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A NEW SPECIES AND SUBSPECIES OF BAT OF THE
HIPPOSIDEROS BICOLOR-GROUP FROM PAPUA NEW GUINEA,
AND THE SYSTEMATIC STATUS OF *HIPPOSIDEROS*
CALCARATUS AND *HIPPOSIDEROS CUPIDUS* (MAMMALIA:
CHIROPTERA: HIPPOSIDERIDAE)¹

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and J. Edwards Hill³



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**A NEW SPECIES AND SUBSPECIES OF BAT OF THE *HIPPOSIDEROS*
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SYSTEMATIC STATUS OF *HIPPOSIDEROS CALCARATUS* AND
HIPPOSIDEROS CUPIDUS (MAMMALIA: CHIROPTERA:
HIPPOSIDERIDAE)¹**

James Dale Smith² and J. Edwards Hill³

ABSTRACT. A new species of bat of the *Hipposideros bicolor*-group is described from New Guinea and the Bismarck Archipelago. The description of this new taxon was prompted by the study of recently acquired specimens from the Bismarck Islands of New Britain and New Ireland. In addition, this new material has allowed for the clarification of a long-standing problem concerning *Hipposideros calcaratus* Dobson 1877 and *Hipposideros cupidus* Andersen 1918. We find these latter two species to be conspecific and referable to *Hipposideros calcaratus* (by priority) and distinguishable from the new taxon on the basis of numerous qualitative and quantitative features.

The geographic variation of the new taxon and *Hipposideros calcaratus* was assessed by computing principal component and discrimination analyses for 11 cranial and 10 wing variables. Sufficient geographic variation was found to merit recognition of geographic races in both *H. calcaratus* and the new species. In the former, populations from the Bismarck and Solomon Islands, as well as the island groups off the southeastern coast of New Guinea, are assigned to *Hipposideros calcaratus calcaratus* and populations of this species from New Guinea are assigned to *Hipposideros calcaratus cupidus* (new combination). The nominate race of the new species is restricted to the Bismarck Islands, and a new subspecies is described to accommodate populations of the new species from New Guinea.

INTRODUCTION

For many years, two medium-sized species of the *Hipposideros bicolor*-group have been thought to coexist in New Guinea, the Bismarck Archipelago, and the Solomon Islands. One of these, *Hipposideros calcaratus*, was described from Duke of York Island in the Bismarcks by G.E. Dobson in 1877; the other, *Hipposideros cupidus*, was described by Knud Andersen in 1918 from Papua (New Guinea). Andersen's description of *H. cupidus* (issued on his behalf by Oldfield Thomas) was brief and basically defined it as being smaller than *H. calcaratus*.

In his comprehensive review of the Indo-Australian species of *Hipposideros*, Tate (1941) introduced the notion of apparent sympatry of these two species in New Guinea and provided diagnoses with additional characteristics to distinguish them. Tate's assessment and conclusions regarding these two species were based primarily on collections in the American Museum of Natural History.

Sanborn and Beecher (1947:390) first reported *H. cupidus* from the Solomon Islands; identification of this material was credited to Tate. In first recording the occurrence of *H. calcaratus* in the Solomons (Rennell Island), Hill (1956) noted that, in this region, Tate's criteria of size and height of the pos-

terior canine cusp apparently were not reliable diagnostic features. Nevertheless, in his monographic treatment of the genus *Hipposideros*, Hill (1963) adopted most of Tate's other diagnostic characteristics to distinguish between these two species. At the time, Hill's assessment was limited to specimens in the collections of the British Museum (Natural History), which included the type material of *H. cupidus* and *H. calcaratus* and some specimens from the Solomons. Since then, additional material has been obtained from the Solomons (Hill 1971, and BMNH) and Papua New Guinea (McKean 1972). This material was reported and identified primarily on the basis of Tate's diagnostic features.

In the summer of 1979, the Taylor South Seas Expedition from the Natural History Museum of Los Angeles County, led by one of us (Smith), conducted extensive field investigations on the bat fauna of New Ireland and New Britain Islands (Bismarck Archipelago). In the process of identifying the species of *Hipposideros* in this collection, it became apparent that there were two similar taxa that differed mainly in size; one small, presumed to be *H. cupidus*, and the other large, presumed to be *H. calcaratus*. Subsequent examination and comparisons with other material, including the holotypes of both species, clearly demonstrated that Tate (1941) wrongly assigned specimens of his larger species from New Guinea and the Bismarcks to *H. calcaratus*, which does not possess the sphenoidal characteristics he ascribed to it. Furthermore, it is even more apparent that Tate incorrectly identified specimens of *H. calcaratus* from the Solomons as *H. cupidus*.

After considerable study, we have found that Tate's sphenoidal character and other features that he employed to distinguish *H. calcaratus* from *H. cupidus* do not, in fact, differentiate between these two species. His diagnostic features do, however, distinguish a generally larger species from a generally smaller one. The holotypes of *calcaratus* and *cupidus* both correspond with the smaller of these two species. We propose that,

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in the absence of compelling, qualitative characteristics to the contrary, there are no bases for maintaining *Hipposideros calcaratus* and *H. cupidus* as separate and distinct species. The larger species, referred by Tate (1941) and others to *Hipposideros calcaratus*, represents an undescribed species. The geographic variation and nomenclature of these taxa are considered below.

METHODS

Five hundred and fifty-six specimens of *Hipposideros calcaratus* (including *cupidus*) and the new species were examined in the preparation of this study. Lists of referred specimens are given under each subspecific account. Institutional abbreviations are as follows: American Museum of Natural History, New York (AMNH); Bernice P. Bishop Museum, Honolulu (BBM); British Museum (Natural History), London (BMNH); Universitetets Zoologiske Museum, Copenhagen (CN); Field Museum of Natural History, Chicago (FMNH); Natural History Museum of Los Angeles County, Los Angeles (LACM); Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); Natur-Museum Senckenberg, Frankfurt (SMF); United States National Museum, Washington (USNM); Museum Für Naturkunde der Humboldt-Universität zu Berlin, Berlin (ZMB). In these lists of referred specimens, localities are reported within provincial boundaries or islands (arranged alphabetically) and within these, localities are listed from north to south, the westernmost listed first in cases where two localities lie at or near the same latitude. As indicated in the lists, some localities were not plotted on the distribution maps because undue crowding of symbols would have resulted. Also, localities where sympatry was noted between *H. calcaratus* and the new species described in this paper are noted.

Specific and subspecific variation were assessed on the basis of qualitative features and quantitative measurements taken from the skull and wing. Eleven cranial measurements included: zygomatic breadth; breadth of the braincase; mastoid breadth; breadth of the interorbital constriction; condylocanine length; breadth across the canines; length of the maxillary toothrow; breadth across the last upper molars (M3/); length of the palatal bridge; length of the mandibular toothrow; and length of the mandible. Ten alar measurements included: length of the forearm; length of the third, fourth, and fifth metacarpals; length of the proximal phalanx of the third, fourth, and fifth digits; and length of the distal phalanx of the third, fourth, and fifth digits (see Smith and Starrett 1979). These measurements were taken with dial calipers and were recorded to the nearest tenth of a millimeter. All measurements given in the text are in millimeters, and dental notations follow Miller (1907).

Statistical analyses of the data were carried out at the computer center of the University of Southern California, Los Angeles, using an unpublished program of discriminant analysis (DISANAL) written by Richard A. Pimentel (Department of Biology, California Polytechnic University, San Luis Obispo). This multivariate program assesses the morphometric variation among variables by computing principal components (PCA)

and discriminant analyses with classification and matrices of generalized distance. For a discussion of the program and analyses, see Pimentel (1979) and Smith and Starrett (1979).

SYSTEMATICS

Order Chiroptera Blumenbach 1779
Suborder Microchiroptera Dobson 1875
Family Hipposideridae Miller 1907
Hipposideros calcaratus (Dobson 1877)
Spurred leaf-nosed bat

Figures 1-4, 7-8 and Table 1
(Synonymy under subspecies)

DISTRIBUTION. Papua New Guinea (Bismarck Archipelago and mainland); West Irian; and Solomon Islands (Fig. 4).

DIAGNOSIS. Size moderate (mean length of forearm, 51.74, range 55.8-46.2; mean condylocanine length, 18.16, range 19.5-15.9). Calcar relatively short, approximately one-half length of tibia. Tail with five equal to subequal tail vertebrae; fifth tail vertebra not especially shortened. Soft palate with nine interdental ridges, area between ridges divided into numerous small cells giving palate a honeycombed appearance. Bony palate with shallow depression on each side adjacent to lingual corner of M2/ and M3/. Mastoid process moderately developed and flangelike. Upper canine moderately large, not bulbous at base; posterior supplementary cusp well developed, but small, extending from base one third or less along length of tooth. First upper premolar (P2/) small, not crowded out of toothrow; canine and second upper premolar (P4/) not in contact. Hypocone on M1/ and M2/ distinct. Lower incisors trifold, equal or subequal in size, not overly crowded between lingual cingula of lower canines. Mandibular symphysis moderately broad. Lower molars relatively broad; trigonid and talonid of M/1 and M/2 equal to subequal in size. Hypoconid, hypoconulid, and entoconid forming distinct cusps on M/1-3. Coronoid process moderately low; posterior margin markedly concave. Angular process long, slender, and deflected laterally. Sphenoid bridge relatively narrow and emarginated, not concealing large, round optic foramina. Basisphenoid depression shallow and troughlike.

DESCRIPTION. Face (Fig. 1) moderately long, narrow, and rising gently to low crown of head. Muzzle, lateral and anterior to noseleaf, with moderate number of vibrissae, which emerge from small, round, and purplish epidermal glands; vibrissae on lower lip less numerous. Noseleaf (Fig. 1B) simple, secondary leaflets absent. Lateral narial lappets not well developed, sub-tubular, and squared off above external nares. Intermediate noseleaf simple, medial ridge a large, prominent, conical bump, two lateral ridges smaller and less prominent. Each lateral ridge bears a long vibrissa seated in a purplish epidermal gland similar to those on muzzle and lower lip. Posterior noseleaf relatively long, with three strong vertical septa; middorsal portion of upper margin with a tiny, rounded bump. Small, wartlike

tubercle above each small eye and behind dorsolateral corner of posterior noseleaf; several long vibrissae with basal epidermal glands protrude from apex of each tubercle. Frontal sac of males relatively small, horizontal, and not much elevated above posterior noseleaf, which sometimes partially obscures it. Ears

relatively long, broadly subtriangular, and funnel-shaped with rounded tips; 10 to 13 transverse ridges traversing inner surface of each pinna; short, round tragus concealed within ear conch. Antitragus relatively low, round, and moderately convex. Wing membrane attached to side of foot at level of proximal metatarsus. Calcar short, approximately one-half length of tibia. Tail with five vertebrae, equal to subequal in length; fifth tail vertebra not noticeably short or absent.

Pelage and coloration. Dorsal surface (including crown and nape) with long, silky pelage; sides of muzzle sparsely haired; cheeks below eye more densely so, with relatively long hairs (Fig. 1). Ventral pelage long, dense, and woolly. Inner surface of ear moderately hairy, inner margin and antitragus more strongly so (Fig. 1). Dorsal pelage dark brown, hairs unicolored, a slight paler "V" over the shoulders; ventral pelage grayish white; wing membranes naked, blackish brown. The pelage is occasionally bleached with a reddish-orange tinge.

Soft palate. Nine interdental ridges traverse soft palate (Fig. 2). First ridge extends from posterior border of canine forward to a sharp point, then abruptly rearward to form a deep notch; it is fused on midline. Second ridge originates at anterior border of second premolar; middle portion of this ridge is roundly bowed anteriorly. Third ridge extends from near protocone of second premolar and is gently bowed anteriorly. Fourth, fifth, sixth, and seventh ridges extend from sides of first molar; these are nearly straight with slight anterior bow near midline. Eighth ridge extends in a similar fashion from between first and second molars. Ninth ridge originates at anterior margin of second molar and bows gently rearward to fuse on midline. Numerous cells between palatal ridges give soft palate a distinct and characteristic honeycombed appearance (may be less pronounced or absent in young individuals). There are no interdental ridges behind level of second molar; this portion of palate is flat and granular.

Cranium. Skull (Fig. 7 C,D,G,H) teardrop-shaped (viewed dorsally), lightly built, and generally similar to those of other unspecialized members of the *bicolor*-group. Rostrum long, narrow, subtubular, only slightly broader than interorbital constriction. Anterior nasal tubercles slightly inflated, but not exaggerated above nasal profile (Fig. 8 C,D). Top of rostrum flat and lacking pits or depressions. Braincase slightly oblong (viewed dorsally), low and elongate in profile, not abruptly vaulted above facial plane. Some individuals with low sagittal crest on frontals; crest may be weak or absent on parietals; lambdoid crest weak. Infraorbital foramen relatively short and slitlike. Zygomatic arches moderately strong, not markedly arched dorsally; malar flange well developed. Mastoid process well developed and flangelike. Premaxillaries long; anterior palatal emargination terminating posteriorly on or near line joining anterior margins of first molars. Palate moderate, its posterior emargination near a line joining rear faces of last molars, flat, with a shallow depression on each side adjacent to lingual corner of M2/ and M3/. Pterygoid wings relatively long and hooked rearward. Sphenoidal bridge narrow and noticeably emarginate (Fig. 7 G,H). Optic foramina large and rounded. When ventral aspect of skull is viewed, optic foramina extend laterally well beyond narrow sphenoidal bridge. [Tate (1941:362, 364) em-

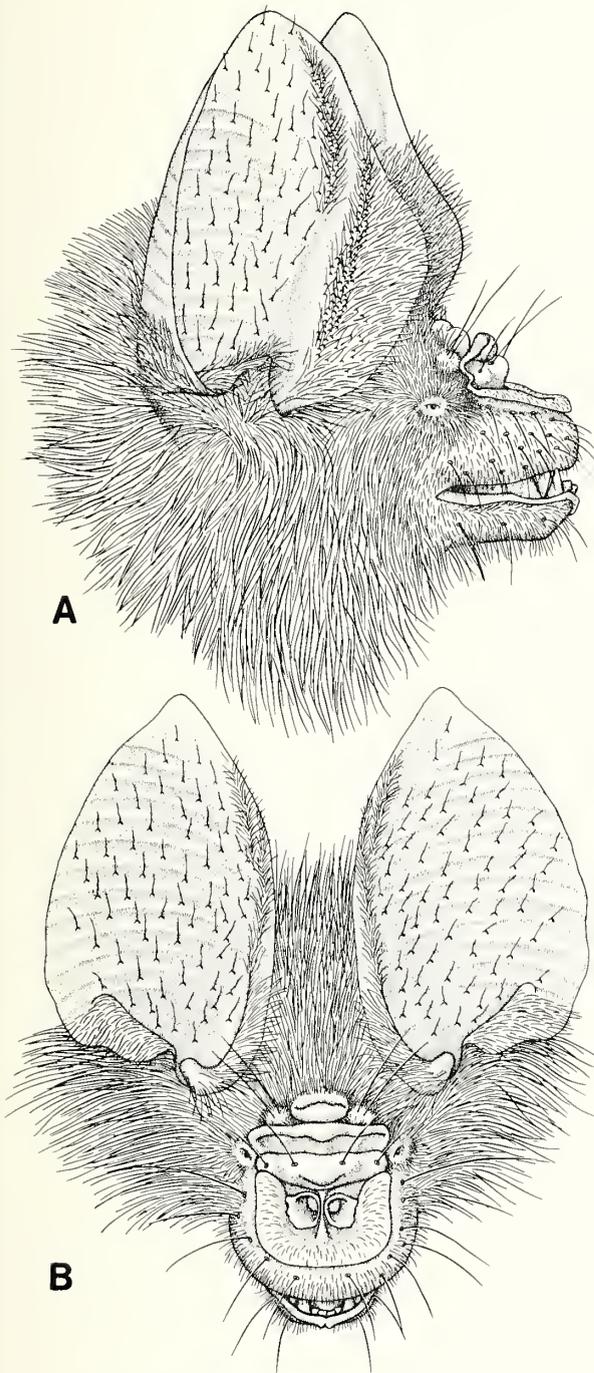


Figure 1. Lateral (A) and frontal (B) views of the head and face of *Hipposideros calcaratus*.

Table 1. Means and ranges (in parentheses) of selected cranial and external measurements of *Hipposideros calcaratus*. Letters in parentheses following locality names coincide with centroids plotted on the canonical graphs in Fig. 10. Superscript numbers indicate sample size different from those given in left-hand column.

Locality	N	CONCAN	ZYGOMA	MASTOD	INTORB	CANINE	MAXTOH	PALWID	PALLEN	MANDIB	DENTAR	FORARM
<i>Hipposideros calcaratus calcaratus</i>												
Madina (A)	11	18.1 ¹⁰ (18.5–17.4)	11.2 (11.5–11.0)	10.2 ¹⁰ (10.4–9.8)	3.5 (3.7–3.3)	4.3 (4.7–3.8)	7.5 (7.8–7.3)	6.9 (7.3–6.8)	3.6 (4.0–3.4)	8.9 (9.2–8.6)	13.9 (14.3–13.5)	51.8 ²² (53.5–49.3)
South New Ireland (B)	20	18.3 ¹⁹ (18.5–18.1)	11.2 (11.5–10.8)	10.3 (10.6–10.1)	3.5 (3.7–3.3)	4.5 (4.7–4.2)	7.3 (7.6–6.9)	7.0 (7.4–6.6)	3.6 (4.1–3.3)	9.0 (9.3–8.8)	14.1 (14.6–13.8)	52.5 ⁵⁶ (55.2–50.5)
Tabar Island (C)	4	17.9 (18.1–17.8)	11.0 (11.4–10.7)	10.1 (10.3–9.9)	3.4 (3.4–3.3)	4.5 (4.7–4.3)	6.9 (7.1–6.9)	6.9 (7.2–6.7)	3.9 (4.2–3.7)	8.8 (8.9–8.8)	14.0 (14.2–13.8)	50.9 ⁵ (52.2–49.0)
East New Britain (D)	33	18.4 ³² (19.5–17.9)	11.5 (11.8–11.1)	10.5 (10.7–9.9)	3.6 (3.8–3.3)	4.5 (4.8–4.2)	7.2 (8.0–6.8)	7.2 (7.4–6.8)	3.9 (4.1–3.6)	9.0 (9.3–8.4)	14.3 (14.7–13.4)	52.5 ⁶⁸ (55.8–49.7)
Kiritwina Islands (E)	3	18.1 (18.2–18.1)	11.2 (11.3–11.0)	10.2 (10.3–10.2)	3.5 (3.6–3.3)	4.4 (4.5–4.3)	6.8 ⁴ (7.2–6.5)	6.8 (7.0–6.7)	4.0 ⁴ (4.3–3.8)	8.9 ⁴ (9.0–8.8)	14.1 (14.2–14.0)	52.8 ⁴ (53.2–52.5)
San Jorge Island (F)	16	18.6 ¹³ (18.9–18.2)	11.1 (11.5–10.8)	10.1 (10.5–9.9)	3.4 (3.6–3.3)	4.6 ¹⁷ (4.8–4.1)	7.8 ¹⁷ (8.0–7.5)	6.9 ¹⁷ (7.4–6.7)	3.9 (4.2–3.6)	8.4 ¹⁷ (8.6–8.3)	14.0 (14.4–13.8)	51.6 ⁶¹ (54.0–49.3)
Malaita Island (G)	14	19.1 (19.5–17.9)	11.2 (11.6–11.0)	10.3 (10.6–10.1)	3.6 (3.9–3.5)	4.4 (4.7–4.1)	7.8 (8.0–7.2)	7.0 (7.3–6.9)	4.2 (4.4–3.8)	8.6 (9.1–8.4)	14.3 (14.7–14.0)	53.3 ¹⁶ (55.1–50.0)
Rennell Island (H)	5	19.2 (19.5–19.1)	11.4 (11.5–11.2)	10.2 (10.3–10.0)	3.5 (3.6–3.4)	4.2 (4.4–4.1)	8.0 (8.1–8.0)	7.0 (7.2–6.9)	4.1 (4.2–4.0)	8.8 (8.9–8.7)	14.1 (14.4–13.8)	52.3 (52.9–51.6)
<i>Hipposideros calcaratus cupidus</i>												
Japen Island (I)	11	17.5 ⁷ (18.1–16.7)	10.3 ⁸ (10.7–10.0)	10.1 ⁷ (10.3–9.9)	3.3 (3.4–3.2)	4.1 (4.3–3.8)	7.1 (7.4–6.4)	6.6 (6.9–6.4)	3.6 ¹⁰ (3.7–3.3)	7.8 (8.2–7.6)	13.1 (13.7–12.5)	48.5 ¹² (49.5–46.9)
Djayapura (J)	7	16.8 (17.3–16.5)	10.4 (10.6–10.1)	10.1 (10.3–9.8)	3.3 (3.4–3.1)	4.2 ⁶ (4.4–4.0)	6.5 (6.8–6.3)	6.5 (6.7–6.3)	3.6 (3.8–3.3)	8.4 (8.6–8.3)	13.0 (13.5–12.8)	49.7 ⁴ (51.1–48.8)
Mt. Diamond Mine (K)	7	16.6 (17.3–16.2)	10.2 (10.3–10.1)	9.7 (9.8–9.6)	3.3 (3.4–3.2)	3.9 (4.0–3.7)	6.6 (7.0–6.3)	6.4 (6.5–6.3)	3.4 (3.6–3.0)	8.1 (8.6–7.6)	12.7 (13.0–12.5)	47.5 (48.2–46.2)
Javareri (K)	5	16.2 (16.3–15.9)	10.0 (10.2–9.9)	9.7 (10.0–9.5)	3.3 (3.5–3.2)	3.9 (4.1–3.7)	6.5 (6.7–6.4)	6.4 (6.6–6.3)	3.4 (3.5–3.2)	8.1 (8.3–7.9)	12.5 (12.7–12.4)	49.0 ⁶ (51.3–47.9)
Madang (L)	5	17.6 ⁴ (17.9–17.3)	10.8 ⁴ (10.9–10.8)	10.3 ⁴ (10.5–10.2)	3.4 (3.5–3.3)	4.3 (4.5–4.2)	6.8 (6.9–6.7)	6.8 (6.9–6.7)	3.7 (4.2–3.3)	8.6 (8.7–8.5)	13.4 (13.6–13.1)	49.9 (50.7–49.2)

CONCAN, condylocanine length; ZYGOMA, zygomatic breadth; MASTOD, mastoid breadth; INTORB, breadth of the interorbital constriction; CANINE, breadth across the canines; MAXTOH, length of the maxillary toothrow; PALWID, breadth across the last upper molars (M3/); PALLEEN, length of the palatal bridge; MANDIB, length of the mandibular toothrow; DENTAR, length of mandible; FORARM, length of the forearm.

ployed this character complex to distinguish "*H. calcaratus*" from "*H. cupidus*." Basisphenoid constricted between cochleae (no broader than width of one cochlea). Basisphenoidal depression shallow and troughlike. Ectotympanic not especially broad; inner margin of auditory meatus without toothlike projection (Fig. 8 C,D). Mandibles lightly built, not particularly attenuated anteriorly. Chin abrupt, symphysis relatively deep. Anterior mental foramen opening anterodorsally, situated approximately halfway up on chin. Lateral mental foramen directed anterodorsally and situated below anterior margin of first premolar. Postdental portion of mandible rotated anterodorsally thus elevating articular facet above dental plane. Coronoid process moderately low, posterior margin markedly concave; masseteric fossa deep and well developed. Angular process long, slender, and deflected laterally; coronoid not so deflected.

Dentition. Dental formula: I 1/2; C 1/1; P 2/2; M 3/3 = 30 (Fig. 3). **Incisors.** Upper incisors slender, indistinctly bifid, curved toward midline. Lower incisors trifold, outer and inner pair equal to subequal in size, not overly crowded. **Canines.** Upper canines moderately large, with pronounced lingual shelf and faint labial cingulum. Posterior supplementary cusp well developed, but small, extending no more than one-third length of tooth from base; not forming a strong, longitudinal shear facet with main cusp of canine. Lower canines long and slender; strong cingulum circumscribes each tooth. **Premolars.** First upper premolar (P2/) single-rooted, small (nearly equal to a lower incisor in size), not excluded from toothrow, and having a low longitudinal ridge with an indistinct central cusp. Second upper premolar (P4/) triple-rooted, only slightly shorter than an upper first or second molar; central cusp moderately long, somewhat slender; posterior longitudinal blade low; labial cingulum distinct; lingual shelf well developed with pronounced protocone and hypoconal basin. First lower premolar (P/2) single-rooted, nearly equal to second lower premolar in length; longitudinal blade high, rising over well-developed central cusp, which is only slightly lower than that of second lower premolar. Second lower premolar (P/4) moderately large with strong, slender central cusp, its thin, lingually oblique blade connecting central cusp with lower, posterolingual supplementary cusp; a strong cingulum circumscribes tooth. **Molars.** First and second upper molars (M1/ and M2/) nearly identical in size and coronal morphology; both with typical W-shaped ectoloph. On M1/, paracone and metacone nearly equal in height, metacone situated slightly more lingually than paracone. On M2/, metacone is noticeably higher than paracone. Protocone of both molars low and indistinct; pre- and postprotocrista well developed; hypoconal shelf descends abruptly to low, narrowly rounded hypoconal heel bearing a low but distinct hypocone. Last upper molar (M3/) markedly reduced in size and coronal morphology; pre- and postmetacrista of ectoloph absent, this tooth standing slightly in front of the anterior extent of postpalatal emargination. First and second lower molars (M/1 and M/2) nearly equal in size and coronal morphology; both moderately broad, with trigonid and talonid equal to subequal in size. Para-

cone not shifted labially, and, on all three lower molars, it is low and noticeably separated from other cusps of trigonid. Talonid cusps (hypoconid, hypoconulid, and entoconid) all distinct and not absorbed into connecting commissure that encompasses talonid. Talonid of M/3 moderately reduced, but not especially compressed laterally.

INTRASPECIFIC VARIATION. Much of the confusion in the past regarding *Hipposideros calcaratus*, *H. cupidus*, and the new species described herein apparently has resulted from a misunderstanding of the qualitative and quantitative variation of these taxa. In his brief description of *H. cupidus*, Andersen (1918) alluded to its generally smaller size compared to that of *H. calcaratus*. As noted previously, Tate (1941) attempted to ascribe qualitative characteristics to a large species (presumed to be *calcaratus*) and a small species (presumed to be *cupidus*). While Tate's qualitative features, and others described herein, do distinguish a generally larger from a generally smaller species, the larger is not *calcaratus*, as he thought, but instead the new species described beyond. Later, Tate identified two specimens, sent to him by C.C. Sanborn and W.J. Beecher, from the Solomon Islands (one from New Georgia and the other from Banika) as *H. cupidus*. Their account (Sanborn and Beecher 1947:390) of Tate's conclusions illustrates his apparent misunderstanding of the quantitative variation among these taxa. He noted the "slightly" larger forearms (50.5 and 53.0) of these two bats from the Solomons, which would have placed them within the size range of the larger species that he recognized as "*calcaratus*." However, on the basis of his qualitative characteristics of the skull, he assigned them to the smaller species, which he understood to be "*cupidus*." Ultimately his as-

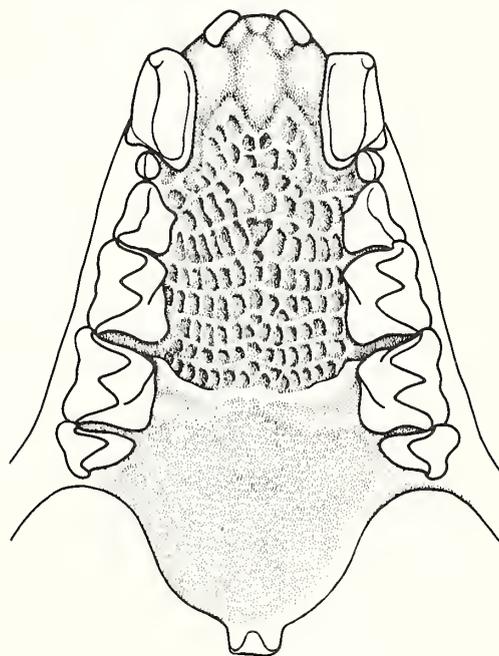


Figure 2. Soft palate of *Hipposideros calcaratus*.

signment of these bats to the smaller species (herein designated *calcaratus*) was correct. However, his disregard for size in this instance led subsequent workers into confusion. Hill (1956:78 and 1963:38) commented that "criteria of size appear not to hold good in the Solomon Islands." On the surface and in a restricted sense, as will be shown below, this statement also is true. However, these statements caused others (McKean 1972; Topal 1975; Vestjens and Hall 1977; and Koopman 1979) to adopt the erroneous notion that large individuals of the taxa under consideration here were *calcaratus* and that smaller bats were *cupidus*. Actual sympatry, except in the Solomon Islands, among these taxa also has further confused the issue.

On the basis of many qualitative features, *Hipposideros calcaratus* and *H. cupidus* are conspecific (herein assigned to *H. calcaratus* by priority) and distinct from the new species diagnosed below. An extensive multivariate analysis of the quantitative, intraspecific variation of *H. calcaratus* indicates that this species is divisible into two geographic races: *H. c. calcaratus* (Bismarck Archipelago, Trobriand, and Louisiade Islands, and Solomon Islands) and *H. c. cupidus* (Japan Island and mainland of New Guinea). This distinction is based on overall size and allometric synergy (shape) among the variables analyzed in this study. The results of the principal components (PCA) and discriminant function analyses of 10 wing and 11 cranial variables (analyzed separately) are shown in Figure 10 and Table 2; PCA canonical graph is not shown. Means and ranges (in parentheses) of 11 selected cranial and external variables of se-

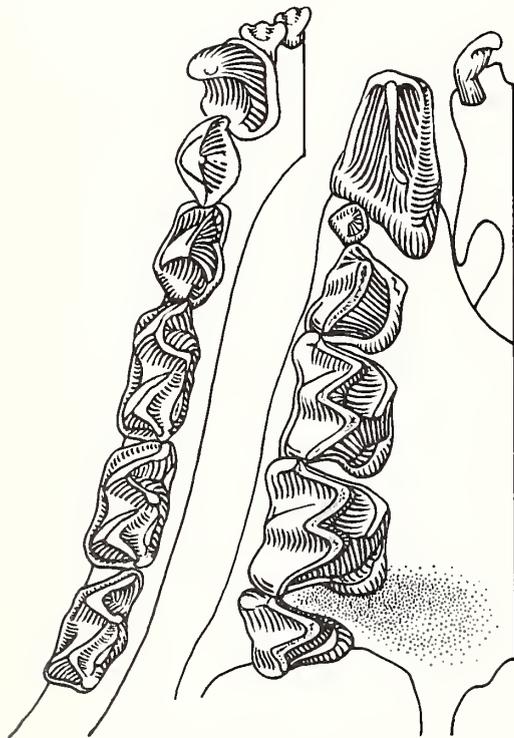


Figure 3. Upper and lower dentition and bony palate of *Hipposideros calcaratus*.

lected populations from throughout the geographic range of *Hipposideros calcaratus* are shown in Table 1.

Cranial and wing variables exhibit separate, although similar, patterns of variation. Individuals of *calcaratus* from the Bismarck and Solomon Islands are generally larger, in all respects, than those from the mainland of New Guinea (Table 1). Specimens from Kiriwina (Trobriand group) and Misima (Louisiade group) Islands agree in size with those from the Bismarcks and Solomons. This pattern may be seen in the ordination of group centroids (Fig. 10 A-H compared to I-L).

Cranial variables appear to be better discriminators of groups than are wing variables. This may be seen in the component scores shown in Table 2. The first component of the direction cosines (PCA) usually is a strong size component; that is, with coefficients having the same sign. It will be noted that the coefficients in this component vary in their sign, thus expressing their contribution to allometric shape. Only condylocanine length weighs heavily in this component axis. The second component of the PCA is more typically an overall size component with all coefficients negative in sign. In the discriminant analysis, the standardized canonical vectors (Z-scores) all express allometric shape in the first three component axes. In the canonical graph for cranial variables (Fig. 10), Bismarck and Solomon centroids (A-H) ordinate together along the first component axis; centroids for samples from the mainland of New Guinea (I-L) ordinate farther to the left (small-size quadrant) along this axis. Solomon Island centroids (F-H) disassociate, somewhat, from Bismarck centroids (A-D) along the second component axis; the centroid for Kiriwina Island (E) ordines with Bismarck centroids. There is little discrimination in the third canonical axis. Zygomatic breadth, breadth of the interorbital constriction, length of the mandibular toothrow, length of the dentary, and condylocanine length are the strongest discriminators among the cranial variables examined.

Although the two geographic races of *calcaratus* may be identified readily on the basis of the length of the forearm (Table 1), wing variables generally exhibit a greater degree of variation. Again, the Bismarck and Solomon Island populations are generally large in overall size compared to those from the mainland of New Guinea, and their respective centroids tend to ordinate together (Fig. 10). The centroids for mainland samples are less strongly ordinated from the island samples of *calcaratus*, although these (I-L) are ordinated into the small-sized quadrant of the canonical graph. The first component of the PCA (Table 2) expresses a strong overall size influence (all signs negative); the second component likewise expresses a considerable amount of overall size. Although the coefficients in the discriminant analysis exhibit allometric shape in the first three component axes, most of the ordination of centroids shown in the canonical graph (Fig. 10) appears to be related to interspecific variation.

Perhaps the most interesting aspect of the variation of wing variables is the pattern of interspecific variation. We have already commented on the apparent past confusion associated with overall size of "*calcaratus*" and "*cupidus*." Until now,

large-sized individuals from the mainland of New Guinea were thought to be "*calcaratus*" and small-sized individuals were thought to represent "*cupidus*." The former are, in fact, the new species described below. The confusion rests in the general similarity in wing size between Solomon Island samples and the large taxon (thought to be *calcaratus*) from the mainland of New Guinea. This interspecific variation is illustrated in the canonical graph for wing variables (Fig. 10) in which Solomon and Bismarck centroids, to a certain extent (F-H and A-E, respectively), show only a small amount of ordination from mainland centroids of the new species (P-W) along the first component axis. The generalized distance (based on wing variables) between Malaita and San Jorge (Solomons) samples of *calcaratus* and mainland samples of the new species average 4.28 (5.22-3.36) compared to an average distance of 3.95 (5.23-2.04) between the Solomon samples and mainland samples of *calcaratus*. The generalized distance between these samples, based on cranial variables, is 10.98 (14.65-7.66) and 7.45 (9.57-5.66), respectively.

Hipposideros calcaratus calcaratus (Dobson 1877)

Phyllorhina calcarata Dobson 1877:122 (Duke of York Island); Jentink 1888:168 (Duke of York Island).

H[ipposideros]. calcaratus, Andersen 1918:383.

Hipposideros calcaratus, Sanborn 1931:24 (Papua New Guinea, Nissan Island); Tate 1941:362, 392 (*in part*: Duke of York Island); Laurie and Hill 1954:55 (*in part*: Duke of York Island; Russell Island; New Georgia Island; Nissan Island); Hill 1956:76 (Rennell Island); Hill 1963:37 (*in part*: Duke of York Island; Russell Island; New Georgia Island; Nissan Island; Rennell Island); Hill 1968:55 (Rennell Island); Hill 1971:574 (San Cristobal Island; San Jorge Island; Malaita Island).

Hipposideros cupidus, Tate 1941:392 (*in part*: Duke of York Island [no specimen cited]; Tabar Island); Sanborn and Beecher 1947:390 (New Georgia Island; Banika Island—identification of these specimens credited to Tate); Koopman 1979:9 (New Britain Island; Duke of York Island; Tabar Island).

HOLOTYPE. BMNH 77.7.18.13, an adult female (preserved in alcohol, skull removed) from Duke of York Island, East New Britain Prov., Papua New Guinea (lat. 4° 10'S long. 152° 28'E).

DISTRIBUTION. Papua New Guinea: Bismarck Archipelago, Trobriand Islands, Louisiade Islands, and possibly some others of the inshore islands of New Guinea; Solomon Islands (Fig. 4).

DIAGNOSIS. Qualitative features same as for species. Overall size large: length of forearm, 52.33 (55.8-49.0); condylocanine length, 18.50 (19.5-17.4); length of maxillary toothrow, 7.43 (8.1-6.5). See Table 1 for the mean (range) of selected cranial and external measurements.

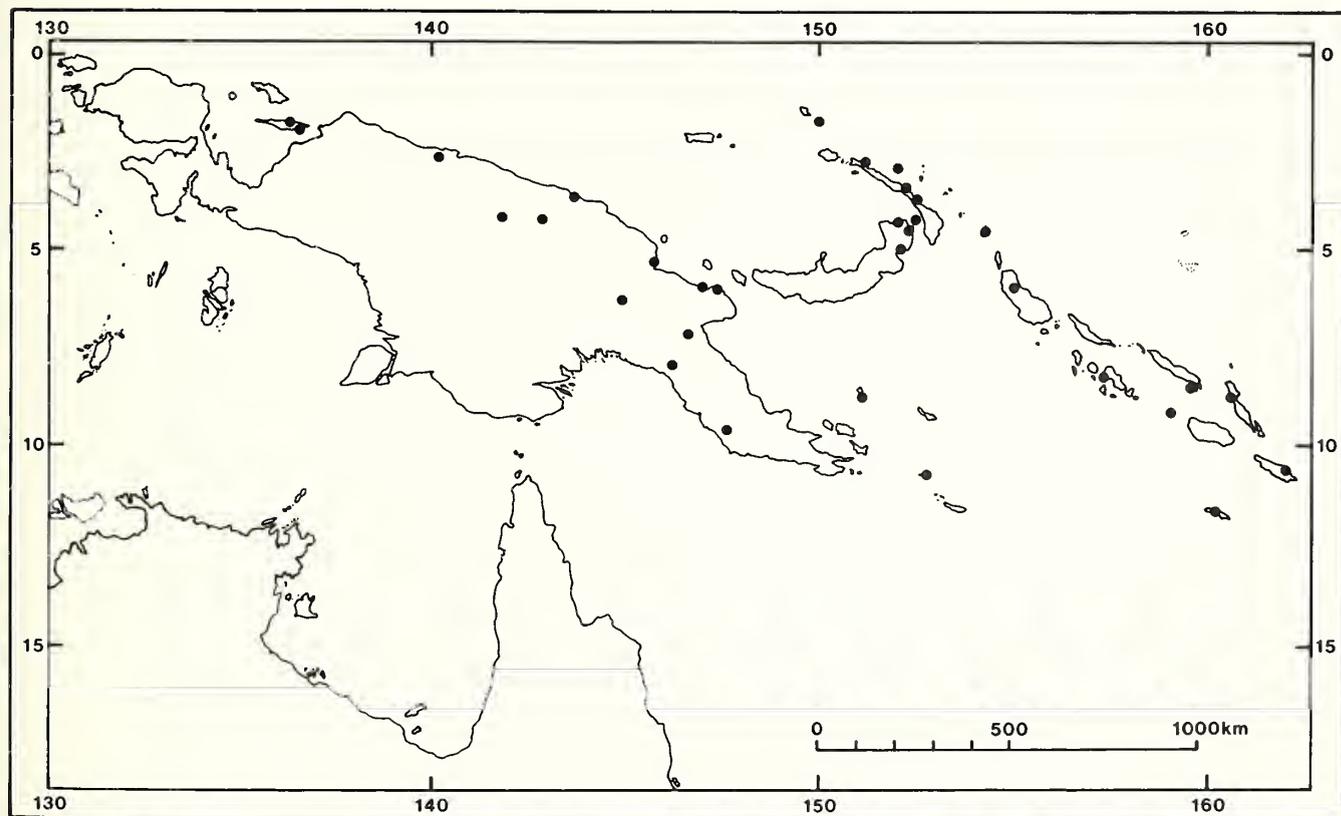


Figure 4. Geographic distribution of *Hipposideros calcaratus*. See lists of referred material for key to plotted localities.

REFERRED MATERIAL (307 specimens examined). PAPUA NEW GUINEA. BOUGAINVILLE PROV.: *Nissan Island*, (4°30'S 154°10'E), 1 (AMNH 99904), *Bougainville Island*, Togarau, base Mt. Balbi, ca. 600m, (5°58'S 155°4'E), 1 (BBM-NG 61370). EAST NEW BRITAIN PROV.: *Duke of York Island*, (4°10'S 152°28'E), 1 (BMNH 77.7.18.13, Holotype); *Ulu Island*, (4°15'S 152°25'E), 1 (AMNH 99844);⁵ *New Britain Island*, 1 km E Kurakakual DPI Station, 40m, (4°13'S 152°8'E), 21 (LACM 66348-68); *Taliligap*, 1000 ft, (4°19'S 152°9'E), 2 (BBM-NG 20987, 20994);⁵ *Keravat*, 500 ft, (4°21'S 152°2'E), 3 (BBM-NG 20879, 20881, 20884);⁵ 3 km SW Gunanur Plantation, 60 m, (4°24'S 152°15'E), 12 (LACM 66369-80); 2 km S Gunanur Plantation, 80 m, (4°24'S 152°16'E), 47 (LACM 66381-427);^{4,5} *Gaulim*, 400 ft, (4°26'S 152°6'E), 5 (BBM-NG 20813, 20817, 20827, 20840, 20854);⁵ *Wide Bay*, Bayalong, 2500 ft, (5°15'S 152°5'E), 1 (AMNH 99823). MILNE BAY PROV.: *Kiriwina Island (Trobriand Group)*, *Liluta*, 10 m, (8°40'S 151°5'E), 5 (AMNH 159356-60); *Misima Island (Louisiane Group)*, *Ehaus Cave*, 50 m, (10°40'S 152°45'E), 2 (AMNH 159361, 159992). NEW IRELAND PROV.: *Emirau Island (St. Matthias Group)*, (1°38'S 150°0'E), 1 (MVZ 109754); *New Ireland Island*, *Laburua Cave*, 1 km S, 2 km W Laburua, 80 m, (2°53'S 151°12'E), 11 (LACM 66276-86); *Lengmebung Cave*, 1.3 km S, 3 km E Lakuramau Plantation, 80 m, (2°54'S 151°16'E), 5 (LACM 66287-91);^{4,5} *Panagapok Cave*, 2.5 km S, 1 km E Madina High School, 80 m, (2°56'S 151°23'E), 4 (LACM 66292-95);⁵ *Madina Cave*, 3 km S Madina High School, 200 m, (2°56'S 151°22'E), 4 (LACM 66296-99);^{4,5} *Riri Cave*, 1 km SW Kalom, 80 m, (3°29'S 152°13'E), 20 (LACM 66300-19); *Marabeke Cave*, *Bakan Village*, 40 m (3°33'S 152°21'E), 11 (LACM 66320-30);⁵ *Kabis Cave*, 3 km SW Sohun 2, 220 m, (3°43'S 152°30'E), 11 (LACM 66331-41); *Loula Cave*, 3 km S. Balai, 100 m, (3°51'S 152°38'E), 6 (LACM 66342-47);⁵ *Tabar Island*, (3°0'S 152°0'E), 5 (AMNH 99488-90, 99847-48).

SOLOMON ISLANDS. CENTRAL DIST.: *Russell Island (Russell Group)*, *Talaena*, (9°4'S 159°12'E), 1 (BMNH 33.11.11.2); *Banika Island (Russell Group)*, (9°5'S 155°13'E), 1 (FMNH 54755);⁵ *Rennell Island*, (11°38'S 160°14'E), 5 (BMNH 54.878-882); *Kongaata Cave at Tinggoa*, (11°51'S 160°38'E), 10 (CN 2863-72);⁵ *San Jorge Island (Santa Ysabel Group)*, *Talise*, (8°25'S 159°35'E), 78 (BMNH 67.1957-2034). EASTERN DIST.: *San Cristobal Island*, confluence *Warihito and Goge Rivers*, ca. 6 mi inland from *Wainoni Bay*, (10°33'S 162°2'E), 1 (BMNH 67.1761). MALAITA DIST.: *Malaita Island*, *Dala*, ca. 20 m, (8°35'S 160°40'E), 1 (BBM-BSIP 24135); *Riba Cave*, near *King George VI School*, *Auki*, (8°48'S 160°44'E), 28 (BMNH 67.2035-2062).⁵ WESTERN DIST.: *New Georgia Island*, (8°20'S 157°30'E), 1 (BMNH 94.10.8.2); *Munda Point*, (8°23'S 157°15'E), 1 (FMNH 54764).

COMPARISONS. As noted above, the nominate race of *H. cal-*

4. Locality of sympatry between *H. calcaratus* and new species.

5. Locality not plotted to avoid overcrowding of symbols (Fig. 4).

caratus may be distinguished readily from *H. c. cupidus* solely on the basis of its larger overall size (Table 1). In a general sense, *H. c. calcaratus* from the Bismarcks, especially New Britain Island, is intermediate in size. Individuals of this subspecies, especially those from the Solomon Islands, approach mainland representatives of the new species in external size; cranially, this similarity in size is less pronounced (Tables 1 and 3), and the two are easily distinguished by various qualitative features outlined herein. It is worth noting here that the narrowness of the sphenoidal bridge and the greatest breadth across the optic foramina appears to be slightly more pronounced among specimens from the Solomon Islands than among other populations of either *H. c. calcaratus* or *H. c. cupidus*.

Hipposideros calcaratus cupidus Andersen 1918 new combination

(?) *Phyllorhina calcarata*, Peters and Doria 1880:693 (West Irian: Andai; Dorei).

(?) *Hipposideros calcaratus*, Jentink 1906:174 (West Irian: Andai; Doreh [= Dorei]); Jentink 1908: 363 (West Irian: Lake Sentani).

H[ipposideros]. cupidus, Andersen 1918:383 (Papua New Guinea: Eaga; West Irian: Jobi).

Hipposideros cupidus, Tate 1941:364, 392 (Papua New Guinea: Javareri, Musgrave River; West Irian: Hollandia; Jobi, Japen Island); Laurie and Hill 1954:55 (*in part*: New Guinea); Hill 1956:78 (*in part*: New Guinea); Hill 1963:38 (New Guinea; Japen Island); McKean 1972: 24-25 (Papua New Guinea: Putei; Ninea; Wagu); Vestjens and Hall 1977:27 (Papua New Guinea, from specimens reported by McKean 1972).

HOLOTYPE. BMNH 97.12.6.4, a subadult male (preserved in alcohol, skull removed) collected by A.S. Anthony (presented by Lord Rothschild) from Eaga, British New Guinea. Eaga is apparently one of two villages now called Ega, one at lat. 7°21'S long. 148°18'E, the other at lat. 6°1'S long. 144°56'E. The first of these localities is just in West Irian, in the lowlands, the second is a little over the northern border of the former territory of Papua (now Chimbu Prov.) and seems to be the more likely as the type locality.

DISTRIBUTION. Japen Island and mainland of New Guinea (Fig. 4).

DIAGNOSIS. Qualitative features same as for species. Overall size small: length of forearm, 48.75 (51.3-46.2); condylocanine length, 16.78 (18.1-15.9); length of maxillary tooththrow, 6.67 (7.4-6.3). See Table 1 for the mean (range) of selected cranial and external measurements.

REFERRED MATERIAL (52 specimens examined). WEST IRIAN. GEELVINK BAY DIST.: *Japen Island*, *Jobi*, (1°42'S 136°27'E), 3 (BMNH 86.11.3.11; USNM 18480-81); 1 mi NW *Sumberbaba*, 1000 ft, (1°47'S 136°39'E), 1 (BBM-NG 22079); *Dawai River Cave*, *Kanyon Batu*, 10 mi E *Sumberbaba*, (1°48'S 136°45'E), 3 (BBM-NG 22121, 22140-41); no specific locality, 9 (ZMB 54620-27, 91837). DJAYAPURA

DIST.: Djayapura (= Hollandia and Sukarnapura), (2° 32'S 140° 42'E), 8 (AMNH 109948, 109950–52, 151547–49, 152695).⁶

PAPUA NEW GUINEA. CENTRAL PROV.: Javareri, Musgrave River, 220 m, (9° 25'S 147° 26'E), 7 (AMNH 108487–90, 108498; SMF 24444–45);⁶ Mt. Diamond Mine, ca. 12 mi E Port Moresby, (9° 27'S 147° 28'E), 7 (BMNH 69.1418–1419; FMNH 110936–37; MVZ 140376–78).^{6,7} CHIMBU PROV.: Ega (= Eaga), (6° 1'S 144° 56'E), 1 (BMNH 97.12.6.4, Holotype). EAST SEPIK PROV.: 7 mi S Wewak, 1100 ft, (3° 40'S 143° 37'E), 1 (MVZ 138588); Wagu (4° 20'S 142° 45'E), 5 (McKean 1972:24).⁶ GULF PROV.: Putei, (7° 48'S 146° 8'E), 19 (McKean 1972:24).⁶ MADANG PROV.: Sempi, 13 mi N Madang, (5° 2'S 145° 46'E), 4 (MVZ 140380–83); South Banup Cave, 6.5 mi S, 4.5 mi W Madang, (5° 18'S 145° 43'E), 1 (MVZ 138587).⁷ MOROBE PROV.: Ninea (= Nineaia), (5° 54'S 146° 54'E), 1 (McKean 1972:24);⁶ Wasu, 40 m, (5° 57'S 147° 11'E), 5 (BBM-NG 53067, 53069, 53074, 53080–81);⁶ Bulolo, (7° 11'S 146° 39'E), 1 (SMF 18891). WEST SEPIK PROV.: Lower May River, (4° 20'S 141° 50'E), 1 (SMF 24513).

REMARKS. The specimens from northwest New Guinea reported as *H. calcaratus* by Peters and Doria (1880) and Jentink (1908) have not been examined by us. However, we consider that these probably represent *H. calcaratus cupidus* since Jentink (1908:364) reports "forearm of 50 mm," which is within the range of this subspecies.

Hipposideros maggietylorae new species

Maggie's leaf-nosed bat

Figures 5–9, 11 and Table 3
(Synonymy under subspecies)

DISTRIBUTION. Papua New Guinea (Bismarck Archipelago and mainland) and West Irian (Fig. 11).

DIAGNOSIS. Largest member of *Hipposideros bicolor*-group (Hill 1963) in the Indo-Australian region (mean length of forearm, 58.41, range 67.2–50.4; mean condylocanine length, 20.38, range 23.5–17.3). Resembles *H. calcaratus* in general appearance. Calcar long, more than half length of tibia. Tail with four conspicuous vertebrae; fifth tail vertebra extremely short or absent. Soft palate with 10 simple ridges. Rostrum moderately long and narrow. Bony palate lacking any noticeable depressions. Mastoid processes not well developed or flangelike. Upper canines large and bulbous at base; posterior supplementary cusp strong and well developed extending from base at least one third (usually more) along length of tooth. First upper premolar (P2/) small and crowded out of toothrow (labially) so that cingula of second upper premolar (P4/) and canine are in contact, or nearly so. Hypocone on M1/ and M2/ indistinct. Lower incisors trifold; inner pair (I/1) smaller than

outer pair (I/2). Mandibular symphysis acutely narrow so that outer incisors are crowded up and behind inner pair, lingual cingula of lower canines are nearly in contact. Lower molars relatively narrow; paraconid merged anterolabially and nearly aligned with protoconid. Lower molars (M/1–3) with reduced hypoconids and entoconids, hypoconids low; entoconids on M/1–2 indistinct, obsolete on M/3. Coronoid process well developed, subtriangular, not deflected laterally, its posterior margin only slightly concave. Angular process strong, knoblike and deflected laterally. Sphenoidal bridge relatively wide, partially or totally concealing elongate optic foramina. Basisphenoidal depression prominent and nearly as wide as long.

DESCRIPTION. Face (Fig. 5) short, relatively broad, and rising to high domed crown. Muzzle, lateral and anterior to noseleaf, and lower lip with numerous vibrissae, which emerge from small, round, and purplish epidermal glands. Noseleaf (Fig. 5B) simple, secondary supplementary leaflets absent. Lateral narial lappets long and slender, not ornamented. Intermediate noseleaf simple, with two ridges lateral to medial ridge; each lateral ridge bears a vibrissa seated in a purplish epidermal gland similar to those on muzzle and lower lip. Posterior noseleaf relatively short with three vertical septa. Large wart-like tubercle above each small eye and behind dorsolateral corner of posterior noseleaf; several long vibrissae with basal epidermal glands protrude from apex of each tubercle. Frontal sac horizontal, large in males, which accentuates shortness of the face and abruptness of the forehead (Fig. 5B). Ears moderately short, subtriangular, and funnel-shaped with rounded tips; nine or 10 transverse ridges traversing inner surface of each pinna; short, knoblike tragus concealed within ear conch. Antitragus short and slightly convex. Wing membrane attached to side of foot at level of proximal metatarsus. Calcar long, more than half length of tibia. Tail with four vertebrae, equal to subequal in length; fifth tail vertebra absent or short.

Pelage and coloration. Dorsal surface densely furred with short (6–8 mm), woolly hairs, somewhat shorter (4–6 mm) and denser on head and upper neck than on back; ventral surface covered with thick woolly fur (6–7 mm), chin and throat less densely haired; inner surface of ear sparsely haired. Dorsal pelage grayish-brown, forming a pale diffuse "V" over shoulders; ventral pelage grayish-white, paler posteriorly; wing membranes naked, brownish-gray. Some individuals with reddish-orange tinge as the result of bleaching. Pelage of juveniles and subadults less dense than that of adults and uniformly gray in color.

Soft palate. Ten interdental ridges traverse soft palate (Fig. 6). First ridge extends between posterior portions of canines and is deeply notched at midline; short, pointed tubercle is situated in front of this ridge and at base of canine. Second ridge bows posteriorly, then anteriorly to midline, originating from in front of second premolar (P4/). Third ridge extends from posterior portions of P4/. Anterior three ridges are more widely spaced than are seven posterior ridges, which are tightly packed and extend between first and second molars. Fourth palatal ridge extends between first molars approximately from level of protocone. Fifth, sixth, and seventh ridges do not join on midline

6. Locality of sympatry between *H. calcaratus* and new species.

7. Locality not plotted to avoid overcrowding of symbols (Fig. 4).

and extend from hypoconal heel of first molars. Eighth ridge does not reach midline and originates approximately from level of protocone of second molars. Ninth ridge (shortest of palatal rugae) extends from just posterior to protocone of second molars to just short of midline. Last palatal ridge is fused on midline where it is curved slightly anterior; it originates from hypoconal heel of second molars. Eighth and tenth ridges appear to encase shorter, ninth ridge. Soft palate behind interdental ridges flat and granular.

Cranium. Skull (Fig. 7 A,B,E,F) teardrop-shaped (viewed dor-

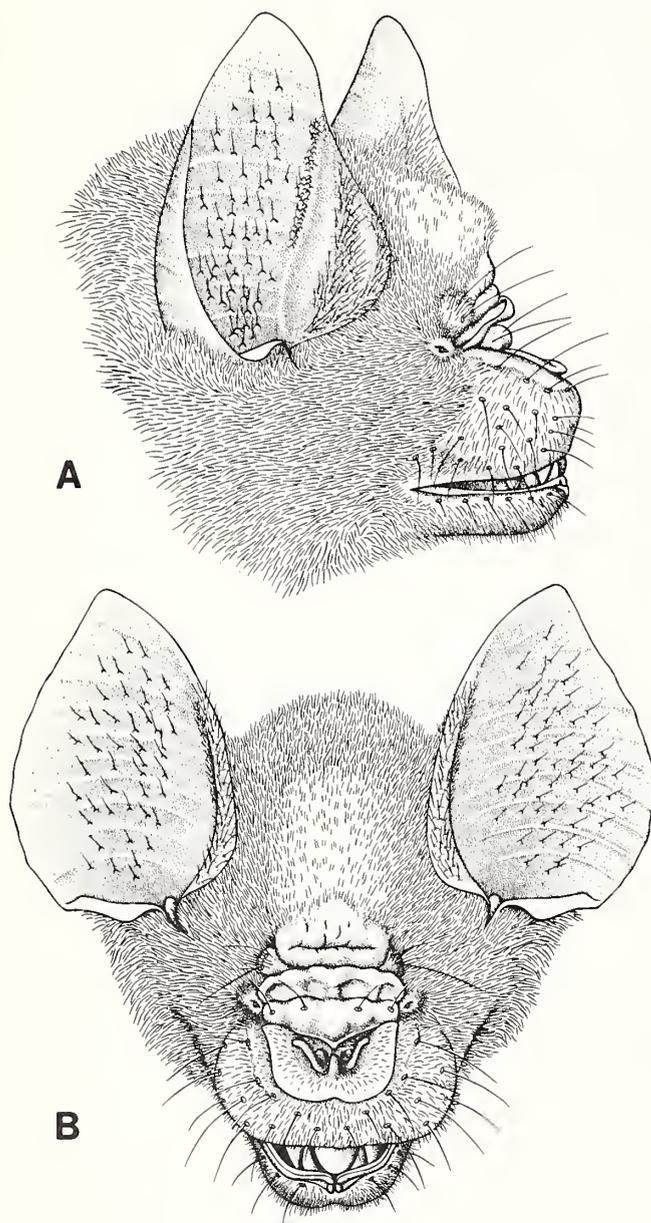


Figure 5. Lateral (A) and frontal (B) view of head and face of *Hipposideros maggietaaylorae*.

sally), lightly built, and generally similar to those of unspecialized members of *bicolor*-group. Rostrum relatively long, narrow, subtubular, and not appreciably broader than interorbital portion of skull. Anterior nasal tubercles not inflated or otherwise exaggerated above nasal profile (Fig. 8 A,B); small pit on midline between tubercles. Braincase slightly elongated and roundish (viewed dorsally), low and slightly oblong in profile, not abruptly vaulted above facial plane. Some individuals with low sagittal crest; lambdoidal crest distinct. Infraorbital foramen long and slitlike. Zygomatic arches strong, not markedly arched dorsally; malar flange distinct. Mastoid processes not well developed. Premaxillaries long, anterior palatal emargination terminating posteriorly on or near line joining anterior margins of first molars. Palate moderately flat and lacking any noticeable depressions or pits; its posterior emargination near a line joining rear faces of last molars. Pterygoid wings relatively long and hooked rearward. Sphenoidal bridge not emarginate (Fig. 7 E,F). Optic foramina elongate and not especially rounded. When ventral aspect of skull is viewed, broad sphenoidal bridge tends to obscure underlying optic foramina. [Tate (1941:362, 364) employed this character complex to distinguish "*H. calcaratus*" from "*H. cupidus*."] Basisphenoid broad; more than breadth of one cochlea. Basisphenoidal depression moderately deep, not elongated and troughlike. Ectotympanic not especially broad; tiny toothlike projection from ventral lip of auditory meatus (Fig. 8 A,B). Mandibles strongly built, sharply attenuated anteriorly. Chin abrupt, symphysis deep. Anterior mental foramen opening anteriorly and situated low on chin. Lateral mental foramen directed anterodorsally and situated directly below canine. Postdental portion of mandible rotated anterodorsally, thus elevating articular facet well above dental plane. Coronoid process high and triangular in shape; masseteric fossa deep and well developed. Angular process long, terminating with a rounded knob, moderately deflected laterally from a perpendicular through the articular process; coronoid not so deflected.

Dentition. Dental formula: $I\ 1\frac{1}{2}; C\ 1/1; P\ 2/2; M\ 3/3 = 30$ (Fig. 9). **Incisors.** Upper incisors slender, bifid, and curved toward the midline; tips nearly in contact. Lower incisors trifold, outer pair slightly larger than inner pair. As the result of the marked attenuation of the anterior lower dental arcade, lower incisors are extremely crowded between anterior cingula of lower canines; outer pair of incisors pushed up and nearly behind inner pair. **Canines.** Upper canines robust and bulbous at base, with pronounced lingual shelf, and lacking labial cingulum. Posterior supplementary cusp strong, well developed, situated one third or usually more along length of tooth. A well-developed shear facet connects supplementary cusp with main cusp of canine and this engages during occlusion with longitudinal blade of lower first premolar (P/2); these shearing surfaces are moderately to heavily worn in most individuals. Lower canines not so large or robust as upper pair, main cusp long and slender; pronounced cingulum circumscribes each tooth. Bases of lower canines in close proximity as a result of acute attenuation of anterior dental arcade. **Premolars.** First upper premolars (P2/) small (only slightly larger than a lower outer incisor), ex-

cluded labially from toothrow. This single-rooted tooth situated in a small notch in the posteriolabial portion of upper canine and has a long longitudinal ridge with an indistinct central cusp. Second upper premolar (P4/) triple-rooted, about as long as an upper first or second molar, with strong central cusp and high posterior, longitudinal blade; labial cingulum absent and posterolingual shelf well developed, protocone absent. Anterior cingulum of this tooth in contact with posterior portion of upper canine. First lower premolar (P/2) single-rooted, about two-thirds length of second lower premolar. Longitudinal blade of this tooth is low, yet strongly developed, and rises over a slightly developed central cusp. Second lower premolar (P/4) large with strong central cusp; short, lingually oblique blade connects central cusp with lower, posterolingual cusp. This blade, although moderately to heavily worn in most individuals, does not occlude directly with any shearing surfaces of the upper dentition; weak cingulum circumscribes each tooth. **Molars.** First and second upper molars (M1/ and M2/) nearly identical in size and coronal morphology; both with typical W-shaped ectoloph. Paracone and metacone situated near the longitudinal midline of tooth; metacone slightly higher and lingual to paracone. Protoconal shelf markedly lower than either paracone or metacone, cusp not distinct, but appears as a short longitudinal ridge. Hypoconal shelf descends from protoconal shelf posteriorly as a low, broadly rounded lingual heel; hypocone absent. Last upper molar (M3/) markedly reduced in size and coronal morphology; pre- and postmetacrista of ectoloph absent; protoconal shelf low and rounded. This tooth situated behind the anterior extent of postpalatal emargination. First and second lower molars (M/1 and M/2) nearly equal in size and shape; both relatively narrow (M/1 narrowest of lower molar arcade); trigonid generally larger than talonid. Paraconid on M/1 shifted anterolabially and nearly in line with protoconid; on M/2 and M/3 paraconid is not so positioned. On all three lower molars, the paraconid is intricately blended with trigonid rather than being distinctly separated from the protoconid and metaconid. Talonid lower than trigonid on all lower molars. Talonid cusps (hypoconid, hypoconulid, and entoconid) indistinct and absorbed into connecting commissure that encompasses talonid. Talonid of M/3 markedly reduced and laterally compressed, reflecting reduction of M3/.

ETYMOLOGY. This new species is named after Mrs. Reese (Maggie) Taylor in recognition of her interest in, and most generous sponsorship of, field research of one of us (Smith) in the Bismarck Islands in the summer of 1979.

INTRASPECIFIC VARIATION. The analysis of intraspecific variation of *Hipposideros maggietylorae* indicates that the species is divisible into two geographic races: the nominate subspecies *H. m. maggietylorae* (Bismarck Archipelago) and a second subspecies, described below, from the mainland of New Guinea. This geographic distinction, like that in *Hipposideros calcaratus*, is marked by a rather pronounced differential in overall size, the Bismarck populations being larger in all respects than those from the mainland (Figs. 7 and 8, Table 3).

Cranial variables, especially zygomatic breadth, length of

the mandibular toothrow, and length of the dentary, are strong discriminators along the first component axis (Table 2 and Fig. 10). The crania of individuals from the Bismarck Islands are massive and more heavily built than are those of individuals from the mainland of New Guinea (Fig. 7 and 8). In profile, the forehead of Bismarck specimens appears to rise somewhat less abruptly than do those of mainland specimens. The posterior margin of the coronoid tends to be slightly more concave in mainland individuals than in those from the Bismarcks.

Again, the wing variables are not as strong as cranial variables in the ordination of group centroids. However, these do separate Bismarck and mainland centroids of *H. maggietylorae* to a greater extent than they do those of *H. calcaratus* (Fig. 10). Finally, New Britain samples, while clearly assignable to *H. m. maggietylorae*, are somewhat intermediate in size between New Ireland populations and those from the mainland.

REMARKS. Specimens of the mainland representative (described below) of this species were identified by the late G.H.H. Tate (1941:392) as *H. calcaratus*, thus leading him to ascribe characters to *calcaratus* that it does not, in fact, possess. This misidentification resulted in further confusion in the literature, having misled authors such as Hill (1956, 1963, 1968, and 1971), McKean (1972) and Koopman (1979). With

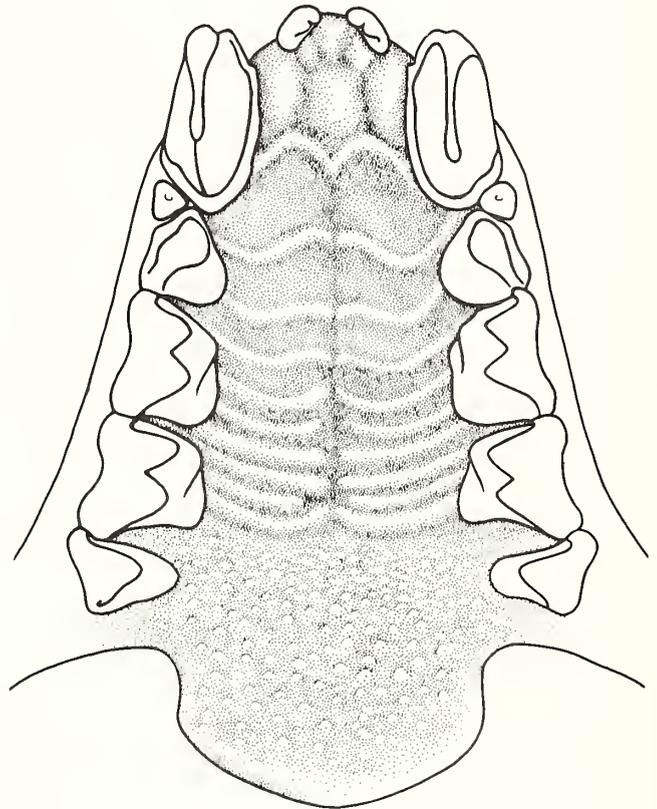


Figure 6. Soft palate of *Hipposideros maggietylorae*.

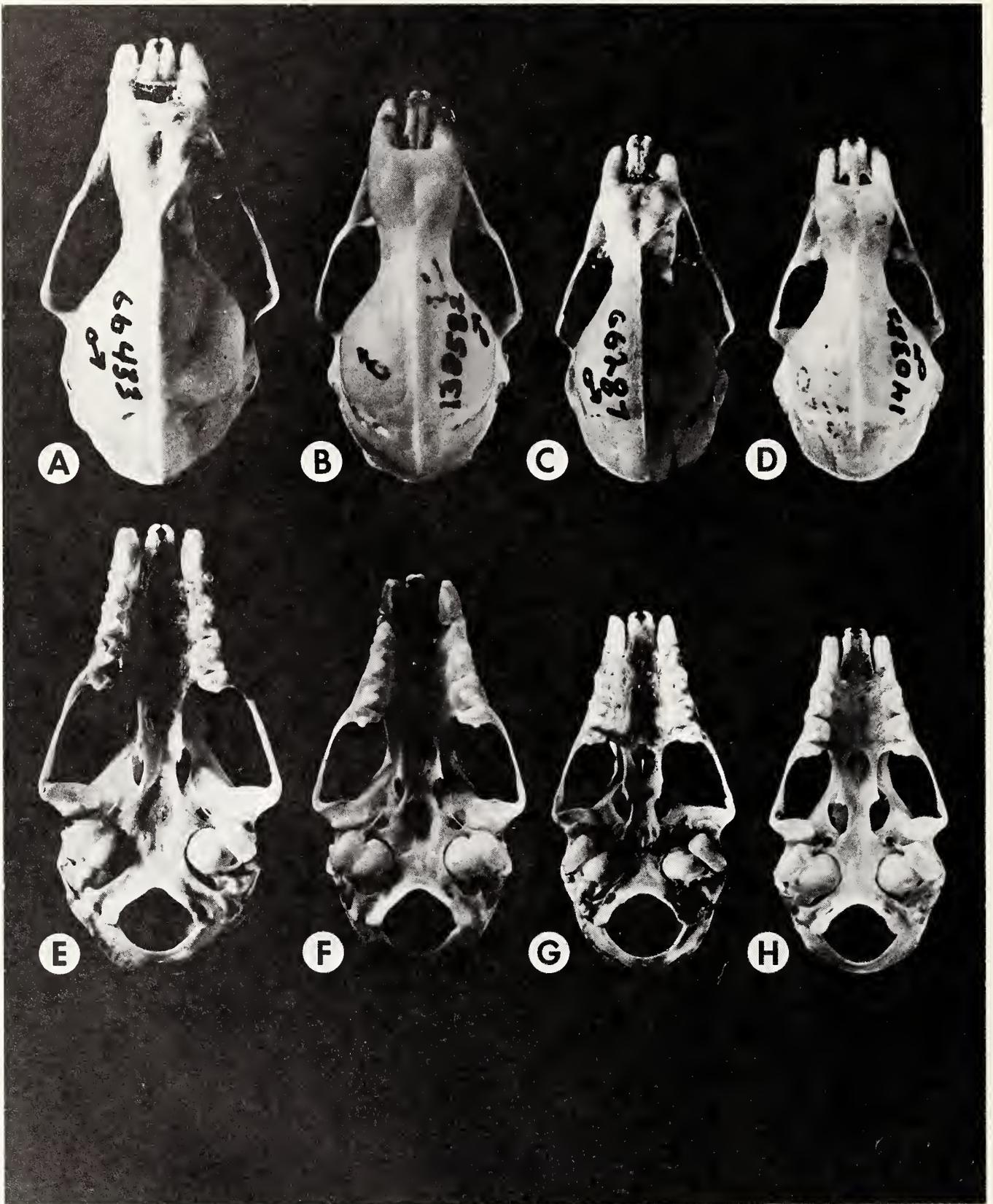


Figure 7. Dorsal and ventral view of cranium of: A, E, *Hipposideros maggietylorae maggietylorae*; B, F., *Hipposideros maggietylorae* new subspecies (see p. 12); C, G, *Hipposideros calcaratus calcaratus*; and D, H, *Hipposideros calcaratus cupidus*.

the advent of extensive additional material from New Guinea and adjacent islands, it has been possible to fully clarify this situation.

Hipposideros maggietylorae maggietylorae

Hipposideros calcaratus, Tate 1941:392 (Duke of York Island).

HOLOTYPE. LACM 66433, an adult male (preserved in alcohol, skull removed) collected 19 June 1979 by Craig S. Hood (original number 275) in Lengmebung Cave, 1.3 km south and 3 km east Lakuramau Plantation, 80 m, New Ireland Island, New Ireland Prov., Papua New Guinea (lat. 2°54'S long. 151°16'E).

PARATYPES. Thirty-five individuals (19 males and 16 females; LACM 66428-32, 66434-35, 66437-48, 66450-63, BMNH 80.391-92) from the type locality captured on 19 June 1979. All are preserved in alcohol; skulls removed from six males and seven females.

DISTRIBUTION. Papua New Guinea: Bismarck Archipelago (Fig. 11).

DIAGNOSIS. Qualitative features same as for species. Overall

size large: length of forearm, 63.14 (67.2-56.9); condylocanine length, 21.93 (23.5-20.8); length of maxillary toothrow, 8.40 (8.8-7.8). See Table 2 for the mean (range) of selected cranial and external measurements.

REFERRED MATERIAL (88 specimens examined). PAPUA NEW GUINEA. EAST NEW BRITAIN PROV.: *New Britain Island*, Keravat, 500 ft, (4°21'S 152°2'E), 4 (AMNH 193718, 193720, 193724-25); Toburtue Village, 40 m, (4°21'S 152°21'E), 5 (LACM 66494-98);⁹ Mt. Raiven, 1 km E Toburtue Village, 100 m, (4°21'S 152°22'E), 6 (LACM 66499-504);⁹ 2 km S Gunanur Plantation, 80 m, (4°24'S 152°16'E), 7 (LACM 66505-11).^{8,9} NEW IRELAND PROV.: *New Ireland Island*, Lengmebung Cave, 1.3 km S, 3 km E Lakuramau Plantation, 80 m, (2°54'S 151°16'E), 36 (LACM 66428-35, 66437-48, 66450-63; BMNH 80.391-92; Type series);⁸ Madina Cave, 3 km S Madina High School, 200 m, (2°56'S 151°22'E), 3 (LACM 66464-66);⁹ Lower Bunbun Cave, 3 km S Lambuso, 220 m, (3°13'S 151°49'E), 27 (LACM 66467-93).

8. Locality of sympatry between *H. calcaratus* and *H. maggietylorae*.

9. Locality not plotted to avoid overcrowding of symbols (Fig. 11).

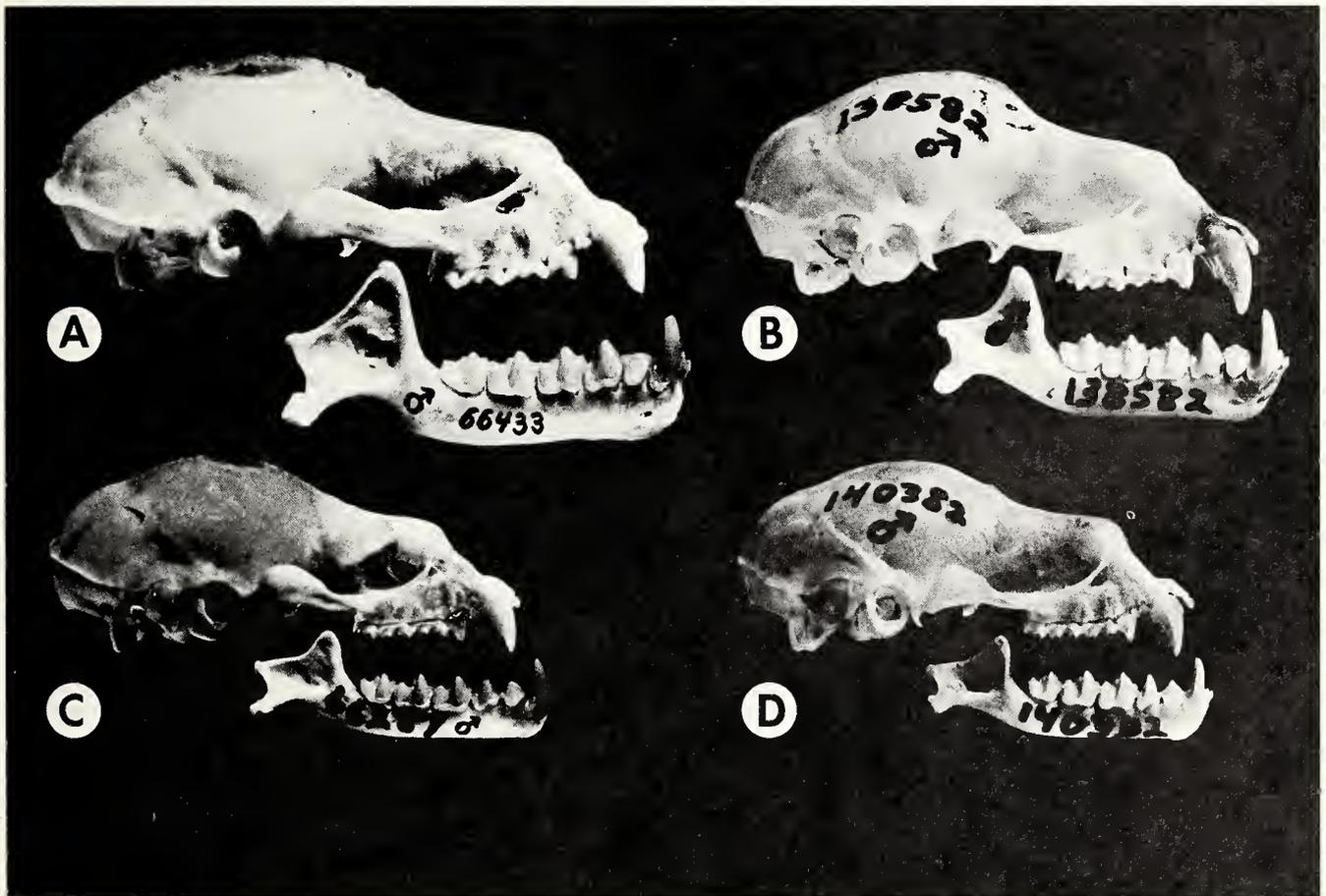


Figure 8. Lateral view of cranium and lower jaw of: A, *Hipposideros maggietylorae maggietylorae*; B, *Hipposideros maggietylorae* new subspecies (see p. 12); C, *Hipposideros calcaratus calcaratus*; and D, *Hipposideros calcaratus cupidus*.

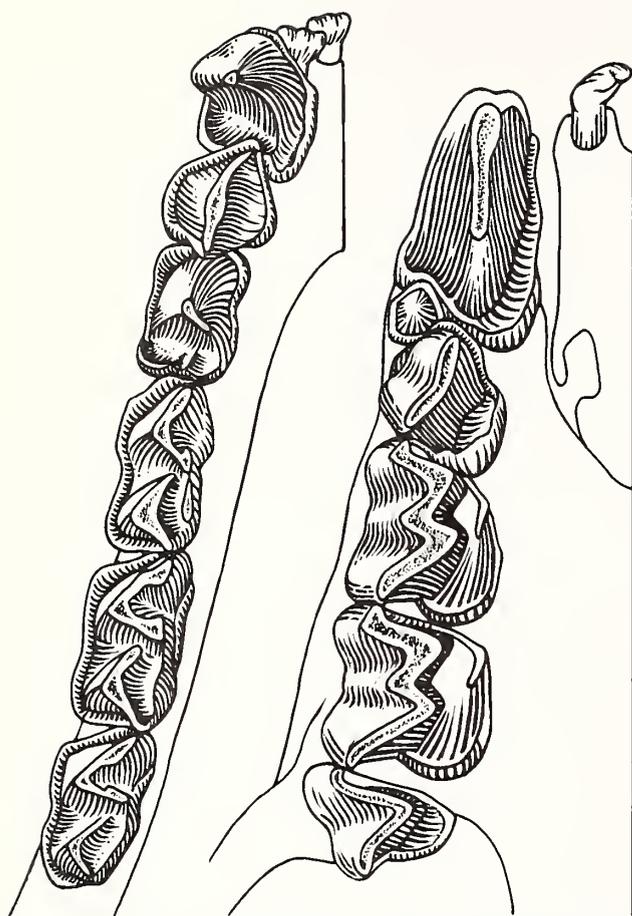


Figure 9. Upper and lower dentition and bony palate of *Hipposideros maggietylora*.

Hipposideros maggietylora erroris
new subspecies

Hipposideros calcaratus, Tate 1941:392 (*in part*: Papua New Guinea: Javareri, Musgrave River; Middle Fly River; Upper Fly River. West Irian: Hollandia); Laurie and Hill 1954:55 (*in part*: New Guinea); Hill 1956:78 (*in part*: New Guinea); Hill 1963:37 (*in part*: New Guinea); McKean 1972:24 (Papua New Guinea: Putei; Ambunti; Ninea; Wagu); Topal 1975:29 (New Guinea); Vestjens and Hall 1977:27 (Papua New Guinea, from specimens reported by McKean 1972).

HOLOTYPE. MVZ 138582, an adult male (skin and skull) collected 23 July 1969 by William Z. Lidicker, Jr. (original number 3045) in Yaguam Sulfur Cave, 5 mi south and 3 mi west Madang, Madang Prov., Papua New Guinea (lat. 5° 17' S long. 145° 45' E).

DISTRIBUTION. Mainland of Papua New Guinea and West Irian (Fig. 11).

DIAGNOSIS. Qualitative features same as for species. Overall size small: length of forearm, 54.32 (57.6–50.4); condylocanine length, 19.59 (21.3–18.6); length of maxillary tooththrow, 7.74 (8.8–7.0). See Table 3 for the mean (range) of selected cranial and external measurements.

REFERRED MATERIAL (109 specimens examined). WEST IRIAN. DJAYAPURA DIST.: Djayapura (= Hollandia and Sukarnapura), (2° 32' S 140° 42' E), 3 (AMNH 109949, USNM 295059–60).¹⁰

PAPUA NEW GUINEA. CENTRAL PROV.: Javareri, Musgrave River, 220 m, (9° 24' S 147° 26' E), 7 (AMNH 108491–97);¹⁰ Mt. Diamond Mine, ca. 12 mi E Port Moresby, (9° 27' S 147° 28' E), 11 (BMNH 69.319–324, FMNH 110939–40, MVZ 140374–75, 140379).^{10,11} EAST SEPIK PROV.: Ambunti, (4° 13' S 142° 50' E), 2 (McKean 1972:24); Wagu, (4° 20' S 142° 45' E), 15 (McKean 1972:24);¹⁰ Kairiru Island, Kairiru Cave, near St. Xaviers Mission, (3° 21' S 143° 36' E), 8 (BMNH 73.2038–2045); St. Xaviers Mission, (3° 21' S 143° 36' E), 3 (BMNH 75.1863–865). GULF PROV.: Bulldog, Lakekama River, (7° 47' S 146° 25' E), 10 (SMF 24621–29, 24446); Putei, (7° 48' S 146° 8' E), 27 (McKean 1972:24).¹⁰ MADANG PROV.: Kaibugu (12 mi SSW Josephstaal), 460 ft, (4° 55' S 144° 57' E), 5 (AMNH 198773–77); near Madang, (5° 12' S 145° 47' E), 1 (MVZ 138589); ca. 10 km S Madang, (5° 15' S 145° 45' E), 2 (BMNH 78.875–876);¹¹ Yaguam Sulfur Cave, 5 mi S, 3 mi W Madang, (5° 17' S 145° 45' E), 12 (MVZ 138646, 138576–84, 140384–85; Type series);¹¹ Tunnel Cave, 7 mi S, 3 mi W Madang, (5° 18' S 145° 45' E), 2 (MVZ 138585–86). MILNE BAY PROV.: Opaigwari, (approx. 9° 37' S 149° 23' E), 7 (AMNH 157420–26); Gwebmantoi Cave, 1 mi N Maneau Village, 300 m, (9° 41' S 149° 21' E), 3 (AMNH 157415–17).¹¹ MOROBE PROV.: Ninea (= Nineia), (5° 54' S 146° 54' E), 1 (McKean 1972:24);¹⁰ Wasu, 40 m, (5° 57' S 147° 11' E), 13 (BBM-NG 53062–66, 53068, 53070–73, 53075–77);¹⁰ Seborgisung Cave, near Finschhafen, 500 ft, (6° 35' S 147° 50' E), 4 (AMNH 194863–66); Oomsis Creek, 10 m, (6° 40' S 146° 48' E), 1 (AMNH 191320); Salamana, (7° 3' S 147° 3' E), 6 (BMNH 80.516–522). NORTHERN PROV.: Budumaga, 125 m, (9° 39' S 149° 18' E), 2 (AMNH 157418–19). WESTERN PROV.: Fly River, 5 mi below Palmer Junction, 80 m, (5° 54' S 141° 32' E), 4 (AMNH 105052–55); Fly River, north bank opposite Sturt Island, (8° 10' S 142° 15' E), 5 (AMNH 105336, 105340, 105354–56).

REMARKS. Individuals of *H. m. erroris* from the western portions of the mainland of Papua New Guinea tend to be slightly smaller, on the average, than those from the eastern parts of the island (Table 3).

ETYMOLOGY. The name chosen for this subspecies reflects the fact that its members have for many years been referred

10. Locality of sympatry between *H. calcaratus* and *H. maggietylora*.

11. Locality not plotted to avoid overcrowding of symbols (Fig. 11).

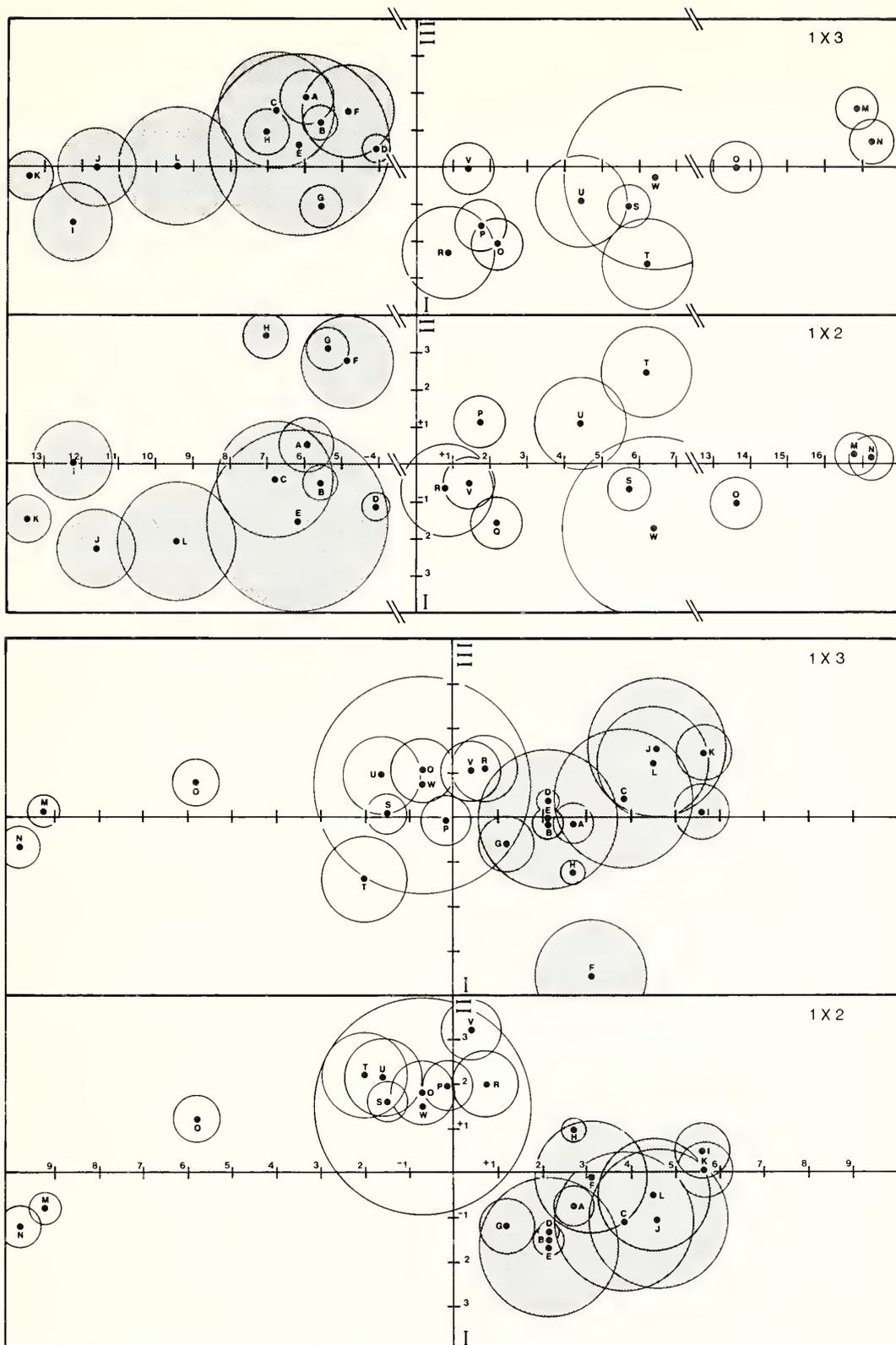


Figure 10. Canonical graphs from discriminant analyses; upper graphs 1 X 2 and 1 X 3 for 11 cranial variables and lower graphs 1 X 2 and 1 X 3 for 10 wing variables. Group centroids are plotted, with their respective confidence circles, as follows: A-H (stippled), *Hipposideros calcaratus calcaratus*; I-L (stippled), *Hipposideros calcaratus cupidus*; M-O, *Hipposideros maggietylorae maggietylorae*; P-W, *Hipposideros maggietylorae* new subspecies (see p. 12); see Tables 1 and 3 for identity of geographic locality of centroid letter codes.

Table 2. Eigenvectors (direction cosines) of principal components (left) and standardized canonical vectors (*Z*-scores) from discriminant analyses (right) for 11 cranial variables (upper) and 10 wing variables (lower). Only the first three component axes are shown because most of the variation is exhibited in these components. The number in parentheses following each component score indicates the percentage of variance contributed by each variable to that respective component:

Variable	Direction Cosines			Standardized Canonical Vectors			Cumulative Percent
	1	2	3	1	2	3	
ZYGOMA	0.006 (0.15)	-0.502 (70.06)	-0.000 (0.00)	0.576 (98.03)	-0.164 (0.16)	0.525 (0.36)	70.21
BRACAS	-0.004 (0.11)	-0.313 (43.56)	-0.096 (2.15)	-0.029 (23.69)	0.042 (1.03)	0.112 (1.54)	45.82
MASTOD	0.012 (0.97)	-0.375 (54.27)	0.108 (2.35)	-0.078 (48.99)	-0.366 (22.38)	-0.664 (15.56)	57.59
INTORB	0.009 (1.09)	-0.097 (7.98)	0.050 (1.11)	0.137 (85.76)	0.024 (0.05)	-0.711 (10.11)	10.18
CANINE	0.006 (0.22)	-0.261 (29.79)	0.119 (3.23)	-0.099 (71.11)	0.242 (8.78)	0.194 (1.19)	33.24
MAXTOH	-0.027 (2.46)	-0.235 (11.84)	-0.785 (69.36)	0.118 (48.54)	0.803 (46.20)	0.162 (0.40)	83.66
PALWID	0.006 (0.23)	-0.270 (32.86)	-0.113 (3.02)	-0.035 (34.93)	-0.218 (28.09)	-0.100 (1.26)	36.11
PALLEN	-0.013 (0.88)	-0.192 (12.51)	-0.052 (0.47)	0.099 (74.16)	0.251 (9.93)	-0.132 (0.58)	13.86
MANDIB	0.004 (0.06)	-0.188 (10.13)	0.553 (45.84)	0.341 (96.06)	-0.289 (1.43)	0.591 (1.26)	56.03
DENTAR	-0.021 (1.73)	-0.482 (53.62)	0.156 (2.93)	0.458 (98.54)	0.230 (0.51)	-0.209 (0.09)	58.28
CONCAN	-0.999 (99.99)	-0.008 (0.00)	0.022 (0.00)	0.078 (85.29)	-0.168 (8.26)	-0.100 (0.62)	99.99
Percent Trace	84.8	5.2	2.7	92.2	2.8	1.6	
Cumulative Percent	84.8	90.0	92.7	92.2	95.0	96.6	
FORARM	-0.383 (57.28)	-0.171 (2.92)	0.131 (1.24)	-0.812 (96.54)	-0.617 (2.85)	0.331 (0.26)	61.44
META-3	-0.429 (65.57)	0.096 (0.84)	0.423 (11.92)	-0.171 (32.14)	1.067 (64.42)	-0.116 (0.24)	78.33
DIG-31	-0.188 (33.76)	-0.213 (11.08)	0.027 (0.13)	-0.393 (90.90)	0.299 (2.70)	0.688 (4.45)	44.97
DIG-32	-0.246 (25.90)	-0.585 (37.28)	-0.522 (21.63)	0.140 (63.00)	-0.429 (30.16)	-0.091 (0.42)	84.81
META-4	-0.554 (66.61)	0.625 (21.64)	-0.528 (11.28)	-0.039 (33.71)	0.120 (16.57)	0.022 (0.18)	99.53
DIG-41	-0.130 (25.57)	-0.095 (3.46)	0.089 (2.24)	0.147 (62.77)	-0.397 (23.46)	-0.317 (4.68)	31.27
DIG-42	-0.094 (10.73)	-0.258 (20.50)	-0.019 (0.08)	-0.195 (79.49)	0.296 (9.35)	0.406 (5.52)	31.31
META-5	-0.448 (67.03)	-0.098 (0.83)	0.447 (12.44)	0.029 (3.56)	-0.254 (14.47)	-0.851 (50.65)	80.30
DIG-51	-0.154 (37.17)	-0.124 (5.52)	0.008 (0.02)	0.251 (83.51)	0.055 (0.21)	-0.422 (3.76)	38.71
DIG-52	-0.130 (13.75)	-0.288 (17.30)	-0.210 (6.75)	-0.034 (19.42)	-0.169 (25.26)	-0.162 (7.20)	37.80
Percent Trace	50.6	12.9	9.4	84.2	8.1	3.1	
Cumulative Percent	50.6	63.5	72.9	84.2	92.3	95.4	

ZYGOMA, zygomatic breadth; BRACAS, breadth of the braincase; MASTOD, mastoid breadth; INTORB, breadth of the interorbital constriction; CANINE, breadth across the canines; MAXTOH, length of maxillary toothrow; PALWID, breadth across the last upper molars (M3/); PALLEN, length of the palatal bridge; MANDIB, length of the mandibular toothrow; DENTAR, length of the mandible; CONCAN, condylocanine length; FORARM, length of the forearm; META-3, META-4, META-5, length of the third, fourth, and fifth metacarpal, respectively; DIG-31, DIG-41, DIG-51, length of the proximal phalanx of the third, fourth, and fifth digits, respectively; DIG-32, DIG-42, DIG-52, length of the distal phalanx of the third, fourth, and fifth digits, respectively.

Table 3. Means and ranges (in parentheses) of selected cranial and external measurements of *Hipposideros maggietaaylorae*. Letters in parentheses following locality name coincide with centroids plotted on the canonical graphs in Fig. 10. Superscript numbers indicate sample size different from those given in left-hand column.

Locality	N	CONCAN	ZYGOMA	MASTOD	INTORB	CANINE	MAXTOH	PALWID	PALLEN	MANDIB	DENTAR	FORARM
<i>Hipposideros maggietaaylorae maggietaaylorae</i>												
Madina (M)	15	22.2 (23.5-21.6)	14.6 (15.0-14.3)	12.2 (12.5-11.9)	4.3 (4.5-4.1)	5.8 (6.1-5.6)	8.5 (8.8-8.3)	8.3 (8.6-8.1)	5.1 (5.5-4.7)	11.1 (11.4-10.4)	18.1 (19.0-17.5)	63.9 ³⁵ (67.2-61.0)
South New Ireland (N)	15	22.2 (22.5-21.6)	14.6 ¹⁴ (15.1-14.0)	12.4 (12.7-11.8)	4.4 (4.5-4.2)	5.9 (6.1-5.5)	8.5 (8.7-8.1)	8.4 (8.6-8.1)	5.2 (5.5-5.0)	11.2 (11.4-10.9)	18.3 (19.0-18.0)	64.7 ²⁰ (66.6-62.6)
East New Britain (O)	13	21.2 ¹² (21.9-20.8)	14.3 (14.5-14.1)	12.2 (12.5-12.0)	4.3 (4.5-4.2)	5.5 (5.7-5.3)	8.2 (8.5-7.8)	8.2 (8.4-8.0)	5.0 (5.2-4.8)	10.7 (11.0-10.4)	17.3 (17.7-16.8)	59.8 ¹⁷ (61.4-56.9)
<i>Hipposideros maggietaaylorae errors</i>												
Mt. Diamond Mine (P)	10	19.6 (20.2-18.9)	12.3 (12.6-11.7)	11.0 (11.4-10.7)	4.0 (4.1-3.8)	4.8 (5.2-4.5)	7.9 (8.4-7.4)	7.4 (7.8-7.2)	4.5 (4.7-4.4)	9.3 (9.7-8.9)	15.5 (15.9-15.3)	52.9 (54.5-51.6)
Javareri (P)	6	19.2 ⁵ (19.7-18.9)	12.3 ² (12.6-12.1)	11.2 ⁴ (11.3-11.0)	4.0 (4.2-3.9)	4.8 ⁵ (5.0-4.6)	7.4 (7.8-7.0)	7.3 (7.5-7.1)	4.6 (4.7-4.5)	9.6 ⁵ (9.9-9.4)	15.4 ⁵ (15.7-15.2)	54.9 (56.0-53.4)
Bulldog (Q)	10	19.2 (19.4-18.9)	12.3 (12.5-12.1)	11.2 (11.4-11.0)	4.1 (4.2-4.0)	4.9 (5.1-4.7)	7.4 (7.6-7.2)	7.6 (7.8-7.2)	4.5 (4.9-4.2)	9.7 (10.0-9.4)	15.5 (15.7-15.1)	54.2 (55.2-52.2)
Palmer Junction (R)	9	18.9 ⁶ (19.3-18.7)	12.1 ⁸ (12.4-11.6)	11.0 ⁸ (11.2-10.7)	4.1 (4.2-4.0)	4.7 (4.8-4.5)	7.4 (7.7-7.0)	7.4 (7.5-7.2)	4.4 (4.6-4.1)	9.6 (9.8-9.3)	15.4 (15.9-15.2)	52.6 (53.8-50.4)
Madang (S)	16	20.0 ¹⁵ (21.3-19.1)	12.9 (13.4-12.5)	11.5 (11.8-11.2)	4.1 (4.3-3.9)	5.0 (5.3-4.8)	7.8 (8.8-7.5)	7.6 (7.9-7.4)	4.4 (4.9-3.9)	9.9 (10.3-9.5)	16.1 (16.6-15.6)	55.5 ²⁰ (57.6-52.9)
Kairiru Island (T)	6	20.8 ⁵ (21.3-20.5)	13.1 (13.5-12.8)	11.5 ⁵ (11.7-11.2)	4.1 (4.3-4.0)	4.8 (5.2-4.5)	8.5 (8.6-8.4)	7.5 (7.7-7.3)	4.5 (4.7-4.4)	9.3 (9.4-9.2)	16.2 (16.5-15.9)	56.2 ⁷ (57.3-55.0)
Salamana (U)	5	19.8 (20.2-19.4)	12.8 (13.0-12.6)	11.2 (11.6-10.6)	4.1 (4.3-3.9)	4.9 (5.1-4.7)	8.1 (8.7-7.7)	7.5 (7.9-7.3)	4.4 (4.6-4.2)	9.7 (10.5-8.8)	15.8 (16.2-15.4)	55.1 ⁸ (56.6-53.4)
Milne Bay (V)	11	19.0 (19.2-18.6)	12.2 (12.4-12.0)	11.0 (11.2-10.8)	3.9 (4.0-3.8)	4.9 (5.1-4.8)	7.5 (7.6-7.3)	7.4 (7.8-7.2)	4.3 (4.5-4.1)	9.7 (10.0-9.5)	15.4 (15.7-15.3)	52.7 (53.8-50.4)
Djayapura (W)	3	20.1 (20.3-19.9)	13.1 (13.3-12.9)	11.7 (11.8-11.6)	4.1 (4.4-3.9)	5.2 (5.4-5.0)	7.7 (7.8-7.6)	7.8 (8.1-7.6)	4.5 (4.6-4.5)	10.2 (10.4-10.0)	16.1 (16.3-16.0)	54.5 (56.2-53.4)

CONCAN, condylocanine length; ZYGOMA, zygomatic breadth; MASTOD, mastoid breadth; INTOR, breadth of the interorbital constriction; CANINE, breadth across the canines; MAXTOH, length of the maxillary toothrow; PALWID, breadth across the last upper molars (M3/); PALLE, length of the palatal bridge; MANDIB, length of the mandibular toothrow; DENTAR, length of mandible; FORARM, length of the forearm.

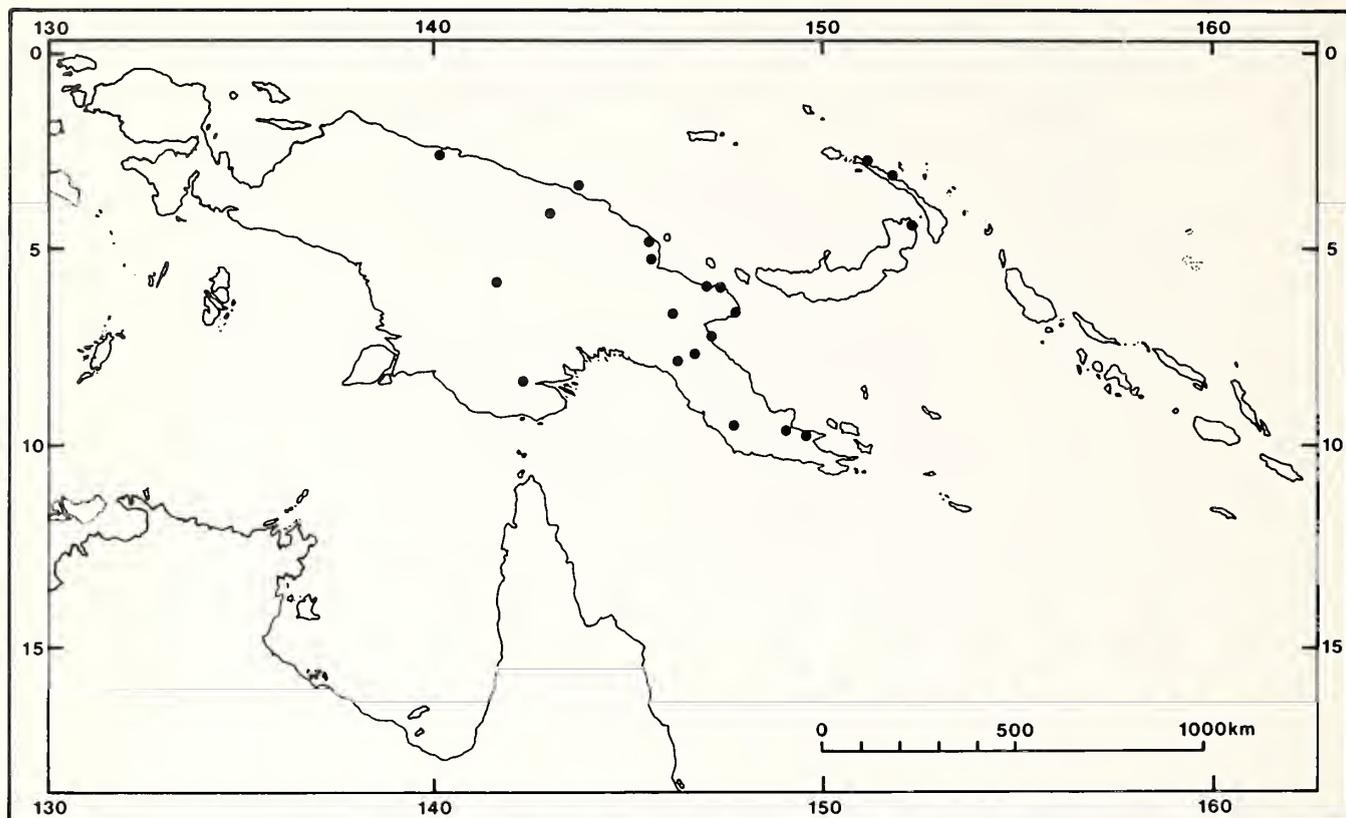


Figure 11. Geographic distribution of *Hipposideros maggietylora*. See lists of referred material for key to plotted localities.

erroneously to *H. calcaratus*, actually represented on New Guinea by the much smaller *H. calcaratus cupidus*.

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Finally, without the early interest, encouragement, and generous support from Mrs. Reese Taylor, the new species described herein would still be foraging, unrecognized by science, through the green mansions of New Guinea.

LITERATURE CITED

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CONTRIBUTIONS IN SCIENCE

CERATIOID ANGLERFISHES OF THE FAMILY GIGANTACTINIDAE:
MORPHOLOGY, SYSTEMATICS, AND DISTRIBUTION

E. Bertelsen, Theodore W. Pietsch,
and Robert J. Lavenberg



Natural History Museum of Los Angeles County • 900 Exposition Boulevard • Los Angeles, California 90007

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**CERATIOID ANGLERFISHES OF THE
FAMILY GIGANTACTINIDAE: MORPHOLOGY,
SYSTEMATICS, AND DISTRIBUTION**

**E. Bertelsen, Theodore W. Pietsch,
and Robert J. Lavenberg**



**Contributions in Science, Number 332
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**Title page illustration: *Gigantactis
vanhoeffeni*, from Chun 1903.**

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GLOSSARY

ANATOMICAL TERMS

A ₂	Adductor mandibulae section A ₂	L.INT.	Levatores interni muscle
A ₃	Adductor mandibulae section A ₃	L.O.	Levator operculi muscle
An	Angular	Mp	Metapterygoid
Ar	Articular	Mx	Maxilla
A _w	Adductor mandibulae section A _w	O	Opercle
Bo	Basioccipital	OBL.D.	Obliqui dorsales muscle
Cbr	Ceratobranchial	P	Parietal
Ch	Ceratohyal	Pa	Palatine
Cl	Cleithrum	Pbr	Pharyngobranchial
Co	Coracoid	Pc	Postcleithrum
CR	2nd Cephalic ray	Pmx	Premaxilla
D	Dentary	Po	Prootic
DEPR.D.	Depressores dorsales muscle	Pop	Preopercle
D.O.	Dilatator operculi muscle	PR.HY.	Protractor hyoidei muscle
E	Epiotic	Ps	Parasphenoid
Ebr	Epibranchial	Pt	Pterotic
EC	Ethmoid cartilage	Ptm	Posttemporal
Eh	Epihyal	Ptp	Pterygiophore of illicium
EREC.D.	Erectores dorsales muscle	R	Radials
Ex	Exoccipital	R.DORS.	Retractor dorsalis muscle
F	Frontal	S	Sphenotic
H	Hyomandibular	SC	Symphysial cartilage
Hh	Hypohyal	Scl	Supracleithrum
IB	Illicial bone	SCAR.A.	Supracarinalis anterior muscle
IMD	Intermandibularis muscle	Se	Supraethmoid
INCL.D. ant.	Inclinatores dorsales muscle, anterior subdivision	So	Subopercle
INCL.D. post.	Inclinatores dorsales muscle, posterior subdivision	STH.	Sternohyoideus muscle
Io	Interopercle	Su	Supraoccipital
L.A.P.	Levator arcus palatini muscle	Sym	Symplectic
LE	Lateral ethmoid	TR.D.	Transversi dorsales muscle
L.EXT.	Levatores externi muscle	Q	Quadrate
		V	Vomer

INSTITUTIONS

AMS	Australian Museum, Sydney.	GMZA	Göteborgs Musei Zoologiska Avdelning, Sweden.
BMNH	British Museum (Natural History), London.	IOAN	Institute of Oceanography, Academy of Sciences of the USSR, Moscow.
BOC	Bingham Oceanographic Collections, Yale University.	IOS	Institute of Oceanographic Sciences, Surrey, England (formerly the National Institute of Oceanography).
CAS-SU	Stanford University collections now housed at the California Academy of Sciences, San Francisco.		

ISH	Institut für Seefischerei, Hamburg.	USNM	National Museum of Natural History, Washington.
LACM	Natural History Museum of Los Angeles County.	ZIAN	Zoological Institute, Akademia Nauk USSR, Leningrad.
MCZ	Museum of Comparative Zoology, Harvard University.	ZIFSUT	Zoological Institute, Faculty of Science, University of Tokyo.
NYZS	New York Zoological Society.	ZMHU	Zoologisches Museum der Humboldt-Universität, Berlin.
SAM	South African Museum, Capetown.	ZMUC	Zoological Museum, University of Copenhagen.
SIO	Scripps Institution of Oceanography, La Jolla.		
UMML	University of Miami Marine Laboratory.		

CERATIOID ANGLERFISHES OF THE FAMILY GIGANTACTINIDAE: MORPHOLOGY, SYSTEMATICS AND DISTRIBUTION¹

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and Robert J. Lavenberg⁴

ABSTRACT. The ceratioid anglerfish family Gigantactinidae is revised on the basis of all known material. The two recognized genera of the family, *Gigantactis* and *Rhynchactis*, are described and compared osteologically. A description and discussion of the myology and functional morphology of the feeding mechanism is also provided. Of the nine nominal species of *Gigantactis* (species based on females), five are recognized: *G. longicirra*, *G. vanhoeffeni* (with *G. exodon* as a synonym), *G. gracilicauda* (with *G. sexfilis* as a synonym), *G. perlatus*, and *G. macronema*. *Gigantactis ovifer* and *G. filibulbosus* are regarded as *incertae sedis*. Twelve additional species of *Gigantactis* are newly described based on females recently collected from the three major oceans of the world. The species are distinguished on the basis of differences in the morphology of the illicium and esca, illicial length, the number, size, and pattern of placement of jaw teeth, caudal fin morphology, and fin-ray counts. The females of *Gigantactis* differ from those of *Rhynchactis* and all other known ceratioids in having the dentaries unfused on the midline and mobile relative to each other. Characters that allow specific identification of *Gigantactis* males to species based on females have not been found. However, males have been divided into six groups based on differences in eye diameter, pigmentation, presence or absence of skin spines, and fin-ray counts.

As far as can be determined, the genus *Rhynchactis* contains a single species. *Rhynchactis* females differ from those of *Gigantactis* and most other ceratioids in lacking a photophore-containing esca bulb.

Both gigantactinid genera are nearly cosmopolitan in geographic distribution and contain species that are for the most part wide-ranging forms. Vertically, gigantactinids are most commonly collected between approximately 1000 and 2500 m.

Rhynchactis has undergone such a drastic reduction and loss of parts that clearly it is the more derived of the two gigantactinid genera. Within the genus *Gigantactis*, *G. longicirra* appears to be the least derived member of the family. Members of the *G. macronema* group, containing *G. macronema* and three newly described forms, are probably the most derived. The remaining species of the genus are more or less intermediate in specialization.

INTRODUCTION

The Gigantactinidae includes elongate, deepsea anglerfishes, the females of which are easily separated from those of allied families by having an exceptionally long illicium, five pectoral radials, and an elongate caudal peduncle. The first of two gigantactinid genera to be discovered was established by Brauer (1902) with the description of *Gigantactis vanhoeffeni*, based on two female specimens collected from the Indian Ocean during the German Deepsea Expedition of 1898–1899. Since that

time, eight additional forms based on females have been described, each from a single specimen: *G. macronema* Regan 1925, *G. gracilicauda* Regan 1925, *G. sexfilis* Regan and Trewavas 1932, *G. exodon* Regan and Trewavas 1932, *G. ovifer* Regan and Trewavas 1932, *G. filibulbosus* Fraser-Brunner 1935, *G. longicirra* Waterman 1939b, and *G. perlatus* Beebe and Crane 1947. A tenth species based on a single metamorphosed male not originally recognized as a gigantactinid, was described by Regan and Trewavas (1932) as *Teleotrema microphthalmus* and referred to *Gigantactis* by Bertelsen (1951).

After examining the then known material of *Gigantactis*, Bertelsen (1951) concluded that the separation of nine nominal species based on a total of 11 metamorphosed females (30–100 mm) must be regarded as uncertain, that the five known metamorphosed males probably represented at least two species and that the 233 larvae in the *Dana* Collections could be divided into three groups based on differences in pigmentation and fin-ray counts.

In this paper, we propose that the 165 known female specimens (11.5–408 mm) of *Gigantactis* now available represent 17 well-defined species. Five of these are previously described forms: *G. longicirra*, *G. vanhoeffeni*, *G. gracilicauda*, *G. macronema*, and *G. perlatus*. The remaining 12 species are recognized as new on the basis of recently collected material from the three major oceans of the world. The nominal species *G. ovifer* and *G. filibulbosus*, each represented only by a poorly preserved holotype, are regarded as *incertae sedis*. The recognition and separation of species based on females is restricted to differences in the morphology of the illicium and esca, illicial length, the number, size, and pattern of placement of the jaw teeth, caudal fin morphology, and median fin-ray counts.

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Females of *Gigantactis* differ from those of *Rhynchactis* and all other known ceratioids in having the dentaries unfused on the midline and mobile relative to each other.

Despite an eight-fold increase in the number of known metamorphosed males, characters that will allow specific identification remain obscure. However, the material has been divided into six groups based on differences in eye diameter, pigmentation, presence or absence of skin spines, and fin-ray counts: *G. longicirra* (recognized by the high number of dorsal-fin rays unique to this species) and five additional groups referred to as Groups I through V. *Gigantactis* male Group I includes "the naked type" of Bertelsen (1951) as well as Parr's (1927) *Laevoceratias liparis* [tentatively included in the Diceratiidae by Bertelsen (1951)]. Group II includes *Teleotrema microphthalmus* Regan and Trewavas (1932), and the remaining three groups are each based on one or two aberrant and previously undescribed specimens. Despite records of several large females (300 to 400 mm), no parasitic *Gigantactis* males have been found.

The genus *Rhynchactis* was established by Regan (1925) with the description of *R. leptonema* based on a single female specimen collected by the *Dana* in 1921. Bertelsen (1951) re-described and figured the holotype and reported finding a single adolescent male and 23 larvae all referred to the same species. Material gathered for this study brings the total number of known metamorphosed specimens to ten (six females and four males) and has added a male metamorphosal stage and two larvae above the previously known size. The material is still insufficient to determine whether the genus contains more than one species. Females of *Rhynchactis* differ from those of *Gigantactis* and most other ceratioids in lacking a photophore-containing escal bulb. They are also unique in having large glands of unknown function lining the oral cavity and, in adult stages, completely lacking premaxillary and dentary teeth.

METHODS AND MATERIALS

Standard length (SL), measured from the tip of the pterygiophore of the illicium to the posteriormost margin of the hypural plate, was used throughout (except where noted) and was taken to the nearest 0.5 mm in specimens less than 100 mm SL, to the nearest millimeter in larger individuals. Measurements were taken on the left side whenever possible and rounded to the nearest 0.5 mm. Jaw-tooth counts are taken from one side only (left side whenever possible). Teeth in early stages of development and teeth in resorption could only be observed in cleared and stained material. In drawings of tooth patterns, the relative position and size of each tooth base was estimated as carefully as possible. To insure accurate fin-ray counts, skin was in most cases removed from the pectoral fins, and incisions made to reveal the rays of the dorsal and anal fins. Caudal-fin rays are numbered from dorsalmost to ventralmost. Illicial length is the distance from the articulation of the pterygiophore of the illicium and illicial bone to the tip of the escal bulb, excluding escal appendages. The escal bulb is the distal swelling of the illicium, excluding escal appendages. The

basal portion of the escal bulb is that part proximal to the photophore.

Terminology used in describing the various parts of the angling apparatus follows Bradbury (1967). Definitions and terms used for the different stages of development follow Bertelsen (1951:10–11). Frequently used abbreviations are given in the glossary. Drawings were made with the aid of a Wild M-5 Camera Lucida.

The osteological and myological evidence presented is based on the following list of specimens. Most of the material was cleared in KOH and stained with alizarin red S. In many cases dissections were made of uncleared specimens to confirm observations made on cleared specimens and to determine ontogenetic changes. Bone and muscle terminology follows Pietsch (1974) and Winterbottom (1974), respectively. All specimens except *Gigantactis meadi* n. sp. were cleared and stained.

- Females. *Gigantactis longicirra* Waterman: ISH 973/68, 209 mm. *Gigantactis vanhoeffeni* Brauer: ISH 802/68, 152 mm; ZMUC P921972, 67.5 mm. *Gigantactis meadi* n. sp.: LACM 11242-12, 353 mm. *Gigantactis macronema* Regan: MCZ 51255, 141 mm. *Gigantactis* metamorphosal stage of Larval Group D: MCZ 54041, 9 mm. *Rhynchactis leptonema* Regan: ISH 2332/71, 60 mm.

- Males. *Gigantactis longicirra* Waterman: UMML 27412, 14mm. *Gigantactis* Male Group I: LACM 30199-26, 17.5 mm. *Gigantactis* Male Group II: LACM 33324-1, 13.5 mm. *Gigantactis* Male Group II: ZMUC P921533, 14.5 mm. *Gigantactis* Male Group V: LACM 32775-1, 14.5 mm. *Gigantactis* unidentified metamorphosal stages: ZMUC P21534, 11.5 mm; LACM 32749-4, 13 mm; LACM 32773-3, 14 mm. *Rhynchactis leptonema* Regan: LACM 37519-1, 17 mm.

- Larvae. *Rhynchactis leptonema* Regan: ZUMC P921751, 7.5 mm.

The systematic revision is based on 165 females (11.5–408 mm), 50 males (10.55–22 mm), and 299 larvae (2.1–15 mm total length) deposited in 19 institutions, the names of which are given in the glossary.

GENERAL DESCRIPTION

Major problems in systematic studies of ceratioid anglerfishes have been the lack of adequately preserved material available for examination and the sparsity of characters that can be used for taxonomic purposes. Ceratioids are, for the most part, soft-bodied animals, subject to damage and deformation during capture, as well as considerable shrinkage due to loss of water during preservation (we have recorded reductions in standard length of as much as 11% over a 3-year period in large individuals of *Ceratias holboelli*). For these reasons, nearly all traditionally utilized morphometric characters are worthless in distinguishing the numerous and morphometrically similar species of gigantactinids. Values for head length, width, and depth, lower jaw and premaxillary length, and caudal peduncle length are difficult to take with accuracy and so highly variable intraspecifically that they are of little importance. Dentary tooth patterns (the number and size of teeth and their arrangement in

longitudinal series), analyzed by us in some detail, are rather irregular and change so considerably with growth that their use as diagnostic characters is limited. The separation of species based on females is thus confined primarily to differences in the morphology of the illicium and esca. Other important characters include the length of the illicium, the shape of the caudal fin, the relative length of the caudal-fin rays, and the number of rays in the dorsal and anal fins (Tables 1 and 2). These and other external characters of general importance are discussed in more detail below. This is followed by an osteological description, and a myological description of the feeding mechanism.

BODY SHAPE

Compared to most other ceratioids, gigantactinid females are slender, streamlined fishes (Fig. 22). Head length and greatest depth of body are usually only 25% SL (compared to 40% or more in most other ceratioids). The caudal peduncle is unusually slender, having a depth of 5 to 10% SL in most specimens. Because of the extreme anterior position of the pterygiophore of the illicium, the snout of *Gigantactis* females is unusually pointed and protruded forward beyond the lower jaw. In *Rhynchactis* females the illicium emerges slightly above and behind the tip of the snout so that the latter is considerably more blunt than that of *Gigantactis*.

ILLICIAM AND ESCA

In all gigantactinids (except for *G. longicirra* and *R. leptonema*) the illicium appears to reach its full relative length by the time females reach a standard length of approximately 30 mm. In the smallest specimens greater than 30 mm (32–38 mm), the illicial length falls within the variation observed in larger conspecific specimens but is shorter than this in all metamorphosed specimens of 25 mm or less. In most of the best-represented species (*G. krefftii*, *G. vanhoeffeni*, *G. meadi*, *G. macronema*, and *G. microdontis*), as well as in the four species known only from two or three metamorphosed females (*G. gibbsi*, *G. gracilicauda*, *G. elsmanni*, and *G. golovani*), the observed intraspecific variation in illicial length is relatively small in specimens greater than 30 mm. However, large intraspecific variations in illicial length are found in larger individuals of some forms (*G. longicirra*, *G. gargantua*, and *G. savagei*).

In *Gigantactis* the bulb of the esca is more or less club-shaped and more slender than in most other ceratioids (Fig. 1). Its basal portion tapers very gradually into the shaft of the illicium without a distinct margin (thus no exact measurement of the length of the bulb is possible). The greatest diameter of the bulb (usually at the photophore) is rarely more than two or three times that of the minimum diameter of the illicium. Distal to the photophore, the bulb is more or less conically prolonged in most species. Generally, the pore of the photophore protrudes as a short tube with a slightly inflated rim, situated, as in all other ceratioids, on the posterior side of the escal bulb. Like the shaft of the illicium, the skin of the basal portion of the bulb is pigmented and spiny in all species of *Gigantactis*.

The pigment and spinule coverage increases with age. In some forms (members of the *G. vanhoeffeni* group) spines are present over the entire surface of the bulb except for a field around the pore of the photophore. As in most other ceratioids, most species of *Gigantactis* have a more or less distinct patch of pigment on the distal portion of the bulb.

The escal appendages of *Gigantactis* species are in the form of filaments and papillae placed directly on the bulb except in *G. longicirra* and *G. perlatus* in which a number of filaments arise from the edge of a pair of peduncle-like lobes situated on the posterior-basal margin of the bulb (Fig. 1). Except for the internally-transparent, distal prolongation of the escal bulb, no appendages with internal light-transmitting tubes occur (as described in several other ceratioid families, Bertelsen and Pietsch 1977).

Great interspecific differences in the length and arrangement of escal filaments are present among species of *Gigantactis* (Fig. 1). Some filaments are short and digitiform, and others are like thin threads or stout tentacles; most are simple, yet branching occurs, especially in larger specimens. In some species (*G. krefftii*, *G. paxtoni*, and members of the *G. macronema* group), the filaments are restricted to the distal part of the bulb; in others, distinct pairs or more or less irregular groups of filaments are also present on more proximal portions of the bulb, as well as on the shaft of the illicium. Generally, the number of filaments (especially those arranged in more irregular groups) increases with standard length.

Three kinds of escal papillae occur: (1) low, distally flattened papillae (unique among ceratioids) that are present in *G. vanhoeffeni* (Fig. 30), *G. meadi* (Fig. 32), *G. paxtoni* (Fig. 37), and *G. gibbsi* (Fig. 34); (2) more or less elongate, unpigmented papillae that are present in juvenile *G. perlatus* and develop into short filaments, completely covering the distal prolongation of the bulb in larger specimens (Fig. 39); (3) one or two papillae that are present on the posterior basal margin of the bulb of *G. krefftii* (Fig. 28) and *G. vanhoeffeni*, respectively, and become distally bifid in larger specimens of the latter species (Fig. 30).

In a histological study of the esca of *G. vanhoeffeni*, Brauer (1908) found nerve fibers entering the filaments and papillae of the esca, supporting his assumption that these structures are organs of touch [“Tastorgane” of Brauer (1908) misinterpreted by Waterman (1948) as “gustatory” in function]. Waterman (1948) showed that the esca of the holotype of *G. longicirra* is innervated by two pairs of large nerves, one trigeminal in origin, the other spinal, both pairs largely sensory in function.

In *Rhynchactis* females, the length of the illicium (in specimens in which it appears complete) varies between 118 and 177% SL (Table 20). The distal part of the illicium is well preserved only in a 27-mm specimen (IOS uncatalogued). In contrast to those of *Gigantactis*, it lacks a photophore-containing escal bulb (Fig. 2). Among other ceratioids, this condition is known only in the Caulophryniidae, in which the slightly club-shaped distal part of the illicium bears a cluster of branched filaments, and in the Neoceratiidae, in which only a subcutaneous rudiment of the illicium is present. In *Rhynchactis*, the slightly inflated distal portion of the illicium bears a series

Table 1. Comparison of important systematic characters among species of *Gigantacris* (tentatively identified specimens excluded)

	<i>G. longicirra</i>		<i>G. krefftii</i>		<i>G. vanhoeffeni</i> group				<i>G. gargantua</i> group		<i>G. macronema</i> group					
	<i>G. longicirra</i>	<i>G. krefftii</i>	<i>G. vanhoeffeni</i>	<i>G. meadi</i>	<i>G. gibbsi</i>	<i>G. gracilicauda</i>	<i>G. paxtoni</i>	<i>G. perlatus</i>	<i>G. elbmani</i>	<i>G. golovani</i>	<i>G. gargantua</i>	<i>G. watermani</i>	<i>G. herwigi</i>	<i>G. macronema</i>	<i>G. savageti</i>	<i>G. microdonotis</i>
Distal prolongation	absent	absent	present	present	present, long	present, long	absent	absent	absent	absent	present	absent	absent	absent	absent	absent
Spines on distal prolongation	absent	present, on base	present	present, reaching tip	absent	present	absent									
Low, distally-flattened papillae	absent	absent	present	present	absent	present	absent									
Distal filaments	single, short	lateral series, short	few to several, short unbranched, unpaired	2-3 long pairs; many short, unpaired	1-2 long pairs; many short	2-4 anterior and lateral pairs	absent									
Proximal filaments	20-25 anterior and lateral	absent	2-4 anterior and lateral pairs	1-2 long pairs; many short	many short	20; most anterior	many, single anterior	several branched	4-5 long pairs, unbranched?	8-10 long pairs	10-18 long, unpaired	8-10 short	absent	absent	absent	absent
Other appendages on or below posterior base of bulb	branched pair	2 papillae unpaired	absent	absent	fringed pair	absent										
Illicial length in % SL ¹	<120	170-200	<110	135-445 (rarely <180)	5-7	4-6	2-3	2-3	2-3	2-3	2-3	2-3	2-3	2-3	2-3	2-3
No. of dorsal-fin rays	8-9	none (longest, 25-35% in most specimens)	none (longest, 25-35% in most specimens)	none (longest, 25-35% in most specimens)	2nd and 7th	4-5	4-5	4-5	4-5	4-5	4-5	4-5	4-5	4-5	4-5	4-5
Prolonged caudal-fin rays ¹ (60-100% SL)	1st and 8th	5-6	3	5-6	3	5	2-3	2-3	2-3	2-3	2-3	2-3	2-3	2-3	2-3	2-3
Dentary teeth	No. of series ¹	Longest in % SL ¹	long, 2.2-7.1 (2.5-5 in most specimens)	long, 2.2-7.1 (2.5-5 in most specimens)	short, 1.1-3.4 (1.5-2.5 in most)											

¹In specimens greater than 30 mm SL.

²Except in largest specimens of *G. gargantua*

Table 2. Frequencies of fin-ray counts for metamorphosal and metamorphosed females of species of *Gigantactis*, including tentatively identified specimens.

Species	Dorsal						Anal				Pectoral (left and right sides)									
	4	5	6	7	8	9	4	5	6	7	14	15	16	17	18	19	20	21	22	
<i>G. longicirra</i>					4	3			4	3	1	5	3		1					
<i>G. krefftii</i>				4					4				3	3	1					
<i>G. vanhoeffeni</i>	11	27	2					9	30	1				20	14	1				
<i>G. meadi</i>		9	1					1	9					4	5					
<i>G. gibbsi</i>		2							2					1	1					
<i>G. gracilicauda</i>	1	2						1	2						2	1				
<i>G. paxtoni</i>		6	2					1	7						2	6	5	1		
<i>G. perlatus</i>	4	3	1					2	5	1			1	3	4	1				
<i>G. elsmanni</i>	2						1	1					2	1						
<i>G. golovani</i>			3						2	1	1	1	1							
<i>G. gargantua</i>	2	3	1						6								3	2	1	1
<i>G. watermani</i>			1					1							2	2				
<i>G. herwigi</i>		1						1							1	1				
<i>G. macronema</i>		8	2						8	2				1	5	4	1			
<i>G. savagei</i>	1	3	2					1	3	2					4	3	1			
<i>G. microdontis</i>	1	4	2					2	3	2				3	6	2				
<i>G. ios</i>		1							1						1					

of short, unpigmented branches (Figs. 2, 63). Histologically, the core of each branch is opaque (Fig. 3), consisting of dense concentrations of cells with large nuclei surrounded by blood vessels.

FIN RAYS

A summary of fin-ray counts shows great similarity among most species (Tables 2, 21). The dorsal fin of *Gigantactis* consists of from four to ten rays, the anal fin from four to eight. *Rhynchactis* has considerably fewer rays in the unpaired fins, the dorsal consisting of from three to five rays, the anal from three to four. All of these rays are biserial, segmented, and unbranched. On the basis of dorsal-fin ray counts, only a single species, *G. longicirra*, can be distinguished from all other species of *Gigantactis* (this species is further unique in having the first and last rays of the dorsal fin distinctly prolonged).

In most species the number of pectoral-fin rays varies between 17 and 19, but especially low counts have been recorded in *G. golovani* (14–16) and *G. longicirra* (14–18), and especially high counts in *G. gargantua* (19–22).

In contrast to other ceratioids (including *Rhynchactis*), all the caudal rays of metamorphosed female *Gigantactis* are unbranched. The ninth caudal ray is very small and completely covered by skin. Extremely prolonged caudal rays (60 to 100% SL) are characteristic of *G. longicirra* and members of the *G. gargantua* group (Table 1). In *G. longicirra*, the first and eighth rays are the longest; in the *G. gargantua* group, the 2nd and 7th rays are prolonged (Fig. 4). Furthermore, considerable differences in the development of the skin coverage of the caudal fin are found among the larger specimens of *Gigantactis* examined (Fig. 4). In individuals of some species (*G. krefftii*, *G. meadi*, *G. perlatus*, and *G. elsmanni*), the proximal one-third to one-half of the fin is covered with undivided skin; in others (*G. golovani* and *G. macronema*), the fin rays are separated nearly

to their bases. The black and spiny skin covering each fin ray may be compressed with broad extensions partially connecting the rays (as in *G. krefftii*, *G. meadi*, and *G. golovani*) or narrowly fitting the cylindrical bony rays (as in *G. macronema*). The diagnostic value of these characters is limited because they are less distinctly developed in juvenile specimens and the number of larger specimens is insufficient at the present time to show the extent of intraspecific variation for most species.

Gigantactinid larvae differ from those of other ceratioids (except for the Caulophryniidae) in the size of the pectoral fins, which vary in length between 40 and 50% SL, extending posteriorly to the caudal peduncle (Bertelsen 1951, figs. 99, 104; Figs. 26, 60). They differ from caulophrynid larvae in lacking pelvic fins (Bertelsen 1951, fig. 11).

DENTITION

Gigantactis

The premaxillary teeth of female *Gigantactis* are small, relatively few, and arranged in either one or two distinct series. In some specimens, a posterior series of anteriorly curved teeth is present (Fig. 13). Although considerable variation in numbers of premaxillary teeth was observed, no clear interspecific differences were found. One of the reasons for this seems to be that, in connection with the reduction of the upper jaw of *Gigantactis*, these teeth are feeble and loosely attached and therefore lost in many preserved specimens.

More distinct differences are found in the heavy dentition of the lower jaw of female *Gigantactis* (Fig. 5). In addition to variation in numbers and in the relative length of the largest fangs, differences in their arrangement in more or less distinct longitudinal series are apparent. To examine to what extent these differences are due to ontogenetic and individual variation, the pattern present in the left dentary of each specimen was drawn. For comparison, dots indicating the bases of the teeth were

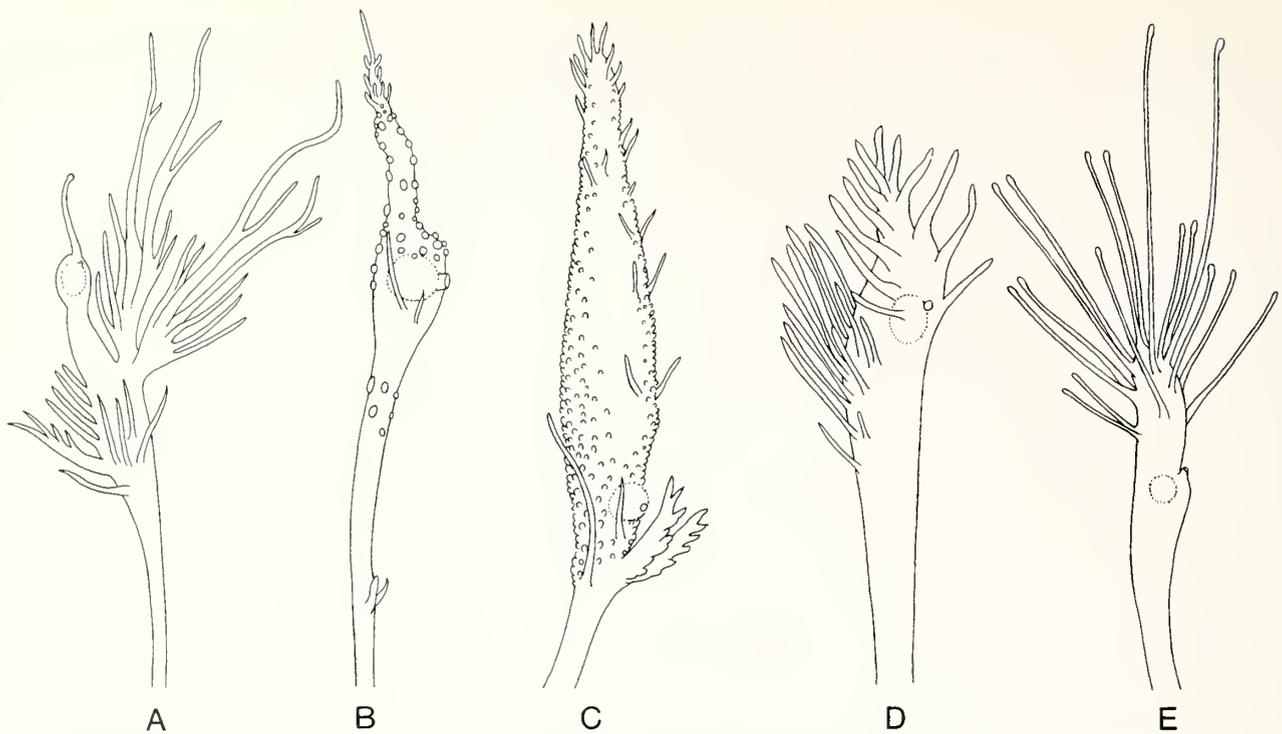


Figure 1. Diagrammatic views of escae of *Gigantactis* showing range of morphological variation: A. *G. longicirra*; B. *G. vanhoeffeni*; C. *G. perlatus*; D. *G. gargantua*; E. *G. macronema*.

drawn with the aid of a camera lucida using the same magnification and, as far as possible, the same dorsolateral angle of view for each specimen. The size and position of teeth partly covered by skin were estimated as exactly as possible. On the basis of a thorough intraspecific comparison as well as a comparison of specimens of a similar size among the best represented species (especially *G. vanhoeffeni*, of which a representative series is shown in Fig. 6), the following statements can be made:

1. In *Gigantactis*, teeth develop externally and internally on the dentaries; in all other ceratioids (except perhaps for *Neoceratias*), replacement teeth of the dentary invariably arise behind and medial to the older teeth.

2. In most species, one to several distinct longitudinal series of teeth occur in the posterior one-half to two-thirds of the jaw, but no distinct pattern can usually be recognized in the anterior part of the jaw. During metamorphosis, all the close-set larval teeth are lost and replaced by a small number of well-spaced tooth rudiments forming a single (median) series that is followed shortly by the first tooth rudiments of the external and, in most species, of the internal series as well. With growth, teeth of gradually increasing size are added externally as well as internally, each series starting anteriorly on the jaw (Fig. 6).

3. The median tooth series, reaching furthest posteriorly and consisting of relatively small and close-set teeth, can be recognized in all specimens with the exception of those of *G. golovani*. Next in relative size are those of the first internal series followed by those of the second internal series, if present. The increase in tooth size (and a corresponding increase in number) is more rapid in the external series, so that the longest of the serial teeth of the lower jaw are found in the posterior part of the exterior-most external series present. Teeth of the irregular

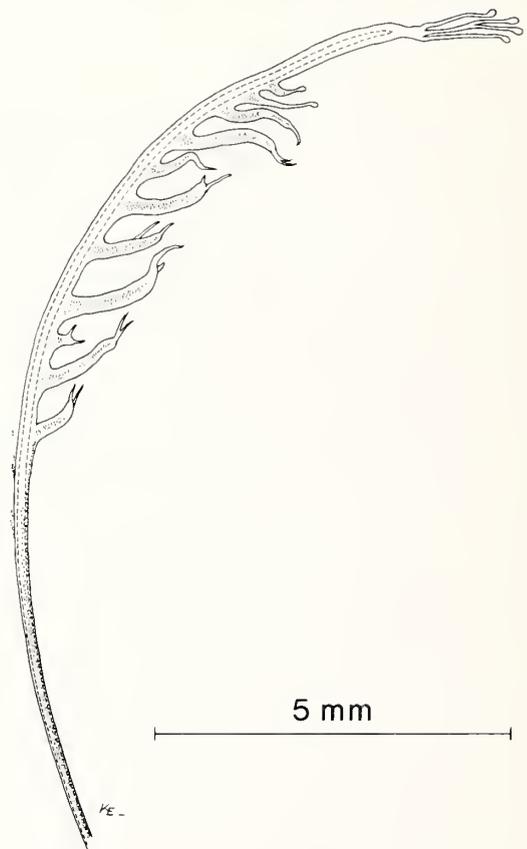


Figure 2. Esca of *Rhynchactis leptonema*, 27 mm, IOS uncatalogued. Drawn by K. Elsmann.

anterior group, however, may reach similar or even greater lengths.

4. Teeth in initial development can be recognized by having soft unossified bases (Fig. 5). Assuming that no further growth takes place after ossification is complete, the ontogenetic increase in size of the teeth can be explained only by tooth replacement. This assumption appears to be correct at least for the smaller, anteriormost serial teeth, which are often found to be partially resorbed and embedded in the bone of the jaw. The possibility, however, that the larger fangs continue to grow throughout life cannot be excluded.

5. According to the position of the smallest and apparently oldest teeth, additions to each tooth series are mainly added in the posterior part of the jaw; but, in contrast to other ceratioids, teeth of increasing size are also added anteriorly along the border of the irregular group on the free anterior end of the dentary.

6. The number of series of lower jaw teeth varies among species of *Gigantactis* (Table 1). *Gigantactis longicirra*, *G. krefftii*, and *G. meadi* have the largest number (five to six series); *G. elsmanni* and members of the *G. gargantua* group are intermediate (four to five); *G. perlatus*, *G. golovani*, and members of the *G. macronema* and *G. vanhoeffeni* groups (excluding *G. meadi*) have the lowest number (two to three series). *Gigantactis golovani*, with two or perhaps three series, seems to be unique in lacking a distinct median series. With some exceptions, species with the largest teeth tend to be those that have the greatest number of series. However, *G. perlatus*, with only two series (representing the median and first external series), has very large teeth, whereas *G. elsmanni*, with five series, has relatively short teeth.

7. The diagnostic value of characters of the dentition is limited because the full number of series may not be developed in smaller specimens, and the series tend to become irregular and therefore difficult to interpret in the largest specimens. Further difficulties arise from the considerable amount of individual variation in both the numbers and size of teeth.

Rhynchactis

Metamorphosed *Rhynchactis* females lack dentary teeth; one or two pairs of premaxillary teeth are present in juveniles (27 and 60 mm SL), but the single larger known specimen (126 mm) is completely toothless. Regan's (1925, 1926) descriptions of the holotype of *R. leptonema* as having "minute teeth in several series" in addition to a "pair of anterior canines" could not be confirmed.

Gigantactinid Males

As in other ceratioids, the jaw teeth of male gigantactinids are lost during metamorphosis and replaced by an upper and lower series of hooked denticles, loosely attached at the symphyses of the maxillae and dentaries, respectively. In *Gigantactis*, the

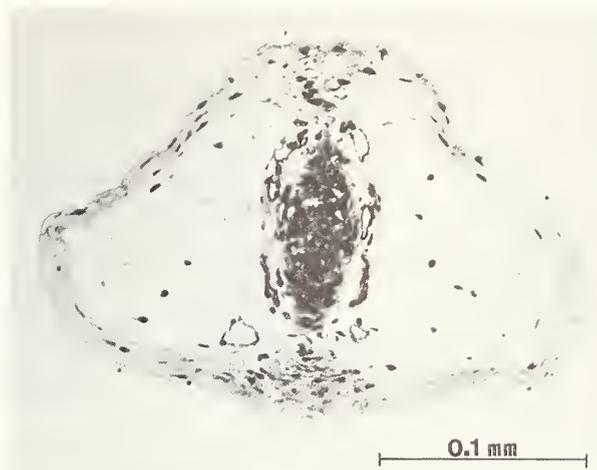


Figure 3. Cross section through single side-branch of esca of *Rhynchactis leptonema*, 27 mm, IOS uncatalogued. Courtesy of Geert Brovad.

denticular teeth are all mutually free and proximally compressed, whereas in *Rhynchactis*, at least some of the teeth are paired and supported by relatively broad bases (Figs. 14, 15).

SENSORY STRUCTURES

Eyes

As in other ceratioids, the eyes of metamorphosed female gigantactinids are very small. Their diameter increases during larval life to approximately 1 mm but then decreases relative to standard length from about 20% to roughly 10% (Bertelsen 1951). After metamorphosis, eyes grow very slowly, reaching a diameter of 2.5 to 3 mm in the largest specimens (300–400 mm) and decreasing to less than 1% SL. Histologically there is no evidence of ocular degeneration (Brauer 1908, Waterman 1948, Munk 1964), but as growth continues, the eyes sink beneath a narrow transparent layer of skin, greatly restricting the visual field. Furthermore, since the lens is situated close to the retina, ocular function is probably reduced to mere light detection.

In contrast to other ceratioids (except Neoceratiidae), the eyes of gigantactinid males are somewhat reduced in actual size during and after metamorphosis. In the five metamorphosal stages available for examination (specimens 11.5–14.5 mm), eye diameter ranged between 0.75 and 1.0 mm (average 0.86 mm), yet in the 42 metamorphosed males available (10.5–22.0 mm), eye diameter was 0.4 to 1.0 mm (average 0.62 mm, Table 19). Expressed as a percentage of standard length, eye diameter varied between 2.9 and 6.9. As in the females, there is no apparent ocular degeneration, but because shrinkage of the eye seems to occur mainly in the scleral and retinal portions, the visual abilities of the males may be even less than those of the females.

Olfactory Organs

In female gigantactinids, the small olfactory organs, each with two tiny nostrils, are raised on short, cylindrical stalks with a

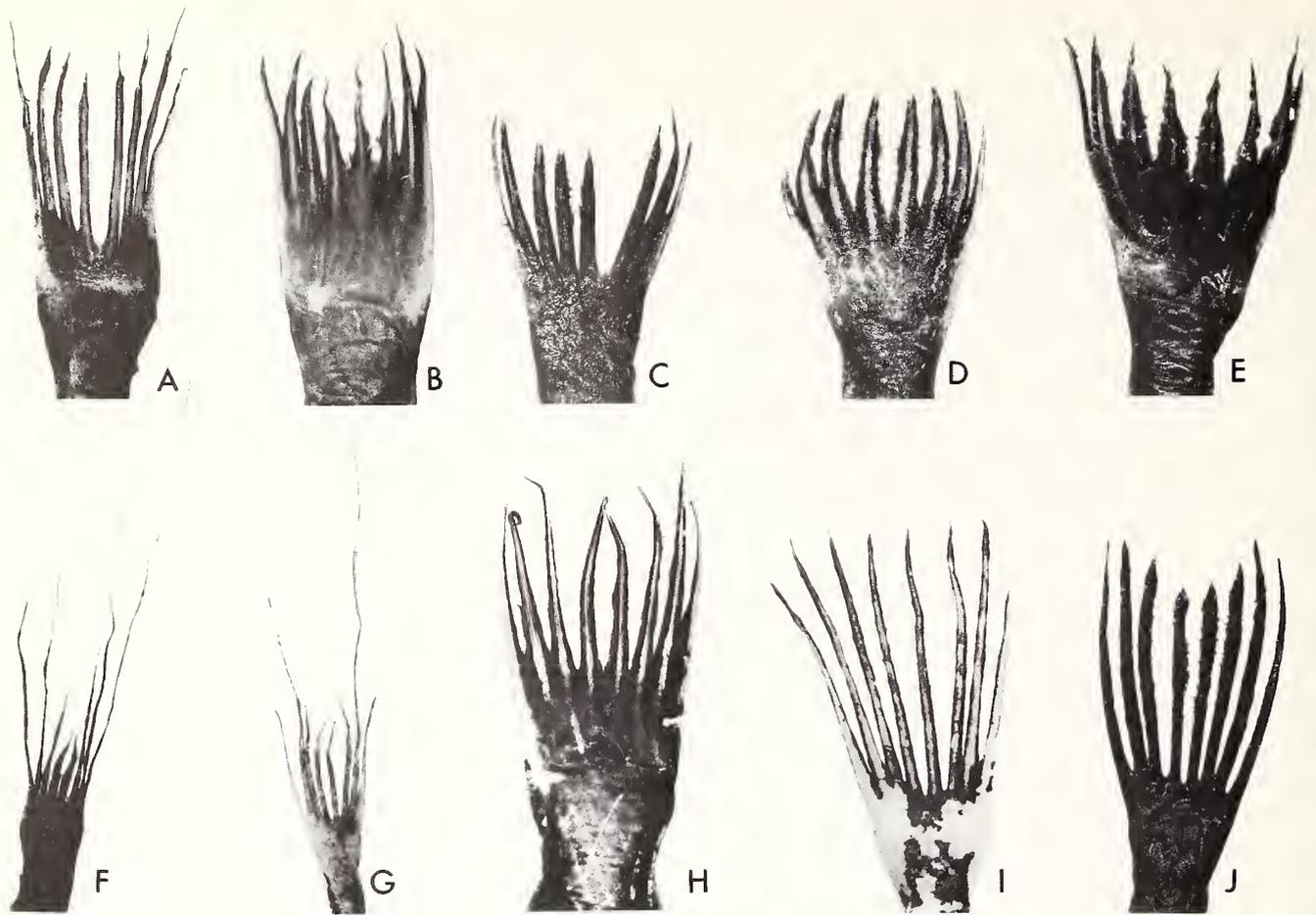


Figure 4. Caudal fins of species of *Gigantactis*: A. *G. vanhoeffeni*, 266 mm, ISH 2480/71; B. *G. meadi*, holotype, 306 mm, MCZ 52572; C. *G. perlatus*, 152 mm, ISH 1466/71; D. *G. krefftii*, paratype, 185 mm, ISH 3236/71; E. *G. elsmanni*, holotype, 384 mm, ISH 1360/71; F. *G. longicirra*, 221 mm, MCZ; G. *G. herwigi*, holotype, 262 mm, ISH 972/68; H. *G. gargantua*, holotype, 408 mm, LACM 6903-32; I. *G. macronema*, 232 mm, ISH 1596/71; J. *G. golovani*, holotype, 179 mm, ISH 2250/71. Courtesy of Geert Brovad.

length of three to four times their width. They are situated anteriorly on the snout very close to the edge of the upper jaw. No distinct olfactory lamellae are present and, as shown by Waterman (1948, fig. 5), the olfactory lobes of the brain are small.

Like those of other ceratioids (except Ceratiidae and Neoceratiidae), gigantactinid metamorphosed males are macrostomatic. The series of olfactory lamellae (11-12 in most specimens of *Gigantactis*, 13-15 in *Rhynchactis*) have a height of 5.2 to 11.8% SL (Table 19). The large, forward-directed anterior nostrils are very close set and separated from the equally large posterior nostrils by a narrow bridge of skin. The distance between the eye and posterior nostril is two to three times the eye diameter. The olfactory lobes of the brain are well developed. (Fig. 7).

Acoustico-Lateralis System

The organs of the acoustico-lateralis system are raised on short stalks or "tags" of pigmented skin (Regan and Trewavas 1932, Waterman 1939b), more or less distinctly connected in series by narrow unpigmented grooves. On each side of the head, the following series can be distinguished (Fig. 8): (1) two supraorbital

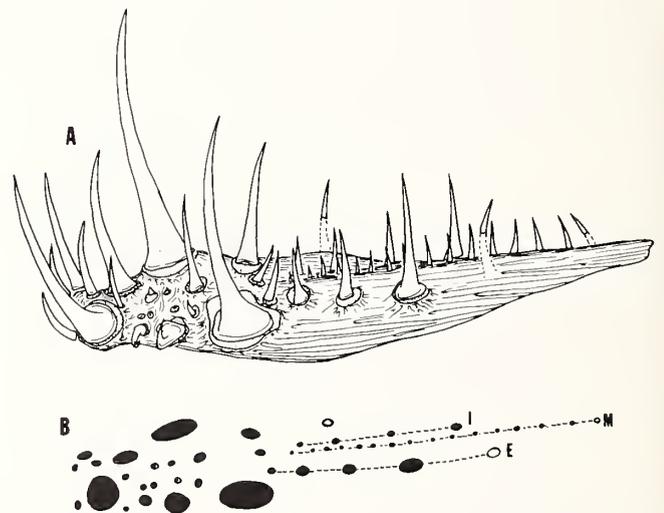


Figure 5. *Gigantactis vanhoeffeni*, female, 152 mm, ISH 802/68: A. Dentary teeth, left lateral view; B. Diagrammatic representation of dentary-tooth pattern. E = external series; M = median series; I = internal series.

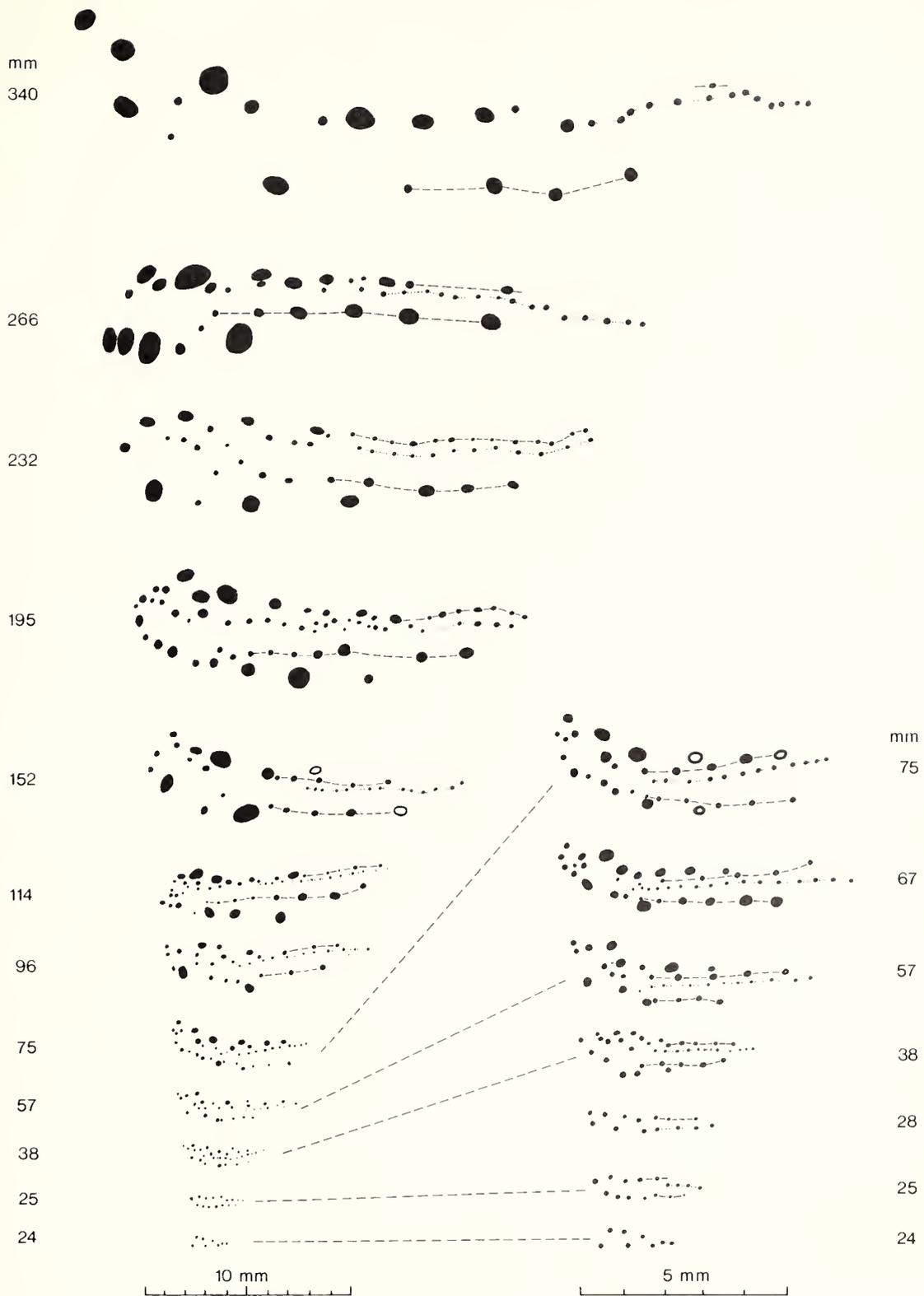


Figure 6. Diagrammatic representation of dentary-tooth patterns of females of *Gigantactis vanhoeffeni* arranged according to stage of development.

tal series meeting anteriorly in front of the nostrils at the base of the illicium, (2) an infraorbital series following along the edge of the upper jaw and meeting posteriorly with (3) an opercular series that connects with the two supraorbital series and spreads out ventrally in an irregularly arranged group of organs below and in front of the gill opening, and (4) two somewhat irregular mandibular series that meet with the opercular series posteriorly and are continuous anteriorly with their counterparts of the opposite side. No distinct cephalic lateral-line commissures between left and right sides are apparent.

The two supraorbital series continue posteriorly in a double lateral line from a very dorsal position in front of the dorsal fin descending to a mediolateral position below the dorsal fin, along the caudal peduncle, and finally out onto each ray of the caudal fin.

Oral Glands of *Rhynchactis* Females

The jaws and oral cavity of metamorphosed *Rhynchactis* females differ from those of other known ceratioid females in the extreme reduction of the jaw bones and lack of dentary and premaxillary teeth and in possessing numerous, large glands that line the inner walls of the jaws. On each side of the upper and lower jaw, a crescent-shaped internal lip is covered with a dense pavement of white papillae, each outlined by pigmented skin (Fig. 9). Each papilla has a more or less distinct central groove that represents the opening of a short tube; each tube is internally walled with large glandular cells that nearly fill the lumen (Fig. 10). Properly fixed material was unavailable for a more thorough histological investigation. No glands were found in the triangular pad of tissue covering the roof of the mouth between and in front of the pharyngeals (Fig. 9); this pad instead consists of tough connective tissue divided into large

close-set papillae, each carrying a distal group of smaller pigmented papillae. In *Gigantactis* females, this part of the roof of the mouth is covered with irregular, transverse folds of pigmented skin.

OSTEOLOGY

CRANIUM, Figures 11-14, 17

The cranial osteology of gigantactinid genera is characterized most strikingly by an extreme reduction and loss of parts. With few exceptions the ethmoid complex of both *Gigantactis* and *Rhynchactis* consists only of widely separated lateral ethmoids. A supraethmoid ossification is present in the 14.5-mm Type V male (LACM 32775-1, Fig. 11F) but greatly reduced in size in the 13.5-mm Type II male (LACM 33324-1). It is absent in larvae and in all metamorphosed male and female specimens examined osteologically except for the 152-mm preparation of *G. vanhoeffeni*, where it is represented by a small rudiment (Fig. 12). An ossified vomer is present in larvae and males (reduced in the 17-mm *Rhynchactis* male, Fig. 11F) but absent in adolescent and adult females of both genera. The frontals are relatively short and broad in the larvae and males of both genera (Figs. 11, 14). However, in metamorphosed females of *Gigantactis*, the frontals are long, narrow, and widely separated throughout their length, approaching each other only slightly at midlength (anteriorly, each frontal lies in close proximity but does not meet with the dorsal process of the respective lateral ethmoid; posteriorly each is overlapped slightly by the respective parietal bone). In *Rhynchactis*, the frontals and parietals are present in larvae and males but absent in the 60-mm female (Fig. 11). The pterosphenoid is absent in *Gigantactis* and *Rhynchactis* of both sexes.

In both gigantactinid genera, the supraoccipital occupies a more anterior position than in other ceratioids. In females, most of the outer surface of this bone lies in the vertical plane, providing a posterior abutment for the pterygiophore of the illicium. In larvae and males of both genera, the entire outer surface of the supraoccipital lies in the horizontal plane.

MANDIBULAR ARCH, Figures 11, 13-15

In *Gigantactis* females, the premaxilla is long and narrow but well ossified, bearing teeth along most of its length (toothless in metamorphosed males and reduced to a small anterior remnant lying just in front of a small symphyseal cartilage, Fig. 15). A small articular process is present, but ascending and postmaxillary processes are absent. The maxilla of *Gigantactis* females is greatly reduced, becoming further reduced with age. In the 141-mm specimen of *G. macronema*, the maxilla is represented by a short anterior portion and a filamentous posterior remnant; in the 146-mm and 209-mm preparations of *G. vanhoeffeni* and *G. longicirra*, respectively, only the posterior filament remains. The elements of the upper jaw are present in *Rhynchactis* larvae but become greatly reduced or lost in adolescents and adults (Figs. 11, 13). The maxilla is absent in the 60-mm female. A thin premaxilla bearing one large, recurved, anterior tooth and a series of minute teeth along its posterior extension is present in the 42-mm holotype of *Rhynchactis leptonema*, but

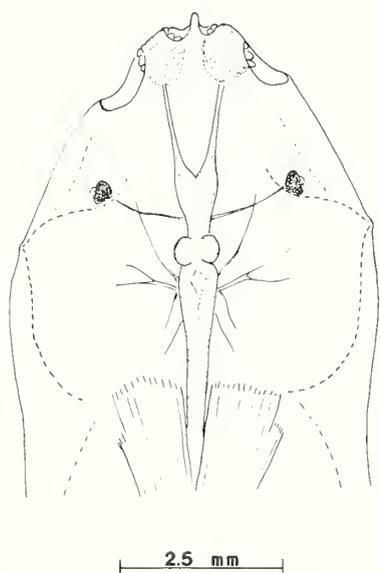


Figure 7. Brain of juvenile male of *Rhynchactis leptonema*, 17 mm, LACM 37519-1, dorsal view.

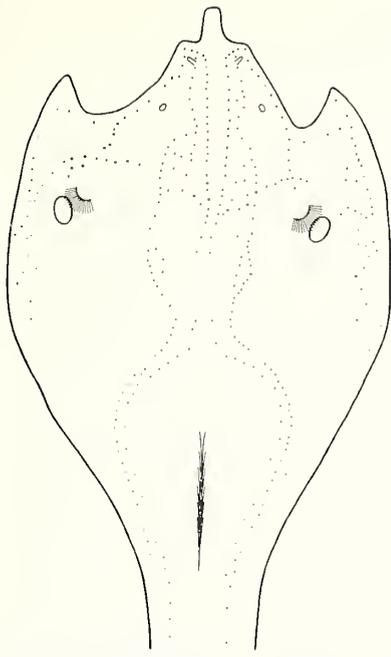


Figure 8. Acoustical-lateralis system of female *Gigantactis van-hoeffeni*, 152 mm, ISH 802/68.

only a small, single-toothed, anterior remnant of the premaxilla remains in the 60-mm specimen (Fig. 13). A symphyseal cartilage is absent in larvae and metamorphosed females of both genera.

Unlike the dentaries of most other ceratioids, those of gigantactinid genera are not forked posteriorly except in males and larvae. The posterior half of the ventral margin of these bones in females forms a relatively loose and mobile connection with the respective articular. Anteriorly, the dentaries curve to approach each other on the midline where they are attached to each other by thick, elastic connective tissue. Compared to females of *Rhynchactis*, the bones of the lower jaw of *Gigantactis* females are thick and well-ossified (Fig. 13). Dentary teeth are absent in *Rhynchactis*; in *Gigantactis*, each dentary bears several rows of recurved, depressible teeth (see "Dentition").

As in other male ceratioids, jaw teeth of male gigantactinids are lost during metamorphosis. The upper and lower denticular teeth (Bertelsen 1951:21) are loosely attached at the symphysis of the maxillae and dentaries, respectively. In *Gigantactis* males, the denticular teeth are all mutually free and proximally compressed; in *Rhynchactis*, at least some of the teeth are paired and supported by relatively broad bases (Fig. 15).

Unlike most other ceratioids, the articular of females of both *Gigantactis* and *Rhynchactis* does not extend back beyond its articulation with the quadrate. Furthermore, there is no ligamentous connection between the angular bone and the reduced interoperculum.

PALATINE AND HYOID ARCHES, Figures 13, 14, 16B

The palatine arch of females of both gigantactinid genera consists of a triangular-shaped metapterygoid and elongate ectopterygoid and palatine bones; the mesopterygoid is absent

except in males and larvae. The hyomandibular bone is large and unforked, forming a single, broad articulation with the cranium. The symplectic is conical in shape and short compared to that of other ceratioids, in females, not extending beyond the dorsal margin of the quadrate. In *Gigantactis* females, the posterodorsal margin of the symplectic is covered laterally by the posterior process of the quadrate; the latter bone is overlapped in turn by the ventral half of the reduced preopercle (Fig. 13A). In *Rhynchactis* females, the posterior process of the quadrate is reduced dorsally so that the remnant of the preopercle lies directly on the symplectic (Fig. 13B).

The epihyals and ceratohyals are narrow and elongate. Each pair bears the heads of six long and slender branchiostegal rays, the anteriormost two of which articulate on the medial surface, the remaining four on the lateral surface. *Gigantactis* females have a single, elongate hypohyal, whereas *Rhynchactis* females have retained both a dorsal and a ventral hypohyal.

As is typical for ceratioids, nearly all examined gigantactinids have six branchiostegal rays. However, in the 14-mm *G. longicirra* male (UMML 27412), there are seven branchiostegal rays on each side: two in an anteromedial position and five in a posterolateral position (Fig. 16B). The 14-mm male in metamorphosis (unidentified, LACM 32772-3) has seven branchiostegal rays on the right side (three anteromedial and four posterolateral) but only six on the left side (two anteromedial and four posterolateral).

OPERCULAR APPARATUS, Figures 13-14

In both gigantactinid genera, the posterior margin of each opercle is deeply notched forming two narrow forks (except in males and larvae), the lower fork slightly longer than the upper. The two forks (the upper one of which is bifurcated on the left side of the 209-mm specimen of *G. longicirra*) are slightly curved in *Gigantactis* but straight in *Rhynchactis*. The subopercle of juvenile females of *Gigantactis* consists of a relatively broad lower portion and a single, short, tapering posterior extension. In larger female specimens, this broad lower portion becomes reduced, sometimes leaving behind a small anterior projection and as many as three filamentous, posterior prolongations, the uppermost of which may be nearly as long as the lower fork of the opercle. The subopercle of the 60-mm female of *Rhynchactis* is a simple, slender, posteriorly tapering bone that is approximately equal in length to the lower fork of the opercle.

In *Gigantactis* females, the preopercle is a small strut of bone that bridges the gap between the hyomandibular and quadrate bones. In *Rhynchactis* females, this element is further reduced, lying on the lateral surface of the symplectic (the latter exposed by the reduced quadrate) but not extending dorsally to the hyomandibular.

BRANCHIAL ARCHES, Figures 13, 16

The elements of the branchial arches are similar in both gigantactinid genera. A pharyngobranchial I is absent. Pharyngobranchials II and III are extremely well developed and heavily toothed (except in males), especially in *Gigantactis*. Epibranchial I is absent. The anterior halves of epibranchials

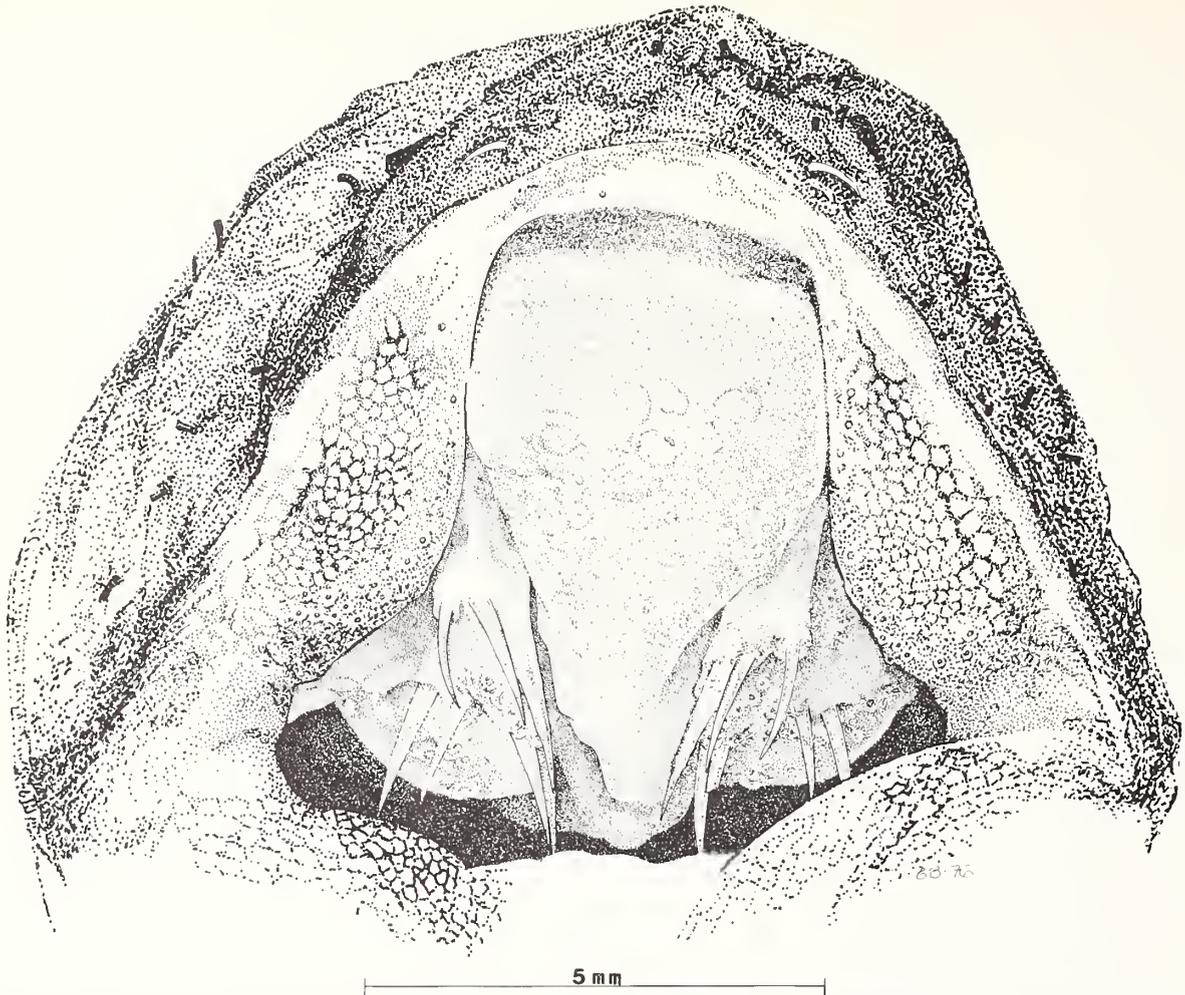


Figure 9. Mouth cavity of female *Rhynchactis leptonema*, 60 mm, ISH 2332/71, showing oral glands. Drawn by Elizabeth Beyerholm.

III and IV are tightly held to each other by connective tissue. Ceratobranchials I through V are complete in males. In females, ceratobranchial I is reduced so that only a small posterior and one or two small ossified remnants of the anterior portion remain; ceratobranchial V is represented only by one or two tiny ossifications (completely lost in the 146-mm preparation of *G. vanhoeffeni*) lying free in the connective tissue matrix. There are no ossified hypobranchials or basibranchials in females; males have a single basibranchial ossification.

VERTEBRAE AND CAUDAL SKELETON, Figure 17

The vertebrae of gigantactinids do not differ substantially from those described for other ceratioids (Pietsch 1972a:36, fig. 16, 1974:12, fig. 12). In all cleared and stained female specimens of *Gigantactis* examined, there are 22 vertebrae. The posterior 15 of these bear complete haemal arches and are thus considered caudal vertebrae. In the 60-mm *Rhynchactis* female there are 20 vertebrae, the posterior 14 of which are caudal.

The caudal skeleton of gigantactinids is like that of other ceratioids in having the ural centra fused with the first pre-ural centrum to form a single, complex half-centrum which is fused

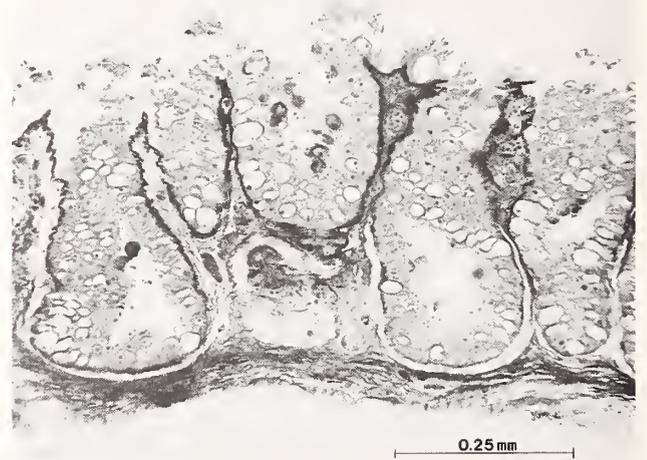


Figure 10. Section through oral glands of female *Rhynchactis leptonema*, 60 mm, ISH 2332/71. Courtesy of Geert Brovad.

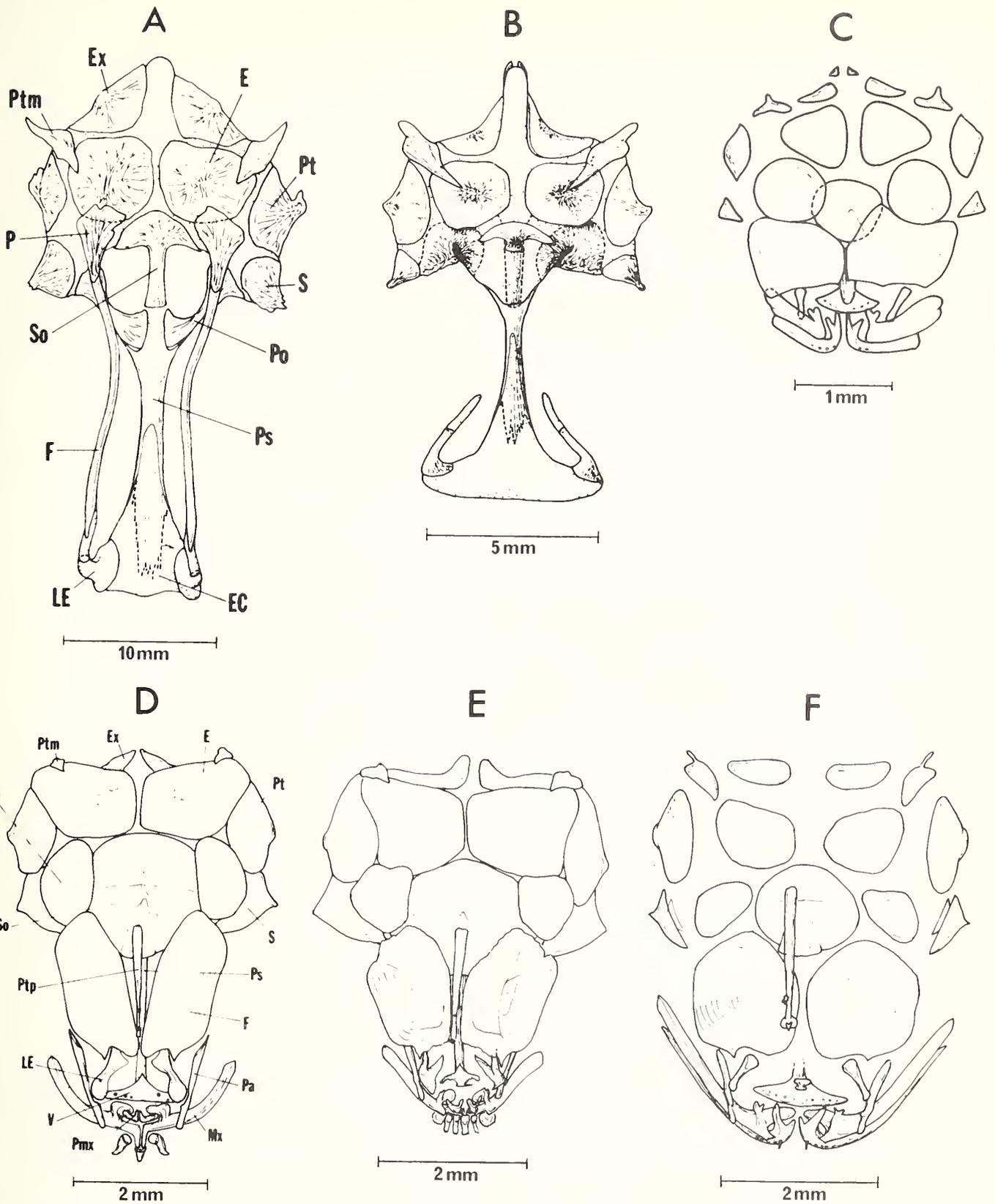


Figure 11. Dorsal views of crania of gigantactinids: A. *G. longicirra*, female, 209 mm, ISH 973/68; B. *R. leptonema*, female, 60 mm, ISH 2332/71; C. *R. leptonema*, larval female, 7.5 mm, ZMUC P921751; D. *G. longicirra*, male, 14 mm, UMML 27412; E. *R. leptonema*, male, 17 mm, LACM 37519-1; F. *G. male* Group V, 14.5 mm, LACM 32775-1.

to a single hypural plate. The hypural plate is unnotched posteriorly and bears the overlapping bases of nine principal caudal rays. These rays are all biserial and segmented. The ninth caudal ray is reduced and embedded within the skin surrounding the adjacent ray. All caudal rays are unbranched in female *Gigantactis*, but rays three (from the top) through six are branched distally in male *Gigantactis* and in both sexes of *Rhynchactis*. In the females of both genera the outermost caudal rays are longer than the inner rays so that, unlike all other ceratioids, the tail fin is emarginate (except in largest females of some species of *Gigantactis*).

ILLICIAL APPARATUS, Figures 11, 13, 14, 17

The pterygiophore of the illicium is exceptionally large and laterally compressed in female gigantactinids. It lies on top of the parasphenoid and ethmoid cartilage and passes between the proximal ends of the huge, dorsally projecting pharyngobranchials II and III, the frontals (in *Gigantactis* females only), and the lateral ethmoids. In females of both genera, the cartilaginous posterior end of this element butts up against the vertical surface of the supraoccipital; the anterior end extends slightly beyond the tip of the upper jaw in *Gigantactis* but terminates just posterior to this point in *Rhynchactis*. A small ossified remnant of the second cephalic ray is present in both genera. The illicial bone is strongly articulated to the distal tip of the pterygiophore.

PECTORAL GIRDLE, PECTORAL FIN, AND PELVIC BONES, Figures 13, 14

The cleithrum of *Gigantactis* females is sharply angled at mid-length, the lower portion being considerably more slender than the upper. The cleithrum of *Rhynchactis* females, on the other hand, is much more like that of most other ceratioids, forming a smooth crescent-shaped curve, the lower portion gradually tapering anteriorly. In both genera, there is a single, elongate

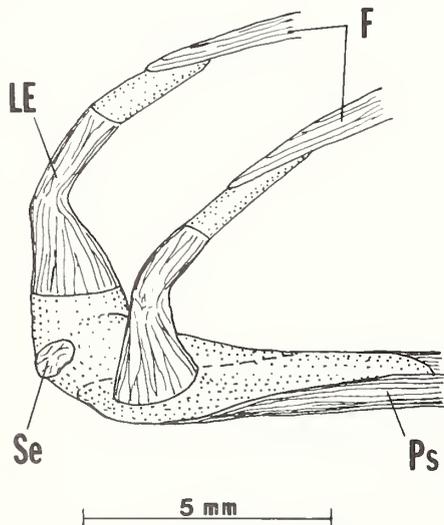


Figure 12. Lateral view of ethmoid region of *Gigantactis vanhooeffeni*, female, 152 mm, ISH 802/68.

postcleithrum. In *Gigantactis* females, the coracoid consists of a small, conical, anterior ossification and an elongate, cartilaginous, posteroventral process that extends backward along the postcleithrum; the scapula remains unossified. In *Rhynchactis*, both the coracoid and scapula are unossified.

In all gigantactinids, there are five pectoral radials. In both genera, it appears that the fourth radial (from the top) tends to become reduced; the proximal end of this radial is absent in most specimens of *Gigantactis* examined. In the 60-mm *Rhynchactis* female, the uppermost pectoral radial extends considerably past the distal tips of the lower four radials. *Gigantactis* has from 14 to 22 pectoral rays, *Rhynchactis* has from 17 to 20 (Tables 2, 20, 21). These rays are all biserial, segmented, and unbranched.

Pelvic bones appear to be absent in all *Gigantactis* examined but represented by small struts of bone in *Rhynchactis*.

SKIN SPINES

Numerous, close-set spines covering the entire body and fins are visually obvious in uncleared specimens of females of all species of *Gigantactis* without microscopic aid. These spines extend out onto the illicium and in some species onto the esca bulb. In *Gigantactis* males, skin spines are present in members of groups II and III (Table 19) but absent in *G. longicirra* and members of groups I, IV and V.

Minute spines are present in the skin of the largest known female (126 mm) of *Rhynchactis* but are absent in males and smaller females.

MYOLOGY OF THE FEEDING MECHANISM

The musculature of the feeding mechanism of gigantactinid females is similar to that described by Field (1966) for the much less derived, shallow-water anglerfish, *Lophius piscatorius*. Differences are mainly in the degree of development of various muscles, and in the reduction and loss of muscle segments due to a corresponding reduction and loss of bony parts. The muscles of the illicial apparatus (cephalic tentacle) of *Gigantactis* were studied by Brauer (1908). These muscles were redescribed by Waterman (1948), and discussion and figures of those of the upper pharyngeals and superficial muscles of the cheek were added. These are reviewed below along with previously undescribed musculature of the lower jaw and floor of the mouth.

CHEEK MUSCLES, Figure 18

Section A₁ of the adductor mandibulae, defined by its dorsal position and insertion on the maxilla (Winterbottom 1974:232), is absent in gigantactinids, corresponding to the severe reduction or loss of this upper jaw bone. In *Gigantactis*, section A₂ (adductor mandibulae superficialis of Waterman 1948:95, fig. 1) has a broad origin on the posterodorsal margin of the hyomandibular and a narrow insertion on the posterodorsal margin of the articular; it does not share a myocomma anteriorly with the posterior fibers of Section A_w (see "Lower Jaw" below). Section A₃ (adductor mandibulae profundus of Waterman 1948:95, fig. 1) lies medial to A₂, originating broadly on the

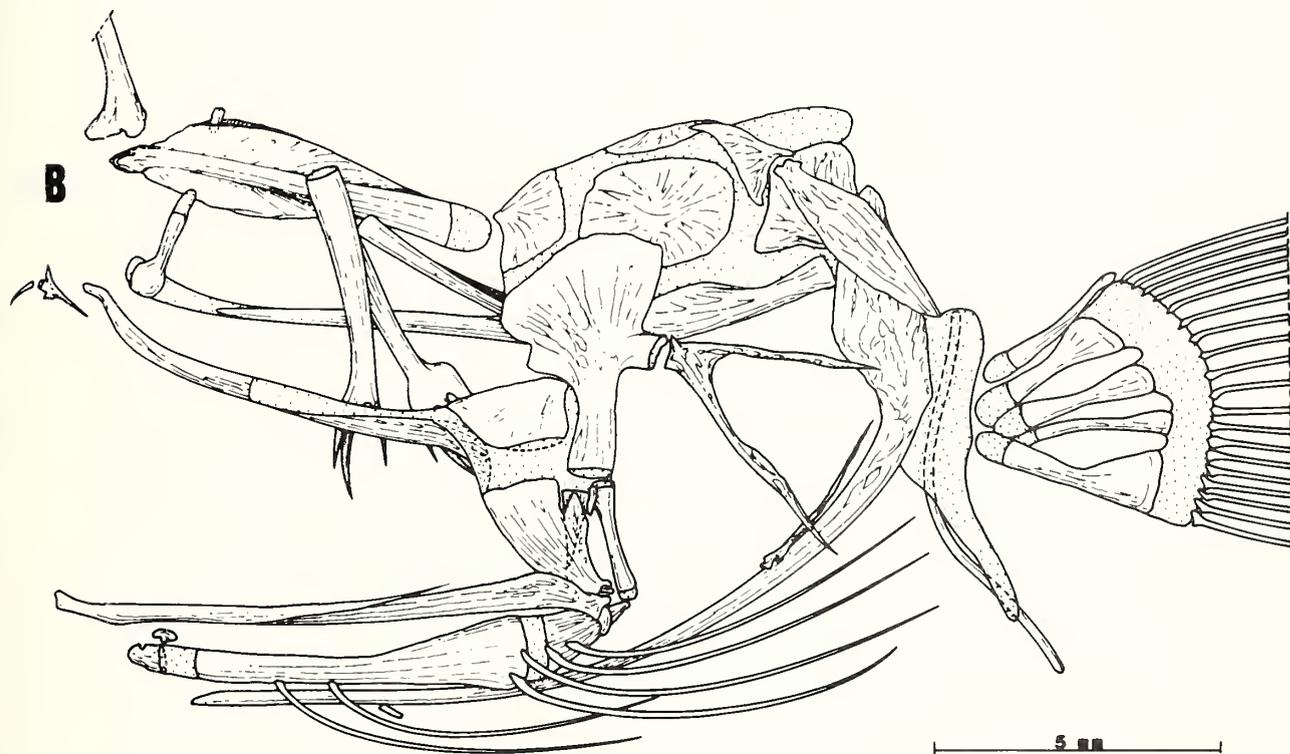
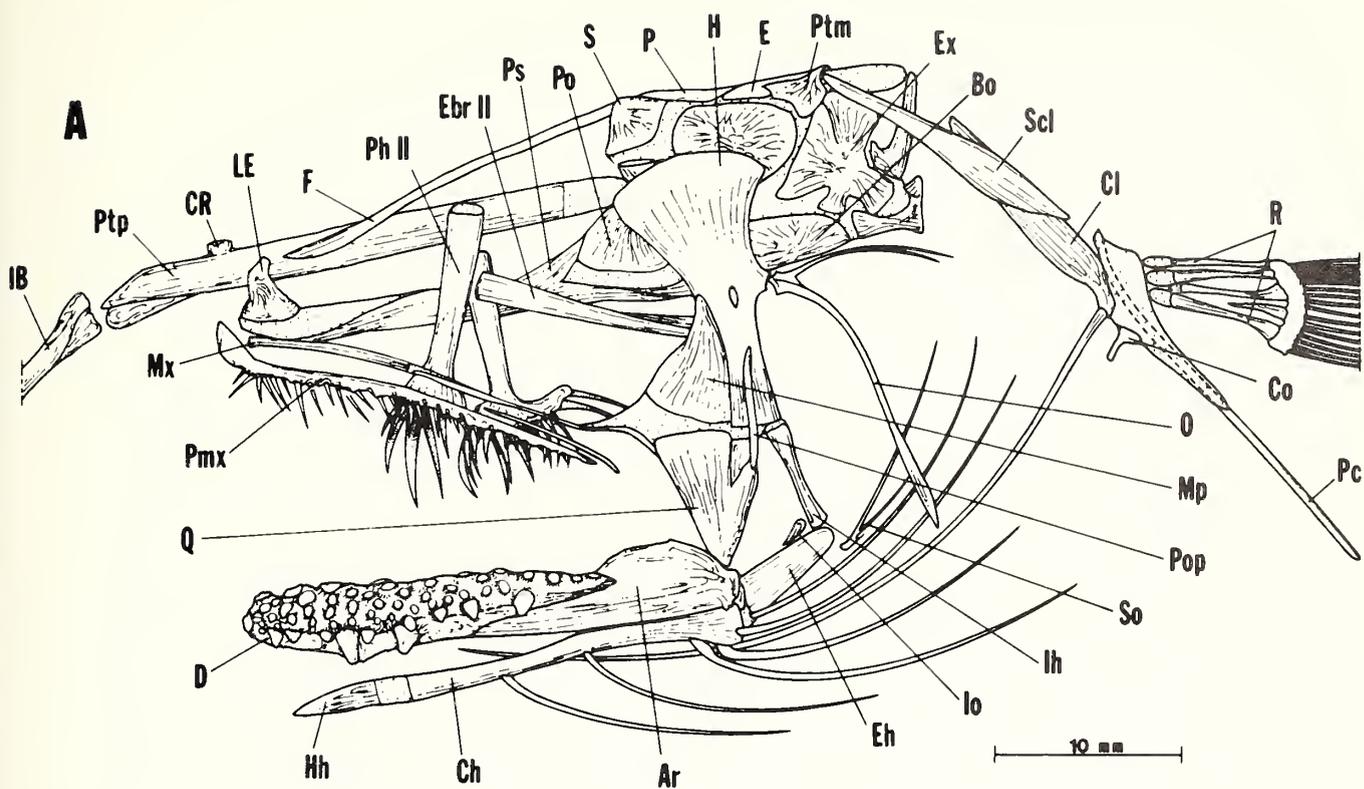


Figure 13. Lateral views of skulls of female gigantactinids with pectoral girdle, opercular apparatus and hyoid apparatus in place: A. *G. longicirra*, 209 mm, ISH 973/71; B. *R. leptonema*, 60 mm, ISH 2332/71.

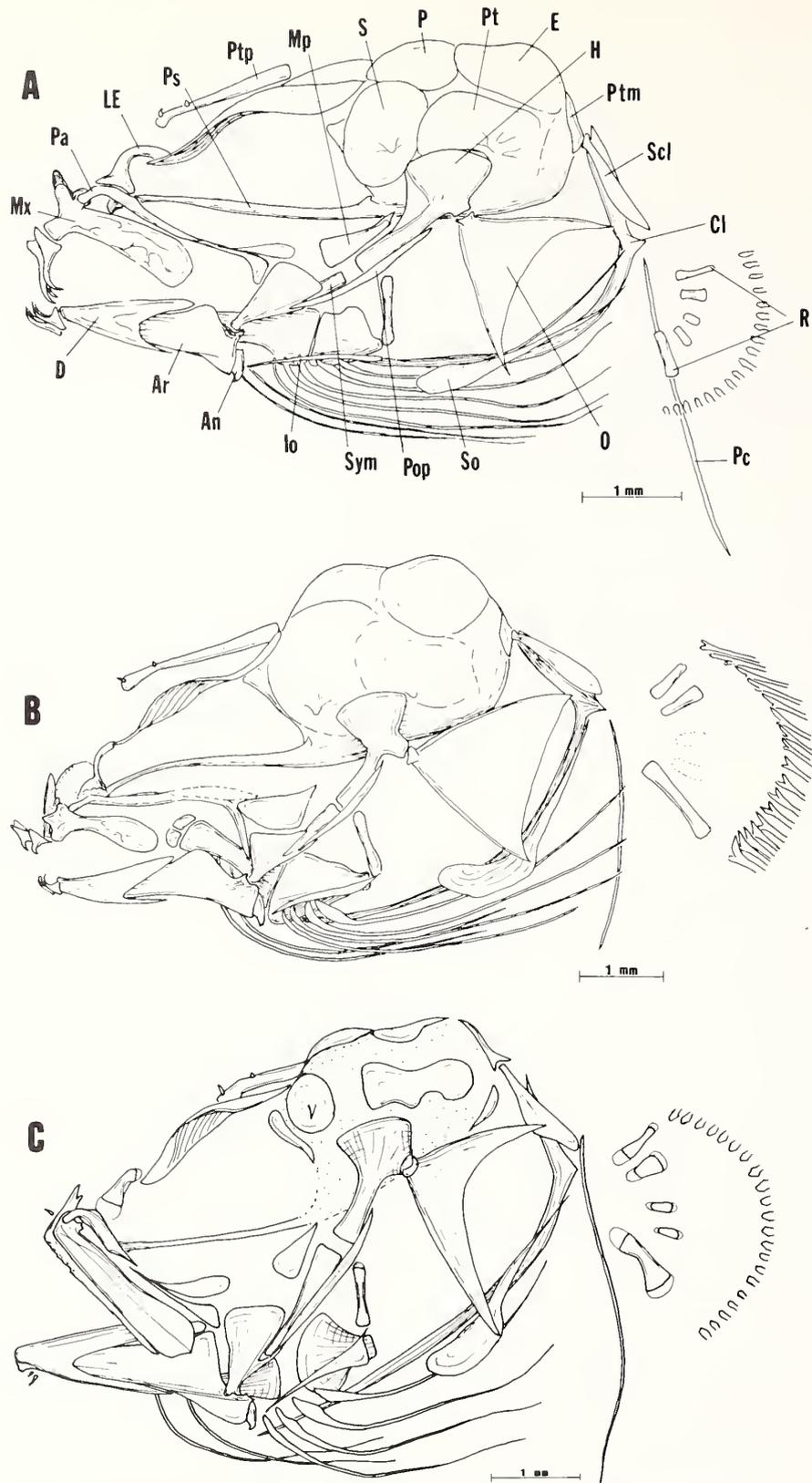


Figure 14. Lateral views of skulls of male gigantactinids with pectoral girdle, opercular apparatus and hyoid apparatus in place: A. *G. longicirra*, 14 mm, UMML 27412; B. *R. leptonema*, 17 mm, LACM 37519-1; C. *G.* male Group V, 14.5 mm, LACM 32775-1.

quadrate, on the anteroventral margin of the hyomandibular and metapterygoid. A small dorsal subdivision originating on the sphenotic is thought to be part of A_3 . All of these muscles are essentially the same in *Rhynchactis*.

The levator arcus palatini (L.A.P.) has its origin on the sphenotic and its insertion on the lateral face of the hyomandibular. A narrow dilatator operculi (D.O.) originates on the sphenotic and inserts on the proximal tip of the opercle. The levator operculi (L.O.) is also narrow, originating on the pterotic and inserting on the upper fork of the opercle. These are all essentially the same in *Rhynchactis*.

LOWER JAW, Figures 18, 19

In *Gigantactis*, section A_w of the adductor mandibulae muscle (articulodentary of Field 1966:54, fig. 4; see also Winterbottom 1974:242) is extremely well developed but has lost all connection with section A_2 becoming purely an intrinsic lower jaw muscle. It covers nearly the entire medial surface of the lower jaw, stretching between the dentary and articular, its oblique fibers running in a anterodorsal-posteroventral direction. In lateral view, it can be seen extending well below the ventral margin of the lower jaw. In the material of *Rhynchactis* available to us, no trace of this muscle could be found. This absence corresponds with the narrow, extremely reduced and toothless bones of the lower jaw of this genus.

FLOOR OF MOUTH, Figure 19A

The intermandibularis (IMD) of *Gigantactis* is a relatively long, narrow muscle that has a broad insertion on the ventral margin of the dentaries just behind the symphysis. Its transverse fibers pass ventral to a thick, crescent-shaped pad of elastic connective tissue that lies between the two halves of the lower jaw preventing them from meeting on the midline. No trace of this muscle could be found in *Rhynchactis*.

The protractor hyoidei (PR.HY.) of *Gigantactis* has a broad origin on the ventral-most margin of the dentary overlapping the insertion of the intermandibularis muscle. Each protractor hyoidei narrows posteriorly, approaching its counterpart from the other side and inserting on a fascia near the midline. From this narrow insertion, each protractor hyoidei widens further posteriorly, attaching broadly to the respective ceratohyal. Only traces of this muscle could be found in *Rhynchactis*.

The sternohyoideus muscle (STH.) of *Gigantactis*, originating on the cleithrum, splits into two sections: a considerably larger, lateral section inserts on the respective hypohyal; the medial section (not shown in Figure 19A) passes to the distal tip of ceratobranchial IV. This muscle has essentially the same morphology in *Rhynchactis* but is slightly larger than that of *Gigantactis* of a similar standard length.

The hypaxial musculature forms a broad insertion along most of the posterior margin of the lower half of the cleithrum in both gigantactinid genera.

UPPER PHARYNGEALS, Figures 18A, 20

As described by Waterman (1948:96, figs. 1, 8), the largest and most complex muscle system in *Gigantactis*, except for the body musculature, is the system that operates the hypertrophied pharyngobranchials and epibranchials of the second

and third branchial arches. These muscles are essentially the same in both gigantactinid genera; *Rhynchactis* is mentioned below only when known differences or additions occur.

The levatores externi muscles (levatores arcuum branchialium externi of Waterman 1948:97, figs. 1, 8), of which only two can be differentiated, originate together on the parietal. The larger, more posterior of these divides distally to insert broadly on epibranchials II and III. The smaller muscle, in contrast to the usual situation (Winterbottom 1974:250), and not mentioned by Waterman (1948), does not insert on an epibranchial but passes down between epibranchials II and III to insert on the posterior margin of pharyngobranchial III just at the base of the pharyngobranchial teeth. The levatores externi muscles appear to be similar in *Rhynchactis* except that, in the absence of the parietal bones, origin takes place on the medial margin of the pterotic.

The levatores interni (levatores arcuum branchialium interni of Waterman 1948), of which we can differentiate only one (most probably those that serve pharyngobranchials II and III have fused to form a single muscle mass; Waterman 1948:97),

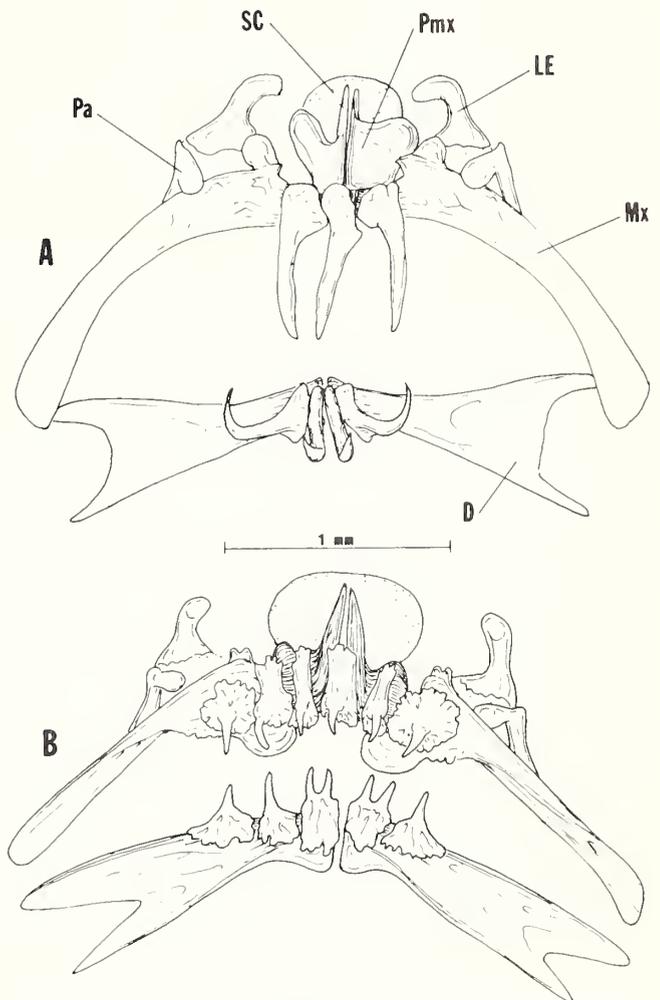


Figure 15. Anterior views of upper and lower jaws of male gigantactinids showing denticular teeth: A. *G. longicirra*, 14 mm, UMML 27412; B. *R. leptonema*, 17 mm, LACM 37519-1.

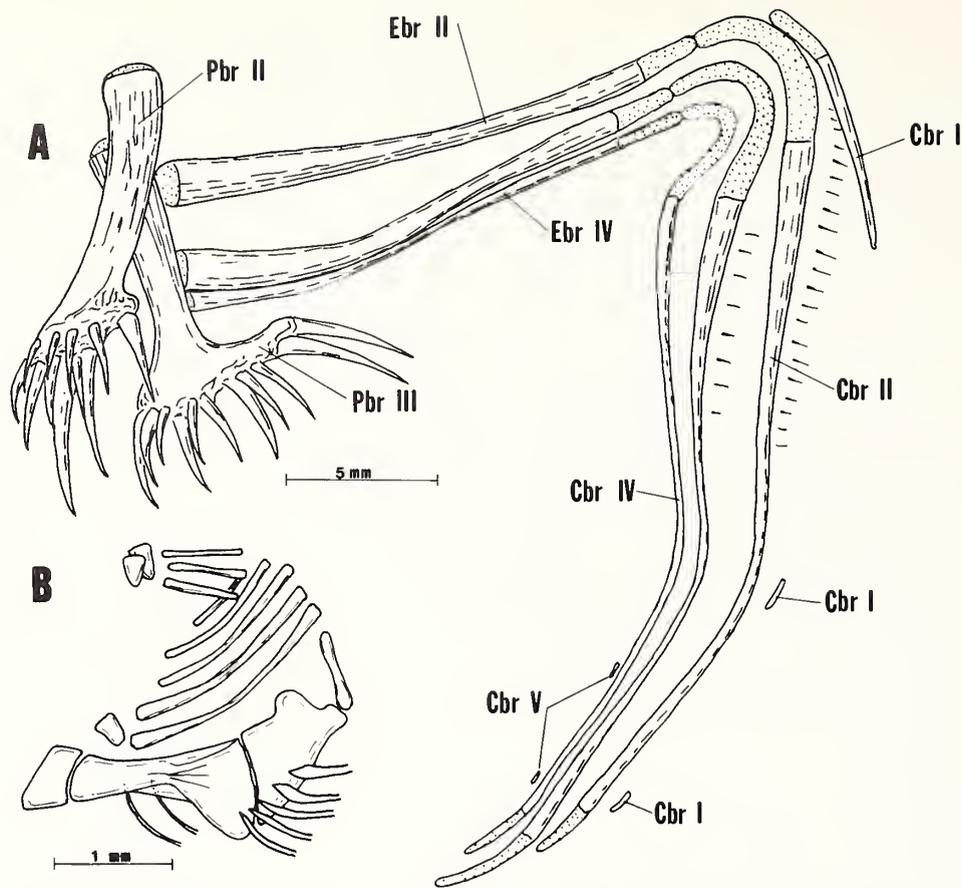


Figure 16. Branchial arches of *Gigantactis longicirra*: A. Female, 209 mm, ISH 973/71; B. Male, 14 mm, UMML 27412, showing hyoid apparatus.

originates on the prootic and sphenotic. It passes dorsal to the retractor dorsalis and medial to the levator externus muscles to insert on the proximal ends of pharyngobranchials II and III.

Three obliqui dorsales muscles (OBL.D.) are present in *Gigantactis*. That serving the second arch (interarcualis dorsalis 2 of Waterman 1948, figs. 1, 8) is especially well developed, originating on the dorsolateral surface of pharyngobranchial II and inserting on the proximal-lateral surface of epibranchial II.

The transversi dorsales (TR.D.) originates partly on the parasphenoid and partly on a fascia near the midline. It passes medial to the levator externus and under the levator internus to form a large, bulbous insertion on the dorsolateral surface of pharyngobranchial II.

The retractor dorsalis (R.DORS.; retractor arcuum branchialium of Waterman 1948:97) is an enormous muscle that originates on the three anterior-most vertebrae and part of the fourth. Insertion is on the posteroventral margin of pharyngobranchial III. In conflict with Waterman's description (1948:97, figs. 1, 8), no fibers on the retractor dorsalis insert on pharyngobranchial II.

ILLICIAL MUSCULATURE, Figure 21

The illicial apparatus is controlled by five pairs of muscles: two intrinsic pairs—the depressor and erector dorsalis I (DEPR.D. and EREC.D., respectively; flexor and extensor, respectively, of

Bertelsen 1951); and three extrinsic pairs—the supracarinales anterior (SCAR.A.: exertor of Bertelsen 1951), and anterior and posterior subdivisions of the inclinator dorsalis II (INCL.D.; inclinator and retractor, respectively, of Bertelsen 1951). The origins and insertions of these muscles have been previously described (Waterman 1948, Bertelsen 1951). Compared to most other ceratioids, the extrinsic illicial muscles of gigantactinids are small. In contrast, the two intrinsic muscle pairs are unusually large.

FUNCTIONAL MORPHOLOGY OF THE FEMALE FEEDING MECHANISM

GIGANTACTIS

Despite its restricted mobility relative to the cranium (only a few millimeters, even in the largest individuals), the pterygiophore of the illicium of *Gigantactis* is equipped with moderately developed extrinsic muscles (the supracarinales anterior and the anterior and posterior subdivisions of the inclinator dorsalis II; Fig. 21). The extrinsic illicial musculature of *Gigantactis* does not provide for gross movement in the antero-posterior and lateral directions, as is the case in most other ceratioids (particularly *Ceratias* and *Oneirodes*, see Bertelsen 1943 and Pietsch 1974, respectively). Instead, it is used to produce vibration that passes out along the stiff illicial bone to the

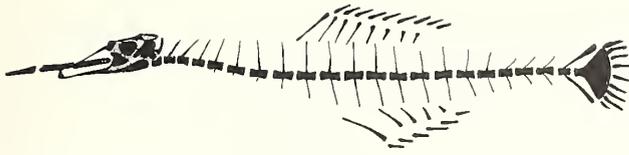


Figure 17. Diagrammatic representation of axial skeleton of *Gigantactis longicirra*, female, 209 mm, ISH 973/71.

esca and esca filaments. That most of this vibration is transferred to the surrounding water by the esca and its filaments rather than by the stem of the illicium was confirmed by one of us (R.J. Lavenberg) through direct observation. Immediately upon capture, the 408-mm holotype of *G. gargantua* was placed live in an aquarium. Several whip-like, backward and forward thrusts of the entire illicium were followed by moderately-strong vibrations of the esca with no apparent movement of the illicium, although quick, rapid contractions could be felt throughout its length. This vibratory action, combined with the bioluminescence of the bait, appears to be the most important mechanism of attracting prey; to what extent sweeping movements of the entire illicium are used in luring is unknown. Feeding on unattracted (or unattractable) prey items may occasionally occur. How female ceratioids detect their attracted (or unattracted) prey is still open to speculation. In *Gigantactis*, this is especially difficult to understand with the large predator-to-prey distance due to the exceptionally long fishing apparatus (Fig. 22). It is unlikely that the small, laterally positioned eyes, lacking stereoscopic vision and an ability to produce a well-defined image (Munk 1964:12), play any role in prey detection. The acoustico-lateralis system of the head, well developed in most ceratioids, may function in this way in those species in which prey is brought up close to the head, but it seems questionable that the system could provide sufficient distance and directional signals at the distance required by *Gigantactis*. Although unsupported by direct observation, the nervous innervation of the esca described by Brauer (1908) and Waterman (1948) indicates that this organ and its filaments are sensitive to touch or to pressure waves produced by moving prey. It is hypothesized that once prey has been attracted to the bait, it is seized by a sudden, forward lunge, for which the streamlined body and powerful caudal of *Gigantactis* seem well adapted (Bertelsen 1951).

The jaw mechanism of *Gigantactis* is similar to that of *Thaumatichthys* (family Thaumatichthyidae) in that it allows the seizure of prey to be made by means of long hooked teeth placed outside the mouth, rather than through suction as is the case in nearly all other anglerfishes (Bertelsen 1951:242; Bertelsen and Struhsaker 1977:29; Grobecker and Pietsch 1979). Although it is the lower jaw of *Gigantactis*, in contrast to the upper jaw of *Thaumatichthys*, which is specialized in this way, the principle of both mechanisms is identical. In both, the bones of the right and left sides of the jaw are free at the sym-

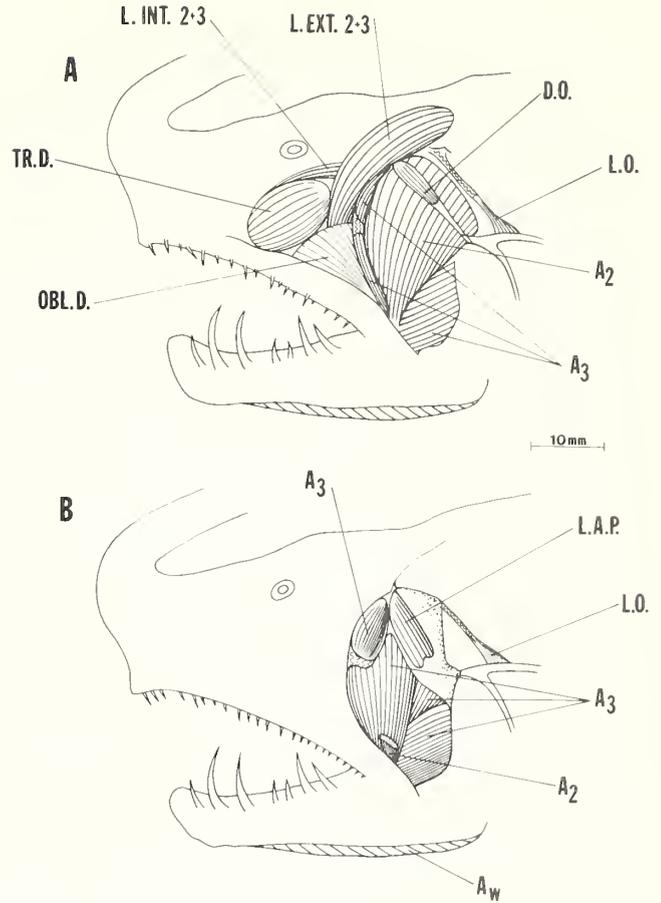


Figure 18. Muscles of the cheek, upper pharyngeals and lower jaw of *Gigantactis meadi*, female, 353 mm, LACM 11242-12; A. Superficial musculature; B. Portions of superficial musculature removed.

physis, connected only by elastic ligaments; each bone can be twisted relative to the other in such a way that their long, curved teeth can be rotated inwards from a widely outstretched, open position to a situation in which the teeth of the opposite side approach each other within the cavity of the mouth (Fig. 23). In both, the relatively small teeth in the opposing jaw (the upper in *Gigantactis*, lower in *Thaumatichthys*) play a secondary role in seizing prey. It seems apparent that in *Gigantactis* the prey is snagged by the outstretched, recurved dentary teeth and brought into the buccal cavity within reach of the huge, upper pharyngeal teeth by a sudden, inward twist of the lower jaw (possibly aided by negative pressure created by a sudden expansion of the buccal and opercular cavities). The elastic connection between the rami of the lower jaw may allow for asymmetrical opening and closing of the mouth (much like the feeding mechanism of a snake); this alternating side to side adduction of the mandible, in association with the hooked and hinged jaw teeth, would facilitate the transport of prey items back towards the reach of the upper pharyngeal teeth. The extreme development and forward position of the upper pharyngeal teeth contribute to the efficiency with which the prey is seized and transferred to the stomach. Morphological evidence as well as direct observation on the living holotype

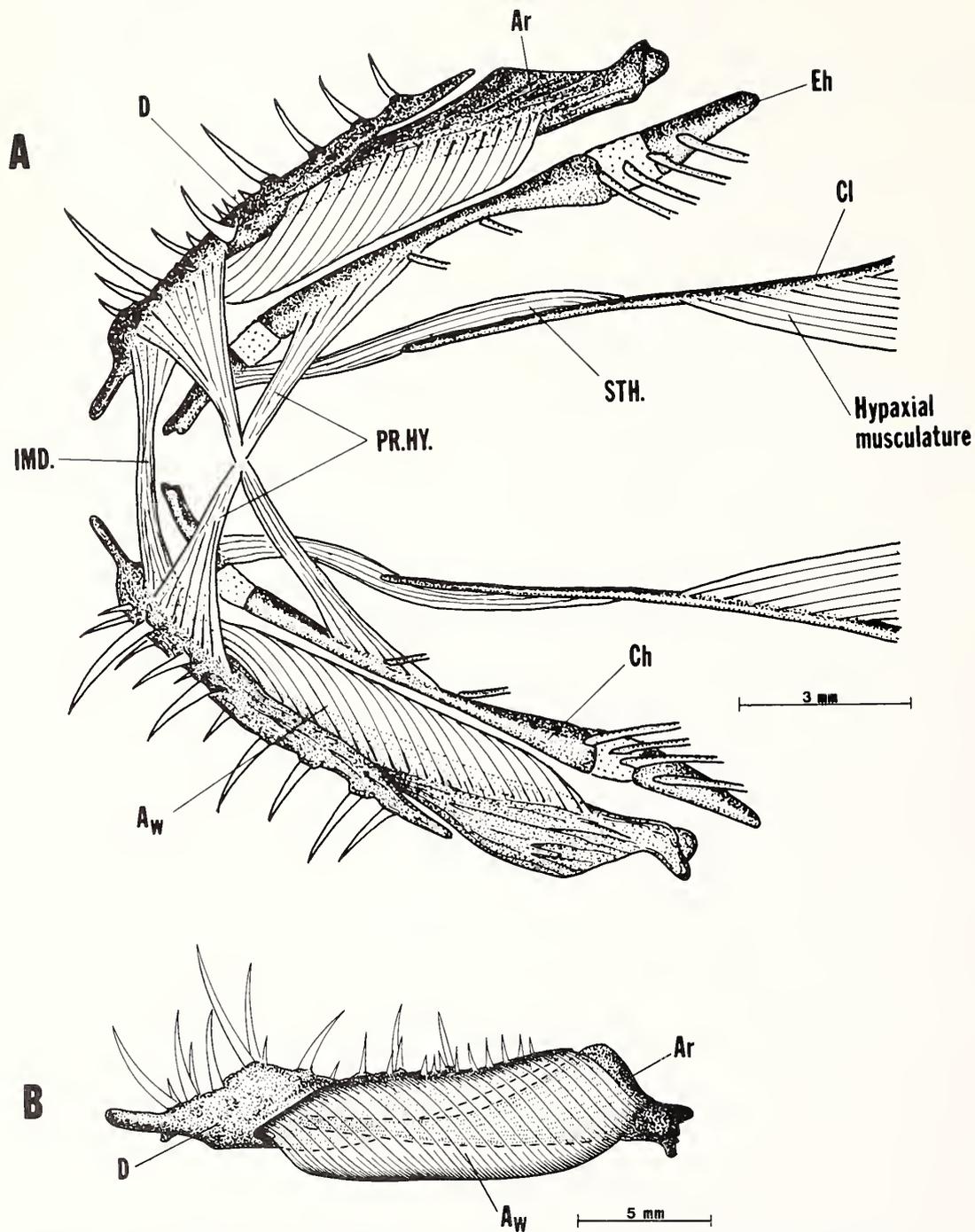


Figure 19. Musculature of the lower jaw and floor of throat of female *Gigantactis vanhoffeni*: A. Ventral view, 67.5 mm, ZMUC P921972; B. Medial view of lower jaw showing intrinsic lower jaw muscle, 152 mm, ISH 802/68, left side reversed.

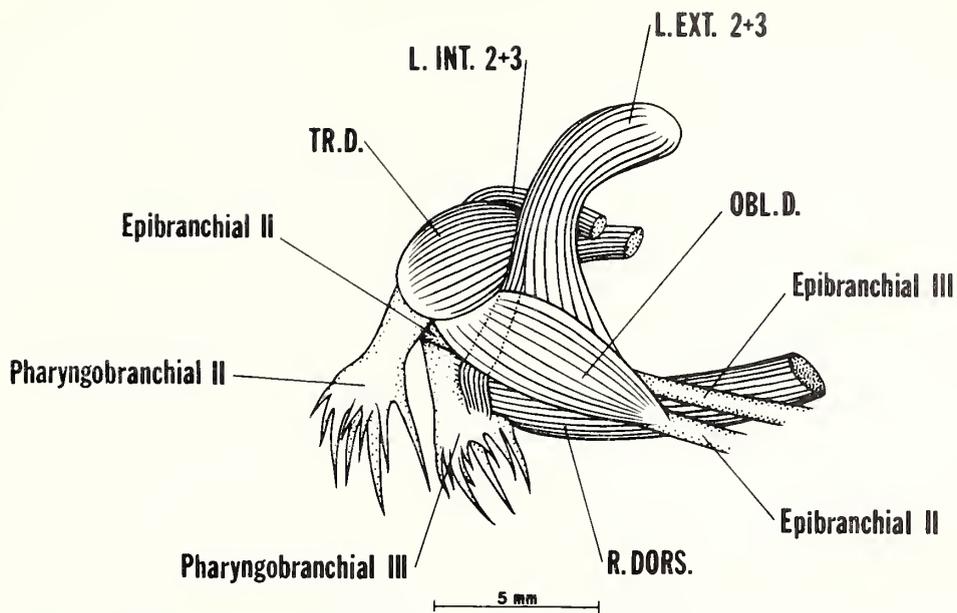


Figure 20. Musculature of upper pharyngeals of *Gigantactis meadi*, female, 353 mm, LACM 11242-12, right side reversed.

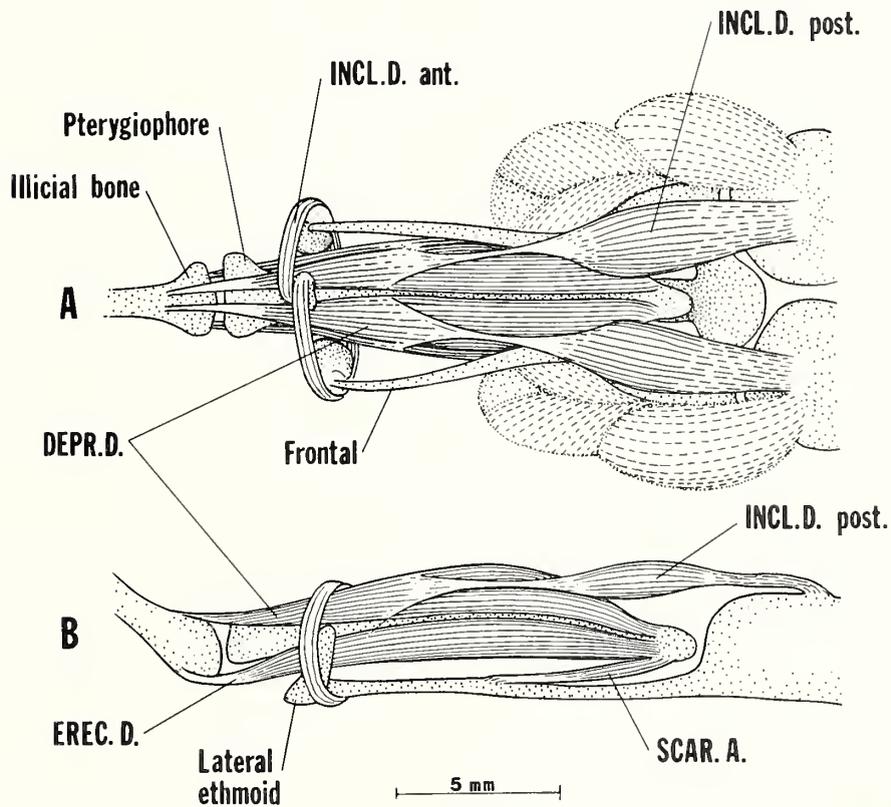


Figure 21. Illicial musculature of *Gigantactis vanhoeffeni*, female, 109 mm, ISH 2331/71, slightly diagrammatic: A. Dorsal view; B. Left lateral view.



Figure 22. *Gigantactis macronema*, female, 232 mm, ISH 1596/71.

of *G. gargantua* shows that the upper pharyngeals work in pairs on each side, each pair alternating with the other, thrusting forward and pulling back with the teeth extended, like the pedals of a bicycle.

Unlike other ceratioids, numerous individuals of *Gigantactis* have been captured with their stomachs everted; this eversion presumably occurs as a reaction to the stress of capture but could also indicate a mechanism by which *Gigantactis* is able to void the stomach of unwanted food.

A stomach contents analysis of all available material of *Gigantactis* was largely unsuccessful. In the majority of specimens examined, the stomach was either empty or everted. The stomachs of only nine individuals contained organisms, most of which showed little or no evidence of digestion and could well have been swallowed while in the net:

- *Gigantactis vanhoeffeni*: LACM 36046-10, 26 mm (one partly swallowed *Cyclothone*); SIO 73-159, 39 mm (one copepod, one *Sagitta*); ZMUC P921972, 67.5 mm (one cephalopod-eye lens); ISH 872/68, 114 mm (one *Phronima* in barrel with a deformed cephalopod); IOAN uncatalogued, 196 mm (one *Argyropelecus*, ca. 40 mm, and one *Nebaliopsis?*, both apparently partly digested).
- *Gigantactis meadi*: MCZ 52572, 306 mm (one *Atolla*, apparently partly digested).
- *Gigantactis gracilicauda* (data taken from Bertelsen 1951:240): ZMUC P92132, 51 mm (eyes and beaks of two squid); ZMUC P92129, 82 mm (eyes and beak of a squid).
- *Gigantactis perlatus* (data taken from Beebe and Crane 1947): CAS-SU 46487, 32.5 mm (one copepod, 6 mm long).

RHYNCHACTIS

As in *Gigantactis*, the restricted mobility of the pterygiophore of the illicium indicates that the primary function of the extrinsic illicial muscles is to create vibratory movement of the illicium and esca. In the absence of an esca bulb providing a site for the maintenance of bioluminescent bacteria, it seems apparent that the *Rhynchactis* esca cannot produce light. If so, perhaps the attraction of prey is based solely on pressure waves produced by pterygial vibration, in addition to other movements of the illicium. The possibility of luminescence, however, cannot be completely disregarded.

In *Rhynchactis*, the reduction of nearly all the elements of the jaws, the loss of jaw teeth, and the reduced musculature reflect a very different kind of feeding mechanism than that found in *Gigantactis*. Prey attracted by the illicial apparatus of both genera is far beyond the reach of the jaws. However, the lack of effective jaw teeth and less slender body of *Rhynchactis* make it unlikely that this genus is able to reach out and seize prey by a sudden forward dart as is supposed for *Gigantactis*. It

seems more likely that the curious oral glands are, in some way, involved in luring the prey the remaining distance from the bait to within reach of the jaws and powerful pharyngeal teeth. The inadequate preservation of the glands available to us does not allow conclusions as to their function; bioluminescence cannot be excluded, nor can the more likely function of secretion of some chemical attractant. If the latter is true, and if the esca has lost the ability to produce light, then perhaps *Rhynchactis* is adapted to feeding on prey that is not attracted by light.

The stomachs of four *Rhynchactis* females examined were empty.

REPRODUCTION

Much of what is known about reproduction in gigantactinids was recently summarized by Pietsch (1976). Although a number of the large *Gigantactis* females examined (353–408 mm) have relatively large ovaries, none approach maturity. Eggs larger than 0.5 mm in diameter have not been found.

The largest of the known males in metamorphosis is 14.5 mm; metamorphosed males of *G. longicirra* and those of Groups II, III, and V are between 10.5 mm and 15.5 mm, whereas those of Groups I and IV are between 15 and 22 mm (Table 19). This relatively large, postmetamorphic increase in size indicates that *Gigantactis* males continue to grow after metamorphosis (beyond the usual change in shape), yet there is still no evidence that postmetamorphic males are able to feed (the stomachs of all metamorphosed males examined were empty). The absence of parasitic males and the relatively large number of large females known might indicate that gigantactinids are among those ceratioid families in which no permanent attachment of males occurs (Bertelsen 1951, Pietsch 1976).

Compared to most other ceratioids, gigantactinid males have small eyes (diameter 4–5% SL in most specimens). It is assumed that they rely to a greater extent on the use of olfaction in locating potential mates.

SYSTEMATICS

Family Gigantactinidae Boulenger 1904a

DIAGNOSIS. Metamorphosed gigantactinid females are distinguished from those of all other ceratioid families by the following combination of characters: body elongate, head length less than 35% SL, caudal peduncle length greater than 20% SL; oral valves absent; upper jaw extending slightly beyond lower jaw; supraethmoid extremely reduced, usually absent; vomer absent; frontals reduced or absent; parietals reduced or absent; sphenotic spines absent; pterospinoventral ab-



Figure 23. Anterior view of *Gigantactis vahoeffeni*, female, 306 mm, MCZ 52572, showing ability of rami of lower jaw to rotate relative to each other: A. Closed position; B. Open position. Courtesy of Geert Brovad.

sent; ascending and postmaxillary processes of premaxillary absent; symphyseal cartilage absent; maxillary reduced to threadlike ossification or absent; dentaries not ankylosed anteriorly but held together by thick elastic connective tissue; anterior maxillomandibular ligament absent; articular and angular spines absent; mesopterygoid absent; hyomandibular with a single head; 6 branchiostegal rays (2 + 4); opercle reduced, bifurcate; interopercle reduced, no ligamentous connection with angular; preopercle reduced; pharyngobranchial I absent; pharyngobranchials II and III heavily toothed; epibranchial and ceratobranchial teeth absent; epibranchial I absent; anterior half of epibranchials III and IV fused; ceratobranchial I reduced, represented only by posterior half and tiny isolated remnants of anterior half; ceratobranchial V absent except for tiny isolated remnants; no ossified hypobranchials or basibranchials; posterior margin of hypural plate entire; caudal fin emarginate (except in largest females of *G. kreffti* and *G. macronema*), with 9 rays, ventralmost ray reduced and embedded within skin surrounding adjacent ray; pterygiophore of illicium exceptionally large, compressed, its posterior end abutting up against supraoccipital; ossified remnant of second cephalic ray present; illicium greater than 60% SL; 5 pectoral radials; pelvic bones reduced or absent.

Metamorphosed gigantactinid males are distinguished from those of all other ceratioid families by the following combination of characters: eyes minute (diameter 3–5% SL in most specimens); olfactory organs large (depth 8–10% SL in most specimens); anterior nostrils close together, opening anteriorly; premaxillae degenerate; jaw teeth absent; denticular teeth all or nearly all mutually free; upper denticular teeth 3–6 (rarely

2), not connected to pterygiophore of illicium; lower denticular teeth 4–7 (rarely 3); hyomandibular with a single head; branchiostegal rays 6 (rarely 7); pectoral radials 5; pelvic bones absent; probably nonparasitic.

In addition to the sexual dimorphism common to ceratioids, gigantactinid males differ from females of the family in having a symphyseal cartilage, a vomer, and a basibranchial ossification. They also differ in having fully developed frontals, parietals, opercular bones, and ceratobranchials.

Gigantactinid larvae differ from those of the other ceratioid families in having exceptionally large pectoral fins (length 45–55% SL), comparable only to those of the Caulophryniidae (Bertelsen 1951, Pietsch 1979). They differ from caulophryniids, however, in the absence of pelvic fins.

KEYS TO THE GENERA OF THE GIGANTACTINIDAE

Females

- 1A. Lower jaw teeth well developed in several rows; dorsal-fin rays 5–9, rarely 4 or 10; anal-fin rays 4–7, rarely 8; esca bulb present *Gigantactis* Brauer 1902
- 1B. Lower jaw teeth absent; dorsal-fin rays 3–4, rarely 5; anal-fin rays 3–4; esca bulb absent *Rhynchactis* Regan 1925

Males

- 1A. Three upper and 4 lower denticles; dorsal-fin rays 5–9, rarely 4 or 10; anal-fin rays 4–7, rarely 8; skin spinulose in some species *Gigantactis* Brauer 1902

- 1B. Four upper and 6 lower denticles; dorsal-fin rays 3–4, rarely 5; anal-fin rays 3–4; skin naked
 *Rhynchactis* Regan 1925

Larvae

- 1A. Dorsal group of pigment weakly developed or absent, when present extending posteriorly to base of dorsal fin but never contiguous with peritoneal pigment; dorsal-fin rays 5–9, rarely 4 or 10; anal-fin rays 4–7, rarely 8
 *Gigantactis* Brauer 1902
- 1B. Dorsal group of pigment strongly developed terminating in front of base of dorsal fin but contiguous with peritoneal pigment; dorsal-fin rays 3–4, rarely 5; anal-fin rays 3–4
 *Rhynchactis* Regan 1925

SYNOPSIS OF GIGANTACTINID CLASSIFICATION

The listing of taxa below summarizes the taxonomic conclusions made in this study. Full descriptions of all taxa and complete generic synonymies follow.

- Genus *Gigantactis* Brauer 1902
Gigantactis longicirra Waterman 1939b
Gigantactis krefftii new species
Gigantactis vanhoeffeni group
Gigantactis vanhoeffeni Brauer 1902
Gigantactis meadi new species
Gigantactis gibbsi new species
Gigantactis gracilicauda Regan 1925
Gigantactis paxtoni new species
Gigantactis perlatus Beebe and Crane 1947
Gigantactis elsmani new species
Gigantactis golovani new species
Gigantactis gargantua group
Gigantactis gargantua new species
Gigantactis watermani new species
Gigantactis herwigi new species
Gigantactis macronema group
Gigantactis macronema Regan 1925
Gigantactis savagei new species
Gigantactis microdontis new species
Gigantactis ios new species
Gigantactis ovifer Regan and Trewavas 1932, *incertae sedis*
Gigantactis filibulbosus Fraser-Brunner 1935, *incertae sedis*

- Genus *Rhynchactis* Regan 1925
Rhynchactis leptonema Regan 1925

Genus *Gigantactis* Brauer

Females: *Gigantactis* Brauer 1902:295–296 (type species *Gigantactis vanhoeffeni* Brauer 1902, by original designation).
 Males: *Teleotrema* Regan and Trewavas 1932:92–93, fig. 149 (type species *Teleotrema microphthalmus* Regan and Trewavas 1932, by original designation). *Laevoceratias* Parr 1927:33, fig. 13 (type species *Laevoceratias liparis* Parr 1927, by original designation).

DIAGNOSIS. The genus *Gigantactis* is distinguished from *Rhynchactis* in lacking pelvic bones and by having D. 5–9 (rarely 4 or 10) and A. 5–7 (rarely 4 or 8). In addition, metamorphosed females differ in having the following characters: frontals present; parietals present; premaxilla developed, with teeth present throughout length; maxilla represented by threadlike remnant; dentary with several rows of strong, recurved teeth; 1 hypohyal; all caudal rays unbranched (in contrast to males); skin spinulose; snout produced in front of mouth bearing illicium on tip; esca with luminous bulb.

Metamorphosed males are distinguished from those of *Rhynchactis* by having the following characters: diameter of eye greater than 3% SL (usually 3.5–5% SL); olfactory lamellae 12 (rarely 10 or 11); depth of nostrils rarely greater than 9% SL; upper denticular teeth 3 (rarely 2 or 4); lower denticular teeth 4 (rarely 2, 3, or 5); all bases of denticular teeth compressed and mutually free; skin pigmented or unpigmented, spinulose or naked (weakly pigmented and naked in *Rhynchactis*).

Larvae of *Gigantactis* differ from those of *Rhynchactis* in having the following characters: dorsal group of subdermal pigment absent or only weakly developed, never contiguous with peritoneal pigment but, when best developed, extending posteriorly behind base of dorsal fin; length of pectoral fin approximately 45% SL.

KEYS TO SPECIES OF THE GENUS *GIGANTACTIS*

Adolescent and Adult Females

Gigantactis ovifer and *G. filibulbosus*, each represented by only a poorly preserved holotype, and here referred to as *incertae sedis*, are omitted from the key.

- 1A. Dorsal-fin rays 8–10, the first and last distinctly longer than intermediate rays; length of first and eighth caudal-fin rays 60–100% SL (esca, Fig. 24)
 *G. longicirra* Waterman 1939b, p. 26
- 1B. Dorsal-fin rays 4–7, all about the same length; length of first and eighth caudal-fin rays less than 40% SL 2
- 2A. Esca with a black, spiny, distal prolongation (*G. vanhoeffeni* group) 3
- 2B. Esca without a black, spiny, distal prolongation 7
- 3A. Esca with filaments on base; illicium 70–120% SL . . . 4
- 3B. Esca without filaments on base (Fig. 37); illicium 160–200% SL *G. paxtoni* new species, p. 39
- 4A. Esca without distally flattened papillae (Fig. 35)
 *G. gracilicauda* Regan 1925, p. 38
- 4B. Esca with distally flattened papillae 5
- 5A. Illicium with a pair of small, papilliform or digitiform appendages on posterior margin below esca; distal prolongation of esca conical and confluent with esca bulb (Fig. 30)
 *G. vanhoeffeni* Brauer 1902, p. 31
- 5B. Illicium without a pair of appendages below esca; distal prolongation of esca constricted at base 6

- 6A. Esca with distal prolongation nearly cylindrical, more than twice as long as wide, and covered with short filaments (Fig. 32) *G. meadi* new species, p. 33
- 6B. Esca with distal prolongation conical, about as long as wide, with filaments restricted to tip (Fig. 34) *G. gibbsi* new species, p. 36
- 7A. Illicial length 60–120% SL 8
- 7B. Illicial length 130–490% SL, rarely less than 200%. 10
- 8A. Esca with a posterior pair of appendages at base, fringed in juveniles, divided into branched filaments in older specimens; conical, distal prolongation of esca longer than diameter of esca bulb (Fig. 39) *G. perlatus* Beebe and Crane 1947, p. 41
- 8B. Esca without posterior pair of appendages; distal part of esca shorter than diameter of esca bulb 9
- 9A. Base of esca bulb with a posterior, median papilla, without long filaments; conical, distal part of esca with lateral series of short filaments (Fig. 28) *G. krefftii* new species, p. 29
- 9B. Base of esca bulb without posterior papilla, but with a pair of long stout filaments; distal part of esca with two pairs of long filaments and several shorter ones (Fig. 41) *G. elsmanni* new species, p. 43
- 10A. Esca with distal filaments branched, and several filaments arising from base and below 11
- 10B. Esca with distal filaments unbranched, and without posterior filaments on or below base 13
- 11A. Esca with a single anteroproximal filament (Fig. 43) *G. golovani* new species, p. 44
- 11B. Esca with several anteroproximal filaments 12
- 12A. Esca with 4–5 pairs of distal filaments (Fig. 45) large specimens of *G. gargantua* new species, p. 46
- 12B. Esca with 8 pairs of distal filaments (Fig. 52) large specimens of *G. macronema* Regan 1925, p. 50
- 13A. Esca with a group of anterior filaments arising from base; distal part of esca bulb bearing 4–5 pairs of stout filaments along posterior margin; second and seventh caudal-fin rays more than 50% SL (*G. gargantua* group) 14
- 13B. Esca without anterior filaments arising from base; filaments of distal part of bulb not as above; longest caudal-fin rays less than 40% SL (*G. macronema* group) 16
- 14A. Esca with less than 10 (7 in a 262-mm specimen) filaments arising from base; distal part of esca bulb only slightly truncated, pigmented swellings at base (Fig. 50) *G. herwigi* new species, p. 49
- 14B. Esca with more than 10 filaments at base; distal part of esca bulb truncated, bearing 4–5 pairs of filaments with pigmented, swollen bases 15
- 15A. Esca with less than 15 (11 in a 99-mm specimen) filaments arising from base; distal filaments swollen and pigmented for one-half their length (Fig. 48) *G. watermani* new species, p. 49
- 15B. Esca with more than 15 filaments at base; distal filaments swollen and pigmented for less than one-fifth their length (Fig. 44) *G. gargantua* new species, p. 46
- 16A. Esca with distal prolongation 17
- 16B. Esca without a distal prolongation 18
- 17A. Esca with distal prolongation truncated, bearing several simple filaments arranged in nearly symmetrical pairs (Fig. 51) *G. macronema* Regan 1925, p. 50
- 17B. Esca with distal prolongation tapering to a point, filaments not arranged in pairs (Fig. 54) *G. savagei* new species, p. 53
- 18A. Esca with a U-shaped series of about 10 short, spatulate filaments surrounding a distal patch of pigment (Fig. 56) *G. microdontis* new species, p. 54
- 18B. Esca with a dense group of 16 short, lanceolate filaments (with tiny, internal bulbs) arising from a distal patch of pigment (Fig. 59) *G. ios* new species, p. 56
- Males**
- 1A. Skin spinulose 2
- 1B. Skin naked 3
- 2A. Skin darkly pigmented; eyes relatively small, diameter 0.4–0.6 mm *Gigantactis* Male Group II
- 2B. Skin unpigmented; eyes relatively large, diameter 0.7–0.8 mm *Gigantactis* Male Group III
- 3A. Distinct V-shaped patch of subdermal pigment on throat (Fig. 62); number of dorsal and anal-fin rays 4 *Gigantactis* Male Group V
- 3B. No V-shaped patch of subdermal pigment on throat; number of dorsal and anal-fin rays 5–7 4
- 4A. Number of dorsal-fin rays 8–10 *Gigantactis longicirra* Waterman 1939b
- 4B. Number of dorsal-fin rays 5–7 5
- 5A. Number of pectoral-fin rays 18–22; eyes relatively large, diameter 0.6–0.9 mm; number of olfactory lamellae 11–12 *Gigantactis* Male Group I
- 5B. Number of pectoral-fin rays 15; eyes relatively small, diameter 0.5 mm; number of olfactory lamellae 8–9 *Gigantactis* Male Group IV
- Larvae**
- 1A. Dorsal and peritoneal pigment well developed 2
- 1B. Dorsal and peritoneal pigment weak or absent 3
- 2A. Dorsal and ventral series of three to four large, subdermal melanophores on caudal peduncle *Gigantactis* Larval Group D

- 2B. No large, subdermal melanophores on caudal peduncle
 *Gigantactis* Larval Group A
- 3A. Number of dorsal-fin rays 5–7, anal-fin rays 5–7
 *Gigantactis* Larval Group B
- 3B. Number of dorsal-fin rays 8–10, anal-fin rays 5–8 (Fig.
 26B)..... *Gigantactis* Larval Group C (= *Gigantactis*
longicirra Waterman)

Gigantactis longicirra Waterman

Figures 1A, 4F, 11A,D, 13A, 14A, 15A, 16, 17, 24–26, 66;
 Tables 1–3, 19

Gigantactis longicirra Waterman 1939b: 82–85, figs. 1–2 (original description, single specimen); Waterman 1949:81–149, figs. 1–10 (comparative anatomy; comparison with other species of the genus, other ceratioid genera and families); Clark 1950:6, 10, 18, 28 (problems in classifying ceratioid lateral line organs, references to Waterman 1948); Bertelsen 1951:150–152, table 31 (comparison with all known material, comments); Grey 1956:269 (synonymy, vertical distribution).

Gigantactis sp., Becker et al. 1975:327 (specimen tentatively referred to *G. longicirra*).

MATERIAL. Eight females (seven metamorphosed [34.5–221 mm] and one in metamorphosis [19.5 mm]), two metamorphosed males (14–14.5 mm) and eight larvae (4.5–7.5 mm).

Holotype of *Gigantactis longicirra*: MCZ 35065, 39 mm, 39°06'N, 70°16'W, closing net at 1000 m, bottom depth 2860 m.

Females: IOAN uncatalogued, 34.5 mm, 18°29'N, 80°33'W, 0–1500 m; ISH 2561/71, 2 (108–118 mm), 7°32'N, 20°54'W, 0–1300 m; ISH 973/68, 209 mm, 4°43'S, 26°39'W, 0–2000 m (cleared and stained); MCZ 52570, 221 mm, Gulf of St. Lawrence; SIO 60-241, 19.5 mm, 7°26'N, 144°29'W, 0–2100 m; SIO 60-215, 72.5 mm, 13°13'N, 127°06'W, 0–2300 m, bottom depth 4612 m.

Males: UMML 27412, 14 mm, 11°40'N, 68°16'W (cleared and stained); UMML 27411, 14.5 mm, 4°56'N, 00°13'E.

Larvae: ZMUC P921656-68, listed as *Gigantactis* "Type C" larvae by Bertelsen (1951:274).

DIAGNOSIS. *Gigantactis longicirra* differs from all other species of the genus in having a relatively high number of dorsal-fin rays (8–10). Metamorphosed females are further distinguished in having three or fewer distal, esca filaments, the first and last rays of the dorsal fin distinctly longer than the intermediate rays, and, in addition, the following combination of characters: illicial length less than 120% SL (39–105%); esca bulb without distal prolongation or papillae; dentary teeth relatively long (longest 3.3–5.0% SL), in 5–6 longitudinal series; first and eighth rays of caudal fin prolonged (60–100% SL).

Metamorphosed males of *G. longicirra* are further characterized by having the following combination of characters: eyes small, diameter 0.45 and 0.5 mm; olfactory lamellae 11; upper denticular teeth 3; lower denticular teeth 4; skin naked, unpigmented (Table 19).

Larvae of *G. longicirra* are further distinguished in lacking dorsal, subdermal pigment (See "Comments" on this species).

Table 3. Counts and measurements in percent of SL of females of *Gigantactis longicirra*.

Character	S10 ¹ 60-241	IOAN uncata- logued	Holotype MCZ 35065	S10 60-215	ISH 2561/71	ISH 2561/71	ISH 973/68	MCZ 52570
Standard length (mm)	19.5	34.5	39	72.5	108	118	209	221
Length								
Illicium	13+	62.3+	38.5	45.1	104	96.6	broken	59.3
Longest premaxillary tooth	0.5	2.6	—	—	1.9	2.7	1.8	1.7
Longest dentary tooth	1.0	4.9	—	5.2	3.7	4.1	3.3	4.7
Longest caudal ray	38.0	broken	60.3	82.3	64.8+	86.4	broken	98.6
Teeth								
Premaxillary	3	5	8	13	20	35	22	23
Dentary	5	9	14	17	41	52	60	22
Dorsal-fin rays	8	8	8	9	8	8	9	9
Anal-fin rays	6	7	6	6	7	6	6	7
Pectoral-fin rays	16	15	18	16	15–15	15–16	16	14–15

¹Metamorphosal stage.

DESCRIPTION OF FEMALES. Illicium without filaments, nearly cylindrical throughout, length highly variable and unrelated to standard length (Table 3). Escal bulb pear-shaped in juveniles, elongated and constricted below photophore in adults, without spines on distal portion; 1–3 short, distal filaments; an anterolateral, proximal group of short filaments; and a posteroproximal group of long filaments. Esca of 39-mm holotype (described and figured by Waterman 1939b) with pear-shaped, unpigmented, and naked bulb; a single distal filament and a total of 20 proximal filaments; all filaments unpigmented and unbranched with slight distal swellings. Escal bulb of 118-

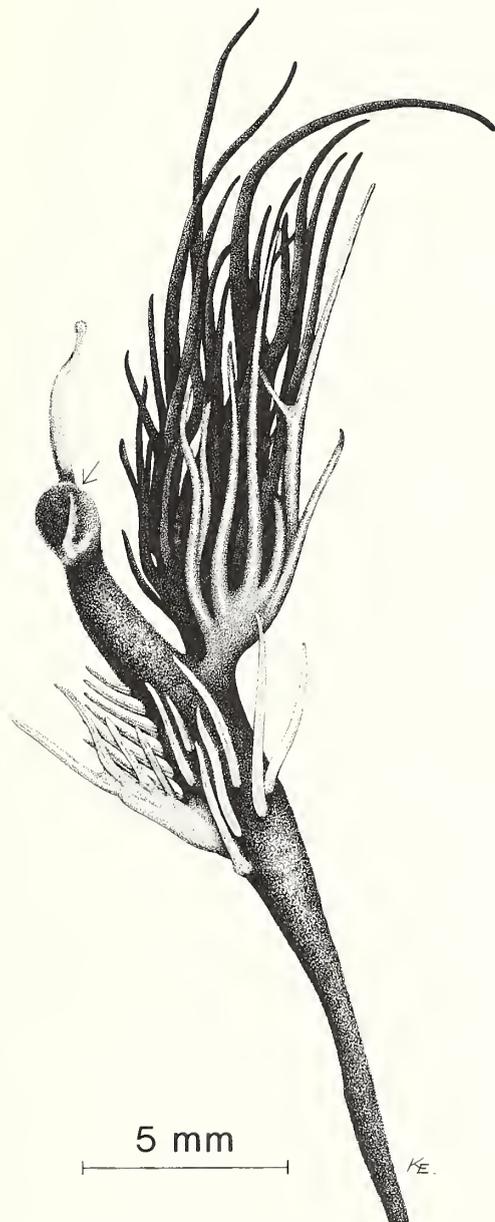


Figure 24. Esca of *Gigantactis longicirra*, 118 mm, ISH 2561/71, left lateral view. Arrow indicates opening of pore of photophore. Drawn by K. Elsmann.

mm specimen elongate and darkly pigmented (Fig. 24), with a distinct constriction below distally placed photophore; skin of proximal part of bulb covered with small spines; a single, unpigmented distal filament bearing a small terminal swelling; all of approximately 25 filaments of anterolateral-proximal group unpigmented and arranged in an anterior series (of which the proximal is branched) and a lateral, more scattered grouping of 6–7 single filaments; posteroproximal group darkly pigmented and arranged in two symmetrical, fan-shaped groups, each consisting of numerous filaments, long and short (some of which are branched), arising from a common base. Esca of 221-mm specimen similar in all major characters to that of 118-mm specimen but differs in having 3 distal filaments, and those of anterolateral-proximal group all unbranched and pigmented.

Number of teeth in each premaxilla increasing with standard length from 5 (34.5-mm specimen) to 35 (118-mm specimen) but decreasing in largest specimens (22 and 23 teeth in the 209-mm and 221-mm specimens, respectively; Table 3); longest premaxillary tooth (present in the anterior portion of the jaw) 1.7–2.7% of SL. Number of teeth in each dentary increasing with standard length from 9 (34.5 mm) to approximately 60 (209 mm), fewer (22 teeth) at 221 mm (this largest specimen, MCZ 52570, has lost many of the older and smaller teeth). Teeth in posterior part of dentary in 5–6 longitudinal series in specimens greater than 100 mm; number of series increasing from 2 (the median and first external) at 34.5 and 39 mm; first internal series appearing at 72.5 mm; second and third internal series present in larger specimens (but many older and smaller lost in the largest specimen, MCZ 52570); longest dentary teeth present in anterior, irregular groups (Fig. 25).

Anal-fin rays 6–8, pectoral-fin rays 14–18 (Table 2); first ray of dorsal fin longest (78 and 80% SL in 108- and 118-mm speci-

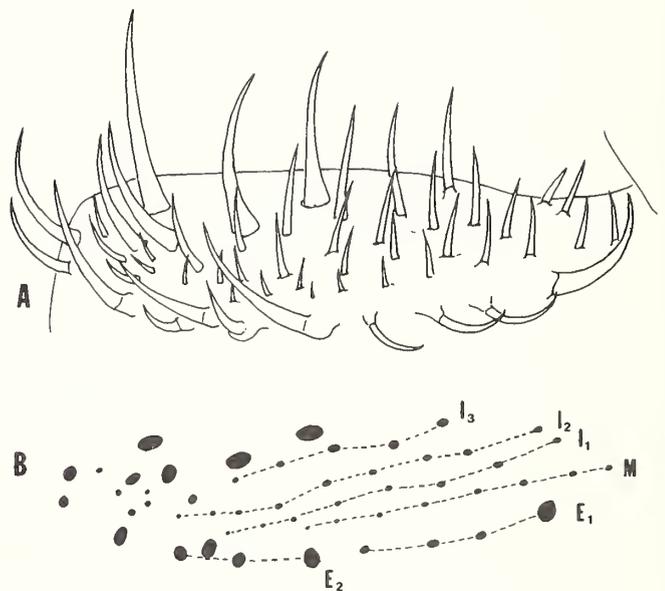


Figure 25. *Gigantactis longicirra*, female, 118 mm, ISH 2561/71: A. Dentary teeth, left lateral view; B. Diagrammatic representation of dentary-tooth pattern. E = external series; M = median series; I = internal series.

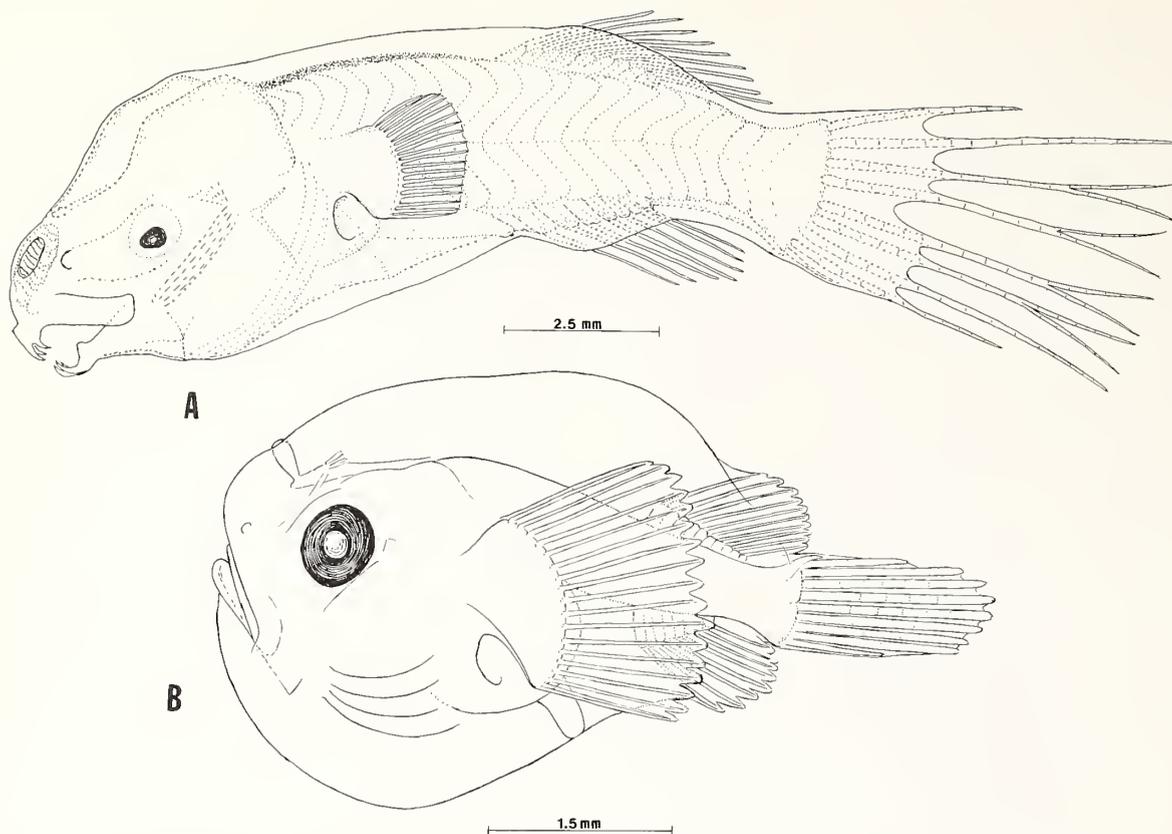


Figure 26. *Gigantactis longicirra*: A. Male, 14 mm, UMML 27412; B. Larval female, 4.7 mm, ZMUC P921668.

mens, respectively; broken in other specimens); caudal rays free nearly to base without remains of connecting membrane, first and eighth rays prolonged 60–100% SL, becoming longer with increased SL (Fig. 4F, Table 3).

Skin spines and lateral line organs on head and body slightly larger than in other members of genus.

The 19.5-mm metamorphosal stage (SIO 60-241) with esca lost; jaw teeth few and rudimentary, those of dentary in a single (median) series; first caudal ray broken, eighth caudal ray 38% SL; seven anteriormost supraorbital lateral line organs enlarged on each side, the longest approximately 5% SL; skin faintly pigmented; subdermal pigment absent.

DESCRIPTION OF MALES AND LARVAE (Fig. 26). See “Diagnosis” above, and “Males” and “Larvae” in the section on *Gigantactis* sp. unidentified.

DISTRIBUTION. *Gigantactis longicirra* inhabits the tropical Atlantic from the Gulf of Guinea in the east to the Caribbean Sea in the west, the western north Atlantic as far north as approximately 50° N, and the eastern tropical Pacific (Fig. 66). All metamorphosed female material of *G. longicirra* was collected by gear fished open at maximum depths of between 1000 and 2300 m. The 39-mm holotype was captured with a closing net at 1000 m.

COMMENTS. The females of *Gigantactis longicirra* are simi-

lar to those of a number of other *Gigantactis* species (Table 1) in having a relatively short illicium and long teeth in several rows in the lower jaw. Except for these similarities, the species shows no distinct affinity with any other species of the genus. The esca is unique in several characters: the low number of distal filaments combined with the lack of a distal prolongation of the bulb, and (in adults) the constriction of the bulb below the photophore as well as the posteroproximal pair of darkly pigmented, fan-shaped appendages. The prolongation of the first and last dorsal ray is found in no other *Gigantactis* species; greatly prolonged caudal rays also occur in *G. gargantua*, *G. watermani*, and *G. herwigi*, but in these species, the second and seventh rays are the longest.

In both metamorphosed males, the testes are relatively short and narrow (0.7 and 0.8 mm in diameter), yet the specimens appear to have passed metamorphosis as evidenced by their well-developed denticulars, resorbed premaxillae, and close-set olfactory organs.

Since *G. longicirra* is unique among the recognized species of the genus in having more than seven dorsal-fin rays, the eight larvae with such high dorsal-ray counts referred to Group C by Bertelsen (1951) no doubt represent this species. On the other hand, the two larvae with seven dorsal rays included in this group by Bertelsen (1951) should be removed to the uniden-

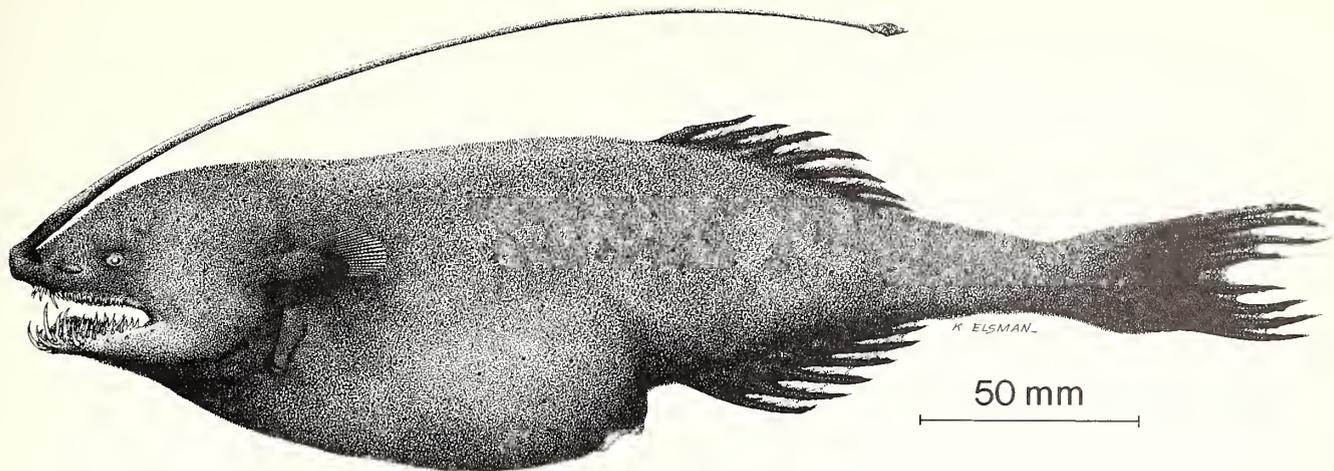


Figure 27. *Gigantactis krefftii*, holotype, 252 mm, ISH 1099/71.

tified larvae of Group B. The absence of dorsal subdermal pigment in *G. longicirra* is confirmed in the identified female metamorphosal stage (SIO 60-241) and in the two metamorphosed males (UMML 27411, 27412).

Gigantactis krefftii new species

Figures 4D, 27–29, 65; Tables 1, 2, 4

MATERIAL. Four metamorphosed females, 44.0–252 mm.

Holotype: ISH 1099/71, 252 mm, 39° 19'S, 3° 15'W, 0–2000 m.

Paratypes: ISH 1262/71, 75 mm, 34° 12'S, 16° 35'E, 0–1550 m; ISH 3236/71, 185 mm (data as for holotype); ZIFSUT 52706, 44 mm, 35° 06'N, 139° 24'E, 0–1000 m, bottom depth 1200–1400 m.

DIAGNOSIS. Metamorphosed females of *G. krefftii* are distinguished from those of all other species of the genus in having the following combination of characters: illicial length less than 120% SL (69–94%); distal esca prolongation with spines at base and several unpigmented, digitiform filaments on lateral margins; esca papillae absent; a posteromedial papilla at base of bulb and a second on illicium below bulb; proximal esca filaments absent; dentary teeth relatively long (longest 2.6–5.2% SL), in 4–5 longitudinal series; rays of caudal fin less than 30% SL.

Males and larvae unknown.

DESCRIPTION. Illicium without filaments, nearly cylindrical throughout, only proximal part slightly compressed, length variable and unrelated to standard length (Table 4). Escal bulb pear-shaped with short, conical distal prolongation; spines covering proximal part of bulb, reaching base of distal prolongation on anterior margin. Escal bulb of 252-mm holotype (Fig. 28D) with distal prolongation and oval area surrounding pore of photophore, naked and unpigmented; remaining surface of esca bulb darkly pigmented and covered with spines; pore of photophore protruding from surface of bulb as a short tube;

lateral margins of distal prolongation bearing approximately 20 digitiform, unpigmented filaments; an unpigmented, stout papilla present posteriorly at base of bulb and a similar, but slightly smaller papilla on illicium about 65 mm (25% SL) below base of bulb (in the freshly caught, unpreserved specimen, the tips of the distal filaments and the papillae were red; beneath the skin below the pore, a bright silvery, circular area was noted). Escae of paratypes (Fig. 28A–C) similar to that of holotype except for some changes with growth: in smaller specimens (44 and 75 mm), esca bulb more spherical in shape; at 44 mm bulb without pigmentation, at 75 mm pigmentation reaching posterior part of base of bulb; number of distal filaments increasing from 4–5 on each side at 44 mm to 7–8 at 75 mm and to approximately 30 at 185 mm; in two smallest specimens, papilla on illicium situated at a distance of about 10% SL below base of bulb (papilla and part of the skin of the illicium are lost in the 185-mm specimen).

Left premaxilla of holotype with 44 teeth of which approximately 10, posteriormost, curved forward; longest tooth in upper jaw 1.3% SL. Number of premaxillary teeth of paratypes increasing from 7 at 44 mm to 17 at 75 mm and 30 at 185 mm; longest premaxillary tooth 1.3–2.5% SL. Holotype with about 47 teeth in each dentary, posteriorly arranged in 5 longitudinal series, one external, one median, and three internal (Fig. 29). Number of dentary teeth of paratypes increasing from 15 at 44 mm to 27 at 75 mm and 42 at 185 mm; 4 posterior longitudinal series present except in the smallest paratype (44 mm) in which second internal series not yet developed.

Dorsal-fin rays 7, anal-fin rays 6, pectoral-fin rays 16–18 (Table 2); skin covering caudal fin for some distance beyond fin base; skin of each ray broad, distally tapering, and basally connected by transparent membrane (Fig. 4D).

DISTRIBUTION. *Gigantactis krefftii*, known from only four metamorphosed females, has an unusual disjunct distribution with three individuals captured in the South Atlantic off the tip of Africa and one in the western North Pacific off Japan (Fig. 64). Probably when this form becomes better known, it will

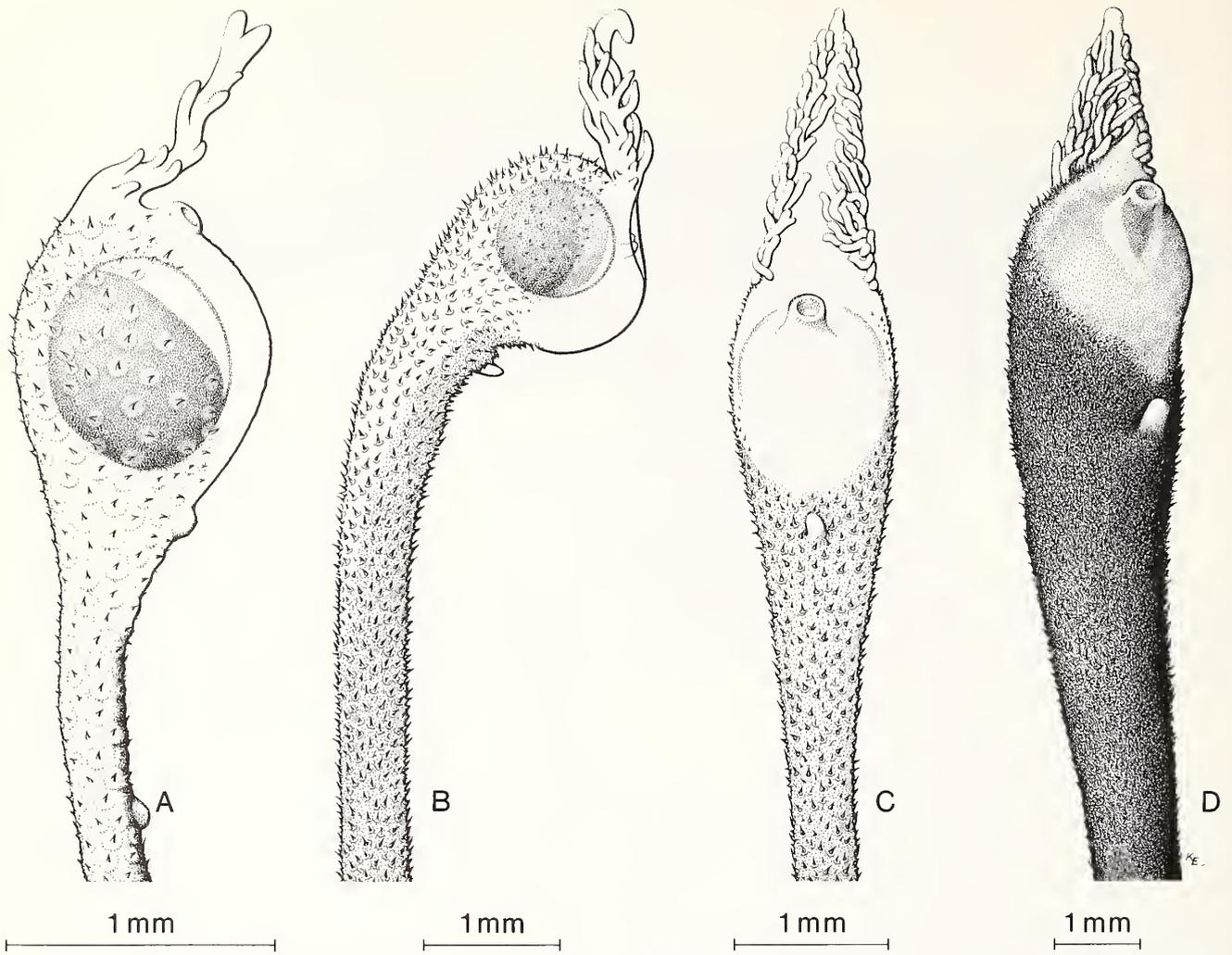


Figure 28. Escae of *Gigantactis kreffii*: A. Paratype, 44 mm, ZIFSUT 52706, left lateral view; B. Paratype, 75 mm, ISH 1262/71, left lateral view; C. Paratype, 185 mm, ISH 3236/71, posterior view; D. Holotype, 252 mm, ISH 1033/71, posterolateral view. Drawn by K. Elsman.

prove to be a wide-ranging if not cosmopolitan species. All material of *G. kreffii* was taken with open gear fished at maximum depths of between 1000 and 2000 m.

ETYMOLOGY. *Gigantactis kreffii* is named for Gerhard Krefft of the Institut für Seefischerei, Hamburg; his interest and energy have established an important ichthyological resource that has immensely expanded our knowledge of the deep-sea fauna.

COMMENTS. *Gigantactis kreffii* is similar to a number of other *Gigantactis* species (Table 1) in having a relatively short illicium and long teeth in several posterior series in the lower jaw. It is similar to members of the *G. vanhoeffeni*-group (including *G. vanhoeffeni*, *G. meadi*, *G. gibbsi*, *G. gracilicauda*, and *G. paxtoni*) in having a relatively spinulose esca with a distal prolongation bearing short filaments but differs from these species in lacking both spines on the distal prolongation and filaments on the proximal part of the esca. The relatively short



Figure 29. *Gigantactis kreffii*, holotype, female, 252 mm, ISH 1099/71: A. Premaxillary and dentary teeth, left lateral view; B. Diagrammatic representation of dentary-tooth pattern. E = external series; M = median series; I = internal series.

Table 4. Counts and measurements in percent of SL of females of *Gigantactis kreffii*.

Character	Paratype ZIFSUT 52706	Paratype ISH 1262/71	Paratype ISH 3236/71	Holotype ISH 1099/71
Standard length (mm)	44	75	185	252
Length				
Illicium	94.0	81.3	68.6	86.5
Longest premaxillary tooth	2.5	1.3	1.4	1.3
Longest dentary tooth	5.2	3.3	2.6	3.4
Longest caudal ray	27.7	27.3	17.8	19.8
Teeth				
Premaxillary	7	17	30	44
Dentary	13	27	42	47
Dorsal-fin rays	7	7	7	7
Anal-fin rays	6	6	6	6
Pectoral-fin rays	18	16-16	17-17	16-17

caudal fin with well-developed skin coverage is similar to those of *G. meadi*, *G. gibbsi*, and *G. perlatus*.

Gigantactis vanhoeffeni Brauer

Figures 1B, 4A, 5, 6, 8, 12, 19, 21, 30, 31, 64;
Tables 1, 2, 5

Gigantactis vanhoeffeni Brauer 1902:296 (original description, two specimens, lectotype hereby designated ZMHU 17712, paralectotype lost, used by Brauer 1908 for anatomical, histological description of the illicial apparatus and esca). Boulenger 1904b:720 (brief description); Brauer 1906:322, pl. 15, figs. 8, 9 (description after Brauer 1902); Brauer 1908:103, 184, pl. 31, Figs. 18-20, pl. 32, figs. 1-5, pl. 34, fig. 14, pl. 44, fig. 1 (anatomical, histological description of illicial apparatus, esca, and eyes); Gill 1909:586, fig. 25 (description, figure after Brauer 1902, 1906, habits); Regan 1926:38 [three additional specimens, two subsequently described as new (*G. sexfilis* and *G. exodon*) by Regan and Trewavas 1932]; Regan and Trewavas 1932:93, 94 (description after Brauer 1902, 1906, in key); Fowler 1936:1345, 1346, fig. 565 (brief description, figure after Brauer 1902, 1906, Regan 1926); Waterman 1939b:85 (lateral line organs on caudal rays, comparison with *G. longicirra*); Beebe and Crane 1947:168 (comparison with *G. perlatus*); Bertelsen 1951:150-152, table 31 (comparison with all known material, comments); Grey 1956:267 (synonymy, vertical distribution); Parin and Golovan 1976:271 (in part, two additional specimens).

Gigantactis exodon Regan and Trewavas 1932:93, 94, 95, fig. 151 (original description, single specimen, in key); Fraser-Brunner 1935:326 (comparison with *G. filibulbosus*); Waterman

1939b:84, 85 (comparison with *G. longicirra*); Bertelsen 1951:150-152, table 31 (comparison with all known material, comments); Grey 1956:268 (synonymy, vertical distribution); Pietsch 1972a:42, 45 (holotype with five pectoral radials).

Gigantactis perlatus, Parin et al. 1973:145-146 (misidentifications, three specimens).

Gigantactis "sp. 2," Parin et al. 1973:146 (typical juvenile).

MATERIAL. Forty-nine females: 46 metamorphosed (19-340 mm), and three in metamorphosis (16.5-21.5 mm).

Lectotype of *Gigantactis vanhoeffeni*: ZMHU 17712, 35 mm, 5°42'S, 43°36'E, 2500 m.

Holotype of *Gigantactis exodon*: ZMUC P92128, 25 mm, 18°50'N, 79°07'W, 2500 m wire.

Referred female material: IOAN uncatalogued, 16.5 mm, 9°09'N, 118°24'W, 0-1000 m; IOAN uncatalogued, 21.5 mm, 3°20'S, 82°02'W, 0-1300 m; IOAN uncatalogued, 23 mm, 3°21'N, 81°02'W, 0-1300 m; IOAN uncatalogued, 29 mm, 16°07'S, 53°39'E, 0-1000 m; IOAN uncatalogued, 37 mm, 32°01'N, 143°15'E, 0-5300 m; IOAN uncatalogued, 48 mm, Akademik Kurchatov Cruise 17, Station 1454; IOAN uncatalogued, 57 mm, 3°22'N, 120°07'W, 0-1000 m; IOAN uncatalogued, 96 mm, 2°03'S, 82°31'W, 0-1500 m; IOAN uncatalogued, 102 mm, 2°03'S, 82°31'W, 0-1000 m; IOAN uncatalogued, 196 mm, 5°03'N, 2°08'E, 0-4000 m; IOAN uncatalogued, 2 (198-205 mm), 10°36'N, 17°38'W, 0-1550 m; IOAN uncatalogued, 285 mm, 8°00'S, 59°27'E, 0-1300 m; IOAN uncatalogued, 340 mm, off Peru, 0-900 m; ISH 2188/71, 38 mm, 2°29'S, 18°58'W, 0-304 m; ISH 661/68, 57 mm, 12°07'N, 23°08'W, 0-2000 m; ISH 2331/71, 3 (75, 109, 232 mm), 1°04'N, 18°22'W, 0-2100 m; ISH 872/68, 114 mm, 0°14'N, 25°22'W, 0-600 m; ISH 802/68, 152 mm, 4°08'N, 24°41'W, 0-600 m (cleared and stained); ISH 721/68, 152 mm, 8°21'N, 24°10'W, 0-520 m; ISH 1959/71, 195 mm, 10°57'S, 11°20'W, 0-1900 m; ISH 2480/71, 266 mm, 4°38'N, 19°41'W, 0-756 m; ISH 376/73, 270 mm, 62°39'N, 33°45'W, 0-2100 m; LACM 36031-1, 17 mm, 4°55'S, 129°48'E, 650-810 m; LACM 31470-1, 22 mm, 00°00', 140°53'W, 0-1170 m; LACM 36039-6, 2 (24-31 mm) 5°08'S, 130°08'E, 650-1000 m; LACM 31526-1, 24 mm, 2°07'S, 169°43'E, 0-1200 m; LACM 36032-1, 25 mm, 4°47'S, 129°52'E, 0-1500 m; LACM 36046-10, 26 mm, 4°54'S, 129°43'E, 0-850 m; LACM 31521-2, 27 mm, 0°18'S, 169°57'E, 0-1200 m; LACM 36131-1, 32 mm, 4°56'S, 129°50'E, 550-815 m; LACM 31513-1, 28 mm, 1°00'S, 170°00'E, 0-1200 m; LACM 31497-2, 29 mm, 0°51'S, 170°04'E, 0-1030 m; LACM 36012-1, 30 mm, Central Tropical Pacific, 600-950 m; LACM 36034-5, 34 mm, 4°58'S, 130°12'E, 0-750 m; LACM 36013-1, 42 mm, 11°17'S, 142°47'W, 0-1200 m; LACM 36954-1, 305 mm, off southern California, 0-1070 m; LACM 37079-1, 315 mm, San Clemente Basin, California (no other data); MCZ 52571, 19 mm, 7°33'N, 64°41'E, 0-500 m; SIO 68-535, 29.5 mm, 4°59'N, 164°14'W, 2550 m of wire out, bottom depth 4575 m; SIO 70-309, 35 mm, 29°32'N, 137°14'E, 0-1900 m, bottom depth 4277-4630 m; SIO 73-159, 39 mm, 31°02'N, 155°04'W, 0-1450 m; UMML 11336, 33 mm, 25°02'N, 79°48'W, 0-320 m; UMML 23821, 92 mm, 4°00'N, 2°46'W, 0-490 m, bottom depth 1995-2233 m; UMML 23973, 232 mm, 6°54'N, 79°58'W, bottom depth 3184 m; ZMUC

P921972, 67.5 mm, 4° 14'S, 44° 52'E, 0–1050 m (cleared and stained).

DIAGNOSIS. Metamorphosed females of *G. vanhoeffeni* differ from those of all other species of the genus in having the following combination of characters: illicial length less than 120% SL (71–112% in specimens greater than 25 mm); escal bulb with an elongate, spinulose, and darkly pigmented distal prolongation; escal bulb and distal prolongation bearing distally flattened papillae; short distal, and slender proximal escal filaments present; illicium with a posterior pair of papillae below escal bulb; dentary teeth relatively long (longest 2.6–5.0% SL) in 3 longitudinal series; rays of caudal fin less than 45% SL.

Males unknown (probably included in *Gigantactis* Male Group II).

Larvae unknown (probably included in *Gigantactis* Larval Group A).

DESCRIPTION. Illicium distinctly compressed in specimens greater than 50 mm SL, depth at base 2–3 times width, length variable and unrelated to SL. Escal bulb gradually tapering into a conical distal prolongation, darkly pigmented proximally, unpigmented and transparent around photophore, and less darkly pigmented distally; bulb covered to distal tip with spines and bearing several large, distally flattened papillae of varying pigmentation, some black, others, especially in skin covering photophore, nearly transparent; distal filaments short and restricted to tip of distal prolongation, increasing in number from one in specimens less than 30 mm to 10–30 in specimens greater than 100 mm; 2–3 thin filaments on each side of bulb immediately below photophore, the longest reaching to base of distal prolongation; a close-set pair of small appendages arising on posterior margin of illicium some distance below bulb, papilliform and very small in juveniles, larger and somewhat compressed in adults, bifurcated in some of largest specimens (Figs. 30–31); distance from base of paired, illicial papillae to tip to distal filaments 10–22% SL in specimens less than 100 mm, 7–14% SL in larger specimens; 1 to approximately 10 (increasing in number with standard length) short filaments present on posterior margin of distal portion of illicium of specimens greater than 70 mm SL (Figs. 30B, 31). In freshly captured, unpreserved specimens, the paired papillae and the tips of the distal filaments are bright red.

Number of teeth in each premaxilla increasing with standard length from 2–8 in smaller specimens to 22–53 in larger (Table 5); longest premaxillary tooth 1.0–1.8% SL in specimens greater than 25 mm SL. Number of teeth on each dentary increasing with standard length from 3–15 in smaller specimens to 32–66 in larger (Table 5); median series of small dentary teeth distinctly developed (Figs. 5, 6).

Dorsal-fin rays 5–7, anal-fin rays 5–6 (rarely 7), pectoral-fin rays 17–18 (rarely 19; Table 2); caudal fin divided between upper and lower lobes nearly to base; caudal-skin coverage weakly developed, skin of fin rays only slightly compressed; remains of transparent membrane between bases of rays present in some specimens (Fig. 4A).

Three metamorphosal stages (16.5 mm, IOAN uncatalogued; 17 mm, LACM 36031-1; 21.5 mm, IOAN un-

catalogued) with illicial length 23.5–41% SL; escae with more or less distinct rudiments of papillae and paired posterior appendages; jaw teeth rudimentary, premaxilla with 2–4 teeth, dentary with 3–5 teeth (representing the median series and one or two of the first external series); four to eight anteriormost supraorbital lateral line organs enlarged, the longest about 7% SL; dark subdermal dorsal and peritoneal pigment.

DISTRIBUTION. *Gigantactis vanhoeffeni* has a cosmopolitan distribution between approximately 63°N and 15°S (Fig. 64; but see “Comments” concerning the northern-most record of this species, ISH 376/73). This species has been taken with open gear fished at maximum depths between 300 and 5300 m,

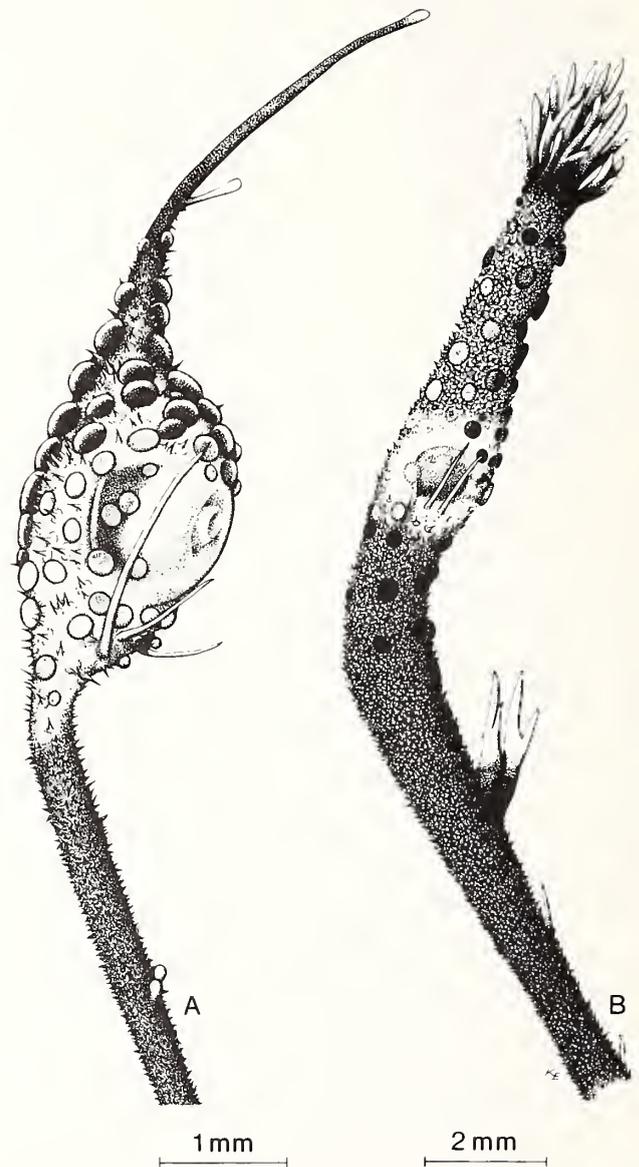


Figure 30. Escae of *Gigantactis vanhoeffeni*, left lateral views: A. 38 mm, ISH 2188/71; B. 152 mm, ISH 721/68. Drawn by K. Elsmann.

but appears to be most commonly found between 700 and 1300 m.

COMMENTS. *Gigantactis vanhoeffeni* is one of several *Gigantactis* species (Table 1) that have a relatively short illicium. It is the type of a group of species (the *G. vanhoeffeni* group, including *G. vanhoeffeni*, *G. meadi*, *G. gibbsi*, *G. gracilicauda*, and *G. paxtoni*) characterized by having a distal, spinulose prolongation of the esca bulb bearing short filaments and (except for *G. paxtoni*) having at the base of the bulb a small number of more slender filaments that reach to the base of the distal prolongation. Like *G. meadi*, *G. gibbsi*, and *G. paxtoni*, this species has distally flattened esca papillae but differs distinctly from these forms in the shape of the distal prolongation of the bulb and in having a posterior pair of papillae on the illicium below the bulb.

Even though the characters that distinguish *G. vanhoeffeni* from its nearest relatives are not mentioned in Brauer's (1902) original description (based on two specimens now lost except for badly damaged remains of one), his excellent figure of the esca (Brauer 1908, pl. 15, fig. 9) shows the characteristic conical shape of its distal prolongation with the filaments restricted

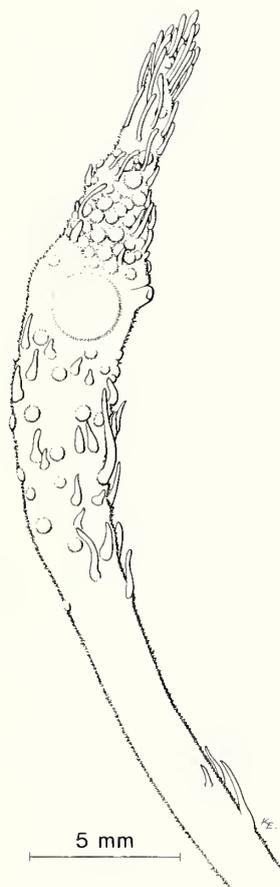


Figure 31. Esca of *Gigantactis vanhoeffeni*, 270 mm, ISH 376/73, left lateral view. Drawn by K. Elsmann.

to the tip, as well as the paired appendages on the illicium below the bulb.

Two of the specimens of the referred material have lost the esca, but in both, the characteristic paired papillae are present on the remaining part of the illicium. In one of them (IOAN uncatalogued), the loss of the esca seems to have happened before capture. The esca has been broken off just below the photophore, leaving a wound that has healed without sign of regeneration of the lost part. A second break just below the paired appendage has healed in such a way that the remains of the esca are attached to the illicium in a twisted and displaced position.

The esca of the 270-mm specimen (ISH 376/73, representing the most northerly capture [63°N] of a gigantactinid) shows some aberrant features (Fig. 31). In addition to the cluster of filaments at the tip of the distal prolongation, it has numerous short, tapering filaments and papillae on the proximal part of the prolongation as well as on the proximal part of the bulb. A pair of filaments on the posterior margin of the illicium below the bulb probably represents the paired appendages characteristic of *G. vanhoeffeni*, but they are neither compressed nor particularly distinct from other filaments present on the illicium in this same region. Although these aberrant features are not present in the three specimens examined of similar or larger size, there is a general tendency among *Gigantactis* species for the number of distal filaments of the esca as well as those of the illicium to increase with increasing size. For this reason, we assume for the present that this variation is due to age, possibly combined with individual differences.

Gigantactis meadi new species

Figures 4B, 18, 20, 23, 32, 33, 64; Tables 1, 2, 6

MATERIAL. Fourteen females: ten metamorphosed (35.5–353 mm), and three in late metamorphosis (19.0–21.0 mm).

Holotype: MCZ 52572, 306 mm, 34°14'S, 64°56'E (depth unknown).

Paratypes: ISH 415/76, 87 mm, 47°45'S, 40°04'W, 0–2000 m; ISH 1004/71, 2 (155–201 mm), 36°49'S, 12°17'W, 0–2000 m; ISH 965/71, 178 mm, 39°45'S, 17°40'W, 0–2000 m; ISH 571/76, 207 mm, 39°08'S, 40°00'W, 0–1850 m; ISH 883/71, 230 mm, 39°55'S, 26°02'W, 0–2000 m; ISH 1465/71, 290 mm, 33°00'S, 7°50'W, 0–2000 m; LACM 11242-12, 353 mm, 39°58'S, 150°31'W, 0–1900 m, bottom depth 5161 m; SAM 27811, 21.0 m, 30°06'S, 31°57'E, 0–750 m; USNM 208032, 35.5 mm, 33°06'S, 83°57'W, 0–1050 m, bottom depth 3731–3822 m.

Referred material: The following are tentatively referred to *G. meadi*: IOAN uncatalogued, 290 mm, 29°35'S, 14°13'E, 0–1300 m (esca lost, illicial length 93% SL, strong filaments on head at base of illicium); SAM 27807, 19 mm, 30°45'S, 30°42'E, 0–830 m; SAM 27808, 20 mm, 31°14'S, 30°21'E, 0–1120 m.

DIAGNOSIS. Metamorphosed females of *G. meadi* differ from those of other species of the genus (except for *G. paxtoni*) in having filaments on the dorsal surface of the head just behind

Table 5. Counts and measurements in percent of SL of females of *Gigantactis vanthoeffeni*.

Character	LACM ¹ 36031-1	ZMUC ² P92128	SIO 70-309	LACM 36013-1	ISH 2331/71	UMML 23821	ISH 2331/71	ISH 872/68	ISH 721/68	ISH 1959/71	IOAN uncata- logued	ISH 2331/71	ISH 376/73	LACM 37079-1	IOAN uncata- logued	
Standard length (mm)	17	25	35	42	75	92	109	114	152	195	205	232	270	315	340	
Length																
Illicium	23.5	68.0	84.3	83.3	100	103	93.6	96.5	83.6	93.8	100	102	100	87.3	112	
Longest premaxillary tooth	<0.5	1.6	1.7	—	1.3	1.6	1.5	1.8	1.2	1.0	1.5	1.6	1.1	1.1	1.0	
Longest dentary tooth	1.2	3.2	4.0	4.5	3.5	4.1	4.7	4.2	3.3	3.6	3.7	2.8	3.3	3.2	2.6	
Longest caudal ray	36.0	30.0	30.0	31.0	34.7	28.1	27.5	31.4	29.6	32.3	23.9	29.4	23.0	22.9	25.6	
Teeth																
Premaxillary	4	3	8	6	20	18	19	22	31	38	53	34	22	37	26	
Dentary	5	15	20	20	40	55	41	53	58	66	64	41	57	56	32	
Dorsal-fin rays	6	6	6	6	6	5	7	6	6	6	6	7	6	6	6	
Anal-fin rays	6	6	6	6	5	6	6	6	6	6	6	7	6	6	6	
Pectoral-fin rays	18	17	18	18	18	19	17	18	17	18	17	17	17	18	18	

¹Metamorphosal stage.

²Holotype of *Gigantactis exodon* Regan and Trewavas 1932.

Table 6. Counts and measurements in percent of SL of females of *Gigantactis meadi*.

Character	SAM ¹ 27811	Paratype USNM 208032	Paratype ISH 415/76	Paratype ISH 1004/71	Paratype ISH 965/71	Paratype ISH 1004/71	Paratype ISH 571/76	Paratype ISH 883/71	Paratype ISH 1465/71	Holotype MCZ 52572	Paratype LACM 11242-12
Standard length (mm)	21	35.5	87	155	178	201	207	230	290	306	353
Length											
Illicium	52.0	87.6	72.4	94.2	94.4	9.1	96.1	79.1	83.4	73.5	78.5
Longest premaxillary tooth	0.8	1.4	1.1	1.4	1.0	1.3	1.0	1.3	1.6	1.8	1.1
Longest dentary tooth	1.9	3.4	3.3	3.6	3.5	3.7	3.8	3.6	3.6	3.3	2.9
Longest caudal ray	33.0	28.2	20.7+	23.9+	23.6	27.4	20.9+	23.0	22.1	28.4	24.9
Teeth											
Premaxillary	4	2	8	20	15	23	20	31	20	20	27
Dentary	13	14	24	51	33	51	53	63	58	51	81
Dorsal-fin rays	6	6	6	6	7	6	6	6	6	6	6
Anal-fin rays	6	6	6	6	6	5	6	6	6	6	6
Pectoral-fin rays	16	18	—	17	17	17	18	18	18	18	17

¹Metamorphosal stage.

the base of the illicium. They are further distinguished in having the following combination of characters: illicial length less than 120% SL (72–96%); short filaments present along entire posterior margin of illicium; esca bulb with an elongate, spinulose, black, distal prolongation, slightly constricted at base; esca bulb and distal prolongation bearing distally flattened papillae; short distal and slender proximal esca filaments present; posterior pair of close-set illicial appendages absent; dentary teeth relatively long (longest 2.9–3.8% SL), in 5–6 longitudinal series; rays of caudal fin short (less than 30% SL).

Males unknown (probably included in *Gigantactis* Male Group II).

Larvae unknown (probably included in *Gigantactis* Larval Group A).

DESCRIPTION. Proximal part of illicium distinctly compressed, its depth at base more than twice width, length variable and unrelated to SL. Esca bulb club-shaped with cylindrical, distal prolongation more than twice as long as wide (about 3 times in the holotype), spinulose except for area surrounding pore of photophore (Fig. 32); small, distally flattened papillae present from tip of distal prolongation to some distance below bulb; papillae white or only weakly pigmented; 15 to approximately 20 short filaments on distal prolongation, most concentrated at tip, a few (only 2 in the holotype) below its base distal to photophore; a posterolateral group of filaments at base of bulb, some slightly longer than those of distal group; filaments along posterior margin of illicium (34 illicial filaments

in holotype, 8–42 in paratypes) continuing onto head forming a cluster (16 cephalic filaments in holotype, 2–18 in paratypes).

Number of teeth in each premaxilla of holotype 20, increasing with standard length from 2–8 in smaller specimens to 20–27 in larger specimens (Table 6); longest premaxillary tooth 1.8% SL in holotype, 1.0–1.8% in metamorphosed paratypes. Number of dentary teeth of holotype 51, increasing with standard length from 14–24 in smaller specimens to 51–81 in larger specimens (Table 6); teeth in posterior part of lower jaw in 5–6 longitudinal series: 2 external series, a distinct median series of small teeth, and 1 or 2 internal series; anterior part of lower jaw of most specimens with a third external series (E3 in Fig. 33) containing largest teeth of jaw, 3.3% SL in holotype, 2.9–3.8% SL in paratypes (Table 6).

Dorsal-fin rays 6–7, anal-fin rays 5–6, pectoral-fin rays 17–18 (Table 2); skin coverage of caudal fin well developed and complete for more than half length of rays; skin of each ray gradually tapering distally and connected by transparent membranes (Fig. 4B).

Two small females (19 mm, SAM 27807; 20 mm, SAM 27808), tentatively referred to this species, and the 21-mm paratype (SAM 27811) represent an ontogenetic series of late metamorphosal stages: illicial length 16, 16, and 52% SL, respectively; distal prolongation of esca short, unpigmented, and naked at 19 and 20 mm, elongate, cylindrical, and pigmented, bearing papillae and short filaments at 21 mm; rudimentary dentary teeth in a single series at 19 and 20 mm,

arranged in three series (a median series of eight teeth, a first external series of four, and a single tooth representing the second external series) at 21 mm; no enlarged lateral-line organs on head; dorsal and peritoneal subdermal pigment well developed.

A third specimen (290 mm, IOAN uncatalogued), tentatively referred to *G. meadi*, has lost the esca but has apparently retained a complete illicial bone (measuring approximately 90% SL). The cephalic filaments present at the base of the illicium, as well as characters of the teeth and caudal fin, agree with the description above.

DISTRIBUTION. *Gigantactis meadi* is circumglobal in and about the subtropical convergence of the Southern Ocean (Fig. 64), where it appears to be a relatively deep-living form. All specimens 87 mm and larger were taken by gear fished open at maximum depths of between 1850 and 2000 m.

ETYMOLOGY. This species is named for Giles W. Mead in recognition of his many contributions to ichthyology, but also for his service as Chief Scientist on the cruise during which the holotype of this new species was collected.

COMMENTS. *Gigantactis meadi* belongs to the *G. vanhoffeni* group characterized by having a black, spinulose, distal prolongation of the escal bulb. In common with three members of

this group (*G. vanhoffeni*, *G. gibbsi*, and *G. paxtoni*), it has distally flattened papillae on the esca. It differs from *G. vanhoffeni* in having a cylindrical, distal prolongation that is somewhat constricted at the base, a cluster of filaments on the head just behind the base of the illicium, and a shorter caudal fin that is covered to a greater extent by skin. It differs from *G. gibbsi* and *G. paxtoni* mainly in the shape and length of the distal prolongation. It further differs from *G. paxtoni* in illicial length.

Gigantactis gibbsi new species

Figures 34, 64; Tables 1, 2, 7

MATERIAL. Two metamorphosed females, 38 and 50 mm.

Holotype: ZIAN 44262, 50 mm, 2°01'N, 3°56'W, 0–465 m.

Paratype: USNM 218613, 38 mm, 33°00'N, 64°06'W, 0–1000 m.

DIAGNOSIS. Metamorphosed females of *G. gibbsi* differ from those of other species of the genus in having the following combination of characters: illicial length less than 120% SL (104–118%); escal bulb with a short, conical, spinulose, black, distal prolongation; escal bulb bearing distally flattened papillae, and short distal and slender proximal filaments; illicium without posterior pair of papillae; dentary teeth posteriorly in 3 longitudinal series; rays of caudal fin less than 50% SL.

Males unknown (probably included in *Gigantactis* Male Group II).

Larvae unknown (probably included in *Gigantactis* Larval Group A).

DESCRIPTION. Escal bulb of holotype pear-shaped with a short conical, distal prolongation, darkly pigmented except at base; skin covering area of photophore and base of distal prolongation unpigmented; spines present on distal prolongation and bulb except around pore of photophore; distally flattened, unpigmented papillae present on proximal part of bulb; approximately 12 short filaments at tip of distal prolongation; a group of filaments of varying length lateroproximal to bulb, longest

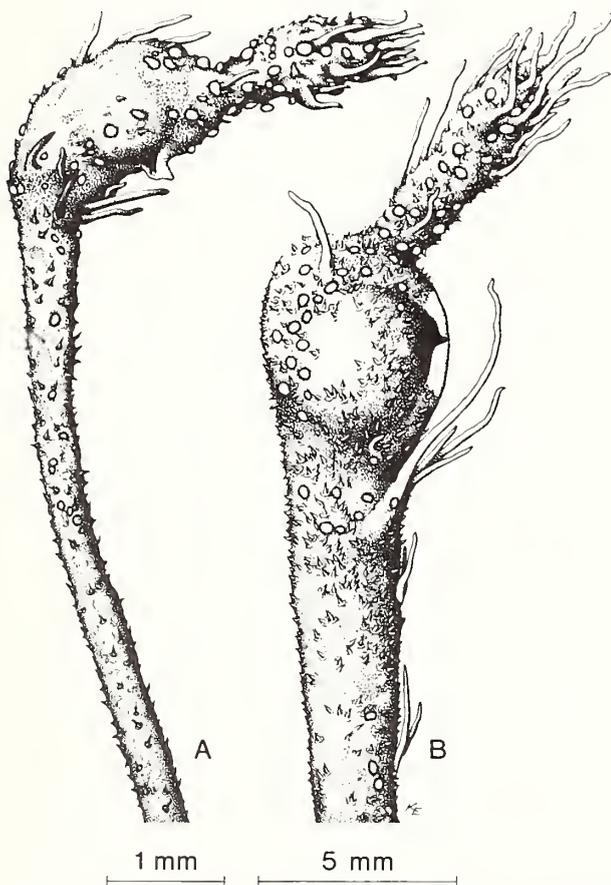


Figure 32. Escae of *Gigantactis meadi*, left lateral views: A. Paratype, 35.5 mm, USNM 208032; B. Holotype, 306 mm, MCZ 52572. Drawn by K. Elsmann.

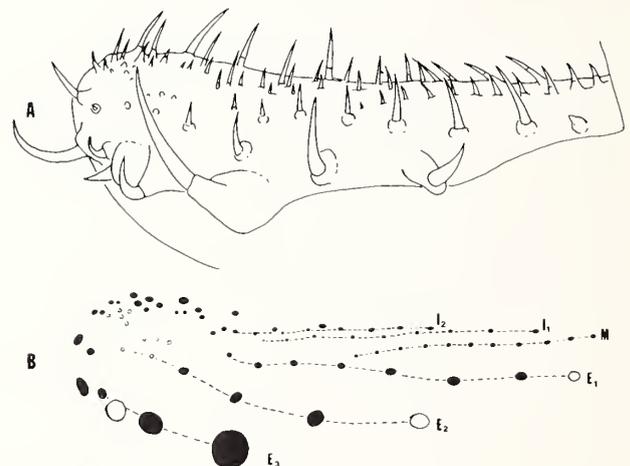


Figure 33. *Gigantactis meadi*, paratype, female, 207 mm, ISH 571/76: A. Dentary teeth, left lateral view; B. Diagrammatic representation of dentary-tooth pattern. E = external series; M = median series; I = internal series.

about equal to width of bulb (Fig. 34A). Juvenile paratype with distal prolongation of esca bulb darkly pigmented and spinulose except at base, bearing a short, terminal filament (Fig. 34B); bulb and base of distal prolongation naked and unpigmented; skin torn away from proximal part of bulb and distal part of illicium, with only a few remains of proximal filaments.

Holotype with 13 teeth (the longest 1.4% SL) in each premaxilla, paratype with 6 (the longest 1.3% SL); holotype with 27 teeth (longest 2.6% SL) in each dentary, paratype with 23 (longest 2.4% SL; Table 7). Tooth pattern similar to that of *G. vanhoeffeni* of similar standard length, with 3 distinct, longitudinal series in posterior part of lower jaw; median series of small teeth well developed.

Dorsal-fin rays 6, anal-fin rays 6, pectoral-fin rays 17–18 (Table 2); longest caudal-fin ray (second and seventh) 49% SL in holotype, 26–28% in paratype; skin coverage of caudal-fin relatively well developed.



Figure 34. Escae of *Gigantactis gibbsi*, left lateral views: A. Holotype, 50 mm, ZIAN 44262; B. Paratype, 38 mm, USNM Z18613. Drawn by K. Elsmann.

DISTRIBUTION. *Gigantactis gibbsi* is known from two specimens collected from the Atlantic Ocean, the holotype taken between the surface and 465 m from equatorial waters of the Gulf of Guinea, and a second individual from between the surface and 1000 m off Bermuda (Fig. 64).

ETYMOLOGY. This species is named for Robert H. Gibbs, Jr., in recognition of his many contributions to deepsea biology.

COMMENTS. *Gigantactis gibbsi* is a typical member of the *G. vanhoeffeni* group (Table 1) having a relatively short illicium, a spinulose, distal prolongation of the esca, and distally flattened papillae on the esca bulb. It differs from *G. vanhoeffeni*, *G. meadi*, and *G. paxtoni* in the shape and length of the distal prolongation and in the length of the longest caudal-fin ray. It further differs from *G. vanhoeffeni* in lacking a pair of papilliform or flattened appendages on the posterior margin of the illicium below the esca bulb, from *G. paxtoni* in illicial length, and from *G. gracilicauda* in having distinct, distally flattened esca papillae.

The two specimens on which *G. gibbsi* is based (38 and 50 mm) are juveniles; older specimens of this form could conceivably undergo ontogenetic changes that would indicate conspecificity with some other species of *Gigantactis*. A comparison of this material with a complete growth series of *G. vanhoeffeni* (16.5–340 mm) indicates that the differences observed in *G. gibbsi* cannot be explained as part of the variation within the more well represented *G. vanhoeffeni*. Some of the differences between *G. gibbsi* and the series of specimens representing *G. meadi* could perhaps be explained in this way, but it seems unlikely that the latter species, known only from the Southern Ocean, would occur north of the equator. Finally, it can hardly be assumed that these two juveniles represent *G. gracilicauda* or *G. paxtoni*; besides involving great ontogenetic changes in the shape of the esca, this hypothesis would also

Table 7. Counts and measurements in percent of SL of females of *Gigantactis gibbsi*.

Character	Paratype USNM 218613	Holotype ZIAN 44262
Standard length (mm)	38	50
Length		
Illicium	104	118
Longest premaxillary tooth	1.3	1.4
Longest dentary tooth	2.4	2.6
Longest caudal ray	28.4	49.0
Teeth		
Premaxillary	6	13
Dentary	23	29
Dorsal-fin rays	6	6
Anal-fin rays	6	6
Pectoral-fin rays	17	18

imply an ontogenetic loss of either the escal papillae or the proximal escal filaments.

Gigantactis gracilicauda Regan

Figures 35, 64; Tables 1, 2, 8

Gigantactis gracilicauda Regan 1925:565 (original description, single specimen); Regan 1926:18, 19, 38, fig. 12, pl. 10, fig. 2 (cranial osteology, description after Regan 1925); Regan and Trewavas 1932:93, 94 (brief description, in key); Waterman 1948:90, 93 (osteological comparison with *G. longicirra*, correction of errors made by Regan 1926); Bertelsen 1951:150–152, table 31 (comparison with all known material, comments); Grey 1956:267 (synonymy, vertical distribution); Pietsch 1972a:42, 45 (holotype with five pectoral radials).

Gigantactis sexfilis Regan and Trewavas 1932:38, 39, 93, 94, figs. 49, 50, 150, pl. 5, fig. 2 (original description, single specimen, osteology of skull and pectoral lobe, in key); Waterman 1939b:84 (comparison with *G. longicirra*, holotype with four pectoral radials after Regan and Trewavas 1932); Waterman 1948:88 (ossification of skull of *G. longicirra* less extensive than that of *G. sexfilis* as figured by Regan and Trewavas 1932);

Bertelsen 1951:150, table 31 (comparison with all known material, comments); Grey 1956:267 (synonymy, vertical distribution); Pietsch 1972a:42, 45 (holotype with five pectoral radials).

Gigantactis sp., Bertelsen 1951:150–152, fig. 100, table 31 (*G. vanhoeffeni* of Regan 1926).

MATERIAL. Three metamorphosed females, 21–82 mm.

Holotype of *Gigantactis gracilicauda*: ZMUC P92129, 82 mm, 13° 47' N, 61° 26' W, 4500 m wire.

Holotype of *Gigantactis sexfilis*: ZMUC P92132, 51 mm, 13° 07' N, 57° 20' W, 4000 m wire.

Referred material: ZMUC P921535, 21 mm, 25° 11' N, 20° 57' W, 5000 m wire.

DIAGNOSIS. Metamorphosed females of *G. gracilicauda* differ from those of other species of the genus in having the following combination of characters: illicial length less than 120% SL (104–107%, 86% in the 21-mm juvenile); escal bulb with an elongate, spinulose, and darkly pigmented distal prolongation; short distal and slender proximal escal filaments present; distally flattened escal papillae absent; illicium without posterior pair of papillae; dentary teeth posteriorly in 3 longitudinal series; rays of caudal fin less than 30% SL.

Males unknown (probably included in *Gigantactis* Male Group II).

Larvae unknown (probably included in *Gigantactis* Larval Group A).

DESCRIPTION. Illicium slightly compressed laterally in larger specimens. Escal bulb gradually tapering to form a darkly pigmented and slender distal prolongation; median portion of bulb containing unpigmented photophore; skin of bulb and distal prolongation covered with spines but without distinct papillae; distal filaments short, restricted to distal part of tapering prolongation; 1 or 2 pairs of slender filaments below escal bulb not reaching base of distal prolongation. Escal bulb of ho-

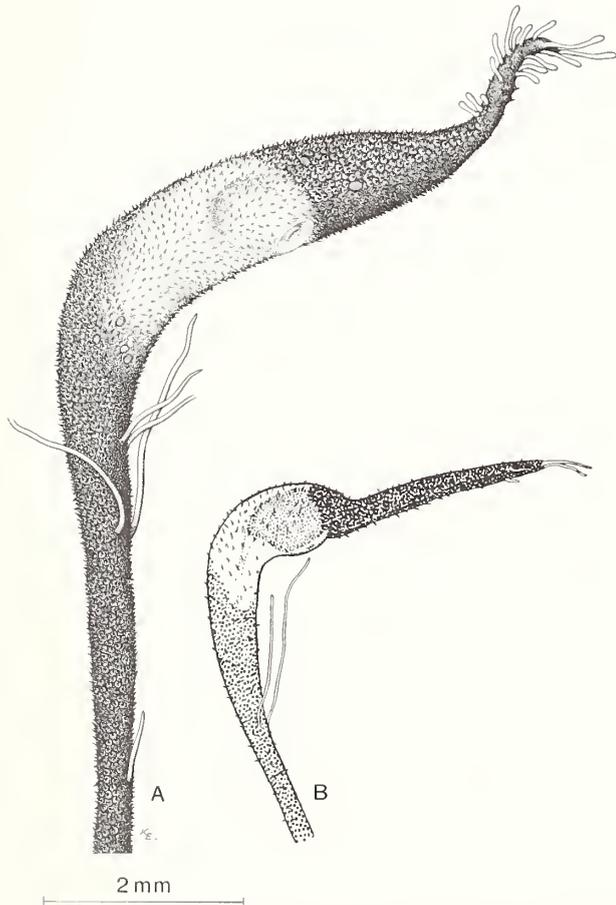


Figure 35. Escae of *Gigantactis gracilicauda*, left lateral views: A. Holotype, 82 mm, ZMUC P92129, drawn by K. Elsmann; B. Holotype of *G. sexfilis*, 51 mm, ZMUC P92132, after Regan and Trewavas 1932.

Table 8. Counts and measurements in percent of SL of females of *Gigantactis gracilicauda*.

Character	ZMUC P921535	ZMUC ¹ P92132	Holotype ZMUC P92129
Standard length (mm)	21	51	82
Length			
Illicium	85.7	104	107
Longest premaxillary tooth	—	1.0	0.7
Longest dentary tooth	—	2.4	2.4
Longest caudal ray	—	30.4	28.0
Teeth			
Premaxillary	—	7	10
Dentary	—	23	43
Dorsal-fin rays	5	6	6
Anal-fin rays	5	6	6
Pectoral-fin rays	19	18	18

¹Holotype of *Gigantactis sexfilis* Regan and Trewavas 1932.

lotype of *G. gracilicauda* (Fig. 35A) with about 20 short, distal filaments, two pairs of slender filaments on posterior margin of illicium just below bulb, and below these, an additional short illicial filament. Bulb of holotype of *G. sexfilis* (Fig. 35B) with 4 short, distal filaments, and a single pair of slender illicial filaments at base of bulb. Esca of juvenile (21.0 mm) unpigmented except for small spot on distal tip, with a few spines, but papillae absent; about 8 short, distal filaments and 2 illicial pairs of very thin, lateral filaments at base of bulb (some tiny filament-like structures, 0.2 to 0.4 mm long, present on the anteroproximal margin of the bulb may be due to abraded skin).

Holotype of *G. gracilicauda* with 10 teeth in each premaxilla (longest 0.7% SL), holotype of *G. sexfilis* with 7 teeth (longest 1.0% SL), juvenile with 4 (all in development; Table 8). Holotype of *G. gracilicauda* with 43 dentary teeth (longest 2.4% SL), holotype of *G. sexfilis* with 23 teeth (longest 2.4% SL), juvenile with approximately 10 (all in development). Tooth pattern similar to that of *G. vanhoeffeni* of similar size, with 3 distinct, longitudinal series in posterior part of lower jaw.

Dorsal-fin rays 5–6, anal-fin rays 5–6, pectoral-fin rays 18–19 (Table 2); longest caudal-fin rays (second and seventh) 26 and 28% SL in holotype of *G. gracilicauda*, both 30% SL in holotype of *G. sexfilis* (both broken in juveniles); skin coverage of caudal fin well developed.

DISTRIBUTION. *Gigantactis gracilicauda* is known from three individuals all collected in the tropical Atlantic Ocean (Fig. 64), where it appears to be a relatively deep-living form. All were taken by gear fished at maximum depths of between approximately 2000 and 2500 m.

COMMENTS. *Gigantactis gracilicauda* is a member of the *G. vanhoeffeni* group (Table 1), having a relatively short illicium and a spinulose, darkly pigmented distal prolongation of the esca bulb bearing short filaments. It resembles *G. vanhoeffeni* and *G. paxtoni* in the shape of the distal prolongation but differs from these species and other members of the *G. vanhoeffeni* group in that it lacks distally flattened esca papillae.

The esca of the holotype of *G. gracilicauda* was not described originally by Regan (1925, 1926) or later by Regan and Trewavas (1932). However, its general shape and presence of some distal filaments is shown in Regan's (1926) illustrations of the whole fish. Our figure (Fig. 35A) is to some extent a reconstruction, as the esca is now rather dehydrated and shrunken. Among the spines in its wrinkled, dark skin are some wartlike protuberances, which could be interpreted as the remains of distally flattened papillae but might well be artifacts. The esca of the holotype of *G. sexfilis* (Fig. 35B), well described and figured by Regan and Trewavas (1932), is still in good condition; no papillae are present. These distally flattened esca papillae characteristic of several well-represented *Gigantactis* species (*G. vanhoeffeni*, *G. meadi*) are developed at metamorphosis and indicate no distinct individual or ontogenetic variation. *Gigantactis gracilicauda* is recognized as a distinct species mainly because these esca papillae are lacking. The differences observed between the holotype of *G. gracilicauda* and the two smaller specimens are within the expected range of variation for this species; for this reason, *G. sexfilis* is regarded as a junior synonym of *G. gracilicauda*.

Gigantactis paxtoni new species

Figures 36, 37, 38, 64; Tables 1, 2, 9

Gigantactis "sp. 1," Parin et al., 1977:68–188 (single specimen).

MATERIAL. Eight metamorphosed females, 50–232 mm.

Holotype: AMS I.20314-018, 237 mm SL, 100 km east of Broken Bay, N.S.W., 33° 28'S, 152° 33'E, 0–900 m over 4200 m, 14 December 1977.

Paratypes: AMS I.20070-016, 124 mm SL, northeast of Cape Howe, N.S.W., 37° 24'S, 150° 30'E, 0–540 m over 3600 m, 1 November 1977. AMS I.20306-007, 142 mm SL, 65 km east of Broken Bay, N.S.W., 33° 31'S, 152° 20'E, 0–900 m over 1800–2900 m, 12 December 1977. AMS I.20314-018, 3 (175–

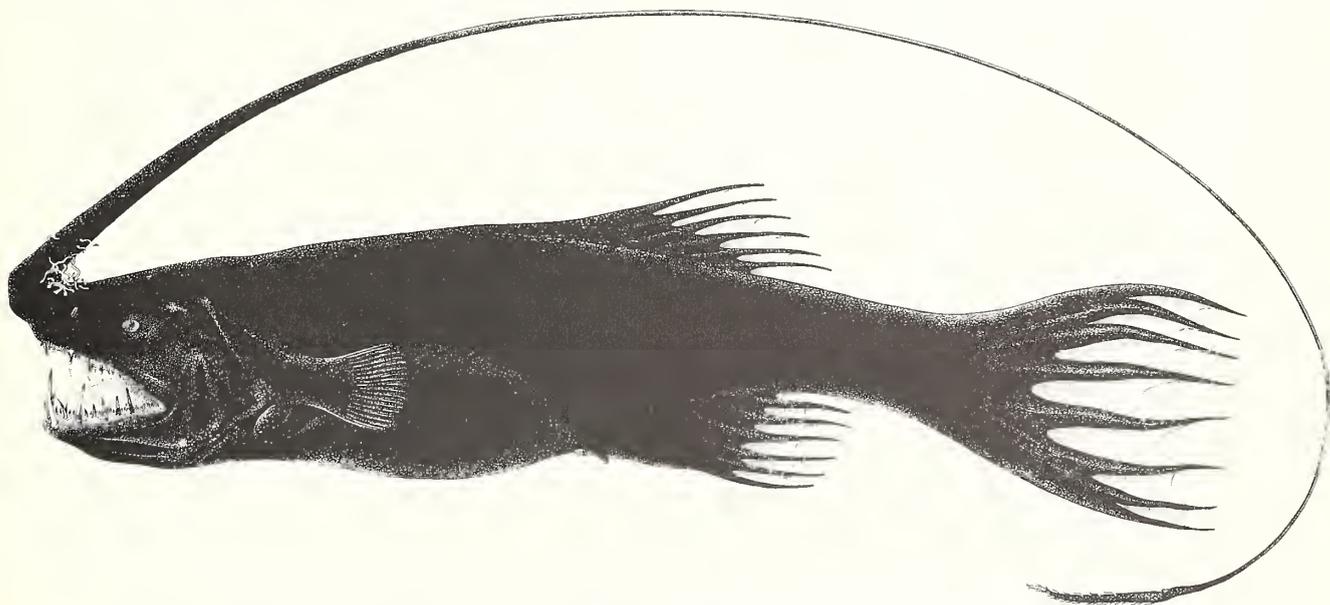


Figure 36. *Gigantactis paxtoni*, holotype, 237 mm, AMS I.20314-018. Drawn by R. Nielsen.

228 mm SL), data as for holotype. IOAN uncatalogued, 50 mm SL, VITYAZ Station 7288, 3°39'N, 131°22'E, 0–1500 m (Parin et al. 1977). IOAN uncatalogued, 210 mm SL, ZWIEZDA KRYMA Station 83, 34°07'S, 44°50'E, 0–1260 m, 1976.

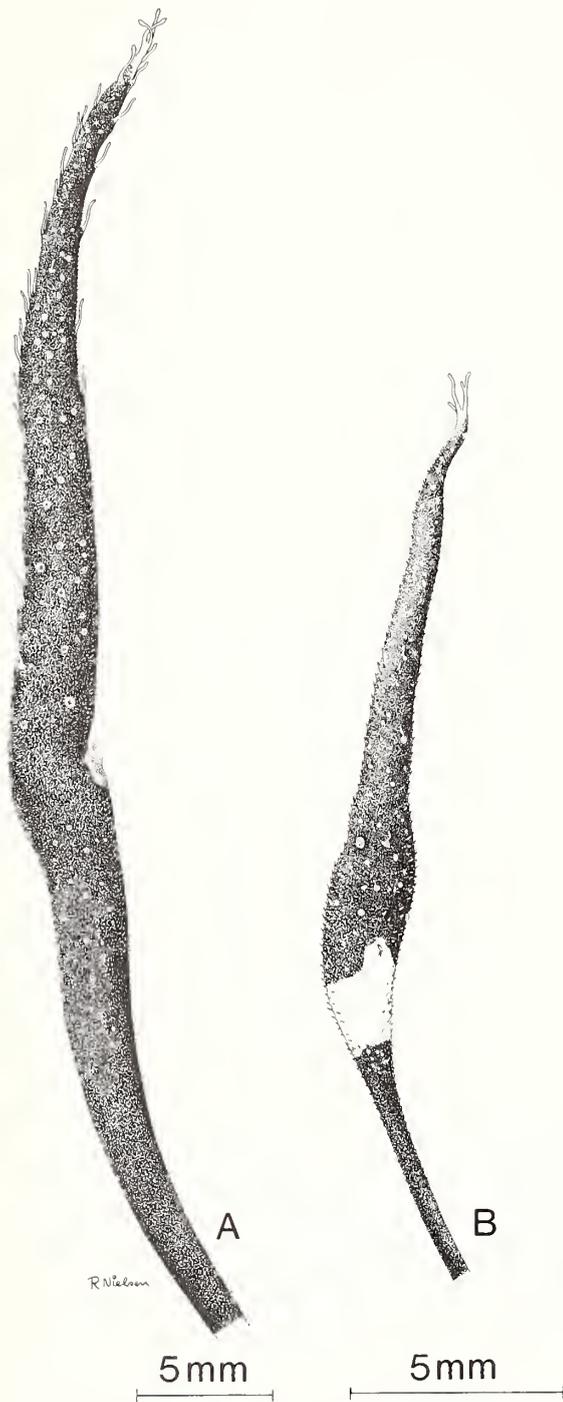


Figure 37. Escae of *Gigantactis paxtoni*: A. Holotype, 237 mm, AMS I.20314-018, left lateral view; B. Paratype, 50 mm, IOAN uncatalogued, left posterolateral view. Drawn by R. Nielsen.

DIAGNOSIS. Metamorphosed females of *Gigantactis paxtoni* differ from those of other species of the genus (except for *G. meadi*) in having filaments on the dorsal surface of the head just behind the base of the illicium. The species is further distinguished by the following combination of characters: illicial length 168–198% of SL; short filaments present on base of illicium; esca bulb gradually tapering into a conical, spinulose and darkly pigmented, distal prolongation measuring 12–28% of SL; esca bulb and distal prolongation bearing low unpigmented papillae; short filaments present on distal prolongation, but absent on base of esca bulb; posterior pair of close-set illicial appendages absent; dentary teeth long (longest tooth 3.4–7.1% of SL), in 3–4 longitudinal series in posterior part of jaw; rays of caudal fin short (27.5–35% of SL).

Males and larvae unknown.

DESCRIPTION. Proximal portion of illicium distinctly compressed, depth at base more than twice width. Escal bulb gradually tapering into a distal prolongation several times as long as wide (approximately 9 times as wide in holotype), spinulose and pigmented except for area surrounding esca pore (Fig. 37); small papillae present from tip of distal prolongation to some distance below esca bulb; papillae low (height less than width), unpigmented, and transparent; approximately 10–30 short filaments on distal prolongation, none proximal to its base; filaments along posterior margin of proximal part of illicium (except in smallest known specimen) continuing onto head and forming an anterodorsal cluster on snout.

Number of teeth in each premaxilla of holotype 15, increasing with standard length from 7 in 50-mm SL specimen to 10–19 in larger specimens (Table 9); longest premaxillary tooth 1.3% of SL in holotype, 1.0–1.8% in paratypes. Number of dentary teeth of holotype 46, increasing from 10 in 50-mm SL specimen to 28–55 in larger specimens (Table 9); teeth in posterior part of lower jaw in 3 longitudinal series; anterior part of

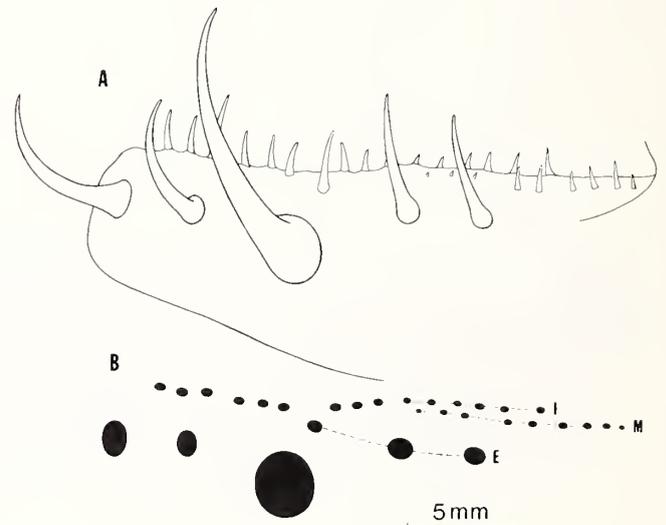


Figure 38. *Gigantactis paxtoni*, paratype, 210 mm, IOAN uncatalogued: A. Dentary teeth, left lateral view; B. Diagrammatic representation of dentary-tooth pattern. E = external series; M = median series; I = internal series.

lower jaw of most specimens with a second external series containing largest teeth of jaw, 5.6% SL in holotype, 3.4–7.1% SL in paratypes (Table 9, Fig. 38).

Dorsal-fin rays 6–7, anal-fin rays 5–6, pectoral-fin rays 18–21 (Table 2); skin coverage of caudal fin relatively well developed and complete for about one-third of length of rays; skin of each ray gradually tapering and connected by transparent membranes.

DISTRIBUTION. Six of the eight known specimens of *Gigantactis paxtoni* were caught off the southeast coast of Australia near the northern boundary of the Subantarctic Water Mass between 33° and 37°S. A seventh specimen was collected from the western South Indian Ocean and an eighth from the western tropical Pacific off the northwest coast of New Guinea (Fig. 64). With the exception of a single individual taken by bottom trawl at 1210–1260 m, the material was collected by pelagic gear fished open at maximum depths of between 540 and 1500 m (over bottom depth of 1800–4200 m).

ETYMOLOGY. This species is named for John R. Paxton of the Australian Museum, Sydney, in recognition of his contributions to deepsea ichthyology and in gratitude for providing most of the material on which this new form is based.

COMMENTS. *Gigantactis paxtoni* belongs to the *G. vanhoeffeni* group characterized by having a darkly pigmented, spinulose distal prolongation of the esca bulb. It differs from all other members of this group in having a considerably longer illicium and a longer distal prolongation of the esca bulb and in lacking proximal esca filaments. In common with three members of this group (*G. vanhoeffeni*, *G. meadi*, and *G. gibbsi*), *G. paxtoni* has distally flattened esca papillae; these pa-

pillae differ from those of the other species, however, in being distinctly lower.

Gigantactis perlatus Beebe and Crane

Figures 1C, 4C, 39, 40, 65; Tables 1, 2, 10

Gigantactis perlatus Beebe and Crane 1947:167–168, text fig. 13, pl. II, fig. 3 (original description, single specimen); Bertelsen 1951:150, 151, table 31 (comparison with all known material, comments); Grey 1956:268 (synonymy, vertical distribution); Mead 1958:133 (holotype transferred from NYZS to SU); Robins and Courtenay 1958:151 (depth distribution); Parin et al. 1973:145–146 (misidentifications, three specimens here referred to *G. vanhoeffeni*).

MATERIAL. Eight females: seven metamorphosed (23–223 mm), and one in metamorphosis (20 mm).

Holotype of *Gigantactis perlatus*: CAS-SU 46487 (originally NYZS 28621), 32.5 mm, 7°08'N, 81°57'W, 0–915 m.

Referred material: ISH 1466/71, 152 mm, 33°00'S, 7°50'E, 0–2000 m; LACM 37518-1, 20 mm, Hawaii, off leeward Oahu, 0–800 m; LACM 36875-2, 36 mm, Hawaii, off leeward Oahu, 670–805 m; MCZ 51327, 23 mm, 39°38'N, 70°03'W, 0–1000 m; SIO 61-31, 222 mm, 11°57'S, 115°22'E; USNM 218614, 41 mm, 32°00'N, 64°00'W, 0–1340 m; USNM 208111, 223 mm, 35°05'S, 91°59'W, 0–1650 m.

DIAGNOSIS. Metamorphosed females of *G. perlatus* differ from those of other species of the genus in having an extremely large distal prolongation of the esca bulb (20% SL in 220-mm specimen), the entire esca densely covered with slightly elongated papillae (not distally flattened papillae as in members of the *G. vanhoeffeni* group). They are further distinguished in

Table 9. Counts and measurements in percent of SL of females of *Gigantactis paxtoni*.

Character	Paratype IOAN uncatalogued	Paratype AMS 20070-016	Paratype AMS 20306-007	Paratype AMS 20314-018	Paratype IOAN uncatalogued	Paratype AMS 20314-018	Paratype AMS 20314-018	Holotype AMS 20314-018
Standard length (mm)	50	124	142	175	210	218	228	237
Length								
Illicium	168	185	190	187	192	190	158 + ?	198
Longest premaxillary tooth	1.0	1.5	1.1	1.4	1.8	1.6	1.3	1.3
Longest dentary tooth	3.4	6.1	7.0	7.1	6.9	5.0	5.0	5.6
Longest caudal ray	28	28.3	35	33	31.5	27.5	30.5	31.5
Teeth								
Premaxillary	7	15	10	17	17	19	19	15
Dentary	10	36	42	55	30	28	39	46
Dorsal-fin rays	6	6	6	6	7	7	6	6
Anal-fin rays	6	6	5	6	6	6	6	6
Pectoral-fin rays	19	18	19–19	20–21	19–19	18–19	20–20	20–20

having the following combination of characters: illicial length less than 120% SL (74–111% in specimens greater than 30 mm); a pair of posterior esca appendages; dentary teeth large (longest 2.2–5.9% SL), arranged in 2 irregular, longitudinal series; rays of caudal fin less than 35% SL.

Males and larvae unknown.

DESCRIPTION. Illicium somewhat laterally compressed in largest specimens, length variable and unrelated to SL. Escal bulb with a tapering, distal prolongation, increasing in size with standard length from 5–6% SL in specimens less than 50 mm to about 20% SL in specimens of approximately 220 mm; entire bulb and distal prolongation without spines, densely covered with unpigmented, slightly elongated papillae; a few, short, paired filaments along posterior margin of distal prolongation; a pair of wing-shaped appendages on posterior margin near base of bulb, with fringed edges in juveniles, divided into numerous branched filaments in older specimens; two pairs of long, proximal filaments, larger pair on lateral margin slightly below base of wing-shaped appendages, smaller pair just below and on each side of pore of photophore (Fig. 39).

Esca of three smaller specimens (23–45 mm) very similar to that of 34-mm holotype (described and figured by Beebe and Crane 1947), having a total length about 10% SL; slightly elongated papillae increasing in number and coverage of bulb with standard length; paired, wing-shaped posteroproximal appendages simple in 36-mm specimen, fringed on posterior edge in other specimens; 2–3 paired filaments along posterior margin of distal prolongation; 2 proximal pairs of larger filaments (Fig. 39A). Distal prolongation of three largest specimens (152–223 mm) greatly lengthened, total esca length 15% SL at 152 mm,

22 and 27% SL at 222 and 223 mm, respectively; bulb and distal prolongation densely covered with small, elongate papillae except for narrow posterior area around tubular opening of pore of photophore; numerous short filaments on distal third of prolongation in addition to paired filaments on posterior margin; all filaments of distal prolongation except proximal pair unpigmented and simple, proximal pair branched in two largest specimens; paired, wing-shaped appendages divided into numerous short branches in 152-mm specimen (Fig. 39B), into numerous, thin filaments in largest specimens. Esca of fresh, unpreserved specimens “completely semi-translucent white” (except for black photophore) in holotype (Beebe and Crane 1947:167); opaque, pearly white except for pink and silvery area around pore of photophore in 152-mm specimen (E. Bertelsen, personal observation); bright red in 223-mm specimen (according to color photo of fresh specimen provided by Anne Cohen).

Teeth few; number of teeth on each premaxilla 10 in 223-mm specimen, 2–3 in all others, longest tooth approximately 1.0% SL; 5–10 dentary teeth in specimens 23 to 41 mm (longest about 6% SL), 14–18 in specimens 153–223 mm (longest 2.2–3.0% SL), teeth arranged in 2 very irregular series throughout length of jaw (Fig. 40).

Dorsal-fin rays 5–7, anal-fin rays 5–7, pectoral-fin rays 16–19 (Table 2); longest caudal rays (second and seventh) 22–31% SL; skin coverage of caudal fin and thin membranes between rays well-developed (Fig. 4C, Table 10).

The 20-mm metamorphosal stage (LACM 37518-1) with illicial length 19% SL; esca with relatively short distal prolongation, no papillae, rudiments of posterior paired appendage and

Table 10. Counts and measurements in percent of SL of females of *Gigantactis perlatus*.

Character	LACM ¹	MCZ	Holotype	LACM	USNM	ISH	SIO	USNM
	37518-1	52573	SU 46487	36875-2	218614	1466/71	61-31	208111
Standard length (mm)	20	23	32.5	36	41	152	222	223
Length								
Illicium	19.0	25.2	108	73.6	107	102	111	94.2
Longest premaxillary tooth	—	—	—	—	—	—	—	—
Longest dentary tooth	—	—	—	5.9	5.0	2.2	3.0	3.0
Longest caudal ray	27.0	—	—	26.4	31.2	22.4	27.0	—
Teeth								
Premaxillary	0	—	—	3	2	3	3	10
Dentary	0	—	10	6	10	17	14	18
Dorsal-fin rays	6	5	5	7	6	5	6	5
Anal-fin rays	6	6	5	7	6	5	6	6
Pectoral-fin rays	19	17	16	18	18	17	18	17–18

¹Metamorphosal stage.

of three pairs of filaments; edge of premaxilla and dentary in resorption; jaw teeth absent; enlarged cephalic lateral line organs absent; skin and subdermal pigment absent (possibly bleached out).

DISTRIBUTION. *Gigantactis perlatus* is known from eight specimens collected from seven widely distributed capture sites: two in the western North Atlantic, one in the South Atlantic off the tip of Africa, one in Indonesian waters, one in the Hawaiian Islands, one in the Gulf of Panama, and one in the eastern South Pacific at approximately 35°S, 91°W (Fig. 65). The 36-mm Hawaiian specimen (LACM 36875-2) was collected with a closing net between 670 and 805 m. The remaining material was captured by open gear fished at maximum depths of between 800 and 2000 m.

COMMENTS. Among the *Gigantactis* species characterized by having relatively short illicia (less than 120% SL; Table 1), *G. perlatus* is distinguished by the characters of the esca: the numerous, small, slightly elongated papillae (not distally flattened as in members of the *G. vanhoeffeni* group), the extreme development of the distal prolongation, and the characteristic pattern of the filaments and appendages. The presence of paired, posteroproximal appendages is shared only with adult specimens of *G. longicirra*; but this species, besides lacking a

distal prolongation of the bulb, differs from *G. perlatus* in tooth pattern, median fin-ray counts, and caudal fin-ray lengths. A similar tooth pattern in which few, relatively large dentary teeth are arranged in two irregular series is found only in *G. golovani*. The latter species is very distinct from *G. perlatus*, however, in the length of the illicium (greater than 180% SL in *G. golovani*) and in nearly all esca characters (Figs. 39, 43).

***Gigantactis elsmanni* new species**

Figures 4E, 41, 42, 65: Tables 1, 2, 11

MATERIAL. Two metamorphosed females (283–384 mm).

Holotype: ISH 1360/71, 384 mm, 10°57'S, 11°20'W, 0–1900 m.

Paratype: LACM 10687-1, 283 mm, 63°00'S, 114°34'W, 0–2932 m, bottom depth 5051 m.

Referred material: The following specimen is tentatively referred to *G. elsmanni*: MCZ 51269, 11.5 mm, 34°26'S, 16°11'E.

DIAGNOSIS. Metamorphosed females of *G. elsmanni* differ from those of other species of the genus in having a single proximal pair and two distal pairs of large esca filaments and in lacking a distinct distal prolongation of the esca bulb. They are further distinguished in having the following combination of characters: illicial length less than 120% SL (93–105%); esca papillae absent; dentary teeth relatively short (longest 2.8% SL), arranged in 5 longitudinal series; rays of caudal fin less than 30% SL.

Males and larvae unknown.

DESCRIPTION. Illicium without filaments, proximal part laterally compressed, depth at base about 3 times width. Esca bulb club-shaped without distal prolongation; proximal part of bulb darkly pigmented, covered with spines to (or slightly beyond) photophore; distal part of bulb above photophore bearing numerous short filaments and 2 pairs of large filaments; a pair of large, proximal filaments reaching beyond tip of longest distal filaments.

Esca extremely similar in two known specimens (the proximal and distal pairs of long filaments arise in exactly the same position and seem to be of very similar relative length, although some appear to be broken in the holotype); number of short, distal filaments somewhat greater, and longest slightly longer in holotype; pigmentation on posterior margin of bulb just below photophore deeply cleft in holotype, forming a rounded inden-

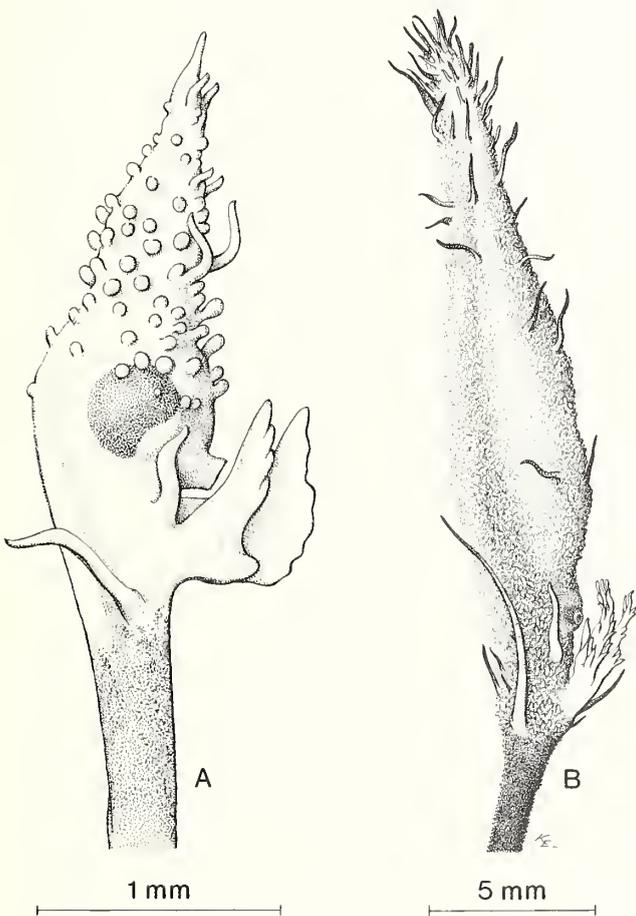


Figure 39. Escae of *Gigantactis perlatus*, left lateral views: A. 23 mm, MCZ 51327; B. 152 mm, ISH 1466/71. Drawn by K. Elsmann.

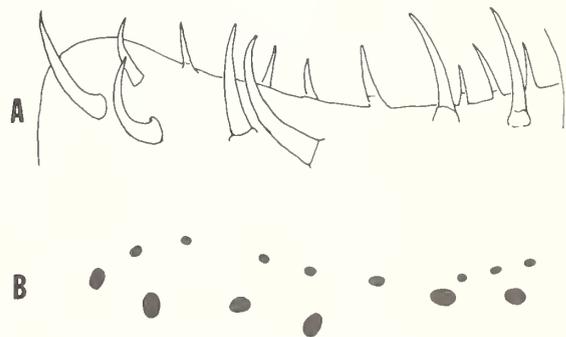


Figure 40. *Gigantactis perlatus*, female, 222 mm, SIO 61-31: A. Dentary teeth, left lateral view; B. Diagrammatic representation of dentary-tooth pattern.

tation in paratype; spines absent on unpigmented part of bulb in holotype, covering proximal part of bulb in paratype (Fig. 41).

Number of teeth on each premaxilla 32 in both specimens, arranged in 2–3 overlapping, longitudinal series, external and posteriormost turned forward; longest premaxillary tooth 1.2% SL in holotype, approximately 1.0% in paratype. Number of dentary teeth 56 in holotype, 35 in paratype, longest 2.8% SL in both; dentary teeth in posterior part of jaw arranged in 5 longitudinal series, an external, a median, and 3 internal (Fig. 42).

Dorsal-fin rays 5, anal-fin rays 4–5, pectoral-fin rays 16–17 (Table 2); longest rays of caudal fin (second and seventh) 21–

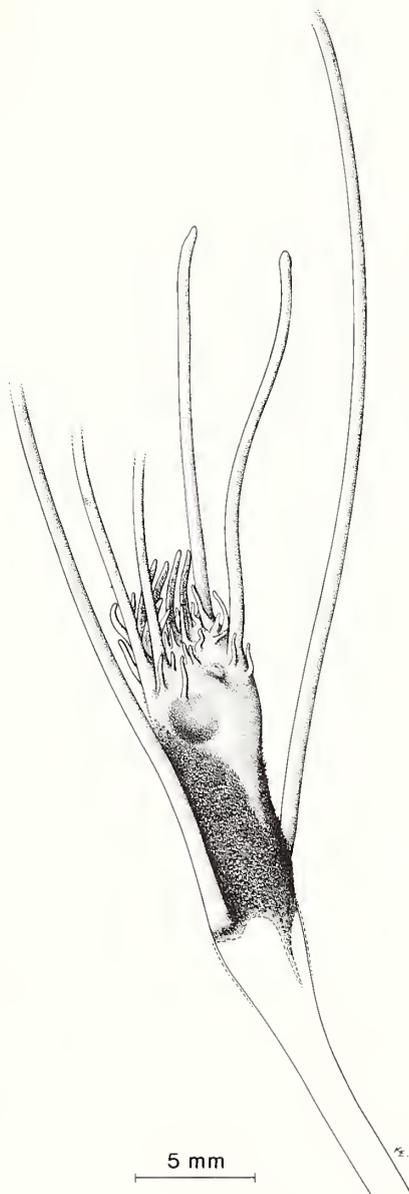


Figure 41. Esca of *Gigantactis elsmanni*, holotype, 384 mm, ISH 1360/71, posterolateral view. Drawn by K. Elsmann.

27% SL; skin coverage of caudal fin and membranes between caudal rays well developed (Fig. 4E).

The 11.5-mm metamorphosal stage tentatively referred to this species (MCZ 51269) with illicial length of about 10% SL; esca with naked, unpigmented skin, a short conical distal prolongation and papilliform rudiments of a pair of filaments on base; edge of jaws in resorption, no rudiments of teeth; on each side, a series of seven or eight enlarged supraorbital lateral line organs, the longest about 10% SL; skin faintly pigmented; no distinct dorsal subdermal pigment (specimen somewhat bleached); differs from holotype and paratype in having four dorsal-fin rays and 18 pectoral-fin rays (Table 11).

DISTRIBUTION. *Gigantactis elsmanni* is known from two specimens: the holotype taken from between the surface and 1900 m in the central Atlantic at approximately 11°S, and the paratype from between the surface and 3000 m in the eastern South Pacific at 63°S. A third specimen, tentatively referred to this species, is from the South Atlantic off Cape Town, South Africa (Fig. 65).

ETYMOLOGY. This species is named for the late Kai L. Elsmann, whose superb illustrations have added immeasurably to this revision.

COMMENTS. Among the *Gigantactis* species with an illicial length of less than 120% SL (Table 1), *G. elsmanni* is clearly distinguished by the characters of the esca: the lack of a distinct, distal prolongation of the esca bulb and the presence of a single proximal and two distal pairs of large filaments. Specimens lacking escae may be identified by using a combination of characters including a low number of fin rays, a relatively high number of posterior longitudinal series of dentary teeth, and well-developed skin coverage on the caudal fin.

Gigantactis golovani new species

Figures 4J, 43, 44, 65; Tables 1, 2, 12

Gigantactis vanhoeffeni, Parin and Golovan 1976:271 (in part, one specimen).

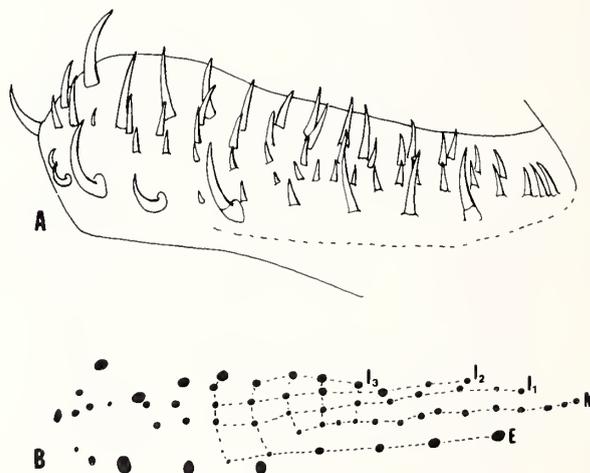


Figure 42. *Gigantactis elsmanni*, holotype, female, 384 mm, ISH 1360/71: A. Dentary teeth, left lateral view; B. Diagrammatic representation of dentary-tooth pattern. E = external series; M = median series; I = internal series.

MATERIAL. Three metamorphosed females (25–179 mm).

Holotype: ISH 2250/71, 179 mm, 2°27'S, 19°00'W, 0–660 m.

Paratypes: ZIAN 44263, 153 mm, 10°36'N, 17°38'W, 0–1550 m; MCZ 51272, 25 mm, 14°43'N, 25°27'W, 0–720 m.

The following specimen, tentatively referred to this species, is not included in the description below (but data given in Table 12): LACM 37517-1, 29 mm, Hawaii, off leeward Oahu, 0–2100 m.

DIAGNOSIS. Metamorphosed females of *G. golovani* differ from those of other species of the genus in having branched, distal esca filaments, a single long filament below the anterior margin of the esca bulb, and several similar filaments on and below the posterior margin of the esca bulb. They are further distinguished in having the following combination of characters: illicial length 180–200% SL (except in juveniles); esca papillae absent; dentary teeth relatively long (largest 4.4–4.5% SL), arranged in 2, possibly 3, very irregular, longitudinal series; rays of caudal fin less than 35% SL.

Males and larvae unknown.

DESCRIPTION. Illicium nearly cylindrical throughout, length 183–199% SL, 72% in 25-mm juvenile. Esca bulb club-shaped without distal prolongation, naked and unpigmented except at base; a group of branched distal filaments; a single, long filament on anterior margin of base of bulb; numerous filaments of different length (some reaching beyond the tip of the distal filaments) on posterior margin of proximal part of bulb and on illicium below bulb (Fig. 43). Esca of larger paratype less well preserved, but number and distribution of filaments quite similar; filaments on proximal part of esca and on illicium shorter, not reaching beyond base of distal filaments. Esca of juvenile paratype (Fig. 43A) with distribution of filaments similar to

Table 11. Counts and measurements in percent of SL of females of *Gigantactis elsmanni*.

Character	MCZ ¹ 51269	Paratype LACM 10687-1	Holotype ISH 1360/71
Standard length (mm)	11.5	283	384
Length			
Illicium	~10	92.6	105
Longest premaxillary tooth	—	1.1	1.2
Longest dentary tooth	—	2.8	2.8
Longest caudal ray	40.0	20.8	27.3
Teeth			
Premaxillary	0	32	32
Dentary	0	35	56
Dorsal-fin rays	4	5	5
Anal-fin rays	5	4	5
Pectoral-fin rays	18	17	16

¹Metamorphosal stage tentatively referred to this species.

that of holotype, but number somewhat less, considerably shorter, and unbranched.

Premaxillary teeth 20 in holotype (longest 1.7% SL), 17 in larger paratype (longest 1.8% SL), 5 in smaller paratype (longest 2.0% SL). Dentary teeth 17 in holotype, 14 in larger paratype, 10 in smaller paratype (Fig. 44).

Dorsal-fin rays 6, anal-fin rays 6–7, pectoral-fin rays 14–16 (Table 2); longest caudal rays (second and seventh) 30–32% SL in holotype, 28–31% SL in larger paratype; caudal-fin rays connected by transparent membranes; pigmented skin covering median caudal rays, which are broad, tapering only at tip (Fig. 4J, Table 12).

The 29-mm juvenile (LACM 37517-1, Table 12), tentatively referred to this species, differs from the type material in having only about four distal esca filaments, five proximal filaments on posterior margin, and none on anterior margin; it is similar to the type material in the arrangement of the esca filaments, in lacking a distal prolongation of the esca bulb, and in the

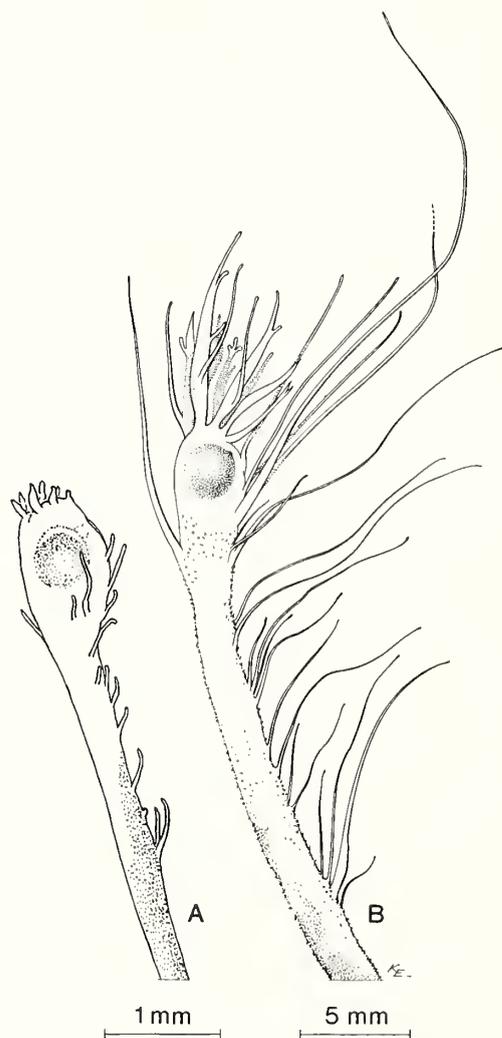


Figure 43. Escae of *Gigantactis golovani*, left lateral views: A. Paratype, 25 mm, MCZ 51272; B. Holotype, 179 mm, ISH 2250/71. Drawn by K. Elsmann.

dentary tooth pattern, which consists of a few (9) large (the six largest 3–5% SL) teeth arranged in two (?) irregular series.

DISTRIBUTION. *Gigantactis golovani* is known from three specimens all collected in the eastern tropical Atlantic Ocean (Fig. 65). The material was captured by open gear fished at maximum depths of between 660 and 1550 m. A fourth specimen, tentatively referred to this species, is from Hawaii, collected between the surface and 2100 m.

ETYMOLOGY. *Gigantactis golovani* is named in honor of George Golovan of the Institute of Oceanology of the Academy of Sciences of the USSR, in appreciation for his making large and valuable collections of ceratioids available to us.

COMMENTS. The intermediate illicial length of *G. golovani* (180 to 200% SL, comparable only to *G. paxtoni*, *G. gargantua* and *G. savagei*) easily separates this from the eight species in which the illicium is less than 120% SL (Table 1), and, at the same time, distinguishes it from all remaining species in which the illicium is considerably longer. In escal characters, *G. golovani* is unique in having branched, distal filaments and a single anterior filament below the base of the escal bulb and several similar filaments on and below its posterior margin. Some branched distal filaments and several filaments on and below the base of the escal bulb are present in large specimens of *G. gargantua* and *G. macronema*; but, in these forms, the proximal filaments are concentrated anteriorly (Figs. 46, 52). In dentary tooth pattern (in which the teeth are relatively long, but few in number and irregularly arranged), *G. golovani* is similar only to *G. perlatus*.

Gigantactis gargantua new species

Figures 1D, 4H, 45, 46, 66; Tables 1, 2, 13

Gigantactis sp. n., Pietsch 1972a:42, 43, 45, fig. 24(2) (otolith described, figured).

MATERIAL. Seven females: six metamorphosed (49–408 mm), and one in metamorphosis (25 mm).

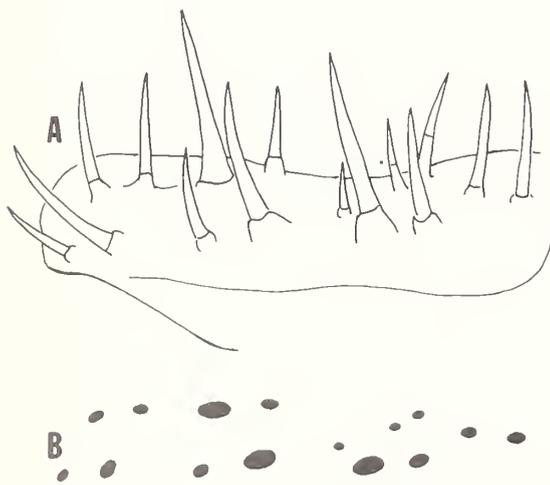


Figure 44. *Gigantactis golovani*, holotype, female, 179 mm, ISH 2250/71: A. Dentary teeth, left lateral view; B. Diagrammatic representation of dentary-tooth pattern.

Holotype: LACM 6903-32, 408 mm, 32° 16'N, 117° 43'W, 0–1250 m, bottom depth 1775 m.

Paratypes: IOAN uncatalogued, 325 mm, 31° 30.8'S, 95° 27.2'E, 0–1400 m; LACM 30415-27, 25 mm, 28° 44'N, 118° 10'W, 0–1850 m; LACM 32749-3, 49 mm, 21° 20–30'N, 158° 20–30'W, 0–1000 m; LACM 30997-2, 105 mm, 31° 32'N, 118° 29'W, 0–1300 m; LACM 30996-16, 106 mm, 31° 54'N, 118° 39'W, 0–500 m; LACM 9748-28, 166 mm, 32° 13'N, 117° 47'W, 0–835 m, bottom depth 1756 m.

DIAGNOSIS. Metamorphosed females of *G. gargantua* differ from those of other species of the genus in having the following combination of characters: illicial length 134–354% SL; 4 to 5 pairs of large, distal escal filaments; 30 to 50 proximal filaments centered on anterior margin of escal bulb; escal papillae absent; dentary teeth relatively short (longest 2.3% SL), arranged posteriorly in 4 longitudinal series; second and seventh caudal-fin rays extremely long (30–47% and 54–76% SL, respectively).

Males unknown (probably included in *Gigantactis* Male Group I).

Larvae unknown.

DESCRIPTION. Illicium usually without filaments (some filaments on distal part of illicium of 325-mm specimen, IOAN uncatalogued), distinctly compressed proximally, depth near base more than twice width in holotype; illicial length 134–216% SL in five metamorphosed specimens from eastern Pacific, 354% SL in specimen from Indian Ocean (325 mm, IOAN uncatalogued). Escal bulb club-shaped with a short, distal prolongation; posterior surface of distal prolongation darkly pigmented, with a distal and 2 or 3 lateral pairs of swellings forming bases for 4–5 pairs (2 on distal pair of swellings) of

Table 12. Counts and measurements in percent of SL of females of *Gigantactis golovani*.

Character	Paratype		Paratype IOAN uncata- logued	Holotype ISH 2250/71
	MCZ 51272	LACM ¹ 37517-1		
Standard length (mm)	25	29	153	179
Length				
Illicium	72.0	93.0	183	199
Longest premaxillary tooth	2.0	1.7	1.8	1.7
Longest dentary tooth	4.4	5.0	4.4	4.5
Longest caudal ray	—	32.0	31.4	31.8
Teeth				
Premaxillary	5	5	17	20
Dentary	10	9	14	17
Dorsal-fin rays	6	5	6	6
Anal-fin rays	6	6	6	7
Pectoral-fin rays	—	17	16	15–14

¹Only tentatively referred to *G. golovani*.

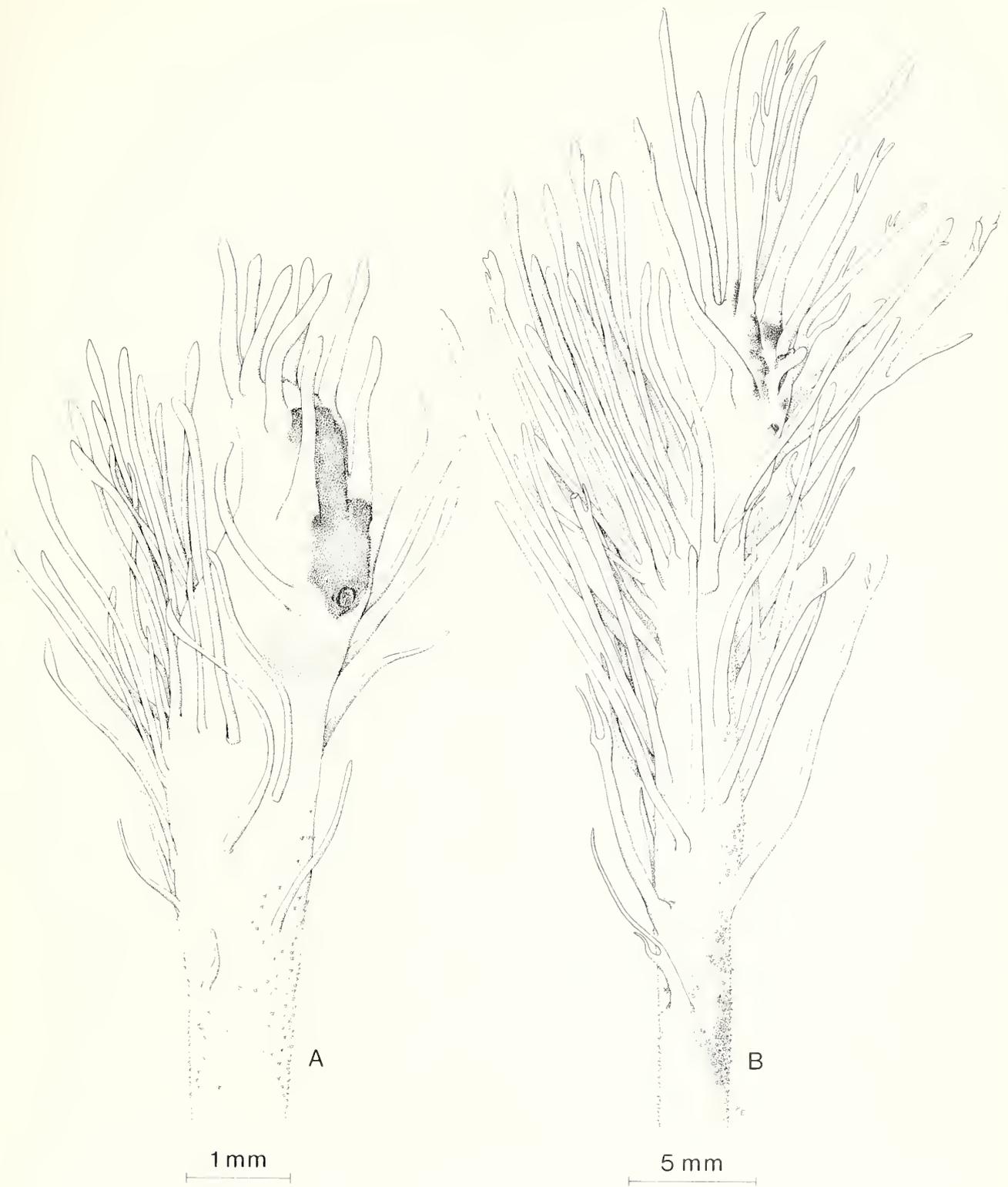


Figure 45. Escae of *Gigantactis gargantua*, posterolateral views: A. Paratype, 105 mm, LACM 30997-2; B. Holotype, 408 mm, LACM 6903-32. Drawn by K. Elsmann.

Table 13. Counts and measurements in percent of SL of females of *Gigantactis gargantua*.

Character	Paratype ¹ LACM 30415-27	Paratype LACM 32749-3	Paratype LACM 30997-2	Paratype LACM 30996-16	Paratype LACM 9748-28	Paratype IOAN uncatalogued	Holotype LACM 6903-32
Standard length (mm)	25	49	105	106	166	325	408
Length							
Illicium	50.0	208	216	190	189	354	134
Longest premaxillary tooth	<0.5	0.8	0.8	0.9	0.7	0.9	0.8
Longest dentary tooth	<0.5	1.6	1.7	2.1	1.9	1.3	2.3
Longest caudal ray	25.0	67.3	54.3	59.4	54.8	76.0	broken
Teeth							
Premaxillary	2	7	15	11	17	34	59
Dentary	5	16	31	35	41	46	75
Dorsal-fin rays	7	6	6	5	6	6	5
Anal-fin rays	6	6	6	6	6	6	6
Pectoral-fin rays	19	19	19-20	20	21	20	22

¹Metamorphosal stage.

large, unpigmented filaments, more or less branched in large specimens (Fig. 45); pore of photophore on a pigmented papilla; proximal part of bulb spinulose, unpigmented, with numerous filaments of different length (longest reaching beyond tip of distal prolongation), longest and most dense on anterior margin. Esca of 408-mm holotype (Fig. 45B) differing from those of paratypes: proximal, right swelling of distal prolongation small, deformed, with only a short filament (possibly in regeneration); division into six pairs of distal filaments less distinct, nearly all branched, some bifurcated near close-set bases; proximal filaments more numerous, group centered on anterior margins surrounding base of bulb. Most esca filaments of type material slightly swollen at tip.

Premaxillary teeth increasing in number with standard length from 7 in smallest paratype to 59 in holotype (longest tooth 0.7-0.9% SL). Dentary teeth increasing in number with standard length from 16 in smallest paratype (longest 1.6% SL) to 75 in holotype (longest 2.3% SL), arranged posteriorly in 4 longitudinal series, some teeth of second external series present anteriorly in the jaw of large specimen (Fig. 46, Table 13).

Dorsal-fin rays 5-7, anal-fin rays 6, pectoral-fin rays 19-22 (Table 2); skin coverage of proximal part of caudal fin well-developed (Fig. 4H).

The 25-mm metamorphosal stage (LACM 30415-27) with illicial length 50% SL; esca with short distal prolongation and indistinct rudiments of distal filaments; teeth in early development; no enlarged lateral line organs on head; dorsal subdermal pigment faint (Table 13).

DISTRIBUTION. *Gigantactis gargantua* is known from six specimens collected in the eastern North Pacific Ocean off southern California and the Hawaiian Islands, and a seventh individual collected in the eastern south Indian Ocean (Fig. 66). The material was taken by open gear fished at maximum depths of between 500 and 1300 m.

ETYMOLOGY. *Gargantua*, a gigantic king, was the hero of a satirical romance written by Rabelais in 1535.

COMMENTS. *Gigantactis gargantua*, *G. herwigi*, and *G. watermani* form a group of closely related forms here referred to as the *G. gargantua* group (Table 1). They are distinguished

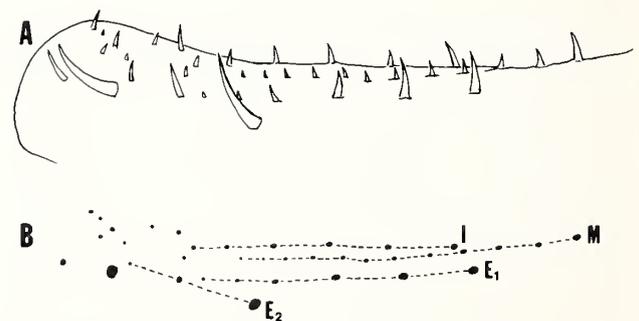


Figure 46. *Gigantactis gargantua*, paratype, female, 106 mm, LACM 30996-16: A. Dentary teeth, left lateral view; B. Diagrammatic representation of dentary-tooth pattern. E = external series; M = median series; I = internal series.

from other members of the genus in having four to five pairs of large, distal filaments arising from swollen bases, a group of proximal filaments centered on the anterior margin of the bulb, and the especially prolonged second and seventh caudal fin rays. *Gigantactis gargantua* differs from *G. watermani* and *G. herwigi* in details of the escal morphology, particularly in having a greater number of proximal filaments (about 20 to 50 compared with 12 and 7 in *G. watermani* and *G. herwigi*, respectively).

The material forming the *G. gargantua* group is quite similar in nearly all characters. However, we recognize three species within the group for the following reasons: the six metamorphosed specimens from the Pacific and Indian Ocean, here described as *G. gargantua*, agree completely in the escal characters that separate them from the two Atlantic specimens; in light of the small intraspecific and ontogenetic variation in these characters observed in other *Gigantactis* species, it seems unlikely that the differences between the two Atlantic specimens could be explained in this way. The variation in illicial length is unusually great in *G. gargantua* compared to that in most other *Gigantactis* species, even within the representatives of the eastern Pacific population. For this reason, the extreme illicial length observed in the specimen from the Indian Ocean (IOAN uncatalogued) is not considered to express specific distinction. For the same reason, the large difference in illicial length between the holotypes of *G. watermani* and *G. herwigi* may not be a diagnostic means of distinguishing these two forms.

Gigantactis watermani new species

Figures 47–49, 66; Tables 1, 2

MATERIAL. A single metamorphosed female, the holotype: ISH 2330/71, 99 mm, 1°04'N, 18°22'W, 0–2100 m.

DIAGNOSIS. Metamorphosed females of *G. watermani* differ from those of other species of the genus in having the following combination of characters: illicial length 231% SL; 5 pairs of large, distal escal filaments; 12 proximal filaments centered on anterior margin of escal bulb; escal papillae absent; dentary teeth short (longest 2.5% SL), arranged posteriorly in 4 longitudinal series; second caudal-fin ray extremely long (70% SL),

seventh caudal-fin ray broken in holotype (remaining portion measures 30% SL).

Males and larvae unknown.

DESCRIPTION. Illicium without filaments, proximal part not distinctly compressed. Escal bulb club-shaped with a darkly pigmented, distal prolongation approximately five times as long as bulb diameter, with proximal one-half greatly swollen; distal prolongation bearing 5 pairs of stout, tapering filaments, all but distal-most pair densely covered with black pigment except for narrow, tapering tip; opening of pore of photophore present in darkly pigmented skin at base of distal prolongation, not raised on a papilla; 12 narrow, unpigmented filaments on anterior margin of base of bulb, longest reaching base of distal-most pair of distal filaments; base of bulb proximal to filaments pigmented and spinulose (Fig. 48).

Premaxillary teeth 16 (longest 1.1% SL); dentary teeth 43, arranged in 4 longitudinal series in posterior part of jaw, some teeth of second external series present anteriorly (Fig. 49).

Dorsal-fin rays 6, anal-fin rays 5, pectoral-fin rays 18–19 (Table 2).

DISTRIBUTION. *Gigantactis watermani* is known only from the holotype collected from between the surface and 2100 m in the eastern tropical Atlantic at approximately 1°N, 18°W (Fig. 66).

ETYMOLOGY. This species is named for Talbot Howe Waterman in recognition of his outstanding contribution to our knowledge of the anatomy of *Gigantactis* (see Waterman 1948).

COMMENTS. *Gigantactis watermani* is a member of the *G. gargantua* group (Table 1). It is distinguished from the other two members of this group (*G. gargantua* and *G. herwigi*) in having a more elongate, distal escal prolongation and larger and more heavily pigmented proximal portions of the distal escal filaments. It is further distinguished from *G. gargantua* in having fewer proximal filaments that are all restricted to the anterior margin of the escal bulb.

Gigantactis herwigi new species

Figures 4G, 50, 51, 66; Tables 1, 2

MATERIAL. A single metamorphosed female, the holotype, ISH 972/68, 262 mm, 4°43'S, 26°39'W, 0–2000 m.

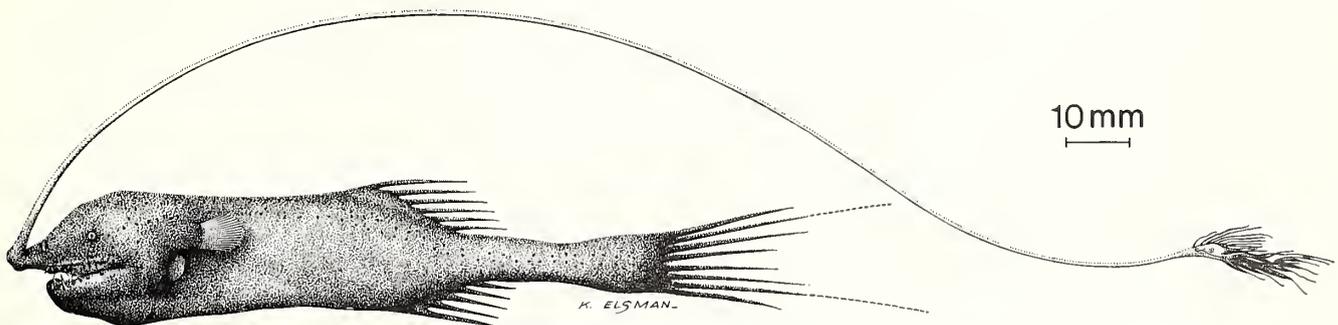


Figure 47. *Gigantactis watermani*, holotype, 99 mm, ISH 2330/71. Drawn by K. Elsmann.

DIAGNOSIS. Metamorphosed females of *G. herwigi* differ from those of other species of the genus in having the following combination of characters: illicial length 373% SL; 4 pairs of large, distal esca filaments; 7 proximal filaments centered on anterior margin of esca bulb; esca papillae absent; dentary teeth short (longest 1.6% SL), arranged posteriorly in 4 longitudinal series; second and seventh caudal-fin rays prolonged (70 and 95% SL, respectively).

Males and larvae unknown.

DESCRIPTION. Illicium without filaments, proximal part slightly compressed laterally. Esca bulb club-shaped, without

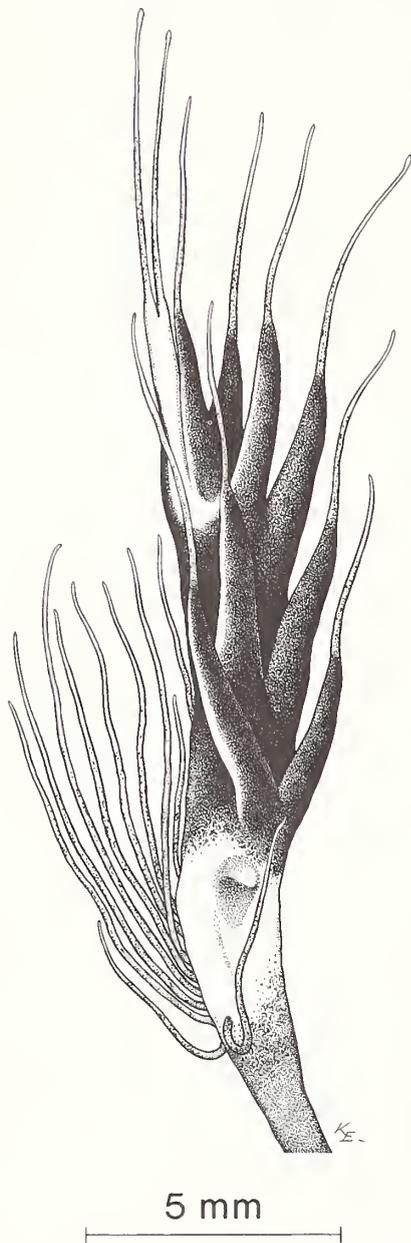


Figure 48. Esca of *Gigantactis watermani*, holotype, 99 mm, ISH 2330/71, left lateral view. Drawn by K. Elsmann.

distinct prolongation, bearing 4 pairs of large, unbranched, distal filaments, slightly swollen and pigmented posteriorly at base; opening of pore of photophore on pigmented papilla; proximal part of bulb spinulose with 7 narrow, unpigmented filaments on anterior margin of base of bulb, longest reaching beyond base of distal filaments (Fig. 50).

Premaxillary teeth 34 (longest 0.7% SL); dentary with approximately 65 teeth, arranged posteriorly in 4 series, some teeth of second external series present anteriorly (Fig. 51).

DISTRIBUTION. *Gigantactis herwigi* is known only from the holotype collected from between the surface and 2000 m in the tropical Atlantic at approximately 4° S, 26° W (Fig. 66).

ETYMOLOGY. This new form is named after the German Research Vessel *Walther Herwig*, which has been used during numerous expeditions since 1966 to collect an outstandingly rich resource of deepsea fishes, including the holotype of *G. herwigi* as well as nearly all *Gigantactis* material catalogued at the Institut für Seefischerei, Hamburg (ISH).

COMMENTS. *Gigantactis herwigi* is a member of the *G. gargantua* group (Table 1). It differs from other members of this group in lacking a distinct prolongation of the esca bulb. It further differs from *G. gargantua* in having all distal filaments of the esca unbranched and proximal esca filaments (7 compared to about 30 in *G. gargantua*) restricted to the anterior margin of the bulb (surrounding the bulb in *G. gargantua*). It further differs from *G. watermani* in having distal filaments that are less swollen and that are pigmented only near the base (swollen and darkly pigmented for more than half their length in *G. watermani*), and in having unpigmented proximal filaments (pigmented in *G. watermani*).

Gigantactis macronema Regan

Figures 1E, 4I, 22, 52, 53, 67; Tables 1, 2, 14

Gigantactis macronema Regan 1925:565 (original description, single specimen); Regan 1926:38, pl. 11 (description after Regan 1925); Regan and Trewavas 1932:93, 94 (description after Regan 1925, 1926, in key); Waterman 1939b:84–85 (comparison with *G. longicirra*, largest known gigantactinid); Waterman 1948:130 (comparison with *G. longicirra*); Bertelsen 1951:150–152, fig. 101, table 31 (comparison with all known material, comments); Grey 1956:267 (synonymy, vertical dis-

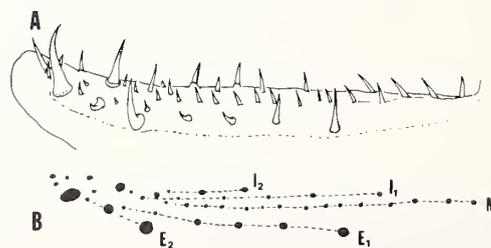


Figure 49. *Gigantactis watermani*, holotype, female, 99 mm, ISH 2330/71: A. Dentary teeth, left lateral view; B. Diagrammatic representation of dentary-tooth pattern. E = external series; M = median series; I = internal series.

tribution); Robins and Courtenay 1958:151 (comparison with additional specimen designated *Gigantactis* sp.); Fitch and Lavenberg 1968:135-137, fig. 74 (distinguishing characters, natural history, fishery information, other family members off California); Pietsch 1972a:29, 34, 35, 41, 42, 45 (comments on osteology, holotype with five pectoral radials).

MATERIAL. Ten metamorphosed females, 34-354 mm.

Holotype of *Gigantactis macronema*: ZMUC P92130, 98 mm, 31°47'N, 41°41'W, 5000 m wire.

Referred material: ISH 1596/71, 232 mm, 27°14'S, 2°56'E, 0-2000 m; LACM 37516-1, 34 mm, Hawaii, off leeward Hawaii, 0-950 m; LACM 32745-2, 37.5 mm, 21°00'N, 158°20'W, 0-930 m; LACM 9036-36, 93 mm, 33°26'N, 118°33'W, 0-1100 m, bottom depth 1270 m; LACM 6902-38,

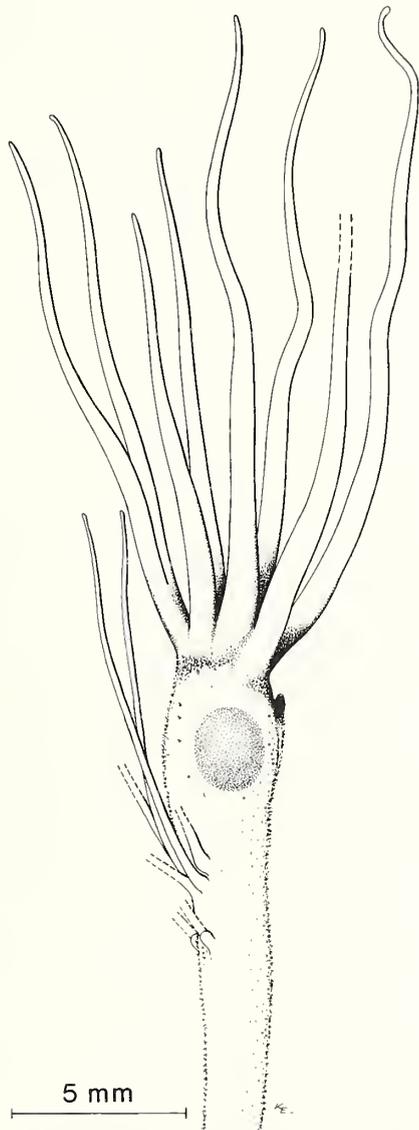


Figure 50. Esca of *Gigantactis herwigi*, holotype, 262 mm, ISH 972/68, left lateral view. Drawn by K. Elsmán.

110 mm, 32°36'N, 118°05'W, 0-650 m; LACM 30599-20, 354 mm, 33°22'N, 118°02'W, 0-650 m; MCZ 51255, 141 mm, 23°04'N, 45°10'W, 0-1100 m (cleared and stained); SIO 73-156, 35 mm, 28°18.5'N, 155°14.5'W, 3000 m wire; SIO 57-46, 62 mm, 28°51'N, 118°11'W, 0-1041 m, bottom depth 1280-1830 m.

DIAGNOSIS. Metamorphosed females of *G. macronema* differ from those of other species of the genus in having the following combination of characters: illicial length 340-447% SL; esca bulb with a lightly pigmented, truncated distal prolongation; 8-20 long distal filaments; esca papillae absent; proximal esca filaments absent; dentary teeth short (longest 1.3-3.4% SL, average 2.3% SL), arranged posteriorly in 2 longitudinal series; length of caudal-fin rays less than 40% SL; skin coverage of proximal part of caudal fin weakly developed, caudal-fin rays free nearly to base.

Males unknown (probably included in *Gigantactis* Male Group I).

Larvae unknown (probably included in *Gigantactis* Larval Group B).

DESCRIPTION. Illicium without filaments (except in the 354-mm specimen, Fig. 52B, in which distal sixth of illicial length covered with unpigmented, short filaments, each with white swollen base), nearly cylindrical throughout length, depth less than twice width; illicial length variable and unrelated to SL. Esca of holotype (not well preserved, see comments below) with remains of at least 8 filaments at tip of distal prolongation; esca bulb of 93-, 141- and 243-mm specimens (all well preserved and quite similar, Fig. 52) elongate and club-shaped, increasing gradually in width from illicium toward unpigmented area surrounding photophore; skin of bulb spinulose except area distal to photophore; pore of photophore raised on papilla, pigmented at tip; distal prolongation truncated, faintly pigmented on posterior margin, length more than twice width at base; 16 distal filaments, symmetrically arranged more or less in close-set pairs, each with a small swelling at tip; esca of 354-mm specimen (Fig. 52B) with somewhat shorter distal prolongation bearing more numerous filaments (approximately 20) that are close-set and less distinctly arranged in pairs, some bifurcated; esca

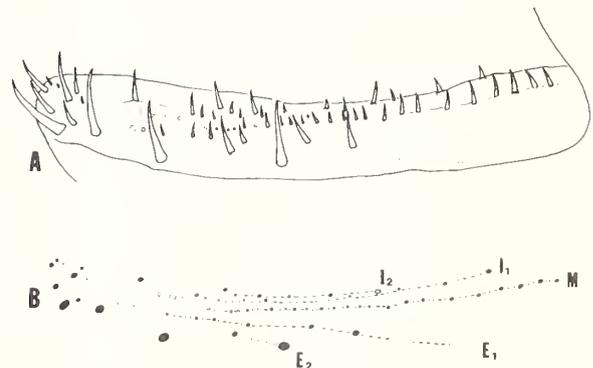


Figure 51. *Gigantactis herwigi*, holotype, female, 262 mm, ISH 972/68; A. Dentary teeth, left lateral view; B. Diagrammatic representation of dentary-tooth pattern. E = external series; M = median series; I = internal series.

of 110-mm specimen with distal filaments lost; esca of 35-mm specimen with about 8 distal filaments.

Number of teeth on each premaxilla increasing with standard length from 3–5 in smaller specimens to 23 in largest, those in posterior part of jaw turned forward (Fig. 53, Table 14); longest premaxillary tooth 0.6–1.6% SL. Number of dentary teeth varying between 18 and 31 in 6 largest specimens, those in posterior part of jaw arranged in 2 longitudinal series (Fig. 53; in the larger specimens, teeth of the second external, and a few of the first internal series are present more anteriorly in the jaw).

Dorsal-fin rays 5–6, anal-fin rays 5–6, pectoral-fin rays 17–20 (Table 2); skin coverage of proximal part of caudal fin less developed than in most other species (Fig. 41), rays free nearly to base, skin nearly cylindrical without connecting membranes; longest caudal-fin rays (second and seventh) 26–37% SL, only slightly longer than intermediate rays.

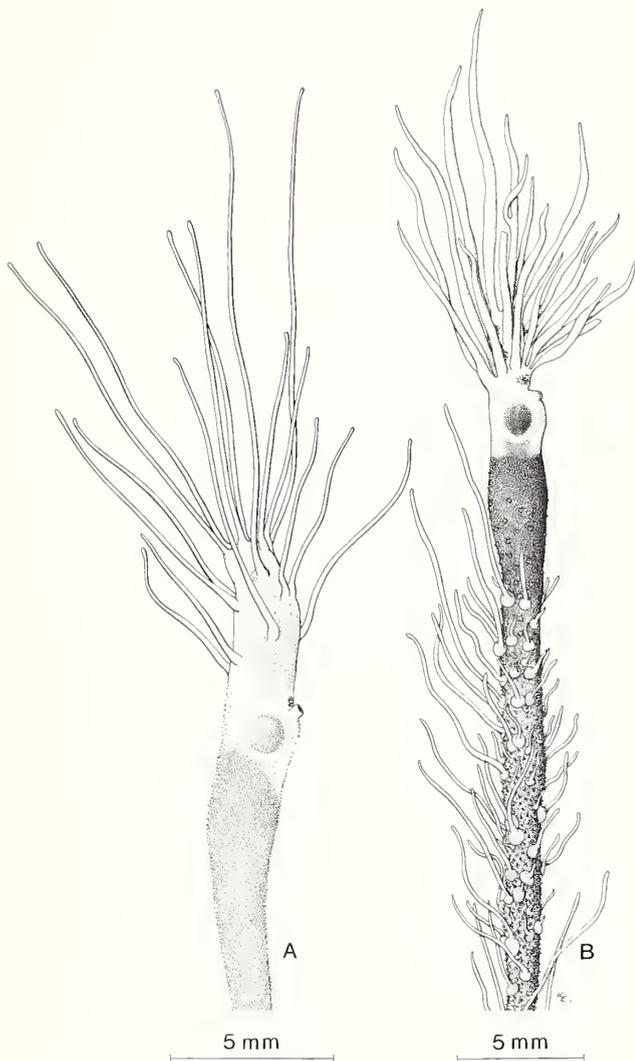


Figure 52. Escae of *Gigantactis macronema*, left lateral views: A. 232 mm, ISH 1596/71; B. 354 mm, LACM 30599-20. Drawn by K. Elsman.

DISTRIBUTION. *Gigantactis macronema* is known from the north and south Atlantic, from the eastern Pacific just north and west of the Hawaiian Islands, and from off the coasts of southern California and Baja California (Fig. 67). The material was captured by open gear fished at maximum depths of between 650 and 2500 m.

COMMENTS. *Gigantactis macronema* is one of a number of *Gigantactis* species that have an illicium that is more than twice the standard length (Table 1). These forms, here referred to as the *G. macronema* group, are further characterized by the absence of filaments on the proximal part of the esca bulb and in having relatively small dentary teeth (those in the posterior part of the jaw in 2, rarely 3 longitudinal series) and a caudal fin with weakly developed skin coverage (the second and seventh caudal rays are the longest, usually 30–35% SL, but only slightly longer than the intermediate rays). *Gigantactis macronema* differs from the other three members of the *G. macronema* group in the length of the illicium (less than 275% SL in the other members) and in the size, shape and pigmentation of the distal prolongation of the esca bulb (dark and tapering in *G. savagei*; with a distal pigmented patch and only slightly raised in *G. microdontis*; distal prolongation absent in *G. ios*). It further differs from *G. microdontis* and *G. ios* in the length of the dentary teeth (the longest in these species is 1.1–1.6% SL, average 1.3% SL).

The esca of the holotype of *G. macronema* was not described in the original description (Regan 1925). A well-developed distal prolongation of the esca bulb and some slender distal filaments, however, are shown in an illustration provided by Regan (1926, pl. 11). The esca is now dehydrated and shrunken so that the position and the number of filaments of the distal

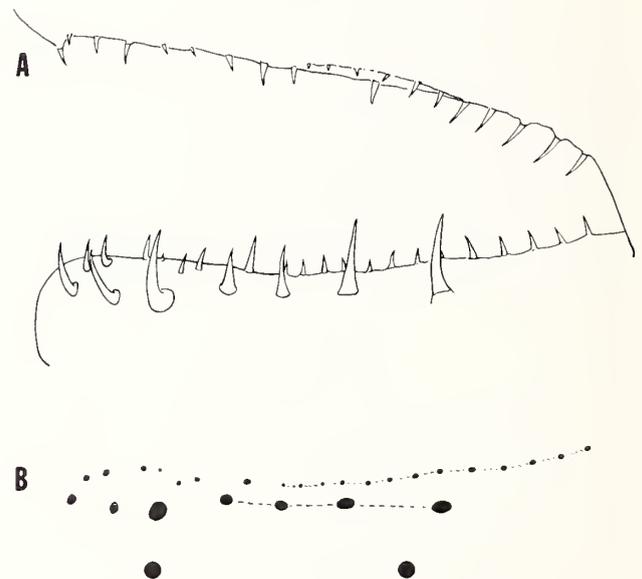


Figure 53. *Gigantactis macronema*, female, 354 mm, LACM 30599-20: A. Premaxillary and dentary teeth, left lateral view; B. Diagrammatic representation of dentary-tooth pattern. E = external series; M = median series.

prolongation is difficult to ascertain; the remains of at least eight filaments are present. Because of the poor condition of the holotype, the allocation of our material to this species is open to some doubt. However, all differ significantly from material of the other three species of the *G. macronema* group in illicial length (in addition to other differences discussed above).

The 62-mm specimen (lacking an esca) is tentatively referred to this species because of the great length of the remaining part of the illicium (281% SL), which appears to have been broken some distance below the esca.

Gigantactis savagei new species

Figures 54, 55, 67; Tables 1, 2, 15

MATERIAL. Three females: two metamorphosed (56–150 mm), and one in metamorphosis (19 mm).

Holotype: LACM 9706-41, 150 mm, 31° 40'N, 120° 23'W, 0–650 m.

Paratypes: LACM 37080-1, 56 mm, Hawaii, leeward Oahu, 0–1250 m; LACM 37520-1, 19 mm, Hawaii, leeward Oahu, 0–985 m. The following material, only tentatively referred to this species, is not included in the description below (but data given in Table 15): LACM 9589-30, 33 mm, 29° 01'N, 118° 00'W, 0–650 m; LACM 9652-32, 44 mm, 31° 31'N, 118° 26'W, 0–500 m; SIO H53-340, 38 mm, 41° 18'N, 168° 21'E, 0–1640 m.

DIAGNOSIS. Metamorphosed females of *G. savagei* differ from those of other species of the genus in having the following combination of characters: illicial length 165–268% SL; esca bulb with a darkly pigmented, tapering distal prolongation; 10–18 narrow, distal filaments; esca papillae absent; proximal esca

filaments absent; dentary teeth short (longest 1.7–2.1% SL), arranged posteriorly in 2–3 longitudinal series; length of caudal-fin rays less than 35% SL; skin coverage of proximal part of caudal fin weakly developed, caudal-fin rays free nearly to base.

Males unknown.

Larvae unknown (probably included in *Gigantactis* Larval Group B).

DESCRIPTION. Illicium without filaments, length variable and unrelated to SL, nearly cylindrical throughout. Esca bulb club-shaped, proximal part pigmented and spinulose, without filaments; tapering, distal prolongation darkly pigmented (except area under swollen bases of filaments), distal filaments not arranged in a distinct pattern, largest and most numerous at tip, each with a series of small swellings throughout length; 18 distal filaments in holotype (8 longest present at tip), 10 in metamorphosed paratype (5 longest at tip); tissue between oval swellings very thin and flexible (Fig. 54).

Number of premaxillary teeth 7–14 (longest 0.8–1.4% SL); number of dentary teeth 17–18 (Fig. 55, Table 15).

Dorsal-fin rays 5–6, anal-fin rays 5–6, pectoral-fin rays 18–20 (Table 2); skin coverage of proximal part of caudal fin less developed than in most other species, rays free nearly to base, skin nearly cylindrical without connecting membranes; longest caudal-fin rays (second and seventh) 30–35% SL, only slightly larger than intermediate rays (Table 15).

The 19-mm metamorphosed stage (LACM 37520-1) has relatively shorter illicium; esca with conical, distal prolongation and four distal filaments; some remains of enlarged supraorbital lateral line organs; skin and subdermal pigment absent (possibly bleached away).

Table 14. Counts and measurements in percent of SL of females of *Gigantactis macronema*.

Character	LACM 37516-1	SIO 73-156	LACM 32745-2	SIO 57-46	LACM 9036-36	Holotype ZMUC P92130	LACM 6902-38	MCZ 51255	ISH 1596/71	LACM 30599-20
Standard length (mm)	34	35	37.5	62	93	98	110	141	232	354
Length										
Illicium	447	340	184 +	281 +	372	350	444	443	432	343
Longest premaxillary tooth	1.2	1.4	0.8	1.6	1.0	0.8	1.2	1.5	1.3	0.6
Longest dentary tooth	3.2	3.1	2.7	3.4	1.9	1.4	3.2	2.7	1.9	1.3
Longest caudal ray	35.0	32.9	29.0	—	30.1	—	37.3	30.5	31.9	26.3
Teeth										
Premaxillary	5	5	3	7	13	11	16	15	16	23
Dentary	7	8	5	17	31	21	22	22	18	29
Dorsal-fin rays	5	5	5	6	5	6	5	5	5	5
Anal-fin rays	5	5	5	6	5	5	6	5	5	5
Pectoral-fin rays	19	17	19	18–19	19	18	18	18	20	18

DISTRIBUTION. *Gigantactis savagei* is known only from the north Pacific Ocean, from off the coast of southern California and the Hawaiian Islands (Fig. 67). This species appears to be a relatively shallow-living form: the holotype was captured in open gear fished above 700 m; the two paratypes were collected by open gear fished at maximum depths of between approximately 1000 and 1250 m.

ETYMOLOGY. *Gigantactis savagei* is named in honor of Jay M. Savage of the University of Southern California in appreciation for his service as principal investigator of grants from the National Science Foundation in support of Ecological Studies of Midwater Fishes in and about Southern California Borderland Region, 1960–1970.

COMMENTS. *Gigantactis savagei* is a member of the *G. macronema* group (Table 1). It differs from the other three mem-

bers of this group (*G. macronema*, *G. microdontis*, and *G. ios*), as well as from all other members of the genus, in esca pigmentation, in the size and shape of the distal prolongation of the esca bulb, and in the structure and position of the distal filaments. *Gigantactis savagei* further differs from *G. macronema* in having a significantly shorter illicium.

The three juvenile specimens (33–44 mm), tentatively referred to this species, represent the *G. macronema* group in illicial length, in lacking proximal esca filaments, and in having relatively short dentary teeth in two longitudinal series (Table 15). In other esca characters, however, they are not in complete agreement with the material here placed within the *G. macronema* group. The largest (44 mm) has nine short distal filaments, each with a series of swellings as is characteristic of *G. savagei*, but the bulb is distally unpigmented and without a distal prolongation. In each of the two smaller specimens, the bulb has a somewhat pigmented, short, conical, distal prolongation with short rudiments of distal filaments (approximately 7 in the 38-mm specimen, indistinct rudiments in the 33-mm specimen), and two additional filaments at the base. From a comparison with specimens of *G. macronema* and *G. microdontis* of a similar standard length, it seems less likely that they represent one of these species than that they represent developmental stages of *G. savagei*.

Gigantactis microdontis new species

Figures 56–58, 67; Tables 1, 2, 16

Gigantactis "sp. 2," Parin et al. 1973:146 (19.5-mm metamorphosal stage).

MATERIAL. Seven females: six metamorphosed (25.5–127 mm), and one in late metamorphosis (19.5 mm).

Holotype: MCZ 52574, 66 mm, 15° 12'S, 75° 44'W, 0–700 m, bottom depth 1060 m.

Paratypes: IOAN uncatalogued, 19.5 mm, 12° 30'S, 87° 45'W, 0–100 m; LACM 32776-2, 25.5 mm, 21° 20'–30'N, 158° 20'–30'W, 0–925 m (juvenile); LACM 32791-3, 38.5 mm, 21° 20'–30'N 158° 20'–30'W, 0–1175 m; LACM 30284-29, 44 mm, 28° 48'N, 118° 10'W, 0–650 m (esca poorly preserved); LACM 9693-34, 118 mm, 31° 45'N, 118° 45'W, 0–600 m (esca previously drawn, but now lost); LACM 32204-2, 127 mm, 28° 20'N, 118° 18'W, 0–650 m (esca poorly preserved).

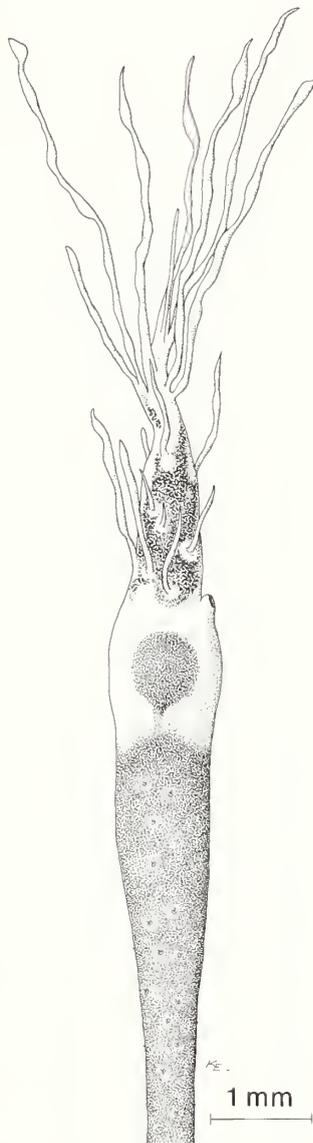


Figure 54. Esca of *Gigantactis savagei*, holotype, 150 mm, LACM 9706-41, left lateral view. Drawn by K. Elsmann.



Figure 55. *Gigantactis savagei*, holotype, female, 150 mm, LACM 9706-41: A. Dentary teeth, left lateral view; B. Diagrammatic representation of dentary-tooth pattern. E = external series; M = median series; I = internal series.

Table 15. Counts and measurements in percent of SL of *Gigantactis savagei*.

Character	Paratype ¹ LACM 37520-1	LACM ² 9589-30	SIO ² H53-340	LACM ² 9652-32	Paratype LACM 37080-1	Holotype LACM 9706-41
Standard length (mm)	19	33	38	44	56	150
Length						
Illicium	~65	273	165	260	268	265
Longest premaxillary tooth	—	1.0	1.2	1.3	1.4	0.8
Longest dentary tooth	<0.5	2.0	2.0	2.5	2.1	1.7
Longest caudal ray	30.0	—	28.2	32.5	30.4	34.7
Teeth						
Premaxillary	0	6	8	6	7	14
Dentary	2-3	11	11	12	17	18
Dorsal-fin rays	6	4	5	5	6	5
Anal-fin rays	6	4	5	5	6	5
Pectoral-fin rays	20	18	18-19	19	18-19	18

¹Metamorphosal stage.

²Tentatively referred to *G. savagei*.

DIAGNOSIS. Metamorphosed females of *G. microdontis* differ from those of other species of the genus in having exceptionally short dentary teeth (longest 1.1–1.6% SL). They further differ in having the following combination of characters: illicial length 216–240% SL (in specimens 38.5 mm and longer); escal bulb with a short, distal prolongation pigmented on distal surface; 8–10 short, distal filaments; escal papillae absent; proximal escal filaments absent; dentary teeth arranged posteriorly in 2 longitudinal series; length of caudal-fin rays less than 45% SL; skin coverage of proximal part of caudal fin weakly developed, caudal-fin rays free nearly to base.

Males unknown.

Larvae unknown (probably included in *Gigantactis* Larval Group B).

DESCRIPTION. Illicium without filaments, nearly cylindrical throughout length. Escal bulb club-shaped, pigmented only near base and on distal part of short, distal prolongation; distal patch of pigment oblong in shape, tapering posteriorly towards pore of photophore; 10 distal filaments in holotype, 9 in paratype, arising from surface of bulb just inside edge of distal pigment patch in 2 nearly parallel, lateral series that meet anteriorly; filaments short, approximately diameter of bulb in holotype, less in paratype, spatulate and compressed distally (Fig. 56); most distal filaments lost in 44-mm and 127-mm specimens (but in illicial length, in the shape of the escal bulb, and remains of the distal prolongation, they are in good agreement with the above description), those remaining differing in

being compressed nearly from base; esca of 118-mm specimen (Fig. 56C, sketched before being lost) lacking a distinct distal prolongation, but bearing 10 filaments of similar shape; late metamorphosal stage and juvenile (19.5 and 25 mm, respectively) with illicium short (33% and 43% SL, respectively), and esca unpigmented with about 8 short, rudimentary filaments close-set on distal surface of bulb (Fig. 56).

Number of premaxillary teeth 8–16 (longest 0.8–1.0% SL). Number of dentary teeth 16–51 (Fig. 57, Table 16).

Dorsal-fin rays 4–6, anal-fin rays 4–6, pectoral-fin rays 17–19 (Table 2); skin coverage of proximal part of caudal fin less developed than in most other species (Fig. 4), rays free nearly to base, skin nearly cylindrical without connecting membranes; longest caudal-fin rays (second and seventh) 30–43% SL, only slightly longer than intermediate rays.

The 19.5-mm IOAN specimen (Fig. 58) is a late metamorphosal stage with nine to ten of anteriormost supraorbital lateral line organs enlarged, largest 10% SL; skin very faintly pigmented, no distinct subdermal pigmentation (possibly bleached).

DISTRIBUTION. *Gigantactis microdontis* is known only from the eastern Pacific Ocean: three records from off southern California, two from the Hawaiian Islands, and two off the coast of Peru (Fig. 67). It appears to be a rather shallow-living form; all material was collected by open gear fished above 1200 m; southern California and Peruvian specimens by gear fished above 700 m.

Table 16. Counts and measurements in percent of SL of females of *Gigantactis microdontis*.

Character	Paratype IOAN uncatalogued	Paratype LACM 32776-2	Paratype LACM 32791-3	Paratype LACM 30284-29	Holotype MCZ 52574	Paratype LACM 9693-34	Paratype LACM 32204-2
Standard length (mm)	19.5	25.5	38.5	44	66	118	127
Length							
Illicium	33.0	43.2	240	226	217	216	226
Longest premaxillary tooth	—	—	1.0	0.9	0.9	0.8	1.0
Longest dentary tooth	—	—	1.2	1.6	1.2	1.1	1.3
Longest caudal ray	30.0	broken	31.4	33.2	33.3	31.8	42.5
Teeth							
Premaxillary	—	—	13	9	8	13	16
Dentary	—	—	28	16	22	28	51
Dorsal-fin rays	4	5	6	5	5	6	5
Anal-fin rays	4	5	6	4	5	6	5
Pectoral-fin rays	17	19	18	18	17	18	19

ETYMOLOGY. The name *microdontis* is derived from the Greek *mikros*, meaning small, and *odontas*, tooth, in reference to the exceptionally small dentary teeth of this species.

COMMENTS. *Gigantactis microdontis* is a member of the *G. macronema* group (Table 1), separated from all other species of the genus by the characters listed for this group (see species account for *G. macronema*); it differs from the other members of this group (*G. macronema*, and *G. savagei* and *G. ios*) in pigmentation, shape and size of the distal prolongation of the escal bulb, and structure and position of the distal escal filaments. It further differs from *G. macronema* in illicial length and from *G. savagei* in the length of the longest dentary tooth.

Gigantactis ios new species

Figures 59, 67; Tables 1, 2

MATERIAL. A single metamorphosed female, the holotype: BMNH 1977.9.13.1, 57 mm, 29° 49' N, 23° 00' W, 1005–1250 m.

DIAGNOSIS. Metamorphosed females of *G. ios* differ from those of other species of the genus in having the following combination of characters: illicial length 256% SL; escal bulb without distal prolongation; a dense group of 14 short distal filaments; escal papillae absent; proximal escal filaments absent; dentary teeth short (longest 1.1% SL), arranged posteriorly in 2 longitudinal series; length of caudal-fin rays less than 35% SL; skin coverage of proximal part of caudal fin weakly developed, caudal-fin rays free nearly to base.

Males unknown.

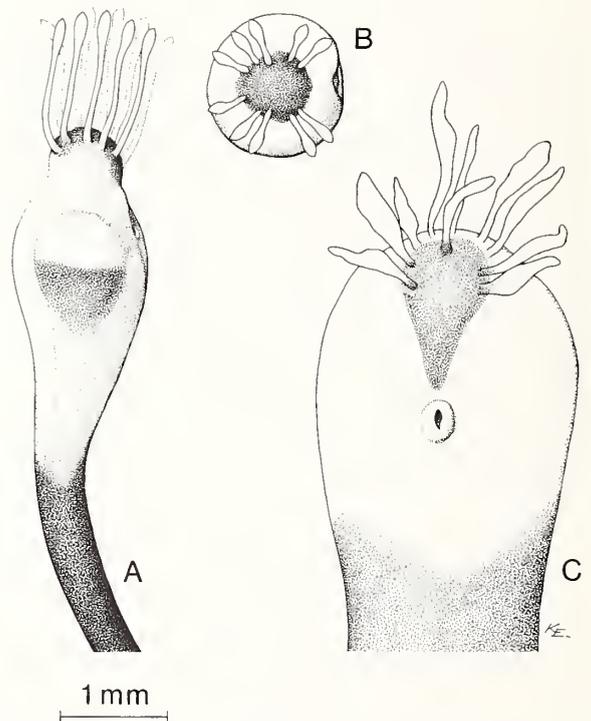


Figure 56. Escae of *Gigantactis microdontis*: A. Holotype, 66 mm, MCZ 52574, left lateral view; B. Holotype, 66 mm, MCZ 52574, dorsal view; C. 118 mm, LACM 9693-34, posterior view. Drawn by K. Elsmann.

Larvae unknown (probably included in *Gigantactis* Larval Group B).

DESCRIPTION. Illicium without filaments. Escal bulb club-shaped; pigment confined to base of bulb except for a small distal spot; distal escal filaments lanceolate with tiny internal, transparent bulbs (Fig. 59).

Premaxillary teeth 16 (longest 0.9% SL); dentary teeth 32.

Dorsal-fin rays 5, anal-fin rays 5, pectoral-fin rays 18 (Table 2); skin coverage of proximal part of caudal fin weakly developed, rays free nearly to base, skin nearly cylindrical without connecting membranes; longest caudal-fin ray (seventh) 31% SL, only slightly longer than other rays.

DISTRIBUTION. *Gigantactis ios* is known only from the holotype collected in a closing trawl between 1005 and 1250 m in the eastern North Atlantic Ocean just southwest of Madeira (Fig. 67).

ETYMOLOGY. The name *ios* (to be pronounced *īos*) is an acronym formed from the initial letters of the Institute of Oceanographic Sciences, Surrey, England, in recognition of important ichthyological contributions made by our colleagues of that institution.

COMMENTS. *Gigantactis ios* is a member of the *G. macronema* group, distinct from other members of the genus in the characters mentioned for this group. It differs from *G. macronema* and *G. savagei* in the same characters that distinguish *G. microdontis*. It is easily separated from *G. microdontis* by the structure, number, and position of the distal escal filaments.

Gigantactis Species *Incertae Sedis*

Gigantactis filibulosus Fraser-Brunner

Gigantactis filibulosus Fraser-Brunner 1935:326 (original description; single specimen, the holotype, BMNH 1934.8.8.92, 25 mm, 53°15'N, 12°28'W, 0–320 m); Waterman 1939b:85 (comparison with *G. longicirra*); Bertelsen 1951:150–152, table 31 (comparison with all known material; comments); Robins and Courtenay 1958:151 (depth distribution); Wheeler

1969:585 (reference to original description); Maul 1973 (listed).

The holotype and only specimen ever referred to this species is a juvenile stage with an undeveloped illicium (84% SL) that gives no indication of what its length might have been when fully developed. The escal bulb is shrunken with no remains of “a slender filament, expanded at tip, on each side of its distal end,” as described and figured by Fraser-Brunner (1935). Among the species recognized here, an esca somewhat similar to this description is found only in *G. microdontis* (Fig. 56); however, this species has about 10 escal filaments. Even if we assume that the pair of filaments present in *G. filibulosus* represents remains of a larger number, the length of the dentary teeth of the holotype (which according to the description and figure reach a length of at least 3% SL) fall well outside the range recorded for *G. microdontis*. Further, since the juvenile holotype has lost the distal portion of the caudal fin and is similar to several *Gigantactis* species in proportions and meristic characters, *G. filibulosus* is regarded as *incertae sedis*.

Gigantactis ovifer Regan and Trewavas

Gigantactis ovifer Regan and Trewavas 1932:93, 95, fig. 152 (original description; single specimen, the holotype, ZMUC P92131, 30 mm, 14°37'N, 119°52'E, 2500 m wire); Fraser-Brunner 1935:326 (comparison with *G. filibulosus*); Waterman 1939b:85 (comparison with *G. longicirra*); Bertelsen 1951:150–152, table 31 (comparison with all known material; comments); Grey 1956:268 (synonymy; vertical distribution); Pietsch 1972a:42, 45 (holotype with five pectoral radials).

The esca of the holotype of *G. ovifer* is damaged. The “two very short terminal appendages” described by Regan and Trewavas (1932:95, fig. 152) represent fragments of torn tissue. The relatively long dentary teeth of this specimen (longest 3.4% SL), and the presence of a few teeth representing a third longitudinal series, only excludes it from the *G. macronema* group. Since it remains doubtful that its illicial length (90% SL) represents the relative length as an adult, and as it in other morphometric and meristic characters is similar to several species of *Gigantactis* recognized here, *G. ovifer* is regarded as *insertae sedis*.

Gigantactis Species Unidentified

METAMORPHOSED FEMALES, Table 17

MATERIAL. Six specimens (23.5–300 mm) with escae and an unknown portion of the illicium lost: IOAN uncatalogued, 24 mm, 20°00'S, 76°42'W (*Gigantactis* “sp. 1” of Parin et al. 1973:146); IOAN uncatalogued, 32.5 mm, VITIAZ St. 7284; ISH 150/68, 177 mm, 33°42'N, 16°19'W, 0–840 m; ISH 1958/71, 292 mm, 10°57'S, 11°20'W, 0–1900 m; LACM 36076-8, 23.5 mm, 2°46'S, 127°54'E, 0–1500 m; LACM 34311-2, 47 mm, off leeward Oahu, 0–800 m; MCZ 52573 300 mm, landed at Gloucester, Massachusetts, ca. 42°30'N, 70°W, 0–310 m.

COMMENTS. All of these specimens lack the diagnostic features of the esca and illicium. The characters given in Tables 1

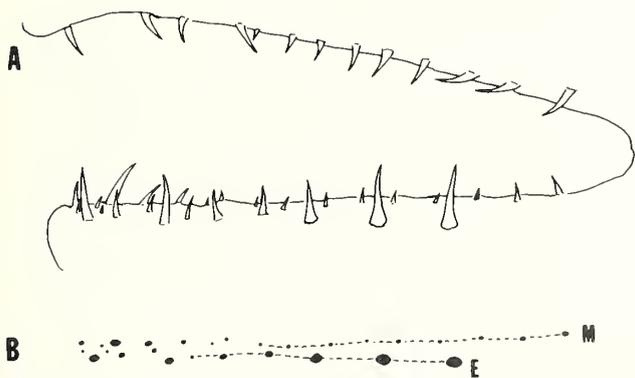


Figure 57. *Gigantactis microdontis*, female, 118 mm, LACM 9693-34: A. Premaxillary and dentary teeth, left lateral view; B. Diagrammatic representation of dentary-tooth pattern. E = external series; M = median series.

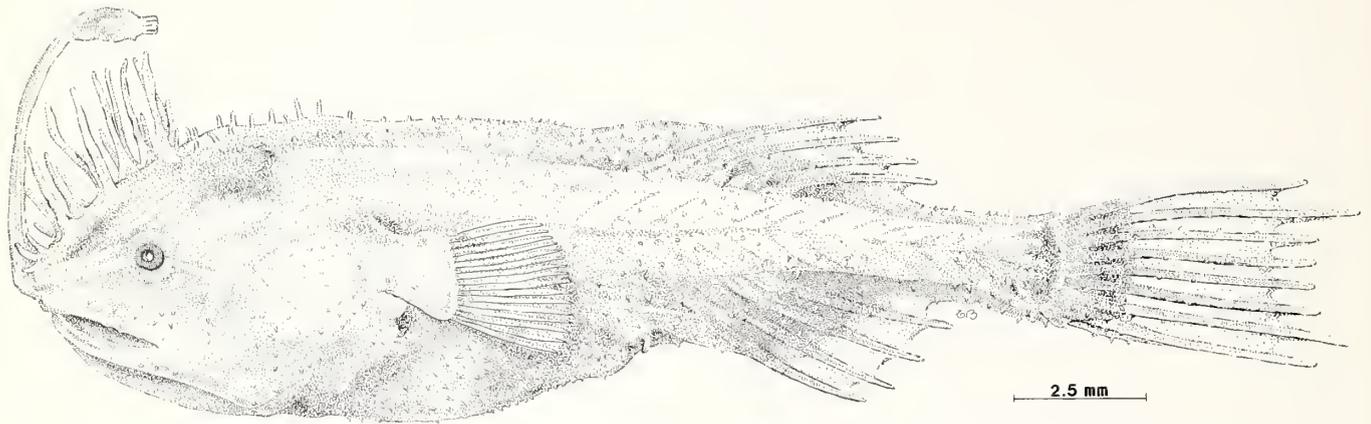


Figure 58. *Gigantactis microdontis*, female metamorphosal stage, 19.5 mm, IOAN uncatalogued. Drawn by Elizabeth Beyerholm.

and 2, combined with observations on tooth patterns and caudal-fin shape, provide an insufficient basis for reliable identification. None of the individuals show a combination of characters that might indicate differences from the species recognized above.

FEMALE METAMORPHOSAL STAGES, Figure 60, Table 18

MATERIAL. Eight specimens, 9–19.5 mm: LACM 34297-2, 14 mm, 21° 20'N, 158° 20'W, 0–1100 m; LACM 32768-3, 19 mm, 21° 20'N, 158° 20'W, 0–900 m; MCZ 54041, 9 mm, 39° 33'N, 42° 47'W, 0–390 m; SAM 27810, 17 mm, 30° 17'S, 31° 25'E, 0–750 m; SIO 61-48, 14.5 mm, 8° 14.5'S, 151° 36.5'W, 0–2500 m; SIO 73-158, 20 mm, 28° 22'N, 155° 02'W, 0–3000 m; ZMUC P921605, 9 mm, 17° 55'N, 24° 35'W, 300 m wire; ZMUC P921655, 19.5 mm, 1° 06'S, 62° 25'E, 4000 m wire.

COMMENTS. Evidence obtained from the pigment patterns of larvae, and from those of identified metamorphosal stages and juvenile females, indicates that some of the unidentified females listed above probably represent the metamorphosal stages of species belonging to the *G. vanhoeffeni* group.

Enlarged supraorbital lateral line organs, unique to *Gigantactis*, are present in some female metamorphosal stages (Fig. 58). In the material examined, they are found in nine specimens (11.5–21.5 mm): two unidentified (listed above), three *G. vanhoeffeni*, and one each of *G. longicirra*, *G. elsmanni*, *G. savagei*, and *G. microdontis*. They are absent in ten metamorphosal stages of a similar size range (14.5–29 mm): four unidentified (listed above), three *G. meadi*, and one each of *G. perlatus*, *G. golovani*, and *G. gargantua*, as well as in the two 9-mm specimens that represent Larval Group D (see Fig. 60). The occurrence of this type of organ thus seems unrelated to the supposed relationships of the species, being present in *G. vanhoeffeni*, but absent in *G. meadi*, the most similar species

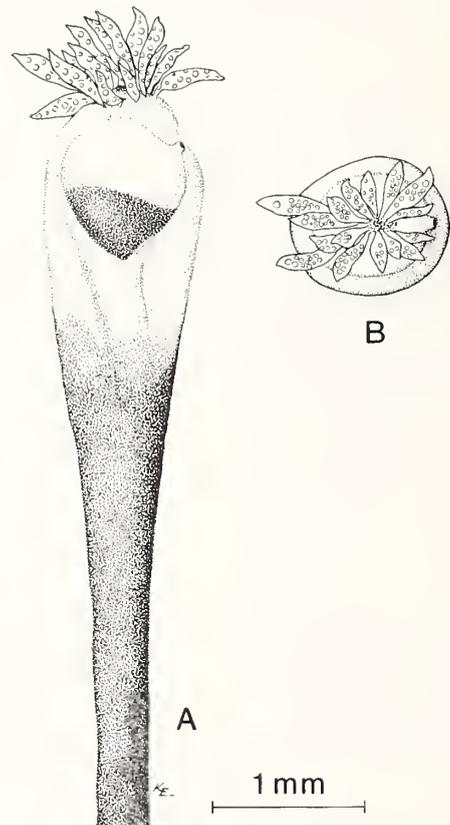


Figure 59. Esca of *Gigantactis ios*, holotype, 57 mm, BMNH 1977.9.13.1: A. Left lateral view; B. Dorsal view. Drawn by K. Elsmann.

within the *G. vanhoeffeni* group (see "Sensory Structures" in the general description).

MALES, Figures 26A, 61, 62, 68; Table 19

Characters previously used to separate *Gigantactis* larvae into groups (the concentration of subdermal, dorsal, and peritoneal pigment and median-fin ray counts; Bertelsen 1951:148) were of limited use in separating the males. The two specimens here referred to *G. longicirra* on the basis of their high dorsal-fin counts agree with larval "Type-C" of Bertelsen (1951:150, fig. 99E-F) in having weakly developed pigmentation. In the remaining material, the density of subdermal melanophores was relatively great but varied without significant relation to other characters. This variation is due to ontogenetic changes but also is probably caused by different preservation and storage times allowing for an unequal loss of pigment.

The size of the olfactory organs, used to distinguish other ceratioid males (Bertelsen 1951), also proved to be of little importance in distinguishing *Gigantactis* males. The thin, fragile skin covering the olfactory lamellae is torn or deformed in most of the specimens so that the only reliable measurement of size is the length of the series of olfactory lamellae (this length varied from 0.8 to 1.8 mm without any significant relation to other characters); but even in the best preserved males, the size of the nostrils of left and right sides differs significantly. There is the impression, however, that the anterior nostrils are slightly smaller and more narrow than the posterior nostrils and have a depth of approximately one-half the length of the series of olfactory lamellae.

The final results of a thorough investigation provided five characters that can be used to separate *Gigantactis* males into groups: (1) eye diameter, (2) dermal pigmentation, (3) subdermal pigmentation (used to separate a single specimen), (4) presence or absence of skin spines, and (5) fin-ray counts (the only character found in males that is also useful in distinguishing species based on females). In evaluating their significance, changes in these characters during metamorphosis were considered in view of the fact that (1) in the larvae the skin is unpigmented and naked, (2) the eyes of larvae are normally developed and relatively large, and (3) the olfactory organs of larvae are small (with few olfactory lamellae) and occupy a lateral position. To judge the relative stage of development, the testes of each specimen were examined and the maximum diameter of the larger of the pair was measured (since each testis is more or less pear-shaped, tapering into a stalk of variable length, no useful length measurement could be obtained). On this basis the material of *Gigantactis* was separated into six groups: *G. longicirra* (two specimens) and five additional groups that are for convenience called Group I through Group V. Group I includes the material referred to as the "naked type" by Bertelsen (1951:152, fig. 102C). Group II includes *G. microphthalmus* (Regan and Trewavas 1932:92, fig. 149; Ber-

telsen 1951:152). The remaining three groups include previously undescribed material. The characters of all known male specimens (including a number of metamorphosed stages that could not be assigned to a group) are compared in Table 19.

Male Group I, Figures 61A, 68; Table 19

Laevoceratias liparis Parr 1927:33, fig. 13 (original description, single specimen); Regan and Trewavas 1932:93 (after Parr 1927); Bertelsen 1951:70, fig. 29 (tentatively referred to Diceratiidae, figure after Parr 1927).

MATERIAL. Ten specimens, 15–22 mm.

Holotype of *Laevoceratias liparis*: BOC 2013, 17 mm, 24° 11' N, 75° 37' W, 2440 m wire.

Referred material: GMZA, uncatalogued, 19.5 mm, *Skagerak* 1946, 38° 25' N, 10° 23' W, 5000 m wire; IOS uncatalogued, 22 mm, 31° 51' N, 63° 47' W, 1260–1500 m; LACM 33316-3, 16.5 mm, Hawaii, leeward Oahu, 0–1100 m (cleared and stained); LACM 35668-2, 19 mm, 21° 20–30' N, 158° 20–30' W, 0–1000 m; LACM 30199-26, 17.5 mm, 31° 48' N, 119° 48' W, 0–1320 m (stained); SIO 68-490, 17 mm, 29° 07' N, 178° 05' W; SIO 70-336, 21.5 mm, 18° 49' N, 124° 22' E, 0–1525 m; USNM 218615, 15 mm, 32° 27' N, 64° 17' W, 0–1536 m; ZMUC P921536, 19 mm, 25° 11' N, 20° 57' W, 5000 m wire.

DIAGNOSIS. Males of Group I differ from other *Gigantactis* males in having the following combination of characters: eyes relatively large, diameter 0.6–0.9 mm (average 0.79 mm); olfactory lamellae 11–12; upper denticular teeth 3 (rarely 2);

Table 17. Counts and measurements in percent of SL of unidentified metamorphosed *Gigantactis* females.

Character	LACM 36076-8	LACM 34311-2	ISH 150/68	ISH 1958/71	MCZ 52573
Standard length (mm)	23.5	47	177	292	300
Length					
Illicium	60+	85+	155+	147+	83+
Longest premaxillary tooth	2.1	2.1	1.4	0.8	0.6
Longest dentary tooth	3.8	3.7	3.2	5.2	0.9
Longest caudal ray	32	28	32	27	40
Teeth					
Premaxillary	7	4	12	23	23
Dentary	12	18	46	63	48
Dorsal-fin rays	7	6	6	6	5
Anal-fin rays	7	5	6	5	5
Pectoral-fin rays	16	17	19–20	17	17

Table 18. Counts and measurements in percent of SL of unidentified female metamorphosal stages of *Gigantactis*.

Character	ZMUC P921605	MCZ 54041	LACM 34297-2	SIO 61-48	SAM 27810	LACM 32768-3	ZMUC P921655	SIO 73-158
Standard length (mm)	9	9	14	14.5	17	19	19.5	20
Illicial length	5	10	19	9	7	24	10	12
Larval teeth	+	+	+	+	+	—	+	—
Post-metamorphic dentary teeth	0	0	0	0	0	11	0	0
Enlarged supraorbital filaments	0	0	7-8	0	0	0	4	0
Subdermal dorsal pigmentation	+	+	faint	+	+	+	+	+
Dorsal-fin rays	6	6	5	5	5	5	6	—
Anal-fin rays	5	6	5	5	6	6	5	—
Pectoral-fin rays	18	19	17	21	21	17	18	—

lower denticular teeth 4 (rarely 3); skin naked, pigmented; dorsal-fin rays 5-6, anal-fin rays 5-7, pectoral-fin rays 18-22 (Table 19).

COMMENTS. The material of Group I differs from other known *Gigantactis* males in length distribution: eight of the ten known specimens are larger than the males of all other groups, ranging from 17 to 22 mm. In two of the smallest known specimens of Group I (15 mm, USNM 218615; 17 mm, SIO 68-490), the anterior nostrils are somewhat separated, but otherwise their metamorphosis seems to be complete. The greatest diameter of the testes of the largest known specimen (22 mm, IOS uncatalogued) is 2.7 mm; in the remaining material, this measurement varies disproportionately with standard length from 0.8 to 2.2 mm.

Male Group II, Figures 61B, 68; Table 19

Teleotrema microphthalmus Regan and Trewavas 1932:93, fig. 149 (original description, single specimen).

Gigantactis microphthalmus Bertelsen 1951:146, 152, 153, figs. 102C, 103E, table 32 (new combination; comparison with all known material).

MATERIAL. Twenty-two specimens: 10.5-15.5 mm.

Holotype of *Teleotrema microphthalmus*: ZMUC P92127, 16 mm, 8°26'N, 15°11'W, 5000 m wire.

Referred material: IOAN uncatalogued, 13 mm, 6°50'S, 103°28'E, 0-2000 m; IOS uncatalogued, 13 mm, 10°45'N, 20°10'W, 0-1250 m; IOS uncatalogued, 13.5 mm, 17°56'N, 24°59'W, 1250-1500 m; IOS uncatalogued, 15.5 mm, 17°43'N, 24°59'W, 1250-1500 m; LACM 36034-1, 2 (12-12.5 mm), 4°58'S, 130°12'E, 0-750 m; LACM 36033-1, 2 (13-14 mm), 4°58'S, 129°43'E, 1000-1500 m; LACM 33324-1, 13.5 mm, 21°20'-30'N, 158°20'-30'W, 0-620 m (cleared and stained); LACM 36032-1, 13.5 mm, 4°27'S, 129°52'E, 0-1500 m; LACM 32800-4, 14 mm, 21°20'-30'N, 158°20'-30'W, 0-

800 m; LACM 32778-1, 14 mm, 21°20'-30'N, 158°20'-30'W, 0-500 m; MCZ 54043, 10.5, 3°55'N, 60°08'E, 0-2000 m; MCZ 54042, 12 mm, 1°20'S, 27°37'W, 0-1100 m; SIO 63-560, 12.5 mm, 00°55'N, 11°29'W, 0-2300 m; SIO 69-354, 13.5 mm, 17°48'N, 143°41'E, 0-525 m; SIO H52-409, 14.5 mm, 01°02'N, 91°46'W, 0-1100 m; SIO 68-482, 14.5 mm, 22°03'N, 171°46'E; SIO 60-232, 15.5 mm, 5°02'S, 135°03'W, 0-2750 m; ZMUC P921537, 11.5 mm, 17°56'N, 64°49'W, 3000 m wire; ZMUC P921533, 14.5 mm, 17°58'N, 64°41'W, 4000 m wire (cleared and stained).

DIAGNOSIS. Group II males differ from other *Gigantactis* males in having the following combination of characters: eyes relatively small, diameter 0.45-0.60 (average 0.54 mm); olfactory lamellae 11-12 (two specimens with 10 and 13, respectively); upper denticular teeth 3 (rarely 4); lower denticular teeth 4 (rarely 3 or 5); skin densely covered with spines, darkly pigmented; dorsal-fin rays 5-6, anal-fin rays 5-7, pectoral-fin rays 16-18 (Table 19).

COMMENTS. In the material of Group II, the diameter of the testes ranges from 0.4-1.9 mm, with some tendency for larger males to have larger testes (diameter less than 1.0 mm in all specimens less than 14 mm SL, greater than 1.5 mm in all material more than 14 mm SL). All known specimens are postmetamorphosal stages.

Male Group III, Figure 68; Table 19

MATERIAL. Two specimens: LACM 34291-3, 14 mm, leeward Oahu, 0-1150 m; LACM 34305-4, 15 mm, leeward Oahu, 0-995 m.

DIAGNOSIS. Group III males differ from other *Gigantactis* males in having the following combination of characters: eyes relatively large, diameter 0.7 and 0.8 mm; olfactory lamellae 10-11; denticular teeth present in only the 15 mm male, 3 upper and 4 lower; skin spinulose, unpigmented; dorsal-fin rays 5-

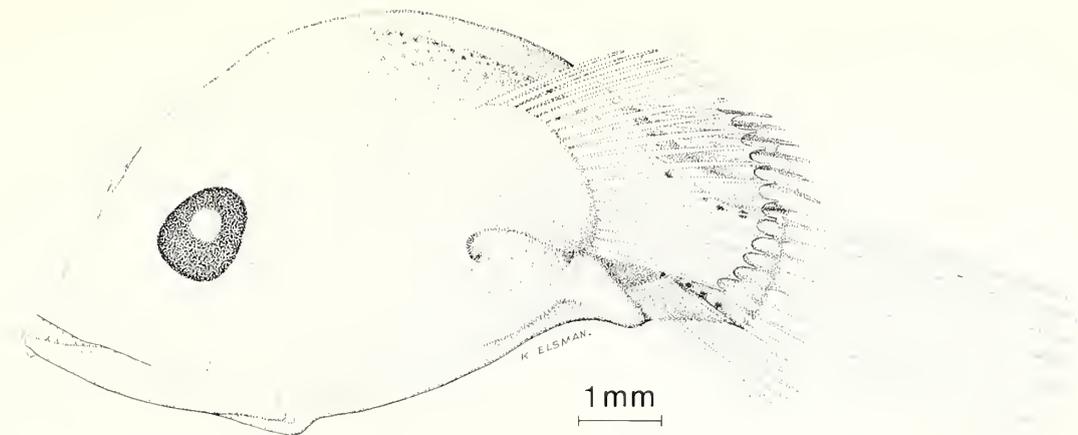


Figure 60. *Gigantactis* sp. female metamorphosal stage, 9 mm, MCZ 54041. Drawn by K. Elsmann.

6, anal-fin rays 5–6, pectoral-fin rays 16–18 (Table 19).

COMMENTS. The diameter of the testes of the Group III males is 1.3 and 1.5 mm. Both specimens are postmetamorphosal stages.

Male Group IV, Figure 68; Table 19

MATERIAL. One specimen in metamorphosis: LACM 36030-1, 16.5 mm, 4° 33'S, 129° 17'E, 0–1100 m.

DIAGNOSIS. The Group IV male differs from other *Gigantactis* males in having relatively low pectoral-fin ray counts (15–15). In addition, this specimen differs in having the following combination of characters: eyes small, diameter 0.5 mm; olfactory organs well-separated with 8 to 9 lamellae; upper denticular teeth 3; lower denticular teeth 4; skin naked, darkly pigmented; dorsal-fin rays 6, anal-fin rays 5 (Table 19).

COMMENTS. The diameter of the testes of the Group IV male is 0.4 mm. The development of the olfactory organs and testes indicate that the specimen is a late metamorphosal stage.

Male Group V, Figures 62, 68; Table 19

MATERIAL. One specimen in metamorphosis: LACM 32775-1, 14.5 mm, 21° 20'–30'N, 158° 20'–30'W, 0–1500 m.

DIAGNOSIS. The Group V male differs from other *Gigantactis* males in having a distinct, V-shaped patch of subdermal pigment on the throat and in having relatively low dorsal and anal-fin ray counts (D. 4, A. 4). In addition, this specimen differs in having the following combination of characters: eyes large, diameter 1.0 mm; olfactory organs in development, not contiguous, with approximately 8 lamellae; denticulars in development with 2 upper teeth and 4 lower teeth; skin naked, unpigmented; pectoral-fin rays 21 (Table 19).

COMMENTS. Despite the relatively large testes of the Group V male (approximately 2 mm long and 1.2 mm wide), the development of the premaxillae (unresorbed), eyes, olfactory organs and denticulars indicate that the specimen is an early metamorphosal stage.

Males Not Referred to Group, Table 19

MATERIAL. Seven specimens, 11.5–14.5 mm: IOS uncatalogued, 13 mm, 30° 14'N, 23° 02'W, 1250–1500 m; LACM

32773-3, 14 mm, 21° 20'–30'N, 158° 20'–30'W, 0–820 m (cleared and stained); LACM 34271-2, 14.5 mm, leeward Oahu, 0–500 m; LACM 32749-4, 13 mm, 21° 20'–30'N, 158° 20'–30'W, 0–1000 m (cleared and stained); SIO 70-327, 11.5 mm, 18° 19'N, 133° 41'E, 0–1500 m; SIO 70-343, 13.5 mm, 18° 06'N, 119° 08'E, 0–1850 m; ZMUC P921534, 11.5 mm, 17° 58'N, 64° 41'W, 4000 m wire.

COMMENTS. The reduction of the premaxillae and development of the denticulars of the 13-mm specimen (LACM 32749-4) indicate that it is a postmetamorphosal stage. It is poorly preserved with torn olfactory organs. The unpigmented and naked skin, combined with its small size, make its reference to any of the groups described above doubtful. The six remaining specimens are in metamorphosis. They have more or less transparent, naked skin and relatively small, well-separated olfactory organs containing eight to approximately ten lamellae. The eyes are unreduced and relatively large (0.75–1.1 mm in diameter), the denticulars are in development (not yet present in the 11.5-mm specimen, ZMUC P921534), and the premaxillae are complete or only slightly resorbed with remains of jaw teeth in some specimens. Fin-ray counts are dorsal 5–6, anal 5–6, pectoral 16–19. The greatest width of the testes ranges from 0.4 to 1.2 mm (Table 19).

Discussion

Except for *G. longicirra*, it is not possible to satisfactorily refer *Gigantactis* males to species based on females. However, there seems little doubt that the best represented Group II contains the males of the most common species, *G. vanhoeffeni*, having the same fin-ray counts. Probably the males of other members of the *G. vanhoeffeni* group are included in Group II as well. The high number of pectoral-fin rays characteristic of Group I indicates that these males correspond to members of the *G. macronema* and *G. gargantua* groups. The fin-ray counts of Group III males are shared with a number of species based on females, thus providing no indication of their identity. The exceptionally low number of pectoral rays in Group IV males (15) corresponds only to *G. golovani*, but since both known females of this species are from the Atlantic and the single Group IV male is from the western Pacific, this evidence seems too slight

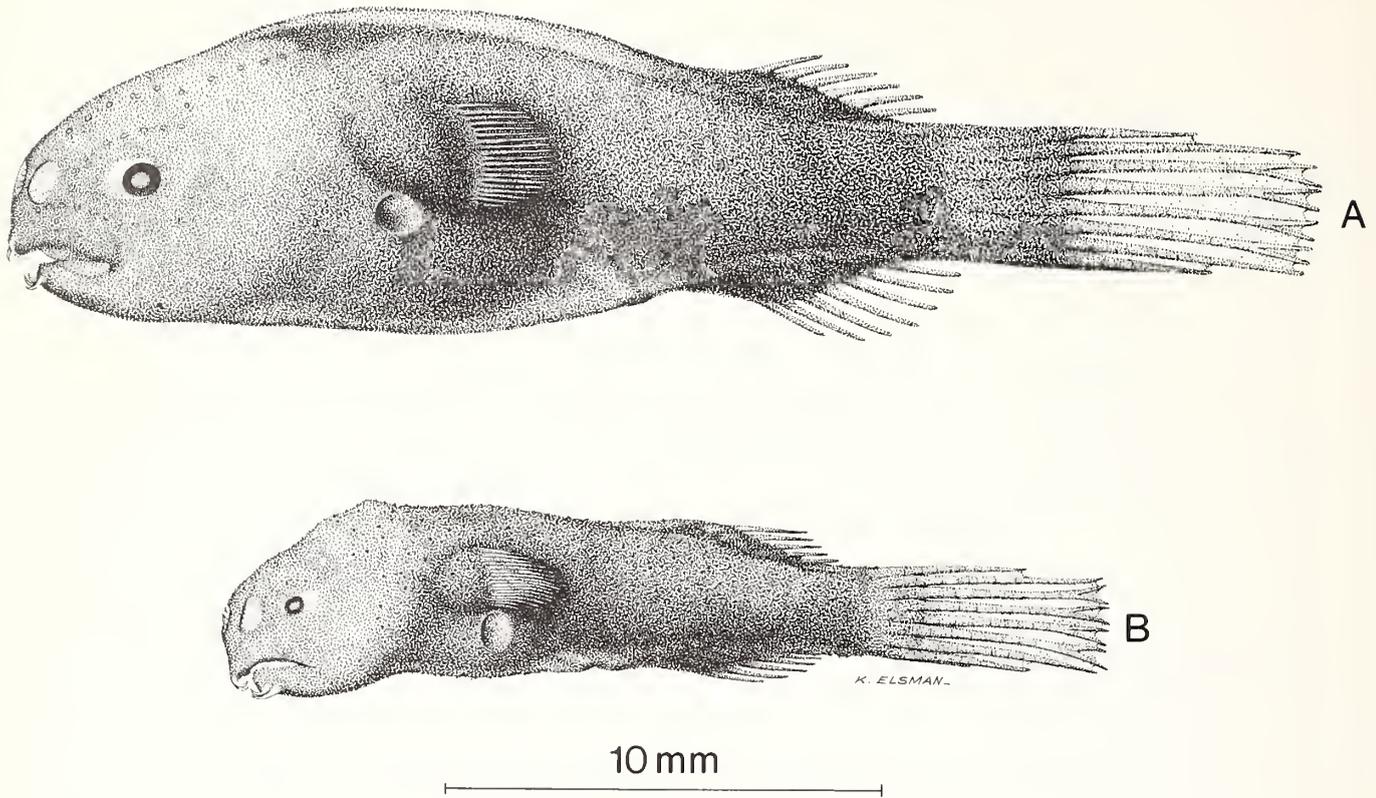


Figure 61. *Gigantactis* sp. males: A. Group I, 22 mm, IOS uncatalogued; B. Group II, 14.5 mm, SIO H52-409. Drawn by K. Elsmann.

to conclude that these forms represent the same species. Similarly, the low number of dorsal and anal rays (4) in the Group V male corresponds only to *G. elsmanni*, *G. savagei*, and *G. microdontis*. Females of *G. savagei* and *G. microdontis* and the Group V male are known only from the eastern Pacific, yet none of the known females have more than 19 pectoral-fin rays, while the Group V male has 21. The presence of a well-developed supraethmoid, and the fact that the subdermal pigment of the Group V male differs significantly from that of all known gigantactinid larvae, males, and juvenile females, possibly indicate that it represents an undescribed genus.

The most conspicuous difference between the groups of *Gigantactis* males is the presence or absence of skin spines. Since this difference is correlated with standard length (spines present in all the smaller specimens, but absent in all the larger specimens), it might be only an ontogenetic difference. This conclusion is clearly contradicted by the difference between Group I and Group II males in pectoral-fin ray counts (Table 19). Furthermore, a decrease in actual eye diameter from the metamorphosal stages (see below) to the small spiny specimens, followed by an increase in the larger naked specimens, is very unlikely. Finally, a comparison of the size of gonads (Table 19)

shows that some of the naked specimens have smaller and probably less advanced testes than most of the spiny specimens.

LARVAE, Figure 68

MATERIAL. In addition to the 233 larvae (2.5–14 mm total length) listed by Bertelsen (1951), we have examined 66 specimens, 4–15 mm total length (18 MCZ, 48 in collections of the National Marine Fisheries Service, Southwest Fisheries Center, La Jolla; see also Maul 1962, 1973).

COMMENTS. Bertelsen (1951) divided the *Gigantactis* larvae into three types (here referred to as groups): Group A, with dorsal and peritoneal pigment well developed, dorsal-fin rays 5–7, anal-fin rays 5–7; Group B, with dorsal and peritoneal pigment weak or absent, dorsal-fin rays 4–6, and anal-fin rays 4–6; and Group C, with pigment as in Group B, but dorsal-fin rays 7–10, anal-fin rays 5–8. The groups, however, could not be sharply distinguished. Several specimens were found to be intermediate in pigmentation, and the chosen limit between groups B and C in fin-ray counts was doubtful. In examination of much of the additional material now available, it was impossible to judge whether differences in the strength of pigmentation in larvae obtained from different sources might be due to

variation in the degree of bleaching caused by differences in preservation and storing time. Furthermore, much of the material is small (2.5–5 mm TL), representing young stages in which the separation between Groups A and B is especially uncertain. No larvae with more than seven dorsal rays were found. For these reasons, the attempt to separate *Gigantactis* larvae into distinct groupings failed. Nevertheless, combined with the much greater information on the genus now available, a reexamination of the larvae revealed some new facts.

Larval Group A

Among the identified female metamorphosal stages (representing seven of the 16 recognized species of *Gigantactis*), only those of *G. vanhoffeni* and *G. meadi* have a well-developed dorsal group of subdermal pigment. Furthermore, distinct remains of this pigment were found under the darkly pigmented skin of the juvenile specimens of *G. gibbsi* (38 mm, USMN 218613) and *G. gracilicauda* (21 mm, ZMUC P921535), the two remaining species of the *G. vanhoffeni* group. This indicates that Group A contains the larvae of species belonging to the *G. vanhoffeni* group, and further infers that this type of pigmentation is unique to the group. If this is correct, five of the eight unidentified female metamorphosal stages listed in Table 18 (LACM 32768-3, SIO 61-48, SIO 73-158, SAM 27810, and ZMUC P921655) also belong to the *G. vanhoffeni* group. Since approximately one-half of the identified *Gigantactis* belong to this group, this possibility is not too unlikely.

Larval Group B

In the identified female metamorphosal stages representing *G. perlatus*, *G. elsmanni*, *G. gargantua*, *G. savagei*, and *G. microdontis*, the dorsal subdermal pigment is either absent or (as in *G. gargantua*) very faint. Since none of the specimens have darkly pigmented skin, the possibility that this lack of subdermal pigment is due to bleaching cannot be excluded. However, it seems probable that the larvae of these species are included among those of Group B (see also "Male Group I").

Larval Group C

Since *G. longicirra* is unique among the recognized species of the genus in having more than seven dorsal-fin rays, the eight larvae with such high dorsal-ray counts referred to Group C by Bertelsen (1951) no doubt represent this species. On the other hand, the two larvae with seven dorsal rays included in this group by Bertelsen (1951) are removed to the unidentified larvae of Group B. The absence of dorsal subdermal pigment in *G. longicirra* is confirmed in the identified female metamorphosal stage and in the two metamorphosed males.

Larval Group D

Two small females (both 9 mm, MCZ 54041 and ZMUC P921605) differ slightly in subdermal pigmentation from other specimens examined. According to the presence of numerous tiny melanophores in the skin and a developing external illicium,

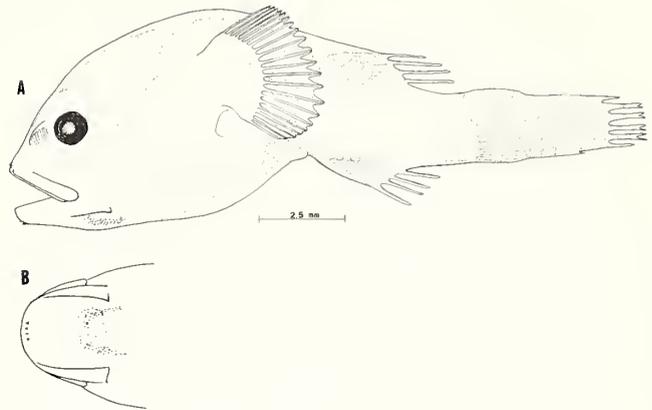


Figure 62. *Gigantactis* male Group V, 14.5 mm, LACM 32775-1: A. Lateral view; B. Ventral view of throat.

um, they represent early metamorphosal stages. Besides having a well-developed dorsal group of subdermal pigment, they both have a short dorsal and ventral series of three to four large melanophores on the caudal peduncle (Fig. 60; see also Bertelsen 1951, fig. 59c). All *Gigantactis* larvae examined lack pigment on the caudal peduncle, whereas metamorphosal stages and juveniles of Group A may have diffuse pigment extending posteriorly to the caudal peduncle. In no other specimens examined is pigment concentrated in large, well-separated melanophores. For this reason, it seems probable that the Group D specimens represent one of the species for which no metamorphosal stages have been yet identified.

Genus *Rhynchactis* Regan

Rhynchactis Regan 1925:565–566 (type species *Rhynchactis leptonema* Regan 1925, by original designation and monotypy).

DIAGNOSIS. The genus *Rhynchactis* is distinguished from *Gigantactis* by having pelvic bones and by having dorsal-fin rays 3–4 (rarely 5), anal-fin rays 3–4. In addition, metamorphosed females differ in having the following characters: frontals absent; parietals absent; premaxilla represented by an anterior remnant bearing 0–2 teeth; maxilla absent (present in larvae); dentaries with minute teeth or toothless; 2 hypohyals; caudal-fin rays 3–6, branched; skin with minute spines in larger specimens, naked in juveniles; snout truncated, bearing illicium slightly behind tip; esca without bulb.

Metamorphosed males are distinguished from those of *Gigantactis* by having the following characters: diameter of eye 2.4% SL in largest specimens (17–18.5 mm); olfactory lamellae 13–15; depth of nostrils 10–12% SL; upper denticular teeth 4–6; lower denticular teeth 6–7; at least some denticular teeth paired with broad, conical bases; skin naked, weakly pigmented (subdermal pigment as in larvae, see below); pectoral-fin rays 17–19.

Larvae of *Rhynchactis* differ from those of *Gigantactis* in having the following characters: dorsal group of subdermal pig-

Table 19. Counts and measurements in percent of SL of males of *Gigantactis* and *Rhynchactis*.

	Standard length (mm)	Eye diameter		Denticular teeth		Olfactory lamellae			Testes diameter		Fin rays		
		Upper	Lower	Upper	Lower	Number	Series	Length	diameter	D	A	P	
<i>Gigantactis longicirra</i> (naked, unpigmented skin)													
UMML 27412	14	3.5	3	4	4	—	—	—	5.7	9	7	7	18
UMML 27411	14.5	3.1	3	4	4	11	~10	—	4.8	9	7	7	18
<i>Gigantactis</i> Group I (naked, pigmented skin)													
USNM 218615	15	4.3	3	—	—	12	6.7	6.7	8.7	6	6	6	19
LACM 33316-3	16.5	4.8	2+	4	4	11	7.9	7.9	13.3	6	6	6	20
SIO 68-490	17	3.5	2	4	4	11-12	8.8	8.8	4.7	6	6	6	18
BOC 2013 ¹	17	—	3	4	4	—	—	—	—	5	6	—	—
LACM 30199-26	17.5	5.1	3	4	4	—	—	—	8.5	6	5	5	22
LACM 35668-2	19	4.2	3	4	4	12-12	8.9	8.9	8.9	5	5	5	21
ZMUC P921536	19	3.9	3	4	4	12	7.9	7.9	4.2	6	6	6	20
GMZA uncatalogued ²	19.5	—	3	4	4	12	—	—	—	6	5	5	19
SIO 70-336	21.5	3.7	3	3	3	12-12	6.5	6.5	7.9	6	6	6	19
IOS uncatalogued	22	3.6	3	4	4	11-12	5.9	5.9	12.2	6	7	7	19
<i>Gigantactis</i> Group II (spiny, pigmented skin)													
MCZ 54043	10.5	4.8	1+	—	—	—	—	—	11.4	5	6	6	16-17
ZMUC P921537	11.5	5.2	1+	—	—	10-12	7.8	7.8	3.5	6	6	6	17
MCZ 54042	12	5.0	3	4	4	—	—	—	6.7	6	5	5	17
LACM 36034-1	11	4.2	—	—	—	—	—	—	5.0	~6	~5	—	—
LACM 36034-1	12.5	3.6	—	—	—	—	—	—	6.0	~6	~5	—	—
SIO 63-560	12.5	4.0	3	4	4	10+	~11	~11	9.6	6	6	6	~17
IOS uncatalogued	13	3.8	1+	4	4	12-12	~10	~10	8.5	6	6	6	18
LACM 36033-1	13	4.6	—	—	—	12-12	6.2	6.2	6.2	6	5	—	—
IOAN uncatalogued	13	3.4	3	4	4	12-12	~10	~10	8.3	6	6	6	17
LACM 33324-1	13.5	—	3	4	4	—	—	—	—	6	5	5	17
IOS uncatalogued	13.5	4.4	1+	4	4	12-13	9.6	9.6	11.0	6	5	5	18
LACM 36032-1	13.5	4.4	—	—	—	11-11	8.1	8.1	7.4	6	5	—	—
SIO 69-354	13.5	4.4	1+	2+	2+	12-12	8.1	8.1	11.0	6	5	5	16
LACM 36033-1	14	3.6	~3	~4	~4	—	—	—	7.5	~6	~6	—	—
LACM 32800-4	14	4.3	1+	2+	2+	12-12	10.0	10.0	10.0	6	6	6	18
LACM 32778-1	14	4.3	3	4	4	—	—	—	10.0	6	6	6	17

ZMUC P921533	14.5	3.1	3	4	11-12	~7	7.6	5	7	18
SIO H52-409	14.5	4.1	3	5	11	8.3	10.4	5	5	17
SIO 68-482	14.5	4.1	3	3	12	9.0	13.1	6	6	17
ZMUC P92127 ³	14.5	3.4	3	4	12	9.0	7.6	5	5	18
SIO 60-232	15.5	3.2	4	4	10+	5.2	10.3	6	6	17
IOS uncatalogued	15.5	3.9	4	4	12	5.2	11.6	6	6	18
<i>Gigantactis</i> Group III (spiny, unpigmented skin)										
LACM 34291-3	14	5.0	—	—	10-10	—	9.3	6	6	16-17
LACM 34305-4	15	5.2	3	4	11-11	7.3	10.0	5	5	18
<i>Gigantactis</i> Group IV (naked, pigmented skin)										
LACM 36030-1	16.5	3.0	3	4	8-9	5.5	2.4	6	5	15-15
<i>Gigantactis</i> Group V (naked, transparent skin)										
LACM 32775-1	14.5	6.9	2	4	~8	~5.5	8.2	4	4	21
<i>Gigantactis</i> (not referred to group) Metamorphosed										
LACM 32749-4	13	6.2	3	4	—	—	8.5	5	5	18
SIO 70-343	13.5	3.7	~3	~4	11-12	—	—	6	5	—
Metamorphosal Stages										
ZMUC P921534	11.5	6.5	—	2	8-9	—	6.1	6	5	18
SIO 70-327	11.5	6.5	2	1	9-9	6.9	5.2	6	5	16
IOS uncatalogued	13	6.9	—	—	8-9	6.0	10.0	6	6	19
LACM 32773-3	14	7.1	3	3	~10	—	5.0	6	6	17
LACM 34271-2	14.5	6.2	3	4	~8	6.9	8.2	6	6	17
<i>Rhynchactis leptotema</i>										
IOAN uncatalogued ⁴	13	5.4	~5	~5	~12	8.5	1.5	4	4	18
SIO 70-334	15	4.7	—	—	—	—	2.0	—	—	18
SIO 60-243	16.5	4.8	5	6	14	10.4	5.4	4	4	~18
LACM 37519-1	17	2.4	6	7	13	11.8	2.4	4	3	17-18
ZMUC P921732	18.5	2.4	4	6	15	10.1	3.2	4	4	19

¹Holotype of *Laevooceratias liparis* Parr 1927.

²After Nybelin 1948, Bertelsen 1951.

³Holotype of *Teleotrema microphthalmus* Regan and Trewavas 1932.

⁴Metamorphosal stage.

ment very dark and contiguous with peritoneal pigment, but never extending back to base of dorsal fin; length of pectoral fin approximately 50–55% SL.

Rhynchactis leptonema Regan

Figures 2, 3, 7, 9, 10, 11B,C,E, 13B, 14B, 15B, 63, 69;
Tables 20, 21.

Rhynchactis leptonema Regan 1925:565–566 (original description; single specimen); Regan 1926:38, pl. 10, fig. 1 (description after Regan 1925). Regan and Trewavas 1932:95 (after Regan 1925, 1926); Waterman 1939b:84 (comparison with *Gigantactis longicirra*); Bertelsen 1951:153–156, fig. 104, tables 33, 34 (diagnostic characters; addition and description of an adolescent male and 23 larvae; *Dana* material listed); Grey 1956:269 (synonymy; vertical distribution); Pietsch 1972a:42, 45 (holotype with 5 pectoral radials); Becker et al. 1975:327 (additional specimen); Parin et al. 1977:107 (additional larval stage).

MATERIAL. Five metamorphosed females (27–126 mm), 4 metamorphosed males (15–18.5 mm), one male metamorphosal stage (13 mm) and 26 larvae (2.5–20 mm).

Holotype of *Rhynchactis leptonema*: ZMUC P92133, 42 mm, 8°19'N, 44°35'W, 3000 m wire.

Females: IOAN uncatalogued, 32 mm, 19°38'N, 74°40'W, 0–1000 m; IOS uncatalogued, 27 mm, 31°47'N, 63°39'W, 910–1000 m; ISH 2560/71, 126 mm, 7°32'N, 20°54'W, 0–1300 m; ISH 2332/71, 60 mm, 1°04'N, 18°22'W, 0–2100 m (cleared and stained).

Males: IOAN uncatalogued, 13 mm, 9°56'S, 86°27'E, 0–4160 m; LACM 37519-1, 17 mm, 8°00'N, 164°33'W, 0–1400 m, bottom depth 4900 m (cleared and stained); SIO 60-243, 16.5 mm, 10°09'S, 147°08'W; SIO 70-334, 15 mm, 19°02'N, 125°46'E, 0–1350 m; ZMUC P921732, 18.5 mm, 7°46'S, 167°10'W, 4000 m wire.

Larvae: IOAN uncatalogued, 20 mm, 11°23'N, 142°51'E, 0–1500 m; LACM 33316-2, 18 mm, 21°20–30'N, 158°20–30'W, 0–1100 m; Ocean Research Institute, University of Tokyo, uncatalogued, 10.5 mm, 17°01'N, 126°16'E, 350 m wire; ZMUC P921732-P921754, 23 (2.5–7 mm SL, 4–10 mm total length), listed by Bertelsen (1951) (P921751, 7 mm, cleared and stained).

DIAGNOSIS. As for the genus.

DESCRIPTION OF FEMALES. Illicium of four specimens (in which it appears complete) 118–177% SL, gradually increasing in proportion to standard length (Table 20); 27-mm specimen (IOS uncatalogued) with unpigmented, naked skin of distal part of illicium intact (Fig. 2), but lacking an esca bulb containing photophore (in contrast to other gigantactinids and most other ceratioids); distal part of illicium of 27-mm specimen bearing distal group of four tiny filaments, each with minute distal swelling (about 0.1 mm in diameter), and 11 short side-branches distributed along distal 9 mm (28% of its length), some with bifurcated tip, others (the two most distal) with minute swelling; core of each side-branch opaque, containing (according to histological section, Fig. 3) dense concentration of cells with large nuclei surrounded by blood vessels; illicium of 42-mm holotype appearing complete, but skin of distal portion dehydrated, shrunken, lacking trace of branches or filaments; 60-mm specimen (ISH 2332/71) with skin of distal portion of illicium lost; 126-mm specimen (ISH 2560/71) with torn bases of about 12 posterior side-branches on partially abraded skin of distal 45 mm (20% of its length); lower-jaw teeth absent, dentary strongly reduced in all metamorphosed specimens; few small, curved teeth present anteriorly in reduced premaxillae of specimens 27–60 mm (on each side, two teeth in 27-mm specimen, one in 42- and 60-mm specimens), premaxillary teeth absent in 126-mm specimen (Table 20, see Comments below).

Dense pavement of white, papillae-like glands covering inner

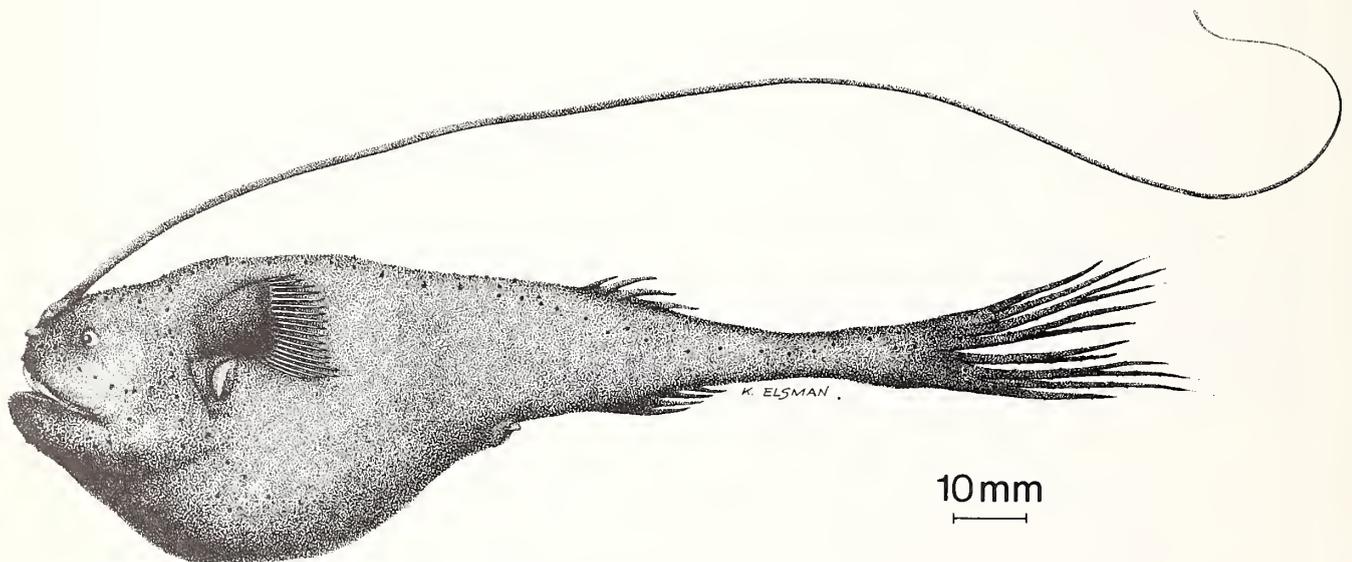


Figure 63. *Rhynchactis leptonema*, 126 mm, ISH 2560/71. Drawn by K. Elsmann.

Table 20. Counts and measurements in percent of SL of females of *Rhynchactis leptonema*.

Character	LACM 33316-2	IOS uncata- logued	IOAN uncata- logued	Holotype ZMUC P92133	ISH 2332/71	ISH 2560/71
Standard length (mm)	18	27	32	42	60	126
Illicial length	8	118	lost	158	166	177
Longest caudal ray	33	37	31	36	broken	42
Premaxillary teeth	2	2	2	1	1	0
Dorsal-fin rays	4	4	4	3	4	4
Anal-fin rays	4	3	4	4	4	4
Pectoral-fin rays	19	17?	17?	18?	19	18

surface of upper and lower jaw present in all metamorphosed females, each gland with more or less distinct central groove and outlined by pigmented skin (Fig. 9); histologically each gland consisting of simple short tube with more or less pigmented wall and internally covered with large glandular cells that nearly fill lumen of tube (Fig. 10).

Caudal fin distinctly divided into upper and lower portions containing four and five fin rays, respectively; longest caudal rays (second and seventh) 31–42% SL in five specimens in which they appear complete (Table 20).

Skin of 126-mm specimen densely covered with minute spines, largest spines with length and diameter of base nearly 0.1 mm; spines apparently absent in all other specimens.

Pectoral-fin rays 17–20, usually 18–19 (Tables 20, 21).

DESCRIPTION OF MALES AND LARVAE. See generic diagnosis.

DISTRIBUTION. *Rhynchactis leptonema* has a wide horizontal distribution in all three major oceans of the world between approximately 32°N and 12°S (Fig. 69). Vertically, metamorphosed specimens appear to inhabit waters between about 800 m and some unknown lower limit. A 27-mm female was captured in an opening-closing net near Bermuda between approximately 910–1000 m.

COMMENTS. Regan's (1925, 1926) description of the holotype of *R. leptonema* having "minute teeth in several series" in addition to a "pair of anterior canines" could not be confirmed. This may be due to a misinterpretation of the series of oral glands that line the inner walls of the upper and lower jaws of all known metamorphosed females (see "Description of Females," Fig. 9). The glandular nature of these structures is clearly shown in histological sections (Fig. 10). Properly fixed material for a more thorough investigation that might reveal the function of the gland was unavailable.

Males of *R. leptonema* are represented by five specimens (13–18.5 mm) including the 18.5-mm specimen (ZMUC P921732) described by Bertelsen (1951). They differ from all known *Gigantactis* males in the number and shape of the denticular teeth (Fig. 15), the number of olfactory lamellae, and in subdermal pigmentation (see *Rhynchactis* diagnosis, Table 19).

The diameter of the testes ranges from 0.2 to 0.6 mm. These are smallest in the 13-mm specimen (IOAN uncatalogued), which according to its rudimentary denticulars and small olfactory organs is in metamorphosis.

Despite its large size, the 18-mm larval female (LACM 33316-2) shows no sign of metamorphosis except for a slight prolongation of the illicial rudiment (8% SL) and some reduction in the relative length of the pectoral fins (approximately 45% SL). The skin is unpigmented, and the bones of the jaws are unreduced and bear larval teeth; the subdermal pigmentation is somewhat dense but has the same distribution as in the largest, previously described larval female (7 mm; Bertelsen 1951, fig. 104A).

DISTRIBUTION

The family Gigantactinidae is widely distributed throughout all the major oceans of the world in a broad belt limited by the Arctic and Antarctic Polar Fronts, with northern and southernmost records at approximately 63°N and 63°S, respectively (Figs. 64–69). The larvae and males, however, have only been caught in tropical and subtropical waters (as in all ceratioids, Bertelsen 1951), with northern and southernmost records at about 48°N and 34°S, respectively (Figs. 68, 69). Gigantactinids are not found in the Gulfs of California or Mexico, and,

Table 21. Frequencies of fin-ray counts for *Rhynchactis leptonema* (uncertain counts excluded).

	Dorsal			Anal		Pectoral			
	3	4	5	3	4	17	18	19	20
Females	1	5		1	5	2	2		
Males		4		1	3	3	1		
Larvae	7	16	1	9	15	7	7	5	3
Total	8	25	1	11	23	7	12	8	3

like all other ceratioids, they are unknown from the Mediterranean Sea (Bertelsen 1951).

Gigantactinids, in common with some ceratioid genera (e.g., *Dolopichthys*, Pietsch 1972b), are not particularly restricted to the more organically productive water and have broad geographic ranges, occurring throughout the central North Atlantic and central Pacific. This situation contrasts with that found for yet other ceratioid genera (e.g., *Oneirodes*, Pietsch 1974), whose species tend to avoid less productive regions and are, for the most part, restricted geographically into oceanic areas defined by distinct physiochemical and biological parameters. With the exceptions of *G. meadi*, *G. gracilicauda*, and possibly *G. golovani*, no species that is known from more than three individuals is restricted to a single water mass.

Since the majority of collections of gigantactinids were made with nonclosing nets, the actual depth of capture is unknown. Furthermore, because sample sizes are small, a statistical treatment of the nonclosing net data is impossible. Assuming, however, that most specimens were caught at depths where gear was fished for the longest period of time, vertical distributions may be roughly estimated by referring to the maximum depth reached by gear for each capture. On this assumption, metamorphosing and metamorphosed members of the Gigantactinidae may be taken anywhere between 500 m and some unknown lower limit exceeding 3000 m, but they are commonly found between roughly 1000 and 2500 m. Although some vertical separation of sympatric species may exist, such forms probably overlap in vertical range wherever they are found.

Four of the 17 recognized species of the family (*G. gibbsi*, *G. watermani*, *G. herwigi*, and *G. ios*) are so poorly represented

that the boundaries of their distributions are unknown; these are not dealt with further. *Gigantactis kreffti*, *G. elsmanni*, and *G. gargantua*, known from four, two, and seven specimens, respectively, are mentioned because of unusual disjunct distributions (Figs. 65, 66): *G. kreffti* with three individuals from the South Atlantic off the tip of Africa, one from off Japan; *G. elsmanni* with one from the mid, tropical Atlantic, and one from the Pacific sector of the Southern Ocean below 60°S; and *G. gargantua* with six specimens from the eastern north Pacific and one from the eastern south Indian Ocean. It is assumed that, when these three species are better known, they will prove to be wide-ranging forms. Horizontal ranges and, to a lesser extent, vertical ranges for the remaining ten species (*G. longicirra*, *G. vanhoeffeni*, *G. meadi*, *G. gracilicauda*, *G. paxtoni*, *G. golovani*, *G. macronema*, *G. savagei*, *G. microdontis*, and *R. leptonema*) are known with some confidence. Three of these have cosmopolitan distributions, two are known from the Atlantic and eastern Pacific, two from the tropical Atlantic, one is Indo-west Pacific, two are confined to the eastern Pacific, and one is endemic to the Southern Ocean.

COSMOPOLITAN FORMS

Gigantactis vanhoeffeni, *G. perlatus*, and *R. leptonema* are wide-ranging forms collected from all three major oceans of the world between approximately 63°N and 35°S (Figs. 64, 65, 69). Vertically, larger metamorphosed specimens of all three species coexist between approximately 800 m and some unknown lower limit (a 232-mm *G. vanhoeffeni*, UMML 23973, was taken in an otter trawl fished on the bottom at 3184 m). On

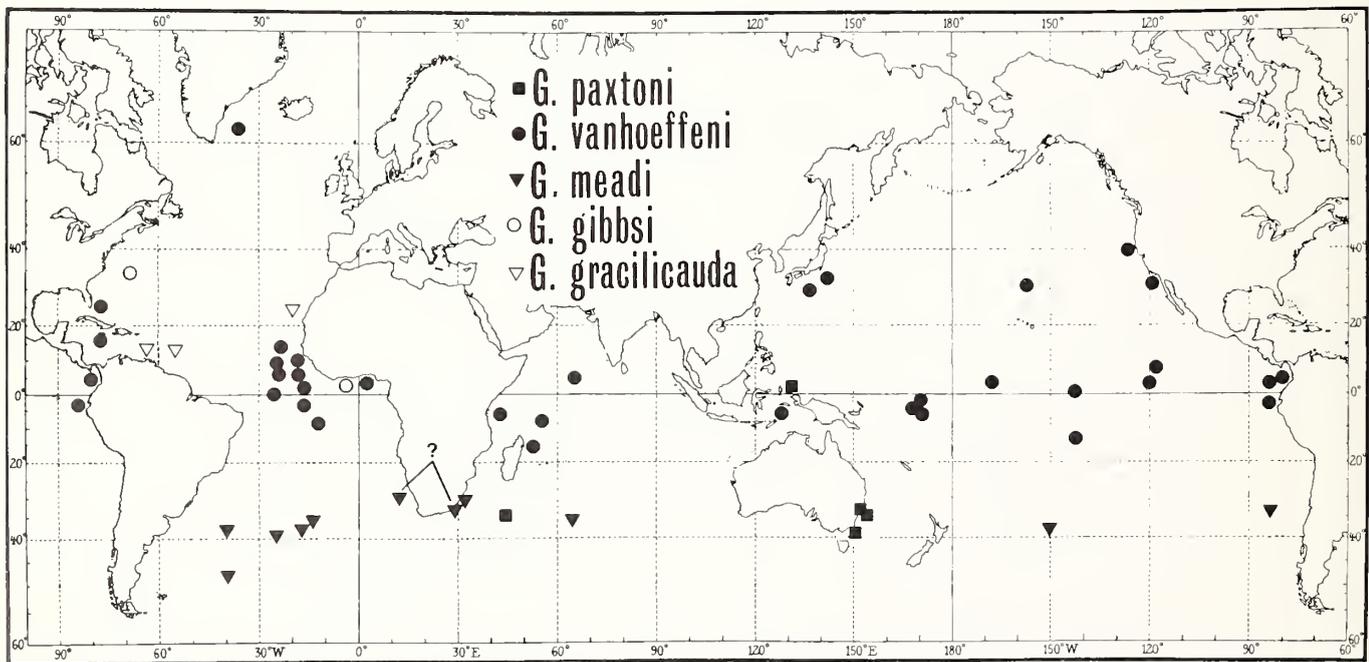


Figure 64. Distributions of five species of *Gigantactis* (*G. vanhoeffeni* group). A single symbol may indicate more than one capture.

the other hand, relatively small individuals have been captured with closing nets at considerably shallower depths: a 32- and 24-mm *G. vanhoeffeni* between 550–815 m and 656–1000 m, respectively; a 32-mm *G. perlatus* between 670–805 m; and a 27-mm *R. leptonema* between 910–1000 m.

ATLANTIC AND EASTERN PACIFIC FORMS

Gigantactis longicirra and *G. macronema* are wide-ranging forms in the North and South Atlantic and in the eastern Pacific (Figs. 66, 67). It is predicted that, as these species become better known, they will prove to have cosmopolitan distributions. Vertically, the metamorphosed material of both forms was captured with gear fished at maximum depths of between 650 and 2300 m. Two rather large *G. macronema* (110 and 354 mm) were caught in the mixed Transition Water off the coast of southern California in gear fished above 630 m. The 39-mm holotype of *G. longicirra* was collected in a closing net at 1000 m.

TROPICAL ATLANTIC FORMS

Gigantactis gracilicauda and *G. golovani*, each known from only three specimens, have been captured only from the tropical Atlantic; *G. gracilicauda* is known from both sides of that ocean, *G. golovani* is perhaps restricted to the eastern side (Figs. 64, 65). Small sample sizes make it difficult to say with any certainty, but *Gigantactis gracilicauda*, having been taken in gear fished open at maximum depths of between 2000 and 2500 m, is perhaps a deeper living form than most other gigantactinids. On the other hand, *G. golovani* may be a relatively

shallow-living form; the 179-mm holotype was taken between the surface and 660 m, the 153-mm paratype between the surface and 1550 m.

INDO-WEST PACIFIC FORM

Gigantactis paxtoni is represented by eight specimens: six collected off the southeast coast of Australia near the northern boundary of the Subantarctic Water Mass, one from the eastern South Indian Ocean, and one from the western tropical Pacific off the northwest coast of New Guinea (Fig. 64). With the exception of a single specimen captured in a bottom trawl at 1210 to 1260 m, the material was collected by pelagic trawls fished open at maximum depths of 540 to 1500 m. These relatively shallow depths contrast with those of *G. meadi* (maximum depths between 1850–2000 m), whose horizontal distribution overlaps that of *G. paxtoni* (Fig. 64).

EASTERN PACIFIC FORMS

Gigantactis savagei and *G. microdontis* are all more or less restricted to the eastern Pacific Ocean (Fig. 67). *Gigantactis savagei* is known only from southern California, the Hawaiian islands, and a single record from the central North Pacific; and *G. microdontis* is known from off southern California and two records from the eastern South Pacific off the coast of Peru. Both species live sympatrically at relatively shallow depths (500 to 650 m) in the mixed Transition Water off southern California. In other regions, *G. savagei* appears to occupy slightly deeper levels, and *G. microdontis* maintains a rather shallow

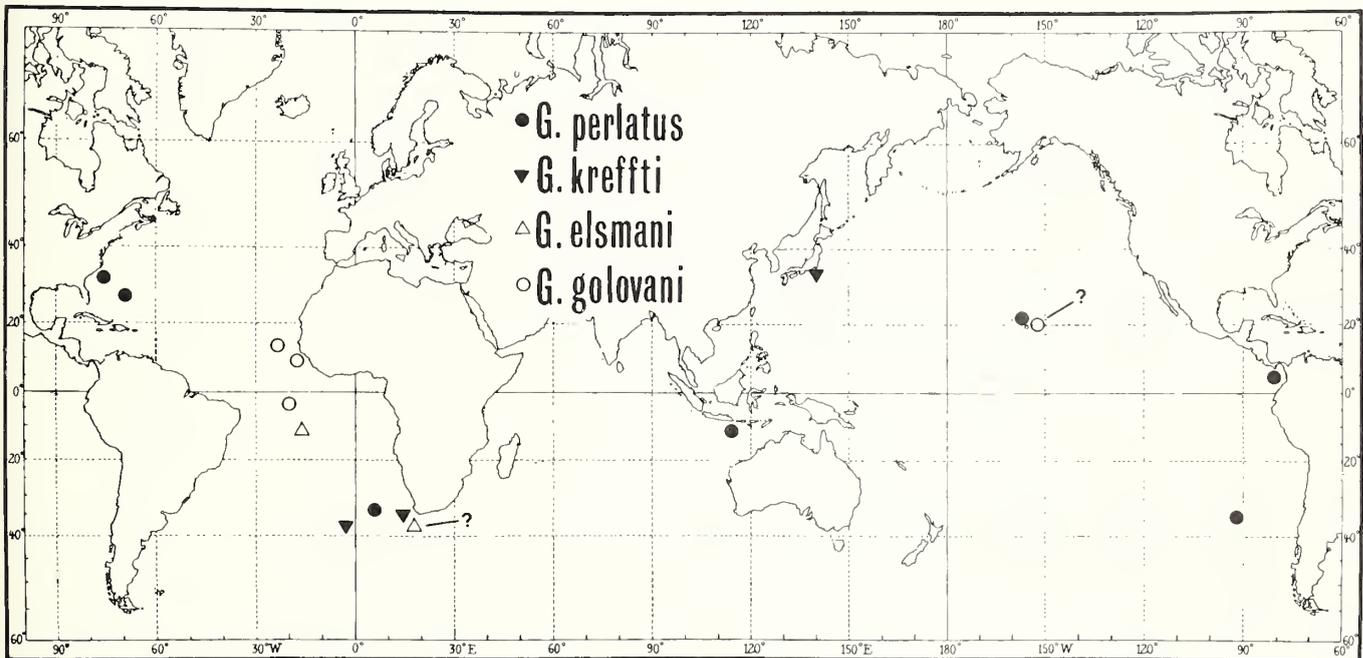


Figure 65. Distributions of four species of *Gigantactis*. A single symbol may indicate more than one capture.

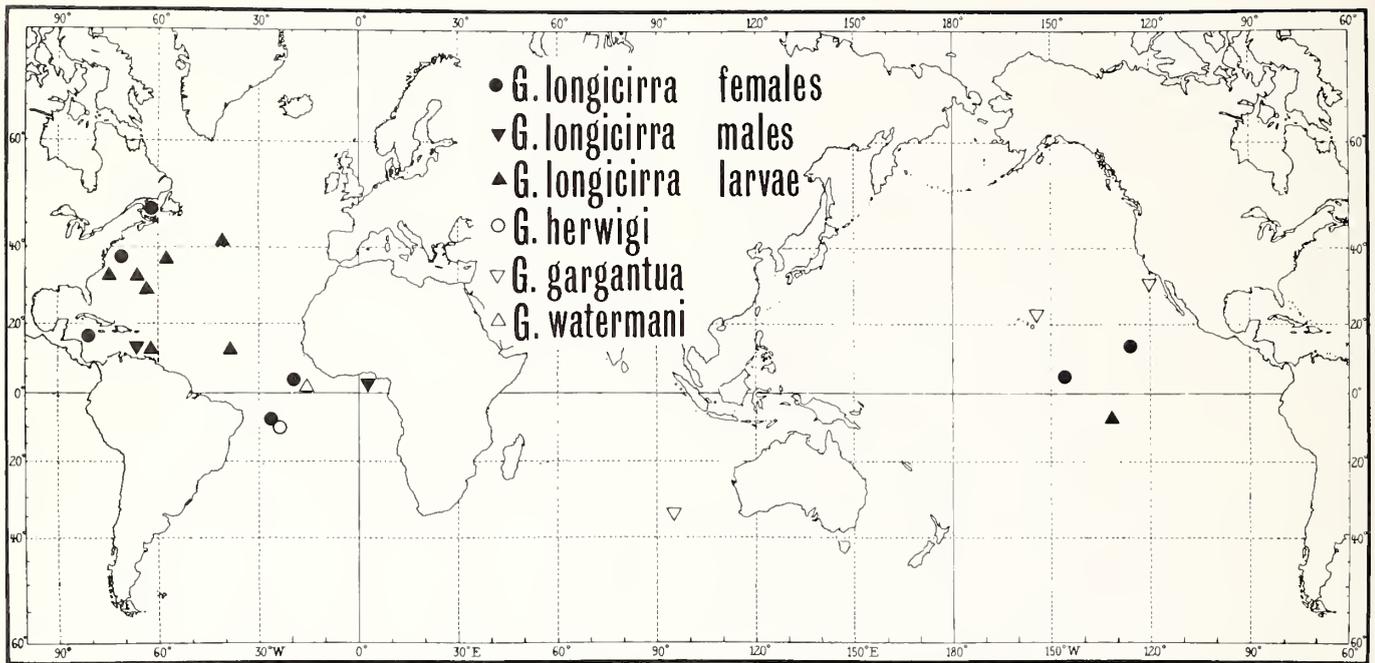


Figure 66. Distributions of four species of *Gigantactis*. A single symbol may indicate more than one capture.

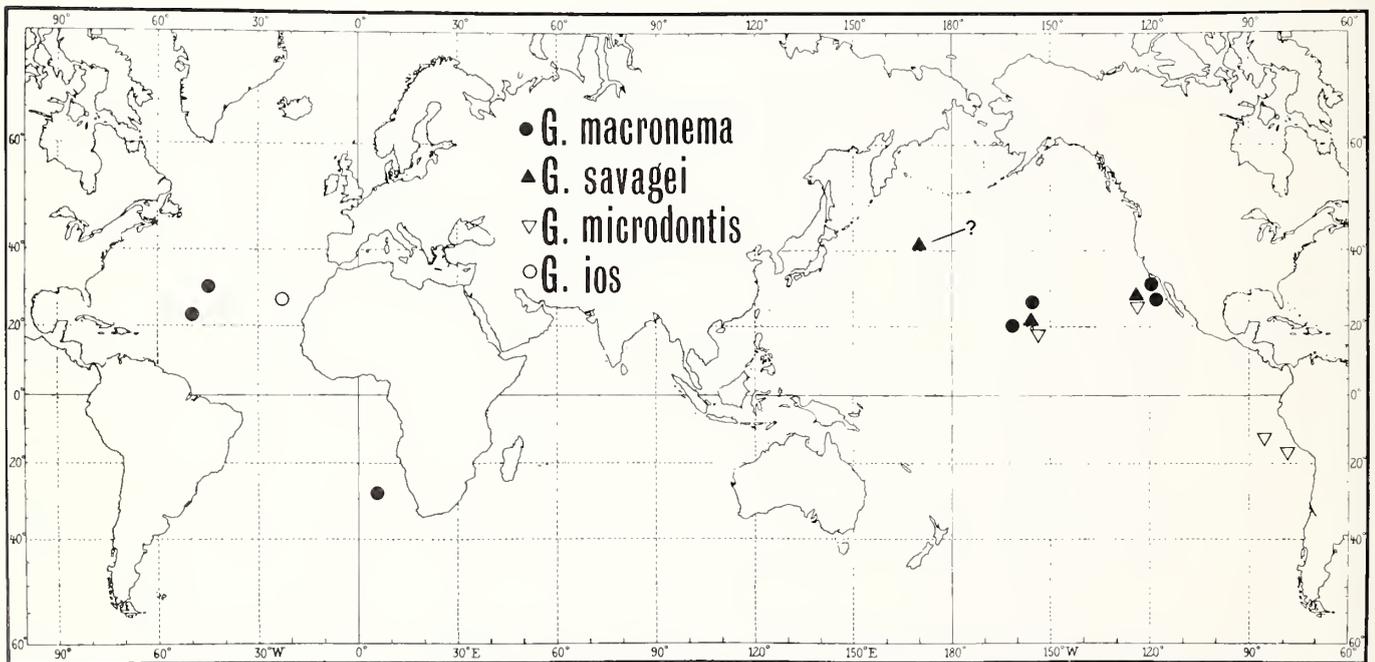


Figure 67. Distributions of four species of *Gigantactis* (*G. macronema* group). A single symbol may indicate more than one capture.

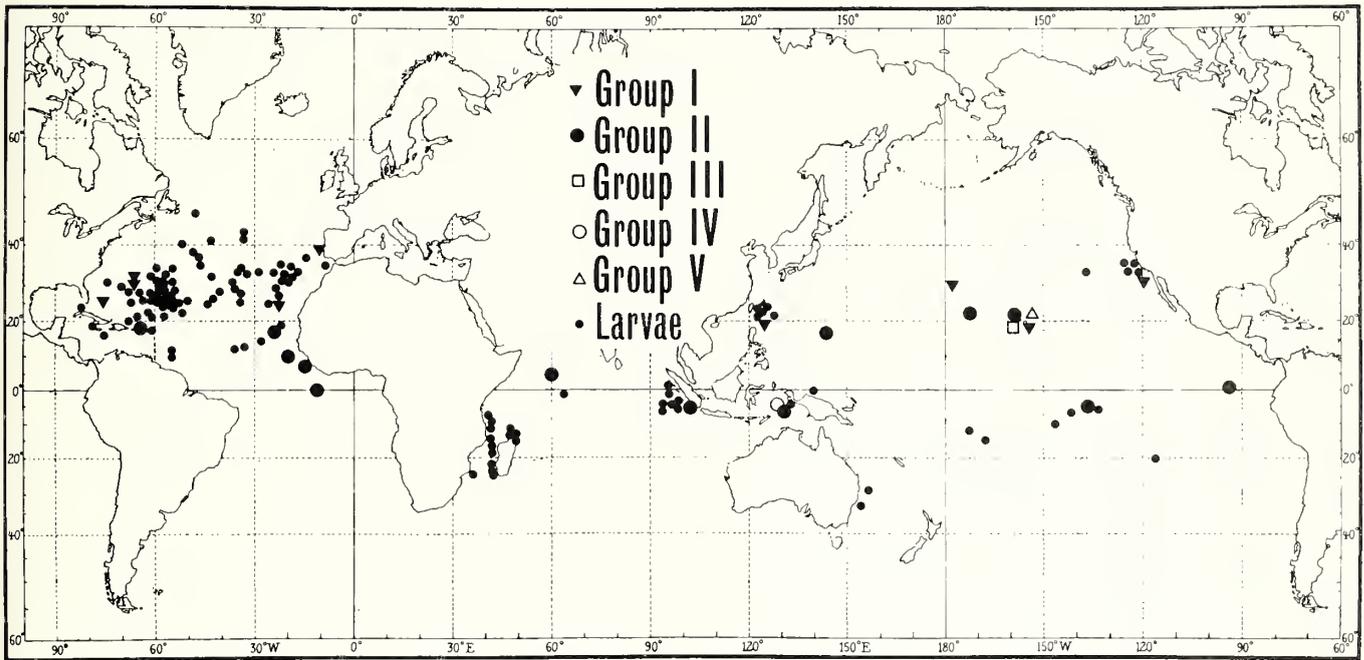


Figure 68. Distributions of males and larvae of *Gigantactis*. A single symbol may indicate more than one capture.

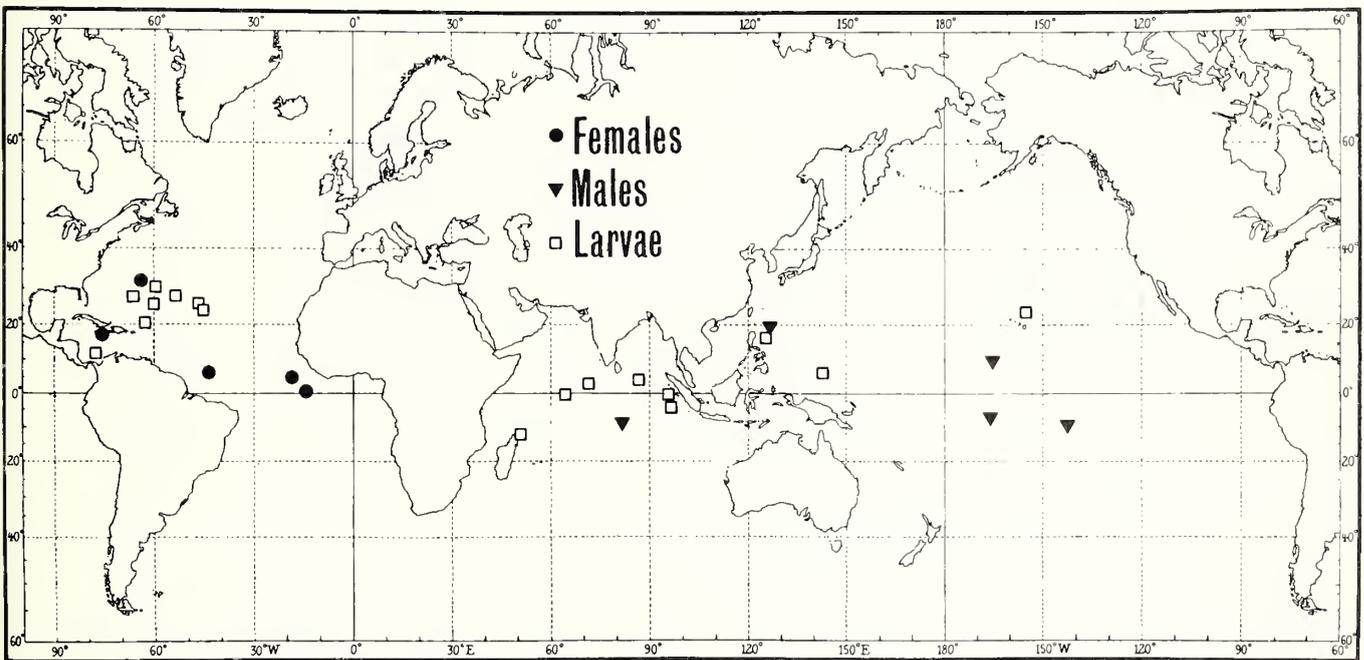


Figure 69. Distribution of *Rhynchactis leptonea*. A single symbol may indicate more than one capture.

distribution; all material of the latter species was captured above 1200 m.

SOUTHERN OCEAN ENDEMIC

Gigantactis meadi has a circumglobal distribution in Subantarctic Water, where it appears to have a relatively narrow but relatively deep vertical range. All specimens 87 mm and larger were taken in trawls fished open between 1850 and 2000 m (Fig. 64).

COMMENTS

At all stages in their life cycle, the more globose ceratioids such as *Oneirodes* are incapable of any prolonged horizontal locomotion and are to a considerable extent passively transported along by water movements. The movement of water masses and current gyres, which help to form and maintain these water masses, are no doubt important in the integration and concentration of distributions of these animals (Pietsch 1974). Gigantactinid females, on the other hand, are probably the most hydrodynamically efficient and most active in terms of prolonged horizontal movement of all ceratioids. Their considerably greater locomotory capabilities, as well as their tendency to inhabit deeper strata where physicochemical differences between water masses are appreciably less, probably account for their broad horizontal as well as vertical ranges.

EVOLUTIONARY RELATIONSHIPS

Rhynchactis has undergone such a drastic reduction and loss of parts that clearly it is the more derived of the two gigantactinid genera (compare generic diagnoses). Within the genus *Gigantactis*, there are four morphological trends that are found within nearly all ceratioid families and speciose genera (Pietsch 1972b, 1974:87, 88) and that seem to characterize anglerfish evolution: (1) an increase in the length of the illicium, (2) a decrease in the number of median-fin rays, (3) a loss of jaw teeth (Table 1), and (4) an increase in morphological complexity of the luring apparatus, in this case, reflected in a general tendency to increase the number of distal filaments of the esca and filaments of the illicium. *Gigantactis longicirra* appears to be the least derived member of the genus, having the shortest illicium, the greatest number of longitudinal series of dentary teeth, the highest dorsal-ray count, and the least number of distal esca filaments. Members of the *G. macronema* group (*G. macronema*, *G. microdontis*, and *G. ios*) are the most derived, having the longest illicium, the fewest series and total number of dentary teeth, the lowest dorsal-ray counts, and numerous distal, esca filaments. The remaining species of the genus are more or less intermediate in specialization. Members of the *G. vanhoeffeni* group, including *G. vanhoeffeni*, *G. meadi*, *G. gibbsi*, *G. gracilicauda*, and *G. paxtoni*, are united in sharing a relatively short illicium and a similar esca morphology. Members of the *G. gargantua* group, including *G. gargantua*, *G. watermani*, and *G. herwigi*, likewise share a similar esca morphology

but are also united on the basis of having a relatively long illicium and an elongation of the second and seventh caudal-fin rays.

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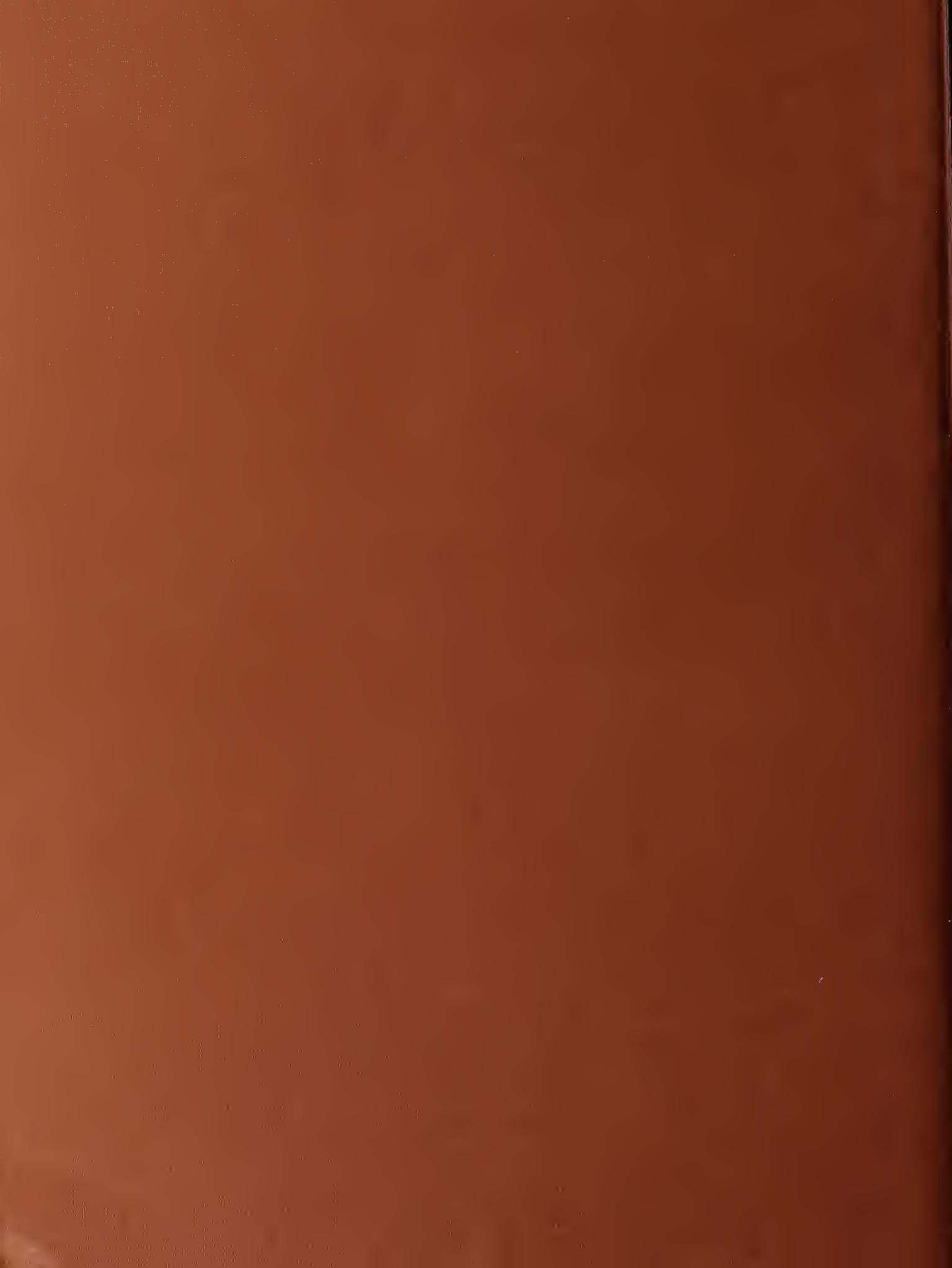
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CONTRIBUTIONS IN SCIENCE

A REVISION OF THE SERRANID FISHES
OF THE SUBGENUS *MIROLABRICHTHYS* (ANTHIINAE: *ANTHIAS*),
WITH DESCRIPTIONS OF FIVE NEW SPECIES

John E. Randall and Roger Lubbock



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A REVISION OF THE SERRANID FISHES
OF THE SUBGENUS *MIROLABRICHTHYS* (ANTHIINAE: *ANTHIAS*),
WITH DESCRIPTIONS OF FIVE NEW SPECIES¹

John E. Randall² and Roger Lubbock³

ABSTRACT. The Indo-Pacific subgenus *Mirolabrichthys* of the serranid fish genus *Anthias* is characterized chiefly by the thickened front part of the upper lip of the male, which is usually pointed and movable. The subgenus is represented by 11 colorful species: *tuka* (Herre and Montalban) from the Philippines, Indonesia, Great Barrier Reef, Papua New Guinea, Solomons, and Palau; the closely related *pascalus* (Jordan and Tanaka) from the Ryukyus and Oceania; *evansi* Smith from the Indian Ocean; *dispar* (Herre) from the central and western Pacific; *bicolor* Randall from Hawaii to Réunion; *lori* Lubbock and Randall from the central and western Pacific; *parvirostris* from the Solomons and Philippines; *smithvanizi* from the western Pacific and Cocos-Keeling Islands; *ignitus* (related to *dispar*) from the Maldives; *bartlettorum* from the Marshalls; and *regalis* from the Marquesas. The last five species are described as new. The most important characters to distinguish these fishes are the number of dorsal, anal, and pectoral rays, the number of lateral-line and circumpeduncular scales, the number of opercular spines (two or three), the presence or absence of prominent papillae on the posterior margin of the orbit, the relative length of dorsal spines (certain spines may be prolonged, especially in males), the presence or absence of scales on the mandible, and color. Most species exhibit sexual dichromatism.

INTRODUCTION

The small colorful seabasses generally classified in the Indo-Pacific genus *Mirolabrichthys* Herre and Montalban (subfamily Anthiinae, family Serranidae) are more abundant than the few records in the literature would indicate. They are among our loveliest of fishes, displaying colors of pink, red, orange, yellow, and violet in various combinations. They often occur in dense aggregations on coral reefs, typically in areas of clear water at escarpments. They feed on zooplankton above the bottom but retire to shelter within the reef at the approach of predaceous fishes. Because of their small size and their immunity from capture by ordinary commercial methods such as trawls and seines, they have no value as food fishes. However, with the development in recent years of the marine aquarium fish trade, these fishes have become economically important. A great need exists to revise the classification of this group, particularly to describe five new species collected by the authors and diving associates.

In his synopsis of the nominal Indo-Pacific serranid fishes of the genus *Anthias*, Heemstra (1973) included the three known species of the related genus *Mirolabrichthys*: *M. dispar* Herre from the Solomon Islands, *M. evansi* (Smith) from Kenya, Aldabra, and the Seychelles, and *M. tuka* Herre and Montalban.

He divided *M. tuka* into two subspecies: *M. tuka tuka* from the Philippine Islands, East Indies, and Solomon Islands, and *M. tuka pascalus* from the Ryukyu Islands, Caroline Islands, and Gilbert Islands. He separated the two on the basis of higher though overlapping pectoral-ray and lateral-line scale counts of *M. pascalus*. He wrote, "In view of the apparent allopatric distribution of these two forms, it seems best to recognize them as subspecies until additional field work is done to confirm these distributions and secure further information on fresh coloration." Whitley (1964) also preferred to treat *M. tuka* and *M. pascalus* as subspecies. The senior author, however, has collected both *M. tuka* and *M. pascalus* in the Palau Islands—on one occasion from the same rotenone station. Thus we conclude that these two forms are closely related species, not subspecies.

Mirolabrichthys has been separated from *Anthias* principally by two characters: the front of the upper lip of the male is developed into a fleshy protuberance, which juts anterior to the lower jaw, and the members of the genus possess two instead of three opercular spines. However, all five new species, *Anthias* (*Mirolabrichthys*) *bicolor* Randall, and *Anthias* (*Mirolabrichthys*) *lori* Lubbock and Randall, have a third opercular spine at the upper end of the gill opening (though, for most, it is obtuse and not well developed). This leaves only the hypertrophied anterior part of the upper lip of the male as a generic character. In aggregations of these fishes, the males are few in number compared to females. They are probably all the result of sex reversal, if we may extrapolate what is known of *Sacura margaritacea* (Hilgendorf) (Okada 1965), *Anthias squamipinnis* (Peters) (Fishelson 1970; Popper and Fishelson 1973), and *Mirolabrichthys pascalus* (Jordan and Tanaka) (Katayama 1974). When collections are made proportional to the percentages of the sexes (as by rotenone), relatively few males are taken, which means that most of the fishes would not be identified as belonging to the genus *Mirolabrichthys*. Furthermore, though one of our new species (*A. parvirostris*) generally resembles the smaller *Mirolabrichthys*, the male has only a slightly thickened upper lip without any pointed protuberance. This fish is so intermediate to typical *Mirolabrichthys* and some *Anthias*

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that it is difficult to decide into which genus to place it. Under the circumstances, it would seem best to regard *Mirolabrichthys* as a subgenus of *Anthias*.

A question still remains: whether the genus *Anthias* should be restricted to the eastern Atlantic and Mediterranean species *Anthias anthias* (Linnaeus) or whether the name should continue to be applied broadly to many Indo-Pacific species. If the genus is restricted to the eastern Atlantic species, the majority of the Indo-Pacific fishes now placed in *Anthias* should be shifted to *Pseudanthias* Bleeker. Phillip C. Heemstra and the senior author are presently trying to clarify this generic problem.

Males of the monotypic genus *Nemanthias* Smith (1954) also have a thickened, somewhat pointed upper lip, but this taxon is here provisionally recognized as distinct from *Mirolabrichthys* in its possession of 11 dorsal spines and prolonged first two dorsal spines. Probably it should also be classified as a subgenus of *Anthias*.

METHODS AND MATERIALS

Standard length (SL) is the straight-line distance from the front of the upper lip to the base of the caudal fin (posterior end of hypural plate). The depth of the body is the maximum depth from the base of the dorsal spines; width of body is measured just posterior to the gill opening. Head length is taken from the front of the upper lip to the most posterior point of the opercular flap; snout length is measured from the front of the upper lip to the fleshy edge of the orbit. Orbit diameter is the greatest fleshy diameter of the orbit, but the interorbital width is the least bony width. The depth of the caudal peduncle is the least depth; the length of the peduncle is the horizontal distance from the rear base of the anal fin to the base of the caudal fin. Fin spine and ray measurements are taken to the extreme bases. Pectoral and pelvic fin lengths are the lengths of the longest rays. The caudal concavity is the horizontal distance between verticals at the distal tips of the longest and shortest rays. The last dorsal and anal rays, though usually divided to the base, are counted as one ray. Pectoral ray counts include the upper rudimentary ray. Gillraker counts include all rudiments.

Type specimens of the new species have been deposited variously in the following institutions: Academy of Natural Sciences of Philadelphia (ANSP); Australian Museum, Sydney (AMS); Bernice P. Bishop Museum, Honolulu (BPBM); British Museum (Natural History), London [BM(NH)]; California Academy of Sciences, San Francisco (CAS; SU); Natural History Museum, Los Angeles County (LACM); Muséum National d'Histoire Naturelle, Paris (MNHN); U.S. National Museum of Natural History, Washington, D.C. (USNM); and Western Australian Museum, Perth (WAM).

Data in parentheses in the descriptions of new species apply to paratypes. Table 1 is a comparison of the principal external characters used to distinguish the species of *Anthias* of the subgenus *Mirolabrichthys*. Tables 2 to 4 present the meristic data of these fishes, Table 7 gives proportional measurements of *Anthias lori*, and the remaining tables give the proportional mea-

surements of the new species. More measurements are given in the last six tables than are summarized in the text.

SYSTEMATICS

Genus *Anthias* Subgenus *Mirolabrichthys*

Mirolabrichthys Herre and Montalban in Herre 1927, p. 413 (type species, *Mirolabrichthys tuka* Herre and Montalban, by monotypy).

Entonanthias Jordan and Tanaka 1927, p. 385 (type species, *Entonanthias pascalus* Jordan and Tanaka, by monotypy).⁴

DIAGNOSIS. Dorsal rays X,15–18; anal rays III,7 or 8; branched caudal rays 13; lateral line in a smooth curve following contour of back, the pored scales 21–36; body moderately elongate, the depth 2.56–4.03 in SL; upper lip of males thickened anteriorly, and pointed (except *A. parvirostris*); patch of villiform teeth on vomer roundish to quadrangular; two or three opercular spines; first dorsal spine never prolonged (but second and/or third spines may be elongate); pelvic fins of males often extending posterior to origin of anal fin.

DESCRIPTION. Dorsal rays X,15 to 18; anal rays III,7 or 8; pectoral rays 15 to 22, generally the upper two and often the lowermost unbranched, pelvic rays 1,5; principal caudal rays 15 (upper and lower unbranched); lateral-line scales 41 to 64; circumpeduncular scales 21 to 36; gill rakers 8–12 + 20–29, usually longer than gill filaments; branchiostegal rays 7; vertebrae 26 (rarely 25); predorsal bones 1–3.

Body moderately elongate, the depth 2.56 to 4.03 in SL, and moderately compressed, the width 1.56 to 2.54 in depth; head length 2.81 to 3.7 in SL; snout 3.1 to 5.59 in head, the upper lip thickened anteriorly in males, with a pointed proboscis-like protuberance (except in *A. parvirostris*), which is freely movable dorsoventrally; diameter of orbit 2.87 to 5.3 in head; margin of posterior half of orbit of some species with prominent fleshy papillae; interorbital space convex, the bony width 3.2 to 4.67 in head; least depth of caudal peduncle 1.92 to 2.93 in head.

Mouth terminal, becoming inferior in males with development of the proboscis at front of upper lip; mouth oblique and moderately large, the maxilla reaching beyond a vertical at center of eye (but rarely posterior to eye); no supplemental maxillary bone (supramaxilla). A band of villiform teeth in jaws, broader anteriorly, the outer row the largest (may be of canine proportions), often inclined forward except anteriorly; a stout canine tooth anteriorly on each side of jaws, those on lower jaw projecting forward and outward; an incurved canine tooth on outer side of lower jaw about one-third distance from front of jaw; villiform teeth in a roundish to quadrangular patch on vomer and in a band on palatines. Tongue pointed, without teeth. Anterior nostril in a membranous tube (higher dorsoposteriorly); posterior nostril large, with little or no rim.

4. Myers (1929) has shown that the name *Mirolabrichthys* has priority over *Entonanthias* by a scant margin of 3 months in publication time.

Gill membranes free from isthmus. Opercle with two or three spines (when a third spine is present, at upper position, it is usually obtuse and indistinct); upper margin of preopercle and often the rounded corner serrate; no serrae or spines on lower margin of preopercle; subopercle and interopercle not serrate.

Scales ctenoid; auxiliary scales present or absent; mandibles scaled or naked; snout fully scaled or with a naked zone anterior to eye that may include nostrils in its upper part; dorsal and anal fins naked or scaled basally; caudal fin with small scales

more than three-fourths distance to posterior margin; pectoral fins with small scales on basal one-fourth to one-third. Lateral line complete, running in a smooth curve following contour of back, the last pored scale usually ending slightly anterior to base of hypural.

Origin of dorsal fin varying from just posterior to upper margin of preopercle to over pectoral base; certain dorsal spines may be prolonged, particularly in males, but never the first; no marked indentation between spinous and soft portions of dorsal

Table 1. Comparison of distinguishing external characters of species of the genus *Anthias*, subgenus *Mirolabrichthys*.

Species	Auxiliary scales	Mandibles	Lateral-line scales	Circumpeduncular scales	Papillae on posterior margin of orbit	Pectoral fin rays	Opercular spines	Prolonged dorsal spines of males
<i>A. evansi</i>	present	scaled	47-50	26-28	absent	16-18	2	none
<i>A. parvirostris</i>	absent	scaled	41-44	21-24	present	17	3	none
<i>A. tuka</i>	present	scaled	45-49	23-26	present	15-17	2	none
<i>A. pascalus</i>	present	scaled	48-52	25-27	present	16-19	2	none
<i>A. smithvanizi</i>	absent	scaled	44-48	23-25	present	16-17 (18)*	3	3rd
<i>A. lori</i>	absent	scaled	49-52	25-28	present	(16) 17-18	3	3rd
<i>A. dispar</i>	absent	scaled	55-63	32-35	absent	(18) 19-20	2	none
<i>A. ignitus</i>	absent	scaled	53-58	29-33	absent?	(19) 20	3	none
<i>A. bicolor</i>	absent	naked	57-64	31-33	absent	19-20 (21)	3	2nd & 3rd**
<i>A. bartlettorum</i>	absent	naked	54-58	29-32	absent	(20) 21	3	2nd
<i>A. regalis</i>	absent	naked	56-62	32-36	absent	21 (22)	3	2nd***

*() = rarely

**third prolonged in females as well as males

***also prolonged in females, though less than in males

Table 2. Fin-ray counts of species of *Anthias*, subgenus *Mirolabrichthys*.

	Dorsal Soft Rays				Anal Soft Rays		Pectoral Rays							
	15	16	17	18	7	8	15	16	17	18	19	20	21	22
<i>A. evansi</i>		4	18	5		27		5	20	2				
<i>A. parvirostris</i>	1	10				11			11					
<i>A. tuka</i>	2	27	1		29	1	3	21	6					
<i>A. pascalus</i>	2	29	3		33	1		3	9	19	3			
<i>A. smithvanizi</i>	2	22	1		24	1		10	14	1				
<i>A. lori</i>		16	1		16	1		1	10	6				
<i>A. dispar</i>		3	25	2	29	1				1	11	18		
<i>A. ignitus</i>		5	3		8						1	7		
<i>A. bicolor</i>		1	22	6	27	2					10	18	1	
<i>A. bartlettorum</i>			8	1	9							1	8	
<i>A. regalis</i>			15	3	18								15	3

fin; fourth anal ray may be prolonged on some species; caudal fin lunate, the lobes often filamentous; pectoral fins rounded to slightly pointed, usually not extending posterior to a vertical at origin of anal fin; pelvic fins generally longer in males than females, principally as a result of prolongation of the second ray (pelvics often extend beyond spinous portion of anal fin).

**KEY TO THE
SPECIES OF ANTHIAS OF THE
SUBGENUS MIROLABRICHTHYS**

- 1a. Lateral-line scales 41 to 52; pectoral rays 15 to 19 (rarely 19) 2
- 1b. Lateral-line scales 53–64; pectoral rays 18 to 22 (rarely 18 or 19) 7
- 2a. A series of prominent papillae along edge of posterior half of orbit; anal soft rays 7 (rarely 8); color not as in 2b .. 3
- 2b. No papillae along posterior margin of orbit; anal soft rays 8; violet to fuchsia with yellow dots, the back above a demarcation from dorsal fin origin to midbase of caudal fin bright yellow; dorsal and caudal fins largely yellow (Indian Ocean) *evansi*
- 3a. Fourth to tenth dorsal spines longest; two or three opercular spines 4
- 3b. Third dorsal spine the longest; three opercular spines... 6
- 4a. Teeth along sides of jaws relatively small (except for canine in lower jaw) and not inclined forward; two opercular spines; auxiliary scales present; lateral-line scales 45 to 52; snout moderately long, 3.2 to 3.8 in head; caudal fin entirely violet or with yellow lobes 5
- 4b. Teeth along sides of jaws relatively large and inclined forward (except anteriorly); lateral-line scales 41 to 44; three opercular spines (though uppermost obtuse and indistinct); no auxiliary scales; snout short, 4.6 to 5.6 in head; caudal fin yellow, the upper and lower margins violet (Solomon Islands and Philippines).... *parvirostris* new species
- 5a. Lateral-line scales 45 to 49 (rarely 49); pectoral rays 15 to 17 (usually 16); females with a band of bright yellow on back, and caudal lobes broadly yellow (Melanesia, Great Barrier Reef, Indonesia, Philippines, and Palau Islands) ..
..... *tuka*
- 5b. Lateral-line scales 48 to 52 (rarely 48); pectoral rays 16 to 19 (usually 18); no yellow band on back, and no yellow on caudal fin (Ryukyu Islands, Japan, and Oceania)
..... *pascalus*
- 6a. Lateral-line scales 44 to 48; depth of body 3.1 to 3.35 in SL; pink with yellow dots on upper two-thirds of body, shading ventrally to light lavender; a narrow band of yellow on back at base of dorsal fin (Western Pacific and Cocos-Keeling Islands, Indian Ocean)
..... *smithvanizi* new species
- 6b. Lateral-line scales 49 to 52; depth of body 3.35 to 4.05 in SL; salmon pink shading to pinkish white ventrally, with a row of subquadrangular red blotches along body beneath dorsal fin (except anteriorly) and a broad horizontal red band nearly covering upper half of caudal peduncle and

extending slightly anterior to it (Central and Western Pacific) *lori*

- 7a. No dorsal spines greatly prolonged (second dorsal spine of males of *A. dispar* may be slightly elongate); two or three opercular spines; dorsal fin primarily red 8
- 7b. Second and/or third dorsal spines of adults greatly prolonged; three opercular spines (though uppermost usually obtuse); dorsal fin not primarily red 9
- 8a. Dorsal soft rays usually 17; opercular spines 2; lateral-line scales 55 to 63 (modally 60); circumpeduncular scales 32 to 35; two irregular rows of small teeth on palatine at widest place (Central and Western Pacific) *dispar*
- 8b. Dorsal soft rays usually 16; opercular spine 3; lateral-line scales 53 to 58; circumpeduncular scales 29 to 33; three to six irregular rows of palatine teeth at widest place (Maldive Islands) *ignitus* new species
- 9a. Second anal spine slightly longer than third; second and third dorsal spines prolonged in adults (the third the longest, but the two spines nearly equal on males, with yellow membranous tips); maximum number of preopercular serrae 36 (serrae increasing generally with size); maximum standard length at least 111 mm (Indo-Pacific).... *bicolor*
- 9b. Third anal spine longer than second; second dorsal spine prolonged in adults; maximum number of preopercular serrae 24; maximum standard length about 65 mm 10
- 10a. Lateral-line scales 54 to 58; circumpeduncular scales 29 to 32; three to five irregular rows of small teeth on palatines at widest place; pelvic fins of large males moderately elongate, reaching posteriorly just to soft portion of anal fin; back and caudal fin yellow, side and ventral part of head and body abruptly violet (Marshall Islands)
..... *bartlettorum* new species
- 10b. Lateral-line scales 56 to 62, circumpeduncular scales 32 to 36; two irregular rows of small teeth on palatines at widest place; pelvic fins of large males very elongate, reaching posteriorly to rear base of anal fin; females orange-yellow, shading to red posteriorly; males violet, the upper postorbital head and nape yellow (Marquesas Islands) *regalis* new species

Anthias evansi
Figure 1, Tables 1–4

Anthias evansi Smith 1954, p. 1, fig. 1 (type locality, Shimoni, Kenya); Smith 1955, p. 342 (Aldabra, islands of the Cosmoledo Group, Seychelles); Smith 1961, p. 363, pl. 35A; Smith and Smith 1963, p. 18, pl. 58A.

Mirolabrichthys evansi Heemstra 1973, p. 207, fig. 3 (top); Burgess and Axelrod 1973b, pp. 648, 651, figs. 113, 114, 117 (Mombasa and Maldive Islands).

DIAGNOSIS. Dorsal soft rays 16 to 18 (usually 17); anal soft rays 8, pectoral rays 16 to 18 (usually 17); lateral-line scales 47 to 50 [Heemstra (1973) recorded 2 of 24 *A. evansi* with 47]; circumpeduncular scales 26 to 28; auxiliary scales present; mandibles scaled; snout fully scaled except for a zone running diagonally downward in front of anterior nostril; teeth along

sides of jaws relatively small (smaller only in *A. tuka* and *A. pascalus*) and not oblique; gill rakers 9-10 + 22-26; three predorsal bones; no papillae on margin of orbit; two opercular spines; origin of dorsal fin over pectoral base; fourth dorsal spine usually longest (but not prolonged); snout length 3.9 to 4.4 in head length; depth of body 3.1 to 3.4 in SL; dorsal and anal fins scaled basally; adult males with second pelvic ray, fourth and fifth anal rays, and tenth to thirteenth dorsal rays prolonged.

Back yellow above a demarcation from origin of dorsal fin to lower caudal base, violet to heliotrope below with scattered yellow dots; an orange band from snout through lower part of

eye to pectoral base; caudal fin yellow; dorsal fin yellow except for small posterior portion and margin, which are violet; remaining fins pale violet.

REMARKS. *A. evansi* is known only from the Indian Ocean. Smith (1954) based his description of the species on six specimens, 82 to 113 mm total length from Kenya (including the holotype from Shimoni, his largest specimen, 87 mm SL) and Pemba, Mozambique.

We have collected *A. evansi* from the Maldives, Réunion, and Mauritius (two from the stomach of a 310-mm specimen of *Aphareus furcatus*). We have examined two lots of specimens from the Cocos-Keeling Islands at the Academy of

Table 3. Lateral-line scales of species of *Anthias*, subgenus *Mirolabrichthys*.

	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64
<i>A. evansi</i>								7	12	8														
<i>A. parvirostris</i>	3	3	3	1																				
<i>A. tuka</i>					3	8	10	7	2															
<i>A. pascalus</i>								1	7	14	9	3												
<i>A. smithvanizi</i>				1	5	6	7	6																
<i>A. lori</i>									1	3	5	6												
<i>A. dispar</i>															1	1	2	5	6	8	3	2	1	
<i>A. ignitus</i>													1	1	1	2	2	1						
<i>A. bicolor</i>																	2	5	4	7	6	2	2	1
<i>A. bartlettorum</i>														5	1	1		2						
<i>A. regalis</i>																1	5	1	4	2	1	1		

Table 4. Gill-raker counts of species of *Anthias*, subgenus *Mirolabrichthys*.

	Upper Limb					Lower Limb										
	8	9	10	11	12	20	21	22	23	24	25	26	27	28	29	
<i>A. evansi</i>		14	13						2	9	9	6	1			
<i>A. parvirostris</i>	1	5	4	1					3	4	4					
<i>A. tuka</i>	2	22	6						5	10	9	5	1			
<i>A. pascalus</i>		6	22	6					2	7	15	6	4			
<i>A. smithvanizi</i>	16	9				2	4	10	8	1						
<i>A. lori</i>	13	4					2	6	7	2						
<i>A. dispar</i>		2	16	10	2				1	10	10	8	1			
<i>A. ignitus</i>				6	2				2	1	4	1				
<i>A. bicolor</i>				13	16								6	15	7	1
<i>A. bartlettorum</i>			4	4					1	5	1	1				
<i>A. regalis</i>			3	12	3					1	7	8	1	1		

Natural Sciences of Philadelphia collected by William F. Smith-Vaniz and associates and one lot from the Seychelles collected by James E. Böhlke and associates. The depth range for all of these specimens was 4 to 30 m. The largest, BPBM 20007, 93 mm SL, is from Réunion.

Anthias parvirostris new species

Figures 2A and B, Tables 1–5

HOLOTYPE. BPBM 15605, male, 48.3 mm SL, SOLOMON ISLANDS, Alite Reef (off Malaita), outer reef slope on west side, bottom mainly rubble, 60 m, dynamite and rotenone, J.E. Randall, W.A. Starck, II, B. Goldman, and W. Doak, 24 July 1973.

PARATYPES. BPBM 20448, 6: 23.3–36.1 mm SL; BM(NH) 1976.9.30.10, 35.8 mm SL; CAS 37886, 29.7 mm SL; LACM 35904-1, 27.4 mm SL; USNM 216490, 39.9 mm SL, SOLOMON ISLANDS, collected with holotype; BM(NH) 1979.1.3.1, 58.9 mm SL, PHILIPPINE ISLANDS, Palawan, 0.5 km N of Tagtuan R., isolated coral on sand, 35 m, R. Lubbock, 17 August 1978.

DIAGNOSIS. Dorsal soft rays 15 or 16 (rarely 15); pectoral rays 17; lateral-line scales 41 to 44; circumpeduncular scales 21 to 24; no auxiliary scales; mandibles scaled; gill rakers 8–11 + 22–24; side of jaws with a row of moderate canine teeth; about five rows of teeth on palatines at widest place; posterior edge of orbit with fleshy papillae; three opercular spines; snout short, 4.6 to 5.6 in head; body depth 2.8 to 3.0 in SL; soft dorsal and anal fins scaled over basal half to quarter; colors of fresh specimens as in Figure 2.

DESCRIPTION. Dorsal rays X, 16 (15 or 16, only one fish with 15); anal rays III, 7; pectoral rays 17 (upper two and lower unbranched); pelvic rays 1, 5; principal caudal rays 15 (upper and lower unbranched); lateral-line scales 43 (41–44); scales above lateral line to origin of dorsal fin 5 (4–5); scales below lateral line to origin of anal fin 15 (14–15); circumpeduncular scales 23 (21–24); gill rakers 10 + 23 (8–11 + 22–24); branchiostegal rays 7; vertebrae 26; predorsal bones 2.

Body somewhat elongate, the depth 3.02 (2.79–2.89) in SL; body moderately compressed, the width 1.99 (1.89–2.13) in depth; head length 3.10 (2.86–2.98) in SL; snout 4.61 (4.60–5.59) in head; front of upper lip of male holotype barely thickened; diameter of orbit 3.63 (2.99–3.48) in head; posterior edge of orbit with fleshy papillae (13–16 in holotype); interorbital space convex, the bony width 3.99 (4.29–4.67) in head; least depth of caudal peduncle 2.29 (2.17–2.35) in head.

Mouth oblique and moderately large, the maxilla reaching to, or posterior to, a vertical at rear edge of pupil; mouth terminal; posterior end of maxilla rounded, its greatest depth 1.43 in orbit of holotype; no supplemental maxillary bone. Upper jaw with a band of villiform teeth, the band broader anteriorly, the teeth at the front enlarged; one (rarely two) large curved canine anteriorly on each side of upper jaw; an outer row of enlarged teeth (15 to 17 on holotype) on side of jaw, inclined forward; lower jaw with a patch of villiform teeth anteriorly, the front ones slightly enlarged; two large curved canine teeth on each side of lower jaw (one laterally at front of jaw, angled outward,

and the other about one-third back in jaw, curved slightly posterior); a row of moderate canines (17 on holotype) on side of jaw posterior to second large canine, inclined forward; vomer with very small teeth; palatines with a band of villiform teeth in approximately five irregular rows at broadest place; tongue pointed, the upper surface with scattered very small papillae. Gill membranes free from isthmus. Gill rakers slender and long (largest 1.48 in orbit of holotype), notably longer than gill filaments (longest gill filament of first arch of holotype 1.45 in longest raker).

Opercle with three flattened spines, the central one the largest and most posterior, the upper just anterior to lower (two lower spines acute, the upper obtuse and rather indistinct); distance between two lower spines about seven-eighths the distance between central and upper spines; lower margin of preopercle smooth, the rounded corner and upper margin serrate (25 serrae on holotype).

Anterior nostril in a short membranous tube (higher dorso-posteriorly) directly anterior to middle of eye about half the distance from edge of orbit to edge of groove separating upper lip from rest of snout; posterior nostril diagonally upward and posterior to anterior nostril, with a low rim anteriorly, and rather large, the greatest diameter of opening about half the distance between nostrils, 10.75 in orbit of holotype.

Scales ctenoid; no auxiliary scales on body; head scaled except throat and gill membranes, lips, extreme front of snout, and a broad zone on side of snout anterior to center of eye that includes nostrils in its upper part; dorsal fin scaled basally from third spine onwards, the scales covering basal half of center of fin, posteriorly covering basal quarter of fin; basal third to quarter of anal fin scaled; caudal fin with small scales more than three-fourths distance to posterior margin; pectoral fins with small scales on basal third or more of fin; pelvic fins with small scales on medial surface.

Lateral line a smooth curve following contour of back, the last pored scale slightly anterior to, or just beyond, end of hypural plate. Some pores of cephalic lateralis system obscured by scales. Prominent are a pore in front of anterior nostril, one between nostrils, one medial to nostrils, two close together in interorbital space above front of eye, a series near edge of orbit around posterior half of eye, about eleven scattered pores between upper margin of opercle and posterior margin of eye, four on suborbital and preorbital region anterior to a vertical through center of eye (two nearest vertical very close together, large, about half greatest diameter of posterior nostril), and six in a mandibular series beginning at end of lower margin of preopercle (last two on chin close together).

Origin of dorsal fin just anterior to a vertical through posterior margin of opercle; no marked prolongation of dorsal spines in males or females; third dorsal spine 10.53 (10.20–11.36) in SL; longest dorsal soft ray 2.23 (2.13–2.60) in head; third anal spine 2.78 (2.97–3.38) in head; caudal fin lunate, the lobes somewhat filamentous, the caudal concavity 7.25 (5.38–6.45) in SL; pectoral fin length 3.04 (2.84–3.08) in SL; pelvic fins moderately long, 3.38 (2.96–3.16) in SL, reaching to anal fin origin in smaller specimens, and to just beyond spinous portion of anal fin in larger specimens.

Color in alcohol: pale with no dark markings. Color of male

holotype when fresh (from transparency): dorsal part of head and body yellow, that on body interspersed with numerous pinkish lavender spots on scale edges; ventral part of head and body pinkish lavender; posterior margin of operculum golden dorsally; heliotrope band from upper front of eye to base of dorsal fin, parallel to a second short broken heliotrope band running backwards from upper posterior margin of orbit; iris magenta with a yellow ring around pupil; dorsal fin heliotrope basally (except rear part of soft portion where yellow en-

croaches onto base of fin), violet distally; anal fin lavender hyaline with light lavender distal margin (except posteriorly); caudal fin yellow, a few pinkish lavender spots near base, yellowish hyaline towards concavity, with broad heliotrope upper and lower margins and magenta submarginal lines; paired fins pinkish hyaline. Color of 36.1-mm-SL female paratype (BPBM 20448) when fresh (from transparency): dorsal part of head and body yellow, the yellow on body interspersed with numerous pinkish lavender spots on scale edges; remainder of head and

Table 5. Proportional measurements of type specimens of *Anthias parvirostris* expressed as a percentage of the standard length.

	Holotype		Paratypes		
	BPBM 15605	LACM 35904-1	BM(NH) 1976.9.30.10	BPBM 20448	USNM 216490
Standard length (mm)	48.3	27.4	35.8	36.1	39.9
Depth of body	33.1	35.8	35.2	34.6	35.1
Width of body	16.6	16.8	17.0	18.3	16.5
Head length	32.3	35.0	34.1	34.3	33.6
Snout length	7.0	6.6	6.1	7.2	7.3
Diameter of orbit	8.9	11.7	9.8	10.5	10.0
Bony interorbital width	8.1	8.0	7.3	8.0	7.8
Length of maxilla	16.4	16.8	15.9	17.2	16.5
Least depth of caudal peduncle	14.1	15.0	14.5	15.8	14.8
Length of caudal peduncle	16.4	13.9	12.8	14.4	13.3
Predorsal length	33.7	36.5	34.4	34.1	35.1
Preanal length	59.4	64.6	66.8	65.1	61.9
Prepelvic length	34.2	35.4	34.9	36.3	34.8
Length of first dorsal spine	3.7	3.6	4.5	4.2	4.0
Length of second dorsal spine	6.8	7.7	6.7	6.6	7.3
Length of third dorsal spine	9.5	8.8	8.9	8.9	9.8
Length of tenth dorsal spine	11.2	10.2	10.9	11.4	11.5
Length of longest dorsal ray	14.5	14.2	13.1	15.5	15.8
Length of dorsal fin base	55.5	54.4	50.6	56.0	56.6
Length of first anal spine	5.6	5.1	5.0	5.0	6.5
Length of second anal spine	9.1	9.9	8.9	9.7	10.3
Length of third anal spine	11.6	10.6	10.1	11.4	11.3
Length of longest anal ray	18.8	23.4	22.6	22.7	22.6
Length of anal fin base	19.0	19.3	17.6	20.2	21.1
Length of pectoral fin	32.9	32.5	34.6	35.2	33.3
Length of pelvic spine	15.7	15.7	16.2	15.8	16.1
Length of pelvic fin	29.6	32.8	32.4	31.6	33.8
Length of caudal fin	36.0	34.3	39.9	39.6	40.9
Caudal concavity	22.2	15.7	24.0	24.1	24.6

body pink, lighter ventrally; a magenta band from upper anterior edge of orbit to just before dorsal fin base; two rather indistinct pinkish lavender bands on head running backward and diagonally upward from hind margin of orbit, fainter posteriorly; iris yellow immediately above and below pupil, otherwise magenta; dorsal fin yellow basally, becoming pink, then yellowish pink, and finally yellow near distal margin; tips of dorsal spines and distal margin of anterior part of soft dorsal fin violet; anal fin yellow with a lavender distal margin (except posteriorly); caudal fin yellow, with pinkish lavender spots near base, yellowish hyaline towards concavity, with narrow heliotrope upper and lower margins; paired fins yellowish hyaline, the pelvics with a lavender anterior margin.

REMARKS. All but one of our specimens have been taken from a single SCUBA station at 60 m off Alite Reef, Solomon Islands. The one other fish was collected off Palawan, Philippine Islands, in 35 m. *A. smithvanizi* was collected in the same Alite Reef station as the series of *A. parvirostris*.

As mentioned in the introduction, the male of this species has only a thickened anterior upper lip, lacking the pointed movable protuberance that is typical of other species of the subgenus. In this respect, it is intermediate to *Mirolabrichthys* and *Anthias* of the subgenus *Pseudanthias*.

ETYMOLOGY. Named *parvirostris* in reference to the relatively short snout.

Anthias tuka

Figures 3 and 4, Tables 1–4

Mirolabrichthys tuka Herre and Montalban in Herre 1927, p. 413 (type locality, Maricaban Island, Philippine Islands); Burgess and Axelrod 1975, pp. 1474–1475, figs. 150–153 (Solomon Islands).

Mirolabrichthys tuka tuka Heemstra 1973, p. 208, fig. 3 (lower) (Philippines, Borneo, Celebes, Moluccas, and Solomons).

DIAGNOSIS. Dorsal soft rays 15 to 17 (usually 16); anal soft rays 7 or 8 (rarely 8); pectoral rays 15 to 17 (usually 16); lateral-line scales 45 to 49; circumpeduncular scales 23 to 26; auxiliary scales present; mandibles scaled; snout fully scaled; teeth along sides of jaws (except canine in lower jaw) relatively small and not inclined forward (teeth larger on other species except *A. pascalus*); gill rakers 8–10 + 22–26; three predorsal bones; a series of prominent papillae along edge of posterior half of orbit; two opercular spines; snout moderately long, 3.2 to 3.8 in head; depth of body 2.8 to 3.3 in SL; dorsal and anal fins scaled basally; origin of dorsal fin over pectoral base; fifth to tenth dorsal spines the longest, subequal; adult males with caudal lobes, second pelvic ray, and fourth anal ray prolonged and most of soft portion of dorsal fin elevated.

Color in life bright heliotrope, becoming yellowish ventrally on head, thorax, and abdomen; females with a band of yellow along back at base of dorsal fin continuing onto dorsal part of caudal peduncle and upper lobe of caudal fin; lower lobe of fin also with a broad band of yellow; males with more yellow on head below level of lower edge of eye, the upper part of head

with a suffusion of orange, the two regions separated by a band of orange running to pectoral base.

REMARKS. We have collected specimens of *Anthias tuka* in the Palau Islands, Solomon Islands, Bismarck Archipelago, southeast New Guinea, Great Barrier Reef, and Ambon, Indonesia, in the depth range of 7 to 15 m; these are deposited in the Bishop Museum and the British Museum (Natural History). We have also examined specimens from the Philippine Islands and Indonesia at the U.S. National Museum of Natural History and the California Academy of Sciences. One lot of 15 specimens labeled as *tuka* from Cagayan Island, Philippines (USNM 164978) consisted of but a single 65-mm specimen of *A. tuka* and 14 of *A. smithvanizi*; the latter have been recatalogued as USNM 215964.

The largest specimen of *A. tuka* examined (SU 26951) measures 80 mm SL; it was taken in Dumaguete, Philippines.

Some specimens of *A. pascalus* have been misidentified as *tuka*.

Anthias pascalus

Figures 5 and 6, Tables 1–4

Entonanthias pascalus Jordan and Tanaka 1927, p. 385, pl. 34, fig. 2 (type locality, Okinawa); Kamohara 1958, p. 35 (Kochi, Japan); Katayama 1960, p. 162, pl. 83.

Mirolabrichthys tuka Randall (*non* Herre and Montalban) 1955, p. 61 (Gilbert Islands); Burgess and Axelrod 1973a, p. 422, fig. 269 (Marshall Islands).

Mirolabrichthys tuka pascalus Heemstra 1973, p. 208 (Caroline Islands).

DIAGNOSIS. Dorsal soft rays 15 to 17 (usually 16); anal soft rays 7 (rarely 8); pectoral rays 16 to 19 (modally 18); lateral-line scales 48 to 52; circumpeduncular scales 25 to 27; auxiliary scales present; mandibles scaled; snout fully scaled; dentition as in *A. tuka*; gill rakers 9–11 + 23–27; two or three predorsal bones; a series of prominent papillae along edge of posterior half of orbit; two opercular spines; fifth to tenth dorsal spines the longest, subequal (fifth generally the longest in small individuals, and the tenth usually longest in large adults); snout moderately long, 3.2 to 3.8 in head; depth of body 2.9 to 3.4 in SL; dorsal and anal fins scaled basally; origin of dorsal fin over pectoral base; adult males with caudal lobes, second pelvic ray, and fourth anal ray prolonged and most of soft portion of dorsal fin elevated (sometimes with posterior rays free at tips).

Color in life bright heliotrope; an orange band from snout along lower edge of eye to pectoral base; head and thorax below this band yellowish; membranes of distal half or more of soft portion of dorsal fin of adult males red.

REMARKS. We have collected specimens of *A. pascalus* from the Ryukyu Islands, Marshall Islands, Gilbert Islands, Tuamotu Archipelago, Society Islands, Samoa Islands, and Palau Islands in the depth range of 5 to 45 m. The Academy of Natural Sciences of Philadelphia has two lots from Fiji, previously unreported, which were collected by William F. Smith-Vaniz, Bruce A. Carlson, Barry Goldman, and Dan M. Popper. The California Academy of Sciences has specimens from

Ifaluk and Kapingamarangi in the Caroline Islands. Pierre Fourmanoir kindly sent on loan two specimens from New Caledonia.

Heemstra (1973) commented on the apparent allopatric distribution of *A. pascalus* and the closely related *A. tuka*, suspecting that they were subspecies of a single species. As mentioned, we have specimens of these two forms from the Palau Islands and thus conclude that they are species.

Although *A. pascalus* is wide-ranging in the Central and Western Pacific, it appears to be absent from the Hawaiian Islands, Easter Island, Pitcairn Group, Rapa, Marquesas Islands, and the Line Islands (Christmas Island of this group not visited by us). The species is not yet recorded from the Philippines or Taiwan but might be expected to occur there.

This is the largest species of the subgenus; the largest specimen we have collected (BPBM 19126, 117 mm SL, 170 mm TL) is from Okinawa. The holotype (FMNH 59184, 104.7 mm SL) was first deposited in the Carnegie Museum; it is now at the Field Museum of Natural History, Chicago.

The stomach contents of seven adult specimens from Enewetak, Marshall Islands consisted of unidentified crustacean fragments (36%), calanoid copepods (24%), cyclopoid copepods (19%), fish eggs (9%) decapod crustacean larvae (6%), pteropods (3%), amphipods (2%), ostracods (1%), foraminifera (0.7%), and fish scales (0.3%).

The specimen from the stomach of a *Caranx melampygus* speared in the Gilbert Islands, which was reported by Randall (1955) as *Mirolabrichthys tuka*, is *A. pascalus*.

Anthias smithvanizi new species

Figures 7, 8A and B, Tables 1-4, 6

HOLOTYPE. BPBM 15606, male, 58.2 mm SL. SOLOMON ISLANDS, Alite Reef (off Malaita), outer reef slope on west side, bottom mainly rubble, 60 m, dynamite and rotenone, J.E. Randall, W.A. Starck, II, B. Goldman, and W. Doak, 24 July 1973.

PARATYPES. USNM 215964, 14: 41-58 mm SL, PHILIPPINE ISLANDS, Cagayan Island, 1-18 m, dynamite, Philippine Expedition, "Albatross," 31 March 1909; BPBM 9632, 3: 53.0-55.1 mm SL, PALAU ISLANDS, Augulpelu Reef, SW edge at base of drop-off, 33.5 m, spear and rotenone, J.E. Randall, 22 April 1970; BPBM 15592, 29.3 mm SL, SOLOMON ISLANDS, Savo, SW side, small coral head, 46 m, dynamite, J.E. Randall, B. Goldman, and G.R. Allen, 17 July 1973; BPBM 19694, 5: 36.1-43.3 mm SL, collected with holotype; AMS I.18093-001, 2: 39-42.3 mm SL, collected with holotype; BPBM 15726, 2: 47-52.6 mm SL, NEW BRITAIN, former submarine base near Rabaul, vertical drop-off, 30 m, spear, J.E. Randall, 8 August 1973; ANSP 134046, 53.4 mm SL, E Indian Ocean, COCOS-KEELING ISLANDS, Turk Reef, N side on drop-off (12° 06' 30" S, 96° 49' 35" E), 7.5-18 m, Sta. 15, rotenone, W.F. Smith-Vaniz and P.L. Colin, 1 March 1974; ANSP 134047, 47.5 mm SL, same locality as preceding, 18-24 m, Sta. 24, rotenone, W.F. Smith-Vaniz and P.L. Colin, 7

March 1974; ANSP 134048, 46.8 mm SL, same locality as preceding, 46 m, Sta. 27, rotenone, W.F. Smith-Vaniz and P.L. Colin, 9 March 1974; ANSP 134049, 51.8 mm SL, Cocos-Keeling Islands, West Island, 1.5-3 km E of N end of island (12° 07' 40" S, 96° 49' 50" E), 6-7.5 m, Sta. 38, W.F. Smith-Vaniz et al., 16 March 1974; ANSP 134050, 49: 26.3-47.8 mm SL, same locality as ANSP 134046, 30 m, Sta. 55, rotenone, W.F. Smith-Vaniz and P.L. Colin, 24 March 1974; BPBM 19269, 9: 22.5-54.5 mm SL, INDONESIA, Molucca Islands, Ambon, Latuhalat (south coast of island), isolated coral block off front of fringing reef, small cave in 36.5 m, rotenone, J.E. Randall and G.R. Allen, 21 January 1975; ANSP 134016, 4: 26.5-50.6 mm SL, same data as preceding; USNM 215264, 4: 30.1-47.8 mm SL, same data as preceding; WAM P.25492-001, 4: 27.3-48.3 mm SL, same data as preceding; BPBM 18389, 8: 28.5-52.4 mm SL, MARSHALL ISLANDS, Enewetak Atoll, Rigili (Leroy) Islet, west side (ocean reef), cave in vertical drop-off, 46 m, rotenone, J.E. Randall, G.W. Tribble, A.Y. Suzumoto, and P. Lamberson, 5 July 1975; LACM 35553-1, 8: 28.2-49.3 mm SL, same data as preceding; BPBM 18434, 54.4 mm SL, Marshall Islands, Kwajalein Atoll, outside reef near small boat passage at south end of atoll, steeply sloping bottom of coral, rock and sand in 32 m, quinaldine, J.E. Randall, 18 July 1975; BM(NH) 1976.9.30.13-14, 2: 52.7-57.3 mm SL, NEW BRITAIN, Nodup (near Rabaul), boulder with caves on coral and rubble bottom 35-45 m, rotenone, R. Lubbock and B. Parkinson, 29 July 1975; BM(NH) 1976.9.30.12, 35.3 mm SL, New Britain, Tawui (near Rabaul), former Japanese submarine base, cave on vertical drop-off, 25 m, quinaldine, R. Lubbock, 4 August 1975, BM(NH) 1976.9.30.15, 57.6 mm SL, same locality as preceding, 30 m, quinaldine, R. Lubbock, 7 August 1975.

DIAGNOSIS. Dorsal soft rays 15 to 17 (usually 16); pectoral rays 16 to 18 (rarely 18); lateral-line scales 44 to 48; circumpectuncular scales 23 to 25; no auxiliary scales; mandibles scaled; gill rakers 8 or 9 + 20-24; a row of small forward-projecting canine teeth on side of jaws; about three rows of teeth on palatines at widest place; posterior edge of orbit with fleshy papillae; three opercular spines; snout 4.0 to 4.3 in head; body depth 3.1 to 3.3 in SL; third dorsal spine of males prolonged; soft dorsal and anal fins scaled only at extreme base; colors of fresh specimens as in Figure 8.

DESCRIPTION. Dorsal rays X, 16 (21 paratypes with 16, two with 15, and one with 17), last branched to base; anal rays 11, 7 (23 paratypes with 7, one with 8), last branched to base; pectoral rays 17 (10 paratypes with 16, 13 with 17, and one with 18), upper two and lowermost unbranched; pelvic rays 1, 5; principal caudal rays 15, the uppermost and lowermost unbranched; lateral-line scales 44 (45-48); scales above lateral line to origin of dorsal fin 5 (4-5); scales below lateral line to origin of anal fin 12 (12-14); circumpunctuncular scales 23 (23-25); gill rakers 9 + 24 (8 or 9 + 20-24); branchiostegal rays 7; vertebrae 26; predorsal bones 2.

Body moderately elongate, the depth 3.22 (3.12-3.33) in SL, and moderately compressed, the width 1.8 (1.79-2.01) in depth; head length 3.29 (3.11-3.37) in SL; snout 4.0 (4.05-4.28) in head, the upper lip hypertrophied anteriorly, moder-

Figure 1. *Anthias evansi* Smith, male, 93 mm SL, BPBM 20007, Réunion.



Figure 2. *Anthias parvirostris*. A. Holotype, male, 48.3 mm SL, BPBM 15605, Solomon Islands. B. Paratype, female, 36.1 mm SL, BPBM 20448, Solomon Islands.



ately pointed in males; diameter of orbit 3.87 (3.05–3.62) in head, the edge of the posterior half of the orbit lined with fleshy papillae (25 in holotype, largest dorsoposteriorly); interorbital space convex, the bony width 3.75 (3.74–3.92) in head; least depth of caudal peduncle 2.08 (2.07–2.19) in head.

Mouth oblique and moderately large, the maxilla reaching posterior to a vertical at center of eye; posterior end of maxilla rounded, the greatest depth 1.7 in orbit of holotype; mouth terminal on small individuals but lower jaw inferior on larger ones due to hypertrophy of upper lip. Upper jaw with a band of very small villiform teeth, broadest anteriorly (a few teeth anterior in band slightly enlarged), and a stout short canine tooth or close-set pair of canines at front corner of jaw adjacent and anterior to villiform band; an outer row of slender small forward-projecting curved canines on side of upper jaw (23 on one side of holotype and 26 on the other); lower jaw with a short stout canine tooth or close-set pair of teeth at front on each side

that project diagonally outward and forward; a small patch of small teeth medial to each canine; a single row of small slender curved canines on side of lower jaw, those toward front inclined inward and those posteriorly inclined forward (27 such teeth on each side of jaw of holotype); a small patch of about 9 very small teeth on vomer; palatine with a narrow band of tiny villiform teeth in about 3 irregular rows; tongue pointed, the upper surface with scattered tiny papillae; inner surface of thickened anterior upper lip plicate. Gill membranes free from isthmus. Gill rakers slender, the longest about equal to longest gill filament, 1.6 in orbit of holotype.

Opercle with three flattened spines, the central one the largest and most posterior, the upper one slightly anterior to the lower; two lower spines acute, the upper forming an angle of about 90 degrees; distance between tips of two lower spines about two-thirds the distance between central and upper spines. Lower margin and rounded corner of preopercle smooth; upper



Figure 3. *Anthias tuka* (Herre and Montalban), male, 62 mm SL, BPBM 16056, Solomon Islands.



Figure 4. *Anthias tuka* (Herre and Montalban), female, 50 mm SL, BPBM 16056, Solomon Islands.



Figure 5. *Anthias pascalus* (Jordan and Tanaka), male, 101.5 mm SL, BPBM 12895, Marshall Islands.



Figure 6. *Anthias pascalus* (Jordan and Tanaka), female, 72.5 mm SL, BPBM 6244, Marshall Islands.

margin with 29 serrae on holotype (serrae increase with size, from 14 on 29-mm specimen to 20 on 36-mm specimen, and 29 to 32 on individuals over 55 mm SL).

Anterior nostril in a short membranous tube directly anterior to middle of eye about half the distance from edge of orbit to edge of groove separating upper lip from rest of snout; posterior nostril diagonally upward and posterior to anterior nostril, with little or no rim, separated by a space from the anterior, which is contained about 4.5 times in orbit.

Scales ctenoid; no auxiliary scales on body; head scaled ex-

cept throat, gill membranes, lips, extreme front of snout, and a broad zone in front of eye that contains nostrils in its upper part; dorsal and anal fins scaled only at extreme base (naked anteriorly); caudal fin with small scales more than three-fourths distance to posterior margin; pectoral fins with small scales on approximately the basal fourth; pelvic fins with rows of small scales paralleling rays basally on medial surface.

Some pores of cephalic lateralis system obscured by scales. Those readily apparent are a snout-supraorbital series beginning with a pore in front of anterior nostril, then one between

Table 6. Proportional measurements of type specimens of *Anthias smithvanizi* expressed as a percentage of the standard length.

	Holotype		Paratypes		
	BPBM 15606	BPBM 15592	BPBM 19694	BPBM 19694	BPBM 9632
Standard length (mm)	58.2	29.3	36.1	41.8	55.1
Depth of body	31.0	32.1	31.4	30.0	30.8
Width of body	17.2	16.7	16.4	16.7	16.2
Head length	30.4	32.1	31.6	30.3	29.6
Snout length	7.6	7.5	7.5	7.2	7.3
Diameter of orbit	7.9	10.2	9.1	9.1	8.2
Bony interorbital width	8.1	8.2	8.3	8.1	7.7
Length of maxilla	15.3	15.0	14.5	14.4	14.7
Least depth of caudal peduncle	14.6	14.7	14.4	14.1	14.3
Length of caudal peduncle	22.2	20.6	20.5	21.2	21.8
Predorsal length	29.6	31.7	31.6	30.8	29.4
Preanal length	56.0	59.0	59.3	57.0	58.2
Prepelvic length	32.6	32.7	33.0	32.9	33.5
Length of first dorsal spine	5.7	5.5	5.6	5.7	5.4
Length of third dorsal spine	18.9	13.6	13.3	13.2	16.5
Length of tenth dorsal spine	abnormal	12.3	12.5	12.4	11.8
Length of longest dorsal ray	20.6	17.4	18.6	17.2	20.9
Length of dorsal fin base	58.4	56.3	58.7	57.3	58.0
Length of first anal spine	8.6	7.9	8.0	8.1	7.9
Length of second anal spine	12.0	13.6	12.5	12.7	11.3
Length of third anal spine	13.6	14.0	13.9	13.2	13.6
Length of longest anal ray	26.6	20.8	20.2	21.0	27.3
Length of anal fin base	23.2	21.8	22.4	22.4	22.1
Length of pectoral fin	30.7	30.7	31.2	30.4	29.3
Length of pelvic spine	15.3	17.1	16.7	16.0	15.8
Length of pelvic fin	30.0	29.4	28.3	27.0	36.3
Length of caudal fin	52.8	40.3	44.9	40.2	53.3
Caudal concavity	39.8	26.0	29.1	26.5	40.0

nostrils, a third medial to this, and three in interorbital space; a series near edge of posterior rim of orbit in close association with the fleshy papillae; another series around posterior and lower part of eye, each at the end of a tube radiating from near edge of eye, six in mandibular series beginning in front of lower margin of preopercle, the anterior two close together near front of chin; a median dorsal pore and one to each side are all that are readily seen of the occipital series.

Origin of dorsal fin above upper end of gill opening (and first lateral-line scale); third or fourth dorsal spines longest, apparently depending on sex; of the eight larger specimens (48.5 to 58.2 mm SL) on which the description is based, all are males and all have prolonged third dorsal spines, the spine length 1.61 (1.67–1.98) in head; fourth dorsal spine slightly longer than third in females (to 47 mm SL), the length of fourth 2.04–2.19 in head; a cirrus from interspinous membrane behind tip of each dorsal spine, the one from the prolonged third dorsal spine of males enlarged (cirrus length in holotype 2 in orbit); longest dorsal soft ray (eleventh to fourteenth) 1.48 (1.42–1.84) in head; origin of anal fin slightly posterior to a vertical at base of first dorsal soft ray; third anal spine 2.23 (2.17–2.29) in head; longest anal soft ray (fourth or fifth) 1.14 (1.08–1.56) in head; caudal fin lunate, the lobes filamentous in males, the caudal concavity 2.52 (2.5–3.84) in SL; pectoral fins long, extending to or beyond a vertical at base of third anal spine, the longest ray (ninth or tenth) 3.26 (3.21–3.41) in SL; edges of distal part of longest pectoral rays serrate (Fig. 7); pelvic fins long, reaching to anus in females and beyond spinous portion of anal fin in males due to prolongation of second ray, the fin length 3.33 (2.76–3.7) in SL.

Color in alcohol: uniformly pale with no dark markings. Color of males when fresh: violet, shading nearly to white ventrally, the edges of the scales orange-red on upper half of body gradually becoming lavender ventrally; numerous small yellow spots on side of body and postorbital region of head; a bright yellow horizontal band from front of upper lip to orbit; a median yellow band on head that continues along entire base of dorsal fin; spinous portion of dorsal fin yellow, the spine tips and cirri violet, with a row of violet spots at base, one per membrane, which increase in size posteriorly and merge to form a band that continues and broadens in soft portion of fin and extends out on posterior rays; yellow of spinous portion of dorsal also continuing into soft portion but soon replaced except for a submarginal band by a broad median zone of red; margin of soft portion of fin violet; anal fin pale lavender pink with faint yellow dots on membranes, a submarginal zone of light yellow, and a narrow pale lavender margin; caudal fin with a broad band (narrowing at ends) of heliotrope on edge of upper lobe; below this a narrow irregular orange line and a band of yellow; a broad median zone of deep orange in fin; lower lobe pale lavender faintly blotched with light orange; paired fins whitish with lavender cast; outer part of iris purplish blue, the inner yellow, the two separated by a narrow ring of heliotrope.

Females are similar in color, but there is less violet in the ground color and none on the dorsal fin except for the margin; also the yellow in the fin (except for basal band) is confined to an indistinct submarginal zone in the spinous portion; the cau-

dal fin has broad bands of red-orange on the lobes, the upper with a narrow margin of heliotrope.

REMARKS. We have collected specimens of *A. smithvanizi* in the Solomon Islands, New Britain, Indonesia, Palau Islands, and Marshall Islands. We have examined specimens from the Philippine Islands taken by the "Albatross" and from the Cocos-Keeling Islands, Indian Ocean, collected by William F. Smith-Vaniz and associates. Our specimens were obtained from the depth range of 25 to 60 m, but the Philippine material was collected from 1 to 18 m and one Cocos-Keeling individual from 6 to 7.5 m. This species usually occurs in aggregations and is generally seen in the vicinity of caves or ledges. Although it appears to feed on zooplankton, it does not venture as far from the bottom as most other species of the subgenus.

ETYMOLOGY. Named in honor of William F. Smith-Vaniz of the Academy of Natural Sciences of Philadelphia who kindly made available his Cocos-Keeling specimens of this species for our study of the subgenus; he had independently determined that his specimens represented an undescribed species.

Anthias lori

Figure 9, Tables 1–4, 7

Anthias lori Lubbock and Randall in Fourmanoir and Laboute 1976, p. 287, figs. on pp. 280, 287 (type locality, Point Mackau, Loyalty Islands).

Mirolabrichthys imeldae Burgess 1977, p. 39, figs. on pp. 40, 41 (Philippine Islands).

HOLOTYPE. MNHN 1976-1, 52.9 mm SL, LOYALTY ISLANDS, Maré, Point Mackau (NW end of island), reef in 50 m, rotenone, P. Laboute and Y. Magnier, 21 November 1975.

PARATYPES. BPBM 8597, 45.0 mm SL, TUAMOTU ARCHIPELAGO, Tikahau, outside reef N of pass, 36.5 m, spear (specimen badly damaged by spear), J.E. Randall, 14 June 1957; BPBM 8437, 36.5 mm SL, Tuamotu Archipelago, Tikahau, outside reef in 33.5 m, spear, J.E. Randall, 15 June 1957; BPBM 9629, 2: 48.4–66.0 mm SL, PALAU ISLANDS, Ngemelis Islands, Bairakaseru Island, S end, vertical drop-off, 36.5 m, spear, J.E. Randall, 23 April 1970; BPBM 13998, 3: 36.7–47.5 mm SL, TUAMOTU ARCHIPELAGO, Rangiroa,

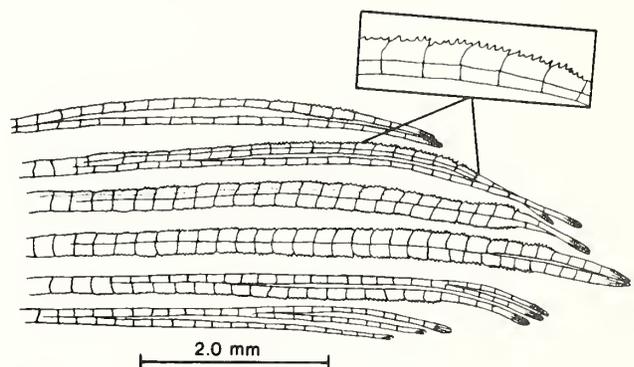


Figure 7. Pectoral fin rays of *Anthias smithvanizi* showing serrae along the edges of the outer part of the longest rays. Drawing by William F. Smith-Vaniz.

Figure 8. *Anthias smithyanizi*. A. Holotype, male, 58.2 mm SL, BPBM 15606, Solomon Islands. B. Paratype, female 43.3 mm SL, BPBM 19694, Solomon Islands.



Figure 9. *Anthias lori*, Lubbock and Randall, paratype, male, 41 mm SL, BPBM 13998, Tuamotu Archipelago.



outside reef 200 m E of Tiputa Pass, 60° slope of coral and sand, 30.5 m. quinaldine, J.E. Randall and D.B. Cannoy, 6 April 1971; ANSP 134017, 47.0 mm SL, collected with holotype; AMS I.18563-001, 33.5 mm SL, collected with holotype; BPBM 14026, 38.6 mm SL, Tuamotu Archipelago, Manihi, outside reef 400 m NW of pass, 27.5 m, spear, J.E. Randall, 11 April 1971; BPBM 14977, 53.6 mm SL, SOCIETY ISLANDS, Tetiaroa, outside reef off west side of Rimatuu Islet, 37–55 m, rotenone, J.E. Randall and R.M. McNair, 19 April 1973; LACM 35552-1, 48.2 mm SL, same data as preceding; USNM 215263, 40.0 mm SL, same data as preceding; WAM P25493-001, 32.7 mm SL, same data as preceding; BM(NH) 1976.9.30.2–3, 2: 50.1–51.5 mm SL, AMERICAN SAMOA, Tutuila, Larsen Bay, 55–60 m, caves at base of steep drop-off, quinaldine, R. Lubbock, 14 September 1975; BM(NH) 1976.9.30.5, 60.4 mm SL, same locality as preceding, quinaldine, R. Lubbock and R.C. Wass, 16 September 1975; BM(NH) 1976.9.30.4, 56.4 mm SL, Society Islands, Tahiti, Arue, 50 m, spear, R. Lubbock, 19 September 1975; BM(NH) 1976.9.30.6–

7, 2: 61.7–64.2 mm SL, PHILIPPINE ISLANDS, Luzon, Batangas Bay, 20 m, R. Lubbock from local aquarium fish collectors, 29 June 1976.

DIAGNOSIS. Dorsal soft rays 16 or 17 (rarely 17); pectoral rays 16 to 18 (rarely 16); lateral-line scales 49 to 52; circumduncular scales 25 to 28; no auxiliary scales; mandibles scaled; gill rakers 8 or 9 + 21–24; a row of small forward-projecting canine teeth on side of jaws; palatines with only a few rudimentary teeth anteriorly; posterior edge of orbit with fleshy papillae; three opercular spines; snout 3.6 to 4.1 in head; body depth 3.4 to 4.0 in SL; third dorsal spine of males prolonged; soft dorsal and anal fins scaled only at extreme base; colors of fresh specimens as in Figure 9.

DESCRIPTION. Dorsal rays X,16 (one of 16 paratypes with 17), last branched to base; anal rays III,7 (one of 16 paratypes with 8), last branched to base; pectoral rays 17 (six of 16 paratypes with 18 and one with 16); upper two and lowermost unbranched; pelvic rays I,5; principal caudal rays 15, the uppermost and lowermost unbranched; lateral-line scales 52



Figure 10. *Anthias dispar* (Herre), male, 54 mm SL, BPBM 16139, Solomon Islands.



Figure 11. *Anthias dispar* (Herre), female ?, 41 mm SL, BPBM 7556, Line Islands.



Figure 12. *Anthias ignitus*, holotype, male, 58.3 mm SL, BPBM 18858, Maldives Islands.

(49–52); scales above lateral line to origin of dorsal fin 5; scales below lateral line to origin of anal fin 14 (13–15); circumpeduncular scales 26 (25–28); gill rakers 9 + 22 (8–9 + 21–24); branchiostegal rays 7; vertebrae 26; predorsal bones 2.

Body elongate, the depth 3.36 (3.46–4.03) in SL, and moderately compressed, the width 2.0 (1.56–1.85) in depth; head length 3.54 (3.28–3.49) in SL; snout 4.1 (3.58–4.0) in head, the upper lip hypertrophied anteriorly, moderately pointed in males; diameter of orbit 3.54 (3.3–3.86) in head; the edge of the posterior half of orbit lined with fleshy papillae 20 (25 on

66-mm paratype, 32 on 41-mm paratype due to very small ones at upper and lower edges of eye that continue anterior to center of eye, especially those on lower edge); interorbital space convex, the bony width 3.93 (3.54–4.02) in head; least depth of caudal peduncle 2.09 (2.06–2.25) in head.

Mouth oblique and moderately large, the maxilla reaching posterior to a vertical at rear edge of pupil; posterior end of maxilla rounded, the greatest depth 1.9 in orbit of holotype. Dentition very similar to that of *A. smithvanizi*, the teeth along side of upper jaw 20 or 23 in holotype (22 or 25 in largest para-

Table 7. Proportional measurements of type specimens of *Anthias lori* expressed as a percentage of the standard length.

	Holotype		Paratypes			
	MNHN 1976–1	BPBM 13998	BPBM 13998	BPBM 13998	BPBM 14977	BPBM 9629
Standard length (mm)	52.9	36.7	41.0	47.5	53.6	66.0
Depth of body	29.8	24.8	25.6	26.6	26.2	28.9
Width of body	14.9	16.5	15.6	14.9	15.0	15.6
Head length	28.3	29.7	30.2	29.6	28.7	30.5
Snout length	6.9	8.3	8.0	7.4	7.4	8.1
Diameter of orbit	8.0	9.0	8.5	8.5	8.0	7.9
Bony interorbital width	7.2	8.0	8.3	7.9	7.4	7.6
Length of maxilla	13.3	15.0	14.7	14.2	13.9	15.2
Least depth of caudal peduncle	13.5	13.9	13.4	13.4	13.9	14.1
Length of caudal peduncle	23.4	23.4	22.9	23.4	23.0	22.4
Predorsal length	30.3	31.9	31.1	29.8	30.4	30.9
Preanal length	58.9	57.2	57.0	56.8	56.3	58.3
Prepelvic length	30.2	31.7	31.7	31.1	32.2	32.9
Length of first dorsal spine	5.5	4.6	4.5	—	5.6	5.7
Length of third dorsal spine	13.2	12.3	15.8	18.1	16.5	25.8
Length of tenth dorsal spine	11.3	10.9	10.3	10.6	10.6	11.2
Length of longest dorsal ray	14.7	15.2	14.4	14.6	15.0	15.4
Length of dorsal fin base	56.4	57.2	56.1	54.2	55.8	56.0
Length of first anal spine	7.0	7.6	6.6	6.4	6.1	7.6
Length of second anal spine	11.1	11.4	11.0	10.5	10.4	10.9
Length of third anal spine	12.1	12.2	12.5	11.7	12.1	13.3
Length of longest anal ray	21.4	20.4	20.0	20.2	22.8	24.1
Length of anal fin base	20.8	21.3	21.4	21.7	21.6	21.6
Length of pectoral fin	29.6	30.8	28.6	28.5	30.1	29.8
Length of pelvic spine	14.2	14.9	13.6	14.3	14.5	14.7
Length of pelvic fin	25.0	25.1	26.8	29.8	29.9	36.1
Length of caudal fin	46.3	35.2	37.9	58.8	47.4	45.5
Caudal concavity	33.8	24.0	25.4	45.7	35.2	34.8

type) and about 27 in lower jaw (26 in largest paratype); vomer with even fewer teeth than *A. smithvanizi*, and palatines with only a few rudimentary teeth anteriorly. Tongue pointed, the upper surface with scattered tiny papillae; inner surface of thickened anterior upper lip plicate. Gill membranes free from isthmus. Gill rakers slender, the longest longer than gill filaments, 1.6 in orbit of holotype.

Opercle with three flattened spines as in *A. smithvanizi*. Lower margin and rounded corner of preopercle smooth; upper margin with 27 serrae on holotype on one side, 30 on other (serrae tending to increase with size from 14 on a 24-mm specimen to 22 on a 39-mm specimen, 24 to 26 on 48-mm specimens, and 29 on 66-mm specimen).

Nostrils, pores of head and scales as in *A. smithvanizi*.

Origin of dorsal fin slightly posterior to upper end of gill opening (over second lateral-line scale); third or fourth dorsal spines the longest, apparently depending on sex, the third spine prolonged on males, 2.14 (1.18–1.91) in head (longer on larger males); fourth spine only slightly longer than third on females (fourth of a 36.7-mm specimen 2.34 in head); a cirrus from interspinous membrane behind tip of each dorsal spine, but not notably prolonged on third dorsal spine of males; longest dorsal soft ray (tenth or eleventh) 1.93 (1.91–2.1) in head; origin of anal fin in line with base of third dorsal soft ray; third anal spine 2.35 (2.29–2.53) in head; longest anal soft ray (fourth or fifth) 1.32 (1.26–1.51) in head; caudal fin lunate, the lobes more elongate in males, the caudal concavity 2.96 (2.19–4.17) in SL; pectoral fins long, extending nearly to or beyond a vertical at origin of anal fin, the longest ray (ninth or tenth) 3.38 (3.24–3.51) in SL; edges of distal part of longest pectoral rays serrate; pelvic fins of females reaching slightly beyond anus, of males to or well beyond origin of anal fin, the length of fin 3.73 (2.77–3.99) in SL.

Color in alcohol: uniformly pale with no dark markings. Life color of holotype not recorded. Color of 41-mm paratype (a small male) when fresh: pinkish tan dorsally shading to whitish ventrally with a lavender cast; edges of many scales yellow and of others dull violet on side of body and dorsally below anterior portion of dorsal fin, thus forming a reticular pattern; a series of five red blotches on back between lateral line and base of dorsal fin, the first four nearly quadrangular in shape, the first (poorly defined) beneath bases of seventh and eighth dorsal spines, the second below last two spines and associated membranes, the third below second to fourth (nearly fifth) dorsal soft rays, the fourth below seventh to ninth soft rays, and the last a smaller semicircular spot below eleventh to thirteenth rays; a broad longitudinal red band, narrowly edged in lavender, posteriorly on body covering most of upper half of caudal peduncle and extending forward to beneath twelfth dorsal soft ray; thickened anterior part of upper lip yellow, the side of lip lavender; tip of lower jaw pink shading to lavender on side of lower lip; dorsal, anal, and paired fins nearly colorless, the dorsal with spine tips lavender and ray tips light blue, with a broad basal zone of light blue and a broader outer zone of dull yellow in spinous portion and dull orange on soft portion; anal fin faintly light bluish with faint yellowish spots; caudal fin with lobes broadly reddish mixed with yellowish with a narrow upper and lower margin of

lavender; central and posterior margin of fin colorless; pectoral fins whitish; pelvic fins clear with a faint tinge of yellow; iris violet with an inner rim of light yellow.

A color slide of the female form of the species was lost; the color was recalled as not being very different from the male. Females also have the series of quadrangular red blotches along the back.

REMARKS. *A. lori* was briefly described by Lubbock and Randall in Fourmanoir and Laboute (1976); a full description is given above. The holotype, collected by Pierre Laboute and Yves Magnier in the Loyalty Islands, was sent to us by Pierre Fourmanoir. We have collected paratypes in the Tuamotu Archipelago, Society Islands, Samoa Islands, Palau Islands, and the Philippine Islands. The senior author has observed the species in 20 m off the island of Manado Tua, north of Manado, Celebes. Bruce A. Carlson photographed an individual of this species in 40 m on a drop-off at the east side of the entrance to Suva Harbor, Fiji Islands.

The senior author and Gerald R. Allen collected three small specimens of *A. lori* (BPBM 19300, 23.8–29.8 mm SL) at Ambon, Molucca Islands, Indonesia on 24 January 1975. The fish were taken with rotenone on a steep drop-off with caves in 24–33 m off a point just NW of the village of Silale on the SE side of Ambon Bay near the entrance to the bay. An accurate lateral-line scale count was possible for only one specimen (49 pored scales); another, however, seems to have 48 scales, which would be the lowest count of the species. Because of the poor condition of the specimens, they are not designated as paratypes.

A. lori is very similar in its mode of life to *A. smithvanizi*.

ETYMOLOGY. Named *lori*, a noun in apposition, after the daughter of the senior author; the illustrated specimen was collected on her birthday.

Anthias dispar

Figures 10 and 11, Tables 1–4

Mirolabrichthys dispar Herre 1955, p. 224 (type locality, Gizo Island, Solomon Islands); Heemstra 1973, p. 208 (New Georgia); Burgess and Axelrod 1975, pp. 1472, 1473, 1476, figs. 147–149, 154 (New Hebrides).

DIAGNOSIS. Dorsal soft rays 16 to 18 (usually 17); anal soft rays 7 to 8 (rarely 8); pectoral rays 18 to 20 (rarely 18); lateral-line scales 55 to 63; circumpeduncular scales 32 to 35; no auxiliary scales; mandibles scaled; side of snout (including region of nostrils) naked; a row of small slender canine teeth along sides of jaws, angled forward (except those anteriorly which are vertical); villiform teeth in a few rows anteriorly in jaws, absent along side of lower jaw but present as a single inner row on side of upper jaw; stout canine teeth in jaws as described for the genus; gill rakers 9–12 + 22–26; one predorsal bone; no papillae on edge of orbit; two opercular spines; snout not very long, 3.1 to 4.2 in head; depth of body 2.7 to 3.2 in SL; soft dorsal and anal fins scaled only basally; origin of dorsal fin slightly anterior to upper end of gill opening; first dorsal spine short; second dorsal spine the longest, but not prolonged; sec-

ond pelvic ray slightly prolonged in females, very elongate in males, reaching beyond base of anal fin; no dorsal or anal soft rays prolonged; caudal lobes slightly produced, more so in males than females; preopercular serrae 7 to 16.

Color of females in life: yellow-orange dorsally shading to whitish ventrally with a tinge of lavender; a horizontal orange band on snout continuing faintly from lower eye toward pectoral base; dorsal fin red (more intensely anteriorly) with a narrow lavender margin; caudal fin yellow, becoming orange red on posterior margin and tips of lobes; remaining fins whitish with lavender tinge. Color of males in life: upper head and anterior body to a diagonal at about base of third dorsal spine heliotrope; back posterior to this demarcation yellow, shading to lavender on caudal peduncle; lower half of head and body lavender; an orange band from snout tip to eye and an orange-yellow band from lower eye to edge of operculum at level of upper pectoral base; dorsal fin red (deep red anteriorly) with a lavender margin and a violet line at base (more evident on soft portion of fin); caudal fin orange-red, shading distally to pink, the upper and lower margins and tips of caudal lobes lavender; remaining fins pale lavender.

REMARKS. *A. dispar* is known in the literature only from Herre's six type specimens (holotype and five paratypes catalogued under number UW 10628, School of Fisheries, University of Washington; the holotype measures 49 mm SL) from Gizo, Solomon Islands, three specimens reported by Heemstra (1973) from New Georgia, Solomon Islands, (now in the U.S. National Museum of Natural History), and five specimens reported by Katayama (1979) from Ishigaki, Ryukyu Islands. We have collected *A. dispar* in the Solomon Islands (Florida Island and Alite Reef), Bismarck Archipelago (New Britain and Admiralty Islands), American Samoa (Tutuila), Marshall Islands (Kwajalein and Majuro), Line Islands (Fanning), and Indonesia (Ambon) in the depth range of 1 to 15 m. These specimens have been deposited in the Bishop Museum and British Museum (Natural History); in addition, the Bishop Museum has a specimen from Fiji collected by Bruce A. Carlson. This species does not appear to range as far eastward in Oceania as French Polynesia, a region extensively collected by us, and it is not known from the Indian Ocean.

The largest specimen, BPBM 17509, 64 mm SL, was collected in American Samoa.

Anthias ignitus new species

Figure 12, Tables 1-4, 8

HOLOTYPE. BPBM 18858, male, 58.3 mm SL, MALDIVE ISLANDS, North Male Atoll, Villingili, lagoon reef, 25 m, spear, J.E. Randall, 16 March 1975.

PARATYPES. AMS I.19219-001, 50.2 mm SL; BM(NH) 1976.9.30.8, 59.4 mm SL; CAS 37888, 47.8 mm SL; LACM 35905-1, 57.9 mm SL; USNM 216494, 49.1 mm SL; MALDIVE ISLANDS, all collected with holotype; BM(NH) 1977.5.11.5-6, 2: 55.5-70.3 mm SL, ANDAMAN SEA, Similan Islands, N tips of Similan Island, 18 m, *Millepora*, quinaldine, R. Lubbock and N. Polunin, 11 March 1977.

DIAGNOSIS. Dorsal soft rays 16 or 17 (usually 16); pectoral

rays 19 to 20 (usually 20); lateral-line scales 53 to 58; circum-peduncular scales 29 to 33; no auxiliary scales; mandibles scaled; gill rakers 11 or 12 + 22-25; a row of moderate forward-projecting canine teeth on side of jaws; five to six rows of teeth on palatines at widest place; no papillae on edge of orbit; three opercular spines; snout 3.8 to 4.5 in head; body depth 2.8 to 3.0 in SL; no prolonged dorsal spines in males; soft dorsal and anal fins naked except extreme base of posterior part of dorsal fin; colors of fresh male as in Figure 12.

DESCRIPTION. Dorsal rays X,16 (16 or 17, three paratypes with 17); anal rays III,7; pectoral rays 20 (19 or 20; one paratype with 19), upper two and occasionally lower unbranched; pelvic rays I,5; principal caudal rays 15, upper and lower unbranched; lateral-line scales 55 (53-58); scales above lateral line to origin of dorsal fin 8 (8-9); scales below lateral line to origin of anal fin 22 (22-25); circumpeduncular scales 31 (29-33); gill rakers 11 + 24 (11-12 + 22-25); branchiostegal rays 7; vertebrae 26; predorsal bones 1.

Body somewhat elongate, the depth 2.87 (2.53-2.97) in SL; body moderately compressed, the width 2.23 (2.05-2.54) in depth; head length 3.15 (3.03-3.24) in SL; snout 3.87 (3.62-4.47) in head; front of upper lip of males thickened, somewhat pointed, and freely movable dorsoventrally; diameter of orbit 4.28 (3.56-4.43) in head; posterior edge of orbit without fleshy papillae; interorbital space convex, the bony width 4.23 (3.81-4.40) in head; least depth of caudal peduncle 2.28 (2.23-2.39) in head.

Mouth oblique and moderately large, the maxilla reaching to or posterior to a vertical at rear edge of pupil; mouth terminal except on large males where it is slightly inferior due to hypertrophy of upper lip; posterior end of maxilla rounded, the greatest depth 1.38 in orbit of holotype; no supplemental maxillary bone. Dentition generally as for *A. bartlettorum*; palatines with three to six irregular rows of villiform teeth at broadest place; tongue pointed, the upper surface with scattered very small papillae. Gill membranes free from isthmus. Gill rakers slender and long (largest 1.10 in orbit of holotype), notably longer than gill filaments (longest gill filament of first gill arch of holotype contained 1.50 in longest raker).

Opercle with three flattened spines, the central one the largest and most posterior, the upper slightly anterior to lower; two lower spines acute, the upper obtuse and indistinct; distance between tips of two lower spines about half the distance between central and upper spines; lower margin of preopercle smooth; rounded corner and upper margin serrate (14 serrae on holotype).

Anterior nostril in a short membranous tube (higher dorso-posteriorly) directly anterior to middle of eye about half the distance from edge of orbit to edge of groove separating upper lip from rest of snout; posterior nostril diagonally upward and posterior to anterior nostril, with little or no rim, and large, the greatest diameter of opening about equal to distance between nostrils, 5.78 in orbit of holotype.

Scales ctenoid; no auxiliary scales on body; head scaled except mandibles, throat and gill membranes, lips, extreme front of snout, and a broad zone on side of snout anterior to eye that includes nostrils in its upper part; dorsal and anal fins naked except extreme base of posterior part of dorsal fin; caudal fin

with small scales more than three-fourths distance to posterior margin; pectoral fins with small scales on basal third or more of fin; pelvic fins basally with small scales on rays.

Lateral line a smooth curve following contour of back, the last pored scale slightly anterior to end of hypural plate. Some pores of cephalic lateralis system obscured by scales. Prominent are a pore in front of anterior nostril, one between nostrils, one medial to nostrils, two close together in interorbital space above front of eye, a series near edge of orbit around posterior half of eye, five or six on suborbital and preorbital region ante-

rior to a vertical through center of eye, and six in a mandibular series beginning at lower margin of preopercle (last two on chin close together).

Origin of dorsal fin on a vertical through posterior margin of preopercle; first dorsal spine short, 12.19 (5.13–11.8) in head; no marked prolongation of dorsal spines, the longest 2.28 in head; longest dorsal soft ray 2.25 (1.98–2.31) in head; third anal spine 3.56 (3.68–4.32) in head; longest anal soft ray 2.07 (2.03–2.31) in head; caudal fin lunate, the lobes somewhat filamentous, the caudal concavity 4.29 (2.97–4.50) in SL; pec-

Table 8. Proportional measurements of type specimens of *Anthias ignitus* expressed as a percentage of the standard length.

	Holotype		Paratypes		
	BPBM 18858	CAS 37888	USNM 216494	AMS 1.19219-001	BM(NH) 1976.9.30.8
Standard length (mm)	58.3	47.8	49.1	50.2	59.4
Depth of body	34.8	35.6	35.0	33.7	34.2
Width of body	15.6	15.1	13.8	15.3	16.2
Head length	31.7	32.6	33.0	31.5	31.3
Snout length	8.2	7.3	8.6	7.6	7.6
Diameter of orbit	7.4	9.0	8.8	8.8	7.7
Bony interorbital width	7.5	7.5	7.5	7.8	7.6
Length of maxilla	16.3	15.7	14.9	15.7	15.5
Least depth of caudal peduncle	13.9	14.6	13.8	14.1	14.0
Length of caudal peduncle	13.7	16.9	14.9	16.3	14.8
Predorsal length	23.3	27.1	27.1	25.1	24.7
Preanal length	64.0	64.6	67.2	64.9	65.0
Prepelvic length	35.7	34.3	36.7	36.7	34.7
Length of first dorsal spine	2.6	3.3	4.5	3.6	6.1
Length of second dorsal spine	9.6	9.2	12.4	12.4	9.5
Length of third dorsal spine	11.7	13.8	11.4	12.9	13.5
Length of tenth dorsal spine	13.9	12.8	14.1	13.1	13.5
Length of longest dorsal ray	14.1	16.5	14.3	14.9	14.0
Length of dorsal fin base	65.4	63.2	62.3	63.1	62.8
Length of first anal spine	2.2	3.8	2.2	3.0	1.3
Length of second anal spine	6.0	7.1	5.7	5.4	5.2
Length of third anal spine	8.9	8.6	8.1	8.0	7.4
Length of longest anal ray	15.3	15.3	14.3	15.5	14.6
Length of anal fin base	18.0	16.5	16.5	16.1	15.3
Length of pectoral fin	27.8	32.0	29.7	31.1	26.4
Length of pelvic spine	11.8	13.4	13.4	13.7	14.3
Length of pelvic fin	39.3	32.4	34.4	41.4	51.7
Length of caudal fin	35.5	38.3	34.8	35.9	41.1
Caudal concavity	23.3	25.1	22.2	23.4	27.1

toral fin length 3.60 (3.13–3.99) in SL; pelvic fins rather long, 2.54 (1.65–3.09) in SL, reaching well beyond spinous portion of anal fin in four largest Maldive specimens and in larger Andaman Sea specimen.

Color in alcohol: light brown with no dark markings. Color of male holotype when fresh (from transparency): head and body orange, becoming reddish-orange dorsally; orange of ventral part of body suffused with lavender, especially just below pectoral fin; head light yellow ventrally; an orange stripe margined with lavender from tip of snout through lower part of eye to edge of operculum immediately anterior to upper pectoral fin base; a small red spot at pectoral fin base; iris orange and lavender ventrally, greenish dorsally; dorsal fin primarily bright red with violet distal margin; base of dorsal fin yellow from about third soft ray backwards, the extent of yellow increasing posteriorly (basal quarter of eleventh, basal half of fourteenth, and basal five-sixths of sixteenth soft rays yellow); anal fin lavender hyaline; caudal fin orange basally shading to red on lobes, becoming yellow centroposteriorly, with narrow violet upper and lower margins; pectoral fins orange-yellow; pelvic fins yellow, shading to lavender distally on filament. Color of female paratype (55.6 mm SL) similar but significantly less intense.

REMARKS. Known only from six specimens speared in the lagoon of North Male Atoll, Maldive Islands, and two specimens from the Similan Islands, Andaman Sea.

A. ignitus is most closely related to *A. dispar*, differing in lower though overlapping dorsal ray and scale counts, higher average number of upper-limb gill rakers, higher number of palatine teeth rows, and in color.

ETYMOLOGY. Named *ignitus* in reference to its flame-like hues.

Anthias bicolor

Figures 13 and 14, Tables 1–4

Anthias bicolor Randall 1979, p. 6, figs. 2 and 3 (type locality, Oahu, Hawaiian Islands).

DIAGNOSIS. Dorsal soft rays 16 to 18 (usually 17); anal soft rays 7 or 8 (rarely 8); pectoral rays 19 to 21 (rarely 21); lateral-line scales 57 to 64; circumpeduncular scales 31 to 33; no auxiliary scales; mandibles naked, snout with a naked zone anterior to eye containing nostrils; a row of small slender canine teeth along sides of jaws, those posteriorly inclined slightly forward; an inner band of villiform teeth in upper jaw and anteriorly in lower jaw; stout canines as described for the genus; vomerine teeth enlarged; gill rakers 11–12 + 26–29; one predorsal bone; no papillae on edge of orbit; three opercular spines; snout 3.4 to 4.3 in head; depth of body 2.7 to 3.0 in SL; soft portions of dorsal and anal fins scaled basally; origin of dorsal fin anterior to a vertical at upper end of gill opening; third dorsal spine prolonged in adult females, and second and third dorsal spines very prolonged in males, the tips fleshy; pelvic and caudal lobes filamentous, particularly in males.

Color in life: upper half of body yellow-orange, lower half lavender pink; males with tips of second and third dorsal spines yellow.

REMARKS. *A. bicolor* is the widest ranging species of the

subgenus. Randall (1979) reported specimens from the Hawaiian Islands (the only member of the subgenus at this locality), Marshall Islands, Loyalty Islands, New Guinea, Maldive Islands, and Mauritius in the depth range of 18 to 68 m.

The junior author collected two specimens [BM(NH) 1977.1.21.4–5, 39.9–42.3 mm SL] at Apo Island off Negros Oriental, Philippine Islands, in 45 m on 24 June 1976.

The largest specimen, BPBM 10173, 111 mm SL, was collected in Hawaii.

Anthias bartlettorum new species

Figures 15 and 16, Tables 1–4, 9

HOLOTYPE. BPBM 17981, male, 54.2 mm SL, MARSHALL ISLANDS, Kwajalein, outer reef off E nubuj Islet at southern end of atoll, upper end of 60° to 70° drop-off, 8 to 10 m, spear and quinaldine, J.E. Randall, 10 December 1974.

PARATYPES. AMS I.19218-001, 42.8 mm SL, MARSHALL ISLANDS, collected with holotype; BPBM 20449, 40.7 mm SL, collected with holotype; BM(NH) 1976.9.30.1, 47.7 mm SL, collected with holotype; CAS 37889, 40.3 mm SL, collected with holotype; USNM 216495, 52.4 mm SL, collected with holotype; BPBM 19969, 2: 53–61.4 mm SL, Marshall Islands, Kwajalein, 100 m NW of small boat passage at S end of atoll (just SE of E nubuj Islet), steep outer reef slope, 10 m, spear, J.E. Randall, 7 April 1976; LACM 35906-1, 51.8 mm SL, same data as preceding; MNHN 1976-125, 58.0 mm SL, same data as preceding.

DIAGNOSIS. Dorsal soft rays 17 or 18 (rarely 18); pectoral rays 20 or 21 (rarely 20); lateral-line scales 54 to 58; circumpeduncular scales 29 to 32; no auxiliary scales; mandibles naked; gill rakers 10 or 11 + 23–26; a row of moderate forward-projecting canine teeth on side of jaws; three to five rows of teeth on palatines at widest place; no papillae on edge of orbit; three opercular spines; snout 3.7 to 4.4 in head; body depth 2.9 to 3.1 in SL; second dorsal spine of males prolonged; dorsal and anal fins not scaled; colors of fresh specimens as in Figures 15 and 16.

DESCRIPTION. Dorsal rays X, 17 (17 or 18, only one fish with 18); anal rays III, 7; pectoral rays 21 (one paratype with 20 on one side), upper two unbranched; pelvic rays I, 5; principal caudal rays 15, upper and lower unbranched; lateral-line scales 55 (54–58); scales above lateral line to origin of dorsal fin 8 (8–9); scales below lateral line to origin of anal fin 23 (21–25); circumpeduncular scales 30 (29–32); gill rakers 11 + 23 (10–11 + 24–26); branchiostegal rays 7; vertebrae 26; predorsal bones 1 or 2.

Body somewhat elongate, the depth 2.93 (2.88–3.05) in SL; body moderately compressed, the width 2.20 (2.04–2.16) in depth; head length 3.27 (3.08–3.19) in SL; snout 4.03 (3.67–4.43) in head; front of upper lip of males thickened, somewhat pointed, and freely movable dorsoventrally; diameter of orbit 3.86 (3.30–3.64) in head; posterior edge of orbit without fleshy papillae; interorbital space convex, the bony width 3.86 (4.00–4.23) in head; least depth of caudal peduncle 2.27 (2.32–2.38) in head.

Mouth oblique and moderately large, the maxilla reaching to



Figure 13. *Anthias bicolor* Randall, male, 99.2 mm SL, BPBM 10146. Hawaiian Islands.



Figure 14. *Anthias bicolor* Randall, female, 83.5 mm SL, BPBM 10173, Hawaiian Islands.

or posterior to a vertical at rear edge of pupil; mouth terminal except on large males where it is slightly inferior due to hypertrophy of upper lip; posterior end of maxilla rounded, the greatest depth 1.4 in orbit of holotype; no supplemental maxillary bone. Upper jaw with a band of villiform teeth, the band broader anteriorly, the teeth at the front enlarged; two large canine teeth anteriorly on each side of upper jaw (one laterally at front of jaw, perpendicular in jaw and not curved, and a smaller slightly curved one that lies nearly flat at posterior edge of the anterior band of villiform teeth); an outer row of enlarged teeth (15 on holotype) on side of jaw, the more posterior ones inclined forward and outward; lower jaw with a patch of villiform teeth anteriorly, the front ones enlarged; two large curved canine teeth on each side of lower jaw (one laterally at front of jaw, inclined outward, and the other about one-third back in jaw, curved slightly posteriorly); a row of moderate canines (11 to 13 on holotype) on side of jaw posterior to second large canine; vomer with small teeth; palatines with a patch of villiform teeth in three to five irregular rows at broadest place; tongue pointed, the upper surface with scattered very small pa-

pillae. Gill membranes free from isthmus. Gill rakers slender and long (largest 1.3 in orbit of holotype), notably longer than gill filaments (longest gill filament of first gill arch of holotype contained 1.5 in longest raker).

Opercle with three flattened spines, the central one the largest and most posterior, the upper slightly anterior to lower; two lower spines acute, the upper obtuse and indistinct; distance between tips of two lower spines about one-third to one-quarter the distance between central and upper spines; lower margin of preopercle smooth; rounded corner and upper margin serrate (19 serrae on holotype).

Anterior nostril a short membranous tube (higher dorsoposteriorly), directly anterior to middle of eye about half the distance from edge of orbit to edge of groove separating upper lip from rest of snout; posterior nostril diagonally upward and posterior to anterior nostril, with little or no rim, and large, the greatest diameter of opening about equal to distance between nostrils, 7.2 in orbit of holotype.

Scales ctenoid, no auxiliary scales on body; head scaled except mandibles, throat and gill membranes, lips, extreme front

of snout, and a broad zone on side of snout anterior to center of eye that includes nostrils in its upper part; dorsal and anal fins naked, caudal fin with small scales more than three-fourths distance to posterior margin; pectoral fins with small scales on basal third or more of fin; pelvic fins with small scales near base.

Lateral line a smooth curve following contour of back, the last pored scale slightly anterior to end of hypural plate. Some pores of cephalic lateralis system obscured by scales. Prominent are a pore in front of anterior nostril, one between nostrils,

a series near edge of orbit around posterior half of eye extending into suborbital and preorbital region, and a mandibular series beginning at end of lower margin of preopercle.

Origin of dorsal fin nearer a vertical at upper end of preopercular margin than upper end of gill opening; second dorsal spine of females 5.81–6.67 in SL; second dorsal spine of males prolonged, 2.95 (2.68–3.57) in SL; longest dorsal soft ray 1.80 (1.89–2.44) in head; third anal spine 3.02 (3.15–3.47) in head; longest anal soft ray 1.75 (1.86–2.16) in head; caudal fin lunate, the lobes filamentous, the caudal concavity 7.13 (6.29–

Table 9. Proportional measurements of type specimens of *Anthias bartlettorum* expressed as a percentage of the standard length.

	Holotype		Paratypes		
	BPBM 17981	CAS 37889	BPBM 20449	BM(NH) 1976.9.30.1	USNM 216495
Standard length (mm)	54.2	40.3	40.7	47.7	52.4
Depth of body	34.1	34.7	33.7	34.6	32.8
Width of body	15.5	16.1	16.5	16.8	15.3
Head length	30.6	32.5	32.4	32.3	31.3
Snout length	7.6	7.4	7.4	8.8	7.1
Diameter of orbit	7.9	9.2	9.8	9.0	8.6
Bony interorbital width	7.9	7.7	8.1	8.0	7.8
Length of maxilla	16.6	15.4	15.7	16.4	16.8
Least depth of caudal peduncle	13.5	14.1	14.0	13.6	13.8
Length of caudal peduncle	13.5	13.9	13.0	13.2	13.1
Predorsal length	24.7	26.6	26.8	7.9	24.8
Preanal length	64.2	66.7	64.1	64.4	66.2
Prepelvic length	33.9	37.2	34.9	37.7	36.5
Length of first dorsal spine	8.9	5.7	6.9	8.2	6.7
Length of second dorsal spine	33.9	17.1	15.0	37.3	17.2
Length of third dorsal spine	8.5	9.4	10.1	9.2	8.4
Length of tenth dorsal spine	12.0	11.7	11.5	12.2	11.5
Length of longest dorsal ray	17.0	15.9	13.3	17.2	13.5
Length of dorsal fin base	64.6	63.8	64.6	64.4	62.2
Length of first anal spine	4.1	3.7	3.7	3.6	3.4
Length of second anal spine	7.6	8.9	8.1	7.5	7.8
Length of third anal spine	10.1	9.4	9.3	9.6	9.9
Length of longest anal ray	17.5	15.4	15.5	17.4	14.5
Length of anal fin base	17.9	18.1	17.0	18.0	16.2
Length of pectoral fin	29.0	31.8	31.0	30.0	28.1
Length of pelvic spine	15.9	14.4	15.5	14.3	14.3
Length of pelvic fin	34.1	28.8	29.7	41.5	26.5
Length of caudal fin	42.8	36.7	38.6	47.0	36.1
Caudal concavity	28.8	22.6	23.6	21.1	24.1

8.33) in SL; pectoral fin length 3.45 (3.14–3.56) in SL; pelvic fins long in males, 2.93 (2.33–2.70) in SL, reaching beyond spinous portion of anal fin; pelvic fins shorter in females, 3.37–3.77 in SL, reaching beyond anus but not to anal fin origin.

Color in alcohol: pale with no dark markings. Color of male holotype when fresh (from transparency): body mainly lavender, becoming lighter ventrally; upper part of body posterior to third or fourth dorsal spines increasingly bright yellow until, at caudal peduncle, the dorsal half is yellow; a short yellow bar over dorsal half of body below eighth and ninth dorsal spines; head lavender, shading to reddish dorsally and pale yellowish ventrally; dusky orange band from tip of snout through lower part of eye, then passing obliquely downward onto preoperculum, fainter posteriorly; iris dusky orange; dorsal fin anterior to fourth or fifth spines lavender with exception of yellow distal half of second spine, remainder bright yellow; anal fin pale lavender with a broad reddish margin on anterior part of fin to fourth soft ray; caudal fin bright yellow, less intense towards concavity, with violet upper and lower margins; pectoral fins hyaline; pelvic fins pale lavender with a broad reddish anterior margin.

Color of 40.7-mm-SL female paratype (BPBM 20449) when fresh (from transparency): upper two-fifths of head and body bright yellow; rest of body abruptly lavender, becoming lighter over abdomen and thorax; postorbital part of head lavender just below dorsal yellow zone, soon shading to whitish ventrally; a dusky orange band from tip of snout through lower part of eye, then passing obliquely downward onto preoperculum, fainter posteriorly; iris dusky orange; dorsal fin yellow, with exception of first and second spines and tips of other spines, which are lavender; anal fin pale lavender; caudal fin yellow, less intense toward concavity, with violet upper and lower margins; pectoral fins hyaline; pelvic fins pale lavender.

REMARKS. This species is known only from the atoll of Kwajalein in the Marshall Islands, though doubtless it will turn up elsewhere in Oceania.

ETYMOLOGY. Named *bartlettorum* in honor of Nathan and Patricia Bartlett, formerly of Kwajalein, Marshall Islands, whose underwater photos of this fish first revealed its existence.

Anthias regalis new species

Figures 17 and 18, Tables 1-4, 10

HOLOTYPE. BPBM 11686, male, 55.2 mm SL, MARQUESAS ISLANDS, Fatu Hiva, just NE of Matahuma Point, rocky bottom with some live coral, 12.5 m, quinaldine, J.E. Randall, 18 April 1971.

PARATYPES. BPBM 11811, 8: 38.8–62.3 mm SL, MARQUESAS ISLANDS, Fatu Hiva, just off point at N end of Hanau Bay, bottom mainly rock, 28–30.5 m, rotenone, J.E. Randall, D.B. Connoy, and R.M. McNair, 21 April 1971; AMS I.19220-001, 42.1 mm SL, same data as preceding; CAS 37887, 60.6 mm SL, same data as preceding; LACM 35903-1, 44.5 mm SL, same data as preceding; MNHN 1976-124, 46.3 mm SL; same data as preceding; USNM 216496, 47.3 mm SL, same data as preceding; BPBM 11026, 5: 23.9–52.3 mm SL, Marquesas Islands, Ua Pou, S side of Vaeho Bay off entrance to

large cave, 0–10 m, rotenone, J.E. Randall, D.B. Cannoy, G.S. Haywood, and J.D. Bryant, 29 April 1971; BPBM 12442, 9: 24.1–48.3 mm SL, Marquesas Islands, Ua Huka, S side of Takatai, rocky area near sand, 27–30 m, rotenone, J.E. Randall, J.R. Haywood, and R.M. McNair, 7 May 1971; BPBM 12751, 58.6 mm SL, Marquesas Islands, Nuku Hiva, W side of Sentinelle de l'Est, steep rocky slope, no sand, quinaldine, J.E. Randall and D.B. Cannoy, 17 May 1971; BM(NH) 1976.9.30.11, 52.0 mm SL, same data as preceding.

DIAGNOSIS. Dorsal soft rays 17 or 18 (usually 17); pectoral rays 21 or 22 (rarely 22); lateral-line scales 56 to 62; circum-peduncular scales 32 to 36; no auxiliary scales; mandibles naked; gill rakers 10–12 + 24–28; a row of moderate forward-projecting canine teeth on side of jaws; two rows of teeth on palatines at widest place; no papillae on edge of orbit; three opercular spines; snout 3.5 to 4.8 in head; body depth 2.6 to 3.1 in SL; second dorsal spine prolonged in adult females, greatly prolonged in males; dorsal and anal fins not scaled; colors of fresh specimens as in Figures 17 and 18.

DESCRIPTION. Dorsal rays X, 17 (17 or 18, usually 17); anal rays III, 7; pectoral rays 21 (21 or 22, rarely 22), upper two and occasionally lower unbranched; pelvic rays I, 5; principal caudal rays 15, upper and lower unbranched; lateral-line scales 57 (56–62); scales above lateral line to origin of dorsal fin 9 (9–11); scales below lateral line to origin of anal fin 27 (26–31); circum-peduncular scales 34 (32–36); gill rakers 11 + 25 (10–12 + 24–28); branchiostegal rays 7; vertebrae 26; predorsal bones 1.

Body somewhat elongate, the depth 2.87 (2.56–3.10) in SL; body moderately compressed, the width 2.50 (2.01–2.53) in depth; head length 3.32 (2.94–3.16) in SL, snout 4.36 (3.52–4.79) in head, the front of upper lip of males thickened, pointed, freely movable dorsoventrally, and relatively long (0.3 in orbit of holotype); diameter of orbit 3.67 (2.87–4.05) in head; posterior edge of orbit without fleshy papillae; interorbital space convex, the bony width 3.96 (3.85–4.37) in head; least depth of caudal peduncle 2.28 (2.26–2.93) in head.

Mouth oblique and moderately large, the maxilla reaching to or posterior to a vertical at rear edge of pupil; mouth terminal except on large males where it is slightly inferior due to hypertrophy of upper lip; posterior end of maxilla rounded, the greatest depth 1.5 in orbit of holotype; no supplemental maxillary bone. Dentition generally as for *A. bartlettorum*, but only two irregular rows of villiform teeth on palatines at broadest place; tongue pointed, the upper surface with scattered very small papillae. Gill membranes free from isthmus. Gill rakers slender and long (largest 1.45 in orbit of holotype), notably longer than gill filaments (longest gill filament of first arch of holotype contained 1.41 in longest raker).

Opercle with three flattened spines, the central one the largest and most posterior, the upper slightly anterior to lower; two lower spines acute, the upper obtuse and indistinct; distance between tips of two lower spines about two-thirds the distance between central and upper spines; lower margin of preopercle smooth; rounded corner and upper margin serrate (19 serrae on holotype; serrae increase in number with size; only 8 on 24.1-mm paratype and 20 on 62.3-mm paratype). The 24.1-mm paratype has two enlarged serrae at the corner of preopercle,

Figure 15. *Anthias bartlettorum*, holotype, male, 54.2 mm SL, BPBM 17981, Marshall Islands.



Figure 16. *Anthias bartlettorum*, paratype, female, 40.7 mm SL, BPBM 20449, Marshall Islands.



especially the lowermost, which extends slightly beyond posterior margin of operculum; one large spine on interopercle; this fish is clearly transforming from the prejuvenile stage.

Anterior nostril in a short membranous tube (higher dorso-posteriorly) directly anterior in middle of eye about half the distance from edge of orbit to edge of groove separating upper lip from rest of snout; posterior nostril diagonally upward and posterior to anterior nostril, with little or no rim, and large, the greatest diameter of opening about equal to distance between nostrils, 6.43 in orbit of holotype.

Scales ctenoid; no auxiliary scales on body; head scaled except mandibles, throat and gill membranes, lips, extreme front of snout, and a broad zone on side of snout anterior to center of eye that includes nostrils in its upper part; small juveniles clearly show five diagonal rows of scales on cheek between orbit and corner of preopercle (plus a single scale as a sixth row just

above upper posterior corner of maxilla); in larger individuals, small scales develop between the orbit and the larger scales and near the margin of the preopercle becoming progressively larger; dorsal and anal fins naked; caudal fin with small scales more than three-fourths distance to posterior margin; pectoral fins with small scales on basal third or more of fin; pelvic fins with small scales basally along rays.

Lateral line a smooth curve following contour of back, the last pored scale slightly anterior to end of hypural plate. Some pores of cephalic lateralis system obscured by scales. Prominent are a pore in front of anterior nostril, one between nostrils, one medial to nostrils, two close together in interorbital space above front of eye, a series near edge of orbit around posterior half of eye, about 12 scattered pores between upper margin of opercle and posterior margin of eye, six on suborbital and pre-orbital region anterior to a vertical through center of eye, and



Figure 17. *Anthias regalis*, holotype, male, 55.2 mm SL, BPBM 11686, Marquesas Islands.



Figure 18. *Anthias regalis*, paratype, female, 37 mm SL, BPBM 12442, Marquesas Islands.

six in a mandibular series beginning at end of lower margin of preopercle (last two on chin close together).

Origin of dorsal fin on a vertical through posterior margin of preopercle; second dorsal spine prolonged in adult females, the length 7.04–10.99 in SL for females, much more prolonged in males, 3.13 (2.58–3.52) in SL; longest dorsal soft ray 2.01 (1.82–2.16) in head; third anal spine 3.14 (3.14–3.58) in head; longest anal soft ray 1.57 (1.56–1.95) in head; caudal fin lunate, the lobes filamentous, the caudal concavity 6.71 (4.54–7.63) in SL; pectoral fin length 3.42 (3.11–3.60) in SL; pelvic fins long, 1.98 (1.93–3.70) in SL, reaching to between anus and anal fin origin in smaller females, to spinous portion of anal fin in larger females, and well beyond spinous portion of anal fin in males.

Color of adults and large juveniles in alcohol: pale with no dark markings (23.9- and 24.1-mm specimens each have a dark

spot in spinous dorsal fin; upper half of body of former darker than lower half). Color of male holotype when fresh (from transparency): dorsal part of head and body anterior to a diagonal from base of approximately ninth dorsal spine to upper pectoral base orange-yellow; remainder of head and body heliotrope, lighter ventrally, with a suffusion of red dorsally and posteriorly; body scales in anterior heliotrope region with light centers; a faint pinkish-orange band with lavender edges from tip of snout through lower part of eye onto preopercle immediately anterior to pectoral fin base (diagonal postorbital part of band broader and fainter); iris pinkish brown; dorsal fin pale lavender with violet distal margin on soft portion; anal fin lavender hyaline with light blue distal margin on anterior half of soft portion; caudal fin reddish basally, becoming yellowish posteriorly, with violet upper and lower margins and red filaments; paired fins pale lavender, the pelvics with a light blue anterior

margin. A color photo of a living male taken underwater by the senior author displays brighter and more contrasting colors of heliotrope and orange-yellow than Figure 17. Color of a 37-mm female when fresh (from transparency): golden orange-yellow, shading to reddish-orange anteriorly on head, to pale lavender ventrally on head, thorax, and abdomen, and suffused with red posteriorly; an orange-red band from tip of snout to lower eye continuing as a broader diagonal orange band edged in lav-

ender onto preopercle, ending at level of upper pectoral base; iris golden; dorsal fin yellowish basally, shading to light red outwardly; anal fin light orangish; caudal fin red, becoming yellowish centroposteriorly; pectoral fins pale pinkish with a large light reddish triangle at base; pelvic fins pale lavender.

REMARKS. Known only from the Marquesas Islands where it is abundant in its rocky bottom habitat at depths of less than 10 to at least 30 m.

Table 10. Proportional measurements of type specimens of *Anthias regalis* expressed as a percentage of the standard length.

	Holotype		Paratypes		
	BPBM 11686	BPBM 12442	BPBM 12442	USNM 216496	BPBM 12751
Standard length (mm)	55.2	24.1	36.7	47.3	58.6
Depth of body	34.8	39.0	33.2	32.3	35.2
Width of body	13.9	15.4	15.8	16.1	15.9
Head length	30.1	34.0	32.7	33.2	31.6
Snout length	6.9	7.1	9.3	7.6	7.3
Diameter of orbit	8.2	11.2	11.4	9.7	7.8
Bony interorbital width	7.6	8.7	8.2	7.6	8.2
Length of maxilla	15.2	14.9	15.5	15.6	16.7
Least depth of caudal peduncle	13.2	11.6	12.8	13.1	14.0
Length of caudal peduncle	15.6	14.1	14.2	12.7	14.3
Predorsal length	24.1	31.1	28.9	26.8	24.4
Preanal length	62.7	63.9	64.3	67.9	67.6
Prepelvic length	33.5	36.5	33.2	37.6	38.9
Length of first dorsal spine	7.8	4.6	4.1	5.3	8.9
Length of second dorsal spine	31.9	9.1	14.2	13.3	38.7
Length of third dorsal spine	11.2	12.4	11.4	12.9	10.6
Length of tenth dorsal spine	10.1	10.8	11.4	11.0	10.6
Length of longest dorsal ray	15.0	15.8	15.5	15.4	17.4
Length of dorsal fin base	63.9	63.1	62.9	62.2	63.0
Length of first anal spine	2.9	7.1	3.5	3.8	3.1
Length of second anal spine	7.8	14.9	9.5	9.1	7.8
Length of third anal spine	9.6	9.5	10.4	9.7	9.6
Length of longest anal ray	19.2	17.4	18.8	18.4	20.3
Length of anal fin base	16.8	19.1	18.3	18.4	16.6
Length of pectoral fin	29.2	30.3	32.2	30.9	27.8
Length of pelvic spine	14.9	16.6	14.7	14.0	13.8
Length of pelvic fin	50.5	27.0	28.1	31.9	51.9
Length of caudal fin	51.1	34.0	37.9	36.4	52.0
Caudal concavity	36.2	12.0	22.6	23.3	38.9

ETYMOLOGY. Named *regalis* in reference to the majestic colors displayed by both sexes.

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CONTRIBUTIONS IN SCIENCE

THE HOLOCENTRID FISHES
OF THE GENUS *MYRIPRISTIS* OF THE RED SEA,
WITH CLARIFICATION OF THE *MURIDJAN* AND *HEXAGONUS* COMPLEXES

John E. Randall and Paul Guézé



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THE HOLOCENTRID FISHES OF THE GENUS
MYRIPRISTIS OF THE RED SEA, WITH CLARIFICATION OF
THE *MURDJAN* AND *HEXAGONUS* COMPLEXES¹

John E. Randall² and Paul Guézé³

ABSTRACT: Three species of *Myripristis* Cuvier are characterized by having two pairs of symphyseal tooth patches outside the gape anteriorly on the lower jaw: *M. hexagonus* (Lacepède) from the western Pacific to the Indian Ocean, but not the Red Sea; *M. xanthacrus* new species, a Red Sea and Gulf of Aden endemic with yellow on the distal ends of the caudal lobes and elevated soft portions of the dorsal and anal fins; and *M. melanostictus* Bleeker with a distribution similar to that of *hexagonus*. The first two have small scales in the axil of the pectoral fins, whereas these are lacking on *M. melanostictus*.

Ostichthys spiniceps Ogilby is a junior synonym of *M. hexagonus*, but *M. australis* Castelnau, previously regarded as synonymous with *M. hexagonus*, is a probable synonym of *M. violaceus* Bleeker.

Apparently only one other *Myripristis* occurs in the Red Sea for which the name *murdjan* (Forsskål) should be applied (*parvidens* Cuvier is a synonym); it ranges to the western Pacific. The species *M. seychellensis* Cuvier and *M. berndti* Jordan and Evermann, both regarded as synonyms of *murdjan* by some authors, are valid. *M. seychellensis* is known at present only from three localities in the western Indian Ocean—Seychelles, St. Brandon's Shoals, and Réunion; it is distinctive in having a terminal mouth or the lower jaw slightly inferior and a patch of vomerine teeth with the posterior border rounded. *M. berndti* ranges throughout the Indo-Pacific and occurs in the eastern Pacific as well; it has a strongly jutting lower jaw (only slightly projecting in *murdjan*), a narrow interorbital space (width 4.3 to 5.2 in head compared with 3.7 to 4.4 for *murdjan*), and orangish-yellow on the outer part of the spinous dorsal fin.

INTRODUCTION

The senior author collected specimens of a soldierfish (Holocentridae: *Myripristis*) in the Red Sea off Sudan in 1974 and 1975 and in Djibouti, Gulf of Aden, in 1977 that seemed unique in having the caudal lobes and elevated parts of the soft dorsal and anal fins broadly tipped with bright yellow. Only *M. chryseres* Jordan and Evermann (1903), known from Hawaii, Japan, and Réunion,⁴ has solid yellow on these fins, but this color is not restricted to the distal part in this species. Furthermore, *M. chryseres* has 32 to 38 lateral-line scales, whereas the Red Sea and Gulf of Aden species has 26 to 29.

In his useful revision of the genus *Myripristis*, Greenfield (1974) recognized 15 species, of which three were recorded from the Red Sea: *M. murdjan* (Forsskål 1775), *M. parvidens* Cuvier (1829), and *M. hexagonus* (Lacepède 1802). Our yellow-tipped specimens key to *M. hexagonus* in Greenfield's paper in having two pairs of symphyseal tooth patches, one above the other, at the front of the lower jaw (just outside the

gape—see Greenfield's fig. 3). They also possess small scales in the axil of the pectoral fins (usually present on *hexagonus*, according to Greenfield). There is, however, no mention of yellow on the fins in Greenfield's account of *hexagonus*, which caused us to compare our specimens with those identified as *hexagonus* in various museums. The collections of the British Museum (Natural History) contain three fish that Greenfield had identified as *hexagonus* but which proved to be the same species as our Red Sea specimens. Our study also revealed two other species, one with scales in the axil of the pectoral fins and one without, among the specimens labelled *hexagonus* in these museums.

To determine which of these species would bear Lacepède's name *hexagonus*, the type specimen (Fig. 14) at the Muséum National d'Histoire Naturelle in Paris was examined. This specimen (MNHN A. 5423) is a dried, varnished half skin 112 mm in standard length. The two pairs of symphyseal tooth patches may be clearly seen at the front of the lower jaw; there are small scales in the axil of the pectoral fins; the lateral-line scale count is 27. The type locality was not given, but Lacepède (1802) stated that the fish was a gift from the Dutch, thus making the eastern Indian Ocean or Indonesia, and not the Red Sea, the likely locality.

Greenfield listed three nominal species as junior synonyms of *M. hexagonus*: *M. melanostictus* Bleeker (1863), *M. macrolepis* Bleeker (1873), and *M. australis* Castelnau (1875). The holotype of *M. melanostictus* and the types of *M. macrolepis* at the Rijksmuseum van Natuurlijke Historie at Leiden were examined. The former (RMNH 5157, 149 mm SL, Greenfield 1974, fig. 18) is a specimen of aberrant color pattern, variously blotched with black pigment. It has two pairs of symphyseal tooth patches on the lower jaw but no scales in the pectoral

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4. The Indonesian record of this species given by Greenfield (1974) is based on a specimen at the Rijksmuseum van Natuurlijke Historie in Leiden (No. 5414). The true locality of this specimen, however, is Réunion. Recently *M. chryseres* was collected at Tutuila, American Samoa, by Richard C. Wass; the specimen is deposited in the Bishop Museum. Phillip C. Heemstra (pers. comm.) reported the capture of a specimen at Aliwal Shoal off Durban, South Africa.

axil. *M. macrolepis* is clearly a synonym of *M. hexagonus*. The type of *M. australis* is apparently lost (see discussion under the account of *M. hexagonus*), but it appears to be a synonym of *M. violaceus* Bleeker (1851).

Therefore, there are three species among the specimens identified as *M. hexagonus* by Greenfield: the true *hexagonus*, *melanostictus*, and the Red Sea and Gulf of Aden species, which is described herein as new.

Other than the new species, the senior author's collections of *Myripristis* from the Red Sea seem to contain only a single species that is not clearly *M. murdjan* or *M. parvidens* as defined by Greenfield (solely on the relative width of the interorbital space). As is discussed in the remarks under *murdjan* below, we determined that Greenfield was in error in recording both *murdjan* and *parvidens* from this locality. All of his Red Sea *parvidens* are referable to *murdjan*.

A problem then arose as to what name to apply to the species from outside the Red Sea that Greenfield had called *M. murdjan*. Our study has shown that two of the nominal species he referred to the synonymy of *murdjan*, *M. seychellensis* and *M. berndti*, are not *M. murdjan* but valid species.

To permit differentiation of the three closely allied species of the *hexagonus* complex and the three we might term the *murdjan* complex, we present a key to the ten large-scale species of *Myripristis* (which includes the last seven species listed in Greenfield's table 1), followed by accounts of the six species of the *hexagonus* and *murdjan* complexes in the order they appear in the key. Color photographs of fresh specimens of these six species, underwater photos of five of them (plus *M. violaceus*), and meristic data (Tables 1 and 2) are also provided. Greenfield's key and his counts of lateral-line scales, soft rays of the dorsal and anal fins, and gill rakers continue to be fundamental to the identification of the other species of the genus.

METHODS AND MATERIALS

The last two dorsal and anal soft rays were counted separately, even if closely spaced, as long as each had its own basal element. Pectoral-ray counts include the short upper ray. The upper-limb gill rakers are listed first; the raker at the angle is contained in the lower-limb count. Rudiments were included in the gill-raker counts except for roundish, entirely sessile plates (sometimes rather large), which are occasionally seen at the end of the raker series.

An important character in differentiating species of *Myripristis* is the presence or absence of small scales on the fin side of the axil of the pectoral fins and the extent of this scalation when present.

Standard length (SL) was taken from the medial anterior point of the upper lip to the midbase of the caudal fin (posterior end of hypural plate). Depth of body is the maximum depth, often just anterior to the base of the pelvic fins. Head length was measured from the median anterior point of the upper lip to the most posterior edge of the opercular membrane. The orbit diameter is the maximum diameter of the bony orbit. The interorbital width is the minimum bony interorbital distance. The depth of the caudal peduncle is the least depth. The length

of the caudal peduncle was measured horizontally between verticals at the rear base of the anal fin and the base of the caudal fin. The length of the dorsal spines was taken from the edge of the groove into which the spines fold, whereas the anal spines were measured to their extreme bases. Caudal concavity is the horizontal distance between verticals at the tips of the longest and shortest caudal rays (with the fin in normal position).

In the description of the new species, data in parentheses refer to paratypes when different from the holotype. More measurements are given in Table 3 than are summarized in the text.

Specimens of *Myripristis* were examined at or obtained on loan from the following museums: Academy of Natural Sciences of Philadelphia (ANSP); Australian Museum, Sydney (AMS); Bernice P. Bishop Museum (BPBM); British Museum (Natural History), London [BM(NH)]; California Academy of Sciences, San Francisco (CAS, SU); Hebrew University, Jerusalem (HUJF); Natural History Museum of Los Angeles County (LACM); Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); Muséum National d'Histoire Naturelle, Paris (MNHN); Queensland Museum, Brisbane (QM); Rijksmuseum van Natuurlijke Historie, Leiden (RMNH); J.L.B. Smith Institute of Ichthyology, Rhodes University, Grahamstown (RUSI); U.S. National Museum of Natural History, Washington, D.C. (USNM); and Western Australian Museum, Perth (WAM).

KEY TO THE SPECIES OF MYRIPRISTIS WITH LOW LATERAL-LINE SCALE COUNTS⁵

- 1a. Margin of median fins black, broadest on lobes of caudal fin and elevated parts of soft dorsal and anal fins (black on distal third of highest part of dorsal and anal fins); spinous dorsal fin blackish with a submarginal unpigmented zone; scales in life rimmed with deep blue dorsally and salmon pink on sides and ventrally; a single scale (rarely two) in pectoral axil (lower half); largest species of genus (to 250 mm SL) (Indo-West-Pacific)*adustus*
- 1b. Margin of median fins not black (although there may be a black blotch or streak distally on caudal lobes or on elevated parts of soft dorsal and anal fins); spinous dorsal fin not blackish; scales in life rimmed with brownish red, red, or pink (except anterodorsally on *M. violaceus* where the scales are dark purplish); either no scales or numerous scales in axil of pectoral fins2
- 2a. Third anal spine distinctly longer (and much stouter) than fourth (fourth spine contained about 1.2 in length of third spine); third anal spine 1.5 to 1.8 in head; no scales in pectoral axil (southern and western Pacific)⁶.....*randalli*
- 2b. Third anal spine shorter than or subequal to fourth spine; longest anal spine 1.9 to 2.65 in head; scales present or absent in pectoral axil3

5. Average number of lateral-line scales less than 32.

6. *M. randalli* Greenfield was described from specimens collected in the Austral Islands and Pitcairn at a depth of 40 to 46 m. It has since been collected by Richard C. Wass in American Samoa.

Table 1. Fin-ray and lateral-line scale counts of species of *Myripristis* of the *hexagonus* and *murdjan* complexes.

Species	Dorsal Soft Rays			Anal Soft Rays					Pectoral Rays			Lateral-Line Scales							
	13	14	15	10	11	12	13	14	14	15	16	25	26	27	28	29	30	31	32
<i>melanostictus</i>	1	15	1		1	16			1	15	1			1	15	1			
<i>hexagonus</i>	3	56	7			46	20		10	53	3	1	3	48	14				
<i>xanthacrus</i>	9	54	1	1	11	50	2		25	39			4	42	14	2			
<i>seychellensis</i> ¹		1	9				11		3	8					11				
<i>berndti</i>	5	90	2		3	87	7		6	88	3				3	63	28	3	
<i>murdjan</i>	1	49	16		1	30	34	1	5	56	5			1	10	40	11	2	2

¹One specimen with deformed dorsal soft rays; no dorsal-ray count made.

- 3a. Two pairs of symphyseal tooth patches, one above the other, at tip of lower jaw just outside gape (lower pair usually absent in specimens smaller than about 90 mm SL).....4
- 3b. A single pair of symphyseal tooth patches at tip of lower jaw just outside gape6
- 4a. Small scales in axil of pectoral fins; no black on fins; total gill rakers 36 to 46; maximum size to 153 mm SL5
- 4b. No scales in axil of pectoral fins; a prominent black blotch distally on caudal lobes and elevated portions of soft dorsal and anal fins; total gill rakers 32 to 38; maximum size to 243 mm SL (western Pacific and Indian Oceans)
.....*melanostictus*
- 5a. Soft dorsal, anal, and caudal fins not tipped with yellow; total gill rakers 36 to 43 (western Pacific and Indian Oceans, but not Red Sea or Gulf of Aden).....
.....*hexagonus*
- 5b. Soft dorsal, anal, and caudal fins tipped with yellow; total gill rakers 39 to 46 (Red Sea and Gulf of Aden)
.....*xanthacrus* n. sp.
- 6a. No scales in axil of pectoral fins; lateral-line scales 30 to 34 (Oceania⁷)*woodsi*
- 6b. Small scales present in axil of pectoral fins; lateral-line scales 27 to 317
- 7a. Scales on upper part of body with broad blackish rims (deep purplish or blue to dark brown in life), those on interorbital and nape almost completely dark; upper-limb gill rakers 12 to 16 (modally 14); lateral-line scales 27 to 29 (modally 28) (Indo-West-Pacific).....*violaceus*
- 7b. Scales on upper part of body without blackish rims; upper-limb gill rakers 11 to 15 (modally 12 or 13); lateral-line scales 27 to 32 (modally 29 except *seychellensis* with 28)8

- 8a. Mouth terminal or lower jaw slightly inferior when mouth fully closed; posterior border of patch of teeth on vomer rounded (Fig. 1A), at least on adults; dorsal soft rays 15 (western Indian Ocean)*seychellensis*
- 8b. Lower jaw projecting when mouth closed (except juveniles); posterior border of patch of teeth on vomer straight (Fig. 1B); dorsal soft rays modally 149
- 9a. Interorbital space relatively narrow, the bony width 4.3 to 5.2 in head length; lower jaw of adults strongly projecting when mouth fully closed; a broad zone of orangish-yellow on outer part of spinous dorsal fin in life (eastern Pacific and Indo-West-Pacific, but not Red Sea).....*berndti*
- 9b. Interorbital space relatively broad, the bony width 3.8 to 4.4 in head length; lower jaw of adults slightly projecting when mouth fully closed; outer part of spinous dorsal fin red in life (Indo-West-Pacific, but absent from Hawaii and French Polynesia).....*murdjan*

SPECIES ACCOUNTS

Myripristis melanostictus Bleeker
Figures 2,8; Tables 1,2

Myripristis melanostictus Bleeker 1863:237 (type locality, Ternate).

Myripristis murdjan (*non* Forsskål) Fourmanoir and Laboute 1976:156, col. figs.

DIAGNOSIS. Dorsal fin rays X-I, 13 to 15 (usually 14); anal fin rays IV, 11 or 12 (usually 12); pectoral fin rays 14 to 16 (usually 15); lateral-line scales 27 to 29 (usually 28); rows of scales between lateral line and middle of spinous dorsal fin 2½; gill rakers 11 to 13 + 21 to 26.

Depth of body 2.12 to 2.45 in SL; head length 2.67 to 2.98 in SL; snout 4.21 to 4.69 in head; orbit diameter 2.09 to 2.48 in head; interorbital width 4.49 to 5.64 in head; maxilla extending posteriorly to a vertical at hind edge of pupil, its length 1.63 to 1.78 in head; least depth of caudal peduncle 3.15 to 3.75 in head; fourth (rarely third or fifth) dorsal spine the longest, 2.05

7. Will be reported from the Ryukyu Islands by Yamakawa and Shimizu.

to 2.67 in head; longest dorsal soft ray (usually the second) 1.34 to 1.52 in head; fourth anal spine usually slightly longer than third, 2.25 to 2.69 in head; longest anal soft ray (second or third) 1.38 to 1.57 in head; caudal fin 1.32 to 1.41 in head; pectoral fins 1.50 to 1.65 in head; pelvic fins 1.35 to 1.53 in head.

Two pairs of tooth patches, one above the other, at symphysis of lower jaw just outside gape; vomerine teeth in a triangular patch with rounded corners, the posterior border slightly indented; no scales in pectoral axil.

Color in alcohol light brown with a silvery cast, the edges of the scales darker than centers; upper opercular membrane blackish, the pigment disappearing about half the distance from opercular spine to level of upper pectoral base; only a trace of dark pigment in a small area in upper axil of pectoral fins; a blackish spot on about outer third of soft dorsal fin between third and sixth rays, and a comparable dark spot on about outer fourth of anal fin between second and fourth or fifth rays; caudal lobes tipped with a blackish spot. Color when fresh as illustrated in Figure 2.

REMARKS. The proportional measurements given above are based on 15 specimens, 127 to 243 mm SL.

The holotype (RMNH 5157, 149 mm SL) was examined by the senior author in Leiden. It has been illustrated by Greenfield (1974: fig. 18). As pointed out by Weber and de Beaufort (1929) and Greenfield (op. cit.), this specimen is melanistic. It has large black areas on the fins and random black blotches over the head and body. Greenfield stated that he found 37 specimens of four other species of *Myripristis* that exhibit similar aberrant coloration.

M. melanostictus seems to be a relatively rare species. The Bishop Museum has only five specimens: one from a fish market at Negombo on the west coast of Sri Lanka (Ceylon), two speared by the senior author in dead reef area at 30 m in the lagoon of North Male Atoll, Maldive Islands, and two from the Cebu City fish market, Philippines. In other museums, we found 12 additional specimens from the following localities: Ternate and Bourou, Indonesia; Bulan Island and Zamboanga, Philippines; Sri Lanka; and Tanegashima, Japan. Fourmanoir and Laboute (1976) have two color illustrations of this species (as *M. murdjan*) in their book on fishes of New Caledonia and the New Hebrides. The senior author observed and photographed an adult individual in 28 m off Sodwana Bay, Kwazulu, South Africa (27° S).

The species from southern Japan identified as *M. melanostictus* by Masuda, Araga, and Yoshino (1975:194, pl. 306) is *M.*

adustus. Although not mentioned by Greenfield (1974), *adustus* often has a second pair of tooth patches below the first pair at the front of the lower jaw. These lower patches are generally smaller than the upper ones; however they can be larger, as is the case for a specimen from Assumption Island, Seychelles (RUSI 7385, 247 mm SL). Specimens of *M. adustus* can generally be identified by the broad black zone distally on the soft dorsal, anal, and caudal fins (although the black is broader at the tips of these fins, it is not confined to the tips as on *M. melanostictus*). If the fins are damaged or faded, another helpful character is the presence on *adustus* of one or two moderately large scales on the lower half of the pectoral axil (a single scale found in axil on one side of one of 14 specimens of *melanostictus*).

M. melanostictus has most often been confused with *M. hexagonus* because of the double pair of symphyseal tooth patches on the tip of the chin of both species and the incomplete meristic separation. The presence of numerous small scales in the axil of the pectoral fins of *M. hexagonus* is the most useful means of separation. Because *M. hexagonus* is a relatively small species (maximum about 155 mm SL), the larger size of *M. melanostictus* can also be helpful in distinguishing the two species. The largest specimen of *M. melanostictus* (BPBM 22437) measures 243 mm SL. Thus it is the second largest species of the genus (after *M. adustus*).

Five of the seventeen specimens of *melanostictus* examined (USNM 218390-93, 218457), all adults, were taken by bottom trawling at Wadge Banks (7 to 8° N; 77 to 81° E) off Sri Lanka in 44 to 71 m in 1969, and a sixth specimen (USNM 216719) was taken from the same bank (depth and gear not recorded). Since species of *Myripristis* usually remain close to coral reefs or rocky areas (they tend to hide in caves or crevices during daylight hours), the capture of these specimens by trawling was unexpected. The label with one specimen (USNM 218391) taken at a station in 64 m, however, stated that the haul was terminated when the net "hung up on rocks."

Myripristis hexagonus (Lacepède)

Figures 1C, 3, 14; Tables 1,2

Lutjanus hexagonus Lacepède 1802:213-214 (type locality, Sumatra).

Myripristis macrolepis Bleeker, 1873:181,195 (type locality, Java, Nias, Celebes, Buro, and Ambon).

Ostichthys spiniceps Ogilby 1908:31 (type locality, Great Barrier Reef).

DIAGNOSIS. Dorsal fin rays X-I, 13 to 15 (usually 14), anal fin rays IV, 12 or 13 (usually 12); pectoral fin rays 14 to 16 (usually 15); lateral-line scales 25 to 28 (modally 27); scale rows between lateral line and middle of spinous dorsal fin 2½; gill rakers 12 to 15 + 24 to 29.

Depth of body 2.10 to 2.51 in SL; head length 2.66 to 3.00 in SL; snout 4.59 to 5.07 in head; orbit diameter 2.04 to 2.39 in head; interorbital width 4.10 to 5.13 in SL; maxilla extending to a vertical at or slightly beyond hind edge of pupil, its length 1.64 to 1.75 in head; least depth of caudal peduncle 3.38 to 3.89 in head; third to fifth (usually the fourth) dorsal spine the longest, 2.10 to 2.42 in head; second or third dorsal soft ray

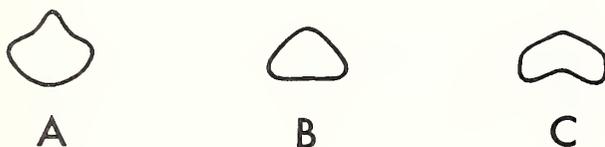


Figure 1. Approximate shape of the patch of vomerine teeth of species of *Myripristis*. A. *seychellensis* B. *berndti* and *murdjan* C. *hexagonus* and *xanthacrus*.

longest, 1.43 to 1.60 in head; longest anal spine (usually the third) 2.39 to 2.65 in head; second or third anal soft ray the longest, 1.42 to 1.60 in head; caudal fin 1.22 to 1.50 in head; pectoral fins 1.38 to 1.52 in head; pelvic fins 1.37 to 1.52 in head.

Two pairs of tooth patches, one above the other, at symphysis of lower jaw just outside gape [lower pair absent in juveniles (may be seen in individuals as small as 75 mm SL, but one of 105 mm lacked them)]. Vomerine teeth in a broad "V"-shaped patch (Fig. 1C). Small scales on fin side of pectoral axil, usually extending almost to dorsal edge of fin base.

Color in alcohol silvery brown, the edges of the scales narrowly brown (darker dorsally); opercular membrane blackish, the dark pigment nearly reaching ventrally to level of upper pectoral base; upper part of pectoral axil blackish; no dark pigment in fins. Color when fresh as illustrated in Figure 3.

REMARKS. The proportional measurements given above are based on 18 specimens 90 to 153 mm SL.

The holotype of *M. hexagonus* (MNHN A.5423, 112 mm SL) was examined in Paris. It is a dried varnished skin of the right side (Fig. 14). In order to determine if there are small scales in the axil of the pectoral fin, a bit of varnish was removed with slender forceps from the axil and dissolved in acetone; a small cycloid scale was found in the residue.

Bleeker (1873) described *M. macrolepis* from 25 specimens, 130 to 190 mm in total length, from five different islands in Indonesia: Java, Nias, Celebes, Buro, and Ambon. The Rijksmuseum van Natuurlijke Historie in Leiden has three lots of

macrolepis collected by Bleeker, the lectotype (RMNH 24910, 134 mm SL) that was selected by D. W. Greenfield, 11 paralectotypes (RMNH 5421, 109 to 138 mm SL), and two other specimens (RMNH 24912, 103 to 111 mm SL). These specimens were examined by the senior author, as was another Bleeker specimen from Nias in the Muséum National d'Histoire Naturelle in Paris (MNHN 2577, 126 mm SL). All are *M. hexagonus*.

The holotype of *Ostichthys spiniceps* Ogilby, a name overlooked by Greenfield (1974), QM I.1203, 101 mm SL, was kindly sent on loan by R.J. McKay of the Queensland Museum. It proved to be *M. hexagonus*. Ogilby gave the type locality as "South Sea Islands"; however, the locality on the original label, written in Ogilby's handwriting, is "Great Barrier Reef" (McKay, pers. comm.).

Greenfield (1974:25) placed *Myripristis australis* Castelnau (1875) in the synonymy of *M. hexagonus*. He did not list the type of *M. australis*, a four-inch specimen from Cape York, Australia, among his "Material Examined" of *M. hexagonus*. Castelnau's description of *M. australis* is brief, and there is no illustration. Nothing in the description indicates that *M. australis* is synonymous with *M. hexagonus*. There is, however, one remark in the description on color, "each scale of the back has a broad edge of dark purple," which strongly suggests that Castelnau had a specimen of *M. violaceus* Bleeker (illustrated herein as Fig. 9). An effort was made to locate Castelnau's type specimen. R.J. McKay of the Queensland Museum in Brisbane, Joan M. Davis of the National Museum of Victoria in Mel-

Table 2. Gill-raker counts of species of *Myripristis* of the *hexagonus* and *murdjan* complexes.

Species	Upper Limb						Lower Limb										
	11	12	13	14	15	16	21	22	23	24	25	26	27	28	29	30	31
<i>melanostictus</i>	6	9	2				2	1	6	6	1	1					
<i>hexagonus</i>		6	28	30	2					3	7	13	21	18	4		
<i>xanthacrus</i>			11	38	13	2						6	17	20	10	7	4
<i>seychellensis</i>		1	5	4	1						2	2	4	2	1		
<i>berndti</i>	8	51	33	4					3	14	33	26	19	2			
<i>murdjan</i>		6	40	17	3					2	11	30	18	3	2		
							Total Gill Rakers										
	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46		
<i>melanostictus</i>	1	2	1	7	4		2										
<i>hexagonus</i>					1	1	8	8	15	16	13	4					
<i>xanthacrus</i>								4	8	11	13	17	4	5	2		
<i>seychellensis</i>						1	1	1	2	4	1	1					
<i>berndti</i>				5	14	20	26	18	10	3	1						
<i>murdjan</i>					1	4	9	20	19	7	4	1	1				

bourne, Douglass F. Hoese of the Australian Museum in Sydney, and Marie-Louise Bauchot of the Muséum National d'Histoire Naturelle in Paris all wrote that the specimen is not in the fish collections of these museums. McKay stated in his letter, "I have made a careful search of the collection and find no trace of the type of *Myripristis australis* Castelnau. The type may have been the specimen registered 1206 *Ostichthys australis* (cast), Cape York, 'Show Collection' (no other data) destroyed 20.11.1950, as no other *O. australis* from Cape York is registered in the early register."

The most useful character in separating *M. hexagonus* and allied species *melanostictus* and *xanthacrus* from other species of the genus (except occasional *adustus* — see remarks on *melanostictus*) is the presence of a double pair of tooth patches at the tip of the chin. It should be noted, however, that juveniles of *hexagonus* less than about 90 mm SL usually lack the lower pair of tooth patches. The smallest *hexagonus* with detectable lower tooth patches that we have seen is QM 65241, 75 mm SL.

M. hexagonus is a small species. The largest specimen we have seen, USNM 192511, from Mindoro, Philippines, measures 153 mm SL.

We have examined specimens of *M. hexagonus* from the following localities: many islands of Indonesia and the Philippines (the specimen illustrated in Fig. 3 was collected in 40 m off Batangas, Luzon); Gulf of Thailand (10–12°N; 99–101°E); Yirrkala near Cape Arnhem, Northern Territory, Australia (reported as *M. macrolepis* by Taylor, 1964); Palm Islands and Lizard Island, Great Barrier Reef; Cairns and Bowen (20°S), Queensland (Queensland Museum specimens were identified as *M. australis* by T.C. Marshall 1964:132, pl. 30, fig. 146); Kendrew Island, Dampier Archipelago (20°28'S; 116°32'E); Mahé, Seychelles; Nossi Be, Madagascar; Inhaca Island, Mozambique; Zanzibar; Bird Island, Suva, Fiji Islands; and Tuuila, American Samoa.

The specimens from Fiji (AMS I 18354–028, 2: 111–140 mm SL) and Samoa (BPBM 26368, 2: 147–147.5 mm SL), the only known from Oceania, differ from the other *M. hexagonus* in their high gill-raker counts (15 + 30 or 31); meristic data from these four fish are not included in Table 2. In other respects, they seem typical of *M. hexagonus*.

T. Yamakawa and T. Shimizu (MS) will record *M. hexagonus* from the Ryukyu Islands and southern Japan.

Myripristis xanthacrus new species

Figures 1C, 4, 10; Tables 1–3

Myripristis hexagonus (non Lacepède) Greenfield, 1974 (in part): 24 (Red Sea).

HOLOTYPE. BPBM 19784, 100.9 mm SL, Red Sea, Sudan, Suakin Harbor, S side near harbor entrance, fringing reef front, caves in 15–17 m, J.E. Randall, P.J. and P. Vine, 15 October 1975.

PARATYPES. BM(NH) 1960.3.15.100–101, 2: 86.6–93.8 mm SL, Red Sea, Mersa Sheikh Ibrahim, "Manihine," 1950–51; BM(NH) 1960.3.15.111–113, 3: 45.3–118.5 mm SL, Red Sea,

Khor Inkeifail and Sanganeb, "Manihine," December 1950; USNM 216608, 17: 75.8–121.3 mm SL, Red Sea, Ethiopia, N end of Isola Delemme just E of Ras Coral (15°30.5'N, 39°54'E), depth to 3 m, rotenone, V.G. Springer, 7 August 1969; USNM 216609, 12: 103.3–134.1 mm SL, Red Sea, Ethiopia, ½ mile off SW shore of Sciumma Island (15°32'31"N, 40°0'E), depth to 7 m, rotenone, V.G. Springer, 9 August 1969; USNM 216610, 5: 98.4–115 mm SL, Red Sea, Ethiopia, Ethiopian Naval Base, Massawa, depth to 1.8 m, rotenone, V.G. Springer, 12 August 1969; USNM 216611, 117 mm SL, Red Sea, Ethiopia, Sheikh el Abu, off lighthouse just W of S end of Harat Island (16°08'N, 39°26.5'E), depth to 4 m, rotenone, V.G. Springer, 14 August 1969; BPBM 20381, 2: 71.0–71.5 mm SL, Red Sea, Sudan, Suakin Harbor, off marine lab. jetty, rocks in 1 m, rotenone, J.E. Randall and P.J. Vine, 12 October 1974; BPBM 20443, 2: 101–109.3 mm SL, Red Sea, Sudan, 100 m S of entrance to Port Sudan Harbor, cave in 18 m, spear, J.E. Randall, 17 October 1974; BPBM 20469, 6: 87.7–107.5 mm SL, ANSP 137869, 88.2 mm SL, CAS 38534, 105.2 mm SL, HUJF 8374, 90.2 mm SL, LACM 36278-1, 96.2 mm SL, MNHN 1977.1, 92 mm SL — all collected with holotype; MNHN 1977-452, 7: 81–118 mm SL, Gulf of Aden, Djibouti, Gulf of Tadjoura, Maskali Island, W side, 10–15 m, rotenone, J.E. Randall and L.A. Maugé, 14 May 1977; BPBM 21568, 2: 65–127 mm SL, Gulf of Aden, Djibouti, Seven Brothers Islands (Sawabi Is.), Tolka Island (Ile Basse) 12°27.7'N, 43°24.9'E, N side, cave in 12 m, rotenone, J.E. Randall and L.A. Maugé, 19 May 1977.

DIAGNOSIS. Dorsal fin rays X-I, 13 to 15; anal fin rays IV, 10 to 13; pectoral fin rays 14 or 15; lateral-line scales 26 to 29 (modally 27); scale rows between lateral line and middle of spinous dorsal fin 2½; gill rakers 13 to 16 + 26 to 31.

Depth of body 2.22 to 2.45 in SL; head length 2.68 to 2.83 in SL; snout 4.43 to 4.97 in head; orbit diameter 2.13 to 2.69 in head; interorbital width 4.30 to 4.77 in head; maxilla reaching posteriorly between verticals at hind edge of pupil and hind edge of orbit; least depth of caudal peduncle 3.22 to 3.92 in head; fourth dorsal spine longest, 2.15 to 2.41 in head; second dorsal soft ray longest, 1.32 to 1.80 in head; second or third anal spine longest, 1.92 to 2.59 in head; caudal fin 1.17 to 1.28 in head, pectoral fins 1.51 to 1.77 in head; pelvic fins 1.41 to 1.69 in head.

Two pairs of tooth patches, one above the other, at symphysis of lower jaw just outside gape; vomerine teeth in a broad "V"-shape; small scales in axil of pectoral fins.

Color in alcohol silvery brown, the edges of the scales darker brown, especially dorsally; opercular membrane dark brown to about level of lower edge of pupil; only a little dark pigment dorsally in pectoral axil, but a dark spot present above pectoral base; fins pale.

Color in life silvery pink, the edges of the scales brownish red dorsally, red on sides and ventrally; opercular membrane brownish red; median fins red except distal tips of soft dorsal, anal, and caudal lobes, which are yellow; upper and lower margins of caudal fin, leading edge of soft dorsal and anal fins distal to initial spines, and lateral edge of pelvic fins white.

DESCRIPTION. Dorsal fin rays X-I, 14 (13 to 15); anal fin rays

IV, 12 (10 to 13); pectoral fin rays 14 (14 or 15); pelvic fin rays 1, 7; principal caudal rays 19 (upper and lower unbranched); upper procurrent caudal rays 5 (the first four spinous); lower procurrent caudal rays 4 (the first three spinous); lateral-line scales 27 (26 to 29); scales above lateral line to origin of dorsal fin 3; scales above lateral line to middle of spinous portion of dorsal fin 2½; scales below lateral line to origin of anal fin 5½; predorsal rows of scales about 9½; circumpeduncular scales 12; diagonal rows of scales on cheek 4; gill rakers 14 + 28 (13 to 16 + 26 to 31); pseudobranch lamellae 32 (18 to 36, generally more

on larger specimens); branchiostegal rays 8; vertebrae 11 + 15.

Depth of body 2.33 (2.22 to 2.45) in SL; width of body about 2 in depth; head length 2.79 (2.68 to 2.83) in SL; snout 4.79 (4.43 to 4.97) in head; orbit diameter 2.40 (2.13 to 2.69) in head; interorbital space flat, the width 4.58 (4.30 to 4.77) in head; maxilla reaching posteriorly between verticals at hind edge of pupil and hind edge of eye, its length 1.72 (1.67 to 1.77) in head; depth of caudal peduncle 3.35 (3.22 to 3.92) in head.

Lower jaw slightly protruding when mouth closed; front of

Table 3. Proportional measurements of *Myripristis xanthacrus* new species, expressed as a percentage of the standard length.

	Holotype		Paratypes			
	BPBM 19784	BPBM 20381	BPBM 20469	BPBM 20735	USNM 216609	USNM 216609
Standard length (mm)	100.9	71.0	87.9	98.5	117.9	134.1
Depth of body	42.8	43.8	40.8	43.3	44.9	42.7
Head length	35.9	35.3	37.3	35.5	35.5	36.3
Snout length	7.5	7.1	7.7	7.6	7.9	8.2
Orbit diameter	14.9	16.2	17.5	14.4	13.6	13.5
Bony interorbital width	8.0	8.2	8.2	8.2	7.9	7.6
Length of upper jaw	20.9	21.1	21.8	21.3	21.1	20.5
Depth of caudal peduncle	10.7	10.0	9.5	10.4	11.0	10.6
Length of caudal peduncle	14.2	14.3	13.5	13.6	13.7	13.9
Predorsal length	41.6	42.5	42.4	40.4	42.8	42.1
Preanal length	70.3	69.7	70.8	71.2	70.0	73.0
Prepelvic length	41.3	39.4	40.6	40.7	40.1	42.0
Length of 1st dorsal spine	10.9	10.6	10.4	8.9	11.5	11.2
Length of 2nd dorsal spine	14.5	13.1	13.7	12.4	13.7	13.3
Length of longest dorsal spine	16.7	16.2	16.1	14.0	15.7	15.1
Length of 10th dorsal spine	5.4	4.8	5.0	5.3	5.6	5.1
Length of 11th dorsal spine	11.5	abnormal	10.4	10.5	11.4	10.4
Length of longest dorsal ray	24.6	26.6	broken	broken	22.8	20.2
Length of 1st anal spine	2.2	2.5	1.4	1.4	1.6	2.0
Length of 2nd anal spine	6.9	6.8	7.4	5.6	7.5	7.1
Length of 3rd anal spine	17.3	18.4	17.0	14.8	16.3	14.0
Length of 4th anal spine	19.6	17.2	17.0	15.7	16.1	15.0
Length of longest anal ray	25.3	25.8	25.1	24.0	23.7	22.1
Length of caudal fin	29.3	29.5	29.2	broken	30.2	29.1
Caudal concavity	15.9	16.5	15.9	broken	15.9	16.0
Length of pectoral fin	23.8	22.8	23.0	23.0	22.9	20.6
Length of pelvic fin	24.8	25.0	22.9	23.4	23.6	21.5
Length of pelvic spine	18.4	17.1	16.3	15.3	16.5	15.4



Figure 2. *Myripristis melanostictus*, 195 mm SL, BPBM 19044, Sri Lanka.



Figure 3. *Myripristis hexagonus*, 159 mm SL, BPBM 23473, Luzon, Philippine Islands.



Figure 4. *Myripristis xanthacrus*, holotype, 100.9 mm SL, BPBM 19784, Sudan, Red Sea.



Figure 5. *Myripristis seychellensis*, 159 mm SL, BPBM 21155, Seychelles.



Figure 6. *Myripristis berndti*, 153 mm SL, BPBM 8456, Guam, Mariana Islands.



Figure 7. *Myripristis murdjan*, 128 mm SL, BPBM 19804, Sinai Peninsula, Red Sea.

upper lip and front of lower jaw nearly straight when viewed from above; two pairs of protuberant tooth patches at front of upper jaw, one directly above the other, the symphyseal gap between each pair approximately equal to the diameter of one of the patches (one of the two paratypes of BPBM 20381, 71.0–71.5 mm SL, lacks the lower pair of tooth patches, and they are very small in the other paratype); a foramen in lower jaw immediately behind each lower tooth patch. Villiform teeth in a band in jaws, the band of the upper jaw notably broader than that of the lower; outer row of teeth in jaws enlarged, nodular, with nearly truncate ends, those at anterior corner of the upper jaw the largest and those on midside of lower jaw the largest (teeth progressively larger anteriorly within the enlarged outer row of jaws); villiform teeth in bands on vomer and palatines, those on vomer in a broad "V"-shape (Fig. 1C); tongue moderately rounded, the upper surface finely papillate. Longest gill filament of first gill arch contained about 1.7 times in longest gill raker.

Pattern of longitudinal bony ridges and intervening mucous channels on the top of the head typical of the subgenus *Myripristis* as illustrated by Greenfield (1974: fig. 11C). Opercular spine not very large, the adjacent serrae of some specimens nearly as large. Lower margin of maxilla with a few truncate serrae near posterior edge. Margins of suborbital, opercle, subopercle, and double margin of preopercle with numerous sharp serrae, a few at angle of preopercle slightly enlarged. Nasal fossa triangular, usually with a few serrae on posterior edge.

Scales strongly ctenoid, as is characteristic of the Holocentridae, with as many as 38 ctenii on scales on midside of body of holotype. Specialized scales forming a sheath along base of soft dorsal and anal fins. Small scales extending well out on caudal fin (variously missing on type specimens); small pointed scales basally on pectoral fins; small scales in axil of pectoral fins; pointed axillary scale of pelvic fins about one-third length of pelvic spine.

Fourth dorsal spine the longest (but third and fifth may be nearly as long), its length 2.15 (2.18 to 2.41) in head; second dorsal soft ray the longest, 1.46 (1.32 to 1.80) in head; third anal spine much stouter than fourth, but the two subequal in length, the third 2.07 (1.92 to 2.59) in head, and the fourth 1.83 (2.05 to 2.59) in head; second anal soft ray the longest, 1.42 (1.37 to 1.65) in head. Caudal fin forked, its length 1.22 (1.17 to 1.28) in head, the caudal concavity 2.25 (2.13 to 2.34) in head; pectoral fins pointed, the second or third rays the longest, 1.51 (1.54 to 1.76) in head, the upper two and lowermost rays unbranched, the uppermost ray less than half length of second ray; pelvic fins nearly reaching anus, 1.45 (1.41 to 1.69) in head.

Color in alcohol silvery with a brownish yellow cast, the scales on upper part of body rimmed with brown, particularly those above lateral line; opercular membrane brown, the dark pigment diminishing ventrally at about level of lower edge of pupil; only a trace of dark pigment at upper end of pectoral axil, but a moderate amount of pigment above pectoral base forming a broad blotch, which aligns with dark color of opercular membrane; fins entirely pale.

Color in life, as illustrated in Figure 4, silvery pink, the

edges of the scales red (brownish red dorsally); opercular membrane and a zone below leading to pectoral base brownish red; median fins red, the color concentrated in the rays of the soft portions, the tips of the soft dorsal and anal fins and caudal lobes bright yellow; distal half of first soft rays of soft dorsal and anal fins and most of the uppermost and lowermost principal caudal rays whitish.

ETYMOLOGY. Named *xanthacrus* from the Greek "xanthos" for yellow and "akros" for tip or at the end, in reference to the yellow areas distally on the soft dorsal fin, anal fin, and caudal lobes.

REMARKS. *M. xanthacrus* is known thus far from the southern half of the Red Sea and the Gulf of Aden.

Only one other species of *Myripristis*, *M. chryseres*, has yellow on the median fins, but this color is not confined to the tips of the fins. *M. chryseres* is not a close relative; it differs notably from *M. xanthacrus* in having 32 to 38 lateral-line scales and only a single pair of symphyseal tooth patches at the front of the lower jaw. *M. xanthacrus* is most closely related to *M. hexagonus* and may be an allopatric derivative of this species. It differs from *M. hexagonus* in the yellow on its median fins, higher average gill-raker counts (see Table 2), and shorter pectoral fins.

Myripristis seychellensis Cuvier

Figures 1A, 5, 11; Tables 1, 2

Myripristis seychellensis Cuvier in Cuvier and Valenciennes 1829: 172 (type locality, Seychelles).

Myripristis murdjan (non Forsskål) Greenfield 1974 (in part): 20.

DIAGNOSIS. Dorsal fin rays X-I, 14 or 15 (rarely 14); anal fin rays IV, 13; pectoral fin rays 14 or 15 (usually 15); lateral-line scales 28; rows of scales between lateral line and middle of spinous dorsal fin 2½; gill rakers 12 to 15 + 25 to 29 (counts based on 11 specimens).

Depth of body 2.19 to 2.38 in SL; head length 2.58 to 3.02 in SL; snout 4.75 to 5.28 in head; orbit diameter 2.27 to 2.48 in head; interorbital space 4.19 to 4.50 in head; maxilla extending to between verticals at hind edges of pupil and orbit, the maxillary length 1.71 to 1.82 in head; least depth of caudal peduncle 3.39 to 3.83 in head; third or fourth dorsal spines longest, 2.29 to 2.49 in head; second or third dorsal soft ray longest, 1.44 to 1.73 in head; third and fourth anal spines subequal, 2.12 to 2.46 in head; second or third anal soft ray longest, 1.31 to 1.58 in head; caudal fin 1.16 to 1.29 in head; pectoral fins 1.47 to 1.56 in head; pelvic fins 1.46 to 1.66 in head.

Lower jaw terminal or inferior when mouth fully closed; a single pair of tooth patches at symphysis of lower jaw just outside gape; vomerine teeth of adults with the posterior border distinctly rounded (Fig. 1A) (the shape of the tooth patch of juveniles seems to resemble that of *M. murdjan*); pectoral axil with small scales except on approximately the upper one-eighth.

Color in alcohol brown, the edges of scales of body darker than centers; opercular membrane blackish to or nearly to level

of upper base of pectoral fins; unscaled dorsal part of pectoral axil blackish; fins pale except for broad blackish streaks on each caudal lobe centered on second and third branched rays (darker distally), and on about outer three-fourths of elevated portions of soft dorsal and anal fins (mainly on third and fourth rays and adjacent membranes, but continuing faintly to basal anterior part of fins); longest pelvic ray (second) tipped with blackish.

Color when fresh as illustrated in Figure 5. The outer part of the spinous dorsal fin is mainly red (a small amount of yellow pigment may be present).

REMARKS. The proportional measurements given above are based on nine specimens, 92 to 176 mm SL.

The holotype, as reported by Bauchot (1970:23), is in the Muséum d'Histoire Naturelle in Paris; this specimen (MNHN 9518), which was collected by Dussumier, measures 159 mm SL. She listed one paratype, MNHN 7579, 176 mm SL, also collected by Dussumier, though this fish was not mentioned by Cuvier in the original description.

The name *Myripristis seychellensis* has been used by very few authors. Sauvage (1891) applied it to specimens from Madagascar, but his illustration and lateral-line scale count of 38 clearly indicate that he did not have the true *seychellensis* (though it doubtless occurs in Madagascar). Günther (1859), Weber and de Beaufort (1929), and Herre (1953) all erroneously regarded *M. seychellensis* as a synonym of *M. pralinius* Cuvier in Cuvier and Valenciennes (1829). Greenfield (1974) placed *M. seychellensis* in the synonymy of *M. murdjan*.

The senior author speared two specimens of this species (BPBM 21155, 156–169 mm SL) on the S and W sides of North Islet, Mahé, Seychelles, in caves in 15 m on 11 June 1977. Observed in the same caves were *M. murdjan*, *M. adustus*, *M. kuntee*, *M. violaceus*, and *M. berndti*, all of which were more common than the *M. seychellensis*.

We have examined only 11 museum specimens that we can identify with confidence as *M. seychellensis*: the two types, the two mentioned above in the Bishop Museum, four from St. Brandon's Shoals (Cargados Carajos, 16° 28'–45'S; 59° 34'–37'E, USNM 218412–13 and USNM 218460, 131–175 mm SL) collected in 4 to 21 m in April 1976 by V.G. Springer and associates, and three more from the Seychelles collected during the International Indian Ocean Expedition by James E. Böhlke and associates (ANSP 106575, 164 mm SL) and Margaret G. Bradbury and party (CAS 35356, 92–117 mm SL). A color photo of a fresh specimen from Réunion by the junior author leaves little doubt that the species occurs there as well as in the Seychelles and St. Brandon's Shoals.

Two small specimens (CAS 35356) from the Seychelles, which we identify as *M. seychellensis*, have the posterior border of the patch of vomerine teeth only slightly rounded. Other small specimens, mostly less than 90 mm SL, from the same locality, have the correct meristic data for *M. seychellensis* and an inferior lower jaw but a straight border to the patch of vomerine teeth. Since *M. murdjan* of this size may have a terminal mouth or slightly inferior lower jaw, these Seychelles specimens would seem to be *murdjan*. However, it seems likely that the vomerine teeth of *seychellensis* begin in a triangular

pattern in juveniles and develop the rounded posterior border with age. If this is the case, young *seychellensis* and *murdjan*, as here diagnosed, may be indistinguishable.

Myripristis berndti Jordan and Evermann

Figures 1B, 6, 12, Tables 1, 2, 4

Myripristis berndti Jordan and Evermann 1903: 170 (type locality, Honolulu).

Myripristis murdjan (non Forsskål) Randall 1973: 181.

Myripristis murdjan (non Forsskål) Greenfield 1974 (in part):20.

Myripristis amaenus Fourmanoir and Laboute 1976:155, col. figs.

DIAGNOSIS. Dorsal fin rays X-I, 13 to 15 (usually 14); anal fin rays IV, 11 to 13 (usually 12); pectoral fin rays 14 to 16 (usually 15); lateral-line scales 28 to 31 (modally 29, often 30); rows of scales between lateral line and middle of spinous dorsal fin 2½; gill rakers 11 to 14 + 23 to 28.

Depth of body 2.32 to 2.62 in SL; head length 2.67 to 2.84 in SL; snout 4.62 to 5.30 in head; orbit diameter 2.25 to 2.73 in head; interorbital space narrow, the bony width 4.30 to 5.21 in head; maxilla extending to between verticals at hind edge of pupil and posterior edge of orbit, the maxillary length 1.66 to 1.78 in head; least depth of caudal peduncle 3.27 to 3.68 in head; third to fifth dorsal spines the longest, 2.15 to 2.59 in head; longest dorsal soft ray (usually the second) 1.53 to 1.74 in head (relatively longer on smaller individuals); third and fourth anal spines subequal, 2.14 to 2.42 in head; longest anal soft ray (usually the second) 1.50 to 1.62 in head; caudal fin 1.19 to 1.39 in head; pectoral fins 1.41 to 1.57 in head; pelvic fins 1.49 to 1.73 in head.

Lower jaw of adults prominently projecting when mouth is closed; a single pair of tooth patches at symphysis of lower jaw just outside gape; vomerine teeth in a triangular patch with rounded corners; lower one-half to three-quarters of pectoral axil with small scales.

Color in alcohol brown, the edges of the scales darker (especially dorsally on body); opercular membrane blackish to a short distance (about half a pupil diameter) below opercular spine, becoming dusky ventrally; unscaled portion of pectoral axil black, some of this pigment generally extending above pectoral base; fins pale or with dark pigment submarginally near ends of caudal lobes and elevated parts of soft dorsal and anal fins, the pigment on some specimens developed as a distinct band that parallels the rays.

Color when fresh as shown in Figure 6. The most significant color feature is the outer yellow or orangish-yellow part of the spinous dorsal fin.

REMARKS. The proportional measurements given above are based on 12 specimens, 99.6 to 231 mm SL.

This species has been confused with *M. murdjan* and *M. seychellensis*. Usually it has been misidentified as *murdjan*.

Randall (1955) gave a detailed color note of the species from a Gilbert Islands specimen. Underwater photographs in color have been published by Bagnis et al. (1972, pl. on p. 251) and



Figure 8. Underwater photo of *Myripristis melanostictus*, Maldives Islands, 30 m.



Figure 9. Underwater photo of *Myripristis violaceus*, Maldives Islands, 10 m.



Figure 10. Underwater photo of *Myripristis xanthacrus*, Sudan, 12 m.



Figure 11. Underwater photo of *Myripristis seychellensis*, Seychelles, 14 m.



Figure 12. Underwater photo of *Myripristis berndti*, Kwajalein, Marshall Islands, 10 m.



Figure 13. Underwater photo of *Myripristis murdjan*, Sudan, 5 m.

Table 4. Comparison of gill-raker counts of *Myripristis berndti* from the Pacific and Indian Oceans.

	Upper Limb				Lower Limb					
	11	12	13	14	23	24	25	26	27	28
Eastern Pacific Ocean	3	14	4		2	7	9	3		
Central and Western Pacific Ocean	5	30	19		1	7	21	16	9	
Indian Ocean		8	10	4			3	7	10	2

by Fourmanoir and Laboute (1976, right hand figures of p. 155, as *M. amaenus*).

M. berndti has the broadest distribution of all the species of the genus: East Africa to the eastern Pacific (Clipperton, Cocos, and Galapagos Islands); it is not known, however, from the Red Sea or Persian Gulf. In the western Pacific, it ranges from southern Japan to Australia; the senior author observed it at Lord Howe Island (31.5°S). It is one of the most common species of *Myripristis* at islands of Oceania and the Indian Ocean. The Bishop Museum has specimens from the Hawaiian Islands, Line Islands, Society Islands, Pitcairn Group, Rapa, Cook Islands, Samoa Islands, Gilbert Islands, Marshall Islands, Mariana Islands, Wake, Marcus, Solomon Islands, New Hebrides, Mauritius, Réunion and Seychelles. These have been collected in the depth range of 1 to 30 m, but the species occurs at least as deep as 45 m. We have identified other specimens from Mozambique, Kwazulu in South Africa, Indonesia, Borneo, Philippines, Ryukyu Islands, Caroline Islands, Clipperton Island, Pacific coast of Costa Rica, and Cocos Island, Costa Rica. The largest specimen (BPBM 3755), 237 mm SL, was collected at French Frigate Shoals, Hawaiian Islands.

There is a difference in the average number of gill rakers between the specimens of *M. berndti* from the Pacific and Indian Oceans (Table 4).

A problem exists with respect to specimens of *Myripristis* from the Marquesas Islands; these fish have only a few small scales at the extreme ventral part of the pectoral axil and a less projecting lower jaw than typical specimens of *berndti*. The life color of these specimens is unknown. If normal specimens of *berndti* were shown to occur in the Marquesas, then the ones with few axillary scales probably represent an undescribed species. More material from the Marquesas is needed to provide a full analysis of the apparent population differentiation of *berndti* in this archipelago.

Myripristis murdjan (Forsskål)

Figures 1B, 7, 13, Tables 1, 2, 5, 6

Sciaena murdjan Forsskål 1775:48 (type locality, Jeddah, Red Sea).

Myripristis parvidens Cuvier 1829:151 (type locality, Port Praslin, New Ireland).

Myripristis axillaris Valenciennes in Cuvier and Valenciennes 1831:491 (type locality, Mauritius).

Myripristis melanophrys Swainson 1839:207 (new name for *M. murdjan* Rüppell, 1828).

Myripristis bowditchae Woods in Schultz et al. 1953:202, pl. 18B (type locality, Bikini Atoll, Marshall Islands).

DIAGNOSIS. Dorsal fin rays X-I, 13 to 15 (usually 14, rarely 13); anal fin rays IV, 11 to 13 (rarely 11); pectoral fin rays 14 to 16 (usually 15); lateral-line scales 27 to 32 (modally 29); rows of scales between lateral line and middle of spinous dorsal fin 2½; gill rakers 12 to 15 + 24 to 29.

Depth of body 2.30 to 2.49 in SL; head length 2.68 to 3.06 in SL; snout 4.89 to 5.30 in head; orbit diameter 2.11 to 2.49 in head; interorbital space relatively broad, 3.78 to 4.43 in head; maxilla extending to between verticals at posterior margins of pupil and orbit, the maxillary length 1.68 to 1.89 in head; least depth of caudal peduncle 3.09 to 3.72 in head; third or fourth dorsal spines longest, 1.96 to 2.48 in head; second dorsal soft ray longest, 1.38 to 1.68 in head; third and fourth anal spines subequal, 2.07 to 2.49 in head; second anal soft ray longest, 1.38 to 1.66 in head; caudal fin 1.12 to 1.33 in head; pectoral fins 1.31 to 1.49 in head; pelvic fins 1.50 to 1.73 in head.

Lower jaw of adults slightly projecting when mouth fully closed; a single pair of tooth patches at symphysis of lower jaw just outside gape; vomerine teeth in a triangular patch with rounded corners; lower one-fourth to three-fourths of pectoral axil with small scales.

Color in alcohol light brown with a faint longitudinal linear pattern due to concentration of dark pigment along the centers of the scales; upper part of opercular membrane dark brown, the pigment diminishing a short distance below principal opercular spine, but some scattered dark dots persisting to level of pectoral base; upper unscaled portion of pectoral axil dark brown to blackish, with some pigment continuing above pectoral base along edge of gill opening; fins pale or with dusky soft rays (particularly on Pacific specimens), with or without a concentration of dark pigment anteriorly in the soft dorsal and anal fins and the caudal lobes.

Color when fresh as illustrated in Figure 7. The outer part of the spinous dorsal fin is bright red.

REMARKS. The proportional measurements given above are based on 24 specimens, 92 to 177 mm SL, twelve of which are from the Red Sea.

As indicated by Klauswitz and Nielsen (1965:19, pl. 15), the holotype of *M. murdjan* in the Zoological Museum, Copenhagen, consists only of a part of the skin of the body and portions of the median fins; the head, nape, abdomen, and paired fins are missing.

Table 5. Comparison of fin-ray counts of *Myripristis murdjan* from the Red Sea and other localities.

	Dorsal Soft Rays			Anal Soft Rays				Pectoral Rays		
	13	14	15	11	12	13	14	14	15	16
Red Sea		29	3	1	20	11		5	26	1
Other localities	1	20	13		10	23	1		30	4

Table 6. Comparison of proportional measurements¹ of *Myripristis murdjan* from the Red Sea and other localities.

	Red Sea		Other Localities	
	Range	Mean	Range	Mean
Depth of body	2.34-2.46	2.41	2.30-2.49	2.40
Head length	2.68-3.03	2.89	2.68-3.06	2.83
Snout length	4.89-5.30	5.10	4.94-5.26	5.11
Orbit diameter	2.11-2.49	2.26	2.13-2.39	2.27
Interorbital width	3.88-4.43	4.16	3.78-4.43	4.02
Maxillary length	1.68-1.82	1.76	1.76-1.89	1.83
Depth of caudal peduncle	3.12-3.72	3.40	3.09-3.54	3.34
Longest dorsal spine	1.96-2.48	2.21	2.01-2.48	2.20
Longest dorsal ray	1.39-1.68	1.57	1.38-1.62	1.52
Longest anal spine	2.07-2.49	2.27	2.19-2.36	2.28
Longest anal ray	1.38-1.66	1.53	1.38-1.60	1.50
Caudal fin	1.12-1.29	1.20	1.15-1.33	1.21
Pectoral fins	1.37-1.49	1.44	1.31-1.42	1.39
Pelvic fins	1.50-1.61	1.57	1.57-1.73	1.65

¹The first 2 measurements (depth of body and head length) are given as a ratio of the standard length, and the last 12 as a ratio of the head length.

Based on 12 Red Sea specimens from 103.5 to 154.3 mm SL and 12 specimens extralimital to the Red Sea, 92 to 177 mm SL.

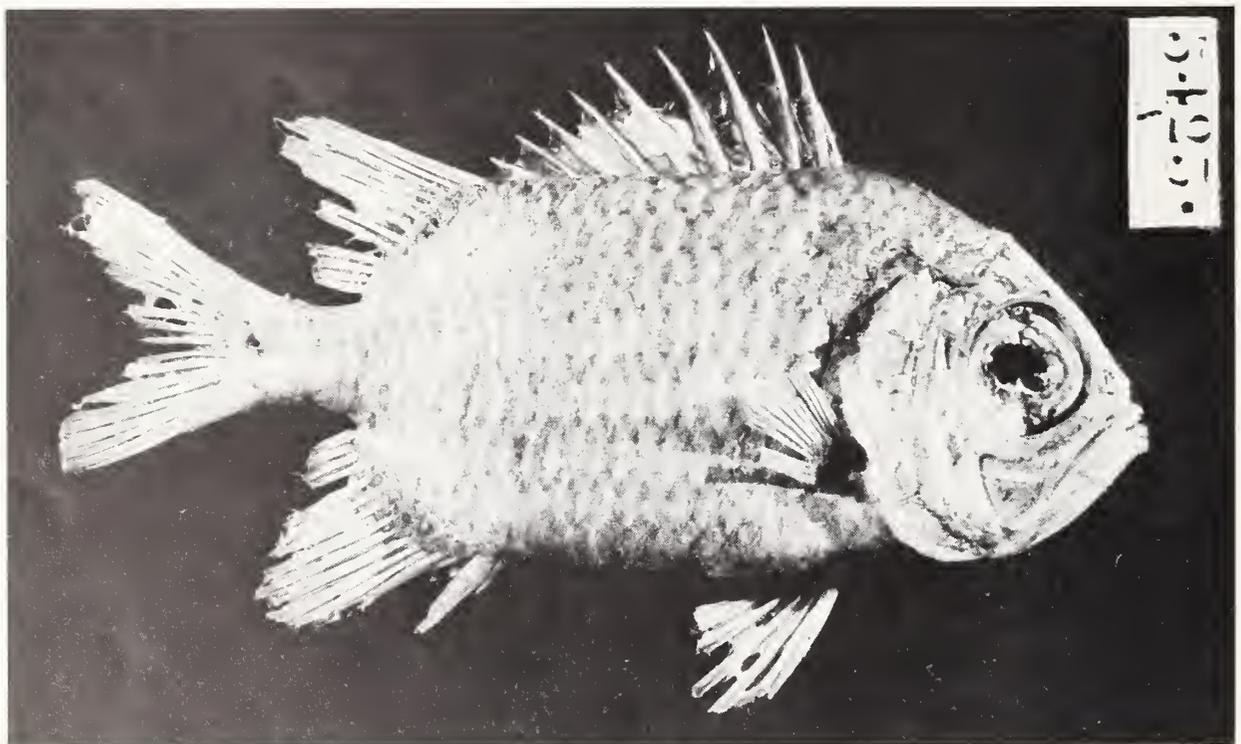


Figure 14. Holotype of *Myripristis hexagonus* (Lacepède), 112 mm SL, MNHN A.5423.

Greenfield (1974) recognized three species of *Myripristis* in the Red Sea: *M. hexagonus* (which we have referred to *xanthacrus*), *M. murdjan*, and *M. parvidens*. He distinguished the latter two on the basis of the relative width of the interorbital space, that of *murdjan* supposedly contained 4 times or more in the head and that of *parvidens* less than 4. Since the interorbital width of the holotype of *murdjan* cannot be determined from Forsskål's fragmentary description or from the fragmentary holotype, Greenfield arbitrarily selected the species with the broad interorbital to bear the name *murdjan* in his revision.

Apart from *M. xanthacrus*, the senior author has collected numerous specimens of *Myripristis* in the Red Sea that seem to be one species. The interorbital width of these fish varies from about 3.8 to 4.4 in the head. If separated into two groups strictly on whether the interorbital is more than or less than 4 in the head, no other basis for separation can be found. Noting that Greenfield listed only one lot of four specimens of *M. murdjan* from the Red Sea in his "Material Examined," we asked for a loan of these four specimens and some Red Sea specimens he identified as *parvidens* from the British Museum (Natural History). We conclude that all represent one species. The name *murdjan* must therefore be applied to this species. The specimens which Greenfield identified as *parvidens* are here referred to as *murdjan* (along with the four Red Sea specimens he called *murdjan*).

Greenfield should nonetheless be credited with noticing the difference in interorbital width among specimens of closely related species of *Myripristis*. As shown in the Key in this paper, the interorbital width is the principal character that distinguishes the true *murdjan* from *berndti*, even though there is some overlap (interorbital width of *berndti* 4.3 to 5.2 in head). The point of division in interorbital width of the two species is not 4.0, however, but about 4.35.

The authorship of *Myripristis parvidens* is usually attributed to Cuvier in Cuvier and Valenciennes; however Bauchot (1970) has shown that the description of this species in Cuvier's Règne Animal appeared in March 1829, hence prior to the appearance of Cuvier and Valenciennes' volume 3 of Histoire Naturelle des Poissons in April 1829.

The holotype of *M. axillaris* (MNHN A.70, 153 mm SL) was examined by the junior author at the Muséum National d'Histoire Naturelle in Paris.

We can confirm the following localities for *M. murdjan*: Red Sea, Gulf of Aden, Comoro Islands, Seychelles, Maldive Islands, Réunion, Mauritius, Indonesia, New Guinea, New Ireland, Solomon Islands, New Hebrides, Philippines, Japan, Caroline Islands, Samoa Islands, Mariana Islands, Marshall Islands, and Pratas Reef in the South China Sea [specimens of *M. murdjan* at the California Academy of Sciences identified as *M. parvidens* and *M. murdjan* by Greenfield (1974) and listed by him as from Taiwan are actually from Pratas Reef].

The species is not known from the Hawaiian Islands and evidently is absent also from the Line Islands and French Polynesia. The record of *M. murdjan* from the Society Islands by Randall (1973:181) refers to *M. berndti*.

M. murdjan is generally taken in less than 10 m, at times in as little as 1 m. However, Red Sea collections made by the se-

nior author include specimens from one station in 37 to 49 m.

As indicated in Table 5, there is a slight difference in the count of the soft rays of the anal fin of *M. murdjan* in the Red Sea and outside the sea. No differences were apparent, however, in the lateral-line scale and gill-raker counts. In a search for other possible differences, a comparison was made of 14 proportional measurements of specimens of this species from within and outside the Red Sea (Table 6). With the possible exception of the interorbital width, the length of the maxilla, the depth of the caudal peduncle, and the length of the pelvic fins, there are no significant differences.⁸

The largest specimen examined is BPBM 19643, collected by the junior author in Mauritius; it measures 177 mm SL.

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The photographs of *Myripristis* were taken by the senior author, except for the photo of the holotype of *M. hexagonus*, which was supplied by the Muséum National d'Histoire Naturelle in Paris. Funds for the color separations were provided by the Charles Engelhard Foundation.

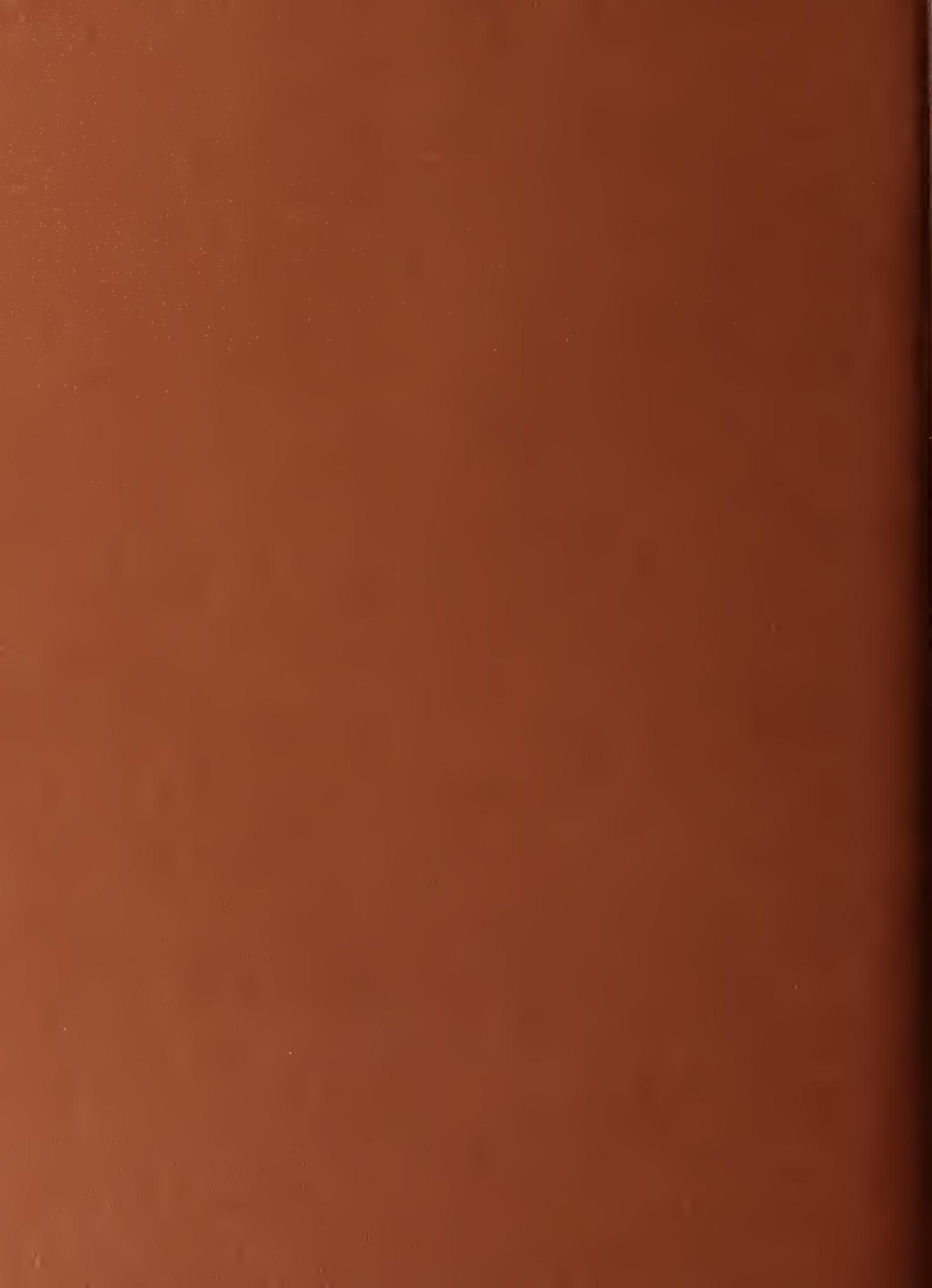
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8. The junior author believes that additional material of *M. murdjan* for this comparison may reveal sufficient differences to warrant nomenclatorial recognition of the Red Sea population. Further study is planned by him.

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CONTRIBUTIONS IN SCIENCE

THE CRANE FLIES (DIPTERA: TIPULIDAE)
OF COCOS ISLAND, COSTA RICA,
WITH DESCRIPTIONS OF FOUR NEW SPECIES

George W. Byers



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**THE CRANE FLIES (DIPTERA: TIPULIDAE)
OF COCOS ISLAND, COSTA RICA, WITH DESCRIPTIONS
OF FOUR NEW SPECIES¹**

George W. Byers²

ABSTRACT. Eleven species of Tipulidae, all in subfamily Limoniinae, are recorded from Cocos Island, Costa Rica. Four new species, *Limonia (Rhipidia) hoguei*, *Limonia (Caenoglochina) paniculata*, *Helius brunneus*, and *Orimarga (Diotrepha) flavescens*, are described and illustrated. The ecology and zoogeography of the tipulid fauna of Cocos Island are briefly considered.

RESUMEN. Once especies de la familia Tipulidae, todas que pertenecen a la subfamilia Limoniinae, se reporta de la Isla del Coco, Costa Rica. Se describe y ilustra cuatro especies nuevas: *Limonia (Rhipidia) hoguei*, *Limonia (Caenoglochina) paniculata*, *Helius brunneus* y *Orimarga (Diotrepha) flavescens*. Se consideré, además, en breve, la ecología y zoogeografía de la fauna de tipúlidos de la isla.

INTRODUCTION

According to legend, there is a fortune in pirate gold buried somewhere on Cocos Island. Since the days of the conquistadores, however, one treasure-seeker after another has come away empty-handed from this tiny tropical island. For those content with less than gold, the remote island, some 500 km (300 mi) southwest of Costa Rica, still has much to offer. For more than 300 years, it served as a source of coconuts and fresh water for passing vessels.

Cocos Island, at 5°32'57"N, 86°59'17"W, is a rugged volcanic island of about 46.6 square km in area and 23.3 km in circumference, with elevations up to about 850 m (2790 ft) (Hertlein 1963). It receives heavy rainfall throughout the year and has temperatures from 20 to 33°C (68 to 92°F). As a result, it has numerous small streams and waterfalls and is covered by a luxuriant growth of palms, ferns, cecropia trees, and other tropical rain-forest plants. Stewart (1912) judged the flora to be that of an oceanic island to which mainland plants had been transported by ocean currents, wind, or birds. It is the consensus of biogeographers who have studied the island that it is a true oceanic island of relatively recent (probably Pleistocene or Pliocene) origin, and that its fauna, other than species evidently introduced by human visitors, was received by transport over the open ocean (Hertlein 1963). That is, although Co-

cos Island rises from an undersea ridge, there is no evidence to indicate it may ever have had a land connection to Central or South America.

Long ago, biologists took an interest in the island because of the contrasts it offers to the near-desert Galápagos some 630 km (350 mi) on to the southwest. While the climate of the Galápagos is affected largely by the cold Peru, or Humboldt, Current that turns westward from the coast of South America as the South Equatorial Current, the Cocos Island climate derives mainly from the warm, eastward-flowing Equatorial Countercurrent. The presence of the Equatorial Countercurrent helps to explain the abundant rainfall on verdant Cocos Island but contributes little to an understanding of the origins of the island's insect fauna. Periodically, however, there have been shifts in the current, which could transport insects living in driftwood, or rafting on floating vegetation, from the coasts of Central America to the island. While July average surface winds over Cocos Island are southerly or from the southeast, those of January blow generally from Central America (i.e., from the northeast) and could introduce mainland insects, especially those that are not strong fliers.

Two recent trips to Cocos Island from the Natural History Museum of Los Angeles County, California, particularly by Charles L. Hogue (Curator of Entomology) and Scott A. Miller (Research Associate), have yielded some 14,000 specimens of insects and arachnids. These add greatly to the small, previously existing collections of arthropods from the island, mostly made incidentally during studies of the vertebrate or plant biota. Hogue and Miller have assembled all extant collections and are attempting to identify the entire entomofauna as part of a biogeographical study.

All collections that include Tipulidae were made at Wafer Bay (named for early explorer Lionel Wafer), where there is safe anchorage and a beach (in contrast to the steep, rocky shoreline of most of the rest of the island). This is at the mouth of the Río (or Arroyo) Genio. Virtually all the crane flies were

1. Review committee for this contribution: Paul H. Arnaud, Jr., Charles L. Hogue, Henry Knizeski, and William J. Turner.

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obtained by use of Malaise traps or were attracted to 15-watt ultraviolet or fluorescent light traps. It should be pointed out that, for some reason, lights attract particularly female crane flies.

A small number of Tipulidae collected on Cocos Island by botanist Ira L. Wiggins in 1967 were recently studied by Professor Charles P. Alexander. From among these, Alexander (1978) described two new species, *Limonia (Geranomyia) co-coensis* and *Limonia (G.) wigginsi*. This collection also included a few species widely distributed in tropical America. All the species found by Wiggins were collected again by Hogue and Miller, who also secured several additional species, of which four—all apparently endemic to Cocos Island—are described as new in the following account.

SYSTEMATICS

Tipulidae of Cocos Island

The crane fly fauna of Cocos Island is restricted to representatives of the subfamily Limoniinae, as is usual for tropical Pacific islands. In the large, virtually cosmopolitan genus *Limonia* (tribe Limoniini), the subgenera *Rhipidia*, *Geranomyia*, and *Caenoglochina* are represented by numerous individuals among the specimens at hand, but curiously there are no flies of the subgenus *Dicranomyia*. *Rhipidia*, *Geranomyia*, and *Dicranomyia* have abundant species in tropical America; the smaller group *Caenoglochina* is wholly neotropical. Species of *Helius* and *Orimarga* (also Limoniini) are also present. Species of the tribes Peditiini and Hexatomini are apparently not found on the island, but the first of these tribes is only poorly represented anywhere in the Neotropical region. Of the Eriopterini, two widely distributed species of *Gonomyia* have reached Cocos Island.

Holotypes, allotypes, and most of the paratypes of the following new species are in the collection of the Natural History Museum of Los Angeles County, Los Angeles, California. A small number of paratypes have been deposited in the Snow Entomological Museum, University of Kansas, Lawrence.

Limonia (Rhipidia) domestica (Osten Sacken)

Three subspecies of this unusually widespread species have been recognized, one in Brazil, one in Ecuador and Peru, and the typical form recorded from eastern North America as far north as Iowa and Maryland, from many parts of the Antillean region, and from northern South America (Alexander and Alexander 1970). Specimens from Cocos Island do not conform exactly to the descriptions of any of these subspecies. Rather than describe them as an insular subspecies, I choose to recognize their specific affinity only. Cocos Island records: Wafer Bay, 17–22 April 1975, C.L. Hogue (1 ♀); in Malaise trap, Sta-

tion 3 (Río Genio), Wafer Bay, 24 March 1978 (1 ♂), same but 25 March (1 ♂, 1 ♀), same but 26 March (1 ♂).

Limonia (Rhipidia) hoguei new species

Figures 1-5

DESCRIPTION. Description based on one ♂, two ♀♀, pinned.

Head. Dorsum dark brown grading into brown at sides, with silvery pollinosity and black bristles. Eyes narrowly separated dorsally by about width of two rows of ommatidia, widely separated ventrally. Rostrum and palps dark brown. Antennal scape and subspherical pedicel blackish brown in both sexes; flagellum dark brown, with 12 flagellomeres. Flagellum of male (Fig. 1): first flagellomere wider than long, second with single, thick ventral lobe over half length of segment; flagellomeres 3–8 bipectinate, or biflabellate, with inner (mesal) flabellations shorter and thicker than outer ones on segments 3, 4, and 8; flagellomere 9 with single ventral pectination; flagellomeres 10–11 not modified, 12 as long as 10 and 11 together; setae on flagellomeres 2–9 conspicuously longer than respective segments. Flagellum of female nodulose, except first flagellomere conspicuously wider than long, as in male; setae short.

Thorax. Pronotum brown. Mesonotal prescutum dull orange with three dark reddish brown longitudinal stripes; broad median stripe and narrower, more lateral stripes connected above pseudosutures in holotype and allotype (somewhat so in paratype), producing four orange spots, two short ones before level of pseudosutures, two longer ones behind. Scutum and scutellum unevenly brown, grading into light brown at sides. Halteres light brown throughout. Pleural surfaces mostly brown, yellowish brown on lower sternopleurite (katepisternum) and meron. Upper ends of coxae brown, lower ends yellowish brown. Femora sordid yellowish brown, slightly expanded and darkened to blackish brown at tips. Tibiae narrowly yellowish brown at base, otherwise dark brown; tarsi dark brown; claws slender, with basal tooth.

Wings patterned approximately as in *L. willistoniana* Alexander (Alexander 1914), with diffuse clouding of grayish brown in all cells, six more distinct darkened areas near anterior border of wing: (1) centered on Sc₂ and R₂, (2) over fork of Rs, (3) at fork of Sc, (4) at origin of Rs, (5) midway between arculus and origin of Rs, and (6) over the humeral cross-vein, arculus, and origin of M (this last spot more diffuse than other five). Clear spots near tip of 2A in cell 1A, in cell R₁₊₂ and extending into cell R₃, in middle of cell 1st M₂, and between darkened spots listed above.

Abdomen of Male. General color sordid yellowish brown; terga 2–5 with darker brown posterior margins; sterna slightly paler than terga; pleural membranes blackish brown. Tergum 8 (Fig. 2) broadly emarginate, tergum 9 much narrower than 8, rounded at sides, with shallow, rounded posterior indentation. Proctiger nearly transparent, two-thirds as wide as ninth

tergum at base, abruptly narrowed near midlength, extending backward beyond rostral tips of ventral dististyles. Basistyles (Figs. 2, 4) each with conspicuous, setiferous ventral lobe. Dorsal dististyle evenly curved, generally blackened but slightly paler near base. Ventral dististyle (Fig. 2, vd) with moderately elongate rostrum bearing two thick spines, their bases well separated, outermost on slight elevation. Gonapophyses (Figs. 3, 5, gon) blackened in upturned apical half, sharply pointed. Aedeagus (Fig. 5) bilobed at apex, with short apicolateral spines and two setae at base on each side.

Abdomen of Female. Terga and sterna sordid brown, indistinctly darker posteriorly; cerci and hypovalves amber-colored. Cerci short, evenly upcurved to sharp tips, closely appressed to each other in dorsal aspect. Hypovalves extending approximately to midlength of cerci.

Length of body, excluding antennae, male (holotype), 4.6 mm; female, 4.3–4.7 mm (allotype 4.7 mm). Wing length, male, 5.0 mm; female, 4.6–5.0 mm (allotype 5.0 mm).

TYPES. Holotype, male, Wafer Bay, 17–22 April 1975, collected by C.L. Hogue; specimen has had abdomen removed, softened, stored in microvial on same pin as rest of specimen. Allotype, female, same data as holotype. Paratype, female, at 15-watt ultraviolet lamp, Station 6 (west bank of Rio Genio, 200 m south of river's mouth), Wafer Bay, 27 March 1978, C.L. Hogue and S. Miller.

DIAGNOSIS. *Limonia (Rhipidia) hoguei* resembles most closely *L. (Rh.) willistoniana* Alexander (originally described as *costalis* by Williston; for best description and figures, see Alexander 1970: 19, 25) from the Windward Islands (St. Vincent, Dominica) and Costa Rica. It is also similar to *L. (Rh.) luquilloensis* Alexander of Puerto Rico (Alexander, 1950: 207). The male of *L. hoguei* differs from both of these in having only six bipectinate flagellomeres (instead of seven) and sharply pointed gonapophyses (instead of bluntly tipped). I have not been able to compare females of these three species to determine in what ways they differ.

ETYMOLOGY. This species is named for its collector, Dr. Charles L. Hogue, in recognition not only of his field studies of the insects of Cocos Island but also his outstanding research on nematoceros Diptera, particularly the Blephariceridae.

REMARKS. Three parasitic Acarina were attached to the ventral surface of the abdomen of the holotype. During the softening process, these became dislodged. They are at present preserved in the vial containing the crane fly's abdomen.

Limonia (Caenoglochina) paniculata new species

Figures 6–11

DESCRIPTION. Description based on 5 ♂♂, 36 ♀♀, pinned.

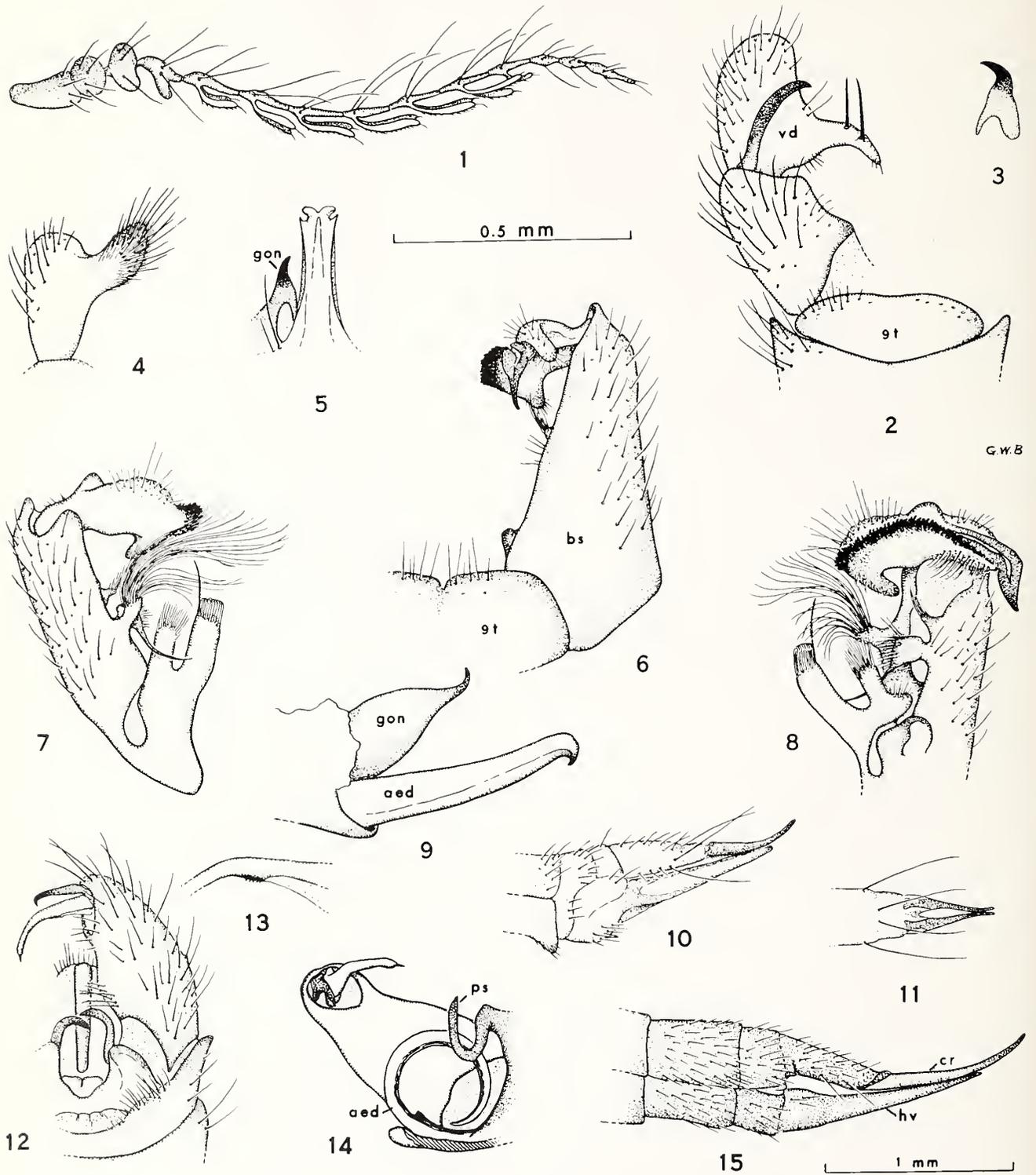
Head. Occiput dark gray with fine, silvery pollinosity. Eyes large in both sexes, contiguous or nearly so both on vertex and beneath rostrum on gular surface. Rostrum and maxillary palps sordid yellowish brown. Scape brown at base; pedicel and apex of scape sordid yellowish brown; flagellum grayish brown with

12 flagellomeres, each pilose, with verticils arising from near midlength; apical flagellomere about 1.4 times as long as penultimate one.

Thorax. Pronotum brown. Mesonotal prescutum polished, yellowish brown with broad brown median stripe abruptly widened in posterior half. Scutum and scutellum brown on elevated parts, yellowish brown where more depressed; mesonotal postnotum light brown. Knobs of halteres dusky brown, stems pale yellowish brown. Pleural surfaces light yellowish brown except for indistinct pale brown spot above anterior coxa. Femora sordid yellowish brown, palest basally, darkest apically; tibiae and tarsi grayish brown; claws apparently not toothed.

Wings lightly tinged with grayish brown, iridescent; stigma not much darker than ground color, its limits indistinct; diffuse brown clouding along vein R_3 , in much of the cell R_2 (especially along costa) and outer cell R_3 . Vein Sc_1 joins C and Sc_2 joins R_1 opposite approximately midlength of Rs. Cell 1st M_2 nearly rectangular in most specimens, basal section of M_3 being in nearly transverse alignment with m cross-vein; when m is more diagonal, M_3 still bends rectangularly.

Abdomen of Male. Terga 2–8 grayish brown, corresponding sterna paler, from sordid yellowish brown to light grayish brown. Ninth tergum yellowish brown with brown posterior and lateral borders, broadly bilobed, with several straight, black setae on posterior one-third (Fig. 6). Basistyles each bearing six tufted lobes of varying complexity, three of these on common sclerotized base joined to ventral base of basistyle and more broadly attached by membrane across deep ventral and mesal notches (Figs. 7, 8). Most ventral of these lobes about 3 times as long as wide, truncate at apex and bearing row of stiff, golden-yellow setae with recurved tips and one long, straight seta at dorsal end of row. Middle lobe of ventral group about twice as long as wide, its rounded apex covered with tuft of yellowish hairs; dorsalmost lobe blunt, with only a few hairs. From ventromesal surface of each basistyle extends a small, flattened lobe (narrower at base than at apex in some males) bearing conspicuous, fanlike array of about 20 long, stiff, yellow setae; this fan divided into more posterior group of longer, sinuous setae and more anterior group of shorter, more strongly curved setae; arrangement fixed, setae springing back, wirelike, when dry and even after boiling in water with trisodium phosphate and preservation in alcohol. Above "fan" a spatulate, strongly sclerotized lobe with long terminal spine curving ventrad and row of dark hairs along apical edge above base of spine. Small, subconical, setiferous lobe on mesal surface of basistyle close beneath dististyle. Single, large dististyle complex, generally concave on lower or inner surface, convex on upper or outer surface, wider dorsoventrally than length from base to mesal edge. Dorsal apex of dististyle a strongly sclerotized, down-curved, acutely tipped blade grooved along its mesal surface (Figs. 6, 8), ventral apex a thick, rounded, hairy lobe curved dorsolaterad; ridge of dense, black, short but thick setae along most of mesal margin. Aedeagus (Fig. 9) elongate but not otherwise modified, with two recurved apical points. Gonapophyses thin, compressed, sclerotized blades,



slightly concave on inner surface, each with upturned, mucronate apex.

Abdomen of Female. Terga 2–8 sordid grayish brown, corresponding sterna 2–7 slightly paler; terga 9–10 yellowish brown except posterior end of tergum 10 slightly darker brown. Cerci and hypovalves amber brown; rounded basal portion of sternum 8 yellowish brown; bases of hypovalves dark brown in ventral aspect. Elongate setae on ventral margins, sides, and dorsum of tergum 10 (Figs. 10, 11). Eighth tergum extended laterally around base of sternum, edges meeting at ventral midline. Cerci bowed slightly apart near midlength (Fig. 11).

Body length (frons to tip of abdomen), male, about 5.0–5.4 mm (holotype 5.4 mm); female, 5.6–6.4 mm (allotype 5.9 mm). Wing length, male, 5.2–5.9 mm (holotype 5.6 mm); female, 5.7–6.5 mm (allotype 6.0 mm).

TYPES. Holotype, male, Wafer Bay, Cocos Island, Costa Rica, collected in Malaise trap, at Station 3 (Rio Genio, 200 m south of river's mouth), 24 March 1978, by C.L. Hogue and S. Miller. Allotype, same label data as for holotype. Paratopotypes: 25 ♀♀, 17–22 April 1975, C.L. Hogue; 1 ♀, 24 March 1978; 1 ♂, 4 ♀♀, 25 March 1978; 1 ♀, 26 March 1978; 3 ♂♂, 4 ♀♀, 27 March 1978; all 1978 specimens from Malaise traps, C.L. Hogue and S. Miller.

DIAGNOSIS. *Limonia* (*Caenoglochina*) *paniculata* most closely resembles *L. (C.) apicata subapicata* Alexander of Florida (U.S.A.) and the Amazonian species *L. (C.) egae* (Alexander) (from Ega, or Tefé, Brazil) and is very similar to *L. (C.) napoensis* (Alexander) (from Rio Napo, an Amazonian tributary, Peru) (Alexander 1921:49–50, figs. 10, 11). *L. (C.) fieldi* Alexander (1967:281, figs. 1, 4), from Honduras, shares with these species the ridge of thick black setae along the margin of the dististyle and the complex basistylar lobes, but it does not have the blackened blade on the dorsal apex of the dististyle. *L. paniculata* differs from all other species in the subgenus in the number, shapes, and arrangement of the basistylar lobes and the complexity of their setae.

ETYMOLOGY. The specific name is derived from the presence of the six setiferous lobes (Latin *paniculata* = tufted).

Limonia (*Geranomyia*) species

Four species of the subgenus *Geranomyia* were identified from among the specimens available. These include *L. (G.) cocoensis*

Alexander, *L. (G.) wigginsii* Alexander, *L. (G.) lycaon* Alexander (= *pallida* Williston), and an apparently undescribed species. Ernest M. May (University of Kansas) is preparing a separate report on *Geranomyia*.

Helius brunneus new species

Figures 12–17

DESCRIPTION. Description based on 19 ♂♂, 4 ♀♀, and one specimen without abdomen, all pinned.

Head. Occiput dark brown; eyes in both sexes large, nearly contiguous, separated on vertex and ventrally by only width of one or two ommatidia. Rostrum and maxillary palps brown; rostrum subequal in length to rest of head in both males and females. Scape and pedicel brown, somewhat depressed; pedicel with subterminal ring of appressed, dark setae; flagellum of 14 flagellomeres, brown, with numerous short, pale hairs, and with most verticils 2–3 times length of their respective segments.

Thorax. Pronotum dull brown; mesonotal prescutum slightly polished brown to light brown, some individuals (including holotype) with indistinct darker brown median line and two submedian, setiferous lines. Depression between scutal lobes yellowish brown to brown. Scutellum and postscutellum light brown. Halteres dull dark brown. Pleural surfaces slightly polished brown to light brown; coxae dull brown, hind coxae with numerous dark setae on posterior surface, other coxae with few, scattered setae. Femora, tibiae, and proximal three-fourths of basitarsi brown, grading into yellowish white on apical one-fourth of basitarsi. Tarsomeres 2–4 nearly white; 5 yellowish. Middle and hind basitarsi with mesal spurlike, elongate seta just beyond end of tibia.

Wings (Fig. 16) strongly tinged with grayish brown, stigma distinct but not conspicuously darker than ground color. Veins R_{2+3} and R_{4+5} generally parallel for half their length beyond level of r-m, diverging near apex of wing. Cross-vein r-m short but present in some individuals, absent by contact of R_{4+5} and M_{1+2} in others. Cell 1st M_2 large, about twice as long as greatest width. Cross-vein m-cu approximately in alignment with r-m, shorter than or subequal to basal section of M_{3+4} .

Abdomen of Male. Dark brown, terga and sterna 2–8 with mostly sparse, short hairs but longer, more numerous hairs near

◆**Figures 1 through 15.** *Limonia hoguei*, *L. paniculata*, and *Helius brunneus*. Upper scale, Figures 1–9, 12, 14; lower scale, Figures 10, 11, 15.

Figures 1 through 5. *Limonia* (*Rhipidia*) *hoguei* n. sp., male holotype. **Figure 1**, right antenna, lateral aspect. **Figure 2**, ninth abdominal tergum (9t), right basistyle, dorsal and ventral (vd) dististyles, dorsal aspect. **Figure 3**, right gonapophysis, mesal aspect. **Figure 4**, left basistyle, ventrolateral aspect. **Figure 5**, aedeagus and left gonapophysis (gon), ventral aspect.

Figures 6 through 11. *Limonia* (*Caenoglochina*) *paniculata* n. sp.; 6–9, male paratype, 10–11, female allotype. **Figure 6**, ninth abdominal tergum (9t), left basistyle (bs) and dististyle, dorsal aspect. **Figure 7**, left basistyle and dististyle, posteroventral aspect. **Figure 8**, left basistyle and dististyle, mesal aspect. **Figure 9**, aedeagus (aed) and right gonapophysis (gon), left lateral aspect (left basistyle removed). **Figure 10**, terminal abdominal segments, left lateral aspect. **Figure 11**, cerci and part of tenth tergum, dorsal aspect.

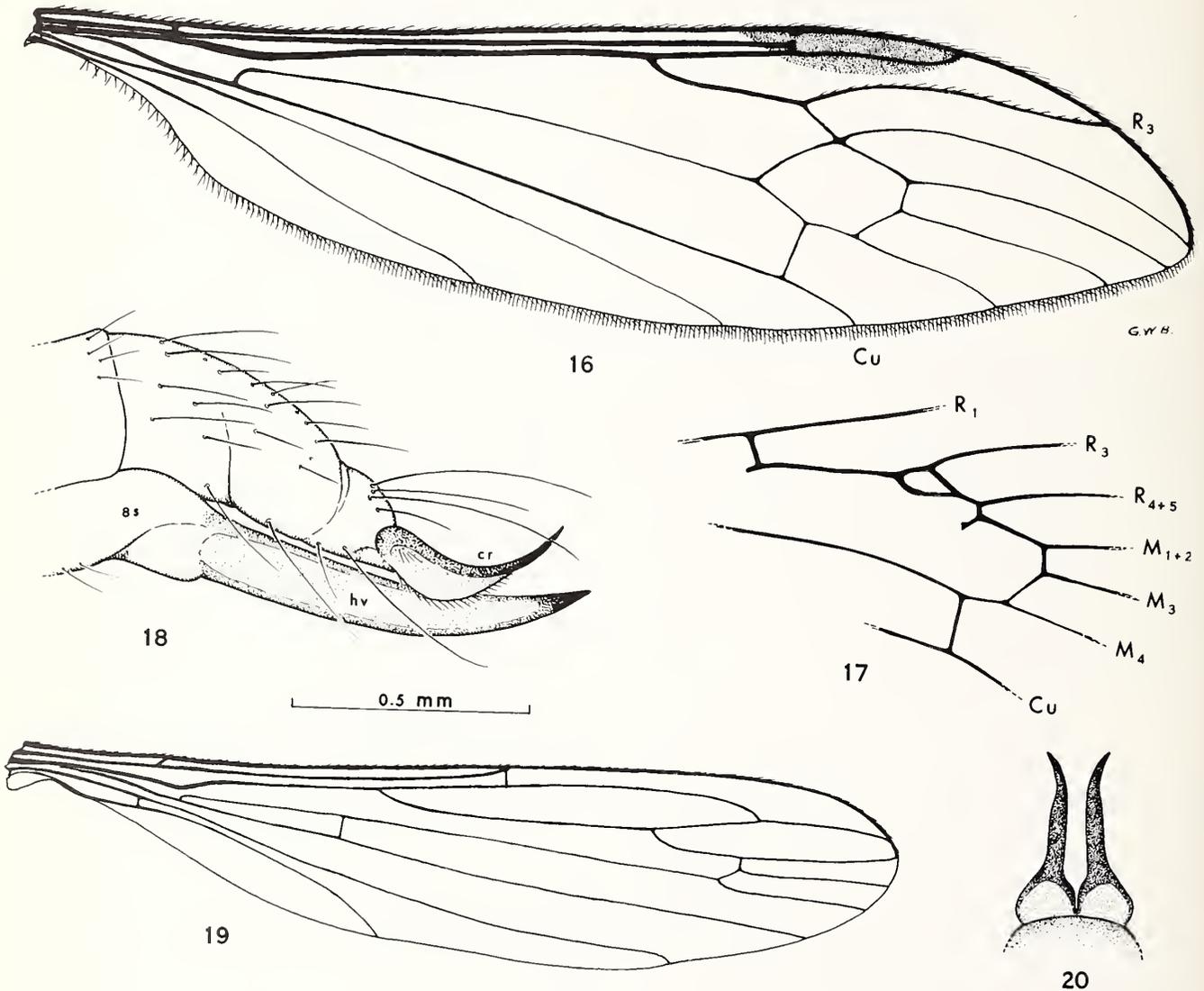
Figures 12 through 15. *Helius brunneus* n. sp., paratypes. **Figure 12**, terminal abdominal segments, male, dorsal aspect (most of right side omitted). **Figure 13**, basal portion of inner dististyle, enlarged to show minute spines. **Figure 14**, left basistyle and dististyles, aedeagus (aed) and phallosome (ps), right lateral aspect (right basistyle removed). **Figure 15**, terminal abdominal segments, female, left lateral aspect.

lateral margins. Ninth tergum (Fig. 12, 9t) with sparse marginal setae at either side of broadly U-shaped median emargination. Outer dististyle darkly sclerotized, slender, abruptly curved near apex to form hooklike tip; no lateral spine. Inner dististyle slender, unevenly curved inward and downward with single spine at apex and group of 4-5 microscopic, blackened spines on mesal surface near midlength (Fig. 13). Basistyle not prolonged conspicuously beyond level of attachment of dististyles. Phallosome bilobed, bearing two elongate, acutely tipped processes directed first downward into genital chamber, then curving upward and mesad (Fig. 14, ps). Aedeagus (Fig.

14, aed) stout, strongly curved to form nearly complete coil. **Abdomen of Female.** (Fig. 15). Dark brown, with sparse, fine hairs shorter on terga than on sterna. Cerci long, slender, straight in basal half, curved evenly upward in apical half. Hypovalves slender, straight, tapering gradually to acute apex.

Length of body exclusive of rostrum and antennae, male, 4.8-6.1 mm (holotype 6.0 mm); female, 5.2-6.5 mm (allotype 5.2 mm). Wing length, male, 5.8-7.2 mm (holotype 6.7 mm); female, 5.8-6.3 mm (allotype 5.8 mm).

TYPES. Holotype, male, Wafer Bay, Cocos Island, Costa Rica, collected at 15-watt ultraviolet light trap, at Station 6



Figures 16 through 20. *Helius brunneus* and *Orimarga flavescens*. Scale, Figures 18, 20.

Figures 16 and 17, *Helius brunneus* n. sp., wings, male paratypes. Figure 16, normal wing venation (wing length 7.3 mm). Figure 17, abnormal wing venation of discal area (R—radius, M—media).

Figures 18 through 20, *Orimarga (Diotrepha) flavescens* n. sp., female holotype. Figure 18, terminal abdominal segments, left lateral aspect; 8s—eighth sternum, cr—cercus, hv—hypovalve. Figure 19, wing venation (wing length 5.1 mm). Figure 20, cerci, dorsal aspect.

(Rio Genio, 200 m south of river's mouth), 27 March 1978, by C.L. Hogue and S. Miller. Allotype, female, and 3 ♂♂, 1 ♀ paratypes, Rio Genio, Cocos Island, 27 March 1978. Additional paratypes: Wafer Bay, 17–22 April 1975 (5 ♂♂, 2 ♀♀, 1 without abdomen); Wafer Bay, at UV light, 27 March 1978 (2 ♂♂); Rio Genio, 25 March 1978 (8 ♂♂).

DIAGNOSIS. *Helius brunneus* belongs to the *albitarsis* group and, on the basis of size, structure, and color, appears to resemble most closely *H. micracanthus* Alexander from the state of São Paulo, Brazil (Alexander 1945a) and, somewhat less closely, *H. rectus* Alexander from the Federal District of Brazil (Alexander 1945b). *H. micracanthus* is slightly smaller in body and wing length, to judge from the type specimen. In *H. brunneus*, the basitarsi are less extensively white than in *micracanthus*, and the halteres are dusky brown, not "dirty white." The inner dististyle is markedly more curved than in *micracanthus*. The two species have in common the strongly curved processes of the phallosome. In *brunneus*, the r-m cross-vein is often absent, but a larger sample of *micracanthus* might show that this is also true of that species.

ETYMOLOGY. Although the body color of *brunneus* is not diagnostic, the species takes its name from that characteristic (Latin *brunneus* = brownish).

REMARKS. A striking venational anomaly was observed in one individual. This involved the area of the discal cell (cell 1st M_2) and the radial sector (Fig. 17). Near its origin, the Rs is angular, with a short spur vein; the discal cell is not formed, and the veins in that area of the wing are thickened and atypically arranged (cf. Fig. 16).

Orimarga (Diotrepha) flavescens new species

Figures 18–20

DESCRIPTION. Description based on one female and one individual with abdomen broken off, both pinned.

Head. Occiput grayish brown with sparse, long, yellow setae; vertex and frons paler, sordid yellowish brown; rostrum and maxillary palps brown. Eyes black, large, only narrowly separated on vertex and ventrally behind rostrum. Antennal scape brown, pedicel light brown, flagellum dull yellowish, with 14 flagellomeres, most bearing verticils subequal to their length, except apical flagellomere with four nearly terminal setae twice its length.

Thorax. Pronotum yellowish brown; prescutum, scutum, and scutellum dull yellowish; postnotum (postscutellum) yellowish brown. Pleural sclerites and coxae dull yellowish. Femora of middle and hind legs nearly white except for apical black band (about 8% of total femoral length). (Both front legs missing from holotype.) Tibiae white, with narrow, black apical band. Basitarsus pale grayish white, tarsomeres 2 and 3 light gray, 4 and 5 dark gray. Ratio of femur: tibia: basitarsus: tarsomeres 2: 3: 4: 5 = 85: 83: 54: 13: 5: 2: 2. Claws simple, strongly curved.

Wings (Fig. 19) lightly tinged with yellowish gray, without stigmal darkening; veins yellow. Sc joins C shortly before level of midlength of Rs; Sc_2 at apex of Sc_1 . R_1 curves evenly to join

R_{2+3} ; no vein R_{1+2} (this vein possibly indicated by faint deflection in R_1 just before junction with R_{2+3}). R_{4+5} nearly perpendicular to Rs and R_{2+3} at their junction. Cross-vein m-cu about three times its length before level of origin of Rs; cross-vein r-m approximately its length beyond fork of M. Halteres grayish yellow.

Abdomen of Female. General coloration yellowish, with light brown, transversely wrinkled annulations at posterior ends of segments 2–4 and paler annulation at end of segment 5. Abdomen long, slender; length of segments 2–6 about 3.5–4 times their greatest diameter. Segments 7–8 short, enlarged abruptly in diameter from 6. Terga 9 and 10 fused dorsally, partially separated laterally (Fig. 18). Cerci short, not contiguous dorsally (Fig. 20), expanded laterally at base, somewhat concave ventrolaterally, with setiferous ventral margin; apex glabrous, densely sclerotized, conspicuously upturned and sharp. Hypo- valves more than twice length of cerci, only slightly upcurved to sharp tip, strongly sclerotized in apical one-third and along dorsal and ventral margins.

Body length (frons to tip of hypo- valves) of female holotype about 7.6 mm. Wing length 5.1 mm. Hind femur 5.0 mm. Antenna about 1.2 mm.

TYPES. Holotype, female, Wafer Bay, Cocos Island, Costa Rica, collected in Malaise trap, at Station 3 (Rio Genio, 200 m south of river's mouth), 26 March 1978, by C.L. Hogue and S. Miller. Paratype (abdomen broken): Chatham Bay, 22 January 1967, I.L. Wiggins.

DIAGNOSIS. *Orimarga (Diotrepha) flavescens* is apparently most closely related to *Orimarga (D.) omissinervis* Alexander, a species known only from Bolivia (Alexander 1913). Like *O. flavescens*, that species has pale legs with darkened femoral and tibial apices and lacks vein R_{1+2} ; however, it has a brown thorax, dark brown abdomen, and grayish wings and is somewhat larger than *flavescens*.

ETYMOLOGY. The specific name refers to the general coloration of this fly (Latin *flavescens* = yellowish).

Gonomyia (Lipophleps) puer Alexander

This species is widespread from southern United States to Mexico, Central America, and northern South America (Ecuador, Guyana, Peru), including the West Indies. Cocos Island records: in Malaise trap, Station 3 (Rio Genio), Wafer Bay, 24 March 1978 (3 ♀♀), same but 25 March (8 ♀♀), same but 26 March (2 ♂♂, 8 ♀♀), same but 27 March (2 ♀♀); light trap, 15-watt UV, Station 4 (400 m south of mouth of Rio Genio), Wafer Bay, 24 March 1978, (2 ♂♂, 1 ♀), same but Station 6 (200 m south of mouth of Rio Genio), 27 March (1 ♂); all collected by C.L. Hogue and S. Miller. On 22 January 1967, I.L. Wiggins collected 13 ♀♀ at Chatham Bay (Bahia de Chatham).

Gonomyia (Paralipophleps) pleuralis (Williston)

Even more widespread than *Gonomyia puer*, this species ranges from southeastern United States through the West Indies and

Bermuda to Brazil, Bolivia, Guyana, and Peru. Cocos Island records: Wafer Bay, 17–22 April 1975, C.L. Hogue (1 ♀); in Malaise trap, Station 3 (Rio Genio) Wafer Bay, 24 March 1978 (1 ♀), same but 25 March (1 ♀), same but 26 March (1 ♂, 5 ♀♀); light trap, 15-watt UV, Station 2 (Rio Genio at first rapids above high tide level), Wafer Bay, 23 March 1978 (3 ♀♀), same but Station 6 (Rio Genio), 27 March (1 ♂); all collected by C.L. Hogue and S. Miller. The I.L. Wiggins collection, made at Chatham Bay, 22 January 1967, contains 30 individuals (2 ♂♂, 28 ♀♀ or lacking abdomen).

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I am particularly indebted to Dr. Charles L. Hogue for making the recent collections available to me for study, and to him and Scott Miller for doing the field work. Their trips to Cocos Island were generously supported by Mr. and Mrs. Richard Steele (1978) and Mr. Timothy Doheny (1975). I thank also Dr. Paul H. Arnaud, Jr., of the California Academy of Sciences, San Francisco, for the loan of many of Wiggins' specimens. For technical assistance, I thank Ernest M. May, Jon K. Gelhaus, and Chen-Wen Young. Finally, I express my gratitude to my colleague in the study of crane flies, Professor Charles P. Alexander, for 30 years of friendly cooperation and encouragement.

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CONTRIBUTIONS IN SCIENCE

ARCOSCALPELLUM HOEK AND *SOLIDOBALANUS* HOEK (CIRRIPEDIA,
THORACICA) FROM THE PALEOGENE OF PACIFIC COUNTY, WASHINGTON,
WITH A DESCRIPTION OF A NEW SPECIES OF *ARCOSCALPELLUM*

Victor A. Zullo



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**ARCOSCALPELLUM HOEK AND SOLIDOBALANUS HOEK (CIRRIPEDIA,
THORACICA) FROM THE PALEOGENE OF PACIFIC COUNTY, WASHINGTON,
WITH A DESCRIPTION OF A NEW SPECIES OF ARCOSCALPELLUM¹**

Victor A. Zullo²

ABSTRACT. *Arcoscalpellum raricostatum* Withers, 1953, previously known from the Italian and Cuban Eocene, and *A. knapptonensis* n. sp. occur in concretions in the basal beds of a chronostratigraphic equivalent of the Lincoln Creek Formation exposed along the Columbia River near Knappton, Pacific County, Washington. The middle units have yielded only fragmentary arcoscappelid remains. The upper beds contain a species of *Solidobalanus* Hoek, 1913, similar to *S. (Hesperibalanus) sookensis* (Cornwall, 1927) from the Sooke Formation (Juanian Molluscan Stage) of Vancouver Island, British Columbia. The molluscan faunas of the middle and upper beds are characteristic of the Matlockian and Juanian Molluscan Stages, respectively (Zemorrian benthic Foraminiferal Stage, or Oligocene). Molluscs are not known from the basal unit, but the arcoscappelids suggest a late Eocene age (Galvinian Molluscan or Refugian benthic Foraminiferal Stage) based on their affinities with late Eocene European species. The two species of *Arcoscalpellum* Hoek, 1907, are the first scalpelloid barnacles to be reported from the Pacific Coast Cenozoic.

INTRODUCTION

Calcareous concretions from marine sediments exposed along the north shore of the Columbia River near Knappton, Pacific County, Washington (Figure 1) contain numerous, well-preserved, but disarticulated capitular plates of two species of *Arcoscalpellum* Hoek, 1907, and the shells and a few opercular plates of an archaebalanid resembling *Solidobalanus (Hesperibalanus) sookensis* (Cornwall, 1927). The arcoscappelids are the first scalpelloid barnacles to be recorded from the Pacific Coast of North America. *Arcoscalpellum* in the traditional sense is an extant, cosmopolitan genus with a fossil record extending back to the Late Cretaceous. It is represented by more than 100 extant species found primarily at bathyal and abyssal depths, and by over 50 fossil species from Upper Cretaceous and Tertiary inshore shelf deposits. Nine fossil species have been reported from North America. As many have perceived, the traditional conception of the genus *Arcoscalpellum* includes a diversity of species whose relationships are not altogether clear. Several attempts have been made to isolate species-groups within the genus, but only Zevina (1978) has proffered a comprehensive revision of the extant species. In Zevina's classification, the species of *Arcoscalpellum*, together with those of *Holoscalpellum* Pilsbry, 1907, are distributed among 12 genera in the subfamily Ar-

coscalpellinae Zevina. No attempt has yet been made to reevaluate the classification of fossil species in light of Zevina's revision. This may not be possible for many fossil species, because generic assignment in Zevina's scheme is dependent upon knowledge of the total armature of the capitulum, and many fossil species are known only from a few disarticulated capitular plates. Buckridge (1980) has proposed a new genus for a group of Tertiary species from Australasia characterized by heavily calcified capitular plates and an absence of pits on the interior of the scutum for the placement of males. The classificatory significance of these features and their distribution in fossil and extant species outside of the Australasian region are unknown.

Archacobalanids are the oldest known balanoid barnacles, first appearing in middle Eocene rocks, and are the most commonly encountered balanoids in Paleogene deposits. Three fossil species have been described from the Pacific Coast Tertiary: *Solidobalanus (Hesperibalanus) cornwalli* (Zullo, 1966) from the middle or upper Eocene Cowlitz Formation of Lewis County, Washington; *S. (H.) sookensis* from the Oligocene Sooke Formation of Vancouver Island, British Columbia; and *S. (H.) proinus* (Woodring, 1950) from the Pliocene of central and southern California (Zullo, 1979a). The extant North Pacific species, *S. (H.) hesperius* (Pilsbry, 1916), is common in Pleistocene deposits of the Pacific Northwest. *Hesperibalanus* Pilsbry, 1916, was synonymized with *Solidobalanus* Hoek, 1913, by Henry and McLaughlin (1967) but was reinstated as a subgenus of *Solidobalanus* by Newman and Ross (1976). Of the four extant and nine extinct species presently included in *Hesperibalanus*, only two, *S. (H.) hesperius* and *S. (H.) proinus*, can be ascribed to this subgenus with certainty. The remainder are included presently as a matter of convenience, awaiting a much needed revision of the free-living Archacobalaninae.

The Knappton Cirripedia are significant in several respects. The presence of arcoscappelids extends the known Paleogene

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distribution of this group into the northeastern Pacific. The occurrence of archaeobalanids supports previous indications that free-living members of this group are widespread in Paleogene deposits (Zullo and Baum, 1979). Perhaps most importantly, the Knappton species suggest that cirripeds are useful biostratigraphic indicators, discussion of which follows the systematic account.

STRATIGRAPHY OF THE KNAPPTON EXPOSURES

The Knappton beds are considered chronostratigraphic equivalents of the Lincoln Creek Formation of Beikman and others (1967) (replacement name for the Lincoln Formation of Weaver, 1912, and of subsequent authors). In the Grays Harbor basin located northeast of the Knappton locality, the Lincoln Creek Formation consists of up to 2,740 m of tuffaceous siltstone and sandstone containing scattered concretions and concretionary beds. The Lincoln Creek Formation is considered to range from the late Eocene to earliest Miocene (Rau, 1958, 1964; Armentrout, 1975, 1977). The lower part of the formation is correlated with the Keasey Formation of Oregon and the Toutle Formation (Gries Ranch beds) of southern Lewis County, Washington. The upper part of the formation is equivalent to the Sooke Formation of Vancouver Island, British Columbia, and the upper part of the Twin River Formation of Washington (Armentrout, 1977).

According to Ray Wells (personal communication, 1980), who has mapped the region and measured and described the section, much of the Knappton section is covered, including the contacts with under- and overlying units. That part of the section considered correlative with the Lincoln Creek Formation consists of about 305 m of thin-bedded and laminated tuffaceous siltstone and sandy siltstone bearing occasional concretions, some of which are several meters in length. This unit is overlain by at least 150 m of concretionary sandstone, sandy siltstone, and silt-

stone that is equivalent to the Miocene Astoria Formation of western Oregon. The underlying unit is not exposed. Fossils from the Knappton exposures, including those described here, were collected by James and Gail Goedert, who divided the "Lincoln Creek" part of the section into four informal faunistic units (Figure 2): (1) a lower unit characterized by barnacle-bearing concretions and an abundance of the trace fossil *Tisosa* De Serres; (2) an overlying unit containing tisoans, sponges, small aturiid nautiloids, and many decapod crustacean and marine vertebrate remains; (3) a glass sponge zone; and (4) an upper unit characterized by an abundance of invertebrate and marine vertebrate remains, including large aturiid nautiloids, but with few sponges and no tisoans. Frey and Cowles (1969, 1972) reported on the single, double, U-shaped, and branching burrows of *Tisosa* from the Knappton locality (primarily unit 1) and noted the presence of the decapod crustacean *Callianassa knapptonensis* Rathbun, 1926, based on a record in Weaver (1942). Armentrout (personal communication, 1979) refers the molluscan fauna of unit 2 to the *Echinophoria rex* zone (= Matlockian Molluscan Stage, = lower Zemorrian benthic Foraminiferal Stage, = lower Oligocene), and that of unit 4 to the *Echinophoria apta* zone (= Juanian Molluscan Stage, = upper Zemorrian benthic Foraminiferal Stage, = upper Oligocene).

CIRRIPEL BIOSTRATIGRAPHY

The two identifiable arcoscappelids are from faunal unit 1 (Natural History Museum of Los Angeles County Invertebrate Paleontology, LACMIP, locality 5844). A new species of *Arcoscappelum* (strict sense), represented by numerous carinae, scuta, and terga, is most similar to *A. gassinensis* (de Alessandri, 1906) from the Eocene Calcare di Gassino on the Bussolino side of Gassino, northeast of Turin, Italy. The second species, represented by partial carinae, is ascribed to *A. raricostatum* Withers, 1953, also described from the Calcare di Gassino near Bussolino. Withers (1953, p. 59) considered the Calcare di Gassino to be Auversian and middle Eocene, and correlative with the Upper Bracklesham beds at Whitecliff Bay, Isle of Wight. Withers's age determination appears to be based on the occurrence of *Nummulites variolarius* (Lamarck) in both units. Herb and Hekel (1973), among others, have shown that *N. variolarius* first appears in the uppermost middle Eocene (Biarritzian) but continues throughout the upper Eocene (Bartonian/Priabonian) in many parts of Europe, including northern Italy. In addition to the current practice of considering the Auversian as basal upper Eocene, Cita (1973), in a review of the Tertiary strata of the Italian Piedmont, regarded the Calcare di Gassino as Priabonian. Thus, it would appear that *Arcoscappelum gassinensis* and *A. raricostatum* are upper rather than middle Eocene species.

The two species of *Arcoscappelum* from the Knappton section thus suggest that the basal part of the exposed "Lincoln Creek" is upper Eocene (= Galvinian Molluscan or Refugian benthic Foraminiferal Stage). This conclusion is supported by the cirriped faunal "facies" of the upper Eocene (Jacksonian Gulf Coastal Plain Stage) Principe Formation in the vicinity of Havana, Cuba. In addition to *A. raricostatum* (see systematic account), this unit contains two other species of *Arcoscappelum*,

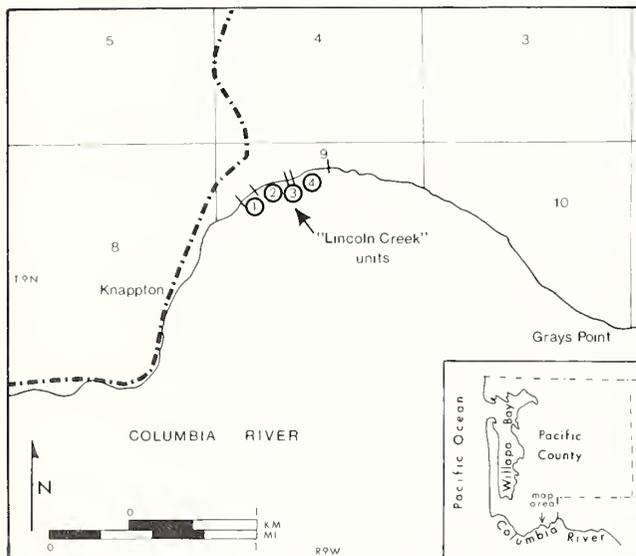


Figure 1. Part of the Knappton, Washington 7.5-minute quadrangle showing location of "Lincoln Creek" faunal units. Inset map shows location of Knappton quadrangle in Pacific County.

A. habanense Withers, 1953, and *A. sanchezi* (Withers, 1926), that are closely related both to *A. gassinensis* and the new Knappton species.

It is unfortunate that the only cirriped remains so far recovered from unit 2 (LACMIP locality 5843) are poorly preserved terga. These plates may represent a species of *Arcoscalpellum*, but terga are not sufficient in distinguishing between the *A. gassinensis* complex and the quite distinctive species of the known Oligocene fauna. Knowledge of the identity of this species might prove helpful in determining the age of unit 2. Many European geologists would place the Eocene-Oligocene boundary at the base of the Rupelian (see Withers, 1953; Van Eysinga, 1975). This shift in the boundary relegates the traditional European lower Oligocene Lattorfian and Tongrian Stages to the upper Eocene. The crux of arguments favoring this change is that Lattorfian and Tongrian faunas are more similar to Bartonian/Priabonian faunas than they are to Rupelian faunas. Rec-

ognition of upper Eocene equivalents and of the Eocene-Oligocene boundary in North America is further complicated by increasing endemism of invertebrate megafaunas and by apparent disagreement in correlation between upper Eocene calcareous nannofossil and planktonic foraminiferal zones. In addition, there is increasing evidence from potassium-argon, rubidium-strontium, and fission track age determinations in Europe, the Caribbean, and the Atlantic and Gulf Coastal Plains that the Eocene-Oligocene boundary is closer to 33 m.y. than to the 37-m.y. date proposed by Hardenbol and Berggren (1978) (Harris and Zullo, 1980). Those faunas and faunal zones whose ages have been related to radiometric age determinations must be reevaluated in light of this evidence.

Although opercular plates are preserved in some of the archaebalanid shells from unit 4 (LACMIP locality 5842), the sediment is too well indurated to permit their intact extraction. The shells are quite similar to those of *Solidobalanus sookensis*,

	FORAMINIFERAL STAGES	MOLLUSCAN STAGES	KNAPPTON BEDS	KNAPPTON CIRRIPEDIA
MIOCENE	SAUCESIAN	NEWPORTIAN	"ASTORIA" FM.	
		PILLARIAN	?	
OLIGOCENE	ZEMORRIAN	JUANIAN	UNIT 4 LACMIP 5842	SOLIDOBALANUS AFF. SOOKENSIS
		MATLOCKIAN	UNIT 3	UNIT 2 LACMIP 5843
UPPER EOCENE	REFUGIAN		GALVINIAN	
			?	

Figure 2. Stratigraphic distribution of Knappton cirripeds and suggested correlation of the Knappton beds (partly after Armentrout, personal communication, 1979).

but the internal morphology of the single scutum examined is sufficiently different to question assignment of the Knappton specimens to that species without additional opercular plate material. It is clear that the Knappton species is unrelated either to the upper Eocene *S. cornwalli* or to true *Hesperibalanus*. The occurrence of a species of *Solidobalanus* similar to *S. sookensis* in unit 4 is in agreement with the Oligocene age assignment derived from molluscan data.

SYSTEMATIC ACCOUNT

Subclass Cirripedia Burmeister, 1834

Order Thoracica Darwin, 1854

Suborder Lepadomorpha Pilsbry, 1916

Family Scalpellidae Pilsbry, 1916

Subfamily Arcoscalpellinae Zevina, 1978

Genus *Arcoscalpellum* Hoek, 1907

Arcoscalpellum knapptonensis n. sp.

Figures 3–7, 9–17

DIAGNOSIS. Broad, slightly bowed carina with arched tectum, faintly ridged parietes, and very narrow, inwardly turned intraparietes; broad, trapezoidal, longitudinally striate scutum with low, flat, apico-basal ridge and decidedly obtuse basitergal angle; tergum subtriangular, longitudinally striate, twice as long as wide, with acute apico-basal ridge and without marked distinction between upper and lower carinal margins. Distinguished from *A. gassinensis* and *A. habanense* by its narrower carina without conspicuous ridges on or bordering the tectum; from *A. sanchezi* and *A. euglyphum* by its carinal parietes that do not flare outwardly; from *A. choctawensis* and *A. toulmini* by its much broader tergum and thicker capitular plates.

LOCALITY. LACMIP locality 5844, "Lincoln Creek Formation," faunal unit 1, on Columbia River approximately 122 m east of boundary between sections 8 and 9, T 9 N, R 9 W, USGS 7.5-minute topographic quadrangle of Knappton (1973 ed.), near Knappton, Pacific County, Washington.

MATERIAL EXAMINED. Disarticulated carinae, scuta, and terga in four concretions. Holotype (LACMIP no. 6270) and paratypes (LACMIP nos. 6266–6269, 6330–6333) are in the invertebrate paleontology collection of the Natural History Museum of Los Angeles County.

DESCRIPTION. Carina slightly bowed, broad, length about four times width; tectum moderately to strongly arched, flattening towards basal margin, sometimes with incipient medial ridge; basal margin broadly V-shaped; parietes half as wide as tectum, normal to tectum, and separated from tectum by one or two inconspicuous, narrow, longitudinal ridges; parietes ornamented by up to five faint longitudinal ridges; intraparietes very narrow, separated from parietes by narrow but conspicuous ridge, and turned inward at approximately a 45° angle.

Scutum strongly arched, trapezoidal, length less than twice width; apico-basal ridge flat, low, slightly curved; occludent margin slightly convex; basal and lateral margins straight, nearly

equal in length, their junction forming an angle greater than 90°; tergal margin concave; tergotergal margin rounded, outer surface ornamented by faint, irregularly placed, longitudinal striae best developed on tergal side of plate; adductor muscle pit shallow, ill-defined.

Tergum subtriangular, elongate, length about twice width, longitudinally striate; apico-basal ridge well developed, acute to flat-topped, straight to gently curved, and situated less than one-third the width of the plate from the carinal margin; a second, low, curved ridge may be present extending from the apex to the scutal margin; carinal margin weakly convex, not sharply divided into upper and lower halves; occludent margin slightly convex, short, about eight-tenths length of scutal margin; scutal margin gently sinuous.

DISCUSSION. Of the Tertiary species whose carinae are known, only the following have arched tecta:

Arcoscalpellum euglyphum Withers, 1924, p. 11, pl. 2, figs. 1–2; Withers (1953, p. 233, pl. 34, fig. 1); Buckeridge (1980, p. 122, fig. 34, as a member of a newly proposed genus); lower Oligocene (Whaingaroan-Dunroonian, = Latorffian-Rupelian), New Zealand.

A. gassinensis (de Alessandri, 1906, p. 252, pl. 13, figs. 10–14, as *Scalpellum michelottianum* var. *gassinensis*); Withers (1953, p. 212, pl. 28, figs. 1–9); upper Eocene, Calcare di Gassino, northeast of Turin, Italy.

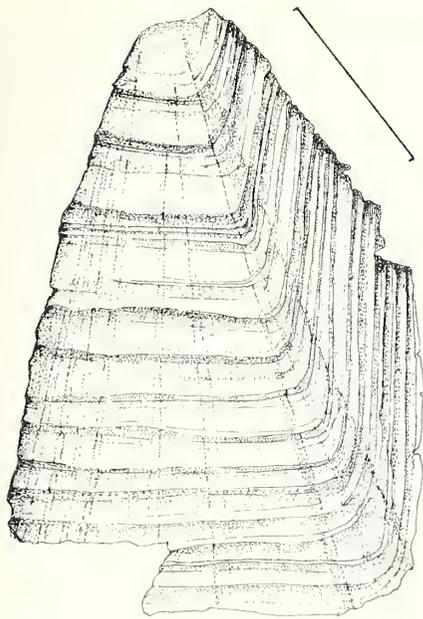
A. habanense Withers (1953, p. 218, pl. 30, fig. 1); upper Eocene, Principe Formation, near Havana, Cuba.

A. hartleyi (Withers, 1936, p. 590, pl. 11, figs. 1–5); Withers (1953, p. 232, pl. 32, figs. 1–5); (?) lower Miocene, Surma Series, Bangladesh.

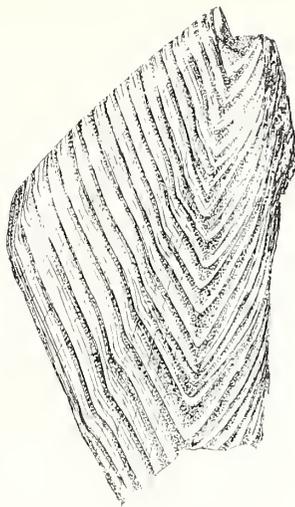
A. sanchezi (Withers, 1926, p. 617, pl. 26, figs. 1–7); Withers (1953, p. 215, text-fig. 84, pl. 29, figs. 1–12); upper Eocene, Principe Formation, near Havana, Cuba.

Arcoscalpellum knapptonensis is most similar to *A. gassinensis* from which it differs primarily in proportions of the plates. *Arcoscalpellum gassinensis* has a broader carina with narrower parietes set off from the tectum by conspicuous ridges, a broader scutum that in other respects is quite similar to that of *A. knapptonensis*, and a tergum that is distinguished by its shorter occludent margin and, conversely, longer scutal margin. *Arcoscalpellum habanense* is readily distinguished by the great breadth of the carina and the presence of prominent, acute, longitudinal ridges on the tectum and parietes. The carina of *A. hartleyi* is quite similar to that of *A. knapptonensis* and differs only in having a less markedly arched tectum. *Arcoscalpellum habanense* and *A. hartleyi* are known only from carinae. The carina of *A. sanchezi* is broader and more strongly bowed than that of *A. knapptonensis*, and its parietes and intraparietes flare outwards. Its scutum is narrower and has decidedly concave tergal and lateral margins. The tergum of *A. sanchezi* is similar to that of *A. knapptonensis*, except that the upper carinal margin is concave rather than straight. The carina of *A. euglyphum* has a strongly arched tectum, and the carinal parietes differ markedly from those of *A. knapptonensis* in flaring outwards and being bordered both on their inner and outer margins by prominent ridges.

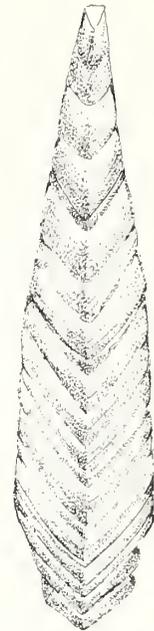
Weisbord (1977) described two species of *Arcoscalpellum* from the Paleogene of Alabama for which the carinae are not



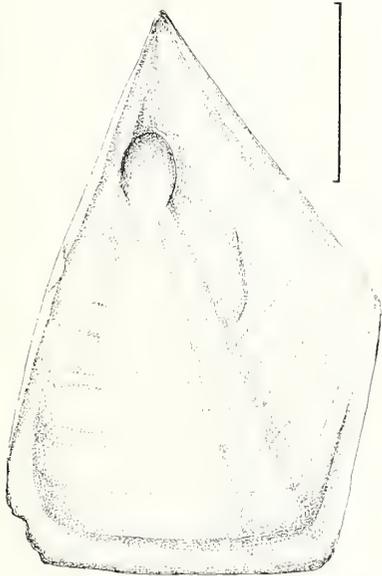
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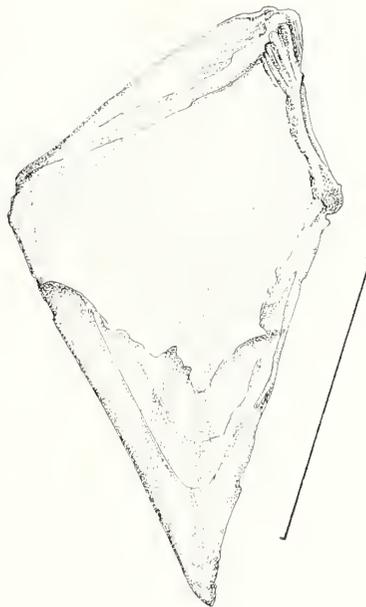
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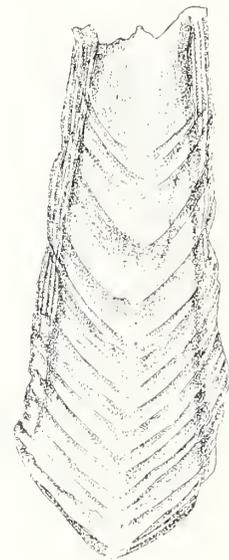
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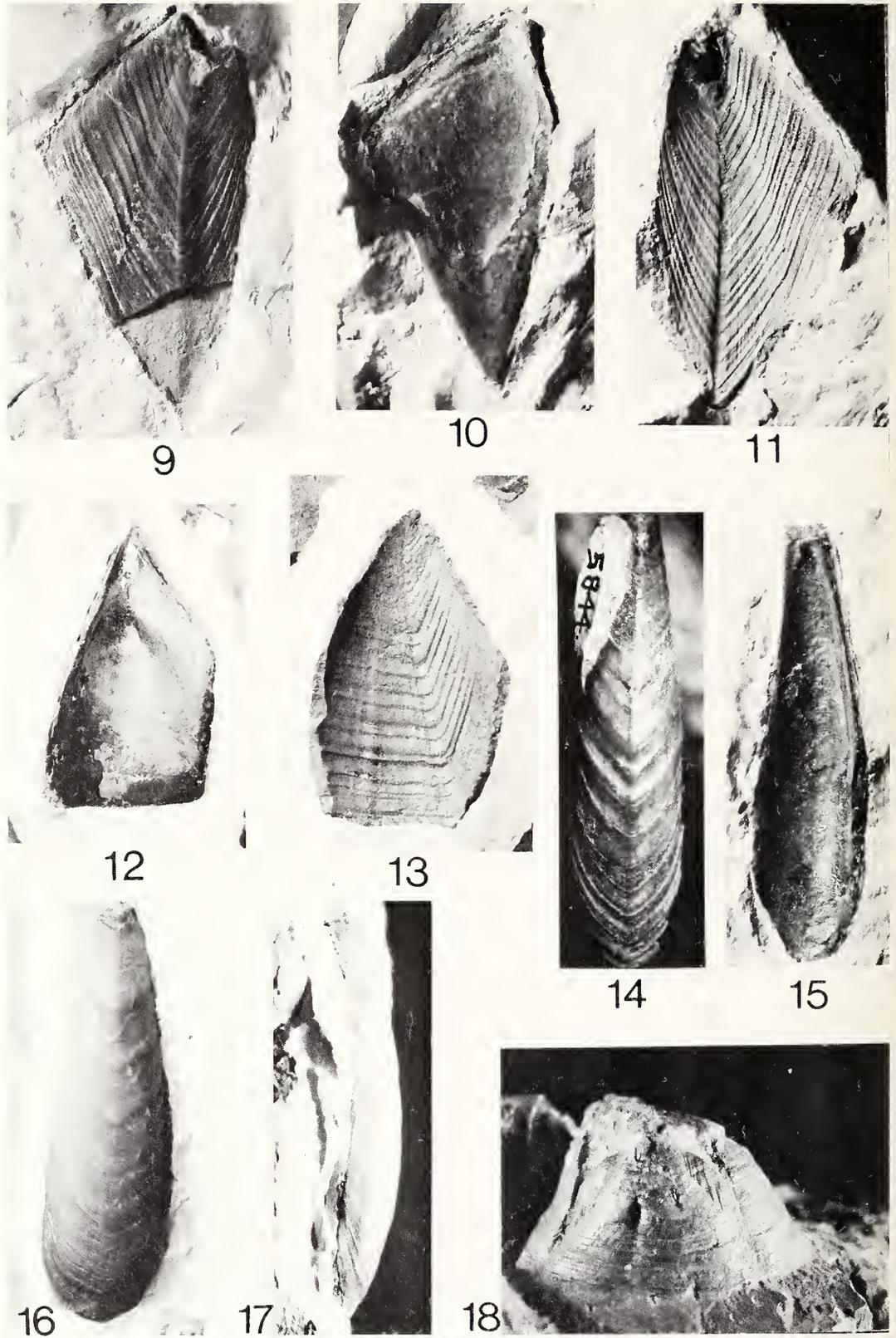


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Figures 3 through 8. *Arcoscalpellum* spp. **Figures 3 through 7.** *Arcoscalpellum knapptonensis* n. sp. (3) exterior of scutum, paratype LACMIP 6266; (4) interior of scutum, paratype LACMIP 6267; (5) exterior of tergum, paratype LACMIP 6268; (6) interior of tergum, paratype LACMIP 6269; (7) exterior of carina, holotype LACMIP 6270. **Figure 8.** *Arcoscalpellum raricostatum* Withers, exterior of carina, hypotype LACMIP 6271. Scale bars represent 5 mm.



known. *Arcoscalpellum(?) choctawensis* Weisbord from the upper Eocene (Jacksonian Stage) North Twistwood Creek Member of the Yazoo Clay has thin scuta and terga; the interior of the scutum is marked by an apical furrow, and the tergum is narrow and elongate. *Arcoscalpellum toulmini* Weisbord from the Paleocene (Landenian Stage) Porters Creek Formation has a narrower tergum than *A. knapptonensis* with a distinctly shorter occludent margin, and a broader scutum with a slightly acute basitergal angle and unequal tergal and lateral margins.

ETYMOLOGY. Geographic, after Knappton, Washington.

Arcoscalpellum raricostatum Withers, 1953

Figure 8

Arcoscalpellum raricostatum Withers (1953, p. 224, pl. 36, figs. 1–2).

Arcoscalpellum aff. *raricostatum* n. sp. Withers (1953, p. 224, pl. 36, fig. 3).

LOCALITY. LACMIP locality 5844, “Lincoln Creek Formation,” faunal unit 1, on Columbia River approximately 122 m east of boundary between sections 8 and 9, T 9 N, R 9 W, USGS 7.5-minute topographic quadrangle of Knappton (1973 ed.), near Knappton, Pacific County, Washington.

MATERIAL EXAMINED. Two carinae in one concretion associated with *A. knapptonensis*: one lacking apical quarter (LACMIP hypotype no. 6271); the other lacking both apical and basal parts (LACMIP hypotype no. 6335).

DESCRIPTION. The carinae are slightly bowed and have flat tecta that are gently arched towards the basal margin. The tecta are bordered by prominent ribs that bear five longitudinal ridglets. The parietes are narrow and normal to the tecta. The basal margins of the carinae are V-shaped.

DISCUSSION. Withers (1953) described *A. raricostatum* on the basis of two carinae from the Calcare di Gassino. Withers also described a basal fragment of a carina from the Principe Formation of Cuba that he considered was similar to but specifically distinct from *A. raricostatum*. The Cuban specimen differs from the types in having a slightly arched tectum with regularly spaced growth depressions and a less V-shaped basal margin. The Knappton carinae agree with the type specimens in the pronounced angulation of the basal margin and in lacking growth depressions but have the basally arched tectum characteristic of the Cuban carina. The Knappton carinae, in sharing features both with the types of *A. raricostatum* and the Cuban carina, suggest that the observed differences merely reflect individual variation within a single, widely distributed species. The morphologic variation seen in these five carinae is no greater than that to be found in the extant descendant of *A. raricostatum*, *A. michelottianum* (Seguenza, 1876) [= *A. velutinum* (Hoek,

1883)], whose geographic distribution includes the Atlantic, Indian, and western Pacific Oceans. For these reasons, I assign the Cuban and Knappton carinae to *A. raricostatum*.

The presence of these carinae amid the numerous capitular plates in the concretions ascribed to *A. knapptonensis* raises the question as to whether some of the scuta and terga may also be referable to *A. raricostatum*. Only the carina is known for this species, but as indicated by Withers (1953), *A. raricostatum* is similar to *A. michelottianum nanum* Withers, 1953, from the middle Miocene (Helvetian) of northern Italy, and to *A. michelottianum michelottianum* from the Pliocene through Recent. If the similarities seen between the carinae of these species extend to the scuta and terga, then there are no observable scuta and terga in the concretions that approach the form seen in *A. michelottianum*. Secondly, the two carinae occur in a single concretion, and the associated terga and scuta that are identifiable in this concentration do not differ from those associated with carinae of *A. knapptonensis* in other concretions.

In terms of Zevina’s revision of scalpellid classification, *A. raricostatum* can be assigned to the restricted genus *Arcoscalpellum* on the basis of its close affinity to the type species of *Arcoscalpellum*, *A. michelottianum*. *Arcoscalpellum knapptonensis*, on the basis of capitular plate morphology, also appears to resemble most closely species of the restricted genus *Arcoscalpellum*.

Suborder Balanomorpha Pilsbry, 1916

Family Archaeobalanidae Newman and Ross, 1976

Subfamily Archaeobalaninae Newman and Ross, 1976

Genus *Solidobalanus* Hoek, 1913

Subgenus *Hesperibalanus* Pilsbry, 1916

Solidobalanus (Hesperibalanus) sp., aff. *S. (H.) sookensis* (Cornwall, 1927)

Figure 18

LOCALITY. LACMIP locality 5842, “Lincoln Creek Formation,” faunal unit 4, on north bank of Columbia River about 1.6 km northeast of Knappton, Pacific County, Washington, center of N ½ of the N ½ of section 9, T 9 N, R 9 W, USGS 7.5-minute topographic quadrangle of Knappton (1973 ed.).

MATERIAL EXAMINED. Six shells in four concretions and one broken scutum; LACMIP hypotype nos. 6334, 6336.

DISCUSSION. The Knappton specimens of *Solidobalanus* agree with those of *S. sookensis* from the Sooke Formation of

Figures 9 through 18. *Arcoscalpellum* and *Solidobalanus* spp. **Figures 9 through 17.** *Arcoscalpellum knapptonensis* n. sp. (9) exterior of tergum, paratype LACMIP 6268, height 27 mm; (10) interior of tergum, paratype LACMIP 6269, height 24 mm; (11) external mold of tergum, paratype LACMIP 6330, height 24 mm; (12) interior of scutum, paratype LACMIP 6267, height 18 mm; (13) external mold of scutum, paratype LACMIP 6331, height 20 mm; (14) exterior of carina, holotype LACMIP 6270, height 30 mm; (15) interior of carina, paratype LACMIP 6332, height 27 mm; (16) exterior of carina, paratype LACMIP 6333, height 26 mm; (17) side view of same carina. **Figure 18.** *Solidobalanus* sp., aff. *S. sookensis* (Cornwall), rostral view of shell, hypotype LACMIP 6334, height 16 mm.

southern Vancouver Island in possessing a recurved carina, a large rhomboidal orifice, broad radii with oblique summits, and an irregularly plicate shell. Opercular plates are difficult to extract from the indurated matrix, and only the interior of a single, broken scutum could be examined in any detail. This scutum differs from those described for *S. sookensis* in lacking a depressor muscle pit and in appearing to have a straight rather than recurved ridge bordering the adductor muscle pit.

Solidobalanus sookensis and the Knappton species differ markedly from the upper Eocene Cowlitz Formation species *S. cornwalli* in having broad, transparietal radii with crenulate sutural edges, rather than narrow, non-transparietal radii with smooth sutural edges, and in possessing an unusually high and thickened ridge bordering the scutal adductor muscle pit. The Pliocene species *S. protnus* and the Pleistocene and extant species *S. hesperius* can be distinguished by their possession of a true scutal adductor ridge and of callosities and rugosities on the interior of the scutum.

BARNACLES AS BIOSTRATIGRAPHIC INDICATORS

Little consideration has been given to the potential of cirripeds as biostratigraphic indicators, particularly in North America. Cheetham (1963) and Weisbord (1977) recognized the value of barnacles in biostratigraphy, but only two authors have attempted to develop biostratigraphic zonations based on barnacle assemblages. Mellen (1973), utilizing Collins' (1973) study of the lepadomorphs from the Upper Cretaceous of Alabama and Mississippi, was able to recognize three zones in the "Selma Chalk." Zullo (1979b, 1980) was able to distinguish four assemblage zones in the middle Eocene through lower Miocene formations of North Carolina. Two of these zones, the upper middle Eocene *Arcoscalpellum subquadratum* zone and the lower upper Eocene *A. jacksonense* zone, can be recognized throughout the southeastern Atlantic and eastern Gulf Coastal Plains.

The Knappton arcoscappelids demonstrate that certain barnacles are useful in interregional and, in this case, intercontinental correlation. If it appears improbable that sessile organisms are capable of attaining rapid and widespread distribution, it is only necessary to compare the modern distribution of a related species. *Arcoscalpellum michelottianum* is found in the North and South Atlantic basins, the Indian Ocean, and the western Pacific between 40 and 2900 m. This species was originally described from the Astian and Plaisancian of Sicily and is considered to have evolved from *A. raricostatum* through the Italian Miocene taxon *A. michelottianum nanum*. The absence of *A. michelottianum* in the eastern Pacific may be an artifact of sampling but is probably related to the closing of Central American seaways during the time that this species was attaining its present distribution. Thus, it appears that *A. michelottianum* achieved virtual worldwide distribution in a three-million-year period through dispersal of planktonic larval stages. Examples of wide-ranging species are not limited to the Lepadomorpha ("goose barnacles"), for several balanomorph species ("acorn barnacles"), including *Balanus trigonus* Darwin, 1854, *B. calidus* Pils-

bry, 1916, and *B. venustus* Darwin, 1854, have developed tropicopolitan or Tethyan distributions by natural means.

Reconnaissance of Tertiary and particularly Paleogene marine units of the Atlantic and Gulf Coastal Plains and the Pacific Coast indicates that an array of lepadomorph and balanomorph remains has been overlooked. Systematic collection and analysis of these cirriped assemblages may provide a valuable tool in stratigraphic interpretations.

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**WOLFCAMPIAN RUGOSE AND TABULATE CORALS (COELENTERATA:
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NORTHERN CALIFORNIA**

Edward C. Wilson



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**WOLFCAMPIAN RUGOSE AND TABULATE
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Edward C. Wilson

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WOLFCAMPIAN RUGOSE AND TABULATE CORALS (COELENTERATA: ANTHOZOA) FROM THE LOWER PERMIAN MCCLOUD LIMESTONE OF NORTHERN CALIFORNIA¹

Edward C. Wilson²

ABSTRACT. Six sections measured across the McCloud Limestone, Shasta County, northern California, are Lower Permian (Wolfcampian Series), represent a composite thickness of at least 5,500 feet (about 1,700 meters), and contain rich invertebrate faunas including at least 49 species of rugose and tabulate corals. Forty-two species in 17 genera of rugose corals are described, including 36 new species and 5 new genera. Seven species in five genera of tabulate corals are described, including four new species. The general generic composition is characteristic of the Durhamid Coral Province known from rocks in the Ural Mountains, Novaya Zemlya, Spitzbergen, Arctic North America, and western North America as far south as southern California. Some genera appear to be endemic to western North America.

The corals did not form reefs but were randomly spaced on calcareous bioclastic substrates in shallow waters of the Cordilleran eugeosyncline near the Permian paleoequator in an area temporarily lacking much volcanic sedimentation.

INTRODUCTION

The primary purpose of this study is to determine the diversity and stratigraphic distribution of the stony corals of the McCloud Limestone, Shasta County, California. Six sections were measured and intensively sampled, and some additional collections were made at localities nearby the measured sections from the southernmost outcrop of the formation to about 20 miles (about 32 km) north along its general northeast trending strike (Fig. 1). In the remaining approximately 14 miles (about 22.5 km) of outcrop north of the measured sections, inspections were made on High Mountain and Bald Mountain, but the few corals collected were very poorly preserved. The section at Tombstone Mountain, which contains the highest Permian (Leonardian) rocks in the formation, is under study.

Fossils were selected for collecting in the following manners: (1) all corals, where feasible, were collected; (2) fusulinids were searched for near the exposed bases and tops of the sections, but within the sections they generally were collected only where abundant; (3) brachiopods were collected at localities where they appeared to be well preserved; (4) bryozoans were collected where abundant; (5) mollusks (bivalves, gastropods, cephalopods, rostroconchs) were collected where well preserved; (6) other conspicuous fossils were collected if well preserved, readily attainable, and of potential stratigraphic significance. The re-

sults are a relatively detailed sampling of the fossil corals of the southern part of the formation and a reconnaissance collection of other fossils. The specimens are deposited in the University of California Museum of Paleontology at Berkeley and the Natural History Museum of Los Angeles County, Invertebrate Paleontology Section.

Field work was pursued during the following intervals: 9–10 March, 19 March–4 April, 19–22 June, 7–11 September 1963; 19–20 April, 26–29 April 1964; 29 June 1967; 19–28 September 1968; 21–22 May 1970; 26 August–6 September 1973; 1–8 October 1976; 21–29 June 1979; 1–15 July 1981.

PREVIOUS WORK

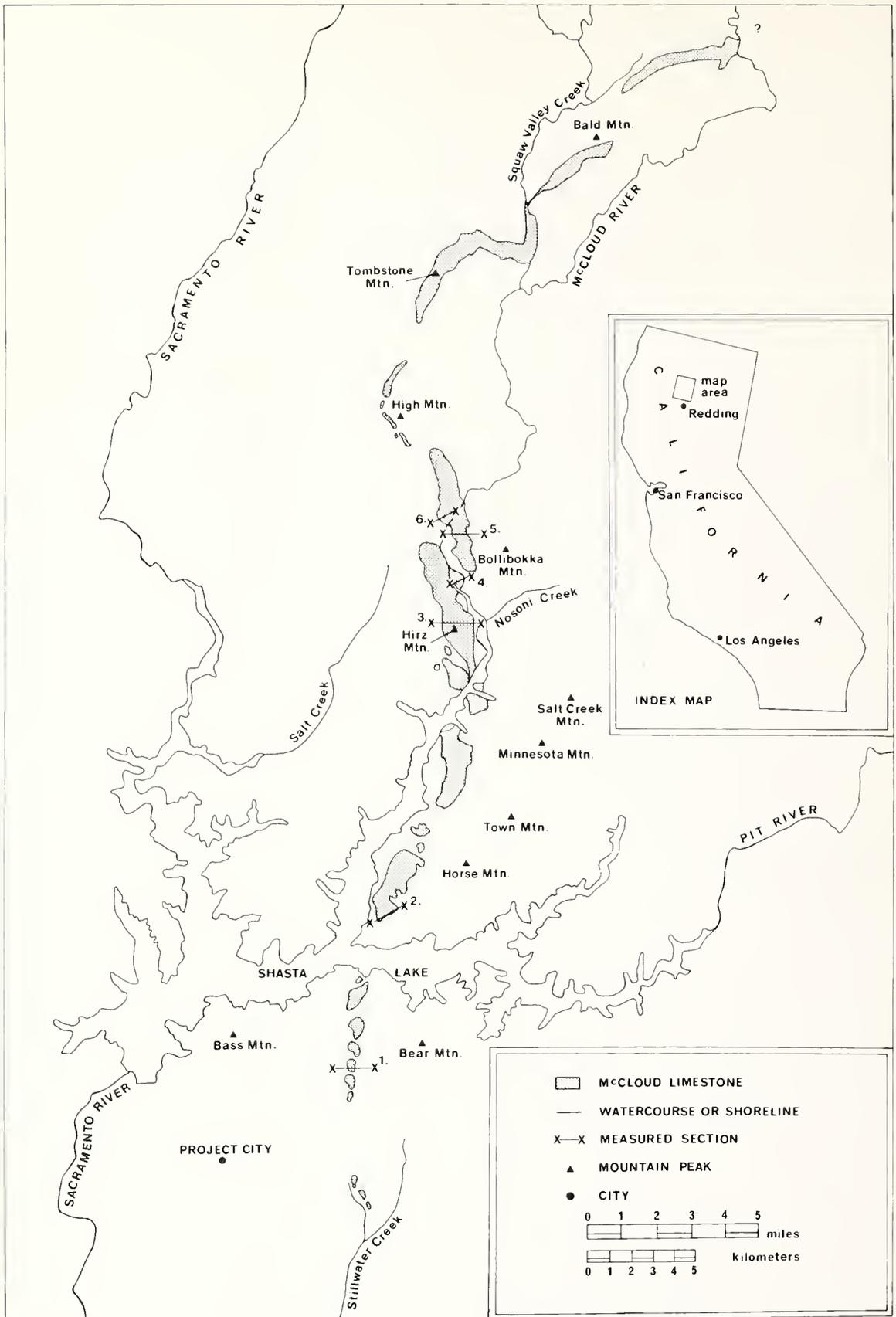
Pioneer work on older rocks in Shasta County was begun by Trask (1853:15), who later found (Trask, 1855:50) a "Carboniferous" limestone there that cropped out from "the Pitt River in a northerly distance for about thirty or forty miles, forming a portion of the canyon of McCloud's Fork. . . ." He was followed by the California Geological Survey under J.D. Whitney, who collected from the limestone on 20 and 21 September 1862 (Brewer, 1930:323). From this collection, Meek (1864) described fusulinids, corals, brachiopods, and a gastropod, all reportedly Carboniferous. Whitney (1865:326) estimated that the formation was 1,000 feet thick and conformable to the formations above and below.

Fairbanks (1893:35) named the formation McCloud Limestone. In a differing opinion, Turner (1894:230) considered it to be part of the Calaveras Formation. The classical study of the Redding Quadrangle by Diller (1906) fixed the name McCloud Limestone and assigned the formation to the Pennsylvanian.

Hinds (1932:273) first placed the McCloud Limestone in the Permian. Using fusulinids, Wheeler (1933) confirmed this determination and later reported (Wheeler, 1935) fusulinids in "seven distinct faunal horizons" from the southern part of the formation. Thompson and Wheeler (1946) described fusulinids from

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the McCloud Limestone and Nosoni Formation as far north as Potter Ridge, concluding that the former formation was Wolfcampian and Leonardian and the latter was Guadalupian in age. Fusulinid paleontology and biostratigraphy were continued by Skinner and Wilde (1965), who showed that the formation represented an aggregate thickness in excess of 7,000 feet and zoned it for its entire outcrop length into eight complexly distributed zones, ranging from possible Upper Pennsylvanian into Lower Permian. Wilde (1971:364) later determined that the lowest zone is Permian.

Additional reports on fusulinids, corals, brachiopods, and mollusks from the formation were published by Hayasaka (1936:64), Langenheim and McCutcheon (1959), Watkins (1973, 1974, 1975), and Wilson (1967a and b, 1970, 1971, 1980:89).

Other information about the formation has continued to accumulate. Coogan (1960), Skinner and Wilde (1965), and Watkins (1973) pointed out that fossils at the top of the underlying Baird Formation at Bollibokka Mountain are Pennsylvanian or Permian, rather than Mississippian as at the type locality. Working farther south, Albers and Robertson (1961) reported that the McCloud Limestone is separated from the overlying Nosoni Formation by the largest fault in the area, the McCloud fault, along which quartz diorite is intruded. Lanphere, Irwin, and Hotz (1968) cited an age of 246 m.y. for the quartz diorite, indicating that the intrusion was a Permian event rather than a Jurassic one as previously believed. Evans (1977) reported on the economic geology of the southernmost McCloud Limestone.

Study of the petrography of the McCloud Limestone indicated to Demirmen and Harbaugh (1965) that it is formed largely of bioclastic sediments that originated in clear waters of a eugeosyncline, somehow protected from the volcanic sediments typical of the rest of the section.

In summary, although considerable work has been done on other aspects of the McCloud Limestone, thorough paleontological study has been limited to the fusulinids, although minor work has been done with the corals, brachiopods, and mollusks.

REGIONAL GEOLOGY

Rocks older than Silurian or younger than Triassic have not been positively identified among the eastward dipping, north-south trending, eugeosynclinal strata that rise south of Shasta Lake from beneath disconformably overlying Cretaceous and younger rocks and disappear northwards beneath the volcanic flows of the southern flanks of Mount Shasta. At least half of the entire rock column is composed of layered volcanic rocks.

Upper Paleozoic rocks represent parts of the Mississippian, Pennsylvanian, and Permian. They are known in ascending order as the Bragdon Formation, Baird Formation, McCloud Limestone, Nosoni Formation, and Dekkas Formation. Various divisions (members, groups) have been proposed based on lithology, and some zones and zonules have been erected based on fossils.

The Bragdon Formation has Mississippian fossils. The Baird Formation contains Mississippian, Pennsylvanian, and possibly Permian fossils. The overlying three formations all are Permian.

The Pit stock, a Permian intrusive, follows the Baird-McCloud contact for many miles, locally intrudes faults in parts of these and other formations, and is followed by the McCloud River for much of its course south from Bollibokka Mountain. In the Potter Ridge area, an intrusion of mafic quartz diorite cuts the Pit stock in places.

STRUCTURE AND RELATIONSHIPS

The Paleozoic and Lower Mesozoic rocks of the Shasta Lake area form a slightly sigmoid north-south trending homocline, which dips eastward at angles varying from 45° to 60°. Coogan (1960:245) reported synclines and anticlines in the Bollibokka Mountain region. An additional small anticline is present in this area on the west bank of the McCloud River near the high-water line north of the McCloud River Bridge and south of Nawtawaket Creek. Albers and Robertson (1961, map) showed a north-south trending anticline in the block of McCloud Limestone north of Marble Creek. For its entire length, the McCloud Limestone is broken by transverse faults into discrete blocks. Numerous high-angle faults occur within some of these blocks.

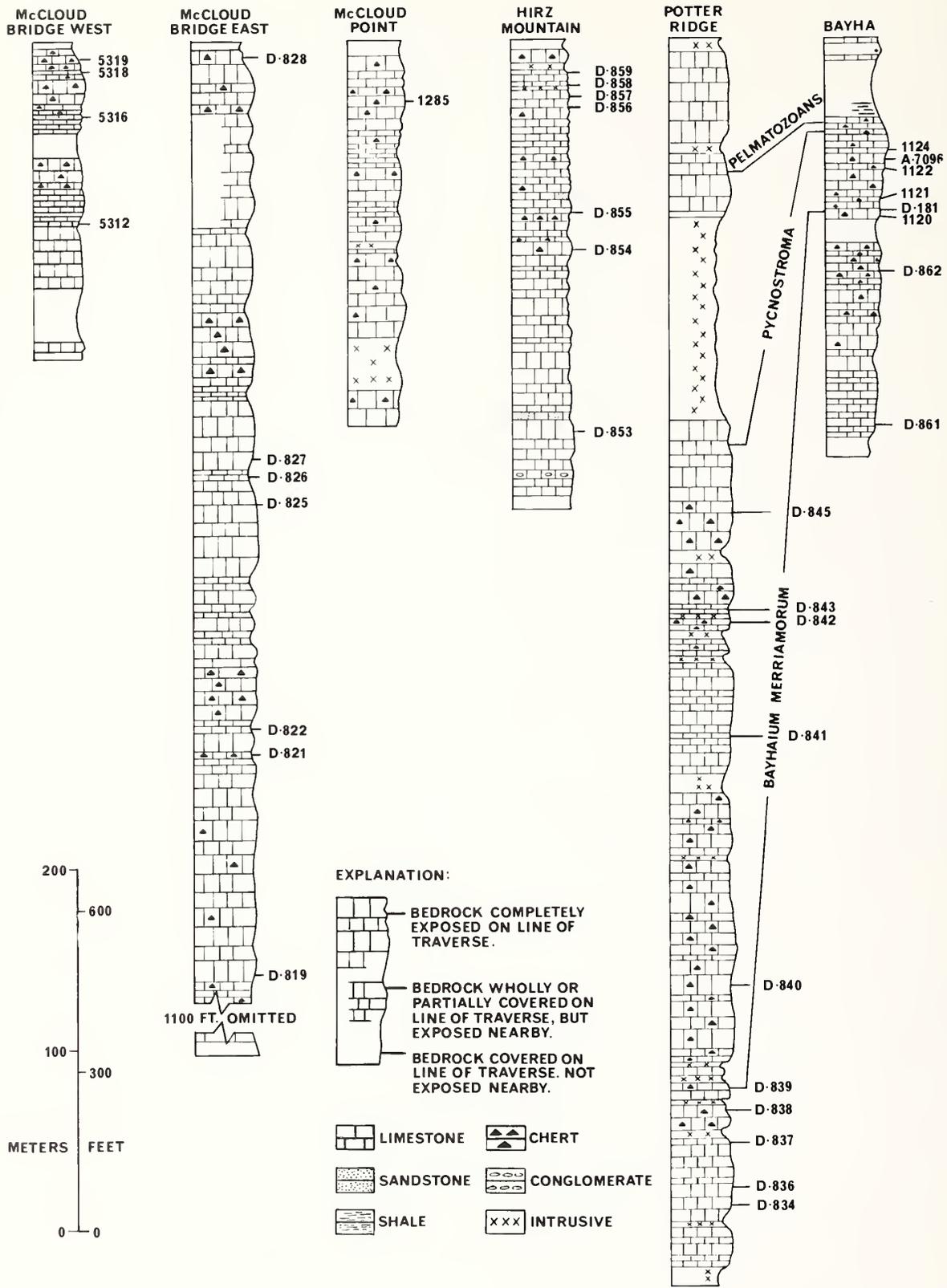
There has been disagreement about the nature of the contact of the McCloud Limestone with the underlying and overlying formations at some localities. Although the scope of this report is primarily the coral paleontology of the formation, the following observations and conjectures may improve understanding of the structural and stratigraphic relationships.

1. On the eastern bank of the McCloud River directly north of the McCloud River bridge, the contact between the McCloud Limestone and the underlying Baird Formation consists of purple tuffaceous sediments, including conglomerate, and interbedded limestone, and seems to be gradational and sedimentary. The gradational rocks here were identified (Coogan, 1960:250; Skinner and Wilde, 1965:11) as the Baird Formation but are higher (Pennsylvanian or Permian) than at the Baird type locality (Mississippian).

2. A high-angle fault separates the McCloud Limestone and the Nosoni Formation along the east side of the ridge crest due east of the McCloud River bridge on Bollibokka Mountain and continues south for at least a mile. Diller (1906, map 3, top structure section) apparently recognized this fault, but some later workers considered the contact to be conformable.

3. About a mile north of the McCloud River bridge on the east bank of the river opposite Wittawaket Creek, Coogan (1960:249) described a depositional contact between the McCloud Limestone and the overlying Nosoni Formation. This is in a different fault block than the McCloud Bridge section of the present study. I inspected Coogan's contact and recognized that the lithology of the apparent top of the McCloud Limestone there

Figure 1. McCloud Limestone exposures in Shasta and Siskiyou Counties, northern California, showing locations of measured stratigraphic sections: (1) Bayha section, (2) Potter Ridge section, (3) Hirz Mountain section, (4) McCloud Point section, (5) McCloud Bridge East section, (6) McCloud Bridge West section.



4 Figure 2. Columnar sections of the McCloud Limestone showing locations of coral collections.

differs from that at the top of the McCloud Bridge section, but I feel that the contact is worth further investigation.

4. At Hirz Mountain, an apparently gradational contact between the McCloud Limestone and the underlying Baird Formation is exposed along the road a few meters above the beginning of the steep upgrade that leads abruptly from the nearby horizontal access road to the summit of the mountain. The gradational contact has limestone beds that contain fusulinids. This contact also was recognized by Watkins (1973:1755), who erected the Hirz Mountain Limestone Member of the Baird Formation for nearby limestone lenses below the Baird-McCloud contact and considered it to be equivalent to fusulinid zone A, now known to be Wolfcampian. If this determination is correct, then the Pennsylvanian-Permian boundary here lies in the upper Baird Formation. It also implies that the fault block along the road should be in fusulinid zone A and therefore must be in a different fault block from the one measured at Hirz Mountain by Skinner and Wilde (1965), who assigned their section at Hirz Mountain wholly to fusulinid zone D. My Hirz Mountain section is not in the same fault block as the road and has zone D fusulinids.

5. Both the upper and lower contacts of the McCloud Limestone on the ridge between Marble and Potter Creeks are with an intrusion of mafic quartz diorite that probably rose along high-angle faults as emphasized by Albers and Robertson (1961:41).

6. In the Bayha section of the present study, both the upper and lower contacts of the McCloud Limestone are covered. A fine-grained shale was dug out here within 2 feet (0.6 meters) of the upper contact. No evidence of a conglomerate was seen. The lower contact, though covered by talus and deep soil, has small springs in places, suggesting the presence of an underlying fault.

7. A pebble conglomerate is present stratigraphically below definite Nosoni Formation rocks on the south side of the summit of the first knoll due south of the Gray Rocks. This hill is greatly faulted, and whether the conglomerate lies within the Nosoni Formation or at the base of the formation is not easily demonstrated because rocks below the conglomerate are not exposed. Fusulinids within the clasts of this conglomerate are referable to species in the McCloud Limestone.

8. Albers and Robertson (1961:57) recognized part of an extensive fault separating the McCloud Limestone and the Nosoni Formation between the Gray Rocks and the Curl Creek areas, named it the McCloud Fault, and described it as dipping west at a moderately steep angle, with left lateral and reverse movement, amount of displacement unknown. The full extent of this fault should be mapped to determine if it had a role in causing the present odd distribution of only older rocks in the southern part of the McCloud Limestone and only younger ones in the northern part.

STRATIGRAPHY, AGE, AND CORRELATION

Relationships of Sections in the McCloud Limestone

By 1935, the discrete fault blocks of the southernmost 9 or so miles (about 14.5 km) of the McCloud Limestone were known to correlate biostratigraphically. It was believed that the same correlation eventually would be obtained everywhere in the formation when its approximately 30-mile (about 48-km) length had

been investigated. This expectation was shown to have been simplistic in 1965 when Skinner and Wilde published their monograph on the fusulinid faunas and biostratigraphy of the formation for its entire outcrop area. They stated (1965:12) that "the maximum thickness observed in any one place . . . is about 2,400 feet, but if the maximum observed thickness of the various [fusulinid] faunal zones were present in a single section the aggregate would be in excess of 7,000 feet." Correlation of the fault blocks proved to be complex. Of their 23 sections measured across the formation, 7 contain only a single zone, 12 have two zones, 3 have three zones, and 1 has four zones. No section has more than four of the eight zones.

The validity of this zonation has been substantiated by its recognition elsewhere in western North America.

Permian corals of western North America are not yet known thoroughly enough to be used more than locally with any assurance as index fossils. In general, however, the results obtained with the corals in the present study support the fusulinid zonation of Skinner and Wilde (1965) in the limited sense that the Potter Ridge and Bayha sections can be correlated using corals, as they can be with fusulinids, whereas the four more northerly sections, which could not be correlated by corals, were shown by Skinner and Wilde (1965) to be at various lower stratigraphic positions in the formation.

Six sections were measured in the McCloud Limestone with Jacob's staff or tape and Brunton pocket transit (Fig. 2). The tables of Mandlebaum and Sanford (1952) were used to compute the thickness of the taped sections. Ranges of coral genera in the formation were tabularized (Fig. 3), and occurrences of coral species were organized into a checklist (Fig. 4). Comments about the sections that relate to their stratigraphy, age, and correlation follow.

Bayha Section. The lower beds of my Bayha section contain very abundant specimens of the Wolfcampian index fusulinid *Pseudoschwagerina*. Four species of corals that occur in the Bayha section also were found in the Potter Ridge section. Seven species of corals found in the Bayha section were not recognized in the Potter Ridge section. Three species of corals described by Meek (1864) were not found by me in the Bayha section or elsewhere, although they reportedly were collected from that area. The large archaogastropod *Omphalotrochus whitneyi* (Meek, 1864) occurs in the Bayha section, and the types were collected from there or nearby. It has a wide stratigraphic range in the McCloud Limestone and is the type species for the genus, now recognized as an index fossil for the Upper Paleozoic in North America, South America, Europe, and Asia. Near the top of the Bayha section are beds with abundant specimens of a biscuit-shaped blue-green alga. These are overlain with beds of particularly abundant and large pelmatozoan columnals that are not present elsewhere in the section. This sequence of algae and columnals also occurs near the top of the Potter Ridge section. The occurrences of coral species common to both sections and the sequential regularity of most of them and other fossils in each section confirm the correlation of the two sections with fusulinids by Skinner and Wilde (1965).

Potter Ridge Section. This section has been correlated with the Bayha section by Skinner and Wilde (1965) with fusulinids. I have described 15 species of corals from there, 4 of which also

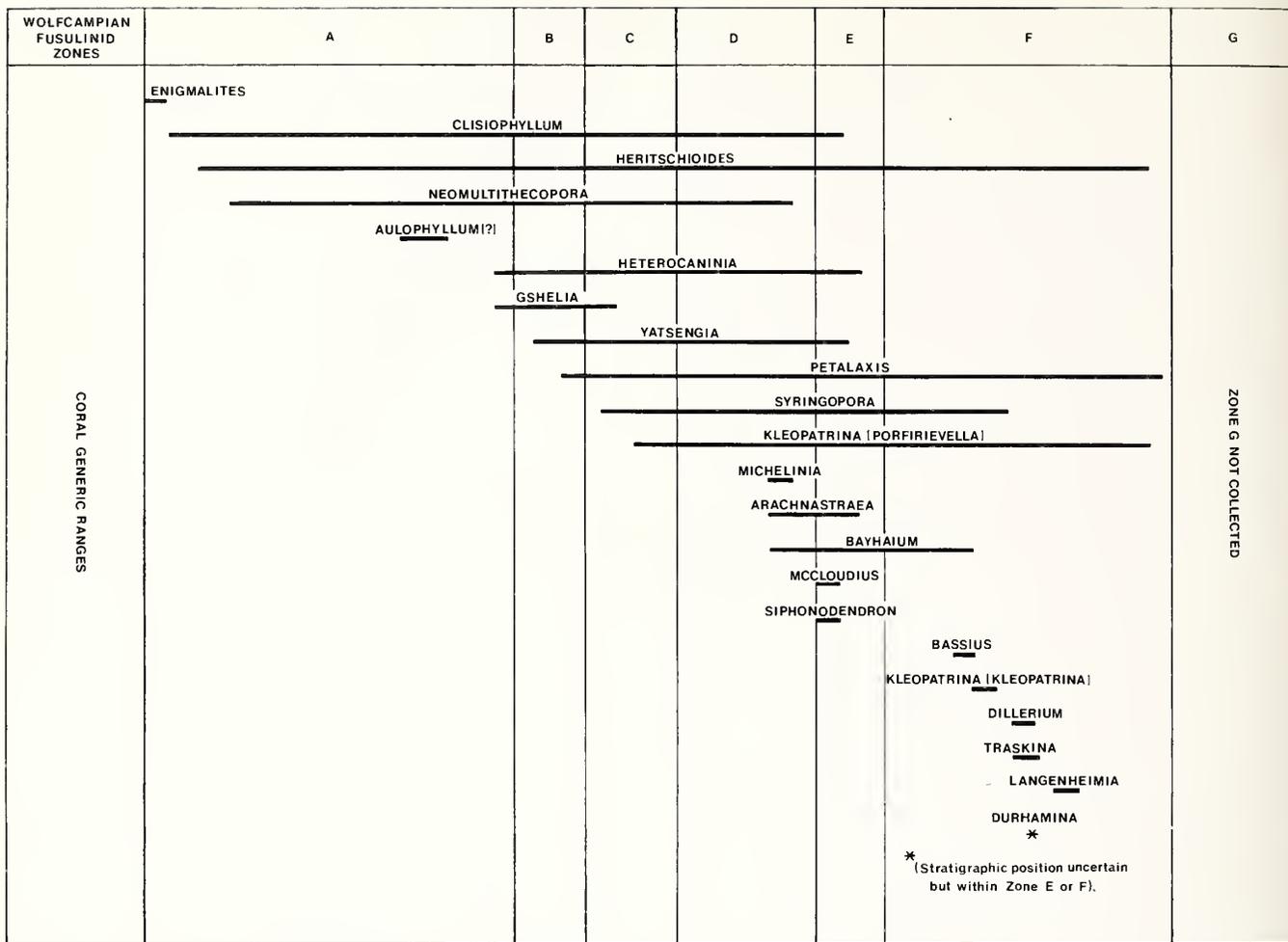


Figure 3. Stratigraphic ranges of coral genera in the McCloud Limestone Wolfcampian Series fusulinid zones of Skinner and Wilde (1965).

were found in the Bayha section and 11 of which were not. Other reasons for correlating the Potter Ridge and Bayha sections are discussed above under the latter section. The differences of the thicknesses of the two sections are likely due to faulting.

Hirz Mountain Section. Skinner and Wilde (1965) placed the Hirz Mountain section in part of a fusulinid zone that lies below the Bayha and the Potter Ridge sections. None of the 11 coral species described from the Hirz Mountain section occur in either the Bayha or Potter Ridge sections, and only 1 occurs in two of my sections measured north of Hirz Mountain. The archaeogastropod *Omphalotrochus* Meek, 1864, occurs at Hirz Mountain.

McCloud Point Section. A single species of coral is described from this section. It was not found in any of the other sections. The fusulinid *Pseudoschwagerina* is common in some beds of the McCloud Point section, but it is a different species from the one in the Bayha section. The archaeogastropod *Omphalotrochus* occurs in the McCloud Point section. Few other fossils were seen in this section, which is rather metamorphosed. Skinner and Wilde (1965) referred the section collected by me (east of the McCloud River) to parts of two fusulinid zones that do not correlate with my three southern sections. The lower part of the section measured by me correlates with the uppermost part of the section east of the McCloud Bridge according to Skinner and Wilde (1965), but the coral was found in the part of the section that is stratigraphically above my two northern sections.

Section East of McCloud Bridge. This section has parts of the lowest three fusulinid zones of Skinner and Wilde (1965). Nine species of corals are described from it and along strike in the great cliff in which it was measured. One coral species also occurs in the Hirz Mountain section and the section west of McCloud Bridge. The other eight species were found only in this section. The archaeogastropod *Omphalotrochus* is widespread in this section, and the type locality of the rostroconch mollusk *Conocardium langenheimi* is here. This fault block is highly fossiliferous and contains other kinds of invertebrates that are not well preserved in some of the other sections.

Section West of McCloud Bridge. Skinner and Wilde (1965) assigned this section to their lowest fusulinid zone and correlated it with the lower part of the section east of the McCloud Bridge. Of the six species of corals described from the section west of the McCloud Bridge, one was found in the section east of the McCloud Bridge and in the Hirz Mountain section. None of the other five species was found in the other sections. The archaeogastropod *Omphalotrochus* and the rostroconch mollusk *Conocardium langenheimi* also were found in the section west of the McCloud Bridge.

Occurrence and Comparison of Related Permian Coral Faunas

The corals described by Merriam (1942) from the Coyote Butte Limestone of Oregon are in part Permian and include species of *Heritschioides* that are not conspecific with species in the part of the McCloud Limestone of this study. According to Skinner and

Wilde (1966), seven species of fusulinids from the Coyote Butte Limestone are Late Wolfcampian in age. Four of these species occur in the highest Wolfcampian zone of the McCloud Limestone, which crops out only north of the area studied by me, and the other three species were described as new. Skinner and Wilde (1966:11) also reported Cooper as having told them that none of his (Cooper, 1957) "latest Leonardian and probably . . . early Guadalupian age" brachiopods described from the Coyote Butte Limestone had fusulinids associated with them. If the Permian coral fauna of the Coyote Butte Limestone also occurs in the McCloud Limestone, it will be found higher in the section than the rocks reported on in the present study.

The type species of *Heritschioides* is from the Blind Creek Limestone of British Columbia (Smith, 1935), which may be Permian or older (Wilson, 1980:91). Although the type species does not occur in the McCloud Limestone, other species of the genus are common there, and the genus also was listed by Watkins (1973:1761) as occurring in the underlying Hirz Mountain Limestone Member of the Baird Formation.

Hoare (1964) described a small fauna of corals from Wolfcampian rocks near the Sunflower Reservoir of Elko County, Nevada, which had no genera in common with the McCloud Limestone corals found by me. Later, Hoare (1966) described a new species of *Bayhaium* from the same formation. This genus was erected for a species in the McCloud Limestone and was found by me to range through parts of three fusulinid zones there (D, E, and F). Wilde (1971:364) suggested that the fusulinids from the Sunflower area correlated with McCloud Limestone fusulinid zone A, at least in part.

Permian corals have been described from White Pine County, Nevada, by Easton (1960), McCutcheon and Wilson (1961), Wilson and Langenheim (1962), and Stevens (1967). They range from probable Wolfcampian to Leonardian. *Syringopora mcutcheonae* Wilson and Langenheim, 1962, occurs rather low in the section in White Pine County and is associated with a large fauna of colonial rugose corals. I found one corallum of *S. mcutcheonae* in the Potter Ridge section of the McCloud Limestone but no other species in the formation conspecific with any from White Pine County. The corals *Kleopatrina* and *Petalaxis*, however, are associated with *Syringopora mcutcheonae* in White Pine County, and their stratigraphic ranges are from below to above the occurrence of this species in the McCloud Limestone. However, the former two genera are represented by different species in the two areas. *Thysanophyllum* Nicholson and Thompson, 1876, is common in the White Pine County fauna but notably missing from the parts of the McCloud Limestone covered by the present paper. Perhaps the White Pine County faunas will be found higher in the more northern parts of the formation. *Durhamina* and *Heritschioides* are present in both White Pine County and in the McCloud Limestone. These genera are present in Leonardian rocks in White Pine County but not in probable Wolfcampian ones. It is curious that the single corallum of *Durhamina* from the McCloud Limestone should have been collected there by the California Geological Survey in 1862 and additional specimens not discovered in the field by me. There is a

suggestion of a mixed collection here. The genus in White Pine County occurs in definite Leonardian rocks where the coralla are present in enormous numbers.

Kleopatrina ftataetea (McCutcheon and Wilson, 1961) was described chiefly from specimens in White Pine County, Nevada, with some paratypes from the Wolfcampian of Clark County, Nevada. Minato and Kato (1965b:69) later erected a new species, *K. wilsoni*, for the figured paratype from Clark County. The genus, but neither of these species, occurs in the McCloud Limestone. McCutcheon (1961:1016) reported *Syringopora multatenuata* McChesney from the Wolfcampian in Clark County, Nevada. This species occurs in the McCloud Bridge section of the McCloud Limestone but has wide geographic and stratigraphic ranges in Pennsylvanian and Lower Permian rocks of the United States and perhaps even the Permian of Spitzbergen (Heritsch, 1939).

The report of *Lonsdaleia cordillerensis* Easton, 1960 (type species of *Durhamina*) in the Lower Permian of San Bernardino County, southern California, marks the southernmost reported existence of the Durhaminid Coral Province.

Thysanophyllum princeps Easton, 1960, was based, in part, on specimens from Millard County, Utah. This is the easternmost geographic record for the Durhaminid Coral Province in the Cordilleran geosyncline, well up on the shelf of the miogeosyncline. Stevens (1975:38) suggested that *Thysanophyllum* shows promise as an important index fossil for Permian rocks of the Cordilleran geosyncline.

Stevens (1977, fig. 6) synthesized studies of Permian corals and fusulinids in the western United States with tectonic research of the area and created a Permian paleogeographic reconstruction showing several north-trending marine depositional provinces beginning in the Idaho, Utah, and Arizona areas with an eastern outer shelf and progressing westward to California through an eastern shelf margin, an axial portion interior sea, an uplifted marginal belt, a back-arc basin, and a volcanic arc perhaps bordered to the west by a trench. On this model, the area of deposition of the McCloud Limestone is within the volcanic arc. Stevens (1977, fig. 7) compared this reconstruction to the present-day plate tectonic and depositional configurations in south-east Asia.

Permian coral faunas east and south of the Cordilleran geosynclinal rocks in North America belong to the Cyathaxonid Coral Province, which has a few widely ranging genera in common with the Durhaminid Coral Province (Rowett, 1975).

Rowett (1969) described species of *Durhamina*, *Heritschioides*, and *Syringopora* from the Wolfcampian or Leonardian of the east-central Alaska Range, Alaska. These genera also occur in the McCloud Limestone, although not the same species. Rowett (1969) also reported other genera from the same area that have not been reported from the McCloud Limestone. *Durhamina* and *Heritschioides* in Alaska are of particular importance in indicating the presence of the Durhaminid Coral Province there, particularly its North American part, which may be characterized by *Heritschioides*.

The generic (and some specific) compositions of Permian coral

faunas in western North America in the eugeosynclinal and miogeosynclinal parts of the Cordilleran geosyncline are so similar that they suggest close geographic occurrences while living. Therefore, I do not believe that the eugeosynclinal coral faunas necessarily lived in a remote area not part of the North American continent that later was moved great distances by continental drift as suggested by Yancey (1975:763; 1976:241). Watkins (1979:36) considered the faunas (chiefly brachiopod and bivalve mollusk) of the Bragdon and Baird Formations, which underlie the McCloud Limestone, to be "... part of an Asiatic province." However, he reported (Watkins, 1973:1761) *Heritschioides* from the Baird Formation. This coral is restricted to western North America, as presently known, and reports of it elsewhere, including Asia, are doubtful or erroneous (Wilson, 1980). The Tethyan Coral Province of Asia is not present in North America.

From Alaska, the outcrops containing corals of the Durhaminid Coral Province turn eastward across Canadian North America to Spitzbergen and Novaya Zemlya and then south through the Ural Mountains of Russia.

PALEOECOLOGY

The fauna of the McCloud Limestone collected in the course of this study consists of algae, fusulinids, sponges, corals, bryozoans, brachiopods, several kinds of mollusks (including ammonoids, and nautiloids), echinoids, crinoids, and pelmatozoan columnals. Of these taxa, only the algae, sponges, bryozoans, and mollusks are known to occur in both fresh and marine waters. The fusulinids and ammonoids are extinct, but they have not been reported from rocks suspected of having been laid down in freshwater or brackish water. Living corals, brachiopods, nautiloids, and echinoderms are known only from marine environments and are stenohaline, except for a few brachiopods. I found no animals or plants that indicate that any of the McCloud Limestone was laid down under terrestrial, freshwater, brackish water, or hypersaline conditions. The entire fauna indicates a sea of normal salinity.

Fusulinids are stratigraphically widespread throughout the formation. Tasch (1957:396) thought that they probably lived in open-sea waters of 5- to 50-foot depths (1.5 to 15 meters). Thompson (1964:387) cited an offshore, open-water environment for them. The biscuit-shaped blue-green algae that are so abundant in some upper beds of both the Bayha and Potter Ridge sections are very much like certain Recent species that have been reported from intertidal and somewhat subtidal wave-affected environments (Ginsburg, 1960). In a study of paleoecology of Mississippian corals, Sando (1980b) used associations of corals and benthonic algae to determine maximum possible depth of occurrence of shallow-water corals. He arrived at a possible depth of 100 meters, which is the depth of the euphotic zone in clear, tropical seawater, but since the blue-green algae are confined to the upper 50 meters of the zone, he concluded that the probable depth for the shallow-water corals may have been mostly less than 50 meters. His conclusions seem applicable to the corals of the McCloud Limestone.

Wells (1957:773) considered Paleozoic colonial rugose corals

to be indicative of well-oxygenated, gently circulating marine water with annual temperature minima of 16° to 21 °C. Most paleogeographic maps show the Early Permian paleo-equator crossing central California or northern Mexico, indicating that the McCloud Limestone was laid down in tropical seas, a theory strengthened by the relatively large number of coral taxa present in the formation.

I conclude that the McCloud Limestone was deposited in clear, shallow, warm marine water with full access to the open sea.

SYSTEMATIC MATERIALS AND METHODS

Morphological terminology has been taken from Moore, Hill, and Wells (1956) with a few additional terms added that are in widespread use. In my opinion, families in the orders Rugosa and Tabulata are so polyphyletic that they will not be useful until they have undergone stringent revision. Therefore, I have grouped the genera and species simply by order and, for the Rugosa, by the forms of the coralla (solitary, fasciculate, cerioid, cerioid-astreoid) and alphabetically within each form. The Tabulata are presented alphabetically.

Locality numbers with a letter prefix refer to the University of California Museum of Paleontology (UCMP) locality register. Locality numbers without a letter prefix refer to the Los Angeles County Museum of Natural History, Invertebrate Paleontology Section (LACMIP) locality register. Pertinent UCMP and LACMIP locality descriptions are placed in the section titled Localities. Existing specimens from the collection used by Meek (1864) now in the Museum of Comparative Zoology, Harvard University (MCZ) are listed as MCZ Meek Collection and, if the specimen bore a number, that number. Numbers preceded by USNM refer to United States National Museum, Washington, D.C., specimens. Types and other specimens are deposited in LACMIP, MCZ, and UCMP. References to fusulinid zones are those of Skinner and Wilde (1965), with age determinations amended by Wilde (1971:364).

SYSTEMATICS

Order Rugosa Milne Edwards and Haime, 1850

Solitary Rugosa

Genus *Aulophyllum* Milne Edwards and Haime, 1850

Aulophyllum (?) sp. Figures 9a–b

External Description. Corallites solitary, large (diameters to 6 cm), cylindrical (?); calyx walls not preserved, but floor beyond ends of septa filled by axial boss 28 mm long, 13 mm wide, 14 mm high, conical, with 34 ridges (septal lamellae forming axial vortex spiraling counterclockwise to apex); corallite length, external walls not observed.

Transverse Section Description. Corallites circular to subcircular, maximum observed diameter 6 cm; major septa number 54 to 57 at 6 cm, 51 at 5.3 cm, all lanceolate and dilate but more so in

cardinal quadrants, 20 to 23 mm long, most touching axial structure and continuous with septal lamellae; cardinal septum shortened, about 16 mm long, 1.5 mm wide where most dilate; cardinal fossula open; minor septa 6 to 11 mm long, not crossing dissepimentarium; dissepimentarium regular, 12 to 13 mm wide, except 7.5 mm wide beneath cardinal septum; dissepiments concentric, angulo-concentric, herringbone, pseudoherringbone, with about 12 to 15 ranks, the axial one thickened into an inner wall; axial structure aulophylloid, 13 mm wide, 20 mm long, filling entire space beyond ends of septa, composed of irregularly twisted septal lamellae, many connected to ends of septa, interspaced with numerous axial tabellae, forming complex mass, but axial vortex not as apparent as in external view of axial boss; corallite wall about 0.1 mm wide.

Longitudinal Section Description. Tabellae of 2 zones, axial and periaxial; axial tabellae of 5 to 10 ranks, steeply dipping from center down (outermost ones may recurve), generally very elongate, a few cystose; periaxial tabellae of 1 to 3 ranks, generally rather straight (few are cystose), sloping down and out gently from axial tabellae; dissepimentarium of 10 to 18 ranks of small, steeply dipping, cystose dissepiments.

Documentation. LACMIP hypotypes 6342–6343. Two thin sections and 11 polished sections from two coralla from LACMIP localities 5318 (hypotype 6342) and 5319 (hypotype 6343) were studied.

Discussion. The two specimens upon which this description is based are fragmentary. The ephebic stages can be reconstructed, but the apices of the coralla are missing so the neanic stages are unknown. *Aulophyllum* and *Auloclisia* Lewis, 1927, both are aulophylloid in the ephebic stages. The former is aulophylloid throughout, but the latter goes through early dibunophylloid and clisiophylloid stages. Therefore, I have questioned the generic assignment. Neither specimen is adequate for erection of a new species, and additional material may be available at the locality, which should be easy to relocate since it is at the summit of a prominent hill.

Aulophyllum apparently has not been reported from the Upper Paleozoic of North America. *Auloclisia deltense* Rowett, 1969, from the Permian of Alaska, is the only species of that genus recognized in North America to date. It is much smaller and has many fewer septa than *Aulophyllum* (?) sp.

Genus *Clisiophyllum* Dana, 1846

Clisiophyllum gabbi Meek, 1864 Figures 5:l, 1a; 6a–f; 7a–h; 8a–d

Clisiophyllum gabbi Meek, 1864, p. 8, pl. 1, figs. 1, 1a, 1b.

External Description. Corallites solitary, trochoid, complete specimen measuring 8.5 cm in length (outside curve) with 3.2-centimeter-diameter calyx, maximum observed corallite diameter 5.7 cm; wall rugose externally with faint growth lines; calyx about 2 cm deep with steeply sloping inner walls and very prominent central axial boss about 1 cm high.

Transverse Section Description, Lectotype. Corallite diameter 23 mm; septa of 2 orders; major septa 38, somewhat lanceolate in cardinal quadrants (not equally so in each cardinal quadrant), thinner in counter quadrants, 6 to 7 mm long, except cardinal

septum 4.5 mm long, about half in contact with axial structure; minor septa very short (at this stage), about 1 mm long, crossing narrow dissepimentarium but not entering tabularium; axial structure clisiophylloid, large, filling most of tabularium, with slightly thickened sinuous medial plate and about 11 somewhat sinuous septal lamellae joined together by axial and periaxial tabellae; dissepimentarium narrow, of 1 to 2 ranks of herringbone, pseudoherringbone, or concentric dissepiments; wall thin, about 0.3 mm wide.

Longitudinal Section Description, Lectotype. Corallite diameter 20 mm; tabellae of 2 zones, axial and periaxial; axial tabellae of about 6 ranks, steeply dipping, cystose to elongate, sloping inwards and upwards to medial plate; periaxial tabellae of 2 to 5 ranks, sigmoid to cystose, gently sloping inwards and upwards to axial tabellae; dissepimentarium of 1 to 2 ranks of small, steeply dipping, cystose dissepiments.

Documentation. A lectotype (Figs. 6b–c) is here designated from the MCZ Meek collection block no. 19, which bears five coralla. It was not figured by Meek (1864). His three figured specimens of this species are not very suitable for preparation of thin sections, and therefore the International Code of Zoological Nomenclature (ICZN) Recommendation 74B (a lectotype should be a figured syntype) was not followed. Two thin sections were made of the lectotype. MCZ Meek collection block no. 23 (about six coralla, including two polished longitudinal sections apparently prepared by Meek), MCZ Meek collection block no. 24 (a laterally crushed fragmentary corallum), two MCZ Meek collection unnumbered coralla (both fragmentary and poorly preserved, including the large specimen figured by Meek [1864, p. 1, fig. 1—apical part now missing]), and the remaining four specimens on MCZ Meek collection block no. 19 here are designated paralectotypes. All the MCZ Meek collection blocks with specimens of this species have labels glued to them reading “*Clisiophyllum Gabbi*, Meek.”

In addition to the above specimens, 12 coralla from UCMP locality D-861 were studied from nine thin sections and numerous polished sections, and more than 100 coralla from LACMIP locality 1119 (UCMP loc. D-861) were examined. Coralla from which thin sections were prepared are designated UCMP hypotypes 37171–37175 and LACMIP hypotype 6344.

Discussion. This species is common in the lower 50 feet of the McCloud Limestone at the Bayha section where it occurs in a coquina of the zone E fusulinid *Pseudoschwagerina robusta*.

The above description is based on thin sections of the lectotype. Measurements and counts of major septa from thin sections showing the ontogeny of one corallum from UCMP loc. D-861 are: 6-mm corallite diameter, 21 septa; 10-mm corallite diameter, 27 septa; 18-mm corallite diameter, 33 septa; 23-mm corallite diameter, 36 septa. Other coralla from the same locality show that the number of septa increases to 38 at 24-mm corallum diameter and 49 at 33-mm corallum diameter. In the latter large specimen, the dissepimentarium has about nine ranks of dissepiments, but the minor septa penetrate only the outer two or three ranks. The largest specimen examined is 57 mm in diameter and has 57 major septa.

There is considerable variation in this species in the dilation of septa in the cardinal quadrants and in the sinuosity of the axial plate. The lectotype has a readily discernible axial plate, whereas

many other specimens have such a sinuous one that it cannot be distinguished in transverse section, although it is easily seen in longitudinal sections cut at right angles to the cardinal-counter plane. Septa of the lectotype are somewhat thinner than those of some other specimens.

The differences of *C. gabbi* and *C. oweni* n. sp. from lower in the McCloud Limestone are noted in the discussion for the latter species.

Clisiophyllum sp. A of Rowett (1969:57, pl. 7, figs. 1, 2), from the Lower Permian McCallum Creek sequence of the east-central Alaska Range, Alaska, is known from only two corallites, but these are very similar to *C. gabbi* and may be conspecific with it.

Clisiophyllum oweni n. sp.

Figures 9c–e

Diagnosis. A species of *Clisiophyllum* characterized by the combination of small corallites, complex symmetrical axial structures from which major septa are withdrawn, and minor septa of variable length but generally confined to the tabularium. It has smaller corallites, smaller and more symmetrical axial structures, and less numerous septa than *C. gabbi*. It has fewer and shorter septa and more symmetrical axial structures than *C. sp. A* of Rowett.

External Description. Corallites solitary, ceratoid or cylindrical; maximum length observed 6 cm (outside), diameter at calyx 1.7 cm; maximum diameter observed 2 cm; wall rugose, highly constricted in places; calyx about 1.5 cm deep, with steeply sloping or overhanging walls and central axial boss of uncertain height.

Transverse Section Description. Corallite diameters 15 to 20 mm; septa of 2 orders; major septa 32 at 20-mm diameter (holotype), slightly dilate in cardinal quadrants, thinner in counter quadrants, 3.5 to 5.2 mm long, except cardinal septum about 4 mm long, septa withdrawn from axial structure; minor septa short, some crossing dissepimentarium, very few entering tabularium as spines; axial structure clisiophylloid, 3 by 4 mm to 4.5 by 5.5 mm, with slightly thickened medial plate and 12 to 22 septal lamellae symmetrically joined by axial and periaxial tabellae; dissepimentarium narrow, of 1 to 4 ranks of herringbone, pseudoherringbone, concentric, or angulo-concentric dissepiments; wall thin, about 0.1 mm wide.

Longitudinal Section Description. Tabellae of 2 zones, axial and periaxial; axial tabellae of 3 to 7 ranks, steeply dipping, elongate to cystose, sloping inwards and upwards to medial plate; periaxial tabellae of 3 to 5 ranks, straight to cystose, gently sloping inwards and upwards to axial tabellae; dissepimentarium of 1 to 4 ranks of steeply dipping, mixed size dissepiments.

Documentation. LACMIP holotype 6345, LACMIP paratype 6346. Three thin sections and five polished sections from two coralla from LACMIP locality 5312 were studied.

Discussion. *Clisiophyllum gabbi*, from much higher in the McCloud Limestone, has larger corallites (to 35 mm), somewhat more septa (33 to 38 septa at 18 to 23 mm, 48 at 35 mm) that are more dilate in the cardinal quadrants, and an axial structure that is larger and less symmetrical. *C. sp. A* of Rowett, 1969, from the Lower Permian McCallum Creek sequence, Alaska Range, Alaska, is comparable in size to *C. oweni*, but the former has

Figure 5. McCloud Limestone rugose corals from Meek (1864).

Parts 1 and 1a. *Clisiophyllum gabbi* Meek, 1864. **Part 1**, MCZ paralectotype, MCZ Meek collection unnumbered specimen. **Part 1a**, MCZ paralectotype on MCZ Meek collection block no. 23.

Parts 1b, 2, and 2a. Identification uncertain. **Part 1b**, no specimen now in the MCZ Meek collection exactly matches this figure. **Parts 2 and 2a**, this specimen is not now in the MCZ Meek collection.

Part 2b. *Heritschioides (?) californiense* (Meek, 1864), MCZ lectotype, on MCZ Meek collection block no. 13.

Part 2c. Identification uncertain; this specimen is not now in the MCZ Meek collection.

Parts 3 and 3a. *Kleopatrina (Porfirivella) whitneyi* n. sp., holotype, MCZ Meek collection corallum no. 15.

Parts 4, 4a, and 4b. *Durhamina sublaeve* (Meek, 1864), holotype, MCZ Meek collection corallum no. 17.

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(Carboniferous.)

PLATE 1.



(Mex. 16)

Young



14 Figure 6. *Clisiophyllum gabbi* Meek, 1864. Fusulinids in Parts a–d and f are *Pseudoschwagerina robusta* (Meek, 1864). **Part a**, MCZ paralectotypes, MCZ Meek collection block no. 23, complete calyx figured by Meek (1864, pl. 1, fig. 1a), x1. **Part b**, MCZ lectotype (lower right) and paralectotypes, MCZ Meek collection block no. 19, x0.8. **Part c**, MCZ lectotype (lower left arrow) and paralectotypes, MCZ Meek collection block no. 19, obverse of Part b, x0.8. **Part d**, MCZ paralectotype, MCZ Meek collection unnumbered corallum, figured by Meek (1864, pl. 1, fig. 1), missing apical part presumed lost, x1. **Part e**, MCZ paralectotype, MCZ Meek collection no. 24, x0.5. **Part f**, MCZ paralectotype, MCZ Meek collection block no. 1, x1.

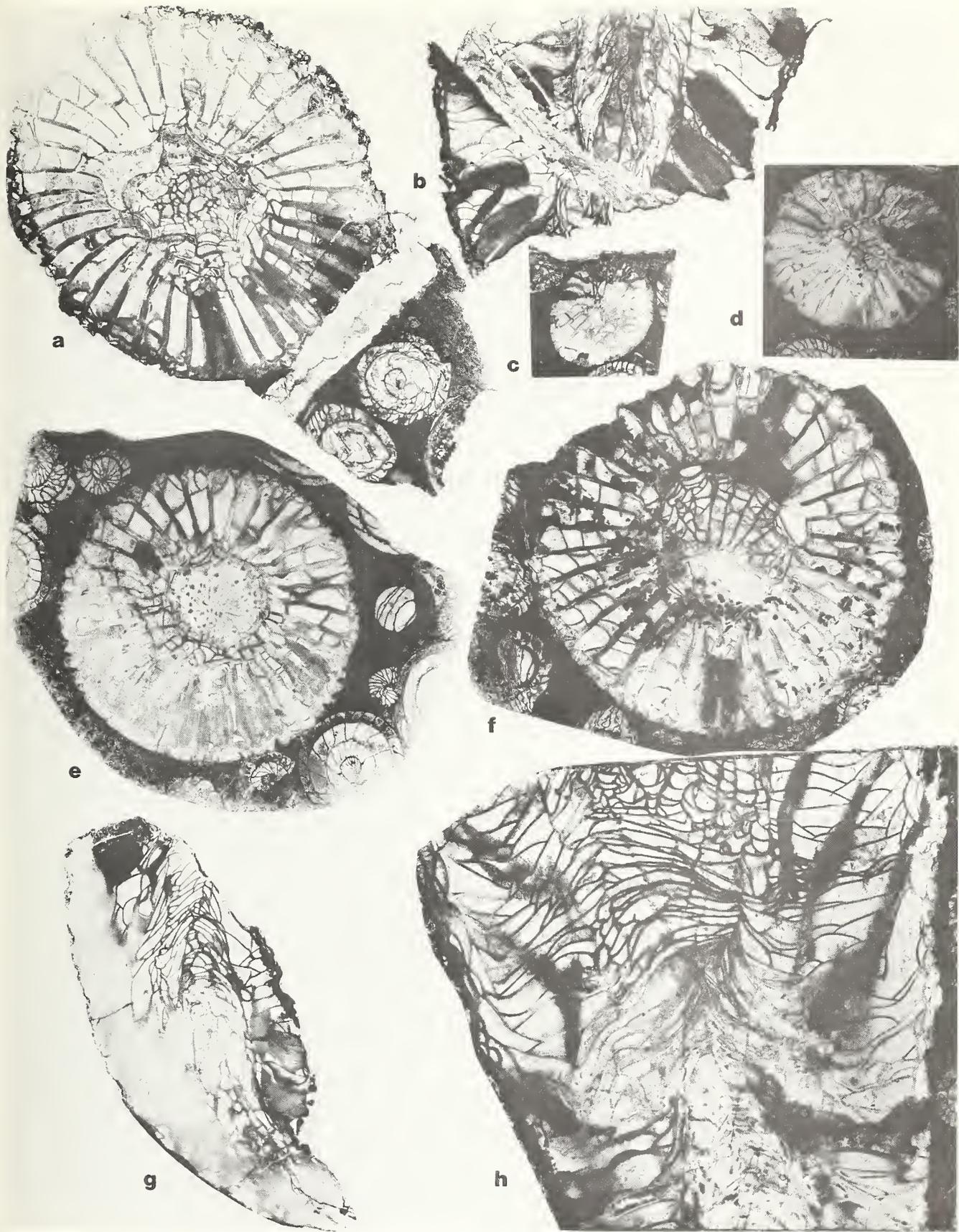


Figure 7. *Clistophyllum gabbi* Meek, 1864. Fusulinids are *Pseudoschwagerina robusta* (Meek, 1864). All parts x3. **Parts a and b**, MCZ lectotype from MCZ Meek collection block no. 19, transverse and longitudinal sections. **Parts c through f**, UCMP hypotype 37171, serial transverse sections through one corallum. **Part g**, UCMP hypotype 37172, longitudinal section. **Part h**, LACMIP hypotype 6344, longitudinal section.



16 **Figure 8.** *Clisiophyllum gabbi* Meek, 1864. Fusulinids are *Pseudoschwagerina robusta* (Meek, 1864). All parts x3., **Parts a and b**, UCMP hypotype 37174, serial transverse sections through one corallum. **Part c**, UCMP hypotype 37173, longitudinal section. **Part d**, UCMP hypotype 37175, longitudinal section.

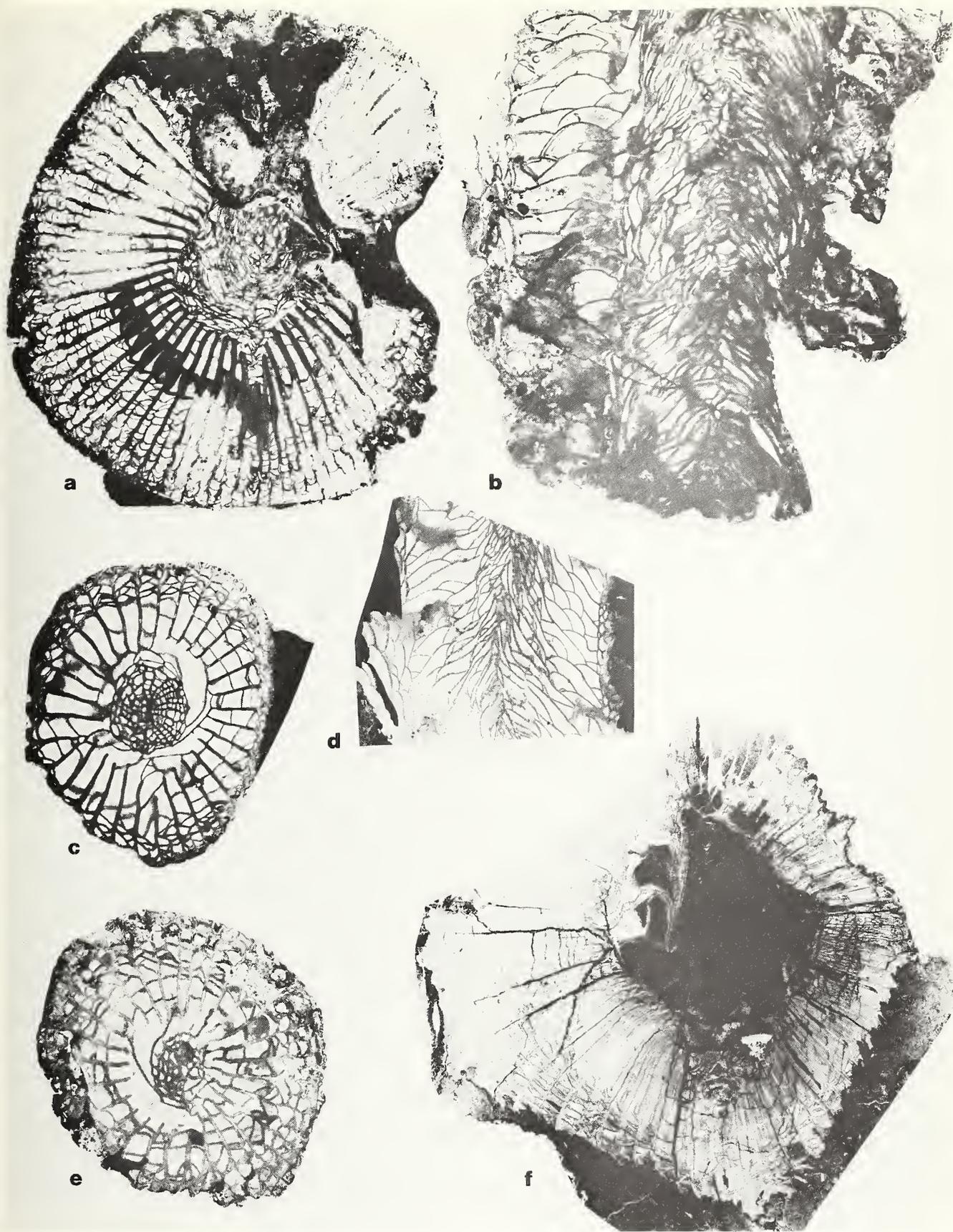


Figure 9. *Aulophyllum* (?) sp., *Clisiophyllum oweni* n. sp., and cyathopsid (?).
 Parts a and b. *Aulophyllum* (?) sp. Part a, LACMIP hypotype 6342, transverse section, x1.5. Part b, LACMIP hypotype 6343, longitudinal section, x3. 17
 Parts c through e. *C. oweni* n. sp., all parts x3. Parts c and d, LACMIP holotype 6345, transverse (c) and longitudinal (d) sections. Part e, LACMIP
 paratype 6346, transverse section.
 Part f. Cyathopsid (?), UCMP hypotype 37176, transverse section, x1.5.



Figure 10. *Gshelia americana* n. sp., LACMIP holotype 6347. Parts a and b, serial transverse sections, $\times 3$. Parts c through e, serial transverse sections, 18×1.5 . Part f, longitudinal section, $\times 1.5$.

more major septa (28 at 8 mm, 39 at 18 to 22 mm), longer minor septa, and a less symmetrical axial structure.

Etymology. The species is named for Mr. Phillip G. Owen.

Cyathopsid (?)

Figure 9f

Description. Corallites large, solitary, exterior unknown; adolescent stages unknown; adult corallite diameters 6 to 7 cm; septa of 2 orders, 76 to 90 each; major septa 14 to 21 mm long, thin in dissepimentarium, somewhat dilate in cardinal quadrants in tabularium, thin in counter quadrants, cardinal septum short, 10 to 16 mm long, and dilate; minor septa short, 3 to 6 mm long, thin, confined to periphery of dissepimentarium; dissepimentarium wide, 6 to 11 mm; dissepiments in 11 to 20 ranks, pseudo-herringbone between minor and major septa, herringbone or complete (many straight, some concentric) between major septa; narrow stereozone on axial row of dissepiments; corallite wall thin, generally not preserved.

Documentation. UCMP hypotypes 37176–37178. Three coralla from UCMP localities D-841 (hypotype 37178) and D-842 (hypotypes 37176–37177) were studied.

Discussion. The preservation of these specimens is poor due to partial crushing, apparent preburial abrasion of most of the external walls and adjacent dissepimentaria, and loss of structures due to stylonite resorption. The corals are not uncommon but difficult to collect. It is important to record the existence of these large solitary corals because they are associated with both cerioid and fasciculate compound rugose corals at these localities.

The description is based upon transverse sections of ephebic stages only. It was not possible to make longitudinal sections of the coralla available. However inadequate the preservation, it seems obvious to me that these specimens are referable to the Cyathopsidae because of their resemblances to *Bothrophyllum* Trautschold, 1879, *Timania* Stuckenberg, 1875, and *Gshelia*. No North American Permian cyathopsid has been described with such a great number (90) of major septa, and therefore comparisons with the few other recorded species are unnecessary.

Genus *Gshelia* Stuckenberg, 1888

Gshelia americana n. sp.

Figures 10a–f; 11a–e; 12a–d

Diagnosis. A species of *Gshelia* characterized by the combination of very large corallites, numerous major septa, and minor septa confined to the dissepimentarium. It has larger corallites and shorter minor septa than *G. rouilleri*. It has shorter minor septa than *G. (?) lonsdalei*. It has longer major septa and shorter minor septa than *G. rouilleri* var. *breviseptata*. It has a more complex axial structure than *G. (?) nikitini*.

External Description. Corallites solitary, cylindrical beyond short apices with angles of 30–35°, straight, irregularly curved, or with abrupt 90° or smaller angle bends, large diameters to 8.1 cm, lengths to 47 cm (incomplete) and more (holotype length 31 cm); epitheca with closely spaced, fine growth lines and widely

spaced annual (?) constrictions; calices deep, sides sloping steeply inwards and downwards, cardinal fossula prominent.

Transverse Section Description, Holotype. Corallite circular to sub-circular, 5.4 cm maximum diameter; septa of 2 orders, 50 to 55 each at maturity, all extending to corallite wall; major septa thin in dissepimentarium, highly dilate in cardinal quadrants in tabularium in adolescent and early adult stages, slightly dilate elsewhere in tabularium, 14 to 19 mm long in adult stage, cardinal septum shortened, 10 to 12 mm long in adult stage; minor septa thin, short, confined to peripheral 1/3 of dissepimentarium in adult stage, not crossing dissepimentarium, not seen at diameters less than 30 mm; major septa at corallite diameters 27, 35, 47, and 50 mm number 48, 51, 55, and 52 (actual decrease), respectively; microstructure of dilate septa shows fibers at right angle to sinus, dark, centerline; cardinal fossula open, with 3 to 5 tabulae arched around axial end in some sections; axial structure present only in adolescent stage, elisiophylloid at 20-mm corallite diameter with slightly dilate medial plate 2.5 mm long and 6 discontinuous septal lamellae united by 5 concentric tabellae (axial structure absent at corallite diameters 30 mm and greater, leaving open tabularium); dissepimentarium wide, width 3 to 9 mm in adult stages, not observed at corallite diameters less than 20 mm; dissepiments in 10 to 17 ranks in adult stage, regular peripherally, herringbone axially; stereozone on axial row of dissepiments in cardinal quadrants; corallite wall very thin, width 0.1 to 0.2 mm, silicified.

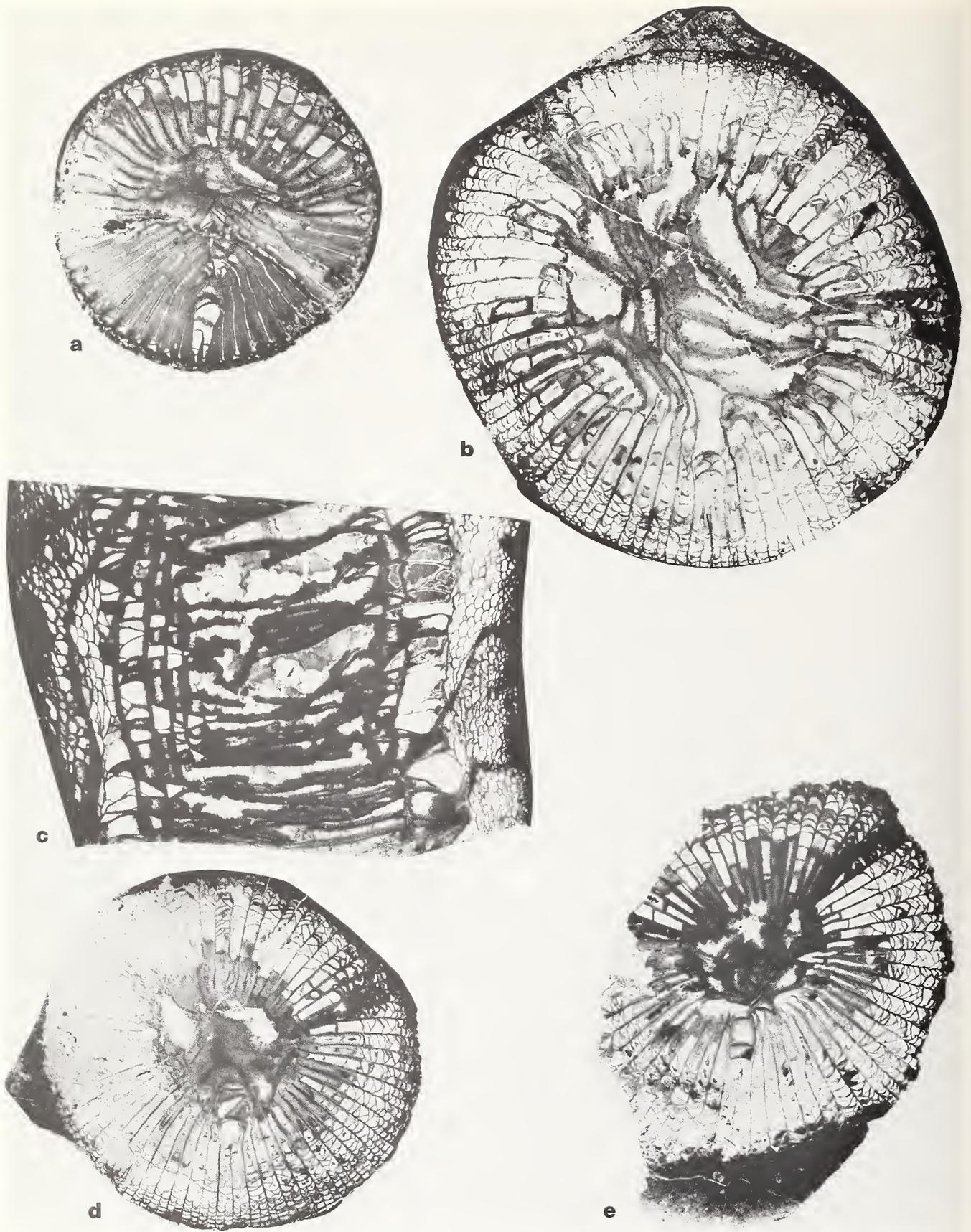
Transverse Section Description, Paratype Variation. Paratype 37183: major septa at corallite diameter 6 mm (smallest diameter sectioned in this species) number 20, all thin, withdrawn from center, without axial structure; major septa at corallite diameter 18 mm number 40, all dilate, with axial structure; major septa at corallite diameter 45 mm number 51, cardinals dilate, counters thin, axial structure absent.

Paratype 37184: major septa at corallite diameter 17 mm number 32, all dilate except 1 counter quadrant on apical side of section, all dilate on calicular side of section.

Paratype 6348: major septa at corallite diameter 37 mm number 49, cardinal quadrant septa dilate, counter quadrant septa thin, cardinal septum short, major septa at corallite diameter 60 mm number 64, cardinal quadrant septa slightly dilate, counter quadrant septa thin, cardinal septum short. This specimen shows middle to late adult stage transition by thinning cardinal quadrant septa.

Paratype 6355 (largest specimen): major septa at corallite diameters 78 mm and 81 mm (sections 95 mm apart) number 60 in each, cardinal septum short, 16 mm long, dilate, cardinal quadrant septa slightly dilate, those neighboring fossula more so, counter quadrant septa thin, major septa length 28 mm total, 9 to 13 mm in tabularium, not meeting; minor septa short, 4 to 6 mm long, not crossing dissepimentarium; dissepimentarium regular, wide, 13 to 19 mm width, dissepiments as in holotype; tabularium 41 mm wide, open in center; wall thin, silicified.

Longitudinal Section Description, Holotype. Dissepimentarium in adult stage (35 mm below calyx, corallite diameter 48 mm) of 10 to 17 ranks of steeply dipping cystose dissepiments, smaller at periphery (presumably where minor septa present), larger axially; tabulae in same section mostly flat with downturned edges,



20 **Figure 11.** *Gshelia americana* n. sp. All parts x1.5. **Parts a through c,** LACMIP paratype 6348, serial transverse sections (a, b) and longitudinal section (c). **Parts d and e,** LACMIP paratype 6349, serial transverse sections.

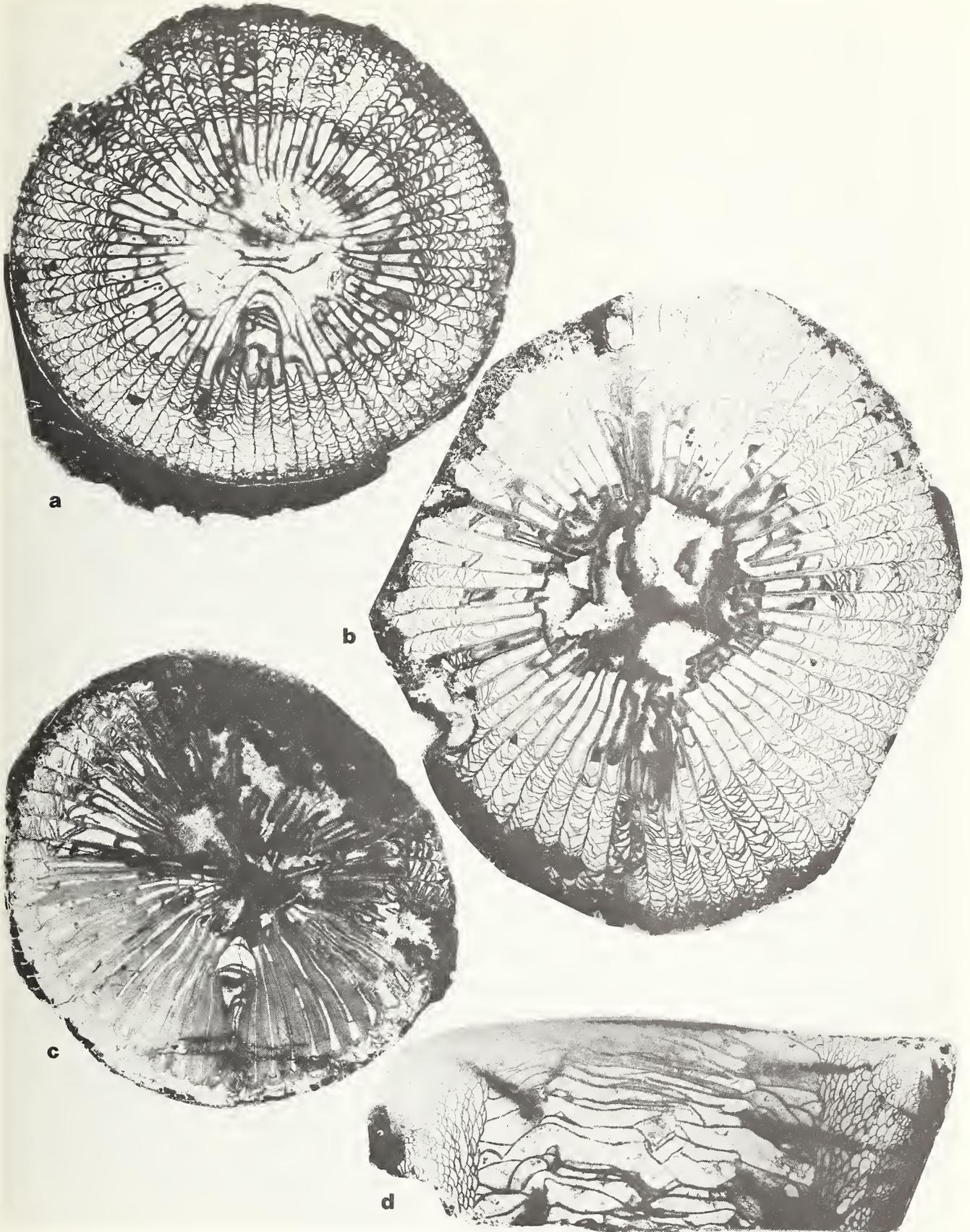


Figure 12. *Gshelia americana* n. sp. All parts x1.5. **Parts a and d**, UCMP paratype 37180, transverse (a) and longitudinal (d) sections. **Part b**, LACMIP paratype 6355, transverse section. **Part c**, UCMP paratype 37182, transverse section.



22 Figure 13. *Heterocamnia langenheimi* n. sp., UCMP holotype 37195, serial transverse sections (Part a, x3; Parts b-e, x1.5).

9 to 12 per cm; tabellae at peripheral edges of some tabular; wall as in transverse section; longitudinal section of adolescent stage not observed.

Documentation. LACMIP holotype 6347, LACMIP paratypes 6348–6357, UCMP paratypes 37179–37194. Twenty-three thin sections and numerous polished sections from 27 coralla from LACMIP locality 1133 (holotype 6347, paratypes 6348–6357), UCMP localities D-800 (paratypes 37183–37184, 37189), D-819 (paratypes 37185–37187), D-821 (paratype 37179), D-822 (paratype 37188), D-826 (paratypes 37180–37181, 37190), D-831 (paratypes 37191–37193), and D-832 (paratypes 37182, 37194) were studied.

Discussion. This species has all the characters of the genus: earliest stages without axial structures, followed by short interval with axial structures, and adult stages lacking axial structures (Dobrolyubova, 1940:71–81). The McCloud Limestone occurrence is the first record of the genus for North America in the Permian. Schoupe (1961:368) stated that *Gshelia* occurs in the “Unterkarbon . . . Nordamerika” but I have not been able to verify this. Hill (1956:292) listed the range as “M. Carb.-U. Carb., USSR-Spitz[bergen],” but it also occurs in the Lower Permian of Russia.

Gshelia americana is comparable to the type species, *G. rouilleri* Stuckenberg, 1888, from the Upper Carboniferous of the Moscow Basin, in size, number of septa, development of the axial structure, and some minor features. *G. americana* has, however, minor septa that are confined to the periphery of the dissepimentarium, whereas *G. rouilleri* has minor septa in many coralla that cross the dissepimentarium and may extend slightly into the tabularium.

Schoupe (1961:367) stated that there are four species of *Gshelia* in Spitzbergen: *G. calophylloides* (Holtedahl, 1913), *G. nikitini* (Stuckenberg, 1905), *G. ruprechtii* (Stuckenberg, 1895), and *G. lonsdalei* (Keyserling, 1854). These were described and figured by Heritsch (1939:37–57) under the genus *Siphonophyllia* Scouler, 1844. Only *G. nikitini* was shown (Heritsch, 1939:54, pl. 2, fig. 3) to have a juvenile axial structure, and that was a simple columella without the axial lamellae present in the type species of the genus. Although the adult stages resemble those of *Gshelia*, there are other genera so similar that I believe the Spitzbergen species' generic assignment to be in doubt until the juvenile stages are figured adequately.

If, however, these four species should turn out to belong in *Gshelia*, the following differences can be pointed out from *G. americana*. *G. (?) nikitini* has a simpler axial structure. *G. (?) calophylloides* appears similar in the adult stages but the juvenile stages are unknown, and Heritsch (1939) figured no longitudinal sections so these cannot be compared. *G. (?) ruprechtii*, as figured by Heritsch (1939, pl. 2, figs. 6, 7; pl. 11, fig. 8) does not exhibit many characters of the genus, is probably not *Gshelia*, and has minor septa that cross the dissepimentarium. *G. (?) lonsdalei*, as figured by Heritsch (1939, pl. 3, fig. 2; pl. 19, fig. 15) has long minor septa that cross the dissepimentarium and extend into the tabularium.

G. rouilleri var. *breviseptata* Dobrolyubova and Kabakovich, 1948 (p. 21, pl. 11, figs. 1–9; pl. 12, figs. 1–3; pl. 13, figs. 1–2),

from the Upper Carboniferous of the Moscow Basin, has longer minor septa and shorter major septa than *G. americana*.

G. elliptica Chi, 1931 (p. 17, pl. 3, figs. 8a–c), does not belong in this genus and is not comparable to *G. americana*.

Both *Gshelia* (?) sp. of Easton and Melendres (1964:413, figs. 1a–1c), from a clast in a Miocene conglomerate in the Philippine Islands, and *Gshelia* cf. *calophylloides* of Schoupe (1961:368, fig. 4), from the Upper Carboniferous of Yugoslavia, are known from specimens inadequately preserved for close comparison with other species.

Etymology. The species is named for North America.

Genus *Heterocania* Yabe and Hayasaka, 1920

Heterocania langenheimi n. sp.

Figures 13a–e; 14a–d

Diagnosis. A species of *Heterocania* characterized by the combination of very large corallites, a modest number of septa, and well-developed minor septa in the dissepimentarium. It has much larger corallites, fewer septa, and better developed minor septa than *H. thohustabulata*.

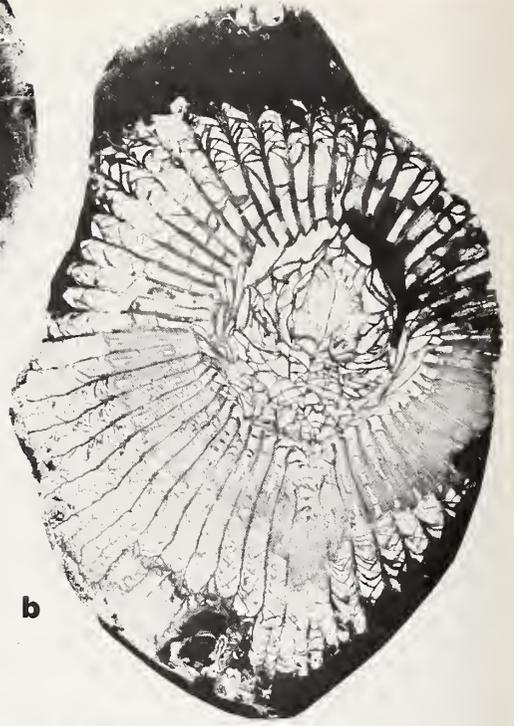
External Description. Corallites solitary, large, trochoid becoming cylindrical, maximum observed length 36 cm, maximum observed diameter 7.6 cm; corallite wall transversely lined and wrinkled, larger wrinkles (rugae) about 1 to 2 cm apart, fine transverse lines number about 30 in 1 cm vertically along corallite.

Transverse Section Description. Corallites roughly circular, diameters to 7.6 cm (generally between 6 and 7 cm); major septa well developed, dilate in cardinal quadrants in tabularium throughout ontogeny, thin in dissepimentarium, thinner in counter quadrants in tabularium but somewhat dilated there in juvenile stages; major septa in holotype number 36 at 23 mm, 43 at 35 mm, 52 at 54 mm, 52 at 57 mm, 57 at 68 mm; septa number 74 in largest (74-mm) paratype, UCMP 37196; cardinal septum short; septa number 24 in youngest observed (diameter 11 mm) paratype, 6359; minor septa well developed, at 11-mm corallite diameter crossing dissepimentarium (2 ranks) and few entering tabularium as nubs on inner wall, in adult stages confined to outer $\frac{1}{2}$ to $\frac{2}{3}$ of dissepimentarium; axial structure large, variable, elisiohyphaloid in juvenile stages, elisiohyphaloid or aulophylloid in adult stages, occupying most of tabularium, regular to irregular, with relatively few septal lamellae abutting straight to sinuous medial plate and connected by axial tabellae; dissepimentarium well developed, as much as 1.5 to 2 cm wide in adult stages; dissepiments highly variable, herringbone, pseudoherringbone, concentric, angulo-concentric, and (in largest adult stages) with some small lateral cystose ones alongside some septa; false wall developed axially on row of dissepiments bordering tabularium in some corallites, thickest in cardinal quadrants and juvenile to early adult stages; corallite wall very thin, 0.1 to 0.15 mm thick, silicified.

Longitudinal Section Description. Dissepimentarium of 12 to 23 ranks of steeply to very steeply dipping cystose to elongate, small to large dissepiments, generally more cystose peripherally, more



a



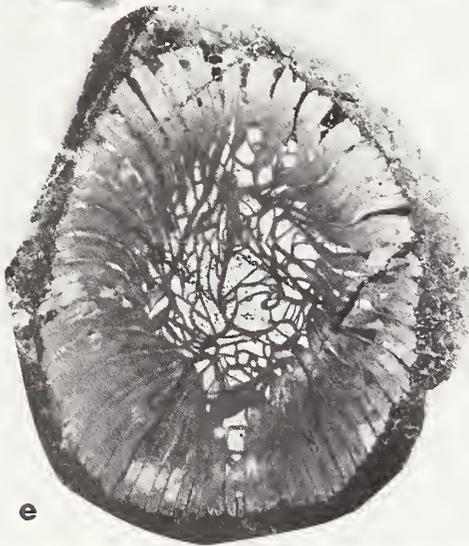
b



c



d



e



f

elongate axially; tabellae of 2 series: axial and periaxial; axial tabellae gently domed inwards and upwards towards and around medial plate and/or septal lamellae, about 15 in 1 cm; periaxial tabellae in 1 or 2 series, horizontal, sagging, or sloping inwards and upwards generally to axial tabellae.

Documentation. UCMP holotype 37195, UCMP paratypes 37196–37202, 37283, LACMIP paratypes 6358–6373. Nine thin sections and numerous polished sections from 24 coralla from UCMP localities D-819 (paratypes 37200–37202), D-822 (paratypes 37196, 37198–37199, 37283), D-826 (paratype 37197), and D-831 (holotype 37195) and LACMIP localities 1132 (paratypes 6366–6370), 1133 (paratypes 6359–6365, 6371–6373), and 4458 (paratype 6358) were studied.

Discussion. Genera of many large solitary Upper Paleozoic corals are badly in need of reinvestigation and redefinition. This coral does not fit readily into any of them. I have chosen to place it in *Heterocania* because the type species, *H. tholusitabulata* Yabe and Hayasaka, 1920, from the Lower Carboniferous of China, has distinctly dilated septa in the cardinal quadrants and a similar appearing axial structure, whereas other genera of the Aulophyllidae and Cyathopsidae with somewhat similar characters do not have such pronounced cardinal quadrant septal dilation. Hill (1956:290) stated that *Heterocania* has “minor septa absent,” but Cotton (1973:95) reported “. . . minors very short and in weathered specimens may not be observed.” *H. langenheimi* has minor septa that do not cross the dissepimentarium in postjuvenile stages, and some specimens have parts of the coral that contained these weathered away.

The genus has not been heretofore recorded in North American Permian rocks. The size and other characters clearly distinguish *H. langenheimi* from any previously described Permian coral.

The specimens occur in growth positions in “log jam” abundance in beds with *Gshelia americana*. The shape of the cylindrical corallum is twisted in many specimens, even as much as 360° in very long specimens, and many specimens exhibit sharp angles (as much as 90°), suggesting that they may have grown upwards until top heavy, fallen over, and then resumed upward growth. Calices of most specimens face towards the upper bedding plane surfaces. Internal structures, such as the cardinal fossula, are randomly oriented to the external curvature of the corallites, which is in contrast to observations made of some other solitary corals.

Etymology. The species is named for Dr. R.L. Langenheim, Jr.

Heterocania (?) sp.

Figures 14e–f

Transverse Section Description. Corallite solitary, circular to sub-circular, maximum observed diameter 29 mm (dissepimentarium missing); major septa number 38 at 20-mm corallite diameter, 41 at 22-mm corallite diameter, all lanceolate and highly

dilate, 6 to 7 mm long in tabularium, many touching axial structure and continuous with septal lamellae; cardinal septum shortened, about 1 mm long in tabularium; cardinal fossula closed; minor septa not observed; dissepimentarium not present due to eroded surface of corallite; axial structure large, filling entire tabularium, composed of highly sinuous medial plate (?) and septal lamellae, many formed from attenuate ends of septa, joined by tabellae; corallite wall not observed.

Documentation. UCMP hypotype 37203. Two thin sections and six polished sections from one corallum from UCMP locality D-861 were studied. Fragments of other corallites were present in the rock.

Discussion. This coral occurs with *Clisiophyllum gabbi* Meek, 1864, which has fewer and much thinner septa and a better defined axial structure. The extreme dilation of all the septa and the nature of the axial structure clearly distinguish *Heterocania* (?) sp. from other species found in the McCloud Limestone. It somewhat resembles *?Clisiophyllum* sp. B of Rowett, 1969 (p. 58, pl. 7, fig. 3) from the Lower Permian of Alaska, but Rowett’s specimen has a greater number of septa and an open cardinal fossula.

The generic referral is questionable since the dissepimentarium was not preserved and no longitudinal section was obtainable. Probably the coral represents a late neanic stage.

Fasciculate Rugosa

Genus *Durhamina* Wilson and Langenheim, 1962

Durhamina sublaeve (Meek, 1864)

Figures 5:4, 4a, 4b; 15a–c; 16a–c

Lithostroton mamillare (?), Castlenau, (sp.). Meek, 1864:5 (*pars*), pl. 1, figs. 4, 4a, 4b.

L. sublaeve Meek, 1864:6 (*pars*), pl. 1, figs. 4, 4a, 4b.

Lithostroton mamillare, var. *sublaevis* Meek, 1864, legend pl. 1, figs. 4, 4a, 4b.

Lithostroton ____? Meek, 1864:7 (not figured).

Not *Lithostroton mamillare*? of Meek, 1864, pl. 1, figs. 3, 3a.

External Description. Corallum phaceloid, maximum observed diameter 15 cm; epitheca with distinct, closely spaced rugae; calyx not observed.

Transverse Section Description. Corallites circular, diameter 10 to 12 mm, touching to as much as 20 mm distant; septa of 2 orders, 19 to 23 each, thin, straight, or slightly sinuous; major septa 2.5 to 4 mm long, generally all but 1 or 2 withdrawn from axial structure; minor septa 0.2 to 1.0 mm long, well developed; dissepimentarium regular, 1 to 3 mm wide; dissepiments concentric, angulo-concentric, straight, or herringbone; axial structure aulophylloid where most fully developed, with very sinuous medial plate (not everywhere distinguishable from axial tabellae) and an indeterminable number of highly sinuous septal lamellae, generally withdrawn from septa except in some corallites 1

Figure 14. *Heterocania langenheimi* n. sp. and *Heterocania* (?) sp.

Parts a through d. *H. langenheimi* n. sp., all parts x1.5. **Part a**, UCMP holotype 37195, longitudinal section. **Parts b through d**, UCMP paratype 37196, serial transverse sections (b, c) and longitudinal section (d).

Parts e and f. *Heterocania* (?) sp., UCMP hypotype 37203, serial transverse sections, x3.

Figure 15. *Durhamina sublaeve* (Meek, 1864), *Heritschioides* (?) *californiense* (Meek, 1864), and *Kleopatrina* (*Porfirievella*) *whitneyi* n. sp.
Parts a through c. *D. sublaeve*, all parts x1. **Part a**, MCZ holotype, MCZ Meek collection corallum no. 17, figured by Meek (1864, pl. 1, fig. 4). **Part b**, MCZ hypotype, MCZ Meek collection corallum no. 16, labeled "*Lithostrotion* ____" by Meek. **Part c**, MCZ hypotype, MCZ Meek collection corallum no. 14, labeled "*Lithostrotion* ____" by Meek.
Parts d and e. *H. (?) californiense*. **Part d**, MCZ lectotype (arrow), paralectotypes, MCZ Meek collection block no. 13, x0.5. **Part e**, lectotype, detail of Part d, figured by Meek (1864, pl. 1, fig. 2b), x1.
Part f. *K.(P) whitneyi* n. sp., MCZ holotype, MCZ Meek collection corallum no. 15, figured by Meek (1864, pl. 1, fig. 3), x1.5.



a



b



c



d



e



f



Figure 16. *Durhamina sublaeve* (Meek, 1864). All parts x3. **Parts a and b**, MCZ holotype, MCZ Meek collection corallum no. 17, transverse (a) and longitudinal (b) sections. **Part c**, MCZ hypotype, MCZ Meek collection corallum no. 14, transverse section. **Parts d and e**, MCZ hypotype, MCZ Meek collection corallum no. 16, longitudinal (d) and transverse (e) sections.

(counter?) or 2; medial plate attached to 1 septum present in some corallites without septal lamellae; corallite wall very thin, 0.1 to 0.2 mm wide.

Longitudinal Section Description. Dissepimentarium of 1 to 4 ranks of various sized (none highly inflated) dissepiments; tabellae of 2 loosely defined ranks, axial and periaxial, both inclined inwards and upwards to medial plate; tabulae tent-shaped where ranks of tabellae break down.

Documentation. Meek's (1864, pl. 1, figs. 4, 4a, 4b) figured specimen is recognized here as the holotype in accordance with ICZN article 73(a): "If a nominal species is based on a single specimen, that specimen is the 'holotype.'" The specimen is no. 17 in the MCZ collection and the only one labeled *Lithostrotion sublaeve*. I prepared two thin sections from it. MCZ specimens nos. 14 and 16 are referred here to *Durhamina sublaeve*. I prepared one thin section of the former and two of the latter. Nos. 14 and 16 were labeled "*Lithostrotion* ____?" and apparently were used by Meek for his description (Meek, 1864:7) under that designation. They are fasciculate, as Meek reported, although a cerioid corallum was figured erroneously by him (Meek, 1864, pl. 1, figs. 3, 3a) with this name.

Discussion. The type locality, as with the other Meek (1864) McCloud Limestone specimens, is presumed to be somewhere in the formation south of the Pit River. Since I did not encounter additional specimens of the species in my field work and since diagnostic fusulinids were not found in the matrix remaining on Meek's coralla, the exact stratigraphic position is uncertain. In this area, the McCloud Limestone is within fusulinid zone E and zone F.

Rowett (1969:43) published a key for eight species of *Durhamina*. *D. sublaeve* compares closely only with *D. cordillerensis* (Easton, 1960) from the Permian of east-central Nevada and southern California and with *D. alaskaensis* Rowett, 1969, from the Permian of Alaska. All three species have "axial tabellae not highly cystose at maturity" and "comparatively small corallites with few speta." *D. cordillerensis*, type species of the genus, is similar to *D. sublaeve*, but the former has a more complex axial structure where most fully developed, with more major septa touching it and more lonsdaleoid dissepiments. *D. alaskaensis* has somewhat larger corallites and a greater number of septa than *D. sublaeve*.

Genus *Heritschioides* Yabe, 1950

Heritschioides carneyi n. sp.

Figures 18a-c

Diagnosis. A species of *Heritschioides* characterized by the combination of large corallites, a large number of septa, a simple axial structure, and minor septa generally confined to the dissepimentarium. It has larger corallites than *H. buttensis*, *H. summitensis*, *H. parvum*, and *H. stevensi*. It has shorter minor septa than *H. hammami*, *H. merriami*, *H. wexoi*, *H. columbicum*, *H. coogani*, *H. durhami*, *H. rowetti*, *H. washburni*, *H. wildei*, *H. gavini*, and *H. smithi*. It has a simpler and more symmetrical axial structure than *H. hillae*, *H. moormanensis*, *H. ochocoensis*, and *H. skinneri*.

External Description. Corallum phaceloid, hemispheroidal, max-

imum observed diameter 18 cm; corallites subparallel, closely spaced to touching; epitheca and calyx not observed.

Transverse Section Description. Corallites circular to subcircular, diameter 12 to 18 mm, closely spaced, touching to as much as 11 mm apart; septa of 2 orders, 25 to 29 each, straight to broadly sinuous, generally thin in dissepimentarium (0.1 to 0.2 mm wide), dilate in tabularium (about 0.3 mm at base) becoming attenuate axially; major septa withdrawn from axial structure (except counter? septum in some), 4 to 6 mm long, except shortened cardinal septum 3 to 5 mm long; minor septa well developed, 1.3 to 2.4 mm long, generally confined to peripheral part of dissepimentarium, some crossing dissepimentarium, few entering tabularium as short spines; fossula small, open, formed by shortened cardinal septum; dissepimentarium regular or herringbone; stereozone developed on some dissepiments separating dissepimentarium from tabularium; axial structure clisiophylloid, generally simple and asymmetrical, relatively small, elliptical to subcircular, dimensions 1 by 3 mm to 3.5 by 4.5 mm; medial plate well developed, straight to sinuous, dilate, width 0.2 to 0.25 mm, length 2 to 4 mm; 2 to 10 sinuously and irregularly developed septal lamellae present; axial tabellae generally few, connecting septal lamellae in somewhat asymmetrical spiderweb pattern; corallite wall about 0.2 to 0.3 mm wide.

Longitudinal Section Description. Dissepimentarium of 1 to 5 (generally 3 to 4) steeply dipping ranks of large and small cystose dissepiments; tabellae of 2 zones, axial and periaxial; axial tabellae small, cystose, dipping inwards and upwards to medial plate; periaxial tabellae variously developed, about 15 per cm, generally 1 or 2 ranks sloping inwards and upwards to axial tabellae, but outer ones may be variously inclined to flat; tabulae present where axial structure consists only of medial plate.

Documentation. LACMIP holotype 6374, LACMIP paratype 6375. Six thin sections and 65 polished sections from two coralla from LACMIP locality 4457 were studied.

Discussion. *H. carneyi* differs from other species of the genus that have similar sized corallites and similar numbers of septa by possessing a variable axial structure that generally is extremely simple with few axial lamellae and by possessing minor septa that generally are confined to the dissepimentarium and appear only as spines in the few instances that they reach the tabularium. These relationships are shown graphically for this and other species in the genus on Figure 17, which informally and artificially combines species of *Heritschioides* based on four readily observable characters.

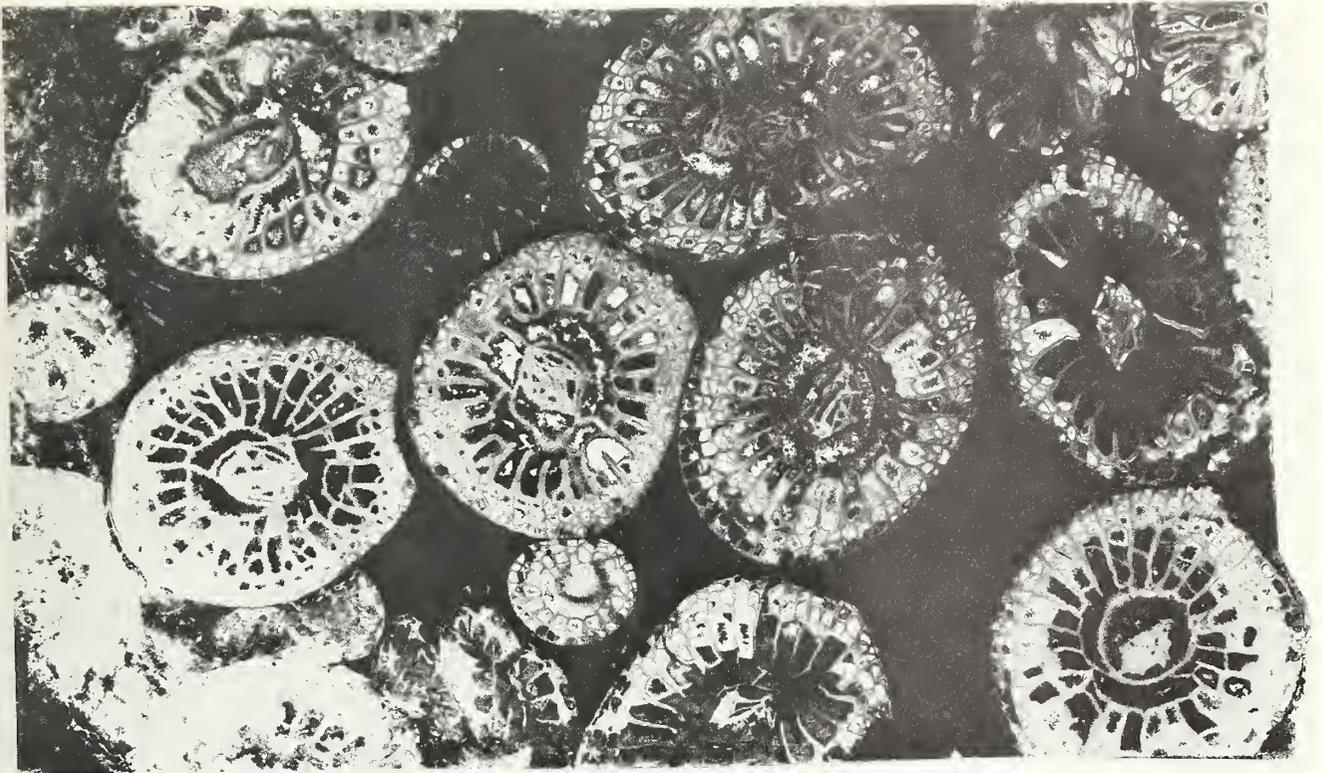
H. carneyi may be the oldest species of the genus recognized thus far. All other species in the McCloud Limestone are stratigraphically higher than *H. carneyi*, as are the species described from Permian rocks in Oregon, Nevada, and most probably Alaska. The exact stratigraphic position of the type species, *H. columbicum* Smith, 1935, is uncertain however (Wilson, 1980:90).

Oekentorp et al. (1978:387) figured a coral from the Upper Permian of Oman and referred it to *H. columbicum*. It should be examined again for characters of the genus. Wilson (1980) considered reports of *Heritschioides* from rocks outside western North America to be doubtful.

Watkins (1973:1761) cited C.H. Stevens as having identified a coral from the Hirz Mountain Limestone member of the Baird

	CORALLITE DIAMETERS GENERALLY LESS THAN 10 MM	CORALLITE DIAMETERS GENERALLY MORE THAN 10 MM	
MINOR SEPTA GENERALLY EXTEND INTO TABULARIUM	<u>H. buttensis</u>	<u>H. hammani</u> <u>H. merriami</u> <u>H. wexoi</u>	MAXIMUM NUMBER OF MAJOR SEPTA 25 OR FEWER
	<u>H. summitensis</u>	<u>H. columbicum</u> <u>H. coogani</u> <u>H. durhami</u> <u>H. rowetti</u> <u>H. washburni</u> <u>H. wildei</u> <u>H. woodi</u>	MAXIMUM NUMBER OF MAJOR SEPTA MORE THAN 25
MINOR SEPTA GENERALLY DO NOT EXTEND INTO TABULARIUM	<u>H. parvum</u> <u>H. stevensi</u>		MAXIMUM NUMBER OF MAJOR SEPTA 25 OR FEWER
		<u>H. hillae</u> <u>H. moormanensis</u> <u>H. ochocoensis</u> <u>H. skinneri</u>	MAXIMUM NUMBER OF MAJOR SEPTA MORE THAN 25
	AXIAL STRUCTURE SYMMETRICAL OR VERY SIMPLE	AXIAL STRUCTURE SYMMETRICAL OR VERY SIMPLE	AXIAL STRUCTURE ASYMMETRICAL

Figure 17. Informal combinations of *Heritschitoioides* species based on corallite diameters, numbers of major septa, lengths of minor septa, and symmetry of axial structures.



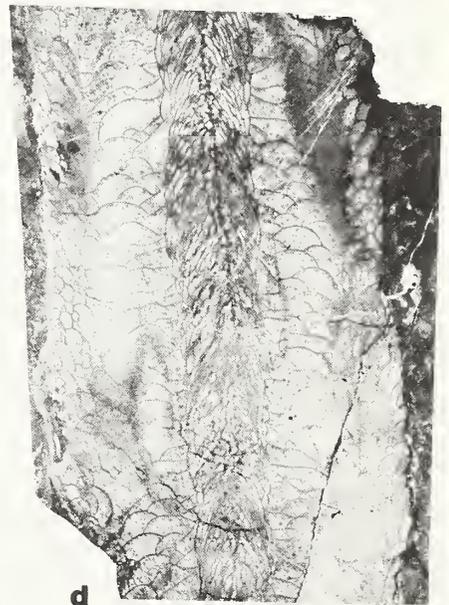
a



b



c



d

Figure 18. *Heritschioides carneyi* n. sp. and *H. coogani* n. sp. All parts x3.
 Parts a through c. *H. carneyi* n. sp., LACMIP holotype 6374, transverse (a, b) and longitudinal (c) sections.
 Part d. *H. coogani* n. sp., LACMIP paratype 6379, longitudinal section.

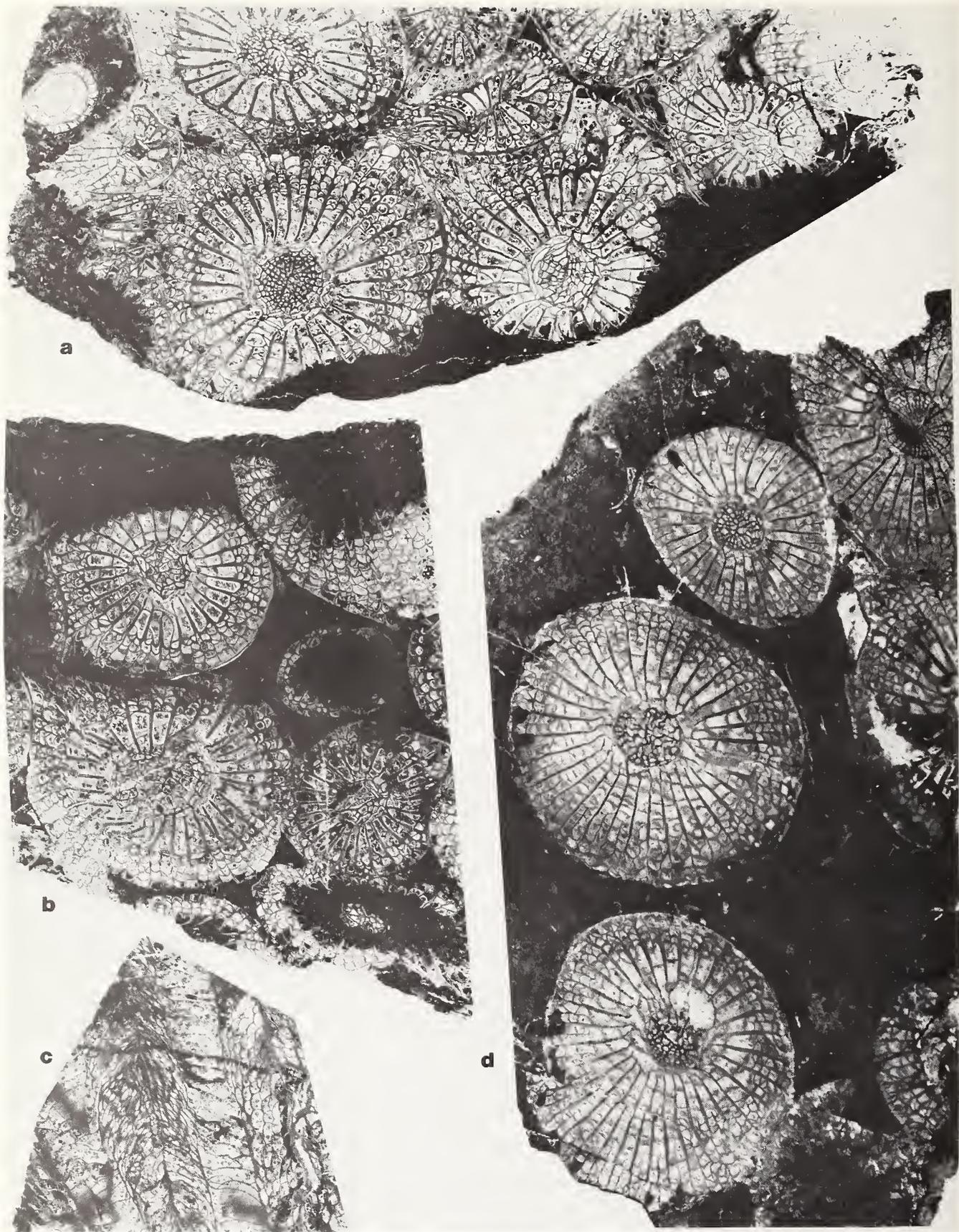


Figure 19. *Heritschioides coogani* n. sp. All parts x3. Parts a through c, LACMIP holotype 6376, transverse (a, b) and longitudinal (c) sections. Part d, LACMIP paratype 6379, transverse section.

Formation on Hirz Mountain as *Heritschioides* sp. This is below the McCloud Limestone and Pennsylvanian or Permian in age (Watkins, 1973:1743). I have not seen this coral.

Etymology. The species is named for Mr. William Alderman Carney.

Heritschioides coogani n. sp.

Figures 18d, 19a-d

Diagnosis. A species of *Heritschioides* characterized by the combination of relatively long and thin septa, a symmetrical and complex axial structure, large corallites, and a large number of major septa. It has thinner minor septa and a more symmetrical axial structure than *H. columbicum*. It has smaller corallites, a more regular axial plate, and shorter minor septa than *H. durhami*. It has larger corallites, more numerous septa, and a more complex axial structure than *H. washburni*. It has more and better developed septal lamellae than *H. wildei*. It has thinner and more numerous septa, shorter minor septa, and more numerous and less sinuous septal lamellae than *H. woodi*.

External Description. Corallum phaceloid, hemispheroidal, maximum observed diameter 12 cm, height 10 cm; corallites parallel to subparallel, very closely spaced (some nearly cerioid); epitheca and calyx not observed.

Transverse Section Description. Corallites circular to subcircular (some angular in part where corallite nearly cerioid), closely spaced, diameter 15 to 19 mm; septa of 2 orders, 25 to 33 each, straight to slightly sinuous, thin in dissepimentarium (about 0.1 mm wide), dilate in tabularium (0.2 to 0.3 mm at base) becoming attenuate axially; major septa touching or slightly withdrawn from axial structure, 6 to 10 mm long (generally 6 to 8), except shortened cardinal septum 4 to 6 mm long; minor septa well developed, 2 to 5.5 mm long, crossing dissepimentarium, many entering tabularium as nubs or dilate septa as much as 1 mm long; fossula small, open, formed by shortened cardinal septum, 1 to 1.5 mm deep; dissepimentarium regular, with dissepiments concentric, angulo-concentric, pseudoherringbone, or concave outwards; stereozone developed on some dissepiments separating dissepimentarium from tabularium; axial structure clisiophylloid, large, complex, symmetrical, generally circular, diameters 3 to 5 mm; medial plate well developed, 3 to 5 mm long, thin or dilate, straight to sinuous, connected to counter septum in some corallites; septal lamellae numerous, 13 to 26, rather evenly developed opposite one another in most complex axial structures; axial tabellae in 3 to 6 ranks, connecting septal lamellae in symmetrical spider-web pattern in best developed axial structures; corallite wall about 0.2 mm wide, rarely fused in closely spaced corallites to form joint cerioid-type wall.

Longitudinal Section Description. Dissepimentarium wide, of 4 to 6 ranks of steeply dipping cystose dissepiments (transverse sections indicate more ranks in some areas of corallites); tabellae of 2 well-defined zones, axial and periaxial; axial tabellae small to large, cystose to straight, dipping inwards and upwards to medial plate in 1 to 6 ranks; periaxial tabellae in 1 to 3 ranks, straight to gently domed, dipping inwards and upwards to axial tabellae.

Documentation. LACMIP holotype 6376, LACMIP paratypes 6377-6379. Six thin sections and 54 polished sections from four

coralla from LACMIP locality 1119 were studied.

Discussion. *H. coogani* is comparable to six other species, as can be seen in Figure 17. *H. wildei* n. sp. is somewhat similar but has far fewer septal lamellae that are less regularly developed on each side of the axial plate. *H. durhami* n. sp. has larger corallites, longer minor septa, and a less regular axial plate. *H. rowetti* n. sp. has much smaller corallites and fewer septa. *H. columbicum* (Smith, 1935), the type species from British Columbia, has longer minor septa that are more dilate and a somewhat less symmetrical axial structure. *H. washburni* (Merriam, 1942), from the Permian Coyote Butte Formation of Oregon, has more septa, larger corallites, and a somewhat smaller and simpler axial structure. *H. woodi* Wilson and Langenheim, 1962, from the Permian (Leonardian) Areturus Formation of eastern Nevada, has longer minor septa, fewer and more sinuous septal lamellae, and somewhat fewer septa.

Etymology. The species is named for Dr. Alan H. Coogan.

Heritschioides durhami n. sp.

Figures 20a-b

Diagnosis. A species of *Heritschioides* that has larger corallite diameters than any other species in the genus.

External Description. Corallum phaceloid and fragmentary, maximum observed diameter 11 cm; epitheca highly silicified, weathered; calyx not observed.

Transverse Section Description. Corallites circular, diameters very large, 17 to 34 mm, touching to as much as 7 mm apart; septa of 2 orders, 26 to 29 each, straight to somewhat sinuous, thin in dissepimentarium (about 0.1 mm), dilate in tabularium (about 0.24 to 0.4 mm); major septa very slightly withdrawn from axial structure (some bent axially near axial structure), 5 to 8 mm long, except shortened cardinal septa (1.7 to 3.2 mm long); minor septa very well developed, 1.7 to 3.2 mm long, extending across dissepimentarium and well into tabularium (about 0.5 mm); fossula small, open; dissepimentarium regular, 2 to 4 mm wide; dissepiments generally angulo-concentric, less generally herringbone, concentric, or straight; stereozone on axial row of dissepiments absent or very inconspicuous; axial structure clisiophylloid, rather symmetrical, large, circular, diameter 5 to 8 mm; medial plate inconspicuous, not dilate; septal lamellae thin, variously developed, 18 to 31, sinuous, curved, or straight, not all traversing axial structure to medial plate; axial tabellae very numerous, generally straight between septal lamellae; corallite wall about 0.1 to 0.15 mm wide, with septa inserted in V-shaped depressions.

Longitudinal Section Description. Dissepimentarium wide, of 4 to 10 ranks of steeply dipping, various sized dissepiments; tabellae of 2 zones, axial and periaxial; axial tabellae of various sizes, cystose to elongate, dipping steeply inwards and upwards to medial plate in 5 to 6 ranks on each side; periaxial tabellae cystose to straight, sloping inwards and upwards to axial tabellae in 2 to 3 ranks.

Documentation. LACMIP holotype 6380. Two thin sections and 13 polished sections from one corallum from LACMIP locality 1125 were studied.

Discussion. The corallite diameters of *H. durhami* are much

larger than those of any other species yet recorded for the genus. A 20-mm diameter is large for any species of *Heritschioides*, but one corallite in this corallum is 34 mm in diameter and the others are 20 mm or more. This alone should clearly distinguish it from other species. In addition, the combination of a large number of septa (as many as 29), the great length of the minor septa, the complex and regularly shaped large axial structure with its thin medial plate distinguishes it from *H. wildei*, which occurs in the same unit and has a similar number of septa, *H. skinneri*, which is much smaller and has much shorter minor septa, and other species with a similarly large number of septa.

Etymology. The species is named for Dr. J. Wyatt Durham.

Heritschioides gavini n. sp.

Figures 20c–d, 21 a–c

Diagnosis. A species of *Heritschioides* characterized by the combination of large corallites, a large number of septa, long minor septa, and an asymmetrical axial structure. It has larger corallites, more septa, and longer minor septa than *H. smithi*.

External Description. Corallum phaceloid, hemispheroidal, maximum observed diameter 27 cm; corallites subparallel, touching to as much as 1.5 cm apart; calyx 19 mm deep in corallite 24 mm in diameter, with large central axial boss; epitheca not observed.

Transverse Section Description. Corallites circular to subcircular, diameters 21 to 27 mm, generally closely spaced or touching; septa of 2 orders, 34 to 36 each, straight to somewhat sinuous, generally thin in dissepimentarium (about 0.2 mm wide), rarely dilate in dissepimentarium (about 0.4 mm wide), dilate in tabularium (0.2 to 0.4 mm wide); major septa slightly withdrawn or touching axial structure, 6 to 8 mm long, except shortened cardinal septum 3.5 to 4 mm long; minor septa well developed, 3.5 to 5 mm long, crossing dissepimentarium and entering tabularium 0.5 to 2 mm; fossula small, open (rarely closed by neighboring septa), formed by shortened cardinal septum; dissepimentarium regular (rarely lonsdaleoid where 1 or 2 septa fail), generally 3 to 4 mm wide; dissepiments pseudoherringbone, concentric, angulo-concentric, or straight; stereozone separating tabularium from dissepimentarium; axial structure clisiophylloid, large, diameter 5 to 8 mm, circular to subcircular, complex, generally asymmetrical (rarely symmetrical), with sinuous medial plate (straight in neanic stages), numerous (15 to 30) septal lamellae crossing several ranks of axial tabellae (rarely all structures coated with stereoplasm); corallite wall about 0.2 mm wide.

Longitudinal Section Description. Dissepimentarium of 3 to 9 (generally 4 to 5) ranks of steeply dipping small globose and few elongate dissepiments; tabellae of 2 zones, axial and periaxial; axial tabellae of 4 to 5 ranks, steeply dipping inwards and upwards to axial tabellae, also some flat, horizontal, or sloping inwards and downwards (rare “clinotabellae”).

Documentation. LACMIP holotype 6381, LACMIP paratypes 6382–6388. Seven thin sections and 78 polished sections from eight coralla from LACMIP locality 1285 were studied.

Discussion. *H. gavini* has corallites among the largest in diameter in the genus. *H. durhami* also has large corallites (17- to 34-mm diameters) but fewer septa (26 to 29) as well as other differences, including an essentially symmetrical axial structure. *H.*

smithi has corallites much smaller in diameters (15 to 21 mm) and fewer septa (26 to 32), although it also has an essentially asymmetrical axial structure. *H. washburni* (Merriam, 1942:375, pl. 55, figs. 2, 5, 7, 9, 11, 13) would seem similar according to the description, but examination of the type specimens (USNM 143427–143431) confirms that they are smaller (largest corallite diameter about 20 mm), although the numbers of major septa (33 to 35) are close, and the axial structure on some specimens is rather asymmetrical but less so than in *H. gavini*. The species is not closely comparable with any other species.

Preservation of the corallites is not good. The beds have been partly metamorphosed, and there is some crushing in most corallites. *Omphalotrochus* sp. was barely discernible as a “ghost” in the same unit. Cerioid rugose corals also were present but impossible to collect.

Etymology. The species is named for Mr. Peter T. Gavin.

Heritschioides hammani n. sp.

Figures 22a–c

Diagnosis. A species of *Heritschioides* characterized by the combination of relatively small corallites, a simple axial structure, long minor septa, and a small number of major septa. It has smaller corallites and a simpler axial structure than *H. merriami* and *H. wexoi* and straighter septal ends than *H. wexoi*.

External Description. Corallum phaceloid, maximum observed diameter 10 cm; corallites parallel, closely spaced; epitheca and calyx not observed.

Transverse Section Description. Corallites circular, diameter 10 to 12 mm, touching or as much as 5 mm apart; septa of 2 orders, 19 to 23 each, dilate in tabularium (many also dilate in dissepimentarium), straight to slightly sinuous; major septa 2.5 to 4.5 mm long, except cardinal septum about 2 mm long, generally slightly withdrawn from axial structure, except counter septum, which may touch axial structure in some; minor septa well developed, 0.5 to 1.5 mm long, generally extending slightly into tabularium as spines; fossula small, open, about 1 mm deep; dissepimentarium regular, 0.5 to 1.0 mm wide; dissepiments concentric or pseudoherringbone; false wall stereozone present; axial structure clisiophylloid, elongate, with only 1 or 2 septal lamellae; medial plate well developed, nearly straight, as much as 4 mm long, connected in some corallites to counter septum; axial tabellae number about 2 or 3 ranks on each side of medial plate, rather symmetrically developed; corallite wall 0.1 to 0.2 mm wide.

Longitudinal Section Description. Dissepimentarium narrow, of 1 to 3 (rare) ranks of small, steeply dipping dissepiments; tabellae of 2 zones, axial and periaxial; axial tabellae of 1 to 3 ranks, elongate, steeply inclined inwards and upwards to medial plate; periaxial tabellae generally of 1 or 2 ranks, horizontal or gently inclined inwards and upwards to axial tabellae.

Documentation. UCMP holotype 37204. Five thin sections and 43 polished sections from one corallum from UCMP locality D-828 were studied.

Discussion. This corallum is stratigraphically the highest colonial rugose coral found in the McCloud Bridge section. It has been so highly altered that many of the corallites are not pre-

served in detail, and most of the limestone matrix has been altered to masses of radiating black crystals that color entire beds black like some limestone beds of the Hirz Mountain section. A few corallites are well enough preserved to observe the structure.

The simplicity of the axial structure, the protrusion of the minor septa into the tabularium as spines, the size, and the number of septa readily distinguish *H. hammani* from other species, except *H. merriami* n. sp. and *H. wexoi* n. sp. *H. hammani* is differentiated in the discussions following the descriptions of these.

Etymology. The species is named for Mr. Howard Hamman.

Heritschioides merriami n. sp.

Figures 23a-c

Diagnosis. A species of *Heritschioides* characterized by the combination of moderately large corallites, a moderately complex and symmetrical axial structure, relatively few major septa, long minor septa, and relatively straight major septal ends. It has larger corallites and a more complex axial structure than *H. hammani*. It has straighter septal ends and a somewhat more symmetrical and complex axial structure than *H. wexoi*.

External Description. Corallum phaceloid, hemispheroidal, maximum observed height 20 cm, width 11 cm; corallites parallel, closely spaced, many touching; epitheca poorly preserved, showing some transverse wrinklings; calyx not observed.

Transverse Section Description. Corallites circular to subcircular, diameter 13 to 15 mm, very closely spaced; septa of 2 orders, 22 to 23 each, straight to somewhat sinuous, thin in dissepimentarium (about 0.1 mm wide), dilate in tabularium (about 0.2 mm at base), thinning axially; major septa 3.5 to 6 mm long, touching or slightly withdrawn from axial structure, except cardinal septum 2.5 to 3 mm long; minor septa well developed, 2 to 3.5 mm long, crossing dissepimentarium and entering tabularium as much as 0.5 mm; fossula small, open, about 1 mm deep; dissepimentarium regular, dissepiments angulo-concentric, straight, pseudoherringbone; thin stereozone formed on some dissepiments at tabularium interface; axial structure clisiophylloid, symmetrical, occupying most of tabularium beyond major septa, elliptical to circular, dimensions 3.5 by 3.5 mm, 2 by 3 mm, 2.5 by 4 mm; medial plate well developed, straight to somewhat sinuous, thin to slightly dilate, length 2.0 to 2.5 mm; septal lamellae number 8 to 14, generally straight to somewhat sinuous, rather regularly developed, many opposite one another on each side of medial plate; corallite wall about 0.1 mm wide.

Longitudinal Section Description. Dissepimentarium of 1 to 6 steeply dipping ranks of large and small cystose dissepiments; tabellae of 2 zones, axial and periaxial; axial tabellae small, cystose, dipping inwards and upwards to medial plate; periaxial tabellae number about 17 in 1 vertical cm, highly varied in inclination, flat, gently domed, generally dipping inwards and upwards to axial tabellae, generally of 1 rank.

Documentation. LACMIP holotype 6389. Three thin sections and 15 polished sections from one corallum from LACMIP locality 1120 were studied.

Discussion. *H. merriami* has corallite diameters generally greater than 10 mm, a maximum number of major septa fewer

than 25, minor septa that extend into the tabularium, and a symmetrical axial structure. As can be seen from Figure 17, it therefore is comparable only with *H. hammani* and *H. wexoi*. *H. hammani* has a much smaller corallite diameter (10 to 12 mm) and a much simpler axial structure than *H. merriami*. It is distinguished from *H. wexoi* in the discussion after that species description.

Etymology. The species is named for Dr. Charles W. Merriam.

Heritschioides rowetti n. sp.

Figures 23d, 24a-c

Diagnosis. A species of *Heritschioides* characterized by the combination of relatively small corallites, relatively few septa, long minor septa, and a symmetrical axial structure. It has smaller corallites and fewer septa than *H. columbicum*, *H. coogani*, *H. durhani*, *H. washburni*, *H. wildei*, and *H. woodi*.

External Description. Corallum phaceloid, large, exact shape not seen, maximum size of largest fragment 33 cm long, 5 cm wide; corallites closely spaced or touching in some coralla, as much as 2 cm apart in others; epitheca with low, rounded, transverse growth wrinklings, irregularly spaced 1 to 3 mm apart; calyx not observed.

Transverse Section Description. Corallites circular to subcircular, diameter 9 to 13 mm, touching to as much as 7 mm apart; septa of 2 orders, 17 to 24 each, generally somewhat dilate in tabularium, straight to slightly sinuous; major septa 3 to 5.5 mm long, except cardinal septum 2.4 to 3.2 mm long, generally very close to or touching axial structure, rare counter septa connected with medial plate; minor septa well developed, 1 to 1.5 mm long, crossing dissepimentarium and generally extending into tabularium as dilate spines; fossula small, open, about 2 mm deep; dissepimentarium regular, 1.3 to 2.1 mm wide; dissepiments concentric or herringbone (very rarely lonsdaleoid); false wall stereozone present; axial structure clisiophylloid, circular to elongate, generally symmetrical appearing, with 4 to 11 septal lamellae; medial plate generally well developed, slightly dilate (rarely thin), straight to somewhat sinuous, 2 to 4 mm long, connected in some corallites to counter septum; axial tabellae in 2 to 4 ranks on each side of medial plate, outer rank dilate in some corallites; corallite wall 0.1 to 0.2 mm wide.

Longitudinal Section Description. Dissepimentarium moderately wide, of 1 to 3 ranks of mixed small and large, steeply dipping dissepiments; tabellae of 2 zones, axial and periaxial; axial tabellae of 2 to 5 ranks, elongate, steeply inclined inwards and upwards to medial plate, not uniform in size; periaxial tabellae generally of 1 or 2 ranks, horizontal or gently inclined inwards and upwards to axial tabellae or sagging or gently inclined outwards and upwards to dissepimentarium.

Documentation. LACMIP holotype 6390, LACMIP paratypes 6391-6399. Four thin sections and 57 polished sections from ten coralla from LACMIP locality 1125 were studied.

Discussion. *H. rowetti* superficially resembles *H. parvum* Stevens, 1967, and *H. buttensis* Stevens, 1967, both from the Leonardian Arcturus Formation of White Pine County, Nevada. It differs from the former species by having longer minor septa and from the latter species by having a narrower dissepimen-

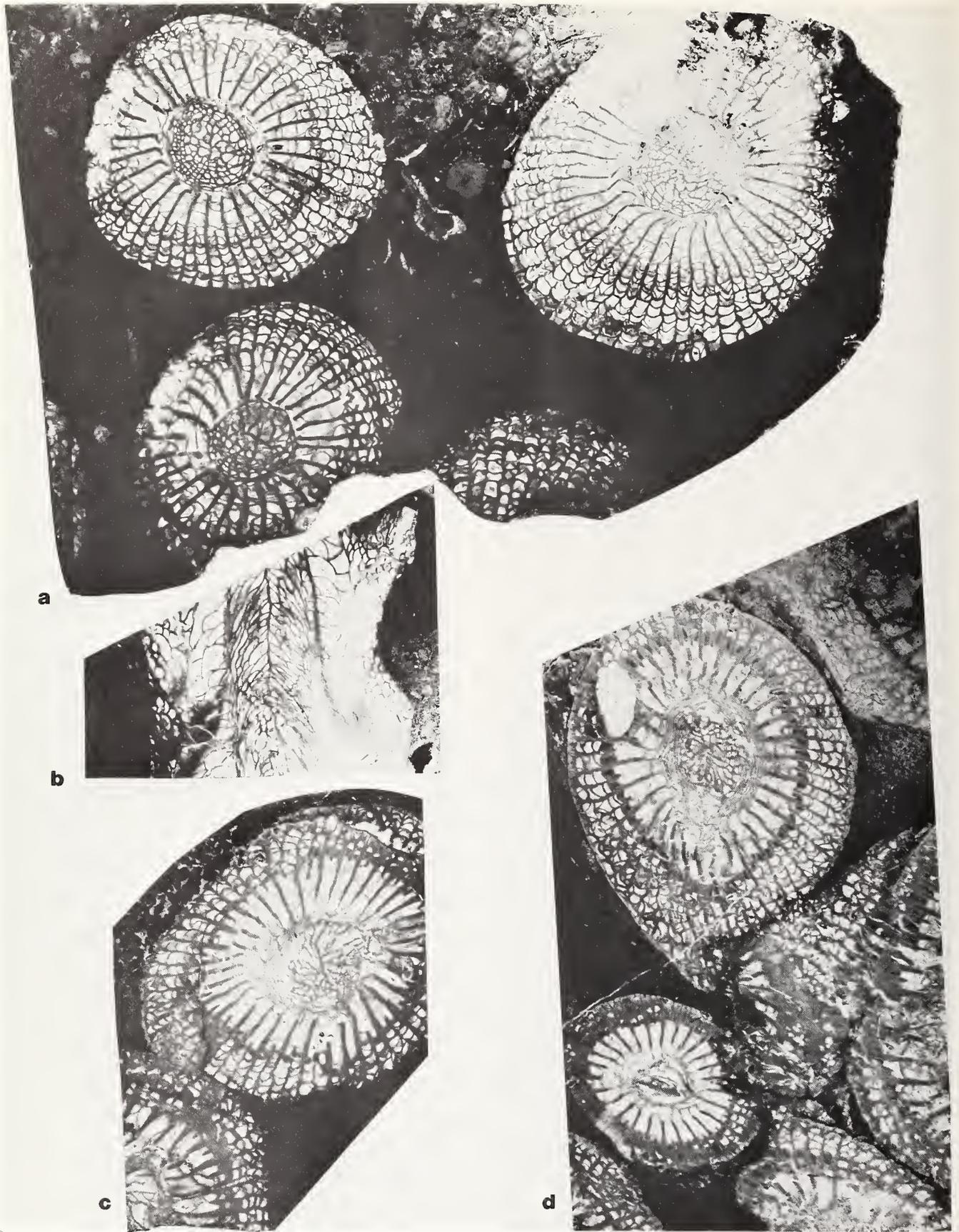


Figure 20. *Heritschioides durhami* n. sp. and *H. gavini* n. sp. All parts x3.
 Parts a and b. *H. durhami* n. sp., LACMIP holotype 6380, transverse (a) and longitudinal (b) sections.
 Parts c and d. *H. gavini* n. sp., LACMIP holotype 6381, transverse sections.



a



b



c

Figure 21. *Heritschioides gavini* n. sp. All parts x3. **Part a**, LACMIP paratype 6383, transverse section. **Parts b and c**, LACMIP holotype 6381, longitudinal sections.

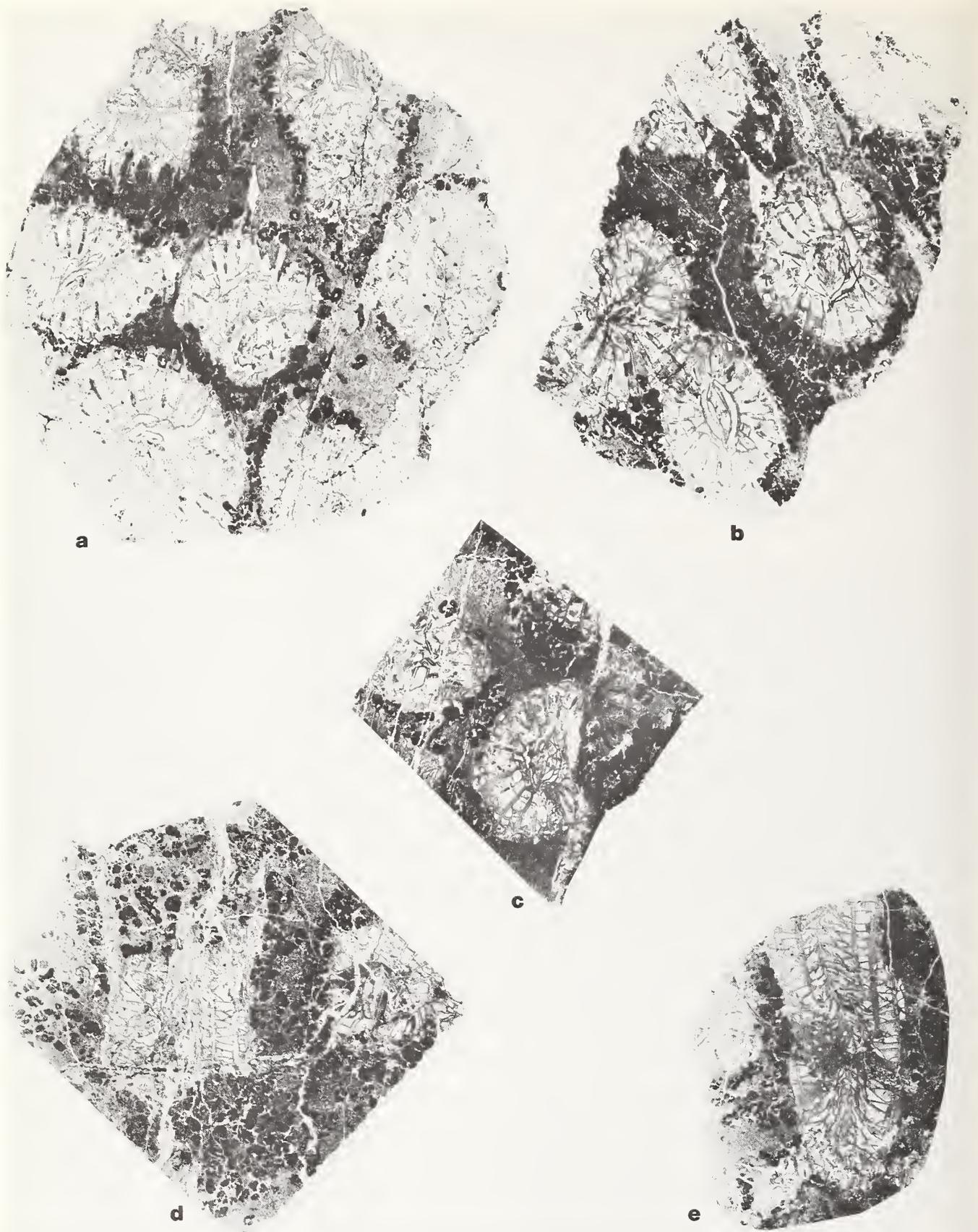


Figure 22. *Heritschioides hammami* n. sp., UCMP holotype 37204, transverse sections (a-c) and transverse and longitudinal sections (d, e). All parts

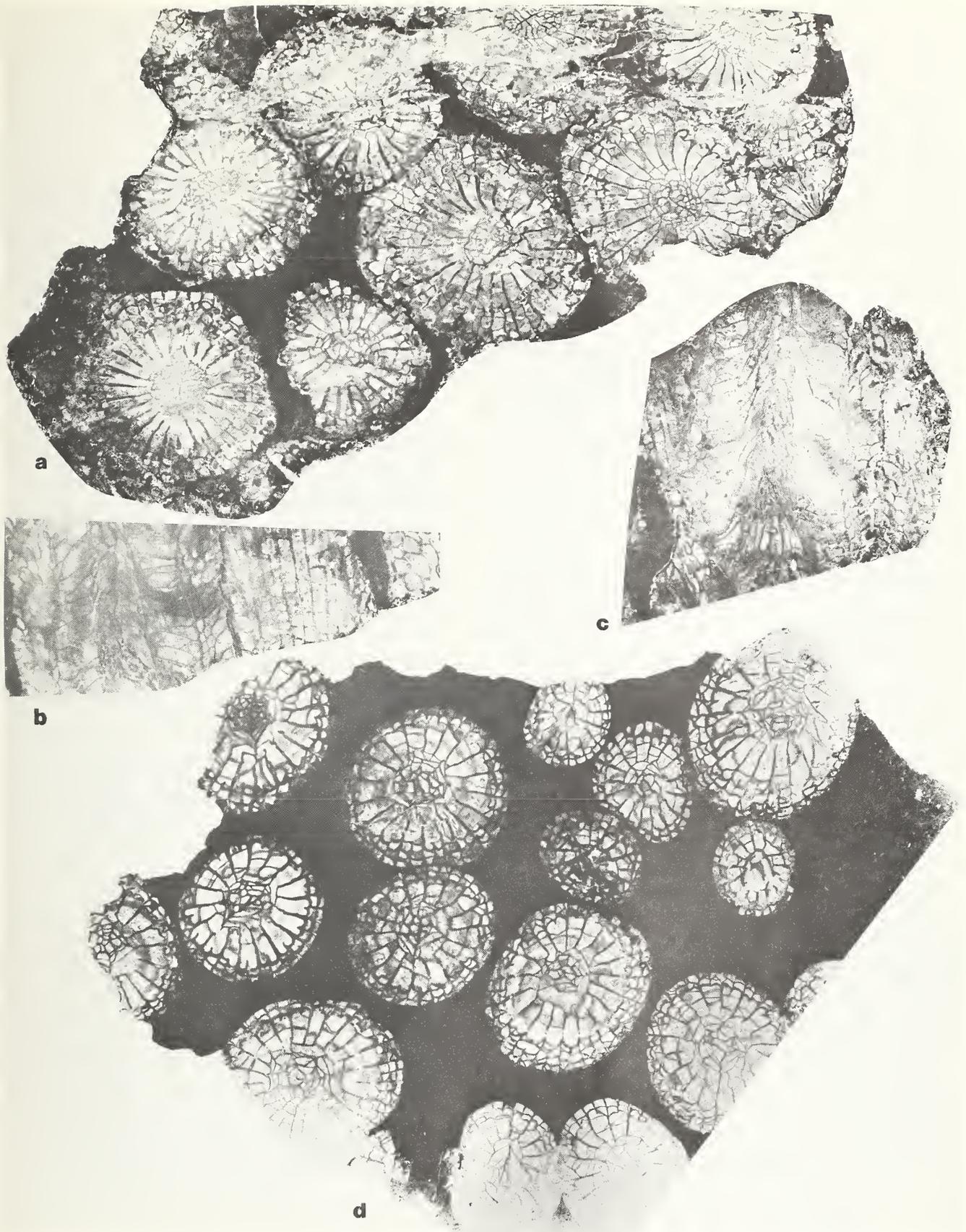


Figure 23. *Heritschioides merriami* n. sp. and *H. rowetti* n. sp. All parts x3.
 Parts a through c. *H. merriami* n. sp., LACMIP holotype 6389, transverse (a) and longitudinal (b, c) sections.
 Part d. *H. rowetti* n. sp., LACMIP paratype 6391, transverse section.

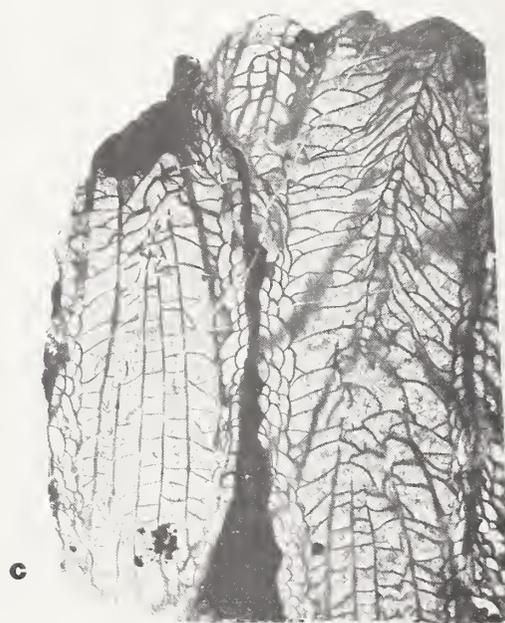
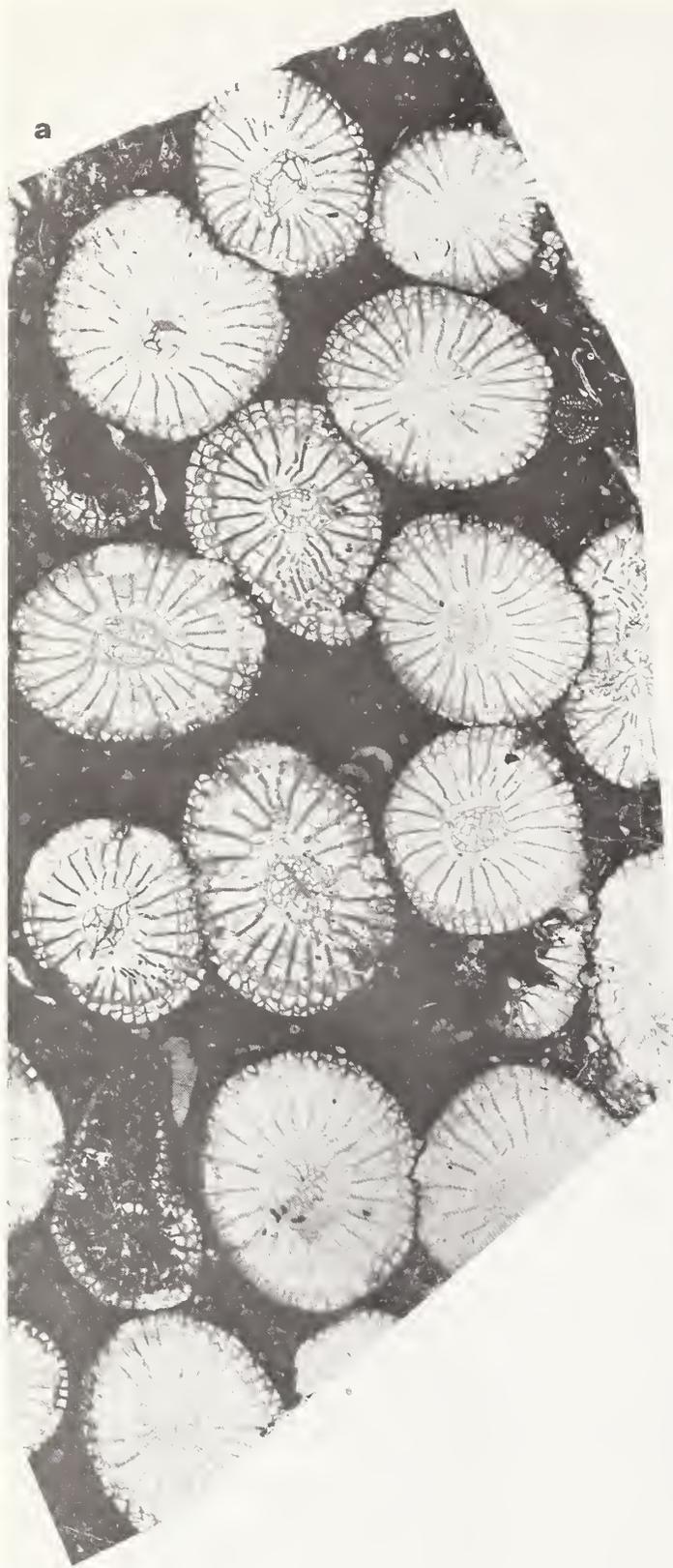


Figure 24. *Heritschioides rowetti* n. sp. All parts x3. Parts a and b, LACMIP holotype 6390, transverse (a) and longitudinal (b) sections. Part c, LACMIP paratype 6391, longitudinal section.

tarium, a smaller axial structure with less sinuous axial lamellae, and a better defined axial plate. There is, however, considerable variation in the corallites of *H. rowetti* in every corallum examined. *H. rowetti* has smaller corallite diameters than other species in its group as shown in Figure 17.

Etymology. The species is named for Dr. Charles L. Rowett.

Heritschioides skinneri n. sp.

Figures 25a–c

Diagnosis. A species of *Heritschioides* characterized by the combination of a moderately asymmetrical axial structure with a relatively well-defined medial plate, a relatively narrow dissepimentarium, large corallites, and a large number of relatively short septa. It has a smaller, less complex, and more symmetrical axial structure than *H. hillae*. It has a more symmetrical and a more complex axial structure and a narrower dissepimentarium than *H. ochocoensis*. It has shorter septa and a more symmetrical axial structure with a better defined medial plate than *H. moormanensis*.

External Description. Corallum phaceloid, maximum observed diameter 11 cm; corallites parallel, closely spaced to 3 cm apart; epitheca and calyx not observed.

Transverse Section Description. Corallites circular to subcircular, diameter 1 to 14 mm, touching to as much as 5 mm apart; septa of 2 orders, 26 to 30 each, some dilate in tabularium, straight to slightly sinuous; major septa 3.5 to 6 mm long, except cardinal septum 2.5 to 4.5 mm long, generally close to but slightly withdrawn from axial structure; minor septa thin, 0.5 to 1.5 mm long, generally confined to dissepimentarium, rarely appearing in tabularium as short spines; fossula small, open, about 0.5 mm deep; dissepimentarium regular, 1 to 2 mm wide; dissepiments concentric or pseudoherringbone; false wall stereozone generally not present, rarely slightly developed; axial structure clisiophylloid, large, asymmetrical, with numerous septal lamellae; medial plate variously developed, highly sinuous to nearly straight, slightly dilate to not dilate, 1.5 to 4 mm long; axial tabellae abundant in many corallites, generally asymmetrically developed in spider-web pattern; corallite wall about 0.1 mm wide.

Longitudinal Section Description. Dissepimentarium narrow, of 1 to 3 ranks of steeply dipping, small dissepiments; tabellae of 2 zones, axial and periaxial; axial tabellae of 2 to 3 ranks, elongate, steeply inclined inwards and upwards to sinuous medial plate, periaxial tabellae of 1 to 3 ranks, gently inclined inwards and upwards to axial tabellae.

Documentation. UCMP holotype 37205. Three thin sections and 32 polished sections from one corallum from UCMP locality D-804 were studied.

Discussion. *H. skinneri* is similar in superficial appearance to the type species of the genus, *H. columbicum* from British Columbia, Canada. In the latter species, however, the minor septa generally extend into the tabularium, whereas in *H. skinneri* they are generally confined to the dissepimentarium. *H. hillae* Wilson and Langenheim, 1962, has a larger and more asymmetrical axial structure than *H. skinneri*. *H. ochocoensis* (Merriam, 1942), from the Coyote Butte Formation of Crook County, Oregon, has a simpler axial structure and wider dissepimentarium. *H. moor-*

manensis Stevens, 1967, from the Arcturus Formation of White Pine County, Nevada, has septa that generally touch the axial structure and a much more asymmetrical axial structure in which the medial plate is so sinuous as to be generally unrecognizable. The other nominal species are not closely comparable.

Etymology. The species is named for Dr. John W. Skinner.

Heritschioides smithi n. sp.

Figures 25d, 26a–c

Diagnosis. A species of *Heritschioides* characterized by the combination of relatively short minor septa, a relatively small and asymmetrical or simple axial structure, relatively small corallites, and relatively few septa. It has shorter minor septa, a smaller axial structure, somewhat smaller corallites, and somewhat fewer septa than *H. gavini*.

External Description. Corallum phaceloid, hemispheroidal, maximum observed diameter 10 cm; corallites parallel to subparallel, very closely spaced or touching; epitheca and calyx not observed.

Transverse Section Description. Corallites circular to subcircular, diameter 15 to 21 mm, touching to as much as 4 mm apart; septa of 2 orders, 26 to 32 each, straight to slightly sinuous, thin in dissepimentarium (0.1 to 0.2 mm wide), dilate in tabularium (0.2 to 0.3 mm wide); major septa 6.5 to 7.5 mm long, except shortened cardinal septum 4.5 to 5 mm long; minor septa well developed, 3 to 4 mm long, generally extending across dissepimentarium into tabularium as spines, fossula small, open; dissepimentarium regular, wide; dissepiments, pseudoherringbone, straight, concentric, or angulo-concentric; false wall stereozone present; axial structure clisiophylloid, variable, simple or asymmetrical where more complex (about 2.5 by 3.5 mm in latter); medial plate slightly dilate (0.1 mm), 3 to 4 mm long, sinuous, connected in some corallites to counter septum; septal lamellae irregularly developed, generally short, 2 to 6 per corallite, not touching septa; corallite wall about 0.2 mm wide.

Longitudinal Section Description. Dissepimentarium 2.5 to 4 mm wide, composed of 2 to 6 ranks of steeply dipping, small and cystose or large and elongate dissepiments; tabellae of 2 poorly differentiated zones: axial and periaxial; axial tabellae tent-shaped, in 1 to 3 ranks; periaxial tabellae horizontal or gently sloping inwards and upwards to axial tabellae (rarely sloping inwards and down), in 1 to 2 ranks, 15 to 20 tabellae per cm.

Documentation. UCMP holotype 37206, LACMIP paratype 6400. Six thin sections and 46 polished sections from the holotype corallum from UCMP locality D-840 and two thin sections and 24 polished sections from the paratype corallum from LACMIP locality 1124 were studied.

Discussion. The only other species of *Heritschioides* with large corallites (more than 10 mm diameter), a large number of major septa (more than 25), minor septa that generally extend into the tabularium, and an asymmetrical (some corallites) axial structure is the type species, *H. columbicum* from British Columbia. *H. columbicum*, however, has a large, well-defined axial structure with numerous septal lamellae and axial tabellae. *H. smithi* has a curiously deformed looking axial structure that is composed in many corallites of simply a twisted medial plate with a few, very short, asymmetrically placed septal lamellae in the simplest forms. Some corallites of *H. smithi* develop a somewhat more

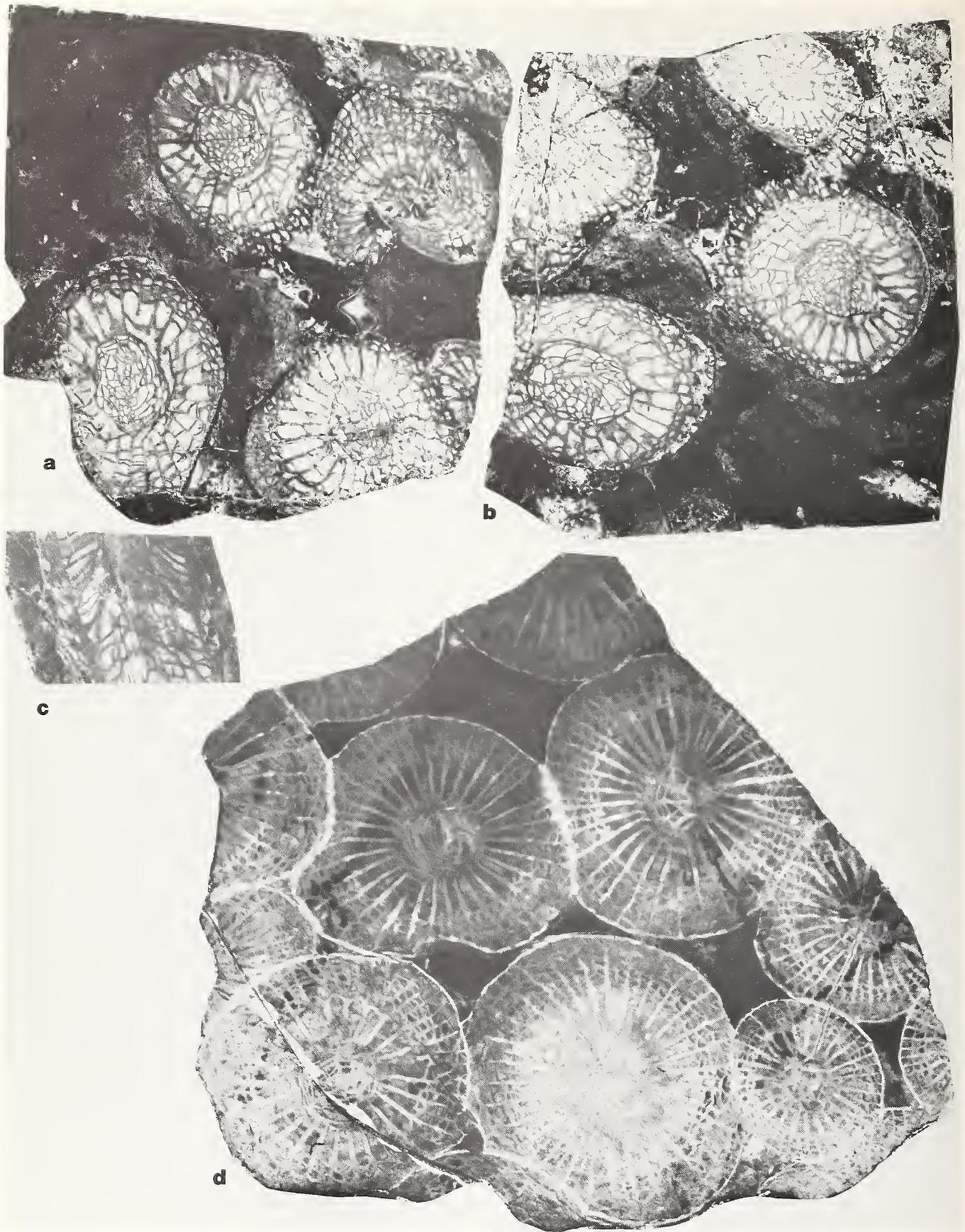


Figure 25. *Heritschioides skinneri* n. sp. and *H. smithi* n. sp. All parts x3.

42 Parts a through c. *H. skinneri* n. sp., UCMP holotype 37205, transverse (a, b) and longitudinal (c) sections.
Part d. *H. smithi* n. sp., UCMP holotype 37206, transverse section.

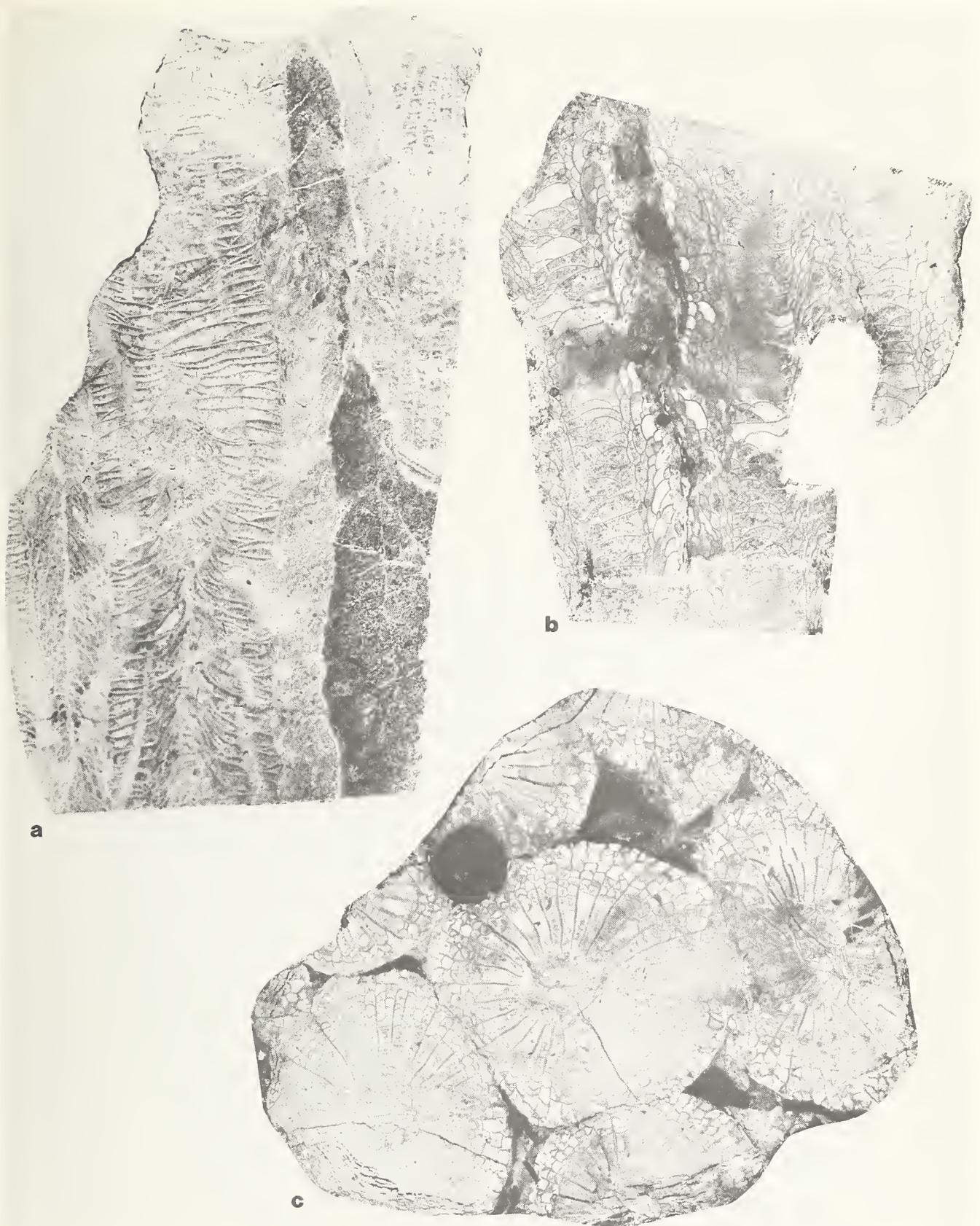


Figure 26. *Heritschioides smithi* n. sp. All figures x3. **Part a**, UCMP holotype 37206, longitudinal section. **Parts b and c**, LACMIP paratype 6400, longitudinal (b) and transverse (c) sections.



Figure 27. *Heruschiooides stevensi* n. sp. and *H. wexoi* n. sp. All parts x3.

- 44 Parts a and b. *H. stevensi* n. sp., UCMP holotype 37207, transverse (a) and longitudinal (b) sections.
Part c. *H. wexoi* n. sp., LACMIP holotype 6401, transverse section.

complex axial structure with longer septal lamellae joined by a few axial tabellae, but these are much more asymmetrical than the axial structure of *H. columbicum*. *H. smithi*'s differences with *H. gavini* are discussed following the description of that species. The holotype corallum is somewhat recrystallized, and the structures are more apparent when studied in polished than in thin section. This has made them difficult to photograph satisfactorily, but the paratype slides photograph better.

Etymology. The species is named for D. Stanley Smith.

Heritschioides stevensi n. sp.

Figures 27a–b

Diagnosis. A species of *Heritschioides* characterized by the combination of small corallites, short minor septa, a small number of major septa, a relatively small and simple axial structure, and a relatively narrow dissepimentarium. It has a smaller and simpler axial structure and a somewhat narrower dissepimentarium than *H. parvum*.

External Description. Corallum phaceloid, hemispheroidal, maximum observed diameter 20 cm; epitheca and calyx not observed.

Transverse Section Description. Corallites circular to subcircular, diameter 8 to 11 mm, touching or as much as 15 mm apart; septa of 2 orders, 18 to 22 each, straight or slightly sinuous, thin throughout; major septa 2.0 to 3.5 mm long, except cardinal septum 2.3 to 3.0 mm long, withdrawn from axial structure except counter in some corallites continuous with medial plate; minor septa short, 0.5 to 1.0 mm long, absent in parts of some corallites, generally confined to tabularium; fossula small; dissepimentarium regular, 0.5 to 1.9 mm wide; dissepiments concentric, angulo-concentric, herringbone, or pseudoherringbone; axial structure elisiophylloid, asymmetrical, very simple, elongate, 1.5 to 2.5 mm long, about 1.0 mm wide, composed of medial plate, septal lamellae, and axial tabellae; medial plate thin, straight to somewhat sinuous, attached to counter septum in some corallites; septal lamellae short, irregularly developed, 1 to 4 in number, corallite wall about 0.1 mm wide.

Longitudinal Section Description. Dissepimentarium of 1 to 4 ranks of dissepiments, various sizes and various inclinations; elongate dissepiments generally gently inclined, small cystose dissepiments generally steeply inclined; tabellae of 2 poorly defined ranks, axial and periaxial; axial tabellae of 1 to 2 ranks, steeply inclined inwards and upwards to medial plate; periaxial tabellae straight to slightly domed, more gently inclined inwards and upwards to periaxial tabellae.

Documentation. UCMP holotype 37207. Two thin sections and 34 polished sections from one large corallum from UCMP locality D-862 were studied.

Discussion. Only one other species, *H. parvum* Stevens, 1976, from the Arcturus Formation of White Pine County, Nevada, is comparable to *H. stevensi* in corallite diameter, numbers of septa, length of minor septa, and simplicity of the axial structure. *H. parvum* may be distinguished readily because it has dilate major septa in the tabularium, a more complex axial structure where it is most highly developed (more axial tabellae), and minor septa

better developed and more consistently present throughout the corallites, a few of which even extend into the tabularium.

Etymology. The species is named for Dr. Calvin H. Stevens.

Heritschioides wexoi n. sp.

Figures 27c, 28a–c

Diagnosis. A species of *Heritschioides* characterized by the combination of a large number of septa, long minor septa, moderately large corallites, a moderately complex axial structure, and axial ends of many septa twisted in vortex fashion. It has larger corallites and a more complex axial structure than *H. hammani*. It has more twisted septal ends and a somewhat less symmetrical and less complex axial structure than *H. merriami*.

External Description. Corallum phaceloid, maximum diameter observed 151 cm, height 46 cm; corallites parallel to subparallel, closely spaced; epitheca with faint rugae; calyx with axial boss, not well preserved.

Transverse Section Description. Corallites circular, diameter 10 to 16 mm, touching or as much as 6 mm apart; septa of 2 orders, 18 to 25 each, dilate in tabularium, major septa 3.5 to 4.5 mm long, except cardinal septum about 3 to 3.5 mm long (some cardinal septa not shortened), straight to sinuous, axial ends attenuate in many, twisted in axial vortex fashion to axial structure, withdrawn and not curved in others; minor septa well developed, 1.25 to 2 mm long, generally crossing dissepimentarium, many extending into tabularium as dilate spines 0.25 to 0.5 mm long; fossula small, open, inconspicuous or absent in some; dissepimentarium regular, 1 to 1.5 mm wide, rarely to 3 mm wide; dissepiments concentric, angulo-concentric, or pseudoherringbone; false wall stercozone present; axial structure elisiophylloid, highly variable, ranging from medial plate with 1 or 2 septal lamellae to complex symmetrical or asymmetrical form, attached to major septa in some, unattached in others; medial plate generally sinuous, slightly dilate, 1 to 3.5 mm long; axial tabellae in 2 to 3 ranks on each side of medial plate, variably developed, in some combined with septal tabellae forming "spider web"; corallite wall about 0.2 mm wide.

Longitudinal Section Description. Dissepimentarium moderately wide, of 2 to 5 ranks of small, steeply dipping dissepiments; tabellae of 2 poorly defined zones, axial and periaxial tabellae of 3 to 4 ranks, tent-shaped, sloping inwards and upwards to medial plate; periaxial tabellae of 1 to 2 ranks, horizontal (few) or inclined inwards and upwards to axial tabellae.

Documentation. LACMIP holotype 6401, LACMIP paratypes 6402–6411. Eight thin sections and 86 polished sections from 11 coralla from LACMIP locality 5316 were studied.

Discussion. *H. wexoi* resembles only *H. hammani* and *H. merriami*. These types have corallite diameters generally greater than 10 mm, 25 or fewer major septa, and minor septa that generally extend into the tabularium, a combination of characters that distinguishes these from other species of the genus.

H. wexoi has widely variable axial structures, some of which are attached to the twisted axial ends of major septa. *H. merriami* differs in having asymmetrical, complex axial structure and no twisted septal ends. *H. hammani* has smaller corallites (10–12

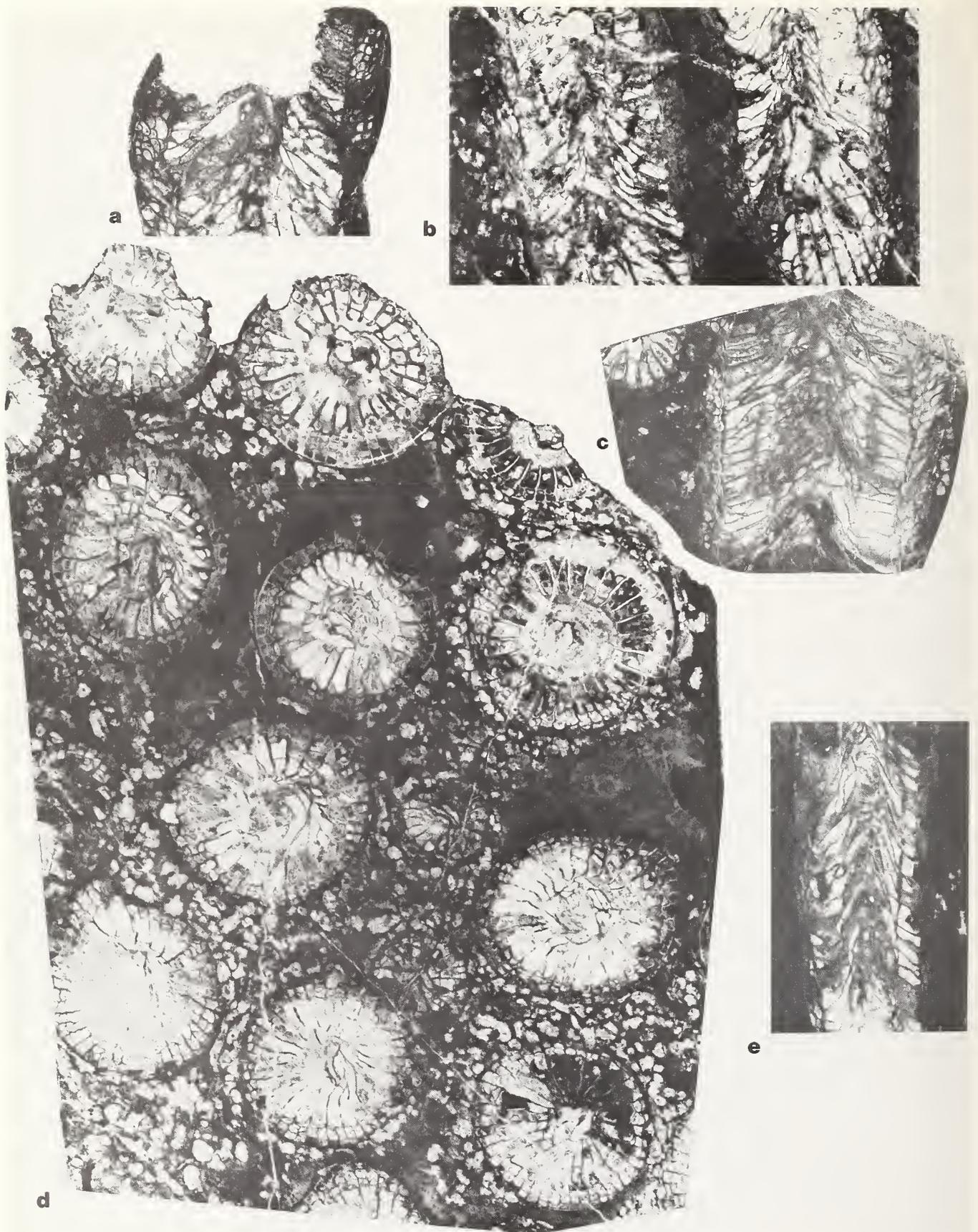


Figure 28. *Heritschioides wexoi* n. sp. All parts x3. Parts a and c, LACMIP holotype 6401, longitudinal sections. Parts b, d, and e, LACMIP paratype 6402, longitudinal (b, e) and transverse (d) sections.

mm), a simpler axial structure, and lacks the twisted septa of *H. wexoi*.

Etymology. The species is named for Mr. John B. Wexo.

Heritschioides wildei n. sp.

Figures 29a-e

Diagnosis. A species of *Heritschioides* characterized by the combination of large corallites, numerous septa, relatively short and thin minor septa, and a symmetrical axial structure with a well-defined medial plate. It has shorter and somewhat thinner minor septa and a better defined medial plate than *H. columbicum*. It has a broader dissepimentarium and generally more dilate major septa in the tabularium than *H. coogani*. It has generally smaller corallites, a somewhat narrower dissepimentarium, and a more symmetrical axial structure with a better defined medial plate than *H. durhami*. It has larger corallites and more septa than *H. rowetti*. It has fewer septa and a more symmetrical axial structure than *H. washburni*. It has shorter and thinner minor septa, fewer herringbone dissepiments, and a somewhat shorter medial plate than *H. woodi*.

External Description. Corallum phaceloid, hemispheroidal, maximum observed diameter 12 cm; epitheca badly preserved, with some transverse wrinklings; calyx deep with walls sloping nearly vertically inwards to depth of about 1.2 cm; calicular floor crossed by prominent septa; axial boss central, large, inversely conical, diameter about 4 mm, height about 4 mm.

Transverse Section Description. Corallites circular, diameter 14 to 18 mm, touching to as much as 5 mm apart; septa of 2 orders, 24 to 30 each, straight to somewhat sinuous, thin in dissepimentarium (about 0.1 mm), dilate in tabularium (about 0.2 to 0.3 mm); major septa generally slightly withdrawn from axial structure, 4.5 to 6.9 mm long, except shortened cardinal septa generally 0.5 to 1.0 mm shorter; minor septa well developed, 1.5 to 3.5 mm long, generally extending across dissepimentarium into tabularium about 0.5 mm, dilate in tabularium; fossula small, open, 0.5 to 1.0 mm deep; dissepimentarium regular, 1.5 to 2.5 mm wide; dissepiments herringbone near corallite wall, otherwise concentric, angulo-concentric, or straight; stereozone on row of dissepiments separating dissepimentarium from tabularium thin; axial structure clisiophylloid, large, circular to subcircular, diameter 3.5 to 5.0 mm; medial plate well developed, dilate and nearly straight to thin and rather sinuous, about 1.5 to 4.0 mm long, 0.1 to 0.2 mm wide where dilate; septal lamellae thin, variously developed, 11 to 19, sinuous to straight, unequal number on each side of medial plate; axial tabellae numerous, intercepting septal lamellae at near right angles, straight, curved, or slightly sinuous (rare); corallite wall about 0.2 mm wide.

Longitudinal Section Description. Dissepimentarium wide, of 4 to 10 ranks of rather steeply dipping, various sized dissepiments; tabellae of 2 zones, axial and periaxial; axial tabellae of various sizes, cystose, dipping steeply inwards and upwards to medial plate in 5 to 8 ranks on each side; periaxial tabellae generally sloping gently inwards and upwards to axial tabellae in 1 to 4 ranks.

Documentation. UCMP holotype 37208, LACMIP paratypes

6412-6413. Five thin sections and 42 polished sections from three coralla from LACMIP locality 1125 (paratypes) and UCMP locality D-852 (holotype) were studied.

Discussion. *H. wildei* occurs in the same beds as *H. rowetti*, but the latter has much smaller corallites and fewer septa. *H. wildei* is closest to *H. woodi* Wilson and Langenheim, 1962, from the Leonardian Arcturus Formation of White Pine County, Nevada, but the latter species has longer and more dilate minor septa in the tabularium, a dissepimentarium composed of a greater number of herringbone dissepiments, and an axial structure that is generally more symmetrical in appearance with a straighter medial plate. *H. washburni* (Merriam, 1942) from the Permian Coyote Butte Formation of Crook County, Oregon, has a greater number of septa, generally less well-developed minor septa, and a generally less symmetrical axial structure. *H. columbicum* (Smith, 1935), from British Columbia has longer minor septa. *H. coogani* has a narrower dissepimentarium.

Etymology. The species is named for Dr. Garner L. Wilde.

Heritschioides (?) *californiense* Meek, 1864

Figures 5:2b; 15d-e; 33b-d; 33c (?)

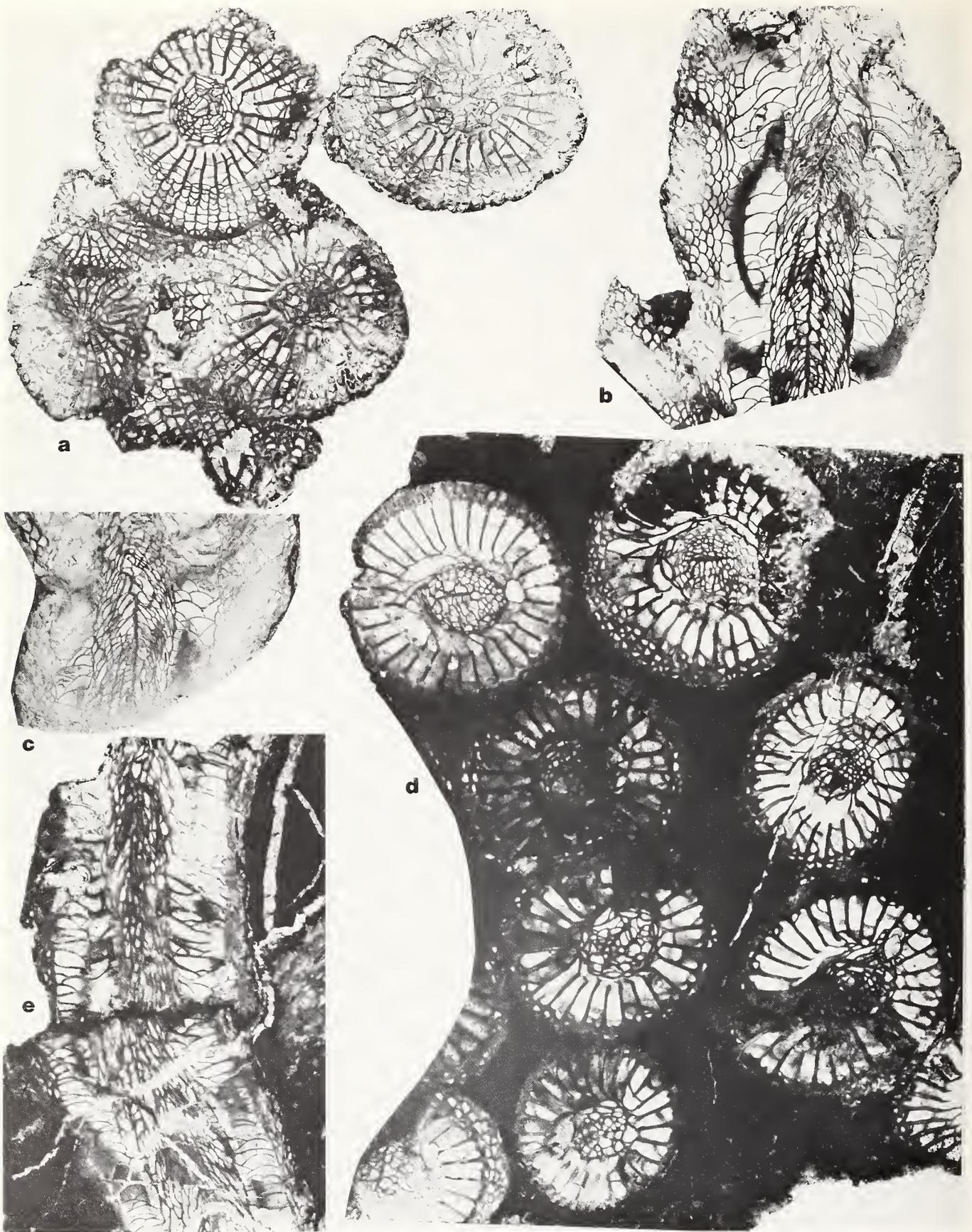
Lithostrotion? *Californiense* Meek, 1864, p. 6, pl. 1, fig. 2b (and (?) 2, 2a, 2c).

External Description. Corallum dendroid (?), maximum observed diameter 22 cm; epitheca apparently smooth except for regularly spaced rugae; calyx deep with walls sloping steeply downwards and inwards to relatively horizontal floor; axial boss prominent, central; septa present in calyx except on axial boss.

Transverse Section Description. Corallites generally circular, diameter 17 to 22 mm, touching or short distances apart; septa of 2 orders, 26 to 34 each, dilate, somewhat thicker in tabularium; major septa 4 to 9 mm long, most somewhat withdrawn from axial structure, few continuous with septal lamellae; minor septa 2 to 4 mm long, extending into tabularium in smaller corallites, confined to dissepimentarium in larger corallites; dissepimentarium regular, as much as 5 mm wide; dissepiments concentric, angulo-concentric, pseudoherringbone, herringbone; false wall stereozone poorly developed; axial structure aulophylloid, very irregular, composed of a loosely arranged group of elements in which the medial plate (if present), septal lamellae, and periaxial tabellae not readily distinguished; corallite wall 0.1 to 0.3 mm wide.

Longitudinal Section Description. Dissepimentarium of 3 to 5 ranks (transverse section shows possible 12) of various size dissepiments (small and cystose to large and highly elongate), steeply dipping; tabellae of 2 rather irregular zones; axial tabellae slope inwards and upwards to septal lamellae (and medial plate?), apparently more steeply inclined in smaller corallites; periaxial tabellae horizontal or sloping gently inwards and upwards (rarely the reverse) to axial tabellae.

Documentation. Three thin sections, one clearly showing a mother and daughter corallite, were prepared and studied from the corallum in the MCZ collection numbered 13. This corallum was figured by Meek (1864, pl. 1, fig. 2b) and is here designated the lectotype. A label glued to the block reading "No. 13



48 **Figure 29.** *Heritschioides wildei* n. sp. All parts x3. **Parts a through c,** UCMP holotype 37208, transverse (a) and longitudinal (b, c) sections. **Parts d and**

Lithostrotion Californiense, Meek” presumably is written in Meek’s hand. A dozen or so other corallites on this block may be the same taxon but were not sectioned.

The type specimens presumably were collected in the McCloud Limestone somewhere south of the Pit River. The absence of *Pseudoschwagerina robusta* in the exposed matrix suggests that they came from higher in the section than the basal 50 feet, where this fusulinid is very abundant. The corals therefore were collected from either fusulinid zones E or F.

Discussion. A transverse section of one corallite in the type corallum suggests the presence of both cardinal and counter open tabular fossulae, but these may be the results of folds in the axial ends of the mesenterics that caused septa to be formed that were doubled back on themselves at the tips. A transverse section of another corallite in the same corallum suggests the presence of an open tabular cardinal fossula. A small transverse section of a single corallite (Fig. 33e) from 210 feet above the base of the Potter Ridge section (UCMP loc. D-836) is very similar in many respects to this species and does have an open tabular fossula and other features questionably like those of *Heritschioides*. I did not collect specimens of this species from the Bayha section (presumably the type area) and, until additional coralla are available, the generic assignment is problematic.

This species is unlike any other nominal species that I have examined.

Genus *Mccloudius* n. gen.

Diagnosis. *Mccloudius* is a phaceloid coral with two orders of septa, a fossula formed by a shortened cardinal septum, a clisiophylloid axial structure, a well-developed regular dissepimentarium that becomes peripherally lonsdaleoid in late ephebic stage, and tabellae of two ranks, both of which slope inwards and upwards.

Type Species. *Mccloudius fluvius* n. sp.

Description. As for the type and only known species.

Discussion. *Mccloudius* somewhat resembles *Lonsdaleia* M’Coy, 1849, but the latter has an almost wholly lonsdaleoid dissepimentarium, no fossula, and is a Lower and Middle Carboniferous genus. *Lonsdaleoides* Heritsch, 1936, was reported originally from the Lower Permian of the Carnic Alps and subsequently from the Upper Pennsylvanian or Lower Permian of Japan and Spain. Its peripheral, sporadically developed series of lonsdaleoid dissepiments is similar to that of *Mccloudius*, but *Lonsdaleoides* has no fossula and its axial structure is much thickened and unlike that of *Mccloudius*. The lonsdaleoid dissepimentarium of *Mccloudius* distinguishes it from *Heritschioides* Yabe, 1950, which has a regular dissepimentarium. Other genera are not closely comparable to *Mccloudius*.

Etymology. The genus is named for the McCloud River.

Mccloudius fluvius n. sp.

Figures 30a–f

Diagnosis. Because the genus *Mccloudius* is erected as mono-

typic, the diagnoses of the genus and of the type species are identical.

External Description. Corallum phaceloid; size, corallite spacing, epitheca, calyx not observed.

Transverse Section Description. Corallites circular to subcircular, diameters 13 to 20 mm, not closely spaced, some touching, others as much as 10 mm apart; septa of 2 orders, 25 to 33 each, straight to slightly sinuous, generally thin in dissepimentarium (about 0.7 mm wide), dilate in tabularium (about 0.3 at base) becoming attenuate axially; major septa generally withdrawn from axial structure (few touching), 4 to 6 mm long, except shortened cardinal septum 3 to 3.5 mm long, extending into tabularium 3 to 4 mm; minor septa well developed in most corallites, poorly in some, generally entering tabularium as spines 0.5 to 1.0 mm long, where present in dissepimentarium, total lengths are 1.5 to 3 mm; fossula small, open, formed by shortened cardinal septum, possible depressed tabellae; dissepimentarium variable with ontogeny: (1) regular in most corallites with diameters less than 14 to 16 mm, dissepiments herringbone, pseudo-herringbone, straight, concentric, angulo-concentric, (2) lonsdaleoid peripherally in corallites with diameters from about 15 to 20 mm, width 1.5 to 3.8 mm, not lonsdaleoid at thinnest widths, peripheral 2 to 3 mm lonsdaleoid at 2.5- to 3.8-mm widths, axial 0.2 to 1.2 mm regular; lonsdaleoid dissepiments axially convex, variable sized, 2 to 6 rows, not naotic; stercozone separating tabularium from dissepimentarium in larger, some smaller, corallites; axial structure clisiophylloid, variable, subcircular, diameter 2 to 6.5 mm, complex, symmetrical to asymmetrical; medial plate 1 to 3 mm long, straight to sinuous, combined with 5 to 12 septal lamellae (some spines in larger corallites), numerous tabellae; corallite wall 0.2 to 0.4 mm thick, with pronounced V-shaped insertions for septal bases except where lonsdaleoid.

Longitudinal Section Description. Dissepimentarium of 1 to 10 rows (5 to 10 in larger corallites) steeply dipping ranks of dissepiments varying in shape from small and cystose to large and elongate; tabellae of 2 zones, axial and periaxial; axial tabellae elongate, dipping inwards and upwards to medial plate, 4 to 5 ranks; periaxial tabellae various developed, 10 to 15 per cm, 1 to 3 ranks sloping inwards and upwards to axial tabellae.

Documentation. LACMIP holotype 6414, LACMIP paratype 6415, UCMP paratype 37209. Eight thin sections and 39 polished sections from three coralla from LACMIP locality 1114 (holotype 6414, paratype 6415) and UCMP locality D-836 (paratype 37209) were studied.

Discussion. The lower beds of the McCloud Limestone on Potter Ridge have abundant fasciculate corals, but they generally are highly metamorphosed by the massive intrusion at the base, which also intrudes the lower beds in many places. It was not possible to determine if *Mccloudius fluvius* is present in the beds below the type locality. Unfortunately also, even though the corallites clearly branch, it was not possible to determine the precise size or nature of the coralla because many of them were broken before burial. However, they clearly are fasciculate.

There is no other species known to me with which this coral can be compared.

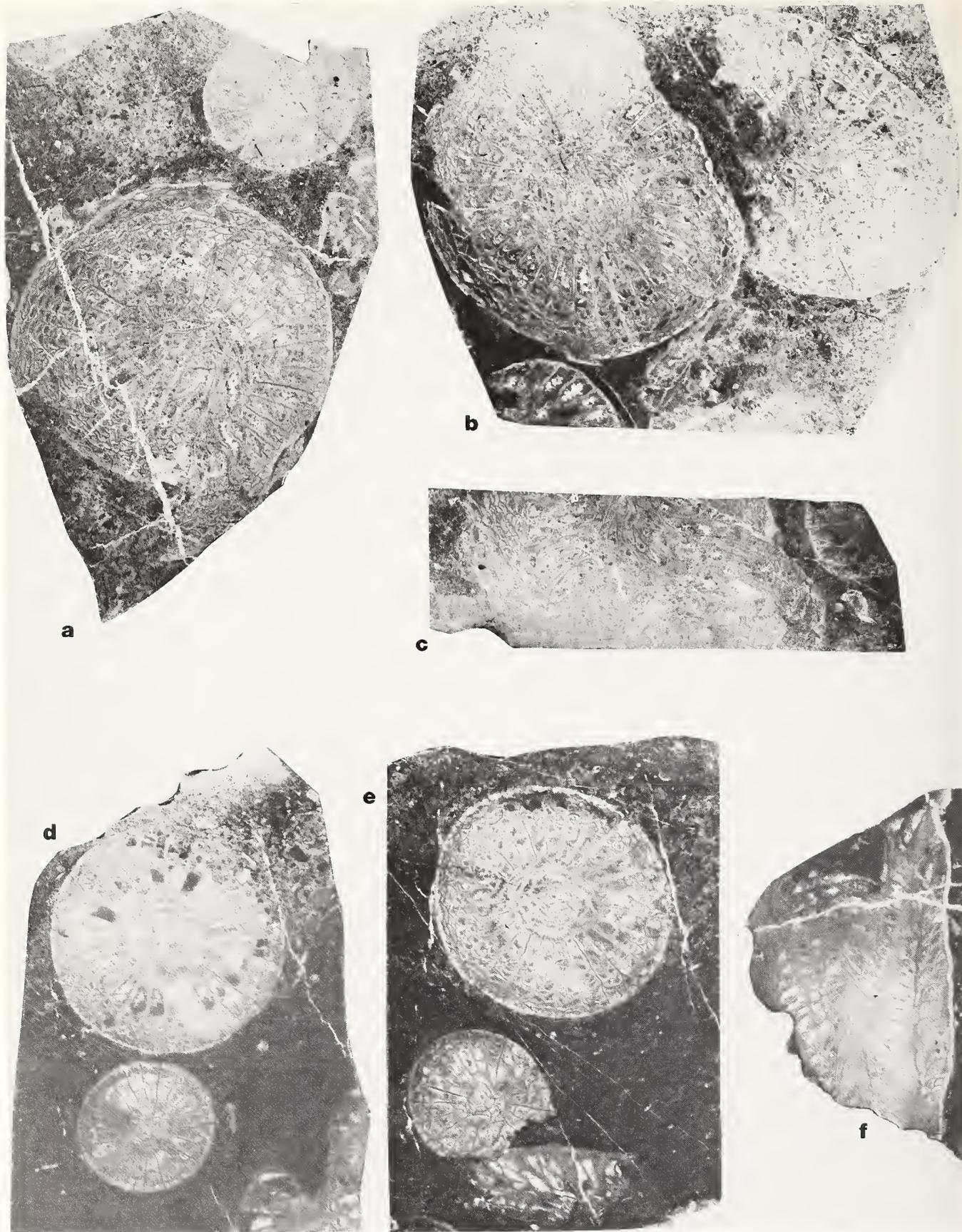


Figure 30. *Mccloudius fluvius* n. gen., n. sp. All parts x3. **Parts a through c**, LACMIP holotype 6414, transverse (a, b) and longitudinal (c) sections. **Parts d and e**, LACMIP paratype 6415, serial transverse sections. **Part f**, UCMP paratype 37209, longitudinal section.

Etymology. *Fluvius*, the species name, is Latin and means river.

Genus *Siphonodendron* M'Coy, 1849

Siphonodendron hongii n. sp.

Figures 31a–b

Diagnosis. A species of *Siphonodendron* characterized by the combination of large corallites, relatively few major septa, very rare dissepiments, and a columella attached to one septum. It has larger corallites, fewer major septa, far fewer dissepiments, and a columella attached to fewer septa than *S. pauciradialis*.

External Description. Corallum phaceloid, external shape not observed, maximum fragmentary diameter 4.5 cm; corallites cylindrical to subcylindrical, parallel, touching to as much as 4 mm apart, many elongated laterally to remain in contact with neighboring corallite; calyx, epitheca not observed.

Transverse Section Description. Corallites circular to subcircular, 5.5 to 7 mm wide, touching to 4 mm apart (generally closer), some attached to nearby corallites by extensions of wall about 5 mm long, 7 mm wide (no internal connections between corallites); septa of 2 orders, 14 to 17 each, straight to somewhat curved, thin; major septa 1 to 2 mm long, thin, withdrawn from columella except 1 (counter?) attached; minor septa rudimentary spines, 0.2 to 0.5 mm long; dissepimentarium absent or present as 1 row; axial structure a columella, simple, elongate, from 0.8 mm long by 0.3 mm wide to 1.1 mm long by 0.6 mm wide, attached to 1 septum (counter); corallite wall 0.1 to 0.3 mm wide.

Longitudinal Section Description. Columella central; tabulae flat, gently sagging, or gently inflated, inclined inwards and upwards to columella, outer ends straight, rarely slightly downturned, 19 per cm; tabellae absent.

Documentation. UCMP holotype 37210. Two thin sections and 27 polished sections from one corallum from UCMP locality B-4837 were studied.

Discussion. *Lithodendron pauciradialis* M'Coy, 1844, the type species for *Siphonodendron*, from the Lower Carboniferous (Mississippian) of Ireland (the type locality), also has been reported from England, Scotland, Russia, and China (Hill, 1940:170). Hill (1940:165) synonymized *Siphonodendron* with *Lithostrotion* Fleming, 1828, which has a cerioid type species. I prefer to use *Siphonodendron* rather than to call this species a "fasciculate *Lithostrotion*."

The type species of *Siphonodendron* has corallites 4 to 5.5 mm in diameter, 18 to 22 major septa, a dissepimentarium, and a columella attached generally to both the counter and cardinal septa. These features clearly distinguish it from *S. hongii*. *S. pauciradialis* and *S. hongii* are, however, remarkably similar at the generic level, both having the lateral attachments of some corallites to others seen in cross section. Unfortunately, the holotype of *S. hongii* occurred in rock near an intrusion and is highly silicified, with well-developed quartz crystals in some vuggy places, so that features of all the corallites are not preserved.

I know of no other Permian species with which *S. hongii* can be

compared. This single corallum appears to be the first record of *Siphonodendron* in the Permian.

Etymology. The species is named for Mr. Chang Ki Hong.

Genus *Yatsengia* Huang, 1932

Yatsengia fletcheri n. sp.

Figures 31c–d

Diagnosis. A species of *Yatsengia* characterized by the combination of large corallites, a large number of septa, and a relatively broad and continuous dissepimentarium. It has larger corallites and more major septa than *Y. kenneyi* n. sp. It has larger corallites and a broader, more continuous dissepimentarium than *Y. scheetzi* n. sp. It has larger corallites and more septa than species of the genus described from Asia.

External Description. Corallum phaceloid, maximum observed diameter 5 cm; corallites subparallel, closely spaced; epitheca and calyx not observed.

Transverse Section Description. Corallites circular to subcircular, diameter 12 to 15 mm, closely spaced, touching to as much as 3 mm apart; septa of 2 orders, 24 to 27 each, thin in dissepimentarium, dilate in tabularium; major septa confluent with septal lamellae, 4.5 to 5.5 mm long, about 0.5 mm wide at periphery of tabularium; minor septa short, 0.7 to 1.5 mm long, confined to dissepimentarium except axial ends dilate and join laterally with major septa to form false wall; dissepimentarium regular, lacking in parts of some corallites; dissepiments straight, concentric, angulo-concentric, pseudoherringbone; axial structure aulophylloid, large; septal lamellae sinuous, confluent with major septa, generally thin, rarely dilate, number equal to or fewer than number of major septa; false wall stereozone as much as 1 mm wide, formed of dilate axial ends of minor septa and dilate peripheral ends of major septa in tabularium, with ends of minor septa either exposed axially to tabularium or covered by extensions of major septa; corallite wall about 0.1 mm wide, with bases of major and minor septa fitted into V-shaped grooves; microstructure of septa fibrous, with fibers at right angles to straight or somewhat sinuous central line.

Longitudinal Section Description. Dissepimentarium of 1 to 3 ranks of steeply dipping, various sized, noninflated dissepiments; tabellae in 2 zones; axial tabellae of 1 to 3 ranks, elongate, steeply inclined inwards and upwards to septal lamella (?) or medial plate (?); periaxial tabellae in 1 to 3 ranks, gently inclined inwards and upwards to axial tabellae; calyx about 8 mm deep, with narrow pointed axial boss about 5 mm high.

Documentation. UCMP holotype 37211. Two thin sections and 13 polished sections from one corallum from UCMP locality D-858 were studied.

Discussion. This species and the following two are referred to *Yatsengia* on the basis of comparisons with the figures and description of the type species, *Y. asiatica* (Huang, 1932:56, pl. 5, fig. 1) and other discussions and figures of this and other species by Yoh (in Yoh and Huang, 1932:32, pl. 9, figs. 3a–3c), Minato

(1955: 117–120, pl. 18, figs. 7–10; pl. 29, figs. 1–4; pl. 37, fig. 10; pl. 41, fig. 3; pl. 43, fig. 3; text-figs. 9A–9M), and Fontaine (1961: 138–143, pl. 8, figs. 3, 4; pl. 9, fig. 4–6; pl. 10, figs. 1, 2; pl. 32, figs. 3–5; pl. 33, figs. 3, 4). These authors erected species from China (the type locality), Japan, and Cambodia. Fontaine (1961:140) also considered the genus to be present in Iran and Turkey. All occurrences seem to be in Permian rocks, ranging from Lower to Upper.

Yatsengia has not heretofore been recorded from North America. My reference of three McCloud Limestone species to it is based on their similarity to the Asiatic species in having axial structures with most septa joined to septal lamellae, apparent lack of medial plates in most axial structures, narrowness or impersistency of the dissepimentaria, shortness of the minor septa, general presence of an excentric false wall, and lack of fossulae or shortened cardinal septa.

It has not been possible to compare the microstructure closely.

Y. fletcheri has a larger corallite diameter (12 to 15 mm) than the Asiatic species of *Yatsengia* (4 to 8.7 mm) and has more septa than any of them (24 to 27 compared with 13 to 20). The differences with *Y. kenneyi* n. sp. are discussed under that species, which is apparently lower in the section although still Wolfcampian. *Y. sheetzii* n. sp., also from the McCloud Limestone, is apparently higher in the section, although also still Wolfcampian, and has smaller corallite diameters (7 to 11 mm) and a much less continuous dissepimentarium than *Y. fletcheri*.

Etymology. The species is named for Mr. William Fletcher.

Yatsengia kenneyi n. sp.

Figures 31e; 32a–b

Diagnosis. A species of *Yatsengia* characterized by the combination of relatively small corallites, a relatively small number of major septa, and a relatively continuous dissepimentarium. It has smaller corallites and more major septa than *Y. fletcheri*. It has somewhat smaller corallites, somewhat fewer septa, and a more continuous dissepimentarium than *Y. sheetzii* n. sp. It has larger corallites and more septa than species of the genus described from Asia.

External Description. Corallum phaceloid, maximum observed diameter 10 cm; corallites generally parallel, closely spaced; epitheca rather smooth with widely spaced rugae; calyx not observed.

Transverse Section Description. Corallites circular to subcircular, diameter 7.5 to 9.5 mm, closely spaced, touching to as much as 8 mm apart; septa of 2 orders, 17 to 20 each, thin in dissepimentarium, slightly dilate in tabularium; major septa 2.0 to 2.5 mm long, generally confluent with septal lamellae; minor septa short, 0.5 to 0.7 mm long, generally confined to dissepimentarium, rarely extending slightly into tabularium as short nubs, axial ends coalescing with lateral extensions of major septa at dissepimentarium-tabularium interface to form prominent false wall stereozone where dissepimentarium present; dissepimentarium regular, absent in parts of some corallites; dissepiments anguloconcentric, concentric, pseudoherringbone, straight; axial structure apparently aulophylloid, large, with irregular septal lamellae generally connected with major septa (if true medial

plate is present, it is too sinuous to be discernible); false wall stereozone as much as 0.7 mm wide, formed of expanded axial ends of minor septa and bases of major septa in tabularium; corallite wall about 0.3 mm wide, with bases of major and minor septa fitted into V-shaped grooves; microstructure of septa fibrous, with fibers at right angles to straight or slightly sinuous central line.

Longitudinal Section Description. Dissepimentarium of 1 to 3 ranks of steeply dipping, various sized, noninflated dissepiments (transverse sections show that it is not present in parts of some corallites, but this not observed in longitudinal sections available); tabellae of 2 zones, boundary irregular in places; axial tabellae of 1 to 2 ranks, various sizes, steeply inclined inwards and upwards to 1 or more thin septal lamellae (medial plate?); periaxial tabellae large or small, in 1 to 3 ranks, inclined inwards and upwards to axial tabellae.

Documentation. UCMP holotype 37212. Three thin sections and 36 polished sections from one corallum from UCMP locality D-805 were studied.

Discussion. *Y. kenneyi* differs from the type and other Asiatic species in its generally greater corallite diameters (7.5 to 9.5 mm compared to 4 to 8.7 mm), generally greater number of septa (17 to 20 major septa compared to 13 to 20), and other characters. It may be distinguished from the two other new species from the McCloud Limestone by its smaller corallite diameters (7.5 to 9.5 mm compared to 12 to 15 mm for *Y. fletcheri* and 7 to 11 mm for *Y. sheetzii*) and fewer number of major septa (17 to 20 compared to 24 to 27 for *Y. fletcheri* and 18 to 26 for *Y. sheetzii*). The dissepimentarium is more discontinuous in *Y. sheetzii* than in *Y. kenneyi*.

Etymology. The species is named for Mr. Paul Kenney.

Yatsengia sheetzii n. sp.

Figures 32c–g; 33a

Diagnosis. A species of *Yatsengia* characterized by the combination of moderately large corallites, a large number of major septa, and a very discontinuous dissepimentarium. It has larger corallites, more major septa, and a less continuous dissepimentarium than *Y. kenneyi*. It has smaller corallites and a less continuous dissepimentarium than *Y. fletcheri*. It has larger corallites and more septa than species of the genus described from Asia.

External Description. Corallum phaceloid, maximum observed diameter 10 cm; corallites subparallel to parallel, closely spaced; calyx and epitheca not observed.

Transverse Section Description. Corallites circular to subcircular, diameter 7 to 11 mm, closely spaced, touching to 3 mm apart; septa of 2 orders, 18 to 26 each, lanceolate throughout; major septa 2.5 to 3.5 mm long, about 0.5 mm wide at base where lanceolate, many confluent with septal lamellae in largest corallites, cardinal and/or counter septa only touch axial structure in smaller corallites; minor septa 0.5 to 0.8 mm long, width where lanceolate as in major septa; dissepimentarium very discontinuous, present only in parts of some corallites; dissepiments straight or pseudoherringbone; axial structure generally aulophylloid, some clisiophylloid or dibunophylloid; medial plate where present thin to slightly dilate, straight to very sinuous;

septal lamellae number 1 to 10, straight to very sinuous, attached to major septa in some large corallites, generally not in smaller corallites; false wall stereozone thin or not present due to discontinuity of dissepimentarium; corallite wall denticulate, with septa set in V-shaped grooves; microstructure of septa fibrous, with fibers at right angles to straight or somewhat sinuous central line.

Longitudinal Section Description. Dissepimentarium discontinuous, may be absent for as much as 1 cm; where present, of 1 to 2 ranks of small, steeply dipping dissepiments, numbering about 6 in 0.5 cm; tabellae of 2 zones; axial tabellae of 1 to 2 ranks, steeply to gently inclined inwards and upwards to medial plate (where present); periaxial tabellae of 2 to 3 ranks, more gently inclined inwards and upwards to axial tabellae, various sizes; corallite wall as much as 0.7 mm wide.

Documentation. UCMP holotype 37213, UCMP paratypes 37214–37218, LACMIP paratype 6416. Seven thin sections and numerous polished sections from seven coralla from UCMP localities D-834 (paratype 37218), D-836 (holotype 37213, paratypes 37214, 37216), and D-838 (paratypes 37215, 37217) and LACMIP locality 1114 (paratype 6416) were studied.

Discussion. The nature of the axial structure in this species, which ranges from aulophylloid through elisiophylloid and dibunophylloid, is troublesome, but all types are present in some coralla and therefore demonstrate that the variation is natural. Two figures of the holotype of *Yatsengia asiatica* Huang, 1932 (pl. 5, figs. 1a, 1b), seemingly show a similar variation.

Y. scheetzi is larger than the Asiatic species and has a greater number of septa. It has somewhat larger corallites than *Y. kenneyi* (7 to 11 mm compared to 7.5 to 9.5 mm) and has more septa (18 to 26 major septa compared to 17 to 20). It has smaller corallites than *Y. fletcheri*, which ranges from 12 to 15 mm in diameter, and has generally fewer septa (*Y. fletcheri* has 24 to 27). The dissepimentarium of *Y. scheetzi* is more discontinuous and narrower than those of the other two species of *Yatsengia* from the McCloud Limestone.

Etymology. The species is named for Mr. James Scheetz.

Ceriod Rugosa

Genus *Bassius* n. gen.

Diagnosis. *Bassius* is a ceriod rugose coral with two orders of septa, elisiophylloid axial structure, wide lonsdaleoid dissepimentarium, thin wall, tabellae of two ranks—axial and periaxial, the former generally clustered dissepiment-like around the columella, the latter generally flat, domed, or slightly sagging, horizontal or sloping inwards and upwards, rarely sloping inwards and downwards.

Type Species. *Bassius mccloudensis* n. sp.

Description. As for the type and only species firmly referred to the genus.

Discussion. *Kleopatrina* (*Porfrievela*) is similar in some characters to *Bassius*, but the latter has a wide and more consistently developed lonsdaleoid dissepimentarium and a much thinner corallite wall. The separation of *Kleopatrina* into two subgenera is largely a subjective matter based on the presence of more or fewer septa that cross the dissepimentarium to the corallite wall.

Even the most lonsdaleoid species of *Kleopatrina*, such as *K. (Porfrievela) arcturusensis* Stevens, 1967, from the Lower Permian of eastern Nevada, have “. . . in large corallites generally less than one-half of the major septa extend to the theca” (Stevens, 1967:427).

Ipciphyllum Hudson, 1958, shares some characters with *Bassius*, but the former is not lonsdaleoid. *Wentzellophyllum* Hudson, 1958, is cerioid, elisiophylloid, and lonsdaleoid, but it has tertiary septa, which *Bassius* lacks. *Wentzelella* Grabau in Huang, 1932, has both tertiary septa and a mostly regular dissepimentarium, unlike *Bassius*, which has neither. *Ipciphyllum*, *Wentzellophyllum*, and *Wentzelella* are Permian and from the classic Tethys area. Only the former genus has been reported in North America (*Ipciphyllum tschernyschewi* Minato, 1960, from the Arctic Islands of the Northwest Territories, Canada).

Lonsdaleia McCoy, 1849, is a Mississippian coral, the type species of which is fasciculate, although Hill (1956:306) would include cerioid coralla in it as well. I consider fasciculate and cerioid coralla to be generic characters and on this basis alone differentiate *Lonsdaleia* from *Bassius*, but in addition they are dissimilar in many other ways. *Lonsdaleia* is restricted to the Carboniferous by most paleontologists.

Hudson (1958:182) referred a specimen from the Permian of northern Iraq to '*Lonsdaleia*' *chaoi* Huang var. The species of Huang (in Yoh and Huang, 1932:35), from the Permian of China, has an aulophylloid axial structure, and the specimens of Hudson are elisiophylloid (Hudson, 1958:183), which are generic differences. Minato and Kato (1965a:211) referred Huang's species to *Wentzellophyllum* and noted that it has tertiary septa. Both these species were reported by Hudson (1958) and Minato and Kato (1965b) to have "clinotabulae" (clinotabellae), a name proposed by Hudson (1958:177) for periaxial tabellae that slope downwards and inwards to the axial tabellae and form a deep groove around the axial boss, as shown in Hudson's (1958, pl. 33, figs. 4a, 4b) reference to his figure of *Waagenophyllum indicum* (Waagen and Wentzel, 1886) as having examples of these structures. Occasional tabellae sloping downwards and inwards in a coral in which they generally slope upwards and inwards do not form the deep groove of *Waagenophyllum* Hayasaka, 1925, and, in my opinion, should not be considered clinotabellae or heavily weighed systematically. I think that the specimens referred to by Hudson (1958:182) as '*Lonsdaleia*' *chaoi* Huang var. do not have clinotabellae, since his figures (Hudson, 1958, pl. 32, fig. 1 and text-figs. 3c–3d) show no such groove.

Minato and Kato (1965a:211) erected *Wentzellophyllum* (?) *gelikhanense* for the '*Lonsdaleia*' *chaoi* Huang var. of Hudson from Iraq and described tertiary septa "locally found along walls as mere short septal ridges." I see no certain evidence of tertiary septa in Hudson's (1958, pl. 32, fig. 2) best transverse section of the holotype. If tertiary septa are lacking, then perhaps *W* (?) *gelikhanense* should be referred to *Bassius*. The thin sections of the holotype should be examined.

Minato and Kato (1965a:213) named *Wentzellophyllum* (?) *tabasense* for a coral from the Permian of Iran. They noted (Minato and Kato, 1965a:215) that it “. . . lacks any trace of the tertiary septa . . . typical to the genus *Wentzellophyllum*.” Their figures (Minato and Kato, 1965a, pl. 20) show transverse and

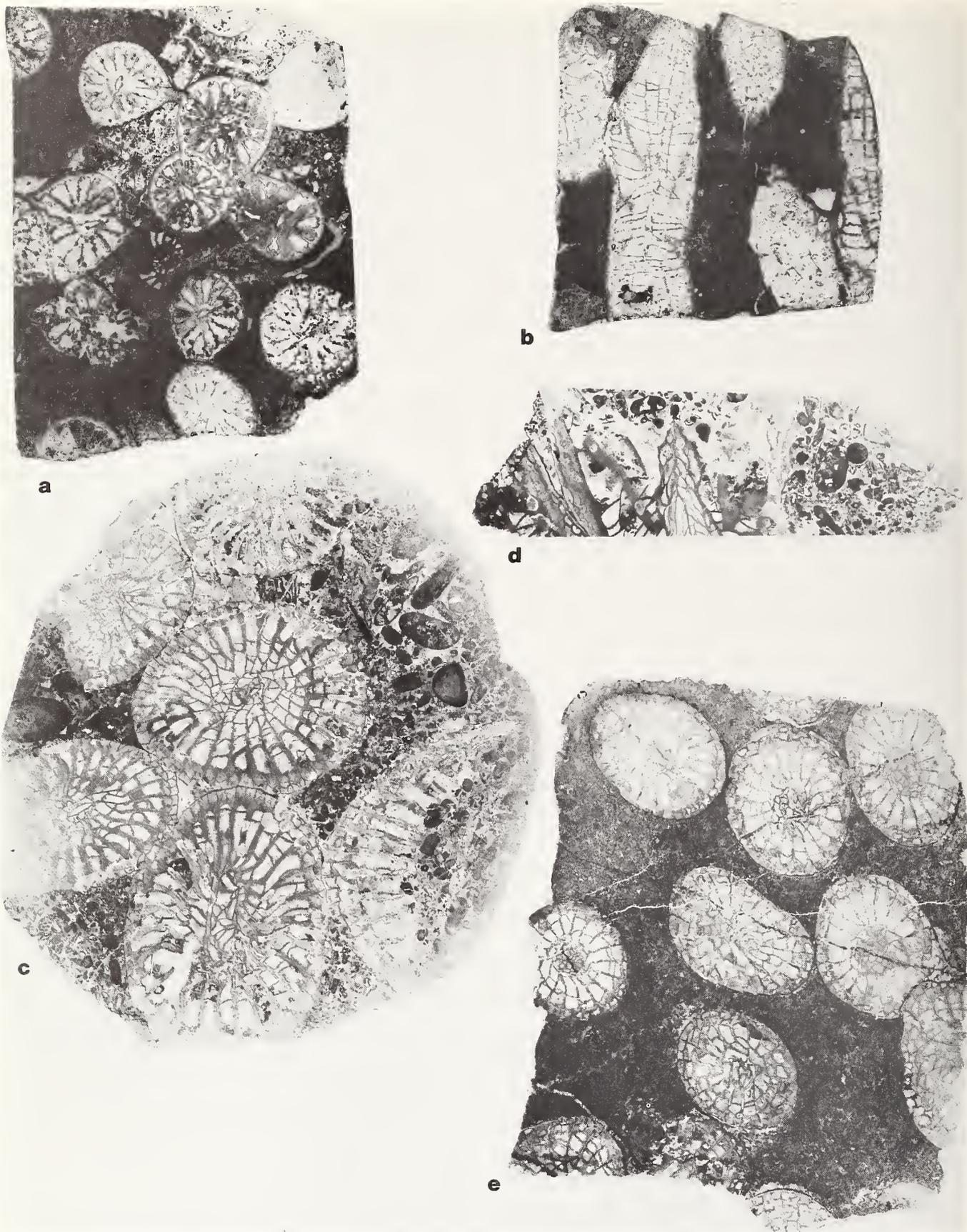


Figure 31. *Siphonodendron hongii* n. sp., *Yatsengia fletcheri* n. sp., and *Y kenneyi* n. sp. All parts x3.

- 54 Parts a and b. *S. hongii* n. sp., UCMP holotype 37210, transverse section (a; note *Pseudoschwagerina* at center) and longitudinal section (b).
 Parts c and d. *Y. fletcheri* n. sp., UCMP holotype 37211, transverse (c) and longitudinal (d) sections.
 Part e. *Y. kenneyi* n. sp., UCMP holotype 37212, transverse section.

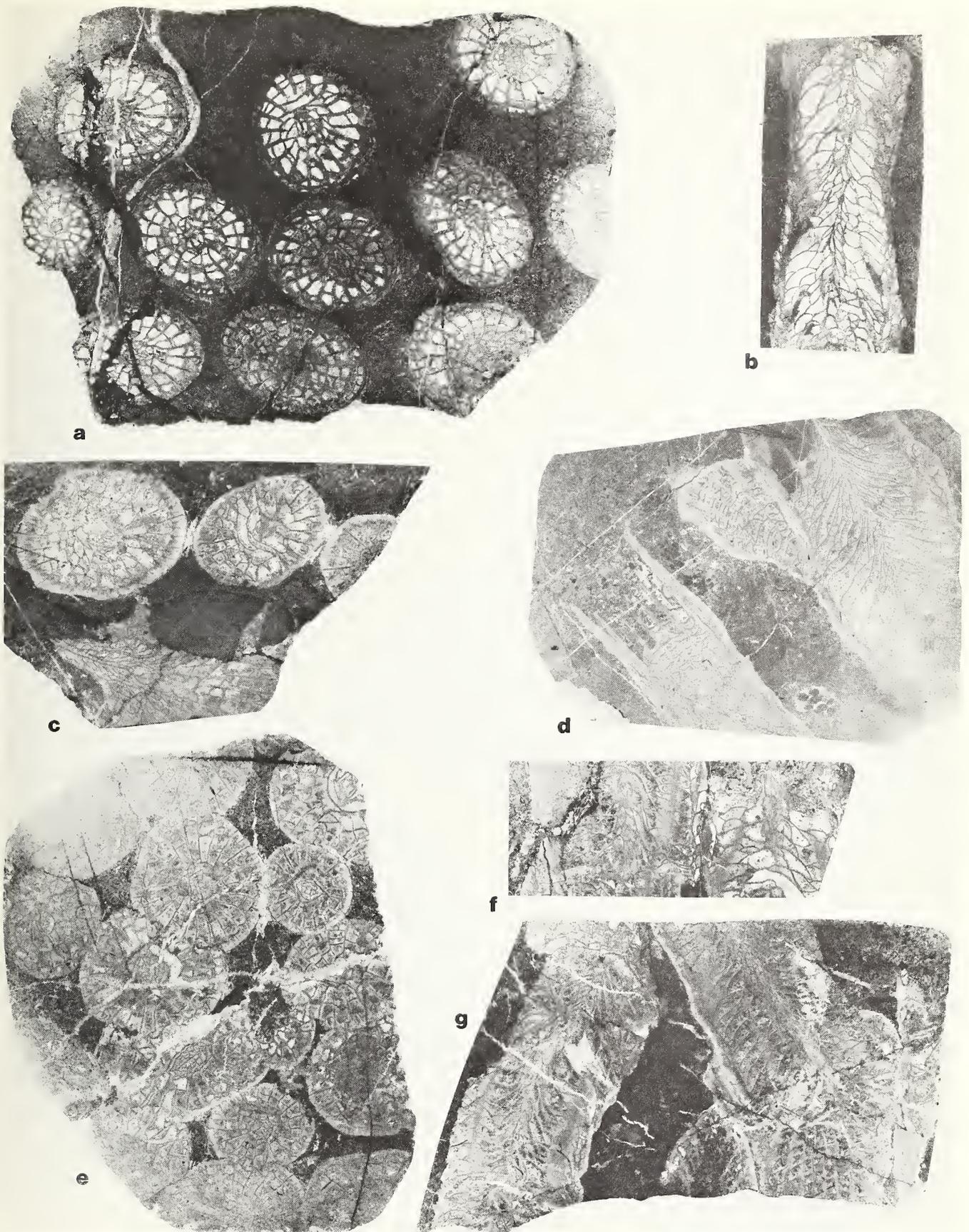


Figure 32. *Yatsengia kenneyi* n. sp. and *Y. scheetzi* n. sp. All parts x3.
 Parts a and b. *Y. kenneyi* n. sp., UCMP holotype 37212, transverse (a) and longitudinal (b) sections.
 Parts c through g. *Y. scheetzi* n. sp. Parts c and d, UCMP holotype 37213, transverse (c) and longitudinal (d) sections. Parts e through g, UCMP paratype 37214, transverse (e) and longitudinal (f, g) sections.



longitudinal sections with characters similar to *Bassius*. The longitudinal sections lack what I consider to be clinotabellae, although Minato and Kato considered them to be present. This holotype also should be examined for possible inclusion in *Bassius*.

If the two species from Iraq and Iran should prove to be referable to *Bassius*, then this would be a rare instance of true *Tethys* massive corals occurring both there and in North America.

Etymology. The genus is named for Mr. John S.P. Bass.

Bassius mccloudensis n. sp.

Figures 34a–c

Diagnosis. Because the genus *Bassius* is erected as monotypic, the diagnoses of the genus and of the type species are identical.

External Description. Corallum cerioid, hemispheroidal, maximum observed diameter 4.5 cm; calyx not observed.

Transverse Section Description. Corallites polygonal, 5 to 7 sided, 11 to 17 mm wide at greatest diameter; septa of 2 orders; major septa 19 to 25 each, 1.5 to 3 mm long, extending into dissepimentarium 0.5 to 1.0 mm, thin in dissepimentarium (where present), represented in places by septal spines on dissepiments, slightly dilate in tabularium, withdrawn from axial structure; minor septa commonly absent in adult corallites or represented by a few septal spines in outer ranks of dissepiments and on wall, absent in tabularium; axial structure elisiophylloid, oval, 2 to 3 mm long, with well-defined axial plate having 5 to 6 short septal lamellae opposite each other on each side, connected by axial tabellae; dissepimentarium highly lonsdaleoid, 3 to 4 mm wide; dissepiments highly lonsdaleoid in peripheral ranks, concave axially, variously sized, with some axial spines, concentric, angulo-concentric, or pseudoherringbone near axial part where major septa present; corallite wall thin and smooth or slightly denticulate, entire, 0.1 to 0.2 mm wide.

Longitudinal Section Description. Dissepimentarium of 2 to 5 ranks of small cystose or larger elongate dissepiments, steeply dipping, about 20 per cm; tabellae of 2 series, axial and periaxial; axial tabellae clustered about columella dissepiment-like or sloping steeply inwards and upwards, 1 to 3 ranks each side; periaxial tabellae flat, domed, or slightly sagging, generally sloping inwards and upwards to axial tabellae, rarely sloping inwards and downwards, about 20 per cm.

Documentation. UCMP holotype 37219. Three thin sections and 19 polished sections from one corallum from UCMP locality D-181 were studied.

Discussion. The only two species known to me with which this species might be compared are from the Permian of Iran and Iraq and have been discussed above under "Remarks" for the genus. It is uncertain if they may be referred to *Bassius*, but if

they should be, then the most obvious difference would be that *B. mccloudensis* has no minor septa in the tabularium whereas both of the other species have well-developed minor septa there.

Etymology. The species is named for the McCloud River.

Genus *Dillerium* n. gen.

Diagnosis. *Dillerium* is a cerioid coral with two orders of septa, a styliiform columella, a regular dissepimentarium, and tabulae that slope inwards and upwards.

Type Species. *Dillerium potterensis* n. sp.

Description. As for the type species since the genus is described as monotypic.

Discussion. *Dillerium* may be distinguished readily from *Kleopatrina* McCutcheon and Wilson, 1963, by the former's greatly thickened columella and possession of tabulae, whereas the latter has a medial plate, variously abutted by septal lamellae, and two well-defined zones of tabellae. It can be differentiated from other somewhat similar appearing cerioid corals by the lack of three orders of septa, the lack of two or three zones of tabellae (no clinotabellae), the lack of a fossula, the lack of an elisiophylloid, aulophylloid, or dibunophylloid axial structure, the lack of an incomplete wall, and the possession, as described in the diagnosis, of complete walls, two orders of septa, a styliiform columella, a regular dissepimentarium, and tabulae.

Etymology. The genus is named for Mr. Joseph S. Diller.

Dillerium potterensis n. sp.

Figures 35a–c

Diagnosis. Because the genus *Dillerium* is erected as monotypic, the diagnoses of the genus and of the type species are identical.

External Description. Corallum cerioid and hemispheroidal; maximum observed diameter 5.5 cm; other external features not preserved.

Transverse Section Description. Corallites 4 to 7 sided, 14 to 16 mm wide at greatest diameter; septa of 2 orders, 13 to 17 each, straight to somewhat sinuous; major septa generally withdrawn from axial structure, 0.5 to 1.5 mm long, generally dilate in tabularium (to 0.15 mm thick), thin in dissepimentarium; minor septa 0.3 to 0.5 mm long, confined to dissepimentarium or extending into tabularium as short spines, thin throughout; dissepimentarium regular, narrow, 0.5 mm wide or less; dissepiments concentric, angulo-concentric, straight, herringbone (rare), or pseudoherringbone (rare); axial structure a highly dilate columella (styliiform), round, oval, lenticular in shape, measuring 1.0 by 1.0 mm, 1.0 by 1.5 mm, to 0.5 by 1.5 mm, with dark line in center representing axial plate and, in some, 1 to 3 short dark

Figure 33. *Yatsengia scheetzi* n. sp. and *Heritschioides* (?) *californiense* (Meek, 1864). All parts x3.

Part a. *Y. scheetzi* n. sp., LACMIP paratype 6416, transverse section.

Parts b through d. *H. (?) californiense*, MCZ lectotype, MCZ Meek collection block no. 13, transverse and longitudinal sections (b), transverse section (c), and longitudinal section (d).

Part e. (?) *H. californiense*, UCMP hypotype 37350, transverse section.



58 Figure 34. *Bassius mcclouidensis* n. gen., n. sp., UCMP holotype 37219, transverse (a, b) and longitudinal (c) sections. All parts x3.

lines representing axial lamellae, not connected to septa; corallite wall 0.15 to 0.3 mm wide, with dark line in center, V-shaped depressions for septal bases.

Longitudinal Section Description. Dissepimentarium of 1 to 2 steeply dipping ranks of small cystose dissepiments; tabulae slope steeply inwards and upwards to columella, generally about 20 per cm.

Documentation. UCMP holotype 37220. Two thin sections and 17 polished sections from one corallum from UCMP locality D-843 were studied.

Discussion. Although the preservation of the corallum on which this new genus and species are based is not very good (somewhat metamorphosed, somewhat crushed), the characters clearly can be made out with some patience. *Dillerium potterensis* is not close to any other species that I have seen, and the genus is erected as monotypic.

Etymology. The species is named after Potter Ridge.

Genus *Kleopatrina* McCutcheon and Wilson, 1963

Subgenus *Kleopatrina* McCutcheon and Wilson, 1963

Kleopatrina (Kleopatrina) raubae n. sp.

Figures 35d–c

Diagnosis. A species of *Kleopatrina (Kleopatrina)* characterized by the combination of large corallites, abundant septa, a complex axial structure, and thin septa in the tabularium. It has larger corallites, more septa, and a more complex axial structure than *K. (K.) ftataeeta* and *K. (K.) wilsoni*. It has larger corallites and/or more septa than all the species of the subgenus described from Russia except *K. (K.) magnifica*. It has a more complex axial structure and septa that are thinner in the tabularium than *K. (K.) magnifica*.

External Description. Corallum cerioid, hemispheroidal, maximum observed diameter 8 cm (probably much greater in uncollected specimens); calyx not observed; corallites parallel.

Transverse Section Description. Corallites 4 to 7 sided, 9 to 14 mm wide at greatest diameter; septa of 2 orders, 16 to 23 each, straight to slightly sinuous, rarely lonsdaleoid; major septa generally withdrawn from axial structure, touching in some corallites, 2.5 to 5.5 mm long, slightly dilate in tabularium or thin throughout; minor septa poorly developed (absent in parts of some corallites), 1.0 to 2.0 mm long, generally confined to outer $\frac{1}{2}$ to $\frac{3}{4}$ of dissepimentarium, but extending into tabularium in places as nubs or spines 0.5 mm long; dissepimentarium generally regular, width 1 to 5 mm, generally about 3 mm; dissepiments concentric, herringbone, pseudoherringbone, or lonsdaleoid (uncommon); axial structure clisiophylloid, circular to subcircular, 1.5 to 2 mm diameter, formed of straight to sinuous, thin or slightly thickened medial plate about 1.5 to 2 mm long with 2 to 8 radiating, straight to sinuous septal lamellae connected by 1 to 2 axial tabellae, generally not touched by axial ends of septa, rarely touched by 1 or more; corallite wall 0.15 to 0.2 mm wide.

Longitudinal Section Description. Dissepimentarium of 4 to 7 steeply to gently dipping ranks of mixed large elongate and large and small cystose dissepiments; tabellae of 2 zones, axial and periax-

ial; periaxial tabellae flat, gently domed, with straight peripheral edges, rarely small and cystose (sloping in and up to periaxial tabellae where axial, sloping in and up to dissepiments where peripheral), 20 to 30 per cm; axial tabellae in 1 to 3 ranks, large to small, elongate (some cystose), steeply sloping inwards and up to medial plate, 20 to 32 per cm.

Documentation. LACMIP holotype 6417, LACMIP paratypes 6418–6419, UCMP paratypes 37221–37222. Eleven thin sections and 64 polished sections from five coralla from UCMP locality D-842 (paratypes 37221–37222) and LACMIP locality 1122 (holotype 6417, paratypes 6418–6419) were studied.

Discussion. *K. (K.) raubae* can be distinguished from the other McCloud Limestone species of *Kleopatrina* described herein by the absence or relative rarity of lonsdaleoid dissepimentaria. The other new species have predominately lonsdaleoid dissepimentaria, which relegate them to the subgenus *Porfirievella* Minato and Kato, 1965b:71, type species *Wentzelella grandis* Dobrolyubova, 1941 (in Soshkina, Dobrolyubova, and Porfiriev, 1941:197, 264, pl. 52, figs. 1a–1b). Minato and Kato (1968:363) suggested later that their name be changed to *Uralnevadaphylum* to avoid confusion with *Porfirievella* Ivanovsky, 1963, which has a one letter difference. ICZN Article 56(a) (International Commission on Zoological Nomenclature, 1964) states that “even if the difference between two genus-group names is due to only one letter, these two names are not to be considered homonyms,” therefore the subgeneric name *Porfirievella* of Minato and Kato cannot be invalidated on the grounds given by them and must stand.

Previously, only two North American species have been referred to the nominal subgenus: the type species, *K. ftataeeta* (McCutcheon and Wilson, 1961), from the Lower Permian of east central Nevada, and *K. wilsoni* Minato and Kato, 1965b, from the Lower Permian of southeast Nevada. Both have smaller corallites, fewer septa, and less complex axial structures than *K. raubae*. Minato and Kato (1965b:69) based *K. wilsoni* on a paratype of *K. ftataeeta* but rejected a longitudinal section (McCutcheon and Wilson, 1961, pl. 123, fig. 5) from the same corallum (their holotype), considering it to belong to *K. ftataeeta*, which illustrates the difficulties of achieving objective systematics when working with variable corals.

K. raubae has greater corallite diameters and/or more abundant septa than the Russian species of *K. (Kleopatrina)*, except for *K. (K.) magnifica* (Porfiriev, 1941, in Soshkina, Dobrolyubova, and Porfiriev:199, 265, pl. 53, figs. 1a–1c; pl. 54, figs. 1a–1b) from the Lower Permian of the Ural Mountains. The latter species, however, has a less complex axial structure and septa that are thickened in the tabularium, which distinguish it from *K. (K.) raubae*.

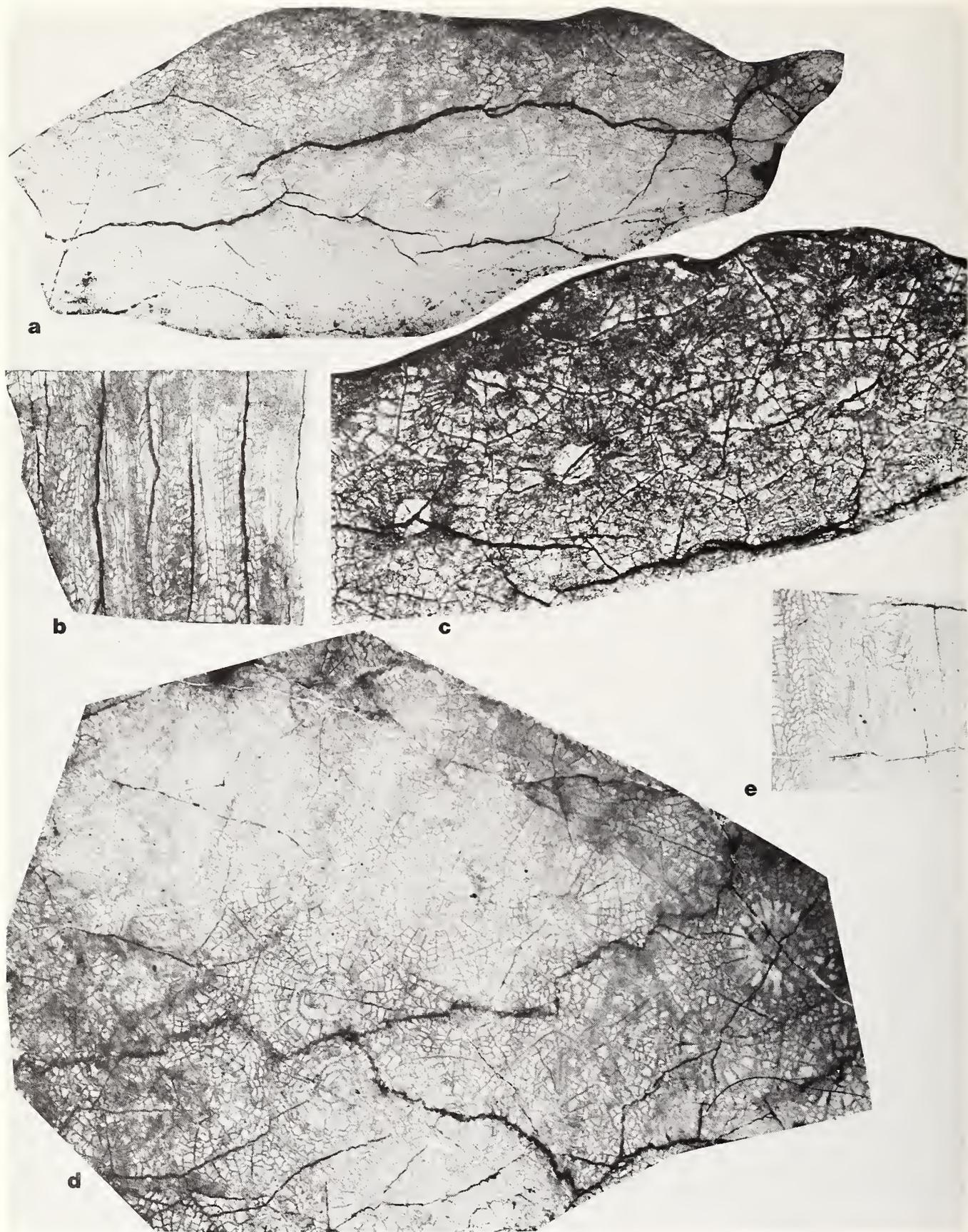
Etymology. The species is named for Mrs. Lenor Raub.

Subgenus *Porfirievella* Minato and Kato, 1965b

Kleopatrina (Porfirievella) mckibbiniae n. sp.

Figures 36c–f

Diagnosis. A species of *Kleopatrina (Porfirievella)* characterized by the combination of a generally simple axial structure



60 **Figure 35.** *Dillerium potterensis* n. gen., n. sp. and *Kleopatrina (Kleopatrina) raubae* n. sp.
Parts a through c. *D. potterensis* n. gen., n. sp., UCMP holotype 37220, transverse section (a, x3), longitudinal section (b, x3), and transverse section (detail of a, x7.5).
Parts d and e. *K. (K.) raubae* n. sp., LACMIP holotype 6417, transverse (d) and longitudinal (e) sections. Both parts x3.

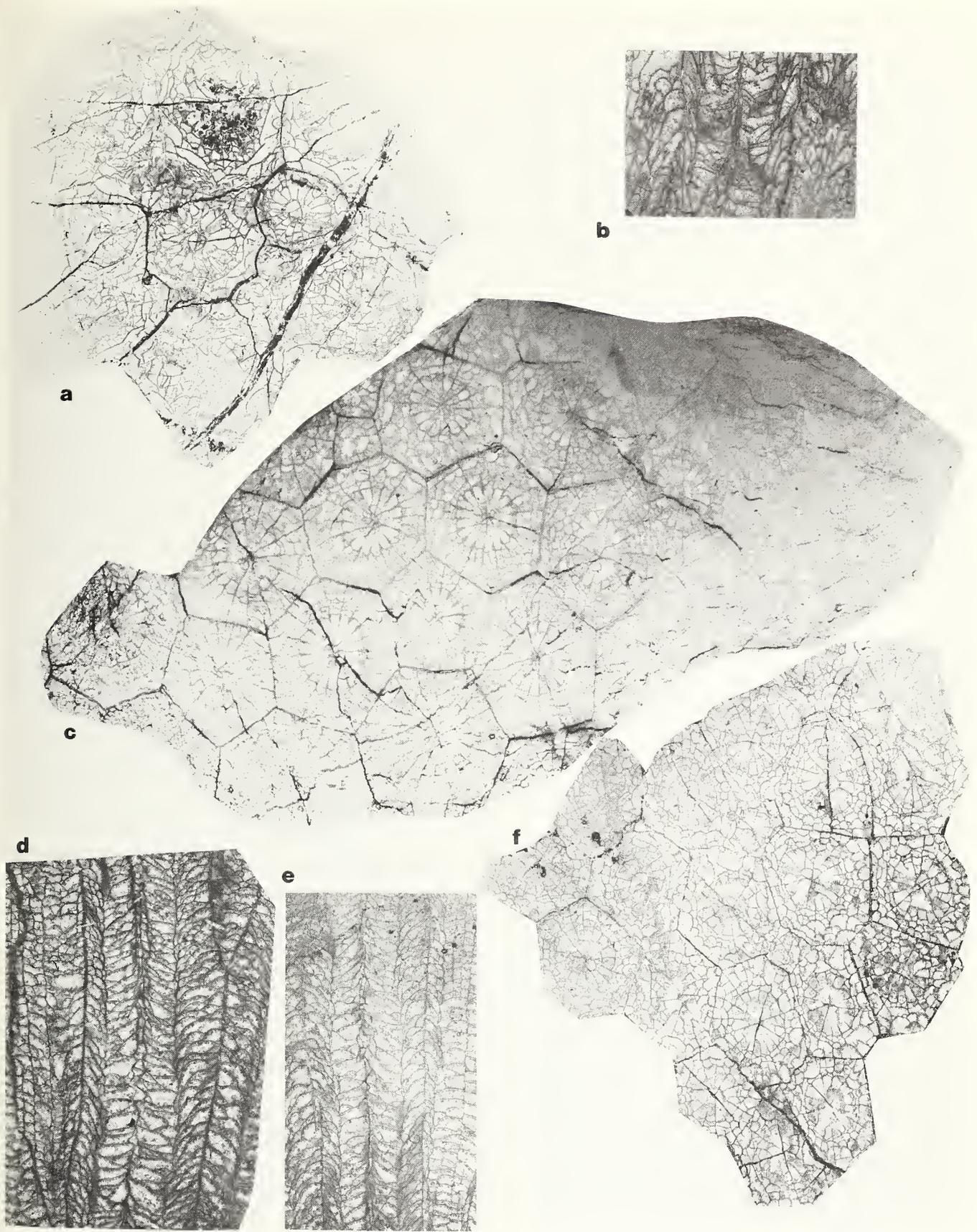


Figure 36. *Kleopatrina (Porfirievella) peggyae* n. sp. and *K. (P.) mckibbiniae* n. sp. All parts x3.
 Parts a and b. *K. (P.) peggyae* n. sp., UCMP holotype 37223, transverse (a) and longitudinal (b) sections.

Parts c through f. *K. (P.) mckibbiniae* n. sp. Parts c through e, UCMP holotype 37224, transverse (c) and longitudinal (d, e) sections. Part f, LACMIP paratype 6420, transverse section.

touched by many septa and a moderately lonsdaleoid dissepimentarium. It has more septa touching the axial structure and a less lonsdaleoid dissepimentarium than *K. (P.) peggyae* n. sp. and *K. (P.) whitneyi* n. sp. It has a less complex axial structure touched by fewer septa than *K. (P.) illipahensis*. It has a less complex axial structure touched by more septa than *K. (P.) arcturusensis*. It has a smaller and less complex axial structure than *K. (P.) nevadensis*. It has an axial structure touched by more septa than *K. (P.) grandis*, *K. (P.) radiata*, and *K. (P.) styliodophylloides*.

External Description. Corallum cerioid, hemispheroidal to sub-hemispheroidal, maximum diameter 13 cm (represented by collected fragments, many from much larger coralla), calyx not observed.

Transverse Section Description. Corallites 4 to 7 sided, 6 to 11 mm wide at greatest diameter; septa of 2 orders, 12 to 20 each (generally 15 to 17), straight to somewhat sinuous, absent or represented by spines on dissepiments where lonsdaleoid; major septa nearly all touching axial structure in some corallites, fewer touching in others, some touching in nearly all corallites, 1.5 to 3.5 mm long, generally thin throughout except few somewhat dilate to 0.2 mm thick in tabularium; minor septa poorly developed, absent in parts of many corallites, 0.5 to 1.5 mm long, rarely crossing dissepimentarium; dissepimentarium width 0.5 to 3.0 mm, generally about 2.0 mm; dissepiments concentric, herringbone, pseudoherringbone, lonsdaleoid (common); axial structure variable, elisiophylloid (connected to counter and cardinal septum in many and appearing dibunophylloid), formed of thin to thickened medial plate 1 to 2 mm long, rarely dilate to as much as 0.6 mm, generally simple with 1 to 7 irregularly spaced, short septal lamellae, some without septal lamellae, some with septal lamellae joined by axial tabellae into complex structure, many of which are touched by attenuate septal ends; corallite wall 0.15 to 0.3 mm wide; corallites rarely seiophylloid.

Longitudinal Section Description. Dissepimentarium of 1 to 6 (generally 2 to 4) ranks of large elongate and small and large cystose dissepiments; tabellae poorly zoned in most corallites, not zoned in some; periaxial tabellae flat, domed, horizontal to gently sloping inwards and upwards to axial tabellae, 18 to 30 per cm; axial tabellae steeply sloping inwards and upwards to columella, 18 to 20 per cm; tabulae tent-shaped or domed, about 20 per cm.

Documentation. UCMP holotype 37224, UCMP paratypes 37225–37229, LACMIP paratypes 6420–6423. Twenty-three thin sections and 183 polished sections from 10 coralla from UCMP localities A-7096 (holotype 37224, paratypes 37225–37226, 37228–37229) and D-842 (paratype 37227) and LACMIP localities I123 (paratypes 6420–6421) and I124 (paratypes 6422–6423) were studied.

Discussion. The numerous coralla of this species examined show it to be variable in the complexity of the axial structure as seen in transverse and longitudinal sections and the consequent zoning, or lack of zoning, in the tabularium as seen in longitudinal section. The holotype has a relatively complex axial structure for the species. A particularly characteristic feature of the species is the common attachment of both the counter and cardinal septa to

the axial structure, giving it a dibunophylloid-like character.

The other three species of *Kleopatrina (Porfirievella)* described herein from the McCloud Limestone are comparable in corallite sizes and septal numbers. The two species from lower in the formation both have much more highly lonsdaleoid dissepimentaria as seen in transverse section and lack the number of septa touching the axial structure. *K. (P.) whitneyi* n. sp.—holotype figured by Meek (1864, pl. 1, figs. 3, 3a)—is somewhat similar in the dissepimentarium, but the axial structure does not show any counter-cardinal septa attachments. Meek's specimen may have come from the Bayha area, but its high degree of silicification is unlike those collected in the Bayha section in this study.

The species of *Kleopatrina (Porfirievella)* from elsewhere show a marked similarity in corallite diameters and septal numbers. However, they differ from *K. (P.) mckibbiniae* in the following manners: *K. (P.) illipahensis* (Easton, 1960) from the Lower Permian Pequop Formation of east-central Nevada has a much more complex axial structure that is touched by almost every septum. *K. (P.) arcturusensis* Stevens, 1967, from the Lower Permian Arcturus Formation of east-central Nevada also has a more complex axial structure and septa that are more withdrawn from it. *K. (P.) nevadensis* Stevens, 1967, from the Lower Permian Arcturus (?) Formation of east-central Nevada has a much larger and far more complex axial structure. *K. (P.) grandis* (Dobrolyubova, 1941) from the Lower Permian of the Ural Mountains of Russia, the type species of the subgenus, has fewer septa touching the axial structure. *K. (P.) styliodophylloides* (Dobrolyubova, 1941) and *K. (P.) styliodophylloides* var. *radiata* (Porfiriev, 1941), also from the Permian of the Ural Mountains, likewise have axial structures that are more withdrawn from the axial ends of the septa.

Etymology. The species is named for Mrs. Jean McKibbin.

Kleopatrina (Porfirievella) peggyae n. sp.

Figures 36a–b

Diagnosis. A species of *Kleopatrina (Porfirievella)* characterized by the combination of a simple axial structure touched by few septa and a highly lonsdaleoid dissepimentarium. It has a simpler axial structure touched by fewer septa than *K. (P.) zulloi* n. sp. It has a more lonsdaleoid dissepimentarium than *K. (P.) whitneyi* n. sp. and *K. (P.) mckibbiniae*. It has a simpler axial structure than *K. (P.) illipahensis*, *K. (P.) arcturusensis*, and *K. (P.) nevadensis*. It has thinner septa and a more lonsdaleoid dissepimentarium than *K. (P.) grandis*. It has more septa and a more lonsdaleoid dissepimentarium than *K. (P.) styliodophylloides* var. *radiata*.

External Description. Corallum cerioid, maximum observed diameter 10 cm; no well-preserved calices or wall observed.

Transverse Section Description. Corallites polygonal, 5 to 7 sided, 7 to 11 mm wide at greatest diameter; septa of 2 orders; major septa number 17 to 18, 2 to 3 mm in length, extending into tabularium 1 to 1.5 mm, thin in dissepimentarium, thin or slightly dilate in tabularium; minor septa absent or represented by septal spines on wall, dissepiments, and (rare) false wall,

fewer than major septa; axial structure variable: columella or medial plate alone, dilate or thin, straight or slightly sinuous, or simplified clisiophylloid with 1 to 4 short septal lamellae; dissepimentarium lonsdaleoid; corallite wall denticulate, 0.3 to 0.5 mm wide.

Longitudinal Section Description. Dissepimentarium of 1 to 4 ranks of inflated dissepiments; dissepiments number about 8 in 1 cm; tabellae of 2 series; axial tabellae small, 1 to 3 ranks on each side of columella, steeply dipping; periaxial tabellae generally horizontal or sloping inwards and upwards to axial tabellae; columella sinuous.

Documentation. UCMP holotype 37223. Two thin sections and 21 polished sections from one corallum from UCMP locality D-827 were studied.

Discussion. *K. (P.) peggyae* has thinner walls, a thinner axial plate, fewer septa touching the axial structure, and generally a simpler axial structure than *K. (P.) zulloi* n. sp. from the Hirz Mountain section. It is more highly lonsdaleoid and differs in other characters from *K. (P.) whitneyi* n. sp. from south of the Pit River and *K. (P.) mckibbinae* from the Potter Ridge section.

K. (P.) illipahensis, *K. (P.) arcturusensis*, and *K. (P.) nevadensis* from eastern Nevada have more complex axial structures than *K. (P.) peggyae*.

The Russian species of the subgenus are not very similar to this species. *K. (P.) grandis*, type species for the subgenus, has major septa dilated in the tabularium and is somewhat less lonsdaleoid. *K. (P.) stylidophylloides* var. *radiata* has somewhat fewer septa and a less lonsdaleoid dissepimentarium.

Etymology. The species is named for Mrs. Peggy McCain.

Kleopatrina (Porfirievella) whitneyi n. sp.

Figures 5:3, 3a; 15f; 37a–b

Lithostrotion mamillare? Meek, 1864, plate 1, figs. 3, 3a.

Diagnosis. A species of *Kleopatrina (Porfirievella)* characterized by the combination of a simple axial structure touched by few septa and a moderately lonsdaleoid dissepimentarium. It has an axial structure touched by fewer septa and a less lonsdaleoid dissepimentarium than *K. (P.) zulloi* n. sp. It has a less variable axial structure and a less lonsdaleoid dissepimentarium than *K. (P.) peggyae*. It has an axial structure touched by fewer septa than *K. (P.) mckibbinae*. It has a simpler axial structure than *K. (P.) arcturusensis*, *K. (P.) illipahensis*, and *K. (P.) nevadensis*.

External Description. Corallum cerioid, maximum observed diameter 3 cm; calices and epitheca not observed.

Transverse Section Description. Corallites polygonal, 4 to 7 sided, 6 to 11 mm wide at greatest diameter; septa of 2 orders; major septa number 17 to 20, total length 2 to 5 mm, extending into dissepimentarium 0.5 to 1.5 mm; generally withdrawn from axial structure; minor septa same number or fewer than majors, extending into tabularium about 0.3 mm in some corallites, absent in tabularium of others, represented in places only by septal spines on dissepiments; axial structure clisiophylloid, with sinuous medial plate 1.5 to 2 mm long; septal lamellae absent or maximum of 6, short, loosely connected by axial tabellae; dissepiments highly lonsdaleoid in parts of some corallites, not lons-

daleoid in others but straight, angulo-concentric, pseudoherringbone, herringbone; dissepimentarium about 4 mm wide at greatest width; wall rather sinuous, not denticulate, about 0.2 mm wide.

Longitudinal Section Description. Dissepiments of 1 to 6 ranks of steeply dipping, small or inflated dissepiments; tabellae of 2 zones, axial and periaxial; axial tabellae large, of 1 rank, sloping upwards to the columella, rarely continuous with periaxial tabellae to form tabulae; periaxial tabellae horizontal in places, generally sloping inwards and upwards gently to axial tabellae, about 16 per cm; columella sinuous.

Documentation. Two thin sections and several polished sections from the holotype corallum, MCZ Meek collection specimen no. 15, were studied. This specimen was labeled “No 15 *Lithostrotion mamillare* Castlenau ? sp.” and is not the “*Lithostrotion* ___?” of Meek (1864:7), which he indicated is figured on his plate 1, figures 3, 3a. The specimen labeled “*Lithostrotion* ___?” is a fasciculate coral and was not figured by Meek.

The type locality is uncertain but probably is somewhere in the McCloud Limestone south of the Pit River at one of the localities collected by the Whitney Survey in September 1862. Other coralla of this species were not collected by me, and the high degree of silicification suggests that the specimen did not come from my Bayha section, where few corals are so highly silicified. Unfortunately, no fusulinids are associated with the holotype, but the formation in this area is within the fusulinid zones E and F. Cerioid corals are common in places in zone F of the Bayha section.

Discussion. *K. (P.) whitneyi* can be distinguished from the other three new species of the subgenus from the McCloud Limestone by the number of septa in contact with the axial structures and the degree of lonsdaleoid development of the dissepimentaria as well as other features. *K. (P.) zulloi* n. sp. from the Hirz Mountain section has many more septa that touch the axial structure and is much more lonsdaleoid. *K. (P.) peggyae* from Bollibokka Mountain has a much more lonsdaleoid dissepimentarium and a different kind of axial structure. *K. (P.) mckibbinae* from the Bayha and Potter Ridge sections has many more septa that touch the axial structure. *K. (P.) illipahensis*, *K. (P.) arcturusensis*, and *K. (P.) nevadensis*, all from the Lower Permian of Nevada, have more complex axial structures and other differences.

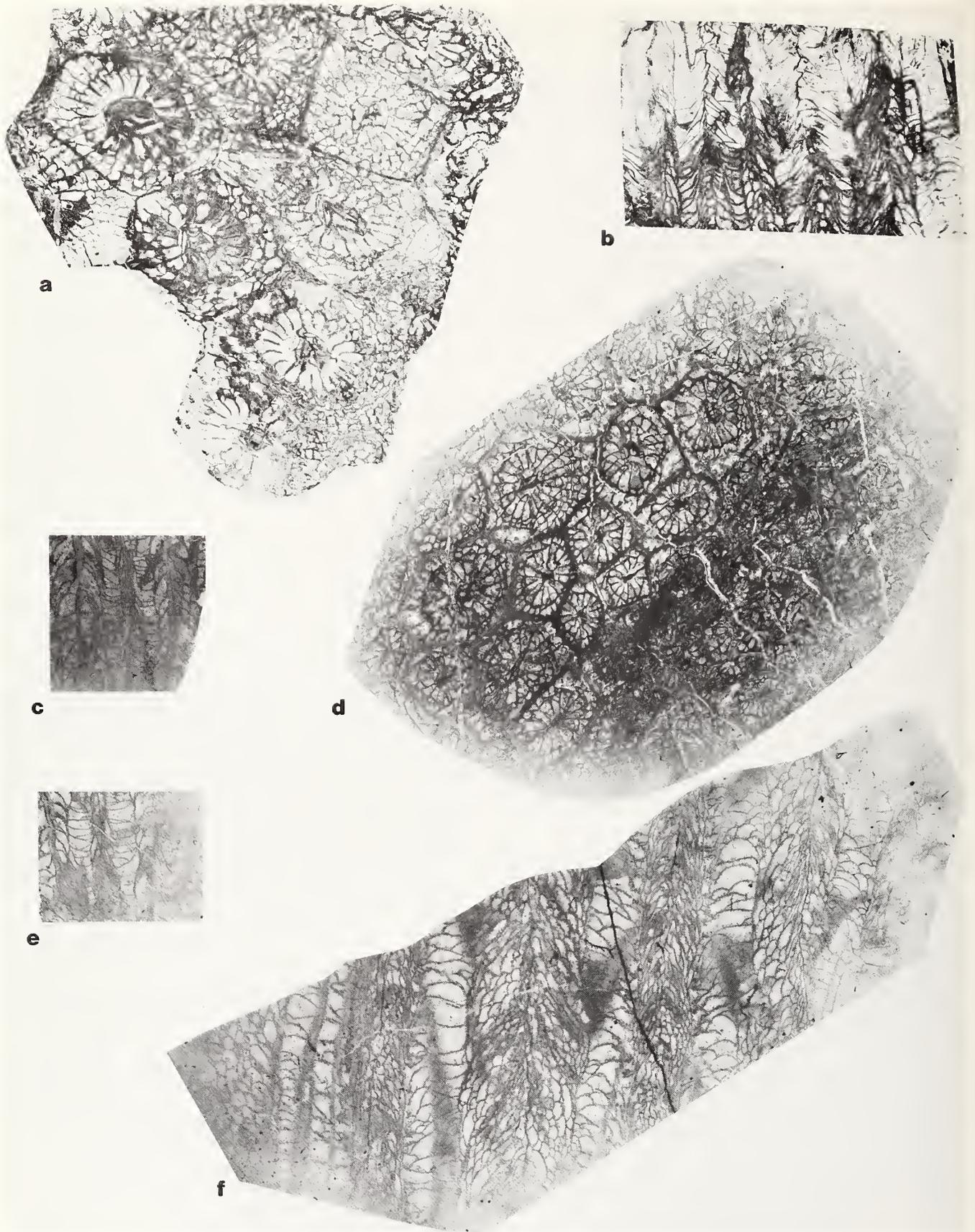
Etymology. The species is named for Mr. Josiah Dwight Whitney.

Kleopatrina (Porfirievella) zulloi n. sp.

Figures 37c–e

Diagnosis. A species of *Kleopatrina (Porfirievella)* characterized by the combination of a moderately simple axial structure touched by many septa and a highly lonsdaleoid dissepimentarium. It has longer septa, a more complex axial structure touched by more septa, and more inflated dissepiments than *K. (P.) peggyae*. It has a more lonsdaleoid dissepimentarium than *K. (P.) mckibbinae* and *K. (P.) whitneyi*. It has a simpler axial structure than *K. (P.) arcturusensis*, *K. (P.) illipahensis*, and *K. (P.) nevadensis*.

External Description. Corallum cerioid, maximum observed di-



64 Figure 37. *Kleopatrina (Porfirievella) whitneyi* n. sp., *K. (P.) zulloi* n. sp., and *Langenheimia klamathensis* n. gen., n. sp. All parts x3.
 Parts a and b. *K. (P.) whitneyi* n. sp., MCZ holotype, MCZ Meek collection corallum no. 15, transverse (a) and longitudinal (b) sections.
 Parts c through e. *K. (P.) zulloi* n. sp., UCMP holotype 37230, longitudinal (c, e) and transverse (d) sections.
 Part f. *L. klamathensis* n. gen., n. sp., UCMP holotype 37231, longitudinal section.

ameter 15 cm, calyx 2 to 3 mm deep, with steeply sloping walls, rather flat floor, tall central axial boss, which may be attached to one side of calyx, presumably by counter septum.

Transverse Section Description. Corallites polygonal, 5 to 7 sided, 6 to 9 mm wide at greatest diameter; septa of 2 orders, 15 to 19 each, thin throughout, or very slightly dilate in tabularium; major septa 1 to 2 mm long, extending into tabularium 0.5 to 0.8 mm; minor septa generally confined to dissepimentarium, about 0.3 mm long; axial structure clisiophylloid, with well-defined medial plate, 1 to 4 septal lamellae, and tabellae (juvenile axial structure a columella attached to counter septum); dissepiments lonsdaleoid in many places, elsewhere concentric and herringbone; corallite wall denticulate, with or without septal spines where lonsdaleoid, 0.2 to 0.3 mm wide.

Longitudinal Section Description. Dissepimentarium of 1 to 3 (rare) ranks of steeply dipping, generally inflated dissepiments; tabellae of 2 series; axial tabellae dissepiment-like against columella; periaxial tabellae generally flat or sagging, rarely sloping inwards and upwards to the axial tabellae; columella somewhat sinuous.

Documentation. UCMP holotype 37230. Four thin sections and 44 polished sections from one large corallum from UCMP locality D-855 were studied.

Discussion. *K. (P.) zulloi* is similar in some respects to *K. (P.) peggyae* from Bollibokka Mountain. The latter, however, has a simpler axial structure from which the septa are somewhat more withdrawn and generally less inflated dissepiments. *K. (P.) whitneyi* and *K. (P.) mckibbinae*, both from higher in the McCloud Limestone, have less highly developed lonsdaleoid dissepimentaria as well as other characters that distinguish them from *K. (P.) zulloi*.

K. (P.) zulloi may readily be distinguished from the three species of the subgenus from Nevada, *K. (P.) illipahensis*, *K. (P.) arcturusensis*, and *K. (P.) nevadensis* by its simpler axial structure.

Etymology. The species is named for Dr. Victor A. Zullo.

Genus *Langenheimia* n. gen.

Diagnosis. *Langenheimia* is a cerioid rugose coral with large corallites, no fossula, septa of two orders, well-defined aulophylloid axial structure, thin and complete wall, tabellae of two ranks—axial and periaxial, the former sloping steeply inwards and upwards, the latter variously inclined but generally gently inwards and upwards to the axial tabellae.

Type Species. *Langenheimia klamathensis* n. sp.

Description. As for the type and only known species.

Discussion. *Langenheimia* has some characters in common with other Permian cerioid rugose corals, but they have the following, among other, important characters that distinguish them from *Langenheimia*. *Wentzelella* Grabau in Huang, 1932, *Wentzelloides* Yabe and Minato, 1944, and *Wentzellophyllum* Hudson, 1958, all have tertiary septa. *Yokoyamaella* Minato and Kato, 1965a, has thick mural septa. *Ipciphyllum* Hudson, 1958, and *Kleopatrina* McCutcheon and Wilson, 1963, both have clisiophylloid axial structures. *Parawentzelella* Fontaine, 1961, also has a clisiophylloid axial structure as well as the controversial “canals” between walls of corallites.

Etymology. The genus is named for Dr. Ralph L. Langenheim, Jr.

Langenheimia klamathensis n. sp.

Figures 37f; 38a–b

Diagnosis. Because the genus *Langenheimia* is erected as monotypic, the diagnoses of the genus and of the type species are identical.

External Description. Corallum cerioid, hemispheroidal; maximum observed diameter 13 cm; calyx and epitheca not seen.

Transverse Section Description. Corallites polygonal, 5 to 7 sided, 15 to 27 mm wide at greatest diameters; septa of 2 orders, 23 to 27 each; major septa 3.5 to 8.5 mm long, extending into tabularium 3 to 3.5 mm, thin in dissepimentarium, dilate and lanceolate in tabularium, maximum width about 0.5 mm near base in tabularium; minor septa thin, 2 to 3.5 mm long, generally confined to dissepimentarium, rarely penetrating slightly into tabularium; axial structure aulophylloid, of numerous irregular cystose tabellae, elongate, 4 to 5 mm long, 2 to 2.5 mm wide, not touched by septa; dissepiments variously angulo-concentric, concentric, herringbone, or pseudoherringbone, with irregular small dissepiments near bases of some septa; corallite wall entire, thin, about 0.13 mm wide.

Longitudinal Section Description. Dissepimentarium wide, of 5 to 10 ranks of small, cystose to large, elongate, steeply dipping dissepiments; tabellae of 2 series, axial and periaxial; axial tabellae small and cystose to larger and elongate, in 3 to 8 ranks each side, steeply inclined inwards and upwards; periaxial tabellae straight, domed, or sagging, in 1 to 3 ranks, variously inclined gently inwards and upwards (generally), horizontal (uncommon), or inwards and downwards (uncommon) to axial tabellae.

Documentation. UCMP holotype 37231, UCMP paratype 37232. Three thin sections and 30 polished sections from two coralla from UCMP locality D-845 were studied.

Discussion. This coral is the only species that presently seems to be referable to the genus. It does not appear to be comparable to any other described Upper Paleozoic coral. A poorly preserved corallum from UCMP locality A-7096 in the Bayha section of the McCloud Limestone may belong to the same genus and species, but detailed observation of morphological characters is impossible due to metamorphism and stylonitic resorption of parts of the corallite.

I have interpreted the longitudinal section as showing two series of tabellae, each consisting of several ranks. The tabellae of the periaxial series are so variously inclined that there might be considered to be three series of tabellae in some parts of the section, but this is not a consistent feature.

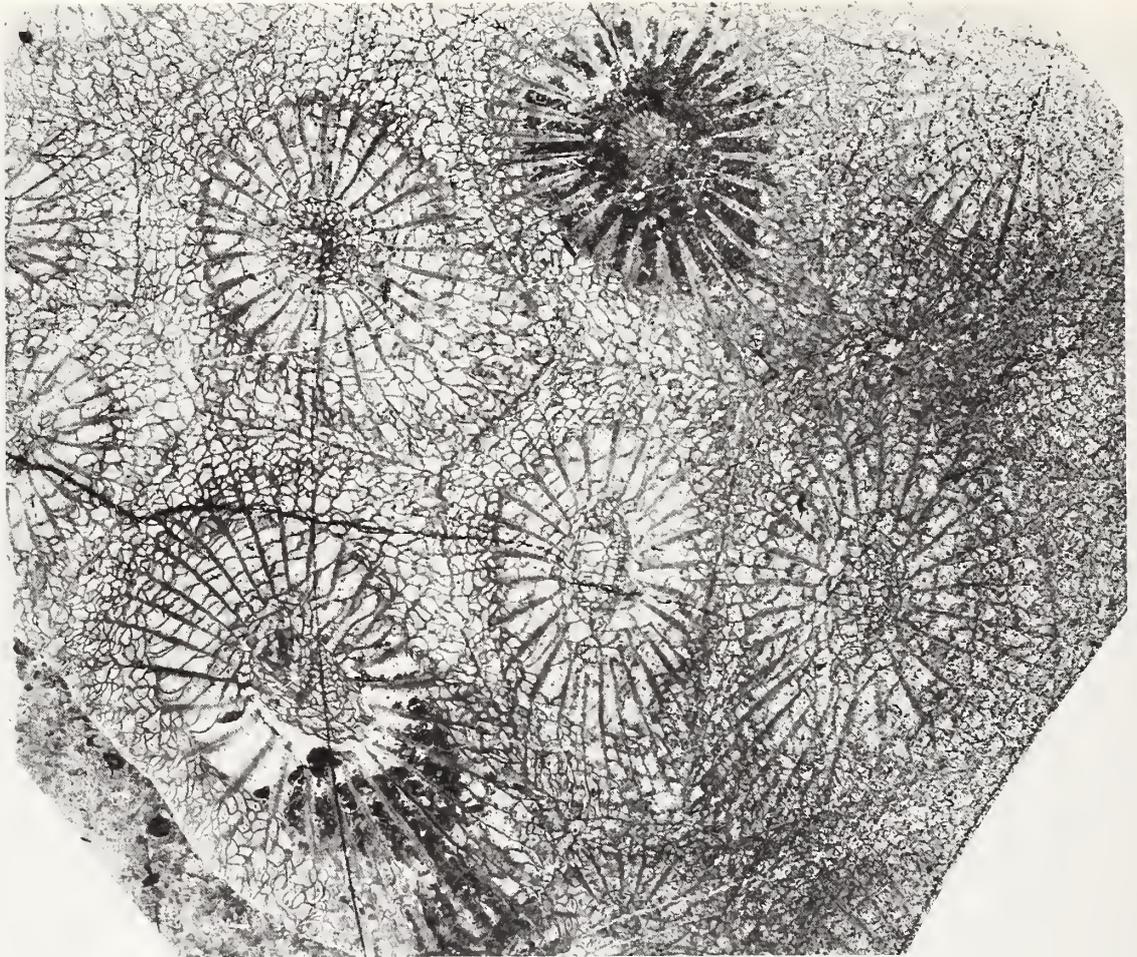
Etymology. The species is named for the Klamath Mountains.

Genus *Petalaxis* Milne Edwards and Haime, 1852

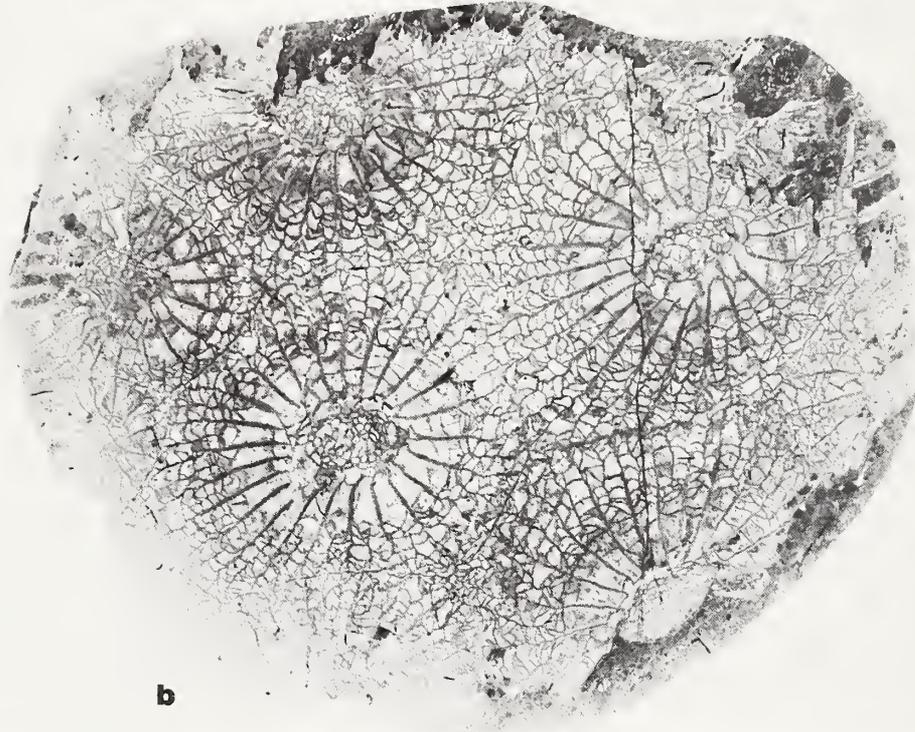
Petalaxis allisonae n. sp.

Figures 39a–b

Diagnosis. A species of *Petalaxis* characterized by the combination of small corallites, a moderately large number of major



a



b

Figure 38. *Langenheimia klamathensis* n. gen., n. sp. Both parts x3. **Part a**, UCMP holotype 37231, transverse section. **Part b**, UCMP paratype 37232, transverse section.

septa, a very dilate columella, and a moderately broad dissepimentarium with few septal spines. It has smaller corallites, fewer major septa, and a somewhat more dilate columella than *P. besti* n. sp. It has smaller corallites and a somewhat less dilate columella than *P. kennedyi* n. sp. It has smaller corallites, a more dilate columella, and a narrower dissepimentarium than *P. pecki* n. sp. It has somewhat smaller corallites, a more dilate columella, and a broader dissepimentarium with fewer septal spines than *P. sutherlandi* n. sp. It has a more dilate columella than *P. brokawi*, *P. mokomokensis*, *P. dilatata*, and *P. occidentalis*.

External Description. Corallum cerioid, maximum observed diameter 5 cm; calyx 3 to 4 mm deep, with steeply sloping walls, small central axial boss.

Transverse Section Description. Corallites polygonal, 5 to 7 sided, 6 to 7.5 mm wide at greatest diameter; septa of 2 orders, 13 to 16 each, fewer minor septa where lonsdaleoid, thin in dissepimentarium, slightly dilate in tabularium; major septa 1 to 2 mm long, extending into tabularium about 1 mm where dissepimentarium lonsdaleoid, generally absent or represented by septal spines on dissepiments; minor septa fewer than major septa in most corallites, extending slightly into tabularium in places; axial structure a columella, generally lenticular, with smooth edges, attached to counter septum, rarely to cardinal septum also, touched by other septa in some corallites; dissepiments lonsdaleoid, generally inflated, many bearing septal spines, forming false wall separating dissepimentarium and tabularium; corallite wall denticulate, about 0.2 mm wide, generally without septal spines where dissepiments highly inflated.

Longitudinal Section Description. Dissepimentarium of 1 to 3 ranks of steeply dipping, somewhat inflated dissepiments; tabulae generally flat and horizontal, some sloping gently inwards and upwards to columella, some sagging, in places broken up into tabellae, with outer series mostly flat and horizontal, inner series gently inclined inwards and upwards or even tent-shaped (rare); columella slightly sinuous, 0.2 to 0.4 mm wide.

Documentation. Holotype UCMP 37233. Two thin sections and 10 polished sections from one corallum from UCMP locality D-803 were studied.

Discussion. *Petalaxis* presently is distinguished by the possession of predominately flat and horizontal tabulae from *Acrocyathus* d'Orbigny, 1849 (a senior synonym of *Lithostrotionella* Yabe and Hayasaka, 1915, according to Easton, 1973), which generally has tent-shaped tabulae (Sutherland, 1977). Although there is considerable variation in the shape and inclination of tabulae in the McCloud Limestone species of *Petalaxis*, many are flat and horizontal, but few are tent-shaped. Some tabulae of the McCloud specimens even sag deeply, which is unlike the type species of either *Petalaxis* or *Acrocyathus*.

Four species from the Permian of North America may be referred to *Petalaxis*: *P. brokawi* (Wilson and Langenheim, 1962), Nevada; *P. dilatata* (Easton, 1960), Nevada; *P. mokomokensis* (Easton, 1960), Nevada; *P. occidentalis* (Merriam, 1942), Oregon.

In addition, unfigured paratypes nos. 6 and 7 (USNM nos. 174371 and 174373) of *Lithostrotionella americana* Hayasaka,

1936, likely are from the McCloud Limestone exposures south of the Pit River and might be referable to *Petalaxis*. I have not seen them. The holotype of *L. americana* is from the Mississippian of Kentucky, and it is improbable that the California Permian paratypes are placed correctly in the same species under current concepts.

P. allisonae does not closely resemble any of the four Permian species listed above, all of which occur in somewhat younger rocks. It is superficially similar, in some characters, to *P. besti* n. sp. and *P. kennedyi* n. sp. from higher in the formation at Hirz Mountain and Potter Ridge, respectively. These two species, however, have larger corallites, more highly denticulate walls, and generally more septa, which are more withdrawn from the columella.

P. allisonae is the lowest record for the genus in the McCloud Limestone.

Etymology. The species is named for Dr. Carol W. Allison.

Petalaxis besti n. sp.

Figures 39c–f

Diagnosis. A species of *Petalaxis* characterized by the combination of large corallites, a great number of major septa, a lenticular columella, and a very broad dissepimentarium with few septal spines. By the large number of septa alone, it can be distinguished from *P. allisonae*, *P. kennedyi* n. sp., *P. pecki* n. sp., *P. sutherlandi* n. sp., *P. brokawi*, *P. mokomokensis*, *P. dilatata*, and *P. occidentalis*.

External Description. Corallum cerioid, maximum observed diameter 8 cm; external features not preserved.

Transverse Section Description. Corallites polygonal, 5 to 7 sided, 7 to 11 mm wide; septa of 2 orders, 17 to 21 each, thin in dissepimentarium and tabularium; major septa 1 to 2 mm long, extending into tabularium 1 to 1.5 mm; minor septa generally represented by spines on inner wall, dissepiments, and outer wall; axial structure a columella, roughly lenticular, with sinuous edges and, in places, 1 or 2 septal lamellae, generally attached to counter septum, not touched by other septa; dissepimentarium lonsdaleoid except in immature corallites, with large dissepiments, some with septal spines; corallite wall highly denticulate, about 0.5 mm wide.

Longitudinal Section Description. Dissepimentarium of 1 (rarely 2) ranks of steeply dipping, inflated dissepiments; tabulae variably inclined: flat and horizontal to sinuous and sloping downwards and inwards to columella, but generally flat and horizontal near columella; columella only slightly sinuous, 0.3 to 0.9 mm wide.

Documentation. UCMP holotype 37234, UCMP paratypes 37235–37237. Four thin sections and 54 polished sections from four coralla from UCMP localities D-857 (three paratypes) and D-858 (holotype) were studied.

Discussion. This species can be distinguished readily from others in the genus from the McCloud Limestone by its greater number of septa, as well as other features. *P. occidentalis*, from

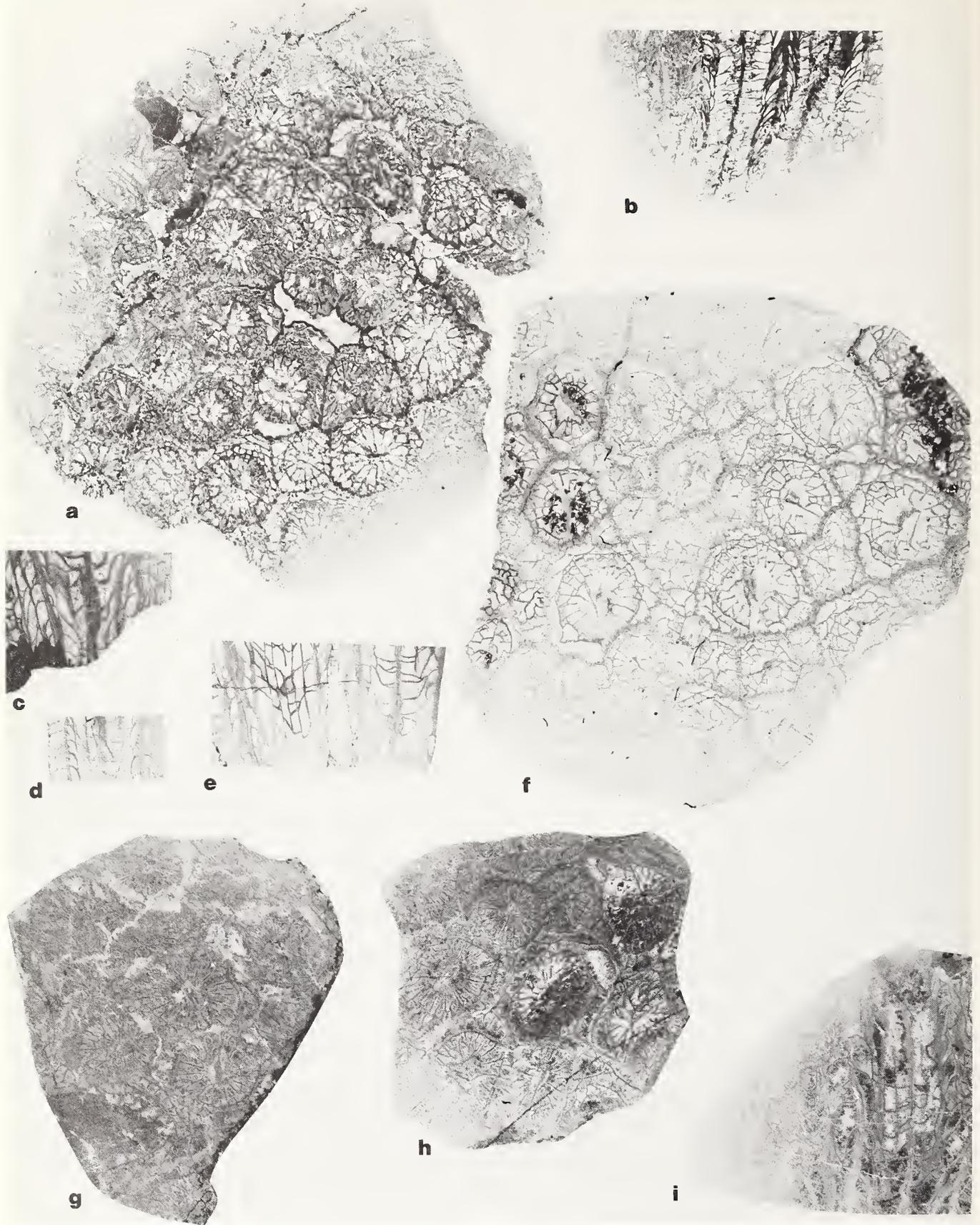


Figure 39. *Petalaxis allisonae* n. sp., *P. besti* n. sp., and *P. kennedyi* n. sp. All parts x3.

68 Parts a and b. *P. allisonae* n. sp., UCMP holotype 37233, transverse (a) and longitudinal (b) sections.

Parts c through f. *P. besti* n. sp., UCMP holotype 37234, longitudinal (c-e) and transverse (f) sections.

Parts g through i. *P. kennedyi* n. sp., UCMP holotype 37238, transverse (g, h) and longitudinal (i) sections.

the Permian of Oregon, has smaller corallites and fewer septa than *P. besti*.

Etymology. The species is named for Dr. R.V. Best.

Petalaxis kennedyi n. sp.

Figures 39g–i

Diagnosis. A species of *Petalaxis* characterized by the combination of large corallites, a moderately great number of major septa, a highly dilate (most circular in transverse section) columella, and a moderately broad dissepimentarium with few septal spines. It has somewhat larger corallites and a somewhat more dilate columella than *P. allisonae*. It has a much more dilate columella than *P. besti*, *P. pecki* n. sp., *P. sutherlandi* n. sp., *P. brokawi*, *P. mokomokensis*, *P. dilatata*, and *P. occidentalis*.

External Description. Corallum cerioid, maximum observed diameter 13 cm; calices and wall not observed.

Transverse Section Description. Corallites polygonal, 5 to 7 sided, 4 to 10 mm wide at greatest diameter; septa of 2 orders, 14 to 17 each, thin throughout or slightly dilate in tabularium; major septa 1.5 to 2.5 mm long, extending into tabularium 0.2 to 0.4 mm; axial structure a dilate, lenticular columella, generally smooth edged, attached to counter septum (rarely to cardinal septum also); dissepiments lonsdaleoid, large, some with septal spines; corallite wall denticulate, with long septal spines in places, 0.3 to 0.6 mm wide.

Longitudinal Section Description. Dissepimentarium of 1 (rarely 2–3) ranks of steeply dipping, very highly inflated dissepiments; tabulae generally flat and horizontal or sloping downwards and inwards, turning up slightly at columella, rarely inwards and upwards; columella straight, about 0.3 mm wide.

Documentation. UCMP holotype 37238, UCMP paratypes 37239–37241, LACMIP paratype 6424. Five thin sections and 76 polished sections from five coralla from UCMP localities D-836 (holotype 37238), D-837 (paratypes 37239–37240), and D-841 (paratype 37241) and LACMIP locality 1116 (paratype 6424) were studied.

Discussion. *P. kennedyi* has similar corallite diameters and numbers of septa to *P. allisonae*, but the latter has much longer septa and many more ranks of dissepiments. *P. besti* n. sp. has a greater number of septa, a thicker wall, and a narrower dissepimentarium than *P. kennedyi*. The other two McCloud Limestone new species of this genus also are from Potter Ridge, but they have much more dilate columellae than *P. kennedyi*. The species is dissimilar in many ways to the other species already known from the Permian of Oregon and Nevada.

Etymology. The species is named for Dr. George L. Kennedy.

Petalaxis pecki n. sp.

Figures 40a–e

Diagnosis. A species of *Petalaxis* characterized by the combination of large corallites, a moderately great number of major septa, a lenticular columella, and a narrow dissepimentarium with many septal spines. It has a thinner columella than *P. allisonae* and *P. kennedyi*. It has a smaller number of septa and a narrower dissepimentarium with more septal spines than *P. besti*. It has a somewhat greater number of septa and a broader dissepimentarium with fewer septal spines than *P. sutherlandi* n. sp.

External Description. Corallum cerioid, maximum observed diameter 8 cm; calices and wall not observed.

Transverse Section Description. Corallites polygonal, 5 to 7 sided, 5.5 to 10 mm wide at greatest diameter; septa of 2 orders, 12 to 17 each, thin, generally absent in dissepimentaria of adult corallites; major septa 0.5 to 1.0 mm long; minor septa well developed, about 0.2 mm long; axial structure a columella (stereocolumella) somewhat lenticular, smooth-edged, maximum observed size about 0.6 mm wide, 1.0 mm long, attached to counter septum, rarely to other septa; dissepiments lonsdaleoid, inflated, some with septal spines; corallite wall denticulate, generally without septal spines in adult corallites, 0.2 to 0.3 mm wide.

Longitudinal Section Description. Dissepimentarium of 1 to 3 ranks of elongate, steeply dipping, inflated dissepiments; tabulae slope steeply downwards and inwards to columella, becoming flat near junction or turning up slightly at columella, breaking down into tabellae in places, with outer series like clinotabellae; columella essentially straight, 0.5 to 0.9 mm wide.

Documentation. UCMP holotype 37242, UCMP paratypes 37243–37245. Seven thin sections and 40 polished sections from four coralla from UCMP localities D-842 (holotype 37242, paratype 37243) and D-843 (paratypes 37244–37245) were studied.

Discussion. *P. pecki* has a thicker columella (stereocolumella) than any other species of the genus from the McCloud Limestone except *P. sutherlandi* n. sp. The latter species may be distinguished by its thicker columella, generally thinner walls, septa, and dissepiments, and more open dissepimentarium as seen in transverse section. *P. occidentalis* from the Permian Coyote Butte Formation of Oregon is similar to *P. pecki* in corallite size, septal number, dilation of columella, and inclination of tabulae/tabellae, but it has a thicker wall, septa closer to the columella, and a false wall in contact with the corallite wall in more places. *P. pecki* is not similar to other Permian North American species of the genus.

Etymology. The species is named for Mr. Joseph H. Peck, Jr.

Petalaxis sutherlandi n. sp.

Figures 40f–i

Diagnosis. A species of *Petalaxis* characterized by the combination of moderately large corallites, a moderately great number of major septa, a lenticular columella, and a narrow dissepimentarium with many septal spines. It has somewhat larger corallites, a thinner columella, and a narrower dissepimentarium with more septal spines than *P. allisonae*. It has somewhat smaller corallites, fewer septa, and a narrower dissepimentarium with more septal spines than *P. besti*. It has a thinner columella and a narrower dissepimentarium with more septal spines than *P. kennedyi*. It has somewhat fewer septa and a narrower dissepimentarium with more septal spines than *P. pecki*. It has a narrower dissepimentarium and a generally more lenticular columella than *P. brokawi*, *P. mokomokensis*, *P. dilatata*, and *P. occidentalis*.

External Description. Corallum cerioid, maximum observed diameter 8 cm; external features not preserved.

Transverse Section Description. Corallites polygonal, 5 to 7 sided,

Figure 40. *Petalaxis pecki* n. sp. and *P. sutherlandi* n. sp. All parts x3.

Parts a through e. *P. pecki* n. sp. **Parts a through c,** UCMP holotype 37242, transverse (a) and longitudinal (b, c) sections. **Parts d and e,** UCMP paratype 37244, transverse (d) and longitudinal (e) sections.

Parts f through i. *P. sutherlandi* n. sp. **Parts f and i,** UCMP holotype 37246, transverse (f) and longitudinal (i) sections. **Parts g and h,** UCMP paratype 37247, transverse (g) and longitudinal (h) sections.



a



b



c



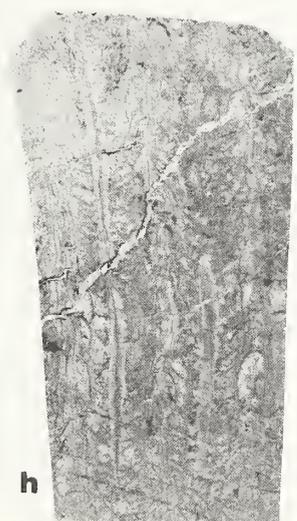
d



e



f



g



h

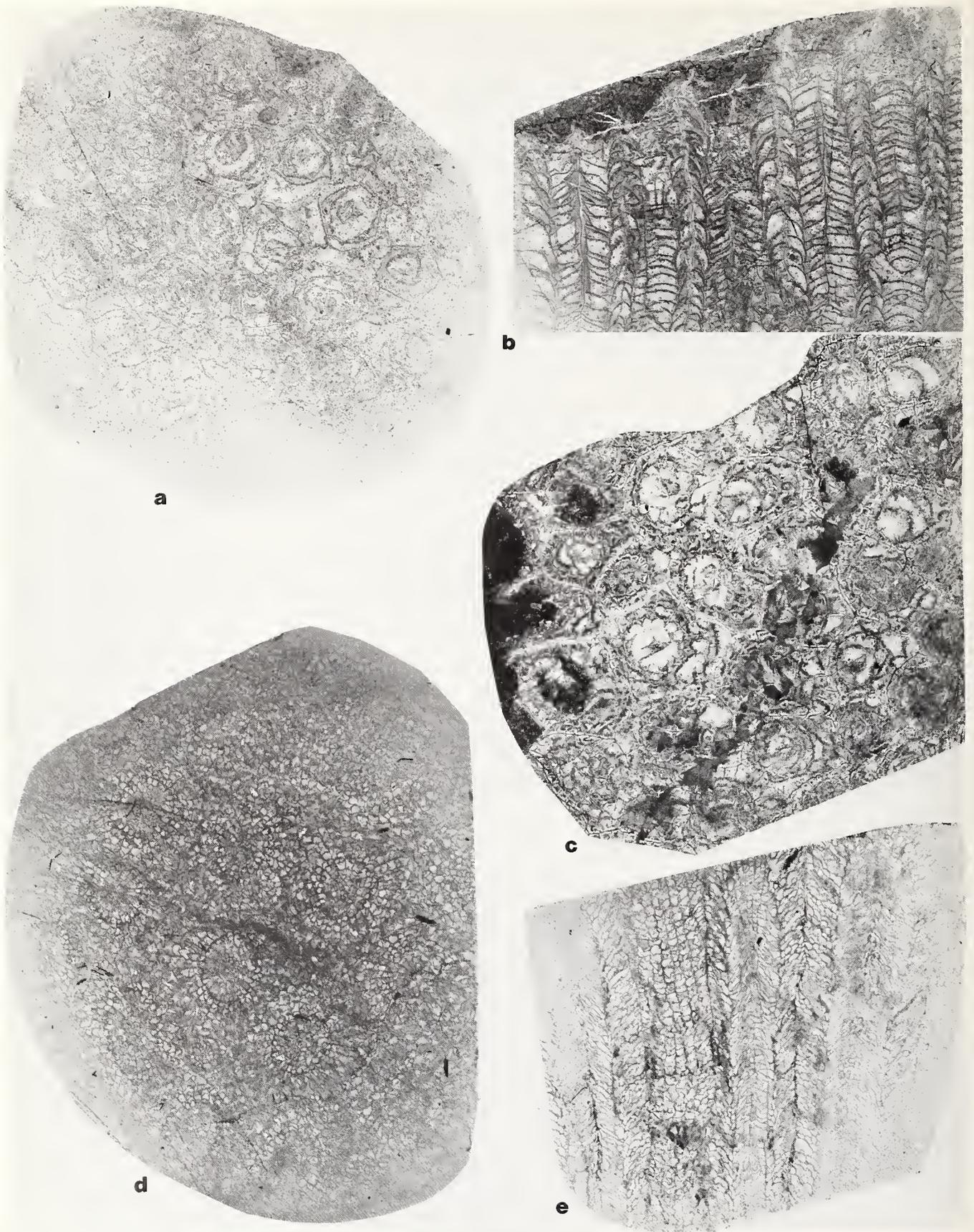


Figure 41. *Traskina shastensis* n. gen., n. sp. and *Arachnastraea fryi* n. sp. All parts x3.

72 Parts a through c. *T. shastensis* n. gen., n. sp. Parts a and b, UCMP holotype 37253, transverse (a) and longitudinal (b) sections. Part c, UCMP paratype 37254, transverse section.

Parts d and e. *A. fryi* n. sp., UCMP holotype 37256, transverse (d) and longitudinal (e) sections.

4 to 9 mm wide at greatest diameter; septa of 2 orders, with most corallites having fewer minor than major septa; major septa 12 to 15 in number, 0.4 to 1.0 mm long, generally present only in tabularium, in places represented by septal spines on corallite wall or dissepiments, thin throughout; minor septa short septal spines in tabularium, absent or reduced in number in some corallites, in places represented by septal spines on corallite wall and dissepiments; axial structure a columella (stereocolumella), round or somewhat oval, generally smooth edged, maximum observed size about 0.7 mm wide, 1.5 mm long, attached to counter septum, very rarely in contact with other septa; dissepiments very large, so few in each corallite that dissepimentarium appears nearly "empty"; corallite wall thin, sinuous, apparently vestigially denticulate, about 0.2 mm wide, with septal spines in few places.

Longitudinal Section Description. Dissepimentarium of 1 row of inflated, very steeply inclined dissepiments, 8 to 9 per cm; tabulae generally straight, sloping gently downwards and inwards toward columella, rarely sigmoid and sloping steeply down (clinotabellae-like); columella straight or slightly sinuous, maximum observed diameter 0.9 mm.

Documentation. UCMP holotype 37246, UCMP paratypes 37247–37252. Four thin sections and 76 polished sections from seven coralla from UCMP locality D-845 were studied.

Discussion. This species probably is related to *P. pecki*, which occurs lower in the same section. Differences are discussed under *P. pecki*. *P. sutherlandi* is not otherwise similar to other species of *Petalaxis* from the Permian of North America.

Etymology. The species is named for Dr. Patrick K. Sutherland.

Genus *Traskina* n. gen.

Diagnosis. *Traskina* is a sciophylloid cerioid rugose coral with two orders of intermittently developed septa, simplified elisio-phylloid axial structure of straight to sinuous medial plate and few sinuous septal lamellae, highly lonsdaleoid dissepimentarium, complete denticulate wall, tabulae sloping inwards and upwards to medial plate, rarely separated into irregular axial and periaxial tabellae with similar inclination.

Type Species. *Traskina shastensis* n. sp.

Description. As for the type and only known species.

Discussion. *Traskina* is superficially similar to *Kleopatrina* (*Porfrierevella*) Minato and Kato, 1965b, but differs by having only vestigial septa (where developed at all), well-developed tabulae, and, in places, poorly zoned tabellae whereas the latter taxon has strongly developed septa and two well-defined zones of tabellae. The axial structures of *Traskina* are a medial plate and septal lamellae, both of which are generally sinuous (even zigzag in places), whereas the same structures of *Kleopatrina* are more nearly straight. Finally, all the skeletal elements of *Traskina* are the thin sciophylloid kind whereas those of *Kleopatrina* are robust.

Traskina has vestigial septa and thin skeletal elements similar to *Sciophyllum* Harker and McLaren, 1950, known from the Upper Mississippian (?) near the Yukon-Alaska boundary, the Lower Pennsylvanian of Japan, and the Lower Permian of east-central Nevada (Wilson and Langenheim, 1962:514) and possi-

bly the Pennsylvanian and Lower Permian of the Ural Mountains, Russia (as *Thysanophyllum aseptatum* Dobrolyubova, 1936). However, *Traskina* has an axial structure and *Sciophyllum* has none.

Etymology. The genus is named for Dr. John B. Trask.

Traskina shastensis n. sp.

Figures 41a–c

Diagnosis. Because the genus *Traskina* is erected as monotypic, the diagnoses of the genus and of the type species are identical.

External Description. Corallum cerioid, maximum observed diameter 10 cm; calices and epitheca not seen.

Transverse Section Description. Corallites polygonal, 5 to 7 sided, 5.5 to 8 mm wide at greatest diameter; septa of 2 orders; major septa number 13 to 15 where well developed (rare), generally numbering fewer than 10, conspicuously absent in parts of most corallites, total length 0.4 to 1.0 mm, extending into tabularium 0.2 to 0.5 mm, generally present as spines on corallite wall and false wall; minor septa rare, present as septal spines, absent in tabularium; axial structure elisio-phylloid, of straight (uncommon), sinuous, or zigzag, thin or somewhat dilate medial plate crossed by 1 to 4 sinuous or zigzag septal lamellae, with medial plate rarely attached to counter septum; dissepiments highly lonsdaleoid, not discernible in many corallites, so that dissepimentarium appears nearly structureless; corallite wall 0.1 to 0.2 mm thick, straight or somewhat denticulate, with septa originating from V-shaped depressions.

Longitudinal Section Description. Dissepimentarium of 1 to 2 ranks of highly inflated, steeply dipping, cystose dissepiments; tabulae straight or slightly domed, with straight or slightly downturned peripheral ends, sloping gently inwards and upwards to columella, 18 to 20 per cm, rarely broken down into tabellae; columella straight to somewhat sinuous.

Documentation. UCMP holotype 37253, UCMP paratype 37254. Five thin sections and 42 polished sections from two coralla from UCMP locality D-843 were studied.

Discussion. There does not seem to be any described species that should be placed in *Traskina* with the type species.

Etymology. The species is named for Shasta Lake.

Cerioid-Astreoid Rugosa

Genus *Arachnastraea* Yabe and Hayasaka, 1916

Arachnastraea fergusonii n. sp.

Figures 42a–e

Diagnosis. A species of *Arachnastraea* characterized by the combination of very large corallites, well-developed and relatively long minor septa, and a complex axial structure. It has larger corallites, better developed minor septa, and a more complex axial structure than *A. fryi* n. sp., *A. molli*, and *A. manchurica*.

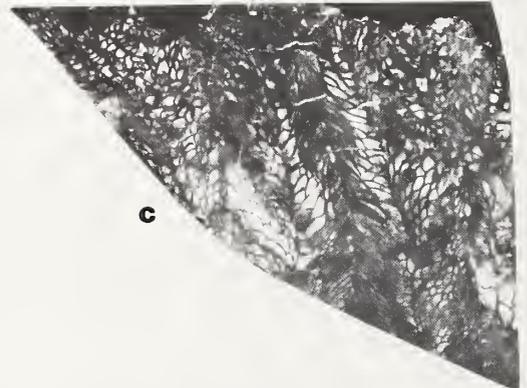
External Description. Corallum cerioid-astreoid; maximum observed diameter 11.5 cm; calices deep with prominent axial boss; external features not well preserved.



a



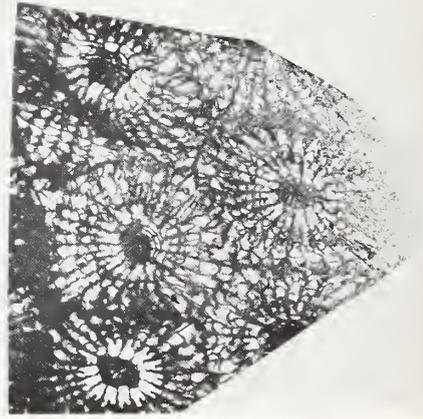
b



c



d



e

Figure 42. *Arachnastraea fergusonii* n. sp. All parts x3. Parts a through c, LACMIP holotype 6425, transverse (a) and longitudinal (b, c) sections. Parts d and e, UCMP paratype 37255, transverse sections.

Transverse Section Description. Corallites polygonal, 5 to 7 sided, 10 to 16 mm wide at greatest diameter; septa of 2 orders, 16 to 18 each; major septa 2.5 to 5 mm long, extending into tabularium 0.5 to 1.5 mm, generally slightly dilate in tabularium, most touching axial structure but not confluent with axial tabellae; minor septa well developed, extending across dissepimentarium and penetrating tabularium as dilate spines; axial structure arachnoid, circular, 2 to 3.5 mm wide, generally symmetrical, with well-developed medial plate and septal number equal to or greater than number of septa, tightly connected by tabellae; dissepimentarium regular; dissepiments straight, angulo-concentric, or pseudoherringbone; corallite wall cerioid-astreoid, very discontinuous, about 0.3 mm wide.

Longitudinal Section Description. Dissepimentarium of 3 to 6 ranks, various sized cystoid or elongate, gently dipping dissepiments, about 22 per cm; tabellae of 2 well-defined ranks, axial and periaxial; axial tabellae elongate, of 2 to 4 steeply dipping ranks, 38 to 40 per cm; periaxial tabellae straight, slightly domed with downturned edges, gently dipping, 20 to 28 per cm; wall about 0.2 mm wide where present.

Documentation. LACMIP holotype 6425, UCMP paratype 37255. Five thin sections and 29 polished sections from two coralla from LACMIP locality 1125 (holotype 6425) and UCMP locality D-852 (paratype 37255) were studied.

Discussion. The UCMP paratype of *A. fergusonii* is a small corallum (4 cm diameter) and has smaller corallites (diameter 6 to 10 mm) and slightly fewer major septa (13 to 16) than the holotype. I consider it to be a juvenile corallum, although the possibilities exist that it may belong to another species or represent variation within the species. Both coralla were closely associated in the same bed.

A. fryi n. sp. from the Potter Ridge section of the McCloud Limestone has smaller corallites, a more continuous wall, and a less complex axial structure than *A. fergusonii*. *A. molli* (Stuckenberg, 1888) from the Middle Carboniferous of Russia and *A. manchurica* Yabe and Hayasaka, 1916 (the type species), from the Lower Permian (?) of Manchuria have smaller corallites (diameter 6 to 8 mm), simpler axial structures, septa more continuous with the axial lamellae, and less well-developed minor septa.

This is the first record for the genus in the Americas.

Etymology. The species is named for Mr. Eugene Ferguson.

Arachnastraea fryi n. sp.

Figures 41d-e

Diagnosis. A species of *Arachnastraea* characterized by the combination of moderately large corallites, well-developed minor septa, and a moderately complex axial structure. It has smaller corallites, somewhat shorter minor septa, and a somewhat less complex axial structure than *A. fergusonii*. It has larger corallites, a more complex axial structure, and better developed minor septa than *A. molli* and *A. manchurica*.

External Description. Corallum cerioid-astreoid, maximum observed diameter 12 cm; calyx not observed.

Transverse Section Description. Corallites polygonal, 5 to 7 sided, 6.5 to 10 mm wide at greatest diameter; septa of 2 orders, 15 to 17 each; major septa 2.5 to 3.5 mm long, extending into tab-

ularium 0.5 to 1.0 mm, thin throughout or slightly dilate in tabularium, generally connected with septal lamellae of axial structure; minor septa well developed, extending across dissepimentarium and barely penetrating tabularium; axial structure arachnoid, with thin, well-developed medial plate, septal lamellae generally equal in number to and confluent with major septa; dissepimentarium regular; dissepiments straight, concentric, angulo-concentric, or pseudoherringbone; corallite wall cerioid-astreoid, about 0.2 mm thick.

Longitudinal Section Description. Dissepimentarium of 4 to 6 ranks of gently inclined dissepiments, about 33 per cm; tabellae of 2 ranks, axial and periaxial; axial tabellae sloping either steeply or gently inwards and upwards to columella; periaxial tabellae sloping gently inwards and upwards to axial tabellae; columella slightly sinuous; wall clearly shows interruptions.

Documentation. UCMP holotype 37256. Two thin sections and 12 polished sections from one corallum from UCMP locality D-837 were studied.

Discussion. In several features, *Arachnastraea fryi* appears to be close to *A. molli* from the Middle Carboniferous of Russia, as figured by Hill (1956, figs. 194, 3a, 3d) and Soshkina, Dobrolyubova, and Kabakovich (1962:343, figs. 106a, 106b). All illustrations show remarkably similar axial structures, partially dilate septa, and denticulate walls, where present. The specimen figured by Hill shows corallites with as many as 21 major septa and apparently no minor septa, whereas that of Soshkina, Dobrolyubova, and Kabakovich has well-developed minor septa and major septa numbering about 14. They may represent different species.

Because it has fewer septa and well-developed minor septa, *A. fryi* is not specifically close to the specimen of *A. molli* figured by Hill. The specimen figured by Soshkina, Dobrolyubova, and Kabakovich has somewhat fewer septa than *A. fryi*, but their *A. molli* has septa that are dilate in the dissepimentarium of some corallites. *A. fryi* has no dilate septa in the dissepimentarium and its dissepimentarium is much wider than that shown in the Soshkina, Dobrolyubova, and Kabakovich illustrations.

Differences with *A. fergusonii* n. sp. also from the McCloud Limestone, are listed in the discussion of that species.

Etymology. The species is named for Dr. Wayne L. Fry.

Order Tabulata Milne Edwards and Haime, 1850

Genus *Bayhaium* Langenheim and McCutcheon, 1959

Bayhaium merriamorum Langenheim and McCutcheon, 1959

Figures 43a-g

Bayhaium merriamorum Langenheim and McCutcheon, 1959: 100, pl. 19, figs. 1-6.

Bayhaium merriamorum Langenheim and McCutcheon. Lafuste, 1963:1127, text-figs. 1-3.

Documentation. UCMP hypotypes 37257-37260. Five thin sections and 14 polished sections from one corallum from UCMP

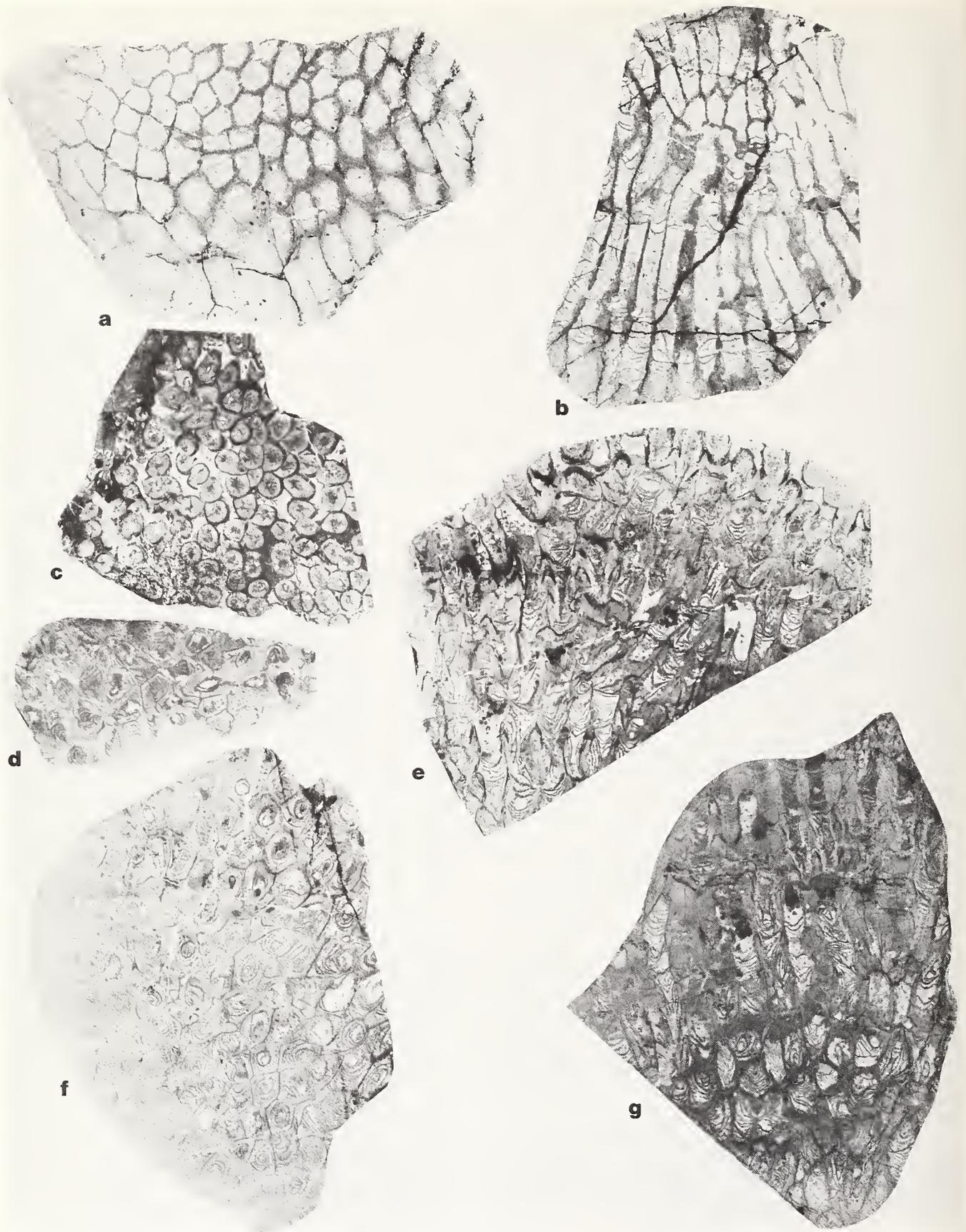


Figure 43. *Bayhaim merriamorum* Langenheim and McCutcheon, 1959. All parts x3. **Parts a and b,** UCMP hypotype 37257, transverse (a) and longitudinal (b) sections. **Part c,** UCMP hypotype 37258, transverse section. **Parts d and e,** UCMP hypotype 37259, transverse (d) and longitudinal (e) sections. **Parts f and g,** UCMP hypotype 37260, transverse (f) and longitudinal (g) sections.

locality D-181 (hypotype 37257), four thin sections and four polished sections from one corallum from UCMP locality D-838 (hypotype 37258), and four thin sections and 21 polished sections from two coralla from UCMP locality D-839 (hypotypes 37259–37260) were studied.

Discussion. Since a very active search was made by me for this coral and I found that it occupied narrow stratigraphic ranges in the Bayha and Potter Ridge sections, I conclude that these occurrences represent a biostratigraphic correlation between the sections and probably the intervening type locality.

Bayhaium virginiae n. sp.

Figures 44a–f

Diagnosis. A species of *Bayhaium* characterized by the combination of thick walls in the immature regions and the rarity of septa and tabulae. It has thicker walls in the immature region and far fewer septa and tabulae than *B. merriamorum*. It has far fewer septa and tabulae than *B. vallum*.

External Description. Corallum cerioid-fasciculate, generally hemispherical, maximum observed diameter 4 cm, outer corallites cylindrical, closely spaced.

Transverse Section Description. In immature portion, corallites cerioid, generally 1 to 1.5 mm in diameter (1 is 2 mm), generally without septa (1 has 3 short septa), with sclerenchyme-thickened walls (generally about 0.3 mm thick on each side of separating dark line, 1 thickened *Multithecopora*-like to 0.9-mm-thick wall and constricted 0.3-mm thick tabularium), with rare infundibuliform tabulae about 0.16 mm thick, no apparent connecting tubules. In mature portion, corallites 1 to 1.5 mm diameter, 0.6 to 1.0 mm apart, with walls 0.3 to 0.5 mm thick.

Longitudinal Section Description. In mature portion, as above, with randomly clumped tabulae, 2 to 4 per mm, generally concave, rarely tabellae or infundibuliform; connecting tubules tunnel-like, rare, randomly scattered, with 0.4- to 0.5-mm wide openings with tabulae passing through; calices as much as 6 mm from top to first tabulae below.

Documentation. UCMP holotype 37261, UCMP paratype 37262. Six thin sections and nine polished sections from two coralla from UCMP locality D-852 were studied.

Discussion. *Bayhaium merriamorum*, the type species of the genus, is known only from the type locality and nearby areas in the McCloud Limestone, which are stratigraphically higher in the formation and south of the locality where *B. virginiae* n. sp. was collected. The latter species has much thicker walls in the immature region, far fewer septa where developed at all, and far fewer tabulae than *B. merriamorum*. *B. vallum* Hoare, 1964, from the Wolfcampian Sunflower Formation of Elko County, Nevada, is more similar to *B. merriamorum* than to *B. virginiae*. The latter species can be distinguished readily from *B. vallum* by many of the same features that distinguish it from *B. merriamorum*, especially the lack of, or poor development of, septa and tabulae. However, both *B. virginiae* and *B. vallum* have thicker walls in the immature parts of the corallum than has *B. merriamorum*.

This is the third species of *Bayhaium* erected. The genus has been reported only from the Lower Permian (Wolfcampian) Cor-

dilleran eugcosyncinal rocks of California and Nevada.

Etymology. The species is named for Virginia A. McCutcheon Langenheim.

Genus *Enigmalites* Tchudinova, 1975a

Enigmalites roberti n. sp.

Figures 44g–h; 45a–c

Diagnosis. A species of *Enigmalites* characterized by the combination of large corallites, poorly developed septal spines and connecting processes, and relatively abundant dissepiments and tabulae. It has fewer septal spines, fewer connecting processes, and more dissepiments and tabulae than *E. lectus*. It has larger corallites than *E. tschernyschewi*, *E. lautus*, and *E. largus*.

External Description. Corallum basally reptant, distally erect, phaceloid, irregularly hemispheroidal, maximum observed height 9 cm, width 9 cm (both incomplete); epitheca with coarse rugae; connecting tubules rare.

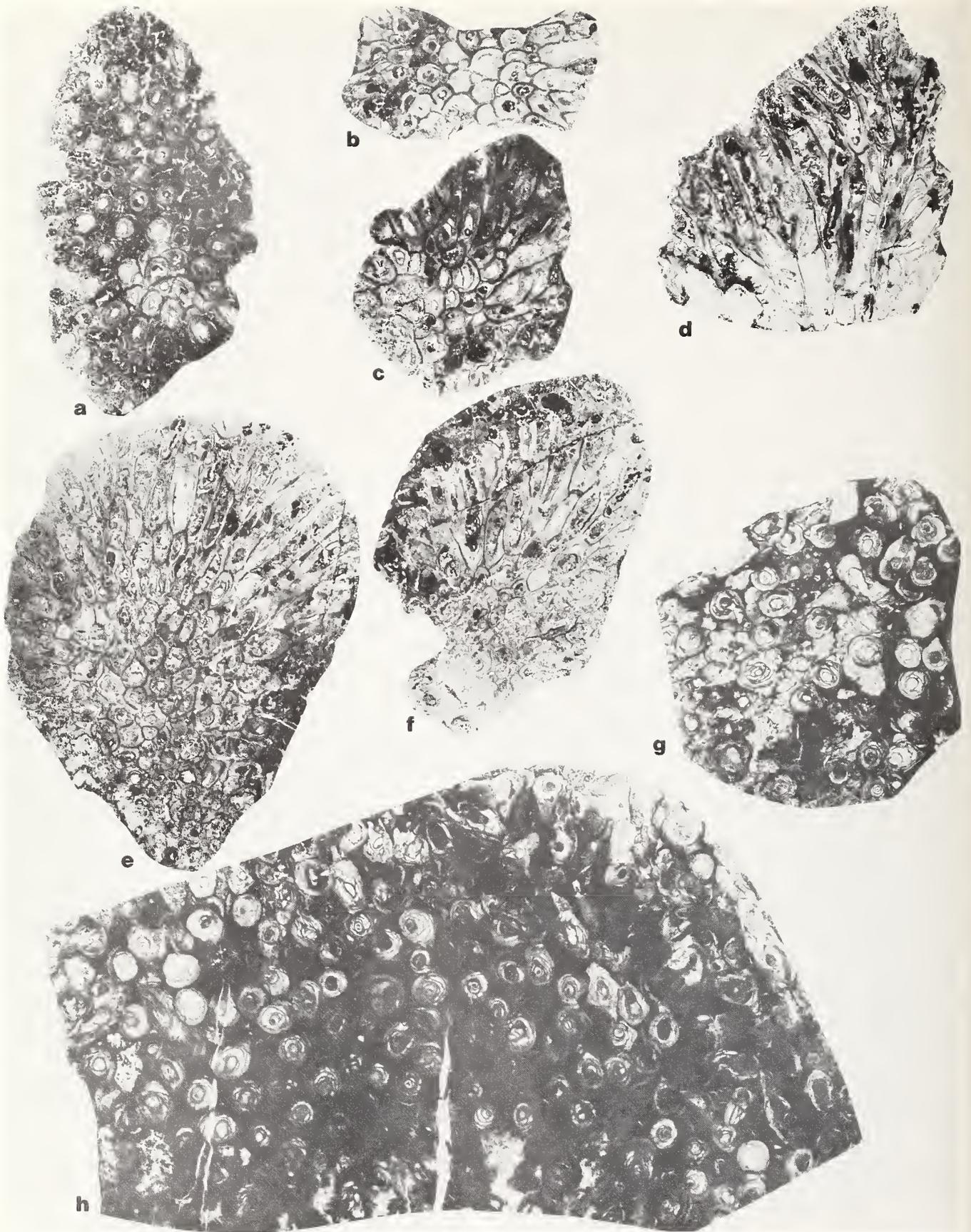
Internal Description. Corallites 2.2 to 2.5 mm in diameter, touching to as much as 1 corallite diameter distant; wall 2-layered, 0.2 to 0.4 mm thick, epitheca microstructure not observed, sclerenchyme layer fibrous, with fibers radially oriented, at right angles to epitheca in transverse and longitudinal sections, not bundled into trabeculae; dissepiments numerous, 1 to 3 ranks, steeply dipping in longitudinal section, circling the interior of the wall in transverse section, leaving central or slightly off-centered tabularium; tabularium open or rarely crossed by flat or slightly domed tabulae; septal spines short, conical, irregularly developed, not present in all corallites, maximum number of 14 where fully developed (rare), generally only a few present on wall, on sclerenchyme, and on dissepiments (lonsdaleoid-like), pointing gently inwards and upwards in longitudinal sections; connecting tubules and mural pores very rare.

Documentation. UCMP holotype 37263, UCMP paratypes 37264–37265. Six thin sections and 57 polished sections from three coralla from UCMP locality A-7101 were studied.

Discussion. Tchudinova (1975a:13) based this genus on a new species and a species of Stuckenberg (1895:19) and later (1975b:429) placed two other new species in it. These specimens were collected in the Ural Mountains. Tchudinova's three species are Lower Permian and Stuckenberg's species is Upper Carboniferous.

The genus is characterized by the combination of an epitheca lined by a thin layer of sclerenchyme, incomplete tabulae taking the form of dissepiments and leaving a tabularium-like central area that is occupied in places by tabulae, septal spines, and rare connecting processes. Probably some species presently placed in *Syringopora* will be assigned by other workers to *Enigmalites*. *E. roberti* is the first report of the genus outside of Russia.

E. roberti is close to *E. lectus* Tchudinova, 1975a, the type species, in corallite size and thickness of the wall. *E. roberti* has fewer and less well developed septal spines, many present on the dissepiments, rarer connecting processes, more abundant dissepiments, and more tabulae than *E. lectus*. Both *E. roberti* and *E. lectus* have larger corallites than *E. tschernyschewi* (Stucken-



berg, 1895), *E. lautus* Tchudinova, 1975b, and *E. largus* Tchudinova, 1975b.

Etymology. The species is named for Mr. Robert B. Spangenberg.

Genus *Michelinia* de Koninck, 1841

Michelinia nelsoni n. sp.

Figures 45d–h

Diagnosis. A species of *Michelinia* characterized by the combination of moderately large corallites, lack of mural pores, and presence of generally complete tabulae. It has smaller corallites than *M. branteri*, *M. harkeri*, and *M. referta*. It has larger corallites than *M. eugeneae*, *M. subcylindrica*, and *M. tenuicula*. It has no mural pores such as those present in *M. exilimura*, *M. latebrosa*, *M. scopulosa*, and *M. spissata*.

External Description. Corallum cerioid, small, maximum observed diameter 2.1 cm, roughly hemispherical, covered ventrally by wrinkled corallite wall; calices 3.5 to 4.5 mm wide, 2 to 5 mm deep, with flat floors and smooth, slightly flaring walls.

Transverse Section Description. Corallites polygonal, 5 to 7 sided, 3.5 to 4.5 mm wide; mural pores not observed, apparently absent; combined thickness of 2 corallite walls 0.3 to 0.5 mm.

Longitudinal Section Description. Tabulae generally complete, irregularly spaced, much thinner than corallite walls, about 0.06 mm thick, 0.5 to 1.5 mm apart, generally flat and horizontal, some slightly sagging or domed, some at angle across corallite.

Documentation. UCMP holotype 37266, UCMP paratypes 37267–37269, LACMIP paratypes 6426–6429. Six thin sections and 16 polished sections from five coralla and three etched coralla from UCMP locality D-852 (holotype 37266, paratypes 37267–37269) and LACMIP locality 1125 (paratypes 6426–6429) were studied.

Discussion. No species of *Michelinia* or its closely related and perhaps synonymous genus *Pleurodictyum* Goldfuss, 1829, has been described previously from the Permian of North America (Sando, 1974, 1980a; Wilson, 1974), although Rowett (1969:15) reported *Michelinia* sp. in the Permian of Alaska, but did not describe it in that paper as he stated he had. Of the 11 species described from the Pennsylvanian of North America (Sando, 1974, 1980a), only four have corallite diameters comparable to those of *M. nelsoni*. These are *M. exilimura* Mather, 1915, from the Morrow Formation near Choteau, Oklahoma, *M. latebrosa* Moore and Jeffords, 1945, from the Otterville Limestone near Ardmore, Oklahoma, and elsewhere in Texas, northwestern Arkansas, and northeastern Oklahoma, *M. scopulosa* Moore and Jeffords, 1945, from the Lower Pennsylvanian of northeastern Oklahoma and northwestern Arkansas, and *M. spissata* Moore and Jeffords, 1945, from the Brentwood Limestone near Brent-

wood, Arkansas. *M. nelsoni* apparently lacks mural pores, whereas all of the above Pennsylvanian species have them variously developed from “not abundant” to “very numerous.” In addition, the tabulae of *M. spissata* are mostly incomplete, whereas those of *M. nelsoni* are mostly complete.

Etymology. The species is for Dr. Samuel J. Nelson.

Genus *Neomultithecopora* Lin, 1963

Neomultithecopora sandoi n. sp.

Figures 46a–f; 47a–f

Diagnosis. A species of *Neomultithecopora* characterized by the combination of relatively large corallites, clumped tabulae, and rare connecting tubules or mural pores. It has larger corallites than *N. syringoporoides*, *N. simplex*, *N. uralica*, and *N. repens*. It has smaller corallites than *N. berkhi*.

External Description. Corallum basally reptant, distally erect, phaceloid, irregularly hemispheroidal, maximum observed height 9 cm, width 7 cm (both incomplete); epitheca with fine and coarse rugae.

Internal Description. Corallites 1.8 to 2.6 mm diameter (generally about 2.0 mm), touching to as much as 2 corallite diameters distant; tabulae distally concave, convex, or elongate and cyst-like, clumped in groups of as many as 6 in 2-mm vertical space, generally only 1 shape in a clump but all shapes may occur in a single corallite, present where sclerenchyme is thin or thick, absent in most parts, some crossing through openings connecting corallites; corallite wall distally thin, elsewhere thickened by sclerenchyme to as much as 1.1 mm thick, leaving tabularium as narrow as 0.1 mm; septal spines regularly superposed and juxtaposed grid-like in longitudinal and horizontal rows, conical, 0.1 to 0.2 mm long, about 0.1 mm diameter at base, dark brown color contrasting with lighter sclerenchyme, in transverse section present on corallite walls and in some on inner layers of sclerenchyme (as many as 30 on former, 15 on latter), in longitudinal section pointing inwards and gently upwards, about 0.1 mm apart, in tangential longitudinal section circular cross sections of spines in 2 or more vertical rows, about 4 or 5 in 1 mm vertically, spines in parallel rows regularly opposite one another; septal spines not present in every corallite or everywhere in corallites that have them; connecting processes scattered, rare, becoming mural pores between touching corallites or, more rarely, connecting tubules as long as 2.5 mm, with diameters to 1.1 mm between more distant corallites; sclerenchyme composed of minute, elongate fibers at right angles to corallite wall in both transverse and longitudinal sections, not bundled into trabeculae.

Documentation. UCMP holotype 37270, UCMP paratypes 37271–37279, LACMIP paratypes 6430–6438. Eighteen thin sections and 202 polished sections from 19 coralla from UCMP

Figure 44. *Bayhaium virginiae* n. sp. and *Engimalites roberti* n. sp. All parts x3.

Parts a through f. *B. virginiae* n. sp. **Parts a through d,** UCMP holotype 37261, transverse (a–c) and longitudinal (d) sections. **Parts e and f,** UCMP paratype 37262, transverse and longitudinal sections.

Parts g and h. *E. roberti* n. sp., UCMP holotype 37263, transverse sections.

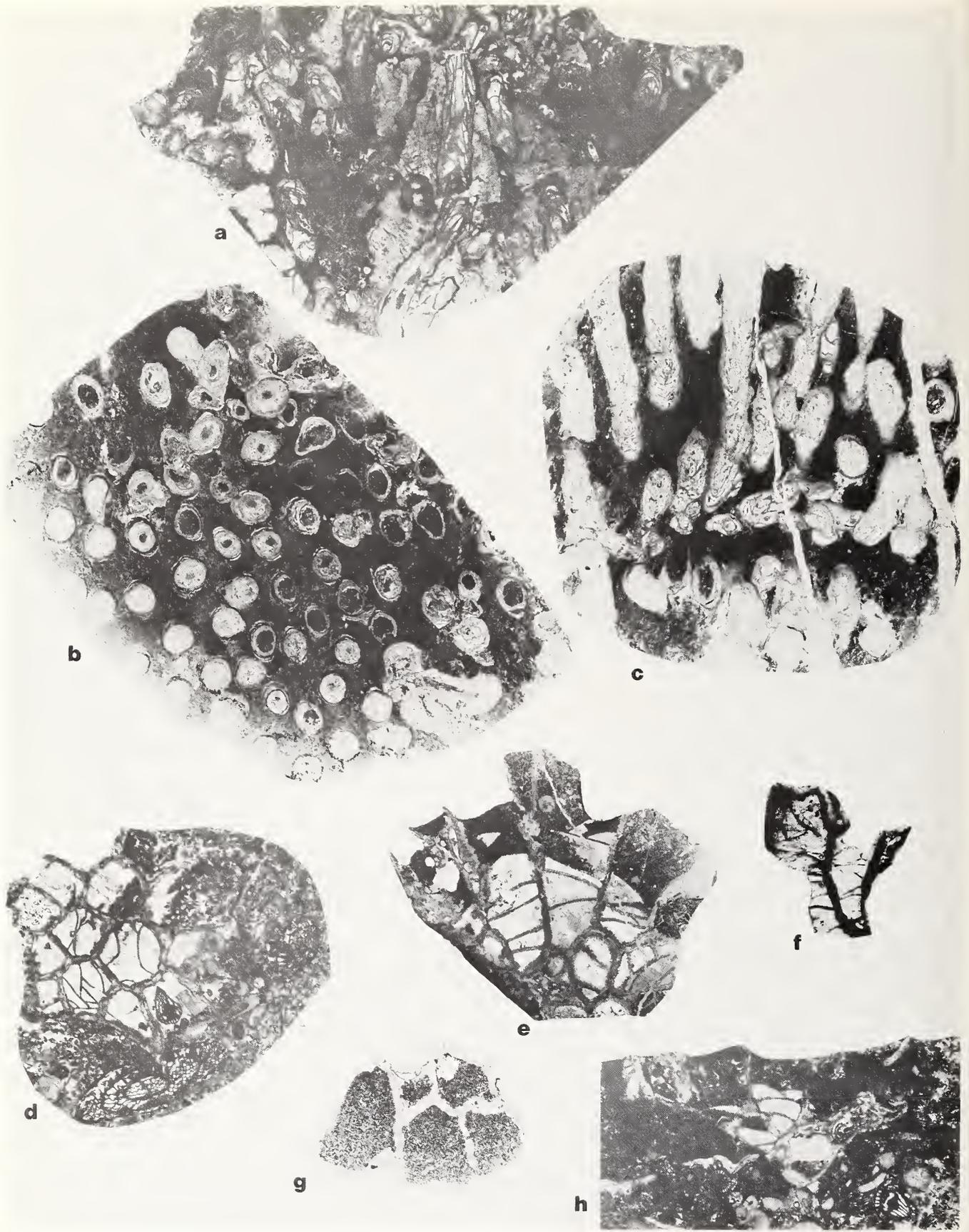


Figure 45. *Engimalites roberti* n. sp. and *Michelinia nelsoni* n. sp. All parts x3.

80 Parts a through c. *E. roberti* n. sp. Part a, UCMP holotype 37263, longitudinal section. Parts b and c, UCMP paratype 37264, transverse (b) and longitudinal (c) sections.

Parts d through h. *M. nelsoni* n. sp. Parts d through g, UCMP holotype 37266, transverse (d, g) and longitudinal (e, f) sections. Part h, LACMIP paratype 6426, longitudinal section.

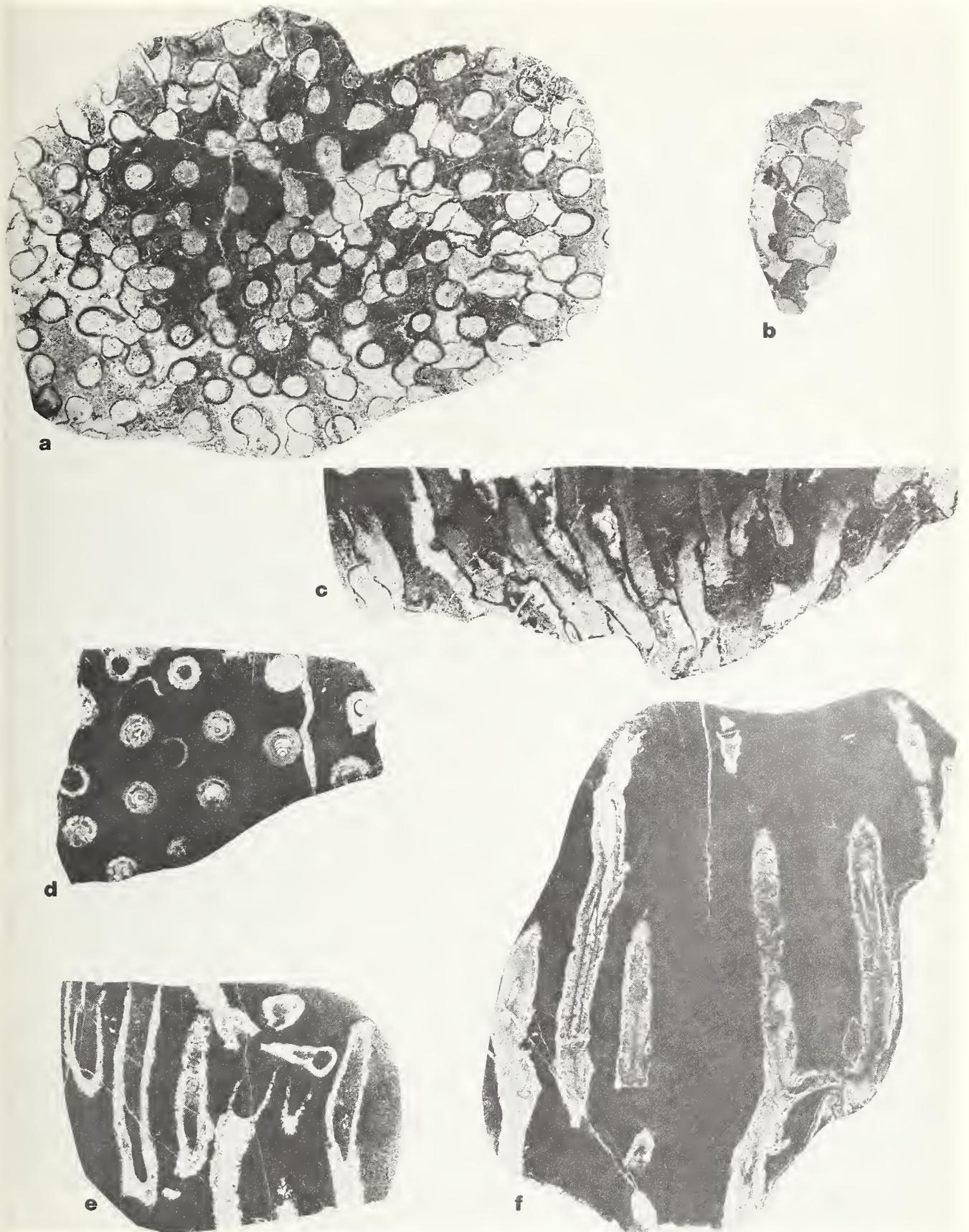
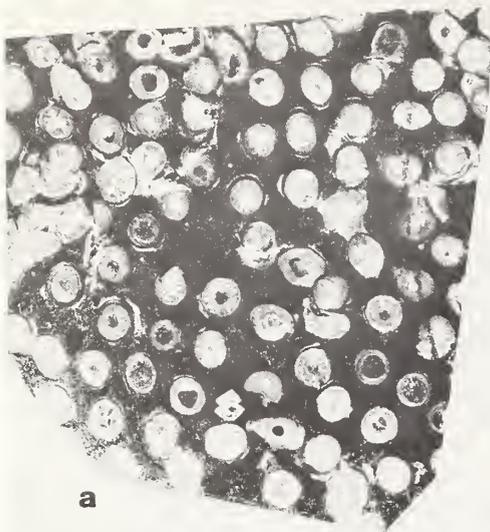


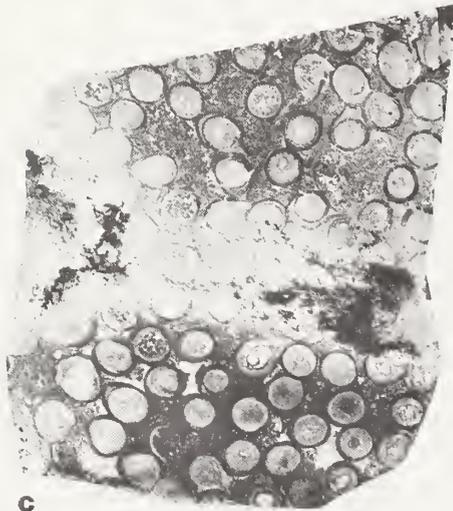
Figure 46. *Neomultihecopora sandoi* n. sp. All parts x3. Parts a through c, UCMP holotype 37270, transverse (a, b) and longitudinal (c) sections. Parts d through f, UCMP paratype 37275, transverse (d) and longitudinal (e, f) sections.



a



b



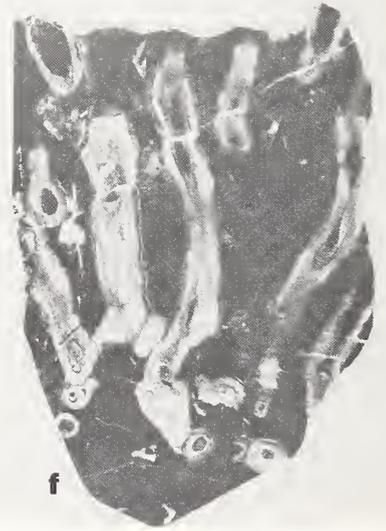
c



d



e



f

82 **Figure 47.** *Neomultithecopora sandoi* n. sp. All parts x3. **Parts a and b,** UCMP paratype 37277, transverse (a) and longitudinal (b) sections. **Parts c and d,** UCMP paratype 37278, transverse (c) and longitudinal (d) sections. **Parts e and f,** LACMIP paratype 6438, transverse and longitudinal sections (e) and longitudinal section (f).

localities D-801 (paratypes 37271–37273), D-803 (holotype 37270), D-822 (paratype 37274), D-831 (paratypes 37275–37276), D-832 (paratype 37277), and D-858 (paratypes 37278–37279) and LACMIP localities 1125 (paratypes 6430–6431), 1132 (paratypes 6432–6433), 1133 (paratypes 6434–6437), and 4457 (paratype 6438) were studied.

Discussion. This is the first report of *Neomultithecopora* in North America and the first record of it in the Permian. The type species, *N. syringoporoides* Lin, 1963, is from the Lower Carboniferous of south China. Other species occur in the Lower Carboniferous, and questionably Upper Carboniferous, of the Ural Mountains and Novaya Zemlya of Russia (Kachanov, 1967:24; Tchudinova, 1975a:17).

This genus is separated from *Multithecopora* Yoh, 1927, chiefly on the basis of the presence of very symmetrically arranged septal spines in the former and perhaps also by microstructural differences of the sclerenchyme. *Multithecopora* seems to have sclerenchyme arranged in concentric layers, whereas *Neomultithecopora* has sclerenchyme composed of radially arranged fibers. The only other tabulate coral with highly thickened walls from the McCloud Limestone, *Bayhaium* Langenheim and McCutcheon, 1959, also has sclerenchyme composed of calcite fibers (Lafuste, 1963), but they differ from those of *Neomultithecopora* in being bundled into trabeculae.

Some of the coralla of *N. sandoi* have wholly or partially silicified walls. The silicified parts are a pale blue, whereas the septal spines are brown. The septal spines are most obvious when observed in reflected light but not always apparent when examined in thin section by transmitted light.

N. sandoi has greater corallite diameters than *N. syringoporoides* from the Lower Carboniferous of south China, *N. simplex* Kachanov, 1967, from the Lower Carboniferous of the Ural Mountains, and *N. repens* (Stuckenbergh, 1895) from the Upper Carboniferous of the Ural Mountains. The latter species is here placed in the genus based on the report of Tchudinova (1975a:17) that it has septal spines.

N. berkhi (Gorskiy, 1951), from the Lower Carboniferous of Novaya Zemlya and the Ural Mountains (Kachanov, 1967:29) has greater corallite diameters than *N. sandoi*.

N. uralica Kachanov, 1967, from the Lower Carboniferous of the Ural Mountains and Novaya Zemlya, has abundant connecting tubules, whereas *N. sandoi* has very few.

Etymology. The species is named for Dr. William J. Sando.

Genus *Syringopora* Goldfuss, 1826

Syringopora mccutcheonae Wilson and Langenheim, 1962

Figures 48a–b

Syringopora mccutcheonae Wilson and Langenheim, 1962:515, pl. 89, figs. 11–13.

S. mccutcheonae Wilson and Langenheim. Langenheim and Langenheim, 1965:235.

Documentation. UCMP hypotype 37280. Five thin sections and 35 polished sections from one corallum from UCMP locality D-842 were studied.

Discussion. This species is geographically widespread in Lower Permian strata of eastern Nevada (Wilson and Langenheim, 1962; Langenheim and Langenheim, 1965). The McCloud Limestone corallum agrees very closely with the Nevada specimens in corallite diameter, absence of septa and septal spines, and general occurrences of connecting processes at the same levels in the coralla. Apparent differential silicification in some corallites gives the impression that sclerenchyme-embedded septa are present.

Syringopora multattenuata McChesney, 1860

Figures 48c–f

Syringopora multattenuata McChesney, 1860:75.

Syringopora multattenuata McChesney, 1867:2, pl. 2, fig. 4.

Syringopora multattenuata McChesney. McCutcheon, 1961:1014, pl. 121, figs. 1–8.

Documentation. UCMP hypotypes 37281–37282. Six thin sections and 30 polished sections from one corallum from UCMP locality D-825 (hypotype 37281) and two thin sections and 26 polished sections from one corallum from UCMP locality D-853 (hypotype 37282) were studied.

Discussion. This species was thoroughly reviewed by McCutcheon (1961), who summarized the geographic occurrence as “widespread in Pennsylvanian rocks of the United States . . . in the Permian of Spitzbergen . . . in the Wolfcampian of the Arrow Canyon Range, Clark County, Nevada.” The McCloud Limestone specimens agree closely with the neotype and hypotypes of McCutcheon (1961), except that the corallite diameters of the McCloud specimens, while generally about 2 mm, do range as high as 2.5 and 2.8 mm in a few corallites, which is somewhat greater than the 2.2-mm maximum cited by McCutcheon (1961:1014).

Sando (1965:32) commented on the differences and similarities of *S. multattenuata* and *S. occidentalis* Meek, 1877, from the Pennsylvanian Weber Sandstone or Permian Park City Formation of Utah, and concluded that “. . . in *Syringopora multattenuata* the axial tube is more clearly defined and the incomplete tabulae are more numerous, more variable in size, and generally more inflated than in *S. occidentalis*.”

LOCALITIES

The following localities are entered in the UCMP and LACMIP locality registers. They all are located in the McCloud Limestone. Abbreviations also are used for United States Geological Survey (USGS), township (T), range (R), north (N), south (S), east (E), and west (W). References to fusulinid zones are those of Skinner and Wilde (1965), with age determinations amended by Wilde (1971:364).

UCMP Localities

A-7096. Bayha section (lower part is the Tunnel Inn section of Skinner and Wilde, 1965). It is on the ridge most likely collected by the California Geological Survey in 1862. The traverse begins at the lowest exposure near the base of the W face of the ridge with summit marked “1693” in the NE ¼ of section 15, T 33 N,



Figure 48. *Syringopora mccutcheonae* Wilson and Langenheim, 1962, and *S. multattenuata* McChesney, 1859. All parts x3.

84 **Parts a and b.** *S. mccutcheonae*, UCMP hypotype 37280, transverse (a) and longitudinal (b) sections.

Parts c through f. *S. multattenuata*. **Parts c and d,** UCMP hypotype 37281, transverse (c) and longitudinal (d) sections. **Parts e and f,** UCMP hypotype 37282, transverse (e) and longitudinal (f) sections.

R 4 W, as shown on the USGS 7.5-minute topographic quadrangle of Project City, California (1957), continues due E over the summit of the ridge, down the E dip slope into cover, offsets slightly S and continues up a smaller limestone hill, down again into cover and ends at the second of two 2-foot (0.6-meter) thick limestone units, which crop out of deep soil in the saddle shown in the NW ¼ of section 14, T 33 N, R 4 W, of the same map. Thicknesses recorded for this section include sills of quartz diorite found in it. A-7096 is 500 feet (152.4 meters) above the base of the section and has abundant cerioid corals, small solitary corals, and rare, large pelmatozoan columns. Fusulinid zone F.

A-7101. W bank of the McCloud River at river level and N of the McCloud River bridge as shown in the NE ¼ of section 31, T 35 N, R 3 W, of USGS 15-minute topographic quadrangle of Bollibokka Mountain, California (1957). Silty limestone with some coquinooid beds of echinoid plates and spines, syringoporida corals, fusulinids. Same as LACMIP locality 1123. Fusulinid zone F.

B-4837. This locality is in the NE ¼ of the SW ¼ of section 35, T 33 N, R 4 W, as shown on the USGS 7.5-minute topographic quadrangle of Project City, California (1957). It is a nearly covered, small limestone outcrop N of a small tributary that flows into the East Fork of Stillwater Creek. A single corallum of a fasciculate coral was collected here by Mr. Chang Ki Hong of Korea in 1962 and brought to me at UCMIP for identification. The matrix on the coral has a specimen of the fusulinid *Pseudoschwagerina robusta* (Meek, 1864). I examined the locality but found no other fossils. Fusulinid zone E.

D-181. Bayha section, 415 feet (126.4 meters) above the base. Cerioid tabulate corals, cerioid rugose corals. Fusulinid zone F.

D-800. Lowest black limestone unit on spur SE of the forest service building ¼ mile S of the McCloud River bridge on Gilman Road as shown in the SE ¼ of section 32, T 35 N, R 3 W, of the USGS 15-minute topographic quadrangle of Bollibokka Mountain, California (1957). Large solitary rugose corals, *Omphalotrochus*, *Hustedia* Hall and Clarke, 1893, fusulinids, fenestellid bryozoans. Fusulinid zone A.

D-801. Estimated 300 feet (91.4 meters) stratigraphically above D-800. Syringoporida corals to 2 feet (0.6 meters) in diameter, large solitary rugose corals, *Omphalotrochus*. Fusulinid zone B.

D-803. Float collection made an estimated 700 feet (213.4 meters) stratigraphically above D-801. Large solitary rugose corals, cerioid rugose corals, syringoporida corals. Fusulinid zone B or C.

D-804. An estimated 150 feet (45.7 meters) stratigraphically above D-803 on spine of spur. Fasciculate rugose corals. Fusulinid zone C.

D-805. Due E of D-804 on spine of spur an estimated 300 feet (91.4 meters) stratigraphically below summit of main N-S ridge. Fasciculate rugose corals. Fusulinid zone B.

D-819. McCloud Bridge East section. Probably same as Skinner and Wilde's (1965) McCloud Guard Station section. This traverse begins at the lowest exposures of the formation on the first spur S of the E end of the McCloud River bridge as shown in the NE ¼ of the SE ¼ of section 31, T 35 N, R 3 W, of USGS 15-

minute topographic quadrangle of Bollibokka Mountain, California (1957), and continues E over the top of the high ridge, stopping at cover in the saddle at the east end of the dip slope as shown in the NE ¼ of the SW ¼ of section 32, T 35 N, R 3 W, same map. D-819 is 1140 feet (347.5 meters) stratigraphically above the base of the section. Many silicified fossils, large solitary corals, *Conocardium langenheimi*, *Omphalotrochus*, fusulinids. Same as LACMIP locality 4458. Fusulinid zone A.

D-821. Wide bench below sheer cliff 410 feet (125 meters) stratigraphically above D-819. Fusulinids, solitary rugose corals, syringoporida corals, brachiopods, bryozoans, bivalves. Same as LACMIP locality 1132. Fusulinid zone B.

D-822. Bench 34 feet (11 meters) stratigraphically above D-831. Large solitary rugose corals, syringoporida corals. Fusulinid zone B.

D-825. Beds 310 feet (94.5 meters) stratigraphically above D-822. Syringoporida corals. Fusulinid zone C.

D-826. Bench 130 feet (40 meters) stratigraphically above D-825. Large solitary rugose corals. Fusulinid zone C.

D-827. Beds 20 feet (6.1 meters) stratigraphically above D-826. Fusulinids and cerioid rugose corals. Fusulinid zone C.

D-828. Topographic summit of main ridge of section, 670 feet (204 meters) above D-827. Fusulinids, fasciculate rugose corals. Fusulinid zone C.

D-831. Approximately 200 yards (183 meters) S of D-819 and about 15 feet (4.6 meters) stratigraphically higher. Fusulinids, abundant large solitary rugose corals, abundant syringoporida corals, *Conocardium langenheimi*. Same as LACMIP locality 1133. Fusulinid zone A.

D-832. Approximately 100 yards (91.4 meters) S of D-831 and an estimated 10 feet (3 meters) stratigraphically higher. Syringoporida corals and large solitary rugose corals. Fusulinid zone A.

D-834. Potter Ridge section. The traverse begins at the lowest exposure of the formation on the W end of the ridge between Potter and Marble Creeks as shown in the SE ¼ of section 23, T 33 N, R 4 W, USGS 15-minute topographic quadrangle of Lamoine, California (1957), and continues up the ridge crest to the base of the intrusive overlying the last limestone unit in the saddle E of the knob on the ridge as shown in the NW ¼ of the SW ¼ of section 24, T 33 N, R 4 W, same map. Thicknesses recorded for this section include sills of quartz diorite. D-834 is 130 feet (39.6 meters) above the base of the section. Fasciculate rugose corals. Fusulinid zone E.

D-836. Beds 80 feet (24.4 meters) stratigraphically above D-834. Fasciculate and large solitary rugose corals. Same as LACMIP locality 1114. Fusulinid zone E.

D-837. Beds 25 feet (7.6 meters) stratigraphically above D-836. Fusulinids, cerioid and cerioid-astroeid rugose corals. Fusulinid zone E.

D-838. Beds 65 feet (19.8 meters) stratigraphically above D-837. Fasciculate rugose corals, cerioid syringoporida corals, *Omphalotrochus*. Fusulinid zone E.

D-839. Beds 10 to 35 feet (3 to 10.8 meters) stratigraphically above D-838. Cerioid syringoporida corals. Fusulinid zone F.

D-840. Beds 230 to 340 feet (70 to 103.6 meters) strat-

igraphically above D-839. Fasciculate rugose corals. Fusulinid zone F.

D-841. Beds 285 feet (86.8 meters) stratigraphically above D-840. Fusulinids, solitary and cerioid rugose corals. Fusulinid zone F.

D-842. Beds 320 feet (97.5 meters) stratigraphically above D-841. Large solitary rugose corals with and without axial structures, cerioid rugose corals, syringoporid corals, large bellerophonid gastropods. Same as LACMIP locality 1116. Fusulinid zone F.

D-843. Beds 20 feet (6.1 meters) stratigraphically above D-842. Fusulinids, large solitary and cerioid rugose corals, gastropods. Fusulinid zone F.

D-845. Beds 105 feet (31.9 meters) stratigraphically above D-843. Large cerioid rugose corals. Fusulinid zone F.

D-852. Summit of Hirz Mountain, dip slope E of the foot of the lookout tower as shown in the SE ¼ of section 7, T 35 N, R 3 W, of the USGS 15-minute topographic quadrangle of Bollibokka Mountain, California (1957). Very rich fauna including fusulinids, syringoporid corals, solitary, fasciculate, cerioid-astroeid, and cerioid rugose corals, brachiopods, and gastropods. Same as LACMIP locality 1125. Probably fusulinid zone D.

D-853. Hirz Mountain section. The traverse begins at the lowest exposure of the formation of the NW face of the N end of the ridge that forms the summit of Hirz Mountain, as shown in the SE ¼ of section 7, T 35 N, R 3 W, of the USGS 15-minute topographic quadrangle of Bollibokka Mountain, California (1957) and continues E over the N end of the summit ridge and down the E face into cover as shown in the SE ½ of section 7 and the SW ¼ of section 8, T 35 N, R 3 W, of the same map. D-853 is 125 feet (37.1 meters) stratigraphically above the base. Syringoporid corals. Fusulinid zone D.

D-855. Beds 420 feet (128 meters) stratigraphically above D-853. Fusulinids, cerioid and fasciculate rugose corals, brachiopods. Fusulinid zone D.

D-857. Beds 240 feet (73 meters) stratigraphically above D-855. Fusulinids, cerioid and fasciculate rugose corals. Fusulinid zone D.

D-858. Beds 10 feet (3 meters) stratigraphically above D-857. Cerioid and fasciculate rugose corals, syringoporid corals. Fusulinid zone D.

D-861. Basal 50 feet (15.2 meters) of the Bayha section. Abundant fusulinids including *Pseudoschwagerina robusta* (Meek, 1864), solitary and fasciculate rugose corals, brachiopods, *Omphalotrochus whitneyi* (Meek). Some of Meek's (1864) specimens were collected from this stratigraphic interval, but not necessarily from this locality. See A-7096 for map description. Same as LACMIP locality 1119. Fusulinid zone E.

D-862. Beds 245 feet (74.7 meters) stratigraphically above D-861. Fusulinids, fasciculate rugose corals. Fusulinid zone F.

LACMIP Localities

1114. See UCMP locality D-836.

1116. See UCMP locality D-842.

1119. See UCMP locality D-861.

1120. Beds in the Bayha section, 380 feet (115.8 meters) strat-

igraphically above base. Fasciculate rugose corals. Fusulinid zone F.

1121. Beds 45 feet (13.7 meters) stratigraphically above 1120. Large fasciculate corals. Fusulinid zone F.

1122. Beds 45 feet (13.7 meters) stratigraphically above 1121. Cerioid and fasciculate rugose corals. Fusulinid zone F.

1123. See UCMP locality A-7096. Fusulinid zone F.

1124. Beds 10 feet (3.0 meters) stratigraphically above 1123. Fasciculate and cerioid rugose corals. Fusulinid zone F.

1125. See UCMP locality D-852.

1132. See UCMP locality D-821.

1133. See UCMP locality D-831.

1285. McCloud Point section. The traverse begins on the E bank of the McCloud River Arm of Shasta Lake at the first limestone exposure on Point McCloud as shown in the NW ¼ of the SW ¼ of section 5, T 35 N, R 3 W, of the USGS 15-minute topographic quadrangle of Bollibokka Mountain, California (1957), and ends at the highest exposure of the formation W of and about the same elevation as Gilman Road. This is the upper part of the McCloud Point section of Skinner and Wilde (1965). In this section, only this locality contained corals. It is 600 feet (182.5 meters) stratigraphically above the base of the section. Fasciculate and cerioid rugose corals. Impossible to collect the cerioid corals. Fusulinid zone G.

4457. Basal 100 feet (30.5 meters) of the McCloud Bridge West section (see 5312 for description), along strike on the SW side of the hill from the line of section and topographically above Gilman Road. Fasciculate rugose corals. Fusulinid zone A.

4458. See UCMP locality D-819.

5312. McCloud Bridge West section. The traverse begins at the lowest exposure of the formation on the SW slope of the hill at the W end of the McCloud River Bridge and NW of Gilman Road and runs NE to the crest of the hill and down the NE side into cover as shown on the NE ¼ of section 31, T 35 N, R 3 W, of the USGS 15-minute topographic quadrangle of Lamoine, California (1957), and the SE ¼ of section 30, T 35 N, R 3 W, of the USGS 15-minute topographic quadrangle of Bollibokka Mountain, California (1957). Locality 5312 is 260 feet (79.2 meters) stratigraphically above the base of the section. Solitary rugose corals, brachiopods, *Omphalotrochus* (?). Fusulinid zone A.

5316. Beds 220 feet (67 meters) stratigraphically above 5312. Enormous fasciculate rugose coralla (largest 5 feet in diameter), *Omphalotrochus*. Fusulinid zone A.

5318. Beds 75 feet (22.9 meters) stratigraphically above 5316, at the summit of the hill. Large solitary rugose corals, brachiopods. Fusulinid zone A.

5319. Beds 1 to 25 feet (0.3 to 7.6 meters) stratigraphically above 5318, at the top of the dip slope. Large solitary rugose corals. Fusulinid zone A.

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CONTRIBUTIONS IN SCIENCE

REVISED STATUS OF NET-WINGED MIDGES OF THE GENUS
BIBIOCEPHALA IN NORTH AMERICA BASED ON
A STUDY OF QUANTITATIVE VARIATION IN THE MALES
(DIPTERA: BLEPHARICERIDAE)

Charles L. Hogue



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REVISED STATUS OF NET-WINGED MIDGES OF THE GENUS
BIBIOCEPHALA IN NORTH AMERICA BASED
ON A STUDY OF QUANTITATIVE VARIATION IN THE MALES
(DIPTERA: BLEPHARICERIDAE)¹

Charles L. Hogue²

ABSTRACT. Samples of male *Bibliocephala* from North America were morphometrically analyzed to determine the presence or absence of subsets of specimens of possible taxonomic significance. Both univariate and multivariate (principal components analysis, unweighted pair group cluster and bloek cluster analysis) techniques were used. Some subsets were recognized, but none was believed to have specific or subspecific significance. A single, moderately variable species exists, *B. grandis* Osten Sacken, 1874.

Bibliocephala kelloggi Garrett, 1922, *B. griseus* Curran, 1923, and *B. nigripes* Alexander, 1965, are synonyms for *B. grandis*. The adult, pupa, and larva of *B. grandis* are redescribed, and the distribution and biology of the species are discussed.

INTRODUCTION

In North America, four nominate species have been referred to the genus *Bibliocephala* Osten Sacken, 1874. The identities of these have never been properly defined, and they have been variously treated in the fragmentary literature dealing with the Blephariceridae. Alexander (1965) gave the only general account of the genus; he recognized two valid and one questionably distinct species. After accumulating all available specimens of this genus from museum and other collections, and finding myself unable to separate the described species, using the characters prescribed by their original authors, I conducted an analysis *de novo* to determine the presence or absence of valid entities, unbiased by previous separations.

My first attempts to reduce the sample by inspective (often called "intuitive" or "classical") taxonomic procedure were totally without success, the specimens possessing an apparent high degree of overall similarity and continuous variation in virtually all characters. Indeed, few characters with consistent and measurable variation could be found at all. Suspecting that quantitative characters might exist by which groups of specimens could be defined, I subjected the material to a regimen of statistical procedures that seemed to me most likely to reveal any such groups that might lie hidden to the purblind eye. My choice of procedures was also partly determined by availability of computer facilities and programs (see METHODS).

Only adult male specimens were available in sufficient numbers for analysis. Females and immatures were too damaged and few in number to give reliable quantitative results, and in no case

were the latter associated with adults; identities, therefore, could not be correlated with decisions made pertaining to the other stages. These stages were measured and univariate statistics calculated for descriptive purposes, however.

My conclusions, having been based only on the one stage, must be considered provisional. However, in the interest of providing a basis for review works now in progress, mainly "Flies of the Nearctic Region" (ed., G.C.D. Griffiths, University of Alberta), I am publishing here a report on my studies of the best material available.

ANALYSIS

OPERATIONAL BASIS

Because past taxonomists concerned with North American *Bibliocephala* have recognized more than one species, my task has been to determine whether or not there are subsets of specimens among the material conforming to pheno-(morpho-)species criteria. These criteria are:

1. Low level of absolute variation in many characters.
2. Variation of most characters unimodal and normal.
3. Significantly higher degree of overall similarity within subsets than between subsets.
4. Suites of associated states (of biologically independent characters) present.

Of course, these elements in the definition of phenospecies are relative, and final decisions of their taxonomic and nomenclatorial application rest with the taxonomist. This section is an explanation of my application and represents only one approach to the problem of species resolution.

MATERIALS

A total of 786 specimens was available for this study, 526 immatures and 260 adults. From the latter, 160 were measured and are

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my "entire" sample; 30 of these were partly dissected for morphometric analysis and constitute the "subsample" referred to in the section on METHODS et seq.

A complete accounting of these specimens and their data is given under SPECIMENS EXAMINED.

TERMINOLOGY

In the following discussions and descriptions, terminology essentially follows that of my other papers on the Blephariceridae (particularly Hogue, 1973, 1978). Abbreviations for taxonomic characters are explained in the following section, those for specimen repositories are as follows: American Museum of Natural History (AMNH), Academy of Natural Sciences of Philadelphia (ANSP), British Museum (Natural History) (BMNH), Brigham Young University, Bean Life Science Museum (BYU), California Academy of Sciences (CAS), California Insect Survey Collection, University of California at Berkeley (CIS), Canadian National Collection, Biosystematics Research Institute, Agriculture Canada (CNC), C.P. Alexander collection, Amherst, Massachusetts (CPA), Cornell University (CU), Central Washington State University (CWS), Illinois Natural History Survey (INHS), Johns Hopkins University (JH), Kansas State University (KS), University of Kansas (KU), Natural History Museum of Los Angeles County (LACM), Museum of Comparative Zoology, Harvard University (MCZ), Oregon State University (OS), Ohio State University (OSU), Royal Ontario Museum (ROM), San Jose State University (SJS), University of Alberta (UAT), University of California at Davis (UCD), University of Idaho (UI), U.S. National Museum of Natural History (USNM), University of Wyoming (UW), and Washington State University (WSU).

Statistical notation follows that in general use plus special terms from Sneath and Sokal (1973).

TAXONOMIC CHARACTERS

Microscopic examination of both external and genital structures of male *Bibiocephala* revealed very few characters with variation adequate for taxonomic purposes. In fact, the vast majority of those characters usually found useful in species definition in the Blephariceridae were simply invariant by any reasonable measure. This logically included characters whose variation was, for practical purposes, indeterminable by reason of their subtlety (integumental coloration), irresoluteness (number of setae on the apex of the outer dististyle), or imperfection (body length).

The characters finally chosen are the following:

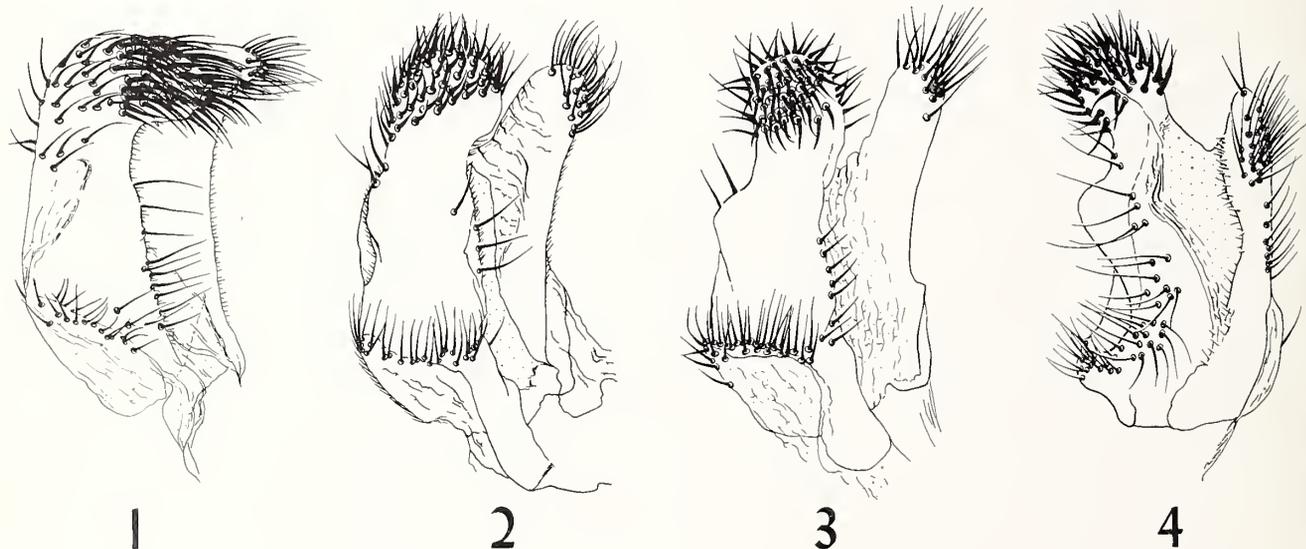
Continuous variates

1. Wing length. (WING)
- 2-10. Lengths of leg segments (femur, tibia, and basitarsus only; the shortness of the remaining tarsal segments precludes accurate measurement). (FEM 1, TIB 1, TAR 1, FEM 2, etc.)
11. Length of outer dististyle of genitalia. (OTDSYL)
12. Length of fused basistyles of genitalia. (BASYL)

Meristic variates

13. Number of median setae on proctiger of genitalia. (PRCTSM)
14. Number of median setae on ninth tergite. (TERSM)
15. Presence or absence of pilosity on upper eye. (EYHAIR)

No qualitative characters were used. Because the configurations of genital structures are generally very useful for species discrimination in the Blephariceridae, I made a careful compari-



Figures 1 through 4. *Bibiocephala grandis*. Outer dististyle of male genitalia. Rotated views to illustrate varied appearance depending on aspect. Figure 1, dorsal; Figure 2, dorsomesal; Figure 3, near mesal; Figure 4, full mesal.

son of these in both male and female specimens and concluded that none had consistent, appreciable states of variation. At first impression, several features seemed to exhibit shape differences; but upon careful stereoscopic inspection, I saw that they were no more than outline changes produced by different viewing angles. The genitalia are complex, and it is therefore difficult to mount them on slides with all parts in a standard position. Thus, with the compound microscope, the same element may look different in plane perspective, depending upon very slight rotations of position relative to other elements. Only by viewing on all sides can the true shape be determined. Examples of this problem are the entire dististyle and the basal lobe of the inner dististyle. As the former is rotated (Figs. 1–4), its appearance changes drastically. The rounded, flat apex of the latter lobe may appear pyramidal if viewed from the oblique position usually assumed in dorsoventral whole mounts of the genitalia.

METHODS

When direct inspection of the samples did not reveal subsets of specimens that met my phenospecies criteria, I sorted them mathematically and applied a variety of reductions and tests. These I chose on the basis of parsimony and the pragmatic availability locally of data processing systems. The analyses were carried out with the aid of packaged computer programs available at the Computer Center of the University of Southern California in Los Angeles and included “Biomedical Computer Programs, P-Series” (Dixon, 1977). Where applicable in the following discussion, the exact programs used from the latter are cited by their system call codes (e.g., “BMDP4M”).

Appropriate direct measures of criteria 1 and 2 are frequency distributions, bivariate correlations (to reveal possible ratio characters and to partially assess character interrelations), and the standard univariate descriptions of variation (standard deviation, coefficient of variation, Chi-square test for goodness of fit to normality, skewness and kurtosis, normal probability, and frequency plots). Interrelations of continuously varying characters were also read from a principal components analysis (PCA) applied to them (BMDP4M).

Criterion 3 was “tested” by means of an unweighted pair group cluster analysis (UPGMA) based on the average distance algorithm (BMDP2M). Distance measure was the sum of squares (Euclidian distance), both between individuals and between ascending clusters of individuals. Two analyses were run, one on the raw data and a second on PCA scores of the 12 continuous mensural characters plus the raw meristic data. The PCA scores were obtained from factoring of a variance-covariance matrix; both these scores and the raw meristic values were standardized by scaling before the distances were calculated. This second procedure follows the example of Agafitei and Selander (1980), who point out its advantages over the first in limiting the effect of a general size factor to a single character and in removing the effect of redundant or correlated characters by transforming them into retrolinear combinations of the originals. To evaluate clusters, I followed the recommendation of Sneath and Sokal (1973:304) that differences between branch points of a dendrogram ought to be more than several standard

errors of the similarity coefficient used in order to be significant.

Some idea of outliers and groupings of specimens can be derived also from the ordination content of PCA. This derives from bivariate plots of the first three components and plots of eigenvectors of each character, which I also completed.

Finally, using what seemed to be the four best uncorrelated and disjunctively variant characters, as determined from the calculations described above (i.e., WING, EYHAIR, PRCTSM, and TERSM), I processed ranked raw data for each according to a block clustering procedure (BMDP3M). To maximize the possibility of recognizing significant subsets and to reflect the trend toward bimodality in their frequency distributions, I ranked the characters into only two classes each. One of the characters was size and was represented by wing length, which—from its dominance of the first principal component—seems to be the best single measure of this character. This method of clustering by modal blocks identifies and groups specimens that have similar patterns for subsets of ranked character states. It seems to me to simulate most closely the methodology of (inspective) taxonomy in which one seeks suites of character states that vary disjunctively in parallel between taxa and thus indicate fundamental (probably genetic) discontinuities characteristic of phenetic and phyletic species. The method is discussed at length by Hartigan (1976).

The univariate statistics and plots were made from the entire sample; a subsample of 30, representing complete specimens from as many distinct localities as possible, was used for the PCA and cluster analysis. The specimens in the subsample are identified under SPECIMENS EXAMINED by the italic number appearing between the parentheses also enclosing the repository abbreviation.

RESULTS

Univariate statistics for the data are given in Table 1. Frequency distributions for all the characters fail the Chi-square goodness-of-fit test for normality at a highly significant level; only wing length has a distribution even approaching normal but is otherwise asymmetrical as are the curves for all the characters. Secondary grouping of class intervals for all characters produces generally flat-topped curves with mild to moderate skewness to the right (most) or left. Several curves have elongate positive tails for which a few very large specimens from an Oregon population are responsible. Primary curves drawn to the original frequencies appear multimodal, although the sample size is not large enough to permit reliable assessment of the detailed form of the distribution. A few characters have slight bimodal trends and were used in the two-state block cluster analyses as described below. Coefficients of variation range from 9.0 to 14.2.

The dendrograms obtained by the two UPGMA cluster analyses are reproduced in Figures 5 and 6. Since the subsample came from a large geographic area and a moderate coefficient of variation was observed for the continuous characters, I felt justified in choosing fairly high multiples of the standard error of the mean of the distances between specimens (Euclidian distance, d_1) to judge significance. With results from the raw data, these values are 10; with scaled data from PCA scores plus raw meristics, 6.

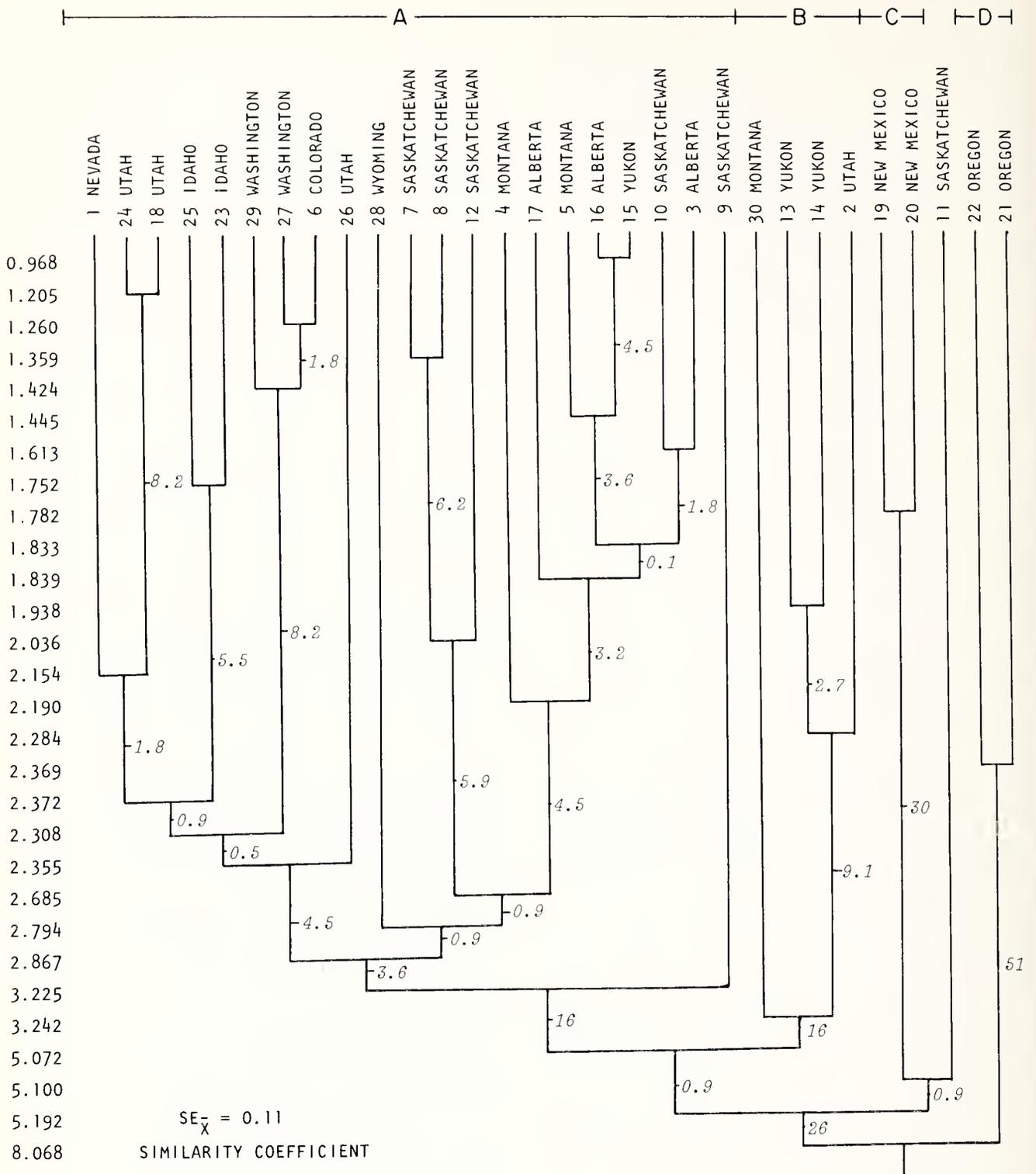


Figure 5. Dendrogram representing results of unweighted pair group cluster analysis of *Bibiocephala* subsample, based on raw data scores. Specimen numbers and general localities at top; amalgamation distance measures at left. Italicized values to right of stems indicate multiples of standard error of similarity coefficient determining the branch. Significance level is 10 with SE of the mean of $d_{ji} = 0.11$.

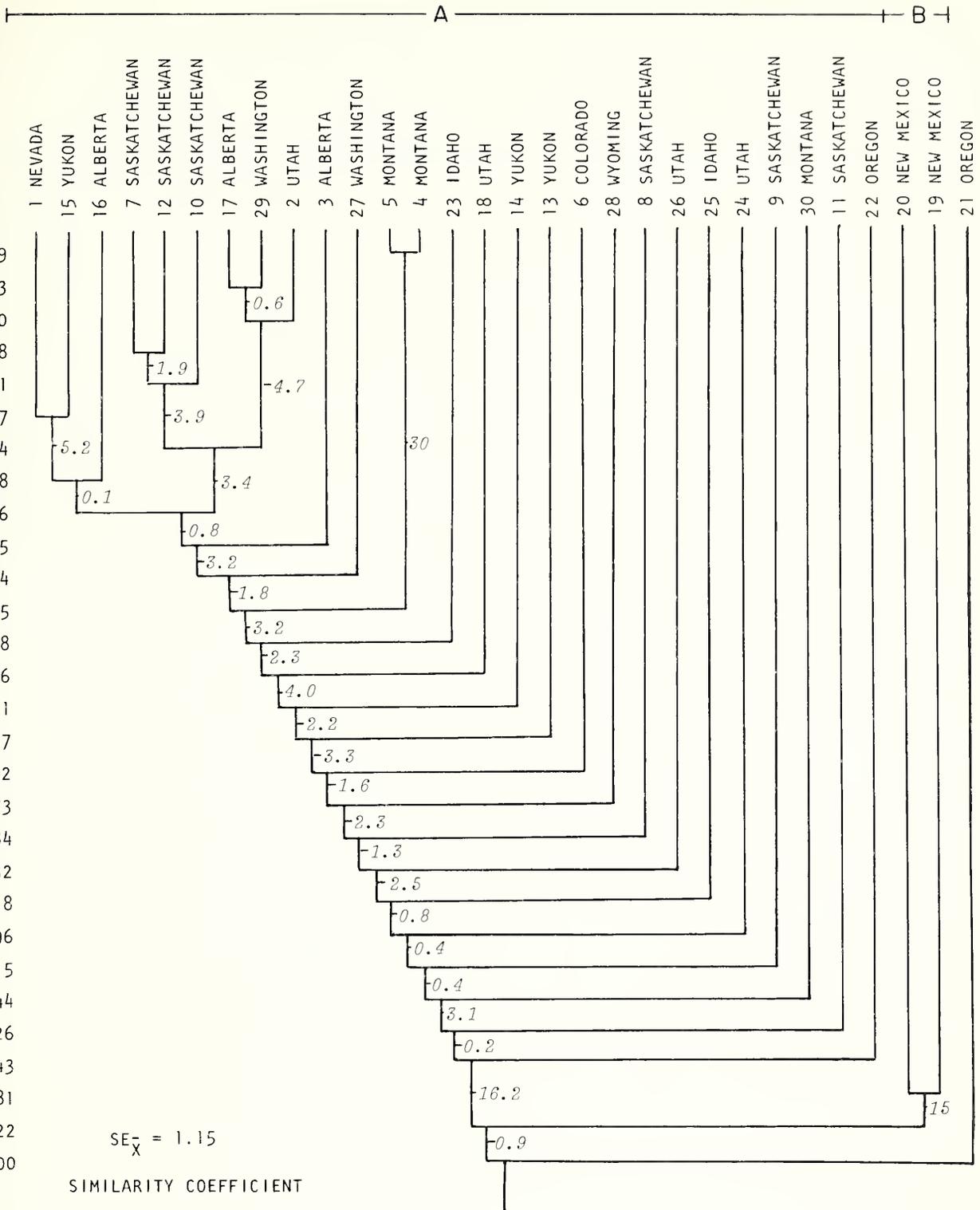


Figure 6. Dendrogram representing results of unweighted pair group cluster analysis of *Bibiocephala* subsample, based on principal components scores of continuous variables. Specimen numbers and general localities at top; amalgamation distance measures at left. Italicized values to right of stems indicate multiples of standard error of similarity coefficient determining the branch. Significance level is 6 with SE of the mean of d_{ij} = 1.15.

Table 1. Univariate statistics of *Bibiocephala* sample, males.

Characters	N	Minimum	Maximum	Inter-quartile Range	Mean (Mode)	SD	Coeff. Var.	Goodness of Fit	Skewness ÷ SE	Kurtosis ÷ SE
WING	102	7.0	11.1	8.3–9.5	8.9	0.80	9.0	0.76	1.28	–0.40
FEM 1	98	2.5	3.9	2.9–3.3	3.1	0.29	9.3	<0.20	0.87	0.43
TIB 1	97	2.6	4.3	3.1–3.5	3.3	0.33	10.1	<0.20	1.76	0.30
TAR 1	97	1.16	2.20	1.62–1.86	1.74	0.18	10.5	0.54	–0.42	0.37
FEM 2	103	2.8	4.8	3.4–3.9	3.7	0.35	9.6	<0.20	1.76	2.02
TIB 2	103	2.7	4.5	3.2–3.6	3.4	0.36	10.6	<0.20	2.63	1.66
TAR 2	102	0.82	1.34	1.00–1.18	1.09	0.11	10.4	<0.20	0.83	–1.41
FEM 3	99	4.3	6.9	5.2–5.9	5.5	0.53	9.5	<0.20	0.48	–0.30
TIB 3	97	3.7	6.0	4.6–5.4	5.0	0.49	9.9	0.33	–0.68	–1.01
TAR 3	92	1.60	2.60	1.99–2.24	2.10	0.20	9.4	0.32	–0.54	0.22
OTDSYL	40	0.45	0.71	0.53–0.58	0.56	0.05	8.5	<0.20	2.33	2.43
BASYL	101	1.20	2.75	1.70–2.02	1.91	0.27	14.2	<0.20	3.82	2.74
PRCTSM	40	2	11	5–8	(6)	2.17	—	<0.20	—	—
TERSM	39	14	42	21–30	(30)	5.67	—	<0.20	—	—
EYHAIR	102	—	+	—	—	—	—	—	—	—

Using this arbitrary standard, the former yielded four significant clusters with more than one individual (Fig. 5, groups A–D). Three of these (A–C, plus specimen 11) form a significant group of a higher order distinct from the fourth (D). The latter dendrogram has only two significant clusters (Fig. 6, A–B).

Cophenetic correlation coefficients were obtained between respective dendrograms and their similarity matrices (raw data: 0.82; PCA scores: 0.78), but a poor match was found between the two dendrograms (0.59).

The total number of data points used in the block clustering analysis was 120; from these, 12 blocks (single and multiple) were developed (Fig. 7). The ratio of data points to blocks recognized is a measure of the significance of the blocks (subsets). In the present instance, the ratio was 0.10, evidence of a “good” analysis according to BMDP3M (Dixon, 1977:647).

The PCA yielded six isolates (Table 2, Fig. 8), only one of which (composed of Oregon specimens 21 and 22) is really distinct. All scores are fairly close to the centroid of the third ordinate, but there are vague linear trends along all axes, especially along the second. There is also a better concordance of groups and general localities than in either of the cluster analyses.

CONCLUSIONS

The reasonable conclusion of inspective analysis of the visually uniform sample—that no taxonomically recognizable subsets are present—is confirmed by metric analysis.

All univariate characteristics are consistent with those expected theoretically from a homogeneous sample, i.e., a sample with many internal minor subsets. This would be expected from a single species distributed over a wide geographic area with multiple populations and small morphological (especially size) differences.

Although a few subsets were formed and measured as significant in the dendrograms from UPGMA clustering, and thus

would appear to meet criterion 3 for phenospecies, they are probably not significant. My greatest reason for this conclusion is the lack of concordance between the two cluster analyses ($r_{C_1C_2} = 0.59$). With the exception of the New Mexico specimens (distinctive character state of EYHAIR) and those from Oregon (large size), there are no concordant groups even of only two specimens. I regard the second analysis (based on PCA scores) as more indicative than the first because of the removal of the effects of correlation. Here, the “staircase” form of the dendrogram is highly reflective of homogeneity, i.e., nearly equal small units. Moreover, the dominating effect of size from many characters (leg segment lengths) is reduced to a single character. Although a vague cline in size is evident from smaller, extreme northern (Yukon) specimens to larger, extreme southern (New Mexico, Oregon) specimens, a single taxonomic entity is indicated for the sample.

The specimens from New Mexico, with pilosity present on the upper eye division, plotted together in both dendrograms and are phenospecies. However, I choose not to give them taxonomic rank at present on the basis of this single character; more material is needed. Note that they (19, 20) do not segregate in the PCA analysis in which EYHAIR was not included (Fig. 8).

The conclusion of homogeneity derives also from assessment of the block cluster analysis. The pattern of clustering, like that in the second UPGMA analysis, indicates homogeneity; many small groups of mixed character states appear. There is no concordance with the results of block and UPGMA clustering, except in the recognition again of the distinctiveness of the New Mexico and Oregon specimens. The distinctiveness of the latter is borne out by their outlying position in the bivariate plots of the first three principal components. Homogeneity of the remainder of the sample is confirmed by this ordination method; points for all other specimens are more or less evenly clustered around the centroids with a slight linear trend along each axis (clinal varia-

tion). (EYHAIR, not being a continuous variate, was not included in the PCA.)

The ultimate conclusion derivable from the results of all the statistical procedures applied to the 15 characters of the present sample is that there are no subsets of specimens clearly and consistently definable as phenospecies. Accordingly, I am making a taxonomic decision to consider all specimens as representing a single species and so recognize them nomenclaturally (see TAXONOMY). Certainly I would urge dipterists to collect *Bibiocephala* assiduously so that this conclusion can be tested in the future on a much larger sample of both males and females, and on immatures also if reared or closely associated with adults.

TAXONOMY

I am foregoing a consideration of the status of *Amika* Kitakami, 1950, relative to *Bibiocephala* and am treating these genera as separate until their relationships can be clarified. Thus the following description for the one species of the latter may be considered the same as for the genus.

Reference to the tribe Blepharicerini is as provisionally defined by Zwick (1977:24, and in personal communication).

Bibiocephala Osten Sacken

SYNONYMY

Bibiocephala Osten Sacken, 1874:564–566. Type species *Bibiocephala grandis* Osten Sacken, 1874, by monotypy.

Bibionus Curran, 1923:266–267. Type species *Bibionus griseus* Curran, 1923, by original designation.

EXSYNONYMY³ (North America only)

Bibiocephala comstocki Kellogg, 1903:192, and of Aldrich, 1905:171; Kellogg, 1907:13; Williston, 1908:152; Cole and Lovett, 1921:229; Walley, 1927:116; Wirth and Stone, 1956:389; Hennig, 1968:42 [*Agathon comstocki* (Kellogg)].

Bibiocephala doanei, of Kellogg, 1903:194–195; Aldrich, 1905:171; Kellogg, 1907:13; Williston, 1908:152 [*Agathon doanei* (Kellogg)].

Bibiocephala elegantulus von Roeder, 1890:230, 232, and of Kellogg, 1903:193; 1907:13; Aldrich, 1905:171; Williston, 1908:152 [*Agathon elegantulus* (von Roeder)].

Bibiocephala snowi Kellogg, 1903:211. *Nomen nudum* [*Agathon elegantulus* (von Roeder)].

Bibiocephala sp. B Johannsen, 1934:52, pl. 23, fig. 206 [*Phylorus californicus* Hogue].

Bibiocephala sp. D Johannsen, 1934:52, pl. 23, fig. 204 [*Dioptopsis sequoiarum* (Alexander)].

Bibiocephala grandis Osten Sacken

SYNONYMY

Bibiocephala grandis Osten Sacken, 1874:566. Fig. wing. Type locality: USA, "Colorado Mountains" (exact locality un-

3. I am introducing this new term here to apply to listings of nominate species originally or at some time combined with a genus under consideration but newly recognized in other combinations.

SPECIMENS		CHARACTERS			
		EYHAIR	PRCTSM	WING	TERSM
1	NEVADA	1	1	1	1
3	ALBERTA	1	1	1	2
12	SASKATCHEWAN	1	1	1	2
10	SASKATCHEWAN	1	1	1	2
8	SASKATCHEWAN	1	1	1	2
26	UTAH	1	1	1	1
17	ALBERTA	1	1	1	1
16	ALBERTA	1	1	1	1
15	YUKON	1	1	1	1
14	YUKON	1	1	1	1
13	YUKON	1	1	1	1
7	SASKATCHEWAN	1	1	1	1
2	UTAH	1	1	1	1
6	COLORADO	1	1	2	1
29	WASHINGTON	1	1	2	1
27	WASHINGTON	1	1	2	1
23	IDAHO	1	1	2	1
11	SASKATCHEWAN	1	1	2	2
4	MONTANA	1	2	1	1
5	MONTANA	1	2	1	2
28	WYOMING	1	2	1	2
18	UTAH	1	2	1	2
9	SASKATCHEWAN	1	2	1	2
30	MONTANA	1	2	1	1
24	UTAH	1	2	1	1
19	NEW MEXICO	2	1	2	2
20	NEW MEXICO	2	1	2	2
22	OREGON	1	2	2	1
25	IDAHO	1	2	2	1
21	OREGON	1	2	2	2

Figure 7. Block diagram showing results of block cluster analysis of *Bibiocephala* subsample. Specimens with similar character states are grouped. Character codes are as follows: EYHAIR absent (1), present (2); PRCTSM (number of setae) 2–7 (1), 8–11 (2); WING (length in mm) 7.0–9.0 (1), 9.1–11.1 (2); TERSM (number of setae) 14–25 (1), 26–43 (2).

known but stated to be between 8,000–10,000 feet elevation). LECTOTYPE male, and four PARALECTOTYPE males, by present designation, from original syntype series of five males, all MCZ.

Bibiocephala kelloggi Garrett, 1922:91. Type locality: CANADA, British Columbia, Cranbrook (? possibly arrived on train from east). Holotype female (erroneously cited as male in original description), CPA. NEW SYNONYMY.

Bibionus griseus Curran, 1923: 268–269. Type locality: CAN-

ADA, Alberta, Nordegg. Holotype male, CNC. NEW SYNONYMY.

Bibiocephala nigripes Alexander, 1965:2–3. Type locality: USA, Idaho, Elmore County, Sawtooth State Forest, near Featherville, 4,900 feet. Holotype male, CPA. NEW SYNONYMY.

Bibiocephala grandis, of Loew, 1877:95; Osten Sacken, 1877:194, 1891:409, 1895:161; Kellogg, 1903, 1907:13; Aldrich, 1905:171; Williston, 1908:152; Coquillett, 1910:514; Cole and Lovett, 1921:229; Walley, 1927:115; Wirth and Stone, 1956:389;

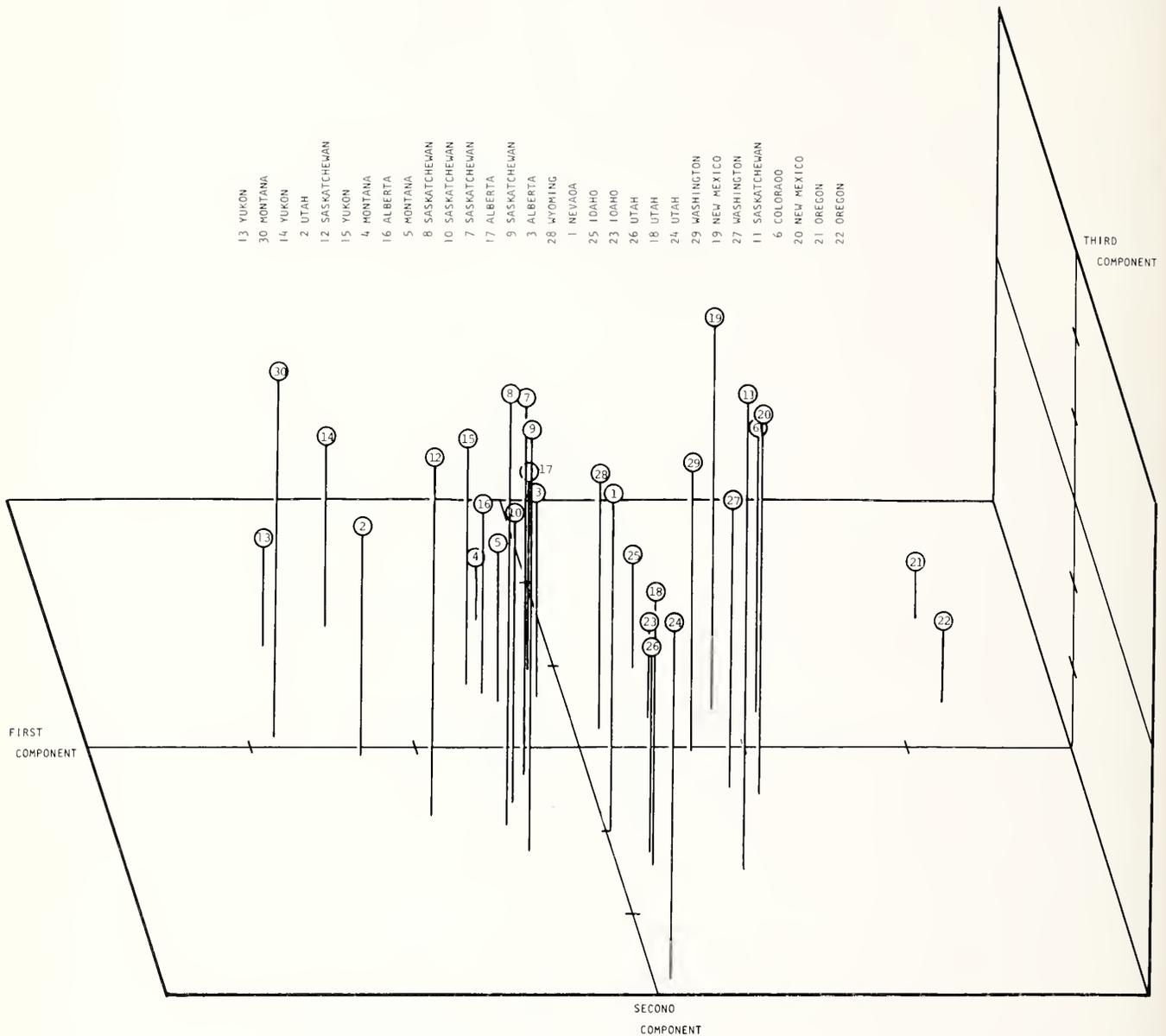


Figure 8. Ordination plot of scores of first three components resulting from principal components analysis of *Bibiocephala* continuous variates. Sequence of specimens and approximate localities at top.

Alexander, 1958:820, 1963:50, 1965; Stone, 1965:99; Cole, 1969:74.

Bibiocephala grisea, of Stone, 1965:99; Cole, 1969:74.

Bibiocephala griseus, of Walley, 1927:115; Alexander, 1958:820, 1963:50, syn. *kelloggi*.

Bibiocephala kelloggi, of Walley, 1927:116; Alexander, 1958:820, 1963:50; Stone, 1965:99; Cole, 1969:74.

Bibiocephala nigripes, of Hogue, 1973:9.

DESCRIPTIONS

Adult (Figs. 9–16)

Rather large, robust, well-pigmented Blephariceridae.

Coloration. Integument generally well sclerotized, gray-brown, legs tending to be yellow-orange basad, darker areas of body with silvery pollinose opalescence. Wing membrane of male infuscate, of female hyaline.

Chaetotaxy. Thorax, abdominal tergite I (laterally), head sclerites, and lower eye division pilose.

Size. Wing length: Range, male (N = 102), 7.0 to 11.1 mm (interquartile range, 8.3 to 9.5 mm), mean = 8.9 mm; female (N = 54), 8.4 to 12.3 mm (9.2 to 10.9 mm), mean = 10.2 mm.

Head. Structure: Generally as found in family. Antennal fossae approximate (slightly closer in male), mesofrons very narrow, slightly convex.

Male (Fig. 11). Sclerites: Suprafrons obliterated dorsad by contiguous eyes, ventral portion triangular, flat; no suprafrontal carina. Parietal sclerite reduced, laterally oblique ventrad. Ocellar lobes joined to form a sessile tubercle, lenses inserted on lobes obliquely. Eyes: Upper division well differentiated from lower, about 3 times larger in area than lower; callus oculi very narrow to obsolete laterad. Proboscis: Short, length of free portion distinctly less than head width. Mandibles absent. Palpus: 5-segmented, length proportions 3:5:5:4:6.

Female (Fig. 12). Sclerites: Suprafrons narrow, interocular distance equal to 5 ommatidial diameters. Eyes: Upper and lower divisions about equal, former only one-fifth larger in area than latter; callus oculi present. Proboscis: Mandibles present. Palpus: 5-segmented, length proportions 3:5:6:4:7. Otherwise similar to male.

Antenna (Fig. 9). Short, length approximately 0.7 times head width; 15-segmented (intersegmental membrane between first two flagellomeres often incomplete; these each slightly longer than remaining flagellomeres); scape oval, pedicel elongate, flagellomeres 3-13 all (including apical) of equal length, ovoid, appearing somewhat contracted in life.

Thorax and Abdomen. Shape of sclerites typical for subfamily.

Wing (Fig. 10). Elongate, subtriangular, broad (broadest across basal third), jugum more expansive than in other genera of Blepharicerini.

Venation: Vein $R_2 + 3$ present, long, straight, joining R_1 near its extreme; $M_3 + 4$ (false crossvein M-Cu) present. Dorsal macrotrichia on veins R_5 and M_3 complete, on $M_1 + 2$ and M_4 apical only; ventral macrotrichia complete on vein R_4 .

Legs. Forefemur strongly upcurved, slightly incrassate. Remaining segments straight and simple; tarsomeres 5, all unmodified. Tibial spurs absent from foreleg, a pair each on mid- and hindlegs. Claws simple, similar, and not enlarged.

Table 2. First three principal components of the covariance matrix of 30 *Bibiocephala grandis* specimens, for 12 continuous variates.

Character	Components		
	1	2	3
WING	0.90	0.27	0.06
FEM 1	0.29	-0.10	0.01
TIB 1	0.36	-0.07	-0.02
TAR 1	0.17	-0.07	0.08
FEM 2	0.41	-0.05	-0.01
TIB 2	0.41	-0.02	-0.05
TAR 2	0.10	-0.04	0.04
FEM 3	0.61	-0.10	-0.06
TIB 3	0.53	-0.17	-0.02
TAR 3	0.18	-0.11	0.12
OTDSYL	0.04	0.02	-0.01
BASYL	0.23	0.08	-0.09
Eigenvalues	2.14	0.16	0.04
Percent total variance	89	6	2

Male Genitalia (Figs. 13–15). Structure: Segment VIII not specially modified; IXth tergite elongate with apicomeral region heavily sclerotized and densely trichiate; lobes of IXth tergite prominent, subtriangular. Basistyle proportionately much larger than in other Blepharicerini, 3.4 times length of outer dististyle, the anterior basistylar extreme projecting below and overriding VIIth sternite. Outer dististyle quadrate, incurved, the apex bifurcate shallowly, the dorsal lobe heavily setate, the inner weakly so; dorsal margin with weakly developed median and basal lobes. Inner dististyle complex, a curved spatulate plate with a basal, short, flat capitate process (appears triangular in some specimens in dorsal view) and a long, apicodorsal, pannuceate, digitiform process, this with a subapicolateral swelling. Parameres and penis filaments very long, former only about twice thickness of latter, hypopygium recurved basad, leading to inverted phallobase. Phallosomal vesica small, nonflanged.

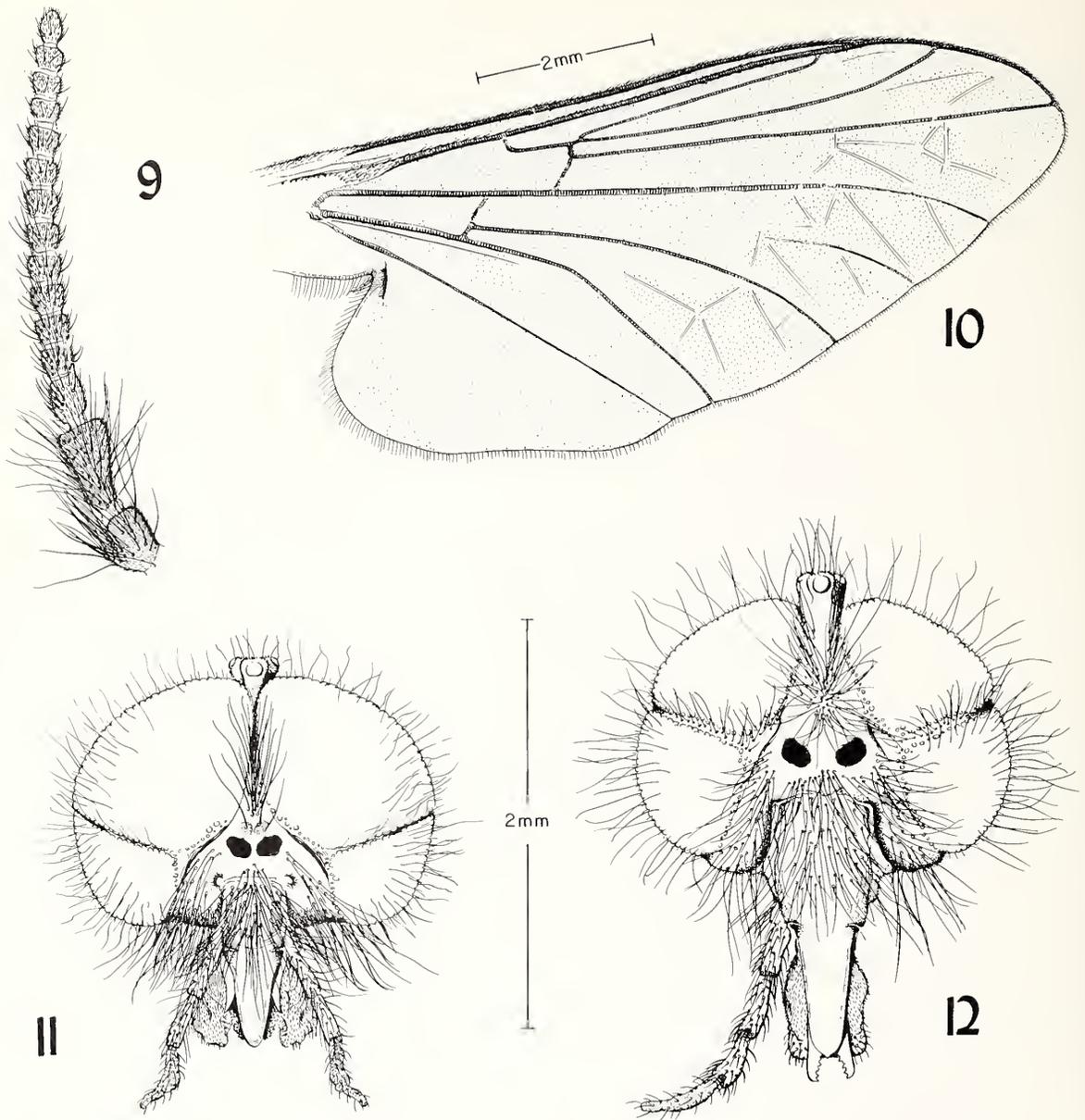
Female Genitalia (Fig. 16). Structure: VIIIth sternite lobe broadly rounded. Oviscapt reduced in overall size, basal portion expanded and convex, lobes not well defined. Dorsolateral portions of IXth tergum developed into a large, separate lobe, larger than cercus, which is reduced. Spermathecae three in number, large, pyriform, with tortuous necks.

Chaetotaxy: Bristles of VIIIth sternite lobes large and numerous. Apex of IXth tergite expansion densely setate, distal margin with row of very long, heavy, incurved setae. Base of oviscapt with central setal group (median bristle series).

Pupa (Figs. 17–19)

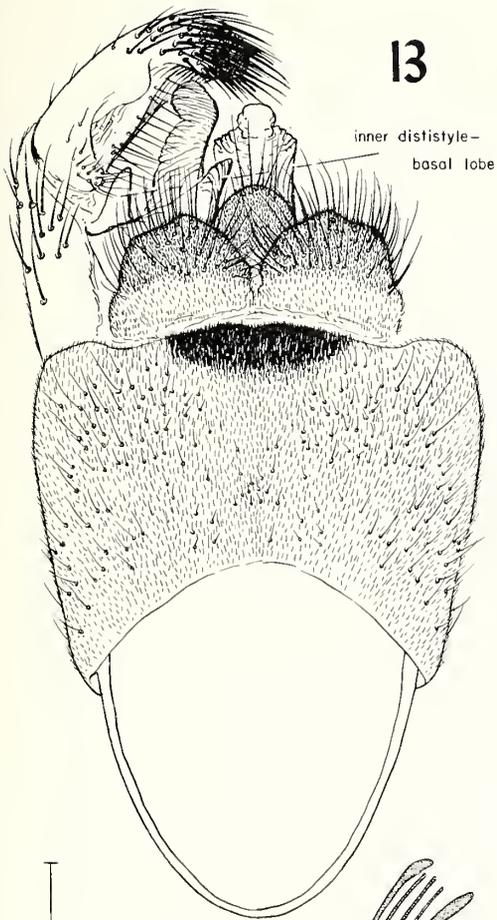
Large, robust. Outline shape hemielliptical (length/width proportions of male 2.2, of female 2.1); body deep, cross-sectional

4. Finely wrinkled, like fingerprint ridges.



Figures 9 through 12. *Bibiocephala grandis*, adult male and female. Structure and terminology used defined in text. Figure 9, antenna; Figure 10, wing (male); Figure 11, head of male, frontal view; Figure 12, head of female, frontal view.

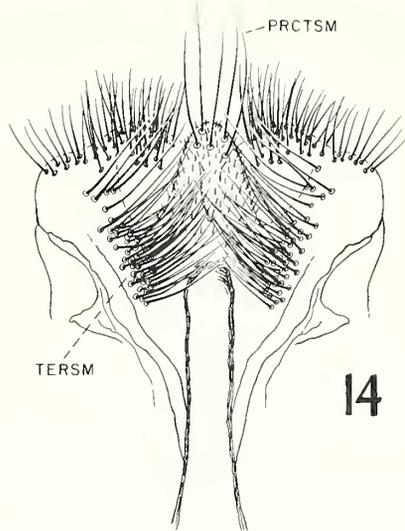
Figures 13 through 16. *Bibiocephala grandis*, genitalia. Structure and terminology used defined in text. Figure 13, external structures, male, dorsal aspect; Figure 14, ninth tergite, male, ventral view, showing setal groups; Figure 15, internal phallic complex, male, dorsal aspect; Figure 16, female genitalia, ventral aspect.



13

inner dististyle-
basal lobe

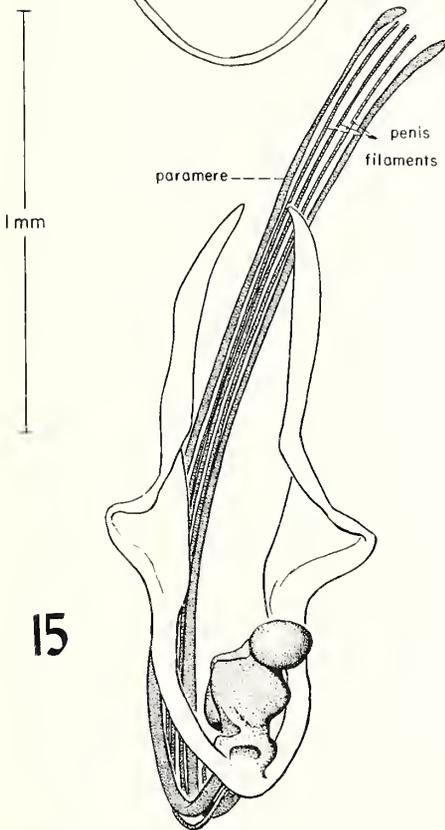
0.5 mm



PRCTSM

TERSM

14



paromere

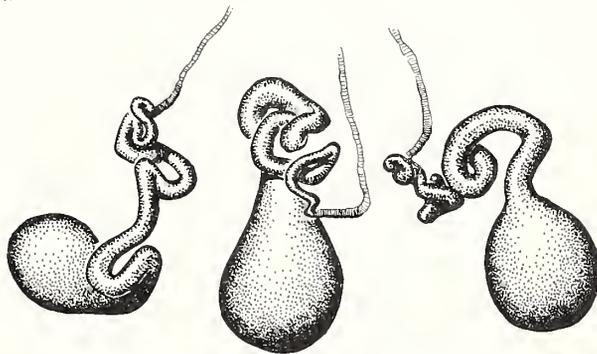
penis
filaments

1 mm

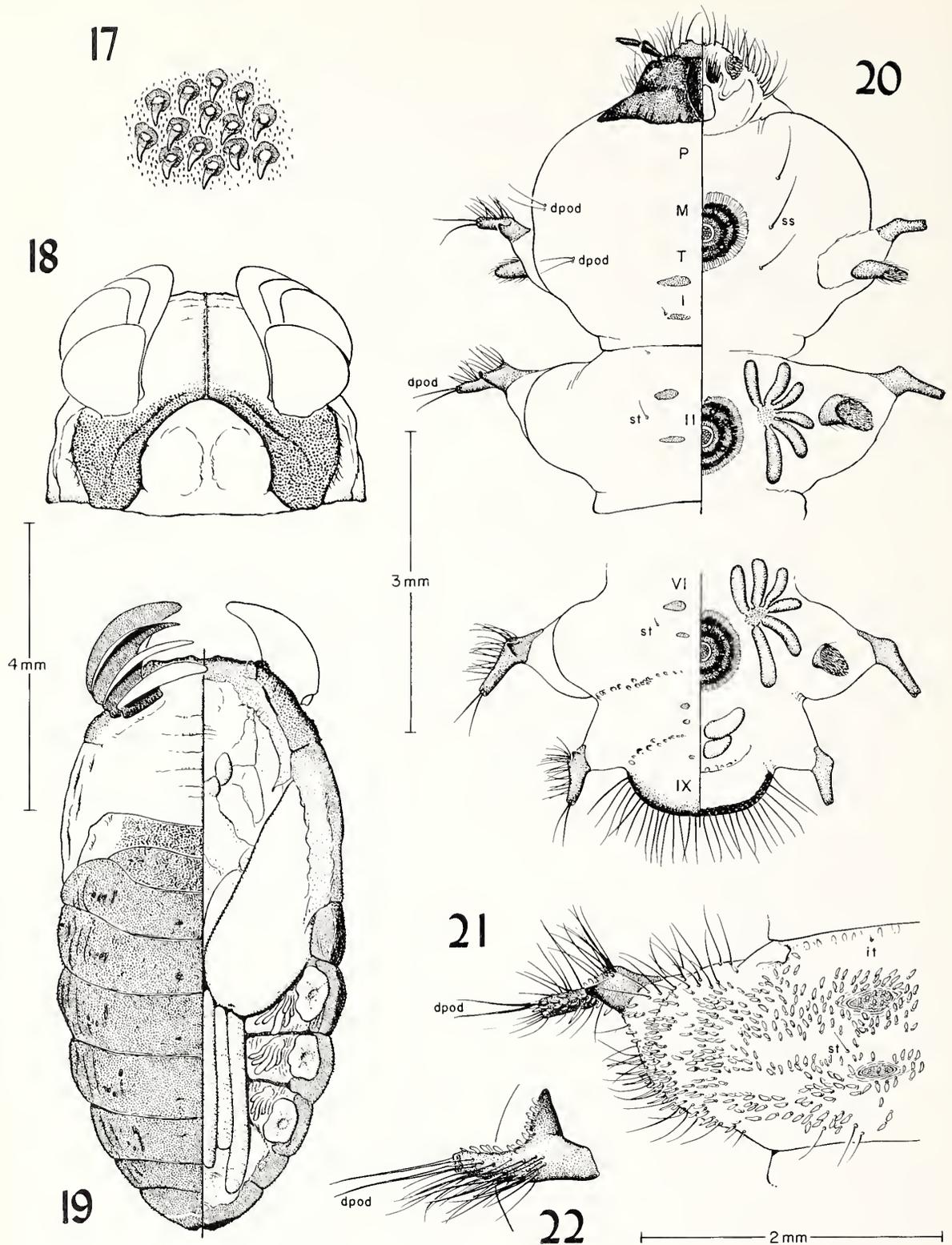
15



1 mm



16



Figures 17 through 22. *Bibiocephala grandis*, pupa and fourth-instar larva. **Figure 17**, denticulae of pupal integument; **Figure 18**, pupa, anterior aspect; **Figure 19**, pupa, general features (dorsal left, ventral right); **Figure 20**, larva, general features (dorsal left, ventral right); **Figure 21**, detailed structure of typical segment, dorsal; **Figure 22**, dorsal pseudopod, anterior view.

shape semicircular to subtriangular. Pleural margins overlap venter laterally.

Coloration. Dorsum and overlapping lateral margins of same black, ventral membranes white.

Size. Body length: Range, male (N = 23) 7.9 to 9.7 mm, mean = 8.8 mm; female (N = 24) 8.65 to 10.5 mm, mean = 9.6 mm.

Width: Range, male (N = 23) 3.35 to 4.5 mm, mean = 3.95 mm; female (N = 24) 3.75 to 5.0 mm, mean = 4.5 mm. Male about 90 percent size (length + width averages) of female.

Structure. Cuticle: Dorsum of metascutal (mesally only), scutellar, and abdominal sclerites, and of subbranchial (with mesal extension) and underfolded portions of branchial sclerite, finely and densely denticulate; denticulae (Fig. 17) recurved (giving surface a rough texture, which may be felt by running the tip of the finger anterad over the dorsum).

Branchiae: Large, porrect, incurving and converging; posteriormost plates contiguous or overlapping in some specimens; all plates projecting appreciably beyond plane of anterior margin. Plates four in number, subparallel (slightly divergent distad), and subequal in size, rigidity, and thickness; individually broadly scutate⁵ in shape.

Dorsal sclerites: Abdominal tergites and scutellum broad, the former appearing to reach lateral margin in dorsal view because of steep pleurae; anteromesal region of frontal sclerite of male with a pair of low, irregular bosses forming a shallow median sulcus, this sclerite evenly rounded in female.

Ventral sclerites: Antennal case short, extending only to base of wing case, apex recurved. Vestigial gills, with 4 to 6 filaments each, present on abdominal sternites III-V. Pattern of extension of leg case apices same in both sexes, tip of hindleg most extended, foreleg less, midleg least extended.

Fourth-Instar Larva (Figs. 20–22)

Large, robust.

Coloration. Dorsum generally well pigmented, black; head and sclerites densely sclerotized, shiny. Venter pale, light-brownish to white.

Size. Body length: Range of randomly selected specimens (N = 122) 5.3 to 13.7 mm, mean = 9.6 mm; of mature specimens only (i.e., pupal branchiae visible) (N = 38) 7.8 to 13.7 mm, mean = 10.5 mm.

Head capsule width: Range 1.4 to 2.2 mm, mean = 1.8 mm.

Structure. Body divisions: Anterior division spherical in mature specimens, subtriangular to quadrate in younger individuals. Terminal division with well-differentiated segment VII–IX; posterolateral lobe of segment VII well developed, bearing large dorsal pseudopod. Intercalary segments developed. A sharp sublateral indentation in dorsal body wall running length of abdomen (I–VI) setting off dorsal pseudopod on a broad lateral lobe.

Head: Small relative to body, anterior portion constricted, lateralia expanded, fused, leaving only a shallow sulcus, which closes completely in many (especially older) specimens. Antenna with two segments, basal segment slightly thicker (expanding slightly distad) but shorter than distal segment.

Integumentary modifications: Dorsum of abdominal segments

5. Sickle-shaped.

I–VII usually with antero- and posterotergal plates, these small, circular or elongate, anterior slightly larger and more oval than posterior, sometimes raised into a small tubercle; segment VIII with a single pair of very small plates; all plates evanescent in some specimens. A small tergopleural tubercle occasionally also present on segments I–VI. Dorsal pseudopods (Fig. 22) well developed on segments I–VII, these of equal size on II–VI, slightly smaller on I and VII; shape antenuoconate, apex truncate, sharply angled posteriorward at basal third, a strong, sharp, erect spine arising just basad of angle.

Pseudopods: Normal, that of segment I more elongate and smaller than others, which are of equal size and shape except that of VI, which is slightly smaller.

Gills: Lateral gills composed of 6 digitiform filaments, arising from contiguous bases and arranged in a plane, hemirosette pattern. Number of filaments and overall size equal on all segments. Anal gills normal.

Chaetotaxy (Figs. 20–22). Dorsum and lateral portions of venter set with dense vestiture of short secondary coniform to claviform sensilla with interspersed setiform types (more so laterad); the former also present on apicodorsal portions of dorsal pseudopods, anteroventral margins of same densely fringed with numerous long, setiform sensilla. Distinctive primary sensilla as follows: subtergal I–VI about in line with outer edges of dorsal plates, slightly closer to posterior plate, that on VII very small and close to posterotergal plate, all setiform; tergopleural M-T members in contiguous pairs, all setiform; dorsopseudopodal I–VII arising from blunt apices of dorsopseudopods, heavy, short setiform. Terminal setae of single row of 20–40 large setiforms fringing terminus of segments VIII–IX.

BIONOMICS

Very little is known about the biology of *Bibiocephala grandis*. It is a typical blepharicerid in its general life cycle and ecological requirements, developing in swift mountain streams and leading a riparian adult life. The adults are active during the summer, most collections indicating June to August as the major flight period, although there are later (September) and earlier (April and even March) records.

The well-developed mandibles of the females indicate a predatory habit; the males, lacking mandibles, probably subsist on liquid food sources (plant nectar and the like). The species is large by family standards, and the females probably can take fairly good-sized prey. The adaptive function of the long pile present over much of the body of both sexes is not known. The curious habit of adults to be attracted to bright silvery objects, possibly mistaking them for the water surface, has been observed by one collector of this species (in this case, "silver metal tanks," Gittins and Barr, Idaho, Slate Creek, 1963).

The winter is presumably spent in the egg stage or as very young larvae. Older larvae are encountered throughout the spring and summer and typically are taken from small to medium-sized rocks in riffles and other completely submerged situations. They apparently are not prone to live on exposed vertical faces of large boulders and fixed rock faces as are the larvae of other blepharicerids. I have found them most frequently on the undersides of stones in gravelly stream beds.

Larvae are frequently found with very heavy coatings of di-

atoms and algae adhering to the dorsum. This may afford them a degree of protective camouflage or may simply be an accident of their lethargic existence.

DISTRIBUTION

Bibiocephala grandis occupies suitable habitats in all of the Pacific and Rocky Mountain states of western North America and the Canadian territories and provinces of Yukon, Alberta, British Columbia, and Saskatchewan. It is not known presently from Alaska or Arizona but is very likely to occur there also. It enters California, Nevada, and New Mexico only in their northern portions, and it is very doubtful if it extends its range into northern Mexico (see Fig. 23).

SPECIMENS EXAMINED

ADULTS

CANADA. ALBERTA. Edmonton, date and collector unknown (♀: UAT). Jasper: 29 August 1932, R.H. Handford (♂: CNC—3); Maligne Lake, 11 August 1926 (♀: CNC); Athabaska Falls, 21 August 1932, E. Hearle (23 ♂♂, 2 ♀♀: CNC—17). Athabaska River, Old Fort Point, 31 August 1932, E. Hearle (4 ♂♂, 4 ♀♀: CNC—16). BRITISH COLUMBIA. Glenora, March 1941, Wickham (♀: USNM). Seton Lake, 2 August 1933, J. McDunnough (♂, ♀: CNC). Lillooet, Seton Lake, 31 May 1926, J. McDunnough (♀: CNC). SASKATCHEWAN. Fenton, 27 May 1948, J.R. Vockeroth (9 ♂♂, 3 ♀♀: CNC—11). North Saskatchewan River, Fort à la Corne, 4 June 1948, J.R. Vockeroth (♂: CNC—10). Nipawin, 2 June 1948, J.R. Vockeroth (11 ♂♂: CNC). Weldon, 27 May 1948, J.R. Vockeroth (13 ♂♂: CNC—7, 8, 9, 12). YUKON TERRITORY. Dawson, 2, 4, 29, 31 August 1962, R. Leech (3 ♂♂, 2 ♀♀: CNC—13, 14). Mile 87, Dempster Highway, 4–8 August 1973, G. and D. Wood (♂, 2 ♀♀: CNC—15). UNITED STATES. CALIFORNIA, *Shasta County*. Pit River Dam No. 5, 14 May 1952, H.P. Chandler (♀: CAS). *Siskiyou County*. Dunsmuir, date unknown, Wickham (♀: USNM). COLORADO, *Clear Creek County*. Exact locality unknown, 9,000 feet, 8 August 1946, R.H. Painter (♀: KS). *Grand County*. Cameron Pass, 11 August 1959, H. Knutson (♀: KS). Poudre River Canyon, 28 June 1931, J. Nottingham (♀: KU). *Gunnison County*. Gothic, 9,500 feet, 15 July 1934, C.P. Alexander (♀: CPA). *Larimer County*. West slope Loveland Pass, 9,850 feet, 8 August 1961, C.H. Mann (♂: CNC—6). "N" Eggers, Roosevelt National Forest, 6,500 feet, 2 July 1936, H. Spieth (5 ♂♂: AMNH). *Weld County*. Platte Canyon, 23 May 1901, H.G. Dyar and A.N. Caudell (♂: USNM). IDAHO, *Idaho County*. Slate Creek Ranger Station, attracted to silver metal tanks (part), 26–27 June 1963, A.R. Gittins and W.F. Barr (50 ♂♂, 20 ♀♀: CAS, SJS—23, UI—25). *Latah County*. Moscow Mountain, 4 June 1910, J. Aldrich (♂: USNM). *Lewis County*. Lawyers Canyon, 26 June 1963, A.R. Gittins (2 ♀♀: UI). *Nez Perce County*. Central Grade, 27 April 1960, A. R. Gittins (♂: UI). Lewiston, 28 March 1953, C. Terhaar (♂: UI); 9 June 1923, A. Melander (♀: USNM). Spalding, 24 April 1949, M. James (♂: USU). *Owyhee County*. Murphy Hot Springs, 20 June 1965, W.F. Barr (♂: UI). *Shoshone County*. Red Ives Ranger Station, 14 July 1969, C. Hornig (♂: UI). MONTANA, *Gallatin County*. Gallatin River, 40 mi S.

Belgrade, Malaise trap, 31 July 1971, H. Telford (1 ♂: WSU—30). Upper Gallatin Canyon, 7,000, 8,100 feet, 10, 20 July 1928, J. McDunnough (7 ♂♂: AMNH, CNC—4, 5). Yellowstone, 20 July 1929, E. Hearle (♀: CNC). *Malvin County*. Madison Creek, 16 July 1948, R. Hays and C. Bishopp (5 ♂♂, 3 ♀♀: USNM). *Park County*. Livingston, 14 July 1903, A. Melander (2 ♂♂, ♀: USNM). NEVADA, *Nye County*. Currant River, Van Burch, 18 June 1936, H. Spieth (♂: AMNH—1). NEW MEXICO, *San Miguel County*. Pecos: 9 June 1903, M. Grabham (10 ♂♂: USNM, BMNH); no date, T.D.A. Cockerell (3 ♂♂: LACM—19, 20). OREGON, *Hood River County*. Hood River, 2, 21, 26 June 1917, 15 June 1919, F. Cole (6 ♂♂, 7 ♀♀: OS—21, 22). UTAH, *Cache County*. Logan, 16 July 1933, T. Thatcher (♂: KU); 14 July, 1 August 1954, T. Miura (3 ♂♂, ♀: KU); 4 September 1950, G. Bohart (♂, 2 ♀♀: UCD—24). Smithfield, 11 July 1937, C. Smith and F. Harmston (3 ♂♂: KU—18, USNM—26). *Duchesne County*. Duchesne River and highway 35, west of Hanna, 12 July 1976, R. Baumann and V. Tipton (2 ♂♂, ♀: BYU—2). *Summit County*. Weber River, below Smith-Morehouse Creek, 5 August 1975, Sakamoto et al. (♀: LACM). WASHINGTON, *Asotin County*. Grand Ronde River near Anatone, 28 April 1963, B.F. Finnigan (2 ♂♂, ♀: WSU—29). Asotin, 22 April 1923, A.L. Melander (♀: USNM). Clarkston, 1 April 1907, A.L. Melander (♂: USNM—27). *Jefferson County*. Olympic Hot Springs, 22 July 1938, E.C. VanDyke (♀: CAS). *Pierce County*. Longmire, Mount Rainier, 3,000 feet, 4 June 1934, Bryant (♀: CAS). *Whitman County*. Almota, 12 April 1941, L.J. Lipavsky (♀: WSU). Pullman, date unknown, A.L. Melander (2 ♂♂: USNM). Wawawai, 24 April 1909, A.L. Melander (♂: USNM); 7 April 1954, M.T. James and J. Quist (♀: WSU). *Yakima County*. Chinook Pass, 29 July 1949, R.H. Beamer (♀: KU). WYOMING, *Yellowstone National Park*. Gallatin Station, Yellowstone Park, 28 July 1923, A. Melander (♂: USNM—28). Firehole River, 7,600 feet, Yellowstone Park, 21 July 1928, J. McDunnough (♂: CNC). Yellowstone Park, date and collector unknown (2 ♂♂, 3 ♀♀: CU). NO DATA (♀: WSU).

IMMATURES

CANADA. ALBERTA. Fiddle Creek, Jasper National Park, 19 June 1962, G.B. Wiggins (1 larva: ROM). BRITISH COLUMBIA. Kicking Horse River, Yoho National Park, 26 April 1964, D.M. Wood (9 larvae: CNC). Thompson's Bridge, Fraser Canyon, August 1967, D. Craig (12 larvae: UAT). Mule Deer Provincial Park, August 1967, D. Craig (9 larvae: UAT). UNITED STATES. CALIFORNIA, *Nevada County*. S Fork Yuba River, 6 mi NW Nevada City, highway 49, 25 June 1973, D.R. Givens and S.D. Smith (8 larvae: CWS). COLORADO, *Archuleta County*. Rio Blanco-Navajo River, 1974, H. Kennedy (19 larvae: LACM). *Boulder County*. Left Hand Creek, near Altona, 18 February 1943, T.H. Frison and H.G. Rodeck (1 larva: USNM). *Gunnison County*. Copper Creek, Gothic, 27 July 1967, T.C. Emmel (36 pupae: LACM). East River, Gothic, 9,500 feet, 28 June 1967, T.C. Emmel (1 larva: LACM). Marble, 4 September 1966, J.T. Polhemus (34 larvae: LACM). *Larimer County*. Big Thompson River, Estes Park, 18 February 1943, T.H. Frison and H.G. Rodeck (2 larvae: INHS). *Mineral County*. Rio Grande River, Marshall Camp, 16 June 1963, D.M. Wood (3 larvae, 18

pupae: CNC). *Rio Blanco County*. S Fork White River, 10 mi S Buford, 4 July 1968, J.T. Polhemus (2 larvae, 20 pupae: LACM). *Rout County*. Elk River, 3 mi S Clark, 18 March 1968, B.R. Oblad (1 larva: LACM). *Summit County*. Stream along US 6, 8 mi W Loveland Pass, 23 August 1968, J. Emmel and O. Shields (2 larvae: LACM). IDAHO, *Custer County*. Herd Creek, 11 mi S Clayton, 11 May 1965, S.D. Smith and E.R. Logan (2 larvae: UI). *Idaho County*. French Creek, 19 mi E Riggins, 25 March 1966, S.D. Smith (11 larvae: UI). Crooked Fork Creek, 4 mi NE

Powell Ranger Station, 30 March 1967, F.H. Everest (5 larvae: UI). *Lemhi County*. Bear Valley Creek, 12 mi SW Lemhi, "7-5-66," H.R. Gibson (2 larvae: UI). OREGON, *Wallowa County*. 6 mi E Lostine, Forest Service Road S-202 at national forest boundary, 24 March 1973, D.L. Peck (1 larva: CWS). Unknown affluent to Wallowa Lake, 24 April 1977, Zack and Raffa (8 larvae: WSU). UTAH, *Cache County*. Logan River, 25 September 1952, collector unknown (6 larvae: USNM). *Duchesne County*. Duchesne River, highway 35 west of Hanna, 12 July 1976, R. Baumann and V. Tipton (3 pupae: BYU). Rock Creek near mouth of Fall Creek, 8 October 1933, Rasmussen (2 larvae: INHS). East fork of Rock Creek, 7 October 1933, Rasmussen (3 larvae: INHS). *Salt Lake County*. Big Cottonwood Creek, 2 mi above power plant, approximately 6,000 feet, 25 February 1968, R. and D. Koss (20 larvae: JH). Big Cottonwood Creek, 5 mi W Brighton, The Spruces, 3 June 1976, C.L. Hogue (63 larvae: LACM). Millcreek, 3 February, 10, 30 April 1966, R.W. Baumann (7 larvae: LACM). Mill Creek, 6 mi E canyon mouth, "The Elbow," 3 June 1976, C.L. Hogue (27 larvae: LACM). Millcreek Canyon Creek, 16 December 1965, R.W. Baumann (1 larva: LACM). *Summit County*. Bear River, near Utah-Wyoming state line, 14 May 1970, R.B. Golightly (4 larvae: LACM). Mid fork Provo River, Slate Gorge, 3 June 1976, C.L. Hogue (10 larvae: LACM). *Uintah County*. White River, Bonanza, 17 September, 8 November 1975, 25 April 1976, E. Hornig (11 larvae: BYU). *Utah County*. American Fork Canyon Creek, 7, 15 April 1966, R.W. Baumann and B.R. Oblad (5 larvae: LACM). North Fork Creek, below Sundance ski area, 5 August 1976, D.K. Sakaguchi (3 larvae, 4 pupae: BYU). WASHINGTON, *Asotin County*. Asotin Creek, 14 April 1935, collector unknown (1 larva: WSU). *Jefferson County*. Hoh River, Hoh River Campground, Olympic National Park, 30 June-1 July 1969, ROM field party (18 pupae: ROM). *Skagit County*. Marble Creek, 10 mi E Marblemount, 30 June 1974, D.L. Peck (1 larva: CWS). *Snohomish ? County*. Pilchuck River, 12 May 1935, collector unknown (2 pupae: WSU). *Whatcom County*. Goodell Creek at Newhalem, highway 20, 1 July 1974, D.L. Peck (1 larva: CWS). WYOMING, *Albany County*. Centennial, Wyoming Summer Camp, 30 June 1936, collector unknown (1 larva, 5 pupae: USNM). Libby Creek along highway 130, below Snowy Range Lodge, Medicine Bow Mountains, 22 August 1968, J. Emmel and O. Shields (19 larvae: LACM). Upper and Lower Libby Creek, Snowy Range Mountains, 23 April, 3 September, 2 October 1955, 14-15, 29 April, 23 June 1956, P.H. Freytag et al. (22 larvae, 1 pupa: OSU, UW). Nash Fork Creek, Snowy Range Mountains, 14 August 1955, P. and R. Freytag (1 larva: OSU). North fork Little Laramie River, 30 April 1955, P. Freytag et al. (1 larva: UW). *Carbon County*. South Brush Creek, 54 mi W Laramie, South Brush Creek Campground, Route 130, 11 September 1966, G. Wiggins et al. (78 larvae: ROM). *Yellowstone National Park*. Gibson River near Norris, Geyser Basin, 23 August 1953, R. Coleman (3 larvae: USNM).

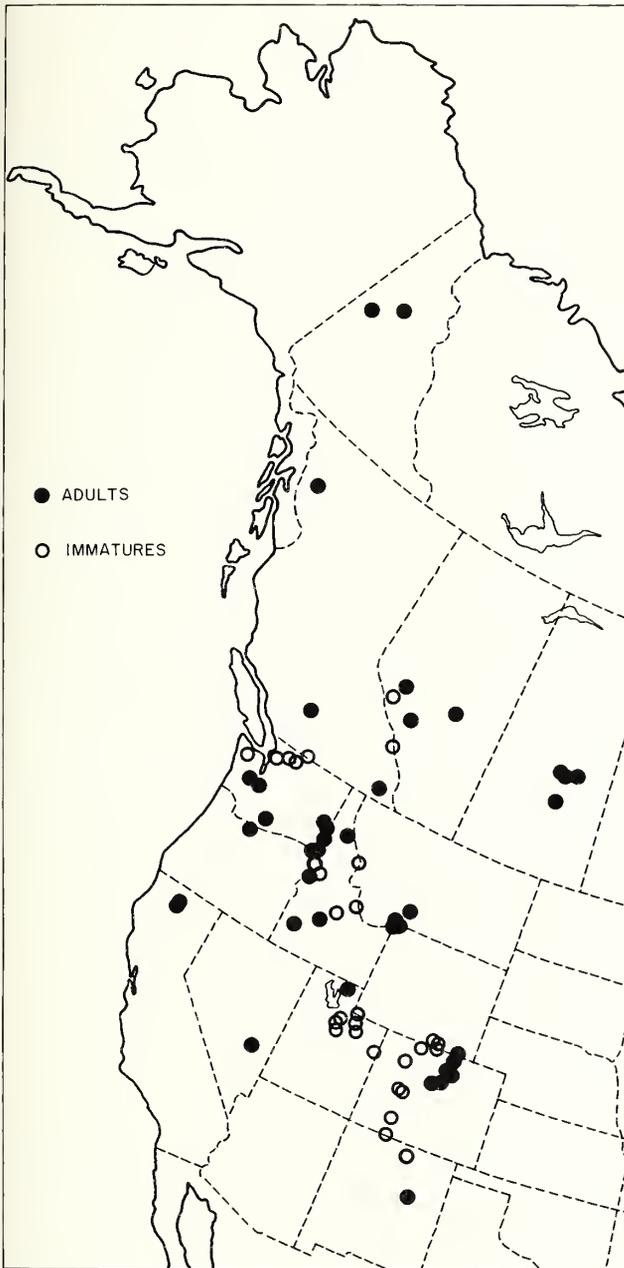


Figure 23. Collection localities of *Bibiocephala grandis* in western North America.

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CONTRIBUTIONS IN SCIENCE

REVISION OF THE EASTERN NORTH PACIFIC ANTHIIN BASSES
(PISCES: SERRANIDAE)

John E. Fitch



Natural History Museum of Los Angeles County • 900 Exposition Boulevard • Los Angeles, California 90007

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REVISION OF THE EASTERN NORTH PACIFIC ANTHIIN BASSES (PISCES: SERRANIDAE)¹

John E. Fitch²

ABSTRACT: Four species of anthiin basses inhabit eastern North Pacific waters: *Pronotogrammus multifasciatus* Gill, 1863; *P. eos* Gilbert, 1890; *Hemanthias peruanus* Steindachner, 1874; and *H. signifer* (Garman, 1899).

Anthias gordensis Wade, 1946, and *Holanthias sechurae* Barton, 1947, are relegated to the synonymy of *Pronotogrammus multifasciatus*. *Pronotogrammus* Gill, 1863, has priority over *Holanthias* Günther, 1868. *P. eos* should be generically reassigned.

Centristhmus Garman, 1899, is relegated to the synonymy of *Hemanthias* Steindachner, 1874. *H. delsolari* is a *nomen nudum* that has been applied to specimens of *H. signifer* in Peruvian waters (Chirichigno, 1974).

Two of the four species occur in Californian waters: *Pronotogrammus multifasciatus* (Hobson, 1975, as *Anthias gordensis*), and *Hemanthias signifer* (misidentified as *H. peruanus* by Wales [1932]).

An identification key is presented; the key utilizes facial scalation, pored lateral-line scale counts, eye diameter, finray counts, and other easily observed characters for differentiating the four eastern North Pacific anthiins. Otoliths (sagittae) of these species are illustrated because of their occurrence as remnants of prey in food habit studies.

INTRODUCTION

An attempt to identify an anthiin that had been caught around 3 February 1977 in 192 meters of water off San Onofre, California, revealed considerable taxonomic confusion and contradiction among accounts of eastern North Pacific Anthiinae. Although an abundance of literature, including original descriptions (Gill, 1863; Steindachner, 1874; Gilbert, 1890; Garman, 1899; Wade, 1946; and Barton, 1947), was available for anthiins in the eastern North Pacific, few faunal reports and identification keys included more than one or two species (Jordan and Evermann, 1896; Hiyama, 1937; Hildebrand, 1946; Hildebrand and Barton, 1949; Berdegue, 1956; Chirichigno, 1974; Walford, 1974; Miller and Lea, 1976; Ramirez and Gonzales, 1976; and Thomson, Findley, and Kerstitch, 1979). In addition, characters given in these publications often were incorrect or inadequate, making it impossible to compare the same features on different species. As a result, numerous anthiins in collections at the California Academy of Sciences (CAS, or SU-CAS), Natural History Museum of Los Angeles County (LACM), Scripps Institution of Oceanography (SIO), and University of California at Los Angeles (UCLA) were misidentified. Obviously, a critical review of eastern North Pacific anthiins was sorely needed.

During the past several years, all eastern Pacific anthiins in the CAS, Cabrillo Marine Museum (CMM), LACM, SIO and

UCLA collections were examined, as was selected material in the University of Costa Rica (UCR) collection.

Proportional measurements in thousandths of standard length (SL), were made on 147 of these specimens representing the known size ranges for the four anthiins that inhabit eastern North Pacific waters (Table 1). The data were used to construct the following key and species accounts. Only primary synonymies have been included in the species accounts.

Otoliths (sagittae) of the four species are illustrated because these frequently occur in digestive tracts and scats of various predators, and might be found in coastal Indian camp sites or in fossil deposits.

Although a new generic name is needed for *Pronotogrammus eos*, such action is being deferred to Phillip C. Heemstra, who is in the process of revising the subfamily for the entire eastern Pacific.

Larvae of three of the four eastern North Pacific anthiins have been described and illustrated (Kendall, 1979), but those of *Hemanthias signifer* have yet to be recognized.

KEY TO THE ANTHIINS OF THE EASTERN NORTH PACIFIC

- 1a. Pored scales in lateral line 36 to 40; eye large, 12 to 16 percent of SL..... *Pronotogrammus eos*
- 1b. Pored scales in lateral line 45 or more; eye smaller, less than 11 percent of SL 2
- 2a. Maxillary, mandible, and anterior part of face and head completely scaled; third dorsal spine only slightly longer than second, about equal to fourth; elongate oval patch of teeth on tongue (often difficult to find); vertebrae 10 + 16...
..... *Pronotogrammus multifasciatus*
- 2b. Maxillary, mandible, and anterior part of face and head without scales; third dorsal spine about three times as long as second, twice as long as fourth; no teeth on tongue; vertebrae 11 + 15 3
- 3a. Margin of urohyal smooth at all sizes; pored scales in lateral line 52 to 59; pectoral rays 16 to 18 (usually 17); total gill rakers 31 to 34 (rarely 34); in fish over 100 mm SL,

1. Review committee for this Contribution: John E. Graves, Robert J. Lavenberg, and C. Richard Robins.

2. Research Associate in Ichthyology and Paleontology, Natural History Museum of Los Angeles County, Los Angeles, California 90007.

Table 1. Comparative measurements, in thousandths of standard length, for the four eastern North Pacific anthiins

Measurement	Species and Number of Specimens Measured			
	<i>P. eos</i>	<i>P. multifasciatus</i>	<i>H. peruanus</i>	<i>H. signifer</i>
Number of specimens	30	27	55	35
Standard lengths (mm)	29–153	66.5–205	71.5–267	60–279
Head length	361–422	322–354	326–385	328–405
Horizontal eye diameter	120–159	081–105	073–102	080–110
Snout length	054–079	064–085	065–088	078–104
Maxillary length	152–183	135–151	139–160	137–161
Bony interorbital width	060–087	065–080	063–078	061–075
Length of first gill raker below angle	060–080	052–071	045–062	044–061
Snout to first D insertion	303–345	283–323	289–329	293–341
Snout to A insertion	610–656	604–695	587–656	587–646
Snout to pectoral insertion	341–382	331–378	316–361	306–380
Snout to pelvic insertion	345–397	350–439	353–417	355–412
Length of anal. fin base	167–199	164–199	179–219	175–208
Length of dorsal fin base	476–561	548–622	509–579	488–557
Dorsal peduncle length	168–199	154–189	184–215	177–201
Ventral peduncle length	231–258	221–256	214–252	217–258
Dorsal fin insertion to pelvic insertion	306–369	303–354	300–341	272–344
Caudal peduncle depth	111–128	091–119	124–148	101–134
Height of first D spine	041–062	046–073	039–056	031–054
Height of second D spine	073–092	063–114	067–090	061–088
Height of third D spine	094–124	105–147	199–352	176–553
Height of fourth D spine	115–155	107–150	086–136	097–138
Height of fifth D spine	118–158	104–150	086–130	096–128
Longest ray in second D fin	190–220	129–173	176–219	127–197
Longest ray in anal fin	196–230	137–190	176–250	137–187
Length of second A spine	115–150	096–147	069–122	066–113
Length of third A spine	115–149	102–140	092–127	092–120
Pectoral fin length	295–339	262–315	226–274	208–254
Pelvic fin length	310–374	301–466	266–536	229–319

middle rays of both upper and lower lobes of caudal fin longest. *Hemanthias peruanus*

- 3b. A sharp, anteriorly projecting spine (visible without dissection) on ventral edge of urohyal in fish longer than about 70 mm SL; pored scales in lateral line 59 to 69; pectoral rays 18 to 20 (mostly 19); total gill rakers 33 to 38 (rarely 33); outermost rays of both lobes of caudal fin longest. *Hemanthias signifer*

SPECIES ACCOUNTS

Pronotogrammus multifasciatus Gill, 1863

Figure 1

Pronotogrammus multifasciatus Gill, 1863:84 (original description, type locality: Cape San Lucas, Mexico).

Anthias multifasciatus (Gill), Jordan and Gilbert, 1882:360 (generic reassignment, redescription).

Anthias gordensis Wade, 1946:225 (original description, type

locality: Inner Gorda Bank, Baja California, Mexico, 70 to 78 fathoms).

Holanthias sechurae Barton, 1947:2 (original description, type locality: Talara, Peru, exact location uncertain).

Holanthias gordensis (Wade). Hubbs, Follett, and Dempster, 1979:21 (checklist of Californian fishes).

MERISTIC DATA. D. X-XI, 14–15; A. III, 7–8; P. 18–20; GR 10–12 + 26–30 = 37–42; pored lateral line scales 45–51; vertebrae 10 + 16.

Twenty-six of the 27 *P. multifasciatus* from which I obtained meristic data had dorsal finray counts of X, 15 and anal finray counts of III, 7.

DIAGNOSTIC CHARACTERS. *Pronotogrammus multifasciatus* is the only eastern North Pacific anthiins with completely scaled maxillary, mandible, and anterior part of the face and head. It also differs from the other three species in having 45 to 51 pored lateral-line scales and an elongate, oval patch of granular teeth on the tongue. It is similar to *P. eos* in lacking an elongate,

filamentous third dorsal spine but differs in having a shorter maxillary and shorter rays in the second dorsal and anal fins (Table 1). *P. multifasciatus* also has a greater number of pectoral rays than *P. eos*, although one of the 27 specimens (LACM 8836) had 18 rays in the left pectoral and 19 in the right.

MAXIMUM SIZE. The largest individual I could find was 205 mm SL (262 mm total length [TL]).

RANGE. Portuguese Bend, Los Angeles Co., California (34° N), to the region off Talara in northern Peru (4° S); 40 to 205 meters.

DISCUSSION. Gill's (1863) description of *P. multifasciatus*, based on a 50-mm (2-inch) specimen collected by John Xantus at Cape San Lucas, contained very little information that could be used to distinguish this species from other eastern North Pacific anthiins. He did note that none of the dorsal spines was especially elongate or filamentous, but this would also be true for a 50-mm long *Hemanthias* and was not of diagnostic value. His pored lateral-line scale count (45) was the only character that could be used to separate this fish from other eastern North Pacific anthiins.

Jordan and Evermann (1896) apparently based their generic description on *P. eos* because they reported that *Pronotogrammus* lacks teeth on the tongue and has a "naked top of head and maxillary." Their account of the species duplicates Gill's (1863) description of the holotype, which—until then (1896)—was the only known specimen. Three years later, Garman (1899) listed three Albatross stations where *P. multifasciatus* had been taken and noted (for the first time) that the entire head and maxillary were covered with scales and that the tongue had a group of teeth on it.

Walford (1974) reported that *P. multifasciatus* was known from "Cape San Lucas to the Galapagos Islands," but I have been unable to locate a single specimen in a west coast collection that had been identified as *P. multifasciatus*.

An inquiry to the National Museum of Natural History regarding the holotype of *P. multifasciatus* (USNM 2762) brought the reply that "the brown body, without skin, scales, head or tail is about 30 mm long" (Bruce B. Collette, pers. commun.). A radiograph of this fragment revealed 16 caudal vertebrae, which eliminated both species of *Hemanthias* but not *P. eos*. Gill's (1863) pored lateral-line scale count eliminated *P. eos*, however.

Anthias gordensis Wade, 1946, and *Holanthias sechurae* Barton, 1947, can not be distinguished and are here considered junior synonyms of *Pronotogrammus multifasciatus*. *Pronotogrammus* Gill, 1863, has priority over *Holanthias* Günther, 1868.

Pronotogrammus eos Gilbert, 1890

Figure 2

Pronotogrammus eos Gilbert, 1890:100 (original description, type locality: Panama).

Anthias eos (Gilbert). Boulenger, 1895 (generic reassignment, list).

MERISTIC DATA. D. X, 14–15; A. III, 7–8; P. 17–18; GR 11–13 + 27–30 = 38–43; pored lateral-line scales 36–40; vertebrae 10 + 16.

Three of the 30 individuals I examined to obtain meristic data

had dorsal finray counts of X, 14, and one had an anal finray count of III, 7.

DIAGNOSTIC CHARACTERS. *Pronotogrammus eos* differs from the other three eastern North Pacific anthiins in having only 36 to 40 pored lateral-line scales and by its large eye, comprising 12.0 to 15.9 percent of SL.

MAXIMUM SIZE: The largest individual I examined was 153 mm SL (207 mm TL).

RANGE. Mid-Gulf of California (28° N) to Panama (7° N); 115 to 325 meters.

DISCUSSION. This species lacks several characters that are of generic magnitude and diagnostic for *Pronotogrammus* (e.g., fully scaled maxillary, mandible, and anterior face and head; patch of granular teeth on tongue; and salient features on its otoliths). Its proper generic assignment must await a revision of eastern Pacific Anthiinae that currently is in progress (Phillip C. Heemstra, pers. commun.).

Hemanthias peruanus (Steindachner, 1874)

Figure 3

Anthias (Hemanthias) peruanus Steindachner, 1874:378 (original description, type locality: Paita, Peru).

Pronotogrammus peruanus (Steindachner). Jordan and Eigenmann, 1890:413 (generic reassignment, redescription).

Hemianthias peruanus Steindachner. Jordan and Evermann, 1896:1222 (subgenus to generic rank, spelling variant).

MERISTIC DATA. D. IX–X, 13–15; A. III, 7–9; P. 16–18; GR 9–10 + 22–24 = 31–34; pored lateral-line scales 52–59; vertebrae 11 + 15.

One of the 55 specimens from which I obtained meristic data had nine dorsal spines, the rest had ten. Forty-eight of these specimens had 14 dorsal soft rays, four had 13, and three had 15. Fifty of the 55 had anal finray counts of III, 8, two had counts of III, 7, and three had III, 9.

DIAGNOSTIC CHARACTERS. *Hemanthias peruanus* is the only eastern North Pacific anthiin in which the middle rays of each lobe of the caudal fin are the longest (not readily visible in specimens smaller than about 90 mm SL). It shares with *H. signifer* an elongate, filamentous third dorsal spine but lacks the antrorse spine that is found on the urohyal of *H. signifer* longer than about 70 mm SL. It also can be distinguished from *H. signifer* by gill raker, pectoral ray, and pored lateral-line scale counts, except at overlap numbers (Table 2).

MAXIMUM SIZE. The largest individual I examined was 305 mm SL (442 mm TL).

RANGE. Hipolito Bank, Baja California Sur (27° N), to Trujillo, Peru (8° S); 10 to 117 meters. Hildebrand (1946) reported the southern range as "Chile," but I could not verify any records south of Trujillo, Peru.

Hemanthias signifer (Garman, 1899)

Figure 4

Centristhmus signifer Garman, 1899:48 (original description, type locality: off Panama at 7° 33' N, 78° 34' 20" W).

Hemianthias peruanus (non Steindachner). Wales, 1932:106 (first California record, misidentified, spelling variant).

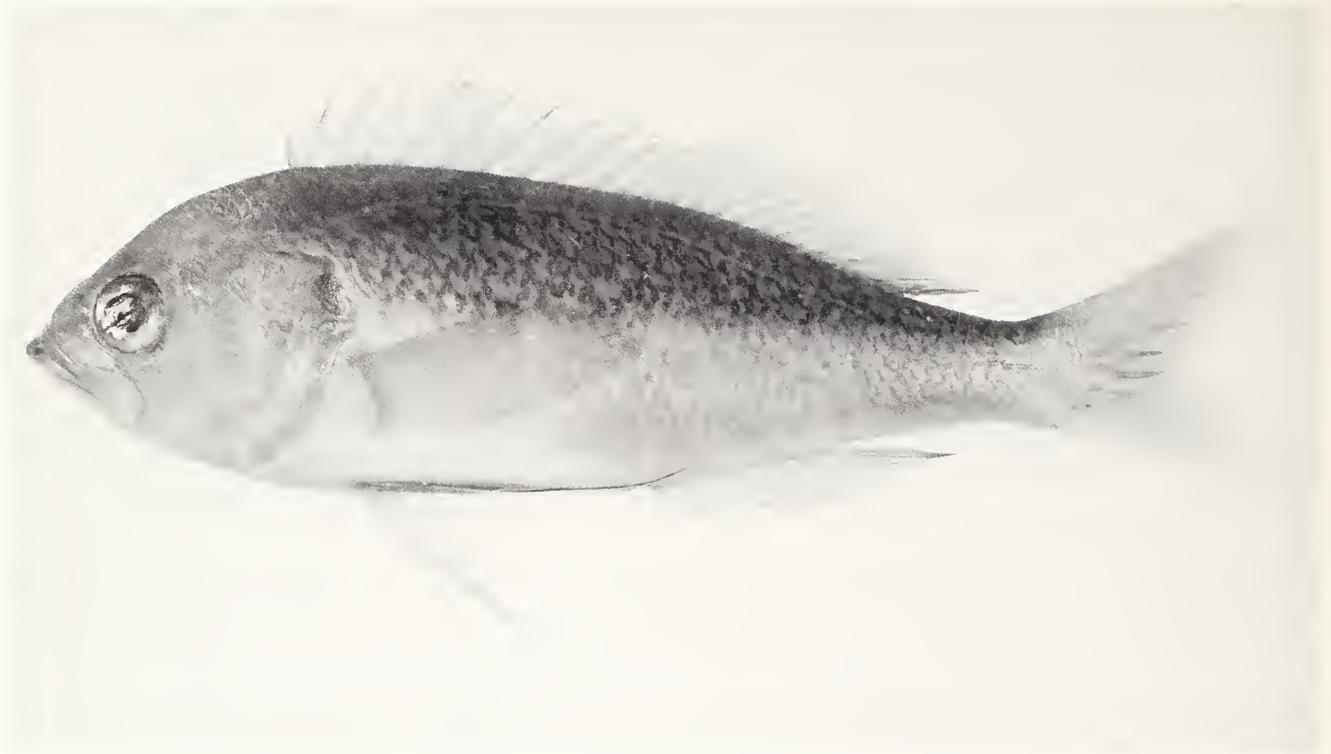


Figure 1. *Pronotogrammus multifasciatus*, 176 mm SL, Uncle Sam Bank, Baja California (LACM 38671). Photograph by Paul Gregory.



Figure 2. *Pronotogrammus eos*, 129 mm SL, middle of mouth of Gulf of Nicoya, Costa Rica (LACM 33827). Photograph by Richard Meier.

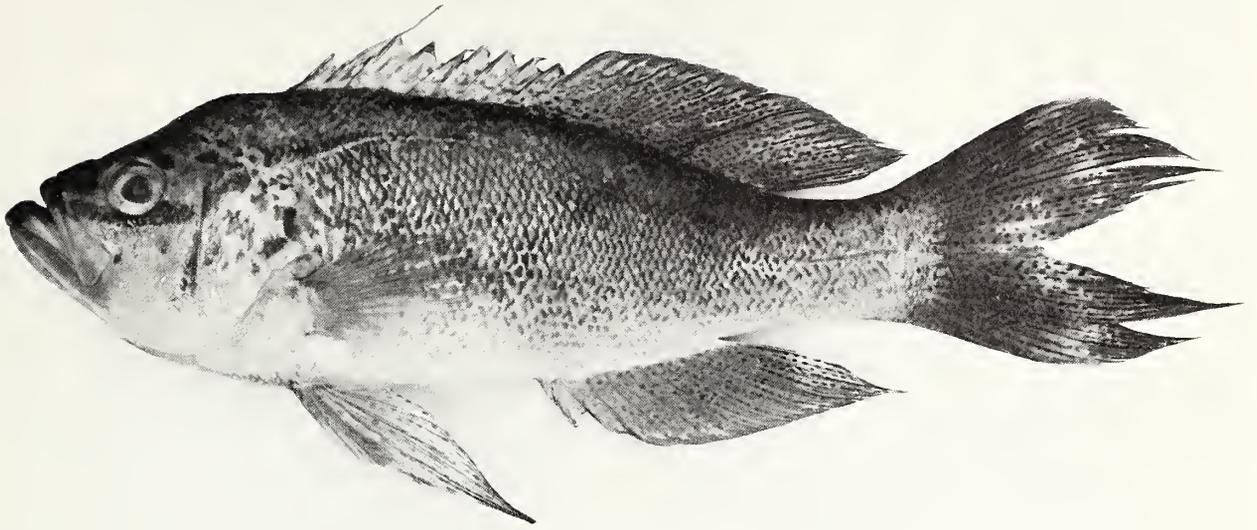


Figure 3. *Hemanthias peruanus*, 267 mm SL, Hipolito Bank, Baja California (LACM W61-124). Photograph by Jack W. Schott.



Figure 4. *Hemanthias signifer*, 201 mm SL, off San Onofre, California (LACM 36401). Photograph by Jack W. Schott.

Table 2. Comparison of pectoral rays, gill rakers and pored lateral-line scales for *Hemanthias peruanus* and *Hemanthias signifer*.

	<i>H. peruanus</i>	<i>H. signifer</i>
Pectoral rays		
16	1	—
17	27	—
18	23	11
19	—	22
20	—	2
Total gill rakers		
31	13	—
32	19	—
33	17	1
34	2	14
35	—	9
36	—	10
37	—	0
38	—	1
Pored lateral-line scales		
52	11	—
53	15	—
54	11	—
55	8	—
56	2	—
57	2	—
58	1	—
59	1	2
60	—	2
61	—	3
62	—	0
63	—	7
64	—	2
65	—	5
66	—	7
67	—	3
68	—	3
69	—	1

MERISTIC DATA. D. X, 13–14; A. III, 7–9; P. 18–20; GR 9–11 + 24–27 = 33–38; pored lateral-line scales 59–69; vertebrae 11 + 15.

One of the 35 specimens from which I obtained meristics had a dorsal finray count of X, 13; all others had X, 14. Except for one individual with seven anal soft rays, and one with nine, this count invariably was eight.

DIAGNOSTIC CHARACTERS. *Hemanthias signifer* longer than about 70mm SL have an anteriorly projecting spine on the urohyal (easily observed by lifting either gill cover) that is unique among anthiins. In the eastern North Pacific, it shares with *H. peruanus* an elongate, filamentous third dorsal spine, but most individuals can be distinguished by counting pored lateral-line scales, pectoral rays, and gill rakers (Table 2). In addition, the outermost rays of both lobes of the caudal fin are the longest—at

all sizes for *H. signifer*, but only for specimens smaller than about 90 mm SL for *H. peruanus*.

MAXIMUM SIZE. The largest individual I examined was 296 mm SL (385 mm TL).

RANGE. Playa del Rey, California (34° N), to off Paita, in northern Peru (5° S); 23 to 306 meters.

DISCUSSION. The unique antrorse spine on the urohyal of this species appears to have been Garman's (1899) primary reason for establishing the genus *Centristhmus*. His *C. signifer*, however, is so closely similar to *Hemanthias peruanus* that, until the spine first appears on the urohyal (at about 70 mm SL), one must count pectoral fin rays, gill rakers, and pored lateral-line scales to determine which of the two species is at hand. In fact, juveniles of both species often have been taken in the same trawl haul, but until now, *H. signifer* seldom was recognized (e.g., SIO 68–66 from La Paz Bay, Gulf of California, in 32 to 42 fathoms [58–77 meters] contained 158 fish labeled *H. peruanus*, but critical examination revealed that only 89 were *H. peruanus* whereas the other 69 were *H. signifer*, none of which had an antrorse spine on the urohyal). Obviously, *Centristhmus* must be considered a junior synonym of *Hemanthias*.

Norma Chirichigno (pers. commun.) described *Hemanthias delsolari* n. sp. in her unpublished thesis (1970), and subsequently (Chirichigno, 1974:289) used the name in her "Clave para identificar los peces marinos del Peru." While her paper was in press, she learned that her *H. delsolari* was a synonym of *Centristhmus signifer* (see last page of "addenda" in Chirichigno, 1974), so the name does not appear elsewhere in reports on the marine fish fauna of Peru. Thus, because *H. delsolari* fails to meet requirements of establishing a new species as spelled out in the International Code of Zoological Nomenclature, it has no status in taxonomic literature.

Wales (1932) reported *Hemianthias* [sic] *peruanus* from Californian waters (based upon a specimen caught off Redondo Beach), but the reported pored lateral-line scale count was diagnostic for *H. signifer*, and examination of the fish in the CAS collection (SU-CAS 24812) revealed the antrorse spine on the urohyal. In February 1977, two additional specimens of *H. signifer* were caught off California: one off San Onofre (LACM 36401) and the other off Playa del Rey (LACM 36944).

OTOLITHS

In the eastern North Pacific, anthiins apparently are a choice prey for many predators. At least two specimens of *Pronotogrammus multifasciatus* in west coast collections came from stomachs of larger fish. One (SIO 59–326) came from the stomach of a yellowtail, *Seriola lalandi lalandi*, and the other (LACM W53–313) from a spotted cabrilla, *Epinephelus analogus*. Otoliths of all four species commonly are found in scats of sea lions, *Zalophus californianus*, that haul out on Islotes Island (north of La Paz), Gulf of California (unpublished data in my files).

When conventional identification characters have disappeared from prey species because of digestive action of the predator, otoliths (sagittae) usually can be found and offer an excellent opportunity to identify the prey to genus or species. Because of this, and the apparent importance of anthiins in the food web,

sagittae of the four eastern North Pacific anthiins are illustrated (Fig. 5).

In identifying otoliths, characters on the inner faces (grooved side) are extremely important for determining family and genus. Overall otolith shape, ratio of height into length, marginal ornamentation, and similar characters are of importance primarily at species level. The illustrated otoliths (Fig. 5) are all inner faces,

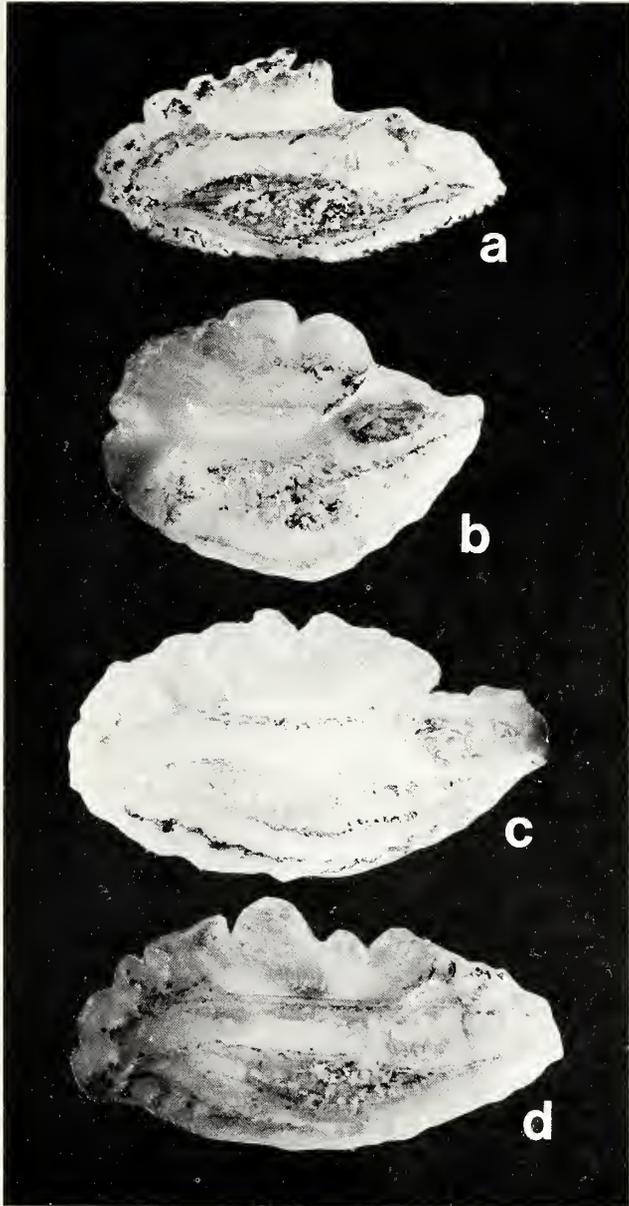


Figure 5. Inner faces of left otoliths (sagittae) of the four eastern North Pacific anthiins: **Part a**, *Pronotogrammus multifasciatus*, 9.1 by 4.6 mm (length and height), from fish 205 mm SL; **Part b**, *Pronotogrammus eos*, 8.7 by 6.3 mm, from fish 130 mm SL; **Part c**, *Hemanthias peruanus*, 10.9 by 6.0 mm, from fish 213 mm SL; **Part d**, *Hemanthias signifer*, 11.0 by 5.5 mm, from fish 256 mm SL. Photographs by Richard Meier.

and all visible features are quite typical of sagittae for other individuals of the same species.

Sagittae of all four anthiins have a "channel" just above the ventral margin and roughly parallel to it; the channel is deepest in *P. multifasciatus* and least developed in *H. signifer*.

In all but *P. eos*, the cauda (posterior portion of sulcus or central groove) flexes slightly downward at its posterior end, and the ostium (anterior portion of sulcus) comprises about 37 to 38 percent of the otolith length. In *P. eos*, the cauda is expanded and indistinct posteriorly, and the ostium comprises slightly more than 40 percent of otolith length. Also, in *P. eos*, otolith height comprises more than 70 percent of otolith length, compared with 50 to 55 percent in the other three species.

In all four species, the crista superior (ridge bordering the sulcus dorsally) is extremely strong and distinct, and the area of the otolith dorsal to it is shallowly to deeply concave. The rostrum (anteroventral projecting portion of the otolith) is least distinct on sagittae of *H. signifer*. When placed outer face down on a flat surface, otoliths of *Hemanthias* are more bowed than those of *Pronotogrammus*; *P. eos* sagittae are the least convex when viewed in this aspect. Otoliths from juveniles usually have margins that are much more lobular, incised, or frilly than is indicated on the illustrated sagittae, which are all from adults.

Sagittae of *P. eos* (five pairs measured) comprise about 6.5 to 7 percent of fish SL, whereas those of the other three species (five pairs of each measured) comprise between about 4 and 5.3 percent.

ACKNOWLEDGMENTS

As with any such project, my investigations of eastern North Pacific anthiins could not have reached fruition without my borrowing specimens, library material, work space, ideas, and the special talents of others that are lacking in me. Phillip C. Heemstra, now with the J.L.B. Smith Institute of Ichthyology, Rhodes University, South Africa, encouraged me and provided information that helped me start in the right direction. My sincere thanks are extended to him and to Lillian Dempster and W.I. Follett (CAS); Steve Crooke, Paul Gregory, William Maxwell, and Jack W. Schott (California Department of Fish and Game); Lawrence L. Jones (CMM); John DeLeon, Teri Kato, Robert J. Lavenberg, Richard Meier, and Camm C. Swift (LACM); Joe Copp, Carl L. Hubbs (deceased), and Richard H. Rosenblatt (SIO); Boyd W. Walker (UCLA); William A. Bussing (UCR); and Bruce B. Collette (USNM). If I have forgotten anyone who helped me, it has not been intentional.

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CONTRIBUTIONS IN SCIENCE

DESCRIPTION OF A NEW SPECIES OF NET-WINGED MIDGE
(DIPTERA: BLEPHARICERIDAE) FROM THE SIERRA NEVADA
DE SANTA MARTA, COLOMBIA

Charles L. Hogue



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DESCRIPTION OF A NEW SPECIES OF NET-WINGED MIDGE (DIPTERA: BLEPHARICERIDAE) FROM THE SIERRA NEVADA DE SANTA MARTA, COLOMBIA¹

Charles L. Hogue²

ABSTRACT. The status of the genus *Limonicola* is reviewed, and a preliminary generic diagnosis provided. The genus presently includes the type species, *L. plurivectis* Lutz, 1928, from Venezuela, *L. leucoptera* Edwards, 1929, from Peru, and a new species named herein *L. davila*, from the Sierra Nevada de Santa Marta, Colombia.

RESUMEN. Se considera el estatus del género *Limonicola* y se da una diagnosis genérica preliminar. Actualmente este género incluye la especie tipo *L. plurivectis* Lutz, 1928, procedente de Venezuela, *L. leucoptera* Edwards, 1929, de Peru, y una nueva especie de la Sierra Nevada de Santa Marta, Colombia nombrada aquí *L. davila*.

INTRODUCTION

The dipteran fauna of torrential waters in South America comprises several taxa whose immatures are highly adapted to life in swiftly flowing streams. Although widespread and common, two of these taxa, the Blephariceridae ("net-winged midges") and the genus *Maruina* Müller, 1895, of the Psychodidae ("lance-winged midges"), are poorly studied. This is unfortunate because their close association with head-water streams, poor dispersal abilities, and great geological age make them particularly useful paleogeographic indicators. Their present distributional patterns can provide data on the positions of tectonic plates and orogenic zones in the past. For this reason, it has long seemed evident to me that these midges might offer significant clues to former relationships between elevated land masses along the Caribbean borderlands of South America, and consequently I have made efforts to collect and analyze material from these areas. One such tectonic unit is the Sierra Nevada de Santa Marta (hereinafter called "Sierra") in northern Colombia that has been the subject of geologic studies (Tschanz et al., 1974) and faunistic investigations on butterflies (Adams, 1973; Adams and Bernard, 1977), reptiles and amphibians (Duellman, 1979:382-4), and plants (Sugden and Robins, 1979).

The present paper is a partial report on my collections of Blephariceridae and *Maruina* made in March of 1980. In future papers, I plan to review my other collections and describe additional species of Blephariceridae (*Paltostoma* Schiner, 1866) and Psychodidae (*Maruina*).

Collection sites pertinent to the present paper are listed by field numbers below with brief habitat descriptions. All distances

are kilometers by road. All localities are situated in the Department of Magdalena except CLH 257, which is in Guajira Department.

CLH 257. Río Ancho and Highway No. 2, 11 March. A wide, shallow river with a bottom entirely of medium-size, rounded boulders. Collections made in morning on both sides of highway bridge crossing the river about 1-2 km from its exit to the sea, on coastal plain at an elevation of only 90 m. Water temperature 25°C.

CLH 259. Quebrada Donama, 5 km northeast of Mamatoco, 12 March. A rushing stream flowing over a hard rock substratum with scattered mixed-sized boulders. Collections made behind a house between road (to Minca) and stream at an elevation of approximately 100 m. Water temperature 25°C.

CLH 260. Quebrada Minca, 12 March. A wide, shallow, cold water (23.5°C) stream flowing through village. Collections made immediately west of village, on medium to small, rounded, loose boulders. Elevation 800 m.

CLH 263. Río Gallina (tributary of Río Sevilla) near Finca California, 11.2 km northeast of Palmar, 13 March. Large stream flowing with considerable velocity through a steep canyon of large, fixed boulders and intermittent rapids. Collections made near bridge just above ranch house at approximately 1,500-m elevation. Water temperature 21°C.

CLH 264. Quebrada Charua (tributary of Río Gallina), near Finca California, 11.2 km northeast of Palmar, 13 March. Small, steep, stepped stream with intermittent dams of large, fixed boulders. Collections made near confluence with Río Gallina.

CLH 267. Río Sevilla, 8.7 km southeast of Palmar, 14 March. Large rushing stream flowing through steep gorge, inclinous, intermittently forming slips over bare rock exposures, falls through gigantic boulder dams, and large pools. Water temperature 24°C. Elevation approximately 800 m.

The water at all localities was free of visible pollution and generally in good ecological condition. All streams appeared to

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be near their lowest normal flows in response to the dry season, which reaches its height on the Sierra in March. Rock types forming their beds are varied, but light-colored granites, quartz diorites, and hard metamorphics predominate.

TERMINOLOGY

Special morphological and descriptive terms applied herein are explained in the text and figures. For the genitalia, I follow the interpretations of homologies as given in my most recent paper (Hogue, 1981). Reference to my papers of 1973 (general) and 1978 (larval chaetotaxy) will provide the reader with further explanations of abbreviations and the particular nomenclature applied to the family.

I refer to the variously shaped, short sensilla of the larval dorsum as "tuberculiform" (sensilla tuberculiforma) to distinguish them collectively from the hairlike sensilla (sensilla chaetica). The tuberculiform types may be further characterized by specific shapes such as conoid (acorn-shaped), clavate, or ovoid; these may be straight or sharply curved at the base (falcate).

SYSTEMATICS

Blepharicerinae and Paltostomatini
sensu Zwick, 1977, and pers. comm.

Genus *Limonicola* Lutz

HISTORY

Lutz proposed the genus *Limonicola* in 1928 to include an unusual blepharicerid that he collected in the Limón River near Maracay, Venezuela. In his publication (Lutz, 1928), he noted that the unique characteristic separating this new entity from other genera was the male's very long hind legs, with swollen basal tarsal segments. He described the type species, *plurivectis*, from complete material of all stages, but his specimens have become lost. A year later, Edwards recognized a new Andean species as belonging to *Limonicola* and described it in his monumental treatment on the Diptera of Patagonia and South Chile (Edwards, 1929:73-74). The species was named *leucoptera* and was based on a single male, the type of which I have not examined.

Because of the absence of good material from Lutz's and Edwards's work for comparative and diagnostic reference, no further species have been added to date (Hogue, 1971), and *Limonicola* has become an enigmatic taxon with undefined boundaries and cryptic affinities. I have material now on hand of these and several additional new species, excluding that from the Sierra described below. From this and good series of all stages from the Sierra, it is now realized that the genus is truly distinct in many characters and contains numerous species widely distributed over the mountainous terrain of northwestern South America.

A full generic definition will not be possible without further study. However, in order to provide a basis for particularization

of the new species, I am providing here a preliminary definition of the genus based on its salient features.

DESCRIPTION

Adult

Small, short-bodied, fragile Blephariceridae.

Coloration. Body integument well sclerotized, dull, velvety-black with opalescent reflections, especially on abdomen; some sclerites and membranes dark brown. Wing membrane infusate in both sexes.

Size. Small, wing length ranges, male 3.5 to 9.5 mm; female 2.8 to 9.0 mm. Male slightly larger than female.

Structure. Head: Colocephalous [amandibulate, misproportioned head, as defined by Hogue, 1970:7] in both sexes. Ocellar lobes slight, ocelli sessile. Eyes disjunct, entire, and without callis oculi [unfacetted strip]; ommatidia subequal, large in male, somewhat smaller in female. Proboscis very short, mouthpart elements greatly reduced and modified: labrum narrowly lanceolate; mandibles totally absent in both sexes; hypopharynx vestigial, slightly larger in female but always less than half the length of labrum; maxillary palpus composed of a single diminutive segment, lacinia similar to palpus but weaker and with obliquely rounded apex; labellum composed of deeply furcate, elongate lobes. Antenna short, 15-segmented; flagellomeres subglobose.

Thorax: Sclerites generally typical for Blepharicerinae; scutum somewhat larger than in most genera and projecting farther forward, giving entire thorax an oblique set in lateral view; katapisternum truncate ventrally; pleural suture sinuous, forked (posterior branch separating dorsal portion of meron, itself broken into two portions, a small triangular lower plate and a larger, upper lobate swelling; the convex anterior part of the latter extends over the pleural suture, forming a pitlike depression beneath).

Wing: Broad as in other Paltostomatini but with a hyperexpanded anal lobe. Venation typical for tribe, with reduced longitudinal veins: subcosta evanescent; fork of R_s near wing apex; M_3 absent; $M_3 + 4$ (false crossvein) lacking; 1A sometimes not reaching wing margin. Posterior veins decidedly more weakly sclerotized than radius and costa.

Legs: Strongly sexually dimorphic: in males very long and slender, especially the hind leg, which is twice the length of others and has inflated tibial apex and tarsal segments 1 and 2; fore femur sinuously curved; all tarsal segments 5 with ventrobasal lobes bearing large setae (calcipalae); tarsal claws elongate and slender, with subbasal tooth. Legs in female short and normally proportioned except fore femur, which is strongly upcurved basally and abruptly swollen apically; hind femur moderately upcurved, hind tibia slightly curved sinuously; tarsal segments 5 and claws simple. Tibial spurs usually lacking from all legs in both sexes, hind tibia of female sometimes with pair of equal spurs.

Abdomen: Short, strongly tapered posteriorly. Sclerites moderately sclerotized, especially sternites; pleural membranes wide. Tergite I very narrow, well sclerotized laterally only.

Male genitalia: Segment VIII ligulate. Tergite IX broad, posterior margin unmodified. Lobes of Xth tergite well developed, ventrolateral portions lobate, converging. Tegmen complex, dorsomesal portion convex, raised into a longitudinal slitlike fold. Vesica large, spherical, with transverse, dorsal, lobate apodeme. Aedeagal rods three, short, equal, attenuate filaments. Lateral tine undeveloped. Genital capsule (fused hypandrium and gonocoxite) broadly membranous mesally. Outer lobe of gonostylus variously shaped, generally with dorsal and ventral lobes; inner lobe of gonostylus transverse, with ventral extension, which is fused with the posterior margin of the genital capsule.

Female genitalia: Tergite VIII narrow, distinct from tergite IX. Sternite VIII well sclerotized medially, developed into a deeply emarginate (bilobed) plate. Oviscapt (hypogynial plate) complex, posterior lobes directed mesad, apices spiculate (and with a few minute setae), midportion constricted. Genital fork well defined, a transverse stirrup-shaped plate. Lateral lobes of sternite IX (normally present in the Blepharicerinae) absent. Proctiger sclerotized basally to form a transverse plate similar to genital fork (but with shorter arms). Lobe of tergite X (cercus, auct.) deeply cleft, with a distinct ventral secondary lobe. Three ovoid spermathecae.

Pupa

Depressed. Outlined shape oval, lateral margins of abdominal segments moderately convex, that of segment II strongly convex (more so in female), thoracic region abruptly narrowed.

Coloration. Upper surface evenly black (in life); lower surface white.

Size. Small to medium-sized, body lengths 2.8 to 7.0 mm. Male pupa slightly larger than female and more elongate.

Structure. General dorsal cuticle and under folded lateral margins of abdomen coarsely and densely verrucose. Scutellar sclerite broad, reaching nearly to lateral extreme of metascutal sclerite; abdominal segments I and II curving strongly anterolaterally. Branchiae with heavy, expanded bases; that of anterior-most lamella bullate laterally; branchial posture porrect, all plates elongate, subtriangular, rigid, with acute apices, and of about equal length but inner pair much narrower than outer. Antennal and mouthpart cases ill-defined. Ventrolateral adhesive organs present on abdominal segments II–V (four pairs).

Fourth-Instar Larva

Size. Small to medium-sized, body lengths 3.7 to 9.0 mm.

Structure. Intercalary convexities (Fig. 11) undeveloped. Head capsule weakly sclerotized (hind margin evanescent), with deep lateral insertions and lateralia. Antenna short, 2-segmented, the proximal segment about one-third length of distal. Dorsal pseudopod absent from segments of anterior and median divisions; present and similar to pseudopods, but smaller, on terminal segment. Dorsal sclerotized plates, tubercles, or other processes entirely absent. Ventral gill filaments digitiform, arranged in two slightly disjunct, stellate clusters, the anterior usually with six filaments, the posterior with four filaments. Pseudopods elongate, directed laterad, only slightly downcurved; subequal in

length (about one-quarter width of segment) except that of segment I, which is one-half the size of others. Ventral integument of each abdominal segment basal to pseudopod, dorsal pseudopod of terminal segment, and sclerotization of terminal lobe with numerous denticles grading to papillae mesad.

Chaetotaxy. Primary trunk sensilla as follows: *ic* slightly ventral on anterolateral corner of segment, minute and difficult to see because of sclerotization in this area; *it* in normal position, minute; *is* double, associated with anteromesal invagination of each segment; *tM-T* forming a quadrate constellation in center of dorsum, chaetiform; *tI-VIII* normal in position, tuberculiform; *stPI-VIII* normally positioned, chaetiform; *stM-T* just lateral to *t*, tuberculiform; *pdpod* not evident; *dpod* on dorsal pseudopod of segment VII only, both chaetiform; *p* not evident; *sp* obscured by proliferation; *ssP-T* in line, large chaetiform; *pdl-VI* normal. Secondary sensilla of small tuberculiform and chaetiform types generally and evenly distributed over dorsum, latter most numerous laterally, former absent from pseudopods but forming a noticeably denser field middorsally (circular concentration); anterior and posterior lobular portions of each segment often free of sensilla; no conspicuously large flat or specially modified sensilla in linear series or otherwise. Terminal setae very small and few in number.

Limonicola davila new species

(Figs. 1–12)

DIAGNOSIS

Limonicola davila is most similar to *plurivectis*. From that species and the only other described species in the genus, *leucoptera*, it may be identified by the following primary structural differences in all known stages.

Adult Male

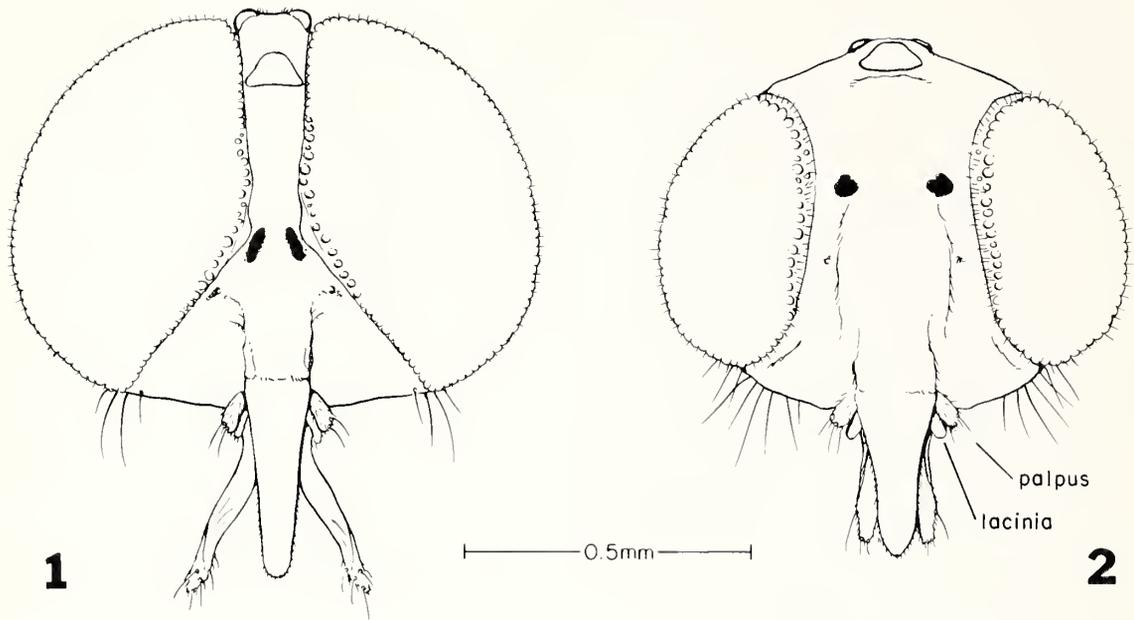
The transverse, strongly asymmetrical, V-shaped dististyle of *davila* is unique; in the two other species, this structure is subhexagonal and roughly symmetrical.

Adult Female

The tarsal claws of both *davila* and *plurivectis* are similar, short and broad, whereas those of *leucoptera* are long and slender. Paralleling this condition is the length of tarsal segment 5 and the presence or absence of calcipalae: long (over twice length of segment 4) and without calcipalae in *davila* and *plurivectis*, short (about equal to length of segment 4) and with calcipalae in *leucoptera*. The shape of the oviscapt lobes of the genitalia also distinguish *davila* from *plurivectis*: with an evenly narrowed apex in the former, broad and basally constricted in the latter.

Pupa

The pupae of *davila* and *plurivectis* are similar but that of the former may be distinguished from the latter most easily by the more extensive verrucae on the scutum and branchial sclerite: in *davila*, the verrucose area of the scutum extends medially to the metascutal sclerite and covers the entire branchial sclerite pos-



Figures 1 and 2. *Limonicola davila*. Heads, frontal view. Figure 1, male; Figure 2, female.

terior to the branchioalar suture; in *plurivectis*, the scutal verrucae are restricted to the central area and cover only the anterior half of the branchial sclerite. Also, the bullate posterior basal extension of the anterior branchial lamella is much larger in *davila* than in *plurivectis*. *L. davila* differs from *leucoptera* by its smaller size (3.0 to 3.4 mm body length versus 3.4 to 4.0 mm), its relatively larger and more widely spaced integumentary verrucae, and the virtual absence of a bullate swelling on the posterior extension of the anterior branchial sclerite base.

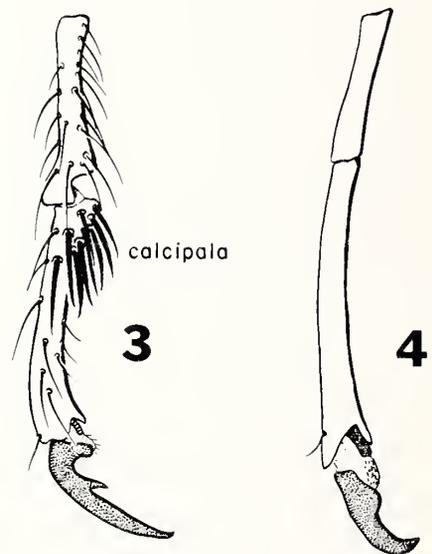
Larva

Gross differences separate the larvae of the three species: *davila* and *leucoptera* are alike in the sparsity of conspicuous, large, dorsal, integumentary, tuberculiform sensilla, which are present in *plurivectis*; the larva of *leucoptera* is easily distinguished from that of *davila* by its significantly larger dorsal pseudopod of the terminal division; the organ also is well separated and extrorse in *davila*, nearly reaching the level of the posterior margin, but is almost adnate to the terminal margin in *leucoptera*.

DESCRIPTION

Adult (Figs. 1-9)

Size. Small, measurements as follows: wing length male (range, N = 10) 3.5 to 3.9 mm, mean 3.7 mm; female 2.8 to 3.8 mm,



Figures 3 and 4. *Limonicola davila*. Hind tarsal segments 4 and 5 and tarsal claws. Figure 3, male; Figure 4, female.

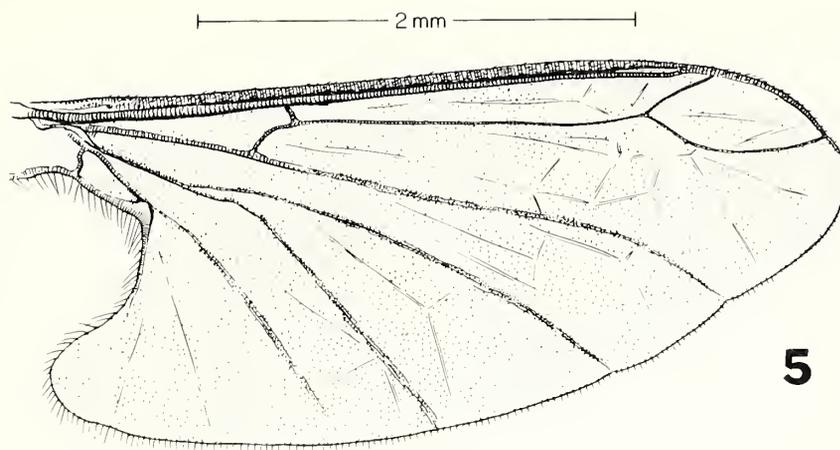
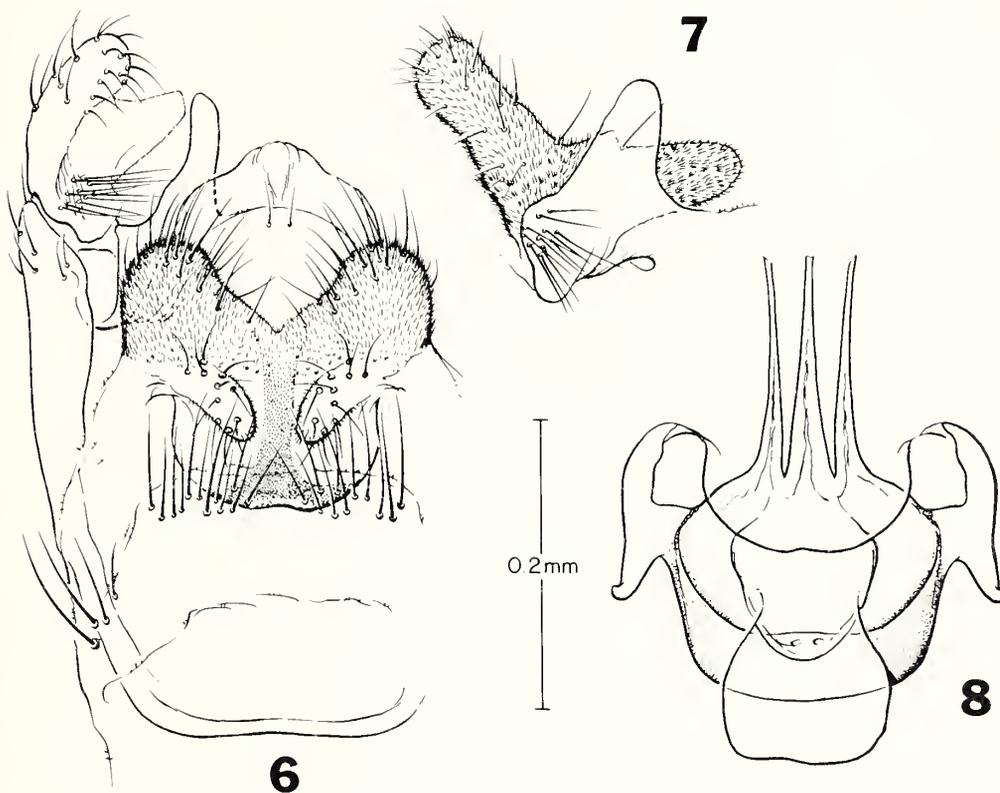


Figure 5. *Limonicola davila*. Wing.



Figures 6 through 8. *Limonicola davila*. Male genitalia. Figure 6, entire structure, dorsal view; Figure 7, inner and outer gonostyles, ventral view; Figure 8, phallic complex, dorsal view.

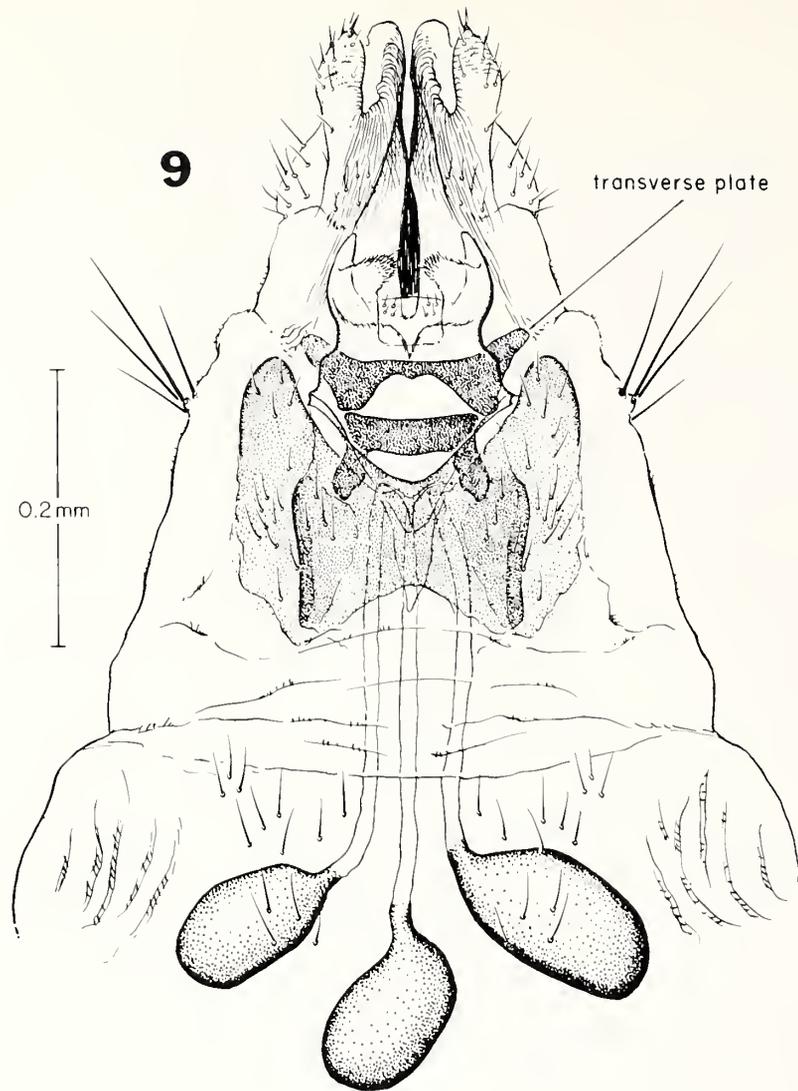


Figure 9. *Limonicola davila*. Female genitalia, ventral view.

mean 3.2 mm. Leg segment lengths given in Table 1.

Structure. Head (Figs. 1–2): Ocular bristles short (about 1.5 width of ommatidium) and single over nearly all of eye. Mouthparts: Labellar lobe short, barely exceeding apex of labrum in male, slightly short of this point in female; lobe with only a few apical setae in both sexes.

Legs: Female tarsal segment 5 over twice as long as segment 4 and without setae except for single, small apicodorsal bristle (Fig. 4). Tarsal claws and calcipalae normal for genus (Figs. 3–4). Tibial spurs entirely lacking.

Wing (Fig. 5): Venation typical.

Abdomen: Setae of sternite VII lacking mesally in both sexes.

Male genitalia (Figs. 6–8): Setae of IXth tergite in two disjunct groups, a posterior group of several medium-sized hairs and an anterolateral group of fewer and generally heavier hairs. Lobe of Xth tergite about as long as broad, apex slightly incurved,

inner margin angled; internal, ventrolateral lobe well developed and with rounded apex. Outer lobe of gonostylus (Fig. 7) transverse, strongly asymmetrical, open V-shaped in mesal view.

Female genitalia (Fig. 9): Lobe of plate formed from sternite VIII narrowly rounded at apex; anterior border of plate emarginate; 29–30 setae on each side of plate. Base of oviscapt (hypogynial plate) only slightly broader than lobular portion; lobe with evenly narrowed, spiculate apex. Necks of spermathecae short, 1.5–2 times width. Transverse inner plate of proctiger (Fig. 9, “transverse plate”) asymmetrically bifurcate laterally, the posterior fork much longer than the anterior.

Pupa (Fig. 10)

General shape and morphology typical for genus.

Size. Small, male body length range 2.9 to 4.1, width 1.7 to 2.5 mm (N = 20; means 3.5 and 2.0 mm); female body length range

Table 1. Leg segment lengths of male and female *Limonicola davila*. Unit of measurement is millimeters; values are ranges (N = 14) followed by means.

	Male	Female
Fore leg		
Femur	1.2-1.5, 1.3	0.66-0.96, 0.79
Tibia	1.4-1.7, 1.6	0.74-1.06, 0.86
Tarsus 1	1.04-1.30, 1.21	0.48-0.65, 0.51
2	0.48-0.59, 0.55	0.20-0.30, 0.25
3	0.29-0.34, 0.31	0.17-0.23, 0.20
4	0.20-0.23, 0.21	0.15-0.20, 0.17
5	0.21-0.26, 0.24	0.30-0.39, 0.34
Mid leg		
Femur	1.3-1.5, 1.4	0.70-0.90, 0.82
Tibia	1.3-1.6, 1.4	0.68-0.92, 0.79
Tarsus 1	1.06-1.16, 1.11	0.41-0.58, 0.48
2	0.44-0.57, 0.51	0.20-0.27, 0.23
3	0.26-0.32, 0.30	0.17-0.23, 0.19
4	0.19-0.24, 0.21	0.14-0.20, 0.16
5	0.21-0.25, 0.23	0.31-0.41, 0.34
Hind leg		
Femur	3.1-3.9, 3.6	1.4-1.9, 1.6
Tibia	3.7-4.5, 4.2	1.4-2.0, 1.7
Tarsus 1	1.44-1.68, 1.56	0.44-0.60, 0.50
2	0.68-0.76, 0.74	0.21-0.30, 0.25
3	0.51-0.58, 0.55	0.17-0.25, 0.20
4	0.32-0.37, 0.34	0.15-0.20, 0.17
5	0.23-0.27, 0.25	0.30-0.40, 0.34

2.8 to 3.8 mm, width 1.6 to 2.2 mm (N = 20; means 3.2 and 1.9 mm). Proportions length/width, male 1.75, female 1.68.

Structure. Verrucae of dorsal integument relatively large and widely spaced (6 in line per 0.1 mm); extensive on thorax: those of median portion of scutal field extending posteriorly to meta-scutal sclerite, and those of lower portion of branchial sclerite covering entire sclerite posterior to the branchioalar suture. Bullate posterobasal portion of anterior branchial lamella large.

Fourth-Instar Larva (Figs. 11-12)

General shape and morphology typical for genus.

Coloration. Generally yellowish gray-brown or medium-brown, intermediate forms with varying amounts of brown mottling on light background: pigmented areas usually confined to escharae (sclerotizations externally marking points of muscle insertions) but may expand transversely over dorsum, often selectively coloring segments III and V, giving larva a double-banded appearance.

Size. Small, body length: range of random specimens (N = 54) 3.7 to 5.5 mm, mean 4.6 mm; of mature specimens only (i.e. pupal branchiae visible) (N = 24) 3.7 to 5.5 mm, mean 4.6 mm; head capsule width, range (N = 54) 0.90 to 1.30 mm, mean 1.11 mm.

Structure and Chaetotaxy (Figs. 11-12). Secondary tuberculiform sensilla of dorsum sparse and mostly very small, conoid to ovoid in shape, including those of median circular group. Dorsal

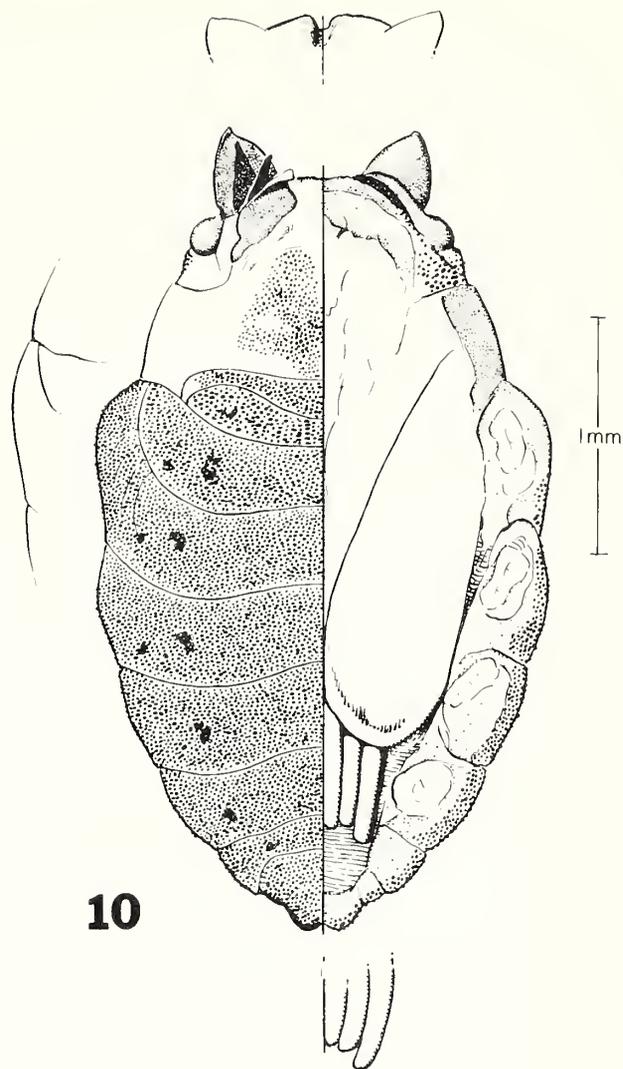


Figure 10. *Limonicola davila*. Pupa, female (dorsal left, ventral right), satellite details of adjacent male features.

pseudopod of segment VII relatively large and well separated and directed away from the terminal lobe.

MATERIAL

Type Material

HOLOTYPE male (completely dissected and mounted on slides Nos. CLH 80-112 a-d): COLOMBIA, Department of Magdalena, Sierra Nevada de Santa Marta, Río Gallina at Finca California, 1,500 m, 13 March 1980, C. L. Hogue, CLH 263. **ALLOTYPE** female (completely dissected and mounted on slides Nos. CLH 80-85 a-d): same data as holotype. 21 male, 23 female **PARATYPES** (pinned, in alcohol, and mounted on slides): same data as holotype.

Holotype and allotype deposited in the collection of the In-

stituto Nacional de los Recursos Naturales Renovables y del Ambiente, Bogotá (INDERENA). One paratype male and female sent to National Museum of Natural History, Washington, D.C. (USNM) and British Museum (Natural History) (BMNH), London. All others in Natural History Museum of Los Angeles County (LACM).

Additional Specimens

COLOMBIA. Department of Guajira, Sierra Nevada de Santa Marta, Río Ancho and Highway No. 2, 11 March 1980, C. L. Hogue, CLH 257 (325 larvae, 75 pupae: INDERENA, USNM, BMNH, LACM). Department of Magdalena, Quebrada Donama, 5 km NE Mamatoco, 12 March 1980, C. L. Hogue, CLH 259 (3 larvae, 4 pupae, 15 males, 1 female: LACM); Quebrada Minca, Minca, 12 March 1980, C. L. Hogue, CLH 260 (142 larvae, 47 pupae, 21 males: LACM); Río Gallina, Finca California, 13 March 1980, C. L. Hogue, CLH 263 (2 larvae: LACM). Quebrada Charua, tributary to Río Gallina, Finca California, 13 March 1980, C. L. Hogue, CLH 264 (8 larvae, 4 pupae, 1 male: LACM); Río Sevilla, 8.7 km SW Palmar, 14 March 1980, C. L. Hogue, CLH 267 (14 larvae, 2 pupae: LACM).

ETYMOLOGY

The species is named for Sr. Francisco E. Dávila Riascos, long time resident and prominent rancher of the Sierra whose gener-

ous assistance during my collecting made the discovery of this species possible.

DISTRIBUTION

Limonicola davila is known only from the Sierra Nevada de Santa Marta and appears to be endemic within that mountain system.

ECOLOGY

In all localities where I found *L. davila*, the larvae and pupae were attached to relatively small (10- to 45-cm diameter), smooth stones that were detachable from the substratum; none appeared on vertical faces of large, implanted boulders or portions of exposed basement rock as is the habitat of *Paltostoma* and other blepharicerid genera elsewhere. Larvae exhibit a distinct preference for lodging in small crevasses or notches on the stone's surface. Most collections were of single specimens or groups of only a few individuals. Water temperatures of streams at collecting sites varied from 22° to 25°C.

Although I was not able to verify it by direct observation, the flight posture of the males and their morphology leads me to the hypothesis that they capture females in flight for mating. *Limonicola* males are unique in possessing swollen hind tarsi on extremely long hind legs, twice the length of the others; all the legs of the female are of normal proportions and without special mod-

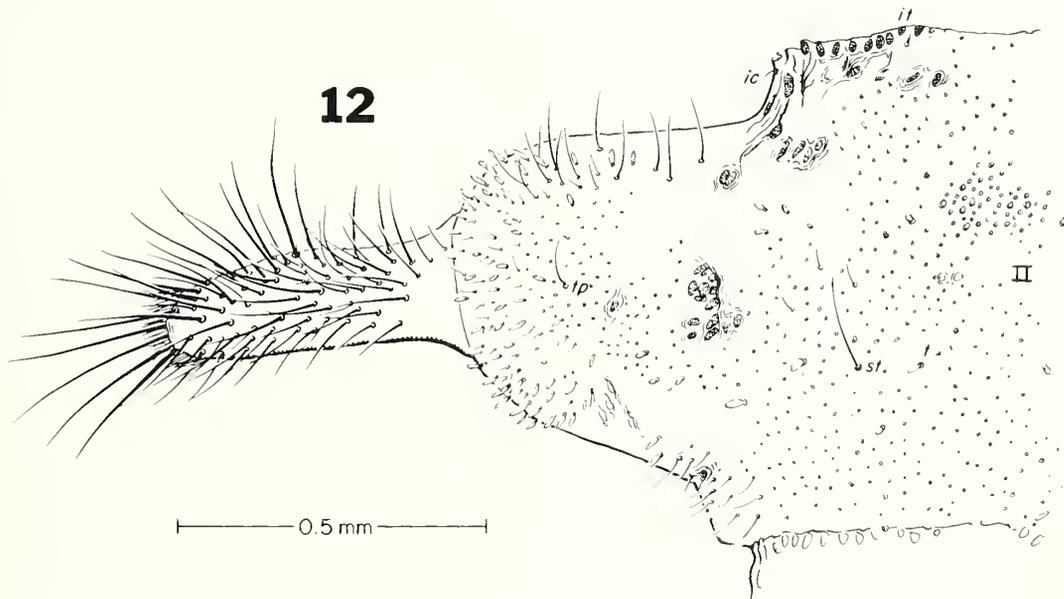


Figure 12. *Limonicola davila*. Larva, fourth instar, dorsal view of left half of abdominal segment II.

Figure 11. *Limonicola davila*. Larva, fourth instar (dorsal left, ventral right), abbreviated sensillar designations explained in Hogue (1978:3-4).

ifications. These features apparently contribute to the male's tendency to fly with the hind legs extended far below the plane of the body in which position they may be used to snare females in flight in a manner similar to the prey capture techniques of certain Mecoptera. This would also explain the sinuously curved fore femora of the females, a configuration that permits them to hold their fore legs upward directly over the body where the male's tarsi could most easily grapple them. That the tarsi of the male are capable of grasping in such a fashion was well demonstrated during field collecting by the way in which adult midges of both sexes become tenaciously entangled by the tarsi of males in a killing tube. The elongate tarsal claws fold back against the calcipalae at the base of the last tarsal segment, creating a very effective clasp device. The female lacks this arrangement, logically, being the passive sex in the precopulatory capture scenario.

Because of their very reduced mouthparts, neither sex could possibly prey on other insects as is normal, at least with the female, in most other Blephariceridae. This, plus their overall small size, indicates an ephemeral, possibly nonfeeding, adult life, paralleling that of other diminutive, short-lived torrenticolous midges, such as the Deuterophlebiidae, Nymphomyiidae, and Thaumaliidae.

ACKNOWLEDGMENTS

I wish to express my very great thanks to the following individuals and institutions for their support and assistance in making possible my field trip and the completion of this report:

The Instituto Nacional de los Recursos Naturales Renovables y del Ambiente (INDERENA) for extending official permission to conduct scientific research in Colombia (by instrument of communication 02475 dated 7 March 1980); Drs. Sergio Duran (president) and Jorge Hernandez C. (chief of the División de la Fauna Silvestre) of this agency for their numerous courtesies, including the authorization of said permission and logistical advice; Dr. Gustavo Maldonado of the Santa Marta office of INDERENA for assistance with transportation; Sr. and Sra. Francisco Dávila of Santa Marta and Dr. Gerardo Reichel-Dolmatoff of Bogotá for their personal interest in my work, reflected in many generous favors during the course of my stay in Colombia; and Sr. Wilfredo Silva for his field assistance and services as chauffeur.

In addition I would like to acknowledge the financial aid extended by the Natural History Museum of Los Angeles County Foundation as well as thank the review committee and my colleagues Peter Zwick, Julian P. Donahue, and Roy R. Snelling for criticism of the manuscript.

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CONTRIBUTIONS IN SCIENCE

FOSSIL BIRDS FROM TERTIARY MARINE BEDS
AT OCEANSIDE, SAN DIEGO COUNTY, CALIFORNIA, WITH
DESCRIPTIONS OF TWO NEW SPECIES OF THE
GENERA *URIA* AND *CEPPHUS* (AVES: ALCIDAE)

Hildegard Howard



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FOSSIL BIRDS FROM TERTIARY MARINE BEDS
AT OCEANSIDE, SAN DIEGO COUNTY, CALIFORNIA, WITH
DESCRIPTIONS OF TWO NEW SPECIES OF THE
GENERA *URIA* AND *CEPPHUS* (AVES: ALCIDAE)¹

Hildegard Howard²

ABSTRACT. The San Luis Rey River Local Fauna, in the lowermost rocks in Lawrence Canyon that are referred to the San Mateo Formation, yielded bones of six species of fossil birds: a murre, *Uria paleoheesperis* n. sp.; a guillemot, *Cephus olsoni* n. sp.; a flightless auk, *Praemancalla* cf. *P. wetmorei*; a loon, *Gavia* sp.; an albatross, *Diomedea* sp.; and an auklet, *Aethia* sp. The holotype of *U. paleoheesperis* has shoulder and wing bones of stockier proportions than in Recent species of *Uria* and has distinctive characters of the scapula, coracoid, and ulna. The holotype humerus of *C. olsoni* is shorter than in Recent *C. columba* and has distinctive characters of the deltoid crest and ectepicondylar process. The partial skeleton of *Praemancalla* cf. *P. wetmorei* includes the first leg bones known for the genus. In the Lawrence Canyon Local Fauna, higher in the formation, abundant fragmentary bones of *Mancalla* occur. *Mancalla milleri*, *M. diegensis*, and *M. cf. M. cedrosensis* are recognized. The presence of *Praemancalla* in the lower beds and *Mancalla* in the upper indicates a major time interval within the San Mateo Formation at this Oceanside site, with a range from latest Miocene to earliest Pliocene.

INTRODUCTION

During the past several years the University of California Museum of Paleontology at Berkeley (UCMP) and the Natural History Museum of Los Angeles County (LACM) have collected vertebrate fossils in Lawrence Canyon at Oceanside, San Diego County, California. Over one hundred bird bones in these collections can be assigned to genus, and 13 taxa are recognized. Personnel of the San Diego Society of Natural History (SDSNH) also continue to collect in the area, and further reports are anticipated.

The Lawrence Canyon localities are at the extreme southern extent of Woodford's (1925:217) mapped outcrop of the San Mateo Formation, a rock unit that he grouped among "Post Capistrano formations." Later, Vedder (1972:167) suggested that Woodford's type section of the San Mateo Formation "may be a channel deposit within the lower part of the Capistrano Formation."

Tentatively retaining the San Mateo Formation designation, Barnes et al. (1981) recognized two separate local faunas based on vertebrate fossils (see Fig. 1). The faunal assemblage in the

lowermost beds (fine gray to white sands that immediately overlie the San Onofre Breccia) was named the San Luis Rey River Local Fauna. The fossils referred to this fauna were collected at locality LACM 4297 (= UCMP V68147) and nearby localities LACM 4298 (= UCMP V68144) and LACM 4299 (= UCMP V68145). The fossil assemblage from a coarser sand and gravel matrix at locality LACM 4301 (= UCMP V68106) and UCMP V6880, some 25 feet higher and near the top of the exposed stratigraphic section, was named the Lawrence Canyon Local Fauna. Both local faunas were assigned to the Hemphillian North American Land Mammal Age, approximately 3.5 to 8.5 million years B.P., which includes the earliest Pliocene and latest Miocene epochs (Repenning and Tedford, 1977, table 1). Bones of sharks, fish, birds, and terrestrial and marine mammals were found in both local faunas. The 26 bird bones from the lower horizon represent approximately half of the vertebrate fossil specimens recognized in the San Luis Rey River Local Fauna and are assigned as follows (number of bones in parentheses): *Gavia* sp.—loon (1), *Diomedea* sp.—albatross (1), *Uria paleoheesperis* new species—extinct murre (9), *Cephus olsoni* new species—extinct guillemot (1), *Aethia* sp.—auklet (1), and *Praemancalla* cf. *P. wetmorei* Howard—extinct flightless auk (13).

Most of the vertebrate bones in the Lawrence Canyon Local Fauna from the upper horizon represent flightless auks of the genus *Mancalla* Lucas, 1901, though only 24 of the 81 so assigned are specifically determinable. The following avian taxa are recognized from this local fauna: Family Sulidae—booby or gannet (1), Family Accipitridae—eagle (1), *Falco* sp.—falcon (1), *Cephus* sp.—guillemot (1), *Mancalla milleri* Howard—extinct flightless auk (9), *Mancalla diegensis* (Miller)—extinct

1. Review committee for this Contribution: Kenneth E. Campbell, Storrs L. Olson, and David W. Steadman.

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flightless auk (3), and *Mancalla* cf. *M. cedrosensis* Howard—extinct flightless auk (12).

METHODS AND MATERIALS

Abbreviations

The specimens cited in text are deposited in the following institutions: Academy of Natural Sciences of Philadelphia (ANSP), Natural History Museum of Los Angeles County (LACM), Museum of Vertebrate Zoology, University of California, Berkeley (MVZ), San Diego Society of Natural History, Natural History Museum (SDSNH), University of California Museum of Paleon-

tology, Berkeley (UCMP), and United States National Museum (USNM).

Methods

The specimens illustrated were coated with a sublimate of ammonium chloride before photographing to present an evenly colored surface.

Materials

FOSSIL. The following holotypes were available for this study: *Mancalla milleri* Howard, 1970 (LACM 2185), *M. cedrosensis* Howard, 1971 (LACM 15373), *Praemancalla lagunensis*

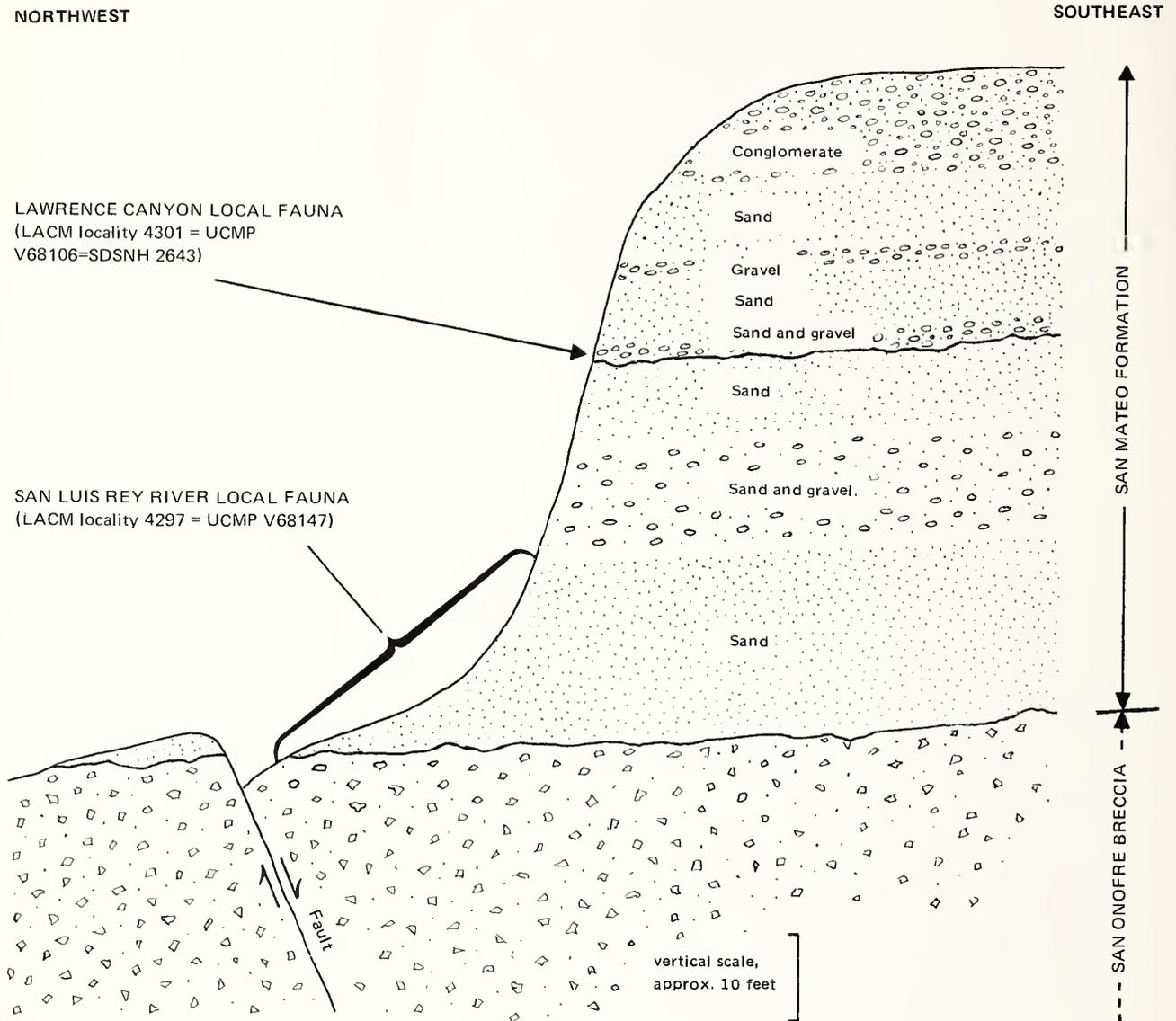


Figure 1. Diagrammatic geologic cross section of part of the San Mateo Formation and the San Onofre Breccia exposed in Lawrence Canyon at Oceanside, showing the stratigraphic occurrence of some fossils making up the two local faunas. Relative thicknesses of the beds are estimated, and the amount of displacement on the fault has not been measured. There is an unconformity at the contact between the San Mateo Formation and the San Onofre Breccia, and another within the San Mateo Formation at the base of the sand and gravel bed that produced the Lawrence Canyon Local Fauna. The San Luis Rey River Local Fauna is derived from the entire thickness of the lowest sand unit resting unconformably upon the San Onofre Breccia. Modified from Barnes et al, 1981, fig. 1. Based on notes and sketches made in the field by Barnes.

Howard, 1966a (LACM 15288), *P. wetmorei* Howard, 1976 (LACM 42653), *Uria brodkorbi* Howard, 1981 (PB7960). Casts of the following holotypes were also available: *Mancalla californiensis* Lucas, 1901 (USNM 4976), *M. diegensis* (Miller, 1937) (UCMP 33409), *Uria antiqua* (Marsh, 1870) (ANSP 13357), *U. affinis* (Marsh, 1872) (ANSP 13358). The following referred material was examined: *Australca* sp., 11 ulnae from the Lower Pliocene Yorktown Formation, Lee Creek, North Carolina (USNM 177833, 179270, 179311, 181106, 183497, 192706, 206457, 210456, 215723, 215905, 242223); *Miocepphus meclungi* Wetmore, 1940, ulna (USNM 237219) from the Miocene Calvert Formation of Westmoreland County, Virginia, and humerus (USNM 25668) from the same formation in Maryland. In addition, large collections of avian fossils from the San Diego Formation (LACM and UCMP), Almejas Formation (LACM), Monterey Formation (LACM), and Repetto Formation (LACM), containing specimens discussed herein, were at hand.

Included with the LACM and UCMP specimens from the San Mateo Formation in the discussions herein are two humeri (SDSNH 119165 and 23568) and a femur (SDSNH 21101) from the Oceanside locality collected by the San Diego Society of Natural History.

RECENT. All skeletal material of Recent species referred to herein is in the LACM collections, with the exception of specimens of the genus *Aethia* Merrem, 1788, which were on loan from MVZ, and *Cephus carbo* Pallas, 1811, and *C. grylle* Linnaeus, 1758, from USNM.

SYSTEMATICS

San Luis Rey River Local Fauna

Order Gaviiformes

Family Gaviidae Forster, 1788

Loons

Genus *Gavia* Forster, 1788

Gavia sp.

REFERRED SPECIMEN. Left tarsometatarsus eroded distally, UCMP 88656. From locality V68145, collected by UCMP field party, August 1968.

DESCRIPTION. In length, the fossil tarsometatarsus is within the size range of tarsometatarsi of the living Pacific Loon, *Gavia pacifica* (Lawrence, 1858) (66.2–75.3 mm, mean 70.1 mm) and close to that of the Red-throated Loon, *Gavia stellata* (Pontopidan, 1763) (68.9–71.4 mm, mean 70.2 mm), though below the mean for either (based on four specimens of each of the Recent species). Relative breadths of shaft and proximal end are within the range of *G. pacifica*, which slightly exceeds *G. stellata* in these measurements. The only notable character of the fossil specimen is found in the very high posterior position of the distal foramen, which is near the level of the proximal edge of the internal trochlea and 6.9 mm above the external intertrochlear notch. In *G. pacifica* and *G. stellata*, the foramen is well below the proximal level of the internal trochlea and only 3.6–5.1 mm above the intertrochlear notch. Of five available specimens of the much larger *G. immer* (Brünnich, 1764), the maximum distance

of the foramen above the intertrochlear notch is only 6.4 mm.

Measurements (in mm): length to center of eroded middle trochlea 68.6, breadth of proximal end 12.0, least breadth of shaft 3.8, greatest depth of shaft 6.9.

DISCUSSION. Four extinct species of the genus *Gavia* have been recorded from the Tertiary of North America: *Gavia brodkorbi* Howard, 1978, from the Upper Miocene Monterey Formation of California; *G. palaeodytes* Wetmore, 1943, from the early Pliocene (Hemphillian age), Bone Valley Formation of Florida; *G. concinna* Wetmore, 1940, from the early-middle, Pliocene Etchegoin Formation of California with referred material from the Bone Valley Formation and the late Pliocene, San Diego Formation of California, and *G. howardae* Brodkorb, 1953, from the San Diego Formation. A fifth species, *G. portisi* (Regalia, 1902), is recorded from the Pliocene of Italy, based only on a cervical vertebra. Three modern species of loons are recorded from the Pleistocene of California (Brodkorb, 1963:225).

The tarsometatarsus has not been recorded for any of the extinct species. However, Robert Chandler of the San Diego Natural History Museum has called to my attention a small tarsometatarsus (SDSNH 22916) from the San Diego Formation that he is referring to *G. howardae* (Chandler MS). It bears the same size relationship to the tarsometatarsus of Recent *G. stellata* (14% shorter) as was previously observed (Howard, 1978:5) for one of the referred humeri of *G. howardae*. Not only is it 8 mm shorter than the Oceanside specimen, it does not have the high position of the distal foramen. The very small size of the holotype ulna of *G. brodkorbi*, which is 23.6 percent shorter than the minimum for *G. stellata* (Howard, 1978), suggests that this species also cannot be represented by the tarsometatarsus from the San Mateo Formation.

Those elements recorded for *G. concinna* and *G. palaeodytes* appear to fall within the size range of *G. stellata* and *G. pacifica*. Since this is also true for the Oceanside tarsometatarsus, it would be ill-advised to attempt a specific assignment of the specimen at this time.

Order Procellariiformes Fürbringer, 1888

Family Diomedidae (Gray, 1840)

Albatrosses

Genus *Diomedea* Linnaeus, 1758

Diomedea sp.

REFERRED SPECIMEN. Distal end of left tibiotarsus, LACM 119353, from locality LACM 4297. Collected by Robert M. McKenzie 9 March 1979.

DESCRIPTION. The fossil tibiotarsus resembles the comparable element in the Black-footed Albatross, *Diomedea nigripes* Audubon, 1839, in having a slight notch on the distal surface of the internal condyle and a rounded contour of the external condyle (viewed laterally). The fossil is narrower in the area of the ligmental bridge and differs in relative depth to breadth of the distal end (depth of distal end 13.5 mm, anterior breadth of distal end 13.6 mm; the same dimensions in *D. nigripes* (LACM 86350) are 15.1 mm and 14.7 mm).

DISCUSSION. A number of albatross bones have been recorded previously from the Miocene of California, although only two species have been described: *Diomedea californica* Miller, 1962 (a large form intermediate in size between the Recent *D. exulans* Linnaeus, 1758 and *D. albatrus* Pallas, 1769) and *D. milleri* Howard, 1966b (a form notably smaller than *D. nigripes*). Both were described from the middle Miocene of the Sharktooth Hill Bonebed in Kern County. *Diomedea californica* is also tentatively recorded from the late Miocene of Orange County (Howard, 1978). *Diomedea milleri*, known only from the holotype ulna, appears to have been even smaller than the species represented by the tibiotarsus at hand, based on the comparable element of *D. nigripes*. Bones assignable to *Diomedea*, and apparently intermediate in size between the two described species, have been found in three California late Miocene sites: in the Valmonte diatomite at Lomita, Los Angeles County (Miller, 1935); and in the Monterey Formation in Laguna Hills, Orange County, at locality LACM 1945 (Howard, 1968) and Laguna Niguel, Orange County, at localities LACM 6902 and 6906 (Howard, 1978). A single species may be represented by these several occurrences, possibly including the Oceanside specimen.

Two other fossils species of *Diomedea* have been described: *D. thryidata* Wilkinson, 1969 from the Miocene of Australia, known only from the holotype rostrum; and *D. anglica* Lydekker, 1891 from the early Pleistocene of England (with referred specimens from the Pliocene of England and Florida (Brodkorb, 1963:242)). The Florida specimen of *D. anglica* is a tibiotarsus of much larger size than LACM 119353 from Oceanside. Extant species of the genus have been recorded from the Pleistocene of southern California (Brodkorb, 1963:242).

Order Charadriiformes (Huxley, 1867)

Family Alcidae Vigors, 1825 Auk-like Birds

Subfamily Alcinae (Vigors, 1825)

Genus *Uria* Brisson, 1760—Murre

DISCUSSION. The coracoid, ulna, and radius of an incomplete skeleton (UCMP 88704) from locality UCMP V68147 more closely resemble the corresponding bones of Recent species of *Uria* than of any other Recent alcid genus in the following characters: coracoid combining a prominent procoracoid process and well-formed foramen with an anteroposteriorly narrow sternal facet; ulna with a stout olecranon, separated from the cotylar rim by a deep notch or channel (as viewed externally); and radius with the ulnar surface of the shaft above the distal end broad, with a distinct, round ligamental attachment on the ligamental prominence. The associated scapula, however, has a narrower, less prominently projected glenoid facet than that of *Uria* or the closely related Razorbill (*Alca torda* Linnaeus, 1758), and, in these characters, more closely resembles the murrelets of the genus *Endomychura* Oberholser, 1899.

Although the scapula suggests generic distinction from *Uria*, I have chosen to place this incomplete skeleton in the genus *Uria*,

in view of the similarities observed in the coracoid, ulna, and radius.

Uria paleohesperis n. sp.

Fig. 2, a–f

HOLOTYPE. UCMP 88704, associated elements including articular end of right scapula, left and right coracoid (both lacking head), complete left ulna and distal end of right ulna, distal ends of left and right radius, distal end of left carpometacarpus, and wing phalanx digit II, phalanx 2. Collected by University of California Museum of Paleontology field party, August 1968.

LOCALITY. UCMP V68147, Loretta Street, Lawrence Canyon, Oceanside, San Diego County, California.

FORMATION AND AGE. San Luis Rey River Local Fauna, San Mateo Formation. Late Miocene.

ETYMOLOGY. The specific name is derived from the Greek *palaio*—ancient, and *hesperos*—of the west, thus indicating an ancient western murre.

DIAGNOSIS. Distinguished from Recent species, *Uria aalge* (Pontoppidan, 1763) and *U. lomvia* (Linnaeus, 1758) as follows: coracoid relatively stouter, with well-formed procoracoid more distinctly pointed at the tip, foramen small, and scapular facet deeply cup-shaped and sharply rimmed; scapula more concave dorsally between acromion and glenoid facet, acromion longer, and glenoid facet narrower and not markedly projected from shaft; ulna relatively stouter, with rounded shaft (less blade-like than in Recent *Uria*), attachment of anterior articular ligament more broadly oval and flatter, and brachial impression broader, extending more than half the depth of the shaft; radius more distally attenuated on internal side of distal articulation; carpometacarpus poorly preserved, but contour of metacarpal 3 in symphyseal region seemingly more rounded than angular; digit II, phalanx 2 less deeply depressed posteriorly and with less sharply developed ridge anteriorly than that of *U. aalge*, closer to that of *U. lomvia*, but with ridge slightly more marked anteriorly; distinguished from extinct species *Uria antiqua* (Marsh, 1870), *U. affinis* (Marsh, 1872), and *U. brodkorbi* Howard, 1981, by smaller size, and also from *U. brodkorbi* by scapula being more concave dorsally and having narrower glenoid facet.

MEASUREMENTS. See Table 1.

DISCUSSION. The proximal end of a humerus (LACM 52018) from the late Miocene, Monterey Formation of Orange County, California, was assigned to ?*Uria* sp. (Howard, 1978). Although only a small fragment, it suggests the stockier proportions of the shaft, in comparison with humeri of Recent species of *Uria*, that are noted in the ulna of *Uria paleohesperis*. Possibly the same species is represented.

Four other extinct species of the genus *Uria* have been described: *Uria antiqua* (Marsh, 1870), from the Lower Pliocene of North Carolina, *U. affinis* (Marsh, 1872), from the Pleistocene of Maine, and *U. ausonia* Portis, 1888, from the Pliocene of Italy, each based on a humerus; and *U. brodkorbi* Howard, 1981, from the Miocene, Sisquoc Formation in California, based on an incomplete skeleton. The small size of the elements of *U. paleohesperis* precludes their assignment to either *U. antiqua* or *U.*

affinis, the holotypes of which are larger than humeri of living species of *Uria*. Furthermore, according to Olson and Gillette (1978), *U. antiqua* should be referred to the genus *Australca* Brodkorb, 1955, rather than to *Uria*. This may be true, as well, of *U. ausonia*. Although the holotype humerus of *U. ausonia* is only a fragmentary distal end, the illustration (Portis, 1891, table 1) that appeared subsequent to the original description suggests that the tricipital grooves are equal in size as in *Alca torda* Linnaeus, 1758, and *Australca grandis* Brodkorb, 1955. The external tricipital groove is notably narrower than the internal groove in the genus *Uria*. The holotype of *U. brodkorbi* consists of the impressions (in diatomite) of an incomplete skeleton, the wing and girdle elements of which are generally larger than those of *U. paleohesperis*. The details of the scapula are best compared in the two species. The scapula in *U. brodkorbi* resembles that of Recent species of *Uria* and differs from that of *U. paleohesperis* in the greater breadth of the glenoid facet and less dorsal concavity.

Ulnae (USNM) from Lee Creek, North Carolina, which Olson (USNM, pers. comm.) assigns to *Australca*, were loaned for this study. All have a more raised and distally pointed attachment for the anterior articular ligament than that of *U. paleohesperis*. This is also true of an ulna (USNM 237219) from the Miocene Calvert Formation of Virginia, which Olson (pers. comm.) assigns to *Miocepphus mcclungi* Wetmore, 1940. This ulna is also notably smaller and more curved than that of *U. paleohesperis*.

One species of murre, *Uria aalge* (Pontoppidan, 1763), occurs today as far south as Newport Beach, Orange County, California, and has been recorded from the Pleistocene of Los Angeles County (Howard, 1936).

Genus *Cepphus* Pallas, 1769 Guillemots

DISCUSSION. A humerus (LACM 107032) resembles that of the guillemots (genus *Cepphus*) as distinguished from all other genera of the family Alcidae in having a rounded, rather than compressed or bladelike, shaft that describes a broad S curvature from proximal to distal end as viewed both laterally and anconally.

Cepphus olsoni n. sp. Fig. 2, g, h

HOLOTYPE. Right humerus, LACM 107032. Collected by Robert M. McKenzie, 19 March 1975.

LOCALITY. LACM 4297, Loretta Street, Lawrence Canyon, Oceanside, San Diego County, California.

FORMATION AND AGE. San Mateo Formation, San Luis Rey River Local Fauna. Late Miocene.

ETYMOLOGY. The species is named in honor of Dr. Storrs L. Olson, of the National Museum of Natural History, in recognition of his extensive studies of fossil Alcidae.



Figure 2. *Uria paleohesperis* n. sp. and *Cepphus olsoni* n. sp. natural size **Parts a through f.** *U. paleohesperis* n. sp., holotype, UCMP 88704. **Parts a and b,** left ulna, external and internal views. **Part c,** right coracoid, dorsal (posterior) view. **Part d,** distal end of left carpometacarpus, external view. **Part e,** distal end of right radius, palmar view. **Part f,** right scapula, dorsal view. **Parts g and h,** *C. olsoni*, n. sp., holotype, LACM 107032, humerus, anconal and palmar views.

Table 1. Measurements (in mm) of *Uria paleohesperis* n. sp. compared to Recent *Uria aalge californica* (7 specimens).

	<i>Uria paleohesperis</i>	<i>U. a. californica</i>		
		Max.	Mean	Min.
Scapula				
Breadth proximal end	10.6	11.5	11.1	11.0
Glenoid facet				
Length	5.9	5.7	5.5	5.0
Breadth	3.7	4.3	3.8	3.6
Shaft near proximal end				
Breadth	4.3	5.2	4.6	4.1
Depth	2.5	2.25	2.15	2.1
Coracoid				
Length from sternal facet to lip of scapular facet	23.4	26.4	25.0	24.3
Breadth of shaft at level of foramen	4.8	4.7	4.5	4.4
Breadth sternal end	14.6	16.2	15.1	14.6
Depth of sternal facet	4.5	5.1	4.5	4.2
Ulna				
Greatest length	62.6	69.5	65.3	61.3
Proximal end				
Breadth	8.5	8.6	8.3	8.1
Depth internally	9.7	10.15	9.9	9.8
Middle shaft				
Breadth	3.85	4.3	4.0	3.8
Depth	5.35	6.6	6.1	5.75
Greatest breadth of brachial impression	3.5	3.4	2.9	2.6
Radius, breadth distal end	5.7	5.9	5.7	5.6

DIAGNOSIS. Compared with the three living species of the genus (in increasing order of size of the humerus), *Cepphus grylle* Linnaeus, 1758, *C. columba* Pallas, 1811, and *C. carbo* Pallas, 1811: between *C. grylle* and *C. columba* in length; relatively stouter of shaft; deltoid crest longer and less abruptly terminated distally; pectoral attachment shorter, with surface concave and more clearly defined; shaft mediad of pectoral attachment sharply ridged, suggestive of condition in *C. grylle*, but space between ridge and median crest narrower and more depressed; bicipital surface distinctly bordered medially and raised from level of shaft; ectepicondylar prominence more evenly rounded in contour, lacking prominent proximal tip; tricipital grooves less distinct (bordering ridges less acute) than in *C. grylle* and *C. carbo*, closer to *C. columba*.

MEASUREMENTS. See Table 2.

DISCUSSION. The genus *Cepphus* was tentatively recorded from locality LACM 6906 in the late Miocene Monterey Formation of Orange County (Howard, 1978:21). Although that speci-

men, an ulna (LACM 47045), suggests a species comparable in size to *Cepphus olsoni*, there is no clear indication that the different elements represent the same species. Apart from these two specimens, there is no other previous fossil record of the genus *Cepphus*. In the material from the upper level of the San Mateo Formation, however, a fragment of a coracoid is herein identified as *Cepphus* sp. According to Storrs Olson (pers. comm.) *Cepphus* has not been found in the abundant alcid material known from the Miocene and Pliocene deposits of the western Atlantic.

That *Cepphus olsoni* is in no way related to *Miocepphus mcclungi* Wetmore, 1940, from the Miocene Calvert Formation of Maryland is evident from the illustration of the holotype humerus of the latter species (Wetmore, 1940:36, figs. 11 and 12), and the shaft measurements provided, as well as by comparison with another humerus (USNM 25668), from a nearby locality in the type formation, which Storrs Olson (USNM, pers. comm.) refers to this species. The shaft in *Miocepphus* is more laterally compressed, the ectepicondylar process more prominent proximally, and the pectoral attachment more elliptical with space between attachment and median crest less sharply depressed than in the holotype of *Cepphus olsoni*. These observations are in keeping with an opinion previously provided by Olson (Howard, 1978:21) that *Miocepphus* is more closely related to *Uria* and *Alca* than to *Cepphus*.

Genus *Aethia* Merrem, 1788

Auklet

?*Aethia* sp.

REFERRED SPECIMEN. Left humerus lacking proximal end, LACM 107031, from locality LACM 4297. Collected by Lawrence G. Barnes, 19 March 1975.

DISCUSSION. This small auklet humerus resembles the referred humerus (LACM 18949) collected and described with the holotype ulna of *Aethia rossmoori* Howard, 1968, from its type locality (LACM 1945) in the late Miocene, Monterey Formation of Laguna Hills, Orange County, California. It also resembles a humerus (LACM 37686) from a slightly later horizon of the Monterey Formation in Orange County (locality LACM 6906) recorded (Howard, 1978:21) as ?*Aethia* sp.

All three specimens differ from Recent specimens of *Aethia pusilla* (Pallas, 1811) and *A. pygmaea* (Gmelin, 1789) by having a more rounded shaft and a greater depression of the brachial area and of the attachment for the anterior articular ligament, with the attachment facing more palmar than laterad. Of the three fossils, only LACM 107031 is complete in the region of the tricipital ridges. It differs from specimens of Recent *Aethia* in that the internal tricipital groove is narrower than the external and lacks the deep depression above the distal edge. In view of this notable distinction, plus the fact that several very small coracoids previously recorded from locality LACM 1945 (Howard, 1968:17) have a well-developed procoracoid with well-formed foramen (unlike the short procoracoid and lack of a foramen characteristic of Recent *Aethia*), it is suggested that an extinct genus of murrelet or auklet is represented in the late Miocene. It is possible that even *A. rossmoori* should be gener-

ically reassigned. It is hoped that further finds of this small alcid will be forthcoming.

Measurements (in mm) of LACM 107031, with those of fossil humeri from Orange County (LACM 18949 and LACM 37686, respectively) in parentheses: breadth of distal end 5.0 (4.1:5.3); least breadth of shaft 2.0 (1.8; 2.3); depth of shaft at same place 2.7 (2.6; 3.3); distance from distal condyle to proximal tip of ectepicondylar process 4.9 (4.5; 5.2).

Subfamily Mancallinae (Miller, 1946) Extinct Flightless Auks

DISCUSSION. The subfamily Mancallinae is best known from the type genus, *Mancalla* Lucas, 1901, in which the wing bones were modified as swimming paddles. Fossil bones of *Mancalla* are abundant in Pliocene deposits in southern California and are recorded herein from the Lawrence Canyon Local Fauna (described later in this paper). Prior records of the genus *Praemancalla* are restricted to the Upper Miocene Monterey Formation in Orange County. The generic name reflects its possible phylogenetic status relative to *Mancalla*. *Praemancalla* has wing bones less highly modified for swimming.

Genus *Praemancalla* Howard, 1966a

DISCUSSION. Two species of *Praemancalla* have been recorded from the Monterey Formation, Orange County, California: *P. lagunensis* Howard, 1966a, and *P. wetmorei* Howard, 1976. The type locality (LACM 1945) of *P. lagunensis* represents a slightly earlier and stratigraphically lower horizon of the Monterey Formation than that of *P. wetmorei* (locality LACM 6906). Only bones of the wing and shoulder girdle and one fragment of mandible were known previously for *Praemancalla*.

Praemancalla cf. *P. wetmorei* Howard, 1976 Fig. 3

REFERRED MATERIAL. Partial skeleton (LACM 107028) consisting of left ulna, left carpometacarpus, right tibiotarsus, left tarsometatarsus, left pedal digit II, phalanx 1, and thoracic vertebra 3. From locality LACM 4297, collected by Robert M. McKenzie, 19 March 1975.

DESCRIPTION OF REFERRED MATERIAL. The ulna resembles the paratype of *Praemancalla wetmorei* (LACM 32429) and is distinguished from the ulna in the several species of *Mancalla* in having (1) olecranon prominent, set off from the cotylae by a deep groove externally and a depression internally (although in the paratype the depression is deeper and more pitlike than in LACM 107028); (2) brachial impression partially palmar and bordered by a long, heavy ridge; and (3) proximal radial depression broad. The distal end, which is missing in the paratype, is distinguished from specimens of the several species of *Mancalla* by having a greatly enlarged projection overhanging the tendinal pit externally and a deep groove separating the carpal tuberosity from the trochlea internally. Although the paratype of *P. wetmorei* lacks the distal end, the length of the Oceanside specimen (36.7 mm) conforms well with the length of the previously re-

Table 2. Measurements (in mm) and ratios (in percent) of humeri of *Cephus olsoni* n. sp., *C. grylle* (2 specimens), and *C. columba* (3 specimens).

	<i>C. olsoni</i>	<i>C. grylle</i>		<i>C. columba</i>	
		Female	Male	Min.	Max.
Greatest length	61.6	59.8	60.6	66.2	69.2
Breadth of proximal end across bicipital crest	15.4	14.4	14.0	14.7	15.1
Breadth of distal end through condyles	7.1	7.0	7.1	7.4	8.0
Breadth of shaft (middle)	4.8	4.3	4.0	4.3	4.8
Depth of shaft from anconal to palmar surface (middle)	3.8	3.4	3.4	3.4	3.7
Ratio, breadth of shaft to length of humerus	7.8	7.2	6.6	6.5	6.9

ferred radius of *P. wetmorei* (LACM 53907, 35.8 mm). Neither ulna nor radius is known for *P. lagunensis*.

The carpometacarpus resembles that of both species of *Praemancalla*, and is distinguished from all species of *Mancalla*, in having a distinct, blunt pisiform process and a more flared internal trochlear crest. It resembles the referred carpometacarpus of *P. wetmorei* (LACM 52216), and is distinguished from the paratype carpometacarpus of *P. lagunensis* (LACM 15287), by having a greater proximal extension of the trochlear crest above metacarpal I, a longer process of metacarpal I (proximodistally), and a less deeply depressed surface above the pisiform process. Distally, it is distinguished from carpometacarpi of *Mancalla* by having a more posteriorly extended distal surface of metacarpal II toward M III, resulting in limited extent of the groove between metacarpal II and III distally. The available carpometacarpi of both *P. wetmorei* and *P. lagunensis* lack the distal end. The contours of the referred specimen of *P. wetmorei* (LACM 52216), as compared with the complete bone from Oceanside, suggest that only 1 mm is lacking from that of *P. wetmorei* and that it was approximately equal in length to the one now at hand.

The tibiotarsus is similar to that of the several known species of *Mancalla* in its general shape and curvature, being relatively broader and flatter of shaft than in species of the subfamily Alcinae, such as the murre (genus *Uria*) or the Great Auk, *Pinguinus impennis* (Linnaeus, 1758). It is distinguished from tibiotarsi of *Mancalla* spp. by having a broader shaft that is less convex anteriorly below the cnemial crests, relatively longer cnemial crests, and a more markedly flared distal end.

The tarsometatarsus is similar to that of *Mancalla* spp. in general shape, with the shaft's anterior surface depressed and

bordered externally by a ridge. It is distinguished from tarsometatarsi of *Mancalla* spp. by the more abrupt narrowing of the shaft distal to the center; more broadly and evenly rounded anterior face of the shaft above the trochleae (lacking the acutely raised area proximal to the middle trochlea); more proximal position of the distal foramen, which is set in a shallower groove; and

more distal position of the internal trochlea. No leg bones have been previously recorded for either species of *Praemancalla*.

The pedal phalanx conforms in general characters to this element in Recent alcids, such as the murre (genus *Uria*), but is markedly larger: length 19.9 mm, proximal breadth 5.7 mm, distal breadth, 3.4 mm. The specimen articulates suitably with



Figure 3. *Praemancalla* cf. *P. wetmorei*, natural size, a–e and g–i, LACM 107028, f, j, k, SDSNH 21101. **Part a**, carpometacarpus, internal view. **Parts b and c**, ulna, external and internal views. **Parts d and e**, tarsometatarsus, posterior and anterior views. **Parts f, j, and k**, femur, external, anterior, and posterior views. **Parts g, h, and i**, tibiotarsus, internal, anterior, and external views.

the internal trochlea of the tarsometatarsus of LACM 107028. This element has not been previously recorded for either *Mancalla* or *Praemancalla*.

The thoracic vertebra was compared with the 3rd thoracic vertebra of *Mancalla cedrosensis* Howard, 1971 (LACM 15425 from locality LACM 65144), the best preserved of the available mancalline vertebrae. The Oceanside specimen resembles LACM 15425 and is distinguished from thoracic vertebrae of Recent species of *Uria* in having a longer costal attachment and a straighter ventral border of the posterior articular surface of the centrum. Anteriorly, the articular surface of the centrum is broadly concave as in *Mancalla* and *Uria*, but it is distinct from both in having a greater dorsoventral dimension at the center. Measurements (in mm): length of centrum 11.9; anterior breadth of centrum 8.4; posterior breadth of centrum 6.5; posterior height of centrum 5.1. Same measurements in *M. cedrosensis* (LACM 15425): 10.0, 7.3, 4.9, and 4.2 respectively. No vertebrae of either species of *Praemancalla* have been previously recorded.

Measurements of wing and leg bones of LACM 107028 are compared with those available for the two species of *Praemancalla* and the largest specimens of *Mancalla diegensis* in Table 3.

TENTATIVELY REFERRED MATERIAL. From locality LACM 4297 and its equivalent, UCMP V68147: scapular end of coracoid (LACM (107030); synsacrum with incomplete pelvic bones of right side including acetabulum and antitrochanter (LACM 119406); axis vertebra (UCMP 102428). From locality LACM 4298 and its equivalent, UCMP V68144: right humerus, abraded distally and in the area of the internal tuberosity (LACM 107029); pedal digit III, phalanx 1 (UCMP 88640). From locality UCMP V68145: poorly preserved proximal end of left scapula (UCMP 95119); left femur poorly preserved both proximally and distally (UCMP 95118). A complete right femur (SDSNH 21101), with characters similar to those of UCMP 95118, was loaned for this study by the San Diego Natural History Museum (locality SDSNH 3003). Judging from the preservation of the specimen and its adhering matrix, it is from the lower level deposits of the San Luis Rey Local Fauna.

DESCRIPTION OF TENTATIVELY REFERRED MATERIAL. Coracoid LACM 107030 resembles this element of *Praemancalla* and is distinguished from that of *Mancalla* by the more medially, less posteriorly oriented triosseal canal and the broad, flat coracohumeral attachment, which is not twisted anteriorly. The specimen is poorly preserved, and the characters that distinguish *P. wetmorei* from *P. lagunensis* are not clearly observable. The only measurement possible (the span from the furcular facet to the top of the glenoid facet) agrees with this dimension in the referred coracoid of *P. wetmorei* (LACM 37637), 10.4 mm. The same dimension in the coracoid referred to *P. lagunensis* (LACM 15289) is 8.4 mm.

The scapula (UCMP 95119) is distinguished from that of the several species of *Mancalla* by the flatter, less concave ventral surface of the proximal end and the longer, more distal extension of the acromion. These characters are suggested in the single, poorly preserved referred scapula of *P. lagunensis* (LACM 15294). The scapula has not been recorded previously for *P. wetmorei*. The proximal breadth of UCMP 95119 (13.8 mm) is greater than that of *P. lagunensis* (12.5 mm).

The following characters of the humerus (LACM 107029) agree with those attributed to the genus *Praemancalla* (Howard, 1976:142): deltoid crest weakly developed; absence of papilla proximal to internal condyle; and presence of a groove separating the base of the ectepicondylar process from the external condyle. It is difficult to determine the profile of the capital groove because the internal tuberosity is broken away. The protrusion of the head over the groove, however, appears to be less than in *Mancalla* spp. and similar to the condition in *Praemancalla wetmorei*. The proximal end of the humerus is not known for *P. lagunensis*. The relative breadth to depth of the shaft above the distal end is 53 percent, as in *P. wetmorei*, contrasted with 66 percent in *P. lagunensis*. For measurements, see Table 3.

The two femora, SDSNH 21101 and UCMP 95118, undoubtedly represent a single species. SDSNH 21101 is complete; UCMP 95118 lacks the proximal surface and has eroded distal contours. Both show the mediad thrust of the distal end, suggestive of the holotype femur of *Mancalla diegensis* (Miller, 1937). They are distinguished from this and all other species of *Mancalla* by the marked depression of the external side of the shaft adjacent to the fibular condyle, which results in emphasizing the prominence of the fibular and external condyles. The popliteal area is deeper than in *M. diegensis* but resembles specimens of *M. milleri* Howard, 1970 as well as those of the Great Auk, *Pinguinus impennis* (Linnaeus, 1758), in this respect. The size of the femur is also similar to that of *P. impennis*. Proximally, the head is large and tilted proximally, and the shaft recedes more abruptly from the head than in *Mancalla diegensis* or *Pinguinus impennis*. The shaft is depressed posteriorly adjacent to the obturator ridge, giving the ridge added prominence. Anteriorly, the trochanter is also prominent and deeply depressed along the internal edge, resembling in this respect the femur of *Uria aalge*, although the trochanter is longer in that species. Both obturator ridge and trochanter are more prominent than in *Mancalla diegensis*. (For measurements, see Table 3.) The mancalline features of the femora and their size, which is proportionate to that of the tibiotarsus and tarsometatarsus associated with the wing elements herein assigned to *Praemancalla* cf. *P. wetmorei*, justify tentative assignment of the specimens to *P. wetmorei*. The ratio of the length of femur SDSNH 21101 to the length of tibiotarsus LACM 107028 assigned to *P. cf. P. wetmorei*, is 65.9 percent. The same ratio in the holotype skeleton of *Mancalla cedrosensis* Howard, 1971 (LACM 15373) is 65.1 percent.

The synsacral section of the pelvis (LACM 119406) resembles a similarly preserved specimen assigned to *Mancalla diegensis* (LACM 2340) from the San Diego Formation in being generally heavier than that of members of the subfamily Alcinae, such as *Uria aalge* and *Alca torda*. It is, however, even heavier than that of *M. diegensis* (LACM 2340), and the median dorsal ridge is broader (greatest breadth of dorsal ridge 3.5 mm; 2.0 mm in LACM 2340).

The axis vertebra (UCMP 102428) was compared with an unrecorded axis of *Mancalla diegensis* (UCMP 45892) from the San Diego Formation. The Oceanside specimen has the facets of the postzygapophyses rounded in contour as in *M. diegensis*, rather than oval as in the Recent murre, *Uria aalge*. These facets, are however, more concave than in *M. diegensis*, and the sides of the vertebra are more deeply depressed toward the anterior end.

Lawrence Canyon Local Fauna
 Order Pelecaniformes Sharpe, 1891
 Family Sulidae (Reichenbach, 1849)
 Boobies and Gannets
 Sulidae gen. and sp. indet.

In this latter respect, the condition is more suggestive of that found in *Uria* than in *Mancalla*. The specimen is markedly larger than *M. diegensis* UCMP 45892 and is in keeping with the large leg bones (LACM 107028) herein assigned to *Praemancalla* cf. *P. wetmorei*. Measurements (in mm): greatest length exclusive of the dorsal spine, 18.5 (*M. diegensis* UCMP 45892, 13.4); breadth and height of posterior surface of centrum, 3.1 and 5.5 respectively (UCMP 45892, 2.7 and 4.0).

The pedal digit III, phalanx 1 (UCMP 88640) suggests in general size digit II, phalanx 1 of the partial skeleton (LACM 107028) assigned herein to *Praemancalla* cf. *P. wetmorei*.

REFERRED SPECIMEN. Digit II, phalanx 1, LACM 119312,
 from locality LACM 4301.

Table 3. Measurements (in mm) of Oceanside *Praemancalla* bones* and those of *P. wetmorei*, *P. lagunensis*, and *Mancalla diegensis* (maximum)

	Oceanside <i>Praemancalla</i>	<i>Praemancalla</i> <i>wetmorei</i>	<i>Praemancalla</i> <i>lagunensis</i>	<i>Mancalla</i> <i>diegensis</i>
Humerus				
Length to intercondylar sulcus	80.8	81.1	—	83.4
Proximal breadth	20.5	22.2	—	20.3
Greatest depth of shaft	9.8	9.6	7.7	10.3
Breadth of shaft at point of greatest depth	5.2	5.1	5.1	5.2
Ulna				
Length to intercotylar ridge	36.7	—	—	32.0
Proximal breadth	7.5	7.5	—	6.6
Proximal depth	11.0	11.3	—	9.3
Breadth shaft (middle)	4.4	4.2	—	3.9
Depth shaft (middle)	6.6	6.2	—	6.8
Carpometacarpus				
Length	36.3	36.3(est)	—	37.2
Breadth proximal trochlea	5.2	5.3	5.2	4.7
Proximal depth through M 1	11.8	12.1	11.7	11.0
Length process of M 1	15.2	15.7	14.0	15.5
Breadth of shaft	4.0	4.0	4.5	3.7
Femur				
Greatest length (external)	69.3	—	—	57.0
Distal breadth	14.4	—	—	11.1
Proximal breadth	14.6	—	—	11.7
Tibiotarsus				
Length to proximal articular surface	105.1	—	—	98.5
Distal breadth	13.5	—	—	10.7
Distal depth	12.1	—	—	9.7
Tarsometatarsus				
Greatest length	47.5	—	—	43.6
Proximal breadth	12.1	—	—	10.7
Distal breadth	11.6	—	—	9.4
Shaft breadth (middle)	6.1	—	—	5.4

*Humerus LACM 107029; Femur SDSNH 21101; all others LACM 107028.

DISCUSSION. This incomplete phalanx resembles the comparable element in the gannet, *Morus bassanus* (Linnaeus, 1758), in general characters but is 2 mm (29 percent) broader.

Although the family Sulidae is no longer represented on the west coast north of Mexico, it is well recorded in the Tertiary and Quaternary of California (Brodkorb, 1963:258–261 and Howard, 1978: 16–19). It is impossible to provide definite identification for this fragment, although its large size is suggestive of *Morus magnus* Howard, 1978, from the Monterey Formation.

Order Falconiformes Seebohm, 1890

Family Accipitridae (Viellot, 1816) Eagles and Hawks

Accipitridae gen. and sp. indet.

REFERRED SPECIMEN. Proximal end of pedal digit I, phalanx 1, LACM 119310, from locality LACM 4301.

DISCUSSION. In size, this specimen suggests assignment to a small eagle or large hawk. Greatest breadth of proximal end is 13.2 mm; the same measurement in the Golden Eagle, *Aquila chrysaetos* (Linnaeus, 1758), is 16.7 mm, and in the Ferruginous Hawk, *Buteo regalis* (Gray, 1844), 11.9 mm. The shape of the proximal end more closely resembles that of the eagle.

There are only two previous records of the family Accipitridae for the Tertiary of California, both of early Miocene age: *Miohierax stocki* Howard, 1944, and *Buteo* indet. (Merriam, 1919). Neither is from a marine deposit. The family is well represented in the Pleistocene (Brodkorb, 1964:269–271, 281–284).

Family Falconidae (Vigors, 1824)—Falcons

Genus *Falco* Linnaeus, 1758

?*Falco* sp.

REFERRED SPECIMEN. Fragment of right clavicle, UCMP 88597 from locality UCMP V6880.

DISCUSSION. This incomplete specimen is suggestive of a falconid clavicle in its prominent, round coracoidal facet. It is similar in size to that of a male Peregrine Falcon, *Falco peregrinus* Tunstall 1771, a species known in California today.

CORRECTION. Owing to a misunderstanding regarding the exact location of UCMP V6880, this specimen was incorrectly cited as being from the San Luis Rey River Local Fauna in Barnes et al. (1981:61).

Order Charadriiformes (Huxley, 1867)

Family Alcidae Vigors, 1825—Auk-like Birds

Subfamily Alcinae (Vigors, 1825)

Genus *Cepphus* Pallas, 1769—Guillemots

Cepphus sp.

REFERRED SPECIMEN. Fragment of right coracoid including glenoid facet and portion of procoracoid, LACM 119260, from locality LACM 4301.

DISCUSSION. The procoracoid is notched 4.6 mm below the upper surface, resembling in this character specimens of living Pigeon Guillemot, *Cepphus columba* Pallas, 1811, a species known today from the coast of California. The few measurements possible on this fragment, compared to those of *C. columba*, are (in mm): length through glenoid facet and scapular facet 9.8 (8.7–9.1 in *C. columba*); depth from tip of procoracoid to shaft 7.8 (7.7–8.1 in *C. columba*). It is impossible to assess the relationship of this fragment to the new species, *Cepphus olsoni*, described herein from a humerus in San Luis Rey River Local Fauna.

Subfamily Mancallinae (Miller, 1946) Extinct Flightless Auks

Genus *Mancalla* Lucas, 1901

DISCUSSION. Five species of *Mancalla* are known: *M. californiensis* Lucas, 1901, from the early Pliocene (Repetto Formation) in Los Angeles, California, with 11 referred specimens (Howard, 1949:196 and 1970:3) from the Repetto Formation in Corona del Mar, Orange County, California; *M. cedrosensis* Howard, 1971, the holotype a nearly complete skeleton, and many referred specimens, all from the Almejas Formation (late Hemphillian) of Cedros Island, Baja California, Mexico; *M. diegensis* (Miller, 1937) and *M. milleri* Howard, 1970, both described and well represented by all principal skeletal elements from the late Pliocene, San Diego Formation in San Diego, California; and *M. emlongi* Olson, 1981, based on an ulna from the San Diego Formation at Pacific Beach, San Diego County.

Eighty bones from locality LACM 4301 and one from locality UCMP V68106 are assignable to this genus. Also available for this study were two complete humeri from locality SDSNH 2643 (equivalent of locality LACM 4301). Preservation of the LACM and UCMP material is poor, but the characters that distinguish *Mancalla* from *Praemancalla* are observable in the coracoids, scapulae, humeri, ulnae, radius, carpometacarpus, tibiotarsi, and tarsometatarsi, as follows: coracoids with scapular facet placed laterally and triosseal canal posterointernally; scapulae concave ventrally, with short acromion, and glenoid facet projecting medially; proximal ends of humeri with notch-like capital groove, and distal ends with papilla above distal condyles; ulna with olecranon not projecting proximad; radius blade-like; carpometacarpus without distinct pisiform process; tibiotarsi without flaring distal end; tarsometatarsi with anterior face of shaft depressed along external side but raised above middle trochlea.

Several bones fall within the size range of the small *M. milleri*. The others are commensurate in size with those of *M. diegensis*, *M. cedrosensis*, and *M. californiensis*. *Mancalla emlongi*, known only from the holotype ulna, was a larger species.

Twenty-six bones, including the two from SDSNH, are assigned, at least tentatively, to three species. The other 57 remain as *Mancalla* species indeterminate.

Mancalla milleri Howard, 1970

REFERRED MATERIAL. From locality SDSNH 2643, complete humerus (SDSNH 23568); from locality LACM 4301,

distal ends of 2 humeri (LACM 119166 and 119272), 2 ulnae (LACM 119283 and 119286), incomplete radius (LACM 119292), proximal end of carpometacarpus (LACM 119290) and proximal ends of 3 scapulae (LACM 119262, 119264, 119265).

DESCRIPTION. The complete humerus agrees in size with that of *M. milleri*. Measurements (in mm): length to internal condyle 62.7 (*M. milleri* 56.4–66.6), proximal breadth 15.7 (*M. milleri* 14.2–16.4), distal breadth 6.0 (*M. milleri* 5.1–6.0). The humerus also has the additional character of the angular distal contour of the bicipital crest, which distinguishes it from the humerus of *M. cedrosensis*. The other specimens are assigned entirely on the basis of small size. Measurements (in mm): distal breadths of humeri 5.4 and 5.7, proximal breadths of ulnae 5.3 and 5.5 (*M. milleri* 4.5–5.7) greatest shaft depth of radius 5.3 (*M. milleri* 4.6–5.6), proximal depth of carpometacarpus through metacarpal I 8.8 (*M. milleri* 8.8–9.3), proximal breadth of complete scapular end 11.6 (*M. milleri* 10.2–11.8).

Mancalla diegensis (Miller, 1937)

REFERRED MATERIAL; From locality SDSNH 2643, complete left humerus (SDSNH 23567); from locality LACM 4301, 2 proximal ends of humeri (LACM 119301 and 119276). An ulna (LACM 119279) is tentatively referred.

DESCRIPTION: The complete humerus has the very angular distal contour of the bicipital crest characteristic of *Mancalla diegensis*, *M. milleri*, and *M. californiensis*, and is further distinguished from *M. cedrosensis* by the broader, more shallow area below the head. It is distinguished from *M. milleri* by larger size and from *M. californiensis* by the muscle scar at the median border of the pneumatic fossa, which does not protrude into the fossa as a distinct groove (Miller and Howard, 1949:209). Although incomplete, the two proximal fragments have the small scar at the distal edge of the bicipital crest that provides the angular contour of the crest as noted above.

The olecranon of the ulna is incomplete but appears to be straighter in anconal contour than in *M. cedrosensis*, and the adjacent depression is small.

Measurements (in mm) compared with those of *M. diegensis* (Howard 1970, table 3): humerus (SDSNH 23567), length to internal condyle, 75.9, proximal breadth, 18.9 (*M. diegensis*, 71.0–85.2 and 17.3–20.3, respectively); ulna (LACM 119279), length 31.7 (*M. diegensis* 28.0–32.1), proximal breadth 6.1 (*M. diegensis* 5.9–6.6).

Mancalla cf. *M. cedrosensis* Howard, 1971

REFERRED MATERIAL: From locality 4301: a nearly complete, but poorly preserved humerus (LACM 119165); proximal ends of 5 humeri (LACM 119222, 119224, 119269, 119273, 119372); complete tarsometatarsus (LACM 119298) and shaft of tarsometatarsus (LACM 119174). In addition, 4 complete ulnae (LACM 119280, 119281, 119287, 119288) are tentatively referred.

DESCRIPTION. The humeri resemble this element of *M.*

cedrosensis and are distinguished from those of *M. diegensis*, *M. milleri* and *M. californiensis* by the characters described (Howard, 1971:12) for the holotype of *M. cedrosensis* (LACM 15273): "... internal contour from shaft through bicipital crest broadly and gradually curved; area below head between pectoral attachment and pneumatic fossa oval and deeply depressed." All are within the size range for *M. cedrosensis* except LACM 119372, which falls between *M. cedrosensis* and *M. milleri* in proximal breadth (16.6 mm in LACM 119372; *M. milleri* maximum 16.4; *M. cedrosensis* minimum 17.0 mm).

The complete tarsometatarsus has the proximal and distal ends flaring as in both *M. cedrosensis* and *M. diegensis*, as contrasted with the more columnar shape in *M. milleri*. In both LACM 119298 and the incomplete LACM 119174, the shaft is more depressed anteriorly than in either *M. diegensis* or *M. californiensis*, and both borders of the anterior face of the shaft are sharply defined as in *M. cedrosensis*. Length (in mm) of LACM 119298, 41.1, proximal breadth 10.1 (same measurements in *M. cedrosensis*, 37.3–42.0 and 9.9–10.9, respectively).

In the tentatively referred ulnae, the olecranon extends beyond the shaft in anconal contour, and there is a deep depression adjacent to the olecranon on the internal side as in *M. cedrosensis*. The depression is also present in the ulnae of *M. milleri*, but the olecranon is less protruded in the smaller species. The four Oceanside specimens fall within the size range of *M. cedrosensis* in length (28.3–30.7 mm; *M. cedrosensis* 28.3–21.7 mm) but are somewhat more slender.

Mancalla sp. indet.

REFERRED MATERIAL. From locality UCMP V68106, incomplete left coracoid (UCMP 88614). From locality LACM 4301, 20 fragmentary humeri (LACM 119167–119171, 119268, 119270, 119271, 119274–119278, 119302–119306, 119407, 121530); 6 incomplete ulnae (LACM 119282, 119284, 119285, 119289, 119311, 119408); 2 carpometacarpi (LACM 119291, 121530); 9 fragments of coracoids (LACM 119223, 119253–119259, 119307); 6 proximal fragments of scapulae (LACM 119172, 119261, 119263, 119266, 119267, 119373); 6 fragments of tibiotarsi (LACM 119173, 119178, 119294–119296, 119371, 121531); 3 fragments of tarsometatarsi (LACM 119297, 119299, 119300); 1 wing phalanx (LACM 119293); 2 pedal phalanges (LACM 119308, 119309); 1 thoracic vertebra (LACM 119252).

DISCUSSION. These fragments probably represent one or more of the species herein specifically assigned with the genus, but it would be ill-advised to attempt to assign them to species.

CONCLUSIONS

This study of the avifaunas of the San Mateo Formation at Oceanside has resulted in the recognition of two new species of the family Alcidae, *Uria paleohesperis* and *Cephus olsoni*, from the San Luis Rey River Local Fauna in the lower level of the formation. Both species add support to the tentative earlier record (Howard, 1978) of the genera *Cephus* and *Uria* from the slightly older Upper Miocene Monterey Formation located farther north, in Orange County, California. The only other con-

firmed Tertiary record of the murre, genus *Uria*, is from the late Miocene Sisquoc Formation, near Lompoc, California (Howard, 1981). The guillemots, genus *Cephus*, have no prior fossil record. A loon (genus *Gavia*), an albatross (genus *Diomedea*) and a murrelet (genus ?*Aethia*) are also known from both the Monterey Formation of Orange County and the lower part of the San Mateo Formation, although there is no proof of specific identities.

Also significant is the occurrence of the extinct flightless auk genus *Praemancalla* in both the lower level of the San Mateo Formation at Oceanside and in the Monterey Formation in Orange County. The partial skeleton from Oceanside is assigned to *P. cf. P. wetmorei*, the species described from the uppermost horizon of the Monterey Formation at locality LACM 6906. The Oceanside specimen includes wing elements, previously recorded for the species, associated with the first tibiotarsus and tarsometatarsus known for the genus. In addition, two isolated femora are the first of this element to be assigned to *Praemancalla*.

In the Lawrence Canyon Local Fauna, in the upper part of the San Mateo Formation at Oceanside, the predominance of the genus *Mancalla* is typical of the marine Pliocene of California. Although it was impossible to specifically identify all of the more than 80 specimens recorded here, three species are noted: *M. milleri* and *M. diegensis* (the predominant species of the late Pliocene, San Diego Formation) and *M. cedrosensis* of the latest Miocene to early Pliocene (Repenning and Tedford, 1977) of Cedros Island, Baja California, Mexico. This is the first record of the association of these three species. The additional fragmentary records from the upper beds add little to the picture, except that the presence of eagle and falcon suggests near-shore deposition.

The occurrence of the highly specialized flightless auk genus *Mancalla* in the upper part of the San Mateo Formation and the related, but more primitive *Praemancalla* in the lower part is important in providing information as to the relative ages of the beds at the two levels. *Mancalla* is the most abundantly represented genus of fossil birds in the Pliocene marine formations (including part of the Capistrano Formation) of the southwest coast. One specimen has also been recorded (Howard, 1970) from Humboldt County in northern California, in beds purported to be as young as Pleistocene in age (Kohl, 1974) with an amino-acid age estimate of 470,000 years B.P. (Wehmiller et al., 1978). *Praemancalla*, on the other hand, has been recorded previously only from the late Miocene, Monterey Formation. If Vedder's (1972:167) postulation that the San Mateo Formation may be a channel deposit within the Capistrano Formation is correct, it is not surprising to find *Praemancalla* in the lowermost beds. For, as he also notes (Vedder, 1972:165-166), in its type-area, the Capistrano Formation is in gradational contact with the underlying Monterey Formation, indicating that there may be no hiatus between these formations. It would appear that the interval between the lower and upper stratigraphic levels of the San Mateo Formation could be of considerably greater temporal extent, allowing time for the demise of the *Praemancalla* and the evolution of *Mancalla*.

As the upper part of the Monterey Formation is of Clarendon-

ian age, ranging roughly from 8.5 to 12 million years B.P., and the lower parts of both the San Mateo and Capistrano Formations are early Hemphillian in age, the geochronologic age of *Praemancalla* is now extended from the Clarendonian into the Hemphillian age.

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CONTRIBUTIONS IN SCIENCE

LARGE ARCHIBENTHAL GASTROPODS OF
CENTRAL CHILE: COLLECTIONS FROM AN EXPEDITION OF THE
R/V ANTON BRUUN AND THE CHILEAN SHRIMP FISHERY

James H. McLean and Hector Andrade V.



Natural History Museum of Los Angeles County • 900 Exposition Boulevard • Los Angeles, California 90007

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LARGE ARCHIBENTHAL GASTROPODS OF CENTRAL CHILE: COLLECTIONS FROM AN EXPEDITION OF THE R/V ANTON BRUUN AND THE CHILEAN SHRIMP FISHERY¹

James H. McLean² and Hector Andrade V.³

ABSTRACT. Fifteen species of large gastropods from off central Chile collected both by an expedition of the R/V ANTON BRUUN in 1966 and by commercial trawling for the shrimp *Heterocarpus reedi* are treated. Nine previously described species are reviewed: *Bathybembix macdonaldi*, *B. humboldti*, *Calliostoma chilena*, *Capulus ungaricoides*, *Fusitriton magellanicus*, *Aeneator fontainei*, *A. loisae*, *Miomelon alarconi*, and *Ptychosyrinx chilensis*. Six species are described as new: *Diodora codoceoeae*, *Calliostoma delli*, *Trophon bahamondei*, *Columbarium tomicici*, *Aeneator castillai*, and *Cancellaria stuardoi*.

RESUMEN. Se estudiaron quince especies de macrogastropodos obtenidos en faenas de pesca camaronera por arrastre y por la expedición del B/I ANTON BRUUN en la zona central de Chile. De estas, nueve especies habían sido ya descritas y se hace la revisión de cada una de ellas: *Bathybembix macdonaldi*, *B. humboldti*, *Calliostoma chilena*, *Capulus ungaricoides*, *Fusitriton magellanicus*, *Aeneator fontainei*, *A. loisae*, *Miomelon alarconi* y *Ptychosyrinx chilensis*. Las seis restantes son consideradas como nuevas y se entregan sus descripciones: *Diodora codoceoeae*, *Calliostoma delli*, *Trophon bahamondei*, *Columbarium tomicici*, *Aeneator castillai* y *Cancellaria stuardoi*.

INTRODUCTION

The marine invertebrate fauna of the lower continental shelf and slope off central Chile is poorly known. This region is one of the few areas of the world not covered by the great expeditions of the last century. In recent years, however, collections from two sources have become available. An expedition of the R/V ANTON BRUUN sampled the region in 1966, and, in subsequent years, the shrimp fishery for *Heterocarpus reedi* Bahamonde, 1955, has yielded abundant material of the larger species.

Over the last 14 years, six mollusks commonly taken by the shrimp fishery have been described from central Chile: Berry (1968) described *Ptychosyrinx chilensis*; Rehder (1971) described *Limopsis ruizana*, *Bathybembix humboldti*, *Calliostoma chilena*, and *Aeneator loisae*; Stuardo and Villarroel (1974) described *Miomelon alarconi*. Other new species have been recognized by marine biologists in Chile but have remained undescribed until now.

From 1976 through 1980, Andrade obtained extensive material of mollusks and other invertebrates incidental to the shrimp

fishery. Specimens were saved by crew members of the trawling vessel GODEN WIND and other vessels based in Quintero. These vessels worked the Chilean coastline to the north and south of Valparaíso between Los Vilos (31°56'S) and Constitución (35°20'S).

The following contributions treating the echinoderms and crustaceans from the Chilean shrimp fishery have been published: Andrade (1980), Andrade and Baez (1977, 1980), Baez and Andrade (1977, 1979), Codoceo and Andrade (1978, 1980, in press), Codoceo et al. (1978), Revuelta and Andrade (1978).

The offshore fauna of northern Peru has been sampled by expeditions of the ANTON BRUUN and by expeditions conducted by the Instituto del Mar, Callao, Peru. These expeditions have produced specimens of some of the species known from central Chile. The Peruvian records of these species are given in this paper.

The present paper is limited to the large gastropods of central Chile that have been taken by the shrimp fishery. Nine previously described species are reviewed, and six additional species are described. For most of the species, we have included a photograph of the radular ribbon as an aid in identification. Full discussion of radular features is beyond the scope of this paper. A more detailed study of radular structure would require the use of scanning electron microscopy.

OCEANOGRAPHIC CONDITIONS OFF CENTRAL CHILE

Depths of samples reported on here from off central Chile are archibenthal, corresponding to the upper part of the continental slope. The benthic fauna is mainly under the influence of Antarc-

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3. Instituto de Oceanología, Universidad de Valparaíso, Casilla 13-D, Viña del Mar, Chile (present address: Station Marine d'Endoume, Rue de la Batterie des Lions, 13007 Marseille, France).

tic Intermediate Water and to a lesser degree of the overlaying Equatorial Subsurface Water, as discussed by Andrade and Baez (1980). Detailed accounts of the physical and chemical properties of the water masses in central Chile are given by Sievers and Silva (1975) and Silva and Sievers (1981).

MATERIALS AND STATION DATA

Station data for the collections reported in this paper are given in Table 1. Localities and depths for material from the shrimp fishery are necessarily less accurate than data for material collected by scientific expeditions. Depths and coordinates are not repeated in the text, except for type localities of the new species.

For lots that define the northern and southern records, the corresponding latitudes are given in the distribution heading.

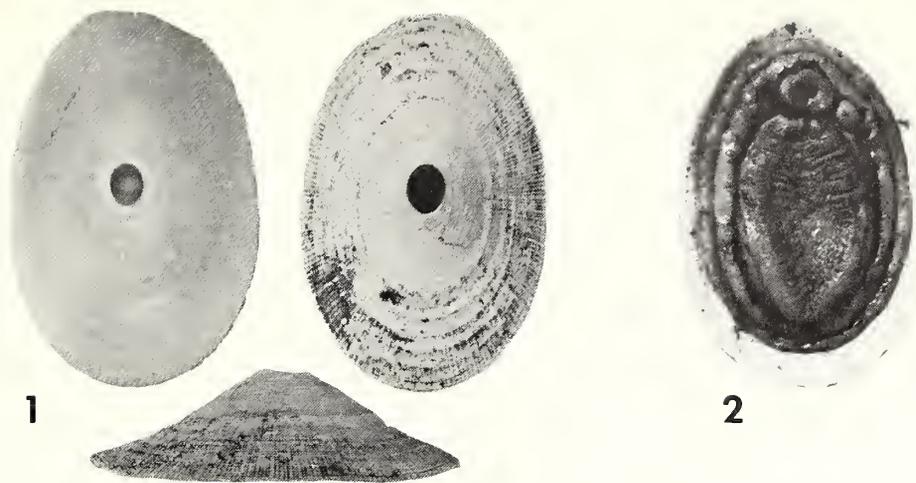
Abbreviations of museums mentioned in the text are as follows: BM(NH), British Museum (Natural History); LACM, Los Angeles County Museum of Natural History, Los Angeles, California, U.S.A.; MNHN, Museo Nacional de Historia Natural, Santiago, Chile; MZICB, Instituto Central de Biología, Universidad de Concepción, Concepción, Chile; USNM, United States National Museum of Natural History, Washington, D.C., U.S.A. Type material of the six new species described herein is distributed among these institutions.

Collections upon which this report is based have been obtained from four sources:

Table 1. ANTON BRUUN, SNP-1, and Chilean shrimp fishery stations arranged north to south.

	Location		Depth (m)
PERU			
W of Lobos de Tierra, SNP-1, sta. 26	06 26 S	81 05 W	1,025
S of Lobos de Tierra, SNP-1, sta. 25	06 42	80 59	785
S of Lobos de Afuera, SNP-1, sta. 13	07 07	80 46	1,200
N of Isla Macabi, SNP-1, sta. 28	07 44	80 30	750–760
W of Isla Macabi, ANTON BRUUN, sta. 754	07 49	80 38	605–735
CHILE			
Junquillar, ANTON BRUUN, sta. 714	25 00	70 40	950
Punta Mar Brava, ANTON BRUUN, sta. 710	29 21	71 25	65–95
Punta Hornos, ANTON BRUUN, sta. 709	29 38	71 21	110
Coquimbo, trawler not identified*	29 58	—	200–400
Los Vilos, GODEN WIND	31 56	71 54	240–400
Pichidanqui, GODEN WIND	32 08	71 54	300–400
Punta Salinas, ANTON BRUUN, sta. 703	32 09	71 43	960
Caleta Molles, ANTON BRUUN, sta. 702	32 17	71 40	580
Papudo, GODEN WIND	32 31	71 54	200–350
Zapallar, GODEN WIND	32 33	71 43	350–450
Quintero, GODEN WIND	32 42	71 48	200–280
Algarrobo, trawler not identified	33 22	71 55	360
Punta Penablanca, ANTON BRUUN, no sta.	33 22	71 54	260–280
Punta Panulcillo, ANTON BRUUN, sta. 701	33 32	71 35	180–175
Puerto San Antonio, ANTON BRUUN, sta. 699	33 39	72 10	1,170–1,480
Punta Toro, trawler not identified	33 06	72 03	270
Bahia Navidad, ANTON BRUUN, sta. 686	33 58	72 05	140
Topocalma, trawler not identified	34 06	72 14	180–360
Punta Topocalma, ANTON BRUUN, sta. 687	34 07	72 19	750–730
Pichilemu, trawler not identified	34 27	72 24	240–350
Mataquito, trawler not identified	35 01	72 10	300
Constitución, trawler not identified	35 20	72 55	260
Cabo Carranza, ANTON BRUUN, sta. 697	35 27	73 01	290–450

*For Coquimbo only, the locality refers to the home port, not the actual station, which is unknown.



Figures 1 and 2, *Diodora codoceae* new species. Figure 1, three views of holotype, LACM 1979, 260 m off Constitución, Chile, length 40.7 mm. Figure 2, LACM 72485, 360 m off Topocalma, Chile, Length 40.6 mm.

1. Cruises of the ANTON BRUUN in Peru and Chile during 1966. This material is deposited in the LACM and USNM.

2. A cruise of the Peruvian naval vessel SNP-1 to the vicinity of the Lobos Islands in northern Peru in January 1974 on which McLean was present. Material from that cruise is deposited in the LACM and the Instituto del Mar, Callao, Peru.

3. Shrimp trawling localities (GODEN WIND and other vessels) in central Chile, 1977–1980. McLean visited the Montemar Marine Laboratory of the Universidad de Valparaíso in August 1978 and examined all of the collections then received by Andrade. This material is now deposited in the LACM, the MNHN, and the Museo Comparativo, Instituto de Oceanología, Universidad de Valparaíso.

4. Shrimp trawling vessels based in Coquimbo, Chile, 1964–1975; collections deposited at LACM by the late Harvey McMillin, Luis Ferreira Osses, and Jorge Tomacic K. In some cases, Coquimbo (29°58'S) is cited as the northern range limit of a species, although it should be understood that the actual occurrence for such a record could have been either to the north or south of Coquimbo.

SYSTEMATIC ACCOUNT

Superfamily Fissurellacea

Family Fissurellidae

Subfamily Diodorinae

Genus *Diodora* Gray, 1821

Type species (monotypy): *Patella apertura* Montagu, 1803 (= *P. graeca* Linnaeus, 1758). Recent, Europe.

Diodora species occur in most temperate and tropical regions of the world in intertidal, sublittoral, and, less frequently, archibenthal depths. Although there is considerable diversity of form

among the species, an adequate subgeneric classification has never been offered.

Diodora codoceae new species

Figures 1–3

DESCRIPTION. Shell large for the genus, thin, conical, basal outline elongate-oval, anterior end slightly narrower than posterior, basal margin lying flat, with ends slightly elevated. Lateral slopes straight, anterior and posterior slopes slightly concave. Foramen nearly central, oval, length of foramen about 10% of shell length, highest point of shell at the posterior rim of the foramen. Periostracum thin, brown, worn away over most of the surface; underlying surface chalky white, worn near summit. Sculpture of numerous fine radial ribs; under magnification, the ribs are rounded, broader than the interspaces, crossed by raised growth lamellae to give a minute beaded appearance; primary ribs remain stronger so that every fourth rib is slightly more prominent than the others. Interior chalky white, the margin finely crenulated and grooved by the ribs; position of the stronger primary ribs marked by corresponding internal grooves. Under magnification, the crossed-lamellar aragonitic structure near the margin is visible. Muscle scar weakly discernible. Callus surrounding the foramen has an oval outline and is slightly truncated and depressed at its posterior edge. Thickness of shell at summit (depth of foramen) approximately equal to the width of the internal callus.

Dimensions: length 40.7 mm, width 27.0 mm, height 11.4 mm (holotype, Fig. 1); length 40.6 mm, width 26.9 mm, height 13.7 mm (Fig. 2).

Animal of preserved specimen (Fig. 2): colorless except for darkly pigmented eyes; contracted to fit completely within the shell; uppermost fold of mantle with a very finely scalloped edge, surface of the mantle folds and the foot sides with negligible development of papillae; cephalic tentacles and epipodial tentacles well developed.

Radula (Fig. 3): typical of the genus, laterals four, rachidian three times wider than the adjacent laterals; first marginal bicuspid as in other species of *Diodora*.

MATERIAL. Chile: Pichidanguí, Zapallar, Topocalma (LACM, Fig. 2), Constitución (LACM, holotype, Fig. 1). Specimens examined: 15.

TYPE MATERIAL. Three specimens from the type locality, collected 25 March 1976, by Andrade, shrimp trawler GODEN WIND. Holotype, LACM 1979; one paratype MNHN 200488, one paratype MZICB 15.527.

TYPE LOCALITY. 260 m off Constitución, Chile (35°20'S, 72°55'W).

DISTRIBUTION. Pichidanguí (34°06'S) to Constitución, Chile (35°20'S). Depth range 180–360 m.

DIAGNOSIS. A species of *Diodora* characterized by its large size, thin shell, oval aperture, and numerous radial ribs. It most resembles *D. tanneri* (Verrill, 1883), known from archibenthal depths in the western North Atlantic, from Delaware to the Caribbean (see Perez-Farfante, 1943:19). *D. codoceoae* differs in having a less conical profile, a proportionately larger foramen, and a more chalky shell surface. We have no information about the animal of *D. tanneri*. *Diodora codoceoae* also resembles *Stromboli beebei* (Hertlein and Strong, 1951), an offshore species in the tropical Panamic Faunal Province ranging from the Gulf of California to Ecuador (see McLean in Keen, 1971:318, fig. 29). Unlike *D. codoceoae*, *S. beebei* has a fleshy mantle that fully envelops the edge of the shell and radial ribs that are uniformly fine, with no distinction between primary and secondary ribs; in addition, *S. beebei* has a sturdier shell than that of *D. codoceoae*.

REMARKS. The internal callus surrounding the foramen is curved on the posterior side in *D. codoceoae*, *D. tanneri*, and *S. beebei*, not straight-edged as in most species of *Diodora*. However, this is a variable feature among species of *Diodora*, particularly those with oval foramina.

ETYMOLOGY. We are pleased to name this species in honor of Prof. Maria Codoceo of the Museo Nacional de Historia Natural, Santiago.

Superfamily Trochacea

Family Trochidae

Subfamily Eucyclinae

Genus *Bathybembix* Crosse, 1893

Type species (original designation): *Bembix aeola* Watson, 1879. Recent, Japan.

Bathybembix species are large mud-ingesting trochids occurring on the outer continental shelf and slope (Merriman, 1967; Hickman, 1981). They are members of the subfamily Eucyclinae, which appeared in the Mesozoic. Such recent genera as *Bathybembix* Crosse, 1893, *Calliotropis* Seguenza, 1903, and

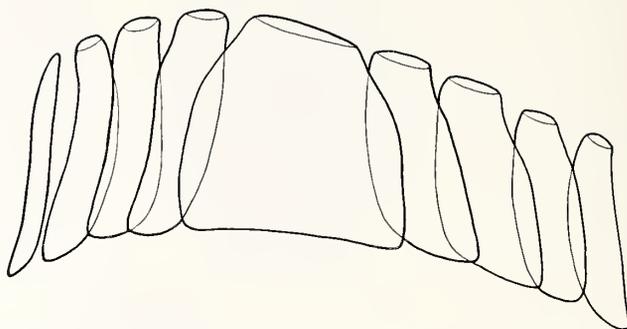


Figure 3. *Diodora codoceoae* new species, radular dentition of holotype, rachidian and lateral teeth, maximum dimension 0.8 mm.

Cidarina Dall, 1909, have been recognized as members of the same group (McLean, 1981:335).⁴

The genus *Bathybembix* occurs in the northern Pacific, with several species in Japan, and one, *B. bairdii* (Dall, 1889), in the northeastern Pacific ranging from the Bering Sea, Alaska, to the Gulf of Tehuantepec, Mexico (McLean in Keen, 1971:331, fig. 62). The two species treated here are common off the coasts of both Peru and Chile. These species are members of the same typical subgenus in which the shells are large, the umbilicus closed, and the periostracum thick and colored greenish brown.

Bathybembix macdonaldi (Dall, 1890)

Figures 4–6

Turricula macdonaldi Dall, 1890:348, pl. 7, fig. 7; 1908:349, pl. 19, fig. 7.

Bathybembix macdonaldi, McLean in Keen, 1971:331, fig. 63.

DESCRIPTION. Shell large, thin, high-spired; final whorl rounded, early whorls strongly carinate. Periostracum thin, yellowish or greenish brown. Protoconch missing, teleoconch whorls eight on intact specimens; early whorls often eroded. Spiral sculpture of two cords per whorl, a prominent projecting peripheral cord, with short projecting spines, and another weaker, noded cord just below the suture, becoming weaker and disappearing on the final whorl. Base with prominent spiral cords. Axial sculpture lacking except for fine growth increments on the periostracum. Outer lip thin, interior nacreous; operculum large, multispiral.

Dimensions: height 69.3 mm, diameter 49.0 mm (Fig. 4); height 75 mm, diameter 60 mm (holotype, Fig. 5).

Radula (Fig. 6): rachidian tooth broadly flanged, overhanging tip bearing numerous fine serrations along the sides; lateral teeth three, marginal teeth numerous.

MATERIAL. Peru: W of Lobos de Tierra (LACM), S. of Lobos

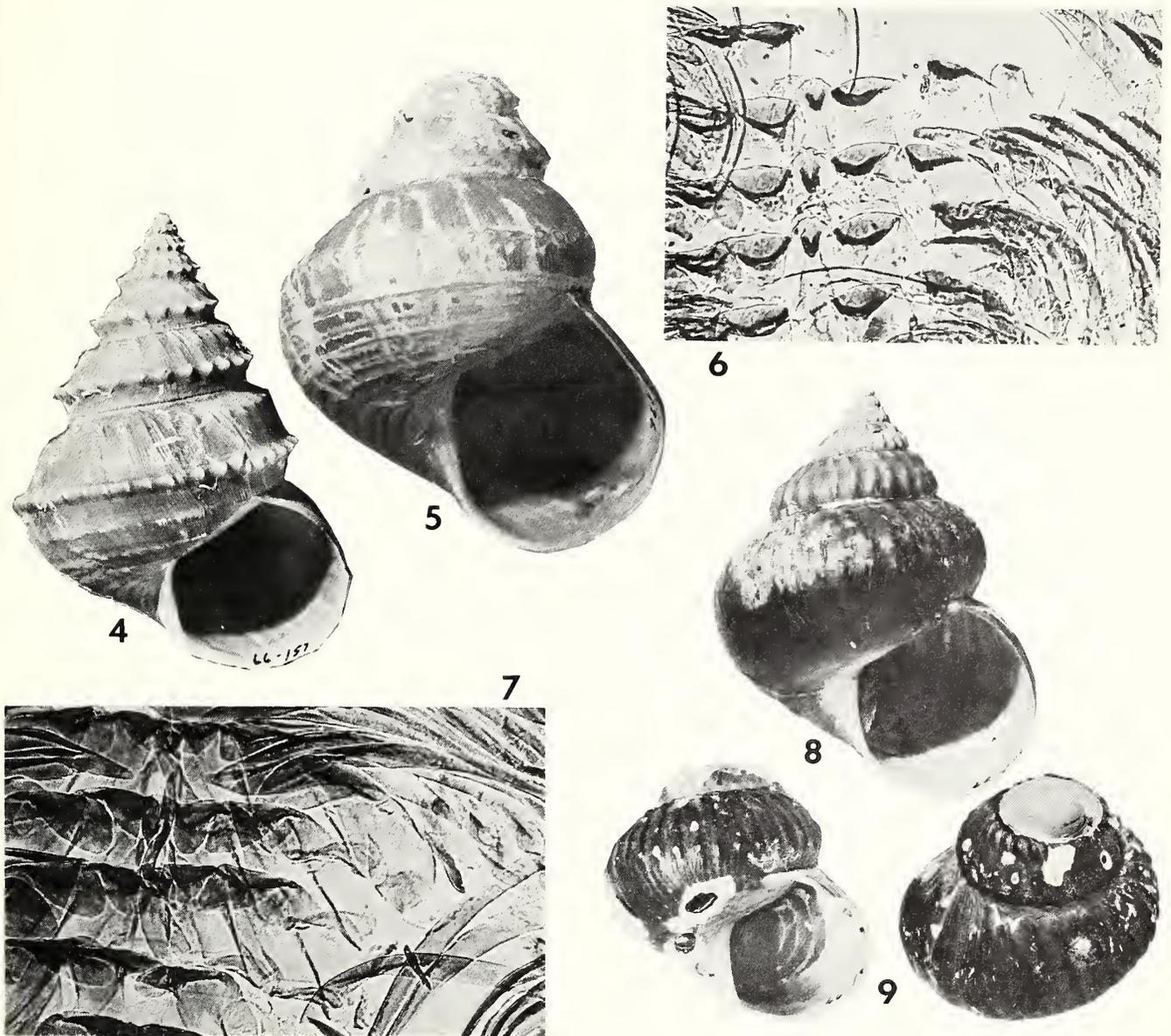
4. McLean (1981) used the subfamily Amberleyinae for this group. That name was proposed at the family level by Wenz, 1938. The older Eucyclinae must be used, a name proposed at the family level by Koken, 1896.

de Tierra (LACM), S. of Lobos de Afuera (LACM). Chile: Junquillar (LACM), Los Vilos (LACM), Punta Salinas (LACM, fig. 4), Caleta Molles (LACM), Papudo, Zapallar, Quintero, Algarrobo, Punta Penablanca (LACM), Punta Topocalma (LACM). Specimens examined: more than 100.

TYPE MATERIAL AND TYPE LOCALITY. Holotype, USNM

96559 (Fig. 5). Type locality: 401 fm (733 m) off Manta, Ecuador.

DISTRIBUTION. Off Punta Mala, Panama (LACM 10369) ($7^{\circ}28'N$) to Punta Topocalma, Chile ($34^{\circ}7'S$). As is the case with *B. humboldti*, northern specimens occurring from Panama to Peru are known only from depths of 780–1,200 m, whereas



Figures 4 through 9, *Bathybembix macdonaldi* and *B. humboldti*.

Figures 4 through 6, *B. macdonaldi*. Figure 4, LACM 66-157, 960 m off Punta Salinas, Chile, height 69.3 mm. Figure 5, holotype, USNM 96559, 733 m off Manta, Ecuador, height 75 mm. Figure 6, radula ribbon, LACM 66-152, 750-730 m off Punta Topocalma, Chile, width of field 0.6 mm.

Figures 7 through 9, *B. humboldti*. Figure 7, radula ribbon, LACM 66-171, 605-735 m, W of Isla Macabi, Peru, width of field 0.7 mm. Figure 8, LACM 66-154, 1,170-1,480 m off Puerto San Antonio, Chile, height 61.7 mm. Figure 9, two views, LACM 66-171, 605-735 m W of Isla Macabi, Chile, height 39.7 mm.

those from Chile occur in similar depths and also as shallow as 200 m.

REMARKS. *Bathybembix macdonaldi* differs from *B. humboldti* in having strong peripheral nodes and a much lighter colored periostracum. Northern specimens tend to have a fainter subsutural cord and more numerous peripheral nodes, as in the holotype (Fig. 5).

Bathybembix humboldti Rehder, 1971

Figures 7–9

Bathybembix humboldti Rehder, 1971:578, fig. 4.

DESCRIPTION. Shell large, thin, suture deeply impressed, whorls rounded. Periostracum thin, brown, varying from yellowish brown to dark brown. Protoconch missing, teleoconch whorls seven on perfect specimens, but usually the early whorls are missing and sealed over with a chalky shell layer. Axial sculpture of low, narrow ribs on the upper half of the whorl, base nearly smooth except for broadly spaced, faintly marked spiral cords. Sculpture of three spiral cords on early whorls, forming elongate nodes where intersecting the axial ribs; one cord just below the suture and two others closer together at the periphery. Aperture nearly circular, outer lip thin, interior nacreous; operculum multispiral.

Dimensions: height 61.7 mm, diameter 46.9 mm (Fig. 8); height 39.7 mm, diameter 40.8 mm (Fig. 9); height 53.1 mm, diameter 44.3 mm (holotype).

Radula (Fig. 7): similar to that of *B. macdonaldi*.

MATERIAL. Peru: N of Isla Macabi (LACM), W of Isla Macabi (LACM, Fig. 9). Chile: Coquimbo (LACM), Los Vilos, Calleta Molles (LACM), Papudo, Zapallar, Algarrobo, Puerto San Antonio (LACM, Fig. 8), Topocalma, Pichilemu. Specimens examined: more than 100.

TYPE MATERIAL AND TYPE LOCALITY. Holotype, USNM 701665, 200 m, 17–18 km NW of Valparaíso, Chile.

DISTRIBUTION. Isla Macabi, Peru (7°44'S), to Pichilemu, Chile (34°27'S). Depth range: 200–1,480 m. In northern Peru, the depth range is 605–760 m; in Chile, the depth range is 200–1,480 m.

REMARKS. This species is characterized by its dark brown periostracum and the predominance of axial sculpture. Most specimens have the apical whorls badly eroded, although such specimens may seal the apical area with internally deposited shell layers (Fig. 9). Populations of *B. humboldti* have uniformly colored periostraca, some darker than others.

Subfamily Calliostomatinae

Genus *Calliostoma* Swainson, 1840

Type species (subsequent designation Hermannsen, 1846): *Trochus conulus* Linnaeus, 1758. Recent, Europe.

Subgenus *Otukaia* Ikebe, 1943

Type species (original designation): *Calliostoma kiheziebisu* Otuka, 1939. Japan.

The calliostomatine trochids have a characteristic radula, modifications in the reproductive system, and a channel in the ventral lip—the pseudoproboscis—directed to the right (Fretter and Graham, 1962, fig. 92). Clench and Turner (1960) reviewed the Atlantic species, but a worldwide generic review has not been offered, and there are varying concepts of genera and subgenera in the family.

The two species of *Calliostoma* in the present material are members of the subgenus *Otukaia* Ikebe, 1943, a group of relatively large-shelled species broadly distributed in deep water throughout the world. They are characterized by a silky white surface layer, rather than a variegated color pattern, and sculpture of three spiral cords on the early whorls, which may or may not persist on later whorls. *Alertalex* Dell, 1956 (type species: *A. blacki* Dell, 1956, from New Zealand), is regarded as a synonym.

Calliostoma (Otukaia) chilena Rehder, 1971

Figures 10–12

Calliostoma chilena Rehder, 1971:590, figs. 2, 5.

DESCRIPTION. Shell large, thin, nonumbilicate; whorls flat to slightly convex, early spire profile slightly concave; color silky white with a gray-green nacreous sheen. Protoconch smooth, rounded, teleoconch whorls nine, early whorls with three spiral cords and axial ribs that produce square cancellations; these cords fade altogether by the fifth whorl. The suture is laid just below the basal keel; base with fine and even spiral cords, more prominent near the columella. Columella thick, slanted, outer lip sharp, thin. Operculum corneous, multispiral.

Dimensions: height 31.7 mm, diameter 26.5 mm (Fig. 10); height 32.7 mm, diameter 29.9 mm (Fig. 11); height 36.1 mm, diameter 31.9 mm (holotype).

Animal: cephalic lappets lacking, left and right neck lobes broad, rolled to form incurrent and excurrent siphons; epipodial tentacles four pairs, two in line with the neck lobes and two adjacent to the operculum; cephalic tentacles broad at the base, eye peduncles short, eyes large.

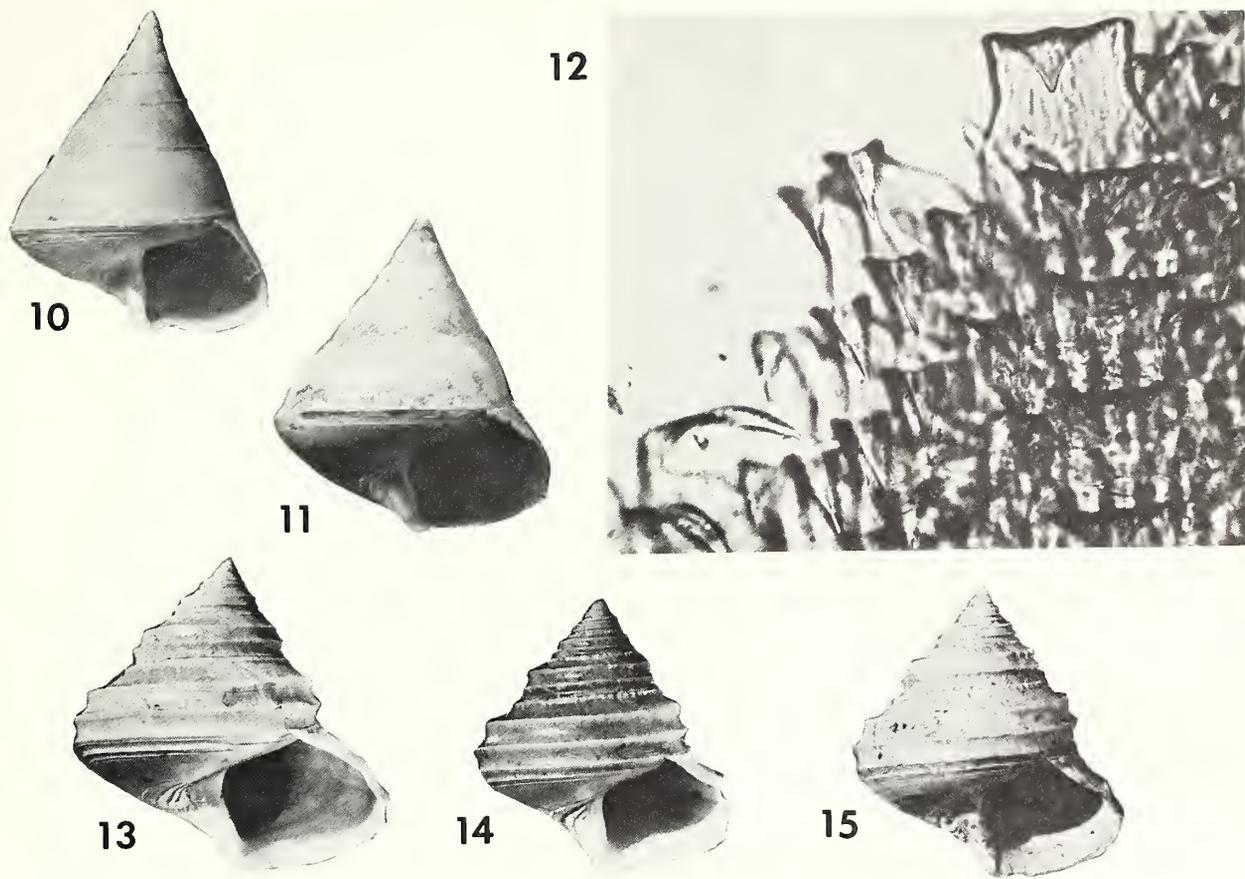
Radula (Fig. 12): the rachidian tooth is more than twice as broad as any of the lateral teeth; there are at least six pairs of lateral teeth, and the serrate, overhanging cusps of the lateral teeth are exceptionally long.

MATERIAL. Peru: W of Isla Macabi (LACM, Fig. 11). Chile: Coquimbo (LACM), Los Vilos, Punta Salinas (LACM, Fig. 10), Papudo, Zapallar, Punta Topocalma (LACM). Specimens examined: 12.

TYPE MATERIAL AND TYPE LOCALITY. Holotype, USNM 701669, 17 km NW of Valparaíso, Chile, 200 m.

DISTRIBUTION. Off Cebaco Island, Gulf of Panama (LACM 10370) (7°32'N), to Punta Topocalma, Chile (34°7'S). Depth range: 200–750 m. The minimum depth in Panama and northern Peru is 560 m; in Chile, the depths range from 200 to 750 m.

REMARKS. *Calliostoma chilena* was described originally from a single specimen. It is still known from rather few specimens. As Rehder noted, *C. chilena* most closely resembles *C. platinum* Dall, 1890, which ranges from British Columbia to southern California at depths of 150–700 m. *Calliostoma platinum* is broader and has convex rather than flat-sided whorls.



Figures 10 through 15, *Calliostoma chilena* and *C. delli* new species.

Figures 10 through 12, *C. chilena*. Figure 10, LACM 66-157, 960 m off Punta Salinas, Chile, height 31.7 mm. Figure 11, LACM 66-171, 605-735 m, W of Isla Macabi, Peru, height 32.7 mm. Figure 12, radular ribbon of specimen in Fig. 10, width of field 0.6 mm.

Figures 13 through 15, *Calliostoma delli* new species. Figure 13, holotype, LACM 1980, 400 m off Los Vilos, Chile, height 29.6 mm. Figure 14, paratype, LACM 1981a, same locality, height 24.3 mm. Figure 15, paratype, LACM 1981b, same locality, height 29.0 mm.

Calliostoma (Otukaia) delli new species

Figures 13-15

DESCRIPTION. Shell large, thin, silky white, nonumbilicate, spire whorls convex. Protoconch of one and one-fourth whorls, teleoconch whorls seven, first teleoconch whorl with three spiral cords, noded to produce square cancellations; sculpture changing by the second whorl to three prominently projecting spiral cords, the uppermost cord beaded, the other two smooth. Mature sculpture of three prominent cords, subsutural cord the least prominent, remaining close to the suture and losing its beading by about the third whorl; second cord sharply defined and separated from the subsutural cord by a broad, smooth area; third cord equally strong and projecting to form the peripheral extent of the whorl. Basal keel sharp; suture laid directly on its lower surface, not forming a channel. Basal cording of about three fine cords on the outer edge and two to three bordering the columellar wall; intermediate area of base smooth except for fine spiral striae. Columellar wall thickened, slanted, forming a spur at the

base; outer lip thin. Operculum corneous, multispiral. Animal and radula as in *C. chilena*.

Dimensions: height 29.6 mm, diameter 30.9 mm (holotype, Fig. 13); height 24.3 mm, diameter 23.2 mm (paratype, Fig. 14); height 29.0 mm, diameter 26.0 mm (paratype, Fig. 15).

MATERIAL. Chile: Los Vilos (LACM, type lot, Figs. 13-15), Papudo, Zapallar, Algarrobo, Punta Penablanca (LACM), Pichilemu, Constitución. Specimens examined: 114.

TYPE MATERIAL. Thirty-three specimens from the type locality, collected 29 May 1977, by Andrade, shrimp trawler GODEN WIND. Holotype, LACM 1980; paratypes, LACM 1981; paratypes, MNHN 200489; paratypes, MZICB 15.528; paratypes, USNM 784738.

TYPE LOCALITY. 400 m off Los Vilos, Chile (31°56'S; 71°54'W).

DISTRIBUTION. Los Vilos (31°56'S) to Constitución, Chile (35°20'S). Depth range 200-450 m.

DIAGNOSIS. A species of the subgenus *Otukaia* characterized by having three spiral cords prominent at all growth stages. It

differs from the similarly sculptured *C. blacki* (Dell, 1956) from New Zealand (see Dell, 1956:46, pl. 7, fig. 6) in being lower spired, and in having a weaker subsutural (first) cord and a stronger second cord.

REMARKS *Calliostoma delli* tends to be broader than high; one of the figured paratypes (Fig. 14) is unusually narrow, compared to most specimens in the type lot.

ETYMOLOGY. We are pleased to name this species in honor of Dr. Richard K. Dell of the National Museum of New Zealand, Wellington.

Superfamily Hipponicacea

Family Capulidae

Genus *Capulus* Montfort, 1810

Type species (original designation): *Patella ungaricus* Linnaeus, 1767. Recent, Europe.

Capulus species are sedentary, protandric, brooding limpets that are usually attached to shells of living bivalves. Most commonly, they are attached to pectinid bivalves, although the European type species may attach to stones or to *Turritella* (Thorson, 1965). Some of their nutrition is derived from filter feeding, as in the calyptraeids, but they also use the pseudoproboscis, an openly grooved proboscis, to take food from the host (Fretter and Graham, 1962). Recently, some species have been found to bore holes in the host shell, inserting the pseudoproboscis directly (Orr, 1962; Matsukuma, 1978).

The capulid in the present material from central Chile was attached to a large bivalve of the family Limidae, identified as *Acesta patagonica* (Dall, 1902). This is the second capulid species associated with a limid rather than a pectinid bivalve. Recently, Dell (1978) described *Capulus novaezelandiae*, attached to an unidentified species of *Acesta* from New Zealand waters. [For a review of *Acesta*, see Vokes, 1963].

Capulus ungaricoides (Orbigny, 1841)

Figures 16–19

Pileopsis ungaricoides Orbigny, 1841:457, pl. 78, fig. 4.

Capulus ungaricoides, Dall, 1909:234; Keen, 1966:3, pl. 1, figs. 14a, 14b; Keen, 1971:467, fig. 833.

"*Capulus chilensis* Dall," Carcelles, 1944:2, fig. 1.

DESCRIPTION. Shell large for the genus, thin but sturdy; outline nearly circular, irregular, conforming to the attachment surface. Apex narrow, strongly incurved, overhanging the posterior margin. Sculpture of fine radial ribs, rib interspaces consisting of narrow grooves. Periostracum and all traces of the radial ribs worn away on apical region but persisting near the margin; periostracum slightly overhanging the shell edge. Interior glossy white; muscle scar horseshoe-shaped.

Dimensions: diameter 39.6 mm, height 15.7 mm (Fig. 18); diameter 24.4 mm, height 9.0 mm (Fig. 16).

Animal: preserved specimens (Fig. 19) have the brood sac with a folded edge unlike that shown in other published illustrations of *Capulus* species. Animal not boring into the shell of its host but producing a notch in the shell edge (Fig. 18, left). The specimen

in Figure 18 (right) is shown attached to the left valve of *A. patagonica*, and in Figure 18 (left), the attachment scar area is shown. The area corresponding to the posterior edge of the foot is eroded in the host shell; this is not a result of boring by the *Capulus*, because it is too far from the position of the head.

Radula (Fig. 17): rachidian and lateral strongly cusped and serrate on the edges, marginals uncusped.

MATERIAL. Chile: Coquimbo (LACM, Figs. 18, 19), Los Vilos (LACM, Fig. 16), Zapallar, Quintero. Specimens examined: six.

TYPE MATERIAL AND TYPE LOCALITY. Holotype, BM(NH) 54.12.4.554. Type locality: Paita, Peru.

DISTRIBUTION. Paita, Peru (5°5'S), to Isla de Los Estados, Argentina (54°47'S). Depth range off central Chile: 200–450 m.

REMARKS. Orbigny's species *Capulus ungaricoides*, described from Paita, Peru, has not been reported (other than in faunal lists) subsequent to its original description. The present material agrees with the original description and with illustrations of the holotype given by Keen (1966), except for lacking reddish rays, which may not be significant. Although the material treated here may not be positively identified with Orbigny's species, it is premature to distinguish separate species until material conforming to Orbigny's holotype can be shown to represent a separate species. Orbigny's holotype was probably not associated with an *Acesta* species, but because many species of *Capulus* are not host-specific, that need not preclude it being conspecific with the present material.

Capulus ungaricoides has the fine spiral sculpture present in *C. chilensis* Dall, 1908, and *C. novaezelandiae* Dell, 1978, but differs from both in having a narrower, more rapidly expanding apex. *Capulus chilensis* has regular early coiling of three distinct whorls, very unlike the narrow recurved apex of *C. ungaricoides*. Type material of *Capulus chilensis* has not previously been figured. The holotype measures 25 mm in diameter; a smaller paratype specimen is figured here (Fig. 20), to show the coiling of the early whorls.

Although Carcelles (1944) reported upon a specimen from Isla de los Estados (east of Tierra del Fuego), Argentina, identified as *C. chilensis*, his description agrees with the present material and forms the basis for the distributional record of *C. ungaricoides* cited above.

Superfamily Tonnacea

Family Cymatiidae

Genus *Fusitriton* Cossmann, 1903

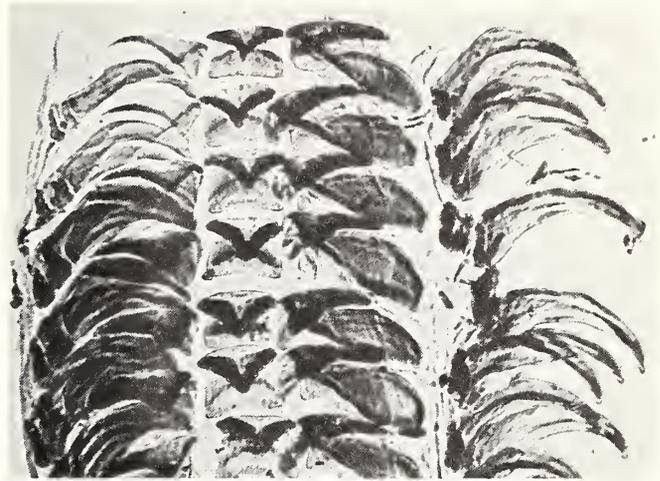
Type species (monotypy): *Triton cancellatus* Lamarck, 1816 [= *Neptunea magellanica* Roeding, 1798]. Recent, Magellanic.

Fusitriton is noted for its bipolar distribution; species are common in shallow water in the North Pacific, South Pacific, and South Atlantic Oceans. At lower latitudes, all of the species become deeply submergent, which helps to explain the presence of the genus in cold waters of both the Northern and Southern Hemispheres.

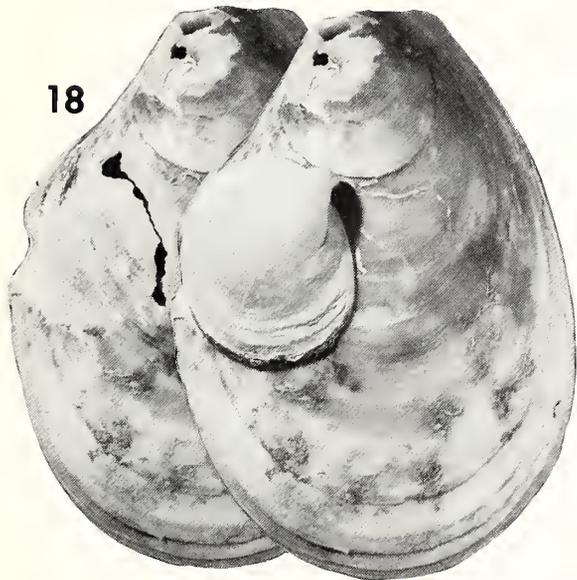
The genus has been thoroughly reviewed by Smith (1970), who discussed the broadly distributed species in the present ma-



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Figures 16 through 20, *Capulus ungaricoides* and *C. chilensis*.

Figures 16 through 19, *C. ungaricoides*. **Figure 16**, preserved but retracted animal attached to shell, LACM 72487, 300-400 m off Los Vilos, Chile, diameter 24.4 mm. **Figure 17**, radular ribbon, LACM 72487, 300-400 m off Los Vilos, Chile, both pairs of marginal teeth on right side of ribbon folded to the right, width of field 0.9 mm. **Figure 18**, two views, LACM 72488, attached to left valve of *Acesta patagonica*, right view with *Capulus* in place, left view showing attachment scar and indentation in host shell corresponding to position of pseudoproboscis, 450 m off Coquimbo, Chile, length of *Acesta* 107.3 mm, diameter of *Capulus* 39.6 mm. **Figure 19**, body of specimen in Fig. 18, showing the folded edge of the brood sac. **Figure 20**, *C. chilensis*, paratype, USNM 96926, "Albatross" station 2781, 636 m "off the Chilean coast," diameter 8.4 mm.

terial at length; her synonymy is not repeated here. Although two names for the Chilean species, *F. magellanicus* and *F. cancellatus*, have been used inconsistently by subsequent authors, Cernohorsky (1977) has recently shown that *F. magellanicus*, credited to Roeding, 1798, has priority over *F. cancellatus*, credited to Lamarck, 1816.

Fusitriton magellanicus (Roeding, 1798)

Figures 21-23

Neptunea magellanica Roeding, 1798:116.

Fusitriton magellanicus, Cernohorsky, 1977:107, fig. 3.

Triton cancellatus Lamarck, 1816:4.

Fusitriton cancellatus, Smith, 1970:475, pl. 42, figs. 4-10.

DESCRIPTION. Shell large, whorls six, rounded. Periostracum thick and bearing projecting hairs. Varices irregular, more frequent in juvenile stages, the mature lip marked by a final varix. Axial sculpture strongest on early whorls, nearly lacking on final whorl. Spiral cords low, with broad, shallow interspaces.

Dimensions: height 94.0 mm, diameter 47.3 mm (Fig. 21); height 85.1 mm, diameter 43.6 mm (Fig. 22).

Animal: Smith (1970, text fig. 2c) gave a sketch of the mantle cavity.

Radula (Fig. 23): typically taenioglossate, rachidian and lat-

eral finely denticulate. See also Smith (1970, text fig. 3d).

MATERIAL. Chile: Los Vilos (LACM), Punta Salinas (LACM), Caleta Molles (LACM, Fig. 21), Pupudo, Zapallar, Algarrobo, Punta Penablanca (LACM), Punta Topocalma (LACM). Specimens examined: 32.

TYPE MATERIAL AND TYPE LOCALITY. Type material unknown, type locality presumed to be the Strait of Magellan.

DISTRIBUTION. Los Vilos, Chile (31°56'S), to Tierra del Fuego; north in the Atlantic to Sarita, Rio Grande do Sul, Brazil (Smith, 1970). Depth range in central Chile: 180–960 m.

REMARKS. *Fusitriton magellanicus* is the only member of the present assemblage of large gastropods also to occur in relatively shallow water in southern Chile. McLean has collected specimens at several localities in the Gulf of Corcovado east of Chiloe Island by diving in depths as shallow as 5 m (Fig. 22).

Superfamily Muricea

Family Muricidae

Subfamily Trophoninae

Genus *Trophon* Montfort, 1810

Type species (original designation): *Murex magellanicus* Gmelin, 1791 (= *Buccinum geversianum* Pallas, 1774). Recent, Magellanic.

The muricid subfamily Trophoninae, of which *Trophon* is the type genus, comprises white-shelled forms with axial lamellae rather than varices, open canals, and simple apertures. It is the least known group in the Muricidae; only the type species of recognized genera were treated by Radwin and D'Attilio (1976).

Trophon is primarily an austral genus with numerous species in the Antarctic and subantarctic region. The type species, which is relatively large, has both axial and spiral sculpture and is common in the intertidal zone in the Fuegian and Patagonian regions. An illustration given by Radwin and D'Attilio (1976, fig. 130), though identified as *Stramonitrophon laciniatus*, is actually *T. geversianus*.

Trophon bahamondei new species

Figures 24–25

DESCRIPTION. Shell moderately large, thin but sturdy, white, spire high, canal long, recurved, open; length of aperture and canal slightly greater than height of spire, aperture shape quadrate, canal constricted. Protoconch eroded, teleoconch whorls six, early whorls bulging at midwhorl, having about 12 thick axial ribs. Mature sculpture of 10 to 13 axial lamellae, suppressed on the shoulder, at the periphery producing open, raised spines that rise above the level of the suture; lamellae sharply raised on the body whorl but suppressed on the siphonal canal; siphonal fasciole with overlapping lamellae; axial sculpture lacking. Aperture simple, lacking denticles or columellar callus.

Dimensions: height 49.4 mm, diameter 26.1 mm (holotype, Fig. 25).

Radula (Fig. 24): typical for the genus, rachidian plate broad and shallow, having five cusps, a strong central cusp and two on either side, the outermost the larger; lateral teeth sickle-shaped.

MATERIAL. Chile: Coquimbo (LACM), Los Vilos (LACM), Papudo, Zapallar, Quintero, Algarrobo, Pichilemu (LACM, holotype, Fig. 25). Specimens examined: 73.

TYPE MATERIAL. Twenty-four specimens from the type locality, collected 25 May 1976, by Andrade, unidentified shrimp trawler. Holotype, LACM 1982; paratypes, LACM 1983, paratypes, MNHN 200490; paratypes, MZICB 15.529; paratypes, USNM 784739.

TYPE LOCALITY. 340 m off Pichilemu, Chile (34°27'S).

DISTRIBUTION. Coquimbo (29°58'S) to Pichilemu (34°27'S), Chile. Depth range: 200–450 m.

DIAGNOSIS. A species of *Trophon* characterized by its quadrate aperture, and sculpture of axial lamellae, which are spinose at the periphery. It most resembles *Trophon* (*Stramonitrophon*) *plicatus* (Solander in Lightfoot, 1786),⁵ a common shallow-water species from southern Chile in which spiral sculpture is lacking, but is smaller with the aperture more quadrate and the canal more constricted. The two species are not closely related, for *Trophon plicatus* has a unique radula in which there are accessory cusps (the feature upon which the subgenus *Stramonitrophon* is based).

REMARKS. There is virtually no variation in *Trophon bahamondei*; all specimens examined are very similar.

ETYMOLOGY. We are pleased to dedicate this species to Dr. Nivaldo Bahamonde N., of the Museo Nacional de Historia Natural, Santiago.

Family Columbariidae

Genus *Columbarium* Martens, 1881

Type species (original designation): *Pleurotoma* (*Columbarium*) *spinicincta* Martens, 1881. Recent, Queensland, Australia.

Columbarium is one of several genera in the Columbariidae, a family restricted to moderately deep water. Shell form and structure of the protoconch resembles that of *Fusinus* Rafinesque, 1815, in the Fasciolaridae, but the radula relates the genus to the Muricacea. Living and fossil Columbariidae of the world were reviewed by Darragh (1969). Japanese species were recently reviewed by Habe (1979).

Although the family is represented in the western Atlantic (Clench, 1944; Bayer, 1971), no species until now has been reported from the eastern Pacific.

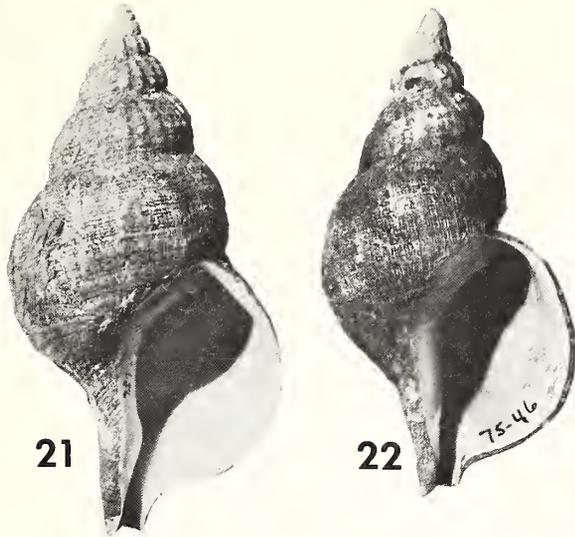
Authors are not agreed as to whether the available taxa should be genera or subgenera, but the new species that follows is clearly a member of *Columbarium*, *sensu stricto*, a genus well represented in the Tertiary and Recent of New Zealand, Australia, and Japan.

Columbarium tomicici new species

Figures 26–30

DESCRIPTION. Shell fusiform, length of aperture and canal about two-thirds the total length, white under a thin brown periostracum. Protoconch eroded, teleoconch whorls six, early

5. *Trophon plicatus* is better known as *T. laciniatus* (Gmelin, 1791) as used by Dell (1971). However, Cernohorsky (1977) showed that *T. plicatus*, credited to Solander in Lightfoot, 1786, is the prior name.

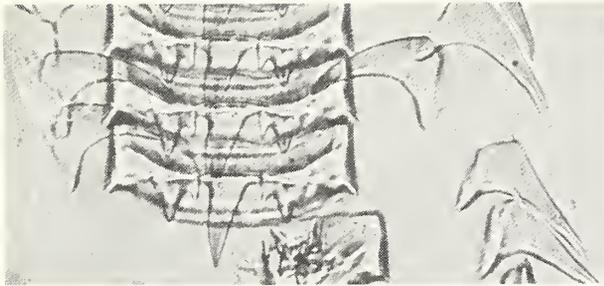


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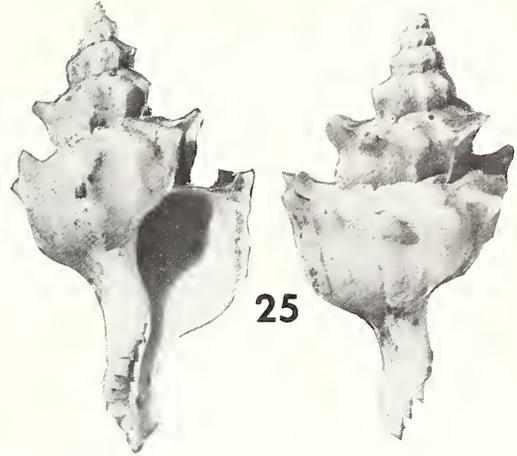
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Figures 21 through 25, *Fusitriton magellanicus* and *Trophon bahamondei* new species.

Figures 21 through 23, *Fusitriton magellanicus*. Figure 21, LACM 66-156, 580 m off Caleta Molles, Chile, height 94.0 mm. Figure 22, LACM 75-46, 5 m, Isla Laitec, Chiloe Province, Chile, height 85.1 mm. Figure 23, radula ribbon, LACM 66-156, 580 m off Caleta Molles, Chile, width of field 1.2 mm. Figures 24 and 25, *Trophon bahamondei* new species. Figure 24, radular ribbon, LACM 72491, 240-400 m off Los Vilos, Chile, width of field 0.35 mm. Figure 25, holotype, LACM 1982, 340 m off Pichilemu, Chile, height 49.4 mm.

whorls with a sharp median carina, at first with weak projections, but changing to thin, triangular, posteriorly directed spines, 9 to 16 on the final whorl. Shoulder and spire whorls smooth or finely striate; suture laid upon, or just anterior to, a stout cord (the anterior carina of Darragh, 1969). Base and canal with prominent, rounded, nonscabrous spiral cords, with interspaces of nearly equal or lesser width, about five across the base and ten more on the canal. Columellar callus thin, not raised to form a columellar lip; aperture subquadrate, lip thin.

Dimensions: height 46.8 mm, diameter 22.8 mm (holotype, Fig. 26); height 78.4 mm, diameter 33.2 mm (Fig. 29).

Radula (Fig. 30): rachidian plate with curved base and three cusps that project over the basal plate of the next row, the middle cusp the longest; lateral tooth with large base and curved tip. The radula is similar to that of other species in the family (see Bayer, 1971:172).

MATERIAL. Peru: S of Lobos de Afuera (LACM, Fig. 29), N of Isla Macabi (LACM). Chile: Junquillar (LACM, holotype, Fig. 26), Coquimbo (LACM, Fig. 27), Los Vilos (LACM), Punta Salinas (LACM), Papudo, Algarrobo. Four other specimens are in the LACM collection from depths of 520-1,200 m in northern Peru (Banco de Mancora, Fig. 28; Chilca, Fig. 30; Mollendo),

received from Dr. Enrique del Solar of Lima, Peru. Specimens examined: 30.

TYPE MATERIAL. Thirteen specimens from the type locality, collected by R/V ANTON BRUUN, station 714, 16 August 1966. Holotype, LACM 1984; paratypes, LACM 1985; paratype, MNHN 200491; paratypes, MZICB 15.530; paratypes, USNM 784740. Although there are single larger specimens from other localities in the material at hand, this lot was selected as the type lot because it contains 13 specimens (only 2 live-collected) of about the same size as the holotype, enabling distribution of paratypes from the type locality.

TYPE LOCALITY. 950 m, W of Junquillar, Chile (25°0'S, 70°40'W).

DISTRIBUTION. Banco de Mancora, Peru (3°25'S), to Algarrobo, Chile (33°22'S). Depth range: 240-1,200 m.

DIAGNOSIS. A species of *Columbarium* characterized by its sculpture of triangular spines at the periphery and regular, nonscabrous cords on the base and canal. *C. tomicici* most resembles *C. veridicum* Dell, 1963, from New Zealand (see Powell, 1979:169, pl. 37, fig. 1), which entirely lacks spiral sculpture on the base and canal. General proportions are similar to those of the Japanese *C. pagoda* (Lesson, 1840), which has a projecting

columellar lip and may have spinose sculpture on the canal, as figured by Habe (1979).

REMARKS. *Columbarium tomicici* has the essential features of *Columbarium*, *sensu stricto*, as diagnosed by Darragh (1969), except that the parietal or inner lip callus is not raised, the spiral cords of the base and canal are nonscabrous, and there is no tooth on the outer lip at the position of the anterior (basal) carination.

ETYMOLOGY. This species is dedicated to Prof. Jorge Tomiic K., of the Universidad de Antofagasta, Antofagasta, Chile.

Superfamily Buccinacea

Family Buccinidae

Subfamily Buccinulinae

Powell (1929, 1951, 1979) has discussed the higher classification of buccinid whelks with particular reference to southern genera. In early publications, he advocated the use of several families based on radular characters, but, more recently (Powell, 1979), he placed genera with a tricuspid rachidian and a tricuspid lat-

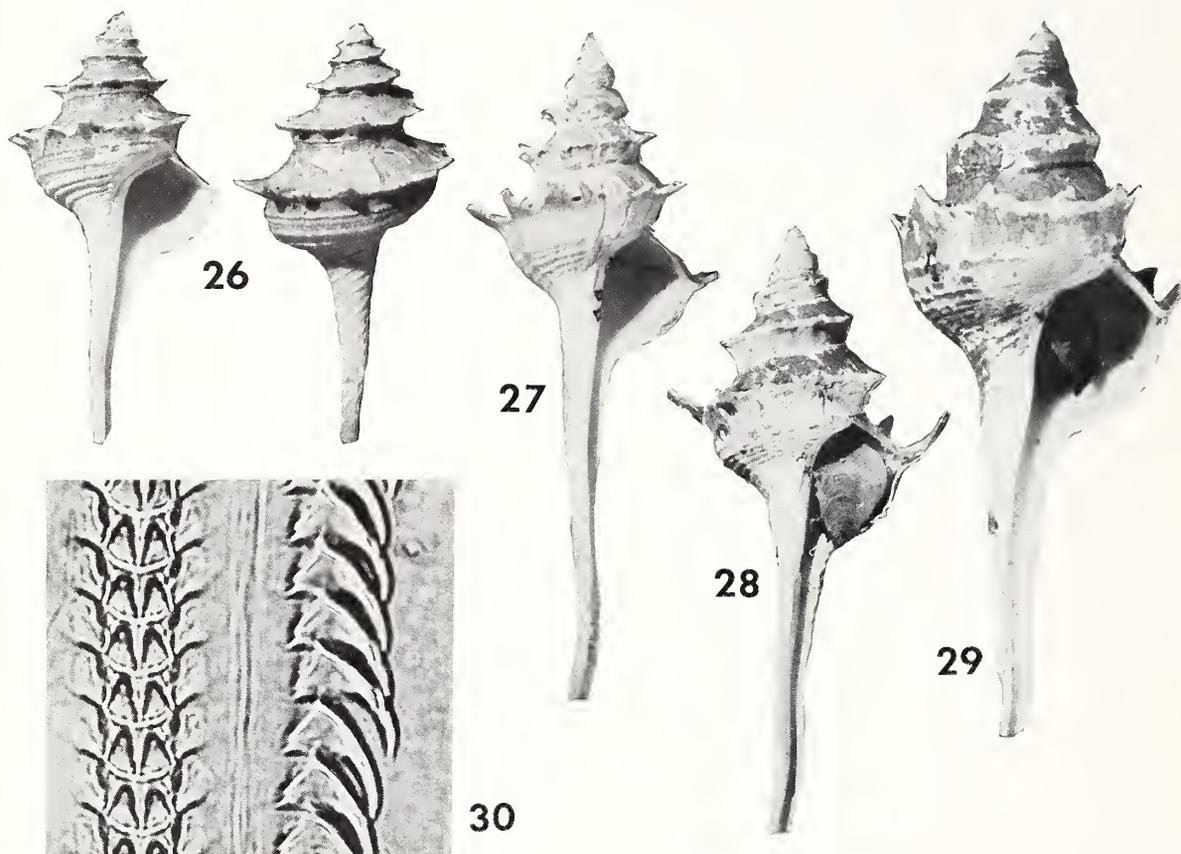
eral in the subfamily Buccinulinae, of which *Aeneator* is a member.

Genus *Aeneator* Finlay, 1927

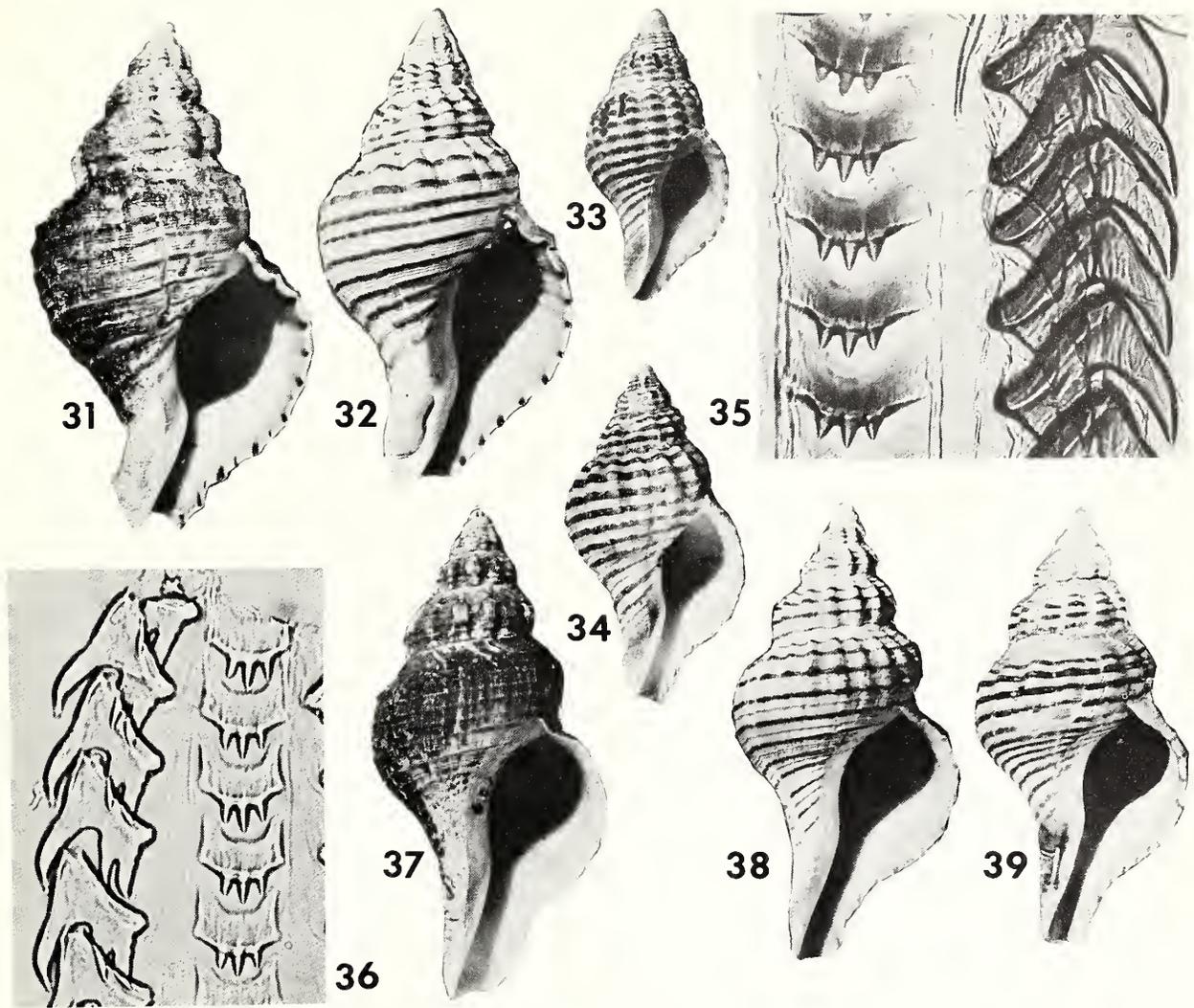
Type species (original designation): *Verconella marshalli* Murdoch, 1924. Pleistocene, New Zealand.

Rehder (1971) introduced the New Zealand genus *Aeneator* to the Chilean fauna with his description of *Aeneator (Ellicea) loisae*, although he did not mention the most common Chilean species of the group, *A. fontainei* (Orbigny, 1841). The latter species was assigned by Dall (1909) and Keen (1966) to *Austrofusus* Kobelt, 1879. *Austrofusus*, however, pertains to a New Zealand group with broad apertures and short, twisted canals.

New Zealand species of *Aeneator* have been discussed by Dell, (1956, 1963), Beu (1979), and Powell (1979). The occurrence of the genus in Chile has not been mentioned by these authors. The Chilean species seem to differ in having a thickened or expanded final lip. However, the living representative of the Pleistocene type species, *Aeneator marshalli separabilis* Dell, 1956, from



Figures 26 through 30, *Columbarium tomicici* new species. Figure 26, 2 views of holotype, LACM 1984, 950 m off Junquillar, Chile, height 46.8 mm. Figure 27, LACM 75-88, depth unknown off Coquimbo, Chile, height 73.7 mm. Figure 28, LACM 71-234, 520 m, Banco de Mancora, Peru, height 65.6 mm. Figure 29, LACM 74-9, 1,200 m S of Isla Lobos de Afuera, Peru, height 78.4 mm. Figure 30, radular ribbon, LACM 72-187, 800 m S of Chilca, Peru, width of field 0.2 mm.



Figures 31 through 39, *Aeneator fontainei*. Figure 31, LACM 75-21, 20 m off Mejillones, Chile, height 70.0 mm. Figure 32, LACM 75-21, same locality, height 66.3 mm. Figure 33, LACM 54737, 40 m off Montemar, Chile, height 39.5 mm. Figure 34, LACM 66-161, 56-95 m off Punta Mar Brava, Chile, height 46.6 mm. Figure 35, radular ribbon, LACM 75-21, 20 m off Mejillones, Chile, width of field 0.5 mm. Figure 36, radular ribbon, LACM 66-150, 260-280 m off Punta Penablanca, Chile, width of field 0.35 mm. Figure 37, LACM 66-159, 110 m off Punta Hornos, Chile, height 67.0 mm. Figure 38, LACM 66-159, same locality, height 64.9 mm. Figure 39, LACM 72493, 270 m off Punta Toro, Chile, height 58.9 mm.

New Zealand, has an expanded outer lip. The allocation of the Chilean species to *Aeneator* is therefore followed here.

Ellicea Finlay, 1927 (type species: *Siphonalia orbita* Hutton, 1855), used by Dell (1956) and Rehder (1971) as a subgenus to distinguish species with strong spiral sculpture, was reduced to synonymy by Powell (1979), who found no clear separation of species on that character.

The following diagnosis of *Aeneator* is offered: fusiform buccinids of moderate size, canal plus aperture more than half the length of the shell, whorls rounded but for a subsutural concavity; lip with a broad shallow sinus below the suture; sculpture of strong axial ribs overridden by spiral cords, rachidian and laterals tricuspid.

Aeneator fontainei (Orbigny, 1841)

Figures 31-39

Fusus fontainei Orbigny, 1841:447, pl. 63, fig. 2.

Austrofuscus fontainei, Dall, 1909:213; Keen, 1966:4.

Fusus alternatus Philippi, 1847, pl. 4, fig. 6; Reeve, 1847, pl. 2, fig. 6.

Siphonalia alternata, Tryon, 1881:137.

DESCRIPTION. Shell large, covered by periostracum, length of aperture and canal more than half the length of the shell. Whorls six, convex except for a concave subsutural area, suture not deeply impressed. Axial sculpture on penultimate whorl of 15-17 rounded ribs, interspaces slightly narrower; axial sculp-

ture usually lacking altogether on the final half whorl. Spiral sculpture of major and minor cords; major cords four on early whorls, raised, dark brown, the interspaces twice as broad as these cords, cords overriding the axial ribs. Minor cords between each brown cord about five, separated by incised grooves. Lip lirate within, edge sharp, thick behind the edge, edge marked with brown at the termination of the cords.

Dimensions: height 70.0 mm, diameter 38.0 mm (Fig. 31); height 67.0 mm, diameter 32.0 mm (Fig. 37).

Radula (Figs. 35, 36): typical for the genus, rachidian and laterals tricuspid.

MATERIAL. Chile: Punta Mar Brava (LACM, Fig. 34), Punta Hornos (LACM, Figs. 37, 38), Coquimbo (LACM), Los Vilos (LACM), Papudo (LACM), Quintero (LACM), Punta Penablanca (LACM), Punta Panulcillo (LACM), Punta Toro (LACM, Fig. 39). Other records: Bahía Independencia and Bahía San Juan, Peru, 20–50 m, collected by the Hancock Expeditions in 1938; Mejillones, Chile (LACM, Figs. 31, 32), collected by McLean in 1975 in 20 m by scuba diving. Specimens examined: more than 100.

TYPE MATERIAL AND TYPE LOCALITY. Five specimens, BM(NH) 54.2.4.517 (Keen, 1966). Type locality: Callao, Peru. Type locality for *F. alternatus*: Mejillones, Chile.

DISTRIBUTION. Independencia Bay, Peru (LACM) (14°13'S), to Punta Toro, Chile (33°1'S). Depth range: 20–350 m.

REMARKS. *Aeneator fontainei* is the only offshore species treated here to occur also in relatively shallow water (at depths of 20 m or more) in central Chile. Three extremes in shell form are noted. Most specimens from shallow water (Figs. 31, 32) have relatively thick shells with pronounced development of siphonal fasciole; the darkly marked cords are prominent. Specimens from archibenthal depths (Figs. 37–39) have a thinner shell and a straighter canal, and the dark cords are less prominent than those of the shallow-water form. A fine, dark intercalary cord may appear in the interspace between major cords, as in Figure 38. At first glance, especially with periostracum intact as in Figure 37, these specimens appear very different from the shallow-water form. However, specimens such as that in Figure 39 seem to be intermediate between the shallow- and deep-water forms. Finally, there is a dwarf form occurring at intermediate depths (Fig. 33), in which there is little subsutural concavity, a more crowded condition of the axials, and more numerous, more closely spaced dark cords. This form shows complete intergradation (Fig. 34) with the usual shallow-water form.

Aeneator loisae Rehder, 1971
Figures 40–44

Aeneator (Ellicae) loisae Rehder, 1971:593, figs. 7, 8.

DESCRIPTION. Shell large for the genus, fusiform, surface chalky white, covered by periostracum, length of aperture and canal more than half the length of the shell. Whorls seven, convex, except for a concave subsutural area; suture not deeply impressed. Axial sculpture on early whorls of about 14 low ribs running from suture to suture, interspaces narrower than the ribs; ribs lacking altogether on body whorl, somewhat indistinct on penultimate whorl but prominent on earlier whorls. Spiral

sculpture of major cords alternating with secondary cords, finer tertiary cords may appear in the interspaces and may be superimposed on the major cords. Major cords about nine to ten on the penultimate whorl, continuing with regular spacing across the body whorl and canal. Lip sinuate on upper part, weakly lirate within, scalloped to correspond with the spiral cords; final lip flared. Canal long, parietal and columellar area well defined, glazed.

Dimensions: height 91.8 mm, diameter 43.7 mm (Fig. 40); height 88.5 mm, diameter 37.9 mm (Fig. 43); height 74.7 mm, diameter 37.3 mm (holotype, Fig. 42).

Radula (Fig. 44): central and lateral teeth tricuspid; see also Rehder, 1971, fig. 8.

MATERIAL. Chile: Coquimbo (LACM), Los Vilos (LACM), Caleta Molles (LACM, Fig. 43), Papudo, Zapallar, Quintero (LACM), Algarrobo, Cabo Carranza (LACM, Figs. 40–41). Specimens examined: more than 100.

TYPE MATERIAL AND TYPE LOCALITY. Holotype, USNM 701667. Type locality: 200 m, 17–18 km NW of Valparaíso, Chile.

DISTRIBUTION. Coquimbo (29°58'S), to Cabo Carranza, Chile (35°27'S). Depth range: 200–450 m.

REMARKS. *Aeneator loisae* differs from both *A. fontainei* and *A. castillai* new species in lacking any brown coloration to the shell. It also has more numerous primary cords than does *A. fontainei*. Its closest relative, as noted by Rehder (1971), is the New Zealand species *A. benthicola* Dell, 1973 (see Powell, 1979:202, pl. 41, fig. 3).

Aeneator loisae is highly variable in proportions. The holotype (Fig. 42) is relatively broad; specimens from Cabo Carranza (Figs. 40, 41) are more slender, and a single specimen from Caleta Molles (Fig. 43) is still more slender.

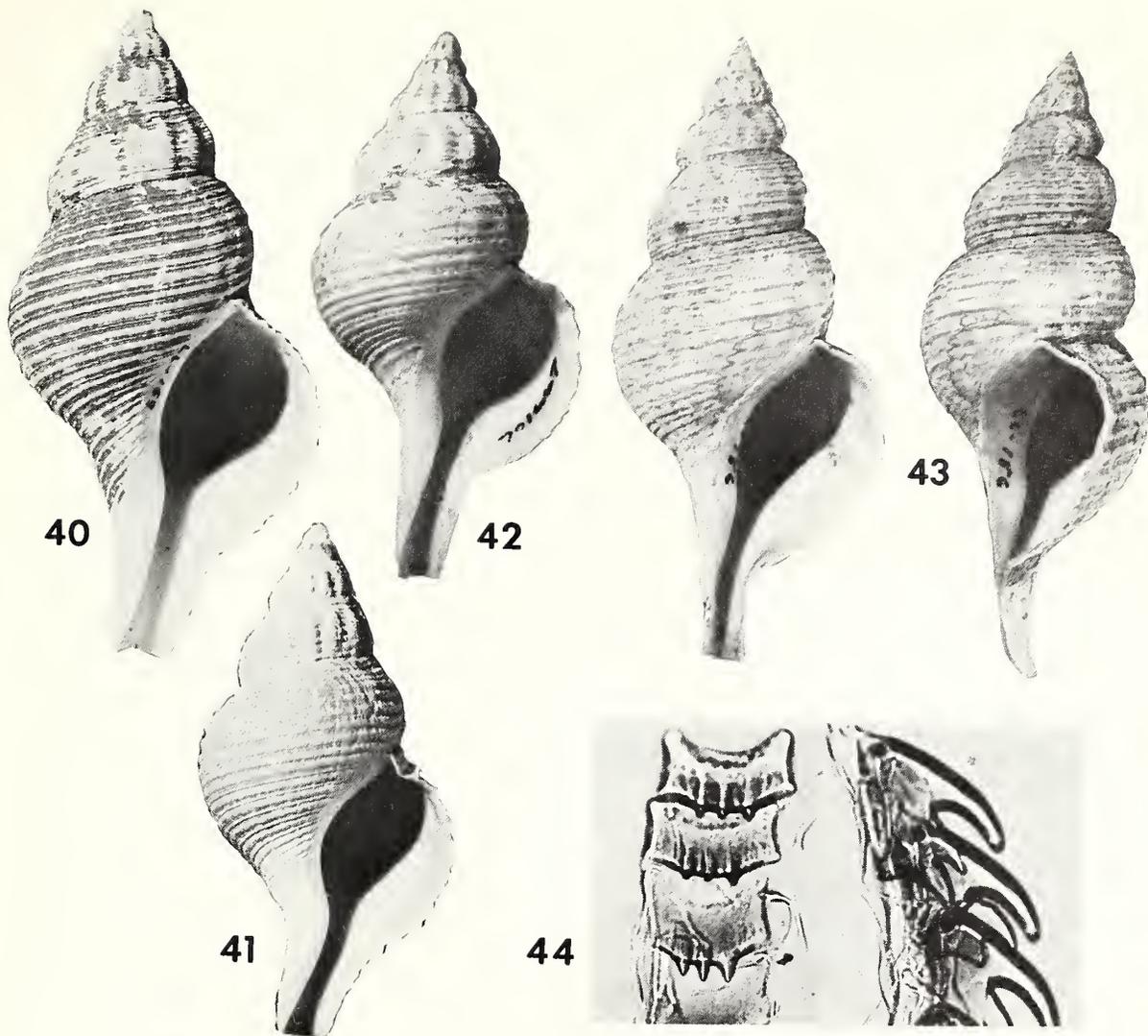
Aeneator castillai new species
Figures 45–50

DESCRIPTION. Shell large, fusiform, length of aperture and canal more than half the length of the shell; canal relatively short, twisted. Shell light brown under a thin periostracum, often with a lighter colored band coinciding with the periphery. Whorls six, protoconch and early whorls eroded; whorls convex but for a concave subsutural area; suture not deeply impressed. Axial sculpture on penultimate whorl of about 16 low ribs, strong across the periphery but faint in the subsutural area; final whorl with weak sculpture; axial sculpture lacking altogether on the final half whorl. Spiral sculpture of fine cords alternating in strength, all cords in the concave subsutural area fine; those of the periphery and base coarser, frequently darker in color. Lip faintly lirate within, sinuate on upper part, final lip not expanded. Parietal and columellar area well defined, glazed.

Dimensions: height 78.7 mm, diameter 39.8 mm (holotype, Fig. 45); height 75.7 mm, diameter 37.8 mm (Fig. 47).

Radula (Fig. 50): typical for the genus, central and lateral teeth tricuspid.

MATERIAL. Chile: Coquimbo (LACM, Fig. 49), Los Vilos (LACM, Figs. 46–48), Papudo (LACM, type lot, Fig. 45), Zapallar (LACM), Quintero (LACM), Punta Penablanca (LACM). Specimens examined: 23.



Figures 40 through 44, *Aeneator loisae*. Figure 40, LACM 66-153, 290-450 m off Cabo Carranza, Chile, height 91.8 mm. Figure 41, LACM 66-153, same locality, height 70.0 mm. Figure 42, holotype, USNM 701667, 200 m off Valparaíso, Chile, height 74.7 mm. Figure 43, two views, LACM 66-156, 580 m off Caleta Molles, Chile, height 88.5 mm. Figure 44, radular ribbon, LACM 66-153, 290-450 m off Cabo Carranza, Chile, width of field 0.5 mm.

TYPE MATERIAL. Nine specimens from the type locality, collected 29 March 1977, by Andrade, shrimp trawler GODEN WIND. Holotype, LACM 1986; paratypes, LACM 1987; paratypes, MNHN 200492; paratypes, MZICB 15.532; paratypes, USNM 784741.

TYPE LOCALITY. 300 m off Papudo, Chile (32°31'S; 71°54'N).

DISTRIBUTION. Coquimbo (29°55'S), to Punta Penablanca, Chile (33°22'S). Depth range: 200–450 m.

DIAGNOSIS. A species of *Aeneator* characterized by its rather short, twisted canal and the absence of axial ribs in the concave subsutural area. It differs from both *A. fontainei* and *A. loisae* in these features. Additionally it differs from the offshore form of *A. fontainei* in having more numerous spiral cords and a flesh colored surface. From *A. loisae*, it also differs in having a brown rather than white shell coloration.

REMARKS. The surface layers of the shell of *A. castillai* are particularly prone to erosion, leaving an unsculptured, chalky shell surface upon loss of the sculptured layer. A number of the specimens are partially or completely eroded (Fig. 49).

ETYMOLOGY. We are pleased to name this species after Dr. Juan Carlos Castilla, of the Universidad Católica, Santiago.

Superfamily Volutacea

Family Volutidae

Subfamily Odontocymbiolinae

Genus *Miomelon* Dall, 1907

Type species (original designation): *Volutilithes philippiana* Dall, 1890. Recent, central Chile.

Miomelon is known from three species occurring in the region from central Chile to the vicinity of the Falkland Islands. The species in the present collection was identified by Weaver and Dupont (1970) and Rehder (1971) as *M. philippiana* (Dall, 1890). Stuardo and Villarroel (1974) showed that Dall's species, which is known only from the single holotype from abyssal depths off central Chile (1,238 m, 38°8'S), differs from the more common archibenthal species, which they described as *M. alarconi*.

Stuardo and Villarroel treated the radula and anatomy of *Miomelon alarconi*, confirming that the genus should be assigned to the volutid subfamily Odontocymbiolinae.

Miomelon alarconi
Stuardo and Villarroel, 1974
Figures 51, 52

Miomelon philippiana (Dall, 1890), of Weaver and DuPont, 1970:132, pl. 56, figs. C, D; Rehder, 1971:594. Not Dall, 1890. *Miomelon alarconi* Stuardo and Villarroel, 1974:140, figs. 4a, 4b, 5a, 5b.

DESCRIPTION. Shell moderately large, aperture length equal to spire height; shoulder concave, siphonal canal broad, outer lip thin. Sculpture of fine axial ribs and less prominent spiral cords, interspaces broad. Columella with three or four plaits, the anteriormost the strongest. Color light brown under a thin brown periostracum; parietal glaze light brown; surface often chalky in specimens that have lost the periostracum.

Dimensions: height 74.9 mm, diameter 32.0 mm (Fig. 52); height 89.7 mm, diameter 39.4 mm (holotype).

Radula (Fig. 51): base of rachidian elongate, strongly tricuspidate. See also Stuardo and Villarroel (1974, fig. 2).

MATERIAL. Chile: Coquimbo (LACM), Los Vilos (LACM), Papudo, Zapallar, Algarrobo, Pichilemu (LACM), Cabo Caranza (LACM, Fig. 52). Specimens examined: more than 100.

TYPE MATERIAL AND TYPE LOCALITY. Holotype, MZICB 5553; paratypes, MZICB 5554, 5555, 5556. Type locality: 125 m, Chanco Bay, Chile (35°45'S).

DISTRIBUTION. Coquimbo (29°58'S), to 37°51'S (Stuardo and Villarroel, 1974), Chile. Depth range: 125–450 m.

REMARKS. *Miomelon alarconi* is larger, heavier, and more broadly inflated and has coarser spiral sculpture than *M. philippiana*.

Superfamily Cancellariacea

Family Cancellariidae

The large new species of *Cancellaria* in the present material was unexpected, for the previously known austral representatives of the family include such genera as *Admete* Kroyer, 1842, and related small-shelled genera (see Carcelles and Williamson, 1951; Powell, 1960, 1979).

The cancellariid radula is unlike that of stenoglossate neogastropods (Olsson, 1970; Keen, 1971), yet other features of can-

cellariid anatomy are typical of those of higher neogastropods (Graham, 1966; Harasewych and Petit, 1982).

Genus *Cancellaria* Lamarck, 1799

Type species (monotypy): *Voluta reticulata* Linnaeus, 1767. Recent, Florida.

Subgenus *Crawfordina* Dall, 1919 [= *Crawfordia* Dall, 1918, not Pierce, 1908]

Type species (original designation): *Cancellaria crawfordiana* Dall, 1891. Recent, California.

The subgenus *Cancellaria*, *sensu stricto*, comprises moderately large shelled forms with reticulate sculpture and prominent columellar plaits. *Cancellaria stuardoi* new species is most closely related to the type species of the subgenus *Crawfordina*. Grant and Gale (1931:614) diagnosed *Crawfordina* as follows: "This section differs from *Cancellaria*, *s. s.*, in the more elongate shape, lighter weight, smaller, more oblique plaits, and shorter columella." Another feature to be mentioned is the minimal development of the parietal callus.

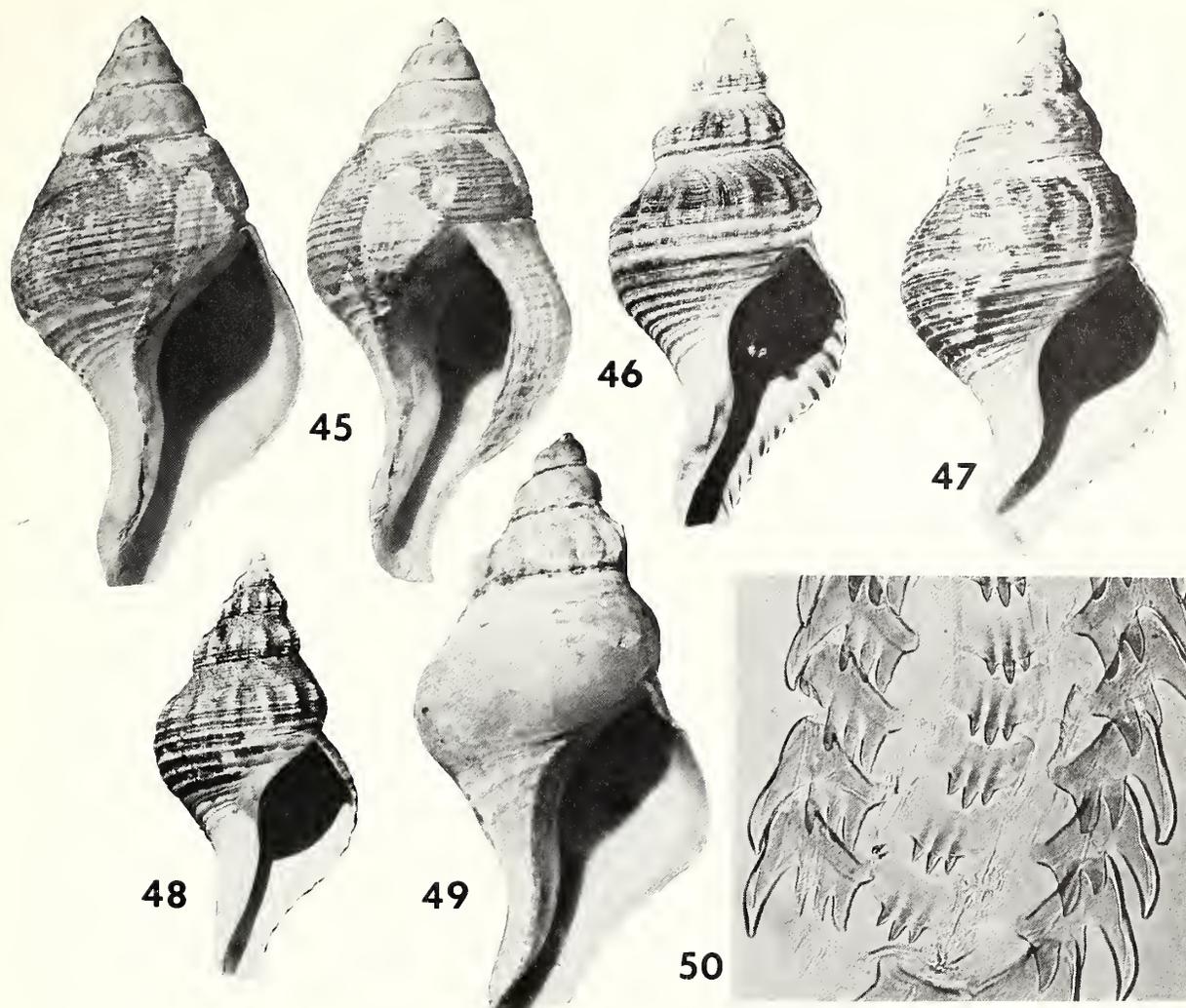
There are three members of the subgenus *Crawfordina*: the offshore Californian type species, the new Chilean species described here, and the connecting link, the deep-water Panamic species, *Cancellaria io* Dall, 1896 (see Keen, 1971:654, fig. 1477), from 589 m, Panama Bay.

Cancellaria (Crawfordina) stuardoi new species Figure 53

DESCRIPTION. Shell large, thin but sturdy, light brown under a thin but persistent light brown periostracum; whorls six, convex and slightly shouldered, suture deeply impressed. Protoconch lost; sculpture eroded on first two whorls. Axial ribs 18 to 20 per whorl, except on the final half whorl, where the ribs become more irregular and tend to be more broadly spaced from growth pauses; ribs crossing the whorls completely; ribs narrower than the interspaces; ribs posteriorly flexed near the suture. Spiral sculpture of broad, low ribs with more or less equal interspaces, 9 on the penultimate whorl and about 20 on the body whorl; spiral cords somewhat indistinct on the shoulder and narrower near the columella. Aperture ovate, columella incurved, columellar callus thin, parietal callus not thick enough to obliterate the sculpture, the anterior end of the columella consisting of a curved fold; two oblique folds higher on the columella, the posteriormost the largest, the folds hardly showing on apertural view, but much stronger within (shell viewed obliquely). Outer lip thin, lirated within. Operculum lacking.

Dimensions: height 61.3 mm, diameter 31.5 mm (holotype, Fig. 53); height 62.9 mm, diameter 31.0 mm (paratype); height 57.5 mm, diameter 30.8 mm (paratype).

MATERIAL. Chile: Coquimbo, Papudo, Pichilemu (LACM, type lot, Fig. 53).



Figures 45 through 50, *Aeneator castillai* new species. **Figure 45**, two views of holotype, LACM 1986, 300 m off Papudo, Chile, height 78.7 mm. **Figure 46**, LACM 72499a, 400 m off Los Vilos, Chile, height 69.3 mm. **Figure 47**, LACM 72499b, same locality, height 75.7 mm. **Figure 48**, LACM 72499c, same locality, height 56.6 mm. **Figure 49**, LACM 61-12, 110 m off Coquimbo, Chile, height 79.8 mm. **Figure 50**, radula ribbon, LACM 72499, 400 m off Los Vilos, Chile, width of field 0.5 mm.

TYPE MATERIAL. Three specimens from the type locality collected by Andrade, 25 May 1976, unidentified shrimp trawler. Holotype, LACM 1988; paratype, MNHN 200493; paratype, MZICB 15.532. Each specimen has the soft parts separately preserved.

TYPE LOCALITY. 240–350 m off Pichilemu, Chile (34°27'S, 72°24'W).

DISTRIBUTION. Coquimbo (29°58'S), to Pichilemu (34°27'S), Chile. Depth range: 200–350 m.

DIAGNOSIS. A species of the subgenus *Crawfordina* characterized by its large size, high spire, convex whorls, and sharp clathrate sculpture. It is remarkably similar to the type species of *Crawfordina*, *C. crawfordiana* from California (Fig. 54). The latter species has a more fibrous periostracum, is somewhat more slender and smaller (attaining a length of about 50 mm), has a slightly more constricted tip to the canal, and has fine pustules on the anterior region of the columellar callus. Despite these dif-

ferences, the two species are clearly related, having similar proportions, sculpture, and the columellar plications visible in oblique view. *Cancellaria io*, the third member of the subgenus, differs from both *C. stuardoi* and *C. crawfordiana* in having subdued spiral sculpture.

ETYMOLOGY. We are pleased to name this species in honor of Dr. Jose Stuardo of the Universidad de Concepción, Concepción, Chile.

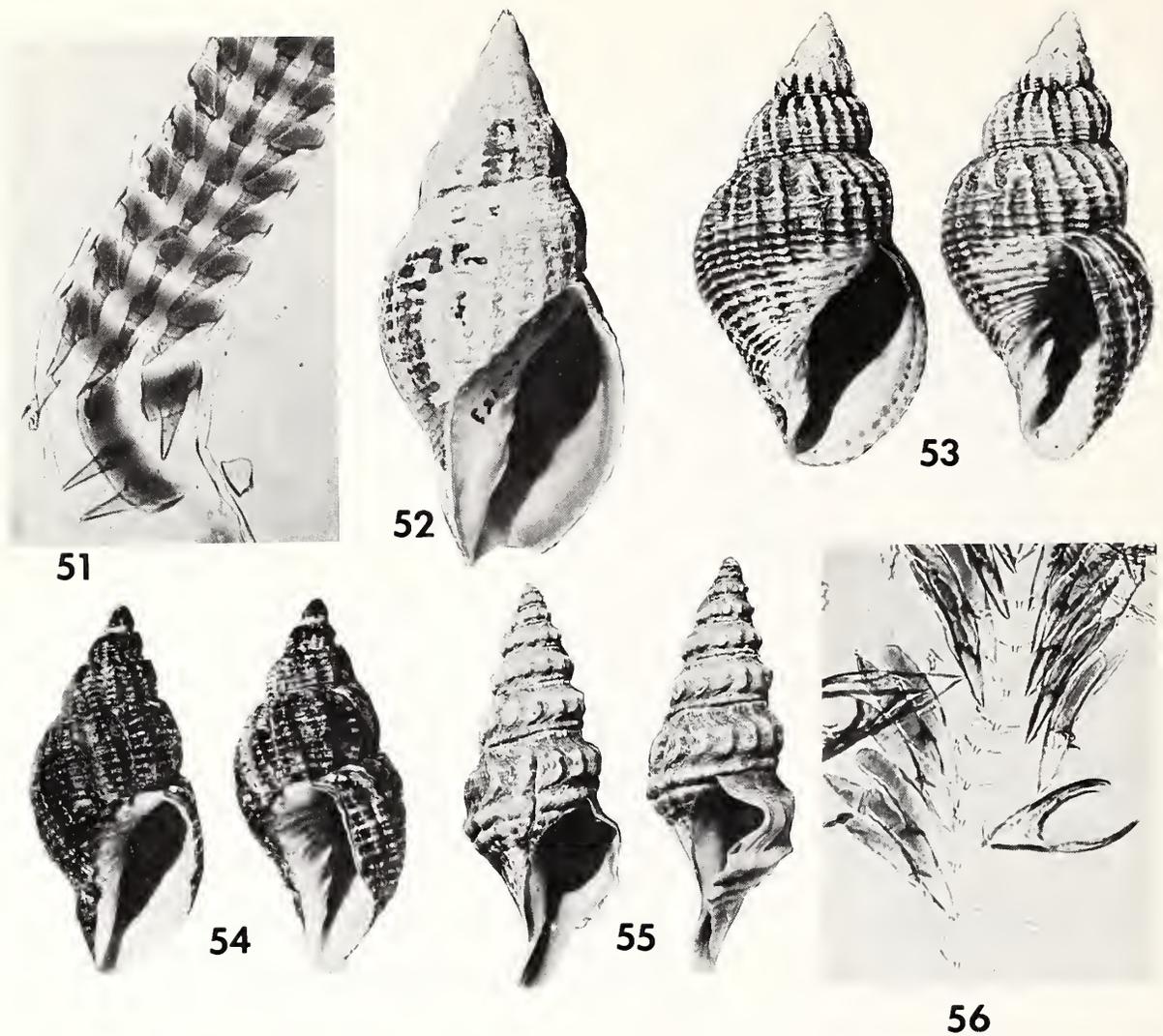
Superfamily Conacea

Family Turridae

Subfamily Turrinae

Genus *Ptychosyrinx* Thiele, 1925

Type species (original designation): *Pleurotoma (Subulata) bisinuata* Martens, 1901. Recent, East Africa.



Figures 51 through 56, *Miomelon alarconi*, *Cancellaria stuardoi*, *C. crawfordiana*, and *Ptychosyrinx chilensis*.

Figures 51 and 52, *Miomelon alarconi*. Figure 51, radular ribbon, LACM 73502, 200-400 m off Coquimbo, Chile, width of field 0.6 mm. Figure 52, LACM 66-153, 290-450 m off Cabo Carranza, Chile, height 74.9 mm.

Figure 53, *Cancellaria stuardoi* new species, two views of holotype, LACM 1988, 240-350 m off Pichilemu, Chile, height 61.3 mm.

Figure 54, *Cancellaria crawfordiana*, two views, LACM 72505, 50-100 m off Redondo Beach, California, height 49.8 mm.

Figures 55 and 56, *Ptychosyrinx chilensis*. Figure 55, two views, LACM 72506, 350 m off Pichilemu, Chile, height 42.4 mm. Figure 56, radula ribbon, LACM 72506, same locality, width of field 0.4 mm.

Ptychosyrinx chilensis is the only eastern Pacific member of its genus, a member of the subfamily Turrinae, in which the excurrent sinus is located at the peripheral keel (see Powell, 1966; McLean, 1971). According to Powell (1966), other species occur in the "deep ocean basins of the Indian Ocean, Natal, East Africa and the East Indies, the north Atlantic, off Bermuda." Hickman (1976) illustrated *P. chilensis* and recorded species of *Ptychosyrinx* from the Oligocene of Oregon.

Ptychosyrinx chilensis Berry, 1968

Figures 55, 56

Ptychosyrinx chilensis Berry, 1968:158; Hickman, 1976:89, pl. 7, figs. 1, 6.

DESCRIPTION. Shell moderately large, length of aperture and canal less than half the length of the shell; color light brown under a fine brown periostracum; shoulder concave, growth line deeply sinuate, periphery marked by strong axial projections, about 15 per whorl; base with three strong spiral cords, the posteriormost retained just above the suture; fasciole with more subdued spiral sculpture.

Dimensions: height 42.4 mm, diameter 15.8 mm (Fig. 55).

Radula (Fig. 56): rachidian rectangular, unicuspid; marginals of "wishbone" type. This is typical for the genus as described by Powell (1966).

MATERIAL. Chile: Punta Mar Brava (LACM), Punta Hornos (LACM), Coquimbo (LACM), Punta Panulcillo (LACM), Bahia Navidad (LACM), Pichilemu (LACM, Fig. 55), Cabo Carranza

(LACM). Specimens examined: more than 100.

TYPE MATERIAL AND TYPE LOCALITY. Holotype, LACM 1912. Type locality: "about 200 fms.," (366 m) off Coquimbo, Chile.

DISTRIBUTION. Punta Mar Brava (29°21'S) to Cabo Caranza, Chile (35°27'S). Depth range: 65–400 m.

REMARKS. *Ptychosyrinx chilensis* resembles the type species of *Ptychosyrinx* but has stronger spiral sculpture on the base and lacks the sinuate projection of the lower lip of that species.

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