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Two new species of poecilostomatoid copepods symbiotic on the venomous echinoid *Toxopneustes pileolus* (Lamarck) (Echinodermata) from Vietnam

Balu Alagar Venmathi Maran · Il-Hoi Kim · Olga A. Bratova · Viatcheslav N. Ivanenko

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Abstract Two new coexisting species of crustacean copepods (Poecilostomatoida) belonging to the echinoid-specific genera *Mecomerinx* Humes, 1977 (Pseudanthessiidae) and *Clavisodalis* Humes, 1970 (Taeniacanthidae) found associated with the venomous flower urchin *Toxopneustes pileolus* (Lamarck) (Echinodermata: Echinoidea: Toxopneustidae) in the South China Sea (Vietnam) are described. The diagnostic features of *Mecomerinx ohtsukai* n. sp. are: (i) three setae and one aesthetasc on the first segment of antennules; (ii) relatively long caudal ramus; (iii) elongated terminal segment of the antenna; and (iv) two claws on the terminal segment of antenna slightly unequal in length. The taeniacanthid copepod *Clavisodalis toxopneusti* n. sp. is distinguished from all seven known congeners by having two-segmented endopod of the legs 2–4 and four setae on the distal endopodal segment of the leg 1. This is the first report on copepods associated with echinoids of the genus *Toxopneustes* Agassiz and the first finding of *Mecomerinx* as well as taeniacanthid copepods in the South China Sea associated with echinoids.

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Introduction

Copepod crustaceans representing orders Harpacticoida Sars M., 1903, Poecilostomatoida Thorell, 1859 and Siphonostomatoida Thorell, 1859 are common and diverse symbionts of both extinct and recent echinoids (Gooding, 1957; Humes & Gelerman, 1962; Humes & Gooding, 1964; Gotto, 1993; Klompmaker & Boxshall, 2015). These symbiotic crustaceans associated with sea urchins are collected over a wide range of latitudes and at depths from shallow to abyssal; the copepods have been found on the host body, its galls or intestine (Humes & Cressey, 1961; Stock, 1968; Boxshall & Ohtsuka, 2001). Some of these copepods exhibit a remarkable microdistribution and evolutionary trends in the group. The siphonostomatoid copepods *Onychocheres alatus* Stock & Gooding, 1986 (Asterocheridae) have been observed moving up and down along the needles of the common sea urchin *Diadema antillarum* Philippi (Stock & Gooding, 1986) in shallow waters of the Caribbean.

Several species of poecilostomatoids of *Clavisodalis* Humes, 1970 (Taeniacanthidae Wilson, 1911) were found in the oesophagus of sea urchins collected at the Great Barrier Reef after dissecting of the Aristotle's lanterns (Humes, 1980; Dojiri & Humes, 1982). Evolutionary host switching revealed in Taeniacanthidae is the rare example of transition from parasitism on fishes to that on invertebrates (Dojiri & Cressey, 1987) and about 116 species have so far been reported from Taeniacanthidae (Venmathi Maran et al., 2016).

The shallow water flower urchin *Toxopneustes pileolus* (Lamarck) (Echinodermata: Echinoidea: Toxopneustidae Troschel) is common and widespread in the Tropical Indo-Pacific and known due to its poisonous globiferous pedicellariae which assist in deterring pests and predators (Fujiwara, 1935; Coppard et al., 2012). The pedicellaria are 2–3 mm long and when open form an isolated space between the test and the tip of pedicellariae. So far, the umagillid turbellarian *Syndesmis longicanalis* Moens, Martens & Schockaert, 1994 (see Moens et al., 1994), the ophiuroid *Ophiosphaera insignis* (Brock, 1888) (Amphiuridae Ljungman) (see Kroh &Thuy, 2013), the crab *Zebrida adamsii* White, 1847 (Pilumnidae Samouelle) (Suzuki & Takeda, 1974), and the alpheid shrimp *Athanas areteformis* Coutière, 1903 (see Kroh, 2015) have been reported as symbionts of the sea urchin *T. pileolus*.

Two new species of poecilostomatoid copepods belonging to the echinoid-specific genera *Mecomerinx* (Pseudanthessiidae Humes & Stock, 1972) and *Clavisodalis* (Taeniacanthidae Wilson) were collected from *T. pileolus* in the South China Sea and described. Their relationships with closest congeners and ecological features are discussed.

Materials and methods

Sampling was conducted in 2013 in Nhatrang Bay and near Cao Island in the South China Sea, Vietnam. Specimens of the flower urchin *Toxopneustes pileolus* (Lamarck) (Fig. 1) were hand-collected by SCUBA diving at depths ranging from 3 to 22 m; each specimen was isolated in a zip-lock plastic bag under water. In the laboratory the echinoids were checked for symbionts by eye, washed with an isotonic solution of magnesium chloride and fixed in 70% ethanol. The copepods obtained by washings were cleared and dissected in lactic acid following Humes & Gooding (1964). All figures were performed with the aid of a drawing tube attached to a light microscope (Nikon Labophot). The morphological terminology follows Humes (1977) and Huys & Boxshall (1991). Lengths of copepod specimens were measured from the frontal margin to the caudal rami, excluding caudal setae. In the armature formula of legs 1–4, Arabic and Roman numerals indicate setae and spines, respectively. For scanning electron microscopy (SEM) analyses copepods were dehydrated through graded ethanol concentrations; critical point dried, mounted on aluminium stubs, coated with gold, and examined in a JEOL scanning electron microscope at the Laboratory of electron microscopy (Biological Faculty of Lomonosov Moscow State University). All measurements are given in micrometres unless otherwise indicated.

Order Poecilostomatoida Thorell, 1859
Family Pseudanthessiidae Humes & Stock, 1972
Genus *Mecomerinx* Humes, 1977

Mecomerinx ohtsukai Venmathi Maran, Kim & Ivanenko n. sp.

Type-host: Flower urchin *Toxopneustes pileolus* (Lamarck) (Echinodermata: Echinoidea: Toxopneustidae).
Type-locality: Off Mun Island, Nhatrang Bay (12°09'52"N, 109°18'36"E), South China Sea, Vietnam; 19.iv.2013; depth 5–10 m; salinity 35‰, annual temperature 23.5–30.3°C.
Type-material: Holotype: adult female, dissected and mounted on a glass slide (NIBRIV0000540725); allotype adult male (NIBRIV0000540726); paratypes: five adult females and one adult male (NIBRIV 0000540727).
Additional material: Off Tre Island, Nhatrang Bay, 12°11′57″N, 109°17′37″E, 22.iii.2013, 3–5 m, 3 specimens; 24-28.iii.2013, 5.5–9.5 m, 26 specimens, 12°09′51″N, 109°18′35″E 2.iv.2013, 10 m, 8 specimens; off Noc Island, 12°11′23″N, 109°20′22″E, 4.iv.2013, 15–22 m, 7 specimens; Dun Island, 12°16′30″N, 109°21′20″E, 11.v.2013, 10 m, 2

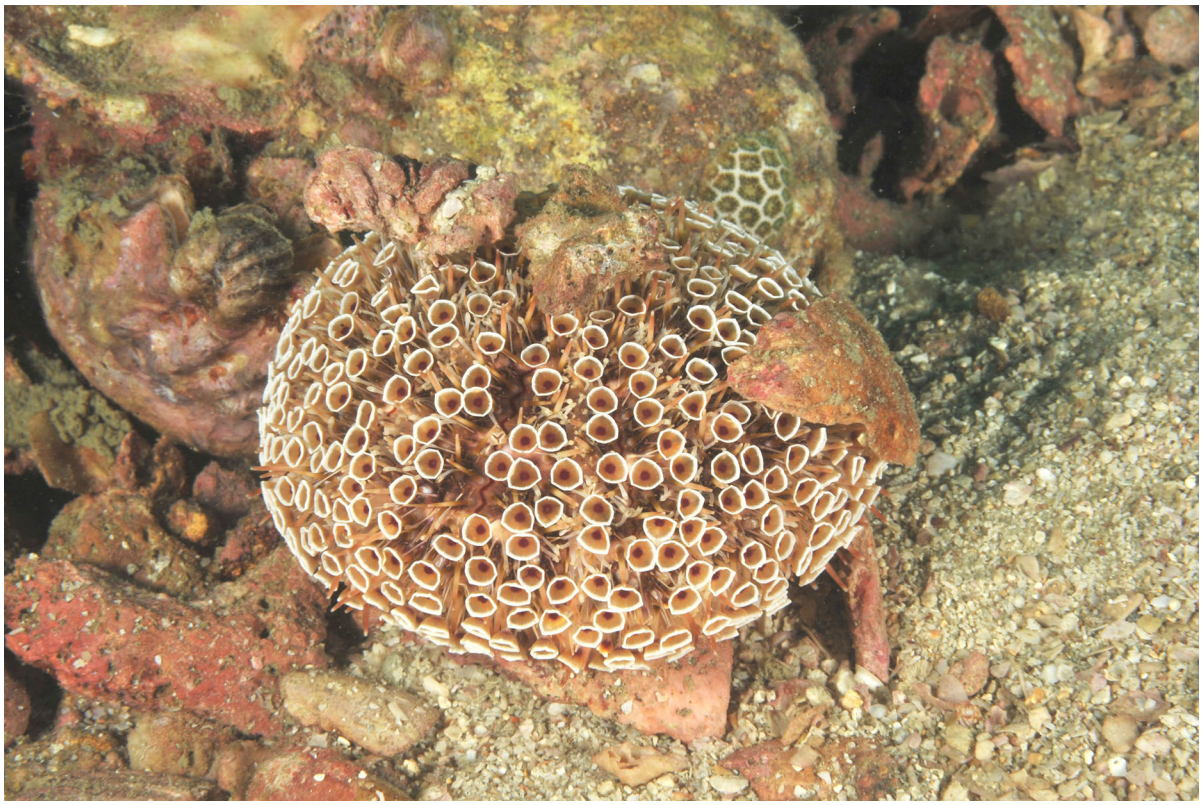

Fig. 1 Habitus of the flower urchin *Toxopneustes pileolus* (Lamarck), host of the new species of symbiotic copepods from Vietnam, natural environment, test diameter 85 mm

specimens; and off Cao Island, 11°13′16″N, 108°49′30″E, 04-05.iv.2013, 8–14 m, 87 specimens; collector OAB. The additional material and specimens used for scanning electron micrograph are in the collection of the Department of Invertebrate Zoology, Lomonosov Moscow State University.

Etymology: The species name is dedicated to Professor Susumu Ohtsuka (Hiroshima University), for his outstanding contribution to the taxonomy of copepods.

Description (Figs. 2–4, 8A–C)

Adult female. Body (Figs. 2A, 8A) cyclopiform, 956 long. Prosome ovoid, 600 × 462. Cephalothorax 400 long, with faint dorsal suture line between cephalosome and first pedigerous somite. Urosome (Fig. 2B) small, 5-segmented. Fifth pedigerous somite 120 wide. Genital double-somite 131 × 117, 1.12 times as long as wide, with convex lateral margins; genital apertures located dorsolaterally slightly posterior to midlength of double-somite. Three free abdominal somites 38 × 81, 29 × 76 and 40 × 75, respectively. Caudal ramus (Fig. 2C) 94 × 34, 2.76 times as long as wide, and armed with 7 setae, including minute, setule-like outer proximal seta; outer proximal, outer subdistal and dorsal setae naked, and other setae plumose.

Rostrum (Fig. 2D) broad, with parallel lateral margins, sclerotised posterior margin connecting to short posterior ridge. Antennule (Fig. 2E) short, 285 long, 7-segmented; armature formula: 3+ aesthetasc, 13, 6, 3, 4+ aesthetasc, 2+ aesthetasc, and 7+ aesthetasc; aesthetasc on first segment long, extending beyond distal tip of antennule; one of setae on first

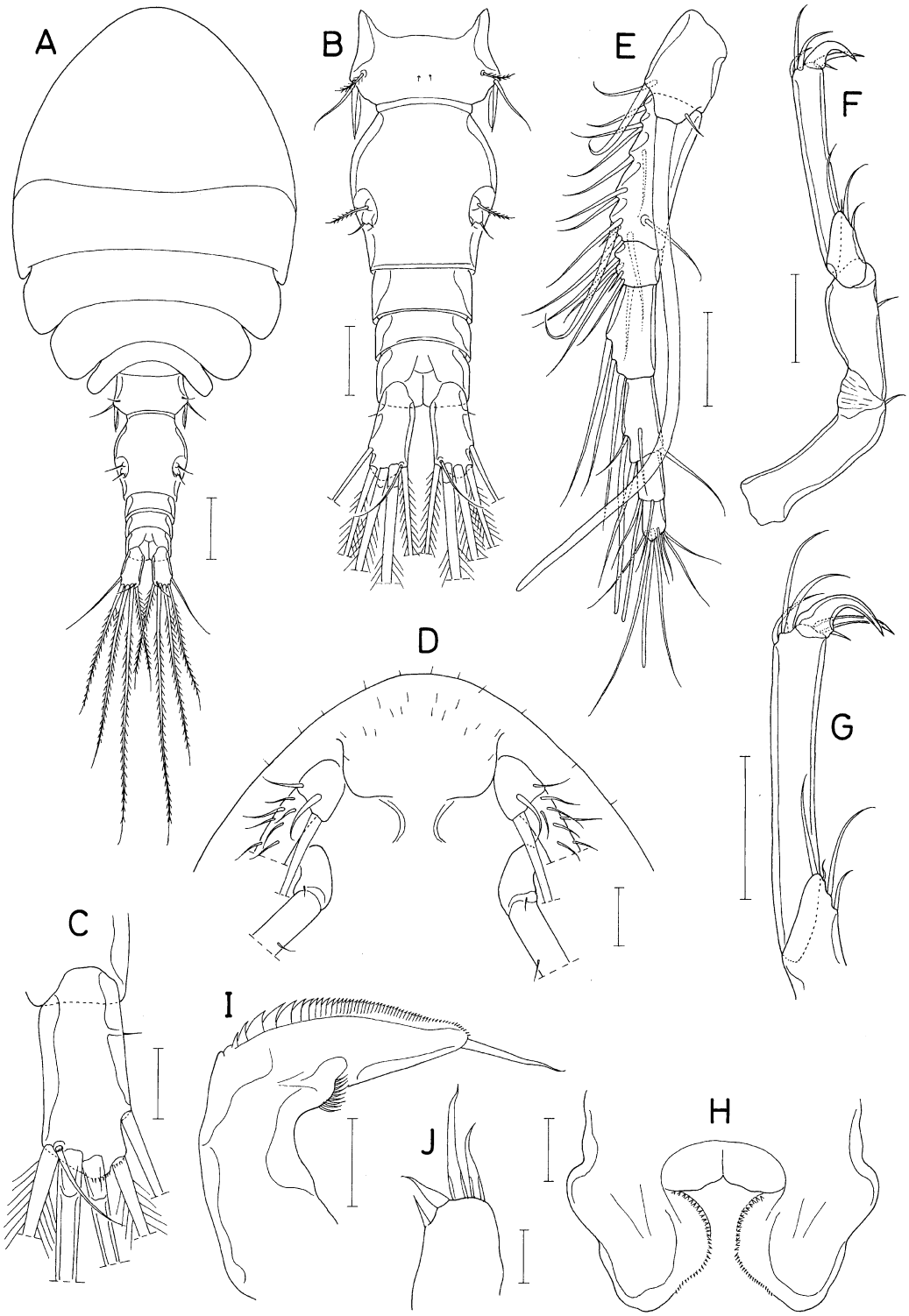

Fig. 2 *Mecomerinx ohtsukai* n. sp., adult female. A, Habitus, dorsal; B, Urosome, dorsal; C, Right caudal ramus, dorsal; D, Rostral area, ventral; E, Antennule; F, Antenna; G, Distal part of antenna; H, Labrum; I, Mandible; J, Maxillule. *Scale-bars*: A, 100 μm; B, D, E–G, 50 μm; C, H, I, 20 μm; J, 10 μm

segment minute and inserted near base of aesthetasc; all setae naked. Antenna (Fig. 2F, G) 4-segmented, consisting of coxobasis and endopod. Coxobasis with 1 seta distally. Endopod 3-segmented; first segment with 1 seta subdistally; short second segment with 4 setae, one of them being rudimentary; third segment 99 × 17 (length as average of outer and inner margins), 5.8 times as long as wide, distally with 2 spines and 4 setae; spines consisting of thick, strongly curved one, 36 long, and slender one, 29 long; one of setae small, inserted at base of large claw.

Labrum (Fig. 2H) with 2 distal lobes and broad convergent posterolateral lobes bearing convex denticulate medial margins (Fig. 8B, C). Mandible (Fig. 2I) narrow, with shallow inner proximal notch, inner row of setules near base of blade, and setiform distal lash; blade tapering, with serrate convex margin and smooth concave margin. Maxillule (Fig. 2J) armed with 3 unequal setae distally and 1 setiform element subdistally. Maxilla (Fig. 3A) 2-segmented; proximal segment (syncoxa) unarmed; distal segment (basis) with 1 naked seta (seta II) on anterior surface and elongate distal lash; distal lash with spinules along convex margin (and row of additional spinules near base of this margin) and graduated fine spinules along distal half of concave margin; setae I and III absent. Maxilliped (Fig. 3B) 3-segmented; first segment (syncoxa) longest, but unarmed; second segment (basis) widest in middle, with 2 similar setae and fine spinules on inner side; third segment (endopod) tapering, acutely pointed distally, with 2 setae (1 proximal and 1 near middle) and row of fine spinules along distal end of inner margin.

Legs 1–3 (Fig. 3C-E) with 3-segmented rami. Leg 4 (Fig. 3F) with 3-segmented exopod and 1-segmented endopod. Outer distal corner of coxa of these legs with several spinules. All of setae on legs 1–4, including outer seta on basis, plumose. Leg 4 without inner seta on coxa; endopod 86 × 21, 4.1 times as long as wide, with setules on proximal half of outer margin; 2 terminal setae of endopod 79 (inner) and 47 (outer), respectively. Armature formula for legs 1–4 as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1	0-1	1-0	I-0; I-1; III, I, 4	0-1; 0-2; I, 1, 4
Leg 2	0-1	1-0	I-0; I-1; III, I, 5	0-1; 0-2; I, II, 3
Leg 3	0-1	1-0	I-0; I-1; III, I, 5	0-1; 0-2; I, II, 2
Leg 4	0-0	1-0	I-0; I-1; II, I, 5	II

Leg 5 (Fig. 3G) represented by 2 setae (one naked) and 1 spine (41 long) at lateral region of fifth pedigerous somite. Leg 6 (Fig. 3G) represented by 2 small lobes bearing 1 plumose seta and 1 naked seta plus 1 small, spinule-like process at genital aperture.

Adult male. Body (Fig. 4A) narrower than that of female, 730 long. Prosome 430 × 303. Cephalothorax 301 long. Urosome (Fig. 4B) 6-segmented. Fifth pedigerous somite 82 wide, much narrower than next somite. Genital somite almost globular, 116 × 135, slightly wider than long. Four abdominal somites 35 × 61, 29 × 60, 22 × 58 and 35 × 58, respectively. Caudal ramus 47 × 25, 1.88 times as long as wide, distinctly shorter than that of female, and armed with 6 setae (seta I not visible).

Rostrum as in female. Antennule (Fig. 4C) 215 long, with 3 additional aesthetascs: 2 on second and 1 on fourth segments, 2 distal aesthetascs small, shorter than segment width. Antenna as in female, without additional ornamentation on inner margin of segments; shortest seta on second endopodal segment longer than in female.

Labrum, mandible, maxillule, and maxilla as in female. Maxilliped (Fig. 4D) 4-segmented; first segment (syncoxa) unarmed; second segment (basis) with 2 small setae and 2 longitudinal rows of fine spinules on inner side; small third segment (first endopodal segment) unarmed; fourth segment (second endopodal segment) represented by elongate, curved claw bearing 1 seta, 1 setule and 1 proximal tubercle, membranous hyaline brim along concave margin, and translucent tip.

Legs 1–4 as in female. Leg 5 also as in female, but both setae naked. Leg 6 represented by 2 naked setae on genital operculum (Fig. 4B).

Remarks

The new species *Mecomerinx ohtsukai* n. sp. differs from its congeners *M. heterocentroti* Humes, 1977, *M. luculenta* (Humes & Cressey, 1961), *M. notabilis* (Humes & Cressey, 1961) and *M. sewellana* Humes, 1977 in having: (i) longer caudal rami; (ii) an elongate terminal segment of antenna; (iii) the two claws on the terminal segment of antenna are short and slightly unequal in length. The new species has three setae and one aesthetasc on the first antennulary segment as in *M. luculenta*. The new species differs markedly from

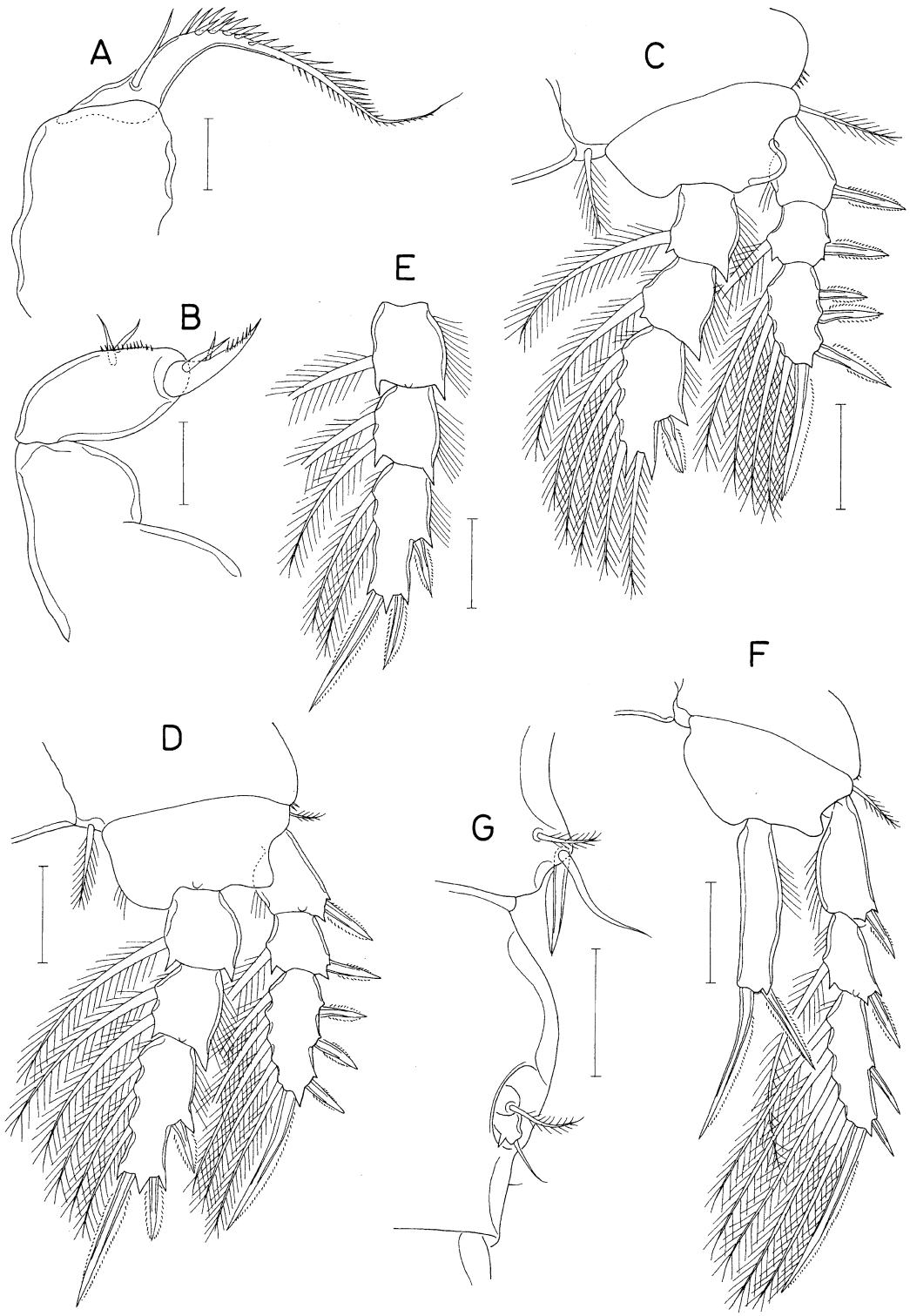

Fig. 3 *Mecomerinx ohtsukai* n. sp., adult female. A, Maxilla; B, Maxilliped; C, Leg 1; D, Leg 2; E, Endopod of leg 3; F, Leg 4; G, Right side of first and second urosomal somites, dorsal. *Scale-bars*: A, B, 20 μm; C–G, 50 μm

its most closely related congener *M. luculenta* in having longer caudal rami (2.76:1 *vs* 1.62:1), a more elongate terminal segment of antenna (5.82:1 *vs* 3.12:1), and in the length of two terminal antennary claws (36 and 29 μm *vs* 88 and 84 μm). Morphological distinctive characters of all five species of the genus *Mecomerinx* including the new species are summarised in Table 1.

About 49% and 63% of the sea urchins examined in Nhatrang Bay and near Cao Island, respectively, were infested by *Mecomerinx ohtsukai* n. sp.; 7 to 22 specimens of the species were found on individual hosts. In 10 of 48 infested sea urchins *M. ohtsukai* n. sp. co-occurred with another new species of the genus *Clavisodalis* described here. The depth range of finding of the sea urchins is 3–22 m. The four other congeners were reported from washings of other four species of sea urchins at a depth range 0.5–3 m in the Gulf of Aqaba, Madagascar, Moluccas, New Caledonia and the Philippine Islands, with no information about co-occurrence on one host individual with other species of symbiotic copepods (Table 1) given. *Mecomerinx ohtsukai* n. sp. is the first member of the genus to be reported in association with echinoids of the genus *Toxopneustes* and the first report of the genus in the South China Sea.

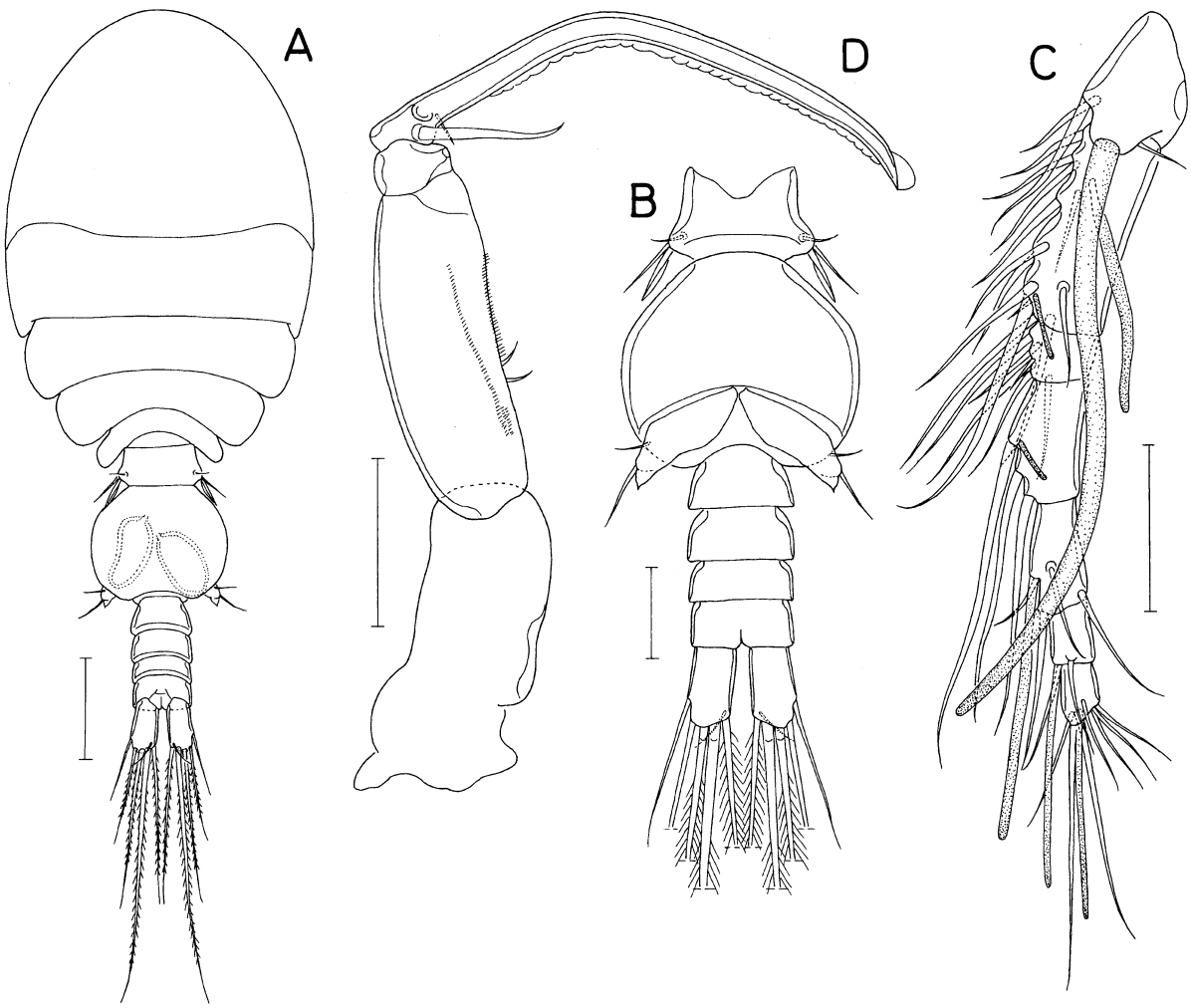

Fig. 4 *Mecomerinx ohtsukai* n. sp., adult male. A, Habitus, dorsal; B, Urosome, ventral; C, Antennule; D, Maxilliped. *Scale-bars*: A, 100 μm; B–D, 50 μm

Order Poecilostomatoida Thorell, 1859
Family Taeniacanthidae C. B. Wilson, 1911
Genus *Clavisodalis* Humes, 1970

***Clavisodalis toxopneustis* Venmathi Maran, Kim & Ivanenko n. sp.**

Type-host: Flower sea urchin *Toxopneustes pileolus* (Lamarck) (Echinodermata: Echinoidea: Toxopneustidae).
Type-locality: Off Mun Island, Nhatrang Bay (12°09′52″N, 109°18′36″E) South China Sea, Vietnam, 19.iv.2013 at 5–10 m depth range, salinity 35‰, annual temperature 23.5–30.3°C.
Type-material: Holotype: female, dissected and mounted on a glass slide (NIBRIV0000540728).
Additional material: Off Tre Island, Nhatrang Bay, 12°11′57″N, 109°17′37″E, 22.iii.2013, 3–5 m, 2 specimens; 12°10′49″N, 109°17′44″E, 22.iv.2013, 5–10 m, 2 specimens; off Noc Island, 12°11′23″N, 109°20′22″E, 04.iv.2013, 15–22 m, 1 specimens; off Mun Island, 12°09′52″N, 109°18′36″E, 11.iv.2013, 12–15 m, 2 specimens; off Dun Island, 12°16′30″N, 109°21′20″E, 11.v.2013, 10 m, 1 specimens; and off Cao Island, 11°13′16″N, 108°49′30″E, 03.iv.2013, 8–10 m, 7 specimens; collector OAB. The additional material and specimen used for scanning electron micrograph are in the collection of the Department of Invertebrate Zoology, Lomonosov Moscow State University.
Etymology: The species name refers to the host genus, *Toxopneustes* L. Agassiz.

Description (Figs. 5–7, 8D)

Adult female. Body (Fig. 5A, B, 8D) laterally expanded, flattened, with large prosome and small urosome. Body length 1.26 mm. Prosome 1.00 mm long, 3-segmented, consisting of fused cephalothorax and pedigerous somites 2-4. Cephalothorax + second pedigerous somite 636 × 614, with truncate anterior apex and constriction between original cephalothorax and second pedigerous somite on dorsal and lateral surfaces. Dorsal cephalic region abruptly depressed and distinctly demarcated from posterior, thoracic region. Third and fourth pedigerous somites 182 × 500 and 159 × 414, respectively, with rounded lateral margins. Urosome (Fig. 5C) 5-segmented. Fifth pedigerous somite 67 × 233. Genital double-somite 121 × 245, consisting of laterally

Table 1 Main differences in the ecology and morphology of females of *Mecomerinx* (Copepoda: Poecilostomatoida: Pseudanthessiidae)

Copepod species	Host	Locality (depth)	Caudal ramus, length/width ratio	Armature of 1st antennulary segment	Antenna		Reference
					Terminal segment, length/width ratio	Length of 2 terminal claws (μm)	
M. heterocentroti Humes, 1977	*Heterocentrotus mamillatus* (L.)	New Caledonia (0.5–2 m)	1.51:1	4 setae	2.69:1	73, 36 (unequal)	Humes (1977)
M. luculenta (Humes & Cressey, 1961)	*Stomopneustes variolaris* (Lamarck)	Madagascar (depth unknown)	1.64:1	3 setae + 1 aesthetasc	3.12:1	88, 84 (subequal)	Humes & Cressey (1961)
M. notabilis (Humes & Cressey, 1961)	*Echinometra mathaei* (Blainville)	Madagascar, the Gulf of Aqaba, New Caledonia (depth unknown)	1.94:1	4 setae	3.27:1	64, 24 (unequal)	Humes & Cressey (1961); Stock (1967); Humes (1977)
M. sewellana Humes, 1977	*Tripneustes gratilla* (L.)	Moluccas and Philippine Islands (1–3 m)	1.69:1	2 setae + 2 aesthetascs	4.84:1	44, 24 (unequal)	Humes (1977)
M. ohtsukai n. sp.		Vietnam (3–22 m)	2.76:1	3 setae + 1 aesthetasc	5.82:1		This study

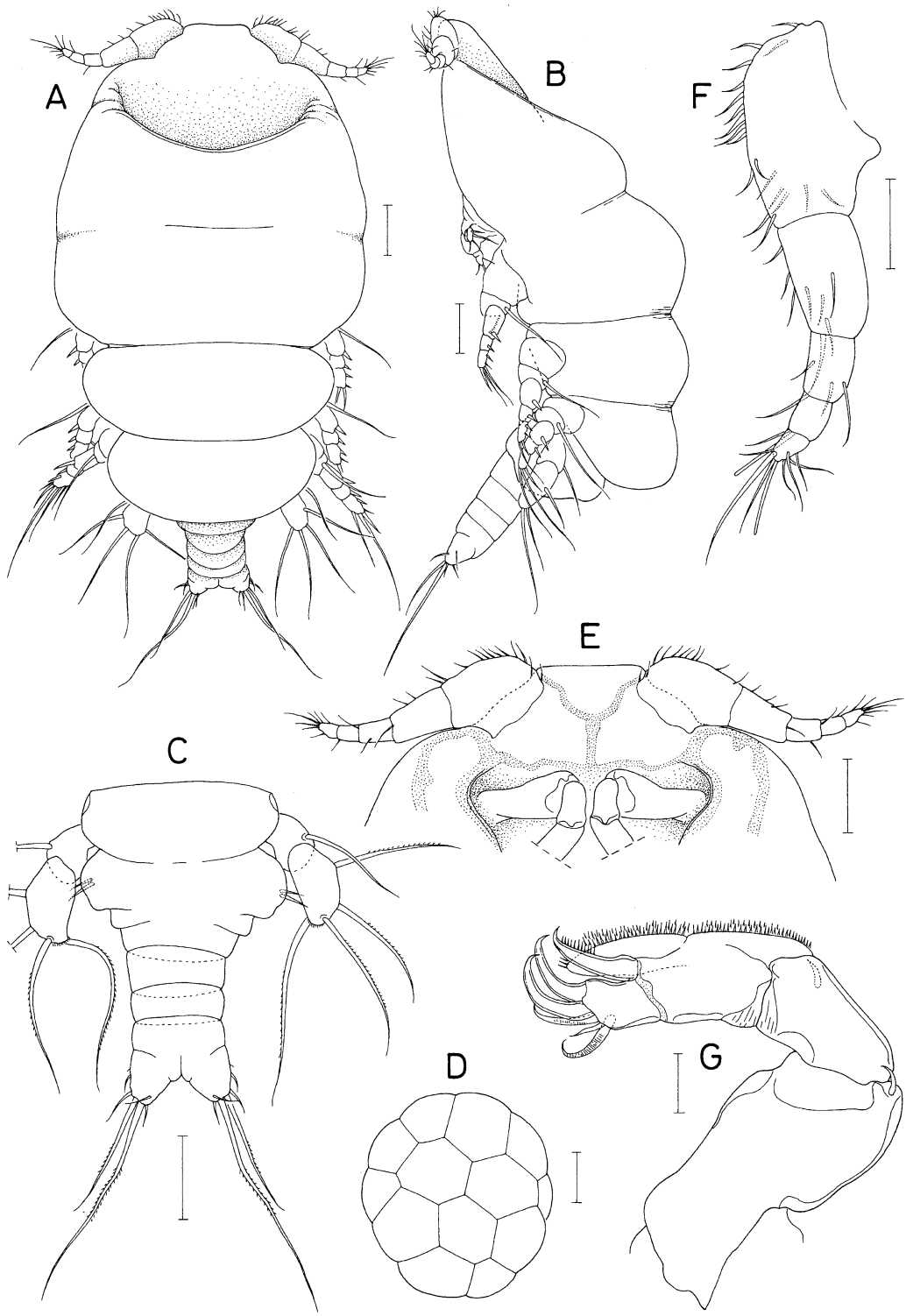

Fig. 5 *Clavisodalis toxopneustis* n. sp., adult female. A, Habitus, dorsal; B, Habitus, lateral; C, Urosome, dorsal; D, Egg-sac; E, Rostral area, ventral; F, Antennule; G, Antenna. *Scale-bars*: A–E, 100 μm; F, 50 μm; G, 20 μm

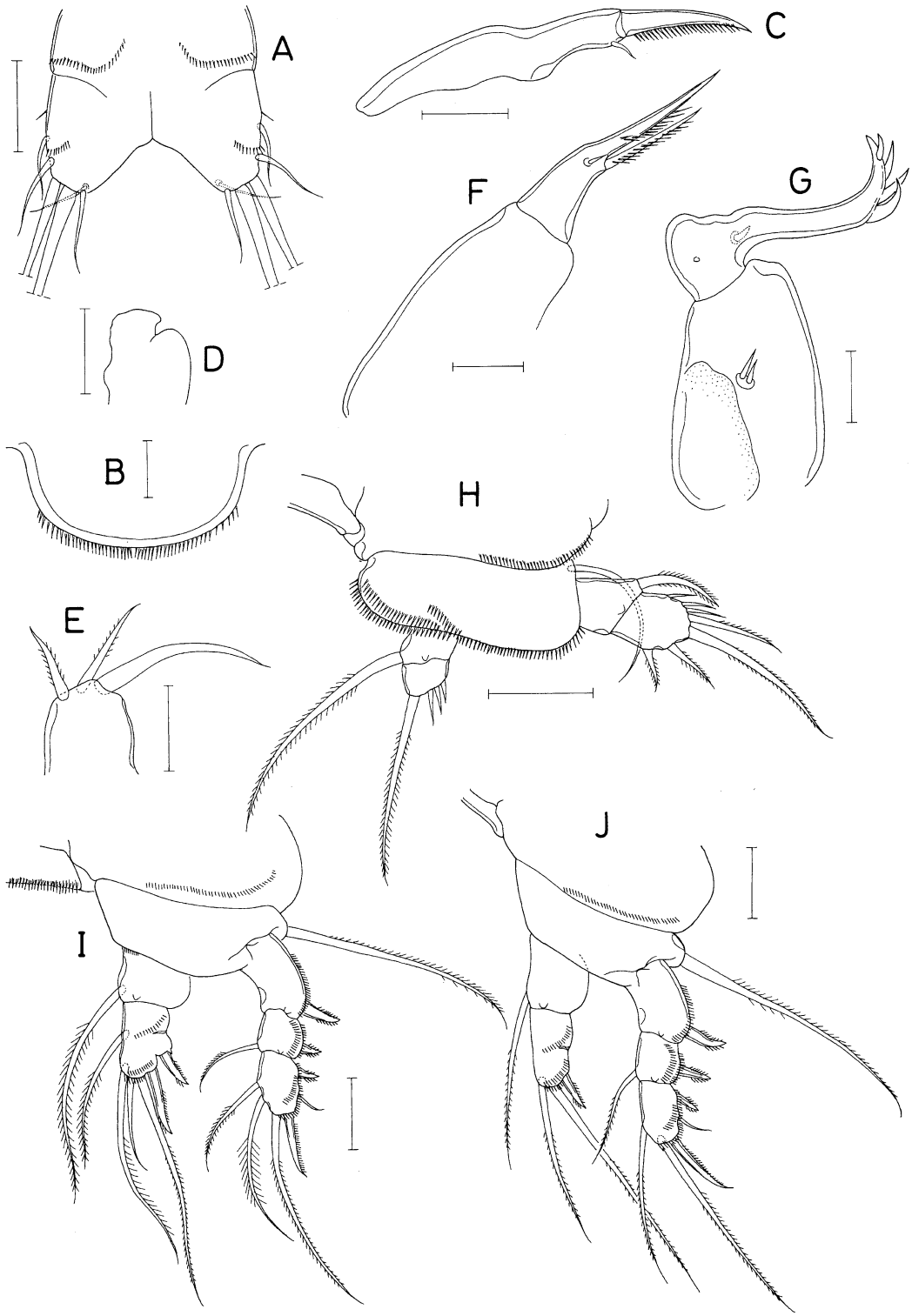

Fig. 6 *Clavisodalis toxopneustis* n. sp., adult female. A, Caudal rami, ventral; B, Labrum; C, Mandible; D, paragnath; E, Maxillule; F, Maxilla; G, Maxilliped; H, Leg 1; I, Leg 2; J, Leg 3. *Scale-bars*: A, H–J, 50 μm; B–G, 20 μm

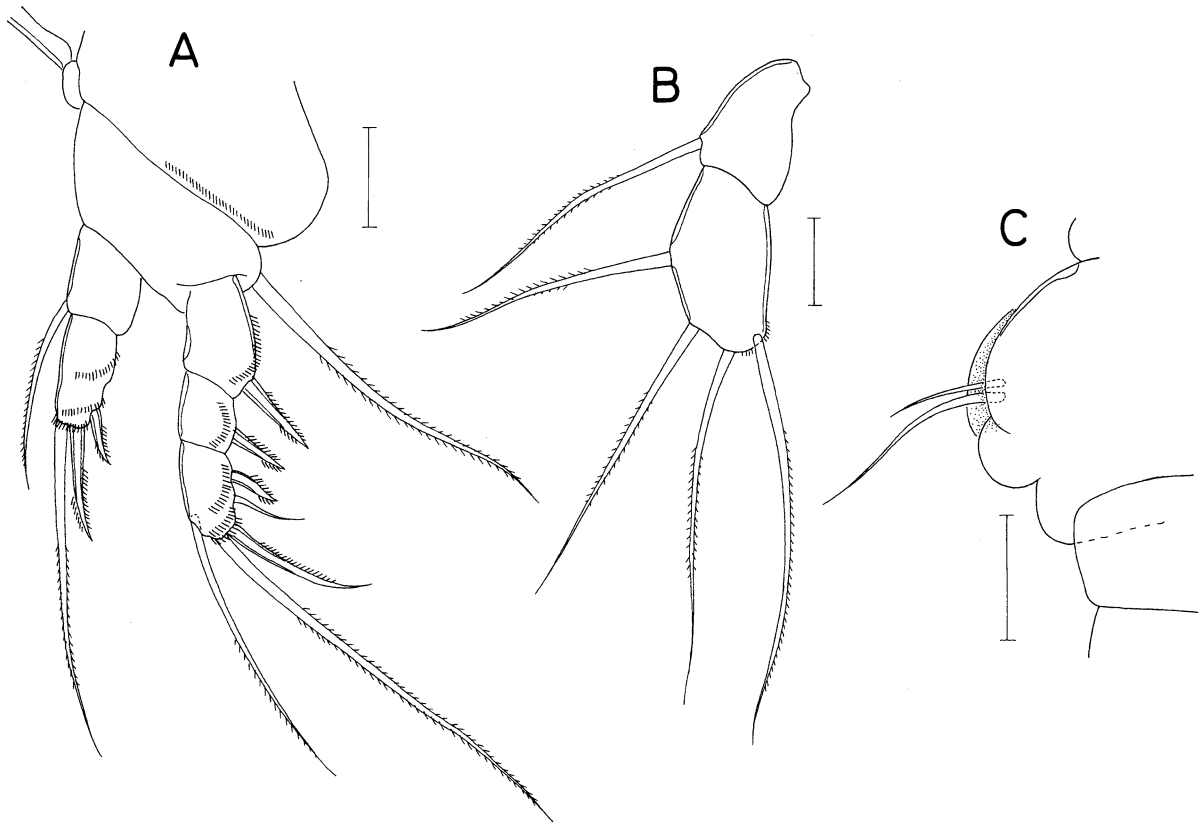

Fig. 7 *Clavisodalis toxopneustis* n. sp., adult female. A, Leg 4; B, Leg 5; C, Right genital area, ventral. *Scale-bars*: 50 μm

expanded anterior half and narrower posterior half; genital area located venterolaterally in middle of expanded anterior half. Three free abdominal somites 45 × 118, 36 × 110, and 45 × 112, respectively, smooth on all surfaces. Caudal rami (Fig. 6A) divergent, incompletely articulated from anal somite, tapering, 53 × 53, and armed with 7 setae including minute outer proximal one; 2 largest median terminal setae with fine spinules along lateral margins; other setae naked. Egg-sac (Fig. 5D) flat, circular, 418 × 386, 2 eggs thick.

Rostrum absent, but rostral region with ventral sclerotised band (Fig. 5E). Antennule (Fig. 5F) 250 long, and 5-segmented; armature formula: 19, 8, 4, 1 + aesthetasc, 7 + aesthetasc; all setae short, naked. Antenna (Fig. 5G) consisting of coxobasis and endopod. Coxobasis with 1 small distal seta. Endopod 3-segmented; first segment with 1 subdistal seta; second segment with densely spinulose ventral (inner) side, broad spinulose subdistal process and spinulose, hook-like spine; third segment with 2 hook-like spines and 3 setae.

Labrum (Fig. 6B) broad, with convex, spinulose posterior margin. Mandible (Fig. 6C) armed with 1 distal spine bearing spinules along concave margin and 1 small, subdistal seta. Paragnath (Fig. 6D) flexible, transparent, with abruptly narrowed distal part. Maxillule (Fig. 6E) armed distally with 3 unequal setae. Maxilla (Fig. 6F) 2-segmented; proximal segment (syncoxa) unarmed; distal segment (basis) with distal spiniform, spinulose process and armed with 1 spinulose spine and 1 minute seta. Maxilliped (Fig. 6G) 2-segmented; proximal segment with 2 medial small setae; distal segment claw-like, elongate, strongly curved proximally and slightly curved distally, with 1 small proximal seta and 4 distal large denticles on convex margin.

Leg 1 (Fig. 6H) with 2-segmented rami. Legs 2–4 (Figs. 6I, J, Fig. 7A) with 3-segmented exopod and 2-segmented endopod. Second endopodal segment of

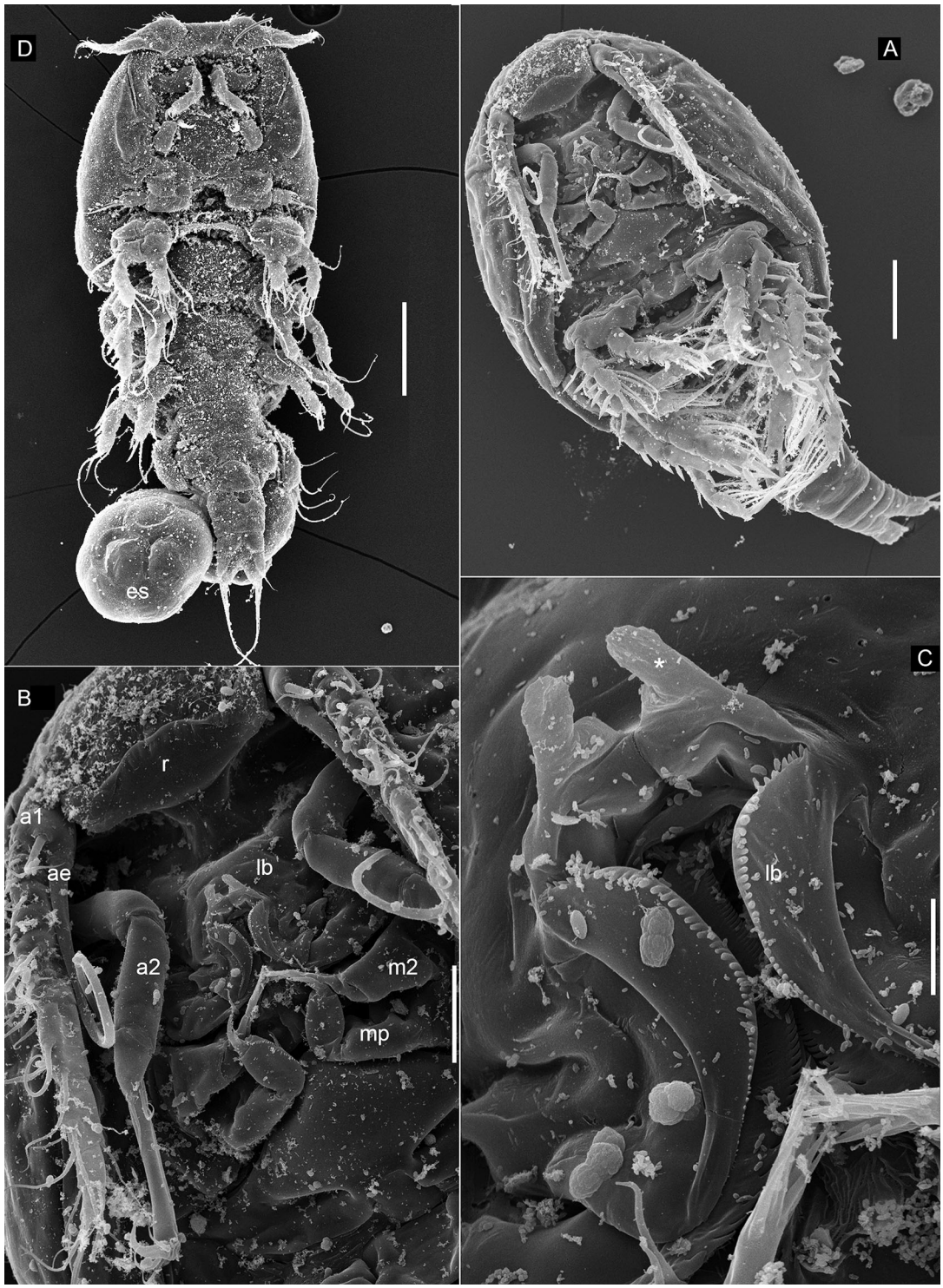

Fig. 8 Scanning electron microphotographs of *Mecomerinx ohtsukai* n. sp., adult female (A–C) and *Clavisodalis toxopneustis* n. sp. (D). A, Habitus, ventral; B, Prosome, ventral; C, Labrum; D, *Clavisodalis toxopneustis* n. sp., adult female, habitus, ventral. *Abbreviations*: a1, antennule; a2, antenna; ae, aesthetasc; es, egg-sac; lb, labrum; m2, maxilla; mp, maxilliped; r, rostrum; *, distal lobe of labrum. *Scale-bars*: A, 100 μm; B, 50 μm; C, 10 μm; D, 200 μm

Table 2 Main differences in ecology and armature elements on exopod (Exp) and endopod (Enp) of legs 1–4 in the species of *Clavisodalis* (Copepoda: Poecilostomatoida: Taeniacanthidae). Number of setal elements on segments (proximal to distal) of rami expressed as x–x–x

Copepod species	Host	Locality, depth (reference)	Leg 1		Leg 2		Leg 3		Leg 4	
			Exp	Enp	Exp	Enp	Exp	Enp	Exp	Enp
Clavisodalis abbreviatus Dojiri & Humes, 1982	*Heterocentrotus mamillatus* (L.)	New Caledonia, 0.1–1 m (Dojiri & Humes, 1982)	1-6	1-8	1-2-7	1-1-5	1-2-6	1-1-3	1-2-6	1-0-3
C. dilatatus Dojiri & Humes, 1982	*Diadema setosum* (Leske)	New Caledonia, 3 m (Dojiri & Humes, 1982)	1-7	1-8	1-2-8	1-2-6	1-2-7	1-2-4	1-2-7	1-2-4
C. heterocentroti Humes, 1970	*Heterocentrotus trigonarius* (Lamarck)	Marshall Islands, depth unknown (Humes, 1970)	1-6	1-7	1-2-6	1-0-5	1-2-6	1-0-3	1-1-6	1-0-3
C. parvibullatus Dojiri & Humes, 1982	*Echinometra mathaei* (Blainville)	New Caledonia, 0–1 m (Dojiri & Humes, 1982	1-6	1-7	1-1-6	1-0-4	1-1-5	1-0-2	1-1-3	1-0-3
C. salmacidis Humes, 1980	Oesophagus of *Salmacis belli* Döderlein	Queensland, depth unknown (Humes 1980; Dojiri & Humes, 1982)	1-7	1-8	1-2-6	1-1-5	1-1-6	1-1-3	1-2-6	1-1-4
C. sentifer Dojiri & Humes, 1982	*Diadema setosum* (Leske), oesophagus of *Diadema* sp.	Moluccas, 2 m Queensland (Dojiri & Humes, 1982)	1-7	1-8	1-2-8	1-2-6	1-2-8	1-2-4	1-2-6	1-1-3
C. tenuis Dojiri & Humes, 1982	*Heterocentrotus mamillatus* (L.)	New Caledonia, 0.1–1 m (Dojiri & Humes, 1982)	1-6	1-7	1-1-6	1-0-4	1-1-5	1-0-2	1-1-5	1-0-3
C. toxopneustis n. sp.	*Toxopneustes pileolus* (Lamarck)	Vietnam, 3–22 m (This study)	1-4	1-7	1-2-6	1-6	1-2-5	1-3	1-1-5	1-3

legs 2 and 3 with vestige of articulation on outer side. Coxa of legs 1–4 lacking inner seta, but with row spinules on outer posterior margin. Leg 1 with exopod inserted on outer margin of basis; posterior margin of basis spinulose, with 3 rows of spinules. Intercoxal plate of leg 2 spinulose on distal margin, but that of legs 1, 3 and 4 naked. Setae of legs 1–4 naked or weakly plumose. Outer seta on basis of legs 1–4 large. Exopodal segments and second endopodal segment of legs 2–4 with rows of spinules on outer or distal sides. Second endopodal segment of leg 1 with 1 long and 3 short setae. Armature formula for legs 1–4 as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1	0-0	1-0	1-0; 7	0-1; 4
Leg 2	0-0	1-0	I-0; I-1; I, 1, I, 3	0-1; II, 4
Leg 3	0-0	1-0	I-0; I-1; I, 1, I, 2	0-1; I, 2
Leg 4	0-0	1-0	I-0; I-0; I, 1, I, 2	0-1; II, 1

Leg 5 (Fig. 7B) consisting of protopod and exopod; protopod with 1 seta on outer distal mardin; exopod 100 × 56, 1,79 times as long as wide, with 4 long setae (2 lateral, 2 distal). Leg 6 (Fig. 7C) represented by 2 unequal setae at genital aperture (Fig. 8D).

Adult male. Unknown.

Remarks

The new species *Clavisodalis toxopneustis* n. sp. can easily be distinguished from other congeners by: (i) two-segmented endopod of the legs 2–4 (*vs* three-segmented); (ii) four setae on the distal endopodal segment of leg 1 (*vs* six or seven setae); and (iii) an unique combination of armature elements of the legs 1-4, as summarised in Table 2.

Copepods of *Clavisodalis toxopneustis* n. sp. co-occurred with *Mecomerinx ohtsukai* n. sp. (see Remarks above). About 24% and 16% of sea urchins collected in Nhatrang Bay and near Cao Is Island,

respectively, were infested by *C. toxopneustis* n. sp. The mean abundance was 2 and 2.6 copepods per sea urchin from Nhatrang Bay and Cao Island, respectively. Half of all of the copepods from Nhatrang Bay and 33% of the copepods from Cao Is Island were ovigerous females. The copepods were collected at a depth range of 3 to 22 m. The other congeners were reported from the oesophagus and washings of other five species of sea urchins at depth range of 0.1–3 m in The Great Barrier Reef, Madagascar, Marshall Islands, Moluccas, New Caledonia and the Philippine Islands (Table 2). *Clavisodalis toxopneustis* n. sp. is the first member of the genus to be found in association with echinoids of the genus *Toxopneustes* and is the first report of a taeniacanthid associating with sea urchins in the South China Sea.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable institutional, national and international guidelines for the care and use of animals were followed.

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