

NEW GENERA IN THE THALASSINIDEAN
FAMILIES CALOCARIDIDAE AND AXIIDAE
(CRUSTACEA: DECAPODA)

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Abstract.—The family Calocarididae Ortmann, 1891, is resurrected and re-diagnosed. Three characters distinguish members of the family: hermaphroditism, eye reduction, and second pleopods having enlarged appendices masculinae along with loss of the distal endopod. The first pleopods are spatulate and somewhat plow-shaped, a character also seen in some axiids. Four genera are included in the Calocarididae: *Calastacus*, *Calocaris*, *Callistocaris*, and *Lophaxius*, the latter two being described as new. Two new genera in the Axiidae are described: *Posthonocaris* and *Sakaiocaris*. A scheme for the derivation of the Calocarididae from more generalized axiids such as the two newly-described genera, is proposed.

The families and many of the genera of the Thalassinidea are extremely poorly defined, with little sense of phylogeny in the currently accepted classification. The Axiidae in particular contains several more or less well diagnosed and probably polyphyletic genera. In the course of a phylogenetic study of the thalassinideans, it became clear that a group of four genera of axiids were more closely related to each other than to the rest of the family. Almost 100 years ago, Ortmann (1891), placed one of these genera in a separate family, the Calocaridae, but this taxon received no recognition and has not been used in the last 50 years. This family is now resurrected and re-diagnosed for this group of four probably monophyletic genera.

Calocarididae Ortmann, 1891

Calocaridae Ortmann, 1891:47, 50.—Stephensen, 1910:75, 77, 189.—Runnström, 1925:14.

Type genus.—*Calocaris* Bell, 1853.

Diagnosis.—Hermaphroditic, generally deepwater forms, with eyes showing some reduction and loss of both pigment and ommatidial facets. *Linea thalassinica* absent.

Maxilla 2 scaphognathite bearing spinulose whip. Maxilliped 3 bearing dentate ischial crest. Pereopods lacking exopods. Pereopods 1 and 2 chelate. Pleopodal rami elongate-slender. Pleopod 1 always present, of 2 articles, directed anteromesially along posterior thoracic sternites, with distal article broadened and flattened, and bearing proximomesial cluster of hooks (fused appendix interna). Pleopod 2 present, showing loss of distal endopod, enlargement of appendix masculina, and eventual fusion of appendix interna with appendix masculina. Uropodal outer ramus with transverse suture.

Genera.—*Calastacus* Faxon, 1893; *Callistocaris*, new genus; *Calocaris* Bell, 1853; *Lophaxius*, new genus.

Remarks.—Ortmann (1891) designated the new family Calocaridae, characterized by four features: rostrum flat, triangular; pleopodal rami narrow; outer uropodal ramus with suture; podobranchs and mastigobranchs present on pereopods. Ortmann further suggested that eventually two subfamilies, the Calocarinae and the Lao-midiinae, would need to be distinguished. Stephensen (1910), in a rather obscure semi-

popular handbook, used the name Calocaridae as a family of the Anomura, though not designating an author. His diagnosis, loosely translated, reads: "The large chelae have straight long fingers, but no tubercles. Two pairs of legs have chelae. Suture across outer branches of uropod. (*Footnote—By a misfortune this suture was dropped from fig. 51). Only one genus and species with us" [presumably meaning 'in Denmark']. Following this diagnosis, is a short discussion and figure of *Calocaris macandreae* Bell. The only other use of the name Calocaridae I have been able to trace, is that of Runnström (1925). This family name (in corrected form), is now resurrected, and its diagnosis expanded, to include several related genera, but not the genera of the Laomidiidae, which are markedly different.

Calastacus Faxon, 1893

Calastacus Faxon, 1893:194.—Borradaile, 1903:539.—de Man, 1925:8, 116.—Balss, 1957:1580.—de Saint Laurent, 1972:353, 354.

Type species.—By monotypy, *Calastacus stilirostris* Faxon, 1893:194.

Diagnosis.—Hermaphroditic. Carapace: supraocular spine present; post-cervical carina and spines lacking; rostrum at lower level than anterior carapace; rostral margins unarmed (except for supraocular spine); median carina entire; submedian carina lacking; lateral carina present only as short posterior extension of lateral rostral margins. Eye lacking pigment, stalk equal to or shorter than cornea. Antennal acicle a slender, elongate spike.

Maxillipeds: exopods on 1–3; epipods on 1–3, with small podobranch on 3; 2 arthrobranches on 3.

Pereopods: lacking exopods; epipods on 1–4, small podobranchs on 1–3; 2 arthrobranches on 1–4; pleurobranches lacking; propodi and dactyli of 3–5 cylindrical, not expanded; pereopod 1 chelipeds slightly asymmetrical, not sexually dimorphic; pe-

reopod 2 chelate; pereopods 3–5, dactyli simple.

Pleopods: rami elongate-slender; appendix interna present on 2–5; pleopod 1 of 2 articles, distal article broad, plow-shaped, appendix interna represented by small mesial lobe bearing hooks; pleopod 2 with small appendix interna fused with basal article of appendix masculina; both articles of latter with double row of setae on mesial margin.

Uropod: outer ramus with transverse dentate suture.

Telson: lacking dorsal spines, longer than wide.

Species.—

Calastacus laevis de Saint Laurent, 1972.

Bay of Biscay, north-east Atlantic, 950–1000 m.

Calastacus stilirostris Faxon, 1893. Pacific Mexico, 1208 m.

Callistocaris, new genus

Type species.—By present designation, *Calocaris alcocki* (McArdle, 1900).

Etymology.—The generic name is derived from the Greek "kallistos"—most beautiful, plus "karis"—a shrimp. Gender: feminine.

Diagnosis.—Hermaphroditic. Carapace: strong supraocular spine present; postcervical carina and spines lacking; rostrum set slightly lower than anterior carapace; rostral margins armed; median carina entire; submedian carina entire; lateral carina entire posterior to supraocular spine. Eye lacking pigment, anteriorly flattened, with mesio-distal tubercle; eye and stalk not differentiated. Antennal acicle fairly well developed, spike-like, but considerably less than half length of peduncle article 4.

Maxillipeds: exopods and epipods (no podobranchs) on 1–3; 2 arthrobranches on 3.

Pereopods: exopods lacking; epipods on 1–4, podobranchs lacking; 2 arthrobranches on 1–4; pleurobranches lacking; propodi and dactyli of 3–5 not expanded; pereopod 1 chelae symmetrical, lacking gape between

fingers; pereopod 2 chelate; dactyli of 3–5 simple. Branchiae simple, lacking pinnae.

Pleopods: rami elongate-slender, appendix interna lacking on 3–5, pleopod 1 uniramous, biarticulate, distal article bilobed, with small mesial patch of hooks; pleopod 2 appendix masculina with indication of fusion of 2 articles, with double row of spines along mesial margin, and with appendix interna fused basally.

Uropod: outer ramus with transverse nondentate suture.

Telson: longer than wide, lacking dorsal spines.

Species.—

Callistocaris aberrans (Bouvier, 1905). Off St. Lucia, Lesser Antilles, 809 m.

Callistocaris alcocki (McArdle, 1900). Bay of Bengal, 992 m.

Callistocaris cf. *alcocki* (McArdle, 1900). SW Indian Ocean, 1000 m.

Calocaris Bell, 1853

Calocaris Bell, 1853:231.—Ortmann, 1891: 50, pl. 1, fig. 5d–i.—Borradaile, 1903: 539.—de Man, 1925:7, 114.—Balss, 1957: 1580.—de Saint Laurent, 1972:353, 354.

Type species.—By monotypy, *Calocaris macandreae* Bell, 1853:233.

Diagnosis.—Hermaphroditic. Carapace: supraocular spine part of lateral rostral spine series; post-cervical carina entire; rostrum at slightly lower level than anterior carapace; rostral margins armed; median carina entire; submedian carina absent; lateral carina armed. Eye lacking pigment, stalk and cornea not differentiated; anteriorly flattened and contiguous along midline. Antennal acicle reduced to barely visible scale.

Maxillipeds: exopods and epipods on 1–3; reduced podobranch on 2 and 3; 2 arthrobranchs on 3.

Pereopods: lacking exopods; epipods on 1–4, small podobranchs on 1–3; 2 arthrobranchs on 1–4; pleurobranchs lacking; propodi and dactyli of 3–5 not expanded; pereopod 1, chelae subsimilar, symmetrical, not sexually dimorphic, broad gape between fin-

gers; pereopod 2 chelate; pereopods 3–5 dactyli simple.

Pleopods: pleopod 1 of 2 articles, distal article expanded, lobed, with patch of hooks on small mesiodistal lobe; pleopod 2, endopod lacking distal portion, appendix masculina slender, mesially setose, of single article, appendix interna articulating at its base.

Uropod: outer ramus with transverse nondentate suture.

Telson: longer than wide, with or lacking two rows of submedian non-articulating dorsal spines.

Species.—

Calocaris barnardi Stebbing, 1914. Off Saldanha Bay, South Africa, 89–180 m. Off Namibia, 338 m.

Calocaris granulatus Grebenyuk, 1975. Gulf of Alaska.

Calocaris macandreae Bell, 1853. Mediterranean; North-east Atlantic, 25–1072 m.

Calocaris sp. Indian 'form' of *C. macandreae* (see Alcock, 1901): Bay of Bengal, Arabian Sea.

Calocaris templemani Squires, 1965. Northwest Atlantic, Newfoundland, Gulf of Maine, 260 m.

Lophaxius, new genus

Type species.—By present designation, *Lophaxius rathbunae*, new species (= *Calastacus investigatoris* Rathbun, 1904, *non* Anderson, 1896).

Etymology.—The generic name is derived from the Greek 'lophos,' a crest or mane, referring to the post-cervical mid-dorsal ridge of the carapace, plus the frequently-used 'axius.' Gender: masculine.

Diagnosis.—Hermaphroditic. Carapace: supraocular spine (part of lateral rostral series) present; post-cervical carina with irregular tubercles present; rostrum at slightly lower level than anterior carapace; rostral margins armed; median carina entire; submedian carina absent; lateral carina only extending short distance posterior to rostrum, with one or two spines. Cornea un-

pigmented, not flattened; stalk subequal to cornea in length. Antennal acicle short. Maxillipeds 1–3 with exopods and epipods; large podobranch on 2 and 3; 2 arthrobranches on 3.

Pereopods: exopods lacking; epipods on 1–4, with large podobranch on 1–3; 2 arthrobranches on 1–4; pleurobranches lacking; pereopod 1 symmetrical, fingers of chelae gaping basally; pereopod 2 subchelate; dactyli of 3–5 simple.

Pleopods: rami elongate-slender; appendix interna present on 2–5; pleopod 1 of 2 articles, distal article spatulate, with small mesial patch of hooks; pleopod 2, appendix masculina slender, tapering, setose, with appendix interna articulating at its base.

Uropod: outer ramus with transverse nondentate suture.

Telson: longer than wide, with dorsal non-articulating spines.

Species. —

Lophaxius investigatoris (Anderson, 1896). Arabian Sea, 1733 m.

Lophaxius rathbunae, new species. North-eastern Pacific, Alaska to California, 549–1190 m.

Remarks.—*Lophaxius* resembles *Calastacus* in having non-pigmented eyes, and with the cornea not flattened as in *Calocaris*. It differs from typical *Calastacus* in having spines on the rostrum, pleopod 1 not as broadly plow-shaped, the appendix masculina of pleopod 2 not as modified, the appendix interna free, in having a well developed postcervical carina, and in having the chela of pereopod 1 with a gap between fingers as in *Calocaris*.

Lophaxius rathbunae, new species

Calastacus investigatoris Rathbun, 1904: 151, non Anderson, 1896.—Schmitt, 1921:112, fig. 75, non Anderson, 1896.

Diagnosis.—Carapace, palm of first chela, abdominal somites, uropods, and telson tuberculate. Merus of pereopod 1 with about 10 spines on anterior (upper) margin, eight

spines on posterior (lower) margin. Outer uropodal ramus with six spines on outer margin; inner uropodal ramus with two or three spines on outer margin.

Material.—Syntypes, USNM 28316, cl 19.5 mm, *Albatross* sta 3347, off Cascade Head, Oregon, 631 m.—USNM 28317, cl 19.1 mm, *Albatross* sta 3210, south of Dan-nakh Islands, Alaska, 884 m.—USNM 28318, ovig. cl 18.4 mm, 17.1 mm, *Albatross* sta 2928, off San Diego, California, 763 m.—USNM 155734, cl 17.1 mm, *Albatross* sta 4352, off San Diego, California, 979–1005 m.

Remarks.—The species *Calastacus investigatoris* Anderson, 1896, from 1733 m in the Arabian Sea is, from the description and figure (Alcock & Anderson 1896:pl. 25, fig. 1) remarkably similar to the north-eastern Pacific species, but differs in having weaker spination on the anterior and posterior margins of the merus of the first chelipeds, and in lacking marginal teeth on the inner uropodal ramus. No doubt further differences would be apparent, were material of the Indian Ocean species available. Indeed, Rathbun (1904:151) mentioned that not all the eastern Pacific specimens agreed with Alcock's description; she also noted some variability in the specimens at her disposal. Given the vast distance between the Indian and Pacific Ocean records, and the differences noted, the two species cannot be regarded as conspecific.

Key to genera of the Calocarididae

1. Post-cervical carina or ridge present on carapace 2
- Carapace lacking post-cervical carina 3
2. Eyes flattened, mesially contiguous *Calocaris*
- Eyes rounded, not mesially contiguous *Lophaxius*
3. Eyes rounded; appendix masculina mesially setose *Calastacus*
- Eyes flattened; appendix masculina mesially spinose *Callistocaris*

Axiidae Huxley, 1878

Posthonocaris, new genus

Type species.—By present designation, *Axius rudis* Rathbun, 1906.

Etymology.—The generic name is a combination of the Greek 'posthon'—one having a large penis (referring to the large appendix masculina), plus 'karis'—a shrimp. Gender: feminine.

Diagnosis.—Gonochoristic, but with hermaphroditic forms occurring in the population. Carapace: cervical groove present; postcervical carina and spines absent; rostral margins armed; median carina entire; submedian carina dentate; lateral carina entire (apart from supraocular spine). Eyes well pigmented; eyestalk rounded, longer than or subequal to cornea. Antennal acicle a well developed spike.

Maxillipeds: exopods on 1–3; epipod present on 1 and 2; 3 with epipod plus podobranch, two arthrobranches.

Pereopods: exopods absent; pereopods 1–3 with epipod plus podobranch; pereopod 4 with epipod only; two arthrobranches on 1–4; one pleurobranch on 2–4. Pereopod 1 chelae asymmetrical. Pereopods 3–5, dactyli simple.

Pleopods: Rami elongate-slender. Pleopod 1 in female slender-elongate, of 2 articles, distal article bearing marginal setae; pleopod 1 of male or hermaphrodite spatulate, of 2 articles, distal article bearing proximomesial clump of hooks; pleopod 2 of male or hermaphrodite with distal setose portion of endopod somewhat reduced, appendix masculina and appendix interna articulating at about midlength of endopod, appendix masculina elongate, setose, reaching well beyond apices of endopod and exopod; pleopods 3–5 lacking appendices interna.

Uropod: Outer ramus with transverse dentate suture.

Telson: With non-articulating dorsal spines; single posterolateral articulating spine.

Species.—

Lophaxius longipes (Bouvier, 1905), off Barbados, 225 m.

Lophaxius rudis (Rathbun, 1906), off Hawaii, 73–426 m.

Sakaiocaris, new genus

Type species.—By present designation, *Axiopsis brucei* Sakai, 1986.

Etymology.—The generic name is a combination of 'sakai,' for Dr. Katsushi Sakai, plus the Greek 'karis'—a shrimp. Gender: feminine.

Diagnosis.—Males, females, and hermaphroditic forms occurring in same species. Carapace: cervical groove present; post-cervical carina a low rounded ridge lacking spines or tubercles; rostral margins dentate; median carina dentate; submedian carina dentate; lateral carina dentate. Eye with reduced pigmentation; eyestalk rounded. Antennal acicle a well developed spike.

Maxillipeds: 1–3 with epipod and exopod, 2–3 with reduced podobranch; two arthrobranches on 3.

Pereopods: exopods lacking; epipod plus podobranch on 1–3; epipod only on 4; two arthrobranches on 1–4; one pleurobranch on 2–4. Pereopod 1, chelae asymmetrical. Pereopod 2 chelate. Pereopods 3–5, dactyli simple.

Pleopods: Pleopod 1 of male of 2 articles, distal article spatulate, with proximomesial clump of small hooks. Pleopod 1 in female (and in only hermaphrodites seen), slender, elongate, of 2 articles, distal article bearing marginal setae; pleopod 2 in male with large exopod and endopod, setose appendix masculina and appendix interna both articulating proximally on endopod. Pleopods 3–5 with free appendix interna.

Uropod: outer ramus with dentate transverse suture.

Telson: with non-articulating dorsal spines; with two articulating postero-lateral spines.

See Sakai, 1986

= Bouvier, 1905

See Sakai, 1986

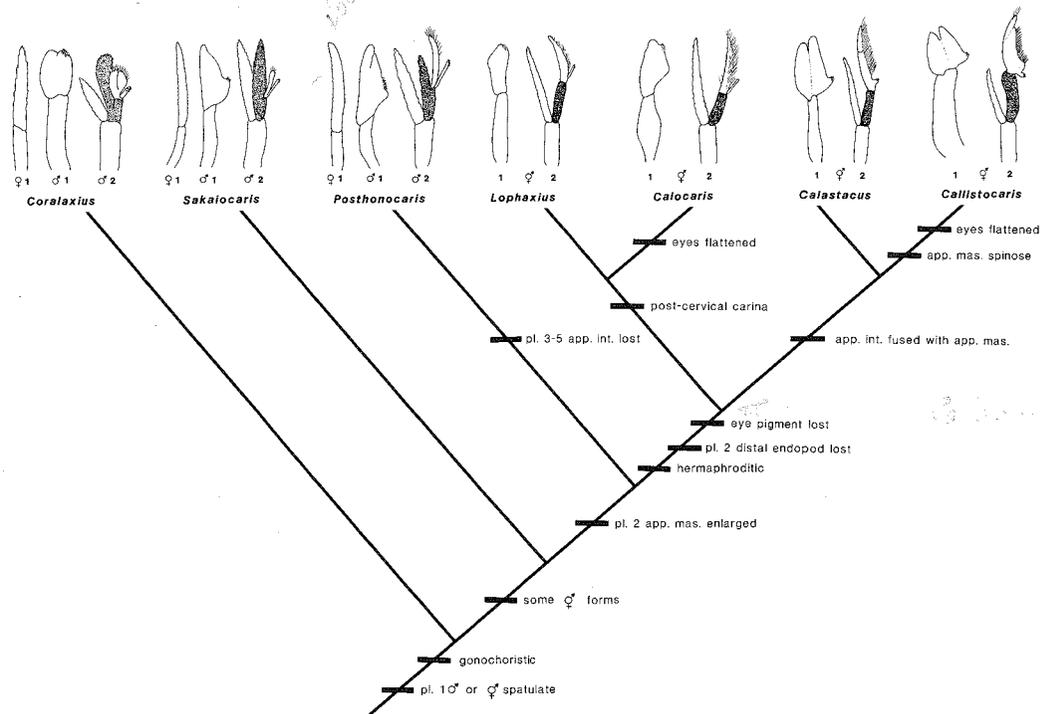


Fig. 1. Hypothetical scheme for derivation of the Calocarididae from more generalized Axiidae, illustrating pleopods 1 and 2, and changes in character-states. Endopod of pleopod 2 shaded. (Abbreviations: app. int.—appendix interna; app. mas.—appendix masculina; pl.—pleopod.)

Species.—

Sakaiocaris brucei (Sakai, 1986); off Western Australia, in hexactinellid sponges, 296–458 m.

Discussion

Three synapomorphies separate the Calocarididae from the Axiidae (s.l.). 1. Invariable hermaphroditism. 2. Enlargement of the appendix masculina of pleopod 2, along with loss of the setose distal element of the endopod. 3. Eye reduction and loss of eye pigment.

A possible pathway in the development of hermaphroditism, from purely gonochoristic forms (e.g., *Coralaxius*), through forms having some hermaphrodites in the population (e.g., *Posthonocaris*, *Sakaiocaris*), to purely hermaphroditic forms (*Calo-*

caris, *Calastacus*, *Callistocaris*, *Lophaxius*), is illustrated in Fig. 1. *Coralaxius* Kensley & Gore, 1981, is purely gonochoristic, and possesses sexually dimorphic first pleopods. In the male, the first pleopod is uniramous and biarticulate, the distal article being spatulate and having a clump of mesial hooks. These latter are presumed to come from the appendix interna which has fused with the endopod; the exopod has either been lost or has fused with the endopod. It is postulated that the genera *Posthonocaris* and *Sakaiocaris* have hermaphroditic forms in the population. In these, the first pleopod of the female or protandrous hermaphrodite is a slender setose, uniramous, biarticulate structure, while in the males, a spatulate first pleopod very similar to those found in the Calocarididae is seen. The presence of pro-

tandrous hermaphrodites in populations of decapod species has been well documented. Policansky (1982) mentions a variety of decapod crustaceans in which protandry occurs, including *Calocaris macandreae* in which the biology, and especially reproduction, has been well examined (see Wollebaek 1909, Runnstrom 1925, Buchanan 1963). Bauer (1986) reported the presence of primary males, primary females, and protandric hermaphrodites that pass through a male phase, a transitional phase, and then become breeding females, in the hippolytid caridean shrimp *Thor manningi*. While ten specimens of *Sakaiocaris brucei* and four specimens of the two species of *Posthonocaris* form too small a sample on which to state with certainty that protandrous hermaphrodites occur in these populations, the dimensions of the specimens (at least of the former species) would seem to suggest this. The only ovigerous female of *S. brucei* seen has a carapace length of 21.9 mm; the three hermaphrodites with their female first pleopods measure 16.1, 19.6, and 20.0 mm (suggesting that these are either in the transitional phase or approaching the breeding female phase), while five males range from 13.8–23.3 mm.

Posthonocaris seems to represent a more advanced stage than *Sakaiocaris*, in this supposed trend towards hermaphroditism. This is seen in the reduction of the setose distal portion of endopod of pleopod 2, an elongation of the proximal non-setose portion, and marked enlargement of the appendix masculina. In the fully hermaphroditic calocaridids *Calastacus* and *Callistocaris*, the final stage of this trend, with complete loss of the distal endopod, and enlargement and specialization of the appendix masculina, with which the appendix interna has fused, can be seen.

There would seem to be a correlation between development of hermaphroditism and depth distribution in this group of thalassinideans. *Coralaxius*, with its spatulate first pleopod in the male, is a shallow (11–76 m) coral reef inhabitant. *Sakaiocaris* inhabits hexactinellid sponges in 296–456 m. Per-

haps there is a reproductive advantage in having a hermaphroditic phase in this species, given its cryptic habit. Species of *Posthonocaris* have been recorded in depths of 73–426 m; *Calocaris* from 89–1072 m; *Callistocaris* from 809–1000 m; *Calastacus* from 970–1208 m; *Lophaxius* from 1733 m.

Loss of eye pigment and corneal facets, along with a breakdown of the distinction between cornea and stalk, can be seen in the four genera of the Calocarididae, suggesting loss of function linked to increased depth distribution. The hypothetical scheme proposed in Fig. 1 requires that anteriorly flattened eyes arose independently in *Calocaris* and *Callistocaris*, which is not unfeasible. Similar flattening of eyes can be seen in several decapod groups such as cave-dwelling hippolytid shrimps, deepsea bresiliid shrimp, as well as in the stomatopod genus *Bathysquilla* (R. B. Manning, pers. comm.).

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