

AN EXAMINATION OF THE SHRIMP
FAMILY CALLIANIDEIDAE
(CRUSTACEA: DECAPODA: THALASSINIDEA)

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Abstract.—One striking character was found to unite the members of the family Callianideidae, viz. the presence of rows of plumose setae, each seta sited in a pit, these rows being found on the carapace, abdominal pleura, and propodi of pereopods 2-4. Several new taxa are described: *Crosniera*, new genus (for *Callianassa minima* Rathbun, 1901); *Michelea*, new genus (for *Callianidea vandoverae* Gore, 1987, *Callianidea leura* Poore & Griffin, 1979, *Callianidea lepta* Sakai, 1987, plus the new species *M. pillsburyi* and *M. lamellosa*); *Mictaxius*, new genus (with the new species *M. thalassicola*); *Marcusiaxius lemoscastroi* Rodrigues & Carvalho, 1972, is redescribed, along with *M. colpos*, new species, while six species of *Meticonaxius* are discussed, with *Meticonaxius bouvieri*, new species described. A cladistic analysis of 11 taxa suggested that, within the Callianideidae, pleopodal respiratory filaments arose twice, that the linea thalassinica and the dentate ischial crest of maxilliped 3 have twice been lost, and that the *Thomassinia-Crosniera-Mictaxius* group of genera are most closely related to the Callianassidae.

In the continuing effort to bring clarity to the systematics of the thalassinidean decapods, individual genera and families are being examined in detail (e.g., Kensley 1989, Kensley & Heard 1990). Morphological characters in particular are being reassessed, in an attempt to establish relationships. With this objective in view, the western Atlantic members of the Callianideidae possessing accessory respiratory filaments of the pleopods were examined, but it became apparent that several thalassinidean species lacking these filaments should also be included in this group; the review was thus expanded beyond the western Atlantic. Of the group possessing respiratory filaments on the pleopods, the genus *Callianidea* is diagnosed, a new genus *Michelea* created to accommodate *Callianidea vandoverae*, two Pacific species, and two new species. In the group lacking pleopodal filaments, the species of the genera *Meticonaxius* and *Marcusiaxius* are reviewed or redescribed, and one new

species of each described; the genus *Thomassinia* is examined, along with the seemingly closely-related '*Callianassa*' *minima* and the new genus *Mictaxius*.

For comparative purposes, material of the Pacific *Callianidea typa* H. Milne Edwards, 1837, was examined from Bikini Atoll, Saipan, Guam, and Tahiti, as was the holotype of *Callianidea lepta* Sakai, 1987, from Japan (USNM 231419).

Common to all these forms is the presence of short plumose setae, each seta sited in a pit-like structure, these pits usually arranged in tight rows. From hereon referred to, for the sake of brevity, as 'setal rows,' these rows are found on the anterolateral carapace, on the pleural region of each abdominal somite, and on the propodi of pereopods 2-4 (Fig. 1). Amongst the callianideid genera, the arrangement and siting of these setal rows fall into three patterns, illustrated in Fig. 2.

The number and position of exopods and



Fig. 1. SEM micrographs of *Marcusiaxius colpos*: A, Setal row from pleuron 2, 350 \times ; B, Setal row from propodus of pereopod 3, 150 \times ; C, Setal row from propodus of pereopod 3, 250 \times .

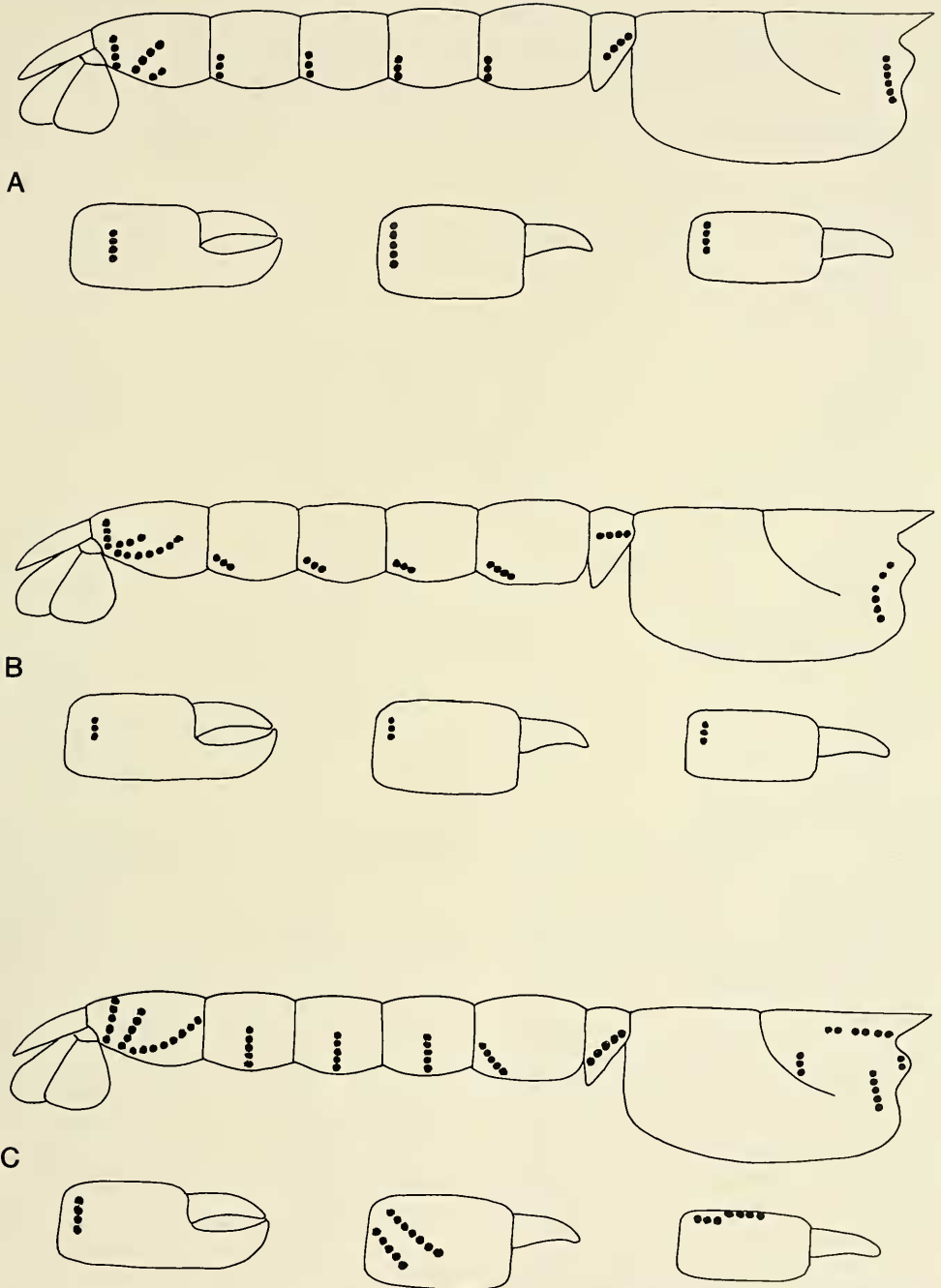


Fig. 2. Diagrammatic representation of three patterns of setal row distribution on carapace and abdomen (above) and propodi of pereopods 2-4 (below): A, *Callianidea* (pattern 0); B, *Crosniera* (pattern 1); C, *Marcusiarius* (pattern 2).

Table 1.—Distribution of exopods, epipods, and gills.

	Maxillipeds			Pereopods				
	1	2	3	1	2	3	4	5
A. <i>Callianidea laevicauda</i>								
Exopod	1	1	1	—	—	—	—	—
Epipod	1	1	1	1	1	1	1	—
Podobranch	—	—	—	—	—	—	—	—
Arthrobranch	—	—	2	2	2	2	2	—
Pleurobranch	—	—	—	—	—	—	—	—
B. <i>Crosniera minima</i>								
Exopod	1	1	1	—	—	—	—	—
Epipod	1	1	1	1	1	1	1	—
Podobranch	—	—	r	r	r	r	—	—
Arthrobranch	—	—	2	2	2	2	2	—
Pleurobranch	—	—	—	—	—	—	—	—
C. <i>Marcusiaxius colpos</i>								
Exopod	1	1	r	—	—	—	—	—
Epipod	1	1	1	1	1	1	1	—
Podobranch	—	—	1	1	1	1	—	—
Arthrobranch	—	—	1 + r	2	2	2	2	—
Pleurobranch	—	—	—	—	1	1	1	—
D. <i>Marcusiaxius lemoscastroi</i>								
Exopod	1	1	—	—	—	—	—	—
Epipod	1	1	1	1	1	1	1	—
Podobranch	—	—	1	1	1	1	—	—
Arthrobranch	—	—	1 + r	2	2	2	2	—
Pleurobranch	—	—	—	—	1	1	1	—
E. <i>Meticonaxius bouvieri</i>								
Exopod	1	1	r	—	—	—	—	—
Epipod	1	1	1	1	1	1	1	—
Podobranch	—	—	1	1	1	1	—	—
Arthrobranch	—	—	1 + r	2	2	2	2	—
Pleurobranch	—	—	—	—	1	1	1	—
F. <i>Meticonaxius longispina</i>								
Exopod	1	1	r	—	—	—	—	—
Epipod	1	1	1	1	1	1	1	—
Podobranch	—	—	r	r	r	r	—	—
Arthrobranch	—	—	1 + r	2	2	2	2	—
Pleurobranch	—	—	—	—	1	1	1	—
G. <i>Meticonaxius microps</i>								
Exopod	1	1	r	—	—	—	—	—
Epipod	1	1	1	1	1	1	1	—
Podobranch	—	—	1	1	1	1	—	—
Arthrobranch	—	—	1 + r	2	2	2	2	—
Pleurobranch	—	—	—	—	—	—	—	—
H. <i>Meticonaxius monodon</i>								
Exopod	1	1	r	—	—	—	—	—
Epipod	1	1	1	1	1	1	1	—
Podobranch	—	—	1	1	1	1	—	—
Arthrobranch	—	—	1 + r	2	2	2	2	—
Pleurobranch	—	—	—	—	1	1	1	—

Table 1.—Continued.

	Maxillipeds			Pereopods				
	1	2	3	1	2	3	4	5
<i>I. Michelea lamellosa</i>								
Exopod	1	r	1	—	—	—	—	—
Epipod	1	1	1	—	—	—	—	—
Podobranche	—	—	—	—	—	—	—	—
Arthrobranch	—	—	r + r	r + r	r + r	r + r	r	—
Pleurobranch	—	—	—	—	—	—	—	—
<i>J. Michelea pillsburyi</i>								
Exopod	1	r	1	—	—	—	—	—
Epipod	1	1	1	1	1	1	1	—
Podobranche	—	—	—	—	—	—	—	—
Arthrobranch	—	—	2	2	2	2	2	—
Pleurobranch	—	—	—	—	—	—	—	—
<i>K. Michelea vandoverae</i>								
Exopod	1	1	1	—	—	—	—	—
Epipod	1	1	1	1	1	1	1	—
Podobranche	—	—	r	r	r	r	—	—
Arthrobranch	—	—	2	2	2	2	2	—
Pleurobranch	—	—	—	—	—	—	r	—
<i>L. Mictaxius thalassicola</i>								
Exopod	1	1	r	—	—	—	—	—
Epipod	1	1	1	1	1	1	r	—
Podobranche	—	—	r	r	r	r	—	—
Arthrobranch	—	—	2	2	2	2	2	—
Pleurobranch	—	—	—	—	—	—	—	—

gills for each species (wherever possible) are presented in Table 1. In these tables, 'r' implies rudimentary or reduced.

Abbreviations: BLM = Bureau of Land Management; MAFLA = Mississippi-Alabama-Florida BLM Program; MCZ = Museum of Comparative Zoology, Harvard University; RMNH = Rijksmuseum van Natuurlijke Historie, Amsterdam; SAM = South African Museum, Cape Town; USNM = National Museum of Natural History, Smithsonian Institution, Washington, D.C.; ZMC = Zoological Museum, University of Copenhagen; ovig. = ovigerous.

In the following systematic section, genera, and species within genera, are arranged alphabetically.

Family Callianideidae Kossman, 1880

Callianideidae Kossman, 1880:80.—Gurney, 1938:343.—de Saint Laurent, 1979:1395.—Poore & Griffin, 1979:221.

Callianideinae De Man, 1928:30.—Melin, 1939:4.—Balss, 1957:1582.—de Saint Laurent, 1973:515.—Sakai & Holthuis, 1987:94.—International Commission on Zoological Nomenclature, 1989:61.

Diagnosis.—Gonochoristic. Carapace somewhat compressed; rostrum short or reduced, lacking spines or teeth, or with few low teeth; cervical groove well developed to obsolete; linea thalassinica complete (i.e., reaching posterior margin of carapace), incomplete, or lacking; anterior region bearing 1 to 4 rows of specialized setae and pits. Abdominal pleura, especially of somite 1, poorly developed, with or lacking lateral anterodorsal lobe for articulation-locking with posterior carapace; 1 or more rows of setal pits present on abdominal somites. Sca-phognathite of maxilla 2 with single elongate spinulose 'whip' seta reaching posteriorly into branchial chamber (very rarely, 2 elongate whips present). Maxilliped 2, ex-

opod well developed or reduced. Maxilliped 3 pediform, becoming somewhat broadened in some forms; dentate ischial crest present or absent. Pereopod 1, chelipeds subsimilar and subequal in size, or markedly different. Pereopod 2 chelate. Propodi of pereopods 2, 3, and 4 expanded in some species, bearing 1 or more rows of setal pits on lateral surface. Epipods present on pereopods 1-4 in all but one species. Pleopod 1 of female uniramous, of 2 articles. Pleopod 1 of male uniramous, of 2 articles, reaching anteriorly to thoracic sternites. Pleopod 2 of male bearing rod-shaped appendix masculina. Pleopods 2-5, rami variously fringed with filaments or lamellae (these presumed to have a supplemental respiratory function), or becoming broad, expanded and lacking respiratory filaments; appendix interna present, free in most species. Uropodal rami lacking transverse suture, lateral ramus bilobed in one species. Telson lacking non-articulating dorsal or lateral spines.

Key to the Genera of Callianideidae

- 1. Respiratory filaments present on pleopods 2
- Respiratory filaments lacking on pleopods 3
- 2. Pereopod 1, chelipeds strikingly dissimilar *Callianidea*
- Pereopod 1, chelipeds subsimilar *Michelea*
- 3. Linea thalassinica present 4
- Linea thalassinica absent 6
- 4. Linea thalassinica reaching posterior margin of carapace *Mictaxius*
- Linea thalassinica not reaching posterior margin of carapace 5
- 5. Maxilliped 3, exopod lacking; Ischium lacking dentate crest *Thomassinia*
- Maxilliped 3, exopod present; Ischium having dentate crest .. *Crosniera*
- 6. Maxilliped 3 lacking dentate ischial

- crest; Rostrum having submarginal dense pile of setae *Marcusiaxius*
- Maxilliped 3 having dentate ischial crest; Rostrum lacking dense pile of setae *Meticonaxius*

Callianidea H. Milne Edwards, 1837

Callianidea H. Milne Edwards, 1837:319.—Boas, 1880:108, 110.—Bate, 1888:10.—Rathbun, 1901:94.—Borradaile, 1903:548.—Gurney, 1938:301, 342.—Balss, 1957:1582.—Melin, 1939:4.—de Saint Laurent, 1973:515.—Le Loeuff & Intes, 1974:23.—Sakai & Holthuis, 1987:93.—International Commission of Zoological Nomenclature, 1989:61.

Type species.—By monotypy, *Callianidea typa* H. Milne Edwards, 1837.

Gender.—Feminine.

Diagnosis.—Carapace lacking linea thalassinica, or with very short anterior linea thalassinica. Anterolateral carapace with vertical row of setae in postantennal area. Abdominal somite 1 with small anterodorsal rounded sclerotized articulating plate, separated by non-sclerotized integument from larger sclerotized posterior plate; latter tapering ventrally but with no free pleuron, with irregular oblique setal row. Somite 2-5 each having short row of few setae in posteroventral angle of pleuron; somite 6 with 3 poorly defined irregular setal rows. Antennular peduncle with article 1 not elongate, article 3 about 1/4 carapace length. Article 4 of antennal peduncle about 1/4 carapace length. Antennal acicle reduced to tiny scale. Lateral epistome bearing cluster of elongate setae. Mandibular incisor having 7 rounded teeth. Maxilliped 2 with well developed exopod. Maxilliped 3 with dentate ischial crest. Pereopod 1, chelipeds highly unequal, similar in ♂ and ♀. Pereopods 2-4, propodus with short vertical setal row proximally on lateral surface. Pleurobranchs lacking. Pleopodal branchial filaments of 2 to 4 articles, borne on mesial and lateral margins of both rami.

Callianidea laevicauda Gill, 1859

Figs. 3, 4, Table 1A

Callianidea laevicauda Gill, 1859:167.—Rathbun, 1901:94.—De Man, 1928:21.—Schmitt, 1924:79; 1935:193, fig. 54; 1936:375.—Rodrigues, 1983:93.

Callianidea laevicauda occidentalis Schmitt, 1939:10.

Callianidea Steenstrupii Boas, 1880:108 [188].

Material examined.—USNM 24663, ♀ cl 14.7 mm, Ensenada Honda, Culebra, Puerto Rico.—USNM 47359, ♀ cl 5.9 mm, Jamaica.—USNM 57514, ♀ cl 8.9 mm, Caracas Bay, Curaçao, under intertidal stones.—USNM 57924, ovig. ♀ cl 11.0 mm, Needham's Point, Barbados.—USNM 67422, ♀ cl 5.1 mm, Kralendijk, Bonaire, under intertidal stones.—USNM 68713, ovig. ♀ cl 10.3 mm, ♀ cl 11.1 mm, Needham's Point, Barbados.—USNM 68722, ♀ cl 11.9 mm, Pelican Is., Barbados.—USNM 122446, ovig. ♀ cl 10.2 mm, Grande Bay, St. Maarten, intertidal.—USNM 221759, ♂ cl 6.3 mm, San Salvador Is., Bahamas, intertidal pool.—USNM 221760, ♀ cl 8.0 mm, Carrie Bow Cay, Belize, back-reef rubble, 1 m.—USNM 243465, 3 ♂ cl 6.6 mm, 7.2 mm, 11.3 mm, 3 ♀ cl 6.0 mm, 8.8 mm, 8.8 mm, Caledonia Bay, Atlantic Panama, intertidal.—USNM 243466, 5 ♂ cl 5.4 mm, 7.2 mm, 8.5 mm, 9.4 mm, 10.0 mm, 3 ♀ cl 5.4 mm, 9.6 mm, 11.5 mm, Smithsonian-Bredin Freelance Expedition sta 73-56, English Harbour, Antigua.—USNM 243467, ovig. ♀ cl 14.2 mm, 3 ♀ cl 6.5 mm, 7.7 mm, 14.0 mm, Smithsonian-Bredin Freelance Expedition sta 21-56, Baradal, Tobago Cays, Grenadines, under intertidal rocks.—ZMC, ♂ cl 12.3 mm, 5 +, cl 4.2 mm, 8.8 mm, 11.1 mm, 12.0 mm, 13.2 mm, Tobago, coll. Dr. Th. Mortensen Expedition 1914-1916.—ZMC, ♀ cl 11.4 mm, St. Johns, U.S. Virgin Islands.—Syntype of *Callianidea steenstrupii* Boas, ZMC, ♀ cl 10.4 mm, Barbados, coll. 1866.

Description.—Carapace with cervical

groove in posterior half, reaching dorsal midline. Rostrum barely demarked, low, apically broadly rounded. Linea thalassinica very short, extending posteriorly from orbit. Irregular vertical row of setal pits in postantennal-postepistomal region.

Eye with cornea demarked, situated laterally at about midlength of eyestalk, mediolateral portion of stalk flattened. Antennular peduncle reaching distal third of antennal peduncle article 4, with articles increasing in length distally, none markedly elongate. Antennal peduncle with acicle reduced to tiny rounded plate, article 4 slender, elongate, article 5 slightly more than half length of article 4. Lateral epistome with band of elongate setae reaching anteriorly almost to distal end of antennular peduncle. Mandible with incisor having 7 blunt teeth, molar broadly rounded with few mesial tubercles; palp of 3 articles, distal article longest, heavily setose. Remainder of mouthparts as figured. Maxilliped 1, endopod with slender digitiform distal article. Maxilliped 2, exopod well developed, with distal segmented flagellum. Maxilliped 3, merus with low blunt spine distally on posterior margin. Pereopod 1, chelipeds strongly dissimilar; larger cheliped with ischium having serrate posterior margin, merus with 2 or 3 low tubercles on posterior margin, chela robust, propodal palm twice length of fingers, propodal carina along posterior margin obscurely crenulate, ridge on mesial face of fixed finger entire, cutting edge with 3 rounded proximal tubercles and strong triangular tooth at about midlength; dactylus strongly curved, cutting edge with strong truncate tubercle proximally, well separated from triangular tooth. Smaller cheliped slender, ischium and merus unarmed; carpus of similar width and about $\frac{2}{3}$ length of propodal palm, latter about $2\frac{1}{2}$ times length of fingers, fixed finger with several triangular teeth distally on cutting edge, dactylar cutting edge entire. Pereopod 2, cutting edges of chela bearing fine spines; propodus with short proximal setal row on lateral surface.

Pereopod 3 almost subchelate, propodus broad, flattened, about $\frac{1}{3}$ longer than wide, with short proximal setal row on lateral surface, posterodistal angle somewhat produced, bearing stout spine. Pereopod 4, propodus with strong posterodistal spine, 2 short setal rows proximally on lateral surface; dactylus somewhat twisted. Pereopod 5, dactylus twisted.

Pleopod 1 in female of 2 articles, distal article slender-lanceolate. Pleopod 1 in male of 2 articles, distal article broadly triangular, with small mesial lobe bearing hooks. Pleopod 2 in male with rod-shaped setose appendix masculina and short free appendix interna. Pleopods 2–5 with both rami bearing marginal slender cylindrical accessory respiratory filaments, each filament proximally of 2 articles, more distal filaments of up to 4 articles. Abdominal somite 6 with 1 vertical row and 2 irregular oblique rows of setal pits posterolaterally, plus short submarginal row near posterolateral angle. Uropod with outer ramus having small basal spine on dorsal surface, margin setose with additional row of small golden spines along most of laterodistal margin; inner ramus with longitudinal dorsal ridge bearing 2 spines in distal half. Telson slightly longer than greatest width, posterior margin subtruncate, setose.

Remarks.—Schmitt (1939) described the new subspecies *Callianidea laevicauda occidentalis*, from Socorro Island (Pacific Mexico) and the Galapagos Islands. In the description, he noted that the only differences from the Atlantic *C. laevicauda* were the somewhat more tuberculate lower propodal carina, and the crenulate mesial ridge of the fixed finger of the larger first pereopod chela. Examination of material from the Galapagos, Lower California, and Pacific Mexico confirmed Schmitt's observations, but revealed some variation in these characters. Separation of Pacific and Atlantic forms of this species is thus based on very thin evidence. Given the wide distribution across the Caribbean and eastern Pacific,

the species would seem to have been well established before any emergence of the isthmus of Panama.

Callianidea typa differs from *C. laevicauda* in lacking any sign of a linea thalassinica, and in having bifurcating pleopodal accessory respiratory filaments that divide up to three times. These features were not thought sufficient to justify separation into two genera, even though these two taxa formed a sister group to the *Crosniera-Mictaxius-Thomassinia* group of genera (see Fig. 25).

Crosniera, new genus

Type species.—By present designation, *Callianassa minima* Rathbun, 1901.

Gender.—Feminine.

Diagnosis.—Carapace with subvertical setal row anterolaterally; linea thalassinica not reaching posterior margin of carapace; rostrum narrowly triangular in dorsal view, just overreaching eyestalks. Abdomen somewhat dorsoventrally compressed. Abdominal somite 1 lacking forwardly-directed lobes; somites 1–5 each with single setal row; somite 6 with 3 setal rows. Mandibular incisor toothed. Maxilliped 1, endopod of 2 articles. Maxilliped 2, exopod well developed. Maxilliped 3, pediform but articles showing some broadening; exopod moderately well developed; dentate ischial crest present. Pereopods lacking setal rows. Pereopod 1, chelipeds subsimilar. Pereopod 3, propodus broadened. Pleopodal rami relatively narrow, about 3–4 times longer than greatest width; rami lacking accessory respiratory filaments. Pleopod 2 in male with appendix interna articulating on appendix masculina. Lateral uropodal ramus not bilobed.

Remarks.—De Saint Laurent (1979) diagnosed the genus *Thomassinia* as having the exopod of maxilliped 3 vestigial or absent, and lacking a dentate ischial crest; in *Crosniera minima* the exopod is moderately well developed, as is the dentate crest. The rostrum in *C. minima* is well developed

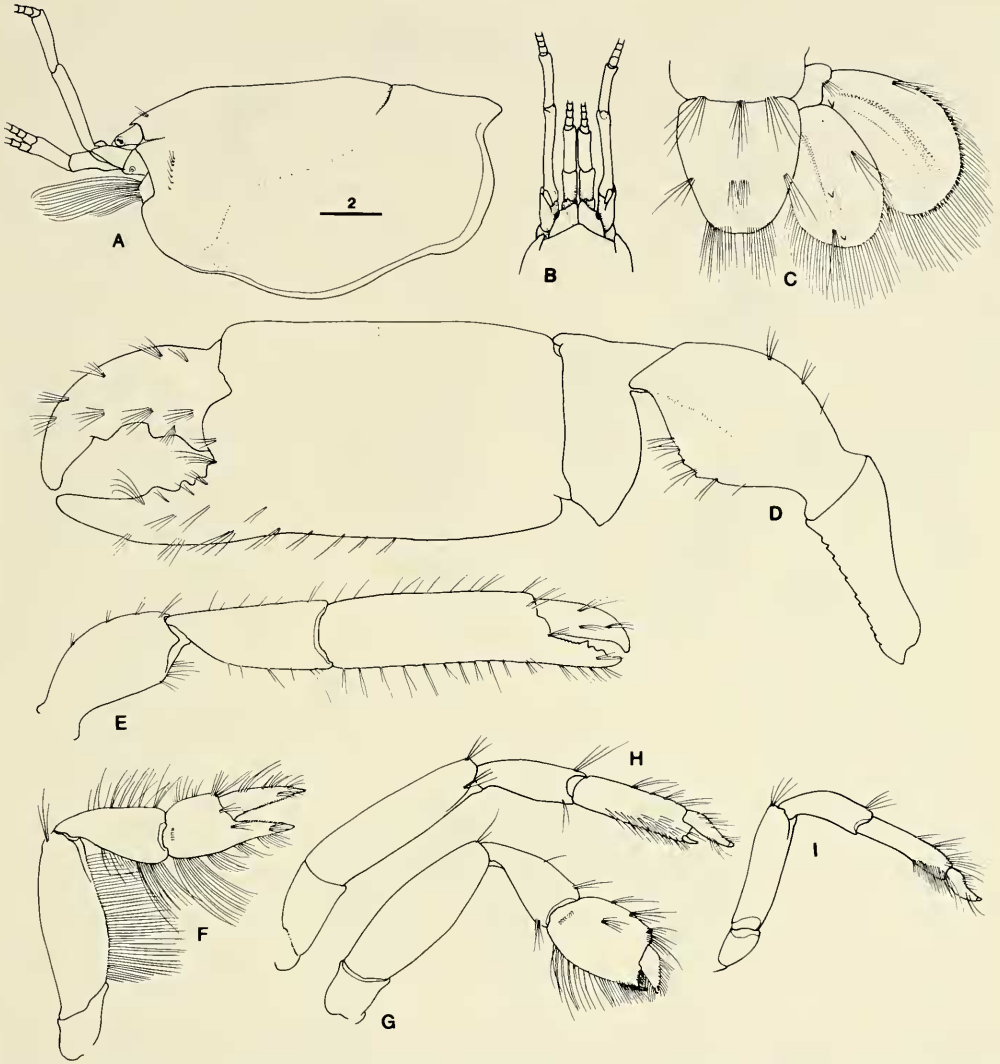


Fig. 3. *Callianidea laevicauda*: A, Carapace in lateral view, scale in mm; B, Anterior carapace, eyes, and bases of antennules and antennae; C, Telson and right uropod; D, Pereopod 1, larger cheliped; E, Pereopod 1, smaller cheliped; F, Pereopod 2; G, Pereopod 3; H, Pereopod 4; I, Pereopod 5.

compared to that of *T. gebioides*, where it is practically lacking. The pereopodal epipods are bifid in *T. gebioides* (G. Poore, 1990, in litt.), but not in *C. minima*. (The upper ramus of these bifid epipods is probably the remnant of a podobranch.) Pleopod 1 of the male is said to be absent in *Thomassinia*. Of seven males of *C. minima* examined, only one possessed first pleopods.

Whether this is an aberration, or a function of maturity, is unknown, and can only be resolved with considerably more male material.

Etymology.—The genus is named for Alain Crosnier, ORSTOM scientist at the Muséum National d'Histoire Naturelle, Paris, renowned carcinologist and valued colleague.



Fig. 4. *Callianidea laevicauda*: A, Maxilla 2; B, Mandible; C, Mandibular palp; D, Maxilla 1; E, Maxilliped 1; F, Maxilliped 2; G, Maxilliped 3; H, Pleopod 1, male; I, Pleopod 2, male.

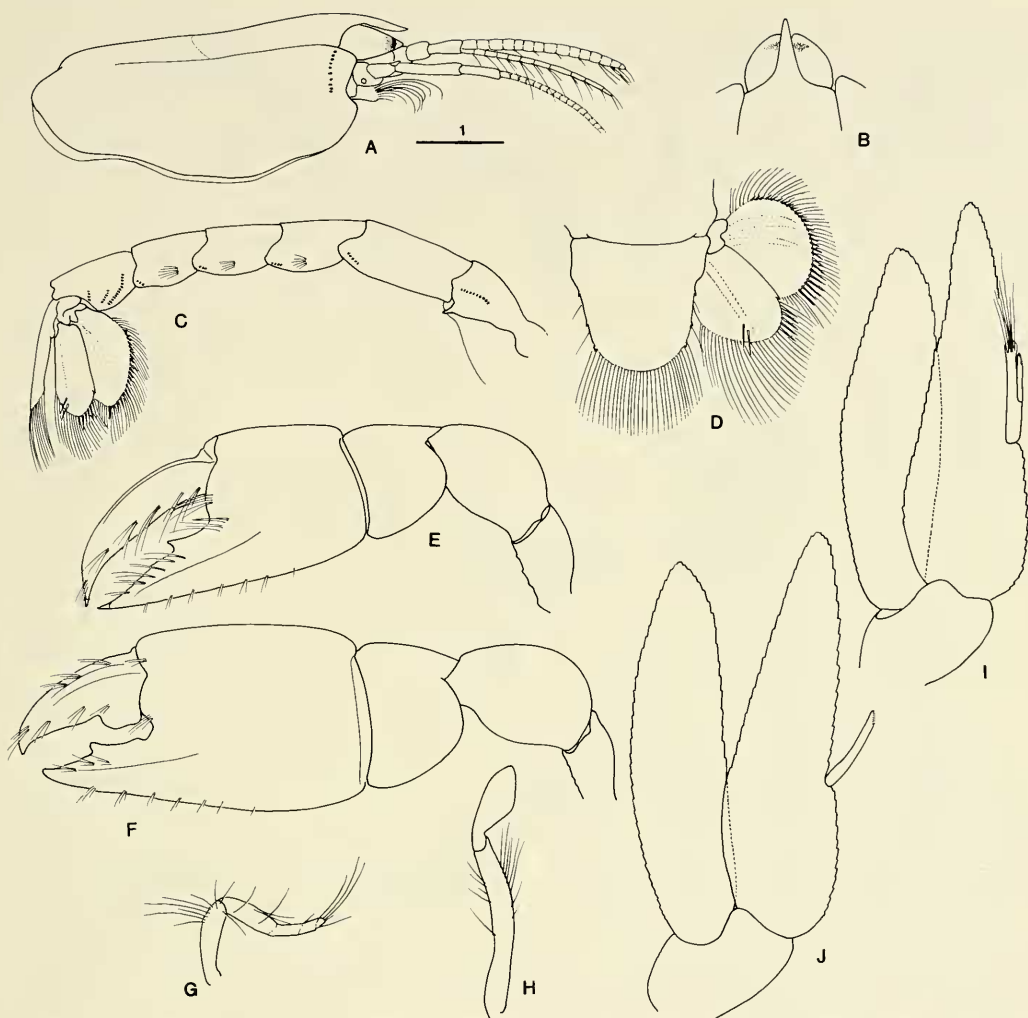


Fig. 5. *Crosniera minima*: A, Carapace in lateral view, scale in mm; B, Rostrum and eyes in dorsal view; C, Abdomen in lateral view; D, Telson and right uropod; E, Pereopod 1, smaller cheliped; F, Pereopod 1, larger cheliped; G, Pleopod 1, female; H, Pleopod 1, male; I, Pleopod 2, male; J, Pleopod 3.

Crosniera minima (Rathbun, 1901)

Figs. 5, 6, Table 1B

Callianassa minima Rathbun, 1901:92, fig. 16.—Schmitt, 1935:5.—de Saint Laurent, 1979:1396.—Manning, 1987:397.

Material examined.—Syntypes, USNM 23779, ♂ cl 2.5 mm, ♀ cl 2.5 mm, *Fish Hawk* sta 6066, Mayaguez Harbor, Puerto Rico, 295–315 m.—USNM 24668, ♀ cl 2.5 mm, *Fish Hawk* sta 6062, Mayaguez Harbor, Puerto Rico, 45–55 m.—USNM 243547,

IEC (Interstate Electronic Corp.) sta A7-3, ♀ cl 3.8 mm, Puerto Rico, 18°29'10.8"N, 66°09'6.6"W, 31 m, 11 Jun 1980.—USNM 243533, IEC sta A20-1, ♂ cl 3.1 mm, ♀ cl 3.0 mm, Puerto Rico, 18°30'42"N, 66°08'47.4"W, 295 m, 11 Jun 1980.—USNM 243534, IEC sta SJA-2, ♂ cl 3.9 mm, Puerto Rico, 18°30'42"N, 66°09'19.8"W, 274 m, 10 Jun 1980.—USNM 243543, IEC sta 731 SJ-010-008, ♂ cl 3.0 mm, Puerto Rico, 18°30'42.0"N, 66°11'36.0"W, 282 m, 10 Jun 1980.—USNM 243542, IEC sta 732

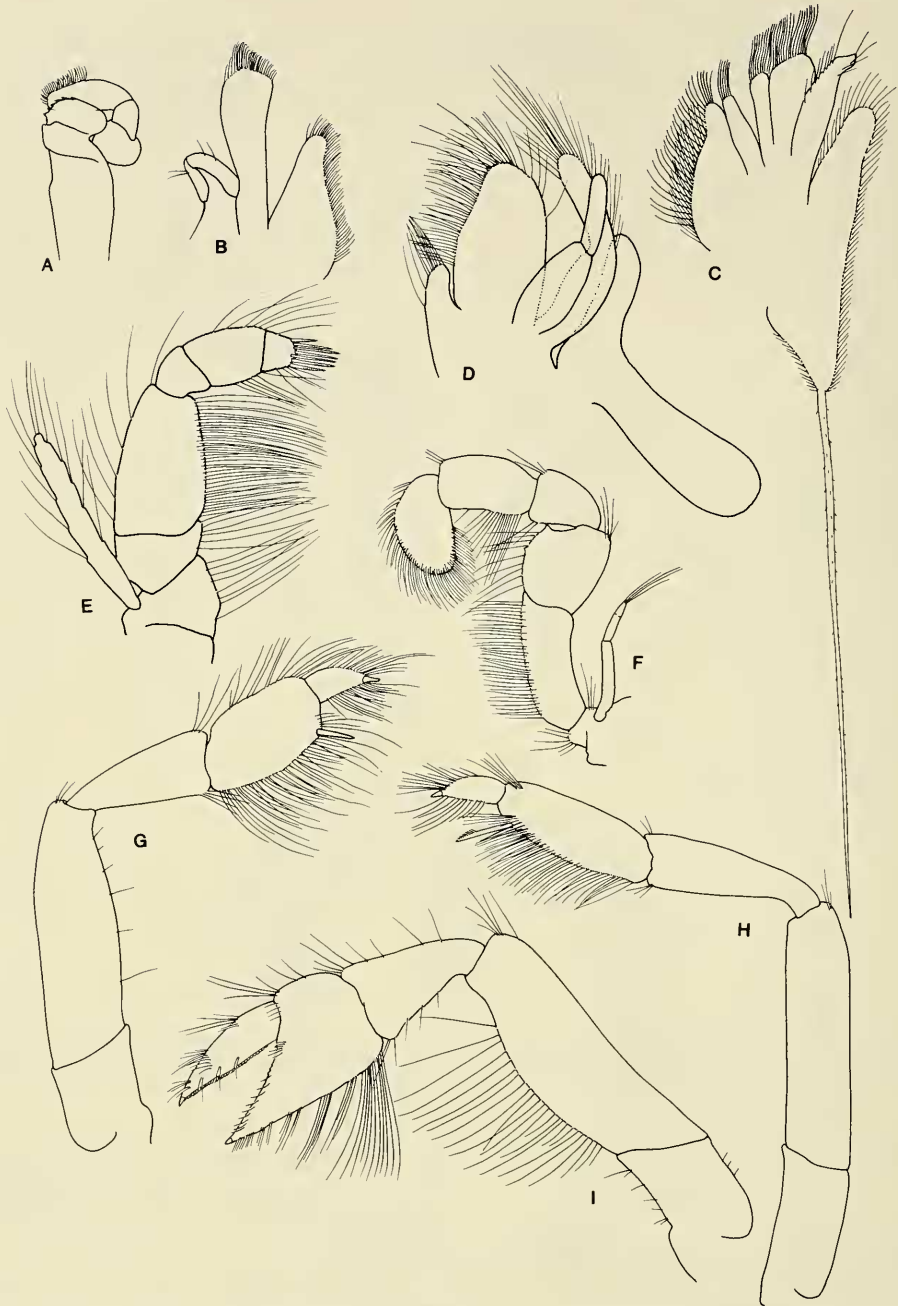


Fig. 6. *Crosniera minima*: A, Mandible; B, Maxilla 1; C, Maxilla 2; D, Maxilliped 1; E, Maxilliped 2; F, Maxilliped 3; G, Pereopod 3; H, Pereopod 4; I, Pereopod 2.

SJ-003-006, ♂ cl 3.0 mm, off Mobile, Alabama, 30°09'36"N, 88°06'37"W, 12 m, 29 Jun 1980.—USNM 243539, IEC sta 732 SJ-002-002, ♀ cl 3.2 mm, off Mobile, Alabama, 30°09'24.6"N, 88°05'24.0"W, 10 m, 28 Jun 1980.—USNM 243538, IEC sta 732 SJ-008-008, ♂ cl 2.8 mm, 1 juv., off Mobile, Alabama, 30°09'23"N, 88°08'14"W, 13 m, 28 Jun 1980.—USNM 243540, IEC sta MO-722-408-010, 1 juv., off Mobile, Alabama, 30°09'25"N, 88°08'30"W, 16 m, 19 Jan 1980.—USNM 243541, IEC sta 731 SJ-004-003, ♂ cl 3.0 mm, Puerto Rico, 18°30'36"N, 66°09'36"W, 276 m, 10 Jun 1980.—USNM 243535, IEC sta 731 SJ-004-009, ovig. ♀ cl 3.0 mm, Puerto Rico, 18°30'30"N, 66°09'31.8"W, 264 m, 10 Jun 1980.—USNM 243537, IEC sta 731 SJ-001-007, 2+ cl 2.5 mm, 3.2 mm, 1 juv., Puerto Rico, 18°30'42"N, 66°09'10.2"W, 302 m, 11 Jun 1980.—USNM 243536, IEC sta 731 SJ-008-004, 1 juv., Puerto Rico, 18°30'42"N, 66°10'31.2"W, 298 m, 11 Jun 1980.

Description.—Rostrum slender, acute, just reaching beyond eyes, directed anteroventrally, with faint middorsal keel; linea thalassinica reaching posteriorly from postorbital margin for $\frac{4}{5}$ of carapace length; vertical row of setal pits in antennal region of anterior carapace; cervical groove barely demarcated. Abdominal somites dorsoventrally flattened; in dorsal view, somite 1 narrow, widening posteriorly, posteroventral angle acute, bearing row of setal pits; somites 2–5 of similar width, pleura posteroventrally rounded with few setal pits; somite 2 longest, somite 6 posteriorly narrowed, with 3 separate rows of setal pits. Telson with 3 small lateral teeth, posterior margin broadly convex.

Eyes flattened, dorsally calcified with sharp lateral margin, cornea not defined, but distal dark pigment visible. Antennule with peduncle article 3 reaching distal margin of antennal article 4; flagella subequal in length, dorsolateral flagellum about twice width of ventromesial one. Antennal acicle reduced to tiny scale; peduncle article 4 twice length

of article 5. Lateral epistome bearing numerous elongate downcurved setae. Mandible with incisor bearing 6 corneous marginal teeth; molar with mesial tubercle; palp of 3 articles, article 3 longest, with dense distal setae. Rest of mouthparts as figured (Fig. 6). Maxilliped 2, dactylus bearing cluster of distal spines; exopod well developed. Maxilliped 3, ischium with strong dentate crest on mesial surface; posterior margin bearing dense fringe of setae; merus somewhat expanded, with 2 small teeth on posterior margin; dactylus ovate, strongly setose; exopod reaching distal margin of ischium, bearing few distal setae. Pereopod 1, chelipeds not sexually dimorphic; chelipeds dissimilar, one slightly wider and longer than other; larger cheliped, propodus carinate along anterior and posterior margins, strong oblique ridge on lateral and mesial surface of palm running onto fixed finger, latter with single tooth at about midlength of cutting edge; dactylus with strong proximal tubercle on cutting edge. Smaller cheliped, propodus carinate along anterior and posterior margins, strong oblique ridge on lateral and mesial surface of palm running onto fixed finger, latter with single proximal tooth on cutting edge; dactylar cutting edge unarmed. Pereopod 2 chelate, articles flattened and strongly setose; cutting edges of propodal fixed finger and dactylus bearing close-set row of hyaline truncate teeth. Pereopod 3, propodus and dactylus strongly setose, propodus broadly ovate, flattened, with single posterodistal spine. Pereopod 4, propodus flattened but more elongate than in pereopod 3, posterior margin strongly setose and with single posterodistal spine; dactylus strongly setose. Pereopod 5 lost in all specimens. Pleopod 1 in female uniramous, proximal article shorter than flexed indistinctly segmented distal article. Pleopod 1 in male of 2 articles, proximal article slender, elongate, distal article about half length of proximal, slightly expanded. Pleopod 2 in male with appendix masculina situated almost at midlength of

mesial margin of endopod, rod-shaped and bearing numerous distal setae; appendix interna articulating at midlength of appendix masculina, not reaching apex of latter; pleopods 3–5 with appendix interna on endopod. Lateral ramus of uropod subcircular in outline, bearing marginal plumose setae; mesial ramus ovate, not lobed, bearing marginal setae.

Marcusiaxius Rodrigues & Carvalho, 1972

Marcusiaxius Rodrigues & Carvalho, 1972: 357.

Type species. — By monotypy, *Marcusiaxius lemoscastroi* Rodrigues & Carvalho, 1972.

Gender. — Masculine.

Diagnosis. — Rostrum at same level as anterior carapace, bearing dense anterodorsal submarginal pile of setae, middorsally with flattened triangular area. Carapace with subvertical setal row in postorbital/postantennal region, few setal pits just below lateral carina, subvertical lateral row just anterior to cervical groove. Abdominal somite 1 with dorso-horizontal setal row; somite 2 with ventro-horizontal, and subvertical posterior setal row; somites 3–5 each with subvertical setal row; somite 6 with 3 setal rows. Dense patches of setae on somites 3–5.

Eyestalk apically subacute, shorter than rostrum; corneal area small, subapical. Antennal acicle half or less than half length of antennal peduncle article 4. Maxilliped 3, exopod reduced or absent; merus lacking spine on posterior margin. Pereopod 1, chelae symmetrical. Pereopod 2 with short proximal setal row on lateral surface of propodus. Pereopod 3 with 2 subparallel proximal setal rows on lateral surface of propodus. Pereopod 4, propodus with setal row along anterior margin. Pleopod 1 in ♂ uniramous, of 2 articles, distal article plow-shaped. Pleopod 2 in ♂ with appendix masculina considerably longer than appendix interna. Pleopods 2–5, rami broad. Mesial uropodal ramus strongly produced disto-

laterally; lateral ramus slightly produced distolaterally. Telson wider than long, lacking non-articulating dorsal spines.

Remarks. — While *Marcusiaxius* and *Meticonaxius* share a number of characters, and appear to be closely related, species of the two may be distinguished on a number of features, as summarized in Table 2.

Key to Species of *Marcusiaxius*

1. Exopod of maxilliped 3 present; Exopod of maxilliped 2 well developed
..... *M. colpos*
- Exopod of maxilliped 3 lacking; Exopod of maxilliped 2 reduced
..... *M. lemoscastroi*

Marcusiaxius colpos, new species

Figs. 7, 8, Table 1C

Material examined. — Holotype, USNM 243404, ♂ cl 13.8 mm, MAFLA sta 2534 G, Gulf of Mexico, 29°40'N, 86°17'W, coarse sand, 73 m. — Paratype, USNM 243405, ♂ cl 14.5 mm, MAFLA sta 2533 A, Gulf of Mexico, 29°42'59.9"N, 85°15'28.6"W, coarse sand, 67 m. — USNM 243406, ? sex, (anterior carapace only), MAFLA sta 2644 F, Gulf of Mexico, 29°36.2'N, 87°23.5'W, medium sand, 75 m. — USNM 243407, ♂ cl 17.0 mm (abdomen missing), MAFLA sta 2747-08, ♀ (carapace damaged), sta 2747-06, Gulf of Mexico, 27°24.2'N, 84°07.3'W, medium fine sand, 74 m. — USNM 243410, juv. cl 4.5 mm, BLM 1974, crustacea 31/F. — USNM 243411, juv. cl 5.1 mm, MAFLA sta 2533 F, Gulf of Mexico, 29°42'59.9"N, 85°15'28.6"W, coarse sand, 67 m. — USNM 243412, juv. cl 3.2 mm, MAFLA sta 2211-10, Gulf of Mexico, 27°56'29.5"N, 83°52'59.5"W, coarse sand, 43 m. — USNM 243413, 2 juv. cl 5.9 mm, 9.8 mm, MAFLA sta 2427 C, 28°49'59.1"N, 85°37'01.9"W, clayey sandy silt, 175 m.

Diagnosis. — Carapace with vertical setal row anterior of weakly defined cervical groove, less compact row just ventral of lat-

Table 2.—Comparison of *Marcusiaxis* and *Meticonaxius*.

	<i>Marcusiaxis</i>	<i>Meticonaxius</i>
Rostrum	With dense anterodorsal pile of setae submarginally	Lacking dense setal pile
Eye	Dorsal flattened triangular region Eyestalk distally pointed Cornea small, discrete	Middorsal rounded to carinate ridge Eyestalk distally rounded or truncate Cornea diffuse
Maxilliped 3	Dentate ischial crest absent	Dentate ischial crest present
Pleuron 2	Anteroventral horizontal, and posterior subvertical setal row present	Posterior subvertical setal row present
Telson	Basal width greater than greatest length	Basal width less than greatest length

eral carina, and short vertical postorbital row; rostrum with submarginal brush of short stiff setae in anterior half; median carina barely demarked, widening posteriorly; lateral carina entire. Abdominal somites having single row of setae-tubercles on pleura 1 and 3–5, 2 rows on pleuron 2, 3 rows on somite 6; dense posteroventral setal patches on 2–5, clumps of dorsolateral setae on 3–5.

Eye with cornea faintly demarked; eyestalk conical. Antennal acicle slightly more than $\frac{1}{3}$ length of peduncle article 4. Maxilliped 2 with exopod elongate; maxilliped 3 lacking spine on merus, lacking dentate ischial crest, exopod reaching distally to base of merus. Pereopod 1, merus with small proximal tooth and larger distal tooth on posterior margin; fingers of chela about $\frac{3}{4}$ length of propodal palm; fixed finger with strong sinuous tooth and few tiny denticles in proximal half of cutting edge; dactylus with proximal emargination in cutting edge. Pereopod 2, merus lacking spines; propodus with short proximal setal row on lateral surface of propodus. Pereopod 3 with 2 subparallel setal rows on lateral surface of propodus. Pereopod 4 with setal row along anterior margin of propodus. Uropod with both rami widening distally, lateral ramus with distolateral corner produced; mesial ramus with distolateral region strongly produced. Telson $\frac{1}{3}$ wider than midlength.

Etymology.—The specific epithet is derived from the Greek 'kolpos,' a gulf or bay, and refers to the Gulf of Mexico.

Marcusiaxis lemoscastroi
Rodrigues & Carvalho, 1972
Figs. 9, 10, Table 1D

Marcusiaxis lemoscastroi Rodrigues & Carvalho, 1972:357.—Carvalho & Rodrigues, 1973:553, figs. 1–21.

Meticonaxius lemoscastroi: Coelho, Ramos-Porto, & Koenig, 1980:39.—Coelho & Ramos-Porto, 1987:33.—Coelho, 1987:63, 68.

Material examined.—RMNH, ♂ cl 11.0 mm, Mucurici, Fortaleza, Ceara, Brazil, collected by beach seine net, 7 Mar 1968.—USNM 243403, ♂ cl 12.2 mm, Pillsbury sta P-758, 11°42.2'N, 69°40.0'W, Gulf of Venezuela, 15–18 m, 27 Jul 68.

Records.—Dredged from the littoral of Amapa, northern Brazil; shallow infralittoral, Gulf of Venezuela.

Diagnosis.—Carapace with rostrum having submarginal band of short stiff setae, median carina narrowly triangular, flattened, widening posteriorly, lateral carina entire. Abdominal pleuron 1 with hooked posteroventral tooth, pleura 2–6 ventrally rounded; pleura 1, 3–5 each with setal row, pleuron 2 with ventral and posterolateral setal row, pleuron 5 with blunt posterolateral lobe; pleuron 6 with 3 setal-rows, pleura 2–5 posteroventrally densely setose.

Antennal acicle slightly more than half length of peduncle article 4. Maxilliped 2 with short exopod; maxilliped 3 lacking exopod, meral spine, and ischial dentate crest. Pereopod 1, merus with strong tooth at mid-

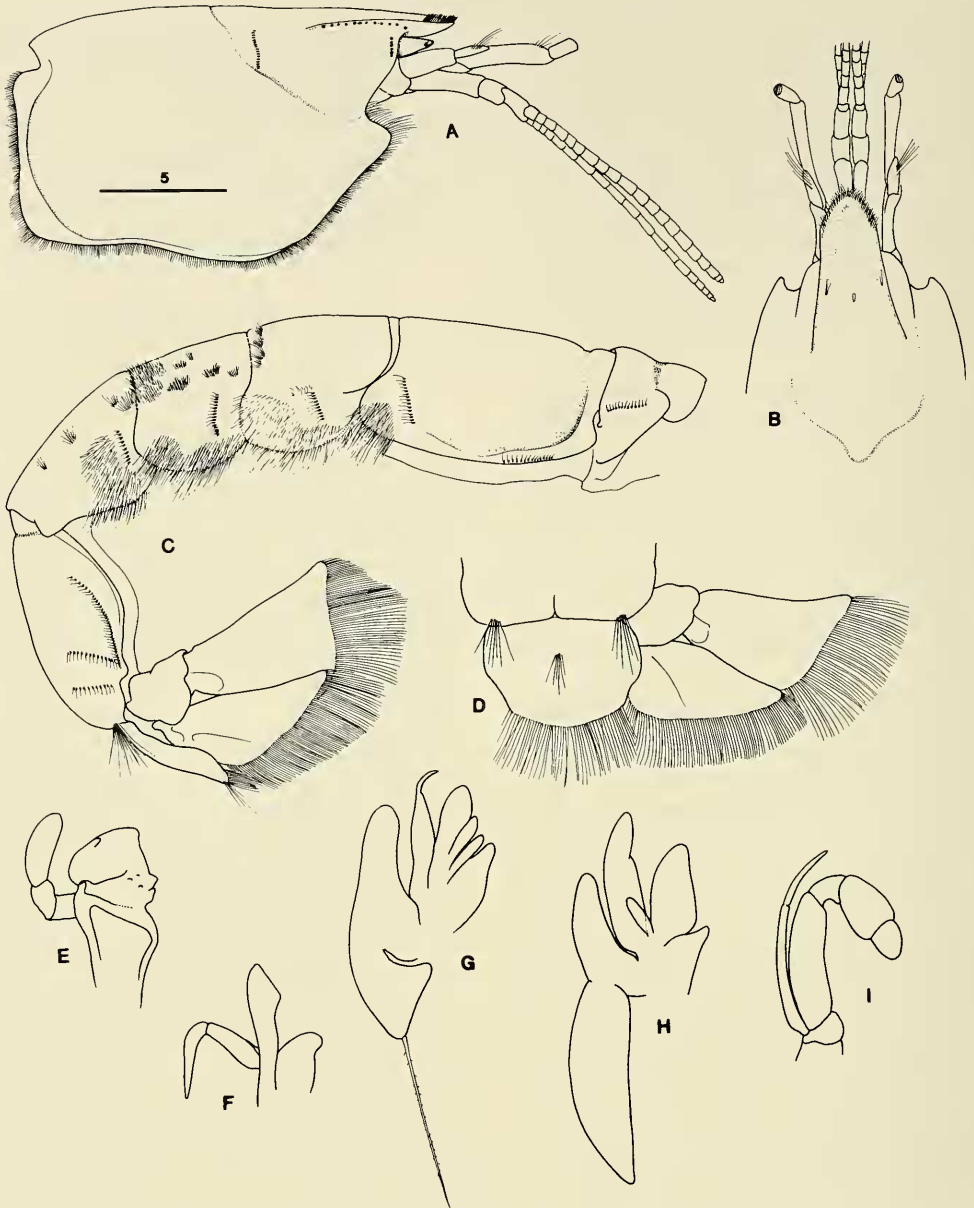


Fig. 7. *Marcusiastixius colpos*: A, Carapace in lateral view, scale in mm; B, Anterior carapace in dorsal view; C, Abdomen in lateral view; D, Telson and right uropod; E, Mandible; F, Maxilla 1; G, Maxilla 2; H, Maxilliped 1; I, Maxilliped 2.

length of posterior margin; fingers slightly shorter than propodal palm, fixed propodal finger with strong triangular tooth in proximal half of cutting edge; cutting edge of dactylus entire. Pereopod 2 lacking meral spines; propodus with short proximal setal

row on lateral surface. Pereopod 3, propodus with 2 setal rows on lateral surface. Pereopod 4 with setal row on anterior margin of propodus. Lateral uropodal ramus distolaterally strongly produced; mesial ramus distolaterally produced, considerably wider

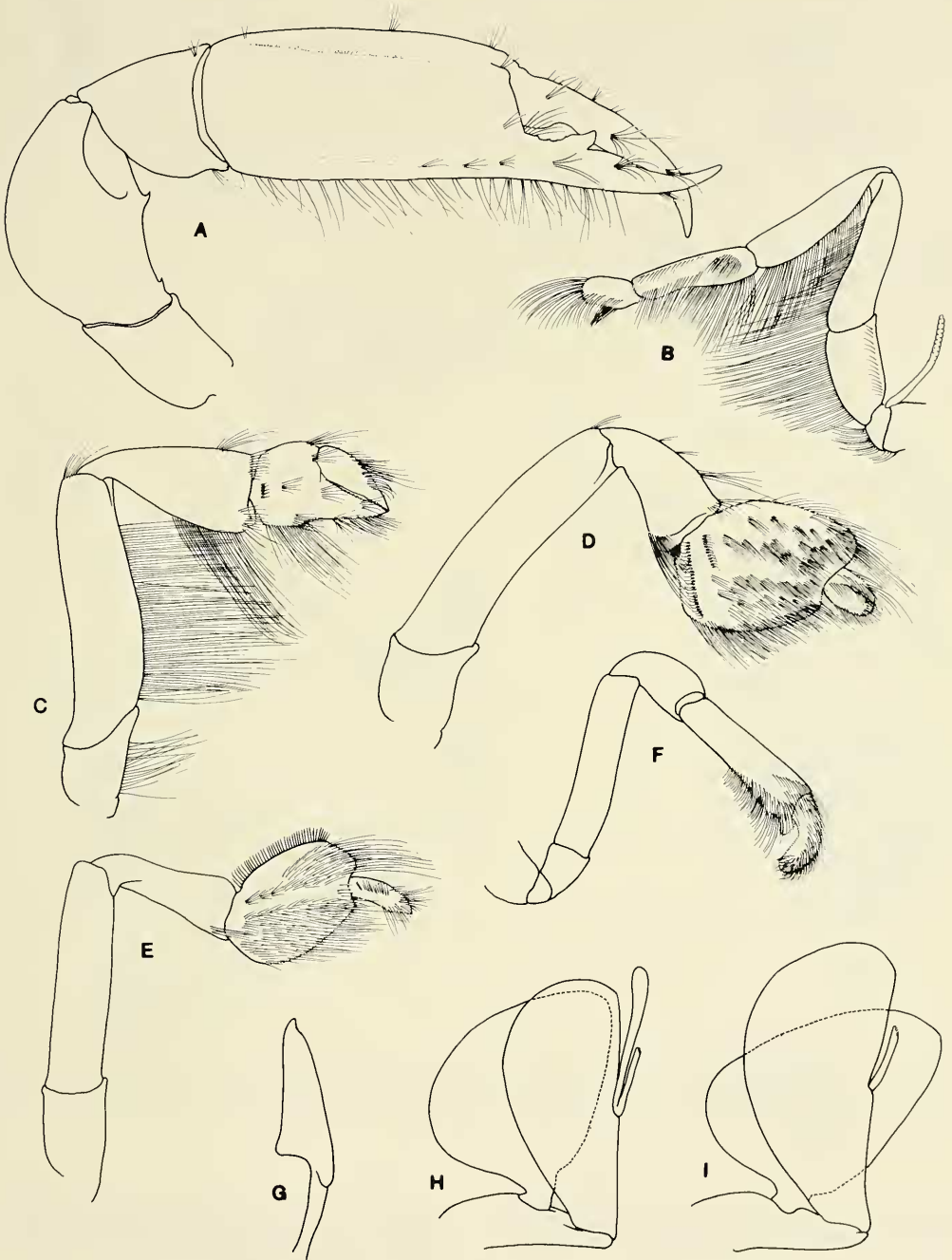


Fig. 8. *Marcusiarius colpos*: A, Pereopod 1; B, Maxilliped 3; C, Pereopod 2; D, Pereopod 3; E, Pereopod 4; F, Pereopod 5; G, Pleopod 1, male; H, Pleopod 2, male; I, Pleopod 3.

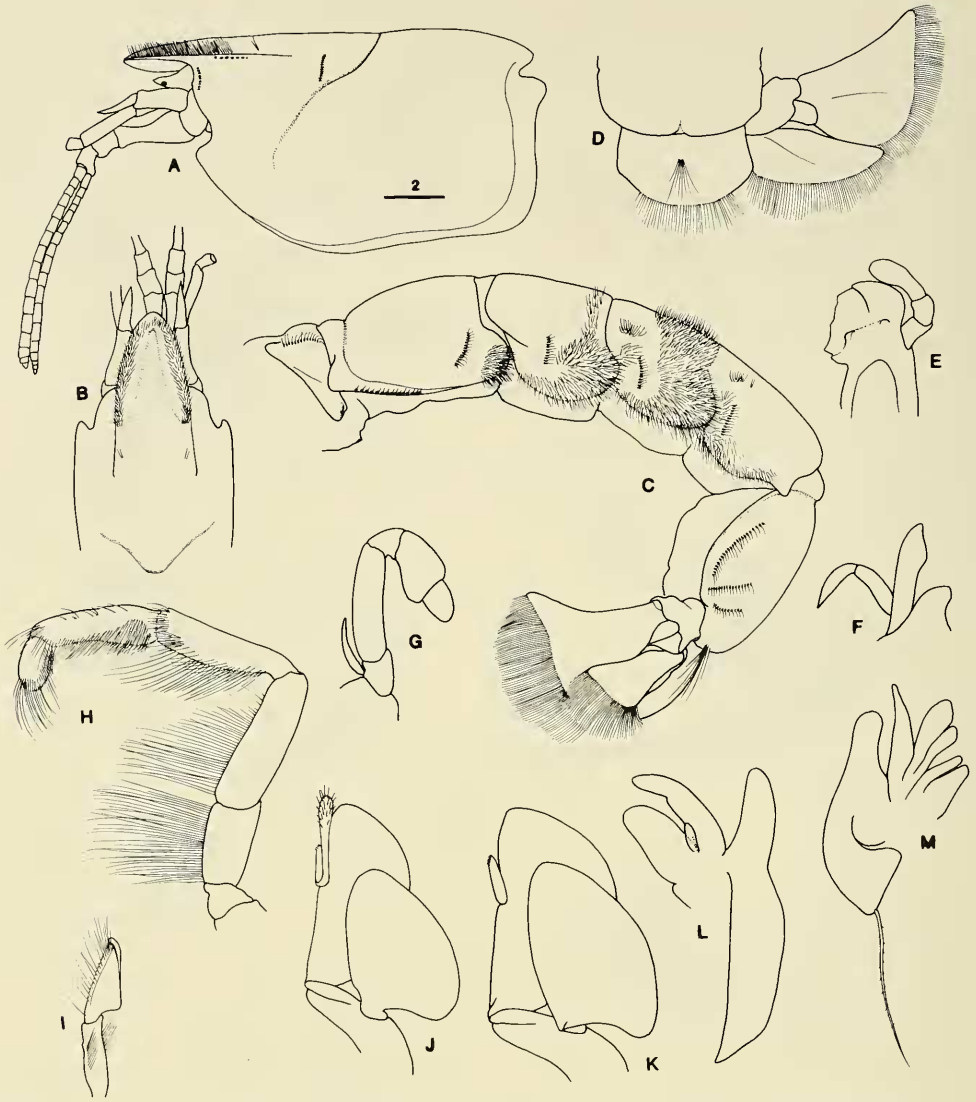


Fig. 9. *Marcusiarius lemoscastroi*: A, Carapace in lateral view, scale in mm; B, Anterior carapace in dorsal view; C, Abdomen in lateral view; D, Telson and right uropod; E, Mandible; F, Maxilla 1; G, Maxilliped 2; H, Maxilliped 3; I, Pleopod 1, male; J, Pleopod 2, male; K, Pleopod 3; L, Maxilliped 1; M, Maxilla 2.

than long. Telson almost twice wider than long, posterior margin broadly convex.

Meticonaxius De Man, 1905

Meticonaxius De Man, August 1905:592; 1925:5, 53; 1928:18, 21, 30, 53.—Barnard, 1950:499.—Balss, 1957:1579.—Le

Loeuff & Intes, 1974:23.—de Saint Laurent, 1973:515, 1979:1397.—Sakai & de Saint Laurent, 1989:9.

Metaxius Bouvier, November 1905:804.—De Man, 1925:8.—Balss, 1957:1582.

Type species.—By monotypy, *Meticonaxius monodon* de Man, 1905:593.

Gender.—Masculine.

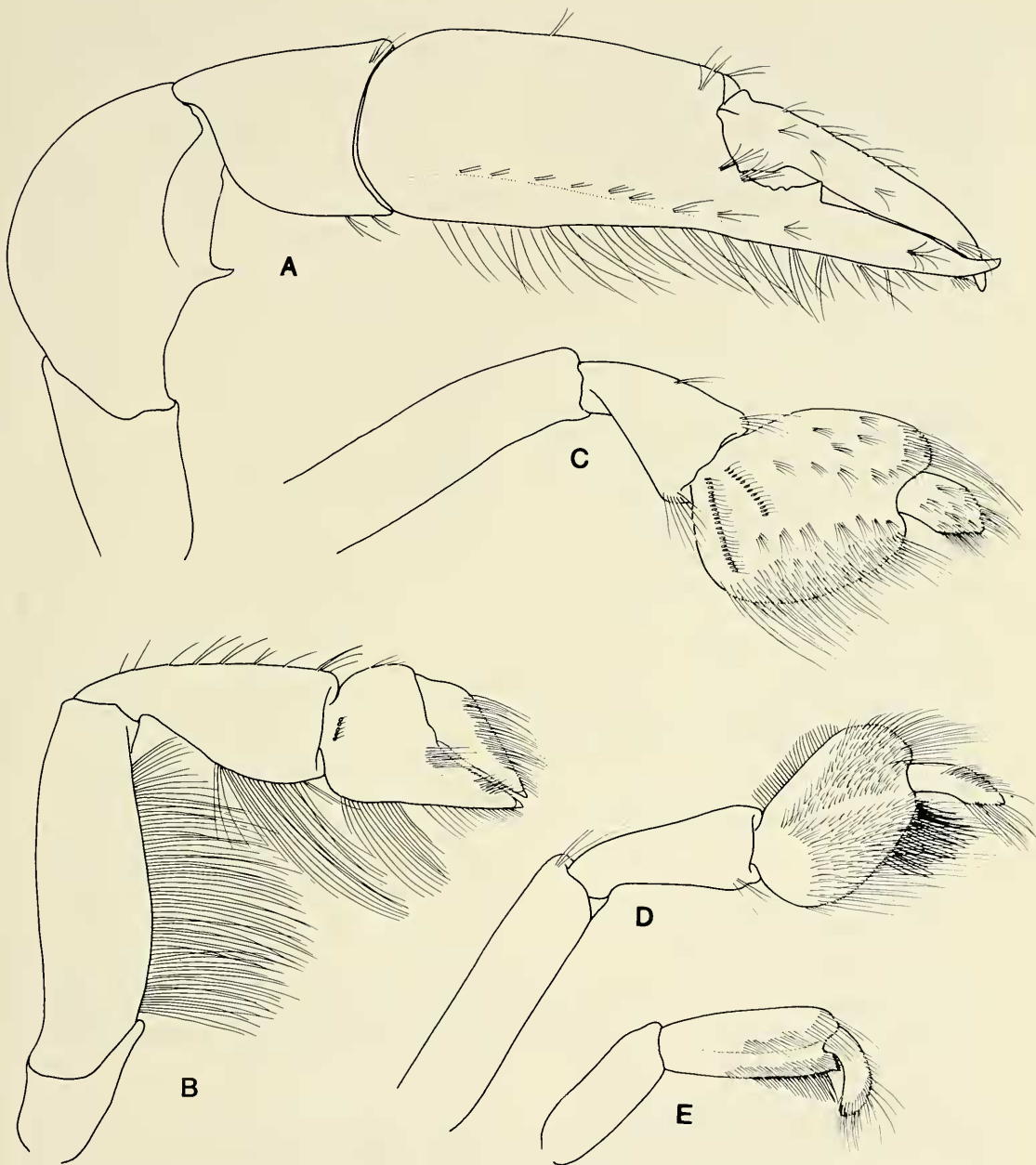


Fig. 10. *Marcusiarius lemoscastrói*: A, Pereopod 1; B, Pereopod 2; C, Pereopod 3; D, Pereopod 4; E, Distal three articles of pereopod 5.

Diagnosis.—Carapace with rostrum at same level as anterior carapace, rostral margins unarmed (single subapical spine on left side in type species may be result of injury). Median carina entire; submedian carina ab-

sent; lateral carina entire. Near-vertical setal row on carapace just anterior to cervical groove, less compact setal row immediately ventral to lateral carina; single row of setal pits on abdominal somites 1–5, 3 rows on

somite 6. Abdominal somites 2–4 with posteroventral region of pleura densely setose.

Eye with cornea undifferentiated or poorly differentiated, weakly to moderately well pigmented; eyestalk shorter than rostrum, distally rounded or truncate-flattened. Antennal acicle about half length or less of peduncle article 4. Maxilliped 3 with exopod reduced; meral spine present or absent; dentate ischial crest present. Chelae of pereopod 1 symmetrical. Pereopod 2 chelate, propodus with short proximal setal row. Pereopods 2–4 each with single pleurobranch present (*M. longispina*, *M. bouvieri*, and *M. monodon*), or pleurobranches absent (*M. microps*). Propodus of pereopods 3 and 4 expanded, that of pereopod 3 with 1 or 2 setal rows on lateral surface, that of pereopod 4 with single setal row. Pleopodal rami broad; appendix interna on pleopods 2–5. Pleopod 1 in ♂ uniramous, of 2 articles, distal article plow-shaped; pleopod 2 in ♂ with appendix masculina and appendix interna. Lateral uropodal ramus lacking suture, distally broad, occasionally produced distolaterally; mesial ramus distolaterally somewhat produced. Telson longer than wide, lacking non-articulating dorsal spines.

Key to Species of *Meticonaxius*
(*M. minutus* excluded due to
lack of information)

1. Rostrum apically acute 2
- Rostrum apically rounded 3
2. Merus of pereopod 1 with single spine on posterior margin; Merus of maxilliped 3 with posterodistal spine *M. monodon*
- Merus of pereopod 1 with 2 strong spines on posterior margin; Merus of maxilliped 3 lacking spine *M. bouvieri*
3. Merus of maxilliped 3 with spine 4
- Merus of maxilliped 3 lacking spine *M. microps*
4. Merus of pereopod 1 with spine on posterior margin *M. capricorni*

- Merus of pereopod 1 lacking spine on posterior margin . . . *M. longispina*

Meticonaxius bouvieri, new species

Figs. 11, 12, Table 1E

Material examined.—Holotype, USNM 243408, ♂ cl 16.0 mm.—Paratypes, USNM 243409, 3 ♂ cl 9.8 mm, 10.0 mm, 13.5 mm, 2 ♀ 15.5 mm (abdomen missing), 12.2 mm (abdomen missing), Pillsbury sta 1261, off Jamaica, 17°13'N, 77°45'W, 722–768 m. — Paratype, USNM 122453, ♂ cl 5.0 mm, north of Long Island, Bahamas, 23°36'N, 75°25'W, 180–360 m.

Diagnosis.—Carapace smooth; rostrum triangular, midventrally keeled, apically acute/subacute, lateral margins unarmed; median carina reaching posteriorly from rostral apex onto carapace, to about posterior level of lateral carinae. Abdominal pleura ventrally rounded.

Antennal acicle reaching midlength of peduncle article 4. Maxilliped 3, exopod reduced to small lobe; posterior margin of ischium and merus unarmed. Pereopod 1, basis with strong spine on posterior margin; merus with 2 strong spines on posterior margin, anterior margin strongly convex; propodal palm longer than fingers, cutting edge of fixed finger with fine denticulations proximally with slightly larger tubercle, strong acute tooth distal of midlength. Pereopod 2 lacking spination, propodal palm subequal to fingers in length (measured along midline of lateral surface); short proximal setal row on lateral surface of propodus. Pereopod 3 with 2 setal rows on lateral surface of propodus. Pereopod 4 with setal row on anterior margin, plus short proximal row on lateral surface, of propodus. Lateral uropodal ramus distolaterally rounded, not produced; mesial ramus distolaterally slightly produced. Telson slightly longer than greatest width, posterior margin evenly convex.

Etymology.—The species is named for the late Eugène Louis Bouvier, renowned French carcinologist.

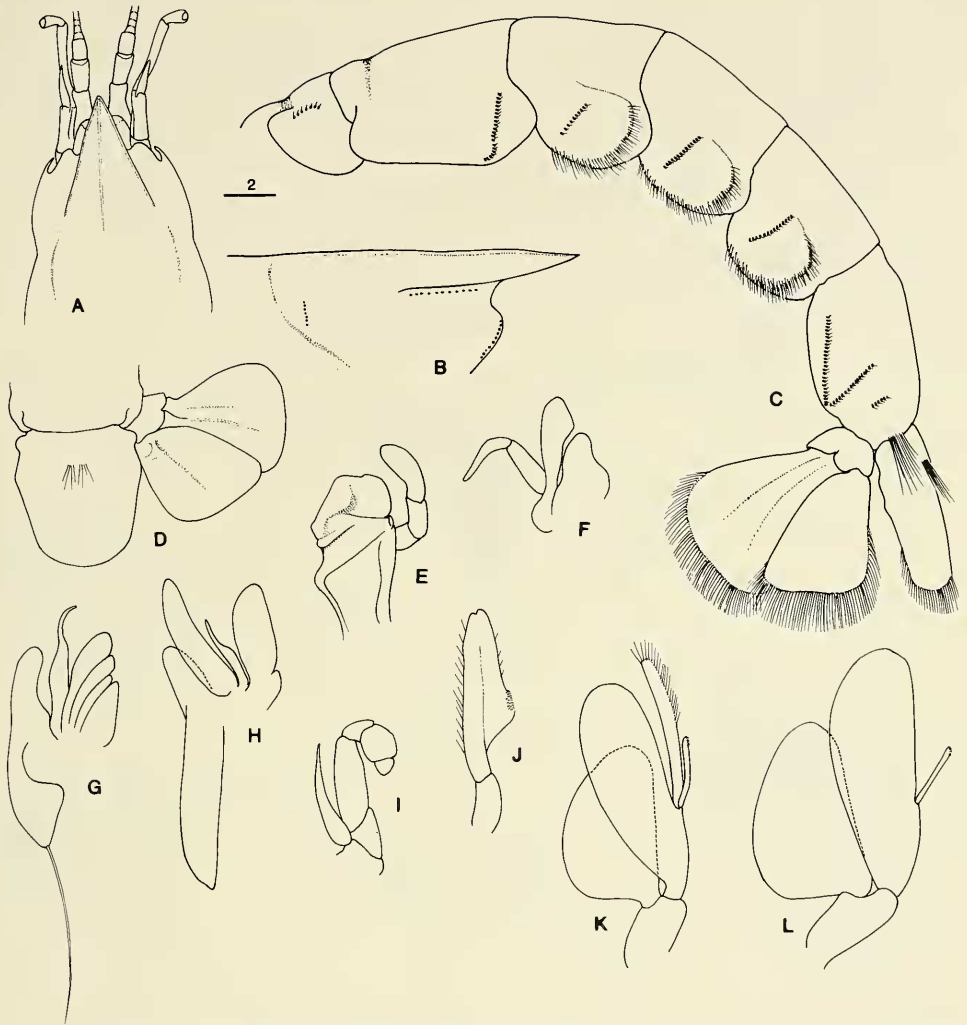


Fig. 11. *Meticonaxius bouvieri*: A, Anterior carapace in dorsal view, scale in mm; B, Anterior carapace in lateral view; C, Abdomen in lateral view; D, Telson and right uropod; E, Mandible; F, Maxilla 1; G, Maxilla 2; H, Maxilliped 1; I, Maxilliped 2; J, Pleopod 1, male; K, Pleopod 2, male; L, Pleopod 3.

Meticonaxius capricorni Coelho, 1987

Meticonaxius capricorni Coelho, 1987:63, 68, figs. 1–3.

Records.—Off Rio de Janeiro and São Paulo states, Brazil, 139–214 m.

Diagnosis.—[Abbreviated; taken from Coelho 1987]: Rostrum subacute, carinate, carina reaching posteriorly onto gastric region of carapace, no raised triangular region. Pleuron of abdominal somite 1 ventrally

spinose. Abdominal somites 3–5 having lateral areas of dense setation. Telson basally slightly wider than long, $\frac{3}{4}$ length of abdominal somite 6.

Maxilliped 3, merus with spine on posterior margin. Pereopod 1, merus with small tooth on posterior margin at about mid-length. Pereopod 2, merus lacking spine. Lateral uropodal ramus distally broadened, but not distolaterally produced; mesial ramus distolaterally produced.

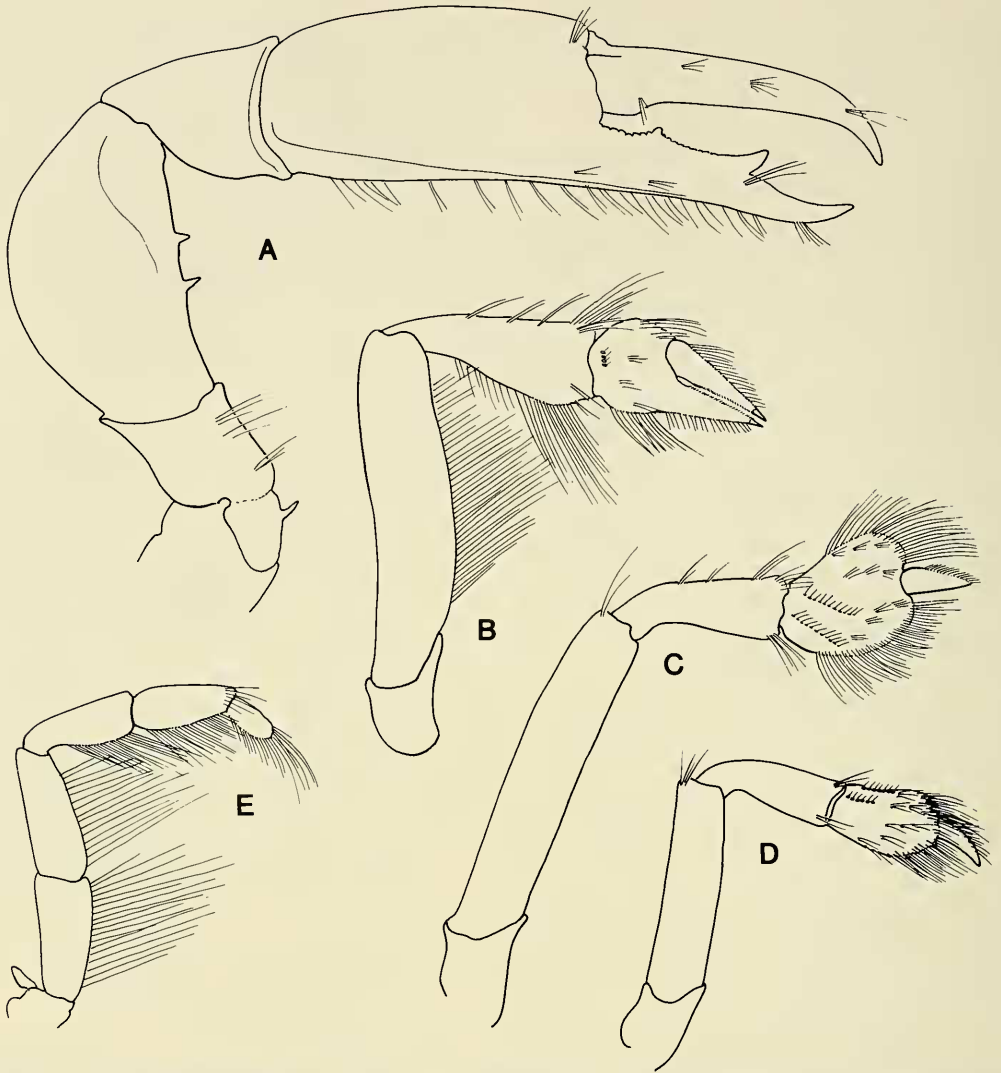


Fig. 12 *Meticonaxius bowieri*: A, Pereopod 1; B, Pereopod 2; C, Pereopod 3; D, Pereopod 4; E, Maxilliped 3.

Meticonaxius longispina

(Stebbing, 1920)

Fig. 13, Table 1F

Axius longispina Stebbing, 1920:265, pls. 106B, 107.

Meticonaxius ?longispina: De Man, 1925:5.

Meticonaxius longispina: Barnard, 1950: 500, fig. 93a-c.—Kensley, 1981:30.—Coelho, 1987:63.

Material examined.—SAM-A2754, juv. ♂ cl 3.8 mm. Pieter Faure sta 13039, off East London, South Africa, 91 m.

Records.—Off Cape Morgan (Indian Ocean), South Africa, 95 m.

Diagnosis.—Carapace with rostral apex broadly rounded, margin faintly crenulate; median carina a rounded ridge; lateral carina entire. Abdominal pleuron 1 ventrally acute; pleura 2–6 ventrally broadly convex;

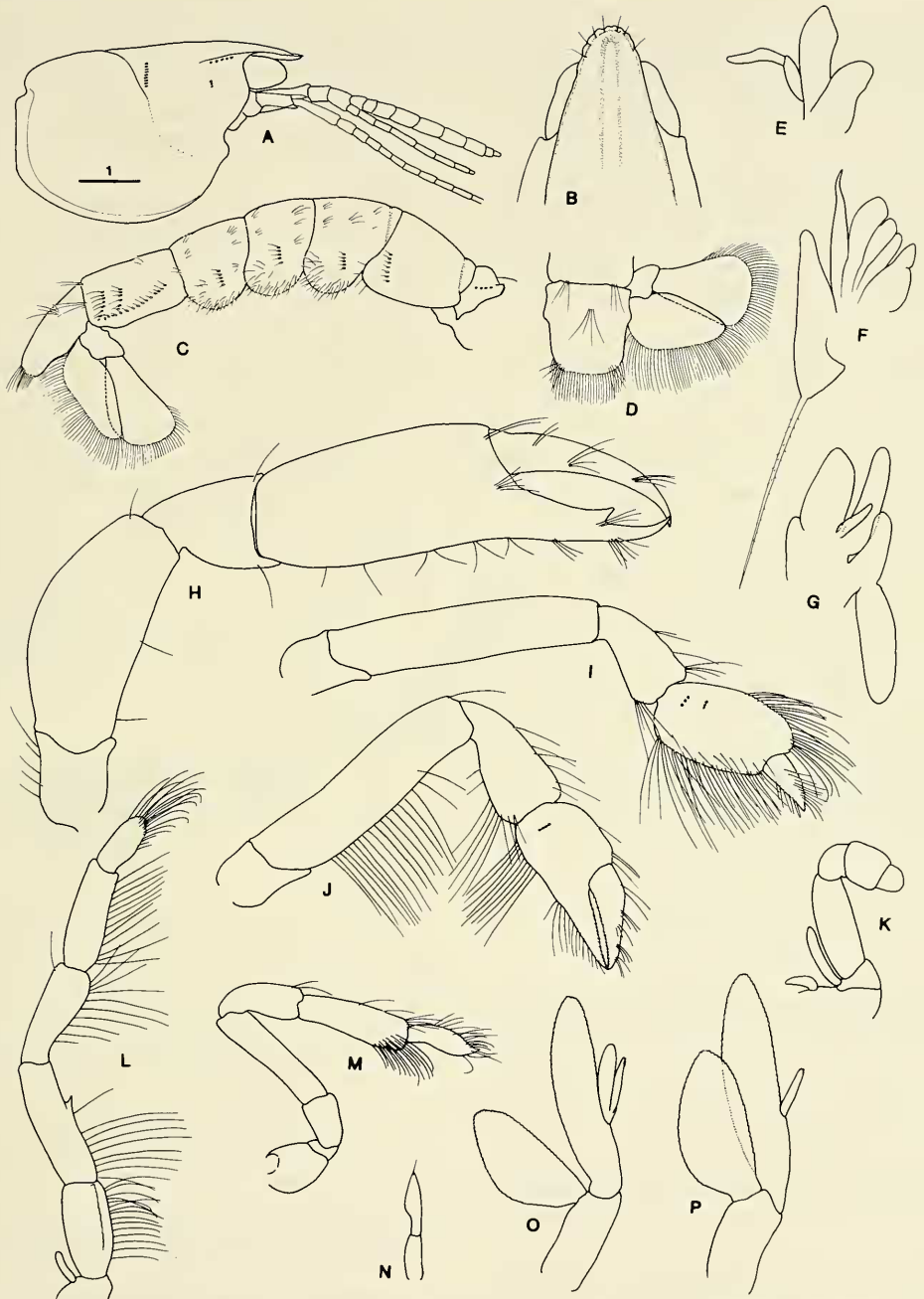


Fig. 13. *Meticonaxius longispina*: A, Carapace in lateral view, scale in mm; B, Rostrum and eyes in dorsal view; C, Abdomen in lateral view; D, Telson and right uropod; E, Maxilla 1; F, Maxilla 2; G, Maxilliped 1; H, Pereopod 1; I, Pereopod 3; J, Pereopod 2; K, Maxilliped 2; L, Maxilliped 3; M, Pereopod 5; N, Pleopod 1, male; O, Pleopod 2, male; P, Pleopod 3.

pleura 1–5 each bearing short row of setose tubercles; pleura 3–5 posteroventrally finely setose; pleuron 6 with longitudinal, and 2 short posterior vertical rows of setose tubercles.

Antennal acicle about $\frac{1}{3}$ length of peduncle article 4. Maxilliped 2 with short exopod; maxilliped 3 having merus with single strong non-articulating spine on posterior (mesial) margin; ischial crest having very low teeth; exopod reduced, less than half length of ischium. Pereopod 1, chelae symmetrical; ischium, merus, and carpus unarmed; fingers shorter than propodal palm, fixed finger with single strong triangular tooth slightly beyond midlength of cutting edge; cutting edge of dactylus unarmed. Pereopod 2, merus unarmed; propodal palm somewhat expanded, short proximal setal row on lateral surface. Pereopod 3, propodus with 2 short setal rows on lateral surface. Uropodal rami distally expanded, lateral ramus evenly so, mesial ramus with distolateral part produced more than distomesial; both rami lacking spines. Telson longer than basal width, lacking both articulating and non-articulating spines.

Meticonaxius microps (Bouvier, 1905)

Fig. 14, Table 1G

Metaxius microps Bouvier, 1905:804; 1925:469, fig. 29.—De Man, 1925:1, 2, 8; 1928:18, 20, 21, 30.—Balss, 1925:210.—Schmitt, 1935:192, fig. 53.—Balss, 1957:1582.—Coelho, 1987:63.

Material examined.—Holotype, MCZ, ♂ cl 3.2 mm, Blake sta 132, off St. Croix, 210 m.

Diagnosis.—Carapace with rostrum triangular, apically narrowly rounded, with several short marginal setae, margins entire and continuing as entire lateral carina, with broadly rounded median ridge widening posteriorly; subvertical setal row just anterior to cervical groove, plus less compact setal row immediately ventral to lateral carina. Abdominal pleuron 1 with horizontal

setal row, ventrally rounded; pleura 2–5 ventrally broadly rounded, each with short vertical row of setose tubercles; pleura 3–5 posteroventrally setose; pleuron 6 with 1 horizontal and 2 vertical rows of setose tubercles.

Eye with cornea faintly demarked, eye-stalk conical, shorter than rostrum. Antennal acicle about $\frac{1}{3}$ length of peduncle article 4. Maxilliped 2 with reduced exopod; maxilliped 3 lacking exopod. Pereopod 1 (only left cheliped present), merus with small tooth in distal half of posterior margin, fingers shorter than propodal palm, fixed finger with low triangular tooth with midlength of cutting edge; cutting edge of dactylus unarmed. Uropod, both rami distally widened, bearing fringe of plumose setae on distal margins, lacking spines; mesial ramus with distolateral corner produced. Telson lacking spines, longer than basal width, posterior margin convex and bearing fringe of plumose marginal setae.

Meticonaxius minutus Coelho, 1973

Meticonaxius minutus Coelho, 1973:345; 1987:63, 68.—Coelho & Ramos-Porto, 1987:32.

Records.—Northern Brazil, off Amapá, 89 m; off Cabo Caciporé and Cabo Norte, 89–91 m.

Diagnosis.—[Abbreviated; taken from Coelho 1973:345, and 1987, Table 1]: Rostrum not reaching beyond article 2 of antennal peduncle, with raised triangular region; anterior margin with fringe of setae. Gastric region not carinate. Cornea situated at median part of ocular peduncle. Antennal acicle short. Pleuron of abdominal somite 1 lacking spine. Abdominal somites 3–5 each with lateral area of dense setation. Telson $\frac{3}{4}$ length of abdominal somite 6.

Meticonaxius monodon De Man, 1905

Fig. 15, Table 1H

Meticonaxius monodon De Man, 1905:593; 1925:5, 54, fig. 10; 1928:20, 21, 30.—Balss, 1925:210.—Coelho, 1987:63.

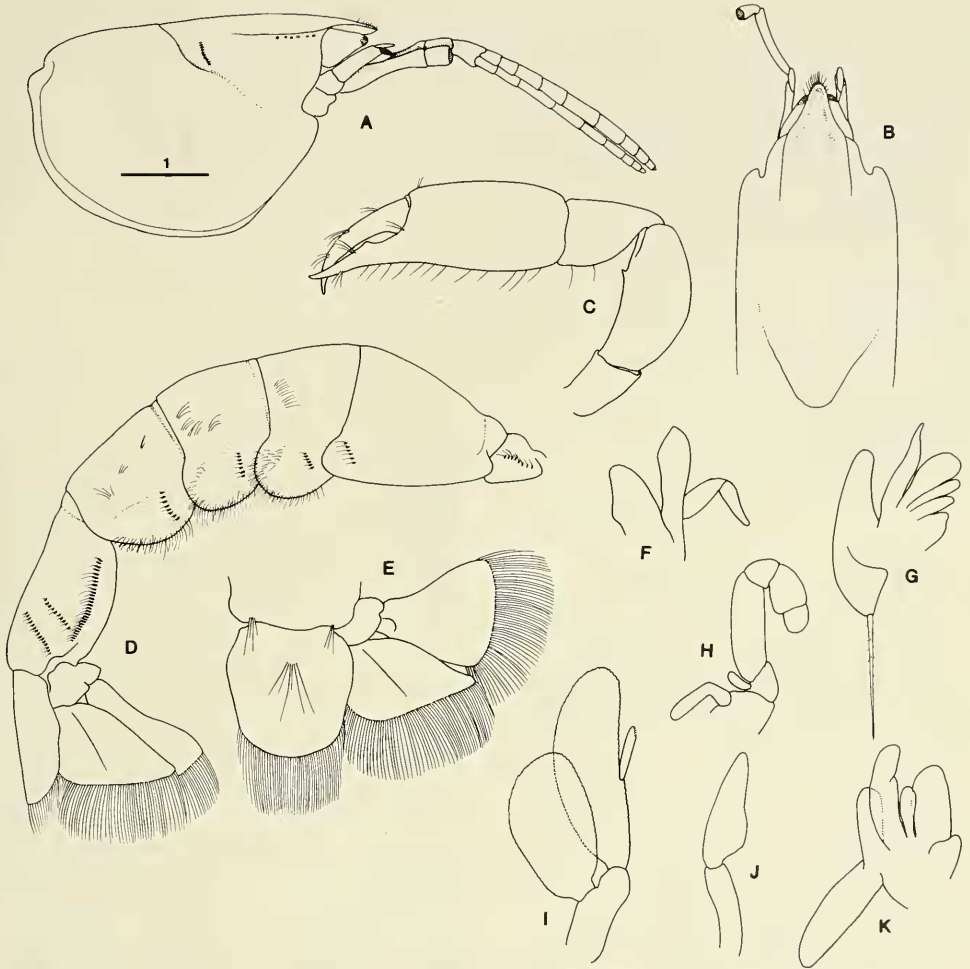


Fig. 14. *Meticonaxius microps*, holotype: A, Carapace in lateral view, scale in mm; B, Anterior carapace in dorsal view; C, Pereopod 1; D, Abdomen in lateral view; E, Telson and right uropod; F, Maxilla 1; G, Maxilla 2; H, Maxilliped 2; I, Pleopod 3; J, Pleopod 1, male; K, Maxilliped 1.

Callianassa (?*Scallasis*) *coeca* Balss, 1925: 212, fig. 16.—De Man, 1928:30.

Material examined.—Holotype, RMNH, ♀ (carapace damaged), north-east of Java, 330 m.

Diagnosis.—Carapace with rostrum apically acute, lacking marginal spines (single subapical spine on left side in holotype perhaps due to injury); median carina entire, rounded ridge; lateral carina entire. Abdominal pleura 1–5 each bearing vertical setal row, pleuron 6 with one longitudinal, and 2 short posterior setal rows; pleuron 1

ventrally narrowly rounded, pleura 2–6 ventrally broadly rounded; pleura 3–5 with posterior part of pleura and dorsolateral part of tergum densely setose.

Antennal acicle reaching slightly beyond midlength of peduncle article 4. Maxilliped 2 with short exopod; maxilliped 3 having very reduced exopod, merus with single distal spine on mesial margin; ischial crest with well defined teeth. Pereopod 1, chelae symmetrical; ischium unarmed; merus with single strong non-articulating spine on posterior margin; carpus and propodal palm smooth, unarmed; fingers shorter than pro-

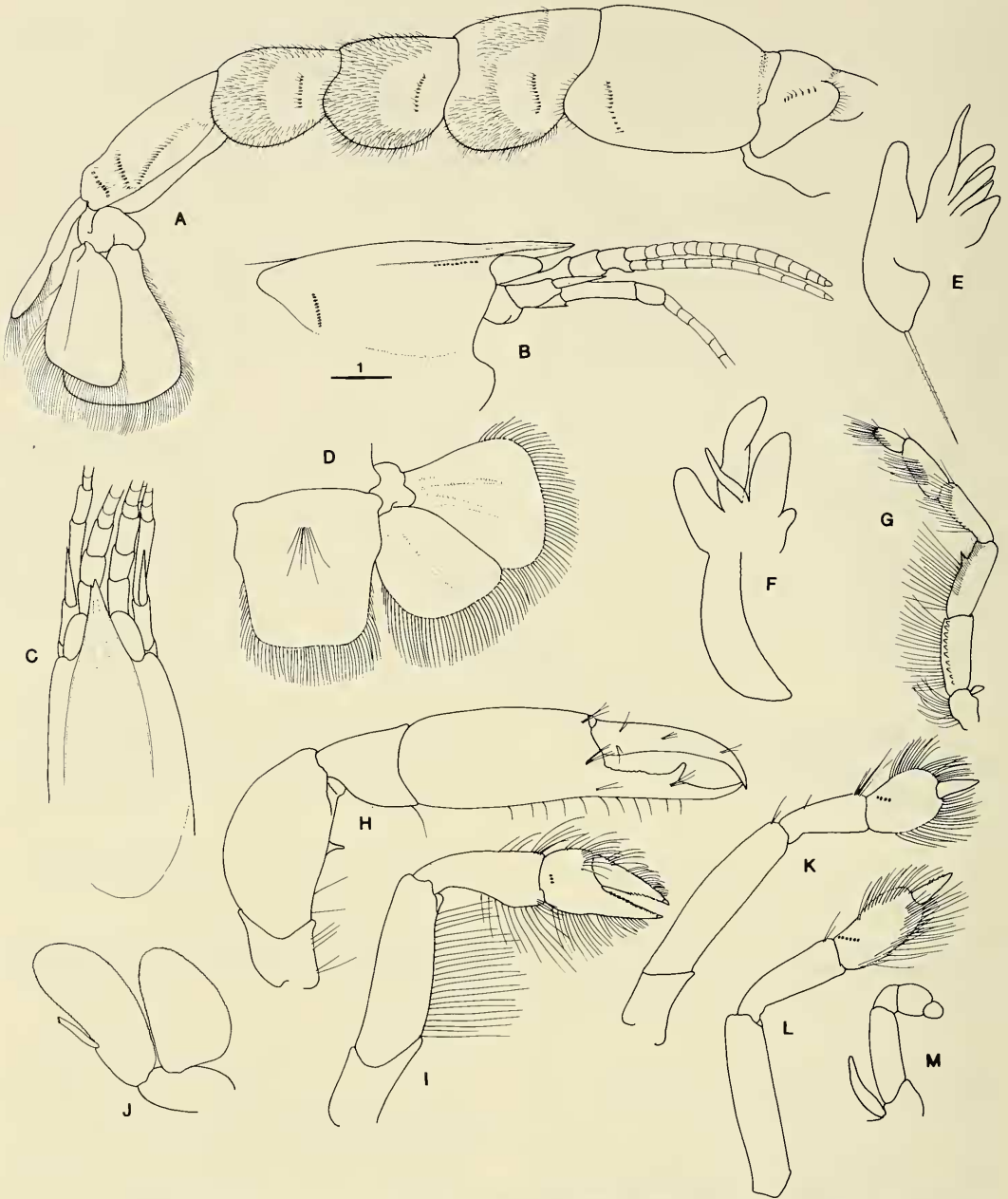


Fig. 15. *Meticonaxius monodon*, holotype: A, Abdomen in lateral view; B, Anterior carapace in lateral view, scale in mm; C, Anterior carapace in dorsal view; D, Telson and right uropod; E, Maxilla 2; F, Maxilliped 1; G, Maxilliped 3; H, Pereopod 1; I, Pereopod 2; J, Pleopod 2; K, Pereopod 3; L, Pereopod 4; M, Maxilliped 2.

podal palm, fixed finger with strong triangular tooth at midlength of cutting edge, dactylar cutting edge entire. Pereopod 2, merus lacking spines; propodal palm some-

what expanded, with very short setal row proximally on lateral surface. Pereopod 3, propodus somewhat expanded, with single setal row on lateral surface. Pereopod 4,

propodus with single oblique setal row proximally on lateral surface. Uropod with both rami distally expanded and bearing plumose marginal setae, lacking articulating and non-articulating spines. Telson having posterior margin broad, truncate, lacking median, dorsal, and marginal spines.

Michelea, new genus

Type species.—By present designation, *Callianidea vandoverae* Gore, 1987.

Gender.—Feminine.

Diagnosis.—Carapace with 4 setal rows anterior to cervical groove; rostrum short, bluntly triangular; linea thalassinica lacking. Abdominal somites 1–5 each with single setal row; abdominal somite 6 with 2 setal rows. Abdominal somite 1 with lateral anteriorly-directed lobe. Eye distally rounded, cornea poorly defined. Article 1 of antennular peduncle about 1/2 carapace length. Article 4 of the antennal peduncle about 1/3 carapace length. Antennal scale spiciform, from 1/2 to 1/4 length of peduncle article 4. Lateral epistome with cluster of short setae. Maxilliped 3 pediform, ischium bearing dentate crest; exopod not reduced. Pereopod 1, chelipeds subequal, similar in male and female; merus with anterior margin strongly rounded, posterior margin straight, with fixed tooth at about midlength. Pereopod 2 with proximal setal row on lateral surface of propodus. Pereopod 3 with 2 short proximal setal rows on lateral surface of propodus; latter flattened and somewhat expanded. Pereopod 4 with short proximal setal row on lateral surface of propodus. Respiratory lamellae present on one or both pleopodal rami, lamellae unbranched, of 1 or 2 articles. Uropodal rami lacking suture; lateral ramus not bilobed.

Etymology.—The genus is named for Michèle de Saint Laurent of the Muséum National d'Histoire Naturelle, Paris, renowned carcinologist and respected colleague.

Remarks.—*Callianidea lepta* Sakai, 1987,

from Okinawa Island, Japan, differs from *Michelea vandoverae* only in having a much smaller spine on the ischium and merus of pereopod 1, and in lacking any branchial filaments on the pleopodal exopods; it should be included in the genus *Michelea*.

Callianidea leura Poore & Griffin, 1979, from Queensland, Australia, differs from *M. vandoverae* in having simple (not biarticulate) branchial filaments on the pleopods, and in having a reduced exopod on maxilliped 2. It does have article 1 of the antennular peduncle and article 4 of the antennal peduncle elongate and the chelipeds of pereopod 1 subequal, but whether a reduced pleurobranch is present above pereopod 4, is unknown.

Key to Species of *Michelea*

- 1. Respiratory lamellae present on both rami of pleopods 2–5 2
- Respiratory lamellae present only on endopods of pleopods 2–5 *M. lepta*
- 2. Respiratory lamellae of pleopods each of single article 3
- Respiratory lamellae of pleopods each of 2 articles *M. vandoverae*
- 3. Pleopodal exopods bearing few (2–3) respiratory lamellae .. *M. pillsburyi*
- Pleopod exopods bearing many respiratory lamellae along most of margin 4
- 4. Thoracic gills strikingly reduced; Pleopodal endopods with proximal spiral lamellae-bearing lobe *M. lamellosa*
- Thoracic gills normal, not reduced; Pleopodal endopods lacking basal lobe *M. leura*

Michelea lamellosa, new species

Figs. 16, 17, Table II

Material.—Holotype, USNM 243468, ♀ cl 9.6 mm, *Pillsbury* sta P-1215, off Jamaica, 17°36.3'N, 77°02.6'W, 24 m.

Description.—Carapace with cervical groove reaching dorsal midline in posterior

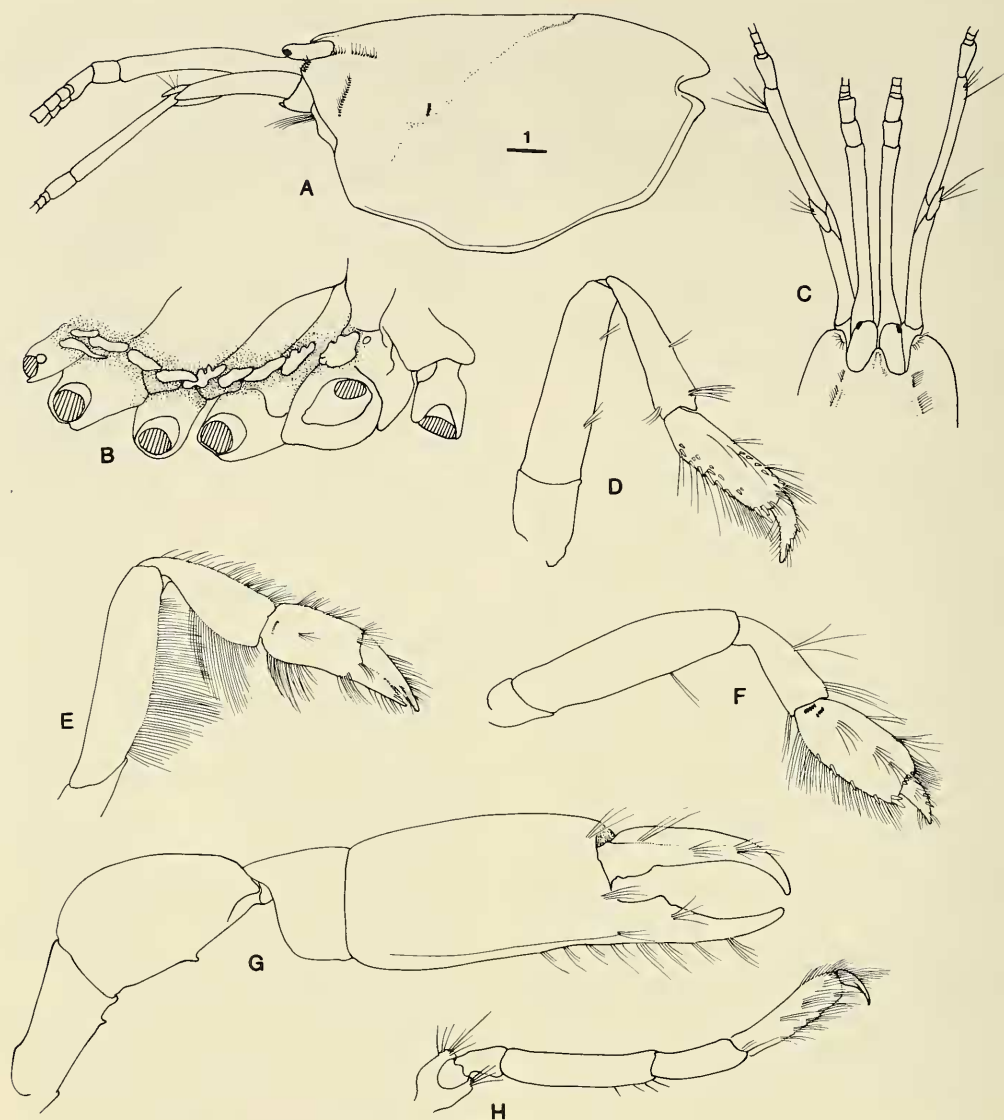


Fig. 16. *Michelea lamellosa*, holotype: A, Carapace in lateral view, scale in mm; B, Left branchial chamber, brachiolegite removed, showing reduced branchiae; C, Anterior carapace, with eyes, and bases of antennules and antennae; D, Pereopod 4; E, Pereopod 2; F, Pereopod 3; G, Pereopod 1; H, Pereopod 5.

half, faintly demarked laterally. Rostrum triangular, with short low middorsal ridge. Row of setal pits on antennal lobe, horizontal row posterior to orbit, subvertical row in postantennal region, shorter vertical row close to lateral cervical groove.

Eyestalk rounded, cornea somewhat demarked, situated distolaterally. Antennular

peduncle article 1 elongate-slender, almost reaching midlength of antennal peduncle article 4. Antennal peduncle with acicle short, spiciform, about $\frac{1}{4}$ length of article 4; article 2 somewhat elongate; article 4 elongate-slender, almost 4 times length of article 5. Lateral epistome with band of short setae reaching anteriorly just beyond antennal ar-

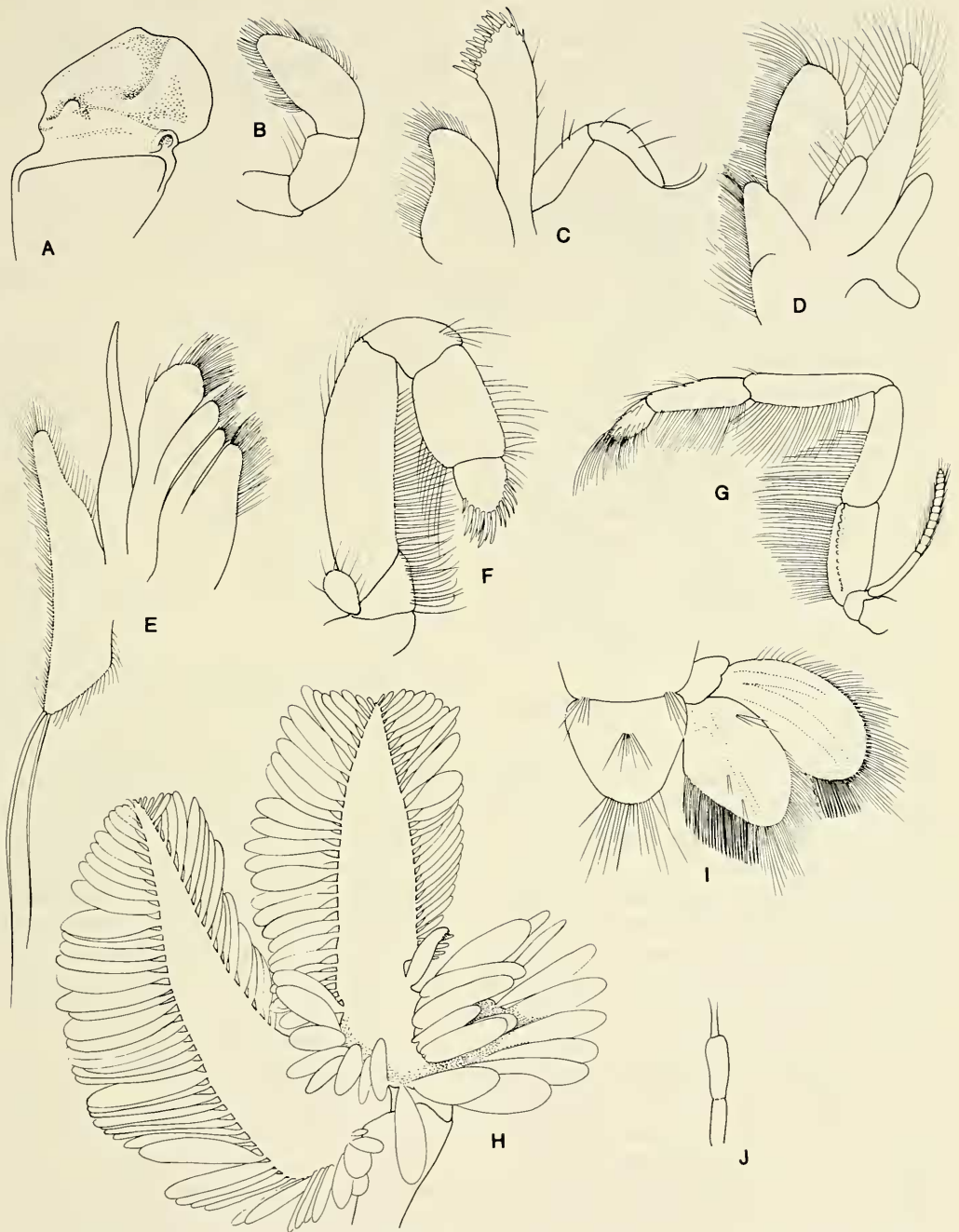


Fig. 17. *Michelea lamellosa*, holotype: A, Mandible; B, Mandibular palp; C, Maxilla 1; D, Maxilliped 1; E, Maxilla 2; F, Maxilliped 2; G, Maxilliped 3; H, Pleopod 2, female; I, Telson and right uropod; J, Pleopod 1, female.

ticle 1. Mandibular incisor with 2 blunt cusps; molar with 2 blunt mesial tubercles; palp of 3 articles, distal article longest, setose. Remainder of mouthparts as figured. Maxilliped 1, endopod of single short article. Maxilliped 2, exopod reduced to short subcircular lobe bearing few setae. Maxilliped 3, posterior margin of merus unarmed. Pereopod 1, chelipeds subequal, ischium with small distal tubercle on posterior margin; merus with small tubercle at about midlength of posterior margin; fingers about $\frac{2}{3}$ length of propodal palm, fixed finger with single triangular cusp proximally on cutting edge; dactylus with cutting edge bearing low truncate tubercle proximally, remainder of edge entire. Pereopod 3, propodus flattened, twice longer than wide, with row of 5 spines on posterior margin including posterodistal spine. Pereopod 4, propodus bearing clusters of spines along posterior margin, row of spines along anterior margin. Gills within branchial chamber very reduced, epipods lacking on pereopods.

Pleopod 1 of female uniramous, of 2 articles. Pleopods 2–5 with free appendix interna; bearing densely packed marginal uniarticulate lamellae; endopod proximomesially produced into spiral lobe also bearing lamellae. Pleuron 1 bearing oblique row of setal pits; pleuron 2 with vertical row of setal pits on posterolateral lobe; pleura 3–6 each with vertical row of setal pits at about midlength. Uropodal outer ramus bearing marginal setae plus row of short corneous spines along distolateral margin; both rami bearing dense thickened golden setae-spines along mesial margin. Telson basal width greater than middorsal length, posterior margin broadly rounded, setose.

Etymology.—The specific epithet refers to the lamellate nature of the pleopodal respiratory filaments.

Michelea pillsburyi, new species

Figs. 18, 19, Table 1J

Material.—Holotype, USNM 243469, ♀ cl 3.6 mm, Caribbean off Panama, *Pillsbury*

sta P-416, 9°22.6'N, 78°08.4'W, 59 m, 19 Jul 1966.—Paratype, USNM 243470, ♀ cl 4.4 mm, off Atlantic Panama, *Pillsbury* sta P-420, 9°30.5'N, 78°26.0'W, 28 m, 19 Jul 1966.

Description.—Carapace with cervical groove weak, not reaching dorsal midline; rostrum short, triangular. Row of setal pits on antennal lobe, longitudinal row posterior to orbit, few subvertical pits in post-antennal region.

Eyestalk rounded, cornea not demarked. Antennular peduncle article 1 elongate-slender, reaching distally to proximal third of antennal article 4. Antennal peduncle with acicle spiciform, about $\frac{1}{4}$ length of peduncle article 4; latter elongate-slender, almost 4 times length of article 5. Lateral epistome lacking setae. Mandibular incisor with 2 blunt cusps; molar with 3 mesial rounded tubercles; palp of 3 articles, distal article longest, setose. Remainder of mouthparts as figured. Maxilliped 1, endopod of single short article. Maxilliped 2, exopod reduced to short lobe bearing few setae. Maxilliped 3, merus with strong distal spine on posterior margin. Pereopod 1, chelipeds sub-similar, equal in length, chela of one slightly wider than other; ischium with strong spine in distal half of posterior margin; merus with strong spine at about midlength of posterior margin; fingers about $\frac{5}{6}$ length of propodal palm, cutting edge of fixed finger with 3 low evenly-spaced teeth; cutting edge of dactylus entire. Pereopod 3, propodus about 3 times longer than wide, flattened. Pereopod 4, propodus with 3 spines on posterior margin, including distalmost spine. Pereopod 5, propodus with strong posterodistal spine. Pleopod 1 of female uniramous, with faint constriction indicating 2 fused articles. Pleopods 2–5 with free appendix interna, endopod bearing uniarticulate lamellae along lateral margin, exopod bearing 2–3 distal lamellae on lateral margin, remainder of margin setose. Uropodal lateral ramus with small spine on lateral margin, latter setose and bearing row of short corneous

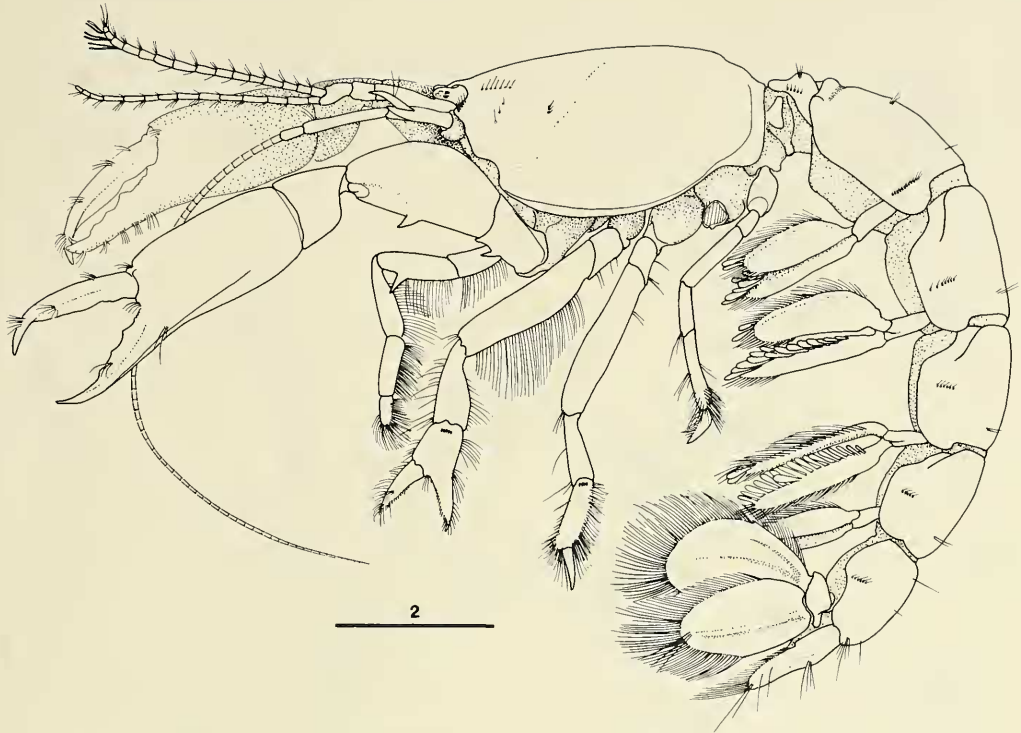


Fig. 18. *Michelea pillsburyi*, holotype, lateral view, scale in mm.

spines; inner ramus bearing numerous marginal setae. Telson length equal to greatest width, posterior margin broadly rounded, setose.

Etymology.—The specific epithet refers to the Research Vessel *Pillsbury*, from which this, and much other valuable crustacean material was collected.

Michelea vandoverae (Gore, 1987)

Figs. 20, 21, Table 1K

Callianidea vandoverae Gore, 1987:186, figs. 1–4.

Material.—USNM 211492, Gulf of Mexico MAFLA sta 2211, 27°56'29.5"N, 83°52'59.5"W, 43 m, coarse sand: sample 2211 A23, ♀ cl 5.7 mm, ♂ cl 4.1 mm; sample 2211 C, juv. cl 2.8 mm; sample 2211 E, ♀ cl 6.2 mm; sample 2211 F22, ♂ cl 6.0 mm; sample 2211 31H, ♂ cl 9.0 mm; sample 2211-07, ♀ cl 10.0 mm.—USNM 211493, Gulf of

Mexico, MAFLA sta 2528, 29°54'58.6"N, 86°04'58.5"W, 37 m, coarse sand: sample 2528H, ♂ cl 5.5 mm.

Description.—Cervical groove at about midlength of carapace, reaching dorsal midline. Rostrum moderately well developed, broadly triangular, with 2 low teeth on lateral margin. Irregular row of setal pits in position of lateral carina, short row on antennal lobe, subvertical row in postantennal region, short vertical row just anterior of cervical groove.

Eyestalk rounded, cornea not defined. Antennular peduncle article 1 elongate-slim, reaching distally to about midlength of antennal article 4. Antennal acicle spiciform, almost half length of elongate article 4. Lateral epistome bearing cluster of short setae, not reaching anteriorly beyond level of basal antennal article. Mandibular incisor having 2 blunt cusps; molar with 3–4 rounded tubercles mesially; palp of 3 ar-

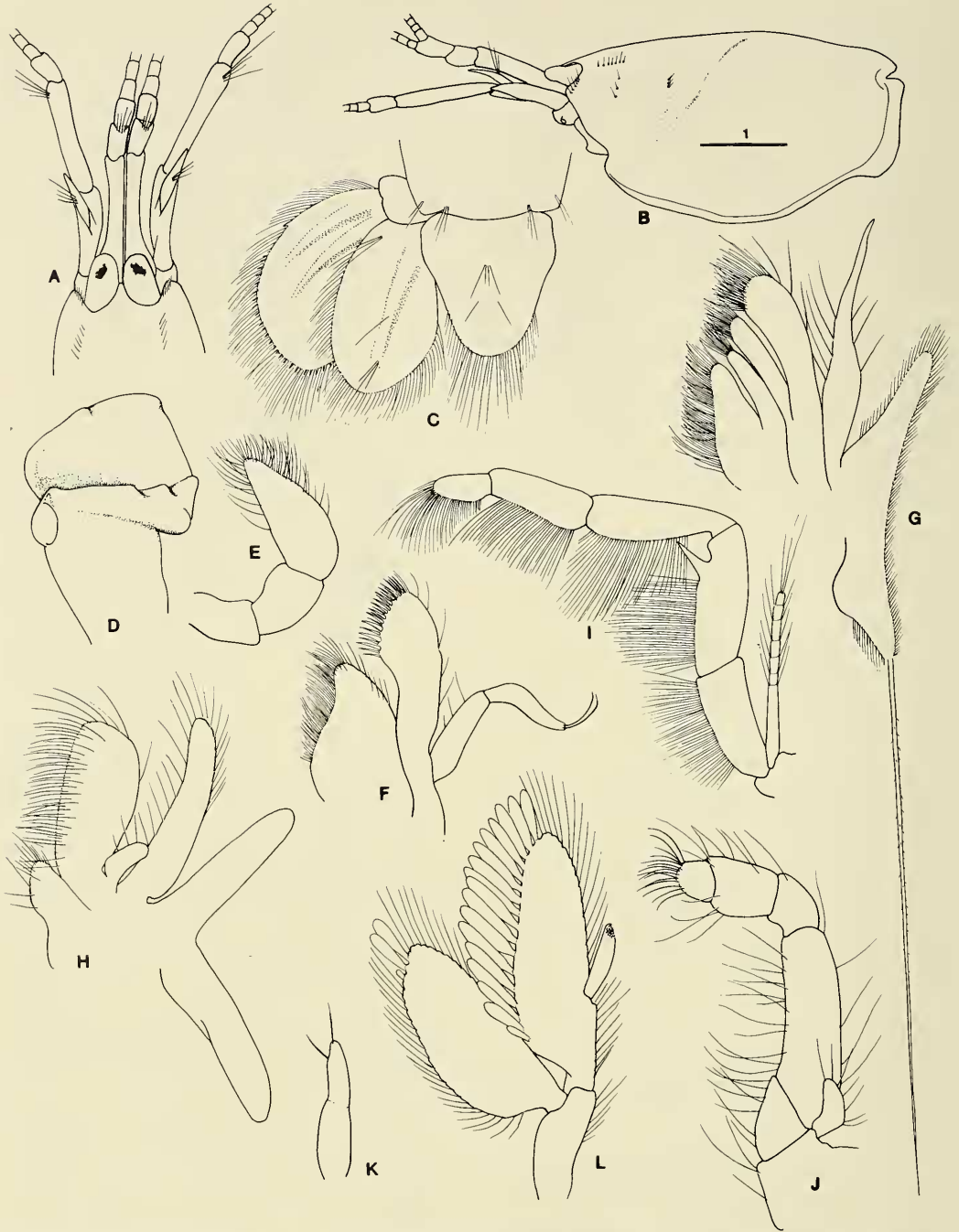


Fig. 19. *Michelea pillsburyi*, paratype: A, Anterior carapace, with eyes, and bases of antennules and antennae; B, Carapace in lateral view, scale in mm; C, Telson and left uropod; D, Mandible; E, Mandibular palp; F, Maxilla 1; G, Maxilla 2; H, Maxilliped 1; I, Maxilliped 3; J, Maxilliped 2; K, Pleopod 1, female; L, Pleopod 2, female.

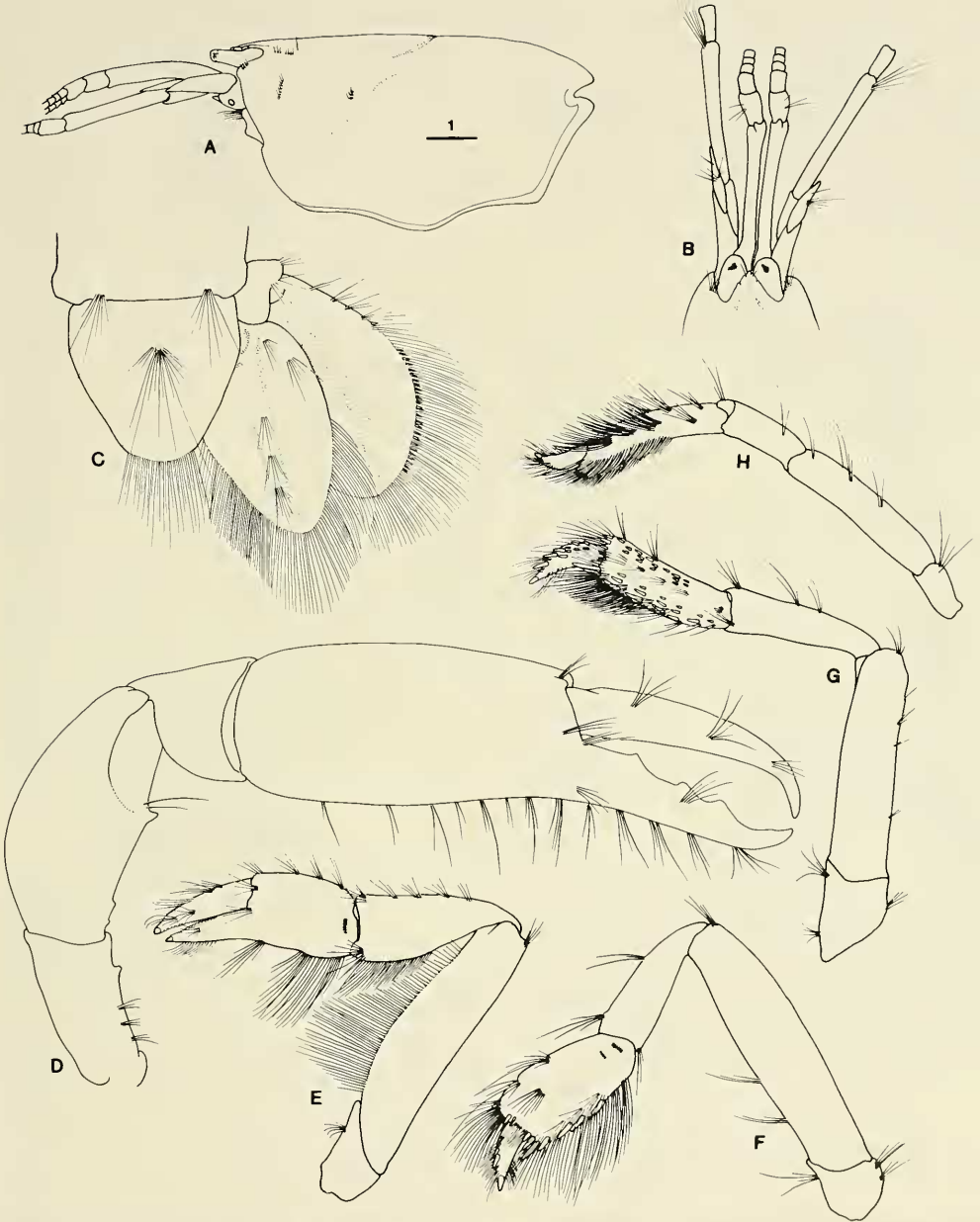


Fig. 20. *Michelea vandoverae*: A, Carapace in lateral view, scale in mm; B, Anterior carapace, eyes, and bases of antennules and antennae; C, Telson and right uropod; D, Pereopod 1; E, Pereopod 2; F, Pereopod 3; G, Pereopod 4; H, Pereopod 5.

ticles, distal article longest, setose. Remainder of mouthparts as figured. Maxilliped 1, endopod with tiny distal article. Maxilliped 2, exopod well developed, with distal seg-

mented flagellum. Maxilliped 3, merus with strong distal spine on posterior margin. Pereopod 1, chelipeds subsimilar, of equal length, propodus slightly broader in one; is-

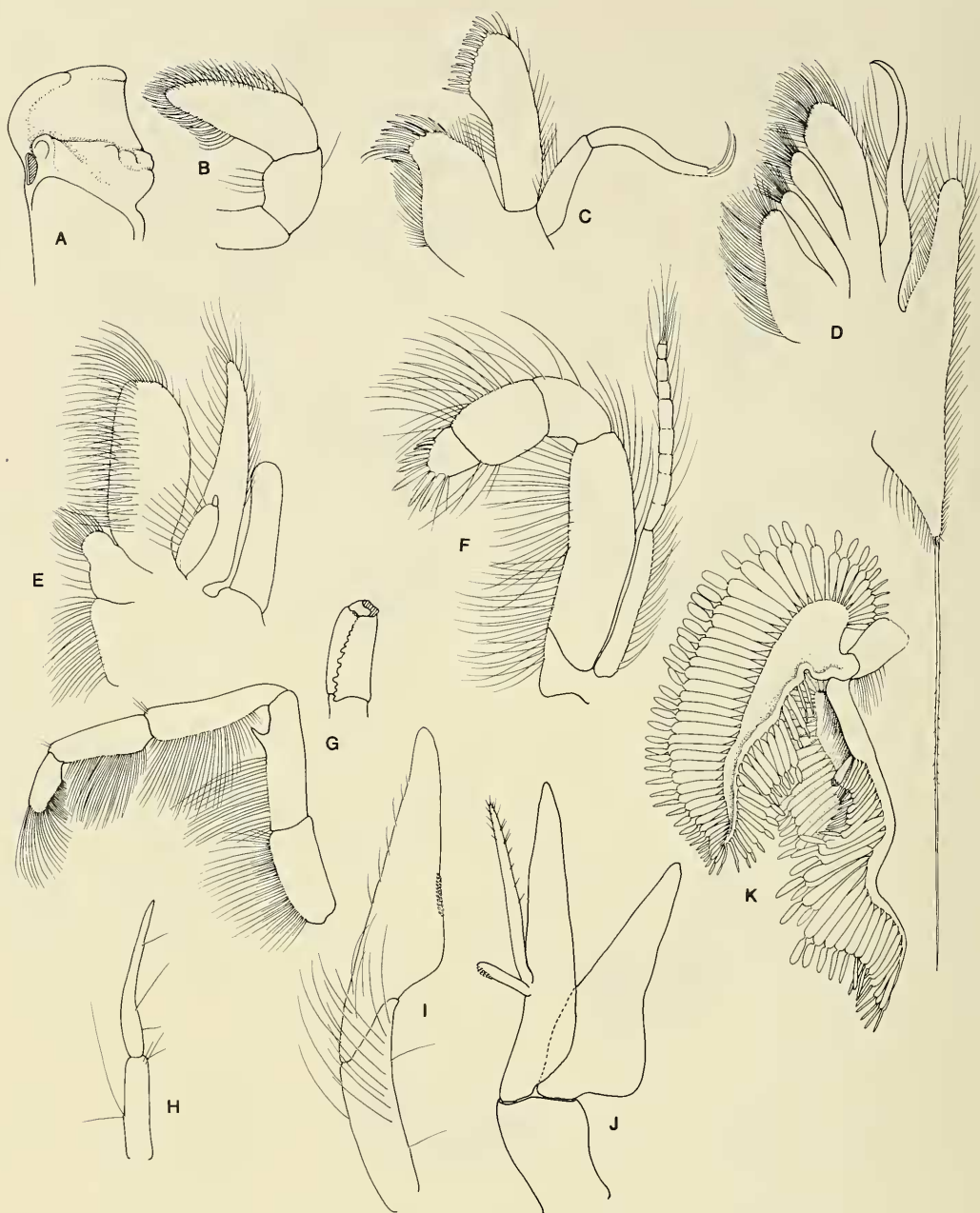


Fig. 21. *Michelea vandoverae*: A, Mandible; B, Mandibular palp; C, Maxilla 1; D, Maxilla 2; E, Maxilliped 1; F, Maxilliped 2; G, Maxilliped 3 with mesial view of ischium; H, Pleopod 1, female; I, Pleopod 1, male; J, Pleopod 2, male; K, Pleopod 3.

chium with 2-3 distal blunt tubercles on posterior margin; merus with single moderately strong blunt spine on posterior margin; propodal palm about one-third longer

than fingers, cutting edge of fixed finger with 3 evenly-spaced low triangular teeth; dactylus entire or with low proximal tubercle. Pereopod 3, propodus moderately broad,

flattened, greatest width about $\frac{1}{2}$ length, with several spines along posterior and distal margins but not subchelate. Pereopod 4, lateral surface of propodus and dactylus spinose.

Pleopod 1 of female uniramous, of 2 articles, distal article about 1.5 times length of proximal, slender and tapering. Pleopod 1 of male with cluster of tiny hooks on mesial margin of triangular distal article. Pleopod 2 of male with appendix interna and appendix masculina situated at about proximal third of endopod; slender tapering appendix masculina with lateral and distal setae, about 3 times longer than appendix interna. Pleopods 2–5, both rami bearing marginal biarticulate flattened lamellae. Outer uropodal ramus with small non-corneous spine on outer margin just short of midlength, row of tiny corneous marginal spines on outer margin from about midlength to just short of apex; both rami with marginal setae becoming denser and thickened proximomesially. Telson length equal to greatest width, broadly rounded posterior margin setose.

Mictaxius, new genus

Type species.—By present designation, *Mictaxius thalassicola*, new species.

Gender.—Masculine.

Diagnosis.—Carapace lacking carinae; cervical groove barely distinguishable; with linea thalassinica reaching from anterior margin in region of eye to posterior margin; row of setal pits present in anterolateral region; rostrum barely demarked, a low convexity at base of eyestalks. Abdominal somite 1 lacking anteriorly-directed lobes; somites 1–6 each with short setal row.

Eyestalk distally pointed, cornea poorly defined, situated subapically, moderately pigmented. Antennal acicle reduced to small immobile scale. Mandibular incisor toothed. Maxillipeds 1 and 2 with well developed exopod. Maxilliped 1 endopod of 2 articles. Maxilliped 3 exopod vestigial, dentate ischial crest on mesial surface moderately well

developed. Pereopod 1, chelipeds asymmetrical, not sexually dimorphic. Pereopods 2–4 each with very short setal row. Propodus of pereopod 3 expanded, subcircular. Pereopods 3–5, dactyli simple. Pleopodal rami somewhat expanded, 2–3 times longer than greatest width; appendix interna present on pleopods 2–5. Pleopod 1 in male absent. Pleopod 1 in female uniramous, of 2 articles. Pleopod 2 in male, appendix masculina and appendix interna fused, resultant lobe-like structure bearing both hooks and elongate setae distally. Telson broader than long, semicircular in outline, lacking spines. Lateral uropodal ramus bilobed, lacking transverse suture.

Etymology.—The generic name is a combination of the Greek 'miktos,' a mixture, and the frequently-used thalassinidean suffix 'axius,' and refers to the seeming mix of callianassid and callianideid features found in the type and only species of this genus.

Remarks.—*Mictaxius* shows several features thought to be advanced amongst the callianideids: antennal acicle very reduced; eyestalk flattened; maxilliped 3 exopod vestigial; linea thalassinica running the full length of carapace. The genus belongs to that group of callianideids that lack respiratory filaments on the pleopods, but the complete linea thalassinica, the fused appendix masculina and appendix interna, and the bilobed outer uropodal ramus (which features appear in the Callianassidae) immediately separate it from the rest of this group.

Mictaxius thalassicola, new species

Figs. 22, 23, 24, Table 1L

Material examined.—Holotype, USNM 243544, ♂ cl 3.9 mm, Paratypes, 3 ♂ cl 2.5 mm, 3.4 mm, 3.9 mm, ovig. ♀ cl 2.5 mm, 2 ♀ cl 3.1 mm, 3.9 mm, Panama Survey sta 115-4, Pico Feo, Atlantic Panama, in shallow-water *Thalassia* patch, 8 Nov 1972.—Paratypes, USNM 243545, 3 ♂ cl 3.1 mm, 3.1 mm, 4.0 mm, ovig. ♀ cl 3.1 mm, 2 ♀ cl 3.4 mm, 3.4 mm, Panama Survey sta 136-

2, Isla Mira, San Blas Islands, Atlantic Panama, in shallow-water *Thalassia* patch, 8 Apr 1973.

Description.—Carapace lacking definite rostrum, anterodorsal margin with slight median bulge, eyestalks completely exposed. Linea thalassinica running full length of carapace; antennal angle of carapace rounded; subvertical setal row situated posterior to antennal region of anterior carapace; cervical groove barely demarked. Abdomen somewhat bilaterally compressed; somite 1, pleuron tapering posteroventrally to acute triangular lobe, with setal row anterolaterally; somite 2 longest, pleuron ventrally broadly convex, with short setal row posteroventrally; somites 3–6 subequal in length, 3–5 each with short setal row posteroventrally; somite 6 with 2 setal rows. Telson semicircular in outline, basally broader than middorsal length.

Eyestalk tapering to narrowly rounded mesiodistal apex, poorly-defined cornea moderately pigmented, situated distal to midlength. Antennule with 3 peduncle articles subequal in length; flagella subequal in length, dorsolateral flagellum broader than ventromesial flagellum. Antennal peduncle with article 4 longest; acicle reduced to tiny immobile scale. Epistome bearing lateral cluster of elongate setae, latter downcurved distally. Mouthparts as illustrated. Mandibular incisor having 9 serrate marginal teeth; molar poorly developed; palp of 3 articles, distal article longest. Maxilliped 2 with relatively well developed exopod. Maxilliped 3, 5 distal articles strongly setose; dactylus broadly ovate; exopod reduced to tiny digitiform process. Pereopod 1, chelipeds dissimilar; larger chela with posterior margin of ischium finely serrate; propodal palm about 1.8 times length of fingers; fixed finger with single triangular tooth on cutting edge; oblique ridge running from palm onto fixed finger on both lateral and mesial surface; dactylus with cutting edge faintly irregular to entire. Smaller cheliped, propodal palm slightly shorter than fingers; fixed finger with

small tooth in distal half of cutting edge; oblique ridge running from palm to distal fixed finger on both lateral and mesial surface; dactylus with cutting edge entire. Pereopod 2 chelate, cutting edges of propodal finger and dactylus bearing obliquely-set hyaline spines; propodus with very short proximal setal row on lateral surface. Pereopod 3, propodus broadly ovate, posterior margin densely setose and bearing single distal spine, very short proximal setal row on lateral surface; dactylus setose, slightly less than half length of propodus, tapering distally. Pereopod 4, propodus 2.5 times longer than wide, posterior margin strongly setose, with single distal spine, very short proximal setal row on lateral surface; dactylus about $\frac{2}{5}$ length of propodus, strongly setose, tapering distally. Pereopod 5, propodus distally strongly setose; dactylus distally rounded, setose. Pleopod 1 in male absent. Pleopod 1 in female of 2 articles, distal article 1.5 times length of proximal. Pleopod 2 in male with fused appendix masculina/appendix interna articulating at about proximal $\frac{1}{3}$ of mesial margin of endopod, bearing cluster of about 8 elongate terminal setae and subapical clump of hooks. Uropod with lateral ramus broadly bilobed, outer lobe bearing marginal spines on distal margin, remainder of margin setose; mesial ramus broadly ovate, with setose margin.

Etymology.—The specific epithet, meaning 'living in *Thalassia*' refers to the fact that all the specimens were collected in shallow beds of this seagrass.

Thomassinia de Saint Laurent, 1979

Thomassinia de Saint Laurent, 1979:1396.

Type species.—By original designation, *Thomassinia gebioides* de Saint Laurent, 1979.

Gender.—Feminine.

Diagnosis.—[Abbreviated, taken from de Saint Laurent 1979]: Carapace with subvertical setal row anterolaterally; linea thalassinica not reaching posterior margin of

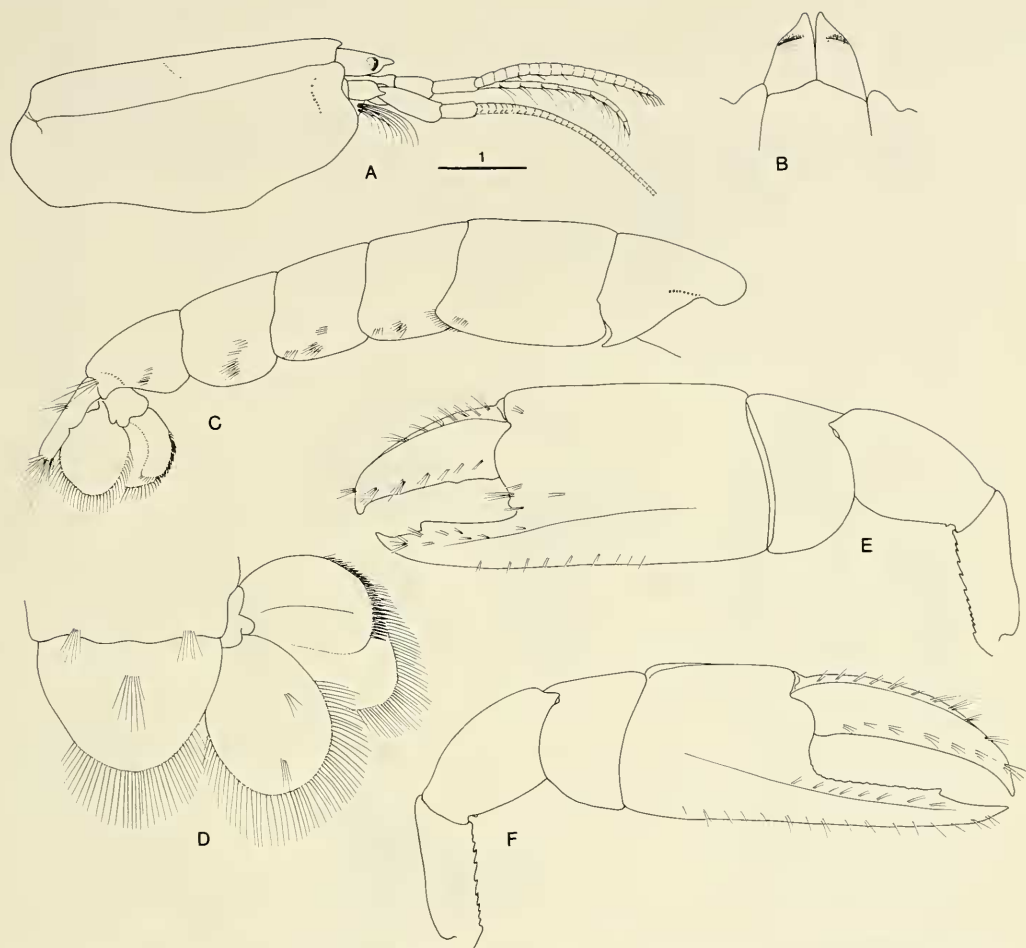


Fig. 22. *Mictaxius thalassicola*: A, Carapace in lateral view, scale in mm; B, Anterior carapace and eyes in dorsal view; C, Abdomen in lateral view; D, Telson and right uropod; E, Pereopod 1, larger cheliped; F, Pereopod 1, smaller cheliped.

carapace; rostrum barely defined, anterodorsal margin of carapace low, triangular. Abdominal somite 1 lacking anteriorly-directed lobes. Antennal acicle vestigial or absent. Mandibular incisor toothed. Maxilliped 2, exopod well developed. Maxilliped 3, articles becoming broadened; exopod vestigial or absent; ischium lacking dentate crest. Pereopod 1, chelipeds subequal. Pereopod 3, propodus broadened. Pleopod 1 in male absent. Pleopods lacking respiratory filaments. Lateral uropodal ramus not bilobed.

Remarks. — *Thomassinia gebioides* de

Saint Laurent, 1979, from Madagascar, has not yet been fully described or illustrated, and with no material available, no further morphological information can be provided.

Discussion

In addition to the 17 species either described or mentioned above, the only other species belonging to the family Callianideidae as defined here is *Callianidea planocula* Melin, 1939, from the Bonin Islands, Japan. (*Callianidea elongata* (Guerin-Méneville,



Fig. 23. *Mictaxius thalassicola*: A, Mandible with palp detached; B, Maxilla 1; C, Maxilla 2; D, Maxilliped 1; E, Maxilliped 2; F, Maxilliped 3; G, Pleopod 1, female.

1832) and *C. mucronata* Kossman, 1880, both appear to be synonyms of *Callianidea typa*.) How these taxa are related was investigated using PAUP (Swofford, 1985), a cladistic program that derives minimum-length trees based on the principle of par-

simony, from which phylogeny may be inferred. Twenty-one morphological characters were used in this analysis.

The characters and character-states used are as follows (0 = plesiomorphic state; 1, 2, 3 = apomorphic states):

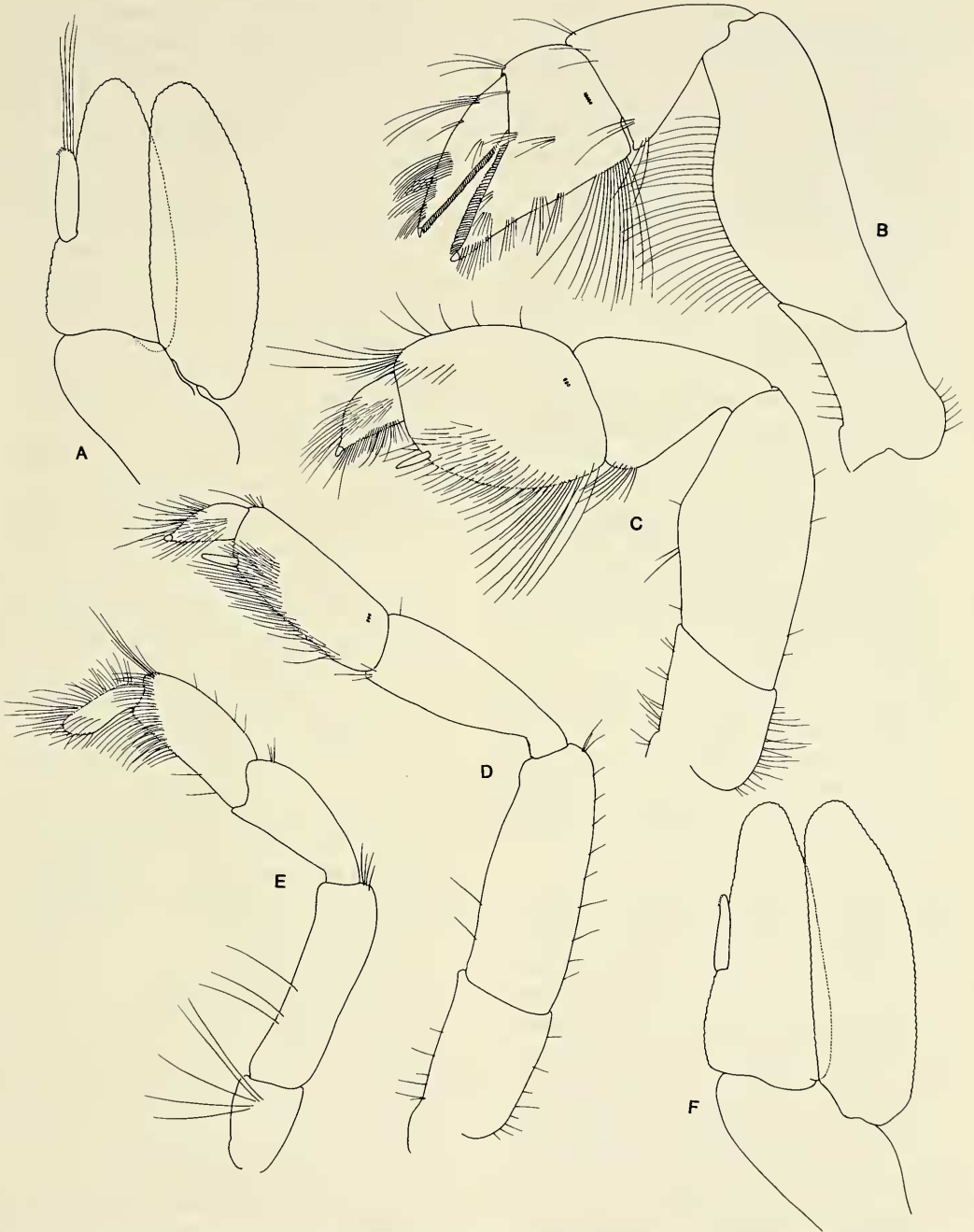


Fig. 24. *Mictaxius thalassicola*: A, Pleopod 2, male; B, Pereopod 2; C, Pereopod 3; D, Pereopod 4; E, Pereopod 5; F, Pleopod 3.

1. Pereopod 1 chelipeds subsimilar (0), or strikingly dissimilar (1).

The condition in *Callianidea* where in both sexes, the chelipeds of pereopod 1 are strongly unequal and dissimilar, implies a specialized separate function for each member of the pair of legs, with the one enlarged cheliped perhaps playing a role in agonistic or mating behavior.

2. Linea thalassinica present (1), or absent (0) [unordered].

There is some uncertainty about whether the linea thalassinica is a primitive or advanced feature, and indeed, whether the linea thalassinica is an homologous structure in the various thalassinideans in which it occurs. Its presence in the callianassids, generally considered to be highly specialized burrowing forms, would suggest that at least in some groups the linea thalassinica is an advanced feature.

3. Pleopodal accessory respiratory filaments absent (0), or present (1).

Development of these supposedly supplementary respiratory structures may have allowed the invasion of habitats characterized by fine sediments and somewhat restricted water flow, as under large intertidal beachrock slabs or in burrows in fine anoxic sediments. Increasing the surface area of the pleopods, which are in more direct contact with oxygen-bearing water than are the gills within the gill-chamber, would allow more effective gas exchange. The possibility of clogging of the gill chamber with fine sediment particles then becomes less critical for respiration.

4. Antennal acicle spiciform (0), or reduced to a small, often immobile scale (1).

In the more specialized burrowing thalassinideans such as the callianassids, the antennal acicle is reduced to the point of being absent.

5. Maxilla 2, scaphognathite whip present (0), or absent (1).

This would be a constant character in the analysis with *Callianassa* deleted, but for *Jaxea* (which has 5–7 elongate whips) which is coded as 9 (= unknown or not applicable).

6. Eye normal, i.e., with cornea delimited and well pigmented (0), or with cornea indistinct and reduced pigmentation (1).

Along with the reduction of pigment, flattening of the eyestalk is seen in several different crustacean groups and is frequently correlated with a burrowing habit.

7. Maxilliped 2, exopod well developed (0), or reduced (1).
8. Maxilliped 3, exopod well developed (0), or reduced or lacking (1).
9. Lateral ramus of uropod distally entire (0), or bilobed (1).

A bilobed lateral uropodal ramus has generally been regarded as characteristic of the more advanced callianassid genera (de Saint Laurent 1973).

10. Lateral ramus of uropod having a transverse suture (0), or lacking a suture (1).
11. Propodi of pereopods 3 and 4 unspecialized and subcylindrical (0), or broadened and flattened (1).
12. Mandibular incisor entire or with one or two low cusps (0), or toothed (1).
13. Setal rows on abdominal somites absent (0), or present (1).
14. Setal rows on pereopods 2, 3, and 4 absent (0), or present (1).
15. Epipods on pereopods 1–4 present (0), or absent (1).
16. Pleopod 2 in male unmodified (0), or modified (1).
17. Pleonite 1 with anteriorly-directed lobes (0), or lacking lobes (1).

The submedian posterodorsal lobes of the carapace fit beneath the anterodorsal lobed part of the first pleuron; simultaneously, the posteromedian convexity of the carapace slides over the anteromedian part of the first abdominal somite. This combination, found in all the axiids, prevents dorsalventral and lateral overextension of

the abdomen, and only functions if the exoskeleton is strongly sclerotized. As thalassinideans become more specialized for permanent burrow or tunnel life, hardened exoskeletons become less necessary, and this interlocking of carapace and abdomen is lost.

18. Setal row pattern (0), (1), (2) [unordered].
19. Pereopod 1 meral pattern (0), (1) [unordered].

The posterior margin of the merus of pereopod 1 is either convex, with or without one or more low serrations (pattern 0), or the posterior margin is straight, with one (rarely 2) strong marginal tooth (pattern 1).

20. Maxilliped 3, ischial crest present (0), or absent (1).
21. Pleopodal respiratory filaments rounded (0), or flattened (1) [unordered].

The data matrix used in the analysis is presented in the Appendix.

Results of PAUP Analysis Fig. 25

Three genera, each from a different thalassinidean family, were chosen to serve as the outgroup for comparison with the eight taxa forming the ingroup: *Axiopsis* (family Axiidae), *Jaxea* (family Laomediidae), and *Callianassa* (family Callianassidae).

When *Callianassa* was included in the analysis as part of the outgroup, the ingroup could not be rooted as monophyletic and the resultant trees were then rooted at the midpoint. With *Callianassa* as part of the ingroup, it was joined with *Thomassinia* to form a sister group to the *Crosniera-Mictaxius* group. As noted above *Mictaxius* in particular possesses features thought to be more characteristic of the Callianassidae; this group thus seems to stand in a position transitional to the Callianassidae. *Callianassa* was thus omitted from the final analyses, making characters 15 and 16 constant for the rest of the taxa.

With *Callianassa* deleted from the anal-

ysis, and characters 2, 18, and 21 unordered, three trees were produced, each of length 25.00, and having a consistency index of 0.760.

The three trees differ only in the configuration of the taxa *Mictaxius*, *Thomassinia* and *Crosniera*, each of the trees having one of the three possible combinations for these three taxa (other than the possibility of an unresolved trichotomy).

Four apomorphic characters define the ingroup: (10) loss of a uropodal suture; (11) broadening of the propodi of pereopods 3 and 4; (13) setal rows present on the carapace and abdomen; (14) setal rows present on the propodi of pereopods 2–4.

The ingroup consists of two sister-groups: 1, the *Michelea-Marcusiaxius-Meticonaxius* group, defined by three characters, viz. loss of a linea thalassinica, acquisition of setal pattern 0, and meral pattern 1 for pereopod 1; 2, the *Callianidea-Crosniera-Mictaxius-Thomassinia* group, defined by four characters, viz. reduction of the antennal acicle, toothed mandibular incisor, loss of somite 1 articulating lobes, non-flattened pleopodal respiratory filaments.

Further examination of character changes in the trees suggests the following:

Character 2: The linea thalassinica has been lost, in the *Michelea-Meticonaxius-Marcusiaxius* group, as well as in *Callianidea typa*.

Character 3: Pleopodal respiratory filaments have been acquired independently in two groups, i.e., in *Callianidea*, and in *Michelea*.

Character 8: The exopod of maxilliped 3 has twice been reduced or lost, in the *Crosniera-Mictaxius-Thomassinia* group and in the *Marcusiaxius-Meticonaxius* group.

Character 14: Setal rows on the pereopods have been lost in *Crosniera*.

Character 18: The setal row pattern of the *Michelea-Marcusiaxius-Meticonaxius* group, as well as that of the *Crosniera-Mictaxius-Thomassinia* group, have been

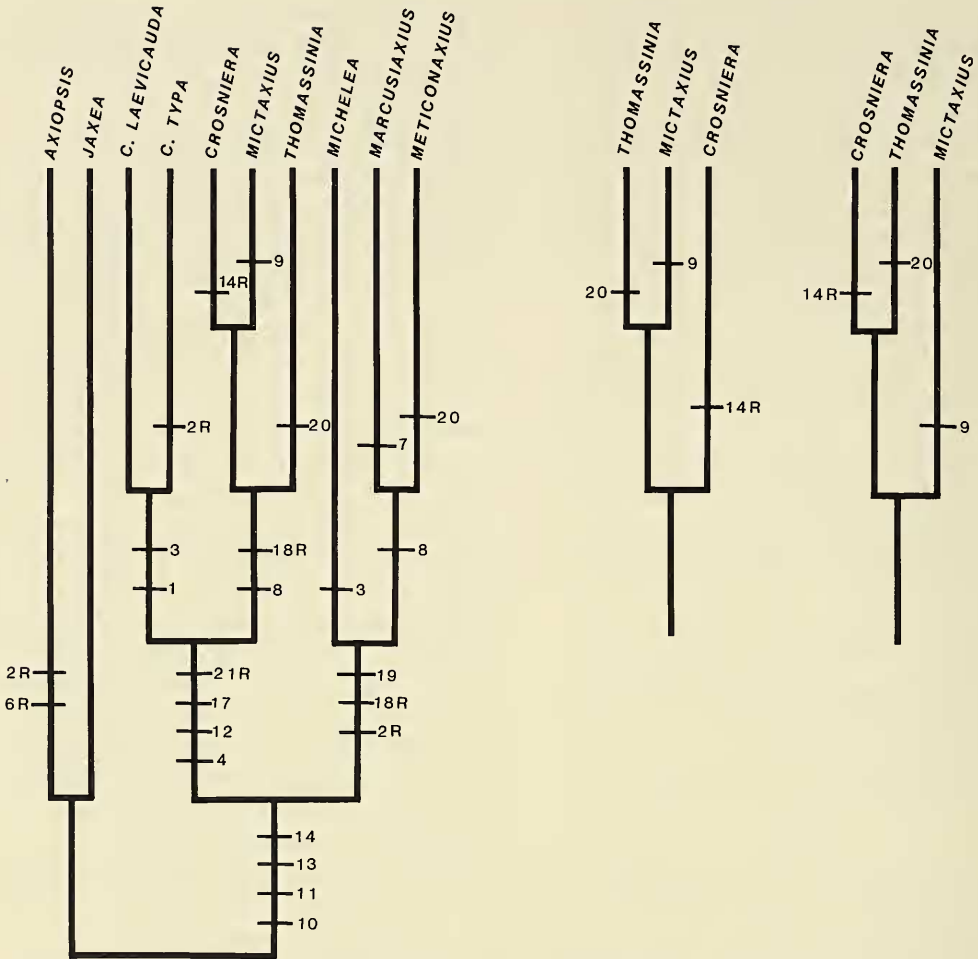


Fig. 25. Cladograms resulting from PAUP analysis of 22 characters and 11 taxa. Numbers refer to characters listed in text. Outgroup = *Axiopsis-Jaxea*. Changes in character-states indicated by bars. R = presumed character reversal.

derived from that of the *C. laevicauda-typa* group.

Character 20: The dentate ischial crest of maxilliped 3 has twice been lost, once in *Thomassinia*, and again in *Meticonaxius*.

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Appendix.—Data matrix used in present analysis.

Taxa	Characters
<i>Axiopsis</i>	*000000000000000009009
<i>Callianassa</i>	*110111111111001119019
<i>Jaxea</i>	*010091000000000009009
<i>C. laevicauda</i>	111101000111110012000
<i>C. typa</i>	101101000111110012000
<i>Michelea</i>	001001000110110010101
<i>Crosniera</i>	010101010111100011009
<i>Mictaxius</i>	010101011111110011009
<i>Thomassinia</i>	010101010111110019019
<i>Marcusiarius</i>	000001110110110000109
<i>Meticonaxius</i>	000001010110110000119

* = Outgroup.