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Caudacalanus* (Copepoda, Calanoida): a new benthopelagic genus from the abyss of the tropical South Atlantic and Southern Ocean

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Abstract

Two species of a new spinocalanoidean genus, *Caudacalanus*, are described from female specimens collected during the German expeditions ANDEEP I–II in 2002 and DIVA-1 in 2000 at abyssal depths above the seabed in the Southern Ocean and tropical waters of the South Atlantic. Segmentation and setation of swimming legs of the new genus are typical of the superfamily Spinocalanoidea. *Caudacalanus* gen. nov. shares the derived morphology of the oral parts and P1 basis and endopod with a monophyletic group of genera, viz. *Arctokonstantinus*, *Foxtonia* and *Sognocalanus*. Arctokonstantinidae is available for this lineage. The new genus differs from other spinocalanoideans by strong asymmetry of the caudal rami, with the right ramus nearly twice as long and wide as the left; setation of maxillule exopod reduced to 0–1 seta; maxilla basis lacking any setae; and maxilliped basis with 1 seta and endopod reduced to 3 segments.

Key words: Copepoda, Calanoida, *Caudacalanus* gen. nov., taxonomy, benthopelagic, South Atlantic

Introduction

Studies of samples collected from pelagic and benthopelagic habitats of the world's Oceans show that the deep-water spinocalanoidean fauna is highly diverse and contains many new genera and species (Hulsemann & Grice 1963; Fosshagen 1967, 1983; Park 1970; Damkaer 1975; Brodsky *et al.* 1983; Fleminger 1983; Grice & Hulsemann 1967; Schulz 1989, 1992, 1996, 2004; Markhaseva & Kosobokova 2001; Ivanenko *et al.* 2007). During the German expeditions ANDEEP I–II to the Antarctic (2002) and the DIVA-1 expedition (2000) to the south-eastern Atlantic, the deep-water benthopelagic environment was sampled using an epibenthic sledge (Brandt *et al.* 2004). Two species of a new genus *Caudacalanus* of the superfamily Spinocalanoidea with asymmetrical caudal rami sorted from these samples are described. Such well-pronounced asymmetry is observed for the first time in a member of spinocalanoidean families.

Material and methods

During the ANDEEP I–II expeditions of RV *Polarstern* in 2002 six females of the new genus were collected from four stations (042–2, 046–7, 131–3, 135–4) in the Southern Ocean to the south of 59°S. Material was collected above the seabed at abyssal depths from 2889 to 4679 m by a closing epibenthic sledge (Brandt & Barthel 1995) with both supranet (sampling layer ca. 1.00–1.30 m above the bottom; mesh size 0.3 mm) and

epinet subsamples (0.27–0.60 m above the bottom; mesh size 0.5 mm). One female was obtained during the DIVA-1 expedition of FS *Meteor* cruise 48–1 from station 344 in the south-eastern Atlantic (17°06'S 04°42'E) by similar gear close to the bottom at a depth of 5415 m.

Material was fixed in 96% ethanol, specimens were stained by adding a solution of chlorazol black E dissolved in 70% ethanol/30% water. Oral parts and swimming legs were dissected, mounted in glycerin and figures prepared using a *camera lucida*.

The following abbreviations are used in the descriptions: P1–P4, swimming legs 1–4. Articulating segments of the antennules are designated by Arabic numerals, ancestral segments by Roman numerals. One seta and one aesthetasc on a segment of the antennule are designated: 1s + 1ae; “1?” indicates that a setal element was broken so that its identity on the antennule could not be determined and only the scar at the location of its attachment was counted.

The segmentation of the antenna is assumed to have an 11-segmented exopod (Schulz 2005). The number sequence for antennal exopod indicates setae present on ancestral segments, a comma represents an arthrodistal membrane, a dash represents the absence of an arthrodistal membrane (Markhaseva & Ferrari 2005). The maxilliped syncoxa is considered to have three praecoxal lobes and one coxal lobe (Ferrari & Markhaseva 2000a, b; Ferrari & Ivanenko 2001).

Type material is deposited at the Zoological Museum Hamburg (ZMH), University of Hamburg, and the Zoological Institute, Russian Academy of Sciences, St. Petersburg (ZIN).

Taxonomy

Superfamily Spinocalanoidea, Vervoort, 1951

Family Arctokonstantinidae Markhaseva & Kosobokova, 2001

Genus *Caudacalanus* gen. nov.

Diagnosis. Female. Cephalosome and first pedigerous somite and pedigerous somites 4–5 separated. Posterior corners of prosome rounded in lateral view and triangular in dorsal view. Rostrum as an elongate cone directed ventrally. Caudal rami asymmetrical, right ramus nearly two times as long and wide as left; right medial seta situated dorsally and inserted more distally than left one, left inserted on ventral surface. Antennules completely or incompletely 25-segmented. Antenna with 2 setae on basis and 1–2 setae on endopod segment 1; endopod longer than exopod. Mandible: basis with 2 setae; endopod segment 1 without seta; endopod segment 2 with 8 setae; gnathobase with 4 teeth; exopod segment 5 with 2 setae. Maxillule: praecoxal arthrite with 9–11 setae; coxal endite well developed with 3–4 setae; coxal epipodite with 7 setae, or without seta; proximal basal endite reduced; endopod fused to distal basal endite, without setae; exopod with 1 seta, or seta lacking. Maxilla: praecoxal and coxal endites with 2 setae each (proximal praecoxal endite sometimes with additional attenuation); basis without seta; endopod with 4 setae. Maxilliped: syncoxa with 2 setae on praecoxa, 1 seta longer than basis plus endopod, curved terminally, and 1 seta on coxal endite; basis with 1 medial seta; endopod of 3 articulated segments armed with 1, 1 and 1–2 setae. P1 endopod 1-segmented, P2 endopod 2-segmented, P3–P4 endopods 3-segmented. P1–P4 exopods 3-segmented. P1 basis without distomedial seta; endopod with 5 setae, without lateral lobe; exopod segments 1 and 2 lacking lateral spines; segment 3 with 4 medial setae, 1 lateral and 1 terminal spine. P2 endopod segment 2 with 5 setae. P3–P4 endopod segments 3 with 6 setae. P2–P4 exopod segments 3 with 5 medial setae. P5 absent.

Male unknown.

Etymology. The generic name (from Latin cauda meaning tail, end) and Calanus (an existing name of a copepod genus) refers to the peculiar caudal rami of the species. Gender masculine.

Type species *Caudacalanus mirus* sp. nov.

Remarks. The new genus *Caudacalanus* together with *Foxtonia*, *Sognocalanus* and *Arctokonstantinus* constitute a monophyletic group of genera in the superfamily Spinocalanoidea. These genera are defined by derived oral parts and P1 characteristics (Table 1); the family name Arctokonstantinidae (Spinocalanoidea) is available for this lineage. Contrary to G.A. Boxshall and S.H. Halsey (2004), the family Arctokonstantinidae is not treated as a junior synonym of Spinocalanidae (Markhaseva 2008), because it is distinguished from Spinocalanidae by the following apomorphies: i) mandibular basis bears less than 3 setae (1 seta in *Foxtonia*, 2 setae in *Caudacalanus*, *Arctokonstantinus* and *Sognocalanus*, vs. 3–4 setae in Spinocalanidae); ii) mandibular endopod segment 1 lacking setae (vs. 2–4 setae in Spinocalanidae); iii) distal basal endite and endopod of maxillule are usually fused with 4 or less (without any setae in *Caudacalanus* and *Foxtonia*, 2 or 4 setae in *Sognocalanus* and *Arctokonstantinus* respectively, vs. distal basal endite supplied with 1–6 and endopod with 7–16 setae in Spinocalanidae, partly or completely separate (fused in *Isaacsicalanus* Fleminger, 1983)); iv) proximal coxal endite of maxilla with fewer than 3 setae (1 seta in *Foxtonia*, 2 setae in *Caudacalanus*, *Arctokonstantinus* and *Sognocalanus*, vs. 3 setae in the Spinocalanidae); v) terminal segment of maxilliped endopod with fewer than 4 setae (1–2 setae in *Caudacalanus*, 2–3 setae in *Foxtonia* and *Sognocalanus*, vs. 4 setae in the Spinocalanidae); vi) P1 medial seta of basis and lateral lobe of endopod absent (present in Spinocalanidae).

TABLE 1. Selected character states of Spinocalanoidea females¹ (diagnostic characters of the family Arctokonstantinidae are in bold).

Character	Spinocalanoidea	
	Spinocalanidae	Arctokonstantinidae
Antennule: number of segments	23–24	23–25
Mandible, nos. setae: ² basis endopod segment 1 endopod segment 2	3–4	1–2
	2–4	0
	9–11	5–8
Maxillule: precoxal arthrite basal exite distal basal endite endopod exopod epipodite	10–11, 13–15	3–4, 9–12
	0–1	0
	1–6	distal basal endite & endopod fused, setation: 0, 2, 4
	7–8, 10, 16	
	8, 10–11	0, 1, 3, 9
	9	0, 1, 4–5, 7
Maxilla: outer coxal seta proximal coxal endite	present or absent	absent
	3	1–2
Maxilliped: syncoxa, precoxal endites basis & incorporated endopod segment 1 articulated endopod segments	1, 2, 3	0, 1, 0(?)
	0, 2, 3	0, 0, 2
	0, 2, 1	
	0, 1, 0	
	2&2	2&1
	3&2	1&2
		1&0
	4, 4, 3, 3+1, 4	2, 1, 1, 1+1, 3
	3, 3, 2, 2+1, 4	1, 3, 1+1, 2
	2, 2, 2, 2+1, 4	2, 1, 1, 1, 3
3, 1, 1, 1, 4	2, 1, 1, 2, 2 1, 1, 1–2	
P1 setation: basis, medial seta endopod, lateral lobe	present	absent
	present	absent

1. References: Hulsemann & Grice 1963; Fosshagen 1967, 1983; Park, 1970; Damkaer 1975; Brodsky et al. 1983; Schulz 1989, 1996, 2004; Markhaseva & Kosobokova 2001; Boxshall & Halsey 2004; Ivanenko et al. 2007; original data.

2. Here and below, number of setae.

Caudacalanus is defined from the other representatives of Arctokonstantinidae by the following apomorphies: i) strongly expressed asymmetry of the caudal rami (slightly asymmetrical in *Foxtonia* (personal observation), symmetrical in *Arctokonstantinus* and *Sognocalanus*); ii) exopod of maxillule without setae, or with 1 seta (vs. 3 setae in *Sognocalanus* and *Foxtonia*, but 9 setae in *Arctokonstantinus*); iii) basis of maxilla lacking setae (setae present in *Arctokonstantinus*, *Sognocalanus* and *Foxtonia*); iv) basis of maxilliped with 1 medial seta (vs. 2 medial setae on basis and 1 seta on endopod segment 1 incorporated into basis in *Arctokonstantinus* and *Sognocalanus*, and 1 medial seta on basis and 2 setae on endopod segment 1 incorporated into basis in *Foxtonia*); v) endopod of maxilliped 3-segmented (vs. endopod 4-segmented in *Sognocalanus* or 5-segmented in *Arctokonstantinus* and *Foxtonia*).

Within Arctokonstantinidae the new genus differs in the antennule morphology, showing a completely or incompletely 25-segmented antennule, the shape of the rostrum (as an elongated cone turned ventrocaudally, vs. absent, or of different shape), and in the praecoxa of the maxilliped bearing 2 setae (only 1 seta in *Arctokonstantinus*, *Sognocalanus* and *Foxtonia*).

***Caudacalanus mirus* sp. nov.**

(Figs 1–3)

Holotype. Dissected adult female (ZMH Reg. no. K-41255), body length 2.70 mm. Collected Southern Ocean, 60°38'S 53°57'W, RV *Polarstern* (ANDEEP I), 30 January 2002, above the seabed at 2893–2889 m.

Paratype. Dissected adult female (ZMH Reg. no. K-41256), body length 2.80 mm. Collected Southern Ocean, 65°19'S 51°31'W, RV *Polarstern* (ANDEEP II), 05 March 2002, above the seabed at 3050 m.

The holotype and paratype are deposited at the Zoological Museum Hamburg, University of Hamburg (ZMH).

Description. Female: total length 2.70–2.80 mm (n=2). Prosome 1.3–1.5 times as long as urosome. Rostrum as an elongated cone (Fig. 1C–D). Posterior corners of prosome as short rounded lobes (Fig. 1A–B, I). Genital double somite symmetrical (Fig. 1H–I, K). Caudal rami asymmetrical; right ramus nearly twice as long and wide as left; both rami with 4 terminal setae; right ramus with a small mediodorsal seta, ventral seta lacking; left ramus with a small medioventral seta, dorsal seta lacking (Fig. 1B, F–G).

Antennule extending to posterior border of prosome somite 3 (Fig. 3A–D), 25-segmented, segments 24–25 incompletely separate, armature as follows: I–1s, II–IV–6s + 1ae, V–2s, VI–2s, VII–2s + 1ae, VIII–2s, IX–2s, X–XI–4s + 1ae, XII–1s, XIII–2s, XIV–2s, XV–1s, XVI–2s, XVII–1s, XVIII–1s, XIX–1s, XX–1s, XXI–2s, XXII–1s, XXIII–1s, XXIV–2s, XXV–2s, XXVI–2s, XXVII–2s, XXVIII–3s+ 1ae.

Antenna (Fig. 2A), coxa with 1 seta; basis with 2 setae; first endopodal segment with 1 seta (2 in paratype), second with 7 (8 in paratype) and 6 setae (13–14 setae in total), endopod about 1.8 times as long as exopod; exopod 8-segmented with 0, 1, 1, 1, 1, 1, 1 and 3 setae, second segment complex of 3 ancestral segments with 0–0–1 setae.

Mandible (Fig. 2B–C), gnathobase with 4 large teeth and seta; basis with 2 setae; endopod segment 1 without setae, segment 2 with 8 setae; exopod 5-segmented with 1, 1, 1, 1 and 2 setae.

Maxillule (Fig. 2D), praecoxal arthrite with 7 terminal spines (8 spines in paratype) and 2 posterior setae; coxal epipodite with 1 seta; coxal endite with 4 setae, 2 long and strongly sclerotized; proximal basal and distal basal endites reduced; endopod fused to exopod, without setae.

Maxilla (Fig. 2E), praecoxal and coxal endites with 2 setae each; basis without setae; endopod 3-segmented with 1, 1 and 2 setae.

Maxilliped (Fig. 2F), syncoxa with 2 setae on distal praecoxal endite, 1 seta longer than basis plus endopod and curved in terminal part; coxal endite with 1 seta. Basis with 1 medial seta. Endopod 3-segmented with 1, 1, and 1 setae.

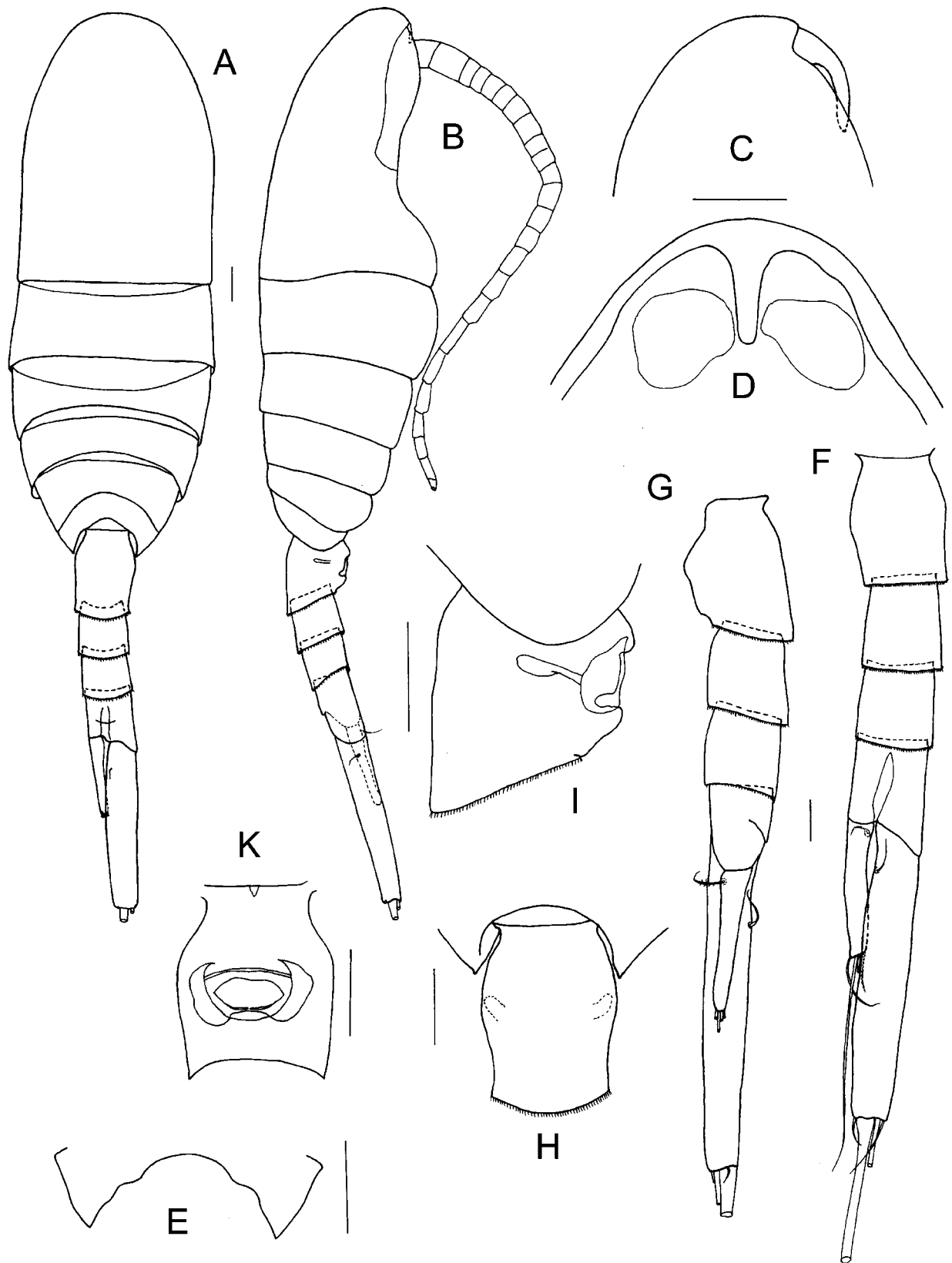


FIGURE 1. *Caudacalanus mirus* gen. et sp. nov. Female. A, habitus, dorsal; B, habitus, lateral; C, rostrum, lateral; D, rostrum, ventral; E, prosome, posterior corners, dorsal; F, urosome, dorsal; G, urosome, lateral; H, prosome, posterior corners and genital somite, dorsal; I, prosome, posterior corners and genital double-somite, lateral; K, genital double-somite, ventral. (C, E–G), paratype, other figures holotype. Scale bars 0.1 mm.



FIGURE 2. *Caudacalanus mirus* gen. et sp. nov. Female, holotype. A, antenna; B, mandible, gnathobase; C, mandible, palp; D, maxillule, a, praecoxal arthrite; b, coxal epipodite; c, coxal endite; d, endopod fused to exopod; E, maxilla; F, maxilliped. Scale bars 0.1 mm.

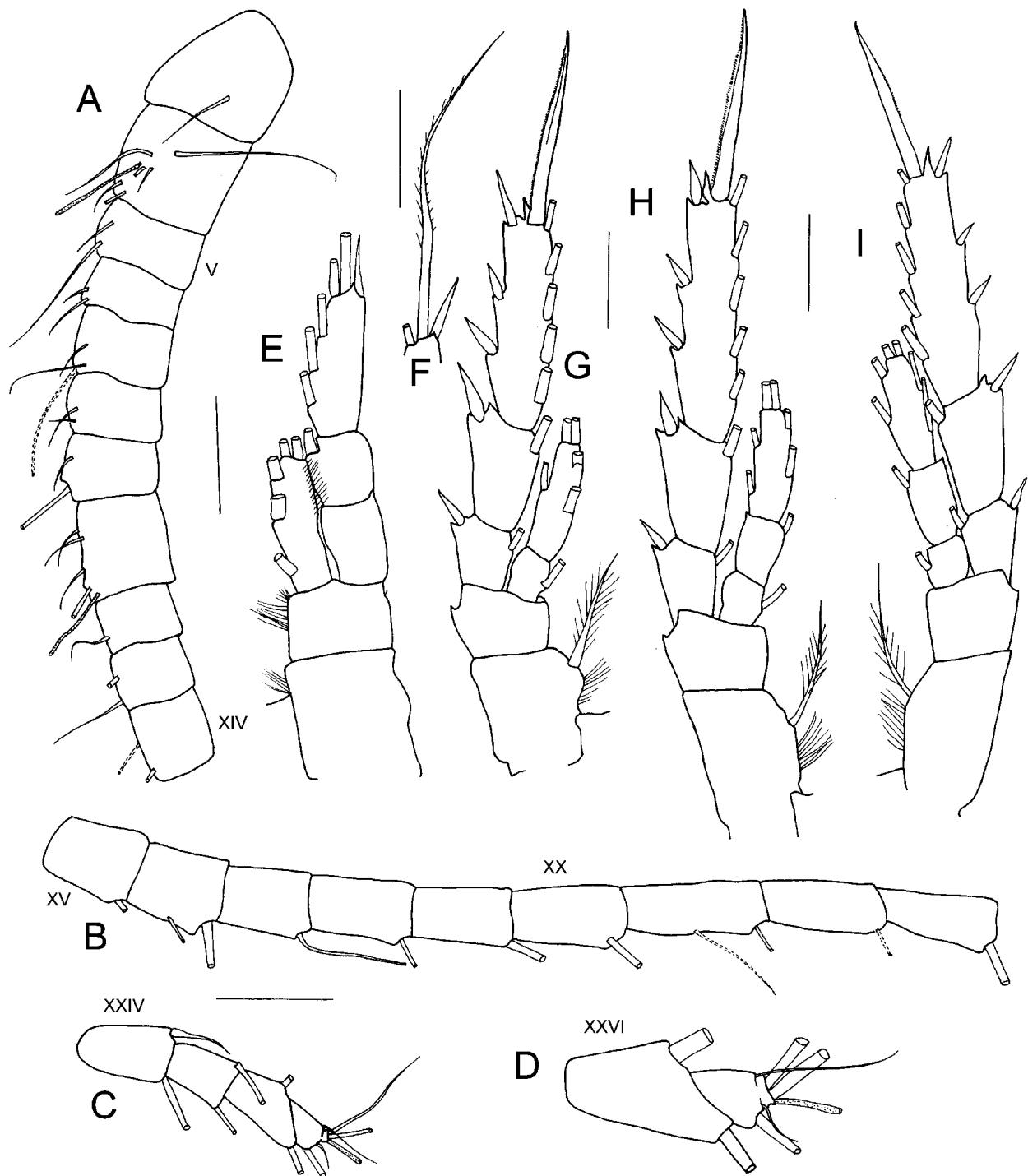


FIGURE 3. *Caudacalanus mirus* gen. et sp. nov. Female, holotype except F. A, antennule, articulated segments 1–11 (ancestral segments I–XIV), dotted setae are additions from paratype; B, antennule, articulated segments 12–20 (ancestral segments XV–XXIII); C, antennule, articulated segments 21–25 (ancestral segments XXIV–XXVIII); D, antennule, articulated segments 23–25 (ancestral segments XXVI–XXVIII); E, P1; F, P1 (from paratype), terminal part of exopod segment 3; G, P2; H, P3; I, P4. Scale bars 0.1 mm.

P1 (Fig. 3E–F), coxa without seta; basis without a medial or lateral seta; endopod 1-segmented with 3 medial and 2 terminal setae, lacking lateral lobe, distal lateral corner smoothly rounded, not reaching suture between exopod segments 2 and 3; exopod segment 1 without setae, exopod segment 2 with 1 medial seta, lateral spine lacking; exopod segment 3 with 4 medial setae, 1 terminal and 1 lateral spine.

P2 (Fig. 3G), coxa with seta, basis without seta; endopod 2-segmented, segment 1 with 1 medial seta, segment 2 with 2 medial, 2 terminal and 1 lateral setae; exopod 3-segmented, segments 1 and 2 with 1 medial seta and 1 lateral spine; segment 3 with 5 medial setae, 1 terminal and 3 lateral spines; terminal spine about as long as exopod segment 3.

P3–P4 (Fig. 3H–I), coxa with seta; basis without seta; endopod segments 1 and 2 with 1 medial seta each, segment 3 with 2 medial, 2 terminal and 2 lateral setae. Exopod as in P2. P3 terminal spine 0.8 times as long as exopod segment 3; P4 terminal spine 0.7 times as long as exopod segment 3.

Etymology. The specific name (from Latin *mirus* meaning wonderful, strange) refers to the exceptional shape of the caudal rami. It is an adjective agreeing in gender with the (masculine) generic name.

***Caudacalanus vicinus* sp. nov.**

(Figs 4–5)

Holotype. Dissected adult female (ZMH Reg. no. K-41257), body length 2.00 mm. Collected Southern Ocean, 65°00'S 43°01'W, RV *Polarstern* (ANDEEP II), 11 March 2002, above the seabed at 4679–4678 m.

Paratypes. Dissected adult female (ZMH Reg. no. K-41258), body length 1.85 mm. Collected Southern Ocean, 60°38'S 53°57'W, RV *Polarstern* (ANDEEP I), 30 January 2002, above the seabed at 2893–2889 m; undissected adult female (ZIN Reg. no 91088), body length 1.80 mm, same collection data as for another paratype.

The holotype and 1 paratype are deposited at the Zoological Museum Hamburg, University of Hamburg (ZMH); 1 paratype is deposited at the Zoological Institute, Russian Academy of Sciences, St. Petersburg (ZIN).

Additional material. Adult female, damaged, not measured. Collected Southern Ocean, 59°40'S 57°37'W, RV *Polarstern* (ANDEEP I), 27 January 2002, above the seabed at 3683–3680 m. Adult female, body length 1.80 mm. Collected south-eastern Atlantic, 17°06'S 04°41'W, FS *Meteor* (DIVA-1), 25 July 2000, above the seabed at 5415 m.

Description. Female: total length 1.80–2.00 mm (n=4). Prosome 1.8–2.0 times longer than urosome. Rostrum as elongated cone (Fig. 4C). Posterior corners of prosome as short rounded lobes (Fig. 4B). Genital double somite symmetrical (Fig. 4D). Caudal rami asymmetrical; right ramus nearly twice as long and wide as left; both rami with 4 terminal setae; right ramus with a dorsal seta, ventral seta lacking, left ramus with a ventral seta, dorsal seta lacking (Fig. 4A–B, D–F).

Antennule exceeding posterior border of prosome somite 3, or as long as prosome (Fig. 4G–K), 25-segmented, armature as follows: I–1s, II–IV–6s + 1ae, V–2s, VI–2s, VII–2s + 1ae, VIII–2s, IX–2s, X–XI–4s + ?, XII–1s, XIII–2s, XIV–2s, XV–1s, XVI–2s, XVII–1s, XVIII–1s, XIX–1s, XX–1s, XXI–2s, XXII–1s, XXIII–1s, XXIV–2s, XXV–2s, XXVI–2s, XXVII–2s, XXVIII–3s + 1ae.

Antenna (Fig. 5A), coxa with 1 seta; basis with 2 setae; first endopodal segment with 2 setae, second with 7 and 6 setae (13 setae in total), endopod about 1.6 times as long as exopod; exopod 8-segmented with 0, 1, 1, 1, 1, 1 and 3 setae, second segment complex of 3 ancestral segments with 0–0–1 setae.

Mandible (Fig. 5B–C), gnathobase with 4 large teeth and seta; basis with 2 setae; endopod segment 1 without setae, segment 2 with 8 setae; exopod 5-segmented with 1, 1, 1, 1 and 2 setae.

Maxillule (Fig. 5D), praecoxal arthrite with 8 terminal spines and 3 dorsal setae; coxal epipodite with 6–7 setae; coxal endite with 3 setae, of them 2 long and strongly sclerotized; proximal basal and distal basal endites reduced; endopod separate from exopod without setae, exopod with 1 seta.

Maxilla (Fig. 5E), proximal praecoxal endite with 2 setae and small attenuation; distal praecoxal and coxal endites with 2 setae each; basis without setae; endopod 3-segmented with 1, 1 and 2 setae.

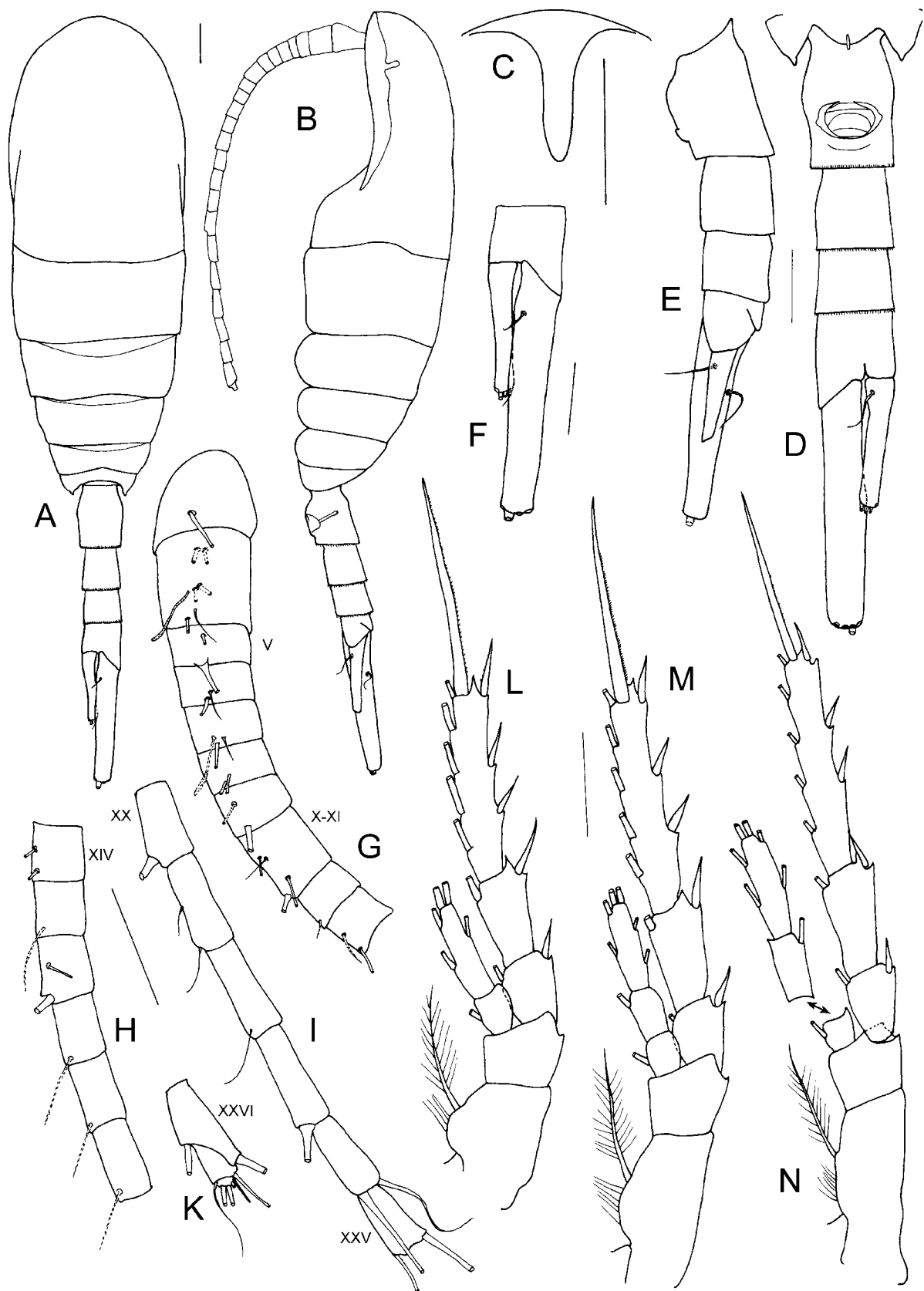


FIGURE 4. *Caudacalanus vicinus* gen. et sp. nov. Female. A, habitus, dorsal; B, habitus, lateral; C, rostrum, ventral; D, urosome, ventral; E, urosome, lateral; F, anal somite and caudal rami, dorsal; G, antennule, articulated segments 1–10 (ancestral segments I–XIII); H, articulated segments 11–16 (ancestral segments XIV–XIX); I, antennule, articulated segments 17–22 (ancestral segments XX–XXV); K, antennule, articulated segments 23–25 (ancestral segments XXVI–XXVIII); L, P2; M, P3; N, P4. E from paratype, other figures, holotype, dotted setae are additions from paratype. Scale bars 0.1 mm.

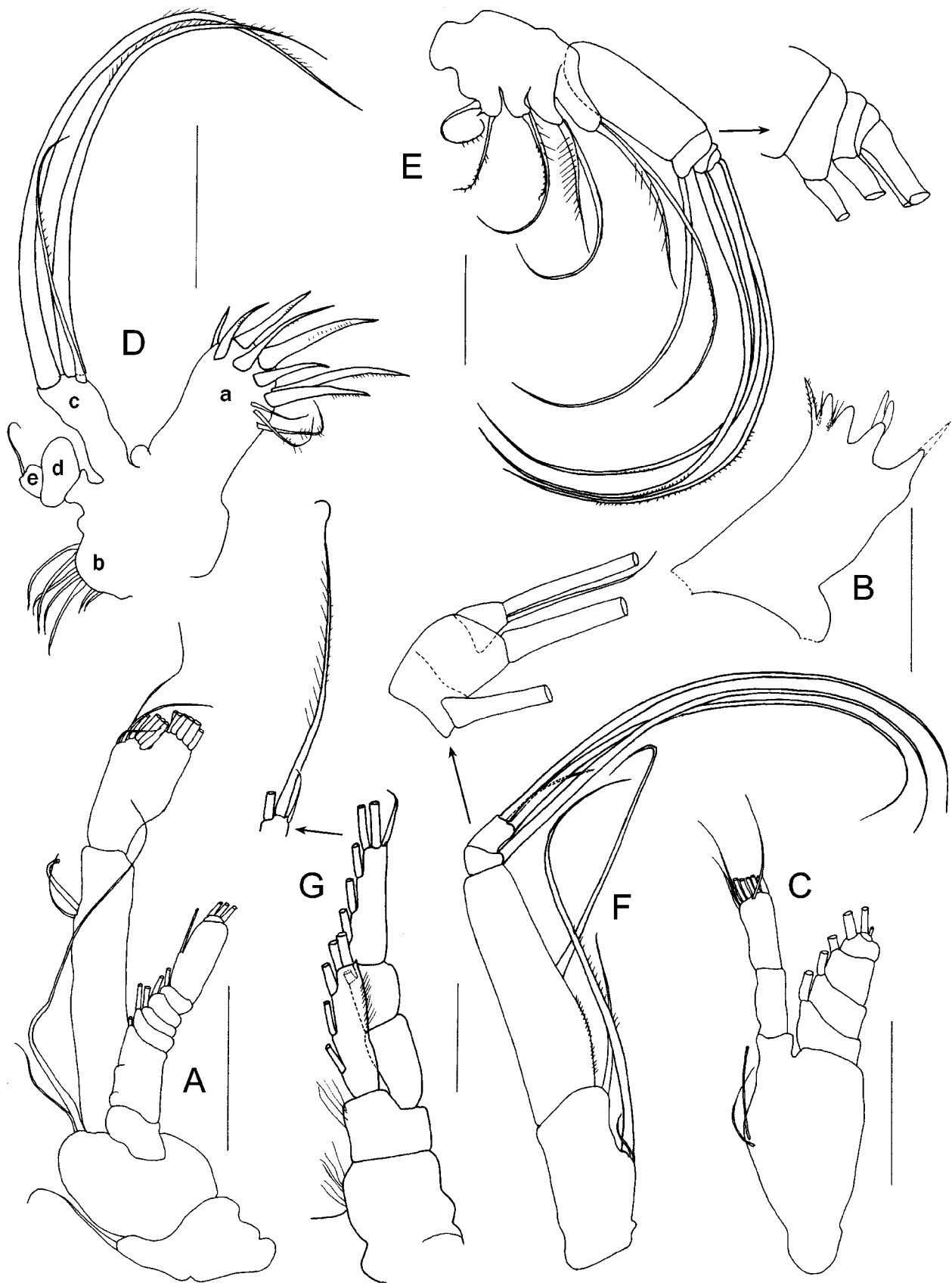


FIGURE 5. *Caudacalanus vicinus* gen. et sp. nov. Female, holotype. A, antenna; B, mandible, gnathobase; C, mandible palp; D, maxillule, a, praecoxal arthrite; b, coxal epipodite; c, coxal endite; d, endopodite; e, exopodite; E, maxilla; F, maxilliped, detail of endopod from paratype; G, P1. Scale bars 0.1 mm.

Maxilliped (Fig. 5F), syncoxa with 2 unequal setae on distal praecoxal lobe, 1 seta curved in distal part, longer than basis plus endopod; coxal lobe with 1 seta; basis with 1 medial seta; endopod 3-segmented with 1, 1, and 2 (1 long and 1 short) setae.

P1 (Fig. 5G), coxa without seta; basis without a medial or lateral seta; endopod 1-segmented, with 3 medial and 2 terminal setae, without lateral lobe; distal lateral corner triangular, slightly exceeding suture line between exopod segments 2 and 3; exopod segment 1 without setae, exopod segment 2 with 1 medial seta, lateral spine lacking, exopod segment 3 with 4 medial setae, 1 terminal and 1 lateral spine.

P2–P4 (Fig. 4L–N) as in *C. mirus* except for P2–P3 terminal spines longer: P2 terminal spine about 1.2 times as long as exopod segment 3, P3 terminal spine about as long as exopod segment 3. P4 terminal spine 0.7 times as long as exopod segment 3.

Etymology. The specific name (from Latin *vicinus* meaning similar) refers to the general similarity of this species with the type species of the genus. The name is an adjective agreeing in gender with the (masculine) generic name.

Remarks. *Caudacalanus vicinus* differs from *C. mirus* in : i) smaller size (1.80–2.00 mm vs. 2.70–2.80 mm in *C. mirus*); ii) praecoxal arthrite of maxillule having 3 dorsal setae (2 setae in *C. mirus*); iii) coxal epipodite of maxillule with 6–7 setae (1 seta in *C. mirus*); iv) coxal endite of maxillule with 3 setae (4 setae in *C. mirus*); v) endopod of maxillule separate from exopod and lacking any seta; exopod with 1 seta (fused to exopod and without setae in *C. mirus*); vi) maxilla proximal praecoxal endite with 2 setae and some attenuation (attenuation absent in *C. mirus*); vii) maxillipedal endopod segment 3 with 2 setae (1 seta in *C. mirus*); viii) P1 endopod slightly exceeding suture between exopod segments 2 and 3 (vs. endopod not reaching suture between exopod segments 2 and 3 in *C. mirus*), with distal lateral corner triangular (smoothly rounded in *C. mirus*); ix) P2 terminal spine about 1.2 times as long as exopod segment 3 (in *C. mirus*, terminal spine about as long as exopod segment 3); x) P3 terminal spine about as long as exopod segment 3 (in *C. mirus*, P3 terminal spine 0.8 times as long as exopod segment 3).

Discussion

Among the Spinocalanoidea, the Arctokonstantinidae are characterized by a reduced segmentation and setation of the oral parts and P1 (Table 1) and appear to be more derived than the Spinocalanidae, the only other family of this superfamily. Three arctokonstantinid genera (*Foxtonia*, *Sognocalanus* and *Arctokonstantinus*) are pelagic deep-water inhabitants, but *Caudacalanus* is benthopelagic. Apparently, Arctokonstantinidae is a later offshoot of the spinocalanids, but it is difficult to speculate if its ancestor was primarily pelagic and invaded the near-bottom secondarily, or was benthopelagic and then invaded the open water column.

Concerning the ancestral mode of life of Spinocalanidae, some speculations are possible. Due to a more primitive morphology of pelagic representatives of spinocalanids, it may be assumed that they probably originated in the pelagic environment. Typically, pelagic spinocalanid genera (*Monacilla* Sars, 1905; *Spinocalanus* Giesbrecht, 1888; *Mimocalanus* Farran, 1908; *Mospicalanus* Schulz, 1996; *Teneriforma* Grice & Hulsemann, 1967) demonstrate diversity of some primitive characters not observed in their benthopelagic relatives (*Damkaeria* Fosshagen, 1987; *Kunihulsea*, Schulz, 1992; *Methanocalanus* Ivanenko, Defaye & Cuoc, 2007; *Isaacicalanus* Fleminger, 1983). The following plesiomorphies are considered typical of pelagic spinocalanids: i) 11 setae on mandible endopod segment 2 in *Spinocalanus* (Park 1970; Brodsky *et al.* 1983), vs. 9–10 setae in other spinocalanids. Here and below the most primitive state of characters described for the genus are given; ii) 15 setae on maxillule praecoxal arthrite in *Monacilla* (Schulz 1989), vs. fewer in other spinocalanids; iii) 6 setae on maxillule coxal endite in *Spinocalanus* (Damkaer 1975; Brodsky *et al.* 1983; Schulz 1989), vs. fewer in other spinocalanids; iv) 6 setae on maxillule distal basal endite in *Teneriforma* (Schulz 1989), vs. fewer in other spinocalanids; v) 16 setae on endopod and 11 setae on exopod of maxillule in *Monacilla*, *Spinocalanus*,

Mimocalanus (but 23 on endopod in *M. crassus* Park, 1970); exopod setation of this type also in *Mospicalanus* (Damkaer 1975; Schulz 1989, 1996), vs. fewer in other spinocalanids; vi) maxilla with 9 setae (2+7) on endopod fused to distal basal endite in *Monacilla* and *Spinocalanus* (Schulz 1989), vs. fewer in other spinocalanids; vii) praecoxal endites of maxilliped syncoxa with 1, 2, 3 setae in *Monacilla* and *Spinocalanus* (Schulz 1989), vs. fewer in other spinocalanids; viii) coxal endite of maxilliped syncoxa with 4 setae in *Monacilla* and *Mimocalanus* (Brodsky *et al.* 1983; Schulz 1989), vs. fewer in other spinocalanids.

Typically, pelagic Spinocalanidae share some primitive characters with more derived benthopelagic spinocalanid genera: i) the primitive type of antenna exopod setation 1, 1–1–1, 1, 1, 1, 1, 1, and 3 setae, is shared by pelagic *Monacilla*, *Spinocalanus*, and *Teneriforma* and the benthopelagic genus *Kunihulsea* (Park 1970; Schulz 1989, 2004); ii) the most primitive condition in the armature of the proximal basal endite of maxillule (4 setae) is found in the pelagic genera *Monacilla*, *Spinocalanus*, *Mimocalanus*, and *Mospicalanus* as well as the benthopelagic *Methanocalanus* (Schulz 1989, 1996; Park 1970; Ivanenko *et al.* 2007); iii) the most primitive armature of the proximal praecoxal endite of maxilla (7 setae) is shared by the pelagic *Monacilla* and the benthopelagic genus *Methanocalanus* (Schulz 1989; Ivanenko *et al.* 2007).

Arctokonstantinidae and Spinocalanidae belong to the Spinocalanoidea, the sister group of the Ryocalanoidea. Diagnostic characters considered to distinguish the superfamily Spinocalanoidea from Ryocalanoidea are not very strong (Andronov 1992; Boxshall & Halsey 2004): male antennule non-geniculate (geniculate in ryocalanoideans) and P1 exopod segment 3 with 1 lateral spine (vs. 2 spines in primitive ryocalanoideans). The recently described benthopelagic spinocalanid genus *Methanocalanus* bears an antennule with traces of geniculation in the male (Ivanenko *et al.* 2007:50). Thus, a possible presence of geniculation in the antennule of adult males, up to now undiscovered, cannot be ruled out, since several males of these genera are still undiscovered (e.g. of the spinocalanids *Kunihulsea*, *Mospicalanus*, and *Isaacicalanus*, as well as of the arctokonstantinids *Foxtonia*, *Arctokonstantinus*, and *Caudacalanus*). As a result, the diagnostic characters of the superfamilies Ryocalanoidea and Spinocalanoidea are not to be considered completely determined.

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