

SYSTEMATICS AND PHYLOGENY OF THE ANCORABOLIDAE
(COPEPODA: HARPACTICOIDA). V. DESCRIPTION OF *LOBOPLEURA*,
NEW GENUS, WITH NOTES ON *PROBOSCIPHONTODES* FIERS

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A B S T R A C T

Both sexes of a new genus and species, *Lobopleura ambiducti* (Copepoda, Harpacticoida), are described from a sandy beach on the Isle of Iona, Scotland. Within the family Ancorabolidae, the new genus is characterised by the following autapomorphies: paired genital system in both sexes; male P3 endopod-2 not secondarily subdivided; P4 endopod with only one apical seta and P5 baseoendopodal armature reduced to one vestigial seta. *Lobopleura ambiducti* is unique within the subfamily Laophontodinae in exhibiting the most plesiomorphic armature pattern on P1 endopod-2. Aspects of pre-copulatory mate guarding behaviour are discussed. Despite the absence of type material for direct comparison, *Laophontodes expansus* Sars, 1908, is transferred to *Lobopleura* based on the following combination of characters: dorsoventrally depressed body shape; somites with laterally produced lobate processes; wide bell-shaped cephalothorax; rostral shape and detailed morphology of antennule, antenna, mouthparts and first to fifth thoracopods. Material previously identified as *Laophontodes* sp. from County Dublin, Ireland, and *Laophontodes expansus* from Gullmarfjord, Sweden, proved upon re-examination to be conspecific with *L. ambiducti*, new genus, new species. An updated generic diagnosis is provided for *Probosciphontodes* Fiers, 1988, resulting from the re-examination of type material of *Probosciphontes stellata* Fiers, 1988, and *P. ptenopostica* Fiers, 1988. The presence of a minute antennary exopod bearing a single (reduced) seta is confirmed in all material of *Lobopleura* and *Probosciphontodes* examined. The strong support for a sistergroup relationship between *Lobopleura* and *Probosciphontodes* is discussed.

The family Ancorabolidae was established by Sars (1909) for four monotypic genera: *Ancorabolus* Norman, 1903; *Arthroposyllus* Sars, 1909; *Ceratonotus* Sars, 1909; and *Echinopsyllus* Sars 1909. Lang (1936a, b) significantly widened the boundaries of the Ancorabolidae by transferring two genera to this family, *Laophontodes* Scott, 1894, from the Laophontiidae, and *Echinocletodes* Lang, 1936, from the Cletodidae.

Lang (1944, 1948) subsequently divided the Ancorabolidae into two subfamilies: the Laophontodinae, containing only *Laophontodes*, and the Ancorabolinae, comprising all remaining genera. The phylogenetic grounds for this subdivision are dubious because several of the few diagnostic characters applied by Lang (1948) are either not exclusive or are ambiguous. For example, the prehensile nature of the P1 endopod has traditionally been used to define the Laophontodinae, whereas the transversely prolonged P1 basis was selected to diagnose the Ancorabolinae. Within the latter, a graded trend in P1 morphology can be noted in the transverse elongation of the basis, the modification of the

endopod (ranging from secondary elongation to complete absence), and the transformation of endopodal armature elements (Conroy-Dalton and Huys, 2000; Conroy-Dalton, 2001, 2003a, b). Similarly, the principal character defining the family Ancorabolidae, the absence of an antennary exopod, is invalid since a minute one-segmented exopod bearing a single seta has been reported in some species (Pallares, 1975; Soyer, 1975; Mielke, 1981) and personal observations confirm this condition to be widespread in the Laophontodinae (see below).

Recent studies on the evolutionary systematics of the Ancorabolinae have resulted in the recognition of two distinct lineages, the *Ancorabolus*-group (Conroy-Dalton and Huys, 2000) and the *Ceratonotus*-group (Conroy-Dalton, 2001, 2003a) and have addressed the taxonomic status of *Echinopsyllus* (Conroy-Dalton, 2003b) and *Echinocletodes* (Conroy-Dalton and Huys, in press). The Laophontodinae has seen the addition of five new genera (*Paralaophontodes* Lang, 1965; *Patagoniaella* Pallares, 1968; *Tapholaophontodes* Soyer, 1975; *Algeniella* Cottarelli and Baldari, 1987; *Probosciphontodes*

Fiers, 1988); however, the relationships among them and to other Ancorabolidae are not well understood. This paper is the first towards a revision of the Laophontodinae, describing a new genus *Lobopleura*, from a Scottish sandy beach and addressing its relationship with *Probosciphontodes*. The revision of the type genus *Laophontodes*, its alleged sistergroup *Paralaophontodes* (cf. Fiers, 1988), and the three remaining genera within the Laophontodinae will be the subject of a forthcoming paper.

MATERIALS AND METHODS

Material of *Lobopleura ambiducti* gen. et sp. nov. was collected by the Karaman-Chappuis method (Delamare Deboutteville, 1954) at the low-tide mark of the sandy beach. Interstitial water was collected and passed through a 38 µm mesh size sieve, and the residue was preserved in 70% ethanol. The harpacticoid copepods were picked out in the laboratory under a dissecting microscope and preserved in alcohol with a few drops of glycerin added.

Specimens were cleared and dissected in lactic acid and the dissected parts were mounted in lactophenol. Preparations were sealed with transparent nail varnish. All drawings have been prepared using a *camera lucida* on a Leitz Diaplan microscope equipped with differential interference contrast.

The descriptive terminology for body and appendages is adopted from Huys and Boxshall (1991). Abbreviations used in the text and figures are: ae, aesthetasc; P1–P6, first to sixth thoracopod; exp(enn)-1(2, 3) to denote the proximal (middle, distal) segment of a ramus; CI–CIV, first to fourth copepodid stage. The term acrothek is used to denote the trifold setal complement found apically on the distal antennular segment.

Type material was deposited in the Natural History Museum, London, UK (NHM). Additional material examined in this study includes: (1) the type material of: *Laophontodes expansus* from the collections of G. O. Sars at the Zoologisk Museum, Oslo, Norway (ZMO); *Probosciphontodes stellata* and *P. ptenopostica* from the collections in the Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussels, Belgium (KBIN); and (2) additional material of: *L. expansus* from the collections of K. Lang at the Naturhistoriska Riksmuseet, Stockholm, Sweden (SMNH); *Laophontodes* sp. from the collections of K. Roe at the National Museum of Ireland, Dublin, Ireland (NMI); and *Lobopleura ambiducti* collected in Ireland by E. McCormack, deposited in the collections of the NHM.

Scale bars in figures are indicated in µm.

SYSTEMATICS

Family Ancorabolidae Sars, 1909 Subfamily Laophontodinae Lang, 1944 *Lobopleura*, new genus

Diagnosis.—Laophontodinae. Body strongly dorsoventrally depressed, tapering slightly posteriorly, without clear demarcation between prosome and urosome; without dorsal processes; with series of lobate, laterally produced processes

on thoracic somites bearing P2–P5, P6-bearing somite (genital half of double-somite in ♀), first abdominal somite (abdominal half of double-somite in ♀) and second abdominal somite; all processes with strong spinules. Cephalothorax wide and bell-shaped; lateral margins fringed with long, fine, closely set spinules. All integumental sensilla simple and unmodified (not branched or flame-shaped). Somatic hyaline frills weakly developed and smooth. Body, swimming legs, P5 and caudal rami with conspicuous tubepores. Anal operculum rounded and setulose. Caudal rami elongate and divergent, with 7 setae; setae I and II inserted halfway along ramus; seta III sub-distal; seta IV fused basally to seta V; seta V well developed, pinnate; seta VI reduced; dorsal seta VII triarticulate at base, inserted subdistally; ♂ caudal rami proportionally more slender than in ♀.

Sexual dimorphism in body size, antennule, P3 endopod, P5, P6, genital segmentation, abdominal ornamentation and caudal rami.

Rostrum large, basally constricted; fused to cephalic shield; with paired membranous projections proximal to sensilla; with distinctive, long midventral tube-pore subdistally. Antennule 4-segmented in ♀, 6-segmented and subchirocer in ♂ (where known), with one segment distal to geniculation; aesthetasc arising from segments 3 and 4 in ♀, segments 5 and 6 in ♂; segment 1 (both sexes) with strong setulose seta; segments 2 (both sexes) and 3 (♀) each with raised spinule tuft along posterior margin. Antenna with allobasis showing partial suture marking original segmentation, abexopodal margin with distal (endopodal) seta; exopod represented by tiny segment bearing 1 seta; endopod with 1 seta and 2 spines laterally and with 6 distal elements (2 spines, 2 geniculate setae, and 1 geniculate pinnate spine basally fused to tiny naked seta). Mandible with slender coxa bearing pinnate dorsal seta; palp 1-segmented with rami completely incorporated, with 6 setae. Maxillule with 2 elements on coxal endite, 1 reduced; basis with 3 setae on proximal and 2 setae on distal endite, endopod and exopod completely incorporated into basis. Maxillary syncoxa with 2 well-developed endites, each with 3 elements; allobasis drawn out into claw with 2 accessory elements; endopod minute with 1 seta. Maxilliped subchelate; syncoxa with 1 seta; endopod drawn out into curved claw with reduced accessory seta.

P1–P4. Intercoxal sclerites transversely elongate; coxae trapezoid (P1), quadrangular

(P2–P4); bases transversely elongate (P2–P4) or rectangular (P1). P1 exopod 3-segmented; exp-3 small with 4 geniculate setae; endopod 2-segmented, prehensile; enp-1 without armature; enp-2 with 1 recurved spine, 1 robust seta, and 2 reduced setae. P2–P4 exopods 3-segmented, without inner setae; exp-3 with 3 outer spines, inner distal seta reduced. P2 endopod absent or 2-segmented; P3–P4 endopods 2-segmented (both sexes); P3 enp-2 ♂ (where known) with short apophysis on enp-2. Armature formula (for both sexes) as follows:

	Exopod	Endopod
P1	0.0.022	0.211
P2	0.0.023	absent or 0.020
P3	0.0.023	0.020
P4	0.0.023	0.010

P5 with fused exopod and baseoendopod; basal setophore cylindrical, demarcated at base; endopodal lobe vestigial, represented by 1 tiny seta and 1 conspicuous tube-pore; exopod elongate with 1 inner, 1 apical, and 3 (♀) or 2 (♂) outer elements. Female genital field located anteriorly; genital system paired; gonopores covered by genital operculum derived from P6, each armed with 1 vestigial element; with small, paired copulatory pores, located at inner limit of genital operculum. Male P6 symmetrical; without armature; both members with functional articulation, represented by membranous flap; with paired gonopores and *vasa deferentia*.

Type Species.—*Lobopleura ambiducti*, new species.

Other Species.—*Lobopleura expansa* (Sars, 1908), new combination.

Etymology.—The generic name is derived from the Greek *lobos* meaning lobe and *pleura* meaning side, and refers to the lobate lateral expansions of the body somites. Gender: feminine.

Lobopleura ambiducti, new species

Synonym.—*Laophontodes* sp. *sensu* Roe (1958), new synonym.

Type Locality.—Isle of Iona, Scotland, UK.

Material Examined.—(a) The Natural History Museum, London, UK: Holotype ♀ dissected and mounted on 11 slides, NHM reg. no. 2003.109; paratypes 1 ♂ and 1 CIV ♀ in alcohol, NHM reg. no. 2003.110–111; all from Seat of the Strand, Isle of Iona, Scotland; sand; low water mark; coll. S. Conroy-Dalton and R. Huys, autumn 1995; (b) The Natural History Museum, London, UK: 1 ♀ dissected and mounted

on 5 slides, 2 ♂♂ dissected and mounted on 9 slides, 3 ♀♀ and 5 ♂♂ in alcohol, NHM reg. no. 2003.673–683; all from Muckinish Inlet, Ballyvaughan Bay, Co. Clare, Ireland; coll. E. McCormack, 3 November 1998; (c) Naturhistoriska Riksmuseet, Stockholm, Sweden: 1 ♀ in alcohol labelled as *Laophontodes expansus*, SMNH reg. no. 15350 from Byxesjär, Gullmarfjord, Sweden; mud; coll. K. Lang, 6 June 1936; (d) The National Museum of Ireland, Dublin, Ireland: 1 ♀ mounted on slide labelled as *Laophontodes expansus* (?), NMI reg. no. 66.1982 from Mulgins Island, Dalkey, Co. Dublin, Ireland; coll. K. Roe, 26 March 1952.

Description of Female (Figs. 1, 3, 4, 5C, 6A–C).—Total body length 472 µm measured from anterior tip of rostrum to posterior margin of caudal rami. Body (Fig. 1A) dorsoventrally depressed (see as for ♂ and CIV ♀ Fig. 2A), tapering slightly posteriorly, without clear demarcation between prosome and urosome; integument moderately chitinized, ornate with series of lateral processes; processes lobate distally, bordered with strong spinules. Somatic hyaline frills weakly developed, smooth (Figs. 1A, 3C); with few hair-like setules around dorsal hind margins (Fig. 1A). Cephalothorax (Fig. 1A) wide, bell-shaped; lateral margins furnished with long fine spinules; sensilla unmodified, arising from tiny pedestals, pattern as in Fig. 1A; with bilaterally symmetrical pattern of 8 conspicuous tube-pores (2 dorsal and 2 laterodorsal pairs).

Free thoracic somites bearing P2–P5, genital and abdominal halves of genital double-somite and second abdominal somite (Figs. 1A, 3C) all with produced lateral processes with associated dorsal sensillum; abdominal half of genital double-somite processes bilobate. Body, P2–P5, and caudal rami with conspicuous tube-pores (Figs. 1, 3C–E, 4F, G, 6A–C). Original segmentation of genital double-somite indicated by bilateral constriction (Figs. 1A, 3C, D); posterior margin without ornamentation. Second and third abdominal somites (Fig. 3C) ventrally with row of fine spinules around posterior margin. Anal somite partly cleft medially (Fig. 3C, E); with paired tube-pore ventrally halfway along somite length and anterolateral margin with pore; anal operculum rounded, with short setules/denticles (Fig. 3E); anal frill finely setulose.

Caudal rami elongate and divergent; 6 times as long as maximum width; anterior half with few strong spinules along inner margin, outer margin anteriorly with 3 spiral rows of spinules, few small spinules present around insertion sites of setae I/II and VI (Fig. 3C, E); with 1 very elongate, lateroventral (arrowed in Fig. 3C) and 1 lateral tube-pore subdistally. Seta I positioned ventral to seta II, seta I reduced, both inserting

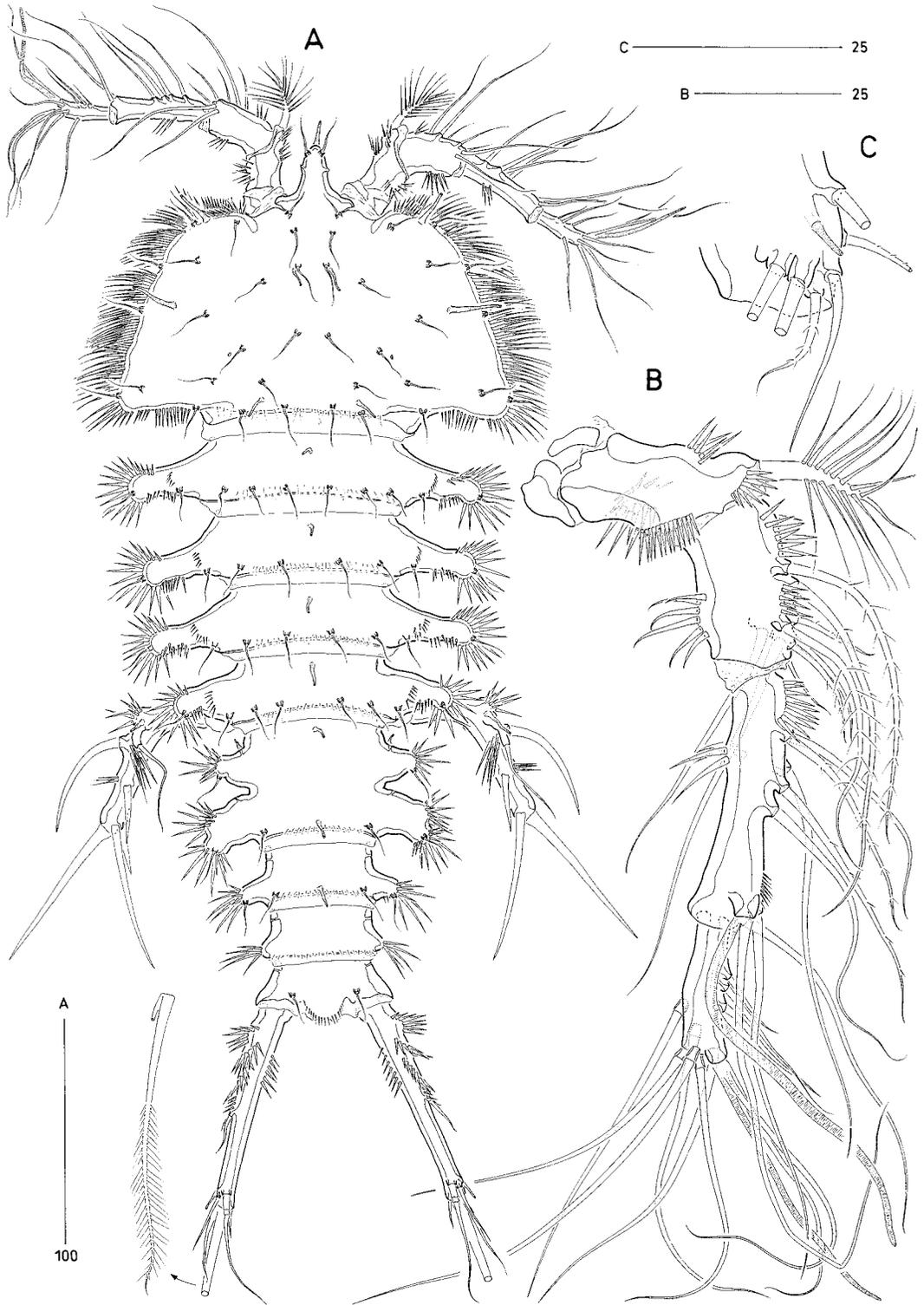


Fig. 1. *Lobopleura ambiducti*, new genus, new species (♀): A, habitus (inset showing full length of caudal seta V), dorsal; B, antennule, ventral; C, distal part of antennule segment-2, dorsal.

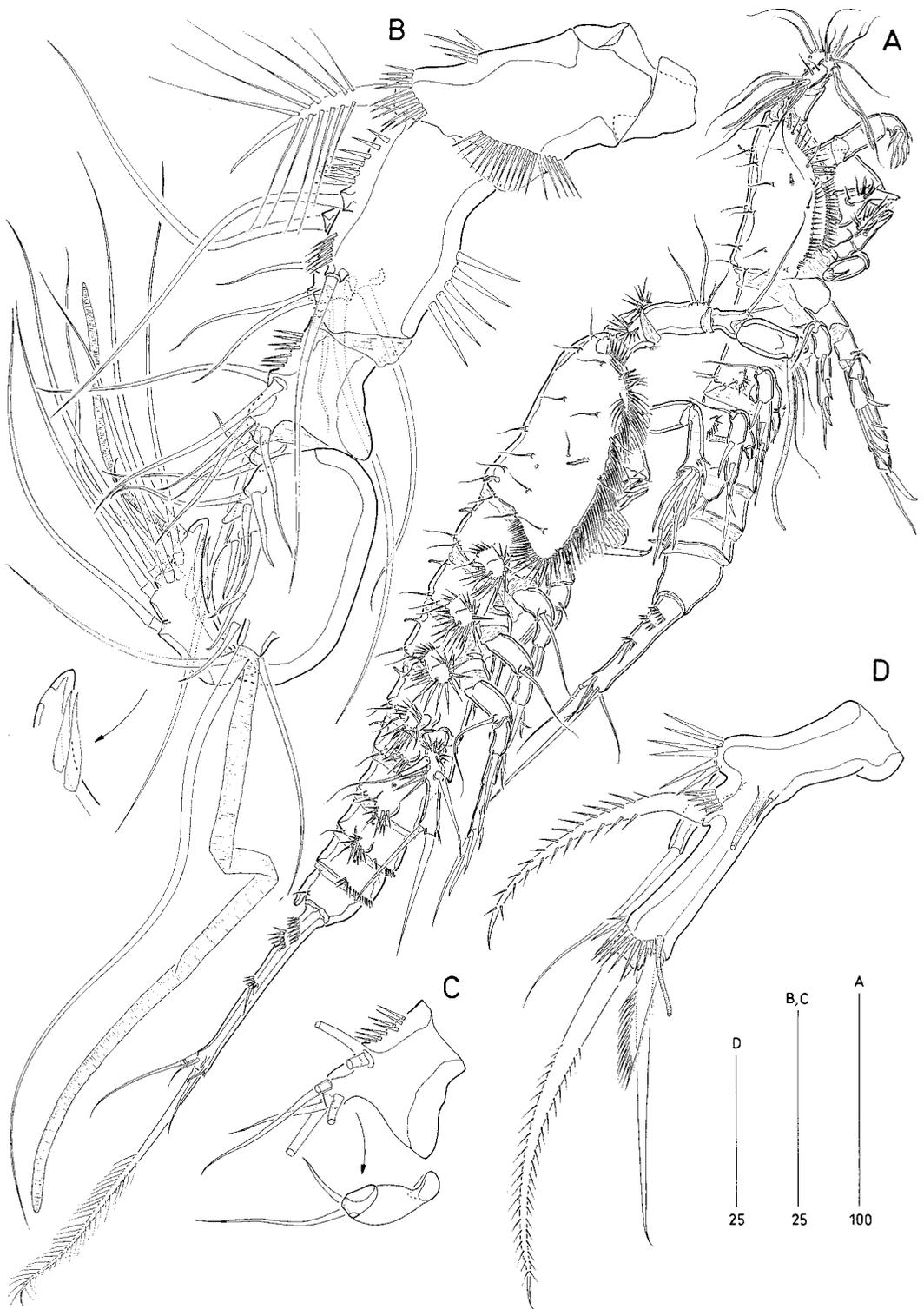


Fig. 2. *Lobopleura ambiducti*, new genus, new species: A, adult ♂ grasping juvenile CIV ♀, lateral; B, antennule ♂ (inset showing modified setae along inner lateral margin of segment-6, enlarged), ventral; C, ♂ antennule segments -3 and -4, disarticulated, ventral; D, ♂ P5, anterior.

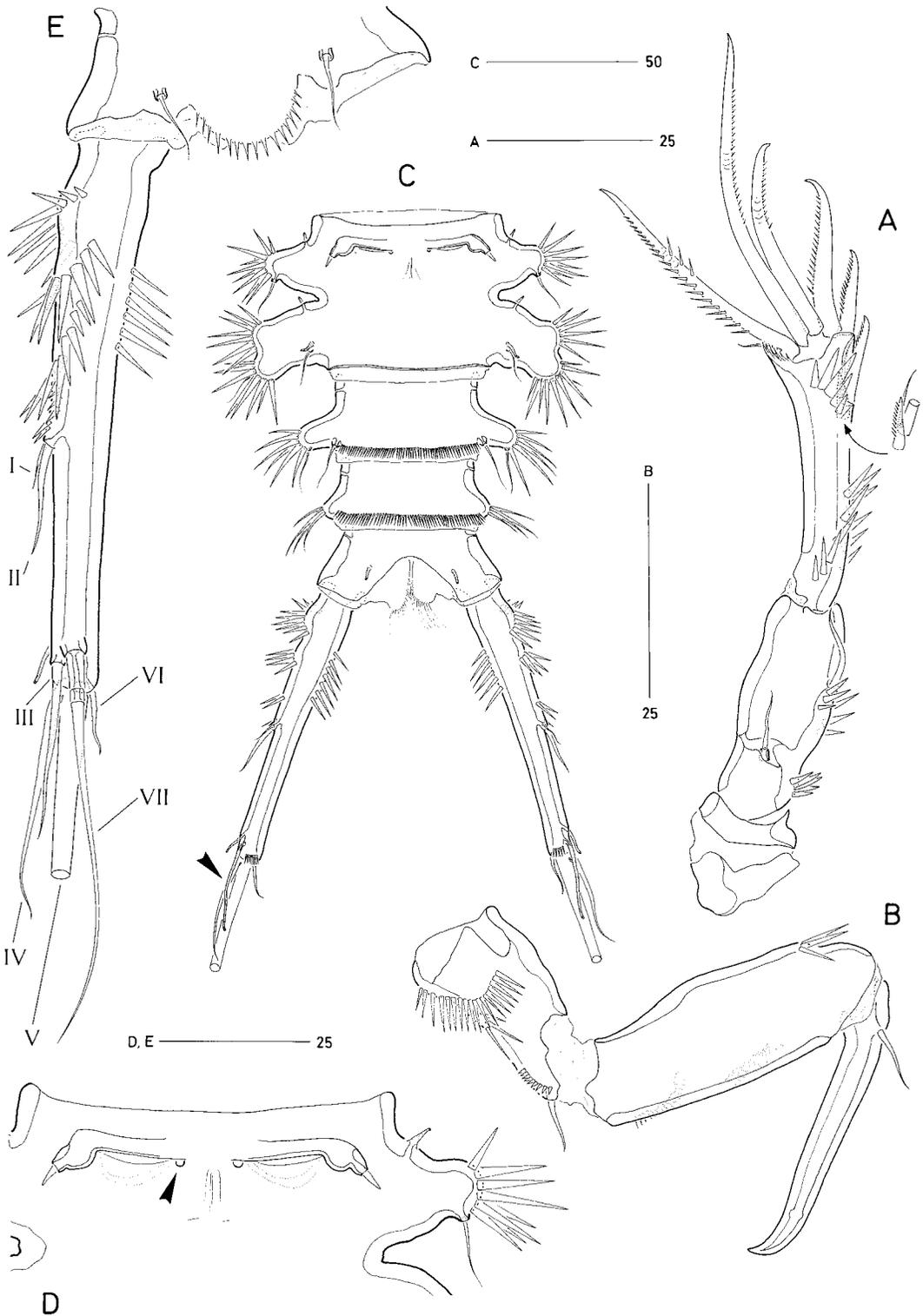


Fig. 3. *Lobopleura ambiducti*, new genus, new species (♀): A, antenna (inset showing lateral armature); B, maxilliped; C, urosome (excluding P5-bearing somite), subdistal elongate tube-pore arrowed, ventral; D, genital field (one of paired copulatory pores arrowed), ventral; E, anal somite and left caudal ramus, (caudal setae labelled with roman numerals I-VII), dorsal.

halfway along ramus (Fig. 3C, E); seta III inserted sub-distally; seta IV fused basally to well-developed seta V (Fig. 3E); seta VI (Fig. 3E) shortest; seta VII triarticulate at base, first socle elongate, arising from minute dorsal pedestal subdistally (Fig. 3E). All setae bare except seta V finely plumose.

Rostrum (Fig. 4A) fused to cephalic shield; moderate size; basally constricted, elongate, with paired sensilla arising from tiny pedestals subdistally; with paired membranous projections laterally; midventral tube-pore, very well developed, proximally reinforced, subdistal.

Antennule (Fig. 1B, C) 4-segmented. Segment 1 with strong setulose element. Segment 2 with 1 dorsal subapical seta arising from bulbous projection, with dorsal tube-pore subapically (Fig. 1C). Segment 3 longest, with aesthetasc (length 66 μ m). Posterior margins of segments 2 and 3 each with raised tuft of short, strong spinules. Segment 4 shortest, with apical acrothek consisting of aesthetasc and 2 slender setae. Armature formula: 1-[1 setulose], 2-[4 bare + 5 finely pinnate], 3-[7 + (1+ae)], 4-[9 + acrothek].

Antenna (Fig. 3A). Coxa represented by well-developed sclerite. Basis and proximal endopod segment fused, forming allobasis; original segmentation marked by incomplete surface suture; abexopodal margin with crown of spinules proximally and few spinules distally, with 1 bare seta in distal (endopodal) half. Exopod represented by minute segment with 1 seta. Endopod with 1 distal surface frill and 2 spinule rows; lateral armature consisting of 2 pinnate spines and 1 seta; distal armature consisting of 2 unipinnate spines, 2 distally pinnate geniculate setae, and 1 (outer) pinnate geniculate spine basally fused to vestigial seta.

Mandible (Fig. 4B). Coxa robust, expanding distally to slender gnathobase bearing 4 multicuspoid teeth; 1 unipinnate seta at dorsal corner. Palp well developed, 1-segmented; with 2 inner setae (representing basal elements), 3 apical setae (representing incorporated endopod), and outer margin with 1 bare seta (representing incorporated exopod).

Maxillule (Fig. 5C). Praecoxa and arthrite slender, elongate. Praecoxal arthrite with 2 setae on anterior surface and few long spinules on posterior surface; distal armature consisting of 6 bare and 2 pinnate spines, and 1 seta as figured. Coxal endite with 1 well-developed and 1 small bare seta. Basis, proximal endite with 3 setae; distal endite with 2 setae. Rami completely

incorporated into basis; exopod represented by 2 setae; endopod represented by 1 seta.

Maxilla (Fig. 4C, D). Syncoxa with 4 spinule patches as figured; with 2 coxal endites, arising from membranous area; proximal endite with 1 pectinate spine and 2 bare setae; distal endite with 2 pectinate spines and 1 seta. Allobasis drawn out into claw; accessory armature consisting of 1 naked seta and 1 pectinate spine. Endopod minute, with 1 seta.

Maxilliped (Fig. 3B). Subchelate. Syncoxa with 3 spinule patches as figured and with 1 small seta. Basis with few spinules along distal outer margin and 2 rows of short spinules along palmar margin. Endopod drawn out into long, curved claw, with 1 accessory seta at base.

P1 (Fig. 4E). Intercoxal sclerite transversely elongate. Praecoxa not discernible. Coxa trapezoid, with anterior spinule row along outer margin. Basis rectangular, with few spinules around insertion site of outer seta; inner and outer setae bare. Exopod 3-segmented, with few setules along inner margin (exp-2) and few spinules along outer margin (exp-1 and -2); outer spines finely unipinnate (exp-1) or geniculate (exp-2 and -3); exp-3 with 4 geniculate setae. Endopod 2-segmented; enp-1 elongate, 5 times as long as enp-2 and twice as long as entire exopod, with strong spinules along inner margin and short spinules along outer margin; enp-2 with few spinules along outer margin, with 1 strong recurved spine, 1 claw-like seta and 2 reduced setae.

P2-P4 (Fig. 6A-C) with wide intercoxal sclerites without ornamentation (see Fig. 6C as for P4). Praecoxae not discernible. Coxae (Fig. 6A-C) quadrangular, with few spinules. Bases transversely elongate, with strong, slender spinules along outer margins; with anterior tube-pore in distal half; outer distal seta bipinnate (P2) or bare (P3-P4). Exopods 3-segmented, without inner setae; exp-3 (P2-P4) inner distal seta reduced. P2 endopod absent, position represented by less chitinized, slightly raised area (Fig. 6A). P3-P4 endopods 2-segmented, enp-1 reduced. Armature formula as follows:

	Exopod	Endopod
P2	0.0.023	absent
P3	0.0.023	0.020
P4	0.0.023	0.010

P5 (Fig. 4F, G). Baseoendopod with raised tuft of strong spinules and long tube-pore subdistally along outer margin; setophore positioned

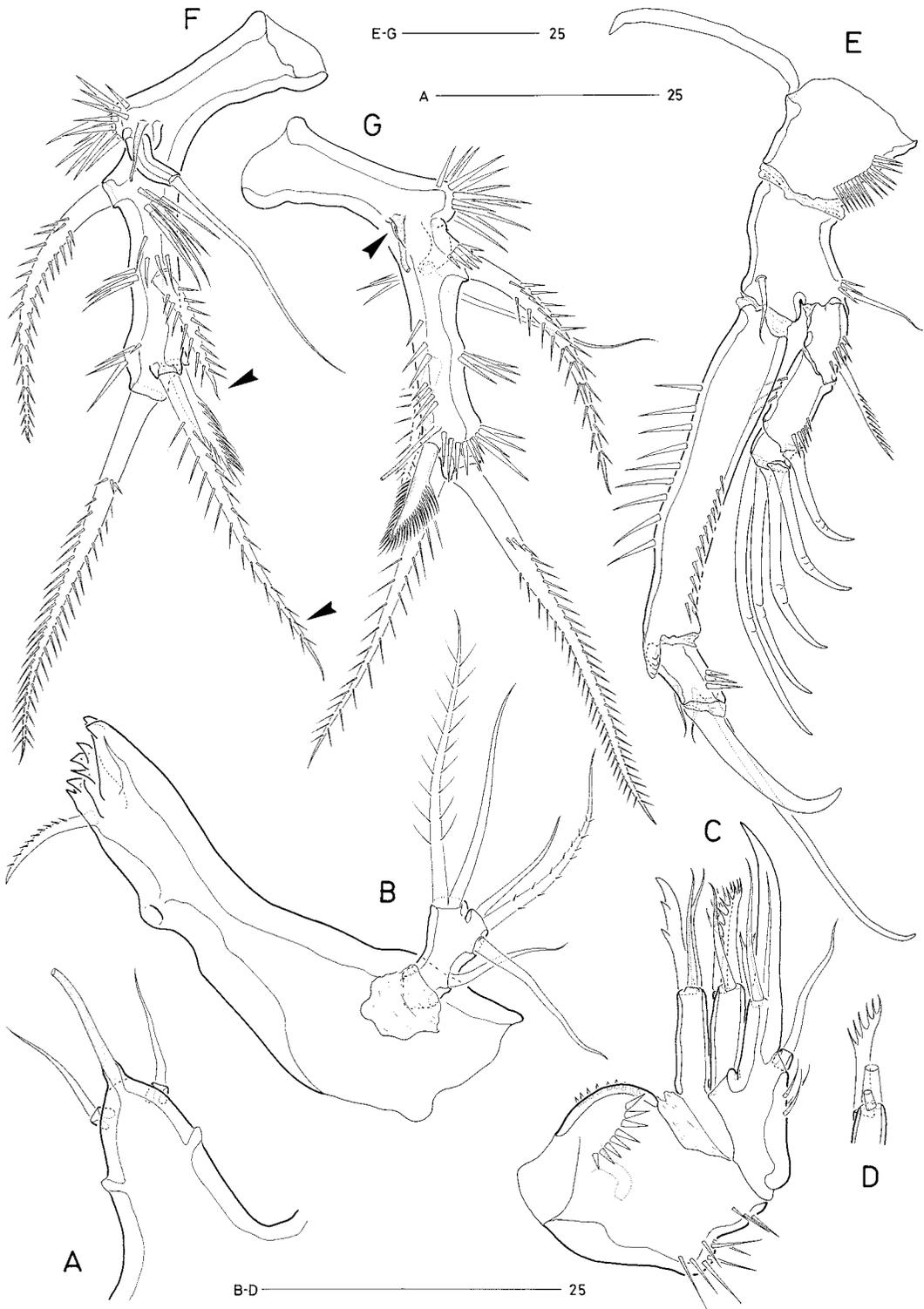


Fig. 4. *Lobopleura ambiducti*, new genus, new species (♀): A, rostrum, ventral; B, mandible; C, maxilla; D, maxilla, distal endite apical part (2 anteriormost elements omitted); E, P1, anterior; F, P5, posterior (2 distalmost outer elements arrowed); G, same, anterior (vestigial endopodal seta arrowed).

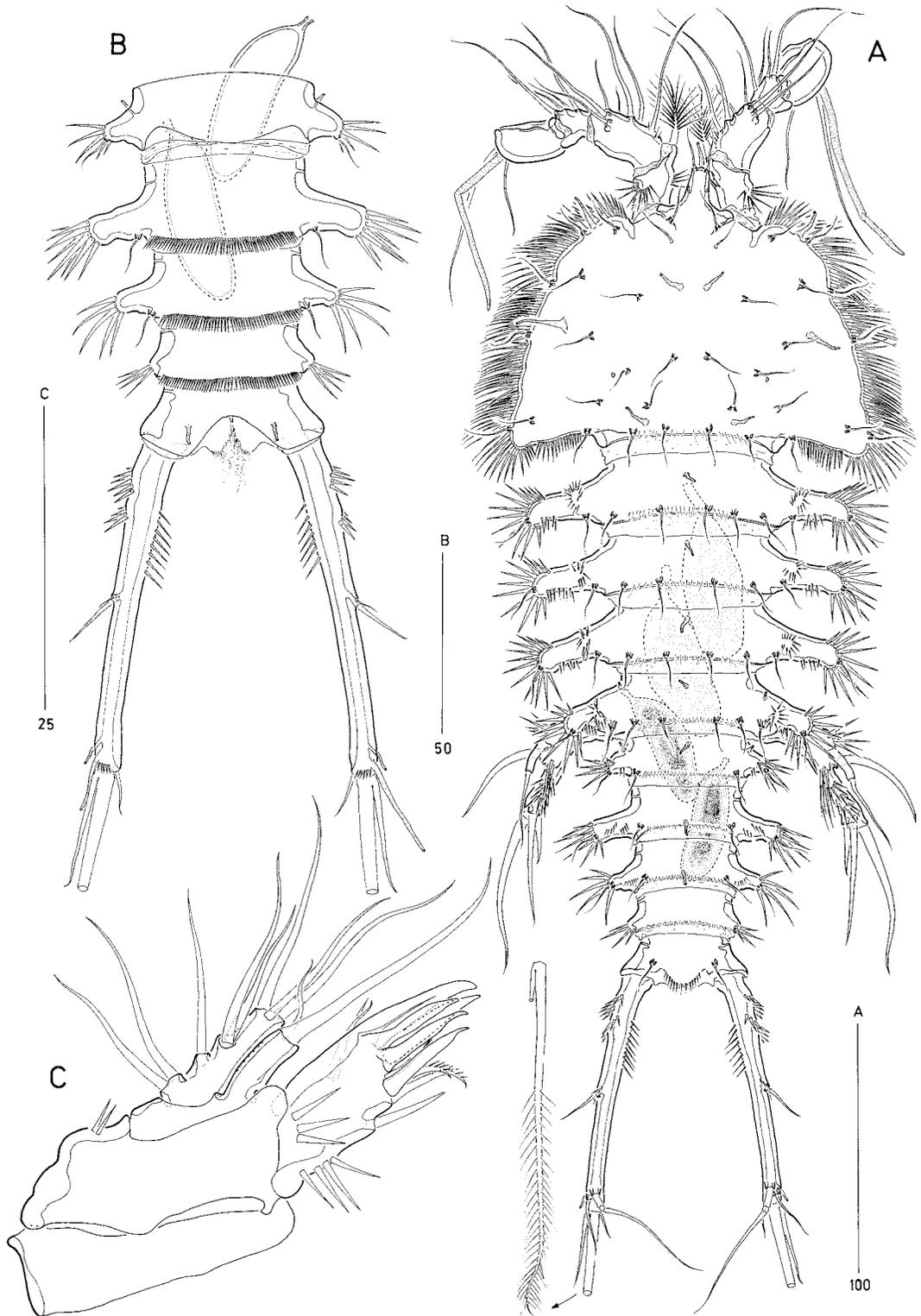


Fig. 5. *Lobopleura ambiducti*, new genus, new species (♂) A, B, (♀) C: A, ♂ habitus (inset showing full length of caudal seta V), dorsal; B, ♂ urosome (excluding P5-bearing somite), ventral; C, ♀ maxillule.

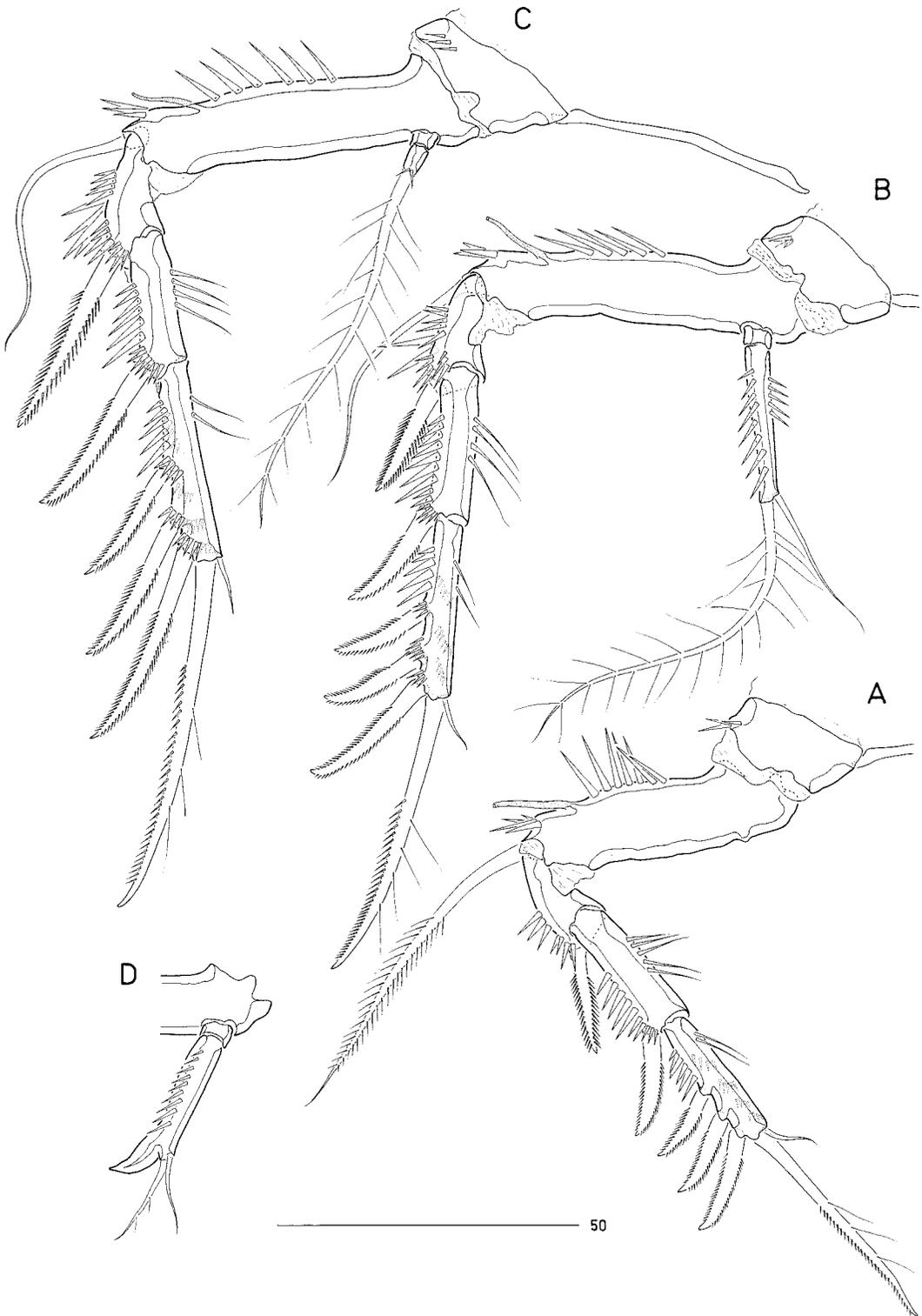


Fig. 6. *Lobopleura ambiducti*, new genus, new species (♀ A–C, ♂ D): A, P2 (♀), anterior; B, P3 (♀), anterior; C, P4 (♀), anterior; D, P3 (♂) endopod, anterior.

posteriorly (Fig. 4F), cylindrical, demarcated at base, bearing bare outer basal seta. Endopodal lobe absorbed, with conspicuous tube-pore and 1 vestigial seta (arrowed in Fig. 4G), visible only in anterior view. Exopod long, fused to baseopod; with subdistal tube-pore anteriorly (Fig. 4G); with 1 distal pinnate seta, 3 outer pinnate setae, and 1 inner serrate seta (Fig. 4F, G).

Genital field positioned anteriorly (Fig. 3C, D); genital system paired, with paired gonopores covered by genital operculum derived from vestigial sixth legs. P6 (Fig. 3D) each with 1 tiny, blunt seta; copulatory pores paired, small (arrowed in Fig. 3D).

Male (Figs. 2, 5A, B, 6D).—Smaller than ♀ (Fig. 5A); total body length 420 µm, measured from anterior tip of rostrum to posterior margin of caudal rami; body dorsoventrally depressed (Fig. 2A). Sexual dimorphism in body size, antennule, P3 endopod, P5, P6, genital segmentation, abdominal ventral ornamentation, and caudal rami morphometrics.

Pattern of body processes and sensilla (Fig. 5A) as in ♀ except: first abdominal somite processes lobate terminally (equivalent processes in ♀ bilobate). Abdominal ornamentation (Fig. 5B) as in ♀, except first abdominal somite ventrally with row of fine spinules.

Caudal rami slightly more slender than in ♀; 8.5 times as long as maximum width.

Rostrum as in ♀ (Fig. 5A).

Antennule (Fig. 2B, C) 6-segmented, subchirocer, geniculation between segments 5 and 6; 1 segment posterior to geniculation; segment 2 with 1 subapical anterior seta arising from bulbous projection; segment 4 represented by a U-shaped sclerite (Fig. 2C); segment 5 swollen, longest; aesthetasc present on segment 5 (length 90 µm) and as part of apical acrothek on segment 6. Armature formula: 1-[1 setulose], 2-[9], 3-[7], 4-[2], 5-[10 + 1 spinous + (1 + ae)], 6-[7 + 2 modified + acrothek]. Modified elements on segment 6 along inner lateral margin, flame-shaped (inset Fig. 2B). Acrothek consisting of 2 bare setae plus aesthetasc.

Antenna, mandible, maxillule, maxilla, maxilliped, P1–P2, P3 exopod, P4 as in ♀.

P3 endopod (Fig. 6D) 2-segmented; enp-2 elongate, anterior distal surface produced into small, recurved apophysis, with 2 small setae subdistally.

P5 (Fig. 2D) as in ♀ except median outer seta absent.

Sixth pair of legs symmetrical (Fig. 5B); both members functional, each represented by unarmed membranous flap. Genital system with paired gonopores and *vasa deferentia* and with 2 fully mature spermatophores, mean length = 52.3 µm ($n = 2$); 2 developing spermatophores also present anterior to mature ones (Fig. 5B).

Etymology.—The specific name is derived from the Latin *ambo*, meaning both, and *ducere*, meaning to lead, and refers to the paired oviducts and *vasa deferentia* present in the female and male reproductive system respectively.

Remarks.—The fifth pairs of swimming legs (in both sexes) are extremely three-dimensional due to the orientation and insertion sites of certain exopodal setae and the basal setophore. In the female for example, the two distalmost outer elements of the exopod (arrowed in Fig. 4F) are posteriorly displaced and typically backwardly directed. The method by which and plane in which this appendage was mounted (in order to minimize squashing effects and preserve the natural orientation of the armature elements) gives the false impression that these setae (Fig. 4F, G) originate from the inner margin. The same situation is exhibited by the male (Fig. 2D) where the distalmost outer element has migrated (the median outer element is absent in males).

In his monograph, Lang (1948) recorded a single female of *Laophontodes expansus* from Gullmarfjord, Sweden, without providing any morphological data directly derived from that individual. Instead, he provided a short synopsis and some illustrations for the species, both of which were based on Sars' (1908) original description and figures. Detailed comparative analysis of Lang's specimen deposited in the collections of the Naturhistoriska Riksmuseet in Stockholm, proved it to be identical in every morphological aspect with *L. ambiducti* described above.

Roe (1958) recorded a single female specimen of *Laophontodes* sp. (slide labelled as *Laophontodes expansus* (?)) from Ireland. Accompanying some notes on the specimen she provided illustrations of the ♀ P2 and P5. Using Lang's (1948) key to species, Roe (1958) identified it as being most similar to *Laophontodes expansus*; however, she also listed several differences from the original description of that species: (1) bases P2–P4 more transversely elongate; (2) enp-2 P2–P3 terminal setae unequal in length with innermost seta shortest; (3) P5 with 5 setae, having

interpreted the P5 figured in Lang (1948) with 6 setae; and (4) female P5 exopod with 1 inner seta. On this basis, she refrained from formally allocating the Irish material to *L. expansus*. Lang (1965) correctly pointed out that the meristic characters (1) and (2) are insignificant and that character (3) was based on Roe's erroneous setal interpretation. He further considered the presence of an inner seta in the female P5 exopod (character 4) as the only valid discriminant between the Irish specimen and *L. expansus* and thus refrained from explicitly regarding the two as conspecific. However, re-examination of Roe's slide material revealed both members of the fifth legs to be severely squashed resulting from mounting technique, giving the false impression that the median outer exopodal seta originates from the inner margin of the ramus. This seta in fact represents an outer element, which has migrated posteriorly, similar to the condition found in *L. ambiducti*. It is also confirmed that Roe's (1958) illustration of the P2 (displaying a 2-segmented endopod) in reality refers to the P3, and that the P2 endopod is completely absent, as in *L. ambiducti*. Detailed comparison revealed no morphological differences between *Laophontodes* sp. sensu Roe (1958) and *L. ambiducti*, providing strong evidence for their conspecificity.

Behavioural Remarks.—The adult male of *L. ambiducti* described above was grasping a juvenile female CIV stage in dorsal aspect, with its antennules positioned just under the female's second pair of swimming legs (Fig. 2A). The most common posture that male harpacticoids assume during this behaviour is to grasp females ventrally, either in a ventral-to-ventral, or dorsal (♂)-to-ventral (♀) contact position. Also, where males in copula are found grasping (juvenile) female swimming legs (as opposed to caudal rami, caudal setae, etc.), the fourth or fifth (in adults) pair of legs are more commonly engaged, as in the Laophontidae (Fiers, 1998). Males attaching around the female's second pair of swimming legs (as in *L. ambiducti*) have only infrequently been reported, such as in some laophontids, where in some instances even the female's first swimming legs are grasped. This posture is typically found in taxa showing an asynchronous development between sexes, with males attaining adulthood and sexual maturity much faster. Such males generally start displaying precopulatory mating behaviour when females are still at an early stage of development,

usually CI or CII, and only the first and second swimming leg precursors are expressed. A striking example of premating behaviour between adult males and female CII stages, is demonstrated in the laophontid *Robustunguis ungulatus* Fiers, 1992 (Fiers, 1998).

***Lobopleura expansa* (Sars, 1908),
new combination**

Synonym.—*Laophontodes expansus* Sars, 1908.

Type Locality.—Saltenfjord (Skjærstadfjord), Norway.

Material Examined.—(a) Zoologisk Museum, Oslo, Norway: ZMO reg. no. F20300, from the type locality; coll. Mr. Nordgaard, det. G. O. Sars; tube found empty.

Remarks.—Despite the type material (2 ♀♀) of *Laophontodes expansus* being no longer available for direct comparison, it is clear from Sars' (1908) original description that the Norwegian species is closely related to *Lobopleura ambiducti*. It differs significantly from other members of *Laophontodes*, principally in the general body morphology (body dorsoventrally depressed, body with lateral lobate processes, the shape of the cephalothorax), in the general structure of the antennule, antennae and mouthparts, and in the morphology and armature of the P1–P5. Sars (1908) probably overlooked and/or misinterpreted some finer morphological details such as the minute antennary exopod; certain armature of antennule and mouthparts; the two reduced posterior setae of P1 enp-2; P2–P4 endopodal segmentation; and P5 baseoendopodal armature. Despite these morphological differences, there is no doubt that *L. expansus* should be formally transferred to *Lobopleura* as *Lobopleura expansa* (Sars, 1908), new combination.

Both Lang (1948) and Roe (1958) overlooked or misidentified the second pair of swimming legs in the European specimens they collected and identified as *L. expansus* and *Laophontodes* sp., respectively (see above under *Remarks* section for *L. ambiducti*). It could therefore be postulated that Sars (1908) also misidentified the true nature of the P2 in his original description of *L. expansus*. Some inferences as to the identity of the appendage figured by Sars (1908) as the P2, can however be made by comparison with the swimming leg morphology of *Lobopleura ambiducti*. The latter species displays a graded trend of elongation in the bases of P2–P4, being shortest in P2 and most elongate in P4. Sars'

(1908) illustrations of *L. expansus* also depict this trend, with the P2 basis least elongate of all the legs. It seems therefore unlikely that Sars inadvertently figured the P3 twice (once correctly and once as the P2). Additionally, in *L. ambiducti*, the innermost apical seta of P3 enp-2 is shorter than the outermost. Sars' (1908) illustrations of *L. expansus* show the same for the P3 endopod (although somewhat less pronounced), whereas the P2 endopod is illustrated with two setae of equal length. Pending the rediscovery of *L. expansa* (preferably from the type locality) to either corroborate or refute the presence of an endopod in P2, there remains no objective ground to contest the accuracy of Sars' (1908) original description. At present, we must consider the presence of an endopod in the P2 as the principal character differentiating *L. expansa* from the type species.

Additional female characters differentiating *L. expansa* from *L. ambiducti* include (1) cephalothorax proportionally less wide, anterior corners rounded; (2) rostrum wider proximally; (3) lateral lobate body processes slightly less developed; (4) processes of abdominal half of genital double-somite not bilobate; (5) P1 exopodal geniculate setae proportionally longer and more slender; (6) P2–P4 outer exopodal spines longer and less robust; (7) P3 enp-2 innermost apical seta longer; (8) P5 exopod proportionally longer; (9) P5 middle outer and inner exopodal setae long. These characters are all morphometric in nature, the taxonomic significance of which cannot truly be assessed without the rediscovery of *L. expansa*.

Probosciphontodes Fiers, 1988

Updated Diagnosis.—Laophontodinae. Body strongly dorsoventrally depressed, tapering posteriorly, without clear demarcation between prosome and urosome; without produced dorsal processes; with series of lobate, lateral processes. All processes furnished with strong spinules. Cephalothorax, medially with paired lobate, laterodorsal processes; posterior margin laterally with elongate pair of lobate processes. Thoracic somites bearing P2–P5, P6-bearing somite (genital half of double-somite in ♀), first (abdominal half of double-somite in ♀), second and sometimes third abdominal somites, with paired lobate processes laterally (Fig. 7E as for P-4 bearing somite). Cephalothorax wide; lateral

margins fringed with long spinules. All integumental sensilla unmodified. Somatic hyaline frills weakly developed, smooth. Body, swimming legs, P5, and caudal rami with conspicuous tube-pores. Anal operculum rounded, spinulose. Caudal rami cylindrical, with 7 setae; setae I minute, inserted ventral to seta II; seta III subdistal; seta IV fused basally to seta V; seta V well developed; seta VI reduced; dorsal seta VII triarticulate at base, inserted subdistally.

Sexual dimorphism in body size, antennule, P5, P6, and genital segmentation.

Rostrum slender, elongate, basally constricted; fused to cephalic shield; lateral margin with long, fine spinules; midventral tube-pore very long, basally reinforced. Antennule 4-segmented in ♀, 6-segmented and subchirocer in ♂, with one segment distal to geniculation; aesthetasc arising from segments 3 and 4 in ♀, segments 5 and 6 in ♂; segment 1 (both sexes) with strong setulose seta; segments 2 and 3 in ♀ each with raised spinule tuft on posterior margin. Antenna with allobasis, abexopodal margin with distal (endopodal) seta; exopod represented by tiny segment bearing 1 minute seta; endopod with 2 spines and 1 seta laterally and 6 distal elements (2 geniculate setae and 3 spines, outermost spine reduced and fused basally to tiny naked seta). Mandible with slender, elongate coxa bearing pinnate dorsal seta; palp 1-segmented, with rami completely incorporated into basis, with 6 setae. Maxillule with 2 elements on coxal endite, distalmost one reduced; basis with exopod and endopod completely incorporated, proximal endite with 2 or 3 setae; praecoxal arthrite slender, elongate. Maxillary syncoxa with 2 endites, each with 2 elements; allobasis drawn out into claw with 2 accessory elements; endopod minute, with 1 seta. Maxilliped subchelate; syncoxa with 1 seta; basis unarmed; endopod drawn out into curved claw with reduced accessory seta.

P1–P4. Intercoxal sclerites transversely elongate. P1 coxa rectangular; basis elongate, rectangular (both longer than wide); basis positioned at right angle to coxa; exopod 3-segmented; exp-3 small, with 4 geniculate setae; exp-2 with geniculate outer seta; endopod 2-segmented, prehensile; enp-1 without armature; enp-2 with 1 claw, 1 geniculate and 1 reduced seta. P2–P4 coxae quadrangular; bases transversely elongate; exopods 3-segmented, without inner setae; exp-3 with 3 outer spines (P4) or 2 outer spines (P2–P3), inner distal seta reduced.

P2–P4 endopods absent. Armature formula (for both sexes) as follows:

	Exopod	Endopod
P1	0.0.022	0.111
P2	0.0.022	absent
P3	0.0.022	absent
P4	0.0.023	absent

P5 with fused exopod and baseoendopod; basal setophore cylindrical, demarcated at base; endopodal lobe vestigial, represented by 2 reduced setae and conspicuous tube-pores; exopod elongate, with 1 inner, 1 apical, and 3 (♀) or 2 (♂) outer elements. Female genital field located anteriorly; paired gonopores covered by genital operculum derived from P6, each armed with 1 vestigial element; single tiny copulatory pore located medially just less than halfway genital double-somite length. Male P6 asymmetrical; unarmed; functional member represented by membranous flap; with single spermatophore.

Type Species.—*Probosciphontodes stellata* Fiers, 1988 (by original designation).

Other Species.—*Probosciphontodes ptenopostica* Fiers, 1988.

Probosciphontodes stellata Fiers, 1988

Type Locality.—Foumbouni, Grande Comore, Comoro Islands, Indian Ocean.

Material Examined.—Koninklijk Belgisch Instituut voor Natuurwetenschappen, Belgium: KBIN reg. no. Cop2886 Holotype ♀ (dissected on slide); Cop2887 Allotype ♂ (dissected on slide); Cop2888–2889 Paratypes (1♀ mounted on slide, 2 ♂♂ in alcohol).

Probosciphontodes ptenopostica Fiers, 1988

Type Locality.—Megiar Harbour, Mandang Province, Papua New Guinea, Pacific Ocean.

Material Examined.—Koninklijk Belgisch Instituut voor Natuurwetenschappen, Belgium: KBIN reg. no. Cop2892 Paratypes (1 ♀ dissected on 12 slides; 3 ♀♀, 2 ♂♂, and 1 CV in alcohol).

Morphological Remarks.—The following amendments and additions apply to both species, unless stated otherwise. Most characters figured here (Figs. 7–9) are based on *P. ptenopostica* and supplement Fiers' (1988) excellent original descriptions.

Rostrum (Fig. 9A) bordered with strong spinules, apical tube-pore elongate.

Antennule 4-segmented in ♀ (Fig. 9B), 6-segmented in ♂ (Fig. 7H). Segment 2 with tube-

pore ventrally. Segments 2 (both sexes) and 3 (♀ only) with tufts of long spinules along posterior margin (Figs. 7 H, 9B). Segment 4 (arrowed in Fig. 7H) in ♂, tiny, represented by U-shaped sclerite bearing 2 setae. Armature formulae as follows: ♀: 1-[1 setulose], 2-[9], 3-[7+(1+ae)], 4-[9+acrothek]; ♂: 1-[1 setulose], 2-[9], 3-[7], 4-[2], 5-[9+1 modified+(1+ae)], 6[9+acrothek]; segment 5 modified seta flame-shaped.

Antenna (Figs. 7A, 8A) allobasis with minute exopod bearing 1 reduced seta. Endopod (8A) with 2 spines and 1 seta laterally, distal armature consisting of 2 spines, 2 geniculate setae, and 1 short unipinnate spine (innermost element) basally fused to vestigial seta.

Mandibular palp (Fig. 8B) uniramous, with 1 outer (representing exopod), 3 apical (representing endopod), and 2 inner (basal) setae.

Maxillule. Praecoxa and arthrite extremely elongate, without surface setae. Coxal endite with 1 well-developed seta and 1 reduced plumose seta (Fig. 7J). Exopod and endopod completely incorporated into basis (Fig. 7B, J). Basis, *P. stellata* (Fig. 7J) with 7 setae, probably 2 exopodal setae, 2 endopodal setae, and 3 setae representing combined proximal and distal endites; basis, *P. ptenopostica* (Fig. 7B) with 5 setae, probably 2 exopodal and 1 endopodal setae, and 2 setae representing combined proximal and distal endites.

Maxilla (Fig. 7C) with 2 coxal endites, each with 1 pectinate and 1 setiform element. Allobasis accessory armature consisting of 1 naked seta and 1 pinnate spine. Endopod incompletely absorbed, bearing 1 seta.

P1 (Figs 7D, 8C, D) coxa medially directed, and basis outwardly directed; basis positioned at right angles with respect to coxa; outer basal seta inserted halfway along segment. Exopod 3-segmented, endopod 2-segmented; both rami forwardly (anteriorly) directed (Fig. 8C). Armature P1–P4 as for genus.

P5 (Fig 7F, 8E) with fused exopod and baseoendopod in both sexes. Basal setophore demarcated at base. Endopodal lobe vestigial, with 2 reduced setae and long tube-pores. Exopod with 1 inner, 1 apical, and 3 outer (♀, Fig. 7F) or 2 outer setae (♂, Fig. 8E).

Abdominal half of genital double-somite, hind margin with 2 ventral spinule patches in *P. ptenopostica* (one side illustrated in Fig. 7G) and continuous ventral spinule row in *P. stellata*.

Female genital field positioned anteriorly (Fig. 7G), with paired gonopores covered by genital operculum derived from vestigial sixth legs. P6

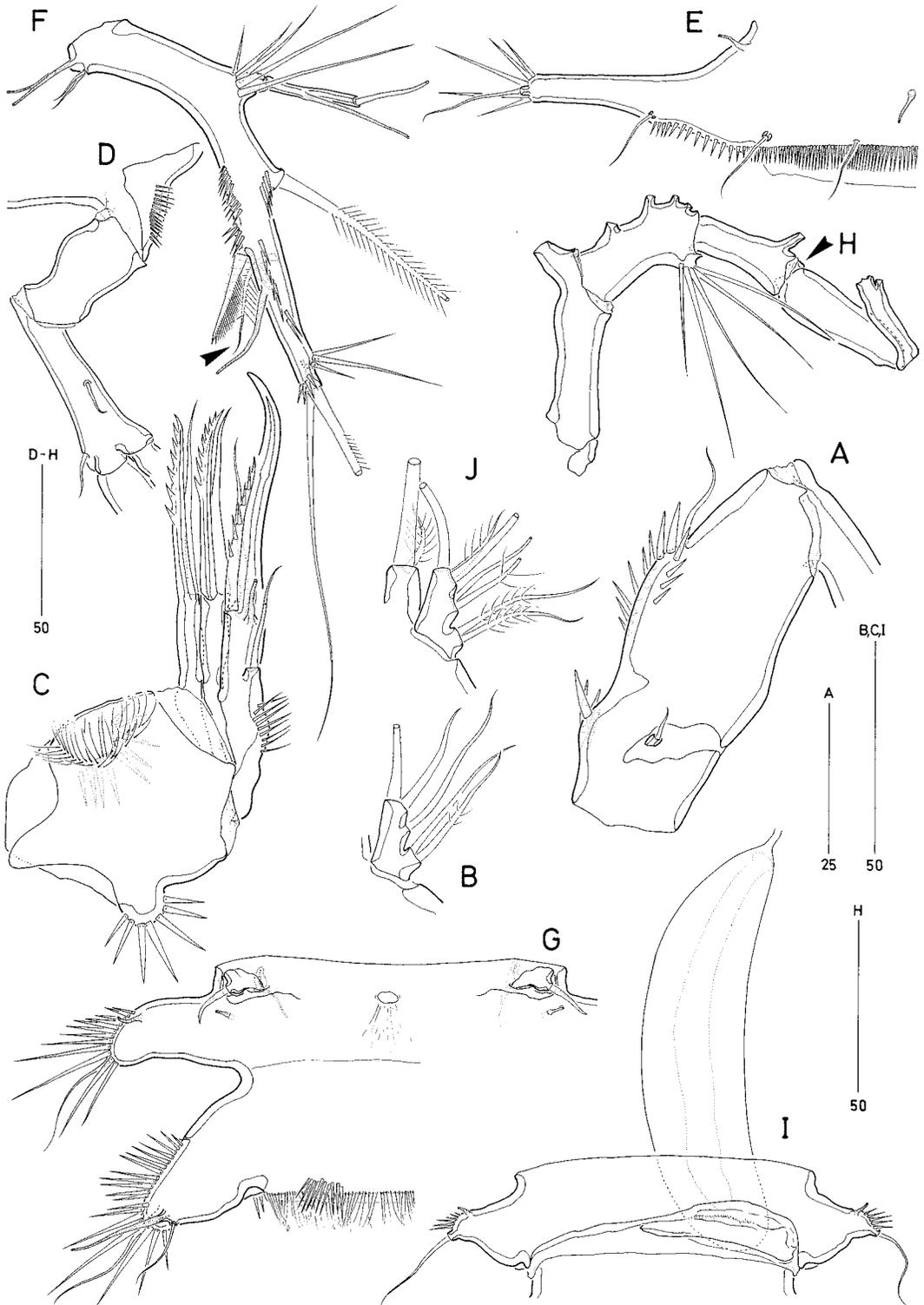


Fig. 7. *Probosciphontodes ptenopostica* (♀) A–G, (♂) H, I: A, antennary allobasis (♀), posterior; B, maxillary basis (♀); C, maxilla (♀); D, P1 protopod (♀), anterior; E, lateral part of P4-bearing somite (♀), ventral; F, P5 (♀), anterior (median outer seta arrowed); G, ♀ genital field, ventral; H, (♂) antennule (armature omitted); I, P6-bearing somite and spermatophore (♂). *Probosciphontodes stellata* (♀): J, maxillule, basis and coxal endite.



Fig. 8. *Probosciphontodes tenopostica* (♀) A–D, (♂) E: A, antenna (♀), anterior; B, mandible (♀) (inset showing distal part of gnathobase rotated); C, P1 (♀), anterior; D, P1 (♀), rotated slightly laterally (prae-coxa and coxa omitted); E, P5 (♂), anterior.

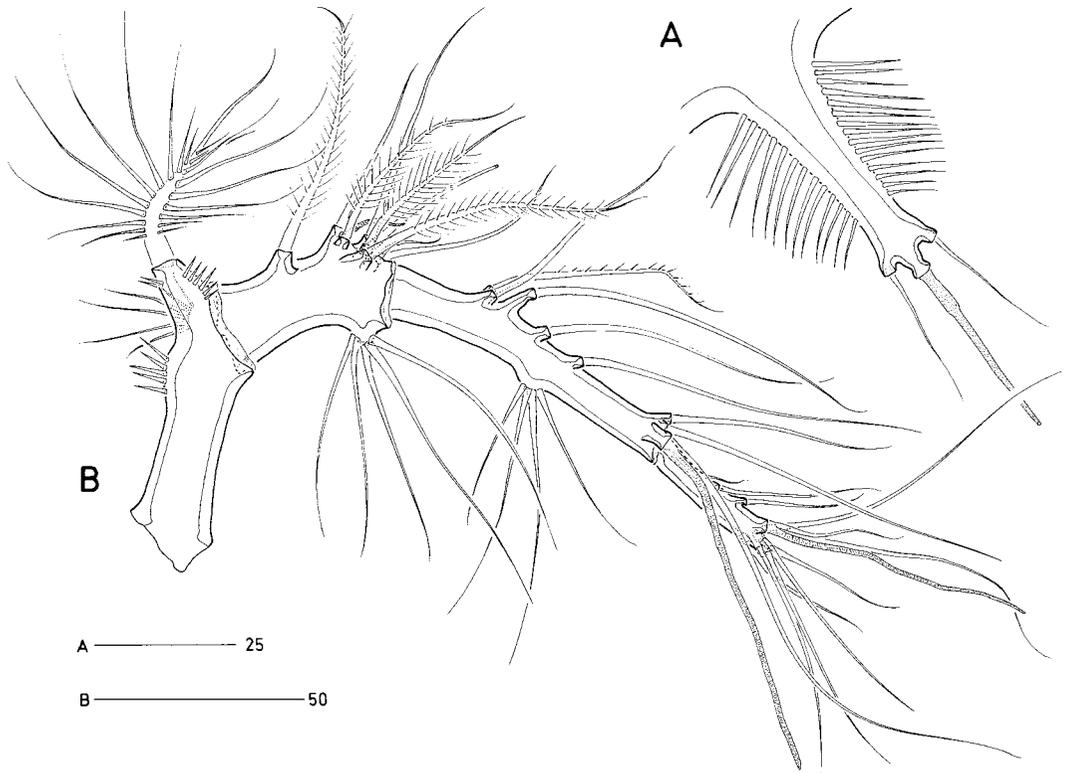


Fig. 9. *Probosciphontodes ptenopostica* (♀): A, rostrum, dorsal; B, antennule, ventral.

(Fig. 7G) each with 1 seta; median copulatory pore located anteriorly.

Male sixth pair of legs asymmetrical (Fig. 7I); functional member represented by unarmed membranous flap. Single, large spermatophore.

Remarks.—Re-examination of the type material has revealed new significant characters, applicable to both species of *Probosciphontodes*. An antennary exopod is present, represented by a minute segment bearing one vestigial seta. Secondly, the P1 is three-dimensional in nature, with both rami being anteriorly (forwardly) directed, and the orientation of the protopodal segments is very distinctive. Finally, the P5 exopodal setation is sexually dimorphic, bearing five setae (♀) or four setae (♂). Fiers (1988) did not describe any sexual dimorphism for this appendage and misinterpreted the setation in the female. Despite having correctly described the female P5 with five exopodal setae, Fiers (1988), however, overlooked the median outer seta (arrowed in Fig. 7F) and misinterpreted a very long subdistal setule as an inner seta. In males, the median outer seta is absent (♀ equivalent arrowed in Fig. 7F).

Fiers (1988) described several characters distinguishing *P. ptenopostica* from *P. stellata*, but only four could be confirmed by the present study: (1) third abdominal somite in both sexes with lobate lateral body processes; (2) anal operculum furnished with fine setules; (3) maxillulary basis with a total of five setae (endopod probably represented by one seta and exopod by two setae); and (4) inner margins of caudal rami straight. In addition, four new characters differentiating *P. ptenopostica* are identified here: (5) maxillulary basis with only two setae apically (representing combined proximal and distal endites); (6) male antennule (Fig. 7H) more slender and elongate, with particular reference to segments 3, 5, and 6; segment 5 only very slightly swollen; (7) hind margin of abdominal half of genital double-somite in ♀ with two ventral spinule patches; and (8) P5 ♀ endopodal setae further reduced.

The following characters identified by Fiers (1988) could not be confirmed here and should therefore be disregarded as reliable species discriminants: (9) dorsomedian pores of last thoracic somites without tubular extensions; (10)

outer apical caudal seta (VII) short, as long as seta VI, and only half the caudal ramus total length; (11) caudal seta VII triarticulate, both socles of equal size. This study failed to reveal a median dorsal pore (character 9) on the genital half of ♀ genital double-somite and the ♂ genital somite, in either species of *Probosciphontodes*. In all specimens of *P. ptenopostica* examined, dorsal median tube-pores were observed on the somites bearing P2–P4 (see Fig. 7E for P4-bearing somite), and in most specimens also on the P5-bearing somite (in two individuals, the pore was short, perhaps due to damage). Body tube-pore patterns are therefore similar in both species. In *P. ptenopostica*, caudal seta IV (character 10) is long, much longer than seta VI and similar to the condition in *P. stellata* (perhaps proportionally very slightly shorter), and the proximal socle of caudal seta VII (character 11) is much longer than the distal one, as in *P. stellata*.

The two remaining characters used by Fiers (1988) to differentiate *P. ptenopostica* are (12) dorsomedian tube pore of first abdominal somite (abdominal half of genital double-somite in ♀) extremely long, reaching to posterior margin of second abdominal somite; and (13) rostral midventral tube-pore long, but shorter than length of rostrum. Both relate to tube-pore characteristics, and should be used with caution. Tube-pores are flexible and retractable to a certain extent (R. Huys, personal communication; personal observation), and those referred to here are extremely elongate and hence vulnerable to damage. In order to assess the validity and robustness of characters (12) and (13) and to rule out variability, observations from a wider range of individuals are desirable. Because both species were collected in very low numbers, these characters could not be categorically confirmed from the material available for study.

DISCUSSION

Fiers (1988) established *Probosciphontodes* to accommodate two new species, differentiated from all other members of Ancorabolidae by two principal characters: the dorsoventrally depressed body shape (although he recognized that *L. expansus* displayed the same condition) and the absence of endopods in P2–P4. He pointed out that *Paralaophontodes*, *Tapholaophontodes*, and *Algeniella* also exhibit endopodal reductions in the swimming legs, but none to the same extent as displayed in *Probosciphontodes*. The prominent rostrum (to which the genus name

refers) and the conspicuous tube-pores in relation to their possible functional and behavioural significance were also highlighted as distinctive generic features.

The Ancorabolidae are generally characterised by their striking visual appearance, with conspicuous body processes and integumental outgrowths. Across the family, body processes bear sensory sensilla apically, and integumental pores frequently exhibit elongate tubular extensions (Fiers, 1988; Schizas and Shirley, 1994a; Conroy-Dalton and Huys, 2000; Conroy-Dalton, 2001, 2003a, b) on the body somites, swimming legs, and caudal rami. Ancorabolids are typically covered by exogeneous material such as detritus (personal observation), obscuring the body contours, but through which the sensilla arising from body processes and the elongate tube-pores protrude. This phenomenon undoubtedly plays a role in enhancing or at least maintaining sensory perception of the animals within their environment. This condition is widespread in the Ancorabolidae (Fiers, 1988; Conroy-Dalton and Huys, 2000; Conroy-Dalton, 2001, 2003a, b, unpublished data). Fiers (1988) also noted a similar phenomenon in *Echinolaophonte* Nicholls, 1941 (Laophontidae) and *Cletopsyllus* Willey, 1935 (Cletopsyllidae) whereas Schizas and Shirley (1994b) reported it in the laophontid genus, *Elapholaophonte* Schizas and Shirley, 1994.

In discussing the relationships of his new genus, Fiers (1988) tentatively recognized two lineages within the subfamily Laophontodinae: the *Laophontodes*–*Paralaophontodes* group and the *Tapholaophontodes*–*Algeniella*–*Patagoniella* group, differentiated from each other by the morphology of the dorsal body surface and P2–P4 bases. Despite admitting some uncertainty as to the affinities of *Probosciphontodes*, Fiers (1988) nevertheless considered it to occupy an intermediary position between these two genus groups.

Within the Laophontodinae, *Lobopleura* and *Probosciphontodes* are instantly recognisable by their strikingly depressed body shape, by the absence of processes on the dorsal body surface, and by the lobate, lateral processes present on most body somites. Their sistergroup relationship is supported by the following synapomorphies: (a) body dorsoventrally depressed; (b) thoracic somites and first two abdominal somites with well-developed lateral, lobate processes, furnished with spinules; (c) antennule segment 1 (both sexes) with well-developed outer, modified

seta (highly setulose); (d) antennule 4-segmented in ♀, segments 3 and 4 having failed to separate; (e) maxillule, coxal endite with one of the two setae reduced; (f) maxillary endopod with only one seta; (g) P2–P4 exp-3 innermost apical element markedly reduced; (h) P5 three-dimensional in appearance, because of the position of the basal setophore and migration of the outer exopodal elements (distalmost two in ♀, distalmost one in ♂); (i) P5 baseoendopodal elements reduced in size (two reduced setae in *Probosciphontodes*, one in *Lobopleura*); and (j) rostrum elongate, basally constricted.

The proposal of the new genus *Lobopleura* for *L. ambiducti*, new species, and *L. expansa*, new combination, is supported by the following autapomorphies: type of modification of male P3 endopod, P4 terminal endopod segment with one apical seta, and P5 baseoendopodal armature reduced to one vestigial seta. In addition, the genus exhibits the following unique plesiomorphy: P1 enp-2 with four armature elements (one claw, one seta and two reduced setae). *Lobopleura ambiducti* is also unique within the Ancorabolidae, with both sexes displaying paired genital systems. The normal condition within the family is: female with single copulatory pore; fused gonopores covered by genital operculum derived from vestigial sixth legs; male with asymmetrical sixth legs, one member fused to the somite and the other, functional member articulating and closing off a single gonopore, with a single spermatophore internally. This condition is typical and universal across the whole canthocamptid complex of families *sensu* Huys and Lee (1998/99) with only one exception. *Nannopus palustris* Brady, 1880 (Huntemanniidae) also deviates from the normal condition, exhibiting a paired system in both the female (Canu, 1892; pers. obs.) and male (pers. obs.) similar to the condition found in *L. ambiducti*. Based on in-group comparison (within the canthocamptid complex) the paired genital system found in *L. ambiducti* is considered here to have developed secondarily from the normal unpaired (dextral or sinistral in the ♂) condition. It is regarded as an autapomorphy for *Lobopleura ambiducti*, having convergently evolved in *N. palustris*.

The type of modification of the male P3 endopod in *L. ambiducti* is also unique within the Laophontodinae. The typical condition across the canthocamptid complex *sensu* Huys and Lee, 1998/99 is three-segmented, which is accomplished at the final moult (from CV to adult) by

secondary subdivision of the distal endopodal segment into two “pseudosegments” and allometric growth of the apophysis. This condition has been interpreted as being plesiomorphic, the apomorphic state being the suppression of the distal secondary subdivision, a condition displayed by the Cristacoxidae, Laophontopsidae, Normanellidae, and the *Ancorabolutus*-lineage in the Ancorabolinae (Huys, 1990; Huys and Lee, 1998/99; Conroy-Dalton and Huys, 2000). In both *Algeniella boitanii* Cottarelli and Baldari, 1987, and *Tapholaophontodes laurenceae* Bodiou and Colomines, 1988 (Laophontodinae), the two-segmented condition of the male P3 endopods is not homologous to that in *L. ambiducti*, because the secondary subdivision of the distal endopod segment is expressed, but enp-1 is not.

Probosciphontodes is considered phylogenetically further advanced within the *Lobopleura–Probosciphontodes* lineage, exhibiting the most elaborate pattern of lateral body processes, having entirely lost the endopods in P2–P4 (in both sexes), and showing armature reductions in several other appendages. The monophyly of *Probosciphontodes* is supported by the following autapomorphies: (1) cephalothorax with median pair of moderately developed lateral expansions and posterior corners laterally produced into well-developed lobate processes; (2) extreme elongation of the rostrum; (3) lateral margins of rostrum with row of strong spinules; (4) antennary endopod distal outermost element further reduced to a short pinnate spine; (5) maxillule without elements representing distal endite; (6) maxilla with both syncoxal endites bearing two setae; and (7) P3 endopod absent in both sexes.

The *Lobopleura–Probosciphontodes* lineage appears to be more closely related to *Tapholaophontodes* and *Algeniella* on account of the absence of distinct dorsal body processes, female antennule segments-2 and -3 with posterior setular tuft, reduced setation of the maxillary basis and maxillary allobasal claw, and the morphology of P1–P4. However, the phylogenetic significance of these characters is not proven and can only be clarified by a phylogenetic analysis of the ancorabolid–cletodid complex as a whole, which is the subject of a forthcoming paper (Conroy-Dalton and Huys, in preparation). Only then can the precise position of the *Lobopleura–Probosciphontodes* lineage, the alleged sistergroup relationship of *Laophontodes* and *Paralaophontodes*, and the supposed relationship between *Tapholaophontodes*, *Algeniella*, and *Patagoniella* be addressed.

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