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Diversity and microhabitat features of crustacean copepods collected in colonization experiments at deep-sea hydrothermal vent field at the Mid-Atlantic Ridge (37°N, Lucky Strike)

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Abstract. Diverse copepods previously unknown were found and described from the Eiffel Tower edifice located in the Lucky Strike vent field (37°N) (Mid-Atlantic Ridge MAR, 1698 m). The copepoda 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 cyclopoid copepod *Heptnerina confusa* Ivanenko & Defaye, 2004 (Cyclopoida: Cyclopinidae), the harpacticoid copepods *Smacigastes micheli* Ivanenko & Defaye, 2004 (Harpacticoida: Tegastidae) and *Tisbe dahmsi* Ivanenko, Ferrari, Defaye, 2011 (Crustacea, Copepoda: Harpacticoida: Tisbidae), and the dirivultid copepod *Aphotopontius atlanteus* Humes, 1996 (Siphonostomatoida: Dirivultidae) were found abundantly in the *in situ* colonization experiments (SMAC arrays) deployed on Bathymodiolus azoricus mussel assemblages at the Eiffel Tower edifice. Another colonization experiment, deployed near a black smoker, exhibits a different pattern with dominance of the harpacticoid families Ameiridae and Argesidae 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 by the Dirivultidae or the Tegastidae, the former being dominant in 67% of the samples.

Keywords: copepods, diversity, microhabitat, deep-sea, hydrothermal vent, Mid-Atlantic Ridge, colonization experiments

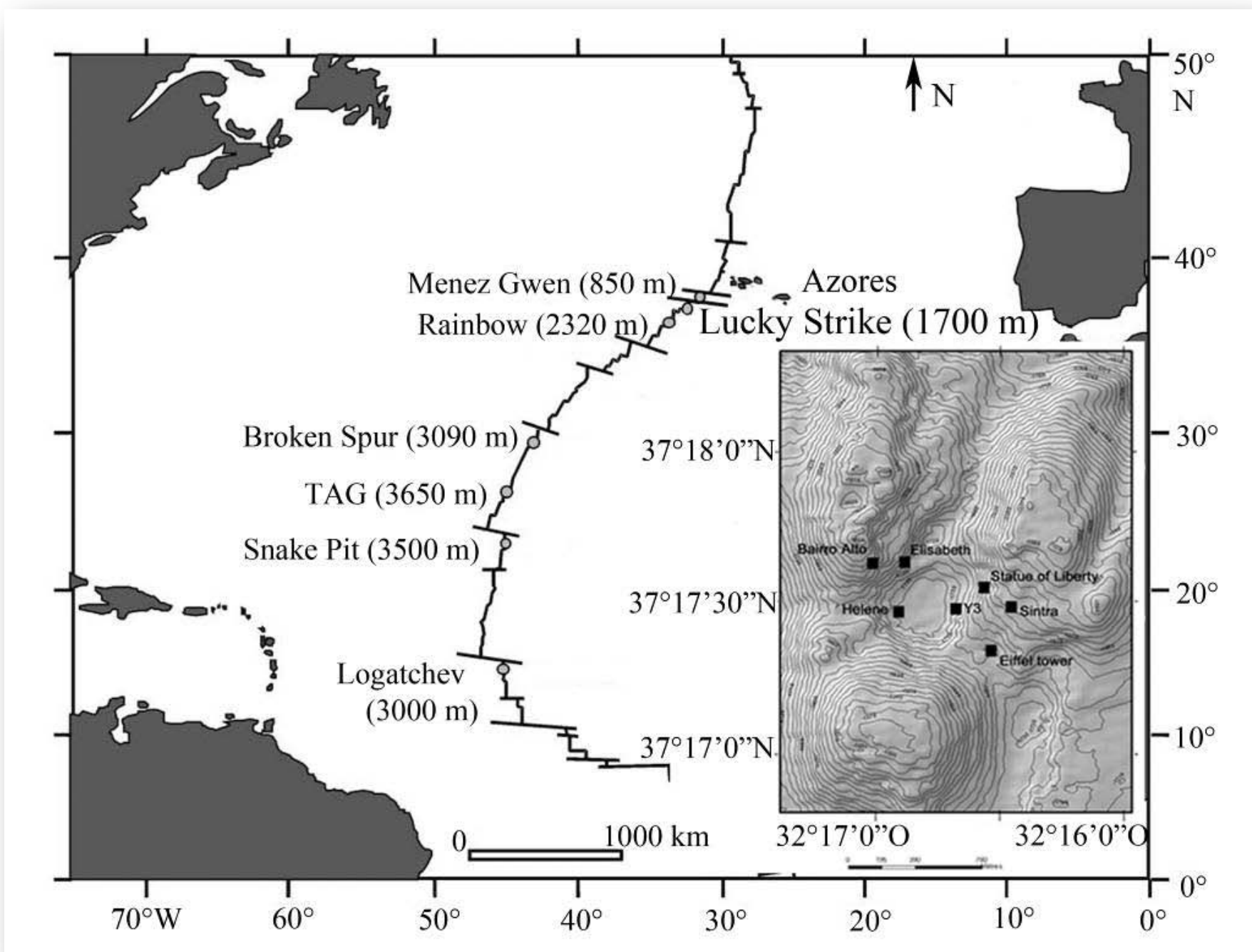
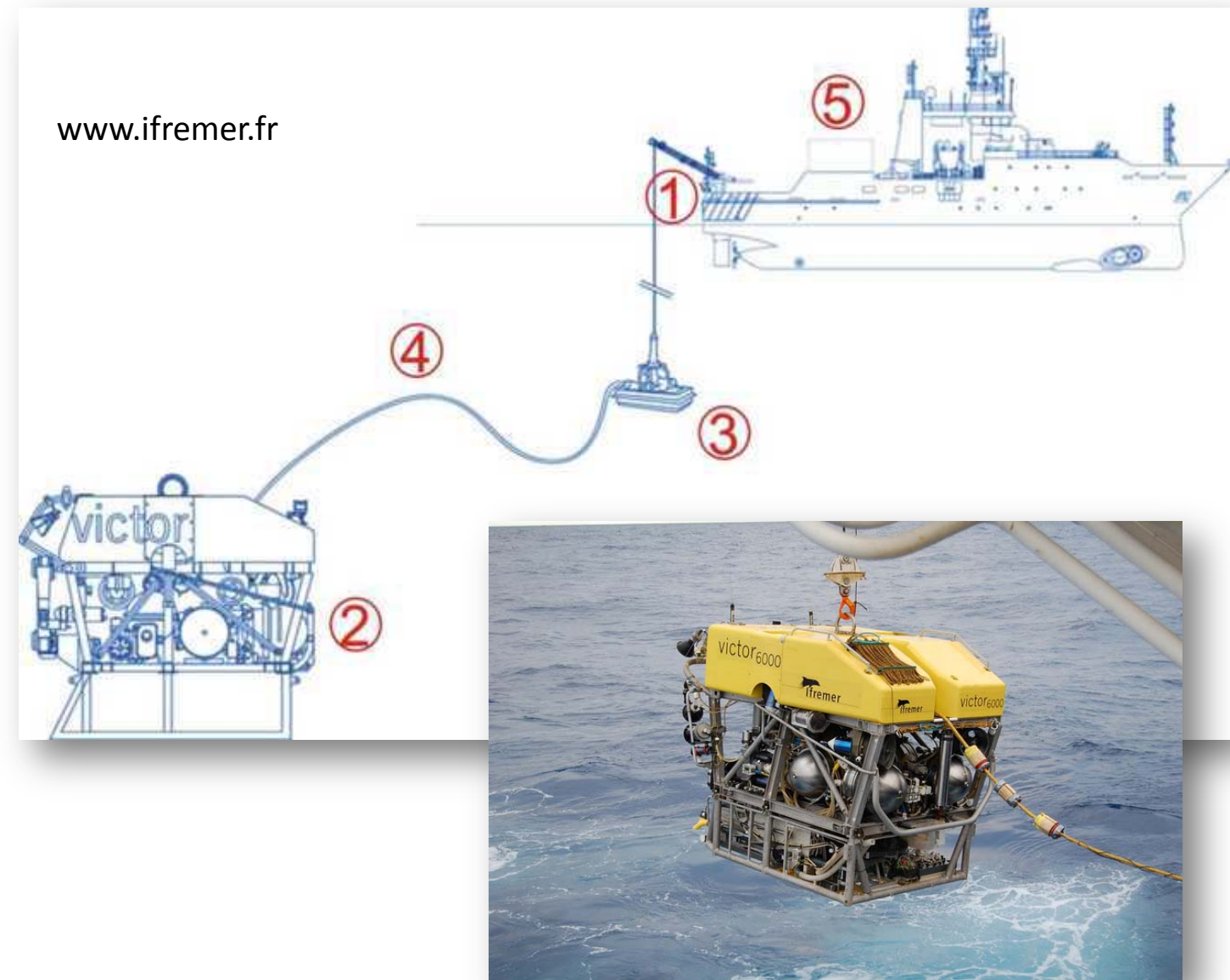


Fig 1. Location of the Lucky Strike vent field on the Mid-Atlantic Ridge (MAR) at 37°17.59N, 32°16.9W. The inset shows the hydrothermal vent field with the localisation of several active sulphide edifices around a central lava lake, including the Eiffel Tower edifice in the south-east. Cuvelier et al 2014



Figs 2-3. The remote controlled vehicle VICTOR 6000 gear includes: A direct-winding hydraulic winch, the 8,500 m 20 mm umbilical, weighing in all: 30 tonnes(1) The vehicle 3.1 x 1.8 x 2.1 m, weight 4 tonnes and 600 kg for the module (2) The hard ballast 1.5 x 0.8 x 0.5 m, weight 1.2 tonne (3) The tether measuring from 100 to 300 m 35 mm (4) 5 20-ft containers (5): vehicle power •winch's hydraulic unit •control room •mechanics •storage

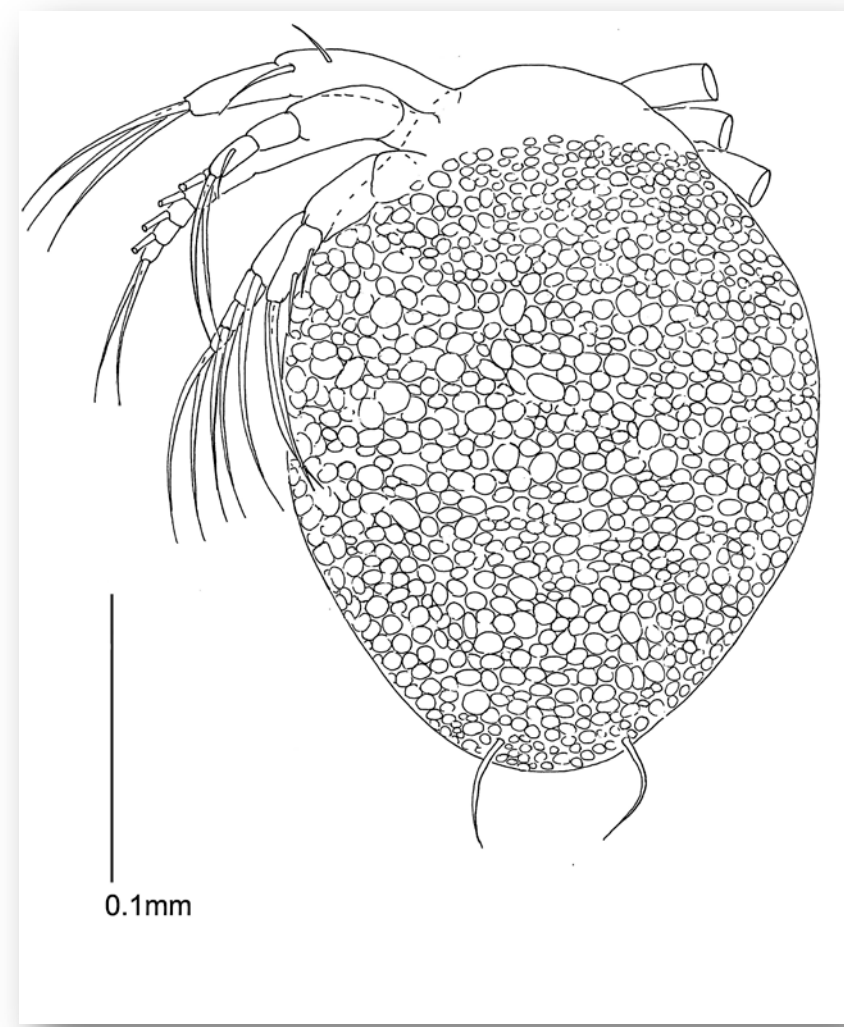


Fig 7. *Stygiopontius pectinatus* Humes, 1987, nauplius of stage I: A, habitus, ventral; B, habitus, lateral, left side; C, antennule, ventral; D, antenna, ventral; E, mandible, dorsal. Ivanenko V.N., P. Martinez Arbizu & J. Stecher. 2007.

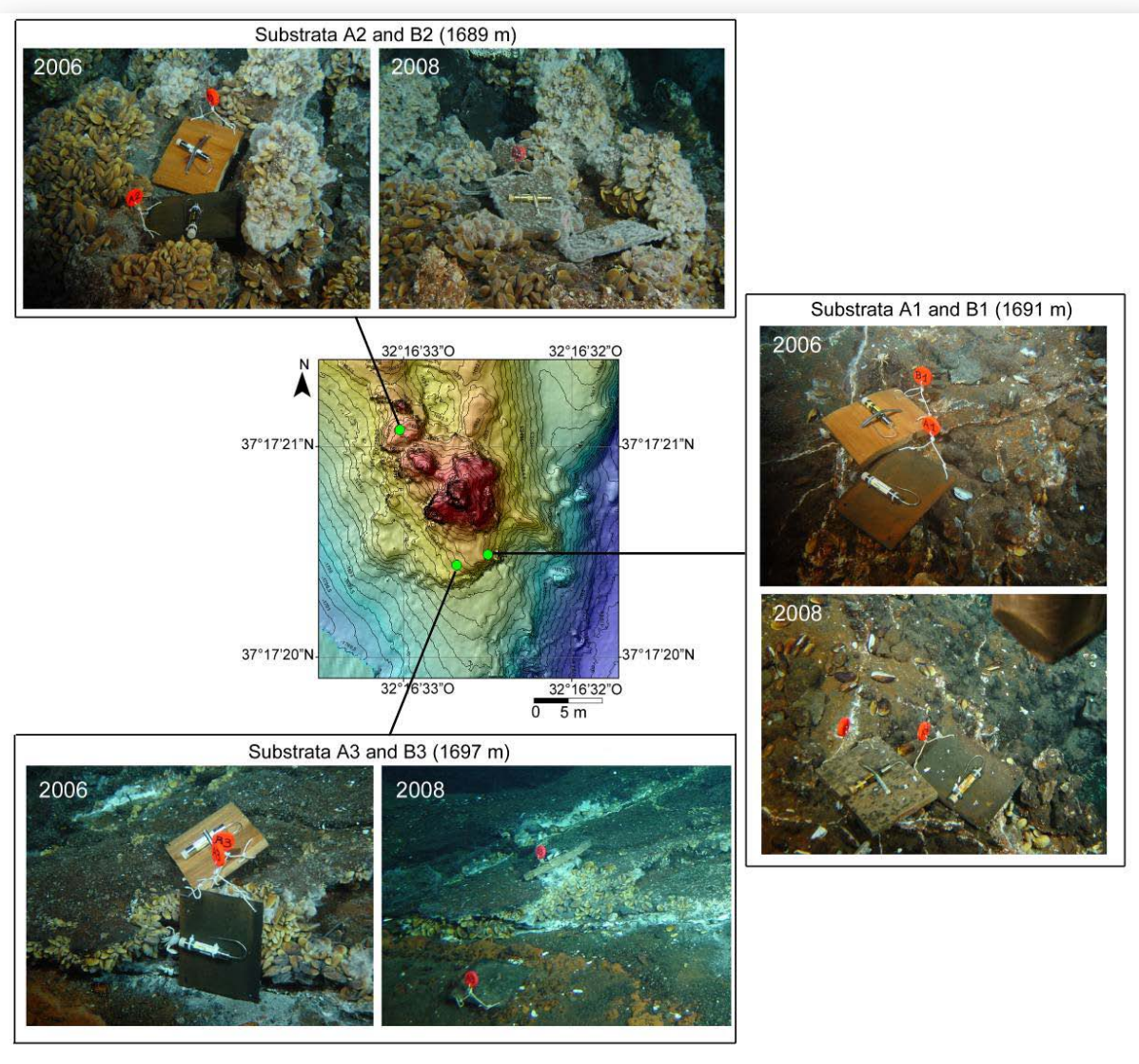


Fig 5. Localisation and depth of the sites at the Eiffel Tower edifice (MAR) at 37°17.59N- 32°16.9W where different substrata were deployed in 2006 and recovered in 2008. On each locality a panel of slate (A) and wood (B), each equipped with a NKE temperature probe, were deployed. Remark the change in localisation of panel A3 in 2008. Cuvelier et al 2014

Results

Copepods from diverse families (Aegisthidae, Ancorabolidae, Canthocamptidae, Cyclopinidae, Dirivultidae, Ectinosomatidae, Lubbockiidae, Miracidae, Oncaeidae, Oithonidae, Pseudotachidiidae, Spinocalanoida, Tegastidae, and Tisbidae), mostly unrecorded for the LS vent field, were found in the 250 µm and 63 µm fractions, while morphologically diverse nauplii were represented mainly in the 63 µm fractions (Figs 6-13).

Physico-chemical characterization of *S. micheli* microhabitats
Mean temperatures conditions on each sampling unit (microhabitat) varied from 4.79°C to 8.79°C, which represents a relatively narrow temperature range for this ecosystem (De Busslerolles et al. 2009). The microhabitats with the warmest temperature values (C2, C8 and C10) also had the highest concentrations of TdFe and TdS. On the other hand, the coolest location C9 had one of the lowest TdS and TdFe concentrations and the highest TdCu concentration. The mean temperatures were near ambient (4.4°C) in C1, C9, C11 and C12. All environmental variables were significantly correlated with temperature but while sulfide and iron concentrations were positively correlated, TdCu and pH showed negative correlations with temperature (De Busslerolles et al. 2009). The pH varied from 6.00 (C10) to 7.34 (C9), being more acidic in the areas of higher hydrothermal influence. Overall, the microhabitats colonized by *S. micheli* were characterized by relatively low temperatures (4.8 to 7.5°C) that represent low hydrothermal inputs. All developmental stages were absent from the most extreme microhabitat (C10) and tegastid abundance was low in the two other hotter microhabitats sampled (C8 and C2). No tegastid copepods were found in C7 despite the presence of intermediate physico-chemical conditions. The faunal and environmental data were transformed prior to a multivariate statistical analysis. Faunal abundance data were transformed to conserve Hellinger, rather than Euclidian, distances in Principle Component Analysis (Legendre & Gallagher 2001). The Hellinger distance gives low weight to rare taxa. This distance is used because in the deep-sea the sporadic appearance of rare taxa in the samples can be attributable to sampling error (Gauthier et al. 2010). The environmental variables were standardized because they are measured in different sampling units and must be reduced to a common scale to calculate meaningful covariance. The procedure consists in centring all descriptors on a zero mean and reducing them to unit standard deviation (Legendre & Legendre 1998). The redundancy analysis (RDA) performed on *S. micheli* abundances from all microhabitats explained 31% of the variance in distribution. An analysis of variance testing for significance of the RDA showed that only the first axis was significant (F=4.6736, p=0.01667, α<0.05) while the second, explaining 10 % of the variance, was not (F=1.5423, p=0.29000, α>0.1). Only three of the five environmental variables tested (TdS, TdCu and T°C) significantly explained the copepod distribution. TdS is the more significant (p<0.015), followed by TdCu (p=0.146) and then, T°C (p=0.434). TdFe and pH were not significant. Fig 14.

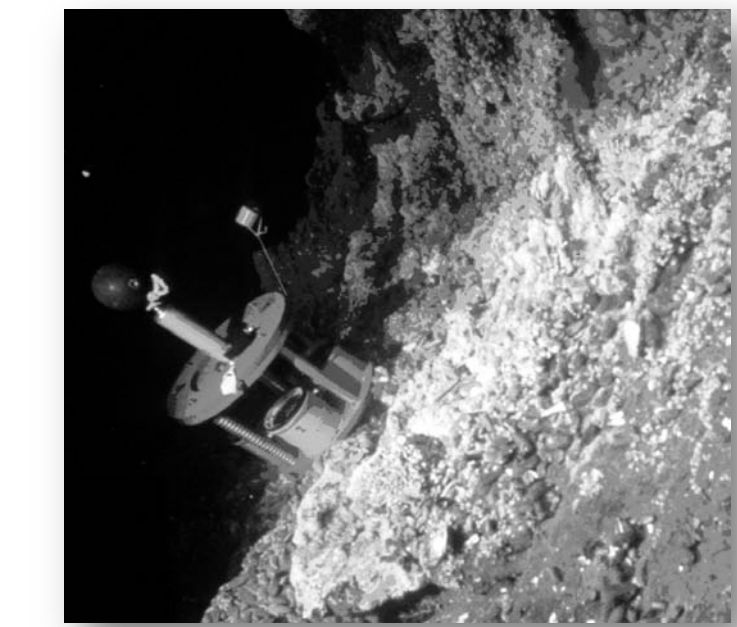


Fig 4. Colonization experiment on the Eiffel Tower edifice of the Lucky Strike vent field. Ivanenko et al. 2011

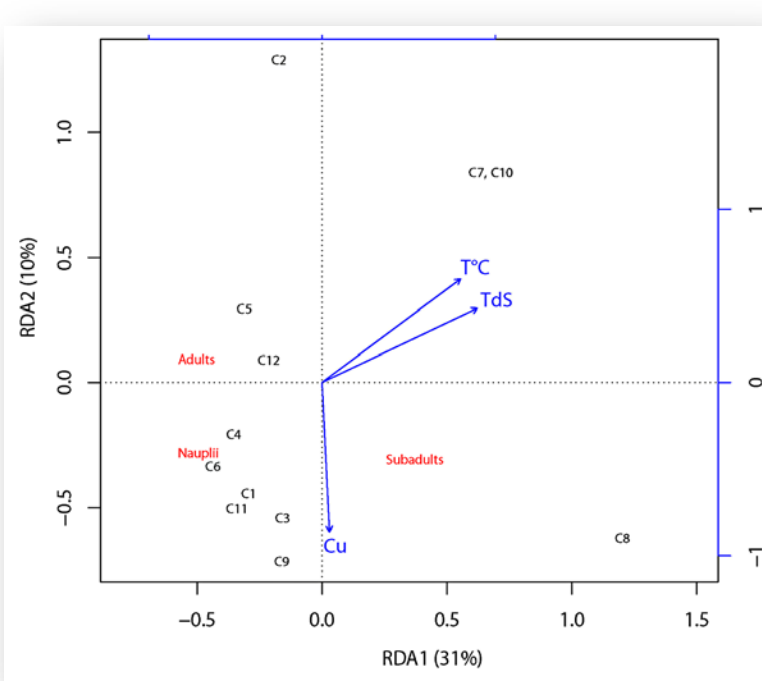


Fig 14. Redundancy analysis (RDA, scaling type 2) performed on the matrix of *Smacigastes micheli* Ivanenko and Defaye 2004 abundances of the different developmental stages (nauplii, subadults, adults) sampled on the Eiffel Tower edifice and the matrix of environmental factors. The first two axes represent 40% of the total variance but only the first axis, explaining 31% of the variance, was significant. Vectors are represented by arrows.

Discussion

This is the first report of abundant and diverse nauplii of copepods in a deep-sea hydrothermal community. Up to now, copepod nauplii were not hypothesized to be living in the extreme conditions (high levels of sulfides, heavy metals and elevated temperatures) present in the vent environment (Tsurumi et al. 2003). Only a few studies report the presence of nauplii (Dinet et al. 1988), and only the leithotrophic nauplius I of a siphonostomatoid copepod from the family Dirivultidae has been positively identified (Ivanenko et al. 2007). In the Eiffel Tower samples, nauplii belonging to the harpacticoid copepod families Canthocamptidae, Pseudotachidiidae, Miracidae, and Tegastidae, as well as nauplii which could not be attributed to a family, were identified. The discovery of several new species 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). 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. In terms of their habitats, the statistical analysis (RDA) showed that the relative abundances of nauplii and adults of *S. micheli* were higher in the microhabitats characterized by the lowest TdS and lowest T°C conditions while the abundance of the subadult stages appears to be linked to slightly higher hydrothermal inputs. This confirms our initial hypothesis concerning the existence of separated environmental niches for the various developmental stages. Whether this distribution is due to differential physiological tolerances, to resource competition between juvenile copepodids and adults, or to different nutritional needs of the different developmental stages is unknown. Presence of nauplii in the mildest microhabitats with the adults may simply result from the fact that nauplii were recently hatched. On the other hand, it is also possible that both the nauplii and adults share the same microhabitat, with different nutritional niches. The separation of adults and subadults in areas of differing hydrothermal input/ higher microbial resource areas may result from differing nutritional requirements. More generally, it seems that copepod diversity is strongly influenced by environmental conditions at vents and that areas with lower hydrothermal influence (lower temperatures, lower concentrations of TdS) harbour a higher diversity (Tsurumi et al. 2003; Zekely et al. 2006; Gollner et al. 2010).

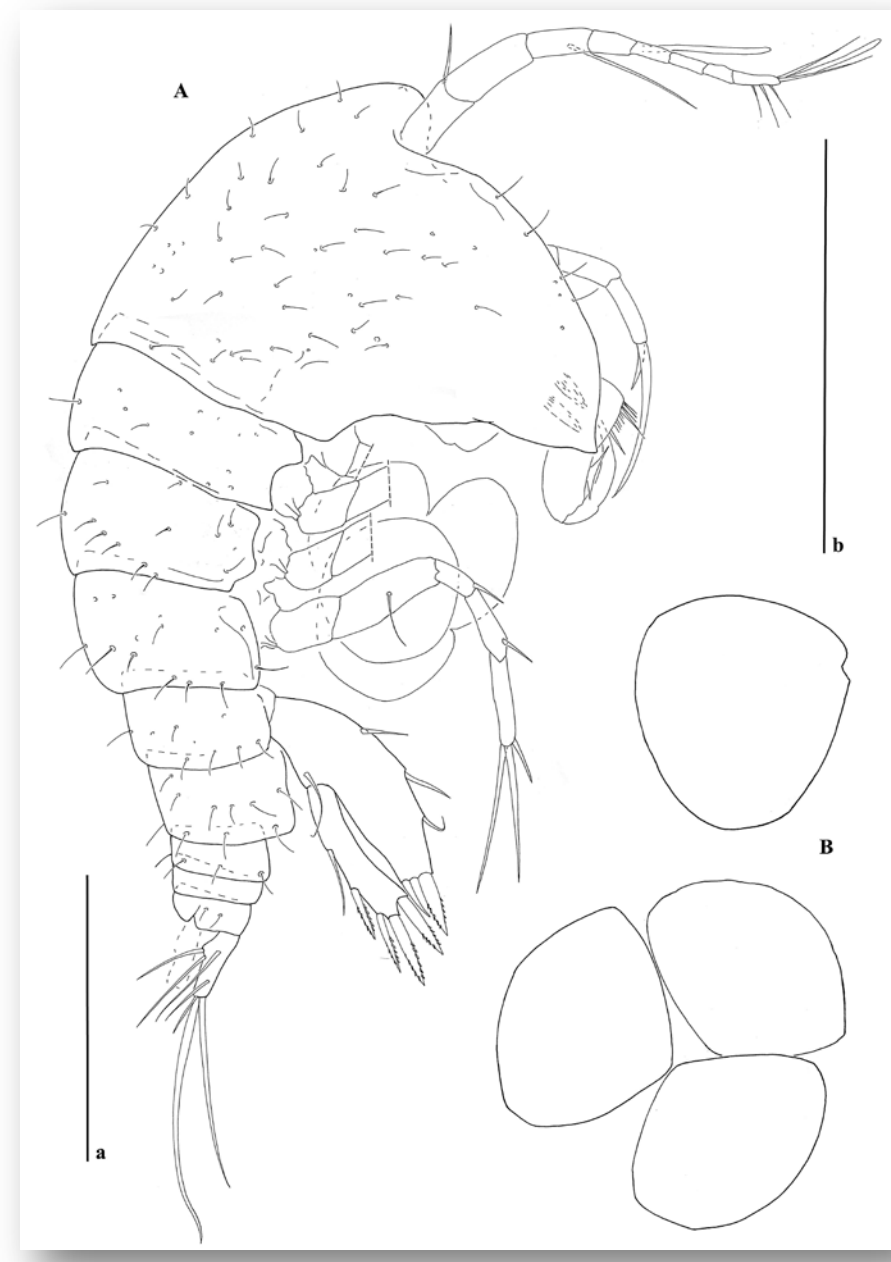


Fig 11. *Smacigastes micheli* Ivanenko & Defaye, 2004 holotype ♀; A, habitus, vue latérale; B, oeufs. Echelles: a, b- 0.2 mm.



Fig 12. *Smacigastes micheli* Ivanenko & Defaye, 2004. Confocal photo of premolting stage VI nauplius. (A) Habitus, ventral. (B) Habitus, dorsal.

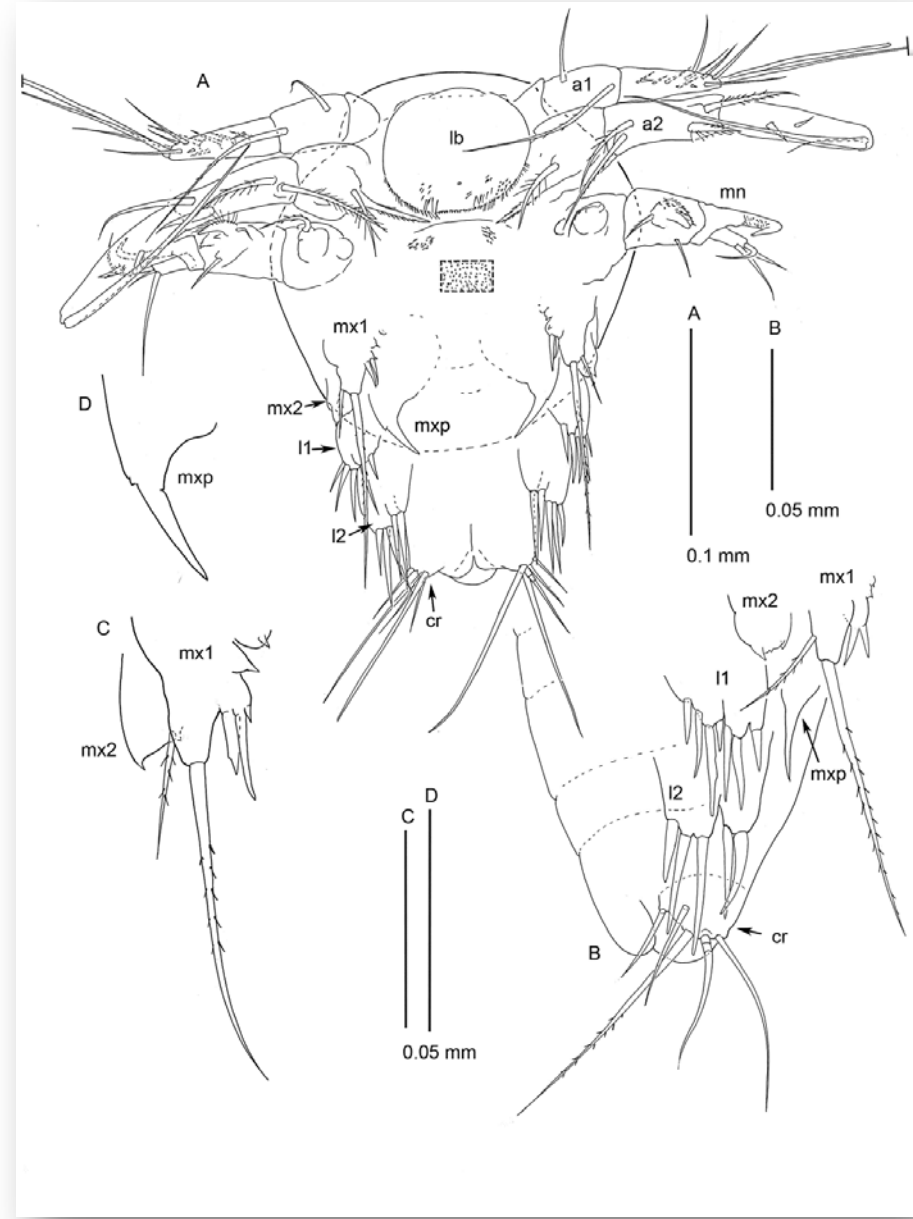


Fig 13. *Smacigastes micheli* Ivanenko & Defaye, 2004. Stage VI nauplius. (A) Habitus, ventral, showing buds of maxillule, maxilla, maxilliped, Leg 1 and Leg 2, papulose surface illustrated within square. (B) Posterior part of body showing buds of maxillule, maxilla, maxilliped, Leg 1 and Leg 2, lateral. (C) Buds of maxillule and maxilla, ventral. (D) Bud of (right) maxilliped. a1, antennule; a2, antenna; mn, mandible; m-1, bud of maxillule; m-2, bud of maxilla; mpx, bud of maxilliped; l1, bud of Leg 1; l2, bud of Leg 2; cr, bud of caudal ramus

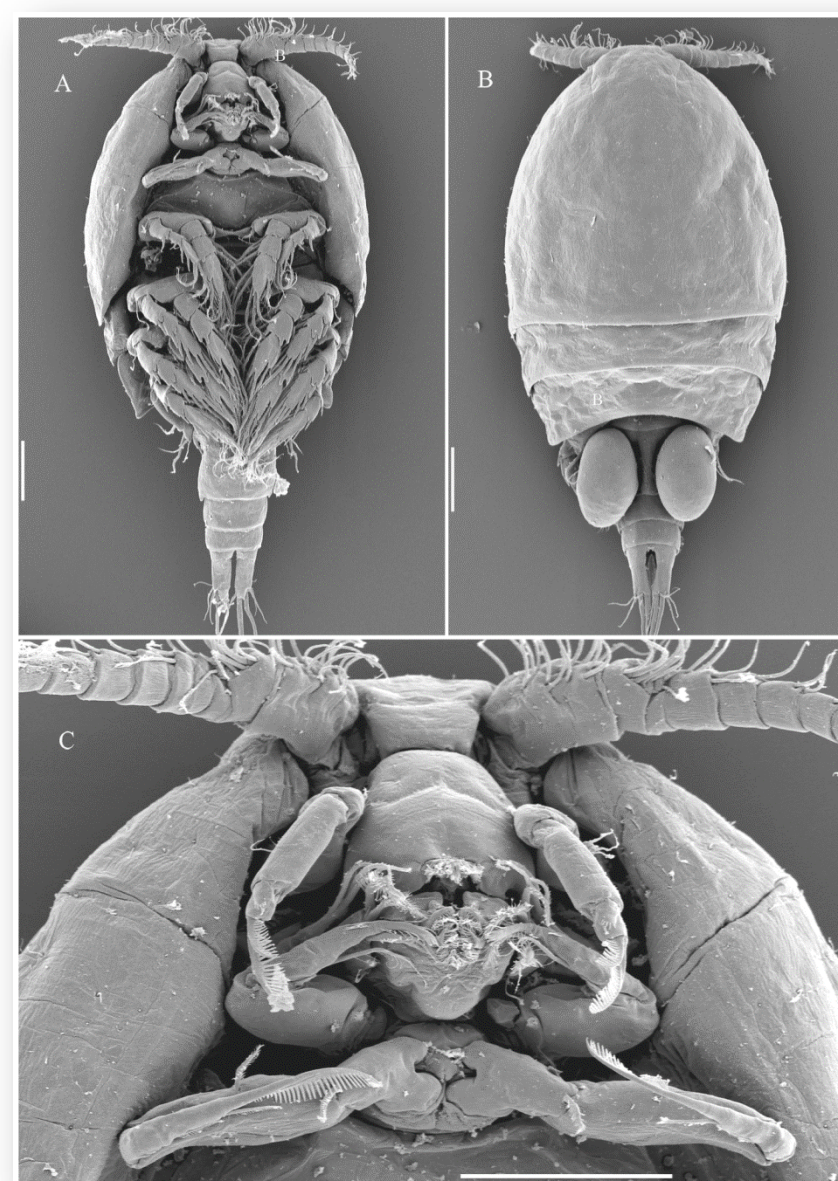


Fig 8. *Stygiopontius pectinatus* (female) SEM micrographs. A: habitus, ventral view. B: habitus, dorsal view. C: oral cone and anterior appendages. Scale bars 100 µm. Gollner S, Ivanenko VN, Arbizu PM, Bright M (2010)

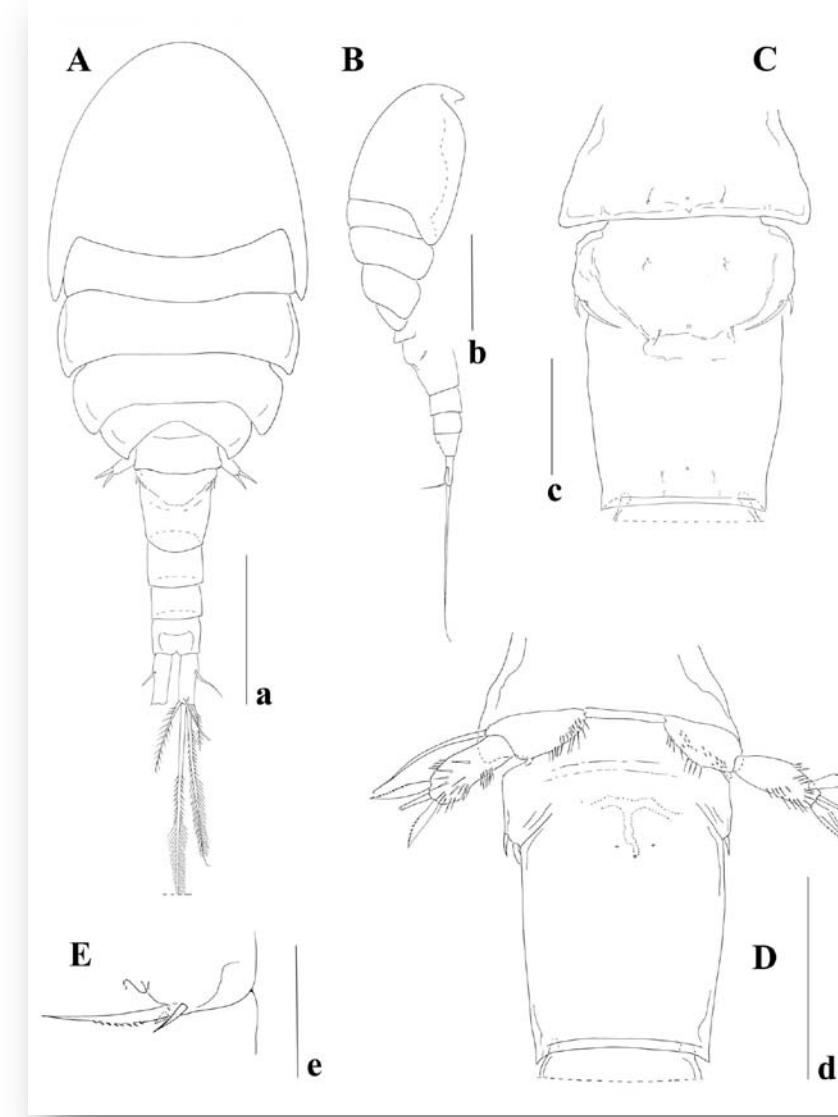


Fig 9. Ivanenko V.N. & D. Defaye. 2004. ♀ holotype: A, habitus, dorsal; B, terminal seta of caudal ramus (shown partially in Fig 1 A); C, leg 6 and genital field, ventral; D, anal somite and caudal rami, ventral; E, labrum, anterior.

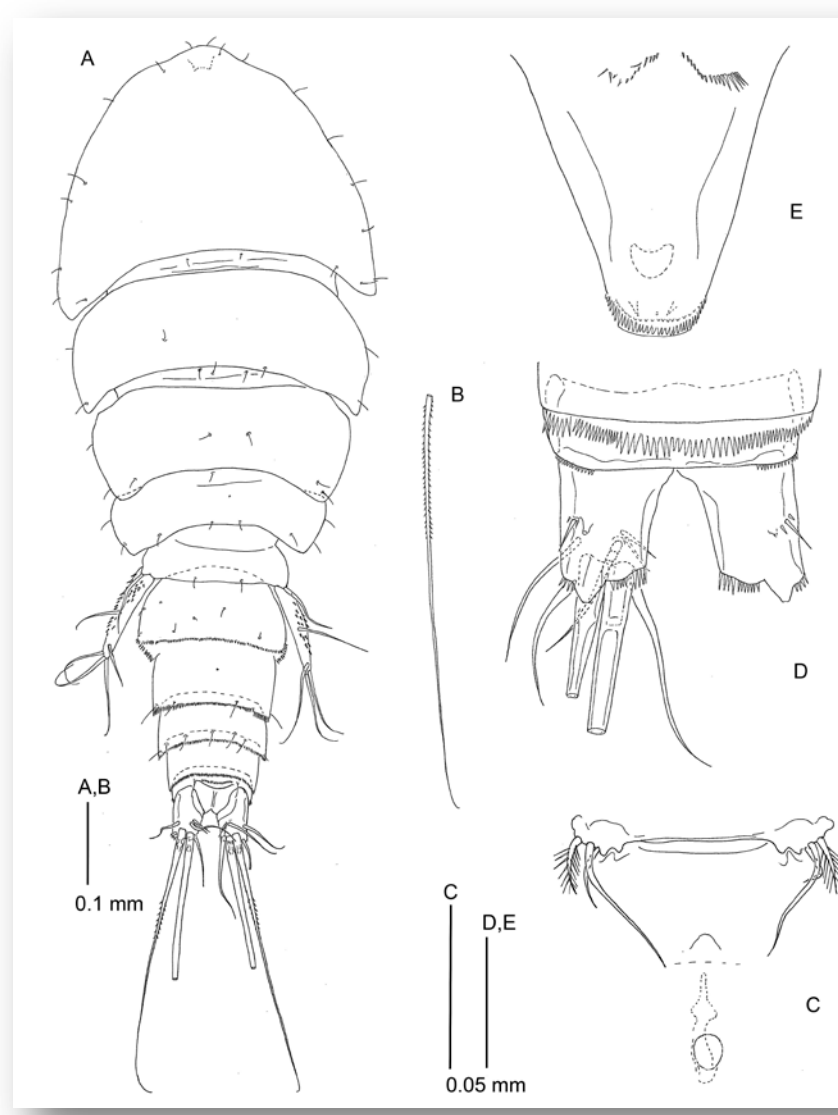


Fig 10. *Tisbe dahmsi* Ivanenko et al. 2011. ♀ holotype: A, habitus, dorsal; B, terminal seta of caudal ramus (shown partially in Fig 1 A); C, leg 6 and genital field, ventral; D, anal somite and caudal rami, ventral; E, labrum, anterior.

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