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R. Huys
Natural History Museum, London

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Enigmas from the past: M'Intosh's (1885) annelidicolous copepods from the voyage of *H.M.S. Challenger*

RONY HUYS
Department of Life Sciences, The Natural History Museum, London SW7 5BD, UK.
E-mail: rjh@nhm.ac.uk

Abstract

The type material of four monotypic genera, *Leaniricola*, *Oestrella*, *Praxillinicola* and *Trophoniphila* (Copepoda, Cyclopoida), described by M'Intosh (1885) from deep water polychaete hosts collected during the *H.M.S. Challenger* expedition, is re-examined. *Leaniricola rotundata* M'Intosh (1885) is removed from its floating status as *species inquirenda* in the Nereicolidae and fixed as the type of a new family, Leaniricolidae **fam. nov.**, based on the presence of an oral cone and massive, three-dimensionally expanded, mandibular gnathobases which are used to anchor the parasite in the parapodial integument of its host. The ectoparasitic *Praxillinicola kroyeri* (M'Intosh, 1885), previously treated as a *species inquirenda* in the Clausiidae, cannot be placed in any of the currently recognized poecilostome families and is here fixed as the type of a new family, Praxillinicolidae **fam. nov.** Females are characterized by unique bilobate antennules, contained within anterior sockets shared with the reduced antennae, and by paired labral hooks, both of which probably serve as auxiliary attachment organs. Despite its highly transformed body *P. kroyeri* has retained the plesiomorphic condition of the female genital system, with the gonopores positioned dorsolaterally and the paired copulatory pores lying close together on the midventral surface. The position of the mesoparasitic *Trophoniphila bradyi* M'Intosh, 1885 in the Bradophilidae is confirmed based on the presence of a median copulatory pore in the female, the disproportionately large egg sacs, the shape of the ectosoma and host utilization. Both sexes of *Bradophila pygmaea* Levinsen, 1878 are re-examined and the male is redescribed in detail. *Flabellicola* Gravier, 1918a is treated as a *genus incertae sedis* in the Bradophilidae. The anal prominence, previously reported in the female of *Oestrella* (= *Melinnacheres*) *levinseni* M'Intosh, 1885 (Saccopsidae), proved upon re-examination to be one of the paired genital apertures. The third and fourth pairs of appendages reported in male saccopsids are here interpreted as the maxillae and maxillipeds, respectively.

Key words: *Bradophila*, *Flabellicola*, *Leaniricola*, *Oestrella*, *Praxillinicola*, *Trophoniphila*, Leaniricolidae **fam. nov.**, Praxillinicolidae **fam. nov.**, Cyclopoida

Introduction

William Carmichael M'Intosh FRS, FRSE (°1838 - †1931) was no doubt one of the most dominating and inspiring central figures in Scottish marine biology and natural sciences for over half a century (Gunther 1977). With the aid of a small grant from the Fisheries Board of Scotland he succeeded in establishing at St. Andrews the first marine laboratory in Great Britain. The St. Andrews Fisheries Laboratory, founded in the old fever hospital in 1884, became subsequently replaced by the Gatty Marine Laboratory in 1896. In addition to this lasting legacy, M'Intosh was best known to the scientific community for his monumental "Monograph of the British Marine Annelids" published by *The Ray Society*, the preparation and publication of which occupied most of his active career. While engaged on this classic he also became involved in the analysis of the material collected during the *R.V. Porcupine* expeditions and the monumental voyage of the *H.M.S. Challenger* (December 1872 - May 1876) which led to a revolution in our understanding of life in the deep sea.

M'Intosh's (1885) report on the polychaete collection obtained during the *H.M.S. Challenger* expedition appeared in two large quarto tomes and took seven years to complete. This landmark publication not only illustrated 334 (226 new) species of polychaetes but also included four new monotypic genera of annelidicolous copepods which M'Intosh identified as "parasitic Crustacea": *Leaniricola*, *Oestrella*, *Praxillinicola* and

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Trophoniphila (Fig. 1). With the exception of *Oestrella*, which was re-examined by Boxshall (1977), all other genera received at most cursory treatment in the literature and, for example, do not feature in Gotto's (1979) review of the parasitic copepods associated with marine invertebrates. Boxshall (1977) convincingly demonstrated that *Oestrella* belongs to the family Saccopsidae (formerly Melinnacheridae) and relegated it to a junior subjective synonym of *Melinnacheres* M. Sars, 1870. Both Gooding (1963) and Stock (1968) alluded to a similarity between *Leaniricola* and the nereicolid genera but were unable to make a strong recommendation for assignment to the Nereicolidae. Boxshall & Halsey (2004) subsequently listed it as a *genus inquirendum* in this family. The genus *Trophoniphila* was at times associated with the Herpyllobiidae (Hansen 1892; Haddon 1912) but its taxonomic position has not been reconsidered properly since its permanent exclusion from this family (Leigh-Sharpe 1926; Lützen 1964). Boxshall & Halsey (2004) tentatively included it as a *genus inquirendum* in the Bradophilidae. The status of *Praxillinicola kroyeri* has remained enigmatic since its proposal. The generic name was not cited in the literature until Southward (1964) listed it as an inadequately described member of the Clausiidae. Boxshall & Halsey (2004) also considered it a potential member of the Clausiidae [but see O'Reilly (1995) for a dissenting opinion].

M'Intosh's (1885) copepod material is still extant and was deposited in The Natural History Museum in London along with the *H.M.S. Challenger* polychaete collection. This paper re-examines the types of *Leaniricola*, *Trophoniphila* and *Praxillinicola* in order to remove them from their current floating status as *genera inquirendae*. It also reassesses the position of *Flabellicola* Gravier, 1918a and provides additional information on the male of *Bradophila pygmaea* Levinsen, 1878 and the female of *Oestrella levinseni* M'Intosh, 1885.

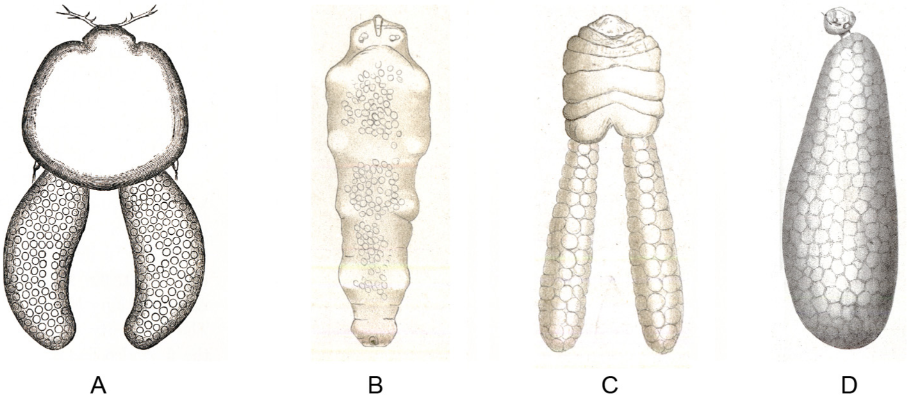

FIGURE 1. Parasitic copepods described by M'Intosh (1885). A, *Leaniricola rotundata*; B, *Praxillinicola kroyeri*; C, *Oestrella levinseni*; D, *Trophoniphila bradyi*.

Material and methods

Habitus drawings were prepared using the hanging drop method (Humes & Gooding 1964) or the "sandwich mounting method" (Huys & Boxshall 1991). Specimens were dissected in lactic acid and the dissected parts were mounted on slides in lactophenol mounting medium. Preparations were sealed with transparent nail varnish. All drawings were prepared using a camera lucida mounted on a Leitz DMR differential interference contrast microscope.

The descriptive terminology is adopted from Huys & Boxshall (1991). Scale bars in figures are indicated in µm except where indicated otherwise. Material examined is deposited in The Natural History Museum, London (NHMUK).

Results and discussion

Order Cyclopoida Rafinesque, 1815

Leaniricola—A copepod chimaera

M'Intosh (1885) proposed this monotypic genus for a new species, *Leaniricola rotundata*, associated with a deepwater sigalionid polychaete collected from the east coast of Japan. The original description based on a single female is very concise, presenting only a woodcut of the dorsal habitus (Fig. 1A). Although the mouthparts were not described, M'Intosh (1885) stated that they presented an arrangement similar to that in *Nereicola* Keferstein, 1863. Gooding (1963) hinted at a relationship between *Leaniricola* and the nereicolid genera *Nereicola* and *Pherma* Wilson, 1923 while Stock (1968) considered the former a *genus inquirendum* in the Nereicolidae. Boxshall & Halsey (2004) adopted this assignment without any further comment. Conradi *et al.* (2015) also listed the genus as a member of the Nereicolidae. Re-examination revealed that *Leaniricola* cannot be accommodated in any of the currently recognized families of the Cyclopoida and, consequently, it is here fixed as the type genus of a new family.

Family Leaniricolidae fam. nov.

Diagnosis. As for the type genus.

Type and only genus. *Leaniricola* M'Intosh, 1885.

Leaniricola M'Intosh, 1885

Generic diagnosis (based on ♀ only). Body rounded in dorsal aspect, consisting of bulbous prosome and slender, ventrally reflexed urosome. Cephalosome separated from remainder of prosome by bilateral constriction. Rostrum offset, fused at base. Somites bearing legs 1–4 fused. Urosome indistinctly 6-segmented; genital and first abdominal somites completely separated; genital apertures paired, located dorsolaterally, without armature; abdominal somites 3–4 fused ventrally; anal somite with unarmed operculum. Caudal ramus elongate, with ventrally recurved lobate outgrowth covered by spinulose pads and five naked setae (setae I and VII absent).

Antennule slender, 6-segmented; segments 1–3 with multipinnate elements. Antenna 4-segmented, comprising coxobasis and 3-segmented endopod; enp-2 with spinulose pad, two setae and one recurved spine; enp-3 small, with six setae, three of which geniculate. Labrum with large, anteriorly directed cylindrical extension forming anterior face of oral cone, and paired lateral folds embracing proximal halves of mandibular gnathobases. Paragnaths fused, forming labium at base of posterior face of oral cone. Mandible without palp; gnathobase very large, entering oral cone via slit between labrum and labium; with strongly chitinized, cylindrical extensions, produced distally into massive, three-dimensionally expanded anchors. Maxillule small, 1-segmented; with three apical setae. Maxilla 2-segmented, comprising syncoxa and allobasis; syncoxa unarmed, with large spinulose pad; allobasis with one strong apical claw and one small accessory element. Maxilliped 3-segmented, comprising syncoxa, basis and endopod; syncoxa robust; basis unarmed, with spinulose pad; endopod represented by strong elongate claw and one vestigial accessory element.

Legs 1–2 biramous, with 2-segmented rami; endopod medially directed; bases with outer seta and spinulose pad(s) on anterior surface; exp-1 with outer spine; exp-2 with seven (leg 1) or six (leg 2) elements; enp-1 with inner seta; enp-2 with five spines/setae. Leg 3 uniramous, 2-segmented, comprising undivided protopod and exopod; protopod with outer basal seta; exopod unisetose. Leg 4 vestigial, represented by ovoid segment with spinulose pad. Leg 5 absent.

Type and only species. *Leaniricola rotundata* M'Intosh, 1885 (by original designation).

Leaniricola rotundata M'Intosh, 1885

(Figs. 2–6)

Original description. M'Intosh (1885): 153–154; Fig. 2.

Host. *Sthenolepis areolata* (M'Intosh, 1885) [as *Leanira areolata* M'Intosh, 1885] (family Sigalionidae).

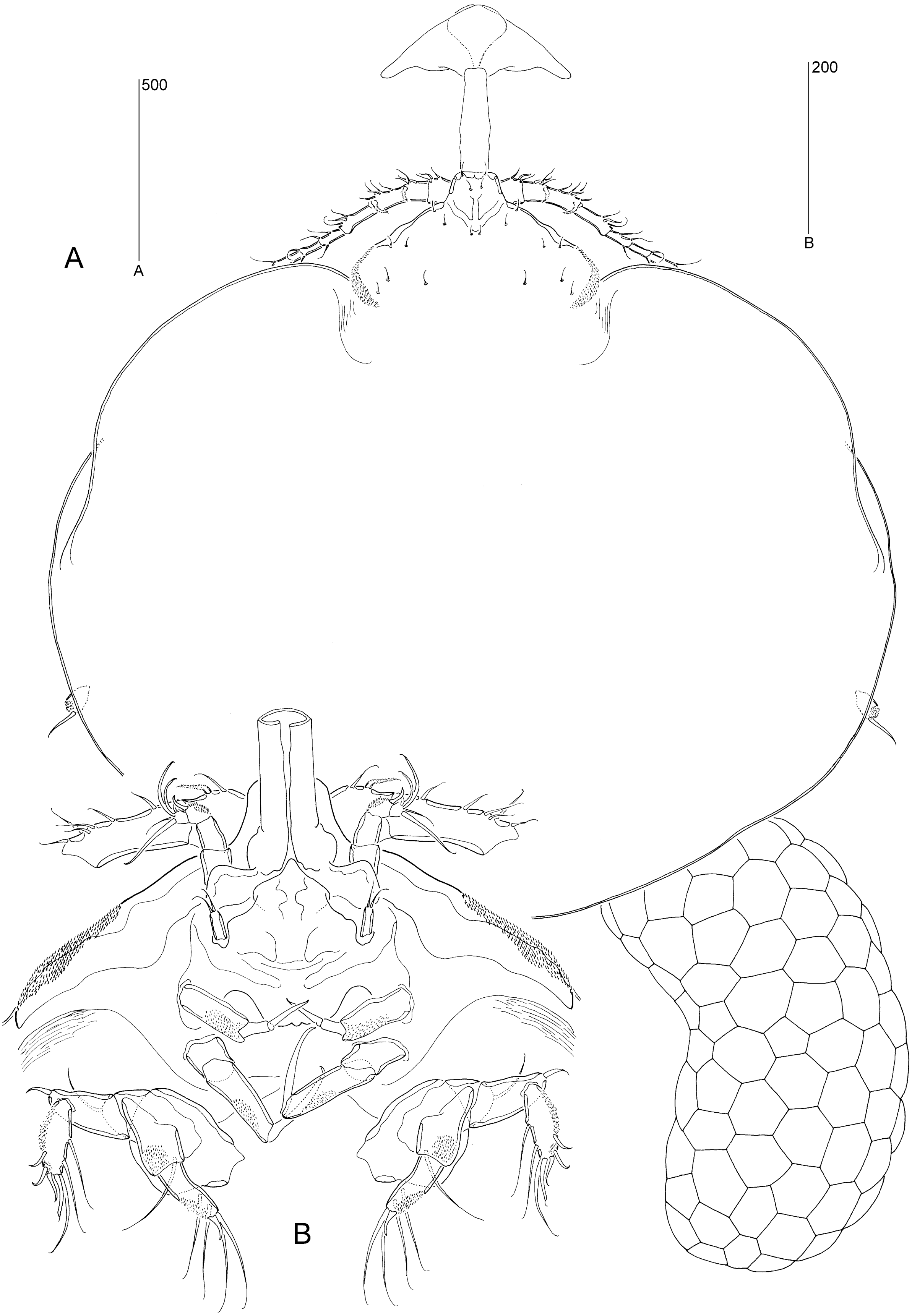

FIGURE 2. *Leaniricola rotundata* M'Intosh, 1885 (♀). A, habitus, dorsal (left egg-sac removed); B, cephalothoracic region, ventral (distal portion of labrum and mandibular gnathobases omitted).

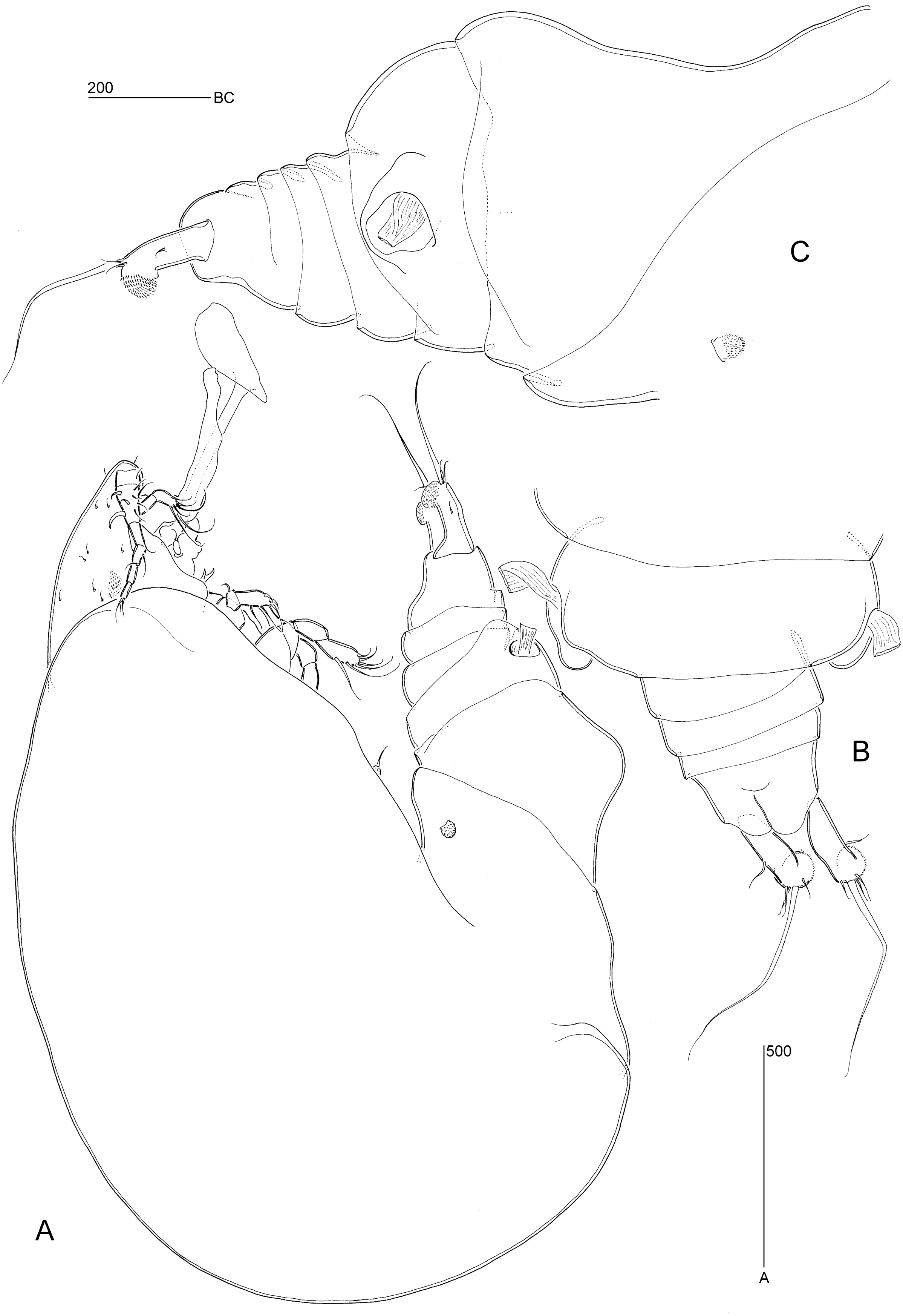

FIGURE 3. *Leaniricola rotundata* M'Intosh, 1885 (♀). A, habitus, lateral; B, urosome, dorsal; C, urosome, lateral.

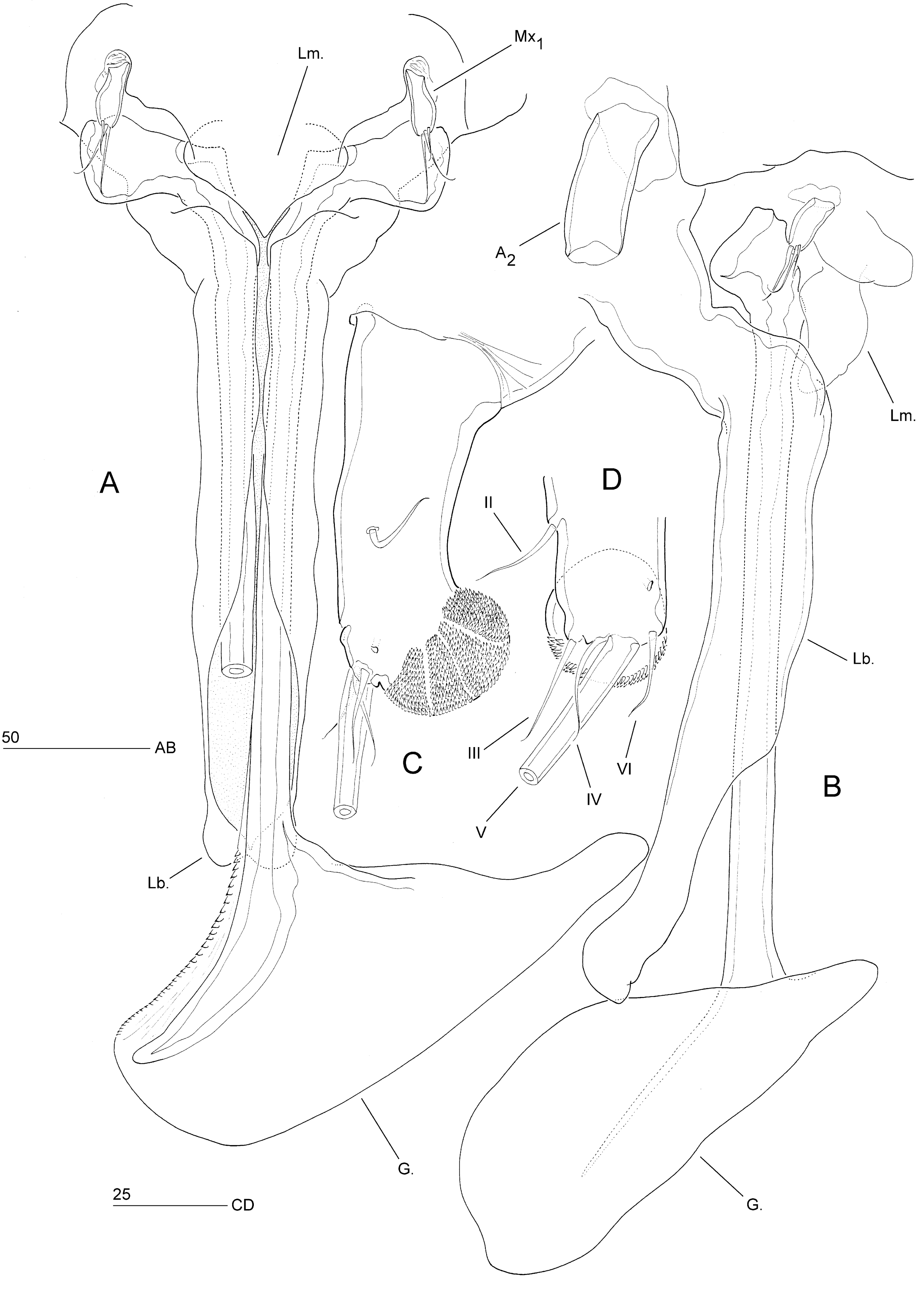

FIGURE 4. *Leaniricola rotundata* M'Intosh, 1885 (♀). A, Oral area showing labrum (Lb.), labium (Lm.), mandible (G.: gnathobase) and maxillule (Mx_1) [left gnathobase omitted], posterior view; B, same, left lateral view (A_2: coxobasis of antenna); C, right caudal ramus, lateral; D, distal portion of left caudal ramus, dorsal.

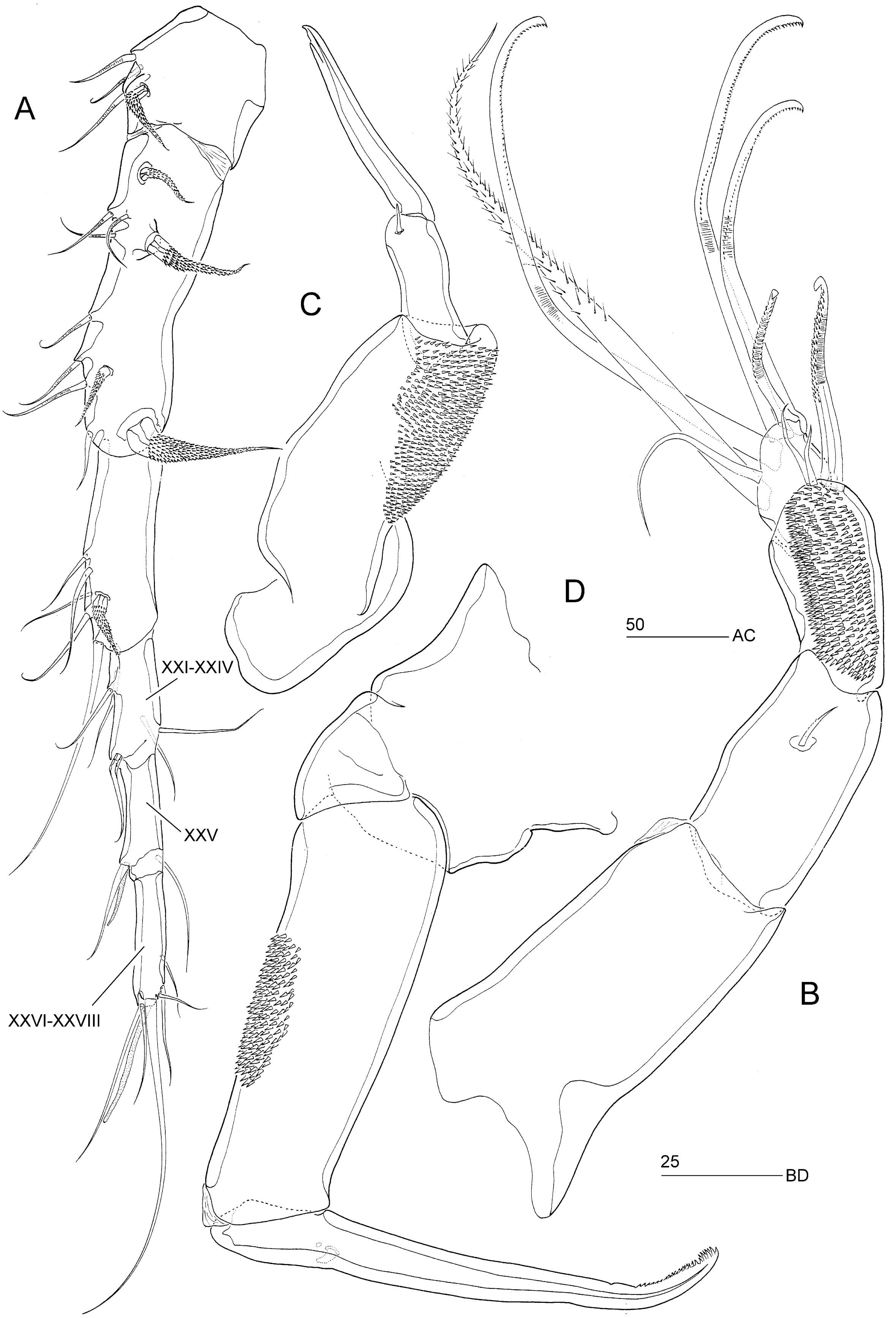

FIGURE 5. *Leaniricola rotundata* M'Intosh, 1885 (♀). A, antennule; B, antenna; C, maxilla; D, maxilliped. Roman numerals in A referring to ancestral antennulary segments (Huys & Boxshall 1991).

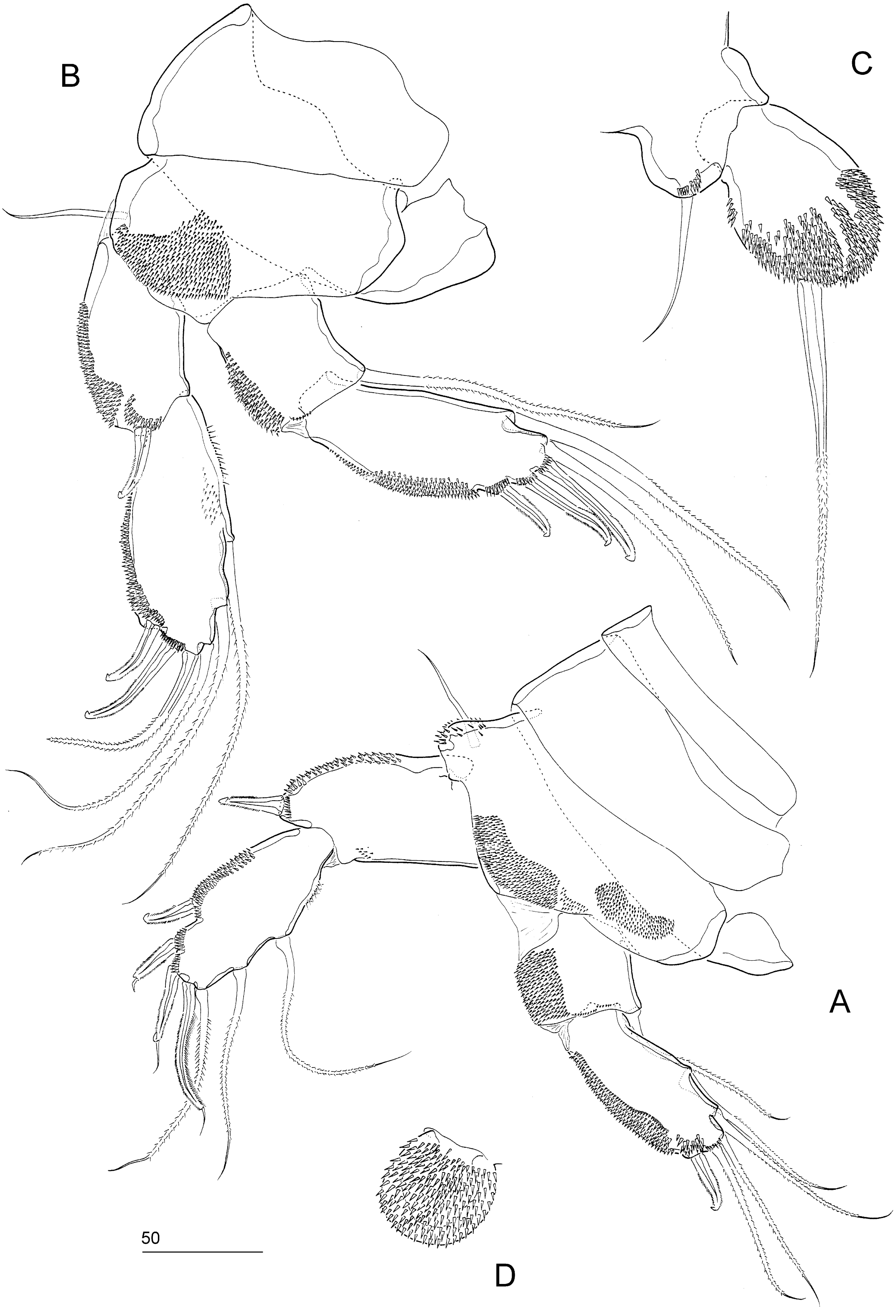

FIGURE 6. *Leaniricola rotundata* M'Intosh, 1885 (♀). A, leg 1, anterior; B, leg 2, anterior; C, leg 3, anterior; D, leg 4.

Type locality. Embedded in the base of a parapodium of the predatory scale worm, *S. areolata*, trawled at *H.M.S Challenger* station 232; south of Tokyo (formerly known as Yedo), Japan, 35°11' N, 139°28' E; depth 345 fathoms (631 m); green mud.

Material examined. The holotype ♀ preserved in ethanol (NHMUK reg. no. 12.5.1875) proved heavily damaged and worthless for descriptive purposes. Inspection of the holotype of *Leanira areolata* (NHMUK reg. no. 85.12.1.116) revealed a second female specimen of *L. rotundata* which was found embedded between its parapodia and is used for the redescription below; collected 12 May 1875.

Redescription of female. Body almost spherical in dorsal aspect (Fig. 2A), maximum width 2,340 µm; consisting of bulbous prosome and slender, ventrally reflexed urosome (Fig. 3A); total body length 4,670 µm, measured along dorsal curvature from anterior margin of prosome to posterior margin of caudal rami.

Cephalosome separated from remainder of prosome by bilateral constriction (Fig. 2A), no functional articulation; triangular in dorsal aspect, with rounded posterolateral angles bearing spinulose pads (Fig. 2A, B); dorsal and lateral surfaces with sensillar pattern as illustrated in Figs. 2A and 3A. Rostrum (Fig. 2A) offset, forming trapezoid projection, fused at base.

Somites bearing legs 1–4 fused, forming bulbous mid-region; no sensillae discernible; region equivalent to somite bearing leg 4 reflexed ventrally, separated from urosome by fully functional articulation (Fig. 3A, C).

Urosome (Fig. 3A–C) not visible in dorsal aspect, 6-segmented, comprising two wide thoracic and four narrow abdominal somites. First thoracic somite limbless (leg 5 not expressed), expanded dorsally forming lobate protrusion. Second thoracic (= genital) somite with paired dorsolateral genital apertures; genital opercula unarmed. Abdominal somites 3–4 fused ventrally, fully separated dorsally (Fig. 3B, C); anal somite with small unarmed operculum (Fig. 3B). Paired egg sacs large, sausage-shaped (Fig. 2A).

Caudal ramus (Figs. 3B, C; 4C, D) elongate, about 3.2 times as long as wide; distal portion forming ventrally recurved lobate outgrowth covered by four spinulose pads; dorsolateral pore present near outer margin. Each ramus with five naked setae (setae I and VII apparently absent); seta V longest and not fused at base to setae IV or VI.

Antennule (Fig. 5A) slender, 6-segmented; segment 2 longest. Armature formula: 1-[3 + 1 multipinnate], 2-[7 + 4 multipinnate], 3-[5 + 1 multipinnate], 4-[5], 5-[2 + aesthetasc], 6-[6 + aesthetasc]. Multipinnate elements spiniform, distalmost one on segment 2 particularly strong.

Antenna (Fig. 5B) 4-segmented, comprising large coxobasis and 3-segmented endopod. Coxobasis without ornamentation. Enp-1 with one small, minutely pinnate seta; without surface ornamentation. Enp-2 with large spinulose pad, two naked setae and one large, finely pinnate, recurved spine. Enp-3 small, partly embedded in enp-2; with three geniculate setae (with fine spinules distal to flexure point), one large multipinnate seta, one short naked seta and one finely pinnate, recurved seta.

Labrum with large, anteriorly directed cylindrical extension with bilobate apex, forming anterior face of oral cone (Fig. 4A, B); discernible in dorsal aspect (Figs. 2A; 3A); with paired lateral folds embracing proximal halves of mandibular gnathobases (Fig. 4A).

Mandible (Fig. 4A, B) very large and of extraordinary shape; palp absent. Gnathobases entering oral cone via slit between labrum and labium and forming strongly chitinized, cylindrical extensions, produced distally into massive, three-dimensionally expanded anchors with serrated medial margin.

Paragnaths fused forming medially pointed lobe (labium) at base of posterior face of oral cone (Fig. 4A).

Maxillule (Fig. 4A, B) small, 1-segmented; with three apical setae.

Maxilla (Fig. 5C) 2-segmented, comprising syncoxa and allobasis. Syncoxa large, expanded basally and with large spinulose pad along distal half of outer margin; unarmed. Basis an elongate segment, partly embedded in syncoxa; with one strong, straight apical claw and one small accessory element near its base; claw slightly bifid near apex.

Maxilliped (Fig. 5D) 3-segmented, comprising syncoxa, basis and endopod. Syncoxa robust, without ornamentation. Basis elongate, unarmed, with spinulose pad halfway along outer margin. Endopod represented by strong elongate claw (longer than basis) with minute serrations along distal quarter of inner margin; with one vestigial accessory element plus pore near base of claw.

Leg 1 (Fig. 6A) biramous, endopod medially directed. Praecoxa and coxa well developed, without surface ornamentation. Basis with two spinulose pads on anterior surface and few spinules near insertion site of outer naked seta. Exopod 2-segmented, segments subequal in length; exp-1 with spinules around outer margin and at base of outer recurved spine; exp-2 with numerous spinules around outer margin and few setules around proximal inner margin, armature consisting of four bipinnate spines (proximal one with recurved tip, others with flagellate extension) and three bipinnate setae. Endopod 2-segmented; enp-1 shortest and widest, with inner bipinnate seta and spinulose pad around outer margin; enp-2 with one recurved bipinnate spine and four bipinnate setae, and spinules around outer margin and bases of outer spine and apical setae.

Leg 2 (Fig. 6B) biramous, endopod medially directed. Praecoxa not discernible. Coxa large, without ornamentation. Basis with spinulose pad on anterior surface near insertion of exopod; outer basal seta naked. Exopod 2-segmented; exp-1 shortest, with spinules around outer margin and at base of outer recurved spine; exp-2 with numerous spinules around outer margin and few spinules around proximal inner margin, armature consisting of two recurved spines and four bipinnate setae. Endopod 2-segmented; enp-1 shortest, with bipinnate inner seta and spinulose pad around outer margin; enp-2 with three recurved bipinnate outer spines and two bipinnate inner setae, and spinules around outer margin and bases of spines.

Leg 3 (Fig. 6C) uniramous, 2-segmented, comprising undivided protopod and exopod; leg members widely separated and discernible in dorsal aspect (Fig. 2A). Protopod fused at base to somatic wall; with naked outer basal seta surrounded at base by few spinules. Exopod a single ovoid segment covered anteriorly by spinulose pad in distal half and with long multipinnate seta.

Leg 4 (Fig. 6D) vestigial, represented by ovoid segment with spinulose pad on anterior surface; anteriorly directed (Fig. 2A, C).

Leg 5 absent.

Male. Unknown.

Remarks. *Leaniricola* differs from all known extant cyclopoid genera by the presence of an oral cone, making it a chimaera displaying both siphonostome and poecilostome characters. However, *L. rotundata* cannot be placed in the Siphonostomatoida based on the segmentation pattern of the female antennule and the morphology of the antenna. The distal part of the female antennule in siphonostomatoids is characterized by the presence of an aesthetasc on ancestral segment XXI and the absence of the boundary between ancestral segments XXIV and XXV (these segments forming a double or even more compound segment) (Huys & Boxshall 1991; Boxshall & Huys 1998). In *L. rotundata* aesthetascs are present on segments XXV and XXVIII but not on segment XXI (Fig. 5A) and segment XXV is expressed as a free segment while segment XXIV is incorporated into a more proximal quadruple segment (XXI–XXIV). The penultimate antennulary segment (XXV) of all copepodid stages of almost every poecilostomatoid thus far recorded is expressed as a distinct segment and carries a seta and an aesthetasc anterodistally and a seta posterodistally (Boxshall & Huys 1998). This free segment represents a characteristic signature for the poecilostome families in the Cyclopoida. The antennary armature in siphonostomatoids is sparse. In species that have retained the 3-segmented condition of the endopod the first segment is always unarmed, the second carries a single seta and the third has a maximum of four setae, one commonly claw-like, around the distal margin. In *L. rotundata* the first segment carries a seta, the second has three elements and the third six elements around the apex. This armature pattern, in conjunction with the fusion of the coxa and basis into a coxobasis and the absence of the exopod, is reminiscent of the poecilostome condition.

The oral cone of siphonostomatoids is formed from the anterior lip, the labrum, and the posterior lip, the labium which represents the paired paragnaths. A genuine oral cone has evolved independently in some harpacticoid families such as the Superornatiremidae and Novocriniidae (Huys 1996; Huys & Iliffe 1998) but has thus far not been reported in the Cyclopoida. Buccal cone-like structures have been observed in the unplaced genus *Endocheres* Bocquet & Stock, 1956 (Boxshall & Halsey 2004) and in members of the Lamippidae (Stock 1988) but their homology with the oral cone of siphonostomatoids and *Leaniricola* is questionable. The labrum and labium are only loosely associated in *L. rotundata* and part readily to allow movement of the mandibular gnathobases between them. The larger part of the oral cone is formed by the muscular labrum with the labium only contributing to its basal section. The female specimen examined in this study was found embedded between the parapodia with its oral cone penetrating the integument of its polychaete host. Presumably the massive, three-dimensionally expanded mandibular gnathobases serve a dual function as feeding appendages as well as anchoring devices. However, it is not known how the oral cone is used to penetrate the host and how nutrients are transported back to the oesophagus.

Although the taxonomic history of the genus *Leaniricola* has been contentious since its inception, most authors have traditionally associated it with the Nereicolidae (M'Intosh 1885; Gooding 1963; Stock 1968; Boxshall & Halsey 2004; Conradi *et al.* 2015). The family currently includes 19 species in seven genera (Boxshall & Halsey

2004; Kim *et al.* 2013) all of which exclusively utilize polychaetes as hosts: *Nereicola*, *Selius* Krøyer, 1837; *Selioides* Levinsen, 1878; *Anomopsyllus* Sars, 1921; *Pherma* Wilson, 1923; *Sigecheres* Bresciani, 1964 and *Vectoriella* Stock, 1968. The distinction between *Selius* and *Selioides* is based solely on the assumption that Krøyer's (1837) observation of the maxilliped is correct. The inadequately described *Chelonidiformis* Hesse, 1869 is not considered here since it is currently considered a *genus inquirendum* (Boxshall & Halsey 2004). Although there is a superficial similarity in gross body morphology, particularly when viewed in dorsal aspect, between *Leaniricola* and members of *Nereicola*, *Selius* and *Selioides* (*cf.* Krøyer 1837; Keferstein 1863; Laubier 1965; Carton & Laubier 1974; Stock 1996) the nereicolid genera are characterized by a strongly reduced urosome which is not reflexed under the prosome as in *L. rotundata*.

The antenna of *L. rotundata* is 4-segmented, comprising a coxobasis and a 3-segmented endopod. Most nereicolid genera (*Anomopsyllus*, *Nereicola*, *Pherma*, *Selioides*, *Sigecheres*) typically share the apomorphic condition in which the middle and distal endopodal segments are fused, forming a 3-segmented antenna. A further derived state is displayed by *Vectoriella* which has a strongly reduced 1-segmented antenna; the condition in *Selius* is unconfirmed. The maxillary basis in members of the Nereicolidae and Clausiidae typically has a rounded tip armed with a spinulose pad (and sometimes with up to two accessory ones). This diagnostic synapomorphy is absent in *Leaniricola* which has a straight apical claw, indicating that the genus cannot be accommodated in either of these annelidicolous families. Based on the presence of an oral cone and the unique morphology of the mandibular gnathobases it is here fixed as the type genus of a new family, Leaniricolidae fam. nov.

According to M'Intosh (1885) a form similar to *L. rotundata* was found on *Leanira hystricis* Ehlers, 1874 from the south-west of Ireland. In one of the 'Porcupine' 1869–1870 expedition reports dealing with the sigalionid polychaetes, M'Intosh (1876: 409) does indeed state "At the anterior end of a fragmentary specimen is apparently a crustacean parasite immersed in the dorsal muscles". However, inspection of this material (four specimens in a bad condition; M'Intosh collection; NHMUK reg. no. 1921.5.1.653) collected off the south-west coast of Ireland at 808 fathoms (1,478 m) depth revealed no additional copepods. The host genus *Sthenolepis* Willey, 1905 belongs to the family Sigalionidae in the infraorder Aphroditiformia (order Phyllodocida). Only two other aphroditiform families serve as hosts to copepods. The Polynoidae (Conradi *et al.* 2015) are most commonly infested by annelidicolous copepods, including members of the Herpyllobiidae (*e.g.* Lützen 1964; Stock 1986, 1996; López-González *et al.* 2000, 2006), Nereicolidae (*e.g.* Carton 1965; Bresciani 1967; Carton & Laubier 1974; Stock 1986, 1996) and occasionally (and probably accidentally) Sabelliphilidae (Bocquet *et al.* 1963). One species of the aphroditiform family Acoetidae serves as host to the catiniid *Cotylemyzon vervoorti* Stock, 1982. *Leaniricola rotundata* is so far the only copepod that utilizes a sigalionid host.

***Praxillinicola kroyeri*—Type of a new family Praxillinicolidae**

M'Intosh (1885) established the genus *Praxillinicola* for a new species found attached to the maldanid *Praxillella abyssorum* (M'Intosh, 1885) in the Antarctic Ocean. Having been collected at 3,510 m depth it constitutes one of the deepest records of a copepod associated with a polychaete host (Conradi *et al.* 2015). M'Intosh (1885) recognized a superficial similarity in body form between *Praxillinicola kroyeri* M'Intosh, 1885 and *Rhodinicola elongata* Levinsen, 1878 (he had no access to the description of the closely related and possibly congeneric *Donusa clymenicola* Nordmann, 1864). Since *R. elongata* had previously been included in the Clausiidae (Giesbrecht 1895; Wilson & Illg 1955) this misleading assertion led Southward (1964) to assign *P. kroyeri* to the same family. *Rhodinicola elongata* is associated with *Rhodine gracilior* Tauber, 1879 and *R. loveni* Malmgren, 1865, also maldanid polychaete hosts, but differs substantially (as M'Intosh admitted himself) in the morphology of the appendages and the reduced abdominal tagma. O'Reilly (1995) claimed that *Praxillinicola* has a caterpillar-like (eruciform) 9-segmented body with only the most rudimentary appendages present. On these grounds he excluded the genus from the nereicoliform group of families (*sensu* Gooding (1963)). Boxshall & Halsey (2004) considered *Praxillinicola* inadequately characterized and treated it as a *genus inquirendum* in the Clausiidae. Conradi *et al.* (2015) also listed *P. kroyeri* as a member of the Clausiidae. Redescription of the holotype below revealed some unique characteristics showing that *Praxillinicola* cannot be included in any of the currently recognized poecilostome cyclopoid families. Consequently, it is here fixed as the type of a new monotypic family.

Family Praxillinicolidae fam. nov.

Diagnosis. As for the type genus.

Type and only genus. *Praxillinicola* M'Intosh, 1885.

Praxillinicola M'Intosh, 1885

Generic diagnosis (based on ♀ only). Body elongate, dorsoventrally depressed; consisting of cephalosome and indistinctly 5-segmented postcephalosomic trunk. Cephalosome bell-shaped, separated from trunk by transverse membranous zone dorsally and ventrally; rostral projection rounded, fused at base. Postcephalosomic trunk probably consisting of four thoracic prosomites and undivided urosome; original somitic boundaries indicated by bilateral constrictions and transverse membranous zones dorsally and laterally. Prosomites limbless, forming continuous unadorned sole ventrally. Urosome 1-segmented, short, with paired dorsolateral genital apertures near posterolateral corners and paired midventral copulatory pores. Anal operculum absent; anal slit positioned middorsally in anterior half of urosome. Caudal rami absent.

Ventral surface of cephalosome with paired anterior sockets containing vestigial antennules and antennae. Antennule 1-segmented, bilobate; outer lobe with strong bipectinate claw; inner lobe with two short spines. Antenna 2-segmented, comprising coxobasis and 1-segmented endopod; coxobasis unarmed; endopod with spinular pad around apex and two small spines. Labrum produced into paired hook-like projections. Paragnaths, mandibles, maxillules and maxillae absent. Maxillipeds comprising robust protopod and 2-segmented endopod; protopod unarmed, with large spinous process on anterior surface; enp-1 unarmed; enp-2 with spinular pad around apex and two short spines.

Legs 1–6 absent.

Type and only species. *Praxillinicola kroyeri* M'Intosh, 1885 (by original designation).

Praxillinicola kroyeri M'Intosh, 1885

(Figs. 7–8)

Praxillinicola kröyeri M'Intosh, 1885—incorrect original spelling (ICZN Art. 32.5.2.1).

Original description. M'Intosh (1885): 409, Plate XXXIX$_{A}$, fig. 10.

Host. *Praxillella abyssorum* (M'Intosh, 1885) [as *Praxilla abyssorum* M'Intosh, 1885] (family Maldanidae).

Type locality. Attached to incomplete specimen of *P. abyssorum* trawled at *H.M.S. Challenger* station 157 (Antarctic Ocean); 53°55' S, 108°35' E; depth 1,950 fathoms (3,566 m); diatom ooze.

Material examined. Holotype ♀ (NHMUK reg. no. 85.12.1.305A); attached to the fifteenth segment of the holotype of *P. abyssorum* (NHMUK reg. no. 85.12.1.305) by "… two small processes on the under surface of the snout …" (M'Intosh 1885: 409); collected 03 March 1874.

Redescription of female. Body elongate and dorsoventrally flattened (Fig. 7A, B); consisting of cephalosome and indistinctly 5-segmented postcephalosomic trunk; total body length 2,190 µm, measured from anterior margin of rostral projection to posterior margin of abdomen (about 2.5 mm according to M'Intosh (1885)); maximum width 677 µm, measured halfway down the second postcephalosomic somite.

Cephalosome bell-shaped, separated from trunk by transverse membranous zone dorsally and ventrally (Fig. 7A, B); dorsal surface with transverse furrow, median pore and four pairs of spiniform sensilla (Fig. 8E). Surface of cephalosome with numerous denticles and spinules as indicated in Figs. 7A, B and 8A, B, E. Rostral projection arising from ventral surface, rounded, fused at base (Figs. 7B; 8E).

Postcephalosomic trunk probably consisting of four thoracic prosomites and undivided urosome (Fig. 7A, B); original somitic boundaries indicated by bilateral constrictions and transverse membranous zones dorsally and laterally; membranous zone between prosome and urosome continuous ventrally but interrupted middorsally by anal slit (Fig. 8H). Prosomites limbless, with numerous spiniform and few setiform sensilla on dorsal surface as indicated in Fig. 7A; forming continuous unadorned sole ventrally (Fig. 7B); fourth prosomite possibly compound as indicated by sensillar pattern. Capacious body cavity mostly filled with several hundreds of oocytes (Fig. 7B).

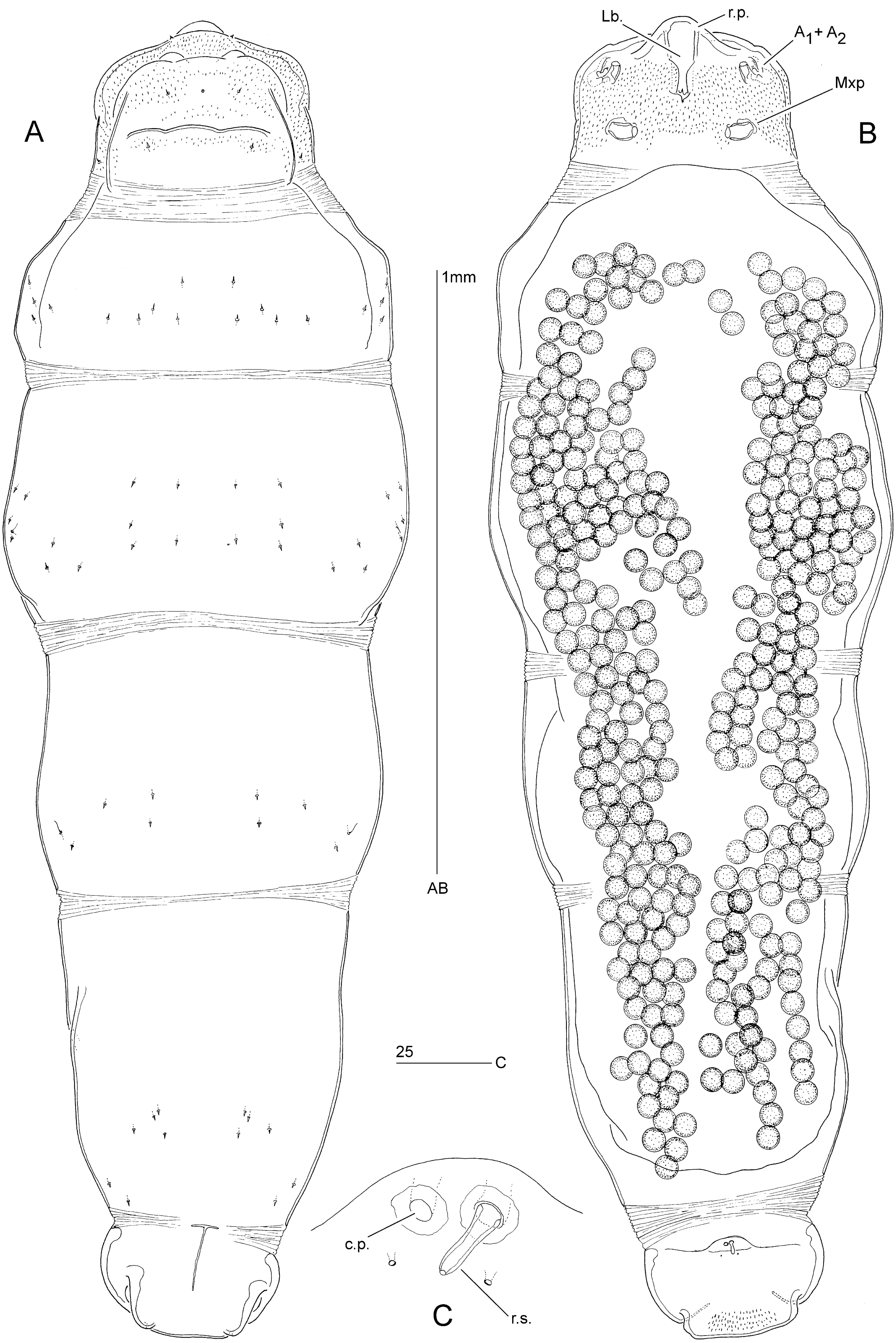

FIGURE 7. *Praxillinicola kroyeri* M'Intosh, 1885 (♀). A, habitus, dorsal; B, same, ventral, showing position of rostral projection (r.p.), socket containing antennule and antenna ($A_1 + A_2$), labrum (Lb.) and maxilliped (Mxp); C, median copulatory pores (c.p.) with remnant of spermatophore neck (r.s.) indicated, ventral.

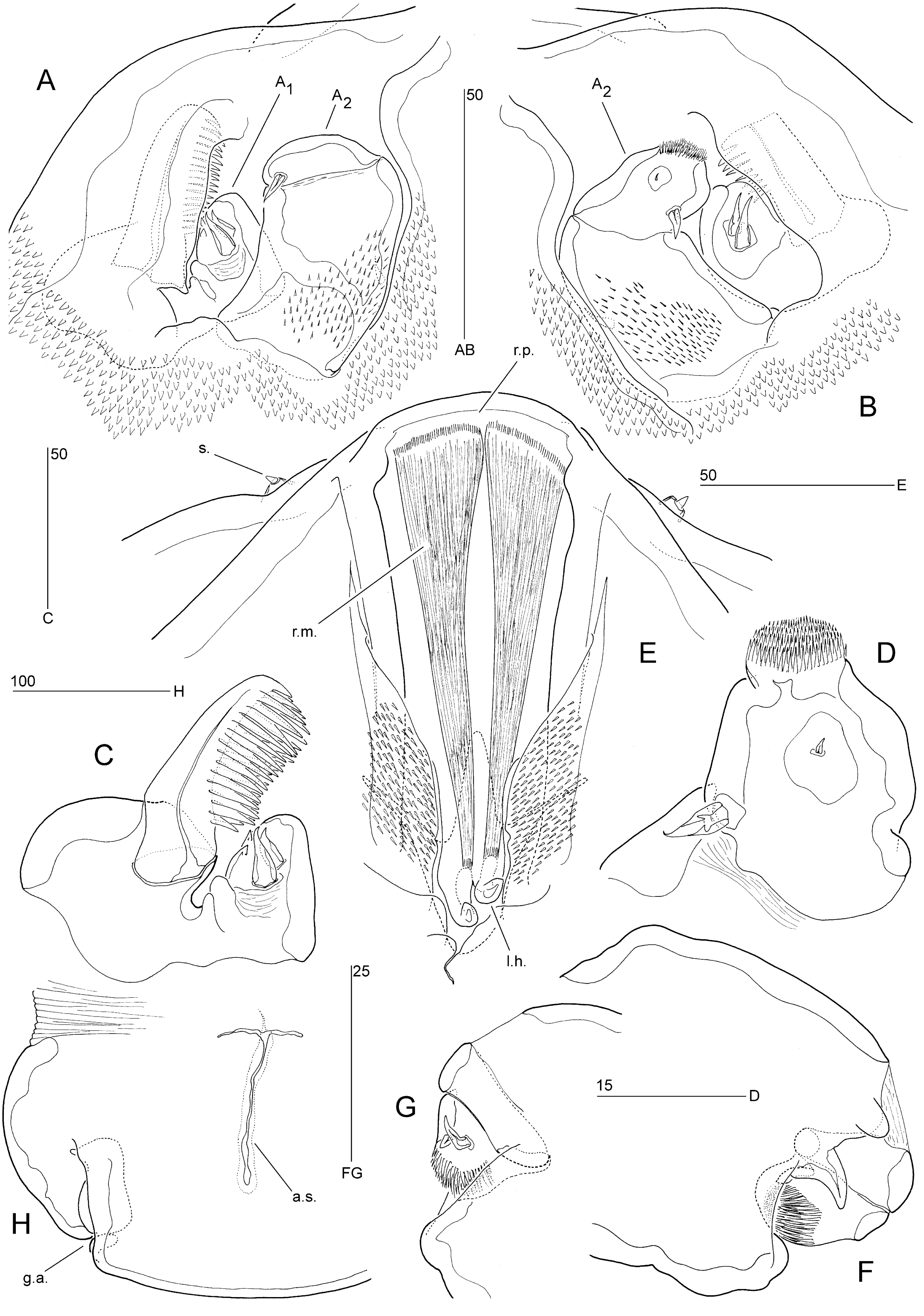

FIGURE 8. *Praxillinicola kroyeri* M'Intosh, 1885 (♀). A, right antennule (A_1) and antenna (A_2, in reflexed condition); B, same on left side (antennulary claw broken); C, right antennule; D, antennary endopod (right side); E, oral area, showing rostral projection (r.p.), labral retractor muscles (r.m.; only one of three pairs drawn), labral hooks (l.h.) and sensilla (s.); F, maxilliped, anterior; G, maxillipedal endopod, posterior; H, anal somite, showing right genital aperture (g.a.) and anal slit (a.s.), dorsal.

Urosome 1-segmented, short, representing about 10% of total body length; about 1.5 times as wide as long; with paired dorsolateral genital apertures (Figs. 7A; 8H) near posterolateral corners, no armature discernible; ventral surface with median depression in proximal quarter, containing paired copulatory pores (with minute associated pores posteriorly) (Fig. 7C), and patch of minute spinules in distal quarter (Fig. 7B). Anal operculum absent; anal slit triradiate (Fig. 8H), positioned middorsally in anterior half of urosome. Caudal rami absent.

Ventral surface of cephalosome with paired anterior sockets containing vestigial antennules and antennae (Figs. 7B; 8A, B). Antennule (Fig. 8A–C) reduced, 1-segmented, consisting of large outer and smaller inner lobe; outer lobe with strong, medially directed, bipectinate claw; inner lobe with two short spines on posterior surface and two spiniform and two rounded extensions along outer margin.

Antenna (Fig. 8A, B, D) 2-segmented, comprising coxobasis and 1-segmented endopod. Coxobasis without armature; posterior surface with numerous minute spinules. Endopod shorter than coxobasis; apex with spinular pad; posterior surface with one short and one minute spine.

Labrum (Fig. 8E) narrow, produced into paired hook-like projections; three pairs of strong retractor muscles originating from frontal wall of cephalosome and inserting on bases of labral hooks (only one pair illustrated in Fig. 8E). Oral opening flanked by dense spinular patches. Paragnaths, mandibles, maxillules and maxillae absent.

Maxillipeds (Fig. 8F, G) compact, located in distal third of cephalosome (Fig. 7B); 3-segmented, comprising robust protopod (fused syncoxa and basis) and 2-segmented endopod. Protopod unarmed but with large spinous process on anterior surface, near articulation with endopod; forming concavity along palmar (medial) margin in which endopod can be withdrawn (Fig. 8F). Enp-1 unarmed, partly fused with protopod along posterior surface (Fig. 8G). Enp-2 narrower than enp-1; apex with spinular pad; posterior surface with two short spines.

Legs 1–6 absent.

Male. Unknown.

Remarks. M'Intosh's (1885) description is very brief, illustrating only the whole animal in ventral aspect (Fig. 1B). He interpreted the body as 9-segmented but it is not clear from his illustration which body regions his "segments" relate to. The abdomen was described as having two dilated somites anteriorly, followed by four narrower ones, the last one being the genital somite presenting a "...central genital aperture". This study revealed that the postcephalosomic trunk probably consists of four thoracic prosomites and an undivided urosome. M'Intosh identified only one pair of appendages which he equated with the antennae (or antennules) with which the copepod attaches itself to the host. From their posterior position in his habitus drawing it appears that in reality he was referring to the maxillipeds. The central projection on the anterior ventral margin referred to as the rostrum by M'Intosh (1885) is here reinterpreted as the prominent labrum.

Praxillinicola kroyeri is unusual in the morphology and arrangement of its cephalosomic appendages. The paragnaths, mandibles, maxillules and maxillae are entirely absent while the strongly reduced antennules and antennae are contained within shared anterior sockets on the ventral surface of the cephalosome. Attachment to its maldanid host is secured by the maxillipeds, at least in females, and both the antennules and labral hooks probably function as auxiliary attachment organs. The distal apex of the maxilliped is blunt and modified into a distinct spinular pad as in other annelidicolous families such as the Anomoclausiidae, Clausiidae, Nereicolidae and Spiophanicolidae.

The antennule of *Praxillinicola* is the most outstanding character of the genus. The bilobate structure of the antennule with a strong, medially directed, bipectinate claw on the outer lobe has not been observed in any other genus of the Cyclopoida. The antennule of *P. kroyeri* shows a remarkable, but deceiving, similarity with the appendage tentatively identified as the antenna in *Phyllodicola petiti* (Delamare-Deboutteville & Laubier, 1960a). Laubier's (1961) Fig. 3j (see also Delamare-Deboutteville & Laubier 1960a: Fig. C) shows a bilobate appendage with an outer branch consisting of two annular sclerites connected to each other by thinner areas of chitin (this condition was interpreted as 4-segmented by Boxshall & Halsey (2004)) and carrying two small claws at its tip, and an inner branch which resembles the bipectinate claw in *P. kroyeri*. However, Laubier's illustration is an optical section through what appears to be a stacked series of semicircular lamellae originating from a common stalk (see his Fig. 3h). A similar structure was observed in the second phyllodicolid genus, *Cyclorhiza* Heegaard, 1942 (Gotto & Leahy 1988). Apart from their morphology being radically different, the structures also cannot be positional homologues since in *Praxillinicola* the claw originates from the outer lobe whereas in both phyllodicolid genera the lamellate structure represents the inner branch. Unlike *P. kroyeri*, adult females in the family Phyllodicolidae are mesoparasitic and utilize exclusively phyllodocid polychaetes as hosts (Heegaard 1942; Delamare-Deboutteville & Laubier 1960a; Laubier 1961; Gotto & Leahy 1988; O'Reilly 2000).

Polychaete hosts are infested by a range of, mostly poecilostome, families (Conradi *et al.* 2015). Approximately 170 species, representing 76 genera and 23 families are known to utilize polychaetes, either as ectoparasites, endoparasites or mesoparasites. None of the ectoparasitic members shows a comparable extreme reduction in body plan and segmentation as in *Praxillinicola*. Although the complete absence of legs 1–5 in the female is also displayed in some species of *Anomopsyllus* (Kim *et al.* 2013) and *Vectoriella* (Laubier & Carton 1973), these nereicolids have an inflated trunk, a 2-segmented urosome and functional caudal rami, as well as a complete suite of cephalic appendages. Despite its highly transformed body *P. kroyeri* has retained the plesiomorphic condition of the female genital system, with the gonopores positioned dorsolaterally and the paired copulatory pores lying close together in a depression on the midventral surface. Among the poecilostome families this condition has been reported only in the Erebonasteridae (Huys & Boxshall 1990; Humes & Huys 1992; Martínez Arbizu 1997). The presence of paired ventral copulatory pores was recently confirmed in the Serpulidicolidae (R. Huys, pers. obs.) and is probably related to the unusual ventral surface to ventral surface mating posture of the diminutive males in this family (*e.g.* Southward 1964; Stock 1979). All serpulidicolids are external parasites of tubicolous, serpulid polychaetes. Although the hosts of most erebonasterids are currently unknown, at least one member is an associate of deep-sea vestimentiferan worms (Humes 1973), a group that is now considered to belong to the polychaete family Siboglinidae (Rouse 2001). Some authorities (Gotto 1979; Ho 1984) have considered the family Serpulidicolidae a member of the "Nereicoliform Group", however, it is equally conceivable that it forms part of a different annelidicolous lineage including the Erebonasteridae and Praxellinicolidae. Maldanid polychaetes are typically, but not exclusively, utilized by members of the Clausiidae (O'Reilly 1995; Kim *et al.* 2013), and occasionally by species of the Clausidiidae (Bocquet *et al.* 1963), but it is unlikely that *P. kroyeri* has a close affiliation to either of these families. Based on the unique characters discussed above it is here fixed as the type of a new family, Praxillinicolidae, which has independently entered into an ectoparasitic association with maldanid hosts.

Trophoniphila—A member of the Bradophilidae?

Trophoniphila was considered a possible candidate for inclusion in the Herpyllobiidae by Hansen (1892) but Leigh-Sharpe (1926) excluded it on the grounds that *T. bradyi* was too defectively described for purposes of classification. Although Delamare-Deboutteville & Laubier (1960b) continued treating it as a valid member of the Herpyllobiidae, this course of action was not adopted by Lützen (1964) in his revision of the family. Boxshall & Halsey (2004) tentatively listed *Trophoniphila* as a *genus inquirendum* in the Bradophilidae pending re-examination or the discovery of new material. Since a proper assessment of this position requires additional observations of the type genus, *Bradophila* Levinsen, 1878, the latter is dealt with first.

Family Bradophilidae Marchenkov, 2002

Marchenkov (1999) suggested that the monotypic genus *Bradophila* belonged in a separate family and formally established it a few years later (Marchenkov 2002). The Bradophilidae is one of six families of mesoparasitic copepods which have adult females that are highly transformed and live partially embedded in their polychaete hosts, the other five being the Herpyllobiidae, Jasmineiricolidae, Phyllodicolidae, Saccopsidae and Xenocoelomatidae (Boxshall *et al.* 2015). Members of the latter family are radically different, mostly internal, parasites maintaining only a small aperture through the host's body wall through which paired egg sacs are extruded. Adults of both sexes lack all trace of appendages and the three known species are cryptogonochoristic, with males reduced to a functional testis housed within a receptaculum masculinum inside the female body (Bresciani & Lützen 1974). In the Saccopsidae both the ovaries and digestive system are contained within the external sac-like body which connects via a short stalk with the internal holdfast or frontal bulla. The latter is a simple ring-shaped thickening of the cuticle surrounding the oral region and penetrates the blood vessels of the host's gills (Bresciani & Lützen 1961) or opens into the connective tissues of the body wall (Bresciani & Lützen 1975). Adult females of the other four families share a bipartite body comprising an ectosoma lying external to the body wall of the host, and an endosoma which is embedded within the host. In the sole member of the

Jasmineiricolidae the female reproductive organs are located in the endosoma (Boxshall *et al.* 2015) while in adult females of the Herpyllobiidae and Phyllodicolidae the ectosoma is essentially the reproductive tagma, containing the ovaries. The condition in the Bradophilidae remains equivocal (see below). Adult females in the family Phyllodicolidae have a unique type of endosoma, represented by a pair of elongate rootlets, and, rather than producing genuine egg sacs, attach their eggs separately to an axial filament originating at the genital aperture (Delamare-Deboutteville & Laubier 1960a; Laubier 1961). Members of the remaining two families, Herpyllobiidae and Bradophilidae, differ from each other primarily in the structure of the female endosoma and the gross morphology of the male (*e.g.* Lützen 1966; Marchenkov 2002, López-González *et al.* 2006). Males of *Bradophila* have large prehensile antennae, robust subchelate maxillipeds and conspicuous caudal processes, all of which are used to attach to the ectosoma of the female (Marchenkov 2002; this study). The highly reduced males in the Herpyllobiidae all lack appendages (except for a pair of putative maxillipeds in *Gottoniella* López-González, Bresciani & Conradi, 2006). While herpyllobiids have dwarf males, typically being at least an order of magnitude smaller than the female, such extreme size sexual dimorphism is not encountered in the Bradophilidae. Unlike in *Bradophila*, male attachment in the Herpyllobiidae appears to be by means of a secretion in the vicinity of the genital apertures of the female. In addition to the type genus, the poorly known genera *Trophoniphila* and *Flabellicola* Gravier, 1918a are here also included in the family on the basis of the absence of cephalic appendages in the adult female, the shape and size of the egg sacs and their utilization of bristle-cage worms (Flabelligeridae) as hosts. Since both genera are only known from the less informative mesoparasitic female it is possible that they will be relegated to junior subjective synonyms of *Bradophila* when information about their respective males becomes available. Bradophilids are very rarely reported but it is known that other as yet undescribed species occur in European waters (Boxshall *et al.* 2015).

Bradophila **Levinsen, 1878**

Levinsen (1878) proposed *Bradophila* for a new species, *B. pygmaea*, associated with the flabelligerid *Brada villosa* (Rathke, 1843). Although he recognized a certain resemblance in gross body morphology with *Herpyllobius* Steenstrup & Lütken, 1861 the difference in the point of origin of the connecting stalk was considered sufficient evidence for maintaining generic distinctiveness. The systematic position of *Bradophila* has been considered dubious for a long time. Hansen (1892) proposed the family Herpyllobiidae in which he included *Herpyllobius*, *Eurysilenium* M. Sars, 1870, *Rhizorhina* Hansen, 1892, and with considerable probability *Saccopsis* Levinsen, 1878 and *Bradophila*, not improbably *Trophoniphila* and possibly *Oestrella*. This classification was largely adopted by Haddon (1912). Applying his own descriptive terminology for the Herpyllobiidae to *B. pygmaea*, Leigh-Sharpe (1926) interpreted the collar-shaped, highly sclerotized anterior part of the ectosoma as the head and described it as having "symmetrically arranged fleshy excrescences with two lateral serrate horns". In reality, the paired excrescences figured by Levinsen represent an optical section through the circular holdfast and the "serrate horns" are not part of the parasite but correspond to torn host integument or tissue located around the point of entry. Levinsen (1878) himself assumed that they were a continuation of the stalk, probably representing the remnants of the anterior, unknown part (endosoma) of a similar structure as seen in *Herpyllobius*. Leigh-Sharpe (1926) pointed out the presence of two spherical processes (as in *Phallusiella* Leigh-Sharpe, 1926) and a small median process (as in *Eurysilenium*) on the ectosoma but nevertheless excluded *Bradophila* from the Herpyllobiidae primarily because the "... head and neck are not perpendicular to the trunk". Delamare-Deboutteville & Laubier (1960b) nevertheless continued listing *Bradophila* as a member of the Herpyllobiidae. Lützen (1964) showed that in herpyllobiids the stalk (neck) issued from a point on the midline of the underside of the ectosoma with which it usually forms a right angle. He excluded *Bradophila* from the Herpyllobiidae without suggesting an alternative placement for it; however, Monod & Laubier (1996) continued to treat the genus as a member of this family. Marchenkov (1997) initially listed *B. pygmaea* as *incertae sedis* in the Siphonostomatoida before designating it as the type of a new family in the Poecilostomatoida (Marchenkov 2002). Boxshall & Halsey (2004) placed the Bradophilidae in a more inclusive Cyclopoida.

Bradophila pygmaea Levinsen, 1878

(Figs. 9–10, 11A)

Bradophila pygmæa Levinsen, 1878—incorrect original spelling.
Bradophila pigmaea Levinsen, 1878—Marchenkov (1999a: 108, 109, 111, 112, Figs. 34, 35; 1999b: 7, 8, 22, Table 1; 2002: 514, 516, 517): incorrect subsequent spelling.
Bradophyla pigmaea Levinsen, 1878—Marchenkov (1998: 15; 1999b: 13, Table 3; 2001: 97; 2002: 517): incorrect subsequent spelling.
Bradophyla pigmae Levinsen, 1878—Marchenkov (2001: 90, 97): incorrect subsequent spelling.

Levinsen (1878) discovered four females, of which two were ovigerous, among museum collections of the flabelligerid polychaete *Brada villosa*. His text description in old Danish and accompanying woodcut figures are remarkably detailed by contemporary standards and reveal details that were even overlooked in modern descriptions (*e.g.* Marchenkov 1999b, 2002). Contrary to Marchenkov's (2002: 514) claim that the hosts were collected off the coast of Greenland by Steenstrup and Lütken no locality data were given (although note that some of the parasitic copepods described in Levinsen's (1878) work did indeed originate from Greenlandic waters, *e.g. Selioides bolbroei*, *Melinnacheres terebellidis*). According to Levinsen the egg sacs of ovigerous specimens extended into the "mouth cavity" of the host while the body was surrounded by, and probably embedded into, the anterior part of the annelid's alimentary tract. Levinsen (1878) doubted whether he had dissected the entire parasite out of the host and his illustrations appear to confirm that he had only obtained the ectosoma. Hansen (1892, 1897) had previously suspected that some tubes must run into the body of the host, otherwise it would be difficult to see how the parasites obtain their food. The second report on *B. pygmaea* is that by Marchenkov (1997) who recorded a single ovigerous female from *Brada villosa* in the Chupa Inlet of the Kandalaksha Gulf, White Sea; no morphological observations were provided. In a conference abstract Marchenkov (1998) subsequently announced the discovery of additional material (four females and three males) from the same locality and host. He confirmed that the adult female body consisted of two portions, ectosoma and endosoma, connected by a well-developed stalk. Applying his newly defined criteria on host-parasite interrelations, Marchenkov (2001) provisionally considered *Bradophila* a potential mesoparasite pending the arrival of anatomical data.

Original description. Levinsen (1878): 371–374, Figs. xyl. (woodcuts) C–E.

Host. *Brada villosa* ((Rathke, 1843) (family Flabelligeridae).

Type locality. Unknown. Levinsen's material was found on polychaete specimens in museum collections, probably in the care of J.J.S. Steenstrup and C.F. Lütken.

Material examined. Damaged ovigerous ♀ with dwarf ♂ attached to ectosoma; obtained from *B. villosa* material collected in the Lofoten Islands and Norway and stored in The Natural History Museum (NHMUK reg. no. 1900.5.1.364–366).

Notes on female. The following is based on Levinsen's (1878) original description in Danish, Marchenkov's (2002) Russian text and personal observations. Ectosoma almost spherical, slightly flattened in dorsoventral direction (on side adjacent to host); colourless or milky white in living specimens; measuring 500–700 µm in diameter (Marchenkov 2002) (330–500 µm according to Levinsen); lacking all trace of segmentation or appendages. Paired genital apertures carried on highly sclerotized genital swellings at posterior end of ectosoma; located ventrolaterally and closed off by strongly chitinized, unarmed opercula. Single copulatory pore located between genital apertures; leading to seminal receptacle(s) via short copulatory duct. Stalk broad, campanulate (bell-shaped) in lateral aspect and passing through surface of host; anterior rim strongly chitinized, collar-shaped and folded backwards. Endosoma filiform, lying in body cavity along digestive tract of host; about 400–700 µm wide; as long as two-thirds body length of host; covered by numerous small rounded tubercles. Paired egg sacs multiseriate, elongate and disproportionately large, measuring 0.9–1.2 mm in length and 0.4–0.7 mm in diameter (Marchenkov 2002) (1.50–1.66 mm long and *ca.* 0.75 mm wide according to Levinsen). Ectosoma with one or two males attached.

Redescription of male. Body (Figs. 9A; 10A) comprising broad, anterior cephalosome and slender elongate postcephalosomic trunk. Body length 530 µm, measured along dorsal curvature from anterior margin of cephalosome to posterior margin of caudal processes. Greatest width (93 µm) measured at cephalosome. Cephalosome (Fig. 9A) subquadrate in dorsal aspect; dorsal surface with pair of spiniform sensilla in anterior quarter; without surface ornamentation; anterior margin with paired lobate outgrowths dorsally (Fig. 9A) and smaller paired protuberances ventrally (Fig. 11). Trunk typically curved ventrally (Fig. 10A); gradually tapering posteriorly in dorsal (Fig. 9A) but not in lateral aspect (Fig. 10A); indistinctly 3-segmented; original segmentation marked by transverse membranous zones dorsally and laterally, and by vestiges of swimming legs 1–3 (arrowed in Fig. 10A). Caudal end with paired, medially directed, non-articulating, lobate processes (probably homologous to caudal rami); each process with spinules along outer margin and on posterior surface, and with dentiform projections on offset apical portion (Fig. 9D, E). Paired genital apertures located ventrally, just anterior to caudal processes (Fig. 9E); spermatophores paired.

Antennules short, located at anterolateral corners of cephalosome (Fig. 9A); short, with large, membranous insert at base dorsally (Fig. 10A); 3-segmented (Fig. 10C). Proximal segment largest, widest at base; distal anterior corner with blunt, posteriorly directed, styliform element. Middle segment subrectangular, positioned at right angle to segment 1; dorsal surface with two spinular patches and one modified conical element; posterior margin with modified rounded element. Distal segment smallest, slightly widening distally; directed at almost right angle to segment 2; carrying two modified elements apically.

Antenna (Fig. 10B) uniramous, anteriorly directed (Figs. 9A; 10A); coxobasis and proximal endopod segment fused forming very long coxo-allobasis; free endopod indistinctly 2-segmented. Coxo-allobasis 3.9 times as long as endopod; with two modified blunt setae. Endopod with incomplete surface suture on ventral surface, indicating original segmentation; with one dorsal and one ventral modified blunt element; distal margin with two curved claws, each with two rows of dentiform projections.

Oral opening minute, probably not functional. Mandible absent. Homology of praeoral processes (Fig. 9B) difficult to assess. Anterior pair of processes (maxillules?) short and subcylindrical; located close to anterior margin of cephalosome, near bases of antennae; each with long naked seta and one modified blunt element (Figs. 9B; 11). Posterior pair of processes (maxillae?) lobate, backwardly recurved and rounded apically (Fig. 10); located either side of vestigial mouth; apical half covered with dentiform projections (Figs. 9B; 11). Pair of minute postmaxillary processes located anterior to maxillipeds (Figs. 9B; 11). Maxilliped (Figs. 9C; 10A) well developed, subchelate; comprising robust proximal segment (protopod) and 1-segmented endopod; palmar margin of protopod with two dentate processes (one proximal, one distal) on anterior surface, and denticular patch and one styliform modified seta on posterior surface (Fig. 11); endopod with strong curved terminal claw.

Remarks. While dissecting females on glass slides, Levinsen (1878) observed two small (200–250 µm) crustaceans, which he considered as belonging to a possibly early developmental stage of *B. pygmaea*. The dorsal view of this stage and accompanying text description leave no doubt that he was dealing with an adult male. According to Levinsen the instar consisted of an anterior, limb-carrying part and a slender, rounded posterior part which was about three times longer. He correctly identified the first pair of limbs as the antennules and described them as 3-segmented, ending in two thorns. The second pair of limbs was described as being the longest, having a large basal part followed by more, clear segments and ending in a thinner part, which also looked like it was segmented. Although this description is more difficult to reconcile with the observations reported here it is conceivable that Levinsen referred to the antennae. The fact that they were figured as posteriorly directed instead of forwardly is probably an artefact due to mounting. The third pair of limbs, which were illustrated as lateral lobes and described as consisting of one piece, which was thick and robust and provided with fine serrations along the anterior margin, can unequivocally be identified as the maxillipeds. Levinsen also observed remnants of a (spent?) putative male, presumably attached near the copulatory pore between the genital apertures of an ovigerous female. His statement that the only obvious parts were a long catching limb ("gribelem") and a short, robust hooked limb ("kroglem") makes a clear reference to the male antenna and maxilliped, respectively.

A fragmentary illustrated description of the male was presented in an unpublished Ph.D. dissertation (Marchenkov 1999a, 1999b) in which it was suggested that *B. pygmaea* belonged in a separate monotypic family. The text description was eventually published as evidence in support of the proposal of the Bradophilidae (Marchenkov 2002) while the illustrations were reproduced in Boxshall & Halsey's (2004) treatment of the family. Unfortunately Marchenkov's description contains several deficiencies and misinterpretations. His statement that *B. pygmaea* possesses dwarf males is misleading because the male (530 µm; 660 µm when antennae are included) is only slightly smaller than the ectosoma of the female (500–700 µm). The male attaches itself to the female by holding the stalk with its prehensile antennae and maxillipeds and using the caudal processes to grasp the ectosoma at the opposite pole. This posture ensures that the male genital apertures maintain close contact with the female copulatory pore, facilitating successful spermatophore transfer. Marchenkov (1999a, 2002) described the antennule

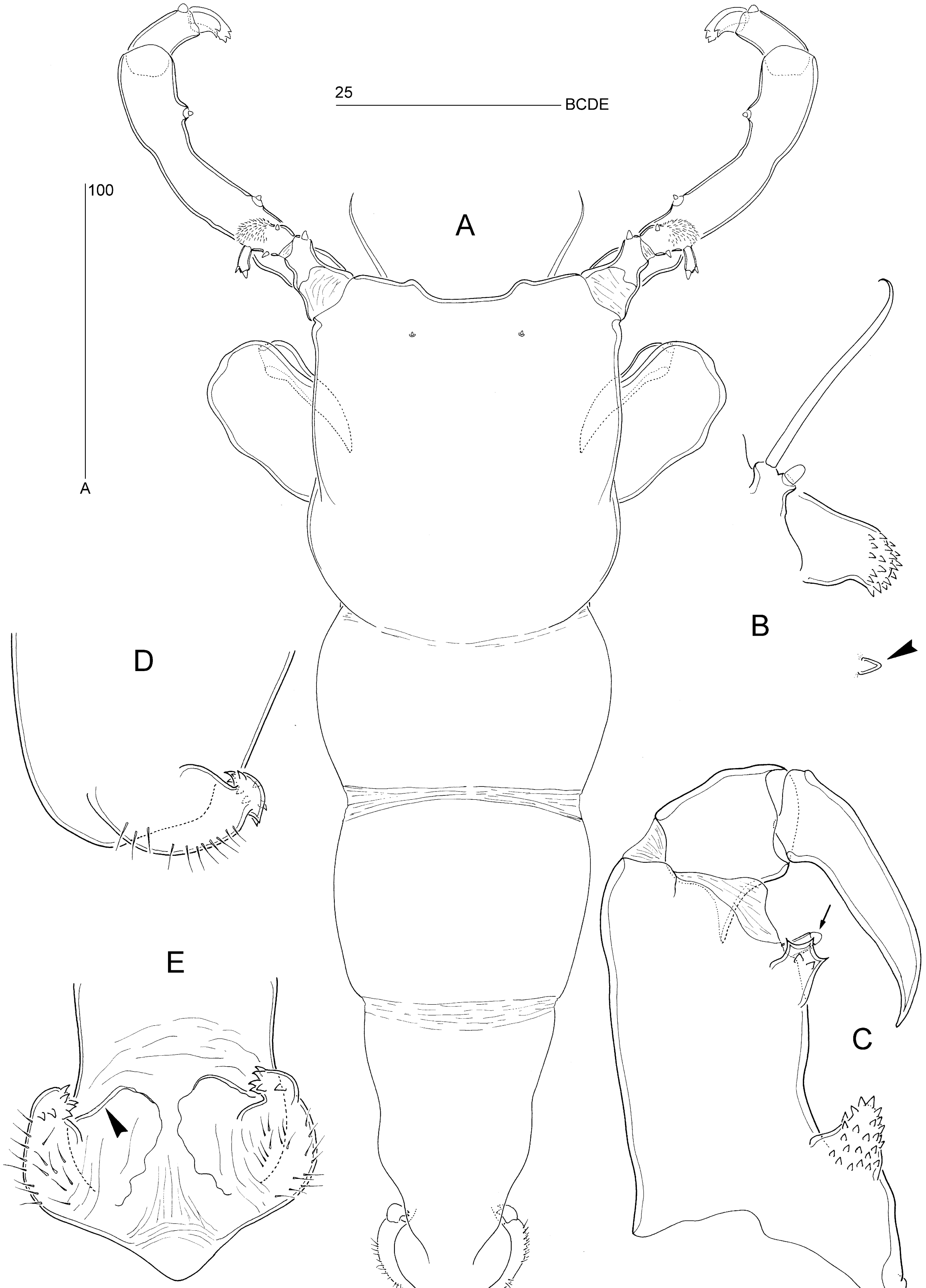

FIGURE 9. *Bradophila pygmaea* Levinsen, 1878 (♂). A, habitus, dorsal; B, mouthparts, lateral (postmaxillary process arrowed); C, maxilliped, anterior (posterior seta on basis arrowed); D, posterior end of trunk, lateral; E, same, ventral (right genital aperture arrowed).

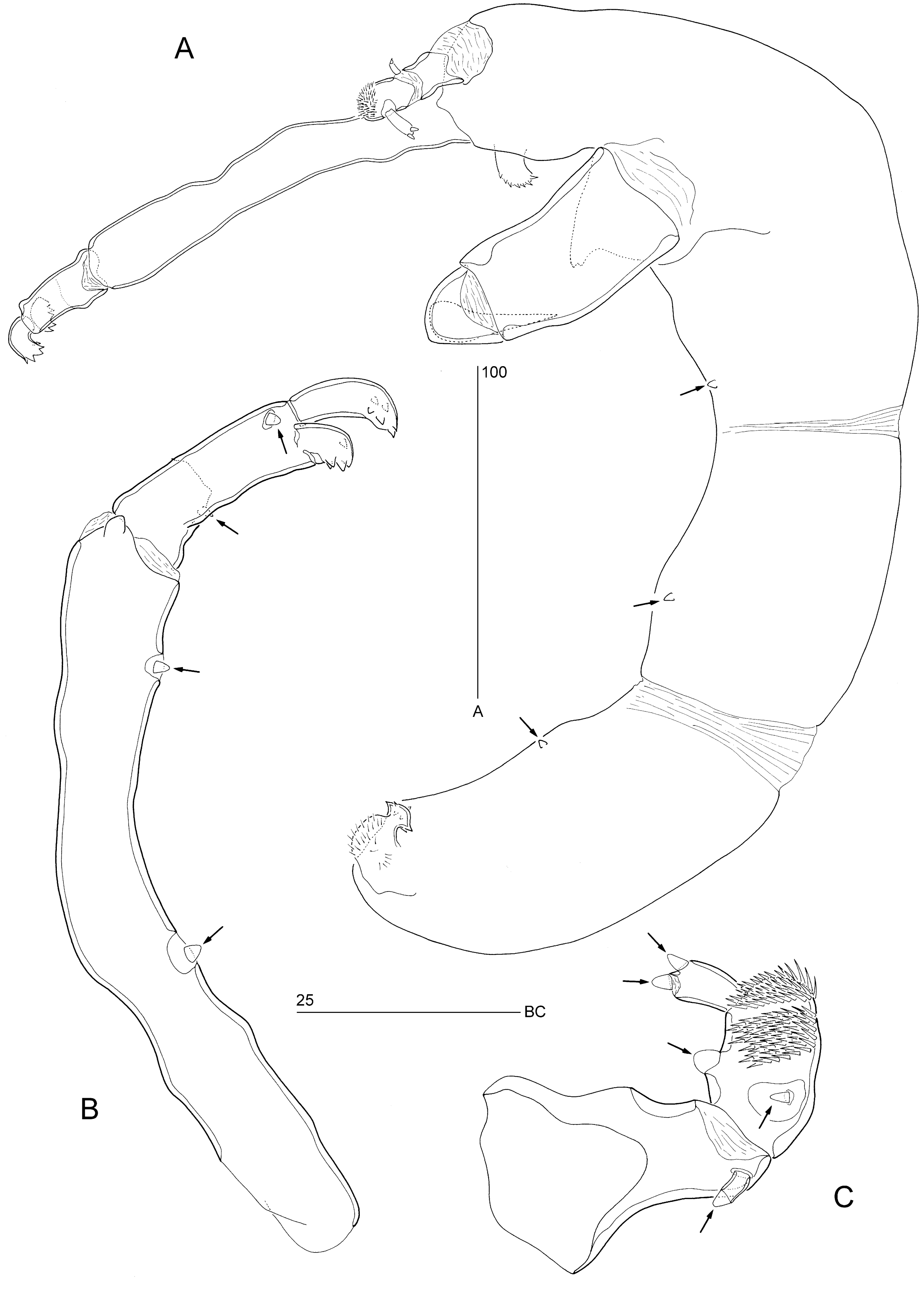

FIGURE 10. *Bradophila pygmaea* Levinsen, 1878 (♂). A, habitus, lateral (rudimentary legs 1–3 arrowed); B, antenna, dorsal (modified setae arrowed); C, antennule, dorsal (modified setae arrowed).

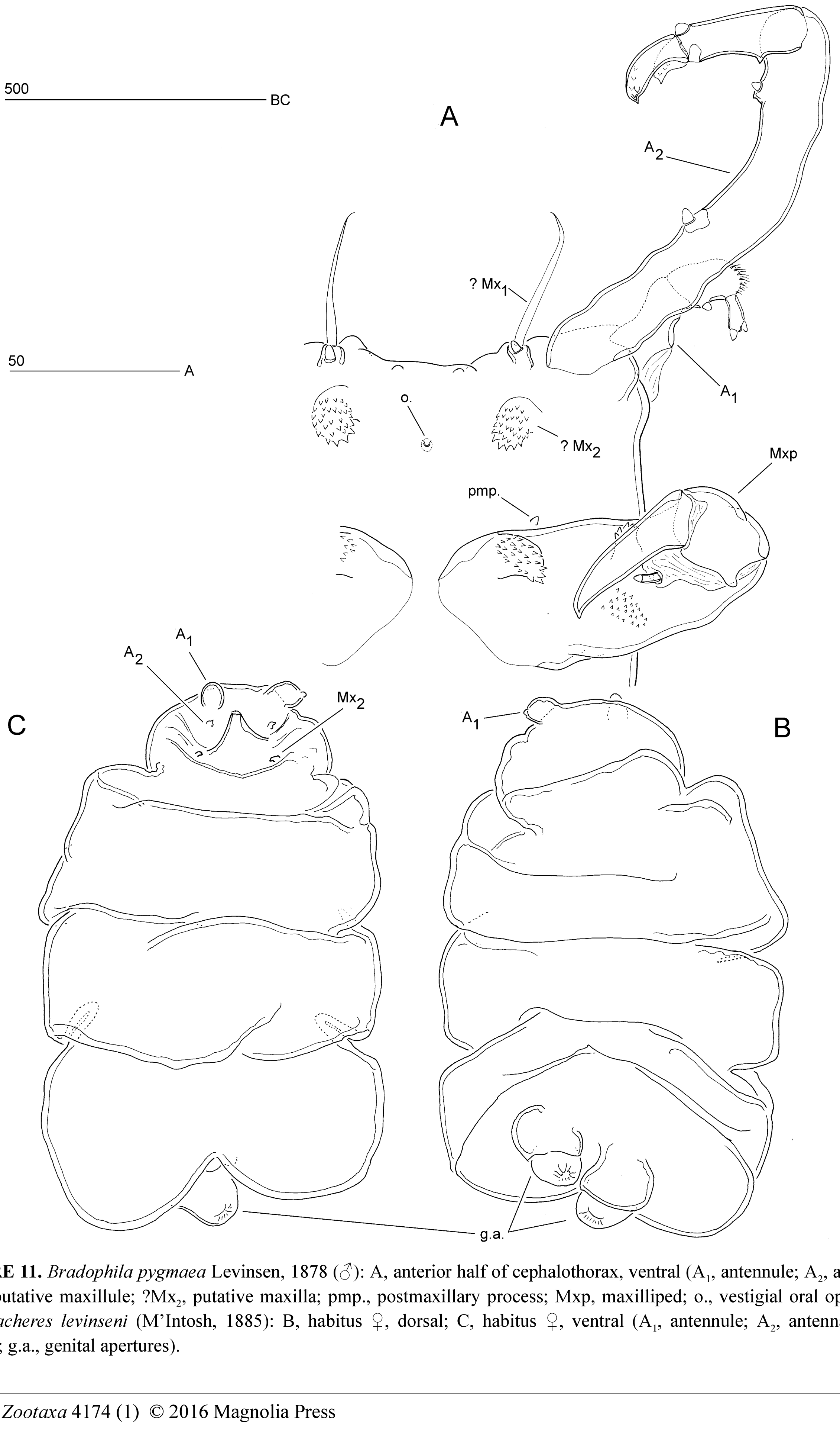

FIGURE 11. *Bradophila pygmaea* Levinsen, 1878 (♂): A, anterior half of cephalothorax, ventral (A_1, antennule; A_2, antenna; ?Mx_1, putative maxillule; ?Mx_2, putative maxilla; pmp., postmaxillary process; Mxp, maxilliped; o., vestigial oral opening). *Melinnacheres levinseni* (M'Intosh, 1885): B, habitus ♀, dorsal; C, habitus ♀, ventral (A_1, antennule; A_2, antenna; Mx_2, maxilla; g.a., genital apertures).

as 4-segmented with the distal two segments being very small and unarmed; however, the apical segment in his drawing is in reality one of the two modified setae of segment 3. The long proximal segment of the antenna was interpreted as the coxobasis, however, the presence of two armature elements on this segment (poecilostome cyclopoids only have one) indicates that it is a compound segment derived by fusion of the coxobasis and the proximal endopodal segment, forming a coxo-allobasis. According to Marchenkov the mandibles are strongly reduced, consisting of a protruding basis, bearing one short seta near the outer margin, and a gnathobase represented by a thin long whip. Our re-examination showed that these limbs are not associated with the mouth opening and most likely represent the putative maxillules, the real mandibles being absent (Fig. 11). The maxillule, erroneously described as an indistinctly 2-segmented, slightly flattened, dentate lobe, in reality represents a different appendage, here identified as the putative maxilla. Marchenkov (1999a, 2002) described and illustrated the maxilla as a reduced lobe bearing small denticles along the inner margin; according to Boxshall & Halsey (2004) it is apparently 2-segmented, comprising a larger syncoxa separated from a tiny claw-like basis by a region of folded integument. Neither description is correct and the appendage labelled as the maxilla in Marchenkov's (1999a) Fig. e could not be confirmed in the male examined herein. Paired minute postmaxillary processes were observed in the same position (Figs. 9B; 11) but it is unlikely that these structures represent remnants of the maxillae. Marchenkov (2002) described the maxilliped as 4-segmented but we could find no evidence for the alleged presence of a syncoxa.

Trophoniphila M'Intosh, 1885

The genus has remained monotypic since its proposal for the subantarctic type species *Trophoniphila bradyi* M'Intosh, 1885. The original description of *T. bradyi* was based on two ovigerous females that lived embedded in the bases of the peristomial gills of their flabelligerid host, *I. wyvillei* (M'Intosh, 1885). M'Intosh (1885) used the spelling *bradii* in the text (p. 368) and the figure legend of plate XXXVI_{A} but explicitly stated that the species was named after George Stewardson Brady. The incorrect original spelling was adopted by Haddon (1912: 403), Gravier (1918a: 504; 1918b: 218), Boxshall & Halsey (2004: 460) and Conradi *et al.* (2015: 153) but is here emended to *bradyi* in accordance with ICZN Art. 32.5.1.

Generic diagnosis (based on ♀ only). Body consisting of endosoma and ectosoma, possibly connected by short frontal stalk; segmentation and appendages completely lacking. Ectosoma rounded, with numerous minute pores on frontal surface. Genital apertures paired, positioned ventrolaterally; closed off by unarmed semicircular opercula; midventral copulatory pore located between genital apertures, connected via copulatory duct with seminal receptacle(s); minute spiniform genital papillae present. Paired egg sacs very large, multiseriate and clavate.

Type and only species. *Trophoniphila bradyi* M'Intosh, 1885 (by monotypy).

Trophoniphila bradyi M'Intosh, 1885

(Fig. 12)

Trophoniphila bradii M'Intosh, 1885—incorrect original spelling.
Trophoniphila Bradii M'Intosh, 1885—Hansen (1892: 21): incorrect subsequent spelling.
Trophoniphila Bradyi M'Intosh, 1885: Hansen (1923: 79) incorrect subsequent spelling.
Trophonophila bradii M'Intosh, 1885: Conradi *et al.* (2015: 153) incorrect subsequent spelling.

Original description. M'Intosh (1885): 368, Plate XXXVIa, fig. 4.

Host. *Ilyphagus wyvillei* (M'Intosh, 1885) [as *Trophonia wyvillei*] (family Flabelligeridae).

Type locality. Embedded in specimen of *I. wyvillei* trawled at *H.M.S. Challenger* station 157 (Antarctic Ocean); 53°55' S, 108° 35' E; depth 1,950 fathoms (3,566 m); diatom ooze.

Material examined. Holotype ♀ in alcohol (NHMUK reg. no. 1939.4.24.1); attached to the bases of the gills; collected 03 March 1874. Inspection of the dissected holotype of *I. wyvillei* (NHMUK reg. no. 85.12.1.261) failed to reveal the second specimen mentioned by M'Intosh (1885).

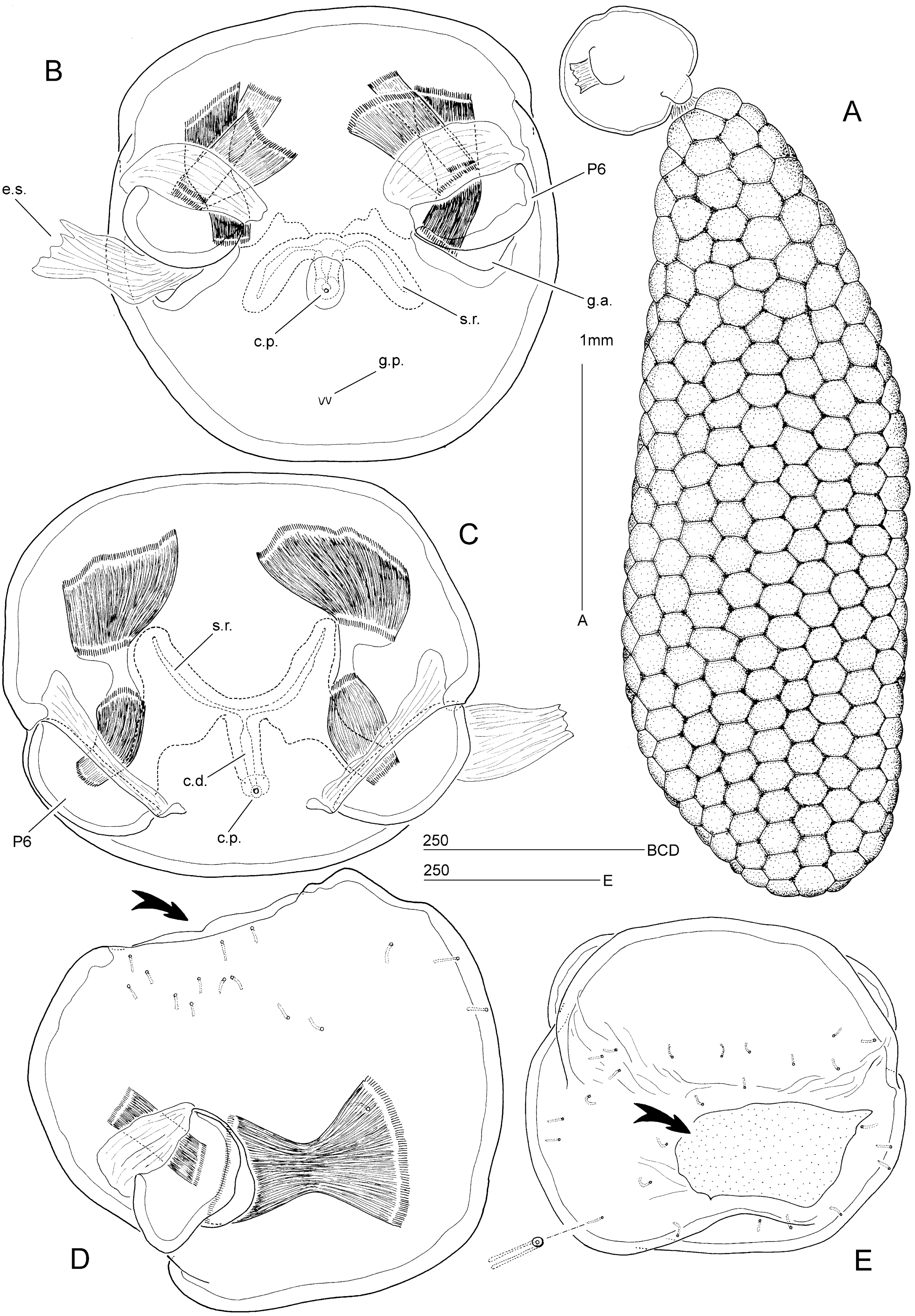

FIGURE 12. *Trophoniphila bradyi* M'Intosh, 1885 (♀). A, ectosoma and left egg-sac; B, ectosoma, posterior (c.p., copulatory pore; e.s., egg sac string; g.a., genital aperture; g.p., genital papillae; s.r., seminal receptacle; P6, genital operculum derived from sixth leg); C, same, ventral (c.d., copulatory duct; c.p., copulatory pore; s.r., seminal receptacle; P6, genital operculum derived from sixth leg); D, same, lateral (arrow indicating connection with endosoma); E, same, anterior, showing connection with endosome (arrowed stippled area) [inset showing detail of integumental pore].

Redescription of female. Body highly transformed and lacking any external trace of segmentation or appendages; consisting of two parts, endosoma and ectosoma, possibly connected by short frontal stalk; stalk and endosoma presumably torn off during dissection. Ectosoma (Fig. 12B) almost spherical, about 520 µm in diameter; frontal surface with numerous minute pores around connection with endosoma (Fig. 12D, E).

Genital apertures paired, located ventrolaterally almost on opposite side of stalk (Fig. 12B–D) and carried on highly sclerotized genital swellings; closed off by strongly developed semicircular opercula, derived from sixth legs; opercula with large membranous insert at base; opening and closing by strong muscles inserting on opercula and posterior wall of genital antra, respectively (Fig. 12B–D). Small median copulatory pore located in shelf-like depression between genital apertures (Fig. 12 B, C), leading via short copulatory duct to seminal receptacle(s); small spiniform papillae discernible, positioned posteriorly to copulatory pore (Fig. 12B).

Egg sacs paired, very large, multiseriate, containing several hundreds of eggs; about 3.6 mm long (approx. 7.0 times diameter of ectosoma) and 1.2 mm wide; clavate.

Male. Unknown.

Remarks. M'Intosh's (1885) original description is restricted to a single text paragraph and an illustration of the female habitus (Fig. 1D). He described the egg sac as fusiform or elongate-ovoid, yellowish, and projecting into the cephalic cage of the polychaete. M'Intosh (1885) referred to Levinsen's (1878) description of *Bradophila* but remarked that the size of the ectosoma and the attachment site of the egg sacs were different between both genera. He also used the number of egg sacs as a discriminating feature, erroneously assuming that only one was present in *T. kroyeri*, and believed the latter was closer to "… the larval form of Levinsen's species" which actually represents the adult male.

The presence of a median copulatory pore in the adult females of both *Bradophila* and *Trophoniphila* is of considerable significance in determining the familial position of these highly modified genera. This character is not displayed by any of the other mesoparasitic families that utilize polychaete hosts; instead the presumably paired copulatory pores are contained within the paired genital apertures of the female. Although Levinsen (1878) did not use the correct descriptive terminology, his account of the female genital system in *B. pygmaea* was remarkably informative. Between the two lateral "protrusions" (genital apertures) he observed another smaller round protrusion with a central opening (copulatory pore), which he assumed to be the genital opening. After clearing in potassium hydroxide this opening was seen to continue upwards as a tube (copulatory duct). Neither a discrete copulatory pore nor duct were observed by Marchenkov (1999b) who overlooked both structures. Re-examination of *B. pygmaea* and *T. kroyeri* showed a striking resemblance in the female genital system, suggesting that both species are closely related and belong to the same family. Additional evidence in support of the assignment of *Trophoniphila* to the Bradophilidae is provided by the disproportionately large egg sacs, the shape of the ectosoma and host utilization.

Flabellicola Gravier, 1918a

The monotypic genus *Flabellicola* was described by Gravier (1918a) from specimens, at different stages of development, parasitic on the flabelligerid polychaete *Flabelligera diplochaitos* (Otto, 1821) in the Gulf of Naples. Although being abundant at the type locality, particularly during April-May when prevalence can be up to 50% (Gravier 1918b), the parasite has not been recorded again since its original description. Adult females of *Flabellicola neapolitana* Gravier, 1918a are mesoparasitic and typically embed themselves in the gills, located dorsally between the two chaetal bundles that form the cephalic cage. Interestingly, similar to the flabelligerid host utilized by *Bradophila*, their presence is betrayed by the paired egg sacs which extend into the cephalic cage of the polychaete. The pyriform ectosoma is about 0.30–0.35 mm in size (measured along its longest axis) and connects via a short neck-like region (stalk) to an internal vesicle (endosoma) which is about twice the length of its external counterpart. Embedded females lack all trace of appendages, digestive tract and external segmentation; however, the endosoma appears to display a transverse constriction dividing it in an anterior and a posterior part (Gravier 1918b). The ovaries are located in the anterior part where they connect to paired oviducts that transport the developing eggs via the remainder of the endosoma and connecting stalk to the external genital apertures of the ectosoma. The paired multiseriate egg sacs are very large, attaining 1.06 mm in size (or over three times the length of the ectosoma). It is not uncommon to observe up to five parasites on the gills of a single host but only the larger specimens are ovigerous. Other females at an earlier stage of development are completely embedded in the branchial tissues and appear to be more numerous than those that have a protruding ectosoma. Gravier (1918a, 1918b) failed to observe males but found spermatozoa, presumably stored in a seminal receptacle, in cross-sections of the female's ectosoma. Contrary to some published claims (Bresciani & Lützen 1966: 804; Gotto 1979: 34) Gravier did not infer that *F. neapolitana* was a self-fertilizing hermaphrodite as previously (but incorrectly) proposed for *Xenocoeloma alleni* (Brumpt, 1897) (Caullery & Mesnil 1919) but concluded that the sperm must have been introduced by an as yet undiscovered male. Based on a series of histological sections Gravier (1918a, 1918b) attempted to reconstruct the female pathway of the life cycle. Although the infective stage is as yet unknown he assumed that it penetrated the host and developed inside the gill tissues. Developing females lack a functional gut and probably absorb nutrients directly through their specialised integument while eggs start developing and gradually fill up the oviducts. At sexual maturity the female penetrates the host integument a second time and protrudes the ectosoma while remaining attached inside with the endosoma. After mating and fertilization, eggs are deposited formings large paired egg sacs and probably remain attached until eclosion takes place. The proposed life cycle is somewhat similar to that of female splanchnotrophids which also penetrate the body wall of their host twice; however, in *F. neapolitana* mating presumably takes place outside the polychaete host while in members of the Splanchnotrophidae it occurs inside the viscera of the nudibranch gastropod (Huys 2001).

Gravier (1918a, 1918b) compared *Flabellicola* with other genera that were known to utilize flabelligeran polychaetes as hosts, claiming that it was probably closest to *Trophoniphila*. Although he suggested a certain affinity with the Herpyllobiidae the genus remained unplaced (*cf.* Gotto 1979) until Boxshall & Halsey (2004) treated it as a *genus inquirendum* in the Saccopsidae. The complete absence of appendages on the female ectosoma, the size and shape of the egg sacs and its utilization of a flabelligerid polychaete as host suggest a possible relationship with the Bradophilidae rather than with the Saccopsidae which typically have three pairs of reduced cephalic appendages, much smaller, sausage-shaped or straight egg sacs and utilize ampharetids, terebellids and trichobranchids as hosts (Sars 1870; Levinsen 1878; M'Intosh 1885; Bresciani & Lützen 1961, 1975). Consequently, *Flabellicola* is here treated as a *genus incertae sedis* in the Bradophilidae.

The positioning of the ovaries in the endosoma of *Flabellicola* rather than in its ectosoma is unusual in mesoparasitic copepods and has so far only been observed in the recently discovered Jasmineiricolidae (Boxshall *et al.* 2015). Whether this character is also diagnostic for the Bradophilidae remains to be confirmed since Marchenkov (1999b, 2002) did not comment on the position of the ovaries in *Bradophila* and no information is available on the condition in *Trophoniphila*.

Flabelligerid polychaetes are rarely reported as hosts for parasitic copepods. The most important diagnostic feature of flabelligerids is their ability to retract the anterior end, including the pro- and peristomium with associated palps and gills, and some of the anterior chaetigerous segments into the body, forming an introvert (Filippova *et al.* 2003). This confined microhabitat is the preferred attachment site for the three mesoparasitic members of the Bradophilidae. The only other copepod that is known to utilize a flabelligerid host is *Flabelliphilus inersus* Bresciani & Lützen, 1962, which was described from off the Swedish west coast (Bresciani & Lützen 1962) but has no bradophilid affinities and occupies a different niche on the host. The species inhabits the gelatinous coat of *Flabelligera affinis* M. Sars, 1829, is known from males only and generally considered of doubtful systematic position due to the incomplete description. Stock (1968) listed *Flabelliphilus* Bresciani & Lützen, 1962 as a *genus inquirendum* in his "nereicolid series" but Laubier (1978) regarded a position in the Nereicoliform Group unlikely. Bresciani (1964) had previously considered it a possible candidate for inclusion in the Clausidiidae. Boxshall & Halsey (2004) ranked it as a *genus inquirendum* based on the clausiid-like antenna and mandible while subsequent workers cited it as a valid genus of this family (Cheng *et al.* 2014; Conradi *et al.* 2015).

Oestrella revisited

M'Intosh (1885) proposed the monotypic genus *Oestrella* for a new species, *O. levinseni* (type by original designation), found attached to the deepwater terebellid, *Ehlersiella atlantica* M'Intosh, 1885, in the northern Atlantic. The original description was based on a single ovigerous female but the presence of three egg sacs in the vial that contained the incomplete host specimen suggested it was infested by two individuals. M'Intosh (1885) did not discuss the possible relationships of the genus nor did he give any justification for its proposal. Hansen (1892) provisionally included *Oestrella* in his newly established family Herpyllobiidae but later admitted that it was too inadequately described for classification purposes (Hansen 1897, 1923). Leigh-Sharpe (1926) excluded the genus from the Herpyllobiidae, a view maintained in Lützen's (1964) revision of the family but not by Monod & Laubier (1996) who continued to treat *Oestrella* as a valid genus in the Herpyllobiidae.

Wilson (1932) placed the genus in the suborder Lernaeopodoida, an artificial taxon characterized by the presence of females, which are permanently attached to their hosts, and pygmy males which attach themselves to the females. He was also the first to recognize the close similarity between *Oestrella* and *Melinnacheres* and distinguished the genera in his key by the position of the "annulus", a structure defined as the chitin ring at the base of the neck where it joins the trunk. Boxshall (1977) re-examined the holotype of *O. levinseni* and relegated *Oestrella* to synonymy with *Melinnacheres*, the type and only genus of the family Saccopsidae.

Family Saccopsidae Lützen, 1964

Melinnacheres levinseni (M'Intosh, 1885)

(Fig. 11B, C)

Œstrella levinseni M'Intosh, 1885—incorrect original spelling (ICZN Art. 32.5.2).
Melinnacheres levinseni (M'Intosh, 1885)—new combination: Boxshall (1977).

Original description. M'Intosh (1885): 477, Plate XXXIX$_A$, fig. 11.

Host. *Ehlersiella atlantica* M'Intosh, 1885 (family Terebellidae).

Type locality. Trawled at *H.M.S. Challenger* station 63 (Mid Atlantic between Bermuda and Azores), 35°29' N, 50°53' W; depth 2,750 fathoms (5,029 m); red clay.

Material examined. Holotype ♀ (NHMUK reg. no. 1934.4.24.2); attached to the posterior fragment of a syntype of *E. atlantica* (NHMUK reg. no. 1934.85.12.1.373; collected 19 June 1873.

Remarks. M'Intosh (1885) described the body as 4-segmented but Boxshall (1977) showed that the grooves separating these segments are only superficial and are probably artefacts caused by shrinkage during preservation and storage. A similar observational error was made by Sars (1870) who stated that the body of *M. ergasiloides* was 5-segmented. Bresciani & Lützen's (1961, 1975) revealed in cross-sections the presence of several pairs of dorsoventral striated muscles which attach to integumental apodemes; contraction of these muscles causes more or less expressed transverse constrictions of the body.

Boxshall's (1977) re-examination of *M. levinseni* revealed the presence of three pairs of minute appendages which he identified as the antennules, antennae and maxillae. All three limbs, particularly the antennule, are much more reduced than in the other three members of *Melinnacheres*. Bresciani & Lützen (1961, 1975) described the antennule in the adult female of *M. ergasiloides* M. Sars, 1870 and *M. steenstrupi* Bresciani & Lützen, 1961 as a moderately elongate, indistinctly segmented appendage carrying up to seven setae. O'Reilly (2016) recently confirmed the same condition in *M. terebellides* (Levinsen, 1870). In *M. levinseni* the antennule is represented by a small, unarmed, lobate outgrowth and the antenna and maxilla do not show the typical striated pads found in the other congeners (Fig. 11B, C). Whether this can be interpreted as evidence in support of resurrecting *Oestrella* as a valid genus will depend on the morphology of the as yet unknown male of *M. levinseni*. Bresciani & Lützen (1961, 1975) identified the third and fourth pair of appendages in the males of *M. ergasiloides* and *M. steenstrupi* as the mandibles and maxillae. The mandibular sexual dimorphism (the mandibles being absent in the female) observed in these species has not been recorded in other copepods and is considered unlikely. The third pair of limbs in the male is here interpreted as the maxillae and the fourth pair as the maxillipeds. This interpretation is in accordance with the condition in highly transformed female poecilostome copepods where maxillipeds are usually expressed in males but often lacking in females.

M'Intosh (1885) observed two rounded lateral prominences at the posterior end of the body where the paired egg sacs attach. These prominences carry the paired genital apertures as in other species of the genus. Bresciani & Lützen (1975) described a small anal prominence dorsally near the genital swellings in *M. ergasiloides* and confirmed its absence in *M. steenstrupi* which lacks a functional anus. According to Boxshall (1977) a much larger conspicuous anal prominence is present in *M. levinseni* and this structure was compared by Stock (1986) with the medio-terminal swelling found between the genital apertures in some *Herpyllobius* species. However, Boxshall (1977) observed the female in ventral aspect only and made no mention of the genital apertures. Re-examination of the posterior region in dorsal aspect (Fig. 11B) revealed the presence of paired genital apertures, the right one of which corresponds to the alleged anal prominence.

Melinnacheres levinseni was collected at 5,029 m depth, representing the deepest record of an annelidicolous copepod so far and the only one recorded below the 5,000 m bathymetric mark. The second deepest record is that of *Ophelicola kurambia* Conradi, Bandera, Marin & Martin, 2015 which was recently collected from an opheliid host at 4987–4991 m in the Kurile Kamchatka trench and abyssal plain (Conradi *et al.* 2015).

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