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A new species of deep-sea Tegastidae (Crustacea: Copepoda: Harpacticoida) from 9°50'N on the East Pacific Rise, with remarks on its ecology*

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Abstract

Both male and female of the new deep-sea species *Smacigastes barti* sp. nov. (Tegastidae, Sars) are described in detail. Copepoda is one of the most diversified taxa at deep-sea hydrothermal vents, but only one species of the family Tegastidae has been described from this habitat and other deep-sea environments. *Smacigastes barti* is the second species of the genus *Smacigastes* Ivanenko & Defaye, 2004, and was found in artificial substrates deployed in the vicinity of and 0.5 m from tubeworm aggregations at the 9°50'N region on the East Pacific Rise at 2500 meters depth. The derived character states of the new species are the lack of coxal endites on the maxilla, and 2-segmented exopods of swimming legs 2 and 3, the latter being the result of the fusion of the 2 proximal segments. An identification key to all known genera of Tegastidae is provided. Interestingly, the distribution of *S. barti* showed that it does not tolerate elevated temperatures and/or the presence of hydrogen sulfide or oxygen fluctuations, although both species of this genus were found in deep-sea chemosynthetic environments.

Keywords

Copepoda; Harpacticoida; Tegastidae; hydrothermal vent; deep-sea

Introduction

Deep-sea hydrothermal vents are globally widespread extreme environments located at the mid-ocean ridge systems. Driven by *in situ* primary production via chemosynthesis, a special vent fauna thrives under highly fluctuating conditions along a gradient of temperature and toxic chemicals such as hydrogen sulfide (Van Dover 2000). Copepoda is one of the most diversified taxa at hydrothermal vents, contributing about 80 described species, which represents more than 15% of the species documented from vents worldwide (Humes & Segonzac 1988, Tunnicliffe et al. 1998, Bright 2006). About 50 described vent copepod species belong to the order Siphonostomatoida, remarkably to the presumably vent-endemic family Dirivultidae Humes & Dojiri. Only 12 species of harpacticoid copepods have been described from vents so far, but this group has been less studied and it is thought

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that the diversity of this group might be higher (Heptner & Ivanenko 2002, Ivanenko & Defaye 2006).

Copepods of the family Tegastidae (Crustacea, Copepoda, Harpacticoida) are characterized by a laterally compressed amphipod-like body, by a modified male genital complex, and by a claw-like mandible in the nauplii (Lang 1948, Ivanenko et al. 2008). Currently 59 species belonging to 6 genera have been described. Except for the deep-sea species *Smacigastes micheli* (Ivanenko & Defaye 2004), all tegastid species have been found in shallow water habitats in association with algae, bryozoans and/or cnidarians (Chislenko 1967, Medioni & Soyer 1968, Chislenko 1977, Humes 1981a, 1981b, 1984, Ferrari et al. 2007). In a previous paper, *S. micheli* was reported from artificial substrates as a part of a colonization experiment deployed at the active chimney “Eiffel Tower” on the Mid-Atlantic Ridge (Ivanenko & Defaye 2004). Here, we describe a new species of the genus *Smacigastes* from deep-sea hydrothermal vents on the East Pacific Rise and provide remarks on its ecology.

Material and methods

Copepods were collected during cruises AT7-26 and AT11-03 on board the RV *Atlantis* to the Northern East Pacific Rise in November 2002 and 2003. Specimens were found associated with artificial substrates that were used to imitate the natural *Riftia pachyptila* Jones tubeworm aggregations. Each artificial aggregation consisted of 80 PVC (polyvinyl chloride) tubes of four different size classes. Four of these artificial aggregations were deployed in each zone: within assemblages of *R. pachyptila*, ~50 cm from *R. pachyptila*, and ~20 m from the natural aggregations at the site Tica (9°50.447'N, 104°17.493'W) at 2500 meters depth. After collection, copepods were fixed in 4% formalin for 24 hours, and transferred to 70% ethanol for shipment and storage (for details see Govenar & Fisher 2007).

For light microscopy, specimens were dissected in glycerin under a Leica MZ8 microscope. Copepods and/or parts of copepods were mounted on slides using glycerin (Higgins & Thiel 1988). Specimens were examined, and drawings were made with bright-field or differential interference contrast, using a Leica DMR compound microscope.

For scanning electron microscopy (SEM), copepods were dehydrated through a series of graded ethanol, acetone and HMDS (hexamethyldisilazane) concentrations, mounted on aluminium stubs, and sputtered with gold (Nation 1983). Specimens were observed using a Philips XL 20 scanning electron microscope.

The description is mainly based on the female holotype and the male paratype 1, which were drawn using light microscopy. Additional SEM pictures from paratypes were used to show more details. For long-term preservation the holotype and paratypes are all mounted on slides in glycerin. The type material is deposited in the Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main, Germany (Holotype, Paratypes 1–8), and in the Oberösterreichische Landesmuseen, Biologiezentrum Linz, Austria (Paratypes 9–13).

Descriptive part

Order HARPACTICOIDA Sars

Family Tegastidae Sars

Genus *Smacigastes* Ivanenko & Defaye

Type species *Smacigastes barti* sp. nov.

Type material

- Holotype dissected ♀, 19 slides (nr. SMF 31411)
Paratype 1: dissected ♂, 13 slides (nr. SMF 31412)
Paratype 2: ♀ (nr. SMF 31413)
Paratype 3: ♂ (nr. SMF 31414)
Paratype 4: ♀ (nr. SMF 31415)
Paratype 5: ♂ (nr. SMF 31416)
Paratype 6: ♀ (nr. SMF 31417)
Paratype 7: ♂ (nr. SMF 31418)
Paratype 8: dissected copepodite stage V, 3 slides (nr. SMF 31419)
Paratype 9: ♀ (nr. OLML 2007/199)
Paratype 10: ♂ (nr. OLML 2007/200)
Paratype 11: ♀ (nr. OLML 2007/201)
Paratype 12: ♂ (nr. OLML 2007/202)
Paratype 13: copepodite stage V (nr. OLML 2007/203)

Type locality

East Pacific Rise (EPR); 9°50.447'N, 104°17.493'W; 2500 m depth. The site Tica is located on the EPR between the Clipperton and Sequeiros transform faults. The site was colonized by the giant tubeworm *Riftia pachyptila* in 1997 (Fornari et al. 2004). Type material was collected from artificial substrates (PVC hoses) deployed in 2002, and recovered one year later (see Govenar & Fisher 2007).

Etymology

The species is named in honor of Breea Govenar who designed the artificial devices from which specimens were collected (BART: Breea's Artificial Riftia Tubes).

Female

Body (Fig. 1a, 1b, 2a) laterally compressed, weakly chitinized, with short sensilla and few pores. Total length of female holotype (rostrum to posterior margin of telson) 420 µm, greatest width 180 µm. Rostrum rounded and prominent (Fig. 1a). Prosoma 4-segmented (cephalothorax and 3 somites bearing legs 2 to 4) (Fig. 2a). Urosome (Fig. 2b) 5-segmented: first urosomite with leg 5, genital-double somite with ventral depression and one gonoporus covered by flap of the minute leg 6 (Fig. 1c, 5b, 5c), and 2 postgenital somites plus telson with furca. Furca 3 times as long as wide, with 7 setae of different length (Fig. 2c).

Antennule (Fig. 2d) 7-segmented; formula of setation: 1, 10, 9, 3+aesthetasc, 6, 4, 6+aesthetasc.

Antenna (Fig. 2e) with small coxa and elongate basis with 1 seta and a field of cuticular spinules. Exopod 2-segmented, proximal segment with 1 inner setae, distal segment with 3 apical setae; endopod 2-segmented, proximal segment with 1 median seta, distal segment with 4 inner setae, 6 terminal setae and a hyaline frill subdistally on outer margin.

Labrum (Fig. 2a) projecting over shield of cephalothorax in lateral view.

Mandible (Fig. 3a) with gnathobase (not shown); palp 2-segmented, with 2 distal setae on basis and 1-segmented endopod bearing 1 outer and 3 terminal setae.

Maxillule (Fig. 3b, c) with praecoxal arthrite bearing 8 spines; coxal endite with 1 seta; exopod with 2 setae; basis elongate with 1 median and 4 terminal setae.

Maxilla (Fig. 3d) syncoxa with two endites, proximal endite with 1, distal endite with 3 spines. Allobasis with 3 lateral setae, two subdistal and one apical spine.

Maxilliped (Fig. 3e, f) 3-segmented, subchelate; syncoxa elongated with 1 distal seta; basis with 2 rows of spinules; endopod 1-segmented, produced into a strong claw, with 2 proximal setae and an inner row of short spinules.

Swimming legs 1–4 biramous; armature formula as in Table 1.

Leg 1 (Fig. 4a) with 1-segmented rami.

Leg 2 and leg 3 (Fig. 4b, 4c) with 3-segmented endopods and 2-segmented exopods; proximal segments of exopods elongated, derived by fusion of former proximal and middle segments.

Leg 4 (Fig. 4d) with 3-segmented rami. Distal exopod segment with an inner seta slightly modified into a spine (Fig. 5a).

Leg 5 (Fig. 5b) with baseoendopod and exopod; baseoendopod with 1 basal outer seta, 3 inner setae, 1 terminal spine, and 1 small terminal outer seta; exopod with 3 outer elements (proximal seta-like; middle and distal ones spine-like), and 2 terminal spines.

Leg 6 a small flap with 1 minute seta (Fig. 5c).

Single egg sac with three eggs, located ventrally between fifth legs (Fig. 1b, 1c, 2a).

Male differs from female in the following:

Length of paratype 1 (Fig. 1d, 6a) 325 μm ; greatest width 150 μm . Genital-double somite (Fig. 1e, 5e) produced ventrally into a large, elongated prominence bearing a distally asymmetrical genital flap representing leg 6.

Antennule (Fig. 6b) 10-segmented; setation formula as follows: 1, 10, 6+aesthetasc, 1, 7+aesthetasc, 1, 2, 1, 4, 7+aesthetasc.

Leg 5 (Fig. 5d) 2-segmented; basis with 1 outer seta, exopod with 1 outer proximal seta, 1 outer subdistal spine, and 2 terminal spines.

Leg 6 (Fig. 1e, 5e) a membranous genital flap on the left side.

One spermatophore stored inside the genital-double somite (Fig. 5e).

Copepodite stage V

Leg 2 (Fig. 6c) and Leg 3 (Fig. 6d) consist of 3-segmented exopods (in contrast to adult) and 2-segmented endopods (shortly before division into the adult 3-segmented endopod).

Taxonomical remarks

Smacigastes barti sp. nov. belongs to the family Tegastidae. This family is characterized by a laterally compressed, amphipod-like, strongly chitinized and sculptured body (Lang 1948, Huys et al. 1996). Six genera belong to the family Tegastidae, namely *Tegastes* Norman, *Smacigastes* Ivanenko & Defaye, *Parategastes* Sars, *Syngastes* Monard, *Feregastes* Fiers, and *Arawella* Cottarelli & Baldari. *Smacigastes* apomorphic characters are its elongate furca and its weakly chitinized body. The other genera can be distinguished by the segmentation of legs 2–4. The key to genera of Tegastidae presented by Huys et al. (1996: 290) and Boxshall and Halsey (2004: 392) turned out to contain typographic inconsistencies. Here, we propose a new identification key that also includes the recently described genus *Smacigastes* (Table 2).

The new species belongs to the genus *Smacigastes* and shares with *S. micheli* the following distinguishing characters: a 10-segmented male antennule, presence of female leg 6, and a furca 3 times as long as wide. Furthermore, both species share a weakly chitinized body, distinguishing them from other tegastids having, according to the family diagnosis, strongly chitinized bodies (Lang 1948, Huys et al. 1996). *Smacigastes micheli* shows 3-segmented exopods of leg 2 and 3. The presumed derived features of *S. barti* are the fusion of proximal exopodal segments 1 and 2 in legs 2 and 3, and the loss of coxal endites of the maxilla.

Interestingly, females of *Smacigastes barti* and *Arawella alexandri* Cottarelli & Baldari possess a slender leg 5, which contrast to all other species of Tegastidae. The females of the other tegastid species have either a swollen baseoendopod and normal exopod (some species of *Tegastes*, *Smacigastes micheli*, *Feregastes wellensi* Fiers, *Parategastes caprinus* Wellerhaus, *P. haphé* Leigh-Sharpe, *P. sphaericus* Claus), a swollen endopod and exopod (some *Tegastes*, *Parategastes coetzeei* Kunz, *P. conexus* Humes, *P. herteli* Jakobi), a swollen baseoendopod and a reduced exopod (*Tegastes georgei* Marcus & Masry, *T. chalmersi* Thompson & Scott, *Syngastes* spp.), or a single swollen rami (*Syngastes* spp. Monard). Most modified female baseoendopods are found in the genera *Syngastes* and *Parategastes*, with a leaf-shaped leg 5. Interestingly, instead of having a broad leg 5, *A. alexandri* developed a special genital somite, produced ventrally into an eaves-shaped structure, and *S. barti* shows a ventral depression of the genital-double somite. We think that the shape of female P5 is important as this is the structure holding and protecting the eggs of tegastids, ensuring the survival of species. However, the development of female P5 has never been discussed or included as a character in tegastid taxonomy. A slender P5 is a plesiomorphic character and in consequence, *Smacigastes* might be a relatively ancient tegastid genera, as already proposed by Ivanenko & Defaye (2004b).

The segmentation of legs 1–4, the character used to distinguish between shallow water tegastids, of *Smacigastes barti* is similar to the genus *Parategastes*. Beside the apomorphic characters of *Smacigastes*, the new species also differs from *Parategastes* in the number of segments of the female and male antennule (7-segmented and 10-segmented antennule in the female and male of *S. barti*, but 6-segmented and 7-segmented antennule in the female and male of *Parategastes*), number of segments of the antennal exopod (2-segmented in *S. barti*, but 1-segmented in *Parategastes*), shape of female leg 5 (slender in *S. barti*, but endopod transformed into a broadened flap in *Parategastes*), length of furca (long in *S. barti*, but shorter than wide in *Parategastes*) (Lang 1948, Jakobi 1953, Wellerhaus 1970, Kunz 1980, Humes 1984, Huys et al. 1996). The 2-segmented exopods of leg 2 and leg 3 and the elongated proximal segments result from the fusion of the proximal and middle segments. The setation formula II-2 of the first elongated exopodal segment of leg 2 and 3 indicates a fusion process. Huys & Boxshall (1991) proposed a setation formula of I-1 and I-1 for the proximal and middle exopodal segments of both legs 2 and 3 for the harpacticoid ancestor.

The fusion process could be proved by studying copepodites of stage V of *Smacigastes barti* having 3-segmented exopods of P2 and P3 (see Fig. 6c, 6d).

Shallow-water tegastid genera can be separated by the segmentation of legs 2–4. *Tegastes* has 3-segmented endo- and exopods of leg 2, 3 and 4. The proximal and middle exopodal segment of leg 2 and 3 are fused in *Arawella*, *Smacigastes*, *Parategastes* and *Syngastes*. Furthermore, *Syngastes* shows a proximal fusion of segments 1 and 2 on the exopod of leg 4. Probable plesiomorphic characters of *Smacigastes micheli* are the 3-segmented endopods and exopods of leg 2, 3 and 4 (Ivanenko & Defaye 2004). Fused proximal and middle exopodal segments of legs 2 and 3 were found by us in *Smacigastes barti* and 2 other undescribed deep-sea tegastid species also belonging to the genus *Smacigastes*. One species was found in samples taken from Gulf of Mexico cold seeps and can be distinguished from *S. micheli* only by shorter spines on the female leg 5 baseoendopod and by its body length (one third shorter). A suture between the first two exopodal segments of leg 2 and leg 3 were observed only from the posterior dorsal view (not from the anterior view) in this cold-seep species. Such suture was not observed in *S. barti*, but a fissure between those segments was observed instead. The other undescribed deep-sea species, found in wood-falls from Gorda Ridge, shows a complete fusion of the proximal exopod segments. These findings might show a general trend in Tegastidae of having fusion processes of exo- and endopodal segments. Whether the fusion processes point to a parallel evolution of shallow-water and deep-sea tegastids, or to characters already developed before the colonization of the deep sea remains to be discussed.

Ecological comments

Thus far, copepods of the family Tegastidae from deep-sea hydrothermal vents have mostly been observed in association with artificial and hard substrates. *Smacigastes barti*, together with a variety of other copepods, nematodes, ostracods and foraminiferans, were found between PVC hoses used to imitate the tubeworm *Riftia pachyptila* (Govenar et al. 2007, pers. obs. SG). Short-term (~ 10 days) and long-term (~ 1 year) deployments were both colonized by *S. barti*, indicating that the species is able to quickly colonize newly formed habitats. Only a few specimens of *S. barti* were found up to now on natural basalt (pers. obs. SG). *Smacigastes micheli* as well as many other copepods were captured in a specially designed array consisting of 4 trays with an artificial substrate of small glass beads, protected from large carnivorous animals by a mesh. It was positioned between *Bathymodiolus azoricus* mytilids at temperatures ranging from 5–13°C at the site Lucky Strike on the Mid-Atlantic Ridge for ~1 year (Ivanenko & Defaye 2004a, 2004b). The yet undescribed tegastid species of the genus *Smacigastes* from the Gorda Ridge was found to be associated with artificially positioned wood. Only copepods of another new and undescribed tegastid species of the same genus were among natural tubeworm aggregations in the Gulf of Mexico cold seeps. The reasons for the attractiveness of artificial substrates are difficult to decipher. Artificial substrates are a system in an early succession stage as they represent a newly opened habitat without former colonizers (Connel & Slayter 1977). It might be that both species, *S. barti* and *S. micheli*, are fugative species, typical for early succession stages, being able to colonize competition-free newly opened habitats.

Smacigastes barti was found associated with artificial substrates deployed at the tubeworm-dominated site Tica on the EPR 9°50'N at 2500 meters depth, but was never found within the natural tubeworm aggregations at the same site (see Gollner et al. 2007). The natural habitat was colonized by *Riftia pachyptila* and was characterized by moderate hydrothermal vent flux with maximum temperatures of 18°C, maximum sulphide concentrations of 176 µM Σ H₂S, and minimum measured pH close to neutrality (Le Bris et al. 2006). Four artificial aggregations each were deployed in an high flow zone within *Riftia pachyptila*

specimens, in a low flow zone with less influence of toxic hydrothermal fluid flux ~50 cm away from *R. pachyptila*, and ~20 m away from the natural aggregations with no influence of hydrothermal fluid flux and constant deep-sea water temperature of approximately 2°C (Govenar & Fisher 2007). The natural *Riftia pachyptila* community at the site Tica was colonized mostly by dirivultid copepods and only some harpacticoid copepods, but not a single tegastid was found (for details see Gollner et al. 2006). Interestingly, the artificial aggregations were successfully colonized by the new tegastid species and from a total of 30 identified *S. barti* specimens, 14 females, 11 males and 4 copepodites were observed. There was no difference in the relative abundance percentage of tegastids in short-term and long-term deployments. 2.2–2.8% of all identified copepods were *S. barti* in the far away zone, and 0–2.6% were found 50 cm away. Not a single specimen was found within the artificial tubes in the high flow zone, except for one artificial aggregation that was originally positioned within *R. pachyptila* but fell out after some time into the low flow zone and is therefore counted to the low flow zone. This indicates that *S. barti* lacks the capability to tolerate varying temperatures and sulfide concentrations of vent flux.

The amphipod-like body of shallow-water tegastids has been interpreted as an adaptation to their co-existence with algae, bryozoans or cnidarians (Huys & Boxshall 1991, Ivanenko & Defaye 2004). Tegastids have never been detected in deep-sea samples from deep-sea abyssal plains (pers. obs. PMA). Their body shape might not be suitable to live in mesopsammal habitats, whose members are usually characterized by worm-shaped bodies allowing them to crawl easily between sand grains (Giere 1993). All of the presently discovered members belonging to the deep-sea tegastids were found close to or in association with hard-substrate chemosynthetic environments. Both *Smacigastes barti* and *S. micheli* were sampled at deep-sea hydrothermal vents. Two other yet undescribed deep-sea tegastid species were found at Gulf of Mexico seeps and at wood-falls from Gorda Ridge. These findings point to a preference of deep-sea tegastids for hard-substrate nutrient-rich environments.

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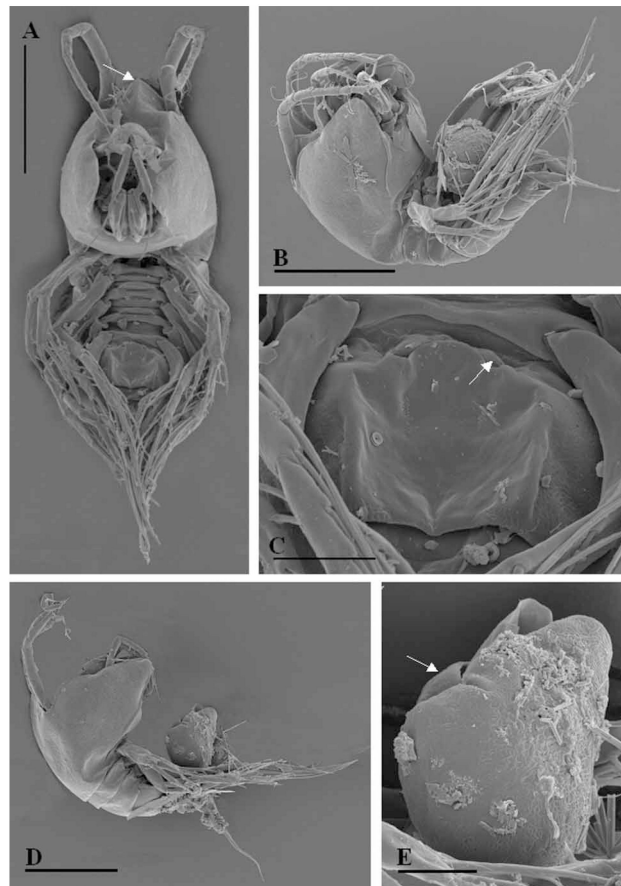


FIGURE 1.

Smacigastes barti sp. nov. SEM photos: ♀ paratype: A, habitus, ventral (rostrum indicated by arrow); B, habitus, lateral; C, genital-double somite with leg 6 (see arrow); ♂ paratype: D, habitus, lateral; E, spermatophore reservoir with opened gonopore and leg 6 (see arrow). Scale bars A, B, D 100 μ m; C, E 20 μ m.

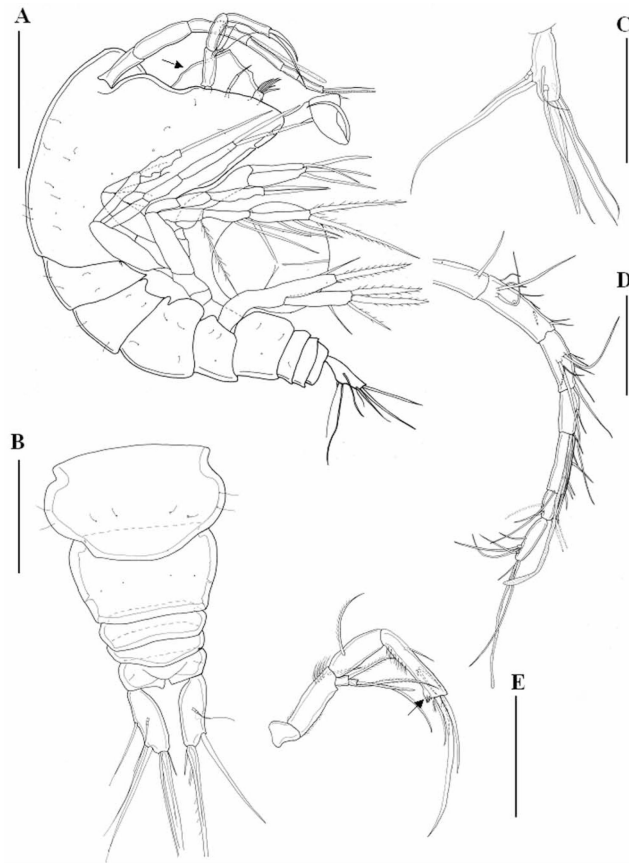


FIGURE 2.

Smacigastes barti sp. nov. ♀ holotype LM drawings: A, habitus, lateral (labrum indicated by arrow); B, urosome, ventral; C, furca, ventral; D, antennule (a seta on 2nd segment broke and is indicated by a circle); E, antenna (frill indicated by arrow). Scale bars A 100 µm; B–E 50 µm.

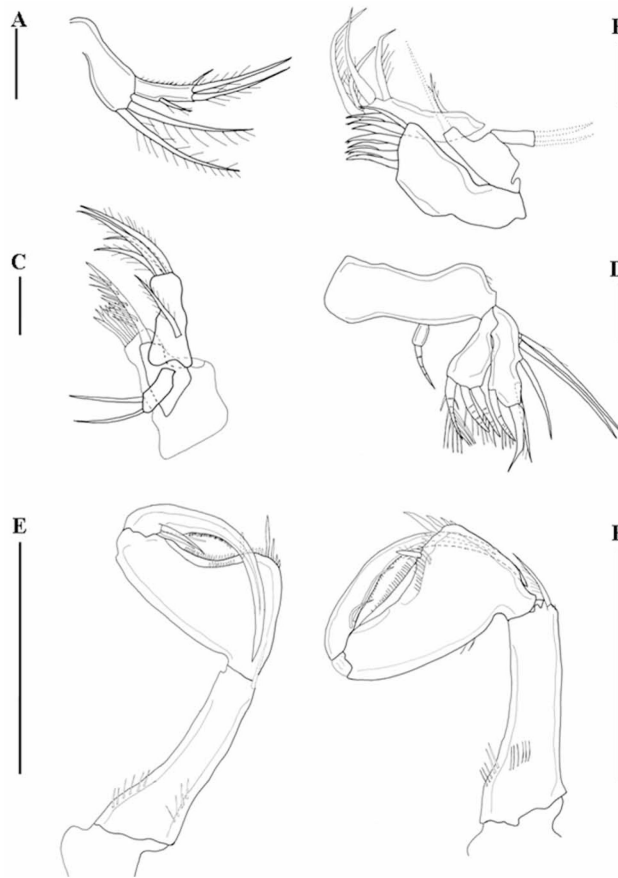


FIGURE 3. *Smacigastes barti* sp. nov. ♀ holotype LM drawings: A, mandible; B, maxillule; C, maxillule (different view, from ♂ paratype 1); D, maxilla; E, maxilliped, posterior; F, maxilliped, anterior. Scale bars A–D 10 μm; E, F 50 μm.

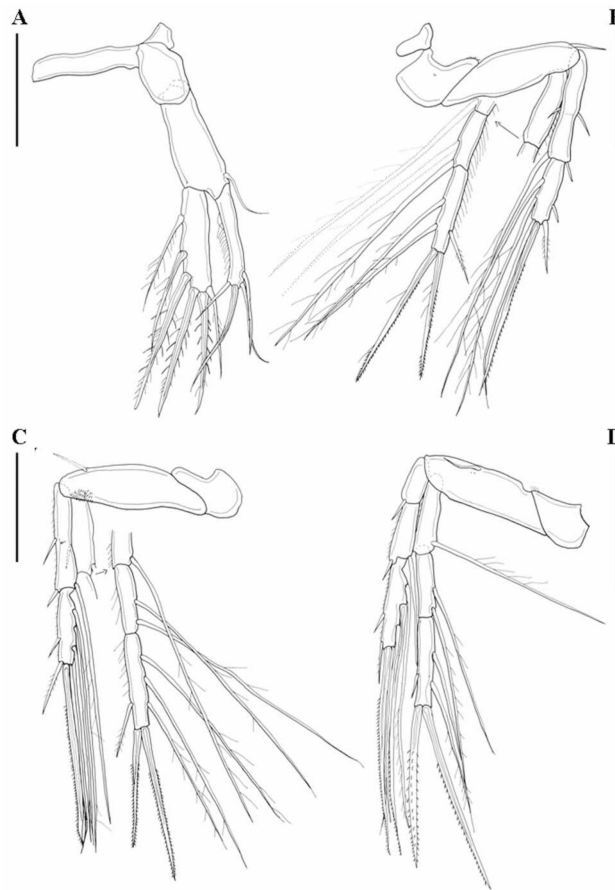


FIGURE 4.
Smacigastes barti sp. nov. ♀ holotype LM drawings: A, leg 1; B, leg 2; C, leg 3; D, leg 4.
Scale bars A–D 50 μ m.

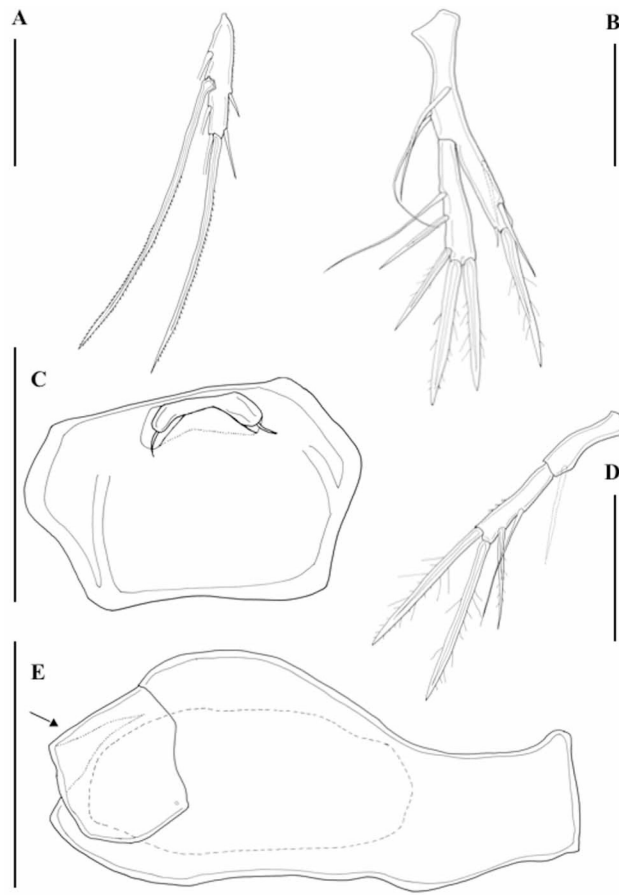


FIGURE 5. *Smacigastes barti* sp. nov. ♀ holotype: A, distal endopod segment of leg 4; B, leg 5; C, leg 6 (♀ paratype 2); ♂ paratype 1 LM drawings: D, leg 5; E, leg 6 (see arrow; ♂ paratype 3). Scale bars A, C–E 50 µm; B 100 µm.

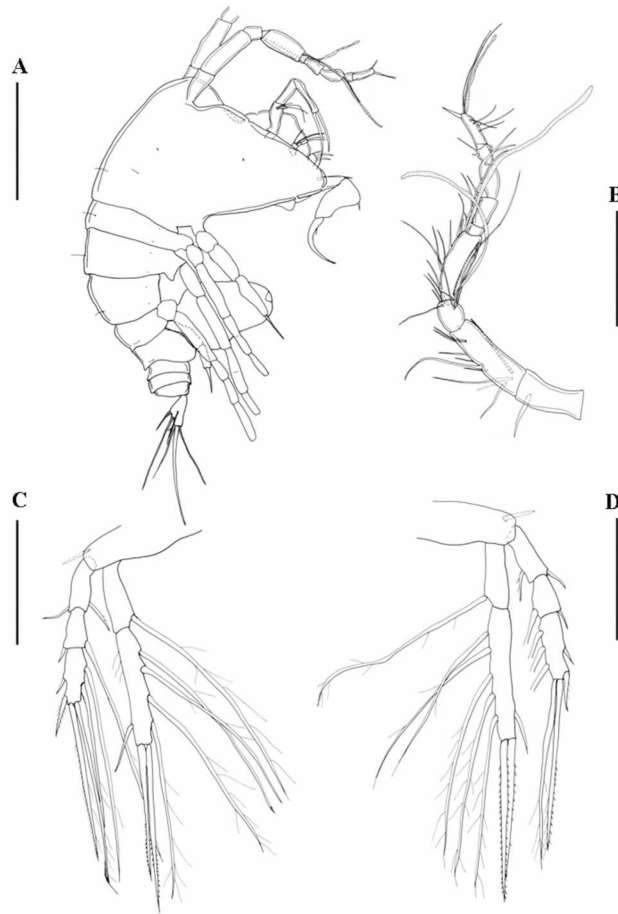


FIGURE 6.
Smacigastes barti sp. nov. ♂ paratype 1 LM drawing: A, habitus, lateral; B, antennule;
paratype 8 copepodite stage V LM drawings: C, leg 2; D, leg 3. Scale bars A–D 50 μ m.

TABLE 1Spine and setal formula of legs 1–4 of *Smacigastes barti* sp. nov.

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

TABLE 2

Key to genera of Tegastidae. In parenthesis number of described species of the genus.

1	Caudal rami 3-times longer than wide	<i>Smacigastes</i> (2)
-	Caudal rami short	2
2	P2–P3 endopods 2-segmented	<i>Arawella</i> (1)
-	P2–P3 endopods 3-segmented	3
3	P2–P3 exopods 2-segmented	4
-	P2–P3 exopods 3-segmented	5
4	P4 endopods 2-segmented	<i>Syngastes</i> (23)
-	P4 endopods 3-segmented	<i>Parategastes</i> (6)
5	P4 endopods 2-segmented	<i>Feregastes</i> (1)
-	P4 endopods 3-segmented	<i>Tegastes</i> (37)