

Systematics and distribution of the genus *Calocarides* (Crustacea: Decapoda: Axiidae)

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Abstract.—The nine currently recognized species of *Calocarides* are reviewed, and two new species are described: *C. capensis* from the south-east Atlantic Ocean off the Cape of Good Hope, and *C. macphersoni* from the Atlantic Ocean off Namibia. Species of the genus are particularly characterized by the possession of dentate median, submedian, and lateral carinae of the carapace, weakly pigmented or unpigmented eyes, and robust, quite heavily sclerotized, tuberculate and/or spinose first pereopods.

The approximately 100 described species of Axiidae show their greatest diversity in shallow tropical and subtropical seas, with several genera confined to the tropics, e.g., *Coralaxius* Kensley & Gore, 1982, *Paraxiopsis* De Man, 1905, *Paraxius* Bate, 1888, *Scytoleptus* Gerstaecker, 1856. A few genera, however, have colonized colder and deeper waters and show considerable diversity and broad geographic range, e.g., *Calocarides* Wollebaek, 1908, and *Eiconaxius* Bate, 1888, the latter an inquiline of hexactinellid sponges. *Calocarides* is geographically widespread in continental shelf-slope regions, and contains cold-water inhabiting, soft-bottom burrowing species, some of which may be associated with zones of upwelling. The genus is reviewed here, two new species are described, and a number of taxonomic and distributional problems noted, relating to species previously included in the genus.

Abbreviations: cl—carapace length; HUMZ—Laboratory of Marine Zoology, Hokkaido University; ICMB—Instituto de Ciencias del Mar, Barcelona; MNHN—Muséum National d'Histoire Naturelle, Paris; SAM—South African Museum, Cape Town; UBZM—Zoological Museum, University of Bergen; USNM—National Mu-

seum of Natural History, Smithsonian Institution.

Systematic Account Family Axiidae

Genus *Calocarides* Wollebaek, 1908

Calocaris (*Calocarides*) Wollebaek, 1908: 3, 23.

Axiopsis (*Calocarides*).—De Man, 1925:1, 2, 6, 67, 71.—Balss, 1957:1579.

Calocarides.—Bouvier, 1940:97.—Sakai & de Saint Laurent, 1989:4, 78.—Poore, 1994:98.

Euconaxius [laps. cal. for *Eiconaxius* Bate, 1888] Trybom, 1904:384.

Type species.—By subsequent designation by Sakai & de Saint Laurent, 1989, *Euconaxius coronatus* Trybom, 1904. Type locality: Skagerrak, North Sea, 230–500 m. Gender: Masculine.

Diagnosis.—Gonochoristic. Carapace having small supraocular spine present, as part of lateral rostral series; post-cervical carina low, rounded, barely discernible in some species, lacking spines; rostrum at same level as anterior carapace, margins armed; median carina dentate; submedian carina dentate; lateral carina dentate.

Eye reaching to about midlength of rostrum, cornea weakly pigmented or unpig-

Table 1.—Branchial formula for *Calocarides coronatus*. r = reduced.

	Maxillipeds			Pereopods				
	1	2	3	1	2	3	4	5
Exopod	1	1	1	—	—	—	—	—
Epipod	1	1	1	1	1	1	1	—
Podobranch	—	—	r	r	r	r	—	—
Arthrobranch	—	—	2	2	2	2	2	—
Pleurobranch	—	—	—	—	—	—	—	—
Setobranch	—	—	1	1	1	1	1	1

mented; eyestalk longer than eye. Antennal scaphocerite elongate. Maxilla 2, scaphognathite having spinulose flagellum. Maxillipeds 1–3 with exopods and epipods. Pereopod 1, chelipeds asymmetrical, somewhat sexually dimorphic. Propodi and dactyli of pereopods 3–5 slender, not expanded, dactyli simple. Pleopodal rami slender elongate; appendix interna present on pleopods 2–5. Pleopod 1 ♂ absent; pleopod 1 ♀ uniramous, of 2 articles. Pleopod 2 ♂ with appendix masculina of single lobe. Uropod with lateral ramus with suture. Telson longer than wide, or at least as long as wide, with dorsal spines.

Branchial formula: see Table 1.

Species:

Calocarides capensis, new species. Off Table Bay, South Africa, 1280 m.

Calocarides coronatus (Trybom, 1904). Swedish and Norwegian fjords, North Sea, 80–700 m.

Calocarides lev (Zarenkov, 1989). Gulf of California, 2000–2036 m.

Calocarides longispinis (McArdle, 1901). Bay of Bengal, 549 m.

Calocarides macphersoni, new species. Off Namibia, 300–480 m.

Calocarides quinqueseriatus (Rathbun, 1902). Off mouth of Columbia River, Oregon, to southern California, 292–2013 m.

Calocarides rostriserratus (Andrade & Baez, 1977). Off Chile, 320–400 m; off Peru, Gulf of Panama, 576–825 m.

Calocarides rudolphi (Zarenkov, 1989). Off Angola, 490–510 m.

Calocarides soyoi (Yokoya, 1933). Off northern Japan, 138–270 m.

Calocarides spinulicauda (Rathbun, 1902). Off Bodega Head, California, 113 m; Puget Sound, 70–256 m; British Columbia, 91–128 m.

Calocarides vigila Sakai, 1992. New Zealand, 74–146 m.

Taxonomic remarks.—The species *Calocarides lev* Zarenkov, 1989, described from a hydrothermal vent at 2000–2036 m in the Gulf of California, is almost certainly a species of *Calocarides*. The proportions and spination of the first chelipeds bear more resemblance to *C. rostriserratus* from Chile, Peru, and Panama, than to *C. quinqueseriatus* from southern California. Given that this species was taken from greater depth than either of the two above-mentioned species, its relative isolation of the Gulf of California, and the lack of males, it seems prudent to await further material before deciding on the status of this species.

Calocarides rudolphi Zarenkov, 1989, from 490–510 m off Angola is likewise a species of *Calocarides*, and bears some resemblance to *C. macphersoni* (see Remarks under *C. macphersoni*).

Although Sakai & de Saint Laurent (1989) tentatively placed *Axiopsis tenuicornis* De Man, 1905, *Axius habereri* Balss, 1913, *Axius armatus* Smith, 1881, and *Axiopsis werribee* Poore & Griffin, 1979, within *Calocarides*, none of these possess a majority of the features that define the genus.

The specific identity of *Calastacus quinqueseriatus* and *Axius spinulicauda amurensis*, both recorded from Japan by Kobajakova (1937) will remain uncertain until the material can be located and examined.

Ecological and biological notes.—Little information exists for species of *Calocarides*, except for *C. coronatus* and *C. quinqueseriatus*. Both of these species are known to burrow into soft bottom sediments. In the case of *C. coronatus*, these sediments are usually mud with a high

(60%) silt content and a temperature of 6°–7.5°C. *Calocarides coronatus* overlaps in bottom distribution with the calocarid shrimp *Calocaris macandreae*, but dominates in deeper water (Brattegard 1966). For all the records of *C. quinqueseriatus*, the bottom sediments were recorded as either yellow or green mud, with temperatures ranging from 13°–16°C.

Even less is known of the prey organisms of species of *Calocarides*. *Calocarides macphersoni* from Namibia was taken from the gut-contents of two bottom feeders, viz. the scorpaenid fish *Helicolenus* sp., and the ray *Raja confundens*, again suggesting that the species burrows in soft sediments.

Regarding reproduction and fecundity, *C. coronatus* produces a about 65 eggs/female, with an egg diameter 15% of carapace length ($n = 2$). *Calocarides quinqueseriatus* produces about 180 eggs/female, with an egg diameter of about 7% of carapace length ($n = 4$). These egg sizes are in the high range for free-living axiids, suggesting that a fairly advanced larva hatches, having a relatively short planktonic larval lifespan. Species which produce thousands of eggs per female generally have much smaller eggs, e.g., *Oxyrhynchaxius caespitosa* with 16,000 eggs/female, egg diameter 1.3% of carapace length; *Axiopsis serratifrons* with 4000 eggs/female, egg diameter 2.7% of carapace length. The commensal species of *Eiconaxius* by contrast, produce far fewer large eggs, 8–30 eggs/female, with an egg diameter 16–38% of carapace length. Elofsson (1959) recorded a 10 mm stage II larva (Gurney 1942) of *C. coronatus* from 600 m.

Distribution.—From the depth ranges of the 11 species of *Calocarides* (see list of species), it is clear that they are continental shelf/slope dwellers, probably with a preference for soft-sediment bottoms into which they can burrow. In several cases, the shelf/slope habitat is also characterized by upwelling of deeper water, e.g., off the Cape of Good Hope and Namibia, off Pacific North America, off Chile, and in localized areas off Norway.

The widespread geographical distribution of the species of *Calocarides*, in the Atlantic, Indian, and Pacific oceans (Fig. 1), along with the most northerly (*C. coronatus*) and most southerly (*C. vigila*) records for the Axiidae, suggests a considerable age for the genus. If, as has been suggested, the axiid-like shrimps evolved from Tethyan ancestors (Kensley 1994), shallow-water precursors of *Calocarides* must have spread with tectonic plate movements and the opening of the present-day oceanic basins, at the same time penetrating to varying depths the waters of the continental shelves. The direction of this invasion from shallow to deeper shelf waters may be reflected in that some eye-pigment is retained in some species (e.g., *C. soyoi*) while other species completely lack eye-pigment (e.g., *C. capensis*).

Calocarides capensis, new species

Fig. 2

Calastacus longispinis.—Stebbing, 1910: 367, non McArdle, 1901.

Calocaris (Calastacus) longispinis.—De Man, 1925:8 (part), non McArdle, 1901.—Barnard, 1950:503, fig. 93 d-f.

Calocaris longispinis.—Kensley, 1981:30, non McArdle, 1901.

Calocarides coronatus.—Sakai & de Saint Laurent, 1989:79, non Trybom, 1904.

Material examined.—Holotype, SAM-A940, ovigerous ♀ cl 19.0 mm (carapace damaged), R/V *Pieter Faure* 40 miles N79°E of Table Mountain, Cape of Good Hope, South Africa, 1280 m.

Diagnosis.—Carapace surface minutely pitted, especially posteriorly; rostrum with 5–6 lateral teeth; median carina well marked, unarmed; submedian carina bearing 1 or 2 spines; lateral carina with 3 or 4 spines. Abdominal pleura ventrally rounded, pleuron 2 widest. Telson with 1 pair of small spines dorsally, 3–4 small mobile spines at posterolateral corner, posterior margin gently convex between posterolateral and median spines.



Fig. 1. Distribution of species of *Calocarides*.

Maxilliped 3, merus with 4 spines on posterior margin; carpus with single small distal spine. Pereopod 1, larger cheliped, ischium with single strong distal spine; merus with strong spine at midlength of posterior margin, few small tubercles in proximal half, anterior margin with 5 distal spines; carpus with few low tubercles on anterior margin and few small tubercles on lateral surface; propodal palm slightly longer than fingers, outer surface with tiny scattered acute tubercles and strong ridge near posterior margin reaching almost to tip of fixed finger, anterior margin with about 11 strong spines, cutting margin of finger finely toothed, with large proximal tubercle; dactylus with few tubercles on anterior margin, cutting edge finely toothed, with proximal tubercle. Smaller cheliped, ischium with strong distal spine; merus with strong spine at midlength of posterior margin, anterior margin with 3 distal spines; carpus with few tubercles on anterior margin and lateral surface; propodal palm longer than fingers, lat-

eral surface with few scattered small tubercles and ridge near posterior margin, anterior margin with about 11 spines; fixed finger and dactylus as in larger cheliped. Pereopod 2, ischium with few small spines and strong distal spine on posterior margin; merus with 3 widely spaced spines on posterior margin. Pleopod 1 consisting of single slender elongate ramus. Pleopods 2–5 each with appendix interna on mesial margin of endopod. Lateral uropodal ramus with single small spine on outer margin; suture bearing 4–8 irregular spines; mesial ramus with 4 spines on middorsal ridge.

Remarks.—See ‘Remarks’ after *Calocarides macphersoni*.

Etymology.—The specific name derives from the type locality, the Cape of Good Hope.

Calocarides coronatus (Trybom, 1904)

Euconaxius coronatus Trybom, 1904:384–390, pl. 20, figs. 1–10, 13, 14, pl. 21, figs. 1–8.

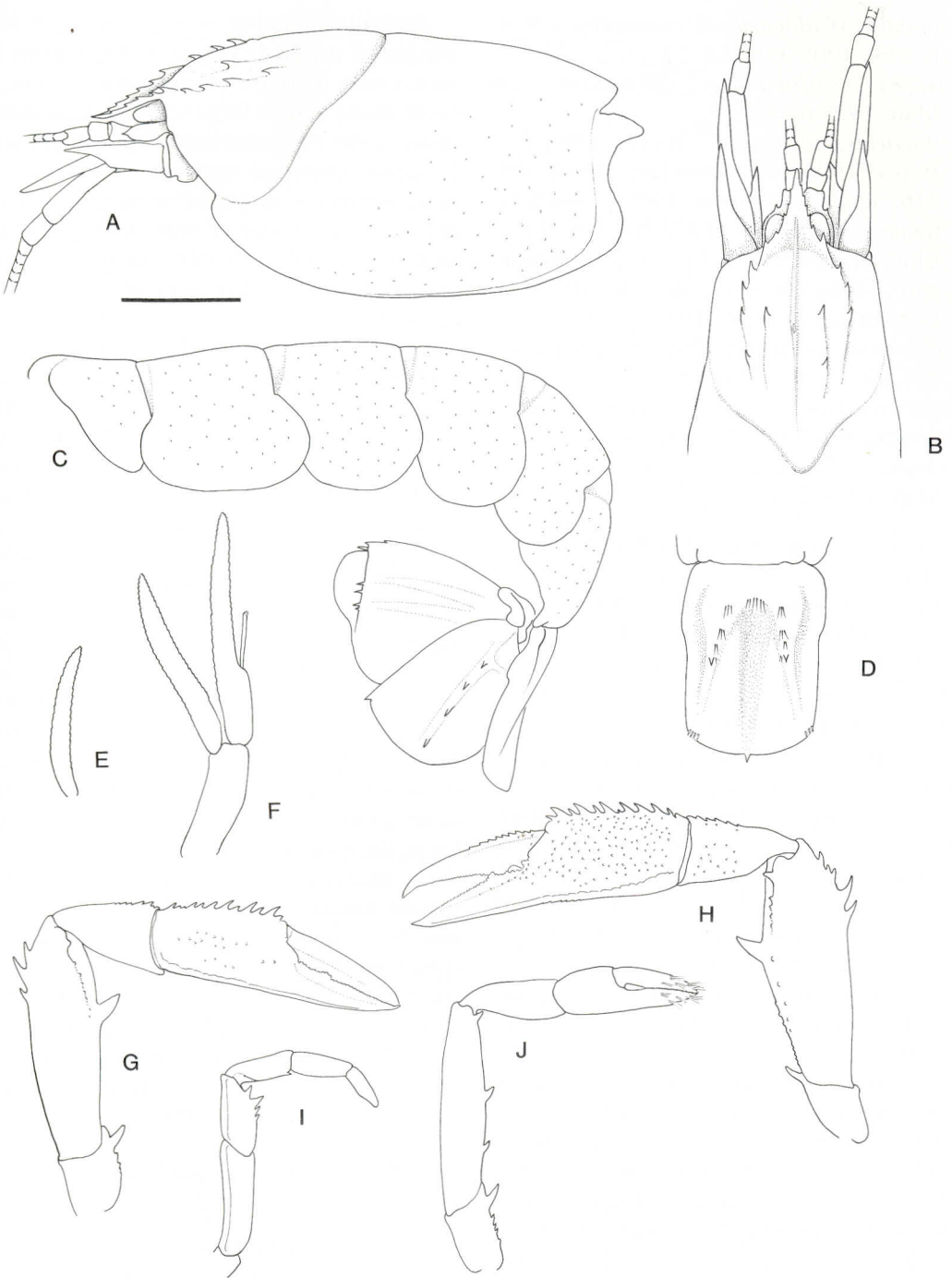


Fig. 2. *Calocarides capensis*, new species: A, Carapace in lateral view, scale = 5 mm; B, Anterior carapace in dorsal view; C, Abdomen in lateral view; D, Telson in dorsal view; E, Pleopod 1, female; F, Pleopod 2, female; G, Pereopod 1, smaller cheliped; H, Pereopod 1, larger cheliped; I, Maxilliped 3; J, Pereopod 2.

Calocaris (Calocarides) coronatus.—Wol-lebaek, 1908:3, 5, 13, 23.

Axiopsis (Calocarides) coronatus.—De Man, 1925:6, 67, 71.

Calocarides coronatus.—Bjorck, 1913:7.—Balss, 1925:209.—Poulsen, 1940:208, 216, fig. 4.—Bouvier, 1940:97.—Christiansen, 1955:1–4; 1972:40, fig. 45.—Elofsson, 1959:3–9, figs. 1–20.—Brattegard, 1966:45–52.—Sakai & de Saint Laurent, 1989:4, 80, 101, fig. 20.

Euconaxius crassipes Trybom, 1904:390–391, pl. 20, figs. 11, 12.

Calocaris (Calocarides) crassipes.—Wol-lebaek, 1908:3, 5–13, 17, 23, pl. 1–7.

Axiopsis (Calocarides) crassipes.—De Man, 1925:6, 67, 71.

Material examined.—UBZM 50400, ♂ cl 14.8 mm, Sorfjord, Norway, 60°11'N, 6°34'E, 589–600 m.—UBZM 49598, 4 ♂ cl 13.5, 13.9, 15.5, 15.5 mm, Kvinnheradfjord, Norway, 59°56'N, 5°45'E, 512 m.—UBZM 49595, ♀ cl 14.0 mm, Kvinnheradfjord, Norway, 59°59'N, 5°53'E, 660–670 m.—UBZM 50461, ovigerous ♀ cl 14.4 mm, Osafjord, Norway, 60°40'N, 6°55'E, 300.—UBZM 49589, Alfjord, Norway, 59°41'N, 5°34'E, 450–465 m.—UBZM, ovigerous ♀ cl 16.1 mm, Fusafjord, Norway, 60°12'N, 5°45'E, 240 m.—UBZM 49591, ♂ cl 15.1, ♀ cl 15.2 mm, Bomlafjord, Norway, 59°40'N, 5°22'E, 360 m.

Distribution.—From Malangenfjord, northern Norway, to southwestern Sweden, 80–700 m.

Diagnosis.—Carapace surface smooth. Rostrum with 4 pairs of lateral teeth, continuous with lateral carina bearing 3 teeth; median carina with 1 tooth anterior to tubercle; submedian carina bearing 2 teeth. Abdominal pleuron 1 ventrally narrowly rounded; pleuron 2 broadly rounded; pleura 3–5 rounded, with 1 or 2 small teeth on anterior margin. Telson with 5 or 6 lateral teeth, 2 mobile spines at posterolateral angle; posterior margin evenly convex, with median tooth; 1 or 2 small spines proximodorsally on rounded ridge.

Antennal scaphocerite reaching distal margin of peduncle article 4. Maxilliped 3, merus with 4 spines on posterior margin, 3 more distal spines large; carpus with small distal spine on posterior margin. Pereopod 1, larger cheliped: ischium with row of acute tubercles on posterior margin, distal-most a large spine; merus with posterior surface expanding distally, mesial and lateral margin defined by row of small acute tubercles, mesial margin with strong spine at about midlength, anterior margin bearing 1 strong spine and few blunt tubercles; carpus bearing small tubercles dorsodistally; fingers slightly more than half length of propodal palm, latter with lateral and most of mesial surface tuberculate, fixed finger with triangular tooth at about midlength of cutting edge; fingers widely gaping, dactylus downcurved, strongly tuberculate, with 1 or 2 stronger tubercles on cutting edge. Smaller cheliped: ischium, merus, and carpus as in larger cheliped; propodal palm with lateral and mesial surface tuberculate, tubercles along anterior margin forming spines, fingers about $\frac{2}{3}$ length of palm, fixed finger with blunt proximal triangular tooth followed by regularly spaced small teeth; dactylus with row of spines along anterior margin, cutting edge with regularly spaced small teeth. Pereopod 2, ischium and basis each with single posterodistal spine; merus with 3 evenly spaced spines on posterior margin. Lateral uropodal ramus with about 18 spines along suture, 2 small distal spines on lateral margin; mesial ramus with single distolateral spine, dorsal ridge bearing 5 or 6 spines.

Calocarides macphersoni, new species

Fig. 3

Calastacus longispinis.—Macpherson, 1983:45, fig. 26; 1991:405, non McArdle, 1901.

Material examined.—Holotype, USNM 243561, ♂ cl 20.4 mm, R/V *Benguela II* sta 66, off Namibia, 20°55'S, 12°23'E, 475–480 m, 9 Sep 1980.—Paratypes, USNM

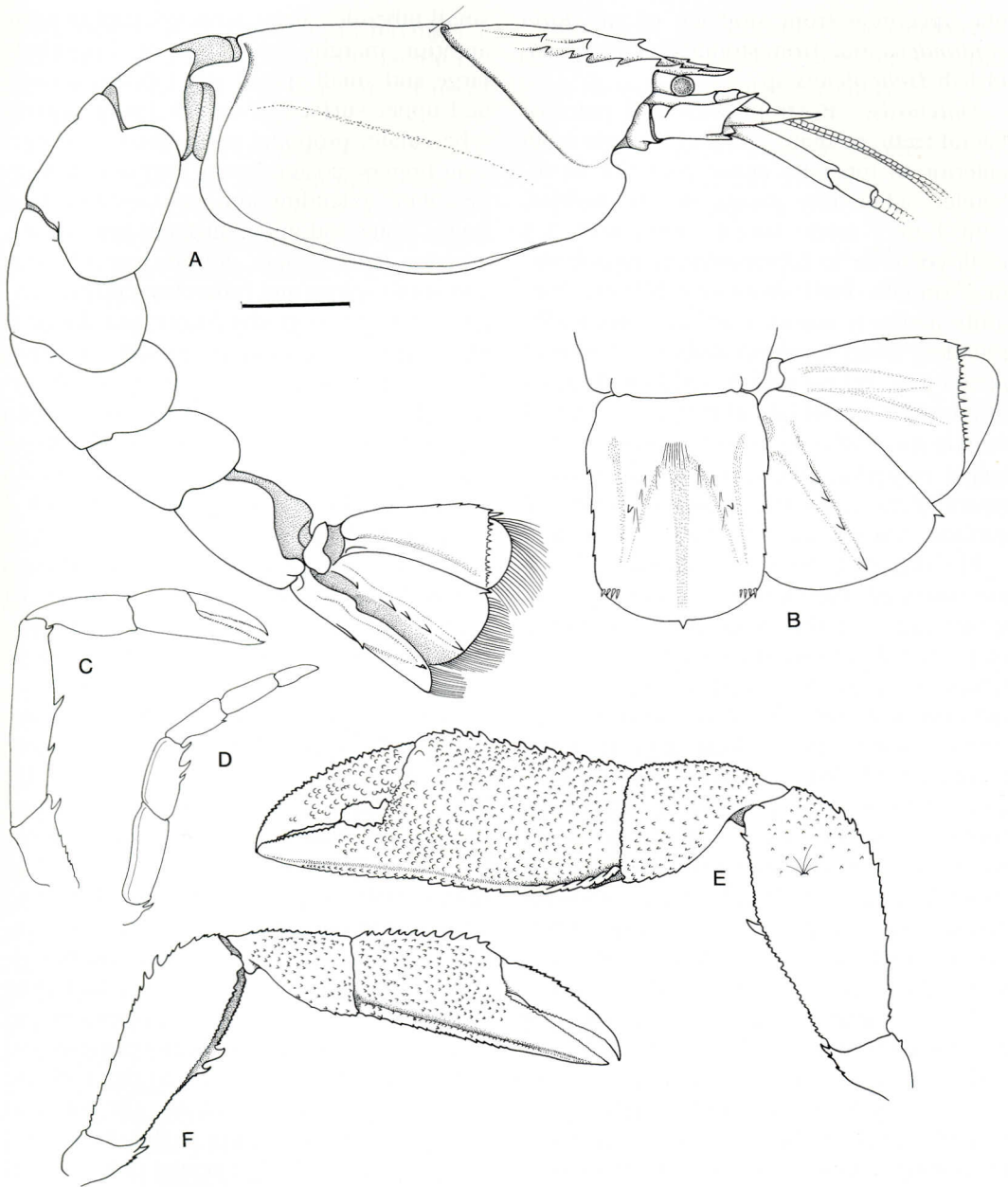


Fig. 3. *Calocarides macphersoni*, new species: A, Lateral view, scale = 5 mm; B, Telson and right uropod in dorsal view; C, Pereopod 2; D, Maxilliped 3; E, Pereopod 1, larger cheliped; F, Pereopod 1, smaller cheliped.

243562, ♂ cl 17.8 mm, R/V *Benguela II* sta 66, off Namibia, 20°55'S, 12°23'E, 475–480 m, 9 Sep 1980.—Paratype, ICMB, R/V *Benguela II* sta P-37, ♂ cl 21.5 mm, off Namibia, 21°33'S, 12°39'E, 380–390 m, from stomach of scorpaenid fish *Helicolen-*

us sp.—Paratypes, ICMB, R/V *Benguela II* sta P-66, 2 ♂ cl 20.3 mm, one damaged, off Namibia, 20°55'S, 12°23'E, 475–480 m.—Paratypes, ICMB, R/V *Benguela IV* sta P-95, 2 ♂ cl 21.0 mm, 21.2 mm, off Namibia, 20°42'S, 12°14'E, 410–417 m,

one specimen from stomach of ray *Raja confundens*, one from stomach of scorpaenid fish *Helicolenus* sp.

Diagnosis.—Rostrum with 2–3 pairs of lateral teeth; median carina with single tooth anterior to tubercle, entire posterior to tubercle; submedian carina poorly defined, with 1 or 2 teeth; lateral carina with 3–5 teeth posterior to supraocular. Carapace surface smooth. First abdominal pleuron ventrally narrowly rounded, pleura 2–6 broadly rounded, small spine on anterior margin of pleura 3–6. Telson with 5 small fixed spines in posterior half of lateral margin, 3–4 small mobile spines mesial to posteriormost lateral spine; posterior margin gently convex between lateral spine and median spine; dorsal surface with one pair of small fixed spines.

Maxilliped 3, posterior margin of ischium unarmed; merus with 3–4 strong distal spines and 2–3 tiny more proximal spines on posterior margin; carpus with small posterodistal spine. Pereopod 1: larger chela, ischium with row of small denticles and single strong spine along posteromesial margin, small distal spine on anterior margin; merus with posteromesial surface tuberculate, having single strong tooth at about midlength, anterior margin with about 5 small spines and several small tubercles; outer and upper surface of carpus evenly tuberculate; propodal palm about $\frac{1}{5}$ longer than fingers, entire surface evenly and fairly densely tuberculate, posterior margin with tuberculate carina extending onto fixed finger, anterior margin with row of somewhat larger tubercles; fingers proximally widely gaping, distally meeting, fixed finger with proximal half of cutting edge having few low rounded tubercles, distal half straight, bearing numerous small rounded teeth; surface of dactylus tuberculate, cutting edge as in fixed propodal finger. Smaller chela, ischium with few small spines and single strong spine on posterior margin, single distal spine on anterior margin; merus with row of small tubercles along posteromesial margin with 1 or 2 strong spines at about midlength, row of

small tubercles along posterolateral margin, anterior margin with row of irregularly large and small spines and tubercles; outer and upper surface of carpus fairly densely tuberculate; propodal palm about $\frac{1}{5}$ longer than fingers, posterolateral carina feebly tuberculate, extending almost to apex of fixed finger, outer and upper surfaces tuberculate, anterior margin with double row of large and small spines and tubercles; cutting margins of fixed propodal finger and dactylus only slightly excavate proximally, remainder of margin bearing row of small evenly-spaced teeth. Pereopod 2, posterior margin with row of small spines and single strong distal tooth; posterior margin of merus with 2–4 spines. Lateral uropodal ramus with 2 or 3 small distal spines on lateral margin, single mobile spine mesial to distalmost, transverse suture armed with row of 13–15 small spines; mesial ramus with single distal spine, dorsal ridge with irregular row of about 8 small spines.

Remarks.—From McArdle's (1901) description, and Alcock & McArdle's illustrations (1902, pl. 57, figs. 2, 2a), and De Man's (1925:118) key, the Bay of Bengal species *Calastacus longispinis* lacks spines on the anterior median carina, has five spines on the free lateral margins of the rostrum, and three spines on the submedian carina. The antennal scaphocerite reaches almost to the end of peduncle article 4. The single female lacked both chelipeds of pereopod 1. Given that the Namibian material has a strong spine anterior to the tubercle on the median carina, and that the antennal scaphocerite reaches only to the distal third of peduncle article 4, it seems unlikely that the Atlantic and Indian Ocean specimens are the same species, especially considering the considerable geographical separation.

The species described above as *Calocarides capensis*, differs from *C. macphersoni* in having more slender and less granular chelipeds of pereopod 1, with relatively more elongate spines on the anterior margin of the propodal palm; in having fewer but stronger distal spines on the anterior margin

of the merus of pereopod 1; in having far fewer spines on the suture of the lateral ramus of the uropod; and in having a more elongate telson.

Major differences between *C. coronatus* and *C. macphersoni* are seen in the size (cl ovigerous ♀ 13.5–16.1 mm vs. cl ovigerous ♀ 17.8–25.0 mm resp.), and in the more spinose upper margin of the merus in *C. macphersoni*.

The species described as *Axius* (*Neaxius*) *laevis* by Bouvier (1915) from 698 m off Cape Bojador, Spanish Sahara, West Africa, (holotype, MNHN, ♀ cl 5.1 mm) was synonymized with *C. coronatus* by Sakai & de Saint Laurent (1989:81, fig. 21). The latter authors illustrated the single damaged specimen of *C. laevis*, the caption of their illustration erroneously referring to *Eiconaxius laevis*. Given the damaged condition of the specimen, and the fact that it lacks spines on the submedian carina, has an antennal scaphocerite shorter than in *C. coronatus*, has pereopod 1 lacking the fine tuberculation of the propodus and the anterior spination of the merus of *C. coronatus*, and a telson longer and narrower than in *C. coronatus*, it seems unlikely that the West African species is synonymous with *C. coronatus*, or indeed, that it is a species of *Calocarides*. From the figure of *Calocarides rudolfi* (Zarenkov, 1989, fig. 3) from Angola, several differences in spination suggests that it differs from *C. macphersoni*. In *C. rudolfi*, the merus of maxilliped 3 bears more elongate and numerous spines, and the merus of both chelae of pereopod 1 has larger and more numerous anterodistal and posterodistal spines than in the Namibian species; the carpus of pereopod 2 bears a posterodistal spine, and the telson bears two pairs of fixed dorsal spines, while *C. macphersoni* lacks a carpal spine on pereopod 2 and the telson bears a single pair of fixed spines. Posterolateral mobile spines on the telson were not illustrated for the Angolan species; *C. macphersoni* bears four such spines on each side.

Etymology.—The species is named for

carcinologist Dr. Enrique Macpherson of Barcelona, Spain, who made the material from Namibia available for study.

Calocarides quinqueseriatus

(Rathbun, 1902)

Figs. 4, 5

Calastacus quinqueseriatus Rathbun, 1902: 887.—Schmitt, 1921:113, fig. 76.—Balss, 1925:209.

Calocaris (*Calastacus*) *quinqueseriata*.—De Man, 1925:8, 118.

Calocarides quinqueseriatus.—Sakai & de Saint Laurent, 1989:79, 103.

Material examined.—Syntypes, USNM 25240, 9 ♂ cl 15.5–22.7, 2 ovigerous ♀ cl 15.4, 18.2, 3 ♀ cl 17.5–19.4, 19.4, R/V *Albatross* sta 3196, San Luis Obispo Bay, California, green mud, 366 m.—USNM 28321, 5 ♂, cl 13.5–21.6, 1 ovigerous ♀ cl 16.9 mm, 9 ♀ cl 15.1–20.5, R/V *Albatross* sta 2909, Santa Barbara Channel, California, 375 m, green mud.—USNM 152525, 22 ♂ cl 18.9–26.0, 9 ovigerous ♀ 20.0–23.3, 11 ♀ cl 21.0–23.0, R/V *Albatross* sta 4436, San Miguel Island, California, 483–496 m, green mud.—USNM 28325, 16 ♂, cl 11.3–18.0, 1 ovigerous ♀ cl 24.0, 7 ♀ cl 10.2–19.2, R/V *Albatross* sta 3195, San Luis Obispo Bay, California, 461 m, green mud.—USNM 28236, 5 ♂ cl 14.8–24.0, 4 ♀ cl 13.0–22.5, R/V *Albatross* sta 3198, off Point Conception, California, 508 m, green mud.—USNM 28327, 7 ♂ cl 12.9–20.5, 3 ovigerous ♀ cl 19.0–20.0, 6 ♀ cl 10.3–19.5, R/V *Albatross* sta 3199, Santa Barbara Channel, California, 426 m, green mud.—USNM 28232, ♂ cl 18.0, 2 ♀ cl 21.0, 21.9 R/V *Albatross* sta 3187, off Point Sur, California, 545 m, brown and grey ooze.—USNM 28320, ♂ cl 20.3, ♀ cl 17.2, R/V *Albatross* sta 2892, off Point Conception, California, 520 m, yellow mud.—USNM 28528, 2 ♂, cl 18.1, 24.1, R/V *Albatross* sta 3200, Santa Barbara Channel, California, 485 m, green mud.—USNM 28319, 1 ♂ cl 19.0, 1 ♀ cl 12.1, R/V *Albatross* sta 2891, off Point Conception, California, 426

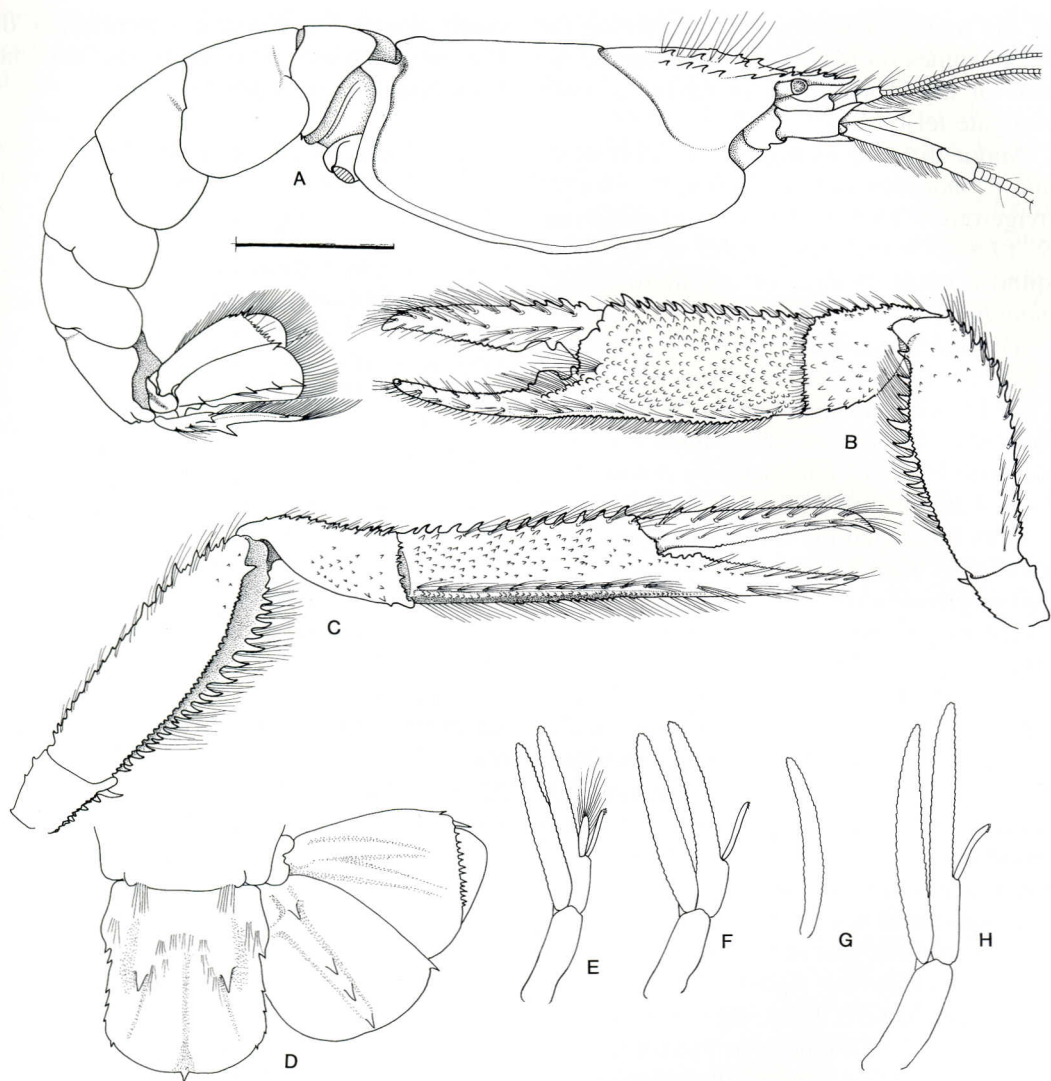


Fig. 4. *Calocarides quinqueseriatus*: A, Lateral view, scale = 10 mm; B, Pereopod 1, larger cheliped; C, Pereopod 1, smaller cheliped; D, Telson and right uropod in dorsal view; E, Pleopod 2, male; F, Pleopod 3, male; G, Pleopod 1, female; H, Pleopod 2, female.

m, brown ooze.—USNM 120119, ♀ cl 18.2, R/V *Commando* sta, mouth of Columbia River, Oregon, 732 m.—USNM 28324, ♂ cl 17.5, ♀ cl 15.0, R/V *Albatross* sta 3193, off San Simeon Bay, California, 293 m, green mud.—USNM 28329, ovigerous ♀ cl 19.5, R/V *Albatross* sta 3201, Santa Barbara Channel, California, 512 m.—USNM 28322, ♂ cl 17.4, R/V *Albatross* sta 2979, off Anacapa Island, California, 710

m, green mud.—USNM 53021, ♀ cl 16.2, R/V *Albatross* sta 4425, off San Nicolas Island, California, 2013 m, green mud, fine sand, globigerina ooze.—USNM 155735, ♂ cl 20.5, R/V *Albatross* sta 4387, off San Diego, California, 1830 m, green mud.—USNM 243350, ovigerous ♀ damaged, R/V *Commando* sta, SW mouth of Columbia River, Oregon, 1556 m.—USNM 243351, ♂ cl 18.4, R/V *Commando* sta, SW mouth

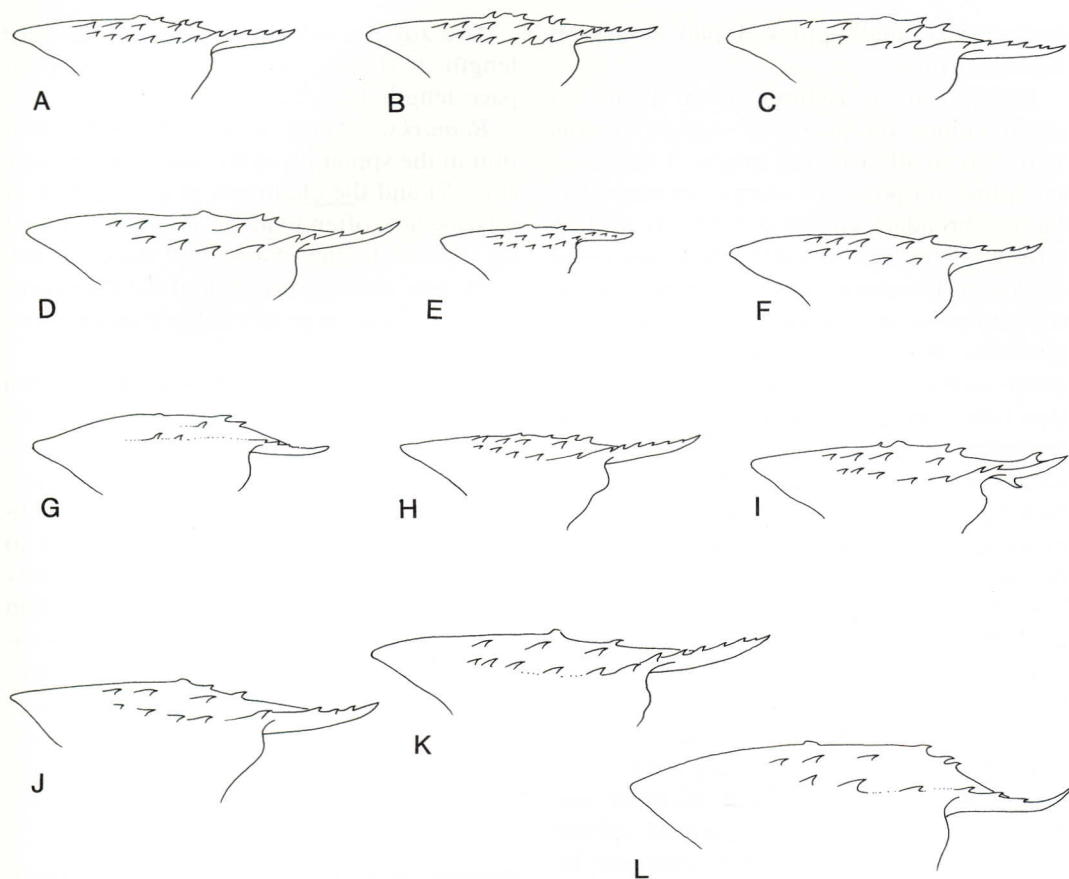


Fig. 5. *Calocarides quinqueseriatus*, variation in rostral and anterior carapace spination: A, Syntype, ovigerous female, San Luis Obispo Bay, California, cl 15.4 mm; B, Syntype, ovigerous female, San Luis Obispo Bay, California, cl 18.2 mm; C, Ovigerous female, San Miquel Is., California, cl 22.0 mm; D, Ovigerous female, San Miguel Is., California, cl 23.3; E, Female, Baja California, cl 12.0 mm; F, Female, Baja California, 20.7 mm; G, Male, Columbia River mouth, Oregon, 18.2 mm; H, Syntype, male, San Luis Obispo Bay, California, cl 19.1 mm; I, Syntype, male, San Luis Obispo Bay, California, cl 20.9 mm; J, Male, San Miguel Is., California, 24.2 mm; K, Male, San Miguel Is., California, cl 26.0 mm; L, Male, Columbia River, Oregon, cl 27.2 mm.

of Columbia River, Oregon, 1373 m.—USNM 243352, ♀ damaged, R/V *Commando* sta, SW mouth of Columbia River, Oregon, 1556 m.—USNM 243353, ♂ cl 17.3, 2 ♀ damaged, R/V *Commando* sta, SW mouth of Columbia River, Oregon, 1922 m.—USNM 243354, ♀ damaged, R/V *Commando* sta, SW mouth of Columbia River, Oregon, 1556 m.—USNM 155737, ♀ cl 20.0, R/V *Albatross* sta 5675, San Cristobal Bay, Baja California, 520 m.—USNM 155736, 2 ♂ cl 19.8–21.0, R/V *Albatross* sta 4433, off Santa Rosa Island,

California, 445 m, green mud.—USNM 243355, 2 ♂ cl 16.5, 2 ♀ cl 13.8–15.0, R/V *Albatross* sta 4351, NE of Point Loma, California, 774 m, soft green mud.

Diagnosis.—Carapace smooth; 5–6 pairs rostral teeth including small supraocular; median carina with 1–4 spines anterior to tubercle, 1–2 posterior; 1–5 spines on submedian carina; 3–7 spines on lateral carina. Abdominal pleuron 1 with ventral spine usually present; pleuron 2 ventrally rounded; pleura 3–6 rounded with spine on anterior margin. Telson with lateral margin

having 5–6 small spines; 1 pair spines on dorsal surface.

Maxilliped 3, ischium with about 10 small spines on posterior margin; merus with 5–6 small proximal spines, 3 large distal spines on posterior margin. Pereopod 1, larger (broader) cheliped: ischium with 1 strong distal and several small proximal spines on posterior margin; merus with inner and outer row of tiny tubercles flanking posterior row of about 17 strong spines, outer surface distally with few scattered tiny tubercles, upper (anterior) margin with irregular row of spines, distal spines largest; carpus with outer surface and distal margin bearing scattered acute tubercles; upper propodal palm subequal in length to fingers, posterior margin of palm and fixed finger a denticulate carina, upper (anterior) margin with about 14 strong spines, mesial and lateral surfaces of palm fairly densely granular/tuberculate, fixed finger with broad tubercle on proximal cutting edge, distally denticulate; dactylus cutting edge with proximal tubercle, distally denticulate, upper margin with several proximal spines. Pereopod 1, smaller (narrower) cheliped: ischium, merus, and carpus as in larger cheliped; upper propodal palm subequal in length to fingers, tuberculation as in larger cheliped, cutting edge of fixed finger with few small tubercles proximally, remainder of edge finely denticulate; dactylus, cutting edge finely denticulate, with about 2 spines on upper margin. Pereopod 2, ischium with 6 small spines on posterior margin; merus with 5 small proximal spines, single strong distal spine. Pleopod 1 in female a slender elongate ramus; pleopod 2 in male with rod-shaped appendix masculina bearing distal setae, slightly shorter than appendix interna; pleopods 2–5 in female, 3–5 in male with appendix interna at about proximal third of mesial margin of endopod. Uropod with lateral ramus having 2 small distal spines on lateral margin, single mobile submarginal spine; about 14 spines along suture; mesial ramus with single distolateral spine, 4 spines on dorsal surface.

Size ranges.—Male, maximum carapace length 26.0 mm; ovigerous females, carapace length 15.4–24.0 mm.

Remarks.—There is considerable variation in the spination of the anterior carapace (Fig. 5) and the chelipeds of pereopod 1 of this species, often made more marked either by injuries to the chelae that have healed, or by loss and regeneration of the chelipeds, resulting in a range of cheliped proportions and armature.

The majority of specimens have been taken from soft bottom sediments, especially from green mud.

The species recorded as *Calastacus quinqueseriatus* from 1150 m off Japan (Kobjakova 1937:142, pl. 2, fig. 8) appears to have the first pereopod chelae relatively shorter, more robust, and less granular than in true *C. quinqueseriatus*. It thus seems unlikely that the Japanese species is conspecific with the California/Oregon species.

Calocarides rostriserratus

Andrade & Baez, 1977

Fig. 6

Calastacus rostriserratus Andrade & Baez, 1977:65, fig. 1.

Calocarides quinqueseriatus.—Sakai & de Saint Laurent, 1989:78, 79, 103, non Rathbun, 1902.

Material examined.—USNM 173366, 4 ♂ cl 15.3 mm, 15.3 mm, 16.3 mm, 17.0 mm, 2 ♀ cl 14.5 mm, 15.9 mm, off Tumbes, Peru, 3°33.8'S, 81°01.4'E, 576 m, 28 Aug 1979.—USNM 243392, ♀ cl 16.1 mm, R/V *Gilliss* sta GS-22, Gulf of Panama, 7°28'N, 79°12'W, 825 m, 18 Jan 1972.

Diagnosis.—Carapace smooth; rostrum with 5–6 pairs of lateral teeth including small supraocular; 2 median carina teeth plus tubercle; 4–5 teeth on submedian carina; 4–6 teeth on lateral carina. Abdominal pleura 2–5 ventrally rounded. Telson with 2–3 pairs small lateral spines, 2 small distal mobile spines at posterolateral angle, 2 pairs spines on dorsal surface.

Maxilliped 3, ischium with 5 small prox-

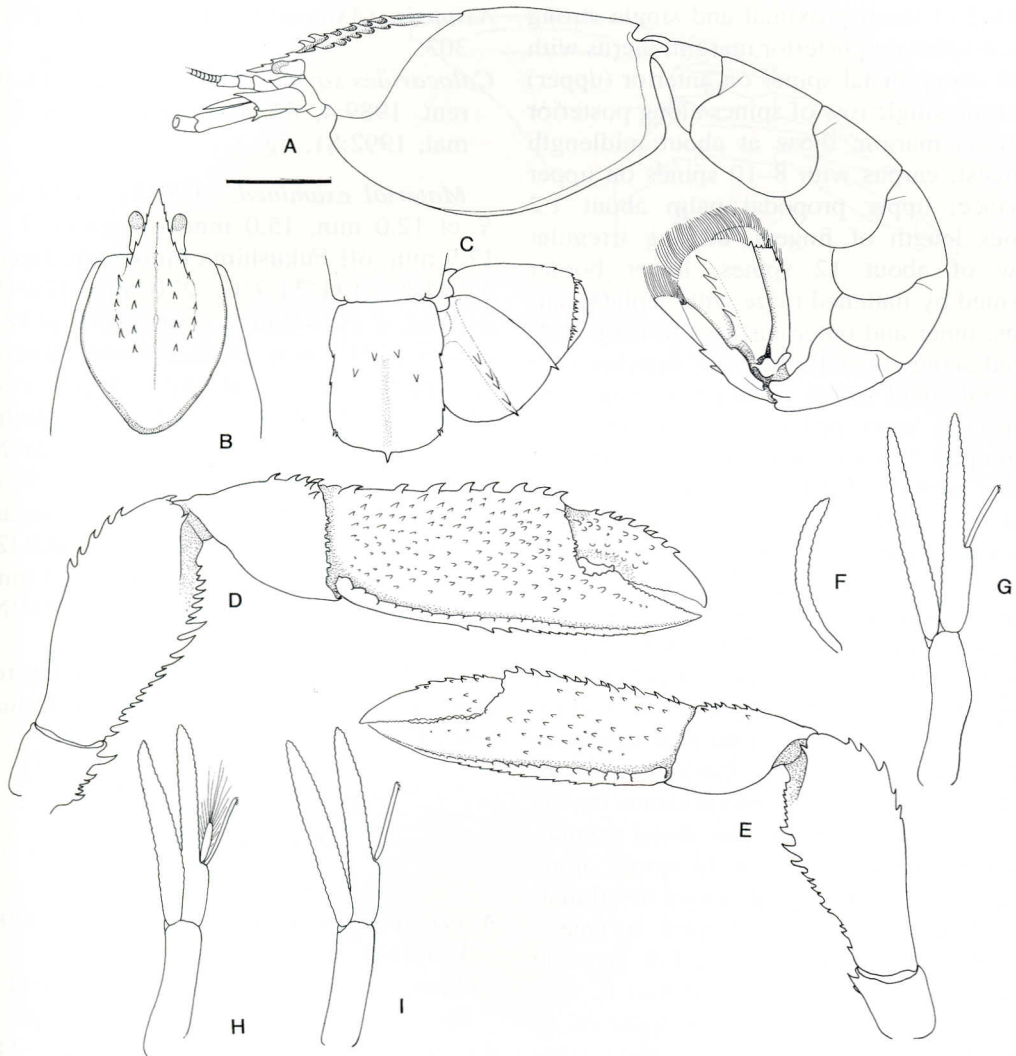


Fig. 6. *Calocarides rostriserratus*: A, Lateral view, scale = 5 mm; B, Anterior carapace in dorsal view; C, Telson and right uropod in dorsal view; D, Pereopod 1, larger cheliped; E, Pereopod 1, smaller cheliped; F, Pleopod 1, female; G, Pleopod 2, female; H, Pleopod 2, male; I, Pleopod 3, male.

imal teeth on posterior margin, distal margin entire; merus with 2 strong distal teeth on posterior margin. Pereopod 1, larger (broader) cheliped, ischium with about 5 small proximal and single strong distal spine on posterior margin; merus with 5 distal spines on upper (anterior) margin, posterior margin with single row of spines of varying length, those at about midlength longest; carpus with several (6-7) small spines on upper surface; upper propodal

palm 1.2 times length of fingers, bearing row of 8 strong spines, lower border consisting of flattened distally narrowed ridge having dentate margins, medial and lateral surfaces bearing moderately dense scattered conical tubercles, cutting edge of fixed finger having rounded proximal cusp; dactylus with upper margin bearing about 8 strong spines, cutting edge having rounded proximal cusps, distally finely denticulate. Pereopod 1, smaller (narrower) cheliped, ischium

with 2–3 small proximal and single strong distal spine on posterior margin; merus with 5–6 strong distal spines on anterior (upper) margin, single row of spines along posterior (lower) margin, those at about midlength longest; carpus with 8–10 spines on upper surface; upper propodal palm about 1.2 times length of fingers, bearing irregular row of about 12 spines, lower border formed by flattened ridge with dentate margins, inner and outer surfaces bearing scattered acute conical tubercles; dactylus with several small spines on upper surface, cutting edge more or less evenly denticulate. Pereopod 2, basis with single spine on posterior surface; ischium with proximal and one or 2 stronger distal spine on posterior margin; merus with 3 or 4 spines in mid-region of posterior margin. Pleopod 1 in female a slender elongate ramus; pleopod 2 in male with rod-shaped appendix masculina bearing distal setae, noticeably shorter than appendix interna; pleopods 2–5 in female, 3–5 in male with appendix interna at about proximal third of mesial margin of endopod. Uropod with lateral ramus having 2–3 small lateral spines plus distal submarginal mobile spine; about 13 spines along suture; mesial ramus with single distal marginal spine, 4–5 spines on upper surface.

Remarks.—In spite of Sakai & de Saint Laurent's (1989:80) statement that *C. rostriserratus* is probably a synonym of *C. quinqueseriatus*, *Calocarides rostriserratus* differs from *C. quinqueseriatus*, its geographically nearest congener, in several easily seen features: in having two pairs of dorsal telsonic spines (one pair in *C. quinqueseriatus*), and two or three lateral telsonic spines (five or six in *C. quinqueseriatus*); and in having the chelae of pereopod 1 broader and less elongate, and with spines only in the distal half of the anterior margin of the merus (full anterior margin of merus bearing spines in *C. quinqueseriatus*).

Calocarides soyoi (Yokoya, 1933)

Axius soyoi Yokoya, 1933:49, fig. 25.—Horikoshi et al., 1982:30, 33, 38, 39, 120, 145, 168.

Axiopsis (Axiopsis) soyoi.—Sakai, 1987:303.

Calocarides soyoi.—Sakai & de Saint Laurent, 1989:4, 83, 103.—Kensley & Komai, 1992:81, fig. 1.

Material examined.—USNM 243563, 2 ♀ cl 12.0 mm, 15.0 mm, ovigerous ♀ cl 17.9 mm, off Fukushima Prefecture, Japan, 37°04'N, 141°31.7'E, 270 m.—USNM 243564, ♂ cl 14.2 mm, ovigerous ♀ cl 18.8 mm, ♀ cl 11.8 mm, off Hachinohe, Aomori Prefecture, Japan.—HUMZ-C990, 3 ♀ cl 11.3 mm, 14.1 mm, 13.0 mm, off Hachinohe, Aomori Prefecture, Japan, 42°52.6'N, 145°22.2'E, 152 m.—HUMZ-C994, ♀ cl 16.9 mm, off Fukushima Prefecture, Japan, 37°17.3'N, 141°21.4'E, 141 m.—HUMZ-C998, 3 ♂ cl 12.4 mm, 15.0 mm, 15.3 mm, off Fukushima Prefecture, Japan, 37°04'N, 141°31.7'E, 270 m.

Remarks.—This species was recently re-described and figured by Kensley & Komai (1992).

Calocarides spinulicauda

(Rathbun, 1902)

Fig. 7

Axius spinulicauda Rathbun, 1902:886; 1904:149, fig. 90.

Axiopsis spinulicauda.—Schmitt, 1921:111, fig. 74.—Butler, 1961:60, figs. 1, 2, pl. 1.

Axiopsis (Axiopsis) spinulicauda.—De Man, 1925:6, 67, 69.

Acanthaxius spinulicaudus.—Sakai & de Saint Laurent, 1989:4, 66, 103.

Material examined.—Holotype, USNM 25239, ♀ cl 15.5 mm, R/V *Albatross* sta 3172, off Bodega Head, California, 113 m.

Diagnosis.—Carapace surface smooth; rostrum with 5 (left) and 6 (right) lateral teeth, including supraocular; median carina barely reaching onto base of rostrum, with 3 spines anterior of tubercle, entire posterior to tubercle; postcervical median carina obsolete except close to posterior margin of carapace; submedian carina short, entire; lateral carina entire posterior to supraocular

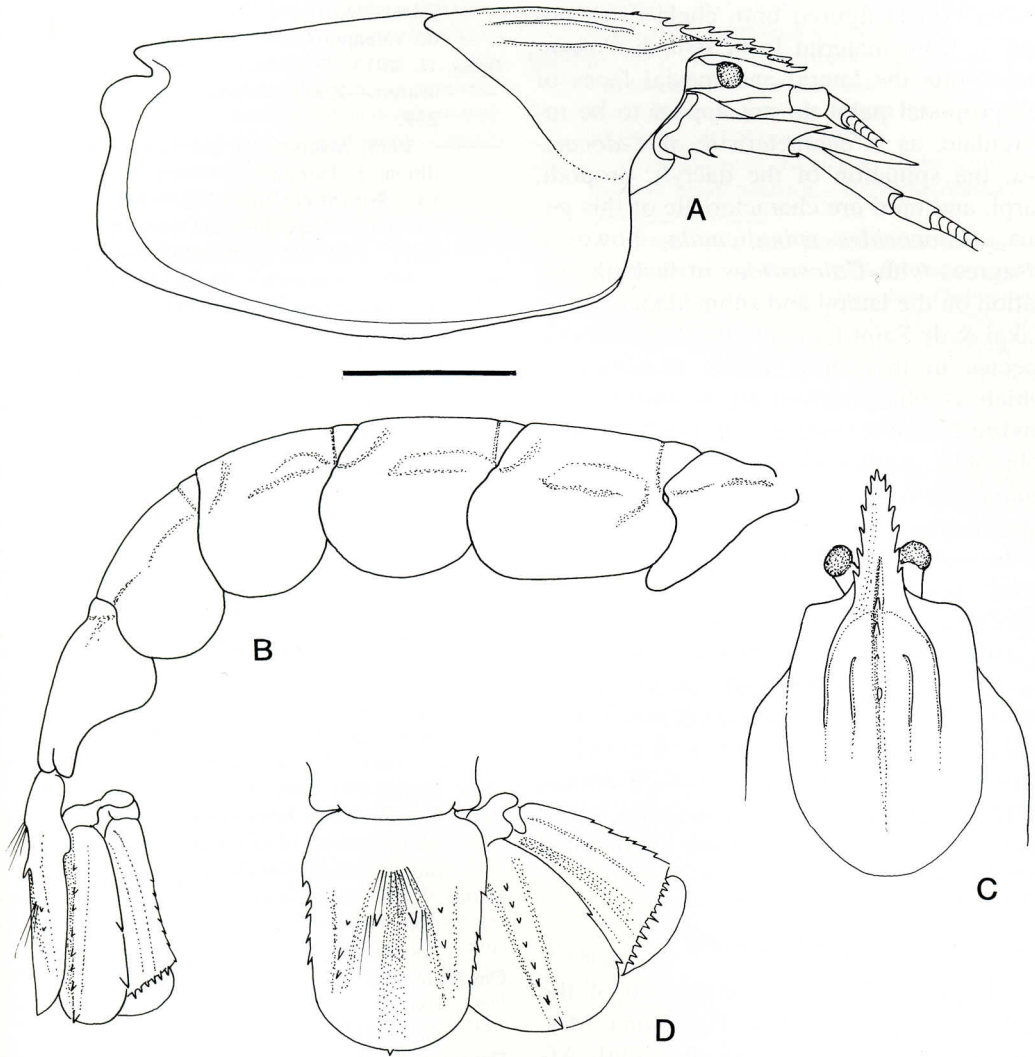


Fig. 7. *Calocarides spinulicauda*: A, Carapace in lateral view, scale = 5 mm; B, Abdomen in lateral view; C, Anterior carapace in dorsal view; D, Telson and right uropod in dorsal view.

spine of rostral series. First abdominal pleuron ventrally narrowed apically rounded with tiny denticle; pleura 2-6 broadly rounded. Telson with lateral margin bearing larger fixed anterior spine, 4-5 small more posterior fixed spines; posterior margin evenly convex; submedian longitudinal ridge bearing 3 fixed spines, pair of fixed anterior spines mesial to longitudinal ridge present.

Maxilliped 3, ischium with 1 or 2 tiny denticles on posterior margin; merus with 3

distal spines on posterior margin. Pereopod 1, both chelipeds missing. Pereopod 2, merus with 2 or 3 well separated spines on posterior margin. Lateral uropodal ramus with 7 small distal spines on lateral margin, transverse suture with row of 11-12 small spines; mesial ramus with 2 strong spines on lateral margin, dorsal ridge with 7 or 8 small fixed spines.

Remarks.—Rathbun (1902), in her description of *A. spinulicauda*, noted that the chelae of the first pereopod were missing.

Butler (1961) figured both chela of pereopod 1, from material from British Columbia. While the lateral and mesial faces of the propodal palm do not appear to be tuberculate, as is characteristic of *Calocarides*, the spination of the dactyli, propodi, carpi, and meri are characteristic of this genus. *Calocarides spinulicauda*, however, disagrees with *Calocarides* in lacking spination on the lateral and submedian carinae. Sakai & de Saint Laurent (1989) placed this species in their new genus *Acanthaxius*, which is characterized by a tendency to having a double cornea, and a lack of pleurobranchs, neither of which are seen in *C. spinulicauda*. With only the female holotype available for examination, the nature of the male pleopods and the first pereopods being uncertain, unambiguous generic placement is almost impossible.

Axius spinulicauda amurensis Kobjakova, 1937, (see also Derjugin & Kobjakova 1935:142), described from the Sea of Japan, while clearly not a subspecies of the Californian *Calocarides spinulicauda* Rathbun, 1902, is difficult to place generically, given the single small figure and the abbreviated description.

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