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Copepods associated with polychaete worms in European seas

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Abstract

Descriptions are given of 18 species of copepods that live in symbiotic association with polychaete worms in European Seas. Three new genera and six new species of the family Clausiidae Giesbrecht, 1895 are described: *Boreoclausia recta* **n. gen. et n. sp.** is described from *Galathowenia fragilis* (Nilson & Holthe, 1985), *Boreoclausia holmesi* **n. gen. et n. sp.** is described from *Myriochele danielsseni* Hansen, 1879, *Sheaderia bifida* **n. gen. et n. sp.** from *Euclymene oerstedii* (Claparède, 1863), *Vivgottoia garwoodi* **n. gen. et n. sp.**, was found inside the tail fragment of a terebellid host (probably *Phisidia aurea* Southward, 1956), *Rhodinicola tenuis* **n. sp.** from an unknown host, and *R. similis* **n. sp.**, from *Rhodine gracilor* (Tauber, 1879). In addition, four other clausiid species, *Clausia lubbockii* Claparède, 1863, *Mesnilia cluthae* (T. and A.Scott, 1896), *Rhodinicola gibbosus* Bresciani, 1964 and *R. rugosum* (Giesbrecht, 1895), are redescribed in detail on the basis of newly collected material. The previously-unknown hosts of *C. lubbockii* were found to be species of the spionid polychaete genus *Dipolydora* Verrill, 1881. *Clausia uniseta* Bocquet & Stock, 1960 were recognized as a junior subjective synonym of *C. lubbockii*, and *Mesnilia martinensis* Canu, 1898 was recognized as a junior subjective synonym of *M. cluthae*. The sole species of the monotypic family Anomoclausiidae Gotto, 1964, *Anomoclausia indrehusae* Gotto, 1964, is redescribed based on new material. The host of *A. indrehusae*, reported here for the first time, is the spionid *Pseudopolydora paucibranchiata* (Okuda, 1937). Four new species of the family Nereicolidae Claus, 1875 are described, three belonging to the genus *Anomopsyllus* Sars, 1921: *Anomopsyllus bifurcus* **n. sp.** from *Notomastus latericeus* M. Sars, 1851, *A. geminus* **n. sp.** from *Ampharete lindstroemi* Malmgren, 1867, and *A. hamiltonae* **n. sp.**, from *Mugga wahrbergi* Eliasson, 1955. The fourth new species is *Vectoriella gabesensis* **n. sp.**, both sexes of which are described from the paraonid *Aricidea catherinae* Laubier, 1967 collected in the Mediterranean Sea off the coast of Tunisia. Another nereicolid, *Sigecheres brittae* Bresciani, 1964 is redescribed based on new material collected from the type host *Sige fusigera* Malmgren, 1865. It is recognized as a junior subjective synonym of *Nereicola concinna* T. Scott, 1902 and the valid name of this taxon becomes *Sigecheres concinna* (T. Scott, 1902) new combination. A new species of the family Spiophanicolidae Ho, 1984, *Spiophanicola atlanticus* **n. sp.**, is described based on European material. Previously European material of *Spiophanicola* Ho, 1984 has been reported as *S. spinulosus* Ho, 1984, but based on consistent differences between the Californian *S. spinulosus* and material from Norway and the British Isles, there is sufficient justification to establish a new species for the European material. Finally one new genus and species is described which cannot be placed, with confidence, in any existing family. This new parasite, *Notomasticola frondosus* **n. gen. et n. sp.**, is based on material from two hosts, a spionid (*Pseudopolydora paucibranchiata*) and a capitellid (*Notomastus latericeus*). It is highly derived and may represent a terminal branch within an existing family. The cluster of families using polychaetes as hosts is in need of revision based on a comprehensive phylogenetic analysis.

Key words: parasitic copepod, polychaete host, new genera, new species

Introduction

Copepods live symbiotic association with virtually every other marine metazoan phylum (Huys & Boxshall, 1991). Eleven families of cyclopoid copepods are recorded exclusively from polychaete hosts, but several other families include one or more species that live in association with polychaetes (Boxshall & Halsey, 2004). In this paper we report on 12 new species of copepods collected from polychaete hosts in European Seas, and provide redescriptions of another six. Parasitic copepods from polychaete hosts are relatively rarely reported and one reason for this might be that they exist at very low prevalence rates, which means that it is necessary, on average, to search large samples of host individuals before encountering parasites. This paper stems from collaboration between specialists working on macrobenthos and copepod taxonomists: the former (A.S. and M.O'R.) have found these parasites while processing large samples of macrobenthic material containing polychaetes, and the latter (I.H.K. and G.A.B.) have generated the descriptions.

Representatives of four families that exclusively parasitise polychaetes are described or redescribed here. The only known species from the monotypic family Anomoclausiidae is redescribed. Three new genera and six new species of the family Clausiidae are described and four are redescribed (*Clausia lubbockii*, *Mesnilia cluthae* and two species of *Rhodinicola*) based on new material. Four new species from two genera of Nereicolidae are described and the only known species of *Sigecheres* Bresciani, 1964 is redescribed. The valid name of this species is *S. concinna* (T. Scott, 1902), as this is shown to be a senior synonym of *S. brittae* Bresciani, 1964. A second species of the hitherto monotypic family Spiophanicolidae is described based on European material. In addition a new genus and species is described but remains of uncertain familial affinity at present.

The Polychaeta is now recognised as a paraphyletic stem group within the Annelida (Nielsen, 1995), but we

use it here in the traditional vernacular sense to encompass those predominantly marine, segmented annelid worms with parapodia and nuchal organs (e.g. as defined in Ruppert *et al*., 2004).

Material and methods

Copepod specimens were immersed in lactic acid before microscopic observation and dissection. Dissections were done using the reverse slide method (Humes & Gooding, 1964). All drawings were made on an Olympus BH-2 microscope using a drawing tube. After drawing, the dissections were mounted in lactophenol and later, sealed with Hoyer's mounting medium. Morphological terminology follows Huys & Boxshall (1991) and host nomenclature was checked against the World Register of Marine Species (WoRMS, www.marinespecies.org). Type and voucher specimens are deposited in the collections of the Natural History Museum, London. Some additional specimens are deposited in the National Museum of Scotland, Edinburgh or remain in personal reference collections of the authors.

Order Cyclopoida Burmeister, 1834

Family Anomoclausiidae Gotto, 1964

The distinction between the families Clausidiidae and Clausiidae is not clear (Boxshall and Halsey, 2004) and the genus *Anomoclausia* appears to be an intermediate taxon, sharing some character states with both of these families. Gotto (1964) noted a number of features shared by *Anomoclausia* and the genera of the Clausiidae, but he placed it in a separate family Anomoclausiidae, due to traits shared with the Clausidiidae, such as the 7-segmented antennules and the well-developed antenna. A phylogenetic analysis of the nereicoliform copepods by Ho (1984) placed the Anomoclausiidae in the Clausidiidae-Anomoclausiidae-Synaptiphilidae lineage. In a subsequent analysis (Ho, 1991) the Anomoclausiidae was placed in a different lineage as sister group to the scleractinian coral-inhabiting Xarifiidae. However, this analysis has repeatedly been shown to be flawed (e.g. Østergaard *et al*., 2003; Huys *et al*., 2012). We temporarily retain the Anomoclausiidae as a family here in this descriptive account, but its validity needs to be reassessed within the context of a full cladistic analysis, ideally incorporating molecular data as they become available.

Genus *Anomoclausia* Gotto, 1964

Anomoclausia indrehusae Gotto, 1964

Anomoclausia indrehusae Gotto, 1964: 221, figs. 1–17.

Material examined: 1 ♀ from *Pseudopolydora paucibranchiata*, Kvitebjørn gas and condensate field, Stn 2-3 (61.076ºN, 2.504ºE), depth 189 m, 01 June 2005; BMNH Reg. No. 2012.1361.

1 ♀ from *P. paucibranchiata*, Statfjord Nord, Stn SFNORD 99, SFNF 4-4 (61.431ºN, 1.981ºE), depth 280 m, 11 June 1999; BMNH Reg. No. 2012.1362.

1 ♀ from *P. paucibranchiata*, Statfjord Nord, Stn SFNORD 99, 8-9 (61.482ºN, 1.852ºE), depth 266 m, 08 June 1999; BMNH Reg. No. 2012.1363.

1 ♀ from *P. paucibranchiata*, Statfjord Nord, Stn SFNORD 99, SFNF 5-4 (61.431ºN, 1.917ºE), depth 255 m, 12 June 1999; BMNH Reg. No. 2012.1364.

1 ♀ from *P. paucibranchiata*, Statfjord Nord, Stn SFNORD 99, SFNF 4-5 (61.431ºN, 1.981ºE), depth 280 m, 11 June 1999; BMNH Reg. No. 2012.1365.

2 ♀♀ (1 ♀ dissected), from *P. paucibranchiata*, Statfjord Nord, Stn SFNORD, SFNF 7-3 (61.438ºN, 1.932ºE), depth 271 m, 12 June 1999; BMNH Reg. No. 2012.1366.

1 ♀ from *P. paucibranchiata*, Vigdis, Stn 25-3 (61.384ºN, 2.141ºE), depth 287 m, 02 June 1999; BMNH Reg. No. 2012.1367.

1 ♀ from *P. paucibranchiata*, Regional, Stn 11-3 (61.2354ºN, 2.6396ºE), depth 313 m, 27 May 1999; BMNH Reg. No. 2012.1368.

Female. Body (Fig. 1A, B) cylindrical and consisting of cephalothorax, second to fifth pedigerous somites, genital double-somite and 2-segmented abdomen. Body length 1.90 mm long excluding caudal setae. Prosome-urosome division indistinct. Metasomal somites separated from adjacent somites only by weak constrictions. Cephalothorax 480×410 μm, wider than metasomal somites, narrowing anteriorly, with truncate frontal margin and convex lateral margins. Fifth pedigerous somite with paired pointed posterolateral processes (Fig. 1C). Genital double-somite and abdominal somites directed posteroventrally (Fig. 1B). Genital double-somite with paired pointed lateral processes posterior to genital apertures. Genital double- and first free abdominal somites each with 3 hyaline chitinous flaps located laterally near posterior margin (Fig. 1D). Genital areas located dorsally. Anal somite about twice as long as preceding somite and unornamented. Caudal rami very widely separated from each other (Fig. 1C), 80×29 μm (ratio 2.76:1); each ramus (Fig. 1E) with 7 setae including 1 minute outer proximal seta (seta I). Egg sac (Fig. 1F) 140 μm wide and longer than body, with multiseriate eggs.

Rostrum forming Y-shaped mid-ventral ridge. Antennule (Fig. 1G) small and 7-segmented; armature formula 2+spine, 6+spine; 5, 2+aesthetasc, 2, 2+aesthetasc, and 7+aesthetasc; all setae naked. Antenna (Fig. 1H) 4-segmented; armature formula 1, 1, 4, and 5+spine; second segment with 2 acute mediodistal processes; setal element on second segment spiniform; third segment with 3 pointed mediodistal processes; terminal segment 35×14 μm (2.50:1); medial terminal seta much smaller than other 4 setae.

Labrum (Fig. 2A) with broadly concave posterior margin flanged with membrane. Mandible (Fig. 2B) with 3 blade-like elements, distal blade articulated at base. Paragnath not recognized. Maxillule (Fig. 2C) weakly bilobed, with 2 apical setae on each lobe. Maxilla (Fig. 2D) 2-segmented, but segmentation incompletely expressed; proximal segment smooth; distal segment digitiform and ornamented with spinules on ventral surface. Maxilliped (Fig. 2E) 4-segmented; first and second segments each with 2 unequal mediodistal setae; short third segment unarmed; terminal segment strongly recurved distally, forming pointed hook, armed with 1 proximal and 1 middle seta, and ornamented with patch of minute spinules on distal margin of hook.

Legs 1–4 with 3-segmented exopod and 2-segmented endopod; both rami armed only with spines. Leg 1 (Fig. 2F) with strong inner spine on basis. Leg 2 (Fig. 2G) to leg 4 identical in shape and in armature formula as follows:

Leg 1: coxa 0-0; basis 1-I; exopod I-0; I-0; II, I, 0; endopod 0-0; 0, I, 0
Legs 2–4: coxa 0-0; basis 1-0; exopod I-0; I-0; II, I, 0; endopod 0-0; 0, I, 0

Leg 5 (Fig. 2H) rotated, as indicated by outer lateral seta being located posteriorly (Fig. 1C), 2-segmented but proximal protopodal segment incorporated into somite, with 1 posterior seta; free distal segment (exopod) nearly rectangular, 1.35 times as long as wide, with 3 spines and 1 seta. Leg 6 represented by 2 spines in genital area (Fig. 1D).

Remarks. The original description of *A. indrehusae* is partly revised in the above redescription, especially the form and setation of the antennule, antenna, maxilla and maxilliped. In addition, the conical posteromedian protuberance of leg 1, mentioned by Gotto (1964), is apparently the inner protopodal spine that is usually found in members of the family Clausidiidae.

Gotto (1964) speculated that spionid polychaetes might be the most likely hosts of *A. indrehusae*. The multiple records here from the spionid *Pseudopolydora paucibranchiata* confirm his suspicions.

Family Clausiidae Giesbrecht, 1895

Boxshall & Halsey (2004) listed 8 genera and 19 species within the Clausiidae, but also noted another four genera inquirenda which might belong in this family. Bjørnberg & Radashevsky (2009) subsequently established a new genus, *Spionicola* Bjørnberg & Radashevsky, 2009, to accommodate a new species *Spionicola mustacia* Bjørnberg & Radashevsky, 2009, parasitic on the spionid *Dipolydora armata* (Langerhans, 1880). Most clausiids are external associates of maldanid and spionid worms, although some species have been recorded in washings of other invertebrate groups, such as sponges (Bocquet & Stock, 1963). Boxshall & Halsey (2004) considered it possible that such records could be based on copepod individuals that had been dislodged from their polychaete hosts during collection, or were associated with polychaetes inhabiting the sponges.

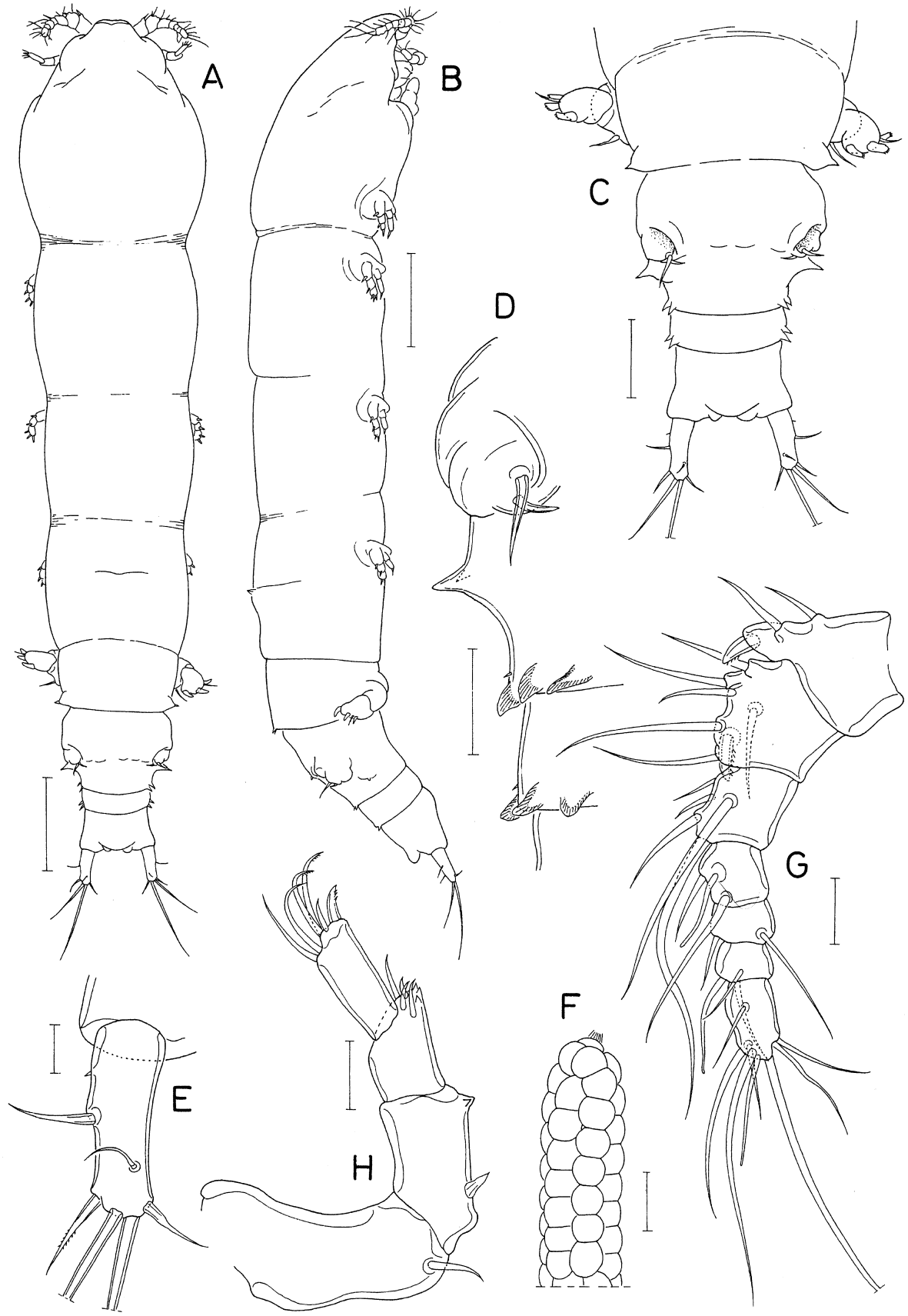

FIGURE 1. *Anomoclausia indrehusae* Gotto, 1964, female. A, habitus, dorsal; B, habitus, lateral; C, urosome, dorsal; D, left side of genital double and first abdominal somites, dorsal; E, left caudal ramus, dorsal; F, egg sac; G, antennule; H, antenna. Scale bars: A, B, 0.2 mm; C, F, 0.1 mm; D, 0.05 mm; E, G, H, 0.02 mm.

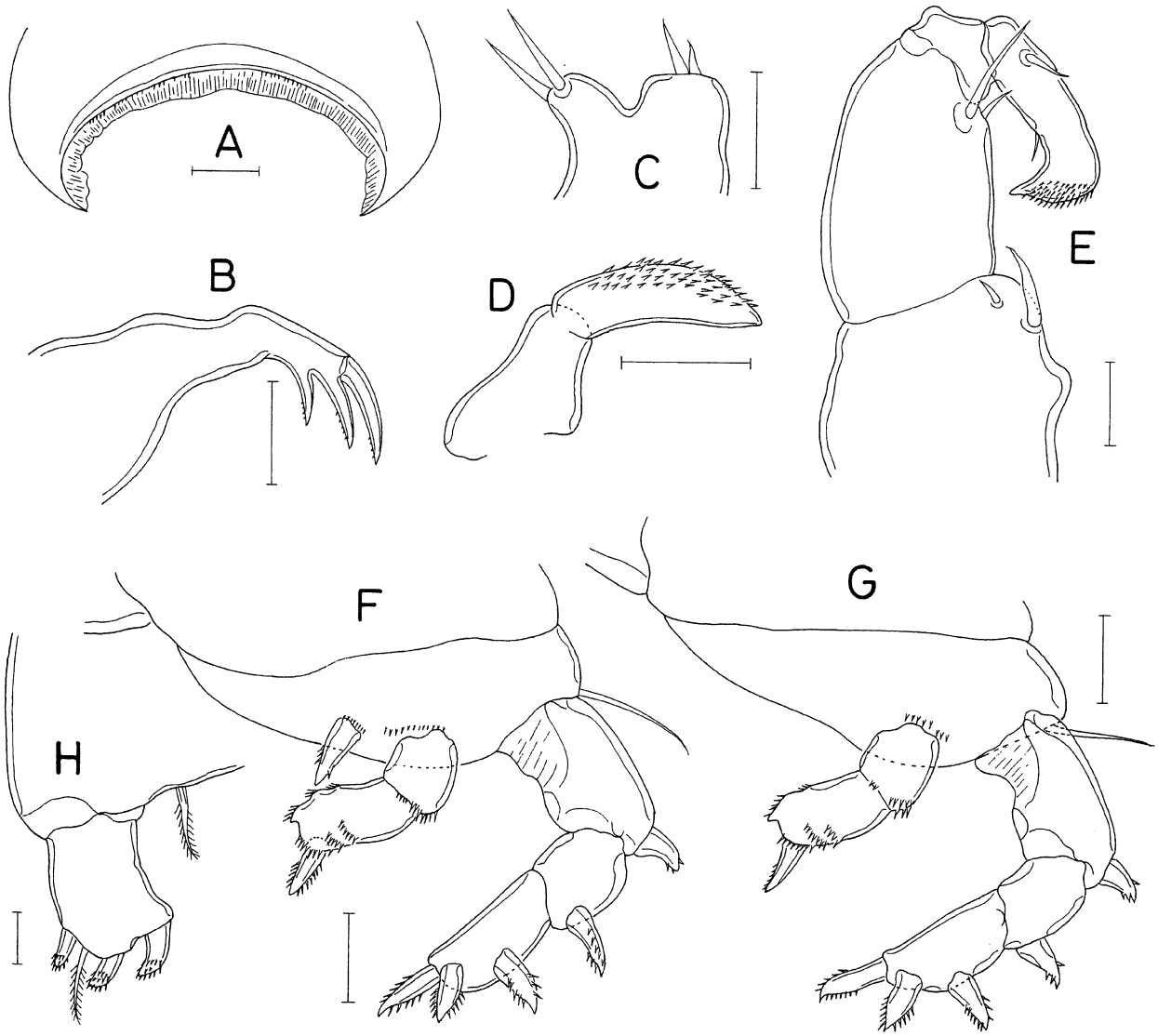

FIGURE 2. *Anomoclausia indrehusae* Gotto, 1964, female. A, labrum; B. mandible; C, maxillule; D, maxilla; E, maxilliped; F, leg 1; G, leg 2; H, leg 5. All scale bars: 0.02 mm.

Genus *Clausia* Claparède, 1863

Clausia lubbockii Claparède, 1863

Clausia lubbockii Claparède, 1863: 94, pl. 17, figs. 7–14; Bocquet and Stock, 1960: 12, figs. 2–5.
Clausia uniseta Bocquet and Stock, 1960: 17, figs.2–5. New synonym.

Material examined: 1 ♀, ovigerous (dissected and figured), from tube with *Dipolydora flava* (Claparède, 1870); Loch Sween, Scotland, SEPA Stn Mid Danna (55° 56.44'N, 5° 40.61'W), depth 16 m; collected by Stephen Nowacki, 04 June 2009.

1 ♀, ovigerous, from *Dipolydora coeca* (Oersted, 1843) agg. (= aggregate); Eastern English Channel, CEFAS Stn H9a (50.41319° N, 0.13736° W), depth unknown (sample taken by Hamon Grab), August 2004; BMNH Reg. No. 2012.1369.

2 ♀ (1 ovigerous), Strangford Lough, Northern Ireland, EHS Stn Green Island (54° 27.73'N, 05° 36.64'W), depth 19.4 m; collected by Tim Mackie, 02 February 2009.

*Female***.** Body (Fig. 3A) elongate and consisting of 4-segmented prosome and 6-segmented urosome. Body

length 2.04 mm. Prosome dorsoventrally depressed, slightly longer than urosome, and consisting of cephalothorax and 3 metasomal somites of similar widths. Cephalothorax 449×553 μm, metasomal somites 209×535, 196×553, and 246×541 μm, respectively. Fifth pedigerous somite 203×400 μm. Genital somite 173×342 μm, twice as wide as long; genital areas positioned dorsolaterally. Four free abdominal somites gradually narrowing from anterior to posterior (Fig. 3C), 119×210, 120×205, 112×173, and 165×146 μm, respectively. Ventral surfaces of abdominal somites unornamented. Caudal rami divergent and widely separated from one another; each ramus (Fig. 3D) tapering, 100×48 μm (ratio 2.08:1), armed with 7 smooth setae, including minute outer proximal seta (seta I); mid-terminal seta (seta V) much larger than other setae, more than 5 times as long as next longest seta III. Egg sac (Fig. 3B) 2.63×0.28 mm, about 1.5 times as long as body and containing 2 rows of eggs; each egg about 154 μm in diameter.

Rostrum (Fig. 3E) anteriorly directed, broader than long, with pointed anterior apex; suture distinct between rostrum and dorsal cephalothoracic shield. Antennule (Fig. 3E) 231 μm long, 6-segmented and gradually narrowing from proximal to distal; armature formula 4, 15, 10, 4, 2+aesthetasc, and 7+aesthetasc; setae on all segments naked. Antenna (Fig. 3F) 3-segmented; first segment (coxa-basis) distally with 1 smooth seta and patch of setules; second segment (first endopodal segment) unarmed but ornamented with 2 patches of minute spinules on medial surface; terminal segment formed by fusion of second and third endopodal segments, 77×27 μm, armed with 1 claw and 2 setae (proximal seta minute) on medial margin, 4 claws of unequal sizes on distal margin, and 2 setae on outer side; ornamented with spinules on medial surface proximal to 3 medial elements and with small patch of spinules proximal to outer setae.

Labrum (Fig. 3G) with strongly tapering posterior margin bearing pair of mid-distal membranous extensions; both sides of labrum ornamented with 2 patches of spinules. Mandible (Fig. 3H) with 2 (distal and subdistal) spiniform elements; distal element with 9 denticles distally (proximalmost thicker than others) and subdistal element shorter than distal, with row of spinules along posterior (outer) margin. Maxillule (Fig. 3I) lobate bearing 1 medial and 3 outer setae, one of latter bearing spinules on both margins. Maxilla (Fig. 4A) 2-segmented; proximal segment unarmed but with bulla-like swelling covered with thin cuticle in middle of ventral surface; distal segment blunt, armed with 2 smooth setae (1 outer and 1 medial) and ornamented with dense distal covering of minute spinules and with rows of spinules in middle of segment. Maxilliped (Fig. 4B) 3-segmented; first segment short and unarmed; second segment expanded in proximal half, with 2 naked setae on medial margin and patch of spinules on subdistal region; terminal segment blunt, with dense distal covering of minute spinules and on distal region of medial margin with 1 claw-like process and 2 small setae.

Legs 1 and 2 (Fig. 4C, D) with 2-segmented rami; endopods distinctly shorter than exopods; all rami ornamented with spinules on outer surface. Inner seta on coxa of leg 1 rudimentary and transparent; that of leg 2 spiniform. Setae small on rami of legs 1 and 2. Leg 3 (Fig. 4E) represented by 2 spinulose setae on lobe. Leg 4 absent. Armature formula of legs 1–3 as follows:

Leg 1: coxa 0-1; basis 1-0; exp. I-0; II, II, 1; enp. 0-1; 0, I, 1
Leg 2: coxa 0-1; basis 1-0; exp. I-0; I, II, 1; enp. 0-1; I, II, 0
Leg 3: 2 on lobe.

Leg 5 (Fig. 4F) directed dorsally and 2-segmented; proximal protopodal segment clearly defined from somite, with 1 small dorsodistal seta; distal segment (exopod) 135×62 μm (ratio 2.18:1), armed with 4 unequal setae and ornamented distally with patches of minute spinules. Leg 6 represented by 1 small simple seta in genital area (Fig. 3C).

Remarks. Bocquet and Stock (1960) redescribed this species based on a female found on a compound ascidian *Didemnum fulgens* (Milne-Edwards, 1841) inhabited by several polychaetes. Our discovery of two females of this copepod from spionid polychaetes of the genus *Dipolydora* indicates that the real host of this copepod is the polychaete, as suggested by Gotto (1993). The specimen from Loch Sween was found alongside its host and was located at setiger 16, with its anterior orientated towards the host anterior.

The dissected specimen shows no significant differences from the redescription of Bocquet and Stock (1960). The labrum is described for the first time and the exact setation patterns of the antennule, antenna and maxilliped are presented here. The lobate leg 3 of one of the ovigerous specimens from Strangford Lough has only a single seta but otherwise resembles the figured specimen.

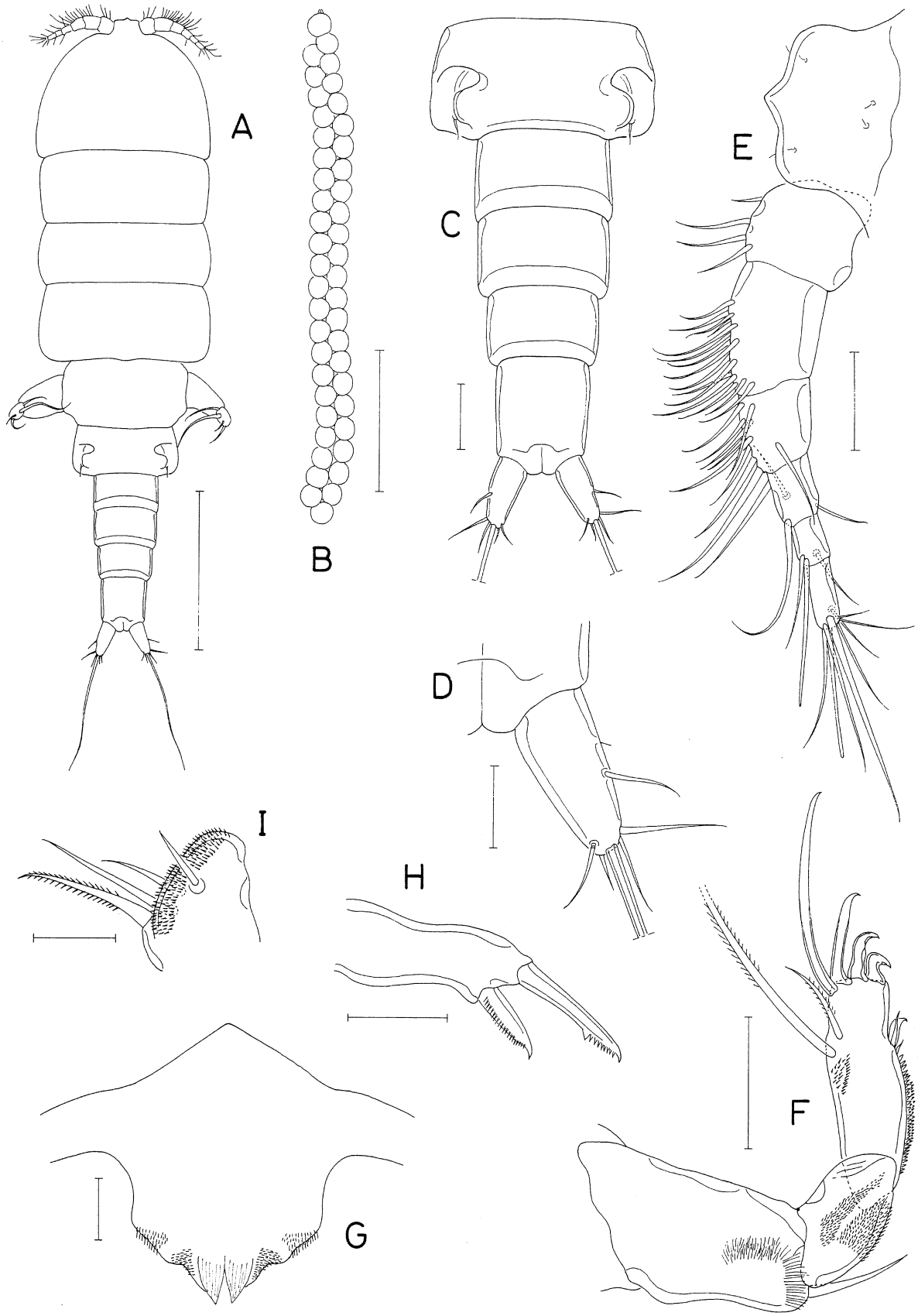

FIGURE 3. *Clausia lubbockii* Claparède, 1863, female. A, habitus, dorsal; B, egg sac; C, genital somite and abdomen, dorsal; D, right caudal ramus, dorsal; E, rostrum and antennule, dorsal; F, antenna; G, labrum; H, mandible; I, maxillule, posterior. Scale bars: A, 0.5 mm; B, 1 mm; C, 0.1 mm; D–F, 0.05 mm; G–I, 0.02 mm.

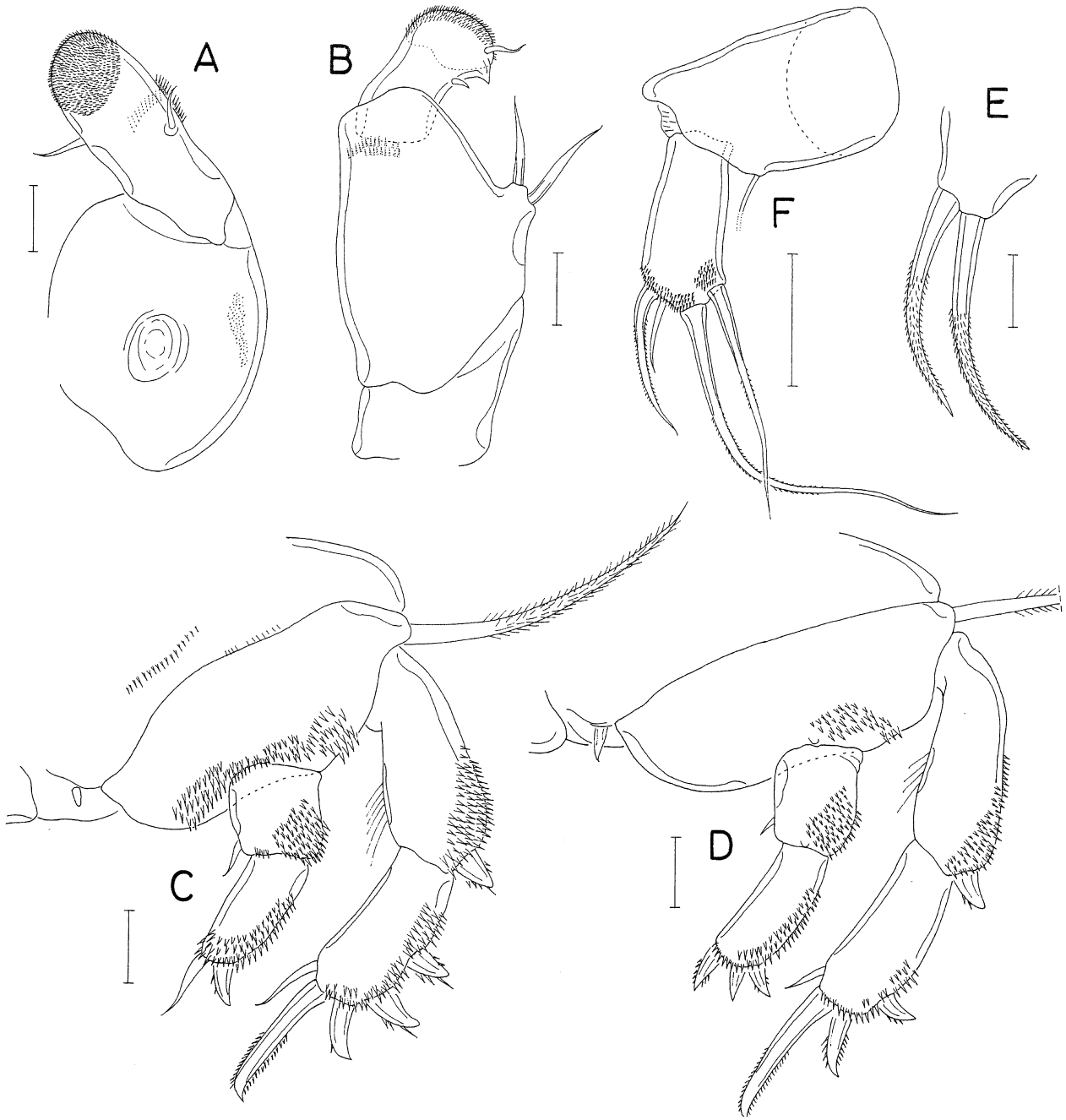

FIGURE 4. *Clausia lubbockii* Claparède, 1863, female. A, maxilla; B, maxilliped; C, leg 1; D, leg 2; E, leg 3; F, leg 5. Scale bars: A–E, 0.02 mm; F, 0.1 mm.

Until now *Clausia lubbockii* has only been recorded from the Channel coast of France at Saint Vaast-la-Hougue and Roscoff, and from the coast of Norfolk, England. A very similar species, *Clausia uniseta* Bocquet & Stock, 1960 was described from a single female, collected on the coast of Norfolk, England. The establishment of *C.uniseta* is based mostly on minor differences in setal length and on the presence of only a single seta on leg 3. *C. lubbockii* has also been recovered from the exact same site as *C.uniseta* (Hamond, 1973) and, as noted above, exhibits variation with either two or only a single seta present on leg 3. We consider that the maintenance of *C.uniseta* as a separate species is unjustified and propose to treat it as a synonym of *C. lubbockii*. With the transfer of *C. antiqua* Kim, 2001 and *C. lobata* Kim, 2000 to *Pontoclausia* Băcescu & Por, 1959 by Ho & Kim (2003), the genus now comprises only *C. lubbockii*.

Genus *Mesnilia* Canu, 1898

Mesnilia cluthae (T. and A. Scott, 1896)

Clausia cluthae T. and A. Scott, 1896: 1, pl. 1, figs. 1–12; Wilson and Illg, 1955: 134.
Mesnilia cluthae: Canu, 1898: 402;
Mesnilia cluthae: Bocquet and Stock, 1959: 5, figs. 1–5.
Mesnilia martinensis Canu, 1898: 401, pls. VIII, IX. New synonym.

Material examined: 1 ♀ (dissected and figured) found among crushed *Turritella* shells in sample where two spionid species were present, *Dipolydora socialis* (Schmarda, 1861) and a smaller species; off Teignmouth, Devon, 3 km from mouth of River Teign, depth 15 m; collected by P. Garwood, 18 April 1990.

1 ♀ found loose in sample which included *Clymenura tricirrata* (Bellan & Reys, 1967) and other maldanid species; Central North Sea, Lundin Block 21-8, Stn 12 – F3 (57°40.3878'N, 00°24.2905'E)**,** depth 104 m, found by S. Hamilton, April 2007; BMNH Reg. No. 2012.1375.

1 ♀ collected from washings of littoral algae/*Sabellaria*; Dovercourt, Essex, England (51°53.3'N, 01°16.3'E), depth intertidal; collected by I. Killeen, found by R. Bamber, 08 March 1993; BMNH Reg. No. 2012.1375.

Additional records. 1 ♀ from clump of *Modiolus* Lamarck, 1799, Loch Creran, Scotland (56 ° 32.76'N, 05 ° 16.14'W), depth 15.5 m, collected by Scottish Natural Heritage/Sue Hamilton, 21 October 2005: deposited in National Museum of Scotland, NMSZ 2008.107.2.

1 ♀ ovigerous, 1 ♂ from tube of *Dipolydora flava*, Sound of Harris, Scotland, Scottish Natural Heritage, Stn SA 105 (57 ° 42.173'N, 07 ° 00.390'W), depth 43 m; collected by Sue Hamilton, 10 November 2005: NMSZ 2008.107.3.

1 ♀, 3 ♂ Stour Estuary, Suffolk, England, Unicomarine Stn 189a, collected by David Hall, 17 July 2008.

1 ♀, Larne Lough, Northern Ireland, EHS Stn LL2 (54° 49.05'N, 05° 45.35'W), depth 3 m; collected by Tim Mackie, 01 November 2008.

1 ♀ Larne Lough, Northern Ireland, EHS Stn LLS2 (54° 48.53'N, 05° 44.37'W), depth 2.6 m; collected by Tim Mackie, 29 January 2009.

1 ♀ Strangford Lough, Northern Ireland, EHS Stn Green Island (54° 27.73'N, 05° 36.64'W), depth 19.4 m; collected by Tim Mackie, 02 February 2009.

1 ♀ in tube with complete *Dipolydora flava*, Shetland, Scotland, SEPA Stn Lerwick UWWTD B (60° 12.60'N, 01° 08.34'W), depth 45 m, found by Stephen Nowacki, 12 January 2012.

Female. Body (Fig. 5A) elongate and dorsoventrally depressed, without prosome-urosome distinction. Body length 2.11 mm (body lengths of other 2 examined specimens 2.38 and 2.17 mm). Body somites distinct, demarcated by constrictions and arthrodial membranes between somites. Cephalothorax and succeeding 3 metasomal somites (second to fourth pedigerous somites) similar in width, 421×462, 185×456, 200×446, and 220×441 μm, respectively. Fifth pedigerous somite 200×364 μm. Genital and abdominal somites gradually narrowing from anterior to posterior. Genital somite 159×313 μm, relatively small; genital areas positioned dorsolaterally. Four free abdominal somites 205×281, 190×256, 144×226, and 179×179 μm, without ornamentation on ventral surface. Caudal rami divergent and distinctly separated from one another; each ramus (Fig. 5B) 108×47 μm (ratio 2.30:1) and armed with 6 smooth setae; mid-terminal seta distinctly larger than other 5 setae.

Rostrum (Fig. 5C) broad, with truncate anterior margin; suture line distinct between rostrum and dorsal cephalothoracic shield. Antennule (Fig. 5D) 229 μm long, 6-segmented, and gradually narrowing from proximal to distal; armature formula 4, 13(?), 10(?), 4, 2+aesthetasc, and 7+aesthetasc; all setae smooth; first segment with patch of spinules on proximal region of anterior surface. Antenna (Fig. 5E) 3-segmented; first segment with 1 seta mediodistally and patches of setules on distal half on medial side; second segment with 1 small seta on ventral surface and ornamented with patch of minute spinules on medial side; terminal segment (fused second and third endopodal segments) about twice as long as wide, armed with 1 claw, broad seta with flagellate tip and 1 small seta on medial margin, 4 claws of unequal size on distal margin, 2 weakly pinnate subdistal setae on outer margin, 1 patch of spinules on outer side and another patch of spinules on proximal half of medial margin.

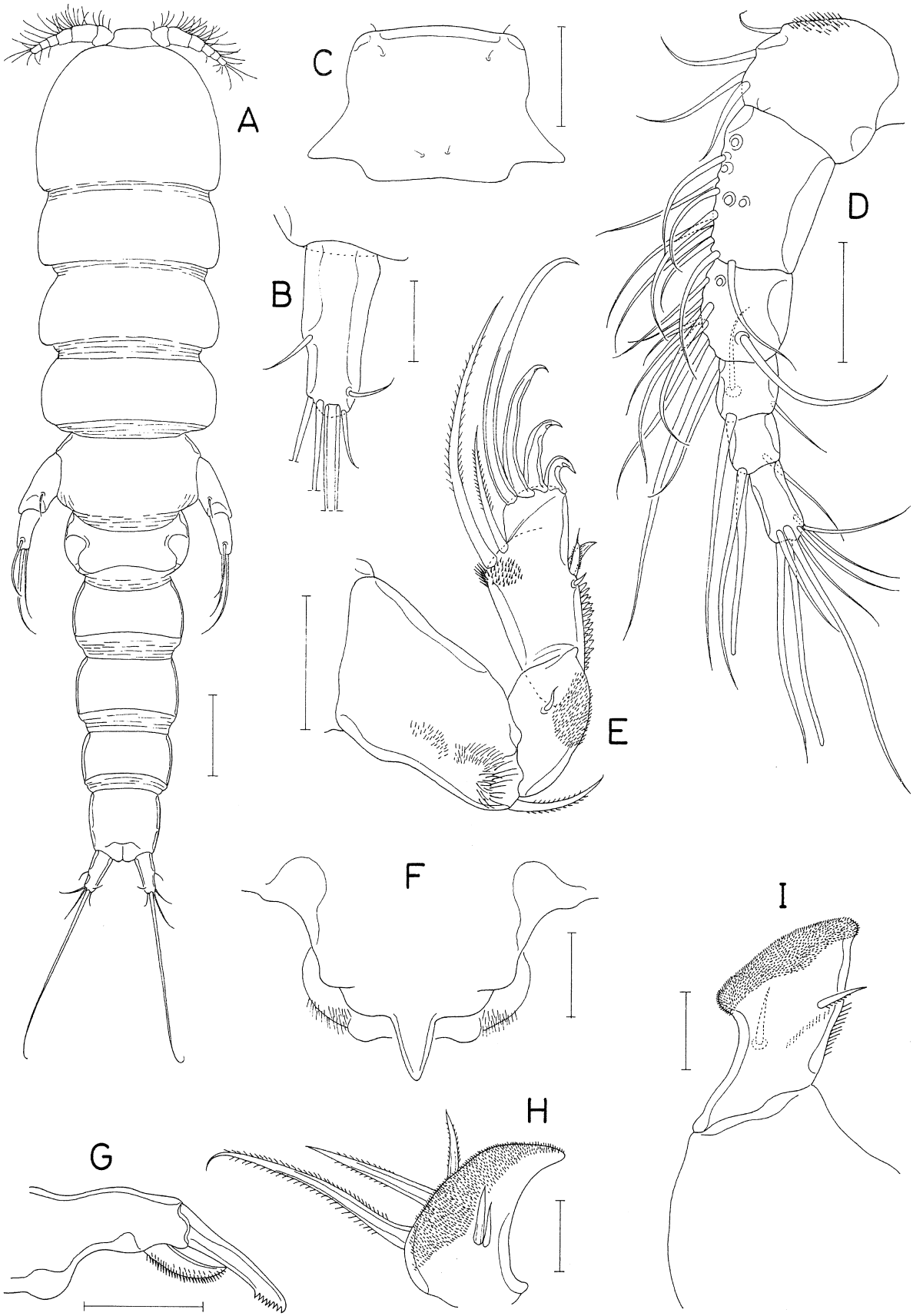

FIGURE 5. *Mesnilia cluthae* (T. and A. Scott, 1896), female. A, habitus, dorsal; B, left caudal ramus, dorsal; C, rostrum, dorsal; D, antennule (open circles indicating insertion scars of missing setae); E, antenna; F, labrum, ventral; G, mandible; H, maxillule, medial; I, maxilla, posterior. Scale bars: A, 0.2 mm; B–E, 0.05 mm; F–I, 0.02 mm.

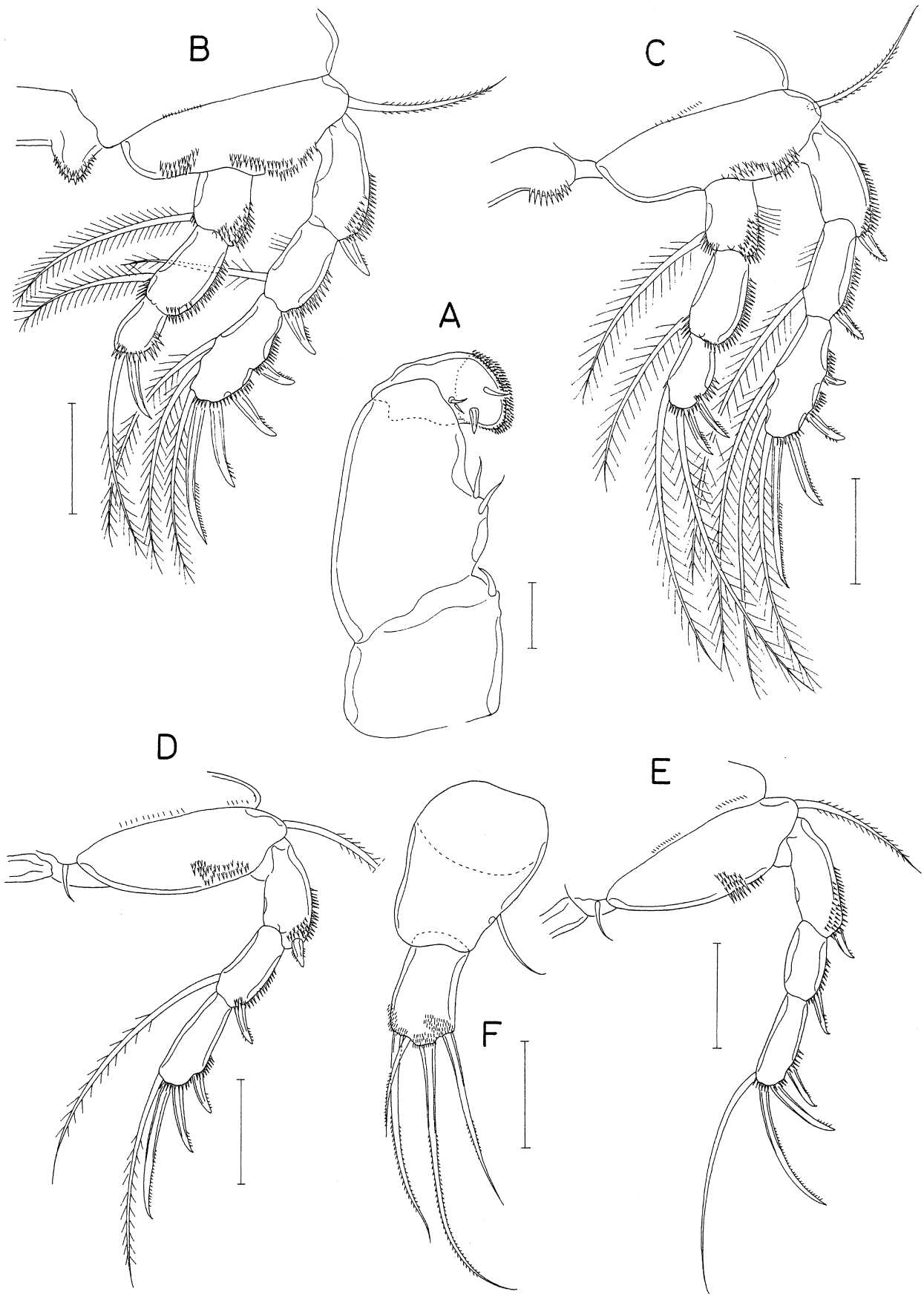

FIGURE 6. *Mesnilia cluthae* (T. and A. Scott, 1896), female. A, maxilliped; B, leg 1; C, leg 2; D, leg 3; E, leg 4; F, leg 5. Scale bars: A, 0.02 mm; B–E, 0.05 mm; F, 0.1 mm.

Labrum (Fig. 5F) with prominent, tapering mid-terminal process on posterior margin and with membranous areas on each side of process; each membranous area with patch of setules. Mandible (Fig. 5G) with 2 spiniform elements; elongate distal element with 8 denticles distally, subdistal element shorter than distal, with spinules on posterior (outer) surface. Maxillule (Fig. 5H) lobate, densely covered with minute spinules on ventral surface and armed with 3 outer and 2 smaller inner setae. Maxilla (Fig. 5I) 2-segmented; proximal segment unarmed and smooth; distal segment truncate, with dense covering of minute spinules on distal surface and 2 setae near middle. Maxilliped (Fig. 6A) 3-segmented; first segment with 1 smooth seta mediodistally; second segment with 2 similar setae on medial margin; terminal segment blunt, with dense distal covering of minute spinules and 4 setae, 2 (one spiniform) located subdistally and 2 smaller setae located proximally.

Legs 1 and 2 (Fig. 6B, C) biramous with 3-segmented rami. Legs 3 and 4 (Fig. 6D, E) uniramous, with 3-segmented exopod, lacking endopod. Second exopodal segment of leg 3 armed with 1 outer spine and 1 inner seta (formula I-1) but occasionally inner seta lacking (formula I-0) (in one of 4 specimens). Both sides of intercoxal sclerite of legs 1 and 2 projecting (those of leg 1 more prominent), with patch of spinules (Fig. 6B, C). Outer margin of rami of legs 1–4 covered with spinules. Armature formula of legs 1–4 as follows:

Leg 1: coxa 0-0; basis 1-0; exp. I-0; I-1; III, I, 3; enp. 0-1; 0-1; 0, I, 1
Leg 2: coxa 0-0; basis 1-0; exp. I-0; I-1; III, I, 3; enp. 0-1; 0-1; I, I, 2
Leg 3: coxa 0-1; basis 1-0; exp. I-0; I-1; II, I, 1; enp. absent
Leg 4: coxa 0-1; basis 1-0; exp. I-0; I-0; II, I, 1; enp. absent

Leg 5 (Fig. 6F) 2-segmented; proximal protopodal segment clearly defined from somite, with 1 dorsal seta; distal segment (exopod) 105×61 μm (ratio 1.72:1), distally with 4 setae and patches of minute spinules. Leg 6 not seen.

Remarks. T. and A. Scott (1896) recorded a single female in their original description of *Mesnilia cluthae* (as *Clausia cluthae*) but they were in fact dealing with a male. The maxilliped (pl. 1, fig. 18) they illustrated is of male form and the morphology of the swimming legs is very different from that of female swimming legs described subsequently by Bocquet and Stock (1959). Similarities in the detailed structure of the male maxilliped and in the strong posterolateral projections on the intercoxal sclerite of leg 1 in both sexes serve to confirm that our specimen and the specimens of T. and A. Scott (1896) and Bocquet and Stock (1959) are conspecific.

Bocquet and Stock (1959) noted discrepancies between their male *M. cluthae* and that described by T. and A. Scott which they attributed to errors on the part of the latter authors. The rudimentary endopods on legs 3 and 4, observed by T. and A. Scott were not seen by Bocquet and Stock or in any of the present material. A very similar species *Mesnilia martinensis* Canu, 1898 was described from the Channel coast of France (near Cherbourg). Canu (1898) was aware of the similarities between *M. cluthae* and *M. martinensis* but only had female material available and did not consider that they might be male and female of the same species. Bocquet and Stock (1959) maintained *M. martinensis* as a separate species based on a number of minor differences in the antennae and mouthparts. It seems much more likely that these differences are simply descriptive inaccuracies by Canu and the two species are treated here as synonymous. The genus *Mesnilia* becomes monotypic, comprising only *M. cluthae*. Specimens examined subsequently by Gotto (1965) from Plymouth, and by Hamond (1973) from Norfolk are consistent with the redescription of Bocquet and Stock (1959). It is now evident that *M.cluthae* is widely distributed around the coast of the British Isles as well as the Channel coast of France.

Genera of the family Clausiidae have typically been distinguished mainly by leg morphology. It is notable that the morphology of cephalic appendages such as the antenna and mandible in *M. cluthae* is very close to that of *Clausia lubbockii* redescribed above, even though they have different leg morphologies.

Genus *Rhodinicola* Levinsen, 1878

Rhodinicola gibbosus Bresciani, 1964

Rhodinicola gibbosa Bresciani, 1964a: 226, figs. 2–5.

Material examined: 1 ♀ (dissected and figured) from *Praxillella praetermissa* (Malmgren, 1866); Troll Vest Stn 16-2 (60.76ºN, 3.445ºE), depth 327 m, 20 May 1995.

1 ♀ from *P. praetermissa*; Korsfjord, Stn 1-1 (70.237ºN, 23.244ºE), depth 160 m, 06 November 2007; BMNH Reg. No. 2012.1370.

1 ♀ detached in sample from unknown host; Barents Sea, depth unknown, 19 May 1995; BMNH Reg. No. 2012.1371.

1 ♀ detached in sample from unknown host; "Resi Stangnes 06", Stn 5-3/4 (68°48.459'N, 16°36.753'E), depth 74 m, 28 June 2006; BMNH Reg. No. 2012.1372.

1 ♀ detached in sample from unknown host; 69º19'01"N, 33º32'28"E, depth 282 m, 24 May 1995; BMNH Reg. No. 2012.1373.

1 ♀ detached in sample from unknown host; Motovsky Gulf, Stn 28-2 (69°35.521'N, 33°09.318'E), depth 226 m, 13 August 2003; BMNH Reg. No. 2012.1374.

Female. Body (Fig. 7A) elongate and consisting of cephalothorax, 4 pedigerous somites, genital double-somite, and 3 free abdominal somites, lacking conspicuous prosome-urosome division. Somites clearly divided by deep constrictions between them. Body length of adult variable: 4.32 mm in dissected specimen, but 6.28 mm in largest specimen from Barents Sea. Cephalothorax triangular in dorsal view, 645×727 μm. Cephalothorax and first to third free metasomal somites (second to fourth pedigerous somites) usually with posterodorsal sub-globular tubercle in midline (tubercles weakly expressed in some specimens). Second to fifth pedigerous somites 600×691, 655×673, 656×618, and 545×600 μm, respectively. Genital double-somite wider than long, with large, paired posteroventral expansions, each expansion distally incised and with genital aperture located within incision; expansions ornamented with rows of minute spinules (Fig. 7B) on ventral surface. Abdomen gradually narrowing from anterior to posterior: first free abdominal somite wider than long, second 275×300 μm, anal somite 215×220 μm, with several patches of minute spinules on ventral surface. Caudal ramus (Fig. 7C) directed posterolaterally, tapering, 208×64 μm (ratio 3.25 : 1), with 7 naked setae including small, setule-like outer proximal seta (seta I); largest distal seta 333 μm long. Egg sac (Fig. 7D) 2.85×0.35 mm; eggs arranged in 3 or 4 rows.

Rostrum as semicircular protuberance on frontal margin (Fig. 7E). Antennule (Fig. 7E) 308 μm long and 5-segmented; first and second segments expanded, distinctly broader than distal 3 segments; armature formula 3+spine, 10+spine, 4+aesthetasc, 2+aesthetasc, and 7+aesthetasc; spine on first and second segments short, with spinulate lateral margins; first segment with large patch of densely-set minute setules on ventral surface; setae on all segments naked. Antenna (Fig. 7F) 4-segmented; segments becoming shorter and narrower from proximal to distal; first segment (coxa-basis) smooth and unarmed; second segment (first endopodal segment) unarmed but with patch of spinules sub-proximally and rows of spinules distally; third segment with 1 distal spinulose claw and several leaf-like hyaline extensions on mediodistal surface; terminal segment 23×12 μm, armed with 2 spinulose claws, 2 long setiform claws, and 2 small subdistal setae.

Labrum (Fig. 7G) with large patches of numerous spinules on each disterolateral area and broad median ridge extending slightly beyond posterior margin. Mandible (Fig. 7H) digitiform with distal membranous extension; armature consisting of distal spine (spine distally bifurcate or trifurcate), and large, transparent plumose seta subdistally. Maxillule lobate bearing 4 naked distal setae, one spiniform. Maxilla (Fig. 8A, B) 2-segmented; proximal segment very broad and unarmed; distal segment stout, distally ornamented with dense covering of minute spinules, armed with 2 claw-like processes, and 1 short but thick medial seta. Maxilliped (Fig. 8C) 4-segmented; first segment unarmed; second segment with 2 unequal naked setae on medial margin and patch of spinules on medial surface; third segment unarmed; terminal segment tapering, with 2 large naked setae, 1 small spine, and spiniform terminal claw ornamented with spinules along medial margin; terminal claw articulated at base.

Legs 1–4 (Fig. 8D–G) with 3-segmented rami; all rami becoming narrower from proximal to distal, with spinules on outer margin and patches of spinules on posterior (dorsal) surface (indicated by dotted circles in Fig. 8D–G). Coxa of legs 1–4 with 1 mediodistal patch of spinules close to inner seta. Basis of leg 1 with posterior patch of spinules between bases of rami. Basis of legs 2–4 with 2 posterior patches of spinules. Setae small on both rami of legs 1–4. Armature formula of legs 1–4 as follows:

Leg 1: coxa 0-1; basis 1-0; exp. I-0; I-1; II, 2, 2; enp. 0-0; 0-1; I, 2, 2
Leg 2: coxa 0-1; basis 1-0; exp. I-0; 0-1; III, 2, 4; enp. 0-1; 0-2; 1, 2, 2
Leg 3: coxa 0-1; basis 1-0; exp. I-0; I-1; I, 2, 5; enp. 0-1; 0-2; 0, 1, 2
Leg 4: coxa 0-1; basis 1-0; exp. I-0; I-1; II, 1, 5; enp. 0-1; 0-2; 0, 1, 2

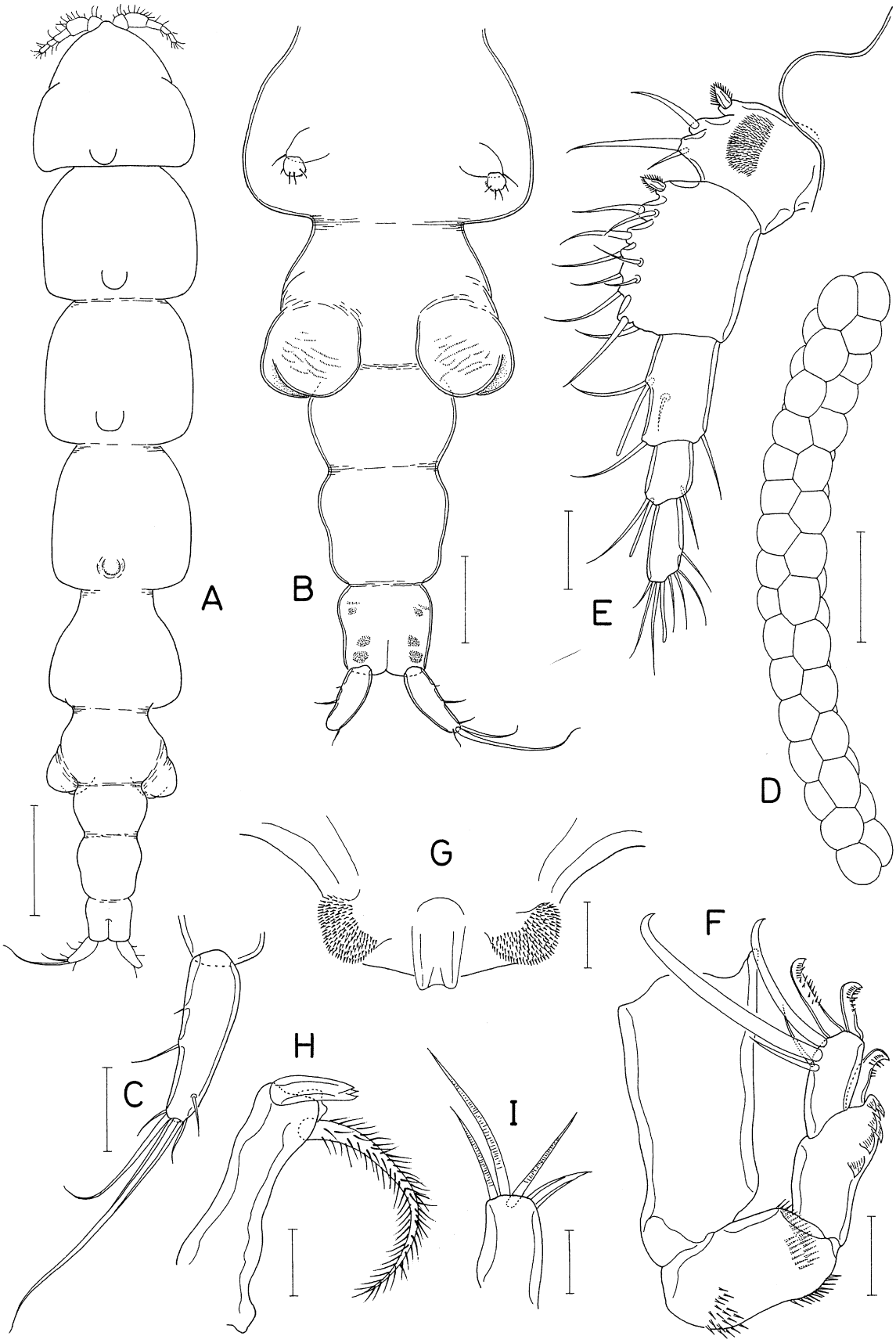

FIGURE 7. *Rhodinicola gibbosus* Bresciani, 1964, female. A, habitus, dorsal; B, urosome, ventral; C, left caudal ramus, dorsal; D, egg sac; E, rostrum and antennule; F, antenna; G, labrum; H, mandible; I, maxillule. Scale bars: A, D, 0.5 mm; B, 0.2 mm; C, 0.1 mm; E, 0.05 mm; F–I, 0.02 mm.

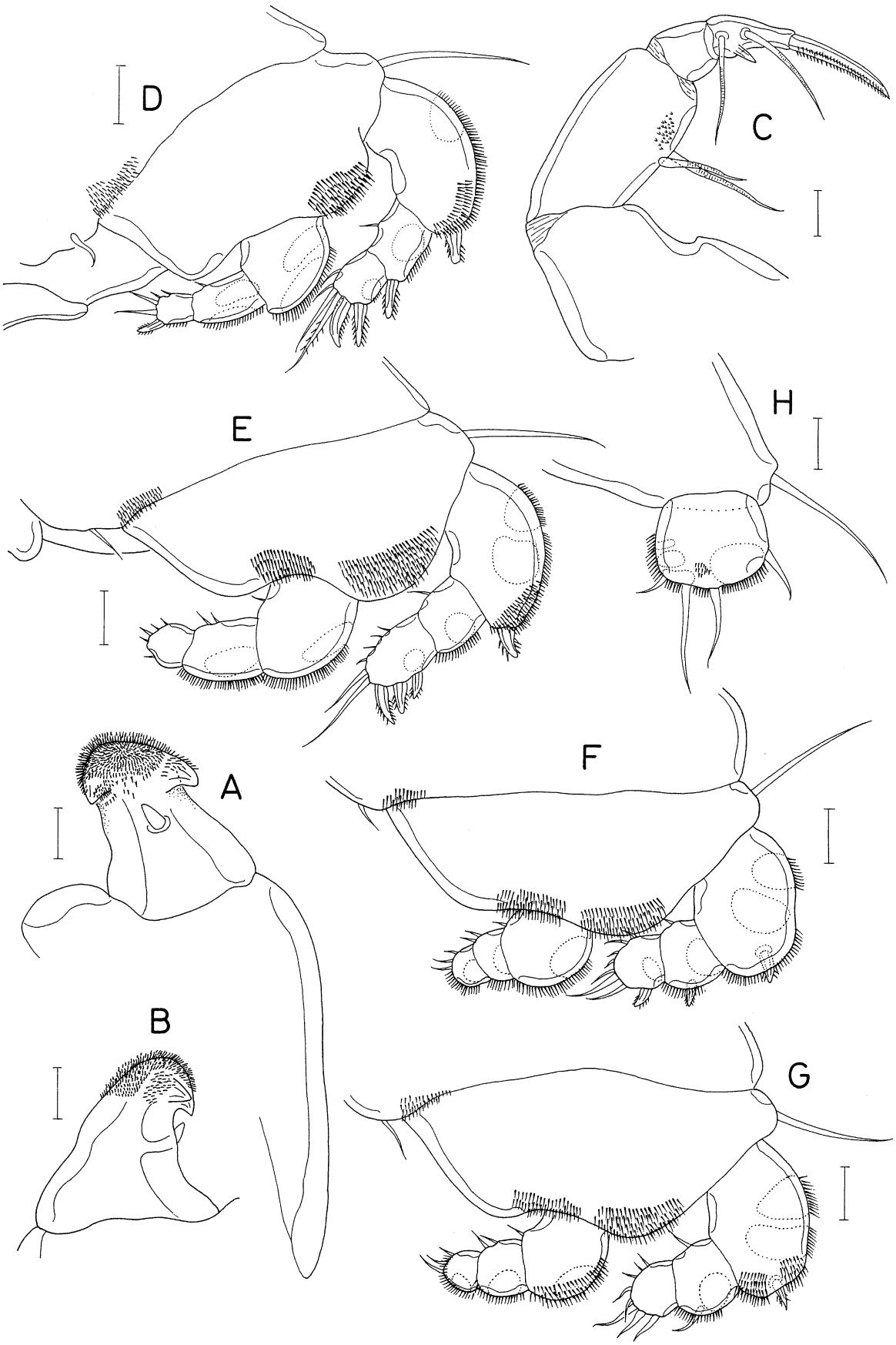

FIGURE 8. *Rhodinicola gibbosus* Bresciani, 1964, female. A, maxilla, medial; B, distal segment of maxilla, ventral; C, maxilliped; D, leg 1; E, leg 2; F, leg 3; G, leg 4; H, leg 5. All scale bars: 0.02 mm.

Leg 5 (Fig. 8H) 2-segmented but proximal protopodal segment incorporated into somite, with 1 posterolateral seta; free distal segment (exopod) roughly rectangular, wider than long, with 4 setae and several patches of spinules. Leg 6 not seen.

Remarks. The large subdistal seta on the mandible was omitted from the original description, probably due to its transparency. We were able to find only four distal elements on the maxillule and were unable to confirm the presence of a subdistal seta as illustrated by Bresciani (1964a). Some of the small setae on the rami of swimming legs were also apparently overlooked in the original description. Our specimens were all taken from the type host, the maldanid *P. praetermissa*, or were found detached in macrobenthos samples.

Rhodinicola rugosum (Giesbrecht, 1895)

Seridium rugosum Giesbrecht, 1895: 223, pl. ix.
Seridium rugosum: Wilson and Illg, 1955: 134.
Rhodinicola rugosa: Bresciani, 1964a: 232.

Material examined: 3 ♀♀ (2 ♀♀ dissected), attached to fragment of *Clymenura* Verrill, 1900; English Channel off Littlehampton, West Sussex (50°40.143'N, 0°31.200'W), depth 15 m (sample taken by Hamon Grab)**,** collected by J. Weir at EMU Ltd, 29 September 2004; BMNH Reg. No. 2012.1377 (undissected ♀).

1 ♀ detached from host; Inner Gabbard Ground off Harwich (51°54.07'N, 01°45.15'E); depth unknown, recovered by David Hall, 14 June 2000; BMNH Reg. No. 2012.1378.

1 ♀ attached to *Euclymene sp.*, Central North Sea, Lundin Block 21-8, Stn 5 (57°40.3878'N, 00°24.4776'E), depth ~104 m, collected by Sue Hamilton, April 2007; BMNH Reg. No. 2013.10.

3 ♀ attached to *Clymenura tricirrata*, Central North Sea, Lundin Block 21-8, Stn 6 (57°40.8664, 00°25.0638'E), depth ~104 m, collected by Sue Hamilton, April 2007; BMNH Reg. No. 2012.1379.

1 ♀ attached *C. tricirrata*, Central North Sea, Lundin Block 21-8, Stn 14 (57°40.3878'N, 00°25.0961'E), depth ~104 m, collected by Sue Hamilton, April 2007; BMNH Reg. No. 2012.1380.

1 ♀ detached from host, Central North Sea, Lundin Block 21-8, Stn 15 (57°40.2902'N, 00°24.6928'E), depth ~104 m, collected by Sue Hamilton, April 2007; BMNH Reg. No. 2013.11.

1 ♀ attached to *C. tricirrata*, Central North Sea, Lundin Block 21-8, Stn 18 **(**57°39.9607'N, 00°24.3614'E), depth ~104 m; collected by Sue Hamilton, April 2007; BMNH Reg. No. 2013.12.

2 ♀ detached but 4 *Praxillella affinis* in sample, 15 miles east of Harwich, Suffolk (51°49.88'N, 01°45.07'E), depth 35 m, collected by Tim Worsfold, May 1998; BMNH Reg. No. 2013.13.

1 ♀ attached to fragment of *P. affinis*, Hastings, East Sussex, CEFAS Stn 169Y (50° 44.05'N, 00° 35.90'E); collected David Hall, July 2001; BMNH Reg. No. 2012.1381.

Additional records:

North Sea:

1 ♀ detached from host, Golden Eagle Oilfield (Blocks 21/1N, 20/1S) Stn 01-FB, 07 March 2008.

1 ♀ immature from maldanid fragment, Arundel/Farragon Oilfield, Stn A09-22-a, 09 September 2009.

1 ♀ attached to *Clymenura* sp., Sycamore Oilfield, Stn ENV-FA, 05 January 2010.

1 copepodite on *Clymenura johnstoni* (McIntosh, 1915), Moray Firth, Stn MSS MF1.2 (57°51.01'N, 03 20.97'W), depth 64 m; found by Stephen Nowacki, 14 January 2010.

Western Scotland:

1 copepodite from *Clymenura* sp., Fishnish, Isle of Mull, collected by Julian Hunter, 2006.

1 ♀ detached from host, Firth of Clyde, Scotland, Stn G03-1 (55° 44.922'N, 04° 53.110'W) collected David Hall, 26 June 2009.

1 ♀ attached at setiger 9 (of 10) on anterior fragment of *Clymenura sp.*, Loch Laxford, SNH Stn 24 (58° 23.67'N, 05° 03.76'W); collected Sue Hamilton, 21 October 2009.

1 ♀ Loch Fyne, SEPA Surveillance site (56° 02.76'N, 05° 18.89'W), depth 43 m; collected Stephen Nowacki, 11 March 2010.

1 ♀ Loch Roag, Isle of Lewis, SEPA site at Fuaigh Beag (58° 12.03'N, 06° 53.63'W), depth 29 m; collected Stephen Nowacki, 24 July 2012.

England:

1 ♀ detached but 16 *Praxillella affinis* (M. Sars, 1872) in sample, 15 miles east of Harwich, Suffolk (51º52.16'N, 01º45.51'E), depth 35 m; collected by Tim Worsfold, May 1998.

Ireland:

1 ♀ on maldanid fragment (*Praxillella?)*, Northern Irish Sea, Block 109, Stn 3 (53º45.27'N, 04º 07.12'W), depth 46 m; collected by Sue Hamilton, September 1995.

1 ♀ northern Irish Sea, Block 109, Stn 12 (53º54.85'N, 04º15.98'W), depth 44 m; collected by Sue Hamilton, September 1995.

1 ♀ attached to *Praxillella sp.*? fragment, Belfast Lough (54º 42.180'N, 05º 35.538' W), depth 25 m; collected by Tim Mackie, 30 April 1999.

1 ♀ and 2 juveniles attached to *Clymenura johnstoni*, Stn 619, Irish Sandbanks Survey, collected by Peter Garwood.

1 ♀ detached from host, Arklow Bank, collected David Hall, 05 October 2006.

1 ♀ detached from host, Belfast Lough, EHS Stn F02-b (54º43.47'N, 05º34.02'W), depth 36 m; collected by Tim Mackie, 04 April 2008.

1 ♀ Larne Lough, Stn LL4-d (54º50.35'N, 05º47.80'W); depth 5 m; collected by Tim Mackie, 01 November 2008.

Female. Body (Fig. 9A, B) elongate, dorsoventrally depressed, and consisting of cephalothorax, 4 pedigerous somites, genital somite, and 4 free abdominal somites, lacking conspicuous prosome-urosome division. Somites clearly divided by deep constrictions between them. Body lengths of 2 dissected specimens 2.79 and 2.47 mm. Cephalothorax triangular in dorsal view, 412×461 μm, with 1 prominent posterodorsal tubercle (Fig. 9A). Second to fifth pedigerous somites 312×486, 369×492, 326×486, and 252×436 μm, respectively; these somites typically rectangular in outline but more sub-circular in inflated specimens, with transverse crease on dorsal surface of each (Fig. 9A, B). Genital somite 369×196 μm, width measured across genital prominences (Fig. 10K), 424 μm; somite broader anteriorly and narrower posteriorly. Four free abdominal somites 135×233, 129×212, 104×184, and 98×146 μm, respectively. Dorsal suture line incomplete between third abdominal and anal somites. Anal somite characteristically narrower than preceding abdominal somites, with patch of minute spinules on ventrodistal surface near base of caudal ramus (Fig. 9C). Caudal rami divergent; each ramus gradually narrowing from proximal to distal, 138×48 μm (ratio 2.88:1), with 6 setae and 1 minute outer proximal seta (Fig. 9C).

Rostrum directed anteriorly and clearly defined from dorsal cephalothoracic shield (Fig. 9D). Antennule (Fig. 9E) 180 μm long and 4-segmented; armature formula 3+spine, 10+spine, 6+2 aesthetascs, and 7+aesthetasc; spines on first and second segment short and spinulose; first segment with large patch of spinules on ventral surface; third segment with 5–8 scale-like processes on distal part of ventral surface. Antenna (Fig. 9F) 4-segmented; first segments (coxa-basis) smooth and unarmed; second segment (first endopodal segment) also unarmed but with 2 patches of spinules on medial side; third segment with 1 claw and 1 seta, and ornamented with 4 or 5 epicuticular scales (proximalmost scale directed distally and remaining scales directed proximally) in mediodistal region; terminal segment 23×11 μm (ratio 2.09:1), armed with 4 claws and 2 smooth setae on distal margin and ornamented with several small spinules on outer margin; 2 medial claws on terminal segments each with rows of fine spinules bilaterally; 2 outer claws each with 3 or 4 spinules on concave medial margin.

Labrum (Fig. 9G) with patch of spinules on each side and a pair of curved digitiform processes in middle of posterior margin. Mandible (Fig. 10A) with 1 large plumose seta distally (this seta transparent and easily detached) and 1 spiniform element with bifurcate apex and lateral membranous flange. Paragnath (Fig. 10B) a densely spinulose lobe with small process on posterior margin. Maxillule (Fig. 10C) lobate, with naked 5 setae. Maxilla (Fig. 10D) 2-segmented; proximal segment unarmed but with 1 pointed ventrodistal process; distal segment stout, distally curved giving claw-like appearance, densely covered with spinules and armed with 1 robust, spinulate spine on dorsal surface and 1 minute, tubercle-like, seta on ventral surface. Maxilliped (Fig. 10E) slender and 4-segmented; first and third segments unarmed; second segment with 2 naked setae in middle of medial margin; terminal segment armed with 2 setae, 1 spine and 1 spiniform process fused to segment, distal seta markedly longer than distal spine.

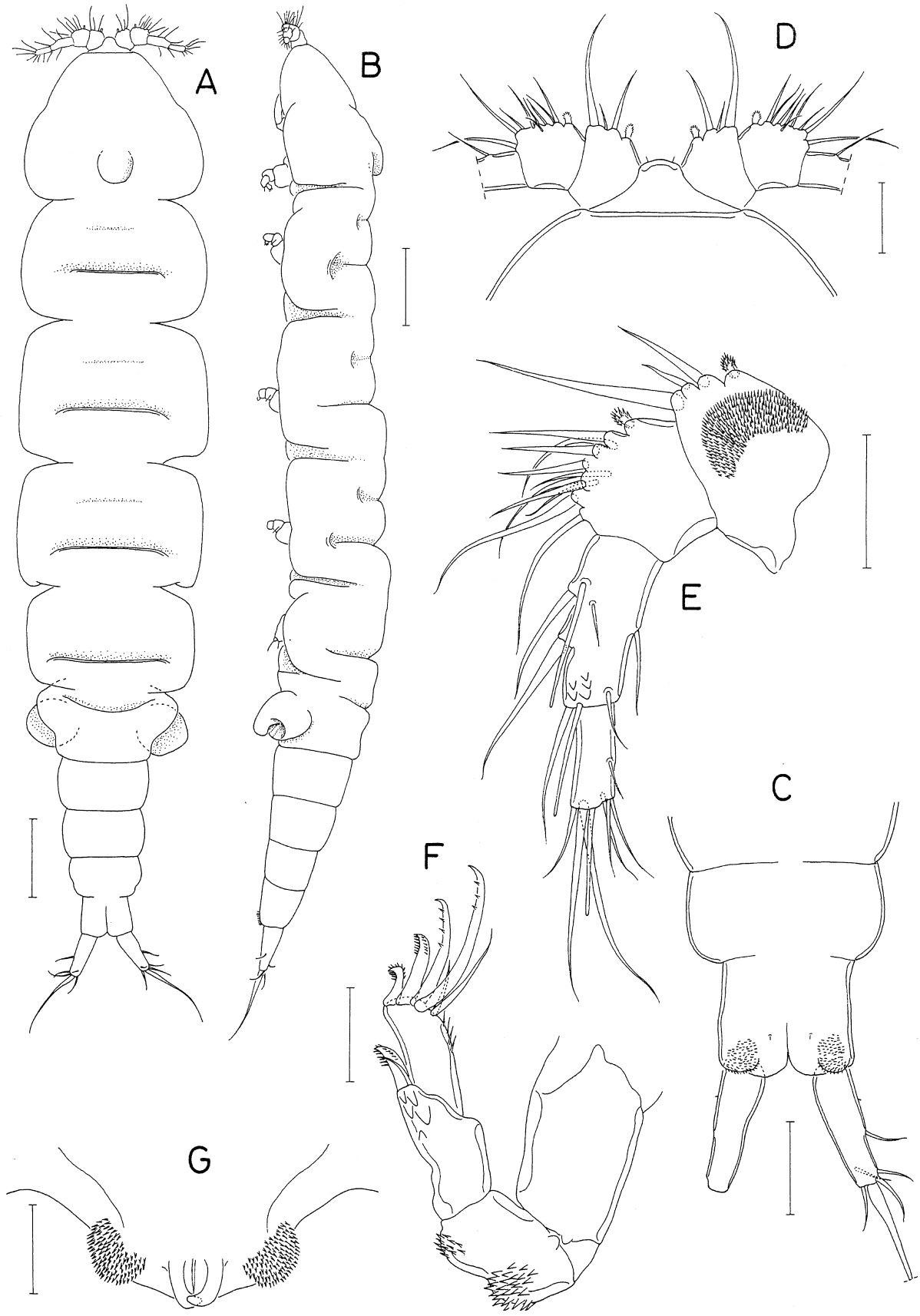

FIGURE 9. *Rhodinicola rugosum* (Giesbrecht, 1895), female. A, habitus, dorsal; B, habitus, lateral; C, posterior part of abdomen with caudal rami, ventral; D, rostral area, dorsal; E, antennule, ventral; F, antenna; G, labrum, ventral. Scales bars: A, B, 0.2 mm; C, 0.1 mm; D, E, 0.05 mm; F, G, 0.02 mm.

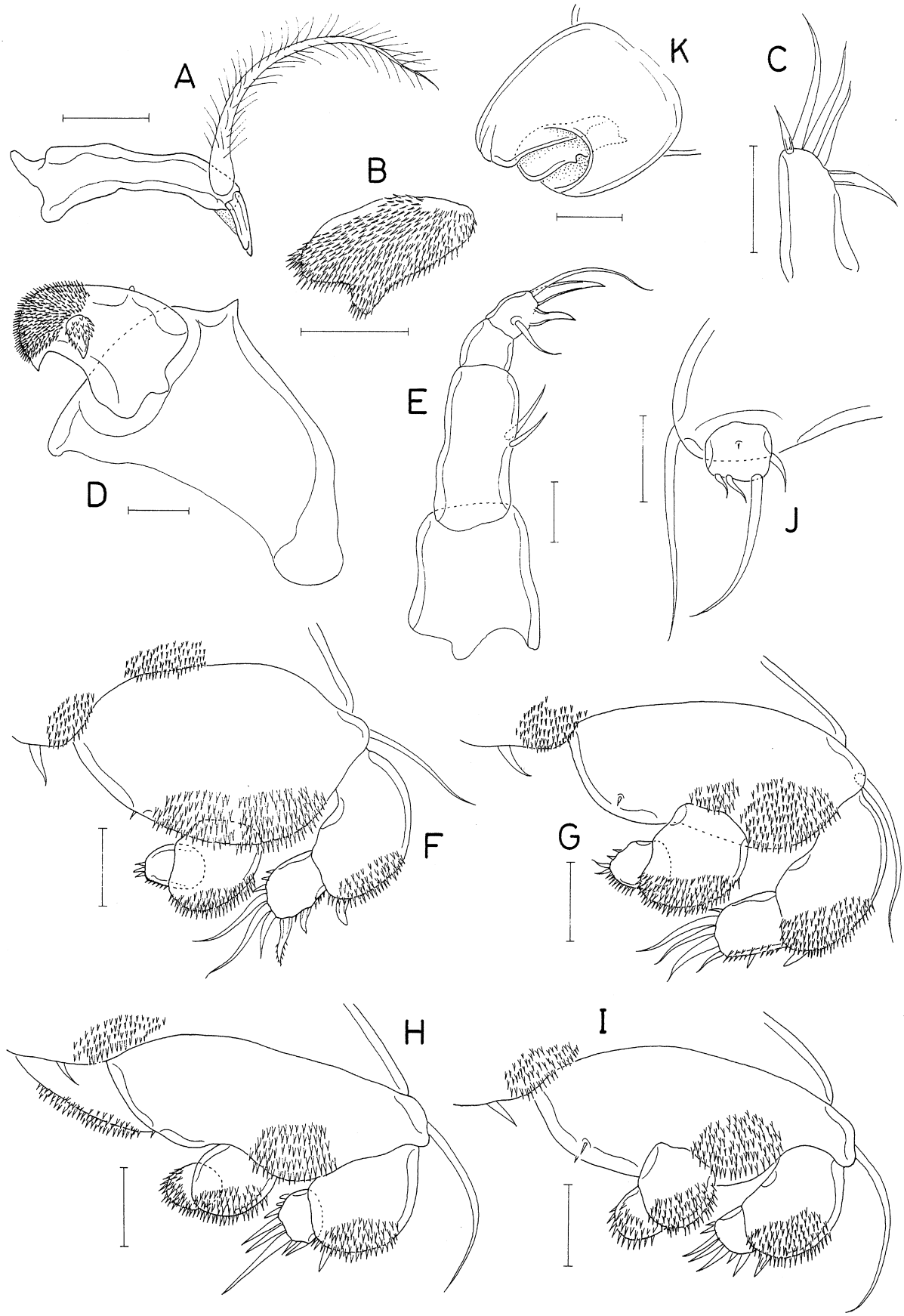

FIGURE 10. *Rhodinicola rugosum* (Giesbrecht, 1895), female. A, mandible; B, paragnath; C, maxillule; D, maxilla, dorsal; E, maxilliped; F, leg 1; G, leg 2; H, leg 3; I, leg 4; J, right leg 5, ventral; K, genital area. Scale bars: A–J, 0.02 mm; K, 0.05 mm.

Legs 1–4 (Fig. 10F–I) biramous, with 2-segmented rami, all ornamented with patches of spinules on coxa, basis and outer surface of rami. Inner seta on coxa of legs 1–4 small and smooth; outer seta on basis of legs large and smooth. Posterior margin of basis of legs 1–4 each with 1 or 2 inner setules. Armature formula of legs 1–4 as follows:

Leg 1: coxa 0-1; basis 1-0; exp. I-0; II, 2, 4; enp. 0-0; 3
Leg 2: coxa 0-1; basis 1-0; exp. I-0; I, 2, 3; enp. 0-0; 4
Leg 3: coxa 0-1; basis 1-0; exp. I-0; 2, 3, 3; enp. 0-0; 0
Leg 4: coxa 0-1; basis 1-0; exp. I-0; 2, 3, 2; enp. 0-0; 0

Leg 5 (Fig. 10J) 2-segmented but proximal protopodal segment incorporated into somite, with 1 posterolateral seta; free distal segment (exopod) small, rectangular, wider than long, armed with 4 setae (1 small seta on medial margin, 1 large plus 2 small setae on distal margin). Leg 6 not seen.

Remarks. In all of four species of *Rhodinicola* observed in the present work (*R. gibbosus*, *R. rugosum*, *R. tenuis* **n. sp.** and *R. similis* **n. sp.**), the mandible is armed distally with a large plumose seta plus either a spiniform process or an articulated element. The plumose seta is transparent and easily detached and, therefore, has probably gone unnoticed in previous descriptions of *R. rugosum* and *R. gibbosus*. The mandibles of *R. elongata* Levinsen, 1878 and *R. thomassini* Laubier, 1970 are in need of re-examination to check for the presence of this plumose seta. However, this characteristic form of mandible, as shared by the four species listed above, differs markedly from the mandible of *R. laticauda* Ho and Kim, 2003 and *R. polydorae* Björnberg & Radashevsky, 2011, both of which have two spiniform elements, one distal and one subdistal (Ho and Kim, 2003; Björnberg and Radashevsky, 2011). In addition, the maxilliped of female *R. laticauda* and *R. polydorae*, which is rudimentary, differs from the well-developed limbs present in females of all other *Rhodinicola* species. We anticipate that *R. laticauda* and *R. polydorae* may well have to be assigned to a new genus in a future revision of the family Clausiidae.

R. rugosum was originally described in 1895 associated with *Praxilla sp*. from Naples. Surprisingly there have been no records since, until its re-discovery by Sue Hamilton in the Irish Sea exactly 100 years later. It appears to be widely distributed around the British Isles on a range of maldanid hosts including *Euclymene sp.*, *Praxillella affinis*, *Clymenura tricirrata* and *Clymenura johnstoni*. One of the observed specimens was still attached to the skin of the host using its left and right maxillae together as pincers. It has also recently been observed on the west coat of Ireland in inner Galway Bay (*pers. comm.* Eddie McCormack, Aqua-Fact International Services Ltd, 2009). The *Rhodinicola sp*. copepodites found by Gotto & O'Connor (1980) in Galway Bay and by Capaccioni *et al* (1993) in the Ebro Delta (western Spain) probably belong to this species.

Rhodinicola tenuis n. sp.

Type material: Holotype ♀ (dissected and mounted on a glass slide) from unknown host; R/V Smolensk, Stn 25-3 (70°08.0'N, 56°58.5'E), depth 69 m, 15 August 2004; BMNH Reg. No. 2012.1382.

Female. Body (Fig. 11A) slender, elongate, and composed of cephalothorax, unsegmented trunk and 4-segmented abdomen. Body length 5.15 mm, excluding caudal setae. Cephalothorax 770×640 μm, slightly expanded posterolaterally, not articulated from trunk but clearly defined from it by prominent lateral constriction. Trunk incorporating second to fifth pedigerous somites and genital somite, narrower than cephalothorax, and gradually narrowing from anterior to posterior, with paired lateral expansions at level of insertions of legs 2–5. Area of genital somite expanded laterally, 570 μm wide across this area; paired genital apertures located ventrolaterally (Fig. 11B). Abdomen small: four free abdominal somites 192×269, 123×246, 92×200, and 192×208 μm, respectively. Caudal ramus (Fig. 11C) rectangular, 119×62 μm (ratio 1.92:1), with 7 naked setae, distal seta much larger than others.

Rostrum as rounded ventral protuberance (Fig. 11D). Antennule (Fig. 11D) 257 μm long and 6-segmented; armature formula 4, 9, 5, 4+aesthetasc, 2+aesthetasc, and 7+aesthetasc; second seta of first segment weakly pinnate; distalmost seta of this segment thick and plumose (Fig. 11D). Antenna (Fig. 11E) 4-segmented; first segment with 1 distal pinnate seta; second segment with 1 small subdistal seta; third segment with 1 claw and 1 seta distally and with longitudinal row of 6 foliaceous scales ornamenting segment; terminal segment 36×21 μm (ratio 1.71:1), bearing 4 claws and 2 long pinnate setae.

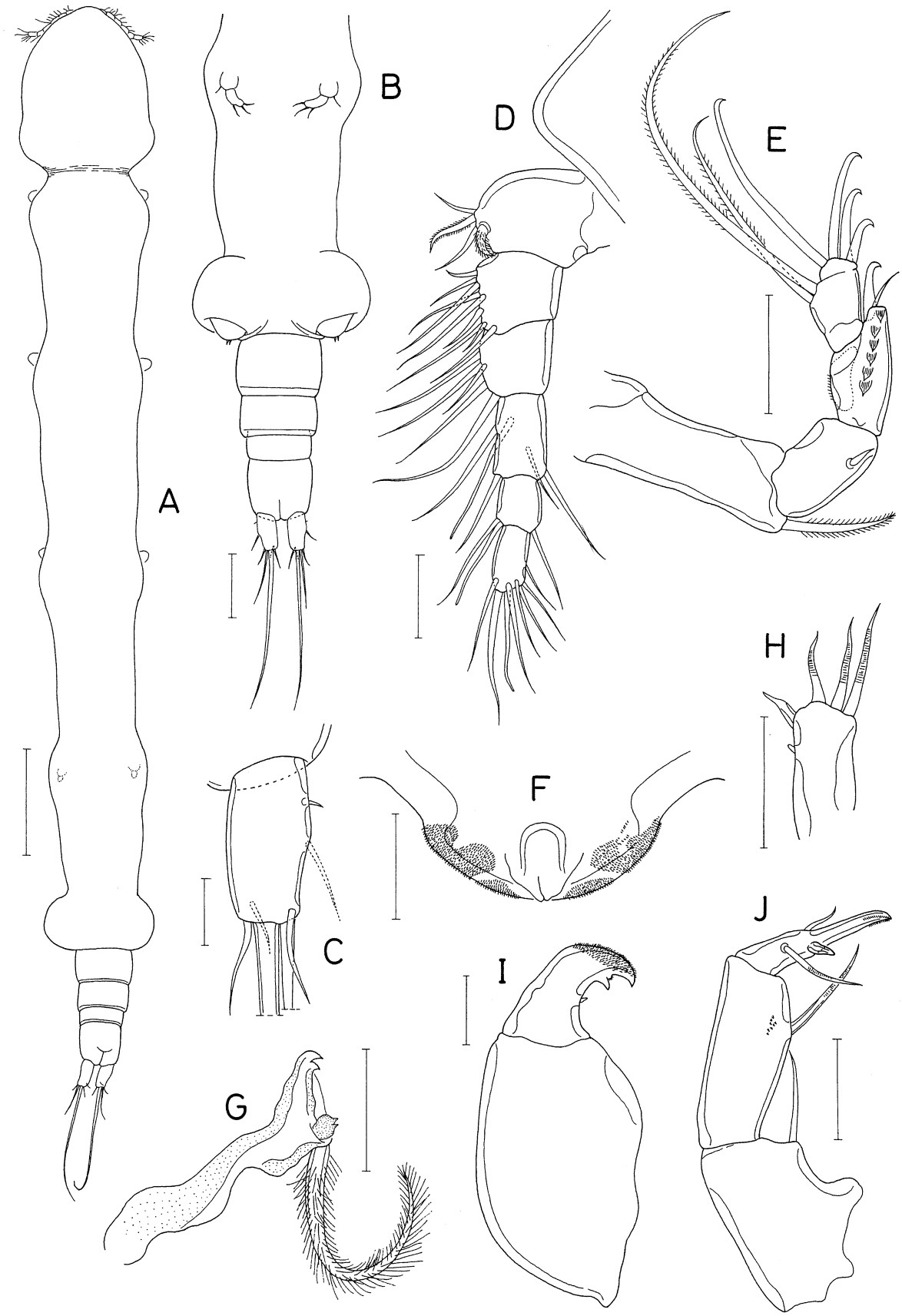

FIGURE 11. *Rhodinicola tenuis* **n. sp.**, female. A, habitus, dorsal; B, urosome, ventral; C, left caudal ramus, ventral; D, rostrum and antennule, dorsal; E, antenna; F, labrum, ventral; G, mandible; H, maxillule; I, maxilla; J, maxilliped. Scale bars: A, 0.5 mm; B, 0.2 mm; C–J, 0.05 mm.

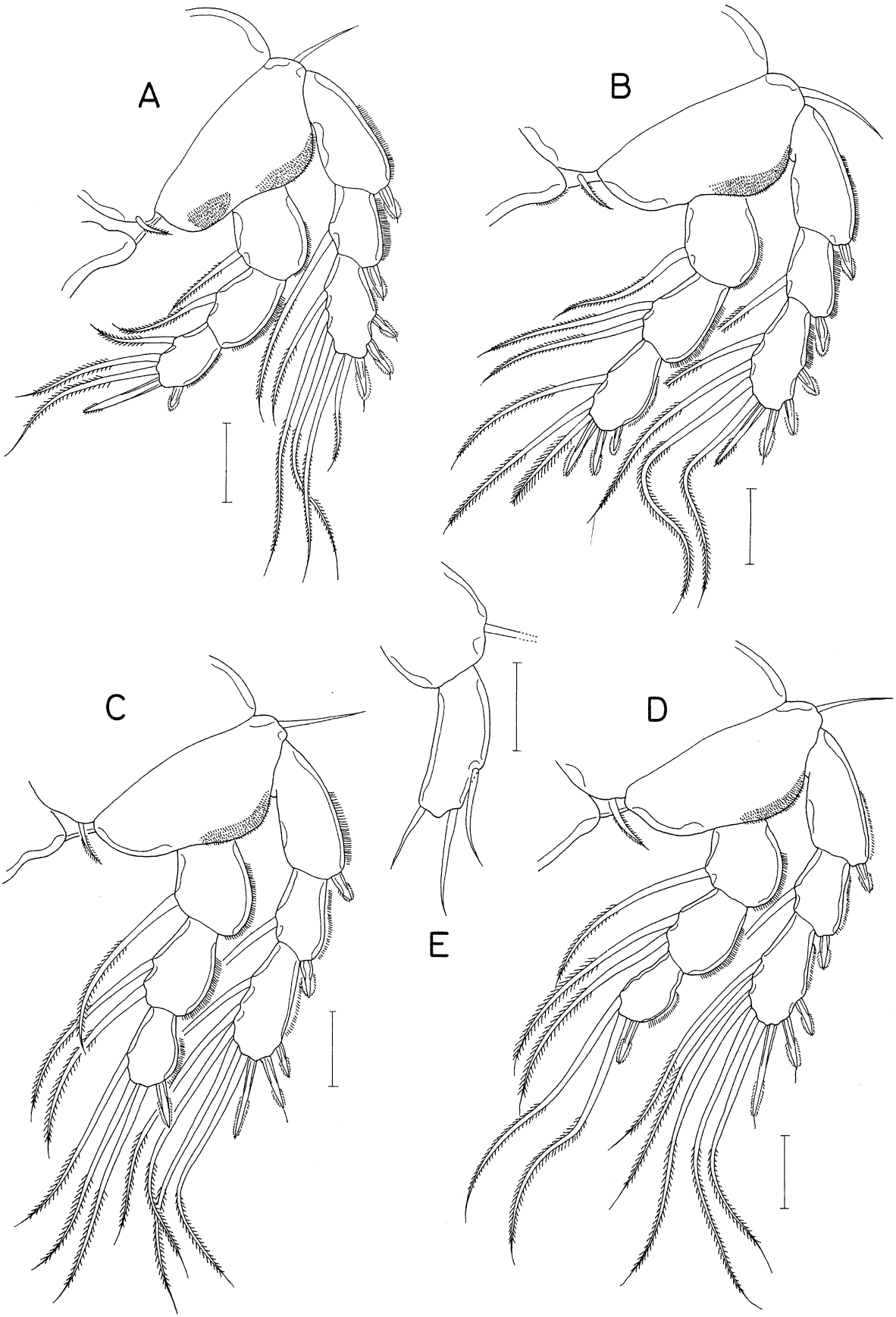

FIGURE 12. *Rhodinicola tenuis* **n. sp.**, female. A, leg 1; B, leg 2; C, leg 3; D, leg 4; E, leg 5. All scale bars: 0.05 mm.

Labrum (Fig. 11F) with roundly convex posterior margin and ornamented with patches of minute spinules. Mandible (Fig. 11G) terminating in 1 or 2 cusps distally and carrying on distal margin 1 large plumose seta and 1 rounded hyaline element terminating in 2 small points. Maxillule (Fig. 11H) with 1 minute lateral, 1 subdistal and 3 distal setae. Maxilla (Fig. 11I) 2-segmented; proximal segment unarmed; distal segment with slightly recurved and pointed apex, armed with 1 minute seta and 1 dentiform process on concave margin and spinulose pad on slightly curved distal margin. Maxilliped (Fig. 11J) 3-segmented; first segment with 1 distal seta on medial margin; second segment with 1 seta in distal third of medial margin; third segment tapering into spiniform distal process with 2 setae and 1 small spine.

Legs 1–4 (Fig. 12A–D) biramous with 3-segmented rami; basis ornamented with 2 patches of spinules in leg 1 and 1 patch in legs 2–4. All segments of both rami of all legs with spinulose outer margins. Inner seta on coxa of legs 1–4 small and pinnate, outer seta on basis, large and naked. All setae on rami of legs 1–4 naked proximally and weakly pinnate distally. Armature formula of legs 1–4 as follows:

Leg 1: coxa 0-1; basis 1-0; exp. I-0; I-1; II, I, 5; enp. 0-1; 0-1; I, I, 3
Leg 2: coxa 0-1; basis 1-0; exp. I-0; I-1; II, II, 4 (or II, I, 5); enp. 0-1; 0-2; I, II, 3
Leg 3: coxa 0-1; basis 1-0; exp. I-0; I-1; II, I, 5; enp. 0-1; 0-2; I, 2, 1 (or 0, 2, 1)
Leg 4: coxa 0-1; basis 1-0; exp. I-0; I-1; II, I, 5; enp. 0-1; 0-2; I, 1, 1

Leg 5 (Fig. 12E) 2-segmented; proximal segment fused with somite, with 1 outer seta; free distal segment (exopod) 82×32 μm (ratio 2.56:1), with 1 outer and 2 distal setae. Leg 6 represented by 2 minute spinules in genital area (Fig. 11B).

Male. Unknown.

Etymology. The specific name *tenuis*, meaning “slender” in Latin, alludes to the slender body of the new species.

Remarks. The new species belongs in the genus *Rhodinicola* because it has three-segmented rami of legs 1–4 and no posteromedian element on the basis of leg 1. The ventral location of leg 5 on its somite is also a feature of *Rhodinicola*, as Boxshall and Halsey (2004) considered it a key character of that genus. The species *R. laticauda* and *R. polydorae* both have a laterally located leg 5, unlike typical *Rhodinicola* species, futher highlighting the need for the affinities of these species to be reassessed. Within the genus *Rhodinicola*, the new species is most closely related to *R. elongata* (as redescribed by Bresciani, 1964a). They share a number of characteristics such as the 6-segmented antennules, the 4-segmented abdomen and antenna, the 3-segmented maxilliped, and the similar shape of the maxilla.

According to the Bresciani’s redescription and illustrations, *R. elongata* has, unlike *R. tenuis* **n. sp.**, two lanceolate spines and three setae on the first antennular segment, only one element on the third antennary segment, a simple mandible bearing only one spiniform distal element, nine or ten elements (having ten is certainly abnormal) on the third exopodal segment of leg 2, and a more slender free exopodal segment of leg 5. These features of *R. elongata* differentiate it from *R. tenuis* **n. sp.** It should be noted that Fig. 1F of Bresciani (1964a), that was labeled leg 1, is in fact leg 4.

Rhodinicola similis n. sp.

Type material: Holotype ♀ (a damaged specimen, with burst prosome and broken abdomen, dissected and mounted on a glass slide), from *Rhodine gracilior* (Tauber, 1879); Loch Creran, Scotland, Rubha Garbh (56°31.59’N, 05°21.25’W), depth 15 m, collected by M.O’Reilly, 11 January 1995; BMNH Reg. No. 2012.1383.

Allotype ♂ (allotype, dissected and mounted on a glass slide) from *R. gracilior*; Irvine Bay, Scotland, Stn H (55°35.92’N, 04°47.40’W), depth 38 m; collected by M.O’Reilly, 08 September 1989; BMNH Reg. No. 2012.1384. Juvenile from *R. gracilior*; Irvine Bay, Scotland, Stn H (55°35.92’N, 04°47.40’W), depth 38 m; collected by M.O’Reilly, 08 September 1989; BMNH Reg. No. 2012.1385.

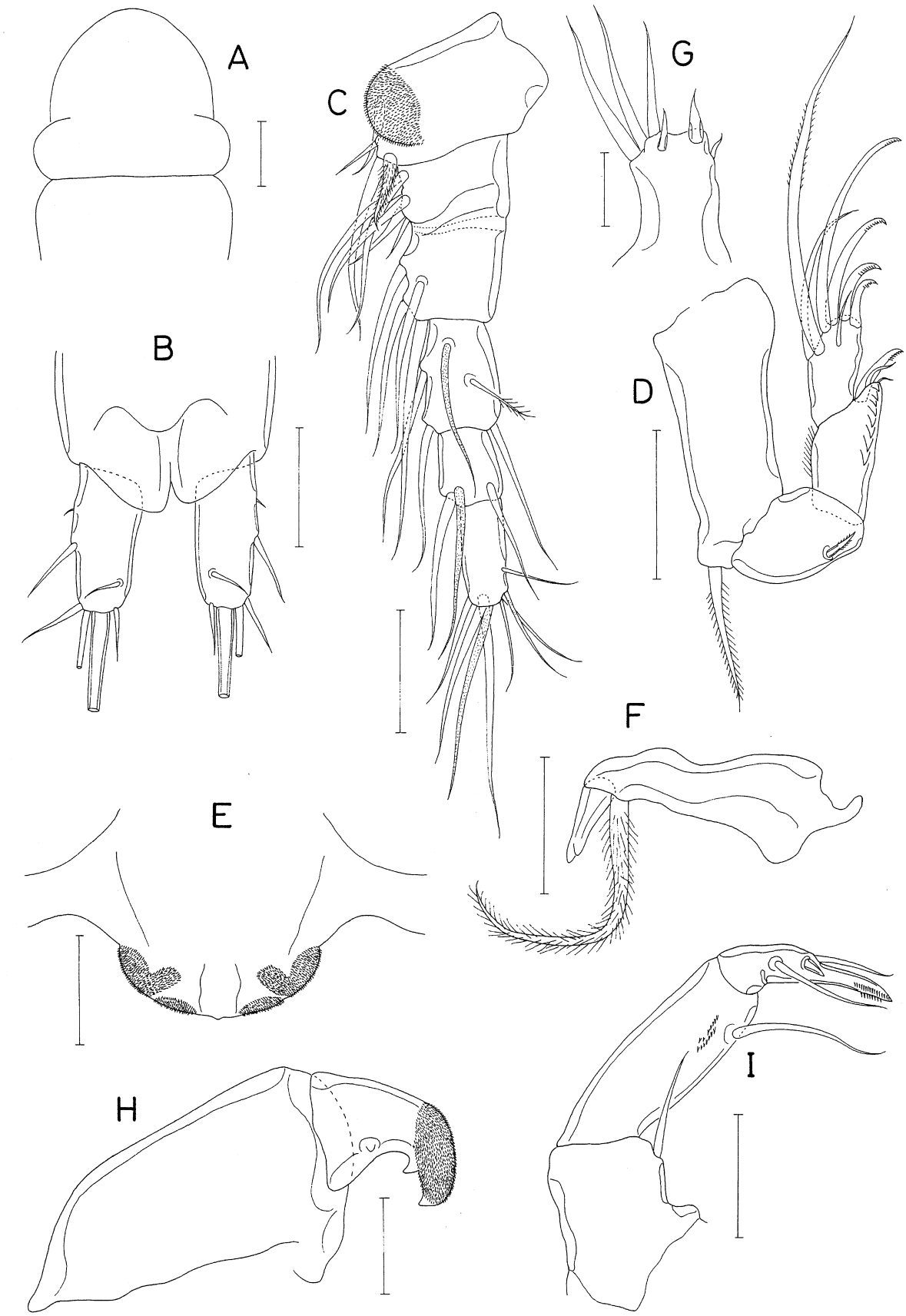

FIGURE 13. *Rhodinicola similis* **n. sp.**, female. A, cephalothorax, dorsal; B, caudal rami, dorsal; C, antennule, ventral; D, antenna; E, labrum, ventral; F, mandible; G, maxillule; H, maxilla; I, maxilliped. Scale bars: A, 0.2 mm; B, 0.1 mm; C–F, H, I, 0.05 mm; G, 0.02 mm.

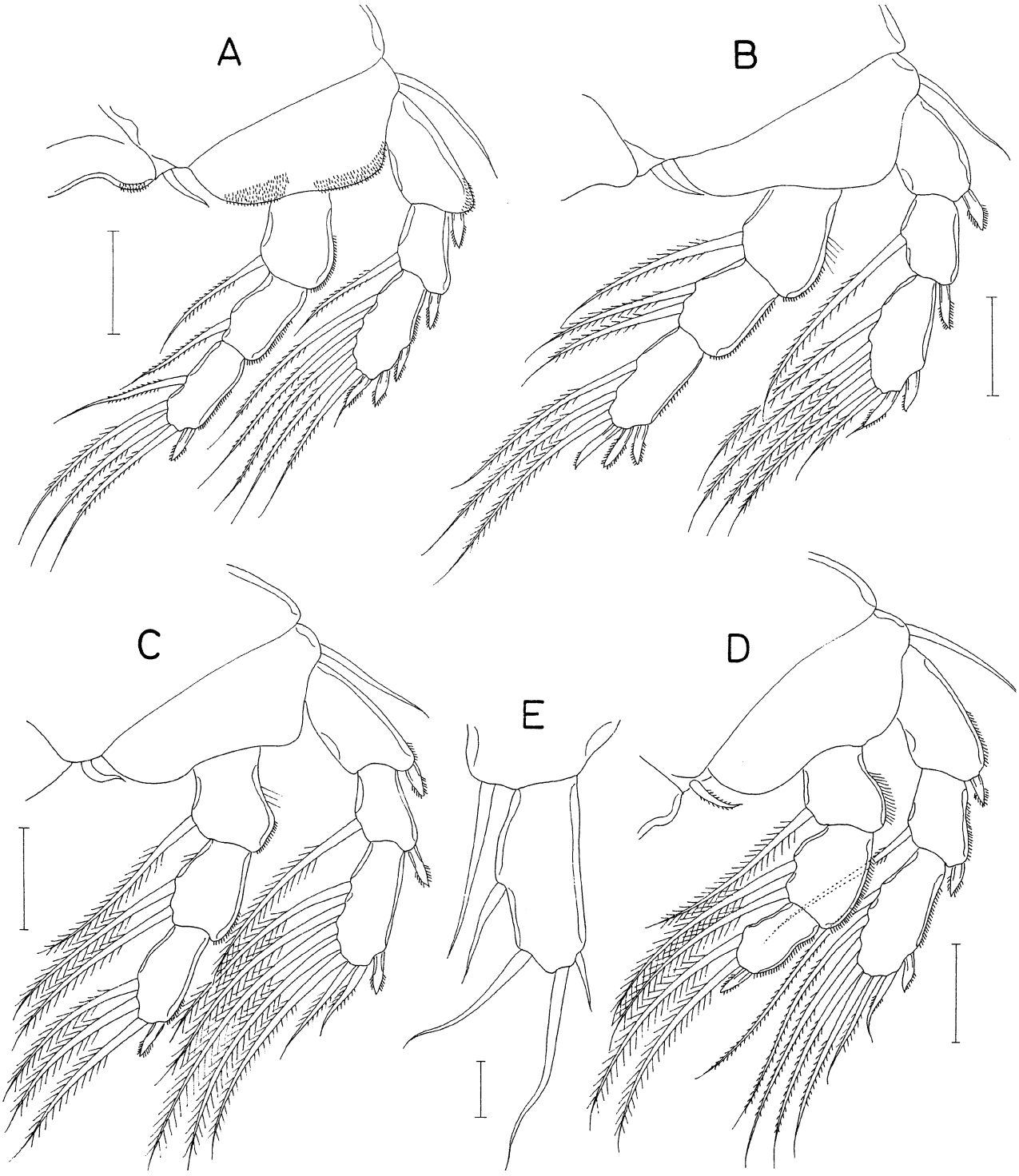

FIGURE 14. *Rhodinicola similis* **n. sp.**, female. A, leg 1; B, leg 2; C, leg 3; D, leg 4; E, leg 5. Scale bars: A–D, 0.05 mm; E, 0.02 mm.

Female. Body similar to that of preceding species in shape and size; slender, elongate and composed of cephalothorax, unsegmented trunk and 4-segmented abdomen. Cephalothorax (Fig. 13A) 508 μm long, consisting of narrower cephalic region (538 μm wide) and laterally expanded thoracic trunk region (608 μm wide). Abdomen clearly 4-segmented, without ornamentation on ventral surface. Caudal rami directed posteriorly (Fig. 13B); each ramus 119×56 μm (ratio 2.13:1), with 7 setae, including small outer proximal seta (seta I); outer lateral seta (seta II) positioned in middle of outer margin. Egg sac 1.10×0.29 mm; containing of 3 rows of eggs; each egg about 190 μm in diameter.

Rostrum absent. Antennule (Fig. 13C) 242 μm long and 6-segmented, with indistinct suture line between second and third segments; armature formula 4, 5, 4, 3+aesthetasc, 2+aesthetasc, and 7+aesthetasc; first segment with large anteroventral patch of spinules; distalmost of 4 setae on first segment plumose; aesthetascs on 3 distal segments distally pointed, setiform. Antenna (Fig. 13D) 4-segmented; first segment with 1 distal pinnate seta; second segment with 1 small subdistal seta; third segment with 1 claw and 2 small setae distally and ornamented with longitudinal row of 8 foliaceous scales; terminal segment about twice as long as wide, bearing 4 setiform claws and 3 setae of different lengths, longest seta spinulate.

Labrum (Fig. 13E) with roundly convex posterior margin and ornamented with patches of minute spinules. Mandible (Fig. 13F) terminating in 1 distal cusp bearing bifurcate or trifurcate apex and carrying 1 large plumose seta subdistally. Maxillule (Fig. 13G) with 1 minute lateral and 5 (3 large and 2 small) distal setae. Maxilla (Fig. 13H) 2-segmented; proximal segment unarmed; distal segment with slightly recurved and pointed apex, armed with 1 small tubercle-like seta and 1 dentiform process on concave margin and spinulose pad on slightly curved distal margin. Maxilliped (Fig. 13I) 3-segmented; first segment with 1 distal seta on medial margin; second segment with 1 seta in distal quarter of medial margin and 1 small patch of spinules near base of seta; third segment tapering into spiniform distal process with 2 setae and 1 small spine; 2 setae on third segment extending to tip of distal process.

Legs 1–4 (Fig. 14A–D) biramous with 3-segmented rami; basis of leg 1 ornamented with patches of spinules. Inner setae on coxae of legs 1–3 small and naked, inner seta on leg 4 pinnate; outer setae on basis large and naked. Armature formula of legs 1–4 as follows:

Leg 1: coxa 0-1; basis 1-0; exp. I-0; I-1; II, I, 5; enp. 0-1; 0-1; I,4
Leg 2: coxa 0-1; basis 1-0; exp. I-0; I-1; I, I, 5; enp. 0-1; 0-2; I, II, 3
Leg 3: coxa 0-1; basis 1-0; exp. I-0; I-1; I, 7; enp. 0-1; 0-2; I, 3
Leg 4: coxa 0-1; basis 1-0; exp. I-0; I-1; I, 7; enp. 0-1; 0-2; I, 2

Leg 5 (Fig. 14E) 2-segmented; proximal segment fused with somite, with 1 outer seta; free distal segment (exopod) 69×30 μm (ratio 2.30:1), with 1 outer and 3 distal setae, innermost smallest. Leg 6 not seen.

Male. Body (Fig. 15A) narrow with clear articulations between somites. Body length 1.37 mm. Prosome 4-segmented, consisting of cephalothorax and 3-segmented metasome. Cephalothorax 423×369 μm. Second to fourth pedigerous somites 119×365, 104×335, and 92×273 μm, respectively. Urosome 6-segmented. Fifth pedigerous somite 73×227 μm. Genital somite 135×242 μm, much wider than long. Abdomen 4-segmented, 115×192, 96×177, 77×154, and 92×123 μm, respectively, from anterior to posterior. Caudal ramus 71×37 μm (ratio 1.92:1), with 6 setae.

Rostrum (Fig. 15B) present as weak anterior protuberance of cephalothorax. Antennule (Fig. 15C) 171 μm long and 6-segmented, with armature formula 5, 7, 7, 4+aesthetasc, 2+aesthetasc, and 7+aesthetasc; aesthetascs on 3 distal segments enlarged, with pointed tip. Antenna (Fig. 15D) similar to that of female, but third segment with row of 10 foliaceous scales, one seta on this segment transformed to spinule-bearing foliaceous element.

Labrum, mandible and maxillule as in female. Maxilla (Fig. 15E) also as in female, but proximal seta on concave margin of distal segment more distinct than that of female. Maxilliped (Fig. 15F) 4-segmented; first segment with 1 seta on medial margin; second segment with serrated protuberance and 1 seta in middle of medial margin; small third segment unarmed; terminal segment forming large claw bearing tapering tip, and bearing 1 minute seta proximally plus 2 large naked setae.

Legs 1–4 (Fig. 16A–D) biramous with 3-segmented rami, but segmentation incomplete between second and third endopodal segments of leg 1. Inner seta on coxa of legs 1–4 well-developed and pinnate. Armature formula as follows:

Leg 1: coxa 0-1; basis 1-0; exp. I-0; I-1; II, I, 5; enp. 0-1; 0-1; I,4
Leg 2: coxa 0-1; basis 1-0; exp. I-0; I-1; III, I, 5; enp. 0-1; 0-2; I, II, 3
Leg 3: coxa 0-1; basis 1-0; exp. I-0; I-1; I+1, I, 5; enp. 0-1; 0-2; I, 3
Leg 4: coxa 0-1; basis 1-0; exp. I-0; I-1; II, I, 5; enp. 0-1; 0-2; 2

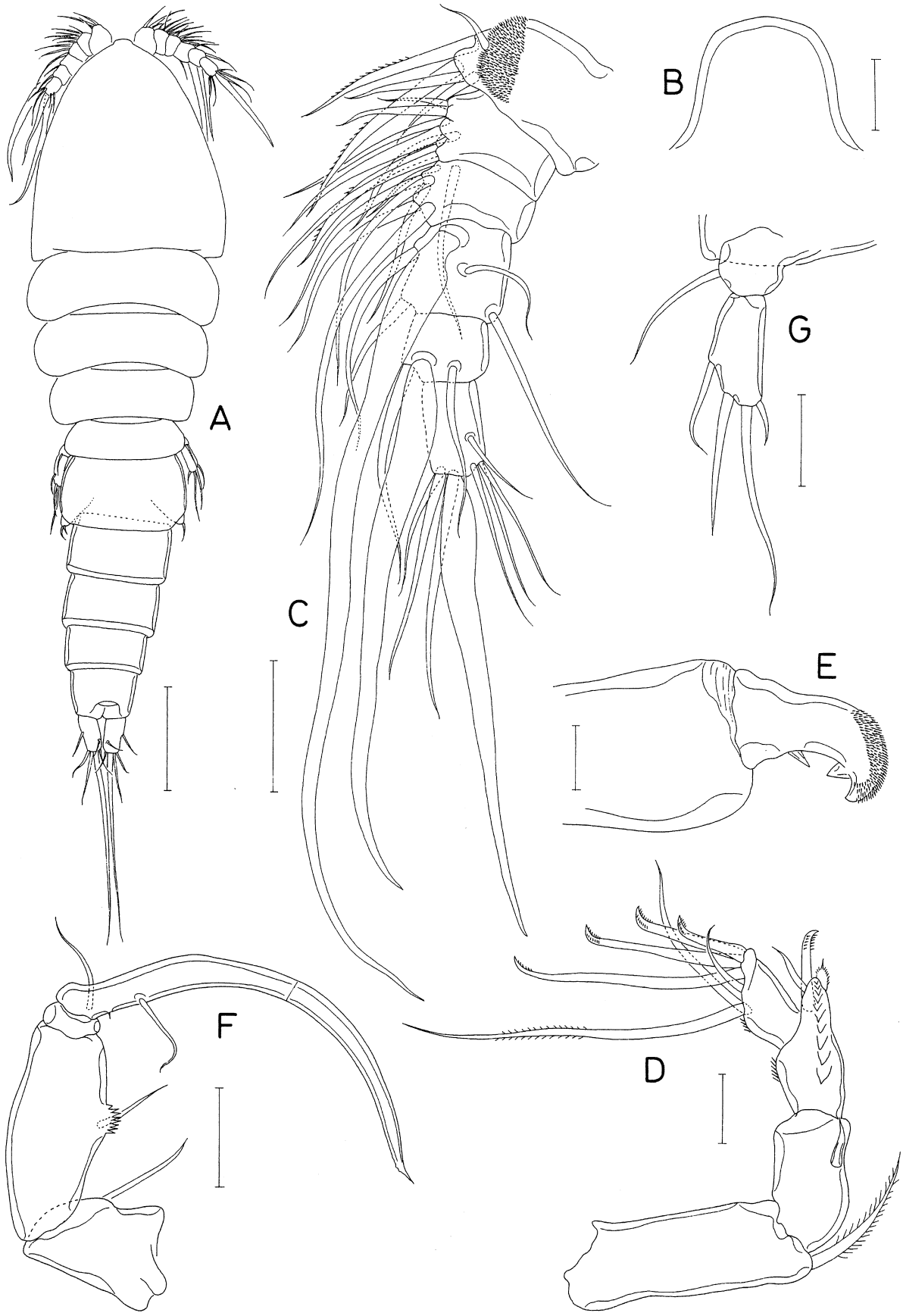

FIGURE 15. *Rhodinicola similis* **n. sp.**, male. A, habitus, dorsal; B, rostrum, dorsal; C, antennule, ventral; D, antenna; E, maxilla; F, maxilliped; G, leg 5. Scale bars: A, 0.2 mm; B, D, E, 0.02 mm; C, F, G, 0.05 mm.

Leg 5 (Fig. 15G) 2-segmented; proximal segment incompletely demarcated from somite; distal segment 60×28 μm (ratio 2.14:1), carrying 4 naked setae. Leg 6 (Fig. 16E, F) represented by 2 or 1 (abnormal?) setae on posterior corner of genital operculum.

Etymology. The specific name alludes to the close similarity between the new species and *R. tenuis* **n. sp.** described above.

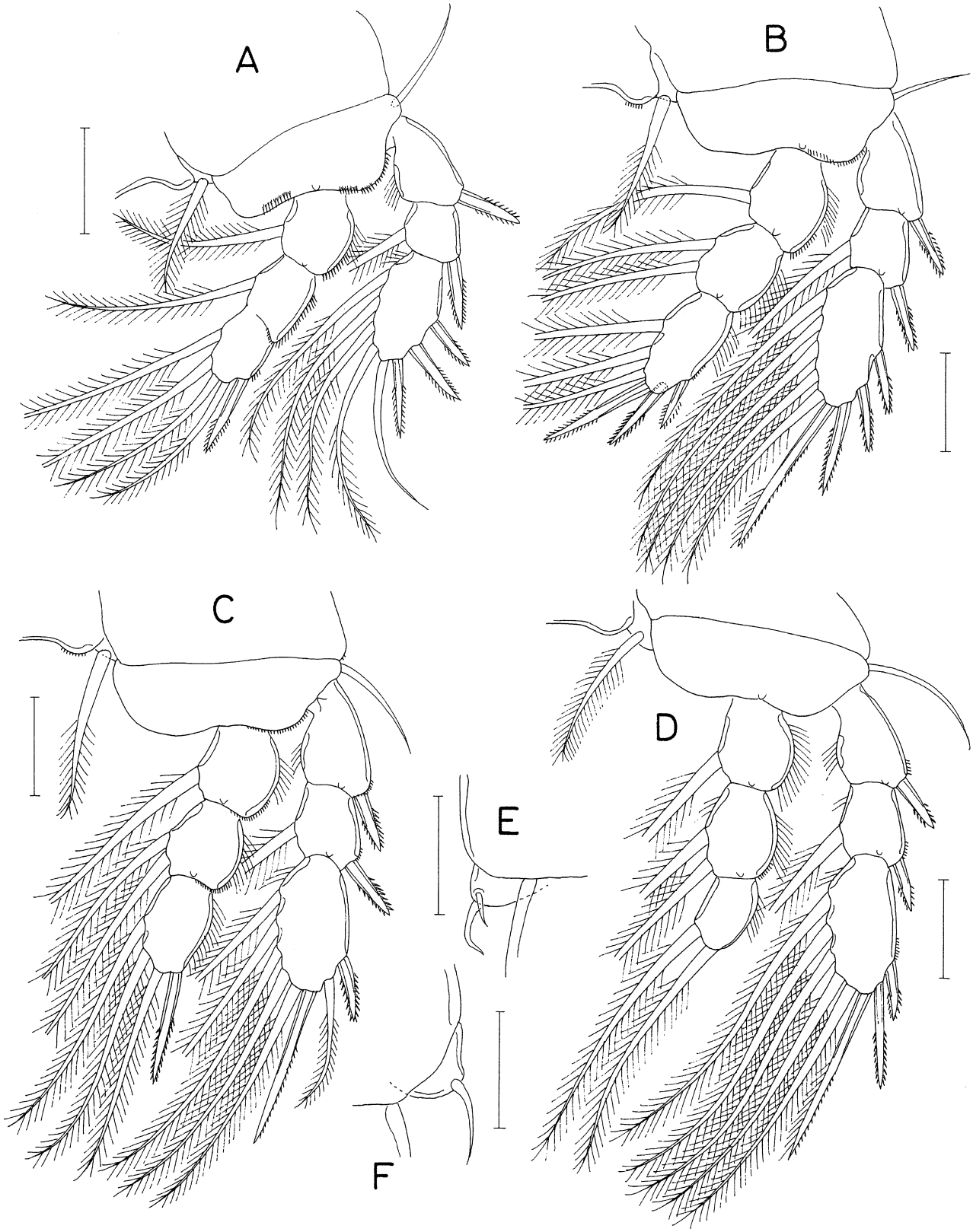

FIGURE 16. *Rhodinicola similis* **n. sp.**, male. A, leg 1; B, leg 2; C, leg 3; D, leg 4; E, F, leg 6, dorsal. All scale bars: 0.05 mm.

Remarks. The male is identified as conspecific with the holotype female on the basis of the following evidence: 1) the labrum, mandible and maxillule are the same in both sexes; 2) both have the unusual number of seven setation elements, rather than six, on the terminal segment of the antenna; 3) both have similar ornamentation on the claws (spinulate distally) on the distal segments of the antenna; 4) both have similar proportional lengths of the setae on the exopod of leg 5; and 5) the aesthetascs on the three distal segments of the antennules taper to a pointed tip.

Rhodinicola similis **n. sp.** most closely resembles *R. tenuis* **n. sp.** in sharing the similar shape of the cephalothorax, labrum, maxilla and maxilliped, the completely 3-segmented legs 1–4 with well-developed setae, and in having caudal rami of similar size and shape. However, they differ in numerous details including: 1) the antennule of *R. similis* **n. sp.** has a patch of minute spinules on the first segment which is absent in *R. tenuis* **n. sp.**; 2) the second and third segments of the antennule of *R. similis* **n. sp.** have 5 and 4 setae, respectively, in the female compared to 9 and 5 setae, respectively, in *R. tenuis* **n. sp.**; 3) the spiniform distal element of the mandible of *R. similis* **n. sp.** is articulated at the base whereas it is not articulated in *R. tenuis* **n. sp.**; 4) the maxillule of *R. similis* **n. sp.** is armed with 6 setae compared to 5 setae in *R. tenuis* **n. sp.**); 5) the third endopodal segment of female leg 1 of *R. similis* **n sp.** is armed with 1 spine and 4 setae (formula I, 4) instead of 2 spines and 3 setae (formula I, I, 3) as in *R. tenuis* **n. sp.**; 6) the armature formula of the third exopodal segment of leg 2 of *R. similis* **n. sp.** is III I, 5 (9 in total), instead of II, II, 4 (or II, I, 5) (8 in total), as in *R. tenuis* **n. sp.**; and 7) the exopod of leg 5 of *R. similis* **n. sp.** is armed with 4 setae compared to only 3 setae in *R. tenuis* **n. sp.**

Boreoclausia n. gen.

Diagnosis. Body elongate, dorso-ventrally flattened, with well-defined pedigerous somites but lacking defined prosome-urosome division. Free abdomen 1-segmented. Caudal ramus with 6 setae. Antennule 5- to 7-segmented, with expanded first segment. Antenna 4-segmented, with spinulose spine on each of third and fourth segments. Mandible with 1 distal spiniform blade fused to segment or articulated at base. Maxillule lobate, with few distal setae. Maxilla 2-segmented; distal segment stout, with spinulose pad. Maxilliped 4-segmented, with spinulose pad distally on terminal segment. Legs 1–3 each with 2-segmented exopod, endopod lacking or small and lobate; setation of exopods much reduced. Leg 4 represented by papilla or lobe bearing few setae. Leg 5 absent or represented by setose papilla.

Type species: *Boreoclausia recta* **n. gen. et n. sp.**, by original designation.

Etymology. The generic name *Boreoclausia* refers to the “boreal” distribution of the host of the type species. The ending of the genus, -*clausia*, is the name of the type genus of the Clausiidae. Gender feminine.

Remarks. In order to confirm the placement of the new genus in a family, we considered the families Nereicolidae, Serpulidicolidae and Clausiidae, all of which contain polychaete-associated copepods having a moderately transformed, or reduced body form and appendages. The genera of the Nereicolidae have in common a body consisting of the cephalosome, an inflated and unsegmented metasome, and 1- or 2-segmented urosome. This body configuration is not shared with the new genus which retains well defined pedigerous somites.

When establishing the Serpulidicolidae, Stock (1979) highlighted that legs 1–4 of the female are positioned lateroventrally rather than mid-ventrally, that leg 5 of the female is enlarged, and that the number of free abdominal somites of the female is reduced to one or two. Although the new genus has only one abdominal somite, it does not share the first two traits. Legs 1–4 of *Boreoclausia* are located ventrally and thus not visible in a dorsal view of the body and its leg 5 is markedly reduced.

The Clausiidae includes a heterogeneous mix of genera exhibiting a broad range of modifications and appendage reductions, depending on genus. The characteristics of *Boreoclausia* are the elongate, linear body, with the well-articulated pedigerous somites, the possession of one free spiniform distal element on the mandible, and the rather well-developed, functional antennae, which are shared with genera of the Clausiidae. We tentatively place *Boreoclausia* in the Clausiidae, although the presence of the greatly reduced leg 5 of the new genus, an unusual feature for the Clausiidae, suggests that this placement should be revisited within the context of a large scale phylogenetic analysis of this cluster of families.

Currently, generic classification in the Clausiidae is mainly based on leg morphology. Within this family, *Boreoclausia* is similar to four other genera, *Clausia*, *Indoclausia* Sebastian and Pillai, 1974, *Pseudoclausia*

Bocquet and Stock, 1960, and *Spionicola*, because they lack leg 4 or have a vestigial leg 4 reduced to a setiferous lobe. However, in all four of these genera both rami of legs 1 and 2 are at least 2-segmented, and none of them exhibits a strongly reduced, lobate endopod, as found in *Boreoclausia*. Leg 3 of *Boreoclausia* is similar to legs 1 and 2 in having a 2-segmented exopod and a lobate endopod. In contrast, leg 3 of the other four genera is reduced to a lobe bearing 1 or 2 setae (in *Clausia*, *Indoclausia* and *Spionicola*) or to a uniramous state consisting of a one-segmented exopod without an endopod (in *Pseudoclausia*). In addition, the mandible of *Boreoclausia* has only 1 distal element, whereas the above four genera have two elements.

Most striking is the reduction of leg 5 in *Boreoclausia* to a pair of setae, which is extremely unusual for the Clausiidae. Sebastian and Pillai (1974) recorded a similar form of leg 5 in their genus *Stockia* which was later removed by Boxshall and Halsey (2004) from the Clausiidae due to its lichomolgoid form of maxilla. We propose to establish *Boreoclausia* as a new genus in order to accommodate two new species.

The reduction of the endopods of the legs and the possession of a 1-segmented abdomen of *Boreoclausia* is reminiscent of the Serpulidicolidae, and the anterodistal process of the first antennular segment resembles that of the Spiophanicolidae (see below). However, these families differ from *Boreoclausia* in many other characteristics.

Boreoclausia recta n. gen. et n. sp.

Type material: Holotype ♀ (dissected and mounted on a glass slide) from *Galathowenia fragilis*: 61.02ºN, 03.4643ºE, Troll C 2004, Stn 99r-1, depth 350 m, 04 June 2004; BMNH Reg. No. 2012.1386.

Female. Body (Fig. 17A) elongate, dorsoventrally depressed, with parallel lateral margins, and consisting of cephalosome, first to fifth pedigerous somites, genital complex and 1-segmented abdomen. Prosome-urosome division not marked. Cephalosome 395×275 μm, with anteriorly produced rostral area. First pedigerous somite shortest of all pedigerous somites. Second to fifth pedigerous somites with rudimentary tergite near posterodorsal border of each somite. Fourth and fifth pedigerous somites longer than anterior pedigerous somites, each incompletely subdivided into anterior and posterior halves by lateral constriction. Anterior hoop-like part of genital complex partially separated as short pseudosomite (Fig. 17A, B). Genital complex 197×245 μm, parallel-sided but narrowing in posterior quarter; genital apertures located dorsolaterally just posterior to midlength. Single-segmented abdomen 140×134 μm, with deep posteromedian incision. Caudal ramus 90×40 μm (ratio 2.25:1), with 6 setae and convex medial margin; longest terminal seta 80 μm long, shorter than caudal ramus.

Rostrum as anterior prominence of cephalosome. Antennule (Fig. 17C) 7-segmented, with armature formula 1+spine, 8, 4+spine, 1+aesthetasc, 2, 2+aesthetasc, and 7+aesthetasc; first segment strongly expanded anterodistally; spines on first and third segments robust. Antenna (Fig. 17D) 4-segmented; first segment unarmed; second segment also unarmed but with row of spinules on medial margin; third segment with 1 thick, spinulose spine, 1 seta, and spinules on medial margin; terminal segment 28×17 μm, with 1 thick, spinulose spine, 3 spinule-tipped setae, and 1 simple seta.

Labrum (Fig. 17E) with straight posterior margin ornamented with patch of spinules laterally, and several patches of minute spinules in posterior half of ventral surface. Mandible (Fig. 17F) tapering distally, with 1 blade-like apical element, articulated at base. Maxillule (Fig. 17G) lobate, with 1 inner and 2 outer setae distally. Maxilla (Fig. 17H) 2-segmented; proximal segment unarmed; distal segment blunt, with 1 proximal seta; distal half ornamented with spinules. Maxilliped (Fig. 17I) 4-segmented; first segment broad and unarmed; second segment longest, with 1 seta; short third segment unarmed; fourth segment with 1 small lateral seta and blunt apex bearing spinulose pad.

Legs 1–3 (Figs 17J, 18A, B) with 2-segmented exopod and small, lobate endopod, that of leg 1 spinulose, others naked. Leg 4 (Fig. 18C) a papilla tipped by 3 setae. Outer spines on exopod of legs 1–3 massive and spinulose. Outer margin of first exopodal segment of legs 1–3 ornamented with spinules. Armature formula of legs 1–3 as follows:

Leg 1: coxa 0-0; basis 1-0; exp. I-0; II, 1, 1; enp. (lobe)
Leg 2: coxa 0-0; basis 1-0; exp. I-0; I, I, 0; enp. (lobe)
Leg 3: coxa 0-0; basis 1-0; exp. 0-0; I, 1, 0; enp. (lobe)

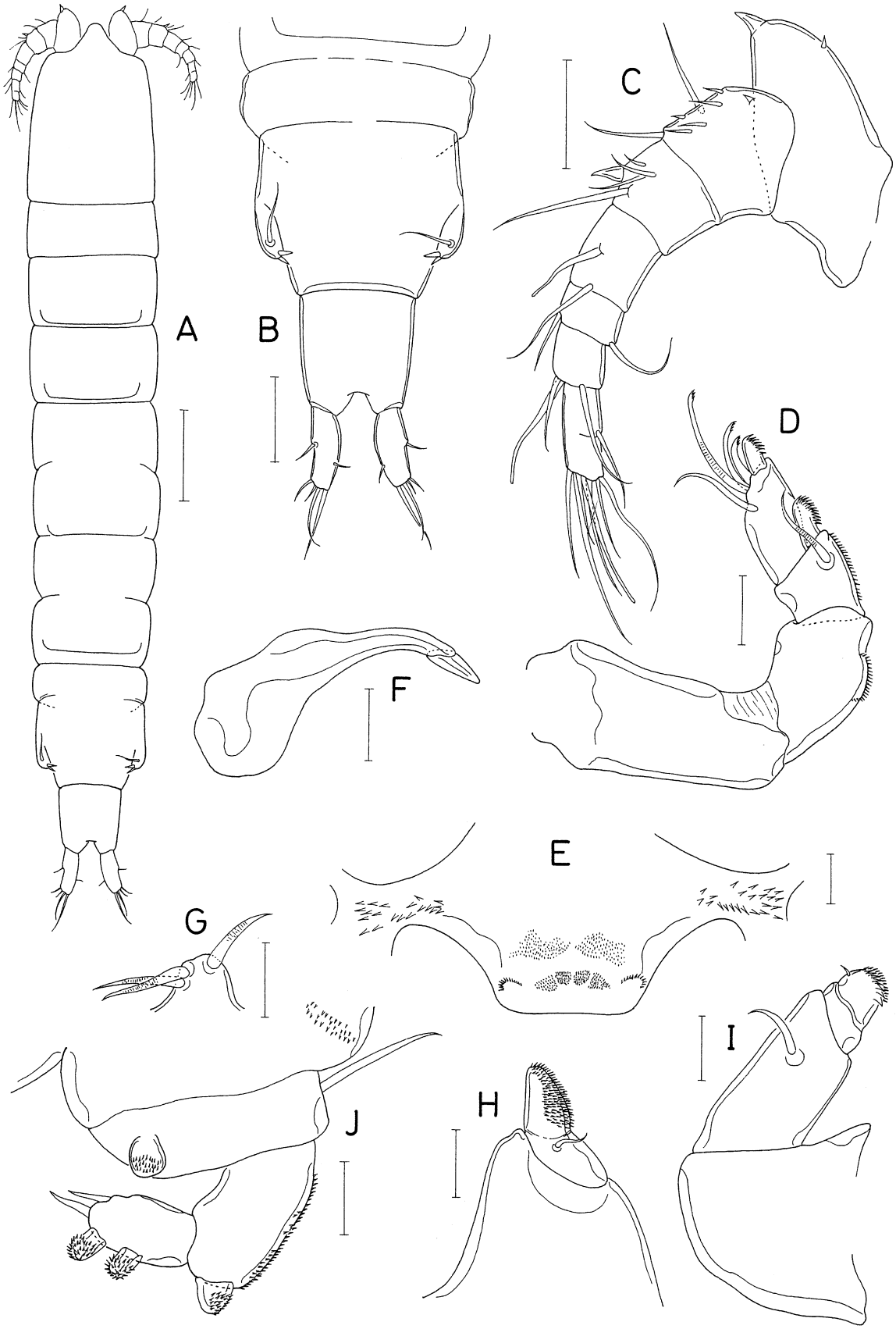

FIGURE 17. *Boreoclausia recta* **n. gen. et n. sp.**, female. A, habitus, dorsal; B, urosome, dorsal; C, antennule; D, antenna; E, labrum; F, mandible; G, maxillule; H, maxilla; I, maxilliped; J, leg 1. Scale bars: A, 0.2 mm; B, 0.1 mm; C, 0.05 mm; D–J, 0.02 mm.

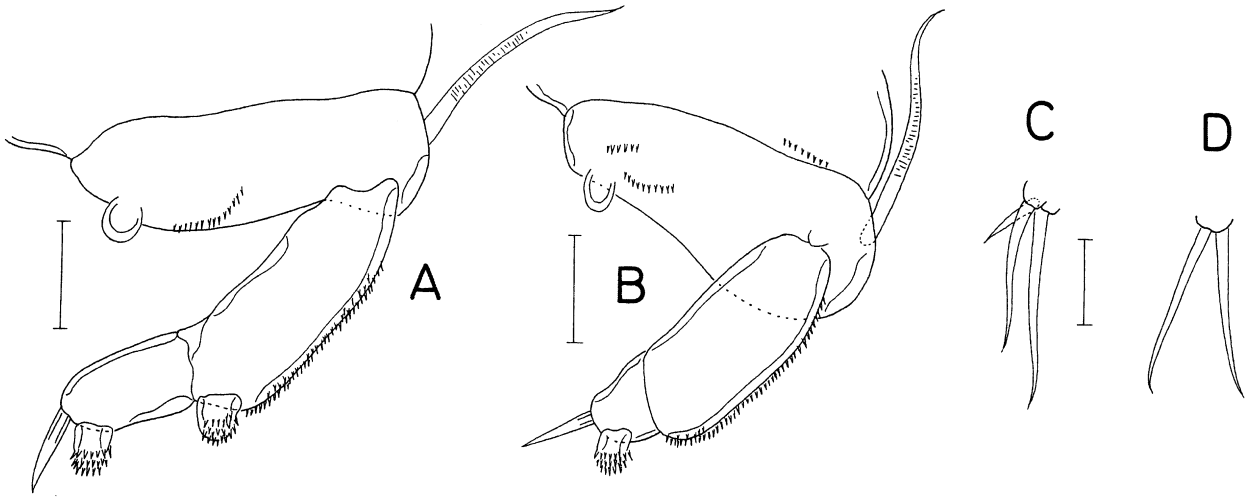

FIGURE 18. *Boreoclausia recta* **n. gen. et n. sp.**, female. A, leg 2; B, leg 3; C, leg 4; D, leg 5. All scale bars: 0.02 mm.

Leg 5 (Fig. 18D) as small papilla tipped by 2 naked setae. Leg 6 represented by 1 seta and 2 spinules in genital area (Fig. 17B).

Male. Unknown.

Etymology. The specific name is derived from the Latin *rectus* meaning "straight" and alludes to the straight body, with parallel lateral margins.

Remarks. The distal blade on the mandible is articulated at its base with the segment in this species.

Boreoclausia holmesi n. gen. et n. sp.

Type material: 3 ♀♀ (intact holotype and 1 paratype and 1 dissected paratype) from *Myriochele danielsseni*; Loch Hourn, Scotland; collected by P. Garwood, 11 May 2005. BMNH Reg. No. 2012.1387 (Holotype) and BMNH Reg. No. 2012.1388 (Paratype).

Paratype ♀ from *Myriochele/Galathowenia* fragment; Sample C2B**,** Selivoe, Shetland [either inner site, 60°12.567'N, 01°23.909'W, depth 11 m, or outer site 60°11.752'N, 01°24.061'W, depth 8–21 m], collected by P. Garwood, July 2000; BMNH Reg. No. 2012.1389.

Paratype ♀ from unknown host; East Shetland basin (61°27.79'N, 01°17.82'E), depth 178 m; collected by P. Garwood, 26 July 2007; BMNH Reg. No. 2012.1390.

Female (dissected paratype). Body (Fig. 19A) elongate, dorsoventrally depressed, with parallel lateral margins, and consisting of cephalosome, first to fifth pedigerous somites, genital complex and 1-segmented abdomen. Body length 1.41 mm. Prosome-urosome division not marked. Cephalosome 308×260 μm, with anteriorly produced rostral area. Lengths of first to fifth pedigerous somites 104, 81, 185, 200, and 196 μm, respectively. Second to fourth pedigerous somites each with rudimentary tergite along posterodorsal border of somite; each tergites ornamented with transverse row of fine spinules near posterior margin. Anterior hoop-like part of genital complex partially separated as short (77 μm long) pseudosomite (Fig. 19A). Genital complex 123×185 μm, parallel-sided but narrowing in posterior third; genital apertures located dorsolaterally at midlength (Fig. 19B). Single-segmented abdomen 81×69 μm, with parallel lateral margins. Caudal ramus 60×27 μm (ratio 2.22:1), with 6 setae; longest terminal seta about 140 μm long, more than twice as long as ramus.

Rostrum as anterior prominence on cephalosome. Antennule (Fig. 19C) 5-segmented but first segment with suture line on dorsal surface; armature formula 12, 2, 2, 2+aesthetasc, and 7+aesthetasc; first segment expanded; setae on first segment usually small. Antenna (Fig. 19D) 4-segmented; first segment unarmed; second segment also unarmed but with patch of spinules on medial surface; third segment with 1 thick, spinulose spine, 1 seta, and 2 patches of spinules; terminal segment 17×14 μm, with 1 thick, spinulose spine and 4 simple setae.

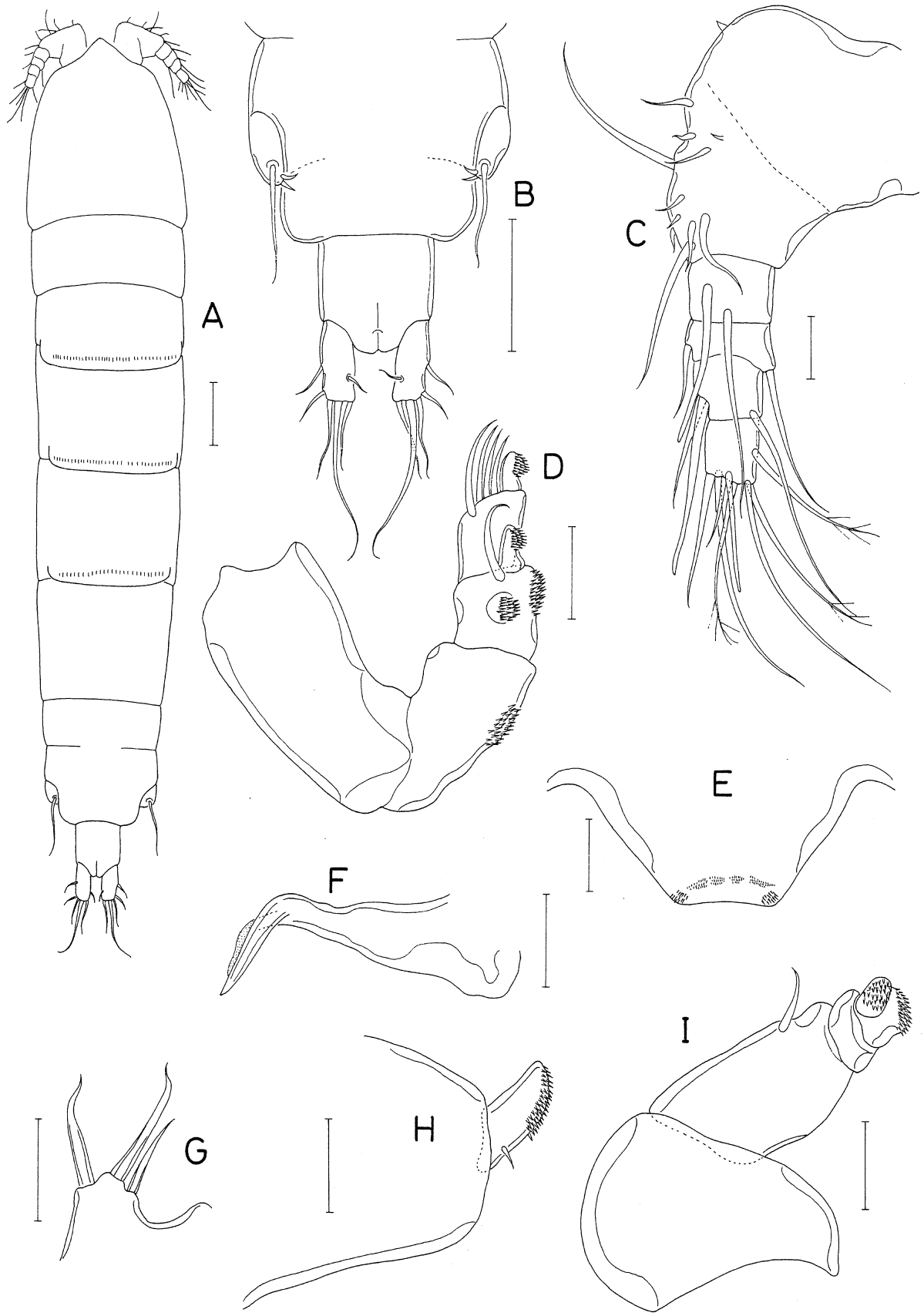

FIGURE 19. *Boreoclausia holmesi* **n. gen. et n. sp.**, female. A, habitus, dorsal; B, genital double-somite and abdomen, dorsal; C, antennule, ventral; D, antenna; E, labrum, ventral; F, mandible; G, maxillule; H, maxilla; I, maxilliped. Scale bars: A, B, 0.1 mm; C–I, 0.02 mm.

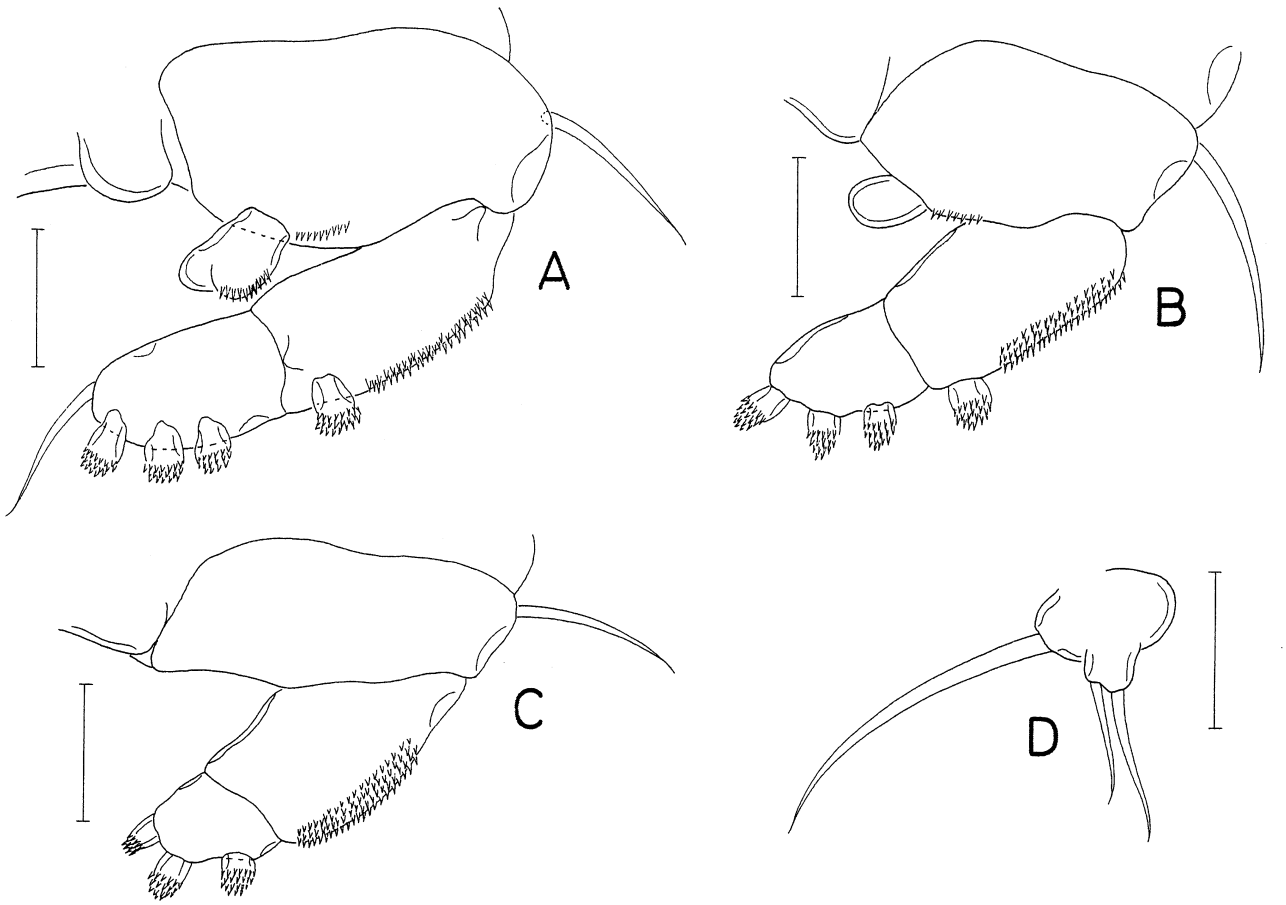

FIGURE 20. *Boreoclausia holmesi* **n. gen. et n. sp.**, female. A, leg 1; B, leg 2; C, leg 3; D, leg 4. All scale bars: 0.02 mm.

Labrum (Fig. 19E) with straight posterior margin and ornamented with several patches of minute spinules posteriorly on ventral surface. Mandible (Fig. 19F) tapering distally, with 1 spiniform apical process; process not articulated at base but with membranous flange along medial (anterior) margin. Maxillule (Fig. 19G) lobate, with 1 inner and 2 outer setae distally. Maxilla (Fig. 19H) 2-segmented; proximal segment unarmed; distal segment blunt, with 1 proximal seta and distal spinulose pad. Maxilliped (Fig. 19I) 4-segmented; first segment broad and unarmed; second segment longest, with 1 naked seta subdistally; short third segment unarmed; fourth segment with 1 stout spinulose lateral spine and blunt apex bearing spinulose pad.

Legs 1 and 2 (Figs 20A, B) with 2-segmented exopod and small, lobate endopod, ornamented with patch of spinules in leg 1, smooth in leg 2. Leg 3 (Fig. 20C) with 2-segmented exopod but lacking endopod. Leg 4 (Fig. 20D) a lobe bearing 1 outer lateral and 0–2 distal setae. Spines on exopod of legs 1–3 massive and spinulose. Outer margin of first exopodal segment of legs 1–3 ornamented with spinules. Armature formula of legs 1–3 as follows:

Leg 1: coxa 0-0; basis 1-0; exp. I-0; II, I, 1; enp. (lobe)
Leg 2: coxa 0-0; basis 1-0; exp. I-0; II, I, 0; enp. (lobe)
Leg 3: coxa 0-0; basis 1-0; exp. 0-0; II, I, 0; enp. (lacking)

Leg 5 absent. Leg 6 represented by 1 seta and 2 spinules in genital area (Fig. 19B).

Male. Unknown.

Etymology. The specific name honours Dr J.M.C. (Mark) Holmes (National Museum of Ireland, Dublin) in recognition of his contributions to the taxonomy of associated copepods. Dr. Holmes sent us sketches some years ago of an undescribed copepod, which appears to be identical to *B. holmesi*, and was found on *Owenia fusiformis* Della Chiaje, 1844 collected near San Sebastian, Spain.

Remarks. *Boreoclausia holmesi* **n. sp.** is placed in the same genus as *B. recta* **n. sp.** as it shares numerous important attributes (see generic diagnosis). *B. holmesi* **n. sp.** can be distinguished from *B. recta* **n. sp.** by the following differences: there are no lateral constrictions on the fourth and fifth pedigerous somites; the fifth pedigerous somite does not have a rudimentary dorsal tergite; the antennule is five-segmented; the distal blade on the mandible is fused rather than articulated at its base as in *B. recta* **n. sp.**; the maxilliped has a massive spine instead of a seta on the terminal segment; the first to third legs have different armature on the distal exopodal segment (3 spines+1 seta in leg 1, and 3 spines in both legs 2 and 3 in contrast to 2 spines+2 setae in leg 1 and 1 spine+1 seta in both legs 2 and 3 in *B. recta* **n. sp.**) and leg 5 is absent.

Sheaderia n. gen.

Diagnosis. Body elongate, dorso-ventrally flattened, comprising cephalothorax, well-defined pedigerous somites 2 to 5, narrower genital double-somite and 1-segmented free abdomen. Caudal ramus with 4 setae. Antennule 5-segmented. Antenna 4-segmented, with 3 claws on third segment and 4 claws on fourth. Mandible with 1 distal blade articulated at base. Maxillule lobate, with 4 distal setae. Maxilla 2-segmented; distal segment stout, with 2 stout setae and spinulose pad. Maxilliped 3-segmented, second segment with 2 inner setae, terminal segment with 1 seta and spinulose pad distally. Legs 1–2 biramous, each with 2-segmented rami densely ornamented with spinules; setation much reduced. Leg 3 represented by lobe bearing 1 apical seta. Leg 4 absent. Leg 5 2-segmented, proximal segment unarmed, distal segment with 3 setae.

Type species: *Sheaderia bifida* **n. gen. et n. sp.** by original designation.

Etymology. The new genus is named in honour of Dr Martin Sheader who first found this parasite in the North Sea and sent it to GAB for study. Gender feminine.

Remarks. On the basis of the absence of leg 4 and the possession of a lobate leg 3, this new copepod appears closely related to the type genus of the family, *Clausia*. The type species *C. lubbockii* was recorded as an associate of an ascidian by Bocquet and Stock (1960) but is reported here to be an associate of polychaetes. *C. lubbockii* exhibits a suite of characters that are relatively plesiomorphic compared to the new genus: it has a 4-segmented abdomen (2-segmented abdomen in the new genus), 6-segmented antennules (5-segmented), 2 spiniform elements on the mandible (1 blade), leg 5 comprising 1 seta-bearing proximal segment (seta absent in the new genus) and 4 setae-bearing distal segment (3 setae), and shorter caudal rami. However the new genus retains a more plesiomorphic condition to the antenna: it has four expressed segments, compared to only three in *Clausia*. The labrum of the new genus is unique in having dorsal and ventral plates; such a structure has never been reported in the Clausiidae. The combination of plesiomorphic, autapomorphic and apomorphic character states is sufficient to justify the establishment of the new genus, although this family and related families are in need of comprehensive revision.

Sheaderia bifida n. gen. et n. sp.

Type material: Holotype ♀ (dissected and mounted on a glass slide) from unknown host; St. Magnus Bay, Shetland (60º 23.44’N, 01º 33.84’W), depth 146 m, collected by S. Hamilton, 04 May 1993; BMNH Reg. No. 2012.1385.

Paratype ♀ (dissected and mounted on a glass slide) from the maldanid *Euclymene oerstedii*, northern North Sea, no other locality data, collected by M. Sheader; BMNH Reg. No. 2012.1392.

Paratype ♀ found loose in sample containing *Clymenura tricirrata* and other maldanid species; central North Sea, Lundin Block 21-8, Stn 6 – F1 (57º40.8664’N, 00º25.0638’E), depth 104 m, April 2007; BMNH Reg. No. 2012.1393.

Female. Body (Fig. 21A) elongate, with well-defined somites. Body length 1.88 mm, excluding caudal setae. Prosome consisting of cephalothorax and second to fifth pedigerous somites. Urosome consisting of genital complex and 2-segmented abdomen (Fig. 21B). Cephalothorax tapering anteriorly and 472×494 µm, with ventrolaterally folded margins to dorsal cephalothoracic shield (Fig. 21D), and rounded frontal margin and posterolateral corners. Second to fifth pedigerous somites well-delimited, with convex lateral margins. Fifth pedigerous somite only slightly narrower than preceding somite and 438 µm wide. Genital complex 157×273 µm,

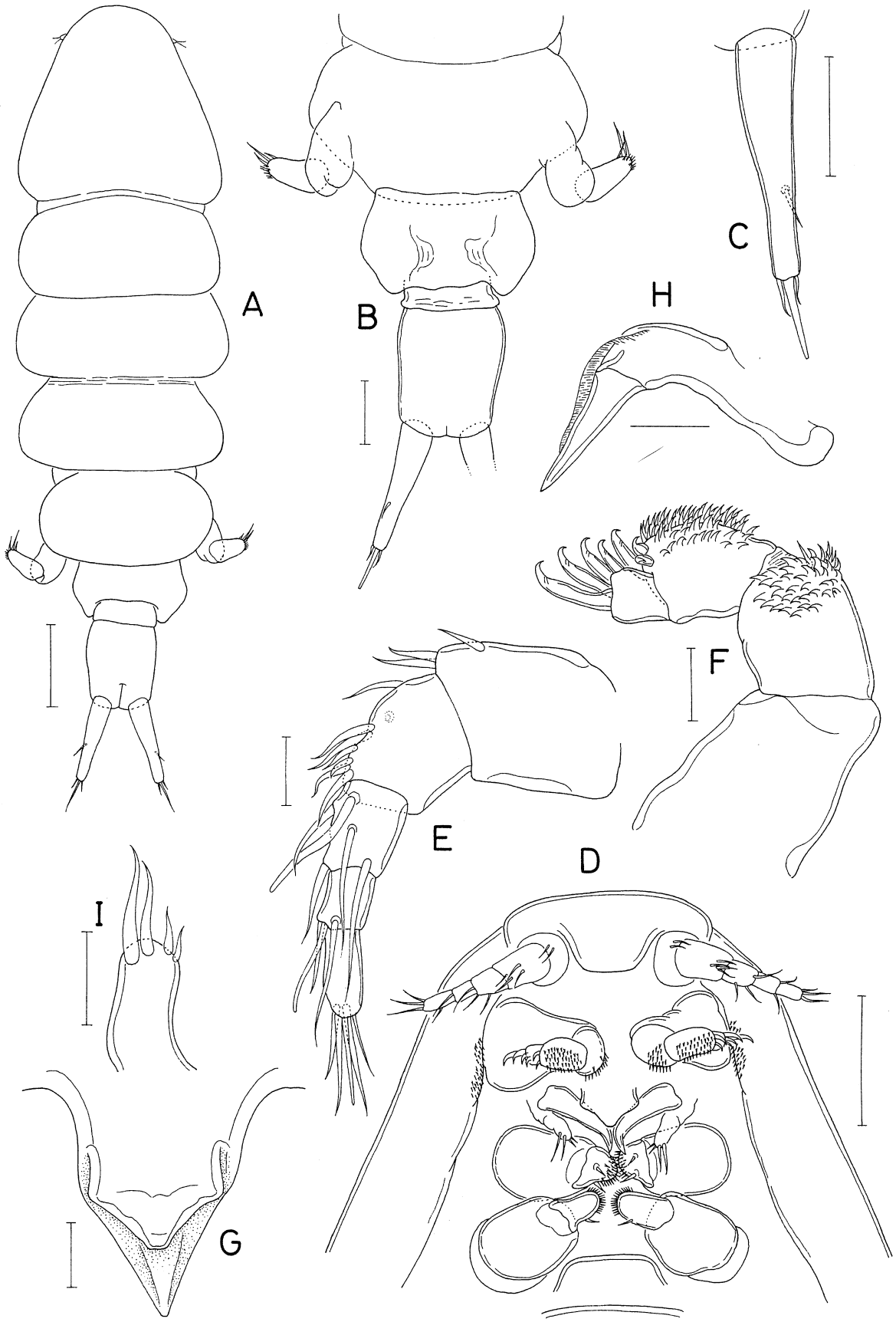

FIGURE 21. *Sheaderia bifida* **n. gen. et n. sp.**, female. A, habitus, dorsal; B, urosome, ventral; C, right caudal ramus, dorsal; D, anterior part of cephalothorax, ventral view showing limbs in situ; E, antennule; F, antenna; G, labrum, ventral; H, mandible; I, maxillule. Scale bars: A, 0.2 mm; B–D, 0.1 mm; E–I, 0.02 mm.

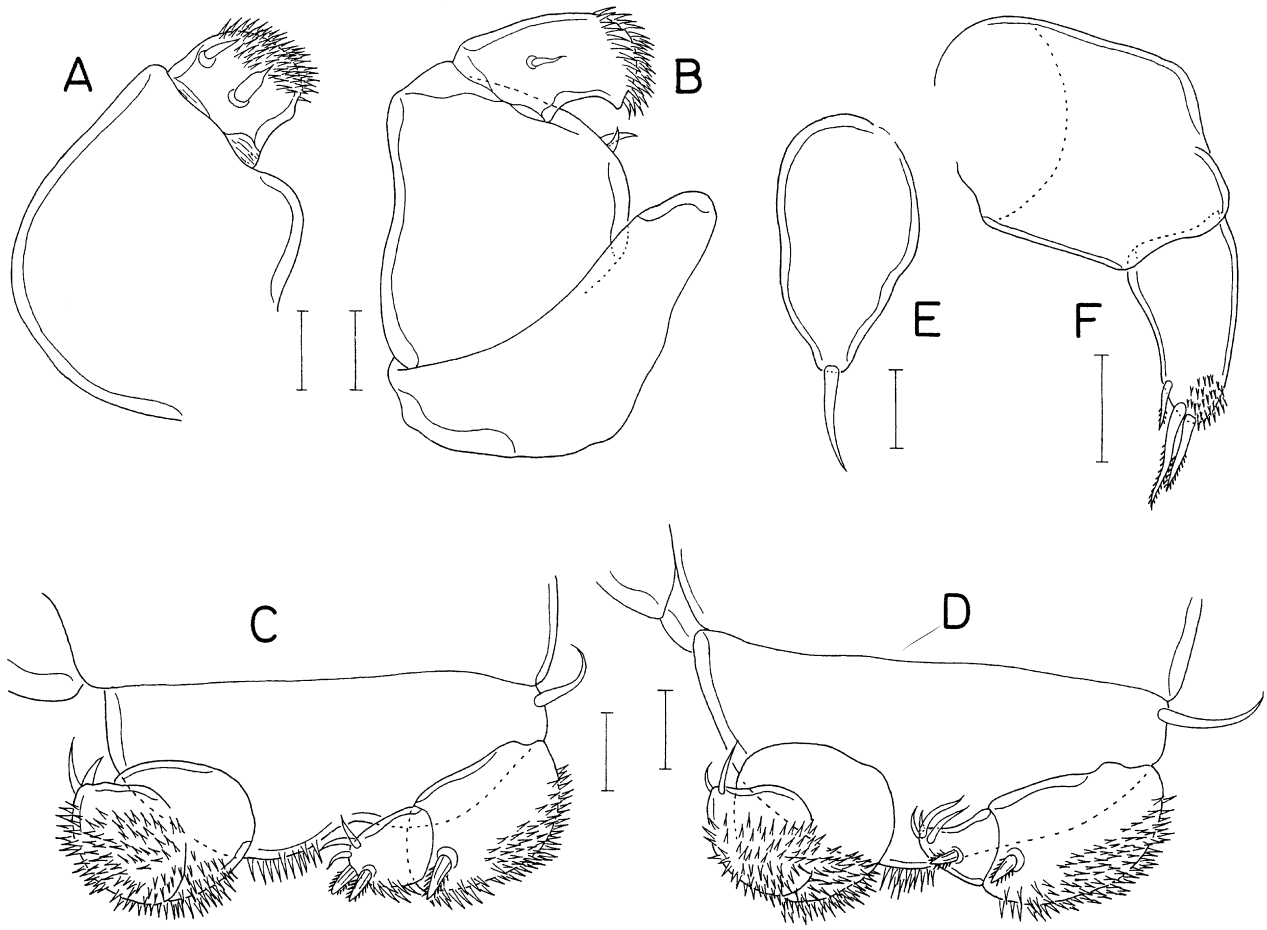

FIGURE 22. *Sheaderia bifida* **n. gen. et n. sp.**, female. A, maxilla; B, maxilliped; C, leg 1; D, leg 2; E, leg 3; F, leg 5. Scale bars: A–E, 0.2 mm; F, 0.05 mm.

with convex lateral margins; genital areas located ventrally but hardly discernible. First abdominal somite very short, about one-fifth as long as anal somite. Anal somite 200×169 μm and unornamented. Caudal ramus (Fig. 21C) slender, tapering and 212×52 μm (ratio 4.08:1), with 1 lateral and 3 distal setae.

Rostrum with truncate posterior margin (Fig. 21D). Antennule (Fig. 21E) small, 5-segmented, gradually narrowing from proximal to distal; armature formula 3, 8, 4+aesthetasc, 2+aesthetasc, and 4+aesthetasc; all setae naked and short. Antenna (Fig. 21F) 4-segmented; first segment smooth and unarmed; second segment with 1 small seta and patch of large spinules mediodistally; third segment with 3 distal claws (two of them small) and ornamented with numerous large spinules on medial surface; terminal segment as long as wide, much smaller than proximal segments and armed with 4 claws.

Labrum (Fig. 21G) comprising small ventral and large dorsal plates; both plates strongly tapering distally. Mandible (Fig. 21H) with 1 large, tapering distal blade articulated at base, with membranous flange along distal part of medial (anterior) margin. Maxillule (Fig. 21I) lobate, distally with 2 small inner and 2 large outer setae. Maxilla (Fig. 22A) 2-segmented; large proximal segment unarmed; stout distal segment wider than long, with 2 thick setae near middle and ornamented with numerous spinules on distal surface. Maxilliped (Fig. 22B) stout and 3-segmented; first segment much wider than long and unarmed; second segment broader than long, with 2 small setae on medial margin; third segment with 1 small lateral seta and dense spinules on distal surface.

Legs 1 and 2 (Fig. 22C, D) with broad coxa and basis, and stocky 2-segmented rami, bearing dense covering of spinules on outer surfaces. Leg 3 (Fig. 22E) lobate and tipped with 1 naked seta. Leg 4 absent. Armature formula of legs 1 and 2 as follows:

Leg 1: coxa 0-0; basis 1-0; exp. I-0; I, I, 3; enp. 0-0; 2
Leg 2: coxa 0-0; basis 1-0; exp. I-0; I, 2, 2; enp. 0-0; 2

Leg 5 (Fig. 22F) 2-segmented; proximal segment large but unarmed; distal segment slightly narrowing distally, 92×53 µm (ratio 1.74:1), with 1 small subdistal and 2 distal setae, and ornamented with distal patch of spinules. Leg 6 not discernible.

Male. Unknown.

Etymology. The specific name *bifida* is derived from the Latin *bifidus*, meaning "split into two parts". It refers to the possession of the double plates of the labrum and the two-segmented abdomen.

Remarks. The undissected paratype female from the central North Sea (BMNH 2012.1393) has a single distal seta on the left leg 3 and two distal setae on the right leg 3. This specimen also has a small papilla-like, unarmed leg 4. However, no other significant difference from the holotype was noted.

Vivgottoia n. gen.

Diagnosis. Body vermiform, elongate, cylindrical, and composed of cephalosome, first to fifth pedigerous somites, genital complex and 1-segmented abdomen. Rostrum shield-like and directed posteroventrally. Antennule 5-segmented, with few setae. Antenna 2-segmented; distal segment perpendicular to proximal segment and inserted on outer margin of proximal segment. Labrum simple, with strongly tapering posterior margin. Mandible with 1 distal blade articulated at base. Maxillule with 2 medial and 2 outer setae. Maxilla 2-segmented; distal segment claw-like. Maxilliped 3-segmented; terminal segment forming strong claw. Legs 1–4 biramous, positioned ventrolaterally and visible in dorsal view of body, lacking intercoxal sclerite, with unsegmented rami; exopod bearing 1 or 2 setae; endopod foliaceous, unarmed. Leg 5 rudimentary, represented by 2 setae.

Etymology. The generic name is in memory of the late Dr. R. V. (Viv) Gotto (Queen's University, Belfast) in recognition of his many contributions to the study of copepods associated with invertebrates.

Type species. *Vivgottoia garwoodi* **n. gen. et n. sp.** by original designation.

Remarks. The elongate vermiform body, the ventrolaterally displaced legs 1–4, and the unsegmented abdomen in the female of *Vivgottoia* **n. gen.** suggest a possible affinity with the Serpulidicolidae. However, the new genus cannot be placed within the Serpulidicolidae because of the vestigial leg 5, the prehensile maxilla, the segmented metasome, and the characteristic form of the antenna and legs 1–4. Unlike the new genus, the genera of the Serpulidicolidae are all ectoparasites of polychaetes.

Like *Vivgottoia* **n. gen.**, copepods of genus *Entobius* Dogiel, 1908, the sole genus of the family Entobiidae Ho, 1984, are endoparasites of polychaetes and have ventrolaterally displaced legs 1–4, a rudimentary leg 5, and a prehensile maxilliped in the female. However, *Vivgottoia* **n. gen.** cannot be assigned to the Entobiidae because the members of this family invariably have elongate rami of legs 1–4 and a simple 3-segmented, antenna, plus they lack a maxilla.

The antenna of *Vivgottoia* **n. gen.** is the most outstanding feature of the genus. The two-segmented condition of this appendage, with the distal segment displaced laterally to the proximal segment, has not been observed in any representative of the nereicoliform families (Nereicolidae, Serpulidicolidae, Entobiidae, Spiophanicolidae, and Clausiidae), all of which comprise copepods living in association with polychaete hosts. The antenna of the new genus probably functions as an attachment organ; the proximal segments of left and right antennae directed towards each other to form pincers (Fig. 23F).

In the Clausiidae, Nereicolidae and Serpulidicolidae the key limbs for securing attachment to the host are the maxillae and/or maxillipeds, at least in females. In these taxa the distal tip of both appendages is blunt and provided with a distinct spinulose pad. In the female of the new genus both the maxillae and maxillipeds terminate in claws, and only the maxilla has a patch of spinules that may represent a vestigial spinulose pad, as found in several families.

The mandible of the new genus terminates in a single blade that articulates with the segment. It closely resembles the mandible of the clausiid genera *Sheaderia* **n. gen.** and *Boreoclausia* **n. gen.** The derived form of this mandible is strongly suggestive of a relationship with the family Clausiidae, but in view of the numerous differences we can only tentatively place *Vivgottoia* **n. gen.** in the Clausiidae.

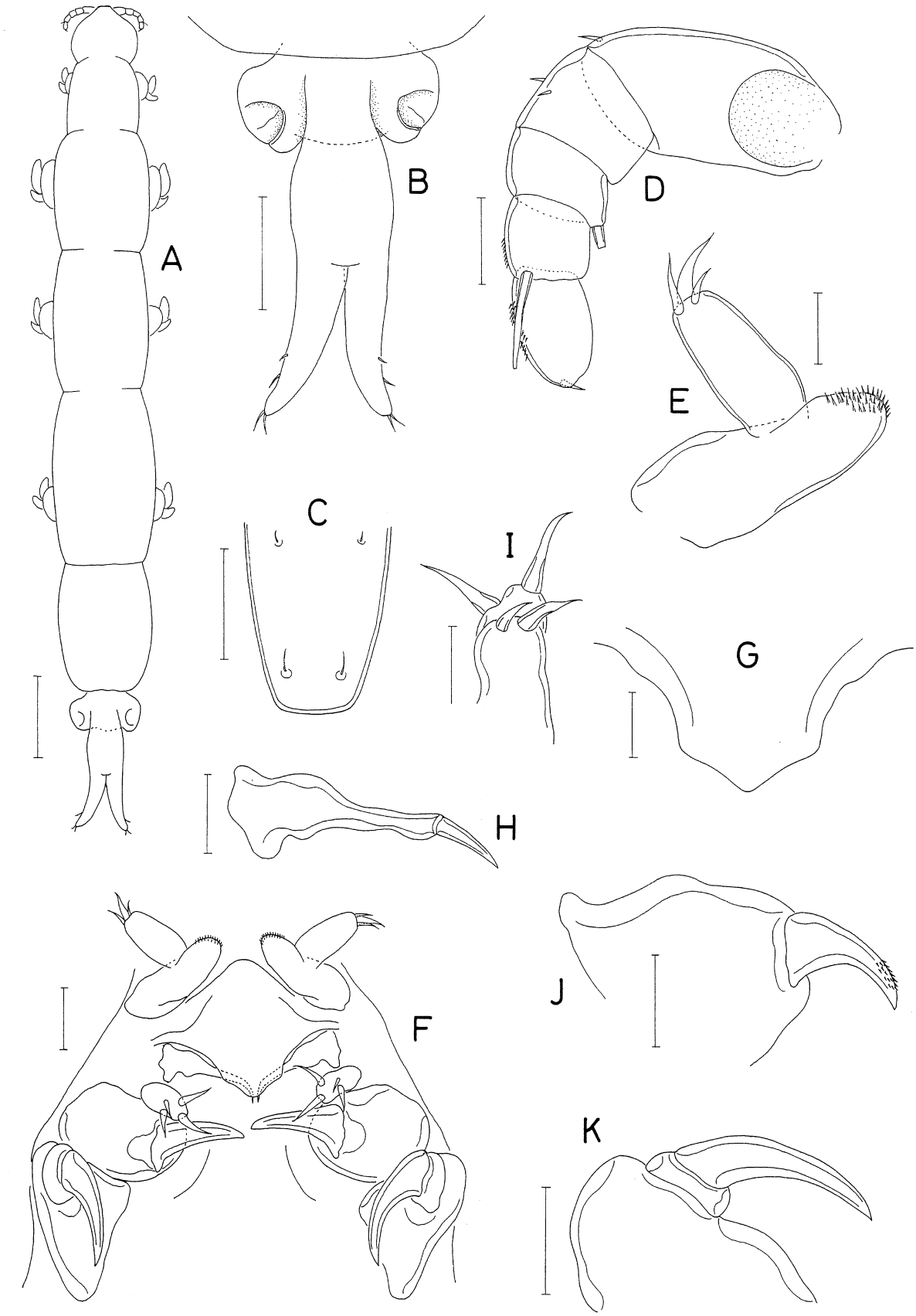

FIGURE 23. *Vivgottoia garwoodi* **n. gen. et n. sp.**, holotype female. A, habitus, dorsal; B, urosome, dorsal; C, rostrum, anteroventral; D, antennule; E, antenna; F, antennae and mouthparts, ventral; G, labrum, ventral; H, mandible; I, maxillule; J, maxilla; K, maxilliped. Scale bars: A, 0.2 mm; B, 0.1 mm; C, D, F, J, K, 0.02 mm; E, G–I, 0.01 mm.

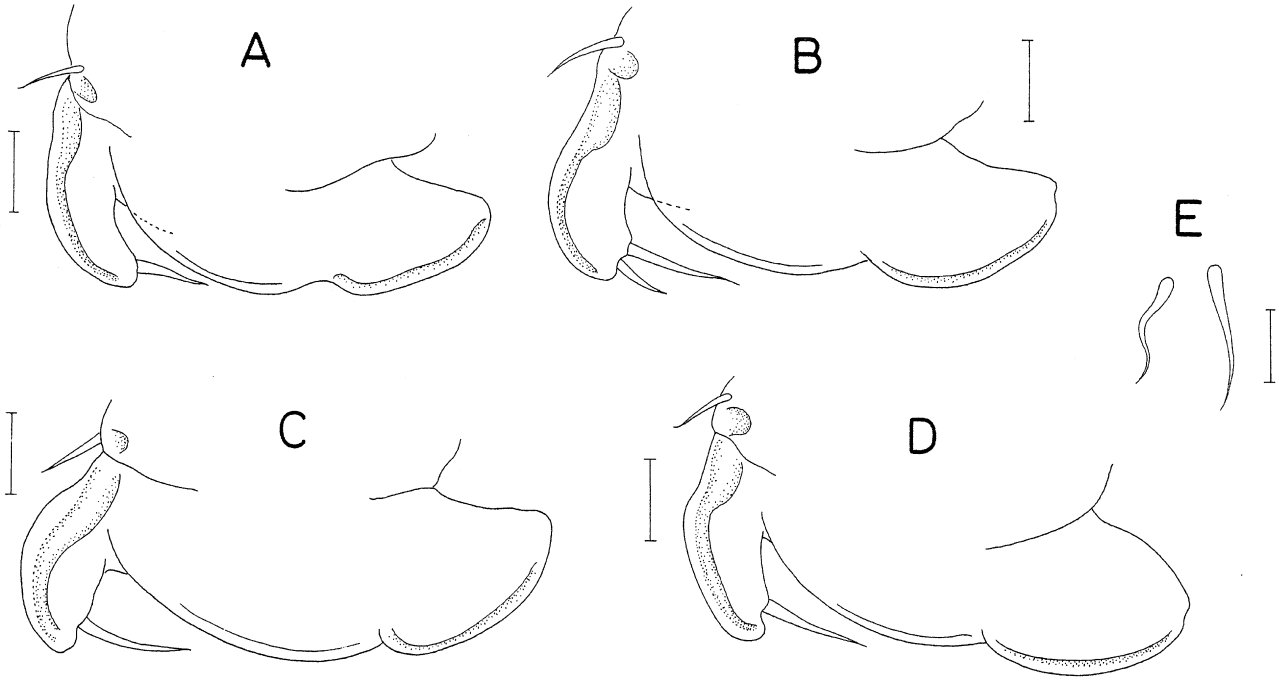

FIGURE 24. *Vivgottoia garwoodi* **n. gen. et n. sp.**, holotype female. A, leg 1; B, leg 2; C, leg 3; D, leg 4; E, leg 5. Scale bars: A–E, 0.02 mm.

Vivgottoia garwoodi n. gen. et n. sp.

Type material: Holotype ♀ ovigerous (dissected and mounted on a glass slide) from inside tail fragment of terebellid polychaete (probably *Phisidia aurea*); Glen Arm, Antrim, Northern Ireland, Stn GL5C (54° 58.20'N, 05° 55.32'W), depth 32 m, collected by P. Garwood; BMNH Reg. No. 2012.1394.

Female. Body (Fig. 23A) vermiform, elongate, cylindrical, and composed of well-marked cephalosome, first to fifth pedigerous somites, genital complex and 1-segmented abdomen. Body length 2.04 mm. Cephalosome smaller than pedigerous somites, 141×166 μm, nearly circular, with slightly produced but truncate frontal margin. First to fifth pedigerous somites distinctly defined from one another by lateral constrictions, 166×178, 295×233, 350×233, 430×255, and 313×231 μm, respectively. Genital complex 81×179 μm; paired genital apertures large and each positioned dorsolaterally on enlarged genital prominence (Fig. 23B). Abdomen 1-segmented, dorsally confluent with but ventrally well defined from genital complex, about 246×91 μm. Caudal ramus tapering, fused to abdomen at base, about 144×44 μm, with 2 lateral and 2 small distal setae.

Rostrum (Fig. 23C) shield-like, directed posteroventrally, longer than wide and truncate at apex, ornamented with 2 pairs of setules on anterior surface. Antennule (Fig. 23D) stout and 5-segmented; first segment longest; armature formula 1, 2, 1, 1, and 1; distal 2 segments with minute spinules along anterior margin. Antenna (Fig. 23E) 2-segmented; proximal segment 2.5 times as long as wide, unarmed but with patch of spinules distally; distal segment twice as long as wide, inserted on outer margin of proximal segment, armed with 3 apical setae, one distinctly larger than other 2.

Labrum (Fig. 23G) unornamented, with strongly tapering posterior margin. Mandible (Fig. 23H) terminating in single blade, articulated at base. Maxillule (Fig. 23I) lobate, armed with 2 outer and 2 medial setae. Maxilla (Fig. 23J) 2-segmented; proximal segment unarmed; distal segment forming strong claw bearing subdistal patch of spinules on convex margin. Maxilliped (Fig. 23K) 3-segmented; first segment expanded but unarmed; second segment small and unarmed; terminal segment forming strong, smooth claw.

Legs 1–4 (Fig. 24A–D) positioned ventrolaterally, all identical in form, biramous, composed of undivided protopod and single-segmented rami; intercoxal sclerites lacking; each protopod with 1 outer seta but lacking inner seta; both rami of legs indistinctly defined from protopod. Exopod of all legs with longitudinal sclerotization along

outer margin and bearing either 1 (in legs 1, 3 and 4) or 2 (in leg 2) simple setae. Endopod of all legs expanded, foliaceous and unarmed, with constriction on outer margin and sclerotization along outer margin of distal part.

Leg 5 (Fig. 24E) rudimentary, represented by 2 simple setae. Leg 6 absent.

Male. Unknown.

Etymology. The specific name honours Dr Peter R. Garwood (Identichaet, Newcastle-upon-Tyne) in recognition of his contributions over many years collecting copepods associated with invertebrates.

Remarks. This is the first clausiid to be reported from a terebellid host, although terebellids are common hosts of symbiotic copepods from other families such as the Saccopsidae and Xenocoelomatidae.

Family Nereicolidae Claus, 1875

Nereicolids are external parasites of a wide range of polychaete families including: Nereidae, Phyllodocidae, Ampharetidae, Paraonidae, Polynoidae and Aphroditidae. They have been reported from shallow coastal waters down to 3,000 m depths in the Atlantic and Southern Oceans, but are rarely recorded (Boxshall & Halsey, 2004).

Genus *Sigecheres* Bresciani, 1964

Sigecheres concinna (T. Scott, 1902) new combination

Nereicola concinna T.Scott, 1902: 455–456, pl. XXV, figs 8–14.
Sigecheres brittae Bresciani, 1964b: 297, figs. 1, 2.

Material examined: 1 ♀ (dissected) from *Sige fusigera*; Brattholmen, FFH 3958, Stn B2A (65.914ºN, 12.2204ºE), depth 102 m; 23 March 2007.

Female. Body (Fig. 25A) consisting of 3 divisions: cephalosome, trunk, and 1-segmented urosome, Body length 1.37 mm. Cephalosome nearly circular, 390×548 µm, defined from trunk by distinct constriction. Trunk subrectangular, 850×850 µm, as long as wide. Abdomen (Fig. 25B) strongly tapering, 185×369 µm, with deep posteromedial cleft. Caudal ramus (Fig. 25C) small, 192×150 µm, with 6 naked setae, one much larger than other 5. Genital areas located ventrally. Egg sac 1.22×0.45 mm.

Rostrum not discernible (Fig. 25D). Antennule (Fig. 25E) 188 µm long and 5-segmented; armature formula 3, 8, 4+aesthetasc, 2+aesthetasc, and 7+aesthetasc; all setae naked. Antenna (Fig. 25F) 4-segmented; first segment large but unarmed; second segment with patch of spinules on mediodistal surface; third segment with 1 blunt spinulose spine and 1 small seta; terminal segment incompletely defined from third segment, with 2 proximal setae and 4 unequal distal spines bearing spinules distally.

Labrum (Fig. 25G) with patch of spinules on each ventrolateral surface and prominent, funnel-like posteromedian extension enclosing mandible (Fig. 25D). Mandible (Fig. 25H) simple, with 12 or 13 teeth arranged along distal margin. Maxillule (Fig. 25I) digitiform, with 1 large, spinulose outer lateral and 3 distal setae. Maxilla (Fig. 25J) 1-segmented and characteristic in bearing large hollow functioning as sucker (pieces of detached host tissue were held within this sucker), with circular, saw-like apparatus in hollow. Maxilliped (Fig. 25K) 3-segmented; all segments unarmed; terminal segment with spinulose pad on truncated distal surface.

Legs 1–6 absent.

Male. Unknown.

Remarks. T. Scott (1902) described a new species of *Nereicola* Keferstein, 1863, *N. concinna*, from a phyllodocid polychaete *Eulalia viridis* Linnaeus, 1767 (as *Eulalia viridis* Oersted) collected at a depth of 100–119 m (55–65 fathoms) in Loch Etive on the west coast of Scotland. His description was detailed, showing the adult ovigerous female, the antennule, antenna, mandible, maxilla and maxilliped, as well as an “immature specimen”. We find no significant differences between our material and the description of Scott (1902). As suspected by Gotto (1993), *Nereicola concinna* is conspecific with *Sigecheres brittae* as described by Bresciani (1964b). The copepod redescribed here was collected from the mid-body region of the same phyllodocid polychaete, *Sige fusigera*, as in the original description of the species (Bresciani, 1964b). Both *Sige fusigera* and *Eulalia viridis* belong to the same subfamily, Eteoninae, of the Phyllodocidae. Some minor emendations to the original description are made here

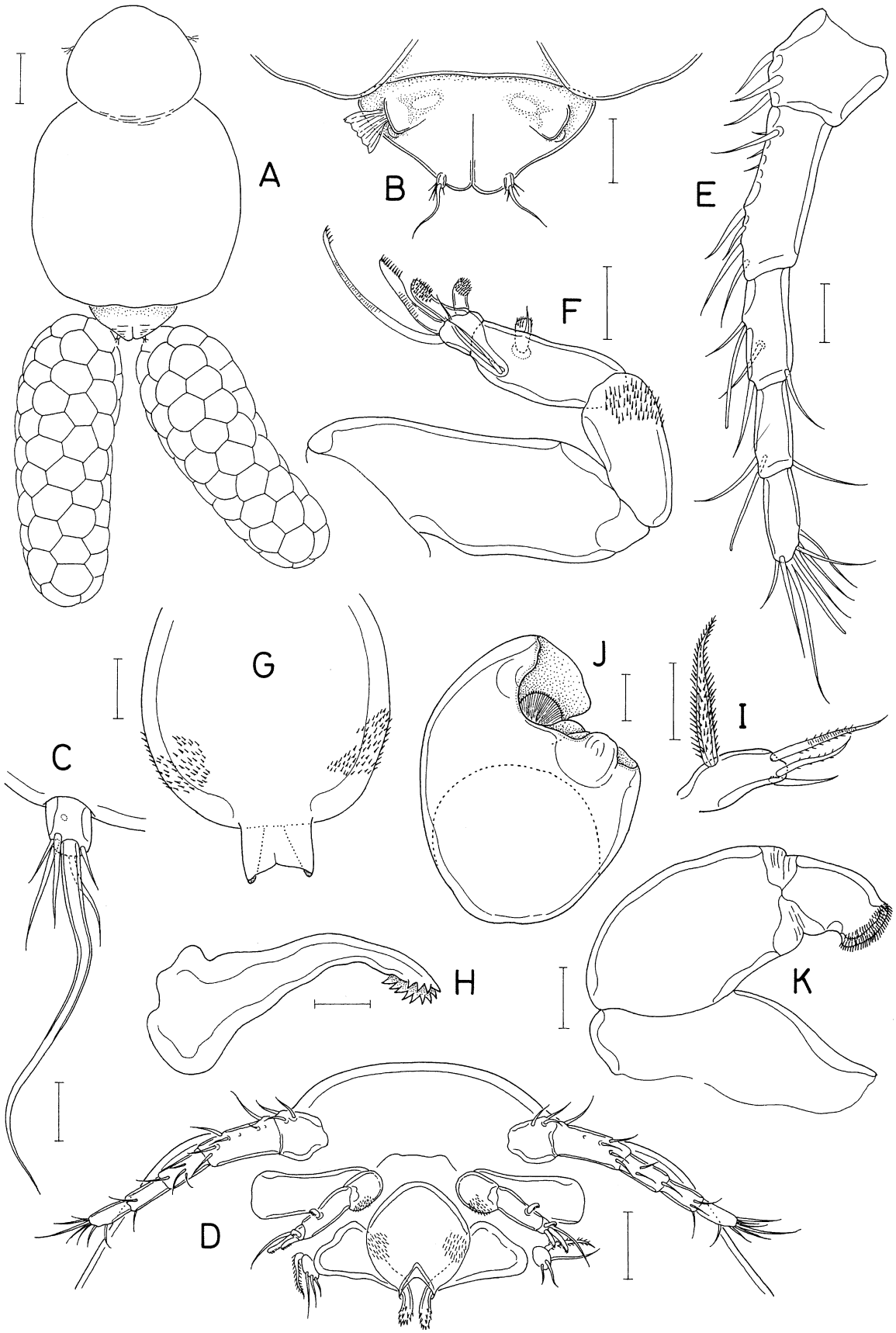

FIGURE 25. *Sigecheres concinna* (T. Scott, 1902) new combination, female. A, habitus, dorsal; B, abdomen, ventral; C, right caudal ramus, ventral; D, anterior part of cephalothorax, ventral; E, antennule; F, antenna; G, labrum, ventral; H, mandible; I, maxillule; J, maxilla; K, maxilliped. Scale bars: A, 0.2 mm; B, 0.1 mm; C, E–K, 0.02 mm; D, 0.05 mm.

with regard to the structure of maxilla, the segmentation of the antenna, and the setation of the caudal ramus and antennule. Bresciani (1964b) pointed to the peculiar form of the maxilla having an excavation. This appendage, acting as a sucker, is the most striking, autapomorphic feature of the genus in comparison with the usual structure of the two-segmented maxilla—with the stout distal segment having a spinulose pad or spiniform elements as found in other genera of Nereicolidae.

We consider that Bresciani (1964b) made a strong case for the classification of this parasite as a distinct genus within the Nereicolidae, and we follow this treatment here. The oldest available name for this taxon is *Sigecheres concinna* (T. Scott, 1902), new combination, and *S. brittae* becomes a junior subjective synonym. *Nereicola* remains monotypic and its type species *Nereicola ovata* Keferstein, 1863 was redescribed by Laubier in 1965.

Genus *Anomopsyllus* Sars, 1921

Anomopsyllus bifurcus n. sp.

Type material: Holotype ♀ (dissected and mounted on a glass slide) from *Notomastus latericeus*; Brattholmen, FFH 3958, Stn B3 (65.928ºN, 12.2518ºE), depth 105 m, 23 March 2007; BMNH Reg. No. 2012.1395.

Female. Body (Fig. 26A) dorso-ventrally flattened and consisting of cephalosome, trunk and urosome. Body length 1.77 mm, excluding caudal rami. Cephalosome (Fig. 26B) subcircular, 250×331 µm, with transparent membranous flange along frontal margin. Trunk flattened, trapezoidal, 1.35×0.68 mm, gradually broadening posteriorly, with truncated posterior margin and no trace of segmentation. Urosome (Fig. 26C) small and consisting of genital complex and 1-segmented abdomen. Genital complex strongly tapering in dorsal view, 288 µm wide and wider than long. Abdomen inserted on ventral surface of genital complex (Fig. 26C), with deep posteromedian anal cleft. Caudal rami not observed (detached).

Rostrum absent. Antennule (Fig. 26D) 197 µm long and 6-segmented; armature formula 1+spine, 6, 2+aesthetasc, 2, 2+aesthetasc, and 7+aesthetasc; spine on first segment large; second segment with transverse sclerotization near proximal one-third. Antenna 3-segmented, with 0, 1, and 8 (3 middle and 5 distal) setae on first to third segments, respectively; all setae simple and naked; first segment with 2 transverse rows of minute spinules.

Labrum not observed (lost during dissection). Mandible (Fig. 26F) with 3 claw-like blades (2 terminal and 1 subdistal) and 1 proximal seta possibly representing palp. Maxillule (Fig. 26G) lobate, with 4 distal setae. Maxilla (Fig. 26H) 2-segmented; proximal segment unarmed; distal segment with 1 proximal seta and spinulose pad on expanded distal surface. Maxilliped (Fig. 26I) 4-segmented; armature formula 0, 2, 0, and 1; first and second segments with numerous minute spinules over surface; terminal segment reflexed, with 2 blunt terminal processes covered apically with fine spinules, broader outer process with trace of articulation at base.

Leg 1 (Fig. 26J) represented by small lobe tipped by 2 setae and 1 nearby seta. Legs 2 and 3 (Fig. 26K, L) vestigial, each formed by small lobe tipped by 1 seta and 1 nearby (protopodal) seta. Legs 4 and 5 absent. Leg 6 probably represented by 1 seta and 2 small spinules in genital area (Fig. 26C).

Male. Unknown.

Etymology. The specific name *bifurcus* alludes to the distally bifurcate terminal segment of the maxilliped.

Remarks. The most characteristic features of *Anomopsyllus bifurcus* **n. sp.** are: the distally blunt, bifurcate terminal segment of the maxilliped, the large spine on the first segment of the antennule, the reduced legs 1–3, each of which is represented by two or three setae, and the absence of legs 4 and 5. The female body of *A. pranizoides* Sars, 1921 in the illustration of Sars (1921) is almost identical in form to that of *A. bifurcus* **n. sp.** However, both *A. pranizoides* and *A. abyssorum* Laubier, 1988 share a similar kind of maxilliped in which the terminal segments bears two claw-like processes and two setae, as illustrated by Laubier (1988). This arrangement differs markedly from the blunt terminal processes of the new species. Neither *A. pranizoides* nor *A. abyssorum* has a strong spinform setal element on the first antennulary segment.

This is the first nereicolid to be reported from a host belonging to the family Capitellidae.

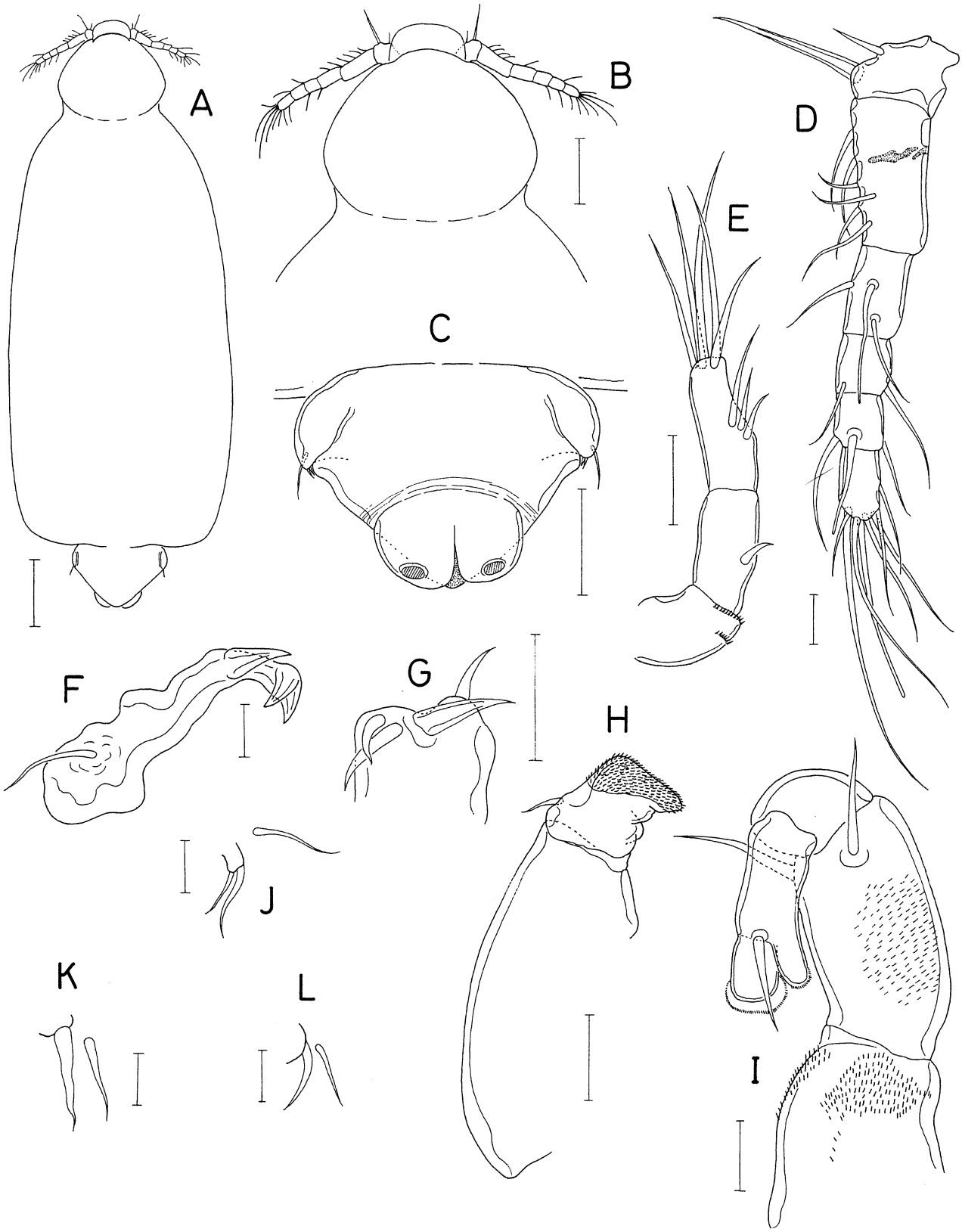

FIGURE 26. *Anomopsyllus bifurcus* **n. sp.**, female. A, habitus, dorsal; B, cephalothorax, dorsal; C, urosome, ventral; D, antennule; E, antenna; F, mandible; G, maxillule; H, maxilla; I, maxilliped; J, leg 1; K, leg 2; L, leg 3. Scale bars: A, 0.2 mm; B, C, 0.1 mm; D–L, 0.02 mm.

***Anomopsyllus geminus* n. sp.**

Type material: Holotype ♀ (dissected and mounted on a glass slide) from *Ampharete* cf. *lindstroemi*; Sandnessjøen, Lille Åsvaer (66.235ºN, 12.3374ºE), depth 45 m; Stn LA2-B, 2007; BMNH Reg. No. 2012.1396.

Paratype ♀ (dissected and mounted on glass slide) attached to abdomen of *Ampharete lindstroemi*; northern North Sea, Stn BYA03a F2 (59º 30.49'N, 01º 29.16'E.), depth 112 m, collected by P. Garwood, 24 August 2006; BMNH Reg. No. 2012.1397.

Female (holotype). Body (Fig. 27A) consisting of cephalosome, inflated trunk, and small urosome. Body length 1.21 mm, excluding caudal setae. Cephalosome subcircular, 200×250 μm, with short anterodorsal ridge and transparent membranous flange along frontal margin. Trunk flattened, 850×539 μm, with slightly undulating, convex lateral margins and truncate posterior margin. Urosome (Fig. 27B) consisting of genital complex and 1-segmented abdomen. Genital complex 110×215 μm, much wider than long, with large dorsal hump (Fig. 27A); genital apertures located ventrolaterally (Fig. 27B). Abdomen much narrower than genital complex, indistinctly articulated from genital complex, and 92×96 μm. Caudal ramus 48×23 μm (ratio 2.09:1), with 6 setae, mid-terminal seta much larger than other 5, 135 μm long.

Rostrum absent. Antennule (Fig. 27C) 123 μm long and indistinctly 5-segmented, with armature formula 6, 3, 2, 2+aesthetasc, and 7+aesthetasc; first segment slightly produced in middle of anterior margin. Antenna (Fig. 27D) 3-segmented; first segment unarmed; second segment with 1 medial seta; third segment 29×12 μm, with 3 medial and 5 distal setae, one distinctly smaller than other 4.

Labrum (Fig. 27E) with concave posterior margin and stout posteromedian process. Mandible (Fig. 27F) with 2 hook-like distal processes and 1 proximal seta representing palp. Maxillule (Fig. 27G) lobate, with 3 thick distal setae (1 medial and 2 outer). Maxilla (Fig. 27H) 2-segmented; both segments unarmed but distal segment with spinulose pad on expanded distal surface. Maxilliped (Fig. 27I) 4-segmented, with armature formula 0, 2, 0, and 2; first and second segments with ornamentation of fine spinules on surface; third segment with membranous flange near outer distal corner; fourth segment reflexed, with blunt tip bearing spinulose pad.

Legs 1–3 (Fig. 27J–L) vestigial, each represented by small, spinulose lobe tipped by 2 setae. Legs 4 and 5 absent. Leg 6 probably represented by 1 small seta and 2 spinules in genital area (Fig. 27B).

Female (paratype). Body length 1.26 mm, excluding caudal rami (caudal rami detached). Body shape as in holotype. Cephalosome without anterodorsal ridge, otherwise same as that of holotype. Trunk and urosome as in holotype.

Antennule, antenna, labrum, mandible, maxillule, maxilla, and maxilliped also as in holotype in shape, segmentation and setation.

Legs 1–3 better developed than those of holotype. Leg 1 (Fig. 27M) with 1 outer seta on protopod and 3 setae on 1-segmented exopod; endopod absent. Leg 2 (Fig. 27N) similar to leg 1, but exopod small, with 2 setae. Leg 3 (Fig. 27O) lobate, with 3 setae.

Legs 4 and 5 absent as in holotype.

Male. Unknown.

Etymology. The specific name *geminus*, from the Latin meaning "double", alludes to legs 1–3 each of which has only two setae.

Remarks. *Anomopsyllus geminus* **n. sp.** differs from its three congeners in having lobate legs 1–3, each bearing 2–3 setae or 1 outer seta plus 2 or 3 setae on 1-segmented exopod, the blunt terminal segment of the maxilliped, and three setae on the maxillule. None of these features has been reported in any congeners. In contrast to the legs, the antennule, antenna and maxilliped are consistent in morphology between the two observed specimens. Therefore, these cephalic appendages may be more reliable than the legs for discriminating taxonomically between species in the genus *Anomopsyllus*.

The holotype was attached to the surface of setiger 14 of the host, with its head end directed towards the posterior end of the worm. The paratype was attached at setiger 16 on the abdomen of its host, the same polychaete species, and was orientated with its head towards the anterior of the worm.

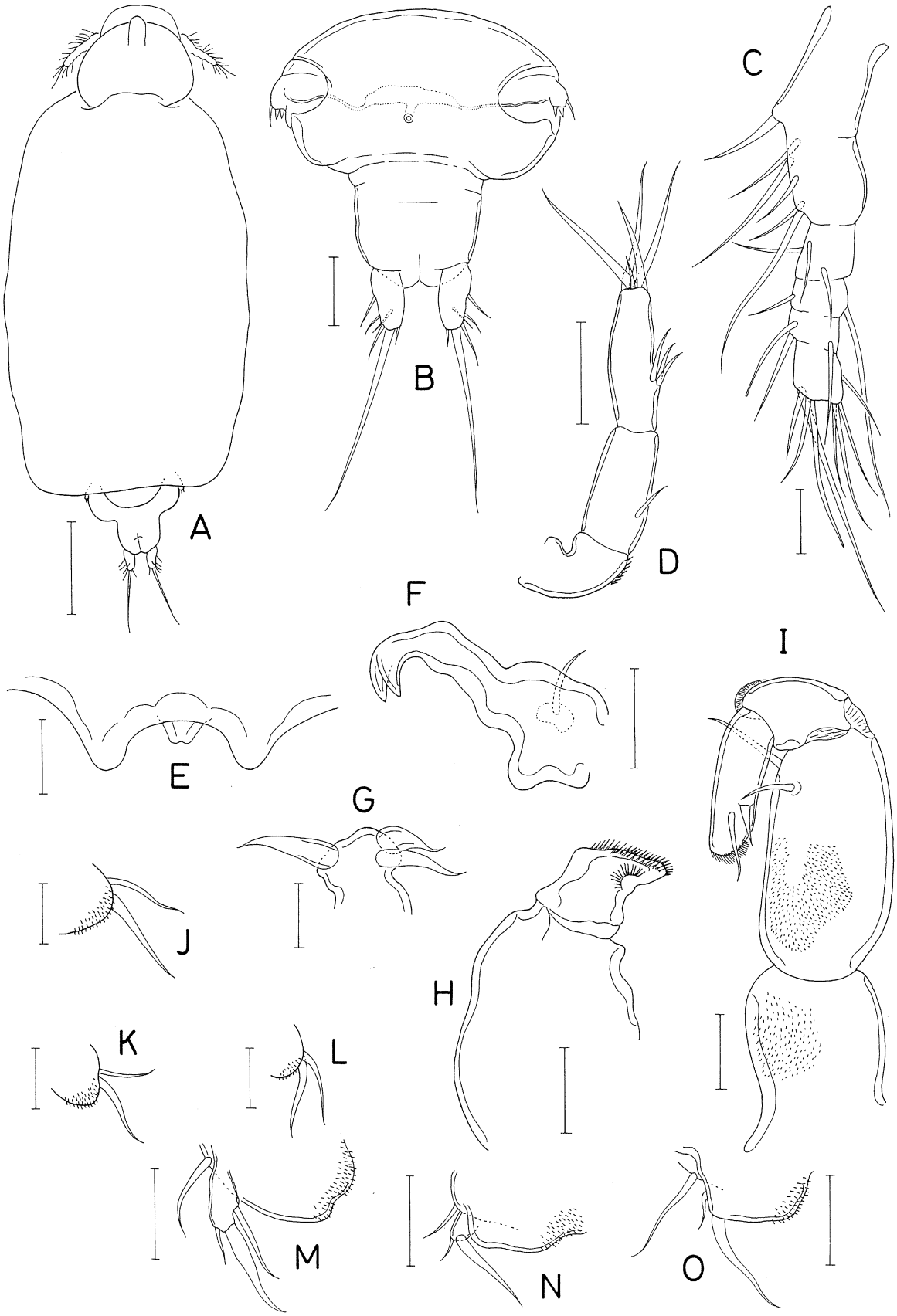

FIGURE 27. *Anomopsyllus geminus* **n. sp.**, holotype female. A, habitus, dorsal; B, urosome, ventral; C, antennule; D, antenna; E, labrum; F, mandible; G, maxillule; H, maxilla; I, maxilliped; J, leg 1; K, leg 2; L, leg 3. Paratype female, M–O, legs 1–3. Scale bars: A, 0.2 mm; B, 0.05 mm; C–O, 0.02 mm.

***Anomopsyllus hamiltonae* n. sp.**

Type material: Holotype ♀ ovigerous (intact specimen) from *Mugga wahrbergi*; northern North Sea, Norwegian sector, Pan Pandora Field, Stn 13 (61°18.51'N, 02°21.33'E), depth 291 m, collected by S. Hamilton, 02 February 2011; BMNH Reg. No. 2012.1398.

Paratype ♀ (dissected on glass slide) from *M. wahrbergi*; Stn S2, 02 October 2007; BMNH Reg. No. 2012.1399.

Paratype ♀ on *M. wahrbergi*, northern North Sea, Norwegian sector, Pan Pandora, Stn 6 (61°17.48'N, 02°22.02'E), depth 285 m; 03 January 2011; BMNH Reg. No. 2012.1400.

Paratype ♀ on *M. wahrbergi*, northern North Sea, Norwegian sector, Pan Pandora, Stn 8 (61°17.97'N, 02°21.45'E), depth 287 m; 10 January 2011; BMNH Reg. No. 2012.1401.

Paratype ♀ ovigerous on *M. wahrbergi*, northern North Sea, Norwegian sector Pan Pandora, Stn.9 (61°17.93'N, 02° 20.64'E), depth 285 m; 14 January 2011; BMNH Reg. No. 2012.1402.

Paratype ♀ on *M. wahrbergi*, northern North Sea, Norwegian sector Pan Pandora, Stn.10 (61°17.86'N, 02°22.02'E), depth 283 m; 25 January 2011; BMNH Reg. No. 2012.1403.

2 paratype ♀♀ on 2 *M. wahrbergi*, northern North Sea, Norwegian sector Pan Pandora, Stn.11 (61°18.13'N, 02°21.62'E), depth 289 m; 27 January 2011; BMNH Reg. No. 2012.1404-1405.

Female. Body (Fig. 28A) consisting of cephalosome, inflated trunk, and small urosome. Body length 846 μm, excluding caudal setae. Cephalosome subcircular, small and indistinctly articulated from trunk, 115×138 μm, with transparent membranous flange along frontal margin. Trunk flattened, 601×323 μm, with 5 indistinct segments corresponding to first to fifth pedigerous somites divided by 4 faint suture lines and weak lateral constrictions. Urosome (Fig. 28B) consisting of clearly defined genital complex and 1-segmented abdomen. Genital complex 93×115 μm, with laterally expanded anterior two thirds and narrower posterior third; genital apertures located ventrolaterally (Fig. 28B). Abdomen 70×54 μm, distinctly longer than wide. Caudal ramus 29×16 μm (ratio 1.81:1), with convex medial margin and 5 setae, one much larger than other 4.

Rostrum absent. Antennule (Fig. 28C) 93 μm long and 6-segmented but articulations indistinct especially among distal 4 segments; armature formula 1, 4, 2, 2, 2+aesthetasc, and 7+aesthetasc. Antenna (Fig. 28D) very small, indistinctly 2-segmented, both segments similar in length; proximal segment with 1 seta; distal segment with 8 setae.

Labrum with concave posterior margin and posteromedian process (Fig. 28E). Mandible (Fig. 28F) with 2 hook-like distal processes and 1 proximal seta representing palp. Maxillule (Fig. 28G) lobate with 3 distal setae (1 medial and 2 outer). Maxilla (Fig. 28H) 2-segmented; both segments unarmed but distal segment with spinulose pad on flat distal surface. Maxilliped (Fig. 28I) 4-segmented, with armature formula 0, 2, 0, and 2; proximal of 2 medial setae on second segment bilaterally spinulate; third segment with membranous flange near outer distal corner; fourth segment with blunt spinulose tip.

Legs 1–5 absent. Leg 6 probably represented by 1 small seta and 2 spinules in genital area (Fig. 28B).

Male. Unknown.

Etymology. The specific name honours Sue Hamilton (freelance marine biologist, Edinburgh) who has found numerous parasitic copepods over many years, including most of the material of this new species, as well as many specimens of other copepod species studied in this paper.

Remarks. In possessing a distally bifurcate mandible and an unarmed but blunt terminal segment on the female maxilliped, *Anomopsyllus hamiltonae* **n. sp.** resembles *A. geminus* **n. sp.**, described above. However, the small, two-segmented antenna and the absence of legs 1–5 are the characteristics that serve to separate the new species from *A. geminus* **n. sp.** and all other congeners.

Anomopsyllus hamiltonae **n. sp.** and other two new species of *Anomopsyllus* described in the present paper share a distally bifurcate mandible with a single proximal seta (although an additional, hook-like subdistal process is present in *A. bifurcus* **n. sp.**), the presence of a brim-like hyaline membrane on the frontal margin of the cephalosome, and the stout terminal segment of the maxilliped. These synapomorphic traits have not been reported in the two previously recorded congeners, *A. pranizoides* and *A. abyssorum*, although the morphology of the mandible of the latter two species is not known precisely. However, the five known species can be assigned to the genus *Anomopsyllus*, as they share the similar body form consisting of a small cephalosome, inflated trunk and

two-segmented urosome, a four-segmented maxilliped with a stout terminal segment, the unmodified, simple setae on the two- or three segmented antenna, and the reduction or absence of swimming legs.

All the copepods in the northern North Sea in the Pan Pandora sector were attached dorsally on the host worm, near the last thoracic segment.

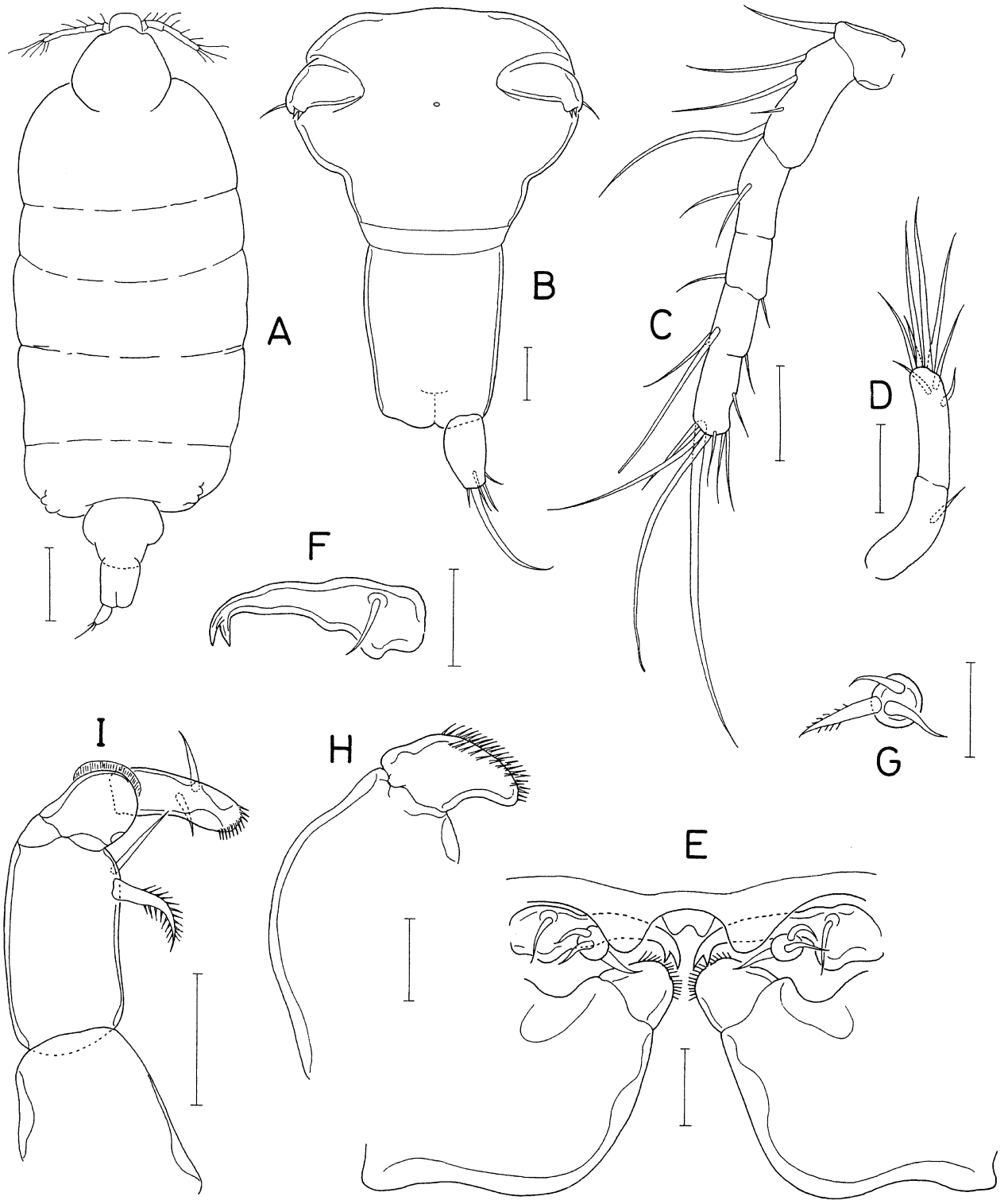

FIGURE 28. *Anomopsyllus hamiltonae* **n. sp.**, female. A, habitus, dorsal; B, urosome, ventral; C, antennule; D, antenna; E, mouthparts; F, mandible; G, maxillule; H, maxilla; I, maxilliped. Scale bars: A, 0.1 mm; B, I, 0.02 mm; C–H, 0.01 mm.

Genus *Vectoriella* Stock, 1968

Vectoriella gabesensis n. sp.

Type material: Holotype ♀ (intact) from *Aricidea catherinae*; Gulf of Gabes, Tunisia (~33º 50.26'N, 10º 36.38'E), depth 13 m, found by David Hall, 28 October 2004; BMNH Reg. No. 2012.1406.

2 ♂♂ (allotype ♂ intact and 1 ♂ dissected paratype) from *A. catherinae*; Gulf of Gabes, Tunisia, (~33º 50.26'N, 10º 36.38'E), depth 13 m, found by David Hall, 28 October 2004; BMNH Reg. No. 2012.1407 (intact), BMNH Reg. No. 2012.1411 (dissected)..

4 paratype ♀♀ (1 ♀ dissected; 3 ♀♀ partly damaged) from *A. catherinae*; Gulf of Gabes, Tunisia, (~33º 50.26'N, 10º 36.38'E), depth 13 m, found by David Hall, October 2004; BMNH Reg. No. 2012.1408-1410 (undissected), BMNH Reg. No. 2012.1412 (dissected).

Etymology. The specific name is derived from the type locality, the Gulf of Gabes, Tunisia, in the Mediterranean Sea.

Female. Body (Fig. 29A) consisting of weakly defined cephalosome, large inflated trunk, and 2-segmented urosome. Body length 508 µm, excluding caudal setae. Cephalosome defined from trunk only by slight lateral constriction. Trunk flattened, about 435×275 µm, slightly broadening posteriorly, with weakly concave lateral margins near middle of trunk. Urosome (Fig. 29B) consisting of genital complex and 1-segmented abdomen. Genital complex much wider than long; genital apertures large and located ventrally (Fig. 29B). Abdomen about 1.5 times as long as wide. Caudal ramus (Fig. 29C) weakly tapering, 39×14 µm (ratio 2.79:1), with 5 naked setae.

Rostrum absent. Antennule (Fig. 29D) 5-segmented, with armature formula 2, 7, 2, 1+aesthetasc, and 4; all of setae simple and naked. Antenna (Fig. 29E) rudimentary, lobate with 2 setae (one small and process-like), and 1 distally bifurcate spine.

Labrum (Fig. 29F) with tapering lateral margins and 2 nipple-shaped processes near concave posteromedial margin. Mandible (Fig. 29G) with 1 large, plate-like distal element covered by spinules. Paragnath (Fig. 29H) as spinulose lobe. Maxillule (Fig. 29I) lobate, with 5 thick setae distally. Maxilla (Fig. 29J) 2-segmented; proximal segment unarmed; distal segment with 3 blunt spinulose spines. Maxilliped (Fig. 29K) 3-segmented; first segment unarmed; second segment with 1 medial seta; third segment unarmed, gradually narrowed distally, with truncate tip covered by spinules.

Leg 1 represented by pair of blunt setae anteriorly on ventral surface of trunk (Fig. 29A). Legs 2 and 3 each represented by 1 blunt seta (Fig. 29A). Legs 4 and 5 absent. Leg 6 represented by 2 small setae in genital area (Fig. 29B).

Male. Body (Fig. 29L) evenly tapering from anterior to posterior and consisting of 7 incompletely articulated somites. Body length 385 µm excluding caudal setae. Maximum width 111 µm. First tagma (cephalothorax) incorporating cephalosome and first and second pedigerous somites. Cephalosomic area of cephalothorax expanded, forming widest part of body. Free abdomen 2-segmented. Anal somite distinctly longer than preceding free abdominal somite. Caudal ramus 58×13 µm (ratio 4.46:1), with 5 setae; medial terminal seta longest, 161 µm long.

Rostrum absent as in female. Antennule segmented as in female but with different armature formula: 2, 7, 3+aesthetasc, 1+aesthetasc, and 4+aesthetasc. Antenna as in female. Labrum (Fig. 29M) sexually dimorphic, directed anteriorly and extending beyond frontal margin of cephalothorax (Fig. 29L), bearing pair of flat, wedge-like elements. Other mouthparts, including maxilliped, as in female.

Leg 1 bilobed: larger outer lobe with 2 setae, smaller inner lobe (endopod) unarmed (Fig. 29L). Legs 2 and 3 with 1 seta on outer lobe and unarmed inner lobe, Legs 4 and 5 absent. Leg 6 each represented by 2 setae on posterior corner of genital flaps closing off paired genital apertures (Fig. 29L).

Remarks. Two species are currently known in the genus *Vectoriella*: both are associates of polychaetes of the family Paraonidae: *V. marinovi* Stock, 1968 associated with *Aricidea (Acmira) cerrutii* Laubier, 1966 (as *Aricidea jeffreysii* (McIntosh)) from the Black Sea (Stock, 1968) and *V. ramosae* Laubier and Carton, 1973 associated with *Aedicira mediterranea* Laubier and Ramos, 1974 (as *Aricidea* (*Aedicira*) *mediterranea*) from the Mediterranean Sea (Laubier and Carton, 1973). Several of the females had remnants of ovisacs and were attached dorsally on their hosts around setiger 14 or 15. The head of the copepod was directed towards the anterior of the worm.

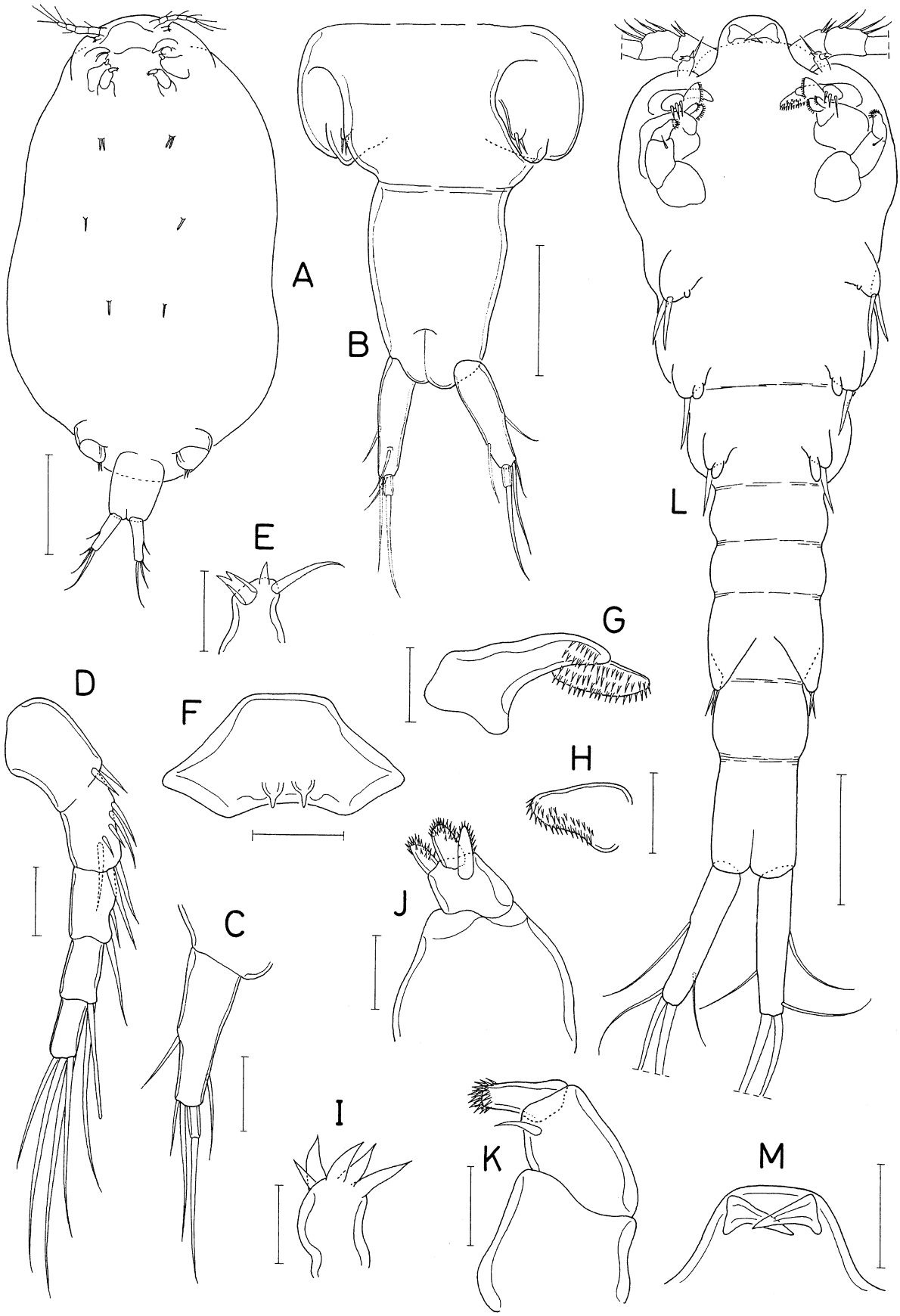

FIGURE 29. *Vectoriella gabesensis* **n. sp.** female: A, habitus, ventral; B, urosome, dorsal; C, left caudal ramus, dorsal; D, antennule; E, antenna; F, labrum; G, mandible; H, paragnath; I, maxillule; J, maxilla, ventral; K, maxilliped. Male: L, habitus, ventral; M, labrum, posterior. Scale bars: A, 0.1 mm; B, L, 0.05 mm; C, F, M, 0.02 mm; D, E, G–K, 0.01 mm.

Vectoriella gabesensis **n. sp.** is more similar to *V. marinovi* than to *V. ramosae* in having a female abdomen that is longer than wide, five caudal setae in the female, three spiniform elements on the distal segment of the maxilla, and the anteriorly projecting male labrum bearing a pair of wedge-like elements. It is notable that Stock (1968) misinterpreted the male labrum as the rostrum, presumably because it forms a rostrum-like anterior protrusion which extends beyond the anterior margin of cephalothorax. It originates from the region posterior to the antenna.

The new species is distinguishable from *V. marinovi* by the following character states: 1) the caudal ramus of *V. gabesensis* **n. sp.** is 2.79 times longer than wide in the female and 4.46 times as long as wide in the male, compared to 4.5 times in the female and 6 times in the male of *V. marinovi* (Stock, 1968); 2) the antenna of *V. gabesensis* **n. sp.** bears 2 setae and 1 spine, unlike that of *V. marinovi* which bears 2 setae only; 3) the terminal (third) segment of the maxilliped, which exhibits no sexual dimorphism, bears only a spinulose pad distally in *V. gabesensis* **n. sp.**, unlike that of *V. marinovi* which bears two pectinate elements; 4) legs 1–3 of *V. gabesensis* **n. sp.** are represented by 1 or 2 setae in the female but those of *V. marinovi* are biramous, although the rami are feebly developed.

Family Spiophanicolidae Ho, 1984

The family Spiophanicolidae currently comprises a single species infesting three or four species of marine polychaetes of the genus *Spiophanes* Grube, 1860. It was described originally from off the west coast of California but was subsequently reported from the outer Clyde Estuary, and the central and northern North Sea by O'Reilly (1999).

Genus *Spiophanicola* Ho, 1984

Spiophanicola atlanticus n. sp.

Spiophanicola spinosus: O'Reilly (1999: 46–47)

Type material: Holotype ♀ from *Spiophanes kroeyeri* Grube, 1860; Motovsky Gulf, Stn 22-5 (69°33.266'N, 32°52.171'E), depth 218 m, 11 August 2003; BMNH Reg. No. 2012.1413.

Paratype ♀ (dissected and figured) from *S. kroeyeri*; off northeastern coast of Svalbad, Prosj. 2302, Stn 8-3 (80.118ºN, 8.778ºE), depth 512 m, 20 May 2003; BMNH Reg. No. 2012.1414.

Paratype ♀ (dissected) detached parasite from unknown host; Hinlopenstretet, Svalbad, Stn VI (78.718ºN, 18.332ºE), depth 433 m, 17 August 2003; BMNH Reg. No. 2012.1415.

Paratype ♀ detached parasite from unknown host; 10 miles off Cullercoats, Northumberland, depth 80 m, Coll. Peter Garwood; BMNH Reg. No.1999.165 (reported by O'Reilly, 1999).

Paratype ♀ from *S. kroeyeri*; northern North Sea, depth unknown, collected by M. Sheader; BMNH Reg. No. 1999.471.

Paratype ♀ from *S. kroeyeri*; northern North Sea, depth unknown, BMNH 2005.2085

Additional material: 1 ♀ from anterior dorsum of *S. kroeyeri*, off Northumberland, England, CEFAS Stn 57A (55º01.189'N, 01º14.960'W), depth 55 m, collected by P. Garwood (possibly 1999); BMNH Reg. No. 2012.1416.

1 tiny copepodid on juvenile *S.kroeyeri* from inner Firth of Clyde, Scotland, off Cloch Point, SEPA Stn CMT7 (55º 56.85'N, 04º 53.65'W), depth 80 m; collected by M.O'Reilly, 11 May 2000; BMNH Reg. No. 2012.1417.

2♀ ovigerous from *S.kroeyeri* from inner Firth of Clyde, Scotland, off Cloch Point, SEPA Stn CMT7 (55º 56.85'N, 04º 53.65'W), depth 80 m; collected by M.O'Reilly, 13 March 2002; BMNH Reg. No. 2012.1418-1419.

1♀ detached from host, inner Firth of Clyde, Scotland, off Cloch Point, SEPA Stn CMT7 (55º 56.85'N, 04º 53.65'W), depth 80 m, collected by M.O'Reilly, 28 April 1999; BMNH Reg. No. 2012.1420.

1♀ on *S.kroeyeri* & 1♀ detached from host, inner Firth of Clyde, Scotland, off Cloch Point, SEPA Stn CMT7 (55º 56.85'N, 04º 53.65'W), depth 80 m; collected by M.O'Reilly, 13 April 2004.

1♀ on *S.kroeyeri* outer Firth of Clyde, Scotland, at SEPA Stn 10 km E. of Johnston's Point (55º19.44'N, 05º21.01'W), depth 48 m; collected M.O'Reilly, 30 November 2010.

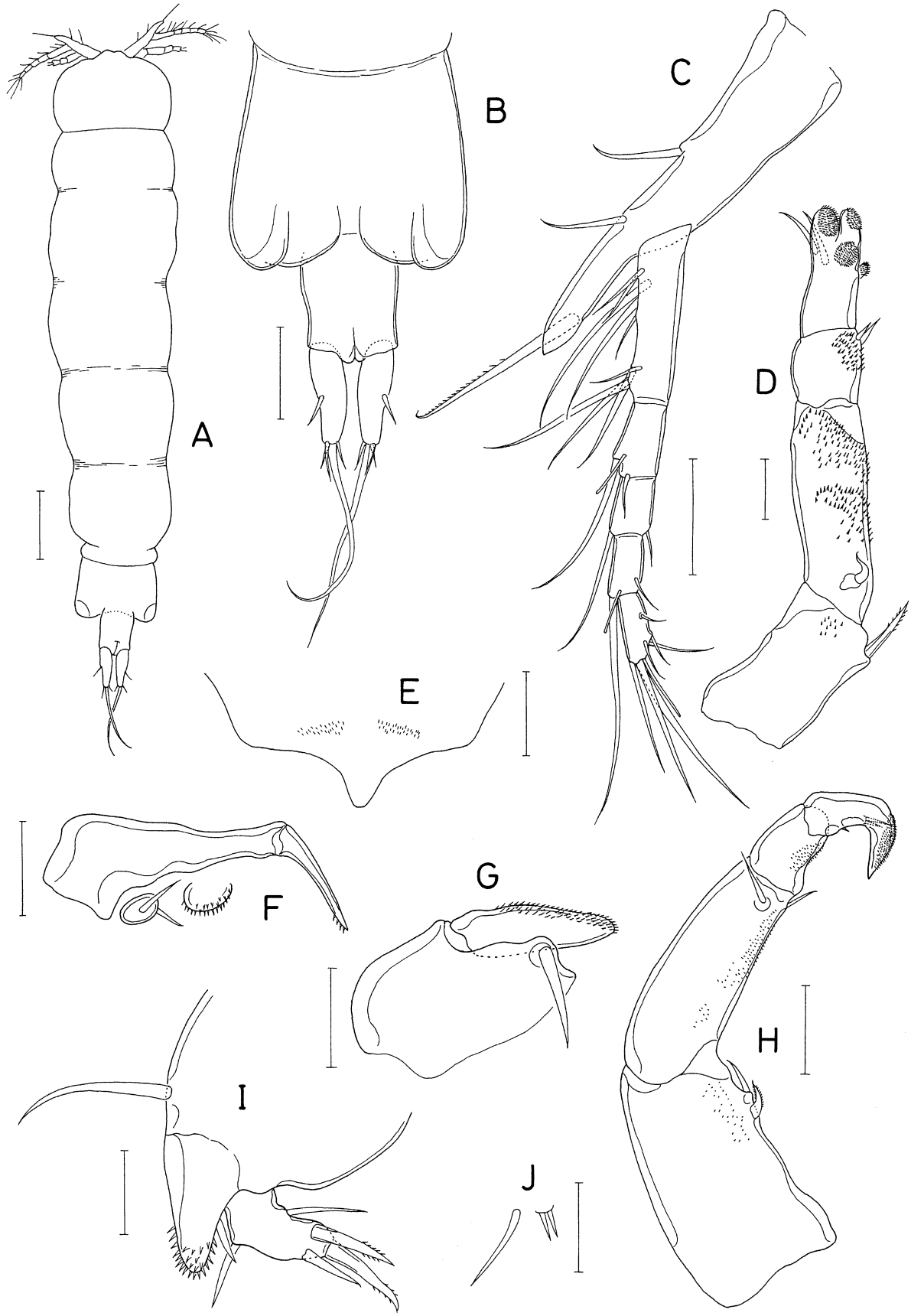

FIGURE 30. *Spiophanicola atlanticus* **n. sp.** female. A, habitus, dorsal; B, posterior part of body, ventral; C, antennule; D, antenna; E, labrum, ventral; F, mandible, paragnath and maxillule; G, maxilla; H, maxilliped; I, leg 1; J, leg 5. Scale bars: A. 0.2 mm; B, 0.1 mm; C, D, H, J, 0.05 mm; E–G, I, 0.02 mm.

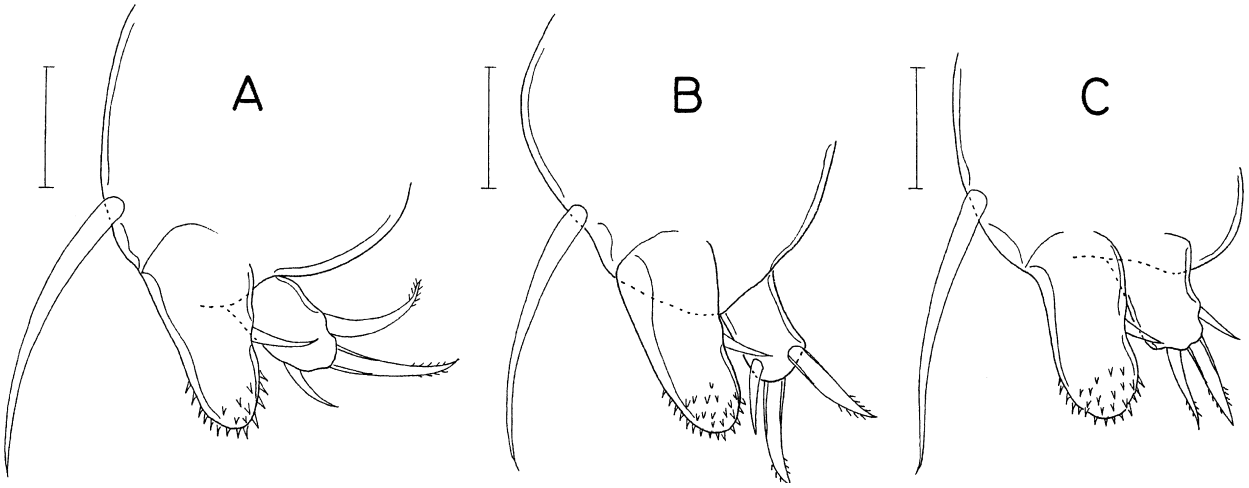

FIGURE 31. *Spiophanicola atlanticus* **n. sp.** female. A, leg 2, B, leg 3; C, leg 4. Scale bars: 0.02 mm for all.

Female. Body (Fig. 30A) elongate and dorso-ventrally flattened. Body length of dissected specimen 1.88 mm. Cephalosome clearly separated from trunk. Trunk consisting of 5 metasomal somites (first to fifth pedigerous somites); each somite defined by weak constrictions. Genital complex slightly wider than long. Abdomen 1-segmented, longer than wide, 125×105 μm. Caudal ramus elongate, 113×37 μm (ratio 3.05:1), with 5 setae (Fig. 30B).

Rostrum absent. Antennule (Fig. 30C) 6-segmented; armature formula 3, 9, 2+aesthetasc, 2+aesthetasc, 2, 2+aesthetasc, and 7+aesthetasc; anterodistal projection on first segment terminating in acute tip, with 1 large, spiniform subdistal seta. Antenna (Fig. 30D) 4-segmented: first segment with distal spine on inner margin; second segment with 1 small proximal seta; third segment with 2 distal setae and 3 spinulose lobes.

Labrum (Fig. 30E) with posteromedian protrusion. Mandible with 1 slender, spiniform distal element articulated at base (Fig. 30F). Paragnath forming spinulose lobe (Fig. 30F). Maxillule lobate, bearing 2 setae (Fig. 30F). Maxilla (Fig. 30G) distinctly 2-segmented; proximal segment with 1 mediodistal seta; spinulose distal segment elongate and unarmed. Maxilliped (Fig. 30H) 4-segmented: first and second segments each with 2 setae distally on medial margin; third segment unarmed; terminal segment forming strongly recurved hook, armed with 3 small setae; first to third segments each with patches of fine spinular ornamentation on medial surface, terminal hook with spinules on outer surface.

Legs 1–4 (Figs 30I, 31A–C) biramous; each comprising protopod partly incorporated into somite, bearing outer seta, partly fused exopod and distinct endopod: exopod of legs 2 to 4 markedly longer than corresponding endopod: exopod of all legs bearing single inner margin seta and having spinulate apex; endopod of leg 1 with 5 setae, legs 2, 3 and 4 each with 3 setae. Leg 5 (Fig. 30J) consisting of 1 small papilla tipped by 2 small setae and 1 nearby seta. Leg 6 not observed.

Male. Unknown.

Etymology. The specific name *atlanticus* is derived from the type locality, as distinct from the Pacific distribution of its only congener.

Remarks. *Spiophanicola spinulosus* Ho, 1984 was described based on specimens associated with three species of polychaetes belonging to the genus *Spiophanes* from the Pacific coast of North America (Ho, 1984). It was subsequently reported from British waters from *Spiophanes kroeyeri*, and possibly from *Spiophanes bombyx* (Claparède, 1870) (O'Reilly, 1999).

There are several differences between the northern European specimens described here and the type material from California used in the original description. In our specimens the anterodistal projection of the first antennular segment terminates in a simple angle whereas it terminates in a distinct hook-like structure in the type specimens. The maxilla is distinctly 2-segmented in our material but the types were described as having unsegmented maxillae (Ho, 1984). There are significant differences in the endopodal setation of legs 1 and 4 which are armed with 5 and 3 setae respectively in our European material, compared with 4 and 2 setae, respectively, in the types. In addition there are differences in the proportional lengths of the rami in legs 3 and 4: in the European material the exopods

are distinctly longer than the endopods whereas in the Californian type specimens the exopods are markedly shorter. Finally, leg 5 is better developed in the type material: it is bilobed and the lobes are tipped with 1 or 2 apical setae. In comparison in the new material described here, leg 5 is represented by a papilla bearing 2 setae plus an adjacent isolated seta on the somite surface nearby.

Differences between the European material and the Californian type material were previously considered to represent variation in a parasite species found on the same host, the polychaete *S. kroeyeri*, in both the Pacific and the Atlantic. However, after examination of new European material and re-examination of one of the specimens (BMNH 1999.165) reported by O'Reilly (1999), we recognise consistent differences between the type material and the European material. We now consider these differences to be significant and propose to establish a new species for the northern European material.

The recognition of *S. atlanticus* **n. sp.** as a sister species of *S. spinulosus* should prompt the removal of the latter species name from the list of alien and invasive species in European Seas (Olenin & Didžiulis, 2009; DAISIE, 2009; Noël, 2011). The wide distribution of *S. atlanticus* **n. sp.** from Norwegian waters to the central North Sea and the west coast of Scotland suggests that this is merely a hitherto overlooked European species rather than an alien.

Family uncertain

Notomasticola n. gen.

Diagnosis. Body elongate and vermiform, without clear body division. Abdomen 1-segmented. Caudal ramus with 6 setae. Antennule broad and 4-segmented. Antenna indistinctly 3- or 4-segmented. Mandible distally armed with 1 ventral lash and 2 dorsal spines. Maxillule bilobed, with setae on lobes. Maxilla 2-segmented; proximal segment unarmed; distal segment forming claw. Maxilliped absent. Legs 1–3 with 2-segmented rami; outer spine of first exopodal segment transformed to claw; endopodal segments enlarged and foliaceous but unarmed. Leg 4 represented by 1 seta. Leg 5 large, located dorsolaterally and 2-segmented but unarmed. Leg 6 represented by 1 seta in genital area.

Type species. *Notomasticola frondosus* **n. gen. et n. sp.**, by original designation.

Etymology. The generic name *Notomasticola* is a combination of an abbreviation of the name of the most frequently reported host, *Notomastus*, combined with the latin suffix *icola* meaning to dwell in or inhabit. Gender masculine.

Remarks. At first glance, the vermiform body and large leg 5 of this copepod led us to infer that it might belong to the family Serpulidicolidae. However, the absence of a maxilliped, the large endopods of legs 1–3, and the very characteristic mandible together suggested that it could not be placed in the Serpulidicolidae. The mandible with its 3 basally articulated elements, and the bilobed maxillule are both clausidiid-like in form. The claw-like distal segment of the maxilla is suggestive of a lichomolgoid affinity. However, the first to third legs have the outer spine of the proximal segment of the exopod transformed to a claw, which forms the anchoring apparatus, and the enlarged but unarmed endopods are autapomorphic features. The 4-segmented and greatly expanded antennule and its possession of enlarged distal setae are also autapomorphic states. This genus cannot readily be placed in any existing family, however it is highly derived and probably represents a terminal branch arising within another family. Therefore we consider this new genus to be *incertae sedis* within the Cyclopoida.

Notomasticola frondosus n. sp.

Type material: Holotype ♀ (intact specimen) from *Notomastus latericeus*; Gullifaks Stn 1-3 (61.094ºN, 02.193ºE), depth 133 m, 17 June 1999; BMNH Reg. No. 2012.1421.

Paratype ♀ (dissected on glass slides and figured) from *Pseudopolydora paucibranchiata*; Huldra 99, Stn 16-9 (61.933ºN, 02.555ºE), depth 125 m, 05 June 1999; BMNH Reg. No. 2012.1422.

Paratype ♀ found in abdomen of *N. latericeus*; Fal Estuary, Cornwall (Stn H5), (GRF 182E336N), collected by P. Garwood, 05 February 1997; BMNH Reg. No. 2013.14.

Paratype ♀ (dissected on glass slide) from the gut of *N. latericeus* fragment; Irish Sandbanks Survey Stn 551, depth unknown, collected by P. Garwood; BMNH Reg. No. 2013.15.

Other material: 1♀ northern North Sea, Conoco Lyell Field, Stn 1 (60º53.944'N, 01º16.287'E), depth 140 m, collected by Sue Hamilton, July 1991; BMNH Reg. No. 2013.16.

1♀ northern North Sea, Total Dunbar Field, Stn 9B (60º37.873'N, 01º39.155'E), depth 130 m, collected by Sue Hamilton, 30 May 1992; BMNH Reg. No. 2013.17.

1♀ northern North Sea, Total Dunbar Field, Stn 6B (60º 37.334'N, 01º39.177'E) collected by Sue Hamilton, 30 May 1992; BMNH Reg. No. 2013.18.

4♀♀ northern North Sea from Statfjord Field (Blocks 33/34); collected by Sue Hamilton, 1996; BMNH Reg. No. 2013.19-22.

1♀ from inside *N. latericeus*, northern North Sea, NW Hutton Field, Stn BP 800ESE(B), collected by P. Garwood, Summer 2002; BMNH Reg. No. 2013.23.

1♀ off Rame Head, Cornwall, England, collected David Hall, 01 May 2007; BMNH Reg. No. 2013.24.

2♀ northern North Sea, NW Hutton Field, Stn BP 1200ESE(B), collected by P. Garwood, Summer 2002.

1♀ Firth of Clyde, Scotland, Stn G03-1 (55º 44.922'N, 04º 53.110'W), collected by David Hall, 26 June 2009.

Female. Body (Fig. 32A) grub-shaped, elongate, consisting of obscurely defined cephalosome, long trunk, indistinct genital complex and 1-segmented abdomen. Body length 3.07 mm. Maximum width 740 µm. Trunk occupying most of body, with many transverse wrinkles and constrictions at irregular intervals. Genital complex much wider than long, 395 µm wide, bearing paired genital apertures dorsolaterally (Fig. 32B). Abdomen 1-segmented, 305×245 µm, slightly tapering. Caudal ramus (Fig. 32C) 58×28 µm (ratio 2.07:1), broadened distally, with 6 setae; one distal seta markedly larger than other 5.

Rostrum (Fig. 32D) as broad lobe on frontal margin of cephalosome. Antennule (Fig. 32E) broad and 4-segmented; terminal segment narrower than proximal 3 segments; armature formula 1, 3, 7, and 8; 3 of setae on terminal segment enlarged, flattened and spinulose. Antenna (Fig. 32F) incompletely 4-segmented, armature formula 1, 0, 1, 1+2 claws; articulation between 2 distal segments obscure.

Labrum (Fig. 32G) with slightly convex posterior margin and large tapering posteromedian process. Mandible (Fig. 32H) armed distally with 1 ventral lash and 2 dorsal, spinulose spines. Maxillule (Fig. 32I) bilobed, with 3 distal setae on small outer lobe and 2 proximal setae on large inner lobe. Maxilla (Fig. 32J) 2-segmented; proximal segment unarmed; distal segment forming claw, with 1 small proximal seta and 4 or 5 subdistal spinules near tip. Maxilliped absent.

Legs 1–3 (Figs 32K, 33A, B) biramous with 2-segmented rami; exopods small; endopods enlarged, with lamelliform segments. Leg 4 (Fig. 33C) represented by 1 seta. Outer spine of exopod of legs 1–3 forming claw, with bifurcate tip. Armature formula of legs 1–3 as follows:

Leg 1: coxa 0-0; basis 1-0; exp. I-0; 2, 3, 0; enp. 0-0; 0-0
Leg 2: coxa 0-0; basis 1-0; exp. I-0; 1, 2, 0; enp. 0-0; 0-0
Leg 3: coxa 0-0; basis 1-0; exp. I-0; 0, 3, 0; enp. 0-0; 0-0

Leg 5 large, located dorsolaterally, and 2-segmented (Fig. 32B); proximal segment expanded, globular and unarmed; free distal segment (exopod) also unarmed. Leg 6 represented by 1 seta in genital area (Fig. 32B).

Male. Unknown.

Etymology. The specific name *frondosus* is from the Latin meaning "leafy" and alludes to the leaf-like endopodal segments of legs 1–3.

Remarks. One of the observed paratypes (from the Irish Sandbanks Survey) was found in the gut of the polychaete host. It was about 3.7 mm in body length and had a smooth body surface, without wrinkles. However, the body of this female had two strong lateral constrictions, one at the level of leg 3 and the other anterior to leg 4 (Fig. 33D). The distance between the two constrictions corresponded exactly to the length of a body segment of the polychaete host, which suggests that the constrictions on the copepod body may have been caused by the muscular constrictions (at the host's internal septa) of the gut of the host. Unlike the other specimens, this female also had maxillipeds (Fig. 33E, F) which were lobate with bulges. Despite the distinctly different body configuration and the possession of vestiges of maxillipeds, the morphological features of other appendages of this specimen, including the characteristic setation of the antennule, are the same as in the other observed specimens.

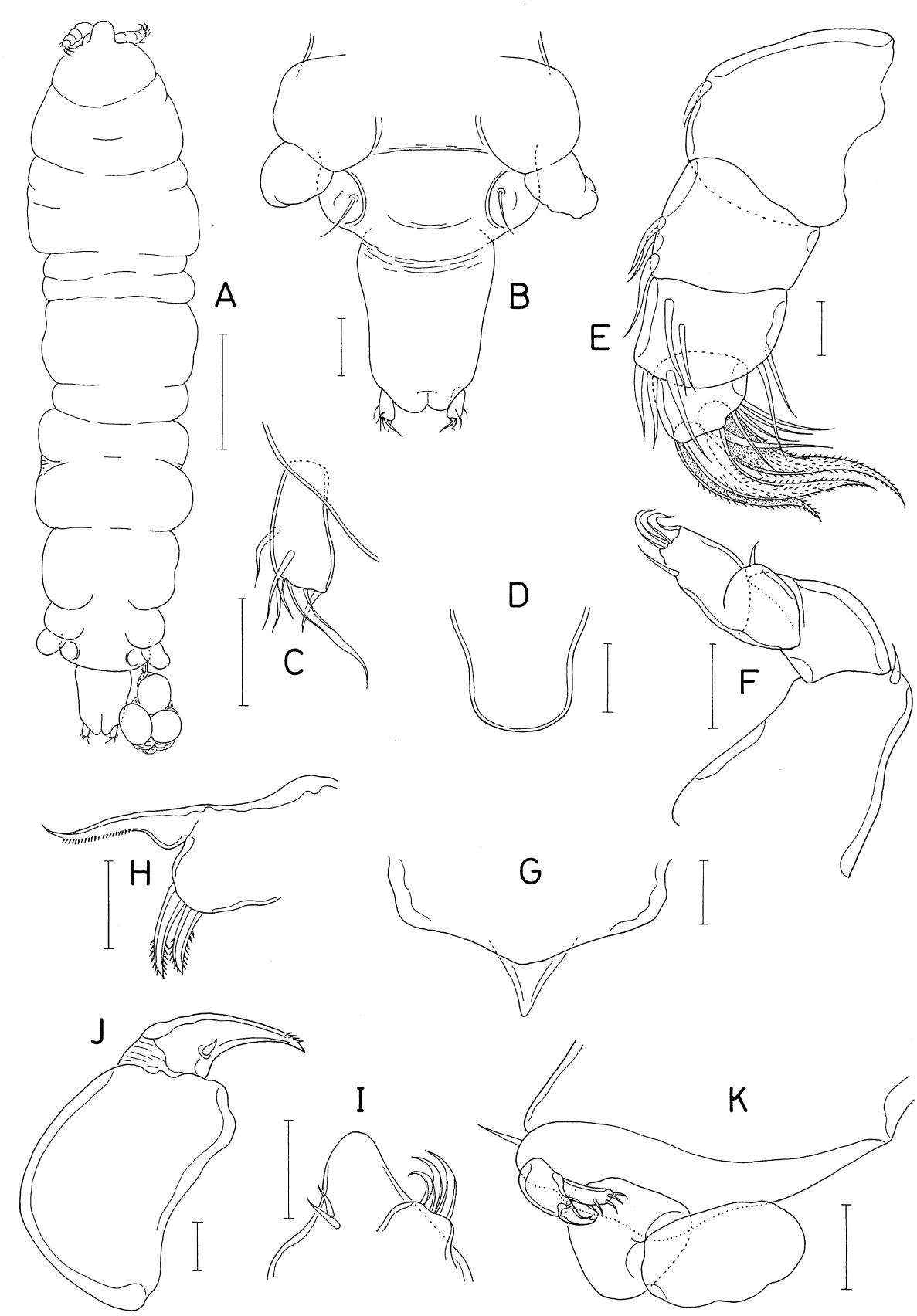

FIGURE 32. *Notomasticola frondosus* **n. gen. et n. sp.**, holotype female. A, habitus, dorsal; B, urosome, dorsal; C, left caudal ramus, dorsal; D, rostrum; E, antennule; F, antenna; G, labrum; H, mandible; I, maxillule; J, maxilla; K, leg 1. Scale bars: A, 0.5 mm; B, 0.1 mm; C, D, K, 0.05 mm; E–J, 0.02 mm.

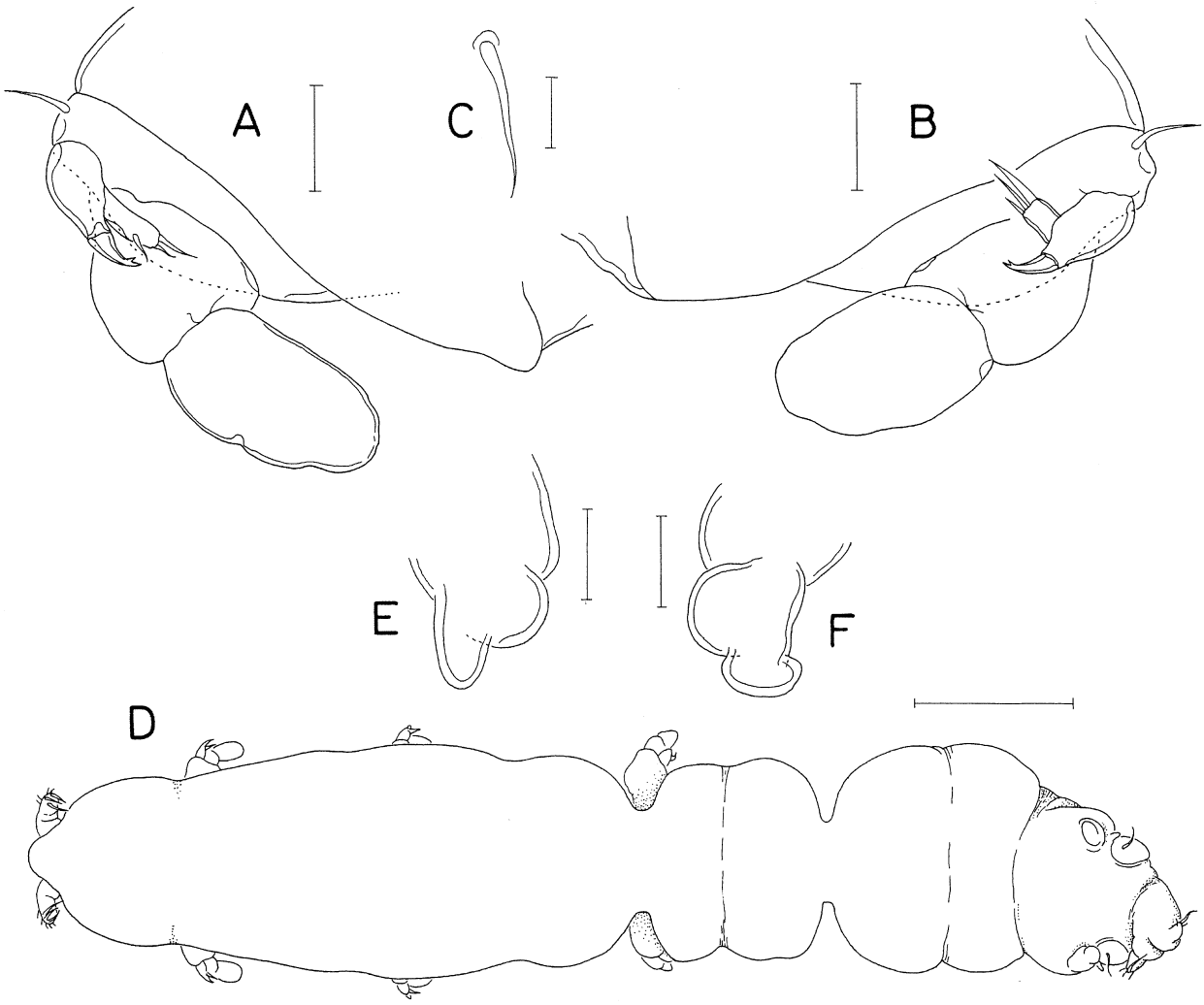

FIGURE 33. *Notomasticola frondosus* **n. gen. et n. sp.**, holotype female. A, leg 2; B, leg 3; C, leg 4. Paratype female, D, habitus; E, F, maxillipeds. Scale bars: A, B, 0.05 mm; C, E, F, 0.02 mm; D, 0.5 mm.

Four of the five specimens associated with hosts lived in the gut of *Notomastus latericeus*, a relatively large polychaete which we believe to be the typical host. We suspect that the other smaller polychaete, *Pseudopolydora paucibranchiata*, is not the usual host.

Discussion

Eleven families of copepods are recorded exclusively from polychaete hosts (Boxshall & Halsey, 2004), but most are rarely encountered and host affiliations are often unknown because specimens had been dislodged from their hosts during the benthic sampling process. Many early records of representatives of families that we now consider to be primarily associated with polychaete hosts refer to material found in washings of other invertebrate groups or in sediment and residues after removal of macrobenthos. The material available here allows us to fill in some of the gaps in our knowledge of the host taxa utilised by copepods associated with polychaetes.

Even in the relatively well-studied European seas the diversity of copepods utilizing polychaetes as hosts has been significantly underestimated, and only the nereicoliform copepods are considered in this paper. However, we have noted a similar, unreported diversity of the more highly transformed copepods, such as those belonging to the families Saccopsidae Lützen, 1964, Phyllodicolidae Delamare Deboutteville & Laubier, 1961 and Herpyllobiidae Hansen, 1892, on polychaetes in European waters. These will be considered elsewhere.

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