

A new and primitive genus and species of deep-sea Tegastidae (Crustacea, Copepoda, Harpacticoida) from the Mid-Atlantic Ridge, 37°N (Azores Triple Junction, Lucky Strike)

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Abstract: *Smacigastes micheli* gen. nov., sp. nov. (Copepoda, Harpacticoida, Tegastidae) is described, from specimens obtained during *in situ* colonization experiments in the Mid-Atlantic Ridge (37°N, Lucky Strike), at a depth of 1698 m. This is the first record of tegastids in the deep-sea. The distinctive and primitive features of the new genus allowing an amendment of the family diagnosis are the elongate caudal rami, the 10-segmented male antennule and the leg 6 represented by 2 small setae on the ventral side of the female genital double-somite. The fusion of the left genital flap with the male genital double-somite and the slight (clockwise from ventral view) torsion of the flaps relative to the dorso-ventral axis of the genital double-somite are the presumed derived features of the new genus.

Résumé: Un genre et une espèce nouveaux et primitifs de Tegastidae profonds (Crustacea, Copepoda, Harpacticoida) de la ride médio-atlantique, 37°N (triple jonction des Açores, Lucky Strike). Un nouveau genre et une nouvelle espèce Smacigastes micheli n.gen.., n. sp. (Copepoda, Harpacticoida, Tegastidae), sont décrits à partir de spécimens collectés au cours d'une expérience de colonisation *in situ* sur la ride médio-atlantique (37°N, Lucky Strike), à 1698 m de profondeur. C'est le premier signalement de Tégastidé en milieu profond. Les caractères distinctifs primitifs sont l'antennule mâle à 10 articles et la P6 femelle représentée par deux soies. La fusion du clapet génital gauche avec le double somite génital mâle, et la légère torsion (dans le sens des aiguilles d'une montre, en vue ventrale) des clapets par rapport à l'axe dorso-ventral du double somite génital sont des caractères supposés dérivés du nouveau genre.

Keywords: Copepoda, Harpacticoida, Hydrothermal vents, Systematics, Deep-sea, Morphology.

Introduction

The Copepoda represent one of the most abundant and widespread groups of invertebrates in the deep-sea hydrothermal vents of Atlantic and Pacific oceans. Among more than 500 species of invertebrates found in the deepsea hydrothermal vents, 73 are copepods, belonging to five orders. Of these, 51 species of copepods belong to the family Dirivultidae Humes & Dojiri, 1980 (Siphonostomatoida) and were observed as free-living or associated to invertebrates in the deep-sea hydrothermal vents only (Humes, 1996, 1997; Humes & Segonzac, 1998; Ivanenko, 1998; Heptner & Ivanenko, 2002; Ivanenko & Ferrari, 2003). Until now, only seven species (from 6 genera and 5

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families) of harpacticoid copepods have been reported from deep-sea hydrothermal vents.

About 60 species of copepods belonging to five orders were described from eleven sites of the Pacific Ocean, six of which are harpacticoid species. Four species are free-living: *Andromastax muricatus* Conroy-Dalton & Huys, 1999 (Aegisthidae) and *Argestoides prehensilis* Huys & Conroy-Dalton, 1997 (Argestidae) from the Galapagos Rift; *Bathylaophonte pacifica* Lee & Huys, 1999 (Laophontidae) from the East Pacific Rise; and *Uptionyx verenae* Conroy-Dalton & Huys, 2000 (Ancorabolidae) from the Juan de Fuca Ridge. Two harpacticoid species of the subfamily Cholidyinae (Tisbidae) parasitize deep water cephalopods: *Genesis vulcanoctopusi* López-González et al., 2000 from the Juan de Fuca Ridge and *Cholidya polypi* Farran, 1914 from the East Pacific Rise (Humes & Voight, 1997).

Fourteen species of copepods have been reported from five sites of the Mid-Atlantic Ridge. The harpacticoid *Bathylaophonte azorica* Lee & Huys, 1999 (Laophontidae) was found in benthic samples at 37°N (Lucky Strike, Menez Gwen). Thirteen species are siphonostomatoids of the family Dirivultidae (Ivanenko & Ferrari, 2003). However, only three dirivultids (*Aphotopontius atlanteus* Humes, 1996, *A. temperatus* Humes, 1997; and *Stygiopontius rimivagus* Humes, 1997) were reported from the Lucky Strike vent field.

Many specimens of cyclopoids (Cyclopinidae, Erebonasteridae), harpacticoids (Ameiridae, Argestidae, Diosaccidae, Ectinosomatidae, Tegastidae, Thalestridae, Tisbidae), and siphonostomatoids (Dirivultidae) were collected during *in situ* colonization experiments conducted at the Lucky Strike vent field, one of the largest active hydrothermal vent fields (Gebruk et al., 1997; Comtet & Desbruyères, 1998; Desbruyères et al., 2000; Gebruk, 2002). These experiments were designed for the sampling of meiofauna and larvae of macrofauna, which are rarely collected in the deep-sea by traditional methods. From this material, a new abundant cyclopoid has been described (Ivanenko & Defaye, 2004) and the description of a new abundant harpacticoid is given here.

Materials and methods

The copepods were collected during PICO cruise (vessel "Nadir", IFREMER, France), by the submersible "Nautile"(dive 1270, 07.VII.1998) at the end of *in situ* colonization experiments. A specially designed array (SMAC A) consisting of 4 trays with artificial substratum of small glass beads, protected from large carnivorous animals by a mesh, was deposited during MARVEL cruise (vessel "Atalante", IFREMER, France) by the submersible "Nautile" (dive 1194, 20.VIII.1997) at the active chimney "Eiffel Tower" covered with mytilids *Bathymodiolus azori*-

cus (Bivalvia, Mytilidae) (see Comtet & Desbruyères, 1998). The array stayed at a depth of 1698 m during 322 days at temperatures ranging from 5 to 13° C.

Adult and copepodid stages of the new tegastid genus were the most abundant among the copepods of six families found in the tray A/2 which had, at the beginning of the experiment, an artificially enriched concentration of H₂S. Other families of copepods found in this tray were Cyclopinidae, Dirivultidae, Erebonasteridae, Thalestridae, and Tisbidae. Unidentified amphipods, gastropods, nematods, nemerteans, ostracods, and polychaetes were also present in the tray A/2 (Segonzac, pers. com.).

For light microscopical studies, the specimens were cleared in lactic acid, stained with a solution of chlorazol black E, and examined with bright-field or differential interference optics. All measurements and dissections were made in lactic acid. Dissections were made with the aid of a Leica MZ8 dissecting microscope. Drawings were made with a camera lucida mounted on a Leica DMLB compound microscope.

For scanning electronic microscopy (SEM), copepods were dehydrated through graded ethanol concentrations, critical point dried, mounted on aluminium stubs, coated with gold, and examined in a JEOL 840 scanning electron microscope.

The description is based on the holotype female, the allotype male and paratypes studied by SEM and light microscope. For long-term preservation, the holotype, the allotype and two paratypes were mounted on slides in glycerol and sealed with Eukitt (O. Kindler GmbH & Co., Freiburg, Germany).

Systematics

Order HARPACTICOIDA Sars, 1903 Family Tegastidae Sars, 1904 Smacigastes gen. nov.

Generic diagnosis

Diagnosis: Tegastidae. Body weakly chitinized. Urosome 5-segmented in both sexes: somite with leg 5, genital double-somite and tree abdominal somites. Male genital double-somite projecting ventrally and asymmetric. Caudal rami elongate. Antennule 8-segmented (with aesthetasc on segments 4 and 8) in female, 10-segmented (with aesthetasc on segments 3, 5 and 10) in male. Antenna with 2-segmented exopod and endopod; proximal segment of exopod with 1 seta, distal segment with 3 setae. Mandible with 1-segmented palp bearing 9 setae. Maxillule with praecoxal arthrite armed with 9 spines, coxal endite with 1 seta, basis with 4 terminal setae, exopod 1-segmented, with 3 terminal setae, endopod represented by 2 setae. Maxilla

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with 3 endites on syncoxa: proximal endite with 4 setae, middle endite with 2 setae and distal endite with 3 spines; allobasis with 3 terminal spines and 3 endopodal setae. Maxilliped subchelate; basis with 1 inner seta and pad-like outgrowth; 1-segmented endopod claw-like with 5 setae (3 anterior and 2 posterior). Leg 1 with 1-segmented rami. Legs 2-4 with 3-segmented rami. Formula of armature of legs 1-4 as in type species. Leg 5 of female 2-segmented with baseoendopod bearing 6 armature elements and exopod with 5 armature elements. Leg 5 of male 2segmented; baseoendopod with 1 seta and exopod with 4 armature elements. Leg 6 of female represented by 2 setae on ventral side of genital double-somite. Leg 6 of male without armature elements and represented by genital flaps; right genital flap apparently articulated; left genital flap fused to genital double-somite; genital flaps forming an angle of about 15° to the body axis.

Type species: Smacigastes micheli sp. nov. (by monotypy).

Etymology: The new generic name is a combination of the name of the sampling apparatus (SMAC) and the generic name of the type genus (*Tegastes*) of the family. The species name is in honour of the marine biologist Dr. Michel Segonzac (IFREMER, France), who has collected so much interesting material from deep-sea hydrothermal vents.

Smacigastes micheli sp. nov. (Figs. 1-9)

Type material: Holotype: dissected

^{\circ}, 1 slide (MNHN-Cp2161). Allotype: dissected ^{\circ}, 1 slide (MNHN-Cp2162). Paratypes: 2 specimens (1 ^{\circ} and 1 ^{\circ}) on one slide (MNHN-Cp2163); 10 specimens (7 ^{\circ} ^{\circ} and 3 ^{\circ}) dried, mounted on aluminium stubs, coated with gold for SEM study (MNHN-Cp2164). Holotype, allotype, and

Scale bars: a, b - 0.2 mm.

oeufs. Echelles: a, b - 0,2 mm.

2 paratypes glycerol preserved. The type material is deposited in the Muséum national d'Histoire naturelle, Paris.

Figure 1. Smacigastes micheli n. gen. n. sp., holotype \mathcal{P} ; A. habitus, vue latérale ; B.

Type locality: Atlantic Ocean, Mid-Atlantic Ridge, Azores Triple Junction, Lucky Strike, 37°17.29'N, 32°16.45'W, chimney "Eiffel Tower", field covered with mytilids





Figure 2. *Smacigastes micheli* gen. nov., sp. nov., \Im paratypes, SEM photos. Female N° 1; **A.** habitus, lateral ; **B.** shield of cephalothorax, lateral surface. Female N° 2; **C.** habitus, ventrolateral; **D.** rostrum and labrum, ventrolateral.

Figure. 2. *Smacigastes micheli* n. gen. n. sp., paratypes Q Q, photographies en MEB. Femelle N°1 ; **A.** habitus, vue latérale ; **B.** détail de la surface latérale du céphalothorax. Femelle N° 2 ; **C.** habitus, vue ventro-latérale ; **D.** rostre and labre, vue ventro-latérale.



Figure 3. *Smacigastes micheli* gen. nov., sp. nov., \Im holotype; **A.** urosome (excluding P5-bearing somite) dorsal; **B.** urosome, ventral; **C.** antennule; **D.** antenna; **E.** Leg 5. Scale bars: a, c, d - 0.2 mm; b - 0.05 mm; e - 0.2 mm.

Figure 3. *Smacigastes micheli* n. gen., n. sp., \mathcal{Q} holotype ; **A.** urosome, vue dorsale ; **B.** urosome, vue ventrale ; **C.** antennule ; **D.** antennue ; **E.** P5. Echelles : a, c, d - 0,2 mm ; b - 0,05 mm ; e - 0,2 mm.



Figure 4. *Smacigastes micheli* gen. nov., sp. nov., paratypes, SEM photos. Female N°3; **A.** genital double-somite, abdominal somite and caudal rami, ventral. Female N°4; **B.** genital apertures on the genital double-somite, ventral. Female N°5; **C.** maxilliped, posterior. Male N°3; **D.** maxilliped, anterior. Setae and spinules at pad arrowed.

Figure 4. *Smacigastes micheli* n. gen. n. sp., paratypes, photographies en MEB. Femelle N°3 ; **A.** double somite génital, urosomites et rames furcales, vue ventrale. Femelle N°4 ; **B.** ouvertures génitales et P6 sur le double somite génital, vue ventrale. Femelle N°5 ; **C.** maxillipède, vue postérieure. Mâle N°3 ; **D.** maxillipède, vue antérieure, flèches : soies et processus couverts de spinules.



Figure 5. *Smacigastes micheli* gen. nov., sp. nov., \Im holotype; **A.** mandible; **B.** maxillule; **C.** maxilla; **D.** maxilliped, posterior; **E.** maxilliped, anterior. Scale bars: a-c - 0.05 mm; d, e - 0.05 mm.

Figure 5. *Smacigastes micheli* n. gen. n.sp., holotype \mathcal{P} ; **A.** mandibule ; **B.** maxillule ; **C.** maxille ; **D.** maxillipède, vue postérieure ; **E.** maxillipède, vue antérieure. Echelles: a-c - 0,05 mm ; d, e - 0,05 mm.



Figure 6. *Smacigastes micheli* gen. nov., sp. nov., \mathcal{Q} holotype; **A.** leg 1, anterior; **B.** leg 2, anterior; **C.** endopod of leg 2, anterior; **D.** leg 3, anterior; **F.** endopod of leg 3, anterior; **F.** leg 4, anterior; **G.** endopod of leg 4, anterior. Scale bars: 0.2 mm.

Figure 6. *Smacigastes micheli* n. gen. n.sp., \mathcal{Q} holotype ; **A.** P1, vue antérieure ; **B.** P2, vue antérieure ; **C.** endopodite de P2, vue antérieure ; **D.** P3, vue antérieure ; **E.** endopodite of P 3, vue antérieure ; **F.** P4, vue antérieure ; **G.** endopodite of P4, vue antérieure. Echelles: 0,2 mm.



Figure 7. *Smacigastes micheli* gen. nov., sp. nov., δ allotype; **A.** habitus, lateral; **B.** urosome, ventral. Scale bars: a, b - 0.2 mm.

Figure 7. *Smacigastes micheli* n. gen. n.sp., δ allotype ; **A.** habitus, vue latérale ; **B.** urosome, vue ventrale. Echelles: a, b - 0,2 mm.

Bathymodiolus azoricus at a temperature from 5 to 13°C. Depth 1698 m; date 07.VII.1998 dive; 1270, submersible "Nautile", vessel "Nadir", cruise PICO (IFREMER, France). Tray A/2 of array SMAC A.

Additional material: 101 specimens (adult and subadult copepodid stages) from tray A/2 of array SMAC A. All specimens ethanol preserved. The material is in the Muséum national d'Histoire naturelle, Paris.

Description

Female: Body (Figs. 1 A; 2 A-C) laterally compressed, weakly chitinized, with long sensillae. Total length of holotype female (excluding caudal setae) 630 µm, greatest width 360 µm. Prosome 4-segmented: cephalothorax (including 2 thoracic somites with maxilliped and leg 1) and 3 somites bearing legs 2 to 4. Shield of cephalothorax produced ventrolaterally into two triangular plates that almost join ventrally; central part of lateral surface pitted. Urosome (Figs. 3 A, B; 4 A, B) 5-segmented: somite with leg 5, genital double-somite and three last short urosomites, of same length; genital double-somite with genital area located ventrally, last urosomite with dorsal anal opening and rounded anal operculum. а Apparently paired gonopores covered by plates representing leg 6 (Fig. 4B). Copulatory pores not observed.

Caudal rami (Figs. 3 A, B; 4 A) elongate, with 7 setae; length to width ratio 2.4:1. Setae IV, V, VI inserted terminally. Only seta V bearing spinules at the beginning of its middle third.

Rostrum (Figs. 1 A; 2 D) a rounded ventral prominence.

Labrum (Fig. 1 A; 2 D) slightly projecting over shield of cephalothorax in lateral view.

Eggs (Fig. 1 B) 4 eggs observed in brood pouch formed by leg 5 and shield of cephalothorax.

Antennule (Fig. 3 C) 8-segmented; formula of setation as follows: 1, 11, 10, 4+a, 2, 4, 4, 7+a. (a = aesthetasc).



Figure 8. *Smacigastes micheli* gen. nov., sp. nov., $\delta \delta$ paratypes, SEM photos. Male N°1; **A.** genital double-somite, ventral; **B.** right genital flap, ventrolateral; **C.** left genital flap, ventrolateral. Male N°2; **D.** abdominal somites and caudal rami, ventral.

Figure 8. *Smacigastes micheli* n. gen. n.sp., paratypes $\delta \delta$, photographies en MEB. Mâle N° 1 ; **A.** double somite génital, vue ventrale ; **B.** clapet génital mâle droit, vue ventro-latérale ; **C.** clapet génital mâle gauche, vue ventro-latérale. Mâle N° 2 ; **D.** urosomites et rames furcales, vue ventrale.



Figure 9. *Smacigastes micheli* gen. nov., sp. nov., \mathcal{J} allotype; **A.** proximal part of antennule; **B.** distal part of antennule; **C.** leg 5, lateral. Scale bars: a, b - 0.05 mm; c - 0.2 mm.

Figure 9. *Smacigastes micheli* n. gen. n.sp., allotype 3° ; **A.** antennule, partie proximale ; **B.** antennule partie distale ; **C.** P5, vue latérale. Echelles : a, b - 0,05 mm ; c- 0,2 mm.

Antenna (Fig 3 D): small coxa and elongate basis with 1 distal inner seta; exopod 2-segmented, proximal segment with 1 distal seta, second segment with 3 terminal setae; endopod 2-segmented, proximal segment with 1 median seta, distal segment with 10 setae (6 terminal and 4 inner setae).

Mandible (Fig. 5 A): gnathobase with 9 terminal teeth; palp 1-segmented with 9 setae of different lengths: 3 terminal setae and 1 inner seta (on process representing endopod), 3 outer (on a lobe interpreted as exopod) and 2 inner (basal) setae.

Maxillule (Fig 5 B): praecoxal arthrite with 9 spines; coxal endite with 1 stout seta; basis elongate with 4 terminal setae and setules; exopod 1-segmented with 3 terminal setae and setules; endopod interpreted as being represented by 2 of the 3 setae at outer margin of basis.

Maxilla (Fig. 5 C): syncoxa with 3 endites: proximal endite with 4 setae, one seta elongate and distally directed; middle endite with 2 spines; distal endite with 3 spines; allobasis with 3 terminal spines and 3 setae at outer margin representing endopod.

Maxilliped (Figs. 4 C; 5 D, E): subchelate, 3-segmented. Syncoxa elongate with plumose seta distally on inner side and rows of long setules proximally. Basis palmar edge with 1 plumose seta inserted at about the middle of rows of long setules and 1 elongate pad-like outgrowth ornamented on its surface with short spinules. Endopod 1-segmented, claw-like, bearing proximally 5 setae (2 on posterior side, 3 on anterior side) and a row of short spinules on its inner side.

Swimming legs biramous ; spine and setal formula, see Table 1.

Leg 1 (Fig. 6 A) with 1-segmented rami. Second inner seta of endopod stout and naked.

Legs 2-4 (Fig. 6 B-G) with 3-segmented rami. Formula for armature of legs 1-4 as in Table 1. Exopod of leg 4: middle inner seta of distal segment stout and unilaterally barbed; inner seta of middle segment smooth.

Leg 5 (Fig. 3 E) 2-segmented, with baseoendopod and exopod; baseoendo-

pod with 6 armature elements: 1 outer seta, 3 inner setae and 2 terminal spines, the inner one very strong; exopod with 5 armature elements: 1 outer seta, 2 outer spines and 2 terminal spines.

Leg 6 (Figs. 3 B, 4 B) represented by 2 plates with setae

 Table 1. Spine and setal formula of legs 1-4 in Smacigastes

 micheli gen. nov., sp. nov.

Tableau 1. Formule des soies et des épines des pattes P1-P4 chez *Smacigastes micheli* n. gen.., n. sp.

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

on ventral side of genital double-somite.

Colour of living specimens unknown.

Male: Differs from female as follows:

Body (Fig. 7 A): total length of allotype male (excluding caudal setae): 570 μ m, greatest width: 310 μ m. Urosome (Fig. 7 B; 8 A-D) 5-segmented: genital somite and first abdominal somite fused, forming genital double-somite as in female, subdivided in ventral view and produced ventrally in a large, elongated prominence bearing distally asymmetrical genital flaps.

Spermatophore (Fig. 7 A) bean-like, stored inside genital double-somite (on figure, placed outside).

Antennule (Fig. 9 A, B) 10-segmented; formula of setation as follows: 1, 11, 8+a, 2, 8+a, 1, 2, 1, 4, 7+a (a = aesthetasc).

Leg 5 (Fig. 9 C) 2-segmented: baseoendopod with 1 outer seta and exopod with 4 armature elements: two unequal terminal spines and 2 lateral setae.

Leg 6 (Fig. 7 B; 8 A-D) without armature elements; 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.

Colour unknown.

Remarks

The new monotypic genus *Smacigastes* gen. nov. belongs to the family Tegastidae, distinguishable from other copepods by the body strongly compressed laterally, the shield of the cephalothorax produced ventrolaterally, and the male genital complex produced ventrally (Huys et al., 1996). About 48 tegastid species belonging to five genera (*Tegastes* Norman, 1903; *Parategastes* Sars, 1904; *Syngastes* Monard, 1924; *Feregastes* Fiers, 1986; and *Arawella* Cottarelli & Baldari, 1987) are known from shallow water, either free-living or in association with algae, bryozoans and cnidarians such as hydrozoans, scyphozoans, as well as actiniarians, alcyonaceans, and scleractinians (Humes, 1981a,b; Humes, 1984; Bodin, 1997; Bartsch, 1999). The discovery of a presumably free-living tegastid in the Mid-Atlantic Ridge is the first report of Tegastidae from deep-sea hydrothermal vents and from the deep sea as a whole.

Smacigastes gen. nov. is the most plesiomorphic genus of the family Tegastidae. The distinctive and primitive features of the new genus are the elongate caudal rami in both sexes and the ten-segmented antennule of the male. These features require an amendment of the existing family diagnosis which indicates a short caudal rami (with length shorter then width), and a up to eight-segmented antennule in the male (Huys et al., 1996: 288). In addition, the leg 6 of female represented in the new genus by two minute setae on ventral side of the genital double-somite was not mentioned in the family diagnosis nor in the previous descriptions of tegastids. Only the new genus and the diverse genus Tegastes share primitive 3-segmented rami of legs 2-4. Other four genera of tegastids possess one or more 2-segmented rami of legs 2-4 (see the generic key in Huys et al., 1996). The new genus has a one-segmented maxillulary exopod with three terminal setae whereas, according to the diagnosis of Huys et al. (1996), the exopod is completely incorporated into the basis. However, one-segmented exopod with terminal setae is present in the first copepodid stage of Tegastes clausi (Scott, 1895) (Dahms, 1993) as well as in adults of several tegastids, such as Tegastes knoepffleri Médioni & Soyer, 1967, Tegastes pygmaeus Marcus, 1977, and Synegaster kunzi Marcus, 1977.

The presumed derived features of the new genus are the fusion of the left genital flap with the male genital doublesomite and a slight torsion (clockwise from ventral view) of the flaps relative to the dorso-ventral axis of the doublesomite. The presumed ancestral male of tegastids had a symmetrical genital double-somite with two articulated genital flaps on both sides of the double-somite as in *Parategastes sphaericus* (Claus, 1863) (Huys et al., 1996: 299, fig. 119, D). A degree of rotation of the male genital flaps to the dorso-ventral axis of the genital double-somite as well as fusion of the genital flaps with the genital somite in *Feregastes wellensi* Fiers, 1986 (Fiers, 1986, Fig.1f-h) and in other tegastids require additional study.

The remarkable feature of *Smacigastes* gen. nov. is the weakly chitinized body and appendages, distinguishing it from other tegastids having, according to the family diagnosis, strongly chitinized integument (Huys et al., 1996).

The five-segmented urosome of male and female, as well as the structure of the somites indicate that the male genital complex of the new genus is double and formed by the genital somite and the first abdominal somite, as in the

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female. This state is shared with the genera *Arawella* and *Feregastes*, and the species *Tegastes cnidicus* (Humes, 1981b; Huys et al., 1996). Males and females of other members of the family (*Parategastes, Syngastes*, and the majority of species in *Tegastes*) possess a more derived state of the genital complex, having the genital double-somite fused with the somite bearing leg 5, thus forming a genital triple-somite (Huys et al., 1996). The male genital double-somite as well as the genital triple-somite are atypical in free-living copepods, being known only in tegastids. The female genital double-somite is a typical characteristic of copepods, with a few exceptions to the rule where the somites articulate (Ivanenko et al., 2001).

The presence of three endites on the maxillary syncoxa was considered to be typical of the family. In fact, it is variable, and particularly in the genus *Tegastes*: for instance, two endites are present in *Tegastes nanus* Sars, 1904 (McAlice & Coffin, 1990), *T. singularisaetus* Marcus, 1977, *T. pygmaeus*, *T. acroporanus* Humes, 1981, *T. paulipes* Humes, 1984, whereas three are present in *T. knoepffleri* Médioni & Soyer, 1967 and *T. cnidicus* Humes, 1981. The new genus conforms to the basic scheme with three well-developed endites.

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References

- Bartsch I. 1999. Three new species of *Syngastes* (Tegastidae, Harpacticoida, Copepoda) from Western Australia. In: *Proceedings of the Ninth International Marine Biological Workshop* (D.I. Walker & F.E. Wells eds), The seagrass flora and fauna of Rottnest Island, Western Australia. Western Australia, January 1996. pp. 95-313.
- **Bodin P. 1997.** *Catalogue of the new marine harpacticoid copepods* (1997 edition). Studiedocumenten van het Koninklijk Belgisch Institut voor Natuurwetenschappen (Documents de Travail, Institut Royal des Sciences naturelles de Belgique) **89**:1-304.
- Comtet T. & Desbruyères D. 1998. Population structure and recruitment in mytilid bivalves from the Lucky Strike and Menez

Gwen hydrothermal vent areas (37°17'N and 37°50'N on the Mid-Atlantic Ridge). *Marine Ecology Progress Series*, **163**: 165-177.

- **Dahms H.-U. 1993.** Comparative copepodid development in *Tisbidimorpha sensu* Lang, 1948 (Copepoda, Harpacticoida) and its bearing on phylogenetic considerations. *Hydrobiologia*, **250**: 15-37.
- Desbruyères D., Almeida A., Biscoito M., Comtet T., Khripounoff A., Le Bris N., Sarradin P.M. & Segonzac M.
 2000. A review of the distribution of hydrothermal vent communities along the northern Mid-Atlantic Ridge: dispersal vs. environmental controls. In: *Island, Ocean and Deep-Sea Biology*. (M.B. Jones, J.M.N. Azevedo, A.I. Neto, A.C. Costa & A.M. Frias Martins eds). *Hydrobiologia*, 440: 201–216.
- Fiers F. 1986. *Feregastes wellensi* gen. nov., sp. nov., a new genus of the family Tegastidae (Copepoda, Harpacticoida) from the Andaman Islands. *Crustaceana*, **51**: 277-285.
- Gebruk A. Ed. 2002. Biology of hydrothermal systems. KMK: Moscow. 543 pp. [In Russian].
- Gebruk A.V., Galkin S.V., Vereshchaka A.L., Moskalev L.I. & Southward A.J. 1997. Ecology and biogeography of the hydrothermal vent fauna of the Mid-Atlantic Ridge. *Advances in Marine Biology*, 32: 93-144.
- Heptner M.V. & Ivanenko V.N. 2002. Copepoda (Crustacea) of hydrothermal ecosystems of the World Ocean. Arthropoda Selecta, 12: 117-134.
- Humes A.G. 1981a. A new species of *Tegastes* (Copepoda: Harpacticoida) associated with a scleractinian coral at Eniwetok atoll. *Proceedings of the Biological Society of Washington*, 94: 254-263.
- Humes A.G. 1981b. Harpacticoid copepods associated with Cnidaria in the Indo West Pacific. *Journal of Crustacean Biology*, 94: 227-240.
- Humes A.G. 1984. Harpacticoid copepods associated with cnidarians in the tropical Pacific Ocean. Zoologica Scripta, 13: 209-221.
- Humes A.G. 1996. Deep-sea Copepoda (Siphonostomatoida) from hydrothermal sites on the Mid-Atlantic Ridge at 23° and 37°N. *Bulletin of Marine Science*, 58: 609-653.
- Humes A.G. 1997. Siphonostomatoid copepods from deep-sea hydrothermal sites on the Mid-Atlantic Ridge west of the Azores. *Cahiers de Biologie Marine*, **34**: 63-77.
- Humes A.G. & Segonzac M. 1998. Copepoda from deep-sea hydrothermal sites and cold seeps: description of a new species of *Aphotopontius* from the East Pacific Rise and general distribution. *Cahiers de Biologie Marine*, **39**: 51-62.
- Humes A.G. & Voight J.R. 1997. Cholidya polypi (Copepoda: Harpacticoida: Tisbidae), a parasite of deep-sea octopuses in the North Atlantic and northeastern Pacific. Ophelia, 46: 65-81.
- Huys R., Gee J.M., Moore C.G. & Hamond R. 1996. Marine and brackish water harpacticoid copepods. Part 1. In: Synopses of the British Fauna (New series), (D.M. Kermack, R.S.K. Barnes & J.H. Crothers eds). The Linnean Society of London and The Estuarine and Coastal Sciences Association London. 352 pp.
- Ivanenko V.N. 1998. Deep-sea hydrothermal vent Copepoda (Siphonostomatoida: Dirivultidae) in plankton over the Mid-Atlantic Ridge (29'N), morphology of their first copepodid stage. *Zoologicheskii Zhurnal*, 77: 1249-1256. [In Russian].

- Ivanenko V.N. & Defaye D. 2004. A new genus and species of deep-sea cyclopoids (Copepoda, Cyclopinidae) from the Mid-Atlantic Ridge (Azores Triple Junction, Lucky Strike). *Zoosystema*, 26: 49-64.
- Ivanenko V.N. & Ferrari F.D. 2003. A new genus and species of the family Dirivultidae (Copepoda, Siphonostomatoida) from a deep-sea hydrothermal vent at the Juan de Fuca Ridge (Pacific ocean) with comments of dirivultid distribution. *Arthropoda Selecta*, 11: 2002: 177-185.

Ivanenko V.N., Ferrari F.D., & Smurov A.V. 2001. Nauplii and

copepodids of *Scottomyzon gibberum* (Copepoda: Siphonostomatoida: Scottomyzontidae, new family), a symbiont of *Asterias rubens* (Asteroidea). *Proceedings of the Biological Society of Washington*, **114**: 237-261.

McAlice B. & Coffin W.L. 1990. First records of *Tegastes falcatus* (Norman, 1868) and *T. nanus* Sars, 1904 (Copepoda: Harpacticoida) from the East Coast of the United Sates and a redescription of *T. nanus. Journal of Crustacean Biology*, 10: 703-707.

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