

**A new species of axiid shrimp from chemosynthetic communities of
the Louisiana continental slope, Gulf of Mexico
(Crustacea: Decapoda: Thalassinidea)**

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Abstract.—*Calaxius carneyi*, new species (Axiidae), is described from two male specimens collected by manned submersibles working near hydrocarbon seeps in deep waters (544 m) on the continental slope off Louisiana, in the northern Gulf of Mexico. Both specimens were taken adjacent to communities of clams that comprise a major constituent of chemosynthetic assemblages at the collection site. The new species is characterized in part by ventrally truncate abdominal pleura, as opposed to the acutely triangular or broadly rounded pleura found in other known members of *Calaxius*, only one of which is known to occur in the Atlantic Ocean. The new species is readily distinguished from its congeners by unique dentition of its heavy triangular rostrum and postrostral carapace, its short eyestalks and antennal acicle, the absence of well-defined teeth on the massive chelipeds, and the narrow, subtriangular telson. Chelipeds, pleopods and uropods of the two known specimens herewith described are covered extensively by long setae, many of which are plumose and densely fouled by flocculent debris.

Recent investigations of methane cold seeps in the Gulf of Mexico have discovered a number of previously undescribed taxa associated with chemosynthetic communities in deep waters of the continental slope (e.g., Gustafson et al. 1998). However, some collections from these unique habitats consist of single specimens, and comparative studies have been deferred pending recovery of additional materials. One such case was presented by the collection of a single, somewhat fragmented, molted integument from the male of an apparently undescribed axiid mud shrimp, collected in 1988 during a dive of the manned submersible *Pisces II*. A second, smaller, intact male specimen, was obtained

from an adjacent site in 1992 with a shallow core sampler deployed by the *Johnson Sea-Link* manned submersible. Collections on subsequent dives by submersibles and vessel-based box coring in this area have brought no additional materials to our attention.

While the female of this species remains unknown, it is readily apparent that the species is undescribed. The marked size difference between the intact specimen and the earlier recovered exuvia provides a glimpse of ontogenetic variation in characters, and allows us to select diagnostic characters that should apply to a wide size range. Also, from familiarity with typical sexual dimorphism in congeneric species, we expect that the description here provided will serve adequately for identification of female specimens, if encountered.

* Deceased.

Upon arrival at the surface, specimens were fixed in 10% formalin (with Rose Bengal stain for only the 1992 collection), transferred to 80% ethyl alcohol, and finally archived in 70% ethyl alcohol. Carapace length (CL) was measured from the posterior margin of the orbit to the posterior margin of the carapace midline. Total length (TL) was measured from the tip of the rostrum to the tip of the extended telson. Specimens are archived in the National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C.

Family Axiidae Huxley, 1879

Calaxius Sakai & de Saint Laurent, 1989

Calaxius carneyi, new species

Figs. 1 & 2

Material examined.—Holotype, USNM 1009165, male, CL 10.1 mm, TL 26.5 mm, *Johnson Sea-Link* submersible sta 3269, box core B, deployed from submersible about 2 m from chemosynthetic mussel community, Bush Hill site, 544 m, Louisiana continental slope, northern Gulf of Mexico, 27°46.904'N, 91°30.286'W, 11 Aug 1992. Paratype, USNM 1009166, exuvia of male, CL 18.3 mm, TL 50.5 mm, submersible *Pisces II* sta 880031 (8831), location and depth same as for holotype, Aug 1988.

Diagnosis.—Rostrum heavy, triangular, extending slightly more than twice length of eyes, bearing flattened, upturned terminal spine and pair of similar upturned subterminal spines. Antennal acicle short, overreaching proximal third of penultimate (fourth) peduncular article. Chelipeds massive, lacking well defined teeth. Carapace bearing dentate lateral and submedian carina. Pereopodal epipods and pleurobranches present. Abdomen with pleura 3–5 ventrally truncate, bearing small anterior and posterior marginal denticles; lacking male pleopod 1; appendices internae on pleopods 2–5; uropodal exopod bearing transverse suture; terminated by narrow, subtriangular telson.

Description of holotype.—Integument firm but pliable, with numerous clumps of elongate, plumose, fouled setae, often obscuring underlying structures on chelae, pleopods, uropods, and telson; calcification most heavy in carapace teeth and chelae. Carapace with posterior midline elevated, bracketed on either side by paired setose punctae, midline elevation becoming a rounded crest in cardiac region where surmounted by a slight but distinct prominence or tubercle, marked dorsally by translucent or worn area (Fig. 1a); rostrum heavily calcified, triangular, slightly more than twice length of eyes, terminal spine subacute, upturned, dorsoventrally flattened, triangular in dorsal view; subterminal pair of spines similar to terminal, also upturned, imparting concave appearance to flattened dorsal surface of rostrum (Fig. 1b, c); supraocular spines (lacking in the paratype, a larger specimen) and supraorbital spines strong, similar in calcification, shape and orientation to subterminal pair; lateral carina originating from supraorbital spine, diminishing immediately anterior to second spine or tooth, continuing as a low ridge toward posterior; submedian carina originating from posteriormost of two slightly offset submedian teeth, becoming ill-defined toward posterior; median carina a weak crest bearing a worn tubercle near its posterior end, and otherwise lacking ornamentation.

Sternite of fourth pereopods (seventh thoracic somite) with deep median slit, thoracic shield produced to form acute, marginally sinuate, triangular flange to either side; 3-branched carina set between articulations of fourth pereopods (Fig. 2a). Abdominal pleuron 1 narrowed, acute ventrally (Fig. 1a); pleuron 2 ventrally broad, with an angular tooth or acute corner at the posteroventral end; pleura 3–5 ventrally truncate, with small acute tooth on anteroventral margin and another on posteroventral margin; pleuron 6 with small acute tooth on anteroventral margin and broad triangular flange at posteroventral margin.

Eyestalks small, subcylindrical, reaching

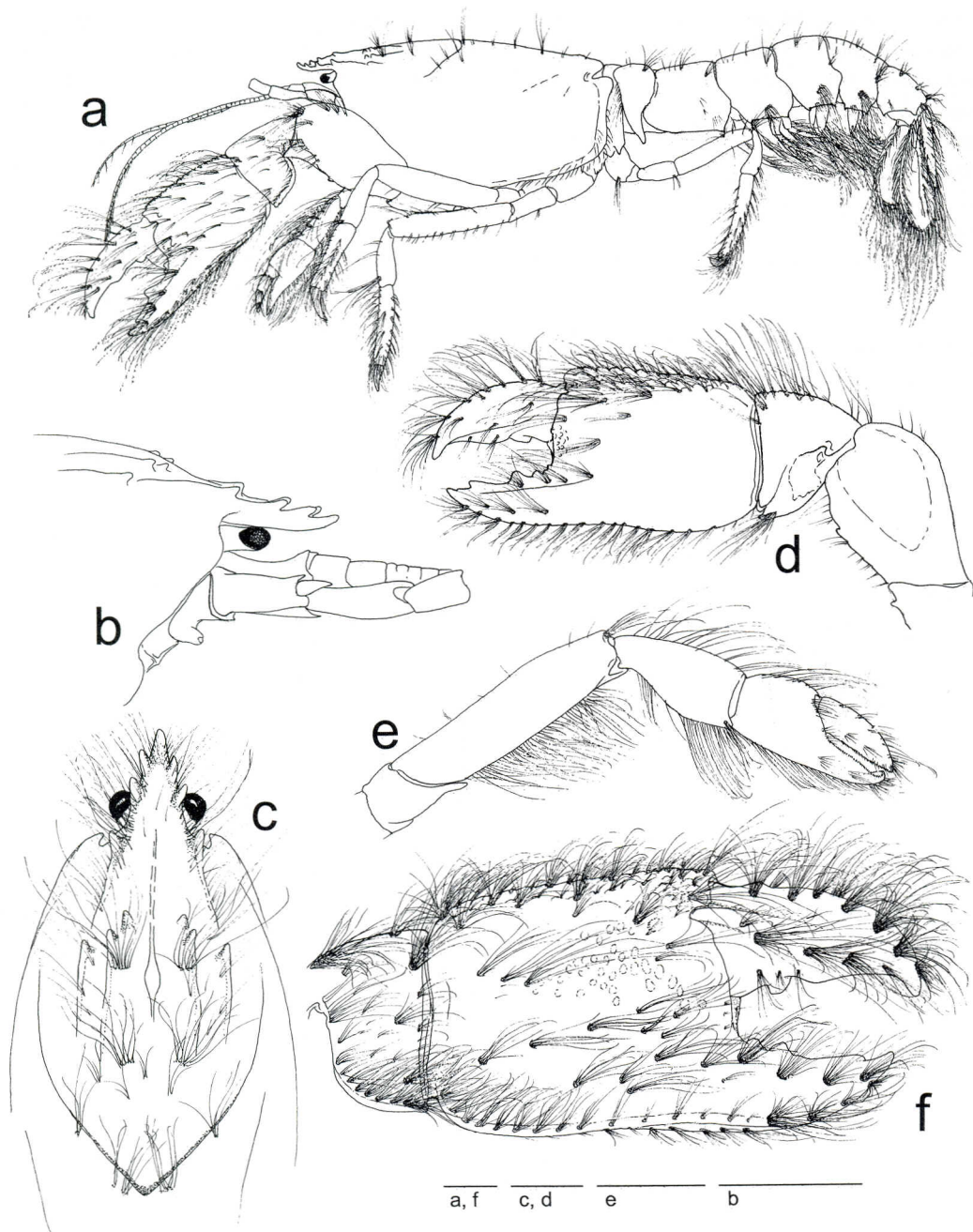


Fig. 1. *Calaxius carneyi*, new species (where setation is shown, setules and flocculent coating of plumose appendages not fully illustrated). a-e, holotype male, USNM 1009165: a, carapace, abdomen, left pereopods 1 and 3-5 in lateral view, with right pereopod 2 internal surface; b, anterior carapace, eyes and antennal peduncles, right side, lateral view, setation not shown; c, anterior of carapace in dorsal view; d, right pereopod 1 or major cheliped, internal surface; e, right pereopod 2, external surface. f, paratype male, USNM 1009166: right pereopod 1 or major cheliped, external surface. Scale bars indicate 2.0 mm.

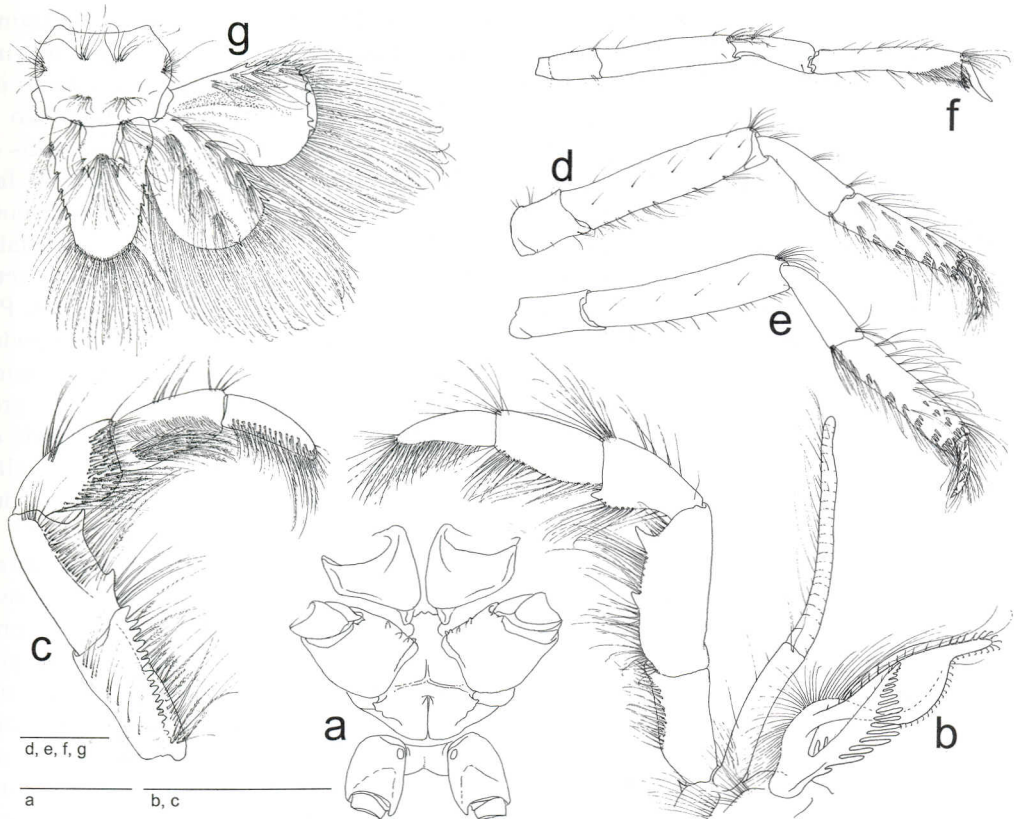


Fig. 2. *Calaxius carneyi*, new species, holotype male, USNM 1009165 (where setation is shown, setules and flocculent coating of plumose appendages not fully illustrated). a, posterior thoracic sternites and coxae of pereopods 3-5, ventral view, setation not shown; b, left maxilliped 3, external surface; c, endopod of left maxilliped 3, internal surface; d, pereopod 3, external surface; e, pereopod 4, external surface; f, pereopod 5, external surface; g, abdominal somite 6, telson and uropods, dorsal surface. Scale bars indicate 2.0 mm.

almost to midlength of rostrum (Fig. 1a, b, c). Cornea terminal, slightly globose, diameter equal to or slightly exceeding that of eyestalk.

Antennular peduncle reaching well beyond rostrum (Fig. 1b). Antennal peduncle bearing produced nephridiopore proximoventrally, second article bearing dorsodistal spine overreaching much of acicle, acicle short, not bifid, overreaching proximal third of penultimate (fourth) peduncular article, third peduncular article distally bearing strong ventromesial spine. Maxilliped 3 basis bearing short, acute mesial spine (Fig. 2b); ischium of endopod with strong, distally elevated crista dentata on internal surface, bearing about 16 spines, distalmost of

which are largest and most strongly directed mesiad (Fig. 2c); merus with two mesial spines, one near or just short of midlength, the other larger and in distal third; carpus with short triangular tooth at distal extreme of flexor margin; all articles of endopods bearing fields of long setae, many dense and heavily plumose, especially on mesiad and internal surfaces.

Pereopods 1-4 bearing epipods. Pereopods 2-4 with pleurobranchs above coxae (on thoracic somites 5-7).

Chelipeds (pereopod 1) similar in form and ornamentation on the 2 sides, right the heaviest (Fig. 1a, d); ischium with single well-defined spine on inferior margin; merus with single flattened spine near mid-

length of inferior margin, which is weakly marked by adjacent sinuation or serration, distal corner of flexor margin on external side forming short, heavy raised spine (Fig. 1a); carpus very short, bearing numerous patches of long setae on external surface, dorsal margin weakly tuberculate, terminating distally in blunt tooth, ventral carina of external surface forming flange distally which terminates in flattened, weakly hooked tooth; propodus very thick and heavily calcified, lacking well-defined teeth on weakly tuberculate dorsal margin, bearing numerous patches of long setae on external surface, including among tubercles of dorsal surface, along well-marked carina of ventral margin, below cutting edge of fixed finger, and proximal to gape, external surface proximal to dactylus with scattered low tubercles and granules, fixed finger bearing two erect teeth on proximal half and single less erect tooth in distal half, terminus spiniform, internal surface with weak carina adjacent to and slightly below cutting edge; movable finger very thick and heavy, with dense patches of long setae externally and dorsally, cutting edge bearing rounded to lobiform tooth in proximal third, broad ill-defined tooth or sinuous lobe in distal two-thirds, terminus weakly hooked and subacute, a carina above cutting edge on internal surface. Pereopod 2 (Fig. 1e) merus lacking marginal spines, combined length of ischium and merus about equal to combined length of carpus and propodus, length of dactyl about half total length of propodus, opposable cutting edges of fingers corneous, finely pectinate, distinctly spooned distally. Pereopod 3 (Fig. 2d) merus lacking marginal spines, external surface of propodus bearing five sets of corneous spiniform setae, set individually or in short transverse rows of two or three near inferior margin, fewer sets and few such setae near superior margin, falcate dactylus with three distinct corneous spiniform setae on external surface, distally with two more very small ones set near flexor margin, and a sharp corneous spine forming terminus. Pe-

reopod 4 (Fig. 2e) merus lacking marginal spines, external surface of propodus bearing six sets of corneous spiniform setae, set individually or in transverse rows of two to four near inferior margin, four such sets of one to three setae near superior margin, falcate dactylus with five distinct corneous spiniform setae on external surface, distally with additional very small corneous seta, sharp corneous spine forming terminus. Pereopod 5 (Fig. 2f) merus and propodus lacking marginal spines, propodus bearing stiff bristles at distal inferior end of propodus, concealed by dense distal fields of setae; lanceolate dactylus twisted laterally, opposed to terminal bristles of propodus when flexed.

Pleopod 1 absent, posterior pleopods all bearing dense cover of long, plumose, heavily fouled setae; appendix interna present on pleopods 2–5. Uropodal exopod (Fig. 2g) bearing four spines along external margin and an articulated spine where this margin meets the transverse suture, five additional spines along transverse suture, and no spines on dorsal surface, long setae forming dense fringe on margins, but on dorsal surface limited to few patches near external margin; endopod with single strong spine at distal end of external margin and another small spine overreaching distal margin at end of weak median ridge, long setae forming dense fringe on margins, and distributed in patches on dorsal surface near external margin and along medial ridge. Telson length distinctly greater than its basal width, tapering toward posterior, widest at lateral lobes in proximal one-quarter of length, single pair of strong fixed dorsal spines in anterior half, two to four fixed marginal serrations or spines posterior to proximal lobes, and two pairs of short, articulated marginal spines in distal third of lateral margins, distal margin evenly convex, densely setose.

Variations.—Paratype: Spination and tuberculation in the exuvia of this larger specimen differ in several minor ways from ornamentation in the holotype. There are few-

er spines on the margin of the rostrum, as the supraoculars are not present. The margin of the rostrum is somewhat broadly concave in this region on the paratype, although it retains an overall triangular shape. Dorsal tuberculation of the propodal palm is less evident than in the holotype. Spines on the cutting edge of the major chela differ slightly in shape from those on the holotype, but the pattern and placement of this spination is conserved (Fig. 1f). Granulation on the internal surface of the propodus in the paratype is stronger than that in the holotype. The external margin of the uropodal exopod in the paratype male bears five rather than four fixed spines, while the external margin of the endopod bears three spines rather than a single one. Lateral margins the telson bear up to five serrations or fixed lateral spines in the paratype, and the pairs of articulated marginal spines are relatively smaller than in the holotype and very difficult to discern. Small angular, acute corners or teeth on the anteroventral margins of abdominal pleurae 3–5 are also more difficult to discern in the holotype. These appear to be somewhat worn or smoothed off in the paratype, although the acute posteroventral margins remain readily evident.

Etymology.—The species is named for Robert S. Carney, Louisiana State University, Baton Rouge, who oversaw collections of the specimens and made these materials available for our study. His own work on hydrocarbon vent communities of the Gulf of Mexico (see Carney 1994) has brought needed attention to these remarkable assemblages of marine organisms.

Remarks.—Ten species were listed in a recent review of *Calaxius* by Kensley & Hickman (2001). The present description accounts for the eleventh known member and only the second species to be found in the Atlantic Ocean. There seems little doubt as to the generic placement of this new species, given the dentate rostrum twice as long as the eyestalks, the dentate carapace carinae, the transverse suture on the uro-

podal exopod, presence of pereopodal epipods and pleurobranchs, the absence of pleopod 1 in the male, and the presence of appendices internae on pleopods 2–5 (see Poore 1994:97). The specimens lack strong dentition on the dorsal surface of the first chelipeds, as seen in *Acanthaxius* Sakai & de Saint Laurent, 1989, which they somewhat resemble.

In contrast to the known congeners and the original generic definition (Sakai and de Saint Laurent 1989:84), the rostrum of *C. carneyi* is heavier and more broadly triangular, the eyestalks and antennal acicle are comparatively shorter, and the palm of the cheliped lacks well-separated and defined teeth dorsally, having at most a covering of low tubercles, and the telson is distinctly narrowed posteriorly or subtriangular. The abdominal pleura of *C. carneyi* resemble neither the acutely triangular plates seen in four other previously described species nor the broadly rounded plates seen in five other species; rather, pleura 3–5 are ventrally truncate with small anterior and posterior marginal denticles.

The only species of *Calaxius* previously reported from the broad geographic area of the Gulf of Mexico and contiguous regions is *C. oxypleura* (Williams, 1974), recorded from the Straits of Florida. This species has abdominal pleura 3–5 ventrally angular or acute, rather than truncate, and a narrow dentate rostrum unlike that of *C. carneyi*.

Ecology.—A dense cover of flocculent materials on plumose setae of both the holotype and paratype exuvia (much of which has disintegrated over time in alcohol, or which was brushed free in the course of morphological studies) may derive from the unique environments inhabited by these animals, but nothing is known of the burrow structure or feeding behavior. The flocculent coatings on the axiid setae could be a passive result of these animals' trophic ties to members of the chemosynthetic community, at a primary or secondary consumer level. Accumulations of mussels and worms near hydrocarbon seeps in the north-

ern Gulf of Mexico do in varied ways depend upon methanotrophic or sulfur-oxidizing bacteria for metabolic resources (see Van Dover 2000:363–366). These bacteria occur in animal tissues as endosymbiotic cells or as scattered mats immediately surrounding the seeps. They may directly exploit methane as both a carbon and energy source or, much as in hydrothermal vent environments, directly oxidize rich cold-seep sources of sulfides for metabolic energy. Precipitates and bacteria might simply accumulate on or among the setules of highly plumose setae, perhaps as these axiids move about or ventilate burrows in these matted settings. While the flocculent materials could simply mask movements among bacterial mats or mussel communities, we cannot rule out that the axiids themselves may directly consume accumulations of chemosynthetic bacteria, either by accessing exposed mats or undertaking behaviors that favor the forming of such accumulations within and along walls of their burrows. It is suspected that other thalassinideans engage in burrow-modulated feeding behaviors that are microbially based, albeit in reduced interstitial waters of shallow hypoxic environments (Felder 2001) where at least one species lives in apparent association with lucinid bivalves harboring chemosynthetic gill bacteria.

Even if *C. carneyi* could be shown to depend upon the chemosynthetic community as a nutritional resource, perhaps by stable isotope measurements, this would not necessarily confirm its restriction to occurrence with chemosynthetic communities of hydrocarbon seeps. As has recently been reported for infaunal worms associated with methane seeps off California (Levin et al. 2000), infaunal thalassinideans are also likely pre-adapted to organic-rich, reducing environments, and may in fact be widely distributed forms that do not strictly exhibit chemosynthesis-based trophic specializations. Owing to very limited general sampling for infaunal macrocrustaceans from slope environments in the Gulf of Mexico

to date, its occurrence in sediments other than those near cold seeps cannot be ruled out.

Acknowledgements

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