



ORIGINAL ARTICLE

A new species of *Ambilimbus* nom. nov., a replacement name for *Amphicrossus* Huys, 1991 (Copepoda, Cyclopoida, Erebonasteridae), from the Mid-Atlantic Ridge at 36°N (hydrothermal vent site Rainbow)

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Abstract

A new deep-sea species of *Ambilimbus* nom. nov. (Copepoda, Cyclopoida, Erebonasteridae) is described from the Mid-Atlantic Ridge (hydrothermal vent site Rainbow, 36°13'N 33°54'W, depth 2285 m). This is the first record for the family Erebonasteridae Humes, 1987 from the Mid-Atlantic Ridge. *Ambilimbus* nom. nov. is here proposed as a replacement name for *Amphicrossus* Huys, 1991, as the latter is preoccupied by *Amphicrossus* Erichson, 1843 (Insecta, Coleoptera). The new species, *Ambilimbus arcuscelestis*, is similar to *A. pacificus* (Huys, 1991) comb. nov. and *A. tuerkayi* (Martínez Arbizu, 1999) comb. nov. in having the third exopodal segments of legs 1 and 2 armed with four and five inner setae, respectively (instead of three and four inner setae as in *A. spinulosus* (Humes, 1989) comb. nov. and *A. altalis* (Humes & Huys, 1992) comb. nov.). It differs from its four congeners by the lack of the inner coxal seta on leg 3. This character and the mid-ventral processes located between the intercoxal sclerites of legs 1–4 are presumed to be apomorphies of the new species.

Résumé

Une nouvelle espèce du genre *Ambilimbus* nom. nov. (Copepoda, Cyclopoida, Erebonasteridae) est décrite de la ride médio-Atlantique, à la latitude 36°N (site hydrothermal Rainbow, 36°13'N 33°54'O, profondeur 2285 m). C'est la première découverte de la famille des Erebonasteridae Humes, 1987 dans la ride médio-Atlantique. *Ambilimbus* nom. nov. est proposé ici comme nom de remplacement pour *Amphicrossus* Huys, 1991, car ce dernier est préoccupé par *Amphicrossus* Erichson, 1843 (Insecta, Coleoptera). La nouvelle espèce, *Ambilimbus arcuscelestis*, ressemble à *A. pacificus* (Huys, 1991) comb. nov. et *A. tuerkayi* (Martínez Arbizu, 1999) comb. nov. en ayant le troisième segment de l'exopodite des deuxième et troisième paires de pattes armé de 4 et 5 soies internes, respectivement (au lieu de 3 et 4 soies internes, comme chez *A. spinulosus* (Humes, 1989) comb. nov. et *A. altalis* (Humes & Huys, 1992) comb. nov.). Elle diffère de ses quatre congénères par l'absence de la soie coxale interne sur la troisième paire de pattes. Ce caractère, ainsi que les processus médio-ventraux situés entre les sclérites intercoxaux des pattes 1 à 4, sont supposés être des apomorphies de l'espèce nouvelle.

Key words: Copepoda, deep sea, hydrothermal vents, Mid-Atlantic Ridge, morphology, systematics

Introduction

The Erebonasteridae Humes, 1987 is a family of deep-water poecilostome cyclopoid copepods including nine species in five genera. Along with all other families formerly placed in Poecilostomatoida it was recently transferred to the order Cyclopoida (Martínez Arbizu 2000; Boxshall & Halsey 2004). The family is remarkable for some of its primitive features

within the poecilostome lineage, including the paired copulatory pores located on the mid-ventral side of the genital double somite and the presence of a discrete mandibular palp. The type genus, *Erebonaster* Humes, 1987, is known from one species found in association with a *Nuculana*-like protobranch bivalve, collected from the Guaymas Basin in the Gulf of California (depth 2002–2025 m). Two other mono-

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typic genera have been described: *Nansennaster* Martínez Arbizu, 1999, collected from sediment in the Russian Arctic between the Kara Sea and the Laptev Sea (depth 156 m) and *Tychidion* Humes, 1973, obtained from a vestimentiferan host on the continental slope off Guyana (depth 500 m) (Humes 1987; Humes & Huys 1992; Martínez Arbizu 1999). The genus *Centobnaster* Huys & Boxshall, 1990 contains two species discovered in sediment samples: one from off New Caledonia (depth 500 m), the other from the Russian sector of the Arctic (depth 135–1017 m) (Huys & Boxshall 1990; Martínez Arbizu 1996/1997). The genus *Amphicrossus* Huys, 1991 includes the type species, *A. spinulosus* (Humes, 1989), from the West Florida Escarpment (depth 3266 m), *A. pacificus* Huys, 1991 off New Caledonia (depth 155 m), *A. altalis* Humes & Huys, 1992 from Juan de Fuca Ridge (depth 2420 m) and *A. tuerkayi* Martínez Arbizu, 1999 from the northern Fiji Basin (depth 1984 m) (Huys 1991; Humes & Huys 1992; Martínez Arbizu 1999). Possible host associations for these four species are as yet unknown. No erebonasterid has thus far been recorded from the Mid-Atlantic Ridge.

Copepods found at five hydrothermal vent fields of the Mid-Atlantic Ridge include one cyclopoid of the family Cyclopinidae (Ivanenko & Defaye 2004a), three harpacticoids belonging to the families Ectinosomatidae, Laophontidae, and Tegastidae (Ivanenko 1998; Lee & Huys 1999; Ivanenko & Defaye 2004b), and 13 siphonostomatoids belonging to the family Dirivultidae (see Ivanenko & Ferrari 2003). None of these copepods has been recorded in the recently discovered deep-sea hydrothermal vents at 36°N (Rainbow) (Humes & Segonzac 1998; Desbruyères et al. 2000; Heptner & Ivanenko 2002).

The purpose of this paper is to describe a new species of Erebonasteridae from the Rainbow site and to replace the preoccupied generic name *Amphicrossus* Huys, 1991 by a new replacement name, *Ambilimbus* nom. nov.

Material and methods

The specimens studied here were collected by the submarine Nautille (on N/O *Nadir*) during the French cruise PICO (Chief Scientist Daniel Desbruyères, Ifremer, 25 May–11 July 1998). The aim of this cruise was to sample the fauna of the hydrothermal sites Lucky Strike (37°N, 1700 m) and Rainbow (36°N, 2300 m) on the Mid-Atlantic Ridge, and to characterize the physicochemical data of their environment. The hydrothermal vent site Rainbow is characterized by some active and numerous inactive chimneys. At the base of dead chimneys, some mytilid bivalves *Bathymodiolus azoricus* Cosel, Comtet & Krylova,

1999 live in shimmering water at ca. 12.8°C (Desbruyères et al. 2001). The copepods were collected in the hydrothermal sediment (iron oxide), among sedentary polychaeta Chaetopteridae and numerous mussel shells, at a few metres of the mussel beds, where the seawater temperature is 3.7°C. On board, the copepods were fixed in formalin, then preserved in ethanol after sorting at the laboratory.

Prior to light microscopy, specimens were cleared in lactic acid and subsequently stained in a solution of chlorazol black E. Material was examined using bright-field or differential interference contrast optics. All measurements and dissections were made in lactic acid. Dissections were made under a Leica MZ8 dissecting microscope. Drawings were made with a camera lucida mounted on a Leica DMLB compound microscope. The description is based on the holotype female and the allotype male. For long-term preservation, the holotype and the allotype were mounted on slides in glycerol and sealed with Eukitt (O. Kindler GmbH & Co).

Systematics

Order Cyclopoida Burmeister, 1835

Family Erebonasteridae Humes, 1987

Genus *Ambilimbus* nom. nov.

Syn. *Amphicrossus* Huys, 1991 *non Amphicrossus* Erichson, 1843.

Type species

Ambilimbus spinulosus (Humes, 1989) comb. nov.

Other species

Ambilimbus altalis (Humes & Huys, 1992) comb. nov.; *Ambilimbus arcuscelestis* sp. nov.; *Ambilimbus pacificus* (Huys, 1991) comb. nov.; *Ambilimbus tuerkayi* (Martínez Arbizu, 1999) comb. nov.

Remark

The genus name *Amphicrossus* Huys, 1991 is preoccupied by *Amphicrossus* Erichson, 1843 (Insecta: Coleoptera: Nitidulidae). *Ambilimbus* nom. nov. is proposed as a replacement name. The new name is “a direct latinization” of *Amphicrossus*, referring to the “setulose ornamentation of the rostrum”.

Ambilimbus arcuscelestis sp. nov. (Figures 1–9)

Type material. Dissected holotype ♀ (MNHN-Cp2069), dissected allotype ♂ (MNHN-Cp2165); 2 ♀ paratypes (MNHN-Cp2166). The type material is deposited in the Museum National d’Histoire Naturelle, Paris, France.

Type locality. Mid-Atlantic Ridge, hydrothermal site Rainbow, marker PP29, 36°13.44’N 33°54.08’W,

depth 2285 m. Date: 02 July 1998. Dive PL 1266, Box 1, Submersible: Nautil; Vessel: N/O *Nadir*; Cruise: PICO.

Etymology. The species name is derived from the Latin name for rainbow, the name of the hydrothermal vent field where the copepods were collected.

Female. Body (Figure 1A, 2A) elongate and flattened, ornamented with setules (on prosome shown in Figure 2B), secretory pores and sensillae; encrusted with tiny grains of sand (not shown in figure). Total length of holotype female (body plus caudal ramus,

caudal setae excluded) 2.35 mm; greatest width 0.51 mm.

Prosome five-segmented comprising cephalosome and four somites bearing legs 1–4. Lateral margin of shield of cephalosome ornamented with setules, as shown in Figure 2B. Epimera of somites slightly developed and rounded. Area between intercoxal sclerites of legs 1–4 provided with processes (Figure 2C). Mid-ventral processes between legs 1–2 and legs 2–3 directed posteriorly; process between legs 3 and 4 represented by two roundish outgrowths covered with long setules.

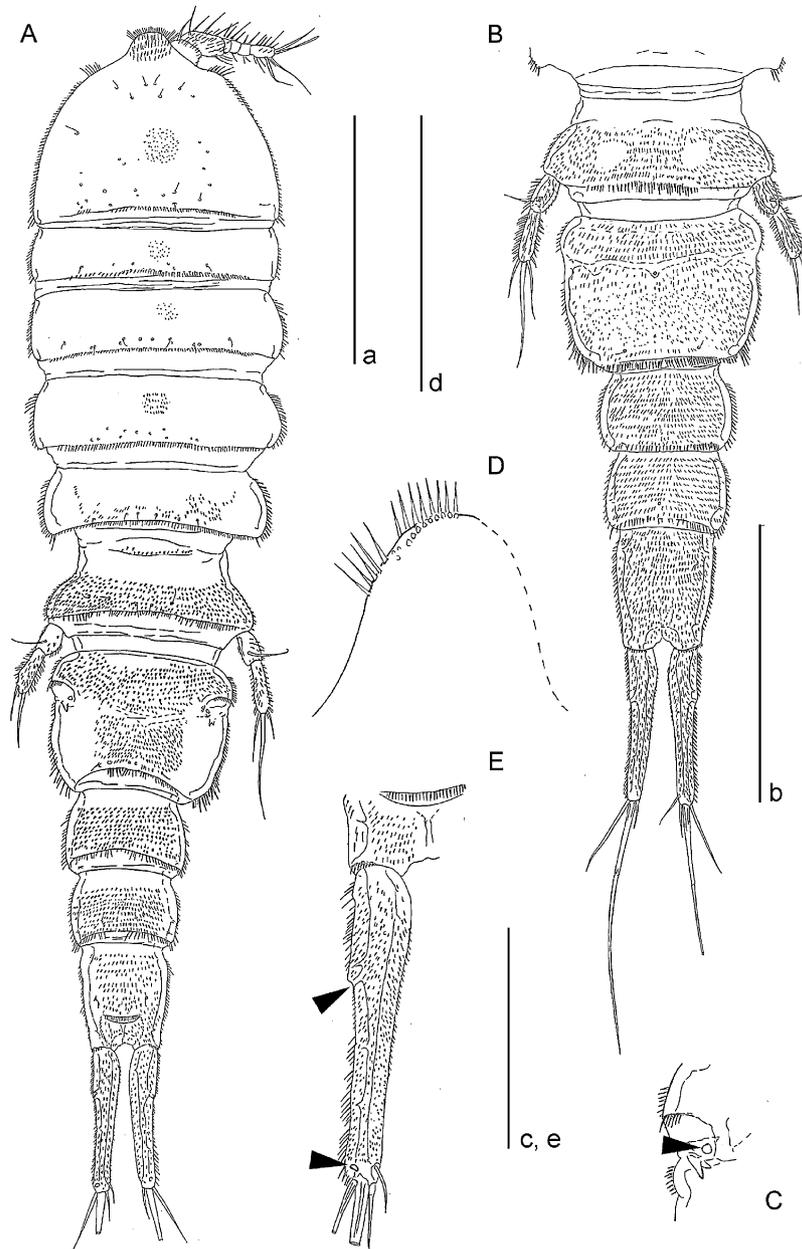


Figure 1. *Ambilimbus arcuscelestis* sp. nov., ♀ holotype. (A) Habitus (ornamentation of prosome shown only in mid-dorsal circular areas), dorsal; (B) urosome, ventral; (C) genital aperture, with scar of missing seta marked by arrow, dorsal; (D) rostrum (damaged), ventral; (E) left caudal ramus, dorsal. Arrowheads indicate positions of missing setae. Scale bars: a, b = 0.5 mm; c, e = 0.2 mm; d = 0.1 mm.

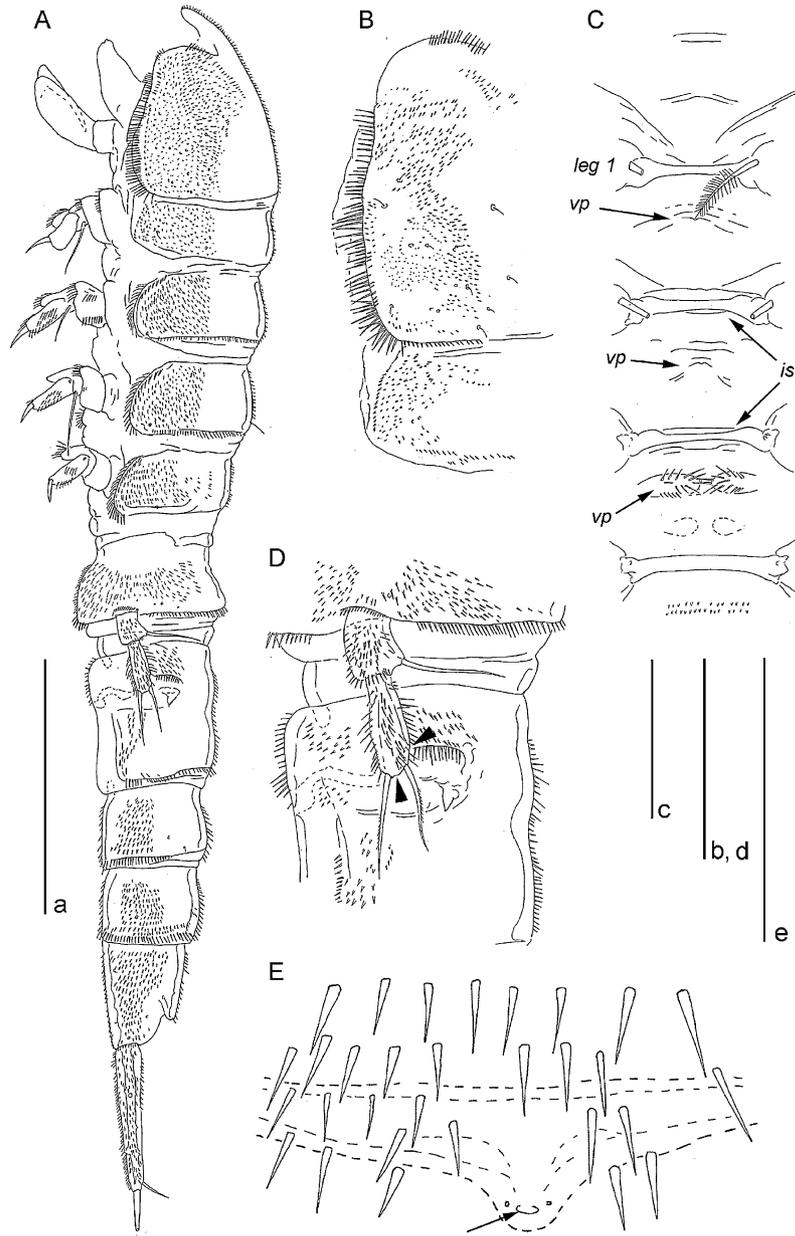


Figure 2. *Ambilimbus arcuscelestis* sp. nov., ♀ holotype. (A) Habitus, lateral; (B) shield of cephalothorax and pleurotergite of first pedigerous somite, lateral; (C) intercoxal sclerites and adjacent sternal areas from P1 (top) to P4, ventral; (D) leg 5 and genital double somite, lateral; (E) copulatory pore, ventral, indicated by arrow. Arrowheads indicate positions of missing setae. Scale bars: a = 0.5 mm; b–d = 0.2 mm; e = 0.05 mm. is, intercoxal sclerites; vp, ventral processes.

Urosome (Figure 1A, B) five-segmented comprising somite bearing leg 5, genital double somite and three abdominal somites. Short pseudosomite separating somite bearing leg 5 and genital double somite. Somite bearing P5, ventrally with two symmetrical spots devoid of ornamentation (Figure 1B). Anal somite with anal opening on dorsal side partially covered by serrate operculum. Genital double somite slightly tapering in posterior half. Copulatory pore (Figure 1B, 2E, arrowed) located mid-ventrally in anterior half of genital double somite. Gonopores (Figures 1C, 2D) located laterodorsally at level of

copulatory pore, covered by plate of P6, bearing one seta and one bifid process.

Rostrum (Figures 1A, D, 2A) prominent anteriorly, with long setules and row of dentiform spinules.

Caudal rami (Figure 1E) elongate, 1.4 times longer than anal somite; slightly divergent from second third, tapering distally; with six setae of different lengths (two setae lost), ornamented with small setules, length/width ratio 5.5:1.

Egg sacs unknown.

Antennule (Figure 3A–C) six-segmented; dorsal surface and margins of segments ornamented with

rows of slender setules of different lengths. Formula for armature: 3; 16; 2+a; 2; 2+a; 7+a (a = aesthetasc). Second segment with one short, seta-like element (Figure 3A); aesthetascs articulate. Segments 1–5 with 3, 15, 1, 1, 1 anterior setae, respectively, which are slender, stout and armed with spinules; distal part of segment 6 with six slender stout setae armed with spinules. Each of segments 2–6 with additional ventral seta having constrictions, appearing as subdivided in several parts.

Labrum (Figure 4A): distal margin with median process, with patch of small spinules and row of dentiform spinules on both sides.

Antenna (Figure 4B) four-segmented, comprising protopod and three-segmented endopod, all segments ornamented with rows of setules, as illustrated. Protopod with inner seta; segments of endopod armed with one, three, and six setae; all setae stout and serrate.

Mandible (Figure 4C) with gnathobase and one-segmented palp; gnathobase slender, with two pectinate spines and two pectinate blades between

spines; one-segmented palp short, with four long serrate setae (three terminal and one subterminal).

Maxillule (Figure 5A): lobe with two groups of setules and five setae: three stout, terminal and two short, subterminal.

Maxilla (Figure 5B) two-segmented; first segment flattened, with one small inner seta and slender setules on outer margin; second segment claw-like, with two outer proximal setae of different lengths and inner median spiniform process.

Maxilliped (Figure 5C) four-segmented, comprising syncoxa, basis and two-segmented endopod; syncoxa with two inner setae; basis with two inner setae and numerous setules on outer and posterior surfaces; first endopodal segment unarmed and with outer spinules; second endopodal segment claw-like, with stout spiniform inner process and two inner setae.

Legs 1–4 (Figures 6–8) biramous, each ramus three-segmented, ornamented with rows of setules, as illustrated. Formula for armature of legs 1–4 as in Table I. Ornamentation of legs 1–4 as illustrated. Basis of leg 1 (Figure 6C) with stout inner spine.

Intercoxal sclerites of legs 1–2 with row of slender setules at distal margin. Coxae of legs 1–2 with plumose inner seta, absent on legs 3–4.

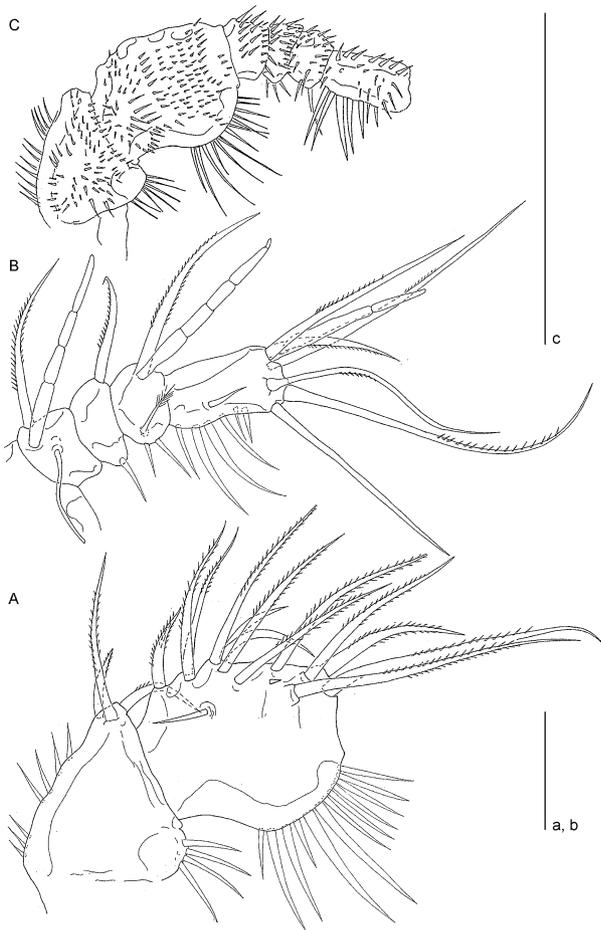


Figure 3. *Ambilimbus arcuscelestis* sp. nov., ♀ holotype: (A) antennule, segments 1–2, ventral; (B) antennule, segments 3–6, ventral; (C) antennule, setae not shown, dorsal. Scale bars: a, b = 0.05 mm; c = 0.2 mm.

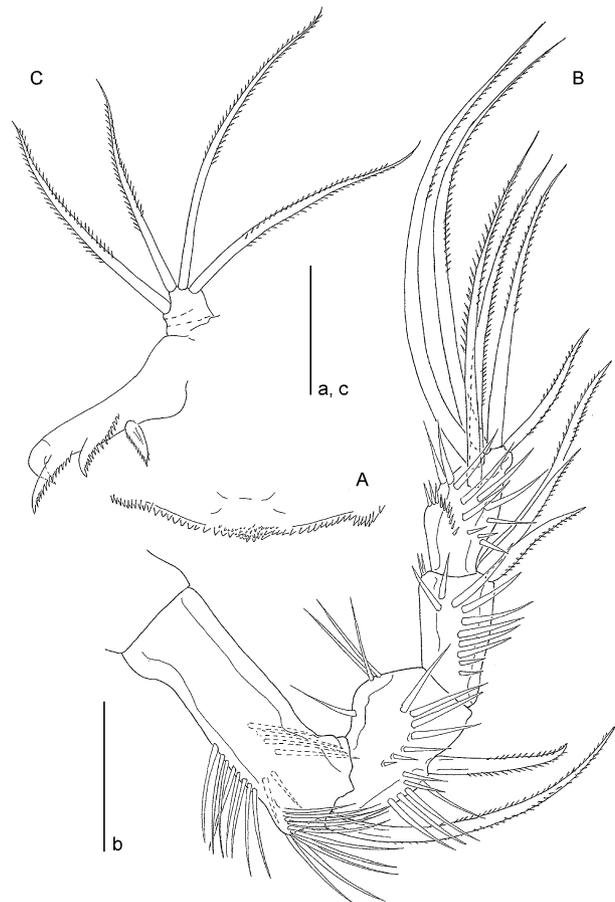


Figure 4. *Ambilimbus arcuscelestis* sp. nov., ♀ holotype. (A) Labrum; (B) antenna; (C) mandible. Scale bars: a–c = 0.05 mm.

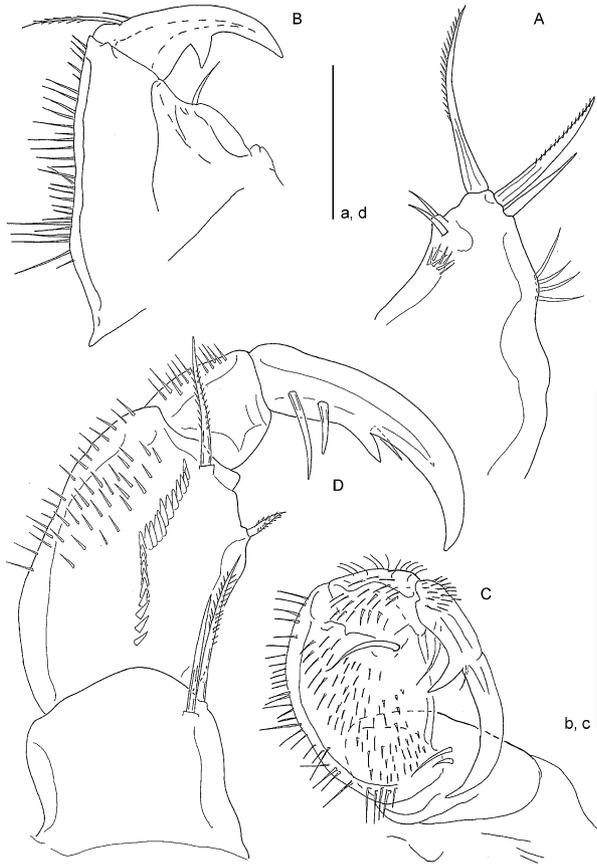


Figure 5. *Ambilimbus arcuscelestis* sp. nov., ♀ holotype: (A) maxillule; (B) maxilla, posterior; (C) maxilliped, posterior. *Ambilimbus arcuscelestis* sp. nov., ♂ allotype: (D) maxilliped, anterior. Scale bars: a, d = 0.05 mm; b = 0.2 mm; c = 0.1 mm.

Leg 5 (Figure 1B, 2D) not joined by intercoxal sclerite, two-segmented, ornamented with spinules; first segment with one outer seta; second segment with four setae (one or two setae lost).

Leg 6 (Figure 1C, 2D) represented by bifid process and seta (lost).

Colour unknown.

Male. Differs from female as follows. Body (Figure 9A): total length of allotype (body plus caudal ramus, caudal setae excluded) 1.65 mm; greatest width 0.49 mm. Urosome (Figure 9A, B) five-segmented, comprising somite bearing leg 5, genital somite and three abdominal somites. Spermatophore (Figure 9A): paired, elongate, pointed anteriorly. Antennule with second segment with three additional aesthetascs on ventral side. Maxilliped (Figure 5D) with additional row of spinules on basis and additional inner seta on distal claw-like segment. Leg 1 with inner spine of basis slightly narrower. Leg 2 (Figure 9C): with large spiniform outer process on distal segment of endopod. Leg 3 (Figure 9D): with small spiniform process on distal segment of endopod. Leg 6 (Figure 9B): represented by posteroventral genital flap, armed with two setae of different lengths.

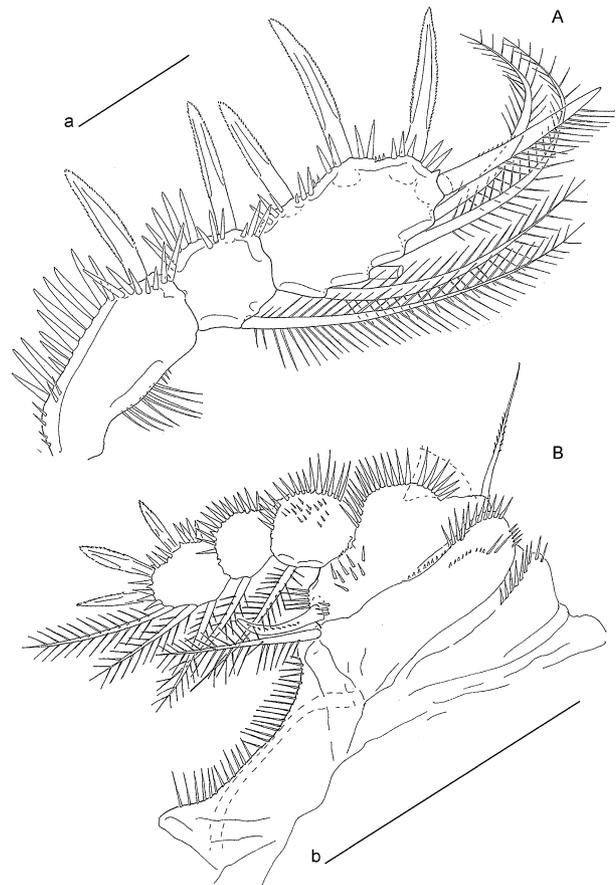


Figure 6. *Ambilimbus arcuscelestis* sp. nov., ♀ holotype: (A) exopod of leg 1, anterior; (B) leg 1, endopod, protopod and intercoxal sclerite, anterior; Scale bars: a = 0.05 mm; b = 0.2 mm.

Ecological note. These specimens were found on a slope in an inactive area, on hydrothermal sediment, among mussels apparently more or less recently dead. This inactive area was located at a few metres from active edifices covered by mussel beds. Pieces of orange tissue were observed between the labrum and the oral appendages, filling the mouth of all specimens examined. This could suggest that these copepods nourish upon mussels.

Remarks

The new species possesses the distinctive features of the genus *Ambilimbus* nom. nov. (Huys 1991; Martínez Arbizu 1996/1997, 1999): the body and appendages covered with numerous spinules, the epimera of somites bearing legs 1–4 rounded and not expanded posteriorly, the rostrum with a row of dentiform spinules and long setules, the claw of the maxilliped with an inner process, and the maxillule without a knob-like process. The presumed apomorphies of the new species are the processes between the intercoxal sclerites of legs 1–4 and the absence of the inner coxal seta on leg 3.

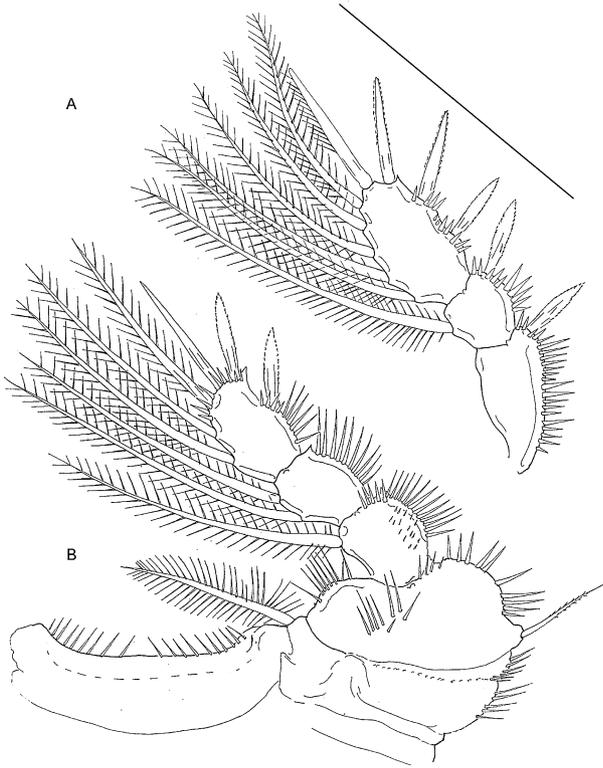


Figure 7. *Ambilimbus arcuscelestis* sp. nov., ♀ holotype. (A) Exopod of leg 2, anterior; (B) leg 2, endopod, protopod and intercoxal sclerite, anterior. Scale bar: 0.2 mm.

The new species, like *A. pacificus* and *A. tuerkayi*, has the third exopodal segment of legs 1 and 2 armed with four and five inner setae, respectively, unlike *A. altalis* and *A. spinulosus*, which have three and four inner setae. It also shares with *A. altalis* the absence of the inner coxal seta on leg 4 and with *A. tuerkayi* the presence of two outer setae on the claw of the maxilla, instead of one seta as in its congeners. The seventh caudal seta I found in *A. spinulosus* could not be observed in the new species because of the dense setulation.

The new species differs additionally:

- from *A. pacificus* in having an elongate body; wider posterior half of the genital double somite; the ornamentation of the intercoxal sclerite of legs 1 and 2, and of the lateral margin of the shield of the cephalothorax; the shorter exopod of leg 5; and the much longer maxillipedal claw in the female (and more prominent spinous process);

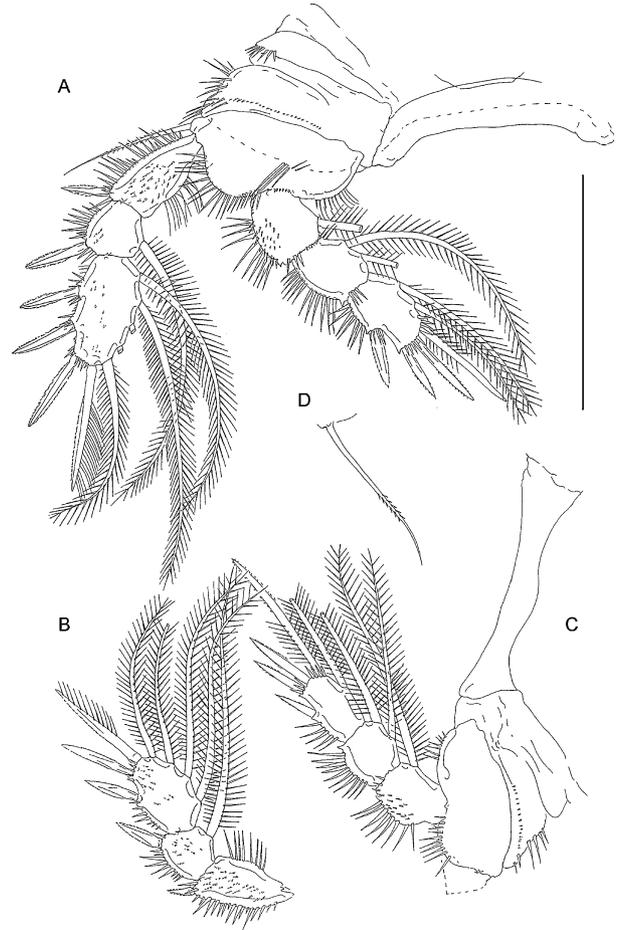


Figure 8. *Ambilimbus arcuscelestis* sp. nov., ♀ holotype. (A) Leg 3, anterior; (B) exopod of leg 4, anterior; (C) leg 4, endopod, protopod and intercoxal sclerite, anterior; (D) outer basal seta of leg 4. Scale bar: 0.2 mm.

- from *A. tuerkayi* in the larger body size (♀♀: 2.35 mm versus 1.51 mm; ♂♂: 1.65 mm versus 1.2 mm); the lack of a suture on the dorsal side of the female genital double somite; the presence of setules on the ornamentation of the genital double somite; the second segment of antennule with 16 setae (15 in *A. tuerkayi*); the maxillule with additional setules; and the more robust maxillipedal claw in the male;
- from *A. altalis* in having ornamentation on intercoxal sclerites of legs 1 and 2 (absent in *A. altalis*); the presence of a spinous process on the maxillary claw, which is also much longer than in *A. altalis*; the wider posterior half of the genital

Table I. Spine and setal formulae of legs 1–4 in *Ambilimbus arcuscelestis* n. sp. Roman numerals indicate spines, Arabic numerals indicate setae.

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

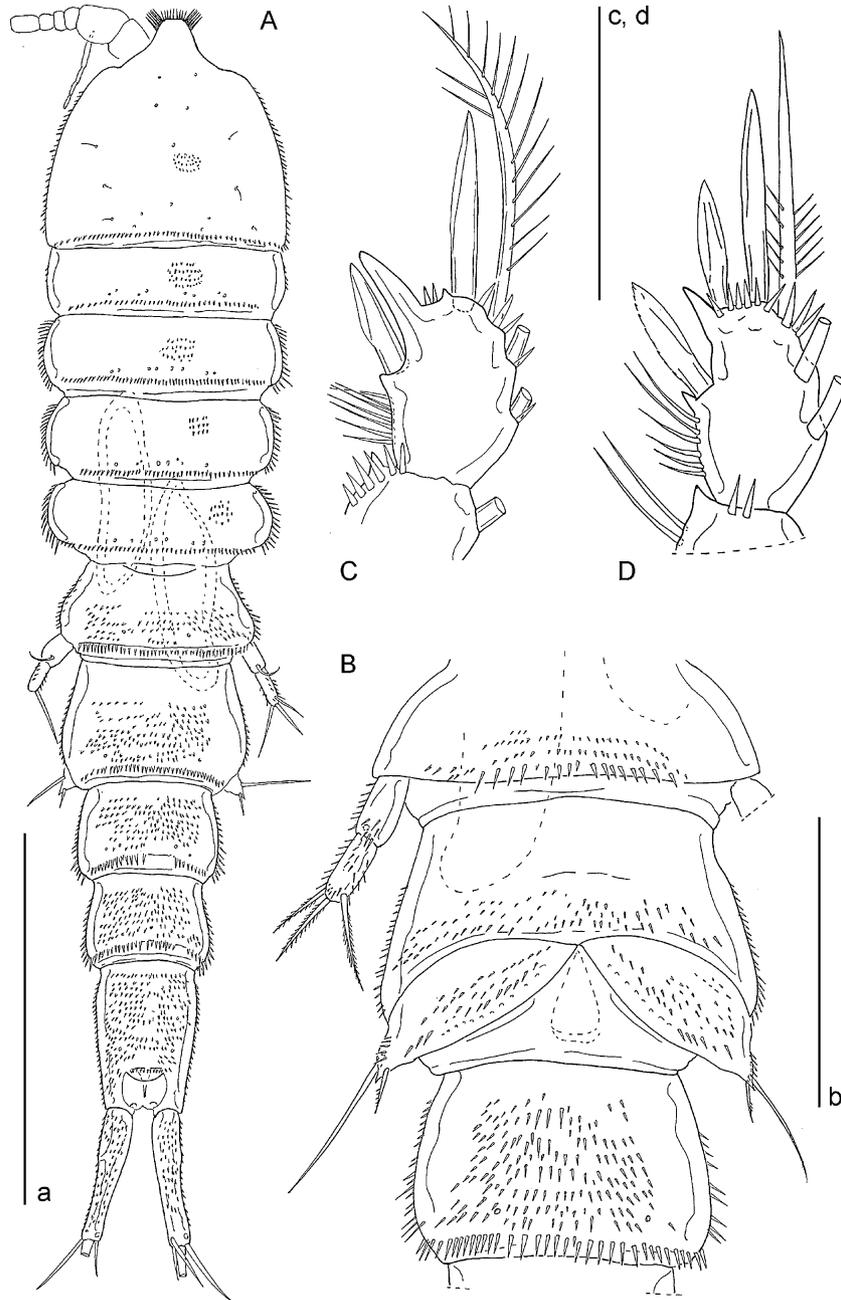


Figure 9. *Ambilimbus arcuscelestis* sp. nov., ♂. (A) Habitus (ornamentation of prosome shown only in mid-dorsal circular areas), dorsal; (B) somite bearing leg 5, genital and first abdominal somite, ventral; (C) distal segment of endopod of leg 2, anterior (outer distal spine omitted); (D) distal segment of endopod of leg 3, anterior. Scale bars: a = 0.5 mm; b = 0.2 mm; c, d = 0.05 mm.

double somite; and the shorter P5 (longer than the genital double somite in *A. altalis*);

- from *A. spinulosus* in the ornamentation of the rostrum; the narrower pedigerous somites; in the size of the longest seta of the maxillipedal syncoxa and basis in the female; and in having ornamentation on the intercoxal sclerites of legs 1 and 2.

Three erebonasterid species are known from deep-sea hydrothermal vents, all in the Pacific Ocean: *Erebonaster protentipes* from the Guaymas Basin; *A.*

altalis from the Juan de Fuca Ridge; and *A. tuerkayi* from the Fiji back-arc Basin. Three other species are described from non-vent areas of the Pacific Ocean: *A. spinulosus*, *A. pacificus* and *Centobnaster humesi*. The present paper provides the first record of erebonasterids on the Mid-Atlantic Ridge and the first description of a copepod from the Rainbow deep-sea hydrothermal vent field.

Ambilimbus arcuscelestis sp. nov. may lead an ectoparasitic mode of life, possibly feeding on bivalves *Bathymodiolus azoricus*, or other inverte-

brates. In effect, the tissues entrapped by the oral appendages might come from such invertebrate hosts. This hypothesis is supported by the earlier finding of erebonasterids in association with vestimentiferans *Riftia pachyptila* Jones, 1981, and bivalves, *Bathymodiolus thermophilus* Kenk & Wilson, 1985, in the Pacific Ocean (Humes 1973, 1987).

Key to the species of *Ambilimbus* (modified after Martínez Arbizu 1999)

1. Armature formula of third exopodal segment of leg 1: III,I,3; of leg 2: III,I,4 2
– Armature formula of third exopodal segment of leg 1: III,I,4; of leg 2: III,I,5 3
2. Second segment of leg 5 2.7 times longer than first segment *A. altalis*
– Second segment of leg 5 1.4 times longer than first segment *A. spinulosus*
3. Second segment of maxilla with two outer setae 4
– Second segment of maxilla with one outer seta *A. pacificus*
4. Inner coxal seta of legs 3–4 present . . . *A. tuerkayi*
– Inner coxal seta of legs 3–4 absent . . . *A. arcuscelestis* sp. nov.

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