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A new species of *Alvinocaris* (Crustacea: Decapoda: Caridea: Alvinocarididae) from Costa Rican methane seeps

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Abstract

A new caridean shrimp, *Alvinocaris costaricensis*, is described from methane seeps in the eastern Pacific off Costa Rica. The new species is the 16th described species of the genus, and by molecular analysis appears closest to *Alvinocaris komaii* from the Lau Basin, southwestern Pacific, but shares certain morphological characters with *A. lusca* from the Galapagos Rift and *A. muricola* from the West Florida Escarpment, as well as with *A. kexueae* from the Manus Basin in the Southwest Pacific.

Key words: Caridea, Alvinocaris, methane seeps, Costa Rica

Introduction

The caridean shrimp family Alvinocarididae is an unusual and interesting assemblage of species known only from hydrothermal vents and cold seeps (Martin & Haney 2005; De Grave & Fransen 2011). Currently, the family consists of nine genera and at least 32 species (Komai & Segonzac 2005; De Grave & Fransen 2011; Yahagi *et al*. 2014; Komai & Tsuchida 2015; Komai *et al*. 2016) (Table 1). More undescribed species are known to exist in various collections around the world (e.g. see Komai & Segonzac 2005), and it is common to encounter undescribed species as new vent and seep sites are explored. The most geographically widespread and speciose genus, *Alvinocaris*, was reviewed by Komai & Segonzac (2005), at which time there were eight described species. Additional species have been described in the twelve years since their review (listed in De Grave & Fransen 2011; see also Yahagi *et al*. 2014; Vereschaka *et al*. 2015; Wang & Sha 2017; Table 2). Below, we describe a new species of *Alvinocaris* from relatively shallow methane seeps off the coast of Costa Rica in the eastern Pacific Ocean.

TABLE 1. Shrimp genera of the family Alvinocarididae as of mid-2018.

Genus	No. of described species
Alvinocaridinides Komai & Chan, 2010	2
Alvinocaris Williams & Chace, 1982	16 (including this paper)
Chorocaris Martin & Hessler, 1990*	5
Manuscaris Komai & Tshuchida, 2015	1
Mirocaris Vereschaka, 1997	2
Nautilocaris Komai & Segonzac, 2004	1
Opaepele Williams & Dobbs, 1995	3
Rimicaris Williams & Rona, 1986	2
Shinkaicaris Komai & Segonzac, 2005	1

*suggested to be synonymous with *Rimicaris* by Vereschaka *et al*. (2015)

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TABLE 2. Species of the genus *Alvinocaris* described as of mid-2018, in alphabetical order, and the general geographic region in which they were discovered.

A. alexander Ahyong, 2009	southern Kermadec Ridge, southwest Pacific
A. brevitelsonis Kikuchi & Hashimoto, 2000	Minami-Ensei Knoll, Okinawa Trough
A. chelys Komai & Chan, 2010	Gueishandao, Taiwan
A. costaricensis (this paper)	Costa Rica, eastern Pacific
A. dissimilis Komai & Segonzac, 2005	Minami-Ensei Knoll, Okinawa Trough
A. komaii Zelnio & Hourdez, 2009	Lau Basin, southwest Pacific
A. kexueae Wang & Sha, 2017	Manus Basin, southwest Pacific
A. longirostris Kikuchi & Ohta, 1995	Okinawa Trough
A. lusca Williams & Chace, 1982	Galapagos Rift, Rose Garden
A. markensis Williams, 1988	Mid-Atlantic Ridge
A. methanophila Komai, Shank & Van Dover, 2005	Blake Ridge
A. muricola Williams, 1988	West Florida Escarpment
A. niwa Webber, 2004	Rumble V seamount, Pacific
A. solitaire Yahagi *et al*., 2014	Central Indian Ridge, Indian Ocean
A. stactophila Williams, 1988	North Central Gulf of Mexico
A. williamsi Shank & Martin, 2003	Menez Gwen, North Atlantic

Materials and methods

Specimens were collected from off the Pacific coast of Costa Rica during two cruises (AT 15-44 and 15-59 in 2009 and 2010, respectively) to study methane seeps, with sampling carried out via the Deep Submergence Vehicle (DSV) *Alvin*. Shrimp were collected via the DSV *Alvin* and photographed alive onboard ship with a Canon PowerShot G9 camera mounted on a Leica S8APO stereomicroscope.

Specimens for morphological study were fixed in 10% seawater-formaldehyde and then preserved in 70% ethanol after rinsing. Two specimens from the 2009 expedition, both from Mound 12 (details below), were sent to the first author for initial examination and illustration. All illustrations in this paper are of the larger (female) of those two specimens, which is designated the holotype. All illustrations were made with the aid of a Wild M5APO dissecting microscope and drawing tube.

Abbreviations used in the description are CL (carapace length) and TL (total length), and OCL (orbital carapace length), and for institutions NHMLAC (Natural History Museum of Los Angeles County), MZUCR (Museo de Zoología, Universidad de Costa Rica), and SIO-BIC (Benthic Invertebrate Collection of the Scripps Institution of Oceanography)

Specimens for DNA analysis were preserved directly in 95% ethanol, and genomic DNA was extracted from legs of seven specimens of the new species using a Qiagen DNeasy Tissue kit. Cytochrome oxidase subunit 1 (COI) (partial, approximately 700 bp) was amplified using the primer pair LCO1490 (5'-GGT CAA CAA ATC ATA AAG ATA TTG G- 3') and HCO2198 (5'-ACT TCA GGG TGA CCA AAA AAT CA-3') (Folmer *et al*. 1994). PCR mixtures contained 12.5 µL ProMega GoTaq Green DNA polymerase (3mM MgCl2, 400 µM each dNTP, 1U Taq), between 50–100 ng DNA, and a reaction profile of 94ºC for 180s, 5 cycles of 94°C for 30s, 47°C for 45s, and 72°C for 60s, 30 cycles of 94°C for 30s, 52°C for 45s, and 72°C for 60s and finally 72°C for 300s was used. The COI sequences, lacking indels, were unambiguously aligned and blasted to other alvinocarids. TCS (Clement *et al*. 2000) was used to construct a COI haplotype network for the seven specimens of *A. costaricensis* **n. sp.**

The seven new sequences (GenBank Accession Numbers MH645099-MH645105) were also combined with a COI dataset of available species of Alvinocarididae in GenBank, largely following those used in Vereshchaka *et al*. (2015), including their choice of outgroup, the acanthephyrid shrimp *Acanthephyra purpurea*. COI sequences were managed in Mesquite (Maddison & Maddison 2011) and aligned using Muscle (Edgar 2004). Pairwise comparisons of COI sequences were conducted, and uncorrected distances were estimated in PAUP* 4.0b15 (Swofford 2002). The sequences were analyzed using maximum parsimony (MP) in PAUP* and maximum likelihood (ML) with RaxML GUI and RaXML 8 (Silvestro & Michalak 2012; Stamatakis 2014). MP analyses were run using heuristic searches (100 random stepwise addition replicates; bisection re-connection (TBR); zero-

length branches collapsed). Clade support was assessed using jackknifing (37% deletion) with 1000 pseudoreplicates with 100 random additions per iteration. The ML analysis was run with the data partitioned by codon using the GTR+Γ model of substitution. Bootstrap support values were estimated by 1000 standard bootstrap pseudo-replicates with the same model and partitions.

Taxonomy

Alvinocarididae

Alvinocaris costaricensis, new species

Material examined. Holotype: SIO-BIC C12202, female (TL ~42 mm, CL 17.4 mm, OCL 10.4 mm, carapace height 6.0 mm), Eastern Pacific Ocean, Costa Rica, Mound 12, *Alvin* dive 4503, 8.9307° N, 84.3072° W, 1005 m, collector Greg Rouse, Feb/24/2009. Paratypes: SIO-BIC C13298, SIO-BIC C13299, same collecting data as for holotype; MZUCR-3569-01, same collecting data as for holotype. NHMLAC LACM CR 2009.1 (ex SIO-BIC C11140-1), ovigerous female (OCL 17.6 mm, TL 55 mm), same collecting data as for holotype. SIO-BIC C11157 and C12203, Eastern Pacific Ocean, Costa Rica, Mound 12, *Alvin* dive 4511, 8.9305° N, 84.3123° W, 1001 m, collector Greg Rouse, March/5/2009; SIO-BIC C12203 1 badly damaged specimen (TL 13.2 mm, OCL 4.9 mm; abdomen disarticulated, sex undetermined). Although damaged, this specimen was sequenced and is the same species. SIO-BIC C11157 was sequenced and is the same species. SIO-BIC C11209, sex not determined, (TL 77.6 mm, CL 30.4 mm, OCL 17.1 mm; left side of carapace slightly inflated), Eastern Pacific Ocean, Costa Rica, Jaco Scarp, *Alvin* dive 4590, 9.1176° N, 84.8395° W, 1800 m, collector Greg Rouse, Jan/11/2010. SIO-BIC C11183, C11186, sex not determined, Eastern Pacific Ocean, Costa Rica, Mound 12, *Alvin* dives 4587 and 4588, 8.9307° N, 84.3072° W, 1005 m collector Greg Rouse, Jan/08 and 09/2010. These specimens were sequenced and are the same species.

Description. Body relatively robust for the genus, integument thin, smooth, shiny. Carapace (Figs. 1, 2) with strong suborbital spine (Fig. 3A) and well developed pterygostomial spine exceeding length of orbital spine, otherwise unarmed.

Rostrum (Figs. 1B, 2, 3A) well developed (tip broken in holotype but well developed in several paratypes), extending forward and only slightly downward, with strong, sharp, anterior-curving teeth in row on dorsal border, extending backward to about, or slightly posterior to, midlength of carapace, bearing 5–7 weakly developed teeth along ventral border. Weak dorsal carina extending backward from rostrum along carapace to posterior border. Larger specimens with rostrum strongly up-turned distally, bearing up to 10 dorsal and forward-directed teeth, exceeding anteriorly beyond tip of scaphocerite and antennular peduncle.

Eighth thoracic sternite with well-developed and acute median tooth directed anteroventrally, produced beyond coxa of pereopod 5 and visible in lateral view (Fig. 2).

Abdomen (Figs. 1A, 2) well developed, somite 6 with sharp posteriorly directed tooth on either side extending posteriorly along telson (Fig. 3D); somite 5 with similar but shorter tooth and with acute posteroventral border; somite 4 with acute posteroventral border.

Telson (Fig 2, 3D, E) long, exceeding length of uropods, lateral margins straight, slightly converging posteriorly; each lateral margin bearing row of 7 movable spines; posterolateral corners each with single large slightly medially-curved spine; posterior border bearing two pairs of small spines and 4 plumose setae; posterior border slightly indented as shown. Uropodal rami each with border of plumose setae; exopod broader than endopod, bearing diaresis and single lateral spine just posterior to acute tooth at border of diaresis, as shown (Fig. 3D).

Eyes fused mesially but distinct, each with small anterodorsal tubercle (Fig. 3A). Cornea with diffuse pigmentation internally but no clear pigmented layer or region.

Antennular peduncle (Fig. 3C) extending beyond antennal scale, with relative lengths of articles 1 > 2 > 3; article 1 with large lateral spine extending clearly beyond similar spine of article 2. Antennal scale (Fig. 3B) broad, distally rounded, with acute anterolateral tooth extending almost to full length of scale.

Mouthparts (Fig. 4A–F) typical of genus (Komai & Segonzac 2005; Vereschaka *et al*. 2015).

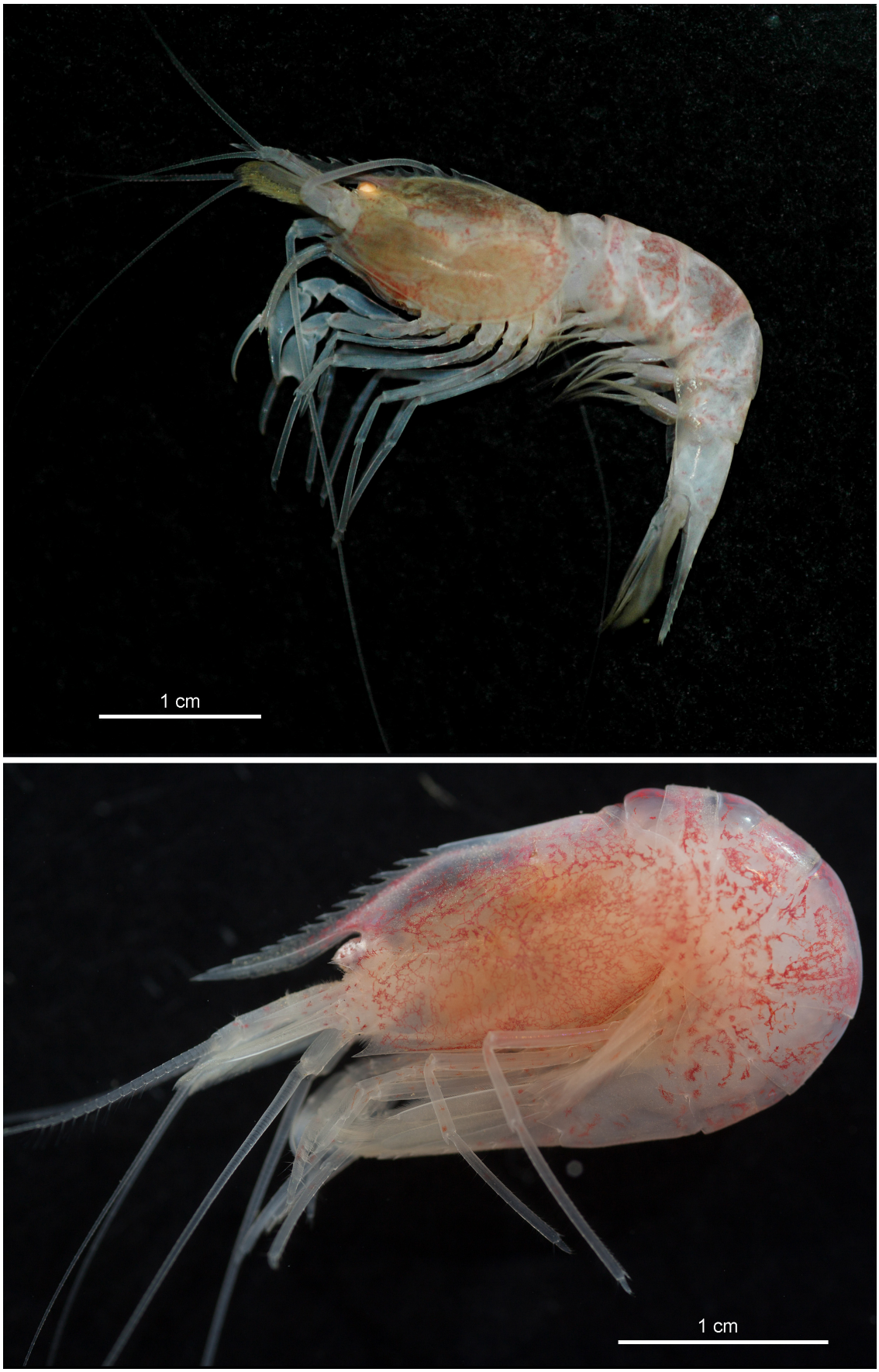

FIGURE 1. A, *Alvinocaris costaricensis* new species, holotype female, SIO-BIC C12202, Eastern Pacific Ocean, Costa Rica, live color photograph. B, same species, paratype female, C11186.

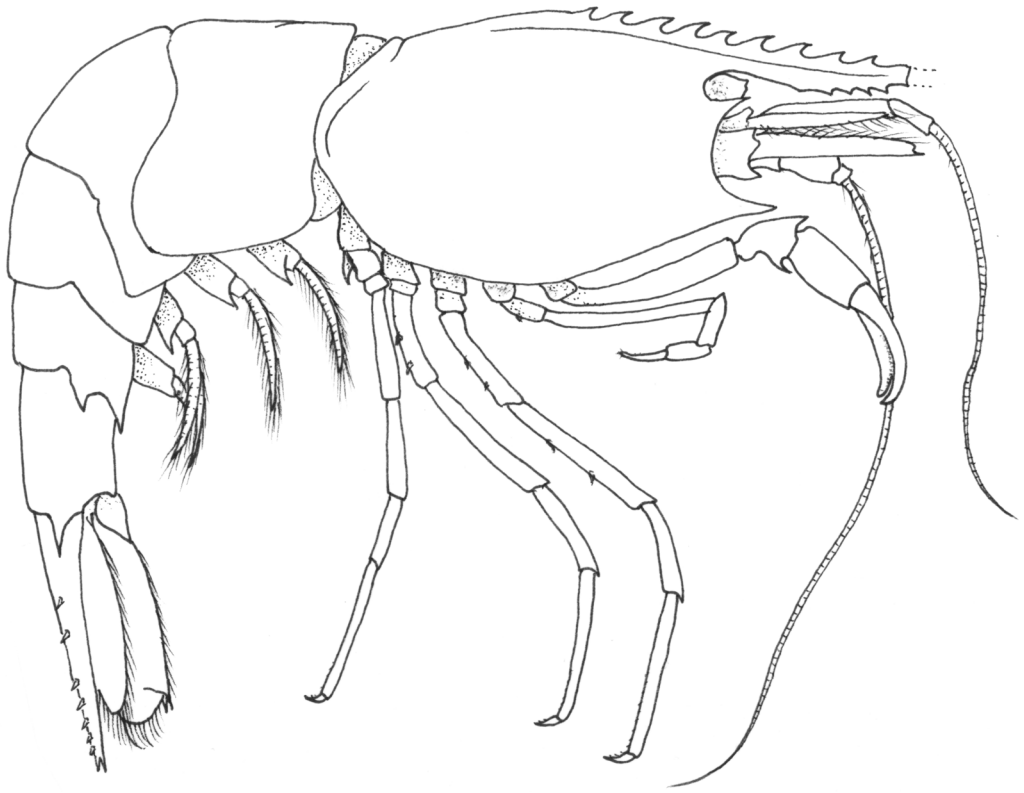

FIGURE 2. *Alvinocaris costaricensis* new species, holotype female, SIO-BIC C12202, Eastern Pacific Ocean, Costa Rica, lateral view, extremity of rostrum broken. Carapace length 10.4 mm (measured from back of the orbital sinus in a straight line to posterior border of carapace).

First pereopod (cheliped) (Figs. 1A, 2, 3F–H) well developed, long, extending beyond bases of antennae when outstretched; chela delicate for genus and strongly curved inward, bearing delicate pectinations along cutting borders of both fingers; fingers of chela approximately 1.5 times length of propodal palm; carpus cup-shaped to receive proximal end of propodus, and bearing brush of "cleaning setae" and large, acute tooth on inner margin.

Second pereopod (Figs. 2, 3I–K) shorter than first; chela delicate, approximately 4 times longer than wide, both fingers bearing pectinate setal borders on cutting margin; fingers slightly exceeding length of palm; ischium with single movable ventral spine.

Third through fifth pereopods (Fig. 5) similar, long and delicate; propodus longer than merus; merus longer than carpus. Dactylus short, stout, with recurved sclerotized tip and ventral single row of 4 or 5 short, sclerotized spines. Propodus with row of regularly spaced short spines along ventral border. Merus with 2 large, ventral movable spines on P3, none on P4 and P5. Ischium with 2 ventral movable spines on P3 and P4, none on P5.

Female pleopod (Fig. 4G) with subequal rami bearing plumose setae; appendix interna short, simple, tapering distally.

Coloration. Photographs of the holotype (Fig. 1A) and one paratype (Fig. 1B) show a largely translucent to white shrimp with a pale or beige carapace, some orange or reddish coloration on the mouthparts, and delicate red reticulations on the carapace and abdomen. The eye, although reflecting light in the photographs, appears to be orange-red.

Etymology. The specific epithet reflects the location of the methane seeps off the Pacific coast of Costa Rica.

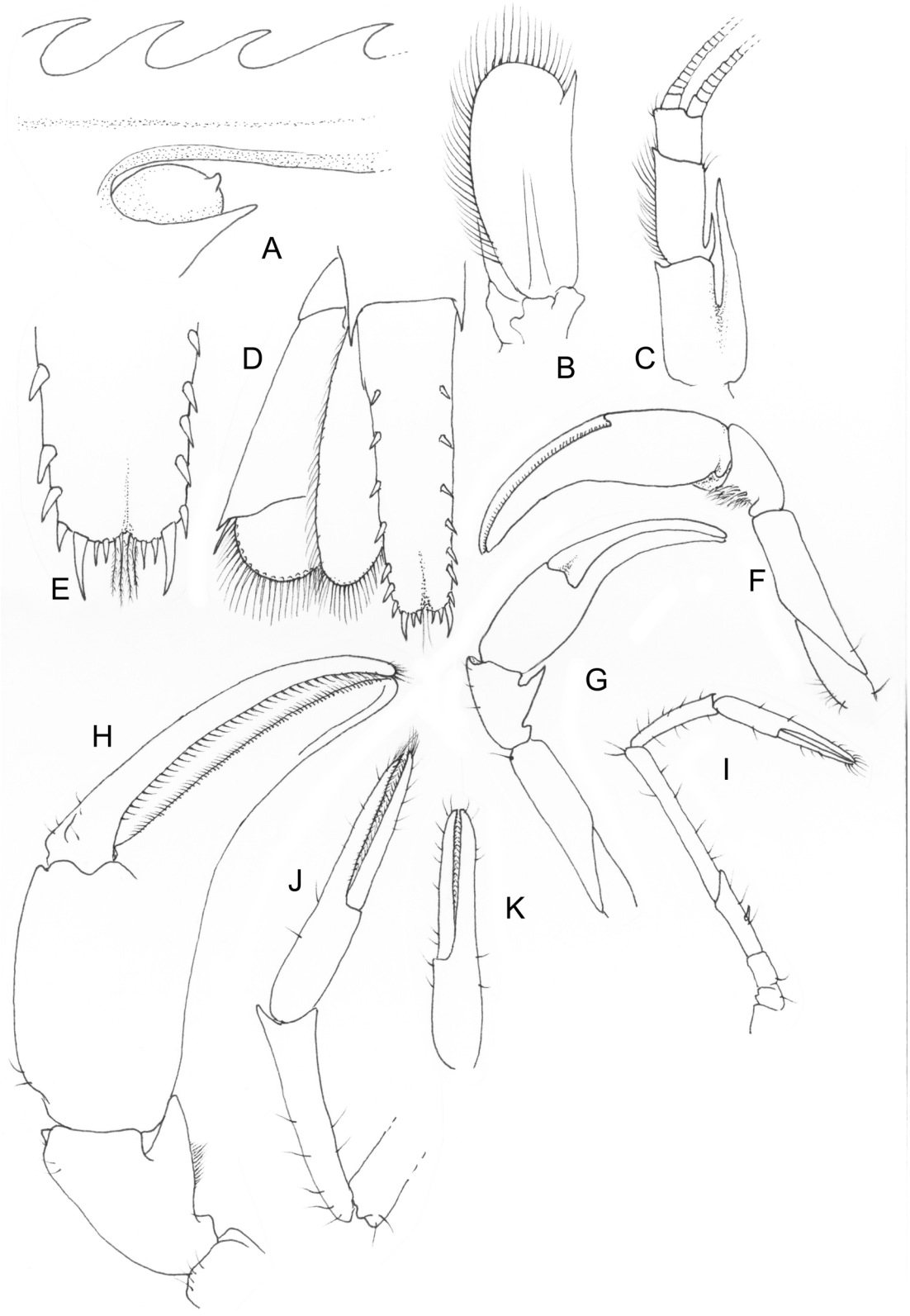

FIGURE 3. *Alvinocaris costaricensis* new species, holotype female, SIO-BIC C12202, Eastern Pacific Ocean, Costa Rica. A, eye and section of rostrum (above) and orbital spine (below); note minute dorsal tubercle on eye. B, antennal scale, right side, dorsal view. C, antennular peduncle, right side, dorsal view. D, telson and left uropods, dorsal view. E, extremity (approximately distal half) of telson. F, pereopod 1 (cheliped), right side, ventro-lateral view. G, pereopod 1, dorsal view. H, higher magnification of pereopod 1, dorsal inner view. I, second pereopod, right side, lateral view. J, pereopod 2 propodus and chela, outer view. K, pereopod 2 chela, inner view.

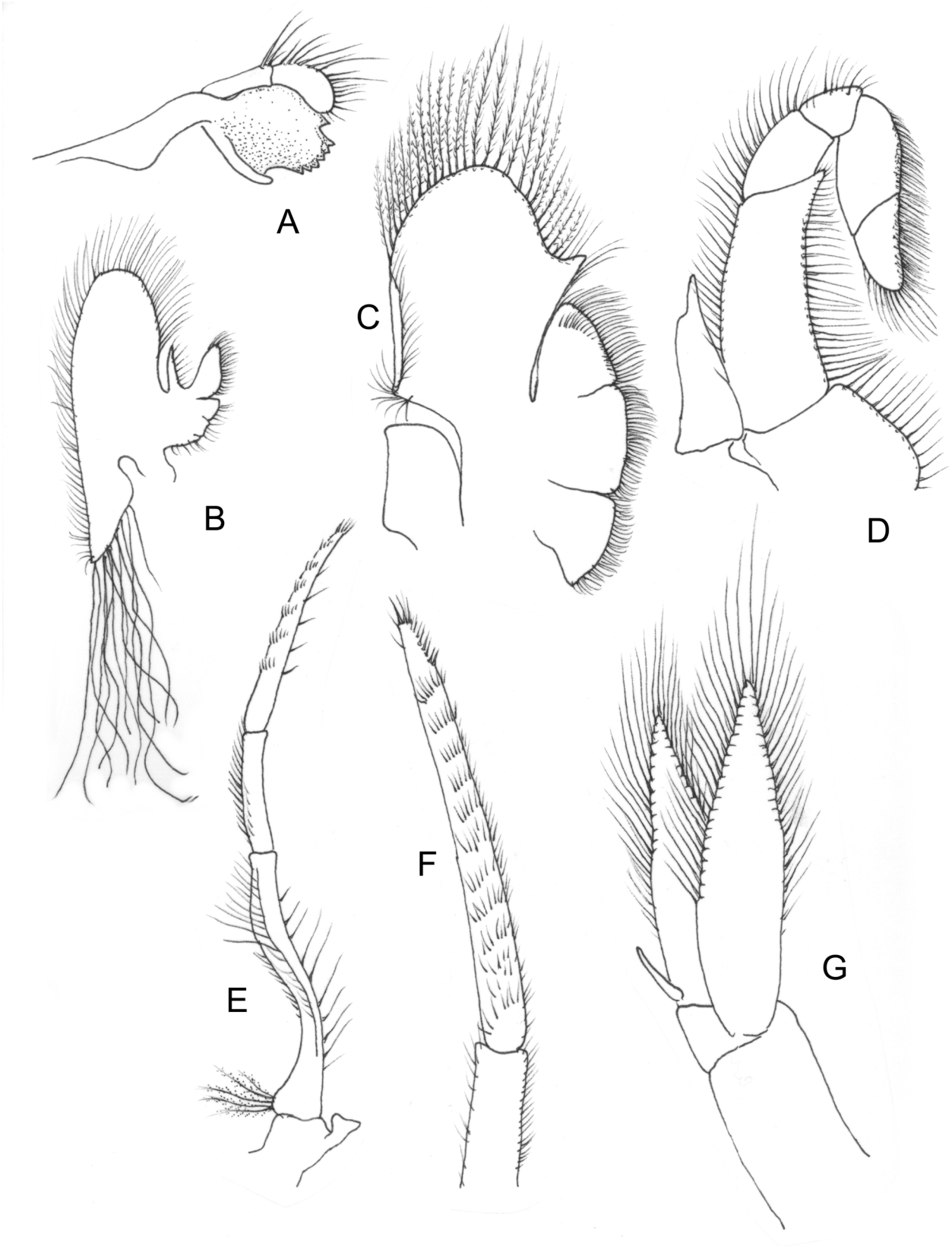

FIGURE 4. *Alvinocaris costaricensis* new species, holotype female, SIO-BIC C12202, Eastern Pacific Ocean, Costa Rica. A, left mandible, inner view. B, maxilla, inner view. C, maxilliped 1. D, maxilliped 2. E, maxilliped 3, lateral view. F, maxilliped 3 dactylus, inner view. G, first pleopod and appendix interna, right side.

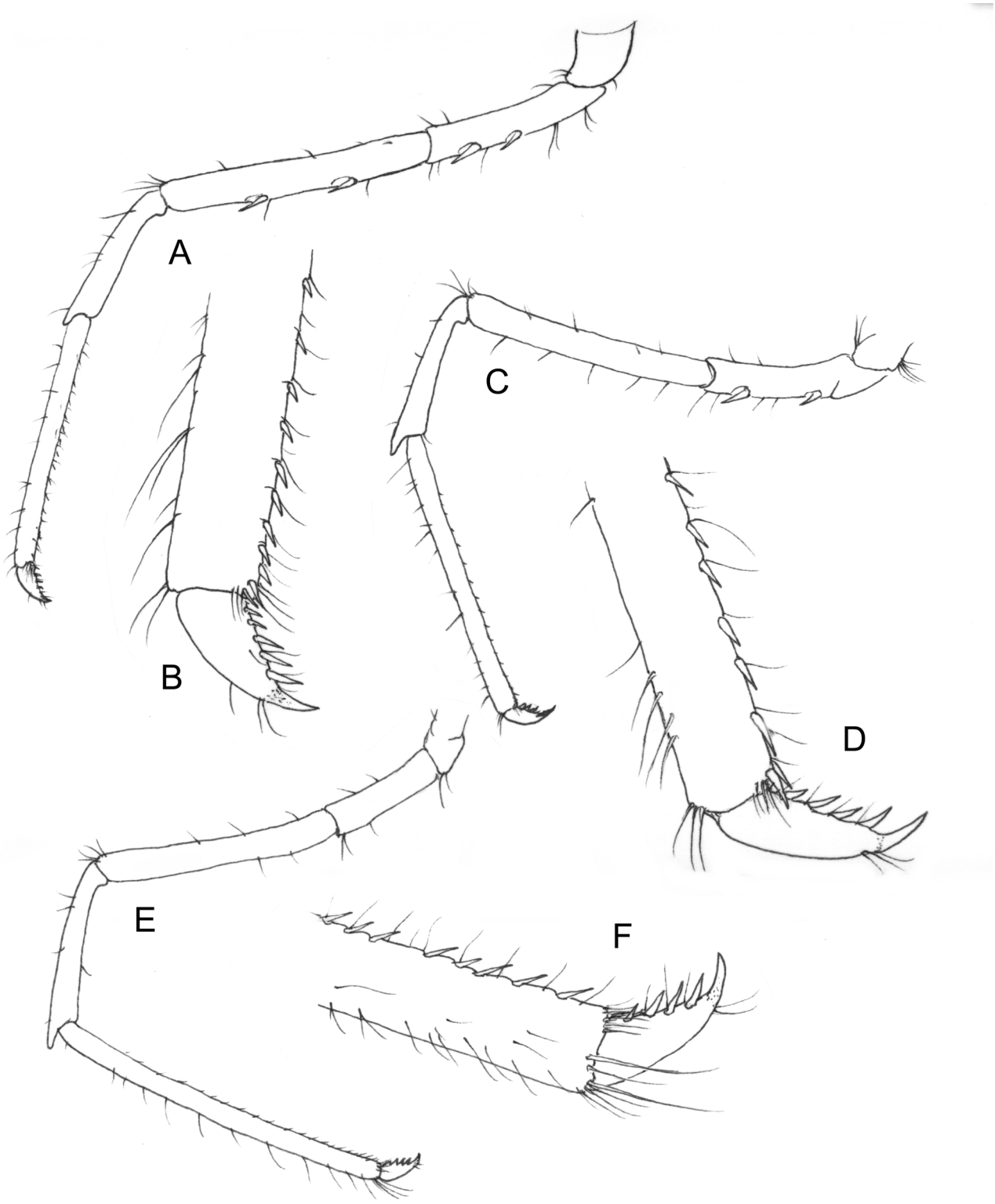

FIGURE 5. *Alvinocaris costaricensis* new species, holotype female, SIO-BIC C12202, Eastern Pacific Ocean, Costa Rica. A, pereopod 3, left side, lateral view. B, same, close up of dactylus and distal half of propodus. C, pereopod 4, left side, lateral view. D, close up of dactylus and distal half of propodus. E, pereopod 5, left side, lateral view. E, close up of dactylus and distal half of propodus.

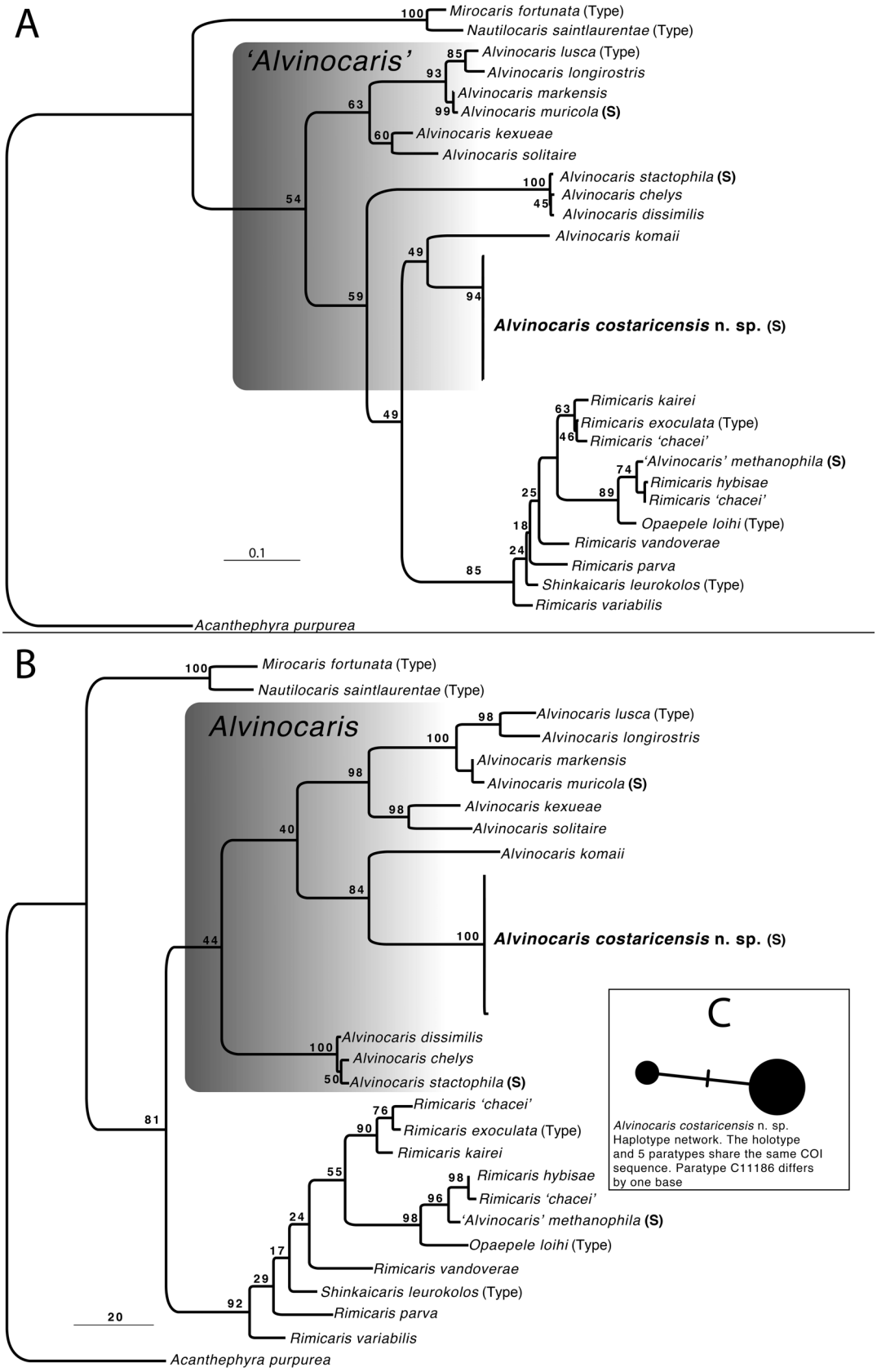

FIGURE 6. Relationships among selected members of Alvinocarididae based on COI sequence data. A, Maximum likelihood topology; numbers at nodes indicate bootstrap values. B, one of eight shortest trees from the maximum parsimony analysis of COI matching jackknife consensus tree; numbers at nodes refer to parsimony jackknife score. C. Haplotype network generated by TCS (Clement *et al*. 2002); holotype and 5 paratypes have identical COI sequences; paratype C11186 differs by one base. Generic type species indicated (Type). Seep-dwelling species indicated (S).

DNA sequence analysis. The seven COI sequences for *A. costaricensis* **n. sp.** were very similar, with six (including that of the holotype) being identical, and one haplotype differing by only one base (Fig. 6C). These had a closest pairwise distance (of ~12%) to *Alvinocaris komaii* (GenBank KP759373) from West Pacific hydrothermal vents. Of the 505 bases in the COI dataset, 323 were constant, 158 were parsimony-informative, and 24 were variable but parsimony-uninformative. The ML analysis (Fig. 6A) recovered *Alvinocaris* as paraphyletic, with *A. costaricensis* **n. sp.** as the sister group to *A. komaii*. The *Rimicaris*+*Opaepele*+*Shinkaicaris* clade was nested within *Alvinocaris* as sister to the *A. costaricensis* **n. sp.** + *A. komaii* clade, though this, and most other deeper nodes, had low support. The four-known seep-dwelling alvinocaridids, *A. methanophila, A. muricola, A. stactophila* and *A. costaricensis* **n. sp.**, were scattered across the phylogeny and all had hydrothermal vent-dwelling taxa as sister groups. The MP analysis (Fig. 6B) found eight shortest trees of length 547. These eight trees varied only slightly; one of the most parsimonious trees with the same topology as the majority-rule consensus tree, and that of the of majority-rule consensus tree for the parsimony jackknife analysis, is shown in Fig. 6B. The MP analysis recovered a monophyletic *Alvinocaris* (with the exception of *A. methanophila*), though with poor support; as in the ML results, *A. costaricensis* **n. sp.** was sister group to *A. komaii.*

Remarks. Morphological comparison. *Alvinocaris costaricensis* **n. sp.** is a large species for an alvinocaridid, with some paratypes (e.g. SIO-BIC C11209 from the Jaco Scarp site) exceeding 75 mm TL and 64 mm OCL. The species is easily identifiable as a member of *Alvinocaris* based on several characters uniquely shared by members of that genus: the laterally compressed, well-developed and toothed rostrum, dentate posterior border on abdominal somite 4, minute dorsal tubercle on the surface of the eye, strongly curved and minutely pectinate chelae, small ischial spine on the second pereopod, parallel rows of small spines on the telson, and spination of pereopods 3 and 4, among other characters (Komai & Segonzac 2005, Vereschaka *et al*. 2015).

Among species of *Alvinocaris*, the new species is similar to *A. muricola* and also to *A. kexueae* in the size (length) of the rostrum, the orientation of the dorsal rostral spination, and the relatively shallow dorsal angle of the carapace. In all three species, the rostrum slopes more gradually, and bears larger teeth, than in most *Alvinocaris* species (Komai & Segonzac 2005). However, there is much morphological variation in the rostrum of *A. muricola*. Using the diagnostic key to species provided by Komai & Segonzac (2005), the new species keys to *Alvinocaris lusca*, another eastern Pacific (Galapagos Rift and East Pacific Rise) species, based on the number of ventral rostral teeth (fewer than 5) and the length/width ratio of the antennal scale. Additionally*, A. lusca* is one of the few species of *Alvinocaris* that shares with the new species, a slightly indented posterior border of the telson (though not as indented as in *A. costaricensis)*. However, *A. costaricensis* differs from *A. lusca* in having a far slenderer major cheliped, 2 (rather than 3) ventral meral spines on pereopod 3, and a much longer lateral spine on the basal article of the antennal peduncle, which barely exceeds the length of the spine of the second article in *A. lusca*.

An interesting departure from typical species of *Alvinocaris* is the absence of ventral meral spines on pereopod 4. Komai and Segonzac (2005) considered the presence of these spines on pereopods 3 and 4 diagnostic for the genus *Alvinocaris*. The new species has prominent meral spines on P3, but not on P4 or P5 indicating that the generic diagnosis requires slight amendment. This difference does not warrant the erection of another genus, as all other characters fit well within the known range of features described for the other 16 species of *Alvinocaris.* The indented terminal border of the telson is also unique among species in the genus, with *A. lusca* being the closest match in that character. However, variation in this character is known (Komai & Segonzac 2005), so we hesitate to suggest this as a determining feature for field identification.

Molecular comparison. We place the new species in *Alvinocaris,* even though there is evidence from the ML analysis (albeit weakly supported) (Fig. 6A) that the genus, as currently construed, could be paraphyletic (and polyphyletic when *A. methanophila* is considered). However, further sequence data are required to properly resolve this situation, and that question is beyond the scope of this study. Vereshchaka *et al*. (2015) also found a paraphyletic *Alvinocaris* based on their analysis of COI and also of the available 16S rDNA sequences, but maintained the genus as currently formulated, although they suggested that the sequence for *A. methanophila* on GenBank (AY163260) was the result of incorrect identification or processing of the material. Vereshchaka *et al*. (2015) did recover *Alvinocaris* (including *A. methanophila)* as a well-supported clade based on morphology, and *A. costaricensis* **n. sp.** shared these features (notably the laterally compressed and carinate rostrum, eyes fused medially with each bearing a small tubercle, and paired dorsal spines on the telson).

Co-occurring species. Another, and smaller, alvinocaridid species, differing both morphologically (with a shorter rostrum lacking the extensive dorsal teeth seen in *A. costaricensis*) and molecularly, was also collected

from the Mound 12 site (AD 4501, 1008 m depth). Further specimens of that species in the SIO collection represent yet another undescribed species.

TABLE 3. Localities and GenBank Accession numbers for alvinocarid shrimp used in this study.

Taxon	Locality of sequenced specimen	Genbank Acc.
Acanthephyra purpurea (outgroup)	Sargasso Sea	GU183787
Alvinocaris chelys	Gueishandao (V)	JX184903
Alvinocaris costaricensis **n. sp.**	Costa Rica (S)	MH645099-MH645105
Alvinocaris dissimilis	Okinawa Trough (V)	LC029870
Alvinocaris kexueae	Manus Basin (V)	KX825835
Alvinocaris komaii	Lau Spreading Centre (V)	KP759373
Alvinocaris longirostris	Not stated, Okinawa Trough (V)?	KP215339
Alvinocaris lusca	Not stated, Galapagos Rift (V)?	KP215340
Alvinocaris markensis	Mid-Atlantic Ridge (V)	AF125408
Alvinocaris methanophila	West Atlantic (S)	AY163260
Alvinocaris muricola	Congo Deep-Sea Fan (S)	KP759377
Alvinocaris solitaire	Central Indian Ridge (V)	LC007114
Alvinocaris stactophila	Louisiana Slope (S)	AF125411
Mirocaris fortunata	Mid-Atlantic Ridge (V)	KT210460
Nautilocaris saintlaurentae	Tonga: Tofua Arc (V)	KF226726
Opaepele loihi	Nikko Seamount (V)	JQ035657
*Rimicaris chacei**	Mid-Atlantic Ridge (V)	AF125415
*Rimicaris chacei**	Mid-Atlantic Ridge (V)	KT210444
Rimicaris exoculata	Mid-Atlantic Ridge (V)	HM125956
Rimicaris hybisae	Mid-Cayman Spreading Center (V)	KJ567003
Rimicaris kairei	Central Indian Ridge (V)	AB813097
*Rimicaris parva**	Manus Basin (V)	AB772278
*Rimicaris vandoverae**	Mariana back arc (V)	AF125418
*Rimicaris variabilis**	North Fiji Basin (V)	AB772283
Shinkaicaris leurokolos	Okinawa Trough (V)	LC029851

*Formerly in *Chorocaris*, synonymized with *Rimicaris* by Vereshchaka *et al.* (2015).

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