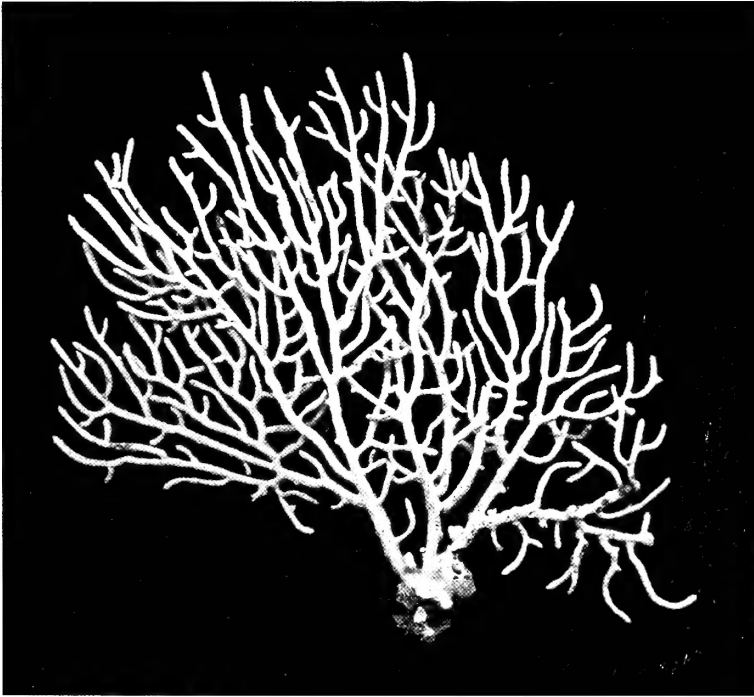


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**The genus *Hymerhabdia* Topsent, 1892 (Porifera:
Halichondrida: Axinellidae) with some remarks on related genera**

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Abstract.—The genus *Hymerhabdia* hitherto contained the species *H. typica*, *H. oxytrunca*, *H. intermedia*, *H. contracta*, *H. papillosa* and *H. topsenti*. Based on our material, a new species is described, *Hymerhabdia diversicolor*, and *H. typica* and *H. papillosa* are redescribed. Moreover, it is proposed to synonymize *H. oxytrunca* and *H. typica*, and to assign *H. topsenti* to the genus *Bubaris*. The new species, *H. diversicolor*, is distinguished by having very particular anisodiametric oxeads, that is, one half tapering to a sharp lanceolate point, the other half uniformly thick and abruptly ending in a tip. This feature clearly distinguishes the species from other known species. The affinity of *Hymerhabdia* to other closely related genera such as *Axinyssa*, *Collocalypta* and *Bubaris* is discussed based mainly on their different types of spicules and choanosomal skeletons. *Hymerhabdia* and *Collocalypta* have a clearly plumose choanosomic skeleton, which consists of erect plumose columns of spicules in *Hymerhabdia*, from which spicule tracts in *Collocalypta* diverge. In the other genera the choanosomal skeleton is disorganised with spicules strewn in confusion and/or composed of vaguely ascending tracts in *Axinyssa*, and with a condensed reticulation of flexuous or vermiform strongyles, with projecting bundles or individual styles ascending to the surface in *Bubaris*.

Hymerhabdia is a small genus with species with a typically littoral Atlanto-Mediterranean distribution (Sarà & Siribelli 1962, Pouliquen 1972, Juan 1987). The genus was erected by Topsent (1892) to include encrusting sponges with a choanosomal skeleton that consists of erect plumose columns of spicules, with centrotylote oxeads sharply curved at the middle and rhabdostyles (Topsent 1904), although the most typical spiculation is formed by long styles that are sometimes sinuous and shorter oxeads (Bergquist 1970). The diagnosis of the genus has been expanded a few times to include a new external morphological characteristic (with vertically ascending projections) (Sarà & Siribelli 1962), or some spicular type previously not found (rhabdos-

trongyles, strongyles) (Sarà & Siribelli 1960, 1962). In material from the Strait of Gibraltar (Southern Iberian Peninsula), we found a new species for the genus characterized by having anisodiametric oxeads which have one-half their length of the same width, and the other half progressively decreasing in width towards a fine or lanceolated point. Besides the new species, there are six others: *H. typica* (Topsent 1892), *H. oxytrunca* (Topsent 1904), *H. topsenti* (Lévi 1952), *H. intermedia* (Sarà & Siribelli 1960), *H. contracta* and *H. papillosa* (Sarà & Siribelli 1962), which share many characteristics with the family Axinellidae, in this work considered to be part of the order Halichondrida (van Soest et al. 1990). Moreover, some species of *Bubaris*,

such as *Bubaris salomonensis* (Dendy 1921) and *B. oxeata* Dendy (1924), were transferred to the genus *Hymerhabdia* by Topsent (1928).

This study seeks to clarify the differences between the known species of *Hymerhabdia*, which allowed a new species to be recognized, and the relation of this genus to related genera such as *Axinysa*, *Collocalypta* and *Bubaris*.

Material and Methods

The specimens were collected by scuba diving off the Iberian coast of the Strait of Gibraltar and preserved in 70% alcohol. Spicule preparation followed the techniques described by Carballo (1994). The new species has been deposited in the Museo Nacional de Ciencias Naturales in Madrid (Spain) (MNCN). Paratype and spicule slides have been deposited in the Laboratorio de Biología Marina (LBM) of the Universidad de Sevilla (Spain). Specimens of other species and genera studied include material collected by the author and material from the museum. The holotype of *Collocalypta digitata* (type-BMNH 1907:2:1:89) has been examined.

Results

Familia Axinellidae Ridley & Dendy,

1887

Hymerhabdia Topsent, 1892

Diagnosis.—Encrusting Axinellidae, sometimes with vertically ascending projections. The spiculation is formed by styles, oxeas, which are frequently centrotylotes or widely curved, rhabdostyles and/or rhabdostrongyles. Modifications of some spicules, such as tylostyles and strongyles also can appear. Without microscleres. There is no ectosomic skeleton. The choanosomic skeleton consists of erect plumose columns of spicules which are continued through the ectosome as loose tufts, which may project beyond the surface.

Hymerhabdia diversicolor, new species
Figs. 1, 2, 5, 6; Table 1

Diagnosis.—*Hymerhabdia* with erect projections. The skeleton in the base consists of tylostyles with the heads on the substratum, from which arise erect plumose columns of spicular bundles (oxeas and styles) that protrude through the surface as small tufts. The spicules are anisodiametric oxeas almost evenly wide for one-half their length, and progressively narrower, ending with a fine or lanceolated point.

Material examined.—Two specimens from Isla de Tarifa (Tarifa), 36°01'8"N, 5°36'22"W, 13 Jul 1995, depth between 10 and 12 m, in small caves. Holotype and spicule slides ref. n° MNCN 1.01/183, Paratype and spicule slides ref. n°s LBM-641 and LBM-642. Type locality. Isla de Tarifa (Strait of Gibraltar, Spain). Coll. J. L. Carballo.

Description.—Sponge consisting of a flat, wide-spreading, encrusting base, about 2–6 mm thick, with a maximum extension of 2.2 by 4.6 cm in the holotype and 2.1 by 4.1 in the paratype, from which erect processes arise. These processes have a length between 0.5 and 2.2 cm, and measure 0.4 cm in diameter at the middle. They usually taper to a sharp apex and are unbranched. The surface of the basal crust is smooth between the processes, but spicule bundles protrude through the surface as small tufts giving it a hispid appearance, without conules. Ectosome conspicuous, translucent, easily detachable from the choanosome. The digitiform processes have a slightly conulose surface with spicule bundles that protrude through the surface. Oscules inconspicuous. The colour in life is white in the holotype and orange in the paratype, and whitish in alcohol (both).

Spicules: The most abundant are anisodiametric oxeas, with one half of constant width and abrupt point, and the other half tapering toward a fine or lanceolated point (Fig. 1A). Oxeas can be straight, slightly curved or even flexuous; at the wider end

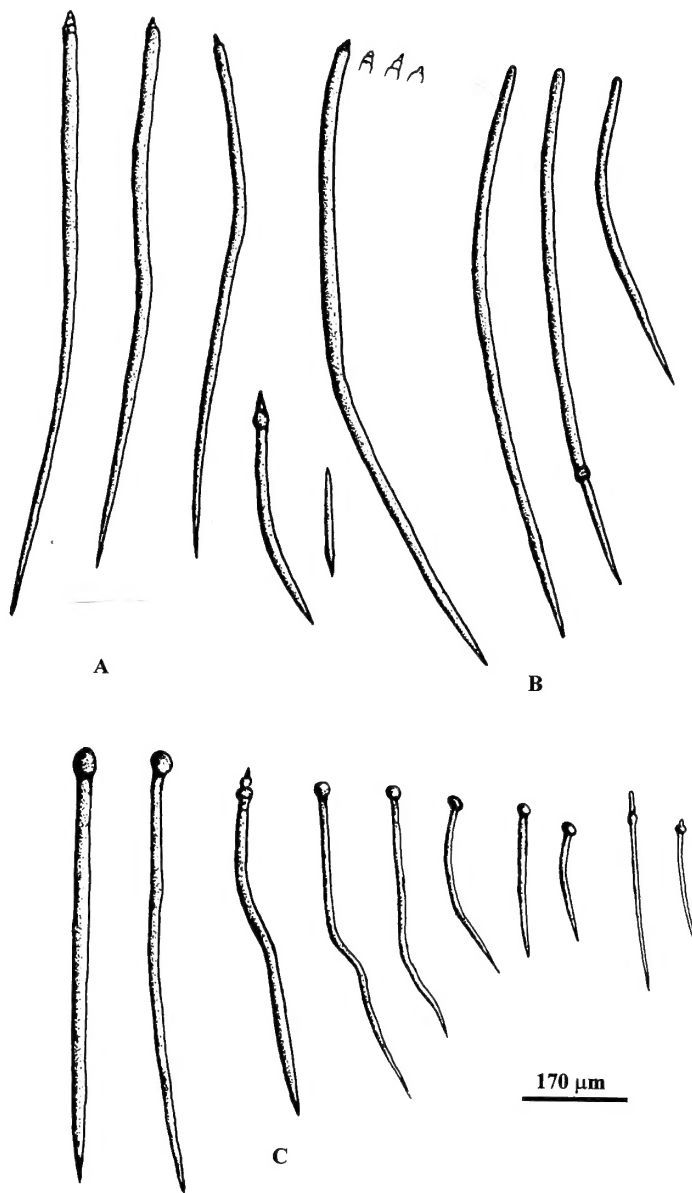


Fig. 1. Spicules of *Hymerhabdia diversicolor*. A) Anisodiametric oxeas. B) Styles. C) Tylostyles.

a series of modifications may appear, most frequently ribbing or successive swelling. Styles are also very frequent, slightly curved (Fig. 1B). Tylostyles are less abundant, with a well formed tyle, straight or curved stem, sometimes at different angles (Fig. 1C).

Skeleton: The skeleton in the basal crust consists of erect plumose columns of oxeas

and styles (Fig. 2), which are continued through the ectosome as a loose tuft, and the apices of these spicules (1–4 spicules) project beyond the surface (Fig. 5F). Sometimes only the basal layer of spicules, which are in bundles, can be observed, from which thin columns of spicules rise to the exterior (Fig. 5E). In the digitiform processes, we find an axial core of spicules,



550 μ m

Fig. 2. Cross section of body of *Hymerhabdia diversicolor*.

from which numerous loose bundles of spicules radiate obliquely outwards and upwards into the surface conuli, beyond which their apices may project (Fig. 6D). There is no ectosomal skeleton.

Etymology.—The proposed name *diversicolor* is from the Latin, *diversus*, in allusion to the two colours observed among the specimens of the species.

Ecology.—The new species has been observed only in Isla de Tarifa (South Iberian Peninsula) where it is relatively common. It is always located on the floor of sub littoral caves with high or moderate silting and with very good water renewal. The white form is more common than the orange. Color is a variable aspect in sponges whose significance is not entirely clear (Sarà 1993); both color types appearing close together could be related to the distribution of light at a micro-scale.

Hymerhabdia typica Topsent, 1892

Fig. 3; Table 1

Hymerhabdia oxytrunca Topsent, 1904

Material examined.—LBM-14, 9 Jul 1990, 15 m, depth, Isla de Tarifa (Strait of Gibraltar, Spain), coll./det. J. L. Carballo.

Description.—Encrusting sponge 1 cm maximum thickness, with numerous cone-shaped projections (2 to 3 mm high), maximum surface area of 2.3 by 1.4 cm. Ectosome not detachable. Oscules have not been observed. Consistency soft, surface hispid. Colour dark orange in life.

Spicules: Styles straight, or slightly curved, sometimes modified to subtylostyles or tylostyles (Fig. 3H). Rabdostyles sharply curved, frequently thickly ribbed and spiny at one end (Fig. 3G). Centrotylote oxeas, some sharply curved, even V-shaped, sometimes with distal microspines (Fig. 3E, 3F).

Skeleton: Vertically-ascending plumose bundles of styles and rabdostyles, giving it a hispid exterior aspect.

Remarks.—By studying *H. typica* material from the Strait of Gibraltar and review-

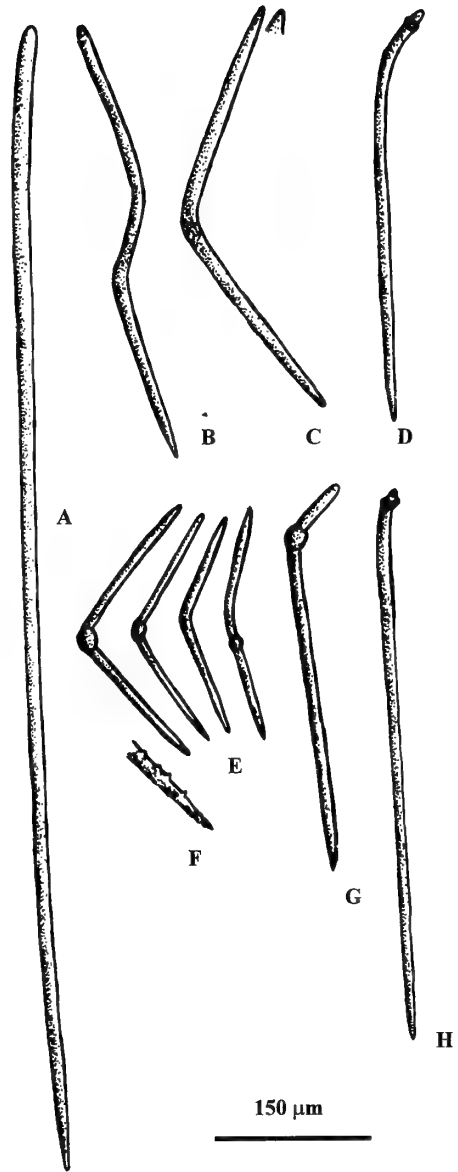


Fig. 3. Spicules of *H. papillosa* (A–D) and *H. typica* (E–H). A–B) Style. C) Oxea. D) Rabdostyle. E) V-Oxeas. F) microspinated oxea. G) Rabdostyle. H) Style.

ing the bibliography on the dimensions and spicule types of *H. typica* and *H. oxytrunca*, an overlap between the species is observed. Both species bear the same spicule types (rhabdostyles, oxeas and styles/subtylostyles), have the same particular characteristics (sharply curved oxeas and rhabdostyles)

(Vacelet 1969), and spicule sizes overlap (Topsent 1904, Sarà & Siribelli 1960, Vacelet 1969, Carballo & García-Gómez 1995) (Table 1). This led me to believe that they could be the same species, and therefore *H. oxytrunca* should be considered a synonym of *H. typica*.

Distribution.—Atlanto-Mediterranean

Hymerhabdia papillosa Sarà & Siribelli, 1962

Fig. 3, 4, 6; Table 1

Material examined.—LBM-45, 10 Feb 1991, 15 m depth, Isla de Tarifa (Strait of Gibraltar, Spain), coll./det. J. L. Carballo, and LBM-Q6, 8 Jan 1993, 15 m depth, Isla de Tarifa (Strait of Gibraltar, Spain), coll./det. J. L. Carballo.

Description.—Encrusting body 0.9 cm thick, from which irregular projections rise vertically up to 1.2 cm high. Maximum substratum coverage of 3.3 by 2 cm. Consistency is soft, surface hispid. Colour is yellow in life.

Spicules: Styles are thin, straight or slightly curved (Fig. 3A). Shorter and thicker styles, curved slightly at the base, resembling incipient rabdostyles (Fig. 3D). Oxeas curved at the center, with pointed ends, or occasionally one rounded end (Fig. 3B).

Skeleton: The spicules are arranged in somewhat dense plumose bundles in the choanosome (Fig. 4A). In the projections, the styles are arranged in tufts from which other styles and oxeas protrude, thus giving it a hispid exterior appearance (Figs. 3B, 6C).

Distribution.—Mediterranean Sea, between 15 to 70 m depth, floor of small littoral caves, and detrital bottoms.

Genera Associated with *Hymerhabdia*

Axinyssa Lendenfeld, 1897

Pseudaxinyssa Burton, 1931; *Axinomimus* de Laubenfels, 1936

Diagnosis.—Massive-amorphous or encrusting Axinellidae. Without ectosomal

Table 1.—Main spicular characteristics of species of *Hymerhabdia* close to *Hymerhabdia diversicolor*. The spicule ranges are the combined measurements of all authors (all spicule sizes in μm ; n.p. = not present).

	Tylostyles	Rhabdostyles	Rhabdostrongyles	Oxeas	Styles/substyles	Distribution
<i>H. typica</i>	n.p.	120–350 × 4–15 ^{1,2,4,7}	n.p.	Centrotylote, V-shaped 136–185 × 5 ^{1,2} .	275–1000 × 8–40 ^{1,2,3,4}	Atlanto-Mediterranean
<i>H. intermedia</i>	n.p.	n.p.	n.p.	Sharply Centrotylote, some modified in strongyles	130–1480 × 3.5–17 ⁵	Mediterranean
<i>H. contracta</i>	512–1600 × 6.2–10 ⁶	102.5–152 × 5–7.5 ⁶	37.5–55 × 7.5–10 ⁶	n.p.	n.p.	Mediterranean
<i>H. papillosa</i>	n.p.	90–350 × 3.7–6 ^{6,7}	n.p.	130–399 × 2.5–7 ^{6,7}	560–1920 × 4–12.5 ^{6,7}	Mediterranean
<i>H. diversicolor</i>	145–500 × 7–13	n.p.	n.p.	anisodiametric, 745– 1130 × 8–19	300–1040 × 7–18	Mediterranean

¹ Topsent 1892, ² Carballo & García-Gómez 1995, ³ Topsent 1904, ⁴ Vacelet 1969, ⁵ Sarà & Siribelli 1960, ⁶ Sarà & Siribelli 1962, ⁷ This work.

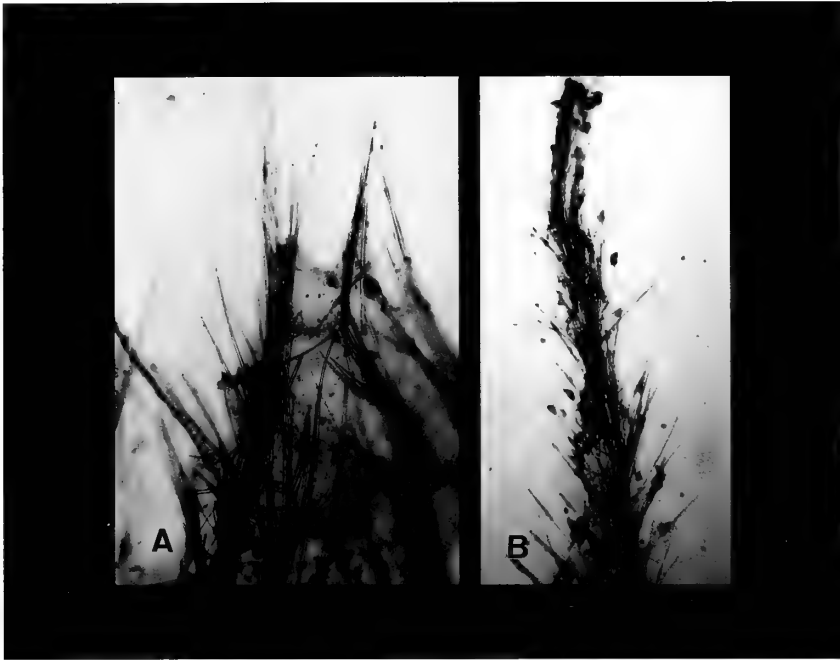


Fig. 4. Skeletal arrangement in choanosome (close to the surface) (A), and projections (B) in *Hymerhabdia papillosa*.

skeleton or with sparsely scattered spicules. Choanosomal skeleton disorganized with spicules strewn in confusion and/or composed of vaguely ascending, widely spaced vertical tracts of large oxeas, forming loose bundles, with spicule tracts protruding through surface to produce conules. Choanosome with poor or moderate spongin fibres but heavy collagen. Spicules oxeas, strongyloxeas or styles usually of only one size class (Soest et al. 1990, Carballo et al. 1996).

Collocalypta Dendy 1905

Figs. 5, 6

Diagnosis.—Axinellidae with fistulose habit and architecture. Ectosomal skeleton absent. Choanosomal skeleton highly collagenous, with a central column of spicules and diverging spicule tracts ascending to the surface, protruding slightly beyond the ectosome, and producing a finely conulose surface pattern. Spicules are oxeas (slightly modified from Soest et al. 1990).

Bubaris Gray, 1867

Ommatosa de Laubenfels, 1936

Diagnosis.—Axinellida with encrusting growth form. Choanosomal skeleton with a condensed reticulation of smooth flexuous or vermiform strongyles, sometimes only, or with straight oxeas, with projecting bundles or individual styles ascending to the surface.

Discussion

The new species, *H. diversicolor*, is mainly characterized by vertical projections from the body of the sponge and by the presence of the anisodiametric oxeas that have one-half of their length different from the other half. The most similar species in external morphology seems to be *H. papillosa* Sarà & Siribelli, 1962. However, its spicular characteristics are clearly different from *H. diversicolor*, as are all the known species of *Hymerhabdia*. Another species found in the Strait of Gibraltar is *H. typica*,

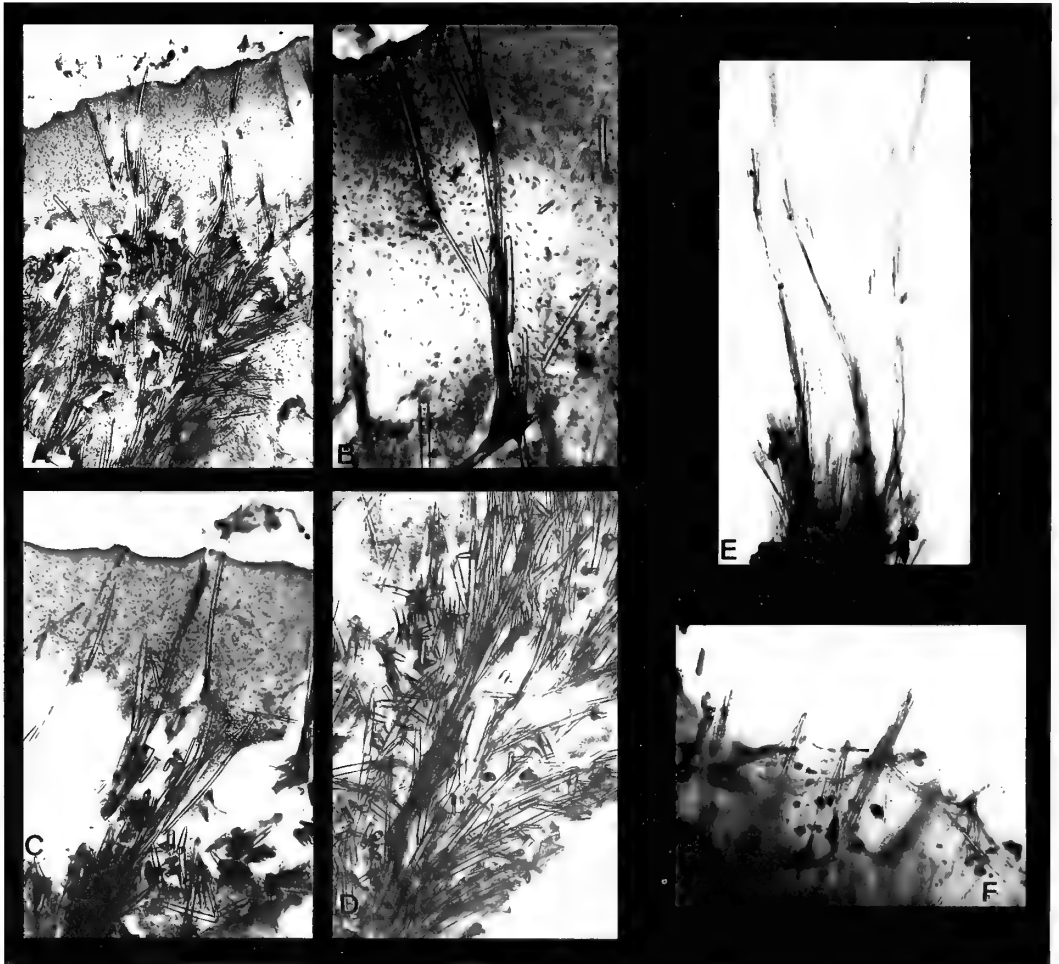


Fig. 5. *Collocalypta digitata* A) Cross section of choanosome. B) Detail of terminal spicule tuft. C) Terminal spicule tuft. D) Detail of erect plumose columns in the choanosome. *Hymerhabdia diversicolor* E) Cross section of choanosomal skeleton. F) Terminal spicule tuft.

which is clearly different from the previous species by having U and V-shaped centrotylote oxeas. The other two species, considered as valid for the genus, have exclusive spicular characteristics, strongyles that are not centrotylote in *H. intermedia* (Sarà & Siribelli 1960), and rabdostongyles derived from rabdostyles in *H. contracta* (Sarà & Siribelli 1962). Others species described in the genus *Hymerhabdia* such as *H. topsenti* Lévi 1952, or transferred to the genus *Hymerhabdia* by Topsent (1928), such as the species *H. salomonensis* (Dendy, 1921 as *Bubaris salomonensis*) and *H. oxeata* (Den-

dy, 1924 as *Bubaris oxeata*), can not be considered as valid species of *Hymerhabdia* because they lack erect plumose columns of spicules in the choanosomic skeleton. *Bubaris salomonensis* (Dendy, 1921) and *B. oxeata* Dendy (1924) have a skeleton consisting of a basal crust of short, interlacing oxea or strongyles, for the most part disposed horizontally, in which are inserted the bases of very numerous, rather close-set styles of various sizes, which project from the basal crust more or less perpendicularly, and match with the genus *Bubaris*. However, these species do not have flexuous or

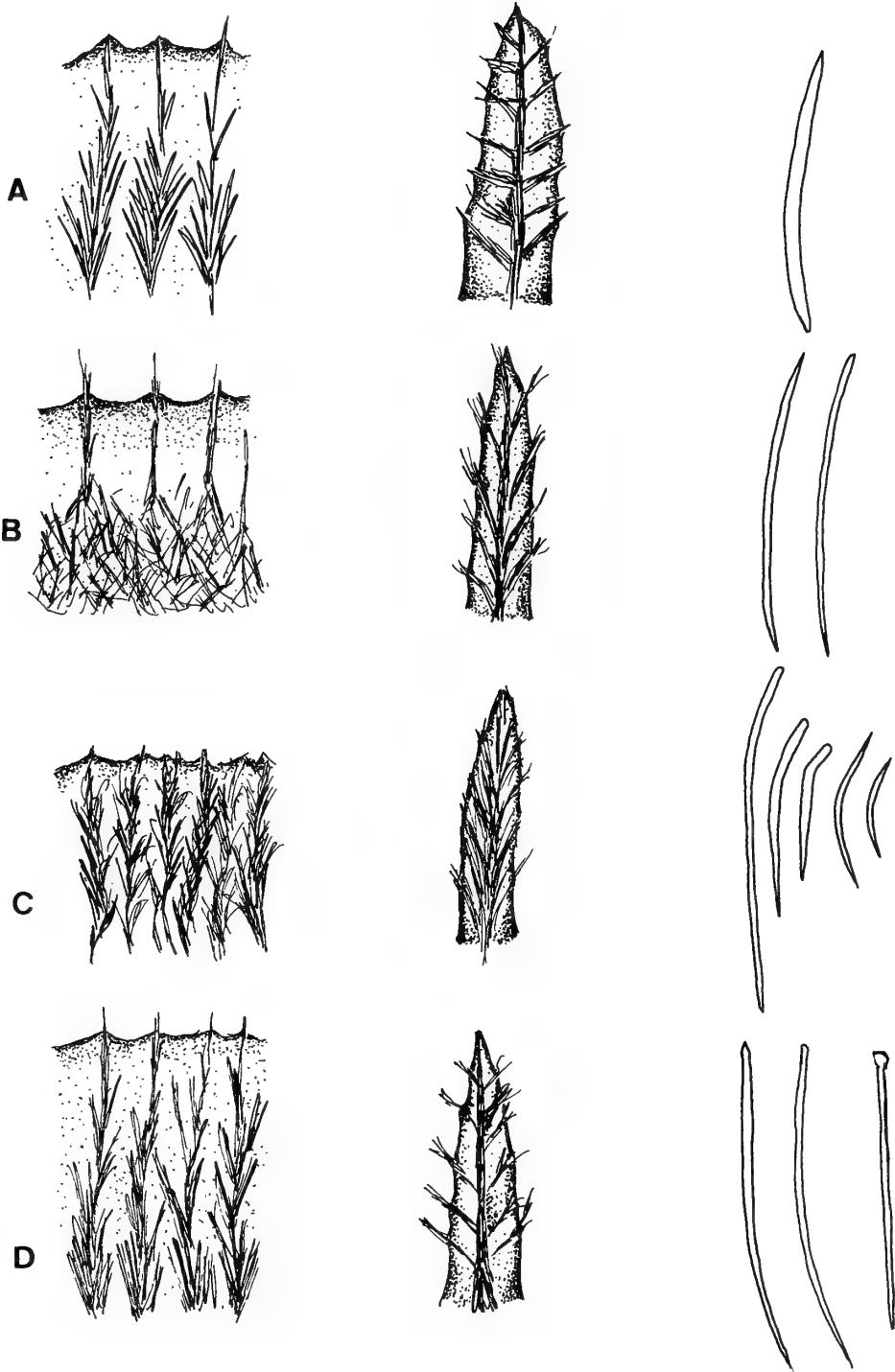


Fig. 6. Skeletal arrangement in choanosome, skeletal arrangement in the projections, and spicules in A) *Collocalypta digitata*, B) *Axynissa digitata*, C) *Hymerhabdia papillosa* and D) *Hymerhabdia diversicolor*.

vermiform strongyles, typical spicules of species of *Bubaris*. Laubenfels (1936) created the genus *Uplexoa* to include *Bubaris oxeata* with the following diagnosis: encrusting growth form; choanosome consists of a basally condensed reticulation of small oxeas lying on the substrate, with an extra-axial skeleton of long thick hastate styles perpendicular to the substrate, with their bases embedded in the basal skeleton and projecting through the surface. This genus is barely differentiated from *Bubaris* Gray, 1867, which has proper sinuous strongyles/oxea, and Lévi (1952) and Bergquist (1970) consider it as a doubtful genus. Later, Kobluk & Soest (1989) found a specimen which was assigned to *Hymerhabdia* sp. This specimen, together with *B. salomonensis*, *B. oxeata* and *Hymerhabdia topsenti*, seems to agree with the diagnosis of *Uplexoa*. In this sense, we suggest a new diagnosis for the genus *Bubaris* in order to include that species, or considering the validity of the genus *Uplexoa* for species of *Bubaris* without proper sinuous strongyles/oxea.

Other genera of the Axinellidae with encrusting body and erect processes similar to *Hymerhabdia* are *Axinyssa* Lendenfeld, 1897 (type species *A. topsenti*), and *Collocalypta* Dendy, 1905 (type species *C. digitata*). In the three genera, however, the skeletal arrangement in the choanosome is clearly different (Fig. 6). In *Axinyssa* there is a basal layer of somewhat disorganized spicules, which clump together into tufts as they rise to the surface and protrude through it (Carballo et al. 1996) (Fig. 6B). In *Collocalypta* the choanosomic skeleton consists of a basal portion of erect plumose columns of megascleres (Figs. 5A–D, 6A), but unlike *Hymerhabdia*, the columns are clearly differentiated, rising more than halfway up the body of the sponge, and transforming into a bundle with a few spicules protruding to the exterior (Fig. 5E, Fig. 6C–D).

On the other hand, the skeleton in the projections is similar in the genera *Axinyssa* and *Hymerhabdia* (Fig. 6). In the digitiform

processes, there is not an axial core of spicular fibre as in the genus *Collocalypta*, where there is a stout central axis from which loose bands of spicules radiate outwards almost perpendicularly. In the other genera, the spicules forming an axis expand obliquely to the exterior as a clear continuation of the axis.

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A new species of *Tethocyathus* (Cnidaria: Anthozoa: Scleractinia: Caryophylliidae), a trans-isthmian azooxanthellate species

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Abstract.—A new species of *Tethocyathus* is described, *T. prahli*, characterized by having a tympaniform corallum shape and no fossa. Specimens were found living at 310 m in the Colombian Caribbean, 303–333 m at Cocos Island (Pacific Costa Rica), and from the early Pleistocene of Pacific Panama, suggesting a relictual distribution of a previously more widespread species. *Tethocyathus prahli* is probably unique among the Scleractinia in having a non-cosmopolitan trans-isthmian distribution. The diagnosis of the genus *Tethocyathus* is emended to conform more closely to that of the type species.

The discovery of an undescribed species of *Tethocyathus* from the Colombian Caribbean and the same species from the Pleistocene of Pacific Panama raised interesting zoogeographic questions. In the course of writing the paper, several more specimens were discovered from the Recent of Cocos Island, reinforcing our zoogeographic interpretation. i.e., that living *T. prahli* represent a trans-isthmian relictual distribution of a moderately shallow-water azooxanthellate species that was more widely and continuously distributed in the early Pliocene of both ocean realms. It is one of the very few scleractinian corals to have an trans-isthmian distribution in relatively shallow water.

Abbreviations

BID: Banco Interamericano de Desarrollo.
COLCIENCIAS: Instituto Colombiano para el desarrollo de la Ciencia y la Tecnología, Francisco José de Caldas.

H:D: Ratio of height to maximum calicular diameter of a corallum.

INVEMAR: Instituto de Investigaciones

Marinas y Costeras “José Benito Vives de Andreis” (Santa Marta, Colombia).

SEM: Scanning Electron Microscope.

STRI: Smithsonian Tropical Research Institute, Panama.

USNM: United States National Museum, Washington, DC (now the National Museum of Natural History).

S_x , C_x , P_x : cycle of septa, costae or pali, respectively, designated by numerical subscript.

$S_x > S_y$: in the context of a septal formula, septa of cycle x are wider than those of cycle y.

Methods

Colombian specimens were collected using a bottom trawl of 9 by 1 m in aperture and 16 m length during INVEMAR Macro Fauna cruise 2 (Dec 1998). Pleistocene corals were collected as part of the Panama Paleontology Project. The Cocos Island specimens were collected on the *Johnson-Sea-Link* Galápagos/Cocos Islands Expedition of 1986, sponsored by the Harbor Branch Oceanographic Institute.

The holotype is deposited at INVEMAR,

paratypes at the USNM and INVEMAR. Paratype images were taken at the USNM using SEM; other images were obtained and processed using methods described by Reyes and Navas (in press).

Systematics

Order Scleractinia Bourne, 1900
Suborder Caryophylliina Vaughan and Wells, 1943
Family Caryophylliidae Dana, 1846
Genus *Tethocyathus* Kühn, 1933

Diagnosis (emended).—Corallum solitary, tympaniform to subcylindrical; attached through a polycyclic base. Septotheca costate, but covered with tectura. Paliform lobes before first cycle of septa; discrete pali before all but first and last cycle of septa. Columella papillose.

Type species.—*Thecocyathus microphylus* Reuss, 1871, by original designation.

Remarks.—The emended diagnosis of *Tethocyathus* is narrower than that given by Cairns (1979) in that it requires a polycyclic base and a thecal tectura (sensu Stolarski 1995 and Roniewicz & Stolarski 1999), both characters found in the type species. Of the three Recent western Atlantic species placed in this genus by Cairns (1979), only one fulfills these requirements: *T. cylindraceus* (Pourtalès, 1868). The other two species, *T. recurvatus* (Pourtalès, 1878) and *T. variabilis* Cairns, 1979, have monocyclic bases. Two additional species exist in the western Pacific: *T. virgatus* (Alcock, 1902) and *T. minor* (Gardiner, 1899). The genus is very similar to *Trochocyathus*, differing in having a polycyclic base, a relatively squat corallum, and tectura-covered theca.

The first cycle of entosepta (i.e., S_1) of *Tethocyathus* may give off one or two crowns of paliform lobes, pali being found before the succeeding entoseptum. The diagnostic character for *Trochocyathus* and *Tethocyathus* "pali before all but the last cycle of septa" (Vaughan & Wells 1943: 205–206, Wells 1956: F423) does not distinguish pali from paliform lobes; therefore,

we propose the diagnostic character be changed to: paliform lobes before first cycle of septa and pali before all but first and last cycles of septa.

Tethocyathus prahli, new species Fig. 1

Description.—Corallum tympaniform (H:D usually < 0.5) and firmly attached by an expanded base. Polycyclic base contains up to 5 visible concentric thecal rings: counting from the center of the holotype, rings 2, 3, 4 and 5 measure 1.12 mm, 1.92 mm, 2.42 mm and 2.97 mm in diameter, respectively. Initial ring can not be seen from above because it is covered by the columella; however, in other coralla the first ring is about 0.7 mm in diameter. Calice round to elliptical; calicular edge slightly serrate. Holotype measures 8.1 by 7.7 mm in calicular diameter and 2.5–3.7 mm in height (H:D = 0.46). Theca (tectura) smooth and bears scalloped growth lines. Inner costae (i.e., those not yet encircled by a thecal ring) thin, ridged, and not granular; outer costae (i.e., those occurring on surface of outermost thecal ring) broader and granular. C_{1-3} equal in size; C_4 thinner.

Septa hexamerally arranged in 4 cycles according to the formula: $S_1-S_2 > S_4 \geq S_3$. One paratype (i.e., the complete fossil and largest specimen, calicular diameter 13.8 by 12.0 mm, height 4.5 mm, H:D = 0.33: Fig. 1d) has 54 septa due to the presence of an extra half-system. S_1 and S_2 equal in size and extend 0.75 to columella; each S_1 bears a small paliform lobe and each S_2 bears a small pali. P_{1-2} small (0.34 mm wide) and occur closest to the columella; only one P_2 is wider (0.55 mm) than the others. S_3 slightly smaller or equal in width to S_4 , extend $2/3$ width of S_{1-2} , and bear a large pali. P_3 3 times wider (0.9 mm) than P_{1-2} , and are recessed from columella. Therefore, two palar crowns are formed: the inner crown formed by 6 paliform lobes (P_1) and 6 pali (P_2), and an outer crown of 12 P_3 . S_4 fuse by their axial edges to adja-

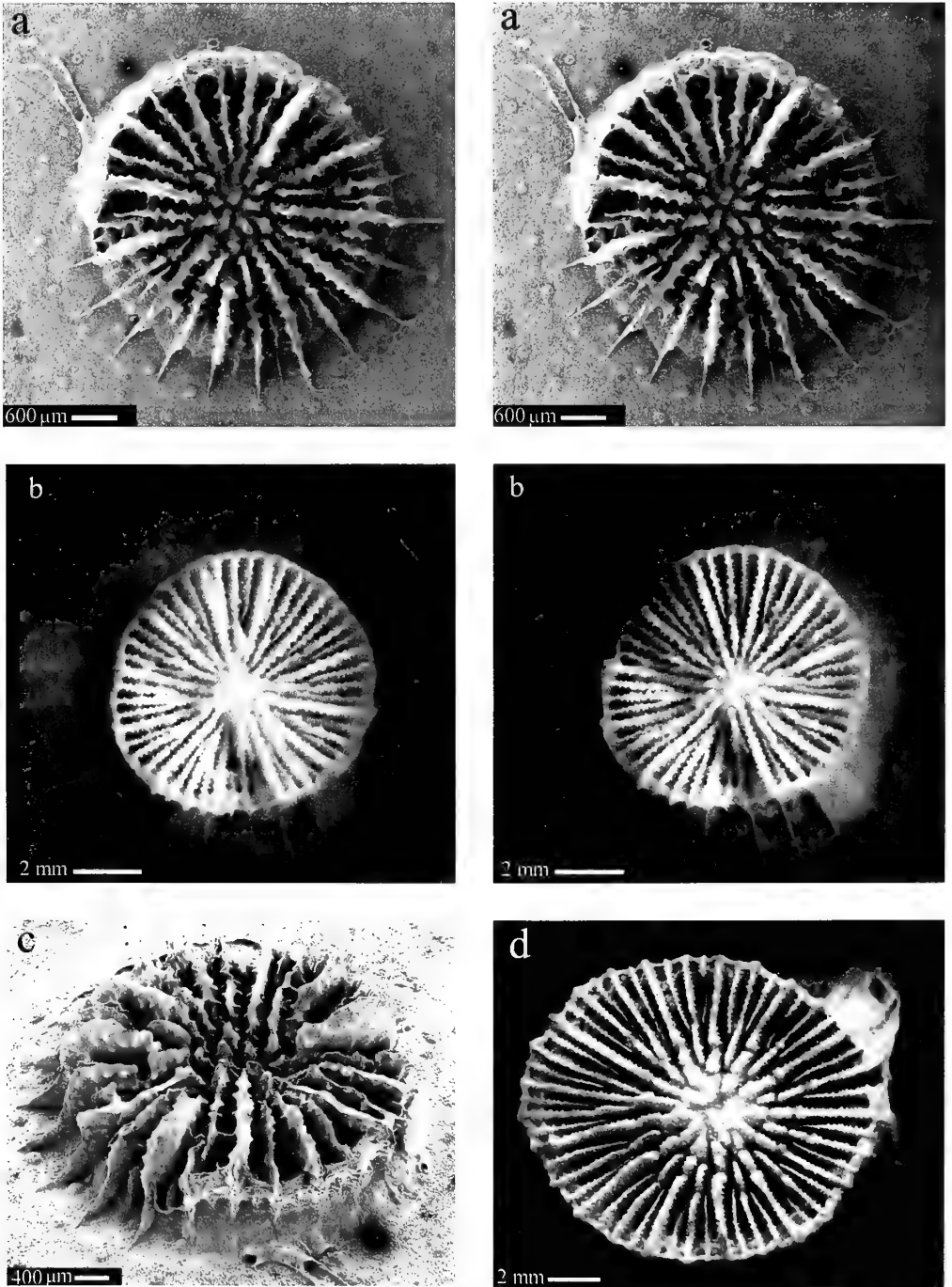


Fig. 1. a–d. *Tethocyathus prahli*. a, c. Recent paratype from Colombia, USNM 100469: a, stereo view of calice; c, oblique calicular view. b, stereo calicular view of holotype. d. Large paratype, Panama Paleontology Project site 148, USNM 95547, calicular view.

cent S_3 or P_3 . Inner edges of S_1 , S_2 and S_4 slightly sinuous; axial edges of S_3 more sinuous. Septal granules numerous, large, and blunt.

Fossa very shallow to non extant. Columella formed of fused papillae: massive and granular, appearing to incorporate part of the P_1 . Each P_{1-2} of fossil corallum have 2 or 3 lobes that extend and fuse to columella.

Discussion.—*Tethocyathus prahli* is quite similar to the type species, *T. microphyllus*, differing from it primarily in shape. *Tethocyathus prahli* has a lower, tympaniform corallum (the H:D ratio of *T. prahli* being between 0.3–0.5), whereas that of *T. microphyllus* is often above 2 and up to 3, i.e., subcylindrical. *T. prahli* also appears to have a larger corallum. *Tethocyathus microphyllus* was most recently described and illustrated by Stolarski (1991). It is known from the Middle Miocene (Badenian) of Poland, Moravia, France, and Morocco. Several voucher specimens from Poland are deposited at the NMNH (USNM 86810 and 96496).

Tethocyathus prahli also differs from *T. cylindraceus* (Pourtalès, 1868) in shape, the latter species being ceratoid to subcylindrical, with a H:D usually over 1. *Tethocyathus cylindraceus* also differs in having a shallow fossa and in having a very thick theca. It is known from the Caribbean (Straits of Florida, Jamaica, Barbados) at 183–649 m (Cairns 2000) and from north-eastern New Zealand (Cairns 1995).

The presence of purportedly the same species in two ocean systems (i.e., the Pleistocene of the eastern Pacific and the Recent of the Caribbean) that have been separated for 3.6–3.5 million years (Coates et al. 1992, Collins 1993), suggests both an evolutionary stasis of that species and the existence of that species in both oceanic realms (i.e., the Gatunian Province) before the closure of the isthmus. Indeed, Collins et al. (1996) logically argue that a deep-water species, such as *T. prahli*, would have been restricted from a trans-isthmian dis-

persal since at least 5.3 Ma. Petuch (1981, 1988:156), based on Neogene and Recent mollusk distributions, has shown there to be several relict pockets within the Caribbean, these faunas containing genera or species surviving from an earlier widespread Late Miocene to Pliocene Gatunian distribution that covered the eastern Pacific and Caribbean regions. One of these relict refugia, which he calls the “Venezuelan Secondary Relict Pocket”, contains several mollusk taxa previously thought to be extinct, and appearing “to be most strongly under the influence of temporal stasis”. The type locality of *T. prahli* lies within this region. We therefore suggest that *T. prahli* existed in the Gatunian Province in both the eastern Pacific and Caribbean in the early Pliocene about 5.3 Ma, freely communicating across the future land bridge when there was still a channel of 150–200 m (Collins et al. 1996). Between 5.3 and 3.5 Ma the genetic exchange was terminated due to the shallowing of the sill depth between the oceans. *Tethocyathus prahli* persisted to the Recent (at Cocos Island) and is documented from the early Pleistocene on the continental margin of the eastern Pacific (Panama), as well as surviving to the Recent in a relictual pocket off Colombia. However, based on so few specimens and the apparent lengthy isolation of the Atlantic and Pacific populations of this purported trans-isthmian species, it is not unreasonable to assume that the type material might represent a cognate species pair or components of a subspecies pair.

No reef corals are known to have a trans-isthmian distribution; however, at least seven azooxanthellate species occur in the Caribbean and eastern Pacific (Cairns et al. 1999). But, all of these species are cosmopolitan in distribution and occur at much greater depths than *T. prahli*. Another two azooxanthellate species appear to have a trans-isthmian distribution: *Madracis pharensis* and *M. asperula*. Both species are well known from both sides of the North Atlantic, and have been tentatively reported

from relatively shallow water (i.e., 16–343 m) from the eastern Pacific (i.e., Nazca Ridge, Chile; Galápagos; Colombia; Rocas Alijos; and Baja California), these occurrences reviewed by Bonilla et al. (1995). However, there is doubt about the identity of these two species with the Atlantic forms, the Pacific specimens always being reported as *Madracis* sp. cf. *M. pharensis*. Thus, *T. prahli* and perhaps two species of *Madracis* constitute the only records of non-cosmopolitan Scleractinia with a transisthmian distribution.

Etymology.—This species is named in honor of Henry Von Prah (1949–1989), who made significant contributions to the knowledge of Colombian corals (Ramos & Lemaitre 1991).

Types.—Holotype: INVEMAR Macro Fauna cruise 2, sta. 49, INVEMAR-COR 241. Paratypes: INVEMAR Macro Fauna cruise 2, sta. 49, 1 SEM stub, USNM 10046, and one corallum deposited at INVEMAR-COR 242. *Johnson-Sea-Link I-1943* (5°26'04"N, 87°07'59"W), Cocos Island, Costa Rica, 303–333 m, 2 Dec 1986, USNM 84868. Panama Paleontology Project site 047, 3 fragments, USNM 95546: eastern coast of Punta Burica, Pacific Panama (8°11'24.0"N, 82°52'34.1"W), 1 km south of supertanker dock, 16 Jan 1986 (Charco Azul Group, Armuelles Formation, early Pleistocene). Panama Paleontology Project site 148, 1 complete specimen, USNM 95547: eastern coast of Punta Burica, Pacific Panama (8°11'20.4"N, 82°52'33.5"W), near Q. Melliza, 21 Feb 1987 (Charco Azul Group, Armuelles Formation, early Pleistocene).

Type locality: INVEMAR Macro Fauna project, sta. 49: 11°05.26'–11°05.12'N; 75°15.33'–75°15.74'W, off Bocas de Ceniiza, Magdalena, Colombian Caribbean, 310 m.

Distribution and age.—Recent: known only from type locality off Colombia and Cocos Island (Costa Rica); 303–333 m. Fossil: early Pleistocene (Armuelles For-

mation, 1.7–1.5 Ma) of Punta Burica, Pacific Panama.

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***Anthopleura sola*, a new species, solitary sibling species to the
aggregating sea anemone, *A. elegantissima*
(Cnidaria: Anthozoa: Actiniaria: Actiniidae)**

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Abstract.—The Sunburst Anemone, a common inhabitant of rocky shores in central and southern California, is here designated as *Anthopleura sola*, new species. This large, conspicuous, solitary sea anemone was previously considered a non-clonal variant of the well-known, clonal Aggregating Anemone, *A. elegantissima*. Although polyps of these two species are similar in appearance and in cnidae, documented differences in population genetics, ecology, biogeography, development, and life history are evidence of a recently evolved sibling-species pair. Where the two species co-occur, they are readily distinguished in the field by differences resulting from their different life histories. In *A. elegantissima*, longitudinal fission results in aggregations of small polyps. *Anthopleura sola* does not divide and instead grows into larger, isolated individuals that have more often been confused with specimens of the Giant Green Anemone, *A. xanthogrammica*.

The sea anemone *Anthopleura elegantissima* (Brandt, 1835), abundant in the rocky intertidal of the northeastern Pacific, has long been recognized as including two sorts of individuals (Hand 1955)—some larger and solitary and some smaller and aggregated. A recent analysis of genetic variation in allozymes by McFadden et al. (1997) has confirmed earlier evidence (Francis 1979) that they belong to two distinct species. Here, we formally designate the solitary form as a new species.

In *A. elegantissima*, repeated episodes of longitudinal binary fission result in clonal aggregations of relatively small individuals. In the solitary polyps of the new species, fission does not occur, and larger, isolated individuals result (Hand 1955, Francis 1979). The presence or absence of fission in the life history yields animals that are readily distinguishable in the field by their

size and aggregated vs. solitary distribution (Fig. 1).

Despite some doubt that the name *A. elegantissima* is properly applied to the most common small intertidal anemone of California [see Cutress (1949) and Hand (1955) for discussion of problems with the original description], this name is so well established in the literature that it should be conserved for the clonal species. No grounds support using this name for the solitary species we are establishing.

Materials and Methods

Specimens of *Anthopleura sola* and *A. elegantissima* were collected at Soquel Point and the breakwater at the Santa Cruz Yacht Harbor, Santa Cruz County, California in summer and autumn, for analysis of cnidae. Cnidae were described (by LF) from both fresh and formalin-preserved

specimens selected to cover a broad range of individual sizes.

To measure cnidae, a sample of tissue was macerated mechanically in a drop of seawater and pressed into a thin layer between a slide and coverslip. Such smears were prepared from tentacles, acrorhagi, column, actinopharynx, and mesenterial filaments for 6 specimens of each species and examined using a light microscope with differential interference contrast optics at 1000 \times and oil immersion. Measurements were to the nearest 0.3 μm using an optical micrometer, and to the nearest 0.1 μm using a computer-linked video camera (image analysis) system.

Measurements were reported separately for cnida types from different parts of the body and also for any subsets that consistently showed strongly discontinuous, variation in shape or size (see 17 categories of data in Table 1). Each slide was scanned systematically (as described by Williams 1996), and the maximum length and width of individual capsules were measured (method of Hand 1954) to establish size ranges. All capsules were measured until the sample size for the most common types or shape variants of the cnidae reached at least 20. For the less common cnidae, an effort was made to measure at least 10. Finally, the slides were rapidly scanned in search of rare cnidae and also any of the more common ones that looked substantially larger or smaller than those already measured. Only clearly visible, intact, unfired capsules with their long axes lying roughly in the plane of the slide were measured.

Family Actiniidae Rafinesque, 1815

Genus *Anthopleura* Duchassaing & Michelotti, 1860

Anthopleura sola, new species

Figs. 1, 2

Morphology and development.—Hand (1955) included *Anthopleura sola* in his thorough description of *A. elegantissima*,

characterizing the shape and coloration of the animals (including the mouth, oral disc, tentacles, column with acrorhagi and verrucae, and pedal disc) and the histology and internal anatomy (including the arrangement of mesenteries, the shape and position of muscles and gonads, the nature of epithelial layers and mesoglea, and the size and distribution of cnidae).

Anthopleura sola shares the morphological characters of *A. elegantissima*, except that *A. sola* is non-clonal and its polyps are large, growing to ~20–25 cm across the tentacle crown. As they do not divide and lack fission scars, regularly arranged mesenteries are to be expected. Given the anatomical similarity between *A. elegantissima* and *A. xanthogrammica*, two well-recognized species with differences in external morphology and in cnidae, repeating Hand's histological work in a search for differences at the anatomical level between *A. elegantissima* and *A. sola* seems unwarranted. No differences between *A. sola* and *A. elegantissima* emerged from our study of cnidae (see below).

Polyps of *A. sola* occur as separate male and female individuals, as do clones of *A. elegantissima*. Females of *A. sola* were observed to spawn (in June, in a large outdoor tank, Santa Cruz, California) at the same time as those of *A. elegantissima*, and the gametes of both species were similar in size and appearance (J. S. Pearse, pers. comm.). Annual sexual reproduction has been studied only in *A. elegantissima* (e.g., Ford 1964, Jennison 1979, Sebens 1981), which is not an asexual lineage or in any way less sexual than *A. sola*, but a normal, sexual species whose individuals grow by replication of many small polyps (e.g., Tsuchida & Potts 1994). The polyps of a clonal aggregation, though disconnected, are comparable to the many polyps of a growing coral colony, in that both result from the development of a unique zygote and represent the growth of one genetic individual (see Pearse et al. 1989, Wasson & Newberry 1997). In contrast, individuals of *A. sola*



Fig. 1. A large solitary specimen of *Anthopleura sola*, new species, about 12 cm across the crown of tentacles, surrounded by a clonal aggregation of *A. elegantissima* in the intertidal at Soquel Point, Santa Cruz, California. (Courtesy J. S. Pearse)

grow into a single large polyp—a major morphological and developmental difference from *A. elegantissima*. The separate identities of the two species are further reinforced by ecological differences and confirmed by evidence for genetic differences (see Discussion).

Cnidom.—Spirocysts, holotrichs, basitrichs, and microbasic p-mastigophores.

Size and distribution of cnidae.—The shapes of the cnidae and their locations within the polyp were the same for *Anthopleura sola* and for *A. elegantissima*. Besides those listed and illustrated by Hand (1955:57–59), we distinguished a third category of relatively rare acrorhagial holotrichs (Fig. 2a, b; a, b in Table 1), especially in the tips of smaller, poorly developed acrorhagi. These were similar to the common,

more slender ones described by Hand (1955, fig. 13D) but most were shorter and more strongly tapered; the tubule, close to its apical point of attachment with the capsule, was more tightly coiled. Like Hand (1955), we identified basitrichs of two shapes in the pharynx, one a slender cylinder of uniform width (Fig. 2c, d), the other typically not of uniform width, often with a bulbous swelling either in the middle or at the base (Fig. 2e, f). In our material, however, the slender cylindrical one was shorter, the bulbous one longer (Table 1)—proportions differing from those recorded by Hand (compare fig. 13J and 13I, respectively). Individual bulbous capsules varied considerably in shape.

For each of our 17 categories of data, size ranges were overlapping but different

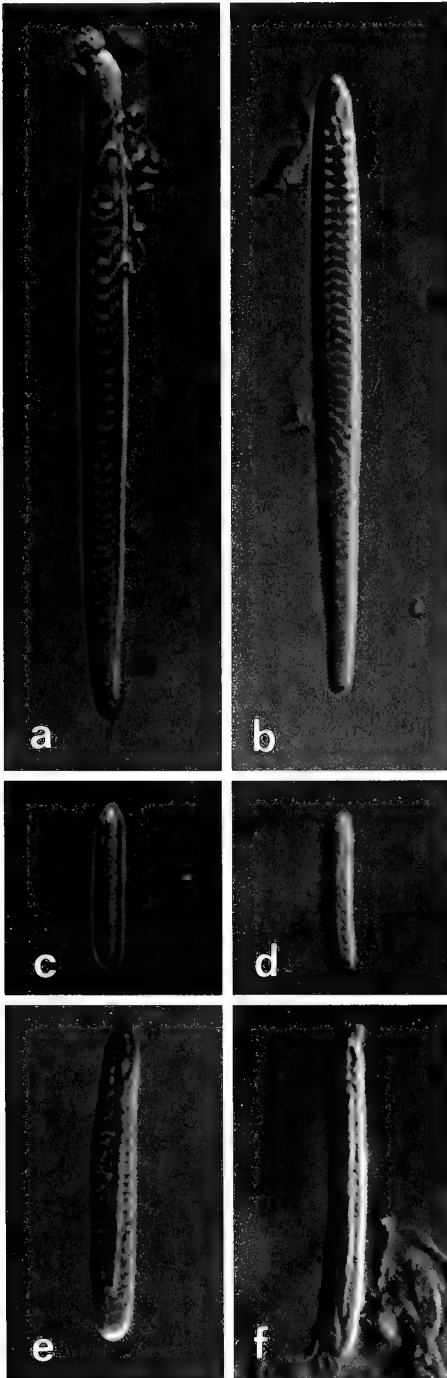


Fig. 2. Some nematocysts found both in *Anthopleura sola*, new species (left: a, c, e) and in *A. elegantissima* (right: b, d, f), photographed at 1000 \times magnification. All at the same scale (scale bar, 10 μ m) and shown with the apex (tubule-bearing end of the capsule) uppermost. (a, b) An acrorhagial holotrich

in the two species (Table 1). Both maximum length and minimum length were greater in *A. sola* than in *A. elegantissima* for 13 of the 17. Polyps of *A. sola* are typically larger than those of *A. elegantissima*: wet weights for specimens of *A. sola* examined were 56.3 ± 74.8 (mean \pm SD, range 2.03–205 g) and for *A. elegantissima* 2.17 ± 2.61 (mean \pm SD, range 0.04–5.93 g). The subtle differences in the size ranges of cnidae reported here seem to relate mostly to polyp size and, consequently, are probably not useful as diagnostic characters for separating these two species.

Type material and locality.—*Anthopleura sola*, new species. Holotype: One solitary polyp, found isolated from any others. Pedal disc, 4 \times 7 cm. Collected 30 Dec 1998 in the mid-intertidal zone at Soquel Point, Santa Cruz, California (36 $^{\circ}$ 57.15'N, 121 $^{\circ}$ 58.29'W) by Vicki Pearse. Holotype (CASIZ 116500) preserved in seawater formalin and deposited in the collections of the California Academy of Sciences, Dept. of Invertebrate Zoology, Golden Gate Park, San Francisco, California 94118, USA. Paratypes, all collected on the same date at the type locality. Deposited at the CAS: two paratypes preserved in seawater formalin (CASIZ 116501 and 116502) and two paratypes preserved in ethanol (CASIZ 116503 and 116504). Deposited at the Santa Barbara Museum of Natural History, Dept. of Invertebrate Zoology, Santa Barbara, California 93105, USA: one paratype preserved in seawater formalin (SBMNH 345318) and one paratype preserved in ethanol (SBMNH

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different from both of the more common ones illustrated by Hand (1955, fig. 13D, E). (c, d) The shorter of our two categories of pharyngeal basitrichs, the capsule a slender cylinder of uniform width, although sometimes curved, as in 2d. (e, f) The longer and more common of our two categories of pharyngeal basitrichs, the capsule typically not of uniform width, many with a bulbous swelling (e.g., bottom of 2f). In smears, the cnidocyte often formed another conspicuous bulge at the capsule apex (top of 2f).

Table 1.—Cnidae of *Aniopleura sola* and *A. elegantissima*. Ranges of lengths and widths of cnidae (17 categories of data by location within the polyp, shape, and size) in the tentacles, acrorhagi, column, actinopharynx, and mesenterial filaments. Samples: the ratio indicates the number of polyps in which each cnida was found out of the 6 polyps of each species examined; the second value indicates the number of capsules measured in all polyps. The uppercase letters A–P designate the corresponding 16 cnidae illustrated for *A. elegantissima* by Hand (1955), fig. 13. The lowercase letters a–f refer to our Fig. 2. The additional category of acrorhagial holotrichs was less common and not measured separately by Hand. The cnidae that were termed atrichs (Hand 1955) do bear minute spines along the thread and are considered to be holotrichs.

Categories	<i>Aniopleura sola</i>		<i>Aniopleura elegantissima</i>		Figure ref.
	Length × width (μm)	Sample	Length × width (μm)	Sample	
Tentacles:					
Spirocysts	13.0–35.0 × 2.0–4.0	6/6: 135	12.0–31.0 × 2.0–4.5	6/6: 120	A
Basitrichs	12.5–33.0 × 1.3–4.0	6/6: 135	14.0–28.5 × 2.0–3.0	6/6: 110	B
Acrorhagi:					
Spirocysts	22.0–45.0 × 2.0–4.0	6/6: 115	14.7–36.4 × 1.8–3.8	6/6: 85	C
Holotrichs	41.0–102.0 × 2.0–5.5	6/6: 135	38.0–89.0 × 2.5–5.0	6/6: 120	D
Holotrichs	59.0–104.0 × 4.8–10.0	6/6: 133	45.5–90.0 × 4.5–10	6/6: 102	E
Holotrichs	34.0–78.0 × 2.8–5.0	4/6: 15	27.7–64.0 × 2.3–4.8	5/6: 49	a,b
Basitrichs	10.0–20.5 × 1.5–3.0	5/6: 52	5.8–28.0 × 1.0–3.0	5/6: 50	F
Column:					
Holotrichs	19.0–28.0 × 3.0–4.0	2/6: 11	15.0–20.5 × 3.0–5.0	4/6: 15	G
Basitrichs	9.5–24.0 × 1.5–3.0	6/6: 135	7.5–16.5 × 1.5–3.3	6/6: 120	H
Actinopharynx:					
Basitrichs	6.0–27.0 × 1.0–3.0	6/6: 113	10.0–19.0 × 1.3–3.0	6/6: 109	I,J?, c,d
Basitrichs	19.0–31.0 × 1.8–5.0	6/6: 130	18.0–31.0 × 2.0–4.5	6/6: 118	I,J?, e,f
Microbasic p-mastigophores	20.0–30.0 × 3.5–6.5	6/6: 108	17.0–28.0 × 4.0–6.0	6/6: 108	K
Filaments:					
Basitrichs	8.5–23.0 × 1.0–3.0	5/6: 114	7.0–13.5 × 1.5–3.0	6/6: 90	L
Basitrichs	28.5–50.0 × 4.5–8.5	6/6: 131	22.0–42.0 × 4.5–9.0	6/6: 104	M
Basitrichs	20.0–33.0 × 1.0–1.5	3/6: 7	29.0–39.0 × 1.0–1.5	4/6: 27	N
Microbasic p-mastigophores	12.0–19.0 × 1.8–4.0	3/6: 7	13.0–30.0 × 2.0–4.5	6/6: 89	O
Microbasic p-mastigophores	20.5–34.0 × 3.8–7.0	6/6: 135	17.0–29.0 × 4.0–5.5	6/6: 120	P

345319). Deposited at the University of Kansas Natural History Museum, Lawrence, Kansas 66045, USA: one paratype preserved in seawater formalin (UKNHM 01208) and one paratype preserved in ethanol (UKNHM 01209).

For comparison, several voucher specimens of *Anthopleura elegantissima*, all collected on the same date and at the same site as the holotype and paratypes of the new species (see above), were also deposited in the collections of the CAS: One polyp from within a cohesive aggregation of many polyps, taken to be a clone because of the intimate contact and identical coloring of its members. Pedal disc, 3 cm. Preserved in seawater formalin (CASIZ 116505). Additional specimens from the same clone: three polyps preserved in seawater formalin (CASIZ 116506) and three polyps preserved in ethanol (CASIZ 116507); pedal discs, 2–3 cm.

Etymology.—From the Latin *sola* (“alone”), referring to the solitary, non-clonal condition, which distinguishes individuals of this species from polyps of the aggregated, clonal *A. elegantissima*. The species name *sola* relates also to the often strikingly pigmented mesenterial insertions and other radial, sun-like (Latin *sol*, “sun”) oral disc patterns, which distinguish the disc in this species from the typically unmarked, uniformly blue-green oral disc in *A. xanthogrammica*, which is also large and non-clonal. For *Anthopleura sola*, we recommend the common name “Sunburst Anemone.”

Previous references.—The other three northeastern Pacific species of *Anthopleura* (*A. artemisia*, *A. xanthogrammica*, *A. elegantissima*) are not being synonymized with the new species, but their names have often been misapplied to it. In the examples listed below, the specific pages and figures cited discuss or illustrate specimens of the new species presented under these older names.

Anthopleura artemisia (Dana, 1846:149–150).—Stephenson & Stephenson, 1972:

235. In a study of the Monterey Peninsula, carried out in 1947.—Hinton, 1987: 55–57, pl. 26.

Anthopleura xanthogrammica (Brandt, 1835:212)—Johnson & Snook, 1935: fig. 79, pl. IV. as *Cribrina xanthogrammica*.—MacGinitie & MacGinitie, 1949, 1968: fig. 16.—Hedgpeth & Hinton, 1961:42, fig. 24.—Hedgpeth, 1962:54 (figure).—Braun & Brown, 1966:22, 24–25.—Ricketts & Calvin, 1968: fig. 53.—Hinton, 1969:53–54, fig. 27, pl. 4. 1987: 55–57, fig. 27, pl. 24.—Snyderman, 1987:77, pl. A-3, no. 9.—Davis, 1991:63, pl. 68.

Anthopleura elegantissima (Brandt, 1835: 213). Only the larger, solitary individuals referred to in the following references belong to the new species.—Hand, 1955: 54–61; see discussion of synonymy, pp. 60–61. 1975:88, 90, 91.—Francis, 1973a, 1973b, 1979, 1988.—Pearse, 1981:216. This photo and the one of *A. xanthogrammica* on the same page illustrate the differences between these species.—Walsh, 1981a.—Annett & Pierotti 1984:204.—Ricketts et al., 1985: fig. 69 (same as fig. 53 in 1968 edition, relabeled.).—Smith & Potts, 1987.—Harris, 1991.—Gotshall, 1994: fig. 51. This photo and the one of *A. xanthogrammica* on the same page illustrate the differences between these species.—Barry et al., 1995:672, 673.—Snyderman, 1998:10 (figure).—Walton, 1998.—Sagarin et al., 1999.

Anthopleura sp. In both references listed here, this designation refers to the new species. McFadden et al., 1997. This study of >800 clonal and non-clonal specimens concluded that the two represent reproductively isolated taxa and referred to the latter as *Anthopleura* sp. throughout.—Secord & Augustine, 2000 also referred to *Anthopleura* sp.

Anthopleura sola.—Shick et al., 1996. The name was used as a nomen nudum in anticipation of its formal designation in the present paper and refers to large solitary

specimens of the new species collected by J. S. Pearse at the type locality.

Discussion

Distribution and interactions with other species.—*Anthopleura sola* tends to thrive in relatively sheltered positions and moderate climates. On a microhabitat scale, these sea anemones usually occupy protected places in quiet pools, at the bases of boulders, and in rock pockets and crevices, seldom on flat rock surfaces (Francis 1979, Harris 1991). Even when much of the pedal disc occupies a flat surface and can be relatively easily detached, a slender toe-like projection from the disc commonly retains a strong anchor-hold in a small hole in the rock (this study and L. G. Harris, pers. comm.), probably the cavity in which the young animal originally settled, long since outgrown. In the subtidal, and sometimes in the intertidal, the anemones are found attached to rocks in sand, the oral disc flush with the sand surface (Harris 1991). This species occurs typically in bays, but also on the open coast, in the middle to low intertidal and into the subtidal (Francis 1979), being found commonly to at least 10 m (Harris 1991, J. S. Pearse, pers. comm.). Its range is along the Pacific coast of North America at least from northern Mexico at Punta Banda, Baja California, to just north of San Francisco Bay at Doran Rocks near Bodega Bay, California (Francis 1979, McFadden et al. 1997).

Harris (1991) discussed possible effects on the species' distribution by predators, which include the sea star *Dermasterias imbricata* and the nudibranch *Aeolidia papillosa*. The large polyps of *A. sola* appear to have an advantage over the smaller ones of *Anthopleura elegantissima*, which are more successfully approached and attacked by these predatory species. Large size is probably the critical factor that permits *A. sola* to occupy subtidal depths that are beyond the vertical range of *A. elegantissima*. Annett & Pierotti (1984) described numerous

occasions on which an "exceptionally large" individual (= *A. sola*) repelled attacks by *D. imbricata*, whereas small individuals of *A. elegantissima* were more readily devoured. Small individuals of the nudibranch *Aeolidia papillosa* thrived when feeding on *A. elegantissima* but could not be raised on *A. sola*; they stopped eating and died (L. G. Harris, pers. comm.). In the subtidal, individuals of *A. sola* surrounded by sand may be partially protected from sea-star predation, but can suffer predation by larger individuals of *A. papillosa* (see Harris 1991).

Zooxanthellae occur as endosymbionts in *A. sola*, as they do also in *A. elegantissima* and *A. xanthogrammica* throughout their ranges. We know of no instance of zoochlorellae occurring in *A. sola*, and, on the basis of the virtually non-overlapping distribution of this anemone species with that of the green symbionts, we do not expect zoochlorellae to be found in this species. The southern limit so far observed for symbiotic zoochlorellae in *A. xanthogrammica*, the area of Bodega Bay and nearby Dillon Beach, corresponds to the northern limit of *A. sola*, and the southern limit observed for zoochlorellae in *A. elegantissima* is central Oregon (Secord 1995, Secord & Augustine 2000). South of these limits, zooxanthellae are the only photosynthetic microalgae symbiotic in *A. xanthogrammica* and *A. elegantissima*. The striking coincidence of the northern limit of *A. sola* and the southern limit of zoochlorellae may hold significant clues to the biology of both the sea anemones and the symbionts.

Similar species.—Three other species of *Anthopleura* are recognized within the range of *A. sola*. Individuals of all four species may be found living within a meter of each other on rocky intertidal shelves along the central California coast, and the observations below relate to specimens from this region.

Anthopleura artemisia, the Moonglow Anemone. Stephenson & Stephenson (1972) presented an elegant and unambig-

uous account of the appearance of *A. sola*, recognizing it as an entity separate from *A. xanthogrammica* and *A. elegantissima*, but under the name *A. artemisia*. Despite occasional references to *A. sola* as *A. artemisia* (see examples in Previous references, above), the latter species was clearly described by Hand (1955) and is readily distinguished from the other local species. Of the four California species of *Anthopleura*, this is the only one in which photosynthetic endosymbionts are not regularly, if ever, present (Hand 1955); the two published reports of zooxanthellae (Haderlie et al. 1980, Walsh 1981b) have a dubious basis (C. Hand, pers. comm.; P. J. Walsh, in litt.). Unlike the other three species, which are primarily green, individuals of *A. artemisia* with any green coloring are uncommon in central California. In all four species, the green color is an animal pigment, not produced by symbiotic algae (Buchsbaum 1968). *Anthopleura elegantissima* and *A. xanthogrammica* may have zoochlorellae that also contribute green coloring, but only in the northern part of their ranges, as discussed above. The body color of *A. artemisia* is typically dull gray or brown; the oral disc and tentacles are variously colored (neutral tones and shades of red are common) and the color is either solid or patterned with white. These anemones are seen most often as isolated individuals attached within deep holes in rock, or attached to rocks beneath the sand so that only the oral disc is visible. However, longitudinal fission has been observed, resulting in small clones, and the aftermath of fission is evident in irregularities of the acrorhagi, tentacles, and mesenteries (Hand 1955 and pers. comm., Haderlie et al. 1980); cloning has yet to be confirmed by genetic data from field populations. In addition to traits mentioned above, several differences in complement and distribution of cnidae distinguish *A. artemisia* from all three other local species of *Anthopleura*. The diversity of holotrich shapes is less in *A. artemisia*, while that of basitrichs is greater and the

distribution within the polyp also differs (see Table 1 and Hand 1955, figs. 11, 13, 15). For example, *A. sola*, *A. elegantissima*, and *A. xanthogrammica* share the absence of one basitrich category present in *A. artemisia* and at least two other actiniids, *Epiactis prolifera* and *Urticina* (= *Tealia*) *coriacea* (see Hand 1955, figs. 9, 19). *Anthopleura artemisia* was reported by Hand (1955) as occurring from Japan(?) and Alaska to southern California.

Anthopleura xanthogrammica, the Giant Green Anemone. This species is the one most commonly confused with *A. sola*, as both are large, greenish, solitary anemones. However, expanded polyps of *A. xanthogrammica* are easily distinguished by their uniformly green or blue-green oral disc and tentacles, lacking the white tentacle bars and other colored stripes and markings on the tentacles, as well as the strikingly pigmented mesenterial insertions and other radial oral-disc patterns, typical of *A. sola* (and *A. elegantissima*). By inserting a finger, one can feel the firm, strong mouth of *A. xanthogrammica*, whereas the mouth is a soft loose opening in *A. sola*. Likewise, the softness of the body of *A. sola* (and *A. elegantissima*) contrasts with the much firmer, less compressible body of *A. xanthogrammica*. Moreover, the column of *A. xanthogrammica* is densely covered with compound verrucae, not arranged in rows, in contrast to the vertical rows of verrucae that are simple on most of the column, compound only on the collar in *A. sola* (and *A. elegantissima*). Below the limbus, the smooth, thin pedal disc of *A. xanthogrammica* typically spreads well beyond the column diameter and is roughly circular in outline, in contrast to the pedal disc of *A. sola*, which is thicker, less regular in outline, and little larger than the column diameter. Despite all these differences, *A. sola* has so often been identified as *A. xanthogrammica* that caution is indicated in interpreting older literature. For example, Barry et al. (1995) and Sagarin et al. (1999) reported a dramatic increase in *A. sola* and decline in

A. xanthogrammica, at a site on Monterey Bay, California, based on comparing their data with those from a 60-year-old study that very likely confused individuals of these two species. In this case, their conclusion is probably correct, based on our experience at the same site over 30 years, but the quantitative comparison is undermined by the taxonomic uncertainties. *Anthopleura xanthogrammica* occurs from Japan(?) to southern California (Hand 1955), but south of Point Conception, it is restricted to a few areas of cooler water near the heads of submarine canyons (Francis 1979).

Anthopleura elegantissima, the Aggregating Anemone. Polyps of this clonal species, when kept submerged and heavily fed in the laboratory, sometimes grow rapidly without dividing and reach sizes not seen in the field. However, such polyps differ in appearance from specimens of *A. sola* of comparable size. The lab-grown clonal polyps look like greatly inflated versions of smaller ones. The tentacles, oral disc, and body wall are translucent. Both the tentacles and the verrucae of the column are large in proportion to the body, and their number does not appear to increase, so that relatively large spaces occur between the rows. Compared to the verrucae of non-dividing specimens of *A. elegantissima*, those of *A. sola* are smaller in proportion to body size and occur in many more, densely packed rows.

In the field, *Anthopleura sola* is usually easy to distinguish from *A. elegantissima*. The most useful clues for separating these species are related to their development and distribution. *A. sola* has non-clonal development: it does not divide and so lacks fission scars; therefore, barring injury, its polyps should have regularly arranged mesenteries. Its polyps grow to large sizes, and they live singly and out of physical contact with neighboring anemones. In contrast, *A. elegantissima* replicates by longitudinal fission, which produces temporary scarring on the columns of recently divided individuals and long-lasting irregularities in the ar-

range of mesenteries (Hand 1955). Fission typically results in smaller anemones, living in more or less compact aggregations of clonemates in contact with each other.

Besides the primary difference in life history—non-clonal vs. clonal development—the two species differ in habitat and biogeographic range. Whereas *Anthopleura sola* is typically found in lower and more protected situations, as described earlier, *A. elegantissima* predominates on open rock surfaces in high to mid-intertidal zones (Francis 1979) and rarely extends to subtidal depths (L. G. Harris 1991; J. S. Pearse, pers. comm.). Hand (1955) noted that large clonal aggregations of *A. elegantissima*—some with thousands of individuals, most with fewer—are common in exposed, wave-washed habitats. The two species overlap throughout southern and central California, but *A. sola* is absent from the extensive northern part of the range of *A. elegantissima* (see Francis 1979). Clones of *A. elegantissima* extend along the west coast of North America north to Alaska (Hand 1955) and south at least to central Baja California (McFadden et al. 1997).

So far, no simple, diagnostic difference in morphology allows us to distinguish a polyp of *A. elegantissima* lacking traces of fission (because it had not yet divided or had not done so recently) from a small individual of *A. sola*. The cnidae in each tissue are the same, and the size ranges of each of our categories overlap in the two species. Like the observed differences in color-type frequencies (Francis 1979) and allozyme frequencies (McFadden et al. 1997), differences in the cnidae are apparent only at the population level. Any species-specific differences in the sizes of cnidae are so far obscured by within-species variability. Nonetheless, the fact that cnidae are generally larger in the larger, non-clonal polyps of *A. sola* than in the smaller, clonal polyps of *A. elegantissima* invites closer inspection of the relationship between cnida size and body size both within and between species of many sea anemones.

Genetic evidence that Anthopleura sola is a species.—Reproductive isolation between the solitary and aggregated anemones was first inferred from differences in frequencies of color markings in populations in southern and central California (Francis 1979). This analysis demonstrated large and highly significant frequency differences between solitary and aggregated anemones from the same sites against a background of within-species variation that increased with geographic distance. Assuming that the color polymorphism is genetically determined and selectively neutral, this result indicates reduced gene flow (if any) between the species. Using standard electrophoretic methods, no fixed differences were found in allozyme electromorphs of *A. sola* and *A. elegantissima* collected from the same sites in La Jolla and Santa Cruz, California; but there were significant frequency differences between the species at the polymorphic locus complex coding for phosphohexose isomerase (Walsh 1981c, L. Francis, P. J. Walsh, & G. Somero, in litt., L. Francis & D. Hedgecock, in litt.).

Smith & Potts (1987) concluded that their electrophoretic allozyme data yielded no evidence of restricted gene flow between the two forms, which they therefore considered a single species. This negative outcome was attributed by McFadden et al. (1997) to limited sampling (small numbers of individuals and few sites in a restricted geographic range) and to pooling of samples from different locations. In their own allozyme study, McFadden et al. (1997) sampled the full range of sympatry of the two forms, doubling the number of sites and individuals (compared to Smith & Potts 1987), and demonstrated significant differences in allele frequencies between solitary and aggregated forms at every site. Populations of aggregated anemones from sites >1000 km apart were more similar to each other (in terms of genetic distance) than to solitaries from the same sites. McFadden et al. (1997) concluded that the aggregated and solitary anemones represent distinct

sister taxa, referring to them as *A. elegantissima* and *Anthopleura* sp., respectively. The latter we now formally designate as *Anthopleura sola*, new species.

A similar case of sea anemones along the Pacific coast earlier identified as a single species also proved to involve a sibling-species pair. In *Metridium senile*, genetic analysis and life-history studies (Bucklin & Hedgecock 1982, Bucklin 1987) established that the smaller, clonal individuals were distinct from the larger, non-clonal ones, later designated as *M. giganteum* Fautin et al., 1989. Although a study of British populations of large, subtidal vs. small, clonal, intertidal individuals of *M. senile* revealed no genetic evidence of reproductive isolation between the two (Bucklin 1985), the history of research using allozymes in *Anthopleura* spp. suggests that the relatively small differences of recent speciation events can go undetected. Other examples of cryptic actinian species documented by a combination of life-history and genetic differences have involved species of *Sagartia* (see Shaw et al. 1987) and *Epiactis* (see Edmands 1995).

Relationship of A. sola and other species of Anthopleura.—*Anthopleura artemisia* was reported by Walsh (1981c) and by Smith & Potts (1987) to be the sister species of *A. sola* + *A. elegantissima*. Some more recent molecular evidence, based on 28S rRNA, 16S rRNA, and COIII sequences, indicates that *A. artemisia* is not closely related to the other eastern Pacific species of *Anthopleura*, but instead belongs to an Asian clade (Walton 1998, J. B. Geller, in litt.). In the same data of Walton and Geller, *A. xanthogrammica*, *A. elegantissima*, and *A. sola* appeared as an unresolved trichotomy in most trees (Walton 1998, J. B. Geller, in litt.). The three species were each separated by fixed changes in one or two base pairs in each gene. However, many features such as coloration, cnidae, the morphology of the mouth, column, and pedal disc, as well as the data of Walsh (1981c) and Smith & Potts (1987), indicate a closer relation-

ship of *A. sola* to *A. elegantissima* than to either *A. xanthogrammica* or *A. artemisia*. For example, small, cylindrical basitrichs (Fig. 2c, d) are present in the pharynx of both *A. sola* and *A. elegantissima* but absent from *A. xanthogrammica*, as well as from *A. artemisia* and other local actiniids (see Hand 1955). Thus, while not excluding the possibility of other topologies, we conclude that *A. sola* and *A. elegantissima* are sibling species.

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A new species of *Leptogorgia* from the eastern Pacific (Coelenterata: Octocorallia: Holaxonia)

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Abstract.—*Leptogorgia styx*, a new species of the holaxonian family Gorgoniidae from the eastern Pacific inhabiting waters unusually deep for this genus is described and illustrated. Scanning electron micrographs of sclerites and morphology of axial mineral are presented.

Family Gorgoniidae

Genus *Leptogorgia* Milne Edwards &
Haime, 1857

Leptogorgia Milne Edwards & Haime,
1857:163 (type species *Gorgonia viminalis* Pallas, 1766, by subsequent designation: Verrill, 1869:420).

Lophogorgia Milne Edwards & Haime,
1857:167 (type species *Gorgonia palma* Pallas, 1766, by monotypy).

Filigorgia Stiasny, 1937:307 (type species
Filigorgia riodouroi Stiasny, 1937, by monotypy).

Leptogorgia.—Grasshoff, 1988:97 (synonymy); 1992:54.—Williams, 1992:231 (synonymy).—Williams & Lindo, 1997:500 (synonymy).

Remarks.—The genera *Leptogorgia* and *Lophogorgia*, long distinguished upon unreliable characters, were unequivocally united by Grasshoff (1988:97).

Leptogorgia styx, new species
Figs. 1–5

Material.—East Pacific Rise, approx. 500 km SSW of Acapulco, Mexico. Seamount 6: 12°43'12"N, 102°36'W, 1900–1950 m, R/V *Atlantis II* Dive AD3016, coll. Scott France and Ewann Berntson, 4 Nov 1996. Holotype USNM 98800.

Description.—The holotype (Fig. 1) is a

broadly flabellate white colony 12.5 cm in height and 15 cm in greatest width, arising from a laminar holdfast covered with coenenchyme devoid of polyps, spreading over solid substrate; three primary trunks produce secondary branches in an irregular, openly pinnate sequence mostly in one plane. The main trunks are 3.5 mm in diameter, the terminal twigs 1.5 to 1.75 mm. Unbranched final twigs are blunt, mostly 2.25 cm or less in length, arising at a wide angle but soon curving upward roughly parallel with the larger branches. Polyps are distributed on all sides, fully retractile into the coenenchyme, which is not elevated around the apertures. A narrow, sinuous groove extending along two sides of the main stems marks the course of the primary stem canals.

Sclerites (Fig. 2) of the coenenchyme are colorless and of the usual gorgoniid design. The longer ones are tuberculate spindles up to 0.15 mm in length, some of them slightly curved (Fig. 2a), the shorter ones blunt tuberculate capstans 0.05–0.08 mm long with two whorls of complex tubercles and terminal clusters (Fig. 2b); the sclerites of the innermost coenenchyme are small rods 0.05–0.08 mm long, with conical, less complex tubercles (Fig. 2c). As usual, a small number of crosses are present, and intergrades in size and form are numerous. The anthocodiae contain narrow, somewhat flat-

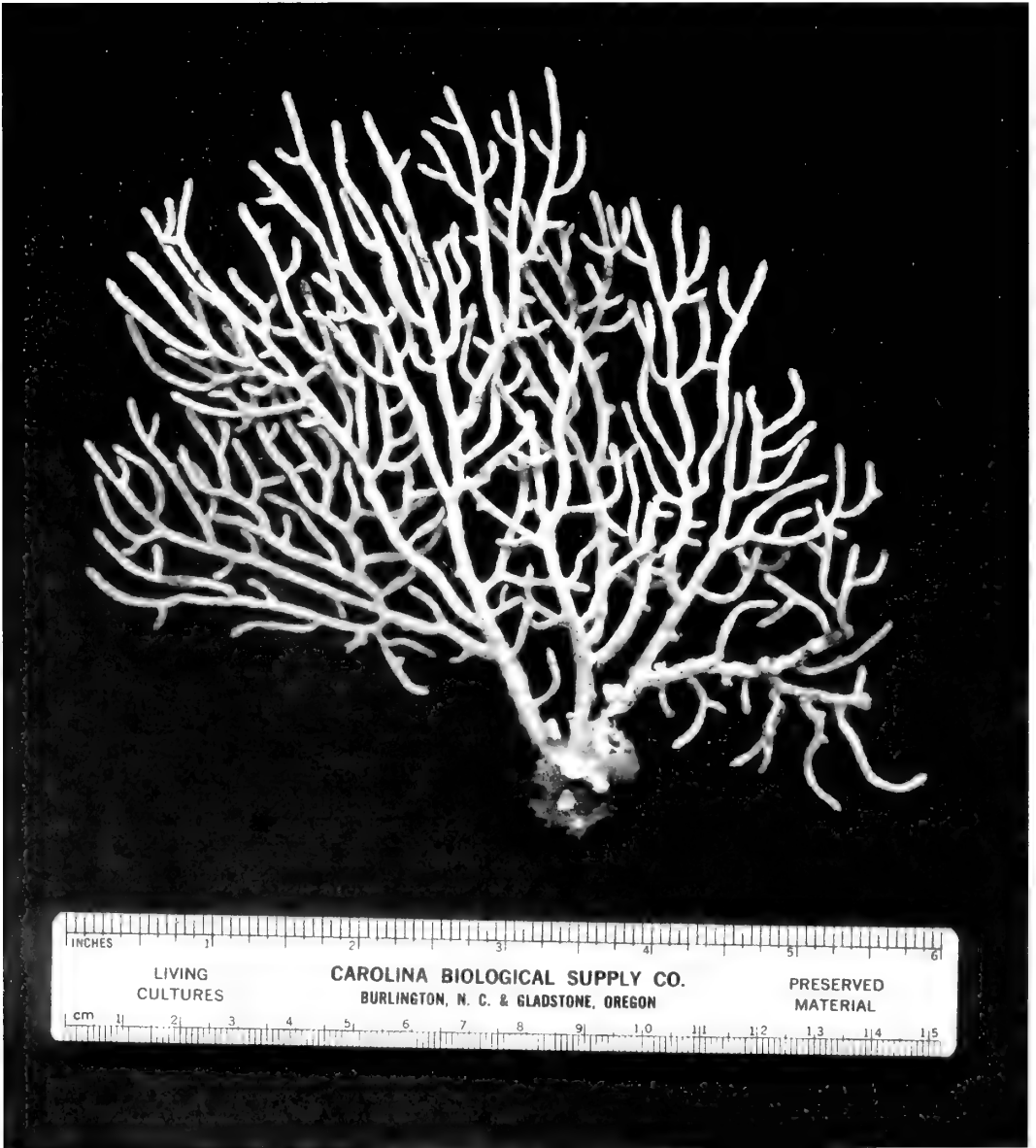


Fig. 1. *Leptogorgia styx*, new species. Holotype colony, USNM 98800.

tened rods, smooth except for a very few marginal projections; dissection of several polyps did not reveal their arrangement and, owing to their relatively small numbers in the preparations, no examples could be found for examination by SEM.

The axis of the terminal branchlets is pale yellow, glassy clear with a clearly visible narrow white chambered central core,

becoming dark brown, almost black, in the larger branches and main trunks; it is marked by irregularly sinuous longitudinal ridges and grooves. The axis effervesces briskly in HCl, indicating dense mineralization.

When exposed by free-hand longitudinal section, the chambers of the core are filled with extremely fine organic filaments, sim-

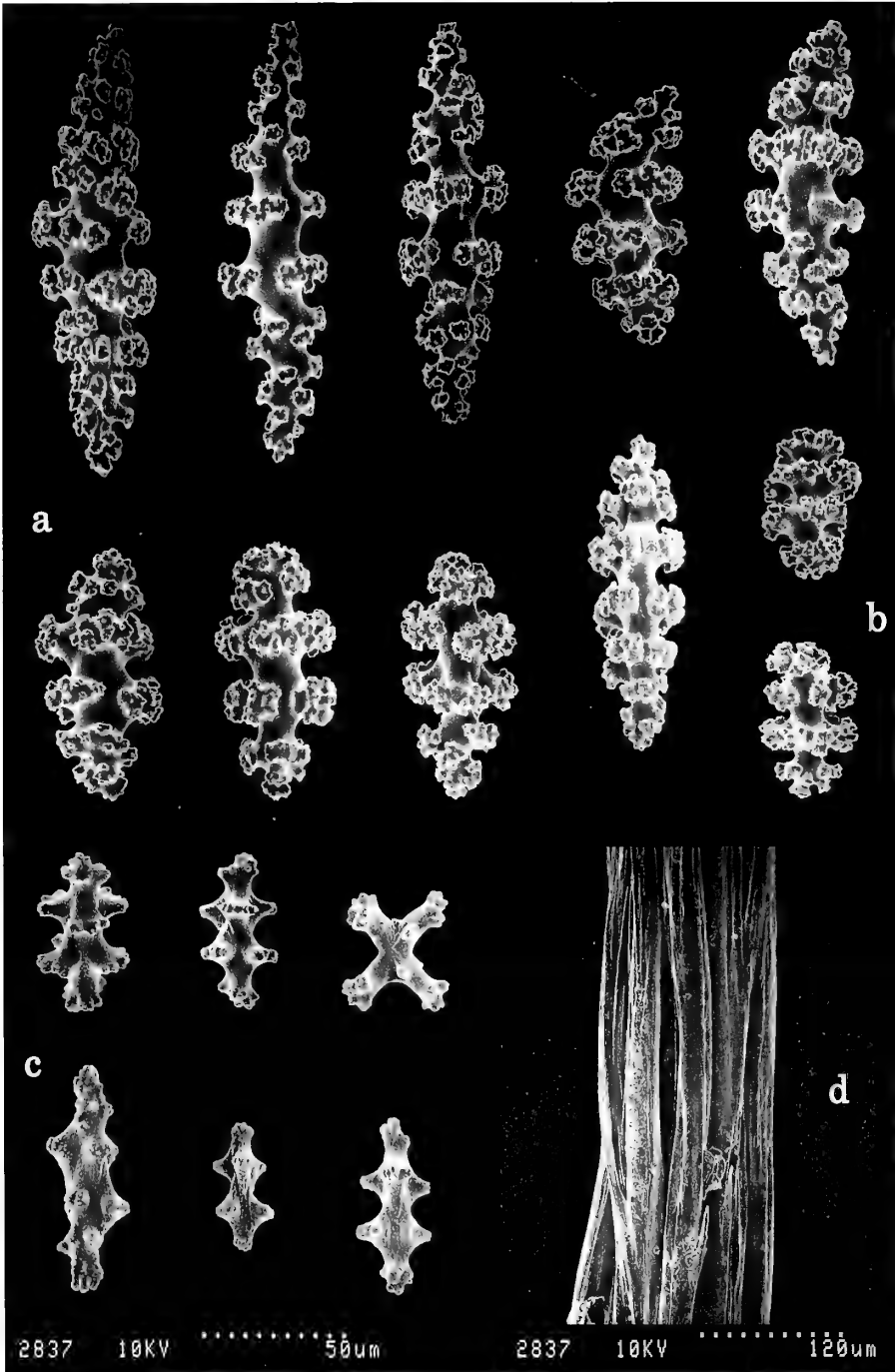


Fig. 2. *Leptogorgia styx*, new species. Sclerites of coenenchyme and axis of terminal twig. a, Tuberculate spindles; b, Blunt capstans; c, Rods of innermost coenenchyme, with cruciform present in all layers; d, Axis of terminal twig after maceration in sodium hypochlorite. (SEM 2837.)

ilar to those first reported in the central core and axial loculi of various gorgonians by Kölliker (1865:150, 151) and later in the central core (“Achsenstrang,” “Zentralstrang”) of *Eunicella verrucosa* by Koch (1878) and of *Pterogorgia pinnata* and several other holaxonians by Neuman (1911: 505. “das Innere jeder Kammer von einem äußerst dichten Netzwerk feinsten Fäserchen durchzogen wird.”) and Schimbke (1915:74. “ein feinstes Hornnetz”), and of *Pseudoplexaura crassa* by Chester (1913: 742, “chambers filled with loosely branching threads”).

The core is surrounded by successive layers of axial cortex (=“sheath” in Macintyre et al. 2000) composed of longitudinally aligned strands of mineralized gorgonin (Fig. 3, top).

After removal of the organic matrix by maceration in 5.25% sodium hypochlorite solution (18 hr), the mineral component of the axis becomes colorless, translucent but faintly cloudy when wet, the opaque core still clearly visible; after washing and drying, it becomes opaque white.

Although the mineral component of the axis of the western Atlantic *Leptogorgia virgulata* has been interpreted as amorphous calcium carbonate (Kingsley & Watabe 1982), Macintyre et al. (2000) have determined that the axial mineral of that species as well as that of the one here described consists of carbonate hydroxylapatite (hereafter abbreviated CHAp) rather than amorphous CaCO_3 .

The filaments of this network are coated with CHAp initially deposited in the form of submicron spheres that sometimes fuse together to form a continuous rodlike coating that retains an indication of the original spherulitic construction (Fig. 4). The individual spheres are up to 0.65 μm in diameter, the columnar mineralized filaments up to about 1.2 μm in diameter.

The CHAp comprising the mineral component of the axial cortex forms the crenulated sheaths around the axial core as reported in Macintyre et al. (2000). The com-

ponent crystallites are too fine for resolution in the available SEM and do not form submicron spheres as in the chambers of the core.

The holdfast extending over the substrate a short distance beyond the main trunk is a fibrous, dark brown to almost black, lamellar expansion consisting of numerous thin layers of gorgonin with intervening locular spaces, covered by coenenchyme devoid of polyps. The locular spaces between the lamellae are filled with fine organic filaments like those of the central core (Fig. 3, bottom).

After the gorgonin matrix of the holdfast is removed by maceration in sodium hypochlorite, the mineral component consists of a white particulate residue including fragments of the much broken mineralized lining of the loculi. The mineral coating the locular walls is composed of CHAp deposited in the form of submicron spheres up to about 0.6 μm in diameter, many of which give rise to rodlike filaments 0.6 μm –0.9 μm in diameter composed of fused spheres and showing clear evidence of deposition in layers (Fig. 5, lower right).

The crystallites comprising the CHAp component of the axis and holdfast of this and other species of *Leptogorgia* are so fine that analysis by X-ray diffraction has not revealed an indication of apatite except in two species, *Leptogorgia stheno* and *L. setacea*, and not in all specimens of those. Morphology of the submicron spheres examined by SEM indicates that the mineral is precipitated initially as a minute spherule at a nucleation site on an organic filament, increasing in size and girdling the filament until meeting on the opposite side (Fig. 5, upper and lower left), often enlarging until all evidence of the point of contact has been overgrown and obliterated. The surface of fully grown spheres and fracture surfaces of the mineral where breaks have occurred during preparation indicate that the CHAp in this species is precipitated in even finer microspherulitic form (Fig. 5, upper and lower left).

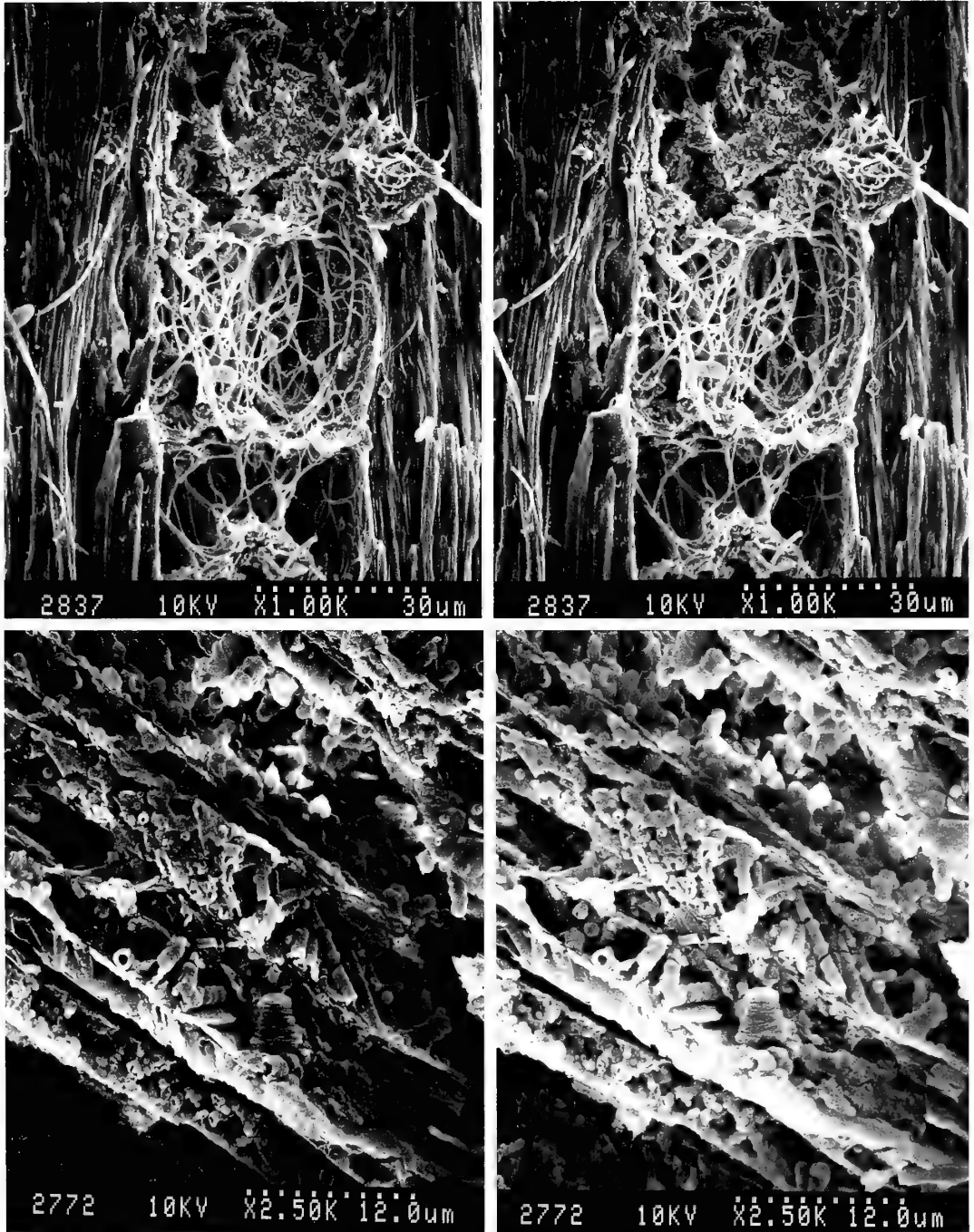


Fig. 3. *Leptogorgia styx*, new species. Structure of axis not macerated in sodium hypochlorite: Top, Longitudinal section of axis showing chambers of core filled with mineralized filaments (SEM 2837, stereo pair); Bottom, Loculi of holdfast showing mineralized filaments (SEM 2772, stereo pair).

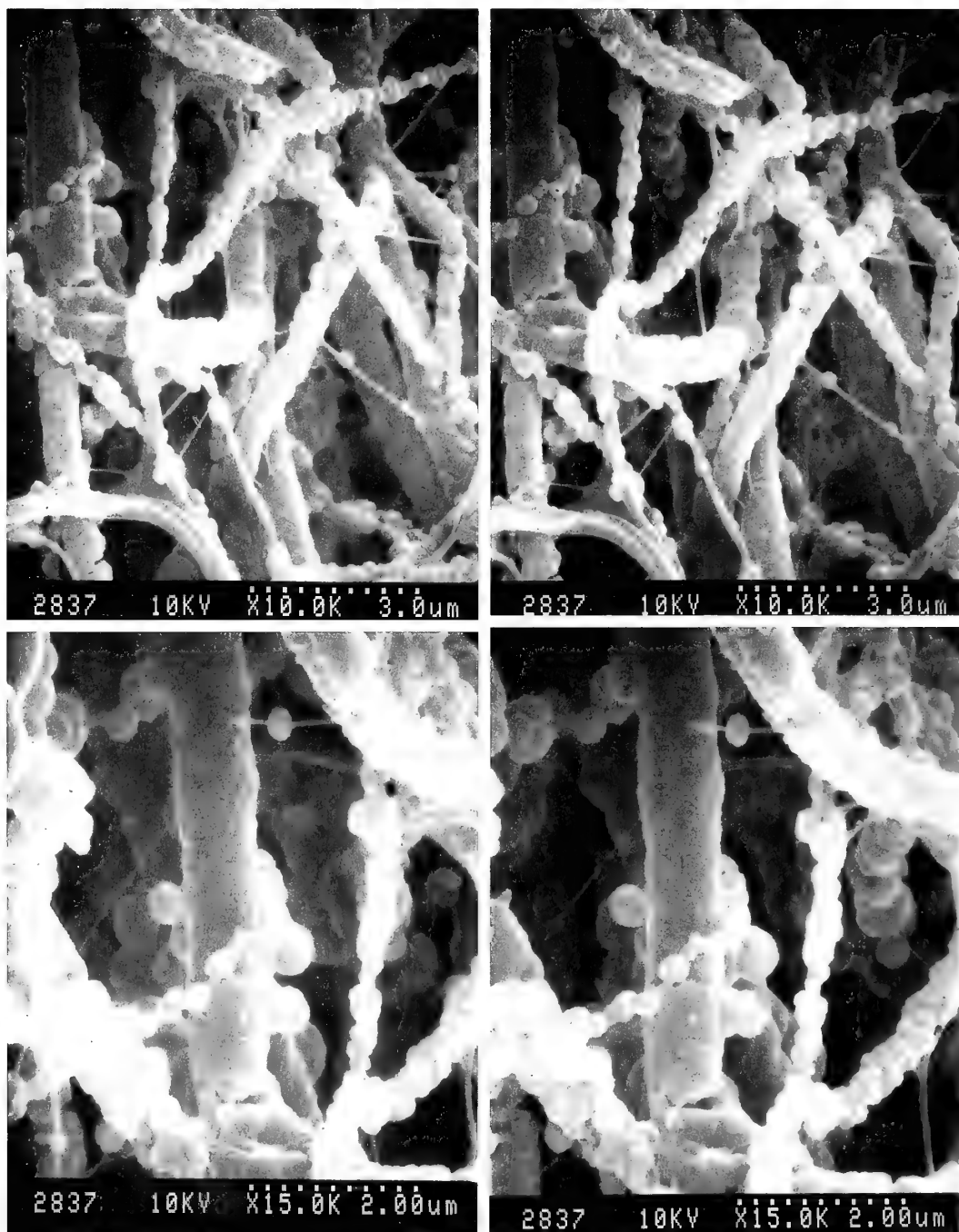


Fig. 4. *Leptogorgia styx*, new species. Mineralized filaments of axial core (SEM 2837, stereo pairs).

Etymology.—Greek *Styx*, the mythical river flowing seven times around the underworld, named for Styx, daughter of Oceanus and Tethys, who dwelt in a lofty grotto

supported by silver columns at the entrance of Hades. A feminine noun used in apposition, alluding to the exceptionally deep habitat of this species.

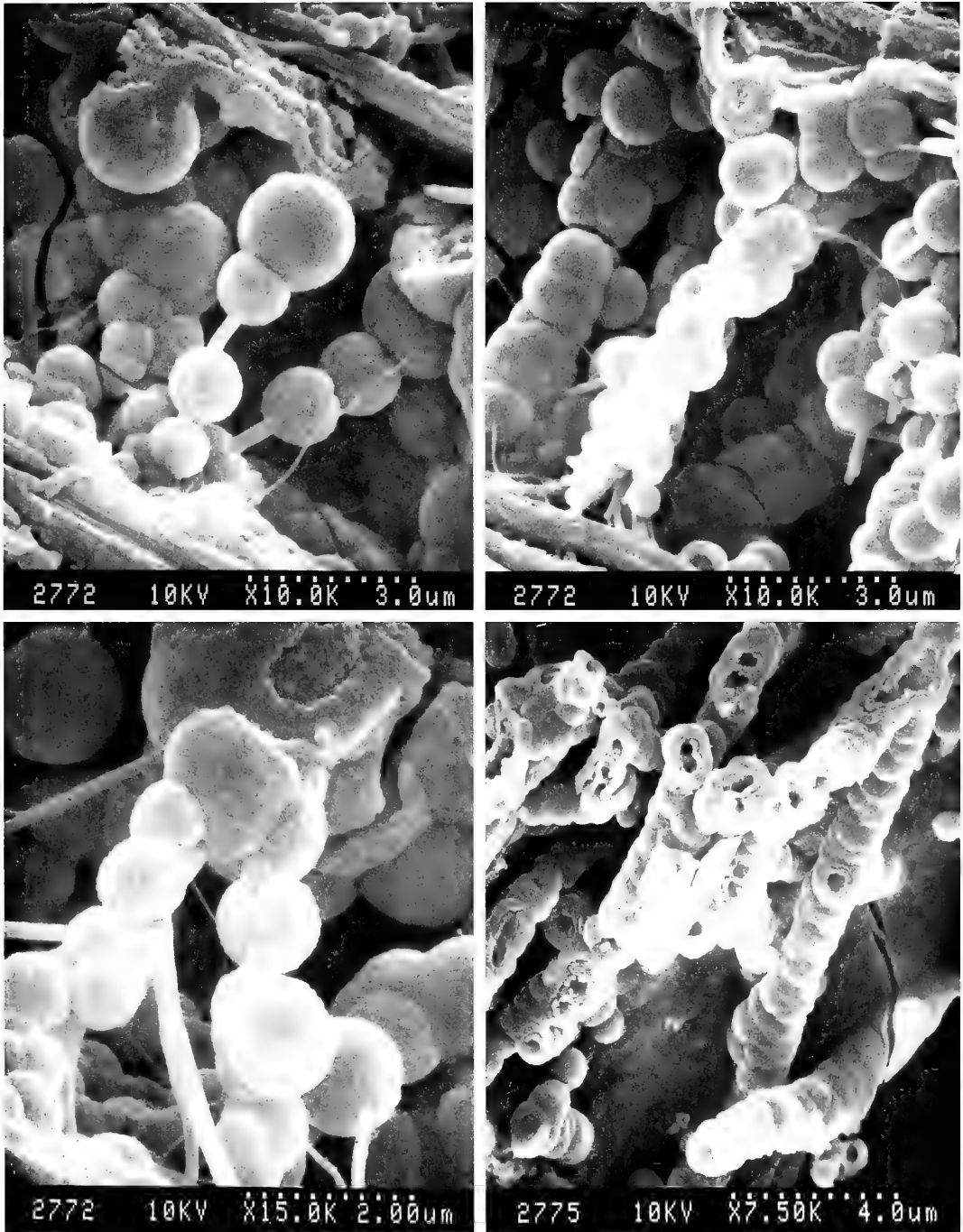


Fig. 5. *Leptogorgia styx*, new species. Mineralized filaments of holdfast loculi. Upper left, Submicron spheres of CHAp on organic filaments show spherulitic microstructure on broken surfaces (SEM 2772); Upper right, submicron spheres of CHAp showing degrees of fusion (SEM 2772); Lower left, Submicron spheres of CHAp on organic filaments show formation of spheres around filament, and microspherulitic structure (SEM 2772); Lower right, Submicron spheres of CHAp coating filaments, fused to form rod-like structures with central lumen originally occupied by organic filament removed by maceration in sodium hypochlorite (SEM 2775).

Remarks.—The flabellate, planar growth form without anastomosis is similar to that of *L. alba* (Duchassaing & Michelotti) and several other species of *Leptogorgia*.

Numerous individuals of a caprellid amphipod were living on this specimen, but so far have not been identified.

Acknowledgments

Dr. Scott France and Dr. Ewann Berntson collected the type specimen of *Leptogorgia styx* and kindly made it available for study. The mineral of the axis was analyzed by Mr. William Boykins. Dr. D. L. Pawson and Mr. W. R. Brown made the scanned image of the colony illustrating this paper. Ms. Molly K. Ryan assembled and mounted the plate of sclerites. Facilities of the Scanning Electron Microscope Laboratory, National Museum of Natural History, were made available by Mr. Walter R. Brown and Ms. Susann Braden. Scientific aspects of this report benefitted from numerous discussions with Dr. Ian G. Macintyre, Department of Paleontology, National Museum of Natural History, and Dr. Manfred Grasshoff, Section of Invertebrates, Naturmuseum Senckenberg, Germany. I extend my best thanks to all these colleagues, without whose assistance this paper could not have been written.

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**An illustrated key to the species of *Grania* and *Randidrilus*
(Annelida: Clitellata: Enchytraeidae) of eastern North America,
Bermuda, and the Caribbean area**

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Abstract.—The marine, clitellate genus *Grania* Southern, 1913 is a globally prevalent group of enchytraeids in intertidal and shallow subtidal habitats, showing high diversity in tropical and subtropical latitudes. Due to the rapidly rising numbers of known species of *Grania*, taxonomic revisions, and modifications in species ranges, a basic aid to species recognition is required for systematic, biodiversity, and ecological studies. A dichotomous key using anatomical characters distinguishes the nine species of *Grania* and two species of the co-occurring and structurally similar genus *Randidrilus* Coates & Erséus, 1985, with known distributions within eastern North America, the neighboring islands of Bermuda, and the Caribbean area. Based on examination of type and recent material, annotations on structural details of the male ducts and statocysts of each of the nine *Grania* species are provided.

Grania of the Northwest Atlantic

The coastal habitats of eastern North America, the Atlantic islands of Bermuda, and the Caribbean area have not been extensively surveyed for marine enchytraeid clitellates and new species are regularly found in unsuspected habitats (Healy 1994, Healy & Walters 1994, Healy & Coates 1999). In some of the few taxonomic surveys, the genus *Grania* Southern, 1913 (Enchytraeidae) was relatively diverse or abundant (Kennedy 1966, Lasserre 1971, Erséus & Lasserre 1976, Lasserre & Erséus 1976, Coates & Erséus 1985) (Fig. 1). Based on existing but undescribed collections, the range of unexplored locations and microhabitats, and investigation of new structural and genetic characters, it is expected that a number of new species remain to be discovered in this geographic region. Readily available and accessible information about known species is essential to the recogni-

tion of new species, and ensuing studies of the diversity of *Grania*.

Species of *Grania* are infaunal, sometimes interstitial, indistinctly segmented worms. They are found in well-sorted medium to coarse sand as well as poorly sorted sandy-mud, both intertidally and in the shallow subtidal. Deep water species are found in clay, silt, and sandy-silt. Sexually mature worms range from about 3–15 mm long and from about 0.08–0.25 mm in diameter. Specimens of *Grania* are distinguished from other marine enchytraeids by their robust, straight, pointed setae which occur singly both ventrally and laterally. These setae are lacking completely in at least one species, *Grania levis* Coates & Erséus, 1985. The unpigmented body wall is relatively rigid due to a thick cuticle, causing the worms movements to be stiff and sigmoid, like those of a nematode. The key characteristics for distinguishing species of *Grania* are the shape and distribution of setae, shape of spermathecae, and structure of

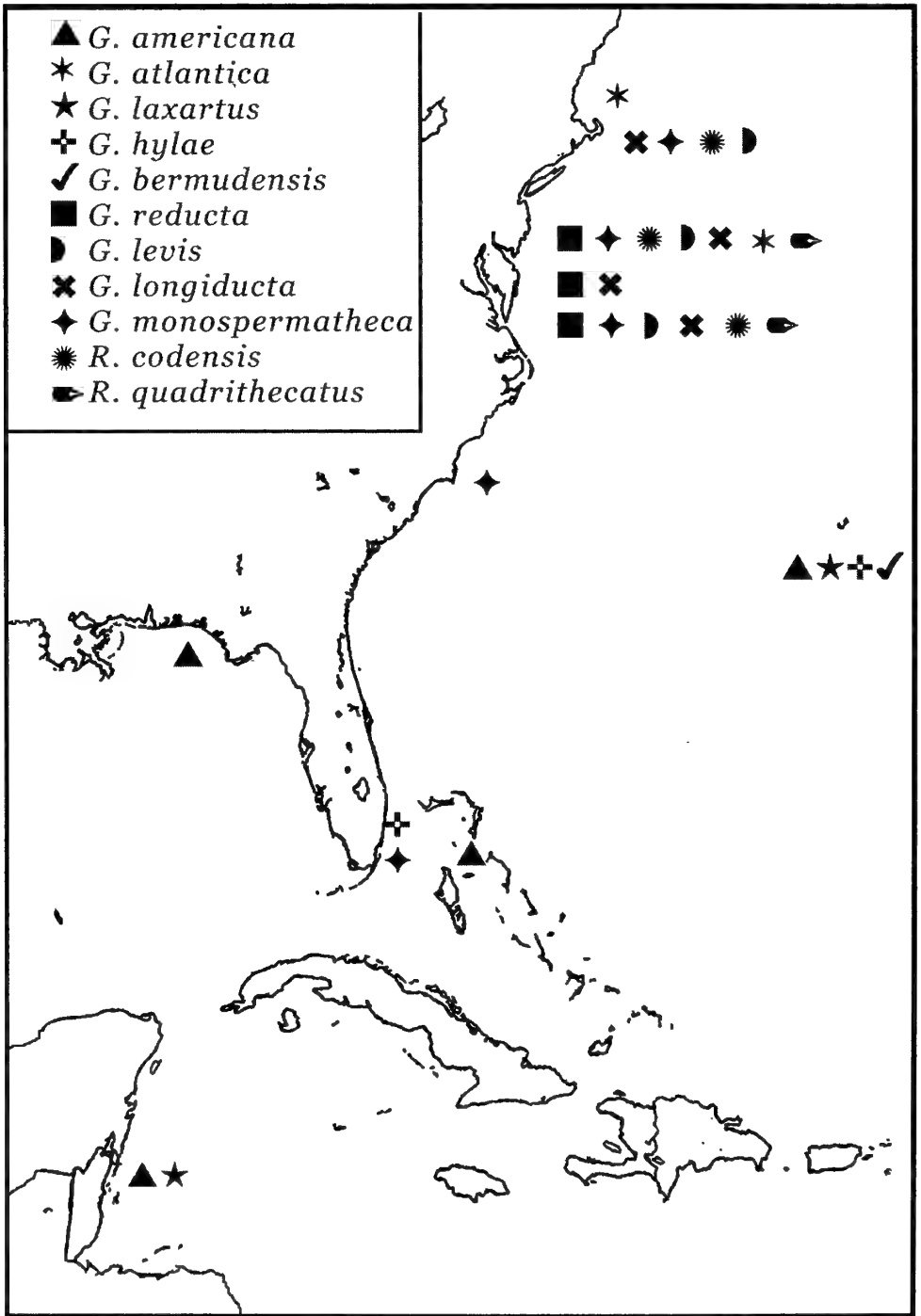


Fig. 1. Known locations of *Grania* species in the Western Atlantic and Caribbean.

the male duct system—the sperm funnel, vas deferens, and penial apparatus (Fig. 2). Specimens must be mature to be identified to species. Nielsen & Christensen (1959) considered any enchytraeid specimens without a clitellum as immature and their reproductive structures incompletely formed.

Grania americana Kennedy, 1966, was the first enchytraeid recorded in a continental shelf habitat of Atlantic North America (Kennedy 1966, Coates & Erséus 1985, Locke & Coates 1999). A few years later, Lasserre (1971), working at the Marine Biological Laboratories of Woods Hole, Massachusetts, recorded three subtidal enchytraeid species, one of which he identified as *Hemigrania postclitellochaeta* (Knöllner, 1935). The genus *Hemigrania* Lasserre, 1971 has since been synonymized with *Grania* (Erséus & Lasserre 1976) and *Grania postclitellochaeta* does not occur in North American waters (see Coates & Erséus 1985). The material reported by Lasserre (1971) has been referred to *Grania longiducta* Lasserre & Erséus, 1976 (Coates & Erséus 1985). The area of Woods Hole remains the northern limit for records of *Grania* in eastern North America. Erséus & Lasserre (1976) made additions to the western North Atlantic fauna with records of *Grania monospermatheca* Erséus & Lasserre, 1976, from Cape Cod, Massachusetts, and *Grania bermudensis* Lasserre & Erséus, 1976 (see also Locke & Coates 1999) from the sub-tropical islands of Bermuda. Coates & Erséus (1985) described three new species, *Grania reducta* and *Grania levis*, from coastal eastern North America and *Grania atlantica* from deep Atlantic waters including the North American continental shelf. The most recently described species in the western Atlantic are *Grania laxartus* Locke & Coates, 1999 and *Grania hylae* Locke & Coates, 1999 from eastern Florida, Bermuda, and the Caribbean area.

Keys to North American Marine Enchytraeids

Cook & Brinkhurst (1973) prepared an annotated key for the northeastern United

States in which they presented information in standard couplet format for four families of “oligochaetes”, Enchytraeidae, Naididae, Tubificidae, and Megascolecidae (=Acanthodrilidae in Cook & Brinkhurst 1973). *Grania* was represented in the key by a single species, *Hemigrania postclitellochaeta*. As noted above, the taxonomic status of the specimens found in North America and originally called *H. postclitellochaeta* has since been amended (Coates & Erséus 1985). Although a number of *Grania* species are now recognized from the northwestern Atlantic (Coates & Erséus 1985, Locke & Coates 1999), a modern, comprehensive key does not exist for these species or for any other marine enchytraeids (Milligan 1996). In fact, enchytraeids have been excluded from all keys to aquatic oligochaetes of North America (see Brinkhurst 1986, Kathman & Brinkhurst 1998), and from regional keys (Strayer 1990; Milligan 1996, 1997).

The following key includes nine species of *Grania* recorded from the eastern coast of North America, Bermuda and the Caribbean area. Species of the enchytraeid genus *Randidrilus* Coates & Erséus, 1985, described from the North American coast by Coates & Erséus (1985), are quite similar to *Grania* in morphology and distribution. Due to their occurrence in the same habitats as some eastern North American *Grania* species, the two *Randidrilus* species from the region are included in the key presented here. Species identifications should be confirmed by reference to recent species descriptions (Coates & Erséus 1985, Locke & Coates 1999). Species included within the key are: *Grania americana*, *Grania longiducta*, *Grania atlantica*, *Grania monospermatheca*, *Grania bermudensis*, *Grania reducta*, *Grania hylae*, *Grania laxartus*, *Grania levis*, *Randidrilus codensis* (Lasserre, 1971) and *Randidrilus quadrithecatus* (Coates & Erséus 1985).

Materials and Methods

Whole-mounted specimens of *Grania* and *Randidrilus* were examined by light

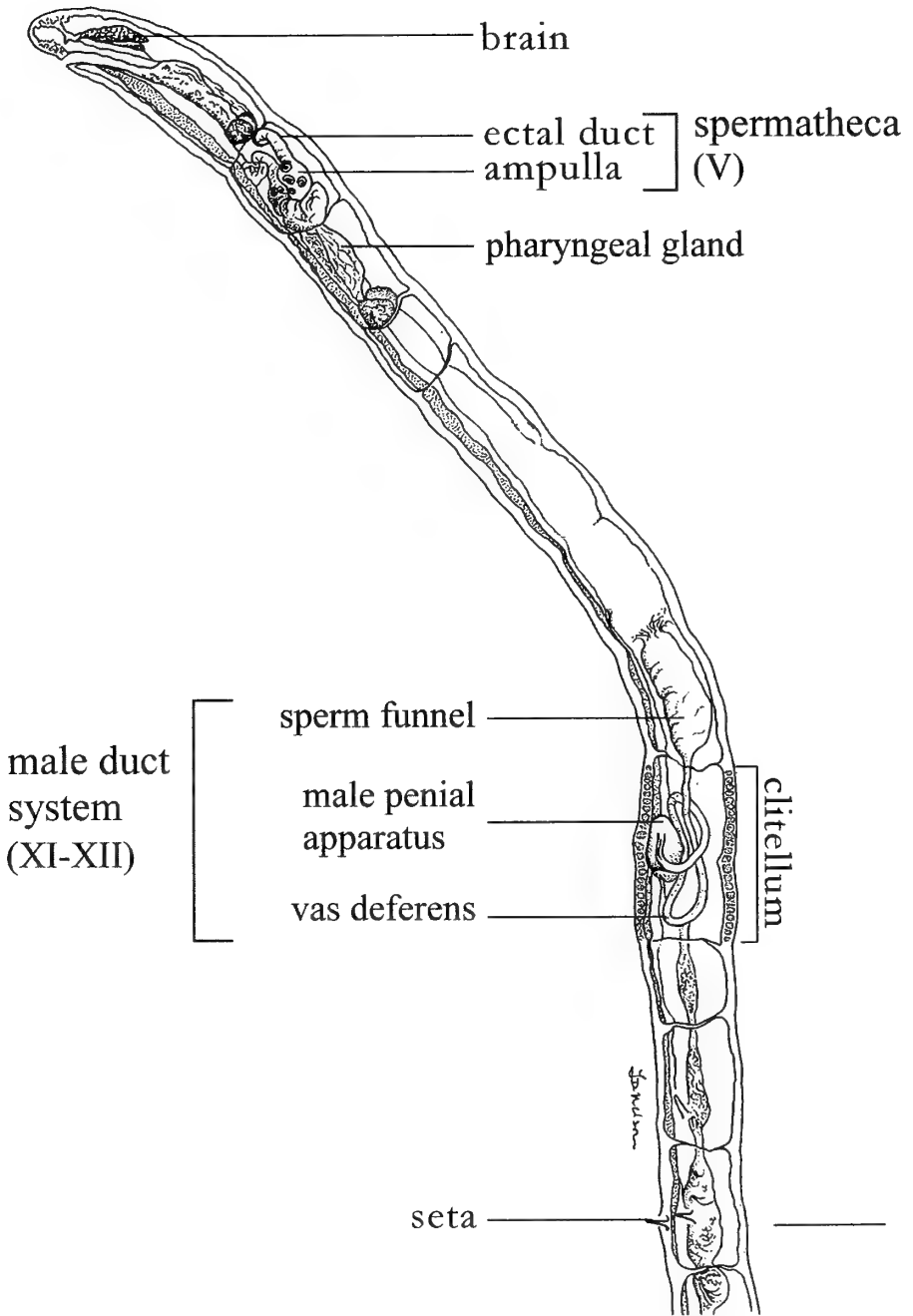


Fig. 2. General morphology of *Grania* species, based on *Grania longiducta*, illustrating main diagnostic characters. Scale equals 100 μ m.

microscopy to confirm characteristics for species included in the key. These included type specimens of *G. americana* USNM 33005, *G. bermudensis* USNM 53202, *G. hylae* USNM 185954, *G. levis* USNM 96509, *G. laxartus* USNM 185951, and *R. quadrithecatus* USNM 96498, from the United States National Museum of Natural History (USNM) (Smithsonian Institution), Washington, D.C. Other material of *R. codensis* ROMIZ 12177 (5 specimens) was borrowed from the Royal Ontario Museum (ROM), Toronto, Ontario, Canada. Specimens of other North American species of *Grania* were from the collections of C. Erséus and K. A. Coates (Locke & Coates 1999).

To separate higher taxa and to identify species, diagnostic characters were determined and definitions for these relevant to the enchytraeids developed (Appendix 1). Primary references for definitions were Nielsen & Christensen (1959), Stachowitsch (1992), Abercrombie et al. (1992) and Webster's Encyclopedic Unabridged Dictionary (1989).

An illustrated key to the species of *Grania* of eastern North America, Bermuda, and the Caribbean area also was developed as a website entitled, "Key to *Grania* of North America, Bermuda, and the Caribbean area." The World Wide Web Universal Resource Locator (URL) address for this website is: <http://www.bbsr.edu/users/kcoates/Grania/Grania.html>. This site is regularly maintained and updated.

Distinctive Characteristics of the Marine Enchytraeid Genera

Enchytraeids (Clitellata) are characterized morphologically by position and form of reproductive structures (Fig. 2) and by their setal shapes. When present, setae are straight, sigmoid or bent, rarely possessing a nodulus and rarely forked at the distal tip. No marine enchytraeids are known with forked setae. Spermathecae are anterior in segment V and rarely in VI. Testes are

Table 1.—Distinguishing characteristics for enchytraeid genera with marine species.

Genus	Distinguishing characters
<i>Achaeta</i>	lack setae head pore at tip of prostomium
<i>Enchytraeus</i>	unbranched peptonephridia
<i>Lumbricillus</i>	lobed testis sacs (except <i>L. semifuscus</i>)
<i>Marionina</i>	dorsal blood vessel bifurcation posterior to brain (few exceptions in marine species, e.g., <i>M. charlottensis</i>)
<i>Stephensoniella</i>	large compact pharyngeal glands thickened septa globose spermathecal diverticulum
<i>Randidrilus</i>	anterior and posterior glands at penial pore
<i>Grania</i>	stout, single setae (rarely absent) complex penial apparatus penial stylet may be present

paired in XI and ovaries are paired in XII. The pores of the male penial apparatuses are in segment XII and paired, glandular, pre-septal sperm funnels originate in XI, often extending or displaced into segments anterior and posterior to XI by body movements and contractions. There are seven genera (Healy & Coates 1999) known to have species in marine habitats, in contrast to about 22 terrestrial and freshwater genera. These genera are: *Achaeta* Vejdovský, 1878, *Enchytraeus* Henle, 1837, *Lumbricillus* Ørsted, 1844, *Stephensoniella* Cernovitov, 1934a (amended by Coates 1983), *Marionina* Michaelsen, 1889, *Grania* Southern, 1913, and *Randidrilus* Coates & Erséus, 1985. All of these have been recorded from the coastlines and continental shelves of eastern North America.

Combinations of a few characters can be used to distinguish among the marine enchytraeid genera. One or two species are atypical of their genus and may lack some otherwise distinguishing characteristics (Table 1).

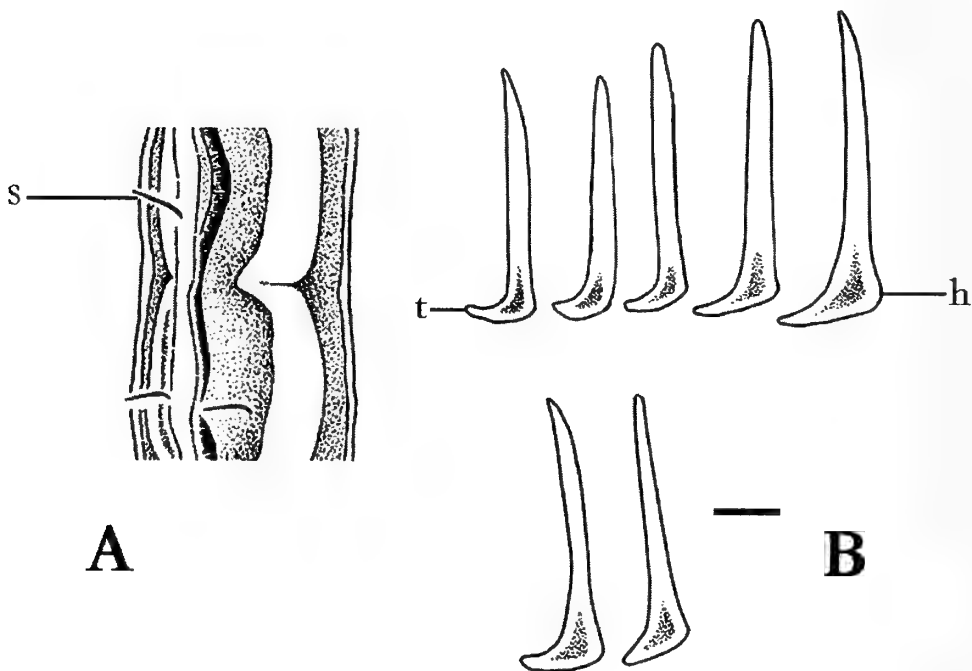


Fig. 3. Setae of *Grania*. A. Position of ventral setae in worm body. B. Setae, illustrating heel and toe characteristic of some species. Scale equals 20 μm for B only. h, heel; s, seta; t, toe.

Specific terms or phrases in the following text are further explained in Appendix 1. The reproductive and nephridial systems mentioned for each of the following genera are paired systems, unless noted otherwise.

Species of *Achaeta* totally lack setae and may have one, two or three pairs of epidermal glands in each segment, called epidermal gland sacs; these sacs are lacking in the single marine species, *Achaeta littoralis* Lasserre, 1968. Spermathecae are in V or extend posteriorly as far as X; the ampullae are without ental ducts or other connections to the esophagus; the brain is convex posteriorly; the sperm sac is small and compact; the penial apparatus includes several small glands around the male pore. The head pore of species of *Achaeta* is near the tip of the prostomium.

Species of *Enchytraeus* possess paired, unbranched post-pharyngeal or esophageal appendages (see Schmelz & Westheide 2000); setae are straight with two or more in a bundle; glands are present at the spermathecal ectal pores; the brain is convex

posteriorly and each penial apparatus has either a single compact gland or a longitudinal row of glands along the ventral body wall.

Species of *Lumbricillus* have a lobed testis sac; setae are usually sigmoid, more than two per bundle; glands are present at the spermathecal ectal pore; the brain is incised posteriorly.

Species of *Marionina* may lack, or have straight or sigmoid, setae, which are single, paired or multiple per segment; spermathecae may have glands along the spermathecal ectal duct and/or at the spermathecal ectal pore; many marine species also have sperm rings, sometimes in distinct diverticula of the ampulla; the brain is incised or convex posteriorly; in each nephridium the nephridial canal extends anterior to the septum; the anterior dorsal blood vessel bifurcation in most species is posterior to the brain with circumpharyngeal vessels looping anteriorly, lateral to the brain (Coates & Ellis 1981, also see Coats 1980).

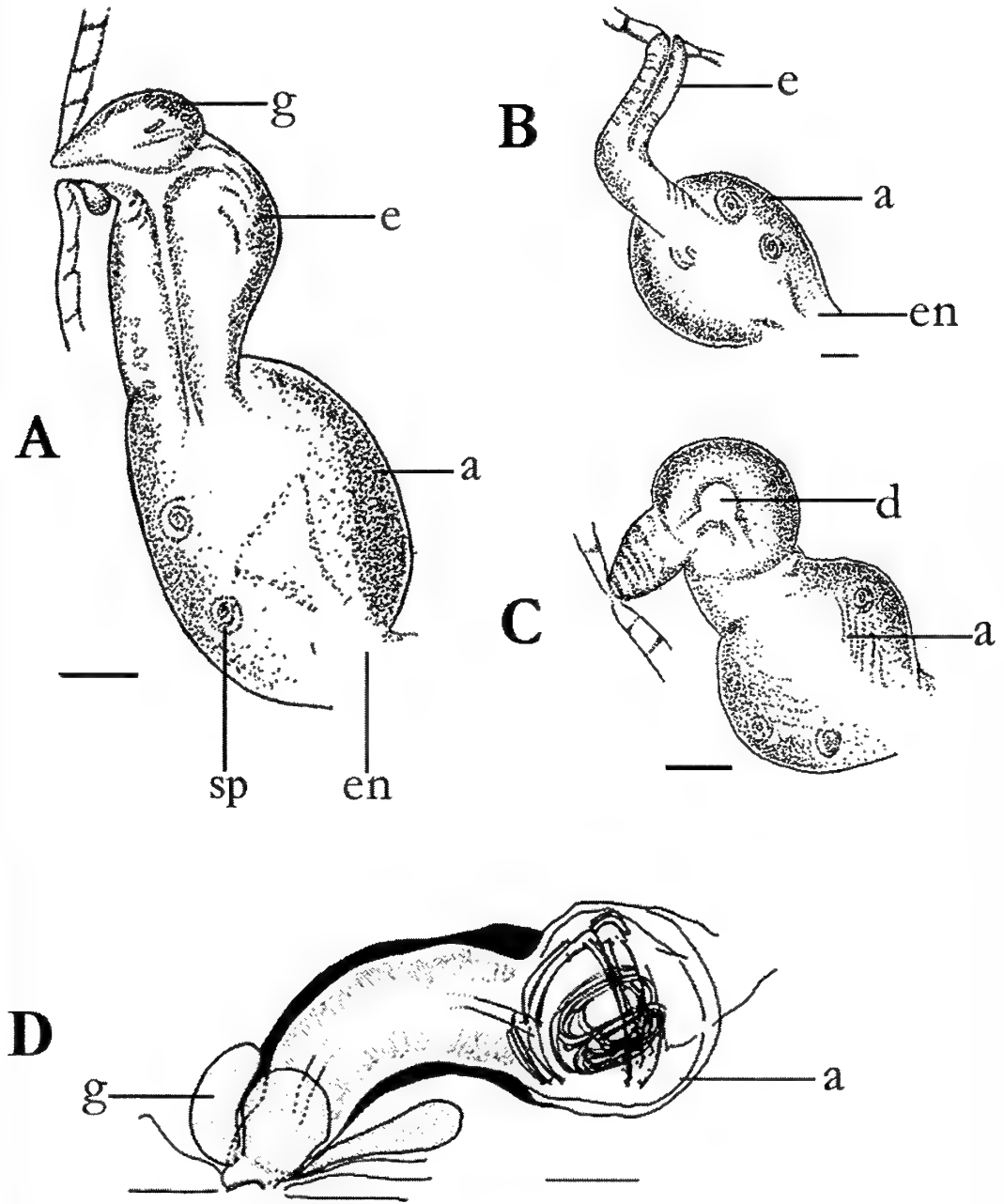
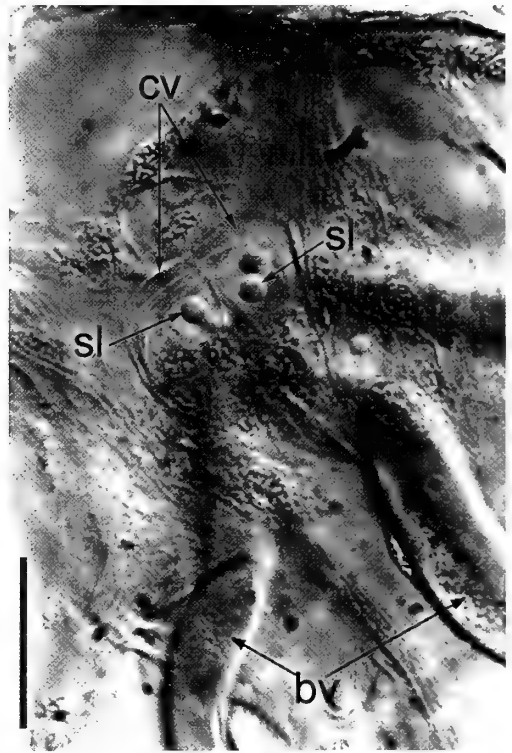
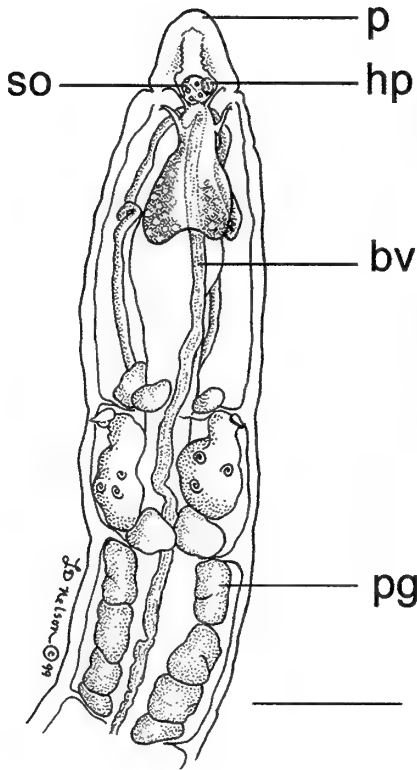


Fig. 4. Spermathecae. A. *Grania americana* with glands at ectal pore; B. *Grania hylae* with narrow ectal duct; C. *Grania laxarta* with distinct dilation of ectal duct; D. *Randidrilus codensis* with glands at ectal pore. Scales equal 20 μm . a, ampulla; d, ectal duct dilation; e, ectal duct; en, ental duct; g, gland; sp, sperm ring.

Stephensiella species have bundles of only two or three slightly sigmoid setae; single compact penial glands; large compact pharyngeal glands and thickened mus-

cular septa from 5/6 to about 8/9; and each spermatheca has a globose or saccate ampullar diverticulum.

Randidrilus species have single, ventro-



A

B

Fig. 5. *Grania americana*. A. Schematic illustration of whole mount showing anterior position of statocyst within the prostomial region. The bifurcation of the dorsal blood vessel is posterior to the statocyst which lies below the head pore. Scale equals 100 μ m. B. Chambered statocyst anterior to blood vessel bifurcation. Three of four statoliths are clearly shown. Scale equals 20 μ m. bv, dorsal blood vessel; cv, chambered statocyst; hp, head pore; p, prostomium; pg, pharyngeal gland; sl, statolith; so, statocyst.

lateral setae present as far forward as II; one or two pairs of spermathecae; and penial apparatuses with separate, compact, anterior and posterior glandular masses at each male pore.

Grania species have stout, single setae (Figs. 2 & 3), but setae lacking from at least some anterior segments; sperm rings in the spermathecal ampulla (Fig. 4); elongate, posteriorly extending sperm and egg sacs; and a diversity of complex penial apparatuses, sometimes with penial stylets.

Key for *Grania* and *Randidrilus*

The following dichotomous key should be used after determining the genus of the

specimens using Table 1 and the information given above. Observation of the characters used in the key requires a compound microscope and sexually mature specimens. Either live specimens or dehydrated, cleared, stained, and mounted specimens can be used (Locke 1999). Major characteristics used in the key are described in Appendix 1.

The hierarchy of the following key is wholly artificial. The numbers in parentheses indicate the couplet from which the current couplet was reached.

- 1. A. Ventral setae occurring anterior to clitellum 2

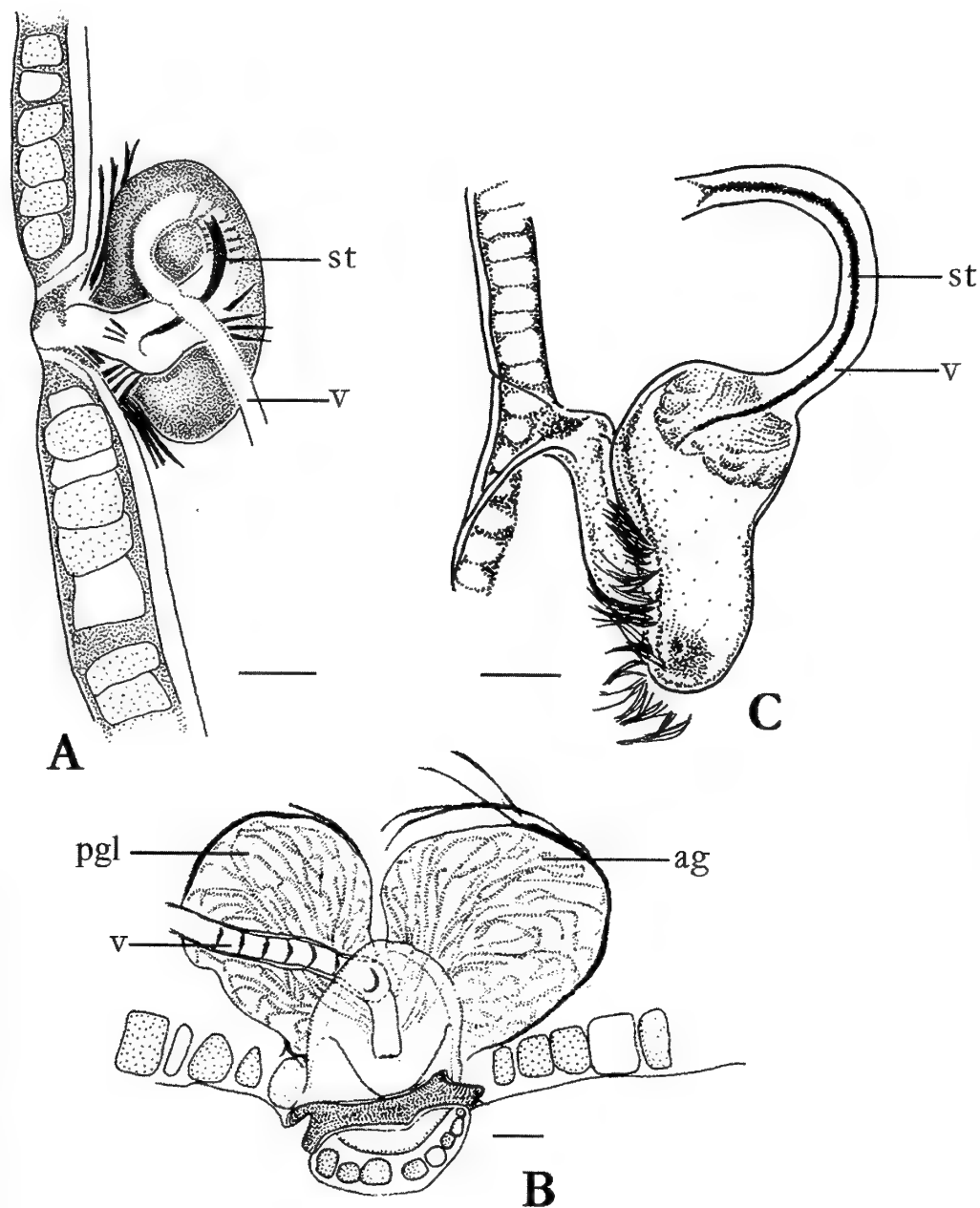


Fig. 6. Male penial apparatuses A. Bulbous gland of *Grania laxarta*, B. Whole apparatus of *Randidrilus codensis*, and C. Bipartite sac of *Grania bermudensis*. Scales equal 20 μ m. ag, anterior gland; pgl, posterior gland; st, stylet; v, vas deferens.

- | | | | |
|-----|----|------------------------------------------------------------|---|
| 3. | A. | Statocyst present (Fig. 5) | 7 |
| (2) | | Penial apparatus with single bulbous gland (Figs. 6A & 7B) | |
| | | Penial stylet absent | |
| | | <i>Grania americana</i> | |
| (1) | B. | Statocyst not present | 3 |
| 2. | A. | No ectal glands present at spermathecal pore | 5 |
| | B. | Ectal glands present at spermathecal pore (Fig. 4A, D) | 3 |

Penial apparatus with anterior and posterior glands at male pore (Fig. 6B)

Penial stylet absent 4

4. A. Two pairs of spermathecae present in V and VI

(3) Ventral seta in II, absent in III to XXI-XXVII

Lateral setae absent
 *Randidrilus quadrithecatus*

B. One pair of spermathecae (Fig. 4D) in V

Ventral setae from II

Lateral setae absent
 *Randidrilus codensis*

5. A. Spermathecal ectal pores dorsal

(2) Penial apparatus a bipartite sac, stylet present (Figs. 6C & 7A) 6

B. Spermathecal ectal pores lateral

Penial apparatus bulbous, stylet absent 10

6. A. Elongate muscular modifications of vas deferens (Fig. 7A)

(5) No statocyst anterior to brain
 *Grania bermudensis*

B. Muscular constrictions of vas deferens

Statocyst anterior to brain
 *Grania hylae*

7. A. Lateral, paired spermathecal pores

(1) Penial apparatus bulbous (Fig. 6A) 8

B. Mid-dorsal, single spermathecal pore

Penial apparatus a bipartite sac
 *Grania monospermatheca*

8. A. Penial stylet absent *Grania reducta*

(7) B. Penial stylet present (Fig. 6A & C) 9

9. A. Setae lacking entirely . . *Grania levis*

(8) B. Setae only postclitellar
 *Grania longiducta*

10. A. Bipartite spermathecal ectal duct

(5) Statocyst present . . *Grania atlantica*

B. Distinct dilation midway along spermathecal ectal duct (Fig. 4C)

Statocyst absent . . . *Grania laxartus*

Systematic Comments

Following are comments on the species included in the key. Particular attention has been given to new taxonomic structures and

our observations are noted as additional comments. Synonymies are found in the most recent references.

Grania americana Kennedy, 1966. Type locality: 0.5 km from North Entrance point, west side of North Bimini, Bahamas. Also known from Florida, Bermuda, and Carrie Bow Cay, Belize. Intertidal and shallow subtidal to 10 m, in sand and sandy-mud. Completely redescribed in Locke & Coates (1999).

Grania atlantica Coates & Erséus, 1985. Type locality: Continental slope off Massachusetts. Known from off the coast of New Jersey, SW of Ireland (NE Atlantic), N of Surinam, Guinea (W Africa) and Luanda, Angola. From depths of 744 to 1518 m, in silty-sand and ooze. Completely described in Coates & Erséus (1985), with new information in Rota & Erséus (1996).

Additional comments on the species: The anterior bilobed brain region consists of a thin extension which connects to an anterior statocyst (Locke 2000), referred to elsewhere as the "head organ" (Rota & Erséus 1996, Rota et al. 1999). The statocyst of *G. atlantica* differs from *G. americana* in that the statocyst vesicle is elongate rather than bulbous, the anterior medial extension of the brain is longer and three to four statoliths are apparent. The relative position of statoliths seem to differ from those of *G. americana* (see Locke & Coates 1999). A statocyst was only clearly visible in three of 21 preserved specimens of *G. atlantica*.

Grania bermudensis Lasserre & Erséus, 1976. Type locality: Castle Island, St. George's, Bermuda. Known only from Bermuda. Shallow subtidal, 8 to 15 m, in coarse coral sand with ripple marks. Completely redescribed in Locke & Coates (1999).

Grania hylae Locke & Coates, 1999. Type locality: ENE of Paget Island, St. George's Bermuda. Also known from Fowey Rocks, Florida. Intertidal, and subtidal, to 17 m, in medium to coarse coral sand, and muddy sand.

Grania laxartus Locke & Coates, 1999.

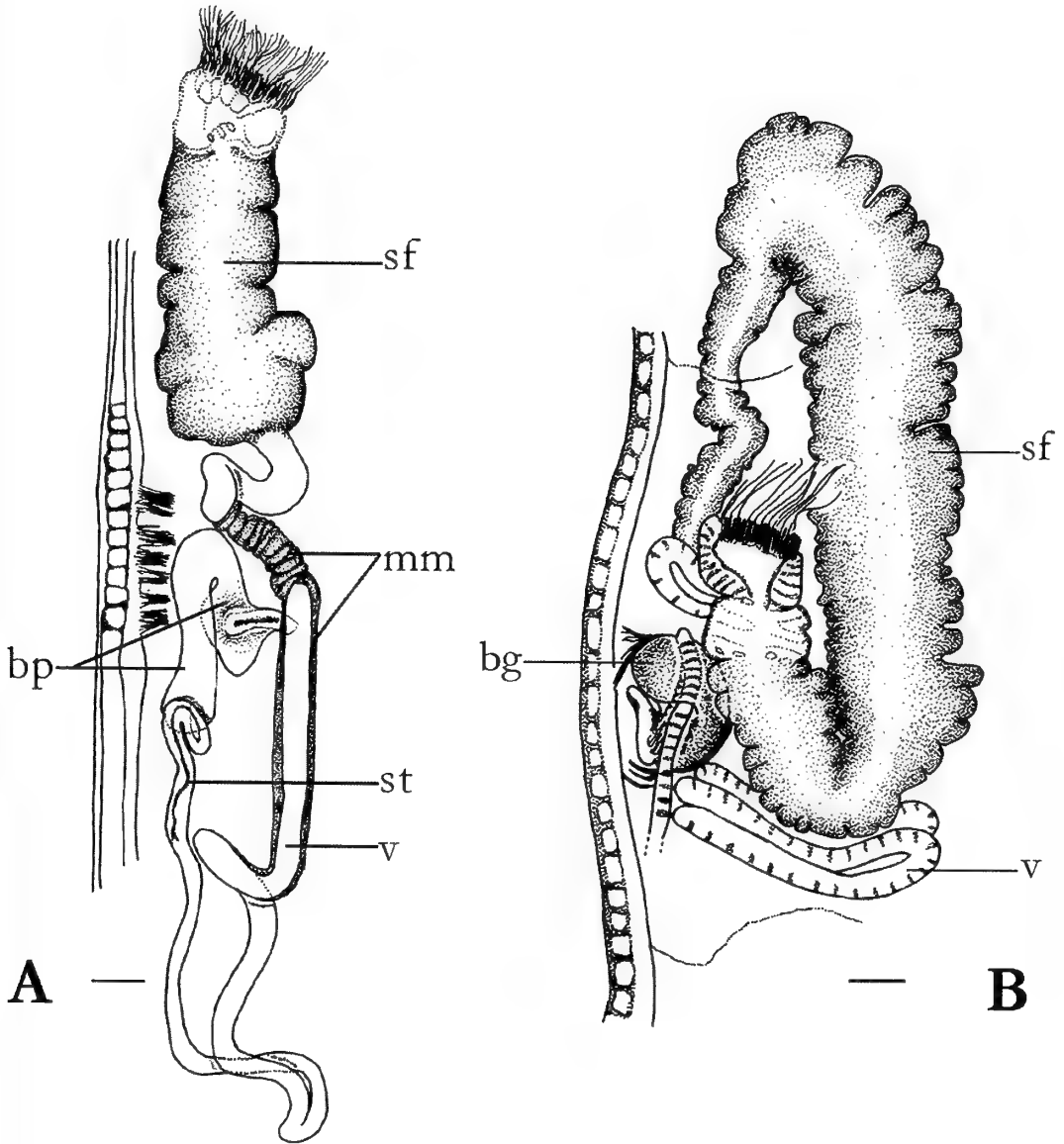


Fig. 7. Male duct systems of A. *Grania bermudensis* and B. *Grania americana*. Scales equal 20 μm . bp, bipartite sac; bg, bulbous gland; mm, muscular modifications; sf, sperm funnel; st, stylet; v, vas deferens.

Type locality: Ferry Point Bridge, St. George's, Bermuda. Also known from Carrie Bow Cay, Belize. Intertidal in poorly sorted coarse biogenic mud and sand.

Grania levis Coates & Erséus, 1985. Type locality: George's Bank (SE of Massachusetts). Also known from off the coast of New Jersey. Subtidal, 42 to 79 m, in medium to coarse sand.

Additional comments on the species: Statocyst not observed in holotype, which appears to be a typical specimen. Thus, it is unlikely that this species has this structure.

Grania longiducta Erséus & Lasserre, 1976. Type locality: Cape Cod Bay, Massachusetts. Also known from George's Bank (SE of Massachusetts), off the coast

of New Jersey, Delaware and Maryland. From depths of 42 to 78 m, in medium to coarse sand. Coates & Erséus (1985) made taxonomic revisions and annotations pertinent to this species.

Additional comments on the species: A narrow, possibly spiraled extension was visible within the anterior region of the bilobed brain; however, a statocyst was not seen anterior to this in 13 fixed and mounted specimens.

Grania monospermatheca Erséus & Lasserre, 1976. Type locality: Cape Cod Bay, Massachusetts. Also known from off the coast of New Jersey, Maryland, North Carolina, NE of Oregon Inlet, Beaufort, North Carolina, and Biscayne Bay, Florida. Subtidal, 3 to 48 m, in sandy-gravel. Redescribed in Coates & Erséus (1985).

Additional comments on the species: The penial apparatus is a terminal bipartite sac, it lacks a bulbous gland and contains a long stylet within a muscular, modified vas deferens. This is called a Type 6 penial apparatus (Coates 1984, Locke & Coates 1999). A statocyst was not seen in any of the 40 preserved specimens observed.

Grania reducta Coates & Erséus, 1985. Type locality: Off the coast of Maryland. Also known from Delaware, and off the coast of New Jersey. From depths of 29 to 65 m, in medium to coarse sand.

Additional comments on the species: Statocyst not observed in two preserved specimens from our collections.

Randidrilus codensis Coates & Erséus, 1985. Type locality: Cape Cod Bay, Massachusetts. Also known from off the coast of New Jersey and Maryland. From depths of 6.7 to 33 m, in medium to coarse sand.

Additional comments on the species: Statocyst not observed in the five preserved specimens that were available.

Randidrilus quadrithecatus Coates & Erséus, 1985. Type locality: off the coast of New Jersey. Also known from Maryland. From depths of 29 to 58 m, in medium to coarse sand.

Additional comments on the species:

Statocyst not seen in holotype, which appears to be a typical specimen. Thus, it is unlikely that this species has this structure.

Acknowledgments

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Appendix 1

Diagnostic characters and definitions for enchytraeids

ampulla (-ae): the ental, enlarged portion of the spermatheca (Figs. 2, 4). Sperm donated by a mate are stored in this part of the spermatheca prior to intracocoon egg fertilization. The ampulla is connected to the exterior of the worm by the ectal duct and an epidermal ectal pore. In species of *Grania* and of the other genera with marine taxa, except *Achaeta*, the ampulla is connected internally to the gut by the ental duct. In most species of *Grania* and some of *Marionina*, sperm rings form in the walls of the ampulla. The ampulla may itself have a single, or several, lateral outpocketings or diverticula.

bi-partite penial sac: a complex sac at the terminus of the penial apparatus, in segment XII, found in species of *Grania*. It consists of two parts joined at a right or acute angle. The ectal or proximal part is an erect invagination of the male pore. The ental or distal part is a longitudinally oriented, muscular sac; when contracted, the walls of this part may be longitudinally ridged. A penial stylet extends into the ridged, ental sac (Figs. 6, 7). The term bipartite, saccate penial apparatus is used for the type of penial apparatus possessing such a sac, Type 6 (Coates 1984, amended by Locke & Coates 1999).

bulbous penial gland: a compact gland, associated with the male pore, in segment XII. Bulbous penial glands may lie alongside and open into an extended invagination of the male pore, or may lie dorsal to and open into a simple, epidermal, male pore. The gland is penetrated by the ectal part of the vas deferens. In species of *Grania*, a penial stylet may extend through the bulbous gland to an extended invagination of the male pore (Figs. 6, 7). In *Randidrilus* there is an anterior and a posterior bulbous gland (Fig. 6B).

clitellum: a region of enlarged, secretory, epidermal cells (see Jamieson 1981) extending from about XI-XIII (Fig. 2). The cocoon into which eggs are released is formed by secretions from the clitellum. In enchytraeids, the epidermal layer of the clitellum is just one cell thick; male (sperm) and female (egg) ducts and pores are within the region of the clitellum; no setae are present ventrally on segment XII once the clitellum is formed.

dorsal blood vessel bifurcation: anteriormost region of the dorsal blood vessel, where it divides to form two, lateral circumpharyngeal vessels (Fig. 5) which travel ventrally, then medially and posteriorly to unite as the ventral vessel. This bifurcation may lie posterior to the brain or near its anterior margin.

ectal duct: duct-like part of the spermatheca lying between the external spermathecal ectal pore and the ampulla (Figs. 2, 4). Sperm from a mate are transported through the ectal duct to the ampulla and, later, out to fertilize eggs. The ectal duct may have glandular cells along its length and/or at its junction with the

ectal pore. The ectal duct may have distinctive dilations or regionation of cell types.

ectal gland: unicellular or multicellular gland at the spermathecal ectal pore (Fig. 4); probably of epidermal origin.

ectal pore: opening of spermathecal ectal duct to the exterior (Fig. 4), located dorsally or ventrolaterally in furrow between segments IV and V, or just posterior to this on segment V and, rarely, VI (see *Randidrilus quadrithecatus*). Usually paired; a few species (e.g., *Grania monospermatheca*) have a single, middorsal pore.

ental duct: duct-like part of the spermatheca between the ampulla and the esophagus; an open canal to the esophagus may be present (Fig. 4). The specific function of an open connection is a matter of speculation (Locke 1999, p. 20; Westheide 1999). It could allow the flow of fluids and intestinal materials between the gut lumen and the spermatheca.

epidermal gland sac: found only in some species of *Achaeta*, all of which lack setae. The solitary sacs are laterally paired and there may be up to three pairs per segment. They are either dorsolateral, or dorso- and ventrolateral, or dorso-, medio- and ventrolateral. Nielsen & Christensen (1959) referred to these as setal follicles or gland sacs but noted that "their true nature is doubtful" (op. cit., p. 16). Setal follicles is synonymous with seta-producing sac or setal sac (Stachowitsch 1992) so the use of that name for the glandular sacs of *Achaeta* implies an homology which is not substantiated.

esophageal (see also oesophageal) appendage: tubular or bulbous organs extending from the posterior of the pharynx or anterior of the esophagus (see Schmelz & Westheide 2000); free floating in the coelom or lying on the dorsal surface of the gut. The unpaired forms are found in the genus *Achaeta*. According to Nielsen & Christensen (1959, 1963) "peptonephridia" are a particular form of these appendages, found only in species of *Enchytraeus*, *Enchylea* Nielsen & Christensen, 1963 and *Fridericia* Michaelsen, 1889. There is no evidence of an ontogenetic relation of these organs to nephridia which is implied by the name peptonephridia (Schmelz & Westheide 2000) and we recommend use of that name be discontinued. At one time there was confusion about the presence of "peptonephridia" in species of *Grania* and this led to the erection of the genus *Hemigrania* for *Grania*-like species which did not have "peptonephridia" (see Locke & Coates 1999). It is now clearly recognized that no species of *Grania* have esophageal appendages (Erséus & Lasserre 1976). The terrestrial genus *Hemienchytraeus* Cernovsytov, 1934b, has a basally unpaired post-pharyngeal or esophageal appendage which Nielsen & Christensen (1959) specifically do not call a peptonephridium. Coates (1987, 1989a, 1989b) studies indicate that this unpaired esophageal appendage had independent origins from the peptone-

phridia of species of *Fridericia* but detailed studies of these structures are in their infancy (Schmelz & Westheide 2000) and nothing is conclusive about their homologies.

head pore: unpaired, dorsal opening from body cavity to the exterior (Fig. 5). Located on the anterior part of the peristomium, at the junction of the peristomium and prostomium, or near the anterior tip of the prostomium as in *Achaeta* and a number of terrestrial enchytraeid genera.

lobed testis sac: lobed, peritoneal membrane enclosing testis, spermatocytes and sperm; originating ventrally on posterior face of septum between segments X and XI (septum 10/11) in the region of the testis. Individual lobes are drop- or pear-shaped. Found in species of *Lumbricillus*. There is one multi-lobed sac for each testis. Stephenson (1930), Coates (1987, 1989a) and Rota (1994) discussed differences between testis sacs and seminal vesicles or sperm sacs.

penial apparatus: the part of the male reproductive system located in segment XII, lying between the ectal end of the vas deferens and the external opening of the male reproductive system (Fig. 2). The penial apparatus of marine enchytraeids may have a penial stylet protruding from the vas deferens, a bipartite sac, a bulbous gland, and an epidermal infolding or invagination at the male pore (Figs. 6, 7). Gustavsson & Erséus (1997) provided a general discussion of atria and prostate glands of aquatic oligochaetes. In that paper, they refer to the penial apparatus of all enchytraeids as the penial bulb. Evolution from a simple male pore to a complex invagination and glandular apparatus at the male pore has occurred within the enchytraeid lineage (Coates 1987, 1989a) so that they do not have homologues of atria and prostates of, for example, tubificid oligochaetes. However, the terms atrium (or genital atrium) and prostate are applied to structurally and functionally comparable or analogous elements of the male reproductive systems of many lineages of animals (Abercrombie et al. 1992), including enchytraeids (Rota 1994). The complex forms of penial apparatus seen in species of *Grania* (Coates 1984, Locke & Coates 1999) were not known when the term penial bulb was first applied to the male pore apparatus of enchytraeids and does not adequately encompass these forms or the simplest forms of the penial apparatus (see Rota 1994).

penial stylet: slender, tapering, tube-like structure in the penial apparatus, reported for some *Grania* species; extends from ectal portion of vas deferens into bulbous penial gland or bipartite penial sac; possibly cuticular (Figs. 6A, C, 7A).

penial gland: a general term for a gland associated with the penial apparatus. In enchytraeids penial glands are usually located, with ducts opening, near or at the male pore. See comments on prostate under penial apparatus.

pharyngeal gland: compact glandular mass which

may occur on the septa at the posterior of segments from IV to VI, or VIII in some species of the freshwater *Cognettia* Nielsen & Christensen 1959, and ventrally in the same segments (Figs. 2 & 5A). Pharyngeal glands are laterally paired in each segment in which they are present. The compound extensions of these glands run ventrolaterally in a compact strand of tissue, anteriorly from the gland masses to the dorsal pharyngeal pad.

post-pharyngeal appendages: see esophageal appendages.

seta(e): also called chaeta(e); chitinous bristles which project from secretory setal sacs in the body wall (Figs. 2, 3); with special epidermal musculature allowing complex movements. Ectal tip single-pointed for all but one freshwater (*Barbidrilus* Loden & Locy, 1980) and one terrestrial (*Aspidodrilus* Baylis, 1914) genus of enchytraeid, variously shaped shaft. General distribution pattern is in four groups or bundles on each segment posterior to the peristomium and anterior to the pygidium. In enchytraeids, the setae are located in two ventrolateral bundles and two more or less lateral bundles on each segment. Setae are never found on the peristomium (i.e., body segment I of oligochaetes); some or all bundles may be missing from one to all other segments. Among marine species, espe-

cially *Grania*, *Randidrilus* and some species of *Marionina*, setae occur singly, rather than in bundles. Jamieson (1981) and Gustavsson (1999) discussed the structure and formation of oligochaete setae.

sperm ring: ring-like bundle of spermatozoa embedded in the walls of the spermathecal ampulla (Fig. 4A–C). Sperm rings are seen in species of *Grania* and marine species of *Marionina*. Mechanism and reason for their formation are unknown. Also see ampulla.

spermatheca(e): female reproductive structure which receives and stores sperm from a mate. Consists of two or three main parts: ectal duct and ampulla, and sometimes an ental duct (Fig. 4); ectal origin in V and, rarely, also in VI; may be paired or single in species of *Grania*.

statocyst: vesicular, ciliate organ with globular inclusions or statoliths (Fig. 5), located anterior to the brain (Rota et al. 1999, Locke 2000); thought to be a geotactic or equilibrium organ; reported only in species of *Grania*; lies below head pore and is dorsal to the anterior bifurcation of the dorsal blood vessel.

vas deferens (vasa deferentia): duct connecting sperm funnel to penial apparatus; with ciliated canal through which sperm travel to the male pore. In species of *Grania*, muscular modifications may be present as bandlike constrictions, knots (short spirals), elongate spirals, and longitudinal bands (Fig. 7).

**Description of a new species and a redescription of
Cirrodrilus aomorensis (Yamaguchi, 1934) with a detailed
distribution of the branchiobdellidans (Annelida: Clitellata) in
northern Honshu, Japan**

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Abstract.—*Cirrodrilus tsugarensis*, a new species, is described and *C. aomorensis* is redescribed from their crayfish host, *Cambaroides japonicus*. A detailed survey of the crayfish and their branchiobdellidans was conducted in Aomori and adjacent Prefectures in northern Honshu, Japan. *Cirrodrilus tsugarensis* was only found in one isolated locality on the Tsugaru Peninsula in Aomori Prefecture, while *C. aomorensis* has an extensive distribution throughout the Prefecture. This survey also confirmed one site containing two introduced species, *Cirrodrilus inukaii* and *C. uchidai*, from Hokkaido.

East Asian branchiobdellidans have been reported as symbionts on freshwater crayfishes and other crustaceans in an area that includes China, southeastern Russia, the Korean peninsula, and Japan (Yamaguchi 1934, Gelder 1987, Timm 1991). Timm (1991:329) divided these branchiobdellidans into two groups—"mainland" and "island" or Japanese. Japan has a high degree of endemism in both the twelve reported species of branchiobdellidans (Pierantoni 1906, 1912; Yamaguchi 1932a, 1932b, 1932c, 1933, 1934) on its only native species of crayfish, *Cambaroides japonicus* (de Haan, 1841). The distribution of *C. japonicus* is restricted to Hokkaido and the northern portion of Honshu Islands. In the latter area, Aomori Prefecture, only one species of branchiobdellidan has been recorded, *Cirrodrilus aomorensis* Yamaguchi, 1934.

Branchiobdella digitata Pierantoni, 1906, is the only reported Japanese branchiobdellidan not belonging to the genus *Cirrodrilus* Pierantoni, 1905. Pierantoni

(1906, 1912) named a number of new species and assigned them to a new genus, *Stephanodrilus*. Professor H. Yamaguchi and others accepted this status until Holt (1967) showed *Stephanodrilus* to be a junior synonym of *Cirrodrilus*. Yamaguchi (1934:196) first questioned the validity of *B. digitata* and later Timm (1991:328) assigned the species to the status of *incertae sedis*, although this status was not included in the world checklist of branchiobdellidans (Gelder 1996a).

The monograph by Yamaguchi (1934) provided the first comprehensive account of East Asian branchiobdellidans. Although a significant resource, its potential value has not been realized because a number of important facts were omitted, including: designation of type specimens, deposition of type specimens in an academic institution for inclusion in their collection's catalogue, description of the exact location where types were collected, and complete type descriptions with independent text and illustrated description of each new species.

When Yamaguchi's preserved specimens, slide collection, and laboratory and field notes appeared to be lost after his death, it seemed unlikely that these omissions could ever be rectified. When Dr. A. Ohtaka rediscovered Prof. H. Yamaguchi's branchiobdellidan slide collection in the care of Dr. Yukiyoichi Kamihira, Hakodate University, Hokkaido, Japan, in 1996, there was hope that the omissions listed above could be redressed from the original specimens and written records. However, this proved impossible as none of the slides had any specimen names on them and the laboratory and field books were not to be found.

As part of a comprehensive review of branchiobdellidans and their crayfish hosts in Japan, the distribution of the native Japanese crayfish, *C. japonicus*, in northern Honshu was studied by Dr. A. Ohtaka and his Japanese colleagues from 1994 to 1999. During this study they found several branchiobdellidan species on the crayfish compared to the single species reported by Yamaguchi (1934). This paper contains a description of a new species, a redescription of *C. aomorenensis*, and the distribution of branchiobdellidans and their hosts found on northern Honshu.

It is usual in Japan to give organisms a common as well as a latinized, Linnean name. This pragmatic system of common names is often used to the exclusion of the Linnean names (Grygier 1993). In recognition of this system and to prevent possible future ambiguity, the Japanese common names are given following the Linnean name in formal descriptions. This will also make it easier to incorporate the taxonomic and distributional information in this paper into the National Survey of Japanese Endemic Species.

Materials and Methods

Unless otherwise stated, branchiobdellidans were removed from *C. japonicus*, fixed in 10% formalin or AFA (Humason 1979) solutions, dehydrated in a graded se-

ries of ethanol and water solutions, cleared in methyl salicylate, and mounted in Canada balsam for examination. The anatomical terminology used in this paper follows that proposed by Gelder (1996b). The term "terete" is used to describe the cylindrical body tapering towards the head and posterior attachment disc, respectively. "Pyriform" refers to a structure that is pear-shaped. Because peristomial appendages are a prime character in the identification of species, particularly in the genus *Cirrodrilus*, a clear definition of the terms "tentacles" and "lobes" is needed. A "tentacle" is an appendage that is as long or longer than wide, while a "lobe" is shorter than it is wide. Some latitude in these terms will always exist due to the contraction or extension of the appendages due to artifacts of fixation. Specimens from the type series of the new species have been deposited in the Division of Biological Sciences, Graduate School of Science, Hokkaido University (ZIHU), Japan, and the National Museum of Natural History (USNM), Smithsonian Institution, Washington D.C., U.S.A.

Cirrodrilus tsugarensis, new species
(Japanese name: Tsugaru zariganimizu)

Fig. 1

Type specimens.—Holotype, ZIHU-1295, on *Cambaroides japonicus* (de Haan, 1841) removed from a stream at the town of Imabetsu, Tsugaru Peninsula, Aomori Prefecture, Honshu, Japan (41°13'13.0"N, 140°33'36.6"E) by A. Ohtaka on the 9 Sep 1997. Paratypes, ZIHU 1296 and 1297, USNM 186574 were collected from the type location on 14 Nov by A. Ohtaka. Seven specimens from the first type collections were mounted in CMCP-10 and after six months the soft-tissues were damaged beyond recognition.

Diagnosis.—Body terete to pyriform, about 1.2 mm long fixed, dorsal segmental appendages absent; head broader than segment 1 and posterior attachment disc; peristomium short, almost as wide as segment

1, tentacle length similar, dorsal lip five tentacles, lateral tentacles three pairs, ventral lip small, not incised, with one pair of lobes laterally; 16 oral papillae present; jaws triangular, similar shape and size, large median tooth with three pairs small teeth across anterior surface; pharynx with one pair of deep sulci; glandular atrium tubular, convoluted, slightly dilated ental half, length about 2.0 times diameter of segment; muscular atrium tubular, length about 1/2 diameter of segment; ovoid bursa length about 1/4 diameter of segment; spermatheca length about 1.3 times segment diameter, pyriform bulb with ental process absent, duct tubular with ental half dilated.

Etymology.—Epithet given for the Tsugaru Peninsular in western Aomori Prefecture, Honshu, Japan, the type locality for this new species.

Description.—Four fixed specimens averaged 1.26 mm in length and ranged from 1.07–1.36 mm long. The body shape is tereete to pyriform with no supernumerary muscles or dorsal segmental appendages (Fig. 1A). The anterior nephridial pores open separately onto the dorso-lateral surface of segment 3. The head slightly broader than segment 1 and posterior attachment disc. The peristomium is shorter than head and nearly as broad as segment 1. There are 11 peristomial tentacles of similar length; five are located on the dorsal lip and three pairs of lateral tentacles. The ventral lip is small, not incised (Fig. 1B, arrowhead), with one small lobe on each side. There are 16 oral papillae. Both jaws are triangular and similar in size with a large median tooth, curved slightly posteriorly, and six small teeth. The median pair of small teeth are located at the base of the large tooth on the anterior margin along with the other two pairs on the lateral crest; dental formula 3-1-3/3-1-3 (Fig. 1C–D). The pharynx has a single deep dorsal and ventral sulcus. A pair of testes is located in segments 5 and 6. The spermatozoa are collected by four sperm funnels. The two funnels in each segment merge into vas efferens that then join

to form a vasa deferentia; each vasa deferentia enters the glandular atrium in its median region (Fig. 1E). The remaining male organs are located in segment 6. The glandular atrium is tubular and convoluted, with the ental half slightly dilated. The total length of the atrium is about 2.0 times the diameter of the segment. This is attached to the muscular atrium, which is about 1/2 the length of the segment diameter. The muscular atrium enters the ovoid bursa, whose length is about 1/4 the diameter of the segment, then merges with an unarmed eversible penis located in the ental half of the bursa. The spermatheca is located in segment 5 and consists of a pyriform bulb without an ental process. The bulb opens into the duct through a small internal papilla. The duct is tubular with the ental half slightly dilated (Fig. 1E). The dorsal epidermis of segment 6 has a thick, localized region of gland cells, two times the thickness of the surrounding clitellum.

Variations.—The median tentacle on the dorsal lip may appear shorter than the other tentacles (Fig. 1B, arrowhead). The ental region of the spermathecal duct and the bulb are usually narrow tubes, but both become distended and rounded when filled with sperm, as shown in Fig. 1E.

Distribution.—Restricted to type locality.

Host.—*Cambaroides japonicus* (de Haan, 1841).

Remarks.—Specimens of this species were found on the surface of the carapace, abdomen, and appendages of the host. No other branchiobdellidans have been found in the type locality.

The small, unincised ventral lip (Fig. 1B) is a constant and important character in the *C. tsugarensis*. Since it is possible that the method of fixation has caused this appearance, the character should be used, but treated with caution. The jaws are shown in Fig. 1D with their teeth pointing posteriorly, a position in which they are usually observed except when feeding. The ingested material in the stomach and intestine of the specimens consisted on small clumps of

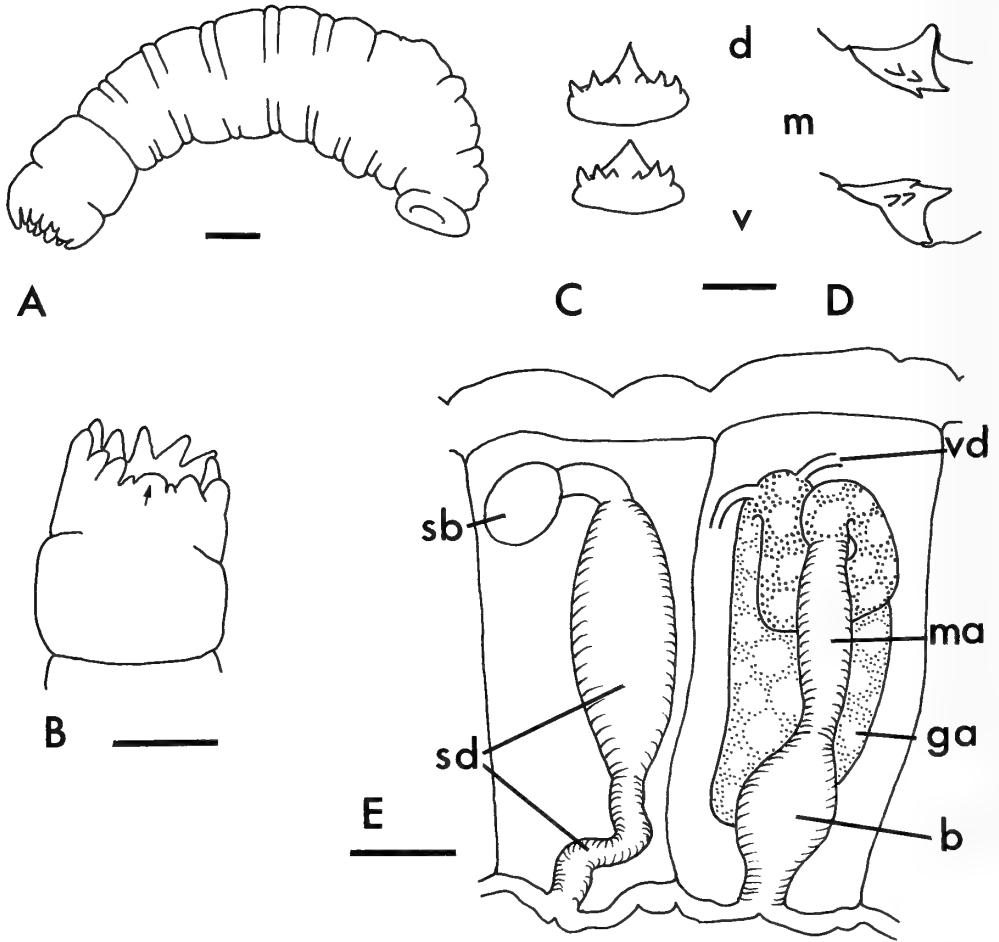


Fig. 1. *Cirrodrilus tsugarensis*: A, Lateral view of holotype, scale bar = 0.1 mm; B, ventral view of the peristomium from a semi-permanent prepared type specimen, scale bar = 0.1 mm; C, jaws of paratype from an anterior aspect, scale bar = 20 μ m; D, jaws of holotype from a lateral aspect, scale bar = 20 μ m; E, segments 5 and 6 with spermatheca and male genitalia respectively from the holotype drawn from the ventral aspect, scale bar = 50 μ m. Abbreviations: b, bursa; d, dorsal jaw; ga, glandular atrium; m, mouth; ma, muscular atrium; sb, spermathecal bulb; sd, spermathecal duct; v, ventral jaw; vd, vas deferens.

“detritus” composed of silt grains and flocculant material. Exoskeletons of arthropod daphnids and the test of a sarcodinid, possibly a cophoderid, were observed.

Discussion.—The combination of features that defines *C. tsugarensis* from other species of *Cirrodrilus* are the number and size of the peristomial appendages, and the morphology of the jaws. However, the form of each of the features is found in other species. The only other described, native branchiobdellidan on Honshu, *C. aomoren-*

sis, is easily distinguishable from *C. tsugarensis* by the seven tentacles of alternating length on the dorsal lip, only two pairs of lateral tentacles, and a dental formula of 4-1-4/4-1-4 with the dorsal median tooth curving anteriorly.

The five dorsal lip tentacles present in *C. tsugarensis* are also found in *C. makinoui*, which is reported only on Hokkaido. In *C. makinoui*, the median tentacle is always shorter than the other four. This character state has been observed once in the new

species. Although Yamaguchi (1934:202) reported that *C. makinoi* had only two pairs of lateral tentacles and an incised, large ventral lip, his drawings of the lateral and ventral views of the peristomium that show three pairs of lateral tentacles or lobes are taken as being accurate. The presence of eight small teeth in a dental formula of 4-1-4/4-1-4, and three pairs of lateral tentacles, separates *C. makinoi* from the new species.

The peristomial tentacle arrangement of *C. tsugarensis* is unlike that on any of the branchiobdellidan species described from the Asian mainland. The new species has a dental formula of, 3-1-3/3-1-3, and this is the same as the following mainland species: *Cirrodrilus kawamurai* (Yamaguchi, 1934), *Cirrodrilus quaditentacularis* (Liu, 1984), *Hidejiodrillus koreanus* (Pierantoni, 1912), and possibly *Cirrodrilus aequiannulus* (Liu, 1984). Whether this dental arrangement is a plesiomorphic condition or a result of convergence is impossible to say at this point. The only other source of anatomical characters is the male reproductive system, which appears to be consistent throughout the genus based on current descriptions.

Emended Species Description

Cirrodrilus aomorensis (Yamaguchi, 1934)
(Japanese name: Aomori-zariganimimizu)

Fig. 2

References.—Yamaguchi 1934:196, Timm 1991:329, Gelder 1996a.

Type material.—None designated by Yamaguchi.

Material examined.—Ten specimens from Professor Yamaguchi's slide collection, probably from Mekasawa or Shichinohe Towns, Aomori Prefecture (Yamaguchi 1934:196); these slides did not carry any species identification, collection data or catalog markings. Additionally 11 preserved specimens that were collected from the Nitose Stream, Tenmabayashi Village, Aomori Prefecture, on 14 July 1999 were

examined. This was supplemented by observations using a Nikon microscope with Normarski Differential Interference Contrast (DIC) illumination on living specimens collected on 24 May 1999 from a branch of the Arakawa River above the Shimoyu Reservoir, Aomori City, Aomori Prefecture. Three specimens from the Tenmabayashi Village collection have been deposited at Hokkaido University museum (ZIHU-1298, 1299, and 1300).

Brief description.—Body terete to club-shaped (Fig. 2A), about 1.3 mm long, dorsal ridges and supernumerary muscles absent, anterior nephridial pores open separately on latero-dorsal surfaces of segment 3, paired lateral epidermal glands on segments 8 and 9; dorsal lip of peristomium with 4 long tentacles alternating with 3 shorter ones, 2 pairs of shorter lateral tentacles, ventral lip with a pair of short lobes laterally and a slight median incision (Fig. 2D); oral papillae 16; jaws dissimilar in size, dorsal larger, large median tooth, 4 pairs of small lateral teeth on anterior margin, ventral jaw smaller with same dentition, dental formula 4-1-4/4-1-4 (Fig. 2B-C); glandular atrium tubular, folded, length about two times diameter of segment, vasa deferentia enter gland three quarters of length from ental end (Fig. 2H); muscular atrium short, spindle-shaped; bursa spherical, penis base sub-conical, narrow, irregularly folded eversible penis entally; spermatheca length is 1.5 times the diameter of segment, sub-spherical bulb entally, a narrow duct, a median spindle-shaped dilation, a prominent papilla separates the median portion and ental chamber.

Variations.—The shape of the body is terete but can appear pyriform if fixation has caused the longitudinal muscles to contract significantly. Similarly, the shape of the peristomial lips and their appendages can vary in proportion to each other in response to fixatives. An optimal view of the peristomium was drawn by Yamaguchi (1934) and was redrawn here (Fig. 2D), however, this condition is rarely found in preserved

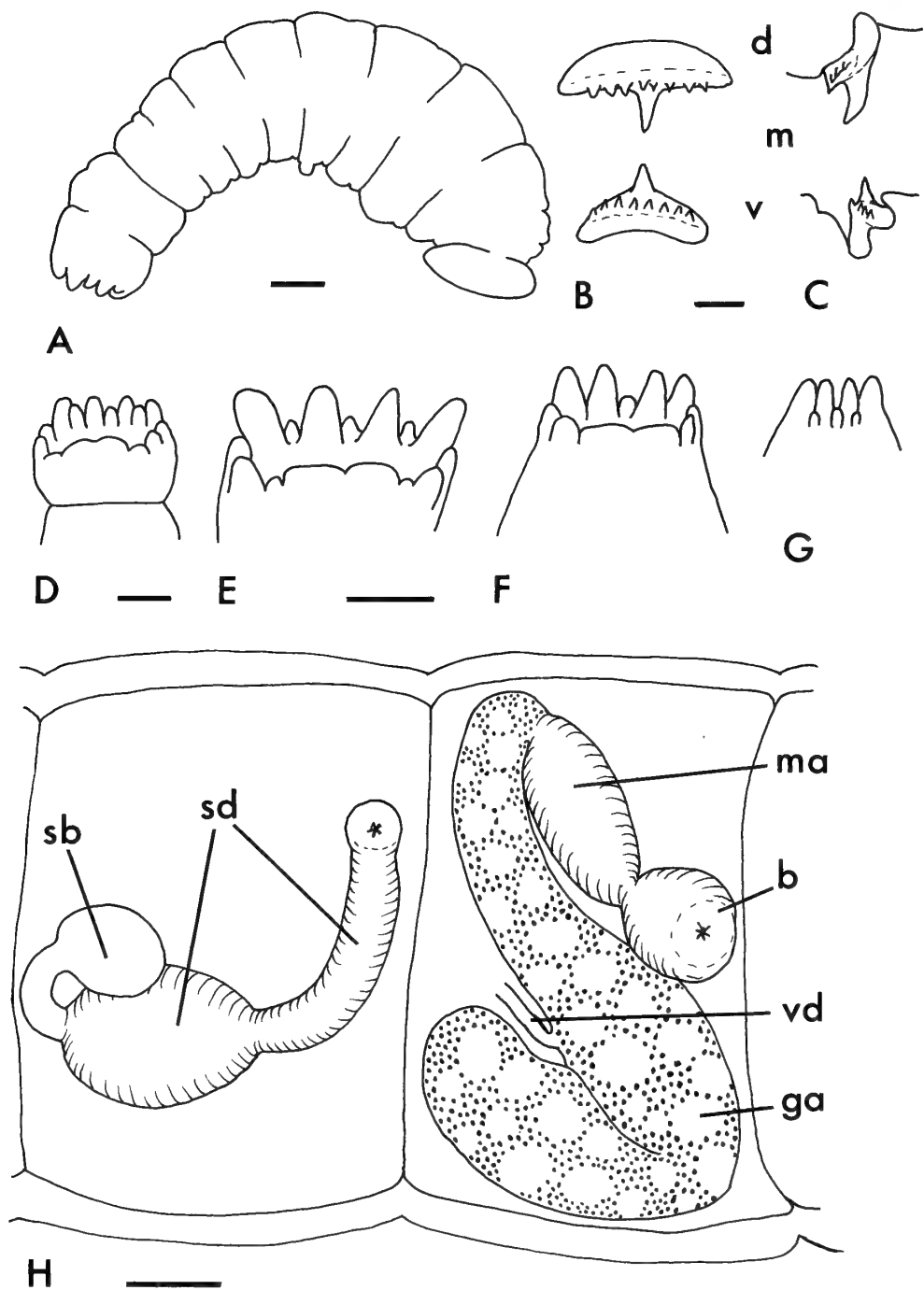


Fig. 2. *Cirrodriilus aomorensis*: A, Lateral view of whole worm, scale bar = 0.1 mm; B, jaws from an anterior aspect; C, jaws from a lateral aspect, scale bar = 10 μ m; D, ventral view of the peristomium redrawn from Yamaguchi (1934:196, fig. 6) scale bar approximately 0.1 mm; drawings of the peristomium of a live specimen E, ventral aspect with light pressure, F, ventral aspect with heavy pressure, G, dorsal aspect with heavy pressure, scale bar = 0.1 mm; H, segments 5 and 6 with spermatheca and male genitalia respectively in a living specimen drawn from the ventral aspect, scale bar = 50 μ m. Abbreviations: b, bursa; d, dorsal jaw; ga, glandular

specimens. Examination of living specimens enables a better and more consistent view of the appendages to be obtained. Even so, the amount of pressure from the cover-glass on the peristomium can significantly effect the number of appendages that are visible (Fig. 2E–G). Note the apparent disappearance of the ventral lip lobes due to increased pressure in Fig. 2F as compared to those shown in Fig. 2E. The small teeth on both jaws may have additional teeth resulting in a dental formula of 5-1-5/5-1-5; spaces in the regular sequencing suggest the position of missing small teeth.

Distribution.—In 20 towns listed in Table 1, and in the towns of Shichinohe and Mekasawa (Yamaguchi 1934), Aomori Prefecture, northern Honshu, Japan.

Host.—*Cambaroides japonicus* (de Hann, 1841).

Remarks.—Specimens of *C. aomorenensis* were found all over the surface of the body, excluding the gill chambers, and never with any other species of branchiobdellidan. The jaws are shown from both an anterior aspect (Fig. 2B) and a lateral aspect (Fig. 2C). The anterior aspect shows the jaws in the greatest detail and is the most useful in identifying specimens. The dorsal jaw is usually found laying parallel to the lumen so that the median tooth points anteriorly out through the mouth (Fig. 2C, m). The lateral teeth similarly point anteriorly and lie just above the cuticle lining of the mouth. In Fig. 2C, the jaws are drawn with the median teeth in dorsal and ventral jaws facing each other; this is a fixation artifact due to the contraction of muscles in the head. The large median tooth on the dorsal jaw in this species is curved anteriorly, which is an unusual but not unique feature. The large median tooth in most species is directed vertically from the jaw or has a slight posterior curve. In these two latter positions, material

ingested into the pharynx would cause the teeth to penetrate the material and hold it in the pharynx. An anterior curve would not act in such a retaining way, but would still puncture the prey while outside of the mouth.

The food and method of feeding has not been reported for specimens of *C. aomorenensis*. Observations on the material in the digestive system show that small oligochaetes, diatoms, and small amounts of organic detritus are ingested. Penetration of the body wall or cell wall during ingestion would release soft materials from the organisms' protective covering for digestion in the stomach. In addition, specimens collected by Yamaguchi and more recently during the present study show the stomach in many specimens to be filled with rounded, amorphous material, the origin of which is not known.

Distribution of Branchiobdellidans and their Host Crayfish in Northern Honshu

Details of the sites from which the crayfish, *C. japonicus*, were collected and its branchiobdellidan symbionts is presented in Table 1. The distribution of four *Cirrodrilus* species in northern Honshu, Japan, is presented in Fig. 3. At this time, *C. tsugarensis* has only been reported from its isolated type locality. Although the extensive distribution of *C. aomorenensis* across most of Aomori Prefecture (Fig. 3) is not unusual, no explanation for the southern limit of both crayfish and branchiobdellidans can be offered at this time. Interestingly, two isolated populations of *C. aomorenensis* on *C. japonicus* were found further south in Akita and Iwate Prefectures. It is possible that crayfish from Aomori Prefecture were introduced into these two locations, or they may be relict populations of a more southern dis-

←

atrium; m, mouth; ma, muscular atrium; sb, spermathecal bulb; sd, spermathecal duct; v, ventral jaw; vd, vas deferens.

Table 1.—Distribution of the crayfish, *Cambaroides japonicus*, and its branchiobdellidans in northern Honshu, Japan, based on specimens collected from 1994 to 1999.

Locality	Prefecture	Species	No. of specimens
Unnamed stream in Sunagamori area, Imabetsu Town	Aomori	<i>C. tsugarensis</i>	10
Unnamed streams, upper Yunokawa River, Kawauchi Town	Aomori	<i>C. aomorensis</i>	25
Unnamed streams, upper Kuchihiro River, Wakinosawa Town	Aomori	<i>C. aomorensis</i>	15
Streams entering Lake Usori, Mutsu City	Aomori	<i>C. aomorensis</i>	36
Unnamed stream in Kamitaya area, Higashidoori Village	Aomori	<i>C. aomorensis</i>	9
Upper Imaizumi River, Higashidoori Village	Aomori	<i>C. aomorensis</i>	30
Unnamed stream on Mt. Fukkoshi-eboshi, Yokohama Town	Aomori	<i>C. aomorensis</i>	12
Unnamed stream, upper Nonai River, Aomori City	Aomori	<i>C. aomorensis</i>	9
Unnamed stream, Shimoyu Reservoir, Arakawa River, Aomori city	Aomori	<i>C. aomorensis</i>	18
Unnamed streams, upper Komagome River, Aomori City	Aomori	<i>C. aomorensis</i>	7
Unnamed stream on Chobo hill, Aomori City	Aomori	<i>C. aomorensis</i>	4
Unnamed stream in Nonaihata area, Hiranai Town	Aomori	<i>C. aomorensis</i>	25
Fudo waterfall on Nishinosawa stream, Hiranai Town	Aomori	<i>C. aomorensis</i>	6
Nitose Stream, Tenmabayashi Village	Aomori	<i>C. aomorensis</i>	20
Unnamed stream in Kuraoka area, Shichinohe Town	Aomori	<i>C. aomorensis</i>	15
Hiyamizunosawa Stream in Fujimori area, Shichinohe Town	Aomori	<i>C. aomorensis</i>	8
Unnamed stream in Tokusaiji area, Namioka Town	Aomori	<i>C. aomorensis</i>	10
Unnamed stream in Oota area, Shiura Village	Aomori	<i>C. aomorensis</i>	10
Unnamed stream, upper Kanagi River, Kanagi Town	Aomori	<i>C. aomorensis</i>	5
Unnamed streams on Mt. Sakai, Goshogawara City	Aomori	<i>C. aomorensis</i>	25+
Upper Tsubokezawa Stream on Mt. Bashin, Goshogawara City	Aomori	<i>C. aomorensis</i>	50+
Magenosawa Stream on Oobuchi River, Goshogawara City	Aomori	<i>C. aomorensis</i>	50+
Upper courses of Iizume River, Goshogawara City	Aomori	<i>C. aomorensis</i>	200+
Unnamed streams in Komozuchi area, Kizukuri Town	Aomori	<i>C. aomorensis</i>	10
Unnamed streams in Kamegaoka area, Kizukuri Town	Aomori	<i>C. aomorensis</i>	8
Streams entering Pond Tubu-numa, Kizukuri Town	Aomori	<i>C. aomorensis</i>	10
Unnamed stream in Maruyama area, Kizukuri Town	Aomori	<i>C. aomorensis</i>	30
Unnamed stream in Yonkenya area, Kizukuri Town	Aomori	<i>C. aomorensis</i>	20
Komorisawa Stream on Mt. Bonju, Namioka Town	Aomori	<i>C. aomorensis</i>	1
Unnamed stream on Mt. Sasamori, Ajigasawa Town	Aomori	<i>C. aomorensis</i>	10
Okushirasawa Stream on Mt. Iwaki, Ajigasawa Town	Aomori	<i>C. aomorensis</i>	30
Upper Chomae Stream on Mt. Iwaki, Iwaki Town	Aomori	<i>C. aomorensis</i>	18
Unnamed stream on Mt. Iwaki in Dake area, Iwaki Town	Aomori	<i>C. aomorensis</i>	8
Unnamed stream in Ishikawa area, Hirosaki City	Aomori	<i>C. aomorensis</i>	38
Unnamed stream in Funada area, Ninohe City	Iwate	<i>C. aomorensis</i>	13
Unnamed stream in Mochida area, Oodate City	Akita	<i>C. aomorensis</i>	3
Unnamed stream in Osarizawa area, Kazuno City	Akita	<i>C. inukaii</i>	20+
		<i>C. uchidai</i>	6

Crayfishes collected by: Doctors A. Ohtaka and S. R. Gelder, and Messers M. Mukohyama, T. Naraoka, M. Oikawa, S. Yamauchi, R. Mayama, A. Abe, M. Sasaki, and Y. Onishi.

tribution. In 1943, *C. japonicus* was introduced into a small stream in Kazuno City, Akita Prefecture (Table 1), from Sapporo, Hokkaido; they were observed to carry *Cirrodriilus inukaii* and *C. uchidai* in 1978 by Mr. T. Komoriya (Japanese Regional report 1978, unpub. obs.). Specimens of the two species were collected by the authors in

May 1999 from the same site in Kazuno City.

Discussion

All of the endemic species of branchiobdellidans reported in Japan are members of the genus *Cirrodriilus* and are found on the endemic crayfish, *C. japonicus*. Although

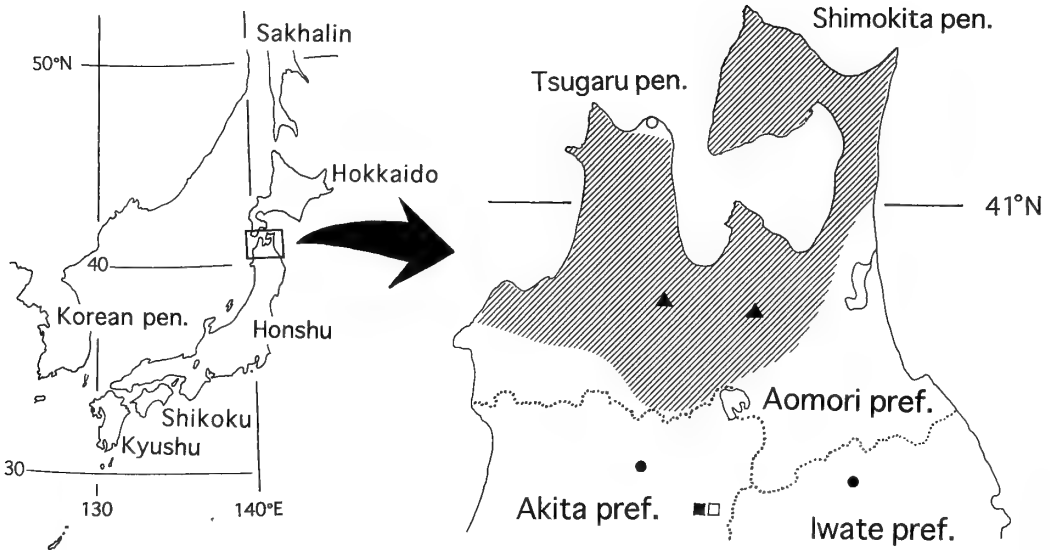


Fig. 3. Map of Japan and adjacent mainland Asia showing the location of Aomori Prefecture in oblong (left). Distribution of branchiobdellidans in northern Honshu, Japan, (right) based on information in Table 1 and other available data: *C. tsugarensis*, open circle; *C. aomorensis*, shaded area (general distribution), solid circles (isolated populations), and solid triangles (original sites from Yamaguchi 1934); *C. uchidai*, solid square; *C. inukaii*, open square.

evidence has been found of *C. japonicus* carrying *Cirrodriulus inukaii* and *C. uchidai* being introduced into Honshu from Hokkaido, no evidence has been found of exotic "mainland" species of crayfish or branchiobdellidans being introduced into Japan. The present work has set the base-line in northern Honshu for observing future developments of the native species as well as the rapid detection of exotic species should they be introduced.

The majority of "mainland" branchiobdellidan species have crayfishes as their hosts, but freshwater shrimps have been adopted successfully as alternative hosts in the following cases: *Caridinophila unidens* Liang, 1963 was found on *Caridina yunnanensis* Yu Shouchie, 1938 in Lake Er-Hai, Yunnan Province, and *Holtodrilus truncatus* (Liang, 1963) on *Neocaridina denticulata sinensis* (Kemp, 1918) from a spring near Sichuan, Hunan Province, and subsequently in the Chanjiang River near Shaoguan, Guangdong Province, China (Liu 1984). The freshwater shrimps, *Neo-*

caridina denticulata (de Haan, 1849), *Paratya compressa* (de Haan, 1849), and *Palaeomon paucidens* de Haan, 1849 have been reported in Japan (Dr. M. Nishino, pers. comm.). Although the distribution of each shrimp species has varying degrees of overlap with *C. japonicus* no branchiobdellidans have been observed on these potential hosts. Therefore, investigators in Japan have a unique opportunity to study the reactions and preferences of branchiobdellidans with respect to potential crustacean hosts other than crayfish. The fact that *N. denticulata* and *P. compressa* are already known to carry the platyhelminth temnocephalid, *Scutariella japonicus* (Matjasic, 1990), which has a very similar ectosymbiotic life style to a branchiobdellidan, makes the project even more intriguing (Gelder 1999).

Although Japan has only one native, crayfish species, crayfishes from North America have been imported into the country for stocking bodies of water since 1926. The history of the introductions of Louisi-

ana red swamp crayfish, *Procambarus (Scapulicambarus) clarkii* (Girard, 1852) and North American signal crayfish, *Pacifastacus leniusculus* (Dana, 1852) into Japan have been reviewed by Kamita (1970). The warm-water species, *P. (S.) clarkii*, is now commonly found from northern Honshu southwards through Japan. Two subspecies of the cold-water signal crayfish, *Pacifastacus leniusculus leniusculus* (Dana, 1852) and *Pacifastacus leniusculus trowbridgii* (Stimpson, 1857) have successfully colonized a mountain reservoir in Shiga Prefecture and another site in Ishikawa Prefecture, both in central Honshu, and in Lake Mashu, eastern Hokkaido, Japan, (Miyake 1973). A new species of branchiobdellidan, *Cambarincola okadai* Yamaguchi, 1933, was described from specimens removed "in 1928" from "crayfish formerly transferred from America into Lake Chuzenji, Nikko" Yamaguchi (1933:191). This species of branchiobdellidan has not been reported in Japan since the original study and further investigations are needed on this exotic symbiosis.

This survey on the distribution of branchiobdellidans and crayfish in northern Honshu has revealed a more accurate picture than was previously available from the two locations of *C. aomorensis* (Fig. 3) reported by Yamaguchi (1934:196). Given the endemism and extremely limited distribution of *C. tsugarensis*, it is easy to see why the species escaped collection previously. It also indicates that other undescribed species may be present in this region. Further studies on the native and exotic species of crayfishes in Japan and their branchiobdellidans are in progress by the authors. These studies are necessary if a clear understanding of the dynamic associations between the native and introduced crayfish and their symbionts is to be obtained.

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***Mahesia ammophila*, a new genus and species of interstitial hesionid (Annelida: Polychaeta) from the Indian Ocean**

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Abstract.—A new small hesionid, *Mahesia ammophila*, new genus, new species, is described from sand sediments of a coral reef flat of the Seychelles island Mahé. A unique combination of characters (e.g., median antenna frontally inserted, exclusively capillary notochaetae, proboscis without distinct papillae) clearly distinguish this new genus and species from other hesionid taxa.

Pleijel's (1998) comprehensive revision of the Hesionidae, including diagnoses and descriptions of all supraspecific taxa, at long last gives us a better overview of the taxonomy of this important polychaete family, which has been so confusing in the past. It will probably provide a further incentive to describe new generic taxa, such as the one presented here. It was discovered in the meiofaunal communities of the littoral sandy sediments around the Seychelles island Mahé. These benthic communities comprise remarkably large numbers of both species and individuals, and have only just begun to be analyzed faunistically and taxonomically (Westheide 2000). The new genus and species described here is one of the relatively numerous interstitial species at this location in this family, although hardly any characters considered to be typical adaptations to the interstitial environment (Westheide 1984) have yet been observed. Among the other interstitial hesionid species are species of *Heteropodarke* Hartmann-Schröder, 1962 (Hartmann-Schröder 1962, Perkins 1984, Ding et al. 1997, Pleijel 1999), *Sinohesione genitaliphora* Westheide, Purschke & Mangerich, 1994 (Westheide et al. 1994) and, especially, the many species of the genera *Microphthalmus* Mecznirow, 1865 and *Hesionides* Friedrich, 1937 (Westheide 1988). The inclusion

of the two last taxa in the Hesionidae has recently been disputed (Pleijel & Dahlgren 1999). Relatively small hesionids can also be found within the genera *Ophiiodromus* Sars, 1862 (e.g., *O. minutus* Hartmann-Schröder, 1959) and *Podarkeopsis* Laubier, 1961 (e.g., *P. arenicolus* La Greca, 1946).

Methods

Animals were extracted from sand with a $MgCl_2$ solution isotonic to seawater (for details see Westheide & Purschke 1988). Live specimens were observed under a light microscope and photographed immediately after sorting. They were fixed in Bouin's fluid; fixed animals were used for making line drawings by means of a camera lucida. Bouin-fixed specimens were also used for scanning electron microscopy; after postfixation in 1% OsO_4 , they were critical-point dried with CO_2 , mounted on aluminium stubs, sputter-coated with gold and examined with a Zeiss DSM 962 scanning electron microscope.

Mahesia, new genus

Diagnosis.—Hesionid with three antennae, the median one frontally inserted. Palps consisting of short palpophore and flask-shaped palpostyle. Four pairs of anteriorly situated biarticulate tentacular cirri

on each side behind prostomium. Chaetigers with capillary notochaetae only; no notoacicula; neuropodium with transparent pointed acicula, heterogomph compound and one to two simple chaetae. Proboscis not armed, without distinct papillae but with ciliary tufts. Anal cirri articulated.

Etymology.—The name *Mahesia* refers to the sampling site of the type species, the Indian Ocean island Mahé.

Type species.—*Mahesia ammophila*, new species, by present designation.

Material examined.—About 20 living specimens from patches of relatively coarse coral sand, covered with shallow water at low tide. Republic of Seychelles, Mahé Island, southern part, east coast, 55°31'E and 4°47'S. Reef flat in front of the beach "Anse Forbans" (22 Feb 1999 and 13 Mar 2000).

Mahesia ammophila, new species

Figs 1–3

Type material.—Holotype whole mounted (glycerine) specimen with 19 chaetigers, deposited at the Senckenberg Museum, Frankfurt, Germany (No. SMF 8897). Two paratypes with 18 chaetigers each in ethanol/glycerine (SMF 8898, 8899) at the Senckenberg Museum and two with 13 and 14 chaetigers in ethanol/glycerine at the Hamburger Zoologisches Museum (P-23240, P-23241). Remaining specimens in the collection of the author.

Etymology.—The first part of the species name is derived from the Greek *ámmos*, sand, the second part is derived from the Greek *philos*, being fond of.

Description.—Pigmentation lacking, animals more or less transparent. Body shape elongated. Length of living animals up to 2.7 mm (23 chaetigers); fixed specimens up to 2.0 mm. Width across body between parapodia ranges from 120 μ m in anterior part and ca. 70 μ m (fixed specimens) in posteriormost part of body trunk, but relatively large parapodial lobes with widely protruding bundles of chaetae giving a

stouter appearance (width including parapodia about 0.5 mm) (Figs. 1, 2B). Number of chaetigers (excluding the anteriorly situated segments with tentacular cirri) between 8 and 23.

Prostomium more or less rectangular, broader than long; lateral margins slightly convex, anterior margin with slightly rounded median indentation (Figs. 2A, 3A). Facial tubercle absent. Palps arising antero-ventrally on both sides of broad upper lip folds leading into mouth opening (Fig. 3B); biarticulated with short palpophore and flask-shaped palpostyle, similar in shape to paired antennae and of nearly same size. Median antenna arising frontally and somewhat dorsally behind paired antennae; latter almost twice as long as median one; all three antennae flask-shaped (Figs. 2A, 3A).

Two pairs of red-pigmented lensed eyes in trapezoidal arrangement (Fig. 2A), anterior pair larger than posterior one. Nuchal organs forming two ciliated fields around posterior edges of prostomial shield; mid-dorsally widely separated (Fig. 3A).

Pharyngeal tube (=proboscis) undivided, straight, reaching posteriorly to chaetigers 3 or 4 (Fig. 1A, B). No jaws or teeth. Terminal part without distinct papillae, but terminal margin with ring of ca. 14 papillate evaginations, each with terminal tuft of cilia; smaller ciliary tufts also in folds between these evaginations (Fig. 3C).

Four pairs of anteriorly situated cirri (tentacular cirri) on each side behind prostomium, each pair consisting of a dorsal and a ventral enlarged appendage; belonging to four segments, the two anterior ones dorsally difficult to distinguish (Figs. 1A, B, 2A, 3A, B). No chaetae detected in these segments, except for one tiny acicula in dorsal cirrophores of segment 4. Cirri biarticulate, with relatively long cylindrical cirrophores; cirrostyles basally slightly inflated, tapered. Dorsal cirri gradually increasing in length from first to third pair; fourth pair distinctly shorter. Ventral cirri shorter than dorsal ones (Fig. 3B).

Chaetigers (Figs. 2B, 3D, E) identical ex-

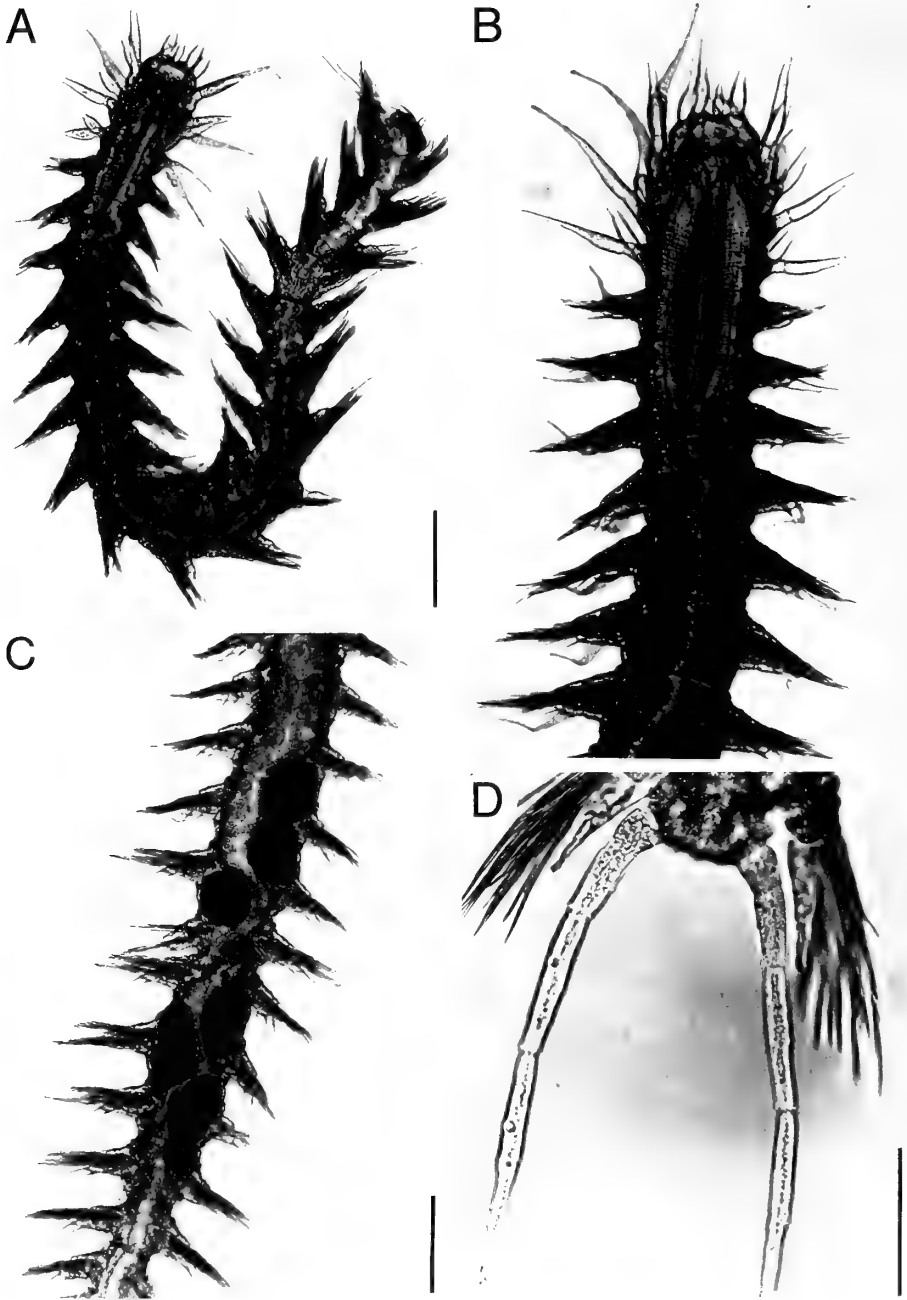


Fig. 1. Micrographs of living *Mahesia ammophila*, new genus, new species. A, entire animal; B, anterior region; C, median region of female with vitellogenic oocytes; D, pygidium with anal cirri. Scale bar in A, C = 200 μ m, in B, D = 100 μ m. Focused on dorsal side.

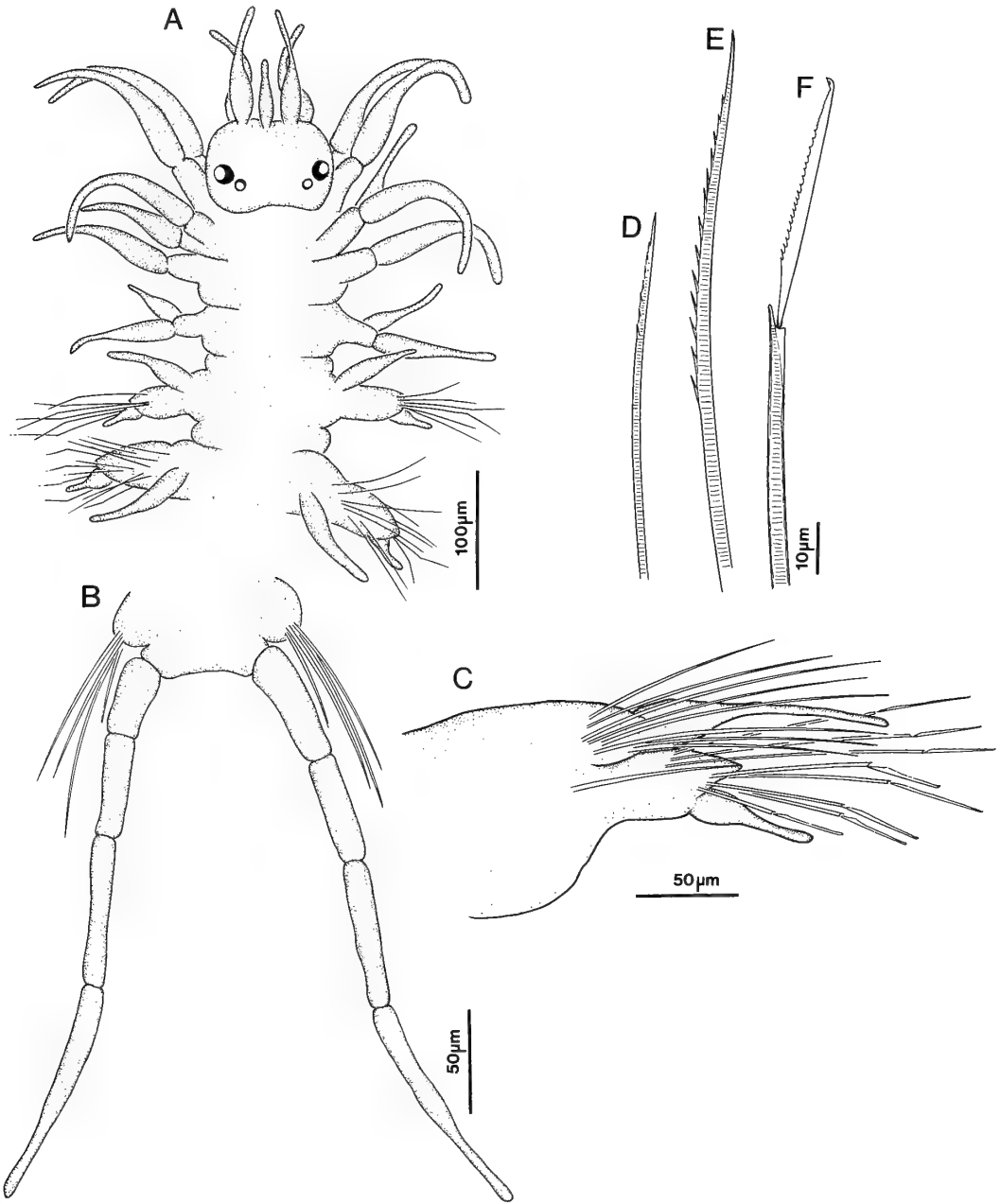


Fig. 2. *Mahesia ammophila*, new genus, new species. A, anterior end, dorsal view; B, pygidium with anal cirri; C, parapodium from posterior part of body, anterior view; D, simple neurochaeta; E, simple notochaeta, only one row of teeth visible; F, compound neurochaeta. Same scale for D-F.

cept for first one (segment 5), lacking notochoetae in larger specimens; in one specimen with 12 chaetigers few notochoetae still present. Dorsal parapodial cirri neither enlarged nor alternating in length, but pos-

teriormost ones slightly or (in large specimens) considerably longer. Dorsal cirri usually not exceeding length of ventral compound chaetae; basal third inflated; tapering, not annulated. From chaetiger 2

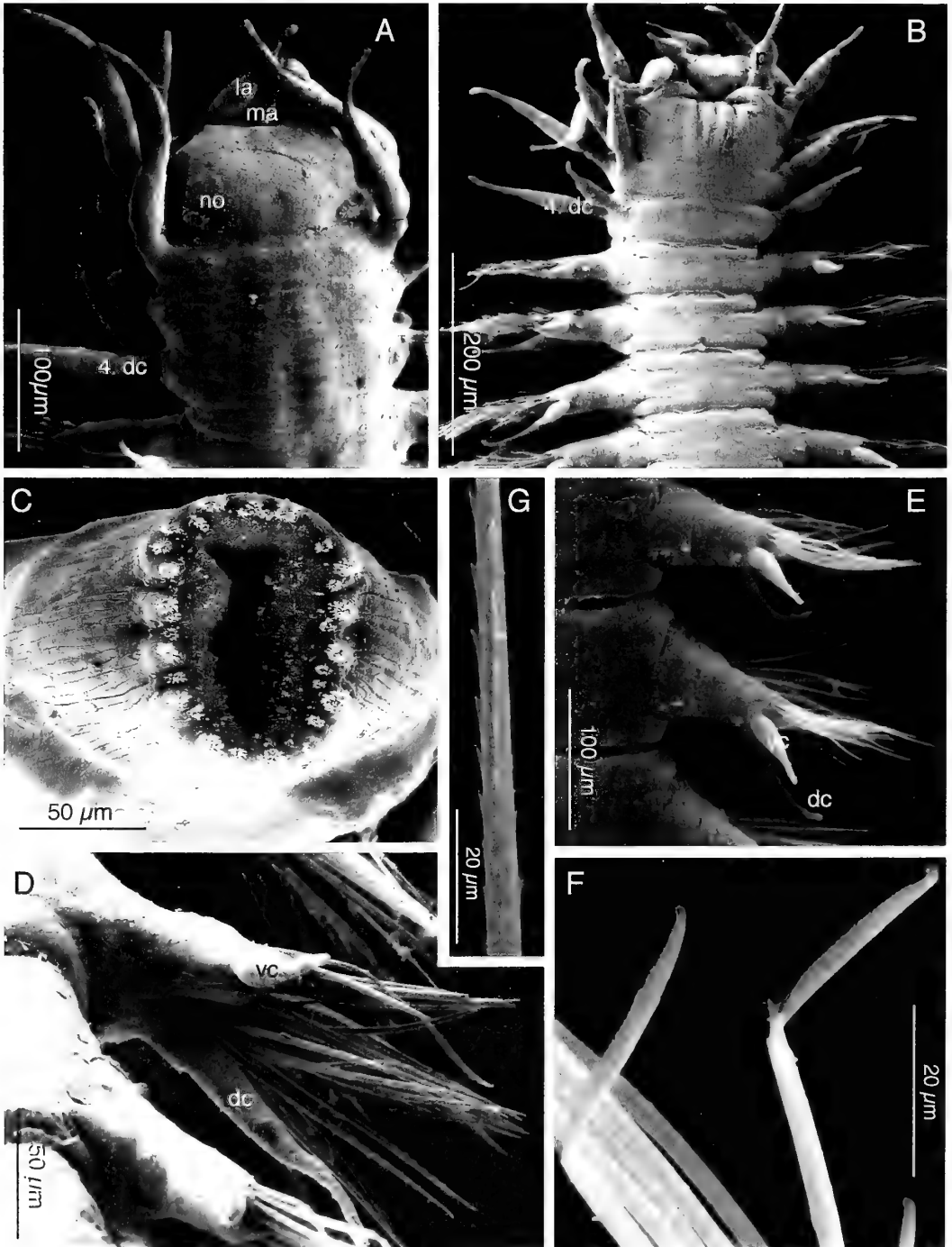


Fig. 3. Scanning electron micrographs of *Mahesia ammophila*, new genus, new species. A, anterior end, dorsal view; B, anterior end, ventral view; C, terminal part of everted pharynx; D, E, parapodia, middle part of body, ventral view; F, compound neurochaetae; G, capillary notochoeta, partly. Abbreviations: dc, dorsal cirrus; la, lateral antenna; ma, median antenna; no, nuchal organ; p, palpus; vc, ventral cirrus.

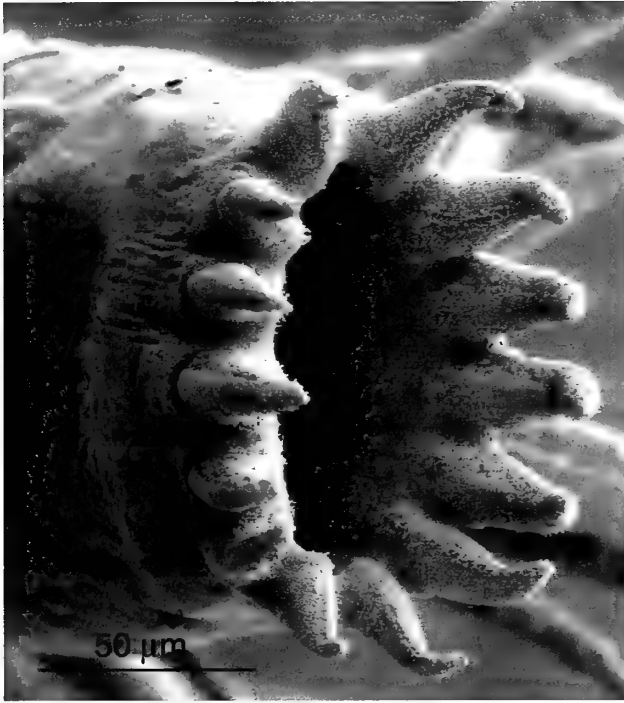


Fig. 4. *Sinohesione genitaliphora* Westheide, Purschke & Mangerich, 1994. Scanning electron micrograph of terminal part of everted pharynx.

posteriorly notopodial lobe with bundle of up to ca. 16 capillary chaetae, slightly bent; slightly increasing in length posteriorly; with two rows of teeth (Figs. 2E, 3G). Notopodial acicular lobes absent; no notoacacula. Neuropodial lobe rhomboidal. Single transparent pointed neuroacacula. Bundle of up to ca. 15 heterogomph compound falcigers with narrow blades of different lengths, densely and uniformly serrated distally, unidentate; blades gradually increasing in length posteriorly (Figs. 2F, 3F). With 1–2 simple capillary neurochaetae (Fig. 2D), anteriorly situated. Number of chaetae different in different specimens, probably age dependent. All chaetae internally chambered throughout entire length (Fig. 2D–F). Ventral cirrus flask-like, without cirrophore; about half as long as dorsal cirrus (Figs. 2C, 3D, E).

Pygidium nearly hemispherical. Two thread-like anal cirri, oriented like a posteriorly open V, up to 300 μm long; with 1–

4 distinct articulations dividing cirri in 2–5 elongate pieces, distal one especially long and tapered (Figs. 1D, 2B). No median unpaired anal appendage. Laterally between last chaetiger and pygidium one or a few chaetae occasionally present, probably indicating development of new parapodia.

Remarks.—Two of the specimens observed alive were females, each carrying up to 8 spherical or oval oocytes (diameter 75–100 μm), positioned between chaetigers 8 and 13 (Fig. 1C), indicating that the species description is based on adult animals.

Discussion

The new species does not fit in any of Pleijel's (1998) generic diagnoses of Hesionidae. It would follow from the cladistic analysis of this author that the frontally inserted median antenna of *M. ammophila* would place it into his subtaxon Ophiodromini. Median antennal furrows and pro-

boscideal papillae would then have to be regarded as reduced. In the taxon *Parasyllidea* Pettibone, 1961, which he also places in this group, the terminal proboscis ring bears no papillae but, instead, fine hairs, presumably cilia (Pettibone 1961, Hartmann-Schröder & Hartmann 1980). This taxon is to some extent consistent with the present species regarding this character, but not in the presence of notochaetae, which are absent in *P. humesi* Pettibone, 1961 and *P. australiensis* Hartmann-Schröder, 1980.

Sinohesione genitaliphora Westheide, Purschke & Mangerich, 1994 resembles *Mahesia ammophila* in the structure of its anterior end (Westheide et al. 1994), but these two species clearly differ in the structure of the terminal ring of the proboscis, which in *S. genitaliphora* bears 14 cone-shaped, broadly based papillae and is here depicted in detail for the first time (Fig. 4). When the new taxon is run with Pleijel's (1998) matrix and both *Sinohesione* and *Mahesia* are scored for 14 papillae, they come out as sister taxa in a cladistic analysis. If this character is excluded, *Mahesia* still falls out within the Ophiodromini but in a different position (F. Pleijel, pers. comm.). Most prominent characters that distinguish *Mahesia* and *Sinohesione* are the external genital organs of the latter in both males and females (Westheide et al. 1994).

Proboscideal papillae are also lacking in *Amphiduros* Hartman, 1959, but this genus has a dorsally inserted median antenna, an autapomorphic character for Pleijel's (1998) hesionid subtaxon Gyptini. However, *Amphiduros* exhibits a number of other similarities to *M. ammophila* (Hartman 1968, Blake & Hilbig 1990, Nuñez et al. 1997, Pleijel 1998): there is no facial tubercle, anterior segments (tentacular cirri segments) 1–4 lack chaetal bundles, notopodial lobes and notochaetae are absent on segment 5, notopodial capillaries have two rows of teeth, furcate notochaetae are absent, and neurochaetae have unidentate blades. This raises the question of the homology of the

position of the median antenna and the importance of this character for phylogenetic reasoning within the Hesionidae. Until more information is available, a close relationship of *Mahesia* with *Amphiduros* is considered no less likely than that of *Mahesia* belonging to the Ophiodromini.

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***Macrothrix marthae*, a new species (Crustacea: Anomopoda: Macrothricidae), a highly specialized macrothricid from Mexico**

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Abstract.—*Macrothrix marthae* new species is described from a tropical epicontinental lagoon, near the gulf coast of Mexico. The structure of the second antenna resembles some taxa related to the *Macrothrix triserialis*-group, but mostly to the South-American *Macrothrix superaculeata* (Smirnov, 1982). However, parthenogenetic females of *M. marthae* are characterized by both morphological differences and strong specialization for scraping in the thoracic limbs I–V. Some of these distinguishing characters are: internal distal lobe of trunk limb I with three strongly pectinate setae, limbs II, III, and V with modified setae bearing well-developed pectens. The postabdomen has small spines, with no lobe formation. The new species was found to be associated with water hyacinth roots, and the adaptations observed are thought to be used to scrape efficiently organic matter from these roots.

Recently, several new species of cladocerans have been found in Mexico. Among them, three new species of *Macrothrix*, *M. mexicanus* Ciroso-Pérez, Silva-Briano & Elías-Gutiérrez, 1996, *M. smirnovi* Ciroso-Pérez & Elías-Gutiérrez, 1997 and *M. sierrafriatensis* Silva-Briano, Quang Dieu & Dumont, 1999, were described from high-altitude aquatic systems, located more than 2000 m above sea level. Our examination of lowland lakes and ponds of southeast Mexico yielded specimens of a new species of *Macrothrix*. These surveys in tropical zones of Mexico have made known several new species of freshwater crustaceans such as copepods (e.g., Fiers et al. 1996, Suárez-Morales & Elías-Gutiérrez 2000) and cladocerans (e.g., Elías-Gutiérrez & Suárez-Morales 1999). These new records resulted from studies in zones and environments such as temporary small ponds and periphytic habitats that were overlooked by specialists until the last decade.

Dumont (1994) suggested that in the tropical areas of the world there is an underestimation of the cladoceran species and predicted that most of the new taxa described will be from these regions. In this paper a new macrothricid cladoceran is described from the coastal plateau of southeastern Mexico, in an aquatic system associated with the Usumacinta river.

Materials and Methods

Samples were collected from water hyacinths by filtering the water from the roots with a 50 μm mesh plankton net; the material was then fixed with sugar formaldehyde (Haney & Hall 1973).

All measurements of the specimens were made following Smirnov's (1971) criteria. Structures were dissected with tungsten needles and then mounted in a glycerin-formaldehyde mixture for a detailed analysis. Drawings were made with the aid of a

camera lucida attached to a Zeiss microscope. Several females were dehydrated in a series of ethanol-water solution from 15% to 100%. After this, animals were dried by the critical point method, mounted, gold-coated, and examined with a Topcon SM-510 scanning electron microscope (SEM) at 10–15 kV. Descriptions were based on both SEM photographs and camera lucida drawings.

Macrothrix marthae, new species

Figs. 1–24

Material.—Holotype: One adult ovigerous female (total length 0.52 mm, height 0.37 mm), preserved in 4% formaldehyde solution, with a drop of glycerol. Vial deposited in The Natural History Museum (NHM), London (1999.1882), 12 January 1998. Paratypes: One ehippial female, in 4% formaldehyde solution, with a drop of glycerol added, NHM 1999.1883, 12 January 1998. Two parthenogenetic females in same medium, Zoological Museum of Moscow University, ZMMU, 12 January 1998. Two adult parthenogenetic females, each dissected and mounted on a slide in glycerine, sealed with DePeX mounting medium. Three parthenogenetic females in formaldehyde solution, deposited at El Colegio de la Frontera Sur (ECO-CH-ZOO 783, 784 and 785).

All remaining specimens and original samples deposited in El Colegio de la Frontera Sur, Chetumal, Mexico.

Type locality and habitat.—Playa del Pozo Lake, located near the Villahermosa city airport, Tabasco State, Mexico (18°00'41"N, 92°17'11"W), 12 Jan 1998: Altitude 10 m above sea level, water temperature of 30.3 °C (air temperature 29.3 °C), pH 6.96, depth 1.66 m, and Secchi disk transparency 0.58 m. *Macrothrix spinosa* King, 1853 was found at the same site.

Etymology.—The species name honors Martha Elena Valdéz-Moreno (wife of Elías-Gutiérrez), for her strong support and understanding to his cladoceran studies.

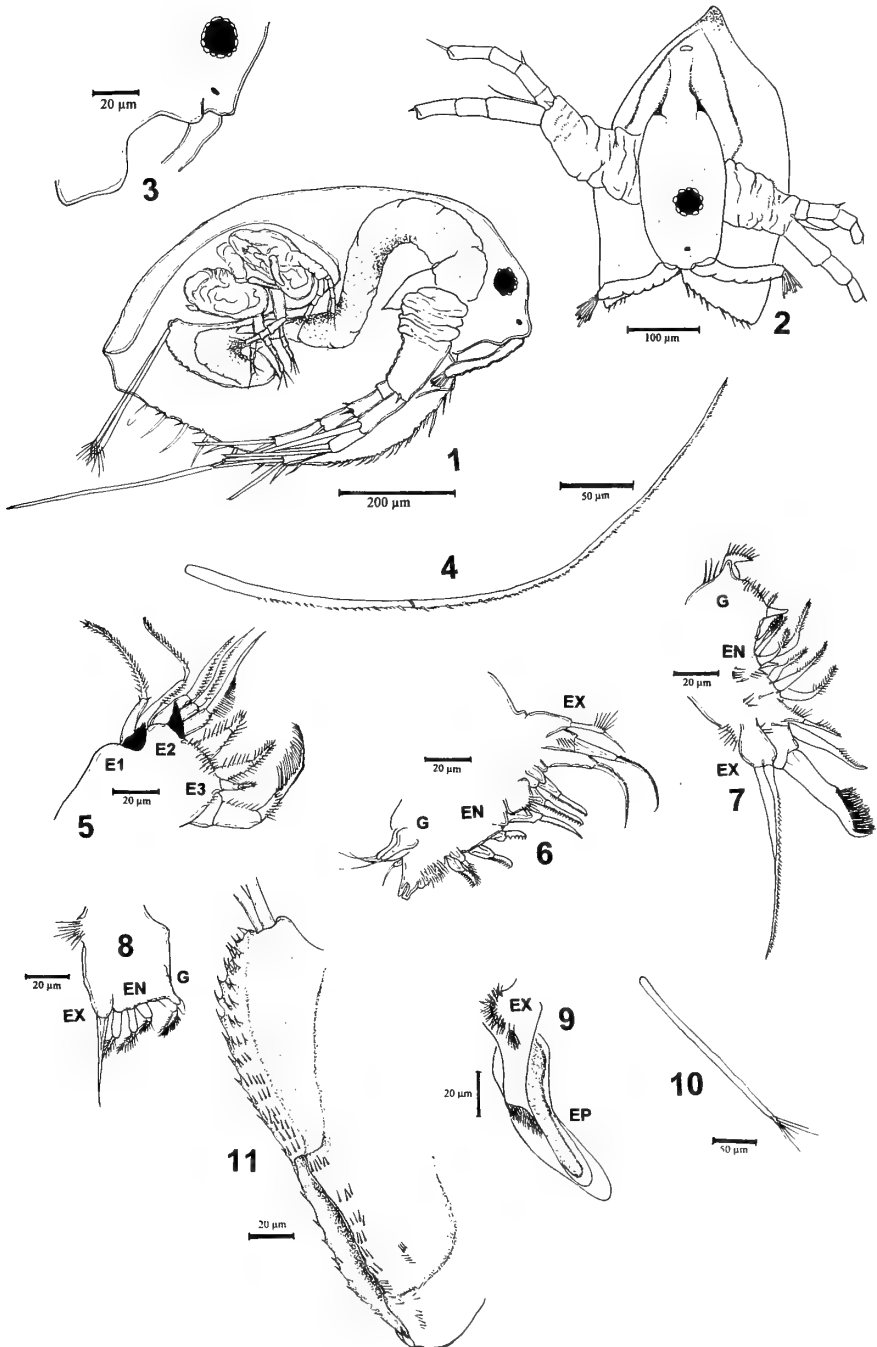
Diagnosis.—This species is characterized by the arrangement of antennal armature, which is one spine on the distal edge of segments 2 and 4 of the endopod branch, plus an accessory spine on segments 2 and 3, about a half length of the other spines; strongly pectenate setae on limbs I, III and V, not seen in any other known *Macrothrix*; postabdomen with no lobe formation, pre-anal postabdominal spinules subequal in size, and arranged in a stripe of several rows. Claws small and pecten-like. Distal segment of postabdominal seta natatoria very short, more than 17 times shorter than proximal segment.

Measurements.—Mature parthenogenetic females: Total length of the body from 0.44 to 0.6 mm, height from 0.27 to 0.39 mm.

Description of parthenogenetic female.—Shape and shell: Body ovoid (length: maximum height = 1.40–1.63). Dorsal margin curved from supraocular region to posterior-dorsal angle (Fig. 1); a pointed keel at the top of the shell (Fig. 2). Dorsal margin of shell without serration, ventral margin serrated, mainly on the anterior half. Two rows of movable different-sized spines inserted along the submarginal edge on the posterior half. External row of sparse leaf-like spines of about the same size, directed outwards. Inner row of smaller spines directed inwards. Each one of the latter alternating with every leaf-like spine. Entire surface of shell dotted and striated with a polygonal pattern.

Head: Evenly rounded, with noticeable supraocular bulge tapering to rostral region (Fig. 1). Frontal part of rostrum trilobed, each lobe subequal in size. Lateral ridges absent. Head pore large and subcircular. Ventral margin of head, in lateral view, with lobe behind insertion of antennule (Fig. 3). Labrum small, triangular, continuing ventral margin of head (Fig. 3). Labral apex blunt. Compound eye located close to midpoint between dorsal and ventral edges. Ocellus close to rostral apex, about 5 times smaller than compound eye.

First antenna (Figs. 12–13): Rod-shaped



Figs. 1–11. *Macrothrix marthae*, new species, Playa del Pozo, Tabasco State, Mexico. Parthenogenetic female. 1, lateral view (distal segments of antennal setae are omitted); 2, frontal view; 3, ventral margin of the head with labrum; 4, seta on first endopodal segment, proximal and distal segments; 5, right first trunk limb, endites 1–3 (from left to right side; outer distal lobe and inner distal lobe are omitted); 6, left trunk limb II, lateral view (in the upper part is the exopod with a soft seta armed with long, tiny setules); 7, right trunk limb III, lateral view (in the lower part is the exopod with two long setae); 8, right trunk limb IV, lateral view (to the left is the exopod with a seta); 9, left trunk limb V, lateral view; 10, seta natatoria of postabdomen; 11, Postabdomen. Abbreviations: E1, endite 1; E2, endite 2; E3, endite 3; EN, endopodite; EX, exopodite; G, gnathobase; EP, epipodite.

(length:width = 5.2–5.3) inserted subapically, not dilated distally, with single ventrolateral basal sensory seta. Distally, relatively long spines surround insertion of aesthetascs. Laterally, the entire surface has 8–10 transverse rows of small spines arranged in groups of 3–5 (Fig. 12). Medially, several groups of two spines, each distributed over the whole surface (Fig. 13). Nine aesthetascs on distal end, all of them unequal in length (Figs. 12 and 13).

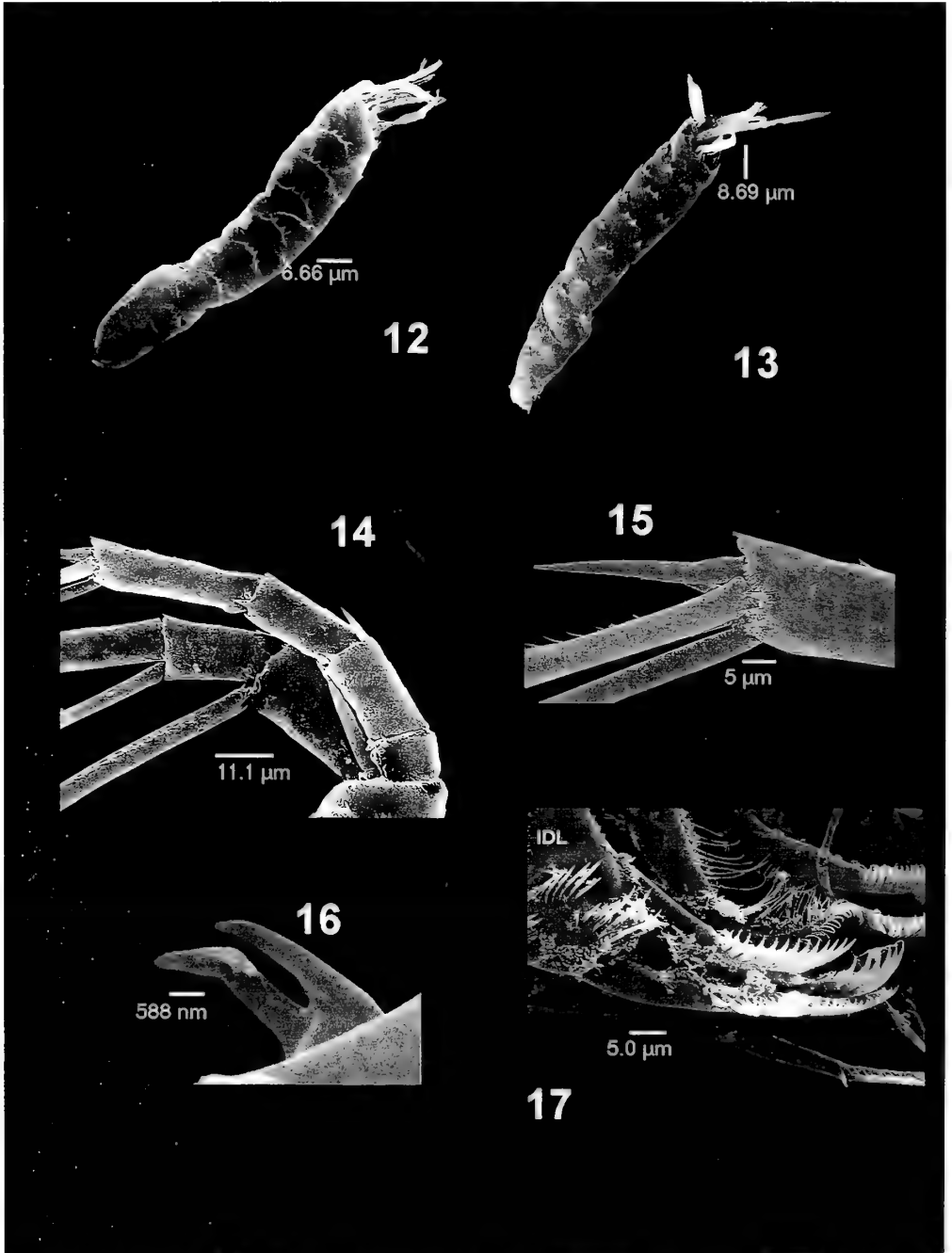
Second antenna (Figs. 14–15): Coxa massive; as in other macrothricids, basal region appears annulated with several folds, with several rows of tiny denticles on lateral margin; one soft seta on middle of medial apical region. Lateral surface of distal portion with a small spine. Swimming setae 0-0-1-3/1-1-3, spines 0-2-1-1/0-0-1. All exopodal setae carry spines on distal segment, except for innermost apical member. Exopod with one spine on distal edge of segments 2 and 4. Internal spine on segments 2 and 3, both subequal in length (Fig. 14). Exopod tip with two different sized groups of spinules. Large ones arranged in groups of 4–5 members, smaller ones in groups of 5–7. Surface of all antennal segments with rows of fine scale-like spinules. First endopodal segment with the longest seta (Fig. 4). This seta is bisegmented (distal: proximal = 1.8), stout, sclerotized, and long (body length:seta length = 1.18–1.34). Convex margin armed with fine spinules on the first $\frac{3}{4}$ of proximal segment, followed in the last quarter by alternating stronger spines and groups of 3–5 fine spinules. This arrangement continues along distal segment, but groups of spines decrease in size distally. Second and third endopodal segments covered by rows of fine spinules.

Trunk limb I (Figs. 5, 16–19): Exopod (outer distal lobe, ODL) slender, bearing an apical seta with chitinized setules along distal third (Fig. 18). Internal distal lobe (IDL) with three strongly pectenate setae, unequal in length (Figs. 17, 18). The two longest ones with second half pectinated. Remaining one with the stronger pecten reduced at

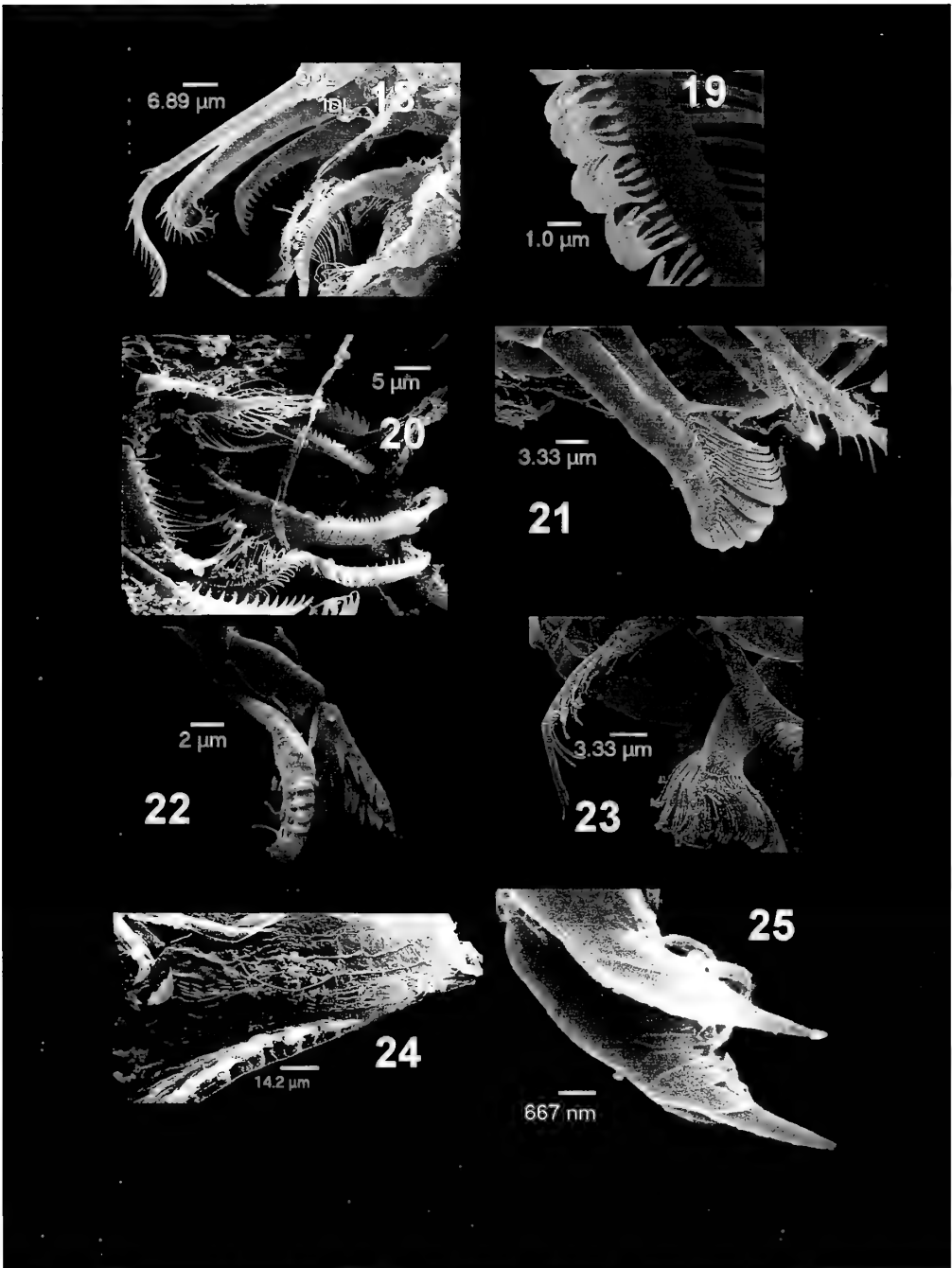
distal third. Posterior surface of IDL with groups of strongly chitinized setae (Fig. 17). Endite 3 with four setae, different in size, two of them equal in length, bisegmented; shortest one segmented, densely pilose at tip. Longest one with peculiar armature formed by approximately six short setules fused into a plate, with successive plates aligned along one margin of the seta (Figs. 18, 19). Opposite side to these plates armed with long setules (Fig. 19). Endite 2 with three bisegmented setae, two of them setulated along distal section and with row of sparse setules on proximal joint. Remaining one with setules only on proximal half of second segment, increasing abruptly in size and decreasing gradually toward tip. Endite 1 with two plumose setae, both of them bisegmented (Fig. 5). Inner spines on endite 1 and 2 with furrow on one of the two teeth where the opposite teeth can be engaged (Figs. 5, 16).

Trunk limb II (Figs. 6, 20): Exopod reduced, with apical soft seta with long, tiny setules at the middle. Endopod with row of eight scrapers, six proximal similar in structure, with a distinct base, and distally with a pecten of strong, sclerotized teeth (Fig. 6). Scrapers 1–3 shorter than 4–6. Scrapers 7 and 8 long, bisegmented, with second segment densely setulate, with triangle-shaped lobe densely ciliated on the apex, located on external surface of the endopod, near the insertion of scrapers 4 and 5. Adjacent to scraper 1, also on the external margin, there is a bisegmented seta, densely pilose on distal section. Gnathobase with reduced filtering comb composed by four small setae, and a probable receptor represented by a reduced seta-like structure.

Trunk limb III (Figs. 7, 21–22): Exopod with two long setae unilaterally setulated. Endopod with distalmost seta stout, sclerotized, with strong pecten developed on distal third (Fig. 21), followed by two smaller setae (Fig. 22), each with a strong brush-like pecten on distal part. External margin with one small setulated seta. Internal armature with seven unequal setulated setae.



Figs 12–17. *Macrothrix marthae*, new species, Playa del Pozo, Tabasco State, Mexico. Parthenogenetic female. 12, first antenna, lateral side; 13, first antenna, medial side; 14, second antenna, medial view; 15, tip of exopod, medial side; 16, trunk limb I, inner spine of endite I; 17, trunk limb I, setae on inner distal lobe (IDL).



Figs. 18–25. *Macrothrix marthae*, new species, Playa del Pozo, Tabasco State, Mexico. Parthenogenetic female. 18, trunk limb I, setae on outer distal lobe (upper side) and inner distal lobe (in the middle). At the lower part is seen the longest seta from endite 3, with plate-like projections; 19, detail of longest seta from endite 3, showing plate-like projections forming successive transverse rows; 20, trunk limb II, scrapers 3–6; 21, trunk limb III, distalmost seta with a strong pecten; 22, trunk limb III, smaller setae after distalmost seta; 23 trunk limb V, strong pectinated seta; 24, postabdomen, dorsal view; 25, postabdominal claws.

Gnathobase sub-rectangular, with two finger-like lobes on each corner and a strongly setulated "L"-like seta on proximal part (Fig. 7).

Trunk limb IV (Fig. 8): Much reduced. One apical naked seta on exopod. Armature consisting of three bisegmented subequal setae, densely pilose plus one tubular sensillum on proximal part. Gnathobase reduced, formed by a densely setose seta and a finger-like lobe. One of the sides of the former armed with more strongly chitinized setules.

Trunk limb V (Figs. 9, 23): Exopod reduced, with small densely pilose seta and a strong, well-differentiated pectinated seta (Fig. 23). Epipodite large, ovoid.

Postabdomen (Figs. 11, 24): Ovoid in lateral view (body length:postabdomen length = 2.36–3.23). Ventral margin somewhat convex, dorsal margin more or less straight, not bilobed, anus subterminal. Anal region bordered on both sides by dorsal stripe of needle-like spinules arranged in several transverse rows (ca. 8–10) which are subequal in length. These two stripes continue proximally into one medial stripe with similar arrangement, composed of 15–25 rows. Claws small, sclerotized, curved, with a lateral face armed by one notable spine, medial margin with a pecten, obliquely arranged (Fig. 25). Claw ornaments visible only with SEM. The setae natatoria (Fig. 10) arising from a sclerotized portion, located proximally on the postabdomen, distal segment much shorter than proximal (proximal segment:distal segment = 17–18), with long, bristle-like setae.

Discussion

Macrothrix marthae has a unique combination of features, which make it difficult to include in any of the species-groups currently recognized. The most significant feature of this new taxon is the strong specialization for scraping, represented by setae modified as scrapers on limbs I, III, and

V as described. No similar structures are found in any other known *Macrothrix*.

However, considering the first antenna structure, its largest seta, and the features of the natatory setae natatoria, this species could be related to the *M. triserialis*-group as is *M. smirnovi*, a species recently described from highlands of Mexico (Ciros-Pérez & Elías-Gutiérrez 1997). *Macrothrix marthae* seems not to have the same ability to grasp objects as described by Fryer (1974) for *M. triserialis*. The rake-like function of the same setae in *M. laticornis* (Fischer, 1851) seems to be stronger and more specialized in *M. marthae*, as can be inferred by its strong pectens.

The *triserialis*-group also includes a species from South America, *M. superaculeata* (Smirnov, 1982) (in Brandorff, 1982), which seems to be the most closely related species to the Mexican species. This is suggested by the presence of several features including the more specialized arrangement of the thoracic limbs to rake rather than to grasp and also by the similarities on the armature of the antennae.

Macrothrix marthae has similarities with other species: the arrangement of the first antennae, the small lobe on the ventral margin of the head, the postabdomen, and the seta natatoria are similar to those of *Macrothrix capensis* (Sars, 1916) which, however, lacks the specialized setae on limbs I, III, and V. A species from Australia, *M. indistincta* Smirnov, 1992 has only one pectinated seta on limb III, and a short distal segment of the seta natatoria, but all the other features of the first antenna, second antenna, and postabdomen are quite different from *M. marthae*.

Other species with a short distal segment of the setae natatoria are *Macrothrix flabeligera* Smirnov, 1992 and *Macrothrix pectinata* (Smirnov, 1976a) from Australia, and *Macrothrix odiosa* Gurney, 1907 from Southeastern Asia. However, as described for *Macrothrix indistincta*, they are quite different in other characters, such as limb

I–V structure, first antenna and postabdomen, so they can be easily separated.

Macrothrix paulensis (Sars, 1900) and *Macrothrix gauthieri* Smirnov, 1976b have accessory spines on the antennal exopod, but differ from *M. marthae* on the following features: the two former have large spines along the first antenna, also the structure of postabdomen and the limbs (Brandorff et al. 1982, Smirnov 1992) are quite different from *M. marthae*.

The adaptations described for *M. marthae* seem to be related to a strictly epiphytic habit. The species was found abundantly associated with the roots of water hyacinth. It seems that this species is a true scraper of the organic matter adhered to the hard substrata represented by the roots instead of the flocculent detritus preferred by other macrothricids (Fryer 1974).

Most surveys on cladocerans omit the fauna associated to the aquatic vegetation, and it is possible that many new species, mainly from the tropics, will be discovered with adequate sampling techniques to collect this specialized fauna.

Finally, the report of this new species increases the number of *Macrothrix* species known from Mexico to thirteen (Silva-Briano 1998, Elías-Gutiérrez et al. 1999, Silva-Briano et al. 1999). Out of these, seven are known to be restricted to south-central Mexico, thus suggesting limited distributional ranges of these forms. Evidence suggests that some species are confined to high altitude systems (e.g., *M. smirnovi* and *M. mexicanus*) and others to lowlands, such as *M. cf. triserialis* sensu Silva-Briano (1998) and *M. marthae*. Other species recorded from this region need further revision (Elías-Gutiérrez et al. 1999), mainly in the structural details of thoracic limbs, first antennae, and postabdomen.

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**Description of *Eusarsiella tampa*, a new species from
Tampa Bay (Gulf of Mexico), Florida
(Crustacea: Ostracoda: Myodocopina: Sarsiellidae)**

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Abstract.—The carapace and appendages of a new species of myodocopid ostracode, *Eusarsiella tampa*, from Tampa Bay (Gulf of Mexico), Florida, are described and illustrated. The new species is a member of the family Sarsiellidae, subfamily Sarsiellinae.

The new species described herein was collected during a benthic monitoring program in Tampa Bay, Florida. The species has also been collected on the Atlantic Shelf off Georgia.

Station data.—Sta 95LTB01: 19 Sep 1995; 27.659°N, 82.597°W; depth 7.32 m; temp. 29.8°C; pH 8.1; sal. 25.3 ppt; dissolved oxygen 5.6 mg/l; silt + clay 3.7%
Sta 96LTB06: 13 Sep 1996; 27.645°N, 82.657°W; depth 3.8 m; temp. 29.4°C; pH 7.9; sal. 31.1 ppt; dissolved oxygen 5.1 mg/l; silt + clay 2.3%.
Sta 96LTB20: 30 Sep 1996; 27.588°N, 82.748°W; depth 4.6 m; temp. 28.2°C; pH 8.14; sal. 34.5 ppt; dissolved oxygen 6.0 mg/l; silt + clay 3.5%.

Sampling device.—Young-modified Van Veen sampler (0.04 m²); sieve size 0.5 mm mesh; relaxant magnesium sulphate; fixative 5% borax buffered formaldehyde + rose bengal; preservative 70% isopropanol.

Disposition of specimens.—Specimens from Tampa Bay have been deposited in the National Museum of Natural History, Smithsonian Institution, and have been assigned USNM (United States National Museum) catalog numbers.

Family Sarsiellidae Brady & Norman,
1896

Subfamily Sarsiellinae Brady & Norman,
1896

Genus *Eusarsiella* Cohen & Kornicker,
1975

Eusarsiella tampa, new species
Figs. 1-5

Sarsiella greyi Darby, 1965:38 (part), pl. 27: fig. 10 [only paratype UMMP 48815].

Eusarsiella species B, Kornicker, 1986:171, fig. 111a.

Etymology.—Named for Tampa Bay in which the holotype was collected; name is used as feminine noun in apposition.

Holotype.—USNM 194616, adult female with large unextruded eggs (appendages on a slide; carapace and furca in alcohol).

Paratypes.—Sta 95LTB01: USNM 194622, ovigerous female. Sta 96LTB06: USNM 194626: 5 adult females (3 ovigerous); USNM 194627, adult female. Sta 96LTB20: USNM 194623, ovigerous female; USNM 194624, ovigerous female; USNM 194625, adult female.

Type locality.—Sta 96LTB06, Tampa Bay, 1996.

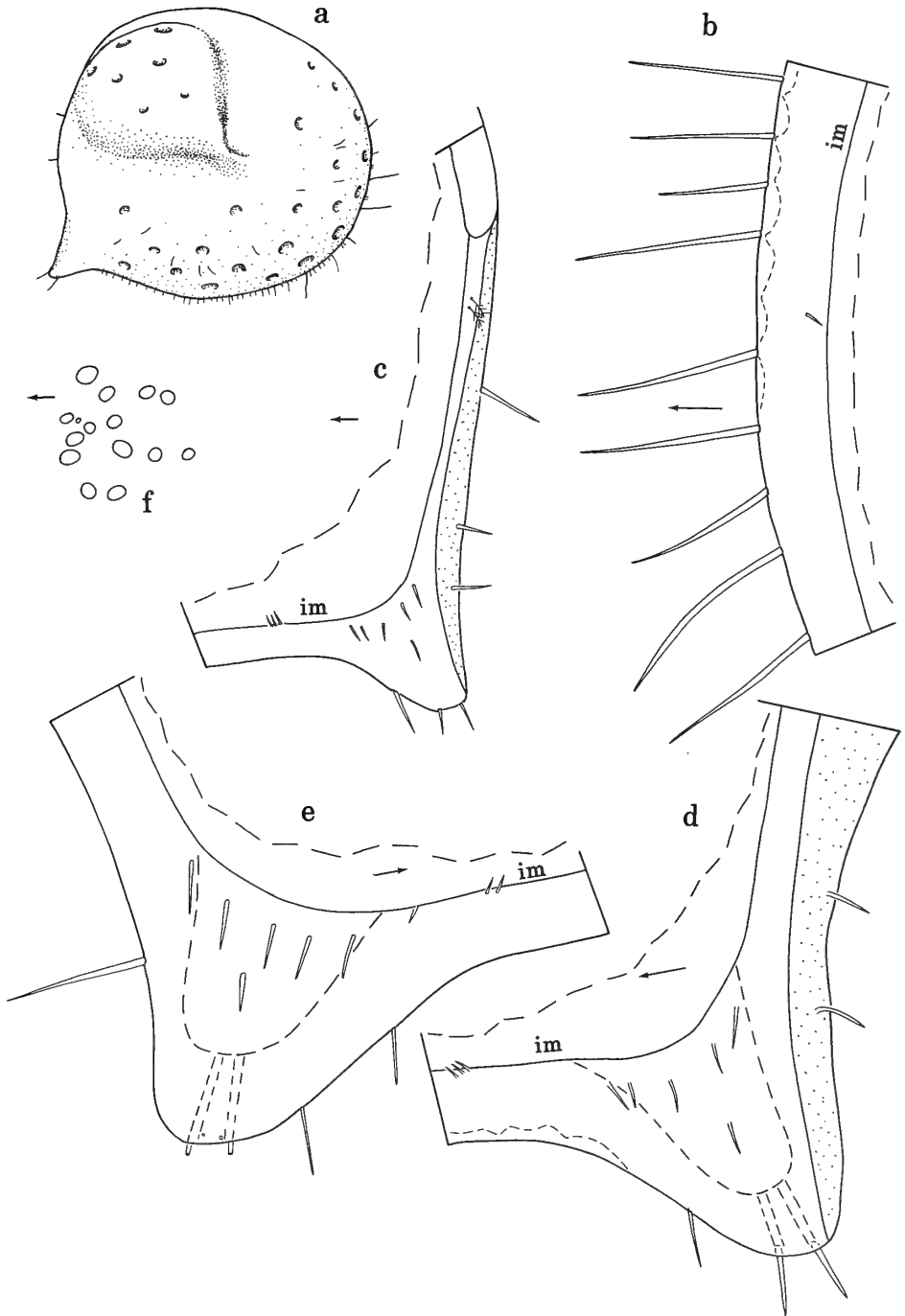


Fig. 1. *Eusarsiella tampa*, new species, holotype, USNM 194616, adult female: a, complete specimen from right side, length 0.91 mm; b, anterior edge of right valve, iv; c, posterior of right valve, iv; d, e, caudal process of right and left valves, respectively, iv; f, ends of central adductor muscle attachments protruding through left side of body with left valve removed.

Abbreviations in Figs. 1-5 are: bas, basale; Bo, Bellonci organ; cx, coxale; cx end, coxale endite; end, endopodite; ex, exopodite; epip, epipodite; es, esophagus; fu, furca; gird, girdle; im, inner margin of infold; iv,

Distribution.—Tampa Bay, depth 3.8–7.32 m. Georgia continental shelf depth 24.7 m (Darby 1965:39).

Description of adult female (Figs. 1–5).—Carapace round in lateral view with short tapered posteroventral caudal process and large projecting posterodorsal bulge (Fig. 1a). Dorsal edge of bulge rib-like on some specimens and with short horizontal or slightly concave anterior extension (concave in reference to valve dorsal margin); extension located just dorsal to central adductor muscle attachments.

Ornamentation.—Surface with numerous widely separated shallow fossae (not all shown in Fig. 1a). Surface of valves, especially around margin, with numerous minute pustules (these less apparent on some specimens). Single bristles abundant along valve margin and sparsely distributed over lateral surface (not all shown in Fig. 1a). Outer surface of valves without gel-like coating. Valves of some preserved specimens with internal calcareous concretions and with brownish color just within ventral edge.

Infold.—Anterior infold with small bristle near inner margin (Fig. 1b). Infold of caudal process with 3–5 proximal bristles forming row and 1 distal bristle (Fig. 1c–e). Posterior infold with 2 setal bristles dorsal to valve midheight (Fig. 1c).

Central adductor muscle attachments.—Obscured on carapaces, but many ovoid attachments visible protruding through body when valve removed (Fig. 1f).

Carapace size (mm).—USNM 194616: complete specimen, length 0.91, height including caudal process 0.88; left valve with body removed: length 0.95, height including caudal process 0.92, height excluding caudal process 0.79. USNM 194622, length 0.92, height including caudal process 0.92,

height excluding caudal process 0.86. USNM 194623, length 0.87, height including caudal process 0.84, height excluding caudal process 0.83. USNM 194624, length 0.89, height including caudal process 0.92, height excluding caudal process 0.80, maximum width 0.72. USNM 194625, length 0.92, height including caudal process 0.88, height excluding caudal process 0.76. USNM 194627, length 0.87, height including caudal process 0.86, height excluding caudal process 0.79. UMMP 48815, length 0.90, height 0.84 (Darby, 1965:39) (present measurements: separated right valve immersed in plastic in dished slide and under cover slip, length 0.89, height including caudal process, 0.93, height excluding caudal process 0.84).

First antenna (Figs. 2a, 5a).—1st joint bare. 2nd joint with dorsal spines and bare dorsal bristle. 3rd joint short, fused to 4th joint, with long bare dorsal bristle and short bare ventral bristle, and medial and ventral spines. 4th joint with dorsal, ventral, and medial spines, and 4 bristles (3 ventral, 1 dorsal). 5th joint with dorsal spines (not shown) and sensory bristle with 2 minute marginal filaments, 6th joint fused to 5th, with small medial bristle near dorsal margin. 7th joint: a-bristle short, bare; b-bristle slender, bare, about twice length of a-bristle; c-bristle about same length as sensory bristle of 5th joint. 8th joint: d- and e-bristles shorter than c-bristle, and d-bristle longer than e-bristle, both bare with blunt tips; f-bristle shorter than c-bristle, with 2 minute marginal filaments; g-bristle about same length as c-bristle, with 2 minute marginal filaments. (The 1st antenna of UMMP 48815 from off Georgia was reexamined and found to have minute filaments on the f- and g-bristles similar to those on the Tampa Bay specimens.)

←

inside view; le, lateral eye; ll, lower lip; lv, lateral view; me, medial eye; mnd, mandible; mo, mouth; mv, medial view; prot, protopodite; ul, upper lip; Y-scl, Y-sclerite. Roman numerals designate endites. Arabic numerals indicate individual joints of a limb. Arrow on illustration indicates anterior.

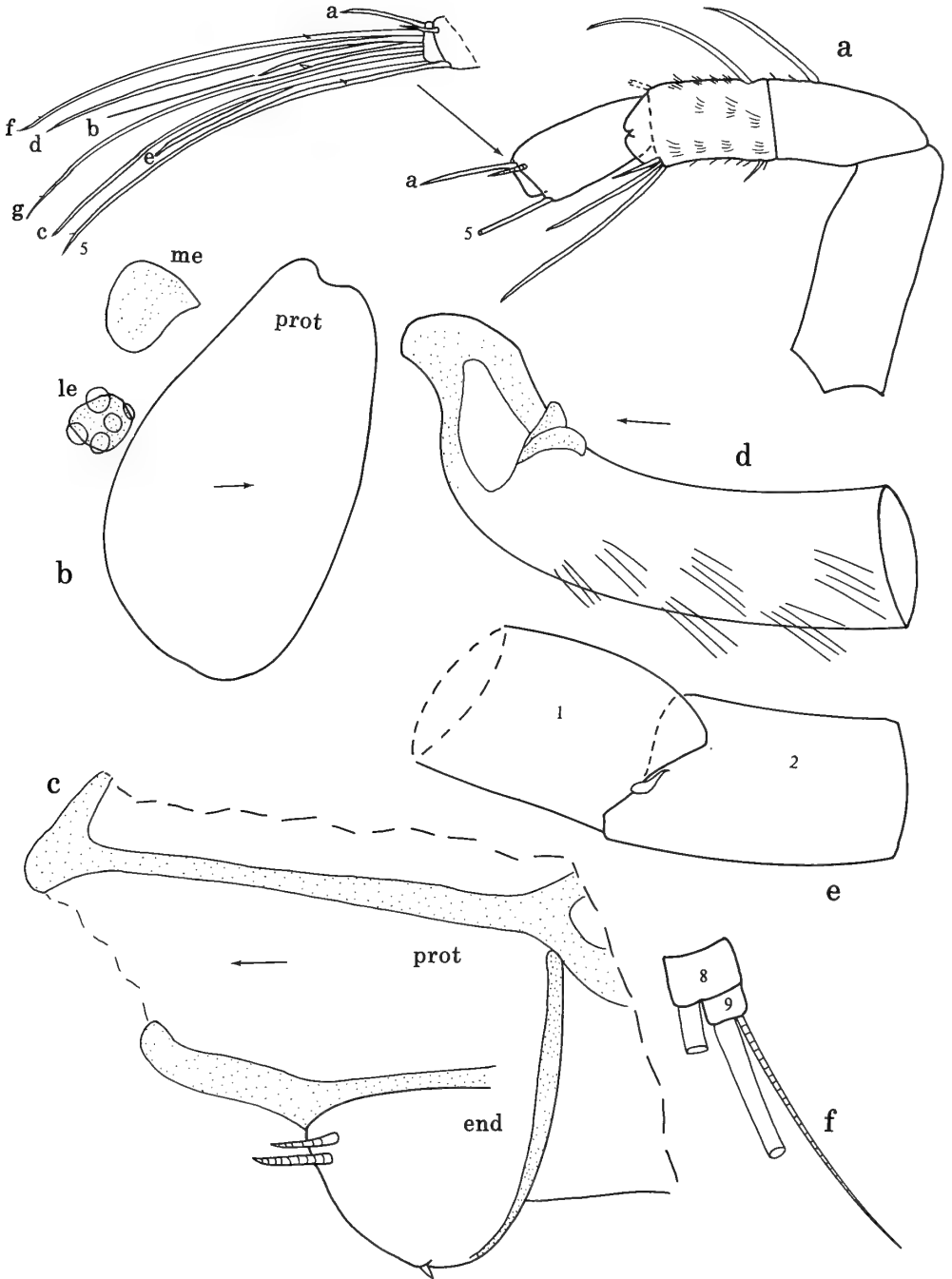


Fig. 2. *Eusarsiella tampa*, new species, holotype, USNM 194616, adult female: a, right first antenna, mv; b, protopodite of right second antenna, pigmented area only of medial eye, and right lateral eye (shown in place on body), lv; c, endopodite and distal part of protopodite of right second antenna, mv; d, proximal part of first exopodial joint of right second antenna, mv; e, distal part of first joint and second joint of right second antenna, mv; f, joints 8 and 9 of exopodite of right second antenna, mv. (For abbreviations see Fig. 1.)

Second antenna (Fig. 2b–f).—Protopodite bare (Fig. 2b, c). Endopodite with 2 small bare proximal bristles and 1 minute unringed bristle on a small terminal node (Fig. 2c). Exopodite (Fig. 2d–f): 1st joint with long proximal ventral spines and small terminal medial recurved tubular bristle (Fig. 2d, e); bristle of 2nd joint long with proximal ventral spines and distal natatory hairs (bristle not shown); bristle of 3rd joint with few proximal ventral spines and distal natatory hairs; bristles of joint 4–7 with natatory hairs, no spines; bristle of 8th joint with few proximal slender ventral spines and distal natatory hairs; 9th joint with 2 bristles (Fig. 2f): ventral bristle with slender proximal ventral spines and distal natatory hairs; dorsal bristle short bare.

Mandible (Figs. 3a, b, 5b–d).—Coxale endite single stout pointed; ventral margin of coxale with long slender spines (Fig. 3a). Basale (Fig. 3a, b): ventral margin with 5 or 6 short bristles; dorsal margin with small bristle at midlength and 2 terminal. 1st endopodial joint with medial spines and spines on distal dorsal corner and slender ventral claw. 2nd endopodial joint with minute distal bristle on dorsal margin and slender ventral claw. 3rd endopodial joint with slender terminal claw and 2 minute bristles (1 ventral, 1 dorsal).

Maxilla (Fig. 3c–e).—Precoxale with dorsal hairs (Fig. 3c). Coxale with short dorsal bristle. Endites (Fig. 3d, e): I with 4 pectinate claws and 2 ringed bristles either bare or with short spines; II with 2 pectinate claws and 2 or 3 ringed bristles; III with 1 pectinate unringed claw and 5 ringed bristles either bare, with marginal spines, or with few marginal teeth. Exopodite with 3 ringed bristles (1 long spinous, 2 short bare about $\frac{1}{2}$ length of long bristle). 1st endopodial joint with dorsal spines and 2 spinous alpha- and beta-bristles. 2nd endopodial joint with 2 short lateral a-bristles, 1 short medial c-bristle, and 5 pectinate end bristles.

Fifth limb (Fig. 4a, b).—Epipodite fragmented, with about 34 bristles. Single en-

dite with small bare bristle. Exopodite: 1st joint with 2 bristles; 2nd joint hirsute with 3 bristles; joints 3–5 fused with total of 6 bristles.

Sixth limb (Fig. 4c).—Single endite with either 1 fairly stout bristle or 2 bristles (1 fairly stout, 1 minute). End joint with 14 bristles (not all shown) followed by space and 2 long plumose bristles; posterior edge of limb hirsute. Closely packed cells present both within limb and within segments of body proximal to limb (cells represented by dots in Fig. 4c). (The 6th limb of UMMP 48815 from off Georgia was reexamined and found to be similar to that of specimens from Tampa Bay.)

Seventh limb (Fig. 4d, e).—Proximal group with 2 or 3 bristles (1 or 2 on each side), each with 2 or 3 bells; terminal group with 6 bristles (3 on each side), each with 2–5 bells; all bristles without marginal spines. Terminus with opposing combs, each with about 6 teeth (not all shown).

Furca (Figs. 3f, g, 5e).—Each lamella with 5 slender claws, except left lamella of USNM 194616 aberrant in having only 4 claws; claw 1 nonarticulated; claws with long and short teeth along posterior edges; proximal teeth of claws 2 and 3 unusually long; each lamella with 2–4 spines along margin following claws; right lamella anterior to left by width of base of claw 1.

Bellonci organ (Fig. 5a).—Elongate with broadly rounded tip.

Eyes.—Medial eye bare with brown pigment (Figs. 2b, 5a). Lateral eye smaller than medial eye, with 5 amber colored ommatidia and dark brown pigment between ommatidia (Fig. 2b, 5a).

Upper lip (Fig. 5b–d).—Single lobe extending anteriorly.

Genitalia (Fig. 5e).—Small round sclerotized ring with attached spermatophore.

Posterior of body (Fig. 5e, f).—Bare.

Y-Sclerite (Fig. 5e, f).—With distal branch typical for genus.

Number and size of eggs.—USNM 194616 with several large unextruded eggs, length of one egg 0.048 mm. USNM

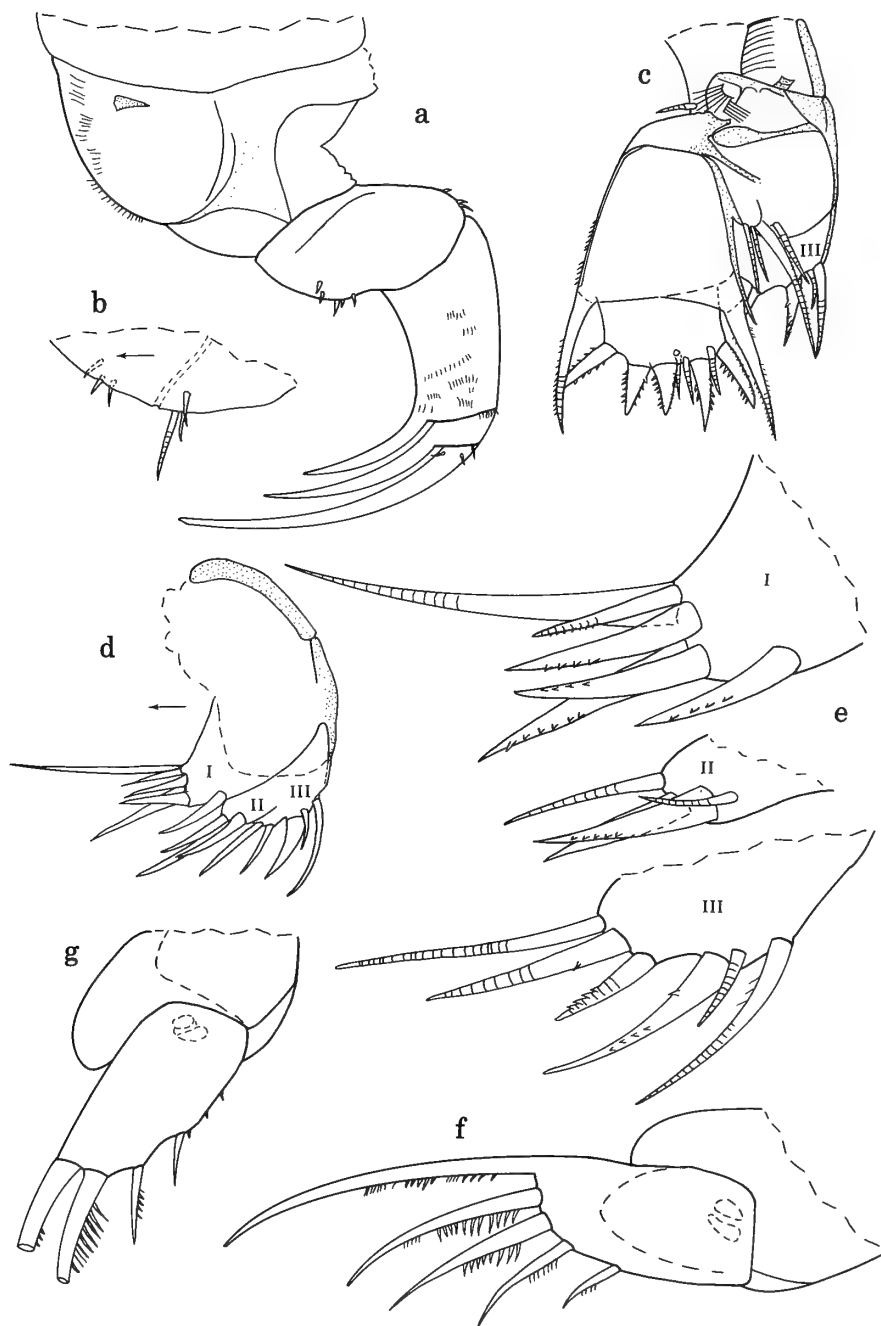


Fig. 3. *Eusarsiella tampa*, new species, holotype, USNM 194616, adult female: a, left mandible, mv; b, ventral margin of basale of right mandible, mv; c, left maxilla (endites I and II not shown), lv; d, e, endites I-III of right maxilla, mv; f, right lamella of furca, mv; g, left lamella of furca, lv. (For abbreviations see Fig. 1.)

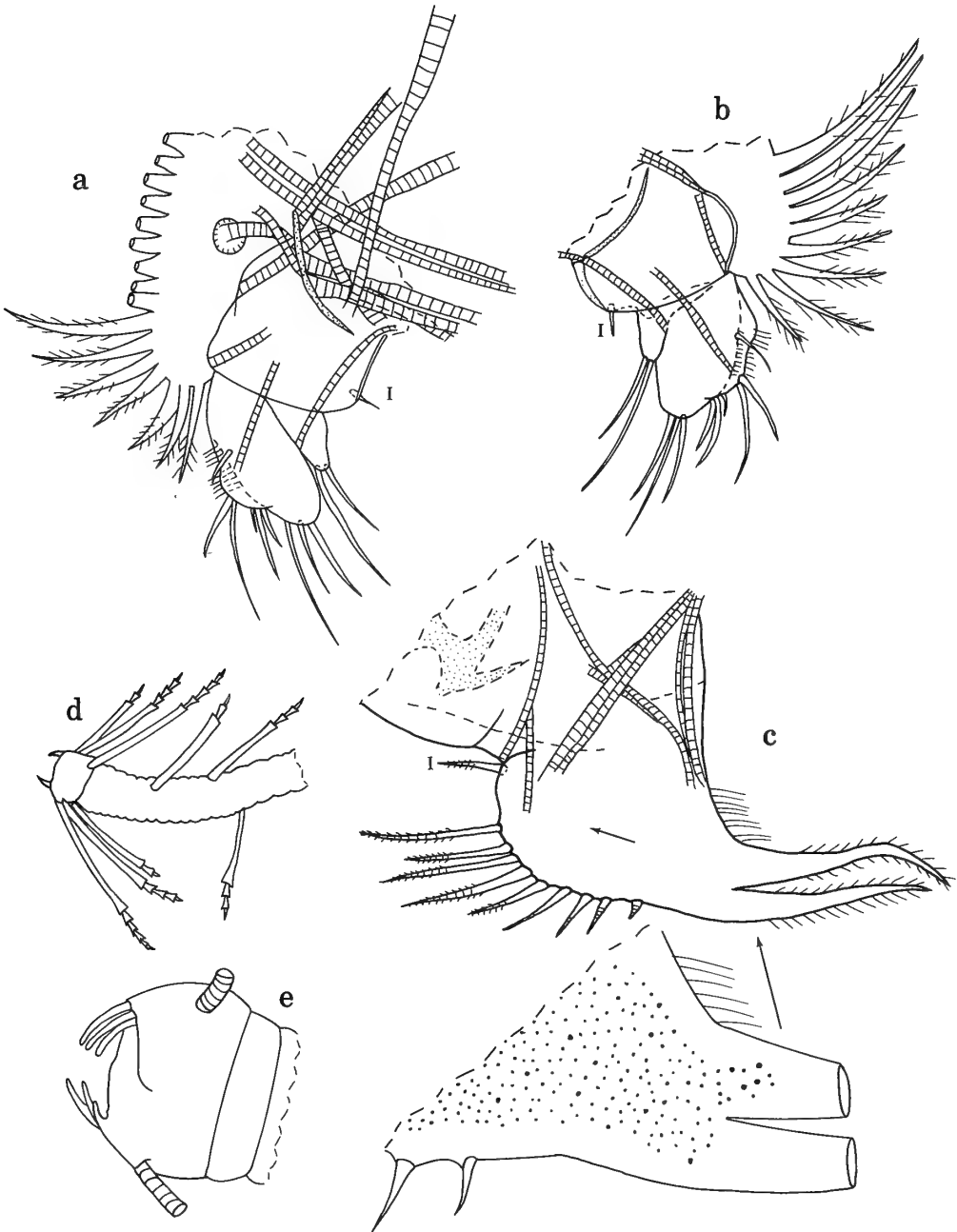


Fig. 4. *Eusarsiella tampa*, new species, holotype, USNM 194616, adult female: a, b, right and left fifth limbs, respectively (muscles striated, sclerites stippled), lv; c, left 6th limb (not all bristles of end joint shown), lv; d, right 7th limb, lv; e, detail of tip of seventh limb (not all bristles shown). (For abbreviations see Fig. 1.)

194622 with 5 eggs in marsupium, length of one egg 0.077 mm. USNM 194623 with 6 eggs in marsupium (oval egg with transparent sheath surrounding an inner brown

mass bearing vestigial appendages), lengths of two eggs (maximum length of sheath/length of inner brown mass (mm)): 0.084/0.059, 0.074/0.058. USNM 194624 with

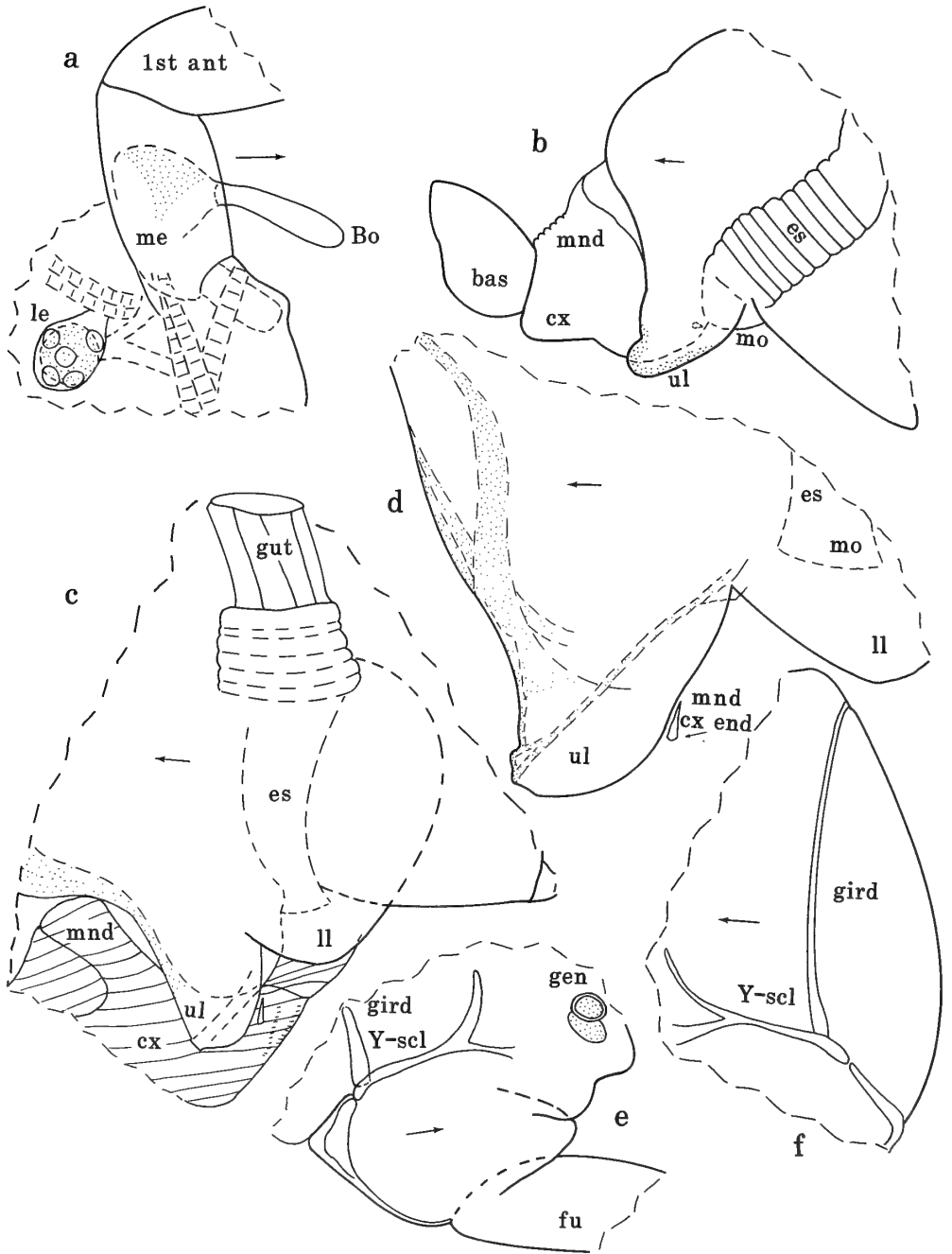


Fig. 5. *Eusarsiella tampa*, new species, holotype, USNM 194616, adult female: a, anterodorsal part of body from right side; b-d, anteroventral part of body from left side; e, posteroventral part of body from right side; f, posterior of body from left side. (For abbreviations see Fig. 1.)

one egg in marsupium, length of egg 0.64 mm. USNM 194627 with six unextruded eggs, length of three eggs: 0.037 mm, 0.039 mm, 0.044 mm. UMMP 44815 with 4 eggs in marsupium (Darby 1965:39).

Gut content.—Gut of USNM 194627 with oval egg with maximum length of 0.051 mm (egg consisting of poorly defined globules and similar in appearance to brown eggs in marsupium of specimen); remainder of gut with unidentified particles. Gut of USNM 194616 with unidentified particulate matter. Gut of UMMP 48815 with complete copepod.

Epibionts.—Carapace of USNM 194624 with abundant threadlike segmented filaments with either rounded or pointed tips. Carapace of one specimen of USNM 194626 with segmented filaments with rounded tips, another with oval egg-like stalked epibiont on posterior edge.

Comparisons.—The carapace of the new species, *E. tampa*, resembles that of *Eusarsiella vema* Kornicker, 1986. The 1st antenna of *E. tampa* bears a ventral bristle on the 3rd joint compared to none on *E. vema*. The caudal process of *E. tampa* is much shorter than that of *Eusarsiella greyi* (Darby 1965).

Correction.—In the “Key to the Species of *Eusarsiella*” in Kornicker (1986:44) couplet 28 should have been as follows:

- 28. First antenna without ventral bristle on third joint 29
- First antenna with ventral bristle on third joint 30

Acknowledgments

Appreciation is extended to the Environmental Protection Commission of Hillsborough County (R. Stewart, Executive Director) and the Tampa Bay Estuary Program (R. Eckinrod, Director) for financial support of the Tampa Bay Benthic Monitoring Program. We thank Matthew D. Kane (volunteer illustrator) for rendering the illustration of the carapace and for inking camera lucida penciled drawings of the appendages by the senior author, Molly Ryan (Smithsonian Institution) for inking additional drawings, and Elizabeth Harrison-Nelson (Smithsonian Institution) for general assistance. We thank the Museum of Paleontology—University of Michigan for the loan of a specimen of *Sarsiella greyi* Darby, 1965 (UMMP 48815, 4 slides).

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Two species of bomolochid copepods (Crustacea) parasitic on marine fishes of Kuwait

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Abstract.—Two species of Bomolochidae (Poecilostomatoida) were found in the gill cavities of marine fishes caught in Kuwait Bay. They are *Nothobomolochus tricerus* (Bassett-Smith, 1898) from *Pampus argenteus* (Euphrasen) and *Orbitacolax hapalogenyos* (Yamaguti & Yamasu, 1959) from *Hemirhamphus marginatus* (Forsskål). Both species are new to the Persian Gulf. A new key to the 30 species of *Nothobomolochus* is provided. *Nothobomolochus trichiuri* Hameed & Kumar, 1988 is a junior synonym of *Nothobomolochus trichiuri* Pillai & Natarajan, 1977.

In their preliminary report on 23 species of parasitic copepods from the marine fishes of Kuwait, Ho & Sey (1996) reported four species of poecilostomatoids belonging to the family Bomolochidae, *Bomolochus stocki*, Roubal, 1981, *Nothobomolochus denticulatus* (Bassett-Smith, 1898), *N. fradei* Marques, 1965 and *N. quadriceros* Pillai, 1973. In this paper, we add to that list two more species of bomolochids: a species of *Orbitacolax* and a fourth species of *Nothobomolochus*.

The concept of the genus *Nothobomolochus* was started by Yamaguti (1939) but the current name of the genus was not given until 23 years later by Vervoort (1962). This genus has become the largest one in the family Bomolochidae, consisting of 30 species. We take this opportunity of adding a species of *Nothobomolochus* to the fauna of the Persian Gulf to create a new key to the species of the genus.

Materials and Methods

The fishes infested with the copepods reported herein were caught in Kuwait Bay

of the Persian Gulf and purchased at a local fish market in Kuwait. Fishes were examined in the laboratory of the Department of Zoology at Kuwait University. Copepod parasites were carefully removed and preserved in 70% alcohol. Subsequent microscopic studies of the parasites were made in a drop of lactic acid. Appendages of the parasites were dissected and examined with a compound microscope magnified up to 1500 times. All drawings were made with the aid of a camera lucida.

Family Bomolochidae Sumpf, 1871

Orbitacolax hapalogenyos (Yamaguti & Yamasu, 1959)

Figs. 1–2

Taeniacanthus hapalogenyos Yamaguti & Yamasu, 1959, p. 95, pl. 3, figs. 44–55; Yamaguti, 1963, p. 21, pl. 19, fig. 8.

Orbitacolax hapalogenyos: Vervoort, 1962, p. 84, Ho & Dojiri, 1976, p. 257, figs. 2A–B.

Orbitacolax hapalogenyos: Cressey & Cressey, 1989, p. 2904, figs. 16–27.

Material examined.—1 ♀ recovered

from gill cavity of *Hemirhamphus marginatus* (Forsskål) caught on 22 Oct 1997 from Kuwait Bay. Dissected specimen kept in junior author's (I-HK) collection.

Female.—Body (Fig. 1A) 1.16 mm in length. Cephalothorax wider than long, $375 \times 495 \mu\text{m}$, with protruded rostral area. Urosome (Fig. 1B) distinctly shorter than prosome, only $384 \mu\text{m}$ long. Genital double somite wider than long, $106 \times 167 \mu\text{m}$, and bearing 3 long, naked setae in egg sac attachment area. All 3 abdominal somites wider than long and bearing a large patch of spinules on ventral surface (Fig. 1C). Caudal ramus (Fig. 1C) longer than wide, $46 \times 27 \mu\text{m}$ (1.70:1), bearing a large patch of spinules on ventral surface and carrying 1 long and 5 short setae.

Rostral area with 2 sharply diverging, pointed tines on ventral surface (Fig. 1D). Antennule (Fig. 1D) with 2-segmented base and 3-segmented terminal section; armature on base consisting of 5, thick setae on first segment and 10 similar setae plus another 10 naked setae on second segment; formula of armature on terminal 3 segments: 4, 2 + 1 aesthete, and 7 + 1 aesthete. Antenna (Fig. 1E) 3-segmented; basal and middle segments bearing a distal seta. Terminal segment bearing rows of spinules on ventral (inner) margin and protruded distally into a large, blunt, cylindrical process with ventral spinules; also armed distally with 4 unequal, curved claws, 3 naked setae, and 2 pectinate processes (Fig. 1F).

Labrum (Fig. 1G) with a large patch of denticles on either side of ventral surface. Mandible (Fig. 1H) a slightly bent, long process tipped with 2 spines bearing serrate, anterior edge. Paragnath (Fig. 1I) a bluntly pointed process fringed basally with cilia and distally with spinules. Maxillule (Fig. 1J) armed with 1 plumose seta and 3 (1 long and 2 short) simple setae. Maxilla (Fig. 1K) 2-segmented; proximal segment unarmed, distal segment protruded posteriorly in basal region and armed distally with 1 small, simple seta and 2 large, spinulated spines. Maxilliped (Fig. 2A) 3-segmented;

proximal segment rod-like, with 2 small protuberances and 1 naked seta; middle segment greatly enlarged carrying 2 extremely unequal setulose setae; terminal segment a sigmoid, sharply pointed claw with an accessory hooklet at distal bend and bearing 1 small, plumose seta in basal region.

Legs 1 to 4 (Figs. 2B, 2C, 2D) biramous, with 3-segmented rami, except exopod of leg 1. Formula of spines (roman numerals) and setae (Arabic numerals) on these 4 legs as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1	0-1	1-0	I-0; III, 6	0-1; 0-1; 5
Leg 2	0-0	1-0	I-0; I-0; II, I, 2	0-1; 0-2; 3
Leg 3	0-0	1-0	I-0; I-1; II, I, 2	0-1; 0-1; 2
Leg 4	0-0	1-0	I-0; I-0; II, I, 2	0-1; 0-1; 3

Basis of protopod and segments on both rami of all four legs bearing rows of spinules. Outer spines on all exopods weakly developed. Setae on ramal segments of legs 2, 3 and 4 sparsely armed. Leg 5 (Fig. 2E) 2-segmented and bearing rows of spinules; proximal segment armed with 1 plumose seta; distal segment, $112 \times 40 \mu\text{m}$ (2.80:1), armed with 2 small outer setae and 2 long terminal setae. Leg 6 represented by 3 long setae in egg sac attachment area (Fig. 1B).

Remarks.—*Orbitacolax hapalogenyos* is the most widely distributed species of the genus, occurring on teleosts in the Seto Inland Sea, Japan (Ho et al. 1983); Great Barrier Reef, Australia (Ho & Dojiri 1976); Gulf of Mexico; Caribbean Sea; and Brazil (Cressey & Cressey 1989). It is characteristic in having two long inner plumose setae (instead of one short simple seta or no seta) on the second segment of the endopod of leg 2. This distinct character state is shared only with *O. aculeatus* (Pillai) among its congeners. However, *O. aculeatus* differs from the present species in having eight elements (2 small + 6 large) [instead of nine elements (3 small + 6 large)] on the terminal segment of the exopod of leg 1. Therefore, the specimen from Kuwait is identified as *O. hapalogenyos*. Neverthe-

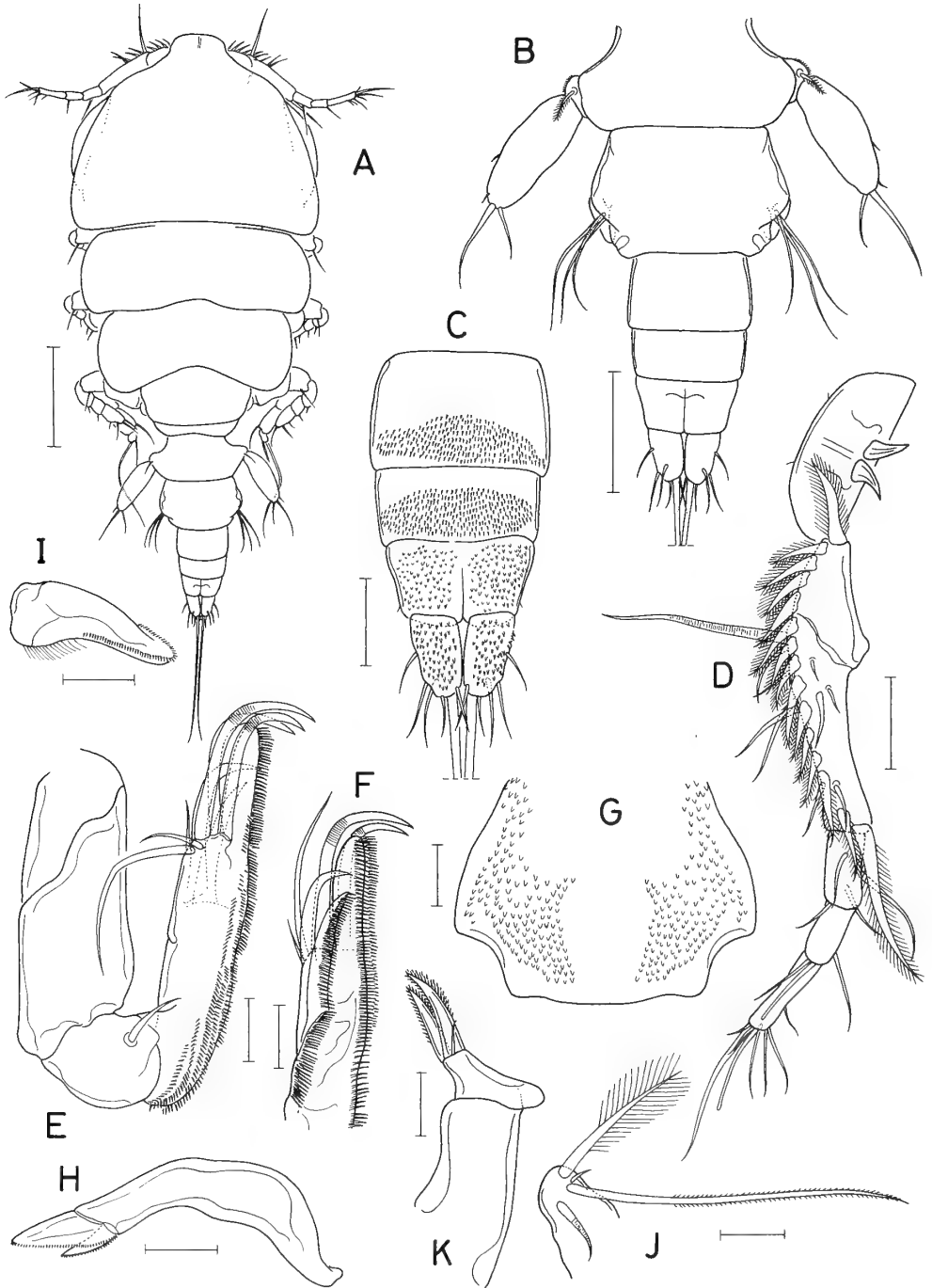


Fig. 1. *Orbitacolax hapalogenyos* (Yamaguti & Yamasu), female. A. habitus, dorsal; B. urosome, dorsal; C. abdomen, ventral; D. rostrum and antennule; E. antenna; F. distal part of antenna; G. labrum; H. mandible; I. paragnath; J. maxillule; K. maxilla. Scale bars: A, 0.2 mm; B, 0.1 mm; C, D, 0.05 mm; E-K, 0.02 mm.

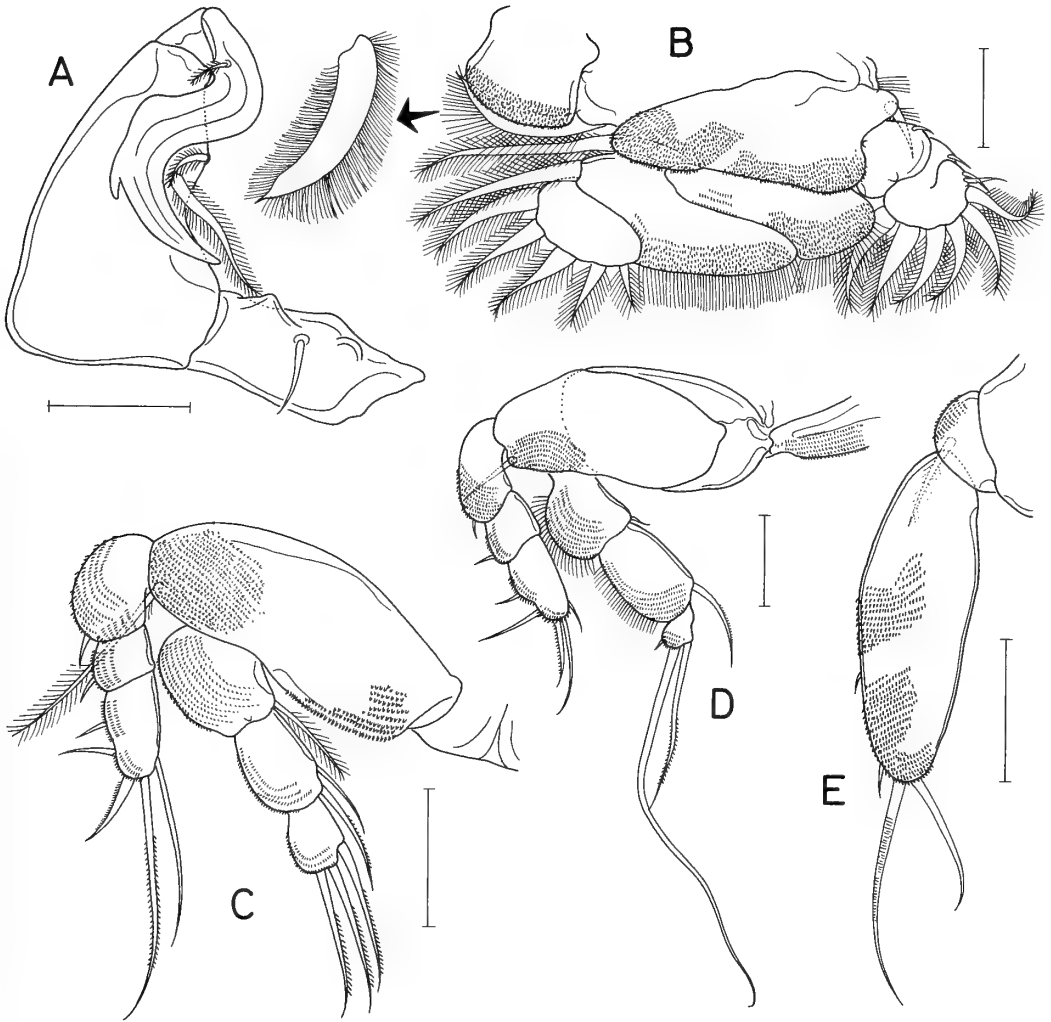


Fig. 2. *Orbitacolax hapalogenyos* (Yamaguti & Yamasu), female. A. maxilliped; B. leg 1; C. leg 2; D. leg 4; E. leg 5. Scale bars: A-E, 0.05 mm.

less, this can only be considered as a temporary identification, because some discrepancies have been detected.

According to Cressy & Cressey (1989), the specimens of *O. hapalogenyos* from the Gulf of Mexico and Caribbean Sea are somewhat different from those found in Japan described by Yamaguti & Yamasu (1959) and redescribed by Ho et al. (1983). There is one extra, small seta on the terminal segment of leg 2 exopod and leg 3 endopod in the specimens from the New world waters (Cressey & Cressey 1989:

Figs. 24, 25; indicated with an arrow). Furthermore, the specimen of *O. hapalogenyos* found in the Great Barrier Reef (Ho & Dojiri 1976) differs from those found in the Seto Inland Sea, Japan and the New world waters in missing the medial, small seta on the terminal segment of leg 4 endopod. Thus, even though our specimen from Kuwait differs from the holotype (from Seto Inland Sea, Japan) in carrying one less seta on the terminal segment of both rami of leg 2, we consider it is better to call it *O. hapalogenyos* for the time being. Since there

is but one specimen from a new host (*Hemiramphus marginatus*) in a new locality (Kuwait Bay), we can not determine if there is an abnormality or geographical variation. Discovery of more specimens from the Persian Gulf will solve this problem.

It is interesting to note that *O. hapalogenyos* has not been found in India. The same host fish, a margin halfbeak (*H. marginatus*) that harbors *O. hapalogenyos* in Kuwait Bay, is known to carry another species of bomolochid, *Bomolochus hemiramphi* Pillai, in Kerala, India (Pillai 1965).

Notobomolochus tricerus (Bassett-Smith, 1898)

Figs. 3–4

Bomolochus tricerus Bassett-Smith, 1898, p. 2, pl. 1, figs. 1a–g; Pillai, 1965, p. 39, figs. 15A–O.

Bomolochus (Pseudobomolochus) managatuwo Yamaguti, 1939, p. 396, pl. 3, figs. 28–19, pl. 4, figs. 30–36; Shen, 1957, p. 304, pl. 4, figs. 33–45.

Nothobomolochus tricerus: Vervoort, 1962, p. 64; Pillai, 1969, p. 149, figs. 1–4; Ho, Do & Kasahara, 1983, p. 9, figs. 82–101.

Nothobomolochus managatuwo: Vervoort, 1962, p. 66.

Pseudobomolochus managatuwo: Yamaguti, 1963, p. 15, pl. 10, fig. 1.

Pseudobomolochus tricerus: Yamaguti, 1963, p. 16.

Material examined—1 ♀ recovered from gill cavity of *Pampus argenteus* (Euphrasen) caught on August 18, 1996 from Kuwait Bay. Dissected specimen kept in junior author's (I–HK) collection.

Female.—Body (Fig. 3A) 1.86 mm in length. Cephalothorax widest part of body, 0.56 mm long and 1.00 mm wide. Urosome (Fig. 3B) distinctly shorter than prosome, only 770 μm long. Genital double somite wider than long, $192 \times 327 \mu\text{m}$, and bearing 3 long, naked setae on a protuberance in attachment area of egg sac (Fig. 3B). All 3 abdominal somites wider than long, anal somite with two patches of spinules on ven-

tral surface (Fig. 3C). Caudal ramus (Fig. 3B) longer than wide, $87 \times 50 \mu\text{m}$ (1.74: 1), and carrying 1 long and 5 short setae. Egg sac (Fig. 3A) longer than urosome, with multiseriate eggs.

Rostral area unarmed. Antennule (Fig. 3D) with heavily sclerotized base (composed of 3 fused segments) and cylindrical, 3-segmented terminal section. Armature on base consisting of 3 equally developed processes on pedestal (tripartite plate) in addition to 12 stout setulose, setae, 11 slender setae and 2 setules. Formula of armature on terminal 3 segments being: 4, 2 + 1 aesthete, and 7 + 1 aesthete. Antenna (Fig. 3E) 3-segmented; basal segment largest and middle segment smallest, both carrying 1 simple seta. Terminal segment bearing spinules along ventral (inner) margin and protruded distally into a blunt, cylindrical process carrying a subterminal seta and a row of ventral spinules in addition to 4 curved claws, 2 naked setae, and 2 pectinate processes.

Labrum (Fig. 3F) with long cilia on lateral margin and 2 large patches of small denticles on ventral surface. Mandible (Fig. 3G) a slightly bent, long process tipped with 2 spines bearing serrated membranous plate on one (anterior) side. Paragnath (Fig. 3H) a bluntly pointed process armed with denticles and cilia. Maxillule (Fig. 3I) armed with 3 unequal plumose setae and 1 naked seta. Maxilla (Fig. 4A) 2-segmented; proximal segment large, carrying 1 small, naked seta; distal segment small tipped with 2 unequal, spinulose processes and 1 small, naked seta. Maxilliped (Fig. 4B) 3-segmented; proximal segment rod-like, carrying a small, naked seta; middle segment greatly enlarged, carrying 2 extremely unequal setulose setae; terminal segment assuming a sharply pointed bent claw bearing 1 large hairy seta at base.

Legs 1 to 4 (Fig. 4C, D, E, F) biramous, with 3-segmented rami, except exopod of leg 1. Formulae of spines (Roman numerals) and setae (Arabic numerals) on these 4 legs as follows:

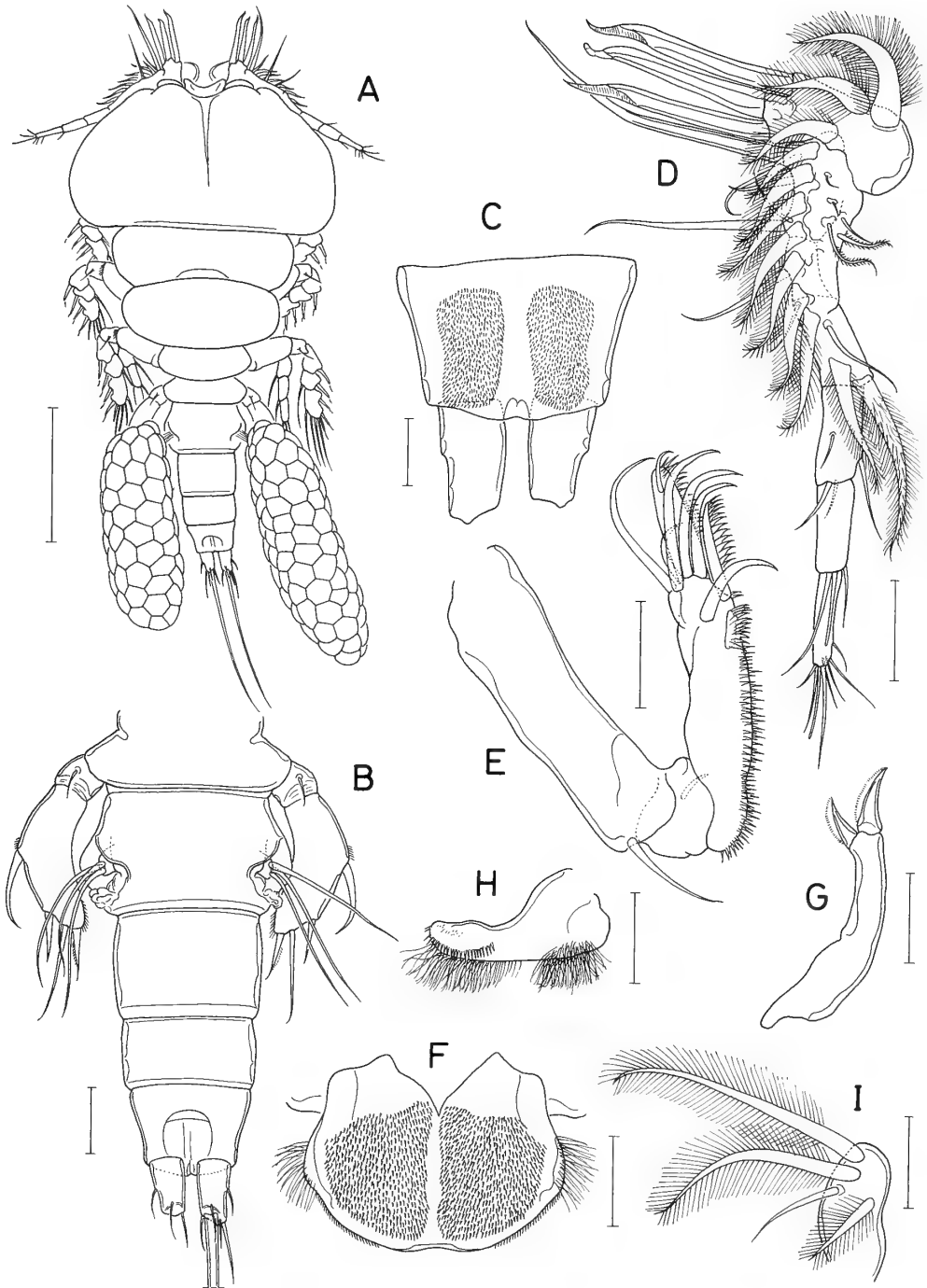


Fig. 3. *Notobomolochus tricerus* (Bassett-Smith), female. A. habitus, dorsal; B. urosome, dorsal; C. anal somite and caudal rami, ventral; D. antennule; E. antenna; F. labrum; G. mandible; H. paragnath; I. maxillule. Scale bars: A, 0.5 mm; B, 0.1 mm; C, E-I, 0.05 mm; D, 0.1 mm.

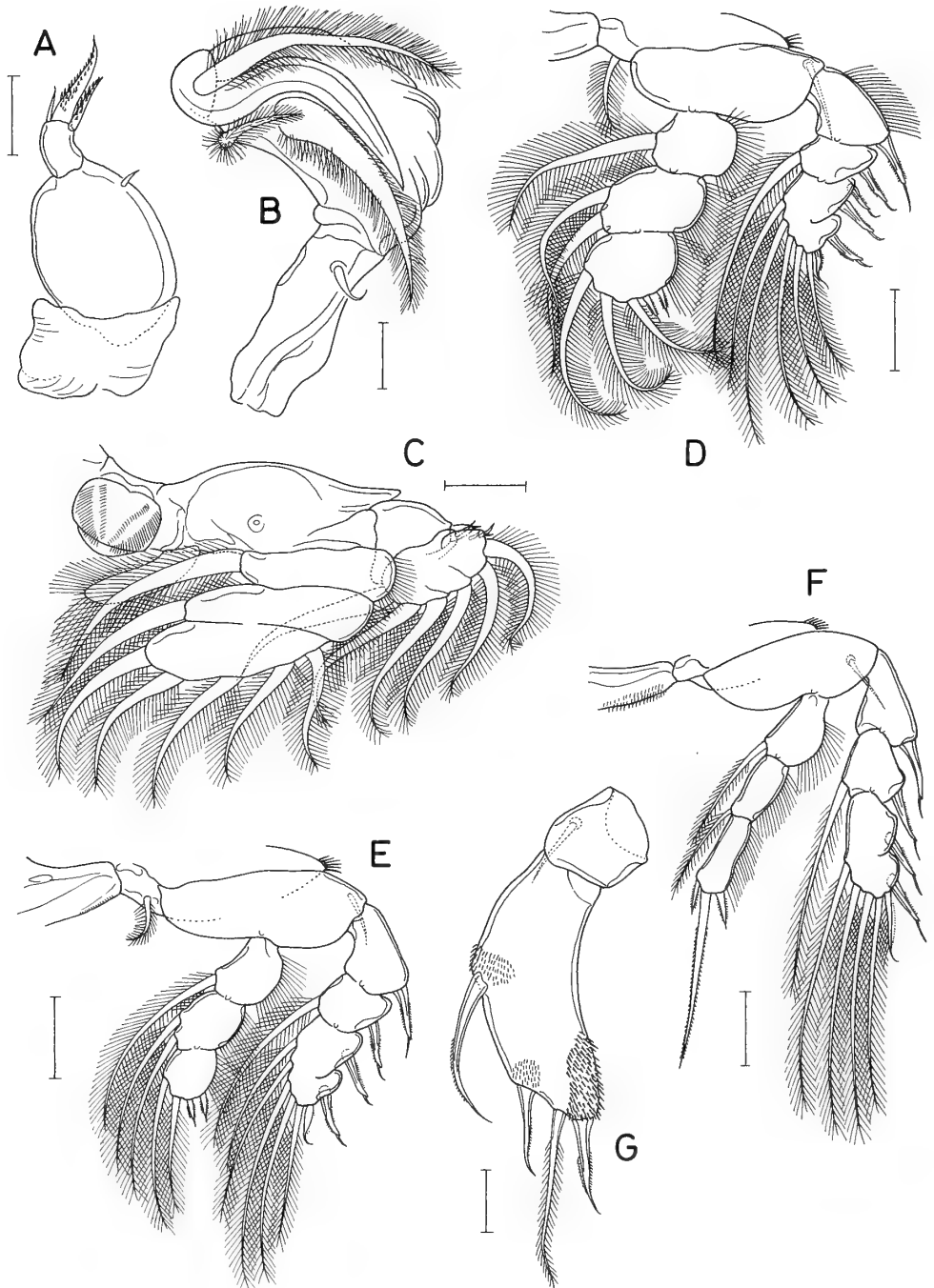


Fig. 4. *Notobomolochus triceros* (Bassett-Smith), female. A. maxilla; B. maxilliped; C. leg 1; D. leg 2; E. leg 3; F. leg 4; G. leg 5. Scale bars: A, B, G, 0.95 mm; C-F, 0.1 mm.

	Coxa	Basis	Exopod	Endopod
Leg 1	0-1	0-0	I-0; IV, 6	0-1; 0-1; 5
Leg 2	0-1	1-0	I-0; I-1; III, I, 5	0-1; 0-2; II, 3
Leg 3	0-1	1-0	I-0; I-1; II, I, 5	0-1; 0-2; II, 2
Leg 4	0-0	1-0	I-0; I-1; II, I, 4	0-1; 0-1; III

Outer spines on exopod of leg 1 weakly developed. Leg 5 (Fig. 4G) 2-segmented; proximal segment slightly longer than wide, $77 \times 69 \mu\text{m}$, and carrying 1 simple, outer seta; distal segment distinctly longer than wide, $212 \times 85 \mu\text{m}$ (2.49:1), and armed with 3 patches of spinules, 3 spines tipped with a flagellum, and 1 plumose seta. Leg 6 represented by 3 setae on a protuberance in egg sac attachment area (Fig. 3B).

Remarks.—This species was first discovered by Bassett-Smith (1898) from the gill cavity of a pampanō [*Pampus argenteus* (Euphrasen)] collected in the Arabian Sea. Since the original description is “very inaccurate” (Vervoort 1962:65), a complete redescription of the Kuwaiti specimen is therefore given above to supplement the original description.

A close comparison of our specimen from Kuwait with the description of *N. tricheros* given by Pillai (1969) from India and by Ho et al. (1983) from Japan indicated that they are conspecific. However, it is interesting to note that while the total length of the specimen from Kuwait (1.86 mm) is not much different from those of India (2.2 mm; Pillai 1985), it is distinctly smaller than those from Japan (3.28 mm; Ho et al. 1983).

Key to Species of *Nothobomolochus* Vervoort, 1962

The most outstanding characteristic of this genus is the possession of a pedestal (well-sclerotized, tripartite plate) on the dorsal surface of the antennule in the basal region and carrying on it the modified third, fourth, and fifth setae. In the following key, these three seta-bearing processes of the plate are respectively called proximal, middle, and distal process. Since these three

processes are constructed differently in different species groups of *Nothobomolochus*, they become one of the best character states for species identification.

Another useful character for the aid in species identification is the extent to which the fourth pediger is covered by a dorsal extension of the third pediger. The fourth pediger is not covered in five species; The fourth pediger is partly covered in nine species, and completely covered (in dorsal view) in 16 species. Since this feature is the easiest to recognize and has been properly illustrated for all nominal species, it is selected as the first morphological discriminator in the following key.

Discovering the above two features present concurrently in certain species of *Bomolochus*, Yamaguti (1939) created the subgenus *Pseudobomolochus* to accommodate the bomolochids with such morphology. However, since the name *Pseudobomolochus* had already been used for another group of bomolochids by Wilson (1913: 205), a new name *Nothobomolochus* was adopted when Vervoort (1962) revised the family Bomolochidae and elevated the subgenus to a generic status. At that time, only 11 species were recognized under the genus *Nothobomolochus* and a key to the species was provided (Vervoort 1962). Later, the addition of 13 newly discovered species created difficulty in species identification. Avdeev (1978) updated the key to the species of *Nothobomolochus*. Since then, six more species have been added to this genus, making it the largest one in the family Bomolochidae with 30 species. Thus, a new key is provided here.

In preparation of the following key, it was discovered that “*Nothobomolochus trichiuri* n. sp.” reported by Hameed & Kumar (1988) is not only bears the same species name but also is conspecific with *N. trichiuri* Pillai & Natarajan, 1977. Therefore, it is proposed to be relegated to a junior synonym of the latter.

Due to the lack of sufficient information in the original descriptions, three species of

Nothobomolochus can not be included in the following key. They are *N. cornutus* (Claus, 1864), *N. scomberesoci* (Krøyer, 1864), and *N. saetiger* (Wilson, 1911) The first species can be keyed beyond bracket 18 and the last two species can be keyed as far as bracket 20. As pointed out by Vervoort (1962:63), these three species need "an accurate redescription".

- | | | | |
|-------------------------------------------------------------------------------------------------------------------------------------------------------|----|------------------------------------------------|--|
| 1. Pediger 3 normally developed | 2 | | |
| Pediger 3 partly concealing pediger 4 | 6 | | |
| Pediger 3 entirely concealing pediger 4 | 12 | | |
| 2. Urosome as long as prosome; terminal claw of maxilliped with outer knob | | <i>teres</i> (Wilson, 1911) | |
| Urosome distinctly shorter than prosome; terminal claw of maxilliped smooth | 3 | | |
| 3. Genital double somite wider than long; 3 processes on antennule much longer than first 2 setae | 4 | | |
| Genital double somite longer than wide; 3 processes on antennule as long as or only slightly longer than first 2 setae | 5 | | |
| 4. Caudal ramus short, 1.67:1; leg 5 with 2 patches of spinules along margin | | <i>quadriceros</i> Pillai, 1973 | |
| Caudal ramus long, 2.67:1; a large patch of spinules covering tip of leg 5 | | <i>vervoorti</i> Avdeev, 1986 | |
| 5. Tip of leg 5 covered by a large patch of spinules; mandible with a row of denticles at base of terminal spines | | <i>elegans</i> Avdeev, 1977 | |
| Tip of leg 5 otherwise; mandible otherwise | | <i>atlanticus</i> Avdeev, 1978 | |
| 6. Claw of maxilliped with auxiliary tooth or outer protrusion | 7 | | |
| Claw of maxilliped smooth | 8 | | |
| 7. Distal segment of leg 5 with spinules on inner margin; middle and distal processes on antennule longer than proximal process | | <i>gazzae</i> (Shen, 1957) | |
| Distal segment of leg 5 with 2 patches of spinules; 3 processes on antennule long and subequal in length | | <i>kanagurta</i> (Pillai, 1965) | |
| Tip of leg 5 covered with a large patch of spinules; middle process on antennule stron- | | | |
| ger (thicker) than other two processes | | <i>ovalis</i> Avdeev, 1977 | |
| 8. Three processes on antennule subequal in length | 9 | | |
| Middle and distal process on antennule distinctly longer than proximal | 10 | | |
| Middle process on antennule blunt and shorter than other two | | <i>thambus</i> Ho, Do & Kasahara, 1983 | |
| 8. Formula of terminal segment of leg 4 endopod I, 1 | | <i>lateolabracis</i> (Yamaguti & Yamasu, 1959) | |
| Formula of terminal segment of leg 4 endopod I, I | | <i>tricerros</i> (Bassett-Smith, 1988) | |
| 9. Proximal process on antennule longer than 1/2 of middle process; tip of leg 5 with patch of spinules along margin | | <i>multispinosus</i> (Gnanamuthu, 1949) | |
| Proximal process on antennule shorter than 1/2 of middle process; tip of leg 5 covered with a large patch of spinules | 11 | | |
| 10. Posterior margin of cephalothorax appearing as an inverted U, with large posterolateral protrusion; caudal ramus long, 2.18:1 | | <i>paruchini</i> Avdeev, 1978 | |
| Posterior margin of cephalothorax straight; caudal ramus short, 1.75:1 | | <i>exocoeti</i> Avdeev, 1978 | |
| 11. Pediger 2 enlarged, wider than cephalothorax; proximal process on antennule longer than other two processes | | <i>marginatus</i> Avdeev, 1986 | |
| Pediger 2 distinctly narrower than cephalothorax; proximal process on antennule shorter than or subequal in length with other two processes | 13 | | |
| 12. Proximal process on antennule distinctly shorter than other two processes | 14 | | |
| Proximal process on antennule subequal with one of other two processes | 19 | | |
| 13. Anterior (dorsal) margin of outer spines on exopod of legs 2-4 heavily denticulated | | <i>denticulatus</i> (Bassett-Smith, 1898) | |
| Anterior (dorsal) margin of outer spines on exopod of legs 2-4 membranous or armed with spinules | 15 | | |
| 14. Posterior margin of cephalothorax appearing as an inverted U, with large posterolateral protrusion | 16 | | |
| Posterior margin of cephalothorax straight | 18 | | |

15. Claw of maxilliped longer than inner seta on corpus
 *cypseluri* (Yamaguti, 1953)
 Claw of maxilliped shorter than inner seta on corpus 17
16. Median process on antennule distinctly stronger and longer than distal process; caudal ramus 1.46:1
 *oxyporhamphi* Avdeev, 1977
 Median process on antennule only slightly stronger and longer than distal process; caudal ramus 2.06:1
 *gibber* (Shiino, 1957)
17. Tip of leg 5 covered with a large patch of spinules; caudal ramus 1.36:1
 *chilensis* Avdeev, 1974
 Tip of leg 5 with 2 patch of spinules along margin; caudal ramus 2.83:1
 *trichiuri* Pillai & Natarajan, 1977
18. Formula of terminal segment of leg 4 endopod I,1; dorsal margin of outer spines on exopod of legs 2-4 heavily denticulated *fradei* Marques, 1965
 Formula of terminal segment of leg 4 endopod I,1,I; armature of spines on exopod of legs 2-4 otherwise 20
19. Claw of maxilliped armed with an auxiliary tooth 21
 Claw of maxilliped smooth 23
20. Formula of terminal segment of leg 4 endopod I,1; middle process on antennule distinctly stronger (thicker) than other two processes 22
 Formula of terminal segment of leg 4 endopod I,1,I; middle process on antennule only slightly stronger other two processes *sagaxi* Avdeev, 1986
21. Claw of maxilliped longer than setae on corpus; terminal segment of leg 4 endopod short, 1.45:1
 *epulus* Vervoort, 1962
 Claw of maxilliped shorter than setae on corpus; terminal segment of leg 4 endopod long, 2.26:1 ... *sagani* Hameed & Kumar, 1988
22. Processes on antennule stout, shorter than first plumose basal seta; paragnath with finger-like terminal processes ...
 *digitatus* Cressey, 1970
 Processes on antennule slender, longer than first plumose basal seta; paragnath armed otherwise *gerresi* Pillai, 1973

Acknowledgments

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**A new calanoid copepod species from South
Carolina, U.S.A.: *Aglaodiaptomus savagei*
(Crustacea: Copepoda: Calanoida: Diaptomidae)**

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Abstract.—*Aglaodiaptomus savagei*, new species, was collected from a seasonal wetland pond in Kershaw County, South Carolina, U.S.A. Additional populations were found in eastern North Carolina, U.S.A. The female most closely resembles *A. forbesi* Light, 1938, and *A. lintoni* Forbes, 1893, but they are separated by the armament of the antennule, body length, and geographic range. Male *A. savagei* can be confused with male *A. spatulocrenatus* Pearse, 1906. Differences occur mainly in the ornamentation of the fifth leg, as well as segment sizes in the fifth leg.

A new species of calanoid copepod was collected during a survey of wetland ponds on the coastal plain of South Carolina, U.S.A. It is the second new species of this genus to be described from southeastern North America since Wilson's (1959) key to the North American calanoids was published. A total of 15 *Aglaodiaptomus* species are known from North America. The new species was first collected only about 140 km from the type locality of another recently described congener, *A. atomicus* DeBiase & Taylor, 1997, which also occurs in wetland ponds. The new species is the third new diaptomid to be recognized from this region since 1959, along with *Skistodiaptomus carolinensis* Yeatman, 1976.

The copepods were fixed and stored in 4% formalin with sucrose (600 g/l), and paratypes were transferred to ethanol. Measurements were made in glycerine, using Image Pro Plus® (Nashville, Tennessee, U.S.A.) image analysis software. Descriptions of whole specimens were made from individuals mounted in glycerine jelly. Individuals were straightened and positioned in melted jelly and held in place until it

solidified. Dissected specimens were mounted in CMC-9®. The specimens were studied using diffusion interference contrast (Nomarski) microscopy, thus they were not stained.

The new species was compared to specimens of *A. spatulocrenatus* Pearse, 1906 to verify that it is indeed a separate species. The *A. spatulocrenatus* specimens were collected from the following locations: Pond near outlet of John Pond, Mashpee, Massachusetts, U.S.A. (USNM 60392); Lily Pond south of Ashmet Pond, Falmouth, Massachusetts (USNM 60388); Clements Pond, Hopkinton, New Hampshire, U.S.A.; Adams Pond, Barnstead and Pittsfield, New Hampshire, and Hall, Upper Pond, Sandwich, New Hampshire (all USNM 210801), M. S. Wilson, collector.

Family Diaptomidae Baird 1850
Genus *Aglaodiaptomus* Light, 1939
Aglaodiaptomus savagei, new species
Figs. 1–3

Type material.—Holotype ♂, USNM 296406; allotype ♀, USNM296407; 12 ♂♂ 6 ♀♀, each dissected on slide in CMC-9,

and 25 ♂♂ 25 ♀♀ + copepodids, undissected and preserved in ethanol; all from Savage Bay, Kershaw County, South Carolina, 34°07'49"N, 80°31'27"W, 7 Aug 1996, B. E. Taylor, collector.

Additional non-type material.—5 ♂♂ 5 ♀♀, dissected and mounted on slides in glycerine, and 30 ♂♂ 30 ♀♀, undissected and preserved in ethanol, USNM 296408, North Carolina, Onslow County, Site 14, 34°37'03"N, 77°18'49"E, United States Marine Corps Camp Lejeune, directly adjacent to unnamed dirt road on northwest side, 210 m southwest of Well Point Road, dirt road intersects Well Point Road 330 m northeast of Well Camp Road. Also 20 ♂♂ 20 ♀♀ dissected on slides in CMC-9, and 200 ♂♂ 200 ♀♀ + copepodids, undissected in formalin, from 9 additional ponds (all located in United States Marine Corps Camp Lejeune, 34°37'03–34°37'59"N, 77°18'49"–77°19'30"E). All collected 4 Feb 2000 by J. C. Mitchell.

Co-occurring Diaptomidae.—None observed in type location or Camp Lejeune Site 14; *Onychodiaptomus birgei* Marsh, 1894 or *Skistodiaptomus reighardi* Marsh, 1895 in 8 Camp Lejeune Sites, *S. reighardi* and *O. birgei* in remaining Camp Lejeune Site.

Male.—Length, excluding caudal setae: 1.0–1.3 mm ($n = 20$, $\bar{X} = 1.25$ mm). Body broadest at pedigers 1 and 2 in dorsal view (Fig. 1A). Pedigers 4 and 5 weakly fused. Thoracic wings nearly symmetrical, with small dorsomedial and ventrolateral sensilla (Fig. 1B). Urosome of 5 segments and caudal rami (Fig. 1B); segment 1 asymmetrical; left posterior distal corner with medium-sized lobe, right posterior distal corner without lobe (Fig. 1C). Both corners tipped with small sensillum. Segments 2–4 symmetrical. Inner margins of caudal rami lined with fine setules.

Antennules reaching distal margin of urosomite 4 (Fig. 1A).

Left antennule 25-segmented (as in Fig. 3B); armature per segment as follows (s = number of setae, a = aesthetasc, sp =

spine): 1(s+a), 2(3s+a), 3(s+a), 4(s), 5(s+a), 6(s), 7(s+a), 8(s+sp), 9(2s+a), 10(s), 11(2s), 12(s+sp+a), 13(s), 14(s+a), 15(s), 16(s+a), 17(s), 18(s), 19(s+a), 20(s), 21(s), 22(2s), 23(2s), 24(2s), 25(5s+a). Setae on segments 17, 19, 20, 22 with stiffly hooked ends.

Right antennule segments 18–19, 20–21, and 22–23 fused; geniculation between segments 19 and 20 (Fig. 1E, F). Segments 10 and 11 each with spine reaching distal margin of succeeding segment; spine on segment 10 distolaterally directed, spine on segment 11 distally directed (Fig. 1D). Distolaterally directed spine on segment 13 about as long as segment 14. Distal spines on segments 14–17 bifurcated at tips. Modified digitiform seta (Fig. 1E) borne on proximal $\frac{1}{4}$ of segment 17, extending to midlength of fused segment 18–19 (a). Additional digitiform setae arising near distal margin of segment 18–19, extending to distal margin of segment (b), and from proximal $\frac{1}{4}$ of segment 20–21, almost reaching distal margin of bearing segment (c). Curved distal process (Fig. 1F) on segment 22–23 about $\frac{1}{2}$ the length of segment 24.

The segmentation and armature of the mouthparts and swimming legs are the same as those of another congener, *Diaptomus* (*Aglaodiaptomus*) *kingsburyi* Robertson, 1975. Leg 2 endopod 2 with well-developed Schmeil's organ on posterior surface (Fig. 2A). Left leg 5 (Fig. 2B–F): Leg (excluding spines) extending to distal margin of right leg exopod 1. Coxa with distolateral lobe tipped with sensillum. Basis with slender, minute lateral seta inserted at $\frac{1}{3}$ segment length from distal margin. Exopod 1 twice as long as exopod 2; hairy pad on distolateral corner (Figs. 2C, D). Exopod 2, distal $\frac{1}{3}$ of posterior surface covered with minute protuberances (Fig. 2C); protuberances covering about 1/10 of anterior surface of distal end (Fig. 2D). Inner margin lined with fine hair-like setules. Processes on exopod 2 subterminal. Inner process with a wide base, slightly shorter than exopod 2; inner margin of process lined

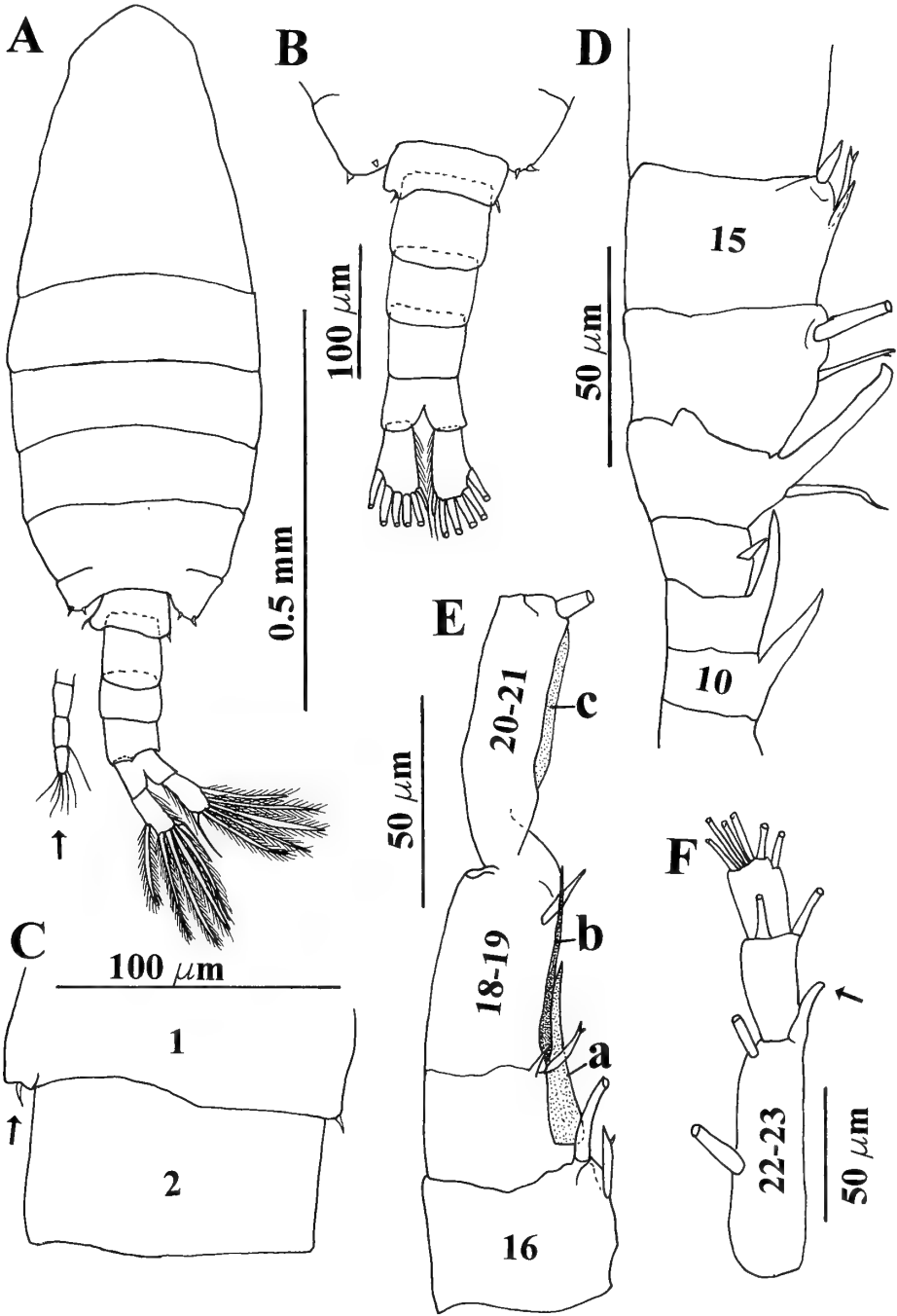


Fig. 1. *Aglaodiaptomus savagei*, new species, male: A, Habitus, dorsal; B, Urosome, dorsal; C, Urosome, segments 1-2, bilobed process indicated by arrow; D, Right antennule, segments 10-15; E, Right antennule, segments 16-21, modified digitiform setae indicated by stippling and labeled "a", "b", "c"; F, Right antennule, segments 22-25, lateral spine indicated by arrow.

with fine setules. Outer process shorter than inner process; distal end rounded and smooth. Endopod, excluding terminal processes (Figs. 2B, E, F), longer than exopod; outer margin with scale-like protrusions in both dorsal and ventral views. Margins of "scales" lined with fine spinules. Inner tip of endopod with pad of fine denticles in posterior view (Fig. 2E).

Right leg 5 (Fig. 2B, G, H): Coxa with distomedial lobe tipped with sensillum (Fig. 2B). Basis with lobed protrusion on medial-posterior face, proximal $\frac{1}{2}$ of segment (Fig. 2G); seta emerging from distal $\frac{1}{3}$ of lateral margin. Endopod greatly reduced, represented by laterally bent lobe, distal $\frac{1}{2}$ of lobe covered with fine setae. Exopod 1 about $\frac{3}{4}$ as long as basis; short with wide bilobed process on distolateral corner (Fig. 2H). Exopod 2 about twice as long as exopod 1. Terminal claw of exopod 1 robust and wide-based; claw equal in length to exopod 2. Inner surface of distal $\frac{1}{2}$ of claw lined with fine denticles. Lateral spine curved, inserted at $\frac{4}{5}$ length of exopod 2; spine $\frac{2}{3}$ as long as segment, inner surface of distal $\frac{1}{3}$ lined with fine denticles.

Female.—Length, excluding caudal setae: 1.4–1.7 mm ($n = 20$, $\bar{X} = 1.51$ mm). Prosome segmentation as in male (Fig. 3A). Antennules 25-segmented, reaching slightly beyond genital segment (Fig. 3A); armature as in male left antennule (Fig. 3B). Thoracic wings nearly symmetrical (Fig. 3C); left inner lobe more dorsally directed than right one. Lobe on each side tipped with small sensillum of approximately equal size. Urosome of 3 segments and caudal rami. Left and right margins of genital segment equal in length, each margin slightly protuberant. Lateral protuberances each tipped with small spine; left lobe and spine placed slightly more proximal than right. Genital operculum with broad proximal plate; distal plate of intermediate width with short arms; transverse plate narrow and crescentic (Fig. 3D). Caudal rami about twice as long as broad; inner margins with fine setules (Fig. 3C).

Mouthparts and swimming legs: As in male.

Leg 5 (Fig. 3E): Coxa with posterior lateral protrusion tipped with sensillum. Basis with slender lateral seta. Exopod 1 slightly shorter than exopod 2 (including claw). Claw on exopod 2 relatively short, slightly curved, with fine denticles on inner and outer margins. No articulation between exopod segments 2 and 3. Lateral spine of exopod 2 about $\frac{2}{3}$ length of outer seta of exopod 3. Inner seta of exopod 3 plumose, outer seta $\frac{2}{3}$ as long as inner seta. Endopod reaching beyond distal margin of exopod 1; tipped with small, rounded, setule-covered protrusion and two setae covered with long, fine setules; setae equal in length and breadth, one terminal, one subterminal (Fig. 3F).

Color.—Pale blue; distal $\frac{1}{3}$ of antennae orange-red. Blue pigmentation is lost with preservation. The red pigment may be lost or become purple-red.

Type locality.—Savage Bay, 34°07'49"N, 80°31'27"W, Savage Bay Heritage Trust Preserve, Kershaw County, South Carolina, U.S.A.

Etymology.—The species name is given after Savage Bay, its type location, and in honor of Henry Savage, Jr. (1903–1990), for whom the location was named. Mr. Savage was a noted naturalist, lawyer, and civic leader in South Carolina, as well as the author of the treatise "The Mysterious Carolina Bays" (1982).

Distribution and ecology.—*Agladiaptomus savagei* is presently known from one Carolina bay in north-central South Carolina and from nine ponds on the southeastern coast of North Carolina, U.S.A.

The type locality of *A. savagei* is a pair of adjacent Carolina bays in the Savage Bay Heritage Trust Preserve. The two basins combined have an area of 8 ha. Carolina bays are shallow, elliptical depressions with a northwest-southeast orientation (Taylor et al. 1999). They occur throughout the sandy Atlantic Coastal Plain from New Jersey to northern Florida, but are most common in

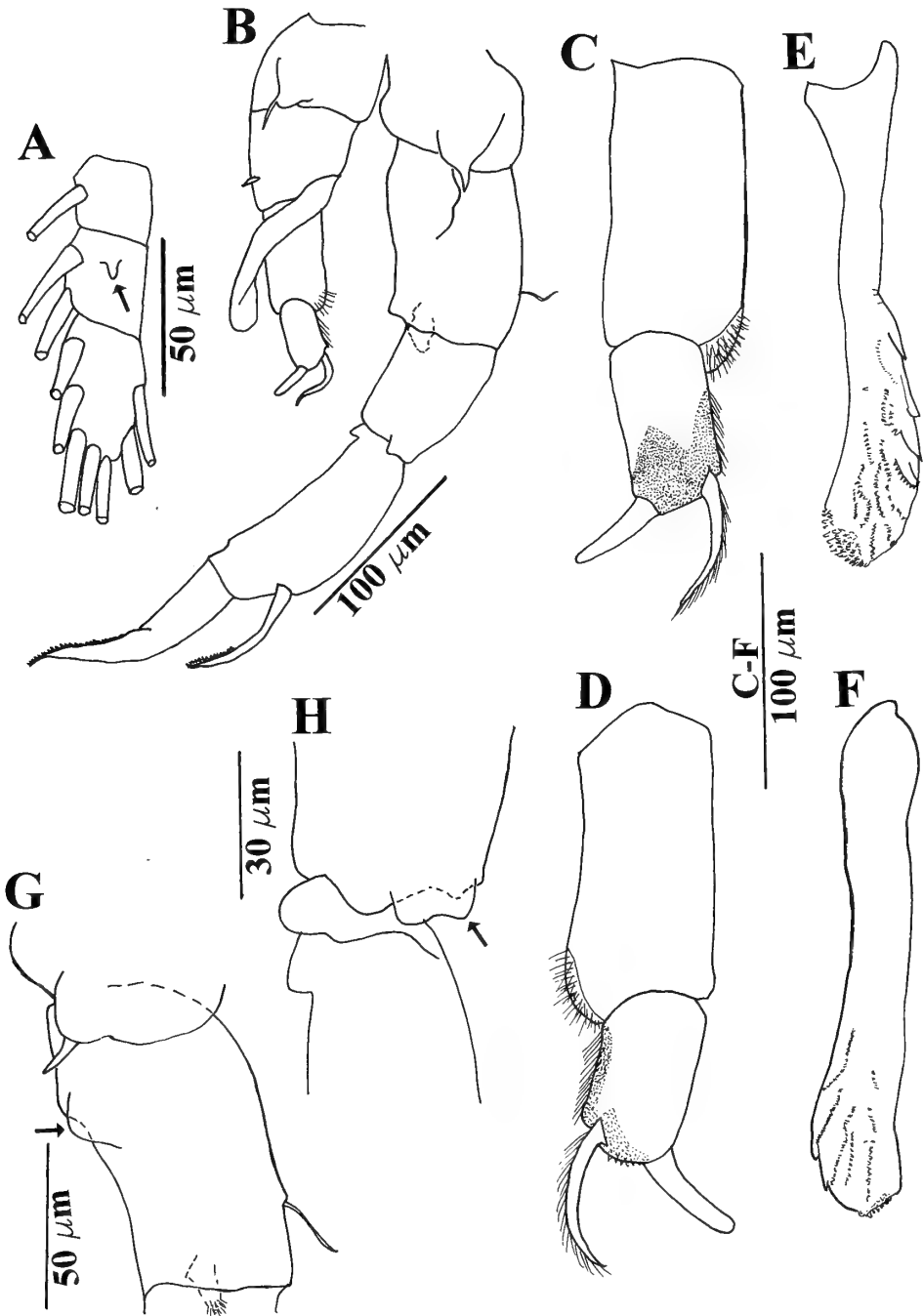


Fig. 2. *Aglaodiaptomus savagei*, new species, male: A, Leg 2 endopod, posterior, arrow indicating Schmeil's organ; B, Leg 5, posterior; C, Left leg 5 exopod 1 and 2, posterior; D, Left leg 5 exopod 1 and 2, anterior; E, Left leg 5 endopod, posterior; F, Left leg 5 endopod, anterior; G, Right leg 5 basis, medial, arrow indicating medial-posterior protuberance; H, Right leg 5, distal end of exopod 1, posterior, arrow indicating bilobed protuberance.

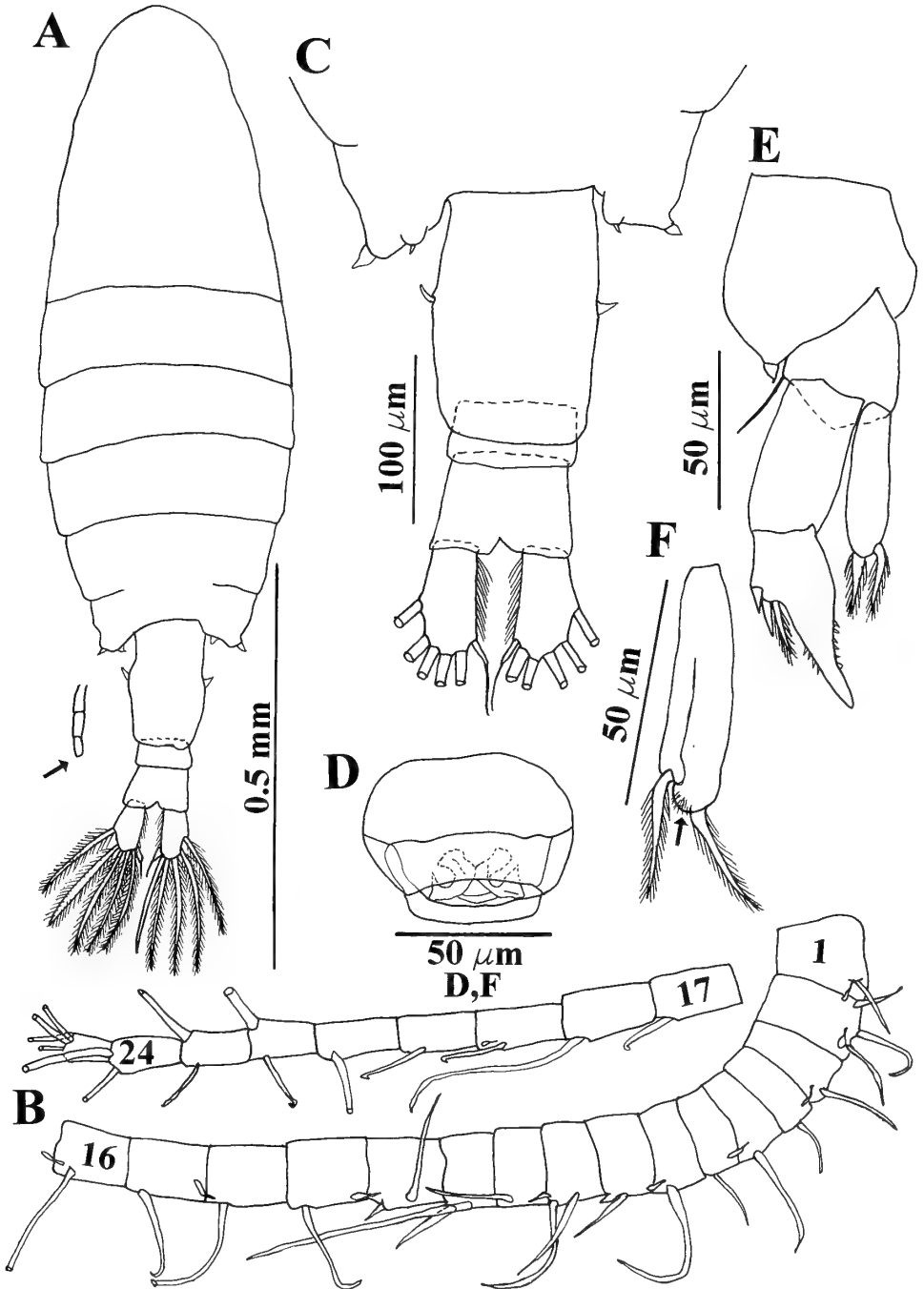


Fig. 3. *Aglaodiaptomus savagei*, new species, female: A, Habitus, dorsal, distal segments of antennule indicated by arrow; B, Antennule, dorsal; C, Thoracic wings and genital compound segment; D, Genital operculum; E, Leg 5, anterior; F, Leg 5 endopod, posterior, arrow indicating hairy lobed process on distal end.

Table 1.—Comparison of female *Aglaodiaptomus savagei* to *A. forbesi* and *A. lintoni*.

	<i>A. savagei</i>	<i>A. forbesi</i>	<i>A. lintoni</i>
Thoracic wings	Symmetrical	Symmetrical	Symmetrical
Genital segment	Slightly elongated, symmetrical	Short, symmetrical	Short, symmetrical
Antennules, segments 13–19 ^a	One seta on each segment	Two setae on segment 16, one seta on each of segments 13–15, 17–19	Two setae on segment 16, one seta on each of segments 13–15, 17–19
Antennule length	Slightly beyond distal end of genital segment	Proximal end of caudal rami	Slightly beyond proximal end of caudal rami
Leg 5, endopod	Longer than exopod 1 by $\frac{1}{5}$ to $\frac{1}{4}$ its length	As long as exopod 1	Longer than exopod 1 by $\frac{1}{5}$ to $\frac{1}{4}$ its length
Length	1.3–1.7 mm	1.3–1.9 mm	1.7–2.5 mm
Geographic range	Eastern North and South Carolina	Pacific coast states, western Canada east to Saskatchewan	Rocky Mountains, Montana to Colorado

^a Also male left antennule.

the Carolinas. Many of these wetlands fill and dry seasonally, and the waters are very acidic. On three dates from February–June 1994, the pH of Savage Bay ranged from 3.80–3.86. We have observed this wetland to dry periodically.

The vegetation of Savage Bay is dominated by pond cypress (*Taxodium ascendens* Brongniart, 1883) with an understory of myrtle-leaf holly (*Ilex myrtifolia* Walter, 1788) and the rare pond spice (*Litsea aestivalis* (L.) Fernald, 1945). Sedges (*Carex* spp.) and sphagnum moss are also common. The dominant vertebrates are amphibians, although pygmy sunfish (*Elassoma* spp.) have also been collected (S. H. Bennett, pers. comm.).

Like many isolated wetland ponds on the Atlantic Coastal Plain of the southeastern United States, Savage Bay harbors a rich community of microcrustacean species. Nineteen species of Cladocera were observed, along with an undetermined number of harpacticoid copepods and ostracods. At least three cyclopoid copepod species have been collected here: *Macrocyclus fuscus* Jurine, 1820, *Tropocyclops extensus* Kiefer, 1931, and *T. prasinus mexicanus* Kiefer, 1938. No Anostraca or Conchostraca have been observed in Savage Bay.

Discussion and comparisons.—Female

A. savagei might be confused with two other congeners: *A. forbesi* Light, 1938, and *A. lintoni* Forbes, 1893. The morphological differences lie primarily in the length and armament of the antennules and relative length of leg 5, exopod, and geographic range (Table 1). Furthermore, *A. lintoni* is substantially larger than the other two species. Besides the obvious size difference in size between *A. savagei* and *A. lintoni*, there is also a difference in color. Live or freshly-preserved *A. savagei* are pale blue with the distal $\frac{1}{5}$ of the antennae being colored orange-red, although the pigments may fade after preservation. *Aglaodiaptomus lintoni* are completely red (Marsh 1907).

The male *A. savagei* might be confused with *A. spatulocrenatus*. There are obvious differences between females of the two species. The males are distinguished by the fifth leg (Table 2).

Three of the six diaptomids described from the United States and Canada since Wilson published her key (1959) belong to the genus *Aglaodiaptomus*. Four of the six species were collected from seasonal ponds, including all three *Aglaodiaptomus* and *Hesperodiaptomus californiensis* Scanlin and Reid, 1996. Carolina bays, vernal pools, and other seasonal wetland ponds in

Table 2.—Major morphological differences between male *Aglaodiaptomus savegei* and *A. spatulocrenatus*.

	<i>A. savegei</i>	<i>A. spatulocrenatus</i>
Leg 5, right, basis	Medial-posterior lobe only	Medial-posterior lobe and distomedial hook-like protrusion
Leg 5, left, endopod	Outer margin with scale-like protrusions	Outer margin scalloped
Leg 5, left, distal processes	Nearly equal in length	Inner twice as long as outer
Leg 5, left, exopod 2	As long as exopod 1	Half as long as exopod 1
Length	1.0–1.3 mm	1.1–1.3 mm
Geographic range	Eastern North and South Carolina	Quebec to east coast; south Atlantic coastal states to Maryland

North America have long been neglected as subjects for study. As more research ensues in poorly studied regions and habitats, it is likely that additional new species will be discovered.

Acknowledgments

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Range extension of *Acanthomysis hwanhaiensis* Ii, 1964, to the San Francisco estuary, California, and notes on its description (Crustacea: Mysidacea)

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Abstract.—The range of *Acanthomysis hwanhaiensis* has been extended from Korea to the San Francisco Bay estuary, California, presumably as the result of ballast water discharge from ocean-crossing vessels. The species is described here because the previous description is out of print and difficult to obtain. Two verified exotic mysid species, and potentially a third, have previously been reported to inhabit the San Francisco Bay estuarine system.

The large amount of shipping from the Far East that enters the San Francisco Bay estuary has brought many exotic marine invertebrates along with it (Cohen & Carlton 1995). Since 1987 eight exotic copepods, most probably transported in ship ballast water, have been discovered (Orsi & Ohtsuka 1999). In addition, two Mysidacea, *Acanthomysis aspera*, common in the coastal waters of Korea and Japan, and *Acanthomysis bowmani*, a species with strong similarities to taxa from the coastal waters of China and Korea, have been found (Modlin & Orsi 1997). A third mysidacean, *Delta-mysis holmquistae*, which was possibly introduced, was described from the estuary (Bowman & Orsi 1992). To these we add a fourth mysid species, *Acanthomysis hwanhaiensis* Ii (1964), a Korean native.

Ii (1964) first described *Acanthomysis hwanhaiensis* from specimens collected in waters around Ryons Mai Island, Hae Ju Bay, Whang Hae do District, Korea. Although his descriptions are complete, the monograph that contains the descriptive material is out of print and somewhat difficult to obtain. Consequently, we have pro-

vided descriptive information and illustrations of several key identifying characters for those specimens of *A. hwanhaiensis* obtained in the San Francisco estuary.

The native mysid fauna of the San Francisco Bay estuary consisted of *Neomysis mercedis*, *N. macropsis* (now *Alienacanthomysis macropsis*), *N. kadiakensis*, *N. ravi*, and *N. costata* (now *Holmesimysis costata*) (Tattersall 1932). These species were all taken during a survey of San Francisco and San Pablo bays in 1912 and 1913 by the USS *Albatross*. Surveys conducted in 1997 and 1998 by the California Department of Fish and Game only collected specimens of *N. kadiakensis*, *N. mercedis*, and *A. macropsis*.

Methods.—All samples were collected by the California Department of Fish and Game (CDFG) with a tow-net mounted on sled-type runners and towed on the bottom for 10 minutes. A General Oceanics meter measured water flow through the net. Mesh size was 505 μm , net mouth diameter 76 cm, and net length 3.35 m. Samples were preserved in 10% buffered formalin with rose bengal dye added to help distinguish the mysids from detritus.

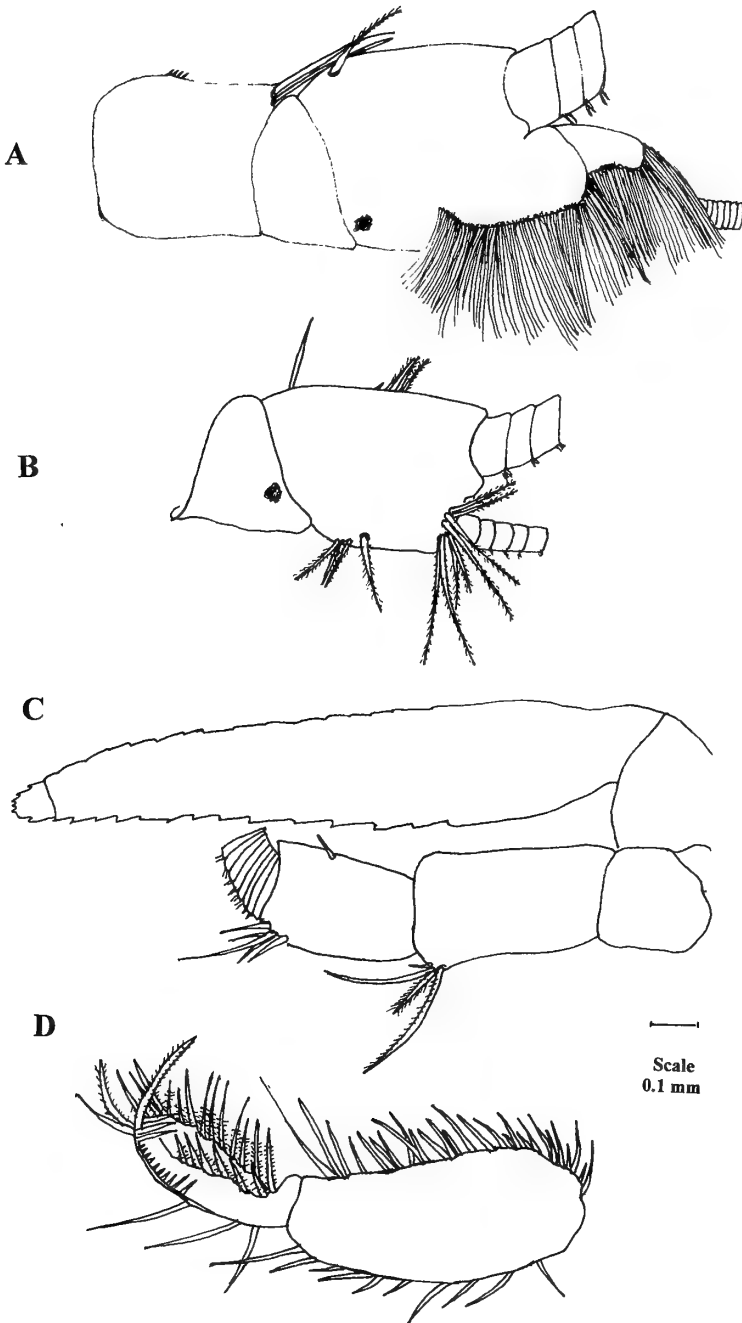


Fig. 1. *Acanthomysis hwanhaiensis* Ii: A. Antennular peduncle, male, 11.1 mm; B. Antennular peduncle segments 2 and 3, female, 12.00 mm; C. Antennal peduncle and scale, male, 10.0 mm; D. Mandibular palp, male, 11.1 mm.

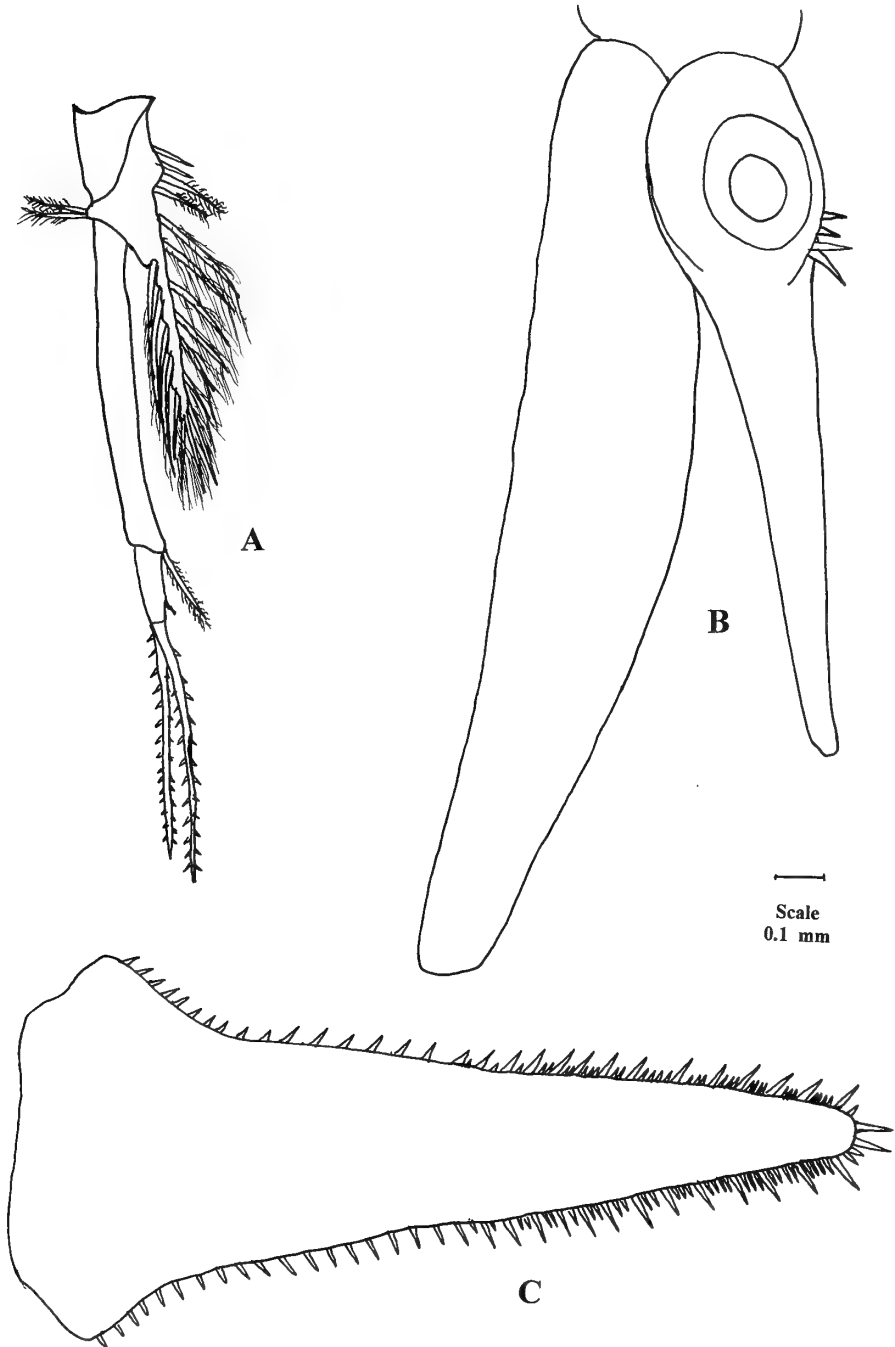


Fig. 2. *Acanthomysis hwanhaiensis* II: A. Fourth pleopod, male, 10.8 mm; B. Uropod, male, 11.1 mm; C. Telson, male, 11.1 mm.

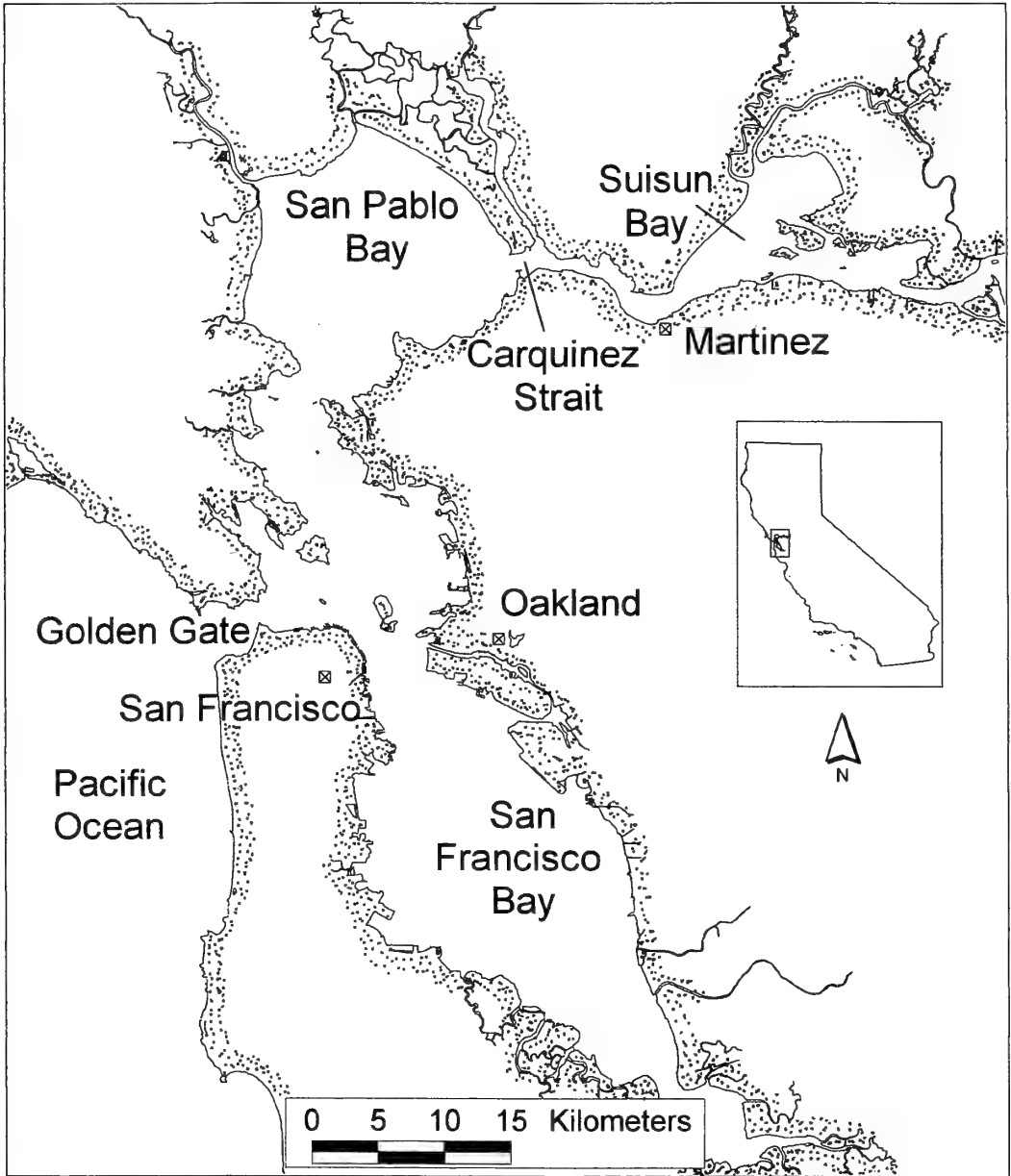


Fig. 3. San Francisco estuary survey area of the California Department of Fish and Game.

Acanthomysis hwanhaiensis Ii, 1964

Figs. 1-2

Material examined.—11 ♂♂, average size = 10.2 mm, range 9.5–11.2 mm; 5 ♀♀, average size = 10.9 mm, range 9.6–12.6 mm. Five ♂♂ and 2 ♀♀ specimens from the San Francisco Bay collection are

on deposit at the USNM of Natural History, Smithsonian Institution, catalog number USNM 291489.

Description.—Antennular peduncle, male (Fig. 1A) 3-segmented; combined length of segments 1 and 2 about 1.3 times length of segment 3; segment 1 with a

group of 4 minute setae on middle of dorsal-lateral margin, 3–4 long setae distal-laterally; segment 2 triangular without setae; segment 3 robust, length to width ratio about 1.0, single proximal plumose seta along dorsal-lateral margin; male lobe conspicuous, heavily setose with fine setae. Female (Fig. 1B) segments 1 and 2 identical to that of male, segment 3 longer than that of male, length to width ratio about 1.4, with 7 plumose setae distally, 4 plumose setae along medial margin, 5 plumose setae laterally, and one spine-like seta directed ventrally on proximal margin. Medial pigmented spot on preserved specimens visible on segment 3 of males and segment 2 of females.

Antennal peduncle (Fig. 1B) 3-segmented; proximal segment 0.6 times length of segment 2, without setae; segment 2, 1.25 times length of segment 3, with a distal-medial group of setae composed of long and small naked setae, a plumose seta and long, robust seta with marginal spinules; segment 3 with distal-medial group of 4 subequal setae and 1 long naked seta, a single medial seta laterally; scale, blade-like, 1.4 times as long as peduncle, setose all around, articulated tip 0.06 times scale length.

Mandibular palp (Fig. 1C) 3-segmented; segment 1 inconspicuous; segment 2 about twice as long as segment 3, robust, medial margin setose along entire length with long, naked setae, lateral margin with 10 naked setae along length; distal segment triangular in cross-section, medial pad surrounded by about 20 robust setae with spinules, lateral margin with 3 long naked setae, apex with 1 naked and 2 long setae with spinules, a row of minute denticle-like spines distal-laterally.

Male fourth pleopod (Fig. 2A) short, length does not reach distal margin of sixth abdominal somite; proximal segment of exopod thick, about 7 times as long as distal segment, short plumose seta on distal-medial edge; distal segment with small inconspicuous naked seta on medial-distal edge,

apex terminating in two long setae, apical setae about 5 times length of distal segment and armed with denticle-like spines along entire length; endopod unjointed, about 0.7 times length of proximal segment of exopod.

Uropod (Fig. 2B) exopod blade-like, about 1.3 times length of endopod, setose all around margin; endopod, margins strongly taper distally, with 4 spines along medial margin near statocyst ventrally, setose all around margin.

Telson (Fig. 2C) linguiform, about 2.1 times longer than width at base, lateral margins with about 30 long subequal spines throughout interspersed in distal half of telson with smaller spines about 0.5 times length of longer ones, number of shorter spines between longer ones increases from 1–4 distally, 1–2 short marginal spines in ultimate position, apex with pair of longer spines.

Remarks.—Except for the differences in the size and setation of antennular peduncle segment 3, males (Fig. 1A) and females (Fig. 1B) are morphologically identical.

Ecological notes.—*Acanthomysis hwanhaiensis* was first taken in San Francisco Bay in September 1997. It has been found at mean water column salinities from 9.8 to 30.4 psu. The range of this species in the estuary encompasses all of San Francisco and San Pablo bays, and Carquinez Strait to Martinez at the western edge of Suisun Bay (Fig. 3). Its highest density, 35.8 individuals/m³, occurred in San Francisco Bay at a bottom salinity of 30.4 psu.

Acknowledgments

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Remarks on the taxonomy of the genus *Ekleptostylis* Stebbing, 1912 (Crustacea: Cumacea: Diastylidae)

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Abstract.—The adult male and female of *Leptostylis vemae* Băcescu-Meşter, 1967 are described and illustrated. This species is transferred to the genus *Ekleptostylis* Stebbing, 1912 and the description of *Ekleptostylis heardi* McLelland & Meyer, 1998 is emended. Both species were found in the Magellan Strait, Beagle Channel, Drake Passage and off Argentina. In addition, *E. vemae* was found off Uruguay. *Diastylis pseudinornata* Ledoyer, 1977 from the Ker-guelen Islands also is transferred to the genus *Ekleptostylis*, resulting in a total of four species now in this genus.

Papers on the cumacean fauna from southern South America have been rather scanty. Most of the species described from this region come from two important expeditions: the “Hamburger Magalhaensische Sammelreise 1892/93” and the “Vema Expeditions” 1958–1961 from the Lamont Geological Observatory, USA (see Zimmer 1902, Băcescu-Meşter 1967, Băcescu 1969, Băcescu & Muradian 1974; Muradian 1976, 1979; Băcescu & Petrescu 1991; Petrescu 1994, 1995).

A large collection of Cumacea from the Magellan region was obtained during the Joint Chilean-German-Italian Magellan “Victor Hensen” Campaign in 1994. Based on this material, some additional samples from Argentina and Uruguay, and the examination of the relevant type material, a study on the genus *Ekleptostylis* Stebbing, 1912 is presented.

In this paper the adult male and female of *Leptostylis vemae* Băcescu-Meşter, 1967 are described and the description of *Ekleptostylis heardi* McLelland & Meyer, 1998 is emended. *Leptostylis vemae* and *Diastylis pseudinornata* Ledoyer, 1977 are trans-

ferred to *Ekleptostylis*, resulting in a total of four species now in this genus.

Materials and Methods

Most of the specimens studied were collected during the Joint Chilean-German-Italian Magellan “Victor Hensen” Campaign, 1994. The largest number of cumaceans was obtained with an epibenthic sledge (see Brandt & Barthel 1995). Other specimens were collected with a small dredge (opening: 0.43 × 0.18 m) equipped with a net of 0.3 mm mesh to sample smaller crustaceans. Only two specimens were obtained with a grab. For more information on this campaign see Arntz & Gorny (1996).

In addition, specimens from Argentina included those taken during the German-Argentine cruise aboard the F.R.V. *Walther Herwig* (WH 31), the Japanese-Argentine cruise aboard the R/V *Shinkai Maru*, both in 1978, and the Argentine cruise OB-08/88 (INIDEP, Mar del Plata). Lastly, specimens from Uruguay were collected during the cruise *Aldebarán 9508* (INAPE, Montevideo).

The abbreviation ZMH refers to the Zoologisches Museum, Hamburg; ZMB, Museum für Naturkunde, Berlin; MNHN, Museum National d'Histoire Naturelle, Paris; USNM, United States National Museum, Smithsonian Institution, Washington, D.C.; GCRL, Gulf Coast Research Laboratory, Ocean Springs, Mississippi; INAPE, Instituto Nacional de Pesca, Montevideo; MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires; INIDEP, Instituto Nacional de Investigación y Desarrollo Pesquero, Mar del Plata.

In addition to the specimens listed in the "Material examined" sections (see below), the following type material was examined:

Ekleptostylis walkeri (Calman, 1907). Golfe de Gascogne, près de l'île d'Yeu, ?100 m: 1 ovigerous female, 1 adult male (Syntypes) (MNHN Cu 111).

Diastylis pseudinornata Ledoyer, 1977. Mission "Marion-Dufresne" 3: Sta. 8 pré. 25, N. île Heard (îles Kerguelen), 90 m, 8 April 1974: 13 ovigerous females, 3 juveniles (Paratypes) (MNHN Cu 137).

In their description of *Ekleptostylis heardi*, McLelland & Meyer (1998) designated a paratype series (USNM 230403) and also included additional specimens (GCRL 1372). However, these two samples contain some specimens of *Ekleptostylis vema* (Băcescu-Meşter, 1967). Therefore, these misidentified specimens have been listed in the "Material examined" section of *E. vema*; the remaining ones have been included in the "Material examined" section of *E. heardi*.

Order Cumacea Kröyer, 1846

Family Diastylidae Bate, 1856

Genus *Ekleptostylis* Stebbing, 1912

Ekleptostylis Stebbing, 1912: 146, 143.—Stebbing, 1913: 129.—Fage, 1951: 124–126.—Day, 1980: 224.—Băcescu, 1992: 336.—McLelland & Meyer, 1998: 278.

Type species (by monotypy): *Leptostylis walkeri* Calman, 1907 (MNHN Cu 111).

Diagnosis.—Carapace smooth, eyes lacking. First antenna with third peduncular article dilated in preadult male and a large number of aesthetascs on first article of the main flagellum in adult male. Second antenna reaching end of body in adult male. Third maxilliped with an exopod in both sexes. Second pereopod not widely separated from third in adult female. Third and fourth pereopods with rudimentary exopods in adult female. Basis of second pereopod distally produced in adult male (the bases of third and fourth pereopods are also distally produced in the adult males of *E. vema* (Băcescu-Meşter, 1967) and *E. heardi* McLelland & Meyer, 1998). Uropod with a 3-articulate endopod, equal to or slightly longer than the exopod. Telson from 4/5 to slightly longer than last abdominal segment in adult female and from slightly longer to almost twice as long as last abdominal segment in adult male; in both sexes telson shorter than uropod peduncle and furnished with 3 or more lateral spines and 2 distal ones, in adult male a broadly laminar preanal part produced over a narrow postanal part.

Ekleptostylis vema (Băcescu-Meşter, 1967), new combination
Figs. 1–6

Leptostylis vema Băcescu-Meşter, 1967: 266–268, figs. 1, 2.—Petrescu & Băcescu, 1991: 390.—Băcescu, 1992: 345.

Material examined.—Vic Hen 1253 (54°55.1'S, 69°19.9'W; 265 m), 4360 specimens (ZMH, K-39571); 20 specimens (MACN 34196). Vic Hen 1246 (54°58'S, 68°49'W; 253 m): 11 specimens, Vic Hen 1247 (54°59'S, 69°05'W; 100 m): 317 specimens, Vic Hen 1248 (54°59'S, 69°02'W; 217 m): 130 specimens, Vic Hen 1263 (54°54'S, 70°13'W; 665 m): 1 specimen, Vic Hen 1270 (54°55'S, 70°45'W; 135 m): 12 specimens, Vic Hen 1307 (54°17'S, 70°52'W; 271 m): 2 specimens; all of them in the collection of the Zoologisches Museum, Universität Hamburg (ZMH, K-

39565 to K-39570). Vic Hen 843 (53°09'S, 70°39'W; 127 m): 18 specimens, Vic Hen 874 (53°44'S, 70°56'W; 335 m): 14 specimens, Vic Hen 887 (53°42'S, 70°57'W; 100 m): 10 specimens, Vic Hen 958 (52°58'S, 70°41'W; 111 m): 7 specimens, Vic Hen 980 (53°43'S, 70°50'W; 522 m): 7 specimens, Vic Hen 1077 (54°53'S, 69°30'W; 347 m): 12 specimens, Vic Hen 1089 (54°55'S, 69°20'W; 272 m): 200 specimens, Vic Hen 1110 (54°55'S, 69°19'W; 96 m): 3 specimens, Vic Hen 1119 (54°56'S, 69°14'W; 208 m): 17 specimens, Vic Hen 1124 (54°59'S, 69°02'W; 202 m): 471 specimens, Vic Hen 1140 (54°55'S, 68°39'W; 310 m): 40 specimens; all of them in the collection of the Museum für Naturkunde, Berlin (ZMB 27312). R/V *Eltanin* Cruise 6, Station 363, 600 km north of Antarctic Peninsula (57°09'S, 58°58'W), 3590 m, 7–8 Dec 1962: 4 ovigerous females, 2 preparatory females, 3 adult males, and 2 juveniles (USNM 230403). R/V *Eltanin* Cruise 6, Station 344, 500 km east of Tierra del Fuego (54°04'S, 58°46'W), 119 m, 4 Dec 1962: 1 ovigerous female (GCRL 1372). WH I-663 (44°33.6'S, 62°59.6'W; 95 m): 1 specimen, WH II-662 (44° 56.7'S, 62°24.6'W; 100 m): 13 specimens, INAPE 9508-17 (35° 53'S, 53°27'W; 95 m): 1 specimen; all of them in the collection of one of the authors (DR).

Description of the adult male.—Total body length 6.3–6.6 mm (from tip of pseudorostrum to tip of telson).

Carapace (Figs. 1A, 6B, C) smooth, glossy with small pits, width approximately 0.8 times length; depth approximately 0.6 times length. Sides with ventral carina starting on posterior margin of carapace, running horizontally, and ending at approximately one-half distance along the carapace. Posterior mid-dorsal area with shallow depression and poorly developed hump. Antennal antero-lateral corner not produced. Antero-lateral margin of carapace with truncate extensions not acutely serrate. Pseudorostrum moderately produced, ocular lobe small, eyes absent. Free

five thoracic segments together approximately one-half as long as carapace. First segment overlapped by carapace and by antero-lateral margin of second segment, followed by four segments with free lateral margins. Abdomen approximately as long as cephalothorax, with a pair of pleopods on first and second segments and 2 pairs of setae on third and fourth segments.

Telson (Figs. 3C, 6D, E): almost twice as long as last abdominal segment, slightly longer than half of uropod peduncle. Pre-anal part strongly produced posteriorly over the postanal part, with a mid-dorsal depression bounded by a sharp carina and bearing 2 tiny sensorial setae near distal end. Postanal part armed with 4–5 spines on each side and 2 stout spines distally.

First antenna (Fig. 1B): Peduncle with first article approximately as long as other two combined. Main flagellum 6-articulate, first article with a conspicuous, thick brush-like tuft of non-segmented aesthetascs, third article the longest, fifth with 1-segmented aesthetasc, sixth article with 1 aesthetasc proximally, similar to that of the preceding article, and 1 long seta distally. Accessory flagellum 4-articulate, fourth article minute with 1 minuscule and 1 long simple seta.

Second antenna: Peduncle, first and second articles with 1 and 2 plumose setae, respectively, first, third and fourth articles subequal, approximately two thirds as long as second; fifth article slightly longer than first four articles together. Flagellum extending slightly beyond end of uropods, with approximately 20 articles (all the antennae examined were twisted/wrinkled, preventing an exact count of articles).

Mouthpart: Mandible boat-shaped, with a lacinia mobilis and 11 setae between incisor and molar processes. First maxilla, palp with 2 distal setae (filaments). Second maxilla with 2 enditae.

First maxilliped (Fig. 1C): Basis slightly longer than remaining articles together, inner margin with a row of 3–5 long plumose setae on dorsal surface (distal one thickest) and 1 distal plumose seta on ventral sur-



Fig. 1. *Ekleptostylis vema* (Băcescu-Meşter, 1967). Adult male. A, habitus; B, first antenna; C, first maxilliped; D, second maxilliped. Scales: A: 1 mm; B, D: 0.3 mm; C: 0.2 mm.

face. Merus with 1–2 denticulations on outer margin and 3 short plumose setae on distal inner margin (not drawn). Carpus with a row of spines on inner margin and numerous setae on inner margin and dorsal surface (not drawn), outer margin with 1–2 denticulations basally and 2 contiguous unequal plumose setae distally. Propodus with 2 unequal plumose setae, 1 simple seta and 2 weak spines distally, and numerous simple setae on dorsal surface (only some drawn). Dactylus with 2 distal spines and 2 subterminal setae.

Second maxilliped (Fig. 1D): Basis slightly shorter than remaining articles together; with 2 plumose setae on inner margin, 1 ventral plumose seta medially, and 2 short, weak spines, and a few transparent scales on outer margin. Ischium wedge-shaped. Merus with 3 large distal plumose setae, 2 on inner margin and 1 on outer margin. Carpus longer than propodus and dactylus together, with 6–7 plumose setae and 1 tooth on distal half of inner margin, and 2 plumose setae at outer distal margin. Propodus with 1 long plumose ventral seta in middle of article, 1 long seta with a few short setules on distal outer corner, and 3 rows of plumose setae at inner margin (only some drawn). Dactylus with distal setae.

Third maxilliped (Fig. 2A): Basis almost twice as long as remainder of appendage, with a row of plumose setae on inner margin, 4 plumose setae on outer distal corner, and a serration of 4–8 teeth on inner distal margin. Ischium with 1 plumose seta on inner margin. Merus with strong tooth on ventral face, 1 plumose seta on distal outer corner, and 2 plumose setae on inner margin. Carpus approximately as long as ischium and merus together, with strong tooth on distal inner corner, 1 plumose seta on distal outer corner, 5 plumose setae on inner margin (only ventral ones drawn). Propodus with 5 weakly plumose setae on inner margin (only ventral ones drawn) and 1 on distal outer corner. Dactylus shorter than propodus, bearing simple and pectinate setae.

Exopod shorter than basis, basal article expanded.

First pereopod (Fig. 2B): Basis slightly more than half as long as remaining articles combined, and approximately as long as propodus and dactylus together, with plumose setae on lateral and distal margins, longest seta extending beyond merus, and simple setae on ventral surface. Ischium subequal to merus, with 1 simple seta on inner margin. Merus with 1 simple seta on inner margin and 2 plumose setae on outer margin. Last three articles with simple setae only. Carpus approximately three fourths as long as propodus. Dactylus approximately 0.8 times as long as carpus. Exopod shorter than basis, basal article expanded.

Second pereopod (Fig. 2C): Basis robust, slightly longer than following four articles together, with several simple and plumose setae; inner corner developed into a conspicuous rounded process extending beyond ischium, bearing 1 plumose seta. Ischium bare, following articles with simple setae. Merus, slightly less than half as long as carpus. Carpus slightly shorter than propodus and dactylus together, with 4–6 spines distally (spine(s) behind propodus not drawn). Propodus with 1 spine distally. Dactylus more than twice as long as propodus. Exopod approximately as long as basis, basal article expanded.

Third pereopod (Fig. 2D): Basis robust, approximately twice as long as the remaining articles combined, inner corner developed into conspicuous rounded process extending as far as ischium, bearing 1 simple seta. Carpus next longest article, with 3 annulate distal setae. Propodus with 1 annulate distal seta. Dactylus with 1 small medial simple seta and 2 extremely unequal distal simple setae: one minuscule, other approximately 3–4 times as long as article. Exopod approximately as long as basis, basal article expanded.

Fourth pereopod as third, except for: Basis being approximately 1.5 times as long as remaining articles combined.

Fifth pereopod (Fig. 2E): Basis weak,

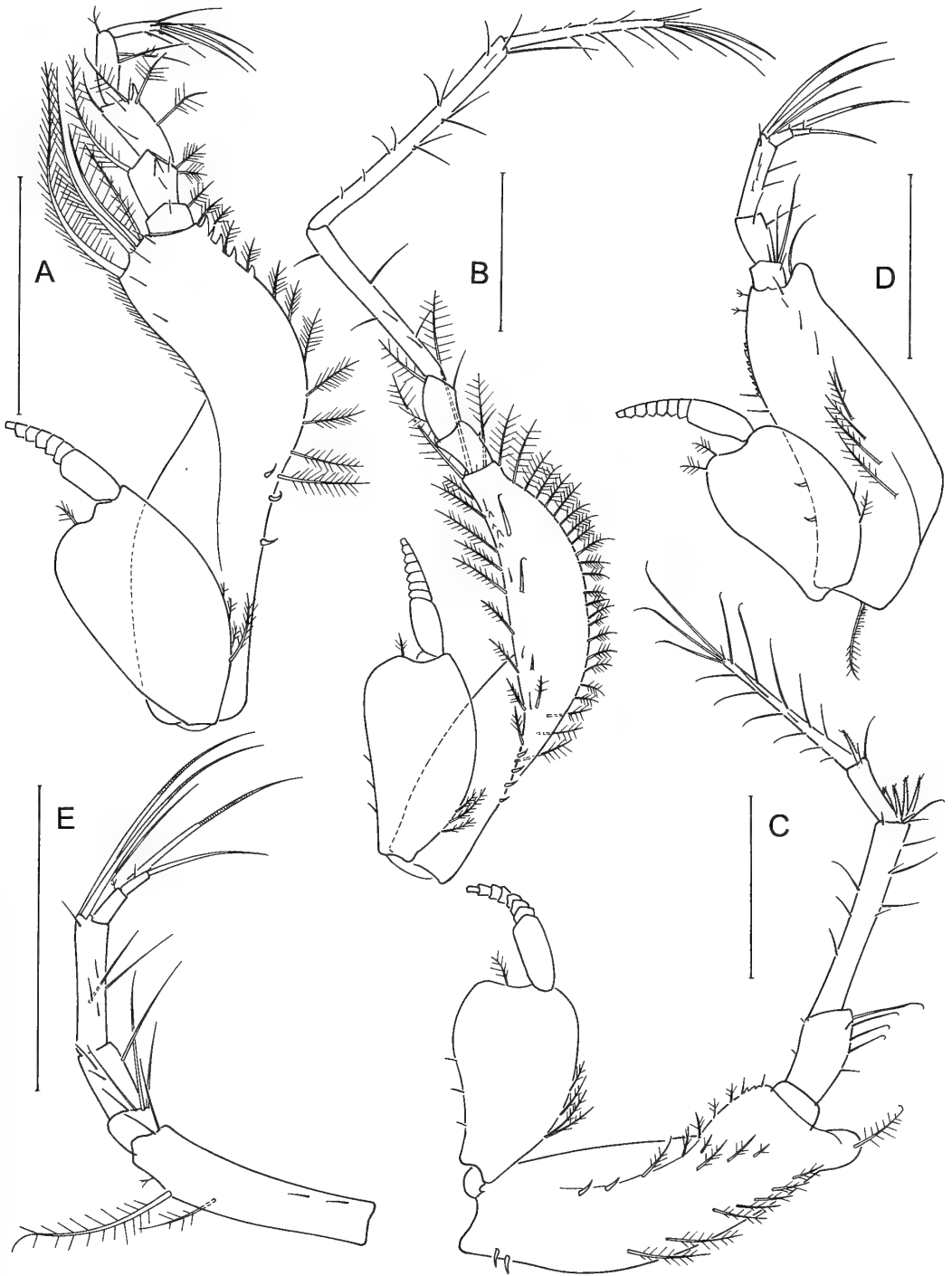


Fig. 2. *Ekleptostylis vema* (Băcescu-Meşter, 1967). Adult male. A, third maxilliped; B, first pereopod; C, second pereopod; D, third pereopod; E, fifth pereopod. Scales: 0.5 mm.

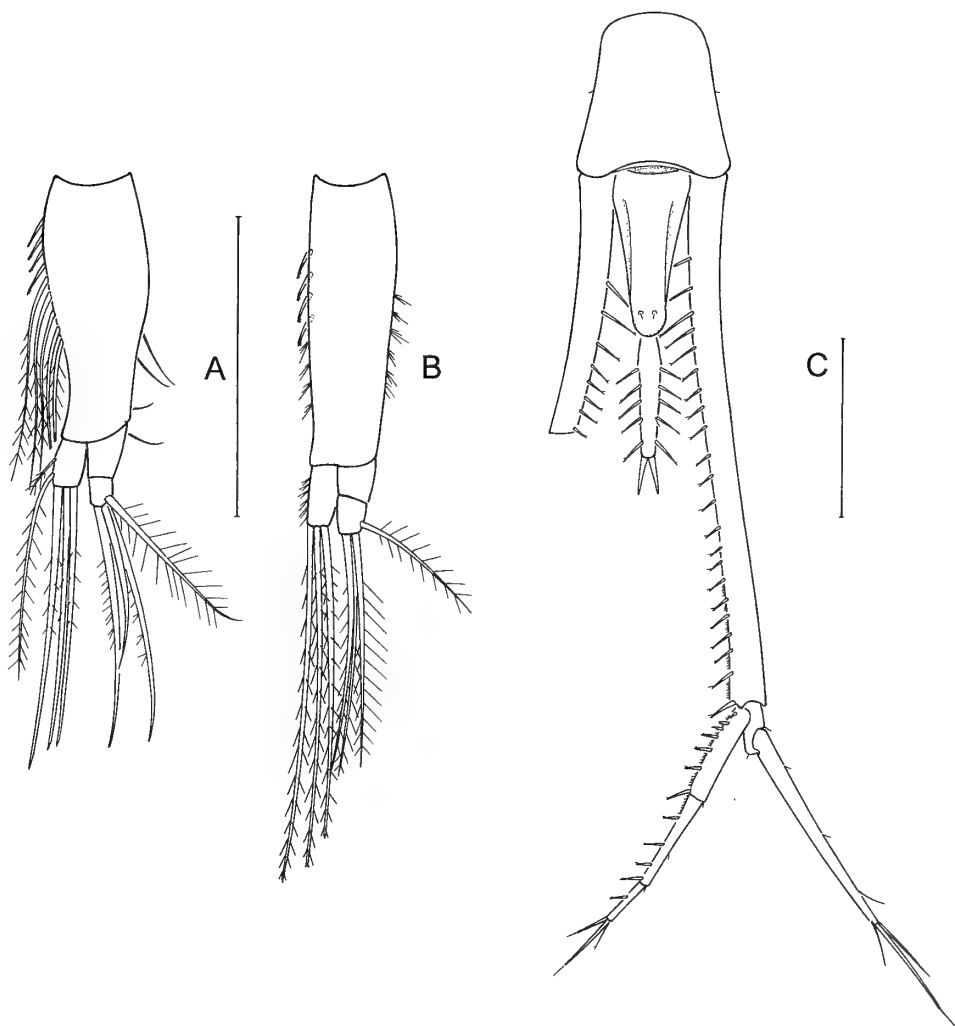


Fig. 3. *Ekleptostylis vema* (Băcescu-Meşter, 1967). Adult male. A, first pleopod; B, second pleopod; C, uropod and telson. Scales: A, B: 0.3 mm; C: 0.5 mm.

shorter than remaining segments combined, with 2 plumose setae laterally and 2 simple setae distally. Carpus, slightly more than half as long as basis. Distal setae of carpus, propodus and dactylus as in third and fourth pereopods.

First pleopod (Fig. 3A): Basis with 3–4 short spines followed by 5–7 plumose setae on inner margin. Endopod 1-articulate, with 2 unequal plumose setae on inner margin and 3 strong, weakly plumose setae distally. Exopod 2-articulate, distal article with 1

plumose seta on outer margin and 3 strong, weakly plumose setae distally.

Second pleopod (Fig. 3B) similar to first, except for: Basis more elongate, inner margin with 4–6 short spines and without plumose setae. Endopod, outer margin without plumose setae. Distal setae of both rami with abundant setules.

Uropod (Fig. 3C): Peduncle with 21–29 spines on inner margin. Rami subequal, approximately half as long as peduncle. Endopod 3-articulate, proximal and medial ar-

ticles subequal, with 7–8 and 4–5 spines, respectively; distal article approximately half as long as proximal ones, with 1 spine laterally, and 2 unequal spines and 1 small simple seta distally. Exopod 2-articulate, with oblique joint; with several small ventral (not drawn) and lateral simple setae along distal article, 1 long distal spine, and 2 small distal setae (or weak spines).

Description of the ovigerous female.—Total body length 3.9–5.6 mm (from tip of pseudorostrum to tip of telson).

Carapace (Figs. 4A, 6A) smooth, glossy with small pits and small setae (setae also present on thorax and abdomen), width approximately equal to length, depth approximately 0.8 times length. Posterior mid-dorsal area with shallow depression and poorly developed hump. Antero-lateral angle poorly developed. As in male, antero-lateral margin of carapace with row of flat-topped teeth. Pseudorostrum moderately produced, ocular lobe small, eyes absent. Free five thoracic segments together slightly more than half as long as carapace, all visible dorsally and laterally; second segment with rounded process on each side. Abdomen approximately as long as cephalothorax.

Telson (Fig. 5B) slightly longer than last abdominal segment, and slightly longer than half of uropod peduncle. Preanal part not produced. Postanal part armed with 3–4 spines on each side and 2 stout spines distally.

First antenna (Fig. 4B): First article of peduncle stout, slightly shorter than second and third articles combined; second article slightly shorter than third. Main flagellum 3-articulate, first article the longest, second with 1-segmented aesthetasc distally, third with 1 aesthetasc proximally, similar to that of the preceding article, and 1 long seta distally. Accessory flagellum 3-articulate, not reaching end of first article of main flagellum.

Second antenna (Fig. 4C) 3-articulate, with 2, 1 and 1 plumose setae on first, second and third articles, respectively.

Mouthparts and first maxilliped as in male.

Second maxilliped as in male, except for basis, without scales on outer distal margin but with a group of approximately 10 scales on ventral surface at two thirds distance along the article.

Third maxilliped (Fig. 4D) as in male, except for basis slender, inner margin with only 1 tooth distally. Propodus with 3 weakly plumose setae on inner margin (only ventral one drawn). Exopod slender.

First pereopod (Fig. 4E) as in male, except for basis approximately half as long as remaining articles together and slightly shorter than propodus and dactylus together. Carpus approximately two thirds as long as propodus. Exopod, basal article not expanded.

Second pereopod (Fig. 5A) as in male, except for basis approximately as long as following three articles together, slender and without rounded process on inner distal corner. Ischium with 1 simple seta. Merus approximately two thirds as long as carpus. Carpus approximately 0.6 times as long as propodus and dactylus together, with 3–4 spines distally (spine(s) behind propodus not drawn). Exopod longer than basis, basal article not expanded.

Third, fourth and fifth pereopods: Bases weak and without distal processes; third one the longest, approximately 1.5 times as long as remaining articles combined, other two, slightly longer and shorter than remaining articles combined, respectively. Distal setae of carpus, propodus and dactylus as in the male. Third and fourth pereopods each with rudimentary 2-articulate exopod.

Uropod (Fig. 5B) as in male, except for peduncle with 10–11 spines on inner margin. Endopod exceeding exopod by its distal article and approximately 0.7 times as long as peduncle; proximal and medial articles with 2 and 2–3 spines, respectively; distal article without lateral spines.

Distribution.—Previously recorded from off Argentina between 70 and 107 m (Bă-

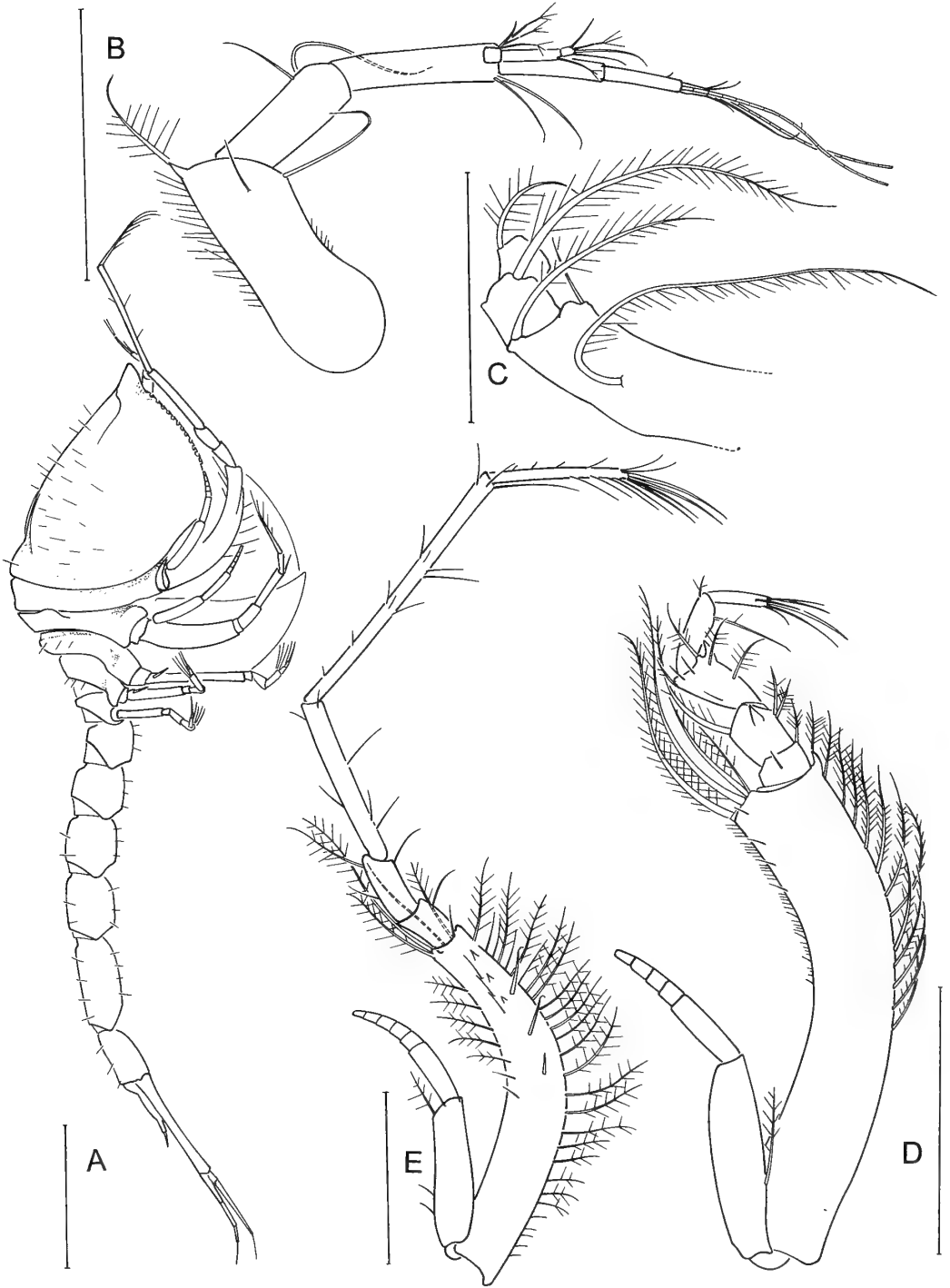


Fig. 4. *Ekleptostylis vema* (Băcescu-Meşter, 1967). Marsupial female. A, habitus; B, first antenna; C, second antenna; D, third maxilliped; E, first pereopod. Scales: A: 1 mm; B: 0.3 mm; C: 0.2 mm; D, E: 0.5 mm.

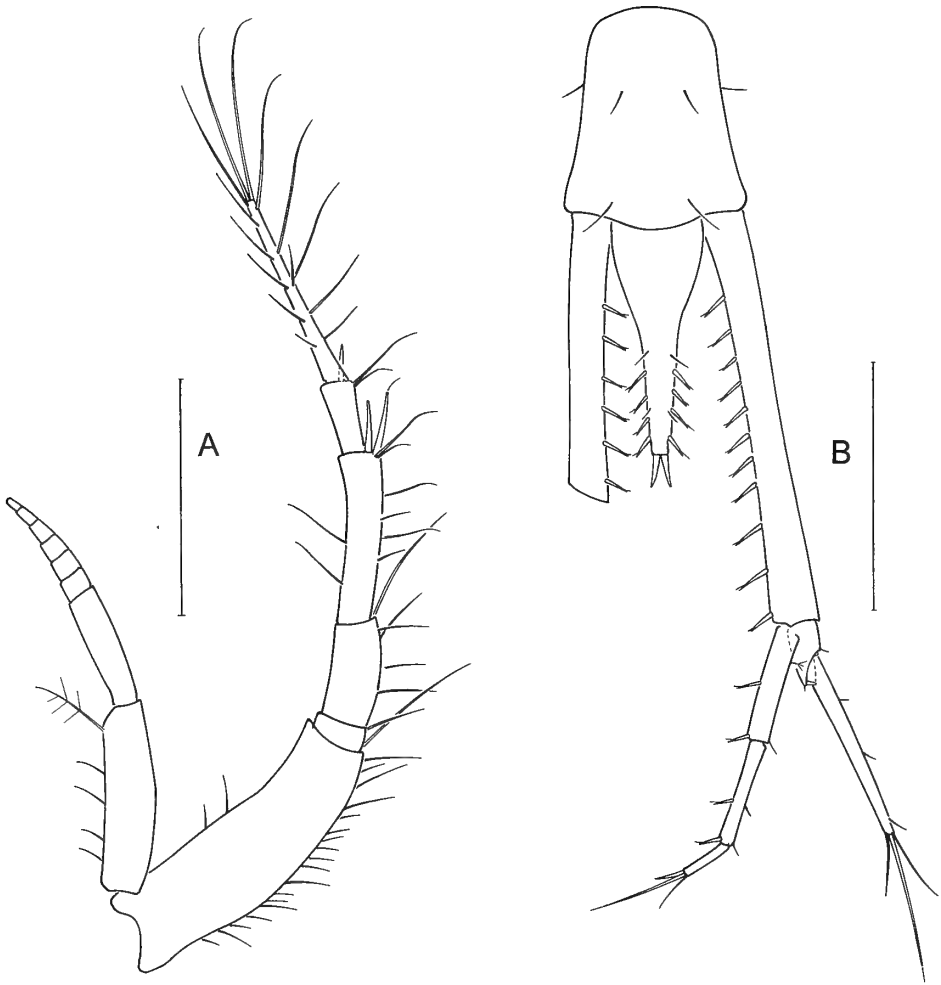


Fig. 5. *Ekleptostylis vemaie* (Băcescu-Meşter, 1967). Marsupial female. A, second pereopod; B, uropod and telson. Scales: 0.5 mm.

cescu-Meşter 1967) and Brazil at 35 m (Petrescu & Băcescu 1991), it has now been found off Uruguay, at additional stations off Argentina, in the Magellan Strait, Beagle Channel and Drake Passage, between 95 and 3590 m.

Ekleptostylis heardi McLelland & Meyer, 1998

Ekleptostylis heardi McLelland & Meyer, 1998:279–285, figs. 1–5.

Material examined.—Holotype (USNM 230401), R/V *Eltanin* Cruise 6, Station 363,

600 km north of Antarctic Peninsula (57°09'S, 58°58'W), 3590 m, 7–8 Dec 1962: 1 preparatory female. Paratypes (USNM 230403), from same sample: 14 ovigerous females, 2 preparatory females, 5 adult males, 2 juveniles. R/V *Eltanin* Cruise 6, Station 344, 500 km east of Tierra del Fuego (54°04'S, 58°46'W), 119 m, 4 Dec 1962: 10 ovigerous females, 7 preparatory females, 6 adult males (GCRL 1372). Vic Hen 1206 (55°48'S, 66°58'W; 66 m): 13 specimens in the collection of the Zoologisches Museum, Universität Hamburg (ZMH, K-39545). Vic Hen 884 (53°43'S,

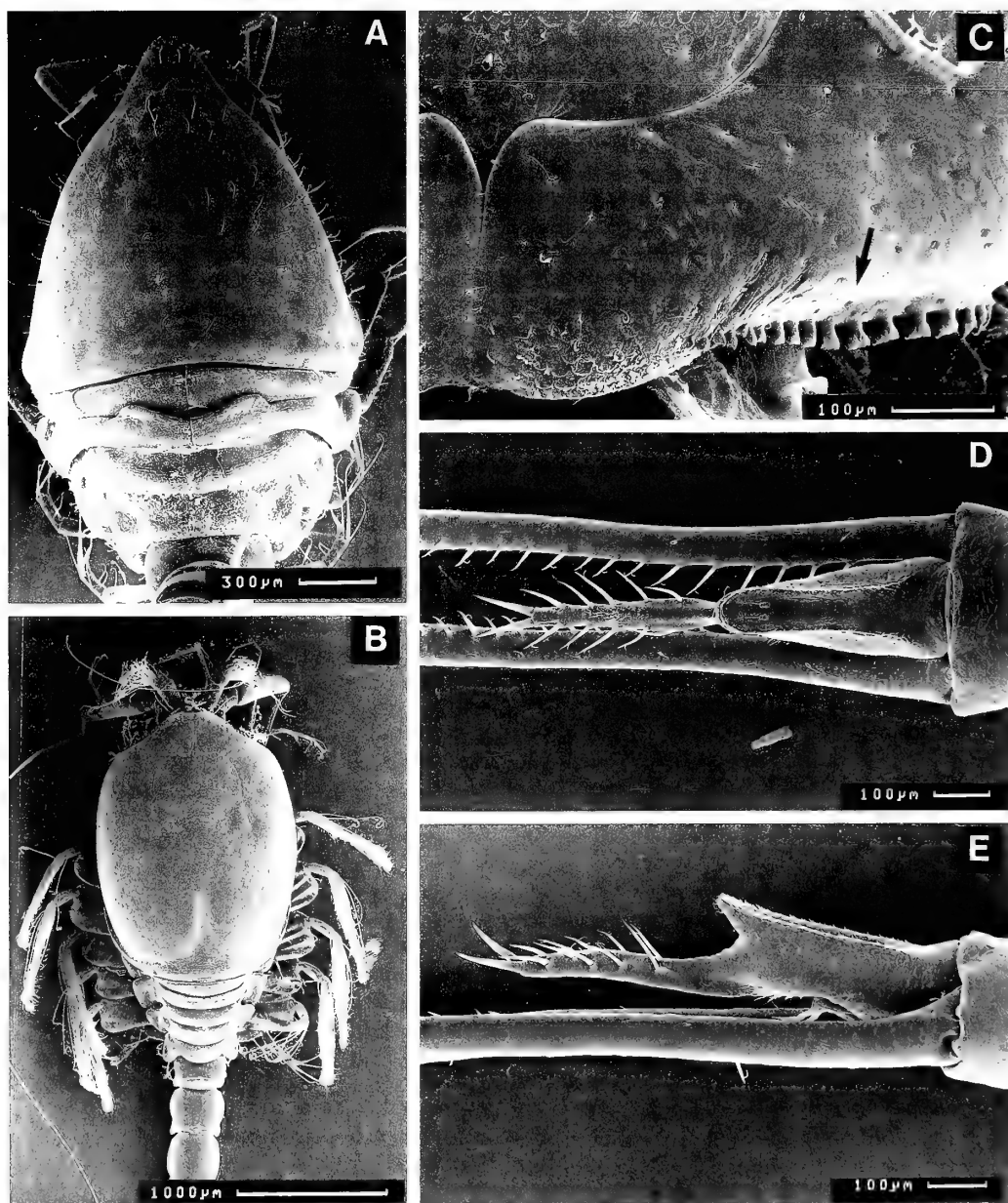


Fig. 6. *Ekleptostylis vema* (Băcescu-Meșter, 1967). SEM photographs. A, Marsupial female: dorsal view of carapace. B–E. Adult male: B, dorsal view of carapace; C, row of flat-topped teeth on antero-lateral margin of carapace (see arrow); D, dorsal view of telson; E, lateral view of telson.

70°57'W; 51 m): 2 specimens, Vic Hen 1192 (55°07'S, 67°02'W; 40 m): 2 specimens, Vic Hen 1210 (55°48'S, 66°59'W; 66 m): 14 specimens, Vic Hen 1240 (55°05'S, 66°48'SW; 33 m): 3 specimens; all of them in the collection of the Museum für Natur-

kunde, Berlin (ZMB 27313). SM IV-14 (37°59.5'S, 55°32.7'W; 99 m): 2 specimens, SM III-19 (38°29.5'S, 55°58.0'W; 92 m): 20 specimens, SM VI-24 (41°05.3'S, 64°24.6'W; 128 m): 20 specimens, SM VII-69 (45°29.6'S, 62°29.7'W; 95 m): 1 speci-

men, OB-08/88 (43°52'S, 64°36'W; depth: ?): 2 specimens; all of them in the collection of one of the authors (DR).

Differing from the original description as follows:

Ovigerous female.—First antenna, aesthetascs arrangement as in *E. vema*, i.e., second and third articles of main flagellum with 1 aesthetasc each; accessory flagellum without aesthetascs.

Second antenna: as in *E. vema*, i.e., composed of 3 articles (not 2) and with 4 (not 3) plumose setae (3 long lateral and 1 short distal).

Second maxilla: 2-articulate maxillary palp mentioned in the original description is a thick, short seta with setules emerging from all around the shaft (pappose seta).

First maxilliped as in *E. vema* except for basis with a row of 6 plumose setae on inner margin.

Second maxilliped: Composed of 7 articles; ischium wedge-shaped. Setation as in *E. vema*, except for basis bearing 3 weak spines (2 in *E. vema*) on outer distal margin and 3 plumose setae on inner distal margin (2 in *E. vema*).

Third maxilliped: Ventral surface of merus and inner distal margin of carpus each with 1–2 strong teeth (it was not possible to confirm if the basis has distal spines on inner margin). Other aspects as in *E. vema*, viz., basis with 4 (not 3) plumose setae on outer distal corner, carpus with 5 (not 3) plumose setae on inner margin, propodus with 3 (not 2) weakly plumose setae on inner margin.

First pereopod: Basis with longest distal seta extending beyond merus.

Second pereopod: Basis slightly longer than next 3 articles combined.

Adult male.—Telson almost 1.5 times as long as last abdominal segment (not 0.69× length of last abdominal segment).

First antenna: First article of the peduncle slightly shorter than other two combined. Other aspects as *E. vema*, viz., main and accessory flagella 6- and 4-articulate (not 5- and 2-articulate).

Third maxilliped as in female, except for: Endopod basis and basal article of exopod thicker; merus without tooth on ventral surface (carpus with tooth on inner distal corner); propodus with 5 weakly plumose setae on inner margin.

Second, third and fourth pereopods with rounded apical process on basis.

Distribution.—Previously recorded from the Drake Passage (3590 m) and off Argentina (119 m) (McLelland & Meyer 1998), it has now been found at additional stations off Argentina, in the Magellan Strait and Beagle Channel, between 33 and 128 m.

Discussion

Stebbing (1912) erected the genus *Ekleptostylis* to include *Leptostylis walkeri* Calman, 1907, a species whose adult male has a telson with a lobe strongly produced over the narrow distal portion. Fage (1951) provided a more thorough description of this species, and added two other important features to the generic diagnosis, presence in adult male of both an apical process on the basis of the second pereopod and first antenna reaching the end of the body. The combination of these three characters adequately diagnoses the genus, although absolute determination is possible only in the presence of adult males.

For a long time the genus *Ekleptostylis* was monotypic and only known for the eastern North Atlantic (Stebbing 1912) and the Mediterranean Sea (Fage 1951, Katağan 1982). Most recently, a new species belonging to the genus *Ekleptostylis* was described for Antarctic and sub-Antarctic waters: *E. heardi* McLelland & Meyer, 1998.

Băcescu-Meşter (1967) described *Leptostylis vema*, on the basis of some immature specimens collected off Patagonia. Among the material studied here were several thousands adult males of this species. We now believe that *L. vema* is congeneric with *Ekleptostylis walkeri* and therefore, we have transferred this species to the genus *Ekleptostylis*.

Diastylis pseudinornata Ledoyer, 1977 from the Kerguelen Islands is another species that we believe should be transferred to the genus *Ekleptostylis*. The fact that this species may belong in the genus *Ekleptostylis* has already been suggested by McLelland & Meyer (1998). Ledoyer (1977) included a male in the paratype series of *D. pseudinornata*, but we were unable to locate this specimen. However, according to Ledoyer's description and figures, the male of *D. pseudinornata* has the second antenna extending to the end of the body and the preanal part of telson strongly produced over the postanal part. In our opinion, these two characters are sufficient to transfer this species to the genus *Ekleptostylis*, although nothing is known about the second pereopod.

The genus *Ekleptostylis* includes now the following four species: *E. walkeri* (Calman, 1907) (type species) from the Mediterranean and east Atlantic (Bay of Biscay), *E. vema* (Băcescu-Meşter, 1967) and *E. heardi* McLelland & Meyer, 1998 from southern South America and Antarctica (Drake Passage), and *E. pseudinornata* (Ledoyer, 1977) from the Kerguelen Islands.

Ekleptostylis walkeri (type species) differs from the other three species of the genus in the adult female having 14–15 lateral spines on the telson and the distal article of the uropod endopod being slightly shorter than the basal article.

Ekleptostylis vema is easily separated from the other three species because the antero-ventral margin of carapace has truncate extensions; pereopods 3 to 5 have one very long and one minute seta at the dactylus, and the antero-lateral angle of the carapace is poorly developed in females.

Ekleptostylis pseudinornata resembles *E. heardi* in the presence of a well-developed antero-lateral angle, the antero-ventral margin of the carapace is serrate, and the dactylus of pereopods 3 to 5 bearing two subequal distal setae; the most striking difference between these two species is that the ovigerous female of *E. pseudinornata* has a

pair of rounded processes on the first two free thoracic segments, which are lacking in *E. heardi*.

Acknowledgments

We would like to thank the Deutscher Akademischer Austauschdienst (DAAD) for the grant (A 9807965 Ref. 415) given to the first author, Prof. Dr. A. Brandt (Zoologisches Museum, Hamburg) for providing work space for both authors, Dr. B. Hilbig for revising the English manuscript, Ms. R. Walter for her assistance with the SEM and Mr. H.-D. Totzke for technical assistance. Many thanks for loaning type material are given to Dr. D. Defaye (Museum National d'Histoire Naturelle, Paris), Dr. M. Schotte (Smithsonian Institution, Washington, D.C.) and Dr. J. McLelland (Gulf Coast Research Laboratory, Mississippi).

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***Eophoxocephalopsis colombus*, a new species
(Crustacea: Amphipoda: Phoxocephalopsidae) from the
southwest Atlantic**

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Abstract.—A new species, *Eophoxocephalopsis colombus*, is described and illustrated from the Chubut province: Golfo Nuevo, and the south of Buenos Aires province. The assignment of the new species to *Eophoxocephalopsis* is discussed. It is separated from the other species of the genus by the shape and number of setae on the inner plate of maxilla 1, and the shape of epimera 2 and 3. The specimens were dredged from sandy substrata at different depths.

The new species described here was found on the southwest Atlantic coast of Chubut province: Golfo Nuevo, Colombo beach, at approximately 42°37'S, 64°16'W, and in the Argentine continental shelf of El Rincón area, in the Buenos Aires province, approximately 39° to 40°S and 61° to 62°W. Specimens were obtained with a small dredge in the first locality mentioned above and with a Van Veen dredge during a survey carried out by the R/V *El Austral* in the second locality. All samples were collected in sandy substrates at different depths in the intertidal and subtidal zones.

The type specimens are deposited in the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina (MACN).

Eophoxocephalopsis Thurston, 1989

Eophoxocephalopsis colombus, new
species

Figs. 1–49

Holotype.—Ovigerous female 3.8 mm (MACN N° 34377), Chubut province: Golfo Nuevo, Colombo beach (approximately 42°37'S, 61°16'W); depth 2 m; 2 Nov 1995.

Paratypes.—9 females 2.5–3.6 mm (MACN N° 34378), 11 males 2.25–3.0 mm

(MACN N° 34379), Chubut province: Golfo Nuevo, Colombo beach (approximately 42°37'S, 61°16'W); depth 2 m; 2 Nov 1995. 4 females 2.75–3.85 mm (MACN N° 34380), Chubut province: Golfo Nuevo, Colombo beach (approximately 42°37'S, 61°16'W); depth 0.4 m; 3 Nov 1995. 1 male 2.8 mm (MACN N° 34381), 39°10'04"S, 61°10'03"W (sta 5); depth 17 m; 3 Nov 1993; 3 females 3.2–3.45 mm (MACN N° 34382), 1 male 2.3 mm (MACN N° 34383), 39°15'10"S, 61°34'41"W (sta 11); depth 14 m; 3 Nov 1993; 2 females 3.2 and 3.3 mm (MACN N° 34384), 1 male 2.05 mm (MACN N° 34385), 39°15'02"S, 61°25'03"W (sta 12); depth 17 m; 3 Nov 1993; 1 ovigerous female 3.5 mm (MACN N° 34386), 1 male 3.25 mm (MACN N° 34387), 39°14'49"S, 61°14'50"W (sta 13); depth 17 m; 3 Nov 1993; 2 males 3.1 and 3.2 mm (MACN N° 34388), 39°24'59"S, 61°50'02"W (sta 18); depth 11.5 m; 1 Nov 1993; 6 males 2.8–3.4 mm (MACN N° 34389), 4 juveniles 1.6–2.8 mm (MACN N° 34390), 40°09'52"S, 61°51'55"W (sta 32); depth 15 m; 2 Nov 1993; 2 females 3.8 and 3.9 mm (MACN N° 34391), 1 male 3.45 mm (MACN N° 34392), 40°19'46"S, 61°51'55"W (sta 34); depth 15 m; 2 Nov 1993; Buenos Aires province: El Rincón.

The samples from Colombo beach were collected by Meijide and Ianovski and donated by D. Roccatagliata. The samples from El Rincón were collected, sorted and donated by D. Roccatagliata and M. Torres Jordá.

Description.—Holotype, ovigerous female, body length 3.8 mm. Head about 79% as long as wide, rostrum about 17% of total body length; cheek somewhat extended ventrally, broadly rounded; eyes without pigment specimens preserved in ethanol (Figs. 1, 2).

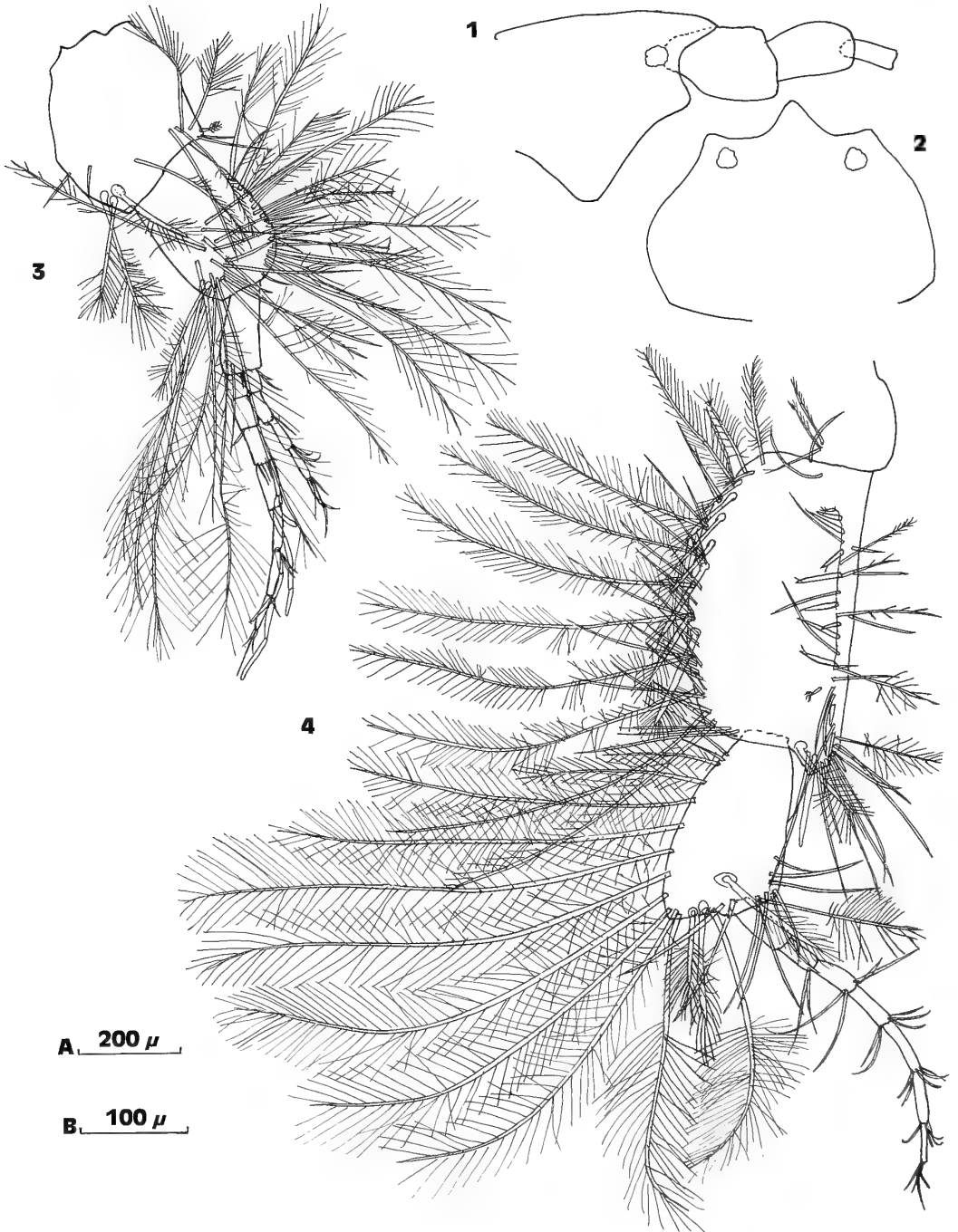
Antenna 1 (Fig. 3), peduncle, article 1 short, dorsolateral armament of 5 plumose and 3 penicillate setae in curved row; article 2 about as long as article 1, with long plumose setae and spines dorsally; article 3 about half as long as article 2; primary flagellum of 7 articles, formula of long aesthetascs 0-0-1-1-1-1; accessory flagellum with 4 articles. Antenna 2 (Fig. 4), peduncle, article 3 with 4 short plumose setae laterally; article 4 facial armature consisting in row of thin spines and simple setae, towards produced apex becoming mixed with plumose setae, ventral margin with numerous stiff penicillate setae, common spines and long plumose setae; article 5 expanded apically, shorter and narrower than article 4, with 3 apicofacial penicillate setae, apical and subapical thin spines, with ventral row of long plumose setae; flagellum geniculate, longer than peduncle article 4, with 7 articles.

Epistome not produced. Upper lip broadly rounded, apically excavate (Fig. 5). Mandible, incisor greatly extended, rather slender, weakly toothed; right lacinia mobilis simple, left acute with 3 accessory teeth poorly developed; rakers stout, serrate, 2 on right mandible, 3 on left; molar stout, toothed, weakly triturative (Figs. 6, 7); palp, article 3 with 9 spine-setae apically and 3 on distal half (Fig. 8). Lower lip, inner lobes large; mandibular process well developed, rounded (Fig. 9). Maxilla 1, inner plate long, thin, bearing 1 apical plumose seta; outer plate with 11 spines, some

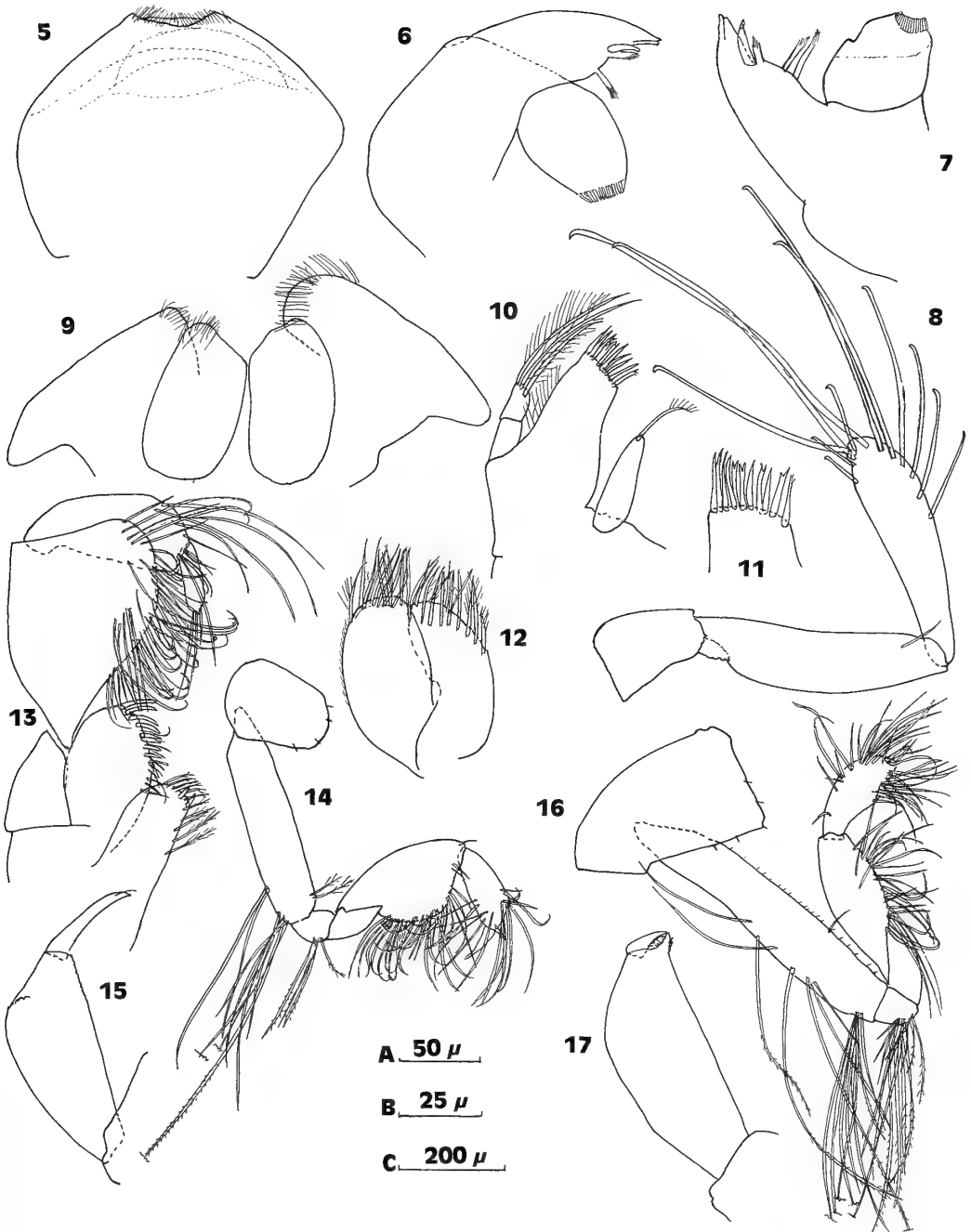
of these dentate; palp short, biarticulate, article 2 about as long as article 1, with 2 apical setae and 1 apicomедial seta, all plumose (Figs. 10, 11). Maxilla 2 (Fig. 12), plates oval, inner plate shorter and narrower than outer, with oblique facial row of plumose setae, simple and plumose setae apically and apicomедially; outer plate with mixed setae on apical and apicolateral margins, and stiff setae on apicoventral margin. Maxilliped (Fig. 13), inner plate with 2 thick apical spines, 6 plumose setae apically and 5 medially; outer plate larger than inner plate, with thick medial spines; palp, article 2 expanded, with high number of marginal and facial spines, article 3 clavate, with facial and distolateral setae, dactylus digitate, blunt, less than half as long as article 3, bearing 2 apical setae as long as article and 1 shorter subapical seta.

Coxae 1-4 progressively larger. Coxa 1, rounded anteriorly, with 4 setules. Coxa 2 subrectangular, moderately expanded distally, with 3 ventral and 2 posterior setules. Coxa 3 subrectangular, expanded distally, with 3 ventral setules, posteroventral corner with 1 setule and 5 medium setae, posterior margin with 4 setules. Coxa 4, anterior margin strongly convex distally, anterior and posterior margins divergent, ventral margin with 3 setules, posteroventral corner bearing 6 medium setae, posterior ventral margin with 3 setules, posterior emargination shallow.

Gnathopods weak, dissimilar. Gnathopod 1 simple, article 2 with long setae on distal half of posterior margin, anterior margin with shorter setae distally; article 3 with weak setal brush posteriorly; article 5 expanded, posterior margin rounded, strongly setose; article 6 short, oval, 63% as long as article 5; dactylus 46% as long as article 6 (Figs. 14, 15). Gnathopod 2 slightly subchelate, article 2 with long setae on posterior margin; article 3 with strong setal brush posteriorly; article 6, 62% as long as article 5, palm almost transverse, excavate medially, distally acutely produced; dactylus short, reaching apex of palm, setose poste-



Figs. 1-4. *Eophoxocephalopsis colombus*. Holotype, ovigerous female. 1, 2, Head, lateral and dorsal views; 3, 4, Antennae 1, 2. Scales: A, Figs. 1, 2; B, Figs. 3, 4.



Figs. 5-17. *Eophoxocephalopsis colombus*. Holotype, ovigerous female. 5, Upper lip; 6, 7, Right and left mandibles; 8, Mandibular palp; 9, Lower lip; 10, Maxilla 1; 11, Outer plate of maxilla 1; 12, Maxilla 2; 13, Maxilliped; 14, Gnathopod 1; 15, Propodus of gnathopod 1; 16, Gnathopod 2; 17, Propodus of gnathopod 2. Scales: A, Figs. 5-10, 12, 13, 15, 17; B, Fig. 11; C, Fig. 14.

riorly (Figs. 16, 17). Peraeopods 3 and 4, article 2, 4 and 5 strongly setose; article 4 much shorter than article 2; article 5 72% and 77% as long as article 4 respectively of peraeopods 3 and 4, spine formula 3 + 1 and 4 + 1 respectively; article 6, spine formula 5 + 3 + 2 and 4 + 4 + 1 respectively; dactylus longer and stouter than spines on article 6, with strong accessory tooth (Figs. 18–21). Peraeopod 5 (Fig. 22), article 2 with medium-length setae on distal half of anterior margin; articles 4–6 broadly expanded and armed with facial spines; article 6 narrower than article 5, about 116% length of article 5; dactylus (Fig. 23) styliform, elongate, slender, with accessory tooth, lacking nail. Peraeopod 6 (Fig. 24) somewhat longer than latter appendage; article 4 with 8 long plumose setae and short spines posteriorly; dactylus (Fig. 25) longer than surrounding spines, with accessory tooth. Peraeopod 7 (Fig. 26) about as long as peraeopod 5; article 2 subcircular; article 4 with 1 medium plumose seta posteriorly, the remainder articles without plumose setae, although distal articles with more shorter simple setae than corresponding articles of peraeopod 6; dactylus (Fig. 27) longer than surrounding spines, with accessory tooth.

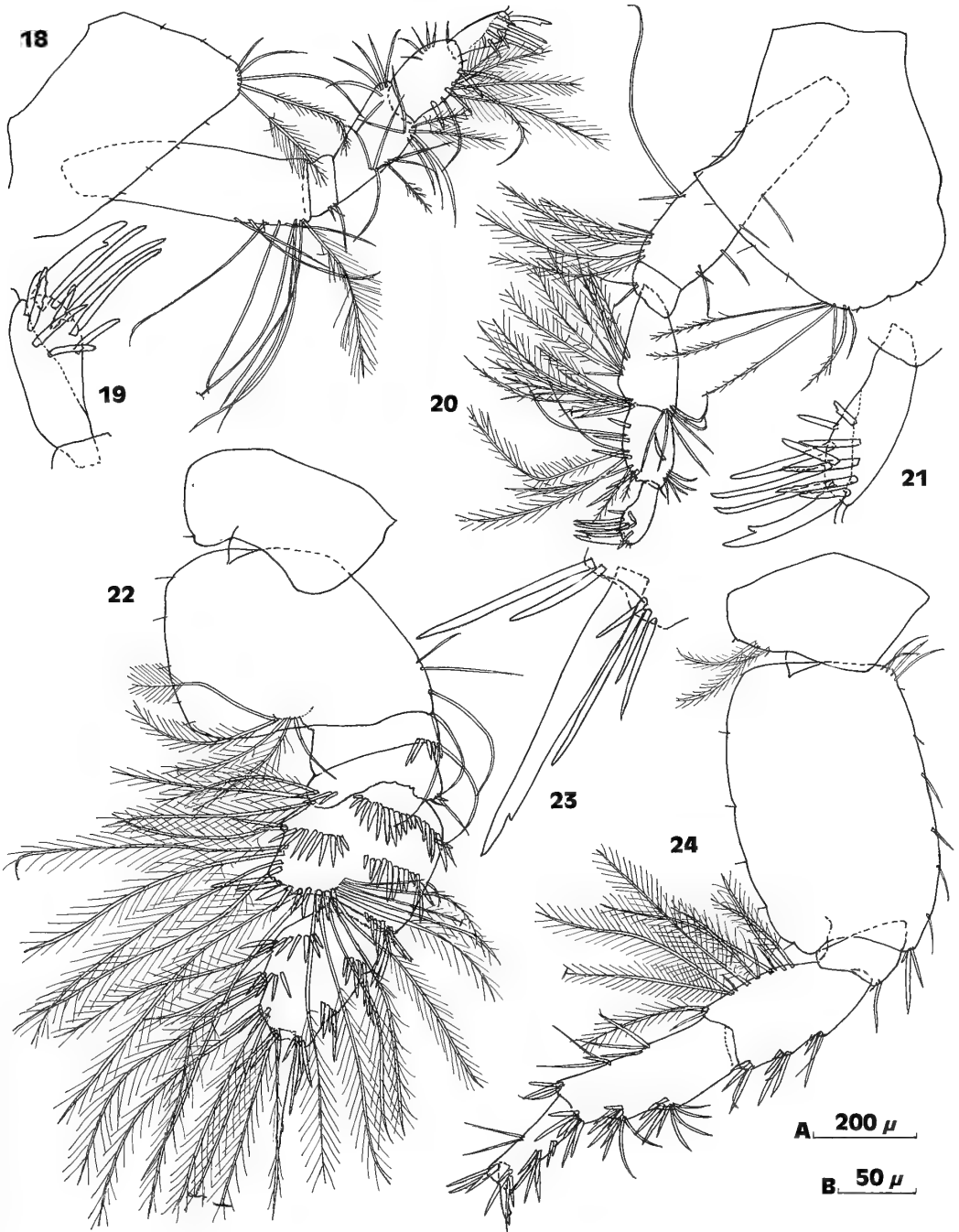
Epimera 1–3 increasing in size posteriorly; epimera 2 and 3 with hooklike tooth at posteroventral angle. Epimeron 1 (Fig. 28), facial armature consisting of many long plumose setae. Epimeron 2 (Fig. 29), posterior margin above angle strongly convex, face with 8 and 2 long plumose setae disposed in 2 rows. Epimeron 3 (Fig. 30), facially with 2 rows of 5 and 2 long plumose setae. Pleopods 1–3 (Figs. 31–34) decreasing in size posteriorly; peduncle of 2 and 3 shorter than that of pleopod 1, each bearing 2 locking spines, with 19 + 13, 15 + 11, 14 + 10 articles on outer and inner rami, basal article of inner ramus with clothespin spine.

Gills present on coxae 2–6, on coxae 5 and 6 small. Oostegites long, slender, setose, on coxae 2–5.

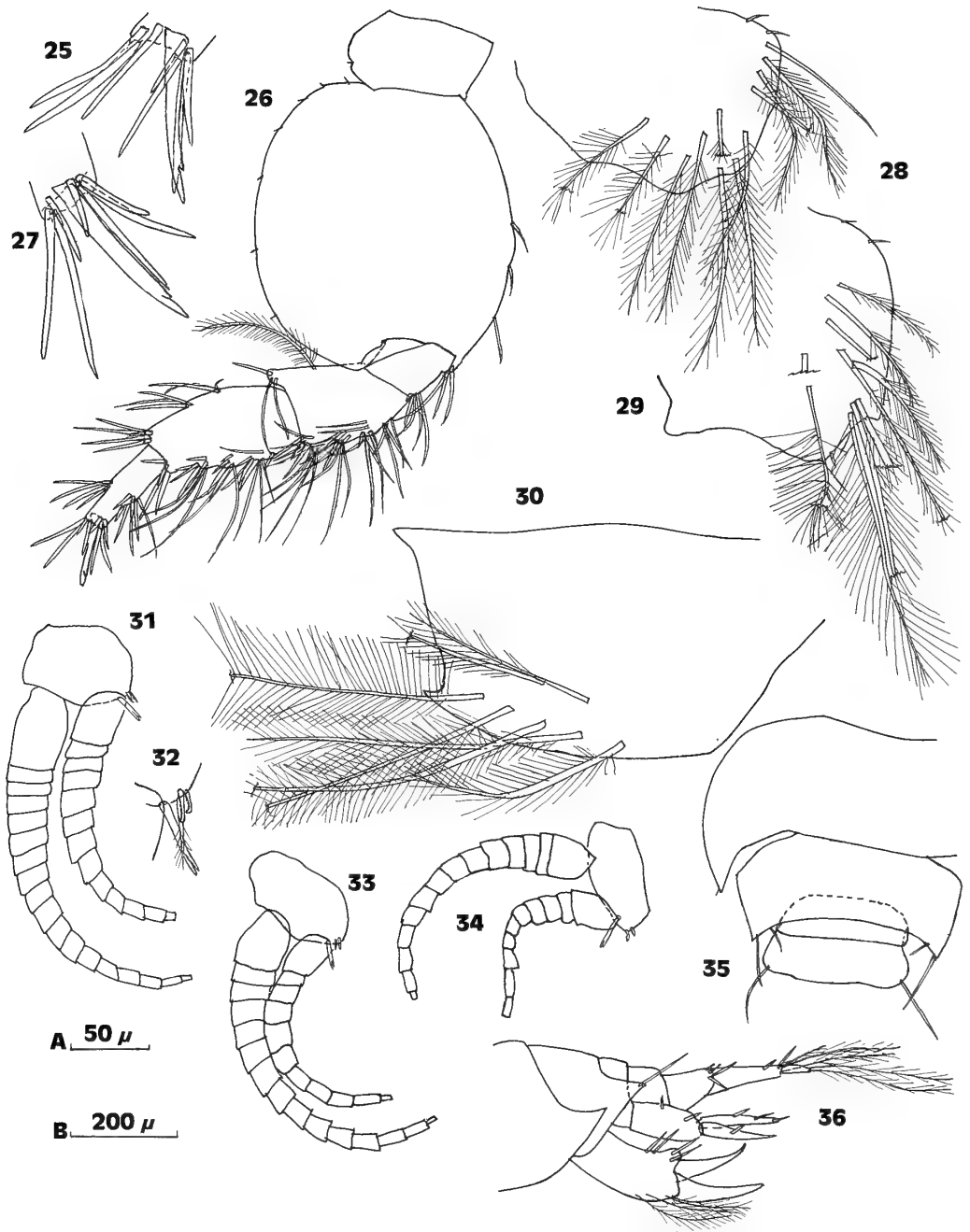
Urosomite 1, lateral projection slightly

longer than urosomite 2, with 1 apical long seta (Figs. 35, 36). Uropod 1 (Fig. 37), peduncle with dorsolateral margin bearing 1 long spine proximally and 1 shorter spine distally, lateral margin with 3 long plumose setae and proximal to these 1 spine, medial margin with 3 spines and 2 setae bearing short plumosity; rami naked, strongly styliform, inner ramus shorter than outer (latter with tip broken). Uropod 1 from opposite side (Fig. 38), peduncle with dorsolateral margin bearing 2 long spines proximally and 1 shorter spine distally, lateral margin with 4 long plumose setae and 1 spine proximally to these, medial margin with 2 spines distally and proximally 2 spines and 4 medium simple setae; rami naked, inner ramus 75% as long as outer, each with an apparent articulating apical nail. Uropod 2 (Fig. 39), peduncle with dorsolateral margin bearing 3 spines, medial margin with 2 spines and 2 long setae; outer ramus styliform with single dorsal spine (tip broken); inner ramus rod-like shorter than outer, with 2 medial and 2 apical spines. Uropod 2 from opposite side (Fig. 40), peduncle with medial margin bearing only 1 seta; outer ramus with only 1 apical spine; inner ramus about 95% as long as outer ramus, with an apparent articulating apical nail. Uropod 3 (Fig. 41), peduncle short, broader than long, 3 spines distolaterally, 2 spines and 7 setae mediolaterally; outer ramus article 1 with 2 groups of 2 spines and 1 long plumose seta laterally, 3 groups of 1 seta each plus 1 spine (except proximal group with only 1 seta) medially, article 2 42% as long as article 1, with 2 plumose setae (one of these broken) and 1 setule at apex; inner ramus with 1 spine and 1 seta laterally, 5 setae medially and 2 apical setae, all long and plumose. Uropod 3 from opposite side (Fig. 42), peduncle with 5 distolateral spines. Telson (Fig. 43) short, broader than long, length 67% of width, cleft 84% of length, apices rounded with 1 spine, each lateral margin with basal pair of spines, 2 plumose setules, 1 spine and single plumose setule.

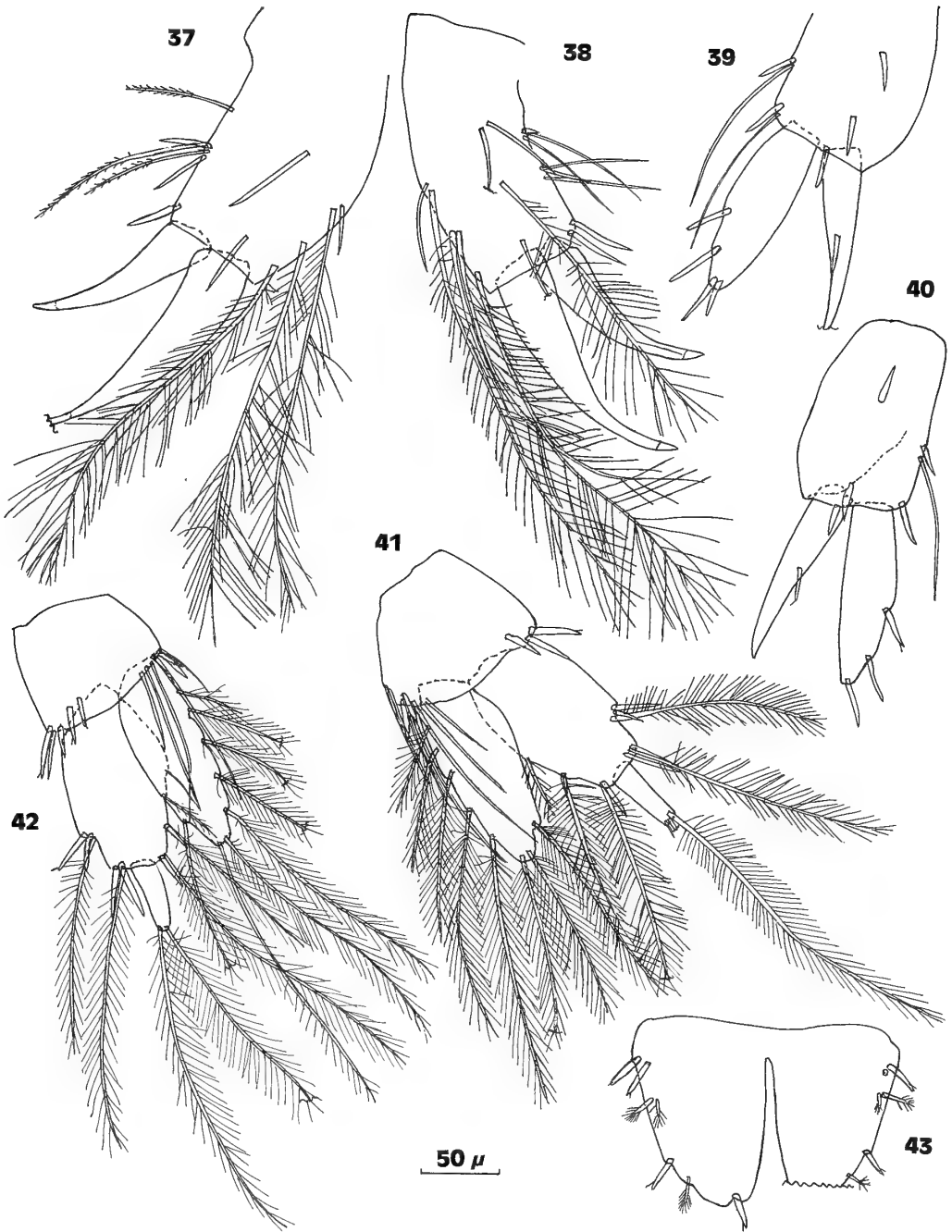
Paratype male from Colombo beach,



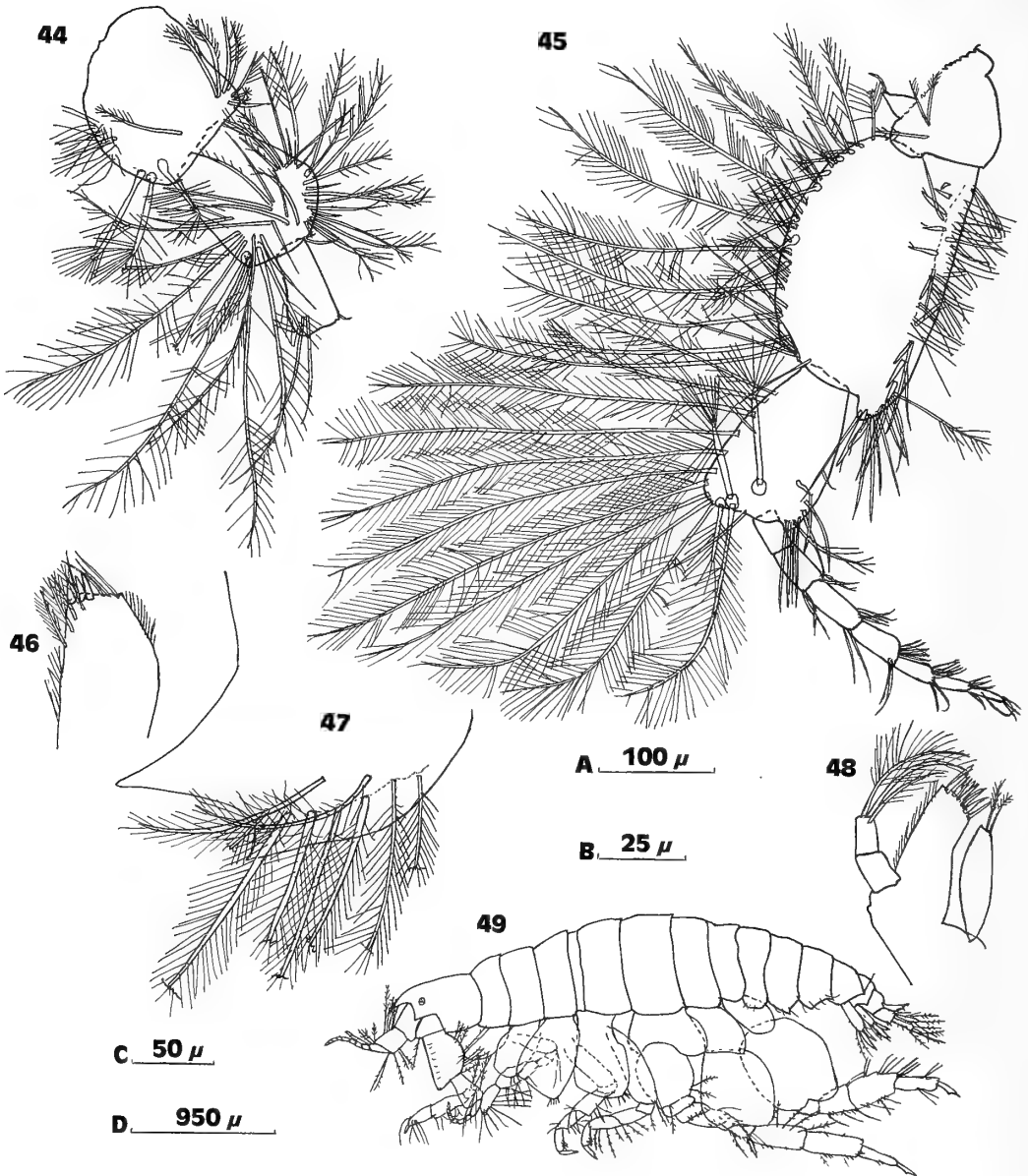
Figs. 18–24. *Ephoxocephalopsis colombus*. Holotype, ovigerous female. 18, Peraeopod 3; 19, Propodus of peraeopod 3; 20, Peraeopod 4; 21, Propodus of peraeopod 4; 22, Peraeopod 5; 23, Dactylus of peraeopod 5; 24, Peraeopod 6. Scales: A, Figs. 18, 20, 22, 24; B, Figs. 19, 21, 23.



Figs. 25–36. *Eophoxocephalopsis colombus*. Holotype, ovigerous female. 25, Dactylus of pereopod 6; 26, Pereopod 7; 27, Dactylus of pereopod 7; 28–30, Epimera 1–3; 31, Pleopod 1; 32, clothespin and locking spines of pleopod 1; 33, 34, Pleopods 2, 3; 35, 36, Urosome, dorsal and lateral views. Scales: A, Figs. 25, 27–30, 32; B, Figs. 26, 31, 33–36.



Figs. 37–43. *Eophoxocephalopsis colombus*. Holotype, ovigerous female. 37, 38, Right and left uropods 1; 39, 40, Right and left uropods 2; 41, 42, Right and left uropods 3; 43, Telson.



Figs. 44–49. *Eophoxocephalopsis colombo*. Paratype male (Colombo beach, depth 2 m). 44, 45, Antennae 1, 2; 46, Inner plate of maxilliped; 47, Epimeron 3. Paratype, ovigerous female (El Rincón). 48, Maxilla 1. Paratype male (El Rincón). 49, Body lateral view. Scales: A, Figs. 44, 45; B, Fig. 46; C, Figs. 47, 48; D, Fig. 49.

depth 2 m, body length 3.0 mm. Similar to holotype, but differs from it as follows. Antenna 1 (Fig. 44), peduncle article 1 with pubescence; primary flagellum with 6 articles, formula of long aesthetascs 3-2-3-3-1; accessory flagellum with 3 articles. Anten-

na 2 (Fig. 45), peduncle article 4 with pubescence; flagellum with 7 articles, some of these more hairy.

Maxilliped, inner plate with 2 thick apical spines and between these a narrower spine (Fig. 46).

Peraeopods 3 and 4, article 6 spine formula $4 + 2 + 1$.

Epimeron 3 (Fig. 47), posteroproximal angle much more produced and acute. Pleopods, rami with fewer articles.

Uropod 3, peduncle with 4 distolateral spines, 3 spines and 4 setae mediolaterally; outer ramus article 1 with 3 groups of 1 spine the most proximal group, and with 2 spines and 1 plumose seta the others; inner ramus with 1 spine and 2 plumose setae laterally, medially with ordinary plumose setae and 1 spine almost distal; plumose setae and spines longer than in female (relative length).

Paratype male, apparently mature, exhibits weak sexual dimorphism, which is particularly denoted on antennae 1 and 2, and uropod 3. Other dissimilarities with regard to holotype are confined to differences in number of spines and setae.

Paratype ovigerous female from El Rincón (Sta 13), body length 3.5 mm. Antenna 1, primary flagellum with 7 articles, formula of long aesthetascs 0-1-1-1-1-1; accessory flagellum with 3 articles. Antenna 2, flagellum with 6 articles.

Maxilla 1 (Fig. 48), inner plate with 2 plumose setae. Maxilliped, inner plate with 2 thick apical spines, and between these another narrower spine.

Peraeopods 3 and 4, article 5, spine formula $3 + 1$; article 6, spine formula $4 + 4 + 1$.

Uropod 1, peduncle with dorsolateral margin bearing 2 spines proximally and 1 distally, lateral margin more spinose. Uropod 2, peduncle with dorsolateral margin bearing 3 spines distally, medial margin with 2 spines plus 2 plumose setae and 1 spine plus 1 plumose seta; inner ramus with 2 medial spines and 1 apical spine. Uropod 3, peduncle with 5 distolateral spines, mediolaterally with 4 spines and 4 simple setae; outer ramus article 1 with 3 groups of 1 spine the most proximal group and the other groups with 2 spines and 1 plumose seta laterally, medially with 3 plumose setae (without accompanying spine), article 2

with 2 long plumose setae and short setule at apex; inner ramus with 2 plumose setae laterally, 4 plumose setae and 2 distal spines in 2 groups medially. Telson, one apex with 2 spines, the other with 1.

Paratype male from El Rincón (Sta 13), body length 3.25 mm (Fig. 49). Antennae 1 and 2 with pubescence as in paratype from Colombo beach, depth 2 m.

Maxilla 1, inner plate with 1 plumose seta. Maxilliped, inner plate with 2 thick apical spines.

Peraeopods 3 and 4, article 5, spine formula $3 + 1$; article 6, spine formula $4 + 3 + 1$.

Uropods 1 and 2 as usual, but with variations in number of spines and setae on peduncle. Uropod 2, inner ramus with 2 apical spines, besides common pair of medial spines.

Variations.—Some variations, especially in number of spines and setae were observed in the different populations from both sampling localities: Colombo beach and El Rincón. This morphological diversity was found also in a same population, among specimens, and in the same individuals, which frequently showed this kind of dissimilarity.

Etymology.—The specific name, a noun in apposition, refers to Colombo beach, the holotype female and paratype male locality.

Relationships.—The new species reported here was assigned to *Eophoxocephalopsis* Thurston, 1989 because it generally agrees with the diagnosis of the genus. The minor morphological differences observed between the taxa do not justify the erection of a new genus, and these can be summarized as follows. The present species has the upper lip incised, versus upper lip anteriorly rounded; the maxilla 1 inner plate is elongate, thin, scarcely setose, and the outer plate bears eleven spines, versus inner plate broad, trapezoidal, setose, and outer plate with eight spines. In addition, the new species can be separated from species of *Phoxocephalopsis* Schellenberg, 1931 and *Puelche* Barnard & Clark, 1982, by the poorly

toothed incisor process, which in both genera is untoothed, the gnathopod 2 with its characteristic palm rather than the subchelate condition, the styliform outer ramus of uropod 2 instead of the rodlike outer ramus. Species of *Phoxocephalopsis* exhibit a strong spinous facial armature on antenna 2 article 5 and an enlarged epimeron 2. Species of *Puelche* lack the typical oblique facial row of setae on inner plate of maxilla 2 described for *Eophoxocephalopsis*.

Eophoxocephalopsis colombus is distinguished from *E. rhachianensis* Thurston, 1989 in that the maxilla 1 inner plate has one seta, or occasionally two, and its outer plate has eleven spines; the upper lip is incised anteriorly; the gnathopod 1 merus is much shorter in relation to the length of this article on gnathopod 2; the gnathopod 2 palm and dactylus are somewhat different; the coxa 4 anterior and posterior margins are strongly divergent; the epimera are different in shape, especially the epimeron 3; the epimeron 3 is larger (relative to epimeron 2); the uropod 1 has fewer dorsolateral spines, and its inner ramus is longer. It can be separated from the other known spe-

cies of the genus, *E. deceptionis* (Stephensen, 1947), which lacks eyes, has epimera 2 and 3 subequal and the uropod 2 outer ramus bears two dorsal spines.

Acknowledgments

I am grateful to Dr. Michael Thurston who revised the species figures and gave me his valuable comments.

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Megalopal and first crab stages of *Porcellanopagurus edwardsi* Filhol, 1885 (Crustacea: Decapoda: Anomura: Paguridea)

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Abstract.—The megalopal and first crab stages of a hermit crab believed to be *Porcellanopagurus edwardsi* Filhol, 1885, are described and illustrated from specimens collected off New Zealand during the U.S. Antarctic Program, 1962–1968. This is the first report of post-larval development in the genus. While the megalopal stage of *P. edwardsi* is generally quite similar to megalopae of other described pagurid genera, a significant difference is seen in the first crab stage. At this stage in most pagurids there typically is reduction in the second pleopods on both sides of the abdomen; the remaining right side pleopods may be reduced or lost entirely, whereas left side pleopods usually undergo only endopod reduction or loss. In contrast, all pleopods of *P. edwardsi* undergo dramatic reduction with the molt to the first crab stage.

Of the 11 species now recognized in the hermit crab genus *Porcellanopagurus* Filhol, 1885a, for none have larvae ever been reared in the laboratory. However, four zoeal stages of *Porcellanopagurus edwardsi* Filhol, 1885b, were described by Roberts (1972) from plankton samples collected in Perseverance Bay, Campbell Island, New Zealand, the type locality of the species. The present post-larval series, containing four megalopae and three first stage crabs was collected during the U.S. Antarctic Program's USNS *Eltanin* cruise 25 at station 370 (43°22'–43°24'S, 175°20'–175°15'E, 95 m, 19 Nov 1966). This area coincides with the reported southern extent of the range of *Porcellanopagurus filholi* de Saint Laurent & McLaughlin, 2000 and the northern limits of the range of *P. edwardsi* (cf. de Saint Laurent & McLaughlin 2000).

Although these two species of *Porcellanopagurus* were confounded under the name *P. edwardsi* for more than a century, adults are readily distinguishable by several characters, particularly the lateral carapace lobes, rostral shapes, and length-width pro-

portions of the ambulatory dactyls and pereopods. Lateral carapace lobes are not present in the megalopal stage and have not reached their full developmental potential during the first crab stage. Similarly, length-width proportions of the ambulatory dactyls and pereopods are expected to be subject to change with growth. No larval or post-larval information is available for *Porcellanopagurus filholi*; however, the similitude seen between the developing rostrum in the megalopa and in first crab stage of the present material and the characteristic sub-adult-adult rostrum of *P. edwardsi* (Fig. 1a) provide reasonable assurance of the identity of these early stages.

The post-larval specimens used in this study have been deposited in the alcohol and slide reference collections of the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM 276169), as have the majority of the small but morphologically mature specimens used for anatomical comparisons. Two megalopae and one first crab stage were stained with chorazol black E, dis-

sected, and mounted in polyvinyl alcohol lactophenol. Whole specimens were examined, drawn, and dissected using a Wild M-5 microscope with camera lucida attachment. Slides were examined and appendages drawn using a Wild M-20 microscope with camera lucida attachment. Information was also obtained from the examination of adult specimens of both *Porcellanopagurus* species belonging to the New Zealand Oceanographic Institute, now part of the National Institute of Water and Atmospheric Research, Wellington, New Zealand. The interpretation of lateral carapace lobes, particularly the tripartite condition of the posterior carapace lobe as defined by of McLaughlin (2000) is applied to the descriptions of the crab stage. Thoracic sternites are indicated by Roman numerals according to the system used by Pilgrim (1973). In other terminology, the recommendations of Clark et al. (1998), as applicable to anomurans, have been adopted. Two measurements, carapace length (cl) and shield length (sl) are used as indicators of specimen size.

Description

Megalopa

Size.—cl = 2.0–2.5 mm; $n = 4$.

Carapace (Fig. 1b).—Shield only faintly indicated; lateral carapace margins smoothly contoured. Rostrum obtusely subtriangular, apex produced, terminating acutely or subacutely. Anterolateral angles of shield (incipient lateral projections) slightly produced and upturned. Ocular peduncles moderately short, corneas slightly dilated; ocular acicles not apparent.

Thoracic sternites (Fig. 1e).—Sternite of third maxillipeds (sternite IX) with anterior margin rounded on either side of median cleft, not distinctly fused with sternite of chelipeds (X). Sternites X and XI partially fused. Sternite XII with incomplete median longitudinal depression or groove. Sternite XIII moderately broad, separated from preceding sternite by thin flexible uncalcified

hinge. Sternite XIV separated from XIII by membranous area.

Antennule (Fig. 3a).—Biramous, considerably overreaching ocular peduncles; peduncle 3-segmented, basal segment with statocyst faintly apparent and with 5 or 6 short lateral setae, 1 long and 2 shorter stiff setae ventrally and sometimes 1 short seta dorsally; penultimate segment usually without setae; ultimate segment with 1 or 2 short setae dorsally and ventrally; endopod (lower ramus) 2-segmented; basal segment with 3 or 4 short setae distally, distal segment with 4–6 short and 2 appreciably longer setae; exopod (upper ramus) 4-segmented, distal segment longer than combined length of first 3, aesthetascs on segments 2–4 as follows: 6, 4–6, 4, penultimate segment often also with 1 or 2 long setae distally, ultimate segment with 3–5 short and 1 long terminal setae.

Antenna (Fig. 2a).—Peduncular segments 3–5 each with 0–2 short setae; second segment with dorsolateral distal angle produced as short spinose process, dorsomesial distal angle rounded; first segment with unarmed ventral protuberance. Acicle short, broad, with 2–4 short setae. Flagella, long, with 20–22 articles each often with 1 or 2 short setae, terminal article with 3 or 4 short and 1 or 2 considerably longer setae.

Mandible (Fig. 2c).—Reduced and simplified, distal margin unarmed or with small tooth; palp 2-segmented, distal segment with 5–9 very short marginal setae.

Maxillule (Fig. 2e).—Coxal endite with 5 or 6 plumose marginal setae; basal endite with 3 or 4 marginal weakly plumose setae dorsally, row of several small teeth on outer margin and adjacent row of few widely-spaced short setae; endopod unsegmented, with short seta subdistally.

Maxilla (Fig. 2g).—Coxal endite bilobed, with 5–7 marginal plumose setae on proximal lobe and 4–6 on distal lobe; basal endite bilobed, with 6–8 plumose marginal setae on proximal lobe and 10–12 plumose marginal setae on distal lobe; endopod unsegmented, with 1 subterminal and 1 termi-

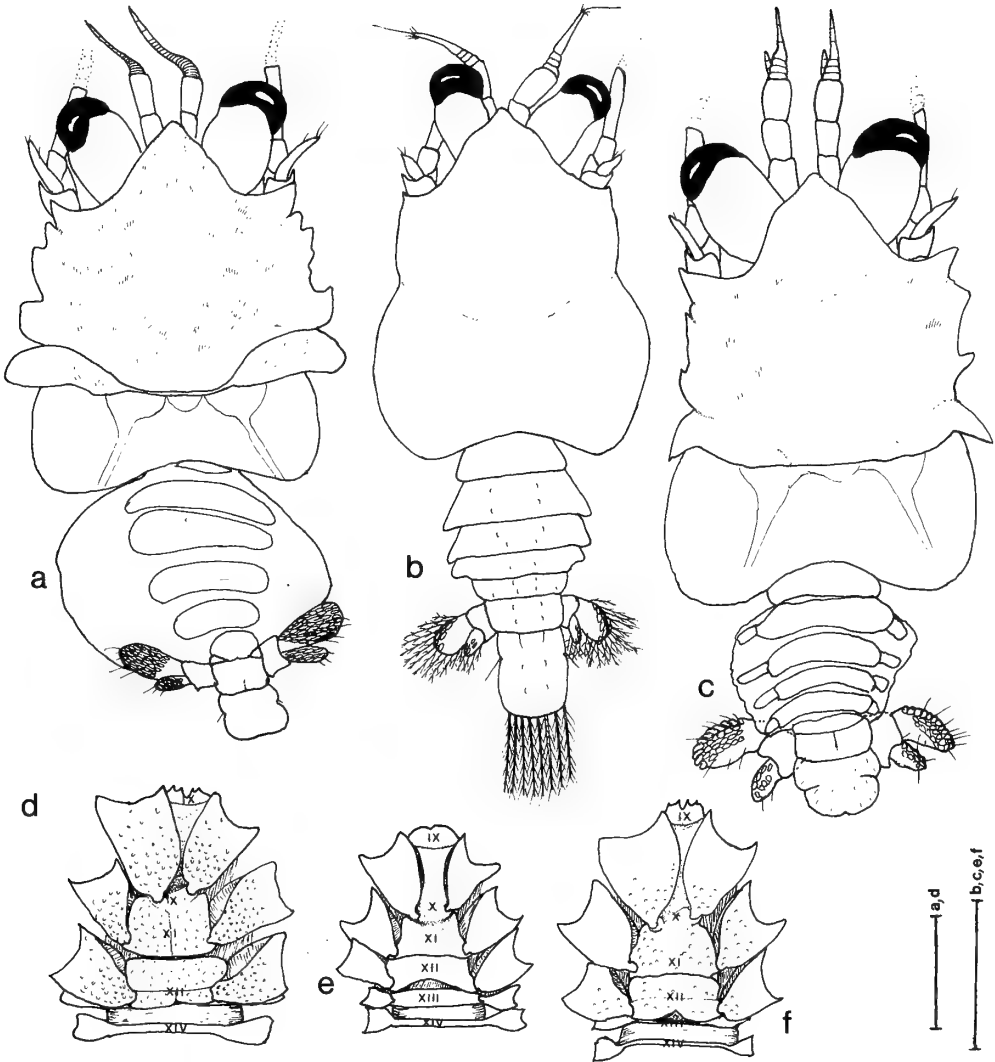


Fig. 1. *Porcellanopagurus edwardsi* Filhol, 1885. a-c, cephalothorax and abdomen (dorsal view); d-f, thoracic sternites (ventral view): a, d, young adult male (sl = 2.3, cl = 3.0 mm, Eltanin cruise 27, stn 1850, 49°40'S, 178°53'E, 103 m, 3 Jan 1967); b, e, megalopa (cl = 2.2 mm); c, f, first crab stage (sl = 1.9, cl = 2.3 mm). Scales equal 1.0 mm.

nal simple seta; scaphognathite with 44-52 moderately short, marginal plumose setae.

Maxilliped 1 (Fig. 2i).—Coxal endite with 2 or 3 simple or weakly plumose setae marginally and sometimes 1 additional seta submarginally; basal endite with 13-15 short marginal plumose setae; endopod unsegmented, 0-2 very short setae terminally and 1 or 2 simple setae on inner margin;

exopod indistinctly 2-segmented, distal segment with 0-1 very short seta.

Maxilliped 2 (Fig. 3c).—Endopod 4-segmented, basal segment with 1 short seta, penultimate segment with 1 or 2 short simple setae, ultimate segment with 4 or 5 terminal simple or plumose setae; exopod 2-segmented, distal segment with 6 long plumose setae.

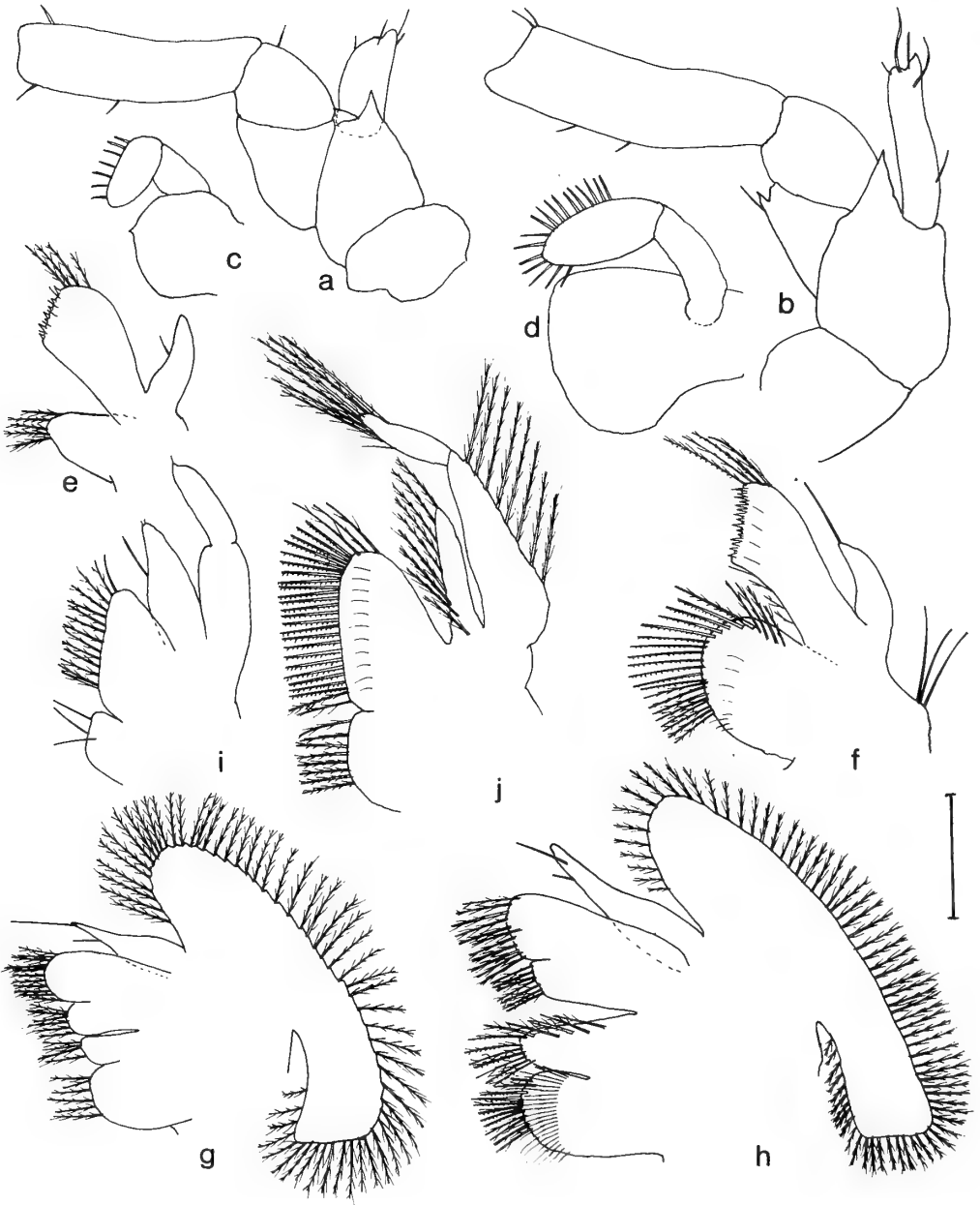


Fig. 2. *Porcellanopagurus edwardsi* Filhol, 1885. a, c, e, g, megalopa (cl = 2.2 mm); b, d, f, h, first crab stage (sl = 1.9, cl = 2.3 mm): a, b, antennal peduncle; c, d, mandible; e, f, maxillule; g, h, maxilla; i, j, first maxilliped. Scale equal 0.25 mm.

Maxilliped 3 (Fig. 3e).—Endopod 5-segmented, all segments with numerous setae, those of ultimate and penultimate segments most frequently serrated or barbed; accessory tooth of developing crista dentata ap-

parent; exopod 2-segmented, distal segment with 6 long terminal plumose setae.

Pereopods (Fig. 4a, c, e, g, i).—Chelipeds unequal, right larger. Cutting edge of dactyl of right with 2 strong calcareous

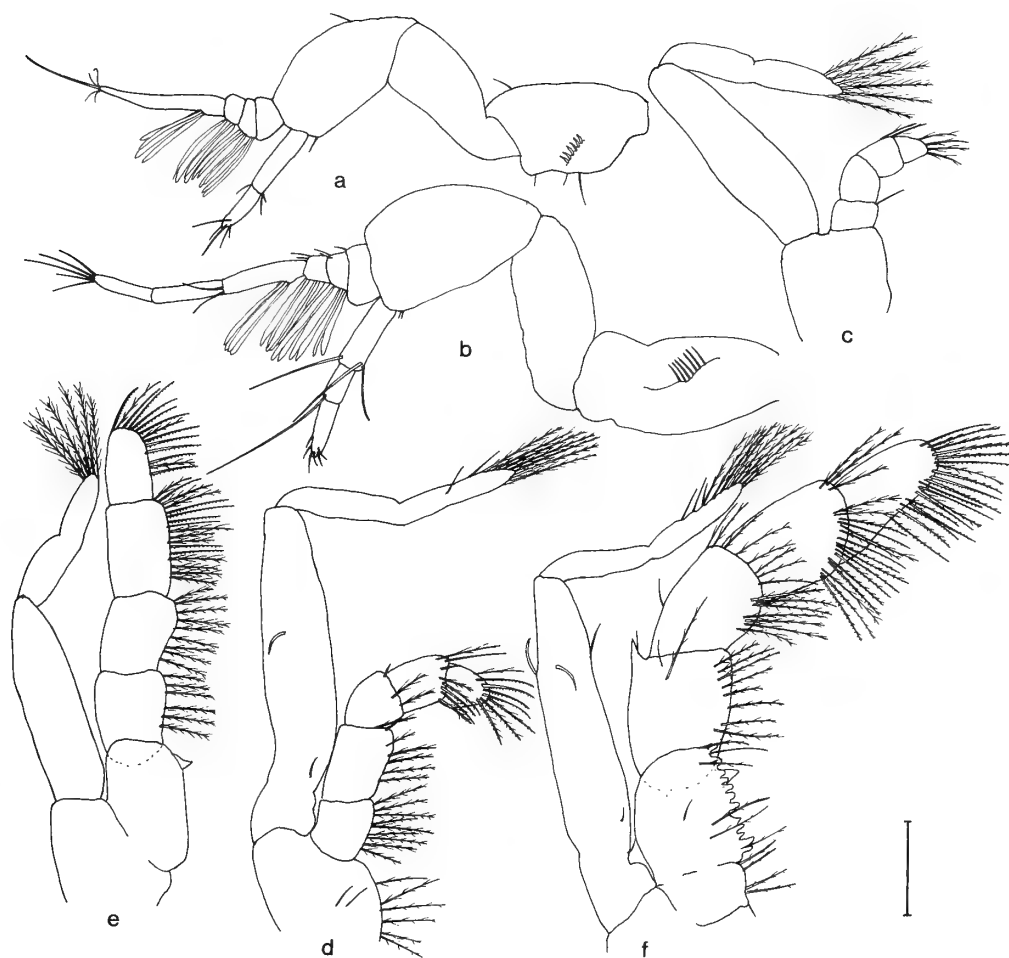


Fig. 3. *Porcellanopagurus edwardsi* Filhol, 1885. a, c, e, megalopa (cl = 2.2 mm); b, d, f, first crab stage (sl = 1.9, cl = 2.3 mm); a, b, antennule; c, d, second maxilliped; e, f, third maxilliped. Scale equal 0.25 mm.

teeth, terminating in corneous claw; chela with faint ridge on dorsolateral margin; carpus and merus each with few low protuberances or short ridges dorsally; ischium unarmed. Cutting edges of dactyl and fixed finger of left with corneous teeth, terminating in corneous claws; chela unarmed; carpus and merus each with few low protuberances on dorsal surfaces; ischium unarmed. Both chelae with few scattered setae. Ambulatory legs generally similar, dactyls of second and third pereopods each with row of 8 corneous spinules on ventral margins, propodi each with 2 widely-spaced spiniform setae on ventral margins

and 2 at or near ventrodistal margin; carpi and meri each with row of few low protuberances setae on dorsal surface. Fourth pereopods semi-chelate with propodal rasp of 1 row of corneous scales; dactyl long, curved; all segments with 1-several scattered setae. Fifth pereopods chelate; with few corneous scales on outer surface and margin of propodus, distal margin with 2 or 3 long curved setae; carpus and merus also with 1 or 2 short simple setae.

Abdomen (Fig. 1b).—Tergites of 6 somites all chitinous, unarmed but with 2 or 3 pairs of short setae as illustrated. Unequally biramous pleopods (Fig. 4k-n) on

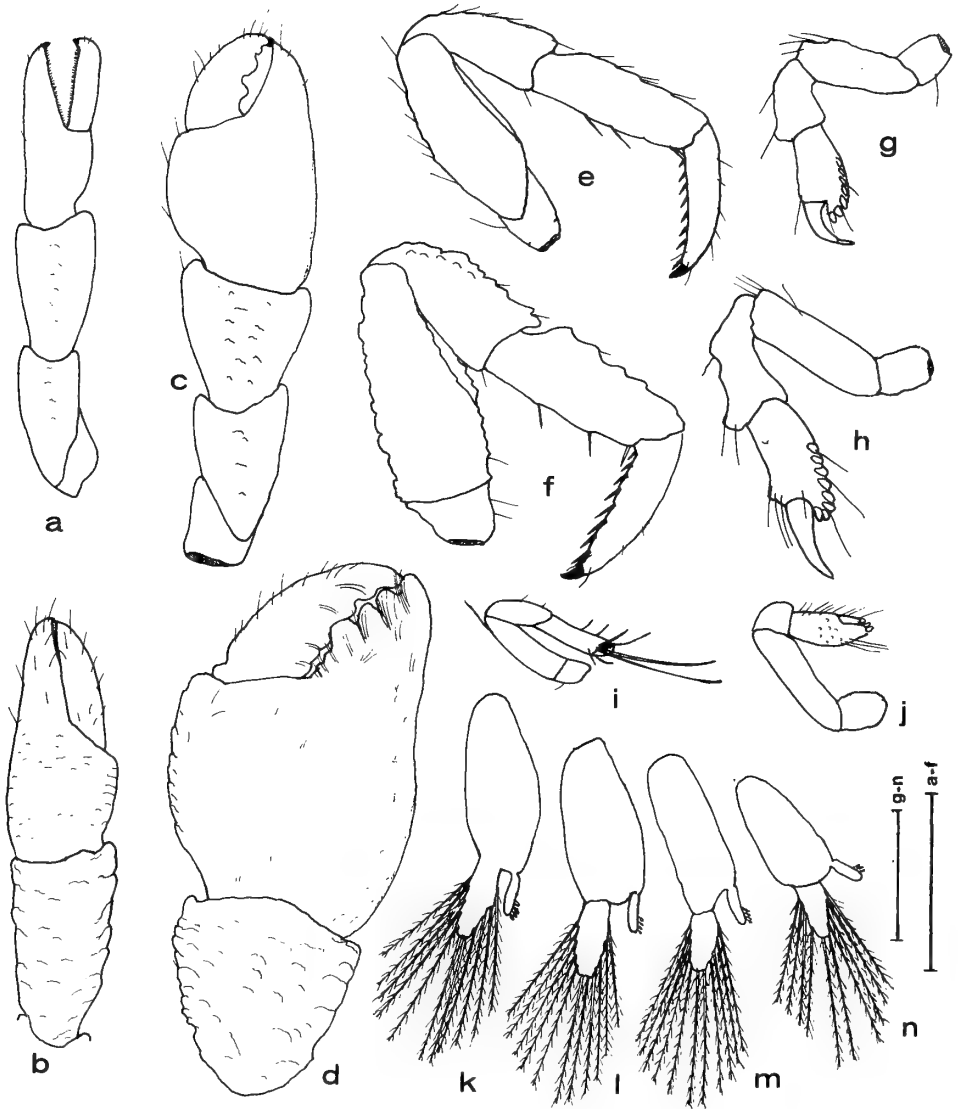


Fig. 4. *Porcellanopagurus edwardsi* Filhol, 1885. a, c, e, g, i, k-n, megalopa (cl = 2.2 mm); b, d, f, h, j, first crab stage (sl = 1.9, cl = 2.3 mm): a, left cheliped (dorsal view); b, carpus and chela of left cheliped (dorsal view); c, right cheliped (dorsal view); d, carpus and chela of right cheliped (dorsal view); e, f, right second pereopod (lateral view); g, h, left fourth pereopod (lateral view); i, j, right fifth pereopod (lateral view); k-n, left pleopods 2-5 respectively. Scales equal 0.5 mm (g-n) and 1.0 mm (a-f).

somites 2-5, exopods of second through fourth each with 11, fifth 10 marginal plumose setae; endopods each with appendix interna consisting of 4 (endopods 2-4) or 3 (fifth) apical hooks. Uropods (Fig. 1b) symmetrical; protopods with 1-3 setae on dorsal surface; exopods 1-segmented, with 15

or 16 simple and plumose setae marginally, 13-15 corneous scales on outer and terminal margins collectively, endopods short, each with 6 or 7 setae and 4-6 corneous scales. Telson with small lateral indentations each accompanied by 1 moderately long seta anterior to mid-length; 2 pairs of

short setae on dorsal surface; terminal margin rounded and with 4 + 4 long plumose setae.

Gills.—Arthrobranchs well developed on chelipeds and pereopods 2–4, rudimentary on third maxillipeds.

First Crab

Size.—sl = 1.8–1.9 mm; cl = 2.2–2.4 mm; $n = 3$.

Carapace (Fig. 1c).—Shield with cervical groove partially to completely delineated, approximately as long as broad (lateral lobes of shield included); dorsal surface with few scattered setae. Posterior carapace with lateral lobes partially to completely delineated, produced beyond level of anterior carapace lobes, directed posteriorly and terminating acutely; no median element developed; posterolateral and posteromedian plates weakly calcified, *cardiac sulci* and *sulci cardiobranchialis* delineated. Rostrum very well developed, occupying at least half anterior margin, obtusely triangular and terminating subacutely; spiniform lateral projections developing anterolaterally. Ocular peduncles short, stout; corneas not dilated; ocular acicles developing as calcified thickenings at peduncular bases, obscured from dorsal view by rostrum.

Thoracic sternites (Fig. 1f).—Sternites IX–XII all with numerous small surface tubercles or granules. Sternites IX (third maxillipeds), X (chelipeds) and XI (second pereopods) now all fused, but suture lines still apparent. Sternite XII (third pereopods) now with transverse median furrow. Sternite XIII (fourth pereopods) now transposed to position posteroventral to XII. Separation of XIV from preceding sternites slightly greater.

Antennule (Fig. 3b).—Peduncle little changed from previous stage; exopod 6-segmented, aesthetascs on second–fourth segments as follows: 6, 6, 4, fourth segment also with 2 short setae distally, ultimate segment with 4 or 5 terminal setae; endopod 3-segmented; basal segment with 2 or

3 moderately long setae; penultimate segment with 1 very long distal seta; terminal segment with 5 or 6 short setae.

Antenna (Fig. 2b).—Fifth and fourth peduncular segments with few setae; third segment with 1 strong spine on ventral margin, second segment little changed from previous stage, first segment unarmed; acicle still subrectangular, with minute terminal spinule and 2 or 3 setae. Flagella missing.

Mandible (Fig. 2d).—Larger and often more strongly calcified but otherwise unchanged; distal segment of palp with 14–17 very short marginal setae.

Maxillule (Fig. 2f).—Coxal endite with several plumodenticulate and 12–16 plumose and simple, submarginal and/or marginal setae; basal endite with 2 rows of teeth and few simple or plumose setae marginally and 4 simple setae submarginally, 3 or 4 additional plumose or simple setae on inner margin; protopod with 3 prominent setae on outer margin; endopod with internal lobe slightly produced and with 1 moderately long bristle, external lobe obsolete.

Maxilla (Fig. 2h).—Coxal endite bilobed, with 10–15 marginal plumose and plumodenticulate setae and row of submarginal plumose setae extending onto lower margin on proximal lobe, distal lobe with 6 or 7 marginal and 5 or 6 submarginal plumose setae; basal endite bilobed, with 7–10 plumose marginal setae on proximal lobe and 9 or 10 marginal and 1 or 2 submarginal plumose setae on distal lobe; endopod with 2 subterminal simple setae; scaphognathite with approximately 75 moderately short, marginal plumose setae.

Maxilliped 1 (Fig. 2j).—Coxal endite with 7 or 8 plumose or plumodenticulate setae marginally; basal endite with 20–30 marginal plumose and plumodenticulate setae and submarginal row of simple or weakly plumose setae; endopod with 8 or 9 plumose setae on inner margin; exopod 2-segmented, distal segment with 1 subterminal simple and 6 terminal plumose setae, prox-

imal segment with 5–8 plumose setae on outer margin.

Maxilliped 2 (Fig. 3d).—Endopod 5-segmented, with setation as illustrated; exopod 2-segmented, distal segment still with 6 or 7 long plumose and 2 short simple setae, proximal segment with 1 seta adjacent to outer margin and 1 proximally near inner margin.

Maxilliped 3 (Fig. 3f).—Endopod 5-segmented, all segments with increased number of setae, more on ultimate and penultimate segments often serrate or barbed; merus with prominent spine at dorsodistal margin, crista dentata with 10–12 teeth and strong accessory tooth; exopod 2-segmented, proximal segment with 1 stiff bristle on outer margin and 2 on or adjacent to inner margin and 1 on outer face, distal segment still with 8 long terminal plumose and 3 shorter, subterminal simple setae.

Pereopods (Fig. 4b, d, f, h, j).—Right cheliped much stronger than left; cutting edges of dactyl and fixed finger of right each with few strong calcareous teeth; palm with row of low faint ridges on dorsomesial margin, few low ridges on dorsolateral margin and scattered setae on dorsal surface; carpus low, scale-like protuberances on dorsal surface, somewhat stronger similar protuberances on dorsomesial margin and dorsolateral margin; merus with scattered granules on dorsal surface, dorsomesial margin with several short transverse ridges, ventromesial margin with row of strong spines; ischium with row of spines on ventromesial margin. Left cheliped with cutting edges of dactyl and fixed finger with several corneous teeth, terminating in corneous claws; palm with scattered low ridges and minute granules, dorsomesial and dorsolateral margins each with few low ridges; carpus with scale-like protuberances or ridges on dorsomesial and dorsolateral margins, dorsal surface with several short transverse ridges; merus with short transverse ridges dorsally, row of subacute spines on ventromesial margin; ischium with row of prominent subacute spines on ventromesial margin.

Ambulatory legs larger, dorsal margins of meri, carpi and propodi now with much more prominent protuberances on dorsal surfaces, carpi each with row of protuberances on lateral face in dorsal half. Fourth pereopods larger but not appreciably changed from previous stage. Fifth pereopods with few more granular-like scales on propodal surface.

Gills.—Increased in size and complexity; no pleurobranch apparent.

Abdomen (Fig. 1c).—Noticeably shortened and swollen; tergites of somites 1–6 somewhat reduced from previous stage; paired, but markedly reduced uniramous pleopods still present on somites 2–5, all lacking setation.

Telson and uropods (Fig. 1c).—Telson with scattered short setae on dorsal surface; transverse suture partially developed; terminal margin with weak median indentation. Uropods symmetrical; protopods each usually with small projection posteriorly; exopods with numerous plumose setae, dorsal surfaces each with 4 or 5 rows of corneous, spiniform scales; endopods each with double row of corneous scales and few short setae.

Discussion

The megalopal stage of *Porcellanopagurus edwardsi* is generally quite similar to megalopae of other described pagurid and diogenid species, except for the marked prominence of the rostrum and lack of a well defined shield. In these characters, *P. edwardsi* might mistakenly be perceived as a lithodid (e.g., *Hapalogaster*, cf. Konishi 1986: fig. 3M; *Placetron*, cf. Crain & McLaughlin 2000b, fig. 1C). Of course with the molt to first crab, the distinctiveness of *Porcellanopagurus* becomes apparent. The lateral carapace lobes begin to develop, the shield becomes delineated, and the lateral projections begin to take on their characteristic prominence. Thoracic sternites IX–XII develop the typically broad, flattened aspect of the adult (Fig. 1d), and

the joint facets of the chelipeds become distinctly asymmetrical. Sternite XIII moves to a posteroventral position beneath XII, while sternite XIV remains a very slender rod-like structure widely separating the coxae of the fifth pereopods. The development of six segments in the antennular exopod is comparable to that reported by McLaughlin et al. (1989) for some specimens of *Pagurus kennealyi* (Stimpson, 1864), although a five-segmented exopod is more common in pagurid crab stage 1 (Carvacho 1988, Ingle 1990, McLaughlin et al. 1992, Crain & McLaughlin 1994, Gherardi & McLaughlin 1995).

More profound differences are seen in the abdomen of the first crab stage of *P. edwardsi*. In the typical pagurid abdomen, the megalopal tergites are considerably reduced, if not lost almost entirely, with segmentation becoming indistinct, or marked simply by transverse fibrils, although some exceptions have been noted in *Discorsopagurus* (cf. Gherardi & McLaughlin 1995). In *P. edwardsi*, some reduction in the size of the individual tergites can be observed, but segmentation is clearly indicated. Additionally, while the typical pagurid abdomen remains elongate and slightly to strongly twisted, or at least flexed, the abdomen of *P. edwardsi* becomes noticeably shortened, with accompanying lateral expansion to give a semi-globular shape. The most significant difference between *P. edwardsi* and the described first crab stages of species of *Pagurus*, *Anapagurus*, *Discorsopagurus*, even the parapagurid genus *Sympagurus*, and the diogenid genera of *Clibanarius*, *Paguristes*, and *Dardanus* (cf. Lemaitre & McLaughlin 1992, McLaughlin et al. 1993, for specific reviews) is seen in the pleopods. Although second pleopods on both sides of the abdomen are typically reduced in most of the above cited genera at the first crab stage, and right side pleopods may be reduced or lost entirely, left side pleopods on somites 3–5 usually undergo only endopod reduction or loss. In some species of *Clibanarius* pleopod loss does

not even begin until the second crab stage (Brossi-Garcia 1987, 1988). In contrast, all pleopods of *P. edwardsi* undergo dramatic reduction with the molt to the first crab stage (Fig. 1c). This type of pleopod reduction heretofore has been reported only in lithodids (i.e., Kurata 1956; Miller & Coffin 1961; Hart 1965; Crain & McLaughlin, 2000a, 2000b). Whether pleopods loss is complete in *Porcellanopagurus*, with females pleopods reappearing with maturity, as has been suggested to be the case in *Lithodes* (cf. Sandberg & McLaughlin 1998), can only be determined when a complete juvenile series becomes available for study.

Acknowledgments

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***Cambarus (Jugicambarus) jezerinaci* (Crustacea: Decapoda: Cambaridae), a new species of crayfish from the Powell River Drainage of Tennessee and Virginia**

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Abstract.—A new species of crayfish, *Cambarus (Jugicambarus) jezerinaci*, is described from first and second order, spring fed streams draining into the Powell River in Tennessee and Virginia. It is believed to be a sister species of *Cambarus (Jugicambarus) parvoculus* and differs in having thickened rostral margins abruptly angled at the cephalic terminus (90°) to form an acumen, a smaller body size, reduced dorsal and ventral ridging of the chelate fingers, reduced lateral impression of chela, immovable finger having four enlarged tubercles (second from base largest), a propodus equal in length to the palm length, and an oval-shaped chela outline.

While evaluating the taxonomic status of *Cambarus (Cambarus) bartonii cavatus* Hay, 1902, the type locality ("Powell River, Tazewell, Tennessee" Hay 1902:435) was visited in an effort to obtain topotypic material of *C. (C.) b. cavatus*. Unable to locate any crayfish that resembled my concept of *C. (C.) b. cavatus* in the Powell River, I began searching smaller and smaller streams in the vicinity of Tazewell, Tennessee. Suspecting that Hay may have obtained his type material while cave exploring, on 18 August 1978, I visited Cave Spring, where a small stream debouches from a cave northeast of Tazewell, Tennessee into Mill Hollow. No specimens resembling *C. (C.) b. cavatus* were found but numerous small, blue or red, sexually mature crayfish of the subgenus *Jugicambarus* Hobbs, 1969 were collected which proved to represent a new species described herein. Other crayfishes of the genus *Cambarus* collected in the area were a species of the subgenus *Puncticambarus* Hobbs, 1969 that has previously been referred to as Species D (Hobbs 1969), and *Cambarus (Cambarus) angularis* Hobbs & Bouchard, 1994.

Material used in this description has been deposited in the Ohio State University Museum of Biological Diversity Crustacean Collection (OSUMC), the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM) and the Cleveland Museum of Natural History (CMNH). Adobe Photoshop 2.5.1 LE® was used to produce computer enhanced photographic illustrations. Systat 5.2.1® was used for regression analysis.

Cambarus (Jugicambarus) jezerinaci, new species

Fig. 1, Table 1

Diagnosis.—Body pigmented. Eyes small. Carapace subcylindrical, slightly dorsoventrally flattened. Rostrum with straight, slightly convergent margins, thickened, without marginal spines or tubercles, abruptly curved cephalically, terminating in upturned corneous acumen. Areola 2.7–5.5 ($\bar{X} = 4.2$, $n = 69$) times longer than wide, comprising 33–37% ($\bar{X} = 35\%$, $n = 69$) of total length of carapace, bearing 1 to 5 punctuations across narrowest part ($\bar{X} = 3$, $n = 69$). Cervical spine and tubercle absent.

Cervical groove continuous or interrupted. Suborbital angle acute, with blunt spine. Postorbital ridge without cephalic spine or tubercle. Branchiostegal spine reduced to small knob. Antennal scale approximately 2.3 times as long as broad, usually broadest at base; distomesial margin strongly converging on lateral margin to form spine on distal end. Basipodite and ischium of antenna lacking spine. Chela lacking tubercles on dorsal and ventral surfaces, length 75% (71–81%) of total carapace length in Form I males ($n = 9$), 66–81%, $\bar{X} = 74\%$ in females ($n = 50$), 1 row of 5–8 ($\bar{X} = 6$, $n = 69$) cristiform tubercles along mesial margin of palm and dorsopalmar furrow running from median dactyl articulation to mesial side of propodus articulation with carpus. Lateral margin of propodus smooth, not impressed at dorsal or ventral surface; longitudinal ridges on finger of dorsal propodus moderately developed, weakly developed on dactyl; dactyl 1.2–1.6 ($\bar{X} = 1.4$, $n = 69$) times longer than mesial margin of palm; palm width 40–52% ($\bar{X} = 46\%$, $n = 69$) of chela length; palm length 70–93% ($\bar{X} = 84\%$, $n = 69$) of chela width; row of 4 enlarged tubercles on opposable margin of propodus finger, second tubercle from base largest; opposable margin of dactyl with row of 3 enlarged tubercles, middle tubercle smallest; lacking subpalmar tubercles; lacking cluster of elongated setae at base of propodus finger. Dorsomesial margin of carpus of chela with 1 distal spine and 1 proximal blunt tubercle; ventral surface with 1 conical tubercle, occasionally none. Ventrolateral ridge of merus usually with 2 or 3 spines. Copulatory hook only on ischium of third pereopod of male. Boss on ischium of fourth pereopod well developed. First pleopods of Form I male contiguous at base, with 2 short terminal elements bent at angle greater than 90° to main shaft; corneous central projection truncated distally, bearing conspicuous subapical notch; mesial process inflated, tapering distally; Form II male pleopods non-corneous, terminal elements more bulbous than Form

I male and bent at angle greater than 90° to main shaft. Females with annulus ventralis deeply embedded in sternum, asymmetrical and having a rounded diamond shaped outline, slightly movable, without cephalolateral prominence.

Holotypic male, Form I.—Body subovate (Fig. 1E), dorsoventrally compressed. Abdomen narrower than cephalothorax (12.3 and 14.9 mm respectively); maximum width of carapace greater than depth at caudodorsal margin of cervical groove (14.9 and 10.4 mm respectively). Areola broad with 3 rows of punctations in narrowest part; 4.2 times longer than wide; length comprising 35.4% of total length of carapace. Rostrum with slightly convergent, thickened, raised margins; rostral margins curved ventrally starting at postorbital ridges; acumen distinctly delimited basally, anterior tip upturned and corneous, reaching base of penultimate podomere of antennular peduncle; dorsal surface of rostrum concave with sparse punctations. Postorbital ridges weak, grooved dorsolaterally, and ending cephalically without spines or corneous tubercles. Suborbital angles prominent; branchiostegal spines absent. Cervical spines represented by small knob. Hepatic and branchiostegal regions granulate. Remainder of carapace punctate dorsally and granulate laterally. Abdomen subequal in length to carapace, pleura short, subtruncate, rounded caudoventrally. Cephalic section of telson with 2 spines on each caudolateral corner. Proximal podomere of right uropod with 9 distal spines on mesial lobe; mesial ramus of uropod with prominent median rib ending distally in small distomedian spine not overreaching margin of ramus, distolateral spine of ramus also strong.

Cephalomedian lobe of epistome (Fig. 1H) short and subpentagonal having angular bends at median margins, ventral surface rather flat; main body with shallow central fovea; epistomal zygoma strongly arched. Ventral surface of proximal podomere of antennular peduncle without acute spine at base of distal third. Antennal peduncle

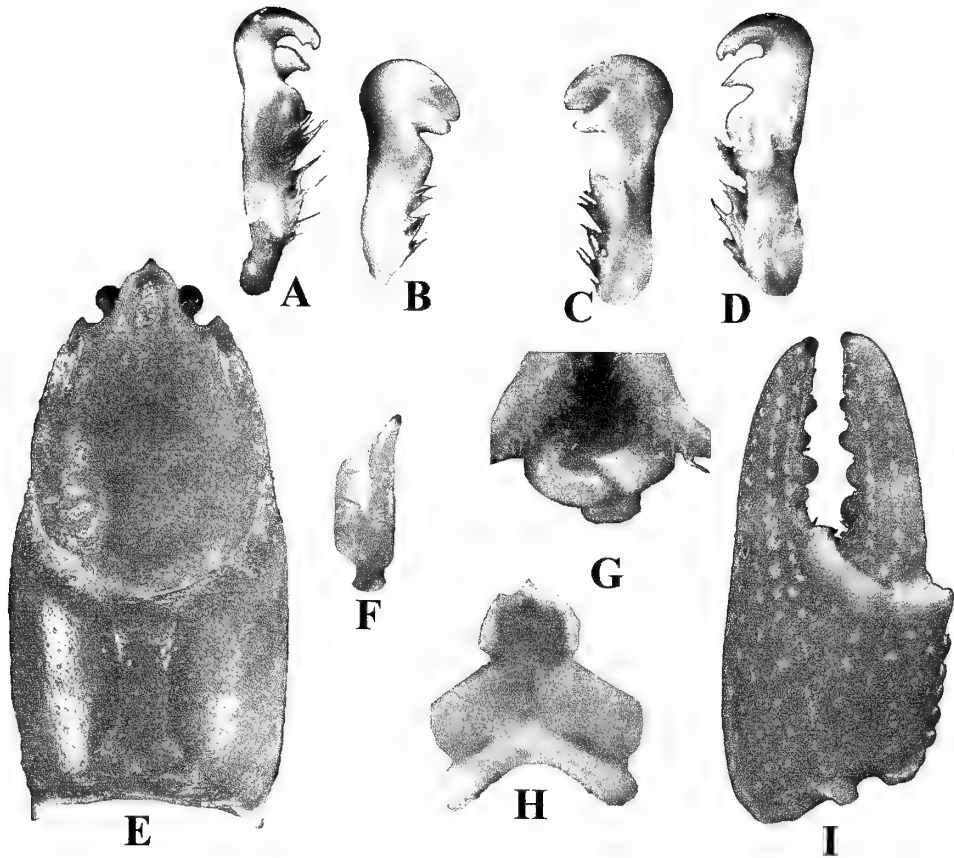


Fig. 1. *Cambarus (Jugicambarus) jezerinaci*, new species: (all from holotype male, Form I (OSUMC 3614), except B and C from morphotype male, Form II (OSUMC 3616), and G from allotype female (OSUMC 3615)) A, B, lateral view of male first pleopod; C, D, mesial view of male first pleopod; E, dorsal view of carapace; F, dorsal view of antennal scale; G, annulus ventralis; H, epistome; I, dorsal view of left cheliped.

without spines; antennal scale (Fig. 1F) 2.5 times as long as broad, broadest at mid-length, mesial margin forming gentle arc; distal spine strong, reaching base of distal extremity of antennular peduncle. Ventral surface of ischium of third maxilliped with evenly spaced rows of tufts of long, flexible setae; submarginal lateral row of seta on podomere small and flexible; distolateral angle not acute; mesial margin with row of teeth alternating large and small, teeth larger distally.

Length of left chela (Fig. 1I) 78% that of carapace (right chela regenerated); width 45.5% of length; palm length 45.5% of chela length; dactyl length 1.3 times palm length. Dorsomesial surface of palm lack-

ing tubercles, mesial margin with row of 6 cristiform tubercles, dorsal surface slightly punctate, punctations very small; lateral surface of palm and fixed finger of propodus not costate; ventral surface of palm less punctate than dorsal, lacking corneous tubercles on articular rim opposite base of dactyl; no subpalmar tubercle. Opposable margin of fixed finger of propodus with row of 5 tubercles (third from base largest) along proximal 66% of finger; single row of denticles between fourth and fifth tubercle, double row of denticles extending distally from fifth tubercle. Opposable margin of dactyl with row of 4 tubercles, (first and third from base larger than second and fourth) along proximal 75%; single row of

denticles between third and fourth tubercle, double row of denticles extending distally from fourth tubercle. Dorsomedian longitudinal ridges on both fingers weakly developed, none expressed ventrally. No dorsolateral impression at base of fixed finger.

Carpus of cheliped with distinct sinuous furrow dorsally; dorsomesial and lateral surfaces smooth; mesial surface with 1 large spiniform tubercle and 2 additional small ones; ventral surface lacking tubercles. Merus with 2 slightly developed pre-marginal dorsal tubercles, ventrolateral row of 3 spiniform tubercles, and ventromesal row of 7 spiniform tubercles, decreasing in size proximally; podomere otherwise smooth. Ventral ridge of ischium with 2 spiniform tubercles.

Ischium of third pereopod with simple hook extending proximally over basioischial articulation, not opposed by tubercles on basis. Coxa of fourth pereopod with vertically disposed caudomesial boss; that of fifth pereopod lacking boss, its ventral membrane bearing oblique rows of small sclerites armed with stiff setae.

First pleopods contiguous at base, reaching coxae of third pereopods; corneous central projection (Fig. 1A, D) bent caudally at angle greater than 90° , tapering distally, with subapical notch and not extending beyond mesial process; mesial process subconical and directed caudolaterally (left more so); lacking caudal knob.

Allotypic female.—Ovigerous. Excluding secondary sexual characteristics, differing from holotype in following respects: areola length 36.2% of total length of carapace and 3.8 times longer than wide; antennal scale 2.4 times as long as broad, widest at base; right chela 74.7% of carapace length, palm width 40.2% of chela length; opposable margin of dactyl with row of 5 tubercles (4 left), second tubercle from base largest; merus with ventrolateral row of 3 tubercles, and ventromesial row of 9.

Annulus ventralis (Fig. 1G) deeply embedded in V-shaped sternum, asymmetrical and having a rounded diamond shaped out-

line, with a narrow sinuous fossa beginning just behind anterior edge and intersecting sinus at posterior margin near midline; tongue extending caudosinistrally in fossa, disappearing beneath thickened caudosinistrally wall; sinus reverse S-shaped and ending under caudal wall slightly dextral to median line. Postannular sclerite oval. First pleopods damaged.

Morphotypic male, Form II.—Differing from holotype in following respects: areola length 35.1% of carapace length and 3.4 times longer than wide; antennal scale 2.4 times as long as broad; left chela (right regenerated) 75.1% of carapace length; palm length 44.6% of chela length; palm width 44.6% of chela length; opposable margin of fixed finger of propodus with 3 tubercles, second from base enlarged; opposable margin of dactyl with 3 tubercles, first and second from base larger; merus lacking pre-marginal tubercles dorsally, with ventrolateral row of 2 tubercles and ventromesal row of 8; central projection of first pleopod (Fig. 1B, C) non-corneous and blunt.

Color notes.—*Cambarus (Jugicambarus) jezerinaci*, new species, exhibits color morphs of red and blue. Red morph individuals grade from a dark brown abdomen to a lighter brown cephalothorax suffused with orange anterior to the cervical groove. Chelae primarily orange mottled with brown, having brown bands on the distal dorsal carpus and merus areas and around the dactyl/propodus joint. Knobs, tubercles, and chela tips orange, the enlarged tubercle of opposable margin of propodus yellow, distal spines of fingers chestnut brown. Merus and distal podomeres of walking legs brown with slight blue tint dorsally and ventrally, orange bands at articulations, podomeres proximal to merus brown dorsally and cream-orange ventrally. Ventral surface of cephalothorax and abdomen white; ventral surface of chela, carpus, and distal merus of first walking legs orange and ventral telson and uropods brown. Eggs of ovigerous females purple. Blue morph individuals concolorous gray-blue dorsally, grad-

ing cream to white ventrally; chela tips cream-orange.

Types.—Holotype male Form I, allotype female, and morphotype male Form II: OSUMC 3614, OSUMC 3615, and OSUMC 3616 respectively; Paratypes: USNM 291280 and CMNH 299.

Type locality.—Virginia, Lee Co., unnamed tributary of Dry Branch, a tributary of Indian Creek of the Powell River drainage, 0.2 miles (0.32 km) east of Chadwell Gap Trail, 1.4 miles (2.25 km) north of Caylor (36°39'16"N, 83°29'55"W).

Range and specimens examined.—*Cambarus (J.) jezerinaci*, new species, appears to have a very restricted range, confined to small tributaries of the Powell River in Lee Co., Virginia and Clairborne Co., Tennessee. Eight lots have been examined: Virginia: Lee Co., 1) OSUMC 3610, type locality (see above), 20 Apr 1986, 36°39'16"N, 83°29'55"W (1♂I, 1♂II, 6♀ ovig.); 2) OSUMC 3608, Hardy Creek adjacent U. S. Rte 58, just downstream of Smiley, 5.0 mi (8.05 km) E of Rose Hill, 20 Apr 1986, 36°41'18"N, 83°17'08"W (1♀ ovig.); 3) OSUMC 3612, trib. Hardy Cr. at culvert on Va. Rt. 790 at intersection of Va. Rt. 658, 3.2 mi (5.15 km) E of Caney Hollow, 20 Apr 1986, 36°40'39"N, 83°15'28"W (2♂I, 6♀ ovig.); 4) OSUMC 3609, large spring trib. to Hardy Cr., 3.7 mi (5.95 km) WNW of Caney Hollow, 1.1 mi (1.77 km) SE of Smiley, 20 Apr 1986, 36°41'05"N, 83°16'13"W (1♂I, 1♂II, 7♀, 1♀ ovig.); Tennessee: Clairborne Co., 5) OSUMC 3611, Mill Hollow tributary (trib.) Powell River, 3.8 mi (6.12 km) ENE of Bacchus, 10.3 mi (16.58 km) SE of Middlesboro, 1 Mar 1984, 36°31'17"N, 83°33'30"W (1♂II, 5♀); 6) Paratypes: CMNH 299 (1♂I, 1♂II, 1I), and USNM 291280 (1♂I, 1♂II, 1♀), Mill Hollow trib. Powell River, 0.75 mi (1.21 km) N of Cave Spring, 4.3 mi (6.92 km) N of Tazewell, 18 Aug 1978, 36°30'56"N, 83°33'15"W; 7) OSUMC 3607, Mill Hollow trib. Powell River, 0.9

mi (1.45 km) N of Cave Spring Church, 4.5 mi (7.24 km) NNE of Tazewell, 13 Aug 1984, 36°30'35"N, 83°33'21"W (4♂II, 8♀); 8) OSUMC 3613, Mill Hollow trib. Powell River, 4.9 mi (7.89 km) NNE of Tazewell, 2.8 mi (4.51 km) NE of Bacchus, 21 Apr 1986, 36°31'44"N, 83°33'41"W (3♂I, 6♀ ovig.).

Variation.—Little variation was seen in *Cambarus (Jugicambarus) jezerinaci*, new species. The most noticeable variation was the presence of 1 or 2 spines on the lateral margin of the antennal scale. This character trait occurred in no discernable geographic pattern, though it appeared to occur more often in females.

Size.—The largest specimen examined was a female with a carapace length (CL) of 33.8 mm. First form male CL ranged from 28.6 to 16.1 mm. For measurements of types see Table 1.

Habitat & life history notes.—Collections have been made in March, April, and August. First form males were observed in April and ovigerous females in April and March. Eight ovigerous females yielded a linear relationship between carapace length and egg number of $y = -94.1 + 6.3x$ and $r^2 = 0.78$, with egg number increasing with carapace length. Other attributes of the life history of this species remain unknown.

This species apparently prefers first and second order, spring feed streams of higher altitude and high gradient. It is a secondary burrower, living under rocks in mid stream and along the stream edges.

Relationships.—*Cambarus (Jugicambarus) jezerinaci*, new species, is most similar morphologically to *C. (J.) parvovulus* Hobbs & Shoup, 1947. It may be a sister species of *C. (J.) parvovulus* and could be derived from populations that crossed the drainage divide from the Cumberland River basin to the upper Tennessee and Powell River basins, subsequently becoming isolated. *Cambarus (J.) jezerinaci*, new species, tends to be smaller than *C. (J.) parvovulus* (Male I, carapace length: 21.5 mm vs. 28.5 mm; Male II, carapace length: 21.6

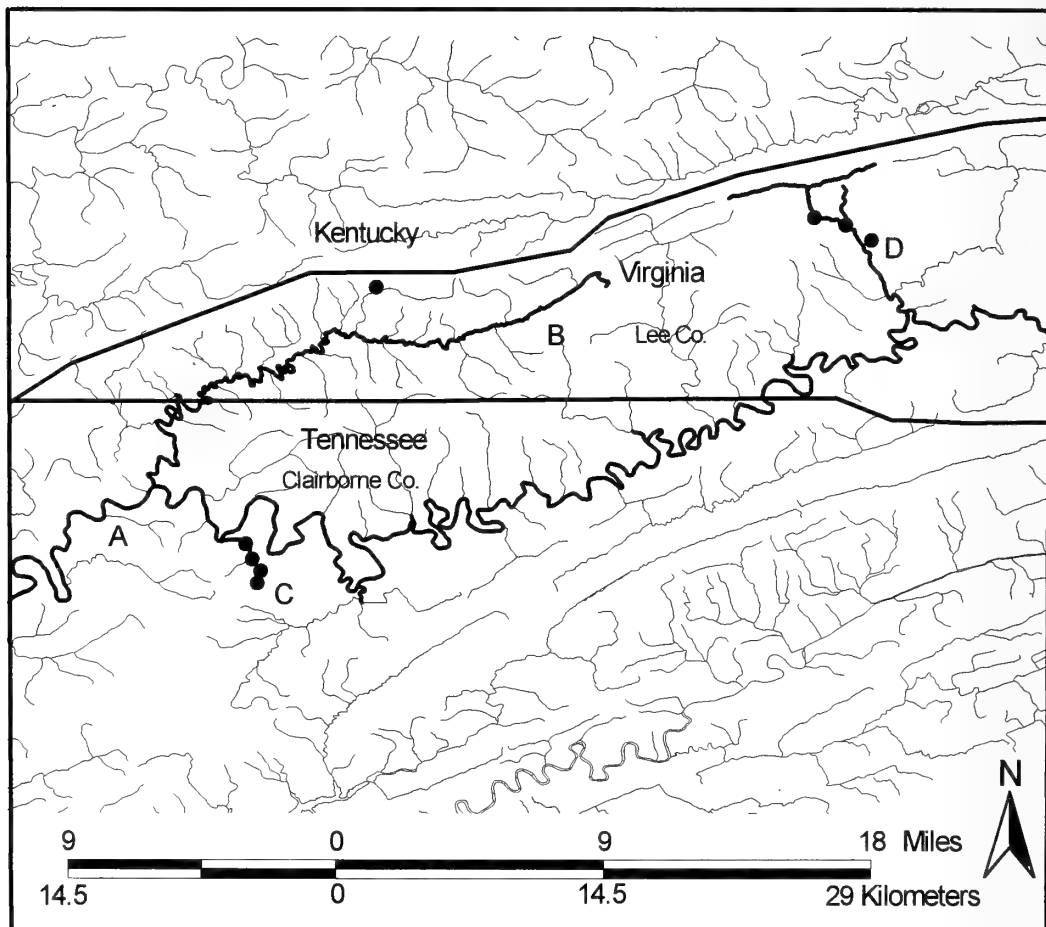


Fig. 2. Distribution of *Cambarus (Jugicambarus) jezerinaci*, new species, in Tennessee and Virginia: A, Powell River; B, Indian Creek; C, Cave Spring; D, Hardy Creek.

mm vs. 25.3 mm; Female, carapace length: 23.2 mm vs. 26.6 mm respectively).

Comparisons.—Like all members of the subgenus *Jugicambarus*, *C. (J.) jezerinaci*, new species, can be distinguished from members of other subgenera in *Cambarus* by the presence of a cristiform row of tubercles on the mesial palm of the chela. Within the subgenus *Jugicambarus*, *C. (J.) jezerinaci*, new species, differs from all other species in its unique tuberculation of the opposable margins of the chela fingers. No other species has an enlarged second tubercle on the opposable propodus and enlarged first and third tubercles on the opposable dactyl. The absence of setae on the chela

distinguishes *C. (J.) jezerinaci*, new species, from many members of *Jugicambarus* and the thickened rostral margins abruptly angled at the cephalic terminus (90°) to form an acumen, a generally smaller body size, reduced dorsal and ventral ridging of the chelate fingers, reduced lateral impression of the chela, immovable fingers having only four enlarged tubercles, a propodus equal in length to the palm length, and an oval-shaped chela outline also aid in separating *C. (J.) jezerinaci*, new species, from *C. (J.) parvoculus* and other members of the subgenus.

Crayfish associates.—*Cambarus (Cambarus) angularis* and a species of *Camba-*

Table 1.—Measurements (mm) of *Cambarus (Jugicambarus) jezerinaci*, new species.

Character	Holotype	Allotype	Morphotype
Carapace			
Height	14.0	16.4	10.2
Width	15.0	17.3	11.4
Length	28.6	33.8	23.2
Areola			
Length	10.1	12.2	8.2
Width	2.4	3.2	2.4
Rostrum			
Width at eyes	3.1	4.0	3.0
Length	4.2	5.0	3.8
Length to anterior postorbital ridges	8.8	9.7	7.2
Distance between postorbital ridges	7.5	8.6	6.0
Chela			
Length	22.2 (left)	25.3 (right)	17.4 (left)
Palm length	9.0	9.0	6.8
Width	10.1	10.2	7.8
Dactyl length	12.1	14.4	10.1
Opposable margin of propodus length	8.4	10.9	7.7
Depth of palm	6.8	6.5	5.2
Abdomen			
Length	29.4	37.3	24.6
Width	12.1	16.3	9.5
First pleopod			
Length	7.2	N/A	5.6
Antennal scale			
Length	4.2	5.2	3.8
Width	1.7	2.2	1.6

rus (subgenus *Puncticambarus* referred to as species D (Hobbs 1969)) were collected with *C. (J.) jezerinaci*, new species.

Etymology.—It is my belated pleasure to name this species after my dear departed friend and mentor, Raymond Felix Jezerinac. He was a devoted carcinologist and good friend, and is sorely missed. Ray contributed greatly to the understanding of crayfish distributions and evolution in the northern U.S.A. He always had a wry sense of humor and would probably agree that some might say “he lived for better or worse, but he’s dead for good.”

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Larval stages of *Paradasygyius depressus* (Bell, 1835) (Crustacea: Decapoda: Brachyura: Majidae) and a phylogenetic analysis for 21 genera of Majidae

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Abstract.—All larval stages and the first crab instar of *Paradasygyius depressus* (Bell) were obtained in laboratory culture. Larval development consists of two zoeal stages, followed by the megalopa. Each larval stage is described in detail. Beginning with the first zoea, the duration of each stage was 4–7 (4.5 ± 0.7), 4–5 (4.5 ± 0.5), and 7 days, the megalopa and first crab instar appearing 11 ± 1 and 15 days after hatching, respectively. A phylogenetic analysis of 21 genera of Majidae is provided based on 34 zoeal and three megalopal characters. The phylogenetic analysis resulted in four equally parsimonious trees 173 steps long (CI = 0.66, RI = 0.71, and RC = 0.47) supporting the monophyly of Oregoniinae, Majinae, and Inachinae (with the exclusion of *Macrocheira* De Haan incertae sedis). Based on general agreement of sister-group hypotheses, we provide sets of larval characters that define Oregoniinae, Majinae, and Inachinae. Our phylogenetic hypothesis suggests that Oregoniinae is the most basal clade within the Majidae, and Majinae and the clade (*Epialtus* H. Milne Edwards + Inachinae [excluding *Macrocheira* incertae sedis]) are sister taxa. Within Inachinae, all trees suggest that *Inachus* Weber and *Macropodia* Leach are sister taxa nested as the most derived clade, followed by *Achaeus* Leach, *Pyromaia* Stimpson, *Paradasygyius* Garth, *Anasimus* A. Milne-Edwards, and the most basal *Stenorhynchus* Lamarck. The sister-group relationships of the clade (*Pisa* Leach (*Taliepus* A. Milne-Edwards + *Libinia* Leach)), *Mithrax* Latreille and *Microphrys* H. Milne Edwards remained unresolved.

Paradasygyius depressus (Bell, 1835) is an eastern Pacific majid crab known from the Gulf of California to Colombia (Garth 1958). Members of this genus were considered to belong to the Inachinae (Rathbun 1925), Inachidae sensu Guinot (1978). However, recent morphological evidence of the skeleton from adults suggests that *Paradasygyius* Garth, 1958 and the nine other American inachine genera *Inachoides* H. Milne Edwards & Lucas, 1842, *Collodes* Stimpson, 1860, *Euprognatha* Stimpson, 1871, *Batrachonotus* Stimpson, 1871, *Ar-*

achnopsis, Stimpson, 1871, *Pyromaia* Stimpson, 1871, *Anasimus* A. Milne-Edwards, 1880, *Leurocyclus* Rathbun, 1897, and *Aepinus* Rathbun, 1897 differ significantly from the remaining Inachinae (Drach & Guinot 1982, Guinot & Richer de Forges 1997). Accordingly, Drach & Guinot (1983) resurrected the family Inachoididae Dana, 1851 to include these genera which here are considered as Inachoidinae for placement within the still widely recognized Majidae (e.g., Griffin & Tranter 1986, Ingle 1992, Melo 1996). Few larvae of in-

achoidines are presently known. The aim of the present paper is to describe the zoeal stages and the megalopa of *Paradasygius depressus*, to compare them to those of other inachoidines and majids, and to provide a phylogenetic hypothesis for 21 genera of Majidae based on zoeal and megalopal characters.

Materials and Methods

Larval development and description.—Specimens of *Paradasygius depressus* were collected 2 July 1992 while trawling at about 70 m depth on the Pacific coast of Costa Rica near Dominical, Puntarenas (9°13'N, 83°48'W). Ovigerous specimens were held in separate aquaria until hatching, which always occurred at night. On 4 July 1992 a numbered series consisting of 50 of the most active, positively phototactic larvae were separated into acrylic jars (2 larvae per jar). Each jar held about 40 ml of filtered sea water with 0.2 mg/ml potassium benzylpenicillin (Squib Brazil Inc.) to prevent bacterial infection. Rearing of this series of larvae was discontinued 17 days after hatching. Larvae from different females were also reared under mass culture conditions to provide additional specimens for analysis.

Newly hatched larvae were fed ad libitum with *Artemia* nauplii. Sea water was changed, and specimens were inspected and fed daily. All acrylic ware was washed in fresh water and air-dried before re-use with fresh sea water the following day. Mean daily water temperature in the tank was 28°C, within about 1°C of the natural environment fluctuation. Average salinity was 32‰. A 12L:12D photoperiod was maintained.

Whenever possible, a minimum of ten specimens was measured and at least five specimens of each stage were dissected for morphological description. For slide preparations polyvinyl lactophenol mounting medium was used with CMC (Turttox) or chlorazol black stain. Morphometric data

were obtained using a microscope-mounted high resolution video camera to a computer equipped with image analysis (OPTIMAS vers. 5.2) and spreadsheet (Microsoft EXCEL 6.0) software. Measurements ($\pm 7 \mu\text{m}$) of zoeal stages include carapace length measured in lateral view from the base of the rostrum to the most posterior margin; carapace width in frontal view at its widest point; the dorsal spine in lateral view from the posterior basal margin to the tip; antenna length in lateral view from the base of the eye to the tip. For the megalopa, carapace length and width were measured in dorsal view, from the vestigial rostrum to the posterior margin, and at its widest point, respectively.

The description of setae follows Pohle & Telford (1981), but here includes only analysis by light microscopy (LM), using an Olympus BH-2 microscope with Nomarski Differential Interference Contrast and camera lucida. Some of the setae designated as plumose herein may be plumodenticulate setae due to the lower resolution limits of LM as compared to scanning electron microscopy (SEM). Denticulettes sensu Pohle & Telford (1981) are generally only visible by SEM but were recorded here when occurring in dense clusters. Description guidelines of Clark et al. (1998) were generally followed. We followed the conventional taxonomic ranking of spider crabs as a single family divided into a series of subfamilies (Rice 1983, Griffin & Tranter 1986, Negreiros-Fransozo & Fransozo 1991, Melo 1996). Specimens of larval stages and a spent female crab have been deposited at the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM 259645, 291488). Slide preparations were banked at the NEBECC Decapod Larval Collection, Núcleo de Estudos em Biologia, Ecologia e Cultivo de Crustáceos, Department of Zoology—IB, Universidade Estadual Paulista, Botucatu, São Paulo, Brazil, accession numbers NEBECCDLC 00003.1–23.

Phylogenetic analysis.—The data matrix

from Marques & Pohle (1998) for 15 genera of Majidae was implemented with additional data from the larval descriptions of *Achaeus cranchii* Leach, 1817 (cf. Paula 1987), *Anasimus latus* Rathbun, 1894 (cf. Sandifer & Van Engel 1972), *Macropodia* sp. (cf. Paula 1987), *Pyromaia tuberculata* (Lockington, 1877) (cf. Fransozo & Negreiros-Fransozo 1997), *Stenorhynchus* spp. (cf. Yang 1976), and *Epialtus brasiliensis* Dana, 1852 (cf. Negreiros-Fransozo & Fransozo 1991) and *E. bituberculatus* H. Milne Edwards, 1834 (cf. Negreiros-Fransozo & Fransozo 2000). Modifications in coding and character argumentation of new characters follow.

An examination of intra- and interspecific variability of antennal morphology among all taxa led to a simplified coding of character states, reduced to four from the original eight states used by Clark & Weber (1991). Character 4, exopod morphology of the antenna: The spinulose tip or spine varies in length relative to a pair of setae. State 0, terminal spine minute, less than half length of smaller apical seta; state 1, terminal exopod spine half or more length of apical setae but not extending beyond tip of setae; state 2, exopod tip extending beyond setae, latter inserted distally to proximal half of shaft; state 3, exopod tip extending much beyond setae, latter inserted on proximal half of shaft.

Six new characters were added to the data matrix in an attempt to resolve sister-group relationships within the Inachinae. Character polarization was inferred with reference to the states observed in *Callinectes* spp. and *Cancer* spp. using the outgroup comparison method (Watrous & Wheeler 1981, Maddison et al. 1984). The following new characters were added to the analysis of Marques & Pohle 1998 (see Table 2):

(32) Posterolateral carapace margin of zoeal stages ornamented with serrulations: Within Inachinae sensu lato, *Inachus*, *Macropodia*, and *Achaeus* are serrulated on the posterolateral margin of the carapace. In

other inachines, as well as oregoniines and the outgroups, the posterolateral margin of the carapace is smooth. According to the outgroup comparison, serrulation on the posterolateral margin of the carapace was considered derived within Inachinae. Character states were coded as: 0, ornamentation absent; 1, ornamentation present.

Character polarization: 0 → 1

(33) Distinct paired acicular (sensu Weber & Wear 1981) curved processes on abdominal somite of zoeal stages: Within Inachinae sensu lato, *Paradasygyius*, *Anasimus*, and *Pyromaia* possess a conspicuous lateral pair of acicular curved processes on somite 2. In other inachines as well as oregoniines and the outgroups, the lateral process on somite 2, although present, is non-acicular. Thus, we considered the presence of acicular processes as derived within Inachinae. Character states were coded as: 0, acicular process absent; 1, acicular process present.

Character polarization: 0 → 1

(34) Separated sixth abdominal somite in the second zoea: Within Inachinae sensu lato, *Inachus*, *Macropodia*, and *Achaeus* do not show a separated sixth abdominal somite. In other inachines, as well as Oregoniinae, the sixth abdominal somite is defined. Unlike Majidae, the outgroups are characterized by more than two zoeal stages. In the latter, the sixth abdominal somite appears in the third zoeal stage. Using Oregoniinae and *Macrocheira* as functional outgroups, we considered the presence of a separated sixth abdominal somite in the second zoeal stage as derived within Inachinae. Character states were coded as: 0, sixth abdominal somite differentiated; 1, sixth abdominal somite not differentiated.

Character polarization: 0 → 1

(35) Megalopa uropods: Pleopods may be present or absent on abdominal somite 6. These uropods are present in the outgroups, while being present or absent in different genera of the ingroup. The absence of uropods was considered as the derived state within the ingroup. Character states

were coded as: 0, uropods present; 1, uropods absent.

Character polarization: 0 → 1

(36) Megalopa antenna exopod process: This lateral, sometimes spine-like process on the basal segment may be present or absent. Within the outgroups, *Cancer* spp. and *Callinectes sapidus* Rathbun, 1896 lack this process, whereas it is present in *Callinectes similis* Williams, 1966. According to the Maddison et al. (1984) algorithm, the presence of the process is considered as the derived state. Character states were coded as: 0, exopod process absent; 1, exopod process present

Character polarization: 0 → 1

(37) Megalopa antennal flagellum: There are a number of articles distal to the basal peduncular segments. In the outgroups there are eight articles, whereas in Majidae the number of articles may range from 3–5. Within the latter fusion of articles 2–3 and/or 4–5 occurred in different genera (Rice 1988). This multistate transformation series was left unordered as the character state observed in the outgroups is not present within the ingroup, and because there are many character states within the ingroup. Character states were coded as: 0, eight flagellar articles; 1, five flagellar articles; 2, articles 4–5 fused; 3, articles 2–3 fused; 4, articles 2–3 and 4–5 fused.

Phylogenetic analysis was performed with PAUP* (version 4.0b1, Swofford 1998) using the heuristic search with 50 replicates and Tree-Bisection-Reconnection (TBR) as the branch-swapping algorithm, and ACCTRAN optimization. Multistate transformation series were considered unordered, characters were equally weighted, and trees were rooted by specifying *Cancer* and *Callinectes* as outgroups, as used by Marques & Pohle (1998). A NEXUS format PAUP* input file containing the data matrix is provided in Appendix 1.

Results

Larval development and description.—Larval development of *Paradasygius de-*

pressus consists of two zoal stages and one megalopa. Figure 1 shows the rearing record for the three stages cultured at ambient temperature (28°C). Beginning with zoea I, the duration of each stage was 4–7 (4.5 ± 0.7), 4–5 (4.5 ± 0.5), and 7 days, the megalopa and first crab instar appearing 11 ± 1 and 15 days after hatching, respectively. Larval morphometrics are given in Table 1. Only morphological changes are described for the stages following the first zoea.

Description

Paradasygius depressus (Bell, 1835)
First zoea (Fig. 2)

Carapace (Fig. 2A).—With long, naked dorsal spine; lacking rostral and lateral spines. On ventral margin with densely plumose “anterior seta” (Clark et al. 1998) posterior to scaphognathite notch, followed by 3 additional sparsely plumose setae. Eyes sessile, with small papilla on peduncle. Small but distinct median ridge frontally between dorsal spine and eyes and a median tubercle on posterodorsal margin. Two pairs of simple or sparsely plumose setae present, one flanking dorsal spine, another longer pair just dorsal to median ridge.

Antennule (Fig. 2C).—Unsegmented, smooth, conical. Terminally bearing two long aesthetascs, 1 shorter aesthetasc and short seta.

Antenna (Fig. 2D).—Biramous, protopod very long and pointed, bearing 2 rows of sharp spinules, increasing in size distally; endopod bud present; one-segmented exopod with long spinulated distal process and pair of serrulate setae about 1/3 from tip.

Mandible (Fig. 2E).—With medial toothed molar process and enlarged lateral incisor process bearing about 10 circularly arranged marginal teeth. Palp absent.

Maxillule (Fig. 2F).—Coxal endite bearing 7 setae, 3 terminal graded plumodenticulate and subterminally 3 plumodenticulate and 1 plumose. Basial endite with 3 terminal plumodenticulate cuspidate setae

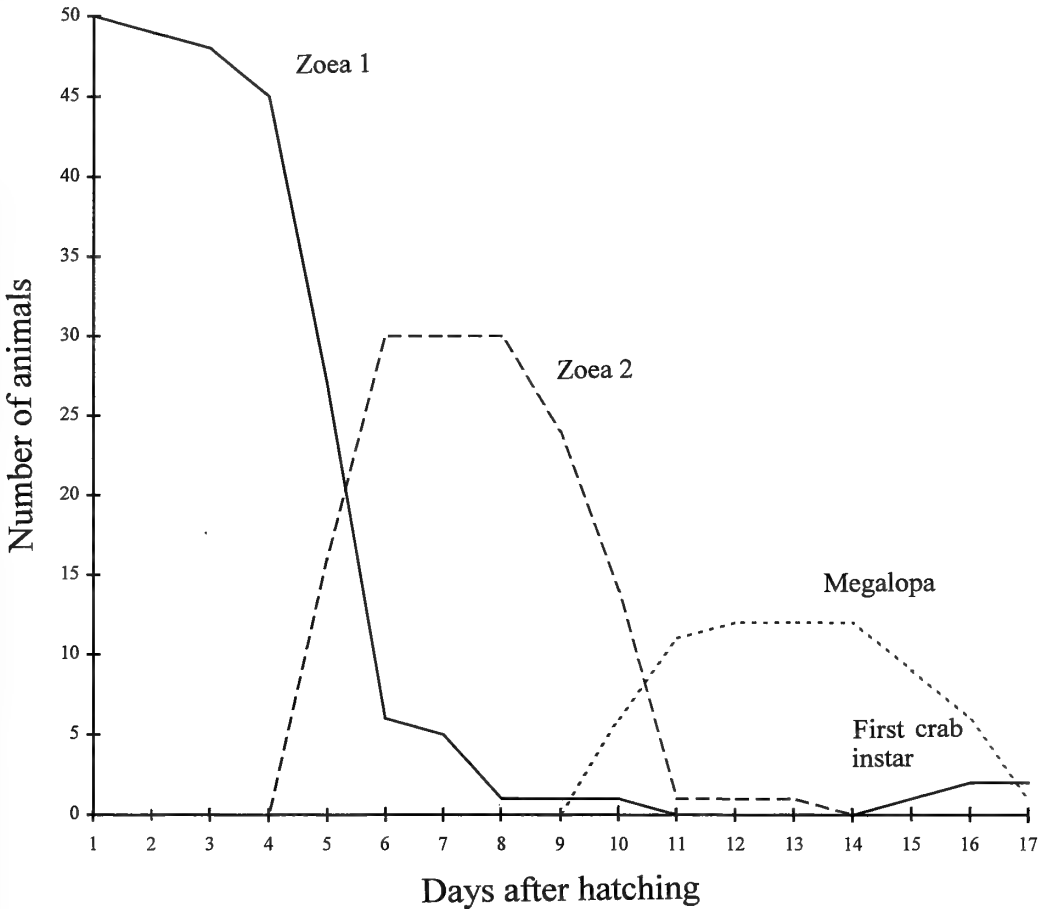


Fig. 1. Rearing record of larval stages of *Paradasygius depressus* at ambient temperature ($28 \pm 1^\circ\text{C}$) and salinity (32‰).

and 4 subterminal setae, 3 plumodenticulate and 1 plumose. Two-segmented endopod with naked proximal segment, distal segment bearing 2 pairs of plumodenticulate setae apically. Exopod seta absent.

Maxilla (Fig. 2G).—Coxal endite bi-

lobed, each lobe with 4 setae, 3 plumose, 1 plumodenticulate. Basial endite bilobed, proximal lobe with 5 plumodenticulate setae, distal lobe bearing 4 plumodenticulate setae. Unsegmented endopod distally slightly bilobed, proximally with single and dis-

Table 1.—Dimensions (mm) of larval structures of *Paradasygius depressus* (Bell, 1835).

Species	Dorsal spine length	Carapace length	Carapace width	Antenna length
Zoea 1	0.67 ± 0.04 (0.57–0.76)	0.69 ± 0.04 (0.60–0.69)	0.53 ± 0.04 (0.49–0.60)	0.60 ± 0.04 (0.50–0.68)
Zoea 2	0.48 ± 0.06 (0.44–0.53)	0.83 ± 0.05 (0.79–0.88)	0.67 ± 0.04 (0.64–0.70)	0.63 ± 0.04 (0.59–0.67)
Megalopa	0.26 ± 0.01 (0.25–0.27)	1.14 ± 0.01 (1.14–1.15)	0.99 ± 0.00 (0.99–0.99)	0.88 ± 0.04 (0.83–0.91)

Note: Values are given as the mean \pm standard deviation, with range in parentheses.

tally with 2 plumodenticulate setae; microtrichia on lateral margin. Scaphognathite marginally with 10–11 densely plumose setae, including distal process.

Maxilliped 1 (Fig. 2H).—Coxa may bear developing seta. Basis with 9 plumodenticulate setae arranged 2,2,2,3. Endopod 5-segmented with 3,2,1,2,1+4 plumodenticulate setae. Incompletely bisegmented exopod with 4 terminal plumose natatory setae.

Maxilliped 2 (Fig. 2I).—Coxa naked. Basis with 3 plumodenticulate setae. Endopod 3-segmented, with 0,1,4 plumodenticulate setae. Incompletely bisegmented exopod with 4 terminal plumose natatory setae.

Maxilliped 3 (Fig. 2J).—Present as small biramous bud.

Pereiopods (Fig. 2J).—Present as small buds.

Abdomen (Fig. 2B).—Five somites. Somite 1 with pair of dorsal plumose setae, somites 2–5 each with pair of shorter sparsely plumose or simple setae. Short posterolateral spines on somites 3–5; somite 2 with pair of curved acicular (sensu Weber & Wear 1981) dorsolateral processes bearing spine-like terminal setal extension. Grouped denticulettes present. Pleopods absent.

Telson (Fig. 2B).—Bifurcated, shallow notch medially, 3 pairs of serrulate setae on inner margin; each furcal shaft proximally bearing lateral spine, furcal shafts and spines covered in rows of spinules to just below tips. Grouped denticulettes present.

Second zoea (Fig. 3)

Carapace (Fig. 3A).—Eyes mobile. Four additional pairs of simple or sparsely plumose setae, two pairs just above eyes, another two further dorsolaterally between dorsal spine and eyes. Lateral margin anteriorly to posteriorly with 5 plumose setae. Small lateral swelling dorsal to eyes.

Antennule (Fig. 3C).—With 6 long and 2 shorter aesthetascs and short seta; endopod absent.

Antenna (Fig. 3D).—Endopod bud enlarged to middle of protopodite.

Maxillule (Fig. 3E).—Basis with additional terminal plumodenticulate cuspidate seta and subterminal plumodenticulate seta; exopod pappose seta present.

Maxilla (Fig. 3F).—Distal lobe of basis with additional subterminal plumodenticulate seta. Scaphognathite with 20 marginal plumose setae.

Maxilliped 1 (Fig. 3A).—Exopod with 6 plumose natatory setae.

Maxilliped 2 (Fig. 3A).—Exopod with 6 plumose natatory setae.

Maxilliped 3 (Fig. 3G).—Present as a trilobate bud.

Pereiopods (Fig. 3G).—Longer, segmentation apparent, chela distinct; some specimens with invaginated setae and dactyl evident.

Abdomen (Fig. 3B).—Additional sixth somite. Somite 1 with 3 dorsal plumodenticulate setae. Somites 2–5 with pair of unsegmented biramous pleopods, endopods very small.

Megalopa (Figs. 4, 5)

Carapace (Fig. 4A).—Dorsally with median dromedary-shaped ridge flanked by short anterolateral spines; posteriorly a median spine; surface covered with many simple setae as shown, lateral margin with two clusters of sparsely plumose setae; area posterior to eyes laterally notched, posterior margin elevated middorsally.

Antennule (Fig. 4B).—Three-segmented peduncle with single simple seta on middle and distal segment; endopod with 1 subterminal and 2 terminal simple setae; three-segmented exopod with naked proximal segment, middle segment bearing 10–11 aesthetascs arranged in two tiers, and distal segment with 3–4 aesthetascs and 1 simple seta.

Antenna (Fig. 4C).—Segments 1–7, progressing proximally to distally, each with 1,2,3,0,0,4,4 simple setae, respectively; two

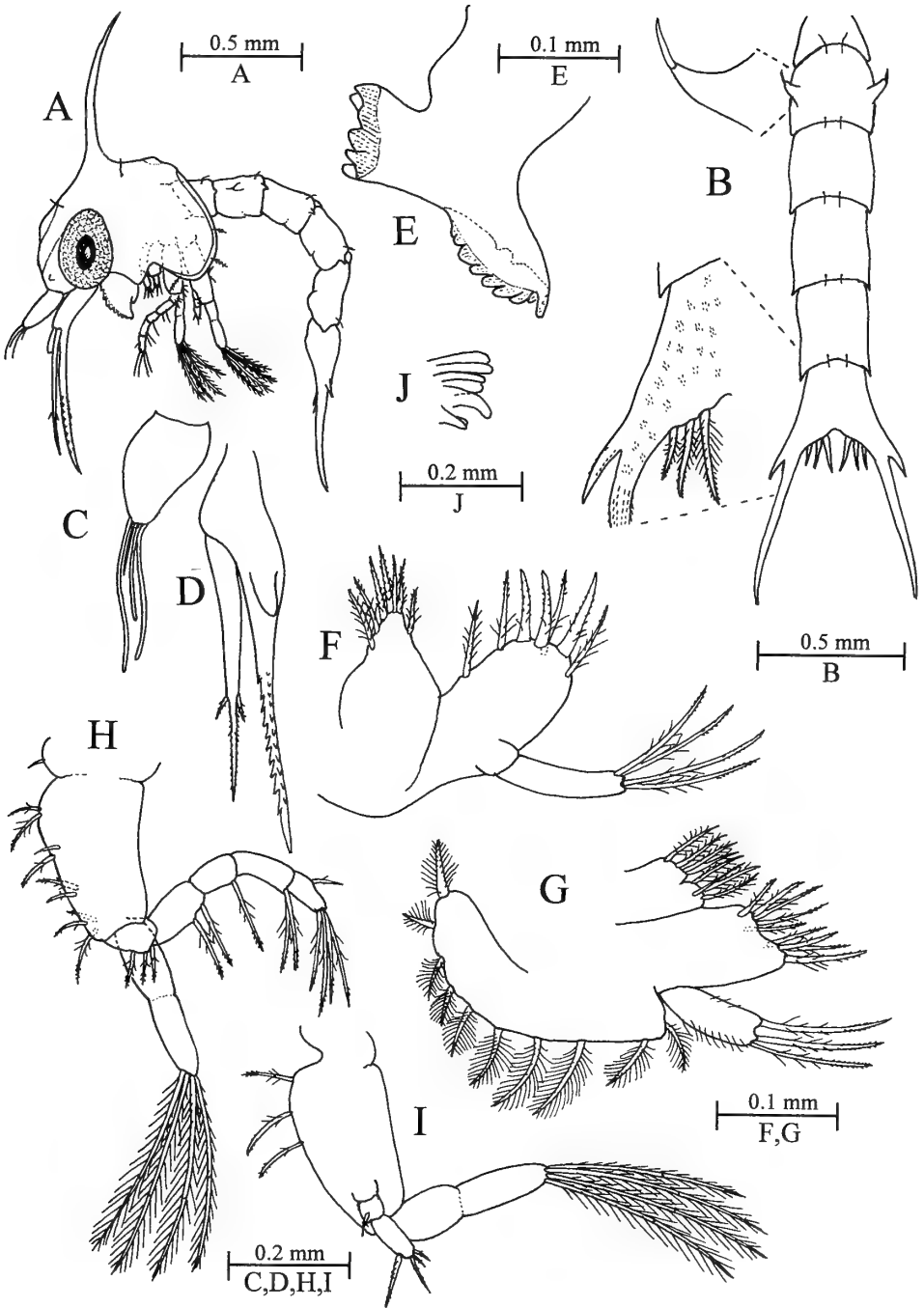


Fig. 2. First zoea of *Paradasygyius depressus* (Bell, 1835). A, lateral view; B, dorsal view of abdomen and telson, with enlargements of projection on somite 2 and proximal part of telson; C, antennule; D, antenna; E, mandible; F, maxillule; G, maxilla; H, maxilliped 1; I, maxilliped 2; J, developing maxilliped 3 and pereopods.

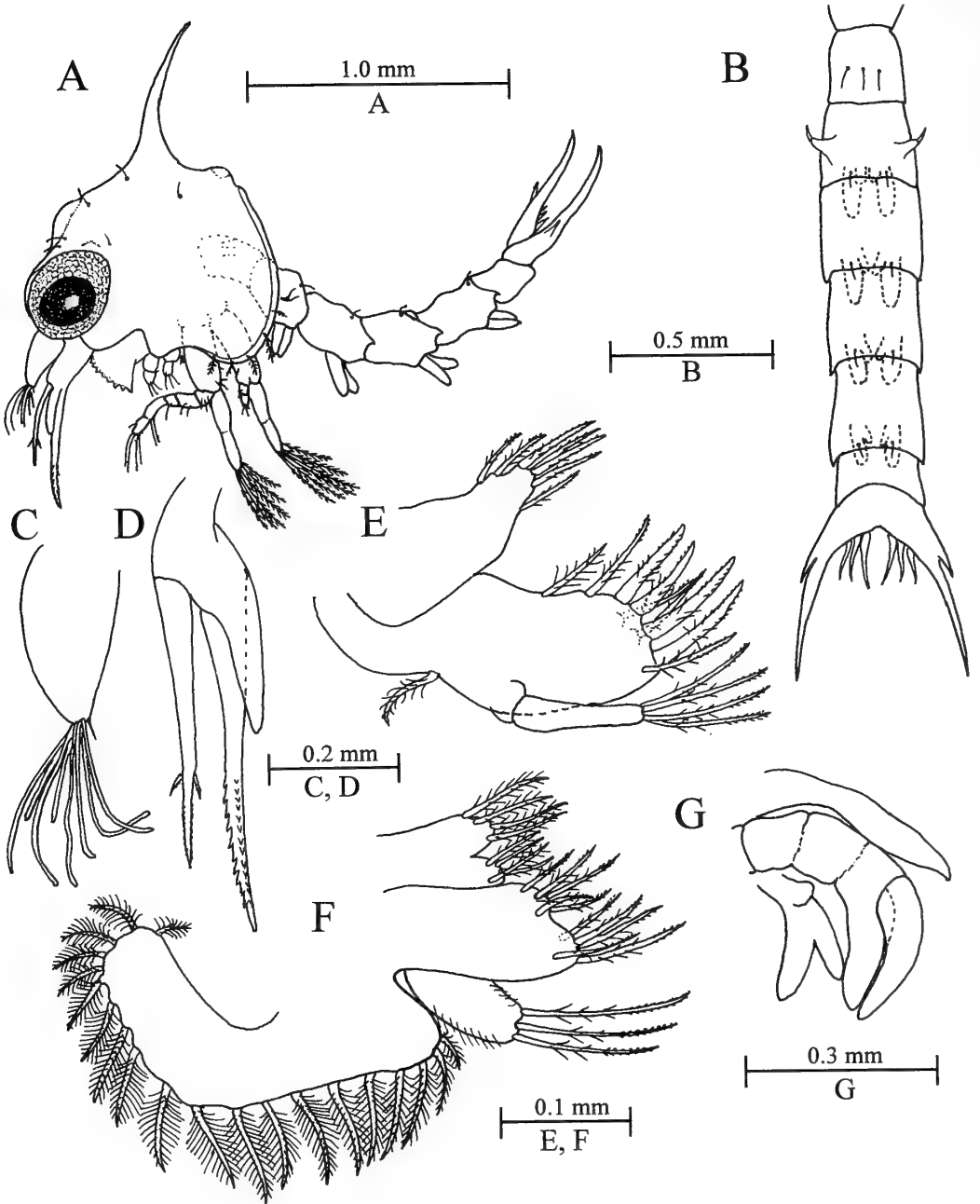


Fig. 3. Second zoea of *Paradasygius depressus* (Bell, 1835). A, lateral view; B, dorsal view of abdomen (ventral pleopod buds shown stippled) and telson; C, antennule; D, antenna; E, maxillule; F, maxilla; G, developing maxilliped 3, cheliped and pereopod 2.

terminal setae very long. Basal segment with exopod spine.

Mandible (Fig. 4D).—Scoop-shaped process with cutting edge and palp bearing 2–4 apical plumodenticulate setae and subterminal simple seta.

Maxillule (Fig. 4E).—Coxal endite with about 10 apical plumodenticulate setae and single exopod seta. Basial endite with 16–17 mostly plumodenticulate setae distal to endopodite and single exopod seta. Endopod setae reduced or lacking.

Maxilla (Fig. 4F).—Coxal endite proximal and distal lobes with 7 and 5 setae, respectively; basial endite with 6–7 setae on proximal lobe, 7 setae on distal lobe. Endopod reduced, may bear single distal seta. Scaphognathite with about 35 marginal plumose setae; blade with 4 simple setae.

Maxilliped 1 (Fig. 5A).—Coxal endite with about 6 setae, basial endite bearing about 12 setae; endopod with 1–2 setae; exopod with pappose seta distally on proximal segment and 4 plumose setae on distal segment; epipod with 3–4 plumodenticulate setae.

Maxilliped 2 (Fig. 5B).—Coxa and basis not clearly differentiated; endopod with indistinct basal segment, subsequent four segments proximally to distally with 0–1, 1, 3 and 4 plumodenticulate setae, respectively; exopod with naked proximal segment and 4 plumose setae on distal segment; epipodite not present on examined specimens.

Maxilliped 3 (Fig. 5C).—Coxa and basis not differentiated, with 4 plumodenticulate setae; endopodite proximally to distally with 13, 7–8, 5, 5 and 4 mostly plumodenticulate setae; ischium with crista dentata; bisegmented exopod with naked proximal segment and 4–5 reduced setae apically on distal segment; epipod with 1–2 plumodenticulate setae proximally and 3 distally.

Pereiopods (Fig. 5D–H).—Covered with mostly serrulate setae; coxa and ischium of pereiopods 1–5 with single spine, merus of cheliped with additional spine; dactyl of pereiopods 1–4 with spinules as shown.

Abdomen (Fig. 4A, 5I).—Dorsally and

laterally ornamented with mostly simple setae, proximally to distally with 3, 4, 4, 6, 6 and 2 setae. Five pairs of pleopods, exopod of pleopods 1–5 with 11, 11, 11, 9 and 2–3 plumose setae, respectively; endopod of pleopods 1–4 with 2–3 cincinnuli each, pleopod 5, i.e., uropod, lacking endopod.

Telson (Fig. 4A).—Rounded posteriorly, bearing a pair of dorsal setae

Phylogenetic analysis.—The phylogenetic analysis generated four equally parsimonious trees 173 steps long, with a consistency index of 0.66, retention index of 0.71, and rescaled consistency index of 0.47 (Fig. 6A–D). These trees and the strict consensus tree show that the data set was able to resolve most of the sister-group relationships (Fig. 7). The present analysis supports the monophyly of Oregoniinae, Majinae, and Inachinae (excluding *Macrocheira* incertae sedis). Our phylogenetic hypothesis places Oregoniinae as the most basal clade within the Majidae, and Majinae and Inachinae (excluding *Macrocheira*) form sister taxa. Within Inachinae, all trees suggested that *Inachus* and *Macropodia* are sister taxa nested as the most derived clade, followed by *Achaeus*, *Pyromaia*, *Paradasygyius*, *Anasimus*, and the most basal *Stenorhynchus*. The sister-group relationship of the clade (*Pisa* (*Taliepus* + *Libinia*), *Mithrax* and *Microphrys*) remained unresolved (Fig. 7).

Discussion

Paradasygyius depressus shares with other majids the presence of two zoeal stages, in which the first stage possesses nine or more marginal setae on the scaphognathite and the maxillule lacks an exopod seta; the second stage is characterized by well developed pleopods (Rice 1980, 1988). Some of these characters are thought to support the monophyly of this family (Rice 1983). However, although the monophyly of Majidae seems to be well supported, the sister-group relationships within the family remain uncertain (Rice 1980, Griffin & Tranter 1986, Clark & Webber 1991,

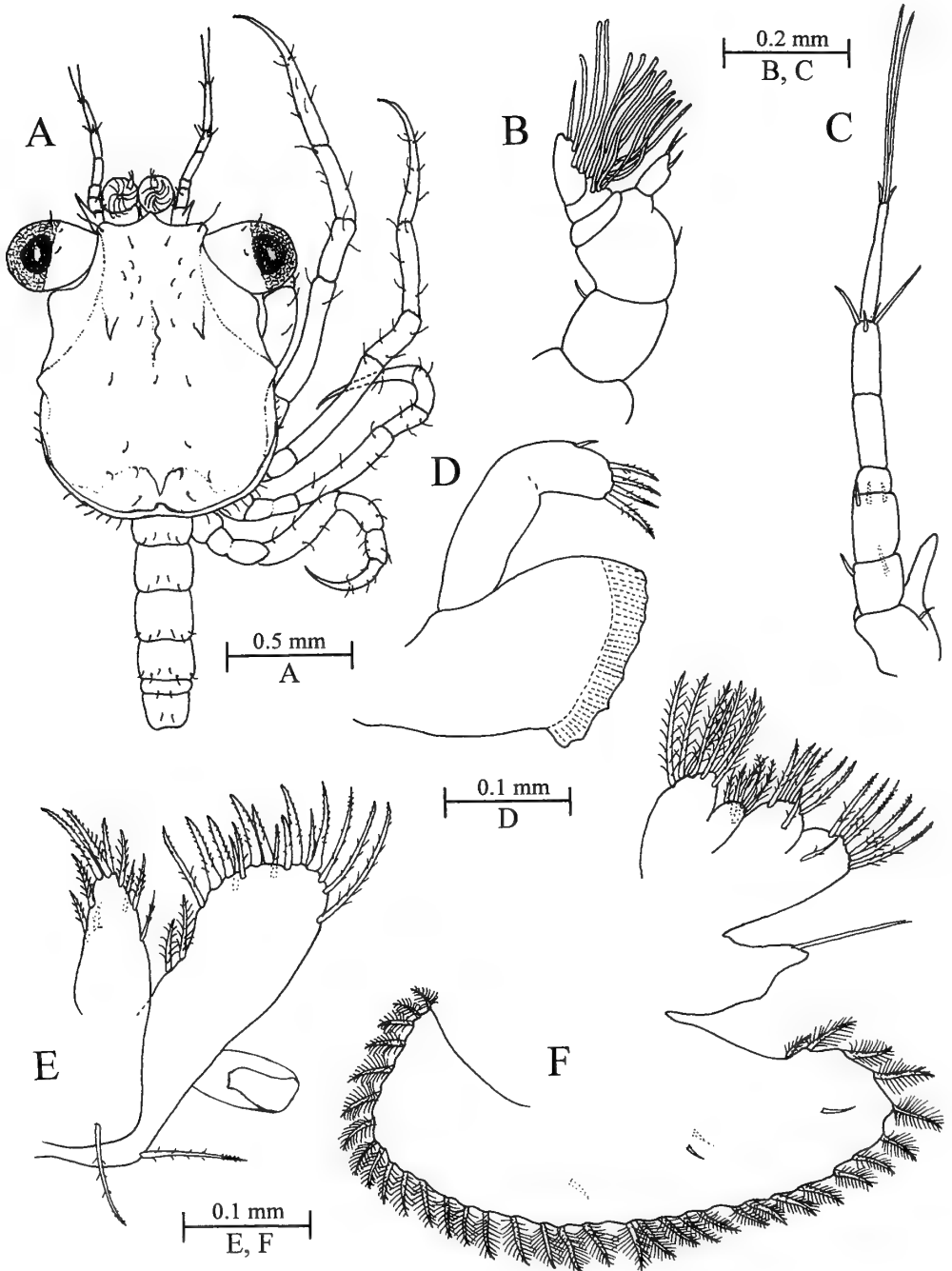


Fig. 4. Megalopa of *Paradasygius depressus* (Bell, 1835). A, dorsal view; B, antennule; C, antenna; D, mandible; E, maxillule; F, maxilla.

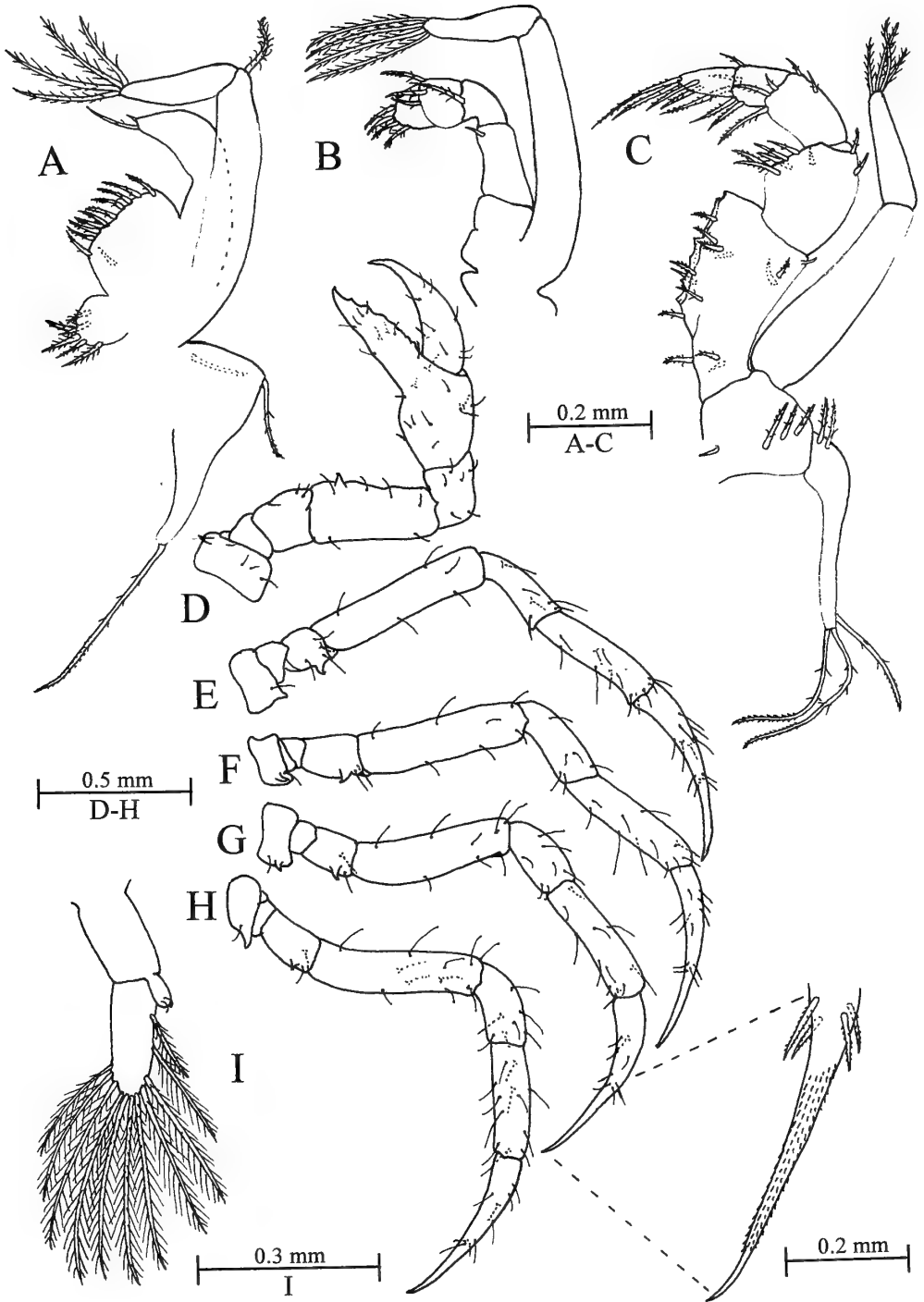


Fig. 5. Megalopa of *Paradasygyius depressus* (Bell, 1835). A, maxilliped 1; B, maxilliped 2; C, maxilliped 3; D, cheliped; E, pereiopod 2; F, pereiopod 3; G, pereiopod 4 with enlargement of distal part of dactyl; H, pereiopod 5; I, pleopod of third abdominal somite.

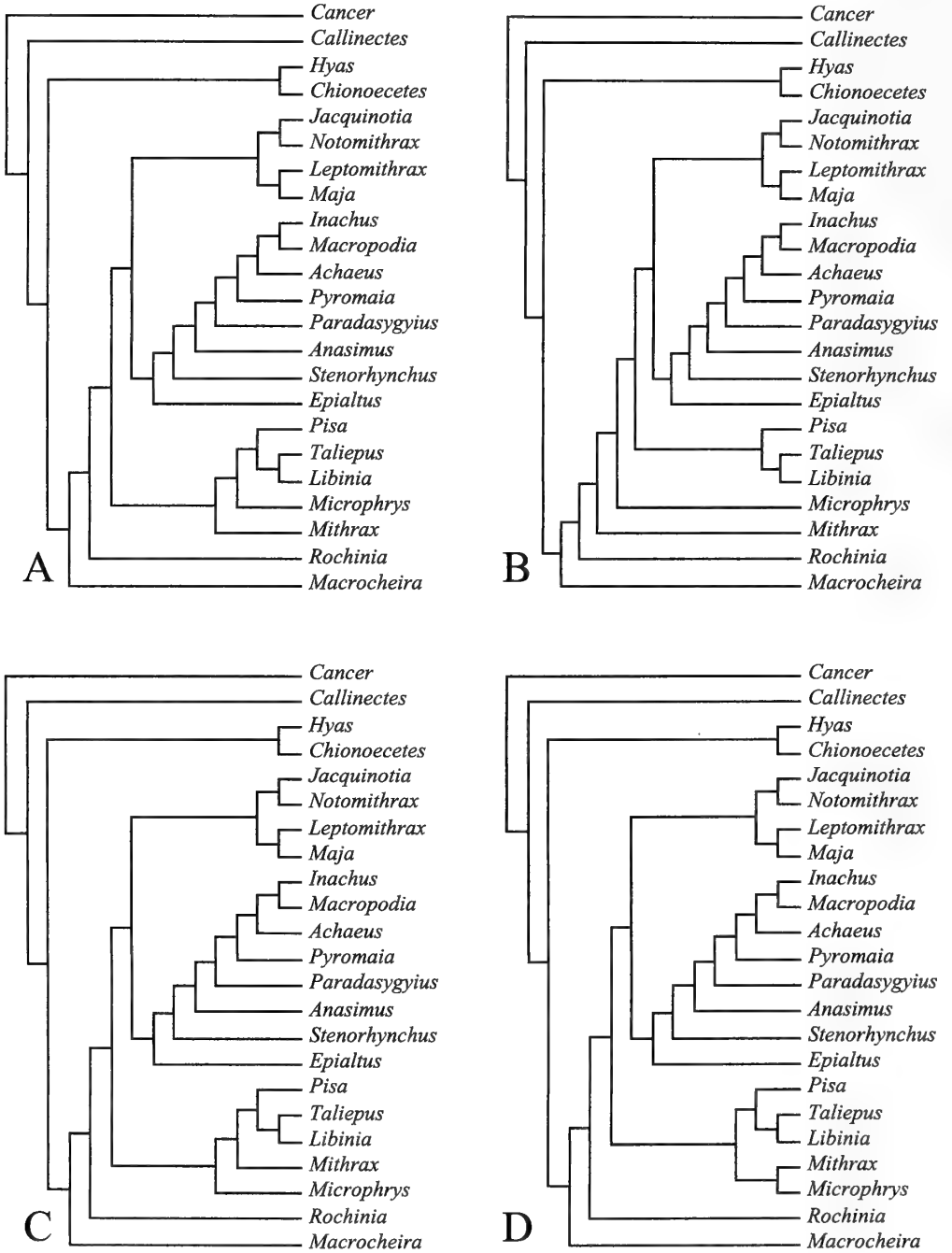


Fig. 6. Four most equally parsimonious trees depicting possible sister-group relationships of 21 majid genera based on 34 zoeal and three megalopal characters.

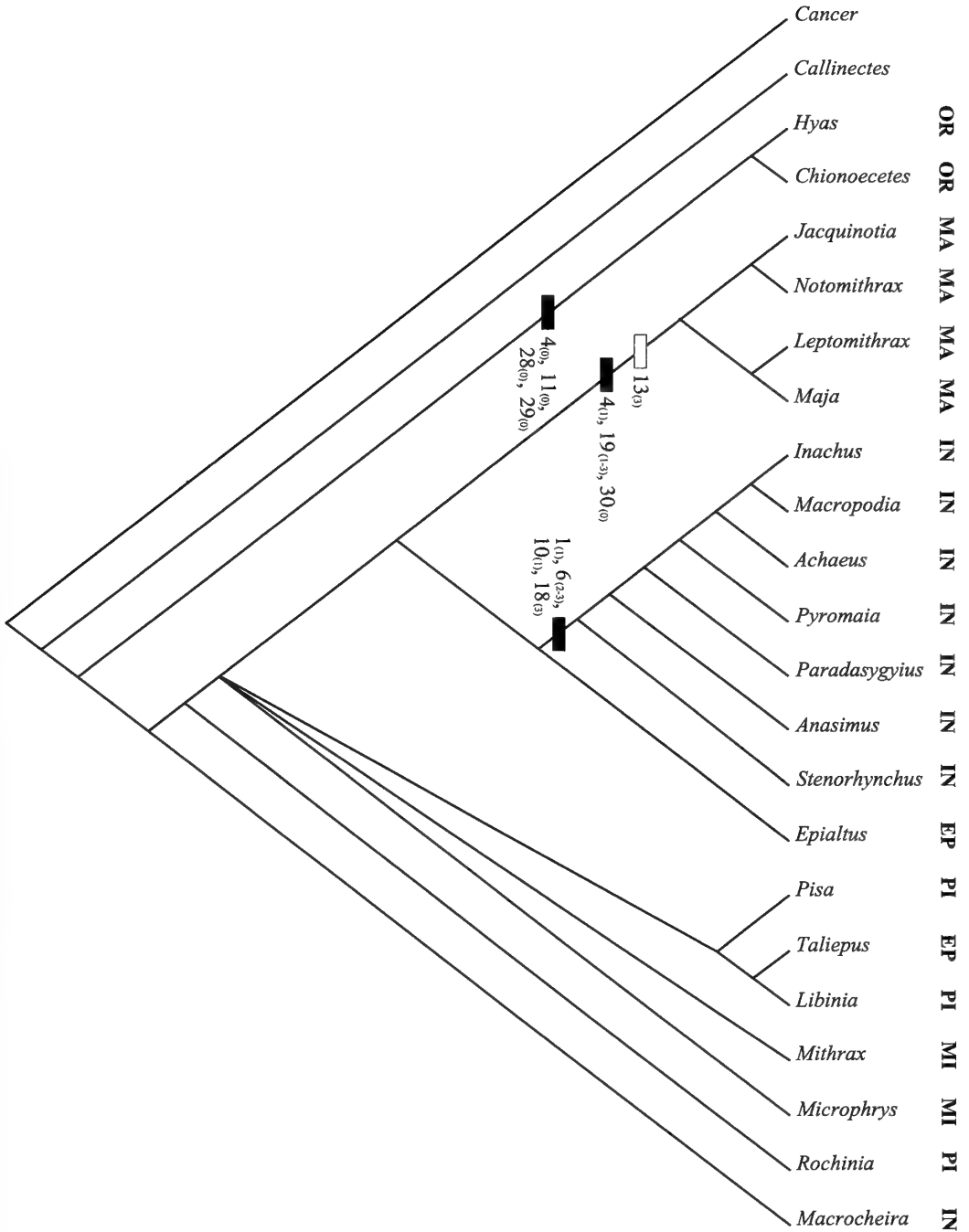


Fig. 7. Strict consensus tree of 4 equally parsimonious trees depicting hypothesized phylogenetic relationships of 21 majid genera based on 37 larval characters. Black rectangles represent character changes, open rectangles reversals. Large numbers represent a given character, small numbers enclosed within brackets represent a character state for a given character (see Marques & Pohle 1998 and materials and methods section of the present study for a detailed description of characters). EP, Epialtinae; IN, Inachinae, MA, Majinae; MI, Mithracinae; OR, Oregoniinae; PI, Pisinae.

Marques & Pohle 1998). Based on adult morphology, the family Majidae presently comprises eight subfamilies: Oregoniinae, Inachinae, Pisinae, Tychinae, Epialtinae, Mithracinae, Majinae, and Inachoidinae. However, most of these subfamilies lack larval synapomorphies to support their monophyly. Recently, Marques & Pohle (1998) found strong support for the monophyly of Inachinae, Majinae and Oregoniinae using zoal characters but not for the remaining subfamilies included in that study. This was corroborated in the present study by the addition of new taxa, stages and characters to the previous data base. Here we primarily discuss the sister-group relationships within Inachinae sensu lato, as most taxa added to the data matrix of Marques & Pohle (1998) belong to this subfamily.

The first attempt to resolve phylogenetic relationships within the Inachinae using larvae was proposed by Rice (1980), suggesting a semi-linear scheme of sister-group relationships. The establishment of these interrelationships were largely based on the assumption that evolution proceeds by oligomerization, where the loss of segments, spines, setae or other larval structures represent the derived condition (e.g., Rice 1980, 1981, 1983; Clark & Webber 1991). On this basis Rice considered *Macrocheira* as the most "primitive Inachinae" and the genera *Stenorhynchus*, *Pyromaia*, and *Anasimus* as intermediate to his "advanced Inachinae" consisting of *Inachus*, *Macropodia* and *Achaeus* (cf. Ingle 1982, Clark 1983, Paula 1987). *Stenorhynchus* (cf. Yang 1976) appeared to be a more derived inachine taxon compared to *Macrocheira* by lacking rostral and lateral carapace spines, having fewer spines on the telson fork, lacking subterminal setae on the distal endopod segment of the maxillule, and the setation of the carapace margin and endopod of maxilliped 2 being intermediate in nature (Table 2). Rice (1980) further postulated that larvae of *Pyromaia* (cf. Webber & Wear 1981, Fransozo & Negreiros-Franso-

zo 1997) and *Anasimus* (cf. Sandifer & Van Engel 1972) fall in between *Stenorhynchus* and the most derived taxa, *Inachus*, *Achaeus*, and *Macropodia*. Subsequent findings by Paula and Cartaxana (1991), based on larval evidence of *Stenorhynchus lanceolatus*, agreed with Rice's ranking of *Stenorhynchus*. However, they also suggested that the intermediate *Pyromaia* and *Anasimus* share some features that positions them closer to the advanced Inachinae.

Previous hypotheses of sister-group relationships among brachyuran larvae were largely based on the assumption that evolution proceeds by oligomerization, where the loss of larval structures represent the derived condition (Rice 1980, 1981, 1983; Clark & Webber 1991). However, Marques & Pohle (1998) showed that this assumption is not valid and that an analysis using outgroup comparison is preferable. For example, for taxa in the present study, zoeas of the most derived taxa *Inachus*, *Macropodia* and *Achaeus* share an ornamented posterolateral carapace margin (Ingle 1992). These structures are apparently absent in zoeas of the other, presumably more basal taxa discussed above. Similarly, the antennal exopod spine in the megalopa is absent in the basal *Macrocheira* and Oregoniinae but present in Inachinae. This violates the assumption that evolutionary events related to oligomerization processes are always derived within Majidae.

Marques & Pohle (1998) found that, among the inachines included in their analysis, *Paradasygyius* was the sister taxon of *Inachus*, while *Macrocheira* nested as the most basal taxon within Majidae, more closely related to Oregoniinae than to Inachinae. Rice (1980) had previously suggested that *Macrocheira* was the most "primitive Inachinae", but he considered the subfamily to be monophyletic. It was Clark & Webber (1991) who first suggested that *Macrocheira* should not be included within Inachinae. They contend that the presence of rostral and lateral carapace spines, more submarginal carapace setae,

the presence of a dorsal process on abdominal somite 3, very well developed postero-lateral abdominal spines, additional spines on the telson fork, subterminal setae on the distal endopodite segment of the maxillule, and more setae on the basis of maxilliped 1 and endopodite of maxilliped 2 were "ancestral zoeal features" that set *Macrocheira* apart from Inachinae. Indeed, *Macrocheira* shares most of these features with the basal Oregoniinae (Table 2). This is also corroborated by the megalopa of *Macrocheira* (cf. Tanase 1967), which resembles that of Oregoniinae in lacking an antennal exopod spine and fused flagellar articles on the antenna (Table 2). As for Clark & Webber (1991) and Marques & Pohle (1998), our study indicates that the inclusion of *Macrocheira* within Inachinae makes the subfamily paraphyletic. Thus, we consider *Macrocheira* as an *incertae sedis* taxon and hereafter reference to the subfamily Inachinae excludes *Macrocheira*.

Our data (Table 2) show that overall phenetic similarities of larval characters support in part the groupings proposed by Rice (1980). The "advanced Inachinae" can be recognized by having a zoeal posterolateral carapace margin ornamented with serrulations, no more than a single basal seta on maxilliped 2, and by the absence of a separated sixth abdominal somite in the second zoea. In addition, uropods are lacking in the megalopa of the "advanced Inachinae". In *Stenorhynchus*, the most basal Inachinae, the flagellar articles 2 and 3, and articles 4 and 5 of the megalopal antenna are not differentiated. *Paradasygyus*, *Anasimus* and *Pyromaia* differ from *Stenorhynchus* in having only fused articles 4 and 5. Thus the proposed groupings are also justifiable based on the overall similarities of zoeal and megalopal characters.

Drach & Guinot (1982, 1983) resurrected the family Inachoididae Dana, 1851, hereafter referred to as Inachoidinae, to include some American majids previously assigned to Inachinae and Pisinae, based on their distinct adult skeletal features. Subsequently,

Guinot & Richer de Forges (1997) suggested that the (i) absence of lateral and rostral spines on the carapace of zoeal stages, (ii) presence of ocular spines, (iii) presence of a pair of acicular processes on abdominal somite 2, (iv) presence of five abdominal somites in zoea I and six in zoea II, and (v) presence of simple pleopodal buds in zoea II comprised a set of larval character states found in *Anasimus* and *Pyromaia* (with the exception of character ii) that could justify the taxonomic status of Inachoidinae. Among the genera transferred to Inachoidinae, *Anasimus*, *Pyromaia*, and *Paradasygyus* were included in our study. Therefore we can provide an improved assessment of the larval support for the Inachoidinae.

Overall similarities of larval characters suggest that *Paradasygyus*, *Anasimus* and *Pyromaia* form a coherent phenetic group since they share a number of morphological larval features that set them apart from some taxa within Inachinae (Table 2). However, our study shows that most characters previously used to characterize groups within Inachinae constitute plesiomorphies. Therefore they are poor indicators of sister-group relationships. For instance, although the absence of dorsal processes on abdominal somite 3 distinguishes these three genera from *Stenorhynchus*, this state is also found in larvae of the "advanced Inachinae" (sensu Rice 1980, 1983). This character is a synapomorphy for all inachinids except *Stenorhynchus*, and thus does not support the monophyly of Inachoidinae.

The same problem of justifying the erection of Inachoidinae arises when examining the larval characters used by Guinot & Richer de Forges (1997). Our results showed that character (i), the loss of lateral spines, is a synapomorphy for a large clade that encompasses members of all subfamilies except Oregoniinae. Also, the loss of rostral spines is a synapomorphy for Inachinae including taxa assigned to the Inachoidinae (character 1_(i), Fig. 7). We found that the presence of a distinct pair of acic-

Table 2.—Comparison of larval characters of selected taxa representing, left to right, presumably derived Inachinae (*Inachus*, *Macropodia*, *Achaeus*), Inachoidinae (*Paradasyggius*, *Anasimus*, *Pyromaia*), intermediate Inachinae (*Stenothyrychus*), ancestral Inachinae (*Macrocheira*), and Oregoninae (*Hyas*, *Chionoecetes*), representing basal Majidae.

Taxon	Derived Inachinae	<i>Paradasyggius depressus</i>	<i>Anasimus latus</i>	<i>Pyromaia tuberculata</i>	Intermediate Inachinae	Ancestral Inachinae	Basal Majidae: Oregoninae
Sources	Clark 1983; Ingle 1982, 1992; Paula 1987	present study	Sandifer & Van Engel 1972	Franzoso & Negro-Franzoso 1997	Yang 1976	Clark & Webber 1991; Tanase 1967	Pohle 1991
Character							
Zoea:							
Carapace spines	dorsal only	dorsal only	dorsal only	dorsal only	dorsal only	dorsal, rostral, lateral	dorsal, rostral, lateral
Carapace spines	smooth	smooth	smooth	smooth	smooth	smooth	spinulose
Carapace post-tuberacle	absent?	present	none shown	indistinct	present	present	present
Posterolateral carapace margin	ornamented	smooth	smooth	smooth	smooth	smooth	smooth
Carapace margin	1-3 setae	3-4 setae	3 (+?) setae	3-4 setae	4-5 setae	8 setae	4-6 setae
Eye papilla or 'spine'	?	small	very distinct	small	present	?	present
Antenna 2 exopod setae	2, midpoint	2, 2/3 distance	2, 2/3 distance	2, midpoint	2, 2/3 distance	2, apically	2, apically
Maxillule endopod segment 1	unarmed	unarmed	unarmed	unarmed	unarmed	armed with seta	armed with seta
Maxillule endopod segment 2	3 (<i>Macropodia</i>) and 4 terminal setae	4 terminal setae	3 terminal setae	4 terminal setae	4 terminal setae	4 terminal setae	4 terminal setae
Maxillule endopod segment 2	no subterminal setae	no subterminal setae	no subterminal setae	no subterminal setae	no subterminal setae	with subterminal setae	with subterminal setae
Maxilliped 1 basis setation	2,2,2,3	2,2,2,3	2,2,2,3	2,2,2,3*	2,2,2,3	2,2,3,3	2,2,3,3
Maxilliped 2 basis	0 or 1 seta	3 setae	3 setae	3-4 setae**	3 setae	3 setae	4 setae
Maxilliped 2 endopod segments	3	3	3	2 or 3***	3	3	3
Maxilliped 2 endopod setation	0,0-1,4-5	0,1,4	0,1,4	1,4 or 0,1,4***	0,1,5	1,1,5	1,1,5

Table 2.—Continued.

Taxon	Derived Inachinae	<i>Paradasysyrius depressus</i>	<i>Anasimus latus</i>	<i>Pyromatia tuberculata</i>	Intermediate Inachinae	Ancestral Inachinae	Basal Majidae: Oregoninae
Abdomen somite 2	non-acicular curved processes	acicular curved processes	acicular curved processes	acicular curved processes	non-acicular curved processes	non-acicular curved processes	non-acicular curved processes
Abdomen somite 3	no dorsal processes	no dorsal processes	no dorsal processes	no dorsal processes	curved dorsal processes	curved dorsal processes	curved dorsal processes
Abdomen postero-lateral spines	well developed	small	small	absent	small	very well developed	very well developed
Abdomen somite 6, zoea 2	not separated	separated	separated	separated	separated	separated	separated
Zoea II endopod pleopod	?	very small	very small	?	?	small	small
Telson fork	1 spine	1 spine	1 spine	1 spine	1 spine	3 spines	2 spines
Megalopa							
Uropods	absent	present	present	present	present	present	present
Antenna exopod spine	present	present	present	absent	present	absent	absent
Antenna fused gellar articles	<i>Macropodia</i> : 2&3	4&5	4&5	4&5	2&3, 4&5	none	none
	<i>Inachus</i> , <i>Achaeus</i> : 2&3, 4&5						

* Webber & Wear (1981) illustrate 2.2.2.3 but state 2.2.2.2 in text, while Fransozo & Negreiros-Fransozo (1997) indicate 2.2.2.2 but now confirm 2.2.2.3 (in litt.);
 ** Fransozo & Negreiros-Fransozo (1997) indicate 4 setae, in litt. revealed 3-4 setae; *** discrepancy between Webber & Wear (1981) and Fransozo & Negreiros-Fransozo (1997), former claiming 2 segments with 1,4 setae, latter giving 3 segments with 0,1,4 setae.

ular curved processes on abdominal somite 2 (iii) could be a putative synapomorphy for the three genera included in Inachoidinae. However, this character did not hold as a synapomorphy for this group when the data were submitted to cladistic analysis. Our analysis suggested that an abdomen composed of five abdominal somites in zoea I and six somites in zoea II (iv) is plesiomorphic for the taxa included in Inachoidinae, since the absence of the 6th abdominal somite in zoea II supports the monophyly of (*Achaeus* (*Inachus* + *Macropodia*)). Finally, the presence of ocular papillae or spines (ii) and simple pleopodal buds in zoea II (v) should be considered in the phylogenetic analysis. However, we found that, among the taxa included herein, it was difficult to define the states of these characters since the taxa differed extensively in the degree of development of these structures or were inadequately described (Table 2).

The inclusion of additional taxa and characters in the matrix used by Marques & Pohle (1998) suggested that the phenetic agreement discussed above does not hold when the data is submitted to cladistic analysis (Figs. 5A–D, 7). Our phylogenetic hypothesis for 21 genera of Majidae supports Rice's (1980) contention that *Inachus*, *Macropodia*, and *Achaeus* are the most derived taxa within the subfamily Inachinae, and that *Pyromaia* and *Anasimus* are nested between the most derived taxa and the basal *Stenorhynchus* (Fig. 7). However, the inclusion of *Paradasygius*, whose larvae were unknown to Rice, suggested that *Pyromaia* is relatively more derived than *Anasimus* (Fig. 7) (contra Rice 1980). Finally, we found no larval evidence to support the monophyly of Inachoidinae despite the phenetic similarities discussed above for three genera presently included within this subfamily (contra Drach & Guinot 1982, 1983; Guinot & Forges 1997).

The most relevant aspect of the phylogenetic hypotheses presented herein is that within Majidae the subfamilies Oregoni-

inae, Majinae, and Inachinae can be defined by sets of larval synapomorphies (Fig. 7). The monophyly of Oregoniinae is supported by four characters: zoea I exopod of the antenna bearing a minute terminal spine, less than half the length of smaller apical seta ($4_{(0)}$); distal basal lobe of the maxilla in zoea I with five setae ($11_{(0)}$); mid-dorsal region of the fourth and fifth abdominal somites with paired setae in zoea II ($28_{(0)}$ – $29_{(0)}$). The subfamily Majinae is supported by the zoeal exopod of the antenna bearing a well developed terminal spine half or more the length of apical setae but not extending beyond the tip of setae ($4_{(1)}$); proximal coxal lobe of the maxilla in zoea II bearing three setae ($13_{(3)}$); scaphognathite bearing 21–28 setae in zoea II ($19_{(1-3)}$); and presence of three lateral spines on the fork of the telson ($30_{(0)}$). Finally, the subfamily Inachinae forms a monophyletic group based on the loss of a rostral carapace spine ($1_{(1)}$); presence of four or three setae on the distal portion of the endopodite of the maxillule ($6_{(2-3)}$); proximal coxal lobe of the maxilla in zoea I bearing four setae ($10_{(1)}$); and the scaphognathite bearing 11 setae in zoea I ($18_{(3)}$).

Our phylogenetic hypothesis showed no larval support for the monophyly of the subfamilies Epialtinae, Mithracinae, and Pisinae. Within Epialtinae, *Epialtus* nested basally to Inachinae, whereas, *Taliepus* nested as sister taxon of *Libinia*, member of Pisinae (Fig. 7). For the subfamily Mithracinae, represented by *Mithrax* and *Microphrys*, the analysis was unable to resolve the relationships between these taxa and other majids, since they nested in a polytomy with the clade (*Pisa* (*Taliepus* + *Libinia*)). However, one of the four most parsimonious trees suggested that *Mithrax* and *Microphrys* are sister taxa (Fig. 6D). Finally, there was no support to the monophyly of Pisinae since *Pisa* and *Rochinia* did not nest as sister taxa (Fig. 6) in any trees.

Three clades, including Oregoniinae, Inachinae, and Majinae, support the taxonomic arrangement based on adult morphology.

Although the taxonomy of Majidae is not based on a cladistic framework, the agreement between the larval phylogeny and adult taxonomy suggests that larval characters covary with adult morphology to the extent that both indicate, with a given degree of fidelity, the same nested groups. If that is true, the disagreement between the larval phylogeny and traditional taxonomy indicates that the adult characters used on the taxonomy of Epialtinae, Inachoidinae, Mithracinae, and Pisinae are poor indicators of sister-group relationships. Thus, some general recommendations can be drawn from our study. First, since larval information was useful to define nested sets, there is no reason to exclude larval data as diagnostic characters on any taxonomic level. However, because most of the characters supporting the monophyly of subfamilies are homoplastic, one cannot delimit these taxonomic groups on the basis of a single larval character. Instead sets of larval characters should be used in defining assemblages among Majidae or other Brachyura. Second, because no larval support was found for the monophyly of Epialtinae, Inachinoidinae, Mithracinae, and Pisinae, further evidence is required to resolve the taxonomic status of these groups. This can be achieved by re-examining adult characters and by using larval information of other genera to define these subfamilies within a phylogenetic framework. Finally, few megalopal characters have been used in phylogenetic analysis despite their high information content (Marques & Pohle 1995, Pohle & Marques 1998). This is mostly due to poor or lacking descriptions in the literature (Clark et al. 1998). If more attention is given to this larval stage by carcinologists working on larval descriptions, a higher number of megalopal characters can be analyzed cladistically to improve and/or test the monophyly of groups already established by zoeal and adult morphology.

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Appendix 1.—Input data matrix of 37 characters and 21 taxa of Majidae in NEXUS file format (Swofford 1998). Outgroups are the first two genera listed. Multistate characters are indicated by brackets and missing data as ?.

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[Pohle & Marques, phylogeny for 21 genera of Majidae]
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MATRIX
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Callinectes           00(01)?(01)0(03)2(03)210(03)(02)(02)014(06)1(01)010311111000(01)0(01)0
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Leptomithrax         0011001122113110222111001011101000???
Rochinia              0012000120100110122011112101121000012
Inachus               1113122121122112235121213111121101114
Macrocheira           0001000001102110000010000111101000001
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Pisa                  0112001110111111234010012011121?0001(23)
Taliepus              0112010110121112232111201001121000012
Notomithrax          011100212211311121311101211110100000(23)
Chionoecetes         000000011100200011(01)000102000010000001
Libinia               011201(01)1111121112(23)(45)011211001121000012
Mithrax               0112000120111111212011(12)11011121000012
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END;

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**Description of *Bermudacaris harti*, a new genus, and species
(Crustacea: Decapoda: Alpheidae) from anchialine caves of Bermuda**

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Abstract.—A new genus is proposed for an unusual new species of alpheid shrimp, *Bermudacaris harti*, inhabiting subterranean anchialine caves on the Bermuda Islands. This unique cavernicolous new species, has been confused with *Automate dolichognatha*, de Man, 1888, a species widely distributed in tropical marine shallow waters. The new genus shows some affinities with *Automate* de Man, 1888 and can be distinguished from the latter genus by several important features, such as subsymmetrical first chelipeds with dactylus in ventral position, and presence of appendix masculina in males. This new species is unusual among the Alpheidae in the considerable reduction of corneal pigmentation, especially in female, most likely an adaptation to the cave environment. The presence of few large eggs in the female suggests that the new species has low fecundity and abbreviated larval development, which might result from its troglobitic lifestyle. The relationships of the new genus to *Automate* are discussed in some detail. Presumably marine ancestors of this troglobitic species entered anchialine caves from neighboring shallow, marine waters.

In an important contribution to the knowledge of the cavernicolous caridean fauna of Bermuda Islands in the Western Atlantic Ocean, Hart & Manning (1981: 453, figs. 56–77) reported *Automate dolichognatha* de Man, 1888 from an anchialine cave near Tucker's Town. Hart & Manning reported two specimens, and included short comments on spinulation of pereopods, branchial formula and color. Although a full description of these specimens was not provided, the figures alone were sufficient to raise suspicions concerning their identity. Possibly, the two specimens were misidentified because *A. dolichognatha* had been previously reported from coastal waters of Bermuda by Markham & McDermott (1980, as *A. gardineri* Coutière). Holthuis (1993) used Hart & Manning's (1981) figures in his recent catalogue of caridean genera.

Automate dolichognatha is presently considered a widely distributed, pantropical species found in shallow marine waters, mainly on soft substrates (Chace 1972, 1988; Banner & Banner 1973, Manning & Chace 1990). Hart & Manning (1981) is the first and only report of a member of the genus *Automate* de Man, 1888 from caves, and the authors suggested that the Bermudan caves could be an "unusual anchialine habitat" for this species.

During a visit to the Smithsonian Institution, Washington, D.C. in 1999, the first author was able to examine the two specimens from Bermuda. A third specimen identified as *Automate dolichognatha*, an ovigerous female, was collected in 1982 in Christie's Cave, Bermuda. After comparisons of these three specimens with those reported as *Automate dolichognatha* from Ascension Island by Manning & Chace

(1990), and with several other specimens reported by Chace (1972, as *A. gardineri*), we have concluded, that the Bermuda specimens are not *A. dolichognatha*, but a new undescribed species having several important features which do not agree with the generic diagnosis of *Automate* de Man, 1888, as given by de Man (1888), Banner & Banner (1973) and Chace (1988). These three specimens could not be assigned to any genus in the Alpheidae, although the presence of the distinct cardiac notch and the robust first chelipeds clearly indicate that they belong to this family. Therefore, a new monotypic alpheid genus is established herein for this new species.

Material and Methods

Specimens were examined and dissected with the aid of binocular microscope and all original illustrations were made using a camera lucida. The material used in this study remains deposited in the National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM), and in the Muséum National d'Histoire Naturelle, Paris (MNHN).

Measurements of carapace length (CL) and total length (TL) are in millimeters. Other abbreviations used in the text: P = pereiopod, Mxp = maxilliped.

The following specimens were used for comparison: *Automate dolichognatha* de Man, 1888, Ascension Island, Atlantic Ocean (USNM 256773), Caribbean Sea (USNM 136069, reported as *A. gardineri* Coutière by Chace 1972), Madagascar (MNHN 4567, 4571); *Automate evermanni* Rathbun, 1901, Principe Island, Gulf of Guinea (MNHN 3450).

Family Alpheidae Rafinesque, 1815

Bermudacaris, new genus

Diagnosis.—Carapace slightly compressed laterally, smooth; rostrum developed as broadly rounded median projection; orbital teeth lacking; pterygostomial region

rounded. Eystalks subconical, anterior portion visible in dorsal and lateral views, corneal pigmentation reduced or absent. Mandible with normally developed incisor and molar processes, and with 2-segmented palp. Ultimate segment of third maxilliped distally armed with slender spines. First pereiopods subsymmetrical, equal in size, carried extended and elevated, with dactylus situated ventrally; chelae laterally compressed, without significant armature; adhesive discs and linea impressa absent. Second pereiopods with 5-segmented carpus, second article longest. Third pereiopods with dactylus simple, propodus armed with spines. Sixth abdominal segment without articulated plate. Second pleopods of male with appendix interna and appendix masculina. Telson distally truncated, with 2 pairs of spines on postero-lateral margin; anal tubercles absent. Branchial formula: pleurobranchs on P1-5, podobranch on Mxp2, arthrobranch on Mxp3, epipods on Mxp1-3 and P1-4, setobranchs on P1-5, exopods on Mxp1-3.

Type species.—*Bermudacaris harti*, new species.

Species included.—Only the type-species.

Etymology.—Generic name derived from the locality of collection, Bermuda Island, and the Greek *karis*, shrimp. Gender is feminine.

Bermudacaris harti, new species

Figs. 1-4

Automate dolichognatha—Hart & Manning, 1981:441, 453, figs. 56-77.—Holthuis, 1986:592; 1993:198, fig. 190 (in part.).—Manning & Hart, 1989:313.

Automate cf. dolichognatha—Iliffe, 1994:420.—Hobbs, 1994:98, 102 (not *Automate dolichognatha* de Man, 1888)

Material examined.—Holotype: ovigerous female (CL 3.9, TL 11.5), Bermuda Isl., Christie's Cave, 24 Oct 1982, coll. T. M. Iliffe, (specimen in excellent condition, not dissected, with both first pereiopods at-

tached) (USNM 250781). Paratypes: male (CL 2.9, TL 10), Bermuda Isl., Tucker's Town, Tucker's Town Cave, 15 May 1980, coll. W. Sterrer and T. M. Iliffe, about 12 m deep (USNM 184014); male (CL 3.6, TL 11), Bermuda Isl., Tucker's Town, Tucker's Town Cave, 26 Aug 1980, coll. T. M. Iliffe & C. W. Hart, about 12 m deep (USNM 184015).

Diagnosis.—Frontal margin lacking orbital teeth, with rounded, rostral projection; subconical eyestalks dorsally exposed, with reduced corneal pigmentation; first pereopods subequal in size and shape, with dactylus in inverted (ventral) position; articulated flap on sixth abdominal segment absent.

Description.—Holotype (Fig. 1a, b). Oviparous female carrying 3 large eggs (maximum size 1.3×1 mm). Carapace smooth, without setae or grooves. Anterior margin of carapace with short, broadly rounded, median rostral projection; orbital teeth lacking; infra-corneal angle only slightly protruding; pterygostomial angle rounded; ventral margin of carapace straight, without emarginations, not fringed with setae; posterior margin of carapace with well marked cardiac notch. Eyestalks subconical, enlarged at base, distal half visible in dorsal and lateral views; cornea reduced, without pigmentation (Fig. 1b). Ocellary beak not distinct.

Antennular peduncles somewhat flattened dorso-ventrally; second article slightly longer than first, and twice as long as third article; stylocerite distally acute, only slightly overreaching first antennular article, with statocyst well developed; ventral carina of first article represented by small acute tooth, situated on mesial margin proximal to second article; strong tooth protruding from base of first antennular article (only visible in ventro-lateral view); stylocerite and anterior margins of articles with conspicuous elongated setae; external flagellum not biramous, with fifth to tenth segments bearing 7 tufts of long aesthetascs. Carapocerite of antenna distinctly overreach-

ing antennular peduncle; scaphocerite broadly rounded anteriorly, with strong lateral spine reaching to about middle of carapocerite; basicerite with small ventral tooth.

Mouthparts not dissected (see paratype description). Third maxilliped reaching far beyond antennular peduncle when extended; exopod short (about 0.6 of length of antepenultimate segment); antepenultimate segment flattened proximally, slightly enlarged and thickened distally; ultimate segment triangular in cross-section, bearing approximately 12 semicircular rows of strong setae on mesio-ventral side, and several groups of spines on distal half of dorsal margin; coxa with blunt lateral plate, and slender strap-like epipod (mastigobranch); corresponding articulation surface of Mxp3 with small arthrobranch.

First pereopods subsymmetrical and almost equal in size, possibly carried elevated and slightly twisted mesially (Fig. 1a); superior margin of ischium with 3 distinct spinules curved anteriorly; merus triangular in section, not enlarged or excavated, with several small spinules on superior margin; distal margins of merus rounded, without acute teeth; carpus cup-shaped, with tiny spinules on dorsal margin; chela and carpus forming angle about 90° with merus and ischium; chela smooth, compressed laterally, palm as long as dactylus; dactylus situated in ventral position; both cutting edges unarmed, with exception of small irregular teeth proximal to dactylar articulation; fingers apically crossing when closed; superior margin of palm and fixed finger bearing conspicuous long setae.

Second pereopods very long and slender, reaching far beyond antennal peduncle when fully extended; merus and ischium elongated and slightly setose; carpus 5-segmented; second segment longest; proportions of carpal articles (from proximal to distal) approximately equal to 10:16:7:6:7; chelae slender, simple; dactylus slightly longer than palm; tufts of small setae present on both movable and fixed fingers.

Third to fifth pereopods slender, setose;

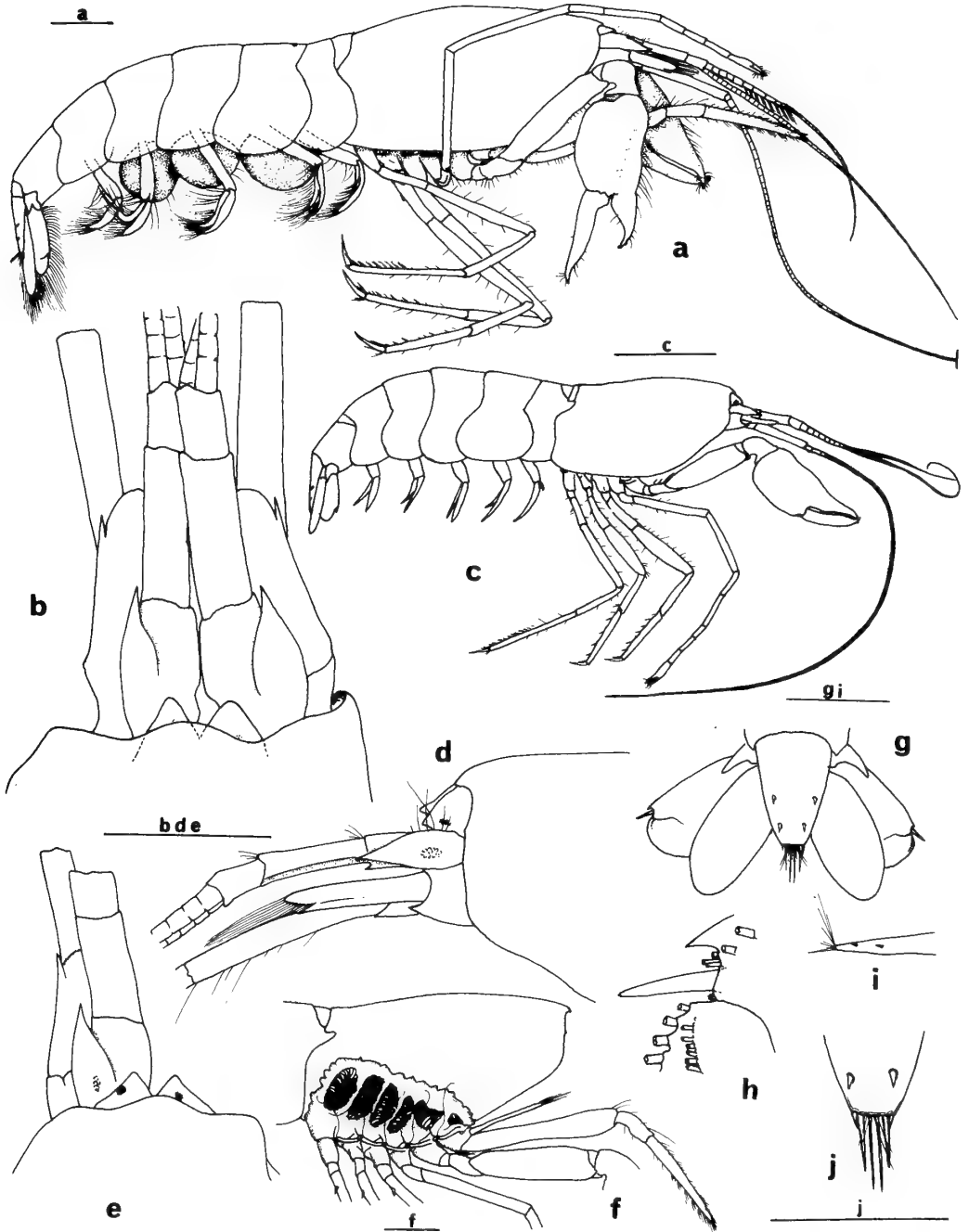


Fig. 1. *Bermudacaris harti*, new species, a, b, female holotype (USNM 250781). c–j, male paratype (USNM 184014). a, habitus with natural position of legs; b, frontal region in dorsal view; c, habitus; d, e, frontal region in lateral and dorsal views; f, gills; g, telson and uropods; h, detail of uropod diaeresis and lateral spine; i, telson, lateral view; j, same, detail of posterior margin. Scales: 1 mm, except for c (2 mm); fig. h without scale. Figs. c, f–i after Hart & Manning, 1981.

ischium with spine on inferior margin; carpus and merus unarmed; propodus of P3 and P4 armed with 6–8 spines on inferior margin, including a pair of slender apical spines proximal to dactylar articulation; propodus of P5 more slender, (about 1.5 times longer than propodus of P3), bearing only few spines and well-developed grooming brush, composed of about 10–12 tufts of long setae; dactylus of P3–5 slender, slightly curved, without trace of secondary unguis; coxae of P1–4 with strap-like epipods.

Abdominal segments rounded ventrally; sixth pleosomite without articulated flap at postero-ventral angle; margin of preanal plate slightly convex, not protruding. First pleopod with reduced endopod. Second to fifth pleopod each bearing long appendix interna, reaching distal margin of endopod. Uropods distinctly exceeding posterior margin of telson; protopod with acute outer tooth; exopod with diarsis slightly curved, ending in acute lateral tooth; lateral spine well developed; endopod without specific structures. Telson relatively broad, tapering distally, with 2 pairs of dorsal spines situated in its distal half, at some distance from lateral margin; posterior margin short, about 0.2 of telson length, almost straight, with 2 spines at each angle, inner spines about 3 times longer than outer, 1 median pair of very long thickened setae overreaching inner spines, and numerous more slender setae directed upwards. Branchial formula as given in generic diagnosis.

Paratypes (Figs. 1c–j, 2, 3, 4). Differ from holotype in external margin of eye-stalks bearing subapically a small but distinct pigmented area (Fig. 1d, e); infra-corneal angle of frontal margin of carapace, above basicerite, apparently more protruding (incorrectly figured as a small tooth by Hart & Manning 1981, fig. 58). Endopod of second male pleopod bears slender appendix interna and much shorter, stout appendix masculina, distally bearing strong setae (Fig. 2k).

Mouthparts (Fig. 4a–h) typical for Al-

pheidae. Mandible complete, with 2-segmented palp, well developed molar process, and robust incisor process distally bearing 5 strong teeth. Maxillula with bilobed palp, each lobe bearing 1 long plumose seta; inferior lacinia with dense cover of setae on distal portion (Fig. 4d) Maxilla bearing narrow scaphognathite fringed with short setae, deeply incised upper lacinia, and small palp. First maxilliped with slender palp bearing short setae on lateral margin; lower endite with several long plumose setae; exopod with rather feebly developed caridean lobe, fringed with plumose setae (Fig. 4g); epipod large and rounded. Second maxilliped without distinguishing characters; exopod elongated; epipod small, mesially with small rounded podobranch (Fig. 4i).

Remarks.—The specimen dissected and illustrated by Hart & Manning (USNM 184014) is in quite poor condition having the frontal and anteroventral regions seriously damaged, and most legs detached. The maxilla and the second maxilliped appear to be missing. To verify Hart & Manning's figures, the mouthparts have been dissected and partly illustrated from another paratype (USNM 184015) in much better condition.

Two additional specimens collected in the caves of Bermuda Island belong to the new species (field notes by T. M. Iliffe), but could not be located in the collections of the USNM. These are not treated as paratypes: 1 ovigerous female, CL 4.5 (with 4 eggs, 1×1.7 mm), Green Bay Cave, New Harrington Sound Passage, 27 Aug 1981, coll D. Williams, caught by hand while swimming in mid-water about 15 m deep. 1 female, CL 4.4, Bat Cave, Government Quarry, 12 December 1981, silt substrate at 22.5 m., coll T. M. Iliffe, by hand, water anoxic between 1 and 10 m, together with *Typhlatya* sp. (not collected) at 10–20 m.

Color in life.—Uniformly whitish, lacking any other color (Hart & Manning 1981). Eggs yellow when collected but brownish after preservation in alcohol.

Etymology.—After Charles Willard Hart

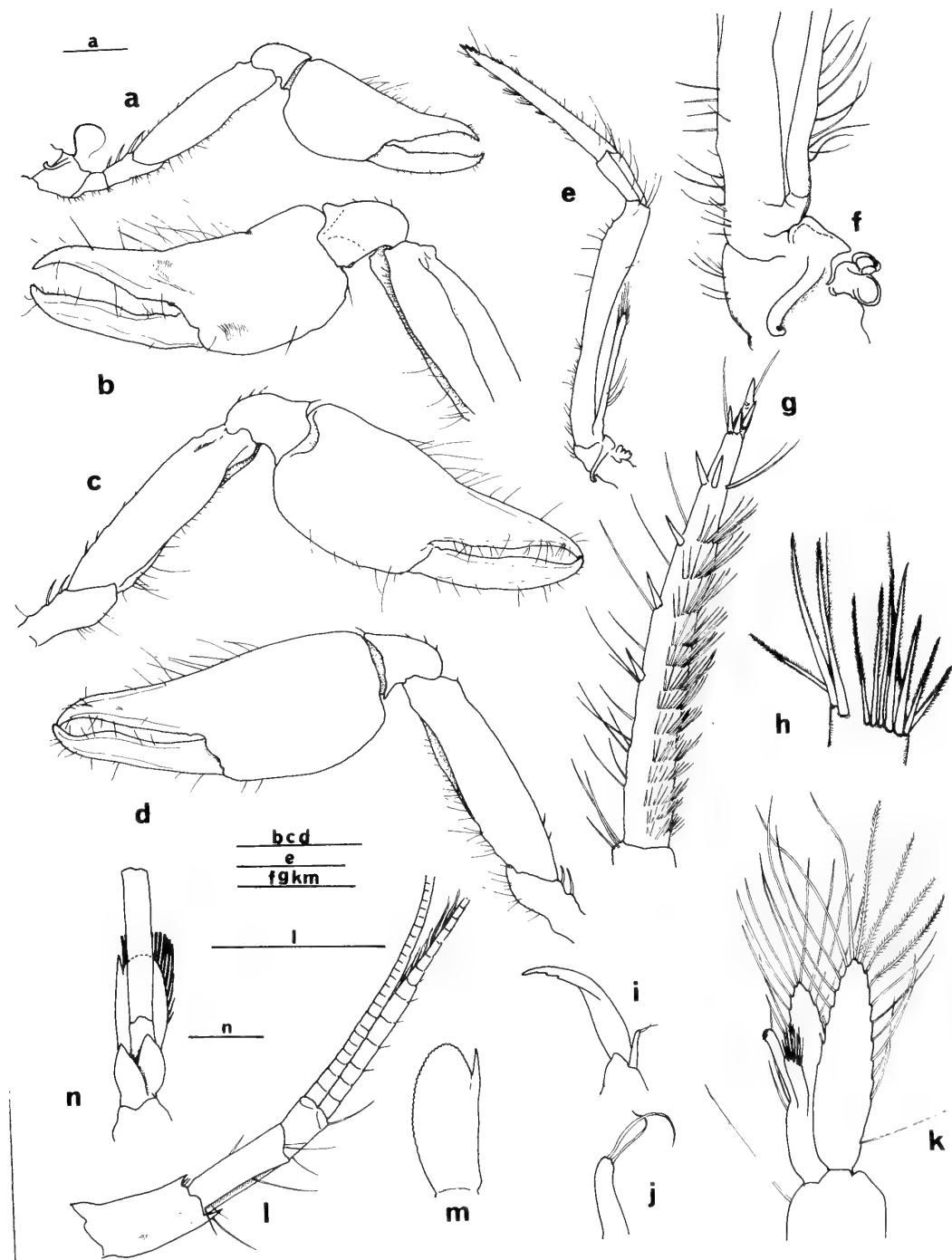


Fig. 2. *Bermudacaris harti*, new species, a–e, h–j, l–n, paratype (USNM 184014); f, g, k, paratype (USNM 184015). a, right first pereiopod, external view; b, same, detail of right chela and carpus, mesial view; c, d, left first pereiopod, inner and outer views; e, third maxilliped; f, same, detail of proximal region; g, h, same, details of ultimate segment; i, first pleopod; j, same, detail of endopod; k, second pleopod; l, antennule, inner view; m, scaphocerite; n, antennal peduncle, ventral view. Scales: 1 mm, except figs. f, g, k, m (0.5 mm); figs. h–j without scale. (Figs. a, h–j after Hart & Manning, 1981).

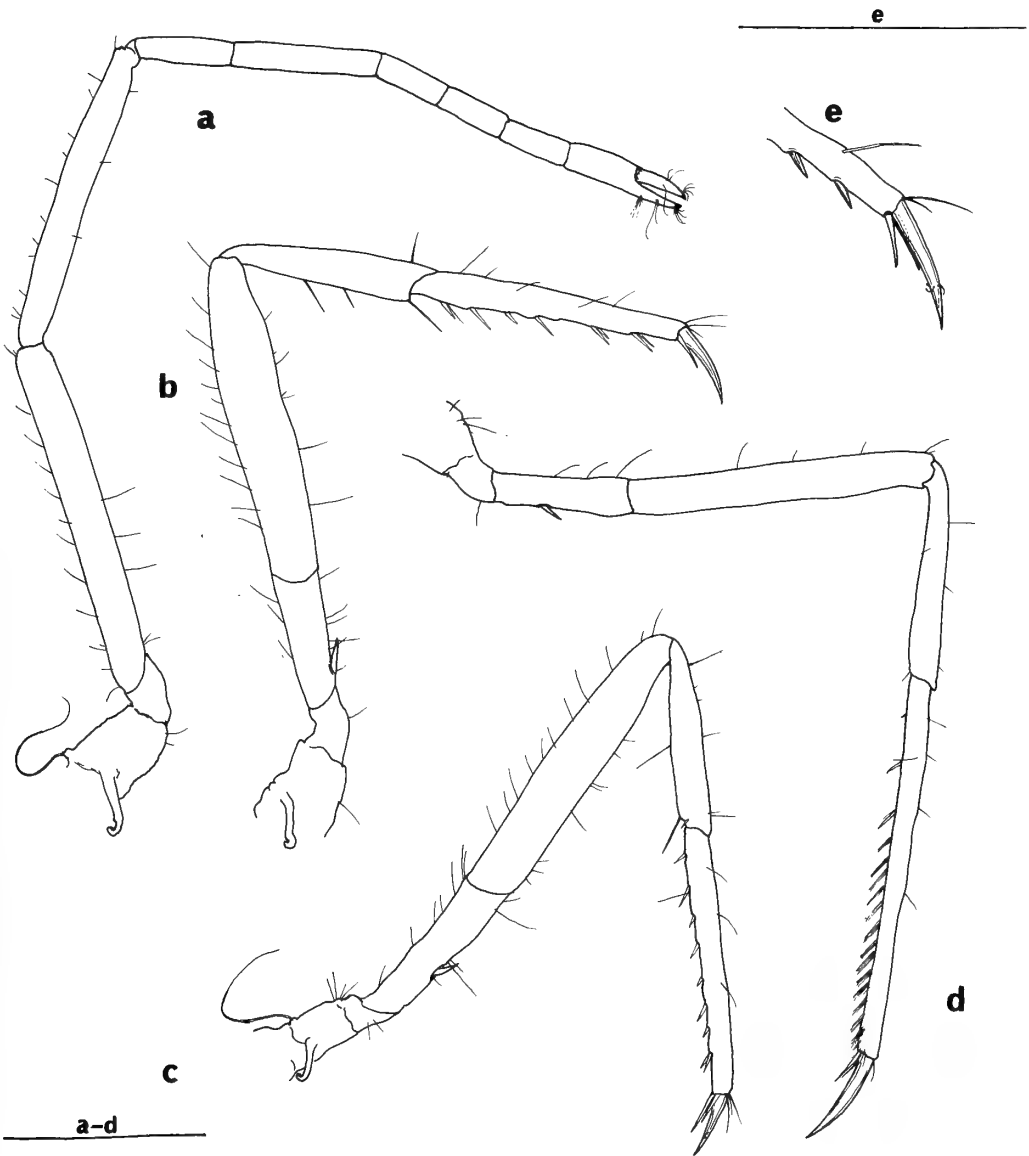


Fig. 3. *Bermudacaris harti*, new species, paratype (USNM 184014). a, second pereiopod; b, third pereiopod; c, fourth pereiopod; d, fifth pereiopod; e, detail of apical part of propodus and dactylus of third pereiopod. Scales: 1 mm.

Jr., retired USNM curator, in recognition of his research on the decapod fauna of Bermudan caves, and who also collected the holotype.

Habitat.—More than 90 anchialine caves are known from Bermuda, most of which are clustered in the area between Castle Harbour and Harrington Sound. They con-

sist primarily of inland limestone caves that extend down to sea level and contain tidally influenced brackish pools. More or less extensive networks of underwater cave passages often interconnect these otherwise seemingly isolated cave pools. An exceedingly rich and diverse troglobitic fauna inhabits these caves, including more than 50

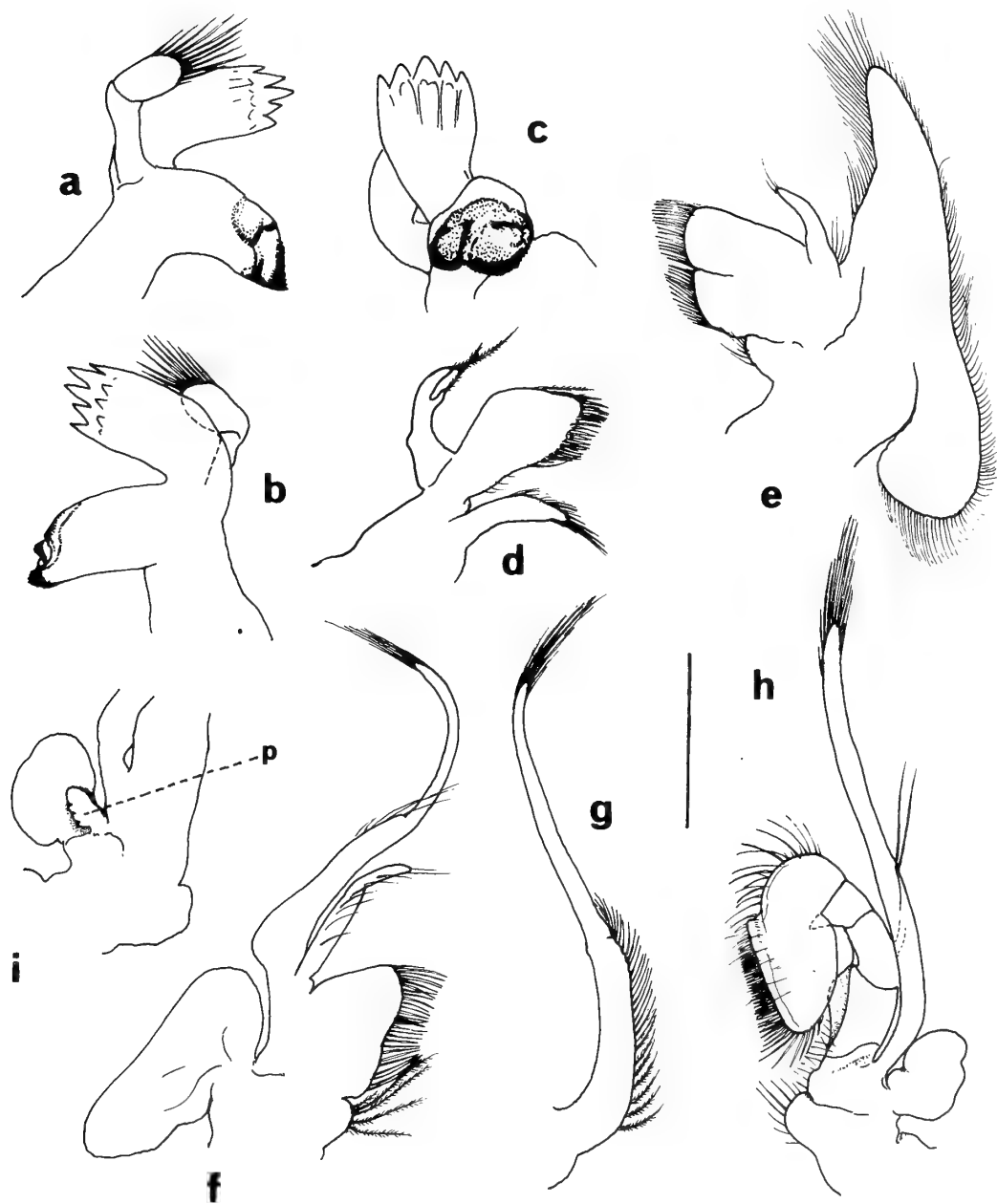


Fig. 4. *Bermudacaris harti*, new species, a–d, f, paratype (USNM 184014); e, g–i, paratype (USNM 184015). a–c, mandible, d, maxillula; e, maxilla; f, first maxilliped; g, same, detail of exopod; h, second maxilliped; i, same in mesial view, detail of podobranch. Scales: 0.5 mm.

endemic species (Sket & Iliffe 1980, Iliffe et al. 1983, Iliffe 1994).

Bermudacaris harti has been found in four caves, all located in the northeastern part of the main island of Bermuda (Fig. 6).

The extensive descriptions of the caves of Bermuda may be found in Kornicker & Iliffe (1989), and Iliffe (1993). Tuckers Town Cave is an isolated cave located on the Tuckers Town peninsula between Castle

Harbour and the South Shore of Bermuda. The cave is entered by way of a 13 m deep vertical shaft that opens into a dimly illuminated, sea level pool measuring 12 by 18 m. The sand-bottom pool slopes steeply down to a large, completely submerged cavern in total darkness with depths to 21 m. This cavern is about 80 m long by 20 m wide, and 10 m high. In October 1981, salinity in the pool was 22.7‰ at the surface, 27.5‰ at 1 m, 34.3‰ at 10 m and 35.5‰ at 21 m. Temperature increased with depth, from 17.8°C at the surface to 21.5°C at 21 m, while dissolved oxygen decreased from 6.11 ml/l at the surface to 2.97 at 21 m. Tides in the cave occur 58 minutes later than tides in the open ocean, and with an amplitude 62% that of open ocean tides. Specimens of *Bermudacaris harti* were collected at about 15 m depth. Other notable troglobitic species in this cave include the shrimps *Typhlatya iliffei* Hart & Manning, 1981, *Barbouria cubensis* (Von Martens, 1872) and *Parhippolyte sterreri* (Hart & Manning, 1981), the mictacean *Mictocaris halope* Bowman & Iliffe, 1985, the halocyprid ostracods *Spelaeoecia bermudensis* Angel & Iliffe, 1987, *Micropolycope styx* Kornicker & Iliffe, 1989 and *Polycopissa anax* Kornicker & Iliffe, 1989, and the calanoid copepod *Enantiosis* sp.

Christie's Cave is located just 30 m from the edge of Castle Harbour. The cave contains a clear 8 m-deep pool just inside a collapsed entrance. No cave passages were found extending away from the pool. In October 1983, surface salinity in the pool was 6.9‰, increasing to 19.5‰ at 1 m. Surface water temperature was 18.2°C, increasing to 20.4°C at 1 m. A *Bermudacaris harti* specimen was collected from the bottom in 8 m depth. Other troglobitic species from this cave include the archiannelid polychaete *Nerilla* sp.; the calanoid copepods *Erebo-nectes nesioticus* Fosshagen & Iliffe, 1985 and *Exumella* sp., and the halocyprid ostracods *Spelaeoecia bermudensis* and *Polycopissa anax*.

Bat Cave (Government Quarry Cave) is

also located along the shoreline of Castle Harbour. The cave was uncovered during quarrying operations in the 1960's. It contained two pools reaching depths of at least 23 m. In December 1981, salinity in the pool was 6.5‰ at the surface, 23.0‰ at 1 m, 35.2‰ at 10 m and 35.7‰ at 19 m. Surface water temperature was 19.1°C, increasing to 21.2°C at 19 m. A specimen of *Bermudacaris harti* was collected in 15–20 m depths, below a layer of polluted, anoxic water. Other troglobitic species from this cave include the shrimp *Typhlatya iliffei*. In 1980, rubbish was bulldozed into one of the cave pools, grossly polluting the water (Iliffe et al. 1984). The cave was completely destroyed by quarrying in the mid 1980's.

Green Bay Cave is the longest cave in Bermuda with more than 2 km of explorer underwater passageways. The cave is located on the peninsula separating Harrington Sound from the North Lagoon. It has two entrances, one at the end of Green Bay on Harrington Sound, and another, an inland sinkhole, known as Cliff Pool. Average depth in the cave is 18 m. In March 1982, salinity in the Cliff Pool entrance was 21.3‰ at the surface, 27.3‰ at 1 m, 36.2‰ at 10 m and 36.3‰ at 18 m. Surface water temperature was 20.0°C, decreasing to 18.7°C at 18 m. A specimen of *Bermudacaris harti* was collected at mid water in 15 m depth from a more hydrologically isolated section of the cave. Other troglobitic species from this cave include the unique shrimp *Procaris chacei* Hart & Manning, 1986; the halocyprid ostracod *Spelaeoecia bermudensis*; and the mictacean *Mictocaris halope*.

Interestingly, two other alpheids have been found in the Green Bay Cave system, but to our knowledge this data has never been published. These are: *Synalpheus* cf. *sanctithomae* Coutière, 1909 (juvenile specimen, CL 3.0, in "yellow sponge"), and *Alpheus* cf. *normanni* Kingsley, 1878 (small male, CL 3.5).

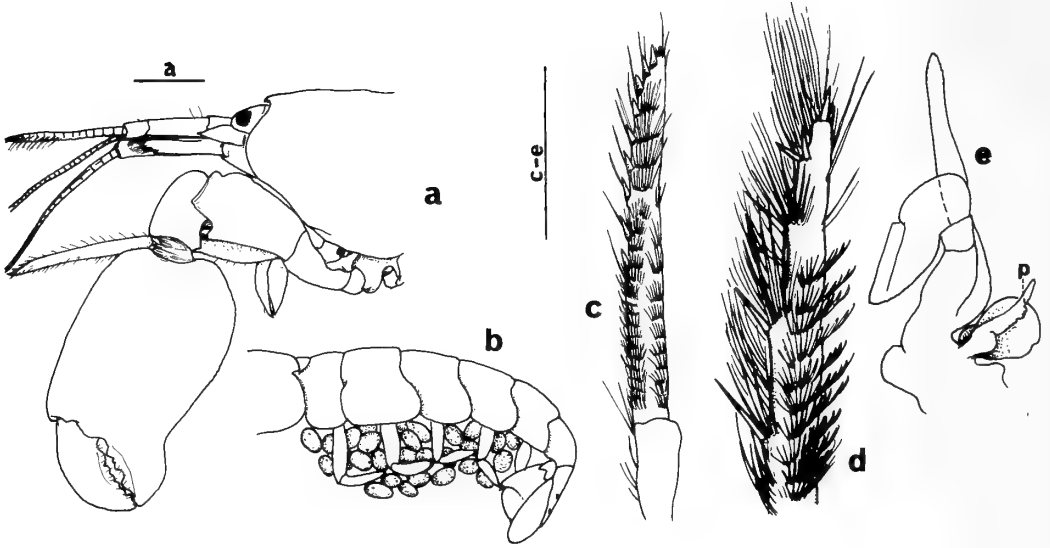


Fig. 5. *Automate dolichognatha* de Man, 1888 (a–c) and *A. evermanni* Rathbun, 1901 (d, e). a, anterior region of *A. dolichognatha* from Ascension Isl. (female, USNM 256773); b, abdomen of ovigerous female of *A. dolichognatha*, probably from Djibouti (after Coutière, 1899, without scale); c, d, details of ultimate segment of third maxilliped of *A. dolichognatha* from Madagascar (MNHN 4571) and *A. evermanni* from Gulf of Guinea (MNHN 3450); e, second maxilliped of *A. evermanni* in mesial view, detail of podobranch (MNHN 3450). Scales: 1 mm.

Discussion

The new genus *Bermudacaris* shares several characters with *Automate* de Man, 1888. In both, the frontal region is similar, with partly exposed parallel eyestalks; the exopod of Mxp3 is short (only slightly overreaching distal half of penultimate segment); the spines on superior margin of ultimate segment of Mxp3 are present; the second pereopod is elongated and has similar proportions of carpal articles; and there is no deep bifurcation on the external flagellum of the antennule. Other features common to these two genera are also shared by numerous other, not closely related alpheid genera.

Using the most recent key of alpheid genera (Holthuis 1993), *Bermudacaris* would key out to *Automate*, but the new genus differs from *Automate* in several important points, notably those concerning first chelipeds and appendix masculina. The first chelipeds of *Bermudacaris* are unique within Alpheidae. In both sexes they are not

especially enlarged, carried extended, elevated, and are almost symmetrical. The merus is slender, the chela rather slim, the cutting edges of both fingers unarmed, and the dactylus is situated clearly in ventral position (Figs. 1c, 2b–d). In contrast to *Bermudacaris*, all species of *Automate* possess asymmetrical and unequal first chelipeds (Fig. 5a), with major cheliped bearing enlarged, rounded or rectangular palm, dactylus always situated in dorsal position, cutting edges of fingers usually armed with large teeth (Fig. 5a), and stout, ventrally excavated merus.

The presence of appendix masculina in male specimens of *Bermudacaris harti* and its absence in all males of species of *Automate* (Coutière 1899, D. M. & A. H. Banner 1973, pers. obs.) is another feature useful for the separation of the two genera. Assuming that the presence of an appendix masculina is a plesiomorphic state for Alpheidae, and for all Caridea, its absence in *Automate* can be explained by a secondary loss.

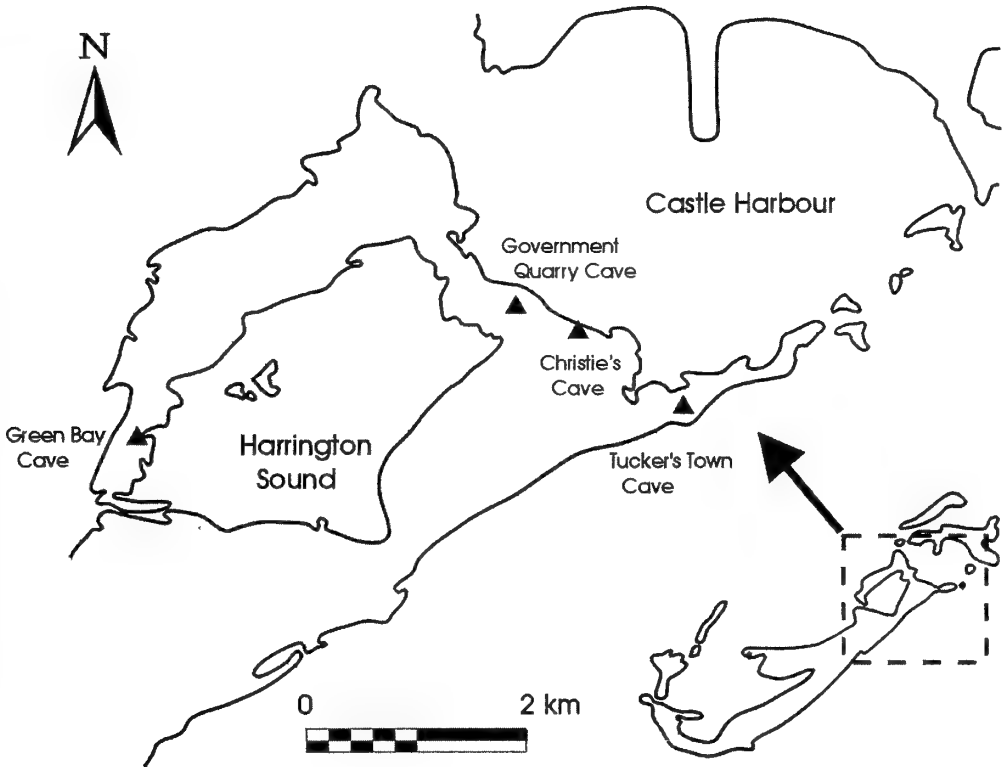


Fig. 6. Map of Bermuda Island showing the locations of caves: Tucker's Town, Christie's, Government Quarry and Green Bay Caves.

Other, less striking points of difference between the new genus and *Automate* are: shape of frontal margin not emarginate in *Bermudacaris* vs. broadly emarginate in *Automate*; shape of eyestalks subconical, not juxtaposed in *Bermudacaris* vs. more or less cylindrical, parallel and juxtaposed mesially in *Automate*; eyes depigmented or with reduced pigmentation in *Bermudacaris* vs. well-pigmented in *Automate* (Fig. 5a); small acute antennular carina present in *Bermudacaris* vs. absent in all species of *Automate*; third to fifth pereopods slender in *Bermudacaris* vs. robust in *Automate*; ischium of fifth leg with small spine in *Bermudacaris* vs. unarmed in *Automate*; few (3 or 4), very large eggs in female of *Bermudacaris* vs. numerous, small eggs (0.3×0.5 mm, Bhuti et al. 1977, Coutière 1899, see fig. 5b, pers. obs.) in females of *Auto-*

mate dolichognatha; pleosomites relatively well developed and more rounded, partially covering large eggs in female of *Bermudacaris* vs. pleosomites weakly developed in females of *Automate* (Figs. 1a, c, 5b). For all the reasons cited above, the new species could not be assigned to *Automate* without significant changes in the diagnosis of this genus.

The observed difference between the female and the males in the pigmentation of eyes is highly unusual for alpheid and possibly for all caridean shrimps. In the holotypic female of *Bermudacaris* almost no pigmented area is apparent on the eyestalks (Fig. 1b), while both paratypic males present a small, but distinct black spot proximal to the anterior margin (Fig. 1e). With only one female specimen, it would be speculative to suggest a sexual dimorphism

in pigmentation of cornea, and more specimens of both sexes are needed to investigate further this interesting feature.

Bermudacaris harti has a small podobranch inserted near the base of the epipod of the second maxilliped. This podobranch was not illustrated by Hart & Manning (1981: 454, fig. 66), but its existence has been noted in the branchial formula. It is generally absent in all members of the family Alpheidae, but its presence has been shown in many Hippolytidae (Coutière 1899). Within Alpheidae a podobranch has been observed in *Automate branchialis* Holthuis & Gottlieb, 1958, *A. rugosa* Coutière, 1902 (see Wicksten 1981), *A. anacanthopus* de Man, 1910, *A. rectifrons* Chace, 1972, and *A. evermanni* Rathbun, 1901 (Fig. 5e), in which it is particularly well developed and acutely produced; the podobranch has not been observed in *A. dolichognatha* and is also lacking in *A. salomoni* Coutière, 1908. The presence of this podobranch could indicate a closer relationship of the new genus to species showing this structure, or in general to the genus *Automate*.

The ultimate segment of the third maxilliped of *Bermudacaris harti*, new species, bears numerous rows of thick setae on its ventral side (Fig. 2h), and strong spines along its superior margin (Fig. 2g). Similar spines are found in *Automate dolichognatha* (Fig. 5c), *A. evermanni* (Fig. 5d), *A. branchialis* (Holthuis & Gottlieb 1958), *A. anacanthopus* and also in other species of *Automate*. To our knowledge, this type of armature has never been observed in other alpheid genera; when strong spines are present on the ultimate segment, they are always situated on its distal part or on the apex itself.

Thus, *Bermudacaris harti* could either derive from the ancestors common to both *B.* and *Automate* or could represent a "highly modified species" of *Automate*, adapted to the unique anchialine cave environment, which is radically different from the usual habitat of recent species of *Automate*. Almost depigmented eyes, and few

very large eggs suggesting highly abbreviated development and low fecundity of *B. harti*, are features certainly related with the evolution in an environment characterized by deficiency of light and fluctuation of salinity.

It is probable that the Bermudan caves were colonized by a marine ancestor of *B. harti*, which could also be those of the modern species of *Automate*. Indeed, all anchialine caves in Bermuda still have an underground connection with the sea as is evidenced by their tidal fluctuations and fully marine salinities at depth (Hart & Manning 1981). Generally, these caves comprise crevicular habitats in rock extending potentially from the sea surface to the deep sea, therefore these habitats could have been entered anywhere in the water column (Manning et al. 1986). This would explain the presence of both deep-sea and shallow water (epigeal), or both old and recent forms in caves.

Bermuda originated on the Mid-Atlantic Ridge and was formed about 100 million years ago (Manning et al. 1986). Hart et al. (1985) stated that there are significant ties between marine cave fauna and the fauna of deep sea, that caves can contain very old elements ("Mesozoic relicts"), and that they could serve as refuges over long periods of time, especially during periods of glaciation (Iliffe et al. 1983). These statements, though partially explaining the distribution patterns of many cave inhabitants, can not explain the origin of *Bermudacaris*. All modern species of *Automate* (and generally all Alpheidae) are found in shallow waters, excluding the hypothesis of an ancestral form coming from the deep sea. Also *Bermudacaris* cannot be considered a relict form, since it shares many characters of modern Alpheidae (such as those shared with *Automate*). A more probable explanation would be the relatively late colonization of Bermudan caves by a marine, probably shallow-water ancestor. This ancestor frequented crevicular habitats (marine caves), from which it could progressively

penetrate into limestone anchialine caves, situated at considerable distance from the sea.

A similar hypothesis has been put forward by Manning et al. (1986: 160–161), to explain the distribution of two closely related species of *Typhlatya*. The salt-water precursors of modern *Typhlatya* species could frequent crevicular habitats along the Mid-Atlantic Ridge while the continents were approximated. Also, Manning et al. (1986) briefly mentioned that a similar scenario could explain the puzzling distribution of the two populations of *Procaris* in the Atlantic.

More recently a common littoral crab, *Panopeus lacustris* Schramm, was reported to be relatively abundant in several Bermudan caves (Manning & Hart 1989). Crabs found in caves differed from those living on the open shore in their colour pattern (being much lighter), and in having little wear on the fingers of the chelae, possibly the initial changes induced by life in a cave environment.

Bermudacaris harti is a seventh alpheid reported from crevicular habitats (marine, anchialine or freshwater), and it seems to be the most adapted to life in caves. Recent cave investigations show that Alpheidae seem to be relatively well represented in this particular environment. Other cavernicolous alpheid species are *Potamalpheops stygicola* (Hobbs, 1973) from freshwater caves in Oaxaca, Mexico (Hobbs 1973, 1983); *Potamalpheops pininsulae* Bruce & Iliffe 1992 from freshwater limestone caves in Ile des Pins, New Caledonia; *Salmoneus sketi* Fransen, 1992 from marine caves in the northern Adriatic Sea; *Yagerocaris cozumel* Kensley, 1988 from marine caves off Cozumel, western Mexico [transferred from Hippolytidae to Alpheidae by Chace & Kensley (1992)], and an undescribed species of *Potamalpheops* from a freshwater cave system in northern Palawan, Philippines (Anker, pers. obs.). Two other stygophilic alpheids have been reported from anchialine lava pools and tubes

in the Pacific Ocean; these are *Metabetaeus Iohena* Banner & Banner, 1960 from Hawaii (Holthuis 1973), and *Hamalpheus acanthops* Bruce & Iliffe, 1991 from Samoa.

In addition to *Bermudacaris harti*, four other species of troglobitic caridean shrimps from three families inhabit anchialine caves of Bermuda: *Parhippolyte sterri*, *Barbouria cubensis*, *Typhlatya iliffei* and *Procaris chacei* (Hart & Manning, 1981, 1986), illustrating the relatively high level of diversity of this habitat: *Procaris chacei*, and *Bermudacaris harti* seem to be very uncommon, in contrast to relatively abundant *Barbouria cubensis* and *Typhlatya iliffei*. Only four individuals of *Bermudacaris harti* were collected in 11 years of cave diving in Bermuda by the junior author. Unfortunately, the anchialine caves of Bermuda are more and more exposed to the anthropogenic activities (Iliffe et al. 1984), but we hope that the unique, endemic cave fauna of this island group can be preserved for the future generations.

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Occurrence of shrimp species (Crustacea: Decapoda: Natantia: Penaeidea and Caridea) in Ubatuba Bay, Ubatuba, SP, Brazil

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Abstract.—The species composition of Penaeidea and Caridea shrimp was studied in Ubatuba Bay, São Paulo, Brazil. Samples were taken monthly from September 1995 to August 1996, using two double-rig trawling nets. A total of 21 marine shrimps species were obtained, belonging to eight families. Sergestoids were represented by a single species of Sergestidae, while penaeoids comprised three families, Penaeidae, Sicyoniidae and Solenoceridae. Caridea shrimps belonged to two superfamilies, the Palaemonoidea, represented by Palaemonidae; and Alpheoidea by three families, Alpheidae, Ogyrididae and Hippolytidae. *Sicyonia laevigata* Stimpson, 1871 and *Nematopalaemon schmitti* (Holthuis, 1950) represent first records in São Paulo State, Brazil.

Seven families of Dendrobranchiata shrimps, represented by 26 genera and 61 species, have been reported for the Brazilian Coast (D’Incao 1995). For the Pleocyemata, Holthuis (1993) listed 15 caridean superfamilies and 31 families. Among these, most representatives belonged to Alpheoidea and Palaemonoidea with 38 and 48 species, respectively (Ramos-Porto 1986, Holthuis 1993). Taxonomic information on Dendrobranchiata and Caridea species found in the Brazilian coast is scant (Corrêa 1977; Christoffersen 1979, 1982; Bond-Buckup & Buckup 1989, D’Incao 1995). Most of the studies dealing with the biodiversity of this group have focused on bioecological aspects of these organisms (Iwai 1973, Abreu 1980, Pires 1992, Nakagaki et al. 1995). The objective of the present study is to determine the composition of marine shrimp species (Dendrobranchiata and Caridea) in Ubatuba Bay, northern coast of São Paulo State, in order to contribute to a better assessment of local marine biodiversity.

Material and Methods

Ubatuba Bay is located on the northern part of São Paulo State (23°25'00" to 23°27'34"S and 45°00'30" to 45°03'30"W), where the coastline consists of several inlets and major bays. According to Castro Filho et al. (1987), this region is affected by three water masses, with different distributional patterns in the summer and winter. Coastal Water (CW) has a high temperature and low salinity (T > 20°C, S < 36‰) Tropical Water (TW) has both a high temperature and salinity (T > 20°C, S > 36‰), and South Atlantic Central Water (SACW) has both a low temperature and salinity (T < 18°C, S < 36‰) following an annual cycle. The dynamics of these currents are responsible for seasonal alterations of temperature, salinity and nutrients concentrations. Ubatuba Bay can be divided into an inner and an outer section. The inner section is affected by direct fresh water drainage from four small

rivers (Indaiá, Grande de Ubatuba, Lagoa and Acaraú) and consequently receives a continuous input of domestic sewage and considerable deposition of organic matter. The outer section is exposed to oceanic influence. Detailed descriptions of environmental factors of the Bay, and the study site characteristics can be found in Mantelatto & Fransozo (1999).

Samples were obtained on a monthly basis from September of 1995 to August of 1996. A shrimp fishery boat supplied with 3.5 m-opening double-rig trawling nets was used. The mesh size was 12 mm except in the cod end where it was 10 mm.

Dendrobranchiata shrimps were identified according to D'Incao (1995) and Pérez Farfante (1997). In the case of juvenile specimens of *Farfantepenaeus* Burukovsky, 1997, the morphology of the last abdominal somite was used for identification as described by Pérez Farfante (1969) and F. D'Incao, pers. comm.

Results

The material obtained contains eight families and 21 species. The Sergestoidea were represented by a single sergestid species. Species belonging to Penaeidae, Sicyoniidae and Solenoceridae were also collected (Table 1). Among the carideans, representatives of two superfamilies were found. Palaemonoidea was represented by the study area by the family Palaemonidae, while the Alpheoidea comprised alpheids, ogyridids and hippolytids (Table 2).

Discussion

This study was restricted to a survey of the soft-sediment bottoms of Ubatuba Bay which is a small area compared to the vast Brazilian coast. This region is located at the Paulista biogeographic Province which comprises the coastal region between Espírito Santo and Santa Catarina States. The mixed feature of the fauna of this region can be explained by the thermal regime of the waters, which can harbor tropical, tem-

perate and subantarctic species (Coelho & Ramos 1972). Nevertheless, Melo (1985) based on the low level of endemism, asserts that the southeastern-south littoral of Brazil does not represent a faunal Province, but a transition area.

The finding of *S. laevigata* and *N. schmitti* is of significance as they represent first records of these species in the State of São Paulo.

The total number of species of Dendrobranchiata now known to occur in São Paulo State is 19. Species not found during our survey include four penaeoideans, such as *Solenocera necopina* Burkenroad, 1939, *Solenocera atlantidis* Burkenroad, 1939, *Mesopenaeus tropicalis* (Bouvier, 1905), and *Parapenaeus americanus* Rathbun, 1901; and three sergestoideans, *Lucifer faxoni* Borradaile, 1915, *Lucifer typus* H. Milne Edwards, 1837, and *Sergia robusta* (Smith, 1882).

Parapenaeus americanus is a species known to occur at depths of 50 to 70 m, much below the deepest trawl performed during the present survey in Ubatuba Bay (up to 17 m). Previous records of *S. necopina*, *S. atlantidis* and *M. tropicalis* in this region were considered atypical (Pires 1992), and this has been confirmed in our survey. Using a lower sampling effort and avoiding rocky coast areas, Nakagaki et al. (1995) did not find *S. laevigata*, *S. parri* and *F. paulensis* in Ubatuba Bay.

Considering the presence of *N. schmitti*, the number of palaemonid species in São Paulo State is now 14, including freshwater and estuarine species. Five of these are considered common marine species but only two were found during this study, *N. schmitti* and *L. paulensis*.

According to Bond-Buckup & Buckup (1989), *P. pandaliformis* preferably inhabits fresh or brackish water environments. However, Ramos-Porto (1986) occasionally found this species in marine habitats. During the present study, two specimens of *P. pandaliformis* were collected near the drainage of a river. Low-salinity conditions

Table 1.—List of shrimp species of Dendrobranchiata collected in the Ubatuba Bay. (SW = shallow water; PE = pelagic zone).

Species	Distribution	Depth (m)
SERGESTOIDEA		
SERGESTIDAE		
<i>Acetes americanus</i> Ortmann, 1893	Western Atlantic: Guyana, Puerto Rico to Brazil (from Pará to Rio Grande do Sul).	PE to 40
PENAEOIDEA		
PENAEIDAE		
<i>Farfantepenaeus brasiliensis</i> (Latreille, 1817)	Western Atlantic: USA (Cape Hatteras, North Carolina) to Brazil (from Amapá to Rio Grande do Sul).	SW to 366
<i>Farfantepenaeus paulensis</i> (Pérez Farfante, 1967)	Western Atlantic: Brazil (from Bahia to Rio Grande do Sul) to Argentina (Mar del Plata).	SW to 150
<i>Litopenaeus schmitti</i> (Burkenroad, 1936)	Western Atlantic: Baía de Matanzas, Cuba to Brazil (from Amapá to Rio Grande do Sul).	SW to 50
<i>Artemesia longinaris</i> Bate, 1888	Western Atlantic: Brazil (from Rio de Janeiro to Rio Grande do Sul) to Argentina (province of Chubut).	2 to 125
<i>Rimapenaeus constrictus</i> (Stimpson, 1874)	Western Atlantic: USA (Chesapeake Bay, Virginia) to Brazil (from Amapá to Santa Catarina).	1.5 to 127
<i>Xiphopenaeus kroyeri</i> (Heller, 1862)	Western Atlantic: USA (Virginia) to Brazil (from Amapá to Rio Grande do Sul).	SW to 70
SOLENOCERIDAE		
<i>Pleoticus muelleri</i> (Bate, 1888)	Western Atlantic: Brazil (from Espírito Santo to Rio Grande do Sul) to Argentina (Santa Cruz).	SW to 600
SICYONIIDAE		
<i>Sicyonia dorsalis</i> Kingsley, 1878	Western Atlantic: USA (Cape Hatteras, North Carolina) to Brazil (from Amapá to Santa Catarina).	3 to 420
<i>Sicyonia typica</i> (Boeck, 1864)	Western Atlantic: USA (North Carolina) to Brazil (from Amapá to Rio Grande do Sul).	SW to 100
<i>Sicyonia laevigata</i> Stimpson, 1871	Western Atlantic: USA (Beaufort, North Carolina) to Brazil (from Amapá to Rio Grande do Sul).	SW to 100
<i>Sicyonia parri</i> (Burkenroad, 1934)	Western Atlantic: USA (North Carolina) to Brazil (from Maranhão to São Paulo).	SW to 87

at the time of sampling (see Mantelatto & Fransozo 1999) probably favored the presence of *P. pandaliformis* at this site.

Alpheoids are represented by 23 species in the State of São Paulo, of which six were obtained during our study. *Ogyrides alphaerostris* occurs preferably in estuaries and was also found with *A. floridanus* and *E. oplophoroides* in marine habitats. *Alpheus intrinsecus* is commonly found in protected embayments areas (Christoffersen 1979, 1980, 1982). The occurrence of the alpheid *A. bouvieri* was also presumably atypical because this species lives in the intertidal zone, frequently in rocky crevices or associated to sand colonies of tubicolous

polychaetes belonging to the genus *Phragmatopoma* Mörch, 1863 (Christoffersen 1979).

Based on data from this study and on others research (Fransozo et al. 1992, 1998; Negreiros-Fransozo et al. 1997) we can infer that Ubatuba Bay represents an important site in the establishment and development of diverse marine shrimp populations. Continuing studies of inshore and offshore areas will provide a more accurate characterization of the diversity of the region.

Acknowledgments

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Table 2.—List of shrimp species of Caridea collected in the Ubatuba Bay. (SW = shallow water; FW = fresh water; IT = intertidal zone; BW = brackish water).

Species	Distribution	Depth (m)
PALAEMONOIDEA		
PALAEMONIDAE		
<i>Leander paulensis</i> Ortmann, 1897	Western Atlantic: USA (Florida) and Brazil (from Maranhão to São Paulo).	SW to 16
<i>Nematopalaemon schmitti</i> (Holthuis, 1950)	Western Atlantic: Guyana and Brazil (from Amapá to São Paulo).	SW to 60
<i>Palaemon pandaliformis</i> (Stimpson, 1871)	Western Atlantic: Antilles, northern South America and Brazil (from Rio Grande do Norte to Rio Grande do Sul).	SW, FW, and BW
ALPHEOIDEA		
ALPHEIDAE		
<i>Alpheus intrinsicus</i> Bate, 1888	Western Atlantic: Tobago, Puerto Rico and Brazil (from Ceará to Santa Catarina). Eastern Atlantic: Western Sahara to Zaire.	IT to 40
<i>Alpheus floridanus</i> Kingsley, 1878	Western Atlantic: Bahamas, USA (southeastern Florida), Mexico (Veracruz). Gulf of Mexico, Cuba, Haiti, Puerto Rico, Antigua, Guadeloupe, Bonaire, Curaçao and Brazil (Atol das Rocas and from Bahia to Rio Grande do Sul).	IT to 78–81
<i>Alpheus nuttingi</i> Schmitt, 1924	Western Atlantic: Bermuda, USA, Cat Cay, Barbuda to Tobago Cays, Panama and Brazil (Alagoas and from Espírito Santo to Santa Catarina).	IT to 2
<i>Alpheus bouvieri</i> A. Milne-Edwards, 1878	Western Atlantic: Bermuda, USA (east coast of Florida), Cuba, Antigua to Tobago, Aruba and Brazil (Fernando de Noronha and from Ceará to Rio Grande do Sul).	IT, between rocky
OGYRIDIDAE		
<i>Ogyrides alphaerostris</i> (Kingsley, 1880)	Western Atlantic: USA (from Virginia to South Carolina, Eastern Florida, Gulf Coast and Louisiana). Dominican Republic and Brazil (Pará and from Rio de Janeiro to Rio Grande do Sul).	0–0.30 to 52
HIPPOLYTIDAE		
<i>Exhippolysmata oplophoroides</i> (Holthuis, 1948)	Western Atlantic: USA (North and South Carolina, Georgia, Texas), Guyana, and Brazil (from Amapá to Pernambuco and from Espírito Santo to Rio Grande do Sul) to Uruguay.	5 to 45

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**On a small collection of Parthenopidae from Indonesia,
with description of a new species of *Pseudolambrus*
(Crustacea: Decapoda: Brachyura)**

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Abstract.—The present paper reports on a small collection of parthenopid crabs from Indonesia. While most of the species have been recorded before, one species, *Platylambrus tumidus* (Lanchester, 1900), is new for the country, while another, *Pseudolambrus sundaicus*, is described as a new species. The latter species differs from all congeners by the structure of the carapace, chelipeds and ambulatory legs.

The parthenopid fauna of Indonesia is remarkably diverse, and 44 species and subspecies are now known (see Flipse 1930, Chiong & Ng 1998). Recently, the authors had an opportunity to study a small but interesting collection of parthenopid crabs in the collection of the Research and Development Centre for Oceanology in Jakarta, Indonesia, which had been collected from various parts of Indonesia. While most were known species, one proved to be a new record, and another, a species of *Pseudolambrus* Paulson, 1875, is here described as new.

The terminology and generic system used here follows that proposed by Ng & Rodríguez (1986). The measurements listed in the material examined are of the carapace width (inclusive of spines and/or teeth) by carapace length (tip of rostrum to posterior margin of carapace). The terminology used follows that proposed by Flipse (1930) with modifications by Ng (1996). The genus *Aethra* Latreille, 1816, classified in the Parthenopidae by many authors, is now regarded as belonging to its own family (Ng & Rodríguez 1986, Guinot & Bouchard 1998). Synonymies are not provided, with most of the information for the species

treated here already present in Flipse (1930) and Tan et al. (1999). Specimens examined are deposited in the Research and Development Centre for Oceanology (RDCO), Indonesian Institute of Sciences, Jakarta, Indonesia; Museum Zoologicum Bogoriense (MZB), Cibinong, Indonesia; Muséum national d'Histoire naturelle (MNHN), Paris, France; and Zoological Reference Collection (ZRC) of the Raffles Museum, National University of Singapore.

Taxonomic Account

Daldorfia horrida (Linnaeus, 1758)

Material examined.—1 male (87.4 × 67.0 mm) (RDCO), 08°37'00"S, 138°18'00"E, mud, coll. research vessel R.I. Jalanidhi, 10 Dec 1967; 1 male (32.4 × 25.0 mm) (ZRC 1999.1459), 1 male (74.7 × 54.4 mm) (RDCO), Pulau Pari, coll. Sukardi, 21 Oct 1973; 1 male (31.2 × 23.5 mm) (RDCO), Pulau Belang Belang, among coral, coll. M. K. Moosa, 6 Nov 1980.

Remarks.—This widely distributed Indo-Pacific species is often common in coral reefs. In the present material, smaller specimens tend to have less eroded carapaces and more distinctly triangular carapaces,

and the chelipeds are also proportionately shorter, with the granules less prominent (Tan et al. 1999).

Platylambrus echinatus (Herbst, 1790)

Material examined.—1 male (43.5 × 33.7 mm) (RDCO), 02°09'00"S, 108°00'00"E, 15 m, 11 Oct 1967.

Remarks.—The taxonomy of this wide ranging Indo-West Pacific species has been discussed by Tan et al. (1999).

Parthenope longimanus (Linnaeus, 1758)

Material examined.—1 female (26.1 × 23.4 mm) (RDCO), Dobo, 10–15 m, coll. Jean, May 1967; 1 male (28.9 × 25.7 mm) (ZRC 1999.1460), 1 male (34.3 × 26.6 mm.), 1 female (36.3 × 32.6 mm) (RDCO), 03°08'08"S, 111°12'08"E, coll. 17 Apr 1973; 1 female (29.0 × 25.8 mm) (RDCO), South Kalimantan, 30 Feb 1982.

Remarks.—This common species has a wide distribution in the Indo-West Pacific, and the problems with its taxonomy have been summarized by Tan et al. (1998).

Platylambrus tumidus (Lanchester, 1900)

Lambrus tumidus Lanchester, 1900: 727, pl. 44, fig. 2.

Material examined.—3 males (31.9 × 23.2 mm, 31.0 × 23.1 mm), 1 female (21.4 × 16.1 mm) (RDCO), 1 male (31.5 × 23.1 mm), 1 female (30.1 × 23.0 mm) (ZRC 1999.1461), Malaka Strait (= Straits of Malacca), coll. R/V *K. M. Madidihang*, 22 Jan 1980.

Remarks.—Many of the older records of *Platylambrus carinatus* (H. Milne Edwards, 1834) and *P. validus* (De Haan, 1839) from Southeast Asia probably refer to *P. tumidus* (Lanchester, 1900), instead, a species first described from Singapore, where it can be quite common (P. K. L. Ng, pers. observation). The presence of this species in the Indonesian part of the Malaka Strait is thus not surprising. *Platylambrus tumidus* is superficially similar to *P. carinatus* and *P.*

validus, and can be easily confused with them. It is formally recorded from Indonesia for the first time. Thus far, *P. carinatus* is known for certain only from the Indian Ocean while *P. validus* is only known for certain from the East China Sea and adjacent areas (Tan et al. 1999).

Pseudolambrus sundaicus, new species

Figs. 1–3

Material examined.—Holotype: male (14.7 × 13.3 mm) (MZB 1429), Pulau Ayer islands, Jakarta Bay, Java, 05°45'S 106°37'E, coll. K. Rohmimohtarto, 25 May 1971. Paratypes, 1 male (12.3 × 10.8 mm), 1 female (10.1 × 9.6 mm) (MNHN), same data as holotype. Non-type:—1 juvenile female (7.8 × 7.5 mm) (MZB), Pulau Kongsii, 5°51'S 106°36'E, Java Sea, intertidal, muddy sand, coll. M. K. Moosa, 26 Sep 1972.

Description of male.—Carapace subtriangular, angle between antero- and posterolateral margins clearly demarcated, angular; dorsal surfaces covered with scattered flattened granules, striae and subsquamate tubercles, granules more pronounced along ridges; progastric, mesogastric, metagastric, mesobranchial, metabranchial, cardiac and intestinal regions distinct, raised; metagastric region separated from cardiac region by shallow groove; cardiac region inflated, protruding obliquely posteriorly, separated from intestinal region by shallow groove; cardiac region separated from branchial regions by deep, relatively broad groove posteriorly, more shallow anteriorly; intestinal region transversely narrow, surface granular. Front deflexed, appearing triangular in dorsal view, weakly trilobate in frontal view, median lobe granuliform, lateral margins weakly granulate, appearing entire; dorsomedian surface with distinct longitudinal depression. Supraorbital margin with 2 deep, narrow clefts; external orbital tooth low but distinct. Hepatic region not swollen, gently granular, relatively entire, clearly demarcated from anterolateral margin by narrow, sinuous cleft.

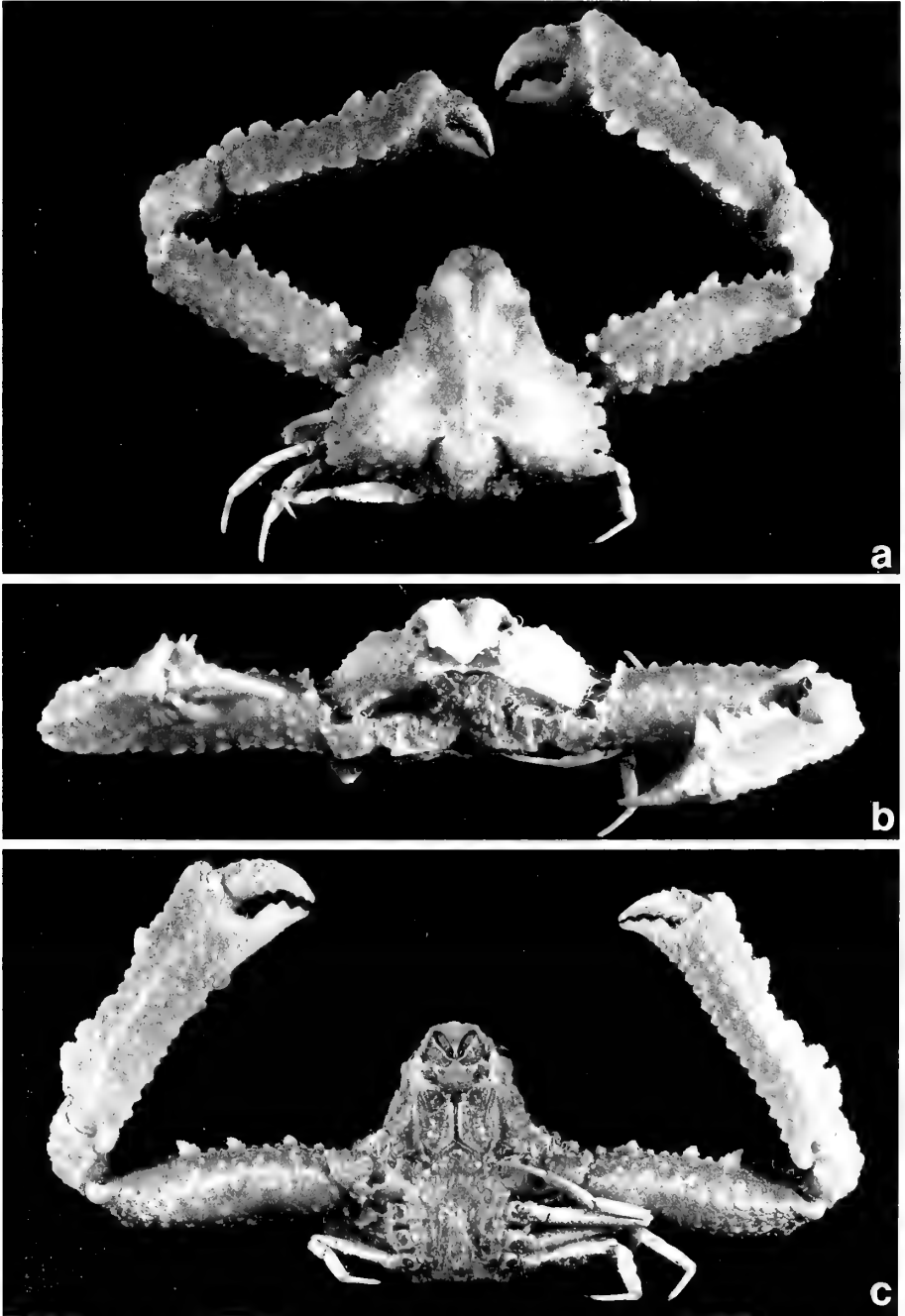


Fig. 1. *Pseudolambrus sondaicus*, new species. Holotype male (14.7 by 13.3 mm) (MZB 1429). a, dorsal view; b, frontal view; c, ventral view.

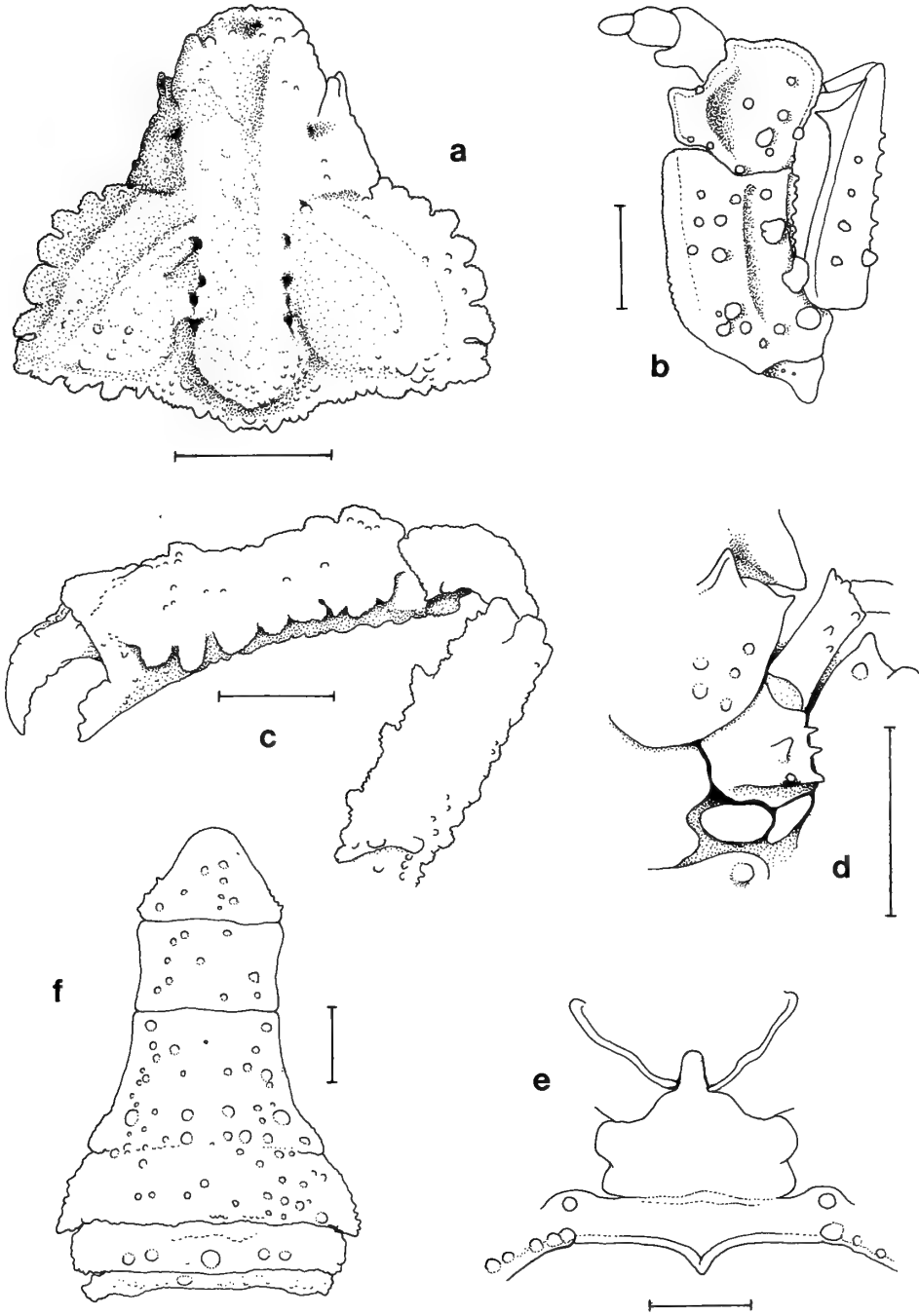


Fig. 2. *Pseudolambrus sundaicus*, new species. Holotype male (14.7 by 13.3 mm) (MZB 1429). a, carapace; b, left third maxilliped; c, right cheliped; d, antennae; e, epistome; f, abdomen. Figures a, b, f, only major granules and regions drawn. Scales: a, c = 5.0 mm; b, d, e, f = 1.0 mm.

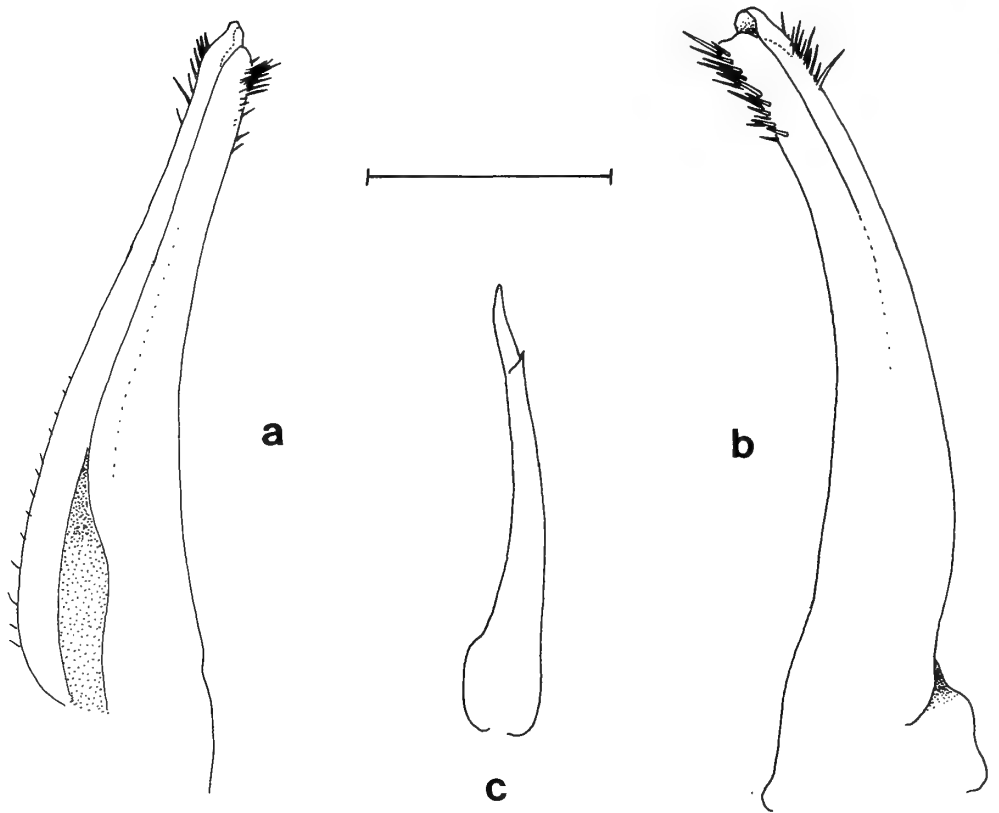


Fig. 3. *Pseudolambrus sundaicus*, new species. Holotype male (14.7 by 13.3 mm) (MZB 1429). a, left male first pleopod (ventral view); b, left male first pleopod (dorsal view); c, left male second pleopod (dorsal view). Scale = 1.0 mm.

Anterolateral margin arcuate, dentate, with 7 or 8 unevenly shaped teeth, with margins finely granulated; teeth gradually becoming larger from anterior to posterior. Posterolateral margin very gently converging towards posterior carapace margin, appearing somewhat subparallel with posterior carapace margin; with 3 or 4 small teeth. Posterior carapace margin with 3 low rounded granules. Branchiostegal surface with prominent sublamelliform tooth which holds cheliped when pushed backwards. Pterygostomial and sub-branchial surfaces granular, but without prominent spines, large teeth or tubercles.

Antennules folding at ca. 45° angle; anterior rim of basal segment cristate. Second antennal segment subquadrate, outer lateral margin with 3 sharp teeth, submedian sur-

face with 2 granules, the anterior one of which is larger and sharper; third antennal segment slightly dorsoventrally flattened, rectangular, anterointernal angle with 3 low tubercles, submedian surface with 3 low granules. Epistome smooth, length subequal in length to width; posterior margin with distinct median lobe.

Outer surfaces of third maxillipeds granular, with granules on outer margins larger. Ischium subrectangular, with relatively deep, oblique median sulcus, clearly separated from basis. Merus subquadrate, with oblique submedian depression; antero-external angle weakly auriculiform. Exopod relatively broad, distal part antero-external angle of merus.

Anterior thoracic sternites with numerous small and large rounded granules; sternites

1 and 2 completely fused; suture between sternites 2 and 3 fused but with shallow median transverse depression demarcating them, suture between sternites 3 and 4 fused but demarcated by shallow transverse groove; sutures between sternites 4–6 medially interrupted; sutures between sternites 6 and 7, and 7 and 8 complete, sternite 8 with deep longitudinal groove.

Right cheliped larger than left. Basis-ischium fused, anterior surface granular. Merus trigonal in cross-section; dorsal and outer surfaces gently granular; surfaces inner margin (between dorsal and inner facets) with 2 large submedian teeth and several smaller teeth, all of which are granular; outer margin (between dorsal and outer facets) with numerous small, low teeth of varying sizes. Carpus with outer surfaces weakly granular, broader distally; inner distal angle with low but distinct tubercle. Manus of larger cheliped trigonal in cross-section; outer and dorsal surfaces gently granular; inner margin (between dorsal and outer facets) with 8 large, lamelliform teeth, those distally larger, more prominent and more clearly demarcated from the rest; outer margin (between dorsal and outer facets) with 3 low teeth; lower margin (between outer and inner facets) gently serrated; outer surface with longitudinal median row of low, rounded granules. Manus of smaller cheliped more slender than larger one, other structures similar but lobes and teeth generally smaller. Fingers relatively short, strongly curved; dactylus strongly curved, distal part of dorsal margin with several rounded granules arranged approximately in 2 indistinct ridges, cutting edge with 3 low teeth and several denticles; pollex shorter than dactylus, cutting edge with 3 prominent teeth, tip hooked upwards.

Ambulatory legs slender; first leg longest. Margins of meri uneven but not distinctly serrated or dentiform; dorsal margin subcristate. Dorsal margin of carpus with 2 or 3 low granules. Dactyli subequal in length to propodus, both articles unarmed; dactylus smooth, styliform.

Male abdomen subtriangular; surface granular, lateral margins lined with granules and short spines. Segment 1 very narrow longitudinally; segment 2 transversely rectangular. Segments 3–5 completely fused, sutures not discernible except for lateral parts of that between segments 3 and 4; lateral margins of segment 3 gently convex, posterolateral angle distinctly produced; lateral margin of fused segments 4 and 5 gently concave. Segment 6 broader than long, lateral margins gently concave. Telson triangular, tip rounded, lateral margins almost straight.

Male first pleopod relatively stout, gently sinuous, tip subtruncate, divided into 2 lobes, outer lateral margins of both lobes lined with numerous stiff setae. Male second pleopod relatively short, ca. 0.6 times length of male first pleopod, distal segment short, ca. 0.25 times length of basal segment.

Female.—The paratype female specimen (MNHN) agrees with the type males in all carapace and ambulatory leg features. The only major difference is that the chelipeds of the female are proportionately shorter. This is especially for the manus of the larger chela.

Remarks.—*Pseudolambrus* Paulson, 1875 (= *Parthenolambrus* Miers, 1879; *Parthenopoides* Miers, 1879), is a very problematic genus, with the degree of infraspecific variation in some species very substantial (e.g., see Monod 1956, Manning & Holthuis 1981, Campbell & Stephenson 1970, Chia & Ng 1993). The validity of the generic synonymy must also be reassessed as it is very unlikely that the genus as presently recognised is monophyletic (P. K. L. Ng & S. H. Tan, pers. observations). Currently, some 29 species and subspecies are classified in *Pseudolambrus* (Flipse 1930, Monod 1956, Sakai 1969, Takeda 1977, Manning & Holthuis 1981).

Pseudolambrus sundaicus, new species, is most similar in general morphology to *P. beaumonti* (Alcock, 1895), especially with regards to the triangular carapace shape and

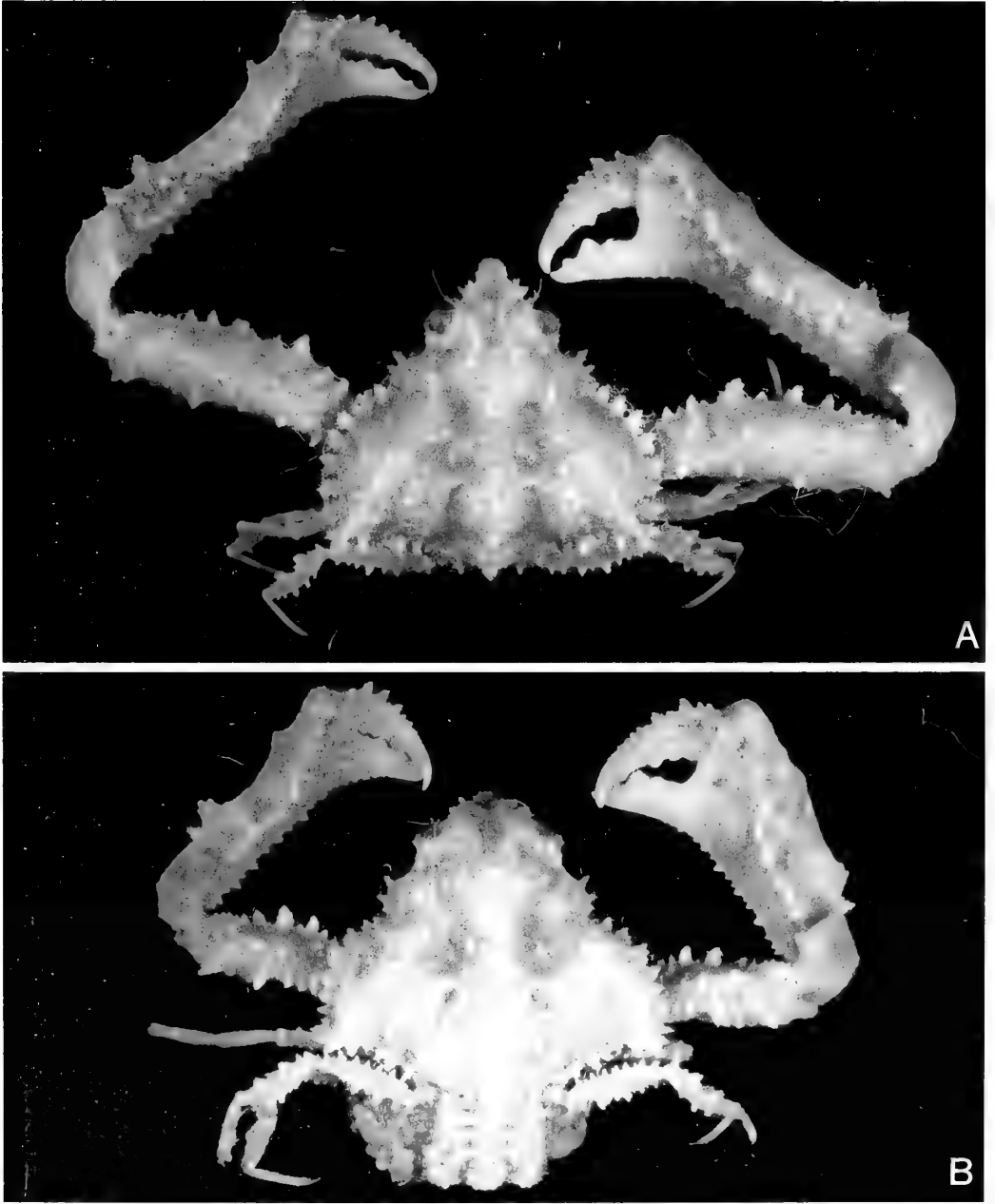


Fig. 4. *Pseudolambrus beaumonti* (Alcock, 1895), syntypes (Zoological Survey of India, Calcutta, catalogue number 11-13/10). A, male (11.3 by 10.5 mm); B, female (9.4 by 9.1 mm).

relatively elongate chelipeds (see Fig. 4; Alcock 1895, Sakai 1976). In most *Pseudolambrus* species (including the type species of the genus, *Parthenope calappoides* Adams & White, 1848), however, the chelipeds are proportionately shorter for both

sexes. *Pseudolambrus sundaicus*, however, can easily be separated from *P. beaumonti* by its relatively broader carapace, more deflexed front which appears almost evenly triangular from dorsal view (against distinctly trilobed with dentiform lateral mar-

gins), higher branchial regions, the hepatic margin being granular but not serrated or spiniform, inner dorsal margin of the chela has distinct, almost petaliform lobes (against the presence of distinct triangular teeth), and the ambulatory merus, carpus and propodus are not armed with prominent spines and teeth.

Pseudolambrus sundaicus is also similar to *P. massena* (Roux, 1830) (Monod 1956, Manning & Holthuis 1981) with regards to its carapace physiognomy, simple front and form of the ambulatory legs. *Pseudolambrus sundaicus*, however, differs from *P. massena* in its more deflexed front, having the posterolateral margin straighter and subparallel with the posterior carapace margin, the carapace distinctly more triangular in shape (against gently converging towards posterior carapace margin and somewhat more hexagonal in shape), and the chelipeds being proportionately longer (cf. Monod 1956, Manning & Holthuis 1981).

The broader than long carapace shape of *P. sundaicus* is diagnostic for this species. Most other *Pseudolambrus* species have carapace widths and lengths subequal, or the carapace is longer than broad. Only in *P. beaumonti* or the very different looking American *P. triangula* (Stimpson, 1860), are their carapace shapes even approaching that of *P. sundaicus* (cf. Garth 1958).

A small juvenile female specimen of *Pseudolambrus* from near the type locality of *P. sundaicus* agrees with the holotype of this species in most aspects. However, its only one cheliped is relatively longer and more slender than that of the holotype male of *P. sundaicus*. Although this is probably size related variation, we prefer not to include it in the type series.

Etymology.—The species name is derived from the Sunda Shelf.

Rhinolambrus longispinis (Miers, 1879)

Material examined.—1 male (42.3 × 41.5 mm) (RDCO), 01° 07'S 105°06'E, otter trawl, sand, 22 m, coll. R. I. J. Alanidhi, 4

Oct 1967; 1 male (24.1 × 24 mm) (RDCO), Jepara, coll. R/V *Samudera*, 14 Oct 1976.

Remarks.—This species has a wide distribution in the Indo-West Pacific. It closely resembles *R. contrarius* (Herbst, 1804) and the differences between the two have been discussed by Tan et al. (1999).

Rhinolambrus turriger (Adams & White, 1848)

Material examined.—1 male (9.8 by 11 mm) (RDCO), 07°41'38"S, 113°15'34"E, 27–23 m, coll. 6 Sep 1975.

Remarks.—This common species has been reported from various parts of the Indian Ocean, Indonesia and Australia. The strength of the spines on the branchial and gastric regions can vary substantially, from very long and spiniform to low and tubercular (S. H. Tan & P. K. L. Ng, pers. observations).

Acknowledgments

The authors are grateful to Mr Tan Swee Hee for his help in sorting out the taxonomy of *Pseudolambrus* and ascertaining the novelty of *P. sundaicus*. Mr Darren Yeo provided us the photographs of the syntypes of *P. beaumonti* in the Zoological Survey of India. The second author was supported by a research fellowship from the Raffles Museum. Part of the work was supported by a research grant to the first author from the National University of Singapore.

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A new species of crayfish (Crustacea: Decapoda: Cambaridae) from Lake Catemaco, Veracruz, Mexico

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Abstract.—*Procambarus (Austrocambarus) catemacoensis*, a new species of crayfish, is described from Lake Catemaco, Veracruz, Mexico. The new species is morphologically similar to *P. (A.) acanthophorus* Villalobos, 1948, from which it can be distinguished by having two or three spines on the anterior border of the carapace, an obliterated areola, smaller and separated spines in the cervical groove, second segment of the antennal peduncle with a spine, gonopod of form I male with bladelike mesial process curved over the lateral border, and annulus ventralis trapezoidal.

Procambarus (Austrocambarus) acanthophorus Villalobos, 1948, was described from “El Castillo”, a locality 4 km west of Tuxtepec, Oaxaca, and having a distribution that included four sites in the neighboring regions of Veracruz. Villalobos (1954), in his review of some species in the *mexicanus* Group, also recorded *P. (A.) acanthophorus* from Espagoya, a marsh area in the northeast section of Lake Catemaco, Veracruz. The range of *P. (A.) acanthophorus* was later modified by Villalobos (1955), extending it to the environs of the Port of Veracruz, and subsequently by Hobbs (1989), who recorded it from Chiapas. A recent detailed examination of these collections revealed that the specimens from Espagoya represented a new species (Rojas 1998), which is described herein.

All specimens cited are deposited in the Colección Nacional de Crustáceos, Instituto de Biología, Universidad Nacional Autónoma de México (CNCR). Other abbreviations used are: coll., collector; RL, rostrum length; TCL, total carapace length.

Procambarus (Austrocambarus)
catemacoensis, new species
Figs. 1–2

Procambarus (Austrocambarus) acanthophorus.—Villalobos, 1954:364; 1955:224; 1983:213.

Diagnosis.—Body pigmented, eyes normally developed. Rostrum with reduced marginal spines, median carina absent. Acumen length 21.1% to 30% of RL (\bar{X} = 24.5%). Carapace with 2 pairs of short cervical spines, both oriented cephaloventrally (Fig. 1a). Areola obliterated, 30.6% to 34.9% (\bar{X} = 32.7%) of TCL (Fig. 1b). Anterior margin of carapace straight, with weak suborbital angle, and 2 to 3 spines of unequal size in addition to branchiostegal spine. Postorbital ridges well marked, cephalic margin with short spine. Antennal scale 2.3 times as long as wide, maximum width at midlength, lateral margin thickened and terminating in spine. Second segment of endopodite of antennal peduncle with spine on distal margin (Fig. 2b). Chelipeds subequal in length, shorter than TCL, covered with squamous tubercles, pubes-

cent; fingers shorter than inner margin of palm, which about twice as long as broad; dactyl with fine, long setae along dorsal surface, opposable margin with prominent tubercle near midlength, finely serrate distally; fixed finger with short setae along ventral margin, opposable margin with 2 or 3 proximal tubercles, finely serrate distally (Figs. 1c–d). Ischium of third pereopod of form I male armed with acute hook, tip of which reaching beyond articulation with basipodite (Fig. 1f). First pair of pleopods (gonopods) of form I male short, symmetrical, devoid of subterminal setae; shoulder on cephalic surface at base of terminal elements wide and strong, distally with 2 borders separated by deep v-shaped depression (Fig. 2c); laterodistal border wide, rounded, lower than mesiodistal border (Fig. 2e); mesiodistal border narrow, inclined, divided by deep notch next to base of cephalic process. In caudal view, lateral border prominent, distal portion rounded, with wide and shallow notch (visible in cephalic view); in lateral view, lateral border extending to midlength of mesial process; in cephalic view, surface of border covered with rounded tubercles and with submarginal groove. Mesial process short, wide, lightly sclerotized, curved laterally, adjacent to lateral shoulder, flattened mesio-laterally, ending in angular tip. Cephalic process small, subtriangular, joining with each vertex central projection, mesial process, and mesiodistal border on cephalic shoulder. Central projection triangular in cephalic view, formed by caudal and cephalic elements. Preannular plate of annulus ventralis complete, extending laterally beyond sternal plates, reaching coxae of fourth pair of pereopods, 4.5 to 5.2 times as wide as long; anterior margin overlapping adjacent sternal plate, posterior margin with wide median concavity, where median lobe fits. Annulus trapezoidal, anterior margin projected cephalically, with deep cephalic groove; apical portion flat, with sigmoidal groove that continues over caudal surface; apical protuberance absent.

Postannular sclerite subtriangular, with apical notch, in contact with annulus (Fig. 2g).

Measurements of types.—See Table 1.

Description of holotypic male, form I.—Body pigmented. Cephalothorax cylindrical, becoming thicker in branchial region, 0.9 times length of abdomen. Areola obliterated, 34.5% of TCL. Dorsal surface of carapace with scattered punctations in gastric region, area next to postorbital ridges with fine punctations; branchial region with punctations of variable size; hepatic region smooth, with few scattered punctations. Anterior border of carapace, between suborbital angle and branchiostegal spine, with 3 spines of unequal size, mesial one largest. Rostrum with reduced marginal spines, dorsal surface smooth, slightly concave; margins of rostrum converging anteriorly, anterior width 2.7 mm, posterior width 5.4 mm; subrostral ridges not visible in dorsal view (Fig. 1b). Acumen length 23.6% of RL, triangular, grooved, tip chitinized, reaching distal margin of ultimate podomere of antennular peduncle. Postorbital ridges parallel, well marked, ending in short cephalic spine. Suborbital margin of carapace straight, infraorbital spine absent. Two short cervical spines each side of carapace, oriented cephaloventrally (Fig. 1a); cervical groove discontinuous.

Abdomen narrower than carapace, tergal region of somites with scarce punctations, pleural surface smooth. Telson covered with short setae dorsally; cephalic portion with 2 spines of equal length in posterolateral angles, external one fixed, internal one articulated; caudal margin of telson straight. Cephalic lobe of epistome subtriangular, anterior vertex with acute cephalomedian projection, caudolateral angles broadly rounded, ventral surface flat with scattered small setae; cephalic lobe delimited posteriorly by strong constriction; body of epistome with raised lateral margins, fovea in cephalomedian section, well defined (Fig. 1e). Antennal scale 2.3 times as long as wide, elongated, slender, with deep longitudinal groove; maximum width at mid-

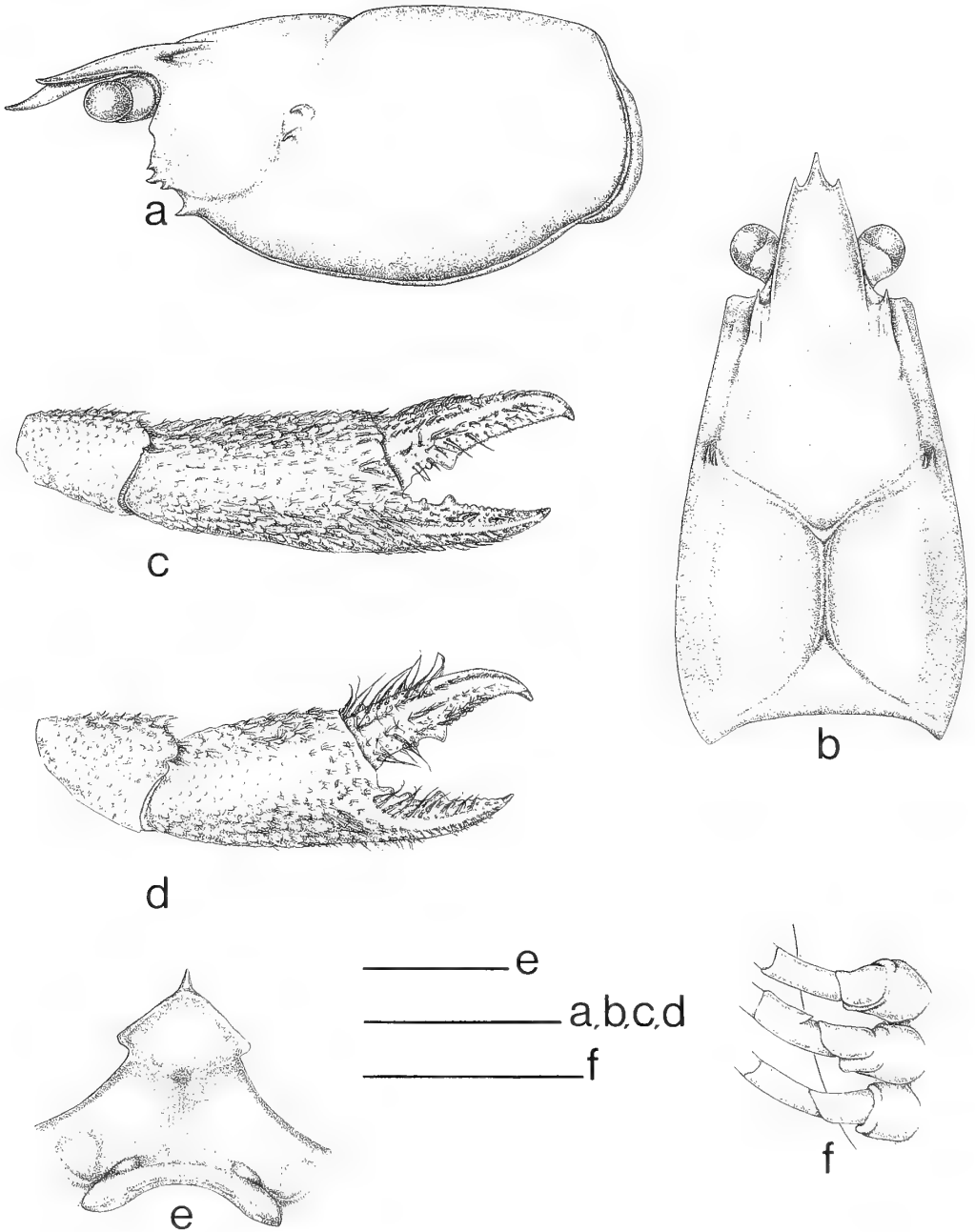


Fig. 1. *Procambarus (Austrocambarus) catemacoensis*, new species, all from holotypic male (CNCR 17993) except d from allotypic female (CNCR 17994): a, carapace, lateral view; b, carapace, dorsal view; c, distal podomeres of right cheliped (male); d, distal podomeres of cheliped (female); e, epistome; f, basal podomeres of left second, third, and fourth pereiopods. Scale bars represent 10 mm (a, b, c, d), 2 mm (e), and 5 mm (f).

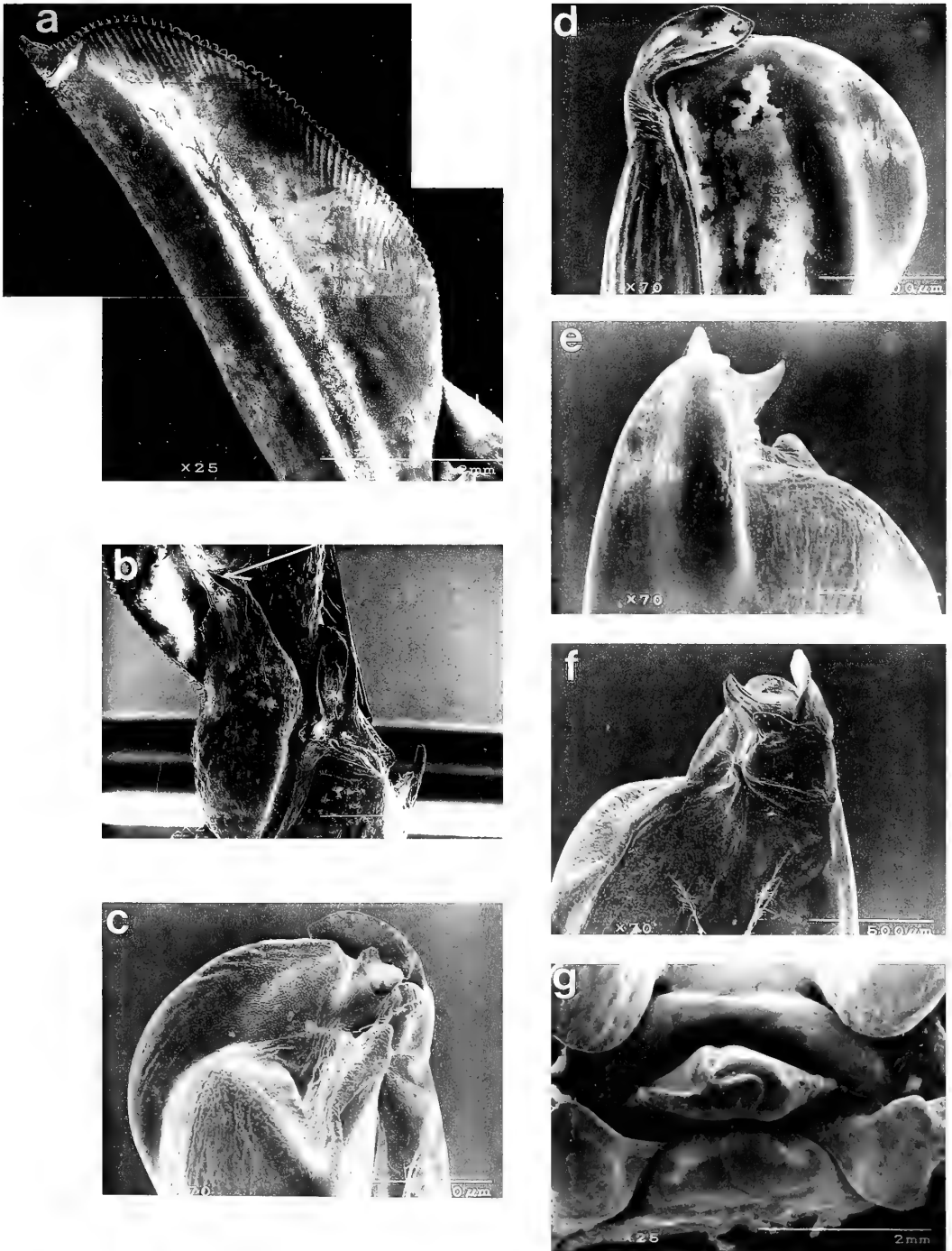


Fig. 2. *Procambarus (Austrocambarus) catemacoensis*, new species, all from holotypic male (CNCR 17993) except g from allotypic female (CNCR 17994): a, antenna scale, dorsal view; b, proximal two segments of antennal peduncle, ventral view; c, left gonopod, cephalic view; d, left gonopod, caudal view; e, left gonopod, lateral view; f, left gonopod, mesial view; g, annulus ventralis, ventral view.

Table 1.—Measurements (mm) of the type specimens of *Procambarus (Austrocambarus) catemacoensis*, new species.

	Holotypic male, form I	Allotypic female
Total length	62.3	64.0
Carapace		
Total length	31.0	32.0
Postorbital length	22.3	23.7
Areola		
Length	10.7	11.0
Width		0.2
Rostrum		
Length	7.2	9.6
Anterior width	2.7	3.7
Posterior width	5.4	6.7
Acumen length	1.7	2.2
Cheliped		
Length of mesial margin of palm	12.7	10.5
Width of palm	6.6	6.5
Length of lateral margin	21.3	18.7
Length of dactyl	10.1	10.2
Abdomen		
Width	10.3	12.0
Length	31.3	33.0

length (Fig. 2a). Antennal peduncle with basis ending in distolateral spine, ischium with ventral spine. Second segment of endopodite of antennal peduncle with spine on distal margin (Fig. 2b). Third maxilliped reaching midlength of second segment of antennal peduncle; ventral surface of ischium with short, fine setae; exopodite extending beyond distal of merus of endopodite.

Chelae shorter than TCL, tuberculate; right chela 3.2 times as long as broad, pubescent, fingers shorter than palm; palm about 1.9 times as long as broad, lateral surface covered with subsquamous tubercles and long, fine setae along dorsal and ventral margins; mesial surface with scattered setae. Fixed finger with cutting edge flanked laterally by longitudinal row of rounded tubercles.

Carpus approximately conical, dorsal and lateral surfaces with scattered small subsquamous tubercles; dorsal surface bearing

distal, sharp, hooklike spine; mesial surface covered with conical tubercles and long setae (Fig. 1c). Merus with spine on distal margin of dorsal surface; mesially, distal margin with row of small tubercles; lateral surface with scattered punctations; mesial surface with 2 longitudinal, parallel rows of spiniform tubercles, setae on space between rows.

Third pereopods with ischium bearing sharp hook, tip not reaching basioischial articulation (Fig. 1f). Fifth pereopods with coxa bearing small tuberculiform projection on mesial surface.

First pair of pleopods (gonopods) as in Diagnosis.

Uropods with short spines on proximal lobes; mesial ramus with premarginal distomedial spine; lateral ramus with 2 spines on distolateral angle, external one fixed, internal one largest, articulated.

Description of morphotypic male, form II.—Unknown.

Description of allotypic female.—Differing from holotypic male in following characters: Areola linear, 34.4% of TCL; anterior border of carapace, between branchiostegal spine and antennal angle, with 3 spines in addition to branchiostegal spine; right chela shorter, 2.9 times as long as wide; fingers as long as palm, covered with long setae; palm 1.6 times as long as wide, devoid of setae on central portion (Fig. 1d); thoracic sternite ridgelike between first and second pereopods, with 3 subacute tubercles, becoming wider between second and third pereopods, smooth between third and fourth pereopods. Annulus ventralis as described in Diagnosis.

Type locality.—Espagoya, Lake Catemaco (altitude 335 m), Municipio de Catemaco, Veracruz, Mexico (18°27'N, 95°6'W).

Disposition of types.—Holotypic male form I CNCR 17993, allotypic female CNCR 17994. Paratypic males form I (2) CNCR 1414.

Material examined.—All specimens from Espagoya, Lake Catemaco, 335 m of

altitude, Veracruz, México: 1 ♂ juv., 3 ♀ juv. (CNCR 1416), 21 Sep 1953, coll. A. Villalobos; 2 ♀, 3 ♂ juv. (CNCR 1413), 8 Dec 1953, coll. A. Villalobos; 3 ♂ form I, 3 ♀ (CNCR 1414), 17 Apr 1957, coll. A. Villalobos.

Etymology.—The species name is derived from "Catemaco" the name of the lake where the type locality is located.

Remarks.—Although the new species *P. (A.) catemacoensis* is morphologically similar to *P. (A.) acanthophorus*, the two can be distinguished by: a wider mesial process of the form I male gonopod, that is completely folded over the lateral shoulder; in lateral view, laterodistal border of cephalic shoulder closer to apex (half the distance found in *P. (A.) acanthophorus*), mesial process and central projection separated; annulus ventralis trapezoidal, with characteristic groove in apical position (caudally positioned in *P. (A.) acanthophorus*); post-annular sclerite subtriangular with apical notch, in contact with annulus (postannular sclerite oval shaped, smooth, and separated from annulus in *P. (A.) acanthophorus*). In addition the following somatic characters can also be used to discriminate between the two species: the number of spines on the anterior border of the carapace, four in *P. (A.) acanthophorus*, two or three in the new species; an obliterated areola in the new species versus a narrow, but not obliterated one in *P. (A.) acanthophorus*; smaller and separated cervical spines in *P. (A.) catemacoensis*; second segment of the antennal peduncle with a spine in the new species. In adult specimens the chelae of both species differ widely, the males of *P. (A.) catemacoensis* have scattered setae along the dorsal and ventral margins, while in *P. (A.) acanthophorus* the whole chela is densely covered with setae. In the females, the chelae of *P. (A.) catemacoensis* are stronger, and possess a large triangular tooth in the middle portion of the cutting edge of both fingers; while in *P. (A.) acanthophorus* the chelae are slender, elongated, and without the large triangular tooth.

Similar to the problem encountered with *Procambarus (Austrocambarus) mexicanus* (Erichson, 1846), where a number of closely related forms classified as the same taxon have proven to be more than one species (Rojas et al. 1999), the new species described herein was previously confounded with *P. (A.) acanthophorus*. New revisions of widely distributed species of cambarids in Mexico will probably result in the discovery of additional new species.

The Los Tuxtlas region supports a remarkably large list of 12 endemic freshwater decapods (Alvarez & Villalobos 1997, Villalobos & Alvarez 1999). In particular, two cambarids, *P. (A.) vazquezae* Villalobos, 1954 and *P. (A.) catemacoensis* new species, one palaemonid shrimp, and two species of pseudothelphusid crabs, are endemic to Lake Catemaco (Alvarez & Villalobos 1997). As more studies are published increasing the number of endemic freshwater species living in Los Tuxtlas, it becomes evident that stronger protection policies need to be developed for this region.

Acknowledgments

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The Identities of *Pinnotheres nudus* Holmes, 1895 and *P. nudus* sensu Weymouth, 1910 (Crustacea: Decapoda: Pinnotheridae)

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Abstract.—The eastern Pacific species *Pinnotheres nudus* Holmes, 1895 is synonymized with *Opisthopus transversus* Rathbun, 1893. *Pinnotheres nudus* sensu Weymouth, 1910, named *P. holmesi* by Rathbun in 1918, also from the eastern Pacific, is shown to be a synonym of the western Atlantic *Zaops geddesi* (Miers, 1880), the second species to be assigned to the genus *Zaops* Rathbun, 1900.

Our ongoing studies of pinnotherid crabs of the Americas continue to yield new information on the identity of American species, newly discovered synonyms for them, and newly recognized genera and species from the Americas, including, *Tumidotheres* Campos, 1989; *Juxtafabia* Campos, 1993; *Epulotheres* Manning 1993; and *Nannotheres* Manning & Felder, 1997.

Here we clarify the identity of two species from California originally placed in the genus *Pinnotheres* Bosc, 1802: *P. nudus* Holmes, 1895, which we show to be a synonym of *Opisthopus transversus* Rathbun, 1893; and *P. nudus* sensu Weymouth, 1910, named *P. holmesi* by Rathbun (1918), which we believe is a synonym of *Zaops geddesi* (Miers, 1880), a western Atlantic species. This latter species probably was introduced in California, where it apparently has not become established.

Rathbun's (1893; 1918) accounts of the two species discussed here are so accurate that we quote them directly. We have added a few additional characters, indicated in italics, to her description of *Z. geddesi*.

Abbreviations used in the text include: cb, carapace width; cl, carapace length;

MXP3, third maxilliped; WL, walking leg(s). The acronym USNM indicates material in collections of the National Museum of Natural History, Smithsonian Institution, Washington, D.C., and UABC in collection of the Laboratorio de Invertebrados, Facultad de Ciencias, Universidad Autónoma de Baja California, México.

Opisthopus transversus Rathbun, 1893
Figs. 1, 2

Opisthopus transversus Rathbun, 1893:252 [type locality: Monterey, California (36°35'N, 121°55'W)]; 1918:172, fig. 110, pl. 37, figs. 4, 5.—Schmitt et al., 1973:131 [complete synonymy].

Pinnotheres nudus Holmes, 1895:563, pl. 20, figs. 1–5 [type locality: Santa Cruz, California].—Rathbun, 1918: 83, pl. 64.—Schmitt et al., 1973:60 [see for a complete synonymy based on the unique original record]. [Not *P. nudus* sensu Weymouth, 1910:53 = *Zaops geddesi* (Miers, 1880).]

Material examined.—2 males, Punta San Miguel, Todos Santos Bay, 13 Oct 1985, in *Aplysia vaccaria* Winkler, Ensenada, Baja California; 3 females (1 juvenile), Punta Sofia, 26–27 Dec 1989, in *Pseudochama*

† Deceased 18 January 2000.

exogyra (Conrad); 1 male, in *Modiolus capax* (Conrad); 2 males, 2 females, 28–29 Dec 1990, in *P. exogyra*. 1 juvenile female, El Rincón, in cultured *Crassostrea gigas* (Thunbergs), 2 males, 3 females, La Bajada, 30–31 Dec 1990, in *Atrina tuberculosa* (Sowerby), Tortugas Bay, Baja California Sur (27°39'N, 114°54'W).

Description (from Rathbun 1918:83, as *P. nudus*).—Carapace a little broader than long, subquadrate with corners rounded, the anterior half nearly same shape and size as posterior half; surface curving downward toward all margins, smooth and naked; regions not defined. Front not protruding. Orbits ovate.

Chelipeds smooth, hands rather thick, widest immediately behind articulation of dactyl; fingers nearly or quite as long as palm, subconical, not conspicuously dentate on inner margin, partly covered by a very short, dense pubescence.

Three anterior legs subequal, fourth smaller; all are smooth, little compressed, and have acute, nearly straight tarsi, those of four pair being relatively longer and more slender than those preceding.

Abdomen of the female nearly circular, covering entire sternal surface, composed of seven separate segments of which the fourth, fifth, and sixth are subequal and larger than the others.

Remarks.—*Pinnotheres nudus* was described and named by Holmes (1895) on the basis of two females (cl 20 mm, cb 24 mm and cl 15.5 mm, cb 19 mm) from Santa Cruz, California. The female holotype and other female collected in Santa Cruz and Monterey, California, respectively, deposited in the California Academy of Sciences, were destroyed in the fire following the San Francisco earthquake in 1906 (Rathbun 1918).

Analysis of the Holmes's (1895) original description of *P. nudus* resulted in our finding that its morphology agrees very well with that observed in actual specimens of *O. transversus* Rathbun, 1893 (Fig. 2A–J). Both have the carapace dorsally smooth and

naked, subquadrate in outline, with rounded corners. They have a MXP3 with a carpus shorter than the spatulate propodus, and a spoon-shaped dactylus that is inserted proximally on the ventral margin of the propodus, with its apex extending beyond the tip of the propodus. Both have the WL1–3 subequal in length and shape, WL4 being shortest; an abdomen, nearly circular, composed of six somites and telson free, with somites 4–6 subequal and larger than the others. Other shared features include the large antennae, visible when dorsally, cheliped shape, and pubescence on the cheliped, MXP3, and abdomen. The lack of a suture between the ischium and merus of MXP3 in the original figure of *P. nudus* (Fig. 1E) is interpreted as an inaccuracy in the original artistic work. Further, that character was not mentioned in the original description. Females of *O. transversus* have a visible suture, although, as in some males, it sometimes is faintly indicated and can be overlooked. Crosnier (1969) reported a male lacking this suture. The carapace of *Opisthopus transversus* is variable in shape, in some specimens more quadrate, in others more rounded (Fig. 2A–C).

Based on the close similarity between actual specimens of *O. transversus* and the description and figures of *P. nudus* we believe that these two taxa should be considered synonyms.

Opisthopus transversus now ranges from Santa Cruz, California, U.S.A. to Laguna de San Ignacio, Baja California Sur, México. It is a symbiont in a wide variety of hosts including amphineuran mollusks, gastropods, bivalves, polychaetes and holothuroids (see Campos et al. 1992).

Zaops geddesi (Miers, 1880), new combination
Figs. 3, 4C–E

Pinnotheres geddesi Miers, 1880:86 [type locality: Veracruz, Mexico (19°11'N, 96°10'W); syntypes in The Natural History Museum, London].—Rathbun,

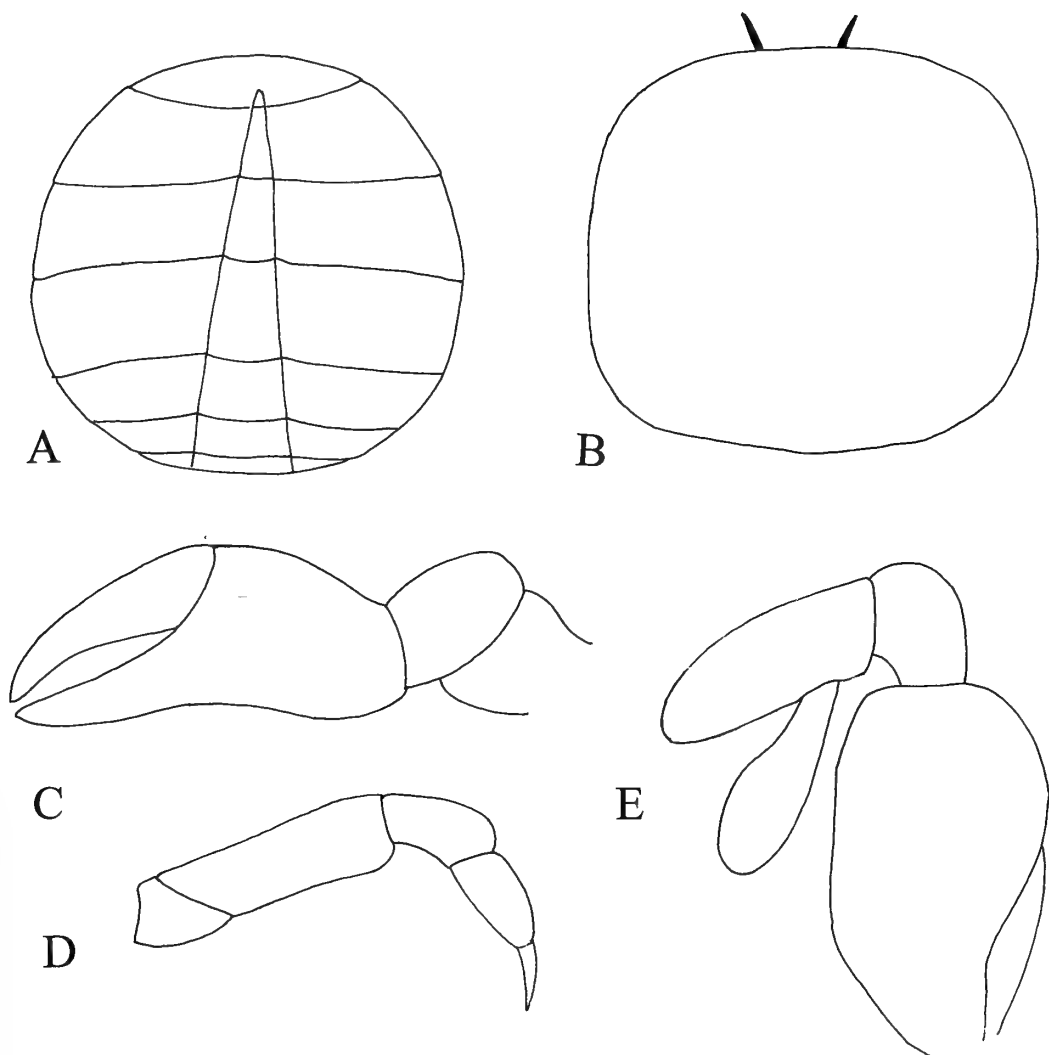


Fig. 1. *Pinnotheres nudus* Holmes, 1895, female holotype. A, Abdomen; B, Carapace; C, Left cheliped, outer aspect; D, Fourth WL; E, MXP3. (from Holmes 1895:pl. 20).

1918:70, fig. 32, pl. 16, figs. 1-4.—Schmitt et al., 1973:45 [complete synonymy].

Pinnotheres ostrearius Rathbun, 1901:20, fig. 3 [type-locality: Mayaguez, Puerto Rico (18°13'N, 67°09'W)]

Pinnotheres nudus.—Weymouth, 1910:53, fig. 1 [Monterey Bay, California (Monterey = 36°35'N, 121°55'W)] [not *P. nudus* Holmes, 1895 = *Opisthopus transversus* Rathbun, 1893].

Pinnotheres holmesi Rathbun, 1918:68, fig.

31, pl. 15, figs. 1, 2 [type locality: ?Pacific Grove, California (36°36'N, 121°56'W)].

Material examined.—*Pinnotheres ostrearius* Rathbun, holotype and paratype, USNM 23767; *P. holmesi* Rathbun, holotype, USNM 51000.

Description (except underlined, from Rathbun, 1918: 70, as *P. geddesi*).—“Carapace very soft and yielding, transversely suborbicular, broad behind. Gastric region

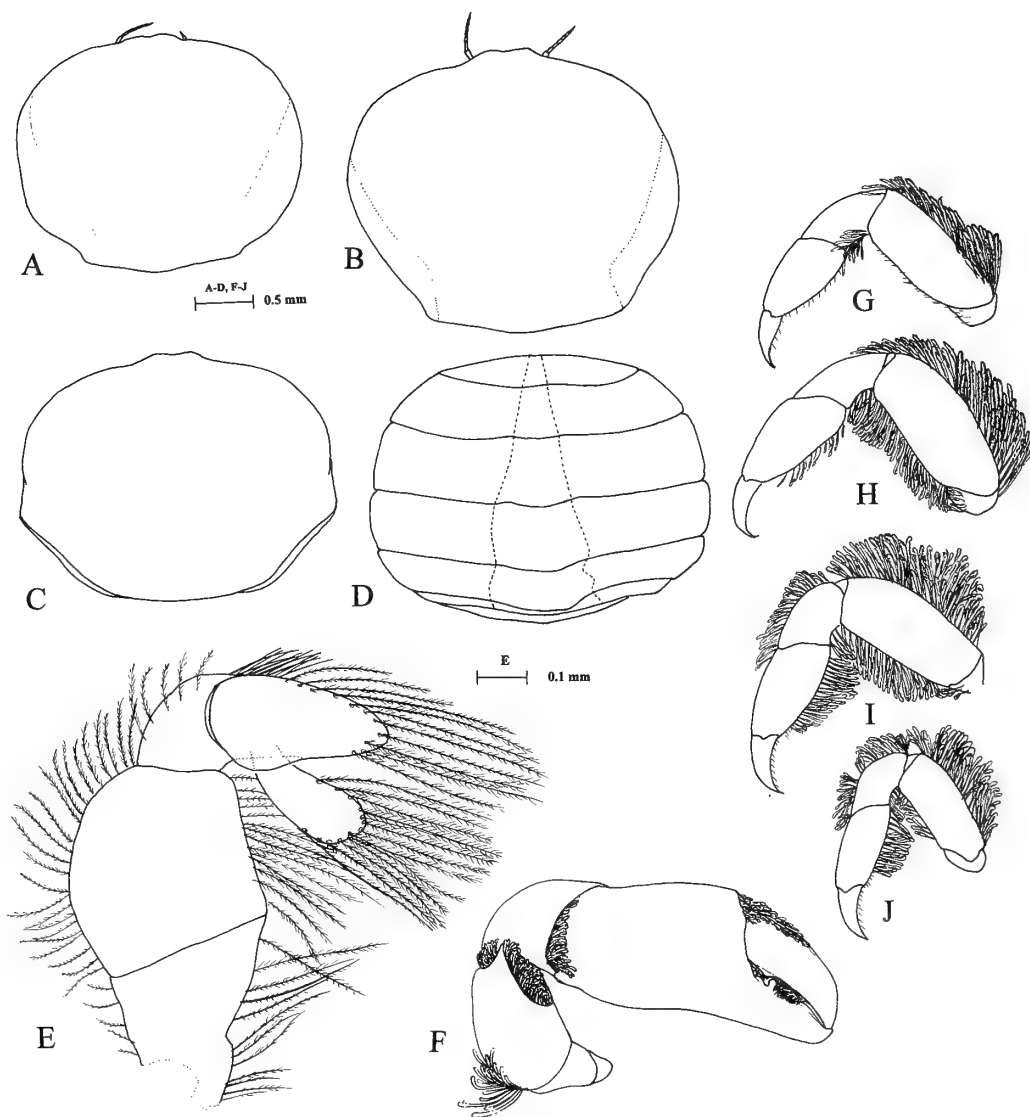


Fig. 2. *Opisthopus transversus* Rathbun, 1893, female UABC uncat. A–C, Carapace; D, Abdomen; E, MXP3; F, Right cheliped, outer aspect; G–J, WL1 to 4 respectively. A, Punta Sofia, Tortugas Bay, Baja California Sur, B, D–J, Punta San Miguel, Todos Santos Bay, Ensenada, Baja California UABC uncat; C from Crosnier, 1969, USNM 50997.

distinctly outlined by a furrow, cardiac region less distinct. Front rounding downward, slightly projecting, truncate in dorsal view. Orbits circular, eyes partly visible in dorsal view.

Ischium-merus of outer maxillipeds robust, outer margin regularly convex, inner margin with bluntly rounded angle near dis-

tal extremity; carpus and propodus robust, the latter rounded and ciliated at distal end; dactyl very slender, styliform, reaching about to extremity of propodus.

Chelipeds smooth; palm rapidly increasing in width from proximal to near distal end, which articulates almost vertically with dactylus; upper margin convex at widest

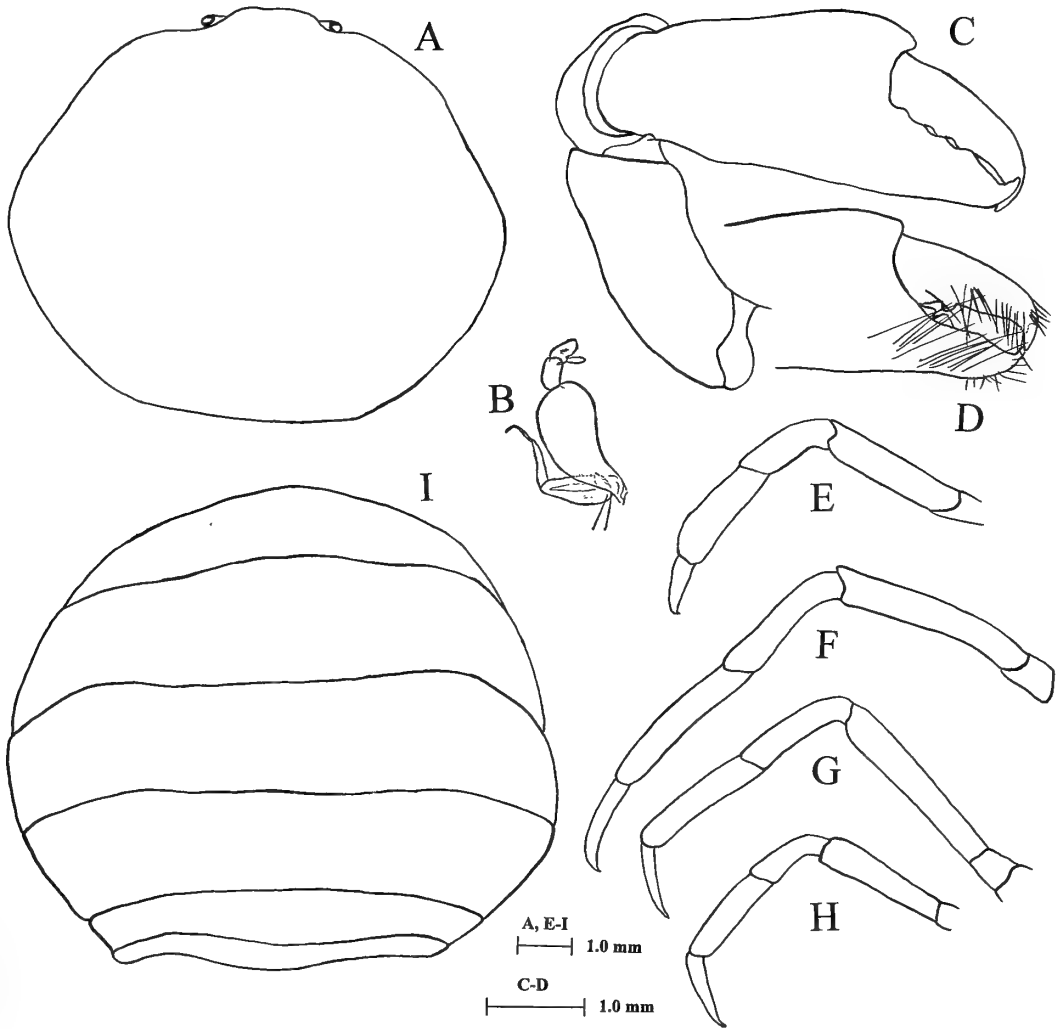


Fig. 3. *Pinnotheres holmesi* Rathbun, 1918, ovigerous female holotype, cl 7.2 mm, cb 8.7 mm, USNM 51000. A, Carapace, dorsal view; B, MXP3 (from Rathbun 1918:fig. 31); C, Left cheliped, outer aspect; D, Left chela, outer aspect; E-H, WL1-4, respectively.

part, lower margin of entire propodus convex; fingers subconical, somewhat hairy, edges meeting and tips crossed when closed.

Legs slender; first one stouter than the others, propodus scarcely widening distally, dactylus about half as long, stout, anterior margin convex, posterior straight; second leg longest, left (106 mm) slightly longer than right (100 mm) in holotype, third subequal to first; fourth reaches about to middle of propodus of third; dactylus of second

leg long, curved, about two-thirds as long as propodus; dactylus of third leg shorter, of fourth still shorter, straighter, and more hairy; third dactylus nearly straight behind, fourth quite straight behind”.

Remarks.—Our initial conclusion from an examination of Rathbun’s (1918) type of *P. holmesi* was that it is conspecific with *Zaops ostreum* (Say, 1818), the common western Atlantic oyster crab. Further study, however, convinced us that *P. holmesi* is identical to *P. geddesi* Miers, 1880, and that

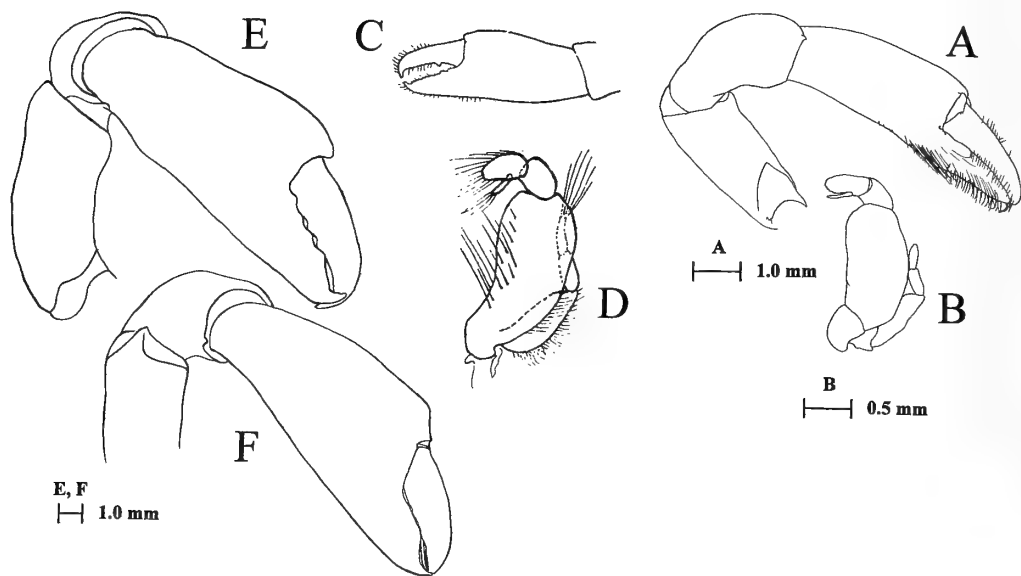


Fig. 4. Species of *Zaops*. A, B, F, *Z. ostreum* (Say, 1818), C–E, *Z. geddesi* (Miers, 1880), new combination (C, D, type of *P. ostrearius* Rathbun, 1901). A, Left cheliped, dorso-inner aspect; B, MXP3; C, Left chela, outer aspect; D, MXP3; E, F, Right chela, outer aspect. (A, B from Manning 1993:fig. 5; C, D, from Rathbun 1901:fig. 3 and Rathbun 1918:fig. 32).

Miers taxon should be transferred to the genus *Zaops*. It is the second species of *Zaops* Rathbun, 1900.

Rathbun [1918:63, (key); 69, (text)] commented that one of the distinguishing features of *Pinnotheres holmesi* is that the palm widens rapidly to a point behind base of fingers (Figs. 3C, 4A); she reported the same character in her account of *P. ostrearius* (1901:20). So far as we can tell, the shape of the palm is almost the same in *Z. geddesi* (Fig. 4E) and *Z. ostreum* (Fig. 4F). The species cannot be differentiated using this character.

The major difference in the chela of the two species lies in the angle of the articulation of the dactylus to the propodus. In *Z. geddesi* the articular surface of the propodus (Fig. 4E) is almost vertical, whereas in *Z. ostreum* that surface is at an oblique angle (Fig. 4F).

Another character mentioned by Rathbun (1918:69) is that the first three legs (WL1–3) are much slenderer in *Z. geddesi* than in *Z. ostreum*. This may not be true, as the length of the propodus is almost seven

times longer than high in *Z. ostreum*, less than six times longer than high in *Z. geddesi*. This may be a feature that varies with size and whether the longer or the shorter WL2 is measured.

A second, possible record for *Pinnotheres holmesi* is mentioned in a letter dated September 5, 1946 from H. W. Clark of Pacific Union College to S. A. Glassell. Clark noted:

“We found a specimen of *Pinnotheres holmesi*, as it appears to be, in the mantle cavity of a large clam. All we can find on it is in Schmitt’s Marine Decapods of California. . . Our specimen varies from his description in several points, not enough to make a new species, but perhaps enough to make a new subspecies. We found it on the Sonoma coast.”

So far as we can tell, this observation has never been published and we have not been able to determine whether the material is extant.

Zaops geddesi is the southern counterpart of *Z. ostreum*, and like *Z. ostreum*, its preferred habitat is in oysters, although no specific host has been mentioned in the literature. *Zaops geddesi* is known from Vera-

cruz, Mexico; Cuba; Puerto Rico; and Brazil (Rathbun 1918).

The single specimen of *Zaops geddesi* known to occur in the eastern Pacific must have been introduced around or before the turn of the century. There is no evidence that the species occurs naturally in the eastern Pacific.

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We thank James T. Carlton, Williams College—Mystic Seaport, Connecticut, for his comments on introduced species in California; to Rafael Lemaitre, Gerhard Pohle and Fernando D’Incao for reviewing our manuscript with great care. Figs. 1 and 2 were prepared by Alma Rosa de Campos and Figs. 3 and 4 by Lilly King Manning. We gratefully acknowledge their contributions. Campos’ studies of pinnotherids are supported by program Crustáceos simbiosites del Pacífico Mexicano. Manning’s studies of pinnotherids were supported by the Smithsonian Marine Station at Fort Pierce, Florida. This is contribution no. 488 from that facility.

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A new raninid crab (Crustacea: Decapoda: Brachyura) from the Kase Formation (lower Miocene) of Kyushu, Japan

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Abstract.—*Carinaranina fudoujii*, new species, a crab of the family Raninidae is described from the lower Miocene Kase Formation in Nagasaki Prefecture, Kyushu, southwest Japan. Recognition of this species of *Carinaranina* from the Miocene of Japan expands the geographic and geologic ranges of the genus, previously known from the Eocene–Oligocene of the Pacific slope of the U.S.A.

Tucker (1998) established the genus *Carinaranina* Tucker (1998) within the family Raninidae De Haan, 1841 and referred five species from Eocene–Oligocene rocks of Washington and Oregon to it. She also suggested using cladistic analysis that *Carinaranina* had close affinities with extant *Raninoides* H. Milne Edwards, 1837 and extinct *Laeviranina* Lörenthey in Lörenthey & Beurlen, 1929.

The purpose of the present paper is to describe a new species of *Carinaranina* from the Miocene of Japan. The specimens were collected from shale of the Kase Formation exposed in a cliff about 1.2 km east of Motogaura (Loc. KS-1), Shikano-cho, Kitamatsu-ura-gun, Nagasaki Prefecture (33°16'28"N; 129°37'03"E) (Fig. 1). *Carinaranina* occurred in the deposits, in association with a pelecypod, *Portlandia watasei* (Kanehara, 1937), and decapods, *Carcinoplax antiqua* (Ristori, 1889), and *Minohellenus* sp. The presence of planktonic foraminifera indicates that the geologic age of the Kase Formation was the earliest Miocene (24.5 Ma and 22.4 Ma) (Sakai et al. 1990).

Specimens are deposited in the Mizunami Fossil Museum (MFM), Yamanouchi, Akeyo, Mizunami, Gifu, Japan, and the Kitakyushu Museum and Institute of Natural History (KMNH IvP), Nishihonmachi 3-chome, Yahatahigashi-ku, Kitakyushu, Japan.

Systematics

Family Raninidae De Haan, 1841
Subfamily Raninoidinae Lörenthey in
Lörenthey & Beurlen, 1929
Genus *Carinaranina* Tucker, 1998

Type species.—*Eumorphocorystes nase-lensis* Rathbun, 1926 by original designation.

Geologic range.—Upper Eocene–lower Miocene.

Carinaranina fudoujii, new species
Figs. 2, 3

Types.—MFM83061, holotype; 7 paratypes, MFM83062–83065, KMNH IvP 300,024–300,026.

Diagnosis.—Large sized *Carinaranina*. Carapace longitudinally ovate in outline, length about 1.4 times width, widest almost at midlength. Orbitofrontal margin narrow. Rostrum triangular, convex dorsally. Upper orbital margin with 2 V-shaped fissures. Outer orbital tooth wide, bifid; internal branch triangular; external branch broad without supplementary spine. Inner orbital tooth small. Anterolateral margin slightly concave. Hepatic spine slender, about 12% carapace length. Posterolateral margin weakly sigmoid. Dorsal surface gently convex, finely punctuate, with median carina. Chelipeds slender, elongate; dactylus and

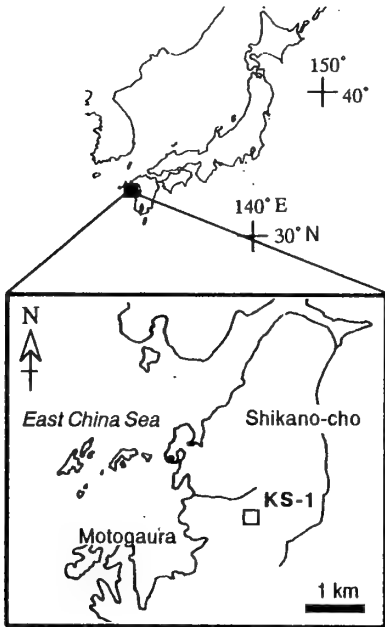


Fig. 1. Locality map.

propodus finely tuberculate; dactylus with granulated ridge on dorsal margin; propodus long, somewhat spinose on ventral margin; merus long. Dactylus of pereopod 2 lanceolate.

Description.—Carapace (Figs. 2.1, 2.3, 2.6b, 2.8, 3.1) large for *Carinaranina*, longitudinally ovate in outline, length about 1.4 times width excluding hepatic spine, widest almost at midlength. Orbitofrontal margin occupying about 0.6 carapace width. Rostrum triangular, convex dorsally, with straight, beaded margins. Upper orbital margin marked by 2 open fissures; inner fissure V-shaped, directed longitudinally; outer fissure also V-shaped, slightly shallower than inner, approximately parallel to lateral margin of external branch of outer orbital tooth. Outer orbital tooth wide, bifid, margins finely granulate; internal branch triangular, longer than external branch but not shorter than rostrum; external branch broad, triangular, without supplementary spine. Inner orbital tooth small, triangular, directed anterolaterally. Anterolateral margin slightly concave; hepatic spine slender, directed

anterolaterally, about 12% carapace length. Posterolateral margin weakly sigmoid, tapering posteriorly, with beaded marginal rim. Posterior margin slightly concave, about half carapace width. Dorsal surface gently convex longitudinally and transversely, medially keeled, finely punctate except for marginal part of hepatic and epi-branchial regions which are covered with fine granules. Dorsal regions poorly defined; only shallow, arcuate branchiocardiac grooves visible. Pterygostomial regions (Fig. 2.7) finely punctated ventrally.

Thoracic sternum (Figs. 2.2, 2.7, 3.2) narrow, elongate, fused through sternites 1–6, with smooth surface; sternites 1–3 separated from sternite 4 by slight emargination; lateral margins of sternite 4 concave, slightly tapering posteriorly; processes between somites 4 and 5 forming widest part of sternum; lateral margins of sternite 5 converging posteriorly; sternite 6 narrower than 5.

Chelipeds (Figs. 2.5a–c, 2.6a–b, 2.8a–b) slender, elongate; dactylus short, about as long as fixed finger, finely tuberculate on lateral and mesial surfaces, bearing granulated, dorsal ridges; propodus long, ovate in cross section, ornamented with fine, irregular tubercles on surfaces, somewhat spinose on ventral margin; fixed finger deflexed ventrally, occupying about 0.25 propodus length; carpus about 0.5 propodus length, cylindrical in cross section, finely granulate on surfaces; merus long, cylindrical in cross section, about equal to propodus length, surfaces covered with fine granules.

Propodus and dactylus of pereopod 2 (Fig. 2.4) lamellate; propodus short, ovoid in lateral view; dactylus lanceolate, keeled medially.

Ischium and merus of maxilliped 3 (Fig. 2.7), long, slender.

Etymology.—The specific name honors Yasuhiro Fudouji, Karatsu, Saga, Japan, who collected the type specimens.

Remarks.—*Carinaranina fudoujii* is most similar to *Carinaranina naselensis* (Rathbun, 1926) from the Oligocene of

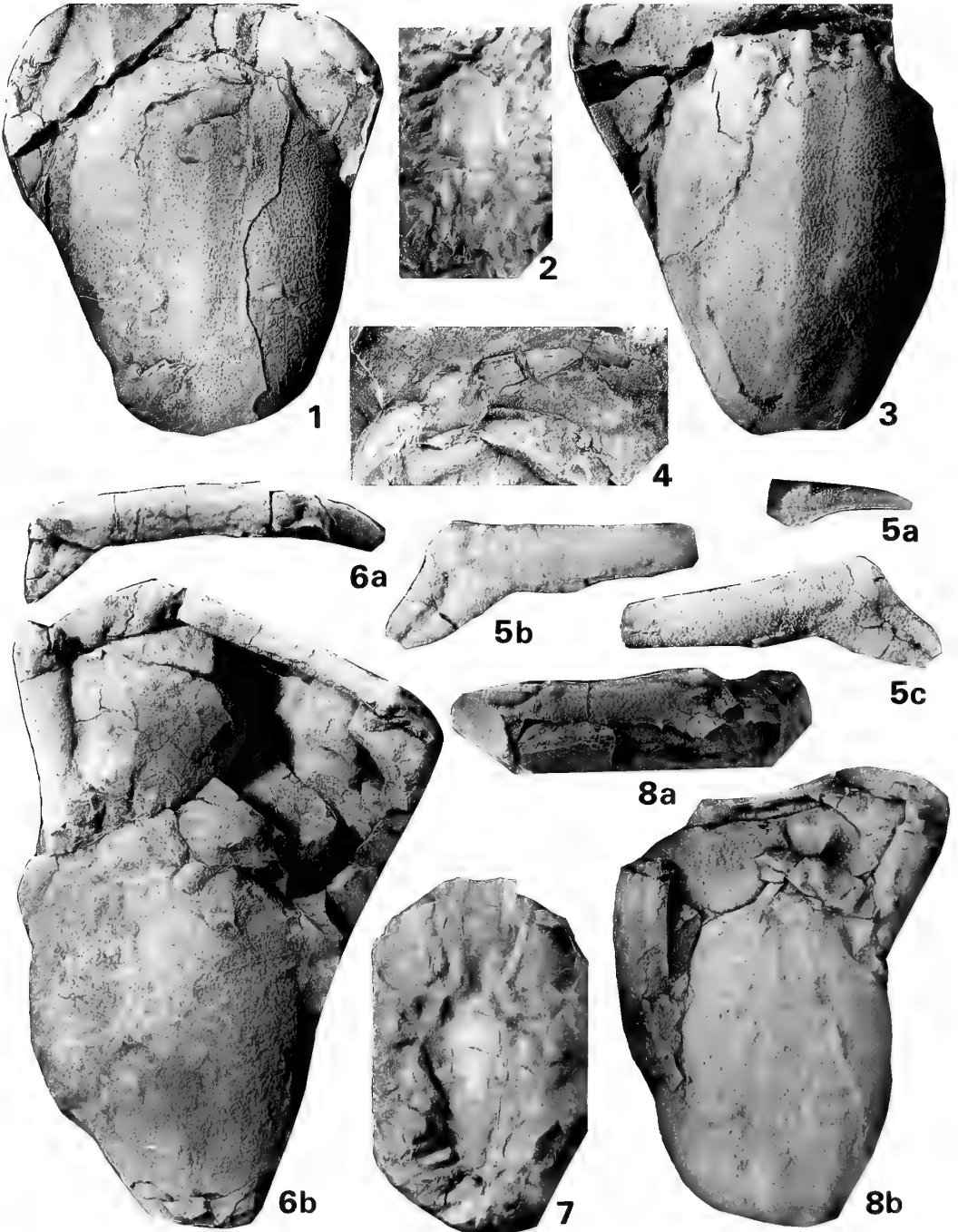


Fig. 2. *Carinaranina fudoujii*, new species: 1, KMNH IvP 300,024 (paratype), carapace and chelipeds, $\times 1.2$, dorsal view; 2, KMNH IvP 300,025 (paratype), thoracic sterna, $\times 1.2$, ventral view; 3, MFM83061 (holotype), carapace and cheliped, $\times 1.5$, dorsal view; 4, MFM83062 (paratype), pereopods 2, $\times 1.2$, lateral view; 5a-c, MFM83063 (paratype), right cheliped, $\times 1.2$, a, dorsal view of dactylus; b, mesial view; c, lateral view; 6a, b, KMNH IvP 300,026 (paratype), carapace and chelipeds, $\times 1.2$, a, lateral view of left cheliped; b, dorsal view; 7, MFM83064 (paratype), thoracic sterna and maxillipeds 3, $\times 1.5$, ventral view; 8a, b, MFM83065 (paratype), carapace and chelipeds, $\times 1.2$, a, lateral view of right cheliped; b, dorsal view.

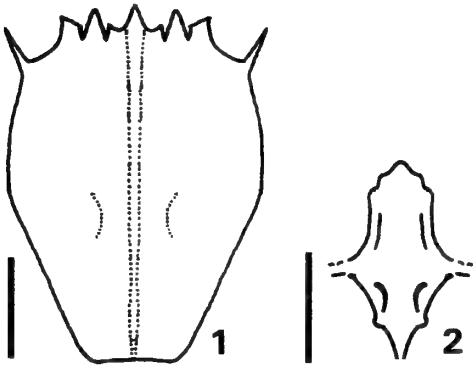


Fig. 3. Reconstruction of *Carinaranina fudoujii*, new species: 1, carapace, dorsal view; 2, thoracic sternites 1-6, ventral view. Scale bar equals 1 cm.

Washington, the type species of the genus, but differs in having a wider orbitofrontal region with two V-shaped open fissures on the upper orbital margin; a large, triangular internal branch of the outer orbital tooth; and a pair of slender, anterolaterally directed hepatic spines. The present new species differs from *Carinaranina willapensis* (Rathbun, 1926) from the Eocene Hoko River Formation of Washington by having a small inner orbital tooth, a broad external branch of the outer orbital tooth without a supplementary spine, and a pair of short hepatic spines. *Carinaranina fudoujii* is distinguished from *Carinaranina schencki* (Rathbun, 1932) from the Eocene Keasey Formation of Oregon by having a wide orbitofrontal margin. Two V-shaped fissures on the upper orbital margin and a short, slender hepatic spine readily distinguishes the present species from *Carinaranina marionae* Tucker, 1998 from the Eocene Hoko River Formation of Washington. From *Carinaranina leucosiae* (Rathbun, 1932) from the Eocene Keasey Formation of Oregon, *C. fudoujii* differs in that the latter exhibits a transversely ovate carapace and lacks spines on the dorsal margin of the propodus of the cheliped.

Hitherto, known members of *Carinaranina* have been recorded from the Eocene-Oligocene of Washington and Oregon

(Tucker, 1998). The discovery of the new species extends the geologic range for the genus from the Oligocene to the early Miocene and the geographic range from the east side of the North Pacific to Japan on the west side of the North Pacific.

Acknowledgments

I thank Dr. J. S. H. Collins (London) for reading my manuscript and Mr. Y. Fudouji (Karatsu, Saga, Japan) for offering fossil crab specimens for study. The manuscript benefited from critical reading by three anonymous reviewers.

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***Medorippe tanabei*, a new species of Miocene dorippid crab
(Crustacea: Decapoda: Brachyura) from the Katsuta Group,
West Honshu, Japan**

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Abstract.—A new dorippid crab, *Medorippe tanabei*, is described from the early middle Miocene Katsuta Group in Okayama Prefecture, Honshu, southwest Japan. The occurrence of *M. tanabei* together with *Medorippe margaretha* (Lörenthey in Lörenthey & Beurlen), new combination, extends the geologic range for the genus back to the middle Miocene. The discovery of the species from the middle Miocene of Japan suggests that the geographic range of the genus early in its history was far greater than it is now. A list of all known fossil species in the world assigned to the subfamily Dorippinae MacLeay is included.

The middle Miocene decapod fauna from the Katsuta Group of southwestern Honshu, Japan was studied by Karasawa (1992, 1993, 1998) and Karasawa & Kishimoto (1996). The decapod fauna consists of 13 species in 13 genera and represents a shallow marine decapod association in the early middle Miocene of Japan (Karasawa 1999).

The purpose of this paper is to describe an additional new species of a dorippid from the Katsuta Group. The material was collected from Shinden, Katsuta City, Okayama Prefecture (35°3'5"N, 134°4'1"E) (Fig. 1). Muddy sandstone of the Yoshino Formation of the Katsuta Group is exposed at the locality (Karasawa 1992). Yoshimoto (1979) assigned the Group to Zones N. 8b–9 (earliest middle Miocene) of Blow's scale of planktonic foraminifera. Karasawa & Kishimoto (1996a) reported nine decapod species from the locality and recognized the decapod assemblage characterized by the predominance of *Callianassa nishikawai* Karasawa, 1993 and *Laurentiella imaizumii* Karasawa, 1993. The assemblage suggests a depositional environment within the intertidal to upper sublittoral zone on a muddy bottom (Karasawa & Kishimoto 1996a).

The specimen is housed in the Mizunami Fossil Museum, Yamanouchi, Akeyo, Mizunami, Gifu, Japan.

Systematics

Family Dorippidae MacLeay, 1838
Subfamily Dorippinae MacLeay, 1838

Remarks.—The subfamily Dorippinae is thought to contain nine Recent genera (Holthuis & Manning 1990) and the Eocene *Titanodorippe* Blow & Manning, 1996. Although Glaessner (1969) placed two extinct genera, *Goniochele* Bell, 1858 and *Orithopsis* Carter, 1872 in the subfamily, both were moved to the Calappidae De Haan, 1833 by Wright & Collins (1972) an arrangement followed by Collins & Smith (1993). In their review of fossil records Holthuis & Manning (1990) included seven species in four genera (*Dorippe* Weber, 1795, *Heikea* Holthuis & Manning, 1990, *Medorippe* Manning & Holthuis, 1981, and *Paradorippe* Serène & Romimohtarto, 1969) within the subfamily. Their review overlooked the occurrence of *Dorippe astuta* Fabricius, 1793 (= *Dorippoides facchio* (Herbst, 1785)) from the Pliocene of Java, described by Van Straelen (1938). Addi-

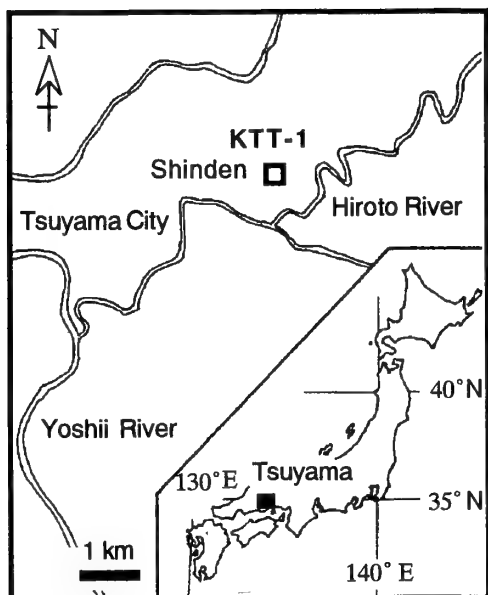


Fig. 1. Locality map.

tional fossil records include *Dorippe frascone tuberculata* Morris & Collins, 1991 from the Pliocene of Brunei, *Nobilum wenchi* Hu & Tao, 1996 from the Miocene of Taiwan, and *Paradorippe granulata* (De Haan, 1841) from the Pleistocene of Japan (Kato & Karasawa 1998).

Although Förster (1979) described *Dorippe? carpathica* Förster, 1979 from the Miocene of Poland, Müller (1996) provisionally placed this species in *Neodorippe*

Serène & Romimohtarto, 1969. Lörenthey in Lörenthey & Beurlen (1929) and Müller (1984) suggested that *Dorippe margaretha* Lörenthey in Lörenthey & Beurlen, 1929, from the Hungarian Miocene, has close affinities with the Recent *Medorippe lanata* (Linnaeus, 1767). The carapace in members of *Dorippe* is longer than wide with distinct dorsal tubercles, while in species of *Medorippe* it is wider than long with some low elevations dorsally. Therefore, *Dorippe margaretha* is here removed from *Dorippe* and placed in *Medorippe*; it differs from *M. lanata* by having obscure lateral branchial and dorsobranchial ridges. Thus 12 species in eight genera of dorippines, including a new species described below, are recognized (Table 1) as fossils.

Genus *Medorippe* Manning & Holthuis, 1981

Type species.—*Cancer lanatus* Linnaeus, 1767 by monotypy.

Geologic range.—Miocene–Recent.

Medorippe tanabei, new species
Fig. 2

Material examined.—MFM39019, holotype, carapace length 10.1 mm × carapace width 12.1 mm.

Diagnosis.—Carapace trapezoidal, wider

Table 1.—Distributions and geologic ranges of recognized fossil species of the subfamily Dorippinae MacLeay.

Species	Age	Locality
<i>Dorippe fankhauuseri</i> Studer, 1892	Middle Miocene	Switzerland
<i>Dorippe frascone tuberculata</i> Morris & Collins, 1991	Pliocene	Brunei
<i>Dorippe quadridens</i> (Fabricius, 1793)	Holocene	Unknown
<i>Dorippoides facchio</i> (Herbst, 1785)	Pliocene	Java
<i>Heikea japonica</i> (Von Siebold, 1824)	Holocene	Japan
<i>Medorippe lanata</i> (Linnaeus, 1767)	Pleistocene	Italy
<i>Medorippe margaretha</i> (Lörenthey in Lörenthey & Beurlen, 1929)	Middle Miocene	Hungary, Portugal
<i>Medorippe tanabei</i> , new species	Middle Miocene	Japan
<i>Neodorippe? carpathica</i> (Förster, 1979)	Middle Miocene	Poland
<i>Nobilum wenchi</i> Hu & Tao, 1996	Miocene	Taiwan
<i>Paradorippe granulata</i> (De Haan, 1841)	Pleistocene–Holocene	Japan
<i>Titanodorippe eocenica</i> Blow & Manning, 1996	Upper Eocene	U.S.A.

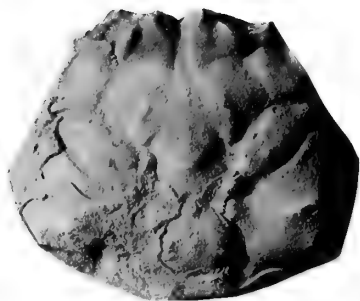


Fig. 2. *Medorippe tanabei*, new species, MFM39019, holotype, $\times 3.8$, dorsal view of carapace.

than long. Front with 2 broadly triangular teeth. Inner orbital angle bluntly triangular. Lateral margin without granules and spines. Dorsal region well defined; protogastric and epibranchial regions with tubercle on each side; meso- and urogastric regions with median tubercle; cardiac region lacking V-shaped ridge, but bearing 3 tubercles; lateral branchial tubercle weakly developed; mesobranchial region with anterior dorso-branchial ridge and posterior dorsobranchial tubercle on each side.

Description.—Carapace (Fig. 2) small, trapezoidal in outline, length about 0.8 its width, widest a little posterior to midlength. Orbitofrontal margin occupying about 0.6 of carapace width. Front consisting of 2 broadly triangular teeth, separated by wide, sulcate, V-shaped emargination. Inner orbital angle bluntly triangular, separated from frontal tooth by shallow, rounded excavation. Upper orbital margin concave, with narrow, rather deep fissure. Outer orbital tooth distinct, but tip broken. Inner suborbital tooth visible in dorsal view, extending slightly beyond frontal tooth. Lateral margin strongly converging anteriorly, without granules and spines; margin anterior to cervical groove nearly straight, margin posterior to cervical groove strongly convex.

Dorsal carapace gently convex longitudinally, almost flat transversely, largely smooth. Dorsal region well defined. Each protogastric region with conical tubercle. Mesogastric region bearing bilobed median

tubercle posteriorly, with 2 oblique submedian pits connected with cervical groove. Urogastric region with small, conical tubercle. Cardiac region inflated, with 3 small, conical tubercles transversely arranged. Hepatic region nearly flat. Cervical and branchial grooves distinct. Epibranchial region with small, conical tubercle on each side. Branchial lobe elevated. Branchiocardiac groove deep, distinct. Meso- and metabranchial regions strongly inflated. Lateral branchial tubercle small, weakly developed. Each mesobranchial region with oblique dorsobranchial ridge and small, conical posterior dorsobranchial tubercle.

Etymology.—The specific name is dedicated to Mr. M. Tanabe who collected the type specimen.

Remarks.—*Medorippe tanabei*, new species, is assigned to *Medorippe* because the carapace is wider than long and it bears some small dorsal tubercles and lateral branchial tubercles. *Medorippe* is represented by a single Recent species, *Medorippe lanata* (see Holthuis & Manning 1990). The new species differs from *M. lanata* by having well separated frontal teeth and having small lateral branchial tubercles. *Medorippe tanabei* lacks the V- or Y shaped cardiac ridge and has low, conical projections on the dorsal surface of the front. Well defined protogastric, mesogastric, epibranchial and posterior dorsobranchial tubercles on the carapace readily distinguish the species from the Miocene *Medorippe margaretha* (Lörenthey in Lörenthey & Beurien, 1929). *Medorippe margaretha* has V-shaped cardiac and transverse urogastric ridges on the carapace which are lacking in *M. tanabei*. In *M. margaretha* the anterior dorsobranchial ridge on the mesogastric region is weakly developed.

The inclusion of *Medorippe tanabei* and *M. margaretha* in *Medorippe* extends the known geologic range of the genus to the middle Miocene. *Medorippe lanata* is now distributed in the Mediterranean Sea, tropical West Africa, southern Africa and Madagascar, and is recorded from the Pleisto-

cene of Italy (Holthuis & Manning 1990). *Medorippe margaretha* is known from the Miocene of Hungary and Portugal (Holthuis & Manning 1990). Recognition of *M. tanabei* from Japan greatly expands the known geographic range of the genus. The fossil records suggest that *Medorippe* had reached Japan and the Paratethys Sea by the middle Miocene.

Acknowledgments

I thank Dr. Lipke B. Holthuis (National Museum of Natural History, Leiden, the Netherlands) for reading my manuscript and Mr. Mitsuo Tanabe (Niimi, Okayama, Japan) for offering fossil crab specimens for study. The manuscript benefited from critical reading by three anonymous reviewers.

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**A new species of diminutive salamander (Amphibia: Caudata:
Plethodontidae: *Nototriton*) from the Montañas del Mico
of Guatemala**

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Abstract.—*Nototriton stuarti*, a new species of salamander belonging to the tribe Bolitoglossini, family Plethodontidae, is described from the Montañas del Mico, north of the Motagua Valley, in eastern Guatemala. The species is geographically isolated from congeneric species, and represents the northwesternmost record for the genus, which ranges from eastern Guatemala to central Costa Rica. This poorly known species is morphologically most similar to *Nototriton barbouri*, which occurs in northwestern Honduras.

Homoplastic evolution has produced diminutive, attenuate salamanders in many different clades of plethodontid salamanders in Middle America. These tiny species are difficult taxonomically and it has taken much effort to recognize that there are many more species than have been named throughout this region. New discoveries and new data have led to taxonomic revisions that are gradually identifying monophyletic groups, and as this process goes forward the generic level taxonomy has changed repeatedly. This is especially true of the genus *Chiropterotriton* Taylor, 1944, which as formerly recognized ranged from northeastern Mexico to Costa Rica, but which was not monophyletic and now has been fragmented into four genera (*Chiropterotriton*, *Cryptotriton* García-París & Wake, 2000, *Dendrotriton* Wake & Elias, 1983, and *Nototriton* Wake & Elias, 1983). At present diminutive plethodontids found to the north and west of the Isthmus of Tehuantepec are assigned to *Chiropterotriton* (Darda, 1994), but, in addition, all members of the genera *Parvimolge* Taylor, 1944, *Lineatriton* Tanner, 1950, and especially *Thorius* Cope, 1869, none closely related to

Chiropterotriton and all endemic to this area, are also diminutive. To the south and east of the Isthmus of Tehuantepec, extending as far as central Costa Rica, diminutive species are found in one well-supported clade (García-París & Wake 2000). This clade includes the genera *Cryptotriton*, *Dendrotriton*, *Nototriton* and *Oedipina*, and possibly the poorly known *Bradytriton* Wake & Elias 1983 (G. Parra-Olea, pers. comm.). *Oedipina* Kieferstein 1868 includes some diminutive species, but also some large and relatively robust, although elongated, species. The phylogenetic diversity of this clade is now understood, at least in broad outlines. *Oedipina* and *Nototriton* appear to be the most deeply nested groups (García-París & Wake 2000), and they are also the most southerly in distribution, extending to Ecuador (moderately large species of *Oedipina* occur in South America, Brame & Wake 1963) and central Costa Rica, respectively. Both occur as far north as Guatemala, and *Oedipina* ranges into Chiapas, Mexico. *Cryptotriton* and *Dendrotriton* range from Honduras into Mexico, the former possibly even north and west of the Isthmus of Tehuantepec [the species

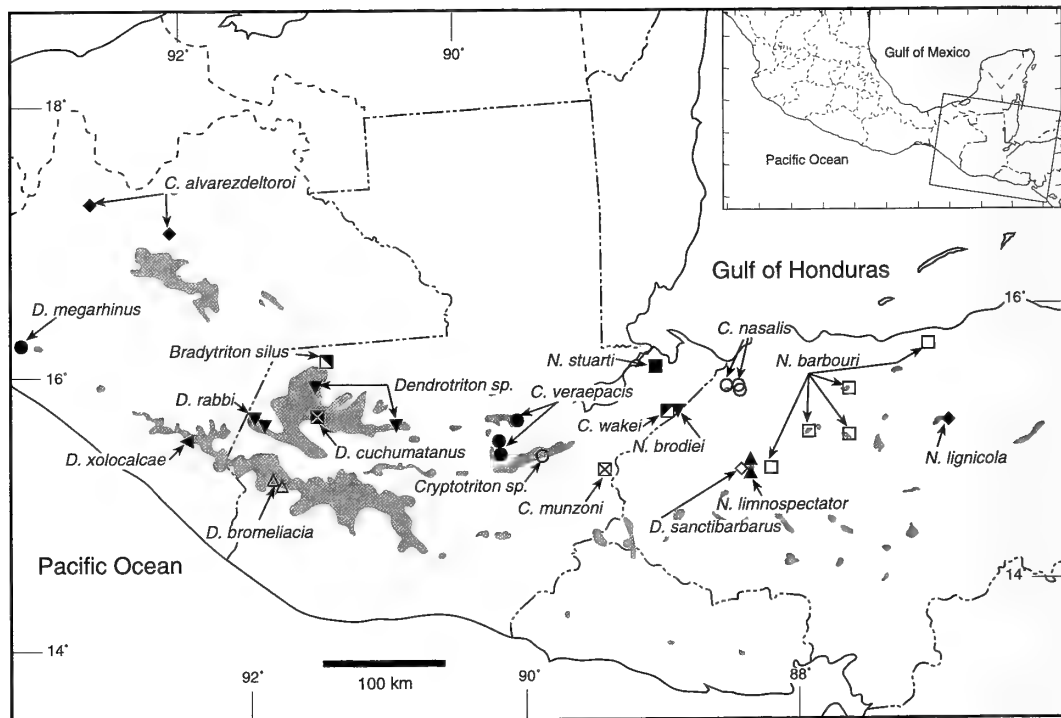


Fig. 1. Distribution of certain taxa discussed in the text from southern Mexico, Guatemala, and Honduras, showing the location of the type-locality of *Nototriton stuarti*. The map shows the location and degree of isolation of morphologically and ecologically similar, diminutive salamanders that have proven to represent several different smaller clades within a larger clade. Shaded areas on map represent regions with elevations in excess of 2000 m.

Cryptotriton adelos (Papenfuss & Wake, 1987) from northern Oaxaca is tentatively assigned to this genus], whereas *Bradytriton* is known only from its type-locality in western Guatemala (Fig. 1).

As revised by García-París & Wake (2000), *Nototriton* includes 11 nominal species, all diminutive (none exceeds 40 mm, snout-vent length), long-tailed forms that have small to moderately enlarged nostrils. Based on molecular data, the genus itself is well supported as a monophyletic group, and there are two well-supported internal clades, one including Costa Rican species, and the other including species from Honduras and Guatemala. The species *Nototriton richardi* (Taylor, 1949) from Costa Rica (and presumably its Costa Rican sister species *Nototriton tapanti* Good & Wake, 1993) is basal to one or the other of these

clades in different analyses, but the consensus view (allozymes plus mtDNA sequences) is that it is most closely related to the other Costa Rican species. The second clade includes one species described long ago but still little known biologically, *Nototriton barbouri* (Schmidt, 1936a), from northwestern Honduras, and three recently described taxa, *Nototriton lignicola* McCranie & Wilson, 1997 and *Nototriton limnospectator* McCranie, Wilson, & Polisar, 1998, the first from north-central and the second from western Honduras, and *Nototriton brodiei* Campbell & Smith, 1998, from extreme eastern Guatemala (Fig. 1). A single specimen representing another species belonging to this clade was collected in the Montañas del Mico in eastern Guatemala and at first confused with small specimens of sympatric *Oedipina elongata*

(Schmidt, 1936b). Fewer than 50 specimens are available for the second clade, but earlier taxonomic judgements based on morphology (McCranie & Wilson 1997, Campbell & Smith 1998, McCranie et al. 1998) have been supported by subsequent molecular studies (García-París & Wake 2000), so we are confident that this morphologically distinct form represents another new species.

Nototriton stuarti, new species
Stuart's Moss Salamander

Holotype.—UTA A-33686, an adult male from 11.6 km (road) WSW Puerto Santo Tomás, Montañas del Mico, Depto. Izabal, Guatemala, 88°40'W, 15°38'N, 744 m elev., collected on 6 Jan 1991 by Jonathan A. Campbell.

Diagnosis.—*Nototriton stuarti* is a member of a clade of northern species of *Nototriton*. It differs from all other members of the clade in having a broader head (0.14 times SL, from tip of snout to posterior angle of vent, whereas males of other northern species have the following values: *barbouri* 0.12, *lignicola* 0.11, *limnospectator* 0.11) and fewer maxillary teeth (36, versus 48–60 in other northern species). It is further distinguished from *lignicola*, *limnospectator*, and *barbouri* by having a larger nostril (0.012 times SL, versus 0.005–0.011 in *barbouri*, 0.005–0.016 in *brodiei*, 0.006–0.009 in *lignicola* and 0.003 in *limnospectator*), although the nostril is small in comparison with some Costa Rican members of the genus. It differs from some species in having longer limbs (combined limb length 0.35 times SL, versus 0.31–0.33 in *brodiei* and 0.30–0.34 in *lignicola*) and narrower feet (foot width 0.05 times SL, versus 0.06 in *barbouri* and *brodiei* and in male *limnospectator*).

Description.—This species is known from a single individual that is about average in size for the genus (32.6 mm, SL). It has small nostrils (0.012 times SL) and a broadly rounded snout (but narrow for an

adult male) of moderate length. The nasolabial protuberances are modest in size and barely protrude below the upper lip. The narrow head has eyes of moderate size that are only slightly protuberant, barely extending to the margin of the jaw. The parotoid glands are distinct but relatively small. The head is rounded rather than flattened, and is little differentiated from the neck and anterior body. Maxillary teeth are relatively numerous (36 in the holotype, with 4 premaxillary teeth), and there are moderate numbers of vomerine teeth (20). The limbs are short (combined limb length SL = 0.35), with narrow hands and feet that bear short, poorly developed digits. The digits are partly fused basally and the outer digits are very short. Digits 2 and 3 of the hand and 2, 3, and 4 of the foot are narrow and have pointed tips. The tail is long (1.26 times SVL) and tapered, with little evidence of basal constriction. The tail is stout basally and is of the same diameter as the posterior end of the body.

Measurements of holotype (in mm).—Snout-vent length 32.6, tail length 41.2, tail depth at base 3.3, tail width at base 3.2, distance between forelimb and hind limb insertions 19.4, trunk width just posterior to forelimbs 3.7, distance from tip of snout to gular fold 6.2, head width 4.5, head depth 2.5, distance between eye and nostril 0.9, elliptical nostril 0.4 × 0.2, distance between nostrils 1.1, eye diameter 1.6, interorbital distance 1.8, forelimb length 5.6, hindlimb length 5.8, width of hind foot 1.6, third toe length 0.4, fifth toe length 0.1.

Osteology.—Information has been obtained from radiographs of the holotype. The skull is relatively well developed, and in general resembles the skulls illustrated for Honduran species of the genus by McCranie et al. (1998), but with some important distinctions. The nasals are relatively large and are fragmented along the anterior margin. The nasolacrimal foramen is clearly evident and is surrounded by bone, but it is unclear if the nasolacrimal duct pierces the prefrontal bone (as in the genus

Cryptotriton) or if the nasal forms the anterior margin of the foramen and the prefrontal the posterior margin (as in some other species of *Nototriton*). The prefrontal is present because there is bone posterior to the duct opening and that bone is separated from the facial process of the maxillary. The premaxillary has a moderately well developed dental process, and paired ascending processes that are not fused basally, remain separated for their entire length, and which are not expanded terminally. The ascending processes are relatively short. No septomaxillary is evident. The maxillaries are relatively long and slender, extending to the posterior margin of the relatively small eye. The preorbital process of the vomer is long and well developed, and bears teeth in a single row. The frontals and parietals are well developed and there is only a small gap that barely qualifies as a mid-dorsal fontanelle. No cranial crests are evident. No columellar process can be seen on the operculum. There are 14 trunk, one sacral, and two caudosacral vertebrae. The tail is incomplete and is regenerating; it may have regenerated twice. The phalangeal formula of the forelimbs is 1-2-3-2, hind limbs 1-2-3-3-2 (digit three is incomplete on one foot). The digits are all well formed. Terminal phalanges of the longest digits are slightly expanded. There is a well-developed tibial spur.

Coloration (in alcohol).—The dorsum of the head, trunk and tail is dark reddish brown, with a series of prominent whitish chevrons (pointing cranially) covering the back. The head is somewhat mottled, with pale patches on the eyelids, between the eyes, and on the temple region, as well as on the nasolabial protuberances. A row of small pale spots creates an irregular and inconspicuous stripe along the upper ventrolateral surface of the flanks. A pair of poorly formed pale spots is found just anterior to the tail base constriction. Irregular whitish spots mark the tail dorsum, and the limbs have abundant small whitish spots. The ventral surfaces are paler than the dor-

sum and are relatively uniform pale gray, but there are some obscure whitish spots on the throat.

Habitat.—The holotype of *N. stuarti* and several specimens of *Oedipina elongata* were found inside logs at the type-locality, and initially the specimen described here was thought to be a member of that taxon. One of this series of salamanders was found dead on a trail, and it may have been in leaf litter and stepped on by collectors earlier in the day.

In contrast to higher, more extensive mountain ranges in Guatemala, the Montañas del Mico do not possess well defined vegetational belts, although above 600 m a lush subtropical wet forest prevails. Cloud forest occurs in the vicinity of the type-locality of *N. stuarti* and on the two highest peaks in the region—Cerro San Gil and Cerro Las Escobas.

The Montañas del Mico are one of the wettest regions in Guatemala. Although weather stations are lacking in these mountains, the lowlands just to the north receive in excess of 4000 mm of precipitation per year (INSIVUMEH 1992), and it is likely that an even greater amount of rain falls on the windward slopes of the Montañas del Mico.

Distribution.—*Nototriton stuarti* is known only from the type-locality (Fig. 1) in the Montañas del Mico, which reach a maximum elevation of 1267 m on Cerro San Gil. These geographically isolated uplands are located to the north of the inhospitable valley of the Rio Motagua and are surrounded by lowland, tropical habitats. To the southwest, a low ridge system (>300 m) connects the Montañas del Mico with that of the Sierra de las Minas.

Etymology.—The species is named in honor of the late L. C. Stuart, who spent his scientific career studying the amphibians and reptiles of Guatemala, and who predicted that the Montañas del Mico would produce a previously undescribed species of salamander.

Comments.—*Nototriton stuarti* repre-

sents the northwestern-most member of the revised genus (García-París & Wake 2000). The species is morphologically distinct, but the differences separating it from other species are subtle. Its closest geographic neighbor is *N. brodiei*, which it resembles in body and nostril size, but it differs markedly in having a shorter tail, fewer teeth, and broader head. Both species, as well as others (often only some individuals of a species) in the genus, have a dorsal color pattern of pale marks arranged in a herringbone pattern. Its morphological characters are matched most closely by those of *N. barbouri*, possibly for the simple reason that that species is known from the largest sample.

Acknowledgements

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A new species of the *calamarina* group of the colubrid snake genus *Tantilla* (Reptilia: Squamata) from Guerrero, Mexico, with a review of and key to members of the group

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Abstract.—A new species of *Tantilla* of the *calamarina* group, *T. sertula*, is described from the Pacific coastal plain of southwestern Guerrero, Mexico. It belongs to a clade that contains *T. calamarina*, *T. cascadae*, *T. coronadoi*, *T. deppei*, and *T. vermiformis*. All these species are endemic to Mexico, except for *T. vermiformis*, which is distributed along the Pacific coastal plain from El Salvador to northwestern Costa Rica. The new species appears to be the sister species of *T. cascadae*. Members of the *calamarina* group are highly adapted to fossoriality.

Mexico is the center of diversity for the speciose genus *Tantilla* (Wilson 1999), which, exclusive of the species described herein, contained 53 species (Wilson 1999). Twenty-seven of these 53 species were noted by Wilson (1999) to occur in Mexico. The majority of our knowledge of the diversity of Mexican *Tantilla* has accrued since 1942, when the last country-wide survey was undertaken by Smith (1942), who listed 19 species, 12 of which are currently considered valid (Wilson 1999). Since Smith's work, 10 valid species have been described from Mexico, and an additional five species have been added to the herpetofauna of that country—either species known previously from elsewhere or taxa elevated to species level.

The *calamarina* group of *Tantilla* is an important assemblage of species in the Mexican segment of the genus. The *calamarina* group was recognized and reviewed by Wilson & Meyer (1981). They included four species in the group, one of which (*T. cascadae*) was described by them. The other three species they included are *T. calamarina*, *T. coronadoi*, and *T. deppei*. Wil-

son et al. (1999) tentatively associated another species, *T. vermiformis*, known from Pacific coastal localities in El Salvador, Nicaragua, and Costa Rica (Wilson 1982, Dueñas et al. 2000), with the *calamarina* group. The four species treated by Wilson & Meyer (1981) are all endemic to Mexico, and occur collectively at elevations from sea level to 2438 m in the western portion of the country from northern Sinaloa to central Guerrero, Morelos, and México, including the Tres Mariás Islands. With the addition of *T. vermiformis* to the *calamarina* group, the distribution of the group extends along Pacific coastal regions from Sinaloa to northwestern Costa Rica.

Although one would expect that other species of *Tantilla* await discovery in the mountainous regions of the southern portion of the country, given that the most recently discovered species are distributed there, it is of interest, therefore, that the next new species to be discovered is from the southern region of Mexico, but not from its mountainous areas. While working on a review of the species of *Tantilla* from Mexico, the senior author contacted the junior

author, who informed him of the existence of a single juvenile specimen of *Tantilla* from Pacific coastal Guerrero that did not fit the description of any of the known species of the *calamarina* group. Examination of this specimen by the senior author confirmed the junior author's suspicions and below we provide a description of this new taxon, which is named:

Tantilla sertula, new species

Fig. 1

Holotype.—The University of Texas at Arlington (UTA) R-38145, a juvenile female from 0.8 km NNE of the junction of Mexico highway 200 on the road to La Unión (17°59'N, 101°49'W), Guerrero, México, approximate elevation slightly above 150 m, collected in July 1978, by J. A. Campbell.

Diagnosis.—A member of the *Tantilla calamarina* group with 7 supralabials; 161 ventrals; 30 subcaudals; two postoculars; 1+1 temporals, contacting one another; a dark middorsal stripe occupying the middle of the middorsal scale row; no dark lateral stripe; a head pattern consisting of a spatulate dark anterior extension of the middorsal dark stripe occupying the dorsum of the head, flanked by pale narrow, longitudinal stripes broadly separated from pale postparietal spots; and uniformly dark brown supralabials.

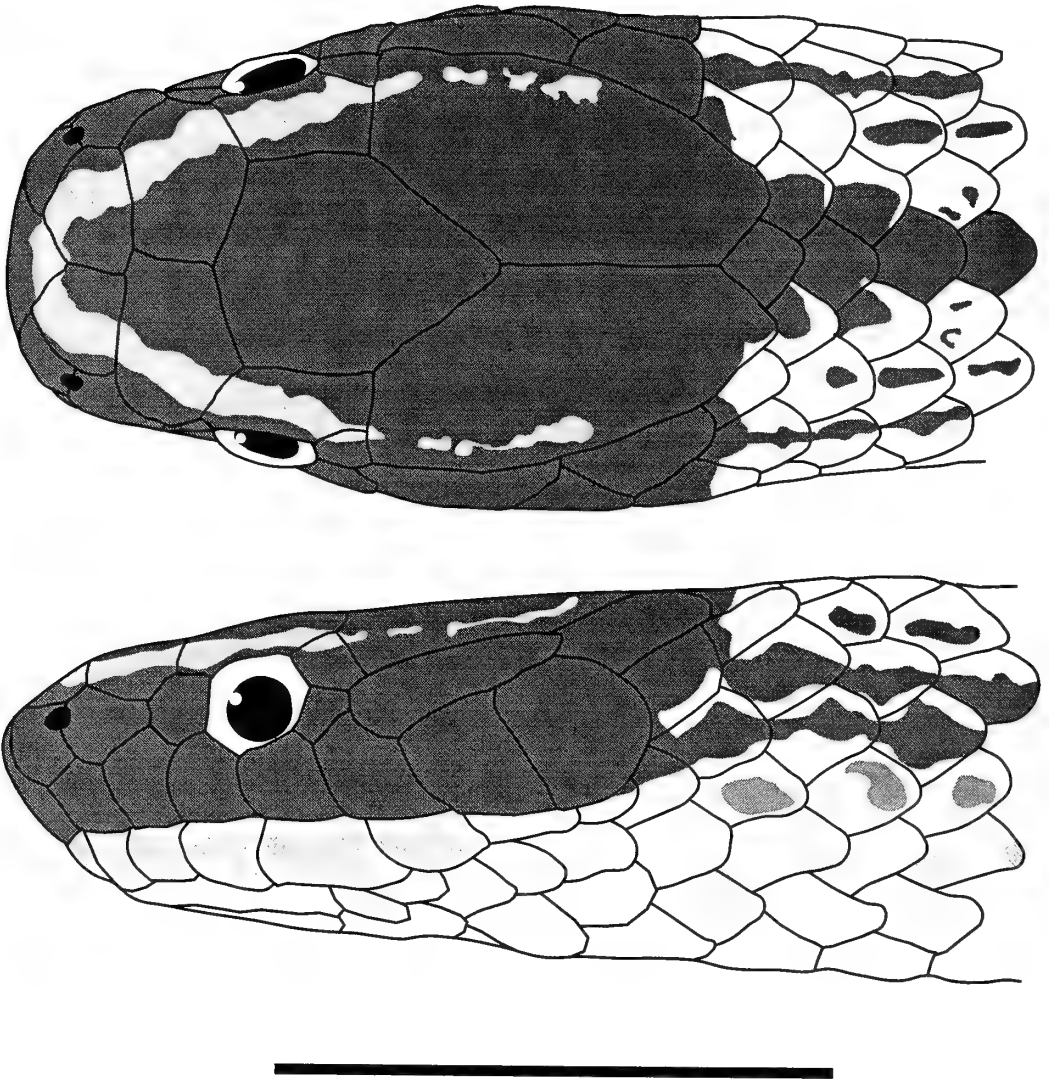
Description of the holotype.—A juvenile female with 15 smooth dorsal scales throughout the trunk, 161 ventrals, a divided cloacal scute (= anal plate), 30 subcaudals, a total length of 99 mm, a tail length of 12 mm, and a tail/total length ratio of 0.121.

Nasal completely divided, posterior section in contact with single preocular on both sides of head; two postoculars, about subequal in size; one anterior and one posterior temporal, in contact with one another, anterior temporal separating parietal and fifth supralabial, posterior temporal elongate, slightly smaller than anterior scale; supral-

abials 7-7, first in contact with rostral, prenasal, and postnasal, second with postnasal and preocular, third with preocular and orbit, four with orbit and lower postocular, fifth with lower postocular and anterior temporal, sixth with anterior temporal, and seventh with anterior and posterior temporals, seventh largest; infralabials 6-6, first four in contact with the anterior chinshields, fifth in contact with anterior and posterior chinshields, 4th largest, first pair broadly separated by contact of mental and anterior chinshields; anterior chinshields larger than posterior pair.

The dorsal ground color in preservative is pale brown, each scale of which has, upon microscopic examination, an irregular concentration of dark pigment along its median portion. A narrow, irregular dark brown middorsal stripe extends down the middle of the middorsal scale row. This stripe expands anteriorly to cover the entire middorsal row and adjacent halves of the paravertebral rows about three dorsal scales posterior to the parietal notch, just before joining the dark head cap. The middorsal row is complete anteriorly, becoming increasingly disjunct posteriorly.

The dorsum of the head is very dark brown, appearing as a dark head cap in the vague shape of a blunt arrowhead. This configuration is created by a pale border that begins on the dorsal apex of the rostral and continues, in gradually diminishing width and intensity, across the anterodorsal corner of the anterior nasal, the middle of the internasal, the canthal region of the prefrontal, the orbital edge of the suprocular, and the dorsal corner of the upper postocular. Beyond this point, this border becomes very narrow and broken until it reaches a point on the lateral edge of the parietal opposite the suture between the anterior and posterior temporal, where it expands into a tear drop-shaped spot. This pale border is separated from a postparietal pale spot, occupying portions of three dorsal scales immediately posterior to the posterolateral portion of the parietal. The post-



3 mm

Fig. 1. Semidiagrammatic representation of dorsal and lateral head scutellation of the holotype (UTA R-38145) of *Tantilla sertula*.

parietal pale spots grade posteriorly into the dorsal ground color. The lateral portion of the head below the pale dorsal border is uniformly dark brown. The chin is cream, with vague smudging along the lingual edge of the infralabials. The venter is immaculate cream.

Distribution.—Known only from the

type-locality, near the village of La Unión, located along the Río La Unión, a few kilometers on an unpaved road from the junction of this road with Mexico highway 200. The type locality is 0.8 km NNE of this junction in the direction of La Unión, and lies on the Pacific coastal plain of southwestern Guerrero. This area is seasonally

dry and is covered with bosque tropical caducifolio (Rzedowski 1988) or tropical deciduous forest (Leopold 1972). This forest type is comparable to the Lowland Deciduous Forest bioclimate (Savage 1975) or the Lowland Dry forest formation (Holdridge 1967).

Etymology.—The name *sertula* is from the Latin meaning a “small garland or wreath,” in allusion to the distinctive pattern on the dorsum of the head.

Discussion

Wilson & Meyer (1981) established the case for the recognition of a *calamarina* group within the genus *Tantilla*, distinct from the *melanocephala* group as recognized by Wilson & Mena (1980). Both of these groups are characterized, in part, by possession of a middorsal dark stripe (although this pattern element is lost in some populations of *T. capistrata* and *T. melanocephala*). The principal evidence used by Wilson & Meyer (1981) to support recognition of the *calamarina* group is similarity of head pattern. The four species included by them all lack a dark nape band, a feature distinguishing them from almost all members of the *melanocephala* group. Wilson & Meyer (1981: 2) further noted that all members of the group “have the central portion of the parietals covered with a spatulate anterior extension of the middorsal dark stripe, which continues anteriorly to cover the remainder of the [central portion] of the head. On either side of this central mark is a postparietal pale spot [except *T. deppei*; see below] that usually grades posteriorly into the ground color of the dorsolateral field (area between the lateral and median dark stripes) and, in its best-developed state, connects anteriorly with a narrow extension that proceeds along the side of the parietal, over the supraocular and onto the side[s] of the prefrontals and internasals.” They (1981: 2–3) further noted that “*Tantilla deppei* has this same narrow pale marking around the rim of the dorsum of

the head but it may or may not connect to a middorsally divided pale collar (the fact that [such a] pale nuchal marking appears more like a broken collar than a pair of nuchal or postparietal spots is due, perhaps, to the narrowness of the connection between the middorsal stripe and the dark pigment on top of the head).” Finally, They pointed out that, “The supralabials of all these forms are generally pale in color, with some dark pigment along their upper borders.” This dark pigment represents the lower edge of the dark mask present below the pale rim of the dorsum of the head.

In discussing the relationships of *T. brevicauda* to members of the *taeniata* group of *Tantilla*, Wilson et al. (1999) indicated that *T. vermiformis* “is characterized by the presence of a ‘thin disjunct dark middorsal stripe confined to the middorsal scale row’ (Wilson 1982), among other features. Given this feature, as well as the small size, relatively low numbers of ventrals and subcaudals, occasional fusion of the primary temporal and the sixth supralabial, pale head markings on the parietal, and the recently-demonstrated presence in El Salvador (Dueñas et al. 2000), it might appear more logical to associate *T. vermiformis* with the members of the *T. calamarina* group (Wilson & Meyer 1981).”

Whereas the view of Wilson et al. (1999) is defensible, it should be noted that the information they provided does not tell the entire story. As is obvious, the genus *Tantilla* consists of a large number of fossorial to semifossorial species. They are all generally small, as is typical of such snakes, although several species can reach total lengths in excess of 600 mm (Wilson 1982, Campbell et al. 1995, Campbell 1998). *Tantilla vermiformis*, as well as the four recognized members of the *calamarina* group and *T. sertula*, are among the smallest members of the genus. The maximum known total lengths (in mm) of four of these species are as follows: *T. vermiformis*—157; *T. coronadoi*—183; *T. calamarina*—202; *T. deppei*—273. The holotype of

Table 1.—Comparison of selected characters among members of the *Tantilla calamarina* group.

Features	<i>T. sertula</i>	<i>T. calamarina</i>	<i>T. cascadae</i>	<i>T. coronadoi</i>	<i>T. deppoi</i>	<i>T. vermiformis</i>
Ventrals in males	—	106–133 (119.7)	—	158	142–151 (145.9)	115–123 (119.6)
Ventrals in females	161	118–140 (129.0)	139	165	153–168 (160.1)	120–129 (124.2)
Subcaudals in males	—	30–43 (36.8)	—	35+(?)	54–62 (57.2)	23–28 (25.3)
Subcaudals in females	30	22–43 (28.8)	37	40	43–50 (46.2)	19–24 (21.0)
Ventrals + subcaudals in males	—	145–166 (156.9)	—	—	196–213 (203.1)	141–147 (144.5)
Ventrals + subcaudals in females	191	146–179 (158.0)	176	205	196–214 (206.3)	140–150 (144.7)
Preocular	Present, in contact with postnasal	Tendency toward decrease in size to complete loss	Present, in contact with postnasal	Present, in contact with postnasal	Present, in contact with postnasal	Present, in contact with postnasal, sometimes fused with prefrontal
Number of postoculars	2	1	2	2	2	2
Number of supralabials	7	Usually 6	6	7	Usually 7	7
Anterior and posterior temporals separated	No	No	No	Yes	No	No
Fusion of anterior temporal and sixth supralabial	No	No	No	No	No	Occasionally
Head pattern	Spatulate dark anterior extension of middorsal dark stripe flanked by prominent pale narrow longitudinal markings confluent with pale postparietal spots	Spatulate dark anterior extension of middorsal dark stripe flanked by two pale spots	Spatulate dark anterior extension of middorsal dark stripe flanked by pale narrow longitudinal markings confluent with pale postparietal spots	Spatulate dark anterior extension of middorsal dark stripe flanked by pale anterior extensions of dorso-lateral ground color	Spatulate dark anterior extension of middorsal dark stripe flanked by pale anterior extension of middorsally-divided pale nuchal band	Dark brown dorsally and laterally with tan, pale lavender, or pale brown blotches on posterior portion of parietals

Table 1.—Comparison of selected characters among members of the *Tantilla calamarina* group.

Features	<i>T. sertula</i>	<i>T. calamarina</i>	<i>T. cascadae</i>	<i>T. coronadoi</i>	<i>T. deppei</i>	<i>T. vermiformis</i>
Body pattern	Dorsum pale brown on rows 5 to 7, dark brown on rows 1 to 4; dark middorsal stripe on middle of mid-dorsal row	Tan to brown with variously-sized dark middorsal stripe and a dark brown lateral stripe on rows 3 and 4	Pale brown with dark middorsal stripe occupying middle of middorsal scale row; dark lateral stripe on rows 3 and 4 only in neck region	Tan to brown with dark middorsal stripe occupying middle of middorsal scale row and dark lateral stripe on rows 3 and 4	Tan to brown with diffusely dark vari-ously-sized mid-dorsal stripe and dark lateral stripe on row 3 or rows 2 and 3; diffuse dark stripe on row 5	Pale brown to brown dorsum with poorly-defined, disjunct dark middorsal stripe confined to middorsal row
Ventral pattern	Immaculate cream	Immaculate cream	Cream with slight amount of dark pigment at lateral apices	Immaculate cream	Immaculate cream	Immaculate white, cream, pale yellow, or pale pink

T. cascadae cannot be measured, due to its desiccated condition, and that of *T. sertula* is a juvenile. Thus, insofar as is known, *T. vermiformis* is the smallest of these species (see Table 1).

Tantilla vermiformis possesses a relatively small number of ventrals (Table 1), comparable to those of *T. calamarina*. It also has the lowest number of subcaudals in the *calamarina* group (Table 1). The anterior temporal and the sixth supralabial are occasionally fused (Wilson 1982). *Tantilla calamarina* and *T. cascadae* also show some fusion or loss of head scales (preoculars, postoculars, and supralabials in the former, supralabials in the latter; Table 1 and Wilson & Meyer 1981). Finally, *T. vermiformis* possesses a head pattern incorporating pale parietal spots, reminiscent of the pale postparietal spots of members of the *calamarina* group (Wilson & Meyer 1981, Wilson 1982), although there are no pale, narrow anterior extensions of the pale parietal spots in this species. Also, it does not possess the dark mask and cream lower supralabials of the members of the *calamarina* group; instead, its head is more or less uniformly dark brown dorsally and laterally (Wilson 1982). Nonetheless, the preponderance of evidence points to a status for *T. vermiformis* as a diminutive member of this group of small species of *Tantilla*, the members of which show varying degrees of greater adaptation to a fossorial lifestyle than is typical for *Tantilla*.

Making a case for inclusion of *T. sertula* in the *calamarina* group is much easier than for *T. vermiformis*. It possesses the head pattern typical for the group members, except for the pale lower supralabials, which are lacking in this taxon (at least in this juvenile). On the other hand, its uniformly colored lateral portion of the head is essentially like that of *T. vermiformis*, a resemblance that assists in linking the latter species to others in this group. These head pattern distinctions in the juvenile holotype of *T. sertula*, as well as those of the body, are expected to hold when material of adults is

secured, as there is no significant ontogenetic change in color pattern known in the *calamarina* group.

With reference to relationships, Wilson & Meyer (1981: 22) concluded that, "With regard to intragroup relationships, it appears that there are probably three subgroups, one containing *T. deppei*, the least specialized member of the group, a second containing *T. coronadoi*, and a third containing *T. calamarina* and *T. cascadae*." They went on to say that "*Tantilla deppei* probably will eventually be shown to have some degree of relationship with members of the *melanocephala* group [which has not been established yet]. It differs principally from those snakes in lacking a dark nape band. *Tantilla coronadoi* seems to be more closely related to *T. calamarina* and *T. cascadae* than to *T. deppei*, judged on the basis of similarity of color patterns."

Wilson & Meyer (1981), thus, hypothesized that the *calamarina* group is monophyletic and that its evolution reflects increasing adaptation to a fossorial lifestyle. In addition, they hypothesized that *T. deppei* is the least derived taxon in the group and that *T. calamarina* the most derived. Finally, they suggested that *T. cascadae* is the sister taxon of *T. calamarina* and that *T. coronadoi* is the sister taxon to a clade containing *T. calamarina* and *T. cascadae*.

Given that two additional species (*T. vermiformis* and *T. sertula*) are proposed herein for inclusion in the *calamarina* group, it is a propitious time to present an identification key to this difficult group of snakes.

Revised key to the members of the *Tantilla calamarina* group

(based, in part, on Wilson & Meyer 1981,
and Wilson 1999)

1. No dark lateral stripe present or, if present, confined to neck region 2
Dark lateral stripe present on trunk 4
2. Supralabials 6; lower portion of supralabials cream colored *T. cascadae*
Supralabials 7; supralabials uniformly dark brown 3

3. Ventrals fewer than 130 (115–129); subcaudals fewer than 30 (19–28) *T. vermiformis*
Ventrals 161; subcaudals 30 *T. sertula*
4. Ventrals 140 or fewer (106–140); postocular single; supralabials 6 *T. calamarina*
Ventrals more than 140; postoculars 2; supralabials 7 5
5. Dark lateral stripe on rows 3 and 4; seventh supralabial in contact with parietal, separating anterior temporal from posterior temporal *T. coronadoi*
Dark lateral stripe on row 3 only or on rows 2 and 3; seventh supralabial separated from parietal, anterior and posterior temporals in contact with one another *T. deppei*

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Systematic relationships of the Verdin: Skeletal evidence (Aves: Passeriformes)

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Abstract.—Recent systematic treatments have placed the Verdin (*Auriparus flaviceps*) in 4 different families. The skeleton of the Verdin is compared with 17 species of 10 genera variously supposed to be close relatives. In 19–20 of 22 skeletal characters, *Auriparus* is close to *Anthoscopus* and *Remiz*, as contrasted with 5–9 in *Microbates*, *Rhamphocaenus*, *Polioptila*, *Aegithalos*, *Psaltriparus*, and *Coereba*. This tends to confirm external anatomy, behavior, and nest characters; the species belongs with the penduline tits, Remizidae.

The relationships and systematic position of the Verdin (*Auriparus flaviceps*) have been variously hypothesized. Until recent years it was placed with the tits in the family Paridae (for example, A.O.U. Check-list, 1957). Snow (1967) segregated it in Remizidae, the penduline tits, along with the Old World genera *Remiz*, *Anthoscopus*, and *Cephalopyrus*. A similar arrangement was followed by Cramp & Perrins (1992). Taylor (1970) thought it belonged in Emberizidae, near *Coereba*. Harrap & Quinn (1995) allowed only a subfamily (of Paridae) for the penduline tits and Verdin. The most recent A.O.U. Check-list (1998) placed it in Remizidae, as did Phillips (1986) and Sheldon & Gill (1996). Sibley & Monroe (1990) placed it in the family Certhiidae, subfamily Polioptilinae, along with the gnatcatchers and gnatwrens, *Microbates*, *Rhamphocaenus*, and *Polioptila*. Among these references, only Cramp & Perrins and Harrap & Quinn gave characterizations based on behavior, nest, and external anatomy. Sibley & Monroe's action was based on DNA study by Sibley & Ahlquist (1990). As Phillips remarked, "this gives the reader plenty of choice!"

Previous studies of the Verdin skeleton were those of Lucas (1890), Beecher

(1953), and George (1962). Lucas found little difference between *Parus* and *Auriparus*, but noted a more incomplete interorbital septum and a smaller mandibular foramen in the latter, concluding that they were close relatives. Beecher (1953) mentioned only one differential skeletal character between his Remizinae (*Anthoscopus* and *Auriparus*) and the other Paridae—the ectethmoid foramen was single rather than pinched. George (1962), studying only the hyoid, put in one group all of the genera I compared, except *Coereba*.

Recent classifications of this group of birds are based on nuclear DNA or on external anatomy, nest, and behavior. Addition of a skeleton character set should improve the situation. I have studied skeletons of all families and nearly all subfamilies of Oscines (Webster & Goff 1979; Webster 1992, 1994, 1997; Webster & Webster 1999). In the present paper the skeleton of *Auriparus* is compared in detail with most of its supposed close relatives—of Polioptilidae *Microbates*, *Rhamphocaenus*, and *Polioptila*; of Aegithalidae (long-tailed tits) *Aegithalos* and *Psaltriparus*, of Remizidae *Remiz* and *Anthoscopus*; of Paridae (true tits) *Parus* and *Melanochlora*; of Emberizidae *Coereba* (Bananaquit).

Table 1.—Results of detrended correspondence analysis ordination. Values are the scores of the skeletal parameters on each of the DCA axes. The last rows indicate the eigenvalues of the axes and cumulative coefficients of determination of the correlations comparing ordination distances between bird species and Euclidean distances in the original data.

Variable	Axis 1	Axis 2	Axis 3
Skull length	21	-185	-21
Premaxilla length/width	-34	123	134
Tibiotarsus length/ulna length	-70	92	-130
Tibiotarsus length/humerus length	-68	80	-68
Tibiotarsus length/femur length	53	157	-44
Ulna length/femur length	203	42	159
Humerus length/femur length	213	16	101
Length/width of interpalatine process	-53	34	76
Length/width of transpalatine process	107	194	8
Length/width of zygomatic process	-12	72	216
Length/width of retroarticular process of mandible	147	250	-100
Length/width of pseudotemporal process of mandible	95	-37	-92
Pneumotricipital fossa of humerus: percent depth of the dorsal fossa to the depth of the ventral fossa	179	-61	-47
Tibiotarsus length/tarsometatarsus length	208	84	-35
Length/width of tarsometatarsus	-61	-24	62
Tarsometatarsus length/skull length	-62	-6	5
Basal width/narrowest width of internal process of mandible	157	28	86
Height/width of basihyale	100	-27	134
Eigenvalue	0.138	0.021	0.009
Coefficient of determination	0.766	0.771	0.832

Methods

Most elements of the skeleton were perused; 39 characters were tabulated. Twenty-two characters are analyzed below; 18 of these are numerical enough to be analyzed statistically. Of the 17 characters not analyzed, 12 were too erratic within species, 4 were too uniform within the entire group, and one had too many missing data because of broken or missing bones. Within the statistically analyzed data, in one case, because of missing bones, a datum from a congeneric species was substituted. This was height/width of the basihyale, where the datum for *Aegithalos concinnus* was used for *A. caudatus*. The four characters not analyzed statistically are marked with an asterisk (*) in the results. In each species where more than one specimen was studied, the number given is the mean of measurements or of ratios of measurements of all specimens. Unfortunately, skeletons of three possibly related genera (*Psaltria*, *Ce-*

phalopyrus, and *Sylviparus*) were not examined, nor were several other species of examined genera (mostly *Parus*).

Eighteen quantitative characters (Table 1) were used in a detrended correspondence analysis (DCA) ordination (Gauch 1982). All data were converted to ranks, but analyses run on non-transformed data produced qualitatively similar results. Analyses were performed using PC-ORD (McCune & Mefford 1997).

Skeletal Specimens Examined

Microbates collaris 3: Peru 2 (LAS121393, LAS111606), French Guiana 1 (RON 125903).
Microbates cinereiventris 3: Costa Rica 1 (LAS63107), Colombia 1 (USNM 428228), Peru 1 (LAS111604)
Rhamphocaenus melanurus 3: El Salvador 1 (MVZ86284), Colombia 1 (MVZ 141823), 1 not recorded
Polioptila caerulea 6: California 2 (MVZ

150800, MVZ69803), Florida 2 (KUN 61089-90), 2 not recorded.

Polioptila plumbea 2: Panama 1 (USNM 430601), Colombia 1 (DEL60776).

Aegithalos caudatus 4: Denmark 1 (LAS 122975), Poland 1 (UFL28538), Russia 2 (UFL28539, UMI33470).

Aegithalos concinnus 3: Captive 2 (BM-51996-53-1, BM-S1999-21-1), China 1 (USNM318461).

Psaltriparus minimus 8: California 2 (DEL49825, KUN23384), Arizona 1 (KUN19035), Oklahoma 1 (CARN9285), Texas 3 (RON125997-8, RON126994), 1 not recorded.

Remiz pendulinus 2: France 1 (UFL28551), Israel 1 (USNM502125).

Anthoscopus caroli 3: Kenya 1 (LAS 28083), Zimbabwe 2 (RON114598, CARN15912).

Anthoscopus parvulus 1: Ghana (UMI 221025).

Anthoscopus minutus 4: Namibia 1 (RON156922), Republic of South Africa 3 (DEL63150-1, DEL63213).

Auriparus flaviceps 12: California 4 (KUN 37094, KUN37101), (UMI151760-1), Arizona 6 (UMI159183, YALE10266, YALE10268, YALE10279, YALE10281-2), Texas 2 (USNM554365, RON 129858).

Parus atricapillus 7: Kansas 2 (MVZ 52869, MVZ60955), Connecticut 5 (YALE5843-4, YALE10619, YALE 5657, YALE5825).

Parus major 2: India 2 (RON125618-9).

Parus bicolor 4: New Hampshire 1 (MCZ 7735), Massachusetts 1 (MCZ7333), Florida 2 (UFL22081, UFL28630).

Melanochlora sultanea 1: Malaya (BM-S1969-1-169).

Coereba flaveola 9: Mexico 2 (RON 112083, RON112141), Costa Rica 2 (both CAS number not recorded), Colombia 2 (DEL61050, DEL63019), Bahamas 1 (BM number not recorded), Grand Cayman 1 (BM1904-8-5-2), 1 not recorded.

Certhia familiaris 2: England 1 (USNM

Table 2.—Zygomatic process of the squamosal. Length/width ratio.

<i>Polioptila</i>	1.3–2.7
<i>Rhamphocaenus</i>	2.2
<i>Coereba</i>	1.9
<i>Microbates</i>	1.2–1.8
<i>Remiz</i>	1.4
<i>Anthoscopus</i>	0.5–1.2
<i>Parus</i>	0.4–1.2
<i>Psaltriparus</i>	1.1
<i>Aegithalos</i>	0.8–1.1
<i>Auriparus</i>	1.0
<i>Melanochlora</i>	0.6

49824), France 1 (USNM number not recorded).

Certhia americana 11: Ontario 1 (RON 127589), United States 5 (FM290725, FM291213, YALE6730, YALE10682-3), 5 not recorded.

Certhia brachydactyla 1: Greece (USNM 488800).

Certhia himalayana 1: China (USNM 319349).

Certhia discolor 1: Thailand (USNM 343078).

Salpornis spilonotus 2: India 2 (RON 125277, RON125624).

Campylorhynchus brunneicapillus 1: California (KUN19009).

Thryothorus ludovicianus 2: Indiana 2 (both CAS, number not recorded).

Troglodytes troglodytes 2: England 1 (BM1984-47-2), Indiana 1 (INST number not recorded).

Results

The retroarticular process of the mandible was long (4–5.5 times as long as wide) in *Remiz*, *Anthoscopus*, and *Auriparus*; moderate (2.4) in *Psaltriparus*; short (0.7–1.3) in *Microbates*, *Rhamphocaenus*, *Polioptila*, *Aegithalos*, *Parus*, and *Melanochlora*: moderate to short (1.0–2.6) in various subspecies of *Coereba*.

The zygomatic process of the squamosal was short in *Auriparus*, in contrast with the gnatcatchers, gnatwrens, and Bananaquit (Table 2).

Table 3.—Tricipital fossa of humerus in some passeriform genera. Numbers in the columns are numbers of specimens examined with this characteristic. Percentages are the proportions of the depth of the dorsal fossa to the depth of the ventral fossa. In the fifth column the septum between the two fossae is prominent except where marked †, where it is a low ridge.

	30%	40–50%	70–90%	100%; septum complete	100%; septum incomplete (= combined fossae)
<i>Microbates</i>	5	1			
<i>Rhamphocaenus</i>	3				
<i>Polioptila</i>		6	2		
<i>Aegithalos</i>		3	3		
<i>Psaltriparus</i>			6	1	1
<i>Remiz</i>			2		
<i>Anthoscopus</i>			6		2
<i>Auriparus</i>			9	2	1
<i>Parus</i>			2	11† in 1	
<i>Melanochlora</i>			1		
<i>Coereba</i>			3	2†	4

A completely or partially bony nasal septum was present in all of *Remiz*, *Anthoscopus*, and *Coereba*, seven of 12 specimens of *Auriparus*, and seven of 13 *Parus*. In contrast, there was no bone in the septum in *Rhamphocaenus*, *Polioptila*, *Aegithalos*, *Psaltriparus*, and *Melanochlora* and very little (one specimen) or none (five specimens) in *Microbates*.*

The ectethmoid foramina were double in *Parus* (pinched in two specimens), *Melanochlora*, and *Coereba*; single in *Aegithalos*, *Remiz*, *Anthoscopus*, and *Auriparus*; an intermediate condition, pinched, or variously pinched or single in *Microbates*, *Rhamphocaenus*, *Polioptila* and *Psaltriparus*.*

The transpalatine process at the caudolateral angle of the palatine was short (0.3–1.4 times as long as wide) in *Polioptila caerulea*, *Microbates cinereiventris*, *Aegithalos*, *Parus*, and *Melanochlora*; moderate (2.1–2.6) in *Rhamphocaenus*, *Polioptila plumbea*, and *Psaltriparus*; long (3.0–10.4) in *Remiz*, *Anthoscopus*, *Auriparus*, *Microbates collaris*, and *Coereba*. (In *Coereba*, seven specimens averaged 10.4, but in two the entire caudolateral part of the palatine was absent.)

The interpalatine process was moderate in size and shape (1.1 to 3.2 times as long as wide) in *Microbates*, *Rhamphocaenus*,

Polioptila, *Aegithalos*, and *Coereba*; but very small and slender (3.0) or short (1.0) in *Remiz*; absent or a slight bump in three specimens or moderate in four of *Psaltriparus*; and absent or a slight bump in *Anthoscopus*, *Auriparus*, *Parus*, and *Melanochlora*.

The pneumotricipital fossa of the humerus in all specimens was double or combined (Table 3). In *Microbates*, *Rhamphocaenus*, and most *Polioptila* the dorsal fossa was only 30–50% as deep as the ventral fossa. In *Aegithalos* the dorsal fossa was 50–70% as deep as the ventral fossa and separated by only a step-down. In *Remiz* and *Melanochlora*, and in most *Psaltriparus*, *Anthoscopus*, and *Auriparus* the dorsal fossa was 70–90% as deep as the ventral fossa and separated by only a step-down. In nearly all *Parus* the fossae were equally deep and separated by a prominent medial bar. In *Coereba* the fossae were equally deep and combined in most specimens. (Bock 1962, Webster 1997.)

The interorbital septum was much more extensively bony in *Parus* and *Melanochlora* than in the other ten genera. Lucas (1890) mentioned this character.*

The premaxilla length/width ratio was high (2.6–4.2) in *Microbates*, *Rhamphocaenus*, and *Polioptila*; moderate to high

Table 4.—Tibiotarsus/tarsometatarsus, ratio of length.

<i>Microbates</i>	1.2
<i>Rhamphocaenus</i>	1.2
<i>Polioptila</i>	1.2
<i>Aegithalos</i>	1.3–1.4
<i>Psaltriparus</i>	1.3
<i>Anthoscopus</i>	1.4–1.5
<i>Auriparus</i>	1.4
<i>Parus</i>	1.4
<i>Coereba</i>	1.4
<i>Remiz</i>	1.5
<i>Melanochlora</i>	1.5

(2.0–3.2 in various subspecies) in *Coereba*; low (1.4–1.8) in the other seven genera (*Auriparus* 1.5).

Shape of the basihyale in these 11 genera varied clearly in two ways. In *Coereba* height at the midpoint was 3.4 times width, whereas in other genera it varied only from 0.7 to 1.2 (George 1962). In all nine specimens of *Coereba*, two of nine *Auriparus*, and five of ten *Parus* the rostral end of the basihyale was sagitate, whereas in the rest the rostral end was blunt with projecting corners absent or nearly so.*

The ratio of length of tibiotarsus/humerus was high (1.9–2.0) in *Microbates*, *Rhamphocaenus*, *Aegithalos*, and *Psaltriparus*. In *Polioptila* it was low or moderate (1.7–1.8). In the other six genera it was low (1.5–1.7).

The ratio of length of tibiotarsus/tarsometatarsus was higher in *Auriparus* than in the gnatwrens, gnatcatchers, and long-tailed tits (Table 4).

The ratio of tarsometatarsus length/skull length was high (1.1–1.2) in *Microbates*, *Rhamphocaenus*, *Polioptila*, *Aegithalos*, and *Psaltriparus*; low (1.0) in the other six genera.

The ratio of length/width of the tarsometatarsus was high (13.6–14.5) in *Microbates*, *Rhamphocaenus*, and *Polioptila*; fairly high (12.0–13.7) in *Aegithalos* and *Psaltriparus*; moderate (10.8) in *Coereba*; low (7.7–9.5) in *Remiz*, *Anthoscopus*, *Auriparus*, *Parus*, and *Melanochlora*.

Table 5.—Length of skull in mm.

<i>Melanochlora</i>	23.8
<i>Rhamphocaenus</i>	18.6
<i>Microbates</i>	18.5–19.4
<i>Parus</i>	17.6–20.2
<i>Coereba</i>	17.4
<i>Auriparus</i>	15.4
<i>Remiz</i>	15.3
<i>Polioptila</i>	15.0–15.6
<i>Psaltriparus</i>	14.5
<i>Aegithalos</i>	14.3–15.5
<i>Anthoscopus</i>	12.9–14.0

Length of the skull was used as a measure of size. *Auriparus* was smaller than the gnatwrens, tits, and Bananaquit (Table 5).

Ratio of tibiotarsus length/ulna length. Range in the 18 species was from 1.20 in *Melanochlora* to 1.72 in *Microbates collaris* with *Microbates*, *Rhamphocaenus*, *Aegithalos*, and *Psaltriparus* higher than the rest.

Ratio of tibiotarsus length/femur length. Range was from 1.68 in *Melanochlora* to 2.03 in *Aegithalos caudatus* and *Psaltriparus* with *Aegithalos* and *Psaltriparus* distinctly higher than the rest.

Ratio of ulna length/femur length. Range was from 1.06 in both species of *Microbates* to 1.42 in *Anthoscopus parvulus*. *Rhamphocaenus*, like *Microbates*, was distinctly low; *Aegithalos*, *Psaltriparus*, and *Polioptila plumbea* were the next lowest.

Ratio of humerus length/femur length. Range was from 0.93 in *Microbates collaris* to 1.21 in *Anthoscopus parvulus*. *Rhamphocaenus* and *Microbates* were lower than the rest.

Internal process of mandible, ratio of width at base/width at narrowest point. Range was from 2.7 in *Microbates collaris* and *Coereba* to 4.5 in *Remiz*. *Microbates cinereiventris* and *Aegithalos caudatus* were next to the lowest.

Pseudotemporal process of mandible, ratio of length/width at base. Range was from 0 (process absent) in *Polioptila plumbea* and *Anthoscopus parvulus* to 0.8 in both species of *Aegithalos*. A prominent process

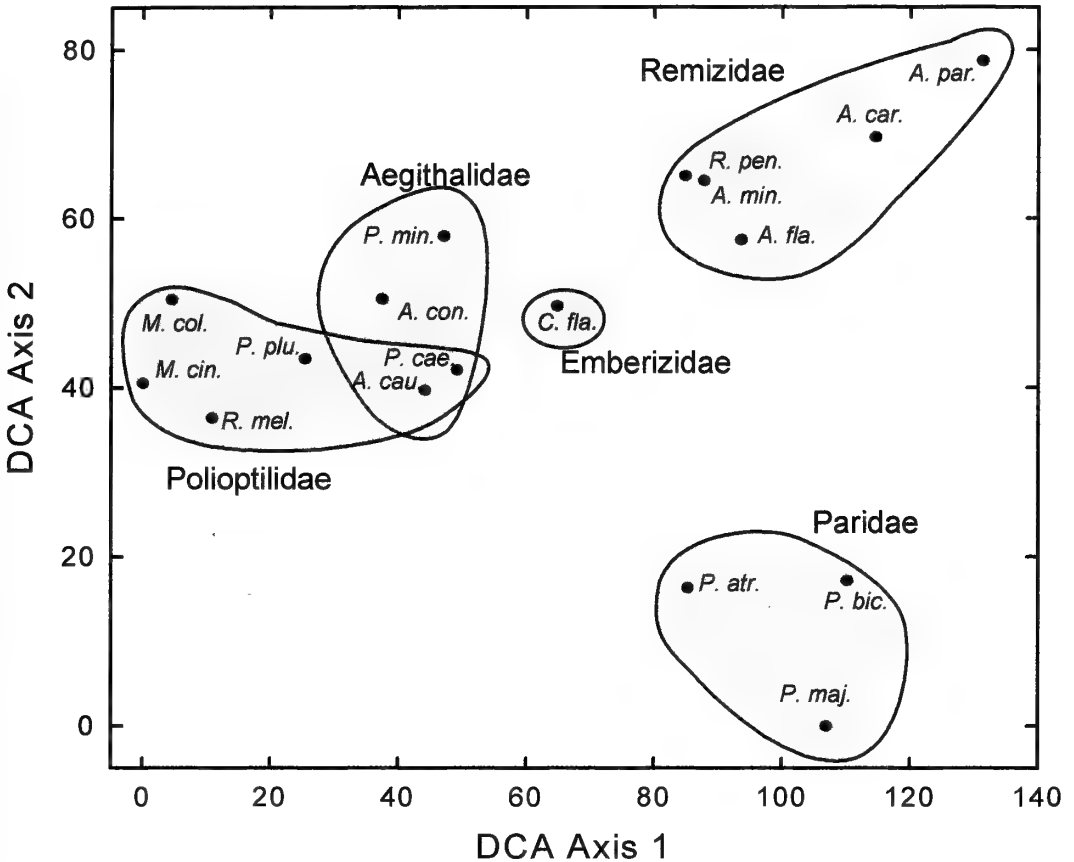


Fig. 1. Results of the detrended correspondence analysis (DCA) of 18 species of songbirds showing the first two DCA axes. Symbols are: *M.cin*—*Microbates cinereiventris*; *M.col*—*M. collaris*; *R.mel*—*Rhamphocœnus melanurus*; *P.cae*—*Polioptila coerulea*; *P.plu*—*P. plumbea*; *A.cau*—*Aegithalos caudatus*; *A.con*—*A. concinnus*; *P.min*—*Psaltriparus minimus*; *R.pen*—*Remiz pendulinus*; *A.car*—*Anthoscopus caroli*; *A.par*—*A. parvulus*; *A.min*—*A. minutus*; *A fla*—*Auriparus flaviceps*; *P.atr*—*Parus atricapillus*; *P.maj*—*P. major*; *P. bic*—*P. bicolor*; *M. sul*—*Melanochlora sultanea*; *C. fla*—*Coereba flaveola*.

(0.7) was also found in *Parus major* and *Coereba*.

Sibley & Ahlquist (1990) and Sibley & Monroe (1990) proposed a fairly close relationship between the Verdin (together with the gnatwrens and gnatcatchers) and the creepers (*Certhia* and *Salpornis*) as well as the wrens (Troglodytidae). I compared skeletons of the creepers and wrens with the 11 genera treated in detail above on all but seven of those 39 characters. Several characters showed differences; these two seem trenchant: height of the basihyale at its midpoint was 2.0 to 2.5 times

width in *Troglodytes* and *Certhia*; 1.0 in *Campylorhynchus*, *Thryothorus*, and *Salpornis*. The pneumotricipital fossa of the humerus lacked a dorsal fossa in *Campylorhynchus*; the dorsal fossa was 30% or less the depth of the ventral fossa in *Thryothorus*, *Troglodytes*, *Certhia*, and *Salpornis* (Table 3). These observed character states (as also those given above for 11 genera) agree with the tabulations of George (1962) for the basihyale and Bock (1962) for the pneumotricipital fossa except for the basihyale of one wren (*Troglodytes*).

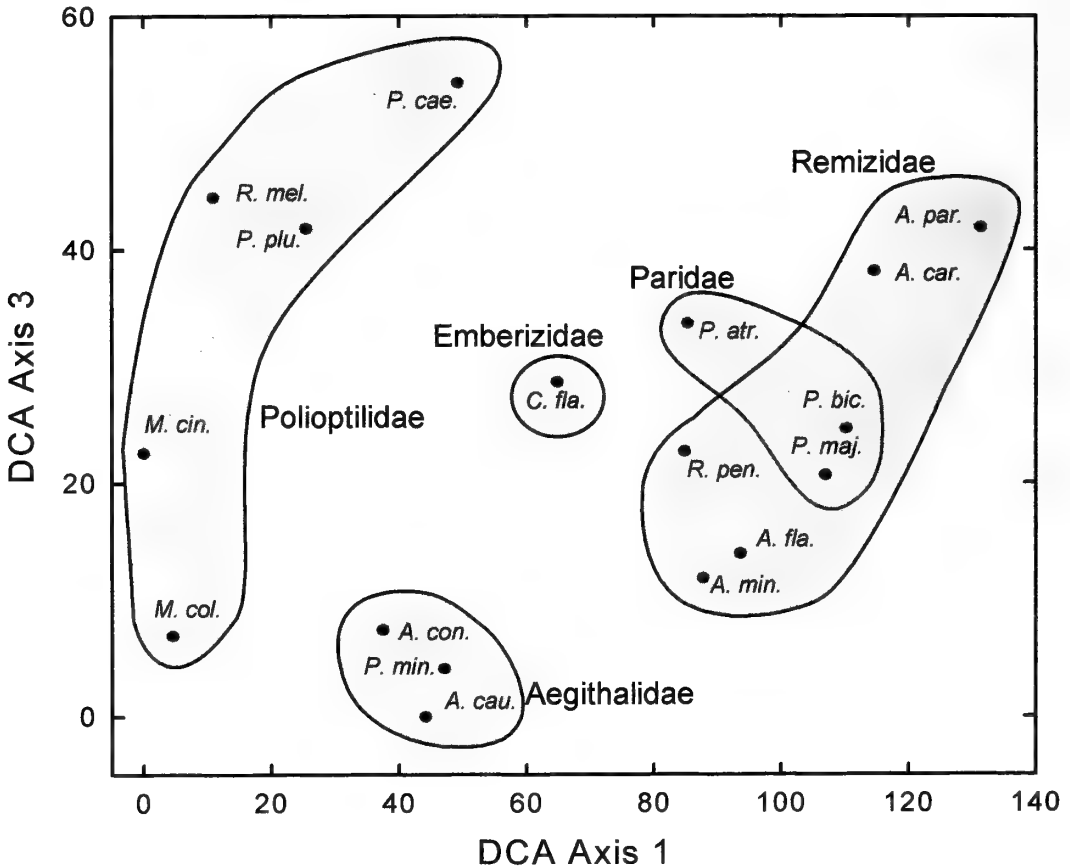


Fig. 2. Results of the detrended correspondence analysis (DCA) of 18 species of songbirds showing the first and third DCA axes. Symbols as in Fig. 1.

Discussion

Results of the DCA ordination (Table 2 and Figs. 1, 2) show fairly clear separation of the five families studied, as recognized by Snow (1967) and the other volumes of *Check-list of the Birds of the World*. Figure 1, however shows some overlap between Polioptilidae and Aegithalidae on these 18 characters, as does Fig. 2 on Paridae and Remizidae. In Fig. 2 the family-enclosing line of Remizidae is drawn on the simplest assumption; it could have been drawn in a bipolar shape to exclude the overlap area with Paridae.

Summarizing the 22 characters analyzed separately above, the skeleton of *Auriparus* agrees with that of *Anthoscopus* in 20 characters, *Remiz* in 19, *Parus* and *Melanoch-*

lora in 12, *Coereba* in nine, *Psaltriparus* in eight, *Polioptila* in seven, *Aegithalos* in six, *Rhamphocaenus* and *Microbates* in five. (Partial or irregular agreement is counted the same as disagreement here.) Similarity to wrens and creepers is slight on the basis of incomplete data. I conclude that skeletal characters agree with the behavioral, nest, and external structural characters mentioned by Cramp & Perrins (1992) and tend to confirm the classification of Snow (1967). The Verdin belongs with the penduline tits, Remizidae.

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Taxonomic notes on hummingbirds (Aves: Trochilidae).
3. *Helianthus violicollis* Salvin, 1891 is a color variant of
***Helianthus strophianus* (Gould, 1846)**

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Abstract.—The holotype of *Helianthus violicollis* Salvin, 1891, reportedly from “Sarayacu” on the Amazonian slope of the Ecuadorian Andes, is hypothesized to be a color variant of *Helianthus strophianus* (Gould, 1846) from the Pacific slope. A second specimen identified by Salvin as an immature male *H. violicollis* represents a female *H. strophianus* in typical definitive plumage. Analysis of plumage color and external measurements revealed no credible evidence for a hybrid origin of *H. violicollis*.

Osbert Salvin (1891:376) characterized *Helianthus violicollis*, a new sunangel procured by Clarence Buckley in Ecuador, as similar to *H. strophianus* (Gould, 1846), “but the upper surface of a darker, more rufescent brown, especially in the middle of the back; the abdomen too has a more bronzy hue; the most obvious difference is in the colour of the throat, which is glittering violet-blue, without any red or rosy tint.” Subsequent taxonomic assessments of *Helianthus violicollis* were anecdotal. Eugene Simon (cited by Hartert 1897) hypothesized that *H. claudia* Hartert, 1895 and *H. violicollis* represented melanistic color aberrations of *H. amethysticollis* (d’Orbigny & LaFresnaye, 1838) and *H. strophianus*, respectively. Oberholser (1902:333) cast further doubt on the taxonomic validity of *H. violicollis*, noting that gorget colors in *H. strophianus* varied from rose to violet and that “too much importance must not be attached to the precise shade of metallic feathers in separating species of hummingbirds.” Cory (1918) listed *H. violicollis* without comment in his catalog, whereas Simon (1921) and Hartert (1922) treated *H. violicollis* as a color variety of *H. strophianus*. Chapman (1926) did not examine the

type, but suggested that *H. violicollis* may be the eastern Ecuadorian form of *H. strophianus*. Finally, Peters (1945) recommended that *H. violicollis*, until rediscovered, was best regarded as an aberration of *H. strophianus*. Later treatments either paraphrased Peters (Zimmer 1951, Fjeldså and Krabbe 1990) or omitted *H. violicollis* altogether (e.g., Sibley & Monroe 1990). Nevertheless, the taxonomic status of *H. violicollis* is still very much in doubt, especially in light of recent discoveries of new species of *Helianthus* with small geographic ranges (Fitzpatrick et al. 1979) or from unknown localities (Graves 1993). Here I provide an assessment of the holotype (BMNH 1887.3.22.901) in The Natural History Museum (formerly British Museum of Natural History), Tring.

Methods

The holotype of *Helianthus violicollis* was supposedly collected in February 1880 at Sarayacu, Province of Pastaza, on the Amazonian slope of the Ecuadorian Andes (Warren 1966). Chapman (1926:728) noted:

“birds in this large collection were labeled by the dealer Gerard, Buckley’s agent, after they reached London. Most of them are credited to Sarayacu, and

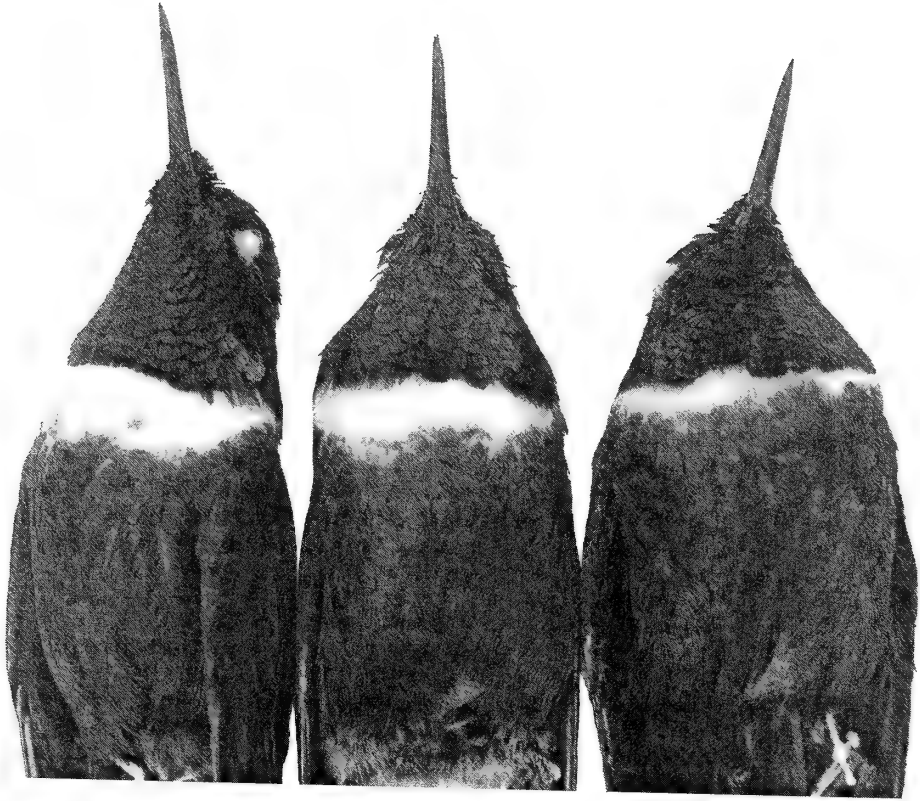


Fig. 1. Ventral view of the holotype of *Heliangelus violicollis* (BMNH 1887.3.22.901) flanked by male *Heliangelus strophianus* in definitive plumage.

this locality on a label attached to a skin from the Buckley collection is therefore to be accepted in a regional sense as any place at or near the settlement of this name and thence to the headwaters of the Rio Pastaza In this connection it may be added that Buckley employed collectors (Illingworth and Villagomez) in western Ecuador whose specimens were also labeled in London. Not only are the localities attributed to them often misleading, but in some instances it is evident that specimens from Buckley in eastern Ecuador have been confused with those from his collectors in western Ecuador."

Similar misgivings about Buckley's entomological localities were voiced by Brown (1941). Accordingly, the possibility that the holotype of *H. violicollis* was collected on the western slope of the Ecuadorian Andes must be considered.

The unsexed holotype of *Heliangelus violicollis* possesses a large (~53 violet-tipped feathers) gorget and relatively large external measurements (Fig. 1, Table 1), in-

dicative of male plumage in the gorgeted species of *Heliangelus*. A few faint striations (visible at 10X magnification) on the right basal margin of the maxillary ramphotheca indicate the specimen is a young adult (see Ortiz-Crespo 1972). A second specimen (BMNH 2000.1.10) from the Gould Collection reported by Salvin (1891, 1892) as an immature male *H. violicollis* is actually a female example of *H. strophianus* in fairly typical definitive plumage (unstriated maxillary ramphotheca, relatively small external measurements, streaked chin and upper throat small gorget [~10 brilliant feathers], see Bleiweiss 1992). I compared the holotype with all taxa of *Heliangelus* deposited in The Natural History Museum, including the type specimen of *Heliangelus amethysticollis laticlavus* (Salvin 1891) (BMNH 1887.3.22.903).

Table 1.—Measurements (range; mean \pm standard deviation in millimeters) of male and female *Heliangelus strophianus* in definitive plumage, the holotype of *Heliangelus violicollis* (BMNH 1887.3.22.901) and a female specimen (BMNH 2000.1.10) of *Heliangelus strophianus* identified by Salvin (1891, 1892) as an immature male of *H. violicollis*.

	<i>Heliangelus violicollis</i> BMNH 1887.3.22.901	<i>Heliangelus strophianus</i>		
		Male <i>n</i> = 15–18	Female <i>n</i> = 6	BMNH 2000.1.10
Wing chord	67.6	66.6–70.7 (68.2 \pm 1.2)	60.4–62.9 (61.5 \pm 0.9)	61.7
Bill length	12.4	12.0–13.5 (12.8 \pm 0.4)	12.7–14.2 (13.4 \pm 0.5)	12.9
Rectrix 1	38.8	35.2–39.4 (37.1 \pm 1.1)	31.9–35.9 (34.3 \pm 1.3)	33.8
Rectrix 2	42.3	38.2–42.5 (40.6 \pm 1.1)	35.5–39.9 (38.0 \pm 1.5)	37.3
Rectrix 3	45.3	41.8–45.2 (43.8 \pm 1.0)	36.6–41.7 (39.9 \pm 1.8)	39.6
Rectrix 4	47.4	44.0–48.2 (48.8 \pm 1.3)	37.1–42.7 (41.0 \pm 2.0)	41.5
Rectrix 5	46.5	46.4–50.4 (48.5 \pm 1.3)	38.6–42.3 (41.2 \pm 1.5)	41.0

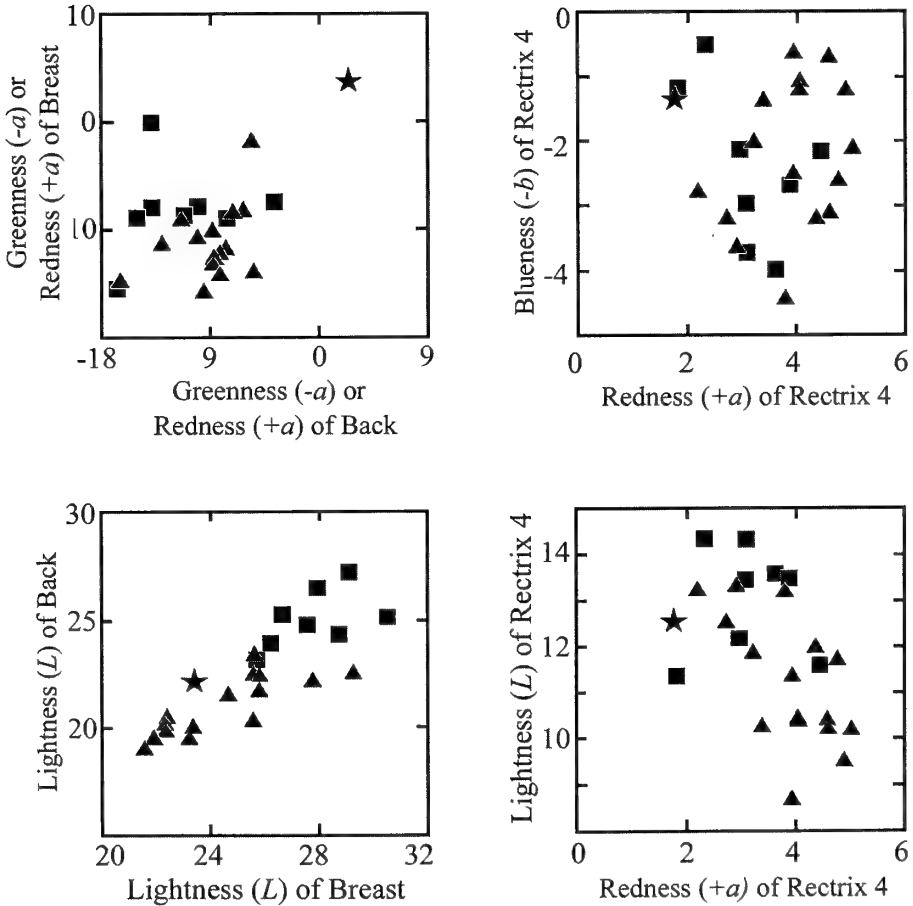


Fig. 2. Bivariate plots of opponent color coordinates (*L*, *a*, *b*) from plumage characters of male (\blacktriangle) and female (\blacksquare) *Heliangelus strophianus* in definitive plumage and the holotype of *Heliangelus violicollis* (\star) (BMNH 1887.3.22.901).

Table 2.—Minima, maxima, means, and standard deviations of opponent color coordinates (L , a , b) reflected from back, crown, breast, and rectrix 4 in male and female *Helianthus strophianus*, the holotype of *Helianthus violicollis* (1887.3.22.901) and a female specimen (BMNH 2000.1.10) of *Helianthus strophianus* identified by Salvin (1891, 1892) as an immature male of *H. violicollis*.

		<i>Helianthus strophianus</i>							
		Male			Female			BMNH 2000.1.10	
<i>Helianthus violicollis</i> BMNH 1887.3.22.901		Min.	Max	Mean \pm SD	Min.	Max	Mean \pm SD		
Crown	L	20.8	18.5	22.1	(20.3 \pm 1.2)	22.1	25.4	(23.8 \pm 1.2)	21.7
	a	3.6	-9.0	0.3	(-4.9 \pm 2.5)	-9.4	0.2	(-4.7 \pm 3.6)	-0.8
	b	12.9	13.9	21.6	(17.0 \pm 1.9)	15.4	22.1	(18.2 \pm 2.8)	15.7
Back	L	22.2	19.0	23.4	(20.9 \pm 1.4)	23.2	27.3	(25.2 \pm 1.3)	24.0
	a	2.4	-16.4	-5.4	(-9.0 \pm 2.8)	-16.7	-3.7	(-11.2 \pm 4.5)	-13.9
	b	15.9	12.1	22.6	(16.4 \pm 2.3)	12.9	23.1	(19.1 \pm 3.3)	20.4
Breast	L	23.4	21.6	29.3	(24.3 \pm 2.3)	25.7	30.5	(28.0 \pm 1.6)	26.2
	a	3.8	-15.9	-1.9	(-11.4 \pm 3.4)	-15.4	0.0	(-8.2 \pm 4.5)	-7.9
	b	13.4	8.6	22.0	(16.4 \pm 3.0)	11.0	20.6	(16.4 \pm 3.2)	13.4
Rectrix 4	L	12.6	8.7	13.3	(11.2 \pm 1.4)	11.4	14.3	(13.3 \pm 1.1)	11.6
	a	1.8	2.2	5.2	(3.9 \pm 0.8)	1.8	3.9	(3.0 \pm 0.7)	4.4
	b	-1.3	-4.4	-0.6	(-2.3 \pm 1.1)	-4.0	-0.5	(-2.5 \pm 1.3)	-2.2

Measurements of wing chord, bill length (from anterior extension of feathers), and rectrix length (from point of insertion of central rectrices to the tip of each rectrix) were made with digital calipers and rounded to the nearest 0.1 mm. Rectrices are numbered from innermost (R1) to outermost (R5).

I evaluated plumage color at five locations with a calibrated colorimeter (CR-221 Chroma Meter, Minolta Corporation) equipped with a 3.0 mm aperture: center of crown, at a line drawn across the posterior border of the eye rings; center of back; center of gorget; upper breast, ~4 mm left of the midline below the pectoral band; and the dorsal surface of rectrix 4 near the tip. The measuring head of the CR-221 uses 45° circumferential illumination. Light from the pulsed xenon arc lamp (C illuminant, 2° observer) is projected onto the specimen surface by optical fibers arranged in a circle around the measurement axis to provide diffuse, even lighting over the measuring area. Only light reflected perpendicular to the specimen surface is collected for color analysis. In order to reduce measurement variation, I held the aperture flush with the plumage surface without depressing the

plumage surface. The default setting for the CR-221 Chroma Meter displays mean values derived from three sequential, in situ measurements. I repeated this procedure three times for each area of plumage, removing the aperture between trials. Each datum summarized in Table 2 represents the mean of three independent measurements.

Colorimetric data from iridescent gorget feathers are acutely dependent on the angle of measurement, the curvature of the gorget surface in museum skins, and the degree of pressure applied to the plumage surface by the Chroma Meter aperture. Because within-specimen measurement error in *Helianthus* was deemed excessive, quantitative assessments of gorget color were omitted from data tables.

Colorimetric characters were described in terms of opponent-color coordinates (L , a , b) (Hunter & Harold 1987). This system is based on the hypothesis that signals from the cone receptors in the human eye are coded by the brain as light-dark (L), red-green (a), and yellow-blue (b). The rationale is that a color cannot be perceived as red and green or yellow and blue at the same time. Therefore "redness" and "greenness" can be expressed as a single

value a , which is coded as positive if the color is red and negative if the color is green. Likewise, "yellowness" or "blueness" is expressed by $+b$ for yellows and $-b$ for blues. The third coordinate L , ranging from 0 to 100, describes the "lightness" of color; low values are dark, high values are light. The more light reflected from the plumage the higher the L value will be. Visual systems in hummingbirds (e.g., Goldsmith & Goldsmith 1979) differ significantly from those of humans. The relevance of opponent color coordinates to colors perceived by hummingbirds is unknown.

I considered five hypotheses: *Helianthus violicollis* represents a genetic color variant of *H. strophianus*; an immature plumage of *H. strophianus*; an intrageneric hybrid; a chemically altered or light faded specimen of *H. strophianus*; or a valid taxon. Methods and assumptions of hybrid diagnosis follow Graves (1990) and Graves & Zusi (1990), as modified by insights on plumage color aberrations associated with hybridization (Graves 1998, 1999). Unless noted otherwise, assessments of plumage characters refer to males in definitive plumage.

Results

Plumage and morphological data are consistent with the hypothesis that *Helianthus violicollis* represents a color variant of *Helianthus strophianus* (Figs. 1, 2). As indicated by Salvin (1891, 1892), portions of the spinal, capital, and ventral feather tracts that exhibit green iridescence in *H. strophianus* are bronze-colored ($+a$ and $+b$ values in Table 2) in the holotype of *H. violicollis*. Viewed head-on, the crown, lores, auriculars, and sides of the throat are sooty black in both *H. violicollis* and *H. strophianus*. The gorget of *H. violicollis* is slightly smaller and narrower than those of definitive-plumaged males of *H. strophianus*, but this is probably attributable to the slight immaturity of the type of *H. violicollis*. Gorget iridescence is violet in *H.*

violicollis as opposed to pinkish-red or rose-red in *H. strophianus*. The size and shape of the pectoral band and pattern of undertail coverts are identical in *H. violicollis* and *H. strophianus*. The rectrices of *H. strophianus* are bluish-black. Those of *H. violicollis* are similar in color, but the central rectrices (R1) are faintly tinted with bronze near the rachis, a trait that is expressed in females and immature males of *H. strophianus*. The external measurements of the holotype of *Helianthus violicollis* fall within the range of those recorded for male *H. strophianus* in definitive plumage (Table 1). The bronze-colored plumage of *Helianthus violicollis* differs significantly from that of *H. strophianus* in immature and definitive plumage, indicating that *H. violicollis* is not merely an ontogenic variant of that species.

I found no evidence that *Helianthus violicollis* represents an intrageneric hybrid. In investigating the possibility of hybridization, I considered five species of sunangels with brilliant gorgets that occur in Ecuador, as potential parental species (i.e., *Helianthus exortis*, *H. micrastur*, *H. strophianus*, *H. viola*, *H. amethysticollis*; taxonomy of Schuchmann 1999). Only four of the ten possible pairwise combinations of species are known to overlap geographically: *H. micrastur* and *H. amethysticollis*; *H. micrastur* and *H. viola*, *H. exortis* and *H. viola*; *H. amethysticollis* and *H. viola* (Fjeldså & Krabbe 1990, Krabbe et al. 1998). However, based on the prevailing knowledge of plumage inheritance in hummingbird hybrids (Banks & Johnson 1961, Graves 1990, Graves & Zusi 1990, Graves & Newfield 1996), none of the possible species combinations could have produced hybrids with broad white pectoral bands (Fig. 1).

Iridescence in hummingbird plumages can be significantly altered by exposure to light (Graves 1991) or chemicals and may even change over time in sealed museum cabinets in the absence of any direct chemical contamination (Graves 1986). The plumage of *Helianthus violicollis* exhibits

none of the tell tale signs of prolonged exposure to light or chemical alteration of structural color observed in some other 19th century specimens of hummingbirds—e.g., sharp color contrast between exposed and concealed portions of imbricated feathers; asymmetric patterns of iridescence within feather barbs, within feathers, or within plumage tracts; matted or stained feather barbules under magnification; or (4) discoloration of the white pectoral band.

Finally, there is no evidence to suggest that *Heliangelus violicollis* represents a valid taxon. The type locality, Sarayacu (700 m), occurs below the known elevational range of sunangels (*Heliangelus* spp.) in the Andes (Graves 1985, Hilty & Brown 1986, Fjeldså and Krabbe 1990). The failure of 20th century ornithological surveys and collecting expeditions (Paynter 1993) to obtain specimens of *H. violicollis* in the upper Rio Pastaza drainage provides additional evidence, albeit circumstantial, that the holotype was erroneously labeled.

In summary, the holotype of *Heliangelus violicollis* is indistinguishable in size, external shape, and plumage pattern from male *Heliangelus strophianus*, differing only in the color of plumage iridescence. All evidence is consistent with Simon's (1921) hypothesis that *H. violicollis* is a color variant of *H. strophianus*. Consequently, the name *Heliangelus violicollis* Salvin, 1891 is correctly placed in the synonymy of *Heliangelus strophianus* (Gould, 1846).

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A new tissue-grade organism 1.5 billion years old from Montana

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Abstract.—“Problematic bedding-plane markings” that resemble a “string of beads” from the Appekunny Formation in the eastern part of Glacier National Park Montana are described as *Horodyskia moniliformis*, a new genus and new species. The matrix shows laminations at an exceptionally fine scale, and, during life these aquatic organisms may have been intermittently lightly covered by wind-blown quartz dust. Growth stages are present: tiny, elongate, benthonic threads develop swellings; swellings grow upward; more robust forms have wide short cones. At all growth stages, the spacing of the cones is approximately proportionally to the diameter of the enlarging cones. To account for this phenomenon, presumably cones intermediate in position along the thread episodically ceased growth. Thus, the organism exhibits a form of colonial growth.

The late R. J. Horodyski (1982) described material from Glacier National Park (GNP) as “problematic bedding-plane markings.” This material is best seen in the field as light spots on a dark matrix, and are informally called “string of beads.” Similar-appearing material has been illustrated and discussed, but not named, from Western Australia (Grey and Williams 1990).

About 2000 meters of strata are exposed in the eastern and central part of GNP (Fedonkin et al. 1994). The fossils of interest are limited to the lower few meters of the 700 meter thick Appekunny Formation. The aquatic Altyn Formation, a stromatolite-bearing limestone at the base of the section, is cut off below by a thrust fault. It is overlain by the clastic Appekunny and Grinnell Formations. The Appekunny is variegated and the Grinnell is distinctly red. The Siyah Formation, another aquatic stromatolitic limestone, is next in sequence and is followed by the Snowslip Formation and the Shepard Formation, both clastic, the Shep-

ard being cut off at its top by another thrust fault. The Pursell Lava lies between the Snowslip and the Shepard and U/Pb dates for that unit range from 1508 to 1845 million years (Alenikoff et al. 1996).

The fossils are known from three adjacent localities (Fedonkin et al. 1994), possibly within the same narrow stratigraphic level. D. W. Winston (in litt.) notes that these beds are unique to the Belt Super-group in being aquatic, rather than terrestrial, red beds. This lower portion of the Appekunny is further remarkable as an exceptionally fine siltite having several microlaminae per mm. In some beds the laminae are gently inclined to form very low hummocky cross-bedding. Higher in this formation, the hummocks are larger, almost all of sequence is of more red beds, and mud cracks and a few shale clasts are present. We interpret the lower fossiliferous beds as quiet water deposits, the sediment forming them being derived from air-borne quartz dust.

Systematic Paleontology

Kingdom, Phylum, and Class Incertae

Sedis

Horodyskia, new genus

Type species.—*Horodyskia moniliformis*, new species.

Diagnosis.—Presumed colonial organisms of small, vertically oriented, short wide cones, hemispherical on the upper surface, growing from a horizontal tube.

Horodyskia moniliformis, new species

Description.—A series of spherical bodies growing from a thin horizontal stolon of variable length and variable orientation relative to troughs and ridges of substrate. Diameter of spherical bodies and spacing between them nearly coequal. As upward growth begins, number of bodies per unit length of string decreases. With further vertical growth, the bodies elongate into wide cones, but remain essentially proportionally spaced. Regardless of the size of individuals, spacing between them remains approximately proportional to diameter of cones and number of cones per unit length of string decreases with increase of cone diameter.

Etymology.—Named in honor of the contributions made by R. J. Horodyski to Precambrian paleontology. The trivial name refers to necklace or string of beads appearance.

Type specimens and related material.—Holotype, United States National Museum (USNM) 508100 (Fig. 1); paratypes USNM 508101–508131, (not figured herein). The type locality is on the Running Wolf Mountain, at approximately the 1700 m contour; this mountain is just north of Two Medicine campground, near the east boundary of GNP, Montana. The primary types are supplemented by about 275 additional slabs; many of these contain more than one string. In addition, ten days were spent in the field examining specimens on the outcrop and collecting.

Systematic position.—The classic divi-

sions of plant or animal cannot be readily applied to some organisms in the fossil record; our material is too complex to fit within the Protista. If a choice must be made between those two entities, we would place *Horodyskia* as an animal. As will be discussed below, the beads were apparently episodically covered by exceedingly fine sediment and this would tend to inhibit photosynthesis as a possible food source. That does not prove a connection to Animalia, but is suggestive.

Preservation.—On all of the strings examined, only two modes of preservation have been noted. Either the individual beads are replaced by silica or they lack an integument and are represented by internal fillings. Specimens are preserved in these two modes on both bedding plane and sole surfaces of slabs. No organic matter has been observed on any specimen. Thus, the prospects for studying any so-called biogenic signals from carbon isotopes is remote, even though, the matrix is little metamorphosed, relative to correlative beds on the western side of GNP.

The slab bearing the holotype (Fig. 1) was selected from a darker colored bed, in part because this may provide the opportunity for geochemical investigations in the future when new techniques might be developed. The string of beads to the upper left of the scale is the holotype and to the upper left of the last bead of the holotype are four smaller beads of another string. In the lower center are at least two more strings with slightly different size beads in each. Because of the fine lamination, the rock splits readily, and, to the far left, two smaller beads of another string are on a triangular-shaped slightly higher surface. Near the top of the slab, two more larger beads are on a slightly lower surface.

Specimens are vertically compressed so as to be nearly one dimensional, but sufficient detail is present to reconstruct the mature form of each "bead" as a low broad cone. The "beads" of *Horodyskia* are upwardly slightly curved plates of silica, this

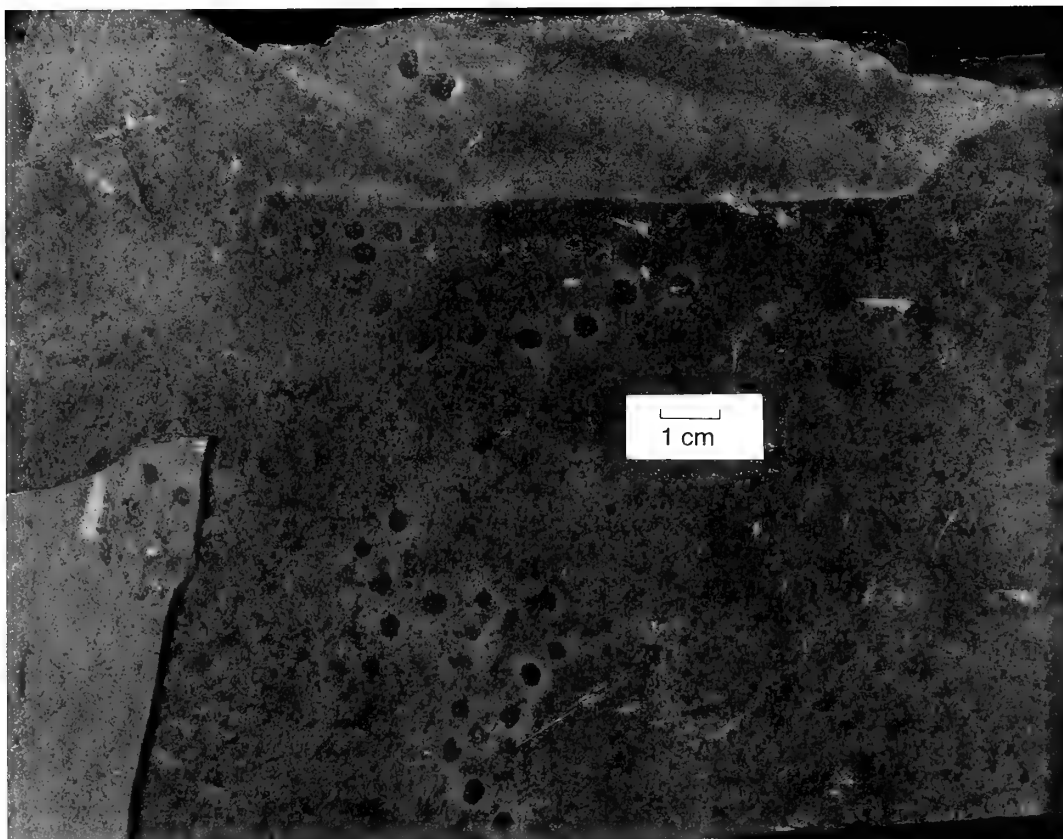


Fig. 1. A relatively smooth upper bedding plane surface from the Appekunny Formation on which a one (1) cm scale has been placed. The holotype is above the scale. USNM 508100, from Running Wolf Mountain, Glacier National Park, Montana, USA (for locality details see Fedonkin et al. 1994, p. 206).

mineral having replaced the original material; the present composition was determined by an electron probe. On the bedding plane surfaces, the internal fillings of the cones stand up as low hemispheres. We estimate that these cones may have grown to a maximum height of about 1 cm during life, but were partially within the sediment throughout their growth. Repeated sectioning of specimens on both sole and bedding plane surfaces and examination under SEM did not produce any details on dimensional shape and mode of growth.

Three lines of evidence suggest the integument of the individual cones was relatively resistant during life. First, some were plucked from the sediment by current action, leaving triangular or quadrangular im-

pressions (Fedonkin et al. 1994, fig. 21). Second, some show current crescents where moving water washed away fine-sized silt around part of the circumference and deposited slightly coarser silt in the depression. Third, some decayed in place and are surrounded by an irregular brown stain. Ancillary evidence that the cones had a thick, resistant wall is given by the absence of any wrinkling of the integument; this is marked contrast to specimens of the younger microfossil *Chuarina* Walcott, which are so wrinkled as to superficially resemble the texture of raisins.

An artistic rendering to show the life position and resistance of the beads is included (Fig. 2). A strong water current from the upper right has excavated current crescents

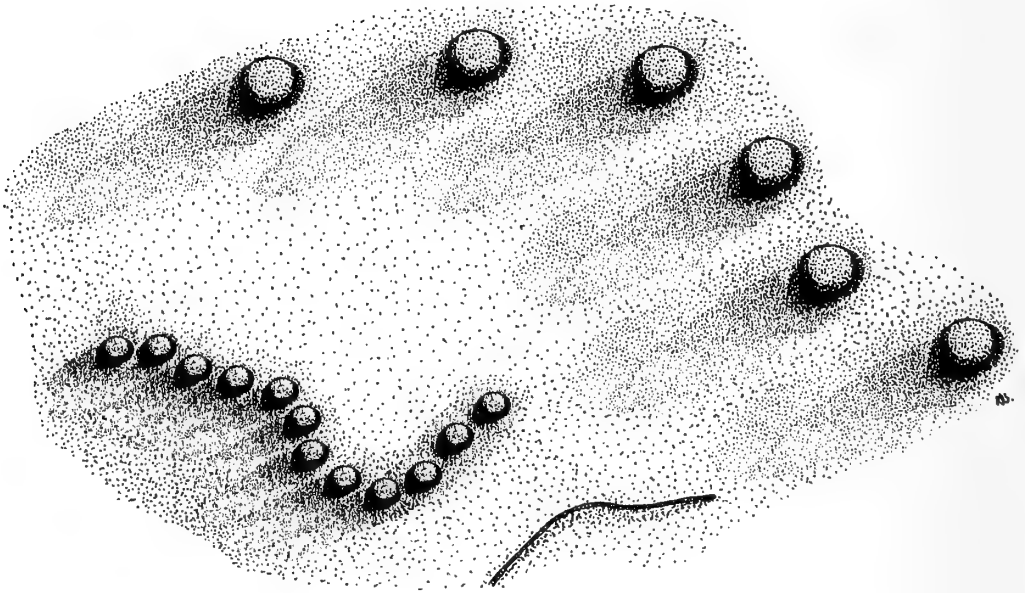


Fig. 2. Artistic rendition of two strings of beads standing in low relief above the bottom, with the sediment affected by their interruption of water movement from the upper right. A stolon which has not yet developed swellings as the first stage of upward growth is lying on the sediment at the lower edge of the drawing. Drawn at approximately natural size.

behind each of the beads of two strings and has left faint current shadows on the fine-grained silt sediment surface.

A few cones appear to have partially flaked away so that the interior may be observed. They may have had interior ridges or rods to strengthen the wall, but the evidence is still relatively inconclusive. Because most of the material is on loose slabs, and has been variously affected by taphonomic processes and subsequent weathering, interpretation of the material is complex and is continuing.

Discussion.—Even though many pseudofossils have been named from the Precambrian, the organic nature of these specimens is defensible. Several forms of traces and inorganic features occur in the Appekunny Formation (Fedonkin et al. 1994), but none of these resemble this material. No sedimentary processes are known which would produce these nearly uniformly spaced spots in elongate strings of varying direction.

On the other hand, the proportionality between the size of the spots and their spac-

ing is remarkable and compelling. No matter how small or how large are these spots, the relative spacing is consistent within the limits of individual effects of preservation and biologic variability. As a general rule, small beads are nearly circular and the larger the beads on a string, the more irregularity there is among the beads. We attribute this irregularity to effects of water currents during life, differential compression and other taphonomic effects.

Many of the strings collected fall within a limited size range for the beads, but it is possible to suggest a gradual increase in spacing with increase in size. At the earliest stage of upward growth, spaces are about the same length as the diameter of the swellings. For the largest known individual the diameter of beads is just over 1 cm and the spacing is just under 2 cm. Organic growth is indicated as the most plausible mechanism to explain the near proportional uniformity of spacing.

Precise measurements are difficult because the boundaries of beads are not al-

ways easy to observe. The values given below are approximate, but are representative of the proportionality of bead size to spacing. The holotype (USNM 508100) has seven beads about 43 mm in diameter and spaced at about 53 mm intervals. For five paratypes the comparable figures are: USNM 508103, 21 beads, 39 mm in diameter and 42 mm spacing; USNM 508110, five beads, 49 mm, and 57 mm; USNM 508112, 22 beads, 27 mm, and 39 mm; USNM 508122, seven beads, 44 mm, and 71 mm; and USNM 508124, eight beads, 41 mm, and 42 mm.

Individual strings vary both in length and in direction, commonly being slightly curved or sigmoidal. The strings show no preferred orientation on hummocky surfaces. On some strings more than 25 beads are present. Specimens on sole surfaces are more common, but this may be because they are easier to observe in the field. Even by the standard of Phanerozoic occurrences of fossils, at the three localities where *H. moniliformis* has been collected, specimens are abundant.

Horodyski published additional illustrations during a decade following his original work, but no more descriptive matter was added and he was never clear that these structures were indeed organic. All his illustrated specimens are from the lower (sole) surfaces of beds, not the bedding planes, as he wrote. No specimens branch, and there is only one form present, two other points in which we disagree with his original informal discussion. Several strings are illustrated in Fedonkin et al. (1994, figs. 20–23). We envision that episodically the growing colony was covered with a slightly thicker than average layer of dust settling through the water column. To insure that the smothered colony did not die, alternate cones presumably transferred part of their substance to adjacent cones, allowing them to grow upward through the sediment. When the next thicker layer settled, the transfer of material from intermediate cones

was repeated. We can think of no other mechanism to explain the spacing of the cones. One factor stimulating cell redistribution and upward growth might be chemotactic attraction to the overlying oxidized environment.

If our interpretation of the growth pattern is correct, it implies a relatively high level of biological organization at a geologically early time. This is colonial growth, but it is unlike colonies which grow by the increase in size of individuals without adding new individuals. We are not aware of any living organisms which are closely comparable to *Horodiskia*.

Acknowledgments

This study was supported in part in 1992 by a grant to Fedonkin from the Smithsonian Institution, Office of Fellowships and Grants and a grant to Yochelson from the National Science Foundation. In the field, Dr. D. W. Winston, University of Montana, shared his wide knowledge of the geology of the Belt Supergroup, as did the late R. J. Horodyski. Authorities of the National Park Service granted a collecting permit. Technical critics A. Cheetham, D. Erwin, and E. Robbins much improved our original draft. We thank V. Krantz, National Museum of Natural History (retired) for the photograph.

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REVIEWERS

The following people reviewed manuscripts for the Proceedings in 1999. N. E. Adams, A. Anker, J. Arroyo-Cabrales, K. Baba, C. C. Baldwin, F. M. Bayer, I. A. E. Bayly, C. W. Beasley, D. Berner, T. Best, R. Boettger-Schnack, J. Bradford-Grieve, A. Brandt, A. J. Bruce, N. L. Bruce, J. E. Cadle, S. D. Cairns, J. A. Campbell, P. Campinho, E. Campos, D. Cannatella, M. D. Carleton, P. Clark, K. A. Coates, P. A. Coelho, C. O. Coleman, N. Cumberlidge, C. d'Udekem d'Acoz, F. D'Incao, P. J. F. Davie, D. Duinot, J. T. Eastman, S. Emslie, C. Erseus, D. G. Fautin, D. L. Felder, C. Ferraris, K. Fitzhugh, O. S. Flint, Jr., B. Richer de Forges, L. Forro, S. Gamo, A. L. Gardner, G. R. Gaston, P. Gipson, O. Gon, L. Grande, D. Greenfield, L. E. Grosso, M. Grygier, E. Hajdu, A. Harold, J. C. den Hartog, M. Harvey, R. W. Heard, S. B. Hedges, M. Hendrickx, W. R. Heyer, B. Hilbig, S. Hiruta, J-s Ho, J. T. Hoag, R. S. Hoffmann, J. R. Holsinger, M. Holynska, P. Houde, P. A. Hutchings, V. N. Ivanenko, K. Izawa, H. James, G. Karaman, B. Kensley, T. Kikuchi, W. Kim, J. C. von Vaupel Klein, K. Konishi, F. Krapp, R. K. Kropp, J. H. Leal, R. Lemaitre, B. Livezey, J. Lundberg, C. Magalhaes, M. Malyutina, R. B. Manning, R. N. Mariscal, J. C. Markham, W. N. Mathis, R. W. McDiarmid, J. McGuire, P. A. McLaughlin, J. McLean, G. S. de Melo, N. A. Menezes, S. Menu-Marque, R. Modlin, E. S. Morales, H. Morino, W. Moser, G. Moura, C. Mourer-Chauvire, U. Muehlenhardt-Siegel, T. Munroe, M. Murano, G. G. Musser, A. Myers, P. Naiyanetr, S. Nates, C. R. Nelson, W. A. Newman, P. K. L. Ng, N. Ngoc-Ho, S. Ohtsuka, J. Olesen, S. L. Olson, L. Parenti, D. W. Pawson, J. Pearse, T. H. Perkins, M. E. Petersen, I. Petrescu, U. Piatkowski, K. de Queiroz, K. Reimann-Zurneck, R. P. Reynolds, S. A. Rice, N. W. Riser, G. Rodríguez, R. Roman-Contreras, L. Ruedas, D. Russell, K. Rutzler, P. Schuchert, K. Schulz, E. Shea, J. Shields, J. B. Slowinski, W. Smith-Vaniz, V. G. Springer, D. Steadman, H. Suzuki, K. Tabachnick, M. Tavares, C. Taylor, R. F. Thoma, F. G. Thompson, J. C. Tyler, R. P. Vari, S. Vassilenko, W. Vervoort, R. Vonk, R. Voss, J-W. Waegele, J. Watson, S. H. Weitzman, B. Werding, M. Wetzell, M. K. Wicksten, E. Willen, D. E. Wilson, G. Wilson, L. D. Wilson, R. Winterbottom, K. Wittmann, K. Wouters, G. Wyngaard, R. Yong, G. R. Zug.

BIOLOGICAL SOCIETY OF WASHINGTON
127th Annual Meeting, 24 May 2000

The meeting was called to order by President Richard P. Vari in the Division of Fishes Conference Room, National Museum of Natural History. Society members present: Brian F. Kensley (President Elect), T. Chad Walter (Treasurer), Carole C. Baldwin (Secretary), Michael D. Carleton, W. Duane Hope, Susan L. Jewett, Rafael Lemaitre, Roy W. McDiarmid, James N. Norris (Elected Council), C. Brian Robbins (Editor), Bruce B. Collette (Finance Committee, Past President), Janet Reid (Past President), and Michael Vecchione.

Minutes of the 126th Annual Meeting of the Society were approved, and President Vari then called on Chad Walter for the Treasurer's Report (Table 1). Society income for the period 1 January 1999 to 31 December 1999 was \$108,514.28; expenses for the same period were \$105,562.69. Total assets for the Society as of 31 December 1999 were \$132,569.46, up from \$129,617.87 in 1998, despite declines in the endowment account due to stock-market fluctuations. The Society's current contract with Allen Press expires this year, and a proposal from Allen Press for a new three-year contract was presented at the meeting. The new contract, which includes a minimal increase in printing costs for 2001 and 2002, was voted upon and unanimously approved.

Editor Brian Robbins then reported that four issues of Volume 112 of the *Proceedings* were published comprising 73 papers and 856 pages, down from 87 and 1008, respectively, in Volume 111. The number of submissions in 1999 was the highest in five years (111, vs. 100 or fewer in 1995–1998). As of 1 May 2000, 45 papers have been submitted for Volume 113, up from 37 in 1999. The new cover design for the *Proceedings* made its debut on Issue No. 1 of Volume 113, an issue that was dedicated to deceased Society member Austin Williams. NMNH scientific illustrator, Molly K. Ryan, was thanked for her creative efforts in designing the new cover. There continues to be no backlog for papers accepted in the *Proceedings*, and new guidelines for authors are currently being revised. The Editor thanked Associate Editors Frederick M. Bayer, David B. Lellinger, Wayne N. Mathis, Gary R. Graves, Stephen L. Gardiner, Frank D. Ferrari, and Rafael Lemaitre for their contributions to the *Proceedings* during the past year.

President Vari then called on Bruce Collette for the Finance Committee Report. Collette reported that he and Thomas Munroe (serving in place of Austin Williams) had examined the Treasurer's records for

Table 1.—Summary financial statement for 1999.

	General fund	Endowment fund	Total assets
ASSETS: JANUARY 1, 1999	25,506.27	104,111.60	129,617.87
TOTAL RECEIPTS FOR 1999	90,076.82	18,437.46	108,514.28
TOTAL DISBURSEMENTS FOR 1999	86,201.87	19,360.82	105,562.69
ASSETS: DECEMBER 31, 1999	29,381.22	103,188.24	132,569.46
NET CHANGES IN FUNDS	3,874.95	(923.36)*	2,951.59

* The income from publication inventory \$4,070.00 and Merrill Lynch loss of value (-\$4,993.36) produced a net reduction of (-\$923.36).

As of 12/31/99 the Merrill Lynch portfolio was valued at \$88,746.18.

1999 and found accounting activity to be in good order.

Custodian of Publications, Storrs Olson, who was unable to attend the meeting, reported through President Vari that the Society's stock of unbound *Proceedings* separates had been sorted by taxonomic category and turned over to the appropriate NMNH Division, each of which can distribute or sell the issues as deemed appropriate.

Results of the 2000 election of officers were then announced as follows: President Elect—Roy W. McDiarmid, Secretary—Carole C. Baldwin, Treasurer—T. Chad

Walter, Elected Council—Michael D. Carleton, W. Duane Hope, Susan L. Jewett, G. David Johnson, Rafael Lemaitre, and Jon Norenburg. President Vari thanked Ronald W. Heyer, Robert Hershler, and Wayne N. Mathis for serving as the nominating committee for the election.

The meeting was then turned over to incoming President Brian F. Kensley, who thanked Vari for his service as President and then adjourned the meeting.

Respectfully submitted,
Carole C. Baldwin
Secretary

INTERNATIONAL TRUST FOR ZOOLOGICAL NOMENCLATURE

Applications published in the *Bulletin of Zoological Nomenclature*

The following Applications were published on 31 March 2000 in Vol. 57, Part 1 of the *Bulletin of Zoological Nomenclature*. Comment or advice on any of these applications is invited for publication in the *Bulletin* and should be sent to the Executive Secretary (I.C.Z.N.), % The Natural History Museum, Cromwell Road, London SW7 5BD, U.K. (e-mail: iczn@nhm.ac.uk).

Case No.

- 3086 *Hyalinia villae adamii* Westerlund, 1886 (currently *Oxychilus adamii*; Mollusca, Gastropoda): proposed conservation of the specific name *adamii* by replacing the syntypes with a neotype
- 3111 *Pachycerianthus* Roule, 1904 (Cnidaria, Anthozoa): proposed designation of *P. multiplicatus* Carlgren, 1912 as the type species
- 2926 *Trichia* Hartmann, 1840 (Mollusca, Gastropoda): proposed conservation; and TRINCHIINAE Ložek, 1956 (Mollusca): proposed emendation of spelling to TRICHIANINAE, so removing the homonymy with TRICHIIDAE Fleming, 1821 (Insecta, Coleoptera)
- 3120 ISCHNURAINAE Fraser, 1957 (Insecta, Odonata): proposed conservation as the correct spelling of ISCHNURINAE to remove homonymy with ISCHNURIDAE Simon, 1879 (Arachnida, Scorpiones)
- 3119 VACHONIAINAE Maury, 1973 (Arachnida, Scorpiones): proposed conservation as the correct spelling to remove homonymy with VACHONIIDAE Chamberlin, 1947 (Arachnida, Pseudoscorpiones)
- 3113 *Betta* Bleeker, 1850 (Osteichthyes, Perciformes): proposed conservation of specific names by the suppression of *Micracanthus marcheii* Sauvage, 1879
- 3134 *Rana cryptotis* Boulenger, 1907 (currently *Tomopterna cryptotis*; Amphibia, Anura): proposed precedence of the specific name over that of *Chirromantis kachowskii* Nikolsky, 1900
- 3033 *Myoxus japonicus* Schinz, 1845 (currently *Glirulus japonicus*; Mammalia, Rodentia): proposed conservation as the correct original spelling of the specific name

The following Applications were published on 30 June 2000 in Vol. 57, Part 2 of the *Bulletin of Zoological Nomenclature*. Comment or advice on any of these applications is invited for publication in the *Bulletin* and should be sent to the Executive Secretary (I.C.Z.N.), % The Natural History Museum, Cromwell Road, London SW7 5BD, U.K. (e-mail: iczn@nhm.ac.uk).

Case No.

- 3133 *Peristernia* Mörch, 1852 (Mollusca, Gastropoda): proposed conservation of *Turbinella nassatula* Lamarck, 1822 as the type species
- 3088 *Doris verrucosa* Linnaeus, 1758 (Mollusca, Gastropoda): proposed conservation of the generic and specific names by designation of a neotype
- 3135 *Scyllarus orientalis* Lund, 1793 (currently *Thenus orientalis*; Crustacea, Decapoda): proposed designation of a neotype
- 3103 *Orsodacne* Latreille, 1802 (Insecta, Coleoptera): proposed conservation by the designation of *Chrysomela cerasi* Linnaeus, 1758 as the type species
- 3118 *Anthaxia* Eschscholtz, 1829 (Insecta, Coleoptera): proposed designation of *Buprestis nitida* Rossi, 1792 (currently *A. fulgurans* (Schrank, 1789)) as the type species
- 3085 *Lacerta undata* A. Smith, 1838 (currently *Pedioplanis undata*; Reptilia, Sauria): proposed conservation of the specific name by the designation of a neotype
- 2980 *Procoptodon* Owen, 1874 (Mammalia, Marsupialia) and the specific names of *P. rapha* Owen, 1874 and *P. pusio* Owen, 1874: proposed conservation
- 3090 *Musca arcuata* and *M. festiva* Linnaeus, 1758 (currently *Chrysotoxum arcuatum* and *C. festivum*) and *M. citrofasciata* De Geer, 1776 (currently *Xanthogramma citrofasciatum*) (Insecta, Diptera): proposed conservation of usage of the specific names by the designation of neotypes for *M. arcuata* and *M. festiva*

Opinions published in the *Bulletin of Zoological Nomenclature*

The following Opinions were published on 31 March 2000 in Vol. 57, Part 1 of the *Bulletin of Zoological Nomenclature*. Copies of these Opinions can be obtained free of charge from the Executive Secretary, I.C.Z.N., % The Natural History Museum, Cromwell Road, London SW7 5BD, U.K. (e-mail: iczn@nhm.ac.uk).

Opinion No.

- 1942 *Haminoea* [Turton] in Turton & Kingston in Carrington, 1830 and HAMI-
NOEINAE Pilsbry, 1895 (Mollusca, Gastropoda): Placed on Official
Lists as correct original spellings.
- 1943 *Pachylops* Fieber, 1858 (Insecta, Heteroptera): *Capsus chloropterus* Kirsch-
baum, 1856 (currently *Orthotylus virescens* (Douglas and Scott
1865)) fixed as the type species.
- 1944 *Papilio sylvanus* Esper, 1777 (surrently known as *Ochlodes sylvanus* or *O.*
venatus faunus; Insecta, Lepidoptera : specific name conserved.
- 1945 *Scarus chrysopterus* Bloch & Schneider, 1801 (currently *Sparisoma chrysop-*
terum; Osteichthyes, Perciformes): specific name conserved and des-
ignated as the type species of *Sparisoma* Swainson, 1839.
- 1946 *Osphronemus deissneri* Bleeker, 1859 (currently *Parosphromenus deissneri*;
Osteichthyes, Perciformes): holotype replaced by a neotype.
- 1947 *Iguanadon* Mantell, 1825 (Reptilia, Ornithischia): *Iguanodon bernissartensis*
Boulenger in Beneden, 1881 designated as the type species, and a
lectotype designated.
- 1948 *Hydrosaurus gouldii* Gray, 1838 (currently *Varanus gouldii*) and *Varanus*
panoptes Storr, 1980 (Reptilia, Squamata): specific names conserved
by the designation of a neotype for *H. gouldii*.
- 1949 *Cacatua* Vieillot, 1817 and CACATUINAE Gray, 1840 (AVES, PSITTACIFORMES):
CONSERVED.

The following Opinions were published on 30 June 2000 in Vol. 57, Part 2 of the *Bulletin of Zoological Nomenclature*. Copies of these Opinions can be obtained free of charge from the Executive Secretary, I.C.Z.N., % The Natural History Museum, Cromwell Road, London SW7 5BD, U.K. (e-mail: iczn@nhm.ac.uk).

Opinion No.

- 1950 *Haliotis clathrata* Reeve, 1846 (non Lichtenstein, 1794) and *H. elegans* Philippi, 1844 (Mollusca, Gastropoda): specific names conserved
- 1951 *Spherillo* Dana, 1852 (Crustacea, Isopoda): *Spherillo vitiensis* Dana, 1853 designated as the type species
- 1952 AUGOCHLORINI Beebe, 1925 (Insecta, Hymenoptera): given precedence over OXYSTOGLOSSINI Schrottky, 1909
- 1953 *Strongylogaster* Dahlbom, 1835 (Insecta, Hymenoptera): conserved by the designation of *Tenthredo multifasciata* Geoffroy in Fourcroy, 1785 as the type species
- 1954 *Labrus* Linnaeus, 1758, *Cichlasoma* Swainson, 1839 and *Polycentrus* Müller & Troschel, 1849 (Osteichthyes, Perciformes): conserved by the designation of *Labrus mixtus* Linnaeus, 1758 as the type species of *Labrus* and *L. bimaculatus* Linnaeus, 1758 as the type species of *Cichlasoma*; and *Polycentrus schomburgkii* Müller & Troschel, 1849; specific name given precedence over *L. punctatus* Linnaeus, 1758

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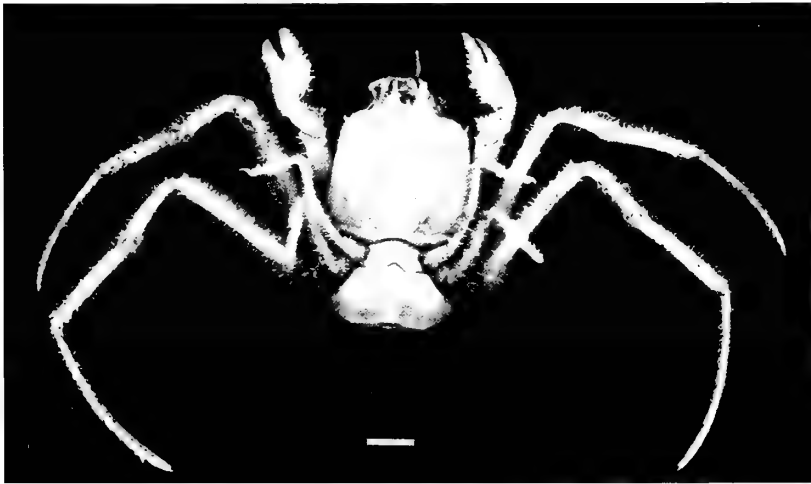
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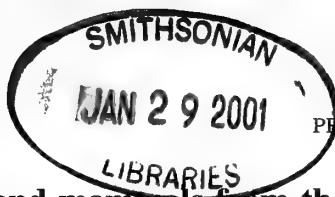
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Land-mammals from the Late Paleocene Aquia Formation: The first early Cenozoic mammals from Maryland

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Abstract.—The late Paleocene Aquia Formation has produced the first early Cenozoic mammal remains from Maryland: a molar of the taeniodont *Ectoganus*, a molar fragment questionably referred to the condylarth *Phenacodus*, and an ungual phalanx of an arctocyonid. They constitute only the third record of Paleocene mammals from eastern North America.

Paleocene mammals are almost unknown from North America east of the Western Interior. Only two such occurrences have previously been reported, one in Louisiana and the other in South Carolina. The first was the highly improbable discovery of a snout and palatal dentition of a Torrejonian anisonchine condylarth, found in a well-core taken at a depth of more than 2400 feet, in Caddo Parish, Louisiana (Simpson 1932). The second is a small collection of late Paleocene mammal fragments recovered from spoil heaps of the Williamsburg Formation, Black Mingo Group, in Berkeley County, South Carolina (Schoch 1985, 1998). In view of this meager record, it is deemed worthwhile to report here a third record of Paleocene mammals from the eastern part of the continent, and the first from Maryland.

Occurrence and Age

The three specimens of the present report come from bluffs along the eastern shore of the Potomac River, about 0.25–0.60 mile north (where the bluff is called the Blue Banks) and about 0.25 mile south of Douglas Point, 3 miles west of Nanjemoy, Charles County, Maryland (Fig. 1; USGS Widewater 7.5-minute Quadrangle). In those areas the exposures are Paleocene, whereas the bluff immediately north and

south of Douglas Point is Pleistocene (G. J. Grimsley & R. E. Weems, pers. comm.). The fossils are from the shallow marine Piscataway Member of the Aquia Formation (Pamunkey Group), which is bracketed within calcareous nannoplankton zones upper NP5-NP8 (Ward & Wiest 1990, Gibson et al. 1991). This corresponds approximately to late Paleocene magnetochrons upper C26r to C25n, spanning roughly 60 to 56 Ma (Berggren et al. 1995, Cande & Kent 1995). According to Olson (1994) and Weems (pers. comm.), the vertebrate-producing zone is in the lower part of this sequence (NP5 or 6), which is approximately equivalent to the middle Tiffanian land-mammal age (Fig. 2; see also Woodburne & Swisher 1995). The Piscataway Member consists of shelly glauconitic sands deposited in an offshore shallow shelf environment, and has produced a diverse fauna of sharks, rays, and bony fishes, as well as two crocodylians and a variety of mainly marine turtles (Weems 1988 and pers. comm., Ward & Wiest 1990). Rare avian fossils are also known, including a peleciform and a new species of *Presbyornis* (Olson 1994). Most or all of these remains represent marine or ocean-loving species. Remains of terrestrial vertebrates are rare.

Above the Aquia Formation in north-eastern Virginia, the early Eocene Potapaco Member of the Nanjemoy Formation (also

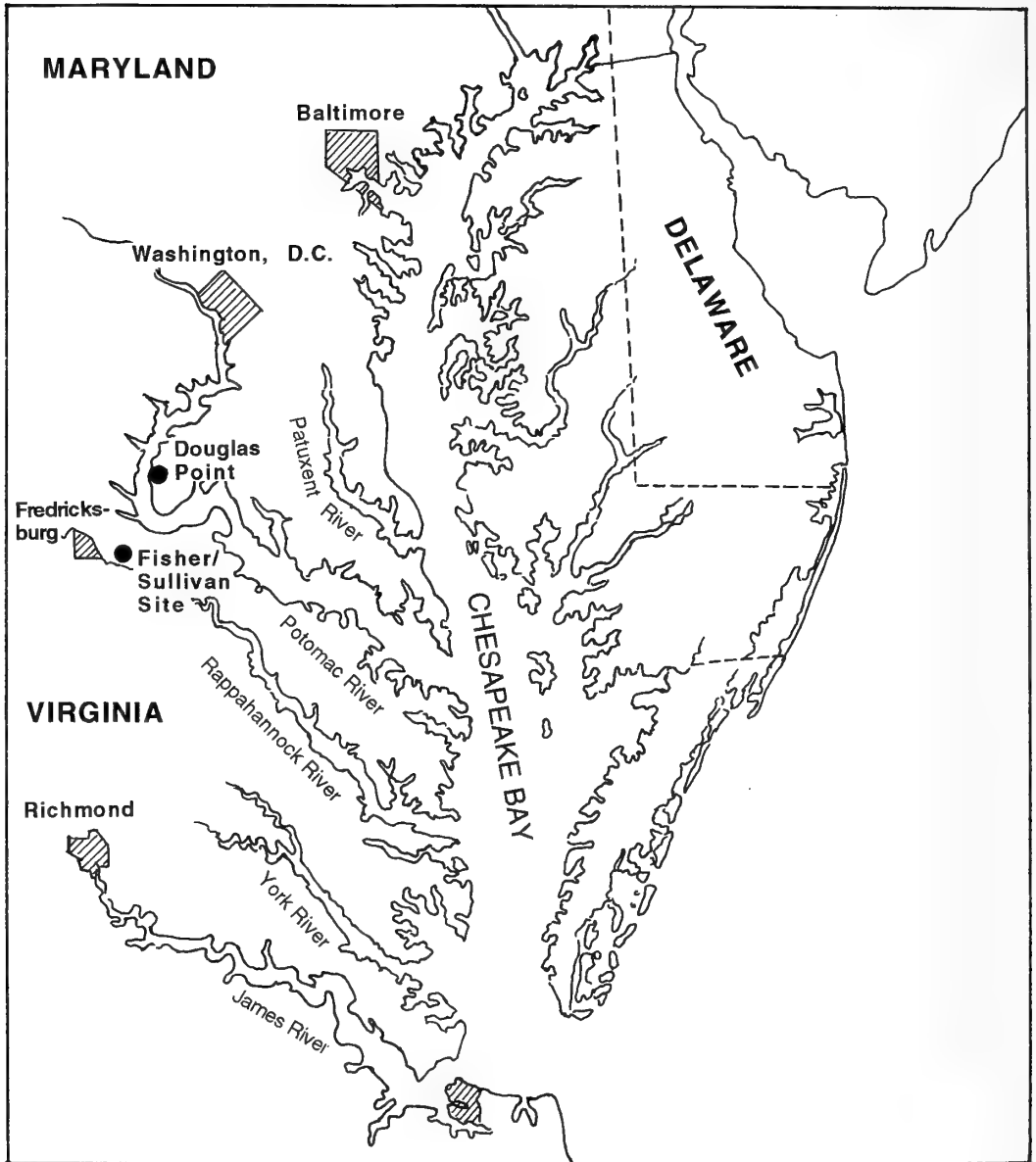


Fig. 1. Location map of late Paleocene Aquia Formation exposures at Douglas Point, Charles County, Maryland. Also shown is early Eocene Fisher/Sullivan Site east of Fredericksburg, Virginia.

Pamunkey Group) has produced a diverse early Eocene vertebrate assemblage (Fisher/Sullivan Site; Weems & Grimsley 1999a; see Fig. 1), including the first early Eocene land-mammals from the central east coast of North America (Rose 1999). The Potapoco Member consists of bioturbated glauconitic sands and clays deposited in neritic

environments, similar to the Piscataway Member of the Aquia (Gibson et al. 1991).

The three very fragmentary mammal specimens described here represent three separate discoveries made over a quarter of a century. Two of the specimens were found in situ in the bluffs, while the third was recovered from beach drift.

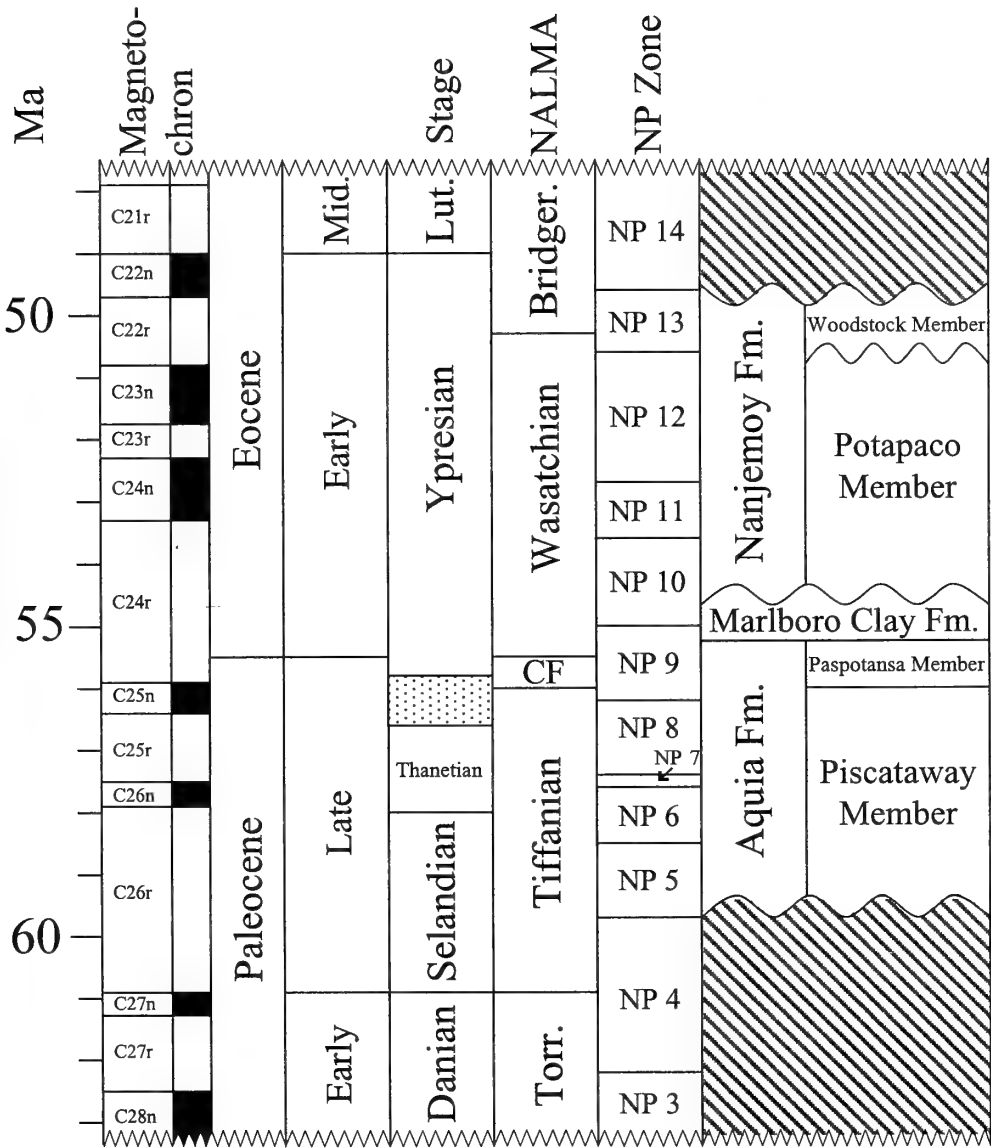


Fig. 2. Stratigraphic and chronologic correlation of the Aquia and Nanjemoy formations relative to magnetochrons, epochs, stages, North American Land-Mammal Ages (NALMAs), and nannoplankton zones. Compiled, with minor modifications, after Ward & Wiest (1990), Gibson et al. (1991), Berggren et al. (1995), Cande & Kent (1995), McKenna & Bell (1997), Berggren & Aubry (1998), and Weems & Grimsley (1999b). Paleocene-Eocene boundary correlations are based mainly on Berggren & Aubry (1998).

Abbreviations used are: ChM—Charleston Museum, Charleston, South Carolina; USNM—Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Order Taeniodonta
 Family Stylinodontidae
Ectoganus cf. *gliriformis* Cope, 1874
 Fig. 3

Referred specimen.—USNM 495534, right m1?; found in situ at beach level about

0.5 mile north of Douglas Point. Collected by R. Harding and G. J. Grimsley, 1999.

Description.—This little-worn, high-crowned taeniodont tooth is very similar to m1 of *Ectoganus* from Wyoming. It is slightly smaller than the specimen of *E. gliriformis* (a p4) from the Black Mingo Group, and differs in having the metaconid slightly higher than the protoconid, and a well-developed talonid with the entoconid as high as the hypoconid (features suggesting it is a molar). In addition, it has a small hypoconulid, two small entoconulids, and a low median paraconid (or anterior cingulid?), all features typical of *E. gliriformis* (Schoch 1986). Dimensions of the tooth are: length = 11.7 mm, trigonid width = 12.0 mm, talonid width = 10.5 mm (all maximum dimensions).

The tooth is also very similar in size and crown morphology to molars of *Psittacotherium multifragum* (e.g., USNM 15417) from the Torrejonian of the San Juan Basin, but differs in being much higher crowned (a characteristic of *Ectoganus*). *Ectoganus gliriformis* is a late Paleocene-early Eocene (late Tiffanian-Wasatchian) species otherwise known from New Mexico, Colorado, Wyoming, and southern Montana, as well as South Carolina.

Order Procreodi (=Arctocyonia)

Family Arctocyoniidae, indeterminate

Fig. 4

Referred specimen.—USNM 446999, unguinal phalanx; found at beach level in the Blue Banks, north of Douglas Point. Collected by C. F. Allison, Jr., 1974.

Description.—This unguinal phalanx is relatively large and morphologically distinctive. It is robust, curved, and only slightly laterally compressed. The proximal articular surface is dorsoventrally concave, slightly higher than wide, and tapered dorsally, with a low sagittal keel separating paired surfaces that articulated with the intermediate phalanx. The unguinal shaft is similarly wider ventrally and tapered dor-

sally, forming a rounded crest along the median dorsal margin, which is shallowly fissured along its distal third. The proximo-dorsal margin is slightly extended into a weak extensor tubercle. Ventrally, the very prominent flexor tubercle (where the deep digital flexors inserted) is wider than the unguinal shaft and gently convex on its plantar aspect. Faint neurovascular grooves run distodorsally from the tubercle toward the tip; near the tip a vascular (or neurovascular) canal opens on each side just below the groove.

In all these details the phalanx closely resembles the unguinal phalanges of the large Paleocene arctocyoniids *Arctocyon* and *Claenodon* (Matthew 1937, Russell 1964) and their early Eocene relative *Anacodon* (Rose 1990). Though slightly damaged at the tip, it is virtually complete. It measures 23.2 mm long and is 6.3 mm wide at mid-length. The proximal articulation is 11.7 mm in dorsoventral dimension (excluding the flexor tubercle) and 10.7 mm at its widest point.

Order Condylarthra

Family ?Phenacodontidae

?*Phenacodus* sp.

Fig. 5

Referred specimen.—USNM 495535, talonid of left m1 or m2; found in beach drift about 0.25 mile south of Douglas Point. Collected by E. Supensky, 1999.

Description.—This heavily abraded molar fragment shows evidence of heavy wear during life, as well as significant postmortem hydraulic abrasion. A scar on the anterior surface indicates where the trigonid has been broken away. The remaining talonid measures 8.0 mm wide and 6.0 mm long, which is at the small end of the size range of the Tiffanian species *Phenacodus grangeri* (Thewissen 1990). The tooth bears a stout root which, from the distal aspect, is divided only at the tip of the roots, but in mesial view consists of two separate roots. The crown is worn nearly flat, with margins and

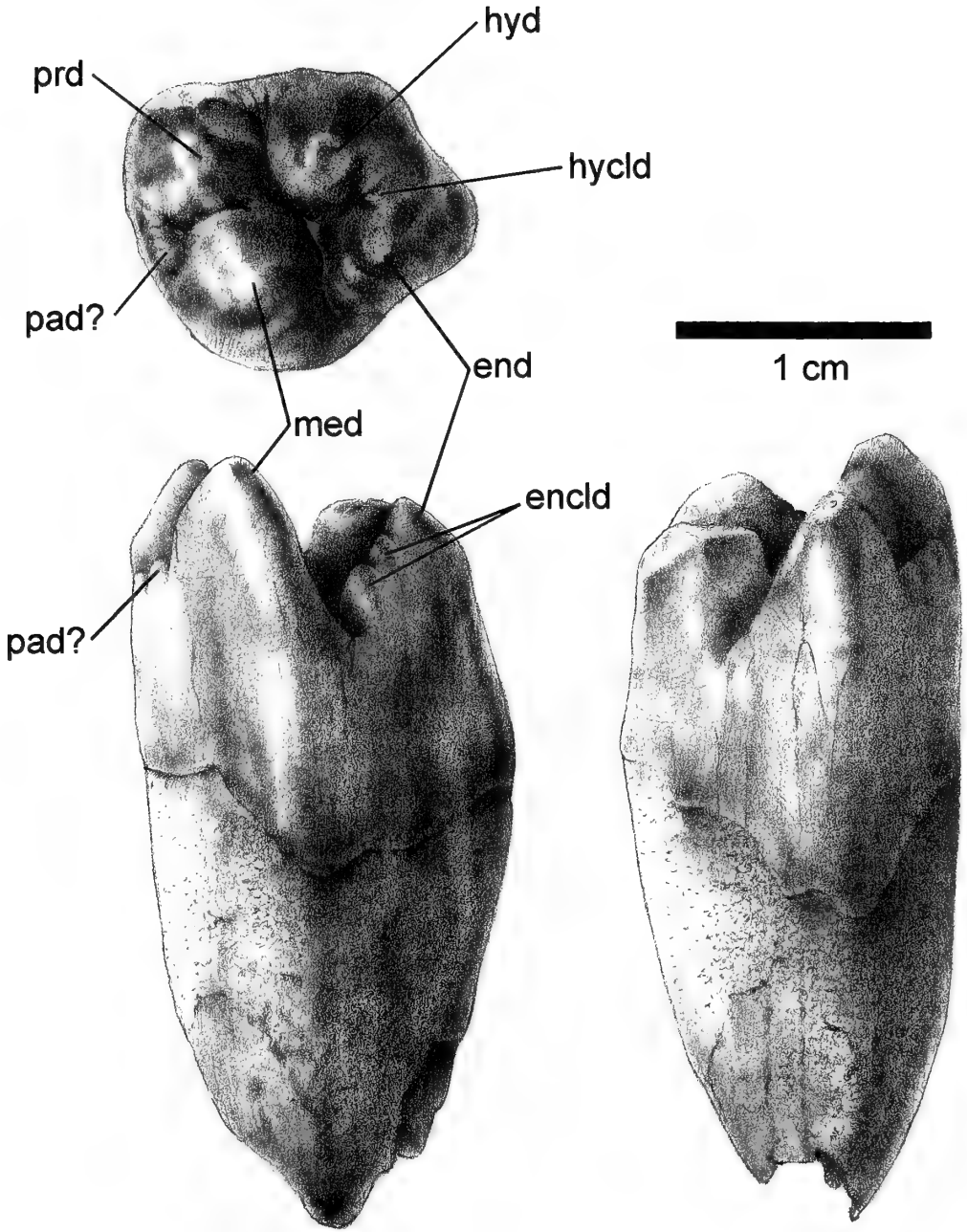


Fig. 3. *Ectoganus cf. gliriformis*, right m1? (USNM 495534), in crown view (above) and oblique lingual (left) and buccal views. Abbreviations: encl—entoconulid; end—entoconid; hcld—hypoconulid; hyd—hypoconid; med—metaconid; pad—paraconid; prd—protoconid.

islands of polished enamel separated by dentine windows. The wear pattern approximates that of heavily worn *Phenacodus* molars more closely than that of any other tax-

on compared. Areas apparently corresponding to large hypoconid and entoconid cusps, a smaller, median hypoconulid, and the cristid obliqua can be identified.

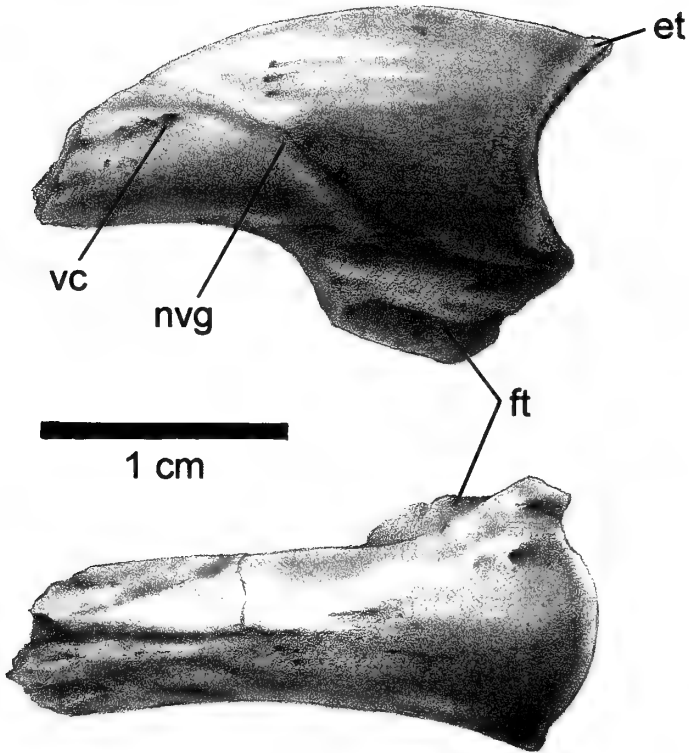


Fig. 4. Arctocyonid unguinal phalanx (USNM 446999), in lateral and dorsal views. Abbreviations: et—extensor tubercle; ft—flexor tubercle; nvg—neurovascular groove; vc—vascular or neurovascular canal.

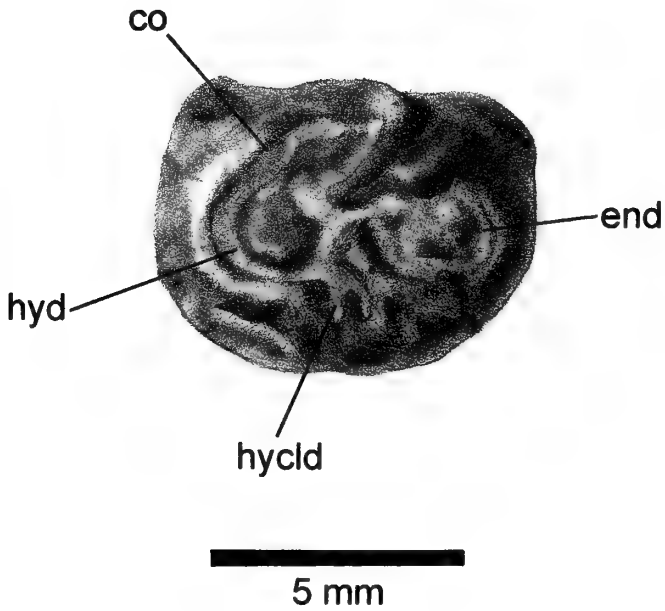


Fig. 5. *Phenacodus* sp., talonid of left m1 or m2 (USNM 495535), in crown view. Abbreviations: co—cristid obliqua; end—entoconid; hycld—hypoconulid; hyd—hypoconid.

Discussion

The *Aquia* mammal specimens provide the first record of Paleocene mammals from Maryland. Because of their imprecise identification, they are not significant chronological indicators, but they are consistent with a late Paleocene age for the Piscataway Member. The taeniodont *Ectoganus* is otherwise known primarily from the Clarkforkian and Wasatchian of Wyoming. Only specimens from the late Tiffanian of the Plateau Valley local fauna, Wasatch Formation of Colorado, and the late Paleocene Black Mingo Group of South Carolina are probably older than the Wyoming material (Schoch 1986), but neither appears to be as old as nannoplankton zones NP5 or NP6, the age suggested for the Piscataway Member. The Black Mingo assemblage is thought to date from nannoplankton zones NP8 or NP9 (Weems & Bybell 1998); Schoch (1998) considered it to be of probable Clarkforkian age. Thus, the *Aquia Ectoganus* appears to be older than any other record of the genus, extending its range well down into the Tiffanian. *Phenacodus* is known from the late Paleocene into the early middle Eocene (Tiffanian-Bridgerian) in the Western Interior, and from the early-middle Eocene of Europe (Thewissen 1990). As mentioned above, large arctocyonids comparable to the one represented in the *Aquia* Formation are also known from both Paleocene and early Eocene beds (late Torrejonian-Wasatchian of North America, Thanetian of Europe).

It seems a remarkable coincidence that of the few Paleocene mammal specimens known from the Black Mingo Group and the *Aquia* Formation, the otherwise rare taeniodont *Ectoganus* occurs in both. It is tempting, though probably premature, to speculate that the east coast provided environments favorable to taeniodonts. The Black Mingo and *Aquia* assemblages may also share the common condylarth genus *Phenacodus*. Large arctocyonids, such as the one represented by the *Aquia* unguis,

were not previously known from the early Cenozoic of eastern North America, although they are present in coeval strata of both the Western Interior of North America and western Europe.

The Black Mingo assemblage includes two other significant mammal specimens, each representing bizarre and distinctive taxa (Schoch 1985). An unidentified tribosphenidan molar talonid (ChM PV2927) is peculiar in presenting a broad, lingually open talonid basin flanked by a lingually directed cristid obliqua (creating a deep hypoflexid) and a straight postcristid that ends in a prominent entoconid. A fracture at the mesial end of the cristid obliqua suggests the former presence of a metastylid. These traits are reminiscent of the late Paleocene-early Eocene condylarth *Meniscotherium*, though the Black Mingo talonid differs in being relatively longer and in lacking an entoconulid, which is often but not invariably present in *Meniscotherium*. The other Black Mingo mammal is a previously unknown form for which Schoch (1985) proposed the name *Mingotherium holtae*. He referred it questionably to the Uintatheriamorpha. The single known upper molar (ChM PV4113) shares with uintatheres a tall protocone and similar wear on the protocone crests; but the paracone and metacone are bunodont and of comparable size, and the postproto-crista does not meet the metacone. These conditions are quite unlike those of uintatheres, in which the paracone is larger than the metacone and both are rather acute, and the paraloph and metaloph run to paracone and metacone respectively, forming a distinct V-shape pattern. Schoch (1985) also compared *Mingotherium* with the Paleocene Asian genus *Pseudictops*, currently placed in the Anagalida (McKenna & Bell 1997), and the same similarities and differences apply to that comparison. Both *Mingotherium* and *Pseudictops* also have well-developed pre- and postcingula on the upper molars. Consequently, McKenna & Bell (1997) included *Mingotherium* within the family Pseudictopidae (thus extending the

range of this otherwise Asian family into eastern North America), although Lucas & Schoch (1998) left it as *Eutheria incertae sedis*. It is also noteworthy that the tall protocone and bunodont paracone and metacone of *Mingotherium* are reminiscent of conoryctine taeniodonts, but the high and prominent pre- and postcingula are unlike taeniodonts. Whether resemblances to any of these groups reflect true relationship or merely convergence will require more substantial evidence than a single tooth. In the meantime, the phylogenetic position of *Mingotherium* will likely remain problematic.

The small glimpse of east coast Paleocene mammalian faunas afforded by the Aquia and Black Mingo assemblages suggests that this region held some taxa in common with contemporary Rocky Mountain faunas, but that the overall composition of east coast faunas may have been rather different. Only with additional samples will it be possible to assess the provinciality of east coast Paleocene faunas.

Acknowledgments

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A new taxon in the *Amazilia viridifrons* (Chordata: Aves: Trochilidae) complex of southern Mexico

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Abstract.—We examined variation among populations of the complex assemblage of hummingbirds presently considered to constitute *Amazilia viridifrons* (Elliott, 1871), of Guerrero, Oaxaca, and Chiapas. A previous author had correctly suggested recognition of most Oaxaca populations as a full species, *A. wagneri* Phillips, 1964. We found that the Chiapas populations are also recognizable as a distinct taxon; because no name had previously been applied to these populations, we name it as a new subspecies, *A. viridifrons villadai*. Populations recently described as *A. viridifrons rowleyi* are actually referable to *A. wagneri*; moreover, that subspecies is not valid as an entity distinct from the remainder of *A. wagneri*.

Resumen.—Se examinó la variación entre las poblaciones del complejo de colibríes que actualmente constituyen *Amazilia viridifrons* (Elliott, 1871), habitando a partes de Guerrero, Oaxaca y Chiapas. Otro autor había sugerido correctamente la separación de muchas de las poblaciones de Oaxaca como *A. wagneri* Phillips, 1964. Nosotros encontramos que las poblaciones también son reconocibles a nivel de especie, y proponemos el nombre de *A. viridifrons villadai*. Argumentamos también que las poblaciones recientemente descritas como *A. viridifrons rowleyi* Howell, 1993 pertenecen más bien a *A. wagneri*, y que la subespecie no se debe de considerar válida.

The taxonomic history of the *Amazilia violiceps* (Gould 1859) and *A. viridifrons* (Elliott 1871) species groups has been complex. A brief historical summary of the taxonomic treatment of the group follows. *Amazilia violiceps* was described in 1860 by Gould, and eleven years later Elliott (1871) described *A. viridifrons* based on a specimen from Putla de Guerrero, in western Oaxaca. Salvin (1892) treated the two forms as separate species, as did Ridgway (1911). Salvin & Godman (1892) described an additional violet-crowned species, *A. guerrerensis*, now in the synonymy of *A. violiceps*.

In general, early treatments recognized violet- (*violiceps*) and green-crowned (*viridifrons*) forms as full species. Peters

(1945), however, not only did not recognize the two forms as full species, but also included both violet- and green-crowned forms within the nominate subspecies of *Amazilia violiceps* (see also Wetmore 1947). Although Friedmann et al. (1950) recognized the green-crowned forms as a full species, Phillips (1964) reduced them again to the rank of subspecies within *A. violiceps* on the basis of the absence of a clear zone of sympatry between the two forms. Most subsequent authors (e.g., AOU 1983, 1998; Binford 1989) have treated the violet- and green-crowned forms as full species.

In the only recent treatment of the group, Howell (1993) also recognized *Amazilia viridifrons* as a species separate from *A.*

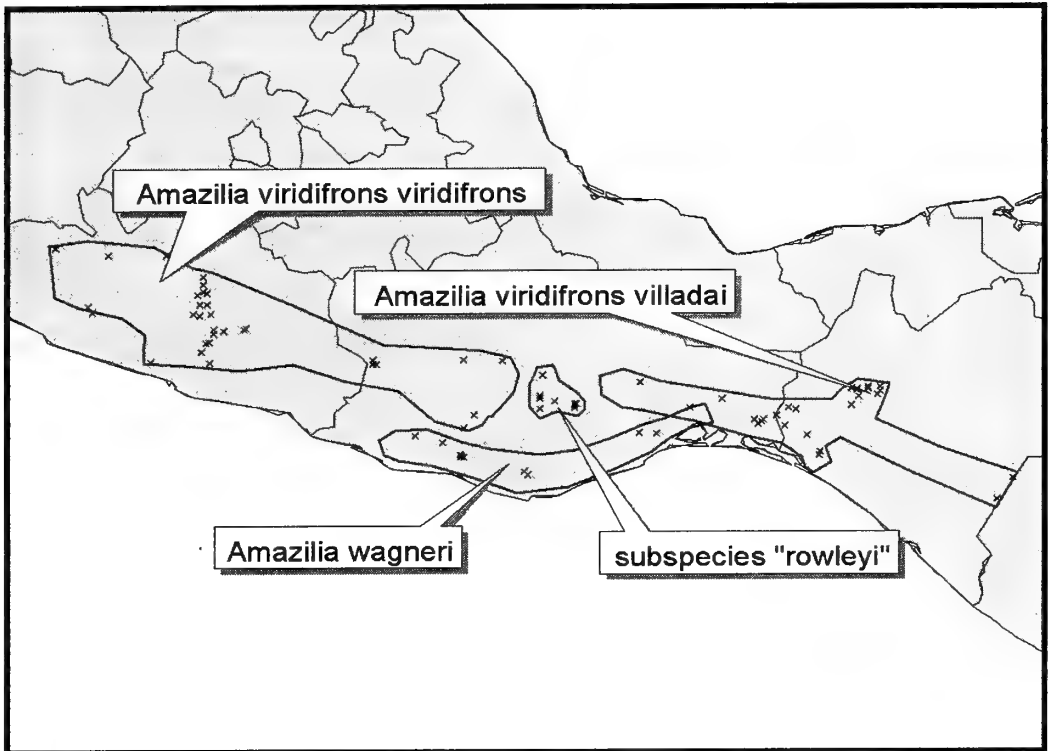


Fig. 1. Map showing geographic distributions of the *Amazilia viridifrons* complex in southern Mexico.

violiceps. He further suggested elevation of the cinnamon-sided populations of southern Oaxaca to species status (*A. wagneri*, Cinnamon-sided Hummingbird), and pointed out the odd geographic situation that resulted, with two green-sided populations separated by cinnamon-sided populations in Oaxaca. Finally, he described a new subspecies (*rowleyi*) from central Oaxaca, which he placed within *A. viridifrons*.

The AOU (1998) did not follow Howell's (1993) recommendation regarding the species status of the cinnamon-sided populations, instead treating them as a "group" within *Amazilia viridifrons*. Our own review indicates that Howell's *rowleyi* is not valid, and in fact that the populations Howell so named should be placed with *A. wagneri*, and not with *A. viridifrons*. Finally, because Howell (1993) ignored characters of size and shape among green-sided forms, he failed to note the marked differentiation

of the western populations (Guerrero and western Oaxaca) from the eastern green-fronted populations (eastern Oaxaca and Chiapas) (Fig. 1), which we herein describe as a subspecies of the biological species *A. viridifrons*.

Materials and Methods

Specimens were assembled for study from numerous scientific collections: Academy of Natural Sciences of Philadelphia (ANSP), Field Museum of Natural History (FMNH), Moore Laboratory of Zoology (MLZ), Southwestern College (Winfield, Kansas, SWC), University of Michigan Museum of Zoology (UMMZ), U.S. National Museum of Natural History (USNM), Delaware Museum of Natural History (DMNH), Louisiana State University Museum of Natural Science (LSUMZ), Western Foundation of Vertebrate Zoology

Table 1.—Summary of measurements (mean \pm standard deviation in mm, n) for *Amazilia viridifrons viridifrons*, *A. v. villadai*, and *A. wagneri*.

Character	<i>viridifrons</i>	<i>wagneri</i>	<i>villadai</i>
Bill length—males	20.3 \pm 0.86, 22	21.1 \pm 0.5, 6	21.3 \pm 0.6, 21
Bill length—females	20.5 \pm 0.7, 13	20.9 \pm 1.8, 7	22.6 \pm 1.1, 22
Wing chord—males	57.5 \pm 1.7, 20	58.5 \pm 0.9, 5	60.3 \pm 1.6, 19
Wing chord—females	56.5 \pm 1.2, 14	56.1 \pm 1.7, 7	58.2 \pm 1.2, 19
Tail length—males	32.4 \pm 1.0, 17	33.9 \pm 1.6, 3	34.5 \pm 1.2, 19
Tail length—females	32.1 \pm 1.1, 12	32.4 \pm 1.2, 6	33.7 \pm 1.3, 21

(WFVZ), University of Kansas Natural History Museum (KUNHM), and Museum of Vertebrate Zoology (MVZ). Sample sizes are presented in Specimens Examined below. Preliminary examinations of interpopulation variation were based on named taxa and geography.

Comparisons of plumage coloration were made under natural light conditions. Measurements on each specimen included bill length from anterior edge of nostril, wing chord, and tail length from base of central rectrices. Measurement data were \log_{10} -transformed; MINITAB (version 11.12, MINITAB 1996) was used for multivariate analyses. Principal components (PC) analyses were based on covariance matrices of \log_{10} -transformed data; percent diagnosability was taken from classification errors for samples available to us in a discriminant function analysis of \log_{10} -transformed data. *T*-tests were used in univariate comparisons of PC scores and raw measurements of sexes within each species to evaluate sexual size dimorphism; *t*-tests were then used to compare populations based on PC scores and raw measurements, with sexes analyzed separately.

Amazilia viridifrons villadai, new subspecies

Holotype.—University of Michigan Museum of Zoology (UMMZ), 102297, adult male from Mexico, Chiapas, Arriaga, 100 m, collected 25 May 1939 by Pierce Brodtkorb.

Diagnosis.—Distinguishable from most *Amazilia* hummingbirds by the combination

of green-and-white-only plumage with relatively large size (Table 1, Fig. 2). Within the species group discussed above, differs from *A. violiceps* in lacking the violet crown, and from *A. wagneri* in lacking cinnamon edging on sides and flanks.

Closely similar to the disjunct *Amazilia viridifrons viridifrons* in coloration, although green flecking and edging on the sides and flanks is less frequent, making the underparts appear whiter overall. Larger in size, with measurements of wing and tail contrasting strikingly (*t*-tests, all three measurements in both sexes, $10^{-5} > P > 10^{-9}$) (Fig. 2). Also differs in having marked sexual dimorphism in size (*t*-tests, $P < 0.001$ for all three PC scores, bill, and wing; $P = 0.051$ for tail), whereas *A. viridifrons* has no detectable sexual size dimorphism (*t*-tests, all $0.86 > P > 0.14$). Based on the limited measurement data (Table 1) available ($n = 74$), discriminant function analysis indicated 86% (30 of 35 individuals) correct classification (diagnosability) of males, and 83% (24 of 29 individuals) correct classification of females.

Distribution.—Known from a restricted zone extending from eastern Oaxaca (vicinity of Tapanatepec), east in the coastal lowlands to western Chiapas (vicinity of Arriaga), and in the interior of Chiapas from north of Arriaga east to the Guatemalan border near Ciudad Cuauhtémoc (Delaware Museum of Natural History, DMNH 24527, 24528, 24530, 24533, 24548). Probably occurs in adjacent areas of western Guatemala as well.

Description of holotype.—Color desig-

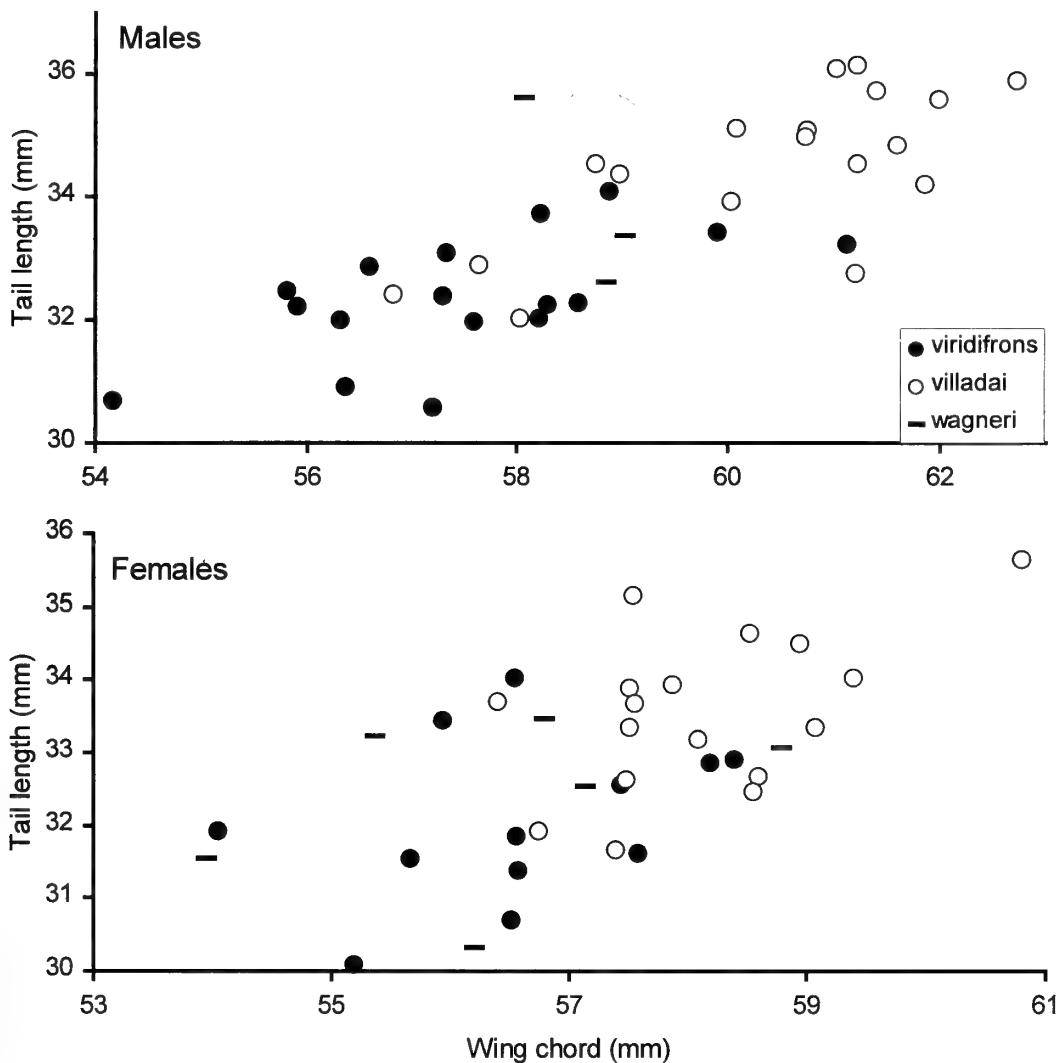


Fig. 2 Bivariate scattergrams of wing chord versus tail length in males and females of the *Amazilia viridifrons* complex in southern Mexico.

nations given as capitalized names are from Smithe (1975); noncapitalized colors are descriptors only. Forecrown very dark green, approaching dusky blackish. Hind-crown and back glossy Parrot Green, tending towards more olivaceous on the rump and upper tail coverts; the latter narrowly fringed white. Dorsal surface of tail glossy Parrot Green strongly tinged with bronzy.

Underparts clean white, with a slight indication of a collar or chest band made up of feathers that are Parrot Green. Sides and

flanks lightly tinged with medium buffy gray. Undertail coverts white. Undersurface of rectrices glossy Parrot Green tinged with bronzy. Bill on dried specimen is light yellow, with tip black. Tarsi and feet on dried specimen are dusky, approaching black.

Measurements of holotype.—Wing chord, 59 mm; tail length, 35 mm; bill from anterior edge of nares, 20.6 mm; total exposed culmen, 22.5 mm; bill depth at anterior edge nares, 2.6 mm; bill width at anterior edge nares, 2.6 mm; body mass not recorded.

Description of female.—Adult female, Louisiana State University Museum of Natural Science, LSUMZ, No. 87570. Closely similar to holotype. Upper tail coverts and rectrices glossy Parrot Green, but with notably more pronounced bronzy tinge. Comparisons of series of males and females indicate little consistent sexual dichromatism in this or any character, nor do they indicate a tendency towards differentiation of eastern and western populations in this regard, contra Howell (1993).

Description of juvenile.—Juvenile male, Western Foundation of Vertebrate Zoology, WFVZ, No. 15610. Similar to holotype. Entire back Olive-Green, with buffy edgings on each feather, giving an overall scaly appearance to the back. Upper tail coverts and rump with whitish edgings. Rectrices glossy Parrot Green, with strong bronzy tinge as in adult female.

Specimens examined.—Adult-plumaged individuals examined are listed here. *Amazilia viridifrons villadai*, western Chiapas: 14 males, 17 females (ANSP 167843, DMNH 24547, 53194-96, FMNH 153210, 208726-28, LSUMZ 40191-93, 44607, 85547, 87570, MLZ 27362, 27364, SWC 8069, UMMZ 102294-99, 109145, USNM 155273-74, WFVZ 15610-12, 19725); eastern Chiapas: 3 males, 2 females (DMNH 24527-28, 24530, 24533, 24548); eastern Oaxaca: 7 males, 4 females (DMNH 24543, LSUMZ uncat., 24350, 40190, 44609, 85657, USNM 57772, 57774, WFVZ 15607-08, 16861); eastcentral Oaxaca near Rancho Las Animas: 13 males, 2 females (DMNH 24544, 45125, 45129, LSUMZ 40188, MLZ 45117, 45120, 45126, 45131, 49538-39, 49543, 54427, 54432, WFVZ 15600-01). *Amazilia wagneri*, Oaxaca, vicinity of Tehuantepec and Juchitán: 3 males (LSUMZ 40189, MLZ 59715, UMMZ 137649); Oaxaca, vicinity of Santiago Matatlán: 5 males, 4 females, 1 unsexed (LSUMZ 24352-53, WFVZ 19598, 19620, 49356-60, 49362); Oaxaca, Sierra de Miahuatlán: 6 males, 10 females (DMNH 24534, 24536-41, 24546, LSUMZ 24352,

27432, WFVZ 21492-94, 21538-39, 21542). *Amazilia v. viridifrons*, Oaxaca, Putla de Guerrero, 1 male (LSUMZ 33092); Guerrero, central: 23 males, 19 females (DMNH 24487, 24490-97, 24499-511, 24513-26, 24550-51, KUNHM 45823, MLZ 10172, MVZ 109971, 113452)

Etymology.—We are pleased to name this species in honor of Manuel M. Villada, influential Mexican naturalist and scientist of the nineteenth century, who produced important works on the hummingbirds of the Valley of Mexico (e.g., Villada 1875).

Discussion

For the *Amazilia viridifrons* complex, errors and misinterpretations began with the super-inclusive "*Amazilia violiceps violiceps*" of Peters (1945). Unfortunately, problems have continued up to the most recent treatment of the group (Howell 1993). The above description of *A. viridifrons villadai* represents one step in setting the situation straight and arriving at a taxonomy for the group in which all distinct biological entities are recognized; several additional considerations follow.

Amazilia wagneri.—Most Oaxaca populations of this complex are easily distinguishable by their warm cinnamon sides of the white underparts. Given their clear differentiation in plumage over very small geographic distances (possible parapatry), we concur with Howell (1993) that they are best treated as a separate species, *A. wagneri*. Variation does exist, however, in the degree to which the species' characters are expressed, deserving some comment.

Examining in detail specimens available, those from the coastal slopes of the Sierra de Miahuatlán uniformly show the cinnamon sides and other characters attributed to *Amazilia wagneri* (Howell 1993). The only four specimens (DMNH 24541, WFVZ 21492, 21538, 21542) available to us from the interior slopes of the Sierra de Miahuatlán, near San Miguel Sola de Vega, however, show no trace of cinnamon on the

sides and flanks, and thus we concur with Howell (1993) that they represent *A. v. viridifrons*. Under our view, however, they represent the eastern extreme of that subspecies' geographic distribution (contra Howell 1993, see below). *A. wagneri*, then, has an extremely restricted geographic distribution in southern Oaxaca, found only along the southern fringes of the Sierra de Miahuatlán and intruding narrowly into the Oaxaca Valley near Santiago Matatlán (see below).

Subspecies Amazilia viridifrons rowleyi Howell.—Among the specimens we examined were 12 individuals (8 adults, 4 immatures) from the series that Rowley collected at a point 13 miles south of Santiago Matatlán, as well as two specimens from 18 miles southeast of Santiago Matatlán from other collectors. Matatlán is located about midway between the Guerrero and Chiapas green-and-white forms, and on the opposite (interior) side of the Sierra de Miahuatlán from the Oaxaca populations. Although, as noted by Howell (1993), specimens collected from the region by other collectors are clear examples of *wagneri*, the plumages of the entire series available to us (11 individuals) from the Rowley collection are worn, and colors seriously faded for unknown reasons (perhaps exposure to sunlight?).

Given the poor condition of the Rowley series, we were concerned about the validity of the subspecies *rowleyi*, which was based principally on that material (Howell 1993). Our inspection, which did not include the type, lead us to conclude that the subspecies is not valid, with diagnostic characters ("Readily distinguished from *wagneri* by duller and less extensive cinnamon on flanks and axillars, lack of rufous or dull cinnamon on wings except as concealed patch in adult ♂, and bronzy to purplish-copper tail"; Howell 1993) based on seriously worn specimen material. All material at hand for *rowleyi*—which according to Howell (1993) agrees well with the type

specimen—is so extremely heavily worn that color comparisons would not be reliable.

Moreover, our inspection of Rowley's Matatlán series leads us to question Howell's (1993) placement of these populations within *Amazilia viridifrons*. All individuals in the series available to us show some degree of cinnamon or buffy on sides and flanks, fall within the range of variation in the series of coastal-slope *wagneri* that we examined, and do not coincide with the green-and-white plumage of *A. viridifrons*. Howell's (1993) confusion is perhaps understandable given the heavy wear and probable fading of the Rowley series, but less so given that specimens *not* collected by Rowley from a nearby locality represent clear examples of *A. wagneri*, unless this were to be a zone of near-sympatry.

Interestingly, about 50 km farther south and east in Oaxaca, in the vicinity of Rancho Las Animas, extensive series have been collected. These individuals are clearly referable to *Amazilia viridifrons villadai*, characterized by large size, no cinnamon edgings, and clear white breasts. Given close proximity to *A. wagneri* populations, and in fact spatial overlap with *wagneri* populations (e.g., at 12 miles E Juchitan, LSUMZ 40189), potential sympatry (or at least interdigitating distributions) exists, yet we see no evidence of intergradation, suggesting that the populations are reproductively isolated.

Systematic characters and species concepts.—This study illustrates clearly the importance of consideration of all available information—geographic and phenotypic—in systematic studies. In the taxonomic history of the group, early workers unfamiliar with the geography of southern Mexico, presented with small and incomplete series of specimens, and using a very inclusive version of the Biological Species Concept, created artificially inclusive taxa in this group. Later, Howell (1993) considered only characters of coloration, ignoring size and shape, and for that reason missed the marked differentiation of the Chiapas pop-

ulations. Although these populations are herein treated as a subspecies of *A. viridifrons*, they are a clearly diagnosable form (size differences, presence of sexual dimorphism), likely monophyletic, and so probably recognizable as a valid evolutionary (Wiley 1978, Wiley & Mayden 2000) or phylogenetic (Zink & McKittrick 1995) species, particularly if additional character suites can be marshaled to the question.

Acknowledgments

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A new species of *Mabuya* (Sauria: Scincidae) from the British Virgin Islands

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Abstract.—*Mabuya macleani*, new species, is a pallid, drab, almost patternless skink which is abundant on Carrot Rock, British Virgin Islands. *Mabuya sloanii* shows character divergence in pattern from the new species concordant with geographic approach to within 400 m. On Puerto Rico, *M. sloanii* has a broad middorsal bronzy area on the anterior dorsum. On most of the smaller islands of the Puerto Rico Bank, as well as the Mona and Desecheo Banks to the west, this middorsal area is much narrowed by the presence of well-developed dark dorsolateral stripes stretching from the head to behind the forelimbs. These two pattern types, which apparently intergrade in the vicinity of northeasternmost Puerto Rico, are recognized as *M. s. nitida* Garman and *M. s. sloanii* Daudin, respectively. The specific name "mabouya" Lacépède, formerly applied to Antillean skinks, is shown to be unavailable. The presence of *M. macleani* and another endemic lizard (*Anolis ernestwilliamsi*) on such a small (1.3 ha), poorly isolated, and young (<3000 y) island as Carrot Rock may be a striking case of rapid divergence of insular populations.

"The coloration is highly interesting . . . several insular forms may be distinguishable when adequate series become available." Karl P. Schmidt (1928)

The scincid lizards of the genus *Mabuya* are nearly tropicopolitan in distribution. We have collected or examined them in numbers from the Antilles, South America, tropical Asia, and Africa. Throughout this vast range, most species are brown with near-black stripes extending the length of the body. A striking exception is on Carrot Rock, a very small (1.3 ha), steep-sided island off the southeast end of Peter Island in the British Virgin Islands (Fig. 1).

On 13 July 1985, while one of us (GCM) climbed the biggest tree on the island in search of anoles, the other (JL) toiled in the dust in the little gully on the windward side of Carrot Rock in which the tree grew, looking for *Sphaerodactylus* geckos. A far larger, drab, pale lizard was turned out, and ran up his sleeve. Although this initial spec-

imen was distinctive, we at first referred to it as *Mabuya mabouya sloanii* (Mayer & Lazell 1988), the common skink of the Virgin Islands (MacLean 1982, Lazell 1983), pending collection of further specimens. Over the next several years JL returned to Carrot Rock occasionally, and found an area where these peculiar pallid lizards were abundant, and succeeded in capturing five more individuals (of dozens seen). These specimens, as well as comparison with *Mabuya* from throughout the islands of the Puerto Rican Bank, have abundantly confirmed the distinctiveness of this population, and also brought into sharp focus a most intriguing evolutionary phenomenon. We here describe this distinctive *Mabuya* as:

Mabuya macleani, new species

Mabuya mabouya sloanii.—Mayer & Lazell, 1988:23 (in part).



Fig. 1. Carrot Rock, British Virgin Islands, viewed from the north, 17 July 1988. Windward is to the left, leeward to the right. The highest elevation is ca. 25 m. From a Kodachrome transparency by GCM.

Holotype.—Museum of Comparative Zoology (MCZ) 170884, collected on Carrot Rock, south of Peter Island, British Virgin Islands, 18°19'45"N, 64°34'18"W, by J. La-zell, 13 Jul 1985 (Fig. 2D).

Paratypes.—All from the type locality: MCZ 182270–72, 17 Jul 1988; MCZ 176728 and University of Michigan Museum of Zoology (UMMZ) 197261, both 26 Oct 1991.

Diagnosis.—A pallid tan to brownish-gray New World *Mabuya* (Dunn 1936, Greer 1970) with one or two pairs of enlarged nuchals (their combined widths more than 75 percent of the width of the parietals); two frontoparietals; parietal overlapping upper anterior temporal (Greer & Nussbaum 2000); midbody scales in 32–34 rows; 16–18 subdigital lamellae under fourth toe of pes; limbs moderately long; dark dorsal markings fragmented or absent on head and separated from dark dorsolateral stripes on nape; nape stripes reduced, separated by all or most of two dorsal scales and not extending more than 21 dorsal scales posterior to parietals; lateral dark stripes poorly developed. *Mabuya macleani*

is distinguished from the geographically nearest populations of *M. sloanii* by the much reduced dorsolateral dark stripe, the continuous stripe beginning behind the head in *M. macleani* (on the head in *M. sloanii*), and extending only to the level of the forelimbs (behind the forelimbs in *M. sloanii*).

Description of the type.—Rostral wider than high, bordered dorsoposteriorly by the nasals and paired supranasals, which are in narrow contact. The frontonasal is broader than long and in contact with the frontal. The paired prefrontals are separated medially by the contact of the frontonasal with the frontal. The frontal is about three quarters as long as its distance from the posterior parietal edge. There are four supraoculars, the second the largest. There are three supraciliaries, the first by far the longest. The two frontoparietals are in contact with the second, third, and fourth supraoculars, bordered posterolaterally by the parietals, and posteriorly by the interparietal, in which the parietal foramen is posteriorly situated. The large, paired parietals are in contact posterior to the interparietal, that on

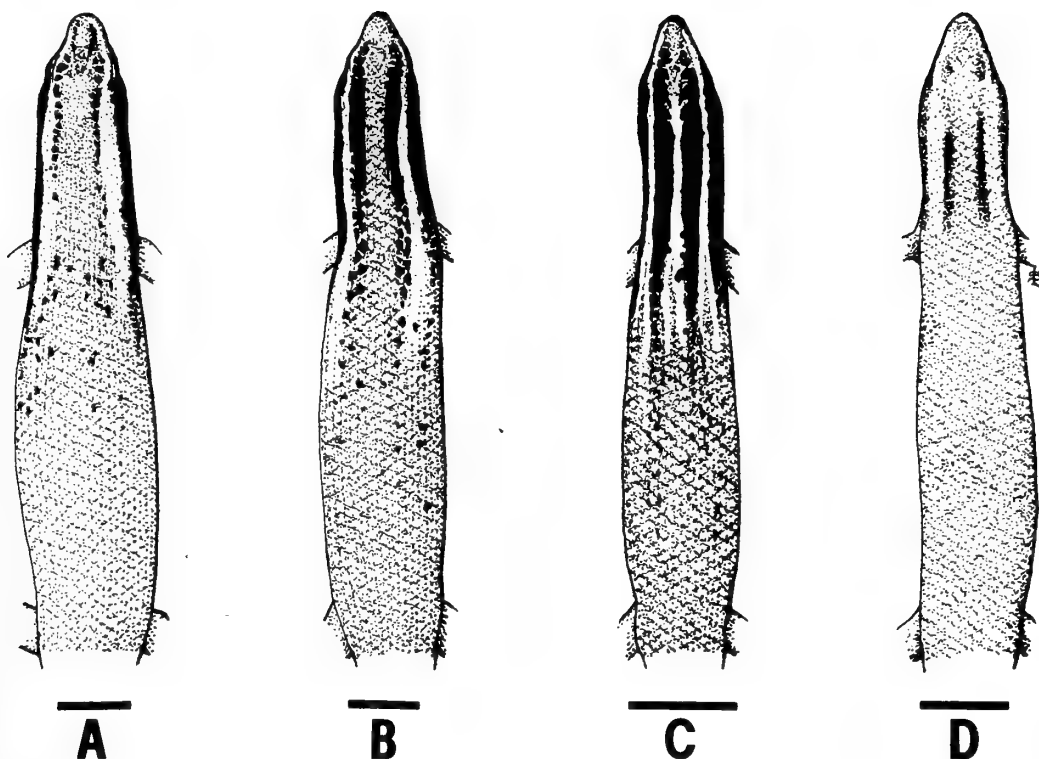


Fig. 2. Dorsal patterns of skins from the Puerto Rican Bank. A–C, geographically approaching Carrot Rock: A) MCZ 6050, lectotype of *Mabuya sloanii nitida*, San Juan, Puerto Rico, ca 164 km WNW of Carrot Rock. B) MCZ 36624, intergrade, *M. s. nitida* × *sloanii*, Cayo Icacos, ca. 102 km WNW of Carrot Rock. C) MCZ 182273, *M. s. sloanii*, Stoney Bay, Peter Island, British Virgin Islands, 400 m N of Carrot Rock. D) MCZ 170884, type of *Mabuya macleani*, Carrot Rock, British Virgin Islands. Bars below lizards indicate 1 cm in each case.

the right extending further posteriorly. The parietals overlap the upper anterior temporal. There is one pair of transversely enlarged nuchals, but the second and third nuchals are enlarged on the left side.

The nasal is subrectangular in side view, with the large nostril posteriorly located, followed by the postnasal and two loreals; the anterior one on the left is much larger than the posterior, but the two are subequal on the right. The anterior loreal is in contact with the prefrontal, but the posterior loreal is separated from the latter scale by a pre-supraciliary. The sixth supralabial on the left, and the fifth on the right, are about twice as long as the others, the enlarged supralabial on each side forming a long subocular. There is a clear disk in the lower

eyelid about as wide as the ear opening. The temporals are larger than the trunk scales. There are no auricular denticles. There are two pairs of chin shields in contact posterior to the mental.

Scales of body and limbs imbricating, subcycloid, regularly arranged in rows. Thirty-four longitudinal rows at midbody, 57 transverse rows dorsally from parietals to anterior edge of hind limb, 61 ventrally from mental to vent. The vent is bordered anteriorly by eight subequal scales. Scales of soles and palms tubercular, transition from imbricate scales of limb to tubercular scales abrupt. Thirteen lamellae under fourth toe of manus, 17 under fourth toe of pes. Adpressed limbs do not meet.

In life, the type was pallid beige-gray

Table 1.—Some characteristics of *Mabuya macleani*. "Scales" are number of rows around trunk at midbody. "Stripe" is the length of the dorsolateral dark stripe in dorsal scales posterior to the parietals (left/right).

	SVL	Scales	Supra-nasals	Stripe	Nuchal Pairs	Adpressed limbs
MCZ 170884	69.5	34	Contact	15/16	1	Fail to meet
MCZ 176728	71.0	32	Contact	18/18	1	Toes barely touch
MCZ 182270	80.5	32	Contact	17/18	2	Fail to meet
MCZ 182271	76.0	32	Contact	18/15	1	Fail to meet
MCZ 182272	63.0	32	Separated	17/18	2	Meet
UMMZ 197261	44.5	32	Fused	21/21	1	Toes overlap

with a faint trace of a lateral stripe extending to just above the axilla. There are two dark dots on the frontonasal and a little dark gray flecking on the supraoculars. The plain lead-gray dark dorsolateral stripes end 15 (left) or 16 (right) dorsal scales posterior to the parietals.

Variation.—Some characteristics of *Mabuya macleani* are given in Table 1, and measurements in Table 2. The holotype is fairly typical of the type series in its squamation, and the paratypes do not present a great deal of variability. Dorsal and ventral head scales of MCZ 182270 are shown in Fig. 3. This specimen shows two unusual conditions: the presence of an intercalary scale separating the first supraocular from contact with the frontal on the left side of the head, and the partial fusion of the fourth

supraocular with the parietal, also on the left side. Contact of the supranasals is variable, being separated in one specimen, touching in four, and even fused medially into a single scale in another. The prefrontals are never in contact medially. In lateral view, the head squamation of *M. macleani* is essentially similar to that of *M. sloanii* shown by Schmidt (1928:122).

The following summary of meristic variation gives for each character the range, followed by the mean and sample size in parentheses. For some bilateral characters the sample size has been reckoned by the number of sides rather than specimens, and this is noted after the sample size. Supraoculars: 4 (4.0, 12 sides); supraciliaries: 2–4 (3.0, 6 sides); supralabial subtending the eye (subocular): 5–6 (5.3, 11 sides); mid-

Table 2.—Measurements (mm) of holotype and three paratypes of *Mabuya macleani*.

	MCZ 170884 Holotype	MCZ 182270 Paratype	MCZ 182271 Paratype	MCZ 182272 Paratype
Snout-vent length	69.5	80.5	76.0	63.0
Tail length	52+	67+	56+	75.5
Axilla-groin length	38.0	45.0	40.5	34.5
Snout length	5.4	5.7	5.7	5.0
Snout width	5.5	5.5	5.4	4.9
Head length	11.9	13.0	12.8	11.4
Head width	8.2	10.2	10.2	8.0
Upper arm length	5.5	6.5	6.0	5.0
Lower arm length	4.9	5.5	6.5	4.7
Palm length	1.9	2.8	2.6	2.9
Fourth finger length	4.5	4.5	4.5	4.0
Upper leg length	8.0	8.0	8.0	7.0
Lower leg length	6.6	7.5	7.3	6.6
Sole length	3.4	3.8	4.3	3.1
Fourth toe length	6.5	7.0	7.0	7.5

+ Tail broken or regenerated.

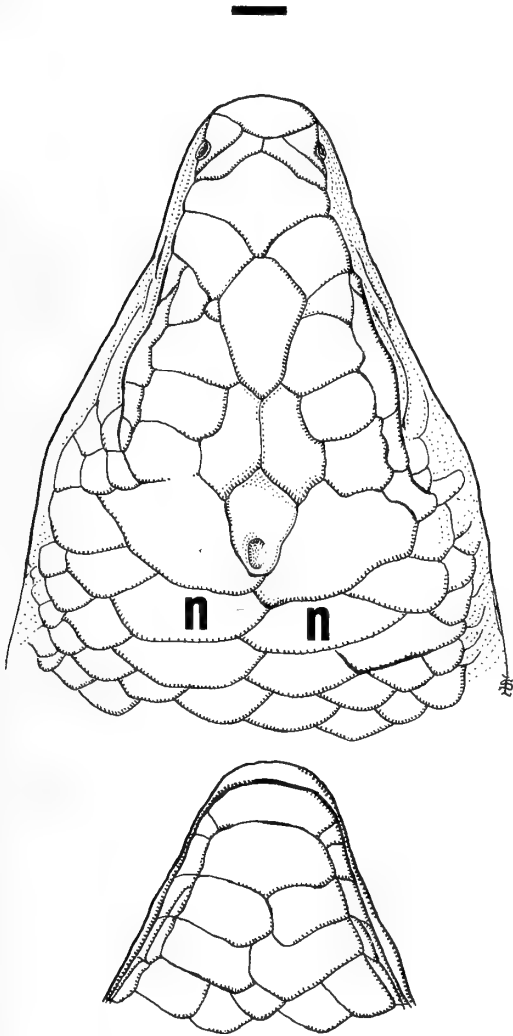


Fig. 3. Aspects of head squamation in MCZ 182770, *Mabuya macleani* paratype. The first pair of enlarged nuchals are marked "n." Bar is 1 mm.

body scale rows: 32–34 (32.3, 6); transverse dorsal rows: 54–58 (56.0, 4); transverse ventral rows: 58–66 (61.2, 6); fourth toe of manus lamellae: 13 (13.0, 4); fourth toe of pes lamellae: 16–18 (17.2, 5).

All *Mabuya macleani* have a much reduced pattern of striping compared to the near-black striping typical of Antillean *Mabuya* (Fig. 2), but the extent of reduction varies, and seems to be size related, with smaller specimens having less reduced markings. All specimens of *M. macleani*

have paired blotches on the frontonasal, but they are scarcely evident on the largest specimen (MCZ 182270), in which, were it not for their presence in the other specimens, they might be taken to be merely two of several scattered dark mottlings on the head, rather than reduced pattern elements. In all specimens the dorsolateral stripe is short and starts on the neck, beginning 3–5 (4.6, 12 sides) scales behind the parietals, and extending to the 15th to 21st (17.7, 12 sides) transverse dorsal scale row behind the parietals; the posterior end is thus at about the level of the forelimbs. There is also size related variation in the intensity of the striping, the dorsolateral dark and light stripes being relatively darker and lighter, respectively, in the second smallest specimen (MCZ 182272) than in the larger ones. The most distinctive pattern variation is in the smallest specimen (UMMZ 197261), which, in addition to the frontonasal blotches and dorsolateral dark stripe (which is longest in this specimen, extending from the 5th to 21st scale row), also has two short stripes on the head, extending from the second supraoculars to the parietals.

There appears to be allometric growth of the limbs. The smallest individual, UMMZ 197261, 44.5 mm SVL, has proportionately by far the longest limbs, and MCZ 187220, 80.5 mm SVL, the largest, has the shortest. The other four are intermediate. The type, at 69.5 mm SVL, has slightly shorter limbs proportionately than MCZ 176728, 71 mm SVL, but the overall impression is that limb length fails to keep pace with body growth. In studies of other New World *Mabuya*, based on larger series than available of *M. macleani*, a similar decline in relative limb length has been demonstrated: Rebouças-Spieker (1974) found this to be the case for most samples in her study of *M. agilis*, *M. caissara*, and *M. macrorhyncha*; Rebouças-Spieker & Vanzolini (1990) found it in *M. carvalhoi*; and Avila-Pires (1995) found it in *M. bistrriata* (= *ficta* sensu Rebouças-Spieker) and *M. nigropunctata* (= *bistrriata* sensu Rebouças-Spieker).

The sexes are similar. Based on broad head, thick tail base, and enlargement of the medial pair of scales bordering the vent, MCZ 182271 was judged to be a male, and dissection confirmed that. Based on narrow head, abruptly tapering tail, and subequal scales bordering the vent, MCZ 187220, the largest available specimen, was judged to be a female, and dissection confirmed that.

Comparisons.—*Mabuya macleani* is morphologically and geographically closest to *M. sloanii*. The latter species is widespread, but nowhere abundant, in the Passage and Virgin Islands, and is also found on Mona and Desecheo (Heatwole et al. 1981, Lazell 1983, 1991, 1995; Mayer 1989). This skink is deep copper to chocolate brown with prominent lateral stripes of near-black and very bold jet black dorsolateral stripes, beginning on the head, and extending continuously down the nape onto the anterior trunk, well past 20 dorsal scales posterior to the parietals (Figs. 2C, 4). The dark dorsolateral stripes are black and separated by silvery-white on the median portions of the two middorsal scale rows. On Puerto Rico, skinks also have near-black lateral stripes extending onto the trunk, but the dark dorsolateral stripes are reduced to heavy blackish blotching on the head, fragmenting and dwindling to speckles on the nape (Fig. 2A). This pattern form was named *M. nitida* by Garman (1887) on the basis of one specimen from Hispaniola and three from Puerto Rico. Stejneger (1904) described this form accurately, mistakenly under the name *M. sloanii*, based on one of two specimens numbered MCZ 6052 from San Juan, Puerto Rico. He also noted the existence of the other pattern type (the actual *sloanii*) under the name *semitaeniata* Wiegmann (1837). Schmidt (1928) also noted the two patterns, and restricted Garman's *nitida* to Puerto Rico. Grant (1931) recognized the distinction in pattern between the Puerto Rican and small island forms as well, using the same erroneous names as did Stejneger. Six Puerto Rican specimens available to us, from San Juan

(MCZ 6050, MCZ 6052 [2 specimens]), Ensenada (American Museum of Natural History [AMNH] 6462), and Bayamon (AMNH 14007, UMMZ 73828) agree with Schmidt and Stejneger's descriptions, as did the Puerto Rican specimens available to Grant (1931).

A seventh specimen, from easternmost Puerto Rico (UMMZ 73829, Cape San Juan), shows some approach toward the *sloanii* pattern. A specimen from Icacos (MCZ 36624), an island just east of Puerto Rico, is intermediate between *nitida* and *sloanii* of the smaller islands to the east (Fig. 2B). Based on these specimens and the literature, we recognize *M. s. nitida* as a valid taxon, and confirm Schmidt's restriction of type locality by selecting MCZ 6050 as the lectotype. A similar pattern of geographic variation, with a Puerto Rican mainland form and a Passage/Virgin Islands form showing signs of intergradation in easternmost Puerto Rico and the adjoining cays is found in *Anolis cristatellus* (Heatwole 1976). It is interesting that *s. sloanii* occupies the islands to the east and west of the Puerto Rican main, with *s. nitida* occupying the main in between; a similar peri-Puerto Rican distribution is shown by *Hemidactylus mabouia* (Kluge 1969) and *Epicrates monensis* (Schwartz & Henderson 1991), with related species on the Puerto Rican main (*H. brookii* and *E. inornatus*).

The overall picture is of Puerto Rico Bank *Mabuya sloanii* showing greater character divergence from *M. macleani* as the latter's geographic distribution is approached (Figs. 2, 5). *Mabuya s. nitida* has less dark anterodorsal pigment than does *M. s. sloanii*; however, *M. s. sloanii* occurs to within 400 m of *M. macleani*, but the latter has the least dark pigment of all.

The Caicos Islands, although geologically part of the Bahamas, share a number of herpetofaunal elements with the Puerto Rico Bank (*Anolis*, *Typhlops*—Thomas 1999). The skinks of these islands appear distinct from Puerto Rico Bank ones based on the specimens we have seen. We have

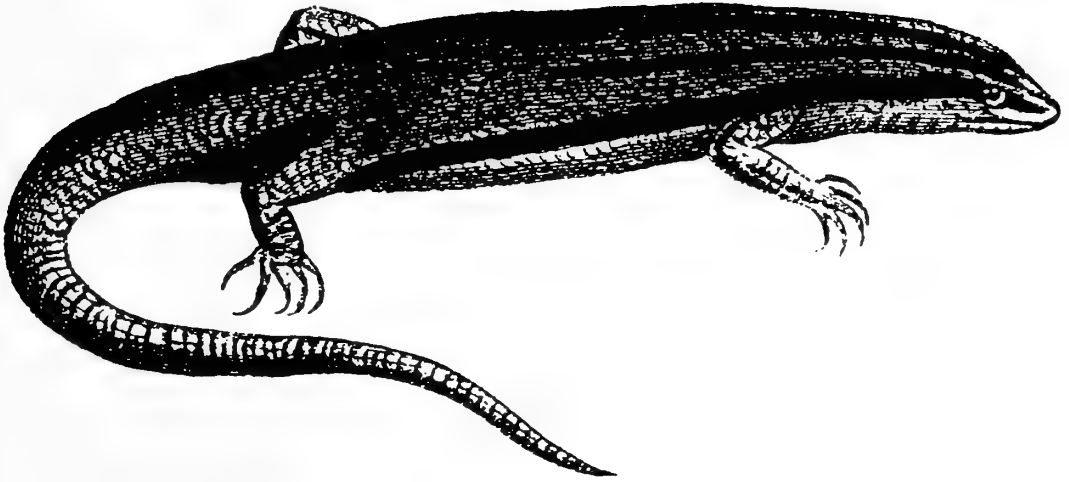


Fig. 4. Daudin's (1802) illustration of his *Scincus sloanii*, the widespread form of the Virgin Islands, showing pattern in side view.

color notes in life for MCZ 182881 from Long Cay, Caicos Bank: dark bronze-brown dorsally, with two very bold cream-white stripes that begin at the snout and ex-

tend dorsolaterally onto the costal region, about one-third of the distance from axilla to groin; these light stripes are bordered ventrally by a near-black field, six scale

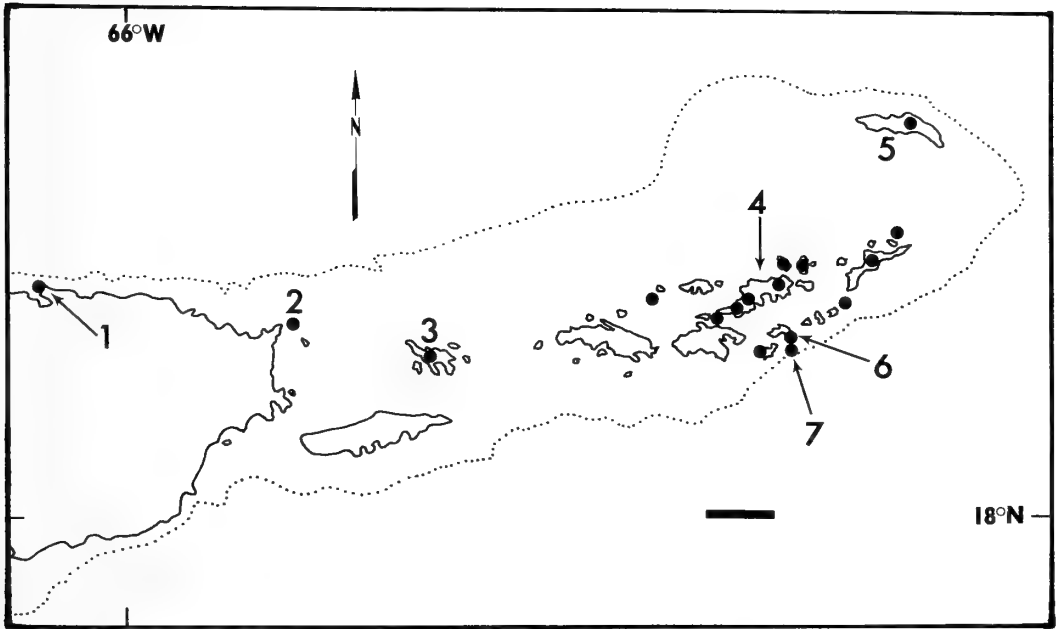


Fig. 5. The eastern portion of the Puerto Rico Bank showing localities from which specimens have been examined. 1, San Juan, Puerto Rico, type locality for *Mabuya sloanii nitida*. 2, Cayo Icacos, represented by an apparent *M. s. sloanii* × *nitida* intergrade. 3, Isla Culebra, 4, Tortola, 5, Anegada, 6, Peter Island, all nominate *M. s. sloanii*. 7, Carrot Rock, type locality for *Mabuya macleani*. Bar indicates 10 km. The dotted line is the edge of the Puerto Rican Bank, ca. 100 m below sea level.

rows wide at the forelimb insertion, and flecked with white speckles. The light dorsolateral stripes are bordered dorsally by near-black stripes one scale wide at the forelimb insertion and separated by four scales across the dorsum at that level. The posterior body is heavily speckled with black dots aligned in longitudinal rows. A preserved series from the same island (AMNH 80125–30) agrees well in pattern with the live specimen described above. The striping pattern most resembles that of the Icos intergrade (Fig. 2B), except that the middorsal brown area is about twice as wide, thus being more like *nitida*, but differing from the latter in having a broader dorsolateral dark stripe, and in that the Icos specimen lacks the heavy, aligned body spotting of the Caicos specimens. Such spotting is variable in *M. s. sloanii*, and may be fairly heavy (Grant 1931; UMMZ 80585 [Buck Island off St. Thomas]). White speckling in the lateral dark stripe, which is also seen in specimens from West Caicos (UMMZ 117392–4) and Six Hill Cays (UMMZ 117394–6), is not found in Puerto Rican region specimens. Further study, beyond the scope of the present work, may reveal that the Caicos *Mabuya* should be recognized as a valid taxon.

Dunn's (1936) description of *Mabuya pergravis* of the western Caribbean, "striping very indistinct; pale with dark dots above," may sound superficially similar to *M. macleani*, but the two forms are amply distinct. *Mabuya pergravis* is much more slender, and has fewer midbody scale rows (28–30—Dunn 1936, Dunn & Saxe 1950). Striping is not indistinct in a single specimen from San Andrés, and in those from Providencia the dark dots are numerous (unlike *macleani*, in which there are few or no dark dots dorsally).

In meristic and measurable characters, all New World *Mabuya*, and most from the rest of the world, are slightly, and often only modally, differentiated; as Greer & Nussbaum (2000) noted, "Few unequivocal characters of scalation are available." *Ma-*

buya macleani differs from *M. sloanii* somewhat in having smaller scales, reflected in higher midbody row counts: 32–34, as opposed to 30–32 in other Puerto Rico Bank *Mabuya* ($n = 20$). It would take larger sample sizes to even demonstrate statistical significance. There may be selection pressure for smaller scales in *M. macleani*. Carrot Rock's other endemic lizard, *Anolis Ernestwilliamsi*, has very small scales and is absolutely distinct from its closest relative in this character (Lazell 1983). Interpreting the adaptive significance of scale size in lizards is, however, fraught with difficulties and apparent contradictions (Lazell 1994, Dmi'el et al. 1997).

Etymology.—The species is named in honor of our late friend and colleague Dr. William P. MacLean, III, of the University of the Virgin Islands, who contributed so much to knowledge of the Virgin Island herpetofauna (MacLean 1982), and who aided and assisted our work, and that of many others, on numerous occasions (Lazell & Mayer 1992). He was one of the first, and still few, professional biologists ever to have set foot upon Carrot Rock, and recognize its biotic uniqueness.

Discussion

Ecology.—Carrot Rock has undergone major ecological changes since it was first visited by JL in 1980 (Lazell 1983). Then, most of the windward (eastern) and northern portion of the top of the island was covered with a sprawling growth of sea grape, *Coccoloba uvifera* (Polygonaceae), which had to be either climbed over or crawled under. There were three thickets of sea grape on the edges of the scarp tall enough to stand in the shade of: one on the leeward coast, one on the northern windward coast, and the biggest in the gully—locally called "ghut"—where the first *Mabuya macleani* was collected.

Severe drought characterized the climate of the Virgin Islands during the eighties. It seemed that more precipitation fell in the

form of dust—said to have blown all the way from the Sahara—than as water. JL's field notes of 13 July 1985 record:

“The Rock is in terrible shape! The sea grape looks 90% dead; places I could crawl under before are now just scattered dry sticks. Trying to dig out leaf litter was a nightmare of dust.”

Despite the drought, *Anolis* remained common, the first *Mabuya* was secured, and *Sphaerodactylus macrolepis* (MCZ 170890) was also collected—all in the one remaining sea grape thicket in the ghut—in 1985 (Mayer & Lazell 1988). This brought Carrot Rock into compliance with the “rule of three” for Caribbean islands, as predicted (Lazell 1983). On 17 July 1988 conditions were no better, but more *M. macleani* were seen and collected than ever before. Over most of the boulder-jumbled surface of Carrot Rock, skinks have the advantage over would-be captors. In one small area near the top, however, there are few rocks, little vegetation, and a soil substrate. Here a group of us simultaneously sighted eight skinks in a 10 × 20 m (200 m²) plot (and caught three of the eight). Excluding the bare rock faces and wave-washed talus of the edges, we estimate the top of the island habitable for skinks at ca. 1.3 ha. Using our crude estimate, the total population of *Mabuya macleani* might be something like 520 individuals. In any case, a density of 12 in 200 m² (400 per ha) far exceeds that of skinks or other comparable ground lizards (e.g., *Ameiva*) anywhere in the Antilles.

On 27 October 1994, three *Mabuya macleani* were seen in about two hours on the Rock. JL's field notes mention “the incredible drought,” and the appearance of the island as “dead gray still” and “really bleak.” Hurricanes Luis and Marilyn struck the Virgin Islands in September 1995. Low-lying areas like Carrot Rock were inundated with sea water, but there was relatively little mitigating rainfall. On this day the Rock was visited with a group of 6 people, but in two hours ashore we saw but two skinks and not a single *Anolis*. Approximately half

the sea grapes in the ghut thicket were dead. The large candelabra cactus, *Pilosocereus royenii*, that had crowned the top of the islet (and housed the largest, uncatchable *Anolis*) was “rotting pulp and stark skeleton.”

Rainfall in the region began to increase in 1996. On 24 October 1996 a group of us checked the Rock briefly. We did not attempt to collect specimens, but we quickly located three *Anolis ernestwilliamsi* and two *Mabuya macleani*, one of the latter perched on a vine ca. 3 cm above the ground (Schwartz & Henderson [1991] note climbing in *Mabuya mabouya*). Again, from JL's field notes: “Seagrapes are regenerating well; the place generally looks much better than last year.”

A brief vegetation survey of Carrot Rock, by Dr. Fred Kraus on 26 October 1991, included, in addition to seagrape and candelabra cactus, *Mammillaria nivosa*, *Melocactus intortus*, and *Opuntia dillenii* (all Cactaceae), and the vines *Capparis flexuosa* (Capparidaceae), *Stigmophyllon periplocifolium* (Malpighiaceae), and *Cavanalia maritima* (Leguminosae). There are “various graminoids including the rare silky foxtail grass *Pappophorum pappiferum*.”

Differentiation on small islands.—The distinctiveness of populations inhabiting small islands, and the apparently rapid evolutionary rates involved in achieving this differentiation, have long been known to students of the zoology of archipelagos (Mayr 1963, Lazell 1972). *Mabuya macleani* appears to be an example of this phenomenon. Two aspects of Carrot Rock's geographic situation, in particular, argue for rapid evolution (Fig. 6). First is its short distance, approximately 400 m, from Peter Island. Given this short distance, and the predominant direction of the currents from the northeast, there seems a considerable probability of waif dispersal of skinks from adjacent parts of Peter Island (where typical *M. sloanii* does occur: MCZ 182273) or other islands to windward. Divergence of the Carrot Rock population, especially by

genetic drift, would have to proceed at a high rate to offset the genetically homogenizing effects of immigration events.

The second aspect is the short time during which Carrot Rock has existed as a separate island. Lowered sea levels during the last glacial period united all of the islands of the Puerto Rico Bank into a single large island (Heatwole & MacKenzie 1967). The age of separation of two islands on the bank can be inferred from the maximum depth of the water now separating them, and the time course of the Holocene sea level rise. We cannot say with certainty what the maximum depth of the channel between Carrot Rock and Peter Island is, because the channel is so shallow and strewn with rocks that only the smallest of boats attempt to pass through the strait, so that accurate soundings are not possible; it cannot be more than a few meters. Based on the time course of Caribbean sea level rise (Fairbanks 1989), a depth of 5 m would correspond to a separation of 3000 years; as the actual depth is almost certainly less than this, this is an upper limit on the time of isolation of Carrot Rock.

The causes of rapid divergence in island populations have long been a matter of contention (Williamson 1981, Berry 1986, Grant 1998), with some arguing for the importance of stochastic factors (e.g., Mayr 1954), while others have stressed the adaptive nature of island differentiation (e.g., Grant 1968, Malhotra & Thorpe 2000). Carrot Rock's proximity to Peter Island argues for a non-stochastic cause, since even a low rate of migration is sufficient to counteract divergence due to founder effect or drift (Crow and Kimura 1970); gene flow is much less effective in counteracting selection (Lande 1980). There is another, in our opinion much stronger, argument for non-stochastic causes: the occurrence on Carrot Rock of another endemic lizard, *Anolis ernestwilliamsi*, which, like *Mabuya macleani*, has a close relative, *A. cristatellus*, widespread on other islands on the Puerto Rican Bank (Lazell 1983; the third

species on the island, *Sphaerodactylus macrolepis* is not distinct). As Mayr (1963) noted, production of evolutionary novelties or new species in small, isolated populations is a rare event; if the initiating genetic events are stochastic in nature, it is highly unlikely that, of all the many islands on the Bank inhabited by *Mabuya* (Fig. 5) and *A. cristatellus* (MacLean 1982, Mayer 1989), these events should occur in both taxa on the same island. We infer that there is something about Carrot Rock itself which is conducive to divergence, rather than that there have been two independent occurrences of a rare stochastic event. We can only suggest that it is the unusual environmental conditions of the island (see above under *Ecology*) that are the common factor in divergence of the two species, but could only speculate about the exact conditions influencing one or the other species. Although it is often argued that evolution proceeds faster in smaller populations, adaptive divergence in fact is faster and greater in larger populations (Weber & Diggins 1990, Coyne et al. 1997), making the situation of two endemic lizards on Carrot Rock even more remarkable.

An alternative explanation for the endemism exhibited by the Carrot Rock saurofauna is that they are relicts, stranded there by post-glacial sea level rise. While we cannot definitively rule out this possibility, the close proximity and very recent separation of Carrot Rock from the main body of the Virgins, and its small size, make it an unlikely refuge for species which have elsewhere gone extinct. Three distributional patterns in the Virgin Islands herpetofauna suggest a relictual distribution, but none match that of the Carrot Rock endemics. *Sphaerodactylus townsendi*, an otherwise Puerto Rican species, occurs in the Virgins only on Frenchcap Cay (Heatwole et al. 1981), but this cay, separated by depths of 22 m, was the earliest of the Virgins to be isolated, about 8000 yr ago when Puerto Rican forms apparently ranged further east on the then exposed bank. Sev-

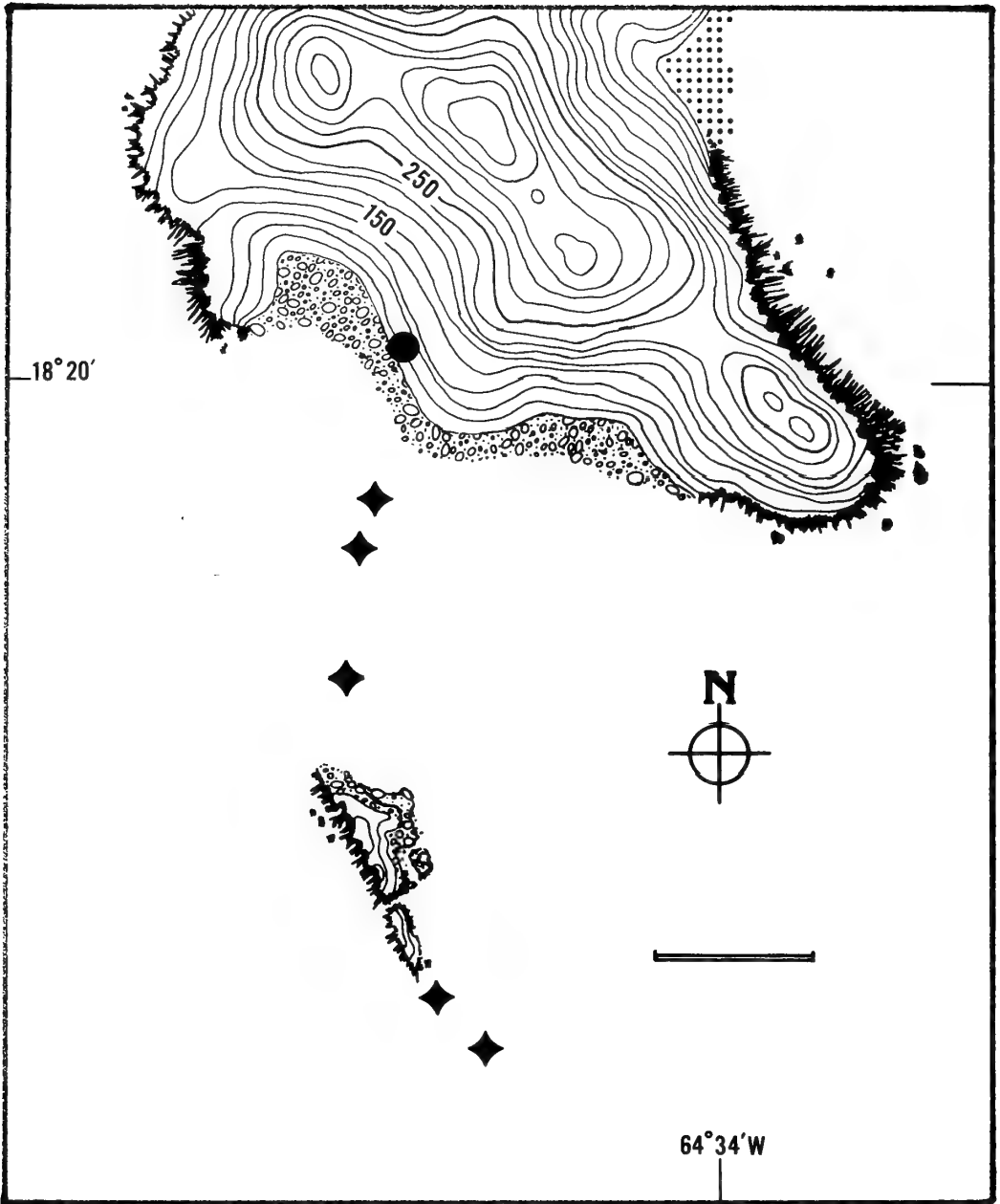


Fig. 6. The south end of Peter Island and Carrot Rock, British Virgin Islands. Dot indicates collection site of *Mabuya s. sloanii*, MCZ 182273, at Stoney Bay. Sand (dots), cobble and scree, and clifed shorelines are indicated. Black diamonds indicate rocks that break at low water (from U.S. NOAA chart 25641, 1984). Contours are at ca 7.62 m or 25 ft. (from British Directorate of Overseas Surveys 346, Series E 837, 1959). Bar, lower right, indicates 200m.

eral species (e.g. *Anolis roosevelti*) which occur today on only one or a few islands, although they must have once occurred more widely when sea levels were low, have persisted on the largest islands (Mayer 1989). Finally, several species have disappeared from some larger islands while persisting on some smaller islands (e.g., *Altophis portoricensis*), but such distributions have resulted from anthropogenic extirpations (Barbour 1930, Mayer & Lazell 1988). The Carrot Rock endemics fit none of these patterns. Furthermore, since close relatives of each are present on Peter Island and throughout the archipelago, supposing that they are pre-sea level rise relicts makes their divergence even more remarkable, or merely pushes the time, but not the mode, of their origin to an earlier glacial cycle. For these reasons, we favor the hypothesis of in situ post-glacial divergence (Lazell 1999).

Nomenclature.—Dunn (1936) referred all Antillean skinks (except *lineolata* of Hispaniola) to the species *Mabuya mabouya* Lacépède (1788), which species he also considered to be widely distributed on the mainland, from Mexico through much of South America. Since then, various authors have studied components of this widespread species or species-group, naming or reviving species as needed, and leaving behind an unstudied residue, to which the name *Mabuya mabouya* might continue to be attached (e.g., Rebouças-Spieker 1974, 1981a, 1981b, Avila-Pires 1995). Lacépède's work, however, is not binominal in its nomenclature, and the name, "mabouya" is thus not available.

Throughout the text of his work, Lacépède uses vernacular names, mostly in French, but some, like "Le Mabouya," deriving from other languages. Some Latin names appear in his "Synopsis methodica," but this is not a table of Linnaean-style binomina, but rather a partial translation into Latin of vernacular names given in the text: French vernacular names are translated, but non-French vernacular names appear un-

changed in the "Synopsis". Thus, the French "Le Sourcilleux" of the text appears as "L[acertus]. superciliosus" in the "Synopsis," while "Le Mabouya" of the text appears simply as "Mabouya," as do other non-French vernaculars such as "Jackie" and "Sheltopusik". Names in the table may be uninominal, binominal, or trinominal. Thus "Le Gecko" of the text appears as "Gecko" in the "Synopsis," "La Salamandre terrestre" as "Salamandra terrestris," and "Tortue marin comun" as "T[estudo]. marinus vulgaris".

Although the word "Lacertus" appears as the name of a "genus" in the heading of the "Synopsis," it cannot be read into the remainder of the table so as to turn uninomina into binomina. (Doing so would also turn some binomina in the table into trinomina.) Those names in the table to which Lacépède attached "Lacertus" are specifically listed as such in the table, most often by prefacing the name with "L.". The rule he generally followed is that when the French name is translated as a Latin adjective, it receives the "Lacertus" appellation (e.g., "Le Silloné" of the text becomes "L[acertus]. sulcatus" in the table), whereas names translated as Latin nouns do not (e.g., "Le Dragon" becomes "Draco"); the latter are thus truly uninominal.

In his genus "Lacertus," Lacépède had 26 uninominal and 30 binominal species names; in his genus "Testudo," he had four uninominal, 19 binominal and one trinominal; and similarly for his other genera. Lacépède's work is thus clearly non-binominal, and must be rejected for the purposes of zoological nomenclature. Brongersma (1972), Vanzolini (1977), Savage (1981), Melville (1986), and Smith (1986) also argued that Lacépède was non-binominal, and should be rejected for nomenclatural purposes, and the Commission agreed (International Commission on Zoological Nomenclature 1987). Unfortunately, all these authors but Vanzolini restricted their attention to Lacépède's second volume, on serpents, so that his quadrupeds have not been

formally rejected. Fortunately, rejection of non-binominal works is automatic under the Code, so action by the Commission is not required.

Lacépède's concept of "Le Mabouya" was composite and confused, with no specific locality. Although largely based on Antillean lizards, he also included Sardinia in its range, and the accompanying figure (pl. XXIV) is not even a *Mabuya*; it appears to be, as surmized by Duméril & Bibron (1839), *Chalcides ocellatus*, which occurs on Sardinia. Losing Lacépède's non-binominal name of dubious application will be no loss.

Recently, some authors (Powell et al. 1996, Hedges 1996, Murphy 1996, Powell et al. 1999, Crother 1999), perhaps aware of the difficulties with Lacépède, have begun using the specific name *bistriata* Spix, 1825 (type locality Belém, Brazil) for Antillean skinks previously (e.g., Schwartz & Henderson 1991) referred to *mabouya*. However, even if the Antillean and Brazilian forms are conspecific, which we consider unlikely, *sloanii* predates *bistriata* by 23 years, and the latter name should not be used.

We thus have not used "mabouya" here for Antillean skinks, but rather use Daudin's (1802; Fig. 4) *sloanii* as the first available name, the type of which still exists (Muséum National d'Histoire Naturelle, Paris 554), has good locality data (St. Thomas), and has been examined for us by G. R. Zug. The Antillean skinks formerly included in the *Mabuya* "mabouya" complex not dealt with in this paper (Lesser Antilles, Jamaica, Hispaniola) are best referred to as the *Mabuya sloanii* complex until their systematics can be resolved.

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Appendix I

Material Examined

Islands in the Puerto Rican area are listed in a roughly west to east sequence, and may be located through reference to the maps in Heatwole et al. (1981) and Lazell (1983), and the gazetteer in Mayer (1989). Numbers in parentheses indicate the number of specimens catalogued as a lot. University of Kansas Museum of Natural History (KU) numbers preceded by a letter are from the Albert Schwartz Field Series.

Mabuya sloanii nitida.—Puerto Rico: AMNH 6462, 14007; MCZ 6050, 6052 (2); UMMZ 73828.

M. s. nitida × *sloanii*.—Puerto Rico: UMMZ 73829. Cayo Icacos: MCZ 36624.

Mabuya sloanii sloanii.—Mona: AMNH 13703, 31896, 31908, 115437; Carnegie Museum (CM) 23774-6; Field Museum of Natural History 215, 134332; UMMZ 73817 (3), 73818 (3), 73824 (15), 73825 (2), 124819; National Museum of Natural History (USNM) 133683. Desecheo: USNM 220995. Culebra: AMNH 14005-6, 32910; UMMZ 73819 (13), 73820 (7), 73822 (16), 73823 (10), 73826 (3); USNM 49586. Cayo Luis Peña: UMMZ 73827. Cayo Norte: University of Puerto Rico Rio Piedras. Culebrita: UMMZ 80786. St. Thomas: MNHN 554, 1088 (by G. R. Zug). Saba Island (off St. Thomas): UMMZ 80580; USNM 304553. Water Island: KU V7409. Buck Island (off St. Thomas): UMMZ 73821 (2), 80585. South Capella Island (adjacent to Buck Island off St. Thomas):

UMMZ 80586. Little Tobago: MCZ 158940. Tortola: AMNH 99522. Guana Island: MCZ 166975, 170883; UMMZ 200131; USNM 306182. Great Camanoe: KU V3982. Peter Island: MCZ 182273. Norman Island: USNM 304551. Virgin Gorda: UMMZ 80581, 80582 (3), 80584. Salt Island: UMMZ 74427. Ginger Island: USNM 304550. Prickly Pear Island: USNM 304552. Necker Island: MCZ 176331. Anegada: AMNH 99523-4; CM 17357-8; UMMZ 80583 (28).

Mabuya sloanii complex from Caicos Bank.—Long Cay AMNH 80125-30; MCZ 182881. Six Hill Cays: 117394-6. West Caicos: UMMZ 117392-3.

Mabuya pergravis.—Providencia: Academy of Natural Sciences, Philadelphia 25791-95. San Andrés: UMMZ 127884.

**An earlier name for the mangrove diamondback terrapin,
Malaclemys terrapin rhizophorarum (Reptilia: Testudines: Emydidae)**

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Abstract.—The name *Malaclemys tuberculifera* Gray, 1844 is shown to pre-date the currently used name for the mangrove terrapin, *Malaclemys terrapin rhizophorarum*. In addition, the type locality of *tuberculifera* is shown to be in error.

The mangrove diamondback terrapin, *Malaclemys terrapin rhizophorarum*, is restricted to the Florida Keys (Conant & Collins 1991) and was described and named *Malaclemmys littoralis rhizophorarum* (= *Malaclemys terrapin rhizophorarum*) by Fowler in 1906. However, this may not be the earliest available scientific name.

A recent examination of the holotype of *Malaclemys tuberculifera* Gray, 1844, The Natural History Museum, London (BMNH) 1947.3.5.29 (38H), a mounted juvenile shell (carapace length 79.2 mm), reveals that this specimen possesses all shell characters used to define *Malaclemys t. rhizophorarum* (Fowler 1906). The carapace of *M. t. rhizophorarum* is best characterized by the bulbous knobs on its medial keel, its oblong shape, and dark scutes that lack light centers; its plastron seams have dark borders (Fowler 1906, Schwartz 1955, Ernst & Bury 1982, Ernst et al. 1994). The plastron of adults may be entirely or almost entirely dark (Carr 1946, 1952). The holotype of *M. tuberculifera* Gray, 1844 has a dark, oblong carapace (widest at the level of the eighth marginals), and knobs on vertebrals 2–4, with those of vertebrals 3–4 very bulbous. Both its light yellow plastron and bridge have dark seams, and there are dark speckles on the bridge. The plastron is not entirely dark like that of many adults,

but the plastron of this subspecies sometimes darkens with age.

Unfortunately, the head and soft parts are unavailable for the holotype of *M. tuberculifera*. These bear distinctive characters in *M. t. rhizophorarum*: the head is streaked with dark marks, the jaws are whitish-cream, the dark spots on the neck coalesce to form streaks, and the hind limbs are longitudinally streaked.

Because of the match of the shell characters of *M. tuberculifera* with those of *M. t. rhizophorarum*, the two represent a single taxon. The name *Malaclemys tuberculifera* is the senior synonym, predating that of *Malaclemys littoralis rhizophorarum* by 62 years. Gray used the name *tuberculifera* again in 1856 and 1873 to denote one of his four varieties of *Malaclemys concentrica* (= *Malaclemys terrapin*), but Boulenger (1889) listed the holotype of *M. tuberculifera* among the specimens of *Malacoclemmys terrapin* (= *M. terrapin*), in the collection of the British Museum (Natural History). His action relegated the name *Malaclemys tuberculifera* to the synonymy of the species name, *terrapin*. Since then, it has appeared only as a synonym of the species, and constitutes a nomen oblitum. Since 1906, when Fowler described it, only the name *rhizophorarum* has been used for the Florida Keys population of diamondback terrapins (Stejneger & Barbour 1917, 1923;

Carr 1940, 1946, 1952; Johnson 1952, Schmidt 1953, Carr & Goin 1955, Schwartz 1955, Duellman & Schwartz 1958, Wer-
muth & Mertens 1961, 1977; Ernst & Bar-
bour 1972, 1989; Godley 1978, Pritchard
1979, Ernst & Bury 1982, Ashton & Ash-
ton 1985, Iverson 1985, Conant 1986, Obst
1986, Müller 1987, Conant & Collins 1991,
Iverson 1992, Lamb & Avise 1992, Wood
1992, David 1994, Ernst et al. 1994, Seigel
& Gibbons 1995, Bartlett & Bartlett 1999).
Because of this almost 100-year usage, we
believe that, in spite of the seniority of *tub-
erculifera*, the name *rhizophorarum* should
continue to be used for this turtle. In com-
pliance with Article 23.9 of the Code of
Zoological Nomenclature, a petition has
been submitted [*Rhizophorarum* Fowler,
1906 (Reptilia: Testudines): proposed con-
servation] to the International Commission
on Zoological Nomenclature requesting the
suppression of the name *Malaclemys tub-
erculifera* Gray, 1844 to conserve the more
commonly known name *Malaclemmys lit-
toralis rhizophorarum* Fowler, 1906.

Gray (1844) gave the type-locality of *M.
tuberculifera* as "California" and stated the
specimen came from "Mr. J. Drummond's
collection." Schmidt (1953) restricted the
type-locality to the "Philadelphia market,"
Pennsylvania, apparently on the assumption
that the name *tuberculifera* was a synonym
of the species name *terrapin*, and so also of
the northern nominate subspecies, *M. t. ter-
rapin*. Because the name *tuberculifera* de-
notes the subspecies occurring in the Flor-
ida Keys, these two type-localities are er-
roneous. However, the designation of a
"correct" type-locality seems unnecessary.

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Comparative cytogenetic analysis of the Chilean leptodactylid frog genus *Telmatobufo*, with the description of the chromosomes of *T. venustus*

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Abstract.—A comparative cytogenetic analysis of the Chilean frog genus *Telmatobufo* show that all the species share $2N = 26$ and $FN = 52$. The chromosomes of *T. venustus* are described here for the first time. A polymorphic condition was detected on chromosome pair 3 of *T. bullocki*. Differences in C-band patterns and nucleolar organizer region (NOR) positions imply karyological differentiation in these species. Transformation of euchromatin to heterochromatin and loss of heterochromatin are hypothesized to have taken place in karyological evolution of some chromosomes in *Telmatobufo* species. Some NORs are considered as specific chromosome markers.

Leptodactylid frogs of the genus *Telmatobufo* (*T. australis*, *T. bullocki*, *T. venustus*) are a rare group (no more than 15 known specimens) endemic to the temperate *Nothofagus* forests of southern Chile (Formas 1979). Venegas (1975) described the karyotype of a single female of *T. bullocki*, and Formas & Pugin (1979) reported the chromosomes of *T. australis* from four tadpoles. Both taxa have a karyotype of $2N = 26$ chromosomes. The karyotype of *T. venustus* has remained unknown until recently. The leptodactylid frogs of the subfamily Telmatobiinae mostly have karyotypes with 26 chromosomes, although some species have 22 or 34 chromosomes (Kuramoto 1990). Reig (1972) considered the formula $2N = 26$ as primitive in the Lepidodactylidae because its most primitive members (*Caudiverbera*, *Alsodes*, *Batrachyla*) have karyotypes with 26 chromosomes.

In this paper we describe for the first time the standard karyotype of *T. venustus*, and redescribe the standard karyotypes of *T. bullocki* and *T. australis*, all of them endemic telmatobiine frogs of central and

southern Chile. Additionally, their C-banding pattern and NOR location were analyzed and compared in order to assess the extent of karyotypic divergence among these frogs, and to establish their karyological similarities.

Materials and Methods

Specimens examined.—The following specimens were used in this study: three females [IZUA (Instituto de Zoología Universidad Austral de Chile) 3159, 3161, 3164], two males (IZUA 3158, 3160), and six tadpoles (IZUA 3169) of *T. australis* (Chiveria, Valdivia Province, southern Chile: $40^{\circ}08'S$, $73^{\circ}40'W$). One male (IZUA 3157) and 26 tadpoles (IZUA 3147) of *T. bullocki* (Ruca-Pehuén, Arauco Province, southern Chile: $37^{\circ}40'S$, $73^{\circ}25'W$). One male (IZUA 3166) and one female (IZUA 3167) of *T. venustus* (Altos de Vilches, Talca Province, central Chile: $35^{\circ}28'S$, $71^{\circ}11'W$). All the specimens were collected by Lila Brieva, John Balladares, César Cuevas, J. Ramón Formas and José Núñez during the summer of 1998.

Chromosome preparations.—Chromo-

some spreads were obtained from duodenal epithelium using the technique described by Formas (1991). The chromosomes of the tadpoles were obtained from the epithelial cells of the tail using the method described by Bogart (1972). C-band patterns and NOR locations were determined by staining according to the techniques of Sumner (1972) and Rufas et al. (1982), respectively. Chromosome complements in several spreads from each individual were counted with a microscope and the best five chromosome spreads were selected for analysis. Centromeric positions were established according to Levan et al. (1964). Relative lengths of chromosomes were determined according to Bogart (1970). The secondary constrictions were not included in the measurements. Idiograms were constructed from the average measurements of ten homologous chromosomes from five well-spread cells.

Results

Standard karyotypes.—The description of the chromosomes of *T. venustus* is based on the analysis of 55 metaphase figures. The karyotype of *T. venustus* (Fig. 1c) has a diploid number of $2N = 26$. All chromosomes are biarmed, so the fundamental number (FN) is 52. When chromosomes are arranged in pairs of decreasing length, pairs 1–4 are large (>100 units), pairs 5 and 6 are intermediate (between 80 to 100 units), and 7–13 small (<80 units). Pairs 1, 4, 7, 8, 9, 10, 11, and 13 are metacentric; 2 and 12 submetacentric; and 3 and 6 subtelocentric (Table 1). The short arms of pairs 5, 6, and 12 show secondary constrictions. In both the female and the male, one member of pair 5 has the secondary constriction much longer than its homologue. No sexual dimorphism was detected in the karyotype.

The redescription of the karyotype of *T. bullocki* is based on the analysis of 30 metaphase spreads. The karyotype of this species (Fig. 1b) consists of 26 chromosomes, all with two arms (FN = 52). A dis-

tinct gap in relative length is evident between 6 and 7; chromosomes are divided into three groups, large chromosomes (1–4), intermediate (5 and 6), and small chromosomes (7–13). Pairs 1, 4, 7, 8, 9, 11, and 13 are metacentric; pairs 2, 10, and 12 are submetacentric; and pairs 3, 5, and 6 are subtelocentric. Pair 12 has a secondary constriction in the short arms (Table 1). A polymorphic condition was detected on pair 3 (Fig. 1b). In the male, the chromosomes of pair 3 are different in size (3'ab), although similar in morphology (st). The same situation was observed in 14 (77%) tadpoles; the remaining six larvae (23%) had the chromosome pair 3 in homomorphic (3 aa) condition (both members similar in size). Secondary constrictions were observed on short arms of chromosome pair 12 and in one member of chromosome pair 3' (b) (Fig. 1b).

The redescription of the chromosomes of *T. australis* is based on the analysis of 80 metaphase spreads. The karyotype of this species (Fig. 1a) has a diploid number of 26 chromosomes, all with two arms; its FN is 52. Chromosomes of *T. australis* form three size groups: large chromosomes (1–5), intermediate (6), and small chromosomes (7–13). Pairs 1, 4, 7, 8, 9, 10, 11, and 13 are metacentric; pairs 2 and 12 submetacentric; and pairs 3, 5, and 6 subtelocentric. Pairs 6 and 12 have a secondary constriction on the shorter arm (Table 1). No sexual dimorphism was detected in the karyotype.

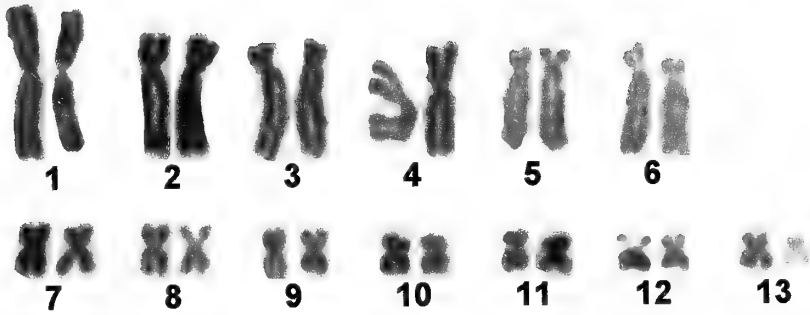
C-banded karyotypes.—The C-banded karyotype of *T. venustus* (Fig. 2e) exhibits constitutive heterochromatin in the centromeric region of all chromosomes, except in chromosome pair 4. Telomeric C-bands occurred on the long and short arms of chromosome pairs 1, 2, 4, 8, 10, 11, and 12; pairs 3, 6, and 9 present only telomeric C-bands (long arms). A polymorphic condition was detected in the C-banded pattern of chromosome pair 5. One member (5a) presents a marked telomeric band on the short arms, which is absent on its homo-

Table 1.—Relative length, arm ratio (mean and standard deviations), and types of chromosomes (m = metacentric; sm = submetacentric; st = subtelocentric) of *Telmatobufo australis*, *Telmatobufo bullocki*, and *Telmatobufo venustus*.

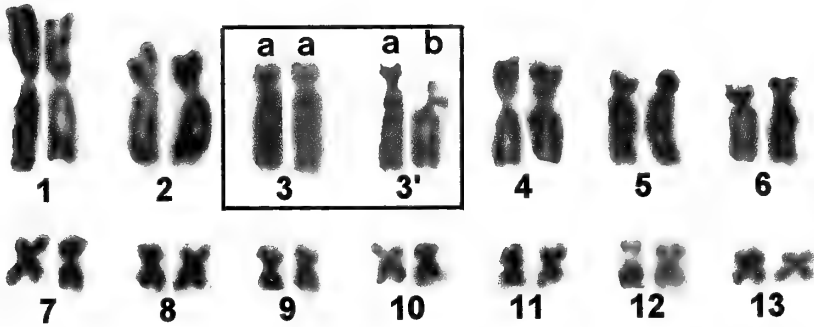
Pair N°	<i>T. australis</i>			<i>T. bullocki</i>			<i>T. venustus</i>		
	Relative length	Arm ratio	Type	Relative length	Arm ratio	Type	Relative length	Arm ratio	Type
1	159.91 ± 6.87	1.22 ± 0.10	m	163.84 ± 0.42	1.35 ± 0.10	m	167.55 ± 3.47	1.25 ± 0.09	m
2	123.78 ± 8.31	2.05 ± 0.27	sm	129.74 ± 3.04	1.87 ± 0.17	sm	124.77 ± 11.45	2.13 ± 0.26	sm
3	113.08 ± 4.57	3.07 ± 0.19	st	125.44 ± 0.84	3.36 ± 0.15	st	111.40 ± 7.95	3.85 ± 0.55	st
3' a				125.26 ± 2.85	3.42 ± 0.25	st			
3' b				*107.10 ± 2.43	5.50 ± 0.12	st			
4	105.06 ± 7.57	1.33 ± 0.07	m	104.31 ± 2.12	1.38 ± 0.08	m	106.68 ± 4.86	1.42 ± 0.12	m
5	100.32 ± 4.61	2.67 ± 0.25	st	95.58 ± 5.44	3.14 ± 0.12	st	* 94.38 ± 5.45	6.80 ± 0.58	st
6	* 87.32 ± 4.80	5.50 ± 0.03	st	80.27 ± 3.67	3.95 ± 0.13	st	* 91.77 ± 7.01	6.00 ± 0.69	st
7	52.99 ± 2.50	1.41 ± 1.41	m	54.83 ± 5.30	1.13 ± 0.14	m	52.35 ± 1.60	1.35 ± 0.11	m
8	49.64 ± 2.12	1.27 ± 0.62	m	50.50 ± 3.53	1.60 ± 0.57	m	47.04 ± 2.37	1.22 ± 0.09	m
9	48.74 ± 1.47	1.11 ± 0.05	m	48.25 ± 1.90	1.24 ± 0.05	m	44.92 ± 5.50	1.88 ± 0.12	sm
10	42.61 ± 3.32	1.20 ± 0.09	m	43.85 ± 4.31	2.10 ± 0.60	sm	40.26 ± 1.35	1.23 ± 0.24	m
11	40.05 ± 1.79	1.45 ± 0.26	m	42.76 ± 3.74	1.54 ± 0.24	m	38.51 ± 2.33	1.30 ± 0.24	m
12	* 39.33 ± 1.86	2.00 ± 0.21	sm	* 38.36 ± 0.63	2.60 ± 0.11	sm	* 36.48 ± 2.35	2.01 ± 0.03	sm
13	35.72 ± 1.39	1.40 ± 0.27	m	33.85 ± 4.31	1.23 ± 0.17	m	32.88 ± 3.30	1.22 ± 0.12	m

* Chromosomes with secondary constrictions.

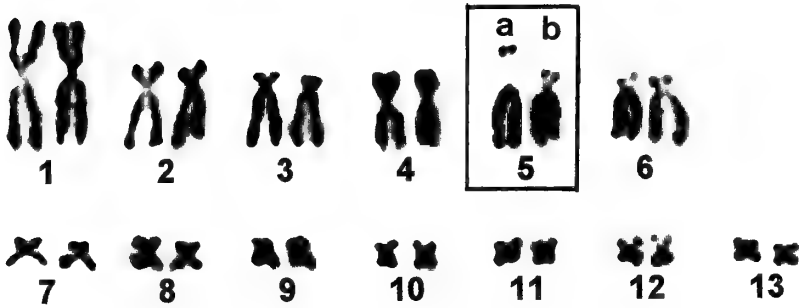
a



b



c



10 um

Fig. 1. (a) Standard karyotype of a male of *Telmatobufo australis*, (b) standard karyotype of a male of *T. bullocki*; the polymorphic condition (aa,ab) detected in the tadpoles (pair 3) is framed, (c) standard karyotype of a male of *T. venustus*; the frame indicates the difference in size of the secondary constriction detected between both member of pair 5.

logue (5b). The polymorphic condition observed in chromosome pair 5 was detected in both female and male. Interstitial heterochromatin was observed in the long arms of pairs 1, 2, 3, and 6. The C-banded idiogram of *T. venustus* is presented in Fig. 3c.

In the C-banded karyotype of *T. bullocki* (Fig. 2c) small heterochromatic bands were observed in the centromeric region of chromosome pairs 2, 3-3', 4, 5, 6, 8, 9, 10, 11, 12, and 13; in chromosome pair 7 the evidence for heterochromatic bands is faint, and it is absent in chromosome pair 1.

Telomeric bands were observed in chromosome pairs 1, 3'b, 4, and 5 (both arms), 2, 3a, 3'a, and 6 (long arms). An interstitial C-band was observed on the long arm of chromosome pair 6. The small chromosomes (7-13) do not show telomeric C-bands. The C-banded idiogram of *T. bullocki* is shown in Fig. 3b.

The C-banded karyotype of *T. australis* (Fig. 2a) shows well-defined bands in the centromeric regions of chromosome pairs 1, 2, 3, 5, 6, 7, 8, 9, 10, 11, and 13; in chromosome pairs 5 and 6 the bands are strongly stained. The stained bands are less marked in chromosome pairs 4 and 12. Pairs 1-4 exhibit telomeric heterochromatic bands (both arms); however, telomeric bands were not observed on the small chromosome pairs (7-13). Chromosome pairs 5 and 6 have no telomeric bands on the short arms. Pairs 3, 5, and 6 have interstitial blocks of constitutive heterochromatin on the long arms. The C-banded idiogram of *T. australis* is shown in Fig. 3a.

Nucleolus organizer regions (NORs).—Silver staining of chromosomes showed the NORs to be located within the secondary (nucleolar) constrictions of the short arms of chromosome pairs 6 and 12 (*T. australis*, Fig. 2b), 12 (*T. bullocki*, Fig. 2d), and 5 and 12 (*T. venustus*, Fig. 2f). A tandem duplication was observed in heterozygotic condition on chromosome pair 5 of *T. venustus* (Fig. 2f).

Discussion

The karyotype of *T. bullocki* as described by Venegas (1975) based on a single female, is only partially congruent with that obtained by us. Firstly, an evident secondary constriction on the short arms of pair 12 (Fig. 1b) was observed here. Second, chromosome pair 3 was subtelocentric, not metacentric, and third, chromosome pair 4 was metacentric, not subtelocentric as previously described by Venegas. Finally, chromosome pair 13 was submetacentric here, not metacentric. Venegas (1975) described chromosome pair 3 as homomorphic (both homologues similar in size); this condition was here reported in six tadpoles, although not in the male analyzed. The former descriptions of the karyotype of *T. bullocki* (Venegas 1975) and the polymorphism here reported for chromosome pair 3 (homologues different in size), suggest the existence of heteromorphic sex chromosomes in *T. bullocki*. This possibility should be tested by analysis of meiotic plates of males and additional mitotic plates of females.

The karyotype of *T. australis* as described by Formas & Pugin (1979) differs in part from our results. Secondary constrictions were observed on pairs 6 and 12; Formas & Pugin (1979) described those karyological features on chromosome pairs 3, 6, and 7. Chromosome pair 3 was submetacentric, not metacentric as previously described. In addition, chromosome pair 5 was metacentric, not subtelocentric. Finally, chromosome pairs 5 and 12 were subtelocentric and submetacentric, respectively, not metacentric as previously described.

The comparison of the standard karyotype of the three species of *Telmatobufo* showed that they do not differ notoriously with respect to the centromeric index; however, the small chromosome pair 10 is submetacentric in *T. bullocki*, although metacentric in *T. australis* and *T. venustus*, and the chromosome pair 9 is submetacentric in *T. venustus*, but metacentric in *T. australis*

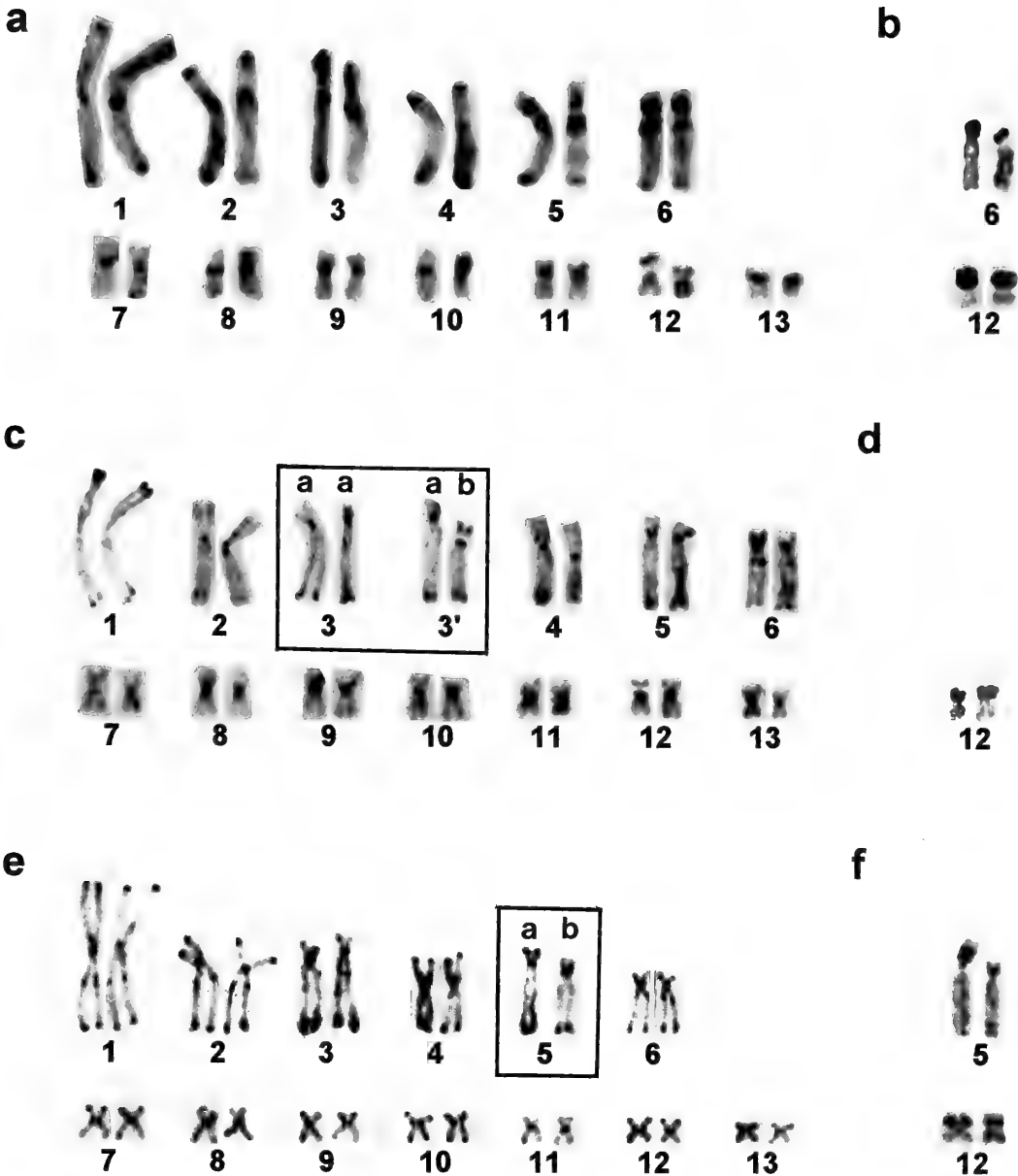


Fig. 2. (a) C-banded karyotype of a male of *Telmatobufo australis*. (c) C-banded karyotype of a male of *T. bullocki*; the polymorphic condition (aa,ab) detected in the tadpoles (pair 3) is framed. (e) C-banded karyotype of a male of *T. venustus*; the frame shows both member of pair 5, they are different in sizes and C-banding patterns. Positions of the NORs in *Telmatobufo* species; (b) pairs 6 and 12 (*T. australis*), (d) pair 12 (*T. bullocki*), (f) and pairs 5 and 12 (*T. venustus*). A tandem duplication is observed in one homologue of pair 5 of *T. venustus*.

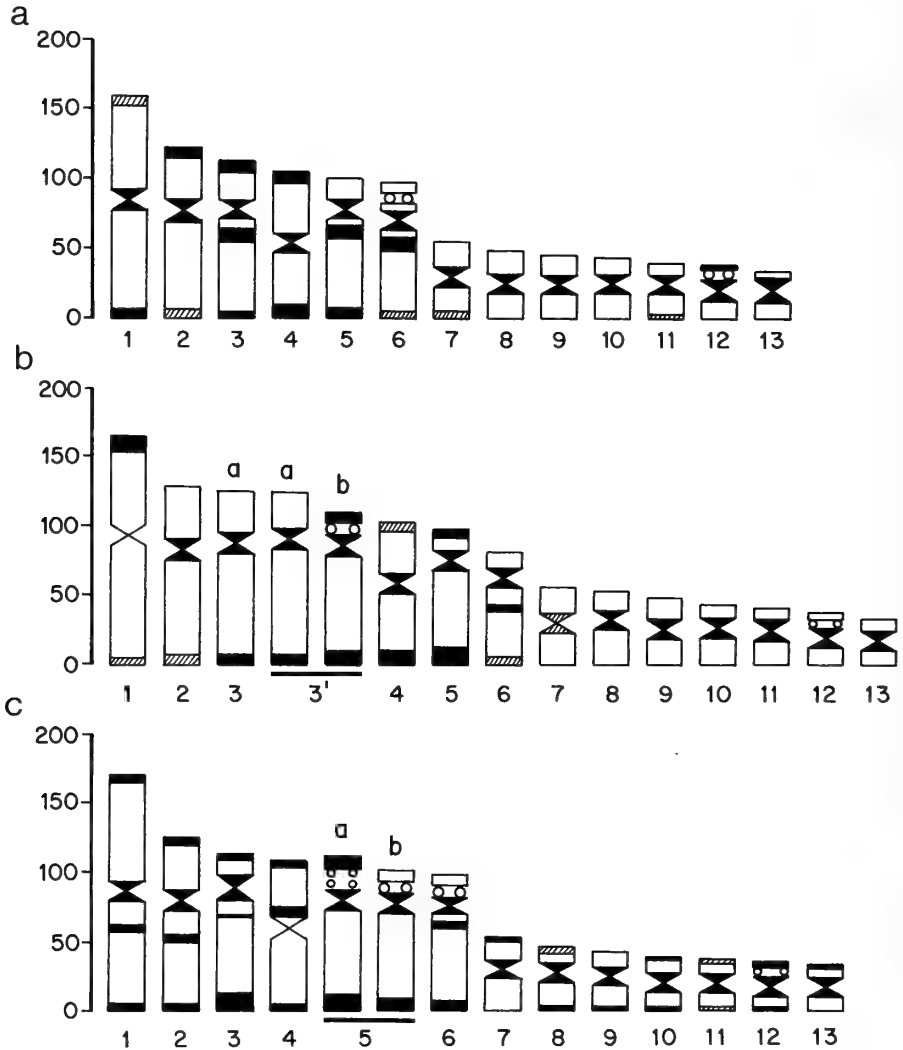


Fig. 3. (a) C-banded idiograms of *Telmatobufo australis*, (b) C-banded idiograms of *T. bullocki*; the bar indicates the polymorphic condition (pair 3) detected in tadpoles, (c) C-banded idiograms of *T. venustus*; the bars shows the differences in sizes and C-banding patterns detected in pair 5. The scale from 0 to 200 refers to the normalized length of the chromosomes relative to the total complement length.

and *T. bullocki*. In terms of number ($2N = 26$) and relative size the karyotypes of *Telmatobufo* species are very similar; however a minor difference was detected. Pair 5 is large in *T. australis*, but intermediate in *T. bullocki* and *T. venustus*.

In contrast to the relative morphological uniformity of the standard karyotypes, important differences were observed in the amount of constitutive heterochromatin, as well as in the position and size of C-bands.

The constitutive heterochromatin of anuran chromosomes presents a highly variable pattern of distribution, in qualitative as in quantitative respects (Schmid 1978a, 1978b; King 1980), and the C-bands have been used to differentiate otherwise closely similar standard karyotypes (Miura 1995, Spasić-Bosković et al. 1997). In most anuran species, the nucleolar organizer regions (NORs) occupy an interstitial or sub-terminal position along the chromosomes,

and interspecific comparisons have shown that the Ag-stained NORs are almost always found in the same chromosomal region in karyotypes of closely related species (Schmid 1982).

The C-banded karyotypes and idiograms of *T. australis*, *T. bullocki*, and *T. venustus* (Figs. 2 and 3) show that *T. australis* and *T. bullocki* share a similar C-band pattern (centromeric bands) on their small chromosome pairs (7–13). In *T. bullocki*, the centromeric band on chromosome pair 7 is less marked. *Telmatobufo venustus* differs from *T. australis* and *T. bullocki* by having a telomeric band on chromosome pairs 7–13 (both arms of 8, 10, 11, and 12, short arms of 7 and 13, and long arm of 9). The three species share an interstitial band on the long arm of chromosome pair 6. In *T. australis*, this band is better developed than in the other species. *Telmatobufo australis* can be differentiated from its congeners by the existence of interstitial large bands of heterochromatin in the long arm of chromosome pairs 3 and 5. On the other hand, the centromeric bands of this species are better developed than in *T. bullocki* and *T. venustus*. *Telmatobufo venustus* is distinguished from *T. australis* and *T. bullocki* by possessing a strong telomeric C-band on the long arm of chromosome pair 3 and interstitial bands on the long arms of chromosome pairs 1 and 2. *Telmatobufo bullocki* differs from its congeners by the absence of centromeric bands on chromosome pair 1.

Transformation of euchromatin to heterochromatin (King 1980, 1991) and loss of heterochromatin, especially in sex chromosomes (Iturra & Veloso 1991, Cuevas & Formas 1996) are processes apparently implicated in the evolution of anuran genomes. The C-banding patterns of *Telmatobufo* species are rather complex and difficult to interpret, and the evolutionary mechanisms cited above are only used to explain the heterochromatin evolution of some of the chromosomes. Frogs in the species group constituting the genus *Telmatobufo* share the same basic karyotype in

terms of gross morphology. This is emphasised by each of the species sharing an interstitial band on the long arm of chromosome pair 6, and strong centromeric bands on all chromosomes, except for chromosome pair 1 in *T. bullocki* (band absent) and chromosome pair 4 in *T. australis* (weak band). The absence of a centromeric C-band in chromosome pair 1 of *T. bullocki* appears to be a derived condition, because the C-banded karyotype of the monotypic genus *Caudiverbera* [*C. caudiverbera*: sister group of the genus *Telmatobufo*, (Lynch 1978)] has centromeric C-bands on all chromosomes (Veloso 1977), and for this reason, we assume loss of heterochromatin.

Transformation of euchromatin to heterochromatin is here postulated to explain the presence of interstitial heterochromatin bands in the long arms of chromosome pairs 1 and 2 of *T. bullocki* due to their absence in the C-banded karyotypes of *C. caudiverbera* (Veloso 1977). Chromosome pair 6 in *T. venustus* and a member of chromosome pair 3 (3'b) in *T. bullocki* show a conspicuous secondary constriction; however, they are negative to Ag-staining. Lack of Ag-staining in these chromosomes can be explained by inactivity of their NORs in the preceding interphase (Schmid 1982).

The presence of NORs in chromosome pair 12 of all three *Telmatobufo* species is one example of the strong similarities among their karyotypes. This feature, along with the presence of centromeric C-bands on all chromosomes and the interstitial C-bands on the long arm of pair 6, provides cytological characters that can be used in the chromosomal diagnosis of the genus, previously based only on osteological (Lynch 1978) and larval characters (Formas 1988). NORs on chromosome pair 6 of *T. australis* and chromosome pair 5 of *T. venustus* are interpreted as specific characters, and could be considered as chromosome markers for these taxa.

Karyotypes with 26 bi-armed chromosomes have been postulated by Reig (1972) as the primitive condition for members of

the family Leptodactylidae. *Caudiverbera caudiverbera*, one of the most primitive members of this group, with fossils reported from the Eocene-Oligocene of Argentinean Patagonia (Shaeffer 1949, Gasparini & Báez 1975, Báez & Gasparini 1975), presents a karyotype with 26 bi-armed chromosomes (Formas & Espinoza 1975). Using an immunological approach (micro-complement fixation), Núñez & Formas (2000) pointed out that *Telmatobufo* and *Caudiverbera* (the unique genera of the Caelyptocephalellini tribe, Lynch 1978) diverged 35 million years ago (Lower Oligocene). The presence of 26 bi-armed chromosomes in *Telmatobufo* and *Caudiverbera* suggests that both genera share an old and primitive karyotype, which constitutes new evidence in support of Reig's hypothesis.

Among the telmatobiine frogs of the temperate *Nothofagus* forests of southern Chile, the primitive 26 bi-armed karyotype has been reported in the genera *Alsodes* [*A. monticola*, *A. tumultuosus*, *A. vanzolinii*, *A. verrucosus*, *A. gargola* (Formas & Vera 1983), *A. australis* (Formas et al. 1997), *A. kaweshkari* (Formas et al. 1998)], *Batrachyla* (*B. antartandica*, *B. leptopus*, *B. taeniata*), *Hylorina* (*H. sylvatica*), and *Insuetophrynus* (*I. acarpicus*) (Barrio & Rinaldi de Chieri 1971). If the karyotype with 26 chromosomes is interpreted as primitive, the presence of 22 chromosomes in *Alsodes nodosus* (Bogart 1970), and 34 chromosomes in *A. barrioi* (Veloso et al. 1981), can be considered a derived condition. As the primitive karyotype does not include telocentric chromosomes, the presence of telocentric chromosomes in *B. taeniata*, *B. antartandica* (one pair) and *A. barrioi* (five pairs) is also postulated to be a derived character. Species of the genera *Eupsophus* (Formas 1978, 1980, 1991; Cuevas & Formas 1996), *Eleutherodactylus* and *Syrrophus* (Bogart 1970) with chromosome numbers both higher and lower than 22 and 26, and numerous telocentric chromosomes, must be interpreted as examples of excep-

tional mechanisms of chromosome evolution within the Leptodactylidae family.

Acknowledgments

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***Sorubim cuspicaudus*, a new long-whiskered catfish from
northwestern South America (Siluriformes: Pimelodidae)**

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Abstract.—*Sorubim cuspicaudus*, new species, is diagnosed herein as the only member of the genus known to occur west of the Andean Cordillera Oriental, occurring in the Sinu, Cauca, and Magdalena Rivers of Colombia and the Lago Maracaibo basin of Colombia and Venezuela. It is distinguished from other *Sorubim* species by the following combination of characters: unique caudal fin shape with both lobes pointed; deep, blackened posterior fontanelle groove on the supraoccipital bone; combination of broad head and elongate body shape. *Sorubim cuspicaudus* is known to attain lengths greater than 80 cm, making it the largest species in the genus and thus a valuable food resource.

Resumen.—*Sorubim cuspicaudus* es una nueva especie que se reconoce como la única del género que habita el occidente de la Cordillera Oriental Andina, presente en al Sinu, Cauca, y Magdalena, ríos de Colombia y cuenca del Lago Maracaibo de Colombia y Venezuela. Se distingue de las demás especies del género *Sorubim* por la combinación de los siguientes caracteres: forma única de la aleta caudal, con ambos lóbulos aguzados, surco fontanelar posterior del hueso supraoccipital negro oscuro; la relación entre el ancho de la cabeza y la longitud del cuerpo. *Sorubim cuspicaudus* alcanza tallas superiores a los 80 cm, siendo la especie más grande del género y representa un importante recurso en el pesquería comercial.

Recent investigations into the systematic status of species assigned to the genus *Sorubim* (Siluriformes: Pimelodidae) have led to the recognition of a new species from the Maracaibo basin of western Venezuela and the Cauca, Magdalena, and Sinu drainages in northwestern Colombia (Littmann 1998). This area is considered ichthyofaunally depauperate despite its large drainage area and diversity of aquatic habitats (Lundberg et al. 1986). The restricted distribution of this species makes it the only member of the genus found west of the Andean Cordillera Oriental. In addition, the new species is a valuable component of the freshwater com-

mercial fishery in Colombia and continues to provide traditional, artisanal fishermen with subsistence protein.

Species of *Sorubim* are characterized by a shovel-like, projecting upper jaw exposing a large premaxillary tooth patch ventrally, laterally positioned eyes, and a distinct, black horizontal stripe stretching from the snout to the caudal fin. Species of *Sorubim* occur in a variety of stream and lentic habitats and are widely distributed throughout most of the major freshwater drainage basins of tropical and subtropical South America.

Twelve zoological names have been his-

torically associated with the genus *Sorubim* (Table 1). One of these names is now known to apply to a species of *Sorubimichthys* (Lundberg et al. 1989), and an additional five names were published only in the synonymy of other nominal pimelodids (Kottelat 1988, Eschmeyer 1998); these names are not available. Of the six remaining names, only *Sorubim lima* (Bloch & Schneider 1801) and *S. trigonocephalus* Miranda-Ribeiro, 1920 represent valid species. *Sorubim infraoculare* Agassiz, 1829, *S. gerupensis* Natterer, 1858, *S. luceri* Weyenbergh, 1877, and *Sorubim latirostris* Miranda-Ribeiro, 1920, are junior subjective synonyms of *S. lima*, the well-recognized senior name and the most widespread species in the genus. *Sorubim trigonocephalus*, represented from only three specimens, occurs only in the Amazon basin (Littmann 1998). We recognize two additional species of *Sorubim*, both unnamed: one is a slender species that occurs syntopically with *S. lima*, to be described in a separate paper in preparation, and the other is described as new below.

The new species has long been considered conspecific with the widely-distributed *Sorubim lima* (Eigenmann & Eigenmann 1890, Miles 1947, Dahl 1961, 1971; Galvis et al. 1997), although the descriptive information presented herein is in disagreement with the past superficial descriptions of species of *Sorubim*. Despite repeated references to *S. lima* in the literature on Colombian fishes, only Dahl (1971:52) and Galvis et al. (1997:72) have illustrated the taxon we describe here as new. Detailed historical, anatomical, and phylogenetic information, including a systematic review of the genus *Sorubim* will be covered in a manuscript now under preparation.

Methods

Point-to-point measurements were made with dial calipers and recorded to the nearest 0.01 mm following Hubbs & Lagler (1974), Lundberg & McDade (1986), and

Lundberg et al. (1991). Measurements, presented as percentage of standard length (SL), were made on the left side of the fish whenever possible. Measurements of small specimens were aided by the use of a Wild dissecting microscope fitted with an ocular micrometer. Distances between fins were taken from landmarks using the terms 'origin' as the anterior and 'insertion' as the posterior points of contact between fin rays or membranes and the body (Cailliet et al. 1996). Fifteen morphometric variables taken from the heads of 17 specimens and 31 taken from the bodies of 8 specimens of the new species were analyzed. Slightly bent specimens were gently forced into a straight position when measured. For comparison, the same set of measurements was made on numerous samples of three other species of *Sorubim*. Effort was made to examine specimens encompassing the known geographic range of the genus.

Gill raker, branchiostegal ray, and vertebral counts were made on cleared and counterstained specimens prepared using methods modified from Pothoff (1984) and Taylor & Van Dyke (1985). Dry skeletons and radiographs were utilized to aid with fin ray and vertebral counts following methods described in Lundberg et al. (1991). Vertebral counts include the fused preural centrum 1 + the ural centrum but do not include 6 vertebral elements fused as part of the Weberian complex. Soft X-rays were used to confirm counts of branchiostegal rays, vertebrae, and anal and caudal fin-rays, following Jenkins and Lachner (1971), Lundberg et al. (1991), and Silfvergrip (1996). Unless otherwise specified, counts of meristic features used in the diagnosis and description are reported as modes with ranges in parentheses. Barbel terminology is as follows: barbels on the anterodorsal surface of the head are termed maxillary; barbels on the ventral surface are termed outer and inner mental barbels, respectively.

A truss network of the body and head shape of *Sorubim* was designed using methods defined in Schaefer (1991), including

Table 1.—List of published names and status of species of *Sorubim* Cuvier 1829. Abbreviations: A = Agassiz; S & A = Spix & Agassiz. Authorship of names used in Spix & Agassiz's "Brazilian Fishes" follows Kottelat (1988).

Name	Taxonomic status	Reference
<i>Sorubim caparary</i> A, in S & A 1829	1st published in synonymy of <i>Platystoma corruscans</i> ; not available	Kottelat 1988, present study
<i>Silurus gerupensis</i> Natterer, in Kner 1858	1st published in synonymy of <i>Platystoma lima</i> ; not available	Gosline 1945, Fowler 1951, Eschmeyer 1998, Nass 1988
<i>Sorubim infraocularis</i> A, in S & A 1829	1st published in synonymy of <i>Platystoma lima</i> ; not available	Whitehead & Myers 1971, Kottelat 1988, Nass 1988, Eschmeyer 1998
<i>Sorubim jandia</i> A, in S & A 1829	1st published in synonymy of <i>Platystoma spatula</i> ; not available	Kottelat 1988, Lundberg et al. 1989
<i>Sorubim latirostris</i> Miranda-Ribeiro 1920	junior subjective synonym of <i>Sorubim lima</i>	Littmann et al. (in press)
<i>Silurus lima</i> Bloch & Schneider 1801	valid as <i>Sorubim lima</i>	Bleeker 1862, Kottelat 1988, several others
<i>Platystoma luceri</i> Weyenbergh 1877	junior subjective synonym of <i>Sorubim lima</i>	Eigenmann & Eigenmann 1890, Gosline 1945, Fowler 1951
<i>Sorubim mena</i> Natterer in Kner 1858	1st published in passing under <i>Platystoma sturio</i> (<i>Platystomaichthys</i>) not available	Eschmeyer 1998
<i>Sorubim pirauaca</i> A, in S & A 1829	1st published in synonymy of <i>Platystoma planiceps</i> ; not available	Lundberg et al. 1989, Eschmeyer 1998
<i>Platystoma planiceps</i> A in S & A 1829	valid as <i>Sorubimichthys planiceps</i>	Kottelat 1988, Lundberg 1989
<i>Sorubim trigonocephalus</i> Miranda-Ribeiro 1920	valid taxon	Eschmeyer 1998, others, present study
<i>Platystoma truncatum</i> A, in S & A	synonym of <i>Pseudoplatystoma</i>	Littmann 1998

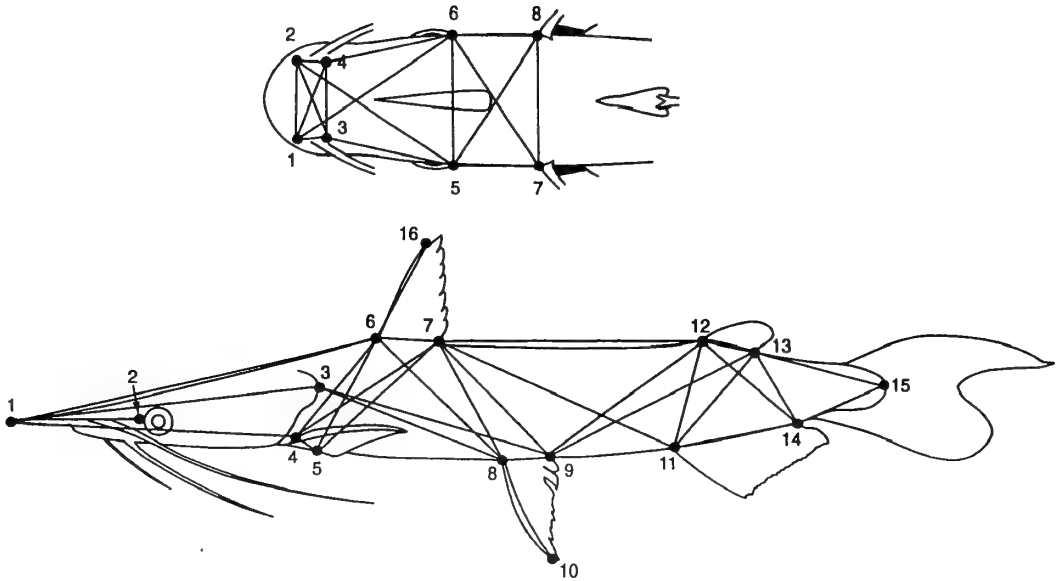


Fig. 1. Diagrammatic representation of 15 head measurements, 31 body measurements, and truss network used in sheared principal component analyses of the species of *Sorubim*. Descriptions of distance measures are provided in Table 2.

46 measurements distributed among three sagittal-plane truss cells with appended posterior and anterior triangles and three dorsal head cells. The truss network consists of a geometric protocol for character selection (Strauss & Bookstein 1982) and incorporates homologous landmarks on the body and head of the fish (Fig. 1). The truss network was used to compare variation in body shape among the different species of *Sorubim*.

Data were analyzed using programs available in SAS 5.18 (SAS Institute Inc. 1997). Multivariate analysis of the morphometric data was accomplished using sheared principal component analysis (PCA) as described by Humphries et al. (1981) and Bookstein et al. (1985) in an effort to eliminate overall size effects. Morphometric characters were log transformed and principal components were factored from the covariance matrix for each analysis, following recommendations by Bookstein et al. (1985).

Institutional abbreviations in text, material examined, and acknowledgments are

taken from Leviton et al. (1985) and Leviton & Gibbs (1988).

Sorubim cuspicaudus, new species
Trans-Andean shovelnose catfish (English)
antioqueno, bagre blanco, blanco pobre,
blanquillo, cucharo, gallego, Trans-Andean
hocico de paletón (Spanish)
Fig. 2b, 3, 4c; Tables 3–8

Holotype.—FMNH 56223, 327 mm SL, Colombia, Departamento de Tolima, Río Magdalena drainage, at Puerto Soplaviento. 11 Jan 1912, C. H. Eigenmann.

Paratopotypes.—FMNH 107492, 2:264–314 mm SL, Colombia, Departamento de Tolima, Río Magdalena drainage, at Puerto Soplaviento. 11 Jan 1912, C. H. Eigenmann.

Paratypes.—FMNH 60305, 3:256–262 mm SL, Colombia, Departamento de Bolívar, Río Magdalena drainage, at Calamar. C. H. Eigenmann. INHS 35428, 145 mm SL, Venezuela, Estado de Zulia, Lago Maracaibo-Río Santa Ana drainage, bridge ca. 8 km SW Alturitas. 2 Feb 1995, L. M. Page

et al. CAS 150404, 420 mm SL, 150406, 367 mm SL, Colombia, Departamento de Caldas, at or near junction of Ríos Samana and La Miel, near La Dorada, 05°29'N, 74°40'W. 27 Feb 1957, T. D. White and J. N. Reynolds. AUM 28756, 2:116–191 mm SL, Colombia, Departamento de Bolivar, Río Magdalena drainage, Ciénega de Jobo at confluence with Canal de Dique, 16 km NW Calamar. 3 Oct 1978, J. S. Ramsey, R. Phelps et al.

Diagnosis.—*Sorubim cuspicaudus* is distinguished from all congeners by the following characters: caudal fin deeply forked; distal caudal margin of lower lobe pointed, not curved and rounded as in other species of *Sorubim*, outer principal rays of upper and lower lobes extending straight back (Fig. 2b); posterior fontanelle elongate, forming a conspicuous groove on the supraoccipital bone, externally pigmented black; other species of *Sorubim* without elongate posterior fontanelle, supraoccipital groove, or black external pigment (Fig. 3b); unique in having the combination of an elongate body and broad-shaped head; other *Sorubim* species have either an elongate body and head, or a stout body with a broad head (Fig. 3b).

Description.—Counts of meristic features and morphometric data appear in Tables 3–8. Largest individual examined was 483 mm SL (CU 47915). Dorsal-fin rays ii,6 ($n = 23$); pectoral-fin rays 9 (8–9); anal-fin rays 19 or 20 (18–22); pelvic-fin rays 6, 1 unbranched and 5 branched ($n = 23$); principal caudal rays in upper lobe always 8, lower rays variable, 8–10; gill rakers on first branchial arch 15–18, 3 to 4 (usually 4) on epibranchial.

Body shape and form shown in Figure 3. Head broad, but body slender and elongate, tapering from the cleithral process to the caudal peduncle. Head length approximately three times gape width ($n = 20$, range 2.5–3.4, mean 2.9); interorbital distance three or more times than eye diameter ($n = 19$, range 3.1–5.1, mean 4.2); anal fin length 1.8–2.3 times adipose fin length (n

= 16, range 1.6–2.6, mean 2.1); and premaxillary tooth patch width 2.4 times or more than its length ($n = 17$, range 2.4–3.2, mean 2.8).

Eyes positioned laterally, visible dorsally and ventrally. Anterior section of lateral line covered externally with very small ossicles (sensu Lundberg & McDade 1986), ovate in shape. Inner mental barbels almost always anterior to or even with gular apex (Fig. 3c). Maxillary barbels extend to pelvic fins. Tooth pattern on vomer highly variable as shown in Fig. 4c. Metapterygoid tooth patches large, fused, and triangular in shape.

Color.—Pigmentation and color variable. Dorsal surface dark to light brown, gray, or black; ventral surface completely white or cream-colored, bisected laterally by a black horizontal stripe extending from tip of snout to the ray tips of lower caudal lobe on its medial edge. Horizontal stripe variable in width, occasionally extending through entire diameter of eye, other times just touching the dorsal edge. Dusky dorsal surface and black horizontal stripe separated by light lateral band, usually white or gray, sometimes light brown.

Fins clear with lemon-yellow at bases of pelvic, anal, and caudal fins, color usually confined to rays, especially in preserved individuals. Fin rays on live or freshly-preserved specimens are primarily clear and lack yellowish color. Posterior rays of anal fin often speckled with melanophores. Most individuals examined had dark, black pigment on outer-most principal caudal-fin rays with a few individuals displaying melanophores on all fin rays. Juveniles exhibit more extensive pigmentation than adults. Maxillary and outer mental barbels pigmented black. Inner mental barbels white, cream, or clear; occasionally pigmented black.

No evidence of sexual dichromatism or dimorphism in any species of *Sorubim* has been identified or reported (Littmann 1998).

Similar species.—*Sorubim cuspicaudus* differs from all other species of *Sorubim* by

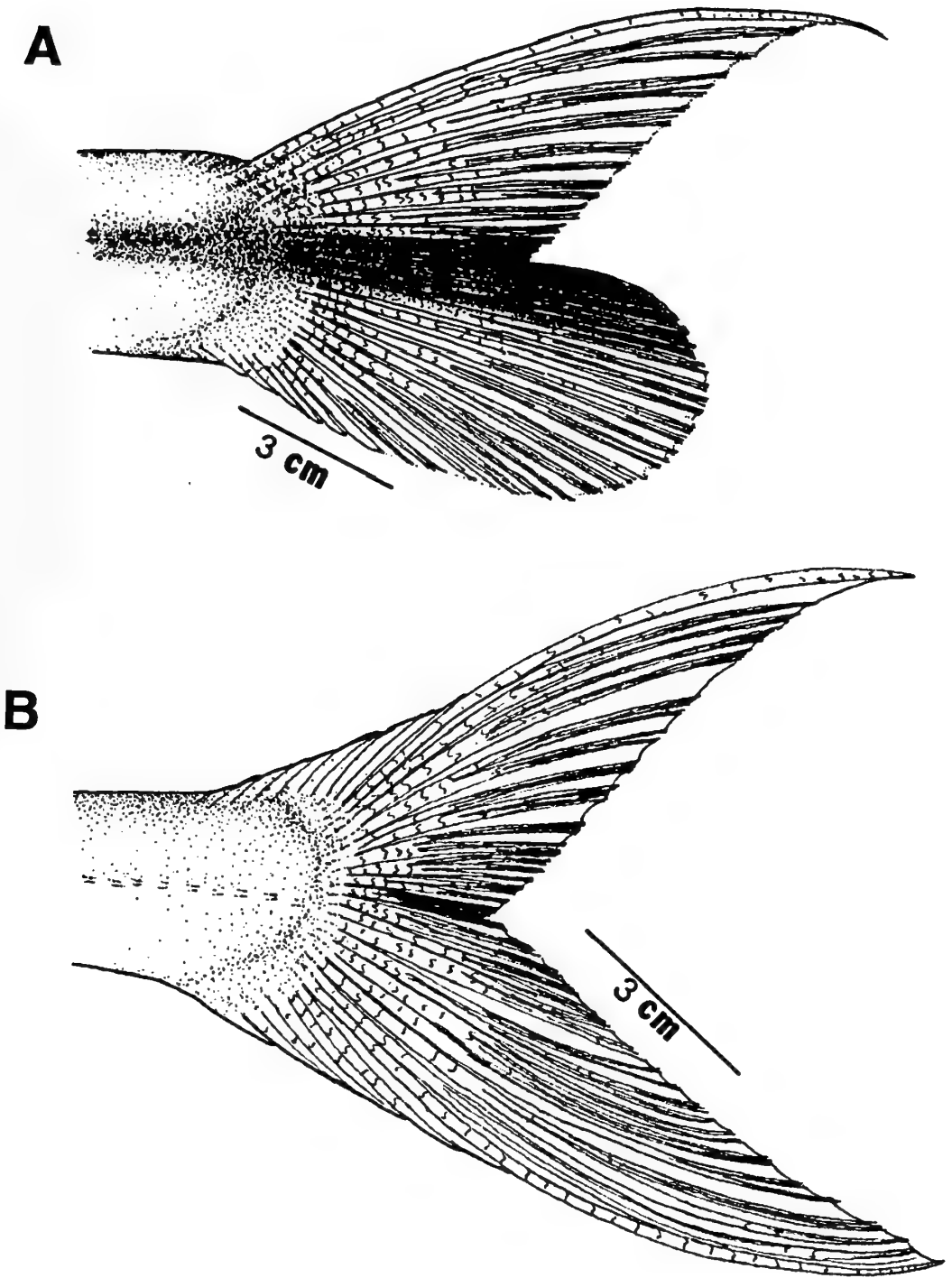


Fig. 2. Schematic illustration of the caudal fin of: A) all species of *Sorubim* except *S. cuspicaudus* n. sp. B) *S. cuspicaudus* n. sp. Illustration by Uriel Buitrago.

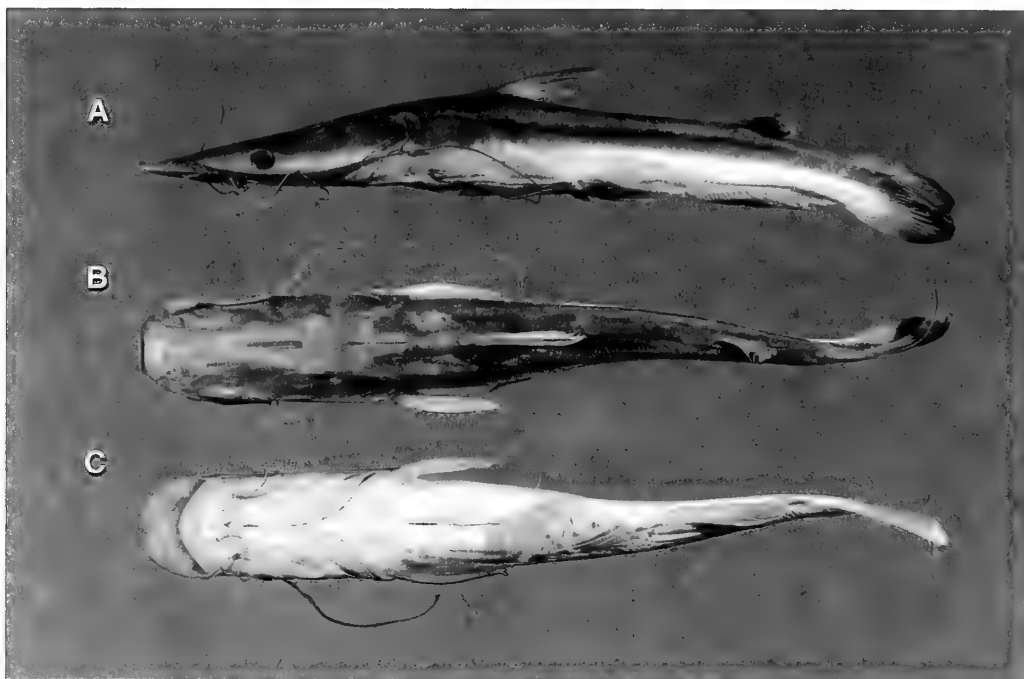


Fig. 3A-C. *Sorubim cuspicaudus* n. sp., holotype, FMNH 56223, 327 mm SL. Photographs by K. S. Cummings.

its unique caudal-fin shape (Fig. 2) and restricted distribution (Fig. 5). It further differs from *Sorubim* n. sp. by having 9 pectoral-fin rays (versus 8), a broader head (Table 9, Fig. 6), and vomerine tooth patches that are connected rather than separated (Fig. 4). Alternatively, the elongate and tapered body shape of *S. cuspicaudus* is similar to *Sorubim* n. sp. but has a relatively longer dorsal spine and dorsal-fin base (Table 10, Fig. 7). The elongate body shape of *S. cuspicaudus* is distinct from the more foreshortened shape of *S. lima* in PCA space (Fig. 7). The new species further differs from *S. trigonocephalus* by having a much shorter premaxillary tooth patch and a broad head that is not triangular in shape. As mentioned in the diagnosis, the combination of a broad head and elongate body is unique within *Sorubim*. *Sorubim lima* has a broad head and fairly stout body, while *Sorubim* n. sp. has both an elongate head and body.

Etymology.—The specific epithet cuspi-

(from *cuspis*), Latin for pointed, and *-caudus*, Latin for tail, refers to the diagnostic pointed caudal-fin lobes. The first part of the English common name “Trans-Andean” describes the general distribution of the fish; the remainder of the name (shovelnose catfish) is familiar to enthusiasts of the aquarium hobby, and differs from that recommended for *S. lima* (i.e., duckbill catfish) by Robins et al. (1991).

Distribution.—*Sorubim cuspicaudus* occurs west of the Andean Cordillera Oriental, and is endemic to three major drainage basins in northwestern South America: Lago Maracaibo, Ríos Magdalena and Sinu (Fig. 5). Miles (1947) reported that this species (as *S. lima*) was not found in the upper reaches of the Río Cauca in northern Colombia. The trans-Andean distribution pattern exhibited by species of *Sorubim* is repeated among other groups of lowland fishes that have been critically examined in recent years (see references in Vari (1988: 350) and Harold & Vari (1994:1)).

Table 2.—Measurements taken on the head and body for morphometric analysis. For diagram of landmark measurements see Figure 1.

Measurement	Truss coordinates
Standard length	1–15
Left anterior nostril to right anterior nostril	1–2
Left posterior nostril to right posterior nostril	3–4
Left anterior nostril to right posterior nostril	1–4
Right anterior nostril to left posterior nostril	2–3
Left anterior nostril to posterior right eye	1–6
Left anterior nostril to left posterior nostril	1–3
Right anterior nostril to posterior left eye	2–5
Left posterior nostril to posterior left eye	3–5
Right posterior nostril to posterior right eye	4–6
Posterior left eye to posterior right eye	5–6
Posterior left eye to right pectoral origin	5–8
Posterior left eye to left pectoral origin	5–7
Posterior right eye to right pectoral origin	6–8
Posterior right eye to left pectoral origin	6–7
Left pectoral origin to right pectoral origin	7–8
Snout length	9–10
Head length	9–11
Snout tip to dorsal origin	9–14
Snout tip to pectoral origin	9–12
Pectoral length at base	12–13
Dorsal length at base	14–15
Dorsal spine length	14–23
Pectoral origin to dorsal origin	12–14
Pectoral origin to dorsal insertion	12–15
Pectoral insertion to dorsal origin	13–14
Pectoral insertion to dorsal insertion	13–15
Posterior margin fleshy operculum to pelvic origin	11–16
Posterior margin fleshy operculum to pelvic insertion	11–17
Pelvic length at base	16–17
Pelvic origin to dorsal origin	16–14
Pelvic origin to dorsal insertion	16–15
Pelvic insertion to dorsal insertion	17–15
Pelvic insertion to adipose origin	17–19
Pelvic insertion to adipose insertion	17–20
Dorsal insertion to anal origin	15–18
Dorsal insertion to adipose origin	15–19
Pelvic insertion to anal origin	17–18
Anal origin to adipose origin	18–19
Anal origin to adipose insertion	18–20
Anal insertion to adipose origin	21–19
Anal insertion to adipose insertion	21–20
Anal fin length at base	18–21
Adipose fin length at base	19–20
Adipose insertion to anterior of caudal fin base	20–22
Anal insertion to anterior of caudal fin base	21–22

Natural history.—Little is known about the biology, life history, and ecology of *S. cuspicaudus*. In the middle and lower Río Magdalena, it occurs in relatively quiet open waters and bays or coves (Dahl 1971,

Valderrama & Zarate 1989), is intolerant of low salinity levels, and is not found in estuarine waters (Dahl 1971).

Adult *Sorubim cuspicaudus* undertake upstream spawning migrations called “su-

Table 3.—Measurements of the head expressed in percentage of standard length for 17 specimens of *Sorubim cuspicaudus*. For diagram of landmark measurements taken on head see Figure 1.

Measurement	Holotype	Mean	Range	SD
Standard length	327.00	288.7	139.0–420.0	71.60
Left anterior nostril to right anterior nostril	0.095	0.086	0.075–0.118	0.009
Left posterior nostril to right posterior nostril	0.080	0.073	0.067–0.100	0.008
Left anterior nostril to right posterior nostril	0.091	0.084	0.077–0.113	0.008
Right anterior nostril to left posterior nostril	0.091	0.084	0.077–0.113	0.009
Left anterior nostril to posterior right eye	0.197	0.188	0.175–0.245	0.016
Left anterior nostril to left posterior nostril	0.033	0.031	0.028–0.041	0.003
Right anterior nostril to posterior left eye	0.196	0.187	0.174–0.244	0.016
Left posterior nostril to posterior left eye	0.130	0.125	0.112–0.161	0.011
Right posterior nostril to posterior right eye	0.130	0.126	0.114–0.161	0.010
Posterior left eye to posterior right eye	0.147	0.141	0.127–0.183	0.014
Posterior left eye to right pectoral origin	0.221	0.212	0.195–0.275	0.019
Posterior left eye to left pectoral origin	0.156	0.148	0.136–0.194	0.014
Posterior right eye to right pectoral origin	0.156	0.149	0.137–0.194	0.014
Posterior right eye to left pectoral origin	0.221	0.212	0.194–0.275	0.019
Left pectoral origin to right pectoral origin	0.149	0.148	0.135–0.185	0.011

Table 4.—Measurements taken on the body expressed in percentage of standard length for 8 specimens of *Sorubim cuspicaudus*. For diagram of landmark measurements taken on body see Figure 1.

Measurement	Holotype	Mean	Range	SD
Standard length	327.00	259.4	139.0–327.0	55.55
Snout length	0.203	0.187	0.153–0.203	0.020
Head length	0.370	0.362	0.349–0.372	0.008
Snout tip to dorsal origin	0.463	0.446	0.432–0.463	0.011
Snout tip to pectoral origin	0.349	0.336	0.319–0.350	0.012
Pectoral length at base	0.033	0.034	0.031–0.037	0.002
Dorsal length at base	0.071	0.072	0.069–0.079	0.003
Dorsal spine length	0.164	0.167	0.153–0.173	0.006
Pectoral origin to dorsal	0.166	0.164	0.161–0.168	0.003
Pectoral origin to dorsal insertion	0.217	0.214	0.206–0.225	0.006
Pectoral insertion to dorsal origin	0.153	0.151	0.144–0.156	0.005
Pectoral insertion to dorsal insertion	0.194	0.189	0.181–0.196	0.006
Posterior margin fleshy operculum to pelvic origin	0.222	0.218	0.192–0.238	0.014
Posterior margin fleshy operculum to pelvic insertion	0.252	0.242	0.222–0.252	0.011
Pelvic length at base	0.030	0.032	0.027–0.038	0.003
Pelvic origin to dorsal origin	0.182	0.176	0.164–0.186	0.009
Pelvic origin to dorsal insertion	0.126	0.121	0.108–0.131	0.006
Pelvic insertion to dorsal insertion	0.134	0.130	0.117–0.137	0.008
Pelvic insertion to adipose origin	0.208	0.207	0.193–0.217	0.009
Pelvic insertion to adipose insertion	0.272	0.280	0.272–0.292	0.008
Dorsal insertion to anal origin	0.265	0.265	0.250–0.277	0.009
Dorsal insertion to adipose origin	0.268	0.262	0.250–0.274	0.008
Pelvic insertion to anal origin	0.157	0.169	0.156–0.197	0.016
Anal origin to adipose origin	0.111	0.108	0.097–0.116	0.005
Anal origin to adipose insertion	0.138	0.143	0.137–0.148	0.004
Anal insertion to adipose origin	0.143	0.144	0.139–0.147	0.003
Anal insertion to adipose insertion	0.073	0.072	0.068–0.076	0.003
Anal fin length at base	0.144	0.146	0.130–0.152	0.007
Adipose fin length at base	0.080	0.088	0.075–0.099	0.008
Adipose insertion to anterior of caudal fin base	0.165	0.159	0.145–0.166	0.007
Anal insertion to anterior of caudal fin base	0.120	0.122	0.118–0.130	0.005

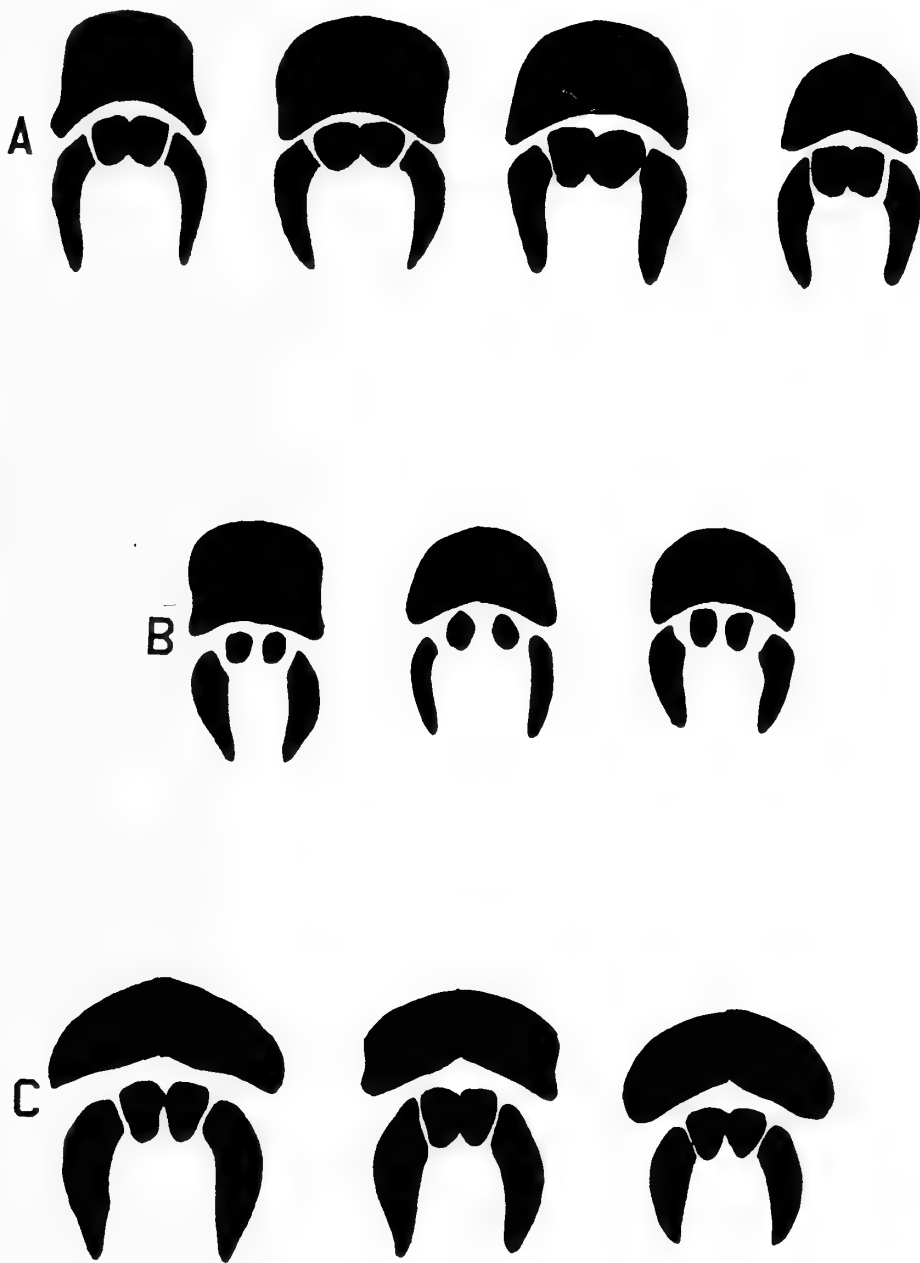


Fig. 4. Ventral view of tooth patterns on upper jaw of: A) *Sorubim lima*, B) *Sorubim* n. sp., and C) *S. cuspicaudus* n. sp.

biendas” during low-water periods (Valderrama & Zarate 1989). The onset of the rainy season initiates reproduction; larvae move downriver along the safety of the banks and littoral zones. Following spawning, adults return to feeding sites in the

floodplains during high-water periods called “bajanzas” (Valderrama & Zarate 1989). Hurtado (1972) reported that *Pseudoplatystoma fasciatum*, a putatively close relative of *Sorubim* spp. (fide Lundberg et al. 1991), spawn in the main channels of

Table 5.—Frequency distribution of number of gill rakers on first branchial arch in four species of *Sorubim* (Littmann 1998).

Species	13	14	15	16	17	18	19	20	21	22	23	33	34	35	36	37	n	mean	SD
<i>Sorubim lima</i>	3	27	35	72	22	1											160	15.54	1.008
<i>Sorubim</i> n. sp.			3	7	15	20	12	25	32	5	3						122	19.27	1.881
<i>S. cuspicaudus</i>			6	4	7	4											20	16.45	1.146
<i>S. trigonocephalus</i>	3																3	13.00	0.000

large rivers where strong currents carry larvae downstream. This behavior has been observed by Bayley (1973) who identified a mechanism for larval dispersal and the early migration pattern of *Prochilodus platensis* as being a drift organism (Valderrama & Zarate 1989). In the Río Madeira, other species of *Sorubim* have been observed migrating upstream through cataracts forming large schools with other members of Pimelodidae (e.g., *Pirirampus pirinampu* and *Calophysus macropterus*) (M. Goulding, pers. comm.). Many local fishermen and scientific researchers agree that such migratory schools may travel distances greater than 1000 km to reach an upstream destination at various times of the year depending on seasonal hydrological regimes. Several authors have expanded on the importance of flow regimes, horizontal movements of fish from flooded forests and “varzea” lakes, and other hydrological matters which directly relate to the success and diversity of the aquatic habitat and its surrounding ecosystem (Goulding 1980, Day & Davies 1986, Sioli 1984).

Fisheries.—Within the Río Magdalena watershed, *S. cuspicaudus* serves as an important food resource for both subsistence and commercial fishery operations (Dahl 1971, Valderrama & Zarate 1989, Galvis et al. 1997), occurring 40% of the time in collections made at 29 sampling sites in the Río Magdalena floodplain system (Kapetsky et al. 1977). Escobar et al. (1983) listed minimum and median catch lengths observed at first sexual maturity for several commercially important species, minimum SL for *S. cuspicaudus* was 319 mm for males and 299 mm for females. In a similar report by Arboleda et al. (1984), median catch lengths were approximately 40–48 cm. Unfortunately, fishing pressures on targeted populations have increased because of the use of better equipment (i.e., seine nets), causing conflicts with cast-net fisherman (Valderrama & Zarate 1989), and undoubtedly elevating the ease of harvest for some species. *Sorubim cuspicaudus* is re-

Table 6.—Frequency distribution counts of vertebrae (including fused preural centrum + ural centrum but not fused elements of Weberian complex) for four species of *Sorubim* (Littmann 1998).

Species	44	45	46	47	48	52	n	mean	SD
<i>Sorubim lima</i>	1	6	17	11	1		36	46.59	0.590
<i>Sorubin</i> n. sp.	2	3	3				8	45.13	0.835
<i>S. cuspidatus</i>		4	1				5	45.20	0.447
<i>S. trigonocephalus</i>						1	1	52.00	0.000

ported to attain a SL of 800 mm or more (Galvis et al. 1997, D. Taphorn, pers. comm.).

Bayley and Petrere (1989) indicated that the potential overharvest of at least one pimelodid species, *Pseudoplatystoma fasciatum*, is imminent. As of 1989, the establishment of temporary fishing bans on this species were considered because of the repeated occurrence of smaller catch sizes relative to the median size reported at maturity. Regulations could have direct impacts on populations of *S. cuspidatus*. Temporary fishing bans on large catfishes have forced fishermen to bring larger quantities

of some smaller species to market that have not been previously utilized commercially. Many authors (Bayley 1981, Bayley & Petrere 1989, Novoa 1989, M. Goulding, pers. comm.) have noted that the majority of fish species in tropical South America are indeed underutilized as food. Thus, the continued collection of annual catch and harvest data are needed for future monitoring of *S. cuspidatus* to help insure its sustainability as a valuable fishery resource.

Biogeography.—Eigenmann (1920) was apparently the first to recognize a “horizontal distribution of fishes,” or close similarity in fish faunal composition between the

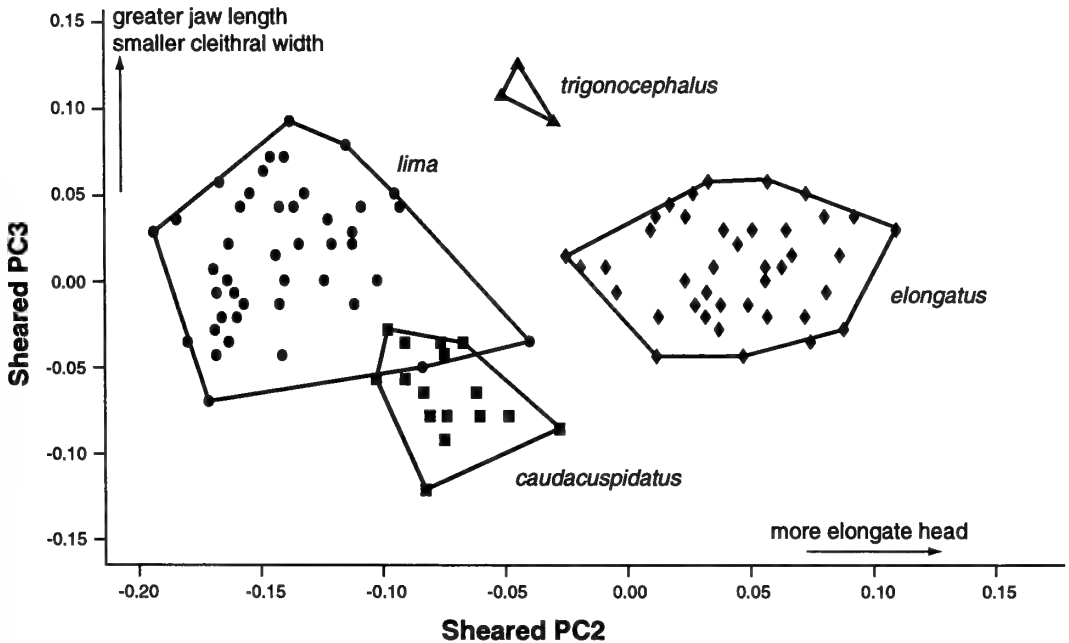


Fig. 5. Morphometric scores of head measurements on sheared PC axes 2 and 3 for 45 specimens of *Sorubim lima*, 43 specimens of *Sorubim* n. sp., 17 specimens of *S. cuspidatus* n. sp., and three specimens of *S. trigonocephalus*.

Table 7.—Frequency distribution of number of pectoral fin rays in species of *Sorubim* (Littmann 1998).

Species	7	8	c	9	10	n	mean	SD
<i>Sorubim lima</i>		4		146	10	160	9.038	0.294
<i>Sorubim</i> n. sp.	7	112		3		122	7.967	0.288
<i>S. cuspicaudus</i>		1		19		20	8.950	0.223
<i>S. trigonocephalus</i>				3		3	9.000	0.000

Magdalena and Orinoco rivers. He included a list of genera and species found on both sides of the Cordillera of Bogota, concluding that the fish fauna of the Magdalena basin was derived “in small part from the ocean and in larger part from Central Amer-

ica,” and that “most of it had an origin in common with that of the Orinoco basin fauna” to the east (Eigenmann 1920, p. 34). One interesting conclusion noted by Eigenmann was that, “the stripes found on the large catfish, the bagre tigre (*Pseudoplatys-*

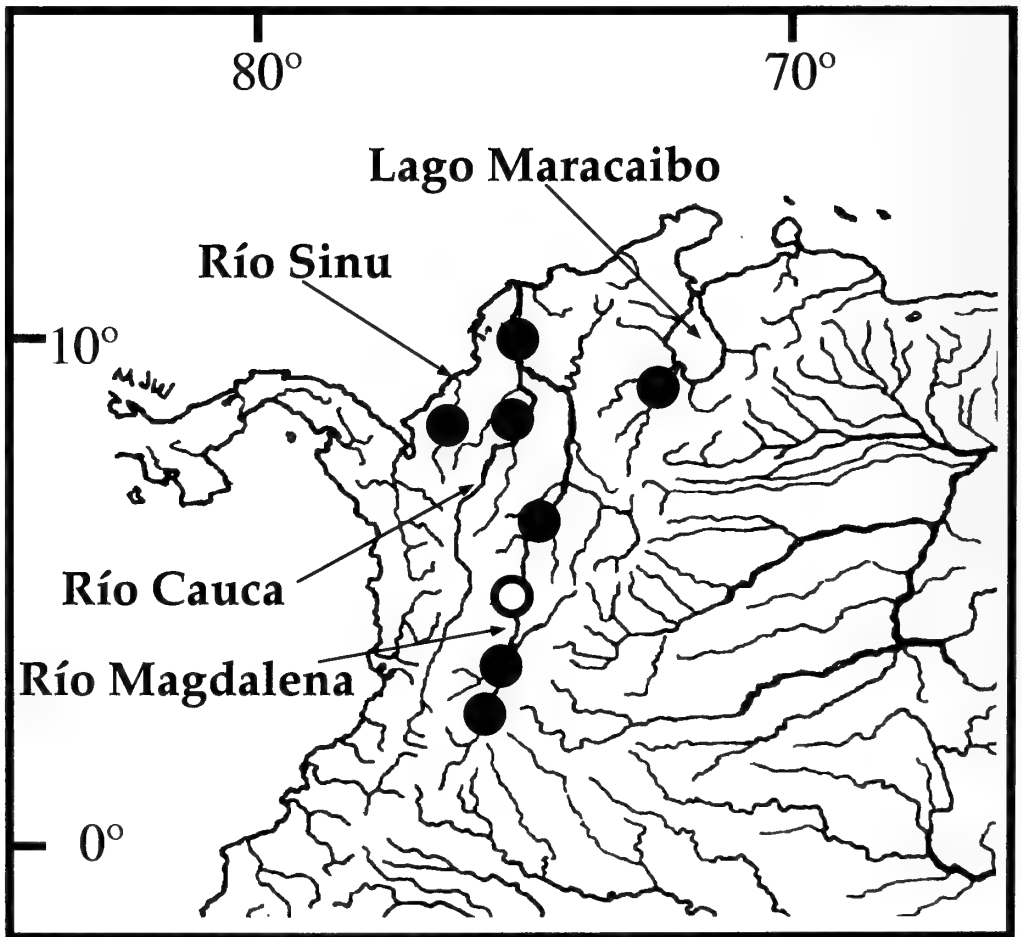


Fig. 6. Record stations in South America of *Sorubim cuspicaudus* n. sp. Open symbol is type locality in Río Magdalena, Puerto Soplaviento, Colombia. Dots may represent more than one lot or locality. Base map by M. Weitzman.

Table 8.—Frequency distribution of number of anal fin rays in species of *Sorubim* (Littman 1998).

Species	18	19	20	21	22	23	24	25	n	mean	SD
<i>Sorubim lima</i>		18	63	66	13				160	20.46	0.800
<i>Sorubim</i> n. sp.			5	35	47	25	8	1	121	21.96	1.004
<i>S. cuspicaudus</i>	1	9	7	2	1				20	19.65	0.933
<i>S. trigonocephalus</i>		1			2				3	21.00	1.732

toma sp.) have persisted during the entire time since the Cordillera of Bogota began to be an effective barrier against the intermigration of the fishes of the two sides." Additional support for this hypothesis can be found in Lundberg (1998), Lundberg et al. (1986) and Lundberg & Chernoff (1992). The occurrence of an endemic species of *Sorubim* west of the Andes Cordillera Oriental in the Magdalena basin is consistent with a pattern repeated among several other lowland fish groups that also have representatives in the Amazon or Orinoco basins (Vari 1988:350, Harold & Vari 1994: 1).

Additionally, the Maracaibo basin and Magdalena drainages are separated from each other by the Sierra de Perija, negating any direct contact between drainage populations of the same species. Historically, a

paleo-Amazon/Orinoco river flowed north, draining into the Caribbean via Lago Maracaibo, a time when no major land barriers existed to divide the area (Lundberg et al. 1998, others). During the late Miocene (11–8 Ma), major uplift caused vicariant events, completely separating ancestral ranges of species into what is now the Lago Maracaibo basin, the Río Magdalena basin, and Pacific coastal drainages in northwestern Colombia.

The presence of *S. cuspicaudus* in both the Magdalena and Maracaibo basins but not east in the western Orinoco basin provides us with a glimpse into their evolutionary history but does not offer the total story. We suggest that ancestral populations of *S. cuspicaudus* were separated from the Orinoco basin species of *Sorubim* (i.e., *S. lima*) by tectonic events giving rise to the

Table 9.—Sheared principal component loadings for morphometric variables taken from the head of 45 *Sorubim lima*, 42 *Sorubim* n. sp., 16 *S. cuspicaudus*, and 3 *S. trigonocephalus*. Highest loading factors are in bold type.

Measurement	Sheared PC 2	Sheared PC 3
Standard length	0.198	0.139
Left anterior nostril to right anterior nostril	-0.328	0.075
Left posterior nostril to right posterior nostril	-0.292	0.030
Left anterior nostril to right posterior nostril	-0.247	0.097
Right anterior nostril to left posterior nostril	-0.246	0.098
Left anterior nostril to posterior right eye	0.050	0.211
Left anterior nostril to left posterior nostril	0.044	0.454
Right anterior nostril to posterior left eye	0.052	0.212
Left posterior nostril to posterior left eye	0.196	0.301
Right posterior nostril to posterior right eye	0.195	0.279
Posterior left eye to posterior right eye	-0.169	-0.288
Posterior left eye to right pectoral origin	0.154	-0.308
Posterior left eye to left pectoral origin	0.462	-0.154
Posterior right eye to right pectoral origin	0.475	-0.157
Posterior right eye to left pectoral origin	0.151	-0.308
Left pectoral origin to right pectoral origin	-0.220	-0.411

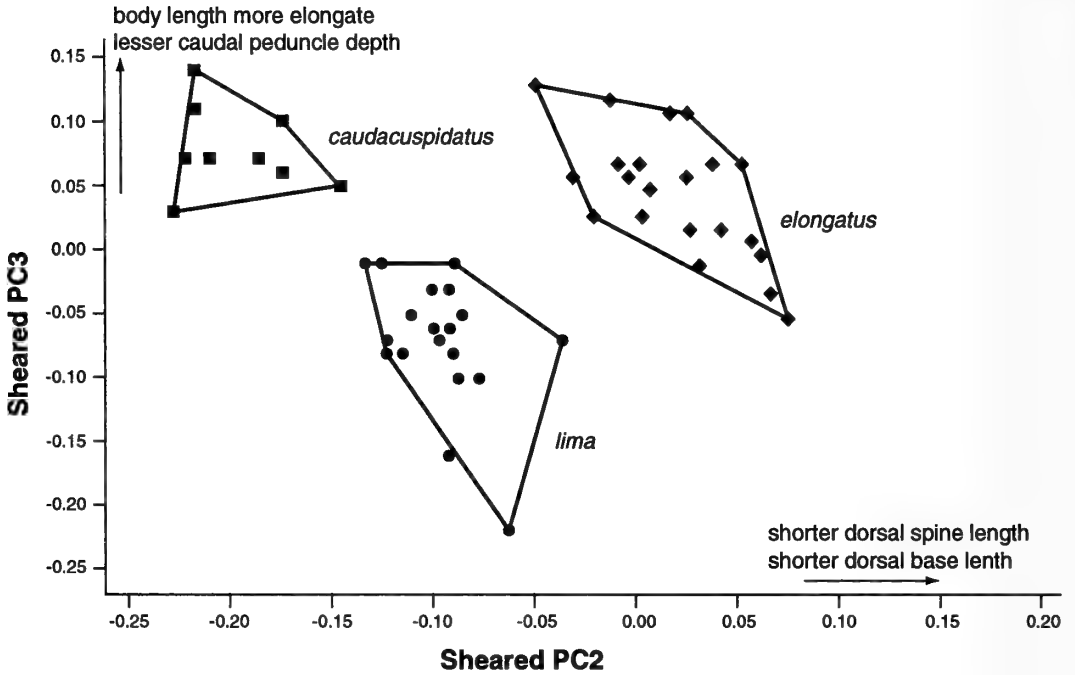


Fig. 7. Morphometric scores of body measurements on sheared PC axes 2 and 3 for 19 specimens of *Sorubim lima*, 21 specimens of *Sorubim* n. sp., and 9 specimens of *S. cuspidatus* n. sp.

Oriental mountain range east of Lago Maracaibo (Lundberg et al. 1998, Galvis et al. 1997). At a minimum, *S. cuspidatus* would have diverged from paleo-Amazon/Orinoco ancestors since the uplift of the Andean Cordillera Oriental during the late Miocene but before geological events leading to the uplift of the Sierra de Perija.

Currently, there are no published hypotheses to explain the historical relationships of *Sorubim*. Vari & Weitzman (1990) discussed the need to study phylogenetic relationships of fishes to develop historical biogeographic hypotheses. They stated that, "... the poor understanding of the recognizable species in South American freshwaters is compounded by the lack of sampling of the fauna." At the present time, preliminary morphological data still under preparation by the first author and collaborators show a sister-species relationship between *S. cuspidatus* and *S. lima*. These findings, including a phylogenetic revision

of *Sorubim*, will be presented in a later paper.

Nontype material.—The following list of material provides detailed locality descriptions of specimens examined for this paper. Comparative material of the other three species of *Sorubim* are listed in Littmann (1998); these data may be obtained from the authors. Specimens whose SL are marked with an asterisk represent those individuals used for the morphometric analyses.

Atlantic Ocean drainage. Colombia. Río Magdalena drainage. BMNH 1900.1.30.12–13, 2:299–353 mm SL, Baranquilla. 30 Jan 1900, Thomson. BMNH 1947.7.1.197, 157 mm SL, Baranquilla. 1 Jul 1947, Miles. CAS 149475, 175 mm SL*, Bolivar, Río San Jorge, San Marcos. Jun 1955, G. Dahl. CU 47915, 483 mm SL, Santander; Lake San Sylvestre by city of Barranca-Bermeja. 7 Sep 1962, J. D. Archer. FMNH 56220, 367 mm SL*, Honda. 28 Jan 1912, C. H.

Table 10.—Sheared principal component loadings for morphometric variables taken from the body of 19 *Sorubim lima*, 16 *Sorubim* n. sp., 8 *S. cuspidus*. Highest loading factors are in bold type.

Measurement	Sheared PC 2	Sheared PC 3
SL	0.198	0.111
Snout length	-0.006	-0.156
Head length	0.019	0.086
Snout tip to dorsal origin	0.072	0.117
Snout tip to pectoral origin	0.021	0.126
Pectoral length at base	-0.223	0.022
Dorsal length at base	-0.543	-0.217
Dorsal spine length	-0.357	-0.038
Pectoral origin to dorsal origin	0.012	-0.014
Pectoral origin to dorsal insertion	-0.056	-0.036
Pectoral insertion to dorsal origin	0.040	-0.030
Pectoral insertion to dorsal insertion	-0.030	-0.061
Posterior margin fleshy operculum to pelvic origin	0.138	0.108
Posterior margin fleshy operculum to pelvic insertion	0.089	0.075
Pelvic length at base	-0.288	-0.196
Pelvic origin to dorsal origin	-0.006	-0.128
Pelvic origin to dorsal insertion	0.181	-0.188
Pelvic insertion to dorsal insertion	0.215	-0.167
Pelvic insertion to adipose origin	0.198	0.087
Pelvic insertion to adipose insertion	0.090	0.208
Dorsal insertion to anal origin	0.156	0.145
Dorsal insertion to adipose origin	0.107	0.338
Pelvic insertion to anal origin	0.090	0.342
Anal origin to adipose origin	0.228	-0.271
Anal origin to adipose insertion	0.035	-0.082
Anal insertion to adipose origin	0.063	-0.068
Anal insertion to adipose insertion	0.264	-0.367
Anal length at base	0.007	-0.118
Adipose length at base	-0.186	0.400
Adipose insertion to anterior of caudal fin base	-0.037	-0.113
Anal insertion to anterior of caudal fin base	-0.269	0.165

Eigenmann. FMNH 57701, 2:305–311 mm SL*, at Puerto Berrio, elevation 429'. 24 Jan 1912, C. H. Eigenmann. FMNH 88180, 3:257–355 mm SL*, at Soplaviento. No date, C. H. Eigenmann. NRM 16254, 107 mm SL, Lower Río Magdalena drainage. No date, Olsson & Ragnar, of Centro de Investigacion de Ciencias Marinas, Cartagena. Río Sinu. NRM 14812, 239 mm SL*, Cordoba, Alto de Quimari, elevation 500 m. Apr 1949, K von Sneidern et al. Venezuela. Lago Maracaibo basin. MBUCV-V-13536, 5:345–380 mm SL, Estado Zulia. 23 Jan 1963, collector unknown.

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A new species of pikeblenny, *Chaenopsis megalops*, from the southwestern Caribbean (Teleostei: Chaenopsidae)

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Abstract.—A new species of blennioid fish, *Chaenopsis megalops*, is described from two specimens trawled in 60–72 m off Colombia. Previously confused with *C. resh* Robins & Randall, 1965, its presumed closest known congener in the western Atlantic, the new species differs in pigmentation pattern, morphometrics, number of vertebrae, gill rakers, and supraorbital pores. It is the only Atlantic species of *Chaenopsis* with a single supraorbital pore on each side of the head. The authorship of *Chaenopsis* Gill, 1865, and its type species, *C. ocellata* Poey in Gill, 1865, are discussed, as is the publication date of three Gill papers.

The blennioid genus *Chaenopsis* Gill, 1865 is represented by two poorly defined species groups (Böhlke 1957). Western Atlantic members of the short-bodied, low count (or *coheni*) group, which have 44–47 total dorsal-fin elements and 29–31 segmented anal-fin rays, were treated by Hastings & Shipp (1980) and include two named species, *Chaenopsis roseola* Hastings & Shipp, 1980 and *C. stephensi* Robins & Randall, 1965. The taxonomic status of one specimen collected in 275 meters on Arrowsmith Bank off Yucatán, Mexico is problematical (Hastings & Shipp 1980), and is either an undescribed species or the second known specimen of *C. stephensi*. Robins and Randall (1965) reviewed the Atlantic members of the long-bodied, high count (or *ocellata*) group, which have 51–57 total dorsal-fin elements and 33–37 segmented anal-fin rays, including *Chaenopsis ocellata* Poey, 1865, *C. limbaughi* Robins & Randall, 1965 and *C. resh* Robins & Randall, 1965.

The new species described herein was first reported by Robins (1971), who identified it as *Chaenopsis resh* despite some obvious differences in color pattern. Color pattern differences were attributable either

to the greater depth of capture of the two Colombian specimens (60–72 m, versus less than 5 m for all other specimens) or to their larger sizes, or both. These specimens also were reported to have fewer gill rakers on the first arch, 14 or 15 versus 19–27 in the five type specimens of *C. resh*, but because gill rakers had not previously been studied in *Chaenopsis* the significance of the discrepancy was difficult to assess. Acero (1987) considered the two Colombian specimens to represent an undescribed species, which he contrasted with *C. resh* in his key to western Atlantic species of *Chaenopsis*. No additional material of this relatively deep-water pikeblenny has become available in over three decades, and I describe it now to make the scientific name available and to further document the biodiversity of the mostly New World family Chaenopsidae. *Neoclinus*, the only chaenopsid genus not restricted to the western Atlantic or eastern Pacific oceans, is represented by nine species (Fukao 1987), three from California, five from Japan, and one from Taiwan.

Although most workers have recognized the Chaenopsidae (tube blennies) as a distinctive group of blennioid fishes, there has

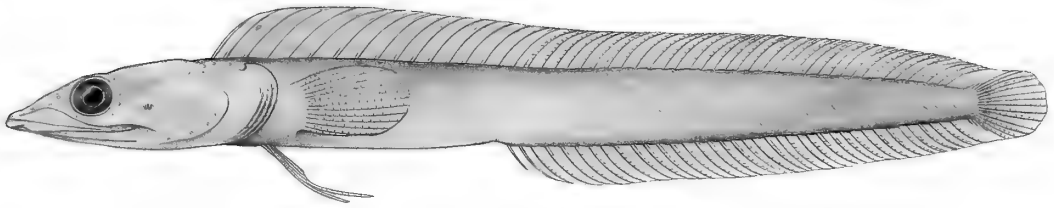


Fig. 1. *Chaenopsis megalops*: holotype, UF 226440, male, 102.3 mm SL, off Gulf of Uraba, S. of Punta Caribana, Colombia; row of nine double spots along side behind pectoral fin which was originally present no longer evident (see discussion of color pattern in species description). Drawn by Tracy D. Pedersen.

been little agreement on familial limits and relationships of the family. I follow Hastings & Springer (1994) who present evidence for recognition of an expanded Chaenopsidae (sensu Stephens 1963), including *Stathmonotus*, *Mccoskerichtys*, and *Neoclinus*. As here recognized, the family consists of 14 genera and at least 80 species.

Methods

Methods follow Hastings & Shipp (1980), except head pore terminology which agrees with that of Hastings & Springer (1994). MP index equals $10 \times$ distance between mandibular pores 3 and 2 divided by the distance between mandibular pores 1 and 2 (Robins & Randall 1965). In the description, counts for the paratype are given in parentheses if different from the holotype, as are measurements of the paratype. All measurements other than standard length (SL) are expressed as a percentage of SL. Collection data for comparative material are abbreviated and the number of specimens, followed by size in mm SL, is given in parentheses. Institutional or collection abbreviations are as follows: ANSP, Academy of Natural Sciences of Philadelphia; UF, Florida Museum of Natural History, Gainesville; UMML, University of Miami Marine Laboratory (collection transferred to UF); USNM, National Museum of Natural History, Washington, D.C.

Chaenopsis megalops, new species

Figs. 1, 2a

Chaenopsis resh (not Robins & Randall).

Robins, 1971:180 (misidentification; two specimens from western Colombian Caribbean; comparison and meristic data); Palacio, 1974:69 (listed; same specimens as Robins 1971).

Chaenopsis sp. Acero P., 1987:7 (underscribed species; diagnosis; in key).

Holotype.—UF 226440 (formerly UMML 26440), 102.3 mm SL, off Gulf of Uraba, S. of Punta Caribana, Colombia, 08°51'12"N, 77°01'36"W to 08°49'06"N, 77°04'06"W, 72 m, 10 ft otter trawl, 17 Jul 1966, R/V *Pillsbury* sta. 402.

Paratype.—ANSP 138519 (formerly UMML 28600), 89.2 mm, off Cartagena, Colombia, 10°20'42"N, 75°39'06"W to 10°18'24"N, 75°38'06"W, 60–66 m [not 73–79 m as reported by Robins (1971)] 10 ft otter trawl, 1 Aug 1968, R/V *Pillsbury* sta. 796.

Diagnosis.—A long-bodied species of *Chaenopsis* with a relatively high number of vertebrae (57), dorsal-fin elements (XVII–XVIII, 35–36; 53 total), and anal-fin elements (II, 36). Nine pairs of double spots present along side behind pectoral fin. Males with small black spot on dorsal fin membrane between spines 2 and 3, and blackish mark on cheek, if present, consisting of small blotch about equal to pupil diameter. A single supraorbital pore on each side of median commissural pore.

Description.—Eighteen precaudal and 39

caudal vertebrae; last pleural rib on 11th vertebra. Dorsal fin low in males, with XVII-(XVIII) spines and (35)-36 unbranched rays, 53 total elements. Anal fin with II spines and 36 unbranched rays. Last dorsal- and anal-fin rays broadly connected to caudal fin by a membrane. Pectoral fin rounded, extending about half distance to level of anus, with 13 unbranched rays. Pelvic fin I, 3; first and second rays elongate, third short and inconspicuous (about four times as long as the short pelvic spine). Caudal fin rounded, with 13 segmented rays and 4 upper and 3 lower procurrent rays. Gill rakers 4 + 10-(11) on first arch.

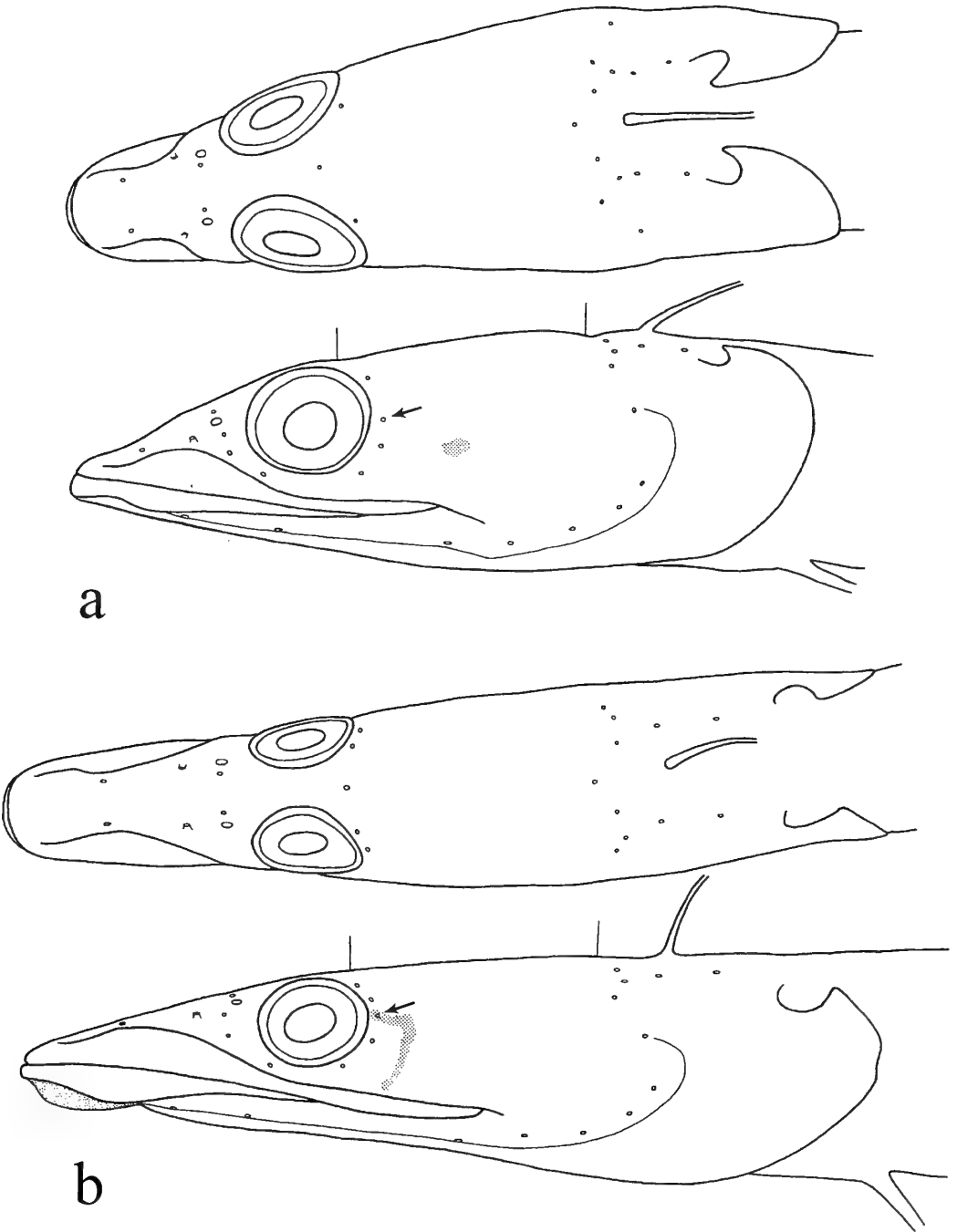
Snout bluntly U-shaped when viewed from above, with forehead sloping when viewed from side. Lower jaw projecting slightly, visible from above. Dewlap on chin poorly developed, not evident in lateral view. Anterior nostril a short tube, its length about 1/3 minimum width of bony interorbital. Posterior nostril with a slightly raised rim. Tongue bluntly rounded, extending only slightly beyond anterior end of palatine tooth row. Median, round fleshy papilla present just behind anterior villiform teeth of either jaw. As noted by Böhlke (1957) in his description of *Chaenopsis coheni*, the papillae of the two jaws are nearly opposed and possibly make contact with each other when the mouth is closed. The lower jaw is greatly expanded distally, then abruptly constricted with the rami straight and almost parallel, similar to the condition described by Rosenblatt & McCosker (1988:108) for species of *Acanthemblemaria*. The following tooth counts are based only on the paratype because the lower jaw of the holotype is strongly locked preventing a clear view of the dentition. Palatine with a single row of 27 bluntly rounded teeth; 16 relatively large teeth anteriorly followed by a series of much smaller teeth. Vomerine teeth absent. Upper jaw anteriorly with an outer row of 17-18 moderately large spatulate incisors (a few of the lateral ones almost conical in holotype) that are continuous posteriorly with a straight

row of 29-30 incisors that become progressively smaller and terminate below anterior margin of orbit. A patch of small villiform teeth behind anterior incisors. Dentition of lower jaw similar to that of upper except about 11 incisors anteriorly and 32-33 uniformly short incisors in straight posterior row.

Cephalic sensory pores as illustrated in Fig. 2a: nasal 1; anterofrontal 1; anterior infraorbitals 3; posterior infraorbitals 3; supraorbital 1; median commissural 1; median supratemporal 1; lateral supratemporal 1; posttemporal 4; mandibular 4 (first pore not shown in figure); common pore (between anguloarticular and preopercle) 1; preopercle 4. Second mandibular pore slightly closer to first than third, MP index 10.1 (10.2).

Measurements.—Predorsal length 22.3 (23.1); preanal length 43.2 (50.3); body depth at dorsal-fin origin 8.2 (8.1); body depth at anal-fin origin 6.8 (6.4); caudal peduncle depth 3.0 (3.4); caudal peduncle length 2.5 (2.7); 3rd dorsal-fin spine length 10.2 (13.0); longest pectoral fin ray 11.6 (12.9); 1st pelvic-fin ray length 11.0 (11.5); 2nd pelvic-fin ray length 15.9 (18.2); head length 28.2 (29.6); head depth 8.3 (9.2); head width 8.1 (7.7); snout length 6.2 (6.6); pigmented eye diameter 4.8 (5.5); least bony interorbital width 1.5 (1.5); upper jaw length 13.4 (15.1).

Color pattern in alcohol.—Both specimens are badly faded after many years of storage in isopropanol (now changed to ethanol) and the illustration of the holotype depicts its present appearance. The following observations, made before the specimens had faded, are those of Robins (1971): "Both specimens are much less boldly marked than Venezuelan males [= *C. resh*] and have 9 pairs of double spots along the side behind the pectoral fin, and one black ovoid mark above the corner of the mouth at the level of the lower edge of the eye. One male has a second spot along the posterior rim of the eye. Pigmentation in the dorsal fin fits the original description, especially with regard to the spot being be-



a

b

Fig. 2. Dorsal and lateral views of head in two species of *Chaenopsis*: a, *C. megalops*, holotype, UF 226440, 102.3 mm SL; b, *C. resh*, holotype; ANSP 102730, 75.2 mm SL. Arrows indicate position of uppermost posterior infraorbital pore in lateral views (infraorbital pores not shown in dorsal views); vertical lines extending from dorsum of head in lateral views indicate positions of median commissural and median supratemporal pores, respectively.

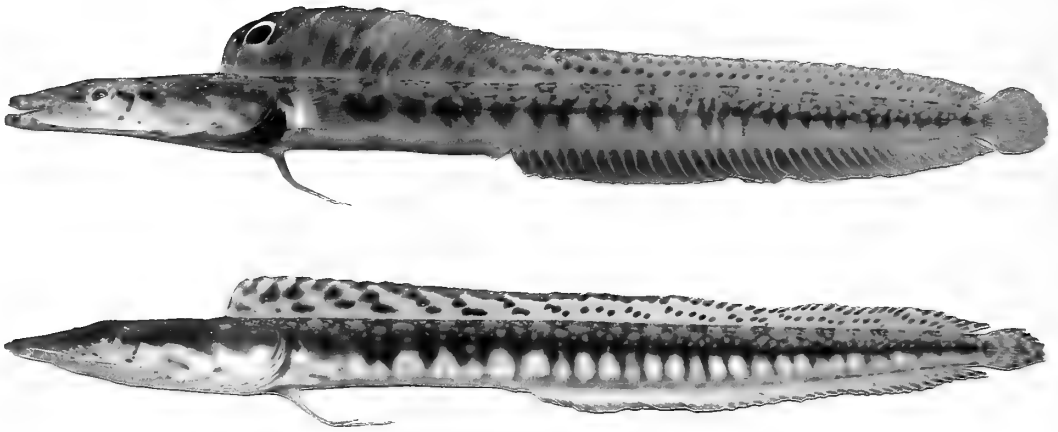


Fig. 3. *Chaenopsis resh*: upper: ANSP 102730, male, 75.2 mm SL, holotype; lower: ANSP 102731, female, 72.4 mm SL, paratype; both from Cubagua Island, Venezuela. After Robins and Randall (1965).

tween spines 2 and 3 but the pattern is much duller." The inner membrane connecting the dentary and maxilla posteriorly is darkly pigmented, and the underlying dark coloration makes the thin maxilla (which is not exposed laterally but slips into a fold of skin below and posterior to the orbit) appear to be partially dark. Branchiostegal membranes are also darkly pigmented in both specimens.

Comparisons.—*Chaenopsis megalops* differs from all other western Atlantic species of *Chaenopsis* in having one (versus two) supraorbital pores (Fig. 2a) on each side of the median commissural pore. Of the high-count Atlantic species, *C. megalops* is most similar to males of *C. resh* in having a black spot or blotch between dorsal-fin spines 2 and 3 (between spines 1 and 2 in males of *ocellata* and *limbaughi*). In the previously described species the spot is more prominent, and either has a complete (*resh*) or partial pale border (*ocellata* and *limbaughi*). *Chaenopsis resh* (Fig. 3) further differs from *C. megalops* in having a dark postorbital mark shaped like the Hebrew letter resh (ר); rows of dark spots extending entire length of soft portion of dorsal fin (forming diagonal rows in females); smaller eye diameter 2.0–4.3 (versus 4.8–5.5% SL); more precaudal (20 versus 18) and total vertebrae (58–59 versus 57), more

total dorsal-fin elements (54–55 versus 53), and more gill rakers on the first arch (19–27 in 5 specimens 50–75.2 mm SL versus 14 or 15).

Robins (1971) confused the new species with *C. resh* primarily because of their similar fin-ray numbers, position of the spot in the spinous dorsal fin, and "the dark spot on the cheek, which, although of different form, seems to be the remnant of the resh-shaped mark that earned the species its name."

Etymology.—The specific name *megalops* is from the Greek *megas* (large) and *ops* (eye), in reference to the relatively large eyes of this pikeblenny.

Comments.—Hastings & Shipp (1980) reported and illustrated *Chaenopsis roseola* as having five infraorbital pores and three supraorbital pores. Examination of the paratypes of *C. roseola* reveals that the species has only two supraorbital pores (on each side), the uppermost pair of posterior infraorbital pores having been erroneously considered to be supraorbital pores. All species of *Chaenopsis* that I have examined have six infraorbital pores, and none has more than two supraorbital pores.

In his Catalog of Fishes, Eschmeyer (1998:1885) gave the authorship of *Chaenopsis* and its type species, *Chaenopsis ocellatus*, as Poey in Gill, 1865. However, in

his species account Eschmeyer (1998:1223) attributed authorship of *Chaenopsis ocellata* to "Gill (ex Poey)," in contrast to previous authors (e.g., Jordan & Evermann 1898, Jordan et al. 1930, Böhlke 1957, Stephens 1963, Robins & Randall 1965, Robins et al. 1991, Springer & Orrell 1996) who credit the species to Poey.

There needs be consensus on the authorship of these taxa, and because Gill's (1865c) paper is not readily available to most readers, discussion of it is included here. The paper begins with "Fam. Chaenopsidae" (Gill is unquestionably the author of the new family name), followed by descriptions of the genus and species under the headings "Genus *Chaenopsis*, Poey," and "*Chaenopsis ocellatus*, Poey Ms." Gill's (1865b) description of *Plagiotremus* Gill, 1865, which was published in the Annals immediately preceding his chaenopsis paper, has the identical style and character order of the *Chaenopsis* description. Thus, I agree with Jordan & Evermann (1898: 203) who credit Gill as the author of the genus. Additional support for that attribution is that, unlike Poey, Gill used the suffix *opsis* for other generic names that he established. The brief description of *C. ocellatus* includes life color observations, and states that a single specimen [USNM 8007] "was obtained by Prof. Poey at Matanzas, and kindly forwarded for my examination." Immediately following the quoted statement, Gill mentioned that a small specimen of *Callionymus* was received with the *Chaenopsis*. He then very briefly described *Callionymus pauciradiatus* [now recognized as *Diplogrammus pauciradiatus* (Gill 1865)] but did not credit the species to Poey. I conclude that Poey should be recognized as the author of *C. ocellatus* because: the contents of the description (life color observations) contain direct evidence that only he could have provided; the inclusion of "Poey Ms." after the species name suggests (although it is not conclusive evidence) that Poey recognized the uniqueness of the specimen and had provided Gill with a description of it in

a letter; and crediting Poey with the description is consistent with majority usage and will cause the least confusion.

Even the date of publication of Gill's chaenopsis paper (article 15), is unclear. In the mid-1800s, journals were printed in sections (signatures), and distribution of separates or reprints of individual articles often preceded issuance of an entire volume. The title page for volume 8 of the Annals is dated 1867, and the signature in which the description appears is dated April 1865, although May 1865 is printed at the bottom of page 139. Most authors have overlooked the illustration of *C. ocellata* (Pl. 3, Fig. 3), which is grouped with other plates at the end of the volume; Figures 1–2 on the same plate are of *Plagiotremus spilistius* Gill, 1865. An explanation for plate 3 appears on page 300 of the signature dated April 1866. Dall (1916) considered 1865 to be the year of publication of Gill (1865a) and, presumably because of the later signature date of plate 3, 1866 for Gill (1865b, 1865c); Dean (1916) made no attempt to provide definitive date determinations and gave the range 1863–1867 for all three Gill papers. The Smithsonian Institution has separates of all three articles, bound together as a single reprint. Plate 3 was not included as part of the reprint but was stapled to the legend sheet as a separate item. On each journal article "Read April 8, 1865" appears below Gill's name, but "Reprinted from the Annals of the Lyceum of Natural History in New York, vol. viii., May, 1865" was substituted on the reprints. Because the page layouts and pagination are the same, it is obvious that all three papers were read, printed, and issued together both as journal articles and as reprints. The upper right corner of the first page of the combined reprint has what appears to be a library stamp that is clearly dated "6 JUL [sic] 65." I conclude from this that the text of all three Gill articles was distributed (published) no later than 6 July 1865, and that plate 3 was published later, probably in 1866.

Comparative material.—*Chaenopsis ocel-*

lata: UF 202319 (1, 67), Florida, Dade Co.; UF 202320 (1, 61), Florida, Dade Co.; UF 202376 (1, 71), Florida, Dade Co.; UF 208723 (1, 92), Florida, Dade Co.; UF 212553 (1, 48), Florida Keys, Islamorada; UF 217843 (1, 45), Florida Keys, Alligator Light; UF 224612 (1, 66), Florida, Dade Co.; UF 229747 (1, 81), Florida, Dade Co.; USNM 8007 (1, 110), holotype, Cuba, Mantanzas. *Chaenopsis limbaughii*: UF 202377 (2, 59–65), Virgin Is.; UF 205624 (1, 70), Virgin Is.; UF 211240 (3, 28–58), Virgin Is.; UF 211241 (1, 72), Virgin Is.; UF 211242 (2, 45–46), Virgin Is.; UF 214678 (3, 50–57.5), Virgin Is.; UF 205980 (2, 28–59), Bahamas, Exuma Cays; UF 217361 (1, 40), Puerto Rico, Mayaquez; UF 217362 (1, 46), Puerto Rico, Culebra Is. *Chaenopsis resh*: ANSP 102730 (1, 75.2), holotype, Cubagua Island, Venezuela; UF 217219 (2, 50–51), taken with the holotype. *Chaenopsis roseola*: UF 27444 (1, 41), 30 km SW of Panama City Beach, Florida; UF 27445 (1, 30), 60 km SSE of Apalachicola, FL. *Chaenopsis* sp. (*stephensi* of Robins 1971): UF 228601 (1, 49.9), Arrowsmith Bank, off Yucatan, Mexico. *Chaenopsis alepidota*: UF 26733 (2, 55–61), Gulf of California. *Chaenopsis schmitti*: USNM 322451 (1, 52), Galapagos Is.

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Redescription of *Squilla fabricii* Holthuis, 1941 (Crustacea: Stomatopoda), and its transfer to *Oratosquilla* Manning, 1968

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Abstract.—The holotype of *Squilla fabricii* Holthuis, is redescribed and transferred from *Oratosquillina* Manning to *Oratosquilla* Manning. Additionally, *O. fabricii* is shown to be a senior synonym of *O. calumnia* (Townsend). Characters previously used to distinguish *O. fabricii* (as *O. calumnia*) from *O. mauritiana*, namely the spination of the first abdominal somite and the shape of the anterior lobe on the lateral process of the seventh thoracic somite are, unreliable. The best character distinguishing *O. fabricii* from *O. mauritiana* is the pitted versus smooth dorsal integument. A key to species of *Oratosquilla* is provided.

Since it was first described from Indonesia, *Squilla fabricii* Holthuis, 1941, presently known as *Oratosquillina fabricii* (Holthuis 1941), has been reported only by Stephenson (1962). The specimen reported by Stephenson (1962) as *Squilla fabricii*, however, was shown by Ah Yong & Norrington (1997) to be a superficially similar species, *Oratosquillina asiatica* (Manning 1978).

Reexamination of the holotype of *Oratosquillina fabricii* shows not only that it belongs in the genus *Oratosquilla*, but also that it is a senior synonym of *Oratosquilla calumnia* (Townsend 1953), a species with a wide Pacific distribution. The confusion over the identity and generic placement of *Oratosquilla fabricii* is largely the result of an error in the type description which attributed an interrupted instead of uninterrupted anterior bifurcation to the median carina of the carapace (Holthuis 1941). The condition of the anterior bifurcation of the median carina of the carapace, whether interrupted or uninterrupted basally, is an important character distinguishing species groups and genera among squilloids (Manning 1971, 1978, 1995). Consequently, *Oratosquilla fabricii* has always been associ-

ated with the species in the ‘*perpensa*’ and ‘*gonypetes*’ groups of *Oratosquilla* (see Manning 1978), each of which were subsequently transferred to the genus *Oratosquillina* Manning, 1995. Thus, the conspecificity of *O. fabricii* and *O. calumnia* has likely escaped detection until now because both have been placed in different species groups or genera. All published records of *Oratosquilla calumnia* are now referable to *O. fabricii*. Four species of *Oratosquilla* are recognized here: *O. fabricii* (Holthuis 1941), *O. kemp*i (Schmitt 1931), *O. mauritiana* (Kemp 1913), and *O. oratoria* (de Haan 1844).

Several major studies of Indo-West Pacific stomatopods are presently in progress, each of which includes material of, or refer to *O. fabricii*. Rather than await completion of those works to correct the nomenclature, however, the present note serves to clarify the taxonomic status of both species in order to simplify the nomenclatural discussion in forthcoming works and to minimize perpetuation of errors in the taxonomic literature.

The holotype of *O. fabricii* is deposited in the Zoological Museum, Amsterdam (ZMA). All measurements are in millimeters (mm). Total length (TL) is measured along

the midline from the tip of the rostrum to the apices of the submedian teeth of the telson. Carapace length (CL) is measured along the midline and excludes the rostral plate. Corneal index (CI) is given as 100 times CL divided by cornea width. Other abbreviations used in this account include: antennule (A1); antenna (A2); abdominal somite (AS); thoracic somite (TS); maxilliped (MXP); median (MD); submedian (SM); intermediate (IM); lateral (LT); marginal (MG).

Family Squillidae Latreille, 1803
Genus *Oratosquilla* Manning, 1968
Oratosquilla fabricii (Holthuis 1941)
Fig. 1

- Squilla nepa*.—Brooks, 1886: 25 [part, see remarks; not *S. nepa* Latreille, 1828].
Squilla oratoria.—Kemp, 1913:66–72 [part, see remarks].—Edmondson, 1921: 287, fig. 1a.—Bigelow, 1931:183–186.—Townsend, 1953:404–406, figs. 2–3 [not *S. oratoria* De Haan].
Squilla fabricii.—Holthuis, 1941:249–253, fig. 1 [type locality: Telok Dalam, Nias, Indonesia].
Squilla calumnia.—Townsend, 1953:410, figs. 8, 9 [type locality: Hilo, Hawaii].
Oratosquilla calumnia.—Manning, 1971: 4–6, fig. 1.—Ahyong & Norrington, 1997:107.—Moosa, 1991:210–211.—Poupin, 1998:37.
Oratosquilla fabricii.—Manning, 1978:7, 11.
Oratosquillina fabricii.—Manning, 1995: 25, 225, 227.
Oratosquilla mauritiana.—Garcia, 1981: 24–26 [not *O. mauritiana* (Kemp 1913)].
Busquilla quadraticauda.—Poupin, 1998: 37 [not *B. quadraticauda* (Fukuda 1911)].
Not *Squilla fabricii*.—Stephenson, 1962: 107–108 [= *Oratosquillina asiatica* (Manning 1978)].

Material.—Holotype: ZMA, female (TL 128 mm), Telok Dalam, Nias, Indonesia, coll. Kleiweg de Zwaan.

Description of holotype.—Dorsal integument distinctly pitted, rugose.

Eye extending beyond midlength but not apex of A1 peduncle segment 1; cornea strongly bilobed, set obliquely on stalk; CI 448. Ophthalmic somite anterior margin faintly emarginate. Ocular scales truncate, separate.

A1 peduncle 0.83 CL. A1 somite with dorsal processes trianguloid, directed anterolaterally, apices pointed but blunt. A2 scale 0.63 CL.

Rostral plate trapezoid, broader than long, lacking median carina. Carapace anterior width 0.49 CL; anterolateral spines not extending beyond base of rostral plate; with MD, IM, LT, MG and reflected MG carinae; MD carina distinct, not interrupted at base of anterior bifurcation; branches of anterior bifurcation distinct, opening anterior to dorsal pit; posterior median projection distinct, obtuse.

Raptorial claw dactylus with 6 teeth, outer margin sinuous, proximal margin lacking basal notch; carpus carina tuberculate; propodus distal margin unarmed; merus outer inferodistal angle acute.

Mandibular palp 3-segmented. MXP1–4 each with epipod. MXP5 basal segment with ventrally directed spine. Pereiopod 1–3 basal segments unarmed; endopod segments fused, styliform.

TS6–8 with distinct SM and IM carinae. TS5 lateral process bilobed; anterior lobe a slender spine directed anteriorly; posterior lobe short, directed laterally. TS6–7 lateral process distinctly bilobed. TS8 anterolateral margin triangular, apex sharp; sternal keel rounded.

AS1–5 with distinct SM, IM, LT, and MG carinae. SM carinae parallel on AS1–5. AS6 with SM, IM, and LT carinae; with small ventral spine anterior to uropodal articulation; sternum posterior margin unarmed; lacking transverse carinae. Abdominal carinae spined as follows: SM 4–6, IM 2–6, LT 1–6, MG 1–5.

Telson flattened, subquadrate, slightly broader than long; with 3 pairs of primary teeth (SM, IM, LT), each with dorsal carina; SM teeth with fixed apices; prelateral lobe

shorter than margin of LT tooth; MD carina interrupted proximally, with short posterior spine; dorsolateral surface with curved rows of shallow pits; lacking supplementary longitudinal carinae; denticles rounded, each with dorsal tubercle, SM 4, IM 8, LT 1. Telson ventral surface with short postanal carina; ventrolateral carina short.

Uropodal protopod terminating in 2 slender spines, with lobe on outer margin of inner spine rounded, narrower than adjacent spine; with minute ventral spine anterior to endopod articulation; protopod inner margin crenulate. Uropodal exopod proximal segment shorter than distal segment; with 8 movable spines on outer margin.

Measurements of holotype.—TL 128 mm, CL 26.9 mm, cornea width 6.0 mm, A1 peduncle 22.2 mm, A2 scale 16.9 mm.

Remarks.—The holotype of *Oratosquilla fabricii* agrees well with the account of *O. calumnia* given by Manning (1971), but differs in lacking a posterior spine on the intermediate carina of AS1, and in bearing a broader anterior lobe on the lateral process of TS7. The two paratypes of *Oratosquilla fabricii*, one from ?Lombok, Indonesia, and the other from an unknown locality, were not studied. Inasmuch as Holthuis (1941) attributed an interrupted anterior bifurcation of the median carina of the carapace to *O. fabricii*, the paratypes may be referable to *Oratosquillina asiatica* which also occurs in Indonesia (Ahyong & Norrington 1997). Specimens reported as *O. calumnia* from New Caledonia (Moosa 1991), Fiji (Ahyong & Norrington 1997), and the Marquesas (Ahyong, unpublished data) show variation in both of these traits: the intermediate carina of AS1 may or may not be armed, and the anterior lobe of the lateral process of TS7 varies from rounded to sharp. Although the holotype of *O. calumnia* is a juvenile (TL 26 mm), large growth series of the species from the Marquesas fully corroborate Manning's (1971) association of the juvenile holotype with adults. Poupin's (1998) record of *Busquilla quadraticauda* (Fukuda 1911) from Tahiti, Society Islands, is based on a

juvenile of *O. fabricii*. Brooks (1886) reported a specimen of *O. fabricii* from Honolulu, Hawaii, as *Squilla nepa*.

Manning (1971) remarked on the close similarity between *O. mauritiana* from the western Indian Ocean and *O. fabricii* (as *O. calumnia*) from the Pacific. In *O. mauritiana*, the intermediate carina on AS1 is always unarmed and the anterior lobe of the lateral process of TS7 is always blunt. In *O. fabricii*, however, the intermediate carina of AS1 may or may not be armed and the anterior lobe of the TS7 lateral process is usually triangular, but may be blunt and obtuse. Thus, the primary characters used by Manning (1971, 1995) to distinguish the two species have limited diagnostic value. Both Kemp (1913) and Manning (1971), however, remarked on the smooth dorsal integument of *O. mauritiana*, and this appears to be the most reliable character distinguishing it from *O. fabricii*, which is pitted and rugose. I have not examined Moosa's (1991) material from New Caledonia, but the holotype of *O. fabricii*, the specimen from Fiji reported by Ahyong & Norrington (1997) as *O. calumnia*, as well as specimens identifiable with *O. calumnia* in the National Museum of Natural History, Smithsonian Institution, bear distinctly pitted dorsal integument. *Oratosquilla mauritiana* reported by Garcia (1981) from the Philippines is referable to *O. fabricii* as it bears a triangular anterior lobe on TS7; that lobe is always blunt in *O. mauritiana*.

Distribution.—Pacific Ocean from Hawaii, French Polynesia, Guam, Fiji, New Caledonia, Indonesia, and the Philippines, at depths of 5–50 m.

Key to species of *Oratosquilla*

1. Raptorial claw merus lacking outer inferodistal spine *O. kempii*
- Raptorial claw merus with outer inferodistal spine 2
2. SM carinae of AS4 unarmed *O. oratoria*
- SM carinae of AS4-6 each with posterior spine 3
3. Dorsum integument smooth, not punc-

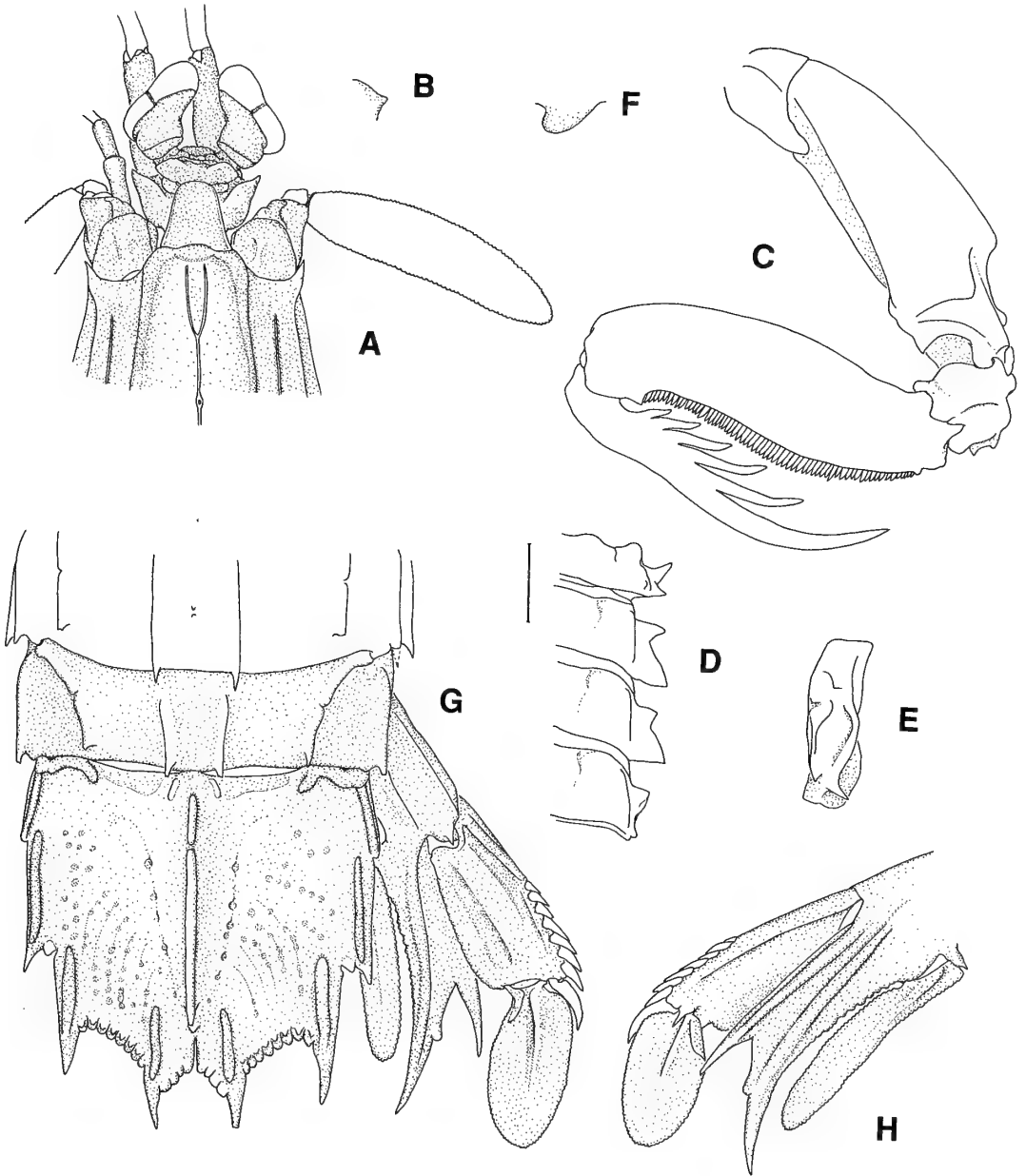


Fig. 1. *Oratosquilla fabricii* (Holthuis, 1941), holotype female (TL 128 mm), ZMA A, anterior cephalon, dorsal. B, A1 somite dorsal process, right lateral. C, raptorial claw, right lateral. D, TS5-8 lateral processes, right dorsal. E, TS5, right lateral. F, TS8 sternal keel, right lateral. G, AS5-6, telson and uropod, dorsal. H, uropod, right ventral. Scale equals 5 mm.

tate. Anterior lobe of lateral process of TS7 blunt *O. mauritiana*
 Dorsum integument distinctly punctate.
 Anterior lobe of lateral process of TS7 pointed to blunt *O. fabricii*

Acknowledgments

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seum of Natural History, Smithsonian Institution, Cees Hof and Dirk Platvoet for providing access to the holotype of *Squilla fabricii* and for providing working space during a visit to Amsterdam in 1998. My stomatopod studies were supported by an Australian Museum Postgraduate grant, a grant from the Joyce Vickery Research Fund (Linnean Society of New South Wales), and an Australian Postgraduate Award from the Australian Research Council, administered by the University of New South Wales.

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Freshwater shrimps of the genus *Caridina* H. Milne Edwards (Crustacea: Decapoda: Atyidae) from Myanmar

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Abstract.—Five species of freshwater shrimps of the genus *Caridina* H. Milne Edwards, 1837 are recognised from Myanmar. Of these, three are described as new: *C. williamsi*, *C. rangoona* and *C. burmensis*. *Caridina annandalei* Kemp, 1918, a species not reported since its original description, is re-diagnosed and figured in detail. The status of *C. weberi* prox. var. *sumatrensis* De Man, 1892 is discussed.

The atyid fauna of Myanmar (formerly Burma, Fig. 1) is very poorly studied, and until now, only two species of *Caridina* H. Milne Edwards, 1837, had been reported, namely *C. annandalei* Kemp, 1918, and “*C. weberi* prox. var. *sumatrensis* De Man, 1892” (Kemp 1918). Recently, the authors had an opportunity to examine several collections of these shrimps in the Swedish Museum of Natural History, Paris Museum, and Raffles Museum of Singapore. Not surprisingly, much of this material represents new species.

The present paper reports on these collections and discusses the status of “*C. weberi* var. prox. *sumatrensis* De Man, 1892” for which no specimens are available. A total of five species are now recognised from Myanmar, of which three are described as new.

Specimens are deposited in the Zoological Reference Collection, Raffles Museum of Biodiversity Research, National University of Singapore, Singapore (ZRC); Swedish Museum of Natural History, Stockholm, Sweden (SMNH); and Muséum National d’Histoire Naturelle, Paris, France (MNHN). The abbreviation cl is used for carapace length, measured from the postorbital margin to the posterior dorsal margin of the carapace.

Genus *Caridina* H. Milne Edwards, 1837
Caridina annandalei Kemp, 1918
Figs. 2, 3

Caridina annandalei Kemp, 1918: 96, pl. 25 (type locality: Inlé Lake, Shan State, Myanmar)

Material examined.—14 specimens (3 ovig. females), syntypes (MNHN-Na663), Inlé Lake, Shan State, Myanmar, exchanged from Calcutta (Indian Museum), entry no. 41-1921, through S. Kemp; 4 ovig. females, cl 3.8–4.3 mm (ZRC.1999.2009), 20°34.87’N, 96°06.33’E, Inlé Lake at Mine Thauk canal, Shan State, Myanmar, pH 7.6, 26 Feb 1999; 4 males, cl 2.5–2.7 mm, 12 females, cl 2.5–3.7 mm, 2 ovig. females, cl 3.2–3.5 mm (SMNH 13504), Inlé Lake, mainly west shore, Salween River drainage, Nyaung Shwe, Shan State, Myanmar, leg. S. O. Kullander, Fang Fang, T. R. Roberts, 26 Feb 1994; 2 ovig. females, cl 2.5–3.0 mm (SMNH 13506), Inlé Lake, west margin, just south of Khaung Taing, Salween River drainage, Nyaung Shwe, Shan State, Myanmar, leg. S. O. Kullander, Fang Fang, 27 Feb. 1994; 1 ovig. female, cl 3.9 mm (SMNH 13507), SOK 94-007B, Inlé Lake, Inlé canal to Nyaung Shwe, Salween River drainage, Nyaung Shwe State, Shan, Myanmar, leg. S. O. Kullander, Fang Fang, T. R. Roberts, 1 Mar 1994; 1 female, cl 3.4 mm,

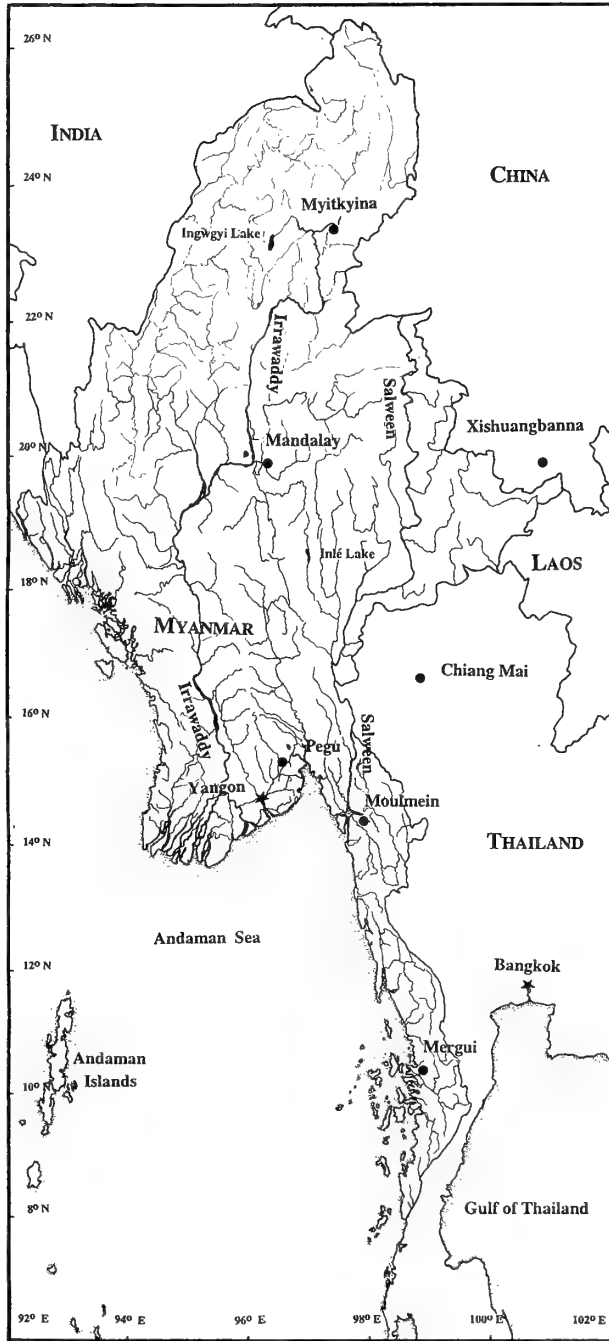


Fig. 1. Map of Myanmar, showing the drainage and collection sites.

19 juv. (SMNH 13903), Inlé Lake, Trungdo, southern Shan State, Myanmar, at 900 m, leg. Malaise, 12 Sept 1934.

Diagnosis.—Rostrum (Figs. 2A, 3A) convex, with tip slightly upturned, reaching to end of second segment of antennular peduncle, or slightly beyond it; rostral formula: 2–4 (mode 3) + 12–21/2–6 (mode 2–4); antennal spine sharply pointed, placed below lower orbital angle, pterygostomial margin broadly rounded; telson (Figs. 2B, C) not terminating in projection, with 5 pairs of distal spines, lateral pair of distal spines subequal to intermediates except median pair only half length of lateral pair; pre-anal carina (Fig. 2D) lacking spine; antennular peduncle 0.85 times as long as carapace, stylocerite 0.8 times length of basal segment of antennular peduncle; scaphocerite (Fig. 2E) 3.5 times as long as wide; epipods on first 3 pereopods only; carpus of first pereopod (Figs. 2F, 3B) 3.0–3.4 times as long as high, chela slightly longer than carpus, 2.3 times as long as broad, fingers distinctly longer than palm; carpus of second pereopod (Figs. 2G, 3C) 7.5–8.0 times as long as high, chela shorter than carpus, chela 3.4 times as long as broad, fingers 1.6 times as long as palm; propodus of third pereopod (Figs. 3D, E) 2.7–3.2 times as long as dactylus, dactylus 4.6 times as long as wide, with 8–12 spines on flexor margin; propodus of fifth pereopods (Figs. 3F, G) 2.2–2.5 times as long as dactylus, dactylus 4.5 times as long as broad, with 44–68 spinules on flexor margin; endopod of male first pleopod (Fig. 2H) sub-rectangular, 2.1 times as long as wide; appendix interna of male second pleopod (Fig. 2I) reaching to 0.8 times length of appendix masculina; uropodal diaeresis (Fig. 2J) with 15 spinules. Egg size 0.55–0.70 to 0.90–1.05 mm.

Habitats.—*Caridina annandalei* was abundant among green weeds in or near Inlé Lake.

Distribution.—Known only from the Inlé Lake basin in central Myanmar.

Remarks.—*Caridina annandalei*, had not been reported since its original description.

Recent collections from Myanmar seem to show that this species is indeed endemic to the Inlé Lake basin. When Kemp (1918) described *C. annandalei*, he noted that it is allied to *C. excavata* Kemp, 1913, and *C. hodgarti* Kemp, 1913, both from Assam in northeastern India, based on the absence of an epipod on the fourth pereopod. This character is, in fact, shared by many other South East Asian *Caridina* species, namely, *C. laevis* Heller, 1862, from Java, *C. excavatoides* Johnson, 1961, from Peninsular Malaysia and *C. fecunda* J. Roux, 1911, from Irian Jaya, Indonesia. *Caridina annandalei*, however, is very different from *C. excavata* and *C. hodgarti* by its much shorter rostrum which never reaches the end of the antennular peduncle (vs. distinctly reaching beyond the end of antennular peduncle in *C. excavata*, and beyond the scaphocerite in *C. hodgarti* (cf. Kemp 1913)). With regards to the short rostrum, the slender first two pereopods and the large egg size, *C. annandalei* is perhaps most similar to *C. laevis* (cf. Heller 1862, Kemp 1918b, Bouvier 1925), but can be distinguished from it by the form of the rostrum, which is convex and sloping (vs. sigmoid in *C. laevis*), and the fifth pereopod having fewer spinules (44–68 vs. 90–100 in *C. laevis*). *Caridina annandalei* differs from *C. excavatoides* (cf. Johnson 1961) by its more elongated antennular peduncle (ratio of the peduncle to carapace length 0.85 vs. 0.64 in *C. excavatoides*); more spinules on uropodal diaeresis (15 vs. 12–13); and larger egg size (0.55–0.70 to 0.90–1.05 mm vs. 0.48 to 0.78 mm). It can also be easily separated from *C. fecunda* (cf. Roux 1911, Bouvier 1925) by the proportionally shorter rostrum; the larger number of spinules on the dactylus of the third pereopod (8–12 vs. 7–8) and fifth pereopod (44–68 vs. 35–40); and the larger egg size (0.55–0.70 to 0.90–1.05 mm vs. 0.50 to 0.80 mm).

Caridina williamsi, new species
Figs. 4, 5

Material examined.—Holotype: ovig. female, cl 4.4 mm (ZRC.1999.2040),

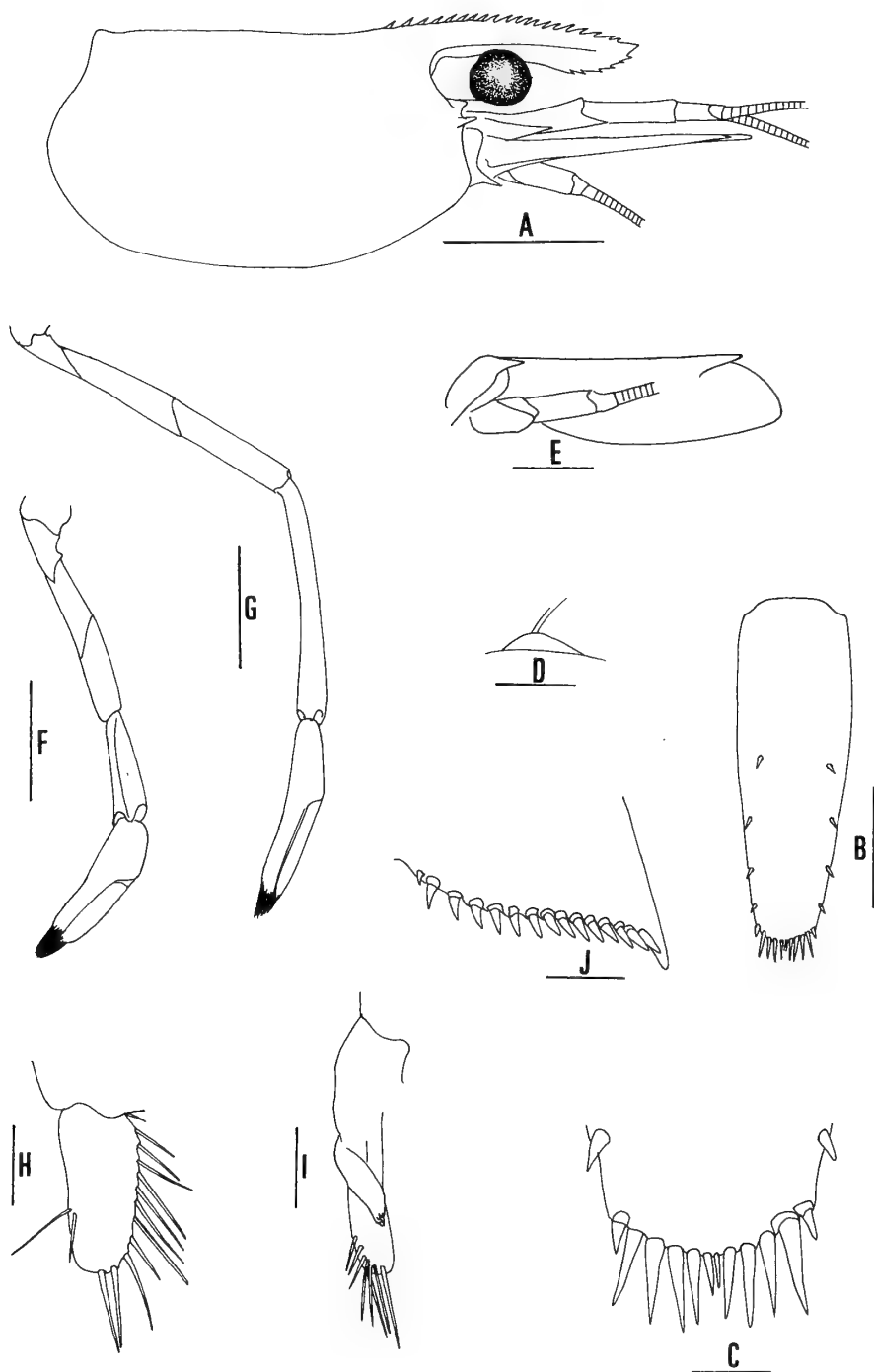


Fig. 2. *Caridina annandalei* Kemp, 1918. A, cephalothorax and cephalic appendages; lateral view; B, telson; C, distal part of telson; D, preanal carina; E, scaphocerite; F, first pereopod; G, second pereopod; H, endopod of male first pleopod; I, appendix masculina of male second pleopod; J, uropodal diaeresis. Scales: A = 2 mm; B, D, E, F, G = 1 mm; C, H, I, J = 0.2 mm. (A–G, J, ovig, female, cl. 4.3 mm, Inlé Lake, central Myanmar, ZRC, 1999.2009; H, I, male, cl. 2.7 mm Inlé Lake, central Myanmar, SMNH 13504)

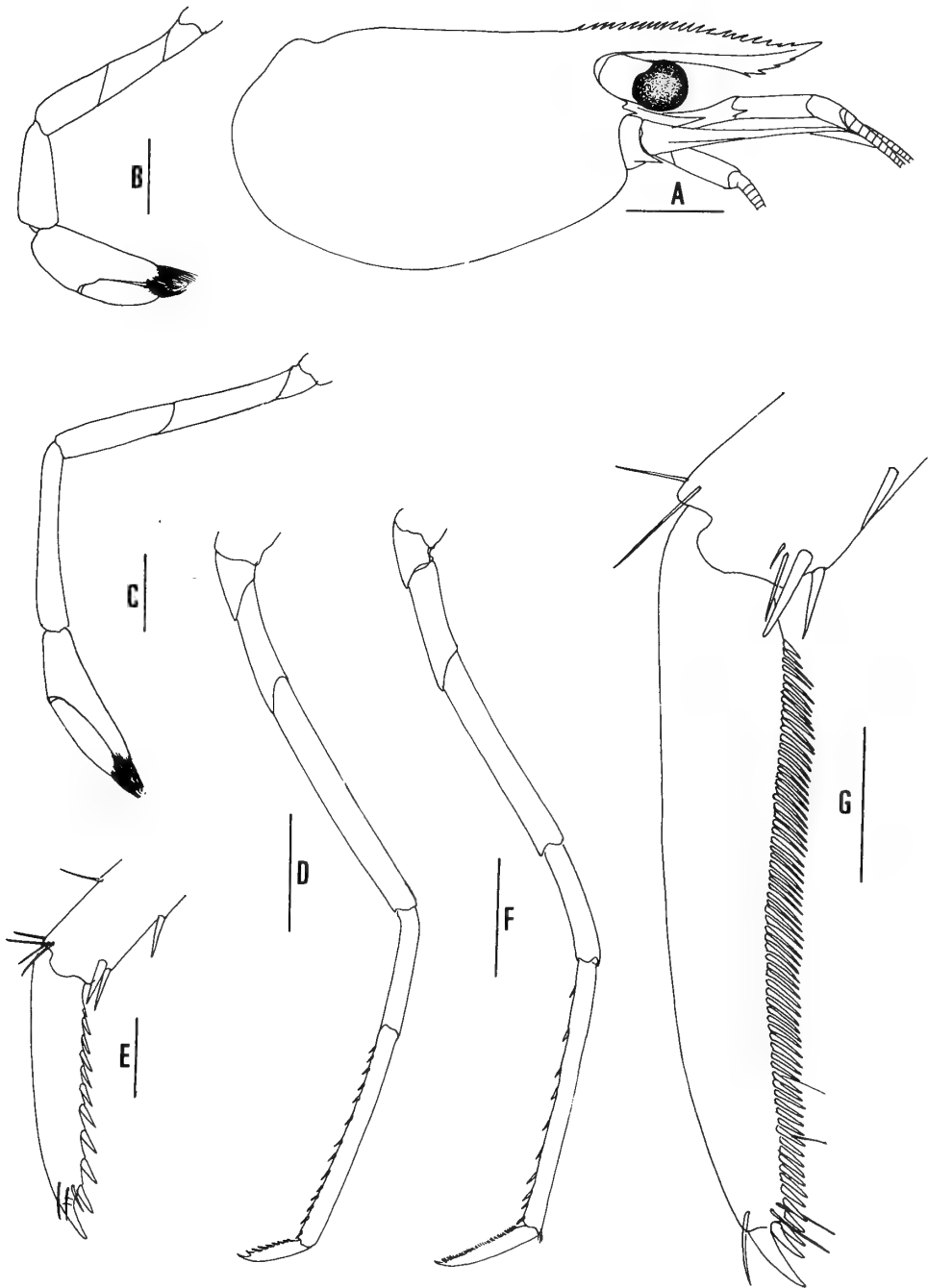


Fig. 3. *Caridina annandalei* Kemp, 1918; ovig. female, cl 3.7 mm, central Myanmar, SMNH 13903. A, cephalothorax and cephalic appendages, lateral view; B, first pereiopod; C, second pereiopod; D, third pereiopod; E, dactylus of third pereiopod; F, fifth pereiopod; G, dactylus of fifth pereiopod. Scales: A, D, F = 1 mm; B, C = 0.5 mm; E, G = 0.2 mm.

17°48.11'N, 96°09.20'E, Balar stream, 12 km Yangon to Mandalay highway, Htauk Kyant, Yangon State, Myanmar. Paratypes: 7 males, cl 1.9–2.2 mm, 8 females, cl 2.8–4.0 mm, 10 ovig. females, cl 3.7–4.2 mm (ZRC.1999.2041–2059), same data as holotype. Others: 18 spec., cl 3.3–4.3 mm (ZRC.1999.2060), 17°09.97'N, 96°09.20'E, Win Paw Hta river, near border between Pegu (Bago) and Yangon, and from fishfolk, Yangon State, Myanmar; 2 females, cl 2.9–3.0 mm, 1 ovig. female, cl 4.8 mm, (ZRC.1999.2061), 20°34.87'N, 96°06.33'E, Inlé Lake at Mine Thauk canal, Shan State, Myanmar; 6 males, cl. 2.1–2.6 mm, 5 females, cl. 2.3–2.5 mm, 20 juv., Yangon (SMNH 13517).

Description.—Rostrum (Figs. 4A, B; 5A) narrow, slender, straight or slightly upturned at distal one third, longer than carapace, reaching beyond end of scaphocerite; armed with numerous teeth throughout dorsal margin, with 4–9 teeth at middle of ventral margin; formula: 2-3 + 23-30/4-9 (mode 5-6). Antennal spine situated below sub-orbital angle. Pterygostonian angle rounded.

Sixth abdominal somite 0.65 times as long as carapace, 2.0 times as long as fifth somite, slightly shorter than telson. Telson (Figs. 5B, C) 3.0 times as long as wide, not terminating in a projection, with 4 pairs of dorsal and 1 pair of dorsolateral spinules; distal margin with 4 pairs of spinules, lateral pair of spine longer than intermediate pairs of spiniform setae, sublateral pair shortest. Preanal carina broadly rounded, lacking spine (Fig. 5D).

Eyes well developed. Antennular peduncle 0.85 to 1.0 times as long as carapace; basal segment of antennular peduncle longer than sum of second and third segment length. Stylocerite reaching 0.8 times length of basal segment of antennular peduncle. Scaphocerite (Fig. 5E) 3.5 times as long as wide.

Incisor process of mandible (Fig. 4C) ending in irregular teeth, molar process truncated. Lower lacinia of maxillula (Fig.

4D) broadly rounded, upper lacinia elongate, with many distinct teeth on inner margin, palp slender. Upper endites of maxilla (Fig. 4E) subdivided, palp short, scaphognathite tapering posteriorly with some long, curved setae at posterior and end. Palp of first maxilliped (Fig. 4F) broadly triangular. Second maxilliped (Fig. 4G) typical of the genus. Third maxilliped (Fig. 4H) reaching to end of second segment of antennular peduncle, with ultimate segment shorter than penultimate segment.

Epipods on first 4 pereopods. First pereopod (Fig. 4I) reaching to end of basal segment of antennular peduncle, merus 3.0 times as long as broad, as long as carpus; carpus excavated anteriorly, shorter than chela, 2.3 times as long as high; chela 2.4 times as long as broad; fingers 1.3 times as long as palm. Second pereopod (Fig. 4J) reaching end of second segment of antennular peduncle, merus shorter than carpus, 5.0 times as long as broad; carpus 1.3 times as long as chela, 6.0 times as long as high; chela 3.0 times as long as broad; fingers 1.4 times as long as palm. Third pereopod (Fig. 5F, G) reaching end of scaphocerite, propodus slightly shorter than merus, 13 times as long as broad, 4.0 times as long as dactylus; dactylus 4.0 times as long as wide (spines included), with 8 or 9 accessory spines on flexor margin. Fifth pereopod (Fig. 5H, I) reaching end of second segment of antennular peduncle, propodus distinctly longer than merus, 13 times as long as broad, 3.1 times as long as dactylus; dactylus 4.0 times as long as wide, with 37 or 38 spinules on its flexor margin. Endopod of male first pleopod (Fig. 5J) triangular, 0.25 times length of exopod, with appendix interna strongly curved inwards. Appendix masculina of male second pleopod (Fig. 5K) half length of endopod, appendix interna reaching distal one-third of appendix masculina.

Uropodal diaeresis (Fig. 5L) with 9 or 10 movable spinules. Egg size 0.75–0.85 to 0.45–0.6 mm in diameter.

Habitat.—*Caridina williamsi*, new spe-

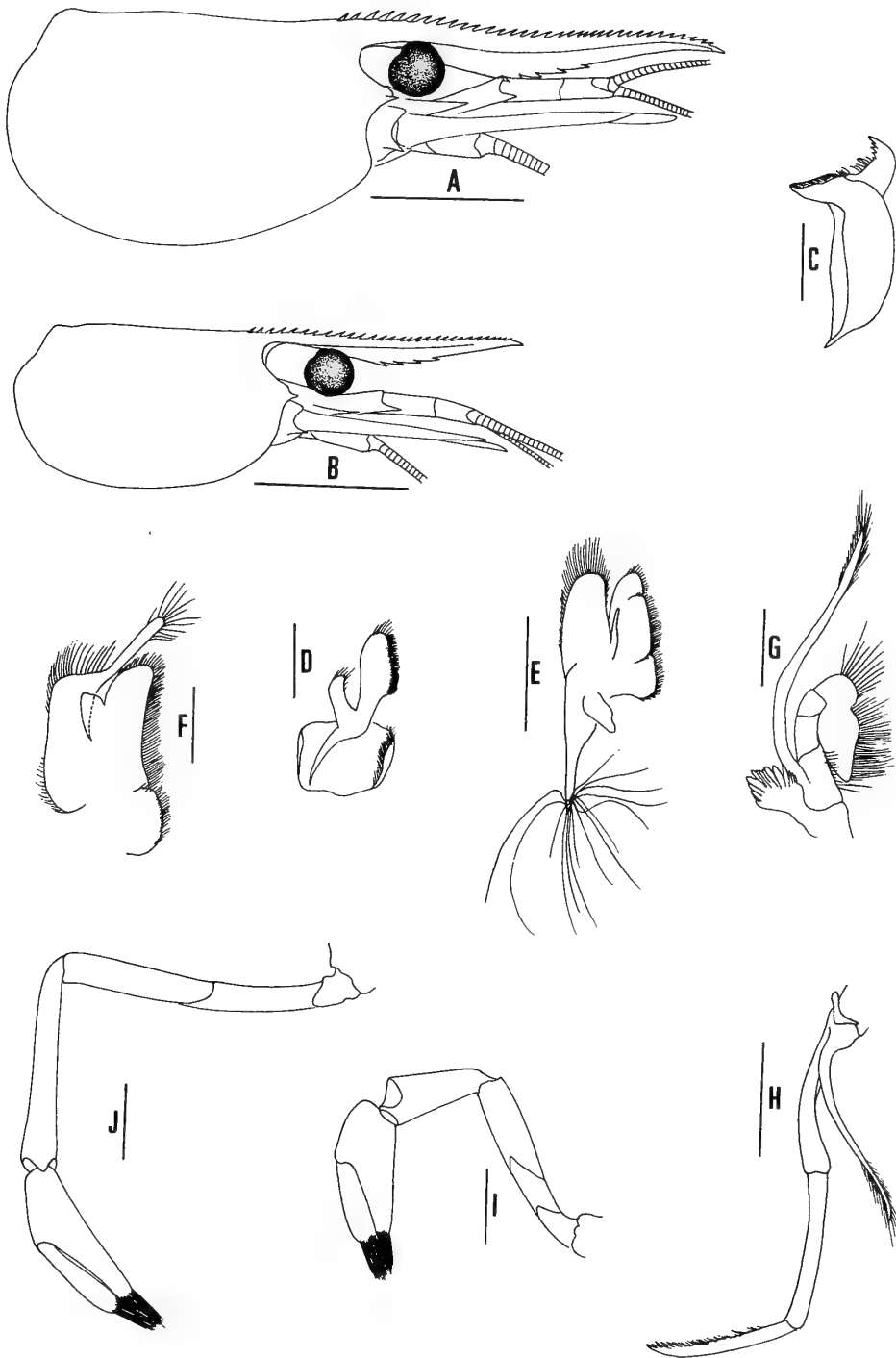


Fig. 4. *Caridina williamsi*, new species. A, B, cephalothorax and cephalic appendages, lateral view; C, mandible; D, maxillula; E, maxilla; F, first maxilliped; G, second maxilliped; H, third maxilliped; I, first pereiopod; J, second pereiopod. Scales: A, B = 2 mm, C, D, F, G, I, J = 0.5 mm; E, H = 1 mm. (A, C-J, ovig. female, cl 4.2 mm; B, male, cl 2.2 mm, paratype, ZRC.1999.2041-2042, Htauk Kyant, Yangon State, Myanmar)

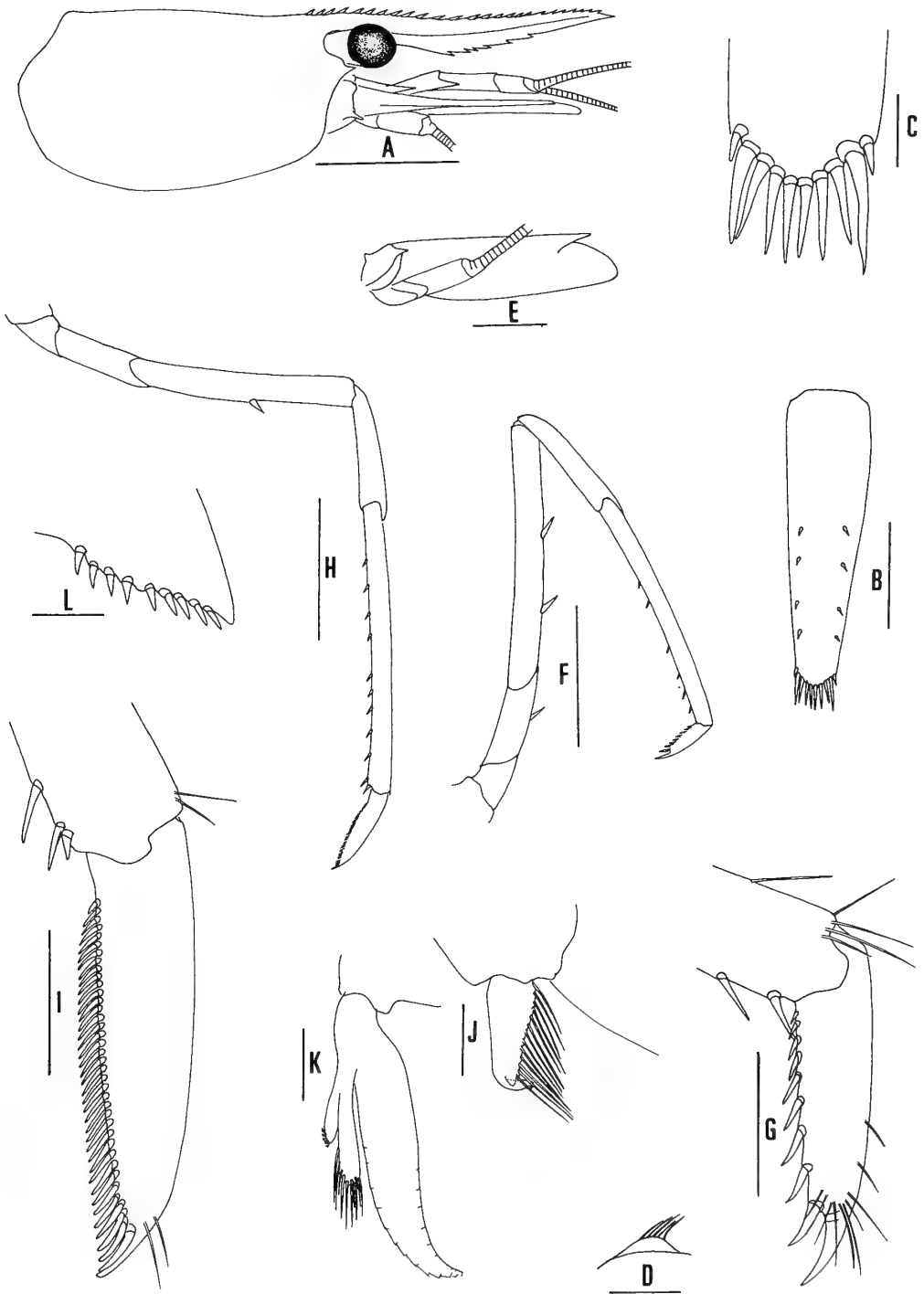


Fig. 5. *Caridina williamsi*, new species. A, cephalothorax and cephalic appendages; lateral view; B, telson; C, distal part of telson; D, preanal carina; E, scaphocerite; F, third pereiopod; G, dactylus of third pereiopod; H, fifth pereiopod; I, dactylus of fifth pereiopod; J, endopod of male first pleopod; K, appendix masculina of male second pleopod; L, uropodal diaeresis. Scales: A = 2 mm; B, E, F, H = 1 mm; C, G, I, J, K, L = 0.2 mm; D = 0.5 mm. (A–I, L, ovig. femal. cl. 3.7 mm, paratype; J, K, male, cl. 2.2 mm, paratype, ZRC.1999.2042–2043, Htauk Kyant, Yangon State, Myanmar)

cies, was collected from water plants along the edges and on the bottom of water bodies.

Etymology.—*Caridina williamsi*, is named after the late Dr. Austin B. Williams, an outstanding zoologist, Systematics Laboratory National Marine Fisheries Service, National Museum of Natural History, Smithsonian Institution, Washington, who contributed immensely to our knowledge of the Caridea.

Remarks.—In the form of the rostrum and large egg size, *Caridina williamsi*, new species, is remarkably close to *Caridina chauhani* Chopra & Tiwari, 1949, from Patna, northern India. The new species, however, can be distinguished by having four to nine ventral teeth (mode 5–6) (vs. 4–14 (mode 7–13) in *C. chauhani*); the dactylus of third pereopod with eight or nine spines (vs. five to six in *C. chauhani*); and the larger egg size: 0.75–0.85 × 0.45–0.6 mm in diameter (vs. 0.62–0.69 × 0.36–0.40 mm in *C. chauhani*).

Caridina chauhani was originally described as *Caridina nilotica* var. *chauhani*. *Caridina nilotica* (P. Roux, 1833), and its allied species (see De Man 1892, 1908; Bouvier 1925), however, have at least some distinct separated sub-apical teeth on dorsal rostral margin, a character absent in *C. n. chauhani*. *Caridina chauhani* is thus, regarded here as a distinct species.

Caridina rangoona, new species

Fig. 6

Material examined.—Holotype: ovig. female, cl 3.5 mm (ZRC. 1999.2010), 17°09.97'N, 96°99.20'E, Win Paw Hta River, near border between Pegu (Bago) and Yangon, Yangon State, Myanmar. Paratypes: 13 females, cl 2.6–3.3 mm, 8 ovig. females, cl 2.6–3.6 mm, 7 juv. (ZRC.1999.2011–2038), data same as holotype. Others: 2 females, cl 3.1 mm, 3 ovig. females, cl 3.5–3.9 mm (ZRC.1999.2039), 17°48.11'N, 96°09.20'E, Balar stream, 12 km from Yangon to Mandalay highway, Htauk Kyant,

Yangon State, Myanmar; 12 females, cl 1.6–2.0 mm (SMNH 13902), Hlaing Lake, Kaw-kareik, near Moulmein, southern Myanmar.

Description.—Rostrum (Fig 6A) short, reaching near end of second segment of antennular peduncle; dorsal margin slightly sloping down, tip slender, acutely pointed, depressed, rostral formula: 4–6 (mode 4–5) + 10–16 (mode 13–15)/2–5 (mode 3–4). Antennal spine situated below sub-orbital angle. Pterygostomian margin sub-rectangular.

Sixth abdominal somite 0.55 times as long as carapace, 1.9 times as long as fifth somite, slightly shorter than telson. Telson (Figs. 6B, C) 3.3 times as long as wide, not terminating in a projection, with 4 pairs of dorsal spinules generally (third pair with only left spine, right one absent in a paratype female) and 1 pair of dorsolateral spinules; distal margin armed with 4 pairs of spinules generally (7 spinules in a paratype female), lateral pair of spine longer than intermediate pairs of spine, median pair shortest. Preanal carina (Fig. 6D) broadly rounded, unarmed.

Eyes well developed. Antennular peduncle 0.80 to 0.85 times as long as carapace; basal segment of antennular peduncle longer than combined length of second and third segments. Stylocerite reaching 0.8 times length of basal segment of antennular peduncle. Scaphocerite (Fig. 6E) 4 times as long as wide.

First maxilliped (Fig. 6F) with palp ending in finger-like structure; rest of mouthpart similar to *C. williamsi*, new species. Third maxilliped reaching to end of basal segment of antennular peduncle, with ultimate segment slightly shorter than penultimate segment.

Epipods present on first 4 pereopods. First pereopod (Fig. 6G) reaching near end of basal segment of antennular peduncle, chela 2.2 times as long as broad; fingers 1.5 times as long as palm; carpus excavated anteriorly, slightly shorter than chela, 2.3 times as long as height; merus 2.3 times as long as broad; ischium as long as merus.

Second pereopod (Fig. 6H) reaching end of second segment of antennular peduncle, merus as long as ischium, shorter than carpus, 4.4 times as long as broad; carpus 1.6 times as long as merus, 1.2 times as long as chela, 6.3 times as long as high; chela 3.5 times as long as broad; fingers 1.5 times as long as palm. Third pereopod (Figs. 6I, J) reaching end of antennular peduncle, propodus shorter than merus, 13 times as long as broad, 3.4 times as long as dactylus; dactylus 4.3 times as long as wide (spines included), with 8 or 9 accessory spines on its flexor margin. Fifth pereopod (Figs. 6K, L) reaching end of second segment of antennular peduncle, propodus distinctly longer than merus, 11 times as long as broad, 2.5 times as long as dactylus; dactylus slender, 5.0 times as long as wide, with 65–67 spinules on flexor margin.

Uropodal diaeresis (Fig. 6M) with 15 or 16 movable spinules. Egg size 0.60–0.70 to 0.31–0.40 mm in diameter.

Habitat.—Specimens of *Caridina rangoona*, new species, were collected from water plants along edges and on the bottom of water bodies, together with *C. williamsi*, new species (H. H. Tan, pers. comm.).

Etymology.—*Caridina rangoona*, is named after the type locality. Rangoon is the old name for Yangon, the capital of Myanmar.

Remarks.—In rostral shape, rostral formula, and slender pereopods, *C. rangoona* is most similar to *C. temasek* Choy & Ng, 1991, originally described from Singapore, but has since been found from many parts of Peninsular Malaysia (unpublished data). *Caridina rangoona*, however, differs by its proportionally broader chela (2.2 times as long as broad vs. 2.4–2.5 in *C. temasek*); the length of ischium in first pereopods (as long as merus in *C. rangoona* vs. distinctively shorter than the merus in *C. temasek*); the ratio of propodus to dactylus of fifth pereopod (2.5 in *C. rangoona* vs. 2.6–3.0 in *C. temasek*); the smaller number of spinules on the dactylus of the fifth pereopod (55–65 vs. 65–75) and the smaller egg

size (0.30–0.40 × 0.60–0.70 mm in *C. rangoona* vs. 0.44–0.54 × 0.70–0.80 mm in *C. temasek*). In the shape of the rostrum, *C. rangoona* is morphologically closest to a Vietnamese species, *C. clinata* Cai, Nguyen, & Ng, 1999, but can be distinguished from the latter (cf. Cai et al. 1999) by the fewer and shorter distal setae on the telson (Cai et al. 1999: figs. 2A, 6C); the longer carpus of first pereopod (2.2 times as long as high vs. 1.5 times in *C. clinata*); the longer finger of the first pereopod (1.5 times as long as palm vs. shorter, subequal in *C. clinata*); the larger number of spinules on the dactylus of the fifth pereopod (65–67 vs. 45–49) and the much smaller egg size (0.30–0.40 × 0.60–0.70 mm vs. 0.60–0.75 × 1.10–1.15 mm in *C. clinata*).

Caridina burmensis, new species

Fig. 7

Material examined.—Holotype: female, cl 3.7 mm (SMNH 13901), Myitkyina, Myanmar, leg. Malaise, 6 Mar 1934.

Description.—Rostrum (Fig. 7A) short, straight, narrow, reaching to end of second segment of antennular peduncle, dorsal margin convex and sloping ventrad anteriorly, with teeth more closely placed posteriorly than anteriorly; ventral margin horizontal, with small teeth; rostral formula: 3 + 11/4. Antennal spine placed below sub-orbital angle; pterygostomian margin rounded.

Abdomen with sixth somite 0.58 times as long as carapace, 1.5 times as long as fifth somite, slightly shorter than telson. Telson (Fig. 7B, C) slightly longer than sixth somite, tapering posteriorly, ending in rounded margin, 1 pair of dorso-lateral spines near distal end; 3 pairs of spiniform setae on distal margin, lateral pair longer than intermediate pairs; preanal carina (Fig. 7D) with a spine.

Eyes well developed. Antennular peduncle 0.8 times as long as carapace; basal segment slightly longer than half of peduncle, third segment shortest; stylocerite reaching

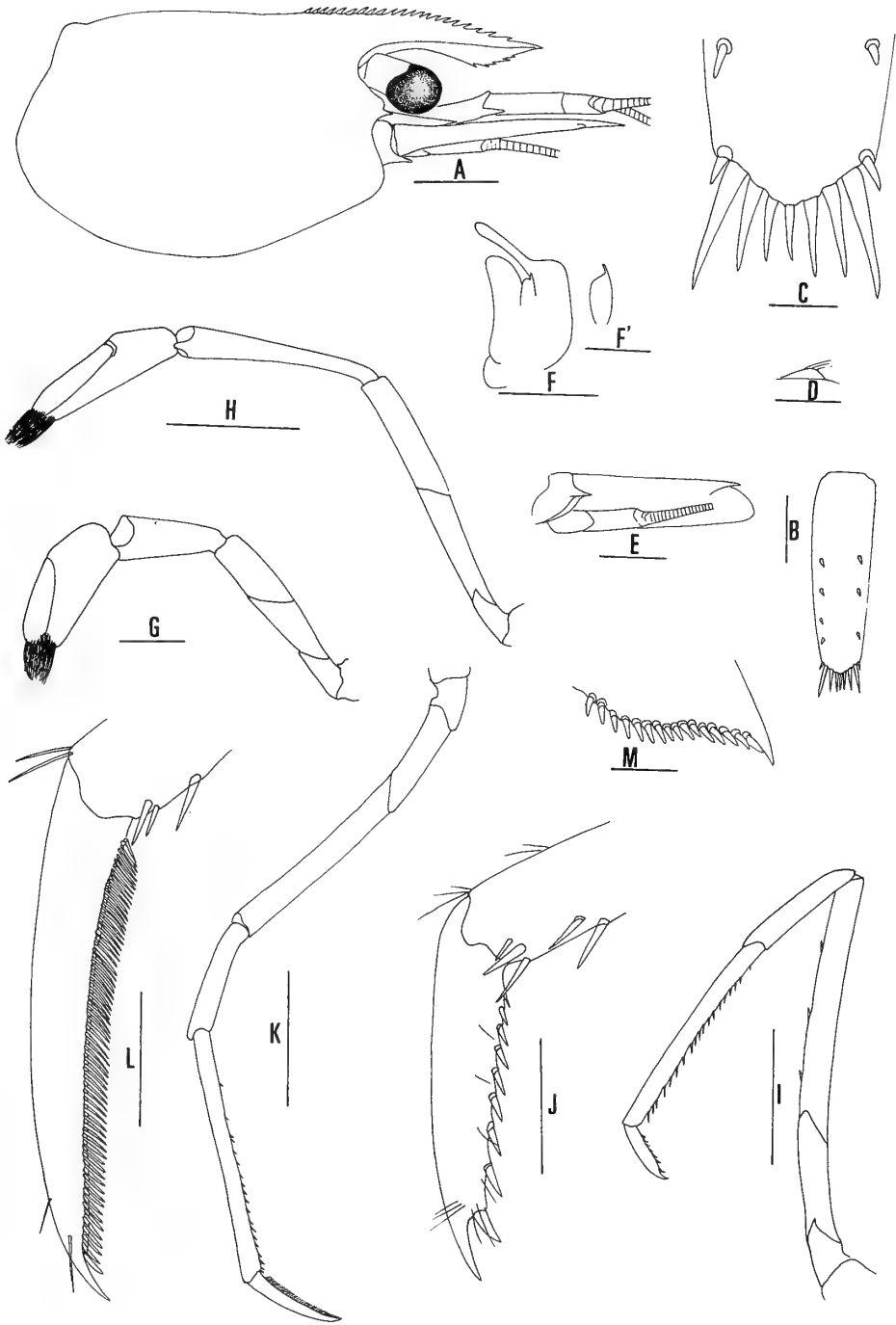


Fig. 6. *Caridina rangoona*, new species, female, cl 3.9 mm, paratype, ZRC.1999.2011, Yangon, Myanmar. A, cephalothorax and cephalic appendages; lateral view; B, telson; C, distal part of telson; D, preanal carina; E, scaphocerite; F, F', first maxilliped; G, first pereiopod; H, second pereiopod; I, third pereiopod; J, dactylus of third pereiopod; K, fifth pereiopod; L, dactylus of fifth pereiopod; M, uropodal diaeresis. Scales: A, B, D, E, F, H, I, K = 1 mm; F', G = 0.5 mm; C, M, J, L = 0.2 mm.

to 0.7 times length of basal segment of antennular peduncle; scaphocerite (Fig. 7E) narrow, reaching beyond distal end of antennular peduncle, about 4 times as long as broad. First maxilliped (Fig. 7F) with palp ending in stout finger-like structure; rest of mouthpart similar to *C. williamsi*, new species. Third maxilliped reaching slightly beyond distal end of antennular peduncle, ending in single terminal claw; ultimate segment slightly shorter than penultimate.

Epipods present on first 3 pereopods only. First pereopod (Fig. 7G) reaching end of antennular peduncle, chela 3.2 times as long as broad, fingers about 1.5 times as long as palm; carpus not excavated anteriorly, about 3.5 times as long as high, shorter than chela, merus shorter than carpus, as long as ischium. Second pereopod (Fig. 7H) long, slender, reaching end of scaphocerite; chela 4.5 times as long as broad, fingers 1.3 times as long as palm; carpus about 6.8 times as long as high, 1.2 times as long as chela; merus shorter than chela, as long as ischium. Third pereopod (Fig. 7I, J) long, slender, reaching beyond end of scaphocerite by dactylus, dactylus terminating in 1 spine, bearing 9 accessory spines on flexor margin; propodus 10 times as long as broad, 3.0 times as long as dactylus. Fifth pereopod (Fig. 7K, L) long, slender, reaching slightly beyond end of scaphocerite; dactylus terminating in a strong claw, with 48 spinules on posterior margin; propodus 12 times as long as broad, 2.6 times as long as dactylus.

Uropodal diaeresis (Fig. 7M) with 17 spinules.

Etymology.—*Caridina burmensis*, is named after the type locality, Burma, the old name for Myanmar.

Remarks.—With regards to the slender shape of the first two pereopods, the shape of the rostrum and the presence of a long and slender antennular peduncle, *Caridina burmensis*, new species, most closely resembles *C. annandalei* Kemp, 1918, from Inlé Lake, and *C. banna* Cai & Dai, 1999, from the Xishuangbanna region of Yunnan

Province, which borders Myanmar in southern China. It can be distinguished from *C. annandalei* by the number (three pairs vs. five pairs) and the form (lateral pair distinctively longer than intermediate pairs vs. subequal with a very small median pair) of the distal spines of telson; the number of dorsal spines of telson (two vs. four pairs); and the presence of a spine on the preanal carina (vs. absent). *Caridina burmensis* can also be separated from *C. banna* by the absence of an epipod on the fourth pereopod; the larger number of ventral rostral teeth (four vs. one or two); the greater number of teeth on uropodal diaeresis (17 vs. 8–11); the merus of first pereopods being as long as the ischium (vs. distinctively longer); and the greater ratio (three vs. 2.5) of the propodus to dactylus of the third pereopod. Although there is only one female specimen available to us, its morphological characteristics are very distinct and can confidently be assigned to a new species.

Caridina sp.

Caridina weberi prox. var. *sumatrensis*.—Kemp, 1918:99.

Remarks.—Apart from the description of *Caridina annandalei*, Kemp (1918) also reported another taxon under the name of “*Caridina weberi* prox. var. *sumatrensis* De Man, 1899; Kemp (1918: 100) noted that this taxon is similar to *C. weberi sumatrensis* but

“differs from *C. weberi* var. *sumatrensis* in a number of particulars which are apparently of subspecific importance: (i) both dorsal and ventral teeth of the rostrum are rather less numerous, (ii) the antero-inferior angle of the carapace is toothed, (iii) the fingers of the second pereopod are proportionately shorter in relation to the palm and the propodus of the third pereopod shorter in relation to the dactylus and (iv) the eggs are very much larger.”

Based on our current understanding of species of *Caridina*, the larger egg size, which is 1.1 mm by 0.7 mm (vs. 0.4 mm by 0.25 mm in *C. w. sumatrensis*), suggests that the larval development of Kemp's Burmese taxon is of the abbreviated pattern. Based

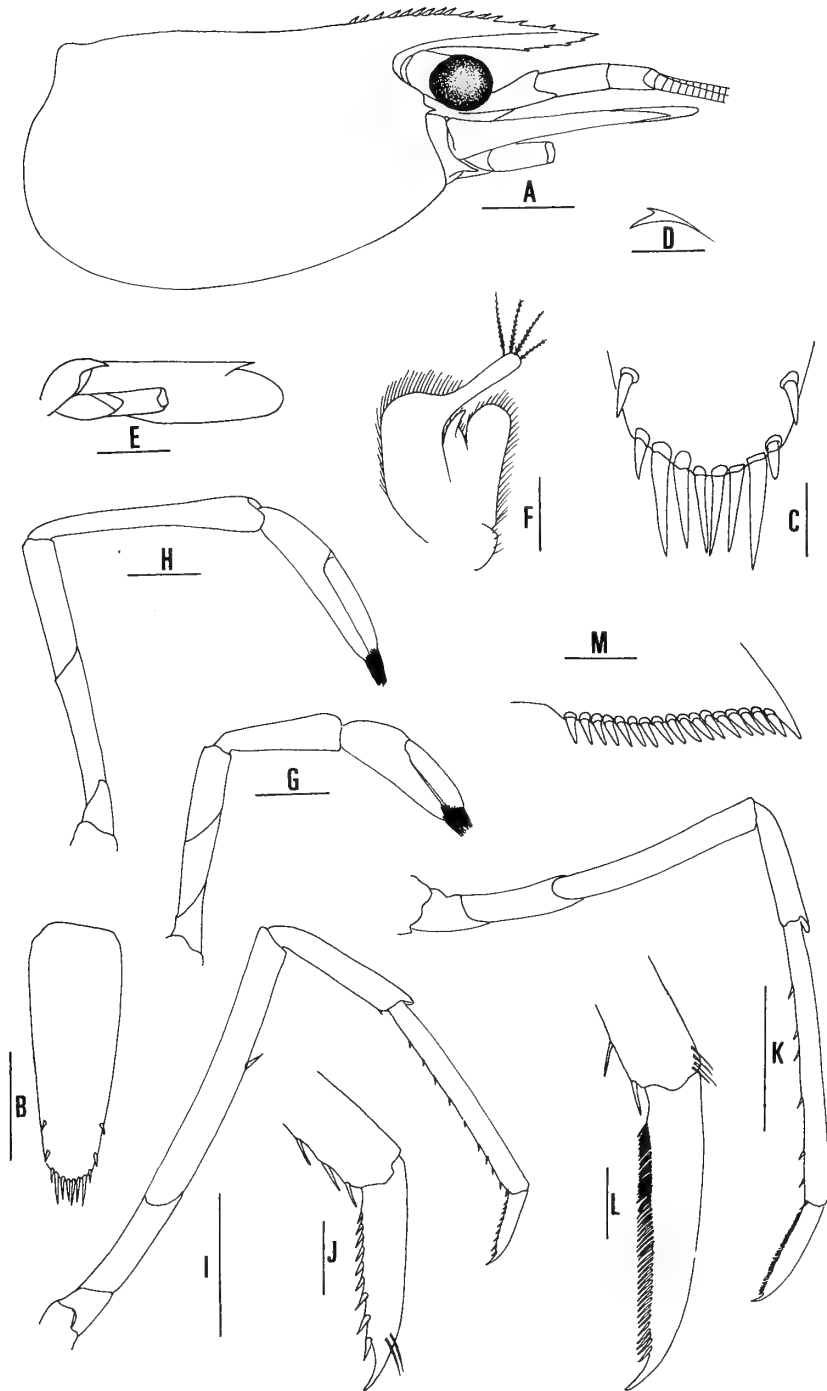


Fig. 7. *Caridina burmensis*, new species, female, cl 3.7 mm (SMNH 13901), holotype, Myitkyina, Myanmar, A, cephalothorax and cephalic appendages; lateral view; B, telson; C, distal part of telson; D, preanal carina; E, scaphocerite; F, first maxilliped; G, first pereopod; H, second pereopod; I, third pereopod; J, dactylus of third pereopod; K, fifth pereopod; L, dactylus of fifth pereopod; M, uropodal diaeresis. Scales: A, B, D, I, K, = 1 mm; C, J, L = 0.2 mm; E, F, G, H = 0.5 mm.

on this consideration, this taxon is thus specifically different from *C. weberi* De Man, 1892, *sensu stricto* and its other known subspecies which have distinctly smaller eggs (De Man 1892, Bouvier 1925). In fact, the overall morphology of Kemp's "form" suggests it cannot be referred to any known taxon. Although we are confident that it is new, the lack of specimens prevents us from naming and describing it for the time being.

Acknowledgments

Thanks are due to Ms. Karin Sindemark (SMNH) for the loan of specimens; Dr. Nguyen Ngoc-Ho (MNHN) for help and hospitality when the first author visited Paris on June 1999, and for checking the type of *Caridina annandalei*; to Mr. Tan Heok Hui and Mr. N. Sivasothi for their fresh collection from Myanmar; to Ms. N. K. Ng, for her help in preparing the map. The present study is partially supported by a research grant (RP950362) from National University of Singapore, to the second author.

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***Calappa pokipoki*, a new species of box crab (Crustacea: Decapoda:
Brachyura: Calappidae) from Hawaii**

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Abstract.—A new species of box crab, *Calappa pokipoki*, is described from Hawaii. This new species resembles *C. gallus* (Herbst), but can easily be distinguished by several carapace features as well as color pattern. *Calappa pokipoki* also resembles *C. bicornis* (Miers), *C. matsuzawa* Galil, *C. sebastieni* Galil and *C. yamasitae* Sakai, but can be separated from these by a suite of distinctive carapace characters.

At present, seven species of calappids are known from Hawaii, *Calappa calappa* (Linnaeus 1758), *C. gallus* (Herbst 1803), *C. hepatica* (Linnaeus 1758), *C. bicornis* (Miers 1884), *Cycloes marierubri* Galil & Clark, 1996, *Mursia hawaiiensis* Rathbun, 1893, and *M. spinimanus* Rathbun, 1906 (Rathbun 1906, Tinker 1965, Galil 1993, 1997; Galil & Clark 1996). Studies of the brachyuran collections in the Bernice P. Bishop Museum showed that Tinker's (1965) record of *C. bicornis* is erroneous, and the specimens which have been referred to this species actually represent a new species, described herein. This new species, while most similar to *C. gallus*, differs from this species in several distinct characters.

Specimens examined during this study are deposited in the Bernice P. Bishop Museum, Honolulu, Hawaii (BPBM); Zoologisk Museum, University of Copenhagen (ZMUC); and the Zoological Reference Collection of the Raffles Museum, National University of Singapore (ZRC). Numerous specimens of *C. gallus*, *C. bicornis* and *C. galloides* from BPBM, ZMUC and ZRC have also been examined for the present comparisons. Measurements provided are listed as the carapace width by length. The abbreviations G1 and G2 are used for the male first and second pleopods respectively.

Taxonomic Account

Family Calappidae

Calappa pokipoki, new species
(Figs. 1, 2, 3a, 4a, 5a-g, 6)

Calappa bicornis.—Tinker, 1965: 74 (not
Calappa bicornis Miers, 1884)

Material examined.—Holotype female (87.8 by 64.5 mm) (BPBM 12073), Kona, Hawaii, coll. research vessel *Townsend Cromwell*, TC 81-01 station 34, 16 Feb 1981.

Paratypes: 1 female (78.8 by 58.8 mm) (ZRC 2000.516), same data as holotype; 1 male (43.5 by 33.5 mm) (BPBM S11259), TC 40 station 2, Penguin Banks, Molokai, 21°09.9'–21°09.8'N, 157°24.1'–157°29.8'W, Hawaii, 182 m, coll. R/V *Townsend Cromwell*, trawl, 6–7 Nov 1968; 1 juvenile (25.3 by 20.0 mm) (BPBM S11255), TC 36 station 33, Penguin Banks, Molokai, 21°02.9'–21°01.6'N, 157°25.9'–157°26.0'W, Hawaii, coll. R/V *Townsend Cromwell*, trawl, 5 Jun 1968; 1 female (46.4 by 36.2 mm) (BPBM S11271), Barber's Point, Oahu, 30 m, Hawaii, coll. 1963; 1 juvenile (13.3 by 11.0 mm) (BPBM S11146), Northwest End, Penguin Banks, Molokai, 21°02.8'N, 157°40.5'W, 182 m, Hawaii, coll. HURL 82-111, *Makalii* submersible, 20 Sep 1982; 1 male (42.4 by

31.6 mm) (ZRC 2000.1798), Molokai, Hawaii, coll. 14 Jun 1959; 1 female (right part of carapace damaged) (BPBM S6688), Hawaii, no other data; 1 male (49.6 by 36.4 mm) (BPBM S5422), 400 yards off Moku- ulua, Oahu, 36 m, Hawaii, coll. Brock, 14 Apr 1949.

Diagnosis.—Carapace dorsal surface covered with relatively large, low, rounded, submammillate granules on anterior half; posterior half with numerous oblique to transverse raised striae; hepatic region strongly depressed; from posterior view, gastric region is highest point, with branchial regions gradually sloping towards margins; frontal margin quadridentate; anterolateral margin with 11 or 12 well marked teeth; clypeiform extension well developed, margin with numerous long, stiff yellow setae which almost completely obscure margin; basal antennal segment with distal margin gently concave; outer surface of manus with well spaced granules; G1 with distal $\frac{1}{4}$ slightly sinuous; G2 subequal in length to G1, distal segment relatively short, tip of flange between distal and basal segments faintly tricuspid.

Description.—Carapace subtriangular in shape; dorsal surface distinctly convex; anterior half covered with relatively large, low, rounded, submammillate granules which are closely appressed basally; posterior half with numerous oblique to transverse raised striae which are longer towards lateral margins; striae near margins more prominent, beaded, appearing almost serrated. Hepatic region strongly depressed. Epigastric region with 2 distinct transverse tubercles. Gastric region strongly raised, median part especially high. Gastric and cardiac regions separated from branchial regions by deep longitudinal groove. Suborbital region with 2 large transverse granules, rest of surface finely granulated. Frontal margin thickened, quadridentate, median part prominently produced anteriorly, median teeth separated by distinct U-shaped sulcus. Supraorbital margin with small but distinct inner tooth; inner half of margin

prominently swollen; outer part with 2 deep narrow fissures. Eyes folding obliquely. External orbital tooth very low, rounded. Anterolateral margin arcuate, clearly demarcated from posterolateral margin by distinct cleft, lined with scattered long, stiff yellow setae which partially obscure margin; first tooth (subhepatic tooth) large, low, conical; subsequent 5 teeth small but clearly discernible, with bicuspid tips, lateral margins with minute denticles; last 6 teeth ca. twice as large as preceding teeth, with sharp tips, lateral margins distinctly denticulate. Posterolateral clypeiform extension well developed, lined with numerous long, stiff yellow setae which almost completely obscure margin; anterior part with 3 broadly triangular teeth (larger posteriorly), each tooth with denticulate margins and median ridge; posterior part with 3 low, broadly triangular teeth, first tooth longest, second tooth slightly shorter than first, third tooth (nearest posterior carapace margin) ca. 0.5 times length of second tooth; each tooth with strongly denticulated margins and median ridge, margin appearing prominently serrated; margins lined with long, stiff yellow setae which almost obscure margin. Posterior carapace margin convex, margin distinctly denticulated, appears serrated, lateral parts lined with long, stiff yellow setae. Basal antennal segment subtriangular, surface finely granulated, distal margin gently concave. Longitudinal endostomial septum with shallow concavity on anterior border, edge just visible when first maxillipeds closed.

Minor left chela (without cutting tooth) with prominent dorsal crest, with 6 lamelliform teeth, first bilobed, low, next 5 high, acutely triangular; outer surface of manus granulated, granules not arranged in distinct rows; upper half with several large granules; lower $\frac{1}{3}$ surface with numerous subsquamose granules, becoming smaller towards tip of pollex; subsquamiform granules on proximal lower surface of manus becoming larger and fewer towards carpus; ventral outer margin lined with row of laterally directed granules, appears distinctly

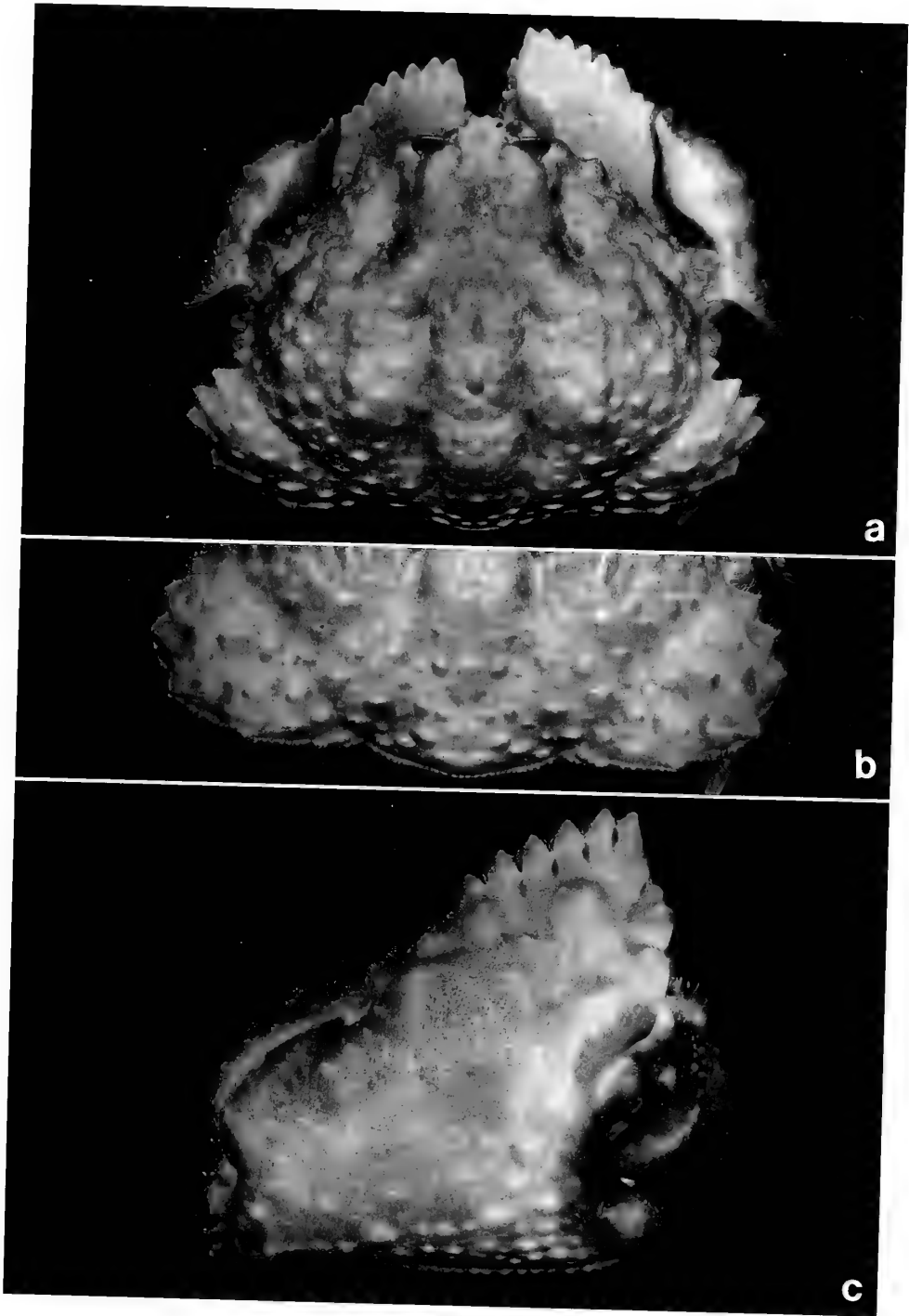


Fig. 1. *Calappa pokipoki*, new species, holotype female (87.8 by 64.5 mm) (BPBM S5422). a, dorsal view; b, posterior carapace margin (dorsal view); c, right chela (outer view).

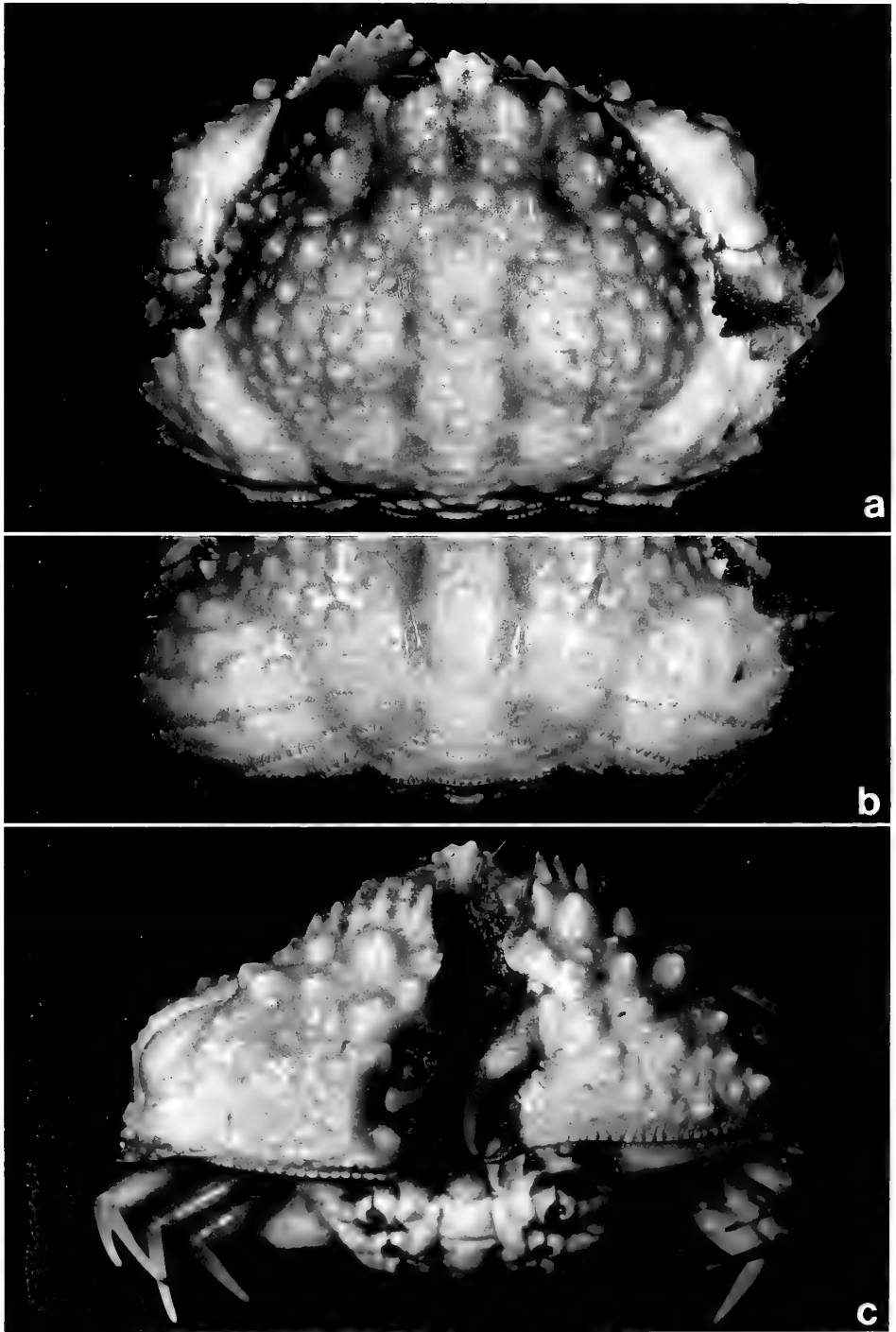


Fig. 2. *Calappa pokipoki*, new species, paratype male (42.4 by 31.6 mm) (ZRC 2000.1798). a, dorsal view; b, posterior carapace margin (dorsal view); c, chelipeds (outer view).

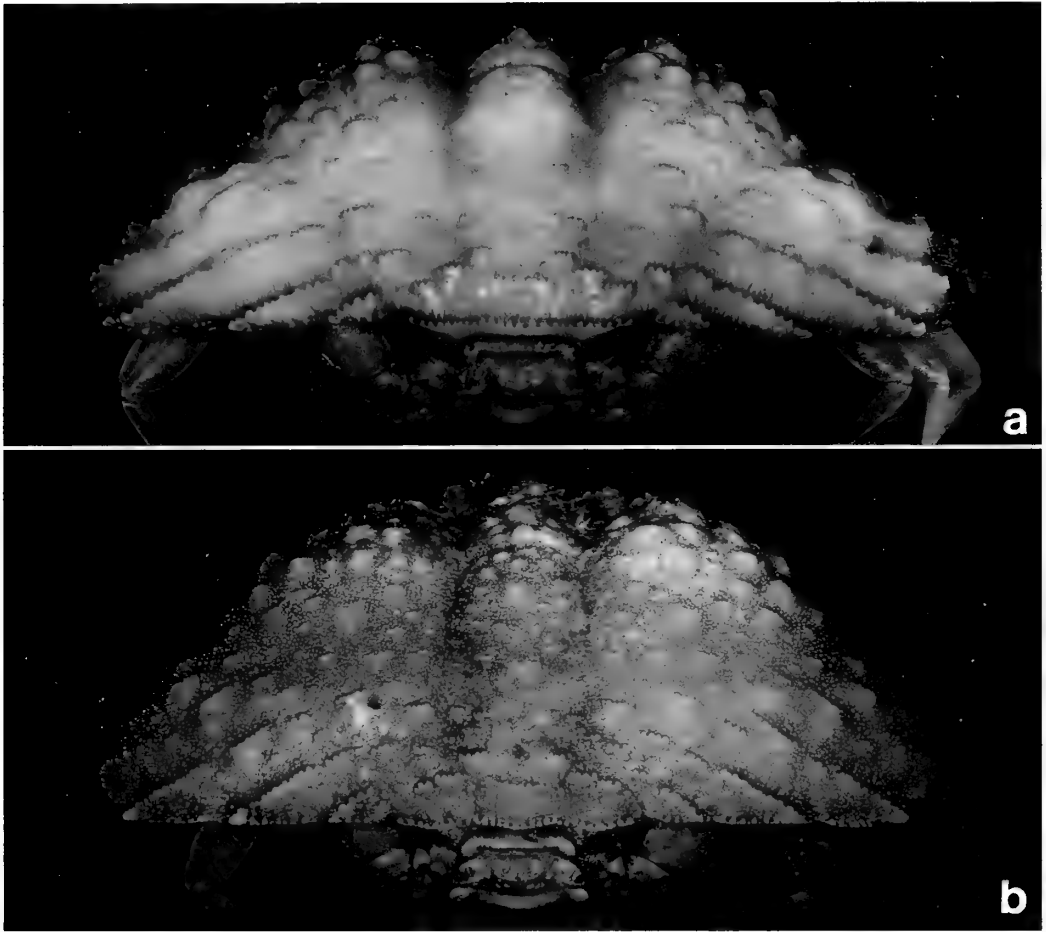


Fig. 3. Carapace showing degree of convexity (posterior view). a, *Calappa pokipoki*, new species, paratype male (42.4 by 31.6 mm) (ZRC 2000.1798); b, *C. gallus*, male (48.4 by 36.4 mm) (ZRC).

serrated, tooth adjacent to carpus low but distinct, subtruncate, sublamelliform; dactylus very slender, recurved, distal half pigmented, smooth; proximal part of dactylus granulated. Major right chela (with special cutting tooth) similar in shape and features to minor chela, but dorsal crest, with 7 lamelliform teeth, first bilobed, low, next 6 high, acutely triangular; entire dactylus pigmented, proximal surface granulated, with subtruncate tooth proximally.

Ambulatory legs relatively slender, unarmed, smooth; second pair longest. Dactylus very slender, styliform, gently curved. Last leg with subdistal part of ventral margin of fused basis-ischium with tuft of long

stiff setae; subproximal part of ventral margin of merus with short row of long stiff setae.

Abdomen narrowly triangular. First segment with proximal margin lined with submedian low granules, appearing gently serrated, with long, stiff yellow setae, outermost parts smooth, glabrous. Second segment with distinct granules on outer and median parts, lined with long, stiff yellow setae, intermediate areas unarmed, glabrous. Third to fifth segments fused, but lateral clefts separating segments still discernible; third segment subrectangular, outer submarginal part with scalloped features, fourth segment trapezoidal, lateral margins

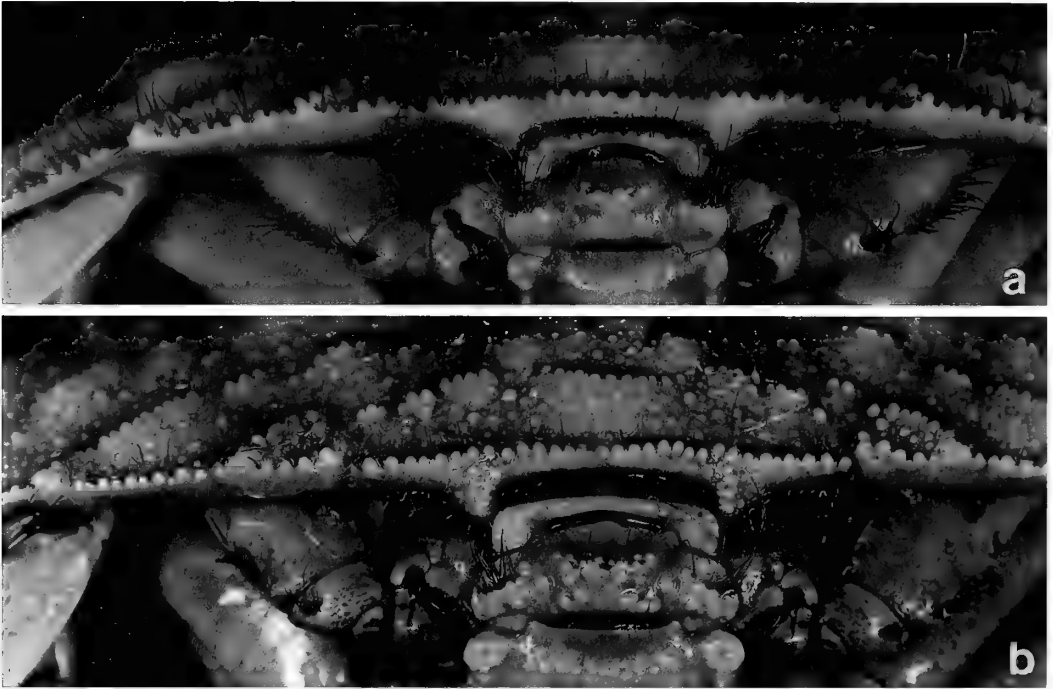


Fig. 4. Posterior carapace margin, first two male abdominal segments and base of last pair of ambulatory legs. a, *Calappa pokipoki*, new species, paratype male (42.4 by 31.6 mm) (ZRC 2000.1798); b, *C. gallus*, male (48.4 by 36.4 mm) (ZRC).

deeply concave; fifth segment almost squarish, with deeply concave lateral margins; sixth segment slightly elongate, lateral margin sinuous. Telson acutely triangular, lateral margin gently concave to almost straight.

G1 relatively stout, almost straight, distal $\frac{1}{4}$ slightly sinuous, more slender than median part; tip truncate; distal surfaces lined with numerous small posteriorly directed spinules. G2 subequal in length to G1, gently curved; distal segment relatively short, tip rounded; junction between basal and distal segments with short flange, tip of flange faintly tricuspid; inner margin of base of basal segment bilobed.

Variation.—The specimens do not vary substantially in morphology, with the non-sexual characters relatively constant. The setation on the carapace margin, ambulatory legs and abdomen is less dense in small specimens (less than 30 mm carapace width). The chela is also relatively higher

in larger specimens, regardless of sex. One paratype female (78.8 by 58.8 mm, ZRC 2000.516) is very unusual in that the special cutting tooth is on the left chela rather than the right. In all known specimens of all other species of *Calappa* Weber, 1795, as well as all the other specimens of *C. pokipoki*, the special cutting tooth is on the right chela and is adapted to peel right-apertured gastropods (see Ng & Tan 1984, 1985).

Color (in preservative).—In adult specimens, anterior half of carapace orange; posterior $\frac{1}{3}$ dirty white with scattered uneven brown spots; zone where 2 color zones meet uneven but well marked. Despite the age of the present specimens, most of them still show the pattern described above quite clearly.

Etymology.—The species name is derived from the Hawaiian name for *Calappa*, “Poki-poki.” The name is used here as a noun in apposition.

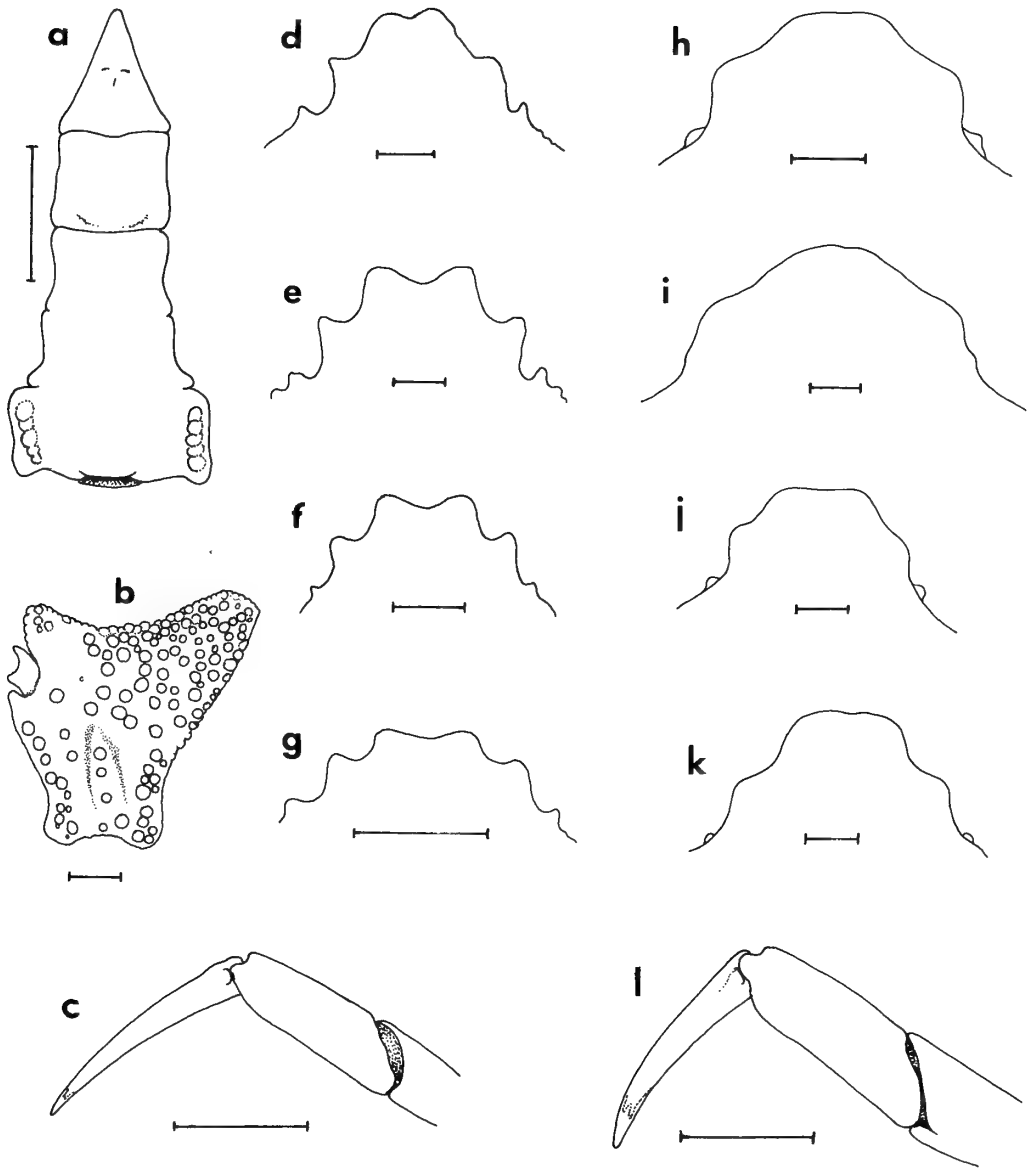


Fig. 5. a–g, *Calappa pokipoki*, new species: a, male abdomen; b, left basal antennal segment; c, l, left second ambulatory leg (dactylus and propodus); d–k, frontal margins; a, b, c, d, holotype female (87.8 by 64.5 mm) (BPBM S5422); e, male (43.5 by 33.5 mm) (BPBM S11259); f, juvenile (25.3 by 20.0 mm) (BPBM S11255); g, juvenile (13.3 by 11.0 mm) (BPBM S11146); h–l, *C. gallus*; h, female (47.2 by 36.2 mm) (BPBM 5078); i, female (46.2 by 35.8 mm) (BPBM 967); j, male (33.2 by 25.5 mm) (BPBM 3303); k, female (46.8 by 37.8 mm) (BPBM 1303). Scales: a, c, l = 5.0 mm; b, d–k = 1.0 mm.

Remarks.—*Calappa pokipoki*, new species, is most similar to *C. gallus* (Herbst 1803), a common species in Hawaii, but the two can easily be distinguished by the frontal margin and carapace physiognomy. The

BPBM has a good series of specimens of *C. gallus* which allows for a very thorough competition of the two species to be made. The frontal margin of *C. pokipoki* (irrespective of sex or size) is more produced,

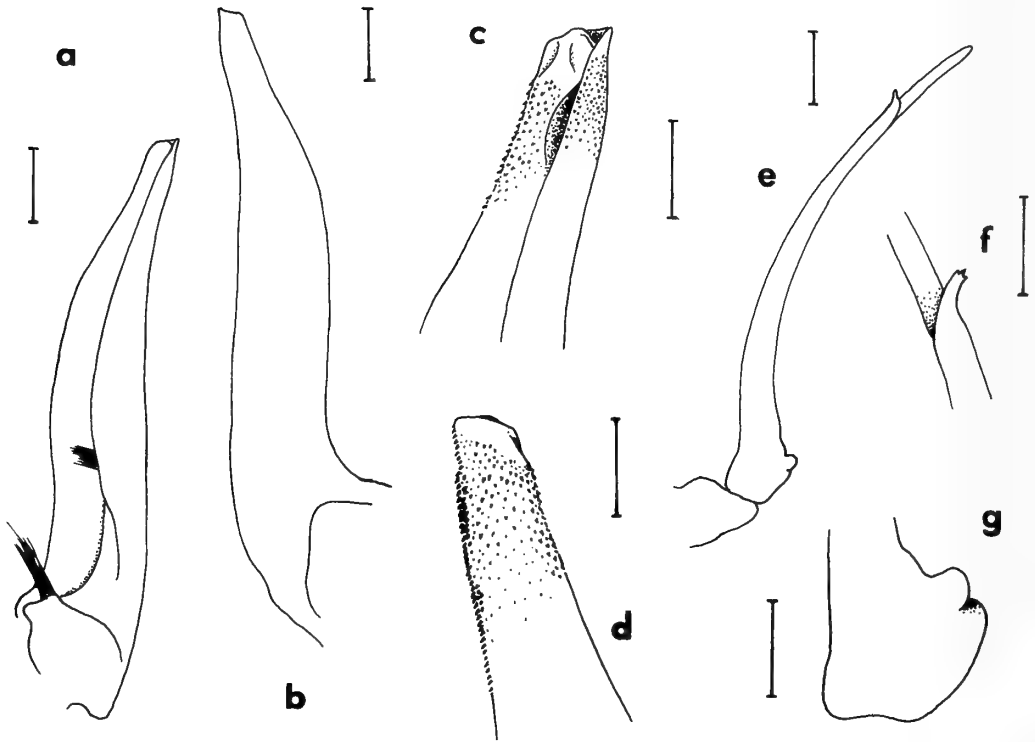


Fig. 6. *Calappa pokipoki*, new species, paratype male (49.6 by 36.4 mm) (BPBM S5422). a, left G1 (dorsal view); b, left G1 (ventral view) (setae not drawn); c, distal part of left G1 (dorsal view); d, distal part of left G1 (ventral view); e, left G2 (ventral view); f, flange at junction of basal and distal segments of G2; g, G2 basal segment. Scales: a, b, e = 1.0 mm; c, d, f, g = 0.5 mm.

with four well defined teeth, the two median ones projecting anteriorly from the lateral ones and are separated by a distinct cleft (Fig. 5d–g). In *C. gallus*, however, the frontal margin is subquadrate, and although the lateral parts may appear stepped, it never develops even a trace of a tooth (Fig. 5h–k). The carapace of *C. pokipoki* is distinctly less swollen compared to that of *C. gallus*. Observed frontally or from the posterior, the branchial regions of *C. pokipoki* in particular, are prominently lower and gradually slope towards the lateral margins from the gastric region which is the highest point of the carapace (Fig. 3a). For *C. gallus*, the gastric and branchial regions are equally high (Fig. 3b, see also Galil 1997, Sakai 1999).

In addition, several more subtle characters can also be used to distinguish the two

species. Specimens of *C. pokipoki* larger than 40 mm carapace width can also easily be distinguished from *C. gallus* by the much denser and longer setae lining the posterolateral margins and chelipedal meral lobe which almost completely obscure the margins (Fig. 4a) from the dorsal view. In *C. gallus*, these setae are much less dense even in large specimens, and never completely obscure the margins (Fig. 4b). The ambulatory dactyli of *C. pokipoki* is also relatively more slender and somewhat longer (Fig. 5c) compared to those of *C. gallus* (Fig. 5l). The second male abdominal segment is also distinctly more granulose in *C. gallus* (Fig. 4b vs. 4a). In contrast, the posterolateral margin of *C. pokipoki* has more widely spaced granules (Figs. 3a, 4a vs. 3b, 4b). In *C. gallus*, the setose parts of the basis-ischium and merus of the last ambu-

latory leg have gentle but distinctly scalloped granules (Fig. 4b), but in *C. pokipoki* these parts are almost smooth (Fig. 4a).

There also appear to be color differences between *C. pokipoki* and *C. gallus*. *Calappa pokipoki* clearly has a "bicolored" carapace when adult, with the anterior half of the carapace darker colored and the posterior part white with scattered brown spots, with the two zones more or less clearly demarcated. This color pattern is similar to that reported for species like *C. undulata* Dai & Yang, 1991, and *C. bicornis* Miers, 1884 (see Miyake 1983, Chen 1993, Ng et al. 2000).

In the form of the frontal margin (and general color pattern), *C. pokipoki* certainly resembles *C. bicornis*, and it is not surprising that Tinker (1965) referred it to this species. Tinker's (1965) material is in the BPBM and his figure is probably based on one of the specimens listed above. *Calappa bicornis*, however, can easily be distinguished from *C. pokipoki* by the dorsal carapace surface of *C. bicornis* having larger and/or more mammillate tubercles, less expanded clypeiform process, relatively much deeper cleft on the frontal margin, deeply clefted anterior margin of the basal antennal segment which appears bidentate (vs. gently concave), serrated supra- and suborbital margins (vs. smooth), proportionately more slender ambulatory meri and much longer dactyli, with the legs appearing banded in life (vs. uniformly colored and patterned) and the distal segment relatively more pod-like (vs. evenly cylindrical with a rounded tip) (present specimens, see also Galil 1997, Ng et al. 2000).

In the morphology and sculpture of the carapace, *C. pokipoki* also resembles *C. matsuzawa* Galil, 1997, described and known only from Japan thus far. The clypeiform process of *C. matsuzawa*, however, is relatively less expanded, the anterior part of the anterolateral margin has no well marked teeth (vs. with 6 distinct teeth in *C. pokipoki*), and the front is less well developed (Galil 1997:304, Fig. 17b). In the

form of the frontal margin, relatively more expanded clypeiform process, granulation features of the suiter surface of the chela and structure of the G1, *C. pokipoki* closely resembles *C. sebastieni* Galil, 1997, known only from the Marquesas. *Calappa sebastieni* can easily be separated from *C. pokipoki* by its less broad carapace (length to width ratio 1.6 vs. 1.3) and much smoother dorsal carapace surface which does not have any prominent large granules on the anterior part of the carapace (Galil 1997: 312, fig. 17f). In the form of its dorsal carapace sculpture, *C. pokipoki* superficially resembles *C. yamasitae* Sakai, 1980, known only from Japan, but the latter species can be separated by its proportionately broader carapace (width to length ratio 1.6 vs. 1.3), bidentate (vs. quadridentate) frontal margin and the dorsal crest of larger chela having more teeth (9–10 vs. 6–7) (cf. Sakai 1980: 5, frontispiece fig. 2).

Calappa pokipoki also bears a close resemblance to the Atlantic species previously referred to "*Calappa gallus*" (see Monod 1956, Manning & Holthuis 1981). Manning & Chace (1990) referred the old records of "*Calappa gallus*" (nec Herbst 1803) from the Atlantic to *C. galloides* Stimpson, 1859. I have examined specimens from various parts of the Atlantic and there appears to be at least two species referable to "*C. galloides*" from there; one with a prominently quadridentate frontal margin and less inflated carapace (*C. galloides* s. str.); and another with a more rounded frontal margin and strongly inflated carapace. In addition, there is one more supposed junior synonym of *C. galloides*, *C. squamosa* Desbonne in Desbonne & Schramm, 1867, described from Guadeloupe. Although the resolution of the taxonomy of these Atlantic taxa is well outside the scope of the present paper, it is nevertheless useful to note that *C. pokipoki* is very unlikely to be conspecific with any of the above taxa. *Calappa pokipoki* can be separated from *C. galloides* (and *C. squamosa*) by its relatively more

expanded clypeiform extension, more rounded posterior carapace margin and much higher dorsal crest of the chela.

Calappa pokipoki is known only from the Hawaiian islands and its vicinity thus far. All the type specimens have been collected from sublittoral waters. *Calappa galus* on the other hand, has a very wide Indo-West Pacific distribution and is common from intertidal to deeper waters.

Acknowledgments

I am most grateful to Lu Eldredge who invited me to Hawaii to work on the crabs in the BPBM, and the Edmondron Fund for supporting the visit. The hospitality and kindness of all the folks in the BPBM also is very much appreciated. Torben Wolff and Danny Jacobsen (ZMUC) kindly allowed me access to their valuable collections.

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First report of *Nematopaguroides* (Crustacea: Decapoda: Paguridae) in the Indo-Pacific, and the description of a new species

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Abstract.—A new species of the hermit crab genus *Nematopaguroides* Forest & de Saint Laurent, *N. reconditus*, has recently been recognized from the South China Sea. This is the first record of the genus outside the subtropical western Atlantic Ocean.

The genus *Nematopaguroides* was proposed by Forest & de Saint Laurent (1968) for *Nematopaguroides fagei* Forest & de Saint Laurent, 1968, and distinguished from *Nematopagurus* A. Milne-Edwards & Bouvier, 1892, by the presence, in males of *Nematopaguroides fagei*, of an externally directed, filamentous right sexual tube, possible absence of a similar extension of the vas deferens from the left, and the absence, in females, of paired and modified first pleopods. A second species, *Nematopaguroides? pusillus* Forest & de Saint Laurent, 1968, was tentatively assigned to the genus based upon a single male specimen in which both right and left sexual tubes were well developed. Both species were collected during the exploratory voyage of the "Calypso" to the east coast of South America in 1961–1962. Although these species have been reported in Brazilian carcinological literature (e.g., Coêlho & Ramos 1972, Coêlho & Santos 1980, Coêlho & Ramos-Porto 1987, 1995; Rieger 1998, Melo 1999), most if not all citations are based upon the original descriptions of Forest & de Saint Laurent (1968). The only additional record of the genus was that of specimens attributed to *Nematopaguroides* cf. *pusillus* by Reed et al. (1982) from off the east coast of Florida.

Extensive surveys in the Hainan Island

region of the South China Sea, conducted by Chinese research vessels (R/V) during the National Comprehensive Oceanographic Survey (NCOS) of 1958–1960 resulted in the collection of a wealth of hermit crabs that are only now being studied. We are already aware of several new records for China that will be reported upon in subsequent publications. However, the discovery of a new species of the genus *Nematopaguroides* warrants particular attention. This is the first report of this genus in the western Pacific. Additionally, the development of a left sexual tube in males of *Nematopaguroides reconditus*, new species, represents an intermediate condition between *N. fagei* and *N. pusillus*, and confirms the accuracy of the assignment of the latter species to *Nematopaguroides*. The holotype and majority of paratypes of the new species are deposited in the Institute of Oceanology, Chinese Academy of Sciences, Qingdao (IOCAS). A pair of paratypes has been deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). An indication of specimen size is given by the shield length (sl) measured from the midpoint of the rostral lobe to the midpoint of the posterior margin of the shield; the abbreviation ovig. refers to the ovigerous condition of some females.

Nematopaguroides Forest & de Saint
Laurent, 1968

Nematopaguroides Forest & de Saint Laurent, 1968:156.

Type species.—*Nematopaguroides fagei* Forest & de Saint Laurent, 1968; gender masculine.

Diagnosis.—Eleven pairs of biserial, phyllobranchiate gills. Rostrum broadly rounded. Maxillule with external endopodal lobe obsolete. Ischium of third maxilliped with well developed crista dentata and 1 accessory tooth; sternite of third maxillipeds unarmed. Chelipeds subequal or somewhat unequal. Males with symmetrical coxae of fifth pereopods, elongate right sexual tube directed obliquely toward exterior and with terminal filament; left coxa with or without sexual tube developed; 3 unpaired, unequally biramous left pleopods (3–5). Females with paired gonopores; no paired, modified first pleopods; unpaired left pleopods 2–5. Telson with prominent lateral indentations dividing anterior and posterior lobes equally or unequally; terminal margin with distinct median cleft.

Remarks.—Forest & de Saint Laurent (1968) remarked on the superficial similarity between species of *Nematopaguroides* and *Nematopagurus*, and that similarity is certainly apparent in *N. reconditus*, new species, as well. The new species differs from both Atlantic members of the genus in being an appreciably larger species, occurring at distinctly greater depths, and morphologically having noticeably more pronounced dilation of the corneas, more distinctly ovate ocular acicles, a roundly rectangular anterior lobe of the sternite of the third pereopods, and telsonal lateral margins provided with several short stiff setae.

The paucity of specimens of the Western Atlantic species of the genus precluded description of the mouthparts of *Nematopaguroides* by Forest & de Saint Laurent (1968). The mouthparts of *N. reconditus*, new species, are described herein.

Nematopaguroides reconditus, new species
Figs. 1, 2

Holotype.—S.E. off Hainan Is., South China Sea, R/V No. 171, Stn. 6144, 18°30'N, 111°00'E, 148 m, soft mud substrate, 22 Apr 1959, ♂ sl = 4.2 mm, IO-CAS L62B.

Paratypes.—S.E. off Hainan Is., South China Sea: R/V No. 121, Stn. 6122, 10°00'N, 111°30'E, 145 m, sandy mud substrate, 19 Oct 1959, 1 ♂ sl = 3.0 mm, 2 ♀ sl = 2.8, 3.3 mm, IOCAS N91B-31; R/V No. 101, Stn. 6123, 18°30'N, 111°30'E, 220 m, muddy sand substrate, 2 Aug 1960, 1 ♀ sl = 2.6 mm, IOCAS N115B; R/V 101, Stn. 6145, 18°15'N, 111°00'E, 173 m, soft mud substrate, 4 Aug 1960, 1 ovig. ♀ sl = 3.9 mm, IOCAS N173B-25; R/V No. 101, Stn. 6162, 18°00'N, 110°30'E, 145 m, mud substrate, 5 May 1960, 1 ♂ sl = 3.9 mm, 1 ♀ sl = 2.3 mm, 1 ovig. ♀ sl = 3.2 mm, IOCAS N198B-8; R/V No. 101, Stn. 6189, 17°00'N, 109°30'E, S, 162 m, coarse sand with mud substrate, 13 May 1960, 2 ♂ sl = 3.1, 4.4 mm, 1 ovig. ♀ sl = 3.5 mm, IOCAS N205B-48, 1 ♂ sl = 2.9 mm, 1 ovig. ♀ sl = 3.1 mm, USNM 253650.

Description.—Shield (Fig. 1A) slightly longer than broad to considerably broader than long; anterior margin between rostral lobe and lateral projections concave; anterolateral margins sloping or weakly terraced; posterior margin roundly truncate; dorsal surface with longitudinal row of sparse tufts of short stiff setae on either side, laterad of midline, few sparse tufts of short setae on or near each lateral margin, 2 sparse tufts of very short setae adjacent to rostral margin. Rostrum very broadly rounded, not produced beyond level of lateral projections. Anterior carapace often distinctly produced anteromesially of lateral projections and conspicuous in dorsal view. Lateral projections subtriangular, with or without laterally directed spinule.

Ocular peduncles short but 0.75–0.85 length of shield; dorsal surfaces each with 2 median sparse tufts of short stiff setae;

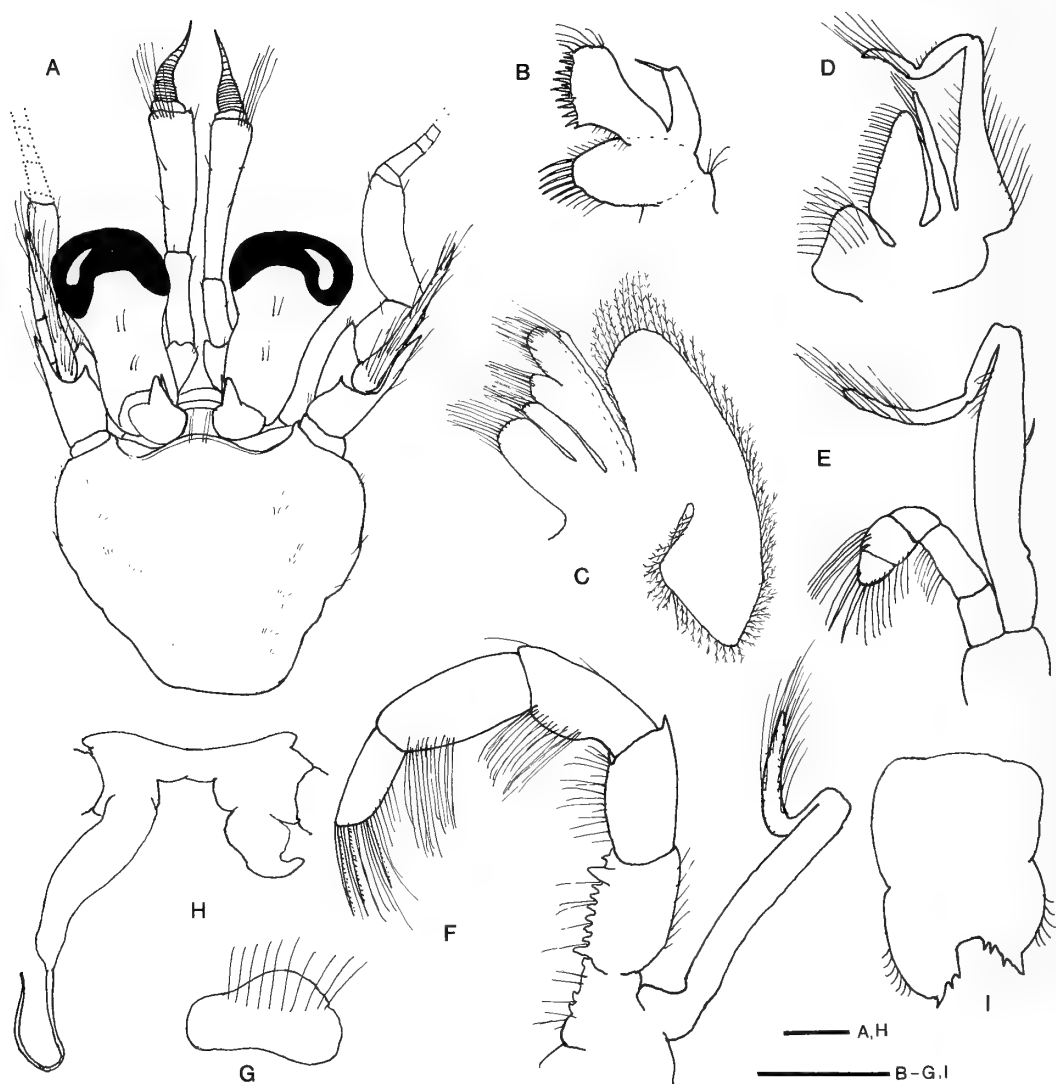


Fig. 1. *Nematopaguroides reconditus*, new species. A, G, H, male holotype, IOCAS L62B; B-F, female paratype from Stn. 6189, IOCAS N205B; I, male paratype from Stn. 6162; A, shield and cephalic appendages (aesthetascs not illustrated); B, maxillule (left, external view); C, maxilla (left, external view); D, first maxilliped (left, external view); E, second maxilliped (left, external view); F, third maxilliped (left, external view); G, anterior lobe of sternite of third pereopods; H, sternite and coxae of male fifth pereopods; I, telson. Scales equal 1 mm.

corneas strongly dilated, corneal diameter 0.65-1.0 of peduncular length, occasionally exceeding peduncular length. Ocular acicles small, ovately triangular, with deeply concave dorsal surface; terminating subacutely and prominent submarginal spine.

Antennular peduncles moderately long, exceeding distal margins of corneas by

nearly entire length of ultimate segments. Ultimate segment with 1 or 2 setae on distal margin laterally, subdistal transverse row of 5 or 6 very long setae, and few additional short setae scattered on surfaces. Penultimate and basal segments each with few scattered setae.

Antennal peduncles, overreaching distal

margins of corneas by 0.10–0.50 length of fifth segments. Fifth and fourth segments with few scattered setae. Third segment usually with small spine and sparse tuft of moderately long setae at ventrodistal angle, occasionally without spine. Second segment with dorsolateral distal angle produced into moderately long spine-like process, usually reaching to mid-length of fourth peduncular segment; dorsomesial distal angle with small spine; lateral and mesial margins with few stiff setae. First segment with spinule on ventrodistal margin. Antennal acicle moderately long, reaching to mid-length of ultimate peduncular segment; arcuate, terminating in acute spine; mesial margin with tufts of long stiff setae. Antennal flagella long, overreaching tip of right cheliped; 2 or 3 moderately short to moderately long setae every 6–10 articles in distal half, more closely-spaced proximally.

Mandible with 3-segmented palp. Maxillule (Fig. 1B) with internal lobe of endopod weakly produced, 1 terminal seta; external lobe obsolete. Maxilla (Fig. 1C) with endopod slender, slightly shorter than distal lobe of basal endite, but overreaching distal margin of scaphognathite. First maxilliped (Fig. 1D) with slender endopod and very slender proximal segment of exopod. Second maxilliped (Fig. 1E) without distinguishing characters. Third maxilliped (Fig. 1F) with 2 or 3 spines on basis; ischium with well developed crista dentata and 1 accessory tooth; merus with prominent dorsodistal spine. Sternite of third maxillipeds unarmed and without noticeable median notch.

Chelipeds subequal; right stouter, but not necessarily longer than left, both moderately to appreciably elongate. Right cheliped (Figs. 2A, B) with dactyl 0.70–1.10 length of palm; cutting edge with 2 widely-spaced, strong calcareous teeth in proximal 0.75, small corneous teeth distally, terminating in small corneous claw and slightly overlapped by fixed finger, dorsal surface with transverse rows of sparse tufts of setae mesially and extending onto rounded dor-

somesial margin, marginal longitudinal row of longer stiff setae extending nearly to tip, few tufts of short setae adjacent to cutting edge. Palm slightly shorter to approximately equaling length of carpus; dorsomesial margin with row of quite small spinulose tubercles, mesial face dorsally with 1 or 2 rows of sparse tufts of long stiff setae; dorsal surface with 9–12 irregular and interrupted transverse rows of stiff setae and occasionally short longitudinal row of 3 or 4 spinules in midline proximally, fewer and more widely-spaced transverse rows of setae on fixed finger, dorsolateral margin with few low tuberculate projections or small spines proximally; sometimes margin elevated to form very low ridge and lined with long stiff setae; lateral and ventral surfaces each with short transverse rows of long stiff setae, fewer in number ventrally; cutting edge of fixed finger with 1 small and 1 large elongate calcareous tooth proximally, row of small calcareous teeth in distal half interspersed with minute corneous teeth, terminating in small calcareous claw; row of tufts of short setae on adjacent dorsal surface. Carpus approximately equal to length of merus; dorsodistal margin with 1 spine mesially and row of stiff setae; dorsomesial margin with row of spines, at least in distal half and each spine usually accompanied by short setiferous ridge, dorsal surface with numerous low, setiferous ridges, dorsolateral margin not distinctly delimited, but with somewhat irregular row small spines, most accompanied by setiferous ridges; lateral and mesial faces each with numerous short transverse or vertical rows of long stiff setae, sometimes capsulate on lateral face; ventral surface with few low ridges and long setae, ventrolateral distal angle with 1 or pair of subacute spines. Merus subtriangular, dorsal margin with irregular row of short transverse scute-like ridges extending onto mesial and lateral faces and accompanied by long setae; ventrolateral margin with row of low transverse ridges and long stiff setae, 2 or 3 moderate to widely-separated spines in distal half; ven-

tromesial margin and ventral surface also with transverse ridges and long stiff setae, ventromesial distal angle usually with small spine, ridges of ventral surface sometimes accompanied by small subacute spines. Ischium with 2 or 3 short transverse ridges and long setae on ventromesial margin. Coxa occasionally with small acute spine at ventromesial distal angle.

Left cheliped (Fig. 2C) reaching nearly to tip of dactyl of right, sometimes beyond; moderately slender. Dactyl 1.5 to approximately twice length of palm; cutting edge with row of small corneous teeth, terminating in small corneous claw and slightly overlapped by fixed finger, surfaces and margins unarmed but with setation as in right. Palm slightly more than half length of carpus; dorsomesial margin with few small blunt or spinulose tubercles, occasionally small spines proximally, decreasing in size and becoming obsolete or appearing only as tiny granules distally; dorsal surface, like that of right, with short irregular and interrupted transverse rows of long stiff setae, occasionally with short longitudinal row of 3–5 small spines on proximal midline, setation of other surfaces also like that of right; dorsolateral margin with slightly elevated, occasionally spinulose ridge lined with long setae; cutting edge with row of widely-spaced, small calcareous teeth interspersed with very small corneous teeth. Carpus approximately equal to length of merus; dorsodistal margin with 1 small spine mesially and often second smaller spine laterally, dorsomesial and dorsolateral margins each with row of spines accompanied by transverse ridges of long setae, spines of dorsomesial margin more prominent and often somewhat hooked, dorsal surface with short transverse setiferous ridges; lateral, mesial, and ventral surface with setation as on right. Merus with setation also as on right; ventromesial and ventrolateral distal angles each with moderately prominent spine. Ischium with 3 or 4 short transverse, tuberculate ridges and long setae, frequently small spine at

ventrolateral distal angle. Coxa sometimes with spine at ventromesial distal angle.

Ambulatory legs (Figs. 2D, E) overreaching right cheliped by 0.50–0.75 length of dactyls. Dactyls long and slender, 1.25–1.75 length of propodi; in dorsal view, distal 0.35 distinctly twisted; in lateral view, distal 0.35 strongly curved ventrally; each terminating in small corneous claw; dorsal surfaces each with row of low protuberances, increasing in strength distally and accompanied by long stiff setae; mesial faces each with row of long stiff setae ventrally, rather widely-spaced in proximal 0.65, but becoming closely-spaced distally; lateral faces each with few sparse tufts of setae, most abundant on left third; ventral margins unarmed. Propodi 0.25–0.40 longer than carpi; dorsal surfaces each with double row of short transverse ridges extending onto lateral faces and set with moderately long stiff setae, lateral face of left third usually with more numerous tufts of setae; mesial and ventral surfaces glabrous or with few scattered short setae. Carpi 0.65–0.90 length of meri; dorsal surfaces of second pereopods each with spine at distal angle and 1–6 additional spines, usually also 1–3 proximally on third right pereopod, all also with row of tufts of stiff setae; lateral faces each with 2 or 3 rows of short transverse ridges and short setae; ventral surfaces each with few setae on distal margin; mesial faces usually glabrous, occasionally with few scattered setae. Meri laterally compressed; dorsal surfaces each with row of transverse scute-like ridges and long stiff setae; lateral faces each with 1 or 2 longitudinal rows of short setae in ventral half; mesial faces glabrous or with very few sparse tufts of short setae; ventral surfaces of second pereopods each usually with 1–5 acute spines or with 1 or 2 spines distally and 3 or 4 blunt or spinulose protuberances proximally, accompanied by tufts of setae; third with only tufts of setae. Ischia each with few setae dorsally and ventrally. Anterior lobe of sternite of third pereopods (Fig. 1G) roundly subrectangular, with long setae on or adja-

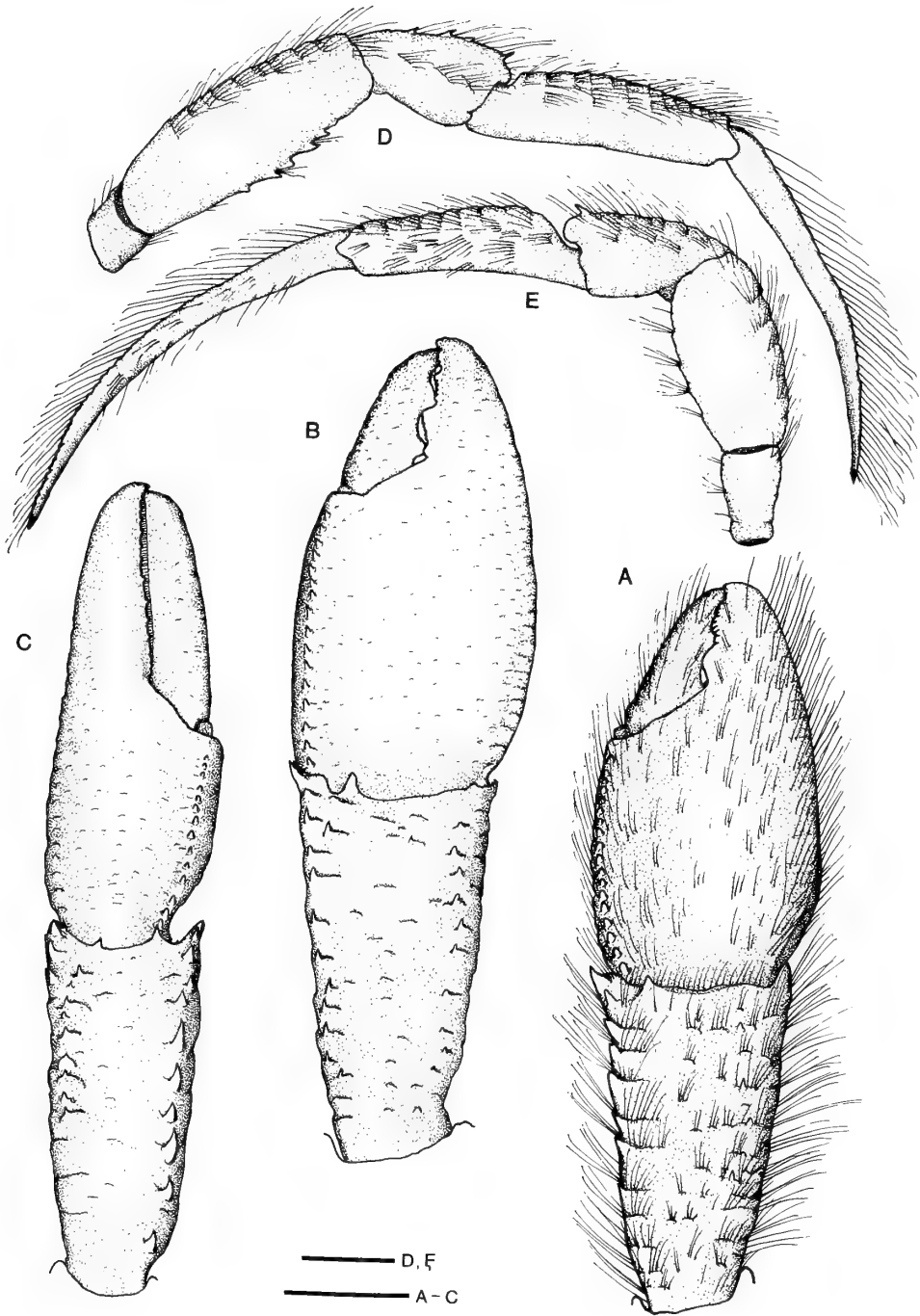


Fig. 2. *Nematopaguroides reconditus*, new species. A, male paratype from Stn. 6162, IOCAS N198B-8; B-E, male holotype, IOCAS L62B: A, carpus and chela of right cheliped (dorsal view, setae omitted); B, carpus and chela of left cheliped (dorsal view, setae omitted); C, carpus and chela of left cheliped (dorsal view, setae omitted); D, right second pereopod (lateral view); E, left third pereopod (lateral view). Scales equal 2 mm.

cent to anterior margin. Fourth pereopods semichelate; dactyls long and slender, usually with prominent preungual process at base of claw; propodi with tufts of long setae dorsally and ventrolaterally; carpi with setose lateral faces.

Males with well developed, elongate sexual tube (Fig. 1H) produced from coxa of right fifth pereopod, stout in proximal 0.35–0.50, filiform distally, coxa of left fifth with short sexual tube, moderately stout proximally, shorter distal portion appreciably more slender but not filiform; unpaired left pleopods 3–5 unequally biramous, fifth with external ramus appreciably longer and more setose than third and fourth. Females with moderately short, but quite dense setae anteriorly on sternite and right coxa of fifth pereopods; egg-bearing pleopods 2–4 with both rami approximately of equal length, non egg-bearing fifth pleopod with considerably longer, more setiferous external ramus, rudimentary internal ramus.

Telson (Fig. 1I) with distinct transverse indentations; anterior often nearly twice length of posterior lobes; posterior lobes symmetrical or nearly so, subtriangular, separated by broad median cleft; terminal margins oblique, each with 2–4 small spines and usually 1 much more prominent spine at apex; lateral margins slightly rounded, each with row of 4–7 moderately short bristles.

Color.—Not known.

Habitat.—Mud and sand substrates, 145–220 m; occupying variety of gastropod shells.

Etymology.—From the Latin *reconditus* meaning concealed, and referring to the superficial similarity of this taxon to species of *Nematopagurus*, which undoubtedly has caused it to be overlooked in the past.

Distribution.—At present recognized only from the Hainan Island area of the South China Sea.

Remarks.—The distinctive male sexual tubes and lack of female modified and paired first pleopods will immediately distinguish *Nematopaguroides reconditus*

from species of *Nematopagurus*. However, the general similarity of the armature and setation of the chelipeds of the new species may easily lead the casual observer to confuse it with those species of *Nematopagurus* that resemble *N. gardineri* Alcock, 1905, *N. meiringae* McLaughlin, 1998, and particularly *N. kosiensis* McLaughlin, 1998.

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Taxonomic studies of snapping shrimp of the *Alpheus* “*Edwardsii*” group from the Galápagos Islands (Decapoda: Caridea: Alpheidae)

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Abstract.—The taxonomy of three species of the *Alpheus* “*Edwardsii*” group from the Galápagos Islands is discussed. Diagnoses of *A. bouvieri* A. Milne-Edwards, 1878 and *A. hebes* Kim & Abele, 1988 are provided. Additional morphological characteristics of *A. hebes* are discussed. Examination of specimens revealed that *A. galapagensis* Sivertsen, 1933 is indistinguishable from *A. canalis* Kim & Abele, 1988. *Alpheus galapagensis* is redescribed and *A. canalis* is synonymized with it. Information on natural habitat and living color of these species is provided.

During field studies in 1998 at the Charles Darwin Research Station (CDRS), Isla Santa Cruz, Galápagos, one of us (MKW) collected specimens of *Alpheus* Fabricius, 1798 from the intertidal zone. The specimens represent four species. One of these shrimp was easily identifiable as *A. panamensis* Kingsley, 1878. The identity of the other three, however, were more difficult to establish. The specimens were compared with previously collected material and with descriptions in the literature. Diagnoses of these species are provided, along with new information on morphology, habitat, and living color.

One of the species could be identified as *A. galapagensis* Sivertsen, 1933 or *A. canalis* Kim & Abele, 1988. In 1925, Alf Wollebaek, Director of the Zoological Museum at Oslo, collected intertidal specimens at Isla Floreana (also called Isla Santa Maria or Charles Island), Galapagos. Sivertsen (1933) reported on these specimens, and designated two ovigerous females and one male as *Alpheus strenuus* Dana var. *galapagensis* Sivertsen, 1933. Subsequently, A. H. Banner & D. M. Banner (1966) and D. M. Banner & A. H. Banner (1982), in their discussions of *A. strenuus*, considered *A.*

galapagensis to be a distinct species. Kim & Abele (1988) were the first to use the species name *A. galapagensis*, yet did not examine any specimens, but based their opinions on Sivertsen’s work. We compared our specimens from the Galápagos with the type material of *A. galapagensis*, paratypes of *A. canalis*, and additional specimens from western Mexico and the Galápagos. *Alpheus galapagensis* is redescribed using the paratype specimen, and *A. canalis* is synonymized with it.

Unless otherwise noted, specimens labeled as CDRS are in the collections of the Charles Darwin Research Station, Isla Santa Cruz, Galápagos. Catalogue numbers for CDRS specimens refer to a photographic catalogue of specimens compiled by Cleveland Hickman, Jr. of Washington and Lee University, Virginia, on behalf of the CDRS. Color data were derived from field notes and from photographs. Additional specimens were borrowed from the National Museum of Natural History, Smithsonian Institution Washington, D.C. (USNM), the Natural History Museum of Los Angeles County (LACM), the University of Southern California (USC), and the Zoological Museum at Oslo (ZMO). Carapace lengths

(CL) are given in millimeters. Anatomical definitions follow Kim & Abele (1988).

Alpheus hebes Kim & Abele, 1988

Fig. 1

Alpheus hebes Kim & Abele, 1988:62, fig. 26.

Holotype.—1 male (CL 7.3) USNM 229919, Isla San Salvador, Galápagos, *Velero III* sta. 333–35, 11 Dec 1935.

Other material examined.—Galápagos: 1 Male (CL 4.1), intertidal rocky area in front of CDRS, S. side Isla Santa Cruz, CDRS 98–599, coll. M. K. Wicksten, 24 Aug 1998, mid-littoral, among rocks and sand; 1 male (CL 2.8), 1 female (CL 4.1), CDRS 98-AA, coll. M. K. Wicksten, 25 Aug 1998, mid-littoral, under rocks; 3 females (CL 2.5–4.5), CDRS 98-BB, coll. by M. K. Wicksten 24 Aug 1998; 1 male (CL 7.7), 1 ovig. female (CL 7.0), USNM 123877, Charles Island, Black Beach, coll. by W. L. Schmitt, 18 Jan 1934; 1 female (CL 2.5), ZMO F89, Floreana, Post Office Bay, coll. by A. Wollibaek, 9 Jul 1925. Mexico: 11 males (CL 3.0–5.0), 12 females (CL 3.5–6.0), Magdalena Island, Tres Marias Islands, 9 May 1939, USC Field Party sta. 972–39 LACM.

Diagnosis.—Rostrum (Fig. 1A–C) very short, noncarinate, barely extending beyond ocular hoods, distal tip curved down. Ocular hoods separated from rostrum by very shallow rounded depression. Telson (Fig. 1E, F) with posterior margins rounded, armed with a pair of spines at each lateral end; lateralmost posterior telson spine curved upward in shape, not straight.

First segment of antennular peduncle (Fig. 1A–C) short; carina on ventral margin very shallow and broadly rounded (Fig. 1D). Second and third segments about equal in length to exposed part of first segment.

First pereopods with merus lacking spine on distoventral margin. Major first pereopod (Fig. 1G, H) with fingers arrayed with sparsely arranged tufts of setae; palm smooth, about 2.3 times long as high. Mi-

nor first pereopod (Fig. 1I) with fingers of chela as long as palm; fingers in male strongly balaeniceps on both inner and outer faces, not balaeniceps in female.

Second pereopod (Fig. 1J) with carpal articles with ratio 10:6:3:3:5.5. Chela about equal in length to proximal carpal article. Third and fourth pereopods (Fig. 1K, L) with movable spine on ischium. Fifth pereopod (Fig. 1M) with ischium without spine.

Color in life.—Chelae orange-brown, progressively darker towards bases of fingers, tips of fingers white. Much of body and legs light gray to green, dorsal area of carapace dark brown with U-shaped orange mark posterior to stomach. Orbital areas white, rostrum brown. Abdomen with transverse bars of dark gray-green to black alternating with light blue-gray bars, tail fan dark olive to black, becoming lighter and fading to white at posterior end, outer edge of uropods red. Red patches on bases of antennae, walking legs and ventrolateral parts of abdominal somites.

Habitat.—mid-littoral, under rocks on sand.

Size.—CL up to 11 mm.

Range.—Eastern Pacific from Baja California to Ecuador, Galapagos Islands.

Remarks.—This species is similar to *A. bouvieri* A. Milne-Edwards, 1878, but is distinguished by the shape of the rostrum (curved down rather than straight), and by the presence of movable spines on the ischia of the third and fourth pereopods. This species has a rostrum similar to that of *A. chilensis* Coutière, 1902 (in Lenz 1902), but can be distinguished by the lack of a spine on the distoventral margin of the merus of the first pereopods. Kim & Abele (1988) depicted the minor chela in *A. chilensis* Holthuis (1952) as being weakly balaeniceps in males. However, the balaeniceps character is well developed in both *A. chilensis* and *A. bouvieri*. This species is also distinguishable from *A. leviusculus* Dana, 1852 by the shape of the rostrum, by the absence of spine on the merus of the first

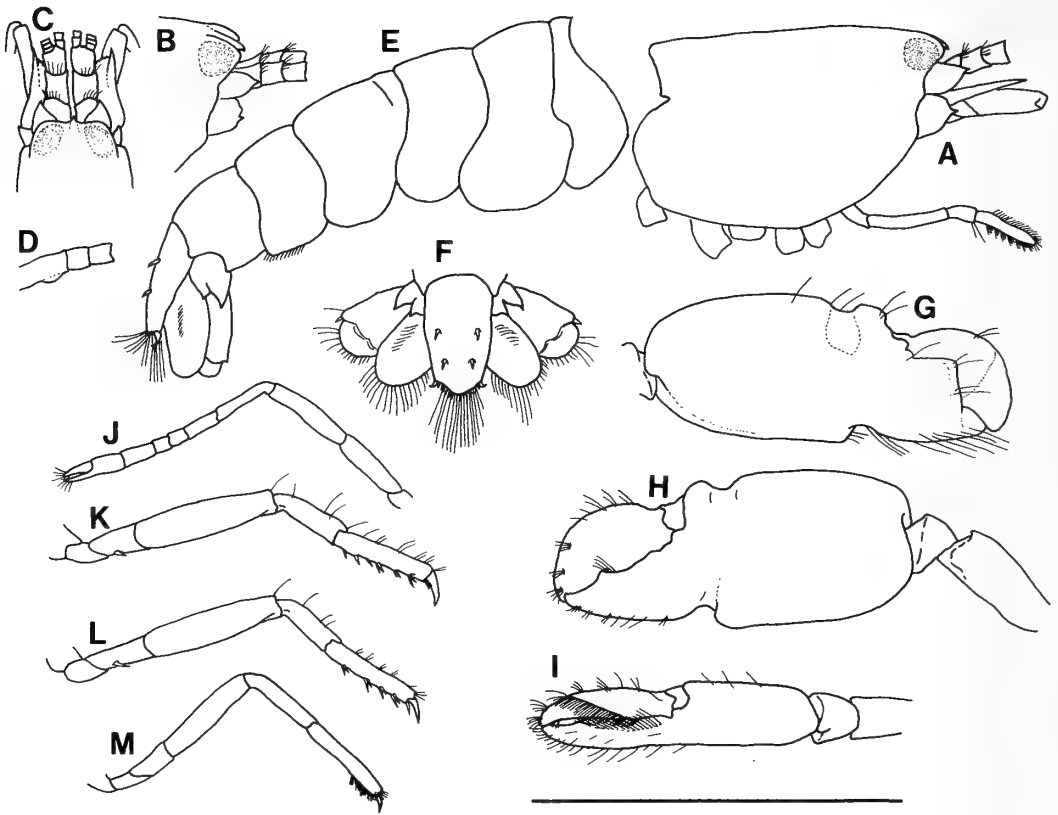


Fig. 1. *Alpheus hebes* Kim & Abele, 1988. Male CDRS 98-599 (CL = 4.1 mm). A, carapace, lateral view (with third maxilliped); B, anterior region of same, dorsolateral view; C, same, dorsal view; D, carina below right first antennular segment; E, abdomen, lateral view; F, telson and uropods, dorsal view; G, left major first cheliped, inner face; H, same, outer face; I, right minor cheliped; J, left second pereopod; K, right third pereopod; L, right fourth pereopod; M, right fifth pereopod. Scale indicates 5 mm.

pereopod, and by the degree of the balaeniceps condition in the minor chela.

Alpheus hebes can also be distinguished from the aforementioned species by the shape of the posterolateral spine on telson, which is curved dorsally rather than straight. This character was not included in the original description by Kim & Abele (1988), but was found to be present in the holotype of *A. hebes* and on all other specimens we have examined.

Examination of specimens used by Chace (1972:64) has confirmed their conspecificity with *A. hebes*. Chace referred to these specimens (USNM 123877) in his remarks on *A. bouvieri* and related species when he mentioned "another, possibly undescribed

species in the Galapagos Islands . . . a male and an ovigerous female without major chelipeds in the Smithsonian collections."

A small and badly damaged female specimen of *A. hebes* was discovered in the lot containing Sivertsen's types of *Alpheus galapagensis*. This specimen is not accounted for in the label, and consists of a cephalothorax, and a detached minor claw and abdomen. Evidently it had remained undetected until the present.

Alpheus bouvieri A. Milne-Edwards, 1878
Fig. 2

Alpheus Edwardsii.—Dana, 1852:542; 1855:11, pl. 34: fig. 2a-f.—Pocock,

- 1890:518 (in part). [Not *Athanas Edwardsii* Audouin, 1826]
- Alpheus Bouvieri* A. Milne-Edwards, 1878: 231.—Coutière, 1898:131, fig. 1 (in part); 1899:15, fig. 291; 1905:907, pl. 85: fig. 44 (in part).
- Alpheus heterochaelis*.—Kingsley, 1878: 194 (in part).—Rathbun, 1900a:152 (in part).—Luederwaldt, 1919:429 (in part). [Not *Alpheus heterochaelis* Say, 1818]
- Alpheus edwardsii*.—Bate, 1888:542, pl. 97: fig. 1.
- Alpheus Edwardsii*.—De Man, 1899:311 (in part).
- Alpheus bouvieri*.—Rathbun, 1900b:312 (in part).—Sourie, 1954:253.—Forest & Guinot, 1958:9.—Ribeiro, 1964:5.—Crosnier & Forest, 1965:606; 1966:273, fig. 22a-j.—Uschakov, 1970:444.—Fausto-Filho & Furtado, 1970:286.—Chace, 1972:63.—Fausto-Filho, 1974:5; 1975:79.—Gore et al., 1978:225.—Christoffersen, 1979:303, figs. 2–5.—Kim & Abele, 1988:58, fig. 24.
- Alpheus bouvieri* var. *chilensis*.—Schmitt, 1924a:162. [Not *Alpheus bouvieri chilensis* Coutière in Lenz, 1902].
- Crangon [Alpheus] Bouvieri*.—Monod, 1933:462, fig. 1A–C.

Material examined.—Galápagos: 6 females (CL 3.0–5.5) intertidal rocky area in front of CDRS, S. side Isla Santa Cruz, CDRS 98-578, coll. M. K. Wicksten, 23 Aug 1998, midlittoral, among rocks and sand; 1 female (CL 5.5) USNM 57710, Eden Island, Williams Galápagos Expedition, 6 Apr 1923; 1 male (CL 6.0), 1 female (CL 6.0), USNM 110395, Clipperton Island, coll. C. R. Harrison, 10–15 Sep 1958. Mexico: 1 male (CL 3.7), 8 females (CL 3.0–5.5), Magdalena Island, Tres Marias Islands, 9 May 1939, USC Field Party station 972-39 LACM.

Diagnosis.—Rostrum (Fig. 2A–C) carinate, short, not reaching 0.5 length of first antennular segment, extending posteriorly about as far as eyestalks. Ocular hoods sep-

arated from rostrum by shallow rostro-orbital depressions.

First pereopods with merus unarmed distoventrally. Major chela (Fig. 2E) thick; weakly setose. Minor chela sexually dimorphic, bearing balaeniceps-shaped setose crest on dactyl and accessory crest on opposable margin in males. Carpus of second pereopods (Fig. 2F) with articles in ratio 10:4.3:3.3:3.0:4.3. Third (Fig. 2G), fourth, and fifth pereopods without movable spine on ischium. Second pleopod of male with appendix masculina overreaching appendix interna. Telson (Fig. 2D) about 1.6 times as long as wide; uropodal exopod with transverse suture forming two conspicuous rounded lobes.

Color in life.—Chelae brown, progressively darker towards bases of fingers, tips of fingers white. Much of body light brown, legs pale. Abdomen with narrow transverse bars of medium brown alternating with pale brown areas, tail fan medium brown and gray, fading to pale brown at posterior end.

Remarks.—*Alpheus bouvieri* can be distinguished from similar species by the following combination of characters: straight tip of the rostrum, absence of a spine of the merus of the first pereopod, presence of a balaeniceps minor chela in the male, and absence of movable spines on the ischia of the third, fourth, and fifth pereopods. *Alpheus bouvieri* and *A. hebes* may be confused with each other due to similarities in major and minor chela shape, and transverse suture of the exopodal uropod. This species can be distinguished from *A. hebes* by the shape of the rostrum (straight rather than downcurved), and by the absence of movable spines on the ischia of the third and fourth pereopods.

Alpheus bouvieri has been treated as a subspecies of *A. leviusculus* by D.H. Banner & A.H. Banner (1982). However, justification of *A. bouvieri* as a distinct species was provided by Kim & Abele (1988).

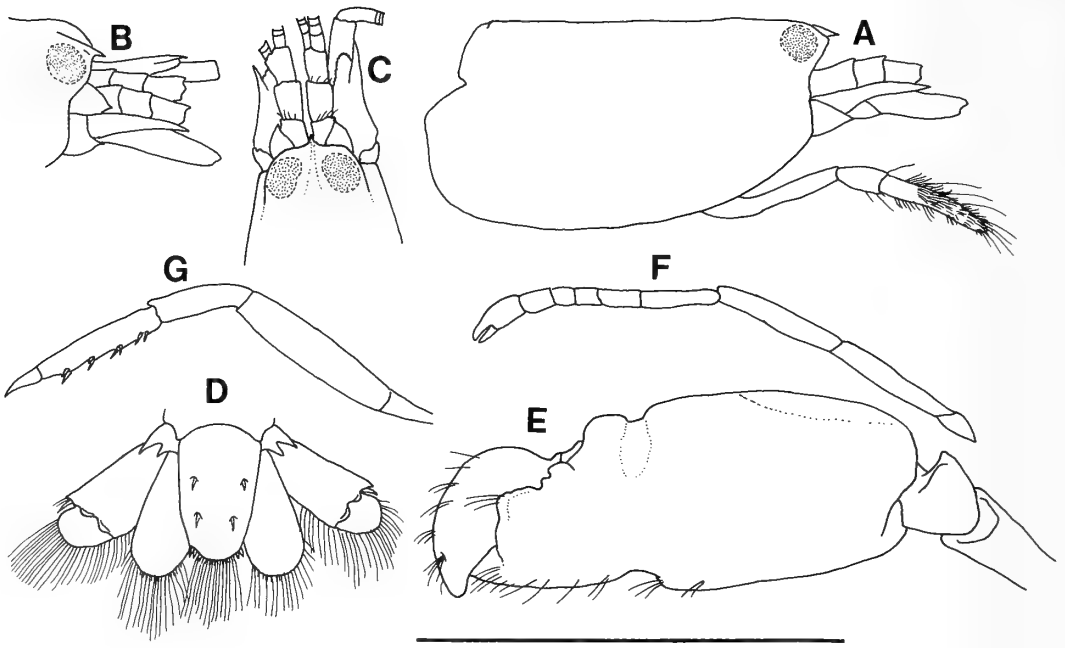


Fig. 2. *Alpheus bouvieri* A. Milne-Edwards, 1878. Female CDRS 98-578 (CL = 4.8 mm). A, carapace, lateral view (with third maxilliped); B, anterior region of same, dorsolateral view; C, same, dorsal view; D, telson and uropods, dorsal view; E, right major cheliped, inner face; F, left second pereopod; G, left third pereopod. Scale indicates 5 mm.

Alpheus galapagensis Sivertsen, 1933

Fig. 3

Alpheus strenuus var. *galapagensis* Sivertsen, 1933:3, pl. 1, figs. 1-5.

Alpheus strenuus galapagensis.—A. H. Banner & D. M. Banner, 1966:184; D. M. Banner & A. H. Banner, 1982:228.

Alpheus canalis Kim & Abele, 1988:72, fig. 30.

Alpheus galapagensis.—Kim & Abele, 1988:102, fig. 43.

Paratypes.—2 ovigerous females (CL 14.5, 10.5), ZMO F89, Isla Floreana, Post Office Bay, shore, Galapagos Islands, coll. A. Wollebaek, 25 September 1925.

Other material examined.—Galápagos: 1 ovigerous female (CL 7.6), Punta Espinosa, Isla Fernandina near Academy Bay, Isla Santa Cruz, coll. G. M. Wellington, 18 Sep 1974, LACM; 1 female (CL 3.4 mm), Academy Bay, near CDRS, CDRS 98-596, coll. M. K. Wicksten, 24 Aug 1998; 1 fe-

male (CL 3.9 mm), same locality, CDRS 98-598; 1 female (CL 6.8mm), same locality, 25 Aug 1998, CDRS 98-618; 1 female (CL 9.2 mm), same locality, sandy tide pool, 25 Aug 1998, CDRS 98-619; 1 female (CL 13.5), Punta Espinosa, Isla Fernandina near Academy Bay, Isla Santa Cruz, CDRS 99-42, coll. C. P. Hickman, 2 Jun 1999. Mexico: 1 male (CL 12.0), 1 ovigerous female (CL 13.0), 1 juvenile (CL 5.5), USNM 229925, San Francisco Island, Baja California, *Velero III* sta. 518-36, 25 Feb 1936 (paratypes of *A. canalis*); 10 males (CL 7.0-15.0), 5 females (CL 12.0-15.0), Guaymas Bay, Sonora, *Velero III* sta. 1041-40, 23 Jan 1940 LACM; 1 male (CL 12.5), Punta Chile, Mazatlán, Sinaloa, in tide pool, Texas A&M University Department of Biology teaching collection, coll. M. K. Wicksten, 8 Jan 1982.

Description of larger female paratype specimen.—Rostrum (Fig. 3A-C) acute, reaching 0.5 times length of exposed part

of first article of antennular peduncle. Rostral carina narrowly rounded dorsally; extending posteriorly past eyes, joining carapace at broad angle when viewed from side. Ocular hoods separated from rostral carina by shallow rounded depressions.

Telson (Fig. 3E) about 1.6 times as long as wide, with 2 pairs of dorsal spines, and bearing longitudinal median depression on dorsal surface. Posterior margin rounded, armed with a pair of spines at each angle.

Antennular peduncle (Fig. 3A–D) with first segment short; shallow carina on ventral margin (Fig. 3D) subtriangular, with rounded apex (see *Remarks*). Second segment long, about 1.8 times length of exposed part of first segment and about 2.0 times length of third. Stylocerite (Fig. 3A–C) barely reaching end of first antennular segment.

Scaphocerite (Fig. 3A–C) about 2.8 times as long as broad. Distal spine reaching to end of or slightly exceeding third segment of antennular peduncle, much exceeding blade; blade reaching 0.5 times length of third segment. Carpocerite (Fig. 3A–C) barely longer than third segment of antennular peduncle. Basicerite with sharp spine.

Major first pereopod (Fig. 3F, G) with movable finger regularly arched in profile except for very slight depression on upper margin near articulation, finger broadly rounded at tip; tip exceeding immovable finger. Both fingers with numerous tufts of setae. Palm about 2.35 times as long as high; superior transverse groove present, proximal shoulder vertical to groove. Superior outer palmar depression large and well-defined, extending to and encompassing oblique suture. Superior inner palmar depression extending proximally and fading toward middle of palm. Inner face of palm with deep longitudinal suture present near top margin at middle of palm; inferior transverse groove deep, slightly directed distally; proximal shoulder rounded and slanted distally. Inferior outer palmar depression narrow, obliquely inverse V-shaped. Inferior inner palmar depression

broad. Inner face of palm with shallow longitudinal depression near inferior margin of palm. Merus about 1.8 times as long as wide, with spine on distoventral margin.

Minor first pereopod (Fig. 3H) with fingers of chela about as long as palm; setose distally. Setae pattern variable (fingers weakly balaeniceps in type specimens, but see *Remarks*). Palm with well-defined oblique suture.

Second pereopod (Fig. 3I) with carpus subdivided into five articles decreasing in length (numbered from proximal end) 1, 2, 5, 3 = 4; articles with ratio approximately equal to 10:6:4:4:5. Finger tips with curved tufts of setae.

Third pereopod (Fig. 3J) with merus about 1.6 times length of carpus; propodus about 1.1 times length of carpus, with 8 sets of spines present more or less in double rows; ischium with very small spine apressed and laying in a small rounded depression (see *Remarks*). Fourth pereopod similar to third. Fifth pereopod with propodus bearing dense combs of setae along distal 0.6 of length; ischium without spine.

Color in life (from field notes and photographs of CDRS specimens).—Upper surface distinctly dappled with faint grayish spots on pea-green to gray background, appearing dull green at distance. Lower surface white, tip of tail fan also white. Abdomen with faint grayish bands running length of lateral surfaces. Major chela darker, tips of fingers white. Minor chela green fading to white at tips of fingers. Walking legs blotched with gray and white. This color pattern is very similar to that observed in the field by MKW of the specimen from Mazatlan.

Habitat.—The specimens from Isla Santa Cruz were taken among tide pools in a lava flow. The area was exposed to strong surf at high tide. All were found in the mid and lower intertidal zone. Except for specimen CDRS 98-619, the specimens were collected under small rocks resting on sand amid small tide pools. Specimen CDRS 98-619 was found under a rock in a large sandy

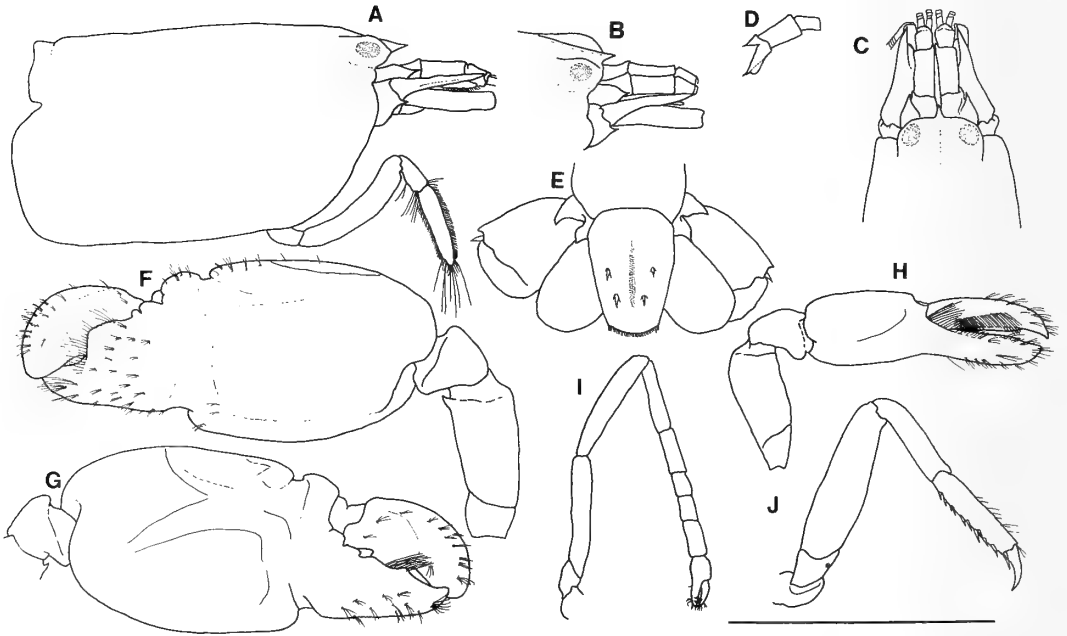


Fig. 3. *Alpheus galapagensis* Sivertson, 1933. Female paratype ZMO F89 (CL = 14.5 mm). A, carapace, lateral view (with third maxilliped); B, anterior region of same, dorsolateral view; C, same, dorsal view; D, carina below right first antennular segment; E, telson and uropods, dorsal view; F, right major cheliped, inner face; G, same, outer face; H, left minor cheliped; I, right second pereopod; J, right third pereopod. Scale indicates 5 mm.

tide pool between two predominately rocky areas.

Remarks.—Our specimens agree in general with the brief description given by Sivertsen (1933), and the subsequent comments by D. H. Banner & A. H. Banner (1982) and Kim & Abele (1988). The type material originally contained three specimens, one male and two females. We were informed, by Cathrine Vollelv at the Museum of Oslo, that the male specimen was lost.

In Sivertsen's (1933:3, pl. 1, figs. 1–5) illustrations, the minor chela is depicted as simple rather than balaeniceps-shaped, and the third pereopod is depicted as lacking a spine on the ischium. This was the basis by which previous authors recognized this as a distinct species, rather than a subspecies of *A. strenuus*. However, these specimens have a small movable spine on the ischium of the third pereopod. Furthermore, the minor claws in the type material have an incom-

plete balaeniceps condition, a rare feature in females of *Alpheus* and characteristic to only a few species, including *A. strenuus*. The minor chelae of the paratype specimens were detached and lacked a distoventral spine on the merus (Fig. 3H), which contrasts the presence of this spine on the major chelae of the paratype specimens (Fig. 3F, G). This, plus the presence of extra detached legs in the lot, casts some doubt as to whether these minor chelae correspond to the two female paratype specimens.

This species can be distinguished from *A. strenuus* Dana by the presence of a median longitudinal depression on the dorsal surface of the telson, a feature previously known from *A. nuttingi* (Schmitt 1924b). This species also differs from *A. strenuus* by the following proportions as provided by D. H. Banner & A. H. Banner (1982, for *A. strenuus strenuus*): the ratio of carpal segments of the second pereopod is 10:6:4:4:5 in the present species, versus 10:10:3:3:6 in

A. strenuus; the second segment of the antennular peduncle of this species is longer in proportion than that of *A. strenuus*; and the antennal blade is much shorter in proportion to the antennal spine in *A. galapagensis*. Furthermore, the movable spine in the ischium of the third pereopod in *A. strenuus* is depicted by D. H. Banner & A. H. Banner (1982) as conspicuous, whereas it is very small in *A. galapagensis*.

Examination of other specimens revealed variability in setal pattern of the minor chelae. Most of the larger specimens (apart from paratypes) showed fingers as densely and evenly setose throughout the distal third of length. However, some of the specimens from Sonora, Mexico had the setae arranged as a row of tufts on both the fixed and movable fingers, a feature that approaches the condition of the paratypes.

The movable spines on the ischium of the third and fourth pereopods are minute and difficult to see. On the specimen illustrated, the tiny movable spine was present on the left third pereopod but was undetectable on the right (the right third pereopod is illustrated with the spine as it is present on the left side). Additional disarticulated pereopods indicate that at least a third specimen was present in the type lot, probably the missing male. One large pereopod, possibly the third, conforms in every way the description above. Two smaller detached pereopods have a conspicuous spine on the ischium which does not match either the legs on the specimens or the other unattached legs, and may have belonged to another species.

Because of the agreement of morphological features, we consider *Alpheus canalis* Kim & Abele, 1988 to be a junior synonym of *Alpheus galapagensis* Sivertsen, 1933. Kim & Abele (1988), in their key to species of *Alpheus*, stated that *A. canalis* and *A. galapagensis* could be distinguished by the shape of the anterior margin between the base of the rostrum and middle of ocular hoods, and by the length of the distal spine of the scaphocerite. However, examination

of additional specimens reveals complete intergradation of these features within populations, as well as for other antennal appendages, ventral carina on first antennular segment, major chelae, walking legs, body proportions, and telson.

Acknowledgments

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A new cyclodorippoidea crab of the genus *Cyonomoides* Tavares, 1993 (Crustacea: Decapoda: Brachyura: Cyonomidae) from the Caribbean coast of Colombia

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Abstract.—A new Cyclodorippoidea crab species, *Cyonomoides fitoi*, of the family Cyonomidae Bouvier, is described and illustrated based on specimens collected from the upper slope region off the Caribbean coast of Colombia. This new species is the fourth known in the genus *Cyonomoides* Tavares, and the third from the western Atlantic. This new species is compared to its congeners, from which it is distinguished by features of the ocular peduncles, dorsal surface of the carapace, and spination on the dactyls of fourth and fifth pereopods.

Resúmen.—Se describe e ilustra una nueva especie de cangrejo Cyclodorippoidea, *Cyonomoides fitoi*, de la familia Cyonomidae Bouvier, en base a especímenes obtenidos en la parte superior del talud continental de la costa del Caribe colombiano. Esta es la cuarta especie que se describe en el género *Cyonomoides* Tavares, y la tercera que se conoce del Atlántico occidental. La nueva especie se compara con las otras del género, de las cuales se distingue por características de los pedúnculos oculares, la superficie dorsal del caparazón, y la presencia de espinas en el margen ventral de los dactilos del cuarto y quinto par de pereópodos.

As part of a study designed to inventory the benthic macrofauna from the continental shelf and upper slope region of the Caribbean coast of Colombia, a number of specimens representing a new crab species of the genus *Cyonomoides* Tavares, 1993, were collected. This genus was placed by Tavares (1993) in the family Cyonomidae Bouvier, 1898, within the Cyclodorippoidea Ortmann, 1892 (see Tavares 1991a, 1991b, 1994). Aside from the type species of *Cyonomoides*, *C. guinotae* (Tavares, 1991), from Cuba, Venezuela, and Brazil, at 592 to 1097 m, two other species have been placed in this genus, *C. cubensis* (Chace 1940), from Cuba, at 990 to 1005 m, and *C. delli* (Griffin & Brown 1975), from Australia, at 675 m. In species of *Cyonomo-*

ides, the carapace is subquadrate; the ocular peduncles are immovable, well calcified and fused at their bases, and lack corneae; the chelipeds are subequal; the second and third pereopods are long and have dorsoventrally flattened dactyls; the fourth and fifth pereopods are reduced and subdorsal in position with dactyls short and curved for grasping; and the abdomen in both males and females consist of seven free segments (including telson). The new species, the fourth in the genus, is herein described, fully illustrated, and compared to its congeners.

Material and Methods

Specimens were collected in November and December, 1998, as part of a joint pro-

gram (INVEMAR-Macrofauna I) between the Instituto de Investigaciones Marinas y Costeras, Punta de Betín, Santa Marta (INVEMAR), and the Smithsonian Institution, designed to inventory the invertebrate and fish fauna of the Colombian Caribbean upper slope zone. A 5-m-opening semi-balloon trawl net with steel doors built by Marinovich Trawl Co., Biloxi, Mississippi, and equipped with a cod-end having a 0.5-cm-mesh size net, was used. Sampling was conducted on board the B/I *Ancón*, a 20-m research vessel operated by INVEMAR. The holotype and some paratypes are deposited in the collections of INVEMAR; and paratypes in Instituto de Ciencias Naturales, Museo de Historia Natural, Universidad Nacional de Colombia (ICN-MHN), and National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM). Terminology used follows Tavares (1991). Measurements listed under material examined are in millimeters (mm), and are given in the order: total carapace length, including rostrum \times carapace width. The width of the frontal region is measured as the distance between the spines located near the base of each antennal peduncle. Abbreviations are: sta, station; ovig, ovigerous.

The images shown in Fig. 1 were prepared using a modified computer flatbed scanner following the methodology described by Reyes & Navas (2001). This method uses a scanner (HP SCANJET 4c) converted into a shallow aquarium 4 cm deep, and filled with water or alcohol. The specimens were immersed and held in place with weights, and scanned using DeskScan II (version 2.5) software. The images produced were processed using CorelPhoto Paint 8 (version 8.232), printed on high quality glossy paper, and mounted as a plate.

Cyonomoides fitoi, new species

Figs. 1–3

Material examined.—Holotype: ♀ ovig 4.8 \times 5.1 mm, INVEMAR-Macrofauna I, off

Bahía Portete, Guajira Department, sta C13, 12°29'19.2"N, 72°15'29"W to 12°28'58.8"N, 72°15'9"W, 22 Nov 1998, 450–430 m, INVEMAR-CRU 2066.

Paratypes: 1 male 3.2 \times 2.9 mm, 1 ♀ 5.3 \times 5.0 mm, INVEMAR-Macrofauna I, off Ciénaga Grande de Santa Marta, Magdalena Department, sta C44, 11°15'18"N, 74°38'19"W to 11°15'22.8"N, 74°38'46"W, 470–472 m, 4 Dec 1998, INVEMAR-CRU 2067.—♀ ovig 6.1 \times 6.2 mm, same data as previous specimens, USNM 276179.—1 ♀ 5.0 \times 4.9 mm, 1 ♀ ovig 4.9 \times 5.1 mm, Palomino, Guajira Department, sta C27, 11°27'3.6"N, 73°42'12"W to 11°27'14.4"N, 73°41'44"W, 490–494 m, 26 Nov 1998, ICN-MHN-CR 1861.

Diagnosis.—Carapace with strong, bifid or multifid hepatic spine on each side; dorsal surface with dense, sharp granules on anterolateral and lateral faces, and with less dense, mostly blunt granules centrally. Ocular peduncles subcylindrical, weakly divergent, and reaching slightly beyond distal margin of second antennal segment; armed with strong spines laterally and mesially. Dactyl of fourth and fifth pereopods with 4–6 corneous spines on ventral margin.

Description.—Carapace (Fig. 1) subquadrate, slightly narrowing anteriorly, with scattered setae. Regions weakly marked except for intestinal and cardiac regions. Dorsal surface covered with minute granules becoming smaller and less dense medially; anterolateral and lateral surfaces with dense, sharp granules or small spines; hepatic spine strong, bifid or sometimes multifid on one or both sides. Frontal region (Fig. 2a) about 0.4 times as wide as carapace width; margins minutely spinulose, laterally curving from base of rostrum around ocular peduncles and ending in strong spine near base of antennal peduncles. Rostrum prominent, triangular, reaching to about proximal third of ocular peduncles; margins spinulose, with well-spaced long setae; dorsal surface with small spines. Orbits lacking.

Ocular peduncles (Fig. 2a) subcylindri-

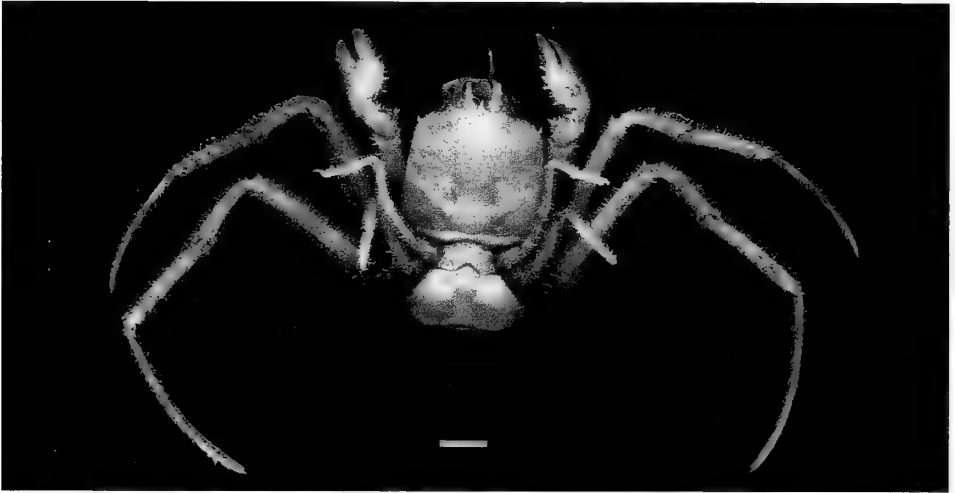


Fig. 1. *Cynomoides fitoi*, new species, paratype, ♀ ovig 6.1 × 6.2 mm, off Ciénaga Grande de Santa Marta, sta C44, USNM 276179. Scale equals 2 mm.

cal, strongly calcified, fused basally, immovable, and weakly divergent; exceeding distal margin of second antennal segment (in dorsal view); lateral and mesial margins armed with strong spines; dorsal faces with small spines. Corneae lacking.

Antennules well developed, long, exceeding antennal peduncle by about 0.8 length of penultimate antennular segment. Fourth (ultimate) segment smooth. Third segment with minute granules. Second segment with small sharp granules on lateral face. First segment very short, unarmed. Antennal peduncle (right antenna abnormally short in paratype illustrated in Fig. 2a) with lateral margins of second and fourth segments spinulose. Epistome with small median bifid spine just below base of rostrum; with small, blunt spine on each side near base of antennular peduncle.

Third maxilliped (Fig. 2b) minutely spinulose on outer surfaces of endopod, ischium, merus and palp; endopod narrow; ischium and merus subequal in length. Ischium with mesial margin densely setose; lateral margin spinulose; outer, distal margin with row of spines mesially. Merus ending in bluntly subtriangular extension with long marginal setae; mesial margin with spines, including 1 or 2 strong spines at level of

articulation of palp, lateral margin with spines. Palp about as long as merus; segments setose.

Chelipeds (Fig. 2c) subequal in size in both sexes; left and right similar in spination; with moderately dense, stiff setae on dorsal, ventral, and outer faces of segments. Fingers with cutting edges consisting of sharp edge lacking distinct teeth; tips curving inward; with several strong spines on dorsal (movable finger) or ventral (fixed finger) margins. Palm with several strong and well spaced blunt or sharp spines on dorsal and ventral faces. Carpus with few spines dorsally and on outer face distoventrally; with strong bifid spine on dorsomesial margin medially. Merus with strong spines on ventral margin; dorsal and lateral faces with small spines or tubercles. Ischium with dorsodistal spine and row of spines on ventrodistal margin; ventral face with small spines. Basis with row of spines on ventrodistal margin.

Second and third pereopods (Fig. 3a, b) long, third longest, exceeding second pereopod by about 0.3 length of dactyl, and about 3.7 times as long as carapace; segments covered with moderately dense, stiff setae. Dactyl broadly curved, terminating in calcareous tip; with row of small, well-

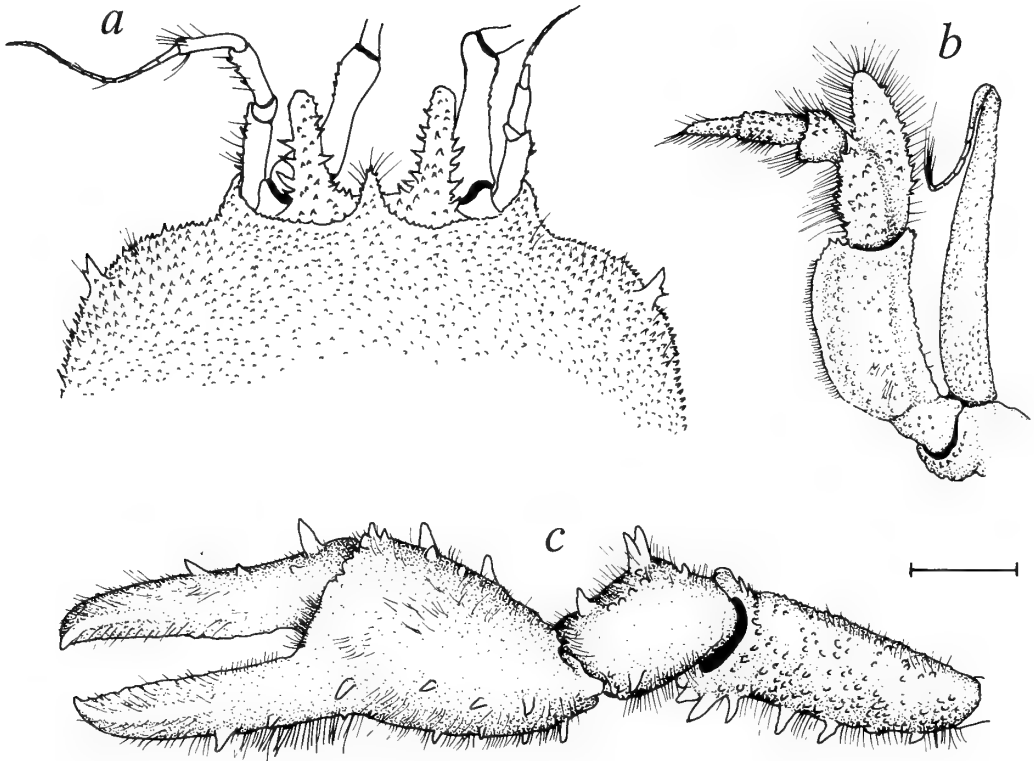


Fig. 2. *Cynomoides fitoi*, new species, paratype, ♀ ovig 6.1 × 6.2 mm, off Ciénaga Grande de Santa Marta, sta C44, USNM 276179: a, anterior portion of carapace, ocular peduncles, first and second antennular segments, and antennae (right abnormally developed), dorsal view; b, third left maxilliped, outer view; c, left cheliped, outer view. Scale equals 1 mm.

spaced spines on proximal third of dorsal margin. Propodus, carpus, and merus with well-spaced, often slender spines, and small blunt or sharp tubercles on all surfaces. Ischium with spines on all surfaces. Coxa with several strong spines on distolateral margin.

Fourth and fifth pereopods (Fig. 3c) reduced, reaching only to distal margin of merus of third pereopod when fully extended; segments covered with moderately dense, stiff setae. Dactyl (Fig. 3d, e) very short, terminating in sharp corneous claw; ventral margin with 4–6 corneous spines, and rounded protuberance proximally. Carpus with row of 2 or 3 strong spines on dorsal margin, and strong dorsodistal spine. Merus of fourth pereopod unarmed or with 1 or 2 slender spines on lateral and mesial faces. Ischium with row of strong slender

spines on ventral margin. Coxa with 1 or 2 spines on dorsodistal margin.

Female abdomen (Fig. 3f) with 7 segments, margins setose; surface minutely granulate, with scattered minute spines; telson width about 2 times the length. Male abdomen about as wide as that of female; telson width about 3 times length.

Color.—In life, generally brownish, fading to a straw color in alcohol.

Etymology.—This species is named after Mr. Adolfo González (affectionately nicknamed “Fito”), in recognition of the invaluable support he has given the junior author during her higher education, and for his encouragement to pursue her interest in marine research.

Distribution.—Known so far only from the Caribbean coast of Colombia, from off Bahía Portete on the north, to off Ciénaga

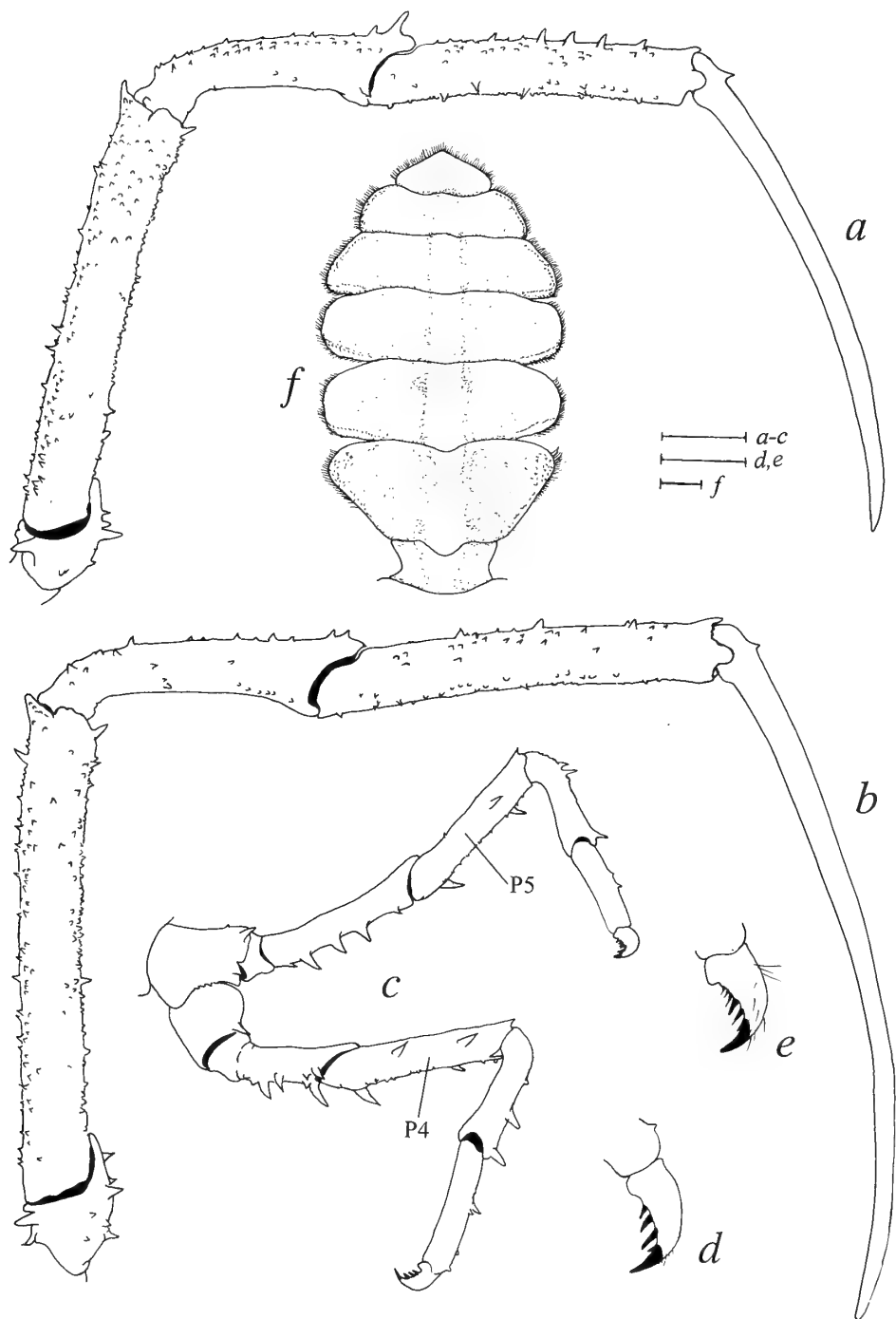


Fig. 3. *Cymonomoides fitoi*, new species, paratype, ♀ ovigerous 6.1 × 6.2 mm, off Ciénaga Grande de Santa Marta, sta C44, USNM 276179: a, second right pereopod, lateral view; b, third right pereopod, lateral view; c, fourth (P4) and fifth (P5) right pereopods, lateral view; d, dactyl of fourth right pereopod, lateral view; e, dactyl of fifth right pereopod, lateral view. Scales equal 1 mm (a-c, f), and 0.5 mm (d, e).

Grande de Santa Marta on the south. Depth: 430 to 494 m.

Remarks.—Among the species of *Cyconomoides*, this new species is most similar to *C. cubensis*. The two differ primarily in features of the carapace, ocular peduncles, and dactyls of the fourth and fifth pereopods. In *C. fitoi*, new species, the granules on the dorsal surface of the carapace are not as dense and strong medially as in *C. cubensis*. The hepatic spine (Fig. 2a) in *C. fitoi*, is multifid and much stronger than in *C. cubensis*. The ocular peduncles (Fig. 2a) are weakly divergent and ornamented with strong spines on the lateral and mesial faces in *C. fitoi* while the peduncles are weakly armed laterally, have small spines mesially, and are strongly divergent in *C. cubensis*. The ventral margin on the dactyl of the fourth and fifth pereopods (Fig. 3d, e) is armed with four to six corneous spines in *C. fitoi*, whereas the ventral margin of the dactyl is unarmed or at most with low, blunt calcareous tubercles in *C. cubensis*.

Cyconomoides fitoi can be easily separated from *C. guinotae* by differences in the rostrum (Fig. 2a) which is prominent, subtriangular and reaches to about the proximal third of the ocular peduncles in *C. fitoi* while the rostrum is short and broad, and barely reaches the basal portion of the ocular peduncles in *C. guinotae*. *Cyconomoides fitoi* distinctly differs from *C. delli* in the ocular peduncles (Fig. 2a), which are subcylindrical in the new species but dorsoventrally flattened in *C. delli*.

Acknowledgments

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Redescription of *Pseudoprotella inermis* Chevreux, 1927, a rare species of caprellidean amphipod (Crustacea) from Ceuta, North Africa

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Abstract.—*Pseudoprotella inermis* Chevreux, 1927 is redescribed based on specimens collected from Ceuta, on the North African side of the Strait of Gibraltar. This species is previously known only from a single specimen collected from the Gulf of Cadiz, in southern Spain. *Pseudoprotella inermis* differs primarily from *P. phasma* (Montagu 1804), the only other species of the genus, by the absence of body projections.

The Strait of Gibraltar has attracted the attention of marine taxonomists because the Strait is situated on the border of the Mediterranean Sea and the Atlantic Ocean (Fig. 1). In 1998 and 1999 the Laboratorio de Biología Marina de la Universidad de Sevilla conducted a research project on benthic animal communities living among algae and hydroids of Ceuta, North Africa, on a coastline facing the Strait, as part of a scientific program to elucidate the marine fauna and flora of the Strait of Gibraltar. Since two new species of caprellidean amphipods have been recently found from Algeciras Bay, on the northern coast of the Strait of Gibraltar (Sánchez-Moyano et al. 1995a, 1995b), we have focused our research on the species diversity of the Caprellidea inhabiting these waters. During this study, several specimens identified as the genus *Pseudoprotella* (Mayer 1903, Krapp-Schickel 1993, Takeuchi 1993) were found. Because these specimens lacked dorsal body spines, they were identified as *Pseudoprotella inermis* Chevreux, 1927 which was previously known only from a single male specimen collected from the

Gulf of Cadiz, southern Spain (Chevreux 1927). In this paper, we redescribe this rare species of caprellidean amphipod, *Pseudoprotella inermis*, based on specimens collected from Ceuta, North Africa.

Specimens (male “a” and female “b”) are deposited in the Museo Nacional de Ciencias Naturales de Madrid (Spain) (n° MNCN 20.04/4646). Additional material are in the Laboratorio de Biología Marina, Universidad de Sevilla (Spain).

Pseudoprotella inermis Chevreux, 1927
Figs. 2–5

Pseudoprotella inermis.—Chevreux, 1927: 135, pl. 14, figs. 3–5.—McCain & Steinberg, 1970:72.

Material examined.—Male “a,” 10.2 mm in length, from the seaweed *Dilophus spiralis* Hamel at Ceuta (35°54'5"N, 5°16'35"W), between 30 and 40 meters deep, August 1999, coll. Juan Rodríguez. Female “b,” 7.2 mm in length, collected together with male “a.” Other specimens: 5 adult males and 4 juveniles with male “a”; 1 adult male and 2 adult females taken

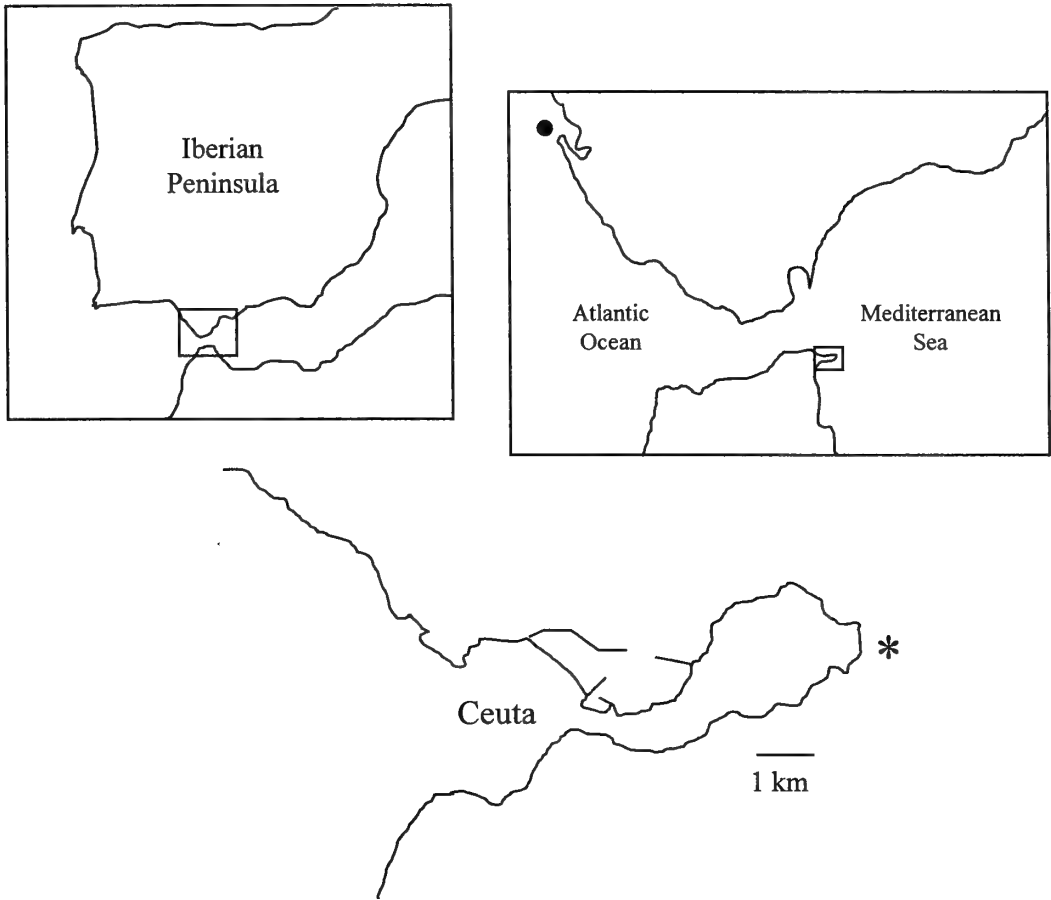


Fig. 1. Location of Ceuta in the Strait of Gibraltar. Gulf of Cádiz (the type locality) is represented by (●). An asterisk (*) indicates the place where *Pseudoprotella inermis* Chevreux, 1927 was collected from Ceuta.

on the hydroid *Sertularella gayi* Lamouroux from the same location.

Diagnosis.—Body smooth, without dorsal projections. Antenna 1 longer than body. Pereonite 3 with a pair of anterior lateral projections in female. Pereopods 5–7 increasing in robustness.

Description.—Male “a,” 10.2 mm in length. Head and pereonites without dorsal projections (Fig. 2a). Head plus pereonite 1 nearly as long as pereonite 2. Pereonites 2, 3 and 4 subequal in length. Pereonite 7 the shortest. Pereonite 2 with a pair of acute ventro-lateral projections near the coxa of gnathopods and a pronounced ventral proximal tubercle.

Antenna 1 longer than the body. Flagel-

lum of 24 articles, a little shorter than peduncle (Fig. 4a). Antenna 2 (Fig. 4b) as long as peduncular articles 1 and 2 of antenna 1; peduncular article 3 to flagellar segment 2 weakly setose. Peduncular articles 1 and 2 very short, article 3 nearly as long as 4.

Mouthparts: Mandibular molar process strong, bordered by robust teeth and with a reticulated inner surface (Fig. 3f, g). Left mandible with incisor divided into 5 teeth followed by lacinia mobilis divided into 5 teeth and 3 pectinate setae. Right mandible with incisor divided into 5 teeth followed by lacinia mobilis divided into numerous minute teeth and 2 pectinate setae. Distal segment of palp with a row of 1 long, 6

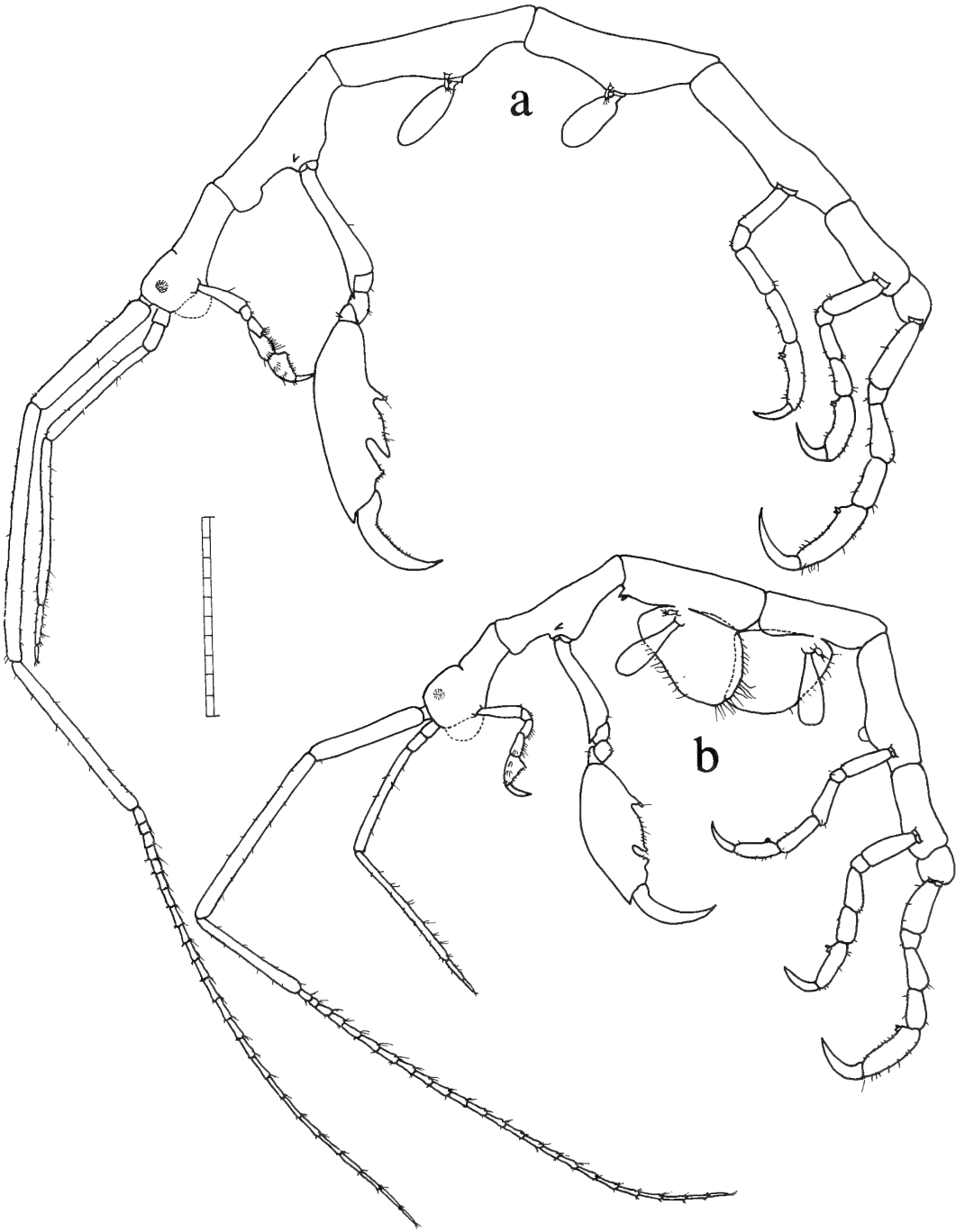


Fig. 2. *Pseudoprotella inermis* Chevreux, 1927 from Ceuta, North Africa. Lateral view: a, male; b, female. Scale bar: 2 mm.

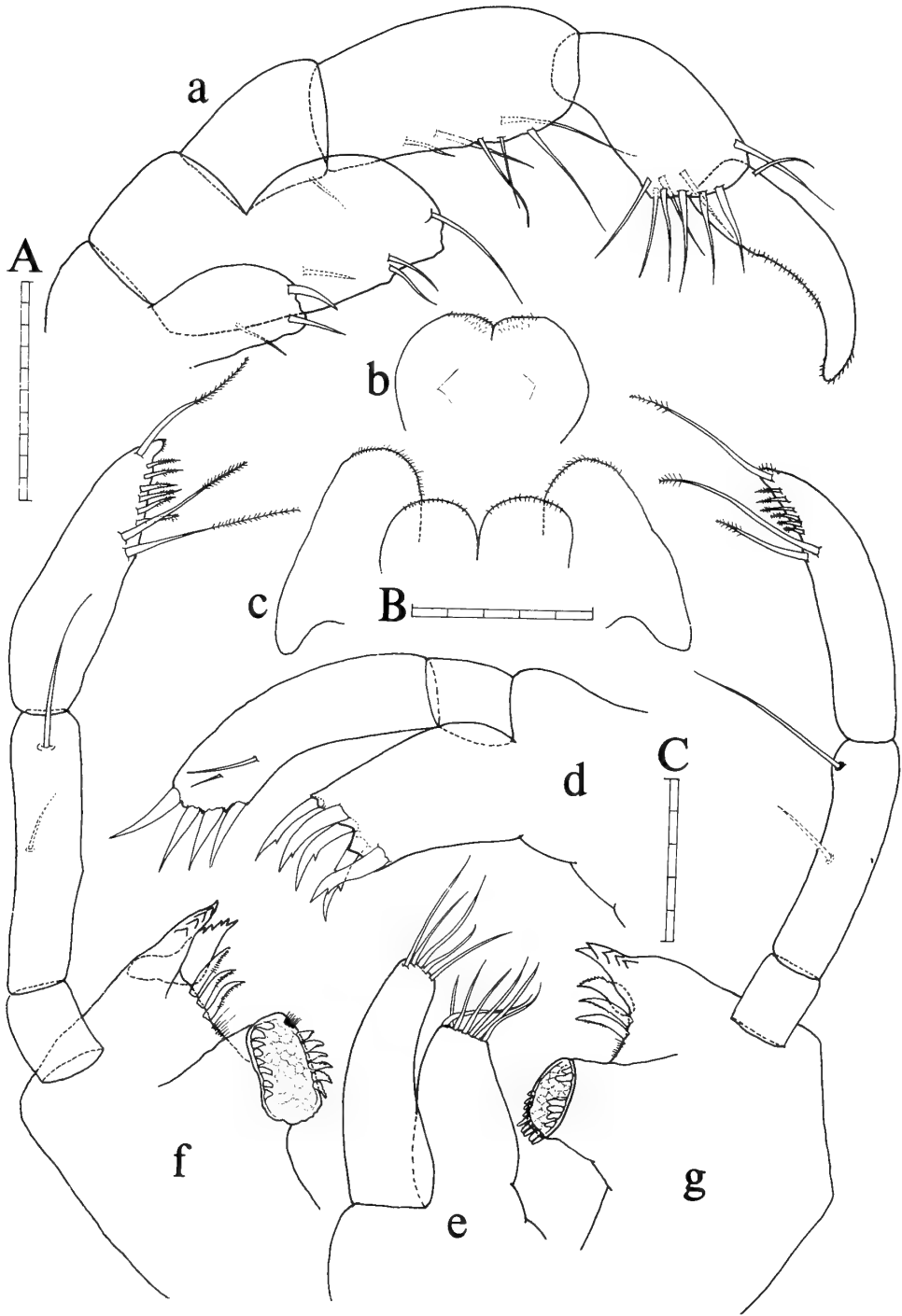


Fig. 3. *Pseudoprotella inermis* Chevreux, 1927 from Ceuta, North Africa. Male: a, maxilliped; b, upper lip; c, lower lip; d, maxilla 1; e, maxilla 2; f, left mandible; g, right mandible. Scale bars: A: 0.1 mm (a, f, g); B: 0.1 mm (b, c); C: 0.05 mm (d, e).

short and 2 long setae, from apex. Maxilla 1 (Fig. 3d) outer lobe with 5 serrate spines, article 2 of palp with 4 distal spines and a pair of dorsal setae. Maxilla 2 (Fig. 3e) inner lobe with 7 apical setae and shorter than outer lobe, with 5 apical setae. Inner plate of maxilliped (Fig. 3a) small and rounded with 2 simple setae; outer plate twice the size of inner one, with 1 prominent seta on end and 4 other setae. Palp 4-articulate; 1st article with 1 seta, inner margin of 2nd article with 6 setae; 3rd article with a row of 8 setae on lateral face and 1 seta on distal dorsal margin; article 4 falcate with rows of setules on grasping margin.

Gnathopod 1 (Fig. 4c) propodus wider but only a little longer than carpus; a pair of proximal grasping spines on palm.

Gnathopod 2 (Fig. 2a) inserted at middle of pereonite 2; basis slender, $\frac{4}{5}$ as long as pereonite 2, with a distal projection shaped like a carina on anterior margin. Ischium, merus and carpus approximately the same size (Fig. 4d). Propodus longer than basis, with acute projection on dorsal end. Length ca. 2.5 times width. Palm of propodus concave with a medial projection bearing a tooth, followed by a submedial projection and "U" notch. Dactylus curved, setose on inner margin.

Gills elliptical, length ca. 2 times width.

Pereopods 3–4 reduced, 2-articulate (Fig. 5a, b). Basal article short; length ca. 1.3 times width. Distal article, twice of basal one in length, with four distal setae.

Carpus of pereopod 5 (Fig. 5c) more slender than those of pereopods 6 and 7 (Fig. 5d, e). Palm of propodus concave with a robust proximal projection, provided with two grasping spines. Homologous articles on pereopods 5, 6 and 7 of increasing thickness from anterior to posterior.

Abdomen (Fig. 5f) with 2 pairs of rudimentary pleopods, uniarticulated, bearing sparse setae. Medial penes.

Female "b," 7.2 mm in length. Ventral proximal tubercle on pereonite 2 less pronounced than in male (Fig. 2b). Pereonite 3 with two ventrolateral acute projections.

Oostegites on pereonite 3 with setose inner margin. Oostegites on pereonite 4 setose only on posterior margin. A pair of lobes in abdomen (Fig. 5g).

Localities.—Type locality: Gulf of Cadiz (36°53'N, 10°52'W), southern Spain, depth 99 m. Other localities: Ceuta (35°54'N, 5°16'W), North Africa, depth 30–40 m.

Remarks.—*Pseudoprotella inermis* was established by Chevreux (1927) based on a single specimen collected from a depth of 99 meters in the Gulf of Cadiz, situated about 120 km west from Ceuta, north African side of the Strait of Gibraltar. The description and figures for *P. inermis* lacked details of the antennae, pereopods, mouthparts and abdomen. *Pseudoprotella phasma* (Montagu 1804), its only congener, is widely distributed in the northwest Atlantic Ocean and the Mediterranean Sea (e.g., Mayer 1890, Chevreux & Fage 1925, Harrison 1940, 1944; McCain & Steinberg 1970, Hughes 1978, Krapp-Schickel 1993). The present study is the second record for *P. inermis*.

The description based on specimens from Ceuta coincides with the original description of Chevreux (1927) in the species diagnosis: absence of dorsal projections from the body and antennae 1 longer than the body. Specimens from Ceuta differ from the original descriptions by Chevreux in only two aspects. The gnathopod 1 of the specimens from Ceuta appears to be larger, and pereopods 3 and 4 are less reduced than those of the specimen described from the Gulf of Cadiz.

The first description of *Pseudoprotella phasma* was given by Montagu (1804) as *Cancer phasma*. Subsequently, several authors have dealt with the taxonomy and biology of *P. phasma* (e.g., Mayer 1890, Chevreux & Fage 1925, Harrison 1940, 1944; Hughes 1978, Krapp-Schickel 1993) from the northwestern Atlantic Ocean and the Mediterranean Sea. Several forms of this species have been described based on the position of dorsal projections and features of the propodus of the male gnatho-

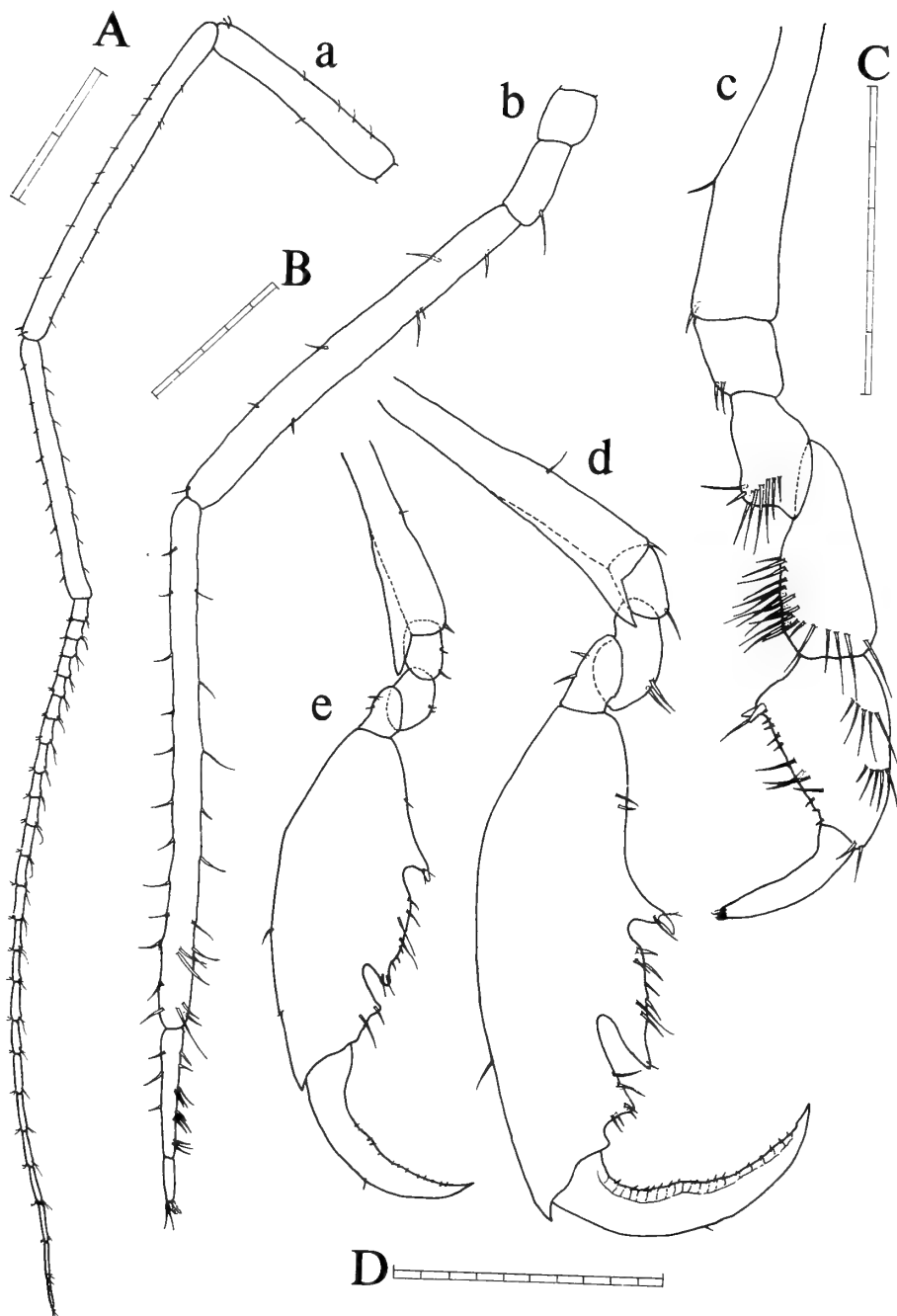


Fig. 4. *Pseudoprotella inermis* Chevreux, 1927 from Ceuta, North Africa. a-d, male: a, antenna 1; b, antenna 2; c, gnathopod 1; d, gnathopod 2; e, female gnathopod 2. Scale bars: A: 1 mm (a); B: 0.5 mm (b); C: 0.5 mm (c); D: 1 mm (d, e).

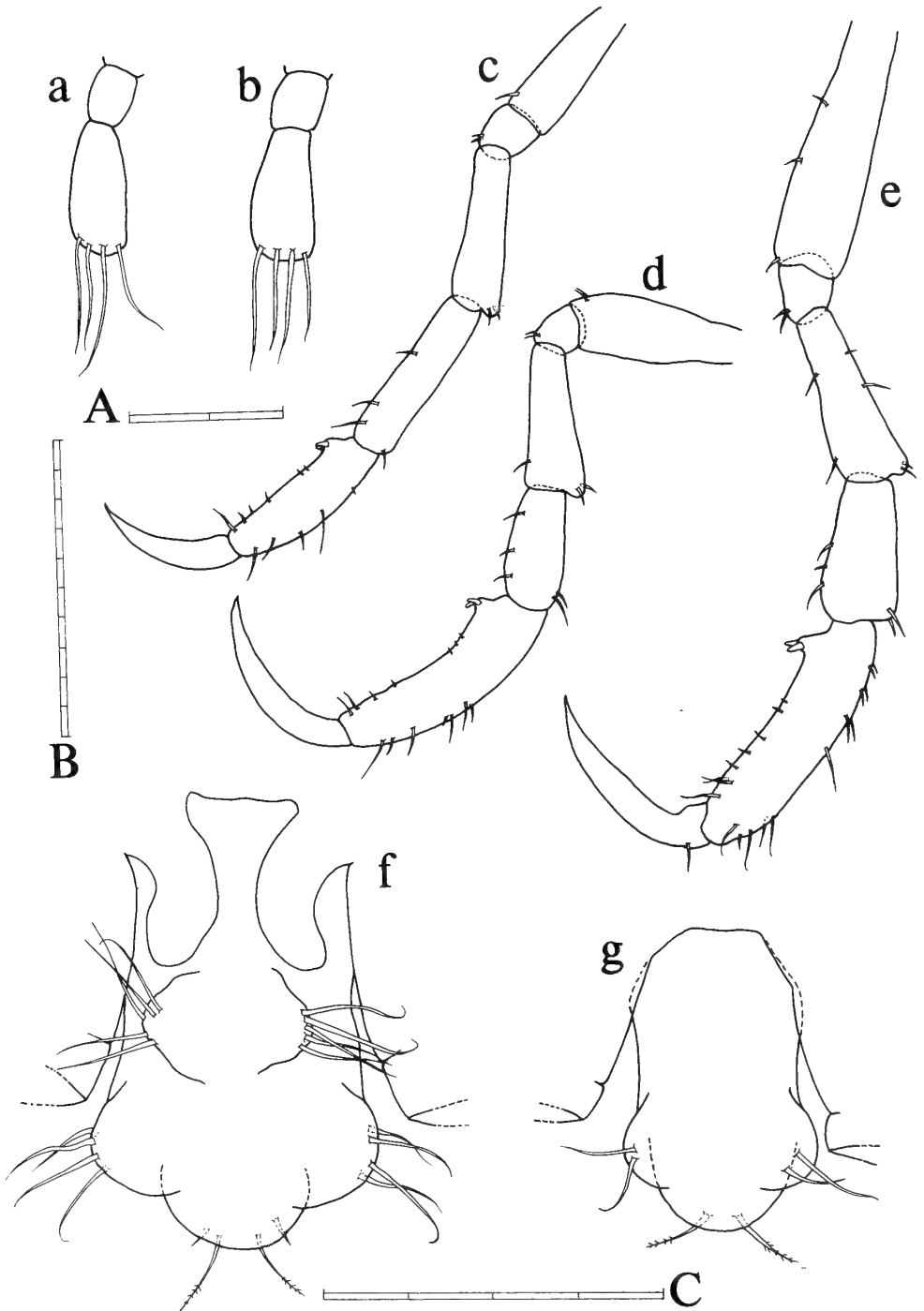


Fig. 5. *Pseudoprotella inermis* Chevreux, 1927 from Ceuta, North Africa. a-f, male: a, pereopod 3; b, pereopod 4; c, pereopod 5; d, pereopod 6; e, pereopod 7; f, abdomen (ventral view); g, female abdomen (ventral view). Scale bars: A: 0.1 mm (a, b); B: 1 mm (c, d, e); C: 0.2 mm (f, g).

pod 2 (Mayer 1890, Chevreux & Fage 1925, Krapp-Schickel 1993). These studies indicate that *P. phasma* has prominent dorsal projections on head to pereonite 2 in the forms *quadrispinis*, *typica* and *minor*, or on the head and pereonite 1 in the form *bispinis*. On the other hand, *P. inermis* has no distinct dorsal projections on the head and first two pereonites. Harrison (1940) reported that *P. phasma* juveniles of less than 5 mm in body length had already developed dorsal projections on the head and pereonite 1. This precludes the possibility that the present specimens of *Pseudoprotella* could be juvenile stages of *P. phasma*.

According to the descriptions of Chevreux & Fage (1925), Harrison (1944) and Krapp-Schickel (1993), *P. inermis* is also distinguished from *P. phasma* as follows: antenna 1 of *P. inermis* is longer than the body, while it is shorter than the body in *P. phasma*. Pereonite 3 of *P. inermis* carries a pair of anterior ventrolateral projections in females, lacking in males, while in *P. phasma* pereonites 3 and 4 each bear anterior lateral projections in males and females. The inner plate margin of maxilliped has 2 simple setae in *P. inermis*, while in *P. phasma* the number is variable, the inner plate with 2 setae (Chevreux & Fage 1925, Harrison 1944) or 3 (Krapp-Schickel 1993). In any case, the inner seta of the inner plate of maxilliped of *P. phasma* is always plumose while in *P. inermis* it is a simple seta. In *P. inermis* pereopods 5–7 increase in robustness respectively, carrying a few setae on the basis to propodus, while in *P. phasma* they are subequal and setose. Pleopods are sparsely setose in *P. inermis*, while densely setose in *P. phasma*.

The present specimens of *Pseudoprotella inermis* from Ceuta were collected from hydroids and algae in an area where visibility is 10–30 meters depending on weather conditions. The area, which is located near the top of the Ceuta's Peninsula, is exposed to the effects of local currents. *Pseudoprotella inermis* lives together with Atlantic caprellids such as *Caprella erethizon* Mayer, *C.*

tuberculata Bate & Westwood, and with *C. santosrosai*, recently described by Sánchez-Moyano et al. (1995b). The dominant posture observed for this species in clinging behavior over substrate was the "upright posture," as categorized by Takeuchi & Hirano (1995). The combination of weak swimming setae on antenna 2 and the long gnathopod 2 basis of the species suggests a predatory mode of life (Caine 1974, 1977).

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***Thermosphaeroma mendozai*, a new species from hot springs in northern Chihuahua, Mexico (Crustacea: Isopoda: Sphaeromatidae)**

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Abstract.—A new species of *Thermosphaeroma* (*T. mendozai*) is described from a collection of specimens found in hot springs in Chihuahua State, Mexico. Apomorphic characters are seen in the frontal lamina, pleotelson, and uropods. A new record is given for *T. subequalum* and the morphology of the female brood pouch is described for *T. smithi*. Bowman's (1981) key to species of *Thermosphaeroma* is amended to include all known congeners.

Of the 95 genera of sphaeromatid isopods, only members of the genus *Thermosphaeroma* are known to occur exclusively in hot springs, whereas other genera in the family have successfully colonized different aquatic habitats around the world. This genus has been found to date only in the southwestern United States and central Mexico between the eastern and western ranges of the Sierra Madre mountains and their northern extensions. The new species is the eighth known congener, described herein. Its discovery represents a westward expansion of the range of the genus.

Material of three *Thermosphaeroma* species was collected in central Mexico over several years by Jerry J. Landye of the U.S. Fish and Wildlife Service and others while searching for freshwater snails in thermal springs in Chihuahua state. Because thermal springs tend to be isolated, there is a high degree of endemism. However in this study, material from Julimes, Chihuahua has been identified as *Thermosphaeroma subequalum* Cole & Bate, 1978 whose type locality is Boquillas del Carmen, Texas, about 150 miles to the east. A third species, *T. smithi* was retrieved from a spring at its type locality and included ovigerous females, hitherto unknown. All material is deposited at the National Museum of Natural History (NMNH).

Family Sphaeromatidae White, 1847
Genus *Thermosphaeroma* Cole & Bane, 1978

Cole & Bane, 1978:225; Bowman, 1981: 105–106.

Thermosphaeroma mendozai, new species
Figs. 1 A–N, 2 A–H, 3 A–G, 4

Material.—Holotype, USNM 291484, non-ovigerous female TL 5.0 mm, Paratypes, USNM 291485, subadult male TL 3.9 mm, 13 juvs., Mexico, Chihuahua State, Ojo de Agua de Casas Grandes, Chihuahua State, 30°24'N, 107°59'E, under gravel and in recreational canal running from multiple spring heads ca. 6 km NNW of main square in Casa Grandes, temperature 29 to 30°C, coll. J. J. Landye and Phil Hines, 16 and 17 Sep 1990.

Diagnosis.—Frontal lamina anteriorly truncate. Pleotelson triangular with straight sides meeting at angled apex. Uropodal exopod lanceolate, held at right angle to broad, parallel-sided, apically square endopod; both rami extending beyond apex of pleotelson.

Description.—Body length 1.4 times greatest width, surface smooth. Sides of pereon subparallel. Pigmentation of preserved specimens various, from even cover to dense, solid black-brown color. Cephalon

with interocular suture. Pereonite 1 longest, pereonites 2–7 and single visible pleonite subequal in length. Sutures at coxal plates very faint. Pleotelson almost twice as wide as long; smoothly domed in lateral view; lateral margins straight, coming together at approximately right angle at apex.

Antennular peduncle, article 1 equal in length to articles 2 and 3 combined, latter article with 4 plumose setae; flagellum with 5 articles, ring-like first article bearing 2 feather-like setae; articles 4 and 5 provided with 1 and 2 aesthetases respectively. Antennal peduncle reaching midlength of cephalon and bearing several plumose setae on terminal article; flagellum consisting of 8 articles.

Frontal lamina, anterior margin straight, one-half of total width; corners angular, arms truncate posteriorly. Clypeus moderately long, anterior margin emarginate.

Mandible, left and right incisors 3 to 4-cusped; left lacinia 3-cusped; left spine row with 5 stout, tufted setae; right spine row with 6 setae, 2 of which tufted. Mandibular palp, penultimate article with 6–7 fringed setae, terminal article with 8–11. Maxilla 1 typical of genus. Maxilla 2, endopod bearing 14 fringed setae apically; exopod, both rami with 9 very long dentate setae. Maxilliped articles 2–4 with lobes on inner margins less produced than in other species; epipod lacking.

Pereopods 1–7 provided with numerous patches of short setae, especially on anterior margins of propodus, carpus, merus and ischium. Pereopod 1 with 2 dentate setae at distal margin of propodus. Pereopods 6 and 7 bearing 4 and 6 stout, dentate setae respectively, on distal margin of carpus. Basis of pereopods 2–7 with patches of scale setules on outer surface.

Pleopods 1–3 evenly covered with pigment. Pleopod 1, with 3 coupling hooks on peduncle, 15 and 22 plumose marginal setae on endopod and exopod respectively. Pleopod 2, 3 coupling hooks, 23 and 31 plumose marginal setae on endopod and exopod respectively. Pleopod 3, 3 coupling

hooks, 10 plumose marginal setae on distal margin of endopod; exopod bearing 41 plumose marginal setae. Pleopod 4, lacking marginal setae; branchial folds very poorly developed, somewhat stronger in endopod; both rami strongly pigmented. Pleopod 5 endopod with many branchial folds; exopod similar to that of *T. smithi*, with deep incision on lateral margin proximal to reniform scale patch.

Uropodal endopod, length almost 4 times greatest width, widening very slightly posteriorly; apically blunt, almost square, with fringe of extremely small setules on distal margin. Exopod lanceolate, shorter than endopod, with tiny setules apically. Both rami somewhat longer than pleotelsonic apex.

Adult male.—unknown.

Etymology.—The species name is a patronym for the New World Mendoza family: Mario, my husband David, Art, and Brandon.

Remarks.—*Thermosphaeroma mendozai* is distinguished from its congeners by the truncate frontal lamina, straight-sided triangular pleotelson and unusual uropods (wide, parallel-sided and truncate at apex), which are found in no other members of the genus. The angled apex of the pleotelson runs counter to the Cole & Bane's original diagnosis (1978), which describes it as "somewhat rounded terminally." The uropodal exopods, as in *T. smithi*, are held at right angles to the endopod. Since the adult male of *T. mendozai* is unknown, the degree of setation on the pereopods may differ from that found in the holotype female described herein. Examination of other *Thermosphaeroma* species in the USNM collection revealed the absence of a maxillipedal epipod, as is the case with many sphaeromatid genera.

Thermosphaeroma smithi Bowman, 1981

Thermosphaeroma smithi Bowman, 1981:
110–113, figs. 4–6, 8e, 9e.

Material.—1 ♂, 3 ovig. ♀, 4 ♀ with brood pouches, 13 juvs. Mexico, Chihua-

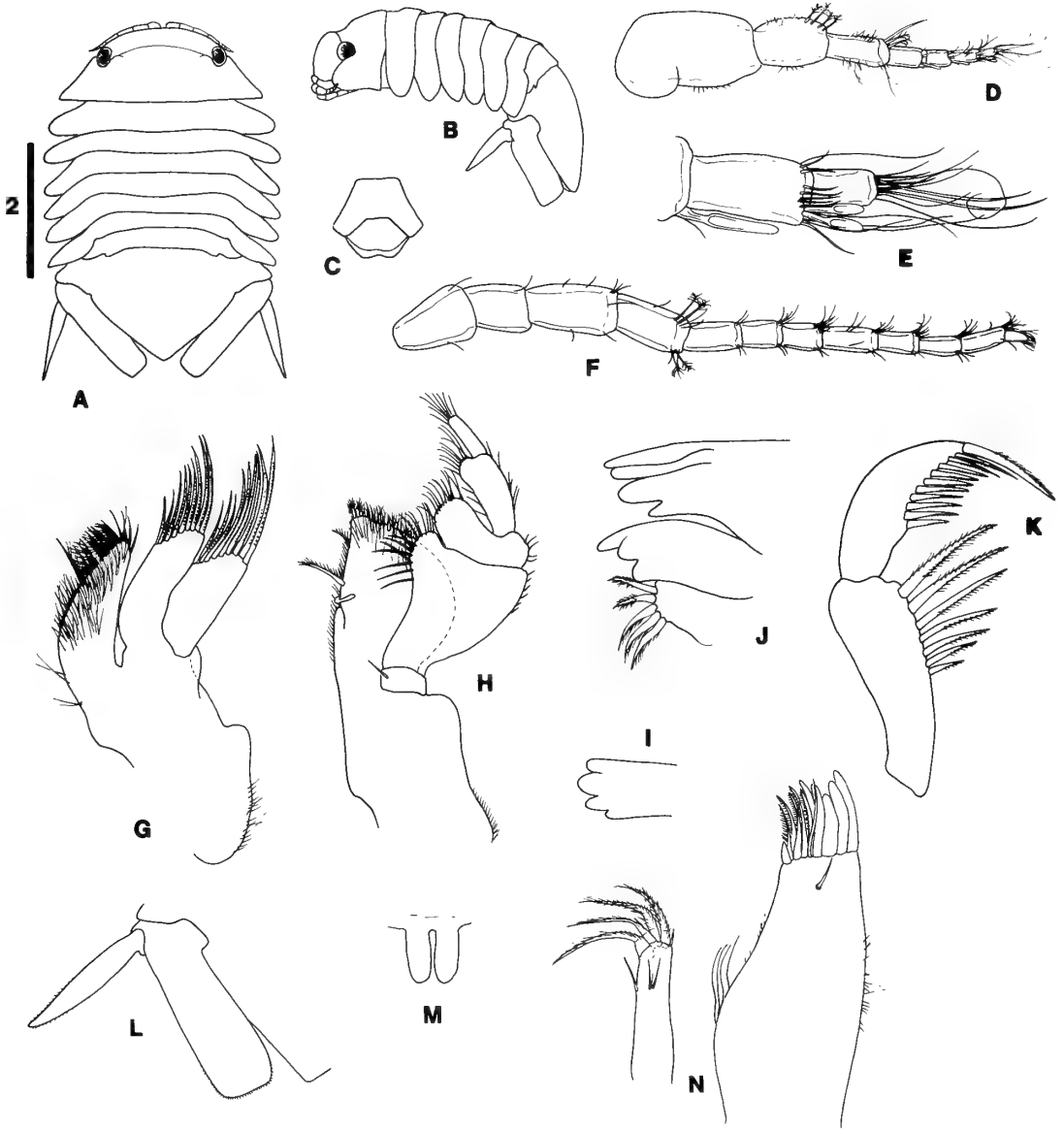


Fig. 1. *Thermosphaeroma mendozai*, n. sp. A, Female holotype; B, Lateral view; C, Frontal lamina; D, Antennule; E, Terminal articles of antennule; F, Antenna; G, Maxilla 2; H, Maxilliped; I, Right incisor; J, Left mandible; K, Mandibular palp (terminal articles); L, Uropods; M, Penes of subadult male; N, Maxilla 1.

hua, Balneario de San Diego (about 37 km E of Ciudad Chihuahua), 28°35.5'N, 105°32.5' W, isolated hot spring on hill E of Rio Chusvucar with lateral springs coming out on N, S and W sides, temperatures 44.7 to 25°C in isolated pool, coll. J. J. Landye et al., 29 Aug 1971.

Remarks.—The type material deposited

at USNM contains no ovigerous females and so the sexual characters for the species were not described. In the present material several females with brood pouches were found. Females resemble males except for secondary sexual characters; the mouthparts are unmetamorphosed; the brood pouch consists of two opposing pockets opening

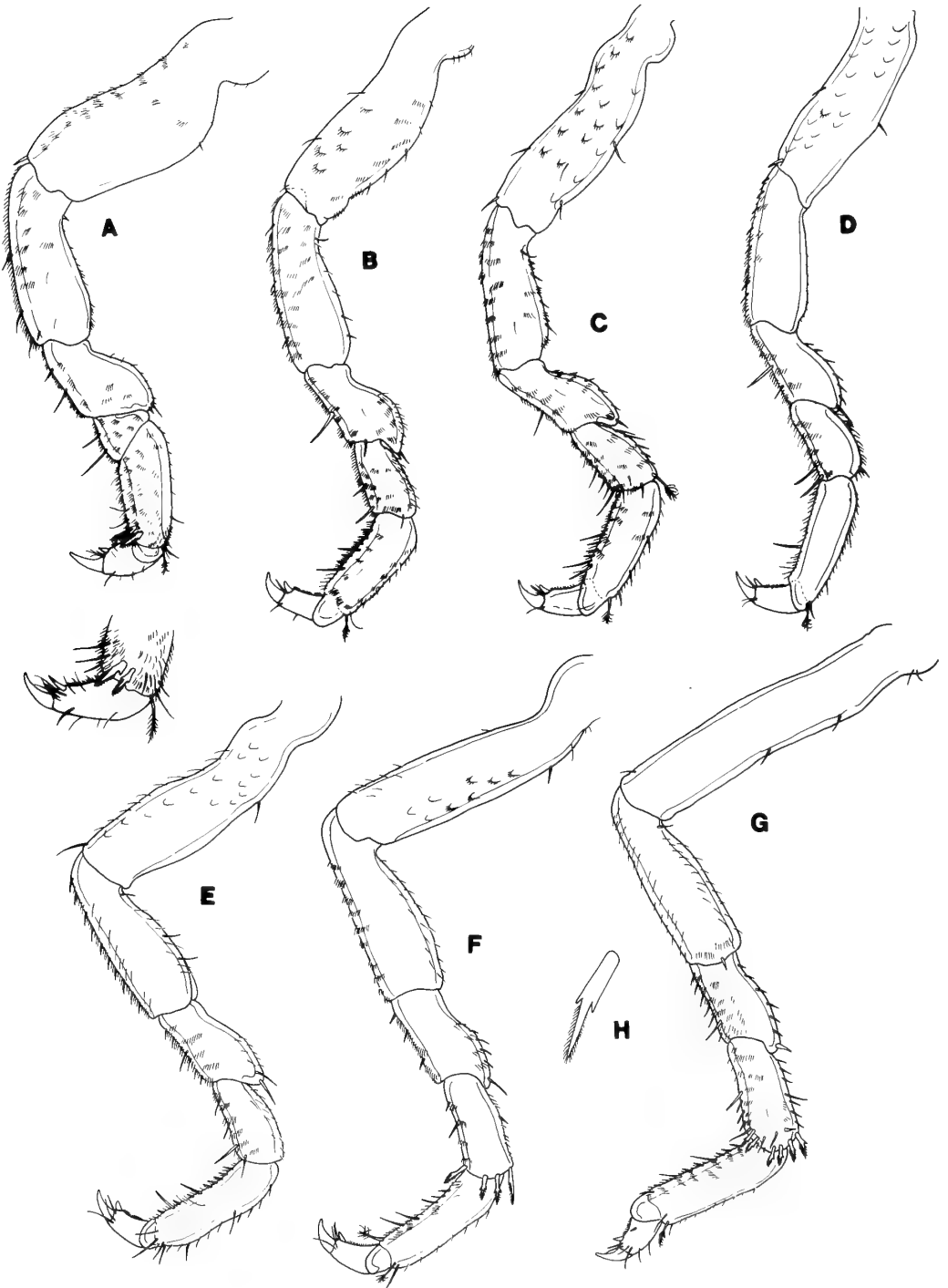


Fig. 2. *Thermosphaeroma mendozai*, n. sp. A, Pereopod 1; B, Pereopod 2; C, Pereopod 3; D, Pereopod 4; E, Pereopod 5; F, Pereopod 6; G, Pereopod 7; H, Dentate seta on carpus.

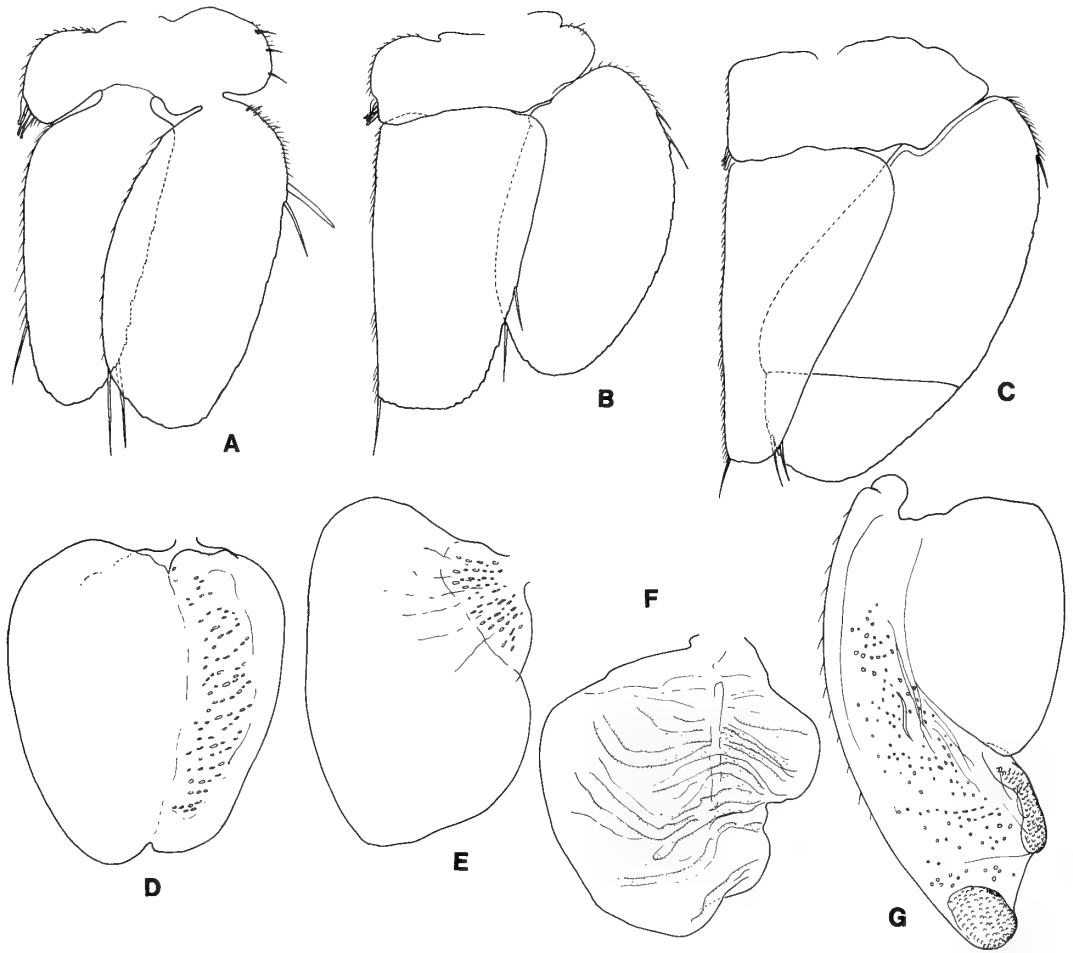


Fig. 3. *Thermosphaeroma mendozai*, n. sp. A, Pleopod 1; B, Pleopod 2; C, Pleopod 3; D, Pleopod 4, endopod; E, Pleopod 4, exopod; F, Pleopod 5, endopod; G, Pleopod 5, exopod.

near fourth pereopods and oostegites are absent. Examination of other type species of the genus in holdings at NMNH yielded no ovigerous females but this character state for *T. smithi* is undoubtedly consistent for the genus.

Thermosphaeroma subequalum Cole & Bane, 1978

Thermosphaeroma subequalum Cole & Bane, 1978:223–228, figs. 1–3.—Bowman, 1981:116–117, figs. 8c, 9c, 10c.

Material.—4 ♂, 9 ♀ with brood pouches, 15 juv. Mexico, Chihuahua, Ojo de Julimes, 28°25'N, 105°25'W, hot springs with mul-

tle sources and common main pool, 44 to 45°C, coll. J. J. Landye and D. Wong, 05 Apr 1991.

Remarks.—The specimens are indistinguishable from type material from Texas, held at USNM. The morphology of the brood pouch in ovigerous females is the same as in *T. smithi*. The uropodal endopod is somewhat longer than the exopod instead of subequal to it (particularly in the case of the juveniles), but otherwise the characters fit those of the type diagnosis exactly. The conspecificity is at first glance puzzling due to the distance between the populations (150 miles) in a genus known for endemism. However, Ojo de Julimes lies in the

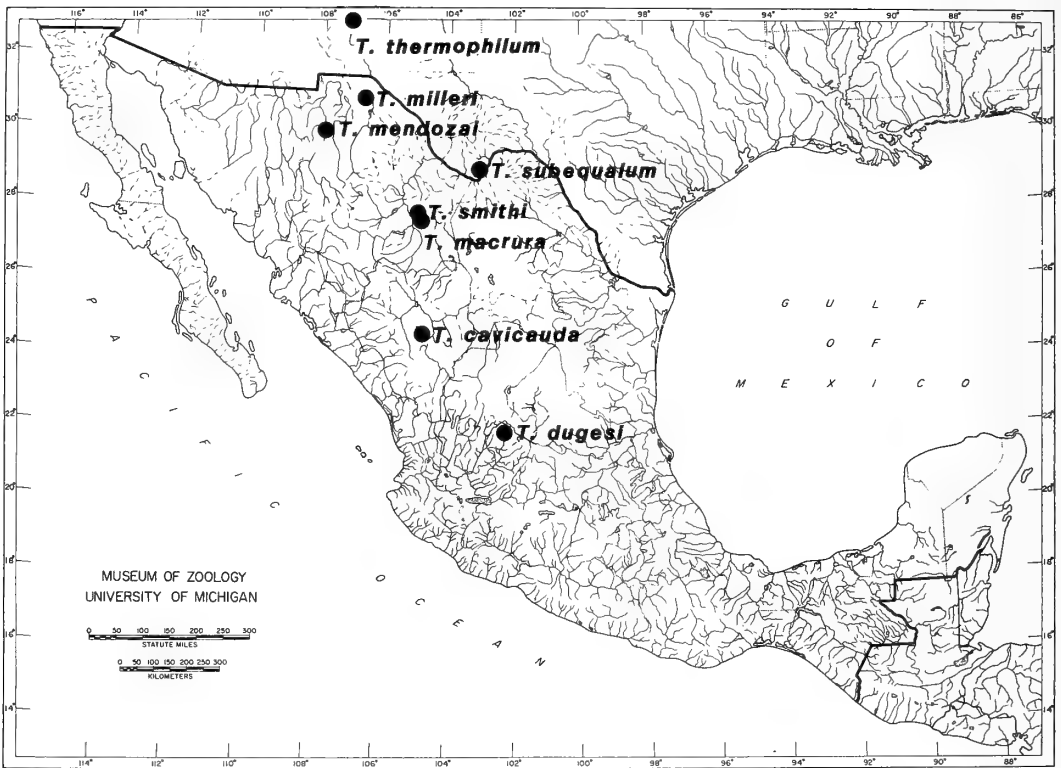


Fig. 4. Distribution of known species of *Thermosphaeroma*. *T. subequalum* has also been found near Julimes, Chihuahua state, near the type locality of *T. macrura*.

watershed of Rio Conchos, which flows into the Rio Grande and ultimately past Boquillas del Carmen, Texas, the type locality. As the two regions are connected by rivers, it is possible that they are also hydrologically connected underground or were so in the recent past.

Bowman (1981) discusses the difficulty of deducing relationships between *Thermosphaeroma* and other isopod groups, and suggests a possible origin of the genus, i.e., a marine sphaeromatid in the Dynameninae family. Such "subfamily" designations, based on branchial folds in the pleopods, are now considered of little use (Bruce 1994). *Thermosphaeroma* differs from other so-called "Dynameninae" in the absence of lateral sutures on the free pleonite, the lack of branchial folds in the fourth pleopodal exopod and the incompletely divided exopod of the fifth pleopod. These character

states are also present in the estuarine species *Cassinidea*, representing another so-called "subfamily" Cassinininae. Until a cladistic analysis of all sphaeromatid genera is performed, discussion of the generic affinities of *Thermosphaeroma* and a possible ancestor would be only conjecture.

Key to known species of *Thermosphaeroma*

- 1a. Apex of pleotelson incised
 *T. cavicauda* Bowman,
 1985 (La Laguna, Durango State, Mexico)
- 1b. Apex of pleotelson not incised 2
- 2a. Frontal lamina truncate, level across
 anterior margin, corners angular; apex
 of pleotelson angled
 *T. mendozai* n. sp.
 (Casas Grandes, Chihuahua State, Mexico)
- 2b. Frontal lamina not truncate anteriorly;
 apex of pleotelson rounded 3

- 3a. Exopod and endopod of uropod subequal in length *T. subequalum*
Cole & Bane, 1978 (Boquillas Canyon, Big Bend National Park, Texas; Ojo de Julimes, Chihuahua State, Mexico)
- 3b. Exopod and endopod not subequal in length 4
- 4a. Exopod of uropod distinctly longer than endopod
. *T. smithi* Bowman, 1981 (Balneario San Diego, Chihuahua State, Mexico)
- 4b. Exopod of uropod distinctly shorter than endopod; lacinia of left mandible 3-cusped 5
- 5a. Apex of endopod of uropod angular 7
- 5b. Apex of endopod of uropod rounded 6
- 6a. Pleotelson evenly and broadly rounded; exopod of uropod about 0.6 length of endopod; appendix masculina of male pleopod 2 curving laterad, longer than endopod *T. thermophilum*
(Richardson 1897) (Socorro, New Mexico)
- 6b. Pleotelson with slightly concave margins just anterior to narrowly rounded apex; exopod of uropod more than 0.7 length of endopod; appendix masculina of male pleopod 2 straight, about as long as endopod
. *T. milleri* Bowman, 1981 (Bolson de los Muertes, Chihuahua State, Mexico)
- 7a. Frontal lamina nearly triangular, anterior margin narrowly rounded
. *T. milleri* Bowman, 1985 (Julimes, Chihuahua State, Mexico)
- 7b. Frontal lamina very broadly rounded

anteriorly, anterior margin almost level *T. dugesi* (Dollfus 1893) (Ojo Calientes, Aguascalientes State, Mexico)

Acknowledgments

I thank Jerry J. Landye, who collected the material, for depositing it at the USNM through his colleague, Dr. Robert Herschler of the National Museum of Natural History. Dr. Brian Kensley kindly reviewed the manuscript for me.

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***Nebalia gerkenae*, a new species of leptostracan
(Crustacea: Malacostraca: Phyllocarida) from the Bennett Slough
region of Monterey Bay, California**

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Abstract.—A new species of leptostracan crustacean, *Nebalia gerkenae*, is described from Bennett Slough, Monterey County, California. The species is similar to *N. hessleri* from deeper waters off La Jolla, California. It differs from *N. hessleri* in the shape and color of the pigmented region of the eyes, armature of the antennule and antenna, the degree that the carapace covers the abdominal somites, dentition of the protopod of the fourth pleopod, and details of the pleonite border spination. Variation in this spination is discussed, and guidelines are suggested for future descriptions of leptostracan species.

The Leptostraca are malacostracan crustaceans characterized in part by a hinged rostrum, bivalved carapace, phyllopodous thoracopods, and the presence of seven abdominal segments (Kaestner 1980, Schram 1986). In the marine environment, these animals are ubiquitous. They have been recorded from a wide range of habitats, including intertidal mudflats, mangrove lagoons, caves, submarine canyons, the bathypelagic zone, and hydrothermal vents. The order Leptostraca includes 32 nominal species in nine genera. However, the true diversity of the group far exceeds this number; the literature includes many references to collections of undescribed species (Dahl 1985, Vetter 1996b, Olesen 1999).

Historically, the leptostracan Crustacea of the Pacific Coast of the United States have all been identified as *Nebalia pugettensis* (Clark, 1932). Although sometimes present in large numbers (Vetter 1994, Gerken 1995), the leptostracan fauna of California is poorly known. Ecological studies on Leptostraca of southern California (Vet-

ter 1994, 1996a) led to the recognition of three taxa, two of which have been described. *Nebalia daytoni* Vetter, 1996a, was recorded from oligotrophic sands off the coast of San Diego. *Nebalia hessleri* Martin et al., 1996, was described from enriched sediments and detrital mats at the head of Scripps Canyon off La Jolla, California. Because Clark's (1932) description was inadequate and type material was not available, Martin et al. (1996) declared *Nebalia pugettensis* (Clark, 1932) a nomen nudum. Actually, the name *Nebalia pugettensis* is available, but a neotype must be established in order to avoid taxonomic confusion. Thus, in addition to *N. pugettensis*, two valid nominal taxa and one undescribed species have been reported from the coast of California. In addition, the identity of populations formerly referred to as *N. pugettensis* is uncertain. New collections of leptostracans from Monterey Bay represent a fourth species of *Nebalia* from the coast of California, described herein.

Materials and Methods

The leptostracans were collected from intertidal algal mats of *Chaetomorpha* sp. and *Gracilaria* sp. Salinity, recorded with a hand refractometer, was 33–34‰. Most specimens were placed directly into 75% ethyl alcohol, but five specimens were preserved frozen using dry ice and later transferred to a freezer held at -80°C .

Written descriptions and illustrations are of the mature females. Additionally, sexually dimorphic features are described. Illustrations were made with the aid of a camera lucida attached to a Wild M5APO dissecting microscope and a Nikon Labophot. Specimens were prepared for scanning electron microscopy according to the method of Martin et al. (1996) and examined with a Cambridge Stereoscan 360. Length measurements were made from the base of the rostrum to the center of the posterior emargination of the carapace (dorsal carapace length) or to the tip of the caudal ramus but excluding the setation (total length). The carapace also was measured in the lateral aspect from the anterior to posterior margin (lateral carapace length) and from the dorsal to ventral margin (carapace height). The female holotype, male allotype, and 60 paratype specimens were deposited in the Crustacea collections of the Natural History Museum of Los Angeles County (LACM). Additionally, 54 paratype specimens (34 of which are juveniles) have been deposited in the National Museum of Natural History, Washington, D.C. (USNM).

Systematics

Order Leptostraca Claus, 1880

Family Nebaliidae Samouelle, 1819

Genus *Nebalia* Leach, 1814

Nebalia gerkenae, new species

Figs. 1–12

Type locality.—United States, California, Monterey County, Bennett Slough, off Jetty Road, north side of bridge before entrance to Moss Landing State Beach, from mudflat

at low tide from surface of fine sediment beneath algal mat consisting of *Gracilaria* sp. and *Chaetomorpha* sp.

Material examined.—Holotype female (Fig. 1a), LACM CR19990191, lateral carapace length 3.7 mm, dorsal carapace length 2.4 mm, carapace height 2.4 mm, total length 9.1 mm, collected 17 Oct 1999 by T. A. Haney; collected in type locality. Allotype male (Fig. 1d), total length 8.9 mm, same collection data, LACM CR19990192. Paratype specimens, same collection data, LACM CR19990193 (37 females, 16 males, 7 juveniles) and USNM 306877 (14 females, 6 males, 34 juveniles). Other specimens destroyed in the course of dissecting for illustrations and/or SEM preparation; these and frozen specimens declared non-paratypic. Non-type material: North Pacific Ocean, United States, California, Monterey County, Elkhorn Slough, 22 miles north of Pacific Grove, station 1590-47, sandflats during -1.6 m tide; collected 5 Feb 1947; collected by R/V *Velero*; LACM CR19470143; 13 specimens (12 females, 1 male) in 4 vials, North Pacific Ocean, United States, California, Monterey County, Elkhorn Slough; collected by E. W. Vetter; no additional data; LACM, unregistered; 8 specimens (4 females, 1 male, 3 juveniles; one female mounted on SEM stub).

Diagnosis.—Average total length of females 5.9 mm ($n = 14$), of males 5.4 mm ($n = 6$), average lateral carapace length of females 3.2 mm ($n = 52$), of males 2.4 mm ($n = 23$). Eye not lobed or subdivided, oval, widest in center, slightly down-turned and laterally compressed; pigmentation extensive, covering at least distal half of eye. Antennule with 2 heavy spine-like setae on apical face of fourth article. Antennular flagellum well developed, with 10 or more segments. Male antennule sickle-shaped, strongly upturned. Dorsum of fourth pleonite with posterior border bearing acute teeth; tooth of postero-lateral border of fourth pleonite (epimeron of Dahl 1985) slightly longer than others and up-turned. Base (proximal podomere or peduncle) of

corresponding pleopod 4 minutely serrated along posterior border, terminating in sharp tooth at postero-lateral corner. Fifth pleopod with 4–6 large spine-like setae on disto-lateral border, with last spine longer than others and located terminally (directed posteriorly). Sixth pleopod with 4–6 spine-like setae along disto-lateral border, 6th seta terminally located terminally, two times as long as others. Rostrum with rectangular keel. Caudal rami in females approximately equal or greater than twice length of telson. Spines along posterior dorsal borders of pleonites acute.

Description of mature female.—Carapace (Fig. 1a): Elliptical laterally, approximately 1.5 to 1.6 times longer than high, with small, u-shaped posterodorsal indentation. Average lateral carapace length in females is 3.2 mm ($n = 38$). Carapace surface smooth, lacking scales. Posterior margin extending to posterior margin of pleonite three and sometimes extending slightly over anterior portion of pleonite four.

Rostrum (Figs. 1a, 2a–c): Rostrum long, clearly extending beyond eye, distally rounded, length approximately 2.4 to 2.6 times width. Average length of rostrum 1.3 mm (0.35 times lateral carapace length; $n = 38$ females). Keel rectangular (Fig. 2b), unpaired, with medial depression, depression bearing field of ctenate setae proximally (Fig. 2c).

Compound eye (Figs. 1b, 4c): Large, well developed, elongate-oval. Pigmentation extensive, covering distal half, with pigmented area more or less reflecting shape of eye. Not lobed or subdivided. Base of eyestalk with minute cuticular scales. Disto-ventral portion of eye bearing patch of simple setae (Fig. 4d). Ocular (supraorbital) plate sharply tapering to acute tip, relatively small, length of ocular plate approximately 0.5 times length of eyestalk, and bearing minute setae (visible via SEM) especially along dorsal and dorso-lateral surfaces.

Antennule (Figs. 3a, 5a–c): Peduncle composed of 4 articles. Second article wid-

est at midpoint, with single long, plumose seta arising proximally on anterior margin, cluster of much longer plumose setae arising subterminally, and group of many simple setae at apex. Third article shorter than second, widest distally, with terminal cluster of simple setae on anterior margin and long, simple seta arising from postero-distal margin. Fourth article (Fig. 5a, c) much shorter than third, with conspicuous row of at least 6 long setae increasing in length distally and with 2 robust spines along disto-lateral border; both spines bear minute tubercles along curved outer surface and minute subterminal pore. Antennular scale (Figs. 3a, 5a–c) oval, blade-like, with anterior margin convex and posterior margin straight; scale approximately as long as third peduncular article, bearing marginal rows of several distinct setal types along anterior margin, including long naked setae, stout, curved setae that are proximally smooth but bear large, blunt serrations distally, and longer, thinner setae that bear smaller, sharper teeth along their entire length. Surface of antennular scale bearing many minute pores. Flagellum well developed, at least 4 times length of antennular scale and composed of at least 10 to 15 articles.

Antenna (Figs. 3b, 4c): Peduncle composed of 3 articles, proximal 2 of which bear an acute disto-dorsal process (Fig. 4c, e, f). Process of first article (Fig. 4f) larger than that of second (Fig. 4e), much broader basally, and covered with minute teeth; process of second article (Fig. 4e) with minute tubercles on dorsal border. First article broader than second and third. First and second articles equal in length. Third article longer than first or second, and bearing approximately 8 short, robust spine-like setae along anterior margin, some of which are similar in appearance to those described for article 4 of antennule. Third peduncular article with proximal cluster of simple setae plus single pinnate seta; long, plumose seta arising from posterior margin at midlength, subequal in length to article; group of plu-

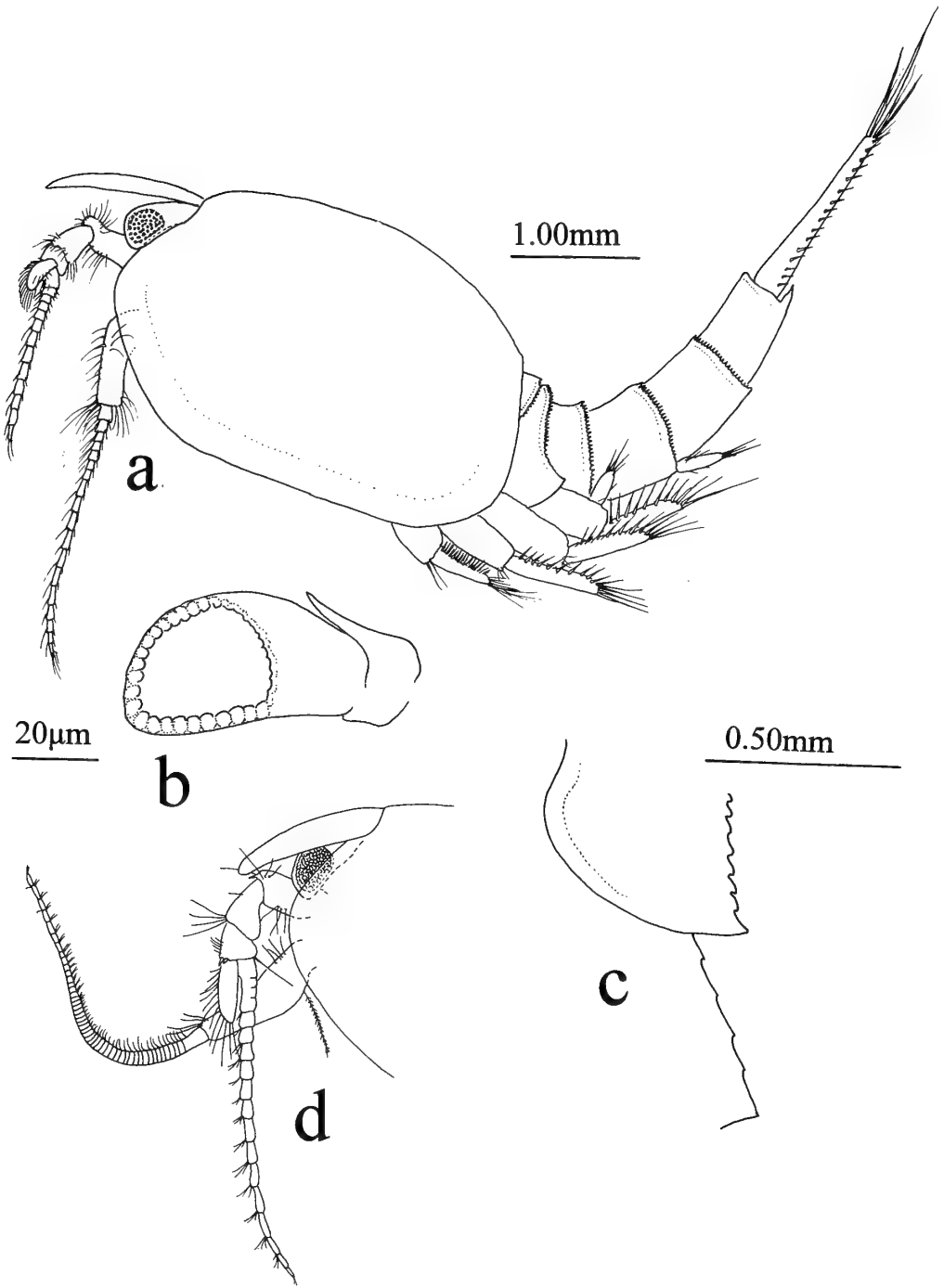


Fig. 1. *Nebalia gerkenae*, new species: a, holotype female, LACM CR19990191, left side; b, eye and ocular plate; c, pleonite four and protopod of pleopod one, postero-lateral margins; d, male allotype, LACM CR19990192, anterior part of left side.

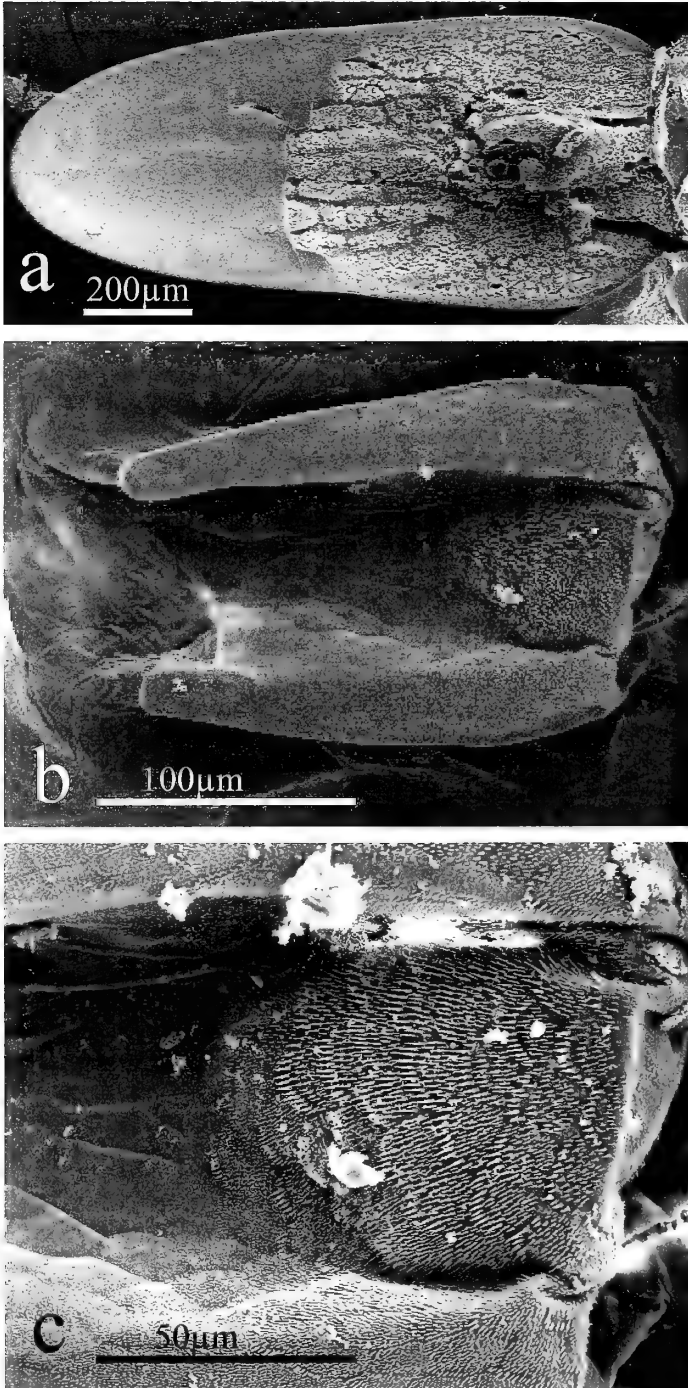


Fig. 2. *Nebalia gerkenae*, new species: a, rostrum, ventral surface, damaged proximally; b, rostral keel; different specimen; c, rostral keel, proximal portion bearing setae.

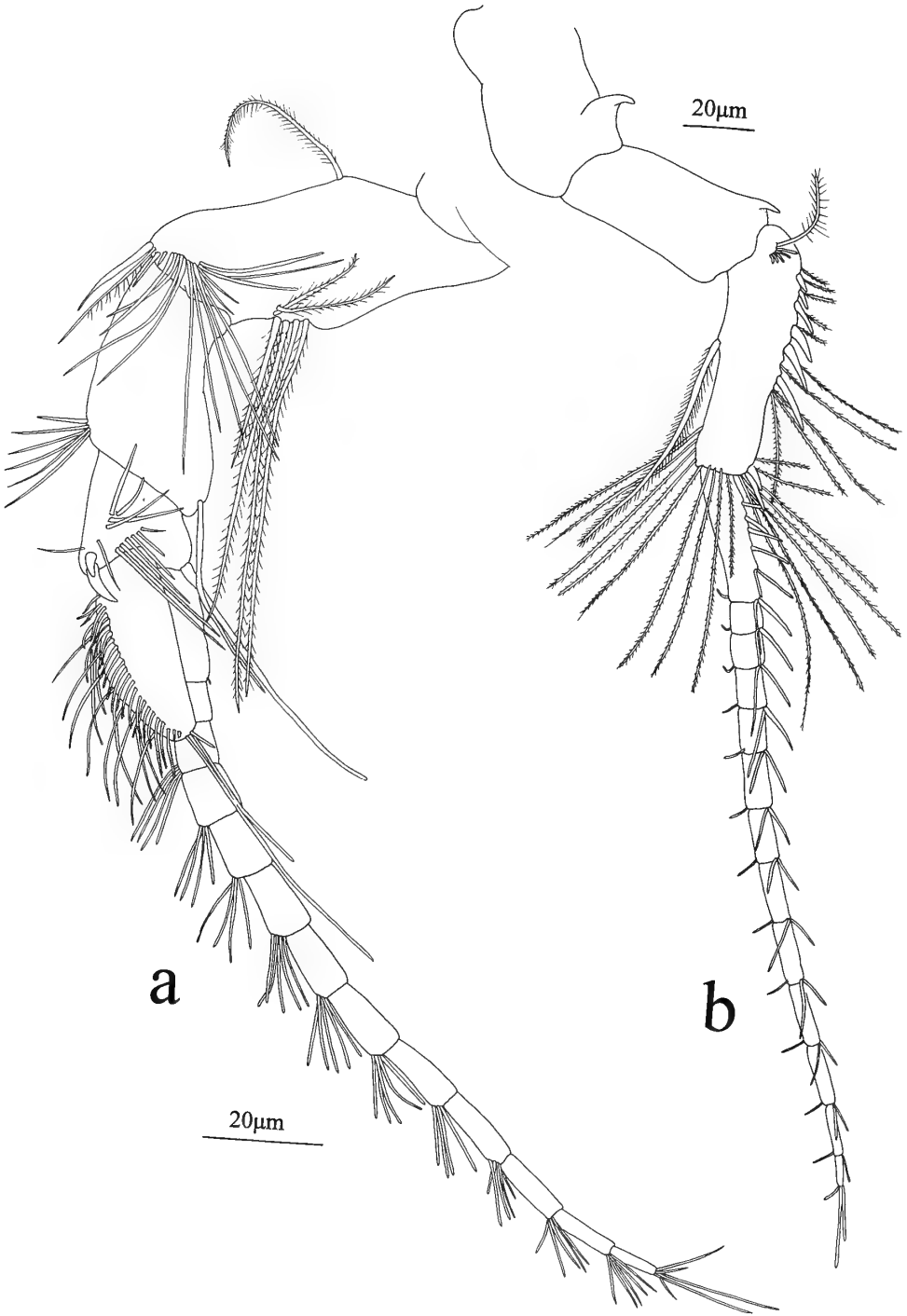


Fig. 3. *Nebalia gerkenae*, new species, female: a, antennule, left, article one not drawn; b, antenna.

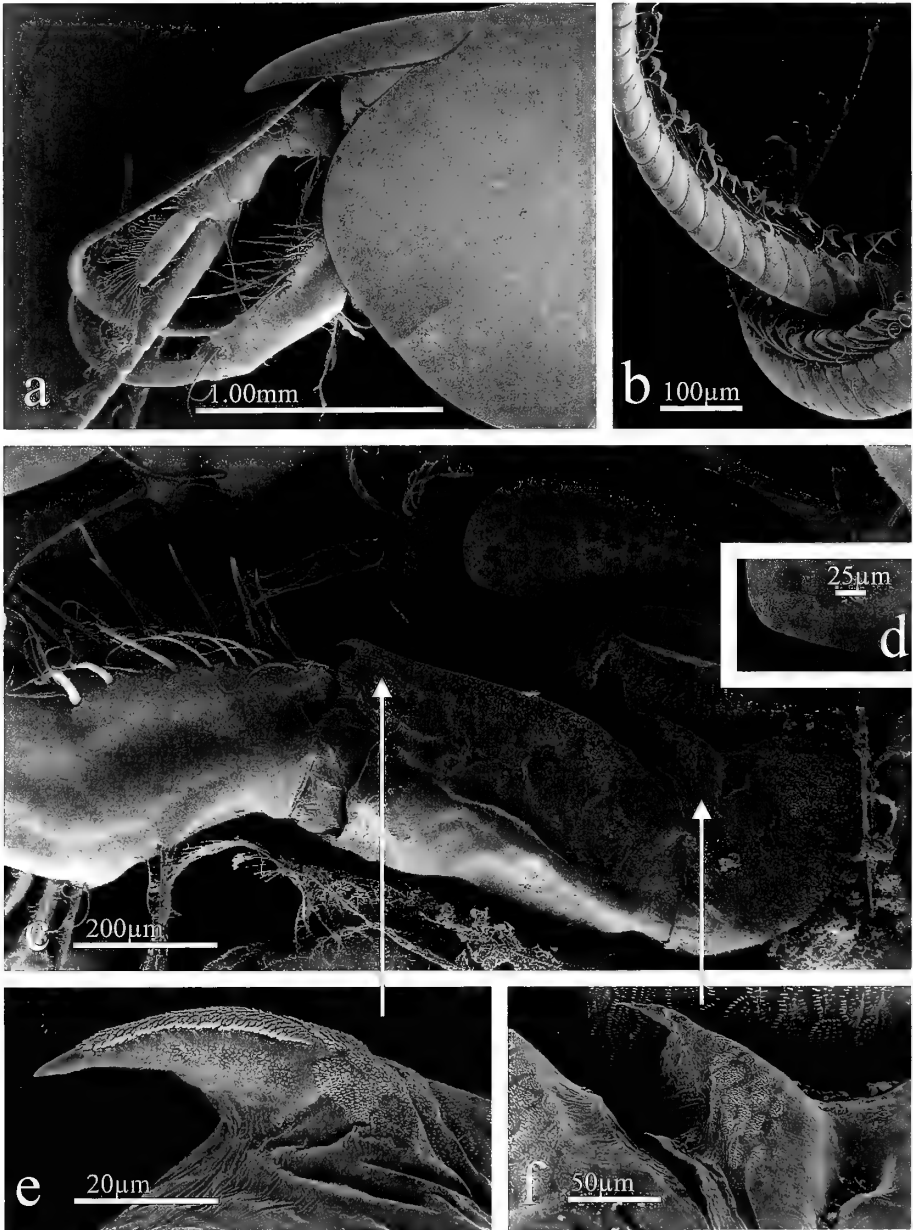


Fig. 4. *Nebalia gerkenae*, new species: a, male anterior, left side; b, antennal flagella of male, showing ribbon-like setae; c, antennal peduncle of male (morphology of which is similar to that of female); d, ventro-distal surface of left eye; e, distal spine of second article of peduncle; f, distal spine of first article of peduncle.

mose setae among short, robust setae of anterior margin, longer plumose setae distally. Flagellum composed of 10 to 16 articles. Flagellum slightly longer than combined articles of peduncle, each flagellar article with

paired terminal and subterminal setae as well as single ventral seta, most of which are unarmed, and covered with minute cuticular scales. Antenna sexually dimorphic; in males, antenna sickle-shaped, strongly

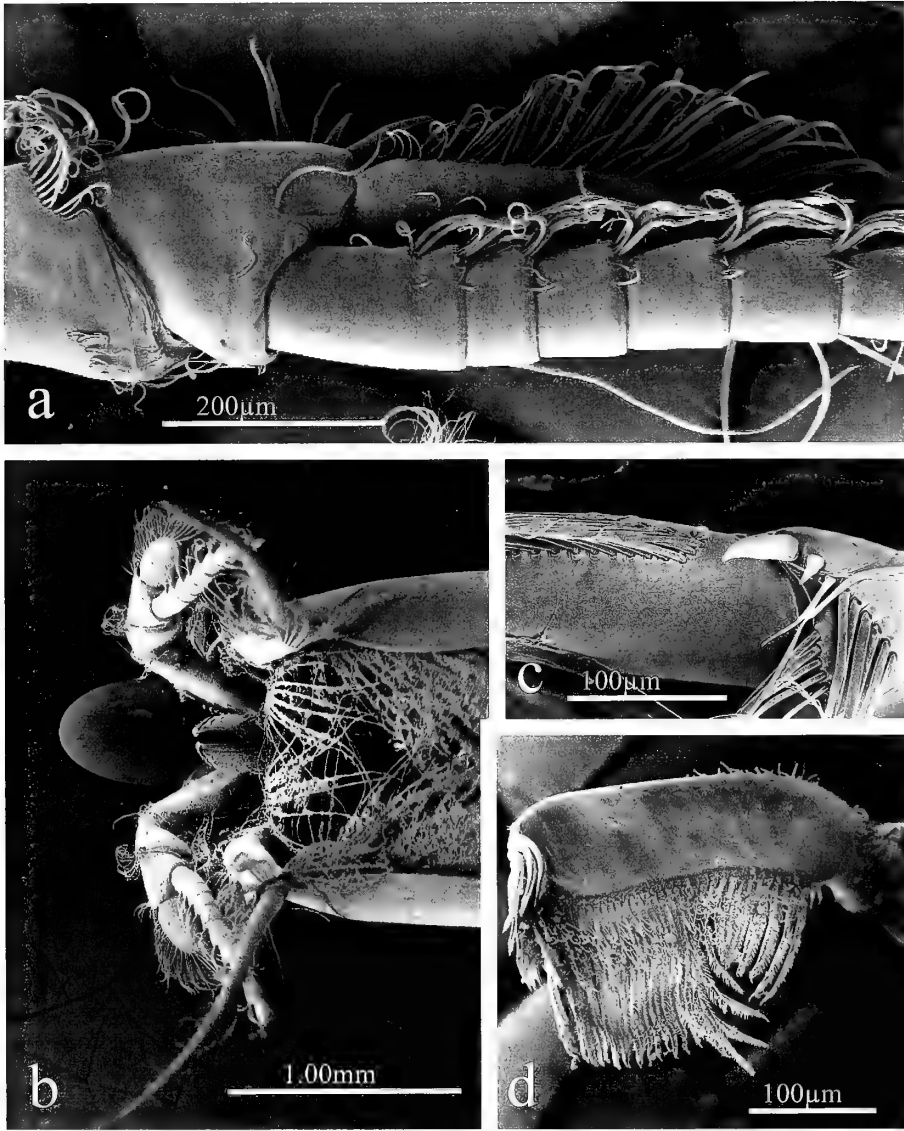


Fig. 5. *Nebalia gerkenae*, new species, female: a, antennule, including distal articles of peduncle, antennular scale and basal articles of flagellum; b, ventral aspect of anterior features; c, distal face of fourth peduncular article of antennule, bearing distal spines and setal rows; d, distal article of right mandibular palp, medial face.

upcurved (Figs. 1d, 4a, b), with articles shorter than those of female, and bearing curved, ribbonlike setae.

Mandible (Figs. 5d, 6a): Molar process 3× as long as wide, subequal in length to first article of palp. Distal margin forming concave grinding surface, with inner field composed of rows of stout, densely spaced teeth, more widely spaced teeth and long

spines on periphery. Incisor process broad basally, with short sharp teeth along inner (medial) face and acute terminal process. Palp well developed, composed of 3 articles; third article subequal to second; second approximately 2× as long as first, bearing two smooth setae, one at midlength and one subterminally. Setation of distal article complex (Fig. 5d), with short field of very

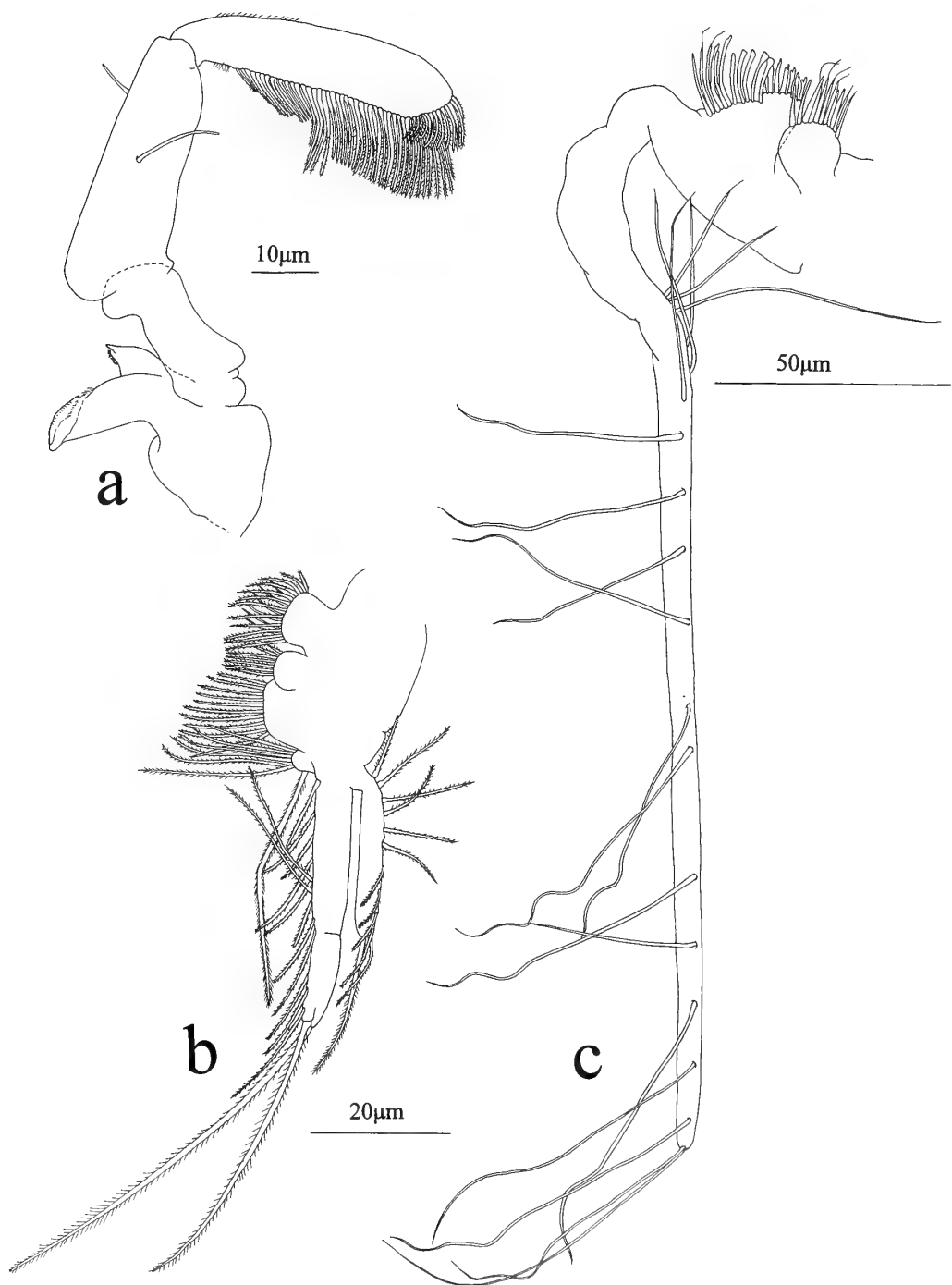


Fig. 6. *Nebalia gerkenae*, new species, female: a, mandible and mandibular palp, left side; b, maxilla, right side; c, maxillule, left side.

fine setae and plumose setae extending from proximal quarter to terminus, and with row of more stout setae overlying distal fourth of this row.

First maxilla (Fig. 6c): Proximal endite with rounded medial margin, bearing robust simple setae. Distal endite 1.6 times as long as proximal and carrying row of stout, spatulate setae just distal to row of trifid setae on outer margin. Several long plumose setae also present on distal part of endite. Trifid setae are nearly smooth basally, giving rise to smooth setules toward distal tip, and with three terminal teeth slightly longer than flanking teeth and bearing small pore (Martin et al. 1996). Palp elongate, approximately 6 times longer than combined length of both endites of protopod, bearing proximal cluster of approximately 6 long setae and 13 widely spaced setae along its length.

Second maxilla (Fig. 6b): Protopod subdivided into 4 endites, with endites 1 and 3 approximately equal in size and larger than endite 2 or 4. Endite 2 approximately 2 \times as large as endite 4, well-rounded. Endopod more than 1.5 times longer than exopod, composed of 2 articles, proximal longest and subequal in length to exopod. All endites, endopod, and exopod bearing plumose setae; distal plumose setae of second article about length of entire limb. Distal seta of exopod subequal in length to exopod.

Thoracopods (Fig. 7a-f): Endopod of thoracopod 1 subequal to length of exopod. Endopod of thoracopods 2-8 longer than exopod. Distal article of endopod of each thoracopod slightly enlarged, typically turned at angle from main axis, and bearing numerous long, plumose setae (Figs. 5b, 7c). Plumose setae of distal article of endopod extremely dense, with setules long and overlapping with those of adjacent setae on the same appendage and also with those of opposing (opposite side) thoracopod, forming floor of brood pouch (Fig. 5b). Endopod articulate, sometimes appearing to have 1, other times 2 or 3, suture

lines separating distal articles. Articulation of distal segment obvious in thoracopods 1 and 8. Exopod extending to approximately 0.8 to 0.9 length of endopod, except in thoracopod 1 which is subequal to endopod, unarmed, with only scattered simple setae along margin.

Pleonites: Cuticle textured with denticular scales (Fig. 8e). Posterior borders of all pleonites dentate (Fig. 8b-d). Posterolateral margin of pleonite 4 expanded (Fig. 8a), with narrow cuticular ridge paralleling outline of the epimeron. Pleonites 5 and 6 longer than pleonites 1 to 4.

Pleopods 1-4: First pleopod (Figs. 9a, 10a, b) protopod 3.5 times width of endopod, with long, simple setae arising proximally and shorter subterminal seta medially; long, simple seta near base of endopod and exopod. Endopod slightly longer than exopod, 2-segmented; distal segment with acute process at apex bearing long, robust terminal seta, lateral and medial borders of distal (longer) segment each with 17-23 plumose setae. Appendix interna bearing 3 short, stout retinaculae distally. Exopod approximately two-thirds as long as protopod. Exopod with row of approximately 26-36 stout, serrate spines along lateral border (Fig. 10b-d), 4 stout smooth spine-like setae on distolateral border, distal longest, approximately 0.6 \times length of exopod, 18 plumose setae along medial margin. Pleopod 2 protopod proximal region bearing simple seta laterally, cluster of 4 to 5 simple setae medially, long, stout spine and long seta distally, row of minute, sabre-like teeth on anterolateral corner (not figured). Endopod lateral and medial borders each with 10-17 long natatory setae; long, stout seta distally; appendix interna with 3 retinaculae. Exopod with three robust setae distally, increasing in size toward apex, row of approximately 5 to 7 spine pairs consisting of long and short spine, all paired and unpaired spines covered with minute triangular cuticular scales on all but tip, and with short subterminal, twisted seta of presumed sensory function (see Martin et al., 1996). Ple-

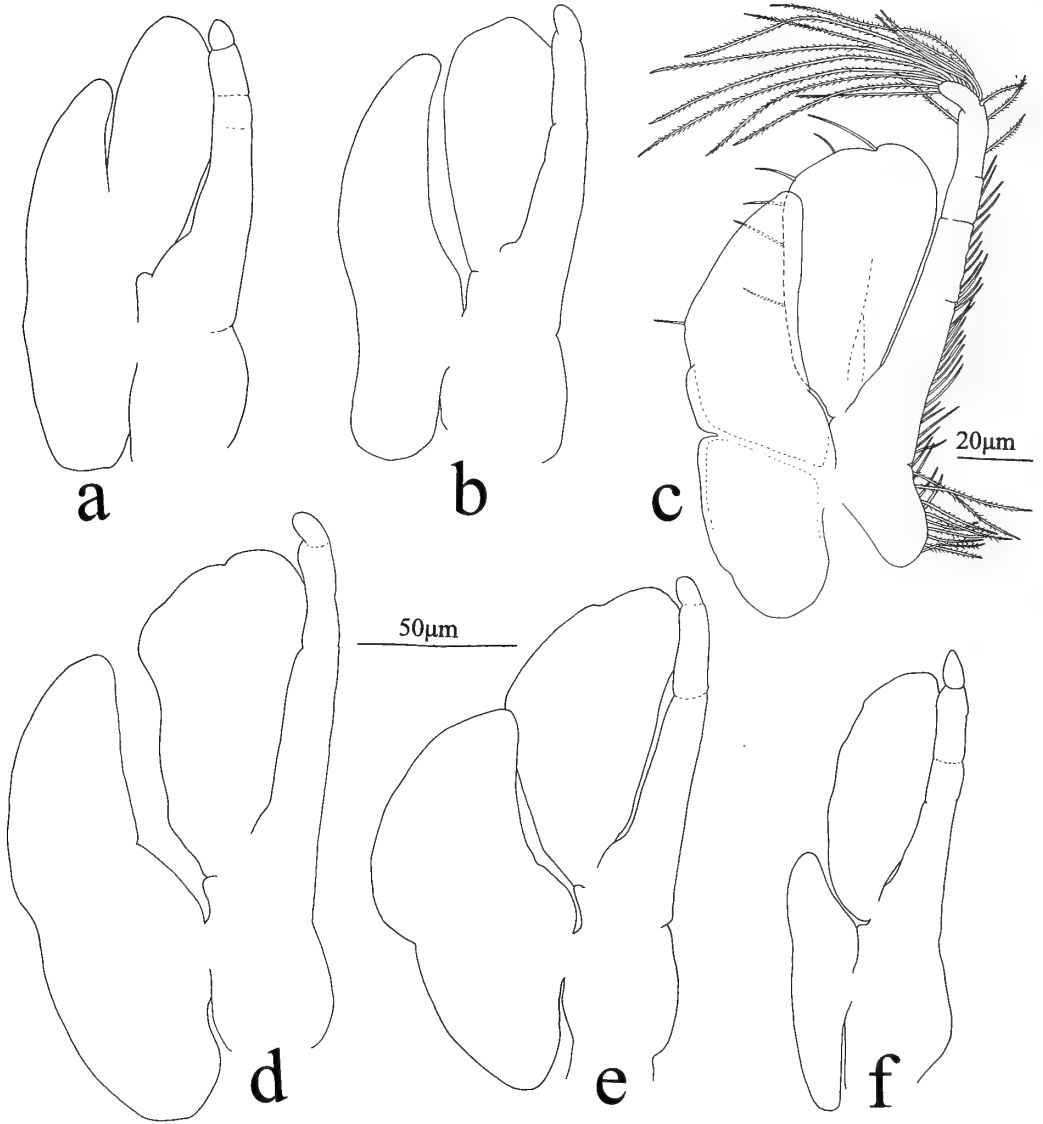


Fig. 7. *Nebalia gerkenae*, new species, female thoracopods of right side (setation shown only for thoracopod three): a, thoracopod one; b, thoracopod two; c, thoracopod three; d, thoracopod six; e, thoracopod seven; f, thoracopod eight.

opod 4 protopod with 4–5 acute serrations along posterior margin (Figs. 1c, 10a, 11b), third and fourth pleopods otherwise similar to second.

Pleopods 5 and 6: Pleopod 5 (Fig. 11a) 2-segmented, uniramous, with 3 to 5 well developed spine-like setae along the distolateral and terminal borders, increasing in size distally, approximately 17 to 30 plu-

mose setae lining medial border of distal article; long setae on medial border are somewhat “jointed” at approximately mid-length, where corrugations of cuticle appear to confer some flexibility on setal shaft (see Martin et al. 1996). Pleopod 6 (Fig. 11c) 1-segmented, uniramous, 4 to 6 robust lateral and distal setae, terminal seta longest, extending beyond posterior margin of pleonite

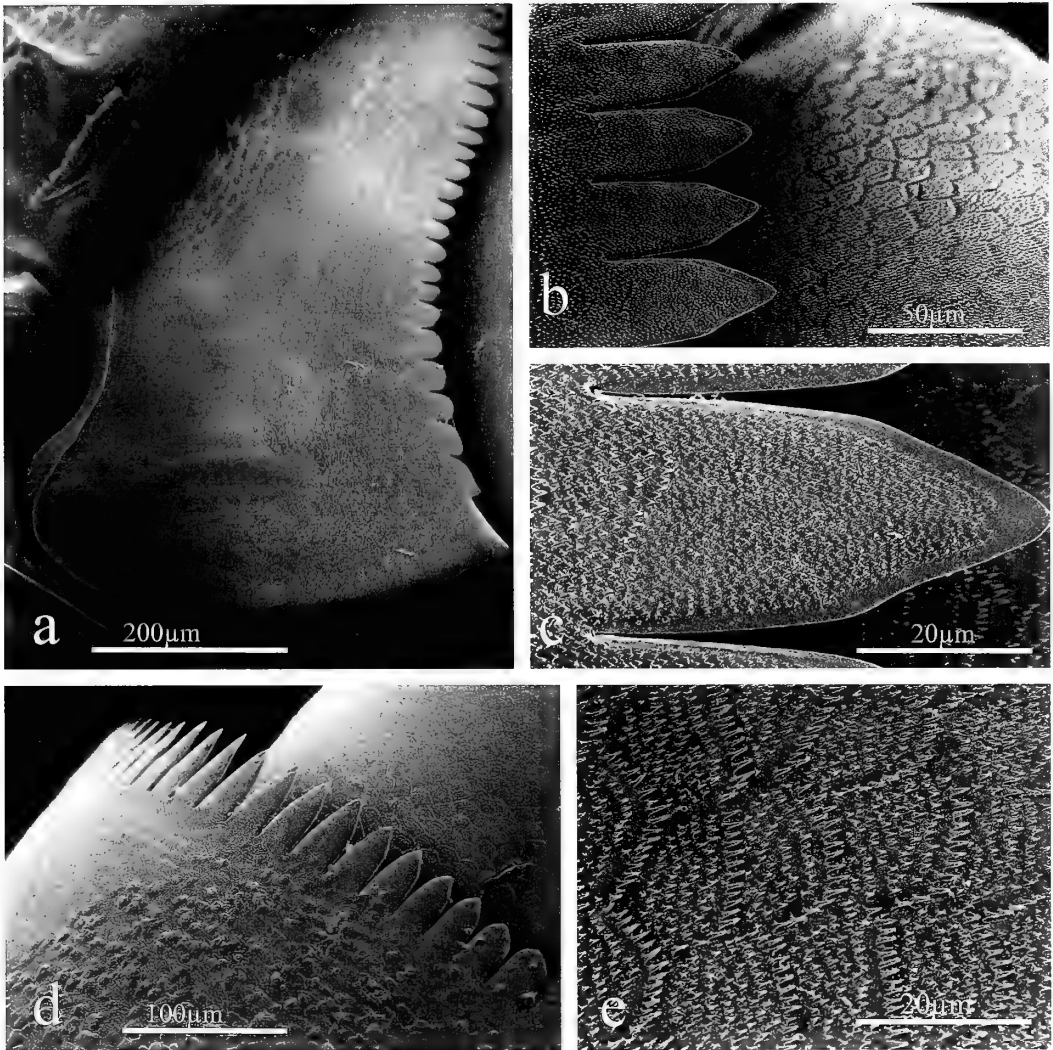


Fig. 8. *Nebalia gerkenae*, new species, female: a, pleonite four, lateral margin; b, pleonite five, dentition of distal margin (with surface of pleonite six visible to the right); c, pleonite five, tooth on distal margin; d, pleonite six, distal margin, showing variation in form of dentition; e, dorsolateral surface of pleonite six (area shown on righthand side of Fig. 8b), showing texture of cuticle.

6. Medial border also bearing few simple setae. Terminus of pleopod where it gives rise to distalmost spine bearing circlet of acute teeth. Lateral and distal spines of both pleopods 5 and 6 covered with short triangular scales and bearing short, twisted subterminal seta, as noted for similar setae of pleopods 1 to 4. Both pleopod pairs with broad triangular ventral process extending posteriorly between bases of rami (Fig.

11a), more acutely triangular and longer in pleopod 6.

Telson, anal plates, and caudal rami: Telson short, approximately as long as wide, averaging length of 0.8 mm ($n = 38$ females), rectangular, sides slightly diverging posteriorly (Fig. 12a, b). Anal plates sharply tapering from broad base to acute extremity, producing Y-shaped medial invagination (Fig. 12a). Caudal rami (Fig. 12b,

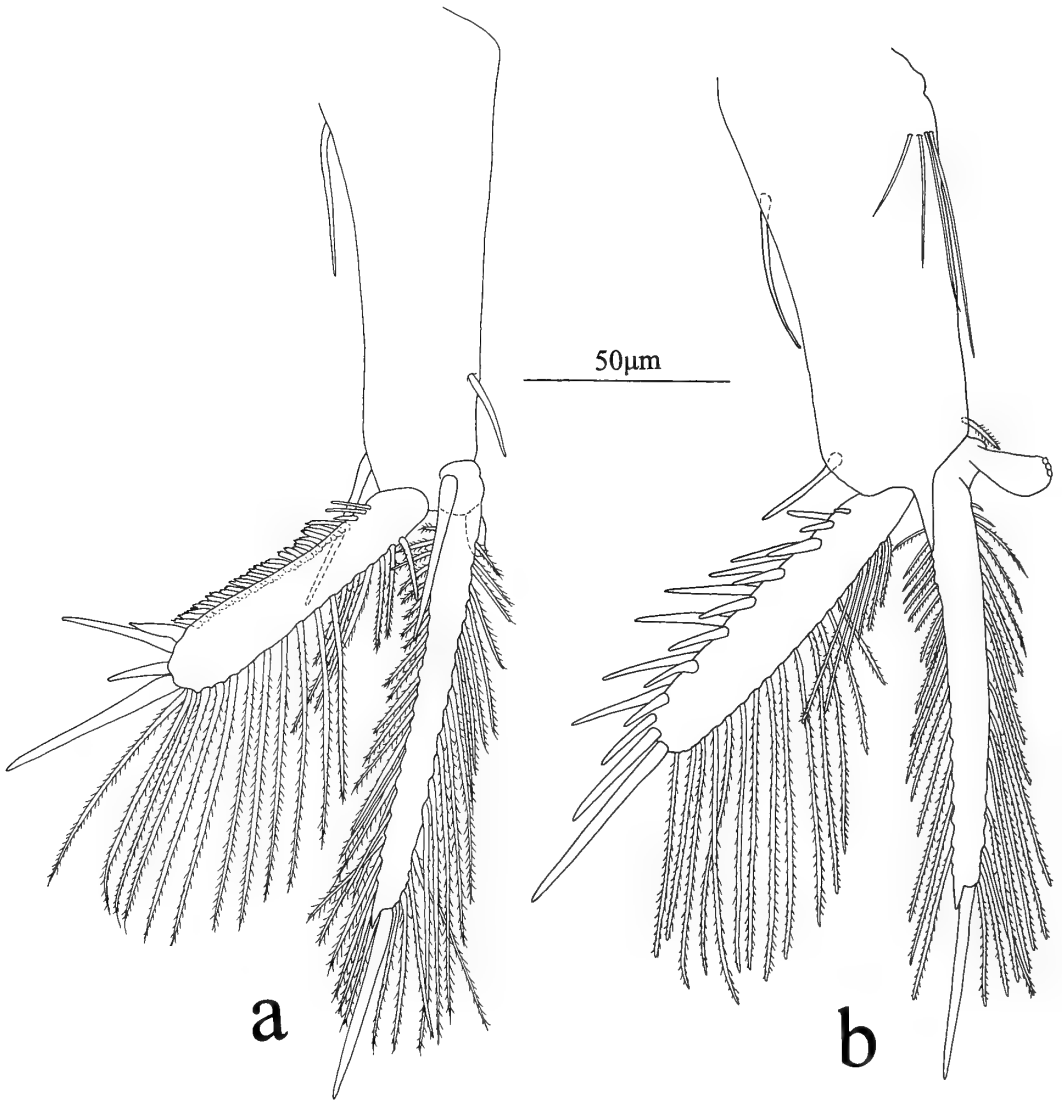


Fig. 9. *Nebalia gerkenae*, new species, female: a, pleopod one, right; b, pleopod two, right.

c) elongate, averaging length of 1.0 mm ($1.4 \times - 2.5 \times$ length of telson). Rami each with 12 to 13 robust setae along inner margin, about 22 robust setae along lateral margin, gradually increasing in length posteriorly with length of two distal setae more than two-thirds length of ramus. Inner margins of each ramus also bear at least 15 fine, pinnate setae.

Sexual dimorphism.—Dahl (1985) recommended that male specimens not be used

in species descriptions. While not in disagreement with Dahl's focus on the morphology of the female leptostracan, we suggest that any sexual dimorphism also be noted in descriptions of new taxa. Gerken (1995) found males to constitute a relatively small proportion of the individuals in a given sample, typically representing less than 15% of the specimens collected. However, Gerken (1995) noted that many of the individuals in each sample were unidenti-

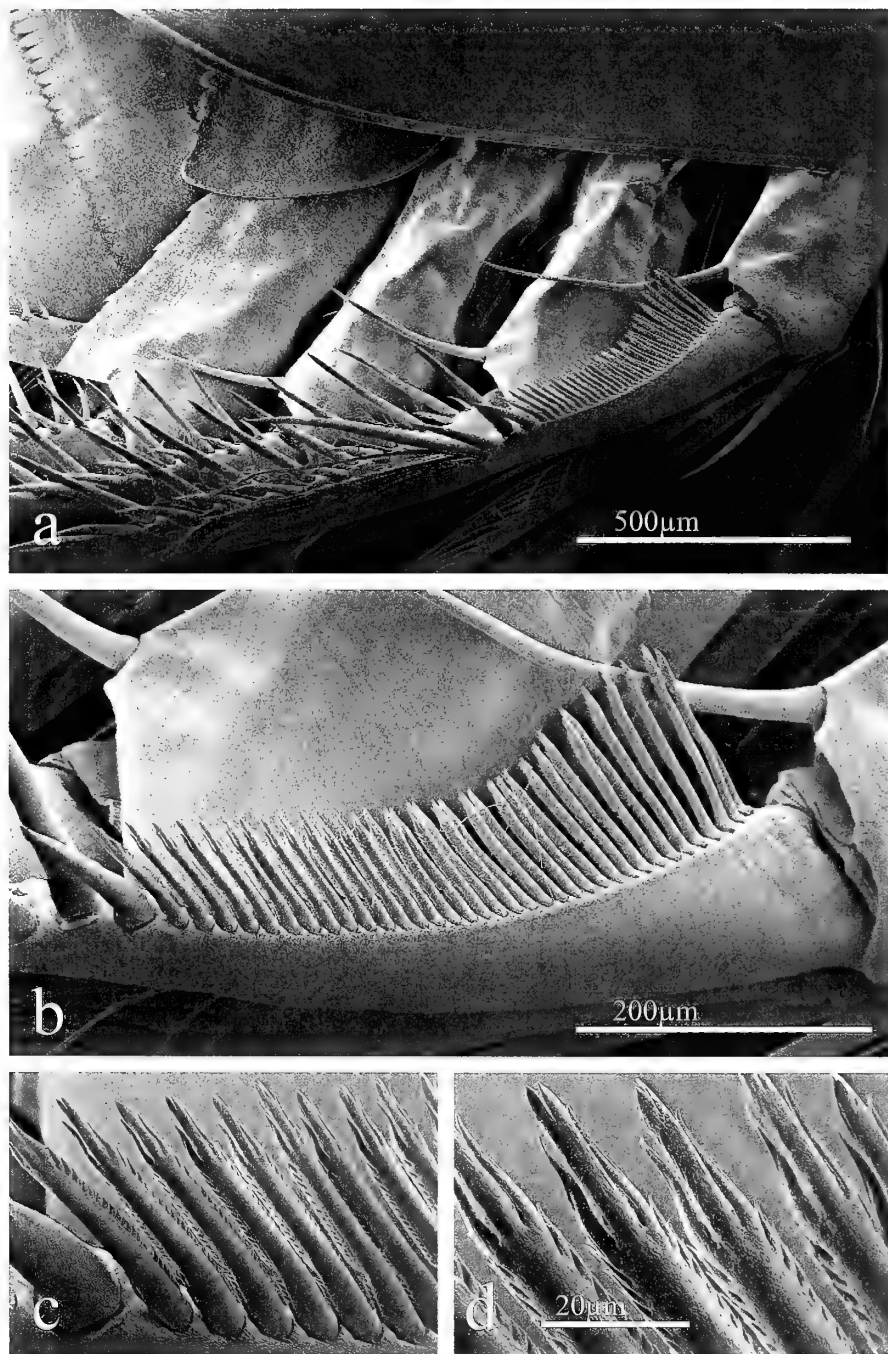


Fig. 10. *Nebalia gerkenae*, new species, female: a, pleopods one-four, right side; b, exopod of pleopod one; c, distal portion of setal row of pleopod one exopod; d, microstructure of setae in setal row of pleopod one exopod.

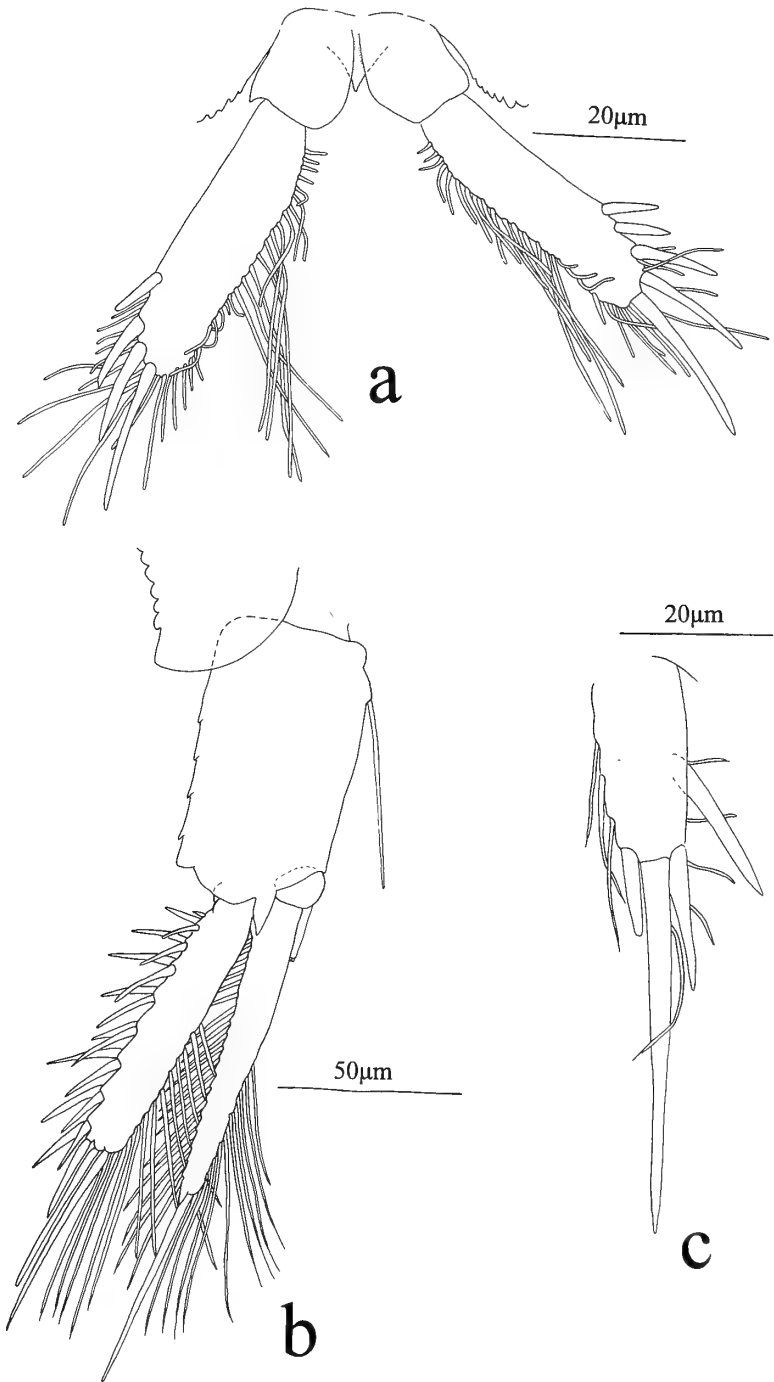


Fig. 11. *Nebalia gerkenae*, new species, female: a, pleopod five, right and left; b, pleopod four, right side; c, pleopod six, left side.

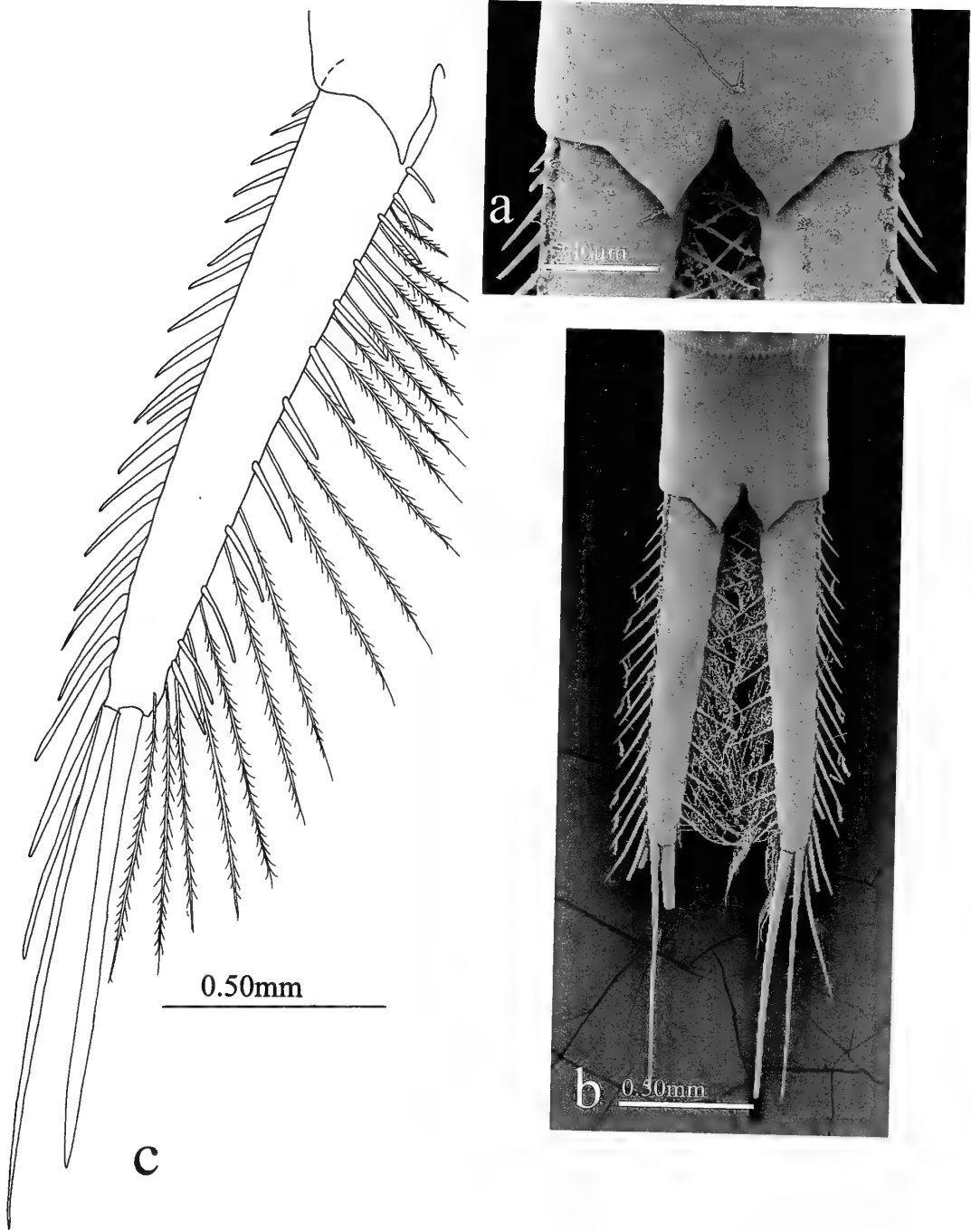


Fig. 12. *Nebalia gerkenae*, new species, female: a, anal plates; b, caudal rami, same individual; c, detail of caudal ramus, right side.

fied, so it could have been the case that many of the unidentified specimens were in fact males. Males were more common in our collections of *N. gerkenae*, constituting 30% of those individuals for which sex could be determined. As also noted for males of *N. hessleri* and Clark's (1932) "*Nebalia pugettensis*," the second antenna of the male of the new species is strongly recurved toward the anterior. Although the curvature of the male's antennular flagellum varies among individuals (see Martin et al. 1996), it differs considerably from the relatively straight and posteriorly directed antennular flagellum of the female. The articles of the flagellum of the male are also notably shorter than those of the female, and the setation of the flagellar articles differs greatly. In males, each flagellar article bears a simple seta and a curved, ribbonlike setae, as described earlier (Fig. 4a, b). The male is typically smaller than the female, with an average lateral carapace length of 2.6 mm ($n = 17$).

Color.—In life, specimens are mostly transparent except for the eyes, which are dark red. The eyes are black in preserved specimens. Overall, the body appears cream-colored in both living and preserved specimens.

Distribution.—To date, the new species is known only from the region of the type locality to the mouth of Elkhorn Slough, Monterey County. The extent to which populations of these animals occur in the upper reaches of Elkhorn Slough is unknown.

Etymology.—We are pleased to name the species for Sarah Anne Gerken, whose MS thesis on the biology of this species (Gerken 1995, as *Nebalia pugettensis*) provided a wealth of information on the animal's natural history.

Remarks.—The new species is most similar in appearance to *Nebalia hessleri* Martin et al., 1996, described from detrital mats at the head of the Scripps submarine canyon. The similarity in the morphology of appendages is striking. However, *Nebalia gerkenae* can be easily differentiated from

N. hessleri by body size, features of the antennule and antenna, length of the carapace relative to the body, and the dentition of the posterior margins of the pleonites. The average total length (excluding setation) of female and male specimens of *N. gerkenae* is 5.9 mm and 5.4 mm, respectively, whereas the average total length of *N. hessleri* was reported as 9.8 mm. The apical face of the fourth article of the antennular peduncle bears a row of four to five robust spines in *N. hessleri* (see Martin et al. 1996: fig. 4b), whereas only two such spines are present in *N. gerkenae* (Figs. 3a, 5c); this number did not vary among the specimens for which it was examined ($n = 20$). Also, the antennular scale arising from the fourth peduncular article of *N. hessleri* is posteriorly directed and crosses the flagellum at an angle. In *N. gerkenae*, however, the antennular scale is typically parallel to the flagellum. The first two articles of the antennal peduncle of *N. hessleri* each bear an acute process distally, and that of the first (proximal) article is considerably smaller; in *N. gerkenae*, the process of the first article is much larger than that of the second article (Fig. 4c). Males possess a sickle-shaped antennule in both taxa. The shape of the endopod of the first pleopod differs somewhat between the two species; the endopod tapers more sharply in *N. gerkenae* and bears a longer spine at its apex. The dentition of the posterior border of each pleonite varies considerably with position along the border; i.e., the apex of the dorsal teeth is acute, whereas that of the teeth occurring on the ventral margin is blunt. Thus, in descriptions of leptostracan taxa, reference should be given to the exact position as well as the shape of the teeth along the posterior margin of the pleonites. In *N. hessleri*, the teeth of the posterior margin of pleonites four through seven taper sharply, producing a fine point distally. The teeth along the dorsal and dorsolateral pleonite margins of *N. gerkenae* taper less strongly; the lateral margins of each tooth are parallel until mid-length, at which point they converge to

form a subtriangular apex. The dentition of the posterior margin of the fourth pleopod also differs between these two taxa, with the protopod of *N. hessleri* bearing approximately eight acute serrations and that of *N. gerkenae* bearing only four or five serrations (Figs. 1c, 11b).

Undoubtedly, close study of leptostracan populations along the western coast of the United States will result in the discovery of additional leptostracan species that will be new to science. Populations of unidentified leptostracans are known, for instance, from intertidal mudflats of Marina del Rey and Long Beach, California. Specimens received from Friday Harbor, Washington, also appear to represent multiple undescribed taxa (one of which is likely the species described as *N. pugettensis* by Clark). Extensive collections of southern Californian leptostracans were made during the cruises of the R/V *Velero IV*, comprising 135 lots and a total of 443 specimens; however, only four of these lots, including material collected near the type locality of *N. gerkenae*, have been examined.

Perhaps more surprising to us than the similarity of *N. gerkenae* to *N. hessleri* is the similarity of *N. gerkenae* to species of Leptostraca from eastern Africa (i.e., *N. brucei* Olesen, 1999) and the Red Sea (i.e., *N. marerubri* Wägele, 1983). Even when examined at high magnification, some characters in this group continue to exhibit considerable morphological similarity across large geographic scales. For example, features such as the setal row of pleopod one, mouthparts, and dentition of the pleonite margins of *N. gerkenae* are nearly indistinguishable among these species (see Wägele 1983: figs. 9–11, 13; Olesen 1999: fig. 6c, e). However, other morphological differences clearly rule out the possibility that the new species is conspecific with either of these taxa. This great morphological similarity, at least as pertains to some features, in part necessitates our use of electron microscopy and detailed figures in the description of new species of Leptostraca.

We recommend that future reports of new leptostracan species include detailed descriptions and SEM and line illustrations of the following features: antennular peduncle, antennular scale, antennal peduncle, antennal flagellum of male, rostrum and rostral keel, eye and ocular spine, carapace, setal row of exopod of pleopod one, posterior margins of protopods of pleopods, dentition of the postero-dorsal margin of pleonites 5–7, and the anal plate. Consideration should also be given to the considerable intraspecific variability exhibited for some features; such is the case, for instance, with the number of articles of the flagella of the antennule and antenna in *N. gerkenae*.

Acknowledgments

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Copepods of the family Oncaeidae (Crustacea: Poecilostomatoida) in the northeast Pacific Ocean and inland coastal waters of Washington State

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Abstract.—Thirty species of the poecilostome copepod family Oncaeidae are recorded from zooplankton samples collected in deep water from the northeast Pacific Ocean and inland coastal waters of Washington State. Seven new species of *Oncaea* are described (*O. canadensis*, *O. thoresoni*, *O. insolita*, *O. rotata*, *O. grossa*, *O. rimula*, and *O. glabra*) and males of five species for which only females were previously described (three *Oncaea*, one *Epicalymma*, and one *Conaea*) are identified and characterized. Comparisons are made of several northeast Pacific species which have also been recorded from the Arctic Ocean, Antarctic Ocean, and waters around New Zealand. Keys are provided for the three Oncaeidae genera included in this study and for the 23 species of *Oncaea*, 4 species of *Epicalymma*, and 3 species of *Conaea*.

In many areas of the oceans, at subsurface depths, the marine zooplankton is dominated numerically by a diverse assemblage of species of the poecilostome copepod family Oncaeidae (Shmeleva 1966, 1968, 1969, Ferrari 1975, Boxshall 1977, Heron 1977, Heron et al. 1984, Heron & Bradford-Grieve 1995, Böttger-Schnack 1995, 1997, 1999).

In this study, 30 species of oncaeid copepods from the northeast Pacific Ocean and inland waters of Puget Sound, Washington, are recorded and discussed. Descriptions are provided for seven new species and for males of five species for which only the females were previously known. Distinguishing characters of similar species are presented and illustrated. Species of the oncaeids can be relatively difficult to identify and consequently considerable confusion exists in the literature about species diversity of the group. A number of sibling species and species groups have sometimes been designated as forms without sufficient definition for subsequent identification.

Several of the northeast Pacific area on-

caeids treated here have also been recorded and studied in collections from other regions: southwest Pacific-Antarctic area (14 species: Heron 1977), Arctic Ocean, Canadian Basin, (8 species: Heron et al. 1984), and the New Zealand area (6 species: Heron & Bradford-Grieve 1995). These observations have considerable biogeographic significance.

Materials and Methods

The copepods discussed in this study were sorted from 80 zooplankton samples collected at oceanic and coastal sites in the northeast Pacific Ocean (Table 1). Oceanic samples were obtained from three areas. One large sample was collected at former Ocean Weather Station P (50°N, 145°W) in the central Gulf of Alaska by hauling a net (0.5-m mouth diameter, 216 μm mesh) vertically from 3000 m to the surface. Three additional zooplankton samples from the Gulf of Alaska were collected at a station to the northeast (Station Q: 51°N, 137°W); an opening-closing Tucker Trawl (Hovecamp 1989) fitted

with plankton nets of 333 μm mesh was used to sample between 360 and 480 m depth. Oceanic waters off Canada, Oregon, and Washington were sampled at various times using a zooplankton net (110 μm mesh) described by Heron & Damkaer (1978). These samples are designated OP (Open Pacific) in Table 1. Oncaeids were also studied from the Strait of Juan de Fuca, Dabob Bay, and Puget Sound, Washington, sorted from 29 zooplankton samples collected for other projects. These samples, designated IW (Inland Waters) in Table 1, were collected in vertical net hauls (1-m mouth diameter; mesh size 73 to 333 μm).

A few additional samples were employed in this study. Audun Fosshagen, Universitetet i Bergen, provided specimens of *Oncaea englishi* collected from Sognefjorden, Norway (61°08'27"N, 5°49'45"E), on 5 May 1966 (1250–0 m), and recently loaned us a sample containing *O. similis* and *Epicalymma vervoorti*, collected from Sognefjorden on 6 Dec 1982 (800–500 m). Specimens of two of the new species of *Oncaea* were also collected in a sample from Prince William Sound, Alaska, 10 Apr 1975, 735–520 m (provided by Douglas B. Dey, NOAA, NMFS, Seattle).

Copepod total length (TL), cephalosome anterior margin to the caudal ramus posterior margin, was measured on glycerine-mounted specimens; in many instances the urosome was flexed and the measurement of the prosome length (PL), anterior to posterior margin, is more useful for comparisons. If TL and PL measurements are not specified below, the size noted refers to the total length. As will be evident, in most instances the length of each sex of a particular species is similar throughout the geographical range of the species.

Figures were drawn with the aid of a Wild M20 drawing tube. In the figure legends, the capital letter following the explanation of each figure indicates the 0.1 mm scale at which the figure is shown; these scales are illustrated in Figs. 3, 4, 5, and 10. Specimens were stained by a solution

of solophenyl blue 2RL dissolved in lactic acid, facilitating the observation of small or hyaline elements and sclerotized areas (English and Heron 1976). Details describing setule and spinule ornamentation of setae and spines, when obvious on figures, has not been included in the text. Type and reference specimens described in this report have been deposited in the National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C. and National Institute of Water and Atmospheric Research (NIWA), Wellington, New Zealand.

Swimming legs are illustrated in anterior view. Armature of the swimming legs is represented as: Arabic numerals (setae), Roman numerals (spines), Si, Se, St (seta or spine on the inner, outer, or terminal border of a segment). The phrase "spine set" of *Oncaea* species refers to the combination of the lengths, shapes, and position of the three or two terminal spines on the endopods of swimming legs 2–4.

Distribution records of other authors are not included unless sufficient description of specific identifying characteristics was provided.

Poecilostomatoida Thorell, 1859
Oncaeidae Giesbrecht, 1892

Based on a cladistic analysis, Huys & Böttger-Schnack (1997) concluded that the family Oncaeidae comprised only three of formerly described genera: *Oncaea* Philippi, 1843, *Conaea* Giesbrecht, 1891, and *Epicalymma* Heron, 1977, plus their new genus, *Archioncaea*. In the family Oncaeidae, the female urosome has five segments plus the caudal ramus while the male urosome has six segments plus the caudal ramus. The male rostral area and mouthparts are similar to those of the female, except for the first antenna and maxilliped, which typically are sexually dimorphic. In the male first antenna, segments corresponding to the terminal three of the female are fused into one segment; armature is similar to the cor-

responding segments of the female, except for absence of the distal seta on the third segment. The male maxilliped is three-segmented, lacking the small segment proximal to the claw of the female. Leg 6 is sexually dimorphic.

Conspicuous similarities and differences between species of the genera *Oncaea*, *Epicalymma*, and *Conaea*, considered in this study, are summarized in Table 2.

Key to genera of Oncaeidae in northeast Pacific and inland Washington waters

- 1a. Caudal ramus with expansion on dorsal surface, surrounding insertion of dorsal seta; leg 4 exopod with outer spine formula I, 0, I 2
- 1b. Caudal ramus without notable expansion on dorsal surface; leg 4 exopod with outer spine formula I, I, II; legs 1–3 exopod segment 3 with outer spine formula III, III, II *Oncaea*
- 2a. Legs 1–3 exopod segment 3 with outer spine formula III, II, II *Conaea*
- 2b. Legs 1–3 exopod segment 3 with outer spine formula II, III, III *Epicalymma*

Genus *Oncaea* Philippi, 1843

In some instances a number of species of *Oncaea* with distinctive characters, such as a dorsoposterior projection on pediger 2, an elongate leg 5, or a less than distinctive pattern of endopod terminal conical projections (cones) or spines for swimming legs 2–4, have caused confusion for discriminating the species from one another. Terminal spines on the endopods of swimming legs 2–4 are important diagnostic characters, usually when considered in addition to a combination of other distinguishing characters. Although the “spine set” may assist in making an identification, it can also cause confusion, when many species have a similar spine set, as shown by figures of terminal endopod spines of legs 2–4 for *Oncaea* species of the northeast Pacific and Washington waters (Figs. 1, 2).

Previously, females of eight *Oncaea* spe-

cies were recognized as having both a dorsoposterior projection on pediger 2 plus a terminal cone on leg 4 endopod between the subterminal and terminal spines: *O. conifera* Giesbrecht, *O. borealis* Sars, *O. antarctica* Heron, *O. inflexa* Heron, *O. furcula* Farran, *O. quadrata* Heron & Bradford-Grieve, *O. derivata* Heron & Bradford-Grieve, and *O. redacta* Heron & Bradford-Grieve. Herein we describe two new species possessing these characters: *O. canadensis* and *O. thoresoni*.

Böttger-Schnack (1999) recently re-described *Oncaea rufa* Boxshall & Böttger, 1987, with the female having a dorsoposterior projection on pediger 2, and she assigned the species to a new genus as *Triconia rufa*. She proposed that the new genus *Triconia* should include all *Oncaea* species where the legs 2–4 endopods of females and males have a conical projection between the terminal and subterminal spines; she also proposed incorporating all *Oncaea* females with a dorsoposterior projection on pediger 2, as well as several species without the projection, in the new genus. Undoubtedly the numerous species in the genus *Oncaea* should and will eventually be distributed among a number of new genera. We do not agree, however, that the generic definition of *Triconia* is sufficient to justify inclusion of all of the divergent species she assigned to the new genus.

Females of four *Oncaea* species with an elongate leg 5 were found in Antarctic samples (Heron 1977) and three of these species also occur in northeast Pacific-Washington waters (*O. damkaeri* Heron, *O. parilla* Heron, and *O. prolata* Heron) in addition to the new species, which is a sibling species of *O. prolata*.

Closely related species with similar features must be separated by considering a combination of morphological characters, including size, lateral and dorsal profiles (including the angle of pediger 4 lateroposterior corner) labrum external form and ornamentation, and the shapes and sizes of the terminal endopod spines and cones of

Table 1.—Sample locations for Oncaeidae specimens (OP: open North Pacific; IW: inland coastal waters of Washington state).

Sample	Vessel	Cruise	Station	Date	Location	Depth (m)
P1	<i>Thompson</i>	TT082	P	8 Aug 73	49°56'N, 144°54'W	3000–0
Q 2	<i>Thompson</i>	TT091	Q	20 Jul 74	51°N, 137°W	420–360
Q 3	<i>Thompson</i>	TT091	Q	20 Jul 74	51°N, 137°W	480–420
Q 4	<i>Thompson</i>	TT091	Q	21 Jul 74	51°N, 137°W	480–420
OP5	<i>Brown Bear</i>	344	4	19 May 64	47°33'N, 126°48'W	1800–0
OP6	<i>Brown Bear</i>	344	5	20 May 64	47°33'N, 128°22'W	2128–0
OP7	<i>Brown Bear</i>	344	7	21 May 64	47°34'N, 130°12'W	2000–0
OP8	<i>Brown Bear</i>	344	9	22 May 64	47°44'N, 132°29'W	2000–0
OP9	<i>Brown Bear</i>	344	11	23 May 64	47°44'N, 134°55'W	2536–0
OP10	<i>Brown Bear</i>	344	17	26 May 64	49°17'N, 143°03'W	4650–0
OP11	<i>Brown Bear</i>	344	18	27 May 64	49°42'N, 144°16'W	1800–0
OP12	<i>Brown Bear</i>	344	19	27 May 64	49°56'N, 144°54'W	4014–0
OP13	<i>Brown Bear</i>	344	21	28 May 64	47°49'N, 144°57'W	4306–0
OP14	<i>Brown Bear</i>	344	25	30 May 64	45°17'N, 141°48'W	4500–0
OP15	<i>Brown Bear</i>	344	26	31 May 64	45°15'N, 132°44'W	2000–0
OP16	<i>Brown Bear</i>	344	29	1 Jun 64	45°23'N, 135°56'W	3500–0
OP17	<i>Brown Bear</i>	344	31	2 Jun 64	45°15'N, 132°44'W	3183–0
OP18	<i>Brown Bear</i>	344	35	4 Jun 64	45°29'N, 126°58'W	2750–0
OP19	<i>Brown Bear</i>	349	25	24 Aug 64	45°19'N, 132°26'W	1800–0
OP20	<i>Brown Bear</i>	349	26	24 Aug 64	45°21'N, 134°34'W	4000–0
OP21	<i>Brown Bear</i>	352	10	16 Jan 65	47°57'N, 135°33'W	2000–0
OP22	<i>Brown Bear</i>	352	12	17 Jan 65	48°29'N, 138°22'W	2000–0
OP23	<i>Brown Bear</i>	352	16	22 Jan 65	45°13'N, 136°04'W	3500–0
OP24	<i>Brown Bear</i>	352	16	22 Jan 65	45°13'N, 136°04'W	4150–0
OP25	<i>Brown Bear</i>	352	20	25 Jan 65	45°22'N, 128°10'W	2000–0
OP26	<i>Brown Bear</i>	352	21	26 Jan 65	45°27'N, 126°33'W	2750–0
OP27	<i>Brown Bear</i>	357	19	20 Apr 65	45°17'N, 138°34'W	4000–0
OP28	<i>Brown Bear</i>	357	19	20 Apr 65	45°17'N, 138°34'W	4150–0
OP29	<i>Brown Bear</i>	357	22	22 Apr 65	47°59'N, 139°58'W	4000–0
OP30	<i>Brown Bear</i>	368	20	10 Aug 65	45°22'N, 128°36'W	2700–0
OP31	<i>Brown Bear</i>	368	21	11 Aug 65	45°21'N, 129°53'W	2750–0
OP32	<i>Brown Bear</i>	368	23	12 Aug 65	45°20'N, 132°28'W	2000–0
OP33	<i>Brown Bear</i>	368	25	13 Aug 65	45°20'N, 134°56'W	2000–0
OP34	<i>Brown Bear</i>	368	28	14 Aug 65	45°17'N, 139°09'W	4250–0
OP35	<i>Brown Bear</i>	368	30	15 Aug 65	46°20'N, 139°50'W	4200–0
OP36	<i>Brown Bear</i>	368	31	16 Aug 65	47°05'N, 139°51'W	2000–0
OP37	<i>Brown Bear</i>	368	32	16 Aug 65	47°58'N, 139°44'W	4000–0
OP38	<i>Brown Bear</i>	368	33	17 Aug 65	47°58'N, 139°44'W	4000–0
OP39	<i>Brown Bear</i>	368	35	18 Aug 65	47°47'N, 137°28'W	2250–0
OP40	<i>Brown Bear</i>	368	36	18 Aug 65	47°47'N, 135°34'W	3700–0
OP41	<i>Brown Bear</i>	368	37	18 Aug 65	47°43'N, 134°17'W	2000–0
OP42	<i>Brown Bear</i>	368	38	19 Aug 65	47°33'N, 132°32'W	3000–0
OP43	<i>Brown Bear</i>	368	39	20 Aug 65	47°42'N, 131°02'W	2000–0
OP44	<i>Brown Bear</i>	368	40	20 Aug 65	47°55'N, 129°09'W	1967–0
OP45	<i>Brown Bear</i>	368	41	21 Aug 65	48°07'N, 127°25'W	2000–0
OP46	<i>Brown Bear</i>	380	11	9 Nov 65	47°37'N, 139°06'W	4100–0
OP47	<i>Brown Bear</i>	380	13	10 Nov 65	45°32'N, 139°48'W	4650–0
OP48	<i>Oshawa</i>	6	11	21 Oct 64	47°20'N, 139°12'W	700–0
OP49	<i>Oshawa</i>	6	11	21 Oct 64	47°20'N, 139°12'W	2500–0
OP50	<i>Oshawa</i>	6	12	22 Oct 64	45°20'N, 139°06'W	2250–0
OP51	<i>Oshawa</i>	6	12	22 Oct 64	45°20'N, 139°06'W	4200–0
IW52	<i>Commando</i>	J. de Fuca Strait		23 Feb 76	48°26'N, 124°30'W	102–50
IW53	<i>Commando</i>	J. de Fuca Strait		24 Feb 76	48°26'N, 124°30'W	176–100
IW54	<i>Commando</i>	J. de Fuca Strait		5 Apr 76	48°26'N, 124°30'W	250–100

Table 1.—Continued.

Sample	Vessel	Cruise	Station	Date	Location	Depth (m)
IW55	<i>Commando</i>	J. de Fuca Strait		6 Apr 76	48°26'N, 124°30'W	185–100
IW56	<i>Snow Goose</i>	J. de Fuca Strait		28 Jun 76	48°26'N, 124°30'W	50–25
IW57	<i>Snow Goose</i>	J. de Fuca Strait		11 Jan 77	48°26'N, 124°30'W	180–100
IW58	<i>Snow Goose</i>	J. de Fuca Strait		23 Feb 77	48°26'N, 124°30'W	180–100
IW59	<i>Snow Goose</i>	J. de Fuca Strait		6 Apr 77	48°26'N, 124°30'W	180–100
IW60	<i>Snow Goose</i>	J. de Fuca Strait		6 Apr 77	48°26'N, 124°30'W	230–100
IW61	<i>Snow Goose</i>	J. de Fuca Strait		26 Jul 77	48°26'N, 124°30'W	180–100
IW62	<i>Hoh</i>	Puget Sound		7 May 71	47°44'N, 122°25'W	200–0
IW63	<i>Hoh</i>	Puget Sound		10 Apr 72	47°44'N, 122°25'W	200–0
IW64	<i>Hoh</i>	Puget Sound		29 Mar 73	47°44'N, 122°25'W	200–0
IW65	<i>Hoh</i>	Puget Sound		2 Jul 73	47°44'N, 122°25'W	200–0
IW66	<i>Hoh</i>	Puget Sound		8 Jul 73	47°44'N, 122°25'W	200–0
IW67	<i>Hoh</i>	Puget Sound		16 Jul 73	47°44'N, 122°25'W	200–0
IW68	<i>Hoh</i>	Puget Sound		23 Jul 73	47°44'N, 122°25'W	200–0
IW69	<i>Hoh</i>	Puget Sound		13 Aug 73	47°44'N, 122°25'W	200–0
IW70	<i>Hoh</i>	Puget Sound		23 Aug 74	47°44'N, 122°25'W	250–0
IW71	<i>Hoh</i>	Puget Sound		24 Apr 75	47°44'N, 122°25'W	15–0
IW72	<i>Hoh</i>	Dabob Bay		21 Jul 76	47°45'N, 122°50'W	105–0
IW73	<i>Hoh</i>	Dabob Bay		7 Jul 77	47°45'N, 122°50'W	184–0
IW74	<i>Hoh</i>	Dabob Bay		16 Sep 82	47°45'N, 122°50'W	105–0
IW75	<i>Hoh</i>	Dabob Bay		25 Apr 85	47°45'N, 122°50'W	180–0
IW76	<i>Hoh</i>	Dabob Bay		26 Apr 85	47°45'N, 122°50'W	180–0
IW77	<i>Hoh</i>	Dabob Bay		20 Jun 85	47°45'N, 122°50'W	180–0
IW78	<i>Hoh</i>	Dabob Bay		24 Jun 85	47°45'N, 122°50'W	180–0
IW79	<i>Hoh</i>	Dabob Bay		22 Oct 85	47°45'N, 122°50'W	110–0
IW80	<i>Hoh</i>	Dabob Bay		5 Feb 91	47°45'N, 122°50'W	110–0

legs 2–4. *Oncaea* species characteristically have a cone between the terminal and sub-terminal spines on the endopods of legs 2 and 3, and, for some species, also leg 4. The size of these cones varies slightly among specimens of a species, while the relative shape and position of the spines remain constant. The cones are incompletely sclerotized at the terminal or subterminal region and support an integumental pore (Bersano & Boxshall 1994).

Recently some investigators have described and illustrated an *Oncaea* female gonopore with a small spiniform process, or minute spinule, in addition to the usual leg 6 setule or seta. There are several layers of overlapping chitinous bands surrounding the insertion of the leg 6 setule (or seta) which complicate interpretation of morphology. On some specimens the possibility of an additional thin spinule or small protuberance can be surmised, but it is never

apparent on both right and left gonopores or consistently on other specimens of the same species for any of the *Oncaea* specimens in our collection.

Males of most species of *Oncaea* are difficult to identify. Several species with a distal cone on leg 4 endopod also have a pattern of very small cuticular pores on the lateral surfaces of the cephalosome, illustrated when visible, which may be useful to assist in preliminary identification of species; often the pores are difficult to discern and may be dissimilar on left and right sides.

Oncaea canadensis, new species
Figs. 1A, 3, 4, 5

Type material.—Holotype female, 1.52 mm, USNM 243731 (type locality, northeast Pacific Ocean); allotype male, 1.18 mm, USNM 243732; 20 paratypes, USNM

Table 2.—Relative characteristics of northeast Pacific Ocean genera of *Oncaea*, *Epicalymma*, and *Conaea* (Sp = spine; Se = seta).

Species	♀ Pediger 2 with dorsal projection	♀ Antenna 2 with reduced inner seta	Labrum with at least one ventral tooth	Mandible with denticles	Mandible with setules	Maxilla 2 with elongate distal seta	♀ Maxilliped segment 2		Legs 2-4 endopod without cone	Leg 4 endopod with cone	Leg 4 endopod seg. 3 with	Leg 5	
							SpSp	SeSe				Segmented	Fused
<i>O. canadensis</i>	+			+			+		+			+	+
<i>O. thoresoni</i>	+			+			+		+			+	+
<i>O. derivata</i>	+			+			+		+			+	+
<i>O. redacta</i>	+			+			+		+			+	+
<i>O. borealis</i>	+			+			+		+			+	+
<i>O. similis</i>				+			+		+			+	+
<i>O. insolita</i>		+		+			+		+			+	+
<i>O. illgi</i>				+			+		+			+	+
<i>O. rotata</i>				+			+		+			+	+
<i>O. brocha</i>		+		+			+		+			+	+
<i>O. olsoni</i>		+		+			+		+			+	+
<i>O. damkaeri</i>		+		+			+		+			+	+
<i>O. parila</i>		+		+			+		+			+	+
<i>O. prolata</i>		+		+			+		+			+	+
<i>O. grossa</i>		+		+			+		+			+	+
<i>O. rimula</i>				+			+		+			+	+
<i>O. macilentata</i>				+			+		+			+	+
<i>O. glabra</i>				+			+		+			+	+
<i>O. lacinia</i>				+			+		+			+	+
<i>O. ovalis</i>				+			+		+			+	+
<i>O. ornata</i>		+		+			+		+			+	+
<i>O. englishi</i>		+		+			+		+			+	+
<i>O. subtilis</i>		+		+			+		+			+	+
<i>E. schmitti</i>		+		+			+		+			+	+
<i>E. umbonata</i>		+		+			+		+			+	+
<i>E. vervoorti</i>		+		+			+		+			+	+
<i>E. exigua</i>		+		+			+		+			+	+
<i>C. rapax</i>		+		+			+		+			+	+
<i>C. succurva</i>		+		+			+		+			+	+
<i>C. hispida</i>		+		+			+		+			+	+

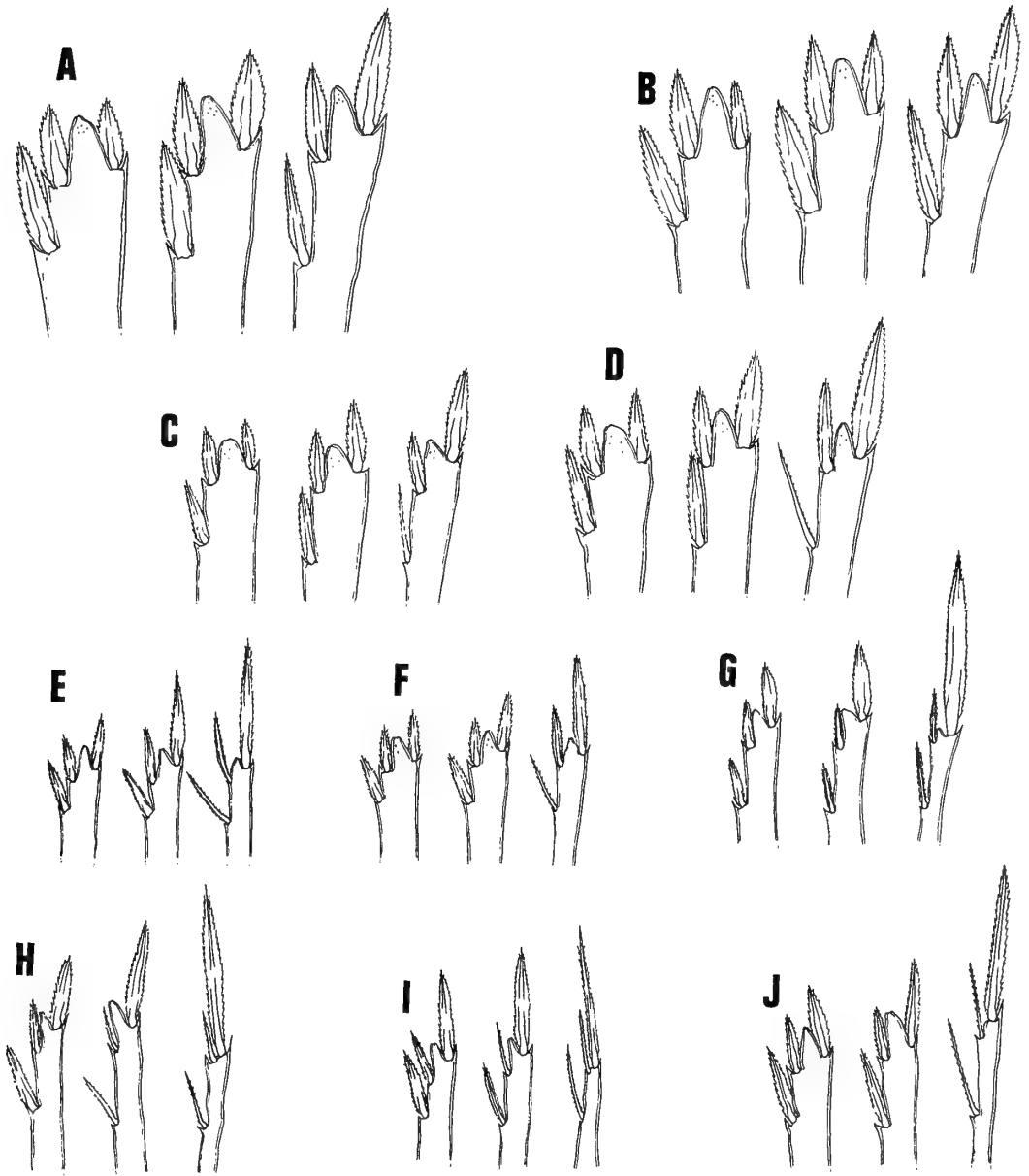


Fig. 1. Northeast Pacific-Washington waters: *Oncaea* legs 2-4 endopod terminal spine set, (leg 2, leg 3, leg 4, left to right). Female, (scale \times): A, *Oncaea canadensis*, new species; B, *Oncaea thoresoni*, new species; C, *Oncaea derivata*; D, *Oncaea redacta*; E, *Oncaea borealis*; F, *Oncaea similis*; G, *Oncaea insolita*, new species; H, *Oncaea illgi*; I, *Oncaea rotata*, new species; J, *Oncaea brocha*.

243733 (10 females, 10 males): *Thompson* Sta P, 8 Aug 1973, 3000-0 m.

Material examined.—See Table 3.

Female.—Mean lengths of 20 specimens: TL 1.47 mm (1.37-1.55 mm), PL 1.01 mm

(0.93-1.07 mm). Body (Fig. 3A-B) robust, exoskeleton heavily sclerotized. Prosome about twice as long as urosome; pediger 2 with dorsoposterior projection in lateral view; pediger 4 with rounded posterior cor-

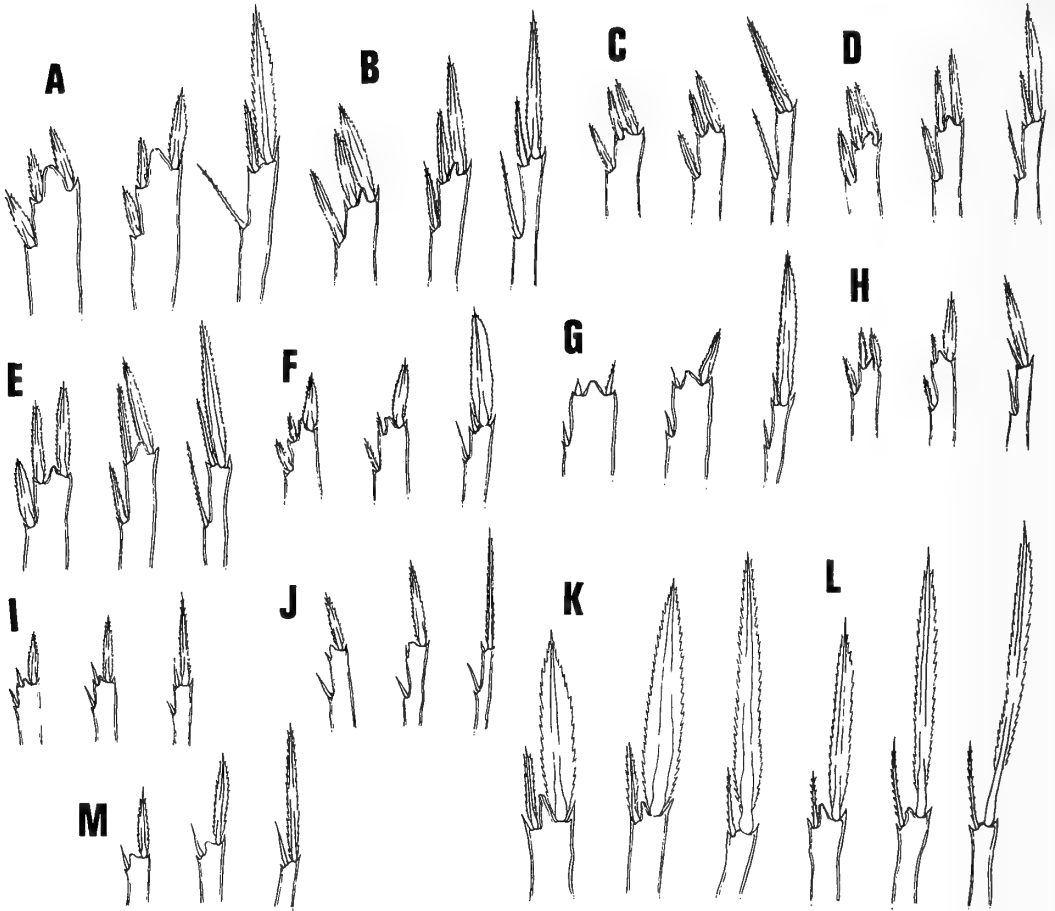


Fig. 2. Northeast Pacific-Washington waters: *Oncaea* legs 2-4 endopod terminal spine set, (leg 2, leg 3, leg 4, left to right). Female (scale \times): A, *Oncaea olsoni*; B, *Oncaea damkaeri*; C, *Oncaea parila*; D, *Oncaea prolata*; E, *Oncaea grossa*, new species; F, *Oncaea rimula*, new species; G, *Oncaea macilenta*; H, *Oncaea glabra*, new species; I, *Oncaea lacinia*; J, *Oncaea ovalis*; K, *Oncaea ornata*; L, *Oncaea englishi*; M, *Oncaea subtilis*.

ner, lateral view. Genital segment length about equal to that of remainder of urosome (Fig. 3C); gonopore, with a spiniform setule just anterior to midregion of dorsal surface; insertion of setule surrounded by complex layers of overlapping chitinous layers. Caudal ramus 4 times as long as wide and longer than anal segment.

Rostral area with thickened, rounded posteroventral margin. First antenna 6-segmented (Fig. 3D) with armature formula 3, 8, 4+1 spinule, 3+1 esthete, 2+1 esthete, 7+1 esthete. Second antenna (Fig. 3E) 3-segmented; first segment with distal inner spinulose seta; second segment with row of

minute dentiform spinules along inner surface and outer rows of setules; terminal segment with row of setules on posterior surface; proximal inner surface with curved, denticulate spine and 3 setae; distally 4 curved long spines and 3 setae.

Labrum (Fig. 3F) posteriorly protuberant; free margin divided into 2 rounded posteroventral lobes, each with a row of dentiform setules on undersurface; lobes separated by quadrate vertex; several thin lamellae extend posteriorly between the lobes; a semicircular ridge bears a row of spatulate setules anterior to the vertex; ovate protuberance anterior to labrum and

Table 3.—Adult female (♀) and male (♂) specimens of *Oncaea*, *Epicalymma* and *Conaea* found and examined in samples from the northeast Pacific Ocean and inland waters of Washington state. Also indicated (+) are previously reported personal records in other regions (Arctic Ocean and Station M, Heron et al. 1984; Southern Ocean, Heron 1977; New Zealand, Heron & Bradford-Grieve 1995).

Species	Station P		Station Q		Open NE Pacific		Washington inland waters		Arctic	Southern ocean	New Zealand	Station M
	♀	♂	♀	♂	♀	♂	♀	♂				
<i>O. canadensis</i>	20	39	103	253	74	85						
<i>O. thoresoni</i>	6	6	7	0	50	32						
<i>O. derivata</i>					44	51	36	41			+	
<i>O. redacta</i>	334	0	10	0	43	18	8	8			+	
<i>O. borealis</i>	2	2					446	242	+			+
<i>O. similis</i>	5	1			243	4	230	14				
<i>O. insolita</i>					66	59						
<i>O. illgi</i>					21	0						
<i>O. rotata</i>	0	1			7	0						
<i>O. brocha</i>	3	1										
<i>O. olsoni</i>	4	2										
<i>O. damkaeri</i>	7	0			19	0	4	0				
<i>O. parila</i>	16	0			1	0						
<i>O. prolata</i>					2	0	2	4	+			
<i>O. grossa</i>	243	304			1	3	200	48				+
<i>O. rimula</i>	2	0			48	2	115	212				
<i>O. macilentia</i>	32	1			11	0	1	3				
<i>O. glabra</i>					20	3	5	0				
<i>O. lacinia</i>					0	1	10	3				
<i>O. ovalis</i>					1	0	18	7	+			
<i>O. ornata</i>					2	0	5	1				
<i>O. englishi</i>					25	12	1	2				
<i>O. subtilis</i>	38	34			196	155	1	0	+			+
<i>E. schmitti</i>	46	1					136	327				
<i>E. umbonata</i>	0	1			51	4			+			+
<i>E. vervoorti</i>					6	1			+			+
<i>E. exigua</i>					1	0			+			+
<i>C. rapax</i>					2	0	4	3	+			+
<i>C. succurva</i>					18	21	3	3				
<i>C. hispida</i>	1	0			3	0			+			+
					7	1			+			+

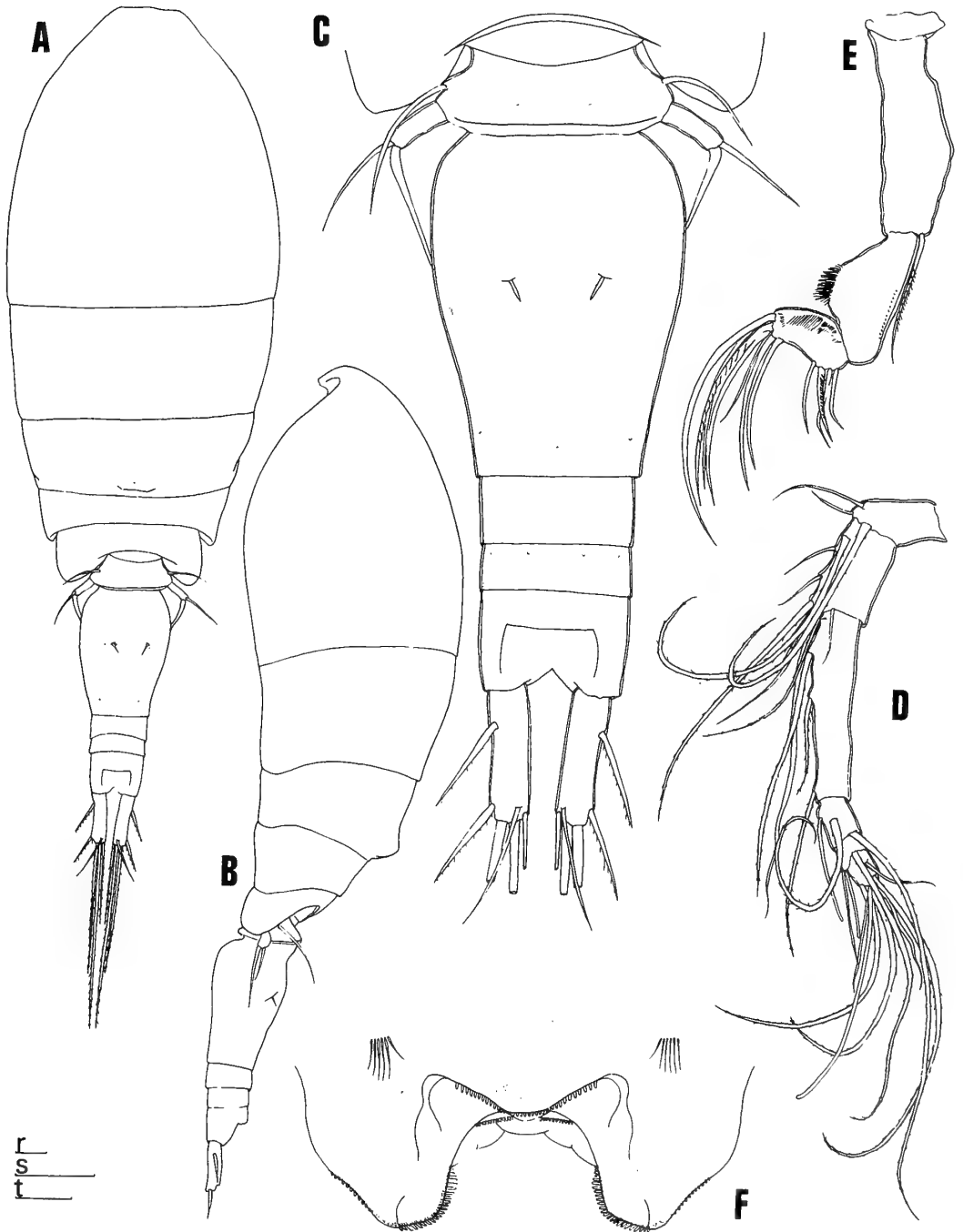


Fig. 3. *Oncaea canadensis*, new species. Female: A, dorsal (scale r); B, lateral (r); C, urosome, dorsal (s); D, first antenna, right (t); E, second antenna, left (s); F, labrum (u).

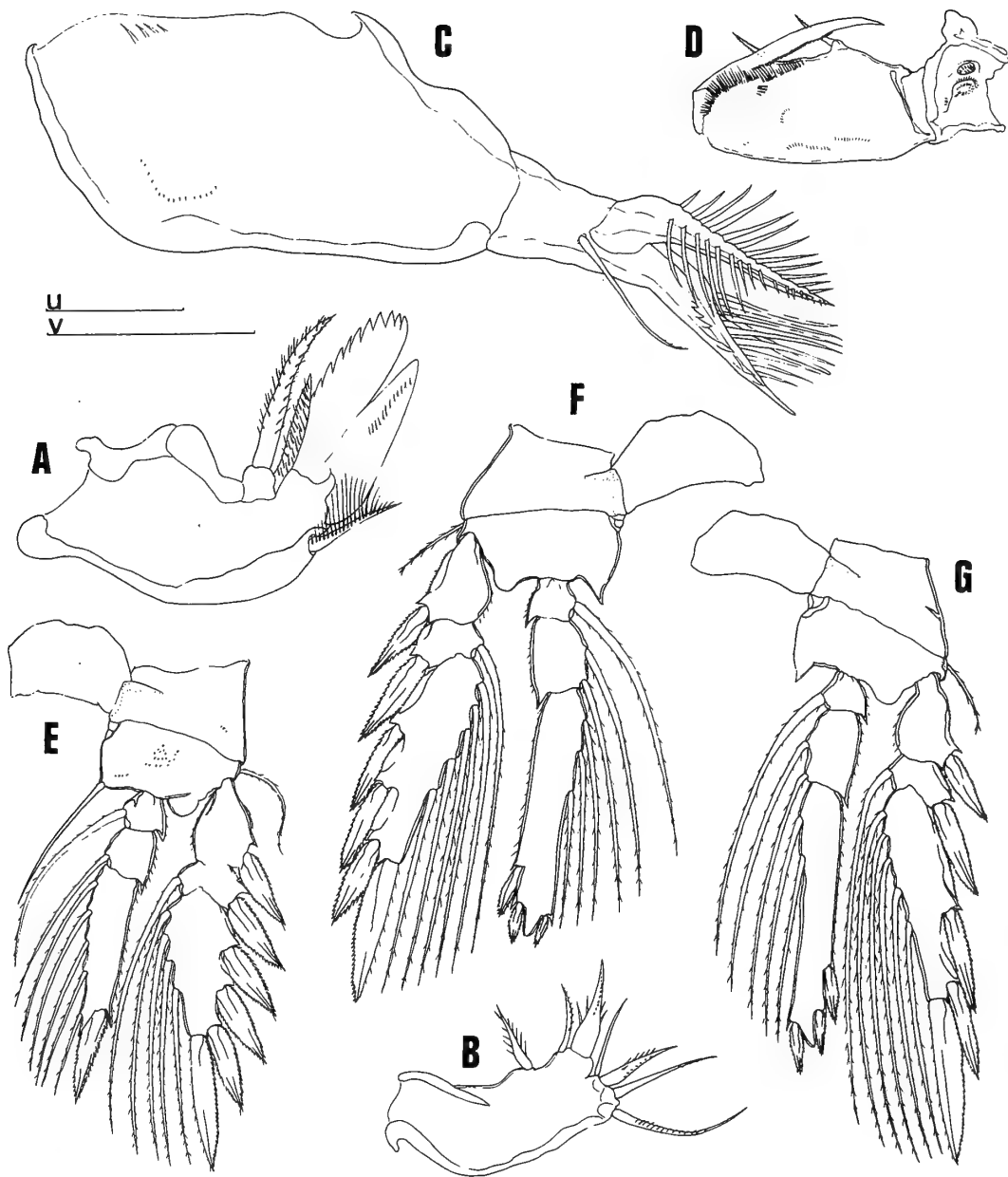


Fig. 4. *Oncaea canadensis*, new species. Female: A, mandible, left (scale v); B, first maxilla, right (u); C, second maxilla, left (v); D, maxilliped, left (t); E, leg 1 (t); F, leg 2 (t); G, leg 3 (t).

lateral setules. Mandible (Fig. 4A) with expanded, triangular base, terminally flattened, bearing 5 elements: outer stout seta with row of long setules; broad element with posterior row of setules and concave inner margin which cups outer basal edge

of adjacent bladlike element with inner dentiform edge; 2 posterior spinulose setae, the shorter seta hyaline.

First maxilla (Fig. 4B) flat, bilobed; 2 setae and 1 spine on inner lobe; 4 setae on outer lobe. Second maxilla (Fig. 4C) 2-segmented;

first segment with expanded base; second segment produced distally as elongate claw, with 2 inner rows of setules and an outer lateral seta; a seta and a curved element with 2 rows of medial setules on proximal inner surface. Maxilliped (Fig. 4D) 4-segmented; first segment with sclerotized areas enclosing clusters of spinules; second segment inner surface with 2 barbed spines, anterior row of setules; terminal segment consisting of long claw with row of setules on concave surface; short element near inner base.

Legs 1–4 (Figs. 4E–G, 5A) with serrate, hyaline flange on spines. Endopods of legs 2–4 with terminal cone. Leg armature, Table 4.

Leg 5 with free segment elongate; 2 terminal setae, the longer spiniform, reaching beyond gonopore, and almost twice the length of the shorter; outer basal seta. Leg 6 represented by long spatulate setule on gonopore.

Male.—Mean lengths of 20 specimens: TL 1.19 mm (1.15–1.27 mm), PL 0.81 mm (0.76–0.85 mm), lacking dorsal projection on third prosomal segment. Body (Fig. 5B–C) with scattered refractile points, usually associated with pores. Prosome twice as long as urosome; cephalosome with posterolateral cluster of small hooded pores; configurations variable (Fig. 5D) but basically circular with a center devoid of pores; pediger 4 with acute angle of lateroposterior corner in lateral view; corner with inner pores. Genital segment length approximately one-third greater than remainder of urosome (Fig. 5E). Maxilliped (Fig. 5F) second segment conspicuously expanded; anterior row of small setules; 2 setae within longitudinal cleft; inner posterior rim with 3 rows of spatulate setules of graduated lengths; terminal claw with narrow element near inner base. Swimming legs as in female. Leg 5 (Fig. 5G) short, not delimited from thoracic segment; armament similar to that of female. Leg 6 represented by posterolateral point-tipped flap on ventral surface of genital segment.

In addition to the specimens listed on Ta-

ble 3, one *O. canadensis* male (TL 1.20 mm, PL 0.81 mm) was identified from Prince William Sound, Alaska.

Etymology.—The specific name *canadensis* was implied by the collection area.

Remarks.—Adults of *O. canadensis* are the largest of the ten *Oncaea* species where the female has both a dorsoposterior projection on pediger 2 and a terminal cone on leg 4 endopod, between the terminal and subterminal spines. *Oncaea canadensis* closely resembles the Antarctic species *O. inflexa* Heron, 1977, with a stout body and elongate caudal ramus. The two species may be separated by comparing differences of the relative lengths of the female genital segment to that of the remainder of urosomal segments as well as the endopod spines of leg 4: *O. canadensis* genital segment length is approximately equal to the length of the remainder of the urosome; the tip of leg 4 endopod subterminal spine reaches to about the midlength of the terminal spine; *O. inflexa* genital segment length is almost 1.5 times as long as the remainder of the urosome, and the leg 4 endopod subterminal spine is almost equal in length to the terminal spine.

Oncaea thoresoni, new species

Figs. 1B, 6, 7, 8A–E

Type material.—Holotype female, 1.33 mm; USNM 243761 (type locality, northeast Pacific Ocean); allotype male, 1.05 mm, USNM 243762; 6 paratypes, USNM 243763 (3 female, 3 male); *Thompson Sta P*, 8 Aug 1973, 3000–0 m.

Material examined.—See Table 3.

Female.—Mean lengths of 20 specimens: TL 1.29 mm (1.22–1.37 mm), PL 0.86 mm (0.81–0.96 mm). Prosome (Fig. 6A–B) less than twice the length of urosome with a ratio of 1.86:1; pediger 2 with dorsoposterior projection, lateral view; pediger 4 with rounded posterior corner, lateral view. Genital segment length ratio to that of remainder of the urosome 1.11:1 (Fig. 6C); gonopore with spiniform setule. Caudal ramus about 3 times as long as wide and approximately same length as that of sum of the 2 segments posterior to genital segment.

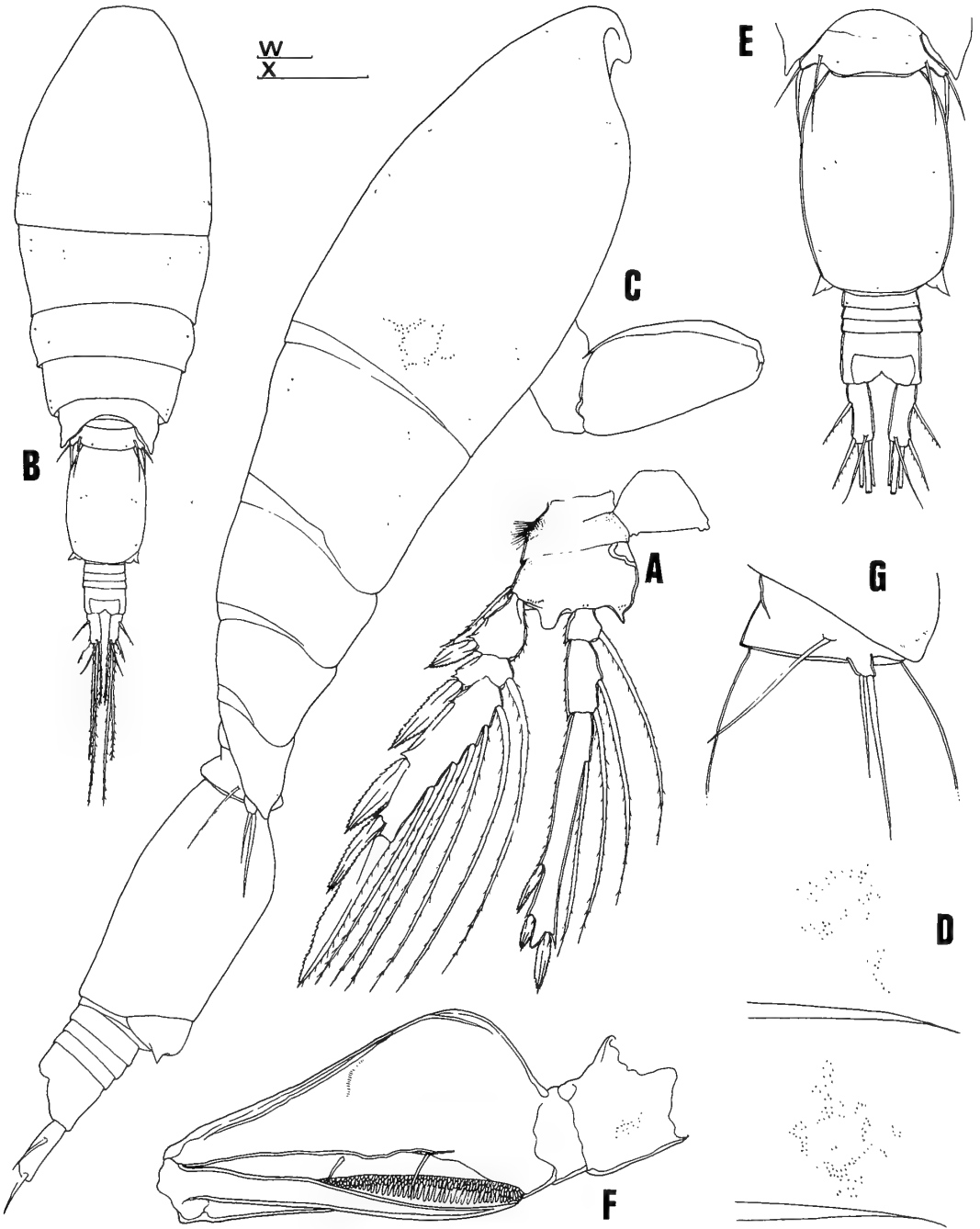


Fig. 5. *Oncaea canadensis*, new species. Female: A, Leg 4 (scale t). Male: B, dorsal (r); C, lateral (w); D, two posterolateral hooded pore clusters from two cephalosomes (x); E, urosome, dorsal (w); F, maxilliped, right (x); G, pediger 4 distal corner, segment of leg 5 (x).

Table 4.—Armature of legs 1–4 of *Oncaea canadensis*.

Leg	Basis		Endopod						Exopod					
	Si	Se	1		2		3		1		2		3	
			Si	Se	Si	St	Se	Se	Si	Se	Si	St	Se	
1	1	1	1	1	5	I	—	I	1	I	4	I	III	
2	—	1	1	2	3	I	II	I	1	I	5	I	III	
3	—	1	1	2	2	I	II	I	1	I	5	I	II	
4	—	1	1	2	1	I	II	I	1	I	5	I	II	

Rostral area with thickened, rounded margin. First antenna (Fig. 6D) and second antenna (Fig. 6E) with armament similar in number to that of *O. canadensis*. Labrum (Fig. 6F) form resembles that of *O. canadensis*. Mandible (Fig. 6G), first maxilla (Fig. 6H), second maxilla (Fig. 7A), and maxilliped (Fig. 7B) with armament similar in number to that of *O. canadensis*. Legs 1–4 (Fig. 7C–F) with armament similar in number to that of *O. canadensis*; endopods of legs 2–4 with terminal cone. Leg 5 with oblong free segment; 2 subequal setae, the longer spiniform; outer basal seta. Leg 6 represented by spiniform setule on gonopore.

Male.—Mean lengths of 20 specimens: TL 1.03 mm (0.94–1.11 mm), PL 0.70 mm (0.63–0.74 mm). Body (Figs. 7G, 8A) with scattered refractile points usually associated with pores. Ratio of length of prosome to that of urosome 1.94:1; cephalosome with lateroposterior cluster of small hooded pores (Fig. 8B), pattern variable, basically with 2 horizontal levels; pediger 4 with acute angle of posterior corner in lateral view; corner with inner pores. Ratio of length of genital segment to that of width 1.42:1, dorsal view (Fig. 8C). Maxilliped (Fig. 8D) second segment expanded with anterior row of small setules; 2 setae within longitudinal cleft; inner posterior rim with 3 rows of spatulate setules of graduated lengths; terminal claw with narrow element near inner base. Swimming legs as in female. Leg 5 (Fig. 8E) not delimited from thoracic segment; armament similar to that of female. Leg 6 represented by posterolateral point-tipped flap on ventral surface of genital segment.

Etymology.—It is a pleasure to name this

species for David S. Thoreson, School of Oceanography, University of Washington, who made a special effort to collect the deep sample at Ocean Station P.

Remarks.—*Oncaea thoresoni* closely resembles *O. canadensis*, but may be distinguished by its shorter total length, relatively smaller sizes of the caudal ramus, and leg 5 segment. Legs 2 and 3 endopodal terminal spines usually differ between the two species: leg 2 of *O. thoresoni* with the terminal spine shorter than the subterminal spine, while *O. canadensis* terminal spine length is about the same as that of the subterminal spine; leg 3 of *O. thoresoni* with terminal spine length about equal to that of the subterminal spine while the terminal spine of *O. canadensis* extends as the longest. One male of *O. canadensis* was observed in which leg 3 terminal and subterminal spines appeared to be nearly the same length, but other characters such as TL, caudal ramus length, and spinule pattern on the distolateral surface of the cephalosome defined it as *O. canadensis*.

Oncaea derivata Heron & Bradford-Grieve, 1995
Figs. 1C, 8F–I

Oncaea conifera.—Moulton 1973: (“bumped” only) 142, 145, 147, 148, 150–154, figs. 4Ac, g, k, 4Bo, s, w. (Not *O. conifera* Giesbrecht, 1891.)

Oncaea derivata Heron & Bradford-Grieve, 1995:25, 29 (female), figs. 9h–j, 10, 11a, 25c.

Material examined.—See Table 3. Reference specimens: NIWA Z9390 (3 fe-

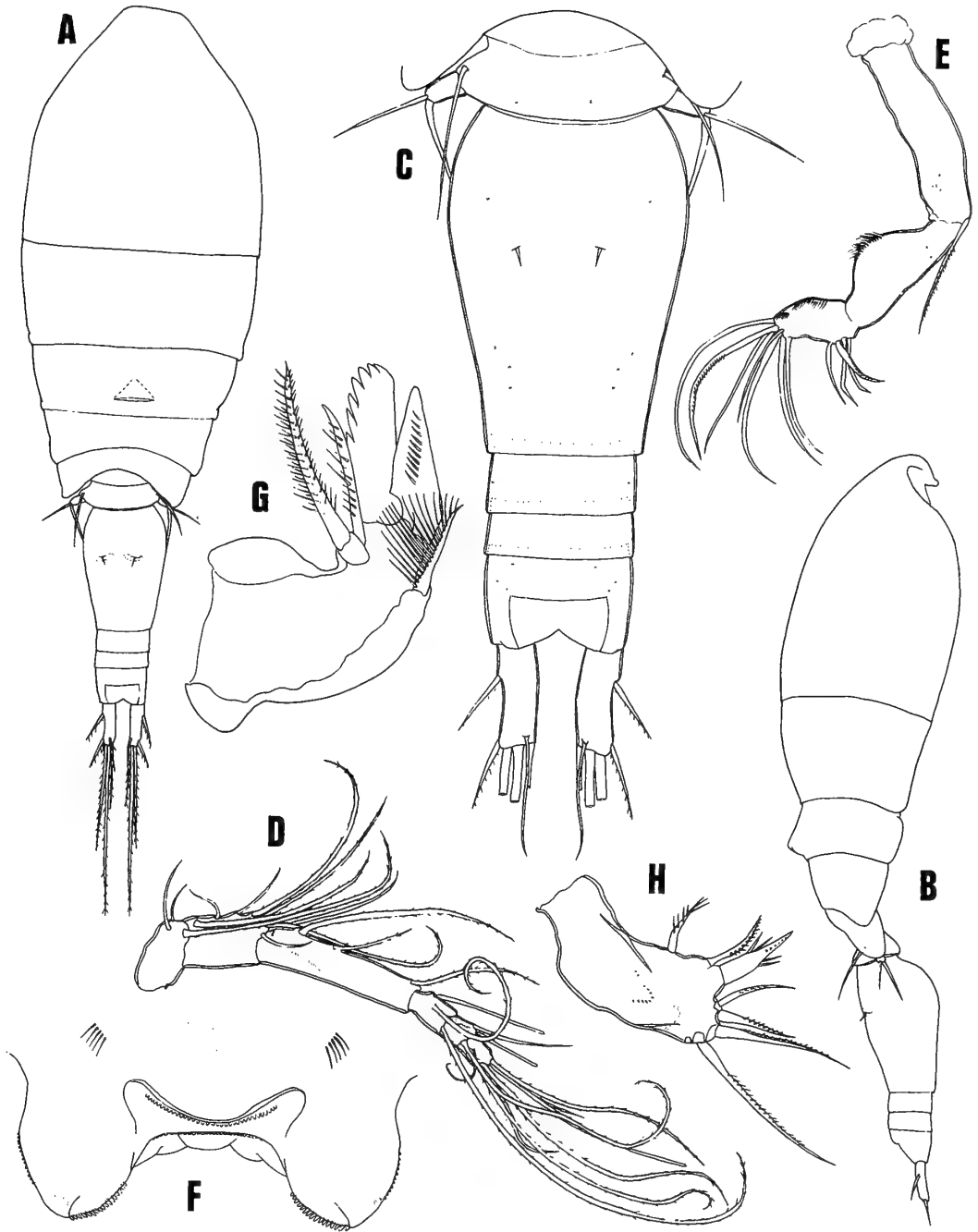


Fig. 6. *Oncaea thoresoni*, new species. Female: A, dorsal (scale r); B, lateral (r); C, urosome, dorsal (s); D, first antenna, left (t); E, second antenna, left (s); F, labrum (u); G, mandible, left (v); H, first maxilla, right (u).

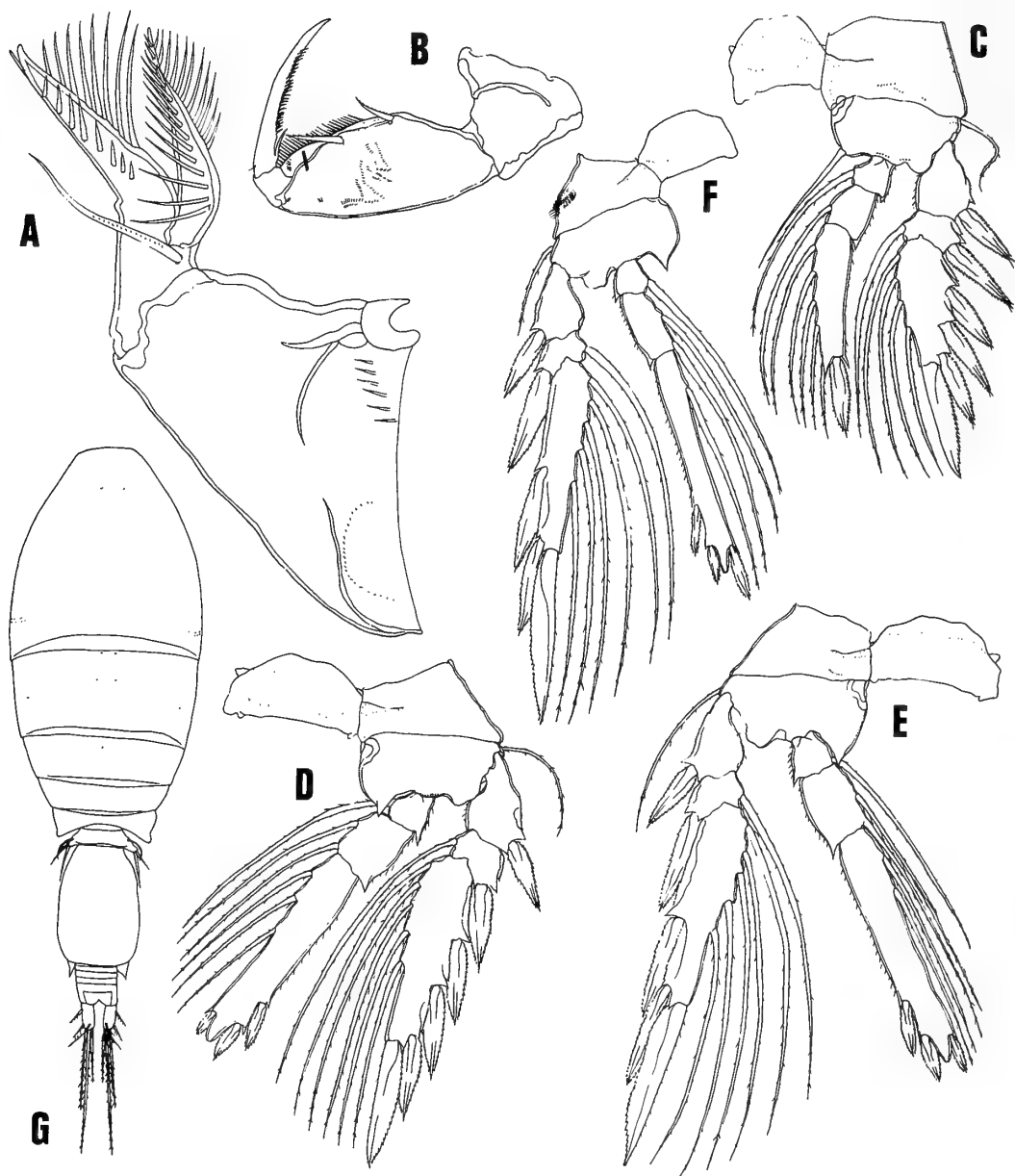


Fig. 7. *Oncaea thoresoni*, new species. Female: A, second maxilla, right (scale v); B, maxilliped, left (t); C, leg 1 (t); D, leg 2 (t); E, leg 3 (t); F, leg 4 (t). Male: G, dorsal (r).

males, 10 males); USNM 243734 (3 females, 10 males): Juan de Fuca Strait, 6 Apr 1977, 180–100 m.

Female.—Mean lengths of 20 specimens: TL 1.09 mm (1.05–1.15 mm), PL 0.73 mm (0.70–0.79 mm).

Male.—The male of *O. derivata* is described for the first time. Mean lengths of 15 specimens: TL 0.70 mm (0.67–0.74 mm), PL 0.47 mm (0.44–0.50 mm). Body (Fig. 8F–G) with scattered refractile points, usually associated with pores. Prosome

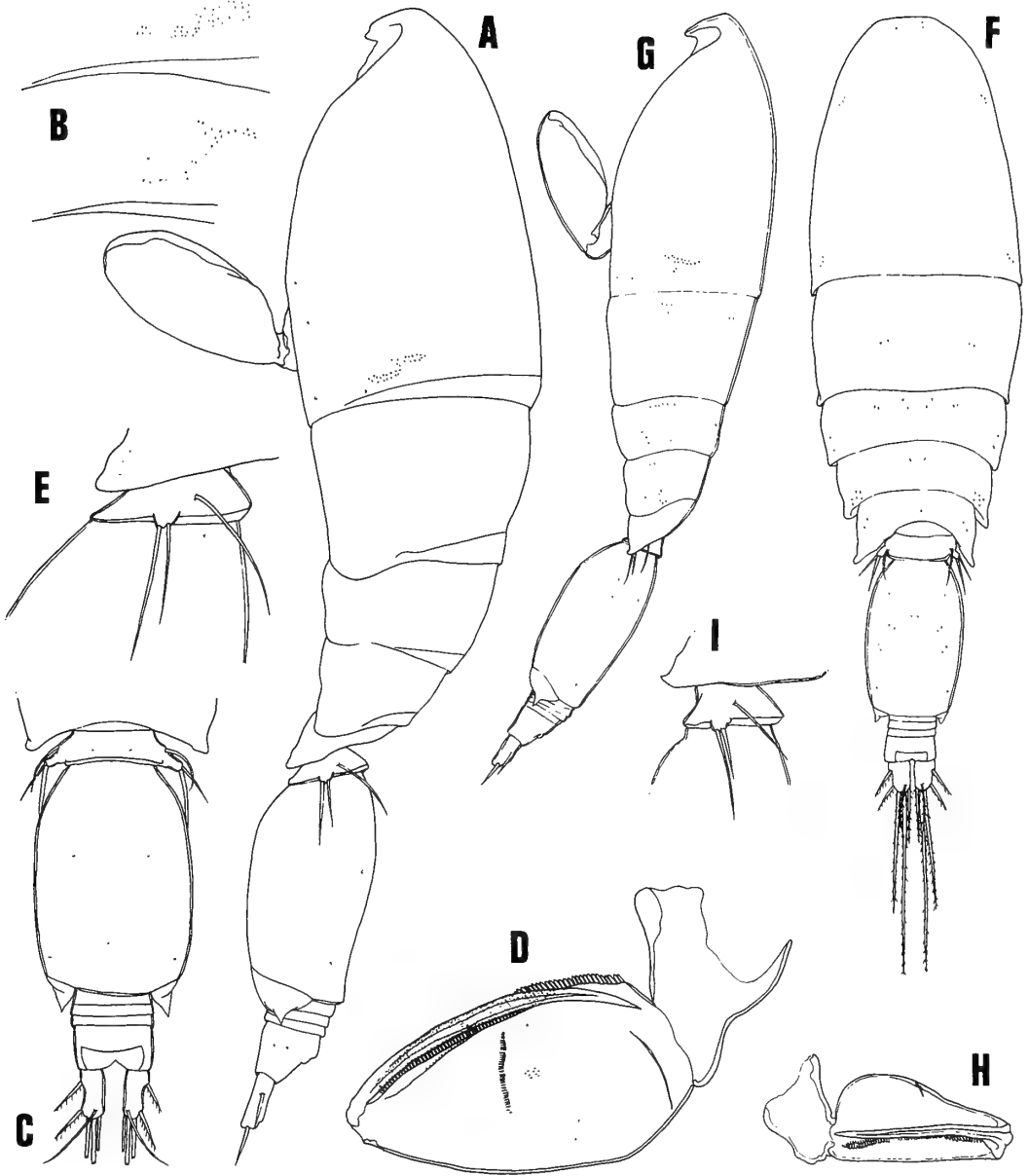


Fig. 8. *Oncaea thoresoni*, new species. Male: A, lateral (scale w); B, two posterolateral hooded pore clusters from two cephalosomes (x); C, pediger 4 posterior corner, urosome, dorsal (w); D, maxilliped, left (x); E, pediger 4 distal corner, segment of leg 5 (x). *Oncaea derivata*, Male: F dorsal (t); G, lateral (t); H, maxilliped, left (x); I, pediger 4 posterior corner, segment of leg 5 (x).

length about twice that of urosome; cephalosome with posterolateral double slanting rows of hooded pores, pattern slightly variable; pediger 4 with acute angle of lateroposterior corner often tilted ventrally.

Maxilliped (Fig. 6J) second segment conspicuously expanded with anterior row of small setules; 2 setae within longitudinal cleft; inner posterior rim with 3 rows of spatulate setules of graduated lengths; ter-

minal claw with narrow process near inner base. Swimming legs as in female. Leg 5 (Fig. 8I) short, not delimited from thoracic segment; shorter terminal seta about three-fifths the length of the longer; outer basal seta. Leg 6 represented by posterolateral point-tipped flap on ventral surface of genital segment.

Remarks.—*Oncaea derivata* females have pediger 4 lateroposterior corner with a blunt or notched margin rather than being smoothly rounded. Females were described from specimens collected in the southwest Pacific, Pacific Panama Basin, Florida vicinity, and from near Liberia. None of the northeast Pacific females had the cephalosome disfigured by a tumorous growth, as found in specimens from New Zealand waters (Heron & Bradford-Grieve 1995).

Oncaea redacta Heron & Bradford-Grieve, 1995
Figs. 1D, 9A–E

Oncaea conifera.—Farran 1936:127–129 (form c only), figs. 25c, f, 26c.—Moulton 1973:142, 144, 145, 147, 148, 150–154 (“minus” only), figs. 4Ab, f, j, 4Bn, r, v. (Not *O. conifera* Giesbrecht, 1891.)

O. redacta Heron & Bradford-Grieve, 1995:29, 32, figs. 11b–i, 12, 27a (female only).

Material examined.—See Table 3. Reference specimens: NIWA Z9391 (1 male); NIWA Z9392 (3 males): *Oshawa* 6–12, 22 Oct 1964, 4200–0 m; USNM 243749 (3 females, 2 males): Juan de Fuca, 6 Apr 1977, 180–100 m; USNM 243750 (3 females): *Brown Bear* 368–36, 18 Aug 1965, 3700–0 m.

Females and males of *O. redacta* were described in 1995 based on 1 female collected from the southwest Pacific and 15 females and 2 males from northeast Pacific samples. After examination and study of additional samples and species, it has been determined that the male described as *O. redacta* in 1995 is actually the male of *O. similis* Sars, 1918, a closely related species.

Female.—Mean lengths of 20 specimens: TL 1.13 mm (1.04–1.22 mm), PL 0.77 mm (0.72–0.81 mm).

Male.—The emended diagnosis of the male of *O. redacta* is as follows. Mean lengths of 20 specimens: TL 0.88 mm (0.83–0.93 mm), PL 0.60 mm (0.53–0.64 mm). Body (Fig. 9A) with scattered refractile points associated with pores; pediger 1–4 segments covered with minute refractile points. Anterior border of cephalosome with 3 anterodorsal sclerotized ridges (Fig. 9B) which appear to each support the opening for a large pore or duct. Prosome length about twice that of urosome; pediger 4 with acute angle of lateroposterior corner. Genital segment length about twice that of remainder of urosome (Fig. 9C). Caudal ramus length about equal to that of anal segment.

Maxilliped (Fig. 9D) second segment conspicuously expanded with anterior row of small setules and a number of refractile points; 2 setae within longitudinal cleft; inner posterior rim with 3 rows of spatulate setules of graduated lengths; terminal claw with narrow element near inner base. Swimming legs as in female. Leg 5 (Fig. 9E) short, not delimited from thoracic segment; armature similar to that of female. Leg 6 represented by posterolateral point-tipped flap on ventral surface of genital segment.

Remarks.—*Oncaea redacta* females with 2 pores in a similar anterodorsal position on the cephalosome, less conspicuous than those of the male, were originally noted by Heron & Bradford-Grieve (1995: fig. 11c). The dorsal pores on the cephalosome and the numerous minute refractile points on pedigers 1–4 assist in the initial identification of *O. redacta* males. The males differ from those of *O. similis* by having a larger size, an acute rather than rounded angle of pediger 4 lateroposterior corner, and the basal seta of leg 5 shorter than the inner, longer of the two terminal setae.

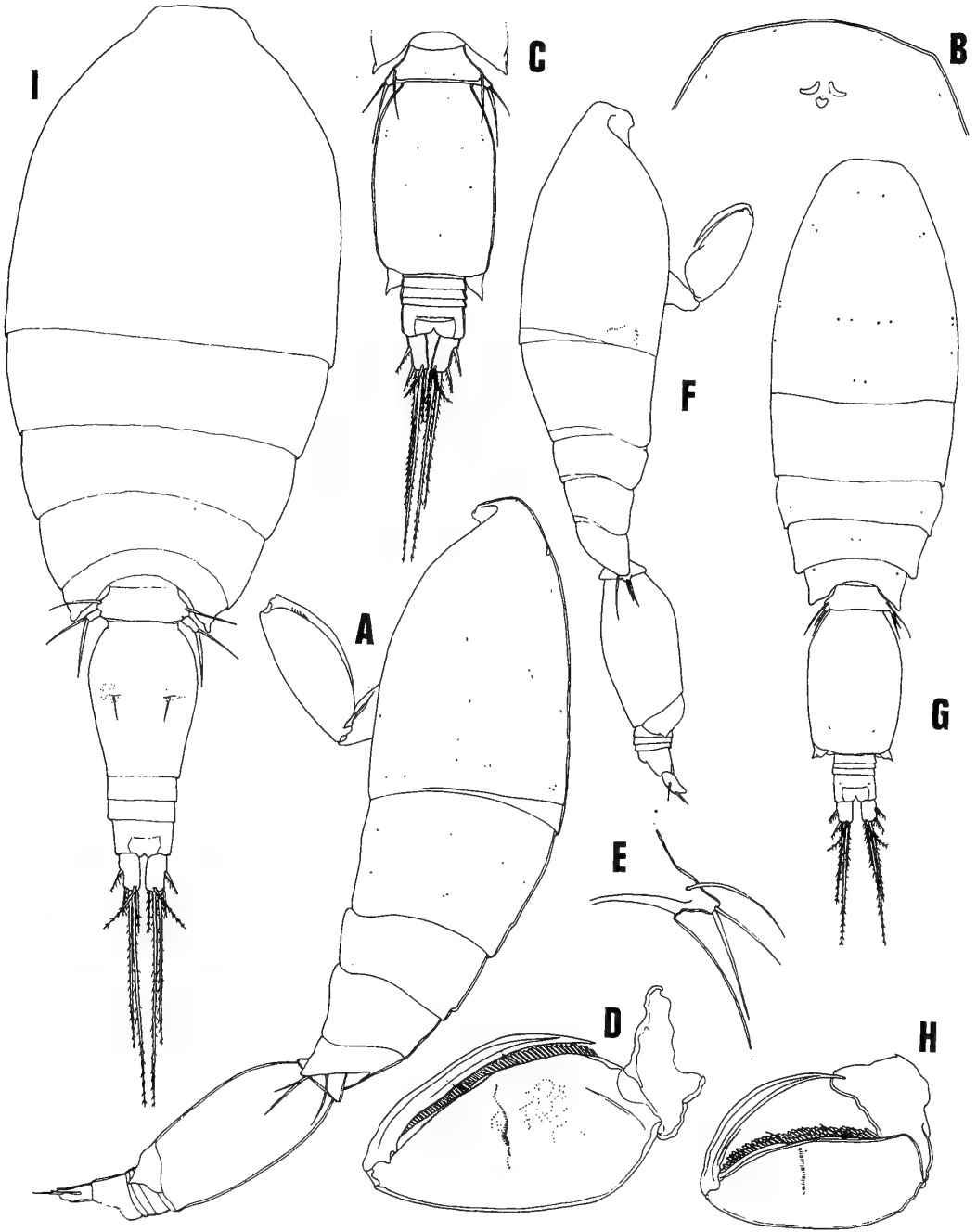


Fig. 9. *Oncaea redacta*, Male: A, lateral (scale t); B, anterior border of cephalosoma, dorsoanterior (x); C, pediger 4 posterior corner, urosome, dorsal (t); D, maxilliped, left (x); E, leg 5 (x). *Oncaea similis*, Male: 0.64mm (Sognofjord specimen); F, lateral (t); G, dorsal (t); H, maxilliped, left (t). *Oncaea insolita*, new species. Female: I, dorsal (t).

Oncaea borealis Sars, 1918

Fig. 1E

Oncaea conifera.—Sars, 1900:113, pl. 32, figs. 15, 16. (Not *O. conifera* Giesbrecht, 1891.)

Oncaea borealis Sars, 1918:191–193, pl. 58.—Malt 1983a:4–6, 9, fig. 2. Heron, English, & Damkaer 1984:466, 467, figs. 9D–G, 10, 11A–D.

Material examined.—See Table 3.

Oncaea similis Sars, 1918

Figs. 1F, 9F–H

Oncaea similis Sars, 1918:193, pl. 109, 10 figs.—Heron 1977:47, 51, figs. 7d–m, 8a–d.—Malt 1983a:4–6, 9, fig. 4.—Malt, Lakkis, & Ziedane 1989:957, 959, figs. 4J, 5A–H.

Oncaea redacta.—Heron & Bradford-Grieve, 1995:29, 32 (male only), fig. 12h–j.

Triconia similis.—Böttger-Schnack, 1999: 44, 45, 48, 50, 52, 53, figs. 2–5.

Material examined.—See Table 3. Reference specimens: USNM 243759 (6 females, 3 males): *Brown Bear* 368–20, 10 Aug 1965, 2700–0 m.

Female.—Inland water: mean lengths of 20 specimens: TL 0.78 mm (0.74–0.80 mm), PL 0.53 mm (0.46–0.56 mm).

Male.—Inland water: mean lengths of 15 specimens: TL 0.64 mm (0.58–0.68 mm), PL 0.43 mm (0.37–0.44 mm). Prosome length approximately twice that of urosome (Fig. 9F, G); cephalosome with posterolateral random scatter of minute refractile points associated with pores. Maxilliped (Fig. 9H) second segment expanded with anterior row of small setules; 2 setae within longitudinal cleft and inner posterior rim with 3 rows of spatulate setules of graduated lengths; terminal claw with narrow process near inner base. Swimming legs as in female. Leg 5 not delimited from thoracic segment; general shape of segment and armature similar to that of female; outer basal seta longer than setae of leg 5. Leg 6

represented by posterolateral flap on ventral surface of genital segment.

Remarks.—The Sognefjorden sample was from near the original collecting locality of Sars' specimens; female: TL 0.74–0.81 mm, PL 0.50–0.55 mm, male: TL 0.59–0.64 mm, PL 0.39–0.44 mm.

Oncaea insolita, new species

Figs. 1G, 9I, 10, 11, 12A–B

Type material.—Holotype female, 0.87 mm; USNM 291274 (type locality, northeast Pacific Ocean); allotype male, 0.70 mm, USNM 291275: *Brown Bear* 344–4, 19 May 1964, 1800–0 m; 7 paratypes, USNM 243742 (5 females, 4 males): *Brown Bear* 344–5, 20 May 1964, 2128–0 m.

Material examined.—See Table 3.

Female.—Mean lengths of 20 specimens: TL 0.86 mm (0.82–0.96 mm), PL 0.59 mm (0.56–0.67 mm). Body (Figs. 9I, 10A) stout, exoskeleton heavily sclerotized; ratio of length of prosome to that of urosome 2.06:1. Genital segment robust in lateral view (Fig. 10B); gonopore at midway of dorsal surface.

Rostral area with thickened, rounded posteroventral margin. First antenna (Fig. 10C) and second antenna (Fig. 10D) with armament similar in number to that of *O. canadensis*. Labrum (Fig. 10E) with free margin divided into 2 posteroventral lobes; each margin with row of short dentiform setules inserted on undersurface; lobes separated by semicircular vertex from which arise several thin lamellae with rows of setules and a central cluster of setules. Mandible (Fig. 10F), first maxilla (Fig. 10G), second maxilla (Fig. 10H), and maxilliped (Fig. 11A) with armament similar in number to that of *O. canadensis*; maxilliped with relatively conspicuous areas of sclerotization on first segment.

Legs 1–4 (Fig. 11B–E) with armament similar in number to that of *O. canadensis*; legs 2–4 endopods with terminal cone. Leg 5 a free segment with 2 subequal terminal setae, the longer slightly spiniform; outer

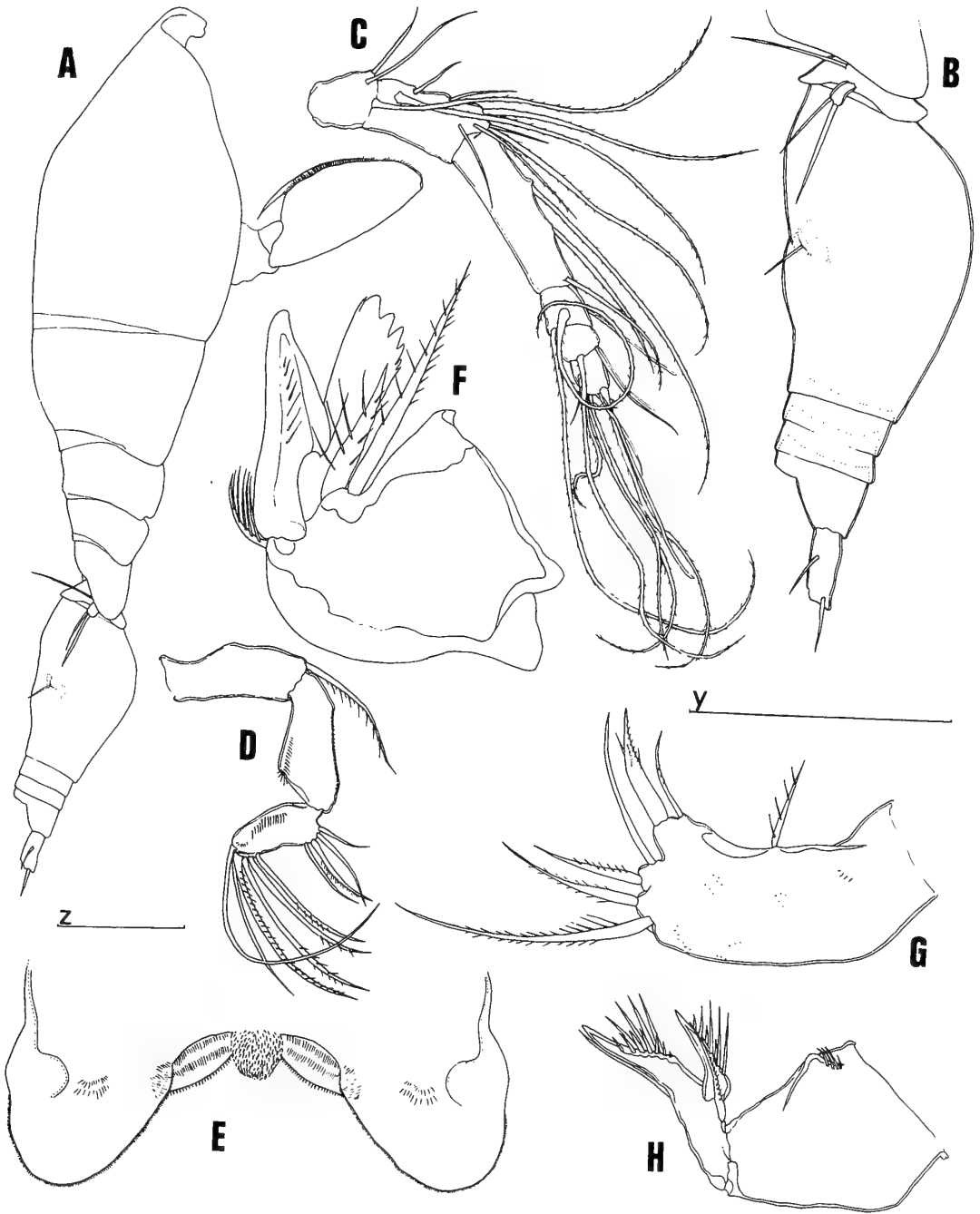


Fig. 10. *Oncaea insolita*, new species. Female: A, lateral (scale x); B, pediger 4 posterior corner, urosome, lateral (x); C, first antenna, left (x); D, second antenna, left (x); E, labrum (v); F, mandible, right (y); G, first maxilla, left (y); H, second maxilla, right (z).

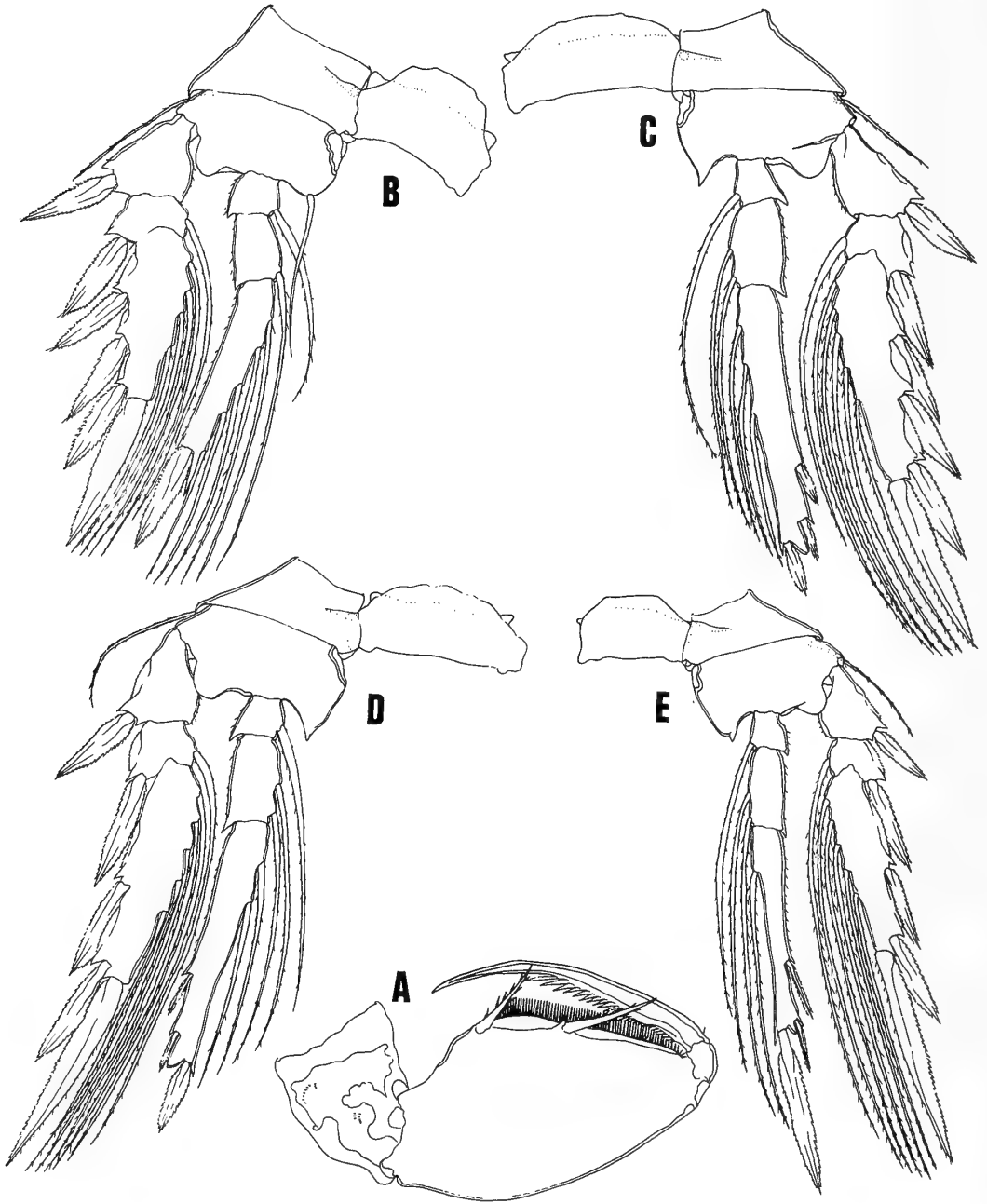


Fig. 11. *Oncaea insolita*, new species. Female: A, maxilliped, left (scale x); B, leg 1 (x); C, leg 2 (x); D, leg 3 (x); E, leg 4 (x).

basal seta. Leg 6 represented by spiniform setule on gonopore.

Male.—Mean lengths of 20 specimens: TL 0.74 mm (0.70–0.81 mm, PL 0.50 mm (0.45–0.56 mm). Body (Fig. 12A) stout,

exoskeleton heavily sclerotized. Maxilliped (Fig. 12B) second segment with outer row of setules and posterior surface with cluster of small spinules followed by prominent protrusion with 2 rows of denticles, each

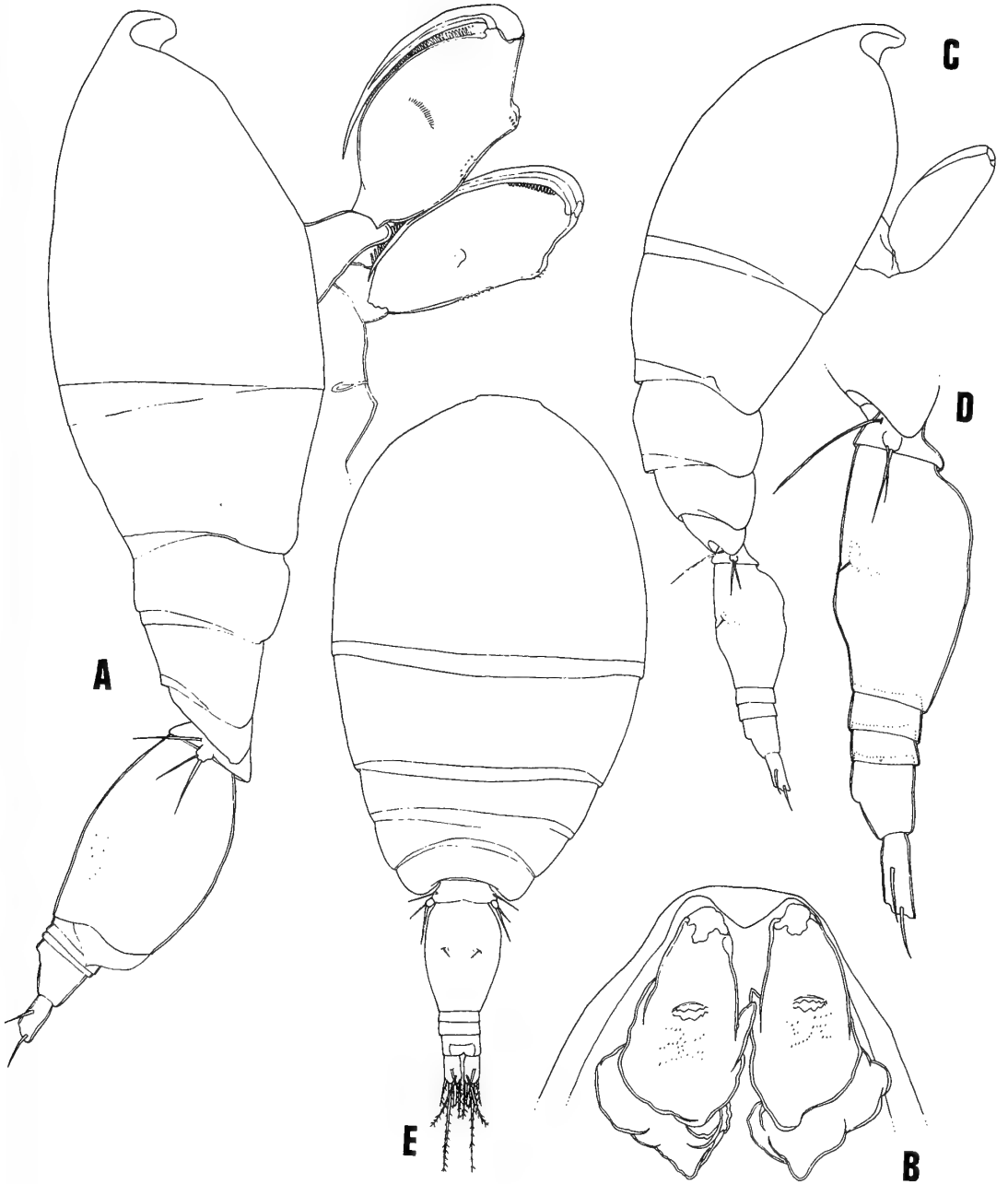


Fig. 12. *Oncaea insolita*, new species. Male: A, lateral (scale s); B, maxillipeds, ventral (s). *Oncaea illgi*, Female: C, lateral (w); D, pediger 4 posterior corner, urosome, lateral (x). *Oncaea rotata*, new species. Female: E, dorsal (w).

associated with small pore; inner surface with stout digitiform outgrowth with inner pore. Swimming legs as in female. Leg 5 not delimited from thoracic segment; ar-

mament similar to that of female. Leg 6 represented by posterolateral flap on ventral surface of genital segment.

Etymology.—The specific name, from

Latin (*insolitus* = unusual, uncommon, strange), refers to the maxilliped of the male.

Remarks.—*Oncaea insolita* shows remarkable resemblance to *O. latimana* Gordejeva, 1975a, excepting the greater size difference, including the conspicuous, unusual male maxilliped. Gordejeva's illustration (Fig. 9) of the *O. latimana* leg 4 endopod does not show a terminal projection, but the subterminal spine, appearing to overlap the terminal spine, could possibly conceal a small projection similar to that of *O. insolita*. We were not successful in attempts to borrow Gordejeva's specimens for comparisons. Gordejeva (1975a) described *O. latimana* from samples collected in the tropical Atlantic Ocean, south of the equator, between 500–1000 m, and from the Gulf of Mexico. *O. latimana* lengths are: females 0.50 mm, males 0.42 mm.

Oncaea insolita resembles *O. illgi* in several characters such as the female stout maxilliped and spine set of legs 2–4. *Oncaea insolita* also shows close affinity to three other species found in Antarctic samples, *O. convexa* Heron, 1977, *O. bowmani* Heron, 1977, and *O. compacta* Heron, 1977. These species all have a relatively large mandible, first maxilla, and second maxilla. The second antenna third segment of the latter four species all have the inner seta, of the distal group of seven elements, considerably reduced. The exterior form and ornamentation of the *O. insolita* labrum is especially similar to that of *O. compacta*.

Oncaea illgi Heron, 1977

Figs. 1H, 12C–D

Oncaea illgi Heron, 1977:51, 55, figs. 10c–k, 11a–k.

Material examined.—See Table 3. Reference specimens: USNM 243764 (4 females): *Brown Bear* 380–13, 10 Nov 1965, 4650–0 m.

Female.—Mean lengths of 20 specimens: TL 0.78 mm (0.76–0.79 mm), PL 0.54 mm (0.48–0.58 mm). Ratio of length of female

prosoma to that of urosome 2.16:1 (Fig. 12C). Ratio of length of female genital segment to that of remainder of urosome 1.15:1 (Fig. 12D). Leg 5 with a faint line of segmentation on ventral surface of some specimens; outer basal seta.

Remarks.—*Oncaea illgi* closely resembles *O. rotata*, new species, *O. bowmani* Heron, 1977, and *O. compacta* Heron, 1977, with a broad, robust prosoma in contrast to a relatively slender, short urosome.

Oncaea rotata, new species

Figs. 1I, 12E, 13, 14A–G

Type material.—Holotype female, 0.69 mm, USNM 243756 (type locality, northeast Pacific Ocean): *Brown Bear* 352–12, 17 Jan 1965, 2000–0 m; allotype male, 0.58 mm, USNM 243757: *Thompson Sta P*, 8 Aug 1973, 3000–0 m; 2 female paratypes, USNM 243758: *Brown Bear* 368–36, 18 Aug 1965, 3700–0 m.

Material examined.—See Table 3.

Female.—Mean lengths of 7 specimens: TL 0.69 mm (TL 0.67–0.70 mm), PL 0.49 mm (0.46–0.52 mm). Prosoma robust in dorsal and lateral view (Figs. 12E, 13A). Ratio of length of prosoma to that of urosome about 2.49:1. Ratio of length of genital segment to that of remainder of urosome about 1.4:1 (Fig. 13B–C). Genital segment with gonopore, bearing a setule, at mid-region of dorsal surface. Caudal ramus with anterior short seta located on mid-dorsal surface rather than more usual lateral position; posterior dorsal seta slightly longer than innermost terminal seta (inner long terminal seta missing on specimens examined).

Rostral area with thickened, rounded posteroventral margin. First antenna (Fig. 13D) and second antenna (Fig. 13E) with armament similar in number to that of *O. canadensis*; second antenna with comparatively slender segments, third segment longer than the second. Labrum (Fig. 13F) with free margin divided into 2 lobes, each margin with an underlying row of setules;

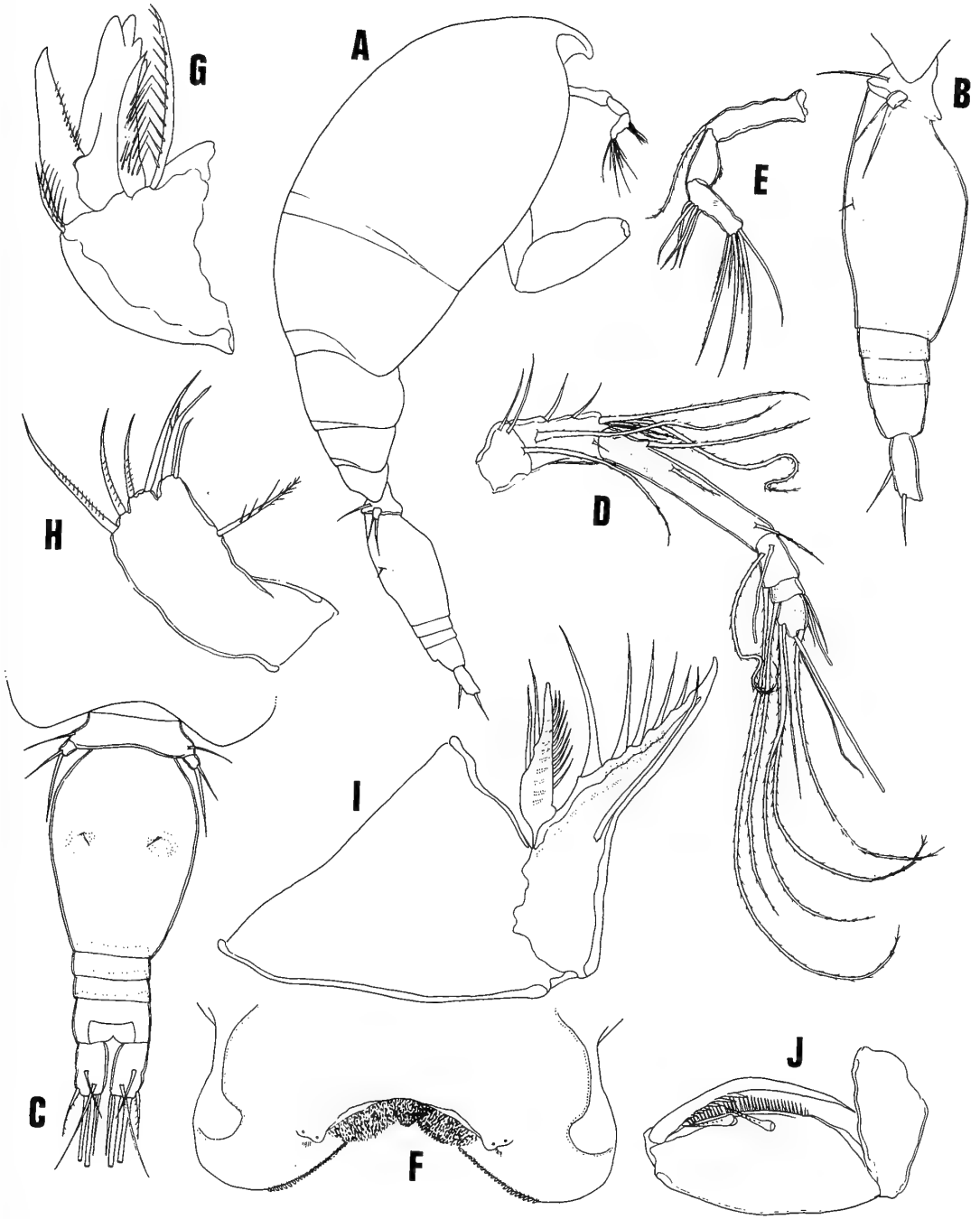


Fig. 13. *Oncaea rotata*, new species. Female: A, lateral (scale w); B, pediger 4 posterior corner, urosome, lateral (x); C, pediger 4 posterior corner, urosome, dorsal (x); D, first antenna, left (x); E, second antenna, left (x); F, labrum (v); G, mandible, right (y); H, first maxilla, left (y); I, second maxilla, right (y); J, maxilliped, right (x).

lobes separated by semicircular vertex from which arises 1 median hyaline lamella and 2 lateral lamellae, all ornamented with thin setules. Mandible (Fig. 13G), first maxilla (Fig. 13H), and second maxilla (Fig. 13I) with armament similar in number to that of *O. canadensis*. Maxilliped (Fig. 13J) 4-segmented, with second segment conspicuously inflated; 2 barbed spines and a row of setules on inner surface; third segment small and unarmed; terminal segment a long claw with row of stout setules of graduated lengths on concave surface; setiform element near inner base.

Legs 1–4 (Fig. 14A–D) with armament similar in number to that of *O. canadensis*; endopods of legs 2 and 3 with terminal cone, leg 4 without. Leg 5 with free segment small; 2 terminal setae, the longer slightly spiniform; outer basal seta. Leg 6 represented by thin, spiniform setule on gonopore.

Male.—The single male (TL 0.58 mm, PL 0.41 mm), found at Station P (Table 2), becomes the allotype of the species and therefore was not dissected. Body (Fig. 14E) with ratio of prosome to that of urosome 2.25:1. Urosome first segment with posterior transverse ridge (Fig. 14F–G). Caudal ramus and caudal setae similar to those of female, including anterior short seta location on mid-dorsal surface. Second antenna with comparatively slender segments. Swimming legs as in female. Leg 5 (see Fig. 14F–G) not delimited from thoracic segment; armature similar to that of female. Leg 6 represented by posterolateral flap on ventral surface of genital segment, pointed posterior corner protruding in dorsal view.

Etymology.—The specific name, from Latin (*rotatio* = turned), refers to the position of the short anterior seta of the caudal ramus, which is located on the mid-dorsal surface, rather than the usual lateral margin.

Remarks.—*Oncaea rotata* appears to have an affinity to *O. illgi* with similar characters such as robust appearance of prosome, diminutive second antenna, and the

exterior ornamentation of the labrum. The shape and length of leg 4 endopod as well as the mid-dorsal location of the proximal short seta of the caudal ramus of *O. rotata* distinguish it from *O. illgi*.

Oncaea brocha Heron, 1977

Fig. 1J

Oncaea brocha Heron, 1977:60, figs. 14f–n, 15a–h.—Malt 1982a:190, fig. 10g–k.

Material examined.—See Table 3.

Female.—Mean lengths of 3 specimens: TL 0.82 mm (0.81–0.83 mm), PL 0.57 mm (0.56–0.57 mm).

Male.—Length of 1 specimen: TL 0.69 mm, PL 0.48 mm.

Oncaea olsoni Heron, 1977

Fig. 2A

Oncaea olsoni Heron, 1977:60, 62, figs. 15i–1, 16.

Material examined.—See Table 3.

Female.—Mean lengths of 10 specimens: TL 0.80 mm (0.72–0.85 mm), PL 0.55 mm (0.52–0.57 mm).

Male.—Length of 1 specimen: TL 0.70 mm, PL 0.48 mm; a second male damaged.

Oncaea damkaeri Heron, 1977

Figs. 2B, 14H

Oncaea damkaeri Heron, 1977:62, 65, figs. 17, 18a–e.

Material examined.—See Table 3.

Female.—Mean lengths of 8 specimens: TL 0.74 mm (0.67–0.78 mm), PL 0.52 mm (0.48–0.53 mm).

Remarks.—The female leg 5 of *O. damkaeri* distinguishes it from other similar species, with the length of the terminal, longer spiniform seta exceeding the length of the leg 5 segment and measuring more than twice the length of the shorter seta (Fig. 14H).

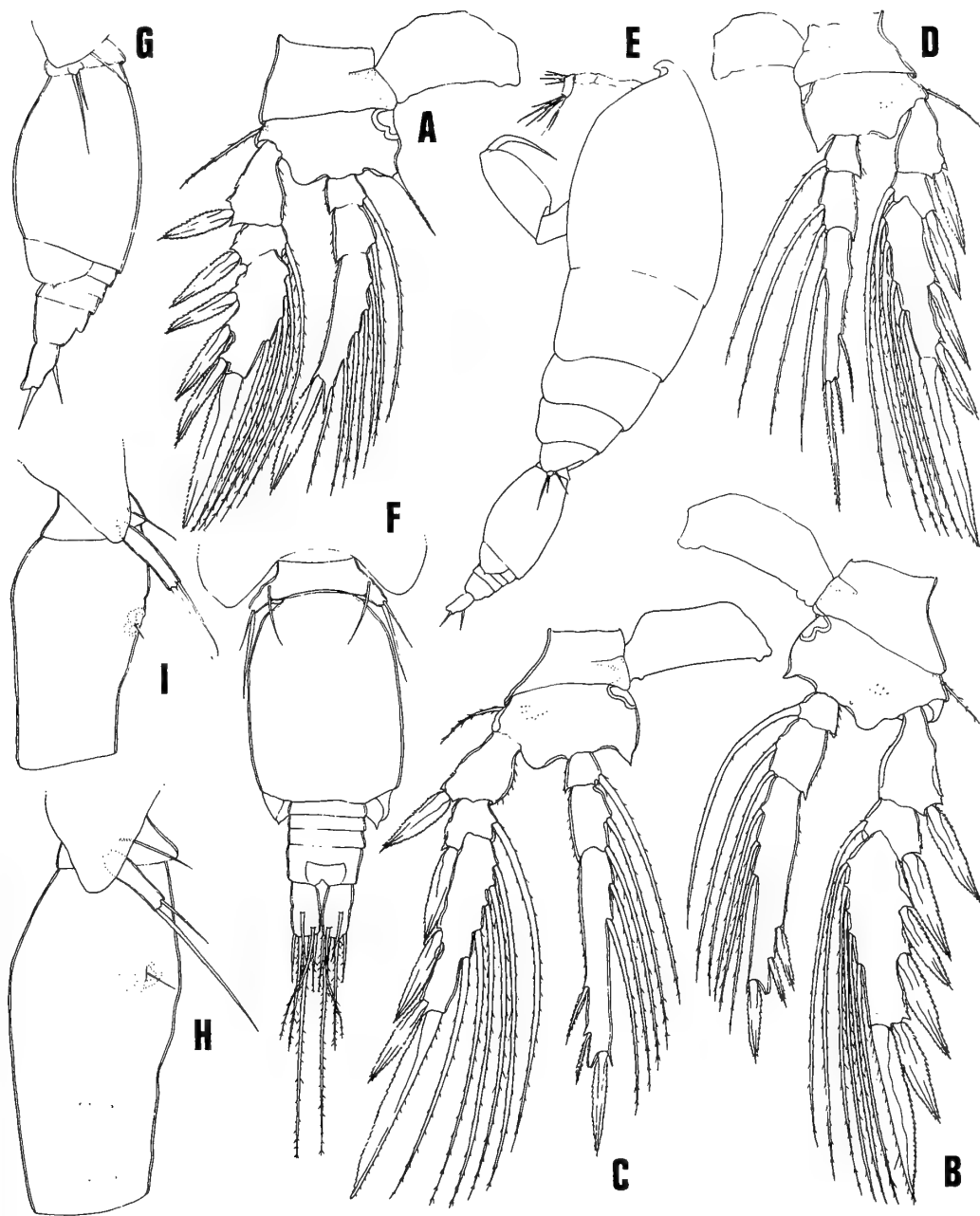


Fig. 14. *Oncaea rotata*, new species. Female: A, leg 1 (scale x); B, leg 2 (x); C, leg 3 (x); D, leg 4 (x). Male: E, lateral (w); F, pediger 4 posterior corner, urosome, dorsal (x); G, pediger 4 posterior corner, urosome, lateral (x). *Oncaea damkaeri*, Female: H, pediger 4 posterior corner, segment of leg 5, genital segment, lateral (x). *Oncaea parila*. Female: I, pediger 4 posterior corner, segment of leg 5, genital segment, lateral (x).

Oncaea parila Heron, 1977
Figs. 2C, 14I

Oncaea notopus Sars.—1900:107, pl. 32, figs. 1-14.—Tanaka 1960:70, 71, pl. 32, figs. 1-7. (Not *O. notopus* Giesbrecht, 1891.)

Oncaea parila Heron, 1977:65, 68 (female), figs. 18j-r, 19a-f.—Heron et al. 1984:470, 472 (male), figs. 11J, K, 12A-C.

Material examined.—See Table 3.

Female.—Mean lengths of 10 specimens: TL 0.62 mm (0.59–0.67 mm), PL 0.41 mm (0.41–0.44 mm).

Male.—Mean length of 4 specimens: 0.48 mm (TL 0.46–0.50 mm), PL 0.34 mm (0.33–0.35 mm).

Remarks.—The female leg 5 of *O. parila* (Fig. 14I) and *O. notopus* Giesbrecht, 1891, both with the lengths of the two terminal setae being approximately equal, display one of the characters useful in distinguishing each of them from other similar species. *Oncaea notopus* differs from *O. parila* by a greater size (female 0.95 mm) and the relatively longer spines on exopods and endopods of legs 1–4 (see Heron 1977, fig. 18f-i).

Oncaea prolata Heron, 1977
Figs. 2D, 15A-B

Oncaea notopus.—Giesbrecht, 1902:41, pl. 13, figs. 1-6. (Not *O. notopus* Giesbrecht, 1891).

Oncaea prolata Heron, 1977:68 (female), figs. 19g-r, 20a-c.—Heron & Bradford-Grieve 1995:41, 42 (male), figs. 19, 20, 26d.

Material examined.—See Table 3. Reference specimens: USNM 243748 (10 females, 10 males): Hoh Dabob Bay, 24 Jun 1985, 180–0 m.

Female.—Mean lengths of 10 specimens: TL 0.68 mm (0.64–0.70 mm), PL 0.47 mm (0.44–0.48 mm).

Male.—Mean lengths of 10 specimens:

TL 0.57 mm (0.56–0.59 mm), PL 0.39 mm (0.37–0.41 mm).

Remarks.—The female leg 5 of *O. prolata* displays one of the important characters for distinguishing it from other similar species: the longer terminal seta is approximately twice as long as the short spiniform seta (Fig. 15A). The male maxilliped (Fig. 15B) has a slight inner swelling and bears two setae and three medial rows of spatulate setules.

Oncaea grossa. new species
Figs. 2E, 15C-J, 16, 17A-C

Type material.—Holotype female, 0.80 mm, USNM 243738 (type locality, northeast Pacific Ocean); allotype male, 0.67 mm, USNM 243739; 40 paratypes, USNM 243740 (20 females, 20 males): Thompson Sta P, 8 Aug 1973, 3000–0 m.

Material examined.—See Table 3.

Female.—Mean lengths of 20 females: TL 0.79 mm (0.76–0.81 mm), PL 0.55 mm (0.50–0.57 mm). Body (Fig. 15C) with ratio of length of prosome to that of urosome 2.16:1. Genital segment length approximately equal to that of remainder of urosome (Fig. 15D-E); anteroventral surface with transverse rows of minute spinules on and around a protruding ledge, followed by horizontal rows of small spinules.

Rostral area with thickened, rounded posteroventral margin. First antenna (Fig. 15F) and second antenna (Fig. 15G) with armament similar in number to that of *O. canadensis*. Labrum (Fig. 15H) with free margin divided into 2 posteroventral lobes; each margin with row of short denticles and 1 large sclerotized tooth, all on undersurface; lobes separated by semicircular vertex from which arise several thin lamellae and a medial tuft with thin setules. Mandible (Fig. 15I), first maxilla (Fig. 15J), second maxilla (Fig. 16A), and maxilliped (Fig. 16B) with armament similar in number to that of *O. canadensis*.

Legs 1–4 (Fig. 16C-F) with armament similar in number to that of *O. canadensis*;

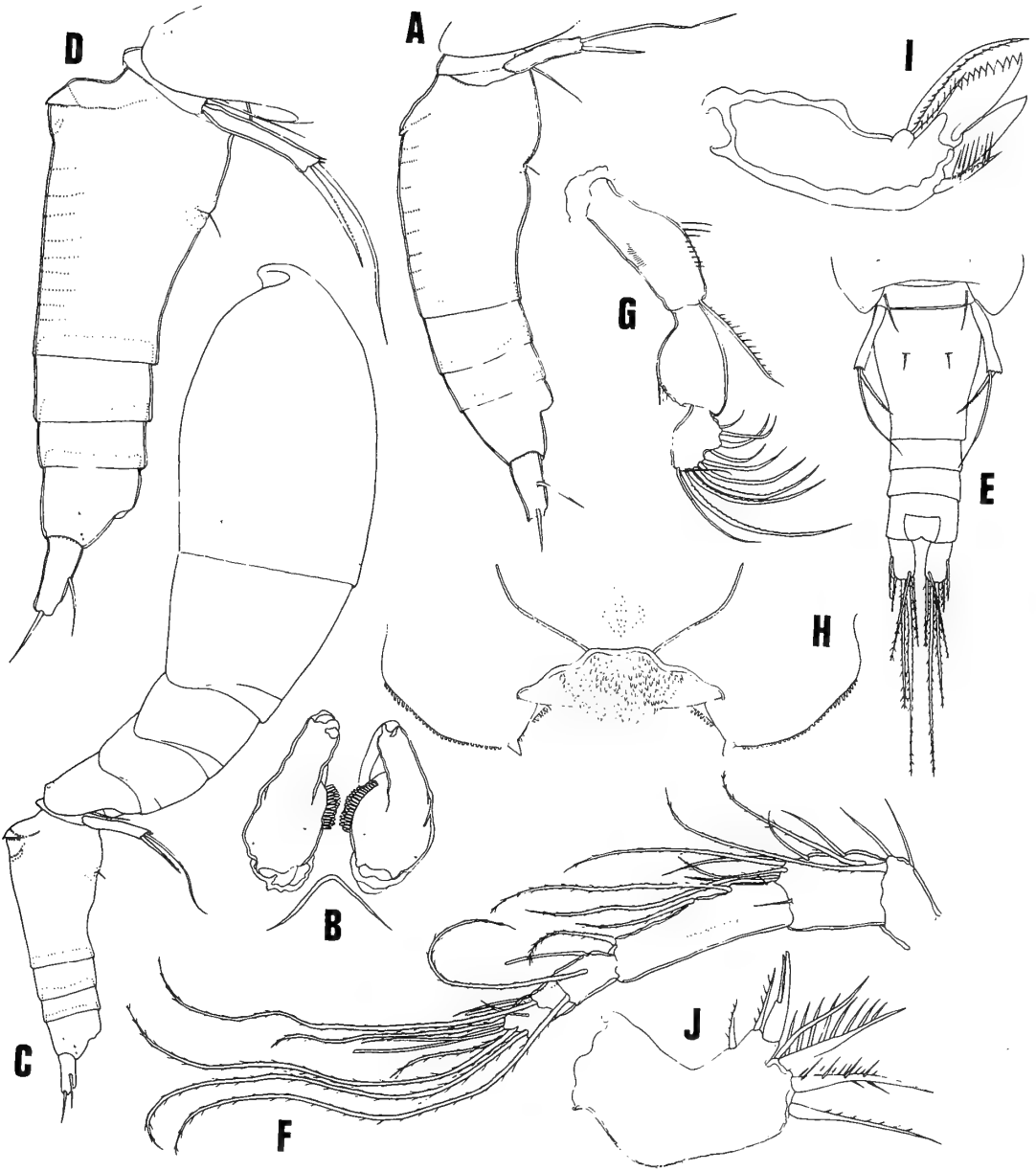


Fig. 15. *Oncaea prolata*. Female: A, pediger 4 posterior corner, urosome, lateral (scale x). Male: B, maxillipeds, ventral (x). *Oncaea grossa*, new species. Female: C, lateral (t); D, pediger 4 posterior corner, urosome, dorsal (t); E, pediger 4 posterior corner, urosome, dorsal (t); F, first antenna, right (x); G, second antenna, right (x); H, labrum (y); I, mandible, left (y); J, first maxilla, right (y).

endopods of legs 2 and 3 with a small terminal cone, leg 4 without. Leg 5 with elongate free segment; 2 terminal setae, the longer less than twice the length of the shorter, which is dentiform; outer basal seta.

Leg 6 represented by spiniform setule on gonopore.

Male.—Mean length of 20 males: TL 0.69 mm (0.63–0.70 mm), PL 0.47 mm (0.41–0.48 mm). Body (Fig. 17A) with ra-

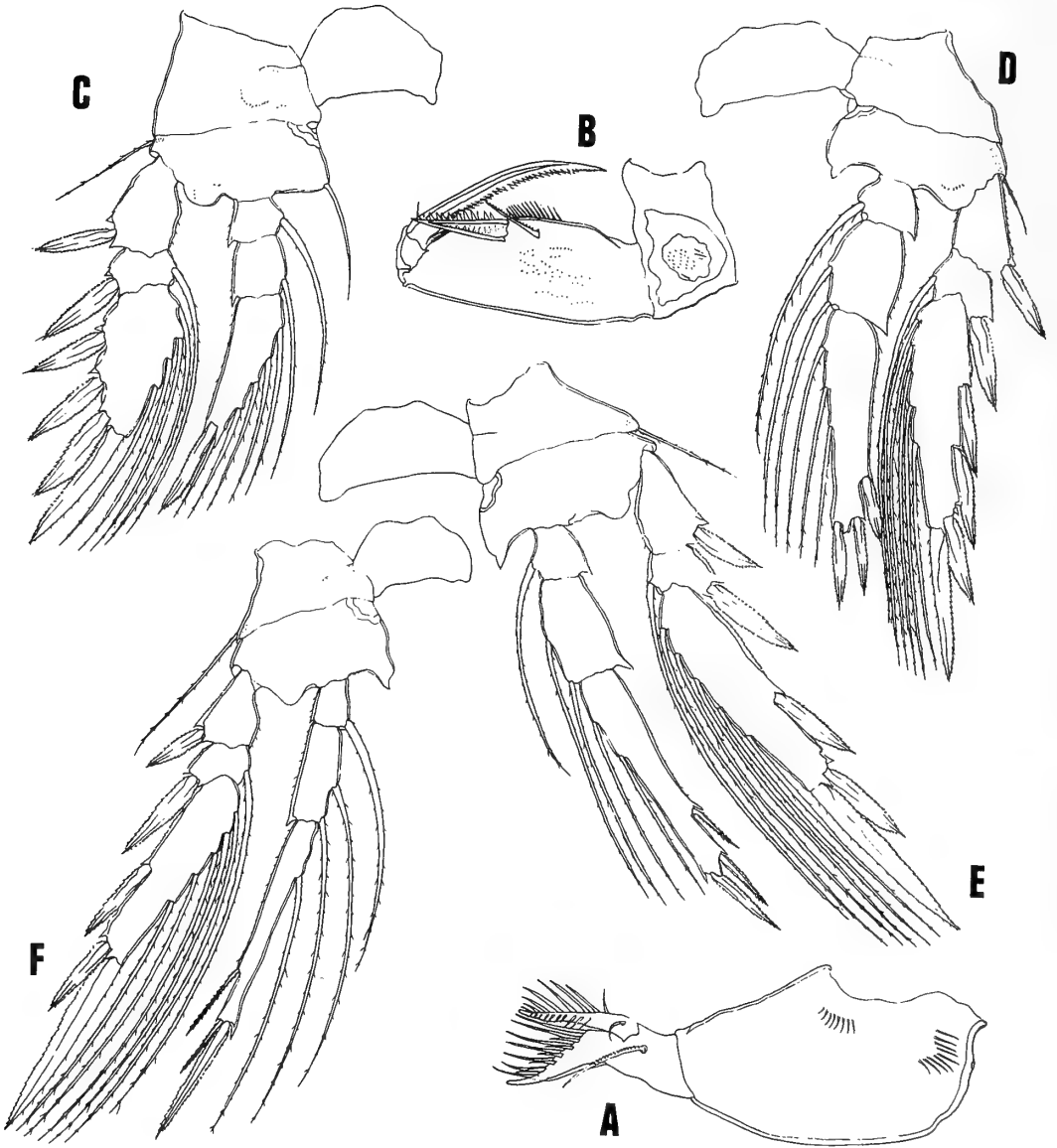


Fig. 16. *Oncaea grossa*, new species. Female: A, second maxilla, right (scale v); B, maxilliped, right (x); C, leg 1 (x); D, leg 2 (x); E, leg 3 (x); F, leg 4 (x).

tio of length of prosome to that of urosome 1.97:1. Urosome (Fig. 17B) with caudal setae proportional lengths as in female. Maxilliped (Fig. 17C) second segment proximally enlarged with 3 rows of wide, lamellate setules on inner posterior rim and conspicuous areas of sclerotization proximally; tip of claw with terminal lamella. Swimming legs as in female. Leg 5 (see

Fig. 17B) not delimited from thoracic segment; armament similar to that of female. Leg 6 represented by posterolateral flap on ventral surface of genital segment.

Etymology.—The specific name, from Latin (*grossa* = big, thick), refers to the conspicuously large size of the male maxilliped.

Remarks.—In addition, 11 females (TL

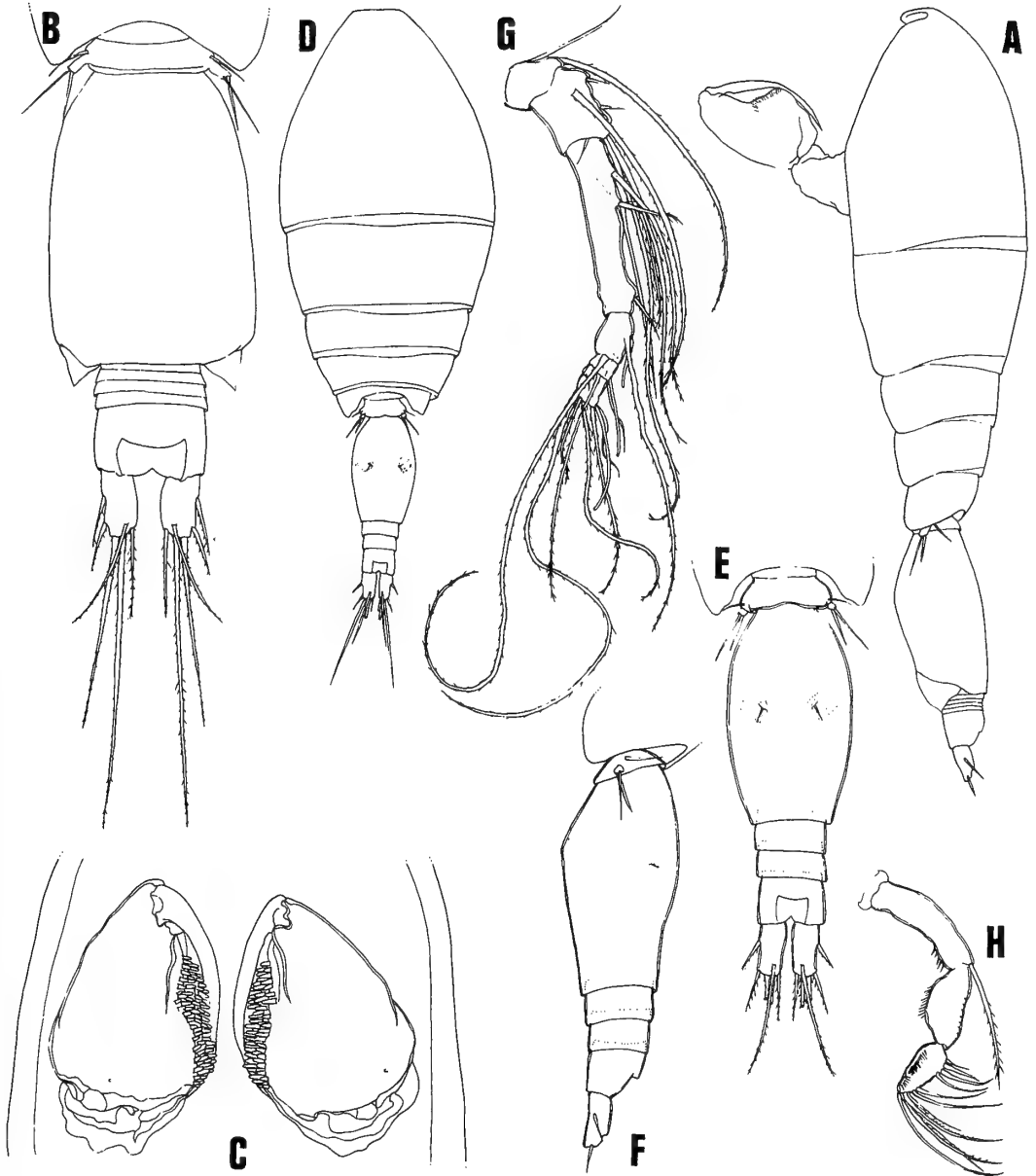


Fig. 17. *Oncaea grossa*, new species. Male: A, lateral (scale t); B, pediger 4 posterior corner, urosome, dorsal (x); C, maxillipeds, ventral (x). *Oncaea rimula*, new species. Female: D, dorsal (w); E, pediger 4 posterior corner, urosome, dorsal (x); F, pediger 4 posterior corner, urosome, lateral (x); G, first antenna, left (x); H, second antenna, left (x).

0.76–0.81 mm, PL 0.56–0.58 mm) and five males (TL 0.63–0.70 mm, PL 0.45–0.48 mm) of *O. grossa* were identified from Prince William Sound, Alaska. *Oncaea grossa* closely resembles *O. prolata* in many characters, but may be separated by

noting the larger size of *O. grossa* and the more robust appearance of the female genital segment in lateral view. The shorter terminal seta of the female leg 5 for both species has a denticulate margin, but denticles are conspicuous for *O. grossa* and obscure

for *O. prolata*. The male maxilliped of *O. grossa* has a robust second segment with rows of conspicuous spatulate setules (see Figs. 15B, 17C), while *O. prolata* male has a recurved terminal claw (Heron & Bradford Grieve 1995:41).

Oncaea rimula, new species
Figs. 2F, 17D–H, 18A–N

Type material.—Holotype female, 0.50 mm, USNM 243751 (type locality, inland coastal waters of Washington and northeast Pacific Ocean): Hoh Dabob Bay, 25 Apr 1985, 180–0 m; allotype male, 0.44 mm, USNM 243752; 1 male paratype, USNM 243753: Hoh Dabob Bay, 24 Jun 1985, 180–0 m; 1 female paratype, USNM 243754: Brown Bear 352–10, 16 Jan 1965, 2000–0 m; 1 male paratype, USNM 243755: Brown Bear 368–25, 13 Aug 1965, 2000–0 m.

Material examined.—See Table 3.

Female.—Mean lengths of 13 females: TL 0.55 mm (0.50–0.60 mm), PL 0.38 mm (0.33–0.41 mm). Ratio of length of prosome to that of urosome 1.97:1 (Fig. 17D). Exoskeleton and setae with thin, fragile cuticle. Cephalosome length about equal to that of width posteriorly, dorsal view. Urosome first segment with dorsoposterior transverse ridge and posterior margin indented midway (Fig. 17E). Ratio of length of genital segment (Fig. 17F) to that of remainder of urosome 1.36:1. Genital segment with gonopore, bearing a spiniform setule, located midway on segment. Caudal ramus longer than anal segment and half the length of dorsal seta (inner long terminal seta missing on specimens examined).

Rostral area with thickened, rounded margin. First antenna (Fig. 17G) and second antenna (Fig. 17H) with armament similar in number to that of *O. canadensis*. Labrum (Fig. 18A) with posterior free margin divided into 2 posteroventral lobes and separated by a semicircular vertex from which arises a thin lamella ornamented with fine setules; imbricated flanges, bearing small

denticles, extend from under inner margin of each lobe. Mandible (Fig. 18B) with inflated, triangular base, terminally flattened, bearing 5 elements: outer stout seta with row of setules, a broad element with a concavity of inner base cupping the outer basal edge of a bladelike element with a setose inner edge; 2 posterior setae, the shorter hyaline, the longer spinulose.

First maxilla (Fig. 18C) and second maxilla (Fig. 18D) with armament similar in number to that of *O. canadensis*; second maxilla with outer flagelliform seta on second segment extending beyond terminal tip of claw. Maxilliped (Fig. 18E) 4-segmented, with first segment unarmed; second segment inner surface with a seta, a spinulose spine, and row of setules; third segment small and unarmed; terminal segment a long claw with a row of fine setules on concave surface and a setose setiform element near inner base. Legs 1–4 (Fig. 18F–I) with armament similar in number to that of *O. canadensis*; endopods of legs 2 and 3 with a small terminal cone, leg 4 without. Leg 5 (see Fig. 17E–F) with free segment small; 2 subequal terminal setae and outer basal seta. Leg 6 represented by spiniform setule on gonopore.

Male.—Mean lengths of 3 specimens: TL 0.44 mm (0.44–0.45 mm), PL 0.30 mm (0.29–0.31 mm). Body (Fig. 18J–K) with ratio of length of prosome to that of urosome 2.04:1. Urosome first segment with dorsoposterior margin indented midway. Genital segment slender, dorsal and lateral view (Fig. 18L–M). (Caudal ramus with inner and outer long terminal setae missing on specimens examined.) Maxilliped (Fig. 18N) second segment with 3 rows of spatulate setules on inner surface, and a seta replacing the spinulose spine. Swimming legs and leg 5 as in female. Leg 6 represented by posterolateral point-tipped flap on ventral surface of genital segment.

Etymology.—The specific name, from Latin (*rima* = cleft), refers to the small indentation on the dorsoposterior margin of the first segment of the urosome.

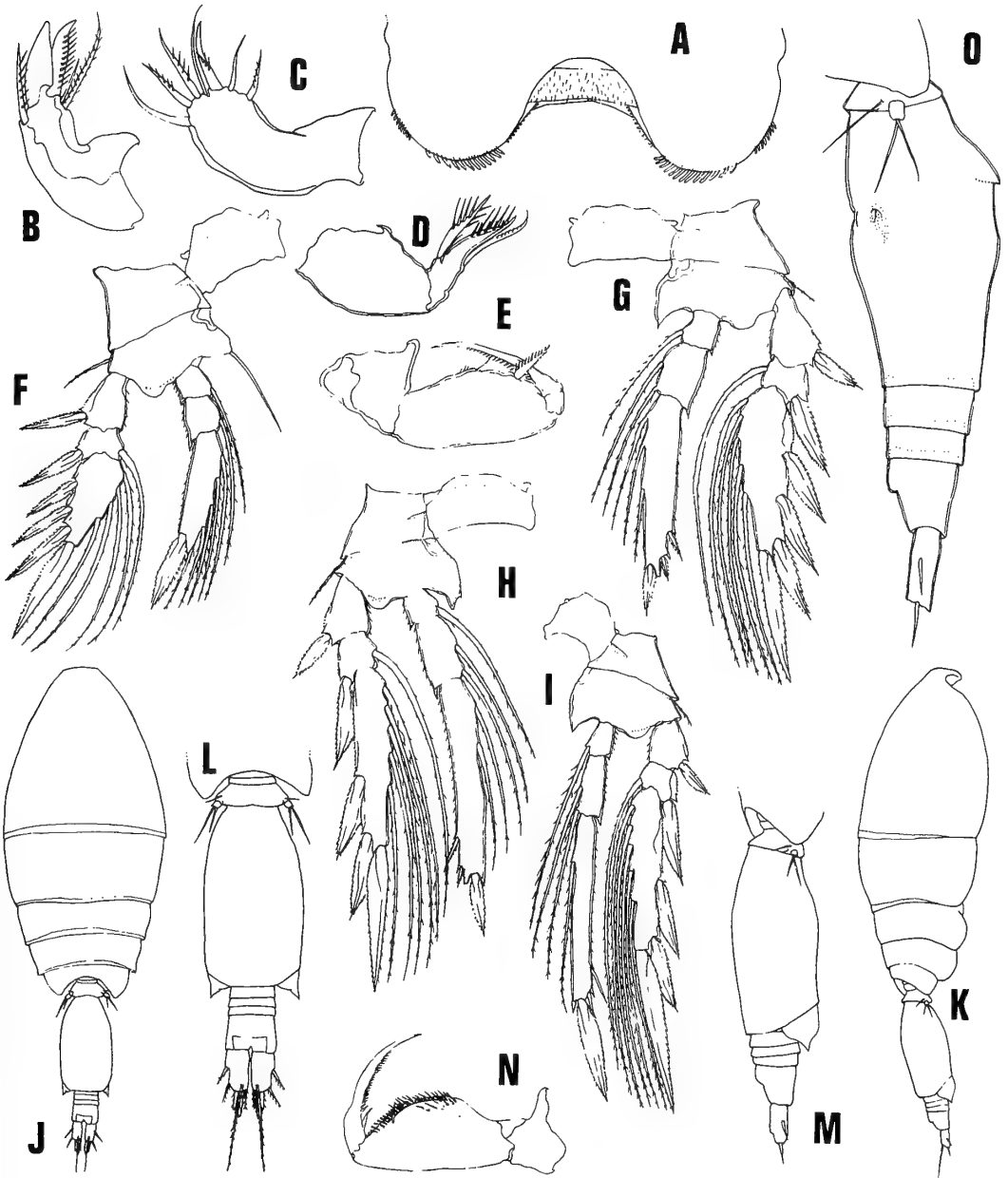


Fig. 18. *Oncaea rimula*, new species. Female: A, labrum (scale y); B, mandible, left (y); C, first maxilla, right (y); D, second maxilla, left (z); E, maxilliped, left (x); F, leg 1 (x); G, leg 2 (x); H, leg 3 (x); I, leg 4 (x). Male: J, dorsal (t); K, lateral (t); L, pediger 4 posterior corner, urosome, dorsal (x); M, pediger 4 posterior corner, urosome, lateral (x); N, maxilliped, left (z). *Oncaea macilenta*. Female: O, pediger 4 posterior corner, urosome, lateral (x).

Remarks.—*Oncaea rimula*, with a thin exoskeleton, is exceedingly fragile. The long caudal setae, when not broken, taper to a very fine distal half of a seta; contrari-

ly, the dentate flange of the swimming legs is prominent. The mandible of *O. rimula* and those of all of the succeeding species differ from the preceding species by the

middle bladlike element bearing a vertical row of setules rather than a row of denticles. *Oncaea rimula*, *O. glabra*, new species, *O. lacinia* Heron et al., 1984, *O. setosa* Heron, 1977, and *O. delicata* Heron et al., 1984, are superficially similar to one another. The outer elongate seta on *O. rimula* second maxilla, extending beyond tip of claw, is similar to that of *O. lacinia*, *O. glabra*, and *O. macilenta* Heron, 1977. The *O. rimula* leg 5 shorter terminal seta reaches to about two-thirds the length of the outer seta; the female genital segment width at the level of the gonopore measures more than half that of the segment length. In order to distinguish each species, comparisons should be made with the shape of the prosome; form and external ornamentation of the labrum; relative lengths of the urosome segments; small, but consistent differences between size and lengths of the terminal spines on endopods of legs 2–4, in relation to the terminal cones, where present; size, shape, and armament of leg 5.

Oncaea macilenta Heron, 1977
Figs. 2G, 18O, 19A–D

Oncaea macilenta Heron, 1977:73, 75, figs. 22o–u, 23a–g (female).

Material examined.—See Table 3. Reference specimens: USNM 243743 (15 females): *Thompson* Sta P, 8 Aug 1973, 3000–0 m; USNM 243749 (1 male): *Brown Bear* 344–25, 30 May 1964, 4500–0 m; USNM 243745 (1 male): *Brown Bear* 368–41, 21 Aug 1965, 2000–0 m.

Female.—Mean lengths of 10 specimens: TL 0.75 mm (0.70–0.79 mm), PL 0.54 mm (0.51–0.57 mm). Females of *O. macilenta* show a squared distolateral corner of pediger 4 with a slight dorsal indentation (Fig. 18O). Genital segment bears a conspicuous anteroventral transverse ridge lined with minute denticles. (Caudal ramus with inner long terminal seta missing on specimens examined.)

Male.—The male of *O. macilenta* is described for the first time. Mean lengths of

4 specimens: TL 0.60 mm (0.57–0.63 mm), PL 0.42 mm (0.39–0.44 mm). Ratio of length of prosome to that of urosome 2.08:1 (Fig. 19A). Exoskeleton with thin, fragile cuticle. Distolateral corner of pediger 4 resembling that of female (Fig. 19B–C). (Caudal ramus with inner long terminal seta missing on specimens examined.)

Second maxilla (Fig. 19D) with outer seta on second segment extending beyond tip of claw, similar to that of female. Maxilliped 3-segmented, lacking small segment proximal to claw of female, although a faint suture line is present on inner surface; second segment slightly elongated compared to that of female; claw with setiform element near inner base and row of setules on concave surface. Swimming legs as in female. Leg 5 (see Fig. 19B) a free segment with 2 slightly subequal terminal setae and an outer basal seta. Leg 6 represented by posterolateral flap on ventral surface of genital segment.

Oncaea glabra, new species
Figs. 2H, 19E–S, 20A–E

Type material.—Holotype female, 0.52 mm, USNM 243735 (type locality, inland coastal waters of Washington); allotype male, 0.48 mm, USNM 243736; 2 paratypes, USNM 243737 (1 female, 1 male): *Hoh Dabob Bay*, 24 Jun 1985, 180–0 m.

Material examined.—See Table 3.

Female.—Mean lengths of 10 specimens: TL 0.51 mm (0.48–0.53 mm), PL 0.35 mm (0.33–0.37 mm). Ratio of length of prosome to that of urosome 2.23:1 (Fig. 19E–F); exoskeleton with thin, fragile cuticle; cephalosome slender, with width posteriorly about same as that of pediger 1, widest point for normal specimens, dorsal view (prosome occasionally expanded abnormally (Fig. 19G) when invaded by unidentified microorganisms). Ratio of genital segment length to that of remainder of urosome 1.11:1 (Fig. 19H). Genital segment with ledge protruding on anteroventral surface, conspicuous in lateral view (Fig. 19I); gon-

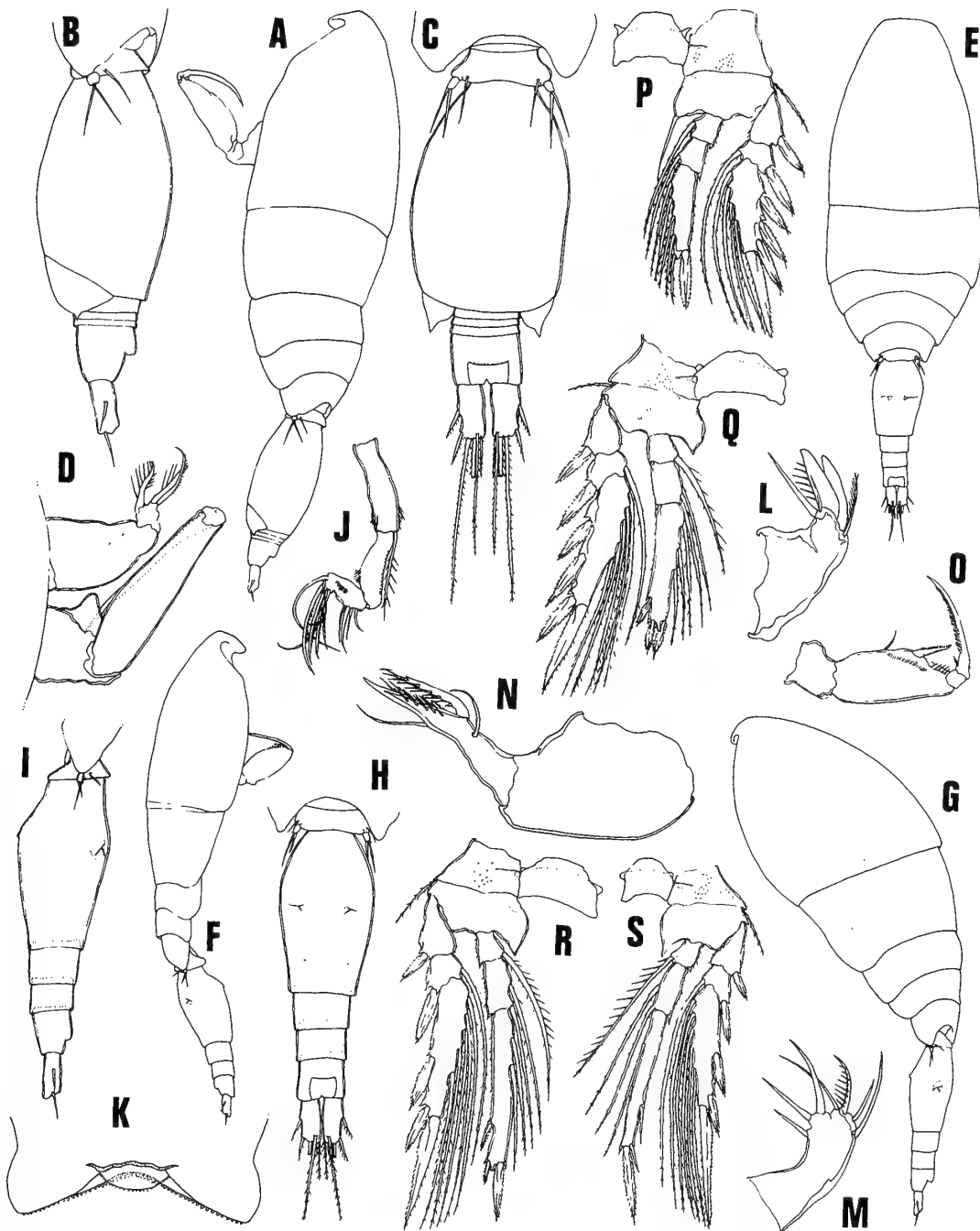


Fig. 19. *Oncaea macilentata*. Male: A, lateral (scale w); B, pediger 4 posterior corner, urosome, lateral (x); C, pediger 4 posterior corner, urosome, dorsal (x); D, second maxilla, maxilliped, lateral (in situ) (x). *Oncaea glabra*, new species. Female: E, dorsal (w); F, lateral (w); G, lateral, abnormally expanded prosome (w); H, pediger 4 posterior corner, urosome, dorsal (x); I, pediger 4 posterior corner, urosome, lateral (x); J, second antenna, left (x); K, labrum (y); L, mandible, left (y); M, first maxilla, left (y); N, second maxilla, right (y); O, maxilliped, right (x); P, leg 1 (x); Q, leg 2 (x); R, leg 3 (x); S, leg 4 (x).

opore, bearing a spiniform setule, located midway on segment. Caudal ramus length approximately equal to that of anal segment and half the length of dorsal seta (inner and outer long terminal setae missing on specimens examined).

Rostral area with thickened rounded margin. First antenna and second antenna (Fig. 19J) with armament similar in number to that of *O. canadensis*. Labrum (Fig. 19K) simple, lacking external ornamentation; posterior free margin divided into 2 posteroventral lobes, outlined with a continuous row of small denticles on undersurface; lobes separated by obtuse, shallow, semi-circular vertex, supported by a narrow sclerotized band, from which extends a thin, short lamella with a border of small denticles. Mandible (Fig. 19L) with armament similar to that of *O. rimula*. First maxilla (Fig. 19M) and second maxilla (Fig. 19N) with armament similar in number to that of *O. canadensis*: second maxilla with outer seta on second segment extending beyond terminal tip of claw. Maxilliped (Fig. 19O) similar to that of *O. rimula*.

Legs 1–4 (Fig. 19P–S) with armament similar in number to that of *O. canadensis*; endopods of legs 2 and 3 with a small terminal cone, leg 4 without. Leg 5 (see Fig. 19E–G) with free segment small; 2 subequal terminal setae and outer basal seta. Leg 6 represented by spiniform setule on gonopore.

Male.—Mean lengths of 4 specimens: TL 0.47 mm (0.46–0.48 mm), PL 0.33 mm (0.33 mm). Body (Fig. 20A–B) with ratio of length of prosome to that of urosome 2.0: 1. Genital segment slender, in dorsal and lateral views (Fig. 20C–D). (Caudal ramus with inner and outer long terminal setae missing on specimens examined.)

Maxilliped (Fig. 20E) second segment elongate with rows of spatulate setules on inner surface, and a seta replacing the spinulose spine. Swimming legs and leg 5 as in female. Leg 6 represented by posterolateral point-tipped flap on ventral surface of genital segment.

Etymology.—The specific name, from Latin (*glaber* = bald, smooth), refers to the unornamented exterior surface of the labrum.

Remarks.—*Oncaea glabra* closely resembles *O. rimula* in many characters, including the delicate, fragile exoskeleton and setae which contrast with the prominent, dentate flange of the swimming legs. *Oncaea glabra* may be separated by distinct differences: form of posterior lobes of the labrum and the short lamella between the lobes; female genital segment width at the level of the gonopore measuring more than half that of the length; tip of the longer, outer seta of leg 5 reaching to about half of the distance to the gonopore; caudal ramus length about equal to that of anal segment. In addition to *O. rimula*, *O. glabra* also closely resembles *O. lacinia*. Separation of these similar species is noted under *O. rimula*, new species (*Remarks*).

Oncaea lacinia Heron et al., 1984

Figs. 2I, 20F

Oncaea lacinia Heron et al., 1984:476, 478, figs. 14F–O, 15A–G.—Heron & Bradford-Grieve 1995:43, 44, fig. 23, 26b.

Material examined.—See Table 3.

Female.—Mean lengths of 10 specimens: TL 0.44 mm (0.42–0.47 mm), PL 0.30 mm (0.29–0.34 mm).

Male.—Mean lengths of 7 specimens: TL 0.37 mm (0.36–0.38 mm), PL 0.24 mm (0.23–0.25 mm).

Remarks.—*Oncaea lacinia* superficially resembles *O. rimula* and *O. glabra* but specific differences may be discerned with careful examination, noted under *O. rimula*, new species (*Remarks*). *Oncaea lacinia* specimens are usually of a smaller size than those of the other two species; the caudal ramus is slightly longer than the anal segment (Fig. 20F); the width of the female genital segment at the level of the gonopore is close to half that of the length; the length of the shorter terminal seta of leg 5 is half or less than that of the outer seta; the tip of

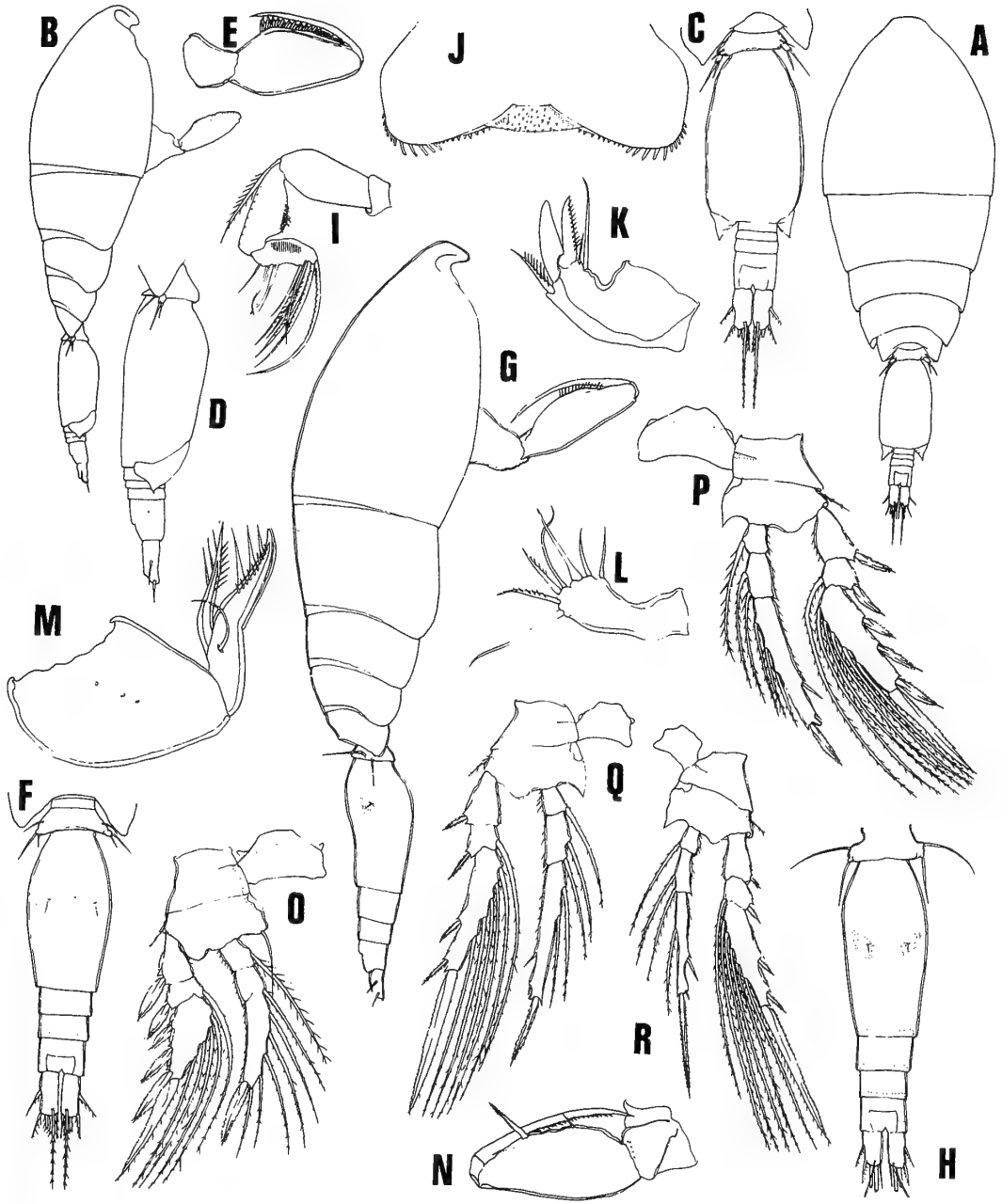


Fig. 20. *Oncaea glabra*, new species. Male: A, dorsal (scale t); B, lateral (t); C, pediger 4 posterior corner, urosome, dorsal (x); D, pediger 4 posterior corner, urosome, lateral (x); E, maxilliped, right (x). *Oncaea lacinia*. Female: F, pediger 4 posterior corner, urosome, dorsal (x). *Oncaea ovalis*. Female: G, lateral (s); H, urosome, dorsal (x); I, second antenna, right (z); J, labrum (y); K, mandible, right (y); L, first maxilla, left (y); M, second maxilla, left (y); N, maxilliped, right (x); O, leg 1 (x); P, leg 2 (x); Q, leg 3 (x); R, leg 4 (x).

the longer, outer leg 5 seta reaches to about one-third of the distance to the gonopore.

Oncaea ovalis Shmeleva, 1966

Figs. 2J, 20G–R, 21A

Oncaea ovalis Shmeleva, 1966:935, fig. 4.—1969:11–13, figs. 8a–i, 9a–i.—Malt et al., 1989:959, 960–962, figs. 5I, 6.

Material examined. See Table 3. Reference specimens: USNM 243747 (2 females, 1 male): Hoh Dabob Bay, 25 Apr 1985, 180–0 m.

Female.—Mean length of 7 specimens TL 0.47 mm (0.41–0.51 mm), PL 0.32 mm (0.26–0.35 mm). Exoskeleton thinly sclerotized. Ratio of length of prosome to that of urosome 1.9:1 (Fig. 20G). Ratio of length of genital segment to that of remainder of urosome 1.24:1 (Fig. 20H). (Caudal ramus with inner and outer long terminal setae missing on specimens examined.)

First antenna and second antenna (Fig. 20I) with armament similar in number to that of *O. canadensis*. Labrum (Fig. 20J) with free margin divided into 2 posteroventral lobes; each margin with row of alternating dentiform spinules and spatulate setules, all on undersurface; lobes separated by a median thin, hyaline lamella, sparsely covered with petaloid setules. Mandible (Fig. 20K), first maxilla (Fig. 20L), second maxilla (Fig. 20M), and maxilliped (Fig. 20N) with armament similar in number to that of *O. canadensis*.

Legs 1–4 (Fig. 20O–R) with armament similar in number to that of *O. canadensis*; legs 2 and 3 endopods terminating with a small vented protuberance between terminal and subterminal spines, leg 4 without. Leg 5 (see Fig. 20G–H) as a small papilla, not delimited from thoracic segment, with 1 terminal seta and an outer long basal seta. Leg 6 represented by spiniform setule on gonopore.

Male.—Length of 1 specimen: TL 0.41 mm, PL 0.27 mm. Ratio of length of prosome to that of urosome 2.22:1 (Fig. 21A). Exoskeleton thinly sclerotized. Cephalo-

some with 2 lateral clusters of small refractile points associated with pores. (Caudal ramus with inner and outer long terminal setae missing on specimen examined.) Maxilliped of the 1 undissected male appears to differ only slightly from that of the female with the second segment bearing a simple seta in place of the spine; terminal claw long and narrowly tapered in both sexes. Swimming legs and leg 5 as in female. Leg 6 represented by rounded flap on ventral surface of genital segment.

Remarks.—Shmeleva described the male of *O. ovalis* (0.31 mm) in 1966 and the female (0.42 mm) in 1969, both from the Adriatic Sea.

Oncaea ornata Giesbrecht, 1891

Figs. 2K, 21B–C

Oncaea ornata Giesbrecht, 1891:477.—1892:591, 593, 600–602, 604–606, pl. 44, figs. 50, 51, pl. 47, figs. 20, 24, 49, 53.—Boxshall 1977:135–138, figs. 17a, c, e–h, 18a–d, f.—Malt 1983a:4, 5, 8, 9, fig. 16.—1983b:449–451, 454, figs. 1A–M, 2A–D, 3A.

Material examined.—See Table 3. Reference specimens: USNM 243746 (2 females, 2 males): Oshawa 6–12, 22 Oct 1964, 4200–0 m.

Female.—Mean lengths of 15 specimens: TL 0.94 mm (0.86–1.01 mm), PL 0.66 mm (0.60–0.70 mm).

Male.—Mean lengths of 13 specimens: TL 0.79 mm (0.77–0.81 mm), PL 0.55 mm (0.52–0.64 mm).

Remarks.—*Oncaea ornata* may be recognized by the distinctive characters of the urosome for both sexes including the ratio of the length of the genital segment to that of remainder of urosome: female 2.15:1 (Fig. 21B); male 2.8:1 (Fig. 21C). There were only two instances in the northeast Pacific samples where *O. ornata* occurred without the co-occurrence of *O. englishi* Heron, 1977, which it closely resembles.

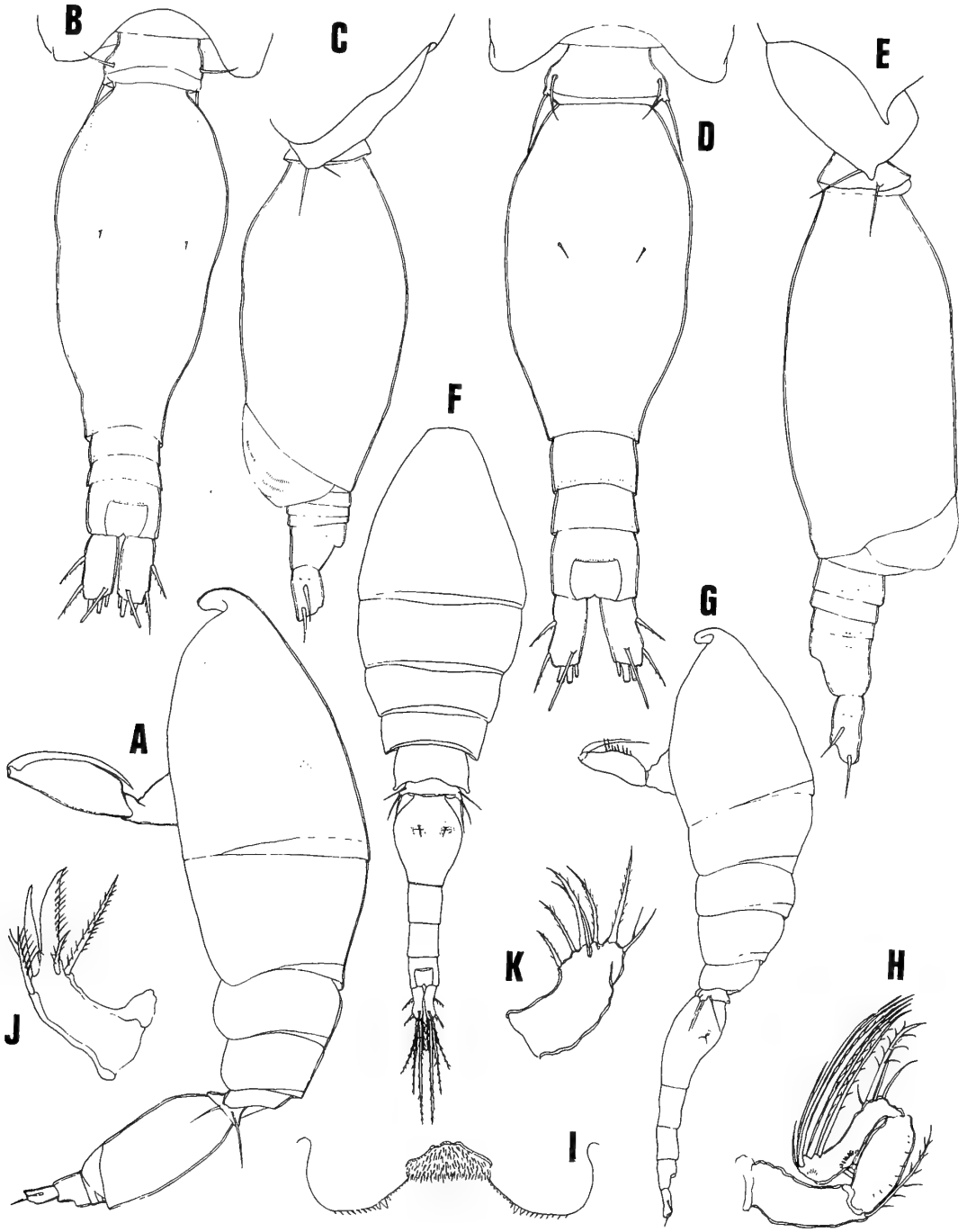


Fig. 21. *Oncaea ovalis*. Male: A, lateral (scale x). *Oncaea ornata*. Female: B, pediger 4 posterior corner, urosome, dorsal (x). Male: C, pediger 3 posterior corner, pediger 4, urosome, lateral (x). *Oncaea englishi*. Female: D, pediger 4 posterior corner, urosome, dorsal (x). Male: E, pediger 3 posterior corner, pediger 4, urosome, lateral (x). *Oncaea subtilis*. Female: F, dorsal (w); G, lateral (w); H, second antenna, right (z); I, labrum (y); J, mandible, right (y); K, first maxilla, left (y).

Oncaea englishi Heron, 1977
Figs. 2L, 21D–E

Oncaea englishi Heron, 1977:79, 82, figs. 25n, o, 26, 27.—Malt 1983a: 4, 5, 8, 9, fig. 17.—1983b:449–451, 454, figs. 1N–W, 2E, F, 3B, C.—Heron, et al., 1984: 478, 479.—Heron & Bradford-Grieve 1995:44, 45, fig. 24a–e, 25d.

Oncaea ornata “Form 2”.—Boxshall 1977:135, 137, 138, figs. 17b, d, i, 18e.

Material examined.—See Table 3.

Female.—Mean lengths of 15 specimens: TL 0.92 mm (0.85–1.04 mm), PL 0.62 mm (0.59–0.74 mm).

Male.—Mean lengths of 15 specimens: TL 0.81 mm (0.76–0.85 mm), PL 0.54 mm (0.50–0.56 mm).

Remarks.—*Oncaea englishi* is a widespread, abundant species. The Sognefjorden sample, 1250–0 m, contained 12 females (0.81–0.89 mm) and 11 males (0.76–0.78 mm) of *O. englishi*. This copepod is one of the most common species in Sognefjorden, below a depth of 1000 m (A. Fosshagen, pers. comm.).

Oncaea englishi may be identified by noting distinguishing characters of the urosome for both sexes, including the ratio of the length of the genital segment to that of the remainder of the urosome: female 1.4:1 (Fig. 21D); male 1.92:1 (Fig. 21E). It closely resembles *O. ornata*, but may be separated by comparing the differences in the relative lengths of the urosome segments as shown in Fig. 21B–E.

Oncaea subtilis Giesbrecht, 1892
Figs. 2M, 21F–K, 22

Oncaea subtilis Giesbrecht, 1892: 591, 596, 598, 599, 601–603, 605, pl. 47, figs. 14, 18, 25, 43, 60.—Gallo 1976:275–280, fig. 1A–I.—Malt 1982b: 134–141, figs. 6–9.—1983a:4, 5, 7, 9, fig. 12.

Material examined.—See Table 3. Reference specimens: USNM 243760 (10 females, 10 males): Hoh Dabob Bay, 24 Jun 1985, 180–0 m.

Female.—Mean length of 15 specimens: TL 0.57 mm (0.52–0.63 mm), PL 0.35 mm (0.32–0.39 mm). Ratio of length of prosome to that of urosome 1.53:1 (Fig. 21F–G). Exoskeleton thinly sclerotized; most setae fragile.

Rostral area with thickened, rounded margin. First antenna and second antenna (Fig. 21H) with armament similar in number to that of *O. canadensis*. Labrum (Fig. 21I) posteriorly protuberant; free margin divided into 2 rounded posteroventral lobes, each margin with row of short setules, 3 sclerotized teeth, and small denticles; lobes separated by vertex from which arises a thin lamella covered with setules. Mandible (Fig. 21J), first maxilla (Fig. 21K), second maxilla (Fig. 22A), and maxilliped (Fig. 22B) with armament similar in number to that of *O. canadensis*.

Legs 1–4 (Fig. 22C–F) with armament of exopods similar in number to that of *O. canadensis*; endopods of legs 2 and 3 with a small terminal vented protuberance, leg 4 without; endopods of legs 2–4 with 1 terminal spine and 1 short subterminal spine. Leg 5 (Fig. 22G) small, not delimited from thoracic segment; 2 terminal and an outer basal setae. Leg 6 (see Fig. 21G) represented by spiniform setule on gonopore.

Male.—Mean lengths of 15 specimens: TL 0.42 mm (0.39–0.46 mm), PL 0.26 mm (0.24–0.29 mm). Ratio of length of prosome to that of urosome 1.79:1 (Fig. 22H–I). Maxilliped (Fig. 22J) second segment with 2 setae within inner longitudinal cleft and 3 rows of setules; claw with narrow element near inner base. Swimming legs and leg 5 (see Fig. 22H–I) similar to those of female. Leg 6 represented by posteroventral flap on ventral surface of genital segment with pointed posterior corner protruding in dorsal view.

Remarks.—*Oncaea subtilis* third endopodal segment of swimming legs 2–4, with two rather than three terminal spines, is similar to the formula for *O. ornata* and *O. englishi*.

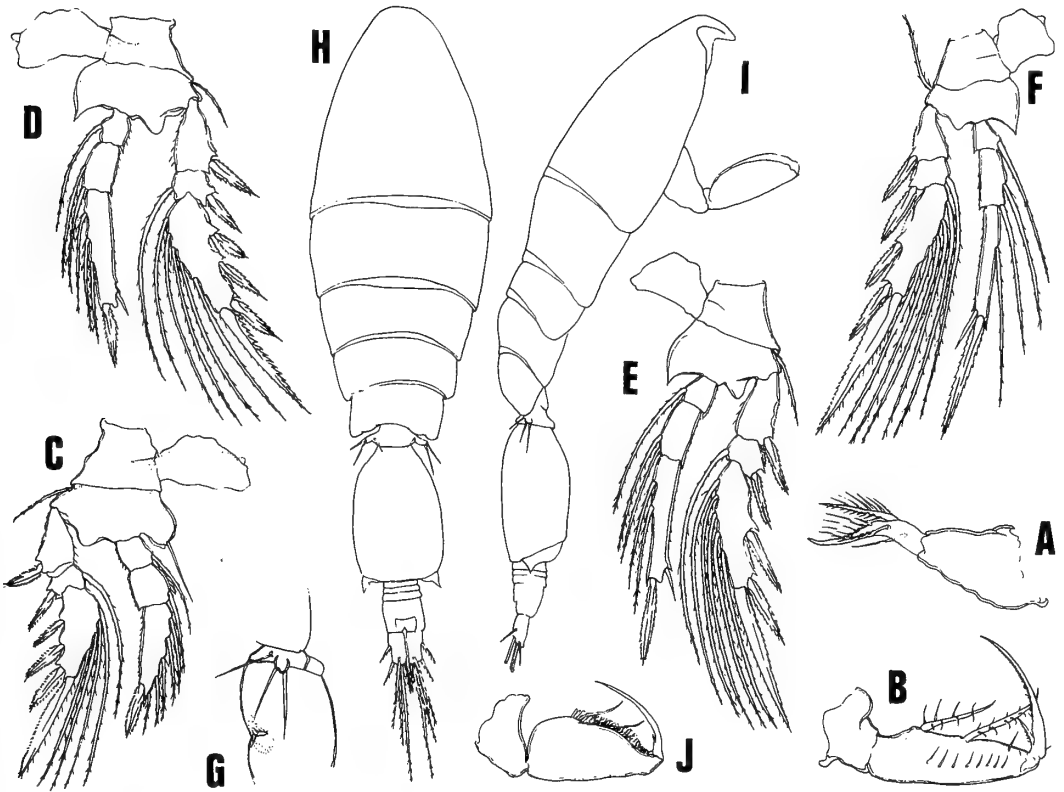


Fig. 22. *Oncaea subtilis*. Female: A, second maxilla, left (scale z); B, maxilliped, right (x); C, leg 1 (x); D, leg 2 (x); E, leg 3 (x); F, leg 4 (x); G, pediger 4 posterior corner and segment of leg 5 (x). Male: H, dorsal (s); I, lateral (s); J, maxilliped, right (x).

Key to species of *Oncaea* in northeast Pacific and inland Washington waters

- 1a. Leg 4 endopod with a conical protuberance (cone) between terminal and subterminal spines 2
- 1b. Leg 4 endopod without cone between terminal and subterminal spines 8
- 2a. Legs 2 and 3 endopods with lateral spines extending to or beyond bases of subterminal spines 3
- 2b. Legs 2 and 3 endopod spines with lateral spines not extending to base of subterminal spines (Fig. 1G) *O. insolita*
- 3a. Leg 4 endopod with lateral spine extending just to subterminal spine base (Fig. 1A) *O. canadensis*
- 3b. Leg 4 endopod with lateral spine extending beyond subterminal spine base 4
- 4a. Leg 2 endopod terminal spine length

- reaching about as far as distal margin of cone (Fig. 1B) *O. thoresoni*
- 4b. Leg 2 endopod terminal spine length extending beyond distal margin of cone 5
- 5a. Legs 2 and 3 endopods with lateral spines extending only to base of subterminal spines; leg 4 endopod subterminal spine barely extending beyond distal margin of cone (Fig. 1C) *O. derivata*
- 5b. Legs 2 and 3 endopods with lateral spines extending beyond base of subterminal spines; leg 4 endopod subterminal spine is twice or more the length of the cone 6
- 6a. Leg 4 endopod with subterminal and lateral spine lengths both about half that of terminal spine (Fig. 1E) *O. borealis*

- 6b. Leg 4 endopod with subterminal and lateral spine lengths greater or less than half that of terminal spine 6
- 7a. Leg 2 endopod with subterminal spine lengths about equal, both shorter than lateral spine (Fig. 1D) *O. redacta*
- 7b. Leg 2 endopod with subterminal and lateral spine lengths about equal 8
- 8a. Leg 4 with terminal spine less than twice the length of subterminal spine (Fig. 1F) *O. similis*
- 8b. Leg 4 with terminal spine twice or more of the length of subterminal spine 16
- 9a. Legs 2-4 third endopod with two spines 10
- 9b. Legs 2-4 third endopod with three spines 12
- 10a. Leg 3 endopod with terminal spine shorter than length of segment, leg 4 endopod with subterminal spine about one-third the length of terminal spine (Fig. 2M) *O. subtilis*
- 10b. Leg 3 endopod with terminal spine as long or longer than length of segment; leg 4 endopod with subterminal spine less than one-third the length of terminal spine 11
- 11a. Leg 2 endopod terminal spine length about twice that of subterminal spine; leg 4 endopod segment about three-fifths the length of terminal spine and more than two times that of subterminal spine (Fig. 2K) *O. ornata*
- 11b. Leg 2 endopod with terminal spine length more than three times that of subterminal spine; leg 4 endopod segment length about two-thirds that of terminal spine and about twice that of subterminal spine (Fig. 2L) *O. englishi*
- 12a. Mandible middle bladeliike element with inner row of setules (Fig. 20K) 13
- 12b. Mandible middle bladeliike element with inner dentiform margin 14
- 13a. Leg 5 with one terminal seta and one basal seta (Fig. 20G) *O. ovalis*
- 13b. Leg 5 with two terminal setae and one basal seta 15
- 14a. Leg 3 endopod with lateral spine not extending as far as base of subterminal spine (Fig. 1H) *O. illgi*
- 14b. Leg 3 endopod with lateral spine extending beyond base of subterminal spine (Fig. 1J) *O. brochia*
- 15a. Leg 2 endopod with subterminal spine extending to less than half the length of terminal spine (Fig. 2I) *O. lacinia*
- 15b. Leg 2 endopod with subterminal spine extending to about same length as that of terminal spine (Fig. 2H) *O. glabra*
- 16a. Caudal ramus with usual lateral anterior short seta located on middorsal surface (Fig. 13C) *O. rotata*
- 16b. Caudal ramus with anterior short seta located in lateral position 17
- 17a. Legs 2 and 3 endopods with length of cones about equal to distance between lateral and subterminal spine insertions (Fig. 2A) *O. olsoni*
- 17b. Legs 2 and 3 endopods with length of cones shorter than distance between lateral and subterminal spine insertions 18
- 18a. Legs 3 and 4 endopods with subterminal spines extending to about midway of terminal spines (Fig. 2B) *O. damkaeri*
- 18b. Legs 3 and 4 endopods without both subterminal spines extending to about midway of terminal spines 19
- 19a. Leg 4 endopod with subterminal spine half the length of terminal spine and lateral spine longer than leg 3 terminal spine (Fig. 2C) *O. parila*
- 19b. Leg 4 endopod with subterminal spine less than half the length of terminal spine and lateral spine shorter than leg 3 terminal spine 20
- 20a. Leg 3 endopod with lateral spine extending about as distal margin of cone (Fig. 2D) *O. prolata*
- 20b. Leg 3 endopod with lateral spine not extending as far as distal margin of cone 21
- 21a. Leg 2 with lateral spine extending beyond distal margin of cone (Fig. 2E) *O. grossa*
- 21b. Leg 2 with lateral spine not extending to base of cone 22
- 22a. Legs 2 and 3 endopod with lateral spine extending to base of subterminal spine (Fig. 2F) *O. rimula*
- 22b. Legs 2 and 3 endopod with lateral spine extending about half as far as

base of subterminal spine (Fig. 2G)
 *O. macilenta*

Genus *Epicalymma* Heron, 1977

Epicalymma schmitti Heron, 1977

Epicalymma schmitti Heron, 1977:82, 84, figs. 28, 29a-e.—Heron et al., 1984: 488.

Oncaea schmitti.—Malt 1982b:190, 191, fig. 11a-d.

Material examined.—See Table 3.

Female.—Mean lengths of 20 specimens: TL 0.59 mm (0.56–0.61 mm), PL 0.39 mm (0.36–0.41 mm).

Male.—Mean lengths of 4 specimens: TL 0.54 mm (0.52–0.56 mm), PL 0.36 mm (0.34–0.37 mm).

Epicalymma umbonata Heron, 1977
 Fig. 23A–E

Epicalymma umbonata Heron, 1977:84, 86, figs. 29f–p, 30a–c (female).—Heron et al., 1984:489.

Oncaea umbonata.—Malt 1982b:191, 193, fig. 11e–h.

Material examined.—See Table 3.

Female.—Mean lengths of 4 specimens: TL 0.70 mm (0.65–0.72 mm), PL 0.47 mm (0.44–0.48 m).

Male.—The male of *E. umbonata* is described for the first time. Lengths of 2 specimens: TL 0.64, 0.67 mm, PL 0.41, 0.44 mm. Body (Fig. 23A, B) with comparatively compact appearance, similar to that of female; ratio of length of prosome to that of urosome 1.77:1. Exoskeleton thinly sclerotized. Genital segment (Fig. 23C) with robust appearance in lateral and dorsal view; caudal ramus with conspicuous expansion on dorsal surface surrounding base of dorsal seta; dorsal seta almost as long as outer long terminal seta; all caudal setae long and resilient.

Rostral area with thickened triangular posteroventral margin. Maxilliped (Fig. 23D) second segment with anterior row of setules; inner longitudinal cleft with 2 setae

and posterior rim with 3 rows of setules; terminal claw with narrow element near inner base and short, fine setules on concave surface. Swimming legs and leg 5 as in female, except leg 1: endopod of leg 1 with modification of terminal spine and seta (Fig. 23E). Leg 6 (see Fig. 23C) represented by posterolateral flap on ventral surface of genital segment, pointed corner protruding laterally in dorsal view.

Remarks.—*Epicalymma umbonata* males are longer than the other three described *Epicalymma* males, and the terminal seta of leg 5 differs by being shorter than the basal seta. The male genital segment posterolateral flap with a pointed corner on the ventral surface may be distinguished from the other three species which have rounded corners.

Epicalymma vervoorti Heron et al., 1984

Epicalymma vervoorti Heron et al., 1984: 483, 485, figs. 17C–I, 18, 19A, B.

Material examined.—See Table 3.

Female.—Lengths of 1 specimen: TL 0.48 mm, PL 0.33 mm.

Remarks.—The one female was also identified from the Sognefjorden, Norway sample, 6 Dec 1982, 800–500 m, loaned by Audun Fosshagen.

Epicalymma exigua (Farran, 1908)

Oncaea exigua Farran, 1908:93, 94, pl. 10, figs. 25–30; pl. 11, figs. 9–11 (female).—Razouls 1974:241, fig. 15.—Gordejeva 1975b:778, figs. 21–27.

Epicalymma exigua (Farran, 1908).—Heron et al., 1984:485, 488, figs. 19C–J, 20.

Material examined.—See Table 3.

Female.—Mean lengths of 6 specimens: TL 0.45 mm (0.43–0.48 mm), PL 0.30 mm (0.29–0.33 mm).

Male.—Mean lengths of 3 specimens: TL 0.40 mm (0.39–0.41 mm), PL 0.26 mm (0.25–0.27 mm).

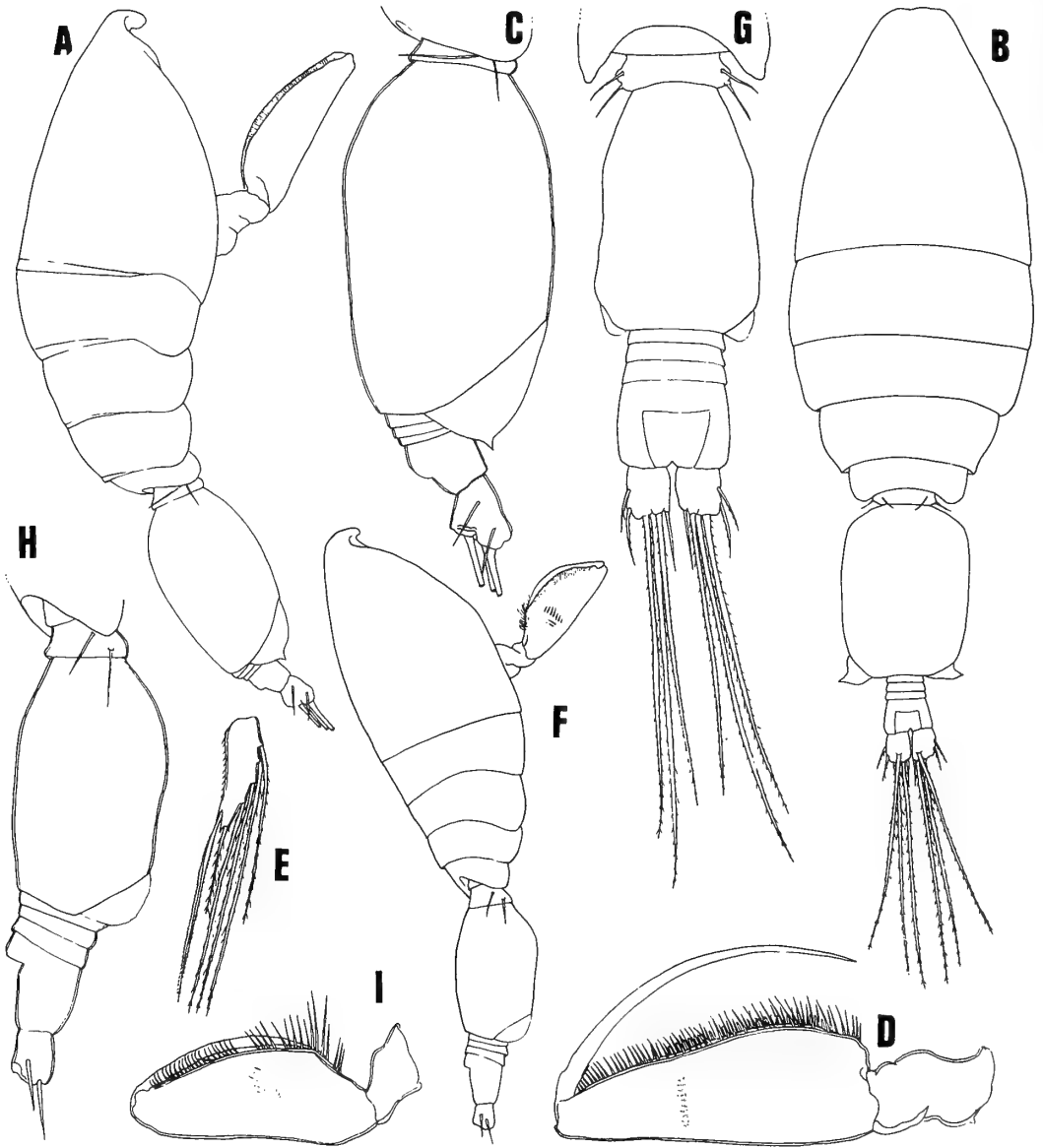


Fig. 23. *Epicalymma umbonata*. Male: A, lateral (scale w); B, dorsal (w); C, pediger 4 posterior corner, urosome, lateral (x); D, maxilliped, right, posterior (x); E, leg 1, third endopod segment (x). *Conaea hispida*. Male: F, lateral (w); G, pediger 4 posterior corner, urosome, dorsal (x); H, pediger 4 posterior corner, urosome, lateral (x); I, maxilliped, right, posterior (x).

Key to species of *Epicalymma* females in northeast Pacific and inland Washington waters

- 1a. Genital segment with gonopore located approximately at midregion of dorsal surface *E. umbonata*
- 1b. Genital segment with gonopore located on anterior third of dorsal surface ... 2
- 2a. Anal segment with operculum margin basically straight 3
- 2b. Anal segment with operculum margin medially distended *E. exigua*
- 3a. Urosome, lateral view, with caudal ra-

mus width as wide at midpoint as that of anal segment (posterior to operculum) *E. schmitti*

- 3b. Urosome, lateral view, with caudal ramus width less than that of anal segment *E. vervoorti*

Key to species of *Epicalymma* males in northeast Pacific and inland Washington waters

- 1a. Anal segment with operculum margin straight 2
 1b. Anal segment with operculum margin medially distended *E. exigua*
 2a. Pediger 4 posterior corner rounded 3
 2b. Pediger 4 posterior corner squared and leg 5 distal seta longer than basal seta *E. vervoorti*
 3a. Leg 5 terminal seta length about same as that of basal seta *E. schmitti*
 3b. Leg 5 terminal seta length shorter than that of basal seta *E. umbonata*

Genus *Conaea* Giesbrecht, 1891

Conaea rapax Giesbrecht, 1891

Conaea rapax Giesbrecht, 1891:477.—1892:82, 605, pl. 48, figs. 50–59.—Heron 1977:86, 88, 90, figs. 30d–j, 31, 32a–d.—Heron & Bradford-Grieve 1995:45, 46, figs. 24f–i, 27c.

Oncaea gracilis (Dana).—Scott 1894:116, pl. 13, figs. 4–12.—Malt 1983a:4, 5, 7, 9, fig. 14.

Conaea gracilis (Dana).—Wilson 1950:191, pl. 5, figs. 36–46 (illustrated and identified as *C. rapax* by G. O. Sars).—Boxshall 1977:145–148, figs. 22, 23.

Material examined.—See Table 3.

Female.—Mean lengths of 12 specimens: TL 1.02 mm (0.97–1.14 mm), PL 0.63 mm (0.60–0.67 mm).

Male.—Mean lengths of 8 specimens: TL 0.92 mm (0.87–1.00 mm), PL 0.59 mm (0.56–0.63 mm).

Conaea succurva Heron, 1977

Conaea succurva Heron, 1977:90, figs. 32e–k, 33a–g.

Material examined.—See Table 3.

Female.—Mean lengths of 3 specimens: TL 0.71 mm (0.70–0.72), PL 0.47 mm (0.45–0.48 mm).

Conaea hispida Heron, 1977

Fig. 23F–I

Conaea hispida Heron, 1977:90, 95, figs. 33h–j, 34.

Oncaea hispida.—Malt 1982a:187, 188, 192, 193, figs. 5, 6.

Material examined.—See Table 3. Reference specimens: USNM 243741 (2 females, 1 male): *Brown Bear* 357–22, 22 Apr 1965, 4000–0 m.

Female.—Mean lengths of 8 specimens: TL 0.60 mm (0.56–0.63 mm), PL 0.40 mm (0.37–0.44 mm).

Male.—The male of *C. hispida* is described for the first time. The single male found was not dissected, except for the right maxilliped. Body with ratio of length of prosome to that of urosome 1.54:1 (Fig. 23F). Lengths of the 1 specimen: TL 0.56 mm, PL 0.37 mm. Exoskeleton thinly sclerotized. Genital segment with slight constriction of lateral margins at midregion, dorsal view (Fig. 23G), similar to that of female. Caudal ramus with slight expansion on dorsal surface surrounding base of dorsal seta (Fig. 23H); dorsal seta nearly as long as outer long terminal seta; all caudal setae long and resilient.

Rostral area with thickened, rounded posterior margin. Maxilliped (Fig. 23I) second segment elongate with anterior setules; inner longitudinal cleft with 2 setae; posterior rim with rows of setules, proximally long. Swimming legs and leg 5 appear to be as in female. Leg 6 represented by posterolateral rounded flap on ventral surface of genital segment.

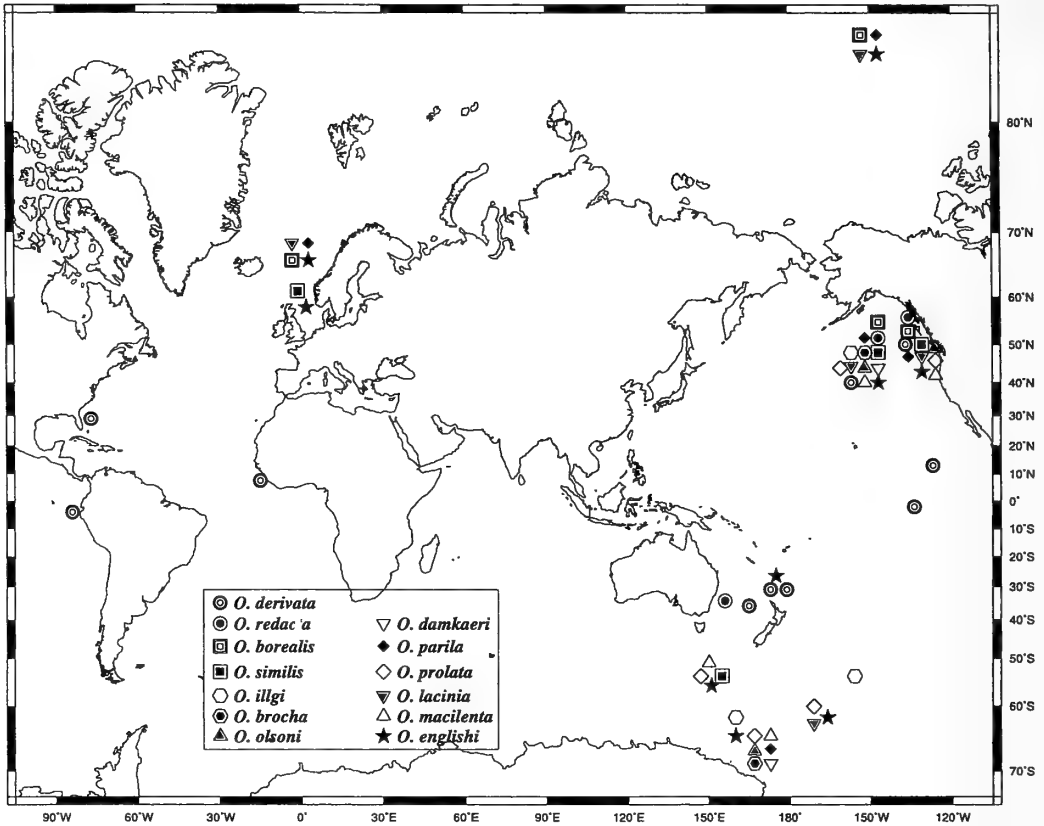


Fig. 24. Locality records for selected species of *Oncaea*. Records include previously published personal observations and data presented in this study (Table 3).

Key to species of *Conaeca* in northeast Pacific and inland Washington waters

- 1a. Leg 2 with third endopod bearing three setae and one spine *C. rapax*
- 1b. Leg 2 with third endopod bearing three setae and two spines 2
- 2a. Leg 2 with outer spine of third endopod approximately one-third the length of inner spine *C. succurva*
- 2b. Leg 2 with outer spine of third endopod approximately half the length of inner spine *C. hispida*

Discussion

Two significant patterns in our results are noteworthy. First, while the seven new species of *Oncaea* described here were found only in our samples from the eastern

Pacific, many of the previously described species that were also collected have much more extensive geographical distributions, occurring in both the northern and southern hemispheres (Table 3, Figs. 24 and 25). In particular, the five most widely distributed species, *O. parila*, *O. englishi*, *O. lacinia*, *Epicalymma umbonata*, and *E. exigua*, occur in polar and subpolar regions of both hemispheres. Bipolar or subpolar amphitropical distributions are well known in planktonic protozoans (e.g., foraminiferans: Bé & Tolderlund 1971; tintinnid ciliates: Pierce & Turner 1993, fig. 18), but not among planktonic metazoa. One of the few remaining cases of a putative bipolar or subpolar amphitropical species of epipelagic crustacean zooplankton was, upon closer scrutiny, ascribed to different spe-

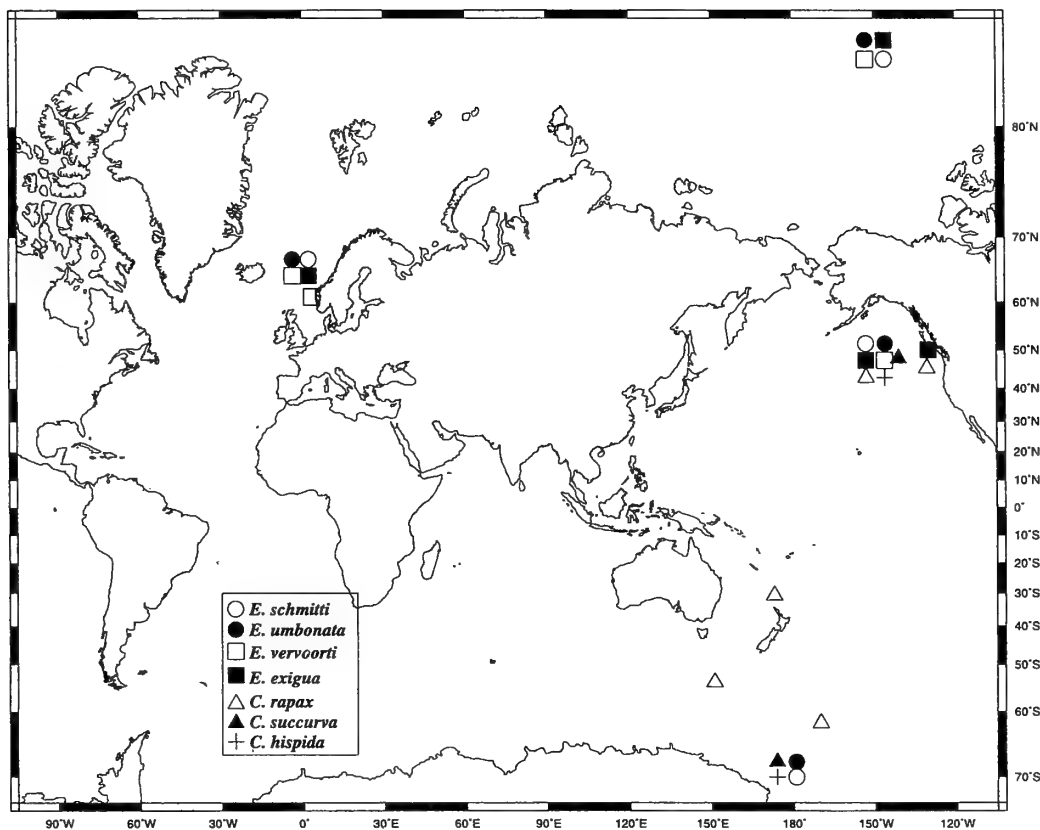


Fig. 25. Locality records for species of *Epicalymma* and *Conaea*. Records include previously published personal observations and data presented in this study (Table 3).

cies in the two hemispheres based on morphological and electrophoretic analyses (e.g., Schneppenheim & Weigmann-Haass 1986).

Second, we found no evidence of morphological divergence between any of the geographically widely separated, apparently disjunct, species of Oncaeidae that occur in the northern and southern polar and sub-polar regions and even in different oceans. Thus our morphological evidence suggests that populations in different ocean basins either share a common gene pool or have not diverged genetically if indeed their distributions are disjunct today. With the advent of DNA sequencing, this is a testable hypothesis.

Possibly the extensive geographical rang-

es of many oncaeid species reflects their broad depth ranges, often extending into the meso- to bathypelagic zones (Heron 1977, Heron et al. 1984, Heron & Bradford-Grieve 1995; fig. 28; Böttger-Schnack 1996, table IV). Such species tend to have much wider latitudinal ranges than oceanic epipelagic species, perhaps by "isothermic submergence" through the subtropical and tropical regions (Briggs 1974, Pierrot-Bults & Nair 1991). It should be noted that the ranges depicted in Figs. 24 and 25 are conservative, being based only on our limited previous observations. We expect that careful analysis of deep samples from subtropical and tropical latitudes will reveal occurrences of many of the polar and subpolar species treated here.

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***Brachycalanus flemingeri* and *B. brodskyi*, two new copepods
(Crustacea: Calanoida: Phaennidae) from benthopelagic waters of
the tropical Pacific**

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Abstract.—*Brachycalanus flemingeri*, new species, has three setae on coxal endite of maxilla 1, a bifurcate worm-like sensory seta on the exopod of maxilla 2, a distal, semicircular protrusion posteriorly on the basis of swimming leg 1, and lacks a medial seta on coxa of swimming leg 4. *Brachycalanus brodskyi*, new species, is differentiated by its large size, 4.0 mm, and a semi-circular row of small denticles distally and posteriorly on the basis of swimming leg 1. *Brachycalanus ordinarius* (Grice, 1972) is redescribed and separated from the remaining species by the exopod of maxilla 2 with a distally constricted worm-like seta with a small lobe near the point of constriction. All three species have nine sensory setae on the distal basal lobe plus exopod of maxilla 2; this number of sensory setae has been reported for one other phaenid copepod and several scolecitrichids. Suggested shared derived character states for the species of *Brachycalanus* Farran, 1905 are epicuticular extensions of the female genital complex and the following two abdominal somites, and knife-like aesthetascs on female antenna 1.

The genus *Brachycalanus* Farran, 1905 includes four species: *B. atlanticus* (Wolfenden, 1904), *B. bjornbergae* Campaner, 1978; *B. ordinarius* (Grice, 1972) and *B. rothlisbergi* Othman & Greenwood, 1988 although Othman & Greenwood (1988) suggested that specimens of *B. atlanticus* reported by Farran (1905) do not belong to the same species as the specimens of Wolfenden (1904). Different species have been reported from the North Atlantic Ocean (Wolfenden 1904, Farran 1905, Grice 1972), the South Atlantic Ocean (Campaner 1978) and the Gulf of Carpentaria in the western tropical Pacific Ocean (Othman & Greenwood 1988); only *B. atlanticus* has been reported more than once, by Wolfenden (1904) and Farran (1905). Specimens of *Brachycalanus* usually are collected from near-bottom localities at depths from 72–100 m (Campaner 1978) to 992–1000

m (Grice 1972). No adult males of a species of *Brachycalanus* have been collected. The two new *Brachycalanus* species described here are the first records of the genus from the eastern tropical Pacific Ocean. *Brachycalanus ordinarius* is redescribed, based a paratype.

Materials and Methods

The specimens from Hawaii collected on 6 July 1997 may have been in a plankton net for up to 12 hours prior to sample fixation with 4% formaldehyde; few internal tissues remain in these specimens. The specimen collected from Volcano 7 during November 1988 was fixed at its depth of capture with gluteraldehyde; most internal tissues remain. Ferrari & Markhaseva (1996, 2000), give further details about collections from Volcano 7 and Hawaii. In the

laboratory, specimens from both localities were preserved in 0.5% propylene phenoxylol/4.5% propylene glycol/95.0% deionized freshwater. During examination, specimens were cleared in steps through 50% lactic acid/50% deionized freshwater to 100% lactic acid, stained by adding a solution of chlorazol black E dissolved in 70% ethanol/30% deionized freshwater, and examined with bright-field and with differential interference optics. Drawings were made with a camera lucida. Dissected and undissected specimens are preserved in 70% ethanol/30% deionized freshwater.

Cephalic appendages are abbreviated A1 = antenna 1; A2 = antenna 2; Mn = mandible; Mx1 = maxilla 1; Mx2 = maxilla 2. Thoracic somites are Th1–7. Appendages on thoracic somites are Mxp = maxilliped (thoracopod 1); P1–5 = swimming legs 1–5 (thoracopods 2–6). The caudal ramus is CR. Measurements are lengths; the length of the whole animal is measured from the anterior edge of the cephalothorax to the posterior edge of the caudal ramus, and does not include the overlap onto the genital complex of the posterior edge of the sixth thoracic somite. Designations of appendage segments follow Ferrari (1995), Ferrari & Dahms (1998) and Ferrari & Markhaseva (2000). The coxa of the maxilliped of copepods has one lobe with a group of setae (Ferrari & Ambler 1992, Martínez Arbizu 1997); the remaining three groups of setae on the calanoid syncoxa belong to the praecoxa. Articulating armament elements of appendages are termed setae regardless of their morphology or degree of rigidity. Two setae and one aesthetasc on a segment of antenna 1 are designated 2+1; “?” indicates that a setal element was broken so that its identity on antenna 1 could not be determined and only the scar at the location of attachment of the seta was counted. Setules are epicuticular extensions of a seta; denticles are epicuticular extensions of an appendage segment; spinules are epicuticular extensions of a somite. An array of denticles whose tips point

toward the distal end of an appendage are distally polarized; an array arranged in a semicircle are radially polarized. Specimens remain deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

Brachycalanus flemingeri new species

Figs. 1–3

Specimens.—Holotype (USNM 307711) a dissected 2.41 mm female; prosome 2.02 mm, urosome 0.44. Paratypes: (USNM 307712) 4 mature females (2.01; 2.04, two specimens; 2.37 mm) and 3 males CV (2.01; 2.07; 2.07 mm) and 1 CIV female (1.65 mm). Type locality: eastern tropical Pacific Ocean, 19°43'27.01"N, 156°04'35.46"W, off Kona, Island of Hawaii, 6 Jul 1997.

CVI Female.—(Fig. 1A) Cephalon and Th1 fused; Th2–Th4 separate; Th5 and Th6 separated but not well articulated. Laterally, posterior corners of prosome triangular; dorsally, acutely triangular and almost reaching mid-length of genital complex (Fig. 1G). Th4 with 2 sensilla laterally; ventral longer; Th5 with 1 short dorsal sensilla laterally. Genital complex and following 2 abdominal somites (Fig. 1D, E, H) with small, scale-like spinules. Genital complex symmetrical.

Rostrum (Fig. 1B, C): subdivided plate with 2 filaments.

A1: reaching Th3 and of 24 articulating segments with groups of setae: 3?, 7?, 3?, 2?, 3?, 2?, 3?, 5?, 1, 1, 3?, 1, 3?, 1, 2?, 1, 2?, 2?, 1, 1, 2?, 2?, 2?, 5+1.

A2 (Fig. 2A): coxa with 1 seta and denticles. Basis with 2 setae. Ri 2-segmented with 2 and 14 (6 terminal and 8 subterminal) setae. Re 7 articulated segments with 0, 1, 1, 1, 1, 1, and 1+3 setae; 2nd segment with several small indentations on medial face and seta minute.

Mn: coxal gnathobase (Fig. 2C) somewhat elongate with 3 compound and 4 simple teeth and 1 seta. Basis with 3 setae (Fig. 2B). Re indistinctly segmented apparently

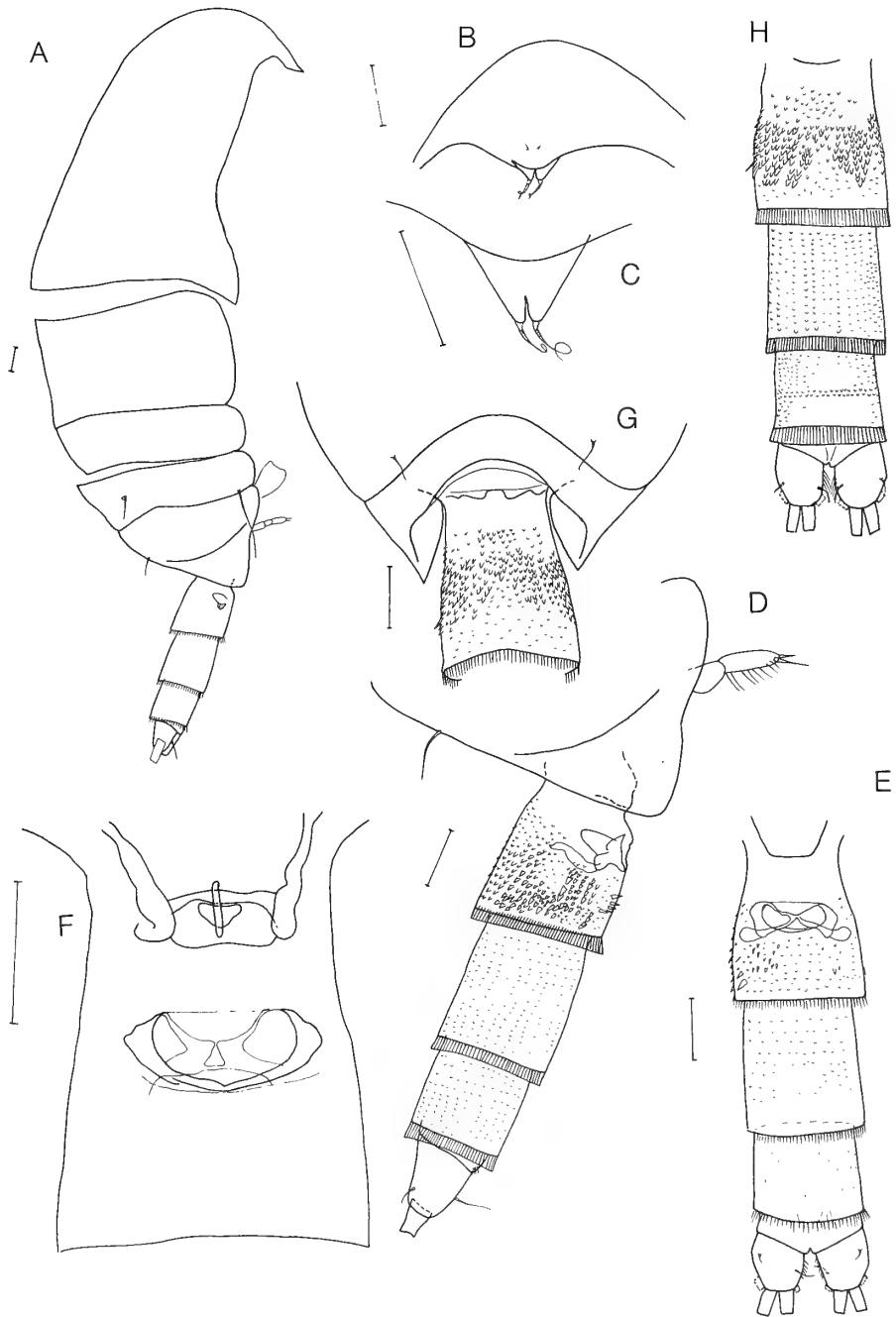


Fig. 1. *Brachycalanus flemingeri* new species. A, habitus, right lateral; B, anterior part of cephalon, ventral; C, rostrum, anterior-ventral; D, Th5-6 and urosome, right lateral; E, urosome, ventral; F, genital complex, ventral; G, posterior Th4, Th5-6 and genital complex, dorsal; H, urosome dorsal. Scale lines are 0.1 mm.

with 1, 1, 1, 1, 2 terminal setae; Ri 2-segmented with 2 and 9 setae.

Mx1: praecoxa elongate with 9 terminal, 1 anterior and 4 posterior setae (Fig. 2E); coxal epipodite with 1 thin, short seta and 8 long, thick setae; coxal endite with 3 setae; 1st and 2nd basal endites with 4 and 5 setae respectively (Fig. 2D). Ri with 11 setae (3+3+5); Re with 10 setae.

Mx2 (Fig. 2G): proximal praecoxal endite with 5 setae; distal with 3 setae, 1 poorly sclerotized. Proximal coxal endite with 1 short, poorly sclerotized sensory seta and 2 long well-sclerotized setae; distal coxal endite with 1 thick and 2 thin setae. Proximal basal endite with 1 long, thick seta, 1 long, thin seta and 2 poorly sclerotized sensory setae. Distal basal lobe + Re with 9 sensory setae; 7 brush-like setae with short setules and 2 worm-like setae, 1 of which is bifurcate toward its distal end.

Mxp (Fig. 2F): syncoxa with 1 worm-like seta on proximal lobe; 1 sclerotized and 1 worm-like sensory seta on middle lobe; 1 sclerotized and 1 brush-like sensory seta with short setules on distal lobe; coxal lobe with 3 setae and distal denticles. Basis with 3 setae on unattenuated proximal lobe and 2 setae on distal lobe; denticles proximally. Ri segments from proximal to distal with 4, 4, 3, 4 (1 lateral), 4 (1 lateral) setae respectively.

P1 (Fig. 3A, B): all segments with denticles, anteriorly and posteriorly. Coxa without seta. Basis with medial seta and distal semicircular protrusion on posterior face. Re 3-segmented, proximal with 1 lateral seta, middle with 1 medial and 1 lateral seta, distal with 3 medial, 1 terminal, 1 lateral setae; lateral seta on proximal segment reaches to base of lateral seta on middle segment and lateral seta on middle segment reaches to base of lateral seta on distal segment. Ri a 1-segmented complex with 3 medial and 2 terminal setae. Anterior face of Von Vaupel Klein's organ with well-developed triangular protuberance, anterior row of long denticles proximally and posterior pore.

P2 (Fig. 3C, D): all segments anteriorly and posteriorly with complex arrays of large and small denticles; arrays may be distally or radially polarized. Coxa with medial seta. Basis without seta. Re 3-segmented, proximal with 1 medial and 1 lateral seta, middle with 1 medial and 1 lateral seta, distal with 4 medial, 1 terminal, 3 lateral setae. Ri 2-segmented, proximal with 1 medial seta, distal with 2 medial, 2 terminal, 1 lateral setae.

P3 (Fig. 3E, F): all segments anteriorly and posteriorly with complex arrays of large and small denticles; arrays may be distally or radially polarized. Coxa with medial seta. Basis without seta. Re 3-segmented, proximal with 1 medial and 1 lateral seta, middle with 1 medial and 1 lateral seta, distal with 4 medial, 1 terminal, 3 lateral setae. Ri 3-segmented, proximal with 1 medial seta, middle with 1 medial seta, distal with 2 medial, 2 terminal, 1 lateral setae.

P4 (Fig. 3G-I): all segments except proximal endopodal anteriorly and posteriorly with complex arrays of large and small denticles; arrays may be distally or radially polarized. Coxa without seta. Basis without seta. Re 3-segmented, proximal with 1 medial and 1 lateral seta, middle with 1 medial and 1 lateral seta, distal with 4 medial, 1 terminal, 3 lateral setae. Ri 3-segmented, proximal with 1 medial seta, middle with 1 medial seta, distal with 2 medial, 2 terminal, 1 lateral setae.

P5 (Fig. 3J): all 3 segments posteriorly with denticles of various lengths. Coxa and basis without a seta. Re 1-segmented with 1 medial, 2 terminal and 1 lateral setae.

CR (Fig. 2E): 4 large, terminal setae, 1 small medial-dorsal seta, and 1 small lateral-ventral seta.

Etymology.—The species name honors Abraham Fleminger of Scripps Institution of Oceanography for his contributions to the systematics of calanoid copepods.

Remarks.—Autapomorphies for *B. flemingeri* include: one bifurcate, worm-like sensory seta on exopod of maxilla 2; basis of swimming leg 1 with semicircular pro-

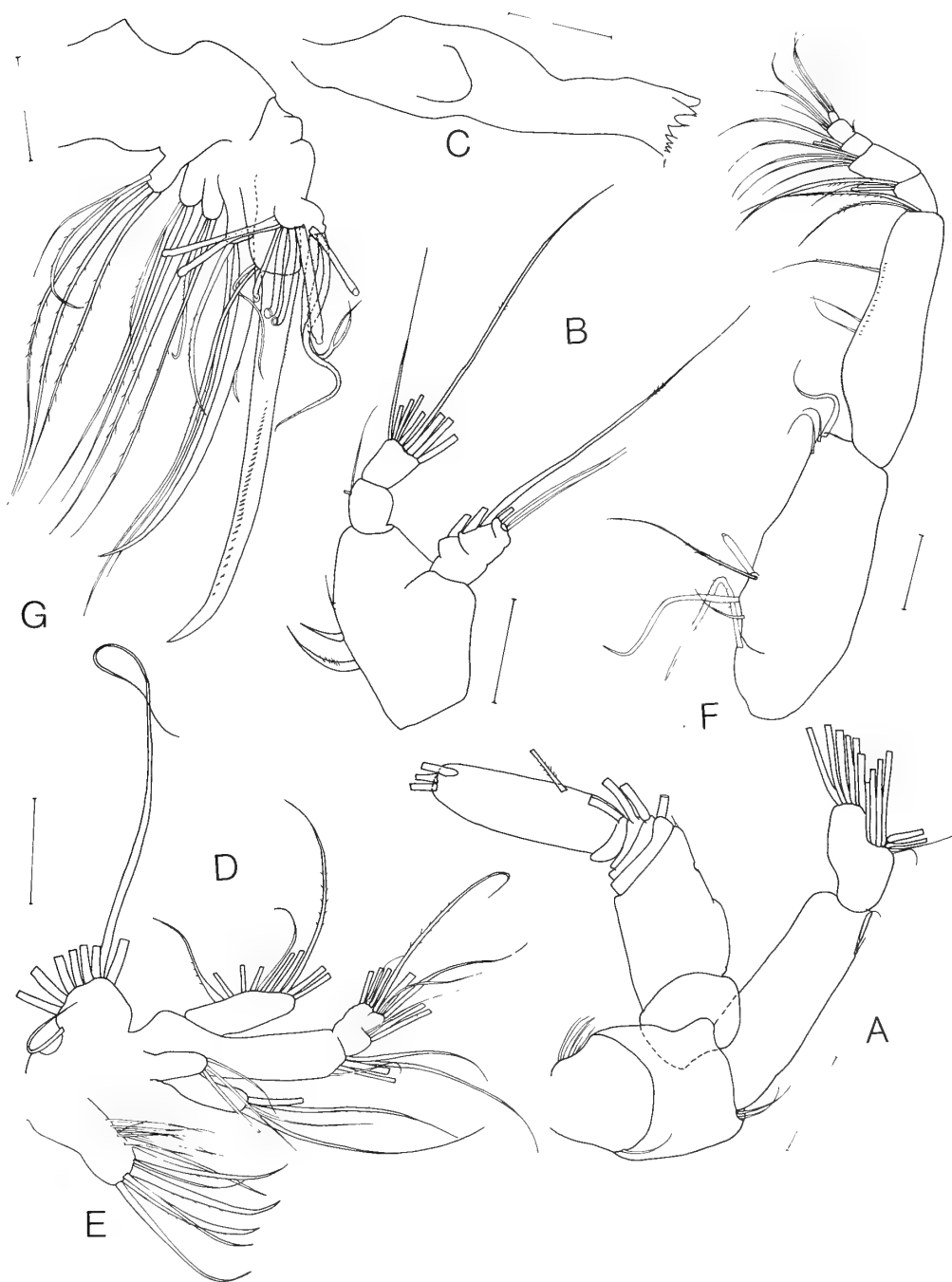


Fig. 2. *Brachycalanus flemingeri*, new species. A, antenna 2, ventral; B, mandibular palp, dorsal; C, mandibular gnathobase, distal; D, maxilla 1, anterior; E, maxilla 1, praecoxal lobe, posterior, distal down; F, maxilliped, anterior; G, maxilla 2 anterior. Scale lines are 0.1 mm.

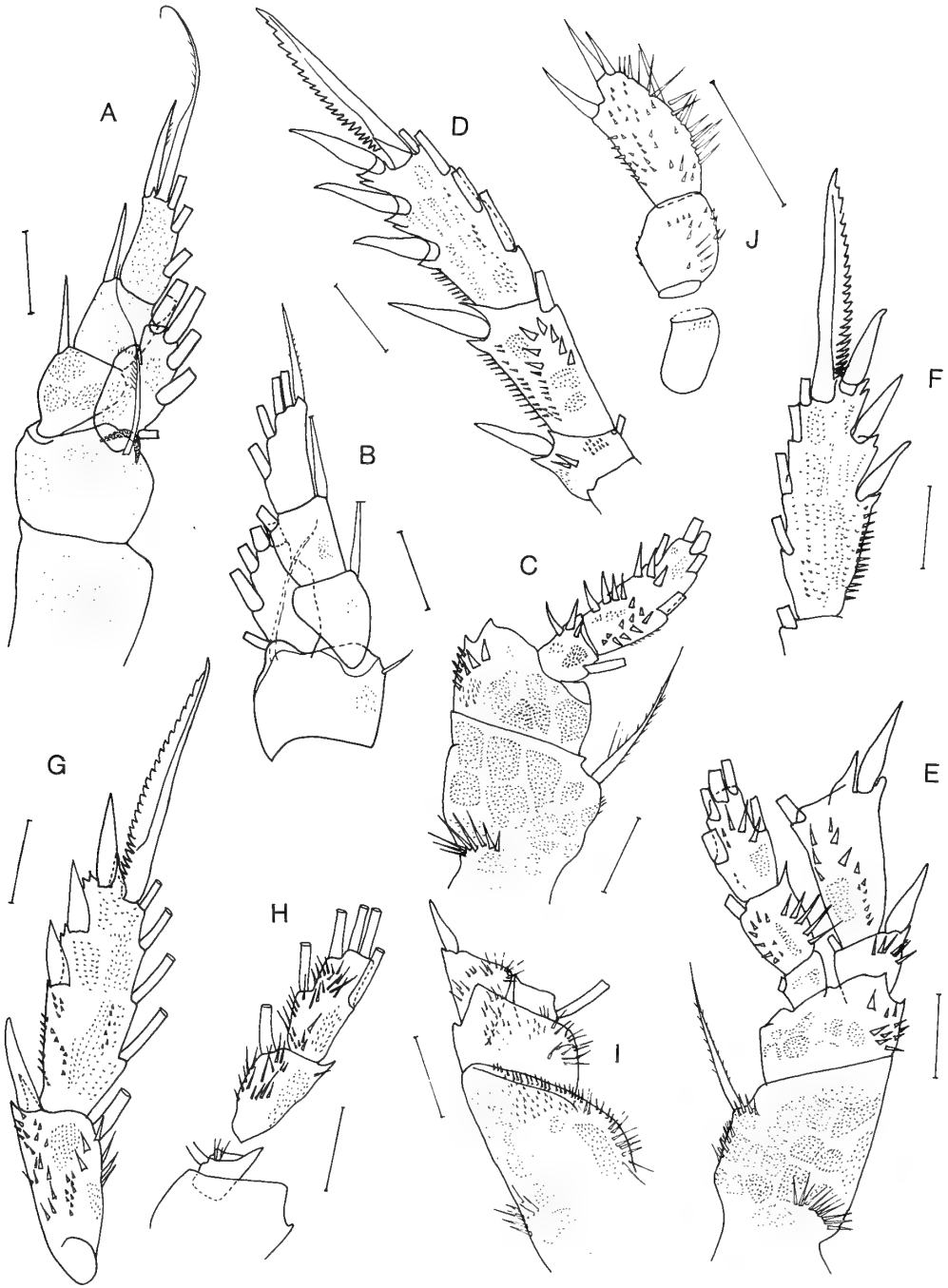


Fig. 3. *Brachycalanus flemingeri*, new species. A, P1, anterior; B, basis and rami of P1, posterior; C, coxa, basis and endopod of P2, posterior; D, exopod of P2, posterior, medial seta of proximal segment missing; E, coxa, basis, endopod and proximal and middle segment of exopod of P3, posterior; F, distal part of middle segment and distal segment of exopod of P3, posterior; G, middle segment and distal segments of exopod of left P4, posterior; H, basis and proximal segment detached from middle and distal segments of exopod of right P4, posterior; I, coxa, basis and proximal ramal segments of left P4, posterior, medial seta of proximal exopodal segment missing; J, P5, posterior, coxa detached. Scale lines are 0.1 mm.

trusion at the base of medial seta; three setae on coxal endite of maxilla 1 (rather than two setae); and swimming leg 4 without a medial coxal seta.

Brachycalanus brodskyi, new species

Figs. 4–7

Specimens.—Holotype (USNM 307714) a dissected 4.0 mm female; prosome 3.3 mm, urosome 1.0 mm. Type locality: eastern tropical Pacific Ocean 1–5 m above bottom at base of Volcano 7 (13°23'N, 102°27'W), at depths of 2945–3010 m, dive 2147, Nov 1988. The anterior seta on praecoxal endite of Mx1 of the single known specimen apparently broken; one seta on the middle praecoxal lobe of Mxp apparently broken.

CVI female.—Differs from *B. flemingeri* as follows: in habitus, dorsally posterior corners of prosome exceeding the middle length of genital somite (Fig. 4H). Genital complex with long denticles posterior-ventrally.

A1 (Fig. 5A–C): 3, 6+1, 2+1, 1+1, 2+1, 2?, 2+1, 4+1, 1, 1, 2+1, 1, 2+1, 1, 2, 1, 2, 1+1, 1, 1, 2?, 2, 2, 5+1. Many setae and aesthetascs present on this specimen.

A2 (Fig. 6A), Mn (Fig. 6B, C), Mx1 (Fig. 6D) as illustrated.

Mx2: proximal and distal coxal endite each with 1 poorly sclerotized sensory seta (Fig. 6E). Distal basal lobe + Re with 9 sensory setae, 8 brush-like with longer setules (Fig. 6F) and 1 worm-like seta.

Mxp: (Fig. 6G, H) as illustrated.

P1 (Fig. 7A, B): basis with a semicircular row of small denticles posterior and distal near origin of endopod, and without semicircular protrusion.

P2 (Fig. 7C, D), P3 (Fig. 7E, F) as illustrated.

P4 (Fig. 7G, H): coxa with medial set; middle and distal segments of both rami lost.

P5 (Fig. 7I) as illustrated.

Etymology.—The species name honors Konstantin Abramovich Brodsky of the

Zoological Institute of the Russian Academy of Sciences, for his contributions to the systematics of calanoid copepods.

Remarks.—*Brachycalanus brodskyi* new species differs from the other species of the genus by its size 4.0 mm (remaining species: 1.52–3.40 mm); basis of swimming leg 1 with semicircular row of small denticles near origin of the medial seta.

Brachycalanus brodskyi shares eight brush-like setae with long filaments and 1 worm-like seta on distal basal lobe + exopod of maxilla 2 with *B. bjornbergae*; this composition apparently is shared also with *B. rothlisbergi* (Othman & Greenwood 1988 fig. 2C). *B. brodskyi* shares with *B. flemingeri* the acute triangular shape of posterior corners of prosome.

Brachycalanus ordinarius (Grice, 1972)

Fig. 8

Xanthocalanus ordinarius.—Grice, 1972: 237, figs. 101–119.

Brachycalanus ordinarius.—Campaner, 1978: 976–977. Othman & Greenwood, 1988: 357.

CVI female, paratype.—USNM 137176; differs from *B. flemingeri* as follows: in habitus, posterior corners of Th6 rounded (Fig. 8A).

A1 (Fig. 8B–D): 24 articulated segments with setal groups containing: 3, 6+1, 2+1, 2?, 2+1, 2, 2+1, 4+1, 1, 1, 2+1, 1, 2+1, 1, 2, 1, 1+1, 1+1, 1, 1, 2, 2, 2, 5+1 setae.

A2: without small distal seta on Re2.

Mx2: distal praecoxal endite without a poorly sclerotized seta; distal basipod lobe + Re with 7 brush-like and 2 worm-like sensory setae (Fig. 8F); 1 worm-like seta constricted distally with a small lobe near point of constriction (Fig. 8G), the other a simple worm-like seta.

Mxp: worm-like sensory seta of proximal lobe with long setules (Fig. 8H).

P1: basis without semicircular row of small denticles or semicircular protrusion near origin of medial seta; lateral seta on

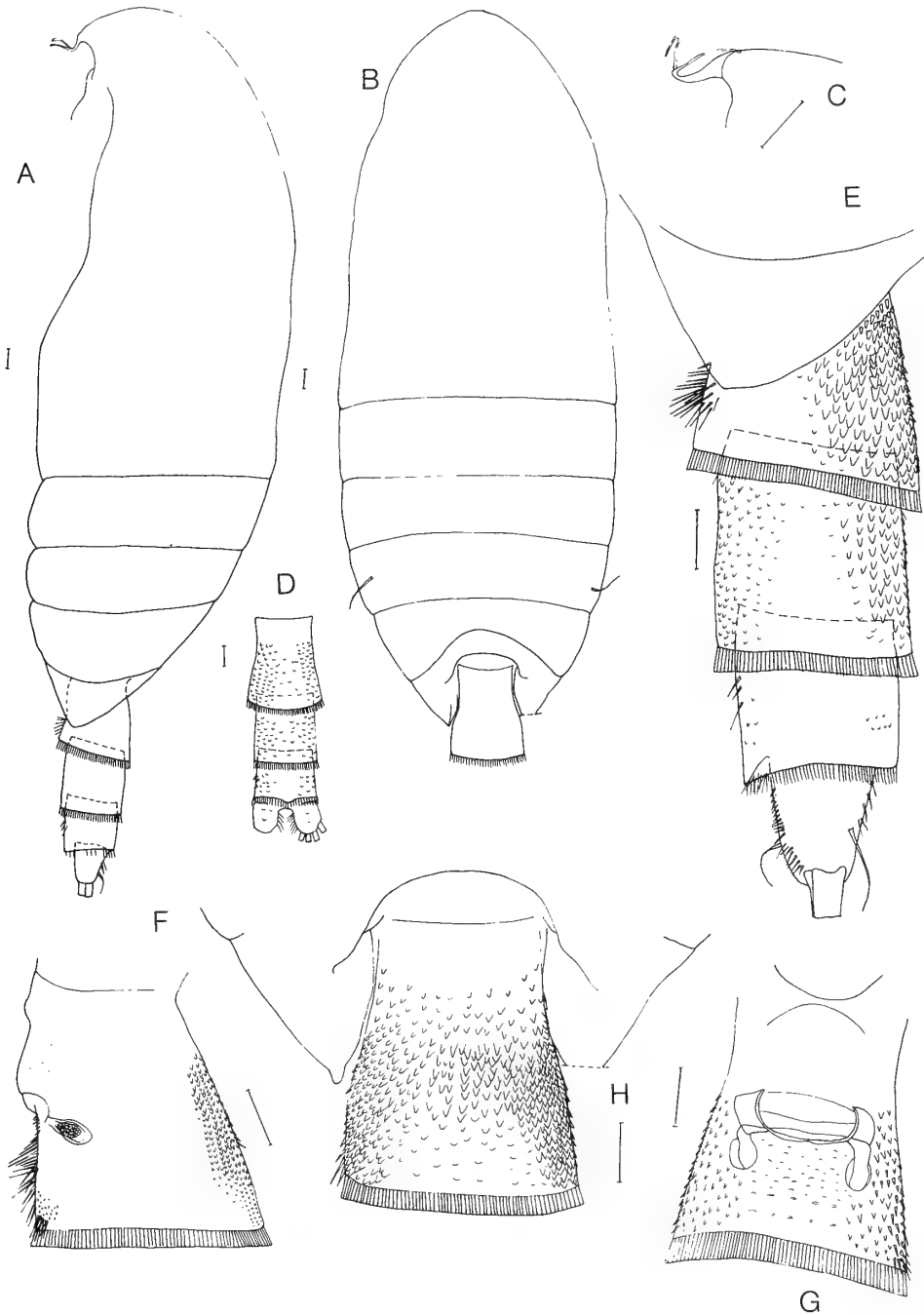


Fig. 4. *Brachycalanus brodskyi*, new species. A, habitus, left lateral; B, prosome and genital complex, dorsal; C, rostrum, lateral; D, urosome, dorsal; E, posterior Th5-6 and urosome, left lateral; F, genital complex, left lateral; G, genital complex, ventral; H, genital complex, dorsal. Scale lines are 0.1 mm.

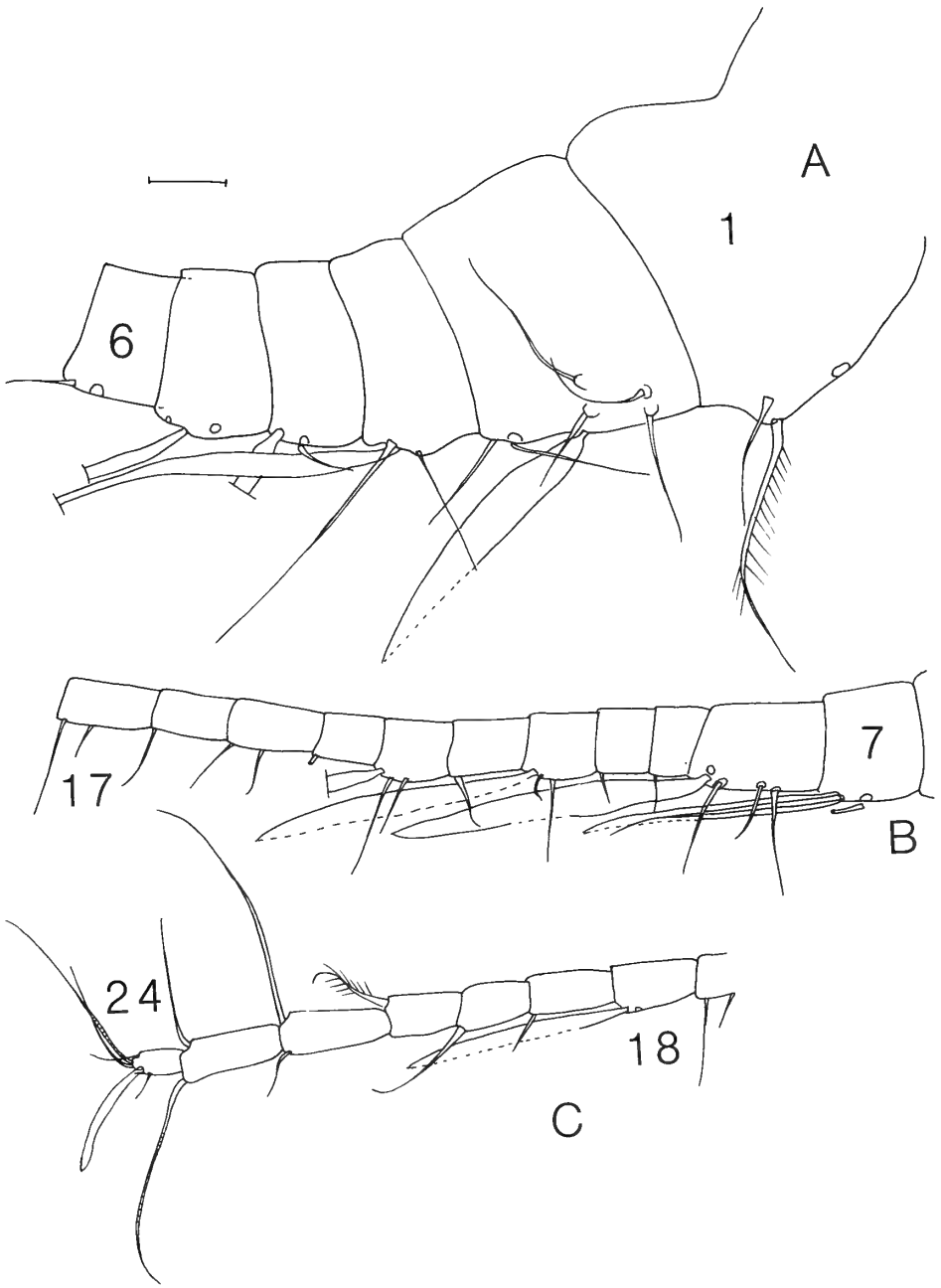


Fig. 5. *Brachycalanus brodskyi*, new species. A, antenna 1, articulating segments 1-6, ventral down; B, antenna 1, articulating segments 7-17, ventral down; C, antenna 1, articulating segments 18-24, ventral down. Broken line indicates poorly resolved edge of aesthetasc. All scale lines are 0.1 mm.



Fig. 6. *Brachycalanus brodskyi*, new species. A, antenna 2, dorsal; B, mandibular palp, ventral; C, mandibular gnathobase, distal; D, maxilla 1, anterior; E, maxilla 2, posterior, distal basal lobe + exopod omitted; F, exopod of maxilla 2 showing 3 terminal aesthetascs; G, syncoxa and basis of maxilliped, anterior; H, endopod of maxilliped, anterior. All scale lines are 0.1 mm.

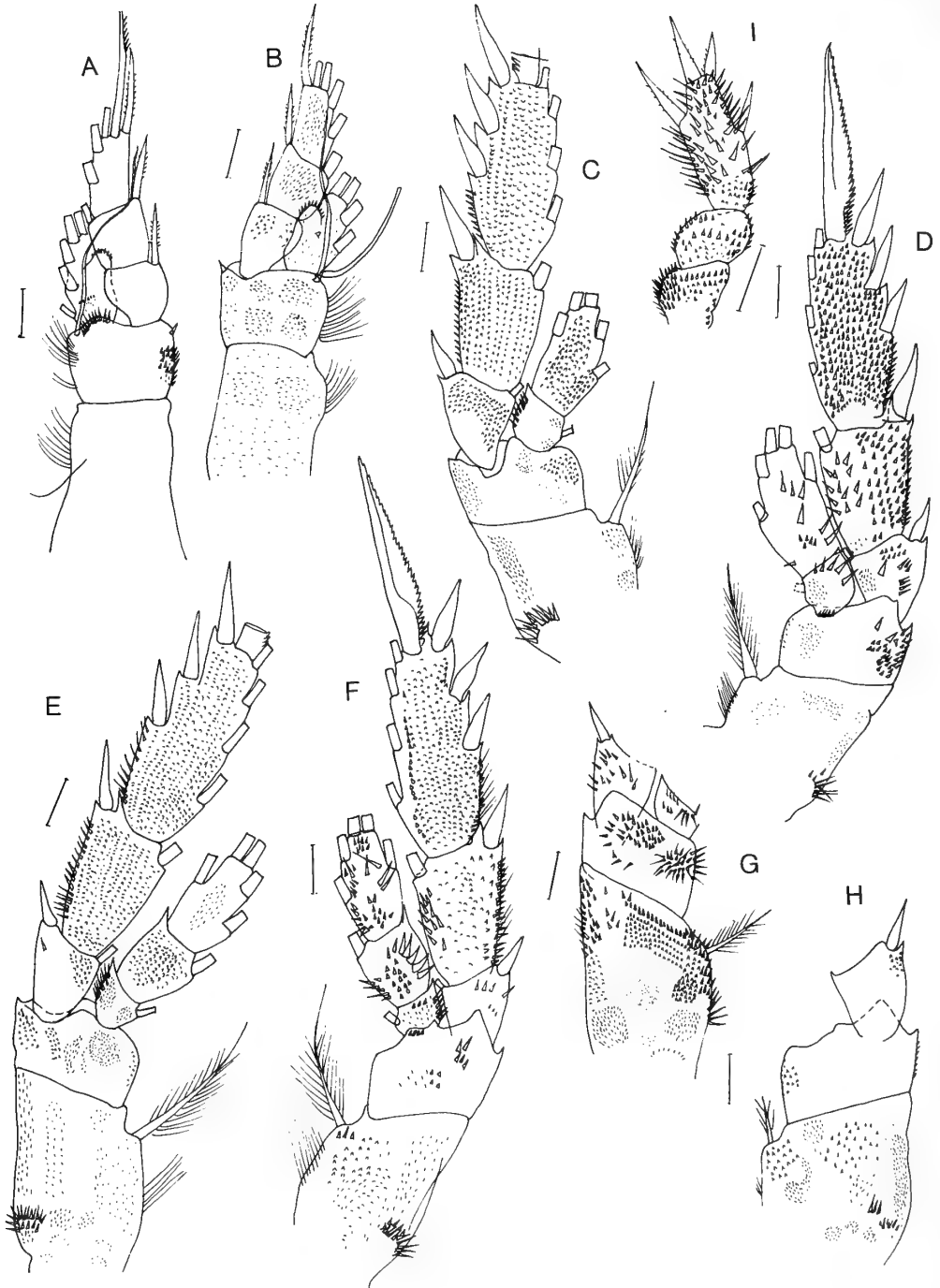


Fig. 7. *Brachycalanus brodskyi*, new species. A, P1, posterior; B, P1, anterior; C, P2, anterior, terminal seta cutoff; D, P2, posterior; E, P3, anterior, terminal seta cut off; F, P3, posterior; G, coxa, basis and proximal ramal segments of P4, posterior; H, coxa, basis and proximal exopodal segment of P4, anterior; I, P5, posterior. All scale lines are 0.1 mm.

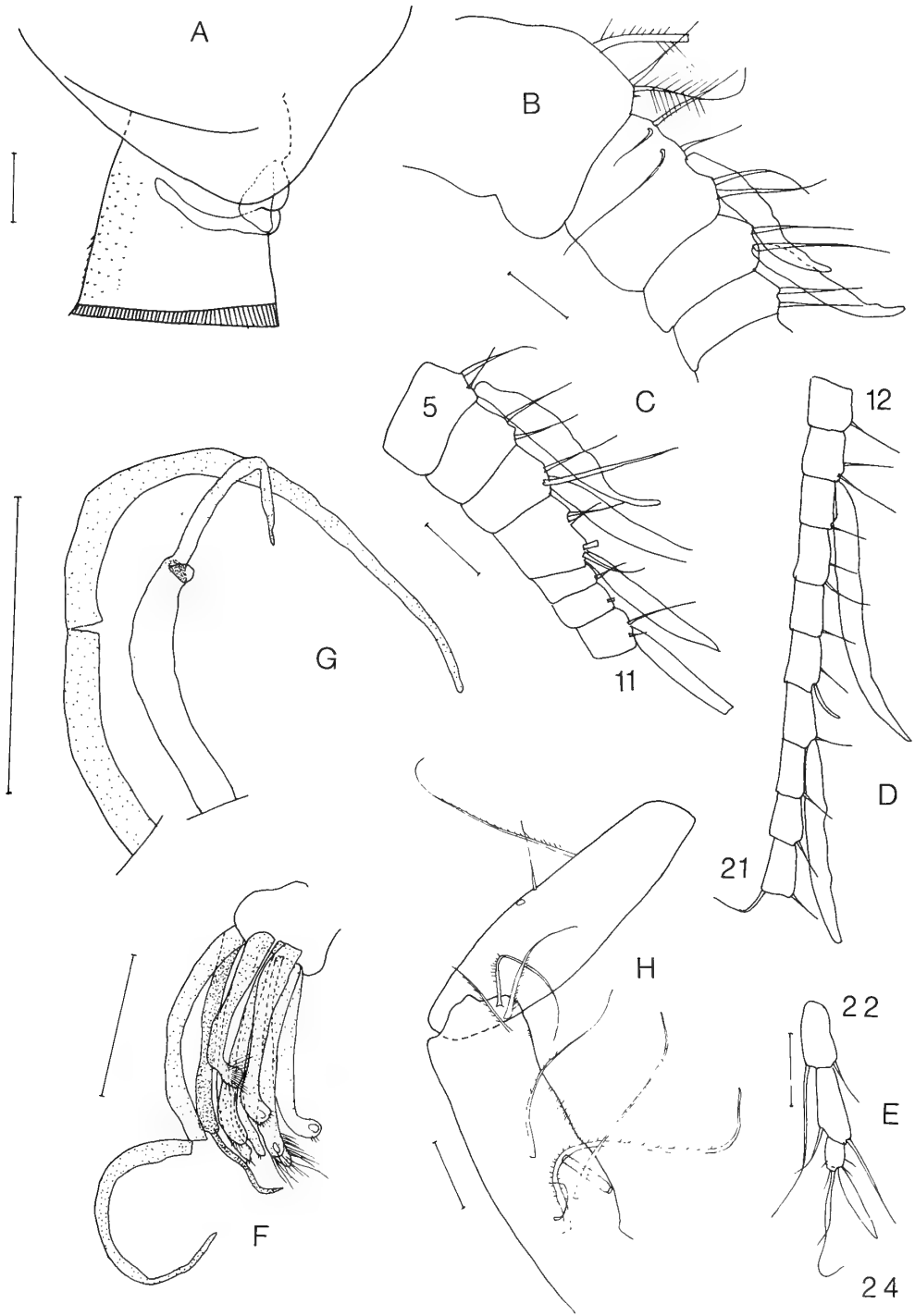


Fig. 8. *Brachycalanus ordinarius* (Grice, 1972). A, posterior Th5-6 and genital complex, right lateral; B, antenna 1, articulating segments 1-4, ventral toward right; C, antenna 1, articulating segments 5-11, ventral toward right; D, antenna 1, articulating segments 12-21, ventral toward right; E, antenna 1, articulating segments 22-24, ventral toward right; F, distal basal lobe and exopod of maxilla 2; G, worm-like setae of exopod of maxilla 2; H, syncoxa and basis, with distal lobe omitted, of maxilliped, anterior. All scale lines are 0.1 mm.

middle segment not reaching base of lateral seta of distal segment.

Remarks.—*Brachycalanus ordinarius* differs from the remaining species of the genus in possessing 1 worm-like seta constricted distally with a small lobe near point of constriction on the distal basal lobe + exopod of maxilla 2.

Discussion

The genus *Brachycalanus* was established by Farran (1905: 41) for three specimens of *B. atlanticus* which were "... washed from sand brought up by a tow net on the trawl . . . (off the west coast of Ireland) . . . They measured 2.5, 2.0 and 1.52 mm respectively." Farran described the largest specimen, except for P5, "which were only found in the smallest specimen, which while appearing fully developed in other respects, still showed immature segmentation of the abdomen". Farran mentioned in the description of the species "While the above was in press a description of this species under the name of *Xanthocalanus atlanticus*, was published by Dr. Wolfenden" (Farran 1905: 42). In establishing the genus, Farran mentioned that it is closely allied to *Xanthocalanus* Giesbrecht, 1892 and noted as distinguishing characters the shape of rostrum and an extremely short A1.

Brachycalanus was diagnosed by Campaner (1978: 976) based on the then three known species; he removed *B. minutus* Grice, 1972 and gave the total number and kind of sensory setae on the ramus of maxilla 2 as 1 worm-like and "(?) 7-8" brush-like setae. In a later diagnosis, Bradford et al. (1983) added that the urosome, and dorsal and ventral (actually anterior and posterior) surfaces of P1-P5 were covered with spines, an important character distinguishing the genus from *Xanthocalanus*. A later discussion of *Brachycalanus* by Othman & Greenwood (1988) noted the presence of knife-shaped aesthetascs on the antenna 1 as derived character state for the genus.

Othman & Greenwood (1988: 355) also suggested that Farran's (1905) specimens of *B. atlanticus* were not conspecific with those of Wolfenden (1904). Ohtsuka et al. (1998) pointed out that *Brachycalanus* shares with at least some species of *Xanthocalanus* a proximal basal endite of maxilla 2 with two worm-like sensory setae, and a syncoxa of the maxilliped with one or two worm-like sensory setae in addition to one brush-like sensory seta. These have not been reported for other phaennid genera.

We found very few differences to separate the three species of *Brachycalanus* studied here from the remaining species. However, the number of autapomorphies and degree of divergence among the species should become more apparent after careful redescription, particularly of the setation of maxilla 1 and maxilla 2, and discovery of males of the five species. Among the three species here that we place in *Brachycalanus*, there are different combinations of worm-like and brush-like setae among the nine sensory setae of the distal lobe and exopod of maxilla 2: one worm-like and eight brush-like setae in *B. bjornbergae* and *B. brodskyi*; two worm-like and seven brush-like in *B. ordinarius* and *B. flemingeri*. However, one worm-like seta each of *B. ordinarius* and *B. flemingeri* appears to be more specialized; one worm-like seta of *B. ordinarius* is similar to a fleshy seta (Campaner 1978: 968) with a small lobe, and one worm-like setae of *B. flemingeri* is bifurcate. It appears that a simple combination of the different kinds of sensory setae cannot be used to diagnose the genus *Brachycalanus*. Whether the number of sensory setae which are not worm-like are phylogenetically significant, remains to be determined. At this time we suggest that synapomorphies for the species of *Brachycalanus* are the presence of spinules on the female genital complex and following two abdominal somites, and knife-like aesthetascs on female antenna 1.

Species of the genus *Brachycalanus* pres-

ently are placed in the Phaennidae, one of five families within the superfamily Clausocalanoidea that possess sensory setae or aesthetascs on the distal basal lobe plus exopod of maxilla 2, and on the maxilliped (Nishida & Ohtsuka 1997). Bradford (1973) and Bradford et al. (1983) suggested that the number and the kinds of these sensory setae be used in diagnosing the Phaennidae and the Scolecitrichidae. Detailed descriptions of this part of maxilla 2 were not provided for the type species of *Brachycalanus* (Wolfenden, 1904) or in the original description of the genus (Farran 1905). In his diagnosis, Campaner (1978: 976) mentioned one worm-like plus "(5?) 7-8" brush-like sensory setae; Othman & Greenwood (1988) described this limb of *B. rothlisbergi* with one worm-like and ten brush-like setae (although only eight brush-like setae can be counted in their fig. 2C); finally, illustrations by Grice (1972: 235, fig. 109b) for *B. ordinarius* show two worm-like plus six brush-like sensory setae. We have observed nine such setae for *B. flemingeri*, *B. brodskyi*, and a paratype of *B. ordinarius*.

The presence of nine setae on the distal basal lobe plus exopod of maxilla 2 of these three *Brachycalanus*, another phaennid, *Xanthocalanus pavlovskii* Brodsky, 1955 as well as all five species of the scolecitrichid *Landrumius* (see Park 1983) and the scolecitrichid *Xantharus renatehaassae* Schulz, 1998 indicates that the number of such setae has not been conserved in these families as they are understood today. Although most descriptions of Clausocalanoidea species with simple, sclerotized setae on the distal basal lobe plus exopod mention eight of these setae, a recent redescription of *Pseudochirella obesa* Sars, 1920 by Vaupel Klein & Rijerkerk (1997) states and figures nine such setae. Ohtsuka et al. (1998) suggested that brush-like setae may be derived from worm-like setae because the dendritic cilia of a worm-like setae are enclosed within a thin cuticle, homologous to the thick cuticle of sclerotized setae, while the cuticle of a

brush-like seta is open distally so that its dendritic cilia are in direct contact with the aquatic environment, as described by Nishida & Ohtsuka (1997). The number present on the ancestral clausocalanoid and the ancestor of the lineage which includes the Aetideidae, Phaennidae and Scolecitrichidae, and the number and kinds of transformations of these ancestral states must await a careful redescription of the species of these families.

Acknowledgments

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Grievella shanki, a new genus and species of scolecitrichid calanoid copepod (Crustacea) from a hydrothermal vent along the southern East Pacific Rise

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Abstract.—Four derived states separate the calanoid copepod *Grievella shanki*, new genus and species, from other scolecitrichids: small integumental bumps on the genital complex; an ear-like extension on articulating segment 22 of antenna 1; two lateral setae on the distal exopodal segment of swimming leg 2; a denticle-like attenuation of the proximal praecoxal lobe of maxilla 2. The first probably is an autapomorphy for the species; the second, third and fourth are presumed synapomorphies for species of the new genus. The last derived state is convergent with some species of the calanoid superfamilies Epacteriscoidea, Centropagoidea and Megacalanoidea, but it is a synapomorphy within the Clausocalanoidea to which *Grievella shanki* belongs. Five setae on the proximal praecoxal lobe of maxilla 2 and three setae on the distal praecoxal lobe of the maxilliped separate *Grievella shanki* from species of Diaixidae, Parkiidae and Tharybidae, and species of Phaennidae, respectively. The states of these characters for *Grievella shanki* may be plesiomorphic to the states expressed in Diaixidae, Parkiidae, Tharybidae and Phaennidae so assignment of this species to the Scolecitrichidae is tentative. The number and kind of sensory setae on the distal basal lobe plus exopod of maxilla 2 alone are not adequate to diagnose the Scolecitrichidae, or to separate all of its species from those of the other families with these sensory setae.

Calanoid copepods belonging to the family Scolecitrichidae usually are collected from pelagic or benthopelagic habitats of marine waters below 200 m. There are over 250 nominal species in 22 genera in the family. Eight of the 22 genera in this family have been described within the last quarter century, reflecting a general increase in interest in the biology of the deep waters of the world's ocean. Here we describe the 23rd genus of the family.

Materials and Methods

The copepod was collected at Droopy Vent, 21°24.027'S, 114°16.184'W on 17 October 1998 with a slurp vacuum sampler

less than a meter above the surface on the side of a small diffusing vent chimney during *Alvin* dive 3287; bottom depth, 2788 m, water temperature, 4.5°C. The specimen was fixed in 70% ethanol/30% seawater. During laboratory examination, the specimen was cleared in steps through 50% lactic acid/50% deionized freshwater to 100% lactic acid, stained by adding a solution of chlorazol black E dissolved in 70% ethanol/30% deionized freshwater, dissected, and examined with bright-field and with differential interference optics. Drawings were made with a camera lucida. The dissected specimen is preserved in 70% ethanol/30% deionized freshwater with a drop of glycerin added.

Cephalic appendages are abbreviated A1 = antenna 1; A2 = antenna 2; Mn = mandible; Mx1 = maxilla 1; Mx2 = maxilla 2. Thoracic somites are Th1–7; appendages on thoracic somites are Mxp = maxilliped (thoracopod 1); P1–5 = swimming legs (thoracopods 2–6). The caudal ramus is CR. Designations of appendage segments are according to Ferrari (1995) as follows: medial lobe of a segment = li, lateral lobe = le; rami are exopod = Re and endopod = Ri; ramal segments of Mx2 are exopodal; the Mxp has a basipod with a distal medial lobe, and with at most five endopodal segments in calanoids (Ferrari & Dahms 1998). Armament elements of appendages are termed setae regardless of their position or degree of rigidity. Two setae and one aesthetasc on a segment of A1 are designated 2+1. Setules are epicuticular extensions of a seta; denticles are epicuticular extensions of an appendage segment; spinules are epicuticular extensions of a somite.

Grievella, new genus

Diagnosis.—Presumed unique synapomorphies of *Grievella* are an ear-like extension anteriorly near distal margin of articulating segment 22 of antenna 1; distal exopodal segment of swimming leg 2 with 2 lateral setae; single denticle-like attenuation of the proximal praecoxal lobe of maxilla 2.

Remarks.—A distal exopodal segment of swimming leg 2 with 2 lateral setae is convergent with some species of the superfamilies Megacalanoidea and Centropagoidea, and with all species of the superfamily Epacteriscoidea. It is assumed to be a synapomorphy for this genus within the Clausocalanoidea to which this species belongs.

Type species.—*Grievella shanki* by monotypy and present designation.

Etymology.—The name *Grievella* honors Janet Bradford-Grieve New Zealand National Institute of Water and Atmospheric Research for her contributions to copepod systematics. The gender of the generic name is feminine.

Grievella shanki, new species

Figs. 1–5

CVI Female.—Holotype, USNM 2617684, (Fig. 1A, B) Cephalon, Th1 and Th2 fused; Th3 and Th4 separate; Th5 fused with Th6. Posterior corners of prosome rounded laterally and not reaching beyond the anterior margin of genital complex. Genital complex (Fig. 1G–J) symmetrical in ventral view; in lateral view, asymmetry results from small integumental bumps; with slight bulge ventrally at copulatory opening; seminal receptacle extending to middle of complex dorsally, and slightly curved posteriorly; oviducal pore anterior. Three articulating abdominal somites posterior to genital complex.

Rostrum (Fig. 1C–E): 2 filaments, each on robust base.

A1 (Fig. 2A–D): reaching Th3, of 24 articulating segments with groups of setae: 3, 6+1, 2+1, 2, 2+1, 2, 2+1, 4+1, 1, 1, 2+1, 1, 2+1, 1, 2, 1, 2, 1+1, 1, 1, 2, 2, 2, 5+1. One denticle proximally on ventral face of segment 7; several smaller denticles distally on dorsal face of segments 19 and 20. Segment 22 with ear-like extension anteriorly with ear cavity facing proximally.

A2 (Fig. 2E): coxa with 1 seta and denticles. Basis with 2 setae. Ri 2-segmented with 2 and 15 (6+1 posterior terminal and 8 subterminal) setae (Fig. 2F). Re 7 articulating segments with 0, 3, 1, 1, 1, 1, 3 setae.

Mx1 (Fig. 3C): praecoxa elongate with 9 terminal, and 3 posterior setae; coxal epipodite with 7 long, thick and 2 short, thin setae; coxal endite with 2 setae; proximal and distal basal endites each with 4 setae. Ri with 10 setae in groups of 3 and 7; Re with 6 setae.

Mx2 (Fig. 4A–C): proximal praecoxal endite with 5 setae and attenuate point, distal endite with 3 setae. Proximal coxal endite with 3 setae, distal coxal endite with 3 setae. Proximal basal endite with 1 long, thick seta, 2 long, thin seta and 1 poorly sclerotized setae. Distal basal lobe + Re

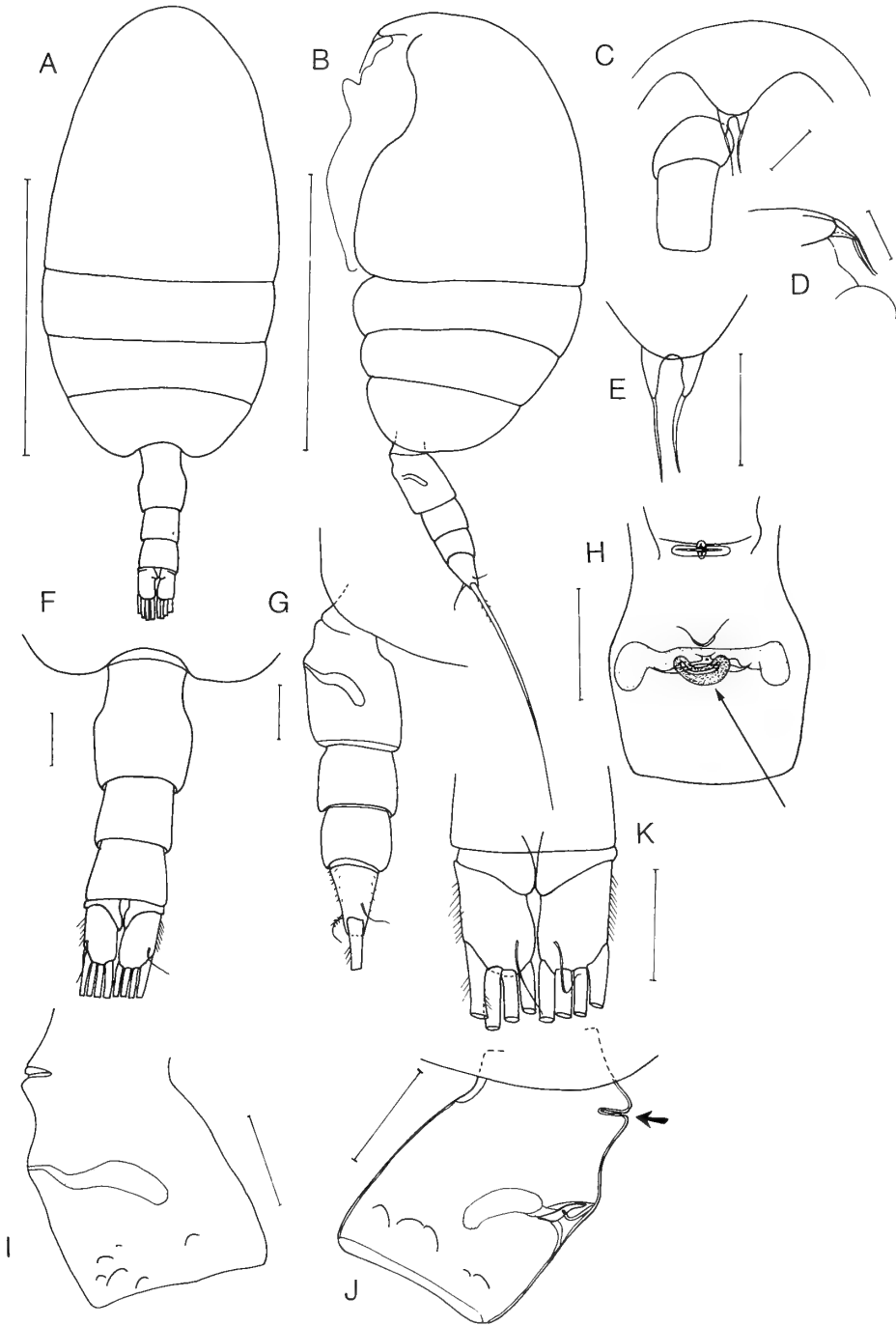


Fig. 1. *Grievella shanki*, new genus and species. A, habitus, dorsal; B, habitus, left lateral; C, rostrum, ventral; D, rostrum, right lateral; E, rostrum, ventral; F, urosome, dorsal; G, urosome, left lateral; H, genital complex, ventral, arrow to location of copulatory opening; I, genital complex, left lateral; J, genital complex, left lateral, arrow to oviducal opening; K, caudal rami, ventral. Scale lines are 0.1 mm.

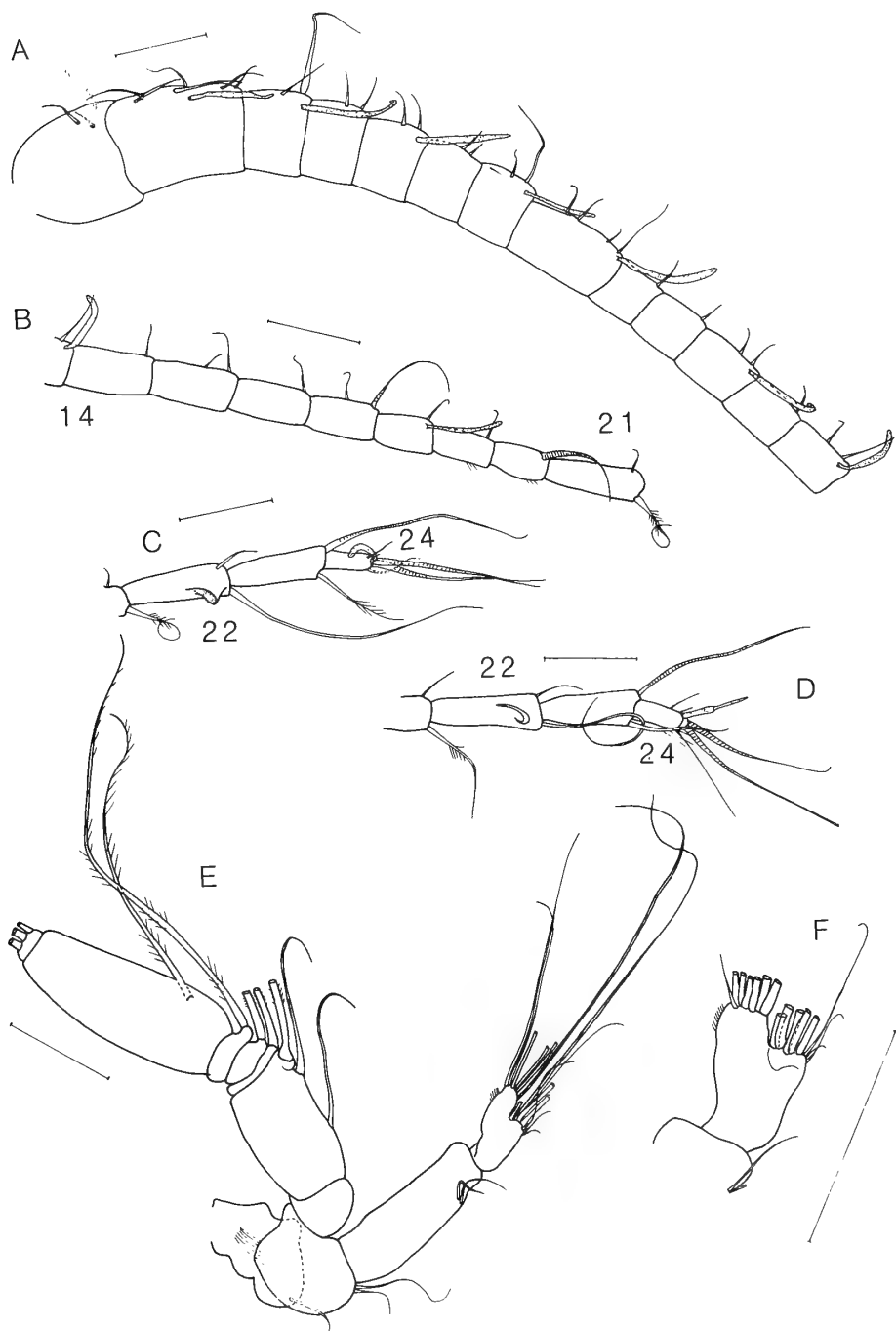


Fig. 2. *Grievella shanki*, new genus and species. A, left antenna 1, articulating segments 1-13; B, left antenna 1, articulating segments 14-21; C, left antenna 1, articulating segments 22-24; D, right antenna 1, articulating segments 22-24; E, antenna 2, posterior; F, antenna 2, distal segment of endopod. Scale lines are 0.1 mm.



Fig. 3. *Grievella shanki*, new genus and species. A, Mn, palp, posterior; B, Mn, gnathobase, posterior; C, Mx 1, posterior. Scale lines are 0.1 mm.

with 9 sensory setae, 3 worm-like setae distally and 6 brush-like setae, all about the same length and with short setules; 3 brush-like setae of the same thickness, 2 thinner, 1 very thin brush-like setae.

Mxp (Fig. 4D, E): syncoxa with 1 long seta on proximal lobe; 2 long setae on middle lobe, both well-sclerotized but 1 broken at its tip; 3 short setae on distal lobe; coxal lobe with 3 setae and denticles on distal face. Basis with 3 setae on unattenuated proximal lobe and 2 setae on distal lobe; proximal denticles short and thick. Ri 5-segmented from proximal to distal with 4, 4, 3, 4 (1 lateral), 4 (1 lateral) setae respectively.

P1 (Fig. 5A, B): coxa without seta but with medial denticles. Basis with medial seta sharply curved. Re 3-segmented, proximal without a seta, middle with 1 medial seta, distal with 3 medial, 1 terminal, 1 lateral setae. Ri a 1-segmented complex with 3 medial and 2 terminal setae; quadrate protuberance of Von Vaupel Klein's organ with anterior row of denticles proximally and posterior pore on lateral edge.

P2 (Fig. 5C): coxa with medial seta and denticles proximally. Basis without seta. Re 3-segmented, proximal with 1 medial and 1 lateral seta, middle with 1 medial and 1 lateral seta, distal with 4 medial, 1 terminal, 2 lateral setae. Ri 2-segmented, proximal with 1 medial seta, distal with 2 medial, 2 terminal, 1 lateral setae.

P3 (Fig. 5D): coxa with medial seta and denticles proximally. Basis without seta. Re 3-segmented, proximal with 1 medial and 1 lateral seta, middle with 1 medial and 1 lateral seta, distal with 4 medial, 1 terminal, 3 lateral setae. Ri 3-segmented, proximal with 1 medial seta, middle with 1 medial seta, distal with 2 medial, 2 terminal, 1 lateral setae.

P4 (Fig. 5E): coxa with medial seta, without denticles proximally. Basis without seta. Re 3-segmented, proximal with 1 medial and 1 lateral seta, middle with 1 medial and 1 lateral seta, distal with 4 medial, 1 terminal, 3 lateral setae. Ri 3-segmented,

proximal with 1 medial seta, middle with 1 medial seta, distal with 2 medial, 2 terminal, 1 lateral setae.

P5 (Fig. 5F): 2 articulating sections. Coxa is proximal; basis without seta fused to 1-segmented Re with 1 medial, 1 terminal and 1 lateral setae is distal complex. CR (Fig. 1F, K): 4 large, terminal setae, 1 small medial-ventral seta, and 1 small lateral-dorsal seta.

Etymology.—The name of this species honors Timothy M. Shank, Woods Hole Oceanographic Institution, who collected this copepod. The epitheton is a noun in the genitive singular.

Remarks.—Four derived character states separate this species from other scolecitrichids: small integumental bumps on the genital complex, an ear-like extension on articulating segment 22 of antenna 1, two lateral setae on the distal endopodal segment of swimming leg 2, and a denticle-like attenuation of the proximal praecoxal lobe of maxilla 2. We believe the first of these may be an autapomorphy.

Grievella shanki shares the absence of an outer spine on both the proximal and middle exopodal segments of swimming leg 1 with a number of other scolecitrichids, e.g., *Scaphocalanus curtus* (Farran, 1926), *S. bogorovi* Brodsky, 1955, *Scolecithricella aspinosa* Roe, 1975 and *S. canariensis* Roe, 1975. We believe this apomorphy of *Grievella shanki* that is shared with these other scolecitrichid species results from convergence; it is not evidence for monophyly.

Grievella shanki shares five setae on the proximal praecoxal lobe of maxilla 2 with the scolecitrichids *Xantharus renatehaassae* Schulz, 1998, one of only two species in this genus, with *Neoscolecithrix antarctica* Hulsemann, 1985, one of six species in this genus, and with all five species of the genus *Landrumius* (see Park 1983). The remaining species of Scolecitrichidae have three or four setae on the proximal praecoxal lobe of maxilla 2. Species of the Phaennidae have five setae on this proximal praecoxal lobe, except for a few species of *Xantho-*

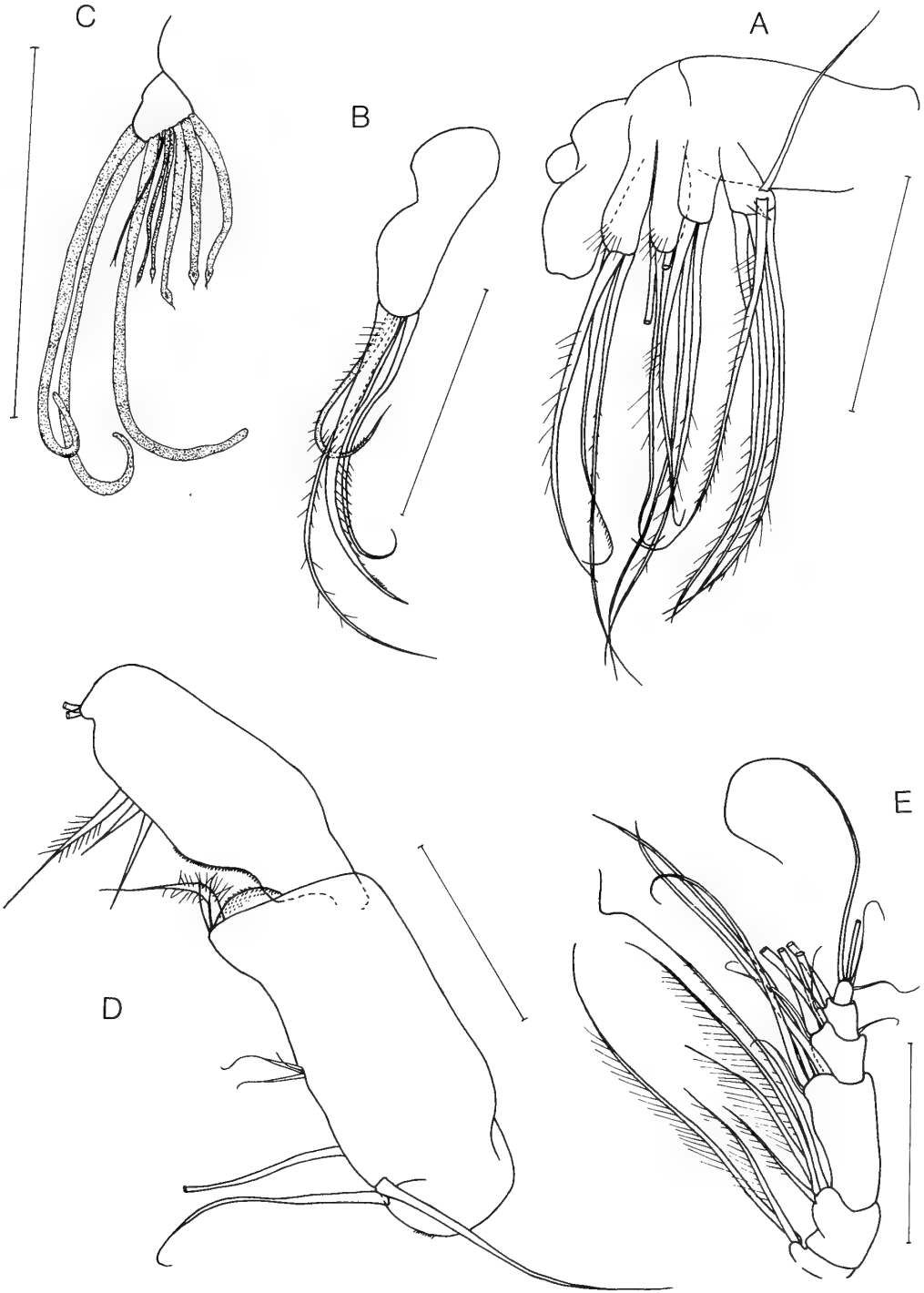


Fig. 4. *Grievella shanki*, new genus and species. A, Mx 2, with setation of praecoxal and coxal lobes, posterior; B, Mx 2, proximal lobe of basis, posterior; C, Mx 2, distal lobe basis plus exopod, posterior; D, syncoxa and basis of Mxp, anterior; E, distal lobe of basis and endopod, posterior. Scale lines are 0.1 mm.

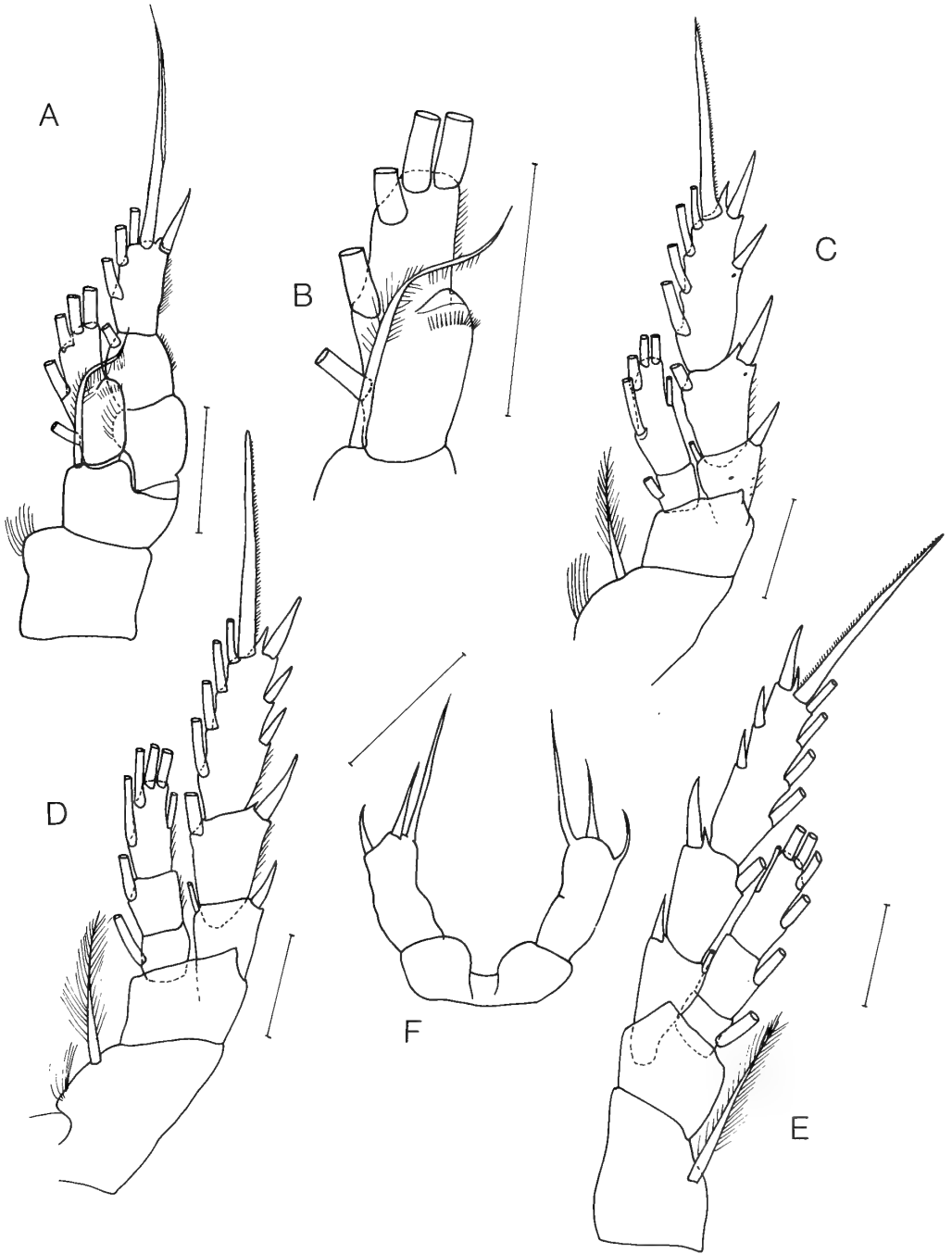


Fig. 5. *Grievella shanki*, new genus and species. A, P1, anterior; B, Von Vaupel Klein's organ of P1, anterior; C, P2, posterior; D, P3, posterior; E, P4, posterior; F, P5, posterior. Scale lines are 0.1 mm.

calanus with four setae. Species of Diaixidae, Parkiidae, and Tharybidae have three or four setae.

Grievella shanki shares nine sensory setae on the distal basal lobe plus exopod of maxilla 2 with all five species of *Landrumius*. The remaining species of Scolecitrichidae have eight sensory setae on the distal basal lobe plus exopod of maxilla 2, with the exception of *Xantharus renatehaassae* which has eight sensory setae and one sclerotized seta. Eight sensory setae is the number most often reported for Phaennidae, Diaixidae, and Tharybidae, although nine sensory setae have been reported for some phaennids (see Ferrari & Markhaseva 2000) and several tharybid-like copepods (unpubl. obs.).

Grievella shanki shares 1, 2, and 3 setae, from proximal to distal, on the three praecoxal lobes of the maxilliped with *Xantharus renatehaassae*, with all five species of *Landrumius*, with *Neoscolecithrix antarctica* and *N. magna* Grice, 1972; however, these latter two species differ quite significantly in other morphological features. Praecoxal lobes with 1, 2, and 3 setae also are known for some diaixids and tharybids (see Ferrari & Markhaseva 1996). Setation for the remaining Scolecitrichidae usually is 1, 2, and 1 setae. For Phaennidae setal numbers 1, 2, and 2 seem to have been conserved.

If we assume that the larger number of elements is the plesiomorphic state (Dogiel 1954, Monchenko & Von Vaupel Klein 1999) for these above three characters of the maxilla 2 and maxilliped, then the states for *Grievella shanki* provide no direct information about its phylogenetic relationships with other copepods sharing the same character states. Among related families Phaennidae, Diaixidae, Tharybidae and Parkiidae, synapomorphies have been proposed only for the latter family. Our decision to place *Grievella shanki* within the Scolecitrichidae is tentative. The number and kind of sensory setae on the distal basal lobe plus exopod of maxilla 2 alone is not

adequate to diagnose the the Scolecitrichidae, or to separate all of its species from those of the Phaennidae and other families with these kinds of sensory setae. Careful redescriptions of the setation of antenna 2, maxilla 1, maxilla 2 and maxilliped are required before the different synapomorphies of the five families with their included genera can be clarified.

Acknowledgments

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**Redescription and designation of lectotypes of the North American
Cambarincola okadai Yamaguchi, 1933
(Annelida: Clitellata: Branchiobdellidae)**

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Abstract.—Unlabelled specimens found in the slide collection of Prof. Hideji Yamaguchi were identified as the North American species, *Cambarincola okadai* Yamaguchi, 1933. As no type specimens had been designated, a detailed redescription was made and the specimens were designated as lectotypes for the species. Specimens of this species were named *Triannulata montanus* Goodnight, 1940, then subsequently redescribed and transferred to *Cambarincola montanus*. The latter two names now become junior synonyms of *C. okadai*.

The export and import of crayfishes between countries and continents for commercial reasons has been practiced for many years. Reviews of the various species and countries involved can be found in Holdich & Lowery (1986) with more recent information in Hobbs et al. (1989). Until recently, little attention has been paid to the detrimental effects the exotic species have caused to the native fauna and environment. The best known instances are the widespread introduction of “crayfish plague” into Europe (Söderhäll & Cerenius 1999), and the destruction of paddy field walls (Ackefors & Lindqvist 1994:199, 189). In addition to pathogens, the introduction of crayfishes into new regions is frequently accompanied by non-pathogenic symbionts such as branchiobdellids and temnocephalidans (Gelder 1999). These exotic ectosymbionts often become part of the local fauna and may adopt endemic species as new hosts (Gelder et al. 1999).

The first significant review of branchiobdellids in Eastern Asia was made by Yamaguchi (1934). He described a number of new species but did not specifically design-

nate any type specimens or record their exact collection sites in his publications. A large earthquake in Hokkaido during 1968 destroyed part of Prof. Hideji Yamaguchi's oligochaete collection, so he asked his assistant, Dr. Yuki-yoshi Kamihira, Hakodate University, Hokkaido, Japan, to look after the remaining material (Ohtaka, pers. comm.). This action was not widely known, so it was generally assumed that the collection had been completely destroyed. Dr. Akifumi Ohtaka found the slide collection and obtained permission from Dr. Yuki-yoshi Kamihira for Dr. Gelder to examine the branchiobdellid slides. At that time, it was realized that the written records supporting the slides had been lost and that none of the slides had been fully labeled.

Four of these unlabeled slides each contained a North American branchiobdellid. Yamaguchi had examined and described a new species of North American branchiobdellid, *Cambarincola okadai* Yamaguchi, 1933, that had been introduced into Japan. Because no type specimens had been designated and no specimens had been reported since the initial examination, *C. okadai*

was considered to be *nomen inquirendum* by Holt & Opell (1993:253). This study was designed to describe in detail the recently acquired specimens, review the information on *C. okadai*, and attempt to clarify the taxonomic status of the species.

Literature Review

Review of the information on Cambarincola okadai Yamaguchi, 1933 and North American crayfish in the collection area.—The description of *C. okadai* was produced “from several specimens . . . attached to . . . crayfish formerly transferred from America into Lake Chuzenji, Nikko”, Tochigi Prefecture, collected by Prof. Y. Okada in 1928 (Yamaguchi 1933:191). He also noted (p. 193) that “there has been no report of crayfish from Lake Chuzenji and adjacent districts except those newly transferred from America.” It is known that *Pacifastacus leniusculus leniusculus* (Dana, 1852) (or Tankai-zarigani) and *Pacifastacus leniusculus trowbridgii* (Stimpson, 1857) (or Uchida-zarigani) were introduced into Japan from Oregon, U.S.A., five times between October 1926 and July 1930 (Kamita 1970). Specimens of these two subspecies were introduced into Tochigi Prefecture (Kamita 1970: fig. 59 for *P. leniusculus*, and fig. 63 for *P. trowbridgii*), but no records have been found to indicate that these crayfishes were actually released into Lake Chuzenji or exactly when they were brought into the Prefecture.

The description of *C. okadai* by Yamaguchi (1933) stated that the longest specimen was 7 mm in length, but no range of variation was given. The elongate, cylindrical body had a distinct head with the peristomium supporting “four distinct digitiform appendages,” (dorsal tentacles), and slightly bilobed ventral lip. No lateral lobes were noted in the text but two small lateral lobes can be seen in his fig. 1. The jaws were illustrated in detail in his fig. 2 showing them to be similar in size and triangular in shape with a large median tooth and two

pairs of small teeth. The width of the jaw base was calculated from his fig. 2 to be 130 μm wide. The single anterior nephropore, “abundant male reproductive cells [spermatozoa]” in segments 5 and 6, tubular spermatheca, and the “spermatic vesicle [glandular atrium] is bifid, having the accessory sperm tube [prostate gland]” are all valuable taxonomic characters that together suggested a member of the North American genus *Cambarincola*. The origin of the prostate gland on the glandular atrium, presence of a protrusible penis together with other details and proportion of the male reproductive system are critical for identifying and defining a species of *Cambarincola*. Unfortunately, most of these details were not included in Yamaguchi’s description. However, based on the information available to Prof. Yamaguchi this was a new species and clearly separable from the sister species of *Cambarincola philadelphicus* (Leidy, 1851) and *Cambarincola chirocephalus* Ellis, 1919. For completeness it should be noted that a year earlier Yamaguchi (1932:456) eluded to examining “a section made from *Cambarincola* sp.” and continued in a footnote to say, “The species was obtained from crayfishes transferred from North America in a Japanese lake and is probably referable to *C. philadelphicus*.”

Reference to *C. okadai* after the type description has consisted of Yamaguchi (1934) repeating the essential information in the type description. However, in a shortened review of the latter paper written in Japanese, Yamaguchi (1935) gave *C. okadai* the Japanese name, Yadorimimizu, Goodnight (1940) in his review of the Branchiobdellidae, quoted the information on *C. okadai* from Yamaguchi (1933), classified the species as “sp. dub.” and added, “appears to the writer to be identical with *Cambarincola philadelphia*, as it differs from it only in the dentation of the lower jaw (p.43).” The species was mentioned incidentally by Hoffman (1963:276), Holt (1986:699), Timm (1991:329), then Holt &

Opell (1993) gave it the status of nomen inquirendum which was accepted in the checklist of branchiobdellidans (Gelder 1996).

Possible branchiobdellid species on North American signal crayfish introduced into Japan.—A review of the currently described branchiobdellids with dorsal lip appendages found on *P. leniusculus* subspecies in the Pacific Ocean drainage region of North America resulted in only two species, *Sathodrilus lobatus* Holt, 1977 and *Cambarincola montanus* (Goodnight, 1940). *Sathodrilus lobatus* is about 2.5 mm long, with six lobes on the dorsal lip, a dental formula of 5/4 (Holt 1977), and is not similar to *C. okadai*. The second species, *C. montanus*, was originally named *Triannulata montanus* Goodnight, 1940, and its type description contained a few errors. These were corrected in an emended description by Holt (1974), resulting in the species being transferred to the *Cambarincola* as a “new comb.”; the holotype number in his paper should read, USNM 20566. This description (Holt 1974:67) stated a body length of about 5.8 mm, triannulate appearance of segments, peristomium with four dorsal lip tentacles, two pairs of lateral lobes and a ventral lip of four lobes; no oral papillae were detectable. Holt (1974:68) reported, “The usual dental formula is 1/1 with prominent blunt teeth. Younger, though large, specimens from the Kalami River, the type-locality, have a dental formula of 5/5, but the lateral teeth are obscure and probably wear away with age.” An examination of about 10 adult specimens of *C. montanus* collected from southern British Columbia, Canada, all showed the large median tooth and two pairs of small, lateral teeth (Gelder & Hall 1990:2355). Given the available information, the 5/5 dental formula appears to be the representative form of the species. The spermatheca and male reproductive system were described in detail and drawn by Holt (1974:68) who also noted that the prostate gland was formed from vacuolated or “differentiated” gland

cells. He reported the distribution of *C. montanus* to extend from Santa Barbara County, California, to northern Washington State along the Coastal and Cascade Ranges on *Pacifastacus leniusculus klamathensis* (Stimpson, 1857), *P. l. leniusculus*, and *P. l. trowbridgii*.

Description of branchiobdellid specimens from Yamaguchi's collection

Cambarincola okadai Yamaguchi, 1933

(Japanese name: Yadorimimizu)

Fig. 1A–F

Material examined.—Four mounted, unnamed specimens from (box.slide numbers: 2.4, 2.9, 2.10, 2.20) the oligochaete slide collection of Prof. H. Yamaguchi are almost certainly all or part of the syntype material; however, only Yamaguchi's ledgers can confirm this. Three of these specimens have been deposited in the Division of Biological Science, Graduate School of Science, Hokkaido University, Japan (ZIHU): slide 2.20 is designated the lectotype (ZIHU-1347) and slides 2.4 and 2.10 become paralectotypes (ZIHU-1348, ZIHU-1349), with the fourth slide—2.9—placed in the National Museum of Natural History, Smithsonian Institution, Washington D.C., U.S.A. (USNM) as the third paralectotype (USNM 186575).

Brief description.—Body rod-shaped (Fig. 1A), ranging in length from 3.4 to 4.7 mm (average length 3.9 mm) with dorsal ridges and supernumerary muscles absent. The segments are not pronounced and each appears to be divided into three annuli. The presence of an anterior nephridial pore could not be verified in these specimens, but it is expected to open medially on the dorsal surface of segment 3. There are paired, lateral groups of epidermal glands on segments 8 and 9. The peristomium has a dorsal lip with four distinct lobes (l) (or short tentacles), two pairs of lateral lobes, and a ventral lip (v) consisting of a pair of short lobes laterally and a central portion with a slight median incision (Fig. 1B).

There are 16 oral papillae present. The jaws are similar in size and triangular in shape with a large median tooth and 4 small lateral teeth on the anterior facing margin; dental formula 2-1-2/2-1-2. The ventral jaw is sometimes slightly smaller than the dorsal, with the base width ranging from 95 to 130 μm (Fig. 1C, D). The glandular atrium is about one third the diameter of the segment, tubular, folded, and with each vas deferens entering an ental lobe. The prostate gland arises at the meeting point of the glandular and muscular atria, and is slightly longer and wider than the glandular atrium (Fig. 1E). The prostate is lined with columnar gland cells which contain neither granular nor vacuolar secretions. The muscular atrium is short, about half the length of the glandular atrium, and leads into a protrusible penis (p) located in the ental portion of the pyriform bursa (b) (Fig. 1F). The length of the spermatheca is about half the diameter of the segment. The ental half consists of a tubular to sub-spherical bulb (sb) connected to a narrow duct (sd) that ends at the epidermis in a small papilla (Fig. 1E).

Variations.—The jaws are virtually the same size. The ventral jaw is usually slightly smaller than the dorsal, and the median region carrying the teeth of both is of constant size. However, the base of the jaws does vary in width; in the specimens examined dorsal jaws range from 95 μm (Fig. 1C) to 130 μm (Fig. 1D).

Comparison of the morphology between the description of C. okadai and the unlabeled specimens.—A comparison of character states of *C. okadai* reported by Yamaguchi (1933) with those observed from the four newly found, unlabeled slide specimens show many to be the same: the shape of the body; segments divided into three annuli; the peristomial appendages having the same arrangement, size and number; identical jaws in shape and dimensions; an unbranched spermatheca in segment 5; a pair of testes in both segments 5 and 6; and the “spermatic vesicle is bifid, having the ac-

cessory sperm tube” [prostate gland] in segment 6.

One character, body length, appears to differ as only a maximum body length of 7 mm was reported by Yamaguchi (1933). However, the specimen in his fig. 1 was calculated to have a length of about 5 mm and this compares well with the longest examined specimen being 4.7 mm. Therefore, the report of a 7 mm long body most probably resulted from the specimen reacting in a slightly different way to the preparation process. Another character dimension in close agreement is the width of the base of the jaws. In two of the type slides the aspect of the jaws has the same appearance as those in Yamaguchi's fig. 2. The measured distance (Fig. 1D) and the calculated distance in his fig. 2 result in both bases being 130 μm wide.

Comparison of the morphology between C. okadai and C. montanus.—The dental formula usually provides the most readily visible character for identification. The reported range in dental formula spans 7/5 (Goodnight 1940) to 1/1 (Holt 1974), however, a 5/5 arrangement was reported by both Holt (1974) and Gelder & Hall (1990), and appears to be the usual configuration. The prostate gland consists of secretory cells with either granular or vacuolar contents. Many fixatives, including that used by Holt (1986:679), preserve these cytological character states so that the state can be included in the species description of a *Cambarincola* species. In *C. montanus* the “cells . . . are highly vacuolated, that is, differentiated” (Holt 1974:68). This character is not always reliable in a specimen because some fixation procedures do not preserve the form of the secretions (Gelder, unpubl. data). The fixatives used on specimens of *C. montanus* collected from British Columbia, Canada (Gelder & Hall 1990), and on *C. okadai* are unknown, but both procedures turned the respective specimens brown indicating a similar postfixation effect. The contents of the prostate gland cells in both of these groups was unclear. There-

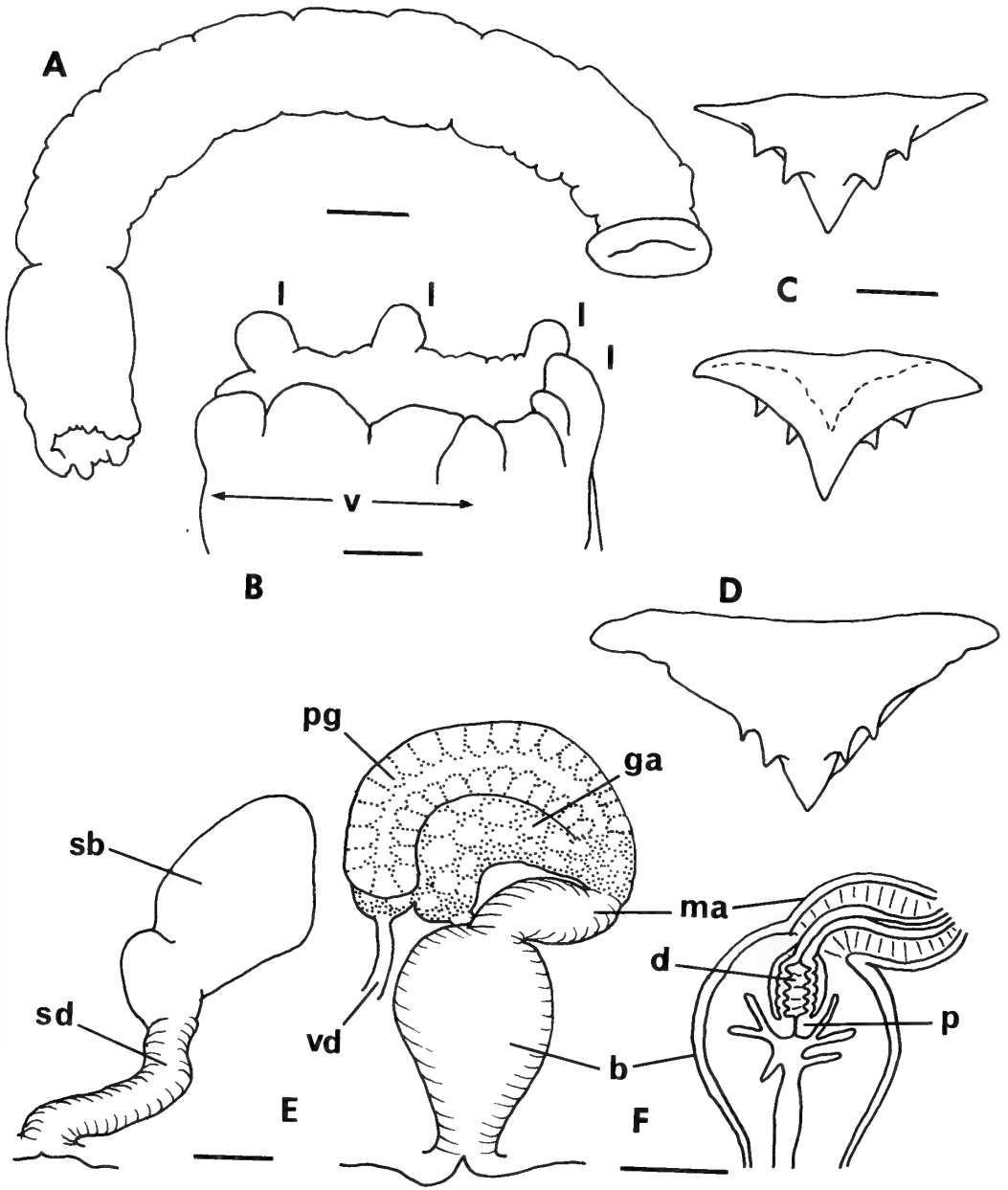


Fig. 1. *Cambarincola okadai*: A, Twisted oblique lateral view of the lectotype, scale bar = 0.1 mm; B, ventral view of the peristomium of a paralectotype, scale bar = 50 μ m; C, dorsal (above) and ventral (below) jaws of a paralectotype from the ventral aspect, scale bar = 25 μ m; D, dorsal jaw of another paralectotype from the ventral aspect, same scale as C; E, segments 5 and 6 with spermatheca (left) and male genitalia (right) respectively from a paralectotype drawn from a lateral aspect, scale bar = 50 μ m. F, optical section of the muscular atrium and penis in the dorsal portion of the bursa, scale bar = 50 μ m. Abbreviations: b, bursa; d, deferent duct; ga, glandular atrium; l, lobes on dorsal lip of peristomium; ma, muscular atrium; p, penis; pg, prostate gland; sb, spermathecal bulb; sd, spermathecal duct; v, ventral lip; vd, vas deferens.

fore, the vacuolar contents reported by Holt may not be significantly different from the cells reported in the Canadian and Japanese specimens. A key character for placing a species in the *Cambarincola* is the presence of a "protrusible" penis. The deferent duct in *C. okadai* is surrounded by the circular muscles of the muscular atrium and then passes into the dorsal portion of the bursa before ending in the penis (p) (Fig. 1F). The last portion of the deferent duct wall is greatly compressed into a concertina form (d) when the penis is retracted into the bursa. The penis in both *C. okadai* and reference specimens of *C. montanus* was found to be identical. The proportions of the spermatheca vary due to its position in the segment, degree of compression and presence or absence of spermatozoa in the bulb. Taking these factors into account, there are no significant differences between the spermathecae of the specimens examined.

Taxonomic conclusions.—The four specimens from the Yamaguchi collection have been identified as *C. okadai* based on their close morphological similarity to the type description. Current studies on crayfishes introduced into Japan require a complete species description of *C. okadai* to be available for comparison with newly collected branchiobdellids from imported crayfishes. Therefore, one of the four specimens was designated the lectotype and the three others as paralectotypes according to Article 74 (I.C.Z.N. 1999). In addition, *C. montanus* now becomes a junior synonym of *C. okadai* due to Article 23, Principle of Priority (I.C.Z.N. 1999).

Reported distribution.—The range of *C. okadai* extends from Santa Barbara County, California, to northern Washington State along the Coastal and Cascade Ranges in the U.S.A. (Holt 1974:68), British Columbia, Canada (Gelder & Hall 1990:2354), and Lake Chuzenji, Tochigi Prefecture, Japan (Yamaguchi 1933).

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Taxonomy and distribution of a new *Cossura* species (Annelida: Polychaeta: Cossuridae) from New Zealand

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Abstract.—The little-known polychaete family Cossuridae is given a detailed taxonomic record from New Zealand for the first time and its sole representative, *Cossura consimilis* new species, is described. The dorsal filament of *C. consimilis* originates on the anterior part of chaetiger 3, and there are at least 28 anterior-region chaetigers (usually 30). Distribution records are mapped from over 70 locations; *C. consimilis* is widespread in the New Zealand region, with most records from the nearshore subtidal, but the species has been found from extreme low water to the mid-continental slope (0–2330 m). The presence of benthic juveniles with extremely long capillaries may indicate a semi-planktonic dispersal phase occurs post-settlement. The taxonomic characters of all cossurid species are tabulated and discussed; the genus *Cossurella* is newly synonymized with *Cossura*.

The polychaete family Cossuridae, unique among polychaetes for possessing just one long branchial filament, has surprisingly not previously gained a substantive taxonomic record for New Zealand. Early polychaete collectors in New Zealand failed to find cossurids during the initial exploration of the fauna (Glasby & Read 1998), and even in recent ecological reports there are relatively few records, and only since the late 1970s. Reasons for this are examined later. In adjacent Australian waters the family has been reported at generic level from southern and eastern coasts, but not identified to species (Hutchings 2000). The brief description in Hutchings & Murray (1984) may indicate a different species from that in New Zealand.

The first cossurids collected in New Zealand waters are from hitherto unpublished records. Specimens were collected in Milford Sound by the Danish Galathea Expedition in 1952, and in Tasman Bay by the New Zealand Oceanographic Institute [now National Institute of Water & Atmospheric Research Ltd. (NIWA)] in 1960. *Cossura*

specimens were subsequently collected from Port Pegasus, Stewart Island in 1972 (survey of J. Lowry 1979), and from Whangarei Harbour in 1977 (survey of R. Mason & L. Ritchie 1979). Now there are many cossurid specimens in the NIWA collection, mostly taken within the last few years from intensive localised surveys.

The first ecological reports of cossurids in the literature are from coastal Hawke Bay (Knox & Fenwick 1978, 1981 (same data), Roper et al. 1989) as an unassigned *Cossura*. In the initial report the worms were found offshore from an ocean outfall at almost all stations from 4 to 17 meters depth. Maximum cossurid density was only about 1900 m⁻² about 2 km offshore. At about the same time the checklist of Day & Hutchings (1979) noted the presence of cossurids in New Zealand, but without giving a locality record. More recently a *Cossura* species was reported from NIWA stations off the northern west coast of South Island (Probert & Grove 1998), and from near Auckland (Cole 1997, and Cole, pers. comm.).

For this paper I have examined all NIWA material and re-examined specimens from the occurrences mentioned above; voucher material of all except the *Galathea* specimens is held in the NIWA collection.

The genus *Cossura* was monotypic until 1955, with *C. longocirrata* Webster & Benedict, 1887 of coastal Maine, U.S.A. as the sole species, and was regarded as belonging in the Cirratulidae until Day (1963) removed it to a family of its own. Cossurids are unique for their type of buccal apparatus as well as their single branchial filament, and are without close affinities to any other polychaete family (Fauchald & Rouse 1997, Rouse & Fauchald 1997). However, there is little diversity in their external morphology and specimens are rarely intact; although 23 cossurid species are named, many are unsoundly differentiated and based on inadequate material. Conversely, there is no evidence yet for the existence of cryptic cossurid species undetectable from gross appearance, but this remains a possibility as the biology of cossurids is poorly known.

Family Cossuridae Day

Cossura Webster & Benedict, 1887

Cossura Webster & Benedict, 1887:743.

Type species *C. longocirrata* Webster & Benedict, 1887. (emended).

Cossurella Hartman, 1976:234. Type species *C. dimorpha* Hartman, 1976.

Heterocossura Wu & Chen, 1977:100. Type species *H. aciculata* Wu & Chen, 1977.

Diagnosis.—Prostomium conical without appendages, without eyes; peristomium achaetigerous, usually subdivided at least dorsally by a transverse furrow. Single branchial filament arising middorsally on chaetiger 2, 3, 4, or 5. Chaetiger one uniramous, thereafter chaetigers biramous; chaetal lobes rarely present. A variable number of narrow anterior chaetigers with chaetal fascicles at anterior chaetal borders; grading thereafter into longer, often beaded

chaetigers with chaetal fascicles emerging at midlength. Anterior chaetae hirsute capillaries (usually in two distinct rows, anterior row with shorter, thicker chaetae); from midbody chaetae fewer and less hirsute, always several per fascicle unless thickened chaetae or short spines present; last few segments may be achaetigerous. Pygidium with three anal cirri, which may be branched; intercirral perianal processes may be present.

Remarks.—The following analysis of the taxonomic characters used in cossurids presents some points of difference from earlier reviews and also a re-evaluation of *Cossurella*.

Misinterpretations in past *Cossura* descriptions have been noted (Fournier & Petersen 1991, Bachelet & Laubier 1994, Hilbig 1996), and, while there is agreement that no achaetigerous post-peristomial segment exists, there is still uncertainty over the demarcation of prostomium and peristomium, difficult to determine in many Polychaeta, although not currently used as a taxonomic character in cossurids. The prostomial-peristomial region usually appears to have two transverse furrows dividing it into three parts, although the clarity of definition is dependant on the state of contraction of the worm. I suggest the prostomium is not subdivided, as has been interpreted by Fournier & Petersen (1991:70) for *Cossura longocirrata* and adopted by Hilbig (1996) for other cossurids. That would be unusual in polychaetes. The zone they regard as a posterior part of the prostomium is more probably the anterior part of the peristomium, as is indicated by Tzetzlin (1994) in his morphological study, and consistent with the earlier usage of Ewing (1984), and with other Polychaeta where nuchal organs are close to the posterior edge of the prostomium. So it is the peristomium, not the prostomium which may appear to be subdivided dorsally, and the peristomium which surrounds the mouth ventrally as expected.

The few external characters useful to

separate species are the point of origin of the branchial filament, the number of anterior region chaetigers, the pygidial ornamentation, and the sometimes-distinctive pattern on the anterior body when stained with methyl green (see Hilbig 1996). The major character is the precise point of origin of the branchial filament, which always occurs between chaetigers 2 to 5, usually just anterior or posterior to the segmental division. In some species this location is unique, but in 16 of the 23 known cossurids the origin is adjacent the segmental division between chaetigers two and three.

A second major character is the number of chaetigers of the anterior region (the so-called 'thoracic' region, but see Bhaud (1998) regarding the inappropriate use of this term for polychaetes) in which segments are wider than long, chaetal fascicles are immediately behind the segmental division, and gametes are always absent. In this region longitudinal musculature mostly fills the body cavity (Rouse & Tzvetlin 1997). This musculature is absent in the middle body where the body wall is thin and the coelomic space is either 'empty' or variably filled with gametes.

A number of authors have been unable to find a clear delineation between body regions. Additionally, most authors have been vague on how they determined when the anterior region ceased, and whether, when a chaetiger range was given, it represented a range between several individuals or a transitional zone in one specimen. The most information on variation is provided by Fournier and Petersen (1991) using material they accumulated of *Cossura longocirrata*. Its anterior region was between 16 and 21 segments long, with a transition in an individual over one or two segments. In all known cossurids the range in the number of thoracic chaetigers is 13 to 35. Differences are likely to be indicative rather than definitive when comparing species, unless based on very extensive meristic data.

The third major feature is the structure of the terminal anus and anal cirri. There is a

raised perianal pad usually with three well-separated, very thin, unbranched anal cirri which may be 2–3 body widths in length, but cirri that are branched, short or solitary have been reported and regarded as diagnostic. In view of the delicacy of these cirri, a single individual with cirri short or missing may be a damaged specimen, and it is doubtful if all such reports describe true species features. The perianal pad may bear radial corrugations, and in one species the pad has distinctive additional short cirri (the 'intercirral' processes) that are not retractable into the anus (Jones 1956).

The chaetal types and arrangements of all cossurids are very similar. In the anterior body there are two rows of capillaries which are distally hirsute, especially along the leading edge. Progressively along the body the number of capillaries decreases and they are more slender and less hirsute. Chaetigers are biramous except for the first. Short thickened chaetae may be present in some cossurids from mid-body, and four species with this character have been separated as the cossurid genus *Cossurella*, Hartman (Hartman, 1976). These spine-like chaetae are slightly hooked, and either occur one per fascicle, or accompanied by a single capillary (*Cossura sima* Fauchald, 1972, juveniles of *C. pettiboneae* (Ewing, 1987)). There are no other features the four have in common, and I consider separation at genus-level is unwarranted and at present unhelpful for cossurid systematics. A fifth species, *C. pseudakaina* (Ewing, 1987) initially placed in *Cossurella*, does not have this type of spine-like chaetae; instead there are single, basally-thickened hairy capillaries, which when broken appear to be blunt spines. This species does not belong with the other four, and its possession of only one chaeta per fascicle posteriorly suggests this cannot be used as a character to support *Cossurella* itself. Accordingly I maintain *Cossurella* and *Heterocossura* are junior synonyms of *Cossura*. *Heterocossura* was previously synonymized with *Cossurella* by Gardiner & Wilson (1979).

Cossura consimilis, new species

Figs. 1–4

Diagnosis.—Dorsal filament originating from anterior median surface of chaetiger 3. Anterior region of at least 28 chaetigers, and adult body with a total of at least 90 chaetigers. Spine setae absent. Pygidium divided vertically into two lobes, with three long cirri and without additional short cirri.

Holotype.—NIWA type collection H-704. A complete specimen, length 10 mm for 89 chaetigers and 0.46 mm wide at chaetiger 10, collected by NIWA divers in a hand-corer sample at NIWA station Z9253 (Transect 7 core 5), 26 m, sandy mud, 15 Mar 1998.

Type locality.—Big Glory Bay, Stewart Island, 46°58'54"S, 168°7'31"E.

Description.—The longest of 816 specimens available for study was incomplete at 17 mm for 79 chaetigers and 0.34 mm wide at chaetiger 10. The few complete specimens ranged from the smallest at 1.8 mm long for 26 chaetigers and 0.22 mm wide, up to the holotype with dimensions as above. The range of widths measured at chaetiger 10 was 0.22–0.66 mm (mean = 0.46 mm, $n = 70$).

Prostomium conical, dorso-ventrally flattened, with bluntly rounded tip. Eyes absent; low transverse ridges of dorsal nuchal organs visible at posterior lateral margin (Fig. 1A). Peristomium usually appearing subdivided, second longer part with the transverse mouth slit on its anterior ventral border. Anterior segments occasionally appearing weakly biannulated. Dorsal branchial filament originating on anterior median border of chaetiger 3, level with chaetal fascicles, with uniform proximal diameter, gently tapering distally, extending to about chaetigers 30–45, or nearly half the body length.

Chaetal fascicles emerging from anterior edges of each segment in the anterior body, but from about chaetiger 30 onwards emerge mid-chaetiger (Big Glory sample with range 28–32, mean = 30.33, $n = 21$).

Over the next few chaetigers the body widens and deepens and becomes more rounded in section, with longer chaetigers, lesser constriction between segments (especially if gametes are present—transition to so-called abdominal region), and more slender chaetae. Segments in posterior third of body are as long as those of the middle region, but appear more bead-like with a lateral dome-like parapodial base bearing the chaetal fascicle, except in far posterior segments, which are short with only slight indentation between them (Fig. 1C). All chaetigers after the first are biramous with a small gap between fascicles in most chaetigers. All anterior fascicles of chaetae in closely situated anterior and posterior rows. Chaetiger 1 with up to 4 chaetae per row, succeeding chaetigers with up to 9 per row. Numbers of noto- and neurochaetae similar, but in each posterior row often one more chaeta. Chaetae in single rows from mid-body, about 4 per fascicle. All chaetae of one basic type of curved capillary, with dense fine hairs covering the convex anterior face of the blade, and with tapering, fine smooth tips (Fig. 2). Anterior row of anterior body chaetae may appear almost spine-like at low magnification, and taper abruptly; posterior row of chaetae of uniformly thinner diameter and with longer tips, with the fascicle spread out fan-like, extending half a body height above and below the body and overlapping succeeding chaetae. Mid-body chaetae long and nearly smooth, posterior body chaetae shorter. Pygidium vertically cleft with three long very fine cirri, up to 1.8 mm long; medial cirrus arising ventral to anal orifice; perianal pad sometimes appearing corrugated or creased but without other processes (Fig. 1C). Pygidium preceded by several narrow segments, with only last 2–3 achaetigerous.

After methyl green staining the prostomium tip is always clear, with the heaviest staining immediately behind, and less intensive staining dorsally to posterior chaetiger 2 (Fig. 1B). Posterior to the pre-branchial region there is a less-stained dorsal median

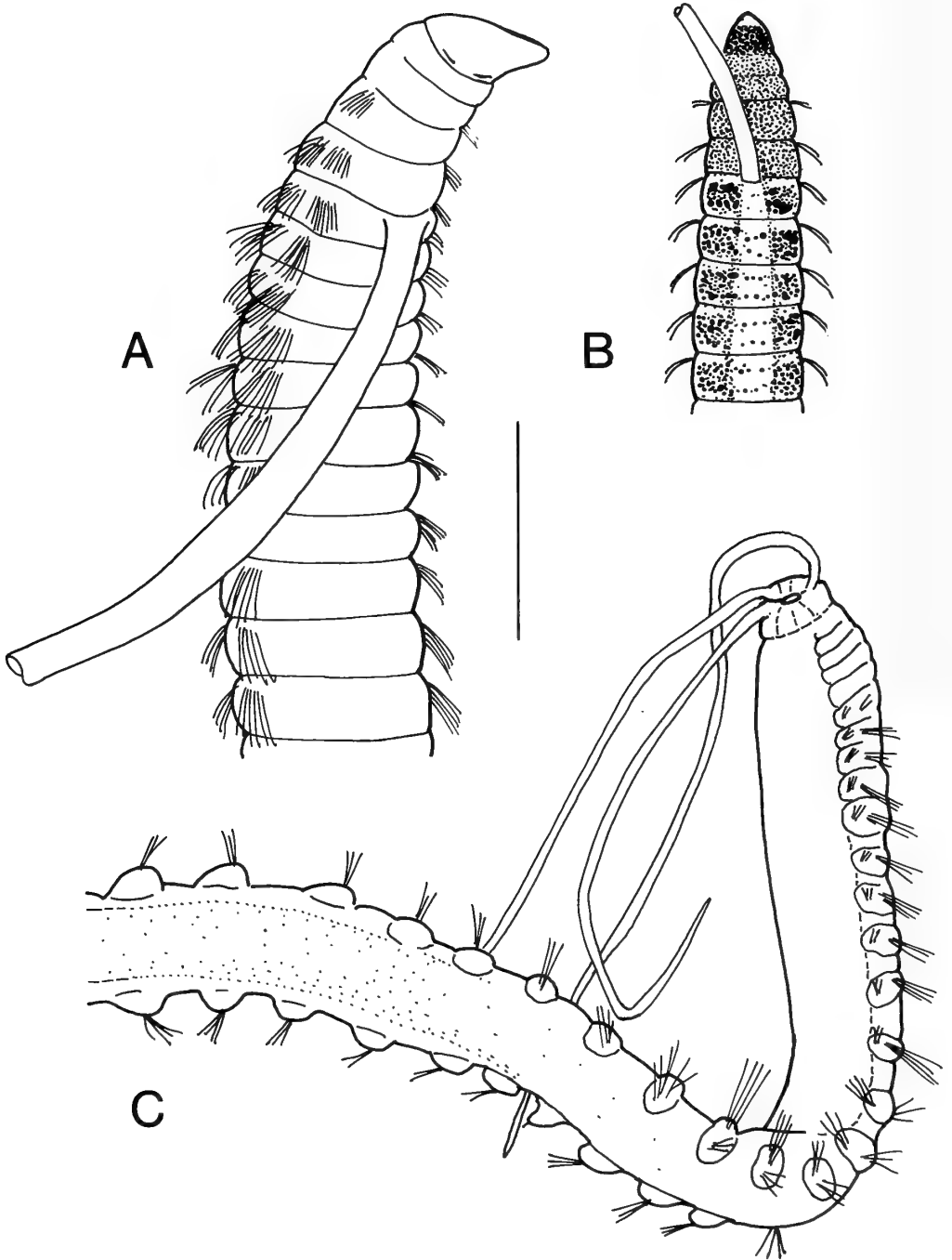


Fig. 1. *Cossura consimilis*, new species. A. Anterior dorsal region. B. Anterior dorsal region methyl-green staining pattern. C. Posterior region (body twisted from ventral to lateral view). Scale 0.5 mm (A and C), 1 mm (B).

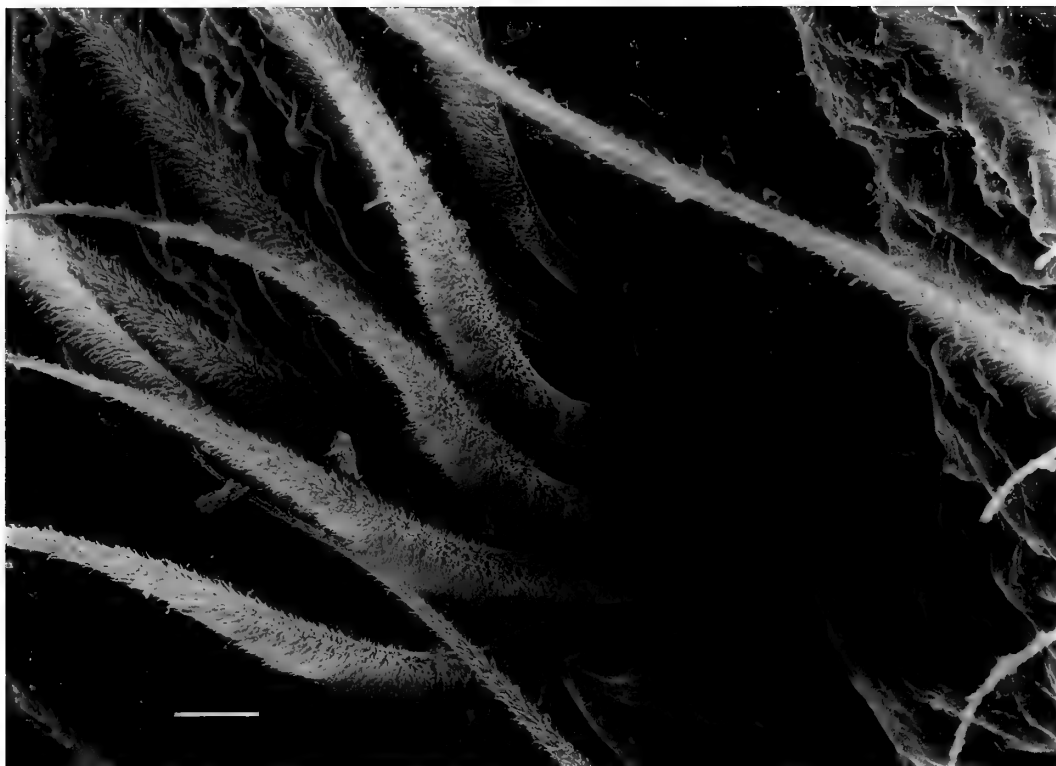


Fig. 2. *Cossura consimilis*, new species. Scanning electron microscope micrograph anterior lateral view of notochaetal fascicle of chaetiger 3. Scale 10 μ m.

strip continuing for a few chaetigers, creating the appearance of block-like lateral patches. Ventrally there are similar median and lateral pigment blocks. In better preserved specimens the staining has a distinct granular appearance as taken up by individual cells, particularly at the margin of 'blocks' (Fig. 1B).

Some juvenile specimens of 30–40 segments (collected in autumn at Clive, Hawke Bay—see material examined) had extraordinarily-long, fine, straight chaetae in both fascicles in the posterior two thirds of the body (from about chaetiger 13) instead of the usual short curved capillaries, with each chaeta up to 1.8 mm long compared to a body width of 0.25 mm (Fig. 3).

Remarks.—As far as is known *Cossura consimilis* is unique to New Zealand seas. If this is not the case its extensive distribution indicates a lengthy establishment in

New Zealand. Specimens occurred in muddy sediments over a depth range from extreme low water at Waiheke Island to 2330 meters depth south of the Chatham Rise, and from the far north to the far south of the New Zealand mainland islands (Fig. 4). *Cossura consimilis* has yet to be recorded from nearshore at the Chatham Islands, but seems likely to occur throughout the New Zealand region where there is suitable habitat. The late discovery of cossurids is probably because pioneering collectors simply overlooked the worms due to their small size, low density, and largely subtidal occurrence (*C. consimilis* probably never occurs exposed in the intertidal: zero depth records notwithstanding). Cossurids are also relatively nondescript in appearance, but it is very unlikely they were previously simply discarded as of no particular interest. Finally, while cossurids may increase

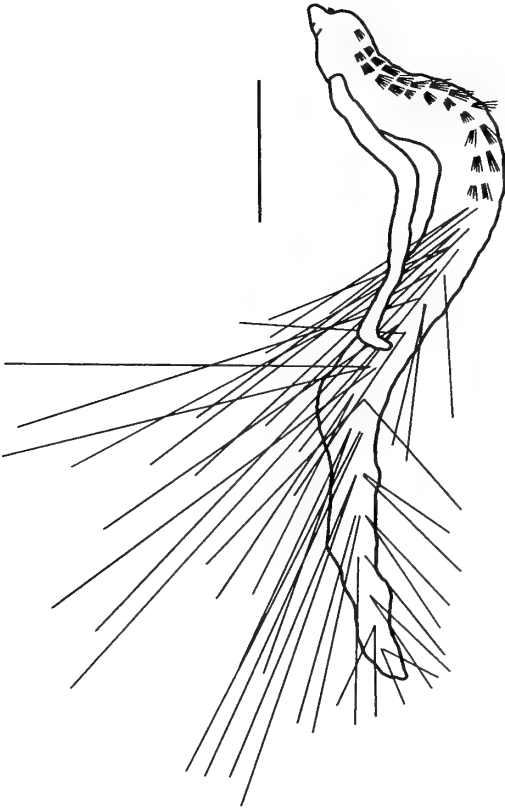


Fig. 3. *Cossura consimilis*, new species. Juvenile with natatory capillaries. The 27 chaetiger individual is near complete but its branchial filament is shortened by breakage. Scale 0.5 mm.

in density in response to local man-induced sediment changes (Olsgard & Hasle 1993), there are no reports of them as trans-oceanic adventive colonisers.

The specimens in the NIWA collection were taken from more than 70 locations (with multiple adjacent samples at some in-shore locations). The limited number of off-shore records is probably an artifact of past sampling techniques. Where appropriately fine sieving of 1 mm or less has been used on the Chatham Rise and off the western coast of the South Island, *Cossura consimilis* has been recorded from shelf to slope depths. However, most records are coastal or comparatively near shore, with occurrences in several major North Island harbours. On the South Island coast *C. consi-*

milis has been found to be widespread in inner Lyttelton Harbour (R. Asher, pers. comm.), also occurring in Timaru Harbour and Milford Sound, but has yet to be recorded from Otago Harbour, even though there has been extensive sampling there (e.g., Rainer 1981, Grove & Probert 1999, and K. Probert, pers. comm.). *Cossura consimilis* also occurs further south in Stewart Island waters.

In incomplete worms the posterior part of the body had broken off anterior to the start of the 2nd body region in 59.6% of worms ($n = 52$, Big Glory samples), and the break averaged between the 25th and 26th segment (25.16, range 17–29, $n = 31$). This indicates that fragmentation on collection is not mainly in the thinner-walled 2nd region (beginning around chaetiger 30) as might be expected. The division into two body regions is not sharply demarcated in *C. consimilis*.

The juvenile benthic *C. consimilis* specimens with extraordinarily-long fine chaetae are unlikely to have retained planktonic-larva chaetae through to such a late stage, and Bachelet & Laubier (1994) showed that juveniles of *Cossura pygodaetyla* have developed adult-type chaetae as early as a four chaetiger stage. A stronger possibility is that a semi-planktonic dispersal phase may occur post-settlement in young worms so equipped with these 'natatory' chaetae. Planktonic cossurid larvae have never been reported with one possible exception; Berkeley & Berkeley (1960) reported a single incomplete "larva" of 22 segments, 2 mm long, with "very long fine larval capillaries." Because of the large size of the specimen I suggest it was not a larval form but rather a post-settlement individual similar to those described here. There are at least two other prior reports of similar unusually long chaetae in postlarval non-reproductive polychaetes. These are the genus *Paraprionospio* spionids of 60 chaetigers found in plankton off Peru (Berkeley & Berkeley 1963), and the asexually-generated young benthic ctenodrilids of genus *Rar-*

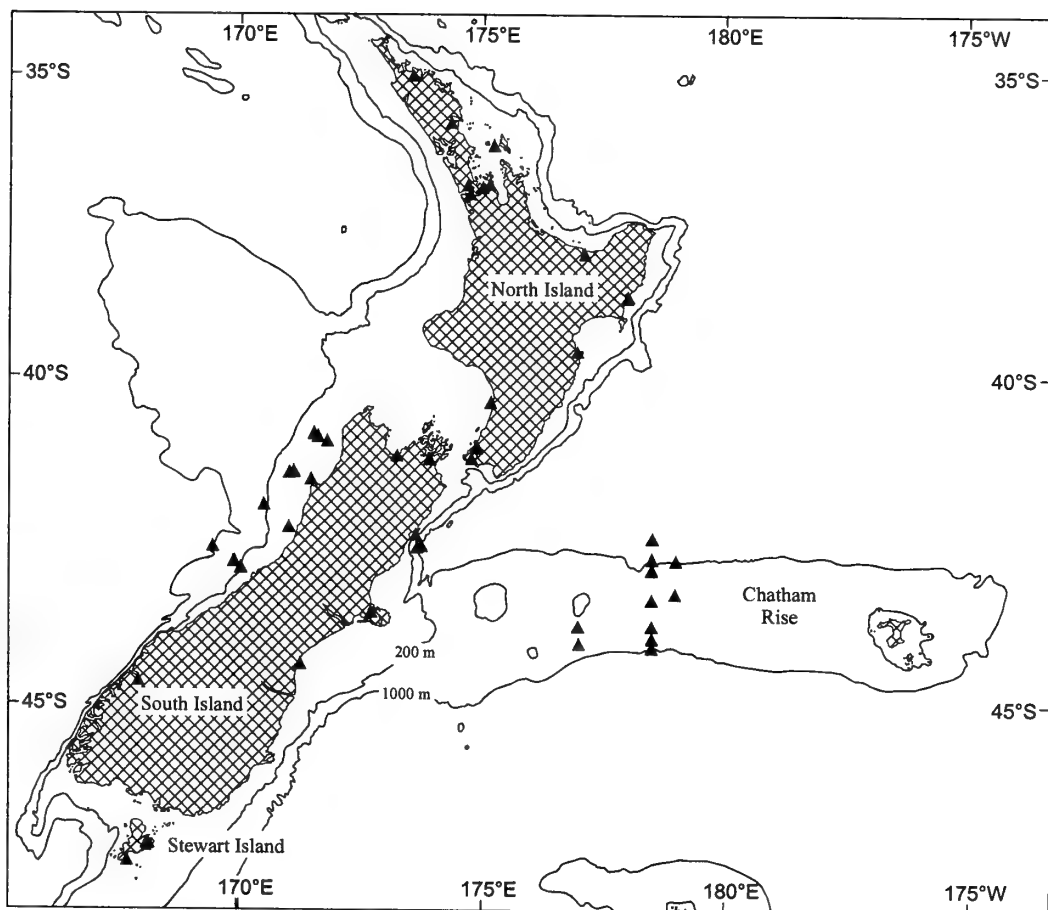


Fig. 4. Distribution of *Cossura consimilis*, new species, in the New Zealand region. Several of the coastline datapoints represent multiple stations (see material examined).

icirrus that Petersen & George (1991) called "dispersal forms".

Methyl green staining was of the basic cossurid pattern and not highly distinctive, except that wedge-shaped blocks were not seen just anterior to the branchial filament, contrary to the pattern in several *Cossura* species off California (Hilbig 1996).

Remarkably, 16 cossurid species are reported from North or South America, including 12 from the Pacific coast (Table 1). Hilbig (1996) was able to recognize several sympatric species from seas at and north of the Point Conception region of California, with up to three species in the same sample. If, as Hilbig maintains, *C. rostrata* is indeed

distinct from the very similar *C. candida*, then six cossurids coexist in this area. Further south the purported four species off the South American Pacific coast are all inadequately described. Of the species outside the Americas four are from the seas around China and Japan, two from the Indian Ocean, and one from the Mediterranean. However, most species are unknown outside their type localities. The four species with possibly wider distributions are: the Californian species *Cossura pygodactylata* Jones, 1956 and *C. brunnea* Fauchald, 1972, both also recorded off the North American Atlantic coast (Hilbig 1996), and the latter also from Korea (Paik 1997); *Cos-*

Table 1.—Characters from original descriptions of *Cossura* (including *Cossurella*) species, ordered by branchial filament placement then date of description. *Cossura lepida*, a synonym of *C. pygodactylata*, is included as a separate entry. Data enclosed by square brackets is from subsequent authors (identified in Remarks column). Distribution data excludes non-taxonomic papers and records categorized as questionable in prior papers.

Species	Anterior chaetigers	Anal cirri	Specimen numbers ^a & maximum dimensions ^b	Depth (m) & sediment	Type locality, further records	Remarks
Branchial filament arising from posterior of chaetiger 2						
<i>C. longocirrata</i> Webster & Benedict, 1887	[16–21]	3 long	1c 0.8 by 19 by 70	[7–887], mud	Maine, [eastern N. America, Arctic, Denmark]	[Fournier & Petersen 1991]
<i>C. pygodactylata</i> Jones, 1956	13–21	3 long	85 (15c) 0.3 by 12 by 64	[1–2720], mud	California, [N. American coasts, S. France & Spain]	6–10 intercirral processes [Hilbig 1996]
<i>C. soyeri</i> Laubier, 1963	31 [20–31]	unknown [3 long]	2 0.4 by ? by ? [0.35 by >7 by >45]	35, [muddy sand]	S. France, [Mediterranean, N. Gulf of Mexico]	incomplete [Bachelet & Laubier 1994]
<i>C. heterochaeta</i> Orensanz, 1976	—	unknown	4 ? by >9 by >37	150–310, sand-mud	Argentina	incomplete anterior neurosetal spines
<i>C. lepida</i> Tamai, 1986 (= <i>C. pygodactylata</i> (fide Hilbig 1996))	13	3 long	21 (1c) 0.3 by 12 by 64	2–21, mud	Japan	20 intercirral processes
Branchial filament arising from anterior of chaetiger 3						
<i>C. laeviseta</i> Hartmann-Schröder, 1962	14?	3 short	13 (1r?) 0.4 by >2.5 by >21	7, —	Peru	ventral peristomial 'eye' pair (pigment spots?) incomplete
<i>C. chilensis</i> Hartmann-Schröder, 1965	—	unknown	5 0.4 by >4 by >28	50–160, mixed	Chile	incomplete
<i>C. abyssalis</i> Hartman, 1967	—	unknown	9 0.5 by >4 by >23	3655, —	Chile	incomplete
<i>C. sima</i> Fauchald, 1972	28	unknown	11 1.5 by >26 by >55	2307–3544, —	W. Mexico	dark spots, spines present
<i>C. dayi</i> Hartman, 1976	—	unknown	465 ? by >7 by ?	16–1006, —	Indian Ocean	incomplete
<i>C. aciculata</i> (Wu & Chen, 1977) new combination	22	unknown	>2 2 by >75 by >112	6, —	China	incomplete spines present
<i>C. duplex</i> Tamai, 1986	14	3 short	45 (1c) 0.5 by 22 by 90	4–16, mud	Japan	biannulate anteriorly
<i>C. pseudakaina</i> (Ewing, 1987) new combination	27–30	1 short, plus papillae	4 (1c) 0.6 by 14 by 81	104–570, sand-mud	Gulf of Mexico, Caribbean Sea	"spines" present

Table 1.—Continued.

Species	Anterior chaetigers	Anal cirri	Specimen numbers ^a & maximum dimensions ^b	Depth (m) & sediment	Type locality, further records	Remarks
<i>C. consimilis</i> new species	28–32	3 long	816 (8c 23t) 0.7 by 17 by 90	0–2330, fine sand-mud	New Zealand	—
<i>C. candida</i> Hartman, 1955	24–35	3 long	Branchial filament arising from midlength of chaetiger 3 ~300 (7c > 1t) 1.0 by 19 by 150	11–2400, sand-mud inshore, clay	California, W. Mexico	—
<i>C. delta</i> Reish, 1958	—	unknown	~100 (0.5 by 66 by >25) ^c	—	N. Gulf of Mexico	incomplete
<i>C. coasta</i> Kitamori, 1960	—	3 long, branched	~100 (2c) 0.6 by 15 by 107	inshore, —	Japan ^d	—
<i>C. brunnea</i> Fauchald, 1972	16–18	3 long	36 0.5 by 8 by >63	[1600–2200], “mixed”	California, [N. American coasts & offshore, Korea]	incomplete, body brown [Hilbig 1996, Paik 1997]
<i>C. rostrata</i> Fauchald, 1972	19–21	[3 long]	16 1.2 by >11 by >57	[6–3348], sand-mud	W. Mexico, [W. N. America]	setae notably hairy [Hilbig 1996]
<i>C. bansei</i> Hilbig, 1996	20–31	3 long?	Branchial filament arising from posterior of chaetiger 3 ~10 (7t) 0.5 by >6 by >71	18–160, sand-silt	California, W. N. America	—
<i>C. dimorpha</i> (Hartman, 1976) new combination	29	unknown	Branchial filament arising from anterior of chaetiger 4 30 0.8 by >10 by >48	34–110, —	Mozambique, N. Indian Ocean	incomplete spines present
<i>C. pettiboneae</i> (Ewing, 1987) new combination	23	unknown	6 1.5 by >34 by >73	257–530, sand-mud	Puerto Rico	incomplete spines present, body brown
<i>C. modica</i> Fauchald & Hancock, 1981	[14–26]	[3 short]	Branchial filament arising from posterior of chaetiger 4 40 0.5 by >6 by >35 [0.5 by 16 by 127]	[985–2955], sand-silt	Oregon, [California]	incomplete [parapodial lobes posteriorly, extra long filament (Hilbig 1996)]
<i>C. alba</i> Hartman, 1967	—	unknown	1 1.5 by >16 by >23	957, —	Chile	filament arises at 4/5 border

^a All specimens are incomplete with tail sections unknown except as noted ((c)omplete, (t)ails).

^b Dimensions are width by length by chaetiger number (prefixed by > if incomplete); lengths rounded to the nearest millimeter and width to nearest 0.1 mm.

^c The *Cossura delta* holotype is abnormally long relative to the number of chaetigers (and to paratypes); the length as published may be a transcription error.

^d The *Cossura coasta* recorded from the Eastern Mediterranean (Bogdanos & Fredj 1983) appears likely to be a misidentification.

sura longocirrata, which may have an ampho-Atlantic occurrence (Fournier & Petersen 1991), although first described from Maine; and *C. soyeri* Laubier, 1963 from the Mediterranean and the northern Gulf of Mexico (Bachelet & Laubier 1994). *Cossura pygodactylata* has also been further recorded from the Bay of Biscay (Bachelet & Laubier 1994), and from Japan (as *Cossura lepida* Tamai, 1986 (fide Hilbig 1996)). *Cossura soyeri* Laubier, 1963 from France is distinct from *C. delta* Reish, 1958 from Gulf of Mexico, although synonymy was advocated by Granados-Barba & Solis-Weiss (1997).

There has yet to be a comparison of types of the putative 23 species. Since 16 of those species were described from incomplete specimens (i.e., head-end fragments only) there may be little benefit from so doing (for the same reasons a table rather than a key has been presented here). Of all cossurids only *C. pygodactylata* was described from several intact specimens. For all other species combined the number of intact cossurids examined is only six specimens in total, with nine species based on rather inadequate material (<10 incomplete specimens). Intact cossurids are very rare in benthic collections, and body pieces other than anterior ends may be mostly discarded unrecognized by sorters.

Cossura consimilis is one of nine species with the dorsal filament arising from the anterior part of chaetiger 3 (Table 1). Of these species, *C. laevichaeta* (Peru) is unique for possessing what were described as ventral 'eyes' (pigmented subdermal structures) on the peristomium and has 3 short anal cirri; *C. duplex* (Japan) has biannulated segments and short anal cirri; *C. pseudakaina* (Gulf of Mexico) has one short cirrus plus papillae; *C. sima* (W. Mexico), *C. aciculata* (China) have thickened chaetae in posterior segments ('*Cossurella*' group); *C. chilensis* (Chile), *C. abyssalis* (Chile), and *C. dayi* (Indian Ocean) are inadequately characterized from incomplete material. Hartman (1976) erected the new name *C. dayi* osten-

sibly for *C. coasta* sensu Day, 1963, which has the branchia on the anterior edge of chaetiger 3 rather than at midlength as in *C. coasta* Kitamori, 1960. However, her description was based only on her own incomplete specimens, which were not from the same geographic area as Day's. Next, if the five species in which the filament is midlength chaetiger three are compared to the New Zealand *Cossura consimilis*, then *Cossura rostrata* (Western Mexico) and *C. candida* (California) appear to be the most similar of this group, but differ in staining pattern as well as branchia position. None of the five species in which the filament is at the posterior of chaetiger two appear to be close in other characters to the New Zealand *C. consimilis*. Finally, species with a similar number of anterior-region chaetigers are: *Cossura sima* and *C. dimorpha* (with spines); *C. pseudakaina* (single posterior capillaries); and *C. candida* (filament arising from midlength of chaetiger three).

It is with some reluctance that I have added another *Cossura* to the genus. I believe that this species does not fit comfortably into any of the previous good descriptions, and that there is little prospect of resolving those that have been inadequately described. As there are no *Cossura* species described yet from New Zealand, Australia, and neighboring South Pacific regions, I elect to provide a benchmark description and establish a name based on the extensive material held at NIWA.

Etymology.—The specific name is from the Latin *consimilis*, meaning "like in all respects." Its derivation follows the example of *Cossura modica* Fauchald & Hancock, which was also named for its ordinariness, as the New Zealand species is unique only by its combination of features.

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Appendix I

Material examined

Samples collected by NIWA (station identifier a letter followed by 4 digits) unless indicated otherwise, arranged in North-South locality order and in alphanumeric order of station within locality. Specimen counts in parenthesis if more than one; sediment type noted as available; sampler abbreviations are 'CB' box corer, 'DA' anchor box dredge.

Mangonui Harbour, 35°00'S, 173°33'E: (2), 0 m, soft sand, hand, G. Read, 15 Feb 1979.

Portland, Whangarei Harbour, 35°48'30"S, 174°20'36"E: (28), T12, 0 m, sandy mud, hand, R. Mason, 1977.

Hauraki Gulf, 36°11'12"S, 175°13'30"E: I0052, 63 m, Agassiz trawl, 9 May 1975.

Te Makuku Bay, Waiheke Island, 36°50'20"S, 175°8'9"E: (2), Z9029, 0 m, muddy sand, hand, 13 Feb 1998.

Waitemata Harbour, 36°50'43"S, 174°41'20"E: (12), L9860, 4 m, muddy fine sand, B. Hayward, Auckland Museum AK130784, 11 Jan 1995.

Pine Harbour marina, Tamaki Strait, 36°53'18"S, 174°59'12"E: (2), PH9, 3 m, sandy mud, R. Cole, 1997. (153) (stations Z9644–46 include 60 samples), Z9644, 17 Jun 1998, Z9645, 16 Jul 1998, Z9646, 28 Sep 1998, 2–6 m, sandy mud, diver dredge, R. Cole.

Pollok Beach, Manukau Harbour, 37°0'0"S, 174°43'59"E: S0696, 0 m, hand dredge, 23 Aug 1986.

Ohiwa Harbour, 37°59'S, 177°6'E (approx): (276) (one complete), 0 m, hand, pooled stations of unpublished MAF Ohiwa Survey, J. Akroyd, voucher set in NIWA collection, Jan 1980.

Gisborne, 38°41'19"S, 178°0'E: (15), stations of Roper et al, 1989, 10 m, D. Roper, voucher set in NIWA collection, 1984. 38°42'54"S, 177°59'24"E, Z9717, 20 m, muddy sand, 1 Feb 1999, R. Cole.

Clive, Hawke Bay, 39°34'48"S, 176°57'12"E: (86(6 complete)), April 1976, 4–16 m, fine sand to very fine silt, grab, 37 specimen lots from 28 stations, G. Knox & G. Fenwick, NIWA Knox collection. 39°34'33"S, 176°58'E: (25), 4–16 m, MOWD outfall survey, D. Roper, voucher set NIWA collection, 1984.

Offshore Wanganui, 40°23'24"S, 175°10'26"E: Z6528, 33 m, muddy sand, Shippek grab, 23 Mar 1989.

Pauatahanui Inlet, 41°5'59"S, 174°52'59"E: M0006A, 0.5 m, mud, suction dredge, 01 Nov 1974. M0042A, 0.5 m, suction dredge, 08 Feb 1975. 41°06'S, 174°54'E: (10), 1.5–2 m, mud, hand core, G. Read, 21 Apr 1979, 12–13 May 1984.

Wellington Harbour, (5 total from 5 adjacent sta-

tions), 41°16'0"S, 174°46'59"E: Z8238, Z8239, Z8240, Z8246, Z8273, 7 m, mud, 1 Mar 1993.

Tasman Bay, 41°13'29"S, 173°14'24"E: C0479, 9 m, soft mud, orange-peel grab, 9 May 1960.

Pelorus Sound, 41°16'12"S, 173°55'11"E: C0939, 9 m, soft mud, orange-peel grab, 12 Feb 1963.

Offshore western South Island, (20 total from 18 stations), 41°28'47"S, 171°1'36"E: Q0703, 202 m, muddy sand, 4 Feb 1982. 42°56'41"S, 170°1'36"E: S0371B, 194 m, mud, CB, 8 Jan 1983. 42°51'11"S, 169°52'30"E: S0374A, 496 m, mud, CB, 9 Jan 1983. 42°50'48"S, 169°53'48"E: (2), S0374C, 464 m, mud, CB, 9 Jan 1983. 42°37'18"S, 169°26'42"E: S0377A, 975 m, mud, CB, 9 Jan 1983. 42°19'36"S, 171°1'0"E: S0382B, 124 m, mud, CB, 2 Feb 1983. 41°58'54"S, 170°30'11"E: S0385A, 497 m, muddy sand, CB, 3 Feb 1983. 40°59'48"S, 171°48'24"E: S0393B, 127 m, sandy mud, CB, 7 Feb 1983. 41°35'24"S, 171°28'12"E: (2), S0394A, 127 m, mud, CB, 8 Feb 1983. 41°35'24"S, 171°28'23"E: S0394B, 126 m, mud, CB, 8 Feb 1983. 41°35'24"S, 171°28'36"E: S0394C, 125 m, mud, CB, 8 Feb 1983. 41°27'47"S, 171°6'47"E: (2) S0395A–B, 178 m, mud, CB, 8 Feb 1983. 40°55'36"S, 171°37'0"E: S0397C, 154 m, sandy mud, CB, 9 Feb 1983. 40°51'59"S, 171°31'59"E: S0398, 175 m, muddy sand, CB, 10 Feb 1983. 40°52'48"S, 171°31'36"E: S0398C, 177 m, muddy sand CB, 9 Feb 1983. 42°31'0"S, 170°10'0"E: S0895A, 836 m, sandy mud, 9 Jul 1991.

Offshore Kaikoura, (26 total from 3 stations), 42°26'23"S, 173°37'54"E: (3), U0231, 38 m, sand, 8 Dec 1982. 42°38'5"S, 173°39'38"E: (3), U0247, 120 m, muddy sand, 1 Dec 1982. 42°36'42"S, 173°44'50"E: (20) U0263, 1496 m, mud, 5 Dec 1982.

Chatham Rise, (30 total from 20 stations), 42°29'43"S, 178°30'47"E: S1049K, 2330 m, CB, 30 Apr 1997. 42°48'16"S, 178°30'19"E: S1053A, 1016 m, mud, CB, 1 May 1997. 42°48'32"S, 178°30'29"E: S1053K, 1004 m, mud, CB, 1 May 1997. 42°48'29"S, 178°30'11"E: (2), S1053L, 1005 m, mud, CB, 1 May 1997. 42°58'19"S, 178°30'26"E: S1054B, 453 m, mud, CB, 1 May 1997. 42°58'19"S, 178°30'18"E: (2), S1054C, 455 m, mud, CB, 1 May 1997. 43°25'52"S, 178°29'43"E: (3), S1055B, 348 m, CB, 2 May 1997. 43°25'54"S, 178°29'35"E: (2), S1055C, 348 m, CB, 2 May 1997. 43°49'38"S, 178°29'50"E: S1060D, 452 m, muddy sand, CB, 3 May 1997. 43°49'37"S, 178°30'13"E: S1060H, 451 m, muddy sand, CB, 3 May 1997. 44°8'31"S, 178°29'55"E: S1065G, 994 m, CB, 5 May 1997. 43°25'59"S, 178°29'53"E: (4), S1066C, 350 m, muddy sand, CB, 6 May 1997. 43°26'0"S, 178°30'1"E: S1066D, 348 m, muddy sand, CB, 6 May 1997. 44°0'13"S, 178°30'16"E: (2), S1071B, 757 m, CB, 7 May 1997. 44°0'10"S, 178°30'10"E: S1071C, 757 m, CB, 7 May 1997. 42°58'32"S, 178°29'38"E: (2), S1072D, 442 m, muddy sand, CB, 7 May 1997. 42°49'50"S, 178°59'32"E: V0369, 1048 m, DA, 1 Sep 1989. 43°20'7"S, 178°58'52"E: V0372, 418 m, muddy sand, DA, 3 Sep

1989. 44°5'4"S, 177°0'0"E: V0378, 663 m, muddy sand, DA, 4 Sep 1989. 43°49'28"S, 176°58'54"E: V0379, 495 m, DA, 4 Sep 1989.

Timaru Harbour, (5 total from 4 stations), 44°23'33"S, 171°15'15"E: Z9045, 10 m, mud, 11 Apr 1998. 44°23'32"S, 171°15'18"E: Z9046, 12 m, mud, 11 Apr 1998. 44°23'33"S, 171°15'24"E: Z9047, 10 m, mud, 11 Apr 1998. 44°23'12"S, 171°15'49"E: (2), Z9059, 11 m, mud, 12 Apr 1998.

Milford Sound, 44°39', 167°55'E: (5), Galathea Station 613, 214 m, mud, Petersen Grab, Galathea Expedition, (Zoological Museum, University of Copenhagen collection), 19 Jan 1952.

Stewart Island, Big Glory Bay (88 total from 9 stations, 1 complete, also 23 tail ends) 46°58'48"S,

168°8'8"E: Z9248, 25 m, core, 13 Mar 1998. 46°58'34"S, 168°7'58"E: Z9251, 25 m, core, 14 Mar 1998. 46°59'9"S, 168°7'36"E: (2), Z9252, 27 m, sandy mud, core, 14 Mar 1998. 46°58'54"S, 168°7'31"E: (10), Z9253, [HOLOTYPE] 26 m, sandy mud, core, 15 Mar 1998. 46°58'41"S, 168°6'53"E: (16), Z9254, 27 m, sandy mud, core, 15 Mar 1998. 46°58'43"S, 168°6'23"E: (7), Z9255, 25 m, core, 16 Mar 1998. 46°58'54"S, 168°6'19"E: (17), Z9256, 27 m, sandy mud, core, 16 Mar 1998. 46°59'13"S, 168°6'29"E: (13), Z9257, 27 m, core, 16 Mar 1998. 46°58'58"S, 168°6'4"E: (21), Z9258, 26 m, core, 17 Mar 1998.

Stewart Island, Port Pegasus, 47°14'S, 167°42'E (approx.) (19), PP1-PP4, 45 m, J. Lowry, NIWA G. Knox collection, 23 Mar 1972.

Revision of the genus *Leonnates* Kinberg, 1866 (Polychaeta: Nereididae), with descriptions and comments on other species described in *Leonnates*

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Abstract.—The genus *Leonnates* Kinberg, 1866 (Polychaeta: Nereididae) is characterized by the presence of both papillae and paragnaths on the pharynx, and either only spinigers or spinigers and falcigers on the notopodia. Although the identity of several *Leonnates* species is in doubt, no systematic revision of the genus has been undertaken. In this study, we examine the validity of the following species that have been described as *Leonnates* or are related to *Leonnates*: *L. indicus* Kinberg, 1866, *L. virgatus* Grube, 1873, *L. pusillus* Langerhans, 1880, *L. jousseaumei* Gravier, 1899, *Australonereis ehlersi* (Augener, 1913), *L. niestrasi* Horst, 1924, *L. decipiens* Fauvel, 1929, *L. insolitus* Gravier & Dantan, 1934, *L. simplex* Monro, 1939, *L. persicus* Wesenberg-Lund, 1949, *Paraleonnates uschakovi* Chlebovitsch & Wu, 1962, *L. decipiens* var. *manilensis* Pillai, 1965, *L. stephensoni* Rullier, 1965, *Websterinereis glauca* Pettibone, 1971, *L. nipponicus* Imajima, 1972, *L. crinitus* Hutchings & Reid, 1991, and *L. bolus* Hutchings & Reid, 1991. Our examination of available type specimens and additional material shows that *L. virgatus* and *L. jousseaumei* are conspecific with *L. indicus*; *L. decipiens* var. *manilensis* is conspecific with *L. decipiens*; *Leonnates bolus* belongs to *Paraleonnates*; *Leonnates niestrasi*, and *L. insolitus*, described from heteronereidid specimens, can not be fully characterized. *Leonnates nipponicus* was not available for examination; its original description indicates a distinct difference from *L. indicus*. Characters of *A. ehlersi*, originally described in the subgenus *Leonnates* in *Nereis*, are discussed. *Leonnates pusillus* is indeterminable to genus. Some specimens originally identified as *L. jousseaumei* are heteronereidids of *Perinereis*. Descriptions of *Leonnates* and related species and a key to atokous *Leonnates* species are provided.

In the original description of the genus (Kinberg 1866), the following characters were used to define *Leonnates*: pharyngeal areas I and V smooth; pharyngeal areas II, III, IV with paragnaths; pharyngeal areas VI, VII–VIII with papillae; anterior and posterior parapodia similar; dorsal and ventral rami separate; with compound spinigers and falcigers; and dorsal cirri not foliaceous.

To date, fourteen species and one variety have been described in the genus, all from

tropical or subtropical coastal areas. There are a number of problems with the described species. The type species, *L. indicus*, was described only briefly and has been considered dubious or unrecognizable by some workers (e.g., Horst 1924, Monro 1939). A number of synonymies between the described species have been suggested, although without convincing evidence [e.g., between *L. indicus* and *L. jousseaumei* by Monro (1931) and between *L. jousseaumei* and *L. virgatus* by Hartman (1959)]. Two

of the species, *L. niestraszi* and *L. insolitus*, were described only from heteronereidid specimens, which have significantly modified parapodia and setae. Three other described species, *L. pusillus*, *Nereis* (*Leonnates*) *ehlersi*, and *L. bolus*, do not belong to the genus at all.

Some original characters defining the genus are also in doubt. The pharynx of *Leonnates* together with *Paraleonnates* Chlebovitsch & Wu, 1962 is characterized by the presence of soft papillae on the oral ring and paragnaths on the maxillary ring. However, papillae were described on area IV of the maxillary ring in *L. virgatus* Grube, 1873 and *L. nipponicus* Imajima, 1972, and Monro (1931) and Hutchings & Reid (1991) noted partially hardened paragnaths on area IV of *L. jousseumei* Gravier, 1899. Furthermore, the setae in the described species of *Leonnates* are predominantly homogomph spinigers and falcigers, which have been described with a variety of terms (Monro 1939, Wesenberg-Lund 1949, Pillai 1965, Rullier 1965, Hutchings & Reid 1991). Some of these terms refer to the same type of seta [e.g., the falcigers of *L. persicus* were said to be heterogomph and fairly heterogomph by Wesenberg-Lund (1949) and slightly heterogomph by Rullier (1965)].

The aim of this study is to address these problems, to redescribe valid species, whenever possible, on the basis of type and non-type material and to redefine the genus *Leonnates*.

Materials and Methods

Line drawings were made with the aid of a camera lucida attached to a stereomicroscope or a video camera attached to a compound microscope. Parapodia used for scanning electron microscopy (SEM) were transferred sequentially from 70% ethanol to de-ionized water, frozen in liquid nitrogen, freeze-dried with a Virtis 12SL drying unit, gold-coated with a Denton Vacuum

Desk II sputter coater, and observed using a JOEL 6300 SEM.

The names of the following institutions are abbreviated in the text: Australian Museum, Sydney (AM); The Hong Kong University of Science and Technology (HKUST); Institute of Oceanology, Chinese Academy of Science, Qingdao (IOCAS); Museum of Natural History, Wroclaw University (MNHWU); Muséum National d'Histoire Naturelle, Paris (MNHN); National Science Museum, Tokyo (NSMT); National University of Singapore (NUS); National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM); The Natural History Museum, London (BMNH); Natural History Museum, Vienna (NHMV); Northern Territory Museum of Arts and Sciences, Darwin, Australia (NTM); Queensland Museum, Brisbane, Australia (QM); Swedish Museum of Natural History, Stockholm (SMNH); Western Australian Museum, Perth (WAM); Zoological Museum, University of Copenhagen (ZMUC); Zoological Institute and Zoological Museum, University of Hamburg (ZIM); Zoological Museum Amsterdam, University of Amsterdam (ZMA).

Systematics

Leonnates Kinberg, 1866

Leonnates Kinberg, 1866:168; Imajima 1972:41; Fauchald 1977:89; Wu et al. 1981:65; Hutchings & Reid 1991:48.

Type species: *Leonnates indicus* Kinberg, 1866 (by monotypy).

Diagnosis.—Eversible pharynx with pair of jaws, soft papillae and occasionally paragnaths on oral ring, paragnaths and occasionally soft papillae on maxillary ring. Prostomium with pair of antennae, pair of biarticulate palps and 2 pairs of eyes. Peristomium with 4 pairs of tentacular cirri. Parapodia biramous, except first 2 pairs. Notopodia with dorsal notopodial ligule, infra-acicular ligule, and often supra-acicular ligule. Neuropodia with presetal acicular

lobe or ligule, postsetal lobe or ligule, and ventral ligule. Notosetae homogomph spinigers and occasionally homogomph falcigers. Neurosetae homogomph or heterogomph spinigers and homogomph or heterogomph falcigers. By SEM, ends of the setal shaft with a large solitary tooth and a circular fringe of smaller teeth.

The currently accepted generic definition of *Leonnates* (e.g., Fauchald 1977) includes the following: pharynx with papillae on the oral ring and paragnaths on the maxillary ring; four pairs of tentacular cirri; biramous parapodia; notosetae homogomph spinigers; neurosetae heterogomph falcigers. Most *Leonnates* species share these features. However, this definition has not taken into account the variation of some of the characters. The papillae on area IV of the maxillary ring of *L. indicus* can be sclerotized to different extents. Paragnaths are present on area VI of the oral ring of *L. simplex*. In addition to spinigers, falcigers are also present on the posterior notopodia of *L. indicus*. Although the neuropodial falcigers of *L. decipiens*, *L. simplex*, and *L. crinitus* are heterogomph, in other species they are homogomph. Some parapodial characters shared by all *Leonnates* species are not included in the generic definition. The neuropodial acicular lobe of *Leonnates* consists of a rounded presetal lobe or a conical presetal ligule and a postsetal ligule or postsetal lobe. The generic diagnosis was, therefore, emended to accommodate these features. This change, however, does not affect its relationship with other nereidid genera.

Leonnates indicus Kinberg, 1866
Figs. 1–3; Table 1

Leonnates indicus Kinberg, 1866: 168.

Leonnates virgatus Grube, 1873: 68.

Nereis (Leonnates) virgata Grube, 1878: 63–64, pl. 4, fig. 7.

Leonnates Jousseaumi Gravier, 1899: 234–237.

Leonnates Jousseaumei Gravier 1901: 160–

164, pl. 11, figs. 34–37; text-figs. 162–165.

Leonnates jousseaumei. Fauvel 1919: 400; Horst 1924: 150; Fauvel 1930: 19, fig. 5A–E; Monro 1931: 43–44, fig. 4A; Fauvel 1932: 85; Monro 1939: 403; Fauvel 1953: 169–170, fig. 86D–F; Day 1967: 330–331; Wu et al. 1981: 67–68, fig. 38; Hutchings & Reid 1991: 52–53.

Material examined.—*Leonnates indicus*: holotype from Knoll, Singapore (SMNH 535); *L. virgatus*: the Philippines, coll. Semper (1 holotype or syntype); *L. jousseaumei*: Obock, Red Sea, 1895, coll. Jousseaume (14 syntypes) (MNHN A78); Suez Gulf and Canal, 1928 & 1933, coll. Fauvel (7 specimens) (MNHN A304); Strait of Makassar, St. 14, 25–34 m, 16 Dec 1908, coll. van Kampen (1 specimen) (ZMA V. Pol. 535); Siboga Expedition St. 164, East of Misool (1°42'30"S, 130°47'30"E) (2 specimens); St. 213, Saleyer anchorage and surroundings, reef (1 specimen); St. 273, Anchorage off Pulu Jedan, east coast of Aru Islands, 13 m (1 specimen); St. 315, Anchorage East of Sailus Besar, Paternoster Islands (1 specimen) (above 5 specimens in ZMA V. Pol. 536); Fenelon Island (14°02'S, 125°43'E), 6 m, 8 Feb 1988, coll. Hutchings (1 specimen) (AM W202841); Princess Charlotte Bay, Queensland (14°07'S, 143°09'E), 12–15 m, Prawn Trawl, 23 Feb 1979 (1 specimen) (AM W202842); Xincun, Hainan Province, China, 1–3 m, coral, 26 Mar 1992, coll. Sun (4 specimens) (HKUST W0002–W0005).

Redescription based on the holotype of Leonnates indicus.—Holotype consisting of 4 fragments, likely from single specimen forming complete worm. Left parapodium of setiger 7 dissected by previous researcher and kept separately. From anterior end, fragment containing 7, 20, 20, and 11 setigers, respectively, for 58 setigers.

Animal colour cream, with darker cream parapodial glands at base of notopodial ligule. Prostomium pentagonal, frontal part including antennae missing (Fig. 1A). Two

pairs of eyes, black with distinct lenses arranged trapezoidally, anterior pair slightly larger. Palps thick, cylindrical, each with small palpostyle. Peristomium tentacular cirri slender, longest reaching setiger 7 (one cirrus on each side missing).

Pharynx everted. Jaws brownish, smooth. Maxillary ring with paragnaths and soft papillae arranged as follows: area I = 0; II = sharp paragnaths, 6 left, 5 right, each in small cluster; III = 3 small soft papillae in transverse row; IV = paragnaths, tips worn off, 6 left, 7 right, each in small cluster. Oral ring with only soft papillae, larger than those on area III: area V = 0; VI = 8 left, 9 right, conical, each in small cluster; VII–VIII = 74, conical, irregularly arranged in 3–4 rows (Fig. 1B).

Parapodia of first 2 setigers uniramous, without notosetae, with dorsal notopodial ligule, neuropodial presetal acicular ligule, neuropodial postsetal ligule, and ventral neuropodial ligule (Fig. 1C). Dorsal notopodial ligule conical, swollen at base, slightly shorter than dorsal cirrus. Neuro-podial presetal acicular ligule conical, smaller than neuropodial postsetal ligule. Ventral neuropodial ligule conical, swollen at base. Dorsal cirrus slender, extending beyond dorsal notopodial ligule; ventral cirrus subulate, shorter than ventral neuropodial ligule.

Remaining parapodia biramous with dorsal notopodial ligule, notopodial supra-acicular ligule, notopodial infra-acicular ligule, neuropodial presetal acicular ligule, neuropodial postsetal ligule, and ventral neuropodial ligule (Figs. 1D, 2A–C). Dorsal notopodial ligule conical, swollen at base, with yellowish glandular region. Notopodial supra-acicular ligule gradually reduced along body (Fig. 2A, B), disappearing by setiger 51 (Fig. 2C). Notopodial infra-acicular ligule becoming slightly smaller along body, but distinct on posterior segments. Dorsal cirrus slender, extending beyond dorsal notopodial ligule. Neuro-podial presetal acicular ligule projecting ventrolaterally, shorter than neuropodial postsetal lig-

ule (Figs. 1D, 2A, B). Ventral neuropodial ligule smaller than but approximately as long as neuropodial presetal acicular ligule. Ventral cirrus subulate, about as thick but much shorter than dorsal cirrus.

Two anal cirri present, extending for length equivalent to 6 posterior setigers.

Notopodia with homogomph spinigers and homogomph falcigers. Spinigers with slender blade (50–150 μm long) fringed on cutting edge; larger tooth at end of shaft, facing cutting edge of blade, approximately as long as circular fringe of smaller teeth (Fig. 3A), present throughout body. Falcigers about 25 μm long, with coarsely serrated, convex blade ending with pointed tip; tooth at end of shaft facing cutting edge of blade, approximately as long as circular fringe of slender teeth. Six falcigers observed on posterior notopodia (one on each parapodium: left setigers 51, 52, 53, 56, and right setigers 52, 53). Neuro-podia with similar spinigers and falcigers. Spinigers present from setiger 3. Falcigers (Fig. 3B) present throughout body, numbering 2–20 per neuropodium.

Female, parapodia with numerous oocytes, 100–105 μm diameter. Parapodia and setae sexually unmodified.

Remarks.—The holotype of *L. indicus* is in poor condition. The frontal part of the prostomium has been damaged and the antennae are now missing. Most coelomic fluid is lost. Some setal blades are missing, which makes it difficult to determine the setiger where notopodial falcigers are first present. However, the remaining 6 falcigers observed on the notopodia of setigers 52–56 suggest that their occurrence starts in the posterior segments. Left parapodium 7 was used for SEM (Fig. 3A, B) after use for a line drawing (Fig. 1D).

The holotype or syntype of *L. virgatus*, originally dried, was rehydrated in 75% ethanol. It consists of an anterior fragment of 20 setigers and a middle fragment of 30 setigers. Animal colour is greyish with darker pigmentation on the palps, prostomium, bases of parapodia, and dorsum (Fig. 2D).

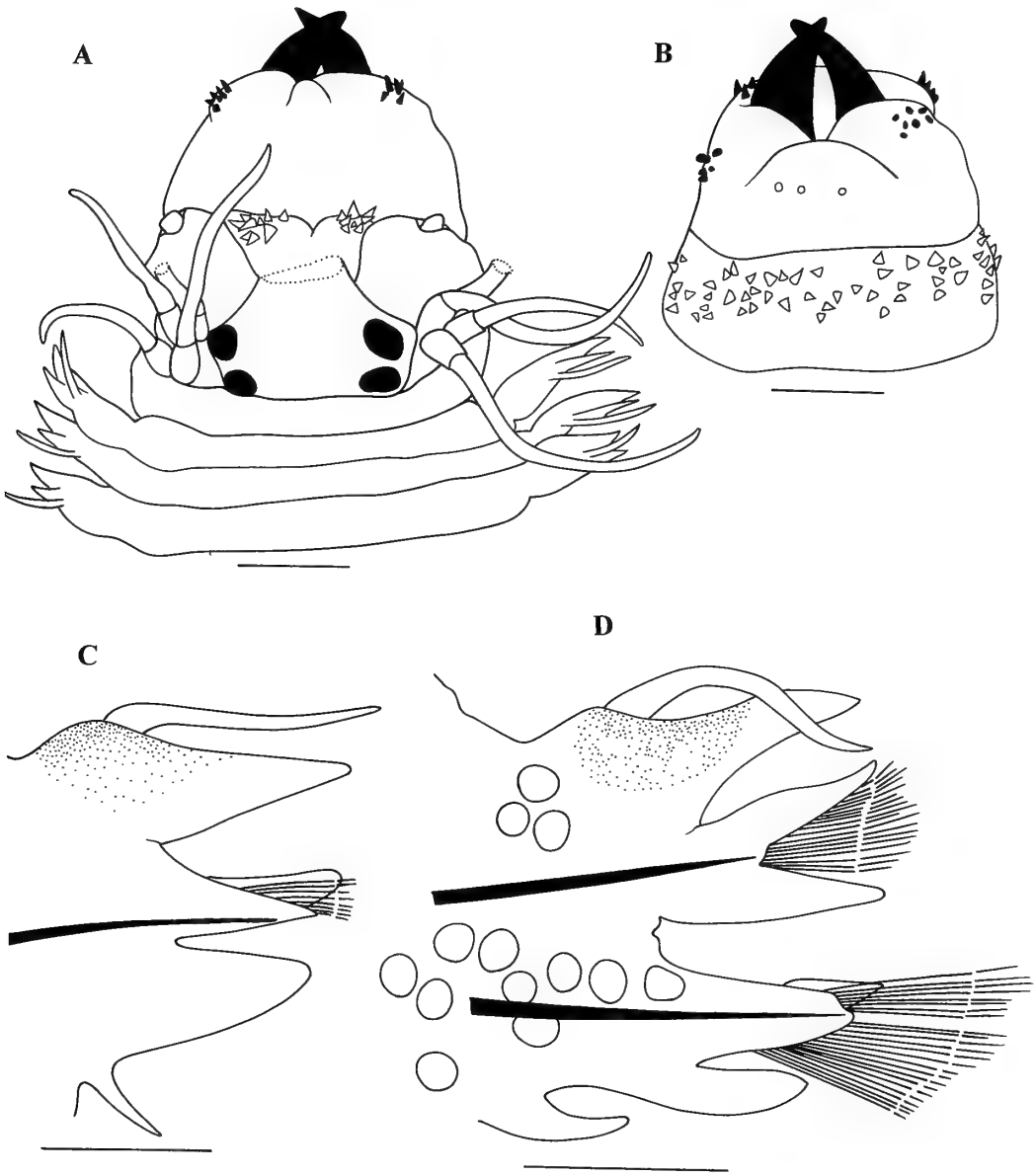


Fig. 1. *Leonnates indicus* (Holotype SMNH 535). A. Dorsal view of anterior region. B. Ventral view of pharynx. C. Anterior view of parapodium 2. D. Anterior view of parapodium 7. (Scale: A, B, D = 0.5 mm; C = 0.25 mm).

The prostomium is pentagonal with a pair of antennae and 2 pairs of uncoloured eyes.

Jaws are brownish and smooth. The maxillary ring of the everted pharynx has chitinized paragnaths and soft papillae as follows: area I = 0; II = paragnaths, 5 on left, 6 on right, each in a small cluster; III = 4

small soft papillae, in a transverse row; IV = paragnaths, 7 on left, 5 on right, each in a small cluster. The oral ring has only soft papillae, larger than those on area III as follows: V = 0; VI = 5 on each side, conical, each in a cluster; VII–VIII = 27, conical, irregularly arranged in 2 rows (Fig. 2D, E).

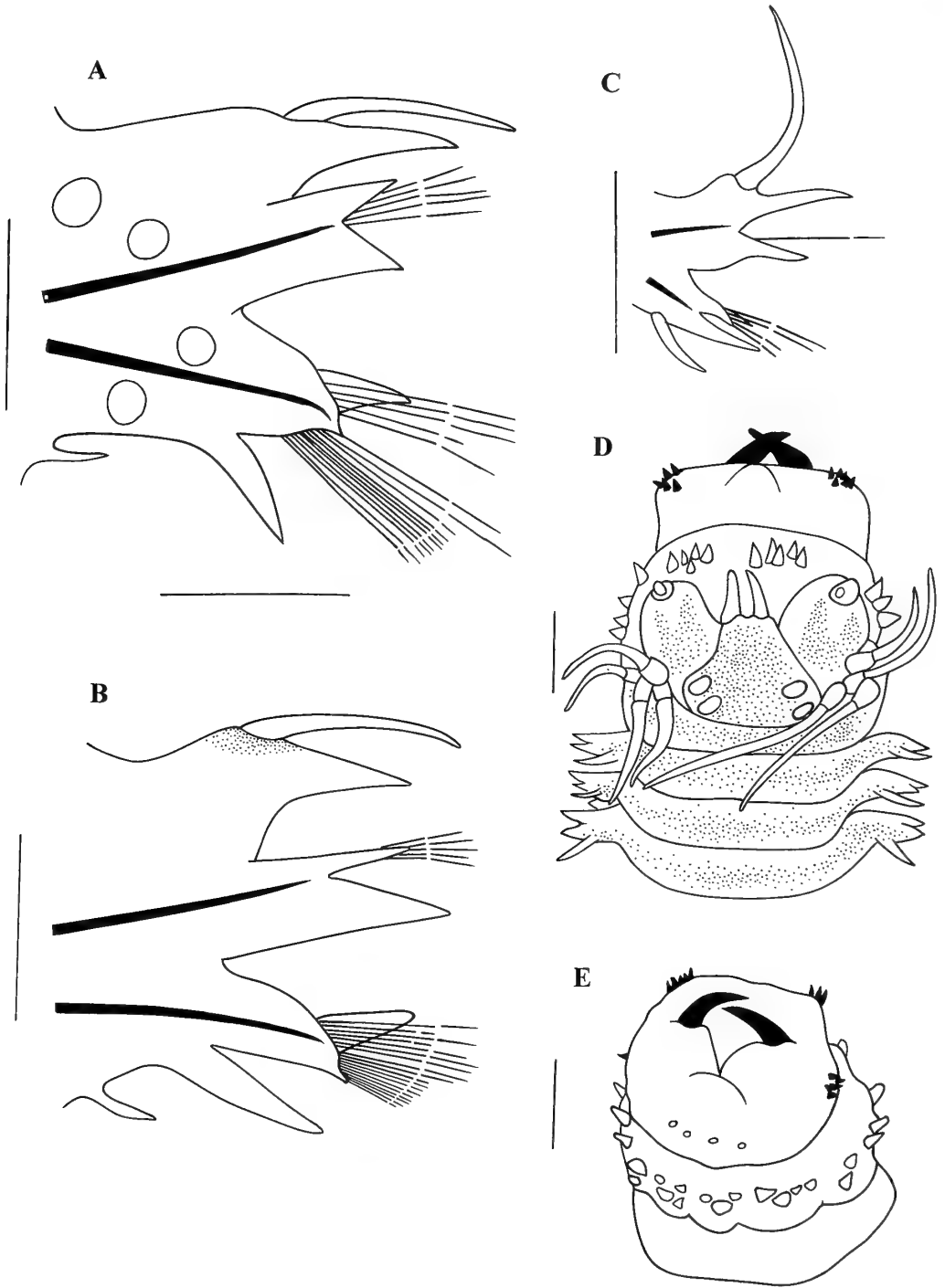


Fig. 2. *Leonnates indicus* (A–C: Holotype SMNH 535; D–E: MNHWU 322). A. Anterior view of parapodium 20. B. Anterior view of parapodium 47. C. Anterior view of parapodium 53. D. Dorsal view of anterior region. E. Anterior view of pharynx. (Scale: A–E = 0.5 mm).

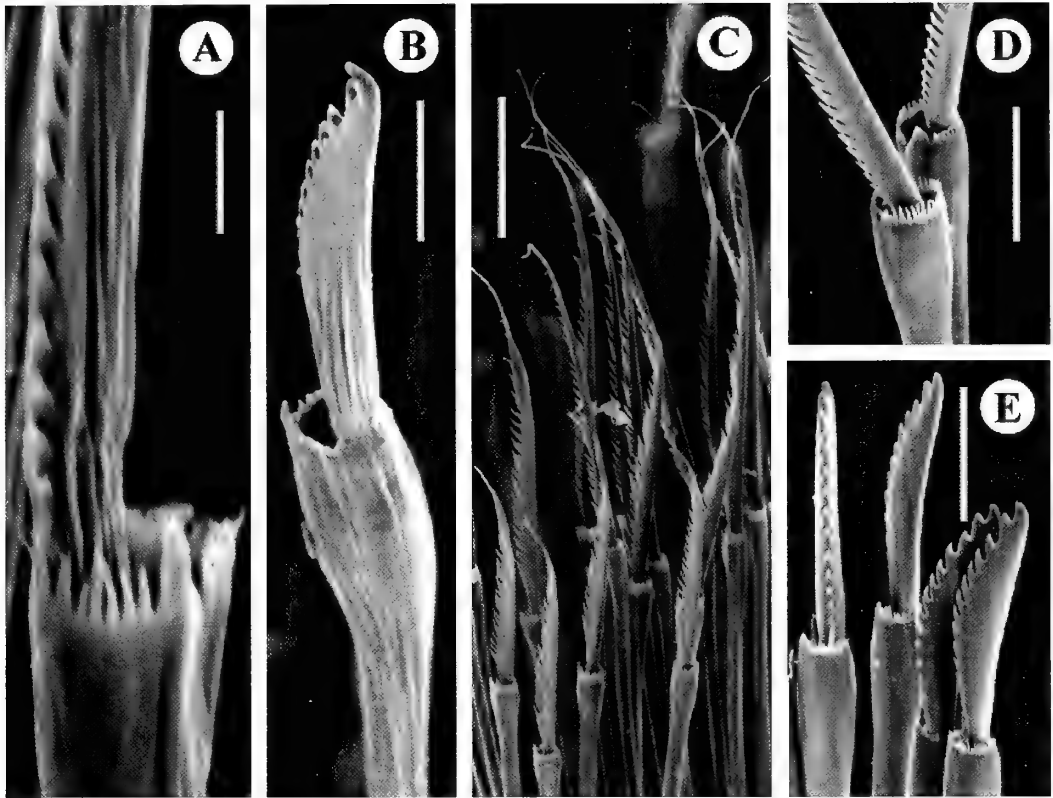


Fig. 3. *Leonnates indicus* (A–B: Holotype SMNH 535; C–E: HKUST W0005). A. Notopodial spiniger from parapodium 7. B. Neuropodial falciger from parapodium 7. C. Notopodial spinigers from parapodium 31, showing blades different in length. D. Enlarged ends of shaft of another two notopodial spinigers from parapodium 31. E. Neuropodial falcigers in different orientations from parapodium 31. (Scale: A = 3 μm ; B = 10 μm ; C = 30 μm ; D = 10 μm ; E = 30 μm).

The pharyngeal armature of the type of *L. virgatus* is very similar to that of the holotype of *L. indicus*, except the latter has more papillae on areas VII–VIII. The shapes of the parapodia of *L. indicus* and *L. virgatus* are also similar, except, in the latter, the notopodial supra-acicular lobe is absent from the middle region (setiger 20) while in the former it is absent from the posterior region (setiger 51) (Table 1). This difference could be an artifact of the long dehydration of *L. virgatus*, since the notopodial supra-acicular lobe is small in the middle and posterior regions and the rehydration may not have made this once-existing structure visible. There is also some mucus-like material covering part of the notopodia, making observation difficult.

The blades of most setae are broken off. Setae with intact blades that remain are of the same types as those found in the holotype of *L. indicus*. Notopodia have homogomph spinigers throughout and 1 homogomph falciger was observed on right setiger 50. Neuropodia have homogomph spinigers from setiger 3 and homogomph falcigers throughout.

Grube (1873) described *L. virgatus*, based on apparent differences from the brief and somewhat inaccurate description of *L. indicus*; his specimen had no incision on the frontal margin of the prostomium, dorsal cirri were longer than dorsal notopodial ligules, and the peristomium was longer than the next three segments. Our observation confirms that the type specimen

Table 1.—Diagnostic characteristics of *Leomnates indicus*. Numbers following original catalogue numbers are added to distinguish the specimens in the same lot. Numbers of processes on the left side and right side of areas II, IV and VI are separated by a slash. Maxillary ring: P = papillae; S = sclerotised papillae; PS = partially sclerotised papillae; N/A = damaged, indeterminate; other numbers represent paragnaths. NSL (notopodial supra-acicular ligule): N/A = posterior region missing or modified, not available for examination.

Specimen cat. no.	Sex	Size (mm)	Maxillary ring						Oral ring papillae		Absence of NSL from setiger	No. of setigers	Notopodial falciger(s) present on setiger(s)
			I	II	III	IV	V	VI	VII-VIII				
SMNH 535	F	3.3 × 24	0	6/5	3P	6/8	0	8/9	74, 3-4 rows	51	58	51-56	
ZMA 535	F	6.5 × 54	0	6/5	7S	6/8	0	9/10	112, 4-5 rows	73	81	59	
MNHN A78.1	F	6.0 × 55	0	4/4	8P	3/3	0	12/11	75, 3-4 rows	76	79	50-73	
MNHN A78.2	N/A	5.3 × 43	0	6/4	6P	10/11	0	5/7	111, 4-5 rows	56	62	55	
MNHN A78.3	N/A	4.3 × 36	0	9/8	7P	14/9	0	7/11	46, 3 rows	57	65	41-58	
MNHN A78.4	N/A	4.2 × 31	0	7/5	6PS	7/11	0	6/8	62, 3 rows	71	76	41-69	
MNHN A403.1	N/A	2.3 × 12	0	4/5	3P	4/4	0	4/4	23, 2 rows	16	56	37-49	
MNHN A403.2	N/A	4.5 × 28	0	3/5	3P	7/7	0	12/15	81, 3-4 rows	57	65	25-59	
MNHN A403.3	N/A	5.5 × 62	0	8/8	5P	8/9	0	11/9	85, 3-4 rows	79	84	44-80	
Siboga 164.1	N/A	4 × 6	0	7/8	6P	14/8	0	11/8	48, 3 rows	N/A	16*	N/A	
Siboga 164.2	N/A	3.2 × 9	0	7/5	4P	7/8	0	5/5	33, 2 rows	N/A	23*	N/A	
Siboga 273	N/A	3.7 × 29	0	5/5	5P	6/8	0	8/6	59, 3 rows	56	69	55	
AM W202841.1	F	2.5 × 19	0	5/6	N/A	5/6	0	6/5	22, 2 rows	48	53*	43-46	
AM W202841.2	N/A	2 × 15	0	6/5	3P	7/7	0	6/6	15, 2 rows	14	61	37-45	
AM W202842	N/A	7 × 48	0	14/10	8PS, 2 rows	16/18	0	15/18	91, 4-5 rows	N/A	43*	N/A	
MNHWU 322	N/A	2.3 × 15	0	5/6	4P	7/5	0	5/5	27, 2 rows	20	51*	50	
HKUST W0002	N/A	4.2 × 43	0	5/7	6P	10/11	0	13/11	83, 3 rows	78	83	63	
HKUST W0003	F	4 × 32	0	6/6	4S	5/7	0	12/9	62, 3 rows	66	72	46	
HKUST W0004	N/A	3.8 × 27	0	18/17	8PS, 2 rows	19/20	0	15/12	84, 4 rows	58	66	44-56	
HKUST W0005	N/A	4 × 28	0	9/9	6PS	11/12	0	14/12	57, 3-4 rows	62	66	31-40	

* incomplete.

of *L. virgatus* has no incision on the frontal margin of the prostomium, which on the holotype of *L. indicus* is missing. However, in none of the other material of *L. indicus* examined is the frontal margin of the prostomium incised. Moreover, in all material examined, the dorsal cirri are longer than the dorsal notopodial ligules. The peristomium is longer than the next three segments on the type of *L. virgatus* only on the ventral side where the lengths of the peristomium and setigers 1 to 3 are 0.40, 0.16, 0.16, and 0.20 mm, respectively; on the dorsal side, however, these segments are of similar lengths, measuring 0.24, 0.24, 0.28, and 0.28 mm, respectively. On the holotype of *L. indicus*, and on all other non-type *L. jousseaumei* material examined, the peristomium and the first 3 setigers are also of similar length on dorsal side, while the peristomium is much longer on ventral side.

The original descriptions of *L. jousseaumei* (Gravier 1899, 1901) were quite detailed, but Gravier did not state on what basis he separated *L. jousseaumei* from *L. indicus* and *L. virgatus*. The pharyngeal armature of *L. jousseaumei* resembles that of the holotype of *L. indicus*, except the former has 3–8 paragnaths, rather than 3 papillae, on area III (Fig. 1B, Table 1). Different extent of sclerotization of papillae on pharyngeal area III of *L. jousseaumei* have been reported and discussed (Fauvel 1919, Hutchings & Reid 1991), and our observation reveals that this phenomenon is common among specimens collected from the same populations (Table 1). The extent to which the papillae on area III are sclerotized does not seem to be associated with the size of the specimen because the papillae of the specimens from the same locality (Xincun, Hainan Province), which are of similar size, vary from soft to completely sclerotized (Table 1). The occurrence of paragnaths on area III (Gravier 1899), therefore, does not sufficiently separate *L. jousseaumei* from *L. indicus* or *L. virgatus*.

Gravier (1899) divided the setae of *L. jousseaumei* into three types: slightly het-

erogomph spinigers with a long and slender cutting edge; almost homogomph falcigers with a distinctively serrated convex cutting edge; and homogomph falcigers with straight thin blade. Later authors (Fauvel 1953, Hutchings & Reid 1991) only recognized two types of setae: homogomph spinigers and homogomph falcigers. As the orientation of a seta affects whether the end of the shaft looks symmetrical or slightly asymmetrical to the long axis of the shaft, the 'slightly heterogomph' and 'almost homogomph' setae (Gravier 1899) are both likely to be homogomph setae (cf., Fig. 3C, showing, at lower left corner, some falcigers with a large tooth slightly longer than the surrounding fringes at the end of the shaft; Fig. 3D, showing another two spinigers that looked perfectly homogomph at higher magnification). Similarly, the orientation of a seta also affects whether its blade looks thin or wide (Fig. 3E). The second and third types of setae of Gravier (1899) are thus considered as likely to be identical.

Gravier (1899) reported the occurrence of falcigers both notopodially and neuropodially on setiger 25, without noting the distribution of falcigers along the body. Monro (1931), Fauvel (1953), and Hutchings & Reid (1991) indicated that falcigers are present on all neuropodia as well as on posterior notopodia. Among the material examined, the most anterior notopodium containing a falciger is setiger 25. Notopodial falcigers were observed only on a few posterior setigers, probably because only a few such setae on each posterior notopodium and they are often broken or with their blades missing.

Siboga Stations 213 and 315 (see Horst 1924) each contains a heteronereidid male specimen with an inverted pharynx. They were assigned to *L. jousseaumei* by Horst (1924) and were subsequently cited by Imajima (1972). The two specimens are quite similar. The pharynx of the specimen from St. 315 has been dissected and is now missing. The specimen from St. 213 has 172 setigers that are divided into two regions:

the anterior 21 setigers and the remaining 151 setigers. The anterior region is not modified, except on the first 7 setigers the bases of the dorsal cirri are swollen. The parapodia of the posterior region are highly modified, having thin accessory flaps in both notopodia and neuropodia and a crenulated lower edge on the dorsal cirrus. The pygidium has a rosette of papillae and two anal cirri. A dissection of this specimen reveals paragnaths, but no papillae, on the pharynx. Therefore, it is not *Leonnates*. The paragnaths are arranged as follows: area I = 1, conical; II = 8, conical, in a cluster; III = 31, conical, in 3 rows; IV = 23–26, conical, in a crescent; V = 1, conical; VI = 2, slightly curved long flat teeth; VII–VIII = 42, conical, in 2 rows. The pharyngeal armature, the parapodia and the setae in the anterior region suggest that this specimen belongs to *Perinereis*. It resembles *Perinereis singaporiensis* Grube, 1878 (sensu Horst 1924: 168–170, pl. 34, figs. 1–2), except that there is only one paragnath (instead of two) on area I, and there are no conical paragnaths between the two elongated teeth on area VI.

Our observation shows that the pharyngeal armature, prostomium, parapodia, and setae of *L. virgatus* and *L. jousseaumei* all resemble those of *L. indicus*; therefore, they are considered to be conspecific. The original description of *Leonnates indicus* (Kinberg, 1866: 168) is unclear, somewhat inaccurate, not accompanied by a figure, and based on one specimen. This has contributed to the erection of the synonyms *L. virgatus* and *L. jousseaumei* for the same species. Specimens of *L. indicus* vary greatly in size (2–7 mm wide by 15–54 mm long) (Table 1). The pharyngeal armature is consistent in having smooth areas I and V, but on other areas there is variation in number of papillae or paragnaths as follows: II = 4–18 paragnaths; III = 3–8 papillae or paragnaths; IV = 3–20 paragnaths; VI = 5–18 papillae; VII–VIII = 15–112 papillae. The number of papillae on area VII–VIII seems to be related to body size as larger speci-

mens usually have more papillae [$Y = 17.4X - 9.22$, $Y =$ number of papillae on areas VII–VIII, $X =$ body width (mm), $n = 20$, $r = 0.837$]. Although the 5 females examined (Table 1) differ substantially in size, they all contain oocytes of approximately the same size (diameter 100–105 μm) and show no signs of heteronereidid modification.

Habitat.—Not mentioned in the original description of the holotype. Other specimens collected from depths of 25–24 m (Horst 1924), 60 m (Monro 1931), and 6–64 m (Hutchings & Reid 1991) were found among coral debris (Hutchings & Reid 1991), co-existing with *Ceratonereis erythraeensis* Fauvel, 1918, or among corals and sponges (Wu et al. 1981).

Distribution.—Australia; Indonesia; Singapore; Malaysia; the Philippines; Hainan; Macassar Strait; Bay of Bengal; Arabian Sea; Persian Gulf; Red Sea.

Leonnates niestraszi Horst, 1924
Figs. 4, 5

Leonnates niestraszi Horst, 1924: 150–151, figs. 4, 5.

Material examined.—Syntypes, Anchorage of North Ubian (6°7'30"N, 120°26'E), Siboga Expedition St. 99, surface, (2 complete specimens) (ZMA V. Pol. 537), (2 anterior fragments and 3 posterior fragments) (ZMA V. Pol. 538).

Description.—The two complete specimens in ZMA V. Pol. 537 measure 1.5 by 7.3 mm for 50 setigers and 2.4 by 9 mm for 55 setigers, respectively. The original description was based on the specimen with an everted pharynx in ZMA V. Pol. 537. Unless otherwise stated, our description is based on this specimen.

Body short with 2 distinctive regions: slightly modified anterior region consisting of 11 setigers and significantly modified posterior region.

Prostomium pentagonal (Fig. 4A), not cleft on frontal margin, with pair of short antennae and pair of biarticulate palps. Two

pairs of enlarged eyes arranged trapezoidally. Peristomium with dorsal tentacular cirri missing. Longest dorsal tentacular cirri reaching setiger 6 on the other specimen of the same lot.

Pharynx everted (Fig. 4A, B). Jaws brownish, with 6–7 denticles. Maxillary ring with paragnaths and papillae arranged as follows: area I = 0; II = paragnaths, 5 left, 3 right; III = 3 tiny papillae, in transverse row; IV = paragnaths, 4 left, 4 right. Oral ring with papillae arranged as follows: area V = 0; VI = 4 left, 6 right, each in 1 small cluster; VII–VIII = 12 in 2 irregular rows.

Parapodia of first 2 setigers uniramous, without notosetae, with dorsal notopodial ligule, neuropodial presetal acicular ligule, neuropodial postsetal ligule, and ventral neuropodial ligule (Fig. 4C). Dorsal notopodial ligule conical. Neuropodial presetal acicular ligule conical, smaller than postsetal ligule. Dorsal cirrus swollen at base, longer than parapodial ligules. Ventral neuropodial ligule longer than neuropodial presetal acicular ligule, shorter than dorsal notopodial ligule. Neuropodial cirrus slightly swollen at base, shorter than parapodial ligules.

Remaining parapodia of anterior region biramous, with dorsal notopodial ligule, notopodial supra-acicular ligule, notopodial infra-acicular ligule, neuropodial presetal acicular ligule, neuropodial postsetal ligule, and ventral neuropodial ligule (Fig. 4D). Dorsal notopodial ligule conical. Notopodial supra-acicular ligule extending about as far as dorsal notopodial ligule, infra-acicular ligule slightly smaller. Neuropodial presetal acicular ligule short, conical, slightly shorter than neuropodial postsetal ligule. Ventral neuropodial ligule conical, not extending as far as neuropodial ligules. Dorsal cirri of setigers 3–7 and ventral cirri of setigers 3–5 also swollen at bases.

From setiger 12, parapodia greatly modified with thin accessory flaps. Dorsal side at base of dorsal cirrus with broad flap, dorsal notopodial ligule expanded, notopodial

infra-acicular ligule expanded, neuropodial postsetal lobe broad and fan-shaped, ventral neuropodial ligule expanded, base of ventral cirrus with broad flaps on dorsal and ventral sides. Dorsal cirrus and ventral cirrus slender (Fig. 4E).

Pygidium surrounded by rosette of papillae; anal cirri missing.

Notopodia with two types of setae: homogomph spinigers on setigers 3–11 and paddle-shaped setae from setiger 12 on. Some spinigers (Fig. 5A, B) modified with short blade and slightly bent shaft tip; others similar to those of *L. indicus* in Fig. 3 (Fig. 5C, D). Paddle-shaped setae with minute serrations on one of two convex edges of blade; end of shaft not fringed with slender teeth (Fig. 5F). Neuropodia with 3 types of setae: homogomph spinigers, paddle-shaped setae, and homogomph falcigers. Spinigers and paddle-shaped setae similar to those in notopodia. Spinigers present in neuropodia 3–11. Falcigers (Fig. 5E) similar to those of *L. indicus* in Fig. 3, present on setigers 1–11, followed by paddle-shaped setae.

Remarks.—This species was described from male heteronereidid specimens. All specimens are consistent in the pattern of heteronereidid modification. The armature of the other specimen with an everted pharynx in ZMA V. Pol. 538 resembles that of the above-described specimen as follows: area I = 0; II = 3 paragnaths; III = 2 tiny papillae in transverse row; IV = 5 paragnaths; V = 0; VI = 4–5 papillae; VII–VIII = 25 papillae in 2 rows.

On both specimens, the parapodia and setae of the posterior region have been modified dramatically, but the pharyngeal armature, parapodia, and setae of the anterior region closely resemble those of atokous *L. indicus* or *L. nipponicus*. Since *L. indicus* or *L. nipponicus* only differ in the presence of notopodial falcigers on posterior segments, and their heteronereidid specimens have not been reported, it can not be determined, based on available material, whether or not *L. niestraszi* is the male heteronereidid.

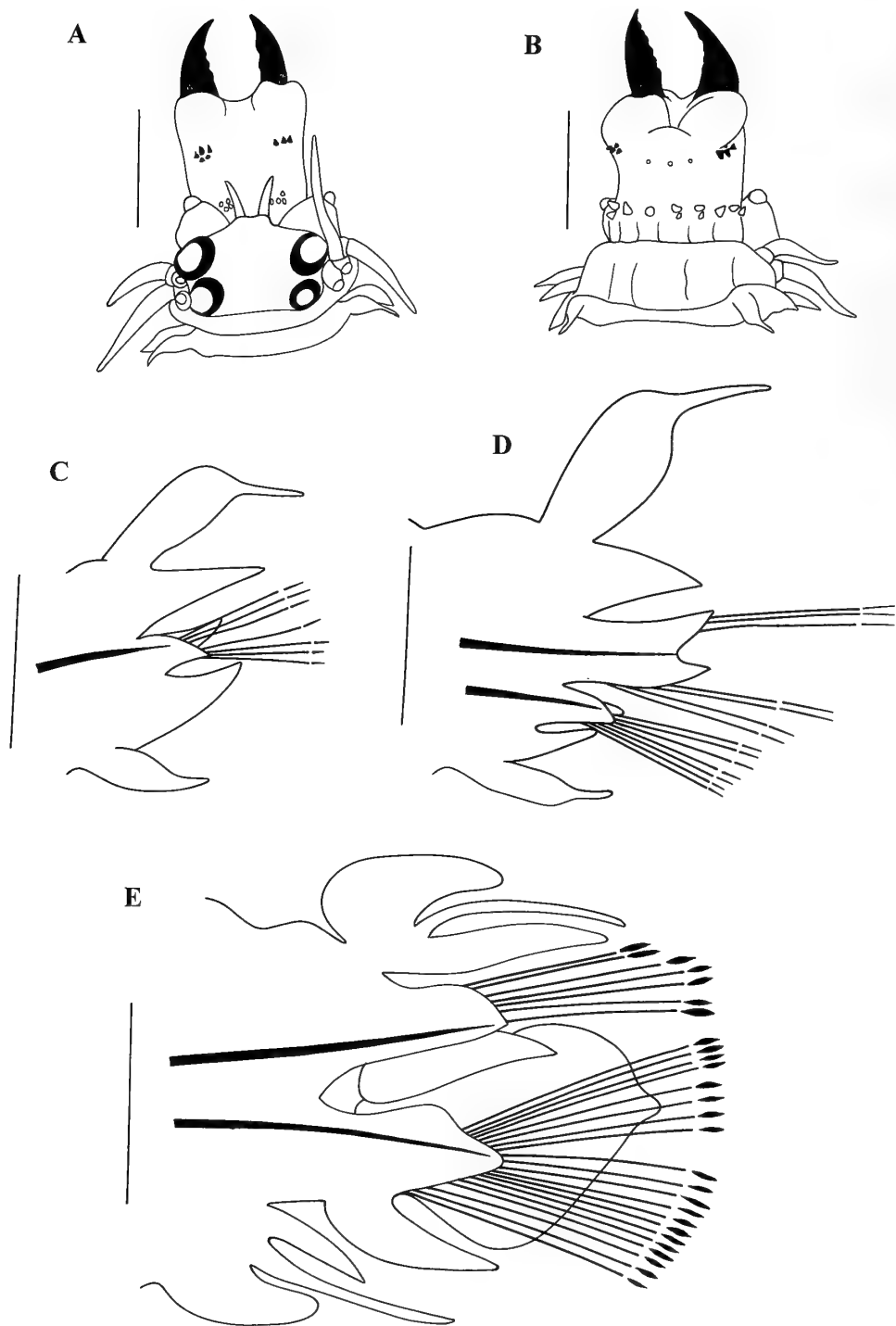


Fig. 4. *Leonnates niestraszi* (ZMA V. Pol. 537). A. Dorsal view of anterior region. B. ventral view of anterior region. C. Anterior view of parapodium 2. D. Anterior view of parapodium 5. E. Anterior view of parapodium 20. (Scale: A-B = 0.5 mm; C-E = 0.25 mm).

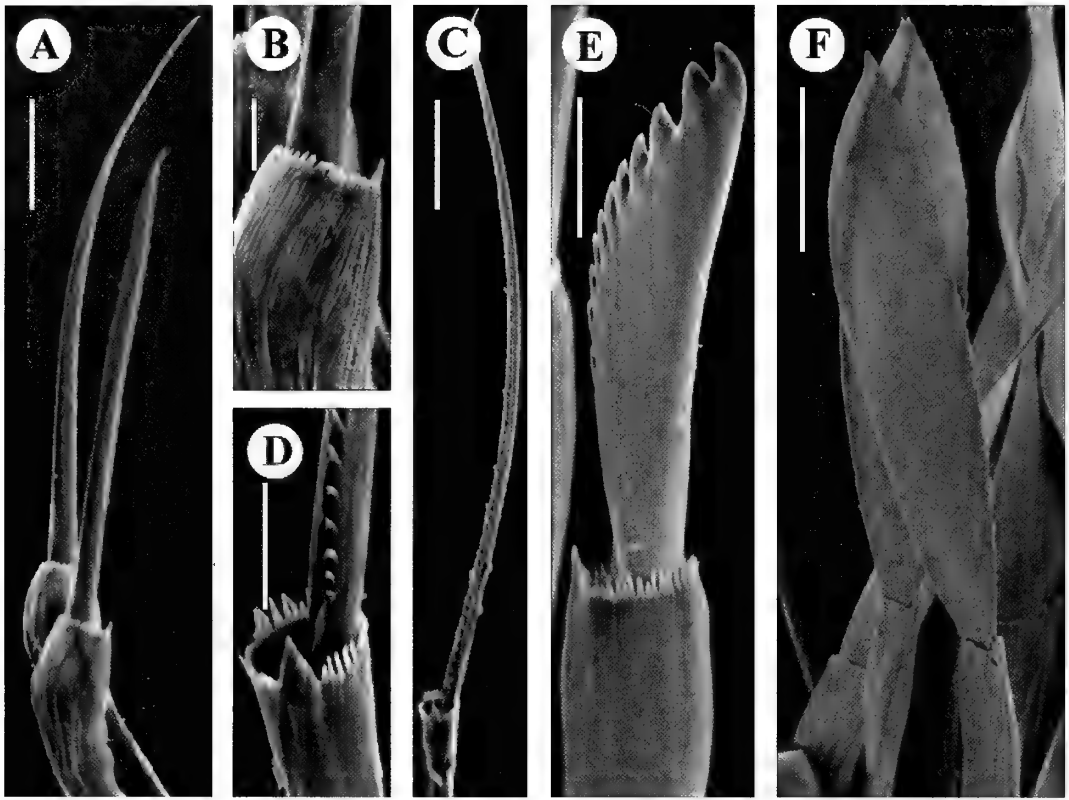


Fig. 5. *Leonnates niestraszi* (ZMA V. Pol. 537). A. Notopodial spinigers from parapodium 5. B. Enlarged end of shaft of one spiniger in A. C. Another notopodial spiniger from parapodium 9. D. Enlarged end of shaft of the spiniger in C. E. Neuropodial falciger from parapodium 5. F. Neuropodial paddle-shaped setae from parapodium 20. (Scale: A = 15 μm ; B = 5 μm ; C = 5 μm ; D = 4 μm ; E = 10 μm ; F = 30 μm).

eidid form of one of these species. However, characters of specific importance can be found on heteronereidid examples, and additional material may allow for the specific status of *L. niestraszi* to be determined. Furthermore, molecular systematic techniques currently available can possibly be used to clarify the status of this species. Although species status is currently questionable, we proposed that this species be maintained.

Leonnates decipiens Fauvel, 1929
Figs. 6A–D, 7A–B; Table 2

Leonnates jousseaumei non Gravier. Fauvel
1927: 427, fig. 106F–H.

Leonnates decipiens Fauvel, 1929: 180–

182, fig. 1; 1953: 171–172, fig. 87; Day
1967: 330, fig. 14.11N–S; Wu et al. 1981:
65–67, fig. 37; Hartman 1974: 196;
Hutchings & Reid 1991: 52.

Leonnates decipiens var. *manilensis* Pillai,
1965: 144–148, figs. 13–14.

Material examined.—*Leonnates decipiens*: Sungei Baloh, Singapore, 12 Apr 1988, St. 1, dredging, 2 incomplete specimens, one of which female with developing oocytes (NUS 1990: 2260–2270); Qisha, Guangxi Province, China, 11 May 1978 (3 incomplete specimens) (IOCAS 08171); Bailongwei, Guangxi Province, China, 26 May 1978 (1 incomplete specimen) (IOCAS 09112). *L. crinitus* non Hutchings & Reid: Coburg, Trepang Bay, Australia

(11°07'S, 113°58'E), St. CP7/1, 5 m, 15 Sep 1981, coll. Hanley et al., (1 incomplete specimen) (NTM W00388). *L. decipiens* var. *Manilensis*: Government Oyster Farm, Binakayan, Cavite, Manila Bay, Philippines, (2 "paratypes") (BMNH 1965 3.11/12).

Description.—The type specimens of *L. decipiens*, collected from the Gulf of Manar and the Suez Canal, were not found in the Muséum National d'Histoire Naturelle, Paris, and they may have been lost. Our description is based on the description by Fauvel (1929) and the characters of the above listed non-type specimens (Table 2).

Prostomium not cleft on the frontal margin. Jaws brownish, smooth. Maxillary ring with paragnaths arranged as follows: area I = 0; II = 3–6, in small cluster; III = 4–21; IV = 5–11, in small cluster. Oral ring with soft papillae arranged as follows: area V = 0; VI = 1; VII–VIII = 4–7, in one row. Longest tentacular cirri reaching back 5–6 posterior segments.

Parapodia of first two setigers uniramous, without notosetae (Fig. 6A). In other anterior segments, neuropodial postsetal ligule with finger-like protrusion on upper tip (Fig. 6B); protrusion reduced along body and absent posteriorly from middle of body (Fig. 6C, D). Neuropodial ventral ligule in middle and posterior regions long and pointing ventrally. Dorsal cirrus shorter than dorsal notopodial ligule; ventral cirrus shorter than dorsal cirrus.

Notopodia with homogomph spinigers throughout. Spinigers identical to those of *L. indicus*, except shaft with large tooth deeply cleft on both sides and with circular fringe of slender teeth (Fig. 7A). Neuropodia with homogomph spinigers and heterogomph falcigers (Fig. 7B). Spinigers similar to notosetae, present throughout, accompanied by falcigers on middle neuropodia. Falcigers with short blade carrying straight terminal projection and fringe of smaller teeth on cutting edge; end of shaft with large tooth extending beyond circular fringe of smaller teeth (Fig. 7B); Falcigers

Table 2.—Diagnostic characteristics of *Leonnates decipiens*. Numbers of processes on the left side and right side of areas II and IV are separated by a slash. In BMNH 1965.3 11/12 the number of falcigers and their occurrence in the exact neuropodia in the middle region were not examined. Numbers following original catalogue numbers are added to distinguish the specimens in the same lot.

Specimen cat. no.	No. of setigers	Size (mm)	Paragnaths on								Papillae on		Neuropodial falciger(s) on setigers		Neuropodial falcigers	
			I	II	III	IV	V	VI	VII–VIII	V	VI	upper fascicle	lower fascicle	upper fascicle	lower fascicle	
NUS 1990.2260–2270.1	10*	2 × 5	0	6/5	21	8/8	0	1	5 in 1 row			N/A		N/A		
NUS 1990.2260–2270.2	58*	1.5 × 16	0	5/6	13	8/10	0	1	6 in 1 row			15–36		1–2		2–5
BMNH 1965 3.11/12	70	1 × 12	0	3/4	3	6/5	0	1	0			Not examined		Not examined		Not examined
NTM W00388	53*	1.9 × 15	0	6/5	11	6/7	0	1	5 in 1 row			13–43		1–2		2–7
IOCAS 08171.1	23*	2 × 11	0	4/5	7	5/7	0	1	7 in 1 row			14–23		1–2		4–6
IOCAS 08171.2	27*	2.1 × 12	0	5/5	11	6/6	0	1	6 in 1 row			13–27		1–3		2–8
IOCAS 08171.3	29*	1.9 × 18	0	3/5	7	8/11	0	1	4 in 1 row			15–39		1–2		2–7
IOCAS 9112	24*	0.6 × 13	0	5/5	4	5/5	0	1	5 in 1 row			13–24		1–2		2–4

* incomplete.

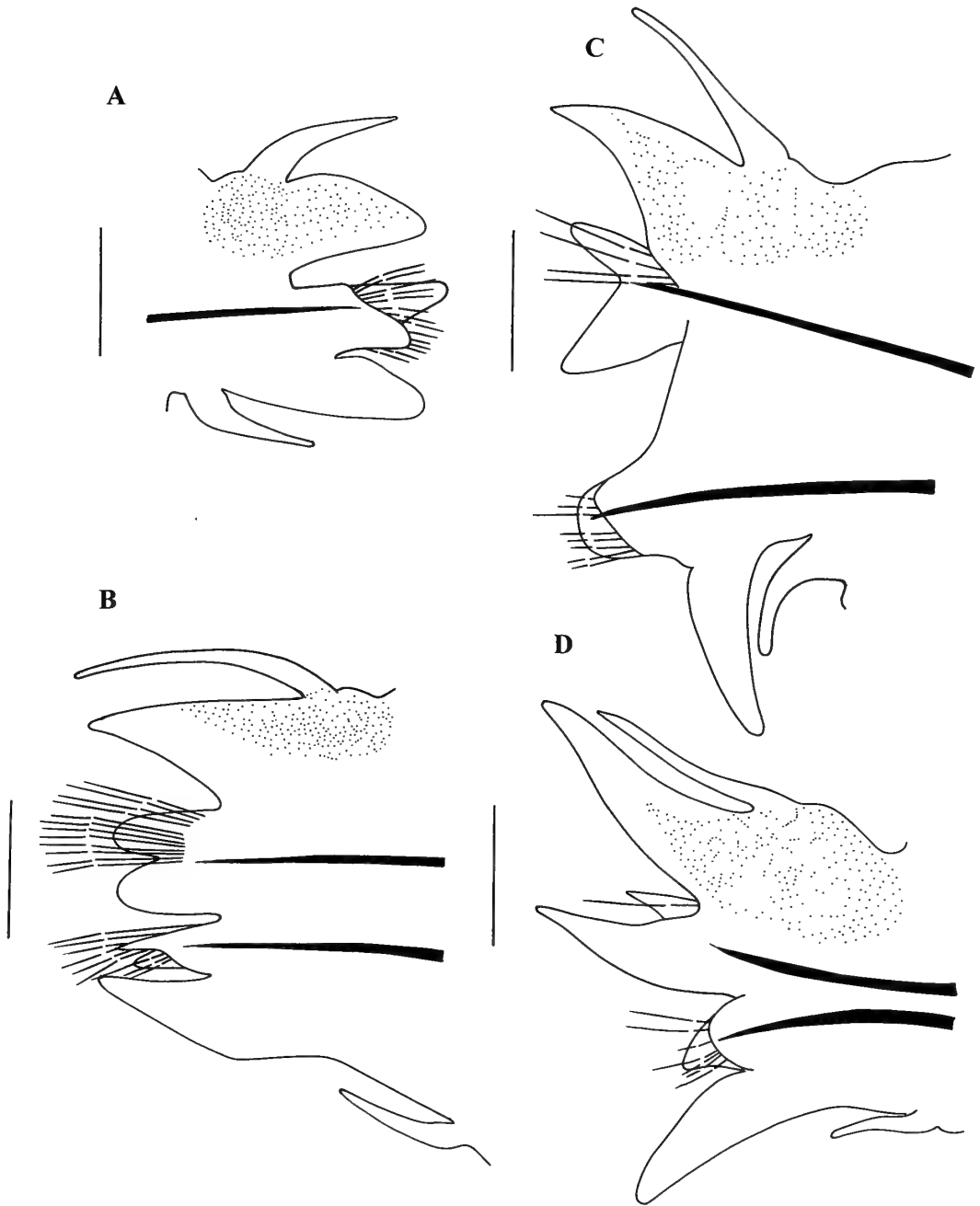


Fig. 6. *Leonnates decipiens* (NUS 1990.2260–2270). A. Anterior view of parapodium 2. B. Posterior view of parapodium 10. C. Posterior view of parapodium 20. D. Posterior view of parapodium 37. (Scale: A–D = 0.15 mm).

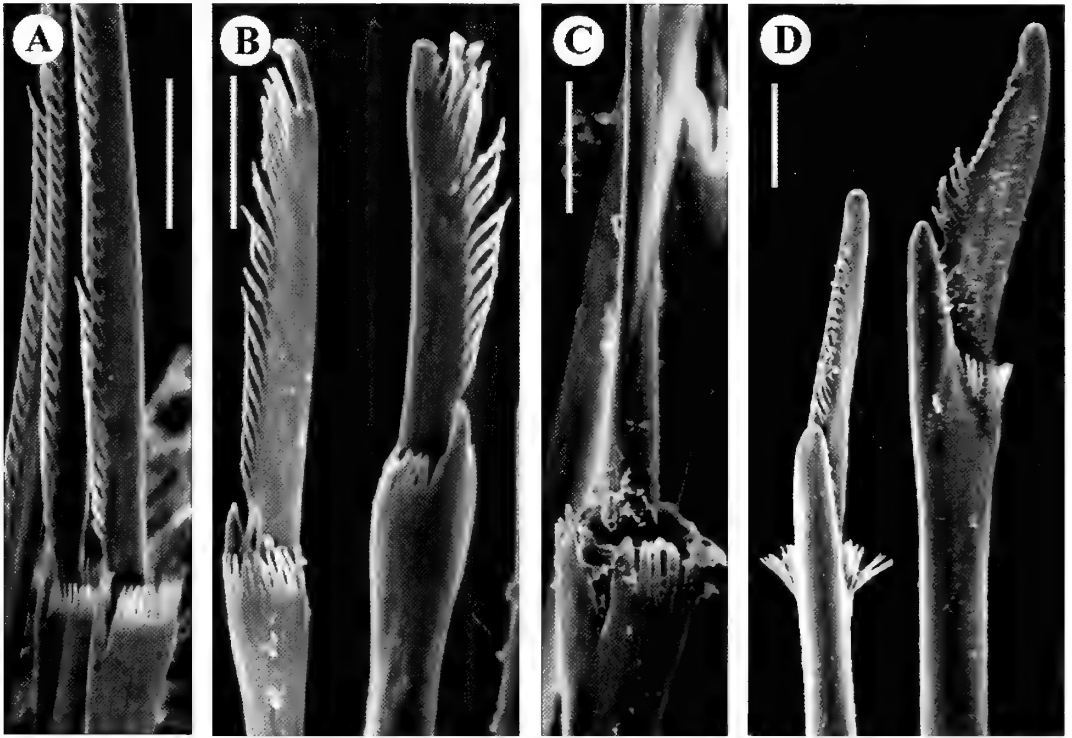


Fig. 7. *Leonnates decipiens* (NUS 1990.2260–2270). A. Notopodial spinigers from parapodium 20. B. Neuropodial falcigers from parapodium 20, the terminal projection of the seta on the right is broken off. *Leonnates simplex* (BMNH 1941.4.4.2). C. Notopodial spiniger from parapodium 20. D. Neuropodial falcigers from parapodium 20. (Scale: A = 10 μ m; B = 10 μ m; C = 7.5 μ m; D = 10 μ m).

present from setiger 13–15 to setiger 23–43, numbering 1–2 in upper fascicle and 2–7 in lower fascicle (Table 2).

Remarks.—Fauvel (1929) differentiated *L. decipiens* from *L. jousseaumei* in that his new species had fewer processes on the pharynx, especially the oral ring, a different shape of falciger, and a different pattern of occurrence of falcigers along the body. The different pharyngeal armature is as follows: area VI = a large papilla; VII–VIII = 7–8 smaller papillae, sometimes more or less absent. The falcigers of *L. decipiens* were described with spinuous convex blade and blunt truncated tip, and occurred only on the neuropodia of the middle region. The non-type specimens examined, although not from the type locality, share the above characters. Apart from the differences in the pharyngeal processes and the shape and pattern of occurrence of the falcigers, *L. de-*

cipiens also differs from *L. indicus* in the shape of parapodia: in the anterior setigers, the neuropodial postsetal ligule has a prominent finger-like protrusion on the upper tip (Fig. 6B), absent on *L. indicus*; in the middle and posterior setigers, the neuropodial postsetal ligules greatly reduced while the ventral neuropodial ligule is much longer than the neuropodial acicular lobe and postsetal ligule (Fig. 6C, D), whereas in *L. indicus* the neuropodial postsetal ligule is similar along the body, and the ventral neuropodial ligule is of similar length to the neuropodial acicular lobe and postsetal ligule. The long and often ventrally pointed ventral neuropodial ligule can be seen in the drawings of Fauvel (1929, fig. 1B; 1953, fig. 87B), but the reduction of the neuropodial postsetal ligule is not shown in his drawings of posterior parapodia (Fauvel 1929, fig. 1B; 1953, fig. 87B).

Pillai (1965) established the nomenclaturally invalid (Article 16, International Commission on Zoological Nomenclature, 1985: "A scientific name proposed expressly as the name of a 'variety' or 'form' after 1960 is infrasubspecific and excluded from zoological nomenclature") *L. decipiens* var. *manilensis* based on the occurrence of fewer (4 instead of 7–8) papillae on area VII–VIII of the proboscis and that these papillae are larger than the paragnaths of the maxillary ring. A "holotype" and two "paratypes" of *L. decipiens* var. *manilensis* were collected from an oyster farm in Manila. The "holotype" (University of Ceylon, RTS 21) was not available for examination. Of the two "paratypes", the one with everted pharynx has no obvious papillae on area VII–VIII (Table 2), and we were not authorized to dissect the pharynx of the other. Fauvel (1929) also reported a lack of papillae on pharyngeal areas VII–VIII of some of his specimens, and his description of the papillae on this area, however, can be interpreted to say that they are much or slightly smaller than those on area VI. On the non-type *L. decipiens* specimens we examined (Table 2), the number of papillae on areas VII–VIII varies from 5 to 6, slightly more than on the "holotype" of *L. decipiens* var. *manilensis*; they are of similar size to the papilla on area VI, but larger than the paragnaths on the maxillary ring. The pharyngeal areas II, III, and IV of this *L. decipiens* var. *manilensis* specimen have paragnaths comparable to those of other *L. decipiens* specimens examined, but they have fewer paragnaths than on the corresponding areas of the *L. decipiens* var. *manilensis* "holotype". The long and often ventrally pointed ventral neuropodial ligule can be seen in the original drawings of Pillai (1965, fig. 14B–D). Pillai also noted that the neuropodial postsetal ligule is lacking in the middle setigers (Fig. 14B, C, *in* Pillai 1965), but it reappears on posterior setigers as a long digit (Fig. 14D, *in* Pillai 1965). This structure is absent from the posterior segments of all the specimens we exam-

ined. The characters that Pillai (1965) used to support the establishment of *L. decipiens* var. *manilensis* are common among specimens of *L. decipiens*, and our opinion is that Pillai's are perfectly good specimens of *L. decipiens* Fauvel.

Habitat.—Fauvel (1927, 1929, 1953), Day (1967) and Hartman (1974) did not give habitat information for their material. The specimens described as *L. decipiens* var. *manilensis* were collected from an oyster farm (Pillai 1965). A male heteronereidid, with significantly modified parapodia, was collected from a pearl oyster farm (Wu et al. 1981). Other specimens described in Wu et al. (1981) were collected from 0–40 m in an estuarine, sandy mud environment. Those in Hutchings & Reid (1991) were found among coral rubble and sandy substrata.

Distribution.—Congo, Senegal, and Mozambique, Africa; Northern Territory, Australia; Gulf of Mannar; Suez Canal; Sri Lanka; Guangdong & Guangxi Provinces, China.

Leonnates insolitus Gravier & Dantan,
1934

Leonnates insolita Gravier & Dantan, 1934:
37–135, figs. 4–8.

Material examined.—None. The original description was based on a heteronereidid collected from the surface water during the night of 29 Jun 1927 in South Viet Nam. The author did not note where the type specimen was deposited. The polychaete curators of the Institute of Oceanography, Nha Trang, and Muséum National d'Histoire Naturelle, Paris found no record of this species in their catalogues.

Description.—Pharyngeal jaws with 6–7 denticles; maxillary ring with paragnaths arranged as follows: area I = 0; II = 3–5; III = 0; IV = 3; oral ring with soft papillae arranged as follows: area V = 0; VI = 1; VII–VIII = 2 rows.

Body divided into two regions: slightly modified anterior region consisting of 9 se-

tigers and highly modified posterior region consisting of remaining.

Anterior region, parapodia after first 2 biramous with dorsal notopodial ligule, neuropodial presetal acicular lobe, neuropodial postsetal ligule, and ventral neuropodial ligule. Dorsal notopodial ligule conical, similar to notopodial acicular ligule. Dorsal cirrus swollen at base. Neuropodial postsetal ligule small, slightly larger than presetal acicular ligule; shorter than notopodial ligules. Ventral neuropodial ligule slightly longer than neuropodial lobe and ligule. Ventral cirrus short with slightly swollen base (Gravier & Dantan, fig. 5, who stated that ventral cirrus was broken off).

Parapodia from setiger 10 greatly modified with thin accessory flaps at base of dorsal cirrus, on postsetal lobe of neuropodial acicular lobe, and at base of ventral cirrus. Dorsal cirrus and ventral cirrus slender. Dorsal cirrus extending beyond dorsal notopodial ligule.

Notopodia of anterior region each with aciculum, but without setae. Neuropodia each with aciculum and few homogomph spinigers. Setae of posterior region of both notopodia and neuropodia paddle-shaped.

Pygidium without rosette of papillae.

Remarks.—Based on the shape of pygidium, Gravier & Danton (1934) suggested their material was a female. They did not report whether oocytes were present in the coelom. Atokous specimens of *L. insolitus* have not been reported, and the extent to which the heteronereidids differ from them is unknown. The pharyngeal armature of this species resembles that of *L. persicus*, but anterior parapodia differ from those of all other *Leonnates* species in lacking setae in notopodia. This lack of setae in anterior notopodia is probably a result of the heteronereidid modification and may not be found on atokous specimen of this species. Currently, the specific status is indeterminable. However, this species is maintained in *Leonnates* in anticipation that additional material from the type locality will allow

for more definitive determination of its status.

Leonnates simplex Monroe, 1939

Figs. 7C–D, 8A

Leonnates simplex Monroe, 1939: 403–405, text-fig. 305.

Material examined.—Holotype: from Aldabra Island, Indian Ocean (BMNH 1941.4.4.2).

Description.—Holotype complete, except pygidium damaged with anal cirri missing, 2.2 by 55 mm, 110 setigers. Animal colour greyish, with darker parapodial glands at base of dorsal notopodial ligule. Prostomium pentagonal, not cleft on frontal margin. Antennae approximately half as long as palps. Two pairs of eyes equal-sized, black. Palps long, cylindrical, with small palpostyles. Peristomium with slender tentacular cirri, the longest reaching setiger 5.

Pharynx everted with jaws brownish, with dentate cutting edge. Maxillary ring with paragnaths arranged as follows: area I = 2; II = 9, each side in small cluster; III = 15 left, 16 right, each in small cluster; IV = 20 left, 23 right, each in cluster. Oral ring with soft papillae and paragnaths arranged as follows: area V = 3 papillae, in triangle; VI = transverse row of numerous minute paragnaths, exact number not determinable; VII–VIII = 21 papillae, in 2 rows.

Parapodia of first 2 setigers uniramous without notosetae, with dorsal notopodial ligule, neuropodial presetal acicular lobe, neuropodial postsetal lobe, and ventral neuropodial ligule. Dorsal notopodial ligule conical, approximately as long as dorsal cirrus. Neuropodial presetal acicular lobe of similar size to neuropodial postsetal lobe, smaller than dorsal notopodial ligule. Ventral neuropodial ligule conical, slightly longer than neuropodial presetal acicular lobe. Ventral cirrus subulate, shorter than ventral neuropodial ligule.

Remaining parapodia biramous with dorsal notopodial ligule, notopodial infra-acicular ligule, neuropodial presetal acicular

lobe, neuropodial postsetal acicular lobe, and ventral neuropodial ligule (Fig. 8A). Dorsal notopodial ligule blunt, with yellowish glandular region at base of dorsal cirrus; ligule becoming slightly smaller on posterior setigers but shape remaining similar. Notopodial infra-acicular ligule similar to dorsal notopodial ligule in shape and size. Dorsal cirrus subulate, approximately as long as dorsal notopodial ligule on anterior setigers, extending slightly beyond dorsal notopodial ligule on posterior setigers. Neuropodial presetal acicular lobe smaller than notopodial ligule, blunt with short, rounded postsetal lobe. Ventral neuropodial ligule smaller than but approximately as long as neuropodial presetal acicular lobe. Ventral cirrus subulate, about as thick but shorter than dorsal cirrus.

Notopodia with 1–3 homogomph spinigers (Fig. 7C); each with slender blade 100–130 μm long, fringed with small teeth on cutting edge; end of shaft with large tooth surrounded by fringe of smaller teeth, all of similar length; both sides of large tooth with split cutting into shaft (Fig. 7C). Neuropodia with spinigers similar to notopodial spinigers and heterogomph falcigers, present throughout, the latter located in the lower position of fascicle. Falcigers with short triangular blade, about 35 μm long, fringed with small teeth on cutting edge; large tooth at end of the shaft facing cutting edge of blade, much longer than surrounding fringe of smaller teeth (Fig. 7D).

Gender indeterminable.

Remarks.—Monro (1939) described this species as differing from *L. indicus* and *L. decipiens* in having only two notopodial ligules, heterogomph falcigers with very short blades, and a quite different pharyngeal armature. The original description is detailed and accompanied by drawings of the head region, parapodia and setae. However, the pharyngeal armature on area VI, originally described as papillae, are sclerotized structures, which should be considered as paragnaths. The occurrence of par-

agnaths on this area has not been reported in any other *Leonnates* species.

Habitat.—Not mentioned in the original description.

Distribution.—Aldabra Islands, Indian Ocean.

Leonnates persicus Wesenberg-Lund,
1949

Figs. 8B–C, 9A–C, 10A–E, 11A–D;
Table 3

Leonnates persica Wesenberg-Lund, 1949:
275–277, figs. 11–12; Day 1967: 328–
329, fig. 14.11. G–M; Wu et al. 1981: 68–
69, figs. 39–40.

Material examined.—2 miles West of Mujgam, Persian Gulf (26°57'N, 53°26'E), 10 Apr 1938 (holotype, ZMUC). Off East Sha Chau, Hong Kong (22°17'N, 113°52'E), Feb 1999 (2 complete specimens) (HKUST W0006–W0007) (1 incomplete specimen) (HKUST W0013); Feb 1998 (5 incomplete specimens) (HKUST W0008–W0012).

Description of holotype.—The original description, based on an anterior fragment with 30 setigers, is incomplete.

Animal colour cream with darker pigmentation at base of dorsal cirrus and dorsal notopodial ligule. Prostomium pentagonal with cleft on frontal margin. Two pairs of black eyes, arranged trapezoidally; anterior pair slightly larger. Palps thick, cylindrical, each with small palpostyle. Antennae digitiform, approximately as long as palps. Peristomial cirri slender and tapering; dorsal most pair missing; remaining longest reaching back to setiger 5.

Pharynx everted with jaws brownish, smooth. Maxillary ring with paragnaths arranged as follows: area I = 0; II = 3 left, 2 right; III = 0; IV = 3. Oral ring with papillae arranged as follows: area V = 0; VI = 1; VII–VIII = 29, in 3 irregular rows.

Parapodia of first 2 setigers with dorsal notopodial ligule, neuropodial presetal acicular ligule, neuropodial postsetal ligule, and ventral neuropodial ligule. Dorsal notopodial ligule asetigerous, conical, with basal

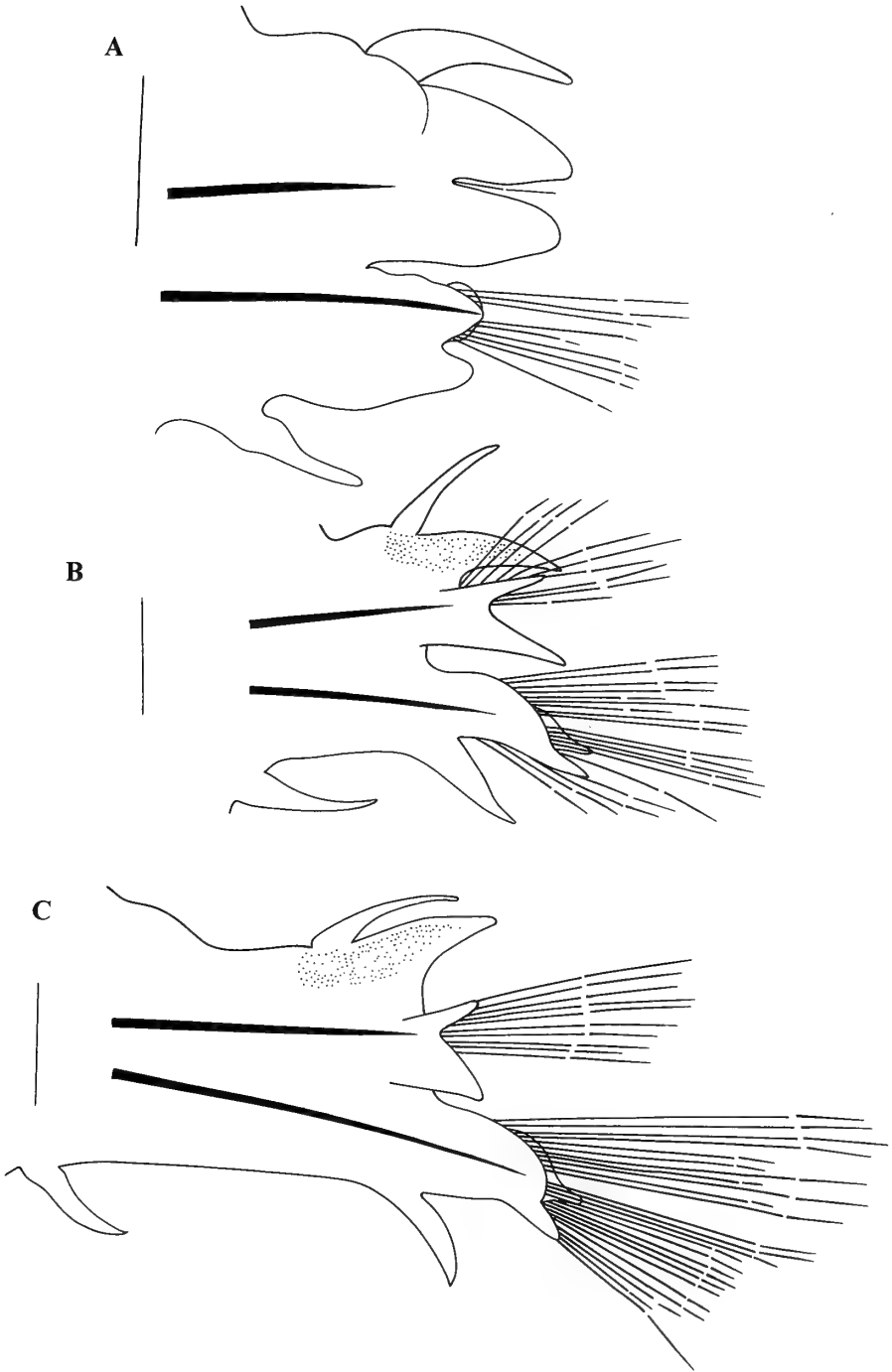


Fig. 8. *Leonnates simplex* (BMNH 1941.4.4.2). A. Anterior view of parapodium 20. B-C. *Leonnates persicus* (Holotype ZMUC). B. Anterior view of parapodium 3. C. Anterior view of parapodium 20. (Scale: A-C = 0.25 mm).

swelling. Dorsal cirrus subulate, slightly shorter than dorsal notopodial ligule. Neuropodial presetal acicular ligule conical, slightly longer than postsetal ligule. Neuropodial ventral ligule conical, of similar length to postsetal ligule. Ventral cirrus subulate, shorter than ventral neuropodial ligule.

Remaining parapodia biramous with dorsal notopodial ligule, notopodial supra-acicular ligule, notopodial infra-acicular ligule, neuropodial presetal acicular ligule, neuropodial postsetal ligule, and ventral neuropodial ligule (Fig. 8B, C). Dorsal notopodial ligule large, conical, swollen at base, with glandular region at upper margin, becoming slightly larger on middle setigers with shape unchanged. Notopodial supra-acicular ligule conical, similar to but smaller than infra-acicular ligule. Dorsal cirrus subulate, shorter than dorsal notopodial ligule. In anterior segments, neuropodial presetal acicular ligule shorter than postsetal ligule, with digit protruding from lower frontal tip (Fig. 8B). In middle neuropodia, presetal ligule and postsetal ligule similar in shape and size (Fig. 8C). Ventral neuropodial ligule conical, smaller than, but of similar length to neuropodial presetal acicular ligule. Ventral cirrus subulate, same thickness as dorsal cirrus but shorter.

Notopodia with homogomph spinigers throughout, each with slender blade fringed with small teeth on cutting edge. Large tooth at end of shaft surrounded by fringe of slender teeth of similar length, with split cutting into shaft on both sides of large tooth (Fig. 9A, B). Neuropodia with two kinds of setae: homogomph spinigers and homogomph falcigers. Spinigers similar to those on notopodia, present throughout fragment, fewer on middle neuropodia where accompanied by falcigers. Falcigers present on neuropodia from setiger 10 to end of fragment (setiger 30), numbering 3–6 in supra-acicular fascicle and 4–16 in infra-acicular fascicle, blades with straight terminal projection, fringed on cutting edge. Tooth at end of shaft fringed by circular

slender teeth of similar length; split cutting into the shaft on both sides of large tooth (Fig. 9C).

Gender of holotype, as well as most of our material, indeterminable. Specimen HKUST W0013 with developing oocytes diameter 60–80 μm , without heteronereidid modification. Female with mature oocytes diameter 100 μm , without heteronereidid modification, and male heteronereidid with modified eyes, parapodia and setae reported by Wu et al. (1981).

Remarks.—Although the original description is quite detailed, it is incomplete as only an anterior fragment was available. The parapodia and setae of our material match well with those of the holotype (Figs. 9A–C, 11, present study; fig. 12, Wesenberg-Lund 1949). In the holotype, as well as all other material described in previous studies (Day 1967, Wu et al. 1981), pharyngeal areas I and III are devoid of paragnaths. Slight variation in the number of paragnaths on areas I and III (0–1 on area I, 0–3 on area III) were found in our specimens collected from the same locality (Fig. 10, Table 3), but we believe this minor variation is intraspecific; some of these specimens have the exact numbers of paragnaths as those occurring on the corresponding areas of the holotype. Greater variation in numbers of soft papillae was found on area VII–VIII: area VII–VIII has 3–4 rows of papillae according to Day (1967) and Wu et al. (1981). The number of rows of papillae on areas VII–VIII of our specimens varies from 2 to 3–4. A correlation between body size and numbers of papillae on area VII–VIII shows this variation is likely to be due to differences in body size: larger individuals usually have more papillae than smaller individuals [$Y = 6.16X + 6.48$, Y = number of papillae on areas VII–VIII, X = Body width (mm), $n = 9$, $r = 0.949$].

The left parapodium 20 from the holotype, which contained both falcigers and spinigers, was the only parapodium of the middle region that was authorized to dissect for SEM. The line drawing and observa-

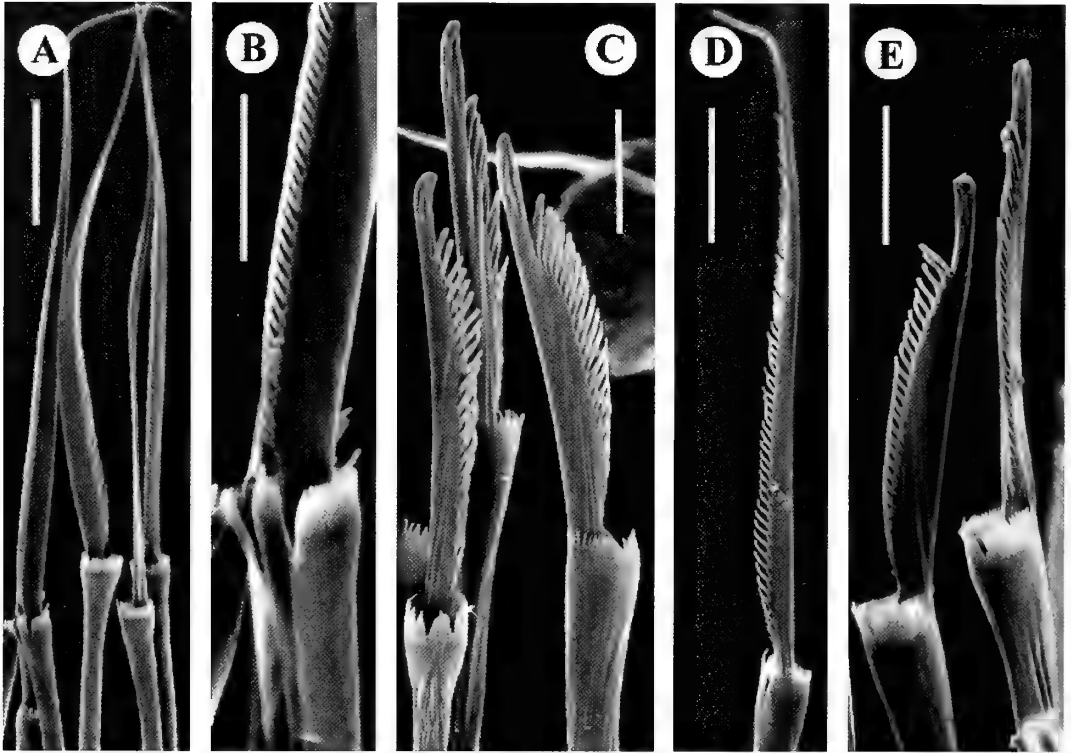


Fig. 9. *Leonnates persicus* (HKUST W0006). A. Notopodial spinigers from parapodium 20. B. Enlarged end of shaft of one of the spinigers in A. C. Neuropodial falcigers from parapodium 20. *Leonnates stephensoni* (AM W10258). D. Notopodial spiniger from parapodium 2. E. neuropodial falciger from parapodium 20. (Scale: A = 25 μm ; B = 10 μm ; C = 10 μm ; D = 15 μm ; E = 15 μm).

tions using dissecting and compound microscopes were successful, but unfortunately, the setae were broken during preparation for SEM. Since substantial evidence indicates that our specimens are *L. persicus*, a parapodium from the same body region of HKUST W0006 was used for SEM.

Our specimens (Table 3) have provided supplemental information on the posterior region of this species. The notopodial supra-acicular ligule gradually diminishes along the body but remains distinct on posterior region (Fig. 9). The notopodial infra-acicular ligule becomes slightly smaller on posterior region. In anterior segments, the neuropodial presetal acicular ligule is blunt, shorter than postsetal ligule, with a digit protruding from the lower frontal margin. In middle and posterior parapodia, the neu-

ropodia presetal ligule and postsetal ligule are of similar shape and size. The pygidium has two anal cirri that extend for a length equivalent to approximately 15 posterior setigers. Neuropodial falcigers disappear from posterior segments.

Habitat.—The holotype was collected from 20 m, in clay with little sand, co-existing with *Pseudeurythoe hirsuta* Wesenberg-Lund, 1949. Our specimens were collected by a grab from 5–11 m depths, in clay with silt; salinity at the site fluctuated on a seasonal cycle, reaching 19.3 ppt during the summer and 32.5 ppt during the winter. The material in Wu et al. (1981) was collected from a variety of localities along the Chinese coast (fig. 18 in Wu et al. 1981) from 1.5–58 m depths, in sandy mud or clay, co-existing with *Venerupis* sp., *Am-*

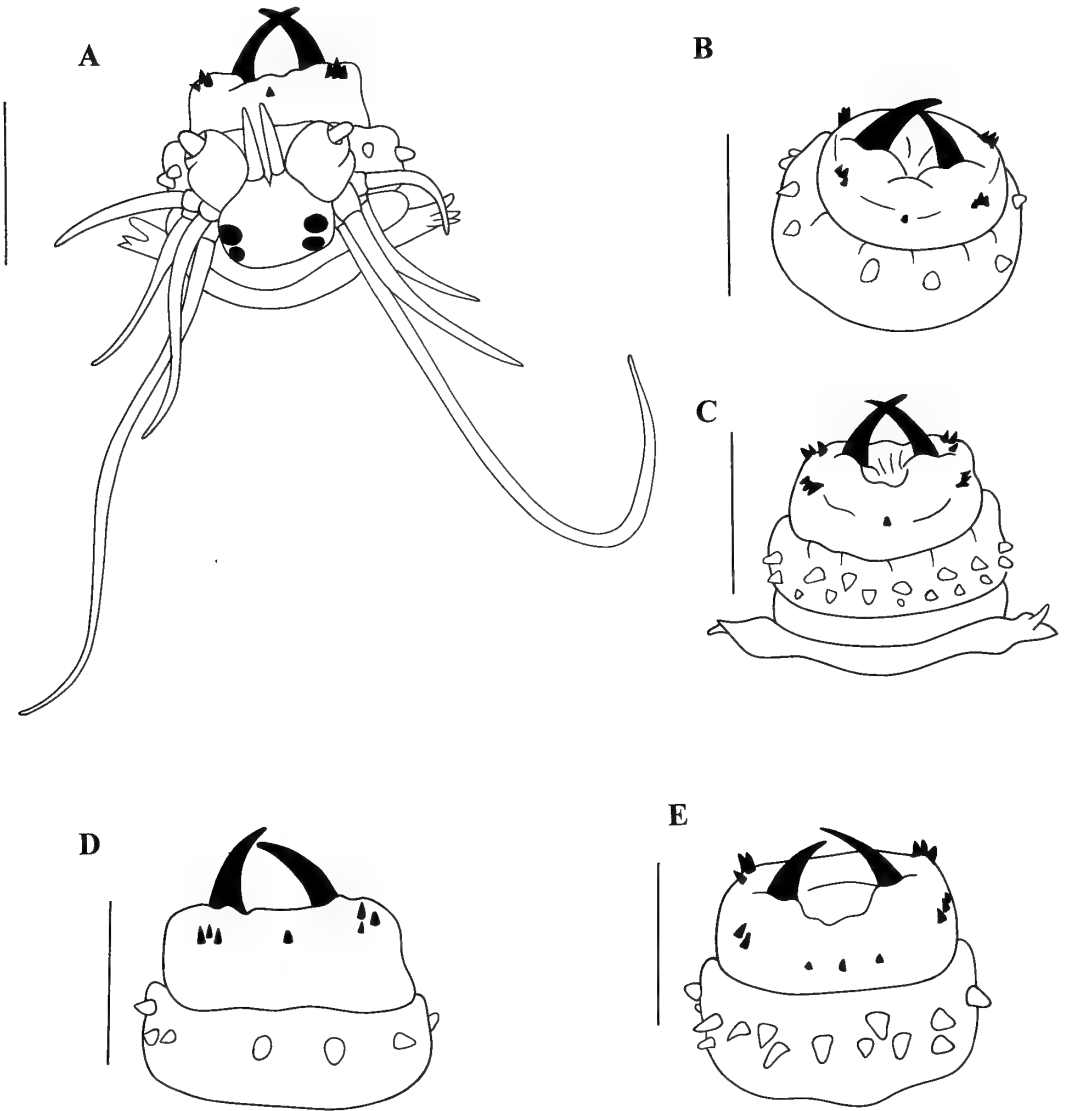


Fig. 10. *Leonnates persicus* (A–C: HKUST W006; D–E: HKUST W008). A. Dorsal view of anterior region. B. Dorsal view of pharynx. C. Ventral view of anterior region. D. Dorsal view of pharynx. E. Ventral view of pharynx. (Scale: A–E = 0.5 mm).

phiura vadicola Matsumoto, *Loimia medusa* (Savigny) and *Eudistylia vancouveri* (Kinberg).

Distribution.—South Africa; Persian Gulf; China.

Leonnates stephensoni Rullier, 1965
Figs. 9D–E, 12

Leonnates stephensoni Rullier, 1965: 174–177, fig. 4A–I; Hutchings & Murray

1984: 36–37, fig. 11; Hutchings & Reid 1991: 53–54.

Leonnates persicus non Wesenberg-Lund.
Gallardo 1967: 64, pl. 14, figs. 1–4.

Material examined.—Calliope River, Queensland (23°55'S, 151°10'E), coll. Saenger, May 1976 (4 specimens) (AM W13513); Auckland Creek, Queensland (23°50'S, 151°16'E), 9–12 Feb 1976, coll. Saenger (1 specimen) (AM W10258).

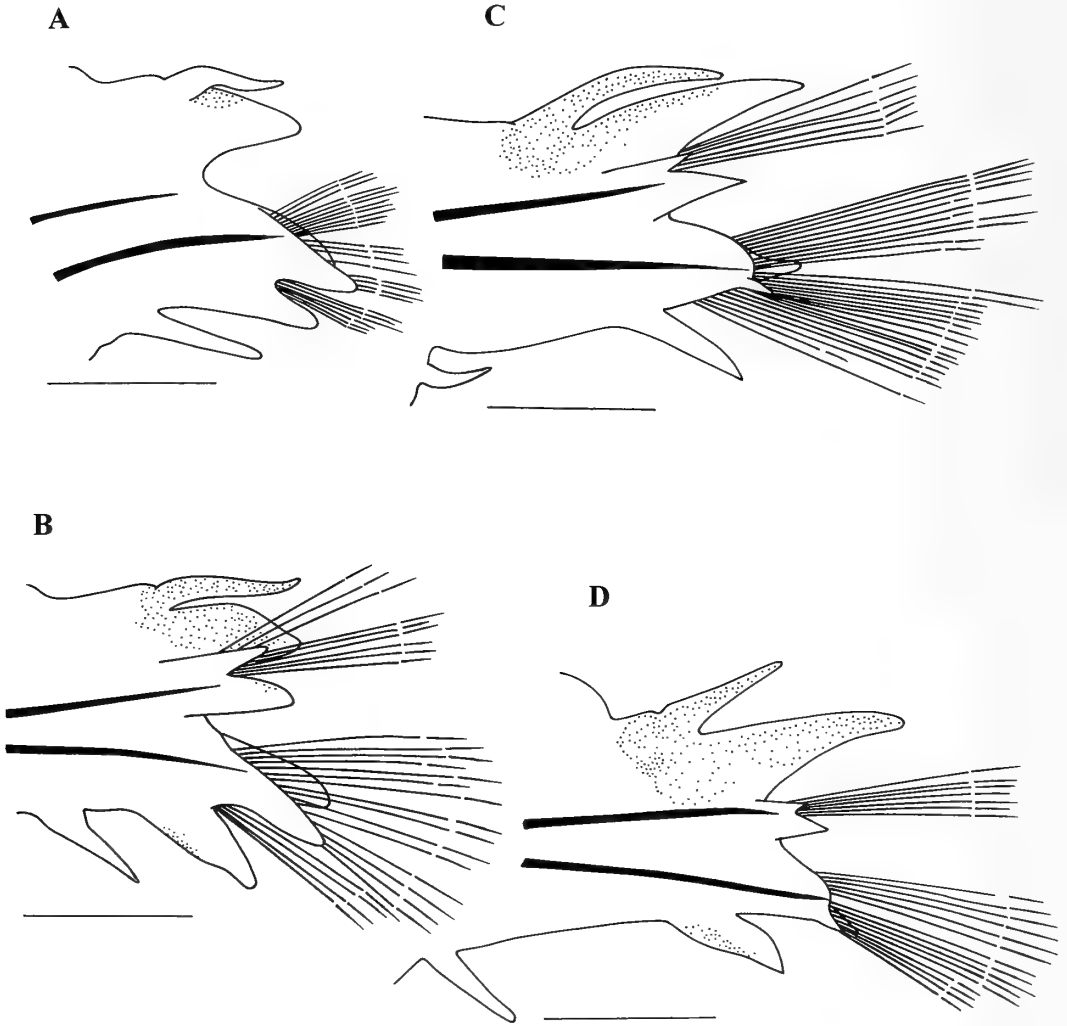


Fig. 11. *Leonnates persicus* (HKUST W0006). A. Anterior view of parapodium 2. B. Anterior view of parapodium 3. C. Anterior view of parapodium 20. D. Anterior view of parapodium 40. (Scale: A-D = 0.2 mm).

Description.—The holotype (AM W3790), an anterior fragment of 27 setigers from Moreton Bay, Queensland (27°25'S, 151°10'E), was not available for examination. All specimens examined were also from Queensland and are incomplete. The longest fragment (AM W10258, 19 mm long with 34 setigers), is the example chosen for description.

Animal colour cream with glandular region at base of dorsal cirrus. Prostomium pentagonal, cleft on frontal margin. Antennae

barely reaching joint between palpopore and palpostyle. Two pairs of eyes in trapezoidal arrangement, anterior pair slightly larger. Peristomium with tentacular cirri, longest reaching back to setiger 10.

Pharynx with slightly denticulate jaws. Maxillary ring with paragnaths arranged as follows: area I = 0; II = 3 left, 1 right; III = 0, IV = 3. Oral ring with papillae arranged as follows: V = 1; VI-VIII = 61 in 3-4 irregular rows.

Parapodia of first 2 setigers with dorsal

Table 3.—Diagnostic characteristics of *Leonnates persicus*. Numbers of processes on the left side and right side of pharyngeal areas II and IV are separated by a slash.

Specimen cat. no.	Size (mm)	Paragnath(s) on area					Papillae on area			Neuropodial falcigers on setigers		Neuropodial falcigers	
		I	II	III	IV	V	VI	VII-VIII	Neuropodial falcigers on setigers	upper fascicle	lower fascicle		
ZMUC**	4.3 × 14	0	3/2	0	3/3	0	1	29 in 3 rows	10-30	3-6	4-16		
HKUST W0006	1.5 × 15	1	3/3	1	3/3	0	1	18 in 2 rows	9-31	2-4	3-14		
HKUST W0007	2.1 × 18	0	3/2	0	3/3	0	1	19 in 2 rows	9-31	2-5	2-16		
HKUST W0008	2.1 × 11	45*	1	3/3	3	2/3	0	19 in 2 rows	8-30	1-3	3-13		
HKUST W0009	2 × 13.5	56*	0	3/3	1	3/3	0	19 in 2 rows	10-29	2-4	2-12		
HKUST W0010	2.4 × 19.4	55*	1	3/3	2	3/3	0	22 in 2 rows	11-33	2-4	2-14		
HKUST W0011	2.6 × 20.5	39*	0	2/3	2	2/3	0	19 in 2 rows	11-34	2-7	6-20		
HKUST W0012	2.6 × 3.3	40*	1	4/3	3	3/4	0	24 in 2 rows	9-34	2-6	2-14		
HKUST W0013	5.2 × 17.5	18*	0	2/4	0	3/3	0	42 in 3-4 rows	10-18	6-10	9-18		

* incomplete; ** holotype, without catalogue number.

notopodial ligule, neuropodial presetal acicular ligule, neuropodial postsetal ligule, and ventral neuropodial ligule (Fig. 12A). Dorsal notopodial ligule asetigerous, large, conical. Dorsal cirrus subulate, shorter than dorsal notopodial ligule. Neuropodial presetal acicular ligule dorsolaterally pointed. Neuropodial postsetal ligule ventrolaterally pointed. Ventral neuropodial ligule conical, similar to neuropodial acicular ligules. Ventral cirrus subulate, about as long as dorsal cirrus.

Remaining parapodia biramous with dorsal notopodial ligule, notopodial supra-acicular ligule, notopodial infra-acicular ligule, neuropodial presetal acicular ligule, neuropodial postsetal ligule, and ventral neuropodial ligule (Fig. 12B, C). Dorsal notopodial ligule large, conical, longer than notopodial presetal acicular ligule. Notopodial supra-acicular ligule slightly smaller than infra-acicular ligule (Fig. 12A, B). Notopodial supra-acicular ligule gradually diminishing along body, but remaining distinct on setiger 34 (last setiger of fragment); infra-acicular ligule similar along body. Dorsal cirrus subulate, shorter than dorsal notopodial ligule. Neuropodial presetal acicular ligule projecting ventrolaterally; neuropodial postsetal ligule projecting horizontally; presetal acicular ligule diminishing posteriorly but present on posterior segments of fragment as small, ventrally located cone. Ventral neuropodial ligule smaller than, but approximately as long as neuropodial postsetal ligule. Ventral cirrus subulate, slightly shorter than dorsal cirrus.

Notosetae all homogomph spinigers, each with slender blade fringed on cutting edge; end of shaft with tooth as long as surrounding fringe of slender teeth (Fig. 9D). Neurosetae homogomph spinigers and homogomph falcigers. Spinigers similar to those on notopodia, present throughout. Falciger present on setigers 9-34 of fragment, numbering 6-8 in supra-acicular fascicle and 9-15 in infra-acicular fascicle; blades with straight terminal projection and fringed cutting edge; shaft ending with

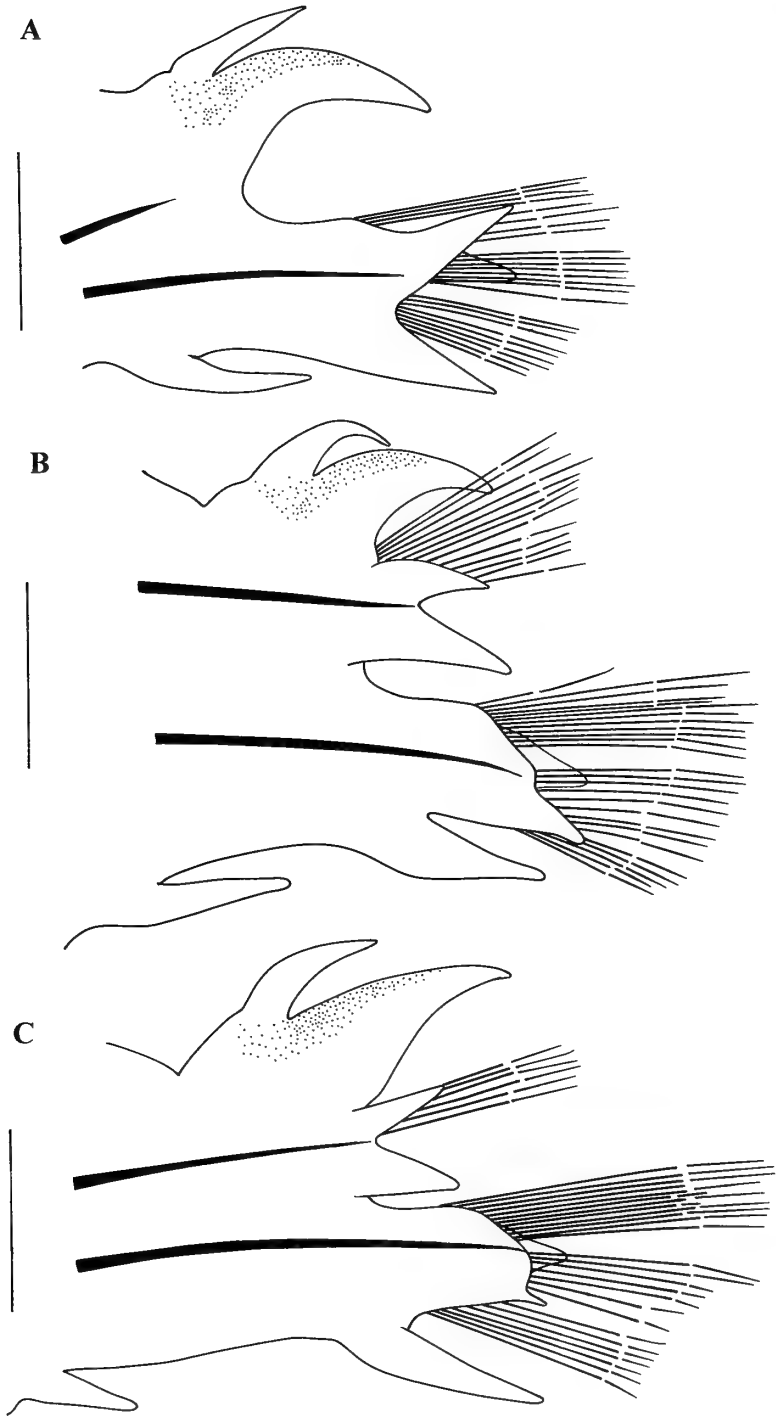


Fig. 12. *Leonnates stephensoni* (AM W10258). A. Anterior view of parapodium 2. B. Anterior view of parapodium 6. C. Anterior view of parapodium 20. (Scale: A-C = 0.3 mm).

tooth extending to the tip of surrounding fringe of slender teeth (Fig. 9E).

Female with developing oocytes diameter 55–70 μm .

Remarks.—According to Rullier (1965), *L. stephensoni* differs from *L. persicus* in having a darkened glandular region on the parapodia, three papillae on area V of proboscis, greater attenuation of falciger blades, a straight tip of falciger blades (rather than a broadly truncated tip) and falcigers with a perfectly homogomph articulation, rather than being slightly heterogomph. Our examination of the holotype of *L. persicus* reveals that it also has darkened glandular regions on the parapodia (Fig. 8B, C), not reported in the original description (Wesenberg-Lund 1949). The non-type *L. stephensoni* specimens also have papillae on the oral ring, but the exact number varies from the 3 reported in the original description: i.e., 1 to 3 on area V, and there are 2–4 continuous rows of papillae on area VI–VIII. SEM shows that the falcigers of *L. stephensoni* and *L. persicus* are very similar in having a homogomph articulation, a straight tip and a fringed cutting edge (Fig. 9C, E). The original description of *L. stephensoni*, which states that the falciger blades are more attenuated than those of *L. persicus*, and that those of *L. persicus* have a slightly heterogomph articulation (Rullier 1965) are incorrect.

Leonnates stephensoni appears to differ from *L. persicus* in having one or more papillae on area V and continuous rows of papillae on areas VI–VIII. Gallardo (1967) reported *L. persicus* from Nha Trang, Viet Nam. His description, however, shows 1 papilla on area V and 40–50 papillae on areas VII–VIII, so his specimen likely belongs to *L. stephensoni*. A specimen (AM W202003), identified as *L. stephensoni* by Hutchings & Reid (1991), resembles *L. persicus* and *L. stephensoni* in parapodial structure and setal type, but the pharyngeal areas V and VI differ from the above two species in having no processes. This specimen was collected from Australia, where

no *L. persicus* has been recorded. The available limited material does not allow a detailed analysis of the intraspecific variation in the pharyngeal areas of *L. stephensoni*. The specific status of this specimen is currently indeterminable.

In the *L. stephensoni* specimens examined, neuropodial falcigers are present from setiger 9–10 to the end of fragment (21–34 setigers), numbering 1–8 in upper fascicle and 3–15 in lower fascicle. In *L. persicus*, falcigers disappear on posterior neuropodia and it is not certain whether this is also true for *L. stephensoni*, because all specimens examined are anterior fragments and no previous reports of this species examined the occurrence of neuropodial falcigers along the body.

Habitat.—Rullier (1965) did not provide habitat information. According to Hutchings & Reid (1991), this species inhabits sandy mud.

Distribution.—Australia; Viet Nam.

Leonnates nipponicus Imajima, 1972

Leonnates nipponicus Imajima, 1972: 41–43, fig. 2A–L.

Material examined.—None. The type specimens (Holotype: NSMT-Pol. H74; Paratype: NSMT-Pol. P75) were not available for examination.

Remarks.—The original description is detailed and accompanied by figures of the head region, parapodia, and setae. This species is very similar to *L. indicus*. Imajima (1972) separated it from *L. jousseaumei* based on its distinctions in pharyngeal area III with 4 small soft papillae, instead of 6–7 chitinized paragnaths and notosetae as exclusively homogomph spinigers, instead of spinigers and a few homogomph falcigers posteriorly. Hutchings & Reid (1991) noted the more anteriorly disappearance of the notopodial supra-acicular ligule along the body of *L. nipponicus* than on specimens of *L. indicus*. As discussed previously, the pharyngeal area III of *L. indicus* contains 3–8 papillae that can be sclerotized to dif-

ferent extents (Table 1). Although the notopodial supra-acicular ligule of most of the *L. indicus* specimens we examined disappears only from far posterior segments, in two specimens this structure is absent before setiger 20 (Table 1). Notopodial falcigers, despite being few in each individual, have been found in posterior parapodia of all *L. indicus* specimens examined. The absence of notopodial falcigers in *L. nipponicus*, appears to differentiate it from *L. indicus*.

Habitat.—Corals.

Distribution.—Southern Japan.

Leonnates crinitus Hutchings & Reid,
1991

Figs. 13, 14A–D

Leonnates crinitus Hutchings & Reid,
1991: 50–52, fig. 2A–G.

Material examined.—Australia, Trinity Bay, Cairns, Queensland, (16°25'S, 145°27'E), intertidal, coll. Australian Littoral Society, 10 Dec 1974 (1 incomplete paratype) (USNM 123355); Wangewanja Cove, Port Essington, Northern Territory (11°23'S, 132°09'E), intertidal, 13 Sep 1985 (1 incomplete specimen) (NTM W3348).

Description.—The holotype (QM GH4683) was not available for examination. All three type specimens were from the same sample. Our description is based on paratype USNM 123355, a 26 mm long anterior fragment with 49 setigers.

Animal colour brownish with glandular region at base of dorsal cirrus. Prostomium pentagonal, not cleft on frontal margin. Antennae barely reaching joint between palpophore and palpostyle. Two pairs of eyes in trapezoidal arrangement, anterior pair slightly larger. Peristomium with tentacular cirri, longest reaching back to setiger 8.

Pharynx half-everted with brownish, smooth jaws. Maxillary ring with paragnaths arranged as follows: area I = 4 in perpendicular row; II = 10 left, 11 right; III = 41; IV = 20 left, 19 right. Oral ring with

papillae arranged as follows: area V = 0; VI = 1; VII–VIII = 8 in transverse row.

Parapodia of first 2 setigers with dorsal notopodial ligule, neuropodial presetal acicular lobe, neuropodial postsetal ligule, and ventral neuropodial ligule. Dorsal notopodial ligule asetigerous, large, conical. Dorsal cirrus subulate, shorter than dorsal notopodial ligule. Neuropodial presetal acicular lobe blunt. Neuropodial postsetal ligule with figure-like digit on upper tip. Ventral neuropodial ligule blunt, similar to neuropodial postsetal ligule. Ventral cirrus subulate, about as long as dorsal cirrus.

Remaining parapodia biramous with 6 ligules on anterior segments, 5 on posterior segments (Fig. 13A, B): dorsal notopodial ligule, notopodial supra-acicular ligule, notopodial infra-acicular ligule, neuropodial presetal acicular ligule, neuropodial postsetal ligule, and ventral neuropodial ligule. Dorsal notopodial ligule large, conical, slightly longer than notopodial supra- and infra-acicular ligules. Notopodial supra-acicular ligule blunt; of similar size to infra-acicular ligule (Fig. 13A); supra-acicular ligule gradually diminishing along body, but remaining distinct on last setiger of fragment; infra-acicular ligule taper in middle region. Dorsal cirrus subulate, shorter than dorsal notopodial ligule. Neuropodial presetal acicular lobe blunt; postsetal ligule with figure-like digit on upper tip; finger-like digit reduced along body and absent from setiger 26. Ventral neuropodial ligule blunt anteriorly, elongated and pointing downward from setiger 23 (Fig. 13B). Ventral cirrus subulate, approximately as long as dorsal cirrus.

Notopodia with homogomph spinigers (Fig. 14A, B) throughout. Neuropodia with supra-acicular homogomph spinigers, infra-acicular heterogomph spinigers (Fig. 14C), heterogomph falcigers (Fig. 14D). Neuropodial spinigers present throughout, accompanied by falcigers in middle region. Neuropodial falcigers present from setiger 12–14 to setiger 42–48, numbering 1–2 in upper fascicle and 2–8 in lower fascicle.

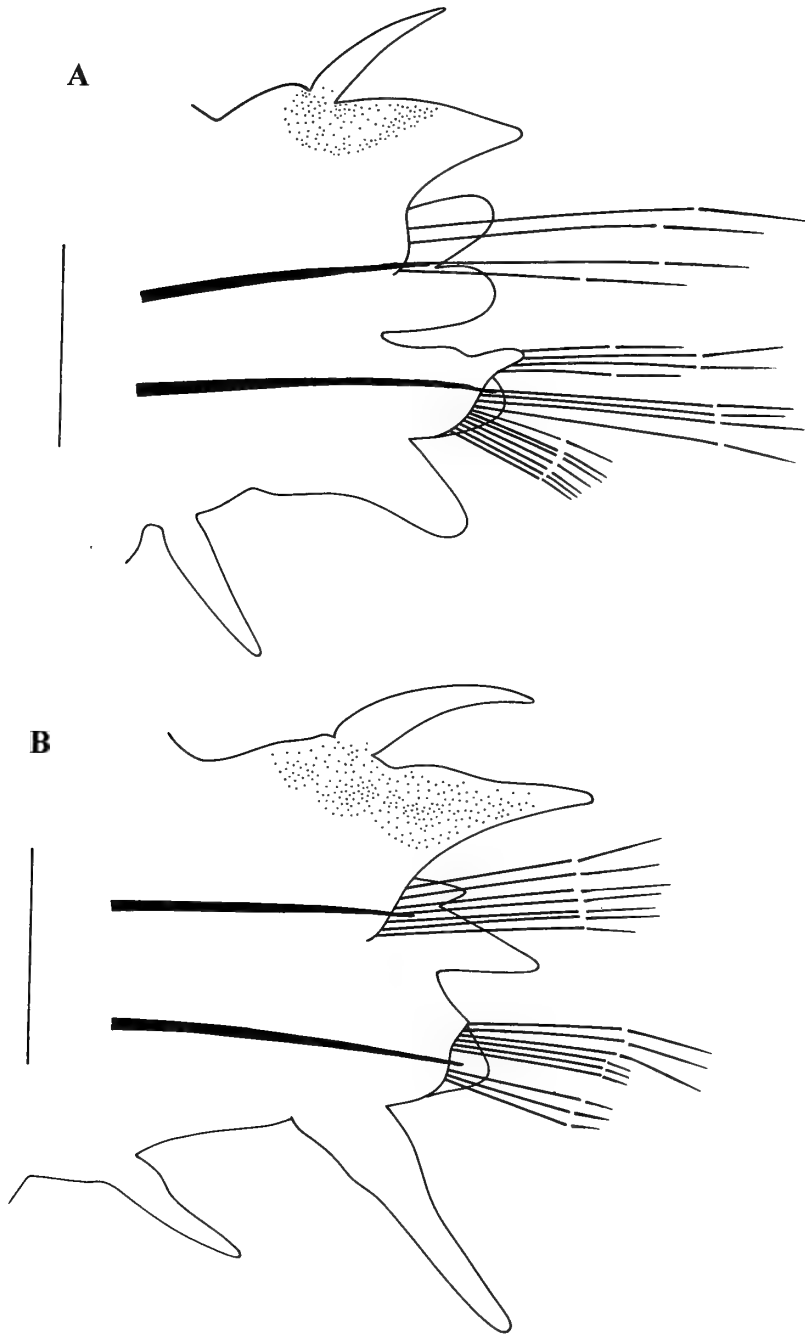


Fig. 13. *Leonnates crinitus* (Paratype USNM 123355). A. Posterior view of parapodium 8. B. Posterior view of parapodium 30. (Scale: A-B = 0.1 mm).

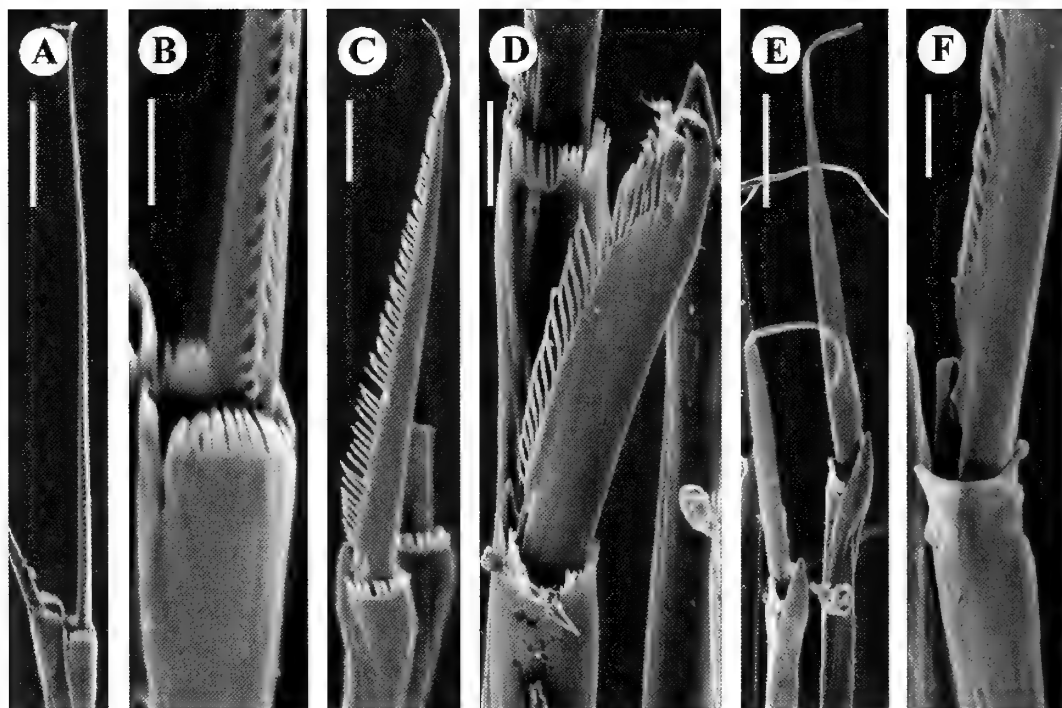


Fig. 14. *Leonnates crinitus* (Paratype USNM 123355). A. Notopodial homogomph spiniger from parapodium 30. B. Enlarged end of shaft of the spinigers in A. C. Neuropodial heterogomph spiniger from parapodium 8. D. Neuropodial falciger from parapodium 30. *Paraleonnates bolus* (USNM 127644). E. Notopodial spinigers from parapodium 4. F. Enlarged end of shaft of another notopodial spiniger from parapodium 4. (Scale: A = 20 μ m; B = 4 μ m; C = 20 μ m; D = 10 μ m; E = 20 μ m; F = 5 μ m).

Remarks.—The characters of the both specimens match well with the original description by Hutchings & Reid (1991). *Leonnates crinitus* is similar to *L. decipiens* in the shape of parapodia and in pharyngeal armature on areas II, IV, and VI, but differs from the latter in having 4–5 paragnaths, instead of none, arranged in a single perpendicular row on area I and a greater number of paragnaths (24–41 vs. 3–21) on area III. The spinigers and falcigers of these two species are also similar, except that heterogomph spinigers, observed in *L. crinitus* (Fig. 14C), were not found in *L. decipiens*. Homogomph falcigers in neuropodial supra-acicular fascicle of *L. crinitus*, reported by Hutchings & Reid (1991, fig. 2G) were not found. This difference, however, may be due to the limited material for SEM observation.

Habitat.—This species inhabits muddy

sand, 0–5 m; specimen NTM W3348 was collected from a rotting bark (Hutchings & Reid 1991).

Distribution.—Australia.

Key to the *Leonnates* species based on atokous specimens

1. Oral ring with paragnaths on area VI *L. simplex*
 - Oral ring with only papillae 2
2. Falcigers present on all neuropodia 3
 - Falcigers not present on anterior neuropodia 4
3. Posterior notopodia without falcigers *L. nipponicus*
 - Posterior notopodia with few falcigers *L. indicus*
4. Pharyngeal area V with papilla(e), papillae on area VI–VIII forming continuous rows *L. stephensoni*
 - Pharyngeal area V without papillae, bor-

- der between areas VI and VII-VIII clearly defined 5
5. In all parapodia, ventral neuropodial ligule slightly shorter than neuropodial acicular ligules *L. persicus*
- In middle and posterior parapodia, ventral neuropodial ligule much longer than neuropodial acicular ligules 6
6. Pharyngeal area I without paragnaths, area III with 3–21 paragnaths *L. decipiens*
- Pharyngeal area I with paragnaths, area III with 24–41 paragnaths *L. crinitus*

Australonereis Hartman, 1954

Australonereis ehlersi (Augener, 1913)

Nereis (*Leonnates*) *ehlersi* Augener, 1913: 142–145, fig. 12A–C, pl. 3, fig. 53.

Leptonereis ehlersi Monro 1938: 618–623, fig. 7–13.

Australonereis ehlersi Hartman 1954: 19–23, fig. 1–11; Hutchings & Reid 1990: 77–78, fig. 4.

Material examined.—Swan River, Western Australia, (19 specimens) (ZIM V-7906).

Description.—None of the type specimens has an everted pharynx. The parapodia and setal structure match well with Hartman (1954). The pharyngeal structure, as revealed by examination of three specimens that have been dissected, also matches Hartman (1954). The tips of pharyngeal papillae are not sclerotized.

Remarks.—*Nereis* (*Leonnates*) *ehlersi* was originally described as having papillae on the oral ring and paragnaths on the maxillary ring (Augener 1913). Monro (1938) found papillae on the maxillary ring only, but he assigned this species to *Leptonereis*, which has a smooth pharynx. *Nereis* (*Leonnates*) *ehlersi* was later assigned to *Australonereis ehlersi* by Hartman (1954). *Australonereis* has a smooth oral ring and a papillate maxillary ring; its notosetae are spinigers and neurosetae are spinigers and falcigers. Hutchings & Reid (1990) provided a detailed description for specimens collected from different parts of Australia. They reported that the tips of the papillae

on the pharynx are sclerotized, and the sclerotization was not seen in all specimens they examined, but it was common and seemed to be independent of gender, size, and locality.

Habitat.—Muddy sand and sand flats.

Distribution.—Australia.

Websterinereis Pettibone, 1971

Websterinereis glauca Pettibone, 1971

Leonnates pusillus Langerhans, 1880: 279, pl. 14, fig. 10.

Leptonereis glauca Claparède, 1870: 454, pl. 7: fig. 3; Fauvel, 1914: 163, pl. 12, figs. 5–23; Ramsay, 1914: 244, pl. 1, figs. 1–10.

Laeonereis glauca Hartman, 1945: 22.

Websterinereis glauca Pettibone, 1971: 27–30, figs. 14–16.

Websterinereis tridentata Fauchald 1977: 90.

Material examined.—Madeiras, (3 specimens) (NHMV 2162).

Description.—Very tiny nereidids (<0.5 cm long), fragile after long storage. Pharynxes not everted. Dissection of one of the specimens revealing no chitinized paragnaths, but other details of pharyngeal structure were not observable. All tentacular cirri missing. Parapodia, except first two pairs, biramous, with no signs of heteronereidid modification. Throughout shape of parapodia and pattern of setal distribution similar. Notosetae homogomph spinigers. Neurosetae homogomph spinigers and heterogomph falcigers. Sex of specimens indeterminable.

Remarks.—*Leonnates pusillus* can not be assigned to *Leonnates* because it does not have both papillae and paragnaths on the pharynx. In the original description *L. pusillus* was depicted as having papillae on both rings, but it was afterwards referred to *Leptonereis glauca* Claparède, 1870 by Fauvel (1914) and Ramsay (1914); *Leptonereis* has a smooth pharynx. Later it was referred to *Laeonereis glauca* by Hartman (1954); *Laeonereis* has tufts of papillae on both pharyngeal rings. Afterwards it was

referred to *Websterinereis glauca* by Pettibone (1971); *Websterinereis* has a smooth maxillary ring and a papillate oral ring. Pettibone (1971) considered *L. pusillus* to be the male heteronereidid form of *W. glauca*, although Langerhans' sample also includes atokous specimens. Fauchald (1977) redefined *Websterinereis* as having a smooth maxillary ring and paragnaths on the oral ring, with *W. tridentata* considered as the sole valid species.

Our observations do not clarify to which genus these specimens belong, but there is no reason for us to state that they are not *W. glauca* as stated by Dr. Pettibone.

Habitat.—Types from old fish cages.

Distribution.—Madeiras.

Paraleonnates Chlebovitch & Wu, 1962

Paraleonnates bolus Hutchings & Reid,
1991

Fig. 14E–F

Leonnates bolus Hutchings & Reid, 1991:
48–50, fig. 1A–E.

Material examined.—Holotype, 1 complete specimen from East Arm, Darwin Harbour, Northern Territory, Australia (12°30'S, 130°55'E), 2.5 by 50 mm, 115 setigers, 14 Dec 1984 (NTM W2518); paratype, 1 incomplete specimen from Port Warrender, Admiralty Gulf, Western Australia (14°35'S, 125°53'E), 2.8 × 45 mm, 86 setigers, Oct 1976 (USNM 127644).

Description.—Unless otherwise stated, our description is based on specimen NTM W2518. Pharynx with paragnaths on maxillary ring and papillae on oral ring, arranged as follows: area I–II = 35 paragnaths in 2 continuous irregular rows; III–IV = 48 paragnaths in 3 continuous irregular rows; V = 0; VI = 2 papillae, one blunt on centre of area, another sharply pointed located near frontal margin of oral ring; VII–VIII = 4 sharply pointed papillae, in transverse row, located near frontal margin of oral ring. Border between areas I and II and border between areas III and IV not clear. Paragnaths on middle of both dorsum and

ventrum of maxillary ring are slightly smaller than those on sides. Centre of area VII–VIII with some dermal folds (Fig. 1B in Hutchings & Reid 1991) but 4 blunt papillae, described on centre of oral ring (Hutchings & Reid 1991), not observed. Similar pharyngeal arrangement in specimen USNM 127644 as follows: areas I–II = 26 paragnaths in 2 irregular rows; III–IV = 34 paragnaths in 3 irregular rows; IV = 7 paragnaths; V = 0; VI = 1 sharply pointed papilla, located near frontal margin of oral ring; VII–VIII = 4 sharply pointed papilla in one transverse row, located near frontal margin of oral ring; on both areas I–II and III–IV, paragnaths on centre slightly larger than those on sides; border between areas I and II and border between areas III and IV not clear. No blunt papillae observed on area VII–VIII.

Parapodia of first 2 setigers subbiramous with 2 aciculae, without notosetae, with dorsal notopodial ligule, neuropodial presetal supra-acicular ligule, neuropodial presetal infra-acicular ligule, neuropodial postsetal lobe, and ventral neuropodial ligule. Dorsal notopodial ligule conical, asetigerous. Dorsal cirrus subulate, extending beyond dorsal notopodial ligule. Neuropodial presetal supra- and infra-acicular ligules conical. Neuropodial postsetal lobe broad. Ventral neuropodial ligule conical, slightly shorter than neuropodial acicular ligules. Ventral cirrus slender, shorter than dorsal cirrus.

Remaining parapodia biramous with dorsal notopodial ligule, notopodial infra-acicular ligule, neuropodial supra-acicular ligule, neuropodial infra-acicular ligule, neuropodial postsetal ligule, and ventral neuropodial ligule. Dorsal notopodial ligule conical, as long as notopodial infra-acicular ligule. Dorsal cirrus slender, longer than dorsal notopodial ligule. Anterior neuropodia with presetal supra-acicular ligule, infra-acicular ligule, and postsetal ligule. Shapes of notopodial presetal acicular ligules similar along body, but postsetal ligule digitiform in anterior segments but absent

from setiger 39 in holotype and setiger 25 in specimen USNM 127644. Ventral neuropodial ligule smaller than neuropodial presetal acicular ligule. Ventral cirrus slender, shorter than dorsal cirrus.

Notopodia and neuropodia with heterogomph spinigers (Fig. 14E–F) throughout. Ends of shaft smooth, hinge with large tooth facing cutting edge of blade. Blade with fringe of small teeth on cutting edge. Smooth, long-bladed heterogomph falcigers in subacicular fascicle of far anterior parapodia, reported from the other paratype (WAM 422–86) in original description (Fig. 1H in Hutchings & Reid 1991), not found in holotype or paratype USNM 127644.

Remarks.—Our examination of the type and non-type specimens of *P. uschakovi* (about 20 specimens, IOCAS 08181, 09188) shows that the prostomium, the pharynx, the parapodia and the setae of *L. bolus* all resemble those of *P. uschakovi*. The original description of *P. uschakovi*, however, does not clearly show a digit-form neuropodial postsetal ligule. The papillae on the oral ring of *P. bolus* also agree well with those of *P. uschakovi*. *Paraleonnates uschakovi* has 1 sharp papilla and 1 blunt papilla on area VI, and 4 sharp papillae and 0–5 blunt papillae on area VII–VIII; the first row of paragnaths on area VII–VIII is sclerotized to higher degree than are those of second and third rows, while in *P. bolus* all paragnaths are quite well sclerotized. This difference may differentiate *P. bolus* from *P. uschakovi*. In the original description of *L. bolus*, one paratype (WAM 422–86, not available for examination) was shown to have long-bladed falcigers on anterior setigers, but neither the other types have such falcigers. Blunt papillae on the centre of oral ring are common to *Leonnates*, but the sharply pointed papillae near the frontal margin of the oral ring have not been reported in any other *Leonnates* species. The shaft of the spiniger of *P. bolus* differs from that of all *Leonnates* species in having a smooth end, instead of being fringed with teeth. The neuropodia of *P.*

bolus differ from those of all *Leonnates* species in having two presetal ligules and a postsetal lobe, instead of one acicular lobe or ligule and one postsetal lobe or ligule. Substantial differences between *Leonnates* and *Paraleonnates*, and the similarities between *P. uschakovi* and *L. bolus* suggest that *L. bolus* be transferred to the genus *Paraleonnates*. *Paraleonnates bolus* is distinguishable from *P. uschakovi* in higher degree of sclerotization in the second and third rows of paragnaths on pharyngeal area VII–VIII.

Habitat.—Mangroves (Hutchings & Reid 1991). Holotype from inside mounds made by burrowing lobster *Thalassina squamifera* de Man.

Distribution.—Northern Australia.

Discussion

Generic separation in Nereididae has been mainly based on the pharyngeal structure and the types of setae present. Intra-generic variation of these characters has been noted (Fauchald 1977). Our examination of all available *Leonnates* species has allowed the assessment of such variation in *Leonnates*. In the pharynx of most *Leonnates* species, the maxillary ring has only sclerotized paragnaths and the oral ring has only soft papillae. However, there are exceptions: in some specimens of *L. indicus*, pharyngeal area III has soft papillae; in *L. simples*, the pharyngeal area III has sclerotized paragnaths. The pharyngeal structure also serves to differentiate *Leonnates* from its closely related *Paraleonnates*; there are pointed papillae and blunt papillae on the oral ring of *Paraleonnates*, the former located near the upper margin, while the later located on the centre; in *Leonnates* there are only blunt papillae on the oral ring, located on the centre. Intraspecific variation in pharyngeal structure also exists: the extent of sclerotization of paragnaths vary in *L. indicus* specimens of collected from the same population. Previous descriptions of pharyngeal area VII–VIII of

Leonnates reported rows, rather than exact numbers of papillae present. Our study reveals that, at least in *L. indicus* and *L. persicus*, the number of papillae present on this area is positively related to the body size, suggesting that the number of rows of papillae alone may not be an effective character for species separation in *Leonnates*.

Six types of setae have been reported in Nereididae (Pettibone 1963, Chambers & Garwood 1992): compound homogomph spiniger; compound heterogomph spiniger; compound homogomph falciger; compound heterogomph falciger; compound paddle-shaped seta; and simple falciger. Of these, simple falciger, which is found on the posterior neuropodia of *Neanthes diversicolor* (Müller, 1776), is a specialized compound falciger whose blade is fused to the shaft. The other five types of setae have been observed in *Leonnates*. Except the paddle-shaped seta, which occurs only in heteronereidids, the other four types of setae found in *Leonnates* share a common character, i.e., the end of shaft has a large tooth, which is fringed by a circle of smaller teeth. This character also serves to differentiate *Leonnates* from *Paraleonnates*, which has a smooth end of setal shaft. However, there are substantial intrageneric difference in the setal blades of *Leonnates*; in *L. indicus*, the blade is convex with short teeth; in other species the blade is fringed with slender teeth, and the shape varies from triangular in *L. simplex* to slender in *L. persicus*, *L. decipiens*, *L. stephensoni*, and *L. crinitus*.

Apart from pharyngeal structure and types of setae present, parapodial structure is also important in the generic identification of Nereididae (Pettibone 1971). In *Leonnates*, the neuropodia consist of an acicular lobe or ligule and a postsetal lobe or ligule; whereas in *Paraleonnates*, the neuropodia consist of two acicular ligules and a postsetal lobe or ligule.

At maturity, many nereidid species undergo significant changes in internal structures such as musculature and gut, and external structures such as parapodial lobes,

setae, prostomial sense organs, and in males, the pygidium. These changes lead to a special stage termed epitoke or heteronereidid with shorter body length, larger parapodia, and broad-bladed setae that aid swimming. The extent of epitokous modification differs from one species to another and between male and female of one species. According to their extent of epitokous modification and the associated mating behavior, nereidids can be divided into three groups (Pettibone 1963): one without an epitokous stage and swarming; ones with a slight epitokous modification but without distinct heteronereidids and with limited swarming activity; and ones with significant modified heteronereidids and active swarming activity. In *Leonnates*, both mature and immature individuals have been reported only in few species. *Leonnates niestraszi* and *L. insolitus* are known only from heteronereidids, while *L. simplex*, *L. nipponicus*, *L. crinitus*, *L. stephensoni* are known only from immature individuals. Heteronereidids of *L. niestraszi* (male), *L. decipiens* (male), *L. insolitus* (female), *L. persicus* (male) have significant modified eyes, parapodial ligules and setae. The females of *L. indicus* and *L. persicus*, both with mature oocytes, however, have no significantly modified external body structures. Based on the above limited information, no pattern of epitokous modification in *Leonnates* can be generalized.

In summary, our study shows that *L. virgatus*, *L. pusillus*, *L. jousseaumei*, *L. decipiens* var. *manilensis*, and *L. bolus* are not valid *Leonnates* species. *Leonnates virgatus* and *L. jousseaumei* are conspecific with *L. indicus*. *L. decipiens* var. *manilensis* is conspecific with *L. decipiens*. *Leonnates bolus* belongs to *Paraleonnates*. *Leonnates niestraszi* and *L. insolitus*, described from heteronereidids with highly modified parapodia and setae, can not be fully characterized. *Leonnates pusillus* is indeterminable to genus. Some specimens originally identified as *L. jousseaumei* are heteronereidids of *Perinereis*.

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***Parapionosyllis macaronesiensis*, a new species of Exogoninae
(Polychaeta: Syllidae) from the Macaronesian Region**

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Abstract.—*Parapionosyllis macaronesiensis* new species, from the Macaronesian region (Canary Islands, Madeira and Selvagens Islands), is described. It is characterized by the shape of the dorsal simple seta, with 2–3 thick spines subdistally on the convex side and the blades of compound setae provided with coarse serrations on the cutting edge, especially the uppermost falcigers.

In a report on the interstitial fauna from Madeira (Núñez et al. 1995), two juvenile specimens of an undescribed species were collected and reported as *Parapionosyllis* sp. Later, more specimens of this species were collected in Lanzarote and Tenerife (Canary Islands) during a study of the interstitial communities of *Cymodocea nodosa* (Ucria) Ascherson (Brito 1999). Most recently two more specimens were collected in the Ilhéu de Fora (Selvagens Islands) during the research project Macaronesia 2000.

This new species differs from all others species of *Parapionosyllis* by its long-bladed uppermost compound setae, with blades having long marginal serrations, and by its solitary dorsal simple seta, provided with 2–3 thick, subdistal spines. In this paper, the new species is described and discussed, and data on its ecology and reproduction are included.

Materials and Methods

The samples from the Canary Islands were collected during a study of the meiobenthos from a sandy bottom and sea-grass (*Cymodocea nodosa*) habitats. Additional material from sandy bottoms from Madeira and Selvagens Islands is included.

The samples were collected by unaided diving and scuba diving from 4–18 m depth. PVC cores covering an area of 16 cm² and pushed into the sediment to a depth of 30 cm, providing 450 cc silt for each sample. Samples were divided into four parts of 0–5, 5–10, 10–20 and 20–30 cm depth for the study of the vertical distribution of species. The sediment was washed and screened through a 100 µm mesh sieve. The samples were treated with MgCl₂ and fixed with 10% formaldehyde in seawater. The specimens were transferred to 70% ethanol. Due to the size of the specimens, they were mounted whole in glycerine jelly and examined with an optical microscope with interference contrast (Nomarski).

The material is deposited in the collections of the Department of Zoology of the University of La Laguna (DZUL) and in the Museum of Natural Sciences of Tenerife (TFMC).

Subfamily Exogoninae Langerhans, 1879
Genus *Parapionosyllis* Fauvel, 1923
Parapionosyllis macaronesiensis, new
species
Fig. 1

Parapionosyllis sp.—Núñez et al., 1995: 6
(list).

Type locality.—Arrecife de Lanzarote (Canary Islands).

Type material.—Holotype (microscopic slide) (TFMCN AN/000204), Arrecife de Lanzarote (Canary Islands), Apr 1993, col. J. Núñez. One Paratype (microscopic slide) (DZUL PO-500), Ensenada de los Abades, Tenerife (Canary Islands), Nov 1994, col. J. Núñez & M. C. Brito.

Additional material.—Two juvenile specimens (microscopic slide) (DZUL PO-501), Laginha, Ponta of San Lourenço (Madeira), Sep 1992, col. J. Núñez. Two specimens (microscopic slide), (DZUL PO-502), Punta do Sul, Ihléu de Fora, (Selvagens Islands), May 1999, col. J. Núñez.

Description.—Body long, thin and filiform, without coloration markings, nearly 3 mm long, 0.16 mm wide, for 29–32 setigers. Prostomium semicircular to ovate, with four small, red eyes in open trapezoidal arrangement; antennae skittle-shaped; median antenna originating between posterior eyes, similar in length to prostomium and palps together, lateral antennae originating in front of anterior eyes, about 0.67 of length of median antenna. Palps broad, similar in length to prostomium, fused along basal half, leaving a middorsal seam and frontal scar (Fig. 1A). One pair of tentacular cirri, originating ventro-laterally to lateral antennae but somewhat short; peristomium dorsally reduced, covered by a dorsal lip of first setiger. Dorsal cirri on all setigers, similar in length or smaller than lateral antennae, sometimes having a pseudoarticulated appearance. Parapodia conical, proportionally short, rounded, with a small distal papilla; ventral cirri digitiform, slightly longer than parapodial lobe. Each segment with 1–2 subdermal, dorsal glands on each side, with yellowish granular material. Anterior parapodia each with one long-bladed compound seta and 5–7 other falcigers with shorter blades (Fig. 1D); progressively, number of falcigers decreasing to 2–5 in posterior parapodia (Fig. 1G). Long blades unidentate, with tips rounded and provided with a subdistal fine spine and long, up-

wardly extending coarse serrations on edge, longer and thicker basally (Fig. 1F), about 35 μm on most anterior parapodia, 55 μm in midbody, 45–50 μm posteriorly. Falcigers similar throughout; blades with rounded tip, provided with a subdistal spine, and long serrations on edge, especially on uppermost setae; anterior dorso-ventral gradation in length of falcigers; anterior falcigers 17 μm above, 10 μm below, posterior falcigers 15 μm above, 10 μm below; shafts becoming thicker more ventrally and posteriorly. Solitary dorsal simple seta from anterior parapodia, unidentate, provided with 2–3 thick, subdistal spines (Fig. 1H). Posterior parapodia each with solitary ventral simple sigmoid unidentate seta (Fig. 1I). Solitary thick aciculum in each parapodium, distally rounded and hollow at the tip (Fig. 1C, E). Pharynx wide, extending through about three segments, provided with a conspicuous, conical middorsal tooth on the anterior rim. Proventriculus shorter than pharynx, extending through about two segments, and with about 18 rows of muscle cells. Pygidium with two anal cirri, longer than dorsal cirri (Fig. 1B).

Reproduction.—The holotype is a mature female collected in April, with one oocyte in setigers 12, 15, 16, 17, 18 and 20. One of the specimens collected from Selvagens Islands in May is a female exhibiting external gestation; juveniles on the dorsolateral body surface above parapodia 15–19. This kind of gestation is a common feature of the Exogoninae (Pierantoni 1903).

Remarks.—*Parapionosyllis macaronesiensis* is very similar to *P. brevicirra* Day, 1954 in having some compound setae with long blades; however they differ in the following:

The compound setae of *P. macaronesiensis*, especially the long bladed ones, have very long, upwardly extending serrations on the margins of the blades; the serrations of the blades of *P. brevicirra* are short and straight.

Parapionosyllis brevicirra was described as lacking parapodial glands (Day 1954,

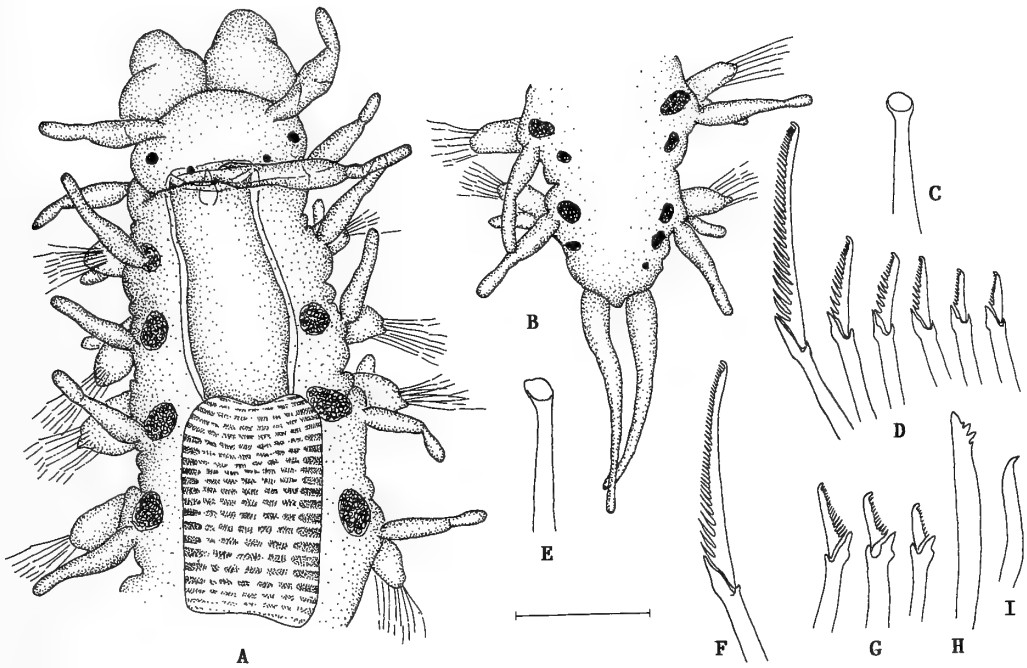


Fig. 1. *Parapionosyllis macaronesiensis*, new species, Holotype. A. Anterior end and midbody, dorsal view. B. Posterior end, dorsal view. C. Aciculum, anterior parapodia. D. Anterior compound setae. E. Aciculum, posterior parapodia. F. Long-bladed compound seta from posterior parapodia. G. Posterior compound setae. H. Dorsal simple seta. I. Ventral simple seta. Scale bar: 90 μm for A, B; 20 μm for C–I.

Hatmann-Schröder 1962, San Martín 1984); however, Alós et al. (1983) described several specimens of this species from the Mediterranean sea, which only differed from previous descriptions in having parapodial glands with fibrillar material; in the same material, several specimens had few glands or lacked them. *P. macaronesiensis* has parapodial glands only with granular material.

The dorsal simple seta of *P. brevicirra* has similar spines on its margin; *P. macaronesiensis* has the dorsal simple seta with spines of different sizes.

Parapionosyllis macaronesiensis differs from *P. minuta* (Pierantoni, 1903), *P. gestans* (Pierantoni, 1903), *P. elegans* (Pierantoni, 1902), *P. labronica* Cognetti, 1965, *P. longicirrata* (Webster & Benedict, 1884) (Perkins 1981), and *P. cabezali* Parapar et al., 2000, mainly in the shape and size of the compound setae. All these species have compound setae with much shorter blades

and also shorter serration on the edge. *P. cabezali*, furthermore, has two kinds of parapodial glands.

Parapyonosyllis uebelackeare San Martín, 1991 is also a very similar species but it has long-bladed compound setae only on the anterior parapodia, which are proportionally shorter and provided with shorter serrations (San Martín 1991). *P. floridana* San Martín, 1991 has longer, apparently biarticulated dorsal cirri, a longer pharynx, lacks parapodial glands and the dorsal simple seta has several, equal serrations.

Ecology.—The collecting depth varied from 4 m in the station of Madeira to 18 m in the Selvagens Islands. The specimens inhabited sandy areas lacking vegetation as well as areas within beds of the seagrass *Cymodocea nodosa*. In reference to the vertical distribution in the sediment, all the individuals were collected in the superficial level (0–5 cm).

Distribution.—Central East Atlantic:

Madeira Islands, Selvagens Islands and Canary Islands.

Etymology.—The *derivatio nominis*, of Greek etymology, refers to Macaronesia (makáro = happiness; nesoi = islands), the biogeographical region in which the specimens of this species were collected.

Acknowledgments

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Metridium farcimen, the valid name of a common North Pacific sea anemone (Cnidaria: Actiniaria: Acontiarina)

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Abstract.—Three older names apply to the species described by Fautin et al. in 1990 as *Metridium giganteum*. They are *Actinia priapus* Tilesius, 1809, *Actinia farcimen* Brandt, 1835, and *Isometridium rickettsi* Carlgren, 1949. We synonymize these four species names. The most senior of the synonyms is a junior homonym; therefore, the valid name of this species is *Metridium farcimen* (Brandt, 1835). We also synonymize with *Metridium* the generic names *Dendractis* Andres, 1883, and *Isometridium* Carlgren, 1949.

Metridium farcimen (Fig. 1) is a conspicuous and distinctive member of the North Pacific coastal fauna. It had been considered an ecotype of *Metridium senile* (Linnaeus, 1761), characterized primarily by large size, solitary habit, and subtidal occurrence. Hand (1956:203, 204) also noted the oral disc of a small specimen is circular, whereas that of a large one is “strongly lobed,” the marginal sphincter muscle may be lacking in a small specimen but is “very strongly developed” in a large one, and a small specimen may bear gonads on its perfect mesenteries “whereas larger ones never do.” Carlgren (1933, 1934) and Hand (1956) documented quantitative differences in cnidae of the acontia. Nonetheless, large and small specimens were considered conspecific; taxonomic considerations centered on whether animals from the Pacific and Atlantic differ subspecifically (e.g., Hand 1956, Williams 1975) and whether the numerous Atlantic variants deserve taxonomic recognition (e.g., Stephenson 1935).

Electrophoretic differences between small, clonal, primarily intertidal specimens and large, solitary, subtidal ones (Bucklin & Hedgecock 1982) convinced us that morphological differences between animals of the two sorts are taxonomically significant.

The former are clearly identifiable as *Metridium senile*. Knowing how common and conspicuous the large animals are, and how many names have been applied to morphological variants of *M. senile*, we were surprised not to find a name that unambiguously referred only to the large specimens. We therefore described a new species, *Metridium giganteum* Fautin, Bucklin, & Hand, 1990. In the course of inventorying taxonomic literature and type specimens of sea anemones (Fautin 1999: Sea anemones of the world, version 2.0. <http://biocomplexity.nhm.ukans.edu/anemones/images/Version.html>), DGF found three older names that refer to the species, the valid name of which is *Metridium farcimen* (Brandt, 1835).

We provide below the formal synonymy of *M. farcimen*. The conflation of *M. farcimen* with *M. senile* has been so great that we do not include the name *M. senile* in the list of synonyms—as occasion arises, scientists may find it useful to identify particular instances of reference to *M. farcimen* under the name *M. senile*.

Metridium farcimen (Brandt, 1835)

non *Actinia Priapus* Forsk.: Gmelin, 1788:3134

Actinia Priapus Tilesius, 1809:405

Actinia farcimen Brandt, 1835:12

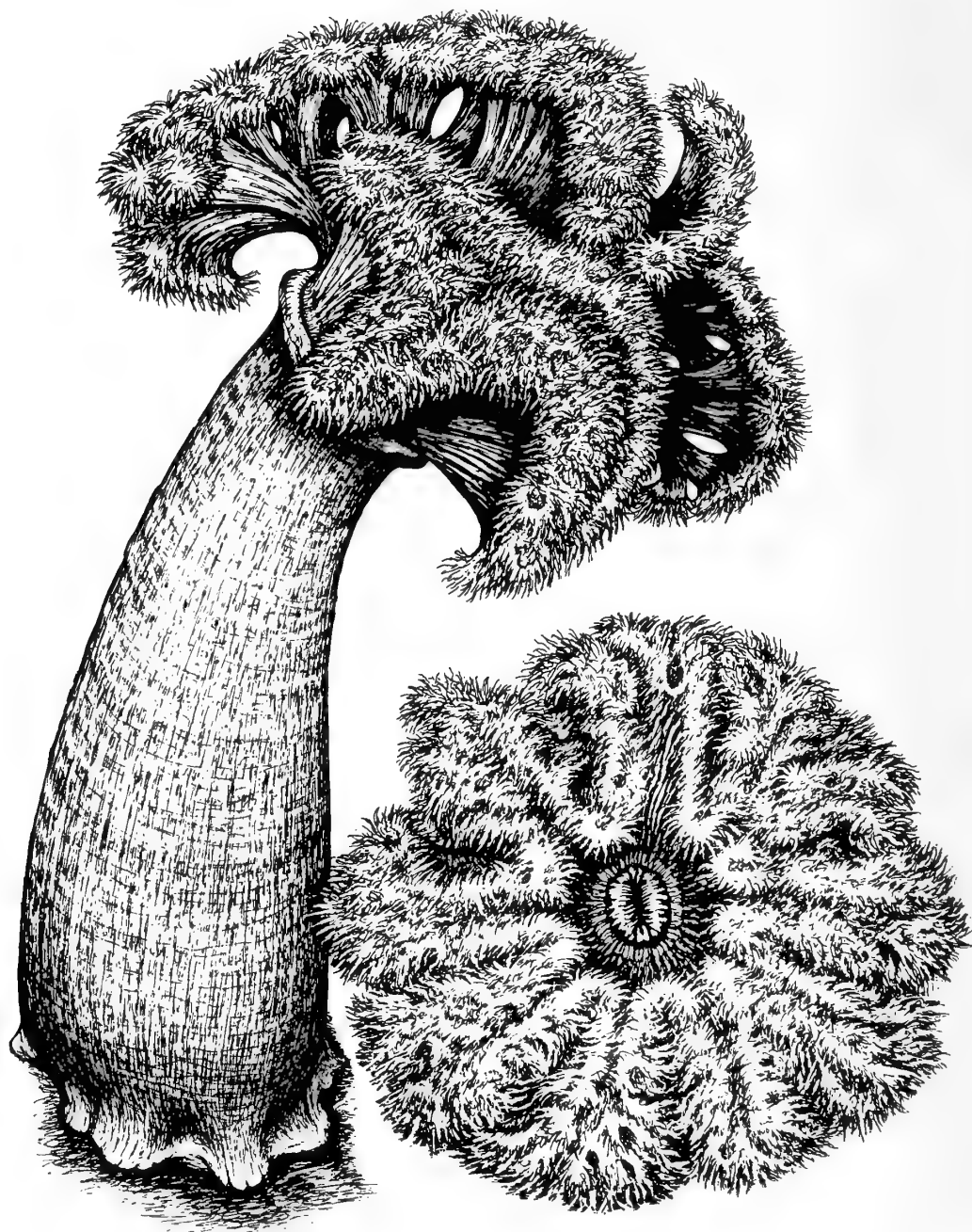


Fig. 1. *Metridium farcimen* (Brandt, 1835) drawn by Steven Sechovec from life.

non *Actinia priapus*, Gmelin: Milne Edwards, 1857:280

L'*Actinia farcimen*, Brandt: Milne Edwards, 1857:289

Heliactis farcimen Brandt: Andres, 1883:

181

Dendractis priapus Til.: Andres, 1883: 364

Isometridium Richettsi Carlgren, 1949: 106

Isometridium rickettsi Carlgren, 1951: 430

Metridium giganteum Fautin, Bucklin, & Hand, 1990:81

History of Names Applied to This Species

The diagnosis of *Actinia priapus* (“*Actinia Kamtschaticae descriptio*”), on page 405 of a long publication by Tilesius (1809) concerned with sea anemone taxonomy, is as follows:

[penis equi ab incolis littoralibus ad Kamtschatkam dicta:] *A. maxima longissima cylindracea, badia vel fusca, transversim rugosa, basi affixa dilatata, lobata; extremitate libera glandiformi praeputio tecta, disco ramoso tentaculifero albedo, tentaculis papillaeformibus numerosissimis fasciculosis. Ore centrali prominulo, cum disco retractili.* (Rendered originally in italics.)

Translation: (called horse penis by the coastal inhabitants of Kamtschatka:) Extremely long and cylindrical, bay or dark colored, wrinkled transversely, with affixed base dilated, lobed [?: probably a misprint for *lobata*, which means lobed; the other possibility is “lipped,” the correct rendering of which would be *labiata*]; free extremity glandiform, covered with foreskin, branched disc with whitish tentacles, very numerous papilliform tentacles in small bundles. Mouth central, somewhat prominent, with retractile disc.

Brandt’s (1835:12) description of “*Actinia (Polystephanus, Entacmaea) farcimen*” was based on notes made by Mertens. We reproduce the description in its entirety.

Corpus fere pedale, admodum elongatum, cylindricum a basi usque supra medium e flavo brunneum lineis e rufo fuscis notatum, parte superiore album. Tentacula alba numerosissima, teretia, conico-filiformia, valde acuminata et attenuata, interiora exterioribus minimis multo quidem longiora, sed disci margine lobati latitudine duplo vel plus breviora.

In sinu Awatschaënsi peninsulae Camtschatkae.

Translation: Body nearly a foot long, completely elongated, cylindrical from the base up to above the middle [where it is] golden brown with fine dark red lines, upper part pale. Tentacles very numerous, white, slender, conico-filiform, exceedingly short and pointed, interior ones much longer than the small exterior ones, but with the disc margin lobate [and] the broad diameter at least twice the shorter.

In Avacha Bay of the Kamchatka peninsula.

In 1940, Ricketts and Steinbeck collected a single specimen listed in Carlgren’s (1951) treatment of the fauna of the Gulf of California as *Isometridium rickettsi*, new genus and new species (Fig. 2). However, Carlgren had included the name in his 1949 catalog to sea anemones of the world, rendered “*rickettsi*.” Williams (1997) interpreted that spelling as an error, an opinion with which we agree, given that, in the paper ostensibly describing the species, the name was rendered “*rickettsi*” and Carlgren (1951:415) noted the specimen was collected “by E. F. Ricketts.” The catalog diagnosis of the genus (reproduced below and differing in only minor ways from that of 1951) differentiated the taxon and thereby made the name available under the provisions of Article 13.1.1 of the International Code of Zoological Nomenclature (ICZN) (International Commission on Zoological Nomenclature 1999). The sole detail Carlgren provided in 1949 (page 106) for the species is its provenance—“Guayamas [sic] [Sonora], Mexico.” We regard that item, combined with the fact the genus contained only a single species, sufficient to differentiate the species. Therefore, genus and species date from 1949, as pointed out by Williams (1997).

Metridiidae ? with broad base. Column divisible into a smooth very thick scapus and a thinner capitulum, the former ends above in a distinct collar. No cinclides. Sphincter mesogloea in the capitulum and in the uppermost part of the scapus. Uppermost part of capitulum and the oral disc drawn out in very numerous permanent lobes. At the apices of these lobes there are extraordinarily numerous, short, filiform tentacles of about same length, their longitudinal muscles ectodermal. Oral disc forming a fold inside the tentacles. Radial muscles well developed, ectodermal on the outer side of the fold and on the inner side of the lobes (in a groove), seemingly absent in other parts. 2 very broad siphonoglyphs. Mesenteries very numerous. Several perfect pairs of mesenteries. The 12 first pairs sterile. Retractors of the mesenteries diffuse, weak. Acontia numerous. Cnidom: spirocysts, basitrichs, microbasic *p*-mastigophors, microbasic amastigophors (and microbasic *b*-mastigophors ?).

The systematic position of this genus is doubtful.



Fig. 2. Original photo of holotype of *Isometridium rickettsi* (specimen 49458 in the Division of Invertebrate Zoology, National Museum of Natural History): at left, oral half and original label; at right, entire specimen.

The nematocysts of the acontia were unexploded so that it was very difficult to clear up their types.

Gmelin (1788) used the name *Actinia priapus* as a replacement name for Forskål's (1775) species *Priapus polypus*. In 1857, Milne Edwards' only use of the name *Actinia priapus* was in the sense of Gmelin; he omitted Tilesius' (1809) species from his scheme, and listed "L'Actinia farcimen" among species too poorly known to assign a place. In the only comprehensive treatment of sea anemone taxonomy to have been published until now, Andres (1883) placed Tilesius' species in a new monotypic genus, *Dendractis*, of uncertain affinity. His generic name recognized the "forma arborescente delle appendici discali" (page 365). Andres (1883:181) listed *Actinia farcimen* as *Heliactis farcimen* under the heading "Sagartidae dubiae." He regarded *Actinia priapus* sensu Gmelin as one of many junior synonyms of *Adamsia rondeletti* Delle Chiaje, 1825.

The names *Actinia priapus* (in the sense of Tilesius) and *A. farcimen* seem mostly to have been ignored during the 20th century. The publications of Tilesius and Brandt were not mentioned in Stephenson's (1920, 1921, 1922) "Classification of Ac-

tinia." Although Carlgren referred to *Actinia priapus* in a 1933 publication (see below), he did not include the species in his 1949 catalog to sea anemones of the world. However, the catalog does contain at least two of Brandt's species, *Actinia xanthogrammica* and *Actinia elegantissima*, the former in the genus *Anthopleura*, the latter questionably in the genus *Bunodactis* (both are now placed in *Anthopleura* [e.g., Hand 1955]). Descriptions of other of Brandt's species are also sufficiently diagnostic to be identifiable: DGF (writing as Dunn 1981) resuscitated the name *Stichodactyla mertensii*.

Hand (1956) mentioned *Isometridium rickettsi* [sic] but considered that insufficient information about it was available for meaningful discussion.

Thus, the oldest synonym for this species, *Actinia priapus* Tilesius, 1809, is, itself, a junior homonym. Therefore, the valid name of this species is *Metridium farcimen* (Brandt, 1835). We consider substitution of this name not to be disruptive to usage and therefore not in violation of Article 23.2 of the ICZN (International Commission on Zoological Nomenclature, 1999). The only names having wide recent

usage for the species are properly applied to another species, *M. senile*. The name *M. giganteum* has only begun to be included in field guides (e.g., Gotshall 1994, Harbo 1999). Because such usages are few, this seems an ideal time to correct our error.

Taxonomic Considerations

Tilesius (1809), Brandt (1835), and Carlgren (1949) all noted the extremely numerous short tentacles and lobed oral disc of the species we (Fautin et al. 1990) named *M. giganteum*. Tilesius (1809) remarked on the animal's characteristic great size but provided no data other than stating the accompanying figure was life size. In our photocopied plate (Fig. 3), the length of the largest specimen is about 110 mm and the basal diameter is 65 mm; according to Andres (1883:365), "Grandi Colonna lunghezza fino a 0^m,15 e 0^m,20; larghezza fino a 0^m,7." Possibly the photocopy, which is the only version of the figure we were able to procure, has been reduced, perhaps the subject of the figure was contracted in length, or perhaps an animal 110 mm long was large in Tilesius' experience. In any case, there is no doubt that Plate XIV of Tilesius (1809) illustrates four specimens of the species in question, the largest moderately expanded and three each with only a tuft of tentacles visible. The image is also available electronically as part of the coverage of *Actinia priapus* in Fautin (1999: Sea anemones of the world, version 2.0. <http://biocomplexity.nhm.ukans.edu/anemones/images/Version.html>). Tilesius (1809) returned the specimens of *A. priapus* he studied to the sea, so no type specimens of it exist. Brandt (1835), whose description was not illustrated, also remarked on the animal's large size, giving the length as nearly a foot (ca. 300 mm). To the best of our knowledge, there are no type specimens of *A. farcimen* (see Fautin 1999: Sea anemones of the world, version 2.0. <http://biocomplexity.nhm.ukans.edu/anemones/images/Version.html>).

The type locality of both species is Avacha Bay (Avachinskaya Guba) (52°30'N, 52°E). Harbors and embayments are typical habitats of the species in question. Carlgren (1934) reported specimens of "*Metridium senile* var. *fimbriatum*" had been collected in Awatcha Bay by the Swedish Kamchatka Expedition in 1921 (he also noted specimens from elsewhere in Kamchatka and from Alaska). DGF examined the five specimens bearing Swedish Natural History Museum catalog number 18350 (old number 995) that are accompanied by labels in Carlgren's hand "Petropavlovsk/Kamtchatka/May 1921/Sw Kamtchatka Exp." and "*Metridium senile* var. *fimbriatum* determ. Carlgren." One specimen is depicted in Fig. 4. The specimens agree in all particulars with the species we (Fautin et al. 1990) named *M. giganteum*. The existence of that species in the type locality of *A. priapus* and *A. farcimen* supports our assertion that the names are synonymous.

DGF examined the holotype of *Isometridium rickettsi*, specimen 49458 in the Division of Invertebrate Zoology of the National Museum of Natural History, Smithsonian Institution. It is the subject of Fig. 2; the photograph of it in Carlgren (1951) is small and lacks contrast. It is strongly contracted although the highly lobed oral disc—which is covered by many short tentacles—is exposed. The diameter of its pedal disc is 105 mm, its diameter at mid-column is 70 × 85 mm, and it is about 100 mm long (it is asymmetrically contracted so its minimum length is about 90 mm and its maximum about 110 mm). Externally, its column differs in two particulars from that of most specimens of *Metridium farcimen* with which we are familiar—it is wrinkled, and it is not a solid color. With regard to the latter feature, in his discussion of *M. dianthus*, which appears to refer to both large and small specimens, Torrey (1902: 395) remarked "... that white and salmon polyps may exhibit blotches of brown ...," and Tilesius (1809) and Brandt (1835) also referred to dark striations on the light col-

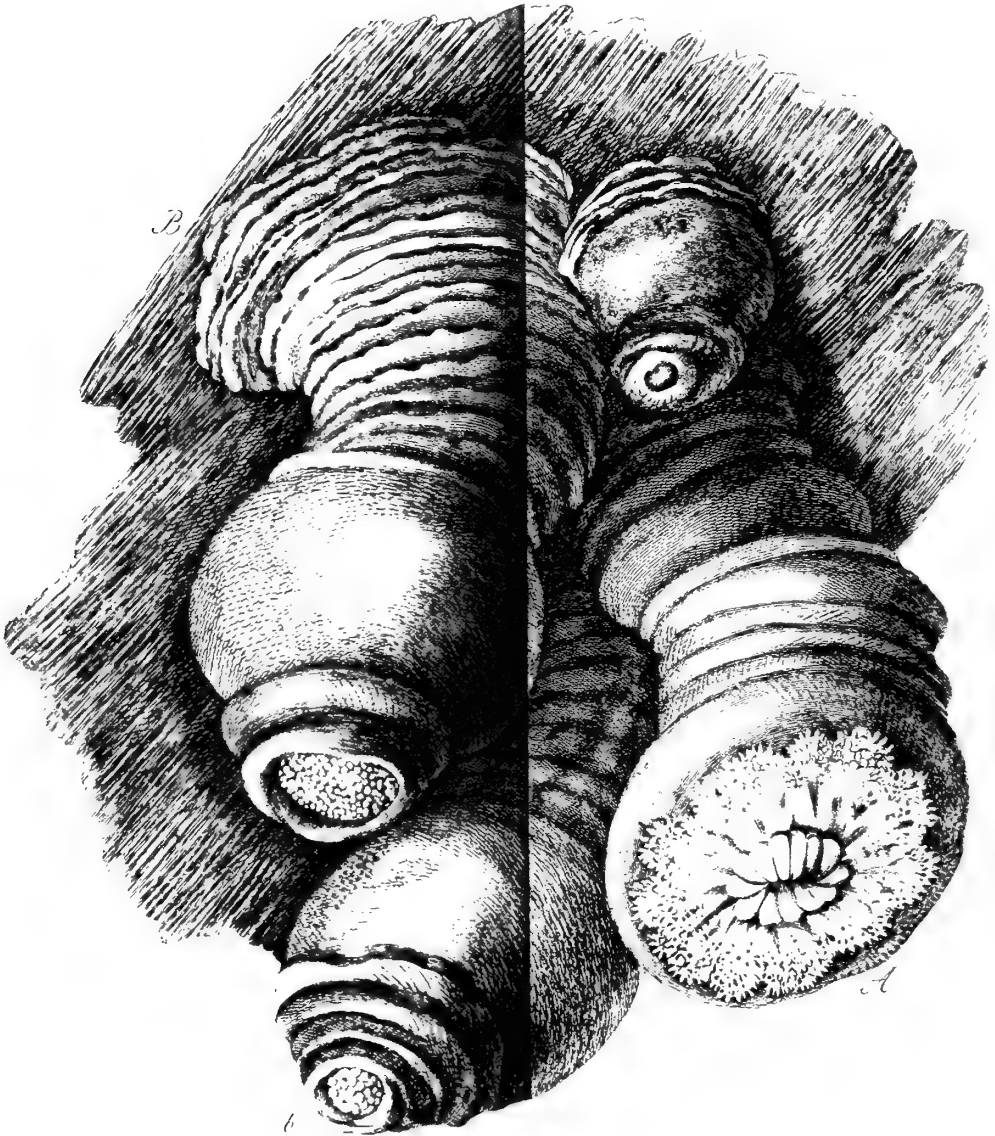


Fig. 3. *Actinia priapus*: Plate XIV from the description of Tilesius (1809).

umn. The wrinkling is probably due to contraction, which could be a result of the animal's having been trawled from considerable depth in a net with many other animals. The individuals illustrated by Tilesius (Fig. 3) are wrinkled, too. Contraction could also produce great column thickness.

In his "description" of *Isometridium*, Carlgren (1951:431) remarked "The ap-

pearance of this very interesting type resembles that of *Metridium*, but its organization is quite different from that of this genus." However, the only difference he explicitly stated is that "the tentacles [are] thin and delicate and extraordinarily numerous, certainly more numerous than those of *Metridium*" (page 432). A point-by-point comparison of Carlgren's (1949)

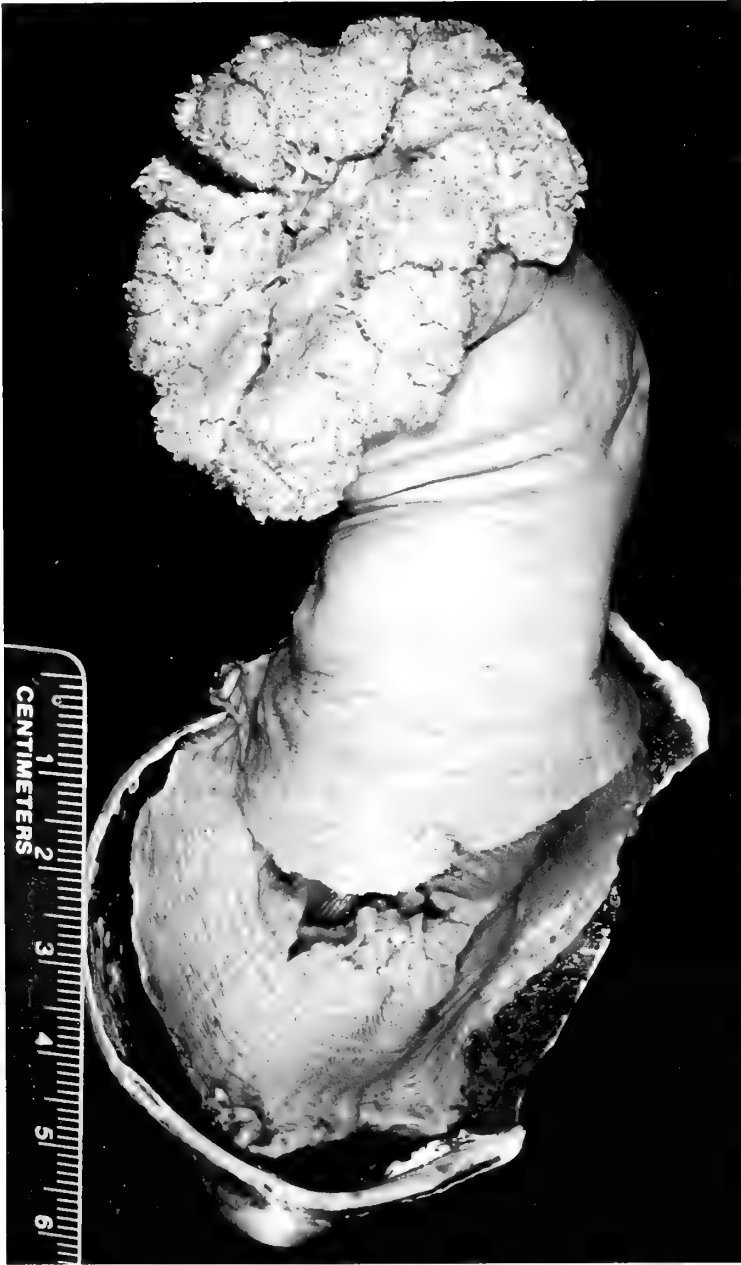


Fig. 4. One of five specimens collected on the 1921 Swedish Kamchatka Expedition (Swedish Natural History Museum 18350 [old catalog number 995]).

diagnoses of *Isometridium* and *Metridium* reveals few other differences: *Isometridium* bears 12 pairs of sterile mesenteries and no cinclides, whereas *Metridium* has cinclides, and mesenteries of the first 6 pairs are sterile in "typical individuals." Carlgren

(1949, 1951) remarked on the marginal sphincter muscle extending into the capitulum of *Isometridium*, but did not comment on its state in *Metridium*.

These differences are in variable characters we consider to distinguish species,

not genera. Thus Carlgren's comparison was really between *Metridium farcimen* and the better-known *M. senile*, which occurs in Europe (as well as both coasts of North America) and with which, therefore, Carlgren presumably was more familiar. The vast number of tentacles was noted by both Telesius (1809) and Brandt (1835). In his treatment of "*M. senile*," Hand (1956:194) noted that a "sphincter is present at the top of the scapus in most specimens; this may be absent or very weak in small specimens." It is not unreasonable, by extension, to expect the muscle to be more extensively developed in larger specimens. Hand also noted the pattern of sterile mesenteries may differ between "younger" and "older" specimens—possibly the difference actually had to do with species, but because this character does appear to be variable, it is not suitable for distinguishing genera. Hand remarked the cinclides could be inconspicuous; thus, their apparent absence in a single contracted specimen should not be used as the basis of a new genus.

The resemblance of animals now placed in the genus *Metridium* to a mammalian penis is manifest in Linnaeus' original generic name of anemones, *Priapus* (see Opinion 1295 of the International Commission on Zoological Nomenclature), as well as Telesius' name and that given to the animals by the people of Kamchatka.

Geographic Distribution

We (Fautin et al. 1990:81) gave the geographical range of *M. giganteum* as "From Alexander Archipelago, Alaska (56–58°N) (or further north) south along Pacific coast of North America through California." We have confirmed the specimens Carlgren (1934) referred to as *M. s. fimbriatum* from Kamchatka belong to the species in question (e.g., that depicted in Fig. 4); Carlgren (1934, 1936) also examined specimens he referred to that taxon from the Aleutians and Norton Sound, and Sitka, respectively. Therefore, the species certainly ranges at

least from the tip of Kamchatka through the Aleutian Islands and down the west coast of Canada and the United States to San Diego. Gotshall (1994:29) wrote that the "White-plumed Anemone *Metridium giganteum*" ranges from "Alaska to Santa Catalina Island, California." Carlgren (1933) considered *M. senile* to be a low boreal form, and not to range into truly Arctic waters.

The occurrence of *M. farcimen* in the Gulf of California is surprising. A distinctive species, it is not included in guides to the shallow water of that region (e.g., Brusca 1973, Kerstitch 1989). The specimen label for the holotype of *Isometridium rickettsi* provides no details about provenance other than Guaymas. However, Chapter 27 of the log of the expedition (Steinbeck & Ricketts 1941, Steinbeck 1951) recounts that on 9 April 1940, "about an hour" after leaving Guaymas, at which no collecting was reported to have been done, the expedition encountered a Japanese fishing fleet. Members of the expedition, Steinbeck and Ricketts among them, were permitted to pick out specimens from the dredge-haul of one of the boats. This was undoubtedly the source of the specimen. Although the only information in the log that might refer to the specimen is the sentence "And there were bottom-samples with anemones and grass-like gorgonians," the date of collection on the museum label (Fig. 2) and in Carlgren (1951) is 9 April 1940.

Few reports specify the depth at which the animals live. In our description of *M. giganteum*, we (Fautin et al. 1990) gave the bathymetric range as intertidal to at least 256 m (collecting depth of the deepest paratype). The Sea of Cortez slopes steeply to a depth of nearly 2000 m west of Guaymas, but the holotype of *I. rickettsi* was collected a short distance south of that city. Trawling in 1940 is unlikely to have been done much deeper than 200 m (Les Watling, pers. comm.), a depth achieved not far from Guaymas. We infer that the upper depth limit declines with latitude, and provides

another example of tropical submergence (Sverdrup et al. 1946). Clearly this species extends further south than had been thought, but presumably only at depths that have not been well studied. It may range much further south than is currently documented.

Nomenclatural Considerations

The generic name *Dendractis* was created by Andres (1883) for Telesius' species *Actinia priapus*, possibly in recognition of the homonymy of *A. priapus* and the distinctiveness of the animal. Therefore, *Dendractis* is a subjective junior synonym of *Metridium*. The name *Metridium* was, itself, proposed by Oken (1815) for the Linnaean species *Actinia senilis*. It was among Oken's names that were declared invalid by Opinion 417 of the International Commission on Zoological Nomenclature. In Opinion 1269, which responded to a request by Dunn & Hulsemann (1979), the Commission ruled that de Blainville 1824, is the author of *Metridium*.

Although the name *M. senile* has been used to refer to both *M. senile* sensu stricto and *M. farcimen* in the North Pacific, there was some effort to distinguish them. Carlgren (1933:23) was of the opinion that a large specimen from Nanaimo (British Columbia) he had examined differed from what he referred to as *M. dianthus*. The name *M. s. fimbriatum* or *M. fimbriatum* was most consistently used for *M. farcimen*, as, for example, by Carlgren (1934, 1936). [In 1936 (page 23), Carlgren wrote (I take the opportunity to rectify a lapsus in my paper *Some Actiniaria [sic] from Bering Sea and arctic waters* (1934, p. 353). Where I have written "var. *marginatum*" read "var. *fimbriatum*.")] However, Hand (1956:203), for example, did not maintain such a distinction, considering *M. s. fimbriatum* to be "*Metridium senile* as it occurs in the Pacific Ocean." He (Hand 1957) deposited two lots of topotypes of *M. s. fimbriatum* in the National Museum of Natural

History, Smithsonian Institution. The four specimens bearing catalog number 50641 appear to be missing; that bearing number 50640 (depicted in Hand 1956:243) was erroneously cataloged as a neotype. Despite Hand's (1957) assertion, two syntypes of *Metridium fimbriatum* Verrill, 1865, exist in the collection of the Yale Peabody Museum (catalog number 9494; Fautin 1999: Sea anemones of the world, version 2.0. <http://biocomplexity.nhm.ukans.edu/anemones/images/Version.html>). The smaller (about 12 mm length and diameter) resembles *M. senile* sensu stricto whereas the larger (about 80 mm long and 30 mm diameter) resembles *M. farcimen* (DGF, pers. obs.). Because of such ambiguities, we (Fautin et al. 1990) coined an entirely new name for the species.

Carlgren (1933:23) further speculated that Telesius' *Actinia priapus* and a specimen from Nemuro, Hokkaido, identified by Wassilieff (1908) as *M. dianthus* "may possibly be identical with *M. fimbriatum* which has been found in several localities between Alaska and San Francisco." Its irregular internal anatomy makes the specimen examined by Wassilieff (1908) likely to have been a specimen of *M. senile*, which can reproduce asexually, a process that can lead to such asymmetry (e.g., Hand 1956, writing in reference to the anemone *Haliplanella luciae*, and Dunn 1981, writing of *Entacmaea quadricolor*).

In light of the broad geographical range of *M. farcimen* and the variability of *M. senile*, both morphological (e.g., Torrey 1902; Carlgren 1933, 1936; Hand 1956) and molecular (Bucklin & Hedgecock 1982), we are concerned that the new species *M. sinensis* and *M. huanghaiensis* described by Pei (1998) may be unwarranted. Color drawings of them (plate I, fig. 3 and 4, respectively) resemble *M. senile*. The animal depicted in Plate I, fig. 2, a color drawing labeled *Metridium senile fimbriatum* (but referred to in the table of contents and some places in the text as *Metridium sensile*) appears to be *M. farcimen*.

Acknowledgments

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Three species of toxic sponges from Cebu, Philippines (Porifera: Demospongiae)

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Abstract.—Three species of sponges toxic to hard corals are described from Mactan Island, Cebu, Philippines. They were most common at depths of 8–12 m, but they occurred between 3 and 32+ m. *Plakortis lita* forms thick crusts or is subglobular or massive and liver brown. Diodes are very densely packed and irregularly distributed. Triodes are rare and microrhabds absent. *Acervochalina hooperi*, new species, forms thin crusts and is dark green. Thick branching spongin fibers are embedded with small oxeas. *Xestospongia vansoesti*, new species, forms thick crusts but can be digitate, and dark green to black. Dense multipiculate tracts contain oxeas. The sponge produces a copious brown mucus.

Since 1994 we have been periodically studying the coral reef community and specifically the sponges of Cebu, Central Philippines. Nishiyama (Nishiyama & Bakus 1999) discovered that all three species of sponges described below were releasing allomones into the surrounding seawater. These allomones were toxic to some hard corals which suggests that the sponges and hard corals are competing for space. Thus, sponge toxins may play an important role in the structuring of coral reef communities. We are herein describing these species of sponges from our ecological field studies.

Materials and Methods

Site description.—Our study site is located approximately 200 m off the Tumbuli Beach Resort on the east coast of Mactan Island near Cebu City (10°17'N, 124°E) (Fig. 1) (Bakus and Nishiyama 1999). Depths surveyed were 3–32 m. The area has a narrow intertidal region followed by seagrasses (principally *Thalassia hemprichii*) to a depth of 5–10 m, then a rich coral reef community to a depth of at least 40 m, with the slope becoming steeper beyond a depth of 20 m. The dominant hard corals in

the region include *Acropora*, *Pocillopora*, *Seriatopora*, *Tubipora*, *Halomitra*, *Parahalomitra*, *Lobophyllia*, *Symphyllia*, *Euphyllia*, *Pectinia*, *Porites*, *Montipora*, *Millepora* and *Fungia* (University of San Carlos Marine Biology section 1979). The average current velocity at the study site was 0.09 m/sec although flow rates as high as about 3.9 m/sec (2 knots) occur occasionally during shifting tides. Current direction during our June–July studies was from 60° NE or 220–240° SW, depending on the tides. The water temperature was 28–31°C although it can get as low as 26°C in February (F. Sotto, pers. comm.). Underwater visibility was 15–30 m. The three species of sponges occurred at depths of 3–32+ m. They were most common at depths of 8–12 m.

Sponges were collected in the field by hand, frozen in a –30°C freezer, and studied later in the laboratory. Scanning electron micrographs (SEM) of spicules were made with a Cambridge 360 SEM. Spicules were measured with a Zeiss Compound Microscope fitted with an ocular micrometer. Sponge skeletons were digitized with a RCA TC 1005 camera connected to a Data Translation 3155 frame grabber board in a

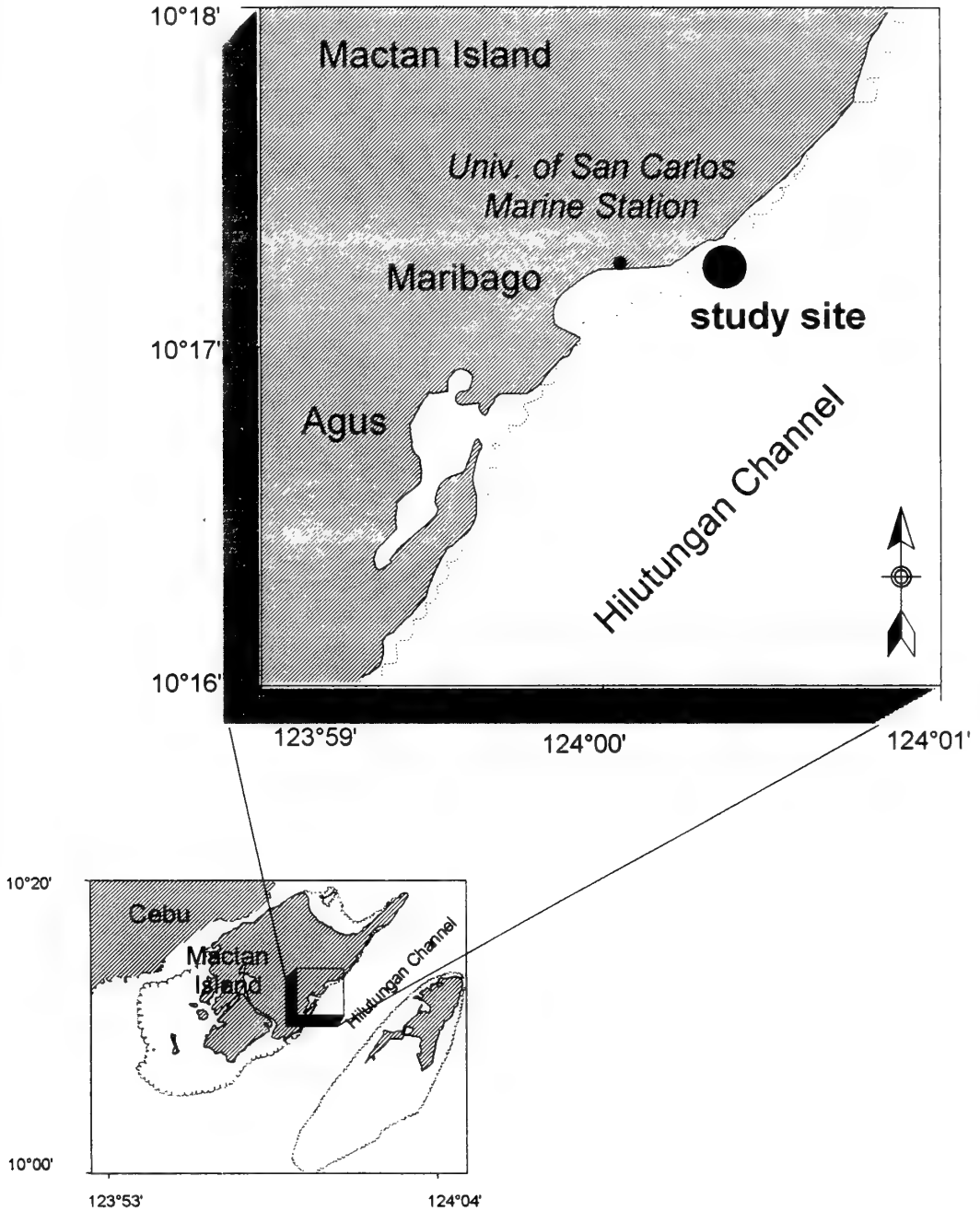


Fig. 1. Mactan Island, Philippines, and study site.

PC computer with an Intel Pentium 233 microprocessor. Current velocities were measured using Rhodamine B dye; nine measurements were made during three days. Current direction was measured using a

compass; three measurements were recorded on each of five days. Water temperature was measured with a scuba regulator thermometer. Water visibility was estimated using a transect line. The GJB-95 series of



Fig. 2. *Plakortis lita* on dead coral.

sponges are deposited in the University of San Carlos marine biological collections, Cebu City, Cebu, Philippines and the holotypes and paratypes are lodged in the collections of the National Museum of Natural History, Washington D.C. (USNM), and the British Museum of Natural History, London (BMNH), respectively.

Species Descriptions

Order Homosclerophorida

Family Plakinidae Schulze, 1880

Genus *Plakortis* Schulze, 1880

Plakortis lita de Laubenfels, 1954

Figs. 2–4

Material examined.—GJB-95-1 and two additional specimens, USNM 51497 and BMNH 1999.1.21.3.

Description.—Thickly encrusting to submassive to globular (Fig. 2). Sponge dimensions are presented in Table 1.

Color.—Dark brown (similar to liver) live and preserved.

Odor.—Similar to old aquarium water. No terpenoid odor.

Texture and consistency.—Firm but rubbery. No tendency to disintegrate in alcohol.

Surface.—Smooth, velvety, with scattered oscula, sometimes with a raised membranous lip. Oscula approximately 1 mm in diameter. No oscula were observed in preserved specimens. Pores 31–62 μm in diameter. Numerous strongly pigmented cells. Ectosome not detachable. No mucus.

Skeleton.—Diodes are very dense and irregularly distributed throughout the sponge. Scanning electron micrographs of spicules are presented in Fig. 3 and spicule measurements in Table 2. Digital photos of the skeleton are presented in Fig. 4.

Mesohyl and canals.—Canals <250 μm in diameter. Very small diodes are numerous. Brown pigmented cells are abundant and characteristic.

Biological associates.—None observed with a dissecting microscope.

Table 1.—Dimensions of three sponge species based on field measurements from Mactan Island, Cebu, Philippines.

Species	<i>n</i>	Median	Mean	<i>SD</i>	Minimum	Maximum
<i>Plakortis lita</i>						
Length (cm)	27	13	18	14.8	5	77
Width (cm)	27	9	12	7.6	2	32
Height (cm)	27	3	3	2.2	1	10
<i>Acervochalina hooperi</i> , new species						
Length (cm)	14	13	14	9.1	3	30
Width (cm)	14	8	9	6.7	2	23
Height (cm)	14	0.2	0.2	0.1	0.1	0.5
<i>Xestospongia vansoesti</i> , new species						
Length (cm)	23	13	19	25.5	5	131
Width (cm)	23	8	12	14.7	2	75
Height (cm)	23	3	4	4.4	0.7	20

Discussion.—Initially only diods were found in microslide preparations. A careful re-examination of the spicules indicated that the sponge contained rare triods but no microrhabds. Moreover, the diods did not have three bends as described by de Laubenfels (1954) in *Plakortis lita* from Truk and Ponape. The diods looked like slightly malformed oxeas and were irregularly distributed. Our sponges are closest to *P. lita* yet lack several of its major characteristics. Diaz and van Soest (1994) reviewed the systematics of the Plakinidae. They described some specimens of *P. lita* with a terpenoid odor and the tendency to disintegrate in alcohol. Our specimens lack these characteristics. Diaz & van Soest (1994) concluded that the variable presence of microrhabds in type specimens of *P. lita* casts doubt over the conspecificity of all reported specimens. They may be part of a *Plakortis* superspecies complex. Because our sponges look like *P. lita* (identified by Kelly Borges) in Colin & Arneson (1995), we are using that name tentatively for our sponges.

Order Haplosclerida

Family Chalinidae Gray, 1867

Genus *Acervochalina* Ridley, 1884

Acervochalina hooperi, new species

Figs. 5–7

Type material.—Holotype: USNM 51495. Collected at 10 m depth off Mactan

Island, Cebu, Philippines, in June 1998. Preserved sponge dark brown, thinly encrusting on most of a dead branching hard coral measuring 11 × 7 cm. Paratype: BMNH 1999.1.21.2.

Material examined.—GJB-95-3, Holotype, paratype and live specimens.

Diagnosis.—Thinly encrusting and dark green, compressible, scattered oscula with membranous lip. Thick branching and anastomosing spongin fibers with embedded small oxeas.

Description.—Thinly encrusting, up to 5 mm thick on dead coral (Fig. 5). Sponge dimensions are presented in Table 1.

Color.—Dark green live. Dark brown after long exposure to air. Dark green to black preserved.

Odor.—Similar to freshly cut grass that has been in water for a day.

Texture and consistency.—Velvet-like, soft, compressible.

Surface.—Superficially undulating, fibrous under dissecting scope. Dermal membrane is often missing in collected specimens; where it occurs in these specimens it generally lacks spicules. Oscula round, about 2 mm in diameter, scattered, often with a raised membranous lip in the field. No oscula observed in preserved specimens. No mucus.

Skeleton.—Ascending fibers with embed-

Table 2.—Spicule dimensions for three species of sponges from Mactan Island, Cebu, Philippines.

Species	<i>n</i>	Median	Mean	<i>SD</i>	Minimum	Maximum
<i>Plakortis lita</i> (GJB-95-1)						
Diod Length (μm)	20	109	110	9.1	90	148
Diod Width (μm)	20	4	3.7	0.4	1	4
<i>Acervochalina hooperi</i> , new species (GJB-95-3)						
Oxea Length (μm)	20	111	113	11.9	86	137
Oxea Width (μm)	20	4	4	0.5	1	5
(Holotype)						
Oxea Length (μm)	20	113	111	11	78	125
Oxea Width (μm)	20	6	5	1.6	3.1	7.8
<i>Xestospongia vansoesti</i> , new species (GJB-95-30)						
Oxea Length (μm)	20	242	240	21.1	152	279
Oxea Width (μm)	20	11	11	0.9	2	12
(Holotype)						
Oxea Length (μm)	20	269	266	27	191	300
Oxea Width (μm)	20	13	13	1.7	11	16

ded oxeas arise from a coral base. Some ascending fibers approximately 250 μm apart measure 62–123 μm at the base then gradually taper towards the upper end until

about 30 μm in diameter at which time the fibers splay out slightly (about 400 μm below the surface). Other fibers have variable diameters (e.g., 15 μm to 45 μm to 30 μm)

Fig. 3. Diod from *Plakortis lita* SEM (X1230).

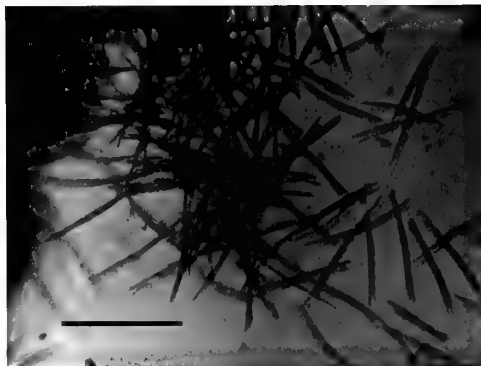


Fig. 4. Digital photos of the choanosome of *Plakortis lita* showing the dioids in confusion. The bars are 100 μm long.

as they ascend. The fibers are echinated occasionally or densely by oxeas (not localized) and are light to medium brown preserved. Most fibers branch or anastomose but single fibers occasionally occur. The mesohyle appears to have few or no oxeas. Scanning electron micrographs of spicules

are presented in Fig. 6 and spicule measurements in Table 2. Digital photos of the skeleton are presented in Fig. 7.

Mesohyl and canals.—Mesohyl is sparse to absent. No canals were observed.

Biological associates.—None observed with a dissecting microscope.

Discussion.—Rob van Soest (pers. comm.) tentatively called this species *Acervochalina* aff. *confusa* Dendy, 1922. However, *A. confusa* is described as being erect or pendant with cored fibers 20 μm in diameter. Our specimens are most closely related to *Acervochalina* (*Cacochalina*) *mollis* Topsent, 1897 from which they differ by their thinly encrusting habitus, dark green to black color in alcohol, thick spongin fibers and small oxeas. We name it *Acervochalina hooperi*, new species, in honor of Dr. John Hooper who has contributed greatly to sponge systematics.

Order Haplosclerida

Family Petrosiidae van Soest, 1980

Genus *Xestospongia* de Laubenfels, 1932

Xestospongia vansoesti, new species

Figs. 8–10

Type material.—Holotype: USNM 51496; Collected from a depth of 10 m off Mactan Island, Cebu, Philippines, on 24 Jul 1996. Preserved sponge dark brown, slightly digitate, on dead coral measuring 9 \times 5 cm and 3 cm thick. Firm, crusty. Paratype: BMNH 1999.1.21.1.

Material examined.—GJB-95-30, Holotype, Paratype and live specimens.

Diagnosis.—Thickly encrusting to digitate, crusty. Dark green to black with copious brown mucus production. Oscula 1–2 cm apart. Dense meshwork of multispicular tracts of oxeas. Spongin sparse.

Description.—Thickly encrusting to digitate (Fig. 8). Sponge dimensions are presented in Table 1.

Color.—Dark green to black live and preserved. The sponge produces a copious brown mucus when handled and especially when damaged. Some untouched specimens



Fig. 5. *Acervochalina hooperi*, new species, on dead coral.

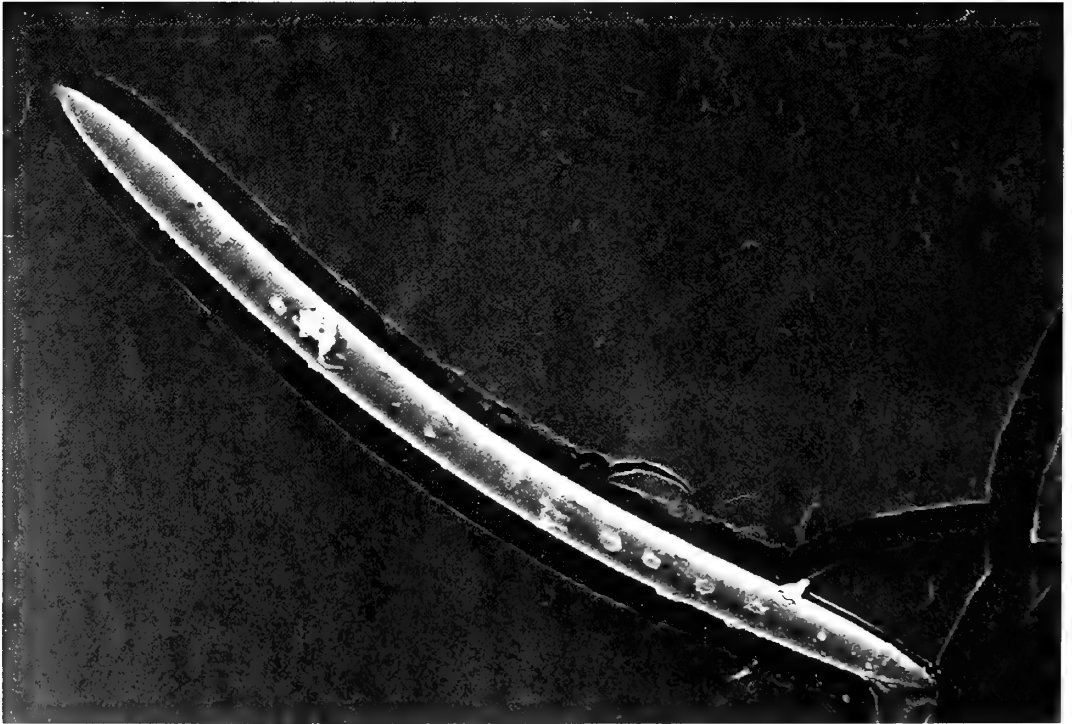


Fig. 6. *Oxea* from *Acervochalina hooperi* n. sp. SEM (X1080).

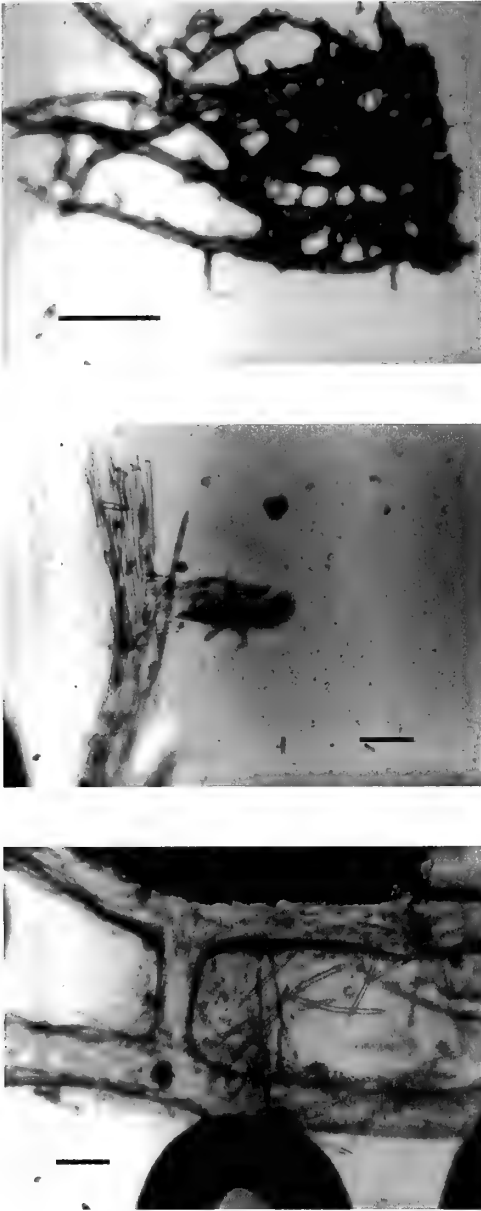


Fig. 7. Skeletal fibers of *Acervochalina hooperi*, new species. The skeleton is shown in the upper photo with the base of the sponge on the right and the upper part of the sponge skeleton on the left. The bar in the upper photo is 500 μm long. The bars in the lower two figures are 100 μm long.

in the field had strings of mucus trailing from the sponge. The alcohol in which they are preserved turns a dark coffee color.

Odor.—Similar to smoke from fireworks.

Texture and consistency.—Rough to the touch, crusty, hard, incompressible.

Surface.—The intact surface is smooth but the dermal membrane is often missing. When missing, the sponge is microrugose with fibers extending upwards, up to 1 mm. The oscula are common, 1–2 cm apart, flush with the surface, and measure up to 3 mm in diameter. Pores are abundant and measure up to 250 μm in diameter. Spicules are generally lacking in the dermal membrane. Numerous, very small subdermal spaces occur.

Skeleton.—A dense meshwork of multipicular tracts, commonly up to 5 spicules or 80 μm thick but sometimes up to 150 μm in diameter. The choanosomal meshes measure approximately 0.5 mm in diameter and the meshes near the surface about 150 μm in diameter. Spongin is sparse. Scanning electron micrographs of spicules are presented in Fig. 9 and spicule measurements in Table 2. Digital photos of the skeleton are presented in Fig. 10.

Mesohyle and canals.—Mesohyle dense, canals moderately numerous.

Biological associates.—None observed with a dissecting microscope.

Discussion.—*Spongia carbonaria* was originally described by Lamarck (1813). De Laubenfels (1936) transferred it to *Pellina* and later described the species from Koror, Palau Islands (de Laubenfels 1954). Hechtel (1965) described it from the West Indies as a new combination, i.e., *Adocia carbonaria*. Bergquist (1965) called her Palau specimens *Pellina carbonaria*. John Hooper (pers. comm.) thought that our sponge was probably a *Xestospongia*, based on a manuscript description. Van Soest (pers. comm.) places our sponge under *Xestospongia* as an undescribed species. A related species, *Reniera viridenigra* Vacelet, Vasseur & Levi, 1976 from Madagascar, differs from our species by having an iridescent green reflection alive, friable consistency, and an ectosome with several layers of a tangential isodictyal network of strongyles with oxete ends. Our species is dark green

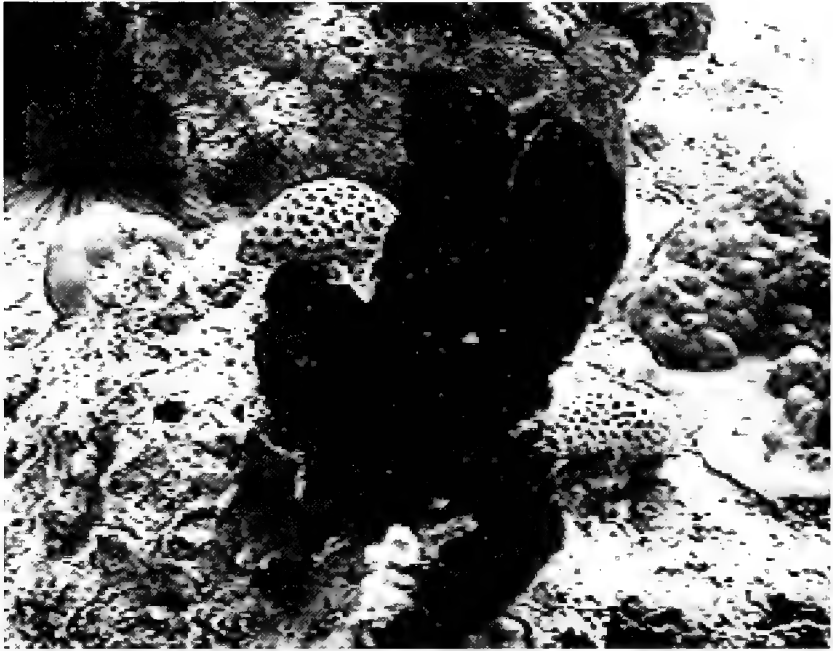


Fig. 8. *Xestospongia vansoesti*, new species, on dead coral.



Fig. 9. Oxea from *Xestospongia vansoesti*, new species. SEM (X470).

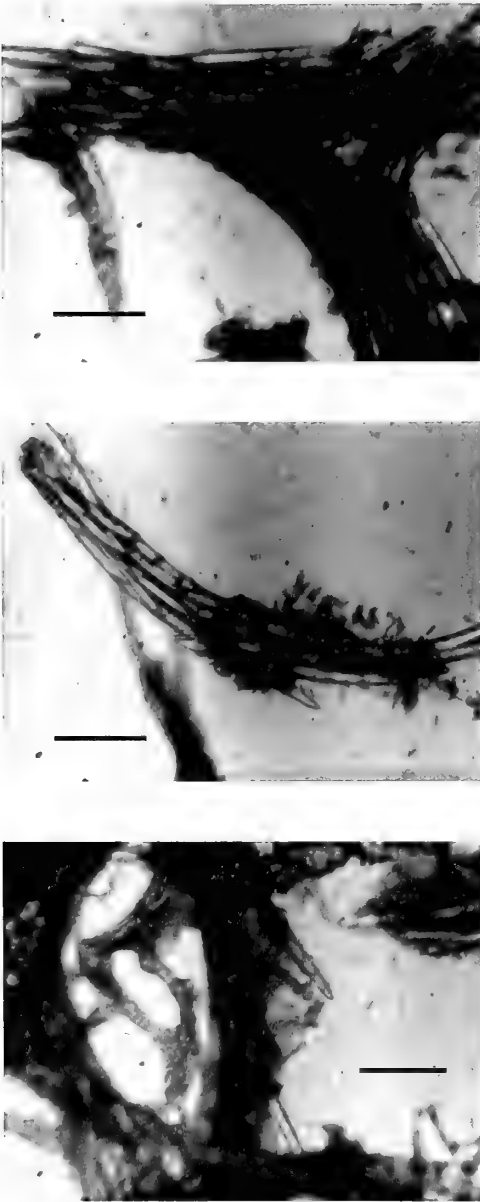


Fig. 10. Skeletal fibers of *Xestospongia vansoesti* n. sp. Note the two pores in the lowest figure. The bars are 100 μm long.

to black and produces a copious brown mucus containing chemicals toxic to hard corals (Nishiyama & Bakus 1999). It is hard, encrusting to digitate (but unlike *Pellina*), and has ascending fiber tracts averaging 80 μm in diameter, but that range up to 150

μm in diameter. Thus it requires a new species name, *Xestospongia vansoesti*, new species, in honor of Dr. R. W. M. van Soest who has contributed greatly to sponge systematics.

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