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Article



Discovery of *Smacigastes* Ivanenko & Defaye, 2004 (Copepoda: Harpacticoida: Tegastidae) in a deep-sea cold seep, with the description of a new species from the Gulf of Mexico*

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Abstract

The new tegastid species *Smacigastes methanophilus* sp. nov. is described from cold-seep samples collected from the Gulf of Mexico in 2006. Besides *Smacigastes micheli* Ivanenko & Defaye, 2004 and *Smacigastes barti* Gollner, Ivanenko & Martínez Arbizu, 2008, this is the third species of the genus *Smacigastes* Ivanenko & Defaye, 2004. To date, this genus contains the only species within the family Tegastidae known from deep-sea habitats. Furthermore, *S. methanophilus* sp. nov. is the first species of Tegastidae found at cold seeps and associated with tubeworm aggregations. It has the same primitive features as *S. micheli* but can be distinguished from the latter by the setation of second and third segments of female antennule and second segment of male antennule, the setation of the mandibular palp, the ornamentation of P5 exopod in both sexes, setation of male P5 exopod, form of the female P5 baseoendopod, and the different shape and length of the P5 setae in female. Moreover, both sexes of *Smacigastes methanophilus* sp. nov. are much smaller than those of *S. micheli*. Compared to *S. barti, S. methanophilus* sp. nov. differs in the segmentation and setation of male antennule, the setation of the maxillule, number of endites of the maxilla, number of setae in P1, the ornamentation of female P5 and setation in male P5.

Key words: Chemosynthetic habitat, deep sea, taxonomy, Harpacticoida

Introduction

Since their first discovery in the early 80s of the last century, many deep-sea cold seeps have been reported in various parts of the world's oceans. Most of them occur in geologically active and passive continental margins, where fluids enriched with methane seep out of the sediment forced by pressure. Regarding the presence of reduced chemical compounds, cold seeps are similar to hydrothermal vents. The similar chemical conditions of these habitats may allow the establishment of similar biological communities as has been detected for the specialized symbiont bearing siboglinid tubeworms and bathymodiolid mussels of these chemosynthetic environments (Levin 2005). However, the existing studies do not show this for the meiofauna communities. In fact, the few studies about cold seep copepods (Robinson et al. 2004; Zekely et al. 2006) indicate that there are no specific copepod communities at cold seeps, but in both cases copepods have been determined on family level only. In contrast to hot vents, where a dominance of specialized siphonostomatoid copepods of the family Dirivultidae can be observed (Heptner & Ivanenko 2002), the cold seeps investigated are dominated by harpacticoid copepods (Gollner *et al.* 2006; Robinson *et al.* 2004; Zekely *et al.* 2006). This was also observed in the meiofauna samples of the "Atlantis" cruise in the year 2006 which aimed to

investigate cold seeps in the Gulf of Mexico as part of the project "Investigations of chemosynthetic communities on the Lower Continental Slope of the Gulf of Mexico" (Bright pers. comm.)

Many families of the Harpacticoida have been found in these samples, including the family of Tegastidae, which up to now contains 56 species belonging to six genera (*Tegastes* Norman, *Parategastes* Sars, *Syngastes* Monard, *Feregastes* Fiers, *Arawella* Cottarelli & Baldari and *Smacigastes*, Ivanenko & Defaye). Before the description of *S. micheli*, tegastids had never been reported from deep-sea samples. Three years after this discovery, another species of *Smacigastes* called *S. barti* was described from a hydrothermal vent in the Pacific (Gollner *et al.* 2008). All other species of Tegastidae were only known from shallow waters . In this paper we describe a new deep-sea tegastid species found at a natural oil seep in the Gulf of Mexico between tubeworm aggregations of the species *Escarpia laminata* Jones, 1985 and an undescribed species of the genus *Lamellibrachia* Webb, 1969.

Material and methods

Samples were taken from a natural oil seep in the Gulf of Mexico (Patchblock GC 852) at approximately 1400 m depth with the aid of DVS Alvin during a cruise in 2006 on board of RV "Atlantis". The habitats sampled during this cruise included aggregations of the tubeworm species *Escarpia laminata* and *Lamellibrachia* sp. nov. as well as mussel beds of the species *Bathymodiolus brooksi*, but the specimens of the new tegastid species were found associated with tubeworm aggregations only. For the collection of tubeworms, the quantitative sampling device called "bushmaster" (Govenar et al. 2005) was used. Meiofauna organisms were sampled together with mega- and macrofauna. The meiofauna was then seperated using a sieve of 32 mm meshwide and fixed in 4% formalin.

The specimens of *S. methanophilus* sp. nov. were sorted in the laboratory at the Forschungsinstitut Senckenberg, department DZMB in Wilhelmshaven, Germany. For light microscopy, specimens were dissected in glycerine under a Leica Mz 12.5 stereomicroscope. The dissected parts of the holotype and paratypes were mounted on several slides using glycerine as mounting medium (Higgins & Thiel 1988). Holotype and paratypes were deposited in the collection of the Forschungsinstitut und Naturmuseum Senckenberg in Frankfurt am Main (SMF), Germany.

Drawings were made with the aid of a drawing tube on a Leica differential interference contrast microscope (DMR with UCA condensor, IC prism and doubler x 1,25 and x 1,6). All drawings were made of female holotype except the maxillule (Fig. 4 from paratype 1) and maxilla (Fig. 4 from paratype 4). The following abbreviations are used in the text: BM = Bushmaster; Cphth = Cephalothorax; A1 = Antennule; A2 = Antenna; Mxl = Maxillule; Mx = Maxilla; GF = Genital field; P1–P6 = first to sixth leg; enp = endopod; exp = exopod; enp-1 (2,3) = proximal (middle, distal) segment of endopod; exp-1 (2,3) = proximal (middle, distal) segment of endopod.

Taxonomy

Harpacticoida Sars, 1903 Tegastidae Sars, 1904 *Smacigastes* Ivanenko & Defaye, 2004 *Smacigastes methanophilus* sp. nov.

Type material: Holotype: female, dissected and mounted on 10 slides, (nr. SMF 32228); Paratype 1: dissected female, mounted on 12 slides, (nr. SMF 32229); Paratype 2: undissected female, mounted on 1 slide, (nr. SMF 32230); Paratype 3: dissected female, mounted on 3 slides, (nr. SMF 32231); Paratype 4: dissected female, mounted on 7 slides, (nr. SMF 32232); Paratype 5: dissected male, mounted on 6 slides, (nr. SMF 32233);

Paratype 6: dissected male, mounted on 3 slides, (nr. SMF 32234); Gulf of Mexico, 27°06.371'N, 91°09.968'E, 1409 m depth.

Additional material: 23 females and 14 males from station BM 4186 stored in glycerine.

Type locality: Atlantic Ocean, Gulf of Mexico, Patchblock Green Canyon 852, Alvin Dive BM 4186 (Bushmaster), 27°06.371'N, 91°09.968'E, 1409 m depth; temperature 4.27°C; associated with tubeworm aggregations of the species *Lamellibrachia* sp. nov. and *Escarpia laminata* Jones, 1985 (Polychaeta, Siboglinidae), growing on muddy sediment and carbonate rocks (Gollner, pers. comm.)

Etymology: The species is named after the methane-rich chemosynthetic-based ecosystem where it has been found.

Description of the female holotype

Body length (with caudal rami) 385 μ m.

Habitus (Figs. 1, 2) laterally compressed with pores and long sensilla up to the first abdominal somite. Following abdominal somite with sensilla, only the last abdominal somite without pores and sensilla. First pedigerous somite completely fused to dorsal cephalic shield building the cphth, which is drawn ventrolaterally into a triangular plate on either side of the body; surface of cphth pitted (Fig. 1B). Thoracic somites bearing P2–P4 with rudimentary epimeral plates. First abdominal somite completely fused with last thoracic body somite, forming the genital double somite which is ventrally extended (Fig. 2A). Genital double somite with 6 sensilla und 4 pores ventrally (Fig. 2A). The 2 remaining abdominal somites reduced; second abdominal somite with altogether, 4 sensilla laterally and ventrally; telson with 2 sensilla laterally. Caudal rami (Fig. 2A-C) elongated, with 7 bare and slender setae. Length:wide ratio 2,5:1, slightly triangular in lateral view, tapering distally.

Rostrum (Fig. 1): rounded and prominent, fused with cephalothorax.

Antennule (Fig. 3A, B): 8-segmented; armature formula starting at first segment: I–1, II–10, III–9, IV–4+aes,V–2, VI–4, VII–4, VIII–7+aes. Both aes fused at base with seta. Segment 3 with 1 articulated seta, segment 7 with 2 articulated setae (sitting on a small pedestal), segment 8 with 4 articulated setae.

Antenna (Fig. 4A): Basis elongated, ornamented with spinules. Endopod 2-segmented; enp-1 with 1 unipinnate inner seta; enp-2 with 4 bare setae laterally, a group of 4 setae subapically, 1 of which bipinnate, 1 unipinnate and 2 bare setae, apically 1 long bare seta and 1 bipinnate seta and 1 outer bipinnate seta subapically; enp-2 with 3 outer rows of spinules. Exopod 2- segmented; exp-1 with 1 bipinnate seta; exp-2 with 1 lateral unipinnate and 2 apical bare setae.

Labrum (Fig. 1): slightly projecting anteriorly over shield of cephalothorax in lateral view.

Mandible (Fig. 4B): Cutting edge of gnathobase with 7 teeth, 1 unipinnate seta at proximal corner. Basis with 4 rows of long spinules and 2 bipinnate distal setae. Exopod fused with basis, represented by a lobe with 2 bipinnate setae. Endopod slightly separated from basis by a suture with 1 bipinnate seta laterally, 3 terminal bipinnate setae and with 1 row of long spinules on the outer margin.

Maxillule (Fig. 4C): Arthrite of praecoxa with 8 spines terminally and one seta at the distal inner corner; praecoxa with one row of spinules; coxal endite with one stout seta; basis elongated with a row of setules, 4 terminal and 3 lateral setae representing enp, one of which small and naked; exopod 1 segmented with 3 bipinnate terminal setae and several spinules.

Maxilla (Fig. 4D): syncoxa with 1 row of spinules distally and with 3 endites bearing 4, 2 and 3 setae; allobasis drawn out to form 1 strong claw, bearing 2 accompanying setae; endopod represented by 3 setae.

Maxilliped (Fig. 5B): subchelate; 3-segmented, comprising syncoxa, basis and 1-segmented endopod; maxilliped inserted on a pedestal; syncoxa elongated with 1 distal seta and 3 rows of long setules; basis edge with row of strong setules; endopod 1-segmented, fused with claw, 2 setae posterior and a row of short spinules.

P1 (Fig. 5A): Coxa without setae, one pore on anterior surface on distal inner margin and a cuticular structure on the outer distal corner. Basis elongated with 1 inner and 1 outer seta and some spinules near outer seta; inner seta unipinnate, outer seta unarmed; one porus on the anterior surface near the outer terminal margin; both rami 1-segmented; exp with 1 terminal spine bipinnate, all other setae bare; anterior and

posterior surface of exp with rows of strong spinules, inner and outer margin also with such rows of spinules. Enp without ornamentation; with 1 inner proximal seta bipinnate, 1 inner spine unipinnate, inner distal spine multipinnate, 1 apical spine bipinnate with one row of setules transversally and 2 apical setae bipinnate.



FIGURE 1. *Smacigastes methanophilus* sp. nov., holotype female: (A) habitus lateral; (B) detail of cuticular surface. Scale bars: (A) = $100 \mu m$, (B) = $50 \mu m$.



FIGURE 2. *Smacigastes methanophilus* sp. nov., holotype female: (A) abdomen ventral; (B) caudal ramus dorsal; (C) caudal ramus lateral. Scale bar = $50 \mu m$.



FIGURE 3. *Smacigastes methanophilus* sp. nov., holotype female: (A) segment 1–3; (B) segment 4–8. Scale bar = 50 μ m.



FIGURE 4. *Smacigastes methanophilus* sp. nov.: (A) paratype 1 female, antenna; (B) paratype 4 female, mandible; (C) holotype female, maxillue; (D) holotype female, maxilla. Scale bar = $50 \,\mu$ m.

P2–P3 (Figs. 6–7): Basis transversally elongated with one outer seta (P3 with a field of spinules on anterior surface). Enp-1 and enp-2 equal in length but shorter than enp-3 which is almost as long as enp-1 and enp-2 combined; posterior surface of each enp segment with outer row of long setules. P2 enp-2 and enp-3 with an additional outer row of small spinules posteriorly; inner endopodal setae bipinnate. Exp-1 and exp-2 incompletely fused, with a suture posteriorly; both segments equal in length but slightly shorter than exp-3; each segment with row of outer spinules; inner exopodal setae and inner apical seta of exp-3 bipinnate; apical seta and outer distal spine of P2 exp-3 unipinnate; apical seta of P3 exp-3 bipinnate, outer distal spine of exp-3 unipinnate.

P4 (Fig. 8): Basis transversally elongated with one outer seta and a field of spinules on posterior surface. Rami 3-segmented. Enp-1 and enp-2 equal in length but shorter than enp-3; enp-1 with 1 outer row of long spinules on posterior and anterior surface; enp-2 with 2 short rows of spinules near the outer margin; surface of enp-3 without spinules; inner endopodal setae bipinnate, with small and strong setules towards there tip; one apical spine unipinnate and one bipinnate, outer seta of enp-3 small, slender and spine-like. Exp-1 and exp-2 distinct; both segments equal in length but shorter than exp-3; exp-3 as long as enp-1 and enp-2 combined; exp-1 with a field of small spinules near the distal corner; exp-2 and exp-3 with outer spinules; inner exopodal setae of exp-3 bipinnate except the middle inner seta of exp-3 which is unipinnate with strong setules; outer distal spine of exp-3 unipinnate; 1 apical seta and the proximal seta of exp-3 with strong setules at the outer side.



FIGURE 5. *Smacigastes methanophilus* sp. nov., holotype female: (A) P1 anterior view; (B) maxilliped. Scale bar = $50 \mu m$.



FIGURE 6. Smacigastes methanophilus sp. nov., holotype female: P2, posterior view. Scale bar = $50 \mu m$.

	соха	basis	exopod	endopod	
P1	0–0	1–1	3,2,0	1,I+1,II+1	
P2	0–0	1–0	I-1; I-1; II,I+1,2	0–1; 0–2; I,II,2	
P3	0–0	1–0	I-1; I-1; II,I+1,3	0–1; 0–2; I,II,3	
P3	0–0	1–0	I-0; I-1; II,I+1,3	0–1; 0–2; I,II,2	

Armature formula P1–P4:

P5 (Fig. 9A) very large, visible in lateral view, left and right P5 separated; exopod and baseoendopod distinct; bnp with 1 outer bipinnate basal seta and 5 setae on endopodal lobe (3 inner setae and 1 spine and 1 seta apically); only outer basal seta and inner apical spine bipinnate, others bare; anterior surface of exp covered with small spinules; exp long and slender, longer than baseoendopod and with 5 elements in total (two apical bipinnate spines and 3 outer setae, proximalmost of which bipinnate).

GF (Fig. 2A): Gonopores covered by 2 medially fused plates, each with 1 seta representing P6.



FIGURE 7. Smacigastes methanophilus sp. nov., holotype female: P3 anterior view. Scale bar = $50 \,\mu$ m.



FIGURE 8. Smacigastes methanophilus sp. nov., holotype female: P4 anterior view. Scale bar = $50 \,\mu m$.



FIGURE 9. Smacigastes methanophilus sp. nov.: (A) holotype female, P5; (B) paratype male, P5. Scale bar = 50 µm.

Male differs from female as follows:

Body length (with caudal rami) 350 µm.

Habitus (Fig. 10, 11): genital somite and first abdominal somite fused, forming genital double-somite as in female, but subdivided in ventral view and produced ventrally into a large, elongated prominence bearing distally asymmetrical genital flaps. Spermatophore of bean-like shape, stored inside genital double-somite.

Antennule (Fig. 12): 10-segmented, armature formula: I–1, II–10, III–8+aes, IV–2, V–8+aes, VI–1, VII–2, VIII–1, IX–4, X–7+aes; segments 1, 2 and 5 together making up more than half of the total length; segment 4 small; segment 10 with 4 articulated setae, and one very thin and pointed distal seta, thickened at the basis; one distal seta fused with aes; proximal seta of segment 7 unipinnate, all others bare.

Leg 5 (Fig. 9B): without inner endopodal lobe; basis with 1 bipinnate outer seta; exopod with 2 apical bipinnate spines and 3 outer setae; proximalmost outer seta bipinnate, others bare; surface of exopod almost completely covered with small spinules, more densely than in female.



FIGURE 10. *Smacigastes methanophilus* sp. nov. holotype male: habitus lateral. Scale bar = $50 \mu m$.



FIGURE 11. Smacigastes methanophilus sp. nov. paratype male: Urosome ventral view. Scale bar = $50 \,\mu$ m.



FIGURE 12. Smacigastes methanophilus sp. nov. paratype male: (A) A1, segment 1–4; (B) A1, segment 6–10. Scale bar = $50 \mu m$.

GF: (Fig. 11) without armature, right genital flap apparently articulated; left genital flap fused with genital double-somite; genital flaps forming an angle of about 15° to the body axis.

Discussion

Smacigastes methanophilus sp. nov. was attributed to the family Tegastidae, mainly because of the laterally compressed body, one single lateral seta on the mandible endopod, the elongate basis of maxillule, the shape of maxilliped syncoxa, basis and endopod, and further the transversally elongate basis of P2–P4. Further, the genital and first abdominal somite are fused to form a ventrally extended genital somite. The remaining abdominal somites are very shortened (Seifried 2003). The affiliation of *Smacigastes methanophilus* sp. nov. to the genus *Smacigastes* is based on the following characters: 10-segmented male antennule, presence of female leg 6, and furca being 3 times longer than wide.

Species morphology and discrimination

Smacigastes methanophilus sp. nov. can be distinguished from its congeners mainly by its smaller size, the setation of female and male A1, setation of A2 and mandibular palp, the segmentation of P2–P3, the setation of male P5, the ornamentation of P5 in both sexes (the cuticular being covered with small spinules) and the shape of the setae of P5.

Smacigastes methanophilus sp. nov. can be distinguished from *S. micheli* by its smaller size, the former being almost one third smaller than the latter. The female A1 of *S. methanophilus* sp. nov. (setation formula: I–1, II–10, III–9, IV–4+aes, V–2, VI–4, VII–4, VIII–7+aes) differs from *S. micheli* (setation formula: I–1, II–11, III–10, IV–4+aes, V–2, VI–4, VII–4, VIII–7+aes) in the number of setae in segment 2 and 3 (10 and 9 setae respectively in *S. methanophilus*, but 11 and 10 setae respectively in *S. methanophilus*. However, both species share the 8 segmented antennule. The female A1 of *S. barti*, in turn, is only 7-segmented due to the fusion (or lack of formation of an arthrodial membrane) of segments 5 and 6. Additionally, *S. barti* possesses only 3 setae in segment 4 and 6 setae in the last segment (setation formula: I–1, II–10, III–9, IV–3+aes, V–6, VI–4, VII–6). The male antennule of *S. methanophilus* sp. nov. (setation formula: I–1, II–10, III–9, IV–3+aes, V–6, VI–4, VII–6). The male antennule of *S. methanophilus* sp. nov. resembles that of *S. micheli* but segment 2 has only 10 setae in *S. methanophilus* sp. nov. (setation formula: I–1, II–10, III–8+aes, IV–2, V–8+aes, VI–1, VII–2, VIII–1, IX–4, X–7+aes) while *S. micheli* possesses 11 setae in this segment (setation formula: I–1, II–11, III–8+aes, IV–2, V–8+aes, VI–1, VII–2, VIII–1, IX–4, X–7+aes). *Smacigastes barti* can be distinguished from its congeners by a reduction of setae in segments 3–5 (setation formula: I–1, II–10, III–6+aes, IV–1, V–7+aes).

The antenna of *S. methanophilus* sp. nov. differs from the other species in having one more seta on enp-2. Additionally, *S. micheli* and *S. barti* possess a seta on the basis of A2, which is absent in *S. methanophilus* sp. nov.

The mandibular palp shows a different setation in each species. The fused exopod is represented by a lobe with 3 setae in *S. micheli*, while *S. methanophilus* sp. nov. possesses only 2 setae on the exopodal lobe. These setae are missing in *S. barti*. Furthermore, *S. barti* can be distinguished from its congeners by the maxillule having only 2 exopodal setae and 1 lateral seta on the basis. *S. micheli* and *S. methanophilus* sp. nov. share the same setation with 3 setae at the exopod and 3 lateral setae at the basis representing the endopod. *S. barti* has no praecoxal seta like the other species. Moreover, the most outstanding and presumed derived feature of *S. barti* is the lack of coxal endite of the maxilla (Gollner et al. 2008).

Smacigastes methanophilus sp. nov. and *S. micheli* can be separated from *S. barti* by the setation of P1. The former two species possess an inner seta on the basis of P1, but in *S. barti* this seta is missing. Additionally, the exopod of P1 has only 2 outer setae instead of 3 in the latter species.

Smacigastes methanophilus sp. nov. resembles S. barti in the segmentation of P2 and P3. Both species share an incomplete fusion of the proximal two exopodal segments. This character distinguishes them from S. micheli which has a 3-segmented exopod of P2 and P3. Smacigastes methanophilus sp. nov. and S. barti can be distinguished by the dorsal suture between exp-1 and exp-2 because S. barti possesses only a fissure between those segments (Gollner et al. 2008). In addition, a good character to distinguish the species of Smacigastes is the P5, visible in the lateral view without high magnification. Mainly the shape of the baseoendopod is different in each species but also the terminal setae of endo- and exopod differ in shape and

size. The P5 baseoendopodal lobe is similar in *S. methanophilus* sp. nov. and *S. micheli*. However, it is slightly more swollen in the latter. In *S. barti*, in turn, the P5 baseoendopod is not swollen. The apical spines of the endo- and exopod differ between *S. micheli* and *S. methanophilus* sp. nov., as they are short, conical, thickened and multipinnate in *S. micheli*. In contrast, the terminal spines of baseoendopod in *S. methanophilus* sp. nov. are more slender and only bipinnate. The most outstanding character of *S. methanophilus* sp. nov. is the ornamentation of the P5 exopod in both sexes. The exopod is covered with small spinules dorsally. None of the other *Smacigastes* species exhibit such ornamentation. Furthermore, the male P5 exopod of *S. methanophilus* sp. nov. possesses 5 elements, while the other two species have only 4.

Another point of discussion is the proximal sclerotized structure in the maxilliped, interpreted by Huys and Boxshall (1991) as a pedestal, a raised area of the ventral body surface. In *S. methanophilus*, this segment looks like a praecoxa, but such an interpretation would be very unlikely, because no Harpacticoida possesses this segment. Only in genera such as *Neobradya* T. Scott, 1892 and *Tachidiopsis* Sars, 1911 is the praecoxal segment partly defined according to Huys and Boxshall (1991). The authors assume, that this segment represents a sclerotized connection between the syncoxa and the body.

Ecological aspects

All deep-sea tegastid species described so far were found in association with artificial hard-substrates close to chemosynthetic environments. This family has developed very efficient capabilities for the colonization of novel substrates. *Smacigastes barti* und *S. micheli* were sampled directly at or near deep-sea hydrothermal vents (see Gollner *et al.* 2008; Ivanenko & Defaye 2004), while another, yet undescribed species, was detected at Gorda Ridge associated with artificially positioned wood falls (Moura pers. comm.). *S. methanophilus* sp. nov. was found at a cold seep associated with tubeworm aggregations.

S. micheli was collected by the submersible "Nautile" at the end of an *in situ* colonization experiment with the aid of a tray. This tray contained small glass beads as an artificial hard-substrate and was positioned between *Bathymodiolus azoricus* mytilids at the Lucky Strike vent on the Mid Atlantic Ridge. It stayed at 1698 m depth at temperatures ranging from 5-13°C (Ivanenko & Defaye 2004).

S. barti was found to be also associated with artificial substrate deployed during a colonization experiment within or nearby tubeworm aggregations of the species *Riftia pachyptila* Jones, 1980. These aggregations were located at a hydrothermal vent site on the East Pacific Rise at 2500 meters depth. The site was characterized by warm fluids with maximum temperatures of 18°C. Maximum sulphide concentrations of 176 μ M Σ H₂S and pH close to neutrality were measured at this site. At the natural hydrothermal vent habitat not a single tegastid has been found so far (Gollner et al. 2008).

The new species described here is the first record of a tegastid from a cold-seep site. *S. methanophilus* sp. nov. was sampled between natural aggregations of *Escarpia laminata* and *Lamellibrachia* sp. nov. growing at a natural oil seep in the Gulf of Mexico. The tubeworms of this site grew on mud and carbonated rocks at a temperature of 4.27°C. Apart from being the first record of *Smacigastes* from a cold seep, this species is the first of the genus which has been found among natural megafauna aggregations on soft substratum. These findings point to a preference of deep-sea tegastids for hard-substrates in nutrient-rich environments. Some potential reasons for the attractiveness of artificial substrates are given in Gollner et al. 2008.

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