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Copepoda from deep-sea hydrothermal sites and cold seeps: description of a new species of *Aphotopontius* from the East Pacific Rise and general distribution

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Abstract: Twenty-four poecilostomatoid and siphonostomatoid copepods are reported from hydrothermal sites in the eastern Pacific and on the Mid-Atlantic Ridge. These include two siphonostomatoids from the East Pacific Rise: *Aphotopontius rapunculus*, new species, and *Stygiopontius mirus*, a species previously known only from the Mid-Atlantic Ridge. Ecological remarks and a synoptic table of 67 species of copepods known at this time from hydrothermal sites and cold seeps are presented.

Résumé : *Copépodes des sites hydrothermaux profonds et des suintements froids : description d'une nouvelle espèce de* Aphotopontius *de la dorsale du Pacifique Oriental et distribution générale.*
Vingt-quatre copépodes (Poecilostomatoida et Siphonostomatoida) sont signalés sur des sites hydrothermaux de la dorsale du Pacifique oriental et de la dorsale médio-Atlantique. Ceux-ci incluent deux siphonostomatoides : *Aphotopontius rapunculus*, nouvelle espèce, de la dorsale du Pacific oriental, et *Stygiopontius mirus*, une espèce connue seulement de la dorsale médio-Atlantique. Des remarques écologiques et un tableau synoptique des 67 espèces de copépodes connus à ce jour des sites hydrothermaux et des zones de suintements froids sont présentés.

Keywords: Copepoda, Poecilostomatoida, Siphonostomatoida, *Aphotopontius*, hydrothermal vents

Introduction

Copepoda, particularly Siphonostomatoida, commonly occur at deep-sea hydrothermal vents on active spreading zones or at cold seeps (Humes, 1991a). They have often been recovered in large numbers from these sites. Certain species are apparently loosely associated with macrofauna, such as tube worms, bivalves, polychaetes, and crustaceans (Humes, 1987).

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Among the 12 genera of Siphonostomatoida (Dirivultidae) already known from deep-sea hydrothermal vents, *Aphotopontius*, with 12 species including the new species described below, ranks second in number of species, after *Stygiopontius*, which contains 22 species. Nine species of *Aphotopontius* have been found in the northeastern Pacific (see Table 1 for authors names and references): *A. acanthinus*, *A. arcuatus*, *A. baculigerus*, *A. flexispina*, *A. forcipatus*, *A. hydronauticus*, *A. limatulus*, *A. mammillatus*, and *A. probolus*. To these, the new species described below may now be added, bringing to 10 the number of species in these areas. The remaining two species of

Aphotopontius, *A. atlanteus* and *A. temperatus*, occur on the Mid-Atlantic Ridge. In this paper, new records and general distribution for 23 species of copepods are reported and one new species of *Aphotopontius* is described.

Materials and methods

The copepods reported in this study come from several French cruises (1991-1995), using the submersible *Nautile*, operating from the N/O *Nadir* (IFREMER). They were collected by means of a slurp gun among the invertebrates living in the hydrothermal fluids or sorted from washings of polychaetes, vestimentiferans, bivalves, or shrimps. The copepods were measured and dissected in lactic acid, following the technique described by Humes & Gooding (1964). The drawings were made with the aid of a camera lucida.

For the previously reported species, the latitudes and longitudes are at times slightly abbreviated. For precise locations, reference should be made to the original publications.

Poecilostomatoida Thorell, 1859
Clausidiidae Embleton, 1901
Hyphalion Humes, 1987
Hyphalion captans Humes, 1987

GUAYNAUT: PL 13, 25 November 1991, Guaymas Basin, site Claire, 27°00.94'N, 111°24.66'W, depth 2025 m. 3 ♀♀ 6 ♂♂.

Locality previously reported: Guaymas Basin (Humes, 1987).

Erebonasteridae Humes, 1987
Erebonaster Humes, 1987
Erebonaster protentipes Humes, 1987

GUAYNAUT: PL 13, 25 November 1991, Guaymas Basin, site Claire, 27°00.04'N, 111°24.66'W, depth 2025 m. 1 ♂.

Locality previously reported: Guaymas Basin (Humes, 1987).

Oncaeidae Giesbrecht, 1892
Oncaea Philippi, 1843
Oncaea praeclara Humes, 1988

HERO 91: PL 07, 11 October 1991, East Pacific Rise, site Brasoucade sud, 09°50.09'N, 104°17.43'W, depth 2500 m. 2 ♀♀;

PL 09, 13 October 1991, East Pacific Rise, site Worm Barbecue, 09°50'N, 104°17'W, depth 2505 m. 1 ♂.

Localities previously reported: East Pacific Rise, Galapagos Rift, and Guaymas Basin (Humes, 1988 a, b).

Siphonostomatoida Thorell, 1859
Dirivultidae Humes & Dojiri, 1980
Aphotopontius Humes, 1987
Aphotopontius acanthinus Humes & Lutz, 1994

HERO 91: PL 06, 10 October 1991, East Pacific Rise, site Worm Barbecue, 09°50'N, 104°17'W, depth 2505 m. 44 ♀♀.

Locality previously reported: East Pacific Rise (Humes & Lutz, 1994).

Aphotopontius atlanteus Humes, 1996

DIVA 1: DV 01, 7 May 1994, Mid-Atlantic Ridge, site Tour Eiffel, 37°17.49'N, 32°16.60'W, depth 1685 m. 25 ♀♀;

DV 03, 9 May 1994, site Statue de la Liberté, 37°17.55'N, 32°16.47'W, depth 1624 m. 28 ♀♀;

DV 14, 22 May 1994, site Menez Gwen, 37°50.46'N, 31°31.35'W, depth 845 m. 39 ♀♀;

DV 16-4, 24 May 1994, site Menez Gwen, 37°50.46'N, 31°31.35'W, depth 845 m. 20 ♀♀;

DV 17, 25 May 1994, site US 7, 37°17.27'N, 32°16.53'W, depth 1700 m. 36 ♀♀;

DV 18, 26 May 1994, site VIII (Isabel), 37°17.36'N, 32°16.64'W, depth 1687 m. 21 ♀♀ ;

DV 19, 27 May 1994, site Nuno, 37°17.50'N, 32°17'W, depth 1727 m. 63 ♀♀.

DIVA 2:

PL 01, 3 June 1994, Mid-Atlantic Ridge, site Isabel, 37°17.36'N, 32°16.64'W, depth 1685. 47 ♀♀, 3 ♂♂, 1 copepodid;

PL 02, 4 June 1994, site Sintra, 37°17.50'N, 32°16.47'W, depth 1622 m. 39 ♀♀;

PL 04, 6 June 1994, site Tour Eiffel, 37°17.32'N, 32°16.51'W, depth 1685 m. 62 ♀♀;

PL 05, 7 June 1994, near site Hélène, 37°17.48'N, 32°16.87'W, depth 1725 m. 92 ♀♀, 1 ♂;

PL 06, 8 June 1994, site Isabel, 37°17.36'N, 32°16.64'W, depth 1685 m. 68 ♀♀;

PL 07, 9 June 1994, site Pagode, 37°17.63'N, 32°16.95'W, depth 1629 m. 93 ♀♀;

PL 08, 10 June 1994, site Tour Eiffel, 37°17.32'N, 32°16.51'W, depth 1685 m. 61 ♀♀, 3 ♂♂, 2 copepodids;

PL 09, 11 June 1994, site Tour Eiffel, 37°17.32'N, 32°16.51'W, depth 1685 m. 3 ♀♀;

PL 11, 13 June 1994, site Menez Gwen, 37°50.54'N, 31°31.30'W, depth 866 m. 26 ♀♀;

PL 12, 14 June 1994, site Menez Gwen, 37°50.54'N, 31°31.30'W, depth 866 m. 82 ♀♀, 1 copepodid;

PL 13, 15 June 1994, site Menez Gwen, 37°50.54'N, 31°31.30'W, depth 866 m. 4 ♀♀;

PL 19, 25 June 1994, site Pagode, 37°17.63'N, 32°16.95'W, depth 1629 m. 15 ♀♀;

PL 20, 26 June 1994, site Tour Eiffel, 37°17.32'N, 32°16.51'W, depth 1685 m. 10 ♀♀.

Localities previously reported: Mid-Atlantic Ridge (Humes, 1996, 1997) .

Aphotopontius limatulus Humes, 1987

HERO 91: PL 06, 10 October 1991, East Pacific Rise, site Worm Barbecue, 09°50'N, 104°17'W, depth 2505 m. 1 ♀;

PL 08, 12 October 1991, site Hole to Tell, 09°50.30'N, 104°17.50'W, depth 2530 m. 1 ♀.

Localities previously reported: East Pacific Rise, Galapagos Rift (Humes, 1987, 1990a).

Aphotopontius mammillatus Humes, 1987

HERO 91: PL 18, 22 October 1991, East Pacific Rise, site Elsa, 12°48.13'N, 103°56.30'W, depth 2630 m. 3 ♀♀.

GUAYNAUT: PL 06, 15 November 1991, Guaymas Basin, site Amandine, 27°00.94'N, 111°24.50'W, depth 2020 m, and site Claire, 27°00.94'N, 111°24.66'W depth 2025 m. 3 ♀♀;

PL 08, 17 November 1991, site Claire, 27°00.94'N, 111°24.66'W, depth 2025 m. 6 ♀♀;

PL 13, 25 November 1991, site Claire, 27°00.94'N, 111°24.66'W, depth 2025 m. 1 ♀.

Localities previously reported: East Pacific Rise, Galapagos Rift, Guaymas Basin (Humes, 1987); East Pacific Rise (Humes, 1989a); East Pacific Rise, Galapagos Rift (Humes, 1990a).

Aphotopontius rapunculus, sp. nov.
Figs 1, 2

Type material: 2 ♀♀, East Pacific Rise, HERO 91, PL 09, site Barbecue, 09°50'N, 104°17'W, depth 2505 m, 13 October 1991. Holotype deposited in the Museum national d'Histoire naturelle, Paris. Paratype (dissected) in the collection of the author.

Female: Body (Fig. 1a) with moderately broad prosome. Length (not including setae on caudal rami) 0.90 mm (0.89-0.91 mm) and greatest width 0.41 mm (0.41-0.42 mm), based on 2 specimens in lactic acid. Greatest dorsoventral thickness 0.27 mm. Somite bearing leg 1 fused with cephalosome, but sides of cephalosome at position of leg 1 showing slight expansion. Epimera of metasomal somites rounded. Ratio of length to width of prosome 1.5:1. Urosome relatively short. Ratio of length of prosome to that of urosome 2.65:1.

Somite bearing leg 5 (Fig. 1b) 70 x 135 μm. Genital double-somite in dorsal view 125 x 166 μm, wider than long, widest near midregion, lateral margins in posterior half slightly undulating. Genital areas located dorsolaterally near widest part of double-somite, both bearing obscure minute seta (Fig. 1b). Three postgenital somites from anterior to posterior 42 x 82, 26 x 78, and 31 x 75 μm. Anal somite with pair of terminal lobes between caudal rami (Fig. 1c).

Caudal ramus (Fig. 1c) short, unornamented, 25 x 18 μm, little longer than wide, ratio 1.39:1. Lateral seta 44 μm, dorsal seta 20 μm, outermost terminal seta 25 (m, innermost terminal seta 19 μm, and 2 median terminal setae 91 μm (outer) and 208 μm (inner). All setae smooth.

Body surface without visible sensilla.

Egg sac not seen.

Rostral area undeveloped (Fig. 1d). Antennule (Fig. 1e) 268 μm long. Lengths of its 10 segments (measured along their posterior nonsetiferous margins): 55 (91 μm along anterior margin), 36, 5, 23, 16, 15, 16, 23, 23, and 37 μm, respectively. Formula for armature: 12, 8, 2, 4, 2, 2, 2, 2, 2 + 1 aesthetasc, and 12. All setae smooth. Antenna (Fig. 1f) 177 μm long not including terminal armature. Basis elongated. Minute exopod with 3 setae. Endopod 2-segmented, first segment broad, width 13 μm, second segment slender, width at midregion 6 μm, bearing 1 subterminal outer seta and 3 terminal setae, longest terminal seta 23 μm.

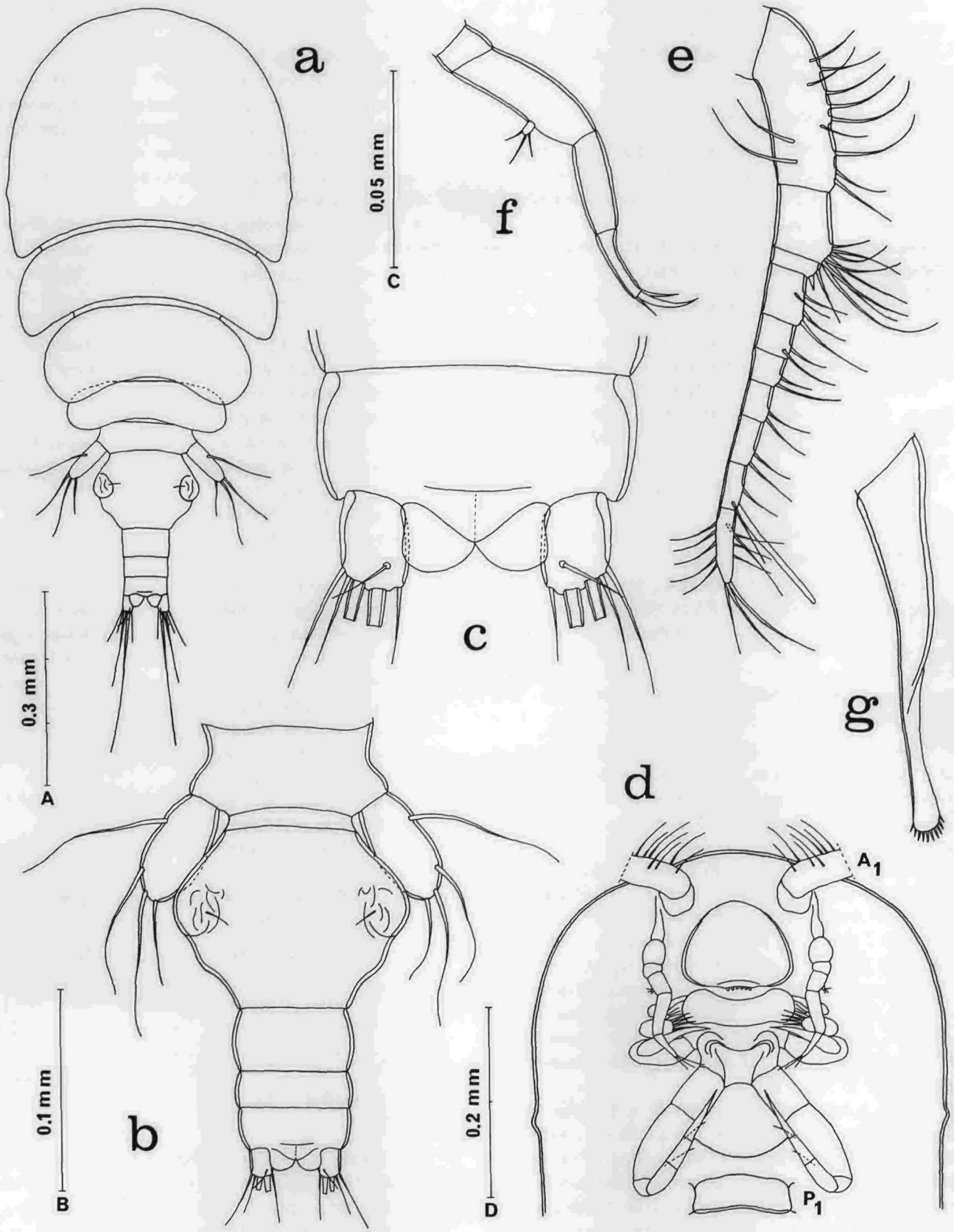
Oral cone (Fig. 1d) with few minute median knobs on posterior (distal) margin of labrum. Mandible (Fig. 1g) elongate, 83 μm, slender in distal half with expanded tip bearing marginal row of setules. Maxillule (Fig. 2a) with outer lobe bearing 4 setae, inner lobe 3 setae. Maxilla (Fig. 2b) 2-segmented, second segment clawlike, slightly sigmoid, with few subterminal setules (long seta usually present in congeners adjacent to clawlike second segment not seen). Maxilliped (Fig. 2c) 4-segmented. First segment with inner distal seta. Long second segment without visible seta. Third and fourth segments (forming part of claw) with 1 seta. Claw 47 μm long.

Ventral area between maxillipeds and first pair of legs (Fig. 1d) slightly protuberant.

Legs 1-4 (Fig. 2d-g) with 3-segmented rami except for 2-segmented endopod in leg 4 (Fig. 2h). Formula for armature as follows (Roman numerals representing spines, Arabic numerals indicating setae):

P_1	coxa 0-0	basis 1-I	exp I-1;	I-1;	III,4
			enp 0-1;	0-2;	1,2,3
P_2	coxa 0-0	basis 1-0	exp I-1;	I-1;	III,I,4
			enp 0-1;	0-2;	1,2,3
P_3	coxa 0-0	basis 1-0	exp I-1;	I-1;	III,I,5
			enp 0-1;	0-2;	1,I,3
P_4	coxa 0-0	basis 1-0	exp I-l;	I-1;	III,I,4
			enp 0-1;	1,1	

Leg 1 with spine on inner side of basis stout, barbed, 33 μm long. Exopod with stout spine on first segment, other spines setiform, especially distal spine on third segment (Fig. 2d). Leg 2 with spines on exopod segments 1 and 2 directed inward (Fig. 2e). Leg 3 with inward directed spine


a
0.3 mm
A
b
0.1 mm
B
0.05 mm
C
f
c
e
g
d
0.2 mm
D
A1
P1

on exopod segment 1; posteroventral margin of intercoxal plate convex (Fig. 2f). Leg 4 (Fig. 2g) with exopod 185 μm long. Endopod (Fig. 2h) with first segment 26 x 21 μm, its inner seta 166 μm; second segment 62 x 29 μm, its inner seta 120 μm and its terminal seta 78 μm.

Leg 5 (Figs 1b, 2i) with 2 segments joined together, only evidence of 2-segmented condition being slight notch on inner margin. Dimensions in dorsal view 78 x 35 μm (Fig. 1b), in lateral flat view 78 x 65 μm (Fig. 2i). Leg 5 bearing usual 4 setae.

Leg 6 probably represented by small seta on genital area (Fig. 1b).

Color of living specimens unknown.

Male: Unknown.

Etymology: The specific name *rapunculus*, Latin meaning a little turnip, alludes to the shape of the female genital double-somite as seen in dorsal view.

Remarks: All species of the genus *Aphotopontius* occur at deep-sea hydrothermal sites: *A. acanthinus* Humes and Lutz, 1994, *A. arcuatus* Humes, 1987; *A. atlanteus* Humes, 1996; *A. baculigerus* Humes, 1987; *A. flexispina* Humes, 1987; *A. forcipatus* Humes, 1987; *A. hydronauticus* Humes, 1989; *A. limatulus* Humes, 1987; *A. mammillatus* Humes, 1987; *A. probolus* Humes, 1990; and *A. temperatus* Humes, 1997. *Aphotopontius rapunculus* differs from all congeners in the shape of the female genital double-somite, with the possible exception of *A. baculigerus*, *A. forcipatus*, and *A. limatulus*. These three species are readily distinguished from *A. rapunculus*, however, by their long slender caudal rami (in the female 13.7:1 and 11.1, 5.64:1, and 10:1, respectively). Other detailed features of *A. rapunculus* are also distinctive: (1) the two lobes of the anal somite between the caudal rami, (2) the absence of a long accessory seta on the maxilla, (3) the apparent absence of a seta on the second segment of the maxilliped, (4) the setiform spines on the second and third segments of the exopod of leg 1, (5) the strongly convex posteroventral margin of the intercoxal plates of legs 3 and 4, and (6) the broad unsegmented leg 5.

Aphotopontius temperatus Humes, 1997

DIVA 2: PL 05, 7 June 1994, Mid-Atlantic Ridge, near site Hélène, 37°17.48'N, 32°16.87'W, depth 1725 m. 2 ♀♀.

Additional locality: Mid-Atlantic Ridge (Humes, 1997).

Ceuthoecetes Humes & Dojiri, 1980
Ceuthoecetes acanthothrix Humes, 1987

HERO 91: PL 07, 11 October 1991, East Pacific Rise, site Brasoucade sud, 09°50.09'N, 104°17.43'W, depth 2500 m. 1 ♂;

PL 09, 13 October 1991, site Barbecue, 09°50'N, 104°17'W, depth 2505 m. 1 ♂.

Localities previously reported: East Pacific Rise, Galapagos Rift (Humes, 1987, 1990a).

Ceuthoecetes aliger Humes & Dojiri, 1980

HERO 91: PL 09, 13 October 1991, East Pacific Rise, site Barbecue, 09°50'N, 104°17'W, depth 2505 m. 1 ♀.

Localities previously reported: East Pacific Rise, Galapagos Rift (Humes & Dojiri, 1980b; Humes, 1990a), East Pacific Rise (Humes, 1989a).

Ceuthoecetes cristatus Humes, 1987

HERO 91: PL 07, 11 October 1991, East Pacific Rise, site Brasoucade sud, 09°50.09'N, 10°17.43'W, depth 2500 m. 1 ♂.

Localities previously reported: East Pacific Rise, Galapagos Rift (Humes and Dojiri, 1980b), East Pacific Rise (Humes, 1987, 1990a).

Rimipontius Humes, 1996
Rimipontius mediospinifer Humes, 1996

MICROSMOKE: PL 20, 5 December 1995, Mid-Atlantic Ridge, site Logatchev (Irina 2), 14°45.18'N, 44°58.76'W, depth 3049 m. 1 ♀.

Locality previously reported: site Snake Pit, Mid-Atlantic Ridge (Humes, 1996).

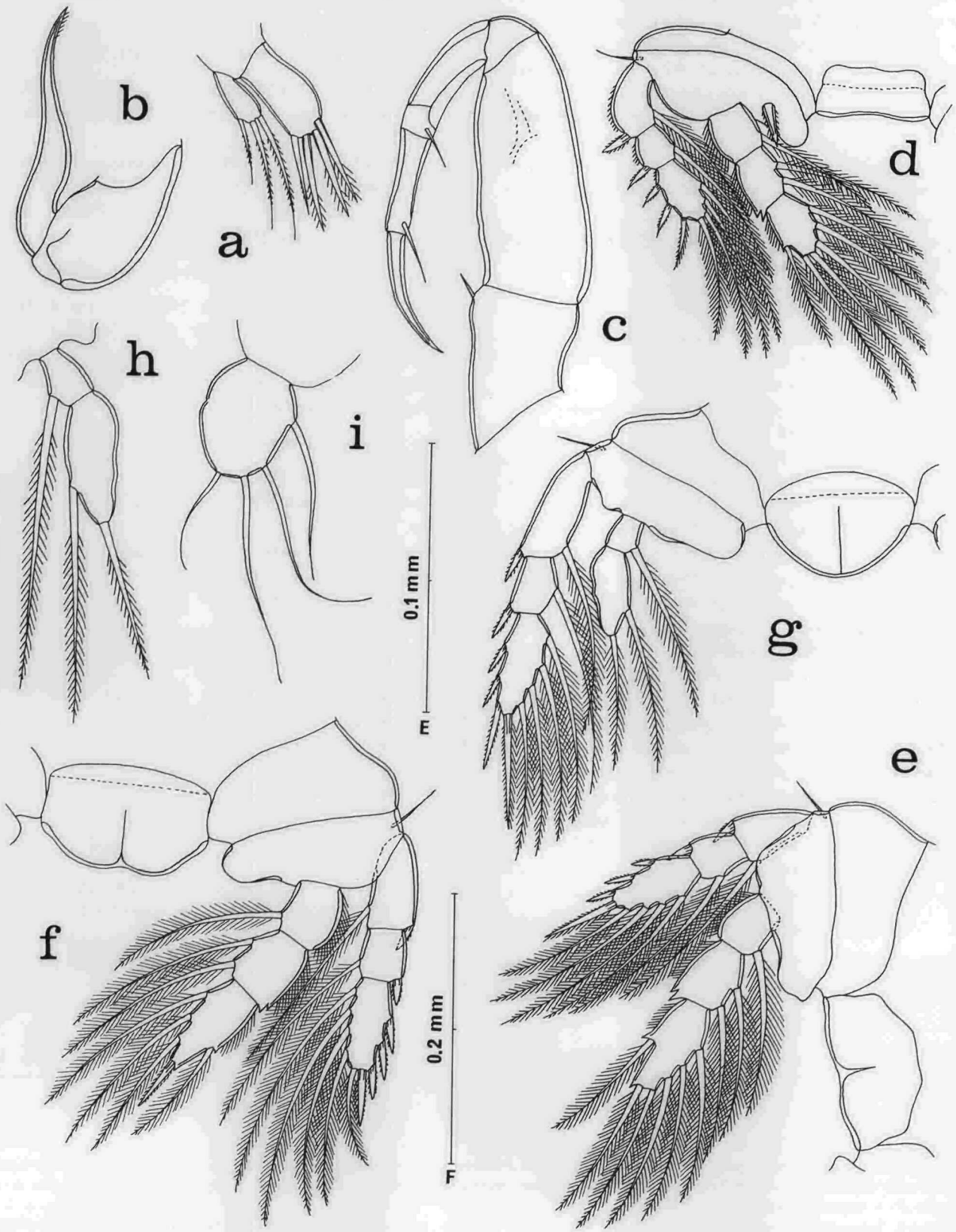
Scotoecetes Humes, 1987
Scotoecetes introrsus Humes, 1987

HERO 91: PL 18, 22 October 1991, East Pacific Rise, site Elsa, 12°48.13'N, 103°56.30'W, depth 2630 m. 5 ♀♀, 4 ♂♂, 1 copepodid.

Locality previously reported: East Pacific Rise (Humes, 1987).

Figure 1. *Aphotopontius rapunculus*, n. sp. Female. (a) body, dorsal (scale A). (b) urosome, dorsal (B). (c) anal somite and caudal rami, dorsal (C). (d) cephalosome, ventral (D). (e) antennule, posteroventral (B). (f) antenna, antero-inner (B). (g) mandible, ventral (C). A_1 = antennule, P_1 = intercoxal plate of leg 1.

Figure 1. *Aphotopontius rapunculus*, n. sp. Femelle. (a) corps, vue dorsale (échelle A). (b) urosome, vue dorsale (B). (c) somite anal et rame caudale, vue dorsale (C). (d) céphalosome, vue ventrale (D). (e) antennule, vue postéroventrale (B). (f) antenne, vue antéro-intérieure (B). (g) mandibule, vue ventrale (C). A_1 = antennule, P_1 = plaque intercoxale de la première patte.


b
a
c
d
h
i
0.1 mm
E
g
e
f
0.2 mm
F

Stygiopontius Humes, 1987
Stygiopontius cinctiger Humes, 1987

HERO 91: PL 06, 10 October 1991, East Pacific Rise, site Worm Barbecue, 09°50'N, 104°17'W, depth 2505 m. 2 ♀♀;
PL 09, 13 October 1991, site Worm Barbecue, 09°50'N, 104°17'W, depth 2505 m. 2 ♀♀.
Locality previously reported: East Pacific Rise (Humes, 1987, 1989a).

Stygiopontius flexus Humes, 1987

GUAYNAUT: PL 06, 15 November 1991, Guaymas Basin, site Amandine, 27°00.94'N, 111°24.50'W, and site Claire, 27°00.94'N, 111°24.66'W, depth 2020 m. 1 ♀;
PL 08, 17 November 1991, Guaymas Basin, site Claire, 27°00.94'N, 111°24.66'W, depth 2020 m. 3 ♀♀.
HERO 91: PL 10 October 1991, East Pacific Rise, site Worm Barbecue, 09°50'N, 104°17'W, depth 2505 m. 2 ♀♀.
Locality previously reported: Guaymas Basin (Humes, 1987).

Stygiopontius hispidulus Humes, 1987

HERO 91: PL 05, 8 October 1991, East Pacific Rise, sites Totem and Genesis, 12°48.80'N, 103°56.46'W, depth 2630 m. 8 ♀♀;
PL 06, 10 October 1991, site Worm Barbecue, 09°50'N, 104°17'W, depth 2505 m. 3 ♀♀;
PL 08, 12 October 1991, site Hole to Tell, 09°50.30'N, 104°17.50'W, depth 2530 m. 236 ♀♀;
PL 09, 13 October 1991, site Barbecue, 09°50'N, 104°17'W, depth 2505 m. 23 ♀♀.
Locality previously reported: East Pacific Rise (Humes 1987, 1989a).

Stygiopontius mirus Humes, 1996

HERO 91: PL 09, 13 October 1991, East Pacific Rise, site Barbecue, 09°50'N, 104°17'W, depth 2505 m. 1 ♂.
Locality previously reported: site Snake Pit, Mid-Atlantic Ridge (Humes, 1996).

Stygiopontius mucroniferus Humes, 1987

HERO 91: PL 09, 13 October 1991, East Pacific Rise, site Barbecue, 09°50'N, 104°17'W, depth 2505 m. 1 ♀.
Locality previously reported: Guaymas Basin (Humes, 1987).

Stygiopontius paxillifer Humes, 1989

HERO 91: PL 06, 10 October 1991, East Pacific Rise, site Barbecue, 09°50'N, 104°17'W, depth 2505 m. 3 ♂♂.
Locality previously reported: East Pacific Rise (Humes, 1989b).

Stygiopontius rimivagus Humes, 1997

DIVA 2: PL 02, 04 June 1994, Mid-Atlantic Ridge, site Sintra, 37°17.50'N, 32°16.47'W, depth 1622 m. 3 ♀♀, 1 ♂;
PL 07, 09 June 1994, site Pagode, 37°17.63'N, 32°16.95'W, depth 1629 m. 1 ♂.
Locality previously reported: site Lucky Strike, Mid-Atlantic Ridge (Humes, 1997).

Stygiopontius sentifer Humes, 1987

HERO 91: PL 05, 08 October 1991, East Pacific Rise, sites Totem and Genesis, 12°48.80'N, 103°56.46'W, depth 2630 m. 2 ♀♀;
PL 06, 10 October 1991, site Worm Barbecue, 09°50'N, 104°17'W, depth 2505 m. 19 ♀♀.
Locality previously reported: East Pacific Rise (Humes, 1987, 1989a).

Stygiopontius verruculatus Humes, 1987

HERO 91: PL 09, 13 October 1991, East Pacific Rise, site Barbecue, 09°50'N, 104°17'W, depth 2505 m. 1 ♂.
Locality previously reported: East Pacific Rise (Humes, 1987).

Ecbathyriontidae Humes, 1987
Ecbathyrion Humes, 1987
Ecbathyrion prolixicauda Humes, 1987

HERO 91: PL 07, 11 October 1991, East Pacific Rise, site Brasoucade sud, 09°50.09'N, 104°17.48'W, depth 2500 m. 3 ♀♀.
Localities previously reported: East Pacific Rise (Humes, 1989a, 1990a), Galapagos Rift (Humes, 1990a).

Remarks on the distribution of copepods at vent areas

The distribution of species of copepods (Poecilostomatoida and Siphonostomatoida) at deep-sea hydrothermal

Figure 2. *Aphotopontius rapunculus*, n. sp. Female: a, maxillule, posterior (scale E). (b) maxilla, posterior (E). (c) maxilliped, posterior (E). (d) leg 1 and intercoxal plate, anterior (F). (e) leg 2 and intercoxal plate, anterior (F). (f) leg 3 and intercoxal plate, anterior (F). (g) leg 4 and intercoxal plate, anterior (F). (h) endopod of leg 4, anterior (B). (i) leg 5, flat inner view (F).

Figure 2. *Aphotopontius rapunculus*, n. sp. Femelle : (a) maxillule, vue postérieure (échelle E) ; (b) maxille, vue postérieure (E). (c) maxillipède, vue postérieure (E). (d) patte 1 et plaque intercoxale, vue antérieure (F). (e) patte 2 et plaque intercoxale, vue ant(rieure (F). (f) patte 3 et plaque intercoxale, vue antérieure (F). (g) patte 4 et plaque intercoxale, vue antérieure (F). (h) endopodite de la patte 4, vue antérieure (B). (i) patte 5, vue intérieure (F).

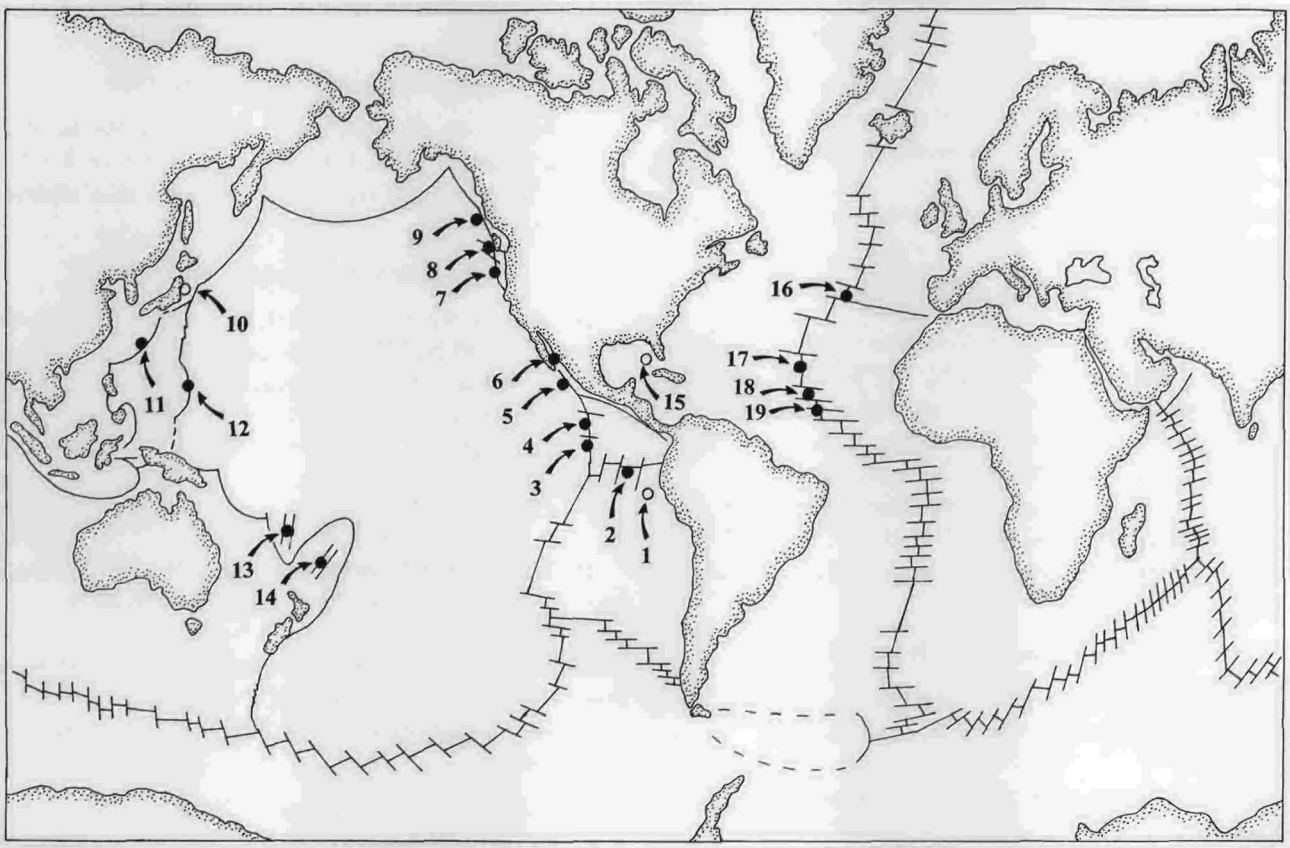


Figure 3. Deep-sea hydrothermal sites (•) and cold seeps (o) from which copepods have been reported. 1 = Paita zone, northern Peru at 5°S; 2 = Galapagos Rift; 3 = East Pacific Rise at 10°N; 4 = East Pacific Rise at 13°N; 5 = East Pacific Rise at 21°N; 6 = Guaymas Basin; 7 = Gorda Ridge; 8 = Juan de Fuca Ridge; 9 = Explorer Ridge; 10 = Sagami Bay, Japan; 11 = Minami-Ensei Knoll, Mid-Okinawa Trough, southwestern Japan; 12 = Mariana Back-Arc Basin; 13 = Fiji Back-Arc Basin; 14 = Lau Back-Arc Basin; 15 = West Florida Escarpment; 16 = Mid-Atlantic Ridge at 37°N (Lucky Strike and Menez Gwen); 17 = Mid-Atlantic Ridge at 26°N (TAG); 18 = Mid-Atlantic Ridge at 23°N (Snake Pit); 19 = Mid-Atlantic Ridge at 15°N (Logatchev).

Figure 3. Localisation des copépodes des sites hydrothermaux (•) et des zones de suintements froids (o). 1 = zone de Paita, nord Peru à 5°S ; 2 = segment des Galapagos ; 3 = dorsale du Pacifique oriental à 10°N ; 4, dorsale du Pacifique oriental à 13°N ; 5 = dorsale du Pacifique oriental à 21°N ; 6 = bassin de Guaymas ; 7 = dorsale Gorda ; 8 = dorsale Juan de Fuca ; 9 = dorsale Explorer ; 10 = baie de Sagami, Japon ; 11 = Minami-Ensei Knoll, fosse d'Okinawa, sud-ouest Japon ; 12 = bassin arrière-arc des Mariannes ; 13 = bassin arrière-arc des Fidji ; 14 = bassin arrière-arc de Lau ; 15 = escarpement ouest Floride ; 16 = dorsale médio-atlantique à 37°N (Lucky Strike et Menez Gwen) ; 17 = dorsale médio-atlantique à 26°N (TAG) ; 18 = dorsale médio-atlantique à 23° (Snake Pit) ; 19 = dorsale médio-atlantique à 15°N (Logatchev).

Table 1. Copepoda from deep-sea hydrothermal vents and cold seeps and their locations. For locations see Figure 3.

Tableau 1. Copépodes des sites hydrothermaux profonds et des suintements froids et leurs localités. Pour celles-ci voir la figure 3.

Taxon	Location	Source
CALANOIDA		
Spinicalanidae		
Isaacsicalanus paucisetus Fleminger, 1983	3	Fleminger, 1983; Grassle, 1986
MISOPHRIOIDA		
Misophriidae		
Misophtiopsis, n. sp. (Humes, in preparation)	8	Humes, in preparation
CYCLOPOIDA		
Cyclopinidae		
N. gen., n. sp. (Humes, in preparation)	8	Humes, in preparation
POECILOSTOMATOIDA		
Lubbockiidae		
Laitmatobius crinitus Humes, 1987 (see Huys & Böttger-Schnack, 1997)	6	Humes, 1987
Clausidiidae		
Hyphalion captans Humes, 1987	6	Humes, 1987; Humes & Segonzac, present paper
Hyphalion sagamiense Toda *et al.*, 1982	10	Toda *et al.*, 1992
Hyphalion tertium Defaye & Toda, 1994	1	Defaye & Toda, 1994
Hyphalion sp.	11	Hashimoto *et al.*, 1995
Erebonasteridae		
Erebonaster protentipes Humes, 1987	6	Humes, 1987; Humes & Segonzac, present paper
Amphicrossus altalis Humes & Huys, 1992	8	Humes & Huys, 1992
Amphicrossus spinulosus (Humes, 1989) (see Huys, 1991)	15	Humes, 1989c
Amphicrossus n. sp., in press	13	Martinez, in press
Oncaeidae		
Oncaea praeclara Humes, 1988	2, 4, 5	Humes, 1988a
Oncaea praeclara	4	Humes, 1989a
Oncaea praeclara	3	Humes & Segonzac, present paper

SIPHONOSTOMATOIDA		
Dirivultidae		
Aphotopontius acanthinus Humes & Luts, 1994	3	Humes & Luts, 1994
		Humes & Segonzac, present paper
Aphotopontius arcuatus Humes, 1987	2, 4, 5	Humes, 1987
Aphotopontius arcuatus	4	Humes, 1989a
Aphotopontius arcuatus	2, 5	Humes, 1990a
Aphotopontius atlanteus Humes, 1986	16	Humes, 1996, 1997; Humes & Segonzac present paper
Aphotopontius baculigerus Humes, 1987	2	Humes, 1987
Aphotopontius baculigerus	5	Humes, 1990a
Aphotopontius flexispina Humes, 1987	5	Humes, 1987
Aphotopontius forcipatus Humes, 1987	9	Humes, 1987
Aphotopontius forcipatus	7	Humes, 1990a
Aphotopontius forcipatus	8, 9	Humes & Huys, 1992
Aphotopontius forcipatus	18	Humes, 1996
Aphotopontius hydronauticus Humes, 1989	4	Humes, 1989a
Aphotopontius limatulus Humes, 1987	2, 5	Humes, 1987, 1990a
Aphotopontius limatulus Humes, 1987	3	Humes & Segonzac present paper
Aphotopontius mammillatus Humes, 1987	2, 5, 6	Humes, 1987
Aphotopontius mammillatus	2, 5	Humes, 1990a
Aphotopontius mammillatus	4	Humes, 1989a
Aphotopontius mammillatus	4, 6	Humes & Segonzac, present paper
Aphotopontius probolus Humes, 1990	2	Humes, 1990a
Aphotopontius rapunculus Humes & Segonzac, present paper	3	Humes & Segonzac, present paper
Aphotopontius temperatus Humes, 1997	16	Humes, 1997; Humes & Segonzac, present paper
Benthoxynus spiculifer Humes, 1984	8	Humes, 1984
Benthoxynus spiculifer	7	Humes, 1990a
Benthoxynus spiculifer	8, 9	Humes & Huys, 1992
Benthoxynus tumidiseta Humes, 1989	4	Humes, 1989a
Bythocheres prominulus Humes, 1988	15	Humes, 1988b
Ceuthoecetes acanthothrix Humes, 1987	2, 4, 5	Humes, 1987
Ceuthoecetes acanthothrix	2, 5	Humes, 1990a
Ceuthoecetes acanthothrix	3	Humes & Segonzac, present paper
Ceuthoecetes aliger Humes & Dojiri, 1980	5	Humes & Dojiri, 1980b; Humes, 1987
Ceuthoecetes aliger	2, 5	Humes, 1990a
Ceuthoecetes aliger	4	Humes, 1989a
Ceuthoecetes aliger	3	Humes & Segonzac, present paper
Ceuthoecetes cristatus Humes, 1987	4, 5	Humes, 1987
Ceuthoecetes cristatus	4	Humes, 1989a
Ceuthoecetes cristatus	5	Humes, 1990a
Ceuthoecetes cristatus	3	Humes & Segonzac, present paper
Ceuthoecetes intoversus Humes, 1987	2, 5	Humes, 1987
Chasmatopontius thescalus Humes, 1990	12	Humes, 1990b
Chasmatopontius thescalus	14	Humes, 1991b
Cheramomyzon abyssale Humes, 1989	4	Humes, 1989a
Exrima dolichopus Humes, 1987	4	Humes, 1987
Exrima singula Humes, 1987	5	Humes, 1987
Nilva torifera Humes, 1987	2, 4, 5	Humes, 1987
Nilva torifera	2, 5	Humes, 1990a
Nilva torifera	4	Humes, 1989a
Rhogobius contractus Humes, 1987	2, 4	Humes, 1987
Rhogobius contractus	4	Humes, 1989a
Rhogobius contractus	2, 5	Humes, 1990a
Rhogobius pressulus	2	Humes, 1989d
Rimipontius mediospinifer Humes, 1996	18	Humes, 1996
Rimipontius mediospinifer	19	Humes & Segonzac, present paper
Scotoecetes introrsus Humes, 1987	4	Humes, 1987, 1989a; Humes & Segonzac, present paper
Stygiopontius appositus Humes, 1989	5	Humes, 1989b
Stygiopontius appositus	4	Humes, 1989a
Stygiopontius brevispina Humes, 1991	14	Humes, 1991b
Stygiopontius bulbisetiger Humes, 1996	18	Humes, 1996
Stygiopontius cinctiger Humes, 1987	5	Humes, 1987
Stygiopontius cinctiger	4	Humes, 1989a
Stygiopontius cinctiger	3	Humes & Segonzac, present paper
Stygiopontius cladarus Humes, 1996	18	Humes, 1996
Stygiopontius flexus Humes, 1987	6	Humes, 1987
Stygiopontius flexus	3, 6	Humes & Segonzac, present paper
Stygiopontius hispidulus Humes, 1987	4, 5	Humes, 1987
Stygiopontius hispidulus	4	Humes, 1989a
Stygiopontius hispidulus	3, 4	Humes & Segonzac, present paper
Stygiopontius latulus Humes, 1996	18	Humes, 1996
Stygiopontius lauensis Humes, 1991	14	Humes, 1991b
Stygiopontius lumiger Humes, 1989	5	Humes, 1989b
Stygiopontius mirus Humes, 1996	18	Humes, 1996
Stygiopontius mirus	3	Humes & Segonzac, present paper
Stygiopontius mucroniferus Humes, 1987	6	Humes, 1987
Stygiopontius mucroniferus	3	Humes & Segonzac, present paper
Stygiopontius paxillifer Humes, 1989	5	Humes, 1989b
Stygiopontius paxillifer	3	Humes & Segonzac, present paper
Stygiopontius pectinatus Humes, 1987	17, 18	Humes, 1987
Stygiopontius pectinatus	18	Humes, 1996
Stygiopontius pectinatus	12	Humes, 1990b
Stygiopontius quadrispinosus Humes, 1987	9	Humes, 1987
Stygiopontius quadrispinosus	7	Humes, 1990a
Stygiopontius quadrispinosus	8, 9	Humes & Huys, 1992
Stygiopontius regius Humes, 1996	18	Humes, 1996
Stygiopontius rimivagus Humes, 1987	16	Humes, 1997; Humes & Segonzac, present paper
Stygiopontius sentifer Humes, 1997	4, 5	Humes, 1987
Stygiopontius sentifer	3, 4	Humes & Segonzac, present paper
Stygiopontius serratus Humes, 1996	18	Humes, 1996
Stygiopontius stabilitus Humes, 1990	12	Humes, 1990b
Stygiopontius stabilitus	4	Humes, 1989a
Stygiopontius teres Humes, 1996	18	Humes, 1996
Stygiopontius verruculatus Humes, 1987	5	Humes, 1987
Stygiopontius verruculatus	3	Humes & Segonzac, present paper
Megapontiidae		
Hyalopontius boxshalli Humes, 1988	2	Humes, 1988c
Ecbathyriontidae		
Ecbathyrion prolixicauda Humes, 1987	2	Humes, 1987
Ecbathyrion prolixicauda	4	Humes, 1989a
Ecbathyrion prolixicauda	2, 5	Humes, 1990a
Ecbathyrion prolixicauda	3	present paper
Ecbathyrion prolixicauda	3	Humes & Segonzac, present paper
Family uncertain		
Fissuricola caritus Humes, 1987	5	Humes, 1987
HARPACTICOIDA		
Cerviniidae		
Neocervinia itoi Lee & Yoo, in press	10	Lee & Yoo, in press
Argestidae insertae sedis		
Argestoides prehensilis Huys & Conroy-Dalton, 1987	2	Huys & Conroy-Dalton, 1997
Ectinosomatidae [Ectinostidae (sic)], in Grassle, 1986, based on A. Dinet, personal communication	5	Grassle, 1986

Four species of copepods have been reported in deep water, but not specifically at hydrothermal sites, and, therefore, are not listed in this table. These include three erebonasterids: *Tychidion guyanense* Humes, 1973, from the vestimentiferan *Lamellibrachia* sp., in 500 m, off Guyana; *Centobnaster humesi* Huys & Boxshall, 1990, in 500 m, off New Caledonia; and *Amphicrossus pacificus* Huys, 1991, in 155 m, of New Caledonia; and one dirivultid: *Dirivultus dentaneus* Humes & Dojiri, 1980a, from the vestimentiferan *Lamellibrachia barhami* Webb, in 1125 m, off southern Calidornia. Other benthopelagic copepods collected above deep-sea cold seeps (see Toda *et al.*, 1994) are not listed here.

vents is very incompletely known. Until now, collections in very deep water at vents have been made in relatively few areas (Fig. 3). Based on presently available information, however, copepods at the eastern Pacific vents are for the most part different from those on the Mid-Atlantic Ridge. From the East Pacific Rise, the Galapagos Rift, the Guaymas Basin, and the Explorer, Juan de Fuca, and Gorda hydrothermal areas, 46 species of copepods are known (1 Calanoida, 1 Misophrioida, 1 Cyclopoida, 6 Poecilostomatoida, and 38 Siphonostomatoida). On the Mid-Atlantic Ridge, 12 copepods have been found, all Siphonostomatoida (Table 1) (Desbruyères & Segonzac, 1997).

Collections of copepods made during the past decade at deep-sea vents, whose geothermal features are characterized by rapid growth and transient nature (Lutz *et al.*, 1994), have not been quantitative. Methods of collection have varied widely, including box cores, slurp guns, and washing macroinvertebrates, such as bivalves, vestimentiferans, and decapods. The number of specimens in the samples has ranged from one to several thousand.

Many species of copepods from deep-sea hydrothermal sites are to some degree associated with invertebrates, such as crustaceans (shrimps and crabs), bivalves, vestimentiferans, and polychaetes: 5 species with Crustacea (*Aphotopontius acanthinus, A. forcipatus, Rimipontius mediospinifer, Stygiopontius cladarus,* and *S. pectinatus*), 14 species with Bivalvia (*Hyphalion sagamiense, Erebonaster protentipes, Aphotopontius arcuatus, A. atlanteus, A. flexispina, A. hispidulus, A. probolus, A. rimivagus, A. temperatus, Ceuthoecetes acanthothrix, C. aliger, C. cristatus, Exrima singula,* and *Nilva torifera*) 4 species with Polychaeta (*Chasmatopontius thescalus, Stygiopontius hispidulus, S. sentifer,* and *S. stabilitus)* and 11 species with Vestimentifera (*Aphotopontius arcuatus, A. flexispina, A. mammillatus, Benthoxynus spiculifer, Ceuthoecetes acanthothrix, C. aliger, C. cristatus, Exrima singula, Nilva torifera, Scotoecetes introrsus* and *Stygiopontius flexus)*. Not all of these associations should be interpreted as true commensalism. A few copepods, such as *Stygiopontius pectinatus* on the mouthparts of shrimps, or *Erebonaster protentipes* in the mantle cavity of *Nuculana*-like bivalves, seem to have a clear relationship with their hosts. Others, such as *Ceuthoecetes acanthothrix, Ceuthoecetes cristatus, Nilva torifera,* and *Exrima singula*, are apparently loosely associated and have been found in washings of more than one type of host. Very little is known about these associations, which may in reality be of a trophic nature (Segonzac *et al.*, 1993).

Information on deep-sea vent copepods is now sufficient to allow certain general comparisons to be made between the eastern Pacific and the Mid-Atlantic Ridge. The genus *Stygiopontius* has several species in the two regions, 15 in the Pacific and 10 on the Mid-Atlantic Ridge. Two species, *Aphotopontius forcipatus* and *Stygiopontius mirus*, occur both in the northeastern Pacific and on the Mid-Atlantic Ridge, and *Stygiopontius pectinatus* has been found both on the Mid-Atlantic Ridge and at the Mariana Back-Arc Basin (Humes, 1990b). *Aphotopontius* has an unequal number of species, 10 in the eastern Pacific, two on the Mid-Atlantic Ridge. *Aphotopontius forcipatus* occurs both on the Mid-Atlantic Ridge and in the northeastern Pacific. *Ceuthoecetes* has four species in the eastern Pacific, but none on the Mid-Atlantic Ridge. Other genera contain too few species to permit generalizations.

A potentially wide-spread distribution of copepods at deep-sea hydrothermal sites is suggested in the case of the dirivultid *Stygiopontius stabilitus* in the Pacific, a species found at the East Pacific Rise at 13°N and at the Mariana Back-Arc Basin.

Although 67 species of copepods are known from hydrothermal vents and cold seeps, discussions of the ecology and biology of vent faunas have centered mostly around their macrofauna (e.g., Tunnicliffe, 1991; Van Dover, 1995; Van Dover *et al.*, 1996; Gebruk *et al.*, 1997b). Gebruck *et al.* (1997a) briefly compared and discussed the fauna at the eastern Pacific vents with that on the Mid-Atlantic Ridge.

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