

Description, distribution and microhabitats of a new species of *Tisbe* (Copepoda: Harpacticoida: Tisbidae) from a deep-sea hydrothermal vent field at the Mid-Atlantic Ridge (37°N, Lucky Strike)

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Abstract: A new species, *Tisbe dahmsi* sp. nov. (Crustacea, Copepoda: Harpacticoida: Tisbidae) is described from the Eiffel Tower edifice located in the Lucky Strike vent field (37°N) (Mid-Atlantic Ridge MAR, 1698 m). The samples were collected in colonization experiments (SMAC arrays) that were deployed in 1997 during the MARVEL cruise and recovered in 1998 during the PICO cruise. Other specimens were collected during the MoMARETO cruise during which a physico-chemical characterization of copepod microhabitats was done. The new species belongs to the *T. gracilis* group based on similarities of the spine-like inner seta on the proximal endopodal segment of the male second swimming leg, which is terminally bifurcate. Re-examination of the closest relative and shallow-water species *T. gracilis* revealed a number of distinctions, including differences in shape and ornamentation of this terminally bifurcate seta. *Tisbe dahmsi* sp. nov. is found abundantly in the *in situ* colonization experiments (SMAC arrays) deployed on *Bathymodiolus azoricus* mussel assemblages at the Eiffel Tower edifice, together with the cyclopoid copepod *Hepterina confusa* Ivanenko & Defaye, 2004 (Cyclopoida: Cyclopinidae), the harpacticoid copepod *Smacigastes micheli* Ivanenko & Defaye, 2004 (Harpacticoida: Tegastidae) and the dirivultid copepod *Aphotopontius atlanteus* Humes, 1996 (Siphonostomatoida: Dirivultidae). Another colonization experiment, deployed near a black smoker, exhibits a different pattern with dominance of the harpacticoid families Ameiridae and Argestidae of the Ectinosomatidae family. These colonization experiments revealed that copepods of the genus *Tisbe* were substantially more abundant in the trays deployed on mussel assemblages than to those in the vicinity of black smokers. Nevertheless, no clear response regarding the effect of organic enrichment on copepod abundance was observed. The type of environment where the arrays were deployed appears to have a stronger influence on copepod abundances and composition than the treatment applied within each tray. Directly on the Eiffel Tower edifice, *Tisbe* copepods were found within different *Bathymodiolus azoricus* assemblages. These assemblages were alternatively dominated (in terms of copepods) by the Dirivultidae or the Tegastidae, the former being dominant in 67% of the samples. In terms of environmental conditions, *Tisbe dahmsi* was found in microhabitats characterized by low temperatures

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(< 8.8°C) and where the estimated hydrothermal inputs vary between 0.22 and 1.38%. The relative abundance of adult Tisbidae within *B. azoricus* assemblages was higher at the higher temperatures as well as at the higher concentrations of sulfide and iron and at lower pH compared to the surrounding sea water. This paper is the first description of a free living representative of the family Tisbidae from deep-sea hydrothermal vents.

Résumé : *Description, répartition et microhabitats d'une nouvelle espèce de Tisbe (Copepoda: Harpacticoida: Tisbidae), provenant d'un champ hydrothermal profond de la dorsale médio-Atlantique (37°N, Lucky Strike).* Une nouvelle espèce, *Tisbe dahmsi* sp. nov. (Crustacea : Copepoda : Harpacticoida : Tisbidae) est décrite à partir de spécimens échantillonnés sur l'édifice hydrothermal Tour Eiffel, situé sur le champ Lucky Strike (37°N) de la dorsale médio-Atlantique, à 1698 m de profondeur. Les échantillons proviennent de substrats de colonisation, déployés en 1997 lors de la campagne MARVEL et récupérés en 1998 lors de la campagne PICO. D'autres spécimens ont été récoltés lors de la campagne MoMARETO (2006), au cours de laquelle a été effectuée la caractérisation physico-chimique de différents microhabitats. La nouvelle espèce appartient au groupe *gracilis*, par certains caractères communs au groupe, en particulier la soie interne spiniforme du segment proximal de l'endopodite de la 2^{ème} patte natatoire dont l'extrémité est bifide chez les mâles. Un nouvel examen de l'espèce la plus proche, *T. gracilis*, vivant en eaux peu profondes, a révélé un certain nombre de caractères distinctifs, incluant des différences dans la forme et l'ornementation de la soie à extrémité bifide. *Tisbe dahmsi* sp. nov. est l'une des quatre espèces de copépodes retrouvées en abondance dans les expériences de colonisation déployées sur les assemblages de *Bathymodiolus azoricus*, situés sur l'édifice hydrothermal Tour Eiffel, avec le cyclopoïde *Heptnerina confusa* Ivanenko & Defaye, 2004 (Cyclopoida : Cyclopinidae), l'harpacticoidé *Smacigastes micheli* Ivanenko & Defaye, 2004 (Harpacticoida : Tegastidae) et le dirivultide *Aphotopontius atlanteus* Humes, 1996 (Siphonostomatoida : Dirivultidae). Une troisième expérience de colonisation, déployée à proximité d'un fumeur noir du même édifice, montre un patron de distribution différent, avec la dominance des copépodes harpacticoides soit des familles Ameiridae et Argestidae, soit de la famille des Ectinosomatidae. Les expériences de colonisation ont montré que les copépodes du genre *Tisbe* étaient substantiellement plus abondants dans les substrats déployés sur les assemblages de modioles que dans ceux situés à proximité du fumeur noir. Cependant, aucune réponse claire n'a été obtenue sur l'effet des différents traitements sur l'abondance des copépodes. Dans les deux expériences sur les modioles, les copépodes du genre *Tisbe* semblent répondre à l'enrichissement organique, mais cette réponse n'est pas visible dans la 3^{ème} expérience. Les caractéristiques de l'environnement où ont été déployés les substrats semblent avoir davantage d'influence sur l'abondance des copépodes que le traitement appliqué. Sur l'édifice hydrothermal Tour Eiffel, les copépodes du genre *Tisbe* ont été trouvés dans différents assemblages de *Bathymodiolus azoricus*. Ces assemblages sont dominés alternativement (en ce qui concerne les copépodes) par les Dirivultidae et les Tegastidae, les premiers étant dominants dans 67% des échantillons. Si l'on considère les conditions environnementales, *Tisbe dahmsi* est retrouvé dans des microhabitats caractérisés par des températures basses (< 8,8°C) et où les apports en fluide hydrothermal varient entre 0,22 et 1,38%. L'abondance relative des adultes Tisbidae au sein des assemblages de *B. azoricus* était plus importante aux températures plus hautes ainsi qu'aux concentrations plus élevées de sulfures totaux et de fer, et aussi à pH plus bas, par rapport à l'eau de mer environnante. Cet article est la première description d'un représentant de la famille des Tisbidae vivant dans les sources hydrothermales profondes.

Keywords: Copepoda • Harpacticoida • Tisbidae • Deep-sea • Hydrothermal vent • Mid-Atlantic Ridge • Systematics • Ecology • Microhabitat • *In situ* experiments • Physico-chemical factors

Introduction

Only sixteen species of crustacean copepods have been described so far from deep-sea hydrothermal vents at the Mid-Atlantic Ridge (MAR) among the more than 80 copepod species described from deep-sea hydrothermal vents world-wide (Humes & Segonzac, 1998; Heptner &

Ivanenko, 2002; Ivanenko & Defaye, 2006; Ivanenko et al., 2006). Twelve of the sixteen species belong to the siphonostomatoid family Dirivultidae, which is endemic to deep-sea hydrothermal communities of the Pacific and Atlantic Oceans (Ivanenko et al., 2006; Gollner et al., 2010). Before our study, only three species of dirivultid copepods (*Aphotopontius atlanteus* Humes, 1996, *A.*

temperatus Humes, 1997, and *S. rimivagus* Humes, 1997) were known at the Lucky Strike (LS) vent field (37°N), one of the largest and active known hydrothermal fields of the MAR (Comtet & Desbruyères, 1998; Desbruyères et al., 2000). However, recent study synonymized *Aphotopontius temperatus* Humes, 1997 with *A. atlanteus* (Ivanenko & Defaye, 2006). A poecilostomatoid copepod *Ambilimbus arcuscelestis* Ivanenko et al., 2005 has been described from the Rainbow vent field (36°N) and is the only record for the family Erebonasteridae Humes, 1987 from the MAR (Ivanenko et al., 2005). A harpacticoid copepod *Bathylaophonte azorica* Lee & Huys, 1999 (Laophontidae), was described from the Menez Gwen vent field (Lee & Huys, 1999). *Heptnerina confusa* Ivanenko & Defaye, 2004 (Cyclopoida: Cyclopinidae) and *Smacigastes micheli* Ivanenko & Defaye, 2004 (Harpacticoida: Tegastidae), have been described from LS (Ivanenko & Defaye, 2004a & b). The monotypic genus *Heptnerina* Ivanenko & Defaye, 2004 is phylogenetically most related to the specious genus *Cyclopinia* Claus, 1863 recorded worldwide from shallow waters. The description of *S. micheli* represented the first record of tegastids from the deep-sea environment, since these copepods are primarily known from shallow waters, either free-living or associated with

bryozoans, cnidarians and algae (Humes, 1981a, b & 1984; Ivanenko et al., 2008a & b). Recent investigations of chemosynthetic communities, such as deep-sea hydrothermal vents of the East Pacific Rise and deep-sea cold seeps of the Gulf of Mexico, as well as from a shallow whale-fall near the Swedish coast, lead to the discovery of new species of tegastid copepods (Gollner et al., 2008; Plum & Martínez Arbizu, 2009; Willems et al., 2009).

During the last decades, a series of *in situ* colonization experiments and faunal sampling have been conducted at the LS vent field, but only recently researchers have started to look specifically at the meiofauna. Furthermore, very few studies have focussed on the distribution of meiofauna in relation to environmental factors. As a result of these colonization experiments, about 22000 specimens belonging to more than 20 copepod species have been collected, representing the orders Calanoida (Spinocalanidae), Cyclopoida (Cyclopinidae), Harpacticoida (Ameiridae, Ancorabolidae, Argestidae, Canthocamptidae, Ectinosomatidae, Miraciidae, Pseudotachidiidae, Donsiellinae, Tegastidae, Thalestridae, Tisbidae), Poecilostomatoida (Erebonasteridae), and Siphonostomatoida (Dirivultidae). Among these specimens, three species were found to be abundant in these

Table 1. *In situ* colonization experiment design. Two colonization devices (SMAC A & B) were deployed directly on *Bathymodiolus azoricus* mussel assemblages while the third device (SMAC C) was deployed near a black smoker. All the experiments were realized on the Tour Eiffel edifice on the Lucky Strike vent field, Mid-Atlantic Ridge. NA = non available.

Tableau 1. Protocole suivi pour les expériences de colonisation *in situ*. Deux dispositifs (SMAC A & B) ont été déployés alors qu'un troisième dispositif (SMAC C) a été déployé près d'un fumeur noir actif. Toutes les expériences ont été effectuées sur l'édifice Tour Eiffel dans le champ hydrothermal Lucky Strike sur la ride médio-Atlantique. NA = données non disponibles.

SMAC A	A1	A2	A3	A4	Duration Site	Depth	Type of habitat	T°C
Tray filling	Glass beads	Glass beads enriched with H ₂ S	Glass beads + 900 g of fish meal + 50 g of S ⁰	Glass beads + 950 g of fishmeal	322 days	1698 m	Mussel assemblage	5-13°C
SMAC B	B9	B10	B11	B12	Duration Site	Depth	Type of habitat	T°C
Tray filling	Glass beads	Glass beads enriched with H ₂ S	Glass beads + 900 g of fish meal + 50 g of S ⁰	Glass beads + 950 g of fishmeal	319 days	1690 m	Mussel assemblage	12.6°C
SMAC C	C5	C6	C7	C8	Duration Site	Depth	Type of habitat	T°C
Tray filling	Glass beads	Glass beads enriched with H ₂ S	Glass beads + 900 g of fish meal + 50 g of S ⁰	Glass beads + 950 g of fishmeal	321 days	1698 m	At the base of a black smoker	NA

hydrothermal vent field samples: the cyclopoid *H. confusa*, the harpacticoid *S. micheli* and a new species of the specious, harpacticoid genus *Tisbe* Lilljeborg, 1853 (Tisbidae). The family Tisbidae has been actively investigated from shallow-waters, as free-living or associated with invertebrates (Humes, 1957; Dahms et al., 1991; Dahms & Schminke, 1993 & 1995; Chullasorn et al., 2009). Only recent studies have revealed the presence of the genus *Tisbe* in the deep sea, from sunken woods, at a hydrothermal vent field in the Pacific Ocean and at the Arctic Håkon Mosby Mud Volcano (Willen, 2004; Van Gaever et al., 2006 & 2009; Martínez Arbizu, personal communication). The aim of this paper is to describe a new species *Tisbe dahmsi* sp. nov. from the deep-sea hydrothermal vent community of the Tour Eiffel (Eiffel Tower) edifice and to characterize the microhabitats and microdistribution of the genus *Tisbe* in terms of physico-chemical factors.

Material and Methods

Specimens of the new species described in this paper were sampled at different time periods: between 1997 and 1998 with *in situ* colonization experiments (SMAC arrays: “Small Module Autonome de Colonisation”) and in 2006, through direct sampling with the ROV VICTOR6000. For *in situ* experiments, the designed arrays (SMAC A, B & C) were deployed in 1997 by the submersible Nautile (during the MARVEL cruise with RV L'ATALANTE) (Fig. 1 & Table 1). Each array contained 4 trays filled with small glass beads and protected from large carnivores by mesh. In addition to the beads, some of the trays were filled with an organic supplement (NordSeaMink quality fish meal) or enriched with either elemental sulfur (S^0) or hydrogen sulfide to mimic the conditions found at hydrothermal vents (see Table 1). Trays A1, B9 and C5 were only filled with beads; trays A3, B11 and C7 were supplied with beads, 900 g of fish meal and 50 g of elemental sulfur whereas trays A4, B12 and C8 contained beads with 950 g of fishmeal. Trays A2, B10 and C6 were equipped with 4 osmotic pumps (ALZET model 2ML1, ALZA Corp., USA) injecting a solution of 80 mmol.L⁻¹ of sodium sulfide in the beads (Na_2S , 9H₂O, Merck, V = 2.3 mL) at a flow rate of ca. 10 μ L.h⁻¹ (Table 1). The three arrays were deployed in 1997 by the submersible Nautile during the MARVEL cruise on the R/V L'ATALANTE. The first two arrays (SMAC A & B) were left for 322 and 319 days respectively on the Eiffel Tower edifice in a mussel assemblage under the influence of 5-13°C hydrothermal fluids. This 11 m high sulfide structure is one of the most active of the LS vent field (Ondréas et al., 2009) and is covered by dense assemblages of *Bathymodiolus azoricus* (Bivalvia:

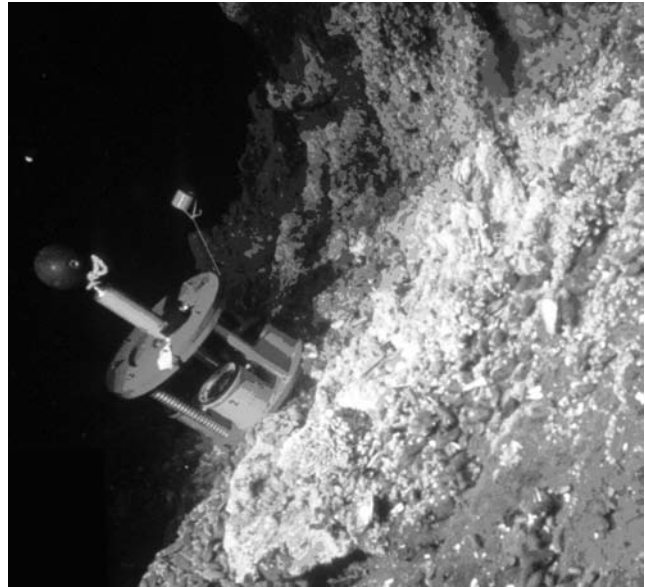


Figure 1. Colonization experiment on the Eiffel Tower edifice of the Lucky Strike vent field (37°N) at the Mid-Atlantic Ridge, depth 1698 m.

Figure 1. Expérience de colonisation sur l'édifice Tour Eiffel du champ hydrothermal Lucky Strike (37°N) sur la dorsale médio-Atlantique, à 1698 m de profondeur.

Mytilidae) (Comtet & Desbruyères, 1998; Cuvelier et al., 2009). The third array (SMAC C) was left for 321 days at the base of a black smoker located on the same edifice (Table 1). The trays were retrieved in 1998 during the PICO cruise on the R/V NADIR with the submersible Nautile. Once on board, the samples were sorted, preserved in 4% buffered formalin and later identified to the lowest possible taxonomic level.

Additional faunal samples were collected during the MoMARETO cruise in 2006 on the R/V *POURQUOI PAS?* with the submersible VICTOR6000. During this cruise, the microhabitats of 12 different *Bathymodiolus azoricus* faunal assemblages (C1 to C12) were characterized in terms of temperature and chemical conditions (Sarradin et al., 2009, De Busserolles et al., 2009). Total dissolved iron (TdFe) and total dissolved sulfide (TdS) concentrations ($H_2S + HS^- + S^{2-}$) were measured *in situ* with the chemical analyser CHEMINI (Vuillemin et al., 2009). Temperature was measured with an autonomous temperature probe (NKE) attached to the sampling inlets. Water samples were collected with the PEPITO sampling device (Sarradin et al., 2009). The pH was measured on board at 25°C using a combined pH electrode (Ingold®) for sulfide-rich medium after calibration with NBS buffers (pH 4 and 7) while total dissolved copper (TdCu) was measured by stripping chronopotentiometry (SCP) with a gold electrode (Riso et al., 1997). A reference temperature was taken outside the

area influenced by hydrothermal fluids. All abiotic sampling and analytical procedures are described in Sarradin et al. (2009). After the physico-chemical characterization of each microhabitat, the fauna was semi-quantitatively sampled using Victor's suction sampler and arm grab. Once brought on board, the faunal samples were washed, sorted and fixed in 4% buffered formalin. After two days, they were transferred to 70% ethanol and, once in the laboratory, identified to the lowest possible taxonomic level.

For their identification, copepods were observed with a light microscope. 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 performed under a Leica MZ8 dissecting microscope. Drawings were achieved 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 at the Muséum National d'Histoire Naturelle (MNHN) in Paris.

The description is based on the holotype female, the allotype male and paratypes studied by SEM and light microscopy. 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). Descriptive terminology follows Ivanenko et al. (2008a); homologies of limb segments follow Ferrari & Ivanenko (2008) and Ferrari & Dahms (2007).

Systematics

Order Harpacticoida Sars, 1903

Family Tisbidae Stebbing, 1910

Subfamily Tisbinae Stebbing, 1910

Genus *Tisbe* Lilljeborg, 1853

Tisbe dahmsi sp. nov.

(Figs 2-8)

Type material

Holotype. Dissected ♀, 1 slide (MNHN-Cp2549). **Allotype:** dissected ♂, 1 slide (MNHN-Cp2550). **Paratypes.** 2 specimens (1 ♀ and 1 ♂) on one slide (MNHN-Cp2551). The type material is deposited in the Muséum National d'Histoire Naturelle, Paris.

Type locality

37°17.29'N-32°16.45'W; Atlantic Ocean, Mid-Atlantic Ridge, Azores Triple Junction, Lucky Strike, Eiffel Tower

edifice; depth 1698 m; date 07.VII.1998; temperature range 5-13°C in SMAC A & B.

Additional material

107 ♀♀ and 118 ♂♂ from tray A4, 2 ♀♀ from tray A1, 1 ♀ from tray A2 of SMAC A array; 1 ♀ from tray B9, 1 ♂ from tray B10, 1 ♂ from tray B12 of SMAC B array; 1 ♀ from tray C7 of SMAC C (for more details see Table 1). All copepods preserved in ethanol and at the Muséum National d'Histoire Naturelle, Paris.

Five ♀♀ and 5 ♂♂ (MNHN-Cp2552) from tray A4 of SMAC A array dried, mounted on aluminium stubs, coated with gold for SEM study are deposited in the Muséum National d'Histoire Naturelle, Paris.

23 specimens (1 ♂ from C3, 12 ♀♀, 3 ♂♂ and 2 copepodids from C4, 4 ♀♀ and 1 copepodid from C6) from faunal sampling in 3 different microhabitats (for more details see Table 4 & Fig. 8), preserved in ethanol at the Laboratoire Environnement Profond, Département Etude des Ecosystèmes Profonds, Institut Français de Recherche pour l'Exploitation de la Mer (Ifremer), Brest.

Etymology

The species name is in honour of the aquatic biologist Prof. Hans-Uwe Dahms who has contributed a lot to the knowledge of copepod crustaceans.

Description

Female. Body (Figs 2A & 8A), total length of holotype female (body plus caudal rami, excluding caudal setae): 0.97 mm, greatest width: 0.39 mm. Prosome 4-segmented: cephalothorax (including 2 thoracic somites bearing maxilliped and swimming leg 1) and 3 articulated somites bearing swimming legs 2 to 4. Urosome of 6 somites with posterior thoracic and anterior abdominal somites fused; posterior toothed fringe on posterior thoracic and anterior three abdominal somites.

Rostrum (Fig. 8A) with weakly developed ventral extension.

Labrum (Figs 2E & 8A-B) trapezoidal, with spinules at base and toothed fringe at tip.

Caudal rami (Fig. 2A & D) with terminal margin with a blunt tooth-like projection laterally and 2 rows of denticles; 4 terminal setae and 2 setae dorsally, dorsomedial seta with 2 adjacent denticles; 1 ventral seta small, with two denticles adjacent to a pore.

Antennule (Fig. 3A & B) 8-segmented; setation: 1, 13, 8 + aesthetasc, 5 + aesthetasc, 1, 4, 3, 6 + bifurcate aesthetasc. Proximal segment with medial denticles; setae medial on segments 1-5, segment 6 with 1 lateral seta, segment 7 with 2 terminal and 1 lateral seta, segment 8 with 4 medial and 2 setae + bifurcate aesthetasc terminal. All setae smooth.

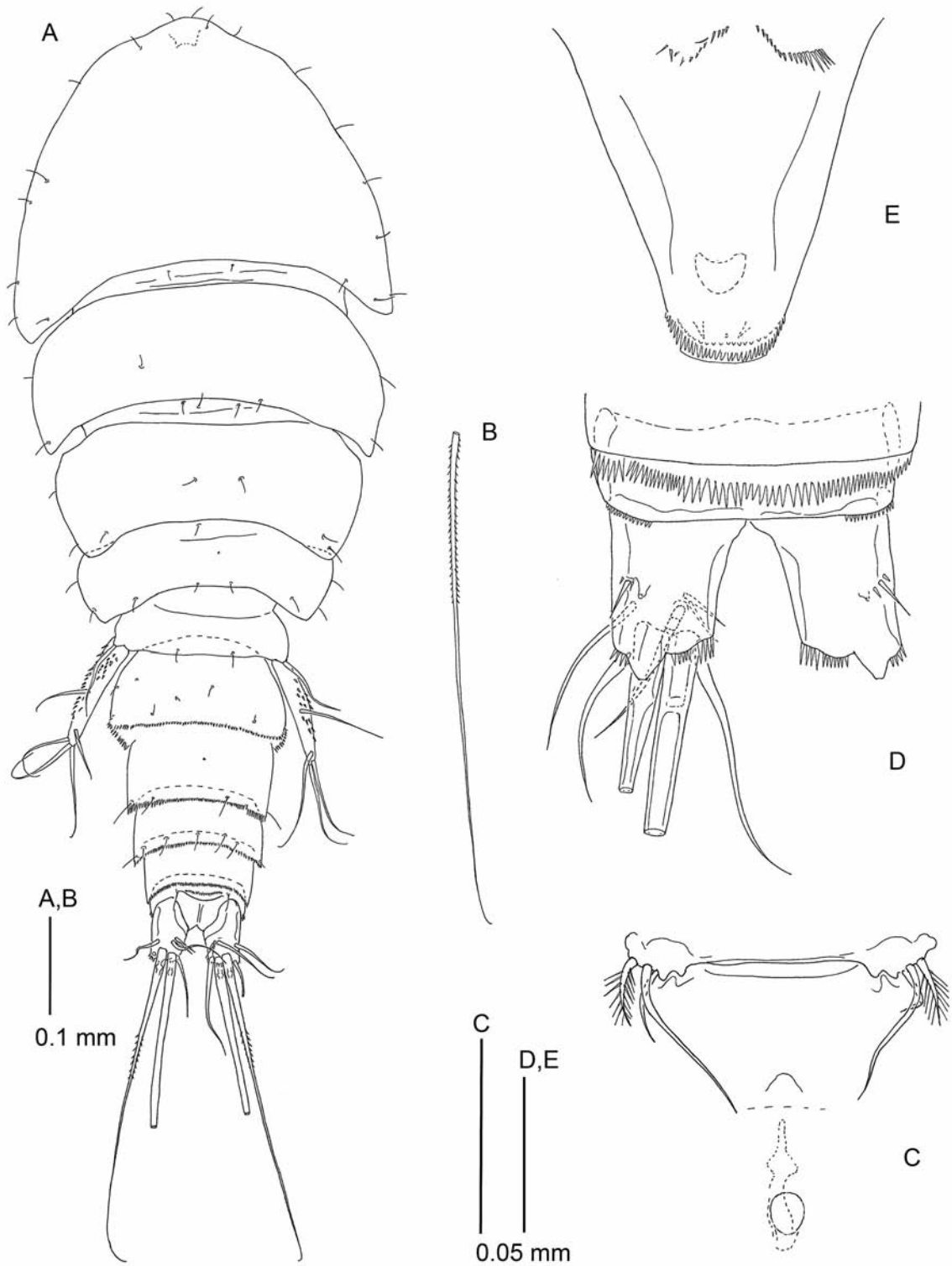


Figure 2. *Tisbe dahmsi* sp. nov. ♀ holotype: **A.** Habitus, dorsal. **B.** Terminal seta of caudal ramus (shown partially in Fig 1 A). **C.** Leg 6 and genital field, ventral. **D.** Anal somite and caudal rami, ventral. **E.** Labrum, anterior.

Figure 2. *Tisbe dahmsi* sp. nov. ♀ holotype : **A.** Habitus, dorsal. **B.** Soie terminale de la rame furcale partiellement illustrée sur la Fig 1A. **C.** Patte 6 et aire génitale ventrale. **D.** Somite anal et rames furcales, ventral. **E.** Labre, antérieur.

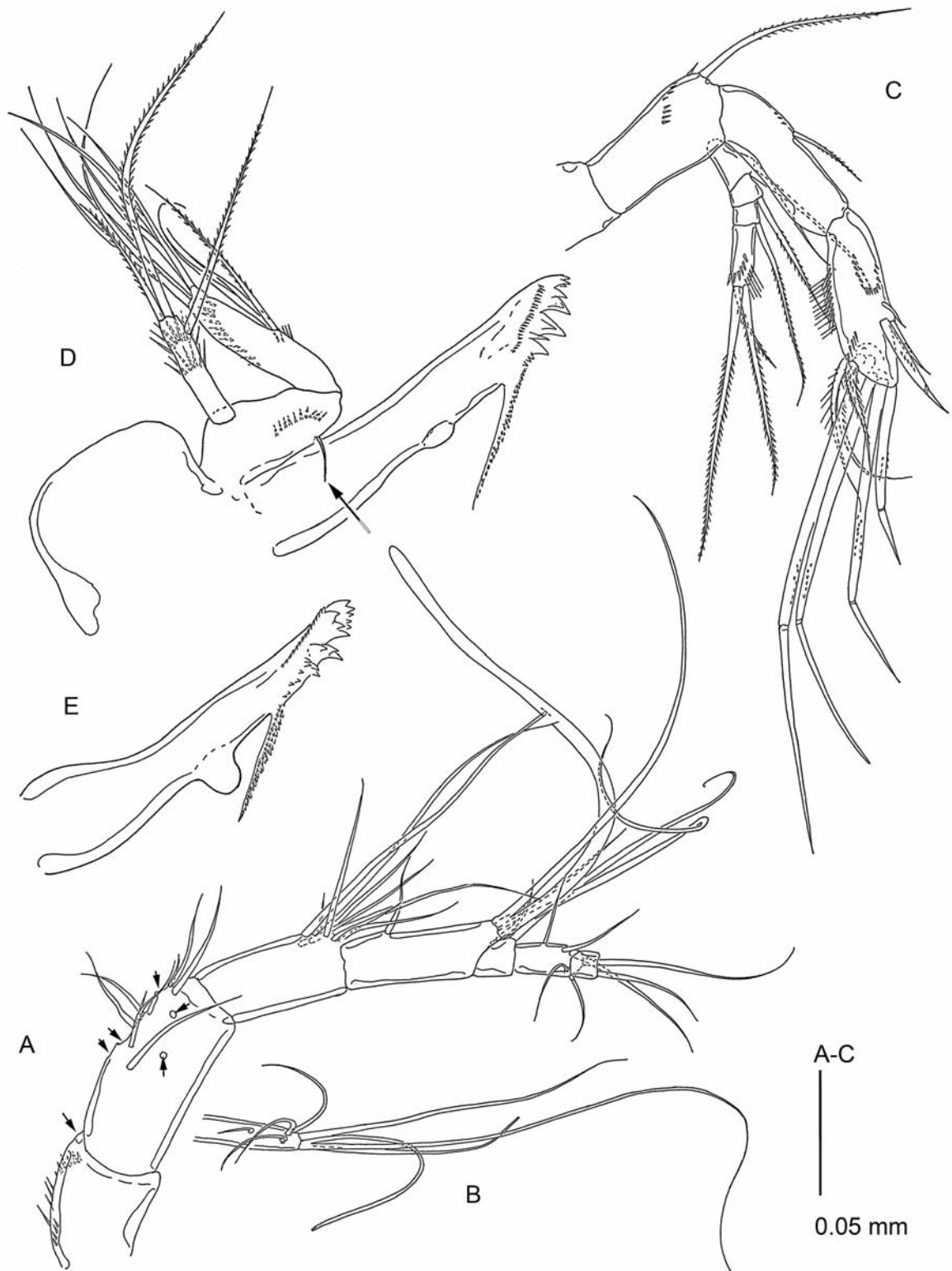


Figure 3. *Tisbe dahmsi* sp. nov. ♀ holotype: **A.** Antennule, segments 1 to 7, insertion places of lost setae arrowed. **B.** Antennule, distal (8th) segment. **C.** Antenna. **D.** Mandible, basal seta arrowed. **E.** Mandibular gnathobase.

Figure 3. *Tisbe dahmsi* sp. nov. ♀ holotype : **A.** Antennule, segments 1 à 7, points d'insertion des soies perdues désignés par des flèches. **B.** Antennule, segment distal (8^{ème}). **C.** Antenne. **D.** Mandibule, soie basale désignée par une flèche. **E.** Mandibule, gnathobase.

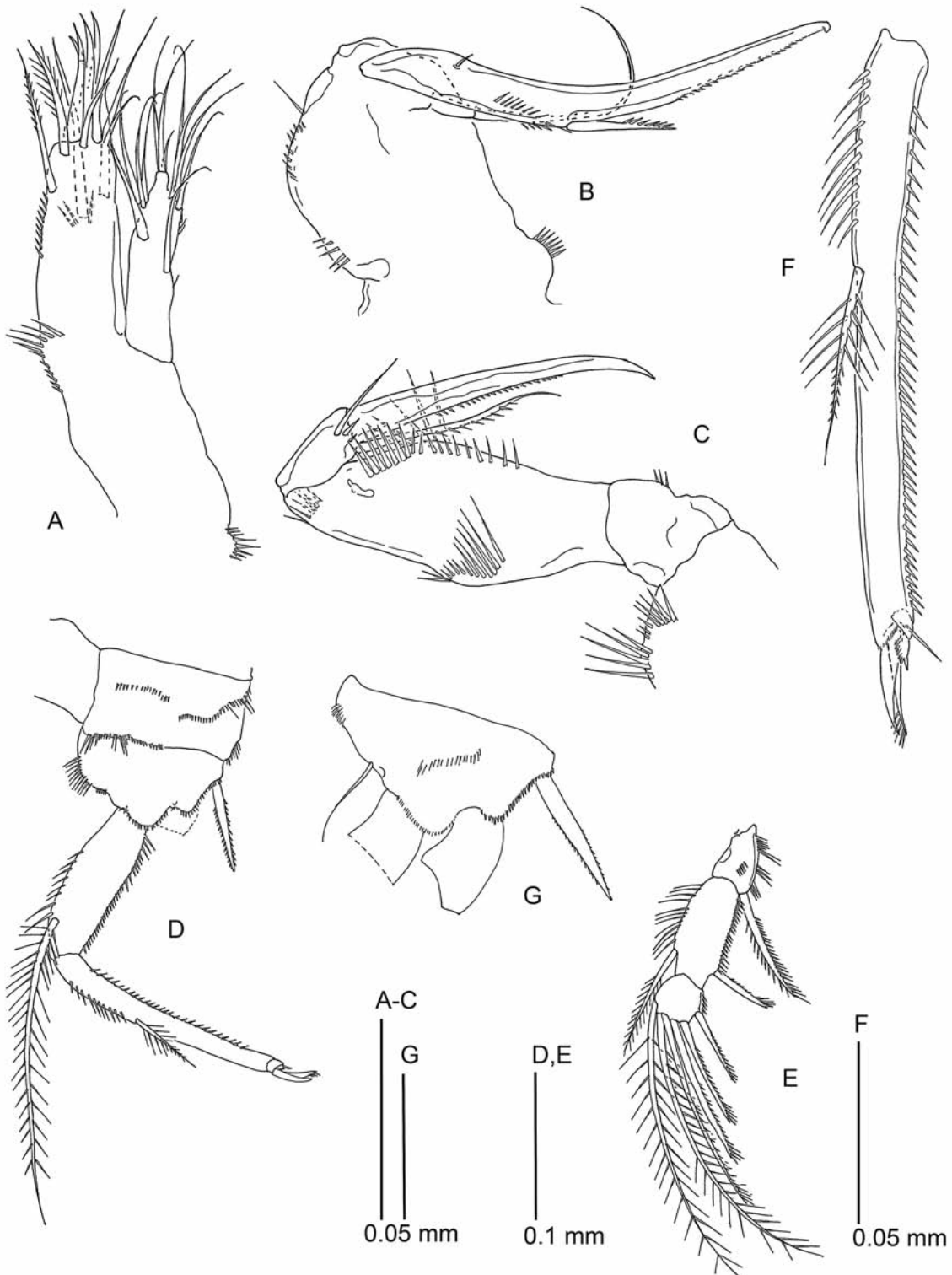


Figure 4. *Tisbe dahmsi* sp. nov. ♀ holotype: **A.** Maxillule. **B.** Maxilla. **C.** Maxilliped. **D.** Leg 1 (exopod not shown). **E.** Exopod of leg 1. **F.** Second and third endopodal segment of leg 1. ♂ allotype: **G.** basis of leg 1.

Figure 4. *Tisbe dahmsi* sp. nov. ♀ holotype : **A.** Maxillule. **B.** Maxille. **C.** Maxillipède. **D.** Leg 1 (exopodite non dessiné). **E.** Exopodite de la patte natatoire 1. **F.** Second et troisième segments de l'endopodite de la patte 1. ♂ allotype : **G.** Basipodite de la patte 1.

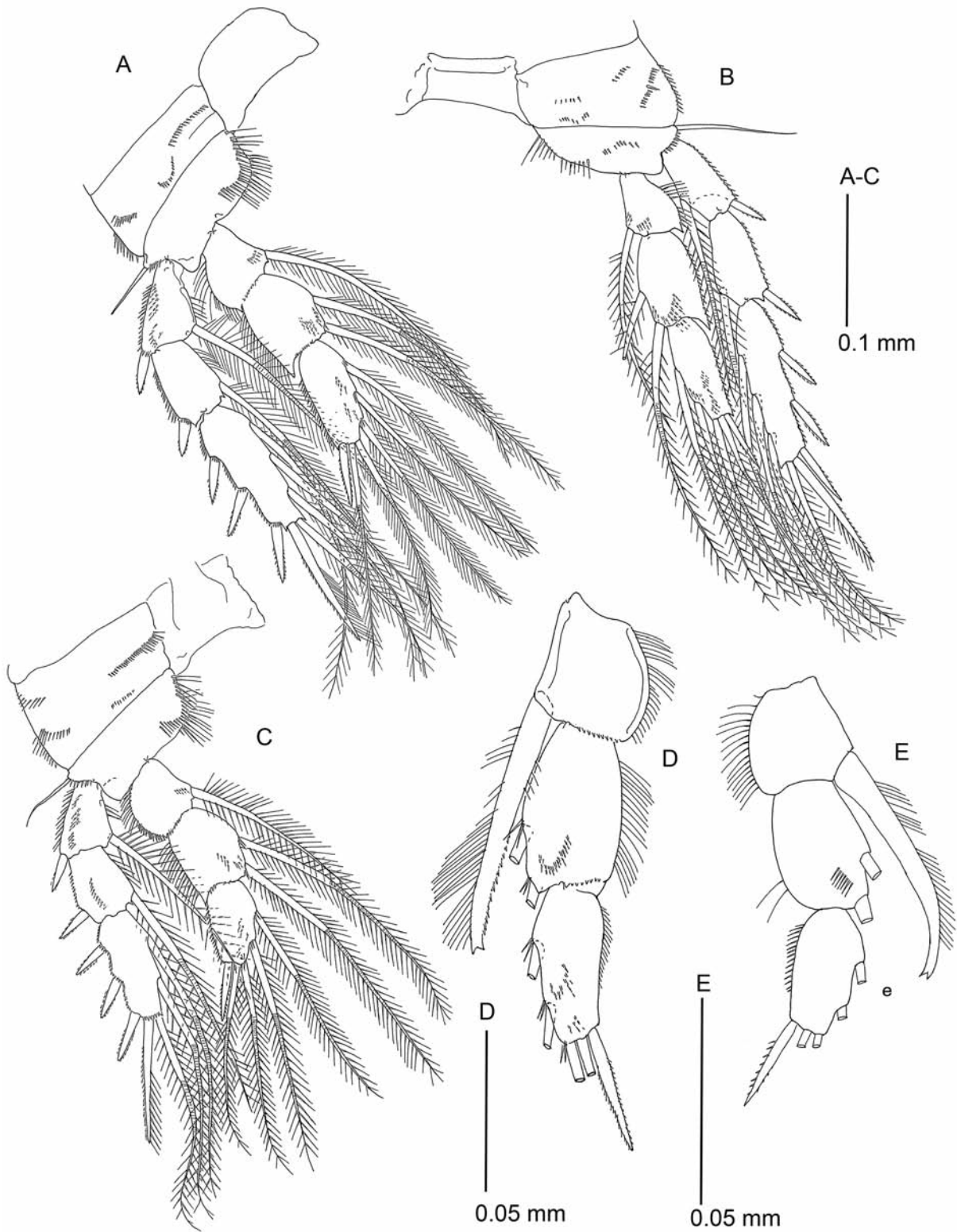


Figure 5. *Tisbe dahmsi* sp. nov. ♀ holotype: **A.** Leg 2. **B.** Leg 3. **C.** Leg 4. ♂ allotype: **D.** Endopod of leg 2. *Tisbe gracilis*, ♂ (USNM 170626): **E.** Endopod of leg 2.

Figure 5. *Tisbe dahmsi* sp. nov. ♀ holotype: **A.** Patte natatoire 2. **B.** Patte natatoire 3. **C.** Patte natatoire 4. ♂ allotype : **D.** Endopodite de la patte 2. *Tisbe gracilis*, ♂ (USNM 170626): **E.** Endopodite de la patte 2.

Antenna (Fig. 3C): small coxa without ornamentation, medial margin of elongate basis with 1 seta and row of denticles. Exopod 4-segmented, segments 1-3 with 1 medial seta with setules; distal segment with 2 rows of denticles and 3 terminal setae. Endopod 2-segmented; proximal segment with 1 medial seta with setules; distal segment with 3 medial setae, 2 of which with articulating plane, and 7 terminal setae with setules, 4 of which with articulating plane.

Mandible (Fig. 3D & E): gnathobase elongate medially with proximal knob, 4 large, multi-cuspid teeth and many unicuspid teeth extending onto a proximal attenuation; basis with 1 row of denticles and 1 small inner seta (arrowed). Exopod 1-segmented with 2 rows of denticles, and 1 medial and 2 terminal setae with setules. Endopod with 2 rows of denticles, and 3 medial setae, 1 with setules, and 6 unarmed terminal setae.

Maxillule (Fig. 4A) coxal endite with 3 sub-terminal and 6 terminal setae and with 4 groups of denticles; basis with denticles and 12 setae.

Maxilla (Fig. 4B) syncoxa with lateral and medial denticles, coxal endite with 2 setae; basis elongate, slightly curved laterally with 2 setae and with apical denticles.

Maxilliped (Fig. 4C) 4-segmented; denticles proximal to coxa; coxa unarmed, with medial denticles; basis unarmed, with medial and lateral denticles. Proximal endopodal segment a complex with 3 short setae anteriorly and 1 long seta medially; distal segment elongate, curved medially at tip with denticles medially.

Swimming legs 1-4 (Figs 4D-G & 5A-C) with 3-segmented rami and complex patterns of denticles. Basis of leg 1 armed with thick, lateral seta and 1 slender, inner seta (Fig. 4G). Distal exopodal segment of leg 1 (Fig. 4E) rounded, with 4 spines and 2 inner setae. Middle endopodal segment of swimming leg 1 with a short inner pinnate seta; distal endopodal segment of leg 1 (Fig. 4F) small, with 2 spines of equal length and 2 small setae, 1 spine ornamented with a patch of spinules. Formula for the armature of swimming legs in Table 2.

Leg 5 (Fig. 6A) baseoendopod fused to 6th thoracic

Table 2. *Tisbe dahmsi* sp. nov. Spine and setal formula of legs 1-4. Roman numerals indicate spines, Arabic numerals, setae.

Tableau 2. *Tisbe dahmsi* sp. nov. Formule des soies et épines des pattes natatoires 1-4. Les chiffres romains indiquent les épines, les chiffres arabes, les soies.

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

somite; lateral basal seta and 3 setae on endopodal projection. Exopod with denticles, and with 2 lateral and 3 terminal setae.

Leg 6 (Fig. 2C) small but ventrally with 3 setae; the median the longest, more than twice the length of the others.

Male. Differs from female as follows:

Body (Figs 6B & 8C-D): total length of allotype male (body plus caudal ramus, excluding caudal setae): 0.80 mm, greatest width: 0.27 mm. Urosome (Fig. 6C & D) 6-segmented: genital somite and first abdominal somite separate. Spermatophore (Fig. 6B) ovoid visible inside genital somite.

Antennule (Fig. 7A-B) 10-segmented; formula of setation as follows: 1, 14, 7 + aesthetasc, 2, 7 + aesthetasc, 1, 2, 1, 4, 7+aesthetasc, geniculation between segments 7 and 8.

Antenna, mandible, maxillule and swimming legs 1, 3, 4 similar to female.

Maxilla (Fig. 7C) slightly curved and slightly re-curved at extremity.

Maxilliped (Fig. 7D & E): coxa, with denticles, not articulated proximally; basis wider than long. Distal endopodal segment with knob-like attenuation medially.

Leg 2 (Fig. 5D): medial seta on proximal endopodal segment spine-like and terminally bifurcate; long setules medially and short setules laterally.

Leg 5 (Fig. 6E): baseoendopod with 2 endopodal setae. Exopod broader and different in shape than in female, almost rounded, without denticles on surface.

Leg 6 (Fig. 6C): a genital flap, with 1 short, inner, thick spine-like seta with short setules, and 2 setae longer, than spine-like seta, without setules.

Taxonomical remarks

Tisbe dahmsi sp. nov. belongs to the *T. gracilis* group in showing the following characters in the female: it lacks a tubercle on the inner margin of the exopod of leg 5, the maxilliped lacks setae with an articulating plane, and the two longest setae on the distal endopodal segment of swimming leg 1 are similar in size but different in morphology (Volkman, 1979). Among the nine species of the *T. gracilis* group (*T. acanthifera* Vervoort, 1962, *T. biminiensis* Volkman-Rocco, 1973, *T. cucumariae* Humes, 1957, *T. denticulata* Volkman, 1979, *T. gigantea* Volkman, 1979, *T. gracilis* (T. Scott, 1895), *T. maraensis* Volkman, 1979, *T. monozota* Bowman, 1962, and *T. pori* Betouhim-El & Kahan, 1972), *T. dahmsi* is most similar to *T. gracilis* based on the spine-like, inner seta on the proximal endopodal segment of the male second swimming leg, which in both species is terminally bifurcate. In *T. dahmsi*, this seta tapers uniformly to a slight curve towards the tip; in *T. gracilis*, the base of the seta is broad, the width

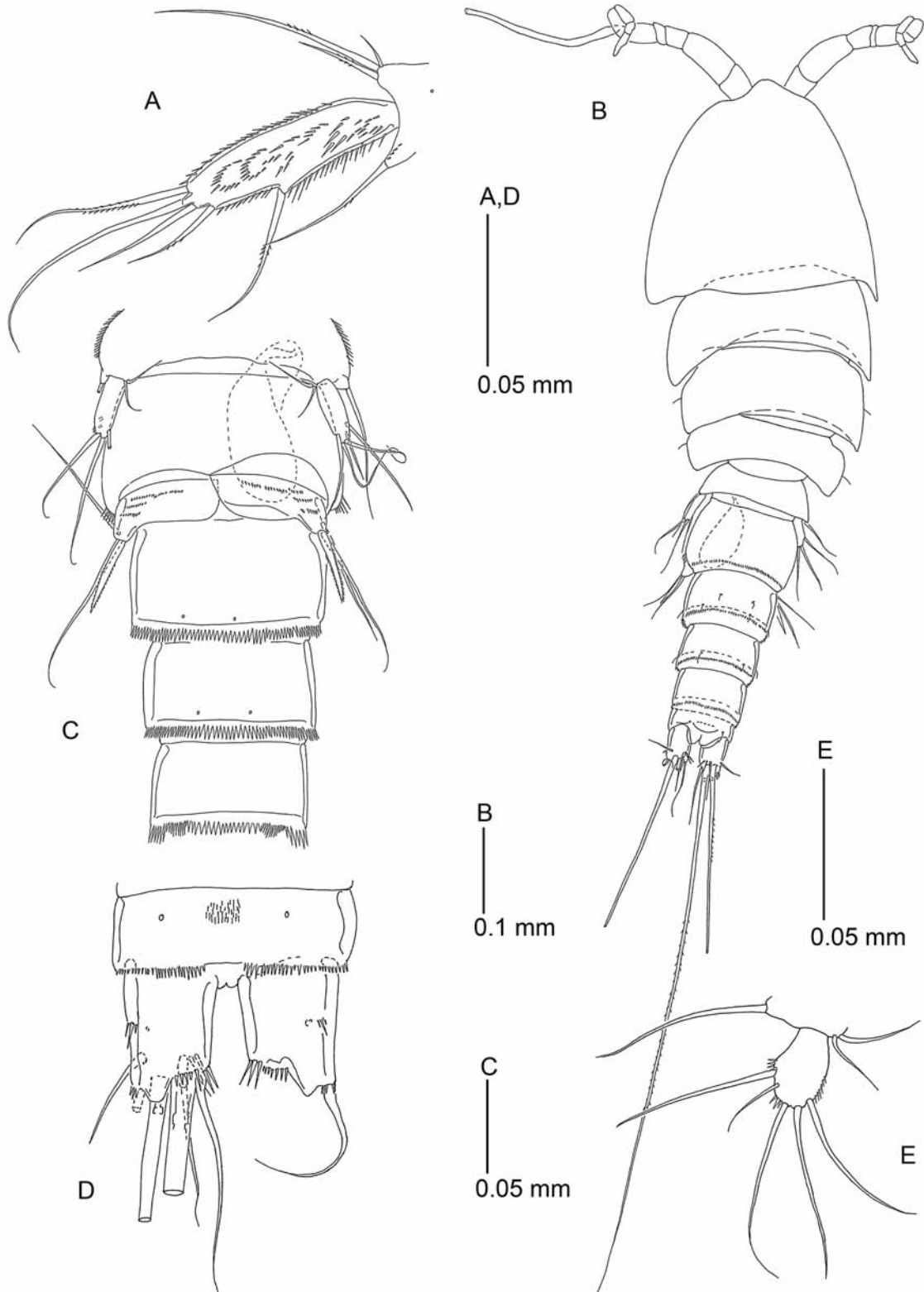


Figure 6. *Tisbe dahmsi* sp. nov. **A.** Leg 5, ♀ holotype. **B.** Habitus of ♂ allotype, dorsal. **C.** Urosome (anal somite and caudal rami not shown), ventral, ♂ allotype. **D.** Anal somite and caudal rami, ventral, ♂ allotype. **E.** Leg 5, ♂ allotype.

Figure 6. *Tisbe dahmsi* sp. nov. **A.** Leg 5, ♀ holotype. **B.** Habitus du ♂ allotype, dorsal. **C.** Urosome (somite anal et rames furcales non dessinées), ventral, ♂ allotype. **D.** Somite anal et rames furcales, ventral, ♂ allotype. **E.** Patte 5, ♂ allotype.

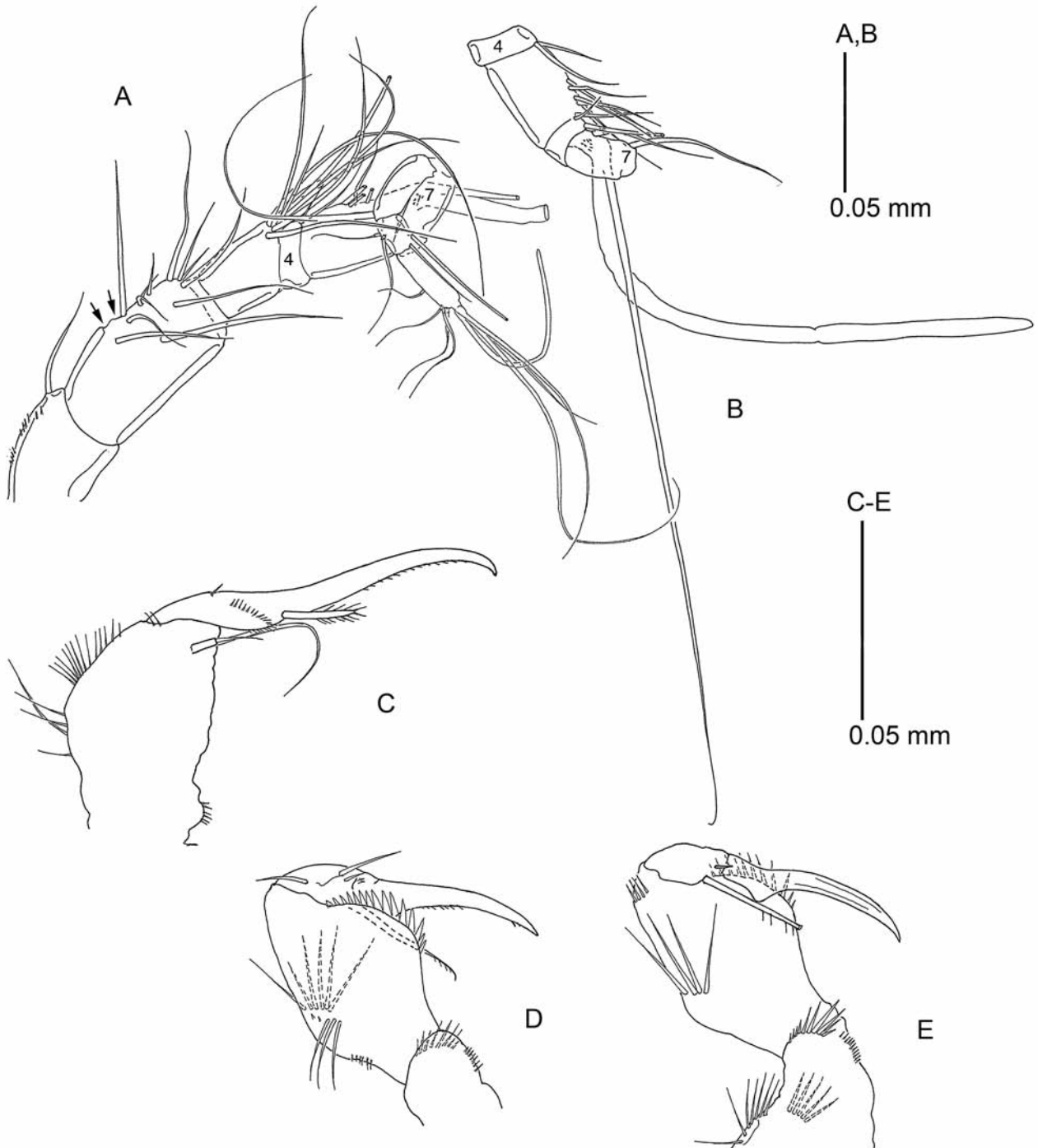


Figure 7. *Tisbe dahmsi* sp. nov., ♂ allotype: **A.** Antennule, insertion places of lost setae arrowed (4, 7 - articulating segment 4 and 7). **B.** Part of antennule (4, 7 - articulating segment 4 and 7). **C.** Maxilla. **D-E.** Maxilliped.

Figure 7. *Tisbe dahmsi* sp. nov., ♂ allotype : **A.** Antennule, points d'insertion des soies perdues désignées par des flèches ; 4, 7 - segments articulés 4 et 7. **B.** Partie terminale de l'antennule, 4,7 - segments 4 et 7. **C.** Maxille. **D-E.** Maxillipède.

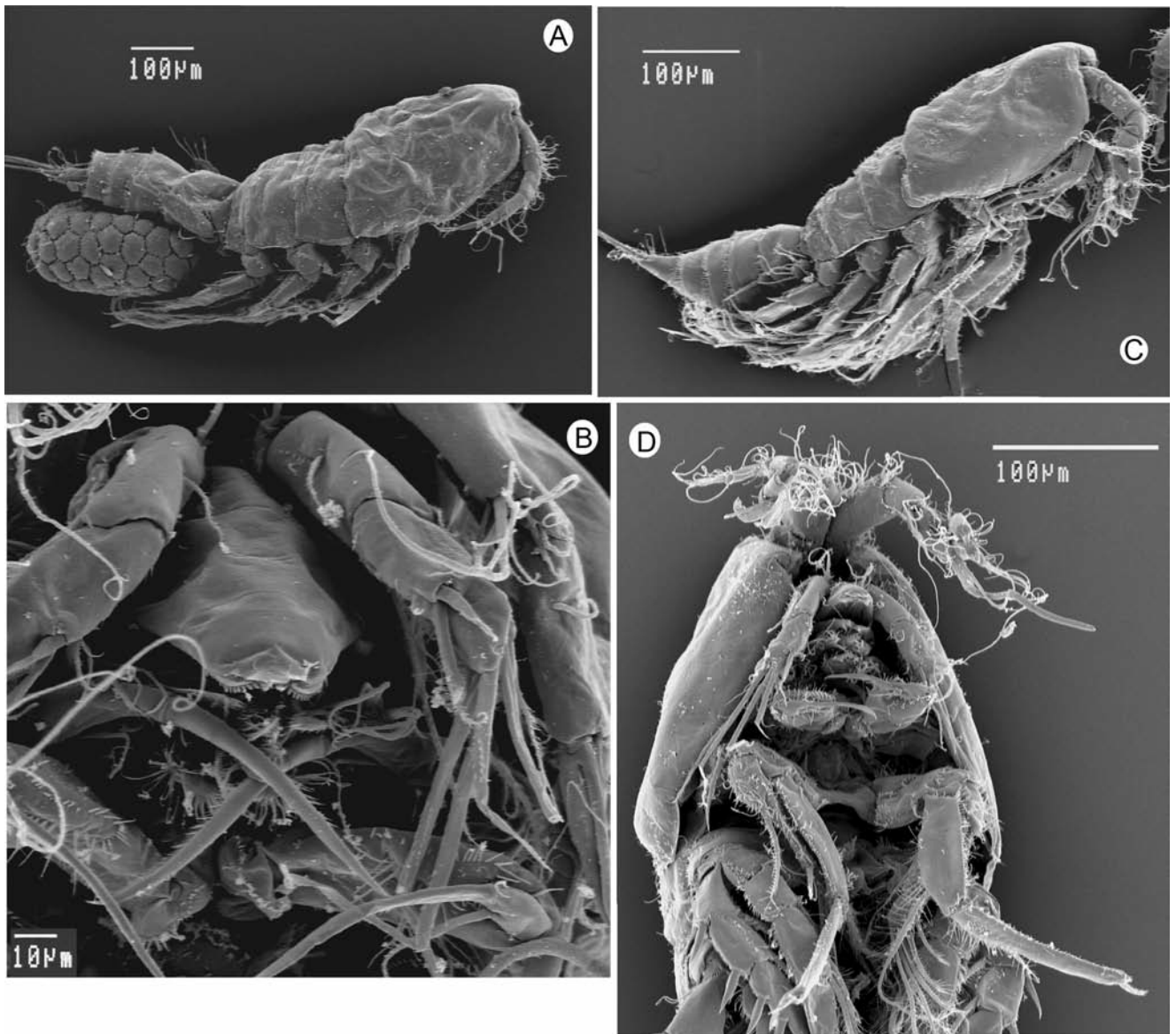


Figure 8. *Tisbe dahmsi* sp. nov., SEM photos. **A.** Habitus, lateral, ♀. **B.** Labrum, antenna, cephalic appendages and maxilliped, ventral, ♀. **C.** Habitus, lateral, ♂. **D.** Labrum and appendages of anterior part of prosome, ventral, ♂.

Figure 8. *Tisbe dahmsi* sp. nov., photos en MEB. **A.** Habitus, latéral, ♀. **B.** Labre, antenne, appendices céphaliques et maxillipèdes, ♀. **C.** Habitus, latéral, ♂. **D.** Labre et appendices de la partie antérieure du prosome, ventral, ♂.

tapers and then broadens again before tapering to a stronger curve towards the tip (Fig. 5E, USNM 170626, slide with dissected male. Collector: B. Volkmann, locality: Atlantic coast of France). Three more species of *Tisbe* have been referred to the *T. gracilis* group since Volkmann (1979), but all differ from *T. dahmsi* with its short seta on the middle endopodal segment of swimming leg 1. In *T. prolata* Waghorn, 1979, this seta reaches well beyond the distal endopodal segment, although Bradford & Wells (1983) showed this seta as reaching only to the distal border of the middle segment (the male is unknown) (Waghorn, 1979;

Bradford & Wells, 1983). In *T. japonica* Ho, 1982, the proximal endopodal segment of swimming leg 1 is incised and the seta on the middle segment reaches the distal border of that segment (Ho, 1982). Furthermore, the morphology of the setules on the spine-like, inner seta of the proximal endopodal segment of male swimming leg 2 appears to be different. In *T. spinulosa* Bradford & Wells, 1983, the seta on the middle endopodal segment of female swimming leg 1 reaches well beyond the distal endopodal segment, and the spine-like, inner seta of the proximal endopodal segment of male swimming leg 2 is not bifurcate at its tip.

Table 3. Relative abundance (%) of different copepod families from three *in situ* colonization experiments (SMAC A, B and C) deployed in 1997 and recovered in 1998 on the Tour Eiffel hydrothermal edifice. Highest values are highlighted in bold.

Tableau 3. Abondance relative (%) des différentes familles de copépodes dans les trois expériences de colonisation (SMAC A, B et C) déployées en 1997 et récupérées en 1998 sur le site hydrothermal Tour Eiffel. Les valeurs les plus élevées sont en gras.

Colonization experiment	A1	A2	A3	A4	B9	B10	B11	B12	C5	C6	C7	C8
Ameiridae-Argestidae	0.67	0.00	0.00	0.00	1.45	0.00	0.51	0.00	76.92	58.00	0.00	0.00
Calanoïd	0.00	0.00	0.00	0.00	0.00	8.33	1.03	0.00	13.46	6.00	0.00	6.67
Cyclopinidae - <i>Heptmerina confusa</i>	79.87	29.12	28.18	7.14	34.78	16.67	25.64	0.00	0.00	6.00	8.33	0.00
Dirivultidae - <i>Aphotopontius atlanteus</i>	0.00	0.55	0.00	0.00	0.00	0.00	1.03	69.57	0.00	0.00	0.00	0.00
Ectinosomatidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.77	16.00	75.00	80.00
Erebonasteridae	2.01	1.65	0.00	0.00	4.35	0.00	1.03	0.00	0.00	0.00	0.00	0.00
Miraciidae	4.70	0.00	0.00	0.00	7.25	0.00	3.08	0.00	0.00	2.00	16.67	13.33
Tegastidae - <i>Smacigastes micheli</i>	7.38	63.19	29.09	10.71	11.59	33.33	26.15	8.70	0.00	0.00	0.00	0.00
Thalestridae	0.00	1.10	0.00	0.00	21.74	0.00	2.56	0.00	0.00	0.00	0.00	0.00
Tisbidae (<i>Tisbe</i> spp.)	5.37	4.40	42.73	82.14	18.84	41.67	38.97	21.74	3.85	12.00	0.00	0.00

Distribution and microhabitats

The *in situ* colonization experiments revealed a diversity of copepods that were unknown before for the LS and other hydrothermal vents at the MAR. Overall, the copepods found in the arrays belong to 10 families (see Table 3). In SMAC A, copepods of 8 families are represented, in SMAC B, 9 families were recovered, while only 6 were present in SMAC C. The Cyclopinidae, Tegastidae and Tisbidae dominated in SMAC A, with one species for each of the first two families and two species for Tisbidae. In SMAC B, representatives of five families were alternatively more abundant, while in SMAC C, copepods of three families of harpacticoid copepods alternatively dominated the samples, the Ameiridae, Argestidae and Ectinosomatidae. The genus *Tisbe* (Tisbidae) (represented by 2 species) was much more abundant in SMAC A (362 individuals) and B (99 individuals) than in SMAC C (10 individuals, Table 3). A similar pattern is also observed with the overall number of copepod individuals found within each array (805 for SMAC A, 299 for SMAC B and 181 for SMAC C). It seems that the type of environment where the arrays were deployed have a stronger influence on copepod abundances than the treatment applied within each tray. Thus, the vicinity of the black smoker significantly affected not only the structure of the copepod community, but also their overall abundance.

Arrays SMAC A and B were deployed on the top of *Bathymodiolus azoricus* mussel assemblages, with temperatures ranging from 5 to 13°C (Table 1). Copepod diversity and density may have been favored by the presence of the mussels which provide food resources as well as shelter for smaller organisms (Comtet & Desbruyères, 1998). On the other hand, the conditions found in the vicinity of SMAC C were maybe too harsh for certain copepod families, which would explain their low diversity and low abundance. In two colonization experiments, the addition of organic supplements led to a decrease in the number of copepod

families in comparison to the trays with only the beads (from 6 to 3 in SMAC A and from 4 to 3 in SMAC C), maybe due to an increase of interspecific competition, leading to the dominance of certain species (Table 3). In fact, in SMAC A and B, Tisbidae were more abundant in the trays bathed with H₂S or native sulfur and in those enriched with organic matter (Table 3), indicating a strong response of this family, enhanced food sources. A different pattern is observed in SMAC C, where only the tray enriched with H₂S exhibited highest abundances of *Tisbe* (Table 3). These chemicals may favour the presence of microbial chemosynthetic communities that may be directly grazed upon by the copepods (De Busserolles et al., 2009).

Among the 12 microhabitats sampled (C1-C12) during the MoMARETO cruise in 2006, a total of 12 copepod families were identified from the 250 µm fraction, while copepods of 14 families (including a number of naupliar stages and families previously unknown from deep-sea hydrothermal communities) were represented in the 63 µm fraction (Sarrazin et al. in preparation). A total of 10 families were present in both fractions. These assemblages were alternatively dominated by Dirivultidae or Tegastidae, the former being dominant in 67% of the samples. Seven of the twelve microhabitats sampled harboured *Tisbe* spp. copepods in different developmental stages (Table 4a & b), but only four of them had adult stages (Table 4a: C3, C4, C5 and C10). A total of nine copepod families were present in microhabitats colonized by *Tisbe* (Table 4a & b). Contrarily to what was found in the colonization experiment, Tisbidae was never dominant, reaching a maximum of 33.3% of relative abundance in C10 (Table 4a). It is interesting to note that juveniles of all copepod families were found within the different microhabitats (Table 4a & b), suggesting ongoing recruitment at the time of sampling.

Concerning environmental conditions, *Tisbe dahmsi* sp. nov. was found in *B. azoricus* microhabitats characterized by

Table 4a. Copepod relative abundance (fraction > 250 μm) in sampling units C3, C4, C5 and C10, taken within different *Bathymodiolus azoricus* mussel assemblages on the Tour Eiffel edifice during the MoMARETO cruise in 2006. Only the sampling units containing Tisbidae are presented. Highest values are highlighted in bold.

Tableau 4a. Abondance relative des copépodes (fraction > 250 μm) dans les unités d'échantillonnage C3, C4, C5 et C10, recueillis au sein de différents assemblages de modioles *Bathymodiolus azoricus* sur l'édifice hydrothermal Tour Eiffel au cours de la campagne MoMARETO en 2006. Seules, les unités d'échantillonnage contenant des Tisbidae sont présentées. Les valeurs les plus élevées sont indiquées en gras.

Copepod families	C3	C4	C5	C10
Cyclopinidae	6.48	3.23	5.70	0.00
Tegastidae	80.77	50.93	91.45	0.00
Tisbidae	0.03	4.59	0.23	33.33
Dirivultidae	3.40	40.08	0.60	66.67
Miraciidae	9.21	0.68	1.95	0.00
Oithonidae	0.03	0.00	0.00	0.00
Pseudotachidiidae	0.09	0.49	0.00	0.00
Ectinosomatidae	0.00	0.00	0.07	0.00

Table 4b. Presence/absence of different copepod developmental stages (fraction > 63 μm and < 250 μm) in sampling units C4, C5, C6, C7, C8 and C10, taken within different *Bathymodiolus azoricus* mussel assemblages on the Tour Eiffel edifice during the MoMARETO cruise in 2006. Only the sampling units containing Tisbidae are presented. 0 = absent, 1 = present. Copepodids – adult and/or subadult stages.

Tableau 4b. Présence/absence des différents stades de développement des copépodes (fraction > 63 μm et < 250 μm) dans les échantillons C4, C5, C6, C7, C8 et C10, recueillis dans différents assemblages de modioles *Bathymodiolus azoricus* sur l'édifice Tour Eiffel au cours de la campagne MoMARETO en 2006. Seuls les échantillons contenant des Tisbidae sont présentés. 0 = absent, 1 = présent. Copépodites – adultes et/ou stades sub-adultes.

Copepod families	C4	C5	C6	C7	C8	C10
Tegastidae (copepodids)	1	1	1	1	1	1
Tegastidae (nauplii)	1	1	1	0	0	0
Tisbidae (copepodids)	1	1	1	1	1	1
Dirivultidae (copepodids)	1	1	1	1	1	1
Dirivultidae (nauplii)	1	0	1	0	0	1
Miraciidae (copepodids)	1	1	1	0	0	0
Miraciidae (nauplii)	1	1	1	1	0	1
Oithonidae	0	0	0	0	0	0
Pseudotachidiidae (copepodids)	1	1	1	1	0	1
Pseudotachidiidae (nauplii)	0	0	0	0	0	1
Calanoida (copepodids)	0	0	0	0	0	1
Ectinosomatidae (copepodids)	0	1	0	0	0	0
Ancorabolidae (copepodids)	1	1	0	0	0	1
Canthocamptidae (copepodids)	1	0	1	0	0	1
Canthocamptidae (nauplii)	1	1	1	1	0	0
Fam sp. gen sp. (copepodids)	0	0	0	0	1	0
Fam sp. gen sp. (nauplii)	1	1	1	1	1	1

low temperatures (< 8.79°C) and by hydrothermal inputs varying approximately between 0.22 and 1.38% (Table 5). The relative abundance of adult tisbids was higher at higher temperature as well as at higher concentrations of sulfide and iron and at lower pH (Tables 4a & 5, Fig. 9). Compared to the overall data set (Sarrazin et al., in prep.), the tisbids were found in the *Bathymodiolus* microhabitats characterized by intermediate to higher hydrothermal influence (Table 5 & Fig. 9, from De Busserolles et al., 2009).

Conclusions

The systematic sampling done during MoMARETO revealed a diverse fauna of copepods and showed that 70% of the copepod families found within the colonization experiments were also present in the Eiffel Tower mussel assemblages (Tables 3 & 4), which probably indicate that most of them are somehow linked to the hydrothermal ecosystem. The harpacticoid copepod families Ameiridae, Argestidae, and Thalestridae (only found within the colonization experiments), as well as representatives of the family Ectinosomatidae, include species that are common members of the deep-sea abyssal fauna (Rose et al., 2005).

The presence of certain copepod families (such as Ectinosomatidae and Oithonidae) in the Tour Eiffel samples is probably due to contamination by background benthic and epibenthic fauna as shown by the low number of individuals collected ($n = 3$) (Rose et al., 2005; Ivanenko & Defaye, 2006; Ivanenko et al., 2007). Poecilostomatoid copepods of the family Erebonasteridae found in the LS are known from different deep-sea chemosynthetic environments and are considered as possible ectoparasites of bivalves and other invertebrates (Ivanenko et al., 2005). A high abundance of a species of *Tisbe* has recently been recorded at the Håkon Mosby Mud Volcano, feeding on methanotrophic bacteria (Van Gaever et al., 2009). Their presence in cold-seep ecosystems rises questions about their ecological and taxonomical similarity with the species found in our hydrothermal vent samples. The remarkable ecological plasticity and morphological diversity of shallow-water copepods of the genus *Tisbe* as well as the difficulties to establish relationships with ecological and taxonomical data, limit comparative analysis of deep- and shallow-water copepods of this genus (Vanden Berghe & Bergmans, 1981; Hockin, 1983; Warwick, 1987; Gómez et al., 2004; Wells, 2007).

Table 5. Mean environmental conditions in the seven sampled microhabitats containing Tisbidae specimens on the Tour Eiffel edifice. The sampling units containing only adults are highlighted in grey. Juveniles (nauplii and copepodids) were found in all sampling units except C3. Standard deviations are given in parentheses. TdS: total dissolved sulfide, TdFe: total dissolved iron, TdCu: total dissolved copper. Adapted from De Busseroles et al., 2009 and Sarradin et al., 2009.

Tableau 5. Conditions environnementales moyennes dans les sept microhabitats échantillonnés sur l'édifice Tour Eiffel et contenant des spécimens de Tisbidae. Les échantillons contenant seulement des adultes sont surlignés en gris. Les juvéniles (nauplies et copépodites) ont été trouvés dans tous les échantillons sauf C3. Les écarts types figurent entre parenthèses. TdS: sulfures dissous totaux, TdFe: fer total dissous, TdCu: cuivre total dissous. Adapté de De Busseroles et al., 2009 et Sarradin et al., 2009.

	T°C	pH	TdS $\mu\text{mol L}^{-1}$	TdFe $\mu\text{mol L}^{-1}$	TdCu $\mu\text{mol L}^{-1}$	Estimated fluid input %
C3	5.35 (0.50)	6.72 (0.20)	3.36 (1.76)	0.36 (0.19)	1.36 (0.21)	0.30
C4	5.67 (0.50)	6.61 (0.09)	6.07 (4.37)	1.69 (0.77)	2.06 (1.29)	0.40
C5	5.11 (0.48)	6.87 (0.10)	1.85 (0.87)	0.14 (0.20)	0.80 (0.42)	0.22
C6	6.04 (0.42)	6.43 (0.04)	7.51 (2.94)	0.39 (0.25)	0.67 (0.43)	0.52
C7	5.55 (0.28)	6.55 (0.04)	6.35 (2.83)	0.41 (0.12)	1.60 (0.06)	0.36
C8	7.49 (1.54)	6.02 (0.38)	33.41 (10.41)	3.53 (2.67)	1.62 (1.96)	0.57
C10	8.79 (2.71)	5.99 (0.38)	34.94 (21.94)	5.25 (3.60)	0.46 (0.65)	1.38

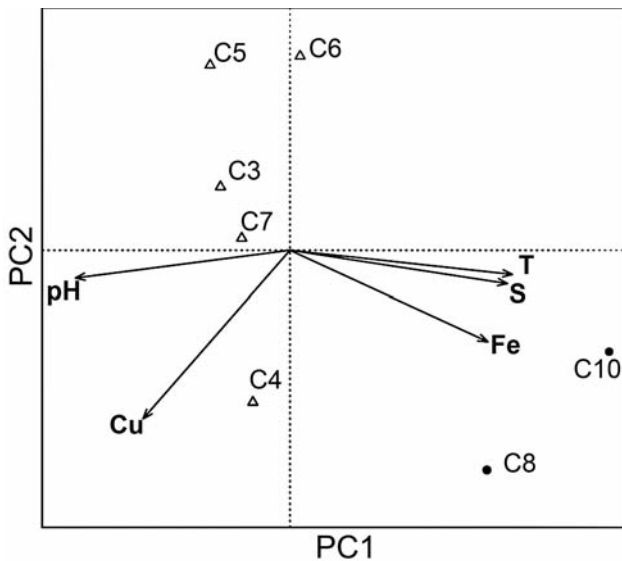


Figure 9. First two principal axes of a Principal Component Analysis (PCA) of mean environmental conditions at each of the 12 sampling units on the Eiffel Tower edifice and representing 95.25% of the total variance (PC1: 79.99%; PC2: 15.26%; Type II scaling). Symbols assign sampling units to one of three groups obtained from k-means partitioning. All variables were standardized prior to analyses. Modified from De Busseroles et al. (2009).

Figure 9. Premiers deux axes principaux d'une Analyse en Composante Principale (ACP) des conditions environnementales moyennes de chacune des 12 unités d'échantillonnage de l'édifice hydrothermal Tour Eiffel et représentant 95,25% de la variance totale (PC1: 79,99%; PC2: 15,26%; mise à l'échelle de type II). Les symboles assignent les unités d'échantillonnages (échantillons) à l'un des trois groupes obtenus à partir d'un partitionnement par la méthode des centroïdes. Toutes les variables ont été standardisées préalablement aux analyses. Modifié de De Busseroles et al. (2009).

The discovery of several new species, such as the *Tisbe* species described here, and a remarkably high diversity of copepods are a result of the improvement in sampling designs and the increased interest for identification of smaller meiofaunal species. With the exception of a few studies, sampling at vents is often limited to the identification of mega- and macrofaunal species and the meiofauna has often been neglected (Gauthier et al., 2010). It is only recently that the meiofauna has really started to be systematically accounted for in vent ecological studies (Tsurumi et al., 2003, Gollner et al., 2006 & 2007, Copley et al., 2007). Indeed, even if this copepod family Tisbidae was never identified before from the LS field, the MoMARETO cruise, which gave more importance to the systematic approach of organisms, has proven that copepods of the genus *Tisbe* were commonly present on the Tour Eiffel edifice (found in 50% of the samples). Future ecological studies at vents will surely benefit from more systematic, small-scale spatial studies of faunal assemblage composition and our portrait of species diversity for these peculiar ecosystems will probably evolve significantly during the up-coming decade.

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