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## Characterization of a monophylum *Echinocletodes*, its exclusion from Ancorabolinae (Copepoda, Harpacticoida), and displacement of *E. bodini* and *E. walvisi* to *Cletodes*, including the description of two new species

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### Abstract

The discovery of two new species of Harpacticoida (Crustacea, Copepoda), *Echinocletodes voightae* **sp. nov.** (Ancorabolidae Sars, 1909) and *Cletodes meyerorum* **sp. nov.** (Cletodidae T. Scott, 1905 sensu Por, 1986), permitted a phylogenetic re-examination of the genus *Echinocletodes* Lang, 1936, whose membership in Ancorabolidae has been increasingly queried in the past decade. *Echinocletodes voightae* was discovered in wood-falls in the Gorda Ridge (Northeast Pacific Ocean). It resembles the type species *E. armatus* T. Scott, 1903, sharing with it seven synapomorphies. In contrast, the other two species in the genus, *E. bodini* Dinet, 1974 and *E. walvisi* Dinet, 1974, were originally collected in the deep Angola Basin (SE Atlantic), and do not exhibit any of these synapomorphies. In fact they correspond more closely with *Cletodes meyerorum*, which is undoubtedly *Cletodes* Brady, 1972, due to the presence of two apomorphies of that genus. Consequently, both *E. bodini* and *E. walvisi* are moved from *Echinocletodes* to *Cletodes*. A revision of ancorabolid apomorphies showed ambiguities, being absent from some Ancorabolidae but present in other non-ancorabolid taxa (like e.g. *Cletodes*). Ancorabolidae were, therefore, considered to be a paraphyletic group that requires extensive re-evaluation, additionally including at least the Cletodidae and Laophontidae T. Scott, 1905. Similarly when comparing *Echinocletodes* with the two ancorabolid subfamilies, Ancorabolinae Sars, 1909 and Laophontodinae Lang, 1944, it was revealed that many species are apparently distributed chaotically over several supraspecific taxa (at least Ancorabolidae and Cletodidae) instead of forming monophyla.

**Key words:** Systematics, *Echinocletodes voightae*, *Cletodes meyerorum*, wood-falls, deep sea, meiofauna

### Introduction

In 1903, Thomas Scott described a peculiar harpacticoid species he named *Cletodes armata* T. Scott, 1903, found in pieces of wood dredged from 159 m in the Faroe Channel. Decades later, Lang (1936a) published a detailed revision of the family Cletodidae T. Scott, 1905. He noted several differences between *C. armata* and the five then known *Cletodes* species and, therefore, established *Echinocletodes* Lang, 1936 transferring *Cletodes armata* into that new genus. Subsequently, Lang (1944, 1948) moved *Echinocletodes* from Cletodidae to Ancorabolidae Sars, 1909, more precisely to the subfamily Ancorabolinae Sars, 1909.

*Echinocletodes* remained monotypic until *E. bodini* Dinet, 1974 and *E. walvisi* Dinet, 1974 were described from the deep Southeast Atlantic (Dinet 1974), and no additional species have been described since. After Lang's (1948) consideration of the genus within a systematic analysis of Ancorabolidae, no subsequent systematic study included it, perhaps because of the unavailability of type material and the rather unsatisfying descriptions of the known species. Most recently, Conroy-Dalton & Huys (2000) listed the taxon as genus inquirendum, and although Conroy-Dalton (2003a, 2004) also noted the unresolved position of *Echinocletodes*, no further phylogenetic insights were provided. Therefore, the systematic status of *Echinocletodes* within Ancorabolidae remains unclear.

During the cruise M 48/1 DIVA 1 of RV METEOR in July–August 2000 several multicorer (MUC) samples were taken at different stations in the Angola Basin (SE Atlantic off Namibia) (Rose *et al.* 2005). Some of these samples contained many specimens of a new copepod species showing a high morphological affinity to both *E.*

*bodini* and *E. walvisi*. Also, despite some apparent similarities with *E. armatus*, the new species shares more characters with *Cletodes* Brady, 1872. It is therefore allocated into Cletodidae as *Cletodes meyerorum* **sp. nov.** and described in this present contribution.

Additional material collected by Dr Janet R. Voight (Field Museum of Natural History, Chicago, U.S.A.) in 2004 from wood falls deployed at the Gorda Ridge (NE Pacific, off U.S.A.) included a male and female of a species strongly resembling *Echinocletodes armatus*. It is described as *Echinocletodes voightae* **sp. nov.**

These new species, combined with an analysis of published data, enabled a reassessment of the genus *Echinocletodes*. The phylogenetic status of the genus is consequently clarified, including a clarification of the relationships between *Echinocletodes* species, and providing the first phylogenetic arguments regarding its relationship with Ancorabolidae. The systematic status of Ancorabolidae has not been questioned since its establishment by Sars (1909) and subsequent refinement by Lang (1948). The main systematic events in the history of this family have been the establishment of two subfamilies, Ancorabolinae Sars, 1909 and Laophontodinae Lang, 1944 by Lang (1944, 1948) and the recognition of two lineages within the Ancorabolinae by Conroy-Dalton & Huys (2000) and Conroy-Dalton (2001), the *Ancorabolus*-lineage and the *Ceratonotus*-group, respectively. Therefore, together with the re-evaluation of *Echinocletodes*, the phylogenetic status of Ancorabolidae is re-evaluated here, including a discussion of the relevant phylogenetic characters and consequent systematic states.

## Material and methods

The type material of the new *Echinocletodes* species (1 female, 1 male) was kindly loaned to the authors by Dr J.R. Voight. It was collected from oak and fir blocks deployed at station VOIJALV4043B, Escanaba Trough (Gorda Ridge), on July 25<sup>th</sup> 2002 and recovered 25 months later on August 30<sup>th</sup> 2004 during cruise FIELD II (Focused Investigations of Environment and Life at Depth) of RV ATLANTIS with Deep Submergence Vehicle (DSV) ALVIN (dive 4043) (J.R. Voight and J. Gerber, personal communication). For detailed sampling and sample treatment information see Voight (2007). The type material was deposited in the collection at the Field Museum of Natural History, Chicago, USA.

The type material of the new *Cletodes* species consists of 10 specimens. It originates from MUC samples taken at station #346 (Northern Angola Basin) during the DIVA 1 campaign (Latitudinal Gradients of Deep-Sea BioDiversity in the Atlantic Ocean) (cruise M 48/1 of RV METEOR) (Balzer *et al.* 2006). Sampling and sample treatment was described by Rose *et al.* (2005). Preserved specimens were dissected and mounted in glycerol on object slides. The type material was deposited in the collection at the Senckenberg Forschungsinstitut und Naturmuseum Frankfurt, D-60325 Frankfurt am Main, Germany.

All drawings were made with the aid of a camera lucida on a Leica DMR compound microscope equipped with differential interference contrast illumination. General terminology follows a literal translation of Lang (1948) with addition terms from Huys & Boxshall (1991). Phylogenetic terminology is translated from Ax (1984); the terms “telson” and “furca” are adopted from Schminke (1976).

Abbreviations used in the text: A1: antennule, A2: antenna, aes: aesthetasc, benp: baseopod, cphth: cephalothorax, enp: endopod, enp-1 (enp-2, enp-3): first (second, third) endopodal segment, exp: exopod, exp-1 (exp-2, exp-3): first (second, third) exopodal segment, FR: furcal ramus/rami, GF: genital field, md: mandible, mx: maxilla, mxl: maxillule, mxp: maxilliped, P1–P6: swimming legs 1–6.

## Taxonomy

### Ancorabolidae Sars, 1909

### Ancorabolinae Sars, 1909

### *Echinocletodes* Lang, 1936

**Type species.** *Echinocletodes armatus* (T. Scott, 1903) by designation.

**Additional species.** *Echinocletodes voightae* sp. nov.

**Generic diagnosis.** Body long and slender (length including FR >1500 µm), cylindrical, with slight lateral depression and densely covered with fine, bristle-like spinules. Cphth reaching about 1/5 of body length (excluding FR), with several pairs of sensilla. Rostrum very small and narrow, with bristle-like spinules, and a long tube pore at its tip. All body somites, except telson, exhibit on dorsal and lateral surface peculiar, triangular-shaped thorn-like spikes each carrying a sensillum laterally. Last thoracic and first abdominal somite fused in female, forming a genital double somite. Telson square-shaped, shorter than the total length of the preceding two somites. Anal operculum with spinules, flanked by 2 sensilla. FR about 8 times as long as maximum width and approximately 1/5 of whole body length, with 7 setae. Female A1 4-segmented, all segments with fine spinules; all setal elements bare. Male A1 8-segmented (not verified for *E. armatus*), subchirocer. A2 without exp; allobasis covered by fine spinules and with 2 short, bipinnate abexopodal setae. Md with strong gnathobase carrying several teeth. Mandibular palp one single lobe with 1 lateral and 3 apical setae. Mxp prehensile, syncoxa subterminal with some spinules but lacking seta. Enp forms claw, with row of spinules at inner margin and long bare seta at base (not verified for *E. armatus*). P1–P4 with weak transverse elongation of basis. P1 not prehensile; P1 enp with 1 or 2 segments, distal (or only) segment with 2 apical setae. P2–P4 enps 2-segmented (for male P3 enp see below). Enp-1 without setae; enp-2 with 2 biplumose apical setae. In P3 and P4 enp-2 with additional bipinnate spines, 1 inner and 1 outer. Exopods 3-segmented; exp-1 and exp-2 each with 1 bipinnate outer spine but no inner seta; exp-3 with 2 bipinnate outer spines and 2 biplumose setae apically, but no inner setae. P5 with small benp and elongate endopodal lobe bearing 2 apical and 2 inner setae. Basal part of benp has long setophore carrying 1 bare seta. Exp distinct, approximately 5 times longer than broadest part, laterally with 1 bipinnate seta and 1 tube pore, apically with 1 outer bipinnate seta and 1 longer biplumose seta. Male P3 enp 3-segmented: first segment shortest, without setation, second segment with peculiarly pointed apophysis terminally, rarely reaching the length of third segment, and ending in winding, hook-like structure. Enp-3 as long as first two segments combined, apically with 2 long biplumose setae. P5 smaller than in female, benp with only 2 apical setae (not verified for *E. armatus*).

***Echinocletodes voightae* sp. nov.**

**Type locality.** Gorda Ridge, Escanaba Trough, Northeast Pacific Ocean, station VOIJALV4043B, at 41°00.016'N, 127°29.685'W, and a depth of 3232 m (Voight 2007). Both specimens described here were taken from lot FMNH-INV 12964 which included more than 25 copepod specimens belonging to several species.

**Holotype.** Female, collection number FMNH-INV 14021 (13 slides).

**Paratype.** Male, collection number FMNH-INV 14022 (7 slides).

**Etymology.** The epitheton *voightae* is given in grateful dedication to Dr Janet R. Voight (Chicago, U.S.A.) who kindly provided the specimens for description.

**Description of female.** Habitus (Figs. 1A, B) very long and slender, cylindrical, with slight lateral depression. Length including FR approximately 1869 µm. Whole body densely covered with fine, bristle-like spinules. Cphth reaching about 1/5 of body length (excl. FR), with several pairs of sensilla. Posterior margin of cphth, free thoracic somites and both components of genital double somite with row of long spinules. Rostrum very small and narrow, with 2 sensilla basally and long, straight tube pore at its tip. All body somites, except telson, exhibit on dorsal and lateral surface triangular-shaped thorn-like spikes each carrying a sensillum laterally (Fig. 1C). Last thoracic and first abdominal somite fused, forming genital double somite; site of fusion indicated by row of long spinules and 3 pairs of thorn-like spikes. Penultimate abdominal somite carrying 8 thorn-like spikes. Telson approximately square, not reaching combined length of preceding somites. Anal operculum with spinules, flanked by 2 sensilla.

FR (Figs. 1A, B, 2D) about 8 times as long as greatest width, approximately 1/5 of whole body length. Seven setae present: I and II close together anteriorly at outer margin; seta I slightly smaller than and located below II; III as long as II, inserted laterally on first half of FR; IV, V, and VI terminal, VI shortest, V longest, reaching length of FR and telson together (cf. Fig. 1B). VII at least biarticulated (broken in Figs. 1A, B, 2D), inserted dorsally on a small hump in centre of FR. Additional slender tube pore subterminally on lateral side of FR.

A1 (Fig. 2A) 4-segmented, all segments with fine spinules; all setal elements bare. First segment with 1 seta. Second segment with 6 setae, one arising from strong protrusion (seta broken in Fig. 2A). Third segment longest

and clearly more slender than all other segments (1, 2 and 4), carrying 7 bare setae, one arising together with an aes from large outgrowth overhanging fourth segment. Fourth segment with 10 setae and 1 small aes. Setal formula: I-1; II-6; III-7 + aes; IV-10 + aes.

A2 (Fig. 2B). Allobasis covered with fine spinules and 2 abexopodal short, bipinnate setae. No exp. Enp as long as allobasis, with row of long spinules and 2 bipinnate setae on inner margin. Subterminally with spinulose frill. Terminally with 3 bipinnate and 2 geniculate setae, plus 1 small bare seta.

Md (Fig. 3A) with strong gnathobase carrying several teeth, and 1 unipinnate seta. Mandibular palp as one single lobe with 1 lateral biplumose seta and 3 apical setae, two of which bare, third bipinnate.

Mxl (Fig. 3B) with spinules on lateral margin. Praecoxa apically with 5 strong spines and 2 unipinnate, articulate setae. Two surface setae arising from broad pedestal; on opposite side accumulation of long spinules and 1 biplumose seta apically. Coxal endite with 2 bare setae. Basis fused with enp and exp, forming single segment; basal endite apically with 2 bare setae, endopod represented by 1 bare seta, exopodal lobe still noticeable, carrying 2 bare setae.

Mx (Fig. 3C) bearing few spinules at lateral margin. Syncoxa with 2 endites. Proximal endite with 2 bare setae and 1 strong bipinnate spine fused to endite. Distal endite with 3 setae, one unipinnate. Basis distinct, with 1 bare seta and 1 strong unipinnate claw-like spine fused with basis. Enp represented by 1 bare seta.

Mxp (Fig. 3D) prehensile, syncoxa subterminal with some spinules but lacking seta. Basis covered with spinules. Enp forming claw, with row of spinules at inner margin and long bare seta at base.

P1 (Fig. 4A) not prehensile. Basis showing modest transverse elongation, with 1 bipinnate inner seta and 1 bipinnate outer seta; tube pore absent. Enp 1-segmented, apically with 2 bipinnate setae. Exp 3-segmented, all segments of approximately same size. Exp-1 and exp-2 each with 1 bipinnate outer spine accompanied by spinules; exp-2 additionally with tube pore. Exp-3 with 2 bipinnate outer spines and 2 geniculate bare setae apically. Pinnae of outer spines notably fine and small.

P2–P4 (Figs. 5A, B, 6A) with moderate transverse lengthening of bases, each bearing 1 bare outer seta but no tube pore. Enps 2-segmented, enp-2 six (P2, P4) to eight (P3) times longer than enp-1. Enp-1 without setae. Enp-2 with 2 biplumose apical setae, P3 and P4 also with 1 inner and 1 outer bipinnate spine. Exps 3-segmented; exp-1 and exp-2 each with 1 bipinnate outer spine; exp-3 with 2 bipinnate outer spines, apically with 2 biplumose setae and tube pore on outer margin.

P5 (Fig. 4B) has small Benp, with elongate endopodal lobe bearing 2 bipinnate apical setae and 2 inner bipinnate setae. One additionally tube pore on anterior surface. Basal part of benp with long setophore bearing 1 bare seta. Exp distinct, approximately 5 times longer than widest part, laterally 1 bipinnate seta and 1 tube pore, apically 1 outer bipinnate and 1 longer biplumose seta.

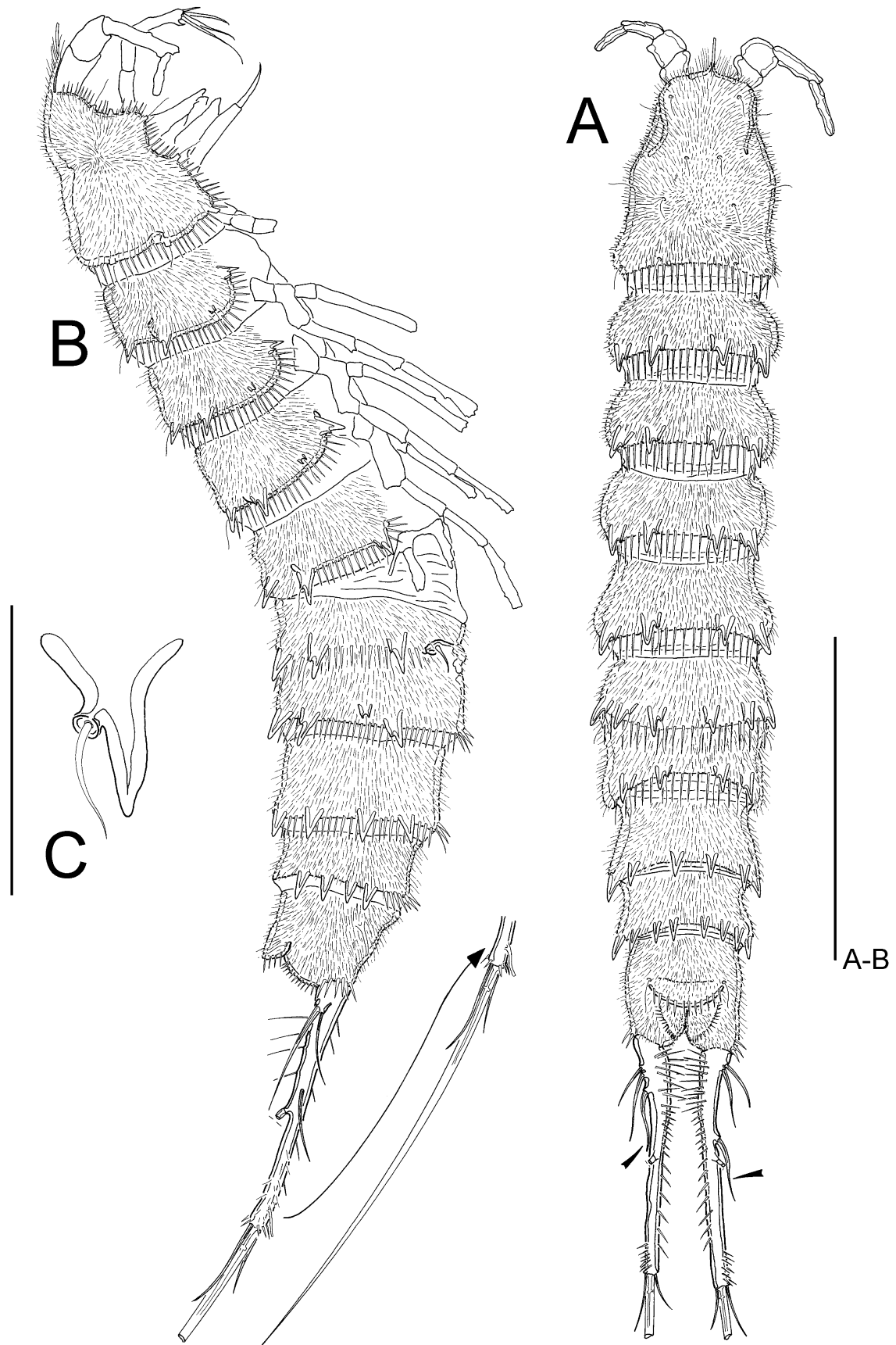
GF (Fig. 2C) difficult to discern, P6 represented by 2 stubby protrusions each carrying 1 small bipinnate seta. Gonopore not seen.

**Description of male.** Male differs from female in following characters: body (not drawn) and appendages slightly smaller, last thoracic and genital somite not fused, shape and setation of A1, P3 enp, and P5.

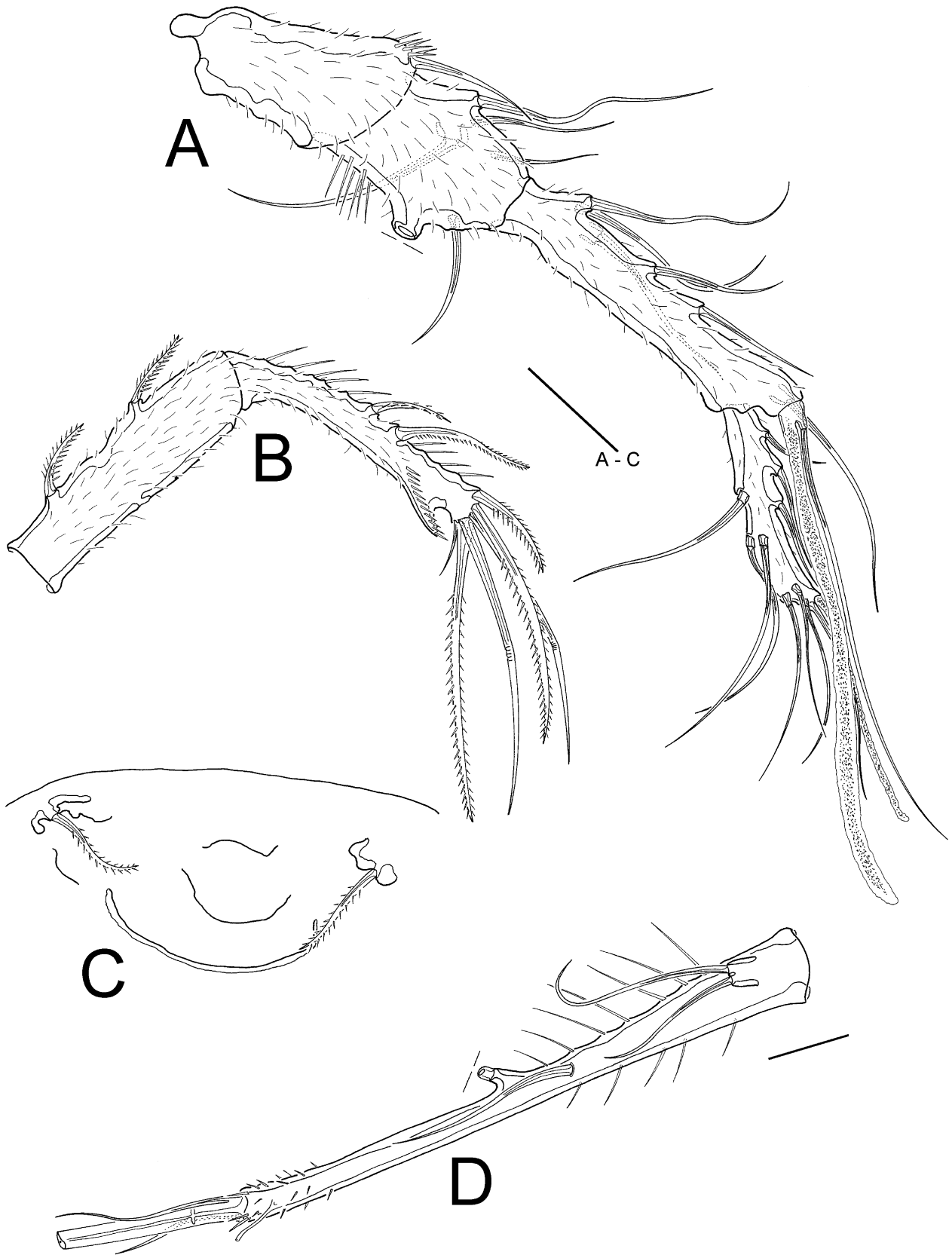
A1 (Fig. 7A) 8-segmented, subchirocer, geniculation between fifth and sixth segment. First segment with 1 pinnate seta, all remaining setae on A1 bare. Second segment with 9 setae, one arising from strong, posteriorly-directed pedestal. Third segment short, with 5 setae. Fourth segment minute, with 2 setae. Fifth segment swollen, with 8 setae along anterior margin, and 1 seta and 1 aes arising from elongate protrusion. Segments 6–8 very narrow: sixth segment with 1 minute and 1 longer seta, seventh segment without setae, and eighth segment tapering distally, with 8 setae and 1 aes. Setal formula: I-1; II-9; III-5; IV-2; V-9 + aes; VI-2; VII-0; VIII-8 + aes.

P3 (Fig. 7B). Basis and exp as in female. Enp 3-segmented, first segment shortest, without setation. Second segment about 1.5 times longer than first, terminally with pointed apophysis rarely reaching the length of third segment. Apophysis ending in hook-like structure that is basally broadened (see \* in Fig. 7B). Enp-3 as long as first two segments combined, apically with 2 long biplumose setae.

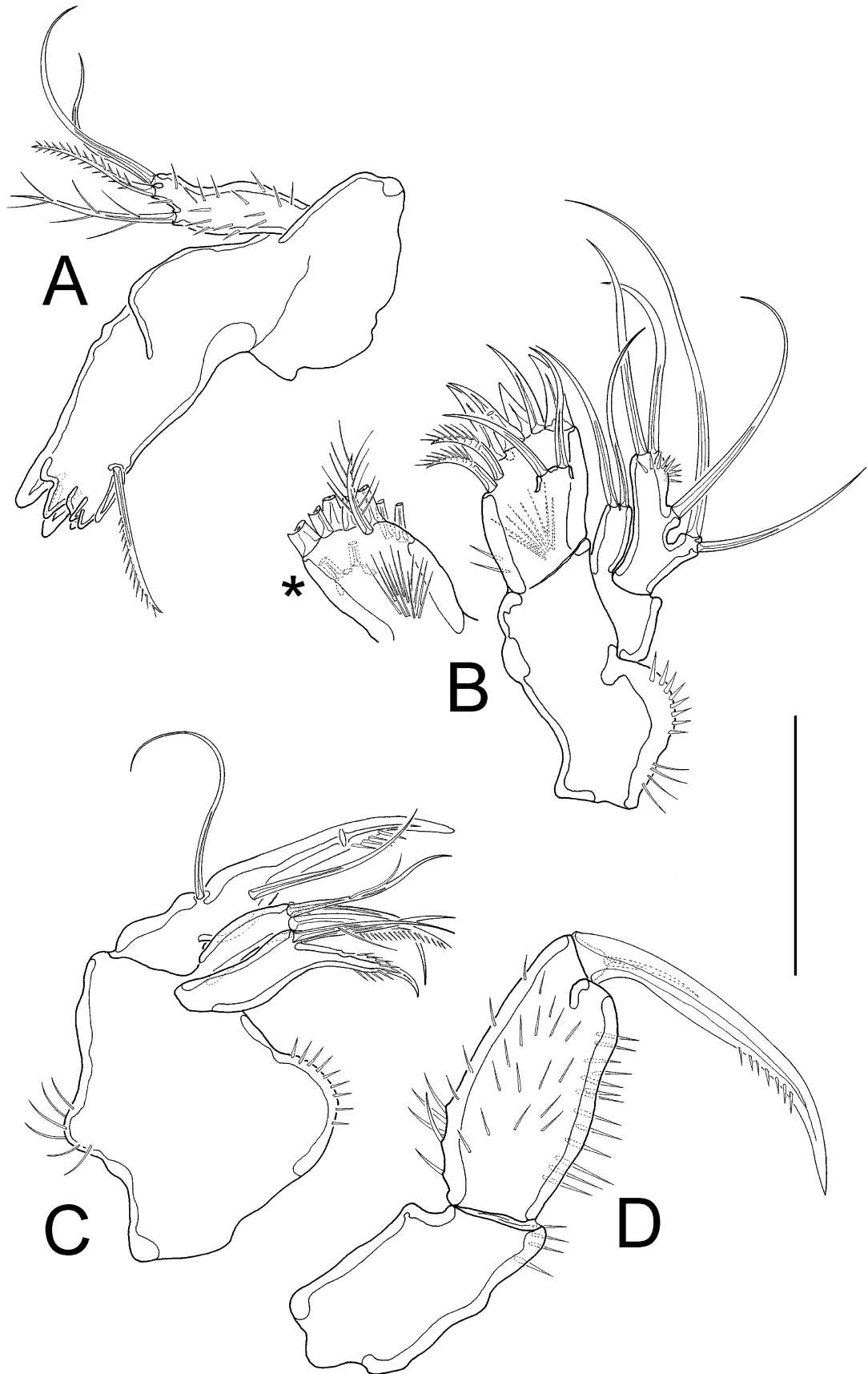
P5 (Fig. 6B) resembles that of female, but smaller. Endopodal lobe more slender, with 2 apical bipinnate setae and 1 tube pore on each of inner and outer margin. Additional tube pore close to setophore, latter with 1 seta. Exp distinct, approximately 5 times longer than broad, laterally with 1 seta and 1 tube pore, apically with 2 bipinnate setae, the innermost almost twice as long as the outer one.



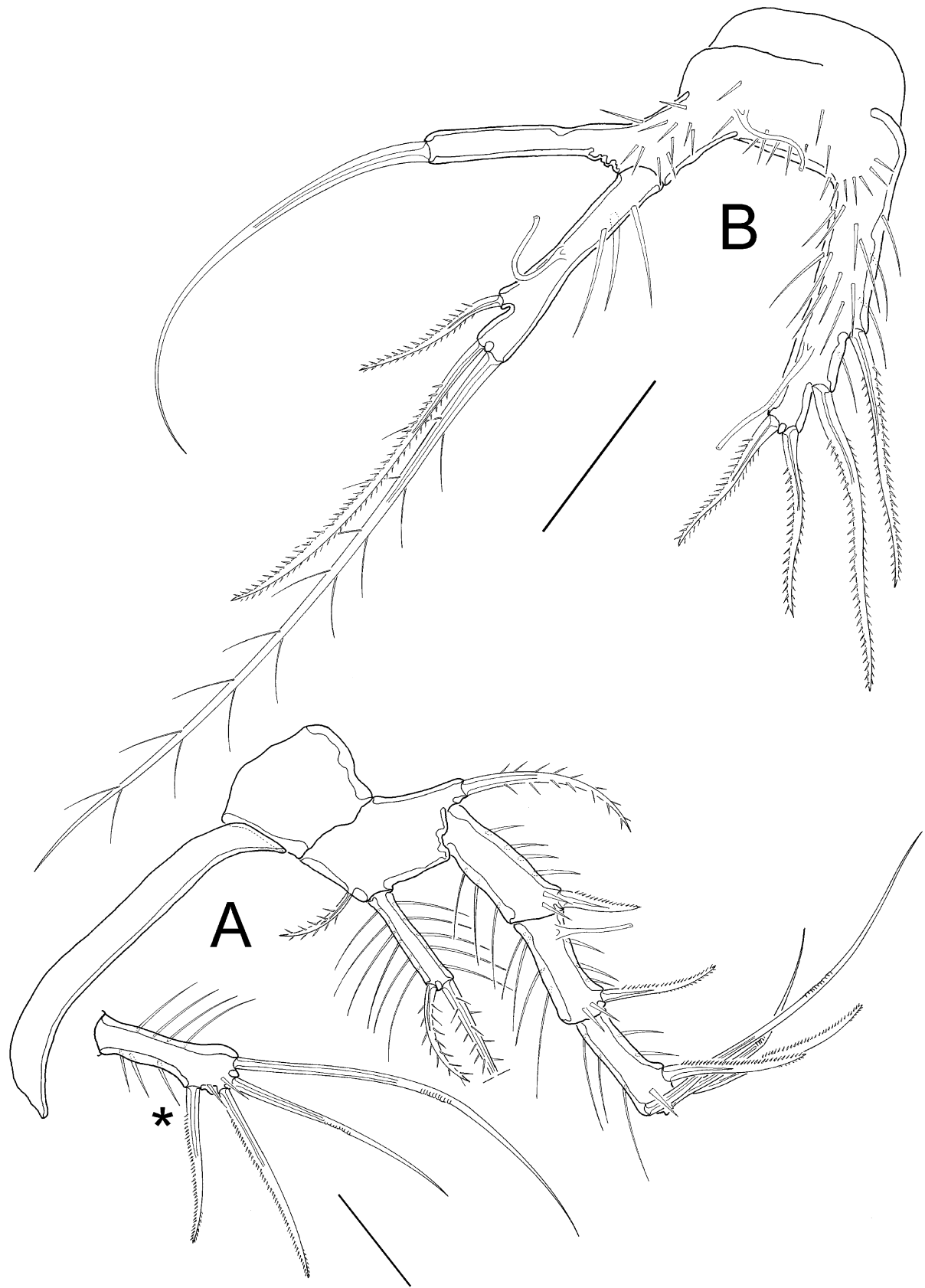
**FIGURE 1.** *Echinocletodes voightae* sp. nov., female. A. Habitus dorsal; triangular arrows indicating different position of furcal seta III in the FR, B. Habitus lateral, C. cuticular spike. Scale bars: A, B: 500  $\mu$ m, C: 50  $\mu$ m.



**FIGURE 2.** *Echinocletodes voightae* sp. nov., female. A. A1, B. A2, C. GF, D. FR (right). All scale bars: 50  $\mu$ m.

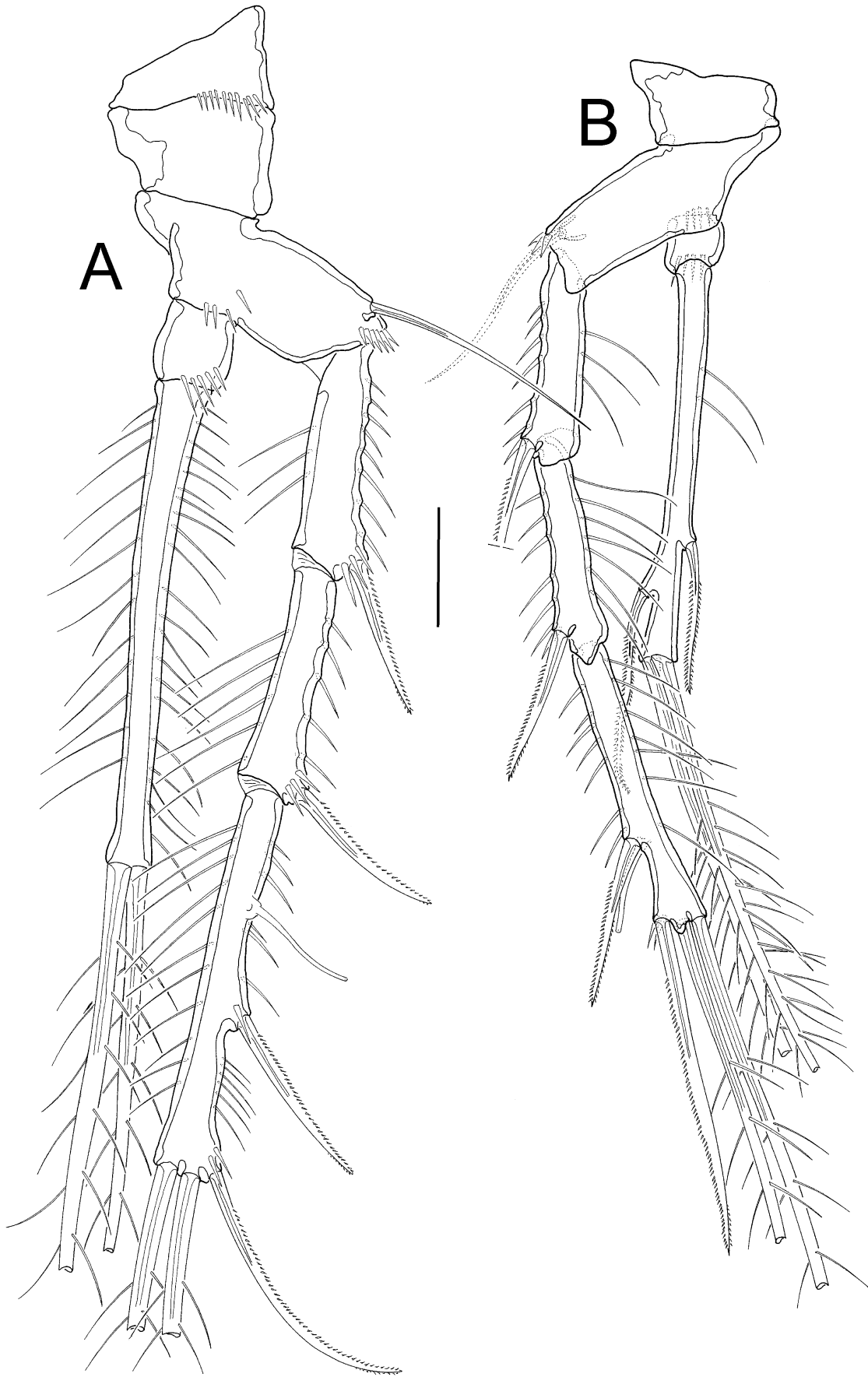


**FIGURE 3.** *Echinocletodes voightae* sp. nov., female. A. Md, B. Mxl, \* showing the other side of the gnathobase, C. Mx, D. Mxp. Scale bar: 50  $\mu$ m.

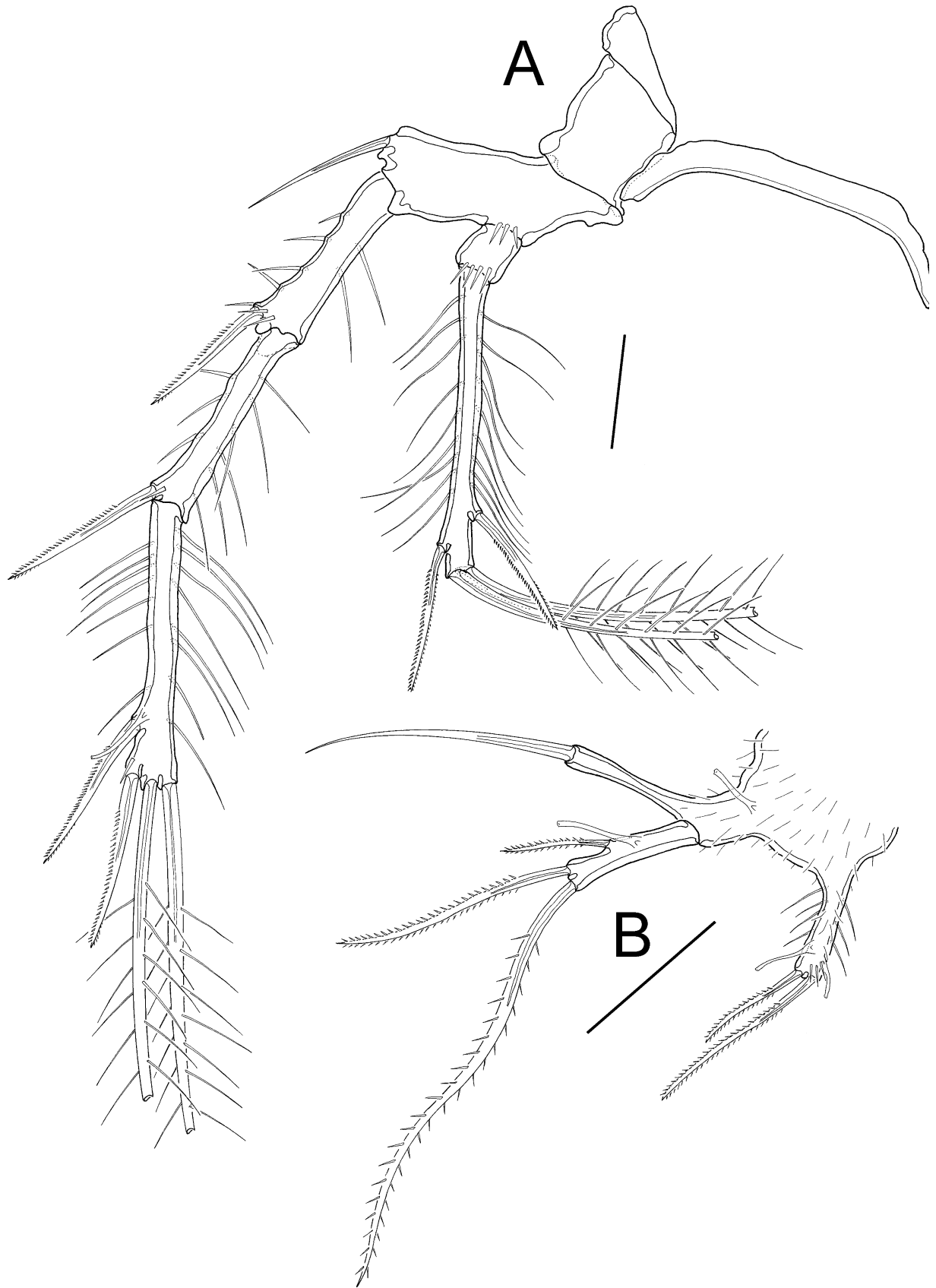


**FIGURE 4.** *Echinocletodes voightae* sp. nov., female. A. P1 with corresponding intercoxal sclerite; \* showing exp-3 of counterpart, B. P5. Scale bars: 50  $\mu$ m.

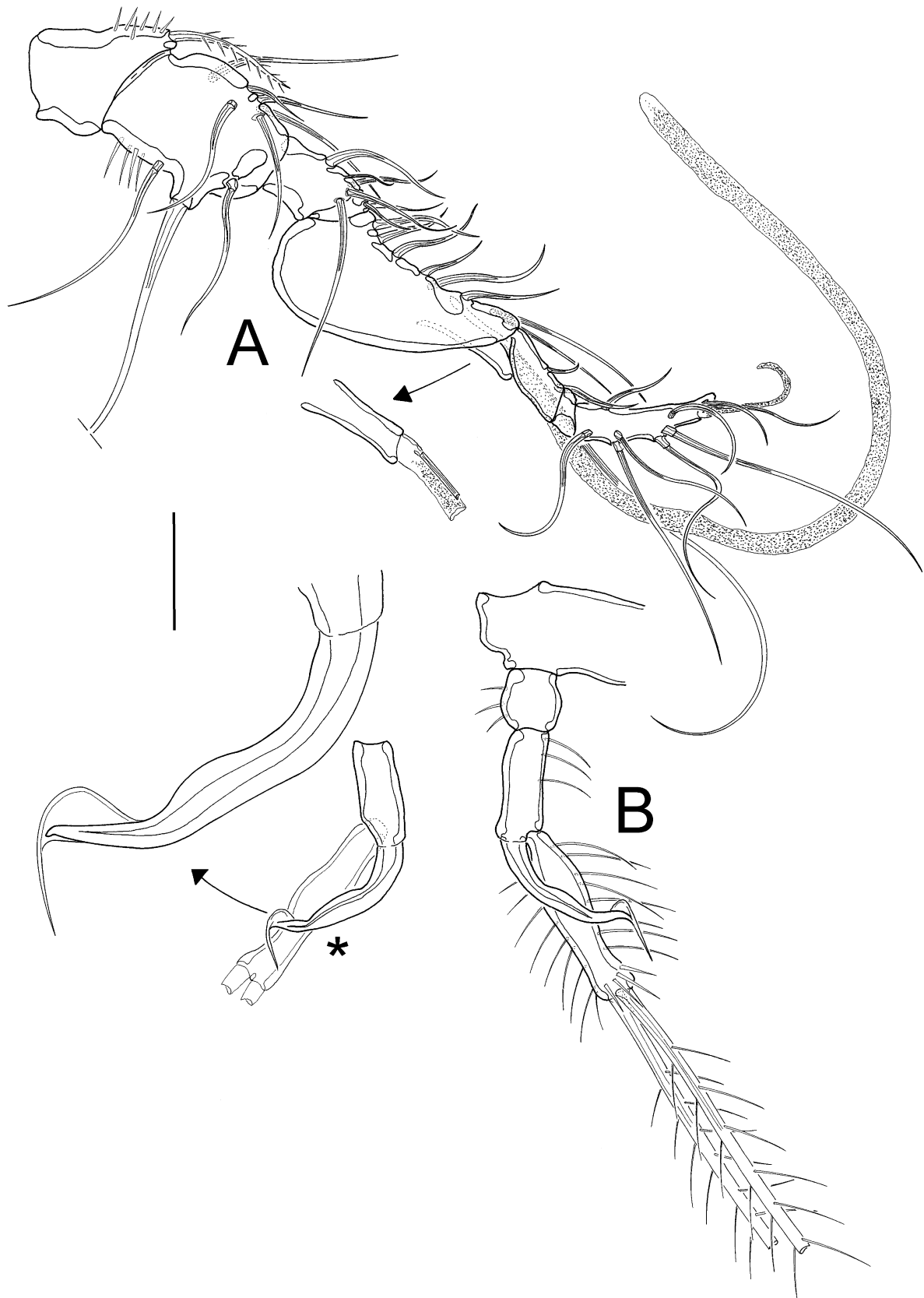




**FIGURE 5.** *Echinocletodes voightae* sp. nov., female. A. P2, B. P3. Scale bar: 50  $\mu$ m.



**FIGURE 6.** *Echinocletodes voightae* sp. nov. A. P4 female, B. P5 male. All scale bars: 50  $\mu$ m.



**FIGURE 7.** *Echinocletodes voightae* sp. nov., male. A. A1, arrow pointing to protrusion of fifth segment that bears 1 seta and 1 aes; B. P3 ep, \* showing enp-2 and enp-3 of the counterpart, with magnification of the apophysis (arrow). Scale bar: 50  $\mu$ m.

**TABLE 1.** Setation of the swimming legs in *Echinocletodes voightae* **sp. nov.**; Roman numerals referring to outer setae/spines.

	Exopod			Endopod	
	1	2	3	1	2
P1	I;0	I;0	II;2;0	0:2:0	–
P2	I;0	I;0	II;2;0	0;0	0;2;0
P3	I;0	I;0	II;2;0	0;0	1;2;1
P4	I;0	I;0	II;2;0	0;0	1;2;1

## Cletodidae T. Scott, 1905 *sensu* Por, 1986

### *Cletodes* Brady, 1872

**Type species.** *Cletodes limicola* Brady, 1872.

**Additional species.** In addition to the herein new described *C. meyerorum* **sp. nov.**, 24 species, plus 1 species incertae sedis (*C. brucei* T. & A. Scott, 1901) and two species inquirendae (*C. longicaudatus* (Boeck) *sensu* Arlt, 1983, *Enhydrosoma* sp. Krishnaswamy, 1957) are known (Wells 2007).

### *Cletodes meyerorum* **sp. nov.**

**Type locality.** Angola Basin, South Atlantic (station #346, 16°117.0'S/05°127.0'E, depth 5389 m).

**Holotype.** Female, collection number SMF 37039.

**Paratypes.** Nine specimens (4 females, 5 males). Paratype 1, male, coll. no. SMF 37040 (1 slide); Paratype 2, male, coll. no. SMF 37041 (1 slide); paratype 3, female, coll. nos. SMF 37042/1–10 (10 slides); paratype 4, female, coll. nos. SMF 37043/1–10 (10 slides); paratype 5, female, coll. no. SMF 37044 (1 slide); paratype 6, male, coll. nos. SMF 37045/1–2 (2 slides); paratype 7, male, coll. nos. SMF 37046/1–2 (2 slides); paratype 8, male, coll. no. SMF 37047 (1 slide); paratype 9, female, coll. nos. SMF 37048/1–2 (2 slides).

**Etymology.** The epitheton *meyerorum* is given in fond dedication to Mrs Grete and Mr Herbert Meyer (Achtermeer, Germany), grandparents of the second author.

**Description of female.** Habitus (Figs. 8A, B) long and slender, narrowing towards caudal end from 95 µm (Cphth) to 45 µm (basis of FR). Length including FR approximately 540 µm, Rostrum (Fig. 10A) small, two sensillate tubercles and two bulbous projections on margin and tube pore on ventral side. Cphth reaching about 1/4 of body length (excl. FR), with 5 additional tube pores and several sensillate tubercles. Posterior margin of cphth, thoracic somites, and first 2 abdominal segments displaying pointed thorn-like spikes (Fig. 8A), each with lateral sensilla. All thoracic somites with dorsal tube pore. Last thoracic and first abdominal somites fused, forming genital double somite. Second abdominal somite with 2 long tube pores dorsally. Telson short, posterior margin with ventrolateral cuticular spinules. Anal operculum with spinules and 2 sensillate tubercles.

FR (Figs. 9A, B) length about ten times width, reaching approximately 1/3 of whole body length. Seven setae present: I and II close together, inserted laterally after proximal 40 % of total FR length, seta I very small and positioned below II, tube pore adjacent; III inserted laterally, close to distal end of FR; IV, V, and VI terminal, IV and VI short, almost equal length, V longest, exceeding total length of free body somites (cf. Fig. 8A). VII triarticulated, inserted dorsally on small hump in middle of FR. On lateral side of FR, between setae III and IV, additional hyaline foliaceous structure (triangular arrows in Figs. 9A, B).

A1 (Fig. 10A, A') 5-segmented, first segment has spinules on inner side, with 1 bipinnate seta. Second segment with 8 setae, 2 bare and 6 bipinnate. Third segment with 5 bare and 1 unipinnate seta and 1 aes; aes and 2 bare setae grouped as trithecata. Fourth segment with 1 bipinnate seta in holotype (\* in Fig. 10A'), in some female paratypes this seta is bare (\* in Fig. 10A; PT 9). Fifth segment with 11 setae and 1 aes; aes, 1 bare and 1 unipinnate seta grouped as trithecata at terminal end; # indicates unipinnate seta in holotype (Fig. 10A') but bare in some paratypes (Fig. 10A; PT 9). Setal formula: I-1; II-8; III-6 + aes; IV-1; V-11 + aes.

A2 (Figs. 10B, B') allobasis with spinules and 1 short, bare abexopodal seta. Exp small, carrying small bipinnate seta. Enp anteriorly with long spinules, 2 bare setae, and 1 bipinnate seta (Fig. 10B'). On the opposite side with 2 spinulose frills. Also, 1 tube pore and 5 setae terminally: The terminal setae vary, 2 bare, long and geniculate, 1 bipinnate, long and geniculate featuring heteromorphic pinnae, 1 monopinnate, and 1 bipinnate and small.

Md (Fig. 11A) forms angle of approximately 110°. Gnathobase with 4 acute teeth and 1 small, bare seta. Mandibular palp formed of one single lobe displaying 1 lateral, 1 subterminal, and 3 terminal setae, all biplumose. Base of subterminal seta surrounded by spinules.

Mxl (Fig. 11B) with spinules on lateral margin. Praecoxa with long spinules and terminally 3 bare and 3 unipinnate strong spines. Subterminally, 1 small unipinnate seta and 2 bare setae. Additional pair of bare surface setae. Coxal endite with 1 bare and 1 unipinnate seta. Basal endite fused with enp and exp, forming single segment which carries 8 biplumose and 3 bare setae.

Mx (Fig. 11C) bearing spinules at lateral margin, proximal spinules long. Syncoxa with 2 endites, each carrying 3 terminal pinnate setae; proximal endite fused with 2 and distal endite fused with 1 terminal setae. Basis fused to syncoxa, with 2 bare setae and 2 strong unipinnate spines, one fused with basis. Enp distinct, with 2 bare setae.

Mxp (Fig. 11D) prehensile, syncoxa bare, with 1 small seta. Basis with one row of tooth-like spinules. Enp forming claw, with row of spinules at inner margin and long bare seta at base.

P1 (Fig. 12A) not prehensile. Basis showing moderate transverse elongation, with 1 long biplumose inner, and 1 bipinnate outer seta as well as 1 long tube pore. Enp 2-segmented, first segment smaller than second, without setation. Enp-2 with 2 apical biplumose setae, medial seta longest. Enp-2 with additional bipinnate outer spine. Exp 3-segmented, all segments approximately same size. Exp-1 and exp-2 each with 1 bipinnate outer spine surrounded by spinules. Exp-3 with 2 bipinnate outer spines and 2 bipinnate terminal setae with heteromorphic pinnae.

P2–P4 (Figs. 12B, 13A, B) with transversely prolonged bases, each bearing 1 biplumose outer spine and 1 long tube pore. Enps 2-segmented, first segments smallest, without setae. P2 enp-2 with 1 small bare outer seta and 2 biplumose terminal setae; P3 and P4 enp-2 with 1 biplumose inner, and 1 bipinnate outer seta and 2 long biplumose terminal setae. Exps 3-segmented: exp-1 and exp-2 each with 1 bipinnate outer spine accompanied by spinules, exp-2 additionally with 1 biplumose inner seta. Exp-3 with 2 bipinnate outer spines and 2 bipinnate terminal setae featuring heteromorphic pinnae.

P5 (Fig. 14B) with small benp having elongate endopodal lobe with 1 bare and 1 bipinnate seta and 1 tube pore. Basal part of benp with tube pore and spinules close to very long setophore which bears 1 bare outer seta. Exp distinct, approximately 14 times longer than broad, laterally with 2, and terminally with 3 bipinnate setae.

GF (Fig. 14C) wrinkled, with fused P6 represented by 2 stubby protrusions each carrying 1 small bare seta. Gonopores covered by trapezoid invagination of the cuticula.

**Description of male.** Male differs from female in the following characters: body and appendages slightly smaller, last thoracic and genital somite not fused, shape and setation of A1, P3 enp, and P5.

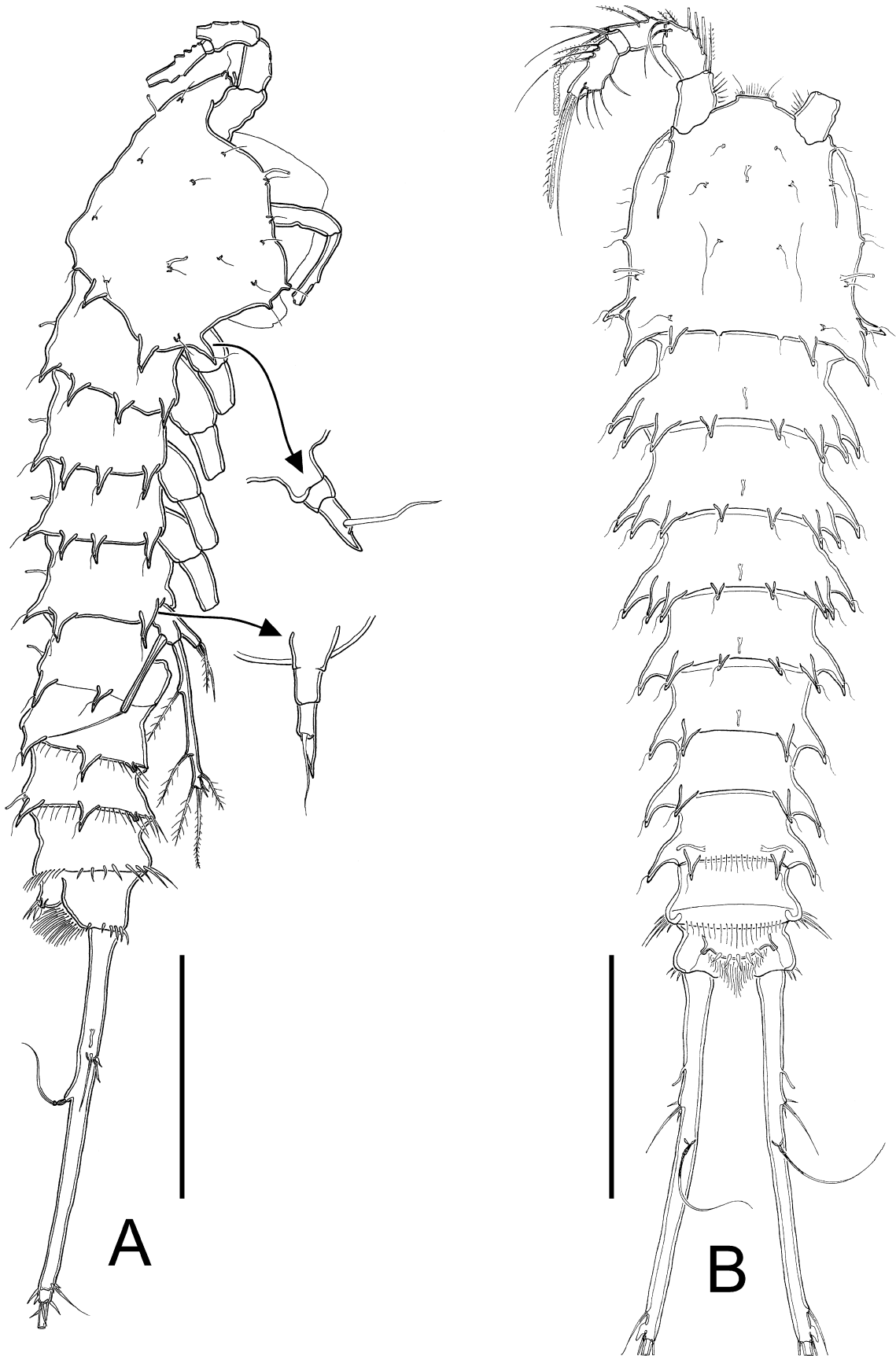
Habitus (Fig. 15A) similar to female in general appearance, but shorter (length including FR approximately 490 µm) and more slender.

A1 (Fig. 15B) 6-segmented, subchirocer. First segment with spinules and 1 pinnate seta. Second segment with 9 setae in total: 2 bare setae and 1 bipinnate seta on dorsal side, 4 bipinnate setae on anterior margin, 2 long bare setae on ventral side. Third segment short, with 6 setae (1 seta broken in Fig. 15B). Fourth segment thickened, with 1 bipinnate seta and 3 bare setae, plus 1 aes and 1 long bare seta located on protrusion. Fifth segment with 3 thick stubby setae on the anterior margin. Sixth segment with 7 bare setae, plus 1 aes and 1 seta located near to distal end. Setal formula: I-1; II-9; III-6; IV-5 + aes; V-3; VI-8 + aes.

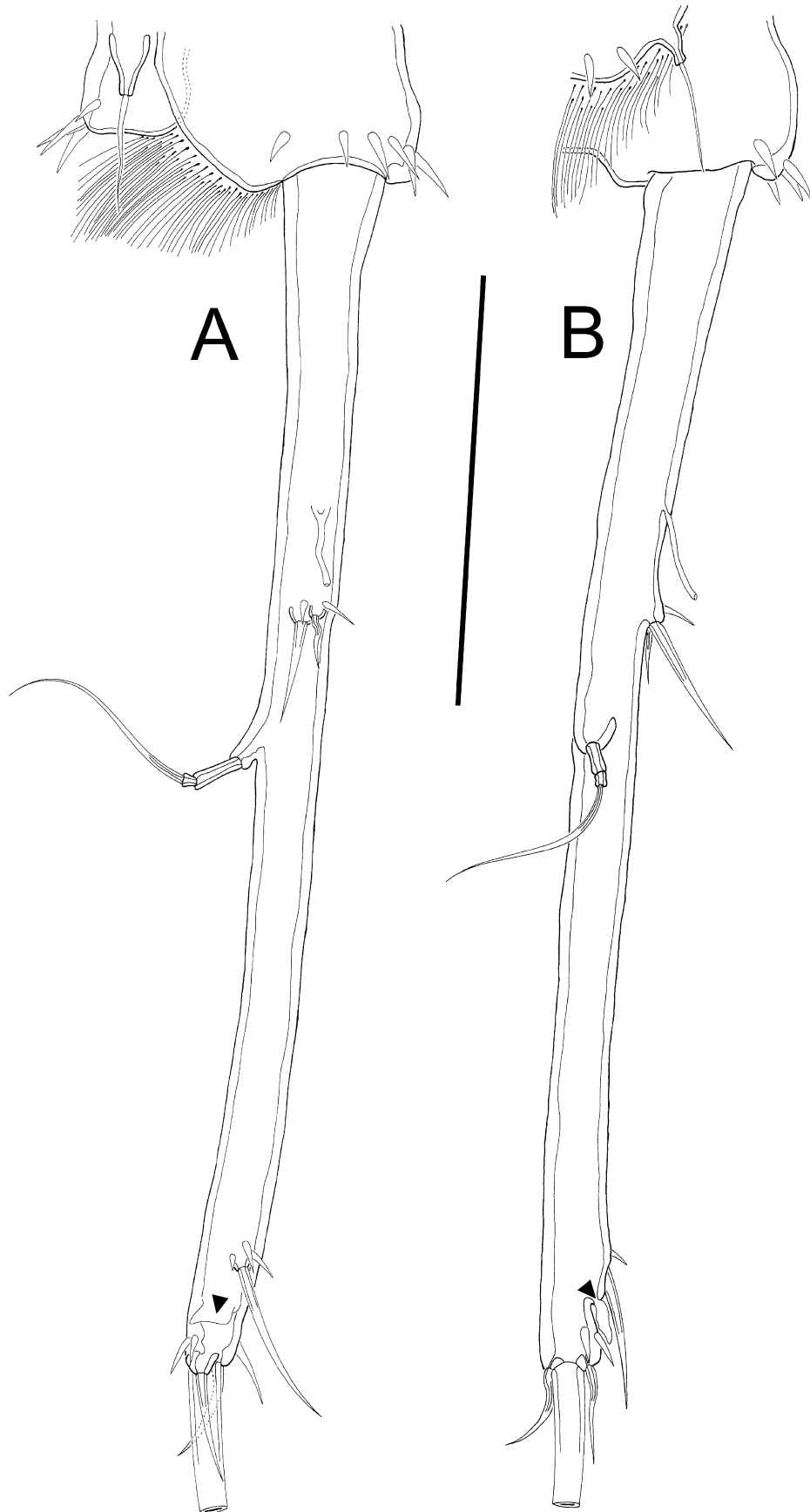
P3 (Fig. 13C). Basis and exp as in female. Enp 3-segmented, first segment short, without setation. Second segment long, terminal pointed apophysis surpassing length of third segment. Enp-3 with 2 terminal long biplumose setae.

P5 (Fig. 14A) similar to female, but smaller. Endopodal lobe only weakly developed, with 1 bare seta, 1 bipinnate seta, and 1 tube pore. Benp additionally has tube pore and spinules close to setophore with 1 bare outer seta. Exp approximately 8 times longer than wide, with 1 lateral and 3 terminal bipinnate setae.

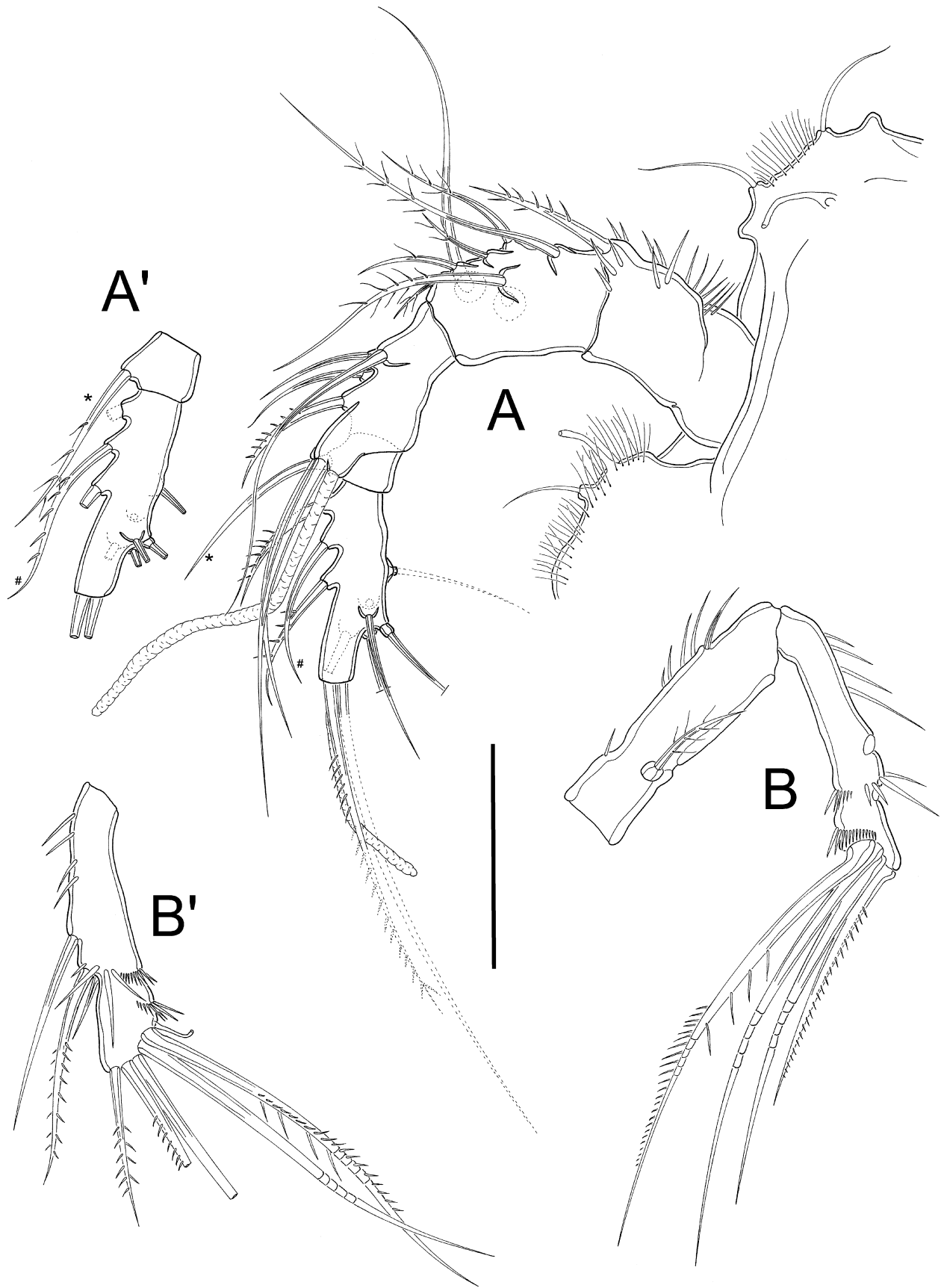
**Remarks.** Apart from a minor variability with respect to the shape of female antennular setae, no intraspecific variability was detected.



**FIGURE 8.** *Cletodes meyerorum* sp. nov., female. A. Habitus lateral, arrows showing cuticular spikes, B. Habitus dorsal. Scale bars: 100  $\mu$ m.

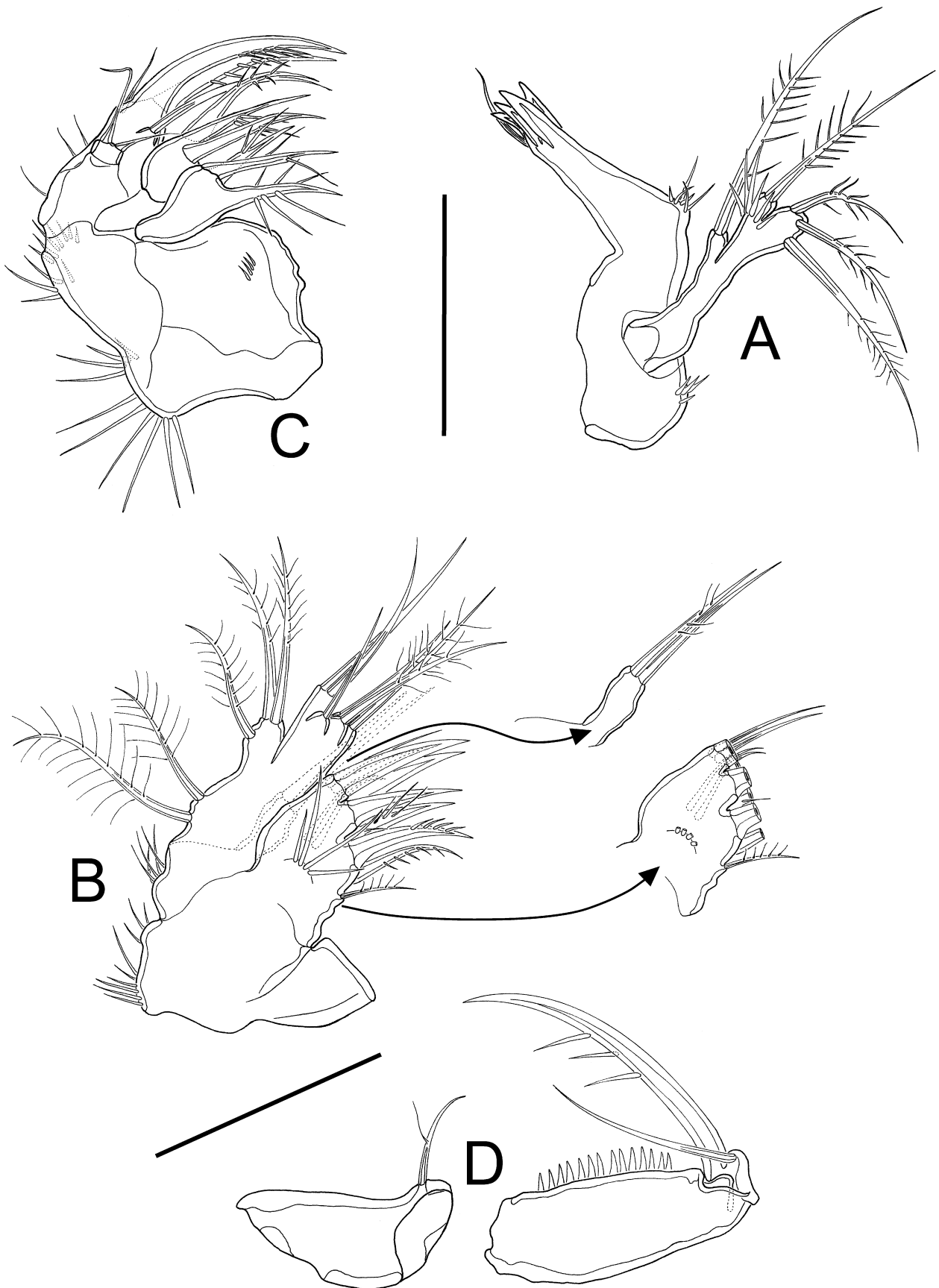


**FIGURE 9.** *Cletodes meyerorum* sp. nov., female. A. right FR, lateral view, B. same FR, dorsal view. Triangular arrows indicating hyaline foliaceous structure. Scale bar: 50 µm.

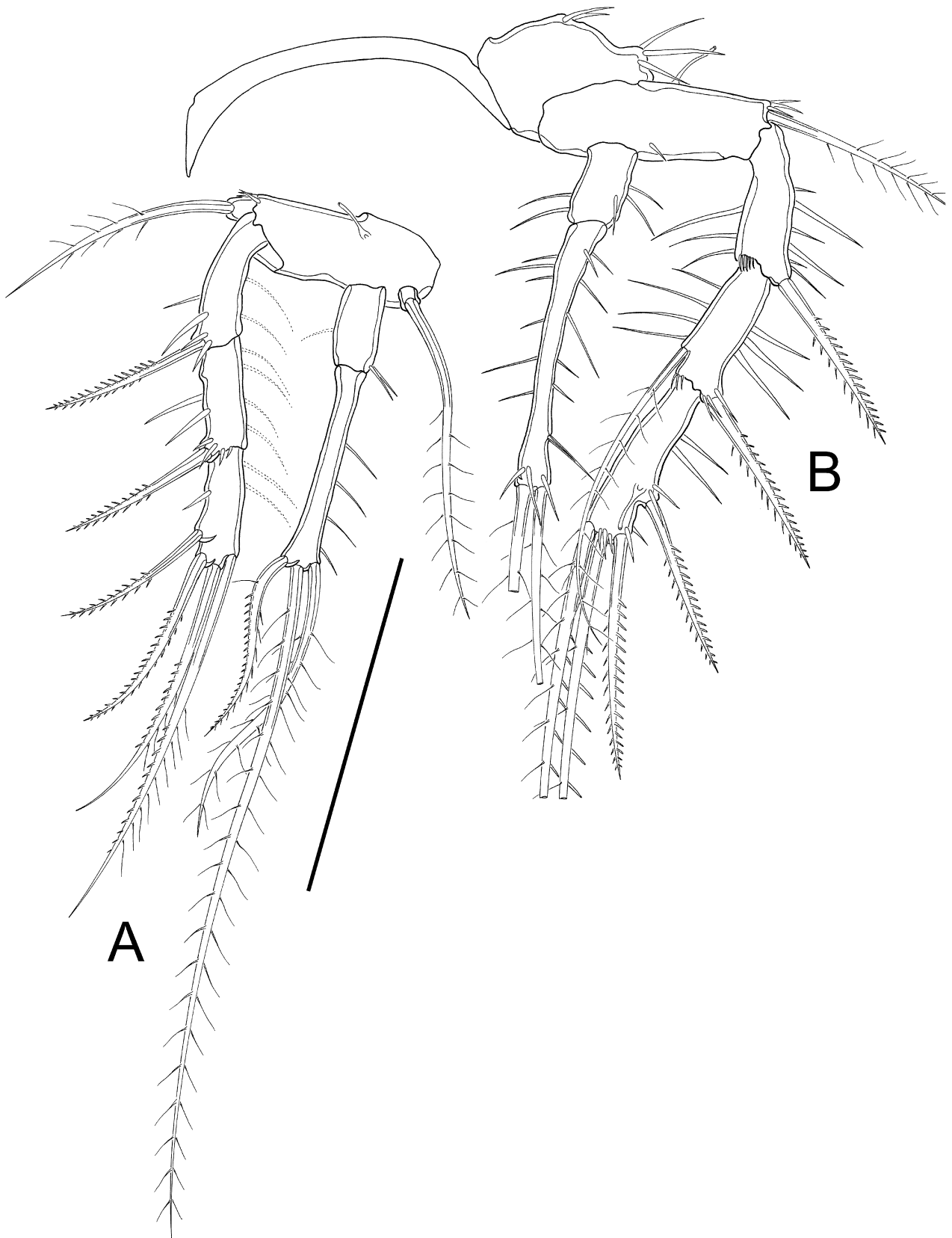


**FIGURE 10.** *Cletodes meyerorum* sp. nov., female. A. A1, A', last 2 antennular segments; \* and # showing homologue setae that are bare in A but unipinnate in A'. B. A2 with some broken elements, B' antennar end of a paratype showing complete setation. Scale bar: 25  $\mu$ m.

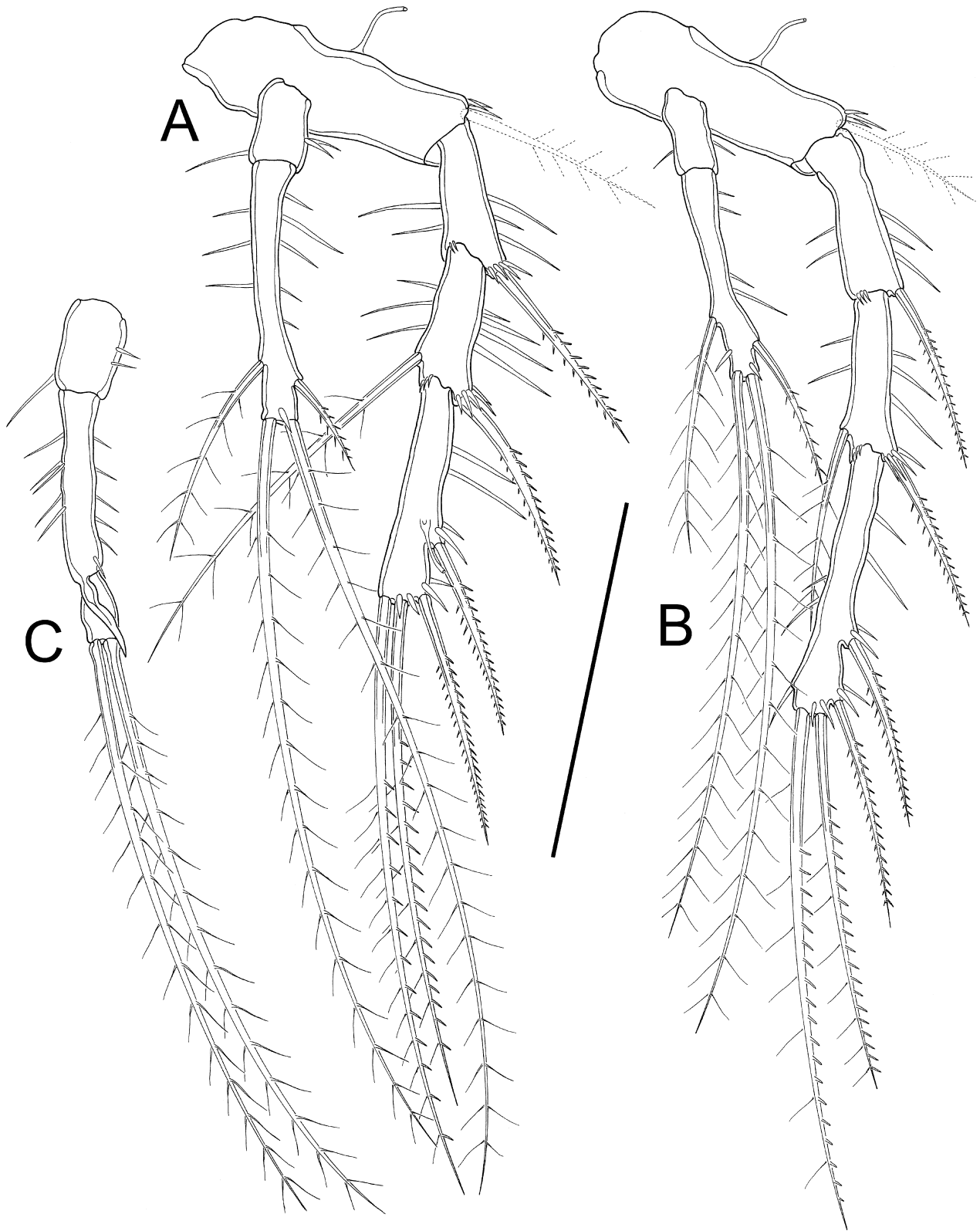




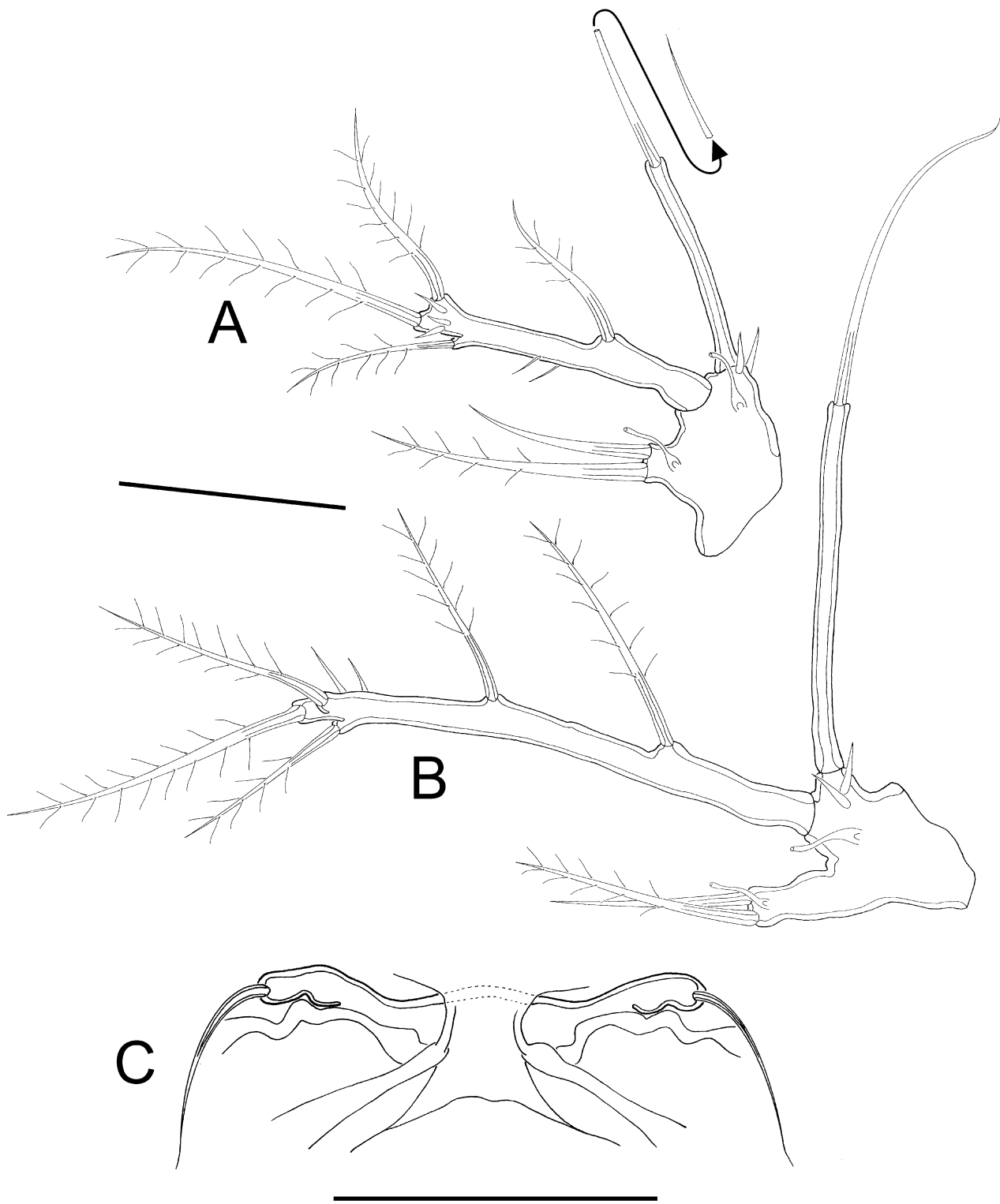
**FIGURE 11.** *Cletodes meyerorum* sp. nov., female. A. Md, B. Mxl, arrows indicate details of gnathopod base and coxa, C. Mx, D. Mxp, Syncoxa and basis broken. Scale bars: 25 μm.



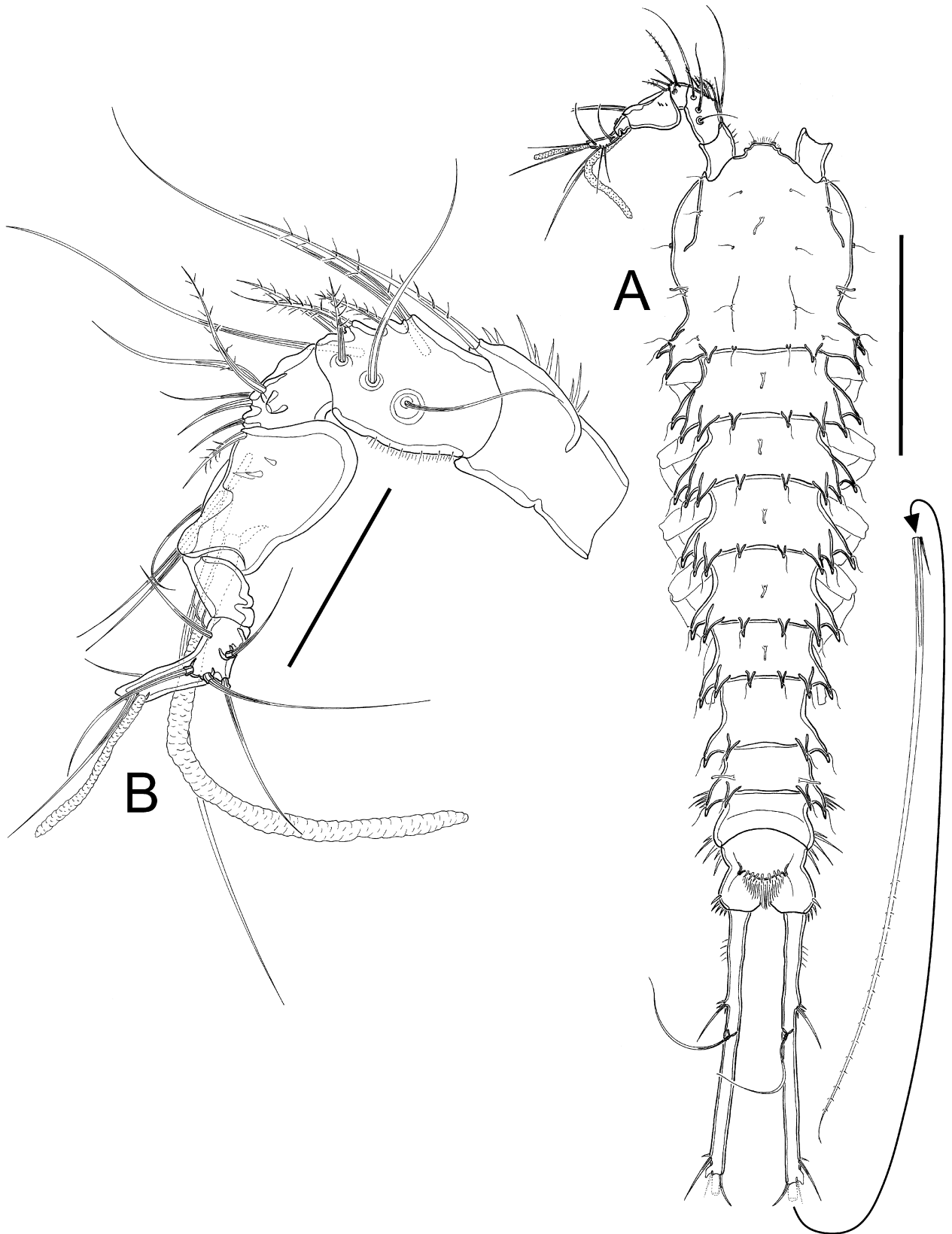
**FIGURE 12.** *Cletodes meyerorum* sp. nov., female. A. P1, B. P2. Scale bar: 50  $\mu$ m.



**FIGURE 13.** *Cletodes meyerorum* sp. nov. A. P3 female, B. P4 female, C. P3 enp male. Scale bar: 50  $\mu$ m.



**FIGURE 14.** *Cletodes meyerorum* sp. nov. A. P5 male, B. P4 female, C. Female genital field. Scale bars: 25  $\mu$ m.



**FIGURE 15.** *Cletodes meyerorum* sp. nov., male. A. Habitus dorsal, B. A1. Scale bars: A. 100  $\mu$ m, B. 50  $\mu$ m.

**TABLE 2.** Setation of the swimming legs in *Cletodes meyerorum* **sp. nov.**; Roman numerals referring to outer setae/spines.

	Exopod			Endopod	
	1	2	3	1	2
P1	I;0	I;0	II;2;0	0;0	1;2:0
P2	I;0	I;1	II;2;0	0;0	1;2;0
P3	I;0	I;1	II;2;0	0;0	1;2;1
P4	I;0	I;1	II;2;0	0;0	1;2;1

## Discussion

The taxon *Echinocletodes* has been subject to repeated shifts within Harpacticoida. Originally placed in Cletodidae by Lang (1936a), that author subsequently transferred the genus to Ancorabolidae Sars, 1909 (Lang 1944, 1948), as it met the then current family diagnosis, and exhibited some of its derived characters such as a maximum of 5 antennular segments, absence of an A2 exp, and transverse elongation of P2–P4 bases. Also, because of the transverse elongation of its P1 basis, Lang (1948) consigned *Echinocletodes* to the subfamily Ancorabolinae and presumed a closer relationship of *Echinocletodes* with *Ancorabolutus* Norman, 1903 and *Arthroposyllus* Sars, 1909. Dinet (1974) described *Echinocletodes bodini* and *E. walvisi* from the deep Angola Basin (SE Atlantic) in muddy sediment. Though claiming their membership to *Echinocletodes*, Dinet (1974) refrained from providing a detailed systematic discussion. In particular, he did not name or discuss the characters on which he based his assumption of a close systematic relationship, however, he did note that despite some similarities to *E. armatus*, the relationship between both Angolan species appeared to be closer (Dinet 1974). The phylogenetic affinity of *Echinocletodes* with Ancorabolidae has been queried subsequently (e.g. Conroy-Dalton 2003a, 2004; Conroy-Dalton & Huys 2000).

This discussion will focus on seven main topics, namely (A) designation of *E. voightae* **sp. nov.** as *Echinocletodes*, (B) designation of *C. meyerorum* **sp. nov.** as *Cletodes* (Cletodidae), (C) displacement of *Echinocletodes bodini* and *E. walvisi* to *Cletodes*, (D) paraphyly of “Ancorabolidae” and possible affinities with *Echinocletodes*, (E) monophyly of Ancorabolinae and possible relationships with *Echinocletodes*, (F) systematic status of Laophontodinae and possible relationships with *Echinocletodes*, and (G) a summary of conclusions.

**Designation of *E. voightae* sp. nov. as *Echinocletodes*.** Comparison of the specimens collected from the Gorda Ridge with T. Scott’s (1903) description of *Echinocletodes armatus* revealed striking similarities. The following seven synapomorphies can be noted, if compared with the remaining Ancorabolidae, supposing them to be the closest relatives (Lang 1948):

Apomorphy 1: body comparatively large. The average body length of Harpacticoida lies between 0.7 and 0.8 mm (Lang 1948). With a body length between 3.0 mm (Sars 1903) and 5.0 mm (Hesse 1867), *Sunaristes paguri* Hesse, 1867 (Canuellidae Lang, 1944) is probably the largest harpacticoid species, and only a few other species surpass a size of 2.0 mm (e.g. *Balaenophilus unisetus* Aurivillius, 1879; *Parathalestris jacksoni* [T. Scott, 1989]). Most Ancorabolidae fit the average harpacticoid body size; the largest known to date are members of the *Ancorabolutus*-group sensu Conroy-Dalton & Huys (2000), which together with *Arthuricornua* Conroy-Dalton, 2001, *Echinopsyllus* Sars, 1909 and *Pseudechinopsyllus* George, 2006 reach body lengths of 0.72–0.9 mm, while most remaining Ancorabolidae range between 0.34 and 0.65 mm (cf. Conroy-Dalton & Huys 2000; Conroy-Dalton 2001, 2003a; George 2006a, b, c; Wandeness *et al.* 2009; Gheerardyn & George 2010; Gheerardyn & Lee 2012). Thus, with a body length between 1.5 and 1.8 mm, *Echinocletodes* is a relative “giant” not only within Ancorabolidae but also within Harpacticoida. The large body size is thus regarded as an apomorphy for the genus.

Apomorphy 2: body densely covered with fine, bristle-like spinules. Both *E. armatus* and *E. voightae* are characterized by a dense covering of very fine, bristle-like spinules on their body somites. A similar state has been observed in Argestinae Por, 1986 (George 2008, 2011) and should be considered as convergent development, since *Echinocletodes* lacks any remaining argestin apomorphies (cf. George 2011). Small bristle-like spinules are also present on certain appendages of Ancorabolinae, namely the antennules and swimming legs (part.) of several species of the *Ancorabolutus*-group, as well as of *Arthuricornua* and *Echinopsyllus*. Nevertheless, none of these

latter taxa (or any other Ancorabolidae) show such a dense coverage on the body somites, which is therefore considered as apomorphic for *Echinocletodes*.

Apomorphy 3: body somites with triangular, thorn-like cuticular spikes. The development of cuticular processes is common and widely distributed, particularly among Ancorabolidae. They are extremely variable in shape and size, but several consistencies have allowed, for instance, the establishment of the *Ancorabolus*-group (cf. Conroy-Dalton & Huys 2000) and the pooling of species into the monophyla *Ceratonotus* (e.g. George & Schminke 1998; Conroy-Dalton 2001; George 2006a) and *Echinopsyllus* (Wandeness *et al.* 2009). The relatively small and thorn-like cuticular spikes of *Echinocletodes* (Fig. 1C), however, are unique in Ancorabolidae and are considered to be derived characters. Although *Cletodes meyerorum* **sp. nov.** has cuticular spikes which are similar to those of *Echinocletodes*, being cuspidate with a lateral sensillum (Fig. 8A), it lacks all remaining apomorphies of *Echinocletodes* and this similarity is consequently interpreted as convergent development.

Character 4: A1 second segment with large, posteriorly-directed seta arising from a pedestal. No Ancorabolidae except *Echinocletodes* bears a similar seta in this position, nor exhibits such a pronounced pedestal. Such seta is admittedly present – and recognized as apomorphic – in the argestid genus *Mesocletodes* Sars, 1909 (Menzel & George 2009). Nonetheless, the designation of *Echinocletodes* as *Mesocletodes* is not justified, owing to the lack of other apomorphies of that genus (cf. Menzel & George 2009). The existence of this character in both taxa must be instead interpreted as convergence and its presence in *Echinocletodes* is regarded as apomorphic.

Apomorphy 5: Mx enp represented by 1 seta. In Ancorabolidae, the maxillar enp is either present or absent, these two conditions being distributed relatively heterogeneously between the species. If a maxillar enp is present, it bears 2 setae (as, for example, in most species of the *Ancorabolus*-group, plus in *Arthuricornua anendopodia* Conroy-Dalton, 2001, *Ceratonotus tauroides* George, 2006, *Dendropsyllus thomasi* Conroy-Dalton, 2003, *Dorsiceratus dinah* George & Plum, 2009, *Polyascophorus martinezi* George, 1998), but they are also maintained even when the enp itself is lost (as, for example, in *Ancorabolus hendrickxi* Gómez & Conroy-Dalton, 2002, *Breviconia australis* [George, 1998], *Ceratonotus pectinatus* Sars, 1909, *Dendropsyllus antarcticus* [George & Schminke, 1998], *Dorsiceratus wilhelminae* George & Plum, 2009, *Touphapleura schminkei* [George, 1998]). The retention of only one seta in *Echinocletodes* is therefore an even more derived condition. This unique condition is interpreted as an apomorphy for the genus.

Apomorphy 6: P2–P4 enp-2 substantially elongated, at least 6 times longer than enp-1. Several harpacticoid families include taxa with a tendency to have diminutive P2–P4 enps. For instance, a 2-segmented P2–P4 enp is widespread in Argestidae, Ancorabolidae, and Cletodidae. Further modification may constitute a narrowing of both endopodal segments, accompanied by a reduced enp-1, and sometimes combined with an elongated enp-2. In Ancorabolidae, the enp-2 is at most up to 3 times longer than enp-1, even in rather basal ancorabolid representatives (e.g. *Laophontodes* T. Scott, 1894). In contrast, both *E. armatus* and *E. voightae* share a remarkable elongation of their P2–P4 enps-2, being at least 6 times longer than the respective enp-1. That elongation has to be regarded as an apomorphic character.

Apomorphy 7: Male P3 enp with peculiar apophysis. Like Ancorabolidae (and many more harpacticoid families), *Echinocletodes* bears an apophysis on male P3 enp. However, it is commonly curved, becoming a bow-like shape pointing backwards or slightly outwards, whilst in *Echinocletodes* the apophysis is somewhat curled inwards (*E. voightae*; Fig. 7B), or even exhibiting a double bend, turning the tip outwards again (*E. armatus*). This extreme curvature, combined with an increased size, is considered to be apomorphic for *Echinocletodes*.

As well as sharing these 7 apomorphies, *E. voightae* and *E. armatus* both show a preference for a submerged wood habitat, a relatively rare ecological niche (e.g. Lang 1948; Hicks & Coull 1983; Huys & Boxshall 1991). Hicks (1988) was the first author to discuss the potential role of harpacticoid species associated with submerged wood when reviewing Donsiellinae Lang, 1944, (Pseudotachidiidae Lang, 1936). This author thought that some donsiellin species (e.g. *Donsiella limnoriae* Stephenson, 1936) were associated with wood-boring organisms such as *Limnoria* Leach, 1814 (Peracarida, Isopoda), whilst others simply inhabited formerly bored wood (even when previously bored in shallower waters) (e.g. *Xylora bathyalis* Hicks, 1988) (Hicks 1988). *E. armatus* and *E. voightae* represent a second harpacticoid group found in submerged wood blocks. *E. armatus* was found alongside the perforations made by the mollusc *Xylophaga dorsalis* (Turton, 1819) (cf. T. Scott 1903), whilst *E. voightae* was found in wood representing the type locality of another wood-boring bivalve, namely *Xylophaga zierenbergi* Voight, 2007 (cf. Voight 2007). However, neither from T. Scott's (1903) description of *E. armatus* nor from an examination of the sample material containing *E. voightae* can any hint of symbiosis be noted; like the donsiellin

*Xylora bathyalis*, both species appear to inhabit previously bored spaces. This may be further supported by the morphological appearance of both *Echinocletodes* species, neither presenting morphological adaptations for such an association [e.g. the P1 in Donsiellinae (Hicks 1988)]. *Echinocletodes* does not share apomorphies with Donsiellinae or Pseudotachidiidae, as discussed by Willen (2000). Compared with the remaining Ancorabolidae, the mode of life of both *Echinocletodes armatus* and *E. voightae* is unique.

Since the derived characters 1–7 listed above are shared only by *E. armatus* and *E. voightae* their synapomorphic state is clear and justifies their placement in the monophylum *Echinocletodes*. It is additional apomorphic differences that require the creation of the new species, *E. voightae*, from the Gorda Ridge:

Apomorphy 8: *E. voightae* presents a 1-segmented P1 enp (it is 2-segmented in *E. armatus*). Following the principle of oligomerisation in copepod evolution (Huys & Boxshall 1991), and based on the fact that the basal endopodal segmentation consists of 3 segments, a 1-segmented P1 enp in *Echinocletodes voightae* is regarded as secondary reduction and hence as autapomorphic for that species, whereas the 2-segmented P1 enp of *E. armatus* is a relatively plesiomorphic condition.

Apomorphy 9: *E. armatus* male P3 enp has an apophysis that is bent twice, the tip pointing outward, whilst in *E. voightae* it is bent only once, with its tip pointing backward. Thus, whilst both *Echinocletodes* species show a derived apophysis in the male P3 enp (Character 7) it is further derived in *E. armatus*, with an additional bend at the tip. Thus, the apophysis of *E. armatus* has a more complex structure than that of *E. voightae*, constituting an autapomorphy.

**Designation of *C. meyerorum* as *Cletodes* (Cletodidae).** When Por (1986) established Cletodidae sensu stricto, he provided a family diagnosis but no phylogenetic characterization. A list of nine potential apomorphies was later presented by Gee (1998), who made the first phylogenetic analysis of Cletodidae. However, a careful examination of these characters shows that some encompass several features, whilst others are in fact widespread across the Harpacticoida. For instance Gee (1998) lists the rostrum fused to the cphth as an apomorphic character, however, it is relatively common within Harpacticoida, and several Ancorabolidae and Cletodidae show the same derived condition. Similarly, the 4–5-segmented female A1 is also an apomorphy of the Ancorabolidae, and is therefore considered at present to be of minor phylogenetic relevance. Several other characters recognised by Gee (1998) as apomorphic for Cletodidae are equally common in the Ancorabolidae.

It is outside the scope of this present contribution to characterize a monophylum Cletodidae, this would require a thorough examination and re-evaluation of all so far described taxa. It is sufficient here to justify the designation of *Cletodes meyerorum* based on the currently accepted genus apomorphies. The new species displays all Cletodidae characters listed by Gee (1998) and all *Cletodes* apomorphies as recognized by Gee (2001). Specifically, it has a small A2 exp, 1-segmented, with 1 seta (plesiomorphy: A2 exp 1-segmented, with at least 2 setae), and elongated segments in P2–P4 exps (plesiomorphy: exopodal segments not elongate).

Gee (2001) listed a third apomorphy, the complete loss of setae on male P5 benp, but noted that at least two species differ from this state (*Cletodes latirostris* Drzycimski, 1967 [1 seta, cf. Drzycimski 1967] and *C. macrura* Fiers, 1991 [2 setae, cf. Fiers 1991]). This is also true for *C. meyerorum* **sp. nov.**, whose male (like *C. macrura*) bears 2 setae on P5 benp. Therefore, this third proposed apomorphy must be rejected. Nonetheless, the assignment of the newly described species to *Cletodes* appears to be sufficiently justified by the two synapomorphies mentioned. In the context of the discussion presented here on *Echinocletodes*, these latter characters become of interest with regards to the comparison of *C. meyerorum* with the SE Atlantic *Echinocletodes* species, revealing a close relationship between the three taxa (see below).

Within *Cletodes*, the new species seems to be close to *C. latirostris*, resembling it in general body shape, shape of the swimming legs, and shape and ornamentation of the FR. However, there are also clear differences: the cuticular spikes are much more pronounced in *C. meyerorum* than in *C. latirostris*; the A2 exp is small, 1-segmented and equipped with 1 seta in *C. meyerorum*, but completely reduced and represented only by 1 seta in *C. latirostris*; the P2 enp-2 lacks an inner seta in *C. meyerorum* which is present in *C. latirostris*; the terminal setae on the male P3 enp-3 are twice as long as the enp itself in *C. meyerorum*, while reaching barely the length of the P3 enp in *C. latirostris*. *C. macrura* and *C. yotabis* Por, 1967 may also be related to *C. meyerorum*, however, of the relationships within *Cletodes* is still awaiting a thorough phylogenetic analysis.

**Transferal of *Echinocletodes bodini* and *E. walvisi* to *Cletodes*.** When assigning the SE Atlantic species *Echinocletodes bodini* and *E. walvisi* to the genus *Echinocletodes*, Dinet (1974) stated their indisputable affiliation to the type (and then only) species *E. armatus*. Yet, he also noted numerous differences between these SE Atlantic



species and *E. armatus*, differences these were: the relative lengths of the antennular segments, the shape, size, and ornamentation of female P5, and the setation of P2–P4 exp-2. The SE Atlantic species are very similar to each other, however, differing only in the FR length, and ornamentation of P4 enp and P5 benp (Dinet 1974).

Considering synapomorphies 1–7 above of *E. armatus* and *E. voightae*, none are shared with *E. bodini* and *E. walvisi*. Therefore, a close relationship between the first and the latter must be refuted: both *E. bodini* and *E. walvisi* are herewith excluded from the genus *Echinocletodes*. Instead, they show a strong similarity with *Cletodes meyerorum*. Like this latter species, both *E. bodini* and *E. walvisi* share the cletodid characters listed by Gee (1998), and they also exhibit one apomorphy of *Cletodes*, the elongated P2–P4 exps. See discussion below regarding other *Cletodes* apomorphies. The morphological features *E. bodini* and *E. walvisi* share with *Cletodes meyerorum* are:

- a) FR elongate, slender;
- b) Furcal seta VII inserting dorsally in the middle of the FR;
- c) a) Female A1 5-segmented; aes on third segment; fourth segment smallest, approximately square;
- d) P1 not prehensile, exp 3-segmented, without inner setae; enp 2-segmented, enp-2 with 1 outer and 2 apical setae;
- c) P3 exp 3-segmented, exp-2 with inner seta; enp 2-segmented, enp-2 with 1 outer, 1 inner, and 2 apical setae;
- f) Female P5 with small benp and long distinct exp, the latter bearing 5 setae.

A detailed phylogenetic evaluation of features a–f would go beyond the scope of the present contribution. However, it can be stated that some may present derived conditions, such as the elongate, slender FR (character a), and the long and distinct female P5 exp (character f).

The here recognized high level of similarity between *Cletodes meyerorum* and *E. bodini* and *E. walvisi* might lead, in the first instance, to the assumption that this new material in fact represented a new record of one of the known species, particularly since not a single representative of either of Dinet's (1974) species was found in the material collected during DIVA 1. However, a detailed morphological comparison reveals that *C. meyerorum* exhibits differences that justify its treatment as a distinct species. Table 3 lists the eight morphological differences observed between the three species. In our opinion they can be interpreted as robust differences that support the three species.

**TABLE 3.** List of differences between *Cletodes meyerorum* sp. nov., *C. bodini* comb. nov. and *C. walvisi* comb. nov.

No.	Character	<i>Cletodes meyerorum</i>	<i>Echinocletodes bodini</i>	<i>Echinocletodes walvisi</i>
1	FR: Longer than broad	11.6x	8.3x	9.6x
2	FR: Position of seta III	Subapically	Subapically	Laterally
3	A2 exp	1-segmented, 1 seta	Absent	Absent
4	Mx enp	Present, with 2 setae	Absent, no seta	?
5	P2 enp-2 setation	0:2:1	0:2:0	0:2:0
6	P4 enp-2 setation	1:2:1	1:2:1	0:2:1
7	P5 benp	2 x longer than broad, clearly exceeding the borderline benp-exp	Small, barely exceeding the borderline benp-exp	Small, barely exceeding the borderline benp-exp
8	Body with cuticular spikes	yes	No	?

One derived character (Tab. 3, no. 3) does confuse the discussions regarding placement of *E. bodini* and *E. walvisi*, that being a small but clearly discernible A2 exp carrying 1 seta as seen in *Cletodes meyerorum* (Fig. 10B). This feature forms part of the autapomorphies of *Cletodes* (Gee 2001), but was not observed in *E. bodini* or *E. walvisi* (Dinet 1974), convincing the author of both species' affiliation to Ancorabolidae. However, such small structures, may be easily overlooked, especially if their presence is not expected (as is the case of an A2 exp in Ancorabolidae). Unfortunately, it was not possible for the current authors to confirm Dinet's (1974) original observations since the type material for both *E. bodini* and *E. walvisi* was not available for examination. Nonetheless, presuming Dinet's (1974) observations to be correct, and therefore that the A2 exps are absent in both

*E. bodini* and *E. walvisi*, this derived state may naturally occur in Cletodidae as in other taxa, and their strong morphological similarity with *Cletodes meyerorum* points to a close relationship between these three species. Thus, combined with the clear affiliation of *C. meyerorum* to *Cletodes*, it is reasonable to move *E. bodini* and *E. walvisi* into *Cletodes*, renaming them *Cletodes bodini* (Dinet, 1974) **comb. nov.** and *Cletodes walvisi* (Dinet, 1974) **comb. nov.**, respectively.

**Paraphyly of “Ancorabolidae” and possible affinities with *Echinocletodes*.** Currently, Ancorabolidae comprises 75 species in 23 genera and 2 subfamilies (Table 4), with 45 species and 15 genera in Ancorabolinae and 30 species and 8 genera in Laophontodinae. As summarized by George (2006c), a monophylum Ancorabolidae can be supported by the following three apomorphies: (i) female A1 at most 5-segmented (plesiomorphy: female A1 at least 6-segmented); (ii) bases of P2–P4 transversely elongate (plesiomorphy: bases not elongate); (iii) P5 exp elongate (plesiomorphy: P5 exp not elongate). These derived features (among other plesiomorphic characters) were defined by Lang (1948) and remain generally accepted without advanced critical revision (see George 2006c). A fourth apomorphy, previously overlooked, can also be recognized: (iv) Coxa strongly shortened (plesiomorphy: coxa rectangular, broader than long). However, a careful examination reveals the ambiguous quality of all four characters for phylogenetic analysis. The main difficulty is that none are unique to Ancorabolidae. The reduction of the female A1 to 5-segments or less is, for instance, widely distributed across the harpacticoid families, and never exceeds 5 segments in six families, namely Adenopleurellidae Huys, 1990 (4 segments), Ancorabolidae (3–5 segments), Canuellidae Lang, 1944 (4–5 segments), Cletodidae (4–5 segments), Cristacoxidae Huys, 1990 (4 segments), and Laophontopsidae Huys & Willems, 1989 (4 segments). Thus, the presence of a 4-segmented female A1 in *Echinocletodes* does not necessarily support its membership in Ancorabolidae (Although T. Scott (1903) described a 5-segmented A1 for *Echinocletodes armatus*, this was erroneous, as demonstrated below).

The transverse elongation of the P2–P4 bases has been assigned as an apomorphic character of Ancorabolidae since Sars’ (1909) erection of the family. However, comparison of ancorabolid taxa reveals a remarkable gradient in basis elongation not only for P2–P4 but also for P1 and it is therefore discussed here briefly. A possible evolution of the coxa and basis of P1–P4 are shown schematically in Figure 16. According to several authors (Lang 1948; Huys & Boxshall 1991; Willen 2000; Seifried 2003), the coxae and bases of P1–P4 in basal (and even the majority of recent) Harpacticoida are of more or less the same size and shape (Fig. 16A). During the course of harpacticoid evolution, however, both basis and coxa of P1–P4 have developed alterations, such as growth, diminution, or a lengthways respectively transverse elongation in some taxa. The bases may be simply shortened longitudinally, the width unchanged and being connected with the coxa along the whole proximal margin; the basis is about half the length of the coxa, and such development is often combined with an outward displacement of the enp (Fig. 16B). This type of swimming leg is observable in, for example, Argestidae Por, 1986, Cletodidae (part.) and Paramesochridae Lang, 1944.

There is, however, (at least) a second type of propodal alteration, characterized by a transverse elongation of the basis accompanied by (a) reduction of the enp (of no further relevance here) and (b) shortening of the coxa (Figs. 16C–E), resulting in a reduced coxa-basis borderline. The cletodid genus *Cletodes*, as well as *Echinocletodes* and some Ancorabolidae (*Arthropysyllus* Sars, 1909, *Calypsophontodes* Gheerardyn & Lee, 2012, *Patagoniaella vervoorti* Pallares, 1968, *Tapholaophontodes laurenceae* Bodiou & Colomines, 1988) represent a rather moderate state for this propodal modification (Fig. 16C): The basis is at most twice as long as the coxal width at the coxal-basal borderline. Similar (but convergent) conditions are also observed in some Idyanthidae (e.g. *Aspinothorax insolentis* Moura & Martínez Arbizu, 2003, *Meteorina magnifica* George, 2004, *Styracothorax gladiator* Huys, 1993). Although an elongation of the basis can be clearly discerned in Cletodidae and the above listed Ancorabolidae, the corresponding swimming legs do not protude laterally. A more advanced state (Fig. 16D) shows the basis approximately 2.5–3.5 times broader than the coxa at the borderline and is seen in most Laophontodinae (*Algeniella* Cottarelli & Baldari, 1987, *Laophontodes* T. Scott, 1894, *Lobopleura* Conroy-Dalton, 2004, *Paralaophontodes* Lang, 1965, *Probosciphontodes* Fiers, 1988) and in *Ancorabolina* (part.). Such pronounced transverse elongation of the basis leads to a clear lateral projection of the respective swimming legs, producing the so-called “spider-like” habitus that is regarded as typical for Ancorabolidae (Huys & Boxshall 1991, p. 409). The most extremely form of this propodal modification is shown in Fig. 16E. Here, the basis is slender as well as being markedly elongated, reaching 4–5 or more times the coxal width at the borderline. This latter pronounced elongation is observable in all Ancorabolinae. It is therefore concluded that the statement “bases of swimming legs transversely elongate” is too vague to be useful as a phylogenetically informative character. Too

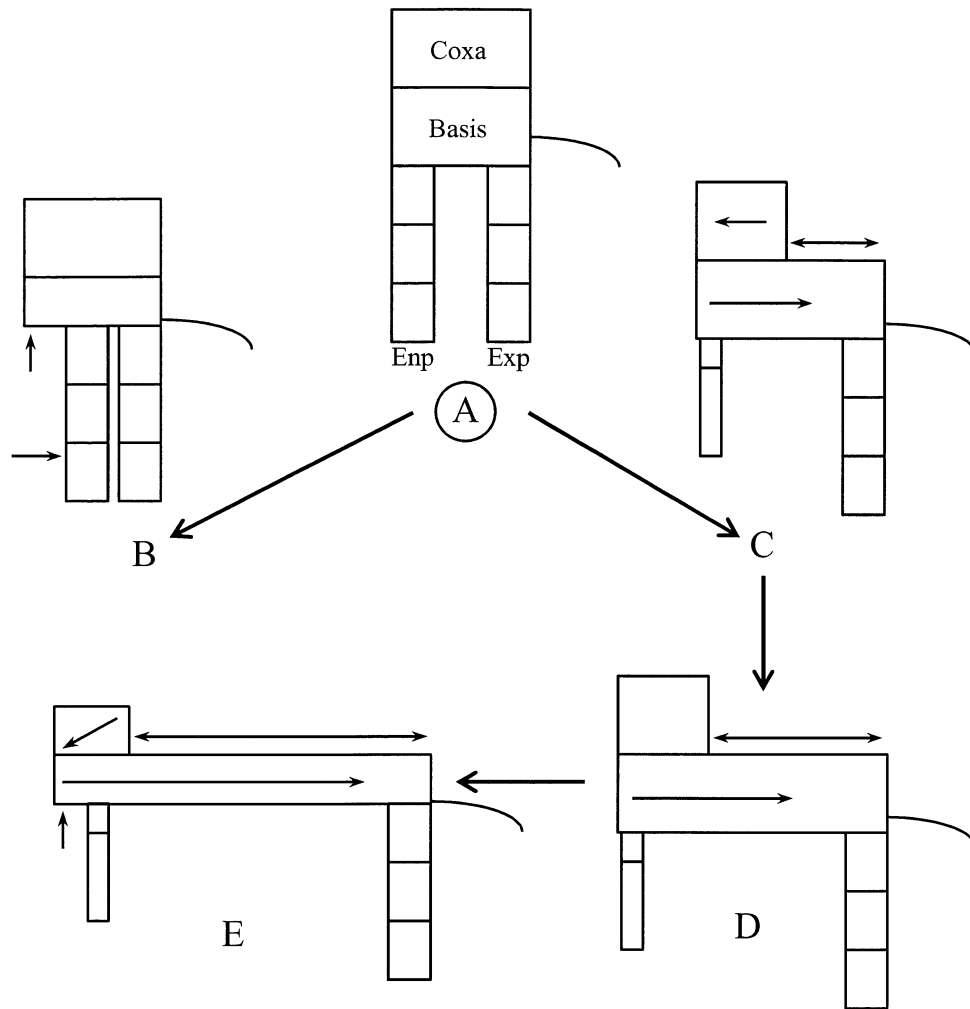
**TABLE 4.** Species list of Ancorabolidae, as valid before the current revision and, therefore, including *Echinocletodes* (grey-marked rows). Both *Cletodes bodini* **comb. nov.** and *C. walvisi* **comb. nov.** are listed in *Echinocletodes*, whilst *E. voightae* **sp. nov.** is not listed.

No.	Taxon	Taxonomic references
	Ancorabolidae Sars, 1909 (75 species)	Sars, 1909; Lang, 1948
I.	Ancorabolinae Sars, 1909 (45 species)	Lang, 1944, 1948
1.	<i>Ancorabolina anaximenesi</i> Gheerardyn & George, 2010	Gheerardyn & George, 2010
2.	<i>Ancorabolina belgicae</i> Gheerardyn & George, 2010	Gheerardyn & George, 2010
3.	<i>Ancorabolina cavernicola</i> George & Tiltack, 2009	George & Tiltack, 2009
4.	<i>Ancorabolina chimaera</i> (type species) George, 2006	George, 2006c; Gheerardyn & George, 2010
5.	<i>Ancorabolina divasecunda</i> Gheerardyn & George, 2010	Gheerardyn & George, 2010
6.	<i>Ancorabolina galeata</i> Gheerardyn & George, 2010	Gheerardyn & George, 2010
7.	<i>Echinocletodes armatus</i> T. Scott, 1903 (type species by designation)	T. Scott, 1903
8.	<i>Echinocletodes bodini</i> Dinét, 1974 (displaced to <i>Cletodes</i> [Cletodidae])	Dinét, 1974; present contribution
9.	<i>Echinocletodes walvisi</i> Dinét, 1974 (displaced to <i>Cletodes</i> [Cletodidae])	Dinét, 1974; present contribution
Ia.	<i>Ancorabolus</i> -lineage (11 species)	Conroy-Dalton & Huys, 2000
10.	<i>Ancorabolus chironi</i> Schulz & George, 2010	Schulz & George, 2010
11.	<i>Ancorabolus confusus</i> Conroy-Dalton & Huys, 2000	Conroy-Dalton & Huys, 2000
12.	<i>Ancorabolus hendrickxi</i> Gómez & Conroy-Dalton, 2002	Gómez & Conroy-Dalton, 2002
13.	<i>Ancorabolus ilvae</i> (species inquirenda) George, 2001	George, 2001
14.	<i>Ancorabolus inermis</i> Conroy-Dalton & Huys, 2000	Conroy-Dalton & Huys, 2000
15.	<i>Ancorabolus mirabilis</i> Norman, 1903 (type species)	Norman, 1903; Conroy-Dalton & Huys, 2000
16.	<i>Arthropysyllus serratus</i> Sars, 1909	Sars, 1909; Conroy-Dalton & Huys, 2000
17.	<i>Breviconia australis</i> (George, 1998) (type species)	George, 1998a; Conroy-Dalton & Huys, 2000
18.	<i>Breviconia echinata</i> (Brady, 1918)	Brady, 1918; Conroy-Dalton & Huys, 2000
19.	<i>Juxtaramia polaris</i> Conroy-Dalton & Huys, 2000	Conroy-Dalton & Huys, 2000
20.	<i>Uptionyx verenae</i> Conroy-Dalton & Huys, 2000	Conroy-Dalton & Huys, 2000
Ib.	<i>Ceratonotus</i> -group (25 species)	Conroy-Dalton & Huys, 2000
21.	<i>Arthuricornua anendopodia</i> Conroy-Dalton, 2001	Conroy-Dalton, 2001
22.	<i>Ceratonotus coineaui</i> Soyer, 1964	Soyer, 1964
23.	<i>Ceratonotus concavus</i> Conroy-Dalton, 2003	Conroy-Dalton, 2003b
24.	<i>Ceratonotus pectinatus</i> Sars, 1909 (type species)	Sars, 1909; Conroy-Dalton, 2003b
25.	<i>Ceratonotus steiningeri</i> George, 2006	George, 2006a
26.	<i>Ceratonotus tauroides</i> George, 2006	George, 2006a
27.	<i>Ceratonotus thistlei</i> Conroy-Dalton, 2003	Conroy-Dalton, 2003b
28.	<i>Ceratonotus vareschii</i> George, 2006	George, 2006a
29.	<i>Dendropsyllus antarcticus</i> (George & Schminke, 1998)	George & Schminke, 1998; Conroy-Dalton, 2003b
30.	<i>Dendropsyllus magellanicus</i> (George & Schminke, 1998)	George & Schminke, 1998; Conroy-Dalton, 2003b; George, 2006a
31.	<i>Dendropsyllus thomasi</i> Conroy-Dalton, 2003 (type species)	Conroy-Dalton, 2003b
32.	<i>Dorsiceratus dinah</i> George & Plum, 2009	George & Plum, 2009
33.	<i>Dorsiceratus octocornis</i> Drzycimski, 1967 (type species)	Drzycimski, 1967; George, 2006b
34.	<i>Dorsiceratus triarticulatus</i> Coull, 1973	Coull, 1973; George, 2006b
35.	<i>Dorsiceratus ursulae</i> George, 2006	George, 2006b

.....continued on the next page

**TABLE 4.** (Continued)

No.	Taxon	Taxonomic references
36.	<i>Dorsiceratus wilhelminae</i> George & Plum, 2009	George & Plum, 2009
37.	<i>Echinopsyllus brasiliensis</i> Wandeness, George & Santos, 2009	Wandeness <i>et al.</i> , 2009
38.	<i>Echinopsyllus grohmannae</i> Wandeness, George & Santos, 2009	Wandeness <i>et al.</i> , 2009
39.	<i>Echinopsyllus nogueirae</i> Wandeness, George & Santos, 2009	Wandeness <i>et al.</i> , 2009
40.	<i>Echinopsyllus normani</i> Sars, 1909 (type species)	Sars, 1909; Conroy-Dalton, 2003a
41.	<i>Polyascopephorus gorbunovi</i> (Smirnov, 1946)	Smirnov, 1946; George, 1998b; Conroy-Dalton, 2001; George <i>et al.</i> , 2012
42.	<i>Polyascopephorus martinezi</i> George, 1998 (type species)	George, 1998b; George <i>et al.</i> , 2012
43.	<i>Polyascopephorus monoceratus</i> George, Wandeness & Santos, 2012	George <i>et al.</i> , 2012
44.	<i>Pseudechinopsyllus sindemarkae</i> George, 2006	George, 2006b
45.	<i>Touphapleura schminkei</i> (George, 1998)	George, 1998b; Conroy-Dalton, 2001
II.	Laophontodinae Lang, 1944 (30 species)	Lang, 1944, 1948
46.	<i>Algensiella boitanii</i> Cottarelli & Baldari, 1987	Cottarelli & Baldari, 1987
47.	<i>Calypsophontodes latissimus</i> (Brady, 1918) (species inquirenda)	Brady, 1918; Gheerardyn & Lee, 2012
48.	<i>Calypsophontodes macropodia</i> (Gee & Fleeger, 1986) (type species)	Gee & Fleeger, 1986; Gheerardyn & Lee, 2012
49.	<i>Laophontodes antarcticus</i> Brady, 1918	Brady, 1918
50.	<i>Laophontodes armatus</i> Lang, 1936	Lang, 1936b, 1965; Pallares, 1968
51.	<i>Laophontodes bicornis</i> A. Scott, 1896	A. Scott, 1896; Pesta, 1959; Griga, 1964
52.	<i>Laophontodes gracilipes</i> Lang, 1936	Lang, 1936c; Kornev & Chertoprud, 2008
53.	<i>Laophontodes hamatus</i> (Thomson, 1882)	Thomson, 1882; Gurney, 1927; Lang, 1934
54.	<i>Laophontodes hedgpathi</i> Lang, 1965	Lang, 1965
55.	<i>Laophontodes macclintocki</i> Schizas & Shirley, 1994	Schizas & Shirley, 1994
56.	<i>Laophontodes mourois</i> Arroyo, George, Benito & Maldonado, 2003	Arroyo <i>et al.</i> , 2003
57.	<i>Laophontodes multispinatus</i> Kornev & Chertoprud, 2008	Kornev & Chertoprud, 2008 (but see also Gheerardyn & Lee, 2012)
58.	<i>Laophontodes ornatus</i> Krishnaswamy, 1957	Krishnaswamy, 1957
59.	<i>Laophontodes propinquus</i> Brady, 1910	Brady, 1910
60.	<i>Laophontodes psammophilus</i> Soyer, 1975	Soyer, 1975
61.	<i>Laophontodes spongiosus</i> Schizas & Shirley, 1994	Schizas & Shirley, 1994
62.	<i>Laophontodes typicus</i> T. Scott, 1894	T. Scott, 1894, 1907; Sars, 1908; Chislenko, 1967
63.	<i>Laophontodes whitsoni</i> T. Scott, 1912	T. Scott, 1912; Pallares, 1975
64.	<i>Lobopleura ambiducti</i> Conroy-Dalton, 2004	Conroy-Dalton, 2004
65.	<i>Lobopleura expansa</i> (Sars, 1909)	Sars, 1909; Conroy-Dalton, 2004
66.	<i>Paralaophontodes echinatus</i> (Willey, 1930)	Willey, 1930; Fiers, 1986
67.	<i>Paralaophontodes elegans</i> Baldari & Cottarelli, 1986	Baldari & Cottarelli, 1986
68.	<i>Paralaophontodes exopoditus</i> Mielke, 1981	Mielke, 1981
69.	<i>Paralaophontodes robustus</i> (Bozic, 1964)	Bozic, 1964; Bodin, 1964
70.	<i>Patagoniaella vervoorti</i> Pallares, 1968	Pallares, 1968
71.	<i>Probosciphontodes ptenopostica</i> Fiers, 1988	Fiers, 1988; Conroy-Dalton, 2004
72.	<i>Probosciphontodes stellata</i> Fiers, 1988 (type species)	Fiers, 1988; Conroy-Dalton, 2004
73.	<i>Tapholaophontodes laurenceae</i> Bodiou & Colomines, 1988	Bodiou & Colomines, 1988
74.	<i>Tapholaophontodes remotus</i> Cottarelli & Baldari, 1987	Cottarelli & Baldari, 1987
75.	<i>Tapholaophontodes rollandi</i> Soyer, 1974	Soyer, 1975



**FIGURE 16.** Schematic illustration of presumed development of swimming legs in Harpacticoida (part.). A. Hypothetical ancestral state, B–E. Evolutionary modification of coxa and/or FR; see text for explanations.

many harpacticoids are convergent with this character, and it exhibits too much variation. It is, therefore, necessary to qualitatively enhance the definition of this character. For Ancorabolidae, the protrusion of the swimming legs may result from two different events which must be regarded as distinct and derived: (i) the development of a transversely elongate, slender basis, surpassing the coxal width at least by 2.5 times, and (ii) the shortening of the coxa itself. Since *Echinocletodes* shows only a moderate transverse elongation of P1–P4 bases, with swimming legs that do not protrude, as seen in other non-Ancorabolidae species (e.g. *Cletodes*, Idyanthidae [part.]), this character does not support its placement in Ancorabolidae.

The possession of an elongated P5 exp is of similar ambiguity. Not only is this character present in several non-ancorabolid species (for example, almost all *Cletodes* species, other Cletodidae, Idyanthidae, Tisbidae Stebbing, 1910 and Zosimeidae Seifried, 2003), but it is absent from some ancorabolid species (*Calypsophontodes latissimus* [Brady, 1918], *C. macropodia* [Gee & Fleeger, 1987]). It is therefore not a character unique to the Ancorabolidae, and its presence in *Echinocletodes* may reflect convergent development.

Even a strongly shortened coxa must be regarded as ambiguous: In combination with an elongation of the bases of at least P2–P4, the coxa often shows a decreased size, becoming small and approximately square or trapezoid in shape. It can be found in all Ancorabolidae (except *Patagoniaella*(?) and *Tapholaophontodes*), but is also seen in the cletodid taxon *Cletodes*, different species exhibiting different states, in Stenocopiinae Lang, 1944, and Argestidae (part.). In *Echinocletodes* the truncated coxae of the swimming legs resemble those found in most *Cletodes* species and in Laophontodinae (part.) rather than those of Ancorabolinae. However, since all Ancorabolidae share this derived feature, it could be interpreted as a family-wide deviation, perhaps shared with *Echinocletodes* (and *Cletodes*).

Thus the retention of *Echinocletodes* within Ancorabolidae remains questionable. *Echinocletodes* does exhibit all derived characters so far assigned as apomorphies to Ancorabolidae, however, they are ambiguous characters, occurring to varying extents in several non-ancorabolid taxa, whilst also being absent from some Ancorabolidae species. Instead of confirming the affiliation of *Echinocletodes* to a monophylum Ancorabolidae, we therefore question the monophyly of the latter. We instead assume a paraphyletic status of Ancorabolidae, a condition that has already been suggested at the subfamilial level for Laophontodinae (cf. George 2006c; Gheerardyn & George 2010; Gheerardyn & Lee 2012). Ancorabolinae is considered to constitute a true monophylum (George 2006c; Gheerardyn & George 2010).

Nevertheless, even if a monophylum Ancorabolidae cannot be justified, preventing therefore an unambiguous phylogenetic allocation of *Echinocletodes* to that group, an affiliation to one of its subfamilies might be determined. Thus follows a discussion on the suitability of assigning *Echinocletodes* to Ancorabolinae or Laophontodinae.

**Systematic status of Ancorabolinae and possible relationship with *Echinocletodes*.** Until 2006, Ancorabolinae was unequivocally characterized by the following derived characters (George 2006c): (i) female A1 at most 4-segmented (plesiomorphy: female A1 5-segmented); (ii) exp3 of P2–P4 with 2 outer spines only (plesiomorphy: with 3 outer spines); (iii) A2 without exp (plesiomorphy: antennar exp present or represented by seta); (iv) basis P1 transversely elongate (plesiomorphy: basis P1 not elongate transversely). Apart from the description of new taxa, phylogenetic investigations concerning Ancorabolinae have focused on minor systematic problems within the subfamily (e.g. George 1998a, b; George & Schminke 1998; Conroy-Dalton & Huys 2000; Conroy-Dalton 2001, George 2001; Conroy-Dalton 2003a, b, 2004; George 2006a, b, c; Gheerardyn & George 2010; George *et al.* 2012) and its monophyly has not been questioned. However, the description of *Ancorabolina chimaera* George, 2006 caused ambiguity regarding its relationship with both ancorabolina sub-groups and to Ancorabolinae in general (George 2006c; Gheerardyn & George 2010). Whilst *A. chimaera* presents the derived condition of characters (iii–iv), it retains the plesiomorphic condition in characters (i–ii). Nonetheless, George (2006c) recognized further derived characters, three of which apparently apply to all Ancorabolinae plus *Ancorabolina* George, 2006: (v) cuticular processes on body (plesiomorphy: body without cuticular processes); (vi) Frontal part of cphth forming a peak (plesiomorphy: cphth without peak); (vii) A1 first segment elongate (plesiomorphy: first antennular segment not elongate).

The relevance of the five derived characters (iii–vii) common to *A. chimaera* and Ancorabolinae was later discussed by Gheerardyn & George (2010). They described four new *Ancorabolina* species, demonstrating that some of the proposed apomorphies display a gradual development within *Ancorabolina* (characters iv and vii) or are also present in some members of the Laophontodinae (character v) and are not therefore apomorphic in Ancorabolinae. Nevertheless, Gheerardyn & George (2010) retained *Ancorabolina* in Ancorabolinae, based on two remaining derived characters (iii, vi). However, even the weakest development of a transversely elongate P1 basis (character iv) as present in *Ancorabolinaanaximenesi* Gheerardyn & George, 2010 and in *A. belgicae* Gheerardyn & George, 2010, and even the weakest (but clearly discernible) elongation of the first antennular segment (character vii) as present in *A. galeata* Gheerardyn & George, 2010 must be, in our opinion, seen as derived when compared with Laophontodinae, the presumed sister-taxon, so the autapomorphic status of characters (iv) and (vii) remain valid for Ancorabolinae. Thus, a monophylum Ancorabolinae (including *Ancorabolina*) may be well supported by four distinct autapomorphies, (iii, iv, vi, and vii). Only character (v) cannot be properly discussed since a comparative examination of the cuticular processes of Ancorabolinae and Laophontodinae is first required.

Having established the strength of the Ancorabolinae apomorphies, the position of *Echinocletodes* relative to this subfamily can be addressed:

A2 without exp (iii). This character state can be found across the Harpacticoida, in Laophontodinae (part.), Cristacoxidae Huys, 1990 (part.), Darcythompsoniidae Lang, 1936 (part.), and Metidae Sars, 1910 (part.) (cf. Lang, 1948; Huys, 1990; Boxshall & Halsey, 2004), suggesting a convergent development. However, it is recorded in all Ancorabolinae, in *E. armatus* (Scott 1903) and in *E. voightae*, which in combination with the other Ancorabolinae apomorphies, supports its autapomorphic character for Ancorabolinae and indicates the similarity of *Echinocletodes* to Ancorabolinae.

Basis P1 transversely elongate (iv). Even the putatively most basal representatives of Ancorabolinae, *Touphapleura schminkei* (George, 1998) (*Ceratonotus*-group) and *Arthropysyllus serratus* Sars, 1909 (*Ancorabolus*-lineage), show a pronounced transverse elongation of the P1 basis (George 1998b; Conroy-Dalton & Huys 2000),

and this is more pronounced still within the subfamily (e.g. Conroy-Dalton & Huys 2000; Conroy-Dalton 2001, 2003a, b; George 1998a, b; George & Schminke 1998; George 2006a, b; George & Plum 2009; Wandeness *et al.* 2009; see also Gheerardyn & George 2010; George *et al.* 2012). In contrast, the transverse elongation of the P1 basis in *Echinocletodes* is, although doubtlessly present, much less pronounced, resembling that of several *Cletodes* species (*C. dorae* Por, 1979, *C. endopodita* [Schriever, 1984], *C. latirostris*, *C. pseudodissimilis* Coull, 1971, *C. pusillus* Sars, 1920, *C. reyssi* Soyer, 1964, *C. smirnovi* Bodin, 1970, *C. tuberculatus* Fiers, 1991) rather than that of Ancorabolinae. Therefore, the membership of *Echinocletodes* to Ancorabolinae is questioned by this apomorphy (iv).

Frontal part of cphth forming a peak (vi). George (2006b) recognized a protruded ancorabolin “forehead” that he named a “peak”. Such a peak has been since found in *Ancorabolina* (George 2006c; George & Tiltack 2009; Gheerardyn & George 2010), but not in Laophontodinae or in Cletodidae. At most, a cphth peak may be inferred for *Echinocletodes* (Fig. 1A), but as shown by the lateral view (Fig. 1B), no protrusion can be clearly noted. Thus, like character (iv), character (vi) also belies an affinity of *Echinocletodes* to Ancorabolinae.

A1 first segment elongate (vii). Ancorabolin antennulae have an elongated first segment, differing completely from Laophontodinae, with exception of *Probosciphontodes* (Fiers 1988; Conroy-Dalton 2004). In *Echinocletodes* only the third antennular segment is elongate, being as long as the first two segments together, these are compact and only slightly longer than broad. Therefore, *Echinocletodes* does not share this apomorphy. It should be noted, however, that deviations of the antennula may be more complex and more variable than has been noted so far. Also, several of these deviations are not restricted to Ancorabolinae but also found in (at least part of) Laophontodinae and/or Cletodidae. Apart from the above mentioned elongation of the first antennular segment in *Probosciphontodes*, there are, for instance, several additional laophontodin species with a 4-segmented A1, fitting the above listed derived “ancorabolin character (i)” (*Laophontodes armatus* Lang, 1936, *L. hedgpethi* Lang, 1965, *L. psammophilus* Soyer, 1974, *Lobopleura* Conroy-Dalton, 2004, *Paralaophontodes* Lang, 1965, and *Probosciphontodes*). Such a heterogeneous distribution of derived antennular features inside a group comprising Ancorabolidae and Cletodidae may suggest paraphyletic status even for Ancorabolinae.

Female A1 at most 4-segmented (i). This feature was considered – along with the absence of A2 exp and a transversely elongate P1 basis – to be an unambiguous autapomorphic character for Ancorabolinae until the description of *Ancorabolina* (George 2006c; George & Tiltack 2009; Gheerardyn & George 2010), which retains a 5-segmented female A1 like most Laophontodinae (and Cletodidae). Since *Ancorabolina* remains in Ancorabolinae (Gheerardyn & George 2010), this character is not considered for the time. However, with respect to a possible affiliation of *Echinocletodes* to Ancorabolinae, it may be of interest: *E. voightae* has a 4-segmented female A1 (Fig. 10A), whilst *E. armatus*, was described with a 5-segmented A1 (T. Scott 1903). Nevertheless, Lang (1948) suspected that the original description was in error, and comparison of T. Scott’s (1905) description of *E. armatus* with *E. voightae*, the remaining “Ancorabolidae” and even other Harpacticoida supports Lang’s (1948) suspicion. For instance, all “Ancorabolidae” including *E. voightae* present a single seta apically on the first antennular segment, which corresponds to the original armature in Harpacticoida (Huys & Boxshall 1991). Yet, according to T. Scott (1903), in *E. armatus* the corresponding seta is located on the second segment, whilst the first segment is unarmed. Such a discrepancy, combined with the shape and ornamentation of the subsequent antennular segments, supports Lang’s (1948) assumption of an error made by T. Scott (1903) when describing the A1 of *E. armatus*. This then corroborates the conclusion that *Echinocletodes* presents a 4-segmented A1 and therefore shares the so far uncertain ancorabolin apomorphy (i). Unfortunately, the type material of *E. armatus* is unavailable, so it is not possible to (dis)prove T. Scott’s (1903) observation until new material is found and re-described.

Despite having the same number of segments, the A1 of *Echinocletodes* differs from that of all Ancorabolinae. The antennular segments of the latter are slender, whilst in *Echinocletodes* the first two segments are very short and compact. Unfortunately though, before considering the segmentation of the A1 for phylogenetic analysis, an overall re-examination of its status in all “Ancorabolidae” and potential relatives (Cletodidae, Laophontidae) is necessary.

P2–P4 exp-3 with 2 outer spines only (ii). This character has been used since Lang (1948) to discriminate between Ancorabolinae and Laophontodinae. Its typological interpretation characterizes Ancorabolinae with the derived possession of 2 outer setae and Laophontodinae with the retention of the ancestral state, which is 3 outer setae. Similar to other characters mentioned above, the loss of one outer seta at P2–P4 exp-3 occurs more than once

in Harpacticoida. Of particular importance for this discussion, the cletodid genus *Cletodes* presents the same apomorphy, as does *Echinocletodes*. Thus, this character may point to a closer relationship between Ancorabolinae, *Cletodes*, and *Echinocletodes*. If this were true, however, such a relationship would conversely weaken the validity of character (ii) as an autapomorphy for Ancorabolinae, making it uninformative for the assignment of *Echinocletodes* to that subfamily.

Contrary to Lang's (1948) assumption, we would conclude that *Echinocletodes* should be excluded from Ancorabolinae. Of the above discussed ancorabolin apomorphies (iii–vi) only the loss of the A2 exp occurs in *Echinocletodes*; the transverse elongation of the P1 basis is too weakly developed to fulfil ancorabolin prerequisites, a cphth peak is not developed in *Echinocletodes*, and the first antennular segment exhibits the plesiomorphic condition in being short. Additional characters (i–ii) are, although shared by Ancorabolinae (part.) and *Echinocletodes*, not defined well enough for an unequivocal validation.

**Systematic status of Laophontodinae and possible relationships with *Echinocletodes*.** Gheerardyn & George (2010, p. 52) determined three derived characters which are widespread in Laophontodinae (and also present in *Ancorabolina*) but absent in the remaining Ancorabolinae. These were: (i) A1 second segment with outer bump bearing long spinules (plesiomorphy: without bump); (ii) P1 coxa elongate lengthways (plesiomorphy: P1 coxa small, square); (iii) P1 seta of (former) exp-2 geniculate (plesiomorphy: element formed as bipinnate seta). Whether these apomorphies may be relevant for supporting a monophylum Laophontodinae must be proved in future analyses. Nevertheless, *Echinocletodes* does not show any of these apomorphies and shares no further derived characters with a laophontodin taxon. Therefore, no closer relationship of the genus with Laophontodinae can be hypothesized.

## Conclusions

The attempt to assign *Echinocletodes* to Ancorabolidae based on morphological apomorphies fails. Instead, the monophyly of Ancorabolidae was rejected, since none of the four supposed ancorabolid apomorphies are sufficiently clear. “Ancorabolidae” must in fact be regarded as a paraphylum, including taxa that share “familiar” synapomorphies but others that do not. Similarly some non-ancorabolid taxa may be closely related to at least some Ancorabolidae (for instance *Cletodes*), but have not been considered in phylogenetic analyses to date.

*Echinocletodes* does share all “ancorabolid apomorphies” and this may indicate an affinity of the genus to at least part of the “Ancorabolidae”. However, any attempt to assign it a position in the family is questionable and first requires an urgent and thorough phylogenetic evaluation of “Ancorabolidae”, incorporating at least Cletodidae and Laophontidae. A detailed review of the two subfamilies highlights similar difficulties as that seen at family level. Ancorabolinae may be justified as a monophylum due to four distinct apomorphies, which although recorded in other harpacticoid families, are only found together in Ancorabolinae. Nonetheless, the monophyletic status of Ancorabolinae remains uncertain, with doubts including the questionable position of *Ancorabolina* and *Echinocletodes*. *Ancorabolina* presents the plesiomorphic condition for Ancorabolinae in two characters, namely the segmentation of the female A1, and the possession of 3 outer setae in P2–P4. In contrast, *Echinocletodes* shares with the remaining Ancorabolinae the derived condition in both characters, but lacks an elongate first antennular segment, a cephalothoracic peak and clearly elongate P1–P4 bases. These latter ancorabolin apomorphies are presented by *Ancorabolina*.

With respect to the presumed paraphylum Laophontodinae, Gheerardyn & George (2010) noted three derived characters whose phylogenetic evaluation might elucidate the systematic status of the subfamily. *Echinocletodes* does not share any derived feature with the Laophontodinae, so a closer phylogenetic relationship with this subfamily appears to be rather improbable.

*Echinocletodes* itself forms a well-supported monophylum as discussed in the present contribution. The large number of autapomorphies may be the result of adaptation to sublittoral and deep-sea wood-falls as very specific habitats. Since the two species *E. bodini* and *E. walvisi* do not conform to *Echinocletodes* apomorphies, they are excluded from the genus. Both species share a high degree of similarity with *Cletodes meyerorum* sp. nov. described here and are therefore moved to the genus *Cletodes* as *C. bodini* comb. nov., and *C. walvisi* comb. nov.



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## References

- Arroyo, N.-L., George, K.H., Benito, J. & Maldonado, M. (2003) A new species of Ancorabolidae (Copepoda, Harpacticoida) from the northern coast of Spain: *Laophontodes mourois* sp. n. *Hydrobiologia*, 498 (1–3), 169–176.
- Ax, P. (1984) *Das Phylogenetische System*. Gustav Fischer Verlag, Stuttgart, 349 pp.  
<http://dx.doi.org/10.1002/iroh.19860710123>
- Baldari, F. & Cottarelli, V. (1986) A new species of the genus *Paralaophontodes* (Crustacea, Copepoda, Harpacticoida) from interstitial waters of Mindoro Island (The Philippines). *Publications of the Seto Marine Biological Laboratory*, 31 (3–6), 163–168.
- Balzer, W., Alheit, J., Emeis, K.-C., Lass, H.U. & Türkay, M. (Eds.) (2006) *South-East Atlantic 2000, Cruise No. 48, 6 July 2000–3 November 2000*. METEOR-Berichte, Universität Hamburg, 06–05, 219 pp.
- Bodin, P. (1964) Recherches sur la systématique et la distribution des copépodes harpacticoides des substrats meubles des environs de Marseille. *Bulletin recueil des travaux de la station marine d'Endoume*, 33(51), 107–183.
- Bodiou, J.V. & Colomines, J.C. (1988) Harpacticoides (copépodes) des îles Crozet. II Description d'une espèce nouvelle du genre *Tapholaophontodes* Soyer, 1974. *Crustaceana*, 55, 104–110.  
<http://dx.doi.org/10.1163/156854088X00285>
- Boxshall, G.A. & Halsey, S.H. (2004) *Copepod Diversity, Vol. I. and II*. The Ray Society, London, 966 pp.
- Bozic, B. (1964) Copépodes Harpacticoides et cyclopoïdes de la Reunion. II Plage St. Pierre. *Bulletin du Musée National d'Histoire Naturelle de Paris*, 36, 481–499.
- Brady, G.S. (1910) Die marinen Copepoden der deutschen Südpolarexpedition, 1901–1903. I. *Über die Copepoden der Stämme Harpacticoida, Cyclopoidea, Nothodelphyoidea und Calipoidea*. *deutschen Südpolarexpedition*, 11 (3), 527–528.
- Brady, G.S. (1918) Copepoda. *Scientific Report of the Australasian Antarctic Expedition 1911–1914*, 5 (3), 1–48
- Chislenko, L.L. (1967) Issledovanija fauni morei VII (XV); gidrobiologicheskie Issledovaniya na Karelskom poberezhe Belogo morya. *Raboty belomroskoi stantsii zoologicheskogo instituta AN SSSR*, 187–189.
- Conroy-Dalton, S. (2001) Systematics and phylogeny of the Ancorabolidae (Copepoda: Harpacticoida). II. Polyphyly of *Polyascophorus* and description of *Arthuricornua*, new genus. *Journal of Crustacean Biology*, 21, 170–191.  
[http://dx.doi.org/10.1651/0278-0372\(2001\)021\[0170:SAPOTA\]2.0.CO;2](http://dx.doi.org/10.1651/0278-0372(2001)021[0170:SAPOTA]2.0.CO;2)
- Conroy-Dalton, S. (2003a) Systematics and phylogeny of the Ancorabolidae (Copepoda: Harpacticoida). IV. Redescription, ontogeny and position of *Echinopsyllus normani*. *Cahiers de Biologie Marine*, 44, 153–169.
- Conroy-Dalton, S. (2003b) Systematics and phylogeny of the Ancorabolidae (Copepoda: Harpacticoida). III. Description of two new species of *Ceratonotus* Sars and *Dendropsyllus*, new genus. *Journal of Crustacean Biology*, 23, 69–93.  
[http://dx.doi.org/10.1651/0278-0372\(2003\)023\[0069:SAPOTA\]2.0.CO;2](http://dx.doi.org/10.1651/0278-0372(2003)023[0069:SAPOTA]2.0.CO;2)
- Conroy-Dalton, S. (2004) Systematics and phylogeny of the Ancorabolidae (Copepoda: Harpacticoida). V. Description of *Lobopleura*, new genus, with notes on *Probosciphontodes* Fiers. *Journal of Crustacean Biology*, 24 (1), 17–36.  
<http://dx.doi.org/10.1651/C-2439>
- Conroy-Dalton, S. & Huys, R. (2000) Systematics and phylogeny of the Ancorabolidae (Copepoda: Harpacticoida). I. The *Ancorabolus*-lineage, with the description of three new genera. *Cahiers de Biologie Marine*, 41 (4), 343–397.
- Cottarelli, V. & Baldari, F. (1987) Interstitial Ancorabolidae (Copepoda, Harpacticoida) from Macquarie Island: *Tapholaophontodes remotus* and *Algeniella boitanii* n. gen. n. sp. *Crustaceana*, 53, 67–77.  
<http://dx.doi.org/10.1163/156854087X00637>
- Coull, B.C. (1973) Meiobenthic Harpacticoida (Crustacea, Copepoda) from the deep sea of North Carolina IV. The families Cletodidae T. Scott and Ancorabolidae Sars. *Transactions of the American Microscopic Society*, 92, 604–620.
- Dinet, A. (1974) Espèces nouvelles de Copepodes Harpacticoides (Crustacea) des sédiments profonds de la dorsale de Walvis. *Archives de Zoologie Expérimentale et Générale*, 115 (4), 567–575.

- Drzycimski, I. (1967) Zwei neue Cletodidae (Copepoda Harpacticoida) aus dem westnorwegischen Küstengebiet. *Sarsia*, 29, 199–206.
- Fiers, F. (1986) A new record and redescription of *Paralaophontodes echinata* (Willey) (Copepoda, Harpacticoida, Ancorabolidae). *Annales de la Société Royale Zoologique de Belgique*, 116 (2), 137–144.
- Fiers, F. (1988) *Probosciphontodes* n. gen., a new genus of the family Ancorabolidae, with the description of two new species (Copepoda, Harpacticoida). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Biologie*, 58, 75–83.
- Fiers, F. (1991) Three new harpacticoid copepods from the Santa Maria Basin off the Californian Pacific coast (Copepoda, Harpacticoida). *Beaufortia*, 42 (2), 13–47.
- Gee, J.M. (1998) A revision of the genus *Limnocletodes* Borutzky, 1926 (Copepoda: Harpacticoida: Cletodidae) with a description of a new species from Southeast Asian mangrove forests. *The Raffles Bulletin of Zoology*, 46 (2), 399–418.
- Gee, J.M. (2001) A reappraisal of the taxonomic position of *Enhydrosoma curvirostre* (Copepoda: Harpacticoida: Cletodidae). *Journal of the Marine Biological Association of the United Kingdom*, 81, 33–42.  
<http://dx.doi.org/10.1017/S002531540100337X>
- Gee, J.M. & Fleeger, J.W. (1986) Two new species of harpacticoid copepod from the South Orkney Islands, Antarctica, and a redescription of *Idyellopsis typica* Lang (Tisbidae). *Journal of the Linnean Society*, 88, 143–165.  
<http://dx.doi.org/10.1111/j.1096-3642.1986.tb01184.x>
- George, K.H. (1998a) A new species of Ancorabolidae (Copepoda, Harpacticoida) from the Beagle Channel (Chile). *Hydrobiologia*, 379, 23–32.
- George, K.H. (1998b) *Polyascophorus*, a new genus of Ancorabolidae (Crustacea, Copepoda), including the description of two new species and the re-allocation of *Ceratonotus gorbunovi*. *Vie Milieu*, 48, 141–155.
- George, K.H. (2001) First record of the "genus" *Ancorabolus* Norman, 1903 from the Southern Hemisphere, including analyses of copepodid development (Crustacea, Copepoda, Harpacticoida, Ancorabolidae). *Senckenbergiana biologica*, 81 (1/2), 23–36.
- George, K.H. (2006a) Ancorabolinae Sars (Copepoda: Harpacticoida: Ancorabolidae) of the deep Atlantic Ocean. *Ancorabolina chimaera* sp. nov. including remarks to ancorabolid phylogeny and to the evolution of the first natatorial leg in comparison with Laophontoidea T. Scott. *Meiofauna Marina*, 15, 157–176.
- George, K.H. (2006b) New Ancorabolinae Sars, 1909 (Copepoda: Harpacticoida: Ancorabolidae) of the Atlantic Ocean. Description of *Pseudechinopsyllus sindemarkae* gen. et sp. nov. and *Dorsiceratus ursulae* sp. nov. from the Great Meteor Seamount, and redescription of *D. octocornis* Drzycimski, 1967, and *D. triarticulatus* Coull, 1973 (part.). *Meiofauna Marina*, 15, 123–156.
- George, K.H. (2006c) New Ancorabolinae Sars, 1909 (Copepoda: Harpacticoida: Ancorabolidae) of the Atlantic and the Pacific Ocean. The taxa *Ceratonotus* Sars, and *Dendropsyllus* Conroy-Dalton. *Meiofauna Marina*, 15, 87–122.
- George, K.H. (2008) *Argestes angolaensis* sp. nov. (Copepoda: Harpacticoida: Argestidae) from the Angola Basin (Southeast Atlantic), and the phylogenetic characterization of the taxon *Argestes* Sars, including the redescription of *A. mollis* Sars, 1910, and *A. reductus* (Itô, 1983). *Zootaxa*, 1866, 223–262.
- George, K.H. (2011) Revision of the taxon *Fultonina* T. Scott (Copepoda: Harpacticoida: Argestidae), including the (re) description of some species, discontinuation of the genus *Parargestes* Lang, and erection of Argestinae Por, subfam. nov. *Meiofauna Marina*, 19, 127–160.
- George, K.H. & Plum, C. (2009) Description of two new species of *Dorsiceratus* Drzycimski, 1967 (Copepoda: Harpacticoida: Ancorabolidae) from Sedlo and Seine Seamounts (Northeastern Atlantic) and remarks on the phylogenetic status of the genus. *Zootaxa*, 2096, 257–286.
- George, K.H. & Schminke, H.K. (1998) First records of the genus *Ceratonotus* G. O. Sars, 1909 (Copepoda, Ancorabolidae) from the Southern Hemisphere, with the description of two new species. *Crustaceana*, 71 (7), 801–817.  
<http://dx.doi.org/10.1163/156854098X00059>
- George, K.H. & Tiltack, A. (2009) A new species of *Ancorabolina* (Copepoda, Harpacticoida, Ancorabolidae) from a Mediterranean submarine cave, with a key to species. *Vie Milieu*, 59 (3/4), 287–300.
- George, K.H., Wandeness, A.P. & Santos, P.J.P. (2012) A new species of Ancorabolidae (Crustacea: Copepoda: Harpacticoida) from the Campos Basin, Brazil, including a phylogenetic review of the taxon *Polyascophorus* George, 1998, and a key to its species. *Zoologischer Anzeiger*, 252 (1), 20–33.  
<http://dx.doi.org/10.1016/j.jcz.2012.02.002>
- Gheerardyn, H. & George, K.H. (2010) New representatives of the genus *Ancorabolina* George, 2006 (Copepoda, Harpacticoida, Ancorabolidae) including remarks on ancorabolid phylogeny. *Zoological Journal of the Linnean Society*, 158, 16–55.  
<http://dx.doi.org/10.1111/j.1096-3642.2009.00567.x>
- Gheerardyn, H. & Lee, W. (2012) *Calypsophontodes* gen. Nov. (Copepoda: Harpacticoida: Ancorabolidae), a new genus of Laophontodinae, including remarks on ancorabolid phylogeny. *Journal of Crustacean Biology*, 32(2), 263–280.  
<http://dx.doi.org/10.1163/193724011x615613>
- Gómez, S. & Conroy-Dalton, S. (2002) Description of *Ancorabolus hendrickxi* sp. nov. (Copepoda: Harpacticoida: Ancorabolidae) from the neotropics and notes on caudal ramus development within oligoarthran harpacticoids. *Cahiers de Biologie Marine*, 43, 111–129.

- Griga, R.E. (1964) Copepoda donnykh biotsenozov Chernogo morya raiona evpatorii. *Trudy sevastopolski biologicheskoi stantsii, akademya Nauk SSSR*, 15, 101–117.
- Gurney, R. (1927) Zoological results of the Cambridge expedition to the Suez-Canal, 1924. Report on the Crustacea: Copepoda (littoral and semi-parasitic). *Transactions of the Zoological Society of London*, 33 (4), 451–577.
- Hesse, E. (1867) Observations sur les Crustacés rares ou nouveaux des côtes de France. *Annales des Sciences Naturelles (Zoologie)*, (5) 7, 199–216.
- Hicks, G.R.F. (1988) Systematics of the Donsiellinae (Copepoda, Harpacticoida). *Journal of Natural History*, 22 (3), 639–684. <http://dx.doi.org/10.1080/00222938800770441>
- Hicks, G.R.F. & Coull, B.C. (1983) The ecology of marine meiobenthic harpacticoid copepods. *Annual Review of Oceanography and Marine Biology*, 21, 67–175.
- Huys, R. (1990) A new family of harpacticoid copepods and an analysis of the phylogenetic relationships within the Laophontoidea T. Scott. *Bijdragen tot de Dierkunde*, 60 (2), 79–120.
- Huys, R. & Boxshall, G.A. (1991) *Copepod Evolution*. The Ray Society, London, 468 pp. <http://dx.doi.org/10.1163/193724092x00193>
- Kornev, P.N. & Chertoprud, E.S. (2008) *Harpacticoid copepods from the White Sea: Morphology, Systematics, Ecology*. KMK Scientific Press, Moscow, 367 pp.
- Krishnaswamy, S. (1957) *Studies on the Copepoda of Madras*. Unpublished Thesis, University of Madras, 168 pp.
- Lang, K. (1934) Marine Harpacticoida von der Campbell-Insel und einigen anderen südlichen Inseln. *Lunds Universitets Arsskrift N.F. Avd.*, 30 (14), 1–56.
- Lang, K. (1936a) Die Familie der Cletodidae Sars, 1909. *Zoologische Jahrbücher*, 68(6), 445–480.
- Lang, K. (1936b) Copepoda Harpacticoida. *Further Zoological Results of the Swedish Antarctic Expedition, 1901-1903*, 3 (3), 1–68.
- Lang, K. (1936c) Beiträge zur Kenntnis der Harpacticiden. 7. Die Familie Anchorabolidae Sars, nebst Beschreibung einer neuen *Laophontodes*-Art. *Zoologischer Anzeiger*, 115 (5–6), 152–156.
- Lang, K. (1944) *Monographie der Harpacticiden (vorläufige Mitteilungen)*. Almqvist and Wiksells boktryckeri AB, Uppsala, Sweden, 39 pp.
- Lang, K. (1948) *Monographie der Harpacticiden*. Two volumes. Otto Koeltz Science Publishers, Königstein (reprint 1975), 1683 pp.
- Lang, K. (1965) Copepoda Harpacticoida from the Californian Pacific Coast. *Kungl. Svenska Vetenskapsakademiens Handlingar*, 10 (2), 1–566.
- Menzel, L. & George, K.H. (2009) Description of four new species of *Mesocletodes* Sars, 1909 (Copepoda, Harpacticoida, Argastidae) and redescription of *Mesocletodes robustus* Por, 1965 from the South Atlantic, including remarks on the *Mesocletodes abyssicola*-group. *Zootaxa*, 2096, 214–265.
- Mielke, W. (1981) Interstitielle Fauna von Galapagos XXVIII. (Laophontidae), Ancorabolidae (Harpacticoida). *Mikrofauna Meeresboden*, 84, 1–106.
- Norman, A.N. (1903) Notes on the natural history of East Finmark. *Annals and Magazine of Natural History*, 7 (11), 1–32.
- Pallares, R.E. (1968) *Patagoniaella*, nuevo género de la familia Ancorabolidae Sars, 1909 (Copepoda, Harpacticoida). *Physis*, 27 (75), 461–469.
- Pallares, R.E. (1975) Copépodos harpacticóideos marinos de Tierra del Fuego (Argentina). I. Isla de los Estados. *Contribuciones Científicas CIBIMA*, 122, 1–34.
- Pesta, O. (1959) Harpacticoiden (Crust. Copepoda) aus submarinen Höhlen und den benachbarten Litoralbezirken am Kap von Sorrent (Neapel). Ergebnisse der Österreichischen Tyrrhenia-Expedition 1952. Teil: VI. *Pubblicazioni della Stazione Zoologica di Napoli*, 30, 94–177.
- Por, F.D. (1986) A re-evaluation of the family Cletodidae Sars, Lang (Copepoda, Harpacticoida). *Syllogeus*, 58, 420–425.
- Rose, A., Seifried, S., Willen, E., George, K.H., Veit-Köhler, G., Bröhdick, K., Drewes, J., Moura, G., Martínez Arbizu, P. & Schminke, H.K. (2005) A method for comparing within-core alpha-diversity values from repeated Multicorer samplings, shown for abyssal Harpacticoida (Crustacea: Copepoda) from the Angola Basin. *Organisms, Diversity and Evolution*, 5 (suppl. 1), 3–17.
- Sars, G.O. (1903) *An account of the Crustacea of Norway with short descriptions and figures of all the species. Vol. V. Copepoda Harpacticoida, Parts I–III: Misophrüidae, Longipediidae, Cerviniidae, Ectinosomidae (part.)*. Alb. Cammermeyer's Forlag, Christiania, 28 pp.
- Sars, G.O. (1908) *An account of the Crustacea of Norway with short descriptions and figures of all the species. Vol. V. Copepoda Harpacticoida, Parts XXIII and XXIV: Laophontidae (cont.)*. Alb. Cammermeyer's Forlag, Christiania, pp. 257–276.
- Sars, G.O. (1909) *An account of the Crustacea of Norway with short descriptions and figures of all the species. Volume V. Copepoda Harpacticoida, Parts XXVII and XXVIII: Cletodidae (concluded), Anchorabolidae, Cyliropsyllidae, Tachidiidae (part.)*. Alb. Cammermeyer's Forlag, Christiania, pp. 305–336.
- Schizas, N.V. & Shirley, T.C. (1994) Two new species of *Laophontodes* (Copepoda, Harpacticoida, Ancorabolidae) from McMurdo Sound, Antarctica. *Zoologica Scripta*, 23 (3), 205–216. <http://dx.doi.org/10.1111/j.1463-6409.1994.tb00385.x>
- Schminke, H.K. (1976) The ubiquitous telson and the deceptive furca. *Crustaceana*, 30, 292–299. <http://dx.doi.org/10.1163/156854076X00657>

- Schulz, M. & George, K.H. (2010) *Ancorabolutus chironi* sp. nov., the first record of a member of the *Ancorabolutus*-group (Copepoda: Harpacticoida: Ancorabolutidae) from the Mediterranean. *Marine Biodiversity*, 40, 79–93.  
<http://dx.doi.org/10.1007/s12526-010-0035-2>
- Scott, A. (1896) Description of new and rare Copepoda. Report on the Investigations carried on in 1895 in connection with the Lancashire Sea-Fisheries Laboratory at University College, Liverpool. *Proceedings and Transactions of the Liverpool Biological Society*, 10, 134–158.
- Scott, T. (1894) Additions to the fauna of the Firth of Forth. Part VI. *Annual Report of the Fishery Board for Scotland*, 12 (3), 231–271.
- Scott, T. (1903) Notes on some Copepoda from the Faroe Channel. *Zoological Journal of the Linnean Society*, 29, 1–11.  
<http://dx.doi.org/10.1111/j.1096-3642.1903.tb00422.x>
- Scott, T. (1907) Some additional notes on Copepoda from Scottish seas. *Report of the Fishery Board for Scotland*, 25 (3), 209–220.
- Scott, T. (1912) The Entomostraca of the Scottish National Antarctic Expedition 1902–1904. *Transactions of the Royal Society of Edinburgh*, 48 (3), 521–599.  
<http://dx.doi.org/10.1017/s0080456800015829>
- Seifried, S. (2003) *Phylogeny of Harpacticoida (Copepoda): Revision of 'Maxillipedasphalea' and Exanechentera*. Cuivillier Verlag, Göttingen, 259 pp.
- Smirnov, S. (1946) New species of Copepoda Harpacticoida from the Arctic Ocean (en Russe, resumée en anglais). *Trudy dreifuyuschei Ekspeditsii Glavsevmorputi Ledokol'nom Parokhode "G. Sedov"*, 3, 231–263.
- Soyer, J. (1964) Copépodes Harpacticoides de l'étage bathyal de la région de Banyuls-sur-Mer: IV. La sous-famille des Ancorabolinae Lang. *Vie Milieu*, 15 (2), 329–340.
- Soyer, J. (1975) Harpacticoides (Crustacées, Copépodes) de l'archipel de Kerguelen. 1. Quelques formes mesopsammiques. *Bulletin du Musée National d'Histoire Naturelle de Paris (3)244 (= Zoologie)*, 168, 1169–1223.
- Thomson, G.M. (1882) On New Zealand Copepoda. *Transactions of the New Zealand Institute of Wellington*, 15, 93–116.
- Voight, J.R. (2007) Experimental deep-sea deployments reveal diverse northeast Pacific wood-boring bivalves of Xylophaginae (Myoida: Pholadidae). *Journal of Molluscan Studies*, 73, 377–391.  
<http://dx.doi.org/10.1093/mollus/eym034>
- Wandness, A.P., George, K.H. & Santos, P.J.P. (2009) First record of the taxon *Echinopsyllus* (Copepoda, Harpacticoida, Ancorabolutidae) from the deep sea of Campos Basin, Brazil, with the description of three new species and their contribution to phylogenetic systematics. *Zoological Journal of the Linnean Society*, 156, 52–78.  
<http://dx.doi.org/10.1111/j.1096-3642.2008.00479.x>
- Wells, J.B.J. (2007) An annotated checklist and keys to the species of Copepoda Harpacticoida (Crustacea). *Zootaxa*, 1568, 1–872.
- Willen, E. (2000) *Phylogeny of the Thalestridomorpha Lang, 1944 (Crustacea, Copepoda)*. Cuivillier Verlag, Göttingen, 233 pp.
- Wiley, A. (1930) Harpacticoid copepoda from Bermuda. I. *Annals and Magazine of Natural History*, 10 (6), 81–114.