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New representatives of the genus *Ancorabolina* George, 2006 (Copepoda, Harpacticoida, Ancorabolidae) including remarks on ancorabolid phylogeny

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Four new species of *Ancorabolina* George, 2006 (Copepoda: Harpacticoida: Ancorabolidae) are described: ***Ancorabolina belgicae* sp. nov.** (from the Porcupine Seabight, north-east Atlantic Ocean), ***Ancorabolina anaximenesi* sp. nov.** and ***Ancorabolina galeata* sp. nov.** (both from Anaximenes Mountain, eastern Mediterranean Sea), and ***Ancorabolina divasecunda* sp. nov.** (from Cape and Guinea Basins, south-east Atlantic Ocean). Furthermore, the generic diagnosis for *Ancorabolina* is provided and the position of the taxon within Ancorabolidae is discussed. The characters originally employed to allocate *Ancorabolina* to the subfamily Ancorabolinae Sars, 1909, are critically evaluated and two true autapomorphies for a monophyletic Ancorabolinae (including *Ancorabolina*) are recognized. Two autapomorphies supporting *Ancorabolina* are proposed: (1) cephalothorax posteriorly with pair of ventrolateral cuticular processes turned backwards and (2) loss of the third setal element subapically on the antennary endopod. The urgent need for a phylogenetic re-evaluation of the paraphyletic subfamily Laophontodinae Lang, 1944 is stressed and evidenced by three characters widespread in this subfamily but also present in *Ancorabolina*. This may be an indication of a closer relationship of *Ancorabolina* with certain members of Laophontodinae.

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ADDITIONAL KEYWORDS: Atlantic Ocean – deep sea – Mediterranean Sea – new species – phylogenetic systematics.

INTRODUCTION

Lang (1944, 1948) subdivided the family Ancorabolidae Sars, 1909 into two subfamilies: Laophontodinae Lang, 1944 and Ancorabolinae Sars, 1909. The subfamily Laophontodinae was considered to be the more primitive (Lang, 1948), but was defined only by plesiomorphies (George, 2006c). Recent phylogenetic studies have mainly focused on the relationships within Ancorabolinae (e.g. George, 1998a, 2006a, b; Conroy-Dalton & Huys, 2000; Conroy-Dalton, 2001, 2003a, b; Gómez & Conroy-Dalton, 2002), whereas the relationships with and within Laophontodinae have been far less explored (e.g. Conroy-Dalton, 2004) and remain mostly unresolved. Recently, the monotypic genus *Ancorabolina* George, 2006 has been described by George (2006c) from the southern Atlantic deep sea. Because of the high number of derived characters in common with Ancorabolinae, an allocation to that taxon was justified.

Within the framework of different projects, several new representatives of the genus *Ancorabolina* have been collected. Besides additional specimens of *Ancorabolina chimaera* George, 2006, the DIVA 2 campaign (in 2005) to the South Atlantic Ocean yielded another new species. The RV METEOR expedition M71/1 (in 2006) to the Anaximander Mountains

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in the eastern Mediterranean yielded two new species, and the RV BELGICA cruise 01/12 (in 2001) to the Porcupine Seabight in the north-east Atlantic Ocean yielded a single specimen of a fourth new species. The description of these four new species herein presented will enhance the phylogenetic characterization of *Ancorabolina*. Moreover, these records extend the distribution range of the genus to the North Atlantic Ocean and into the Mediterranean Sea. The difficulties in allocating *Ancorabolina* within Ancorabolidae clearly indicate the need for a phylogenetic re-evaluation of the subfamily Laophontodinae.

MATERIAL AND METHODS

The material studied in this paper was collected in the Belgica Mound Province of the Porcupine Seabight (north-east Atlantic Ocean), in the Guinea and Cape Basins (in the South Atlantic Ocean), and on Anaximenes seamount (in the eastern Mediterranean Sea). The single specimen from the Porcupine Seabight described in this paper was collected during expedition RV BELGICA 01/12 in May 2001. The sample was taken with a boxcorer in the coral degradation zone of *Lophelia pertusa* (Linnaeus, 1758) reefs, at a depth of 880 m. The surface of the sediment was covered with several dead fragments of this cold-water coral. Treatment of this sample follows Gheerardyn, Seifried & Vanreusel (2008). Stations in the South Atlantic and the eastern Mediterranean Sea were sampled on board RV METEOR with a multiple corer (MUC) (Barnett, Watson & Connelly, 1984) during expeditions M63/2 DIVA 2 (25 February to 30 March 2005) and M71/1 (11 to 24 December 2006), respectively. Sample treatment of these samples follows Rose *et al.* (2005).

Whole specimens and dissected parts of the specimens were mounted in glycerine and preparations were sealed with insulating varnish. Drawings were made with the aid of a drawing tube on a Leica DMR microscope equipped with differential interference contrast (DIC) at 1000 × magnification. Specimens have been deposited in the Invertebrate Collections of the Royal Belgian Institute of Natural Sciences (KBIN) (Brussels, Belgium; labelled COP) and in the collection of the Forschungsinstitut und Naturmuseum Senckenberg (Frankfurt, Germany; labelled SMF). Scale bars in Figures are indicated in μm.

The following abbreviations are used in the text: aes, aesthetasc; P1–P6, first to sixth thoracopod; apo, apophysis; enp, endopod; exp, exopod; enp-1 (2, 3), proximal (middle, distal) segment of endopod; exp-1 (2, 3), proximal (middle, distal) segment of exopod.

SYSTEMATICS

GENUS *ANCORABOLINA* GEORGE, 2006

Ancorabolidae Sars, 1909, Ancorabolinae Sars, 1909

Type species: Ancorabolina chimaera George, 2006

Other species: Ancorabolina belgicae sp. nov.; *Ancorabolina anaximenesi* sp. nov.; *Ancorabolina galeata* sp. nov.; *Ancorabolina divasecunda* sp. nov.

Generic diagnosis: Ancorabolinae. Body cylindrical, slightly tapering posteriorly, without clear demarcation between prosome and urosome. Prosomites and urosomites with a number of small projections along their posterior margins. Body somites bearing P2–P6 (genital half of double-somite in female, except in *A. divasecunda*) with a single tube pore dorsally. Cephalothorax anteriorly slightly constricted, forming a 'peak' as described by George (2006b). Cephalothorax with one pair of lateral processes at the posterior margin, processes slightly curved backwards and each with two sensilla along anterior margin. Telson broader than long, trapezoid in lateral view. Anal operculum bearing row of spinules. Furcal rami elongate and cylindrical, inserted at outer corners of telson and directed upwards, not or only slightly divergent. Furcal rami with seven setae; setae I and II inserted closely together at posterior third of lateral margin; seta III inserted subapically; setae IV, V, and VI inserted apically; setae IV and V fused; seta V longest; seta VII tri-articulate at base. Sexual dimorphism in body size, antennule, P3 endopod, P4 endopod, P5, P6, and genital somites.

Rostrum variable in shape, from small and triangular to strongly elongate and ventrally curved; basally constricted; fused to cephalic shield; with paired sensilla subapically and paired membranous projections laterally. Antennule five-segmented in female, seven-segmented and subchirocer in male (with two segments distal to geniculation); aesthetasc arising from segments 3 and 5 in female, segments 5 and 7 in male; first segment two to five times as long as wide. Antenna with allobasis, abexopodal margin with one slender seta in distal quarter (except in *A. divasecunda*); exopod entirely absent; endopod with two lateral and six distal elements (three geniculate, one small and slender). Mandibular palp one-segmented, with two inner, one outer, one subapical, and two apical setae. Maxillule with one or two setae on coxal endite; basis, endopod, and exopod fused, bearing seven to nine setae. Maxillary syncoxa with two well developed endites, each with three elements (two in *A. divasecunda*); allobasis drawn out into a claw with two or three accessory setae; endopod reduced and represented by two setae. Maxilliped long and slender,

prehensile; syncoxa with one apical seta; endopod drawn out into a long, narrow curved claw, with one accessory seta at base (not discernible in *A. chimaera*).

P1. Coxa cylindrical and slightly elongate. Basis as long as coxa, or distinctly more elongate; slightly to strongly prolonged transversely. Endopod two-segmented, exopod two- or three-segmented. Enp-1 slender, about twice as long as exopod. Enp-2 much smaller, with minute seta along inner margin (not discernible in *A. belgicae*), apically with one anterior claw-like seta and one posterior geniculate seta (two geniculate setae in *A. divasecunda*, two nongeniculate setae in *A. chimaera*). Exp-1 with one outer spine. In the case of a two-segmented exopod: exp-2 with three outer and two apical geniculate setae closely set together near the distal margin. In the case of a three-segmented exopod: exp-2 with one outer geniculate seta; exp-3 with two outer and two apical geniculate setae closely set together near the distal margin.

P2–P4. Coxa small, trapezoid. Basis transversely elongate. Exopods three-segmented, endopods two-segmented. Enp-1 small. Exp-1 and enp-1 without inner setae; exp-3 with three outer spines. Male P3 endopod three-segmented; enp-2 elongate, apically with pointed apophysis; enp-3 with two apical setae. Enp-2 of male P4 additionally with one outer, subapical seta.

P5 with basal setophore; baseoendopod cylindrical, elongate; endopodal lobe vestigial, represented by two minute setae and one or two tube pores; exopod distinct in both sexes and elongate, with one inner, two apical, and two (in female) or one (in male) outer setae. Female genital field located in anterior half of double-somite. P6 represented by two small cuticular plates. Male P6 absent.

ANCORABOLINA BELGICAE SP. NOV.

Type locality: North-east Atlantic Ocean, Porcupine Seabight, Boxcore Bbc01-1205 during Belgica Cruise 01/12, 51°25.9290′N, 11°46.2717′W, 880 m, collected on 7.v.2001, sample of underlying sediment [sediment covered with dead fragments of the cold-water coral *Lophelia pertusa* (Linnaeus, 1758)].

Material examined: From type locality: Female holotype (coll. no. COP 7695/a–n) dissected on 14 slides. Male unknown.

Etymology: The species is named in honour of the crew of RV BELGICA.

Description: Female: Habitus (Fig. 1A) long and slender. Total body length: 342 μm (measured from tip of rostrum to posterior end of furcal rami). Rostrum (Fig. 2B) fused to cephalothorax and elongate, tip reaching distal end of first antennular segment, with paired sensilla distally. Cephalothorax anteriorly slightly constricted, forming a 'peak' as described by George (2006b). Cephalothorax with sensilla and pores as figured. Posteriorly with paired lateral processes, which are strongly cuticularized and curved backwards. Posterior margin of cephalothorax with four sensillate processes. Free body somites 1–4 and anterior somite of genital double-somite with a single mediodorsal tube pore. Free body somites 1–2 with four sensillate projections at their posterior margins. Free body somites 3–4 with inner pair of small processes and outer pair of sensillate processes. Both somites of genital double-somite and following urosomite with several small projections and sensilla at their posterior margins. Posterior margin of penultimate urosomite serrate. Telson broader than long, trapezoid in lateral view (Fig. 6C), anal operculum with row of spinules.

Furcal rami (Figs 1B, 6A, C) long and slender, about 6.5 times as long as wide, with seven setae: I and II inserted closely together at posterior third of lateral margin; III inserted subapically; IV, V, and VI inserted apically; IV and V fused, V longest; VII inserted dorsally at distal margin. Outer margin with tube pore proximally. Furcal rami inserted at outer corners of telson and directed upwards (Fig. 6C).

Antennule (Fig. 2A, B) five-segmented. Armature formula: 1, 8, 5 + (1 + aes), 1, 9 + (2 + aes). First segment slightly elongate (2.5 times as long as wide), with several long spinules along inner surface. Second segment with a small, round bump near middle of outer margin. Second and third segments with several long spinules along outer margin, both nearly equal in length to first segment. Fourth segment shortest, nearly square in shape. Fifth segment slightly shorter than third one.

Antenna (Fig. 2C) with allobasis; exopod absent; abexopodal margin of allobasis with longitudinal row of spinules and one slender seta. Endopod with several spinules, laterally with two bipinnate spines. Apical armature consisting of two unipinnate spines, three long geniculate setae, and one small bare seta (fused basally to seta next to it). Subapically with two cuticular spinular frills.

Labrum well developed (Fig. 3A).

Mandible (Fig. 3B) with strong gnathobase bearing several incised blades and one additional seta. Mandibular palp one-segmented, with two inner, one outer, one subapical, and two apical setae.

Maxillule (Fig. 3C, D). Praecoxal arthrite with two setae on anterior surface; apical armature consisting of six bare and two pinnate spines, and one slender seta. Coxal endite with one well-developed, pinnate spine. Basis, endopod, and exopod fused, bearing eight setae.

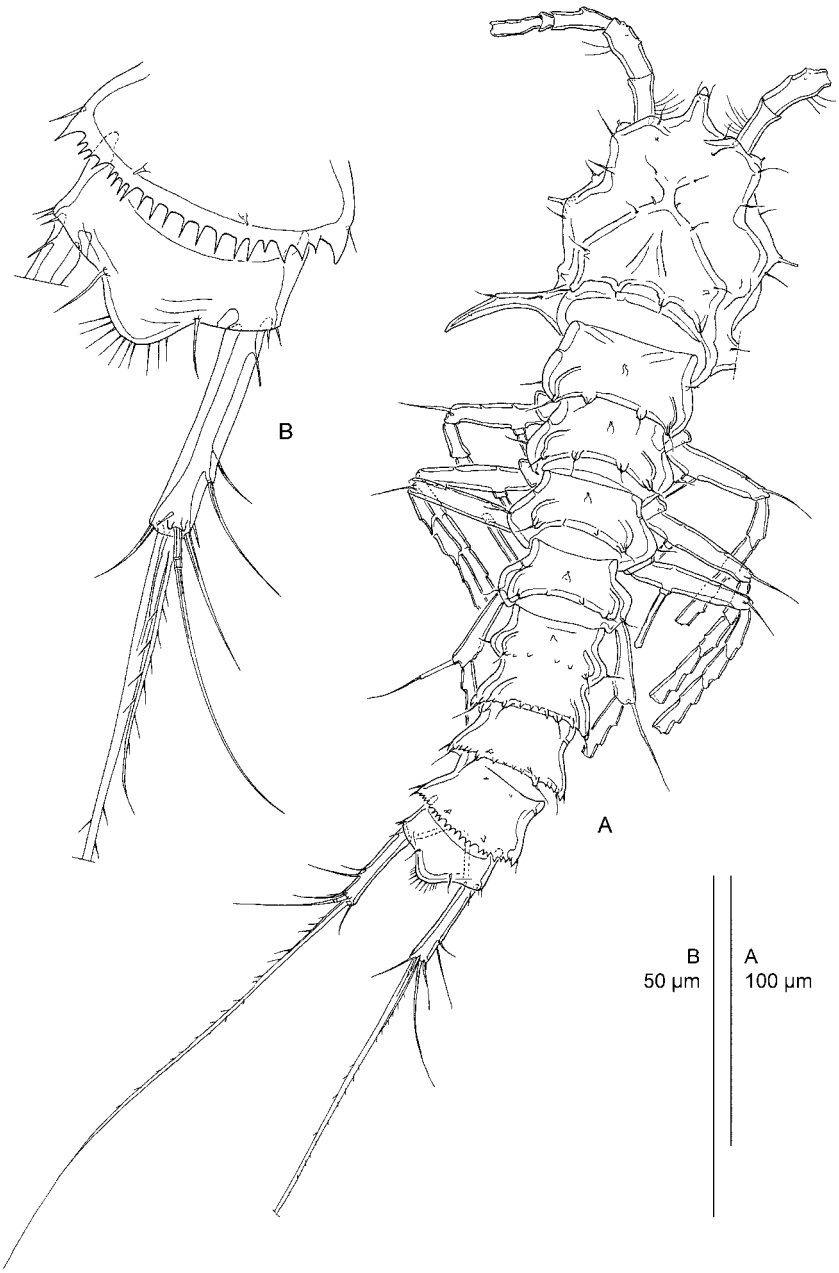

Figure 1. ***Ancorabolina belgicae*** **sp. nov.**, female holotype. A, habitus, dorsal; B, telson and furcal ramus, dorsal.

Maxilla (Fig. 3E). Syncoxa bearing two endites, with long spinules along outer margin. Proximal endite with two setae and one unipinnate spine fused to endite. Distal endite with three setae, one of which is plumose. Basis drawn out into a claw, accessory armature consisting of three bare setae. Endopod reduced and represented by two bare setae.

Maxilliped (Fig. 3F) long and slender, prehensile. Syncoxa apically with a bipinnate seta and several spinules. Basis with a row of small spinules along inner margin and several spinules along outer margin. Endopod drawn out into a long, narrow, curved, finely pinnate claw with one accessory seta at base.

P1 (Fig. 4A) with two-segmented endopod and exopod. Coxa about 1.5 times as long as wide. Basis longer than coxa, slightly prolonged transversely, with inner and outer bipinnate seta. Exp-1 with outer spine, exp-2 with five geniculate setae. Enp-1 twice as long as exopod, with a row of long spinules along inner margin. Enp-2 much smaller, apically with two bare setae (one claw-like and one geniculate).

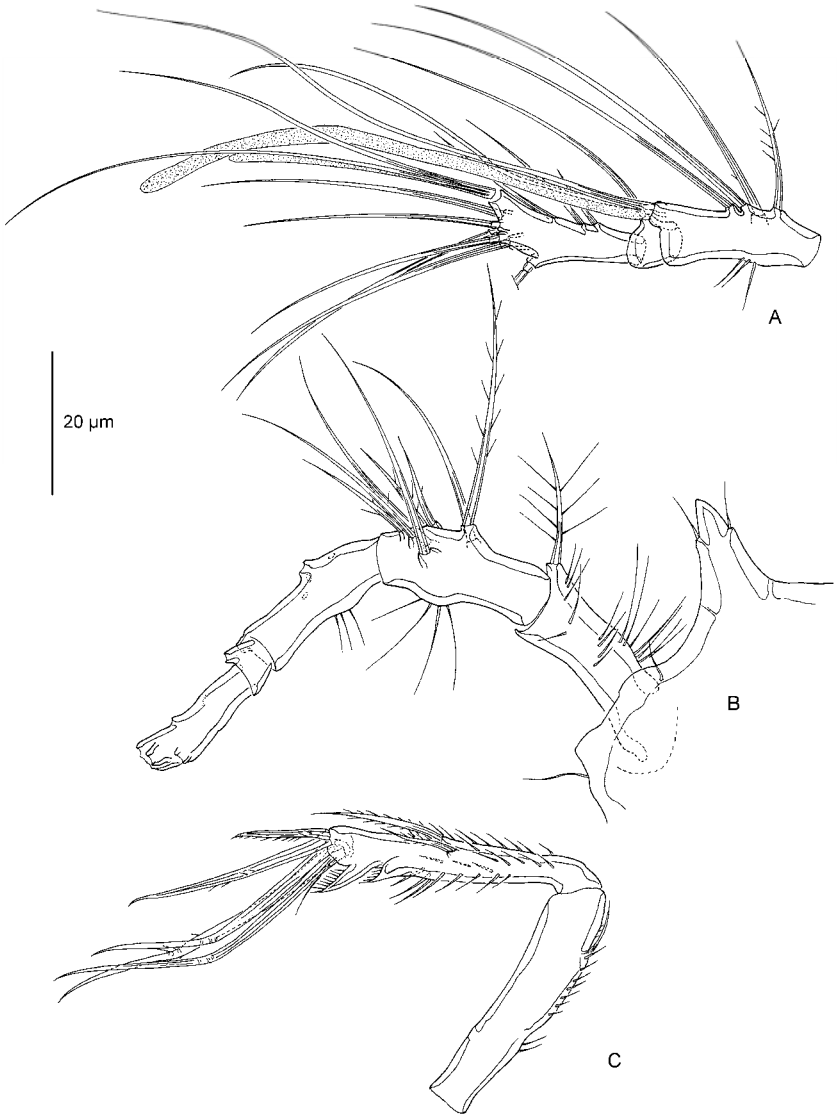

Figure 2. ***Ancorabolina belgicae*** **sp. nov.**, female holotype. A, segments 3 to 5 of right antennule, ventral; B, rostrum and left antennules (armature of segments 3 to 5 omitted), dorsal; C, antenna.

P2–P4 (Figs 4B, C, 5A, B). Basis transversely elongate, with one tube pore in distal half of anterior surface, outer distal seta bipinnate. Exopods three-segmented, outer spines elongate. Endopods two-segmented; first segment very small, without ornamentation. Enp-2 of P2–P4 very long, with two apical setae; enp-2 of P3–P4 additionally with one inner seta. Enp-2 of P2 with inner spinules, of P3–P4 with inner and outer spinules. Armature formula as in Table 1.

P5 (Fig. 6B). Baseoendopod with long outer spinules. Endopodal lobe vestigial, with two small setae and two tube pores. One additional tube pore inserts at the base of the setophore. Exopod distinct and elongate, with one inner, two distal, and two outer bipinnate setae, one tube pore and with long spinules near outer margin.

Genital field (Fig. 6A). P6 represented by two small cuticular plates.

ANCORABOLINA ANAXIMENESI SP. NOV.

Type locality: Eastern Mediterranean Sea, Anaximenes Mountain, multiple corer, station 898 (core 1) during M71/1, 35°28.77′N, 30°12.95′E, depth 914 m, collected on 16.xii.2006.

Material examined: (1) From type locality: female holotype (coll. no. SMF 34163/1–17) and male allotype (coll. no. SMF 34164/1–12) dissected on 17 and 12 slides, respectively. (2) Additionally, 11 paratypes

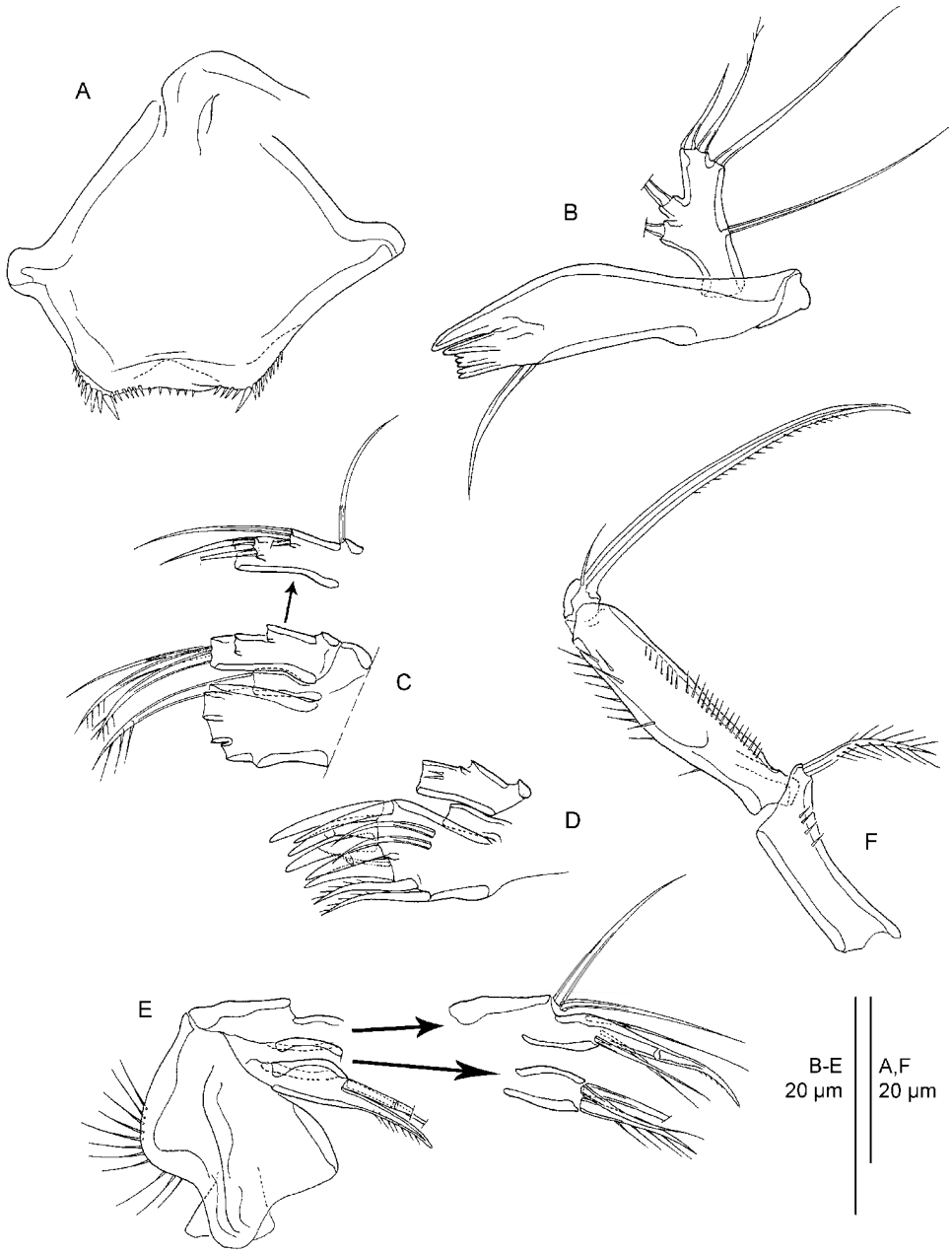

Figure 3. ***Ancorabolina belgicae*** **sp. nov.**, female holotype. A, labrum; B, mandible; C, D, maxillule; E, maxilla; F, maxilliped.

were collected with multiple corer from Anaximenes Mountain during M71/1: 1 ♂ (coll. no. SMF 34165) at station 897 (core 3) (35°28.80′N, 30°12.29′E, depth 904 m) on 16.xii.2006; 1 ♂ (coll. no. SMF 34166) at station 898 (core 2) (35°28.77′N, 30°12.95′E, depth 914 m) on 16.xii.2006; 2 ♀ and 2 ♂ (coll. nos SMF 34167–34169, 34170/1–2) at station 917 (core 2) (35°30.23′N, 30°8.97′E, depth 1965 m) on 18.xii.2006; 2 ♀ (coll. nos SMF 34171, 34172) at station 929 (core 2) (35°29.50′N, 30°10.10′E, depth 1786 m) on 19.xii.2006; 2 ♂ (coll. nos SMF 34173, 34174) at station 931 (core 2) (35°26.04′N, 30°9.90′E, depth 680 m) on 20.xii.2006; 1 ♀ (coll. no. SMF 34175) at station 954 (core 1) (35°27.99′N, 30°17.30′E, depth 1544 m) on 23.xii.2006.

Etymology: The species name *anaximenesi* refers to the type locality of this species, Anaximenes Mountain, which itself refers to the Greek philosopher Anaximenes.

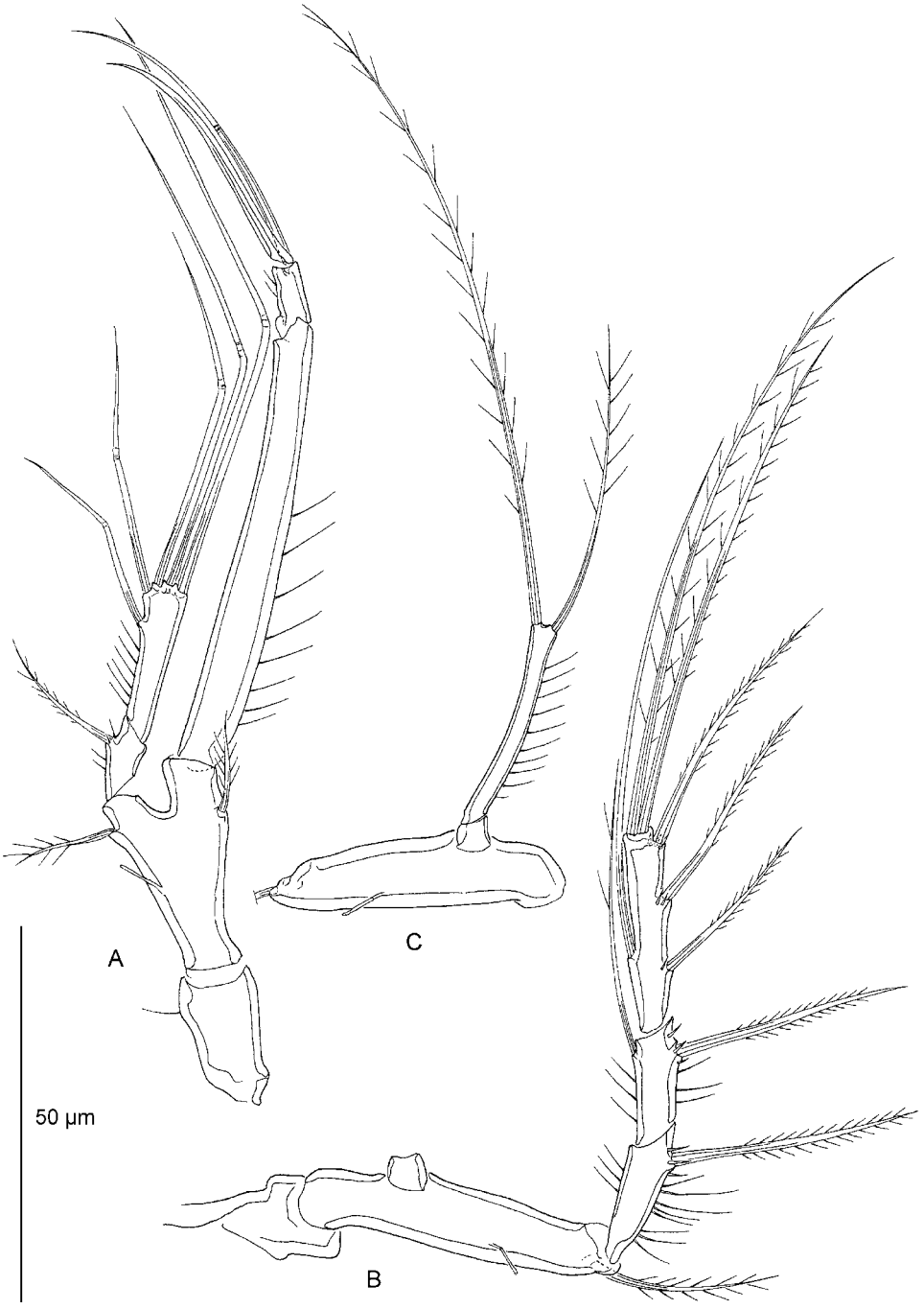

Figure 4. ***Ancorabolina belgicae*** **sp. nov.**, female holotype. A, first thoracopod (P1); B, right P2 (endopod-2 omitted); C, left P2 endopod.

Description: Female: Habitus (Fig. 7A, B) long and slender. Total body length: 294–367 µm (mean = 328 µm; $N = 6$; measured from tip of rostrum to posterior end of furcal rami). Rostrum (Figs 7B, 8E) fused to cephalothorax and elongate, curved ventrally, reaching distal end of first antennular segment in dorsal view, with paired sensilla inserted at two thirds of its length. Cephalothorax anteriorly slightly constricted, forming a 'peak' as described by George (2006b), with small projections laterally from insertion place of antennule, with sensilla and pores as figured. Posteriorly with paired lateral, slender processes, which are strongly cuticularized and slightly curved backwards (Fig. 8D). Each process with a

Figure 5. ***Ancorabolina belgicae*** **sp. nov.**, female holotype. A, third thoracopod (P3); B, P4.

small projection along anterior border, at two thirds of its length. Posterior margin of cephalothorax with inner pair of sensilla, outer pair of small processes, and a row of fine setules. Free body somites 1–4 and anterior somite of genital double-somite with a single mediodorsal tube pore. Posterior margins of free body somites 1–2 with inner pair of sensillate processes and outer pair of sensilla between small processes. Free body somites 3–4 with a pair of sensilla and several small processes along posterior margins. Posterior margins of genital double-somite and following two urosomites strongly serrate. Telson broader than long, trapezoid in lateral view (Fig. 11C), anal operculum with a row of spinules.

Furcal rami (Figs 11C, 12A, B) long and slender, about nine times as long as wide, with seven setae: I and II inserted closely together at posterior third of lateral margin; III inserted subapically; IV, V, and VI inserted apically; IV and V fused, V longest; VII inserted dorsally at distal margin. Outer margin with tube pore proximally. Furcal rami inserted at outer corners of telson and directed upwards (Fig. 11C).

Antennule (Fig. 8A) five-segmented. Armature formula: 1, 8, 5 + (1 + aes), 1, 9 + (2 + aes). First segment slightly elongate (three times as long as wide), with several long spinules along inner surface. Second segment with several long spinules on a small, round bump near middle of outer margin. Second and third segments both nearly equal in length to first segment. Fourth segment shortest, nearly square in shape. Fifth segment slightly shorter than third one.

Table 1. Species of *Ancorabolina* George, 2006

Species	Sex	P1	P2		P3		P4		P5	
		exp	exp	enp	exp	enp	exp	enp	exp	enp
Ancorabolina chimaera	♀	2	0.1.123	0.020	0.1.123	0.020	0.1.123	0.020	5	2
	♂	2	0.1.123	0.020	0.1.123	0.apo.020	0.1.123	0.021	4	2
***Ancorabolina belgicae* sp. nov.**	♀	2	0.1.123	0.020	0.1.123	0.120	0.1.123	0.120	5	2
***Ancorabolina anaximenesi* sp. nov.**	♀	2	0.1.123	0.020	0.1.123	0.120	0.1.123	0.120	5	2
	♂	2	0.1.123	0.020	0.1.123	0.apo.020	0.1.123	0.121	4	2
***Ancorabolina galeata* sp. nov.**	♀	3	0.1.123	0.020	0.1.123	0.120	0.1.123	0.120	5	2
	♂	3	0.1.123	0.020	0.1.123	0.apo.020	0.1.123	0.121	4	2
***Ancorabolina divasecunda* sp. nov.**	♀	3	0.1.123	0.020	0.1.123	0.120	0.1.123	0.120	5	2
	♂	3	0.1.123	0.020	0.1.123	0.apo.020	0.1.123	0.121	4	2

end, endopod; exp, exopod, P1–5, first to fifth thoracopods.
Number of exopodal segments in P1, swimming leg setal formulae of P2–P4 and number of exopodal and endopodal setae in P5.

Antenna (Fig. 8B, C) with allobasis; exopod absent; abexopodal margin of allobasis with spinules and one slender seta. Endopod with several spinules, laterally with two pinnate spines. Apical armature consisting of two unipinnate spines, three long geniculate setae, and one small bare seta (fused basally to seta next to it). Subapically with two cuticular spinular frills.

Mandible (Fig. 9A) with strong gnathobase bearing several incised blades and one additional seta. Mandibular palp one-segmented, with two inner bipinnate setae, one outer, one subapical, and two apical setae.

Maxillule (Fig. 9B). Praecoxal arthrite with two setae on anterior surface; apical armature consisting of six bare spines and one slender seta; subapically with two spines. Coxal endite with one well-developed, pinnate spine and one slender, bare seta. Basis, endopod and exopod fused, bearing eight setae.

Maxilla (Fig. 9C). Syncoxa bearing two endites, with long spinules along outer and short spinules along inner margin. Proximal endite with two setae and one unipinnate spine fused to endite. Distal endite with three setae, one of which is plumose. Basis drawn out into a unipinnate claw, accessory armature consisting of three setae. Endopod reduced and represented by two bare setae.

Maxilliped (Fig. 9D) long and slender, prehensile. Syncoxa apically with a plumose seta and a row of spinules. Basis with a few, long inner and outer spinules. Endopod drawn out into a long, curved, pinnate claw with one accessory seta at base.

P1 (Fig. 9E) with two-segmented endopod and exopod. Coxa about 1.5 times as long as wide. Basis about 1.5 times longer than coxa, slightly prolonged transversely, with inner and outer seta. Exp-1 with outer spine, exp-2 with five geniculate setae. Enp-1 nearly three times longer than exopod, with a row of long spinules along inner margin and a row of short spinules along outer margin. Enp-2 much smaller, subapically with a minute seta along inner margin, apically with two bare setae (one claw-like and one geniculate).

P2–P4 (Figs 10A, B, 11A, B). Coxa short, nearly quadrangular. Basis transversely elongate, with one tube pore in proximal half of anterior surface. Outer basal seta of P3 longest, of P4 shortest. Exopods three-segmented, outer spines elongate. Endopods two-segmented; first segment very small, without ornamentation. Enp-2 of P2–P4 very long, with two apical setae, enp-2 of P3–P4 additionally with one inner seta. Enp-2 of P2 with inner spinules, of P3–P4 with inner and outer spinules. Armature formula as in Table 1.

P5 (Fig. 12C). Baseoendopod with long outer spinules. Endopodal lobe vestigial, with two small setae and two tube pores. One additional tube pore inserts close to the setophore. Exopod distinct and elongate, with one inner, two distal, and two outer setae, with one tube pore on anterior surface and with long outer spinules.

Genital field (Fig. 12A). P6 represented by two small cuticular plates.

Male: The male differs from the female in the following characters: body smaller, second and third urosomite not fused, shape of antennule, endopods of P3 and P4, P5.

Habitus (Fig. 13A, B) as in female, but slightly more slender. Total body length: 263–340 μm (mean = 294 μm; $N = 6$; measured from rostrum to posterior end of furcal rami). Urosome six-segmented, one spermatophore.

Antennule (Fig. 14A–E) seven-segmented, subchirocer, with geniculation between segments 5 and 6. Armature formula: 1, 9, 7, 2, 11 + (1 + aes), 2 + 1 modified, 8 + (2 + aes). First and second segment elon-

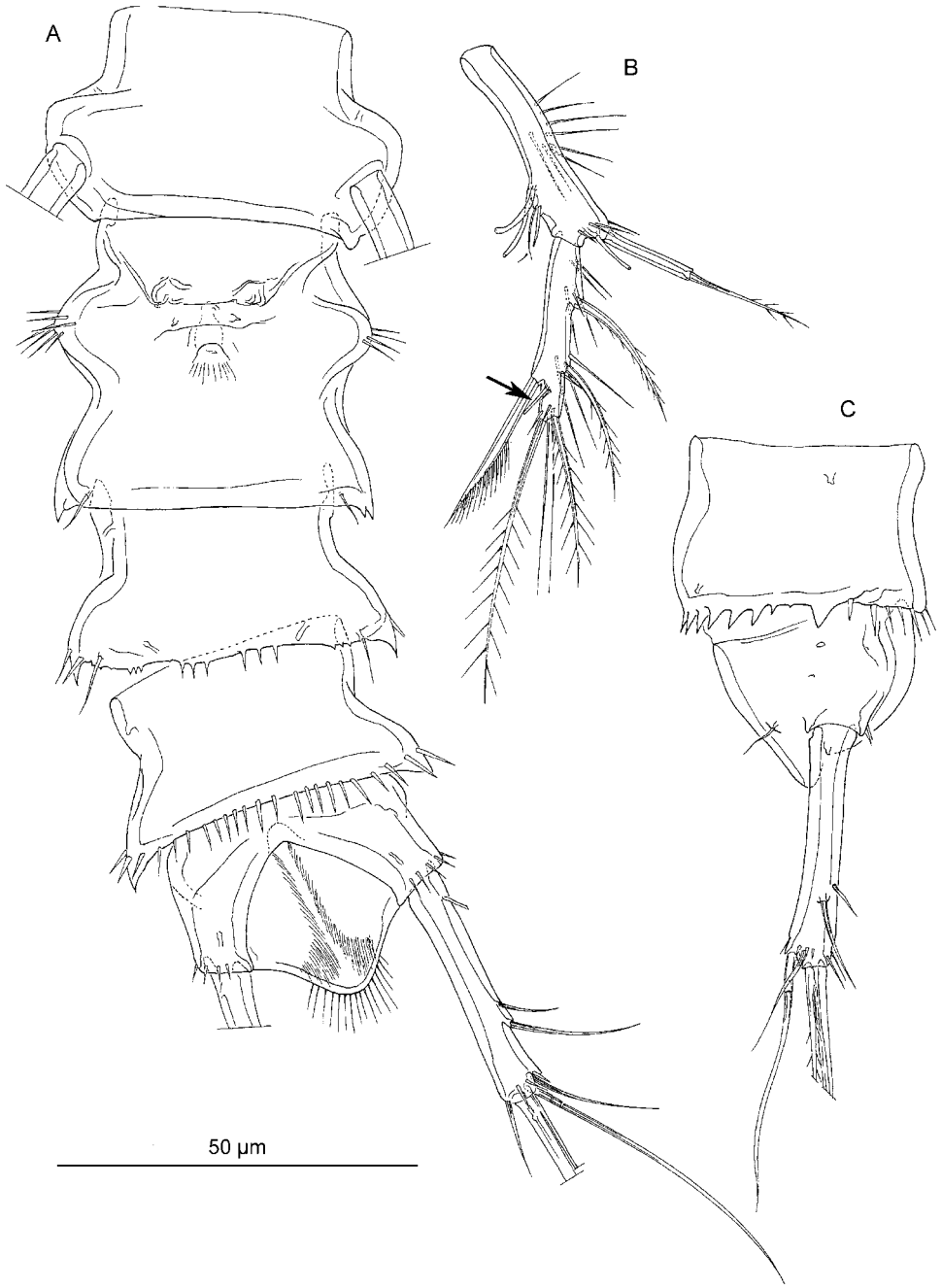

Figure 6. ***Ancorabolina belgicae*** **sp. nov.**, female holotype. A, urosome, ventral; B, fifth thoracopod (tube pore on exopod arrowed); C, telson and furcal ramus, lateral.

gate and of almost the same length. First segment with long spinules along inner margin, second segment with several long spinules on a small, round bump near middle of outer margin. Third segment much smaller than preceding ones, fourth segment smallest. Fifth segment slightly swollen, with one long aesthetasc and 12 setae, one of which bulbous. Sixth segment with one modified element and two setae. Seventh segment with one aesthetasc and ten setae, one of which is very slender.

Antenna, mandible, maxillule, maxilla, maxilliped, P1–P2, exopod of P3, exopod of P4, and furcal rami as in female.

Endopod of P3 (Fig. 15A) three-segmented. Enp-1 very small, without ornamentation. Enp-2 long and slender, with inner and outer spinules, apically with

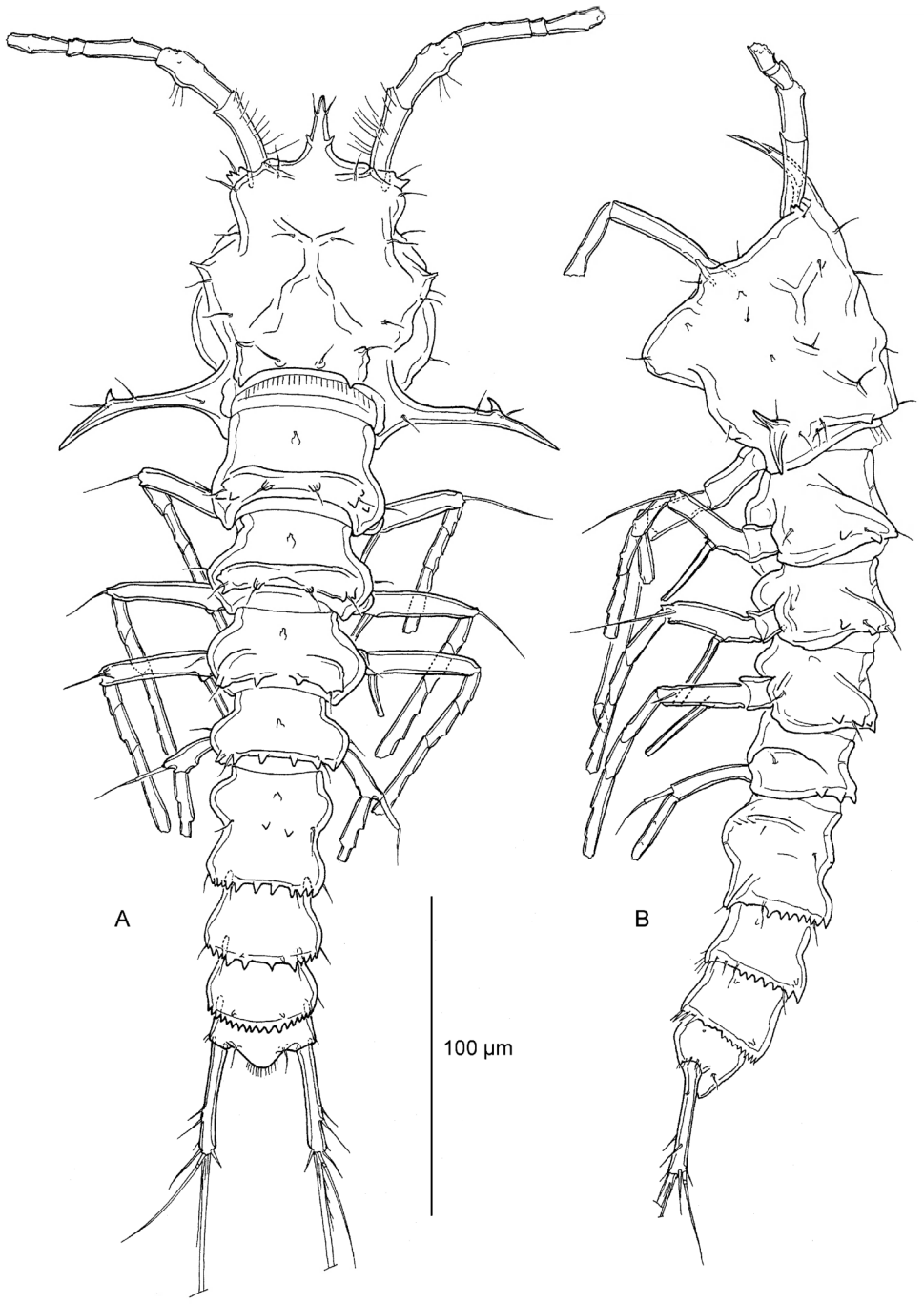

Figure 7. ***Ancorabolina anaximenesi*** **sp. nov.**, female holotype. A, habitus, dorsal; B, habitus, lateral.

lanceolate outer apophysis reaching distal margin of enp-3. Enp-3 small with two apical setae.

Endopod of P4 (Fig. 15B) as in female, but additionally with one subapical, short outer seta.

Baseoendopod of P5 (Fig. 13C) as in female. Exopod distinct and elongate, with one inner, two distal, and one outer setae, with one tube pore on anterior surface and long spinules on posterior surface.

Sixth pair of legs (Fig. 13B) absent.

Variability: In two females and three males (coll. nos SMF 34168, 34171, 34166, 34173, 34174), the rostrum and both posterior processes of the cephalothorax were less developed. The rostrum (Fig. 11D) reached to the middle of the first segment of antennule and did not curve ventrally. The processes (Fig. 11E) were

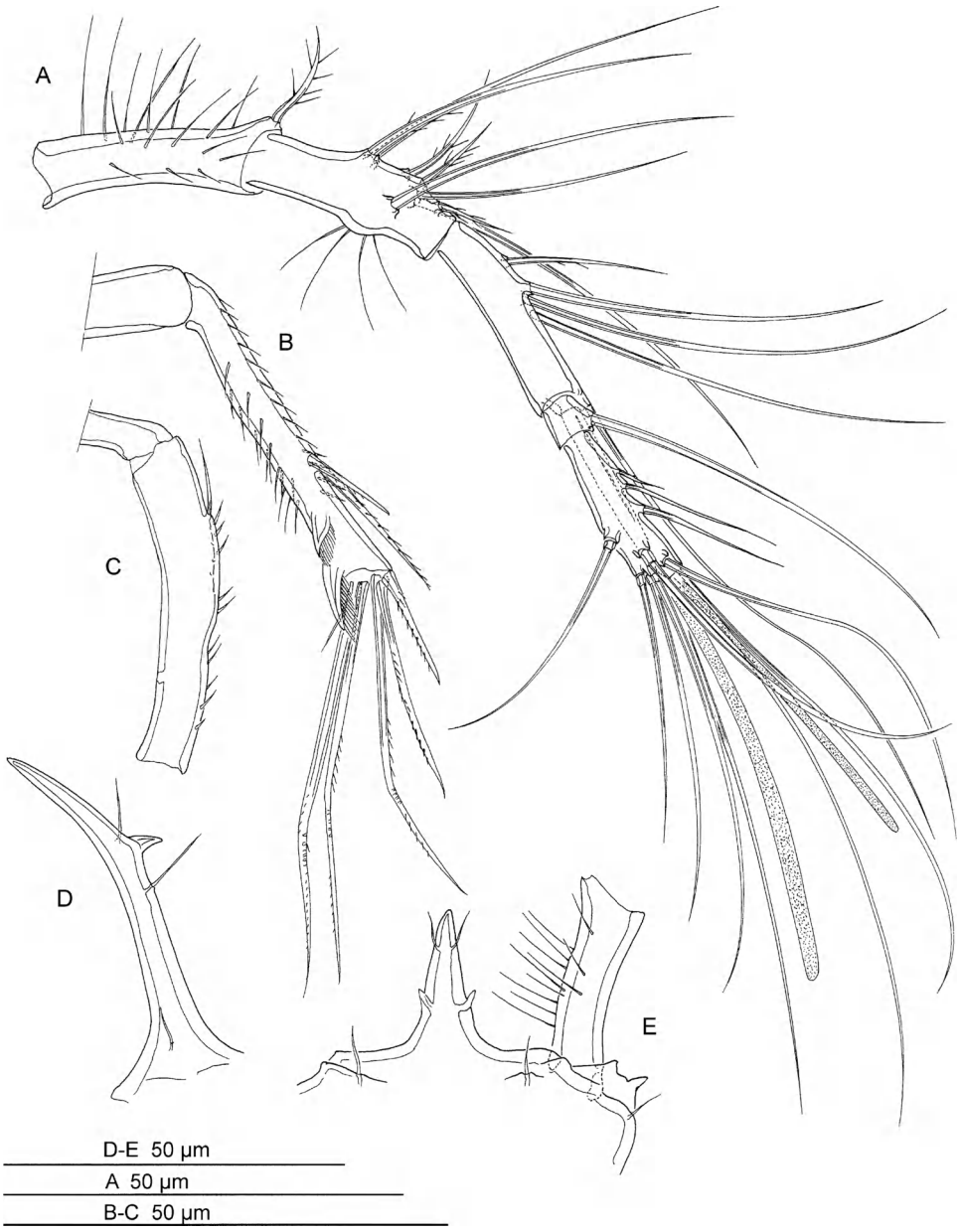

Figure 8. ***Ancorabolina anaximenesi*** **sp. nov.**, female holotype. A, antennule, dorsal; B, endopod of antenna; C, allobasis of antenna; D, process on cephalothorax, dorsal; E, rostrum, dorsal.

shorter and did not show the small projection along the anterior border. However, as all other characters agree completely with the holotype and allotype, these differences are regarded as intraspecific variability and the respective specimens are included as paratypes.

ANCORABOLINA GALEATA SP. NOV.

Type locality: Eastern Mediterranean Sea, Anaximenes Mountain, multiple corer, station 891-3 during M71/1, 35°28.61′N, 30°15.15′E, depth 1254 m, collected on 15.xii.2006.

Material examined: (1) From type locality: Female holotype (coll. no. SMF 34176/1–21) and male allotype (coll. no. SMF 34177/1–18) from core 11 (4/5), dissected on 21 and 18 slides, respectively; 3 ♀ and 8 ♂ paratypes from core 11 (4/5), with 1 ♀ distributed over four slides (coll. no. SMF 34178/1–4) and other paratypes each on one slide (coll. nos SMF 34179–34188); 2 ♀ and 3 ♂ paratypes from core 9

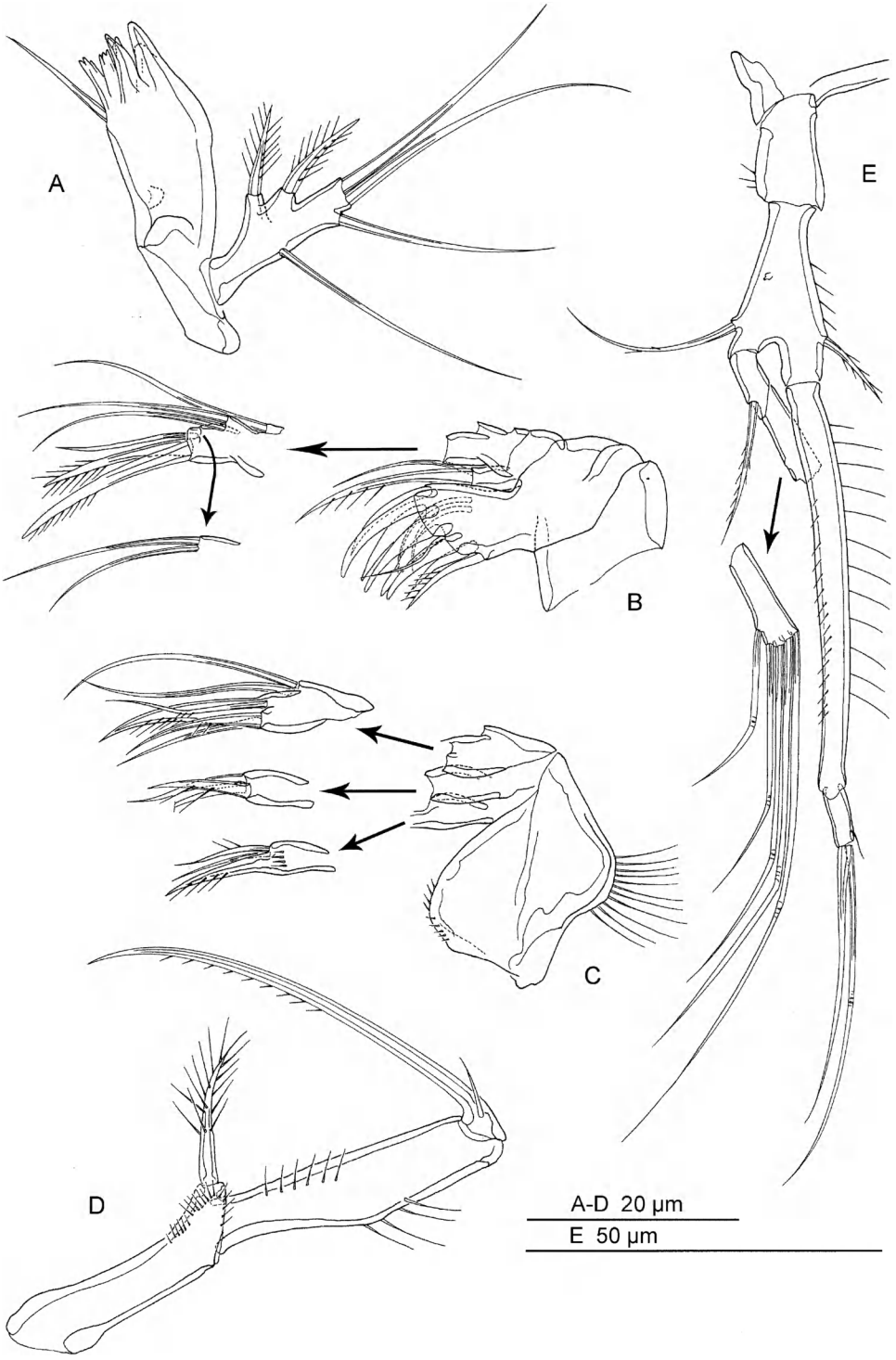

Figure 9. ***Ancorabolina anaximenesi*** **sp. nov.**, female holotype. A, mandible; B, maxillule; C, maxilla; D, maxilliped; E, first thoracopod.

(coll. nos SMF 34189–34193); 3 ♀ and 9 ♂ paratypes from core 11 (coll. nos SMF 34194–34205); (2) Additionally, six paratypes were collected from Anaximenes Mountain with multiple corer at station 891-2 during M71/1, 35°28.61′N, 30°15.13′E, depth 1261 m, collected on 15.xii.2006: 1 ♂ from core 1 (coll. no. SMF 34206), 1 ♂ from qualitative core (coll. no. SMF 34207), 1 ♀ and 1 ♂ from core

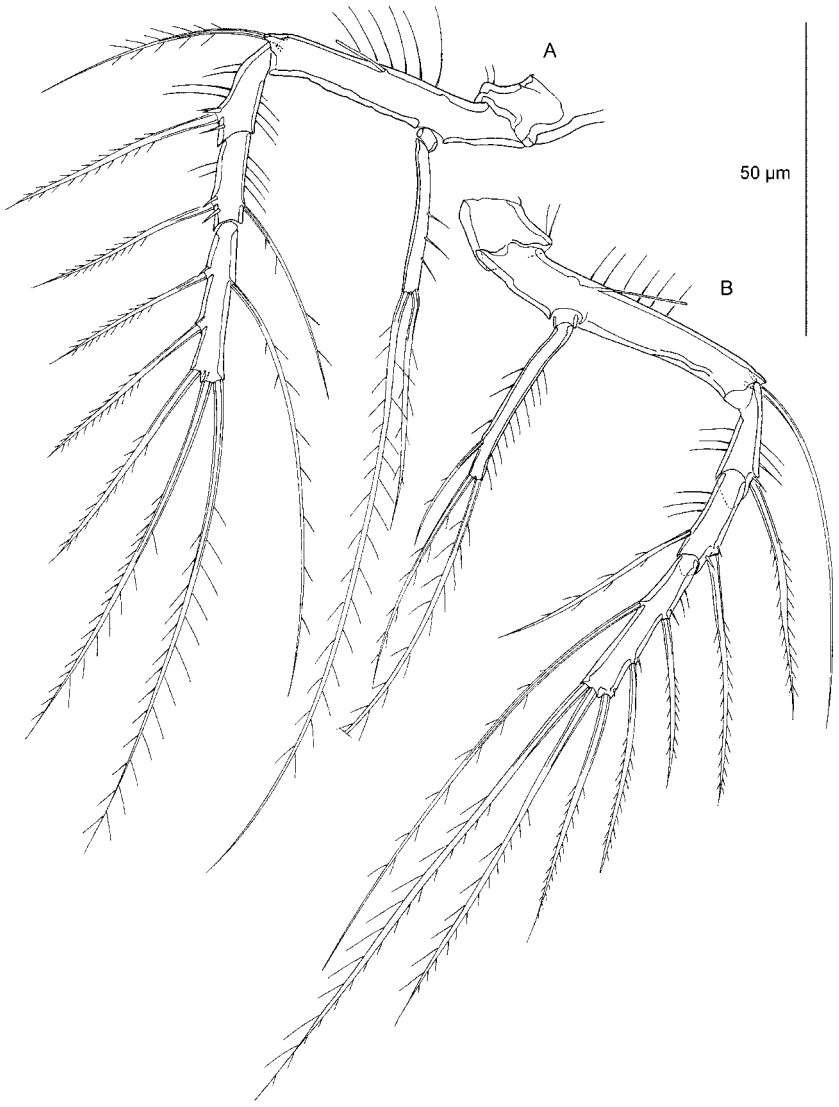

Figure 10. ***Ancorabolina anaximenesi*** **sp. nov.**, female holotype. A, second thoracopod (P2); B, P3.

11 (coll. nos SMF 34208, 34209), 2 ♀ from core 12 (coll. nos SMF 34210, 34211).

Etymology: The species name *galeata* (Latin, helmeted) refers to the helmet-like cephalic shield, with the long rostrum representing the nose guard of the helmet.

Description: Female: Habitus (Fig. 16A–C) long and slender. Total body length: 331–374 µm (mean = 352 µm; $N = 5$; measured from tip of rostrum to posterior end of furcal rami). Rostrum fused to cephalothorax and strongly elongate, curved ventrally, with paired sensilla subapically. Cephalothorax anteriorly slightly constricted, forming a 'peak' as described by George (2006b), and with sensilla and pores as figured. Posteriorly with paired lateral processes, which are strongly cuticularized and curved backwards. Posterior margin of cephalothorax with a pair of sensillate processes. Free body somites 1–4 and anterior somite of genital double-somite with a single mediodorsal tube pore. Posterior margins of free body somites 1–2 with inner pair of sensillate processes and outer pair of sensilla between small processes. Free body somite 1 with additional pair of sensilla just next to inner pair of sensillate processes. Free body somites 3–4 with one pair of sensilla and a row of small processes along posterior margins. Posterior margins of genital double-somite and following two urosomites serrate. Telson broader than long, with a few, fine spinules dorsally (Fig. 21B), and trapezoid in lateral view (Fig. 21C). Margin of anal operculum finely serrate.

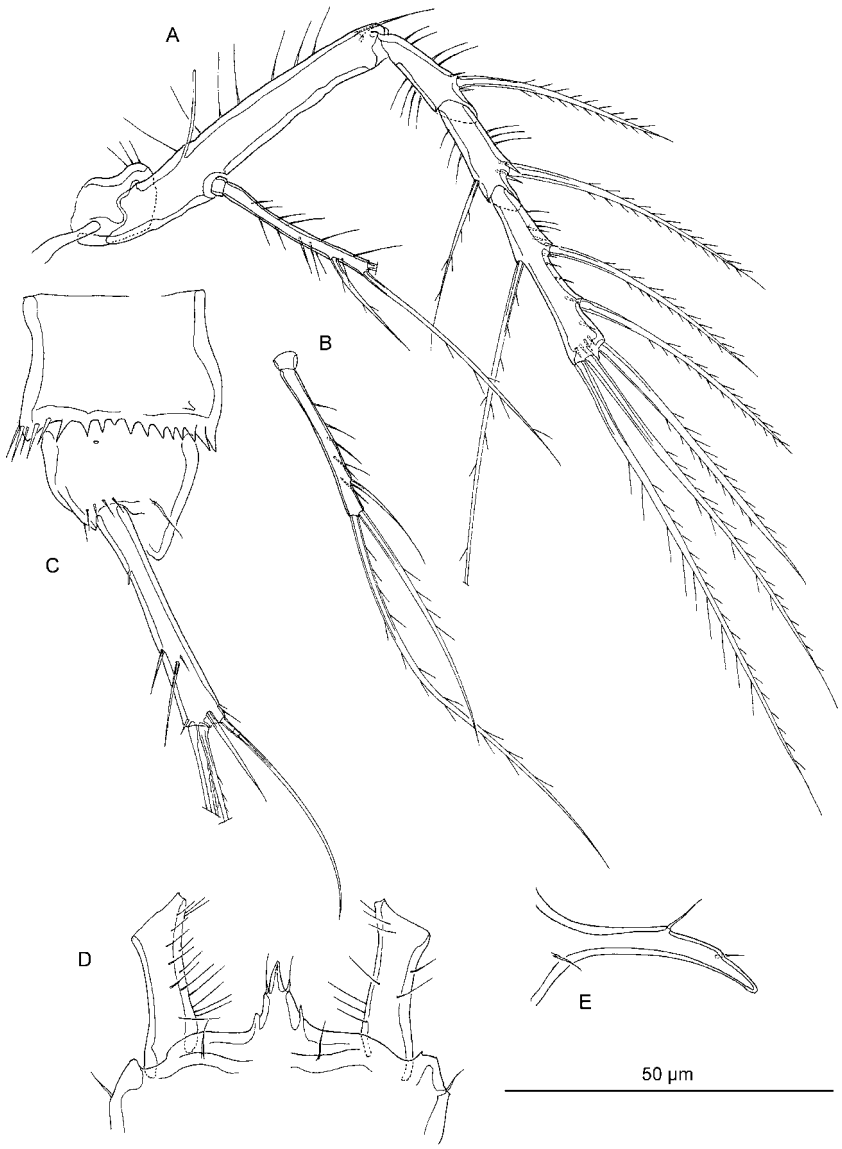

Figure 11. ***Ancorabolina anaximenesi*** **sp. nov.**, A–C, female holotype; D, E, female paratype (SMF 34168). A, fourth thoracopod (P4); B, endopod of right P4; C, telson and furcal ramus, lateral; D, rostrum, dorsal; E, process on cephalothorax, dorsal.

Furcal rami (Fig. 21A–C) long and slender, about eight times as long as wide, with seven setae: I and II inserted closely together at posterior third of lateral margin; III inserted subapically; IV, V, and VI inserted apically; IV and V fused, V longest; VII inserted dorsally at distal margin. Outer margin with tube pore proximally. Furcal rami inserted at outer corners of telson and directed upwards (Fig. 21C), with spinules along outer margin and distally on dorsal surface.

Antennule (Fig. 17A) five-segmented. Armature formula: 1, 7, 5 + (1 + aes), 1, 9 + (2 + aes). First segment about twice as long as wide, with spinules along inner margin. Second segment with several long spinules on a small, round bump near middle of outer margin. Second and third segments nearly equal in length, and slightly longer than first segment. Fourth segment shortest, nearly square in shape. Fifth segment slightly shorter than third one.

Antenna (Fig. 17B) with allobasis; exopod absent; abexopodal margin of allobasis with short spinules and one slender, short seta. Endopod with several rows of spinules, laterally with two pinnate spines. Apical armature consisting of two pinnate spines, three long geniculate setae, and one small bare seta

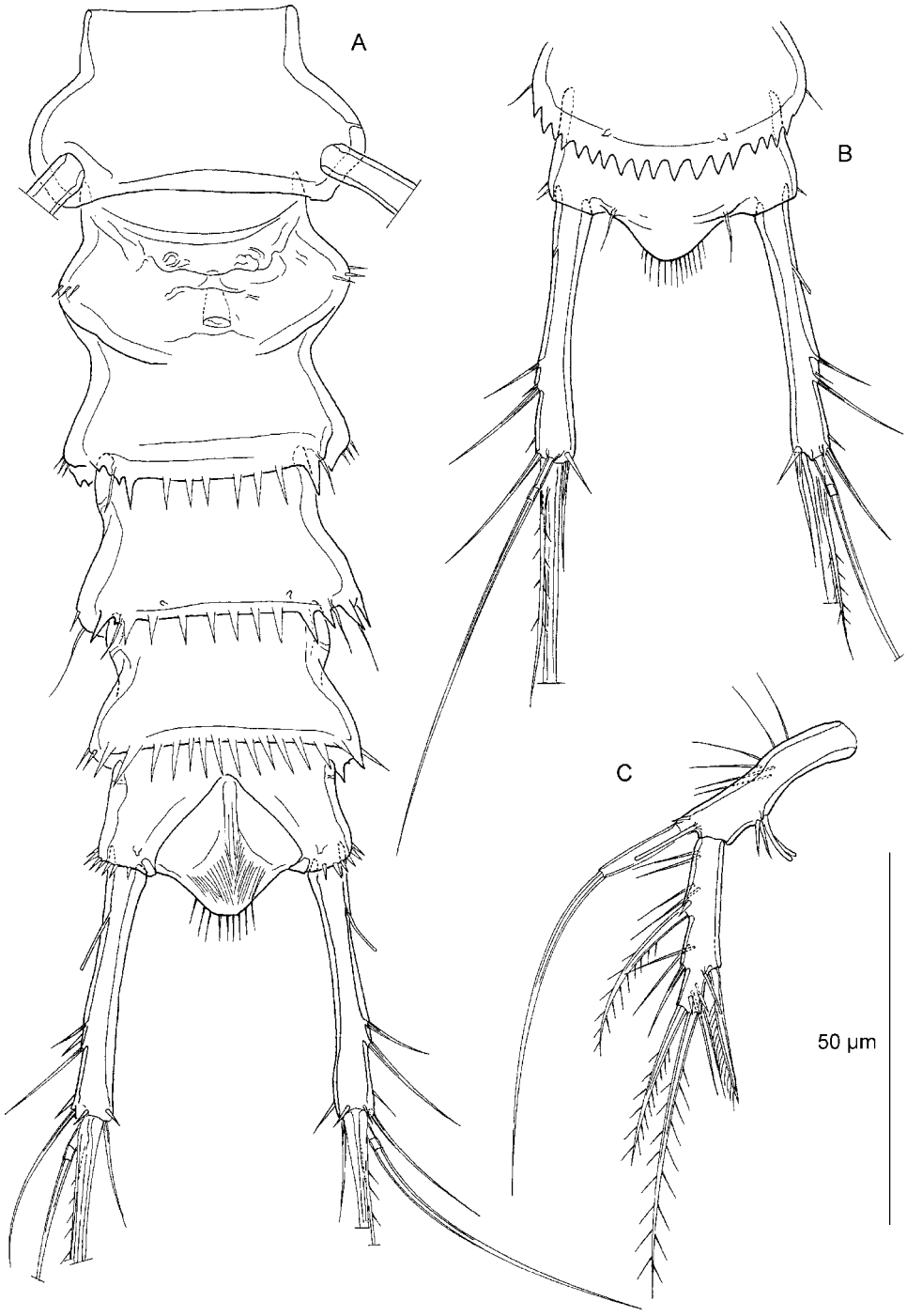

Figure 12. ***Ancorabolina anaximenesi*** **sp. nov.**, female holotype. A, urosome, ventral; B, telson and furcal ramus, dorsal; C, fifth thoracopod.

(fused basally to seta next to it). Subapically with two cuticular spinular frills.

Mandible (Fig. 17C) with strong gnathobase bearing several incised blades and one additional seta. Mandibular palp one-segmented, with two inner bipinnate, one outer, one subapical, and two apical setae.

Maxillule (Fig. 18F). Praecoxal arthrite with two setae on anterior surface and several spinules on posterior surface. Apical armature consisting of six bare spines and one slender seta. Subapically with two pinnate spines. Coxal endite with one well-developed, pinnate spine and one slender, bare seta. Basis, endopod, and exopod fused, bearing eight setae.

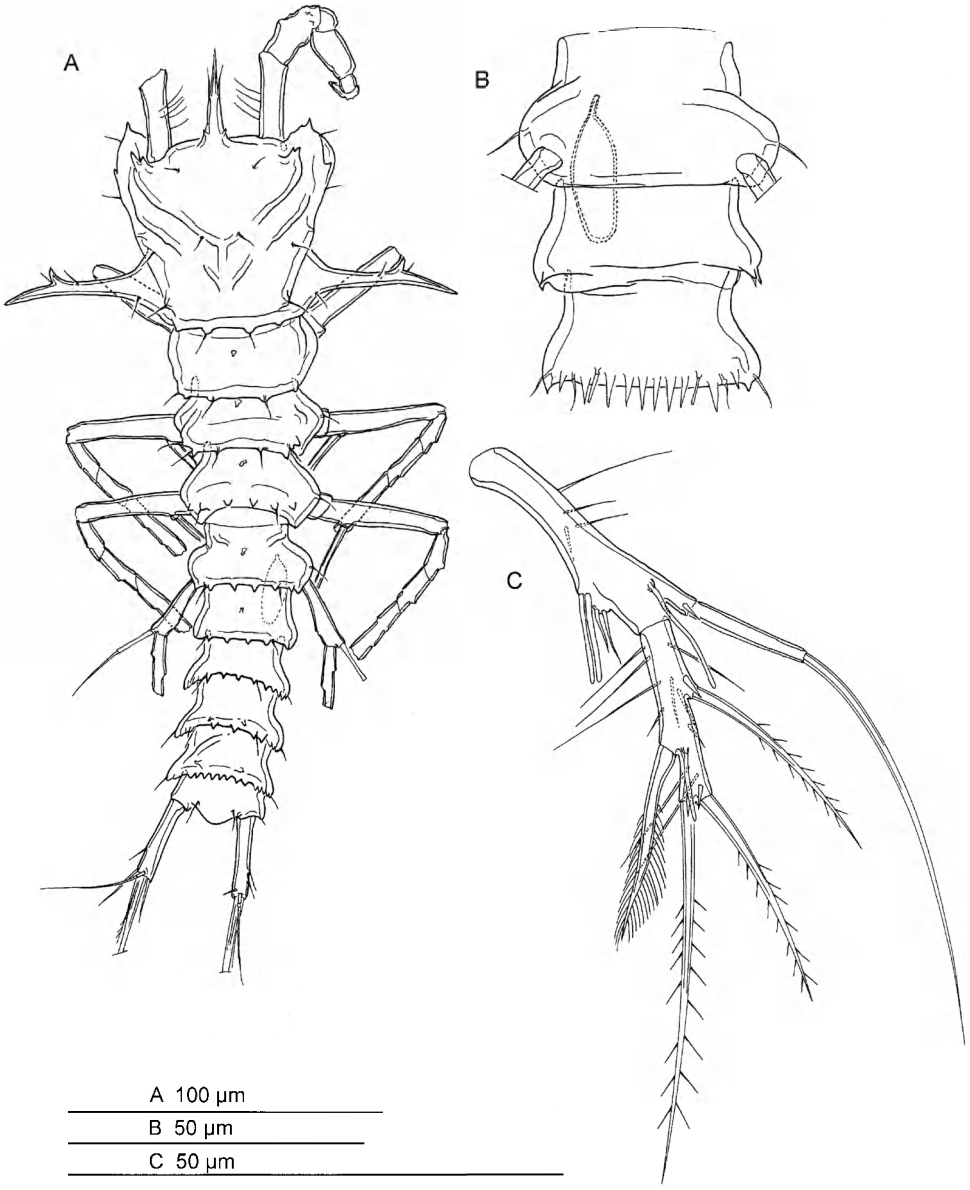

Figure 13. ***Ancorabolina anaximenesi*** **sp. nov.**, male allotype. A, habitus, dorsal; B, first to third urosomite, ventral; C, fifth thoracopod.

Maxilla (Fig. 18E). Syncoxa bearing two endites, with long spinules along outer and short spinules along inner margin. Proximal endite with two setae and one unipinnate spine fused to segment. Distal endite with three pinnate setae, one of which is fused to endite. Basis drawn out into claw, accessory armature consisting of one pinnate and two bare setae. Endopod reduced and represented by two bare setae.

Maxilliped (Fig. 18C, D) long and prehensile. Syncoxa with some outer spinules, apically with plumose seta and a short row of small spinules. Basis with two rows of long inner spinules, and a row of small outer spinules. Endopod drawn out into long, curved, pinnate claw with one accessory seta at base.

P1 (Fig. 18A, B) with two-segmented endopod and three-segmented exopod. Praecoxa with spinules along distal margin. Coxa about 1.5 times as long as wide. Basis strongly prolonged transversely, with inner and outer seta, with spinules along inner and anterior margin and laterally from insertion of endopod. Exp-1 with outer spine, exp-2 with one geniculate outer seta, exp-3 with four geniculate setae. Exp-2 slightly longer than exp-1 and exp-3. Enp-1 slightly more than twice as long as exopod, with a row of long spinules along inner and outer margin. Enp-2

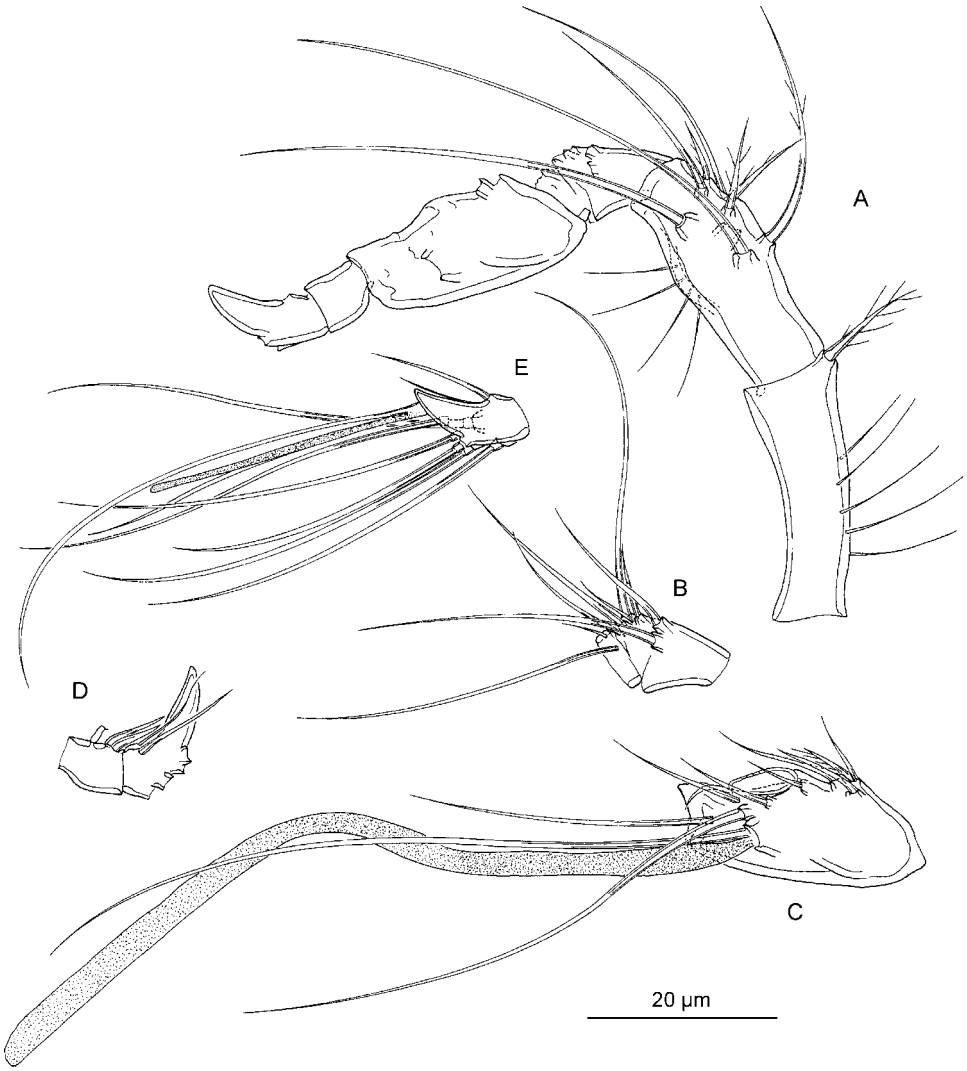

Figure 14. ***Ancorabolina anaximenesi*** **sp. nov.**, male allotype. A, antennule (armature of segments 3 to 7 omitted), ventral; B, segments 3 and 4 of antennule, ventral; C, segment 5 of antennule, ventral; D, segments 6 and 7 of antennule, dorsal; E, segment 7 of antennule, ventral.

much smaller, subapically with a small, slender inner seta, apically with two bare setae (one claw-like and one geniculate).

P2–P4 (Figs 19A–C, 20A). Coxa short, nearly quadrangular. Basis transversely elongate, with one tube pore near middle of anterior surface. Outer basal seta of P3 longest, of P4 shortest, of P2 pinnate, of P3 and P4 bare. Exopods three-segmented, outer spines elongate. Endopods two-segmented; first segment very small, without ornamentation. Enp-2 of P2–P4 very long, with two apical setae; enp-2 of P3–P4 with one inner seta. Enp-2 of P2–P4 with inner and outer spinules. Armature formula as in Table 1.

P5 (Fig. 20B). Baseoendopod with long outer spinules. Endopodal lobe vestigial, with two small setae and one tube pore. One additional tube pore inserts close to the setophore. Exopod distinct and elongate, with one inner, two apical, and two outer setae, with one tube pore on anterior surface and with long spinules on posterior surface.

Genital field (Fig. 21A). P6 represented by two small cuticular plates.

Male: The male differs from the female in the following characters: body smaller, second and third urosomite not fused, shape of antennule, endopods of P3 and P4, P5.

Habitus (Fig. 22A, B) as in female, but slightly more slender. Total body length: 316–340 µm (mean = 328 µm; $N = 11$; measured from tip of rostrum to posterior end of furcal rami). Urosome six-segmented, one spermatophore.

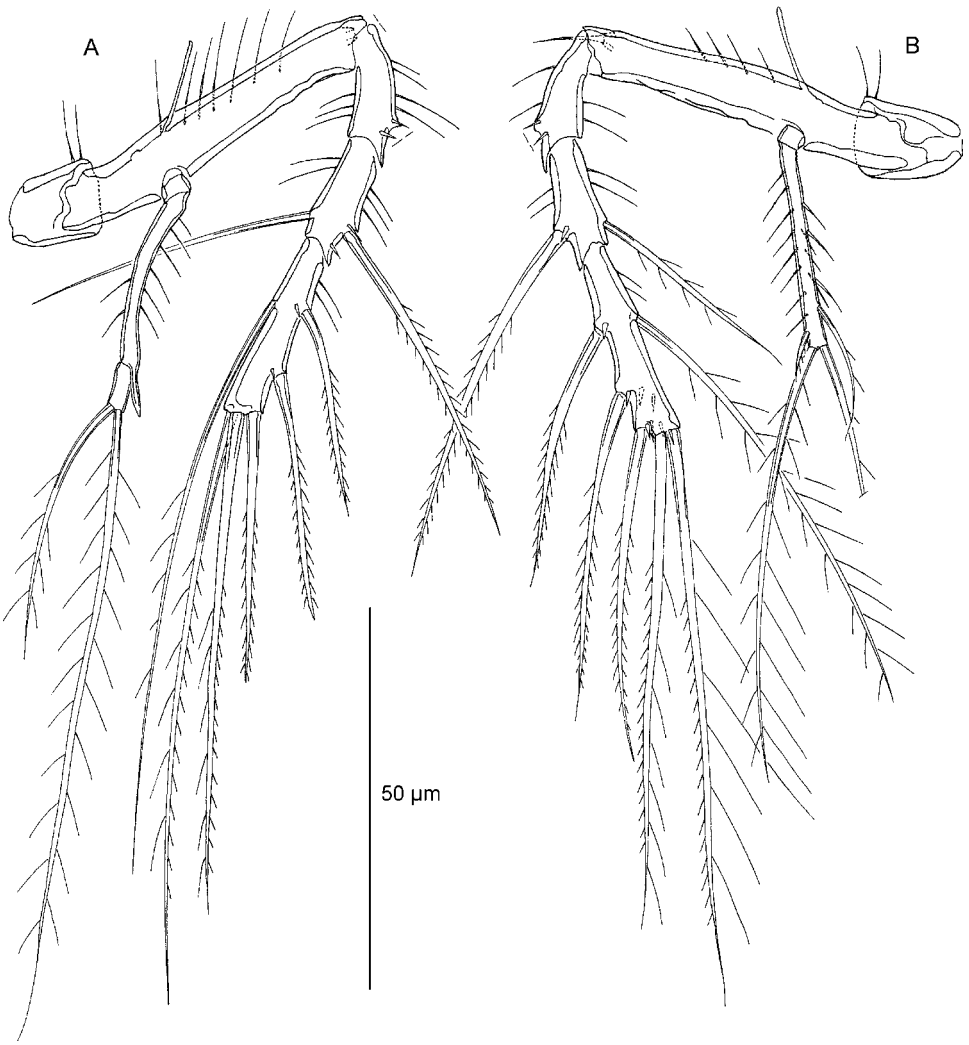

Figure 15. ***Ancorabolina anaximenesi*** **sp. nov.**, male allotype. A, third thoracopod (P3); B, P4.

Antennule (Fig. 23A–F) seven-segmented, subchirocer, with geniculation between segments 5 and 6. Armature formula: 1, 9, 7, 2, 11 + (1 + aes), 2 + 1 modified, 7 + (2 + aes). First segment nearly twice as long as wide. Second segment slightly longer than first segment. First segment with long spinules along inner margin, second segment with several long spinules on small, round bump near middle of outer margin. Third segment much smaller than preceding ones, fourth segment smallest. Fifth segment slightly swollen, with one long aesthetasc and 12 setae, one of which is spiniform. Sixth segment with one modified element and two setae. Seventh segment with one aesthetasc and nine setae.

Antenna, mandible, maxillule, maxilla, maxilliped, P1–P2, exopod of P3, exopod of P4, and furcal rami as in female.

Endopod of P3 (Fig. 24A) three-segmented. Enp-1 very small, without ornamentation. Enp-2 long and slender, with inner and outer spinules, apically with pointed outer apophysis reaching distal margin of enp-3. Enp-3 small with two apical setae. Exp-3 of P3 as in female, but with tube pore near insertion of proximal outer spine.

Endopod of P4 (Fig. 24B) as in female, but additionally with one short subapical seta at outer side.

Baseoendopod of P5 (Fig. 22C) as in female, but endopodal lobe with two tube pores. Exopod distinct and elongate, with one inner, two apical, and one outer setae, with one tube pore on anterior surface and long spinules on posterior surface.

Sixth pair of legs (Fig. 22B) absent.

ANCORABOLINA DIVASECUNDA SP. NOV.

Type locality: South-east Atlantic Ocean, Guinea Basin, multiple corer, station 61/10 during DIVA 2, 0.0°0.0′S, 2.0°24.9′W, depth 5066 m, collected on 15.iii.2005.

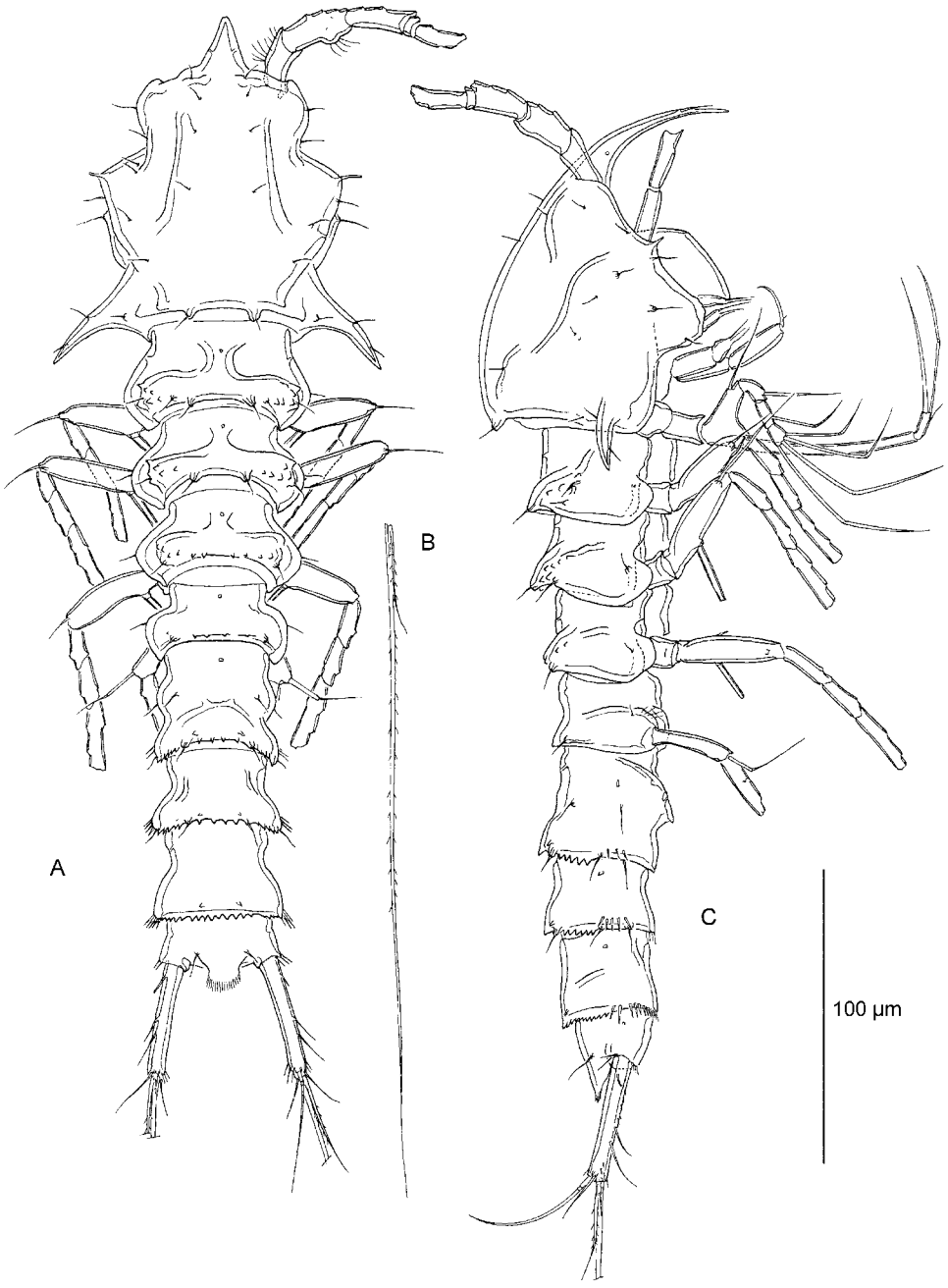

Figure 16. ***Ancorabolina galeata*** **sp. nov.**, female holotype. A, habitus, dorsal; B, furcal setae IV and V; C, habitus, lateral.

Material examined: (1) From type locality: Male holotype (coll. no. SMF 34160/1–12) dissected on 12 slides; (2) Female allotype (coll. no. SMF 34161) on one slide, collected in Cape Basin (south-east Atlantic Ocean) with multiple corer at station 35/7 during DIVA 2, 28.0°6.8′S, 7.0°20.7′W, depth 5033 m, on 3.iii.2005; (3) Female paratype 1 (coll. no. SMF 34162) on one slide, collected in Guinea Basin (south-east Atlantic Ocean) with multiple corer at station 56/1 during DIVA 2, 0.0°0.0′S, 2.0°25.0′W, depth 5064 m, on 14.iii.2005.

Etymology: The specific name *divasecunda* refers to the second cruise of the DIVA project, DIVA 2.

Description: Male: Habitus (Fig. 25A) long and slender. Total body length: 374 µm (measured from tip of rostrum to posterior end of furcal rami). Urosome six-segmented, one spermatophore. Rostrum (Fig. 26C) fused to cephalothorax and considerably elongate, with paired sensilla subapically. Cephalothorax anteriorly slightly constricted, forming a

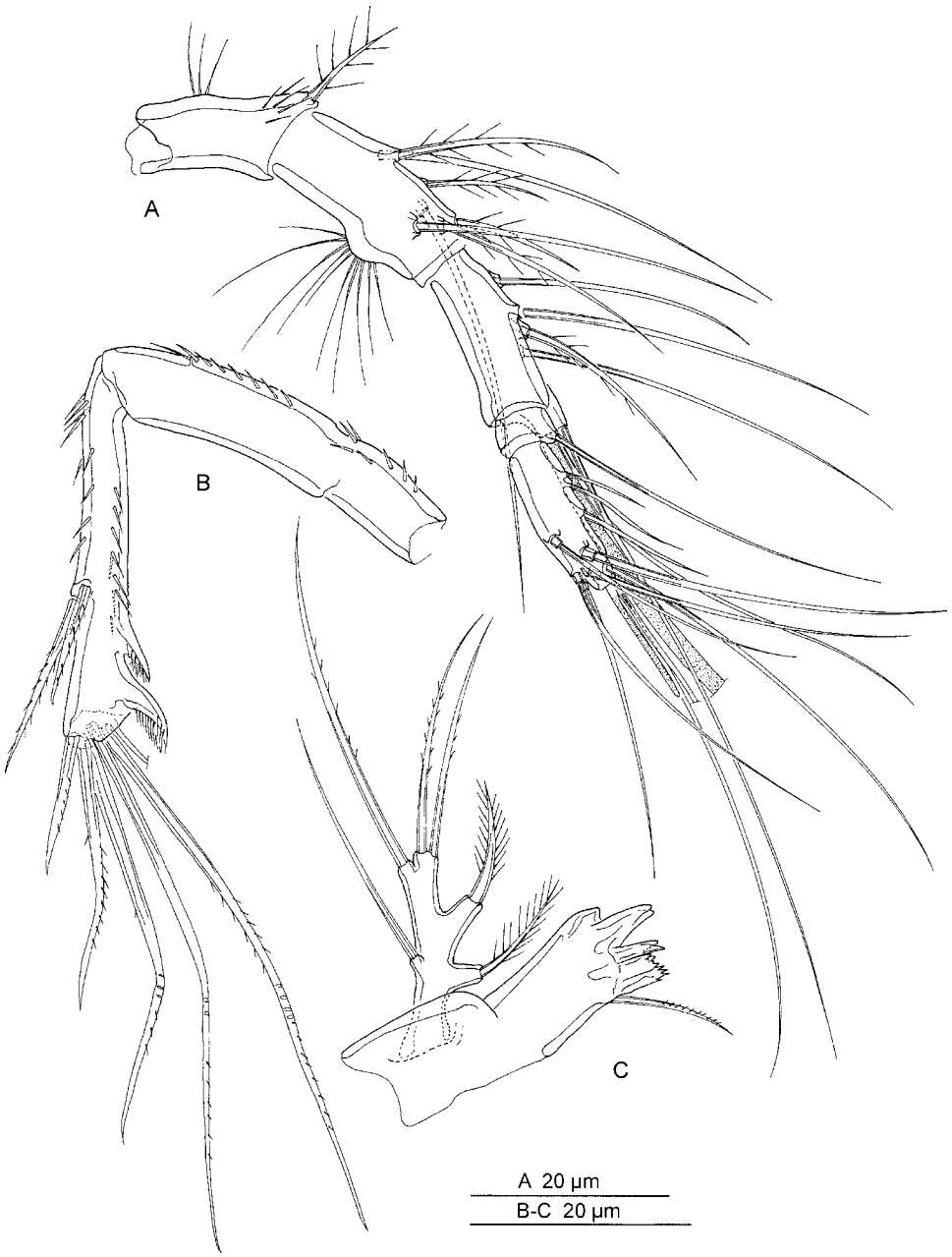

Figure 17. ***Ancorabolina galeata*** **sp. nov.**, female holotype. A, antennule, dorsal; B, antenna; C, mandible.

'peak', and with sensilla and pores as figured. Dorsally with pair of small cuticular projections. Lateral processes (Fig. 26D) strongly cuticularized and curved backwards, subapically with one small cuticular projection each, anteriorly with a few long and fine spinules. Posterior margin of cephalothorax with small sensillate processes. Cephalothorax and all body somites except telson with fine hair-like structures dorsally at posterior margins. Free body somites 1–5 with a single mediodorsal tube pore. Posterior margins of free body somites 1–2 with inner pair of sensillate processes and outer pair of sensilla between small processes. Free body somites 3–4 with a pair of sensilla and a row of small processes along posterior margins. First and second urosomites dorsally with a pair of tube pores and small sensillate processes. Telson (Fig. 25B) broader than long. Margin of anal operculum with small spinules. Furcal rami (Fig. 25B) long and slender, about six times as long as wide, with seven setae: I and II inserted closely together near middle of lateral margin, II being slightly longer than I; III inserted subapically, accom-

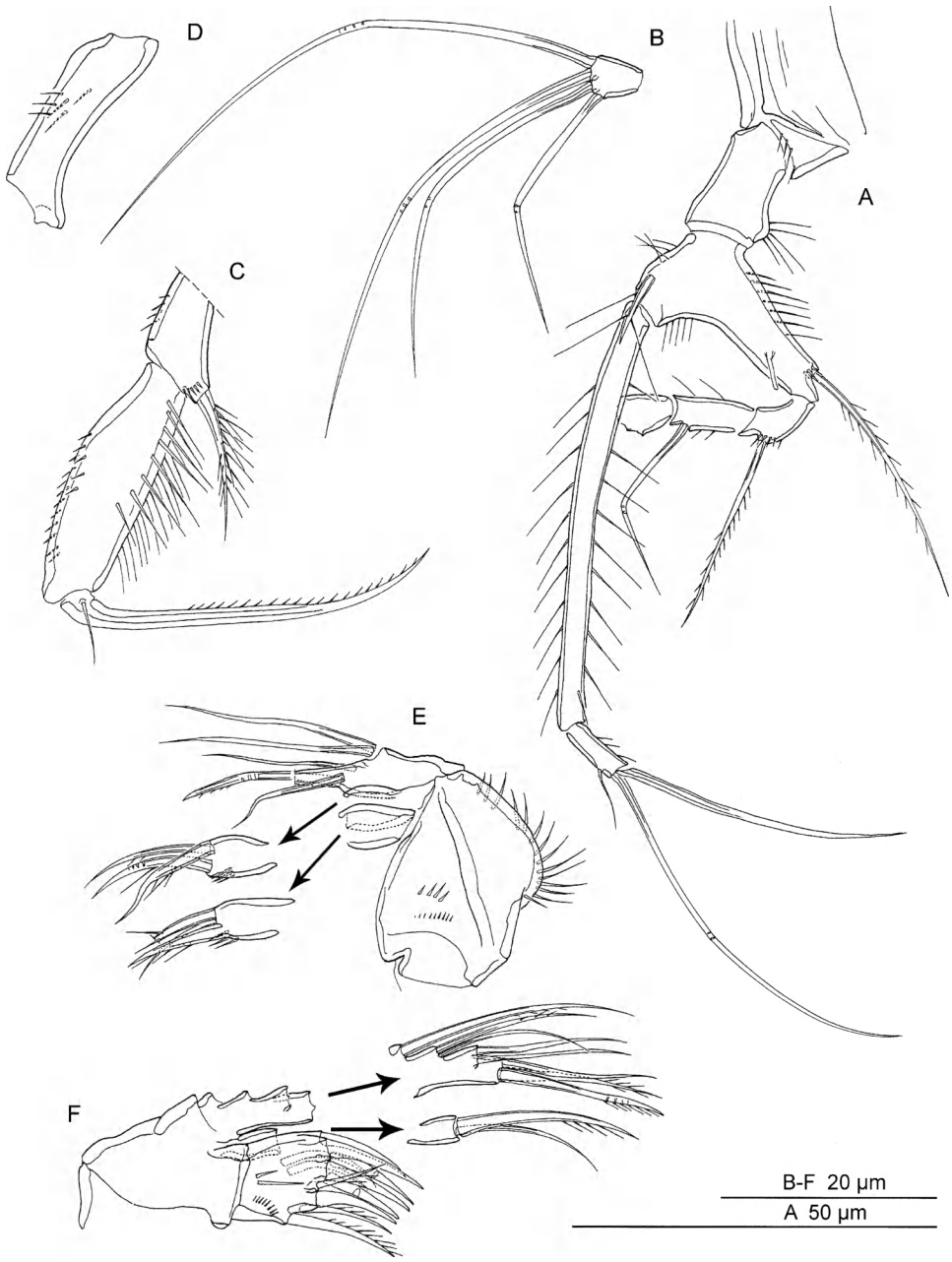

Figure 18. ***Ancorabolina galeata*** **sp. nov.**, female holotype. A, first thoracopod (P1) [armature of endopod-3 (enp-3) omitted]; B, P1 enp-3; C, maxilliped; D, syncoxa of maxilliped; E, maxilla; F, maxillule.

panied by short tube pore; IV, V, and VI inserted apically, IV longer than VI, V longest; VII inserted dorsally at distal margin. Outer margin proximally with tube pore. Furcal rami inserted at outer corners of telson and directed upwards (cf. Fig. 31B), covered with spinules along two thirds of length.

Antennule (Fig. 26A) seven-segmented, subchirocer, with geniculation between segments 5 and 6. Armature formula: 1, 9, 7, 2, 11 + (1 + aes), 0, 7 + (2 + aes). First segment nearly 3.5 times as long as wide. Second segment slightly longer than first segment. First segment with long spinules along inner surface, second segment with some long spinules on a small, round bump near middle of outer margin. Third segment much smaller than preceding ones, fourth segment smallest. Fifth segment slightly swollen, with one long aesthetasc and 12 bare setae. Sixth segment without setae. Seventh segment with one aesthetasc and nine setae.

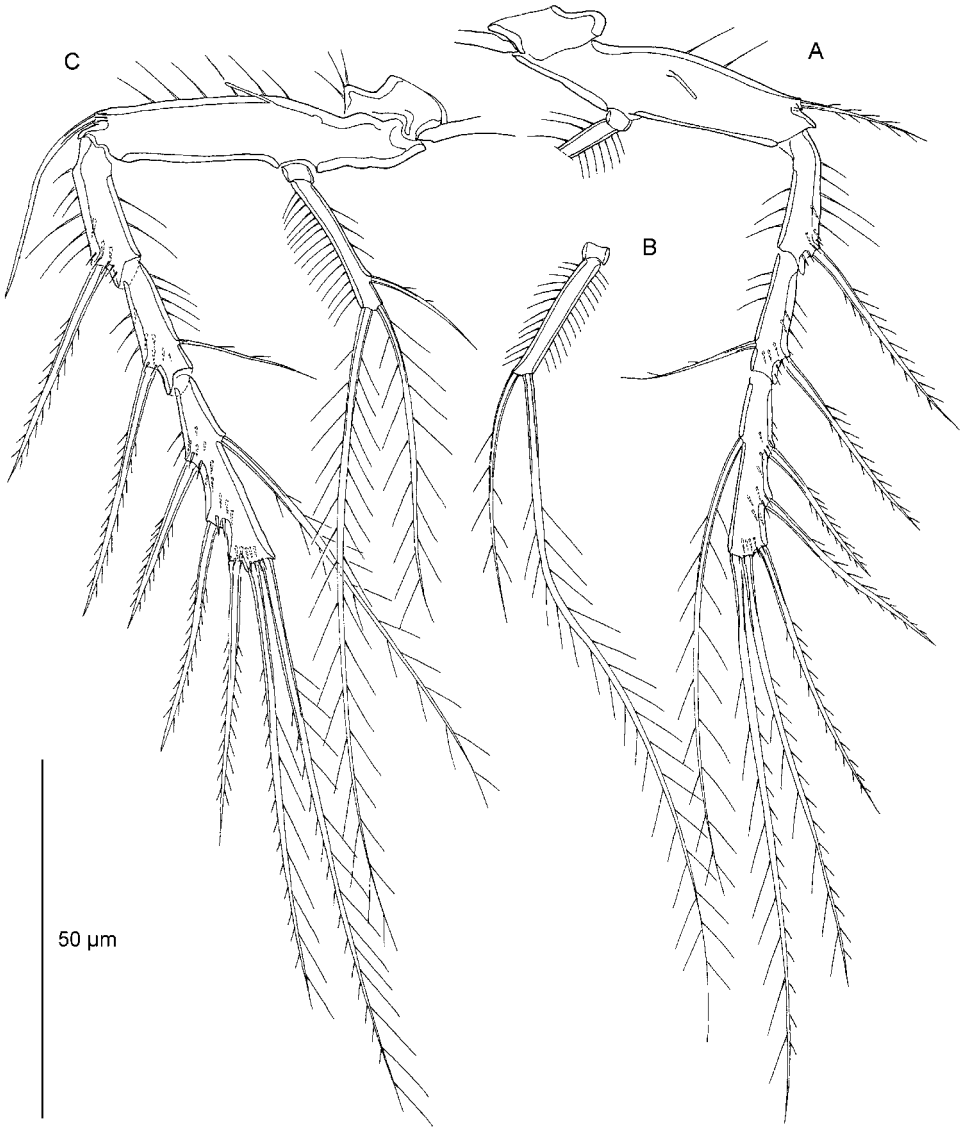

Figure 19. ***Ancorabolina galeata*** **sp. nov.**, female holotype. A, second thoracopod (P2); B, endopod of right P2; C, P3.

Antenna (Fig. 26B) with allobasis; exopod absent; abexopodal margin of allobasis with spinules, without setae. Endopod with several rows of spinules, laterally with two pinnate spines. Apical armature consisting of two pinnate spines, three long geniculate setae, and one small bare seta (fused basally to seta next to it). Subapically with one cuticular spinular frill.

Mandible (Fig. 27A) with strong gnathobase bearing several incised blades and one additional bare seta. Mandibular palp one-segmented, with two inner bipinnate, one outer, one subapical, and two apical setae.

Maxillule (Fig. 27B, B′). Praecoxal arthrite with two setae on anterior surface, and several spinules on posterior surface. Armature consisting of five bare apical spines and one slender subapical seta. Subapically with two spines (one broken). Coxal endite with one well-developed pinnate spine and one slender pinnate seta. Basis, endopod, and exopod fused, bearing seven setae.

Maxilla (Fig. 27C). Syncoxa bearing two endites, with long outer spinules. Proximal endite with one seta and one bipinnate spine. Distal endite with two bare setae. Basis drawn out into a claw (broken in Fig. 27C), accessory armature consisting of three bare setae. Endopod reduced and represented by two bare setae.

Maxilliped (Fig. 27D) long and prehensile. Syncoxa without spinules, apically with a plumose seta. Basis with two rows of long spinules along inner, and a row of long spinules along outer margin. Endopod drawn

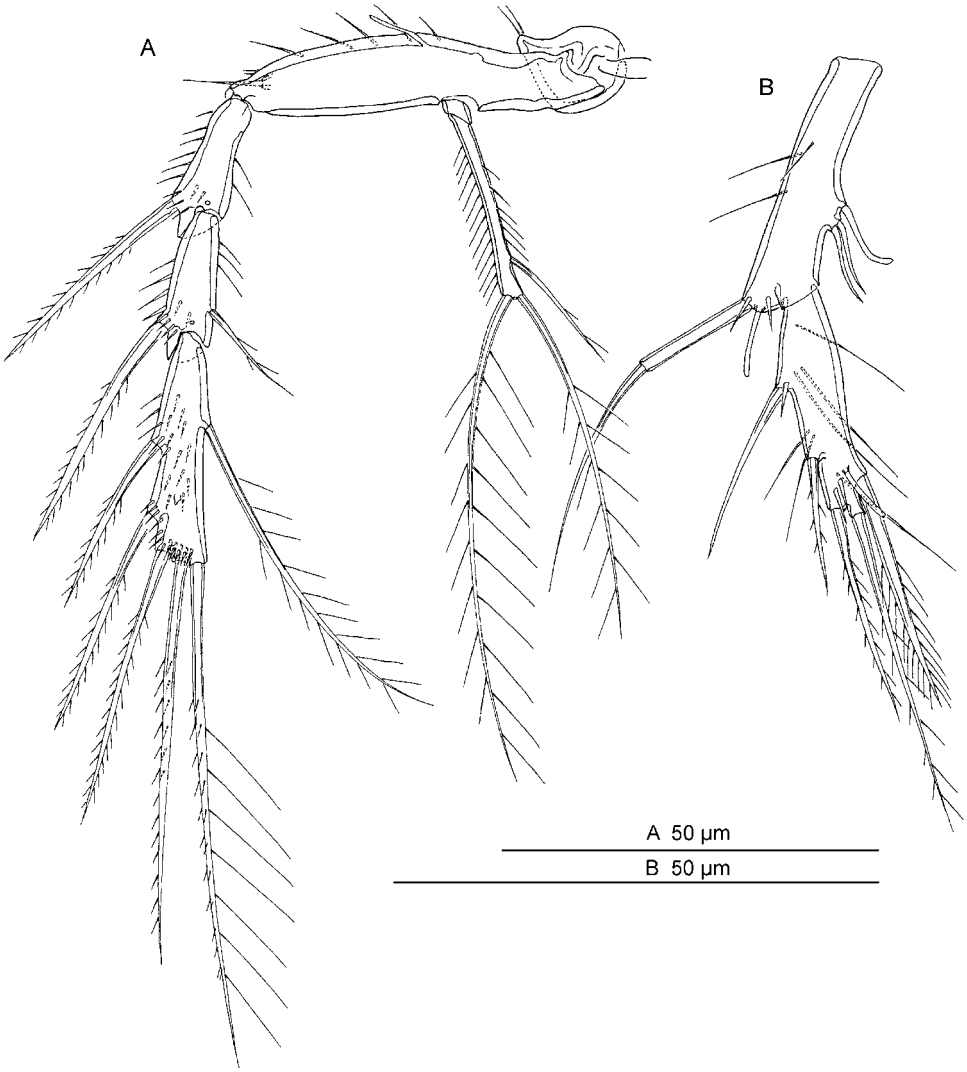

Figure 20. ***Ancorabolina galeata*** **sp. nov.**, female holotype. A, fourth thoracopod (P4); B, P5.

out into long, curved, pinnate claw with one accessory seta at base.

P1 (Fig. 28A) with two-segmented endopod and three-segmented exopod. Praecoxa triangular, without spinules. Coxa about 1.5 times as long as wide. Basis prolonged transversely, with inner and outer seta, with spinules along inner margin. Exp-1 with outer spine, exp-2 with one geniculate outer seta, exp-3 with four geniculate setae. Exp-2 slightly longer than exp-1 and exp-3. Enp-1 approximately 1.7 times as long as exopod, with a row of long spinules along inner and outer margin. Enp-2 much smaller, subapically with a small, slender inner seta, apically with two bare geniculate setae.

P2–P4 (Figs 28B, 29A, 30A). Coxa short, nearly quadrangular. Basis transversely elongate, with several long spinules and one tube pore near middle of anterior surface. Natatory legs with three-segmented exopods, with outer spines elongate. Outer basal seta of P2 (Fig. 29A) longest and bipinnate, of P3 (Fig. 30A) and P4 (Fig. 28B) bare. Endopods of P2 and P4 two-segmented with enp-1 very small, without ornamentation; enp-2 long, with long inner and outer spinules. Enp-2 apically with two setae, P4 enp-2 additionally with an inner and an outer seta. P4 exp-3 subapically with a tube pore. P3 endopod three-segmented; enp-1 very small, without ornamentation; enp-2 long, with long inner and outer spinules, apically with apophysis; enp-3 as long as apophysis, apically with two bipinnate setae. P3 exp-3 with two tube pores. Armature formula as in Table 1.

P5 (Fig. 27E). Baseoendopod with a few long, outer spinules. Endopodal lobe vestigial, with two small setae and two tube pores. One additional tube pore close to the setophore. Exopod distinct and elongate, with long inner spinules, and with one inner, two

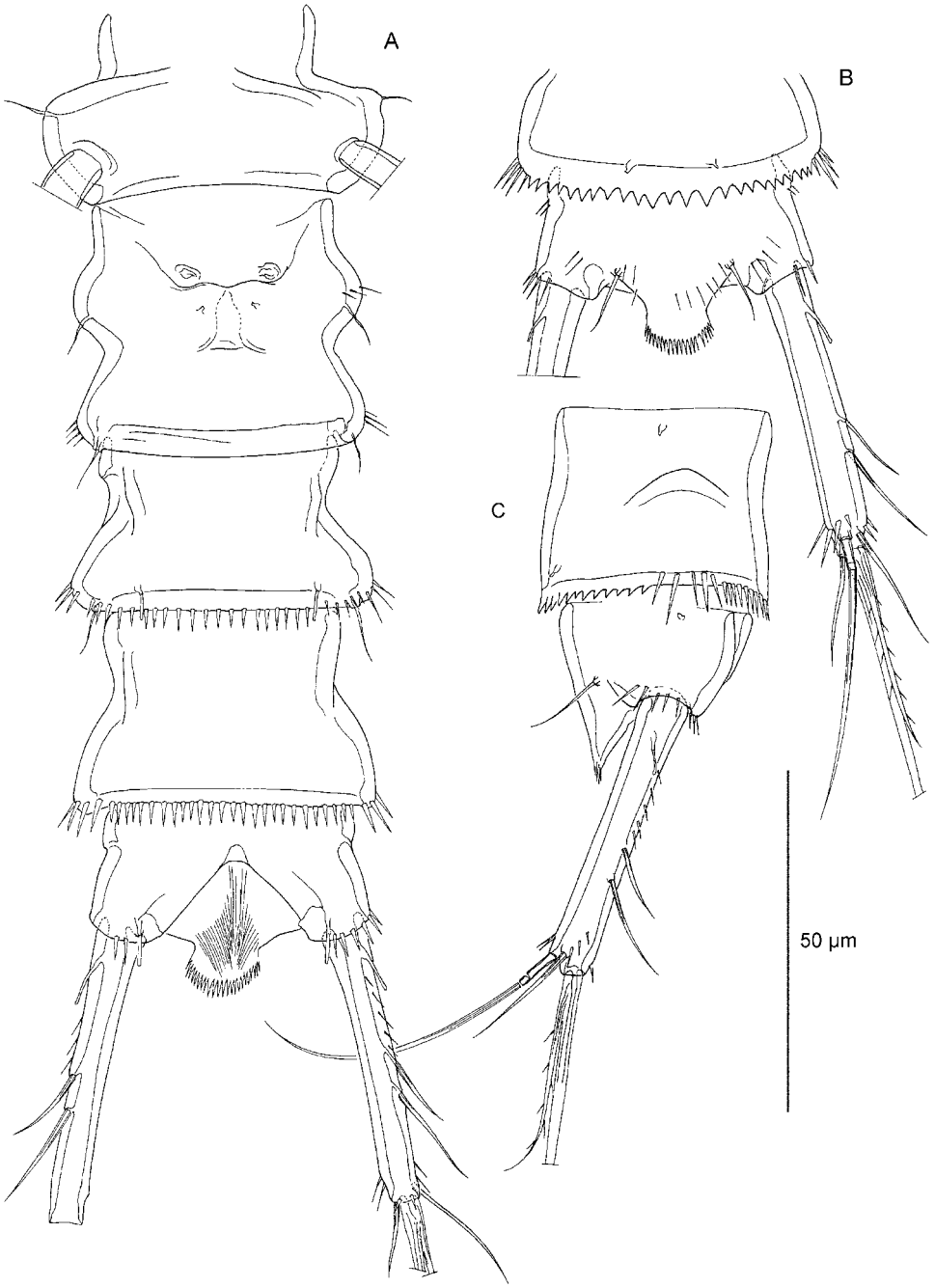

Figure 21. ***Ancorabolina galeata*** **sp. nov.**, female holotype. A, urosome, ventral; B, telson and furcal ramus, dorsal; C, telson and furcal ramus, lateral.

apical and one outer bipinnate setae; one tube pore on anterior surface. The innermost apical seta shows a coarser ornamentation than the remaining ones.

Female: The female differs from the male in the following characters: body remarkably longer, genital double somite present, shape of antennule, endopods of P3 and P4, P5.

Habitus (Fig. 31A, B) long and slender. Total body length: 494–526 µm (mean = 510 µm; $N = 2$; measured from tip of rostrum to posterior end of furcal rami). Genital double-somite with only partial fusion of second and third urosomites; former separation represented by dorsal suture. Genital double-somite and following urosomites dorsally without tube pores. Penultimate body somite without fine hair-like

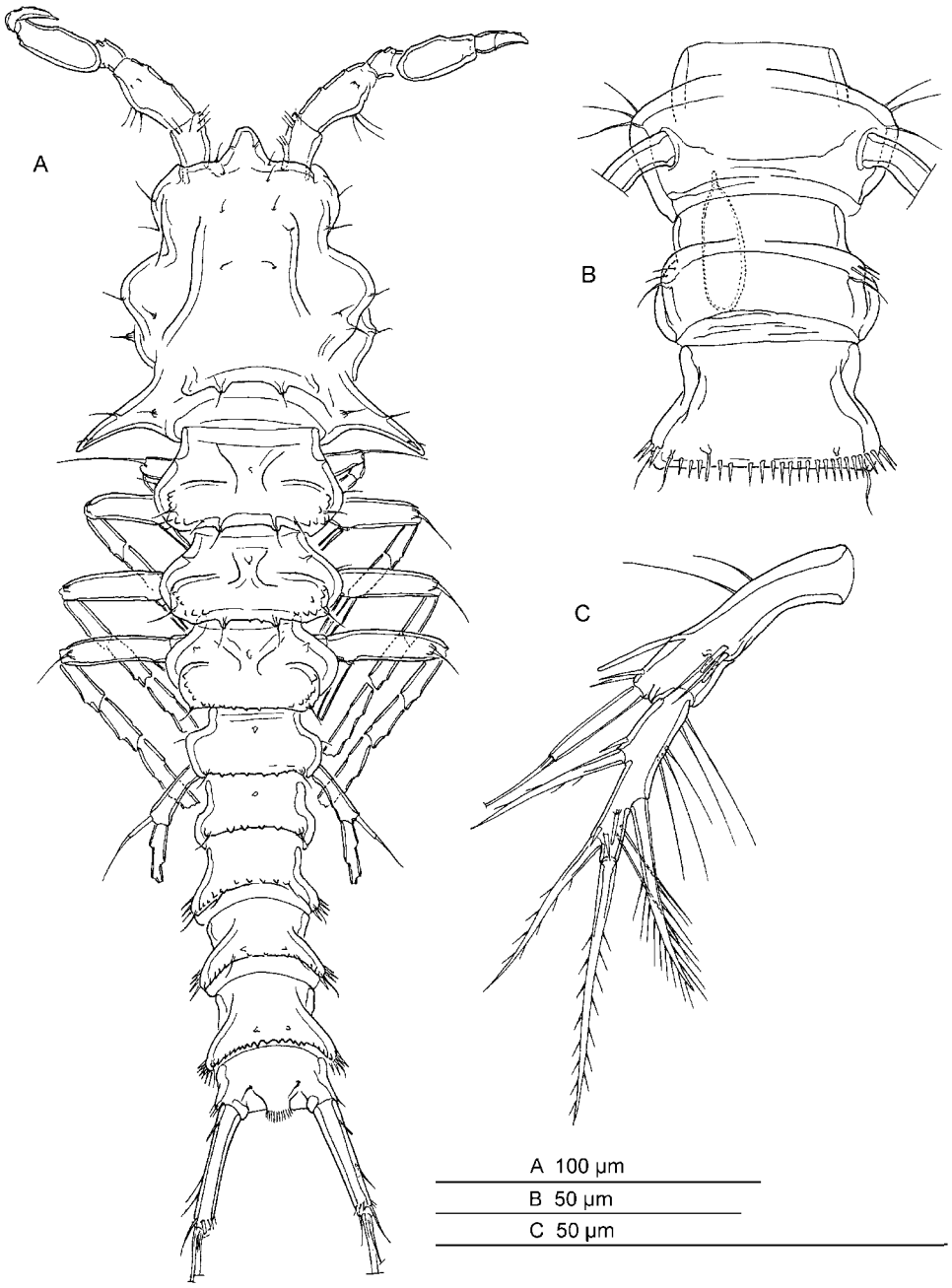

Figure 22. ***Ancorabolina galeata*** **sp. nov.**, male allotype. A, habitus, dorsal; B, first to third urosomite, ventral; C, fifth thoracopod.

spinules at posterior margin. Coverage with spinules on furcal rami more dense than in male.

Antennule (Fig. 32A) five-segmented. Armature formula: 1, 6, 4 + (1 + aes), 1, 9 + (2 + aes). First segment about twice as long as wide, with spinules along inner surface. Second segment with several long spinules on a small, round bump near middle of outer margin. First to third segments nearly equal in length. Fourth segment shortest, nearly square in shape. Fifth segment as long as each of the first three segments.

P3 and P4 endopods (Fig. 29B, C) two-segmented, enp-1 very small, without ornamentation; enp-2 long, with long inner and outer spinules, and with two apical and one inner seta, the latter being smaller in P4 than in P3.

P5 (Fig. 30B). Baseoendopod with a few long, outer spinules. Endopodal lobe vestigial, with two small setae and two tube pores. One additional tube pore close to the setophore. Exopod distinct and elongate, with one inner, two apical, and two outer bare setae,

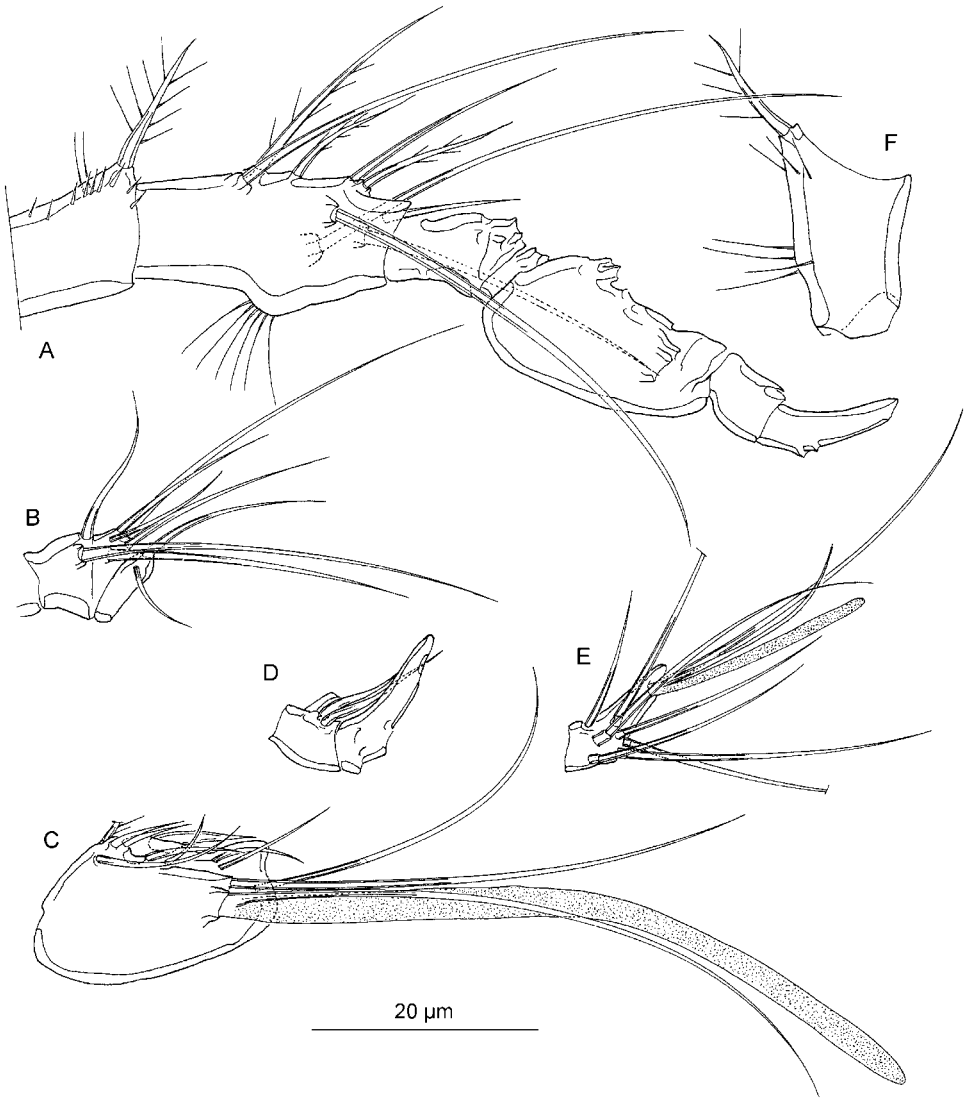

Figure 23. ***Ancorabolina galeata*** **sp. nov.**, male allotype. A, antennule (armature of segments 3 to 7 omitted), ventral; B, segments 3 and 4 of antennule, ventral; C, segment 5 of antennule, ventral; D, segments 6 and 7 of antennule (armature of segment 7 omitted), dorsal; E, segment 7 of right antennule, dorsal; F, segment 1 of right antennule, ventral.

with one tube pore on anterior surface and with some spinules. As in the male, the innermost apical seta shows a coarser ornamentation than the remaining ones.

Genital field (Fig. 30C). P6 represented by two small cuticular plates.

Ancorabolina chimaera George, 2006

Collected and described by George (2006c). See George (2006c) for information on the type material.

Amendments

Careful re-examination of the type material made the following redescriptions necessary:

Male antenna (Fig. 32B). Abexopodal margin of allobasis with one slender, short seta.

Female P5 (Fig. 32C). Exopod with one inner, two apical, and two outer setae.

Drawings were made from holotype and allotype, respectively.

DISCUSSION

Ancorabolina and its systematic status inside Ancorabolidae

The division of Ancorabolidae into the two subfamilies Ancorabolinae and Laophontodinae by Lang (1944, 1948) has been questioned repeatedly (Gee & Fleeger, 1986; Conroy-Dalton, 2004; George, 2006c). Obvi-

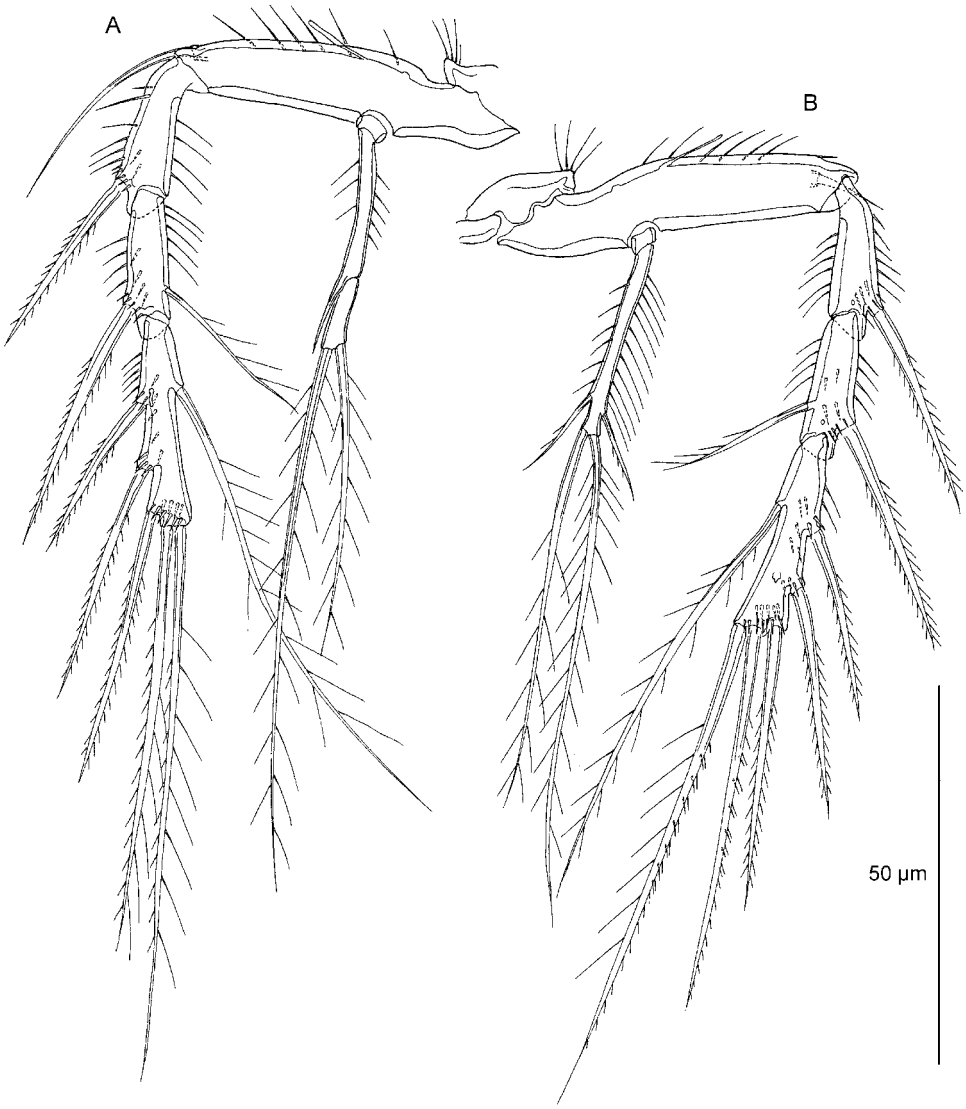

Figure 24. ***Ancorabolina galeata*** **sp. nov.**, male allotype. A, third thoracopod (P3); B, P4.

ously, no autapomorphies have been detected for Laophontodinae so far, being defined by plesiomorphies only (George, 2006c) and therefore constituting a classical paraphylum (cf. Ax, 1984). When carrying out the assignment of *A. chimaera* to Ancorabolinae, George (2006c) based his argumentation on ten derived characters, which are restricted to (at least certain) Ancorabolinae plus *A. chimaera* (plesiomorphies in square brackets):

1. Antenna without exopod (all Ancorabolinae) [antenna exopod present];
2. Basis of P1 transversely elongate (all Ancorabolinae) [basis transversely not elongate];
3. Cuticular processes on cephalothorax and/or body somites (all Ancorabolinae) [cephalothorax/body somites without cuticular processes];
4. Cephalothorax with one pair of lateral processes posteriorly (in *Echinopsyllus* Sars, 1909, *Polyascophorus* George, 1998a, and *Pseudechinopsyllus* George, 2006b) [cephalothorax without lateral processes];
5. Rostrum small and constricted, resembling that of *Arthuricornua* Conroy-Dalton, 2001, *Dorsiceratus* Drzycimski, 1967, *Polyascophorus*, and *Touphapleura* Conroy-Dalton, 2001 [rostrum triangular, of normal shape and size];
6. Frontal part of cephalothorax forming a 'peak' (all Ancorabolinae, cf. George, 2006b) [cephalothorax without 'peak'];
7. Thoracic somites with a single, long tube pore dorsally (all Ancorabolinae) [dorsal tube pore absent];
8. Antennule first segment elongate, with long spinules on inner margin (as in *Ceratonotus*-group

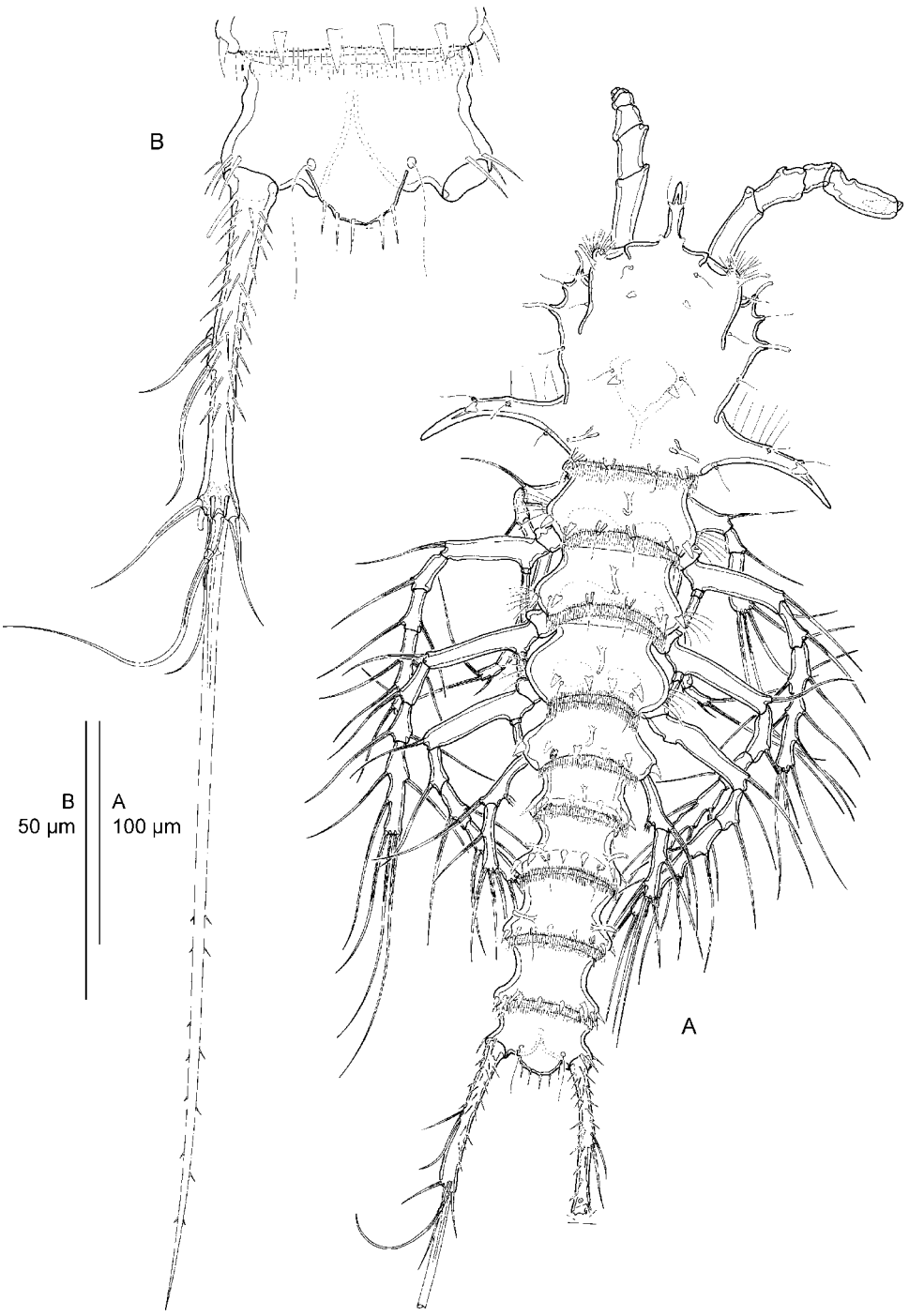

Figure 25. ***Ancorabolina divasecunda*** **sp. nov.**, male holotype. A, habitus, dorsal view; B, telson and left furcal ramus, dorsal view.

sensu Conroy-Dalton, 2001) [first segment not elongate];

9. Telson shorter than broad, trapezoid in shape (as in *Ceratonotus*-group) [telson rectangular];
10. Furcal rami long and divergent, inserted at outer corners of telson and directed upwards (as in *Ceratonotus*-group) [furcal rami not divergent, not directed upwards].

Based on new information from the four new species described in this paper and by thorough comparison with Laophontodinae, the following comments can be made:

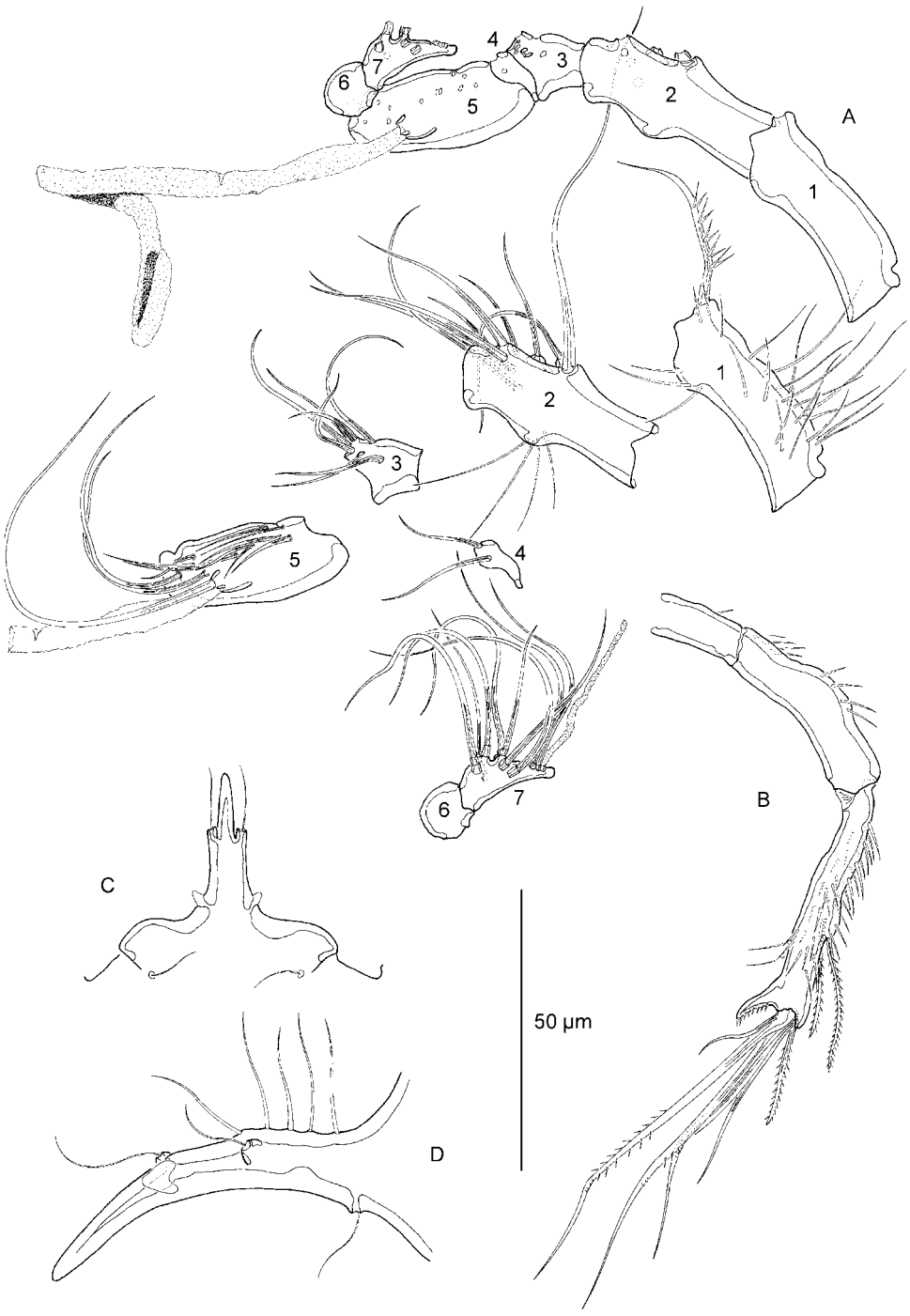

Figure 26. ***Ancorabolina divasecunda*** **sp. nov.**, male holotype. A, antennule, showing segments 1–7 and their corresponding setation; B, antenna (allobasis broken); C, rostrum; D, left cephalothoracic lateral process, dorsal view.

Character 2

Within the genus *Ancorabolina*, there is a gradient from a slightly to a strongly pronounced transverse elongation of the basis in P1. In *A. belgicae* and *A. anaximenesi*, the basis is only slightly elongated transversely and merely forms a pedestal for the exopod, whereas the basis in *A. galeata* is strongly elongated transversely. The intermediate condition is found in *A. chimaera* and *A. divasecunda*. Because this morphocline is not easily dissolved into discrete character states and does not reach the condition as found in the remaining Ancorabolinae (i.e. with a morphology

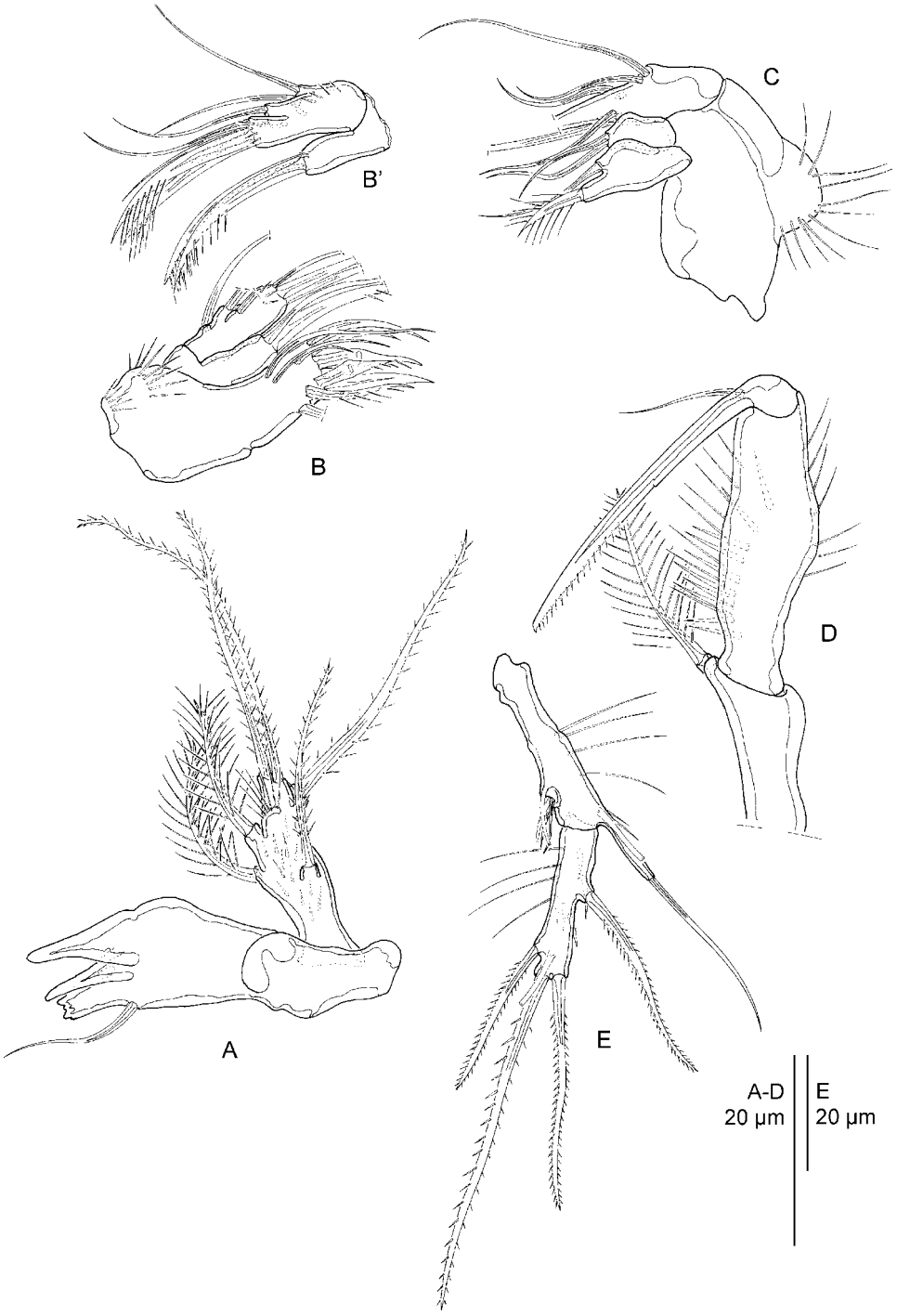

Figure 27. ***Ancorabolina divasecunda*** **sp. nov.**, male holotype. A, mandible; B, maxillule; (B′) maxillular coxa and basis of counterpart; C, maxilla; D, maxilliped; E, fifth thoracopod.

similar to the basis of P2–P4), we prefer to omit that character in our phylogenetic analysis for the moment.

Character 3

Several members of Laophontodinae, i.e. *Paralaophontodes* Lang, 1965, *Laophontodes armatus* Lang, 1936, *Laophontodes hedgpethi* Lang, 1965, and *Laophontodes psammophilus* Soyer, 1975, are characterized by the presence of paired processes along the posterior margins of the cephalothorax, all prosomites, and all urosomites (except for the telson). However, although this character is not restricted to

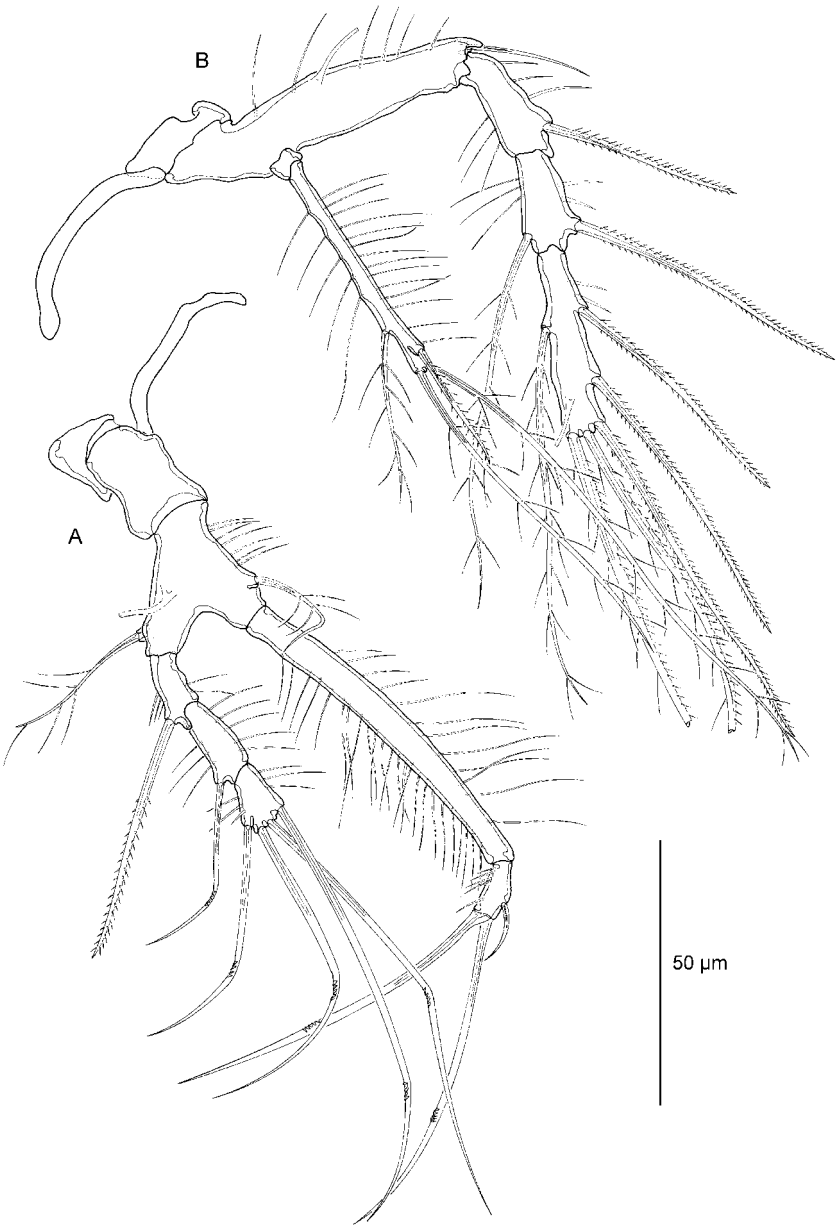

Figure 28. ***Ancorabolina divasecunda*** **sp. nov.**, male holotype. A, first thoracopod (P1); B, P4.

Ancorabolinae, it is clear that its presence in Laophontodinae rather points to the paraphyletic nature of the latter, and illustrates the need for a phylogenetic re-evaluation and the removal of certain taxa from Laophontodinae. Therefore, these cuticular processes should be analysed regarding their homologous development.

Character 4

In addition to *Ancorabolina*, lateral processes posteriorly on the cephalothorax are present in several other ancorabolin taxa, namely *Ancorabolus* Norman, 1903, *Arthropsyllus* Sars, 1909, *Juxtaramia* Conroy-Dalton & Huys, 2000, *Breviconia* Conroy-Dalton & Huys, 2000, *Echinopsyllus*, *Polyascophorus*, *Pseudechinopsyllus*, and *Uptionyx* Conroy-Dalton & Huys, 2000. However, this character should be considered in greater detail, as there are some arguments contradicting the assumption of the processes being homologous:

1. Some processes deviate considerably regarding their shape and ornamentation. Although those of *Ancorabolus*, *Arthropsyllus*, *Juxtaramia*, *Brevico-*

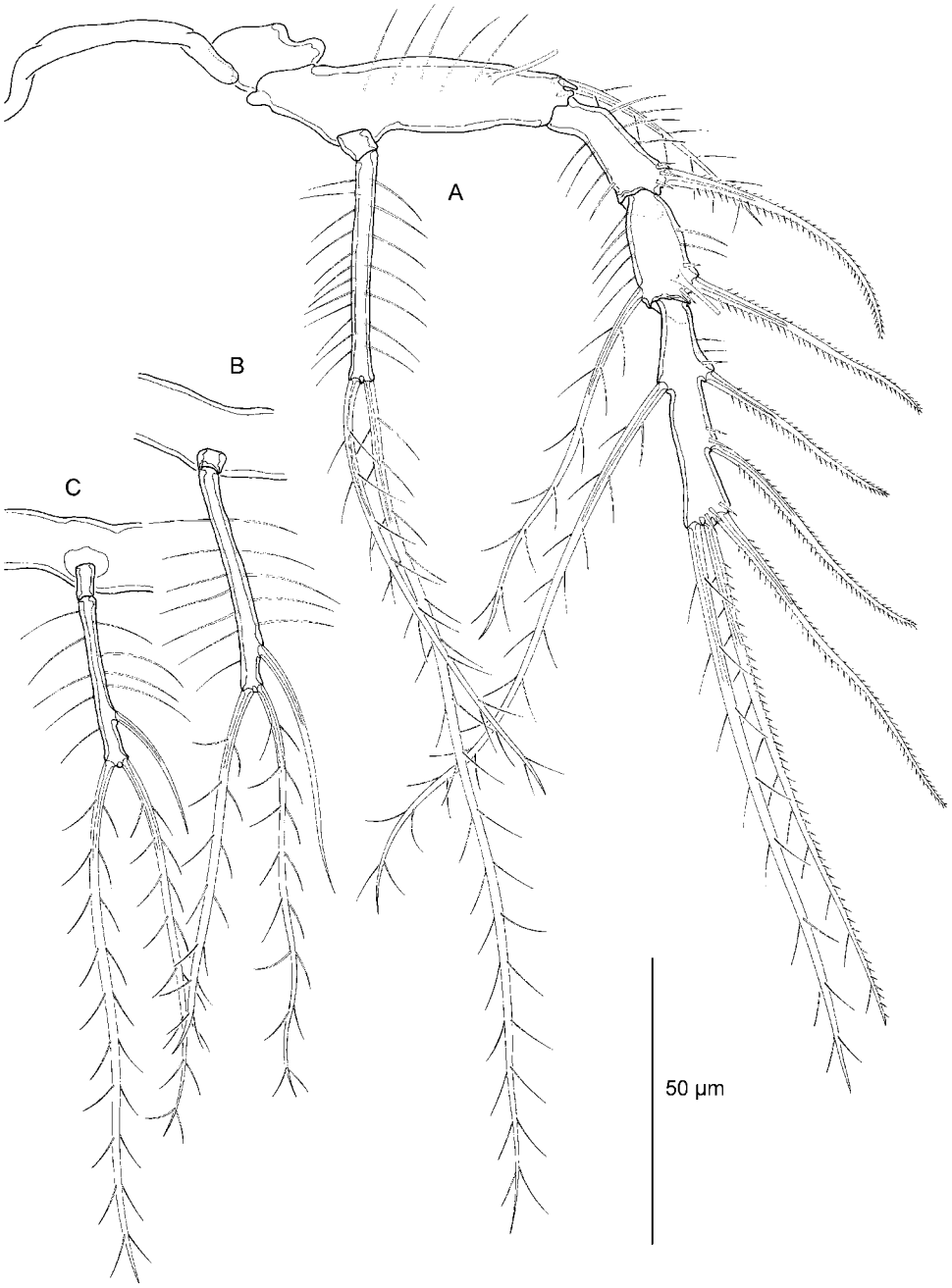

Figure 29. ***Ancorabolina divasecunda*** **sp. nov.** A, male holotype, second thoracopod (P2); B, female paratype 1, P3 endopod; C, female paratype 1, P4 endopod.

nia, and *Uptionyx* may be homologized without problems (Conroy-Dalton & Huys, 2000), the processes of the remaining taxa may not (yet?), showing completely different shape and position of elements (sensilla).

2. Each taxon may be characterized by meaningful apomorphies that are not shared by the other taxa. For instance, *Ancorabolus*, *Arthropsyllus*, *Juxtaramia*, *Breviconia*, and *Uptionyx* form the so-called '*Ancorabolus*-lineage', considered as a monophylum as evidenced by several apomorphies (Conroy-Dalton & Huys, 2000). Also, the remaining genera are well established by unique derived characters (cf. George, 1998a, b, 2006b; Conroy-Dalton, 2003b; Wandeness, George & Santos, 2009).

This suggests a rather convergent development of the lateral processes at least within the so-called

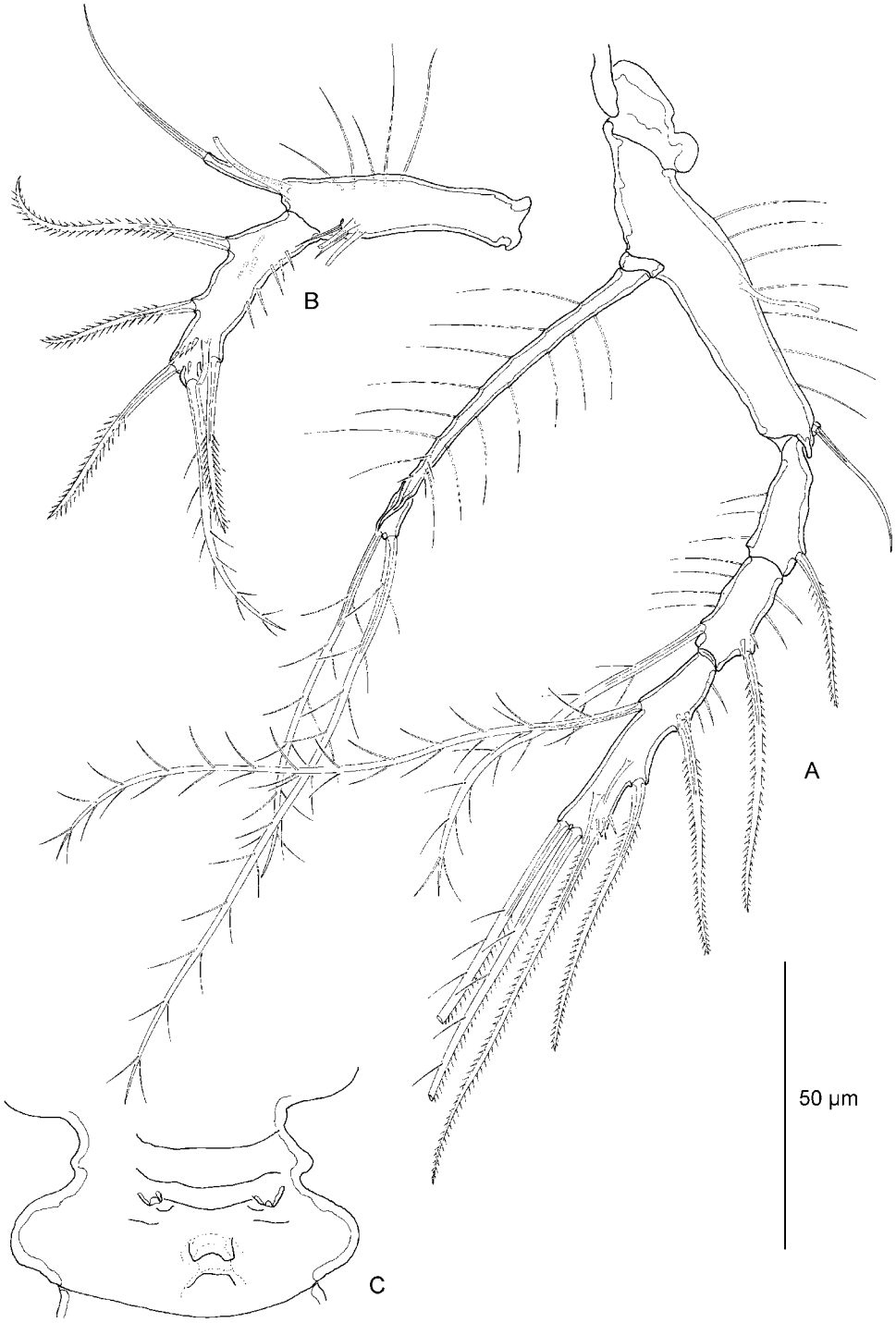

Figure 30. ***Ancorabolina divasecunda*** **sp. nov.** A, male holotype, third thoracopod (P3); B, female allotype, P5; C, female allotype, genital field.

'*Ceratonotus*-group' (Conroy-Dalton, 2001; extended by George, 2006b). The pair of posterior, strongly cuticularized processes of the cephalothorax in *Ancorabolina* are located ventrolaterally and turn backwards (character 16). We consider this character as autapomorphic for *Ancorabolina*. Another species showing such lateral processes is the laophontodin *Laophontodes bicornis* A. Scott, 1896. A more complete comparison between *Ancorabolina* and *La. bicornis* is provided below.

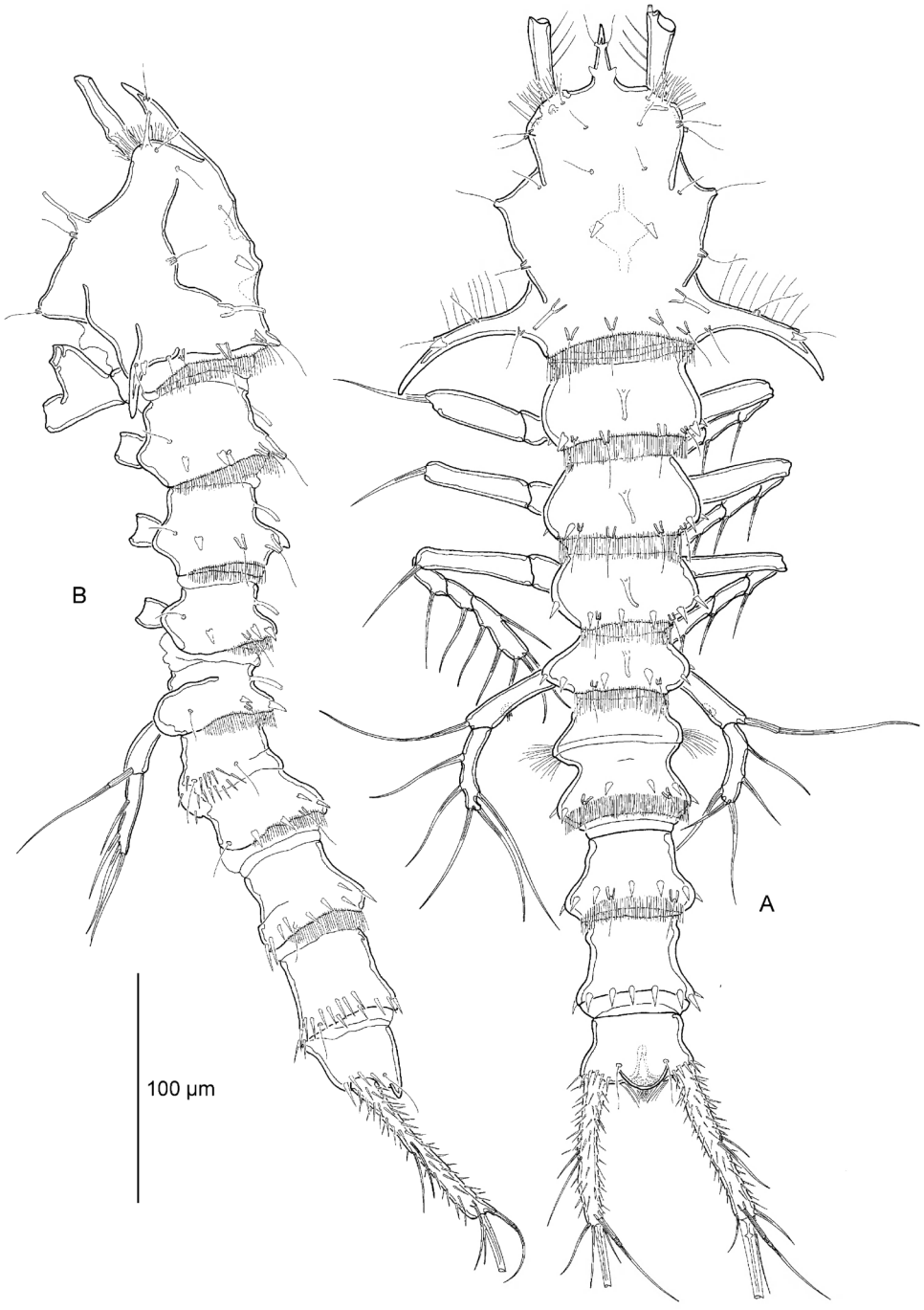

Figure 31. ***Ancorabolina divasecunda*** **sp. nov.**, female allotype, A, habitus, dorsal view; B, habitus, lateral view.

Character 5

The development of a small constricted rostrum is restricted to some members of the *Ceratonotus*-group [*Arthuricornua*, *Ceratonotus* Sars, 1909 (complete loss), *Dorsiceratus*, *Polyascophorus*, *Touphapleura*], whereas the remaining Ancorabolinae (*Ancorabolus*-lineage, *Echinopsyllus*, *Pseudechinopsyllus*), including some species of *Ancorabolina*, deviate from that rostral type, showing an elongation of the constricted rostrum (cf. Conroy-Dalton & Huys, 2000; George, 2001, 2006b, c; Conroy-Dalton, 2003b; Wandeness *et al.*, 2009; present species descriptions).

Character 7

The presence of single, dorsomedian tube pores on thoracic somites is not restricted to Ancorabolinae but

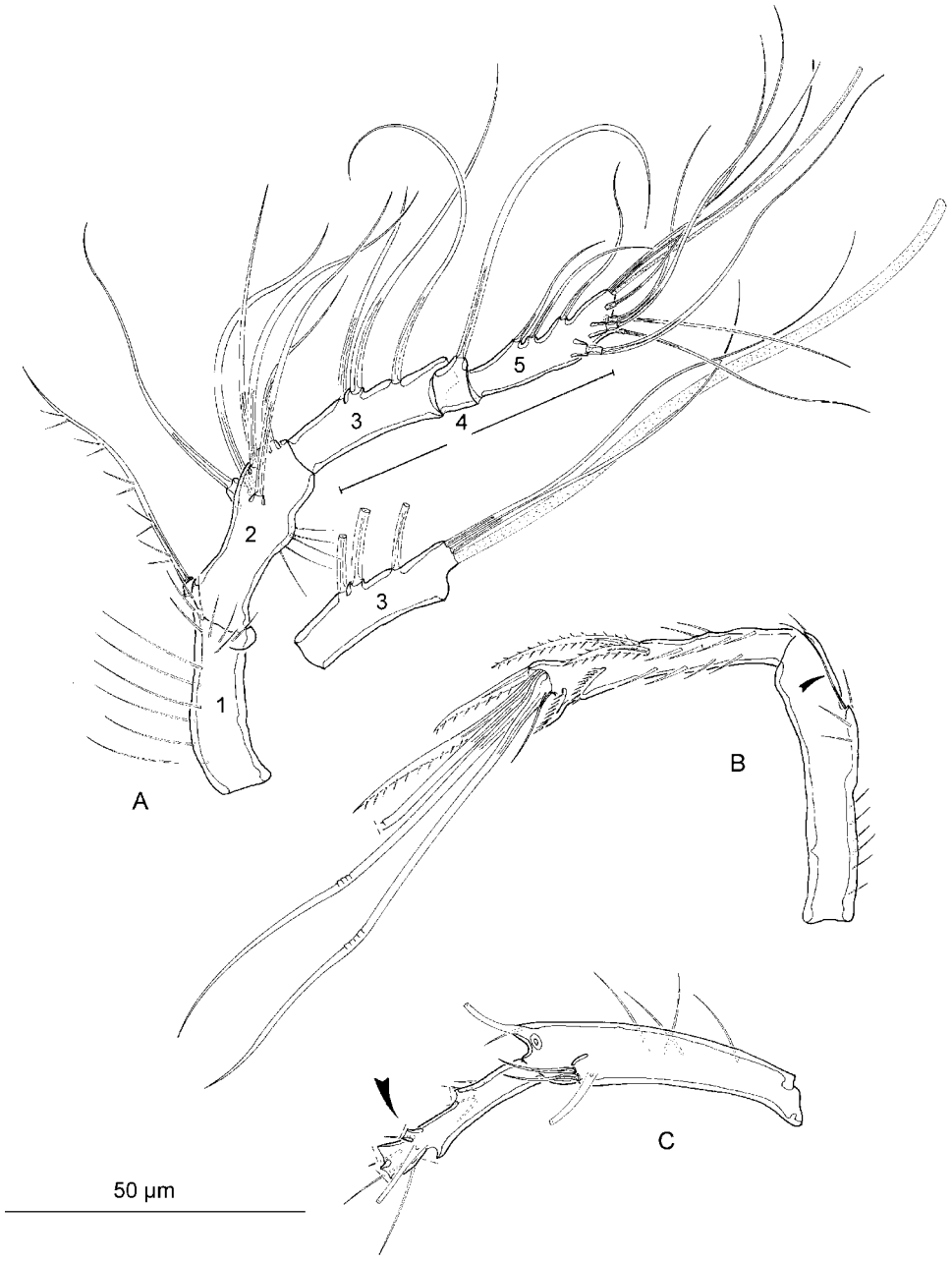

Figure 32. A, ***Ancorabolina divasecunda* sp. nov.**, female paratype (SMF 34162), antennule; B, *Ancorabolina chimaera* George, 2006, male holotype, antenna; C, *Ancorabolina chimaera* George, 2006, female allotype, fifth thoracopod (P5). Arrows indicate structures/elements overlooked by George (2006c).

also detectable in some laophontodin species (e.g. *Laophontodes maccklintocki* Schizas & Shirley, 1994, *Laophontodes spongiosus* Schizas & Shirley, 1994, *Lobopleura ambiducti* Conroy-Dalton, 2004, *Proboscidiphontodes* Fiers, 1988) and therefore worthless for characterization of Ancorabolinae.

Character 8

The elongation of the first antennular segment is least expressed in *A. galeata*. However, when compared with 'typical' *Laophontodes* T. Scott, 1894 species, such as e.g. *Laophontodes whitsoni* T. Scott, 1912, *Laophontodes typicus* T. Scott, 1894, *Laophontodes gracilipes* Lang, 1936, and *La. bicornis*, the segment in *A. galeata* is clearly derived, already showing the shape of all corresponding *Ancorabolina* species.

Sharpening George's (2006c) argument, we state that at present from the listed characters, only two (1, 6) may be recognized as true autapomorphies for a

monophyletic Ancorabolinae (including *Ancorabolina*), being these characters present in all corresponding species. Characters 2 and 3 may further support this assumption, but are presently rather weak in view of the above-discussed difficulties. Furthermore, characters 8, 9, and 10 may even support a closer relationship of *Ancorabolina* to the *Ceratonotus*-group. Nevertheless, the two above-listed apomorphies (1, 6) should sufficiently justify the allocation of *Ancorabolina* into Ancorabolinae, in particular, if the morphological similarity with laophontodin taxa is based on plesiomorphies only, as stated by George (2006c). He based his argument mainly on two additional characters that are usually considered as important apomorphies of Ancorabolinae (Lang, 1948; George, 2006c):

11. Female antennule at most four-segmented [five-segmented];
12. Exp-3 of P2–P4 with two outer spines only [with three outer spines].

All Ancorabolinae present these characters, except *Ancorabolina*, which shares the plesiomorphic conditions with Laophontodinae (George, 2006c). Although no autapomorphies for Laophontodinae have been recognized so far, we detected some characters that are widespread in Laophontodinae and also present in *Ancorabolina*, but absent in the remaining Ancorabolinae:

13. Antennule second segment with outer bump bearing some long spinules [without bump];
14. P1 coxa lengthways elongate [P1 coxa small, square];
15. P1 seta of (former) exp-2 geniculate [element formed as a bipinnate spine];

Character 13

The second segment of laophontodin antennules, as well as those of *Ancorabolina*, show a rounded, bump-like expansion at the outer margin and bear several long spinules. For example, this structure is quite clear in the original descriptions of *Algensiella boitanii* Cottarelli & Baldari, 1987, *La. typicus*, *La. bicornis*, *La. whitsoni*, *La. hedgpethi*, *La. psammophilus*, *La. spongiosus*, *Laophontodes mourois* Arroyo, George, Benito & Maldonado, 2003, *Paralaophontodes exopoditus* Mielke, 1981, *Probosciphontodes*, *Lobopleura* Conroy-Dalton, 2004, and *Tapholaophontodes* Soyer, 1975. Its shape, position, and restriction to certain species point to a homologous structure. Thus, although not necessarily constituting an autapomorphy for a monophyletic Laophontodinae, it may point to a closer relationship between some laophontodin species and *Ancorabolina* if proved to be homologous. This would weaken the assumption of *Ancorabolina* as a member of Ancorabolinae, where the outer margin of the (former) second antennular segment is straight without a tuft of spinules.

Character 14

The remarkable lengthways elongation of P1 coxa is present in all species of *Ancorabolina*. Compared with the remaining Ancorabolinae showing a small and nearly square coxa, this elongation can be considered as apomorphic. However, in view of the remarkable transformation of ancorabolid natatorial legs, both types of coxa – the elongate as well as the shortened one – may constitute derived stages that evolved from a primitive ancestor, which possibly showed cletodid-like coxae and bases on its swimming legs. Although it is a unique and derived character of *Ancorabolina* compared with the remaining Ancorabolinae, a lengthways elongate P1 coxa is rather common within Laophontodinae. Several laophontodin taxa [e.g. *Probosciphontodes ptenopostica* Fiers, 1988, *Paralaophontodes echinata* (Willey, 1930), *Pa. exopoditus*, *La. armatus*, *La. hedgpethi*, *La. macclintocki*] show such an elongate coxa. Although such derivations may occur independently in different taxa, their presence in laophontodin taxa and *Ancorabolina* may be an indication of a closer relationship of *Ancorabolina* with certain members of Laophontodinae. However, as the phylogeny of that supposed paraphylum is not resolved, any assumption remains speculative. Furthermore, especially in older descriptions of laophontodin species, the P1 coxa has not been drawn completely and this hampers comparison.

Character 15

For this character the same argument applies as for character 14. Compared with Ancorabolinae, the transformation of the corresponding spine into a geniculate seta may constitute a true apomorphy for *Ancorabolina*. All remaining Ancorabolinae retain a normal-shaped element, i.e. a nongeniculate, bipinnate spine – this being the 'typical' and plesiomorphic condition widely distributed in Harpacticoida. However, in most species of Laophontodinae, the outer armature element of exp-2 (in the three-segmented exopod) or the most proximal element of exp-2 (in the two-segmented exopod, i.e. in *Pa. exopoditus* and *Tapholaophontodes remotus* Cottarelli & Baldari, 1987) is a geniculate seta, as in *Ancorabolina*. The descriptions of certain species in Laophontodinae are quite poor and probably missed the geniculation of this seta (i.e. in *Laophontodes propinquus* Brady, 1910, *Laophontodes latissimus* Brady, 1918, *La. gracilipes*, *Laophontodes ornatus* Krishnaswamy, 1957, and *Paralaophontodes elegans* Baldari & Cottarelli, 1986). Furthermore, *Pa. elegans*

and *Pa. echinata* only bear four setae on the second segment of their two-segmented exopod, which implies that one seta has been lost. Also, *Patagoniaella vervoorti* Pallares, 1968 forms an exception with a nongeniculate outer spine (but cf. George, 2006c).

The difficulties in allocating *Ancorabolina* within Ancorabolidae clearly demonstrate the urgent need for a phylogenetic re-evaluation of the subfamily Laophontodinae. Furthermore, phylogenetically important characters (such as the geniculation of setae, the presence of minute setae, etc.) probably have been missed in most of the older descriptions, implying the need for redescription of known species. Presently, we retain the genus *Ancorabolina* in the subfamily Ancorabolinae based on two true synapomorphies (1, 6) for the corresponding species.

THE GENUS *ANCORABOLINA* GEORGE, 2006

Comparing the species *A. belgicae*, *A. anaximenesi*, *A. galeata*, *A. divasecunda*, and *A. chimaera* with the remaining Ancorabolinae, they share the following synapomorphies:

16. Cephalothorax posteriorly with pair of ventrolateral cuticular processes turning backwards [no processes];
17. Loss of third setal element subapically on endopod of antenna [minute seta present].

Character 16

We consider this character as autapomorphic for *Ancorabolina* (see discussion of character 4).

Character 17

The subapical armature of the antennary endopod in *Ancorabolina* consists of two bipinnate spines. We propose the loss of a third small seta as a potential autapomorphy for the genus. Many harpacticoids bear this third small and bare seta, and it also occurs within Ancorabolidae. Within Laophontodinae, it is certainly present in *Prohosciphontodes*, *Lobopleura*, and *Pa. exopoditus*. Also, personal observation of additional material of *La. bicornis* and *La. whitsoni* confirms its presence in these taxa. Within Ancorabolinae, it is present in the *Ancorabolus*-group and certain species of the *Ceratonotus*-group. Further study of the Laophontodinae will have to elucidate the phylogenetic relevance of the loss of this seta in *Ancorabolina*.

In addition to these two shared characters, all members of *Ancorabolina* show sexual dimorphism in the endopod of P4, i.e. the outer seta on the male enp-2 is lost in the female. George (2006a) indicated that this kind of sexual dimorphism is present in certain species of *Ceratonotus* (but still has to be confirmed for species described from one sex only). Also, this feature has been considered as apomorphic for *Dorsiceratus* (Conroy-Dalton, 2001), but occurs as well in *Polyascophorus martinezi* George, 1998a. As already stated by George (2006b), this derived state cannot be assigned exclusively to one taxon, and therefore, its phylogenetic value is not considered that high.

ANCORABOLINA AND *LAOPHONTODES BICORNIS*

As mentioned above in the discussion of character 4, the laophontodin species *La. bicornis* strongly resembles the species of *Ancorabolina*. The fact that it shares character 16 with *Ancorabolina* causes some confusion in the phylogenetic interpretation. In fact, the very first examinations of *A. chimaera* (mis-)lead to the assumption of it being a somewhat derived *La. bicornis*. However, we conclude that the differences between *La. bicornis* and *Ancorabolina* are so great that their union is rendered questionable. Table 2 lists several morphological differences based on the redescription by Sars (1908) and personal observations of *La. bicornis* from G. O. Sars' collection and our own. Some of the characteristics (Table 2: 1, 2, 3, 4) are of particular phylogenetic value because their presence in *Ancorabolina* characterize it as a member of Ancorabolinae (George, 2006c; see above), whereas their absence in *La. bicornis* clearly shows its membership of Laophontodinae. At the moment, we refrain from providing a more extensive phylogenetic discussion. Any discussion restricted to *Ancorabolina* and the single laophontodin species *La. bicornis* would be premature as it would ignore the much more complicated conditions within Ancorabolidae and the complex relations between the members of both Ancorabolinae and Laophontodinae. This points again to the urgent need for a phylogenetic re-evaluation of Laophontodinae.

Two other species of *Laophontodes*, *Laophontodes hamatus* (Thomson, 1882) and *La. ornatus*, are also characterized by a pair of ventrolateral cuticular processes on the cephalothorax. The poor quality of the original description of *La. hamatus* led Gurney (1927) to conclude conspecificity with *La. bicornis* and the latter to be regarded as a junior synonym. However, this proposition was later rejected by Lang (1934) based on slight morphological differences in the rostrum and the two last body somites. Pending re-examination of the type material of *La. hamatus*, we refrain from drawing conclusions on the validity of this species. Also, the shortcomings in the original description of *La. ornatus* by Krishnaswamy (1957) obviously cast doubts on the validity of that taxon and prevents any comparison with *Ancorabolina*.

Table 2. Morphological differences between *Ancorabolina* and *Laophontodes bicornis*

Body part/appendage	*Ancorabolina*	*Laophontodes bicornis*
1. First segment of antennule	Elongate	Short
2. First segment of antennule	With long spinules	Without long spinules
3. Rostrum	Narrow, sharpened	Broad at base, not sharpened
4. Cephalothorax	With peak, laterally not extended	Without peak but laterally extended
5. Antenna endopod	Subapically with two bipinnate setae	Additionally with third small seta
6. Maxilliped	Syncoxa with bipinnate seta apically	Syncoxa without apical bipinnate seta
7. Basis P1	Transversely elongate	No transverse elongation
8. P5	Baseoendopod and exopod distinct in both sexes	Baseoendopod and exopod fused in male
9. P5 baseoendopod	With two minute setae and one to two small tube pores	With one (male) or two (female) long bipinnate seta(e), no tube pores
10. P2–P4	Outer spines long and slender, pinnae small and dense	Outer spines short, unipinnate, pinnae long and less dense

P1–5, first to fifth thoracopods.

Phylogeny inside *Ancorabolina*

Species within *Ancorabolina* can be differentiated from each other on account of the proportional lengths of rostrum, first antennular segment and furcal rami, the degree of development of the posterior processes on the cephalothorax, the number of exopodal segments in P1, and the degree of transverse elongation of the P1 basis. There is a clear trend towards progressive elongation in the rostrum (which is also progressively curved ventrally), first antennular segment, and furcal rami, and transverse elongation of the P1 basis. These characters are shown as morphoclines, which are difficult to dissolve into discrete character states. As the species show a mix of less or more derived conditions of the different characters, assessing relationships within the genus is particularly difficult. Contrary to the striking morphological variation of the above characters, the chaetotaxy of P2–P5 is the same in all known species of *Ancorabolina*, except for *A. chimaera* which lacks the inner seta on enp-2 of P4 and female P3.

At present, the genus *Ancorabolina* shows a considerably wide distribution range, from the bathyal north-east Atlantic and eastern Mediterranean Sea to the abyssal south-east Atlantic Ocean.

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