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A new species of *Exrima*, synonymy of four species of *Aphotopontius*, *Stygiopontius* and *Rhogobius*, and record of first copepodid stage of Dirivultidae (Copepoda: Siphonostomatoida) from deep-sea hydrothermal vents of the East Pacific Rise (13°N)

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Females of the new species Exrima walteri *sp. nov. were found in sediment trap samples deployed over different sites of the East Pacific Rise (13°N) at 2600 m depth. Four traps were deposited during the HOPE99 cruise (1999) and recovered during the AMISTAD (1999) cruise on the research vessel 'L'Atalante'. The new species is distinguished from congeners,* E. singula *Humes, 1987 and* E. dolichopus *Humes, 1987, by the following derived characters: first somite of the urosome with 3 (one dorsal and two lateral) stout conical extensions; distal endopodal segment on the swimming leg 4 broad. In addition, many specimens of copepodids I and lecithotrophic nauplii, identified as belonging to Dirivultidae gen. sp., were found in the samples of all sediment traps. This is the first record of copepodids I and of a nauplius of dirivultids from the Pacific Ocean. Study of type and additional material collected during different Ifremer cruises at different vent sites (HERO91, EXOMAR, PHARE and MoMARETO) required synonymy of four species of* Aphotopontius *Humes, 1987,* Stygiopontius *Humes, 1987 and* Rhogobius *Humes, 1987.* Aphotopontius rapunculus *Humes and Segonzac, 1998 is transferred to the genus* Rhogobius *because it possesses all presumed derived attributes of this genus: last abdominal somite with lobes at sides of anal operculum; second segment of antennal endopod elongate and slender. A new study of the type material suggests that:* Aphotopontius temperatus *Humes, 1997 is a synonym of* A. atlanteus *Humes, 1996;* Stygiopontius lumiger *Humes, 1989 is a synonym of* S. sentifer *Humes, 1987 while* S. bulbisetiger *Humes, 1996 is a synonym of* S. pectinatus *Humes, 1987. Females of the three synonymized species were found to be sub-adult females at copepodid V. Leg 6 on these specimens is one seta located dorsolaterally on the posterior part of the genital somite. This position for leg 6 is unknown for copepodid V of other siphonostomatoids whose leg 6 is located ventrally at copepodid V; the dorsolateral position is presumed derived and shared by the dirivultid genera* Aphotopontius *Humes, 1987 and* Stygiopontius *Humes, 1987. A new key to the Dirivultidae genera is presented.*

Keywords: Copepoda, Siphonostomatoida, Dirivultidae, new species, synonymy, new records, deep-sea, hydrothermal vents, East Pacific Rise, Mid-Atlantic Ridge

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INTRODUCTION

Dirivultidae Humes & Dojiri, 1980a is a primitive family of siphonostomatoid copepods whose species have been collected in large numbers from vent fields in the Atlantic and Pacific Oceans (Humes & Segonzac, 1998; Ivanenko & Defaye, 2006a; Gollner *et al.*, 2010; Ivanenko *et al.*, 2011).

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Although specimens of the type species *Dirivultus dentaneus* Humes & Dojiri, 1980a were described from a vestimentiferan not specifically associated with a hydrothermal vent field, species of dirivultids are now considered endemic to deep-sea hydrothermal vent ecosystems. Including the actions proposed in this paper, Dirivultidae currently consists of 51 species in 13 genera: 6 genera (*Chasmatopontius* Humes, 1990, *Fissuricola* Humes, 1987, *Humesipontius* Ivanenko & Ferrari, 2003a, *Nilva* Humes, 1987, *Rimipontius* Humes, 1996 and *Scotoecetes* Humes, 1987) are monotypic; the genera *Benthoxynus* Humes, 1984, and *Dirivultus* Humes & Dojiri, 1980a each contain 2 species, *Exrima* Humes, 1987 and *Rhogobius* Humes, 1987 have 3 species; *Ceuthoecetes* Humes & Dojiri, 1980b, *Aphotopontius* Humes, 1987, *Stygiopontius* Humes, 1987 have 4, 10 and 21 species, respectively. Studies over the last decade have extended our knowledge of Dirivultidae beyond descriptions of adults. All copepodid stages have been reported in plankton over hydrothermal vents (Ivanenko, 1998); a non-feeding lecithotrophic nauplius was described (Ivanenko *et al.*, 2007); their feeding behaviours have been observed (Heptner & Ivanenko, 2002) and their spatial distributions were studied on different substrates from the Juan de Fuca Ridge of the north-east Pacific Ocean and East Pacific Rise at 9°N (Tsurumi *et al.*, 2003; Gollner *et al.*, 2007). The distributional range of the family appears to extend as far as 5°S on the Mid-Atlantic Ridge (Ivanenko *et al.*, 2006).

In this paper, a new species of the genus *Exrima* is described, and the taxonomic status of four species is revised. One species of *Aphotopontius* and two of *Stygiopontius* are synonymized, and one species of *Aphotopontius* is transferred to *Rhogobius*. A key is provided for the genera of Dirivultidae. A number of unknown dirivultid copepodids at stage 1, as well as lecithotrophic nauplii identified tentatively as dirivultids, are reported from the sediment trap samples deployed in the vicinity of hydrothermal vent communities of the East Pacific Rise (13°N). After publications of Humes (1999a–c), this is the fourth paper describing new species of copepods from hydrothermal vents of the eastern Pacific (Ivanenko & Ferrari, 2003a; Ivanenko & Defaye, 2006b; Gollner *et al.*, 2008).

MATERIALS AND METHODS

The copepods of the new species from the East Pacific Rise, 13°N were collected in 1999 by sediment traps that were deployed during the HOPE cruise and recovered two months later during the AMISTAD cruise on the research vessel (RV) 'L'Atalante'. Four specially designed traps (PPS 10, PPS 20, PPS 30 and PPS 40) were anchored over the bottom, in close proximity to hydrothermal vents to collect detrital particles and small planktonic organisms. Experiment setting details are given in Table 1. The sediment trap samples were automatically fixed daily in flacons filled with a solution of NaCl, DMSO and bromophenol blue.

The copepods were studied using the 'hanging drop method' of Humes & Gooding (1964) as modified by Ivanenko & Defaye (2004). All measurements and dissections were made in lactic acid. Dissections were made under a Leica MZ8 dissecting microscope. Prior to examination with a compound light microscope, Leica DMLB, specimens were cleared in lactic acid and stained in a solution of chlorazol black E. Prepared specimens were examined with bright-field or differential interference contrast optics. Drawings were made with a camera lucida. The holotype was mounted on a slide in glycerol for long-term preservation and sealed with Eukitt (O. Kindler GmbH & Co). Descriptive terminology is from Ivanenko *et al.* (2008); homologies of limb segments follow Ferrari & Ivanenko (2008).

RESULTS

SYSTEMATICS
Order SIPHONOSTOMATOIDA Burmeister, 1835
Family DIRIVULTIDAE Humes & Dojiri, 1980
Genus *Exrima* Humes, 1987
Exrima walteri sp. nov. Ivanenko, Defaye & Ferrari
(Figures 1–5)

TYPE MATERIAL
Holotype adult female (MNHN-Cp2553) dissected and mounted on sealed glycerol slide; paratype adult female (MNHN-Cp7870) preserved in 70% ethanol deposited in the Muséum National d'Histoire Naturelle, Paris (MNHN).

TYPE LOCALITY
East Pacific Rise, site Parigo, 12°48.61′N 103°56.42′W, 10 m to the west and 2 m above the bottom, depth 2625 m. Collected in sediment trap PPS 10 (holotype—trap PPS 10, flacon A_{10}, paratype—trap PPS 10 and flacon A4) deployed during HOPE cruise and recovered during AMISTAD cruise.

ADDITIONAL MATERIAL EXAMINED
East Pacific Rise, cruise PHARE (RV 'L'Atalante', remotely operated vehicle (ROV) 'Victor 6000'): adult female (MNHN Cp7867), dive 167-19, suction sampler 4 (ASPI4), 28 May 2002, site PP-Ph08, 12°49.0760′N 103°56.5660′W, 2623 m; adult female (MNHN Cp7868), dive 167-21, small sampling box 2 (PBT2), 30 May 2002, site PP-Ph09, 12°48.6240′N 103°56.3950′W, 2624 m; 2 adult females (MNHN Cp7869), 164-16, PBT2, 25 May 2002, site PP-Ph12, 12°48.6330′N 103°56.4290′ W, 2623 m. All specimens were preserved in 70% ethanol.

ETYMOLOGY
The specific epithet is derived from the family name of T. Chad Walter at the Smithsonian Institution's National Museum of Natural History, Washington, DC who substantially contributed to the development of digital information on Copepoda.

Holotype female
Body (Figure 1 A, B) cyclopiform, elongate. Total length (body plus caudal ramus), excluding caudal setae, 1.52 mm; greatest width 0.53 mm. Shield of cephalothorax and tergites of following three somites pointed posteriorly (Figure 1 B, D, E). Urosome 5-segmented (Figures 1A, B & 2A–C): anterior somite bearing leg 5, genital double-somite and three abdominal somites (last is the anal somite). Anterior somite with one dorsal and two lateral conical extensions (Figure 2A). Genital double-somite (posterior thoracic somite fused to anterior

Table 1. Sediment trap experiment settings on the East Pacific Rise, 13°N. All traps were deployed during the HOPE cruise and recovered during the AMISTAD cruise on the RV 'L'Atalante'.

Site	Coordinates	Trap	Flacons	Distance from site	Depth	Trap opening	Deployment date	Recovery date
Parigo	12°48.61′N 103°56.42′W	PPS10	A1–A9	10 m to the west	2625 m	2 m above bottom	17 April 1999	11 June 1999
Parigo	12°48.61′N 103°56.42′W	PPS20	B1–B10	10 m to the east	2625 m	2 m above bottom	17 April 1999	8 June 1999
Parigo	12°48.67′N 103°56.47′W	PPS30	C1–C10	150 m to the west	2630 m	5 m above bottom	16 April 1999	4 June 1999
Seamount Marginal High	12°42.78′N 103°51.9′W	PPS40	D1–D15	On top	2514 m	50 m above bottom	13 April 1999	6 June 1999

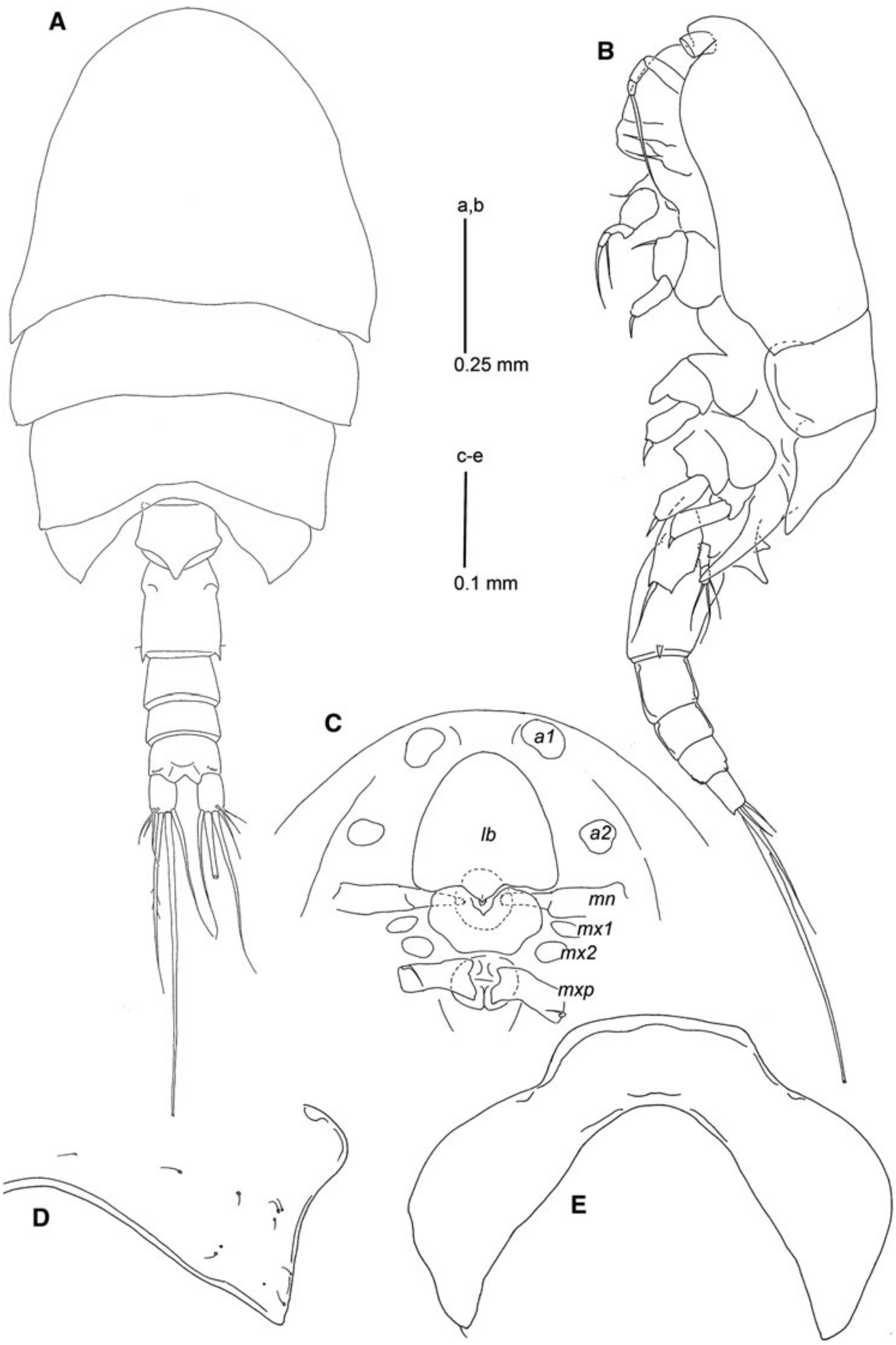

Fig. 1. Holotype female of *Exrima walteri* sp. nov. (A) Habitus, dorsal; (B) habitus, lateral; (C) anterior part of prosome, ventral; (D) right side of tergite of somite bearing swimming leg 3, dorsal; (E) tergite of somite bearing swimming leg 4, dorsal. *a1*, antennule; *a2*, antenna; *mn*, mandible; *mx1*, maxillule; *mx2*, maxilla; *mxp*, maxilliped; *lb*, labrum.

abdominal somite) with spine-like lateral projections near posterior edge; gonopores lateral on the anterior half of the somite, copulatory pores ventral to the gonopores (Figure 2 A, B, D, E). Anal somite bearing caudal rami ornamented with rows of denticles on ventral and dorsal sides near the posterior edge; anal opening dorsal near the posterior margin.

Rostrum (Figure 1 B, C) rounded, slightly pronounced ventrally, fused with shield of cephalothorax.

Oral cone (Figure 1 B, C) short and robust, its opening formed by labrum and labium.

Caudal ramus (Figure 2 F, G) with six setae and a row of flattened denticles on ventral side near the posterior edge; two lateral setae in distolateral position; innermost terminal seta with denticles on inner side.

Antennule (Figure 3 A, B) 11-segmented. Proximal segment longest with fifteen medial setae of unequal lengths. Segment 2 with twelve medial setae, two setae small. Segment 3 with a pair of setae near mid-length and a pair distally. Segments 4–7 with two setae, one seta near mid-length, second seta near distal edge. Segment 8 with one seta at mid-length and one seta and one aesthetasc near distal edge. Segment 9 with one mid-length and one distal seta; segment 10 with mid-length and distal pair of setae each medially and laterally. Distal segment with four lateral setae and three setae and one aesthetasc terminally. All setae smooth.

Antenna (Figure 3C, D): small coxa without ornamentation, lateral margin of elongate basis with row of slender denticles. Exopod small, 1-segmented, with one smooth terminal seta. Endopod 2-segmented; proximal segment elongate, with row of slender denticles on outer margin, without setae; distal segment short bearing four setae, lateral margin with one seta and a row of denticles, two elongate terminal setae with setules.

Mandible (Figure 2H): gnathobase stylet-like, flattened distally, with terminal teeth of unequal size and a row of small teeth on distal margin.

Maxillule (Figure 3E): coxal endite bearing one short and four stout, long setae; basis with three long setae; all long setae with setules.

Maxilla (Figure 3F): syncoxa flattened, with long seta with setules on coxal endite; basis elongate with apical denticles.

Maxilliped (Figure 4A) 4-segmented, syncoxa and basis each with inner seta with setules. Proximal endopodal segment complex with two very short posterio-proximal and two long unequal posterio-distal setae with setules; distal segment with denticles and two terminal setae, one longer and thicker with serrate inner margin.

Swimming legs 1–4 (Figures 4B–D & 5A–C) with 3-segmented rami except for leg 4 with 2-segmented endopod (Figure 5C). Margin of basis expanded medially and distally on swimming legs 1–3, and medially in swimming leg 4. Distal endopodal segments of legs 1–4 wider than exopodal, with denticles as shown in figures. Basis of leg 1 armed with stout inner spine-like seta (Figure 4B). Leg 4 (Figure 5B, C): inner seta of proximal segment of exopod smooth; terminal seta of distal endopodal segment near medial edge of broad terminal margin. Formulae for armature of legs in Table 2.

Leg 5 (Figures 1A & 5D, E) 2-segmented, first segment with one lateral seta; second segment with one lateral and two terminal setae.

Leg 6 (Figure 2 D, E): bud on the anterior half of genital double-somite with one lateral seta.

Table 2. Formula for the armature of legs 1–4 of female of *Exrima walteri* sp. nov. (Copepoda: Siphonostomatoida: Dirivultidae). Roman numerals indicate spines, Arabic numerals, setae.

	Coxa	Basis	Exopod	Endopod
Leg 1	0-0	0-I	I-1; I-1; II,1,4	0-1; 0-2; 1,2,3
Leg 2	0-1	0-0	I-1; I-1; III,I,4	0-1; 0-2; 1,2,3
Leg 3	0-1	0-0	I-1; I-1; III,I,5	0-1; 0-2; 1,I,3
Leg 4	0-0	0-0	I-1; I-1; III,I,4	0-0; 0,I,0

Colour of living specimens unknown.

Egg sacs not observed.

Male

Unknown.

REMARKS

The new species belongs to the genus *Exrima* that is determined by the combination of the following features partly shown in the newly designed key to the genera of Dirivultidae: female urosome with five abdominal somites including anal somite (*Chasmatopontius* with three abdominal somites including anal somite); rostrum weakly developed (projecting anteriorly in *Dirivultus*); caudal ramus with six setae (five setae on *Rimipontius*); proximal fifteen setae on female antennule on one segment (on two segments in *Ceuthoecetes* and *Nilva*); three segments in *Chasmatopontius*, *Stygiopontius* and *Fissuricola*; three or eight segments in *Benthoxynus* (see Humes, 1989a); antennal exopod of female has a simple seta (1-segmented on all other genera); distal antennal endopod with one terminal seta long and slender (modified to claw in *Ceuthoecetes, Dirivultus* and *Nilva*); 2-segmented maxilla (3-segmented in *Dirivultus* or vestigial in *Fissuricola*) with syncoxa bearing seta on coxal endite (seta absent in *Ceuthoecetes*, *Dirivultus*, *Nilva*, and *Rhogobius*); endopod of swimming leg 4 is 2-segmented (endopod absent in *Humesipontius*); setal formula of leg 4 endopod: 0-0; I-0 (0-1; I-1 in *Aphotopontius* and *Rhogobius* and 0-0; I-1 in *Ceuthoecetes, Dirivultus, Nilva, Scotoecetes*, and *Stygiopontius* and 0-1; I-3 in *Fissuricola* and 0-0; 0-3 in *Chasmatopontius*).

The derived features of the new species *Exrima walteri* sp. nov. that clearly distinguish it from two congeners (*E. singula* Humes, 1987 and *E. dolichopus* Humes, 1987; both from the East Pacific Rise) are: three stout conical extensions (one dorsal and two lateral) on the first urosomite (*E. singula* and *E. dolichopus* without extensions); broad distal endopodal segment of swimming leg 4 (simple, cylindrical on *E. singula* and *E. dolichopus*).

KEY FOR THE GENERA OF THE DIRIVULTIDAE*

1. Urosome 4-segmented on female, 5-segmented on male . . . . *Chasmatopontius*
   — Urosome 5-segmented on female, 6-segmented on male 2
2. Endopod of leg 4 absent . . . . *Humesipontius*
   — Endopod 2-segmented 3
3. First segment of endopod of leg 4 unarmed (0-0) 4
   — First segment of endopod of leg 4 with 1 medial inner seta (0-1) 5
4. Second endopodal segment of leg 4 with one terminal spine-like seta (I, 0) 11

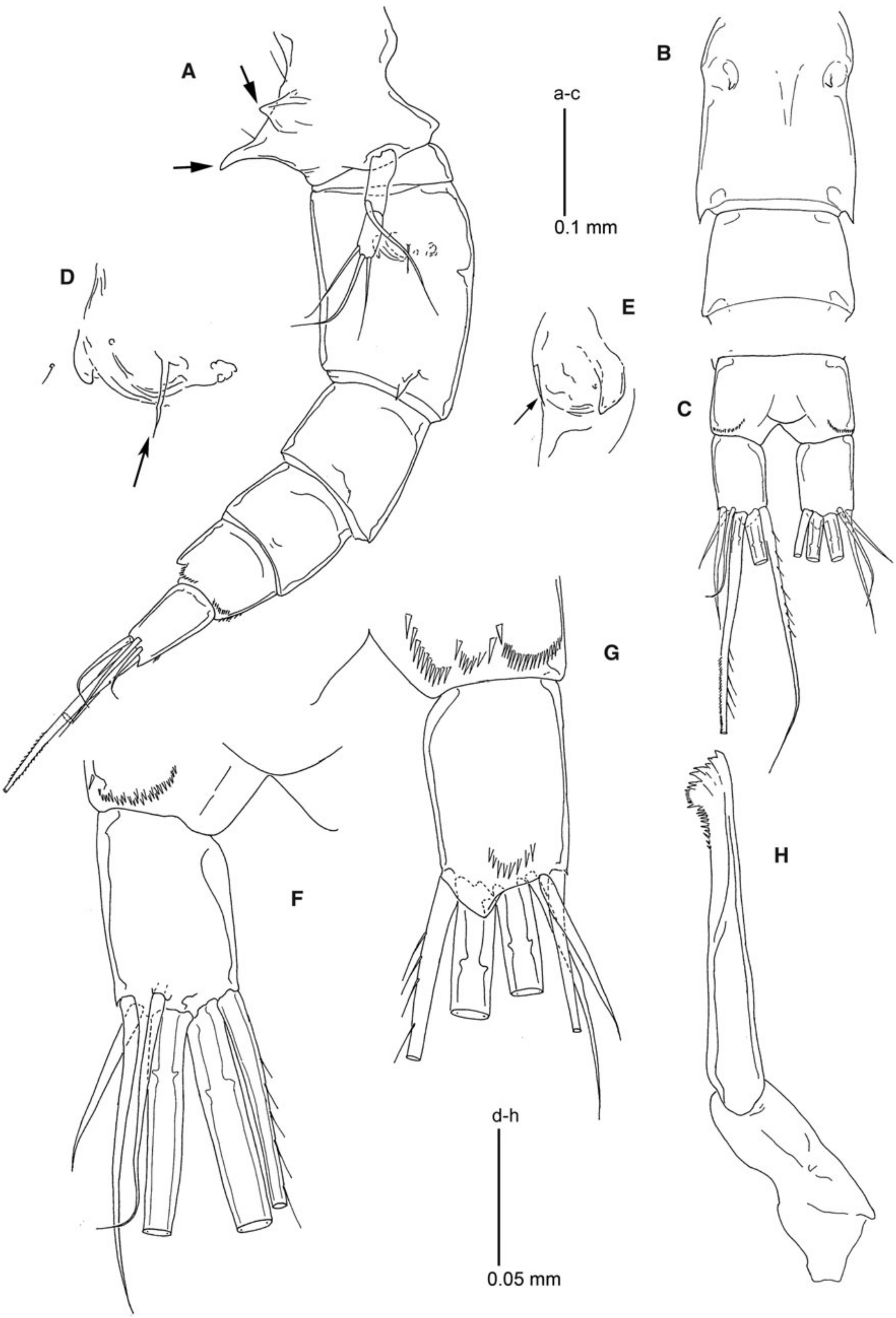

Fig. 2. Holotype female of *Exrima walteri* sp. nov. (A) Urosome, lateral, arrow to ventral and right lateral conical projections; (B) genital double-somite and abdominal somite, dorsal; (C) anal (last abdominal) somites and caudal rami, dorsal; (D) right genital aperture, lateral, arrow to seta of leg 6; (E) left genital aperture, dorsal, arrow to seta of leg 6; (F) left caudal ramus, dorsal; (G) left caudal ramus, ventral; (H) mandible, lateral.

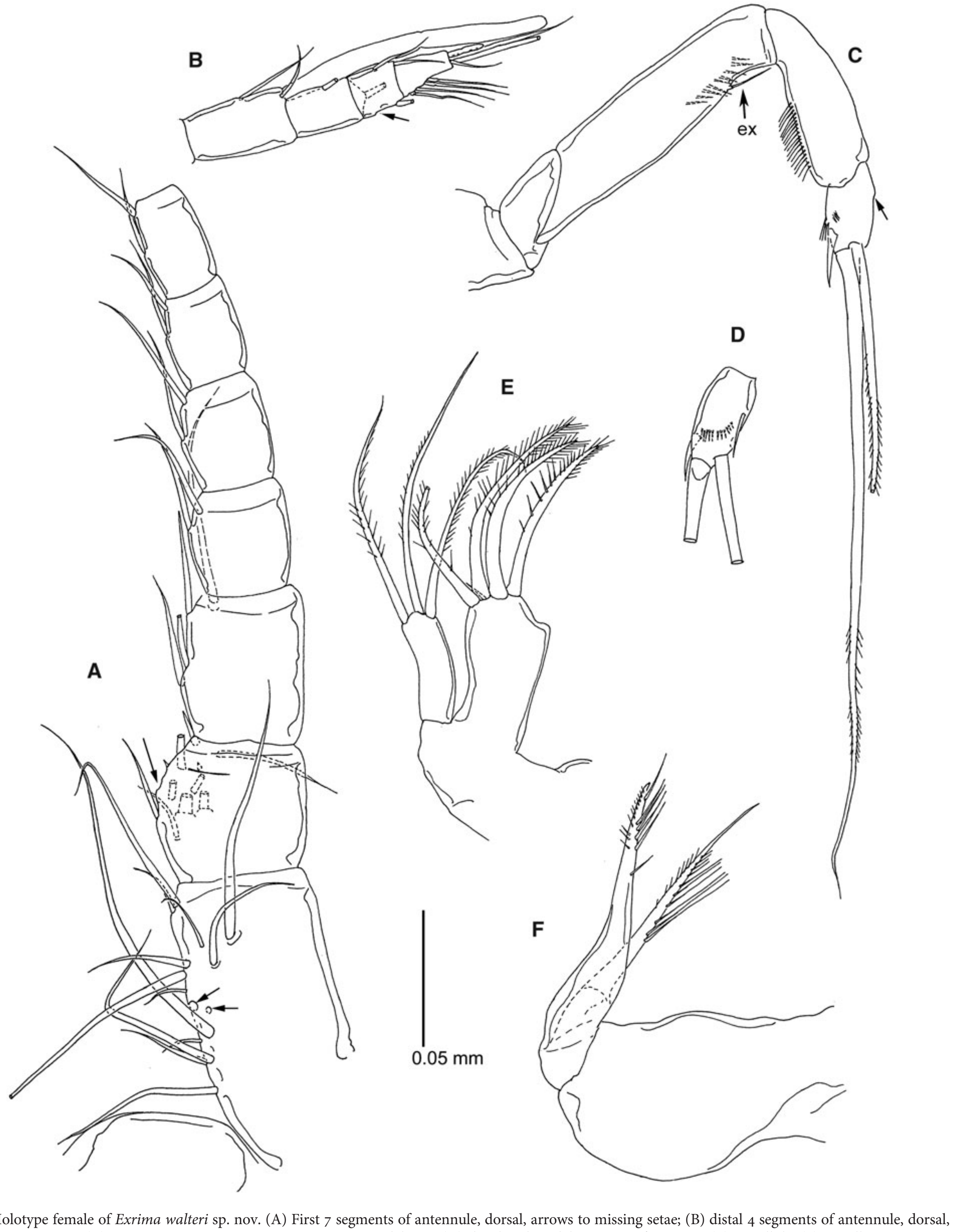

Fig. 3. Holotype female of *Exrima walteri* sp. nov. (A) First 7 segments of antennule, dorsal, arrows to missing setae; (B) distal 4 segments of antennule, dorsal, arrow to missing seta; (C) antenna, arrow to missing seta, ex – exopodal seta; (D) distal endopodal segment of antenna; (E) maxillule; (F) maxilla.

— Second endopodal segment of leg 4 with terminal spine-like seta and medial seta (I, 1) 7

5. Second endopodal segment of leg 4 with two elements (I, 1 or 1,1) 6

— Second endopodal segment of leg 4 with four elements (I, 3) . . . . *Fissuricola*

6. Coxal endite of maxilla with 1 medial inner seta . . . . *Aphotopontius*

— Coxal endite of maxilla without media seta . . . . *Rhogobius*

7. Coxal endite of maxilla with a medial inner seta 8

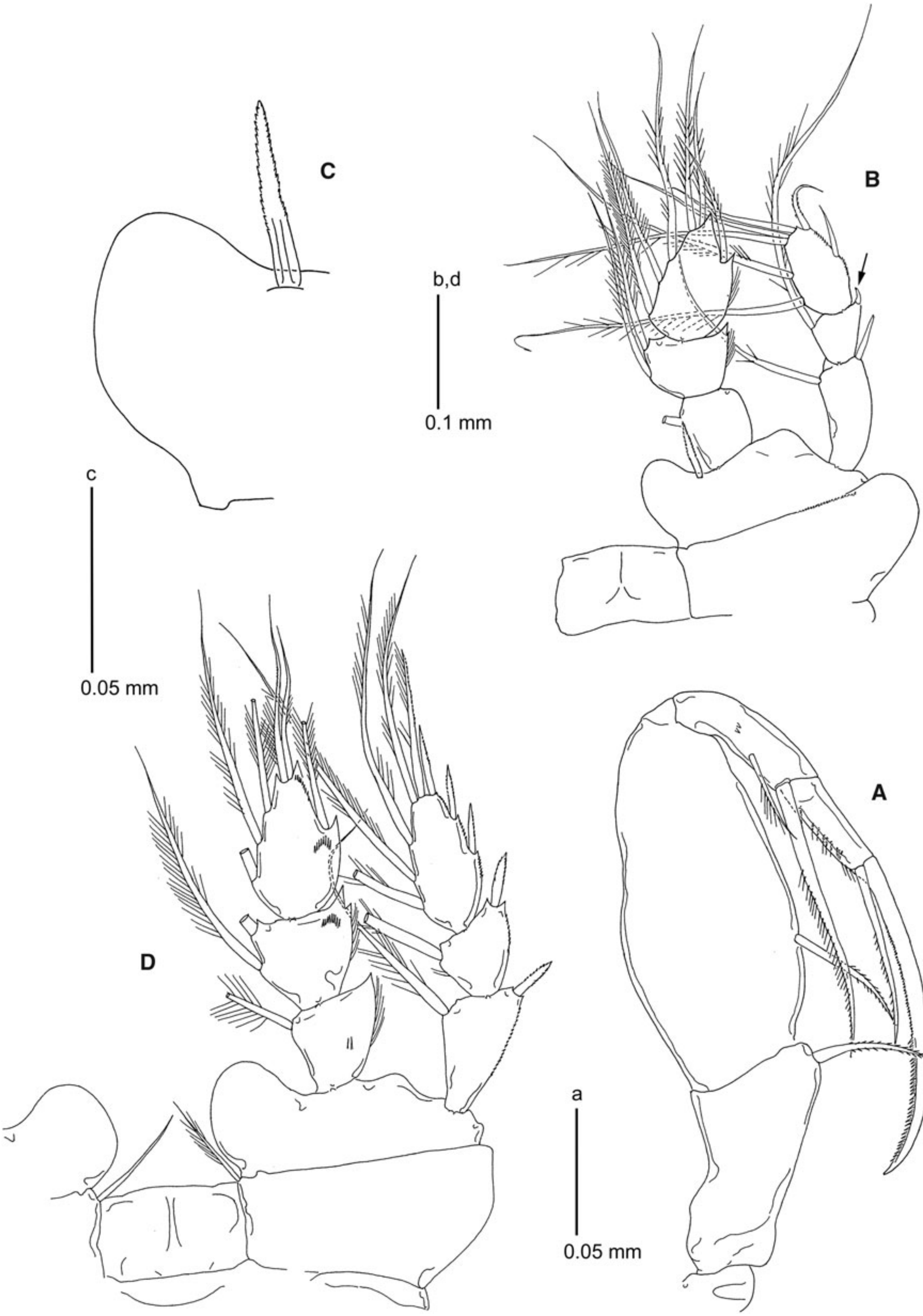

Fig. 4. Holotype female of *Exrima walteri* sp. nov. (A) Maxilliped, posterior; (B) swimming leg 1, anterior, arrow to curved seta; (C) inner seta on basis of leg 1, anterior; (D) swimming leg 2, anterior.

— Coxal endite of maxilla without 1 medial inner seta 9

8. Female leg 1 endopod 2-segmented, a terminal seta turned inward . . . . *Scotoecetes*

— Female leg 1 endopod 3-segmented, terminal seta not so turned . . . . *Stygiopontius*

9. Genital complex with lateral hump . . . . *Nilva*

— Genital complex without lateral hump 10

10. Rostral area projecting anteriorly, oral cone with posteriorly directed dentiform spines . . . . Dirivultus
    — Rostral area not prominent, oral cone without posteriorly directed dentiform spines . . . . .Ceuthoecetes
11. ♀ leg 5 2-segmented; first exopodal segment of leg 3 with medial seta 12
    — ♀ leg 5 a small lobe; first exopodal segment without medial seta . . . . Benthoxynus
12. Caudal ramus with six setae . . . . Exrima
    — Caudal ramus with five setae . . . . Rimipontius

*The key is based on the differential diagnoses of genera by Ivanenko & Defaye (2006a).

SYNONYMY

Aphotopontius Humes, 1987
Aphotopontius atlanteus Humes, 1996

Humes, 1996: 616–622, figures 5–8; Ivanenko & Defaye, 2006a: 329, figure 2.
A. temperatus Humes, 1997: 64–72, figures 1–6.

TYPE MATERIAL EXAMINED

Paratypes of *Aphotopontius atlanteus*: 10 adult ♀ in ethanol (USNM 268308), 3 adult ♀ (USNM 1099033) on sealed glycerol slide, Mid-Atlantic Ridge, 37°20′N 32°17′W, site Lucky Strike, 1636 m.

Types of *Aphotopontius temperatus*: holotype ♀ in ethanol (USNM 285469), 10 paratypes ♀ in ethanol (USNM 285471), 5 paratypes ♀ in ethanol (USNM 1098821) on sealed glycerol slide, Mid-Atlantic Ridge, site Lucky Strike, 37°17′N 32°16′W, 1688 m.

ADDITIONAL MATERIAL EXAMINED

Mid-Atlantic Ridge, 37°N, site Lucky Strike, Tour Eiffel edifice, 1690 m, cruises EXOMAR (July–August 2005; RV 'L'Atalante') and MoMARETO (August–September 2006, RV 'Pourquoi pas?'), ROV 'Victor 6000'. The copepods were collected by small sampling box (PBT) or suction sampler (ASPI) within faunal assemblages of *Bathymodiolus azoricus*; temperature varied between 4.8 and 8.8°C (De Busserolles *et al.*, 2009): 11 ♀, 1 ♂, MoMARETO, dive 303, ASPI1; 16 ♀, 1 ♂, 105 copepodids stage V (♀), 1 copepodids stage V (♂), 4 copepodid stage IV, MoMARETO, dive 303, PBT2, chain 1; 1 ♀, 15 ♂, 74 copepodids stage V (♀), 1 copepodids stage V (♂), 2 copepodid stage IV, MoMARETO, dive 303, ASPI7, chain 1; 1 ♀, MoMARETO, dive 303, ASPI8, chain 1; 1 ♀, MoMARETO, dive 303, ASPI6, chain 7; 1 ♀, MoMARETO, dive 303, PBT2, chain 1; 1 ♀, MoMARETO, dive 303, PBT4, chain 8; 1 ♀, MoMARETO, dive 303, ASPI4, chain 6; 2 ♀, MoMARETO, dive 303, PBT3, chain 1; 4 ♀, MoMARETO, dive 303, PBT5, chain 10; 17 ♀, MoMARETO, dive 303, PBT2, chain 1; 21 ♀, MoMARETO, dive 303, PBT1, chain 6; 33 ♀, 11 copepodid stage V (♀), MoMARETO, dive 303, PBT3, chain 1; 37 ♀, 22 copepodids stage V (♀), MoMARETO, dive 303, PBT3, chain 1; 103 ♀, 54 copepodids stage V (♀), 1 copepodid stage IV, MoMARETO, dive 303, PBT1, chain 6; 162 ♀, 11 copepodids stage V (♀), MoMARETO, dive 303, PBT1, chain 6; 37 ♂, MoMARETO, dive 304, ASPI3, chain 4; 1 ♀, MoMARETO, dive 304, ASPI6, chain 2; 8 ♀, MoMARETO, dive 304, ASPI4, chain 4; 1 ♀, MoMARETO, dive 304, ASPI5, chain 2; 2 ♀, MoMARETO, dive 04, PBT2, chain 3; 2 ♀, MoMARETO, dive 304, PBT4, chain 2; 4 ♀, 146 copepodid stage V (♀), 8 copepodid stage IV, MoMARETO, dive 304, PBT1, chain 4; 108 ♀, 22 copepodids stage V (♀), MoMARETO, dive 304, PBT5, chain 10; 313 ♀, 11 copepodid stage IV, MoMARETO, dive 304, PBT2, chain 3; 313 ♀, MoMARETO, dive 304, PBT2, chain 3; 492 ♀, 11 copepodid stage V (♀), MoMARETO, dive 304, PBT1, chain 4; 21 copepodid stage V, 1 copepodid stage IV, MoMARETO, dive 304, PBT4, chain 2; 60 ♂, MoMARETO, dive 305, ASPI2, chain 11; 253 ♀, 134 ♂, MoMARETO, dive 305, ASPI3, chain 5; 13 ♀, MoMARETO, dive 305, PBT3, chain 12; 1 ♀, MoMARETO, dive 305, PBT4, chain 5; 2 ♀, MoMARETO, dive 305, ASPI1, chain 11; 2 ♀, MoMARETO, dive 305, PBT5, chain 11; MoMARETO, dive 305, PBT5, chain 11; 1 ♀, MoMARETO, dive 306, ASPI1, chain 9; 1 ♂, EXOMAR, dive 252, PBT1; 5 ♂, EXOMAR, dive 253, ASPI2, chain 2; 5 ♂, EXOMAR, dive 253, ASPI3, chain 2; 7 ♂, EXOMAR, dive 253, ASPI4, chain 5; 9 ♂, EXOMAR, dive 253, PBT1, chain 5; 1 ♀, 13 ♂, EXOMAR, dive 253, PBT1, chain 2; 22 ♂, MoMARETO, dive 305, PBT2. All specimens were preserved in 70% ethanol and stored in Ifremer.

PREVIOUS REPORTS

Mid-Atlantic Ridge: 37°N, sites Lucky Strike and Menez Gwen (Humes, 1996, 1997; Humes & Segonzac, 1998); 14°N, Logatchev hydrothermal field (Ivanenko *et al.*, 2006).

REMARKS

Aphotopontius atlanteus Humes, 1996 is found in hydrothermal vent communities throughout the Mid-Atlantic Ridge, and apparently is a widespread species. The adult female of *A. atlanteus* has an urosome of five apparent somites. Leg 6 is a bud with two setae located laterally in the middle of the second somite (Humes, 1996; Figure 5C, D); this location suggests that the genital somite has fused to the anterior abdominal somite to form the genital complex of the adult female. The adult female of *A. temperatus* has an urosome of five apparent somites but second somite lacks genital openings; leg 6 is a bud with 1 seta located laterally but posteriorly on the second urosomite (Humes, 1997; Figure 1B, C). This location of leg 6 and the absence of genital openings suggest that the genital somite has not yet fused with the anterior abdominal somite to form a genital complex. This fusion will take place during the molt to the copepodid VI (adult female). The adult female of *A. temperatus* appears to be a copepodid V female of *A. atlanteus* (Table 3).

Specimens reported as copepodid V females of *A. temperatus* have an urosome of 4 apparent somites and also lack genital openings (Humes, 1997; Figure 4B–D). The rami of the swimming legs 1–4 on these specimens are 2-segmented (Humes, 1997; Figures 4H & 5A–C); leg 6 is a bud with 1 seta located medially and posteriorly on the second somite (Humes, 1997; Figure 4C, D). This location, the number of urosomites and the segmentation of swimming leg rami suggest that these specimens are copepodid IV of *A. atlanteus* (Table 3).

The original description of *A. temperatus* was supplemented with description of the adult male. The adult male of *A. temperatus* shows no clear distinctions from the described adult male of *A. atlanteus*. Specimens reported as copepodid V males of *A. temperatus* have an urosome of

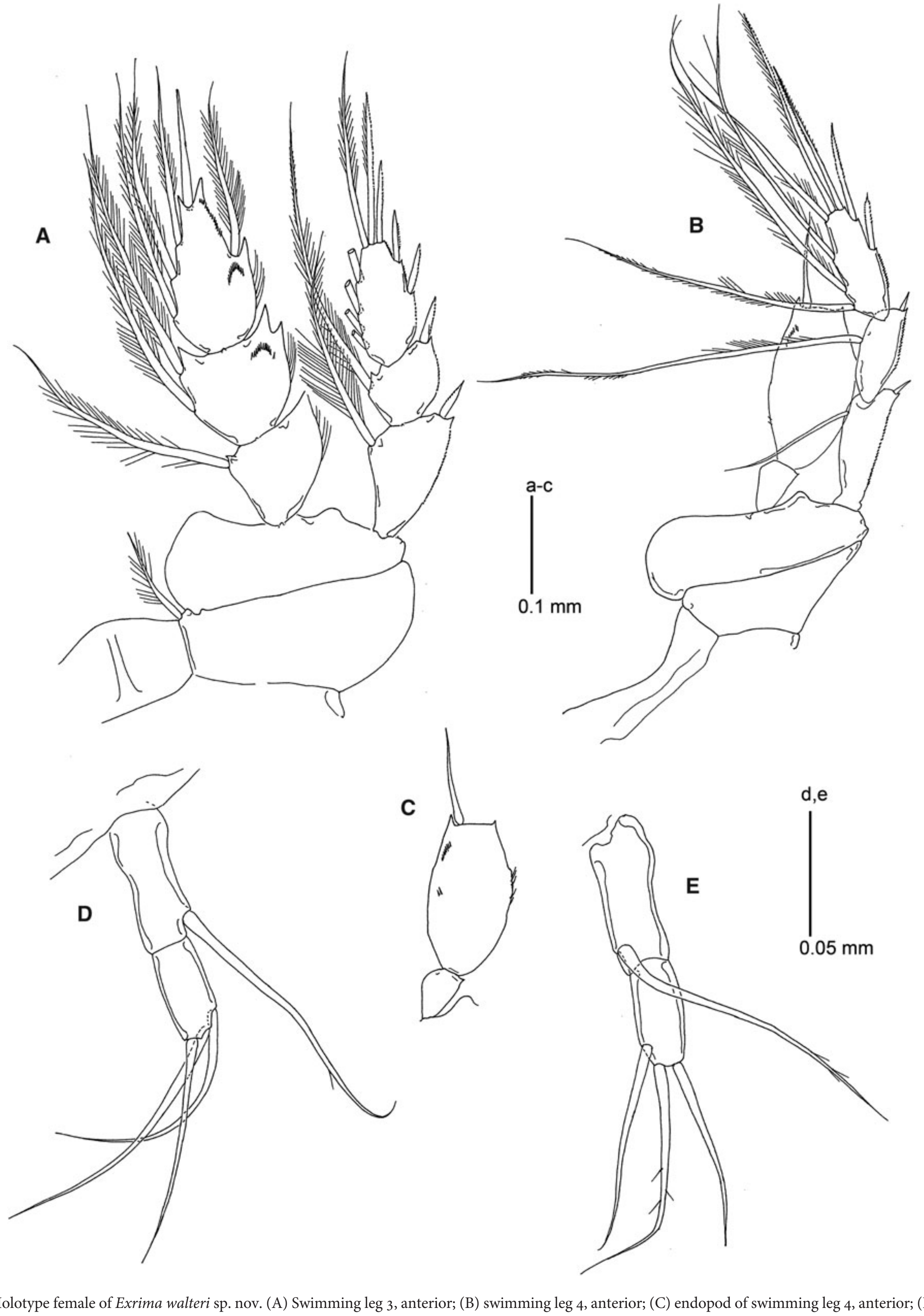

Fig. 5. Holotype female of *Exrima walteri* sp. nov. (A) Swimming leg 3, anterior; (B) swimming leg 4, anterior; (C) endopod of swimming leg 4, anterior; (D) leg 5, lateral; (E) leg 5, dorsal.

five apparent somites and lack genital openings. The rami of swimming legs 1–4 are 3-segmented; leg 6 is a bud with two setae located medially and posteriorly on the second urosomite. These attributes suggest that the specimens are copepodid V males of *A. atlanteus* (Table 3).

Aphotopontius temperatus Humes, 1997 was considered as suggested without comment on a junior synonym of *A. atlanteus* by Ivanenko & Defaye (2006a). The dorsolateral position of leg 6 on females of copepodid stage V, the usual location on most siphonostomatoid copepodid V females, is

Table 3. Reassignment of copepodid stages reported as *Aphotopontius temperatus* Humes, 1997 but now considered *A. atlanteus* Humes, 1996 (Copepoda: Siphonostomatoida: Dirivultidae).

Aphotopontius temperatus Humes, 1997	*Aphotopontius atlanteus* Humes, 1996
Described as copepodid VI female (Humes, 1997; figures 1–2)	= Copepodid V female
Described as copepodid V female (Humes, 1997; figures 4 & 6A–C)	= Copepodid IV female
Described as copepodid VI male (Humes, 1997; figure 3)	= Copepodid VI male
Described as copepodid V male (Humes, 1997; figures 5E–F & 6)	= Copepodid V male

ventrolateral (Ivanenko *et al.*, 2001; Ivanenko & Ferrari, 2003b; Ferrari & Dahms, 2007), complicates the separation of the female copepodid V and copepodid VI. The presence of genital openings defines copepodid VI females and males of all copepods. The unusual dorsolateral position of the leg 6 on females of copepodid V also is shared with two species of *Stygiopontius* considered in this paper and appears to be a derived state at least for these two genera of Dirivultidae. Copepodid VI males of *A. atlanteus* have been observed *in copula* with copepodid stage V females (V.N.I., personal observations) and this behaviour may lead to the incorrect identification of copepodid stage V females as copepodid stage VI females (Table 3).

Stygiopontius Humes, 1987
Stygiopontius sentifer Humes, 1987

Humes, 1987: 724–730, figures 48–50, Ivanenko & Defaye, 2006a: 341.
Stygiopontius lumiger Humes, 1989b: 112–113, figures 6–8; Ivanenko & Defaye, 2006a: 341.

TYPE MATERIAL EXAMINED

Paratypes of *Stygiopontius sentifer*: 10 adult ♀ in ethanol (USNM 231973), 4 adult ♀ (USNM 1099012) on sealed glycerol slide, East Pacific Rise, site Clam Acres, 20°50.0′N 109°06.0′W, 2617 m.

Types of *Stygiopontius lumiger*: holotype ♀ in ethanol (USNM 233776), 10 paratype adult ♀ in ethanol (USNM 233777), 4 paratype ♀ on sealed glycerol slide (USNM 1099008), East Pacific Rise, site Clam Acres, 20°50.0′N 109°06.0′W, 2616 m.

ADDITIONAL MATERIAL EXAMINED

East Pacific Rise, 13°N, cruise PHARE (May 2002 RV ‘L’Atalante’, ROV ‘Victor 6000’). The copepods were collected by small or large sampling boxes (PBT or GBT; respectively) or with a suction sampler (ASPI) and preserved in 70% ethanol: 16 adult ♀ (MNHN Cp7760), 2 adult ♂ (MNHN Cp7766), 1 subadult ♂ of copepodid V (MNHN Cp7768), dive 149, PBT1, site Elsa, 12°48.1420′N 103°56.3090′W, 2621 m; 4 subadult ♀of copepodid V (MNHN Cp7769), dive 149, PBT1, site Elsa, 12°48.1420′N 103°56.3090′W, 2621 m; 10 adult ♀ (MNHN Cp7722), dive 152, PBT3, site PP-Pho1, 12°48.1460′N 103°56.3080′W, 2621 m; 3 adult ♀ (MNHN Cp7732), dive 153, PBT1, site PP-Pho3, 12°49.3460′N 103°56.6390′W, 2621 m; 18 adult ♀ (MNHN Cp7727), dive 154, PBT2, site PP-Pho1, 12°48.1470′N 103°56.3070′W, 2622 m; 1 adult ♀ (MNHN Cp7718), dive 156, ASPI1, site PP-Pho6, 12°48.1690′N 103°56.3430′W, 2622 m; 7 adult ♀ (MNHN Cp7783), dive 156, ASPI3, site PP-Pho6, 12°48.1670′N 103°56.3430′W, 2622 m; 4 adult ♀ (MNHN Cp7724), dive 157, ASPI1, site PP-Pho6, 12°48.1800′N 103°56.3100′W, 2620 m; 3 adult ♀ (MNHN Cp7721), dive 157, ASPI4, site PP-Pho6, 12°48.1800′N 103°56.3100′W, 2620 m; 7 adult ♀ (MNHN Cp7734), dive 157, PBT1, site PP-Pho6, 12°48.1780′N 103°56.3120′W, 2620 m; 10 adult ♀ (MNHN Cp7858), dive 159, PBT1, site PP-Pho5, 12°48.6180′N 103°56.4390′W, 2621 m; 35 adult ♀ (MNHN Cp7729), dive 159, PBT2, site PP-Pho5, 12°48.6150′N 103°56.4390′W, 2621 m; 3 adult ♀ (MNHN Cp7726), dive 160, PBT1, site PP53, 12°48.5570′N 103°56.4170′W, 2623 m; 3 adult ♀ (MNHN Cp7819), dive 161, PBT1, site PP-Pho3, 12°48.0750′N 103°56.2890′W, 2621 m; 3 adult ♀ (MNHN Cp7818), 1 subadult ♀ of copepodid V (MNHN Cp7781),dive 161, PBT2, site PP-Pho3, 12°48.3340′N 103°56.6420′W, 2621 m; 26 adult ♀ (MNHN Cp7797), dive 162, PBT1, site PP-Pho5, 12°48.5860′N 103°56.3920′W, 2622 m; 1 adult ♀ (MNHN Cp7809), dive 164, ASPI2, site PP12, 12°48.6330′N 103°56.4290′W, 2623 m; 1 adult ♀ (MNHN Cp7715), dive 164, PBT1, site PP12, 12°48.6370′N 103°56.4190′W, 2624 m; 6 adult ♀ (MNHN Cp7717), dive 165, ASPI8, site PP-Pho6, 12°48.1790′N 103°56.3080′W, 2621 m; 1 adult ♂ (MNHN Cp7817), dive 166, ASPI1, site PP-Pho8, 12°49.0770′N 103°56.5550′W, 2621 m; 1 adult ♂ (MNHN Cp7751), 6 subadult ♀of copepodid V (MNHN Cp7800), dive 166, ASPI2, site PP55, 12°49.8580′N 103°56.8110′W, 2627 m; 2 adult ♀ (MNHN Cp7763), dive 166, ASPI3, site PP55, 12°49.8590′N 103°56.8110′W, 2626 m; 38 adult ♀ (MNHN Cp7761), 1 adult ♂ (MNHN Cp7762), 1 subadult ♀ of copepodid V (MNHN Cp7772), dive 166, ASPI4, site PP55, 12°49.8600′N 103°56.8080′W, 2627 m; 7 adult ♀ (MNHN Cp7805), dive 166, ASPI5, site PP55, 12°49.8510′N 103°56.8050′W, 2626 m; 3 adult ♀ (MNHN Cp7845), dive 166, ASPI6, site PP55, 12°49.8470′N 103°56.8050′W, 2626 m; 21 adult ♀ (MNHN Cp7810), dive 166, ASPI7, site PP55, 12°49.9940′N 103°56.5970′W, 2627 m; 28 adult ♀ (MNHN Cp7851), 2 adult ♂ (MNHN Cp7853), dive 166, ASPI8, site PP55, 12°49.8540′N 103°56.8050′W, 2627 m; 29 adult ♀ (MNHN Cp7839), 1 subadult ♀of copepodid V (MNHN Cp7847), dive 166, PBT3, site PP55, 12°49.8550′N 103°56.7830′W, 2627 m; 4 adult ♀ (MNHN Cp7798), 1 adult ♂ (MNHN Cp7801), dive 167, ASPI4, site PP-Pho8, 12°49.0760′N 103°56.5660′W, 2623 m; 6 adult ♀ (MNHN Cp7848), 1 adult ♂ (MNHN Cp7850), dive 167, ASPI5, site PP-Pho8, 12°49.0760′N 103°56.5640′W, 2623 m; 1 adult ♀ (MNHN Cp7753), dive 167, ASPI8, site PP-Pho8, 12°49.1920′N 103°56.3270′W, 2621 m; 3 adult ♀ (MNHN Cp7846), dive 167, PBT1, site PP-Pho8, 12°49.0790′N 103°56.5520′W, 2623 m; 23 adult ♀ (MNHN Cp7712, MNHN-Cp7719), dive 168, GBT, site PP-Pho1, 12°48.1520′N 103°56.2660′W, 2620 m; 4 adult ♀ (MNHN Cp7794), 1 adult ♂ (MNHN Cp7825), dive 168, PBT1, site PP-Hot3, 12°48.1450′N 103°56.2670′W, 2624 m; 10 adult ♀ (MNHN Cp7791), 1 adult ♂ (MNHN Cp7793), dive 168, PBT3, site PP-Hot3, 12°48.1430′N 103°56.2650′W, 2624 m; 7 adult ♀ (MNHN Cp7827), dive 169, ASPI4, site PP-Pho5, 12°48.6080′N 103°56.4030′W, 2622 m; 2 adult ♀ (MNHN Cp7828), dive 169, ASPI5, site PP-Pho5, 12°48.6220′N 103°56.3890′ W, 2622 m; 2 adult ♀ (MNHN Cp7830), dive 169, ASPI6, site

PP-Pho5, 12°48.6220′N 103°56.3890′W, 2622 m; 2 adult ♀ (MNHN Cp7812), dive 169, ASPI7, site PP-Pho5, 12°48.6180′N 103°56.3970′W, 2622 m; 7 adult ♀ (MNHN Cp7833), dive 169, ASPI8, site PP-Pho5, 12°48.6190′N 103°56.3990′W, 2622 m; 1 adult ♀ (MNHN Cp7773), dive 169 PBT2, site PP-Pho9, 12°48.6240′N 103°56.3950′W, 2624 m; 58 adult ♀ (MNHN Cp7788), 2 ♂ (MNHN Cp7832), dive 169, PBT3, site PP-Pho9, 12°48.6310′N 103°56.3970′W, 2624 m.

LOCALITY REPORTED

East Pacific Rise, 9°N, 13°N and 21°N (Humes 1987, 1989b; Humes & Segonzac, 1998; Ivanenko & Defaye, 2006a).

Stygiopontius pectinatus Humes, 1987

Humes, 1987: 723–724, figures 46–47; Ivanenko & Defaye, 2006a: 341, figure 2.
Stygiopontius bulbisetiger Humes, 1996: 641–644, figures 21–22; Ivanenko & Defaye, 2006a: 341.

TYPE MATERIAL EXAMINED

Paratypes of *Stygiopontius pectinatus*: 10 adult ♀ in ethanol (USNM 231969), 4 adult ♀ (USNM 1098834) on sealed glycerol slide, Mid-Atlantic Ridge, site TAG, 26°08.3′N 44°49.6′W, 3620–3650 m. Types of *Stygiopontius bulbisetiger*: holotype ♀ in ethanol (USNM 268320), 1 ♀ (USNM 1099005) on sealed glycerol slide, Mid-Atlantic Ridge, site Snake Pit, 23°23′N 44°56′W, 3520 m.

ADDITIONAL MATERIAL EXAMINED

14 adult ♀ from Mid-Atlantic Ridge, cruise EXOMAR (July–August 2005, RV 'L'Atalante', ROV 'Victor 6000'), dive 259, PBT2, 12 August 2005, site TAG, 26°08.2276′N 44°49.5731′W, 3774 m. All specimens were preserved in 70% ethanol and stored in Ifremer.

LOCALITY REPORTED

Marianna Back-Arc Basin (Humes, 1990); Mid-Atlantic Ridge: 4°S, 23°N, 26°N and, 29°N (Humes, 1987, 1996; Ivanenko, 1998; Ivanenko *et al.*, 2006).

REMARKS

Stygiopontius lumiger Humes, 1989b and *S. bulbisetiger* Humes, 1996 known only from females are synonymized respectively with *S. sentifer* and *S. pectinatus* as suggested without comment by Ivanenko & Defaye (2006a). Adult females of *S. lumiger* and *S. bulbisetiger* are considered the female copepodid V of *S. sentifer* and *S. pectinatus*, respectively. The genital somite of adult females of *S. lumiger* and *S. bulbisetiger* lack genital openings and leg 6 is represented by one seta located laterally on the posterior part of the somite. The logic of the analysis follows that for *A. atlanteus*.

Table 4. Records of subadult copepodid and naupliar stages of Dirivultidae collected in sediment traps at the East Pacific Rise, 13°N. For details of traps' settings see Table 1.

Trap	Flacon	Number of specimens	Stage
PPS 10	A1	30+	Copepodid I
PPS 10	A2	46	Copepodid I
PPS 10	A3	14+	Copepodid I
PPS 10	A4	6	Copepodid I
PPS 10	A5	18	Copepodid I
PPS 10	A6	15	Copepodid I
PPS 10	A7	55+	Copepodid I
PPS 10	A8	90+	Copepodid I
PPS 10	A9	12	Copepodid I
PPS 20	B1	3	Copepodid I
PPS 20	B2	4	Copepodid I
PPS 20	B3	2	Copepodid I
PPS 20	B4	4	Copepodid I
PPS 20	B6	10	Copepodid I
PPS 20	B7	50	Copepodid I
PPS 20	B8	50+	Copepodid I
PPS 20	B9	2	Copepodid I
PPS 20	B10	15	Copepodid I
PPS 30	C1	1	Copepodid I
PPS 30	C2	12	Copepodid I
PPS 30	C3	18	Copepodid I
PPS 30	C4	8	Copepodid I
PPS 30	C5	3	Copepodid I
PPS 30	C6	5	Copepodid I
PPS 30	C7	19	Copepodid I
PPS 30	C8	19	Copepodid I
PPS 30	C9	3	Copepodid I
PPS 40	D3	1	Copepodid I
PPS 40	D12	1	Copepodid I
PPS 10	A6	1	Copepodid II
PPS 20	B4	1	Nauplius
PPS 30	C2	1	Nauplius
PPS 40	D3	1	Nauplius
PPS 40	D4	3	Nauplius
PPS 40	D12	1	Nauplius
PPS 40	D14	1	Nauplius

Rhogobius Humes, 1987

Rhogobius rapunculus (Humes & Segonzac, 1998) comb. nov. Ivanenko, Segonzac & Ferrari

Aphotopontius rapunculus Humes & Segonzac, 1998: 53–55, figures 1 & 2; Ivanenko & Defaye, 2006a: 328, 338.

TYPE MATERIAL EXAMINED

Paratype 1 ♀ (USNM 1098800) on sealed glycerol slide, East Pacific Rise, dive 614 (September–November 1991, cruise HERO91, RV 'Nadir', manned submersible 'Nautile'), site Barbecue, 9°50′N 104°17′W, 2505 m.

REMARKS

The species *Aphotopontius rapunculus* Humes & Segonzac, 1998 is here transferred to the genus *Rhogobius* Humes, 1987 because it possesses the hypothesized derived features of this genus: last abdominal somite with lobes at sides of the anal operculum; second segment of the antennal endopod elongate and slender (Ivanenko & Defaye, 2006a). In addition, *Rhogobius rapunculus* (Humes & Segonzac, 1998), as well as its congeners *R. contractus* and *R. pressulus*: (1) possesses setal formula of leg 4 endopod (0-1; I) identical to all species of *Aphotopontius*; and (2) lacks a seta of the coxal endite of the maxilla, an attribute that these species share with all species of *Ceuthoecetes*, *Dirivultus* and *Nilva*, as well as with most copepods of the order Siphonostomatoida (see Mahatma *et al.*, 2008).

NAUPLII AND COPEPODIDS OF DIRIVULTIDAE GEN. SP.

MATERIAL EXAMINED

East Pacific Rise, 13°N, sediment trap PPS 10, PPS 20, PPS 30, and PPS 40 deployed during HOPE cruise and recovered during AMISTAD cruise (see Table 1). 516+ copepodids of stage I of Dirivultidae gen. sp. (Copepoda: Siphonostomatoida) in 29 samples obtained by all four sediment traps; 1 copepodid of stage II of Dirivultidae gen. sp. in 1 sample obtained by the sediment trap PPS 10 over Parigo site; 8 nauplii of Dirivultidae gen. sp. in 6 samples obtained by 3 sediment traps: PPS 20, PPS 30 and PPS 40 over sites Genesis and Parigo and seamount 'Marginal High' (see Table 4). All specimens were preserved in 70% ethanol and stored in the Muséum National d'Histoire Naturelle, Paris.

REMARKS

A large number of dirivultid copepodids I and some lecithotrophic nauplii identified as Dirivultidae have been recovered from sediment trap samples from around deep-sea hydrothermal communities of the East Pacific Rise, 13°N. More specimens of dirivultid copepodid I were collected in the sediment traps than any other copepodid stage, including adults, or any other category of invertebrates such as polychaetes, gastropods, amphipods, ostracods, and decapod larvae.

The first record for a dirivultid copepodid I is from the Atlantic Ocean in plankton samples taken over a hydrothermal vent on the Mid-Atlantic Ridge between 2260 and 2280 m at 29°10′N 43° 10′W (Ivanenko, 1998). Later lecithotrophic dirivultid nauplii, without labrum or mouth, were hatched in shipboard aquaria from embryo sacs of the female dirivultid *Stygiopontius pectinatus* Humes, 1987 that had been washed from freshly collected specimens of the shrimp *Rimicaris exoculata* from the Mid-Atlantic Ridge at 5°S (Ivanenko *et al.*, 2007). The dirivultid copepodids I were found with a few other juvenile dirivultid copepodid stages and adults of *Rimipontius mediospinifer*, *Stygiopontius cladarus* and *S. pectinatus*. Specimens of copepodid I are characterized by different body lengths, and presumably represent different species of dirivultids. Lecithotrophic nauplii tentatively identified as dirivultids co-occurred with these copepodids.

Specimens of copepodid I and co-occurring nauplii from the East Pacific Rise were found in samples that included several species of adult dirivultids (*Exrima walteri* sp. nov., *Exrima singular*, *Aphotopontius* sp., *Stygiopontius* sp., *Ceuthoecetes* sp., *Humesipontius arthuri* Ivanenko & Ferrari, 2003a and *Scotoecetes introrsus* Humes 1987), as well as adult harpacticoids belonging to Tegastidae (*Smacigastes* sp.) and copepodid I of Cerviniidae, cyclopoids belonging to Cyclopinidae (*Barathricola* sp.), poecilostomatoids belonging to Oncaeidae (*Oncaea* cf. *praeclara* Humes, 1988), the mormonilloid *Neomormonilla extremata* (Ivanenko & Defaye, 2006b), and adults and copepodid I of Misophriidae (Misophrioida). Remarkably only one copepodid stage 2 and no other subadult stages of Dirivultidae have been observed in the samples collected by the sediment traps. Nauplii were found usually in the sediment traps that were farthest from hydrothermal vents and 50 m above the hydrothermal field. Juvenile copepodids of dirivultids were found in largest numbers in sediment traps that were closest to the hydrothermal field. Our observations and cultivation of shallow water siphonostomatoids suggest that copepodid I of dirivultids may not feed despite possessing a well-developed feeding apparatus if it retains naupliar yolk and moults to copepodid II relatively quickly (Ivanenko *et al.*, 2001; Ivanenko & Ferrari, 2003b). It appears that copepodid I specimens develop from nauplii that occur higher in the water column above the hydrothermal field. The presence of nauplii higher in the water column may happen if females with embryo sacs migrate upward before releasing embryos, although it is also possible that nauplii of dirivultids were insufficiently collected in the sediment traps on which dirivultid copepodid I specimens were found. The absence of juvenile dirivultid copepodids of later stages in the plankton samples over hypothermal fields suggests that copepodid I is either the settlement stage or the stage that associates with sediment flock collected by the sediment traps (Ivanenko *et al.*, 2007).

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