



CALYPSOPHONTODES GEN. NOV. (COPEPODA: HARPACTICOIDA: ANCORABOLIDAE), A NEW GENUS OF LAOPHONTODINAE, INCLUDING REMARKS ON ANCORABOLID PHYLOGENY

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ABSTRACT

Both sexes of *Laophontodes macropodia* Gee and Fleeger, 1986 (Ancorabolidae, Laophontodinae) are redescribed in detail based on type material from the South Orkney Islands and other material from King George Island (South Shetland Islands). The species is fixed as the type of a new genus *Calypsophontodes* on account of the sexually dimorphic setation on enp-2 of P4 (inner seta present in female, absent in male) and the sexual size dimorphism in P2-P4. The taxon further displays a number of plesiomorphic characters, such as the presence of an outer spine on enp-2 of female P3 and the protruding endopodal lobe in female P5. *Laophontodes latissimus* Brady, 1918 is regarded as species inquirenda within *Calypsophontodes*. The geniculation of the outer seta on exp-2 of P1 and the presence of an outer bump with long spinules on the second antennular segment are proposed as potential synapomorphies of Laophontodinae (including *Ancorabolina*).

KEY WORDS: Ancorabolidae, Antarctica, *Calypsophontodes*, new genus

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INTRODUCTION

Ancorabolidae Sars, 1909 after its establishment was subsequently divided into the two subfamilies Ancorabolinae Sars, 1909 and Laophontodinae Lang, 1944 by Lang (1944, 1948). Since then, Laophontodinae has grown from the single genus *Laophontodes* T. Scott, 1894 to seven genera with a total of 28 species (two of which are incertae sedis) (Wells, 2007). Recently, Kornev and Chertoprud (2008) added *Laophontodes multispinatus* Kornev and Chertoprud, 2008 from the White Sea, but this species will be transferred to the genus *Lobopleura* Conroy-Dalton, 2004 in a subsequent paper. Several authors (Conroy-Dalton, 2004; George, 2006c) pointed out that the subdivision into two subfamilies is dubious, as not a single autapomorphy for Laophontodinae has been identified so far. Gheerardyn and George (2010) detected several features, viz., second antennular segment with outer bump bearing some long spinules, coxa of first swimming leg lengthways elongate, armature element of (former) second exopodal segment of first swimming leg geniculate, that are widespread in Laophontodinae and also present in *Ancorabolina* George, 2006, but absent in the remaining Ancorabolinae; however, the true phylogenetic significance of these characters remains to be evaluated. As certain phylogenetically important characters (such as the geniculation of setae and the presence of minute setae) likely were overlooked in certain older descriptions, the need for redescriptions of known species is evident. Conroy-Dalton (2004) started the revision of *Laophontodes* by transferring *Laophontodes expansus* Sars, 1908 to the newly es-

tablished genus *Lobopleura*, and demonstrated a strong relationship between *Lobopleura* and *Probosciphontodes* Fiers, 1988. Obviously, a further revision of *Laophontodes* is necessary to assess phylogenetic relationships within Laophontodinae.

During a study of the harpacticoid copepods at Marian Cove (King George Island, South Shetland Islands, Antarctica), we rediscovered *Laophontodes macropodia* Gee and Fleeger, 1986, which was originally described from the South Orkney Islands (Antarctica). At the moment of description, Gee and Fleeger (1986) expressed doubts as to whether this species can be included in *Laophontodes*, because of differences in the setation of the second to fourth swimming legs and especially on account of the shape of the fifth leg. Furthermore, they suggested a close relationship with *Laophontodes latissimus* Brady, 1918 (described from Macquarie Island, south of Australia), as demonstrated by similarities in body shape and ornamentation, structure of the last abdominal somite, caudal rami, and the fifth leg. Lang (1948) had already questioned whether the latter species could be included in *Laophontodes* because of its distinctly different fifth leg. Gee and Fleeger (1986) refrained from formally establishing a new genus to accommodate these two species, instead attributing the deviating fifth leg to intrageneric variability and basing their decision on comparison with a similar degree of variability ascribed to other ancorabolid genera at that time. *Laophontodes macropodia* is redescribed here from the type material

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and transferred to a new genus, which furthermore includes *L. latissimus*.

MATERIAL AND METHODS

Syntype and additional material of *Laophontodes macropodia* Gee and Fleeger, 1986 was borrowed from the Natural History Museum, London (NHMUK). Dissected parts of one female from the non-type material were mounted in glycerine and preparations were sealed with insulating varnish. Drawings were made with the aid of a drawing tube on a Leica DM 2500 microscope equipped with differential interference contrast. As most structures in the syntype slides are in a rather bad condition, certain drawings were made from one female and one male specimen from the additional non-type material. However, all characteristics of the latter specimens were thoroughly checked and found to agree completely with the syntypes.

Additional material of *Laophontodes macropodia* examined in this study was collected during two expeditions (in 2002 and 2007, Korea Antarctic Research Program) to Marian Cove (King George Island, Antarctica) and is kept in the collection of the Laboratory of Biodiversity, Hanyang University, Seoul. Sediment samples were collected by gravity corer and preserved in 5% neutral formalin.

The descriptive terminology is adopted from Huys et al. (1996). Abbreviations used in the text are: A1, antennule; A2, antenna; ae, aesthetasc; exp, exopod; enp, endopod; P1-P6, first to sixth thoracopods; exp(enp)-1(2,3) for the proximal (middle, distal) segment of the respective ramus. Scale bars in figures are indicated in μm .

SYSTEMATICS

Ancorabolidae Sars, 1909

Laophontodinae Lang, 1944

Calypsophontodes n. gen.

Diagnosis.—Laophontodinae. Body fusiform, tapering posteriorly; body somites markedly distinct from each other and strongly sclerified. P2-P6-bearing somites (genital half of double-somite in female) each with single mediodorsal tube pore. Genital double-somite and following urosomite in female extended ventrolaterally into pair of posteriorly directed lateral processes. Anal somite short, with strongly protruding, round anal operculum. Caudal rami slightly longer than wide, with convex inner margin, with 7 setae; setae I and II inserted at two thirds of outer margin, seta III subapically and dorsally; IV, V and VI apically; setae IV and V fused at base; seta V well-developed; seta VII tri-articulate at base. Sexual dimorphism in body size, antennule, P2-P6, urosome width, genital segmentation, and ventral abdominal ornamentation.

Rostrum fused to cephalic shield, elongate-triangular and strongly curved ventrally, with pair of sensilla subdistally. Antennule 5-segmented in female, 6-segmented and chirocer in male (with 1 segment distal to geniculation); segments 2 and 3 with outer bump; aesthetasc arising from segments 3 and 5 in female, segments 5 and 6 in male. Antenna with allobasis, without abexopodal seta; exopod represented by minute segment with 1 seta; endopod with 3 lateral and 6 distal elements. Mandibular palp 1-segmented, with

2 inner and 3 apical setae. Maxillule with 2 elements on coxal endite; basis, endopod, and exopod fused and bearing 9 setal elements. Maxillary syncoxa with 2 endites, each with 3 spines; allobasis drawn out into claw, bearing 3 setae; endopod minute, with 2 setae. Maxilliped subchelate; syncoxa with 1 seta; endopod drawn out into curved claw, with 1 accessory seta.

P1-P4. Precoxa well developed, triangular. Coxa as long as wide (P1) or short (P2-P4). Basis longer than coxa and forming distinct pedestal for enp (P1) or transversally elongated (P2-P4). P1 exp 3-segmented; exp-2 longest, with 1 outer, geniculate seta; exp-3 with 4 geniculate setae; enp 2-segmented and prehensile; enp-1 almost twice as long as exp; enp-2 short, with 1 small inner seta, apically with 1 recurved spine and 1 geniculate seta. P2-P4 exopods 3-segmented, without inner setae; exp-3 with 3 outer spines. Endopods 2-segmented; enp-1 small, without armature; enp-2 elongate. Male P3 endopod 3-segmented; enp-2 with apophysis. Enp-2 of P4 with inner seta in female, this seta absent in male. Entire male P2-P4 proportionally larger than in female. Male P3 and P4 exopods more strongly developed than in female.

P5 robust, with basis, exp, and enp fused to one plate. Basal seta on demarcated setophore. Exopodal part bearing 1 inner, 1 apical, and 3 (female) or 2 (male) outer strong setae; endopodal lobe bearing 2 (female) or 1 (male) strong seta(e). Female genital field positioned anteriorly, with medial copulatory pore. P6 represented by small cuticular plates, each with 1 minute seta. Male P6 represented by unarmed membranous flaps; one member fused to ventral wall of supporting somite, one member articulating.

Type Species.—*Laophontodes macropodia* Gee and Fleeger, 1986 = *Calypsophontodes macropodia* (Gee and Fleeger, 1986) n. comb.

Species Inquirenda.—*Laophontodes latissimus* Brady, 1918 = *Calypsophontodes latissima* (Brady, 1918) n. comb.

Etymology.—The generic name refers to Calypso (Καλυψώ), a nymph in Greek mythology who lived on a remote island, and alludes to the type locality of its type species. Gender: feminine.

Calypsophontodes macropodia
(Gee and Fleeger, 1986) n. comb.
Figs. 1-10

Laophontodes macropodia Gee and Fleeger, 1986.

Type Locality.—Signy Island (60°43'S, 45°38'W) (South Orkney Islands, Antarctica), between Billie Rocks, Small Rock, and Cam Rock in Borg Bay, sublittoral fine sand (24.7% silt/clay, median grain size 100 μm), 15 m water depth.

Material Examined.—(a) Syntypes (from type locality): 3 females dissected on 1 slide each (NHMUK 1985.33-35), 2 females mounted on 1 slide (NHMUK 1985.36-37), 2 males dissected on 1 slide each (NHMUK 1985.38-39), and 2 males mounted on 1 slide (NHMUK 1985.40); (b) additional non-type material (from type locality): 1 female dissected on 18 slides (NHMUK 1985.41), 1 male (NHMUK 1985.42), and 6 females (NHMUK 1985.43-48) preserved

in alcohol; (c) 1 male (collection of Laboratory of Biodiversity, Hanyang University) from Marian Cove (62°13'14"S, 58°46'73"W) (King George Island, Antarctica), sublittoral muddy sediments, around 30 m water depth, collected in December 2002 by Hyun Woo Bang; (d) 2 males (collection of Laboratory of Biodiversity, Hanyang University) from same site, collected on 30 April 2007 by Jungho Hong; (e) 1 male and 1 female (collection of Laboratory of Biodiversity, Hanyang University) from Edgell Bay (62°15'50"S, 58°58'30"W) (Nelson Island, Antarctica), around 20-40 m water depth, collected in December 2002 by Hyun Woo Bang.

Remark.—Gee and Fleeger (1986) erroneously reported 3 (instead of 4) male syntypes in the slide material (NHMUK 1985.33-40). They listed 8 females and 2 males as additional non-type material, but in fact the tube contained 7 females and 1 male of *Laophontodes macropodia* (NHMUK 1985.41-48), 1 female *Idyellopsis typica* Lang, 1948 (NHMUK 1985.49), and 1 female *Amphiascoides* cf. *neglectus* (Norman and T. Scott, 1905) (NHMUK 1985.50).

Redescription of Female.—Total body length measured from tip of rostrum to posterior end of caudal rami (in dorsal view) 787 μ m; largest width measured at posterior margin of cephalic shield 274 μ m (both measures from NHMUK 1985.41). Body (Figs. 1A, 6A, 10A) fusiform, tapering posteriorly; body somites markedly distinct from each other and strongly sclerified. Cephalothorax with smooth posterior margin, slightly serrate near posterolateral corners; lateral sides with small constriction in posterior third; pattern of sensilla and pores as figured; tegument of entire cephalic shield with irregular pits and ridges (as in Fig. 1D). Rostrum (Figs. 1A, 3G) fused to cephalic shield and elongate-triangular; strongly curved ventrally; with pair of sensilla inserted subdistally.

Body somites bearing P2-P5 and anterior somite of genital double-somite each with single mediodorsal tube pore. Dorsal surface of all body somites with minute denticles, lateral margins (except in penultimate and anal somite) bordered with row of strong spinules, posterodorsal margins serrate (that of penultimate somite strongly serrate). Second and third urosomites fused to form genital double-somite, with dorsal transverse row of spinous processes indicating original segmentation. Ventral surface of urosome (Figs. 4C, 6A) smooth with few striae, with 2 short rows of fine spinules in middle of genital double-somite. Genital double-somite and following urosomite both distinctly extended ventrolaterally into posteriorly directed lateral processes. Posteroventral margins of genital double-somite and following urosomites bearing several rows of spinules. Anal somite (Figs. 5E-F, 6A-B) very short, partly cleft medially, with strongly protruding, rounded anal operculum. Margin of anal operculum serrate.

Caudal rami (Figs. 5E-F, 6A-B) slightly longer than wide, about as long as anal somite; with convex inner margin; ventral surface with 3 tube pores; short row of spinules along inner margin and ventrally along apical margin. Setae I and II inserted closely together at two thirds of outer margin; seta III inserted subapically and displaced dorsally; setae I, II, and III subequal in length; setae IV, V, and VI inserted apically; with IV and V fused at base; seta V longest and

multipinnate in middle third; seta VII tri-articulate at base, arising from dorsal pedestal.

Antennule (Fig. 2A-C) 5-segmented. Armature formula: 1-[1], 2-[9], 3-[6 + (1 + aes)], 4-[1], 5-[10 + (2 + aes)]. Dorsal surface of each segment with minute spinules. First segment short, bearing several rows of spinules along inner margin and 1 setulose seta. Second segment longest; outer margin forming bump with patch of strong spinules; tegument next to most proximal outer seta on dorsal surface slightly elevated and more strongly developed. Third segment with outer bump bearing row of spinules.

Antenna (Fig. 2D). Coxa represented by well-developed sclerite. Allobasis with row of spinules along abexopodal margin and small spinules proximally. Exopod represented by minute segment bearing 1 seta; tegument near insertion of exopod slightly thicker than surrounding membranous area. Endopod with several rows of spinules, laterally bearing 2 pinnate spines and 1 slender seta. Apical armature consisting of 2 unipinnate spines, 3 long, geniculate, pinnate setae, and 1 small, naked seta (fused basally to seta next to it). Outermost geniculate seta with strong pinnule proximal to geniculation.

Labrum with spinules as figured (Fig. 3A).

Mandible (Fig. 2E-F) with strong gnathobase bearing several multicuspid teeth and 1 bifid seta. Mandibular palp one-segmented, with 2 inner pinnate setae (representing basal elements), 3 apical setae (representing incorporated endopod), and no exopodal setae.

Paragnaths (Fig. 3D) developed as distinct lobes with several rows and patches of short, fine spinules.

Maxillule (Fig. 3B-C) with precoxal arthrite bearing 2 setae on anterior surface, short row of long spinules on posterior surface, and row of small spinules along inner margin. Apical armature of arthrite consisting of 10 setae/spines. Coxal endite with row of spinules on anterior surface, apically with 1 pinnate spine and 1 naked seta. Basis, endopod, and exopod fused. Proximal basal endite with 1 pinnate spine, 1 pinnate seta, and 1 naked seta. Distal basal endite with 2 naked setae. Endopod represented by 1 pinnate and 1 naked setae. Exopod represented by 2 naked setae.

Maxilla (Fig. 3E) with syncoxa bearing 2 endites, row of long spinules along outer margin and short spinules along inner margin. Proximal endite with 3 pinnate spines, one of which robust and fused to endite. Distal endite with 3 pinnate spines. Allobasis drawn out into claw, with accessory armature consisting of 1 pinnate and 2 naked setae. Endopod minute, bearing 2 naked setae.

Maxilliped (Fig. 3F) subchelate. Syncoxa apically with 1 bipinnate seta and several short rows of spinules. Basis with row of spinules along inner margin, with hair-like spinules next to it and short row of spinules distally along outer margin. Endopod drawn out into long, curved, pinnate claw with 1 accessory seta at base.

P1 (Fig. 4A) with slender intercoxal sclerite. Precoxa well developed, triangular, with few outer spinules. Coxa about as long as wide. Basis longer than coxa, forming distinct pedestal for insertion of enp; with 1 strong, inner unipinnate spine, 1 outer bipinnate spine, and 1 anterior tube pore. Exp 3-segmented and enp 2-segmented. Exp-1 bearing 1

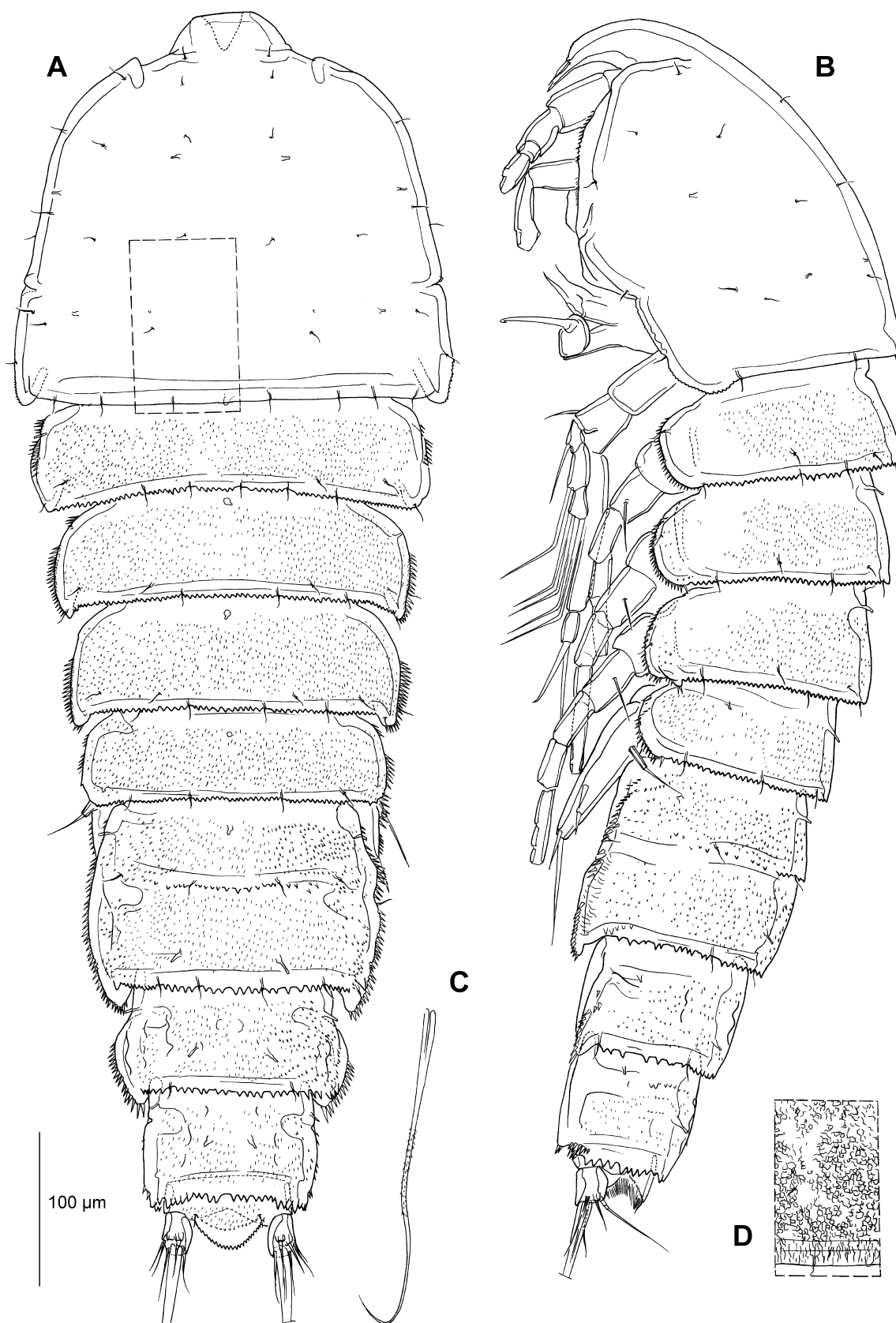


Fig. 1. *Calypsophontodes macropodia* (Gee and Fleeger, 1986). Female, NHMUK 1985.41. A, Habitus, dorsal; B, Habitus, lateral; C, Left caudal seta V; D, Tegumental ornamentation of part of cephalic shield (indicated in A).

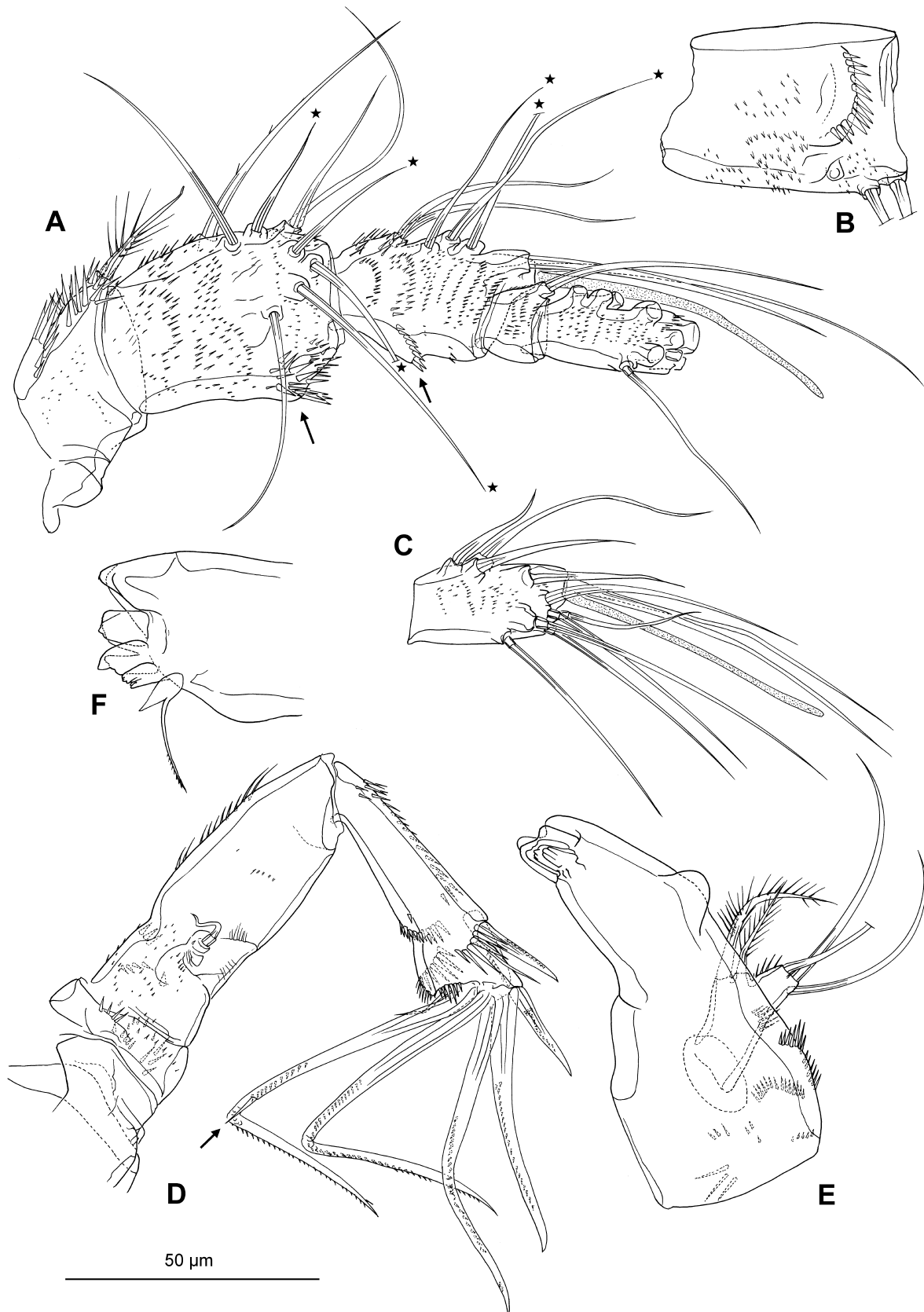


Fig. 2. *Calypsophontodes macropodia* (Gee and Fleege, 1986). Female: (A, B, D, E) NHMUK 1985.41; (C) NHMUK 1985.34; (F) NHMUK 1985.35. A, Antennule, dorsal (asterisks indicate setae added from NHMUK 1985.34, outer bumps on segments 2 and 3 arrowed, setae of segment 5 broken off); B, Antennule segment 2, view of outer margin; C, Antennule segment 5; D, Antenna (pinnule on outermost geniculate seta arrowed); E, Mandible; F, Gnathobase of mandible.

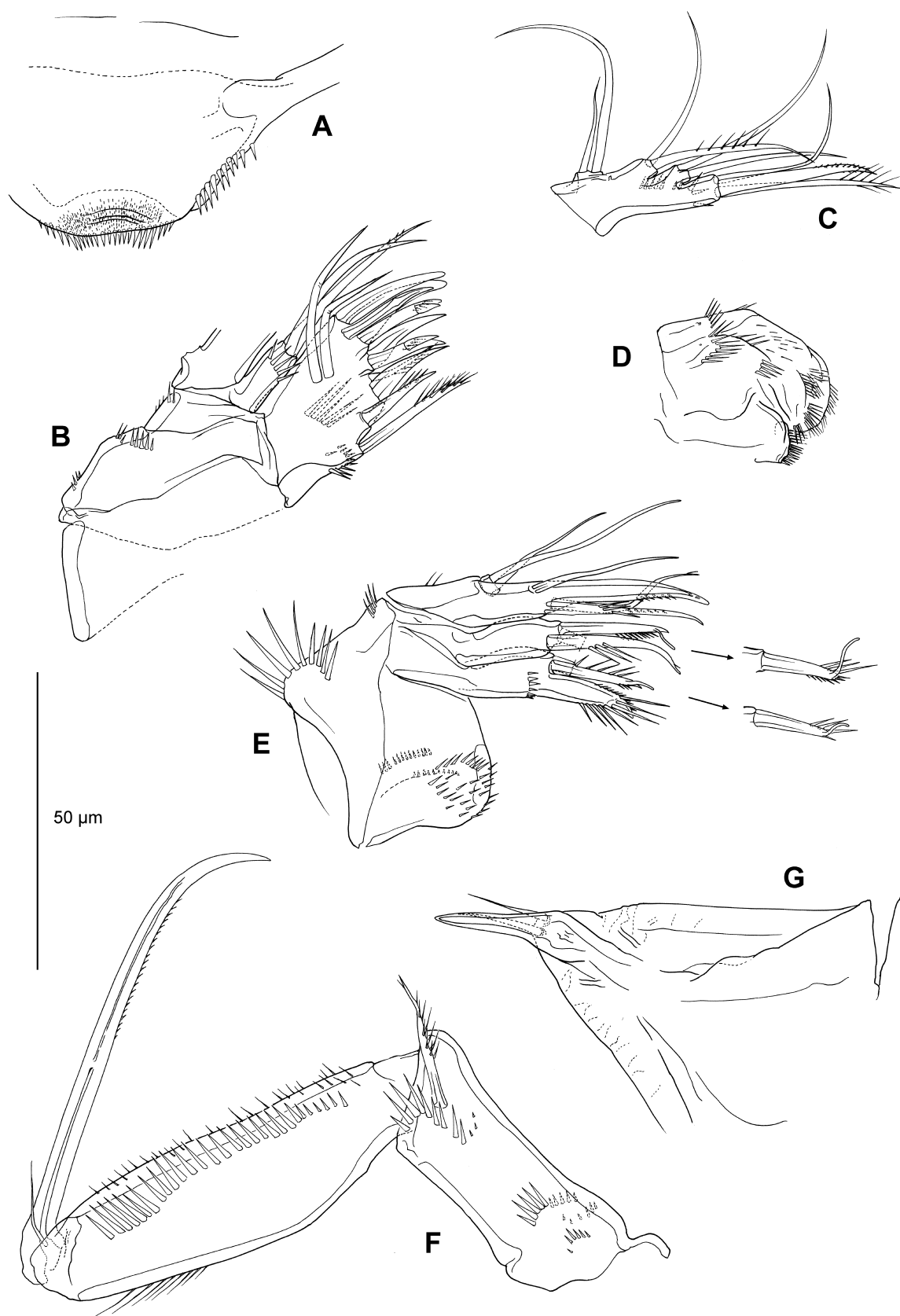


Fig. 3. *Calypsophontodes macropodia* (Gee and Fleeger, 1986). Female, NHMUK 1985.41. A, Labrum, posterior; B, Maxillule (basis, endopod and exopod broken off); C, Basis, endopod and exopod of maxillule; D, Paragnath; E, Maxilla (with posterior spines of proximal and distal endite drawn separately); F, Maxilliped; G, Rostrum, ventral.

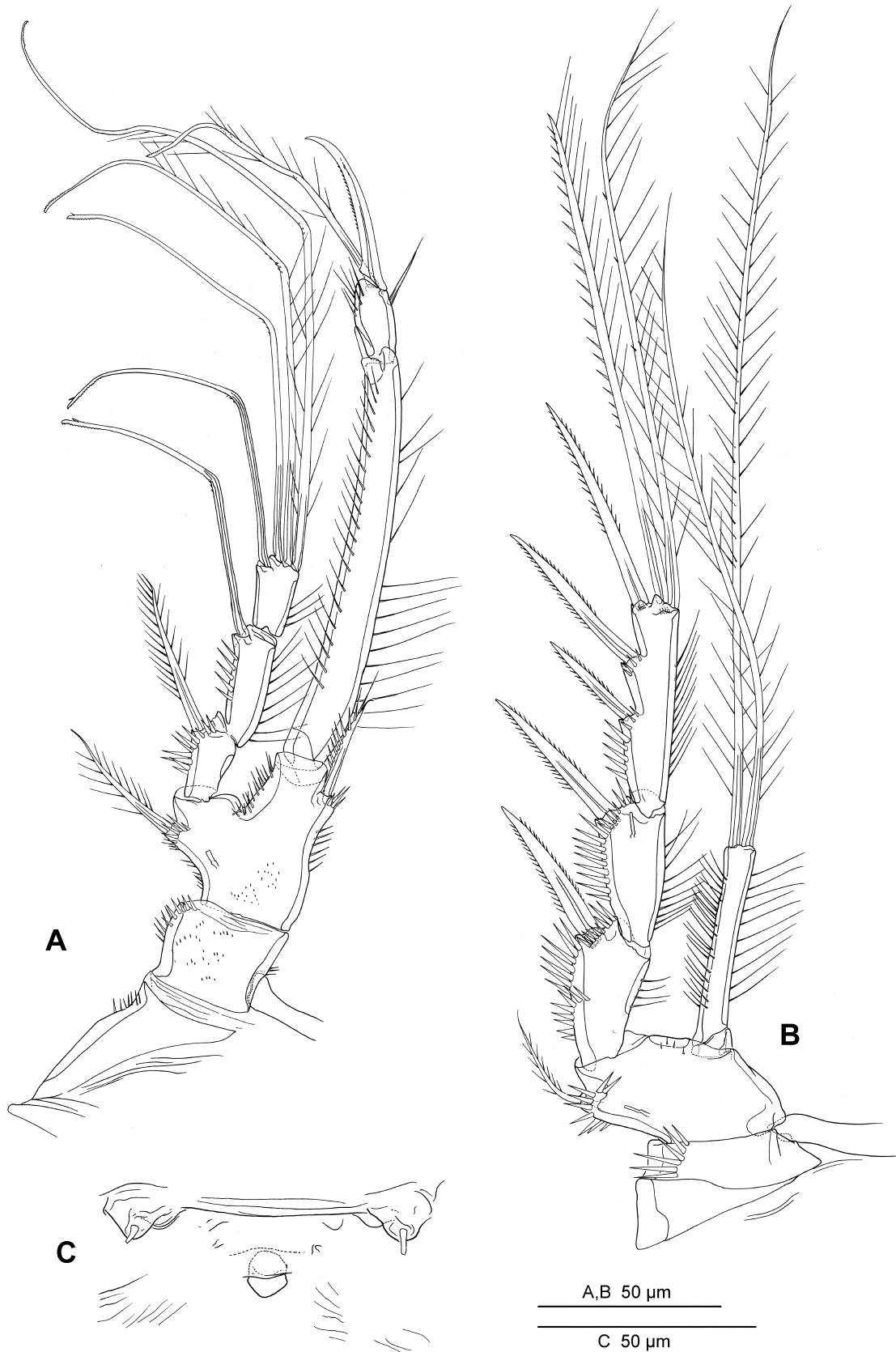


Fig. 4. *Calypsophontodes macropodia* (Gee and Fleege, 1986). Female, NHMUK 1985.41. A, P1; B, P2; C, Genital field.

outer bipinnate spine. Exp-2 longest segment, with 1 outer geniculate, distally serrate seta. Exp-3 bearing 4 geniculate, distally serrate setae, all inserting apically. Enp-1 elongate and slender, 1.7 times as long as exp, with inner and outer row of long spinules. Enp-2 twice as long as wide, with 1 short, slender inner seta, apically with 1 anterior strong, pinnate recurved spine and 1 posterior geniculate, bipinnate, distally serrate seta.

Swimming legs P2-P4 (Figs. 4B, 5A-D) with slender intercoxal sclerites. Precoxae well developed, triangular. Coxae short, with short outer row of strong spinules. Bases transversally elongated; with outer seta bipinnate (P2) or naked (P3-P4); with strong spinules along outer margin, short, fine spinules along inner margin, and 1 anterior tube pore. Exopods 3-segmented, lacking inner setae, with strong spinules along outer margins, and fine, long spinules along inner margins. Exp-2 of P2, exp-3 of P3, and exp-3 of P4 with 1, 2, and 1 tube pore(s), respectively. Endopods 2-segmented. Enp-1 very small, lacking ornamentation. Enp-2 of P2-P4 elongate, with 2 long apical setae; enp-2 of P3-P4 additionally with 1 inner naked seta and 1 outer bipinnate, short spine. Armature formula in Table 1.

P5 (Fig. 6C) robust. Basis, exp, and enp fused to a single plate, about 2 times as long as wide; with anterior tube pore proximally and strong spinules along outer margin. Basal seta on setophore; setophore demarcated at base. Exopodal part with fine spinules along inner margin; bearing 3 outer bipinnate setae, 1 apical tripinnate seta, and 1 inner pinnate seta. Endopodal part protruding, with 1 tube pore medially and 1 spinous process laterally; bearing 2 strong bipinnate setae.

Genital field (Figs. 4C, 6A) positioned anteriorly, with medial copulatory pore. P6 represented by pair of small cuticular plates; each bearing 1 minute blunt seta.

Redescription of Male.—Total body length 630 μm (measured from tip of rostrum to posterior end of caudal rami, in dorsal view); largest width measured at posterior margin of cephalic shield 241 μm (both measures from NHMUK 1985.42). Habitus (Figs. 6D-E, 7A, 10B) as in female, except for fully separated second and third urosomites and distinctly more slender urosome. Posteroventral margin of third urosomite with row of strong spinules. Posterolateral edges of third and fourth urosomites slightly extended laterally and posteriorly. Sexual dimorphism in body size, antennule, P2-P6, urosome width, genital segmentation, and ventral abdominal ornamentation.

Antennule (Fig. 7B-E) 6-segmented, chirocer, geniculation between segments 5 and 6; 1 segment distally to geniculation. Segment 1 short, bearing several rows of spinules and 1 setulose seta. Second segment longest, with striae and small denticles on dorsal surface; outer margin forming bump with patch of strong spinules; tegument next to most proximal outer seta on dorsal surface slightly elevated. Segments 3 and 4 very small. Segment 5 swollen. Segment 6 with 3 modified elements along inner margin, with blunt process on dorsal surface. Armature formula: 1-[1], 2-[9], 3-[8], 4-[2], 5-[11 + 2 modified + (1 + aes)], 6-[8 + 3 modified + (2 + aes)].

Antenna, mandible, maxillule, maxilla, maxilliped, and P1 (Fig. 8A) as in female.

P2-P4 proportionally larger than in female (Figs. 8B, 9A-B, 10B).

P3 (Fig. 9A) with exp slightly flexed inwardly; outer exopodal spines and outer apical spine on exp-3 slightly more strongly developed than in female. Enp 3-segmented; enp-2 elongate with anterior, distal surface produced into elongate apophysis; apophysis twice as long as enp-3 and slightly curved outwardly; enp-3 twice as long as wide, bearing 2 long, plumose apical setae.

P4 (Fig. 9B) with exp flexed inwardly; exopodal segments more robust than in female; outer exopodal spines and outer apical spine on exp-3 more strongly developed than in female. Enp as in female, but lacking inner seta on enp-2.

P5 (Fig. 8C) robust. Basis, exp, and enp fused into single plate; with anterior tube pore proximally and spinules along margins. Basal seta on setophore; setophore demarcated at base. Exopodal part with anterior tube pore near insertion of apical seta; bearing 2 outer bipinnate, 1 apical tripinnate, and 1 inner bipinnate setae, all strong. Endopodal part with 1 tube pore medially; bearing 1 strong bipinnate seta.

Sixth pair of legs (Fig. 6D-E) represented by unarmed minute, membranous flaps; one member fused to ventral wall of supporting somite, one member articulating. Single spermatophore.

Variability of Syntype and Additional Material from Type Locality, and of Own Material from King George Island.—Measurements of body length and width from wholly mounted syntype specimens were not reliable as preparations were in a rather bad condition. Total body length of females in additional material from type locality varied between 687 μm and 789 μm ($n = 5$; mean = 754 μm ; measured from tip of rostrum to posterior end of caudal rami, in dorsal view). The single male NHMUK 1985.42 from additional non-type material measured 630 μm . Total body length of males from King George Island ranged between 661 μm and 743 μm ($n = 4$; mean = 710 μm), while the single female from there measured 796 μm . Swimming legs P2-P4 drawn from male NHMUK 1985.39 are proportionally larger than P2-P4 drawn from female NHMUK 1985.41, a difference that is also clearly noticeable when comparing to the size of the respective P1. The urosome (excluding P5-bearing somite) of dissected male NHMUK 1985.39 measured 278 μm long and extrapolation by using the urosome/body length ratio (of male NHMUK 1985.42: 0.36) gives an estimated body length of 772 μm , which is almost equal to the length of female NHMUK 1985.41. Current observations show that there is sexual dimorphism in size of swimming legs P2-P4, also clearly noticeable when observing the legs in situ (Fig. 10A-B).

In male NHMUK 1985.42, the second endopodal segment of right P1 bears 3 additional long setules along the inner margin (Fig. 9C).

In certain specimens, the anal somite seemed to be partly enclosed by the penultimate somite (in Fig. 1A, but not in Fig. 10A). This might not represent the natural situation, as contraction of body somites due to fixation may be responsible.

Certain structures were overlooked in the original description, namely: 1) pores, sensilla, and fine tegumental ornamentation on body and appendages; 2) certain setae on fe-

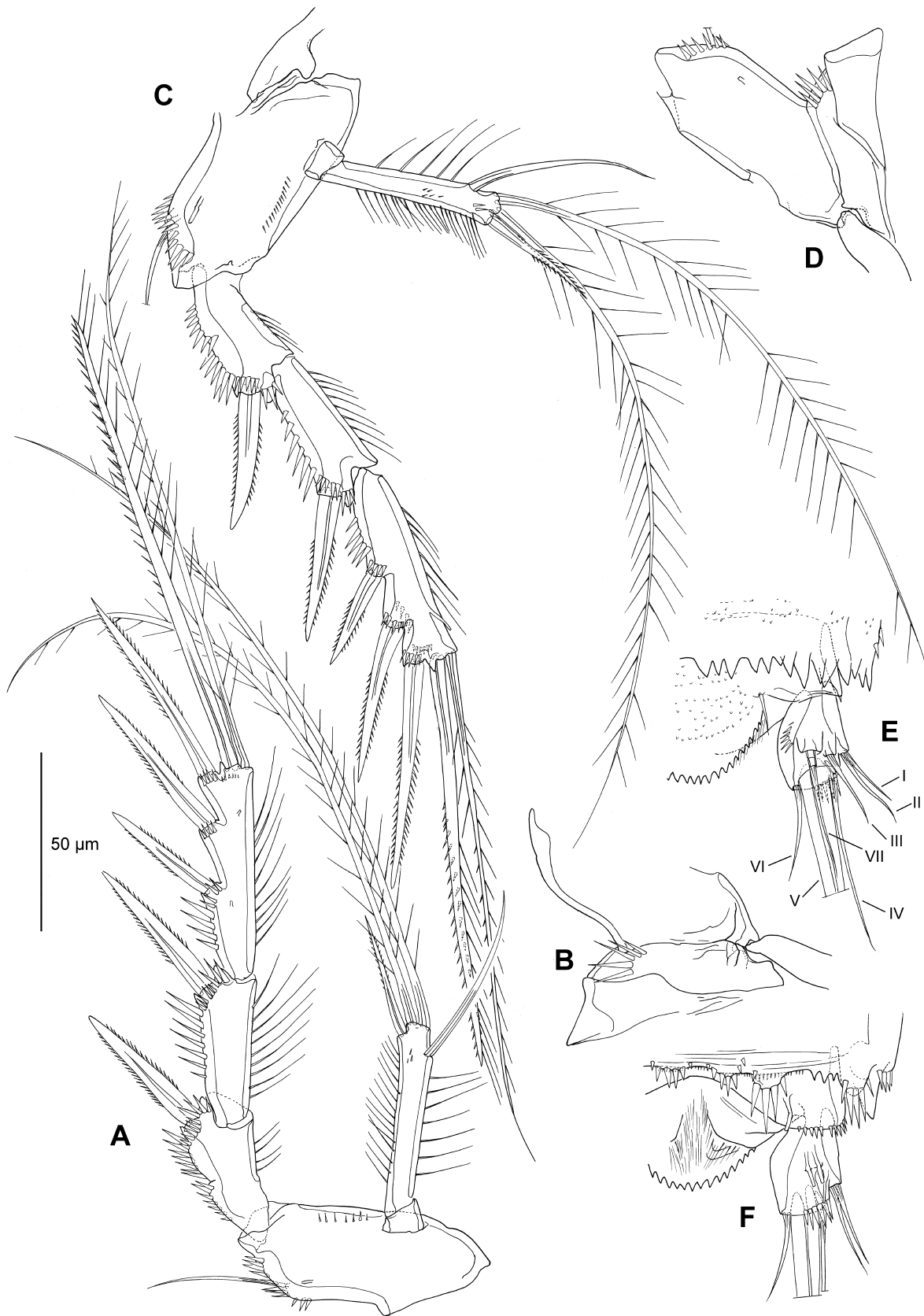


Fig. 5. *Calypsophontodes macropodia* (Gee and Fleeger, 1986). Female: (A, C, E, F) NHMUK 1985.41; (B, D) NHMUK 1985.34. A, P3; B, Precoxa, coxa and basis of P3; C, P4 (basis damaged); D, Precoxa, coxa and basis of P4; E, Caudal ramus (caudal setae labeled with roman numerals I-VII), dorsal; F, Caudal ramus, ventral.

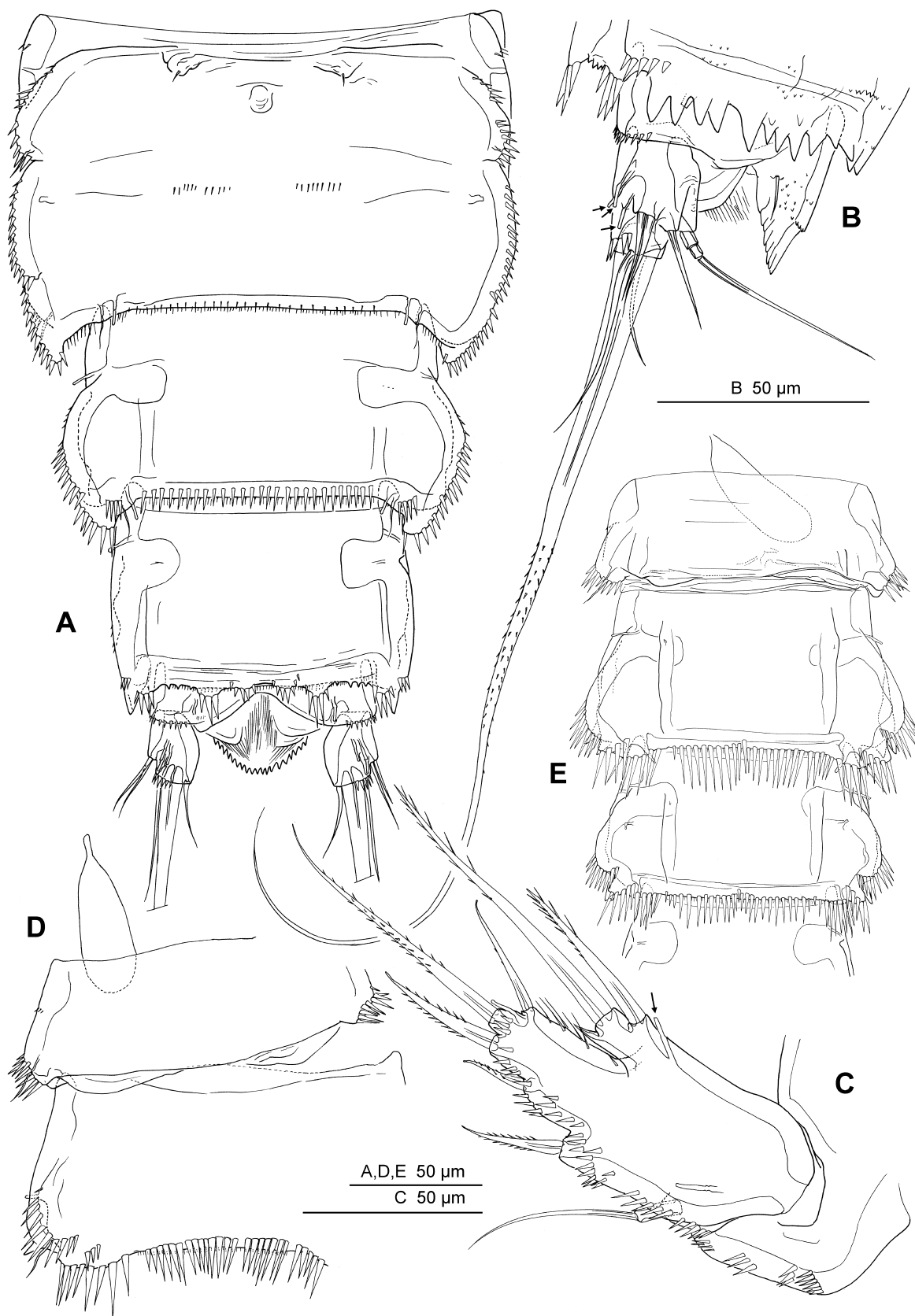


Fig. 6. *Calypsophontodes macropodia* (Gee and Fleeger, 1986). Female: (A, B, C) NHMUK 1985.41. Male: (D) NHMUK 1985.38. Male: (E) own material from Marian Cove. A, Urosome, ventral; B, Penultimate somite, anal somite and caudal ramus (three tube pores arrowed), lateral; C, P5 (tube pore on endopodal lobe arrowed); D, Spermatophore, second and third urosomite (damaged); E, Second to fourth urosomite.

Table 1. *Calypsophontodes macropodia* (Gee and Fleegeer, 1986). Swimming leg setal formula.

	Coxa	Basis	Exopod	Endopod
P1	0-0	I-I	I-0; 1-0; 2,2,0	0-0; 1,I + 1,0
P2	0-0	1-0	I-0; I-0; III,I + 1,0	0-0; 0,2,0
P3	0-0	1-0	I-0; I-0; III,I + 1,0	0-0; I,2,1 [♂: 0-0; 0-0; 0,2,0]
P4	0-0	1-0	I-0; I-0; III,I + 1,0	0-0; I,2,1 [♂: 0-0; I,2,0]

male and male A1, A2, Mx1, and Mx2; 3) antennary exopod; 4) the detailed structure of certain setae, e.g., distally serrate, presence of pinnules; 5) the structure of male P3 endopod as 3-segmented with an apophysis on enp-2 (not as 2-segmented with a subterminal, stout outer spine); 6) sexual size dimorphism in swimming legs P2-P4; and 7) the distinct nature of precoxa and coxa in swimming legs P2-P4 (originally drawn as fused).

Calypsophontodes latissima (Brady, 1918) n. comb.

Laophontodes latissimus Brady, 1918: p. 32-33, plate XI: figs. 1-9.

Type Locality.—Off Macquarie Island, station 1 (tow-net, 2 fathoms (about 3.7 m), 21 June 1912) and station 5 (tow-net at sunrise, 11 June 1912).

Material.—None examined. Brady (1918) reported 2 females, but did not indicate the place of deposition.

Material.—This species is only known from two females collected off Macquarie Island at two stations sampled during the Australian Antarctic Expedition of 1911-1914 (Brady, 1918). Brady (1918) described another two species of *Laophontodes* (*L. antarcticus* Brady, 1918 and *L. echinatus* Brady, 1918) collected during this expedition, but the deficient descriptions forced Lang (1936, 1948) to place all three as species incertae sedis in *Laophontodes*. Conroy-Dalton and Huys (2000) relegated *L. echinatus* to *Breviconia* Conroy-Dalton and Huys, 2000 as a species inquirenda, on account of close similarities with *B. australis* (George, 1998) in body processes, antennule, P3, and P5. *Laophontodes antarcticus* should probably be retained in *Laophontodes* (as shown by the elongate caudal rami and certain characteristics of antennule, P1, and P5), but no firm conclusion can be made because of the lack of detail in the original description. Lang (1948) expressed doubts about the inclusion of *L. latissimus* in *Laophontodes*, as the structure of P5 significantly differs from the condition in other species of this genus. Gee and Fleegeer (1986) considered *L. latissimus* to be closely related to *L. macropodia* based on similarities in body shape and ornamentation, and the structure of last abdominal segment, caudal rami, and P5, but ruled out conspecificity because of differences in setation.

Indeed, certain characteristics point to a close relationship with *L. macropodia*, namely the protruding endopodal lobe of female P5, the absence of inner setae on P3 exopod, the second segment of female A1 being longest, the short caudal rami, and the strongly protruding anal operculum with a serrate margin. Brady's (1918) illustration of the habitus of *L. latissimus* does not show the complete number of body somites, because the anal somite is not properly depicted;

however, in his fig. 3, he shows the anal somite as very short and partly enclosed by the penultimate somite (see above). The antennule was described as 5-segmented, but his drawing (showing 6 segments) is presumably erroneous with the third segment subdivided into two distinct segments. The sutures drawn distally on antennary endopod and proximally on P1 endopod most probably represent observational errors. We consider the distinct endopodal lobe on female P5 (as drawn in his fig. 9) as problematic and maybe representing a malformation, while the short proximal endopodal segments of P2-P4 were probably overlooked. However, based on the above-mentioned similarities with *L. macropodia*, *L. latissimus* is transferred to *Calypsophontodes*, as *C. latissima*, and treated as a species inquirenda. Despite the shortcomings of the original illustrations, conspecificity with *L. macropodia* should be ruled out because of the different setal formula of P3 endopod. In *L. latissimus*, this carries 1 short outer apical seta (which, however, might be the subdistal outer spine) and 1 long inner apical seta, while in *L. macropodia* there are 2 long apical setae, 1 short inner seta, and 1 short outer spine on enp-2 of P3.

DISCUSSION

Gee and Fleegeer (1986) included *L. macropodia* in *Laophontodes* because of similarities in general body shape and ornamentation, the structure of P1, the segmentation of P2-P4, and the presence of three outer spines on the terminal segments of these limbs. Although they noted that the deviating form of the fifth leg might support the establishment of a new genus in Ancorabolidae, they refrained from taking action, instead attributing these differences to intrageneric variability. Based on a thorough comparison with other Laophontodinae, the following comments can be made:

1) Female antennule: In *L. macropodia*, the outer margin of the second and third segments of the female antennule form a slight swelling ('bump'), with a patch (in the second segment) and row (in the third segment) of stout spinules. Conroy-Dalton (2004) identified the presence of posterior setular tufts on the second and third antennular segments as one of the characters indicating a close relationship of the *Lobopleura-Probosciphontodes* lineage with *Tapholaophontodes* Soyer, 1974 and *Algensella* Cottarelli and Baldari, 1987. These tufts as well as inserted on bump-like projections along the outer margins. Gheerardyn and George (2010) pointed out that an outer bump with long spinules on the second antennular segment is widespread in Laophontodinae (and also *Ancorabolina*), and this structure appears not to be exclusive to the above-mentioned genera. Certain older descriptions probably missed this structure, and this prevents us from drawing firm conclusions now, but potentially this structure represents an apomorphy for Laophontodinae (including *Ancorabolina*). On the other hand, a bump-like projection with spinular/setular elements on the third segment of the female antennule appears to be restricted to *L. macropodia*, *Lobopleura*, *Probosciphontodes*, *Tapholaophontodes*, and *Algensella*, indicating a possible close relationship between these taxa.

The tegument next to one subapical dorsal seta on the second antennular segment is strongly developed and slightly elevated in *L. macropodia*. Conroy-Dalton (2004) detected a

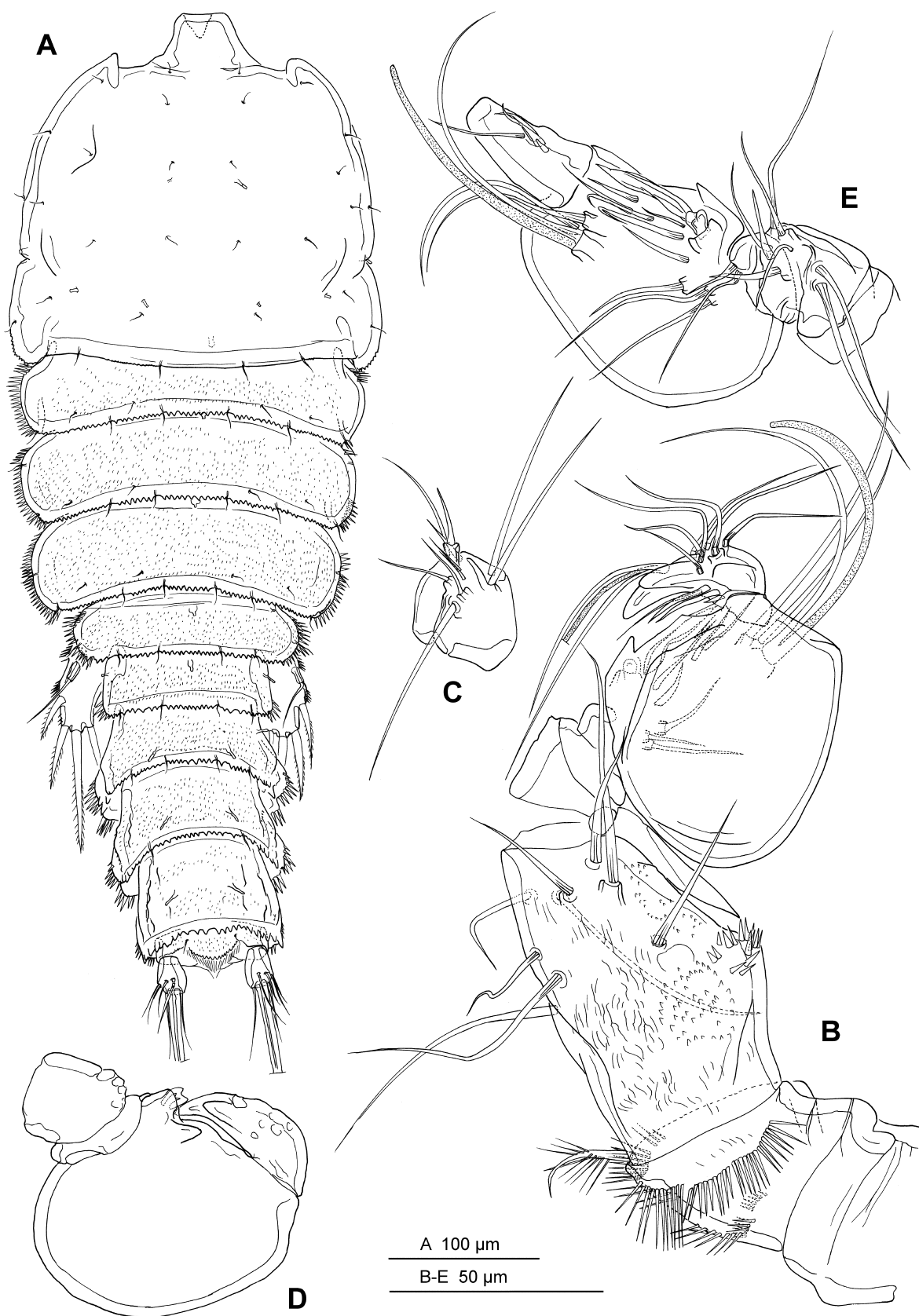


Fig. 7. *Calypsophontodes macropodia* (Gee and Fleeger, 1986). Male: (A, C, D) NHMUK 1985.42; (B) NHMUK 1985.40; (E) own material from Edgell Bay. A, Habitus, dorsal; B, Right antennule (ornamentation of segments 3 and 4 omitted), dorsal; C, Segments 3-4 of left antennule; D, Segments 3-6 of right antennule (ornamentation omitted), dorsal; E, Segments 3-6 of right antennule (ornamentation of segment 6 partly omitted), ventral.

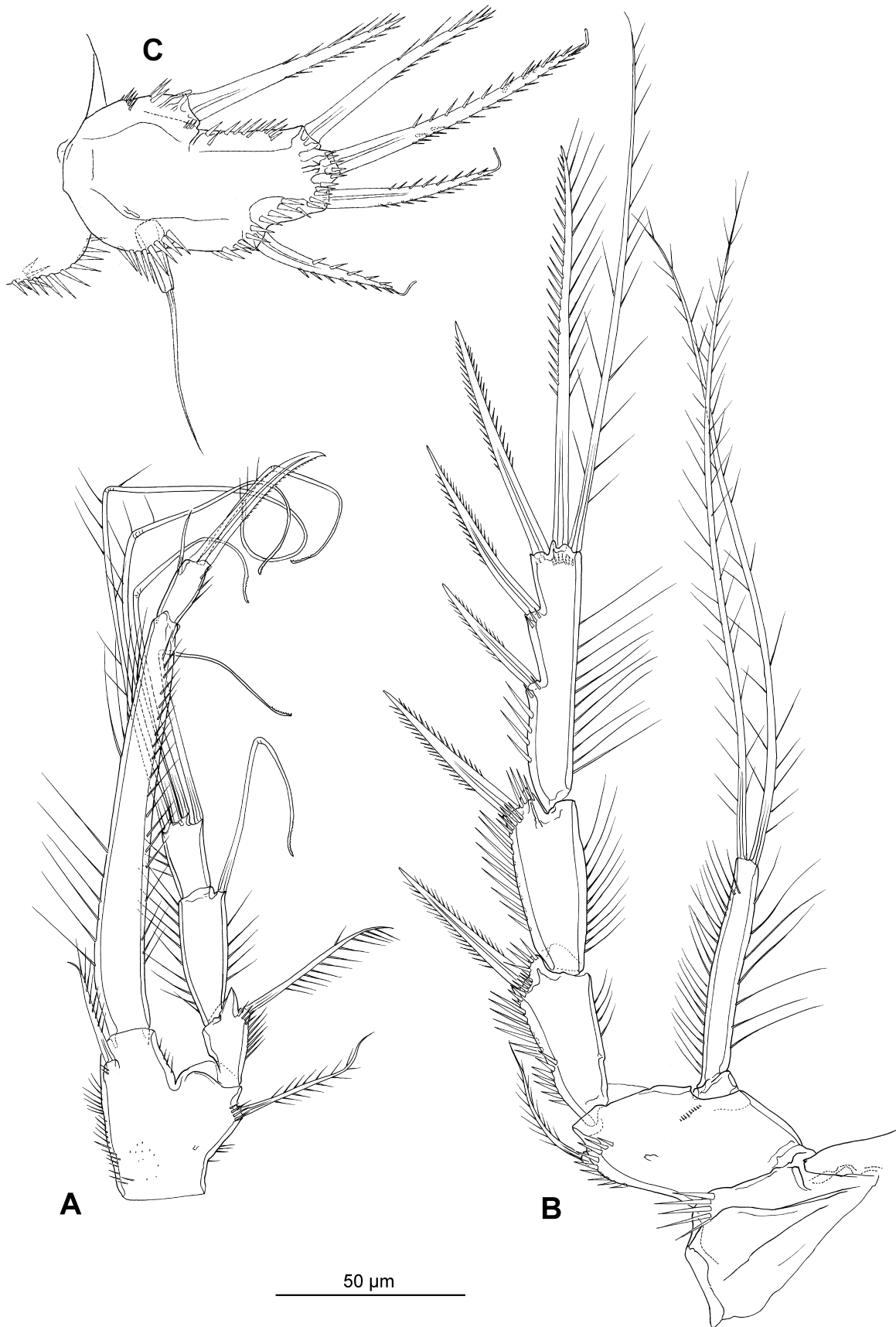


Fig. 8. *Calypsophontodes macropodia* (Gee and Fleege, 1986). Male: (A-B) NHMUK 1985.39; (C) NHMUK 1985.38. A, P1; B, P2; C, P5.

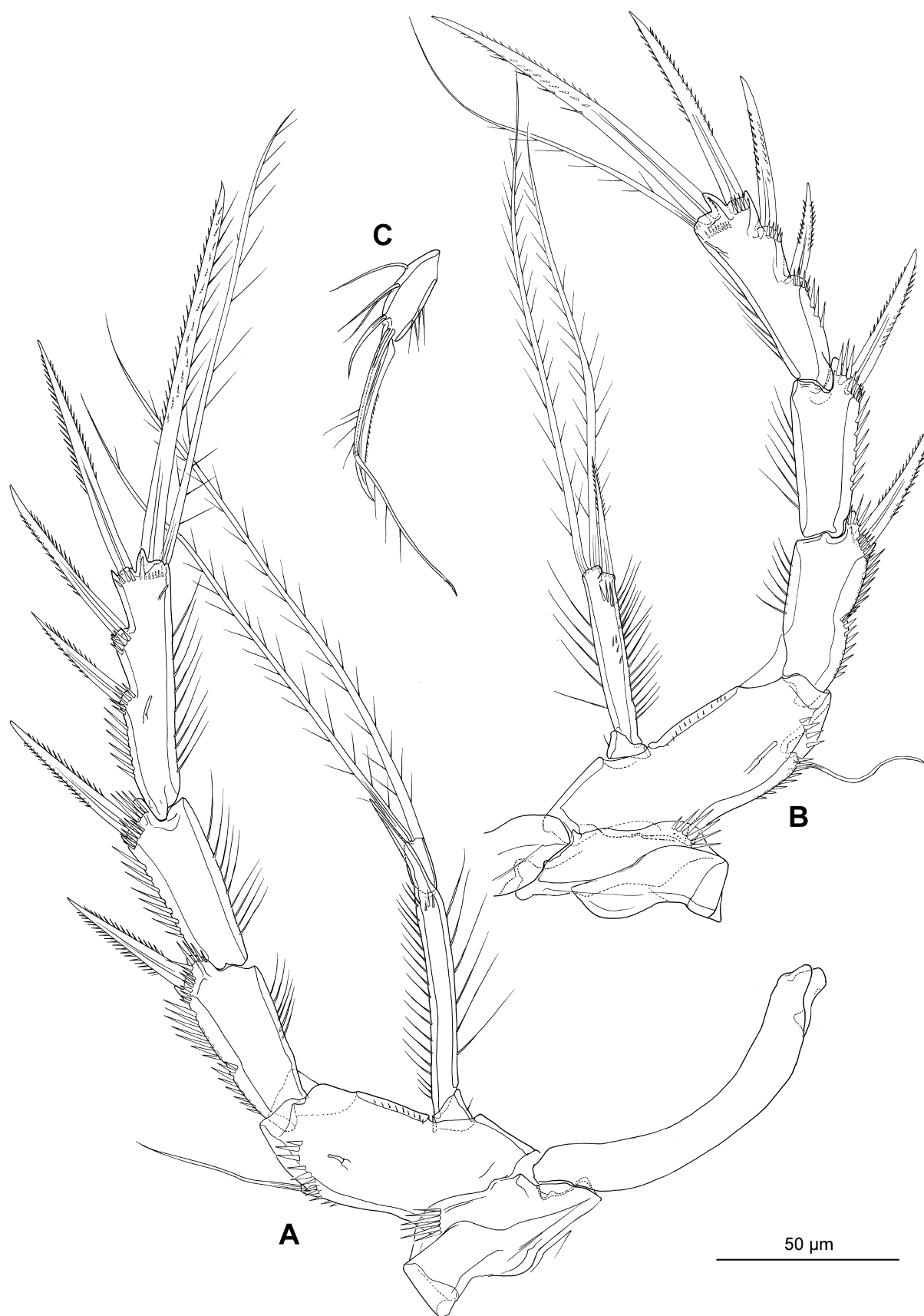


Fig. 9. *Calypsophontodes macropodia* (Gee and Fleege, 1986). Male: (A-B) NHMUK 1985.39; (C) NHMUK 1985.42. A, P3; B, P4; C, enp-2 of right P1, posterior.

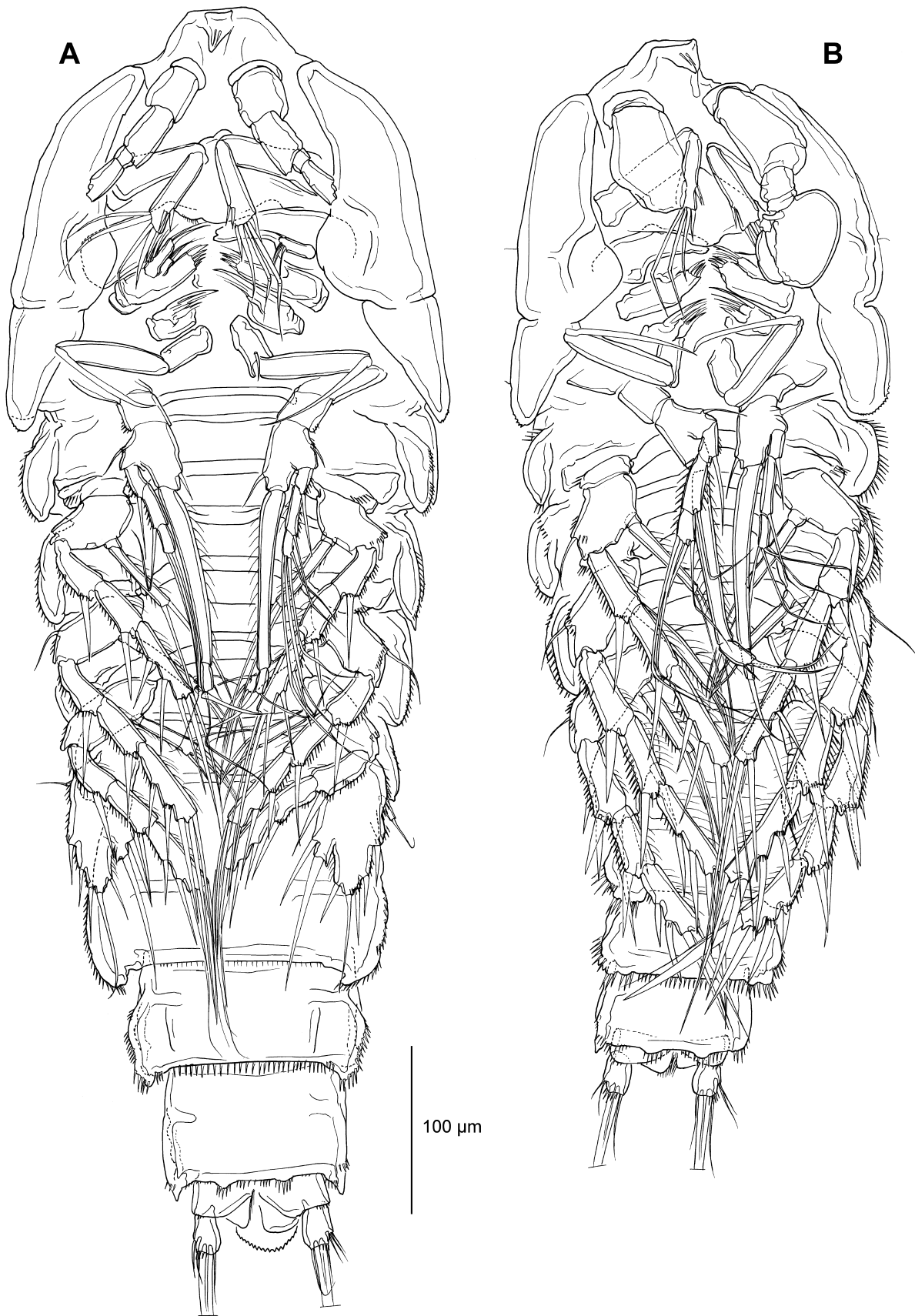


Fig. 10. *Calypsophontodes macropodia* (Gee and Fleege, 1986). Female: (A) NHMUK 1985.43. Male: (B) NHMUK 1985.42. A, Habitus, ventral; B, Habitus, ventral.

similar structure at the same site on the antennule of *Lobopleura ambiducti* Conroy-Dalton, 2004, and described it as “1 dorsal subapical seta arising from a bulbous projection.” As this structure is easily overlooked, it is impossible to assess its presence in other Laophontodinae from the available descriptions and, therefore, its phylogenetic significance remains unclear at present. However, this observation draws attention to the need of homologizing processes on the antennular segments, which can be important in assessing phylogenetic relationships at higher taxonomic levels.

2) Structure of P1: In the ground pattern of Laophontodinae the P1 endopod consists of an elongate proximal segment (with no inner seta) and a short distal segment that bears one short, slender inner seta and two apical elements, namely an anterior claw-like spine and a posterior long seta. The second small inner seta on enp-2 of P1 in *L. ambiducti* should be considered as a supernumerary element and not constituting the ground pattern, as it appears not to be present in remaining Laophontodinae nor in any related major taxa. The exopod of P1 primitively consists of three segments, with an outer spine on the first, an outer geniculate seta on the second, and two outer and two apical geniculate setae on the third segment. The geniculate nature of the outer seta on the second exopodal segment of P1 might be a synapomorphy for all Laophontodinae (including *Ancorabolina*). The only exceptions occur in certain older descriptions (in which the geniculation was likely overlooked, i.e., in *L. ornatus* Krishnaswamy, 1957, *L. propinquus* Brady, 1910, and *L. latissimus*); in *Paralaophontodes elegans* Baldari and Cottarelli, 1986 and *P. echinatus* (Willey, 1930) (which bear only four geniculate setae on the second segment of their two-segmented exopod, implying that one seta has been lost); and in *Patagoniaella vervoorti* Pallares, 1968 (the inclusion of which in Laophontodinae is unsatisfactory, as shown by the strongly deviating P1). All Ancorabolinae (excluding *Ancorabolina*) retain the primitive condition of a non-geniculate outer spine on the second exopodal segment of P1 (or the equivalent element in a two-segmented exopod). In this subfamily, there is only one clear exception, in *Echinopsyllus brasiliensis* Wandenness, George, and Santos, 2009, in which the geniculation of this element has evolved convergently. Also, Smirnov's (1946) drawing of P1 in *Polyascophorus gorbunovi* (Smirnov, 1946) seems to show a geniculate element but lacks sufficient detail to be certain. Gheerardyn and George (2010) drew attention to the widespread occurrence of a lengthways elongate P1 coxa in Laophontodinae and *Ancorabolina*, but concluded that the usefulness of this character is limited. In *Laophontodes macropodia*, the P1 coxa seems rather short.

3) Swimming legs P2-P4: Gee and Fleeger (1986) stated that *L. macropodia* differs in setation of the first four swimming legs from other species of *Laophontodes* (at that time), without providing further details. Within Laophontodinae, *L. macropodia* is the only species retaining an outer spine on the second endopodal segment of the female P3, evidence of its basal position in the subfamily. In her redescription of *L. armatus* Lang, 1936 based on material from Puerto Deseado (Argentina), Pallares (1968b) showed the P3 endopod with one subdistal seta. As no other parts of the swimming leg were drawn, it is unclear whether she depicted an inner

or outer seta. Her redescription differs significantly in number of endopodal setae on P3, P4, and P5 from *L. armatus* described by Lang (1936) from the Falkland Islands, and we suspect the material from Puerto Deseado represents another species. Despite the absence of ontogenetic evidence, it is likely that the outer apophysis in the male P3 endopod of *L. macropodia* is homologous with the outer spine on the female second endopodal segment. This would be consistent with the statement by Huys and Lee (1999) that the modification of the male P3 endopod in the “canthocamptoid complex” (including Cletodidae, Ancorabolidae, Canthocamptidae, and the families of Laophontoidea) is derived from a single ancestral pattern.

Within Laophontodinae, *L. macropodia* shows a unique sexual dimorphism in the endopod of P4, in which the inner seta on the second segment is lost in the male. *Laophontodes hedgpethi* Lang, 1965 also shows sexual dimorphism in this leg, but with the inner subdistal seta present in the male and absent in the female. In Ancorabolinae, the loss of the inner seta on male enp-2 of P4 is considered an autapomorphy of *Arthropsyllus* Sars, 1909 (Conroy-Dalton and Huys, 2000), and should be regarded as having occurred convergently with *L. macropodia*.

Male swimming legs P2-P4 in *Laophontodes macropodia* are proportionally larger than in the female, with an increase in size from P4 to P2. In addition, in the male the P3 and P4 exopods are slightly flexed inwardly, with all outer spines and the outer apical spine on the third segment more strongly developed than in the female. This is clearer in P4, in which additionally the exopodal segments are more strongly developed. Sexual dimorphism in size (rather than form) of P2-P4 has not been reported before in Laophontodinae, and might be unique to *Calypsophontodes*.

Within Laophontodinae, exopodal modifications of the swimming legs have only been reported within males of *Tapholaophontodes*. Bodiou and Colomines (1988) described the exopodal segments of P4 in *T. laurenceae* Bodiou and Colomines, 1988 as being shorter in males than females, and bearing a very strong outer spine on the two proximal segments. Also, their drawing of the male P3 seems to show the third exopodal segment slightly shorter than in the female. In *T. rollandi* Soyer, 1974, the outer spines on the third exopodal segment of P3 are more strongly developed in the male than the female and the P4 exopodal segments are short and very robust, with the outer spines and outer apical spine very strongly developed (Soyer, 1974).

4) Structure of P5: As pointed out by Gee and Fleeger (1986), the robust, broad P5 with a protruding endopodal lobe in the female is highly different from the typical situation in *Laophontodes*, and the presence of an endopodal lobe is a less derived state compared to the remaining Laophontodinae. In *Laophontodes typicus* T. Scott, 1894 (and for example also in *L. bicornis* A. Scott, 1896, *L. whitsoni* T. Scott, 1912, and *L. macclintocki* Schizas and Shirley, 1994), the baseo-endopod and exopod are longitudinally elongated and slender, and there is no protruding endopodal lobe. Further, in these species the exopod and baseo-endopod of P5 are distinct in the female but fused in the male, while in *L. macropodia*, they are fused in both the male and female. However, the fusion of baseo-endopod and exopod in the female P5

occurs throughout Laophontodinae, even in species closely related to *L. typicus* (e.g., *L. mourois* Arroyo, George, Benito and Maldonado, 2003 and *L. spongiosus* Schizas and Shirley, 1994). This fusion probably occurred several times convergently, which renders its phylogenetic value low.

5) Body shape: The robust habitus of *L. macropodia* is considerably different from that in *Laophontodes typicus* and other 'typical' *Laophontodes* species (such as *L. bicornis* and *L. whitsoni*), which exhibit a narrow and elongated body shape with virtually cylindrical body somites. In *L. macropodia*, the genital double-somite and following urosomite are ventrally flattened and their pleural regions are ventrolaterally expanded into posteriorly directed processes. This shape seems to be unique within Laophontodinae, and different from the situation in *Lobopleura* and *Probosciphontodes*, in which these somites are laterally extended into lobate processes. Ventral flattening and ventrolateral expansion with posteriorly directed processes in the genital double-somite and following urosomite occurs quite commonly within the Laophontidae (see Fiers, 1993: figs. 5c, 9a; Lee and Huys, 1999: fig. 2B; Gheerardyn et al., 2006: figs. 4A, 9A), and can also be recognized, albeit less distinctly, in the Cletodidae (Fiers, 1996: fig. 2A) and Normanellidae (Lee et al., 2003: fig. 2A). Furthermore, the presence of lateral extensions on all but the last two body somites is considered a synapomorphy shared by all genera of the *Ancorabolutus*-lineage (Conroy-Dalton and Huys, 2000). The shapes of body somites are, however, difficult to homologize and a phylogenetic analysis of the complete "canthocamp-toid complex" is needed to elucidate whether these similarities point to common ancestry or are the result of convergent evolution.

Laophontodes macropodia is here fixed as the type of a new genus *Calypsophontodes*, on account of the sexually dimorphic setation on the second endopodal segment of P4 (inner seta present in female, absent in male) and the sexual size dimorphism in swimming legs P2-P4. The following diagnostic characters might also prove to have some phylogenetic significance: the strongly elongate and ventrally curved rostrum [but also present in *Laophontodes gracilipes* Lang, 1936 (see redescription by Kornev and Chertoprud, 2008) and within *Ancorabolina*], the broad shape of male and female P5, and the well-developed anal operculum with serrate margin. In addition, *L. macropodia* exhibits a number of plesiomorphic characters: 1) presence of antennary exopod, 2) presence of ten apical elements on precoxal arthrite of maxillule, 3) presence of outer spine on second endopodal segment of P3, 4) protruding endopodal lobe in female P5, and 5) short caudal rami. The description of *L. latissimus* lacks detail, but the transfer of this species to *Calypsophontodes* as a species inquirenda is supported by strong similarities in the female P5, anal somite, and caudal rami.

Within Laophontodinae, Conroy-Dalton (2004) provisionally placed the *Lobopleura-Probosciphontodes* lineage as most closely related to *Tapholaophontodes* and *Algen-siella* on account of the common absence of distinct dorsal body processes, presence of posterior setular tufts on female antennule segments 2 and 3, reduced setation of the maxillary basis and maxillary allobasal claw, and the morphology

of P1-P4. She warned, though, that the phylogenetic significance of these characters had not been proven. With this group of genera, *Calypsophontodes* appears to share the absence of dorsal body processes, the rather short bases of P2-P4, and the presence of a bump with spinules on the third segment of the female antennule (see above), with the last character probably being the only apomorphic one. The newly established genus seems to be less closely related to *Laophontodes* and *Paralaophontodes*, which have been regarded as sister-taxa by Fiers (1988) on account of the sculpted dorsal body surface and the transversely strongly extended bases of P2-P4. Further, Fiers (1988) noted that the lateral sides of the bodies in members of these two genera are strongly sclerified and the lateral side of their cephalothorax features one or two curved expansions. With certainty, and as already mentioned by Fiers (1986) and George (2006a), *Laophontodes armatus*, *L. hedgpethi*, and *L. psammophilus* Soyer, 1974 are very closely related to *Paralaophontodes* Lang, 1965 based on following shared derived characteristics: 1) second endopodal segment of P1 strongly elongated, 2) cephalothorax with dorso-median ridge-like structure and two pairs of triangular expansions laterally, and 3) presence of dorsal processes along the posterodorsal margin of all somites (except the anal somite). Re-examination of most other species of *Laophontodes* (and especially of the type species *L. typicus*) is necessary to confirm the condition of above-mentioned characters in these species, because at least in older (re)descriptions (Sars, 1908), details of the dorsal body surface have been omitted (according to Fiers, 1988).

As mentioned in the introduction, Gheerardyn and George (2010) detected several characters that are widespread in the Laophontodinae and also present in *Ancorabolina*, but absent in the remaining Ancorabolinae. Further research should clarify whether the bump with spinules on the second antennular segment and the presence of a geniculate seta on the second exopodal segment of P1 are synapomorphies that would support the inclusion of *Ancorabolina* into Laophontodinae, thereby rejecting the inclusion of *Ancorabolina* within Ancorabolinae on account of the absence of an antennary exopod and the presence of a 'peak' (as described by George, 2006b) on the cephalothorax.

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