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Porcellidiidae of Australia (Harpacticoida, Copepoda). I. A Reassessment of the European Species of *Porcellidium*

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ABSTRACT. A new species, *Porcellidium rastellum*, is described from NSW bringing the total number of species in that genus for Australia to seven. Unlike other Australian genera in the Porcellidiidae, *Porcellidium* Claus, 1860 is ill defined. *Porcellidium viride* (Philippi, 1840) is considered the type species to the genus, but it has never been adequately characterized. This has led to considerable disagreement on the characters that define the genus. *Porcellidium viride* can be identified from a species specific character shown by Brady's (1880) drawing of the male antennules. Another species, *Porcellidium fimbriatum* Claus, 1863, can also be identified by species specific characters shown in the more complete description by Claus (1889). This enables new specimens of these two species to be identified with a high degree of certainty. In the present study, specimens collected from Oban, Scotland, identified as *P. viride* and *P. fimbriatum*, have been used to redescribe both species in detail and select species specific characters for a diagnosis of each species. A new diagnosis for the genus *Porcellidium* is given, based on the characters of *P. viride*. Extensive enquiry suggests that Philippi's and Claus' type material is lost. To ensure taxonomic stability of the genus *Porcellidium*, a neotype of *P. viride* is designated. From this study it is shown that *P. lecanoides* Claus, 1889 and *P. sarsi* Bocquet, 1948 are junior synonyms for *P. viride*. The new diagnosis for *Porcellidium* excludes many of the species originally placed in that genus. *Porcellidium tenuicauda* Claus, 1860 and *P. scutatatum* Claus, 1889 are examples of species that possess apomorphic characters excluding them from *Porcellidium* sensu stricto. A new genus, *Porcelloides* gen. nov. is proposed to take Claus' two species, as *Porcelloides tenuicaudus* (Claus, 1860) comb. nov., and *Porcelloides scutatatus* (Claus, 1889) comb. nov. Keys to the known species of *Porcellidium* and *Porcelloides* are given.

KEYWORDS: Porcellidiidae, *Porcellidium*, *Porcelloides*.

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Considerable progress has been made in our understanding of the family Porcellidiidae from recent studies on the fauna of the West Pacific Ocean. The works of Gamô (1969), Ho (1986), S. Kim & W. Kim (1996), Harris & Iwasaki

(1996a,b), Il-H. Kim & H.-S. Kim, (1997) and Harris & Iwasaki (1997, 2009) have described in detail 17 new species from Japan and Korea while another 23 new species have been described from Aotearoa (New Zealand) and Australia,

Hicks (1971), Hicks & Webber (1983), Harris & Robertson (1994), Harris (1994, 2002), Walker-Smith (2001). These studies provided a wealth of information on porcellidiid structure and a clearer understanding of the wide range of features that could be used as taxonomic characters.

Many of the new species collected from Australia could not be assigned to *Porcellidium* as understood at that time. This led Harris & Robertson (1994) and Harris (1994) to erect five new genera to accommodate the rejected species. Huys *et al.* (1996) considered that these new genera were “based on dubious grounds” and “without any prior revision of the highly speciose type genus *Porcellidium* it does not seem justified to maintain these Australian genera.” The problem was that *Porcellidium viride* Philippi, 1840 had never been described in sufficient detail to compare it with the Australian species, despite the fact that it is considered the type species to the genus. Without a detailed description of both male and female of the type species it was impossible to give a definitive diagnosis for *Porcellidium*.

Among recent authors there is no complete agreement on the characters that define *Porcellidium*. The diagnoses of Harris & Robertson (1994), Huys *et al.* (1996), Harris & Iwasaki (1996) and Walker-Smith (2001) all fail on the following grounds: (a) there is no clear statement as to the criteria upon which genera are defined, (b) absence of detailed information about males of the four European species upon which the genus is based and (c) freedom from the ideas and synonymies of previous authors, such as Lang (1948). The description of Japanese and Australian species have provided a wealth of information on fine morphological detail, particularly of the male antennule, and a clearer understanding of the range of apomorphic and plesiomorphic characters that can be used for taxonomic purposes. Walker-Smith (2001) has pointed out that genera should be based on apomorphic characters and it can be shown that the new genera proposed by Harris & Robertson (1994), Harris (1994, 2002), Harris & Iwasaki (1996b, 1997, 2009) all display apomorphies that separate them from one another.

Porcellidium is no longer regarded as the only genus in the Porcellidiidae. *Tectacingulum* and *Brevifrons*, Harris (1994) and *Clavigofera* and *Kushia*, Harris & Iwasaki (1996b) have been accepted by Bodin (1997), Walker-Smith (2001) and Wells (2007). *Dilatatiocauda* Harris (2002) has been accepted by Wells (2007). But the genus *Porcellidium* still remains poorly defined and the number of species that should be assigned to it is uncertain. It is important, therefore, that the European species, upon which *Porcellidium* was originally based, should be redescribed in detail so that a new diagnosis can be given for the genus.

A description of *Porcellidium viride* was given by Brady (1880). Although this description is inaccurate and hopelessly confused, his illustration does show one species specific character (related to the male's antennule) that makes it possible to recognize the species with a high degree of certainty. Consequently it has been possible to identify specimens, collected from Scotland in the present study, as *Porcellidium viride*. This enabled a full redescription of the species to be made with a clearer understanding of its species specific characters. *Porcellidium viride* is regarded as the type species to the genus (Apostanov & Marinov, 1988) and so it is now possible to give a definitive diagnosis for the genus *Porcellidium* from the new description of *P. viride*. To give taxonomic stability to the taxon, an adult male *P. viride*

collected at Clachan, Seil Sound, Oban is designated as the neotype. Among other places in Scotland, Brady records the species from Loch Fyne not far from Seil Sound, Oban. Brady (1880) misidentified the adult female of his *P. viride* and called it *Porcellidium fimbriatum*. This was largely due to the inadequate description Claus (1863) gave for *P. fimbriatum*, but the error was perpetuated by other early authors, Thompson & Scott (1903), Sars (1904), Monard (1928), Lang (1948), (see also Appendix 1).

In 1889 Claus redescribed *Porcellidium fimbriatum* and his illustrations show species-specific characters that allowed positive identification of animals collected from Oban, Scotland. The species is redescribed in detail.

A direct consequence of re-diagnosis for *Porcellidium* is that many species originally placed in that genus are now excluded and must be assigned to other genera. For example *Porcellidium tenuicauda* Claus, 1860 and *P. scutatum* Claus, 1889 both have apomorphic characters that are not found in *Porcellidium* or any other genera of the Porcellidiidae. It is proposed to assign them to a new genus, *Porcelloides* gen. nov., as *Porcelloides tenuicaudus* (Claus, 1860) comb. nov., and *Porcelloides scutatus* (Claus, 1889) comb. nov.

The new descriptions of European species means that they can now be compared with Japanese and Australian species to expand our understanding of character diversity in the family.

Methods and nomenclature

Longitude and latitude of collecting sites were made by extrapolation from Ordinance Survey maps and are only approximate. Dates are given as day/month/year.

Animals were collected by washing a sample of seaweed for about three minutes in a bucket containing a 50/50 mixture of soda water saturated with CO₂ (from soda siphon or bottled soda water) and fresh water. This appears to anaesthetize copepods and other small marine animals, these were then collected by removing the seaweed, allowing another three minutes for the animals to sink to the bottom and then pouring off most of the water (which was used again). Five percent formalin was then added to fix the animals. Porcellidiid copepods were extracted using a dissecting microscope and then preserved in 5% borate buffered formalin. This method of collection has the advantage that the male antennule remains fully extended and is easy to study. Specimens usually retain their colouration for several years in the buffered formalin.

For each new Australian species an adult male was chosen as holotype and an ovigerous female as allotype from the type series selected from one of the samples washed from seaweeds. Nearly all the illustrations are drawn from paratype material. This is because fine details that show species specific characters are difficult to measure or draw from the type specimens without dissection. To overcome this problem, paratype specimens from the type series were dissected and used to draw the unique and general structures of each species. Dissections were mounted in polyvinyl lactophenol. Drawings were made either by means of a drawing-tube attachment or from digital photographs. Numbers on some of the drawings refer to the slides from which they were drawn. Measurements were made using a calibrated micrometer eyepiece or from calibrated digital

photographs. The delicate hyaline membrane that surrounds the cephalosome and metasome segments is not shown in the drawing of adult animals, but may be illustrated in detail elsewhere. The extremely fine hair-like setules and “feathering” of setae found on mouthparts and ambulatory limbs is only indicated diagrammatically in the drawings.

Terminology follows Harris & Robertson (1994). Members of the Porcellidiidae are poor swimmers. Their antennae and limbs P2, P3 and P4 are highly specialized for movement over the surface of seaweed and will be referred to as “ambulatory limbs”. Comparison of caudal setae with other copepods is difficult because the furca is modified for protecting the egg mass. The rami are flattened and the setae greatly shortened. There are two dorsal setae (α and β) plus a third (γ) which is usually inserted at the lateral region of the posterior border. Typically there are four terminal setae (T1–T4) on the posterior border of the caudal ramus (Figs 21E, 22H), but T1, T2 or T3 may be missing on certain species. Wells (2007:871, fig. 120) gives a diagram illustrating the differences between the above notation and that of Huys & Boxshall (1991). The terms “serrulate” is used to denote very fine short serration on setae, “plumulose” is used to describe very fine “feathering” on antennule setae and “pinnate” for fine feathering on terminal caudal setae. Because the caudal rami can be held in line with the body or depressed downwards, some animals may appear much shorter than others. A more reliable measure is the distance from rostrum to the extremity of the genital double-somite. This is denoted by the symbol L_{URS} and the distance to the extremity of the caudal furca by the symbol L_{MAX} . The male antennule is measured in the fully extended position. The position of α and β seta relative to the posterior border of the female caudal ramus is a useful parameter in distinguishing between some species. Here it is expressed as the Hick’s index defined as the distance of either α or β seta from the posterior border of the ramus divided by the length of the ramus expressed as a percentage (i.e., $\alpha/\text{ramus length} \times 100$).

The following abbreviations are used. NHM—Natural History Museum, London; NMI—National Museum of Ireland, Dublin; AM—Australian Museum, Sydney.

Systematics

Family Porcellidiidae Boeck, 1865

Type genus: *Porcellidium* Claus, 1860

Diagnosis. Antennule of adult male subchirocer, six segmented, less than half body width, segment 3 partly fused with segment 4, coupling denticles on ventral surface of segment 4; antenna exopod of one segment with six setae; large mandibular palp, anterior lobe with four bulbous setae, posterior lobe with one annulate seta and five bulbous setae, endopod with nine setae; cephalosome surrounded by hyaline membrane (in one genus the hyaline membrane is located on the ventral surface of the cephalosome) with eight embedded border sensilla (six or seven sensilla in species where the anterior border of the cephalosome is turned ventrally); epipleural lobe of metasome segment 3 expanded in male, reduced in female; urosome consists of 5th somite, genital double-somite, anal somite and caudal furca; furca

composed of two flat plates or rami each with seven setae, setae never longer than ramus, (α and β dorsal, γ terminal, plus four terminal setae [may be reduced to three or two in some species]); strong sexual dimorphism.

Generic composition. *Porcellidium* Claus, 1860; *Tectacungulum* Harris, 1994; *Murramia* Harris, 1994; *Brevifrons* Harris, 1994; *Acutiramus* Harris & Robertson, 1994; *Clavigofera* Harris & Iwasaki, 1996b; *Kushia* Harris & Iwasaki, 1996b; *Kensakia* Harris & Iwasaki, 1997; *Mucrorostrum* Harris & Iwasaki, 1997; *Dilatatiocauda* Harris, 2002; *Porcelloides* gen. nov.

Genus *Porcellidium* Claus, 1860

Type species. *Porcellidium viride* (Philippi, 1840).

Diagnosis [an alternative (apomorphic) character state is known for all characters marked with an asterisk]. Spermatophore elongate* (sausage shaped), female receives only one spermatophore during her life span, usually deposited on ventral surface of the genital double-somite at time of metamorphosis from stage V copepodid to adult, attachment to female ephemeral (shed before egg laying starts); body oval*, dorsoventrally compressed*; male cephalosome truncated anteriorly*, female not truncated anteriorly*; animals do not conglobate*; dorsal organs absent*, no massive honeycomb-like cuticle; hyaline border surrounds cephalosome*, marginal glands open dorsal to hyaline border*; female genital double-somite broad*, divided into anterior and posterior lobes*, rounded posteriorly*, lateral striations absent*; male genital somite never fused to metasome segment 4 and P5 baseoendopod*; female caudal ramus rectangular*, setae T1 to T4 always present* (T1 may be recessed), never pinnately clavate or evenly spaced*; no ridge-plates on labrum*; six setae on maxillule endopod*; maxilliped coxae touch in midline*, basis with fimbriate process*; limbs P2, P3, P4 with three external spinous setae on exopod segment 3*; P5 shorter than genital double-somite*, ventral expansion absent*; male antennule segment 3 setae δ and δ' always present*, anterior comb absent*, blade or knob-like ventral process may be present, segment 4 with three denticles*, brush-pad never present*; male P5 trapezoid with six setae*.

Species composition. *Porcellidium viride* (Philippi, 1840); *P. fimbriatum* Claus, 1863; *P. roscoffensis* (Bocquet, 1948) comb. nov. (northeast Atlantic coast of Europe and Mediterranean Sea); *P. rubrum* Pallares, 1966 (Argentina); *P. erythrum* Hicks, 1971 (Aotearoa, New Zealand); *P. hartmannorum* Tiemann, 1978; *P. algoense* Hicks, 1982 (East and West coast of South Africa); *P. hormosirii* Harris & Robertson, 1994; *P. ocellum* Harris & Robertson, 1994; *P. pulchrum* Harris & Robertson, 1994; *P. erythrogastrum* Harris & Robertson, 1994; *P. naviculum* Harris & Robertson, 1994; *P. phyllosporum* Harris & Robertson, 1994; *P. londonarum* Harris, 1994 (name correction for *P. londonii* by Wells, 2007); *P. rastellum* sp. nov. (East Coast of Australia); *P. ofunatense* Harris & Iwasaki, 1996; *P. kiiroum* Harris & Iwasaki, 1996; *P. akashimum* Harris & Iwasaki, 1996; *P. wandoensis* Kim & Kim, 1997; *P. brevicavum* Kim & Kim, 1997 (Japan and Korea).

Key to the species of *Porcellidium*

The antennules of male porcellidiids provide numerous species specific characters, consequently any male animal, for which the antennule has been described in detail, can be identified with a high degree of certainty. In marked contrast, very few species specific characters have been found on female members of the genus *Porcellidium*, consequently the females of less than half of the 20 recognized species can be identified. This is because female characters are based upon shape, position, size or number of body parts which will vary within a species and their measurements or ratios may overlap with other species.

The following key will rely heavily on characters of the male antennule which must be viewed from the ventral side in the fully extended position (see *Methods and nomenclature*). Female ratios are given to help confirm the identity of the female animals. [Abbreviations: CR caudal ramus; GDS genital double-somite; L length of animal; H.I. Hicks' index for α or β setae; * see Hicks, 1982:64].

- | | | |
|---|---|---|
| 1 | Male antennule with ventral process or “blade” on segment 3 (see Fig. 12D, F) | 2 |
| — | Male antennule with “peg” or swollen knob on segment 3 (see Fig. 7F) | 3 |
| — | No blade, peg or knob on segment 3 of male antennule | 4 |
| 2 | Ventral process short ($\frac{1}{4}$ length of segments 3+4), coupling denticle 1 on segment 4 flat with serrated edge, denticles 2 and 3 very small, botryoidal, segment 6 distinct (not fused with segment 5). Ventral surface of male and female cephalosome wrinkled (Fig. 12A). Female GDS with deep cleft between anterior and posterior lobe. Body length male 0.56 mm, female 0.77 mm, CR/L = 18%, CR l/w = 2.8, H.I. for β = 25%, setae T1–T4 pinnate. Colourless with broad band of dark blue down middle of back. Europe. (Plate 1C,E, p. 67) | <i>P. fimbriatum</i> (Claus, 1863) |
| — | Ventral blade almost as long as segments 3+4, segment 3 with spine ventral to δ seta, denticle 1 on segment 4 comb-like, 2 and 3 serrate, segment 5 hooked, fused with 6. Body length male 0.55 mm, female 0.71 mm, CR/L = 7%, CR l/w = 1.2, H.I. for β = 20%. Colour yellow with broad red dorsal stripe. Australia. (Plate 2B, p. 69) | <i>P. pulchrum</i> Harris & Robertson, 1994 |
| — | Ventral blade bifid, $\frac{1}{2}$ length of segments 3+4, denticle 2 on segment 4 spherical with surface serrations, denticle 3 large flat triangle with distal border serrated, segment 5 not hooked fused with 6. α seta on female CR thicker than other setae. Body length male 0.50 mm, female 0.68 mm, CR/L = 12%, CR l/w 1.7, H.I. for β = 22%. Amber colour. Australia | <i>P. hormosirii</i> Harris & Robertson, 1994 |
| — | Ventral blade $\frac{1}{2}$ length of segments 3+4, segment 3 with finger-like lobe pointing forward ventral to δ seta, denticles 1, 2 and 3 triangular with double serrated edge, segment 6 fused with 5. Body length male 0.56 mm, female 0.67 mm, CR/L = 6%, CR l/w 1.5, H.I. for β = 32%, GDS with lateral notch. Colourless with red area round ocellus and larger red dot in middle of back. Australia. (Plate 2H, p. 69) | <i>P. ocellum</i> Harris & Robertson, 1994 |
| — | Ventral blade $\frac{1}{2}$ length of segments 3+4, denticle 1 on segment 4 comb-like, 2 and 3 with serrated edge, segment 5 small, fused with 6. Body length male 0.61 mm, female 0.83 mm, CR/L = 5.5%, CR l/w 1.45, H.I. for β = 10%, GDS with lateral notch. Colourless with areas of thickened ventral cuticle dark red. Australia. (Plate 2A, p. 69) | <i>P. erythrogastrum</i> Harris & Robertson, 1994 |
| — | Ventral blade $\frac{3}{4}$ length of segments 3+4, denticle 1 on segment 4 double serrated, 2 tooth-like, 3 with serrated edge, segment 5 hooked, fused with 6. Body length male 0.57 mm, female 0.75 mm, CR/L = 11%, CR l/w 2.2, H.I. for β = 9%, GDS with scar and very small notch. Coral pink with small iridescent light blue areas at trabeculae, GDS scar and between metasome segments. Australia. (Plate 2F, p. 69) | <i>P. londonarum</i> Harris, 1994 |

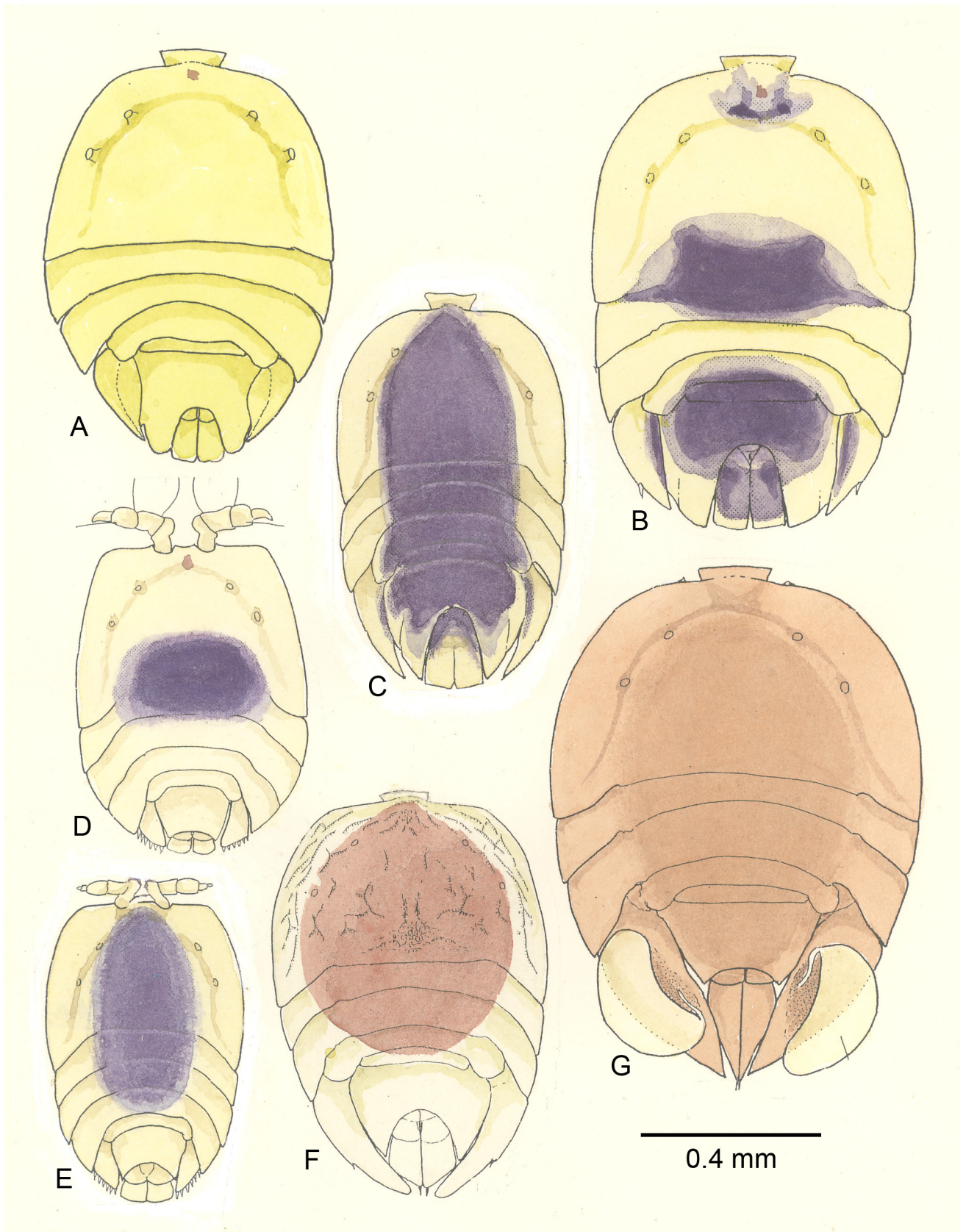


Plate 1. (A) *Porcellidium rastellum* sp. nov., female (Australia). (B) *Porcellidium viride* Philippi, 1880, female (Scotland). (C) *Porcellidium fimbriatum* Claus, 1863, female (Scotland). (D) Male *P. viride*. (E) Male *P. fimbriatum*. (F) *Porcelloides scutatus* (Claus, 1889) female (Ireland). (G) *Porcelloides tenuicaudus* (Claus, 1860) female (Scotland). Scale bar: 0.4 mm.

- Ventral blade slightly more than $\frac{1}{2}$ length of segments 3+4, large thorn-like spine ventral to δ seta. P1 endopod with band of minute setules down medial edge and smaller area on lateral edge. Distance between T3 and T4 on female CR = 10% of CR width, T1 = T4 in length. Body length, male 0.46 mm, female 0.61 mm. Female CR/L = 9%, CR l/w = 1.4, H.I. for β = 15%, GDS cleft with lateral notch. [Original description incomplete]. S. Africa *P. algoense* Hicks, 1982
- Ventral blade as long as segments 3+4, talon-shape*. Ventral seta on male P5 baseoendopod 95% of exopod length. Female CR seta T4 > twice length of T1, distance between T3 and T4 25% of ramus width, Body length male 0.61 mm, female 0.69 mm. Female body L/W = 1.6, CR/L = 11%, CR l/w = 1.5, H.I. for β = 23%, GDS w/l = 1.4. Ruby red. Argentina, Tristan da Cunha *P. rubrum* Pallares, 1966
- Ventral blade present*. Ventral seta on male P5 baseoendopod 40% of exopod length. Female T1 = T4 in length, distance between T3 and T4 10% of ramus width. Body length male 0.55 mm, female 0.76 mm, female body L/W = 1.7, CR/L = 11%, CR l/w = 1.8, H.I. for β = 15%, GDS w/l = 1.3. Red-brown. SW. Africa *P. hartmannorum* Tiemann, 1978
- 3 First seta on male antennule segment 2 > twice length of setae 2 and 3, five plumulose setae on segment 2, denticles on segment 4 denticulate pads (Fig. 7A). Male P5 almost rectangular, apical angle 75°. Body length male 0.62 mm, female 0.91 mm, CR/L = 15%, CR l/w 2.3, H.I. for β = 50%. Border of boundary between anterior and posterior lobes of GDS marked by a clear area without dorsal pits or border setules. Large serrated seta on P3 1.4 times length of endopod. Colourless with variable pattern of dark blue/purple areas. Europe. (Plate 1B,D, p. 67) *P. viride* (Philippi, 1840)
- First seta on male antennule segment 2 same length as setae 2 and 3, no plumulose setae on segment 2. Ventral surface of male rostrum with U-shaped ridges (Fig. 14F). Male P5 trapezoid, apical angle 40°. Body length male 0.70 mm, female 0.85 mm, CR/L = 14%, CR l/w 2.4, H.I. for β = 16%. GDS with slight indentation without setules. Dorsal surface of CR with pits. Large serrated seta on P3 1.4 \times length of endopod. Europe *P. roscoffensis* (Bocquet, 1948)
- First seta on male antennule segment 2 same length as setae 2 and 3, no plumulose setae on segment 2, first denticle on segment 4 finger-like with serrulate edge, segment 5 expanded laterally. Hyaline border of cephalosome striated. Female rostrum obscured by anterior bulge of cephalosome. Body length male 0.69 mm, female 0.84 mm, CR/L = 8%, CR l/w = 1.95, H.I. for β = 33%. GDS with notch. Large serrated seta on P3 short, 1.1 times length of endopod. Yellow with red dorsal stripe. Japan. (Plate 2G, p. 69) *P. akashimum* Harris & Iwasaki, 1996
- 4 P1 endopod segment 1 with band of minute setules down medial edge (Fig. 2E) 5
- P1 endopod segment 1 without any minute setules down medial edge 6
- 5 Female body elongate, length to width ratio = 2.18, cephalosome width/rostrum = 3.3. Male antennule segment 4 denticle 1 pointed with serrulations along both edges, denticle 2 tooth-like, 3 with serrulate edge. Body length male 0.57 mm, female 0.72 mm, CR/L = 6.5%, CR l/w = 1.25, H.I. for β = 7.7%, GDS width/length = 1.25, arch 26% of length. Amber colour. Australia. (Plate 2E, p. 69) *P. naviculum* Harris & Robertson, 1994

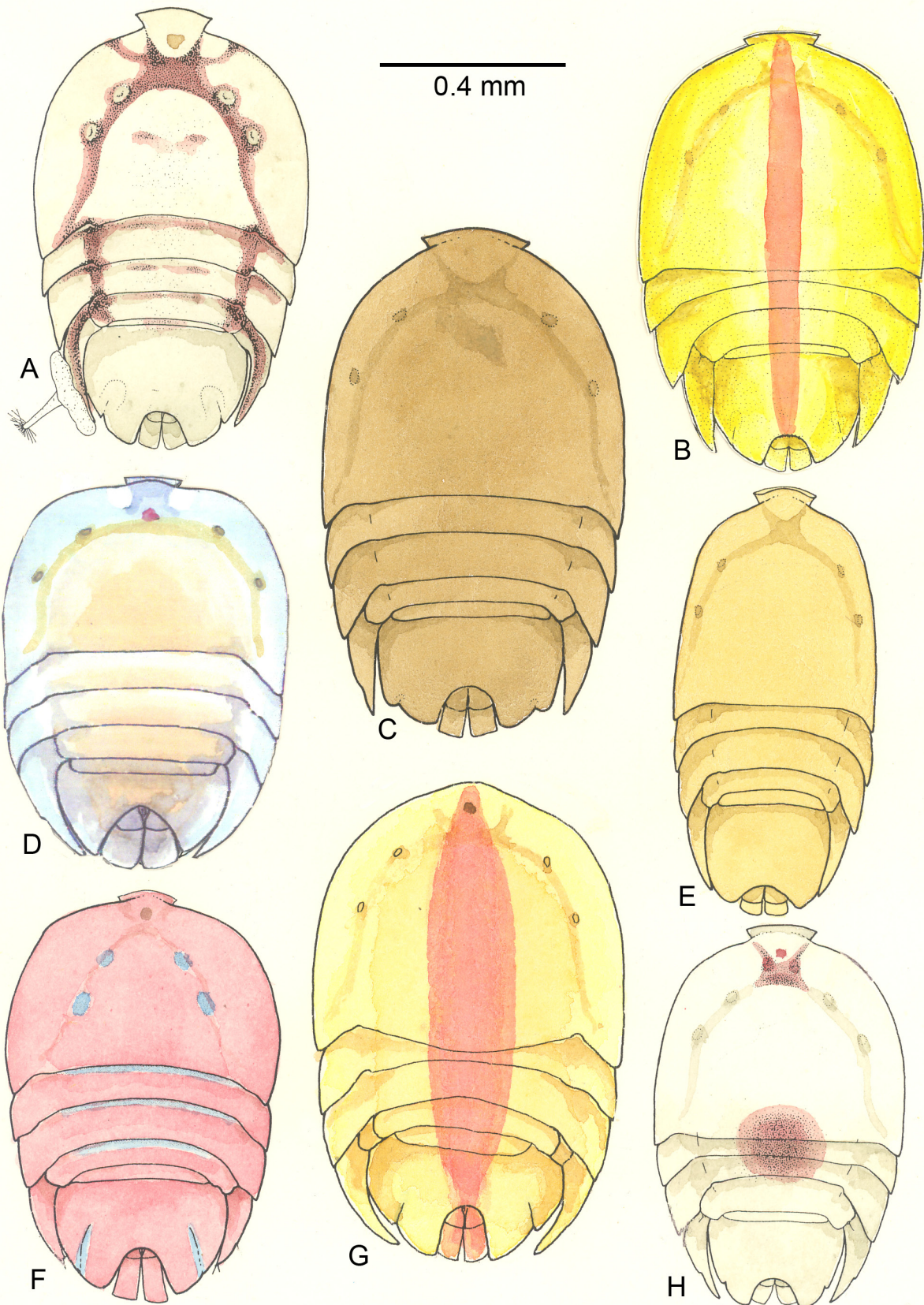


Plate 2. (A) *Porcellidium erythrogastrum* Harris & Robertson, 1994, female (Australia). (B) *P. pulchrum* Harris & Robertson, 1994, female (Australia). (C) *P. phyllosporum* Harris & Robertson, 1994, female (Australia). (D) *P. wandoensis* Kim & Kim, 1997, female (Korea and Japan). (E) *P. naviculum* Harris & Robertson, 1994, female (Australia). (F) *P. londonarum* Harris, 1994, female (Australia). (G) *P. akashimum* Harris & Iwasaki, 1996, female (Japan). (H) *P. ocellum* Harris & Robertson, 1994, female (Australia). Scale bar: 0.4 mm.

- Female body broad oval, length to width ratio = 1.7, rostrum very broad, cephalosome width/rostrum = 2.8. Male antennule segment 2 triangular, denticle 1 on segment 4 C-shaped. Body length male 0.73 mm, female 0.93 mm, CR/L = 5.8%, CR l/w = 1.05, H.I. for β = 25%, GDS very broad width/length = 1.6, arch 20% of length. Orange brown colour. Australia. (Plate 2C, p. 69) *P. phyllosporum* Harris & Robertson, 1994
- Large lateral area of fine setules on P1 endopod. Female rostrum (Fig. 11) a horizontal bar in ventral view (not triangular), not broad, cephalosome width/rostrum = 4.48. Denticle 1 on segment 4 of male antennule with serrate edge, 2 small with lateral serrulation, 3 long, tooth-like. Body length male 0.54 mm, female 0.79 mm, CR/L = 11%, CR l/w = 2.4, H.I. for β = 14. GDS width/length = 1.5. Colour pale yellow. Australia. (Plate 1A, p. 67) *P. rastellum* sp. nov.
- Ventral blade absent* Small lateral area of fine setules on P1 endopod. Female P5 very broad, internal seta on baseoendopod very long, 85% of falciform ridge. Large serrated seta on P3 very long, 1.7 times length of endopod. Body length* male 0.48 mm, female 0.57 mm, CR/L = 5.5%, CR l/w = 1.4, GDS w/l = 1.34. Colour blood red. Aotearoa (New Zealand) *P. erythrum* Hicks, 1971
- 6 First denticle on male antennule segment 4 pointed, comb-like, 2 and 3 rounded denticulate or serrulate 7
- Denticles on male antennule segment 4 swollen or bulbous (not serrated or denticulate) 10
- 7 GDS arch short, arch height/width 0.9, arch height/GDS length = 35% 8
- GDS arch high, arch height/width > 0.9, arch height/GDS length = > 40% 9
- 8 First denticle on male antennule pointed, 2 and 3 rounded serrulate. Body length male 0.63 mm, female length 0.73 mm, width/rostrum = 3.9, CR/L = 8.2%, CR l/w = 1.75, H.I. for β = 26%. Arch height 30% of GDS length, arch height/width = 0.7. Korea, Japan *P. brevicavum* Kim & Kim, 1997
- 9 First denticle on male antennule segment 4 pointed, comb-like, 2 and 3 denticulate pads, spine attached to anterior lobe at base of δ seta. Body length male 0.68 mm, female 0.94 mm, cephalosome width/rostrum = 4.2, CR/L = 11%, CR l/w = 2.4, H.I. for β = 40%. Arch height 45% of GDS length, arch height/width = 1.1. Colour orange brown. Japan, Korea *P. ofunatense* Harris & Iwasaki, 1996
- First denticle on male antennule segment 4 pointed, comb-like, 2 and 3 small denticulate pads, no spine attached to anterior lobe. Body length male 0.58 mm, female 0.81 mm, cephalosome width/rostrum = 3.6, CR/L = 10.5%, CR l/w = 2.6, H.I. for β = 41%. Arch height 45% of GDS length, arch height/width = 1.2. Bright yellow. Japan *P. kiiroum* Harris & Iwasaki, 1996
- 10 Denticles on segment 4 of male antennule bulbous (rounded) with feint serrulation unlike the typical pointed, tooth-like or denticulate pad of other species), short thick seta at base of anterior lobe, unique pinnate seta anterior to the first denticle on segment 4. Body length male 0.61 mm, female 0.76 mm, CR/L = 17%, CR l/w = 2.1, H.I. for β = 40–45%. Colour pale blue or pale brown with blue edge. Korea, Japan. (Plate 2D, p. 69) *P. wandoensis* Kim & Kim, 1997

Remarks. The above generic diagnosis is based on animals collected from Oban Scotland and identified as *Porcellidium viride* from Brady's (1880) illustration which shows a species specific character of the male antennule. Brady collected specimens from the same region of Scotland.

Fifty-nine species of *Porcellidium* have been named in the literature, but 18 of these cannot be counted as valid species for the following reasons. Seven names are synonyms for other species i.e., *P. dentatum*, and *P. ovatum* for *Porcelloides tenuicaudus*; *P. lecanoides* and *P. sarsi* for *P. viride*; *P. penicilliferum* for *Dilatatiocauda tristanensis*; *P. acutum* for *Kensakia acuta*; and *P. aofuchidorum* for *P. wandoensis*, three are given to juvenile stages (*subrotundum*, *rotundum*, *australe*) and another eight species cannot be identified or placed in a genus because the original description is devoid of specific characters, (*P. fulvum*, *P. interruptum*, *P. tuberculatum*, *P. affine*, *P. charcoti*, *P. wolfendeni*, *P. scotti*, and *P. malleatum*), however, some of these may prove to be valid species if redescribed in detail.

This leaves 41 species sufficiently well described to be identified and assigned to a genus, though only 20 of these can be assigned to *Porcellidium* on the diagnosis given above. The remaining 21 species possess apomorphic characters that exclude them from *Porcellidium* and must be transferred to other genera within the Porcellidiidae.

The genus *Porcellidium* is not based on apomorphies, but on a combination of characters all of which may be found in other genera either in an apomorphic or plesiomorphic state.

Porcellidium rastellum sp. nov.

Figs 1–3

Type material. HOLOTYPE adult male, length 0.55 mm, P81207; ALLOTYPE adult female, length 0.80 mm, P81208, collected from *Sargassum* sp., sublittoral, Pontoon Rocks, Ballina, NSW, Australia, (28°52'S 153°36'E), V. A. Harris, 1982. PARATYPE specimens P81209 (20 ♀♀, 10 ♂♂, 10 ♂♂ + juvenile) and paratypes P88552, P88553, P88554, all deposited at AM, Sydney. Specimens from the type series and Cronulla, Sydney (50 ♀♀, 30 ♂♂ + 50 ♂♂ coupled to juv. ♀), deposited at NHM, London.

Diagnosis. Female rostrum horizontal bar, (in ventral view not V-shaped (Fig. 1I), anterior edge of cephalosome folded ventrally (Fig. 1D), hyaline border not modified; maxilla with conspicuous rake-like claw (Fig. 2G); P1 exopod segment 1 with conspicuous crescent of denticulate setules, endopod with extensive lateral and medial peg areas consisting of minute denticles arranged in rows (Fig. 2E); male antennule first seta on segment 2 same length as second seta, no plumulose setae on segment 2, segment 3 without ventral process, three denticles on segment 4 none are denticulate pads; female P5 with broad medial dorsal expansion (Fig. 1C). Spermatophore elongate, ephemeral on female.

Biometric data. *Females* (N = 15): maximum length (L_{\max}) 0.79 mm, range 0.76–0.81 mm, body length to end of genital double-somite (L_{urs}) 0.77 mm, range 0.74–0.81 mm; cephalosome width (W) 0.55 mm, range 0.54–0.56 mm; rostrum width (R) 0.12 mm; genital double-somite width 0.28 mm, length 0.19 mm, arch 0.9 mm; caudal ramus length 0.12 mm, width 0.05 mm.

Ratios: L_{urs}/W 1.41; W/R 4.6; genital double-somite w/l 1.5; caudal ramus 15% of L_{urs} , ramus, l/w 2.4, Hicks' index for α 72%, for β 14%.

Males (N = 9): maximum length (L_{\max}) 0.55 mm, body length (L_{urs}) 0.54 mm; cephalosome width 0.45 mm; antennule length 0.135 mm.

Ratios: L_{urs}/W 1.2; antennule 30% of L_{urs} ; segment 2 30%, segment 3+4 46% and dactylus 23% of antennule length.

Description. *Adult females* (Fig. 1A; Plate 1A, p. 67): colour pale yellow, rostrum a horizontal bar in ventral view (Fig. 1I, not V-shape), wide ($W/R = 4.2$). The anterolateral edge of the cephalosome and hyaline border is folded ventrally as far as the second border sensillum, but without modification in structure (Fig. 1D), hyaline border 8–10 μm wide, granular in appearance. Dorsal pits are conspicuous, very few dorsal sensilla. Labrum without ridge plates. Genital double-somite (Fig. 1F) bordered with strong setules, dorsal surface pitted, anterior and posterior lobes separated by deep notch, posterior lobe rounded, arch about half length of genital double-somite. Caudal rami rectangular (Fig. 1E), dorsal surface with pits, no setules on medial or lateral edges, terminal setae pinnate, T1 not recessed, T2 and T3 close together, T4 set in from medial corner which is slightly bevelled, β seta close to posterior border, fringe of setules on posterior edge between T3 and medial corner (Fig. 1H). Structure and setation of ambulatory limbs and mouthparts typical of family. Basis of antenna with oblique double row of setules (Fig. 2A), endopod segment 2 with three lateral setae, end part of geniculate setae plain, terminal claw comb-like. Mandible (Fig. 2F) with strong molar process, small group of setules on anterior lobe of palp, maxillule (Fig. 2C), maxilla endopod with conspicuous rake-like or ctenoid claw (Fig. 2G), maxilliped (Fig. 2B) normal. First ambulatory limb P1 with conspicuous crescent of rod-like denticles parallel to edge of exopod segment 1, endopod has broad band of denticles down medial edge and a large latero-central area of denticles which occupies nearly $\frac{1}{4}$ of the area anterior to the fimbriate crescent, denticles are minute and arranged in parallel rows, endopod l/w = 1.35 (Fig. 2E). Serrulate spinous seta on P2 endopod segment 3 almost as long as endopod (Fig. 3A). Serrate spinous seta on P3 endopod segment 2 (Fig. 2F) shorter than endopod (0.8:1), large serrate spinous seta on segment 3 much longer than endopod (1.4:1). P4 endopod segments 2 with straight serrulate spinous seta, serrulate spinous seta on segment 3 J-shape (Fig. 3B). Ventral seta on base/endopod of P5 reaches back to level of lateral seta on exopod, P5 exopod (Fig. 1C) lanceolate with broad dorsal medial expansion which partly covers genital double-somite (Fig. 1A, C), there are two sub-apical dorsal setae and one short apical seta, dorsal surface of P5 pitted. Females carry eight or 10 eggs in brood chamber.

Adult males (Fig. 1B) colour, dorsal pits and hyaline border as for female. Cephalosome truncated, shoulders smoothly rounded, lateral corner of antennule socket not prominent, anterior edge of cephalosome and hyaline border reflexed ventrally (as in female) but not modified. Dorsal surface of genital double-somite pitted. Caudal ramus (Fig. 1G, J) with bevelled medial corner makes ramus appear pentagonal, dorsal surface with pits. Setae as for female with β seta close to posterior border, T1 not recessed, T4 set in at base of bevelled medial corner, posterior fringe of setules extends past T4 along bevelled edge. Antennule (Fig. 2D) segment 2 short triangular without plumulose setae, first seta not longer than 1.5 times other setae on segment, no ventral process or blade on segment 3, segment 4 with three coupling

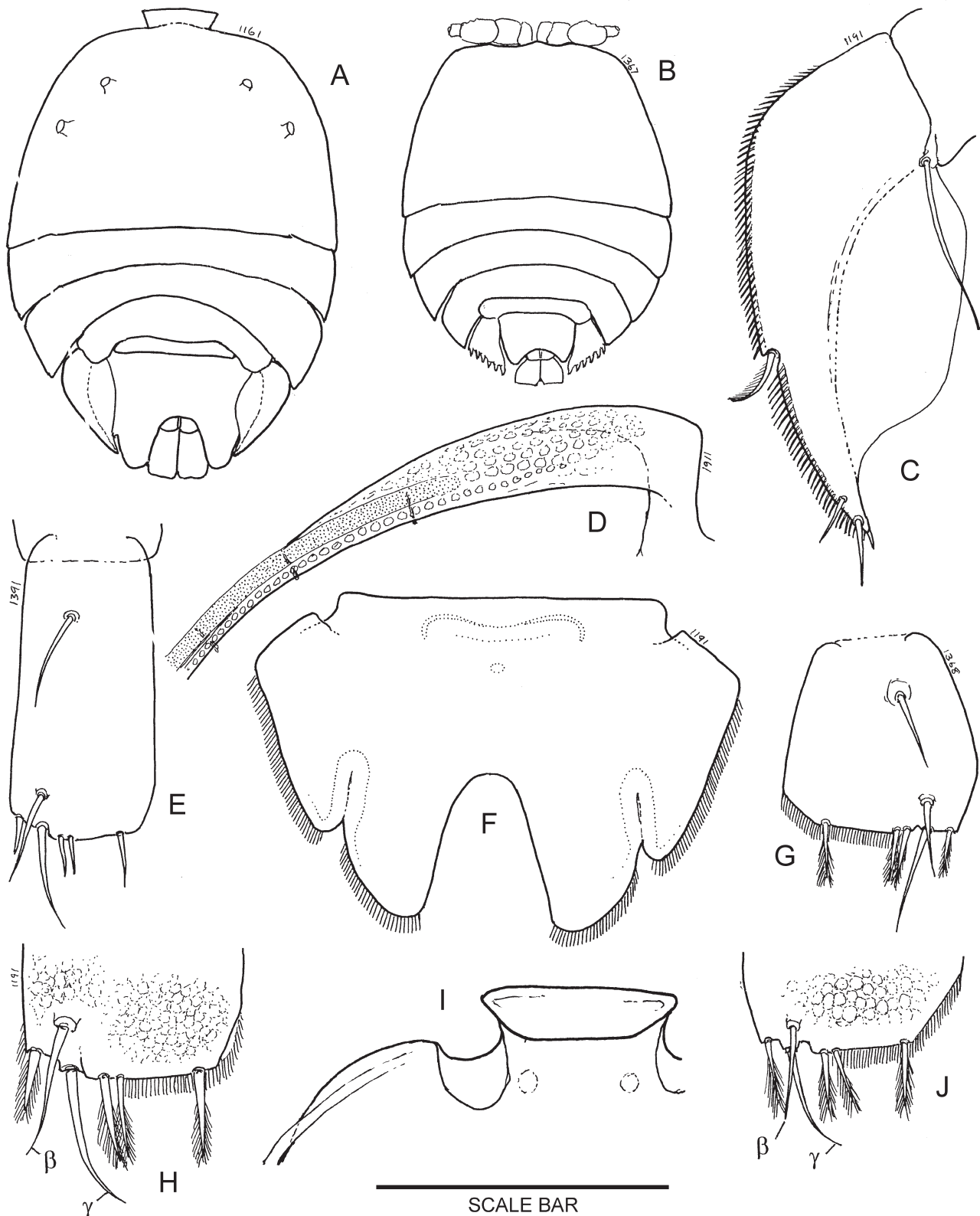


Figure 1. *Porcellidium rastellum* sp. nov. Female: (A) adult; (C) P5 (ventral); (D) anterior edge of cephalosome showing folded edge (ventral); (E, H) caudal ramus; (F) genital double-somite; (I) rostrum (ventral). Male: (B) adult; (G, J) caudal ramus. Scale bar: A, B, = 0.52 mm. C, D, G = 0.09 mm. E = 0.12 mm. F, I = 0.17 mm. H, J = 0.06 mm.

denticles, dactylus short, broad, segment 6 very small. Remaining limbs as for female except that P2 endopod has only two terminal setae (Fig. 3D) and setae on P4 endopod segments 2 and 3 are not spinous (Fig. 3E). P5 trapezoid with

ventral row of setules to lateral seta but no setules at base of terminal setae, dorsal surface pitted (Fig. 3C).

Etymology. The specific name refers to the rake-like claw on the maxilla, (*L. rastellum* = a small rake Fig. 2G).



Figure 2. *Porcellidium rastellum* sp. nov. Female: (A) antenna; (B) maxilliped; (C) maxillule; (E) P1; (F) mandible; (G) maxilla (*rake-like claw on endopod). Male: (D) antennule. Scale bar: A, B, E, F = 0.12 mm. C, D, G = 0.06 mm.

Remarks. *Porcellidium rastellum* differs from most other members of the genus in the large areas of very small denticles that appear to be arranged in rows on the ventral (anterior) surface of the P1 endopod. Another unusual feature is the way in which the anterior part of the cephalosome

border is folded ventrally. This results in a portion of the hyaline border lying in a ventral position. However, this does not correspond to the condition in *Tectacingulum* because there is no modification of the hyaline border and only the anterior part of the border is reflexed.

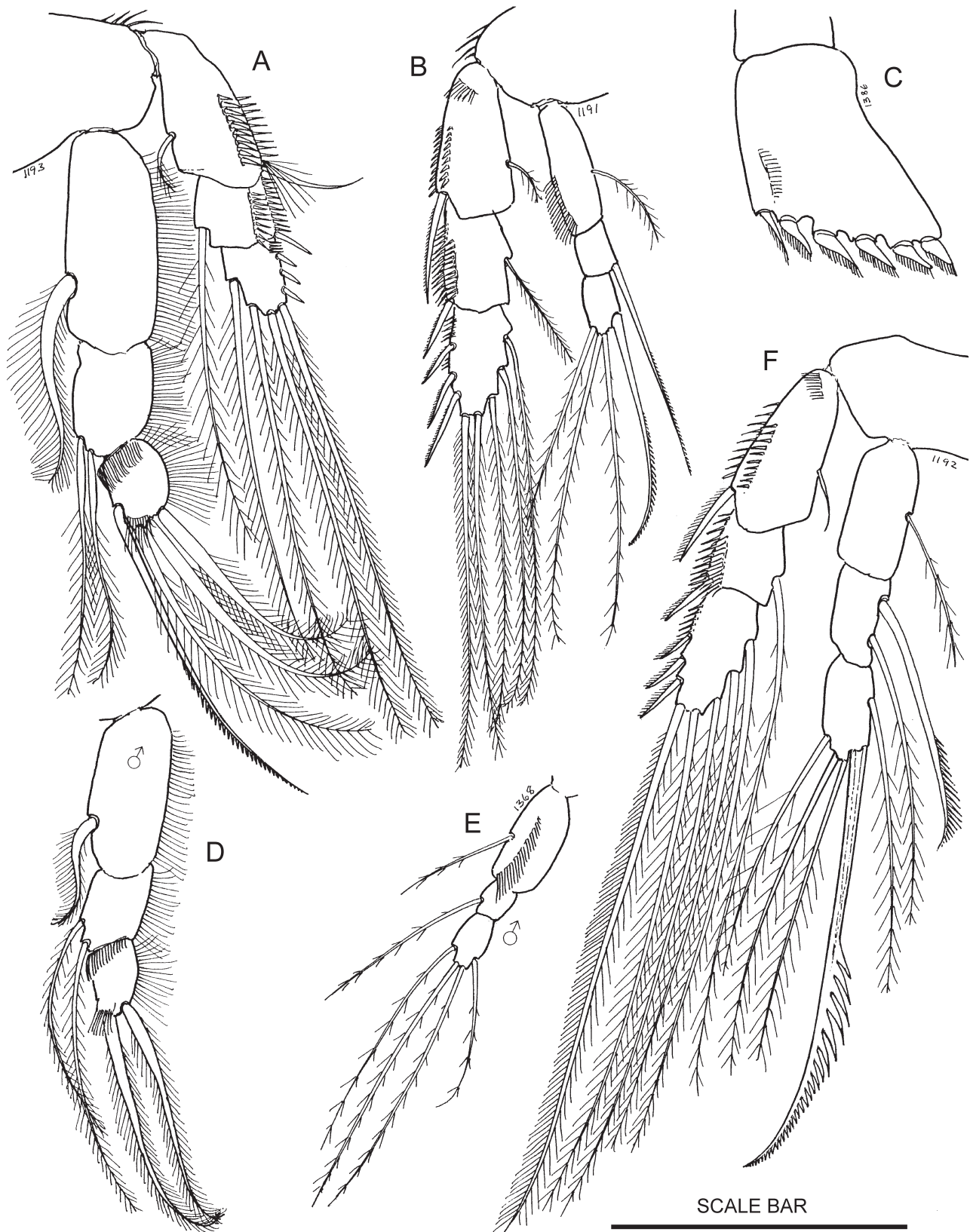


Figure 3. *Porcellidium rastellum* sp. nov. Female: (A) P2; (B) P4; (F) P3. Male: (C) P5; (D) P2 endopod; (E) P4 endopod. Scale bar: A–F = 0.09 mm.

Distribution. The species has been recorded as abundant on several algal species from Nambucca, northern NSW (30°37'S) to Broulee (35°52'S), but not from Hervey Bay, Queensland (25°15'S) or Eden, southern NSW (37°06'S). Collected from *Sargassum* sp., Ballina, Bal12.11/82, 162

♀♀, 44 ♂♂ + 90 ♂♂ coupled to juvenile female: Nambucca, Nb6.11/82, 141 ♀♀, 160 ♂♂ mostly coupled. *Rhodymenia?* Type series, Ballina, Bal14.11/82, 225 ♀♀, 176 ♂♂. *Lobophora* sp., Cronulla, Sydney, Cr19.8/75: Cr33.2/77, 100+, V. A. Harris 1975, 1977, 1982.

***Porcellidium viride* (Philippi, 1840)**

Figs 4–8

Thyone viridis Philippi, 1840:190, pl. IV, fig 2.*Porcellidium subrotundum* Norman, 1868.—Brady, 1880: 169–170.*Porcellidium lecanoides* Claus, 1889.—Holmes & O'Connor, 1990: 66; Huys *et al.*, 1996: 308; Walker-Smith, 2001: 656; Wells, 2007:79.*Porcellidium viride*.—Brady, 1880: 168–169; Lang, 1948: 420–422; Apostanov & Marinov, 1988: 101–102; Harris & Robertson, 1994: 301; Bodin, 1997: 65.*Porcellidium fimbriatum* Claus, 1889.—Brady, 1880 (female): 167; Thompson & Scott, 1903: 227; Sars, 1904: 76–77.*P. fimbriatum* var. *heraldicum*.—Monard, 1928: 324–326; Monard, 1935.*Porcellidium sarsi*.—Bocquet, 1948: 237–259; Holmes & O'Connor, 1990: 66–67; Harris & Robertson, 1994: 301; Huys *et al.*, 1996: 308; Walker-Smith, 2001: 656; Wells, 2007: 79.*Thyone viridis* Philippi.—Vervoort, 1964: 119.

Type material. Due to the apparent absence of a type specimen for Philippi's *Thyone viridis*, a male specimen, (identified as *Porcellidium viride* from Brady's illustration of the antennule) is here designated NEOTYPE to give taxonomic stability to the genus *Porcellidium* and to allow sufficient definition of the specific characteristics to ensure recognition of *Porcellidium viride*.

Neotype designation. NEOTYPE adult male with antennules extended, length 0.63 mm, P90778 deposited at the Australian Museum, Sydney; collected from *Laminaria digitata*, Clachan, Seil Sound, Oban, Scotland (56°19'N 5°35'W), V.A. Harris 1997.

Material examined (specimens here determined to be conspecific with the neotype): an adult female with egg mass detached, length 0.92 mm (AM P90779) and other specimens (20 ♀♀, 8 ♂♂ and coupled ♂ + juv. ♀, AM P89054), deposited at AM, Sydney. Specimens from the same locality and species of seaweed (100 ♀♀, 50 ♂♂ and 6 ♂♂ + juv. ♀, and 4 slide mounted specimens) have been deposited at NHM, London. Slide material in NHM, London (*Porcellidium* 339) and NMI, Dublin (see Appendix 1 and 2). Living material, identified as *Porcellidium viride* from a species specific feature of the male antennule shown in Brady's (1880) illustration, was collected from Castle Head, Dale, Pembrokeshire (51°42'N 5°10'W), Clachan, Seil Sound, Oban, Scotland (56°19'N 5°35'W) and Loch Hyne, Co. Cork, Ireland (51°30'N 9°17'W) and is part of the material examined. The following description is based on the neotype and this material examined.

Diagnosis. Male antennule segment 2 with first (proximal) seta more than twice length of second or third seta, five setae on segment 2 finely plumulose, segment 3 with ventral process or "peg", three coupling denticles on segment 4 are conspicuous denticulate pads, dactylus (segment 5) expanded, hooked distally, segment 6 inconspicuous; ventral surface of male rostrum smooth, no U-shaped wrinkles or ridges, ventral surface of female rostrum V-shape (Fig. 6F); female caudal ramus rectangular, l/w = 2, terminal setae T2 and T3 thin, plain, very close together, posterior border between setae T3 and T4 > ½ width of ramus, Hicks' index for β seta 45–50%; boundary between anterior and posterior lobes of female genital double-somite marked by a clear triangular area without border setules or dorsal pits, border of posterior lobe with three sensilla at edge; male P5 exopod almost rectangular,

posterior angle 80°; females carry 24 eggs. Spermatophore elongate, ephemeral on female.

Biometric data. *Females* (N = 50): maximum length (L_{max}) 0.91 mm, body length to end of genital double-somite (L_{urs}) 0.89 mm, range 0.83–0.95 mm; cephalosome width (W) 0.60 mm, range 0.56–0.62 mm; rostrum width (R) 0.15 mm; genital double-somite width (N = 5) 0.38 mm, length 0.26 mm; caudal ramus length (N = 15) 0.14 mm [ramus dissected, laid flat], width 0.06 mm.

Ratios: L_{urs}/W 1.48; W/R 4.0; genital double-somite 63% of cephalosome width, w/l 1.45; caudal ramus 16% of L_{urs} , l/w 2.3, Hicks' index for β seta 50%.

Males (N = 16): maximum length 0.62 mm, body length to end of genital segment 0.49 mm; cephalosome width 0.52 mm; antennule (N = 7, fully extended) 0.15 mm; apical angle of P5 75–80°; spermatophore length 0.21 mm.

Ratios: male antennule 30% of cephalosome width; antennule segment 2, 33%, segment 3+4 37%, dactylus 24% of antennule length; first seta on segment 2 of antennule is 2.5–2.8 times length of seta 2; spermatophore 43% of body length L_{urs} .

Description. *Adult females* (Fig. 4A; Plate 1B, p. 67): pale yellow or colourless with variable patches of dark blue/purple on cephalosome and posterior of body (see Figs 4A, 8A, F, G, H, I and *Remarks* below). Cephalosome semicircular, rostrum broad (w/l 4.2), V-shape in ventral view (Fig. 6F). Hyaline border with eight border sensilla surrounds cephalosome, 10 µm wide. Dorsal surface ornamented with circular pits 4–5 µm, surface ridge near antennule socket (Fig. 8B, C), ventral surface of cephalosome smooth (not wrinkled). Labrum with oval patch of minute setules (Fig. 4F). Genital double-somite (Fig. 4C) broad, semicircular in outline, no cleft or notch but clear triangular area without border setules or dorsal pits marks boundary between anterior and posterior lobes, three very small sensilla at edge of posterior lobe (Fig. 4D). Posterior arch deep (½ length of genital double-somite), encloses almost whole of caudal rami. Genital opening (Fig. 4E). Caudal rami (Fig. 4B) long, rectangular, feint ridges on dorsal surface, β seta half way down ramus, γ seta and pinnate T1 slightly recessed at lateral corner, T2 and T3 plain, slender, very close together (T2 pinnate on some specimens), space between T3 and T4 greater than half width of ramus, T4 pinnate at medial corner (Fig. 4G). Some of the setae on segment 2 of female antennule finely plumulose (Fig. 5A). Structure and setation of mouthparts and ambulatory limbs typical of family. Antenna (Fig. 5B), endopod segment 2 with two lateral setae, ends of geniculate setae plain, claw comb-like (Fig. 5C). No patch of setules on anterior lobe of mandibular palp (Fig. 5E). Maxillule (Fig. 5G) with single bulbous seta on exopod, six setae on endopod. Coxae of maxilliped meet in midline (Fig. 5H). Limb P1, endopod segment 1 triangular, broad (l/w = 0.95), peg area inconspicuous (Fig. 5F). Serrulate spinous seta on segment 2 of P3 endopod (Fig. 6G) almost as long as endopod (0.9:1), large serrate spinous terminal seta on segment 3 longer than endopod (1.4:1). Spinous setae on P4 endopod segment 2 and 3 (Fig. 6C) longer than endopod (1.3:1). P5 exopod lanceolate with two plain dorsal setae (one sub-terminal and one apical), minute third seta present on some specimens (Fig. 6H). Females carry 24 eggs per brood.

Adult males (Fig. 8A; Plate 1D, p. 67). Dark blue/purple area only on cephalosome, posterior of body colourless. Cephalosome truncated, anterior border straight, shoulder

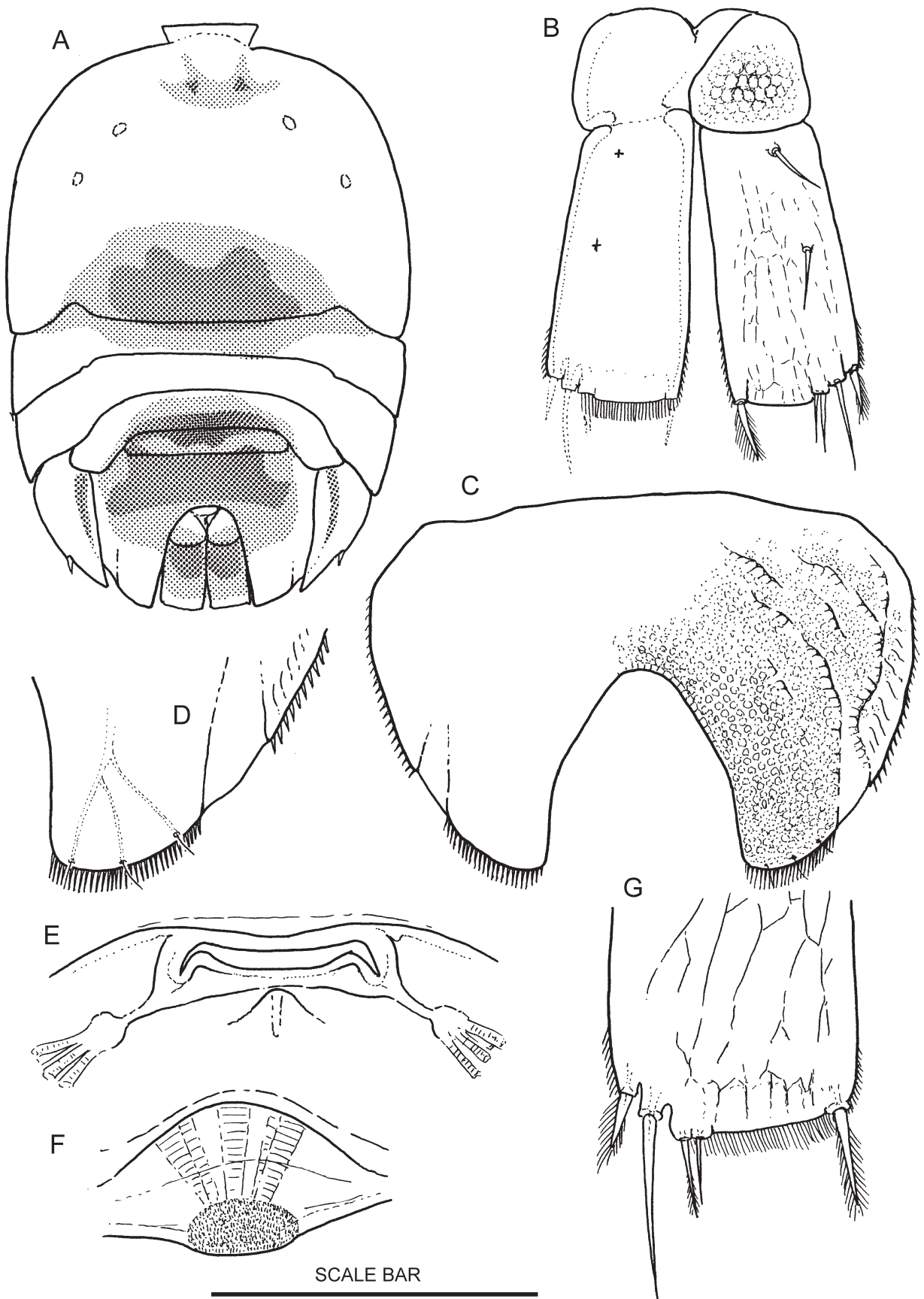


Figure 4. *Porcellidium viride* (Philippi, 1840). Female: (A) adult showing typical colour pattern; (B) caudal rami (left ventral, right dorsal); (C) genital double-somite; (D) detail of genital double-somite posterior lobe; (E) genital opening; (F) labrum; (G) caudal ramus, terminal setae. Drawings of specimens from Scotland. Scale bar: A = 0.5 mm. B = 0.15 mm. C = 0.23 mm. E, F = 0.13 mm. G = 0.08 mm.

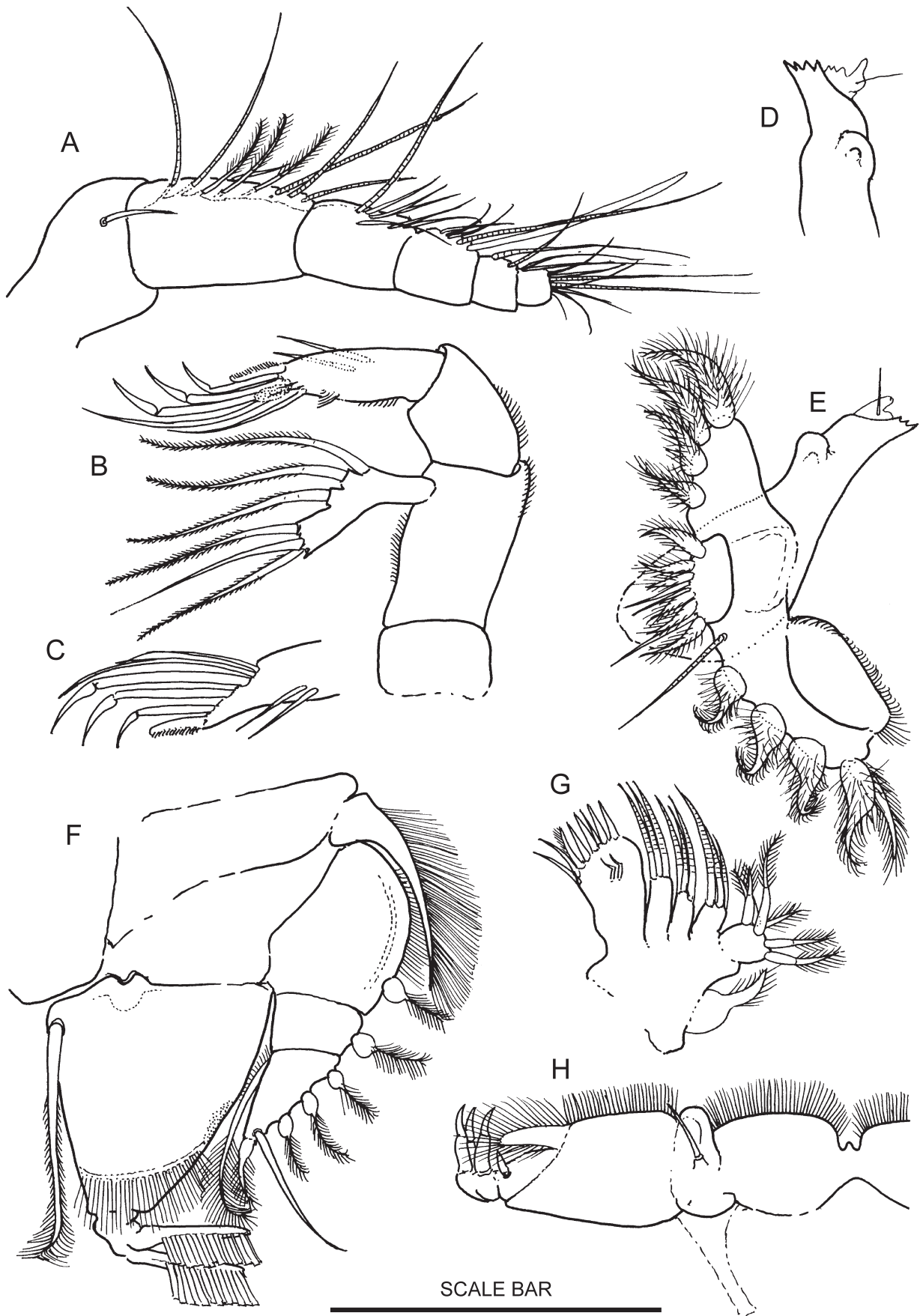


Figure 5. *Porcellidium viride* (Philippi, 1840). Female: (A) antennule; (B, C) antenna; (D, E) mandible; (F) P1; (G) maxillule; (H) maxilliped. Scale bar: A, B, G, H = 0.08 mm. E, F = 0.13 mm.

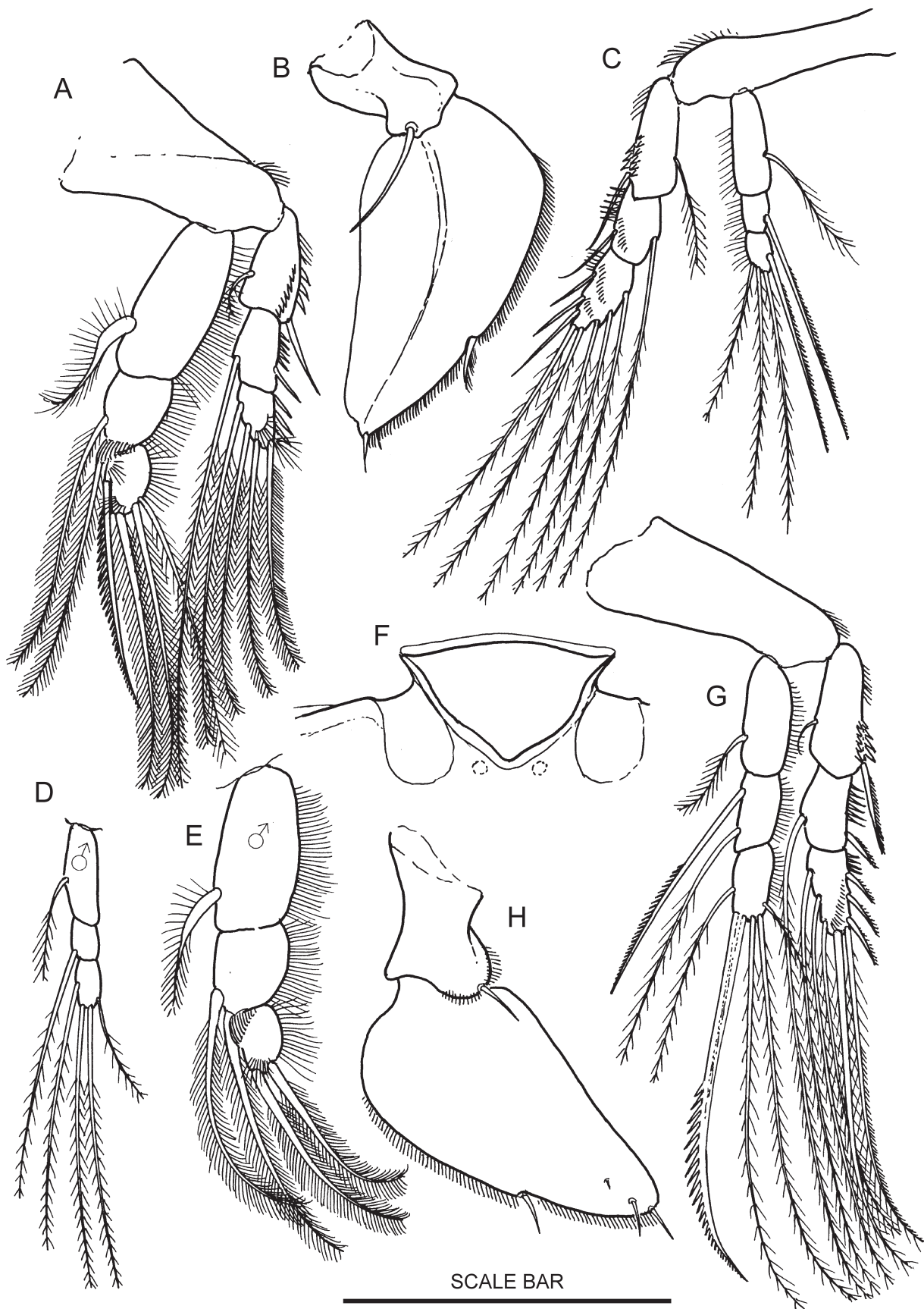


Figure 6. *Porcellidium viride* (Philippi, 1840). Female: (A) P2; (B, H) P5 (ventral and dorsal); (C) P4; (G) P3; (F) rostrum (ventral). Male: (D) P4 endopod. (E) P2 endopod. Scale bar: A, C, G = 0.18 mm. B, F, H = 0.23 mm. D, E = 0.15 mm.



Figure 7. *Porcellidium viride* (Philippi, 1840). Male: (A) detail of antennule coupling denticles; (B, C) P5 (ventral); (D) maxilla; (F, G) antennule (* peg or ventral process). Female: (E) showing extent of colour pattern of specimens from Loch Hyne, Ireland. Scale bar: A = 0.06 mm. B, D, F, G = 0.08 mm.

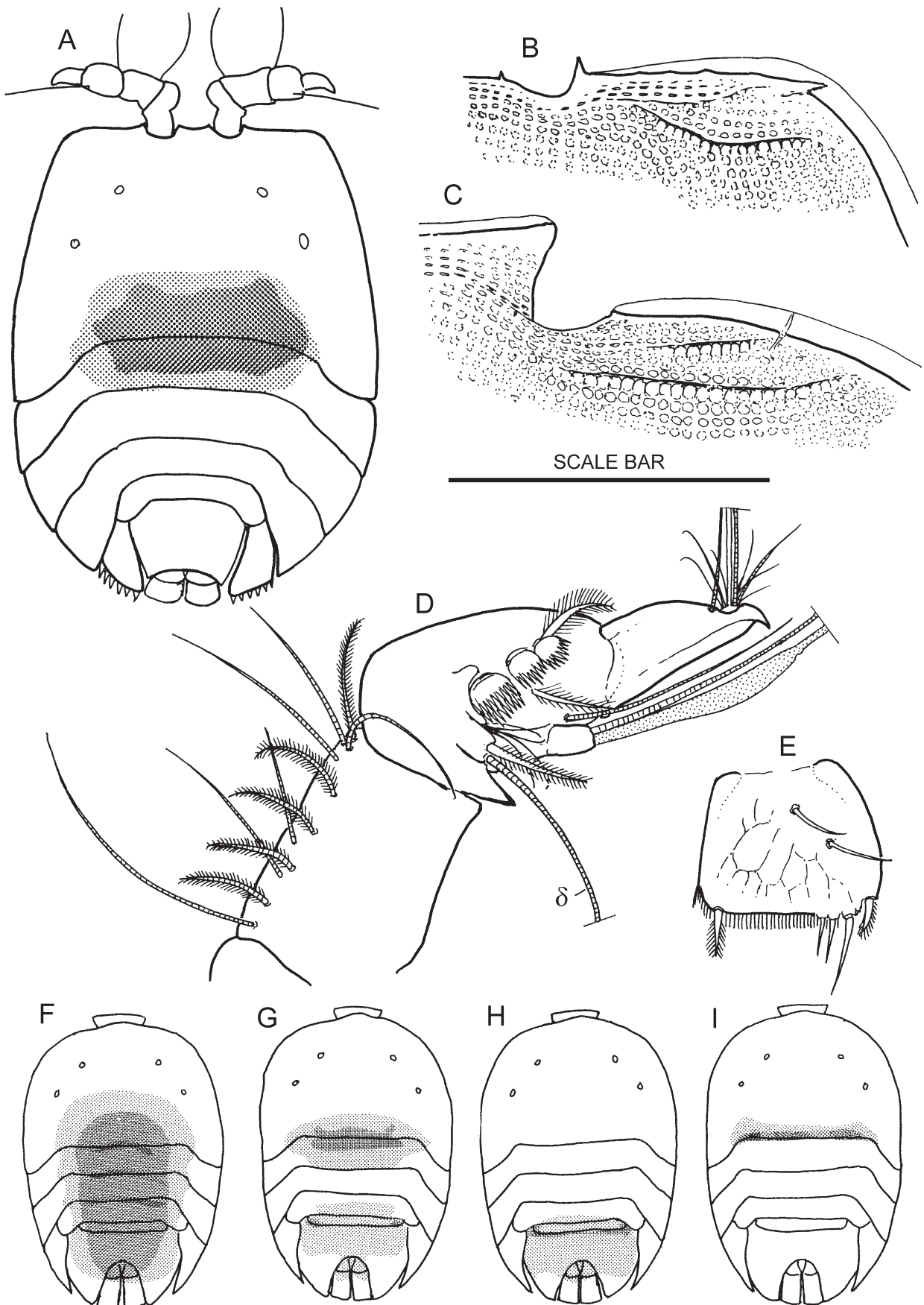


Figure 8. *Porcellidium viride* (Philippi, 1840). Male: (A) adult showing typical colour pattern; (B) anterior cephalosome (dorsal); (D) antennule (anterior); (E) caudal ramus. Female: (C) anterior cephalosome (dorsal); (F, G, H, I) colour patterns (see text). Scale bar: A = 0.45 mm. B, C = 0.13 mm. D, E = 0.08 mm.

tightly rounded. Hyaline border, dorsal pits and ventral surface of cephalosome as for female, no ridges or wrinkles on ventral surface of rostrum. Caudal ramus sub-quadrate (l/w 0.75), medial edge straight, lateral edge convex, dorsal surface with feint ridges, β seta $\frac{1}{2}$ way down ramus (Fig. 8E). First seta on antennule segment 2 more than twice length of second and third seta (Figs 7G), five plumulose setae on segment 2. Segment 3 with knob-like ventral process (no blade). Segment 4 with three conspicuous denticulate coupling denticles, (in some views they may appear as two denticulate pads, compare Figs 7A and 8D). Aesthetasc short (more than twice length of segment 3+4). Segment 5 of dactylus broad, $\frac{3}{4}$ length of segments 3+4, hooked terminally, segment 6 very small, fused to segment 5 (Fig. 7F). Other limbs as for female except for the following: P2 endopod with two plumose terminal setae (Fig. 6E), setae on segments 2 and 3 of P4 endopod all plumose (Fig. 6D), P5 rhomboid (almost rectangular, Figs 7B, C), first (lateral) seta longer than other setae, no setules at base of terminal setae, apical angle of P5 80°. Spermatophore $\frac{1}{3}$ body length.

Remarks. Although Brady's *Porcellidium viride* can be identified, the same does not apply to Philippi's *Thyone viridis*. The reason Brady thought his animal was the same as Philippi's *Thyone viridis* is the similarity of the P5 limbs. He says "There seems little reason to doubt the identity of this species [*P. viride*] with Philippi's *Thyone viridis*; the serration of the lower border of the fifth foot is very distinctive..." but this is a feature of nearly all male members of the Porcellidiidae. It may seem strange that Brady thought his animals the same as Philippi's, but it is clear from his description and figure that he thought his own copepodid was an adult female. Brady had found *P. tenuicauda* (which he illustrates), and the adult female of *P. viride* which he identifies as *P. fimbriatum*, thus the only other animal he could compare with his (male) copepodid was *Thyone viridis*. It is important, therefore, to consider whether Brady's synonymy is justified.

Philippi gave a short (Latin) diagnosis of *Thyone* and then an extremely brief description of his *T. viridis*, "Almost $\frac{3}{4}$ " long, common. Masticatory apparatus extremely complicated". The only clue to the animal's identity is a confusing sketch (Fig. 25A). It shows an animal with six segments to its antennule, but they are not transformed like an adult male members of the Porcellidiidae. This tells us that it is not an adult male or male copepodid: it must be an adult female. But the posterior end of the body clearly shows male P5 limbs with six terminal setae and quadrate caudal rami, therefore Philippi's animal must be a sage IV or V male copepodid. Thus there is a conflict as to the sex of the animal. The shape of the body is even more confusing (see Fig.

24A). It is egg-shaped and sharply truncated anteriorly with maximum width $\frac{1}{3}$ down body. Adult animals of Claus' *P. tenuicauda* are egg-shaped, but neither male nor female is truncated anteriorly. The males of both *P. viride* and *P. fimbriatum* are truncated anteriorly, but are not egg-shaped nor do they taper posteriorly. The females of these two species are oval and not truncated anteriorly. The copepodid of *P. viride* illustrated by Brady (1880) is not egg-shaped; the posterior half is broadly semicircular like other copepodids (Fig. 25B). It is clear that Philippi's animal cannot be identified with any of the European species nor can Brady be justified in thinking it was the same as his animal. Philippi does not say whether he designated type specimens for his animal and no evidence has been found that suggests he did. Brady would not have provided a type specimen for his *Porcellidium viride* because he regarded it as a synonym for *T. viridis*. However, Brady (1880) illustrates the male antennules of *P. viride* which show the unique long first seta on segment 2. This feature is species specific and has not been found on any other member of the family. It allows the species to be identified with a high degree of certainty and is the basis on which the present redescription of *Porcellidium viride* rests. Sars (1904) also shows this long seta in his illustration of *Porcellidium fimbriatum* which proves that his animals were *P. viride*.

Specimens from Wales and Scotland have a variable dorsal colour pattern of dark blue or purple on a pale yellow body colour (Figs 4A, 8F,G,H,I and Plate 1B,D, p. 67). The frequency of colour variability found in one sample is shown below (Table 1). Animals collected from Loch Hyne, Ireland, have a single pale pink dorsal patch (Fig. 4E).

Collection data. *Porcellidium viride* has been collected from the following algae. *Himantalia elongata* at Great Castle Rocks, Dale, Pembrokeshire Wales, (CB7.7/70, 209 ♀♀, 88 ♂♂, 4 coupled ♂♂ + juvenile), V. A. Harris 1970, 1974. *Laminaria saccharina* at Clachan, Seil Sound, Oban, Scotland ES12.9/74, 71 ♀♀ (18 with eggs), 21 ♂♂, 4 ♂♂ coupled to juveniles; ES14.9/74, 14 ♀♀, 3 ♂♂; ES17.9/74, 85 ♀♀ (7 with eggs), 60 ♂♂, 13 ♂♂ coupled to juveniles; ES18.9/74 (holdfasts), 55 ♀♀, 12 ♂♂, 2 ♂♂ coupled to juveniles. *Laminaria digitata* at Clachan, Seil Sound, Oban, Scotland ES19.10/74, 55 ♀♀, 12 ♂♂; ES20.10/74, 58 ♀♀, 23 ♂♂; ES23.9/97, 41 ♀♀, 9 ♂♂; ES25.9/97, 55 ♀♀ (25 with eggs), 39 ♂♂, 2 ♂♂ coupled to juveniles, V. A. Harris 1970, 1974, 1987, 1997. *Ulva lactuca* at Loch Hyne, near Skibbereen, Co. Cork, Ireland LH3.9/97, 8 ♀♀, 6 ♂♂, V. A. Harris, 1997.

Samples collected from *Laminaria digitata* also contain populations of *P. fimbriatum*.

Table 1. Frequency of colour patterns in a population of *Porcellidium viride* from Scotland.

	large purple area on all segments and posterior of body Fig. 8F	large purple patches on cephalosome Figs 4A, 8G	only posterior of body purple Fig. 8H	rear of cephalosome purple, posterior of body not purple Fig. 8A, I	animals pale yellow, no purple	total
female animals						
1		43	63	33	6	146
male animals						
0		0	0	104	2	106

***Porcellidium fimbriatum* Claus, 1863**

Fig. 9–12

Porcellidium fimbriatum Claus, 1863:140, taf. xxii, fig. 1.*P. fimbriatum*.—Claus, 1889: 32, figs. VII 1–18, VIII 1–8 (redescription); Bocquet, 1948: 247–250; Harris & Robertson, 1994: 301; Huys *et al.*, 1996: 308; Walker-Smith, 2001: 656; Wells, 2007: 79.*P. viride*.—Lang, 1948: 420.*P. lecanoides*.—Norman & Scott, 1906: 182.*Thyone viridis*.—Vervoort, 1964: 119.

Type material. The description and illustrations Claus gave of *P. fimbriatum* (1863) are misleading for they do not show a single species specific character that would confirm the animal's identity. It is possible that Claus was looking at mixed material because, as shown above, *P. fimbriatum* and *P. viride* may be found in the same sample. In 1889 Claus redescribed his *P. fimbriatum* giving eight or more species specific characters which should have cleared up any misunderstanding between the two species, but his synonymies show that he believed his animals were the same species as Brady's *P. "fimbriatum"* which is known to be the female of *P. viride*. Moreover, *P. lecanoides* Claus, 1889 is a junior synonym for *P. viride*. In order to stabilize the taxonomy of *Porcellidium fimbriatum* in the apparent absence of a type specimen, a male with antennules extended to show species specific features has been selected as a NEOTYPE for *Porcellidium fimbriatum* Claus, 1863.

Neotype designation. NEOTYPE adult male with antennules extended, to show coupling denticles, length 0.56 mm, P92561 deposited at the Australian Museum, Sydney; collected from *Laminaria saccharina*, LW spring tide at Clachan, Seil Sound, Oban, Scotland (56°19'N 5°35'W), V. A. Harris, September 1997.

Material examined (specimens determined to be conspecific to the neotype): slide material in NHM (*Porcellidium* 339), (see Appendix 1); specimens from Castle Heads, Dale Pembrokeshire, Wales (51°42'N 5°10'W) and Clachan, Seil Sound, Oban, Scotland (56°19'N 5°35'W), identified as *P. fimbriatum* from Claus (1889); specimens collected from *Laminaria digitata* at Clachan, Scotland, AM P89055 (15 ♀♀, 8 ♂♂ + 3 coupled ♂♂, V. A. Harris, 1997). Other specimens (60 ♀♀, 30 ♂♂ + 8 coupled ♂♂, V. A. Harris, 1997) and slide mounted dissections have been deposited at NHM, London. The following description is based on the neotype and material examined.

Diagnosis. No finely plumulose setae on male antennule segment 2, first seta on segment 2 not longer than remaining setae, short blade-like ventral process on segment 3, three coupling denticles on segment 4 (proximal with serrated edge, two distal denticles small, botryoidal, no denticulate pad present), dactylus short (< ½ length of segment 4) segment 5 not expanded, segment 6 clearly visible, not fused to segment 5; no U-shaped wrinkles on ventral surface of male rostrum; female caudal ramus long, rectangular (l/w = 2.7–2.8), terminal setae T1–T4 all conspicuously pinnate, gap between T3 and T4 < ½ width of ramus, Hicks' index for β seta 25%; female genital double-somite with deep cleft or scar between anterior and posterior lobes (clear triangular

area absent), no sensilla on border of posterior lobe; male genital segment with two rows of three dorsal sensilla; ventral surface of male and female cephalosome with fine lines (wrinkles); male P5 exopod trapezoid, apical angle 50°. Spermatophore elongate, ephemeral on female.

Biometric data. *Females* (N = 43): maximum length (L_{max}) 0.77 mm, body length (L_{urs}) 0.76 mm (range 0.73–0.79 mm); cephalosome width 0.45 mm (range 0.43–0.47 mm); rostrum (R) 0.095 mm; genital double-somite width 0.32 mm, length 0.27 mm; caudal ramus length 0.14 mm, width 0.05 mm.

Ratios: L_{urs}/W 1.7; W/R 4.7; genital double-somite width 70% of cephalosome width, w/l 1.2; caudal ramus 18% of L_{urs}, l/w 2.8, Hicks' index for β seta 25%.

Males (N = 25): maximum length (L_{max}) 0.56 mm, body length (L_{urs}) 0.50 mm; cephalosome width (W) 0.38 mm; spermatophore 0.15 × 0.03 mm; antennule fully extended 0.135 mm.

Ratios: L_{max}/W 1.47, L_{urs}/W 1.32; antennule 35% of cephalosome width, segment 2 30%, segment 3+4 42% and dactylus 15% of antennule length; spermatophore 27% of L_{urs}.

Description. *Adult females* (Fig. 9A; Plate 1C, p. 67): colourless or pale yellow with broad band of deep violet or dark blue down middle of back, including genital double-somite and caudal rami. Body outline elongate oval, sides of body almost parallel, rostrum narrow (W/R = 4.7). Dorsal surface of cephalosome, metasome and genital double-somite ornamented with dorsal pits (5–6 μm in diameter), ventral surface of cephalosome with fine wrinkles (see Fig. 12A). Hyaline border 8 μm wide. No patch of setules on labrum. Genital double-somite (Fig. 9H) relatively long (w/l = 1.2), posterior arch deep, slight notch or indentation between anterior and posterior lobes with transparent scar (scar appears as deep cleft when compressed with cover glass, *cf* Claus' 1889 illustration). No sensilla on edge of posterior lobe (Fig. 9E), border setules on posterior lobe longer than those on anterior lobe. Genital opening (Fig. 9G). Caudal rami (Fig. 9C, D) long (18% of body length), rectangular (l/w = 2.8), almost completely enclosed in arch of genital double-somite, dorsal surface with network of fine ridges but no pits. Medial edge straight, slightly bevelled distally, lateral edge slightly convex, both edges with setules posteriorly. Beta seta about ¾ down ramus (Hicks' index = 25%), terminal setae T1–T4 conspicuously pinnate, equal in length, T2 and T3 very close on slight prominence midway between T1 and T4, distance between T3 and T4 equal or less than ¼ width of ramus, very fine terminal fringe of setules between T3 and T4. No finely plumulose setae on segment 2 of antennule. Structure and setation of mouthparts and ambulatory limbs typical of family. Antenna (Fig. 10C). Mandible with small group of setules on anterior lobe of palp (Fig. 10B). Segment 1 of P1 endopod elongate triangular, narrow (l/w = 1.5), coxa with internal seta (Fig. 10A inset). Serrulate spinous seta on segment 2 of P3 endopod (Fig. 11C) shorter than endopod (0.8:1), large serrate spinous seta on terminal segment considerably longer than endopod (1.7:1). P4 with internal serrulate spinous seta on segments 2 and 3 (Fig. 11A). P5 (Fig. 10F, G), exopod broadly lanceolate, with dorsal pits, one sub-terminal dorsal seta and two apical setae. Females carry 12–14 eggs per brood.

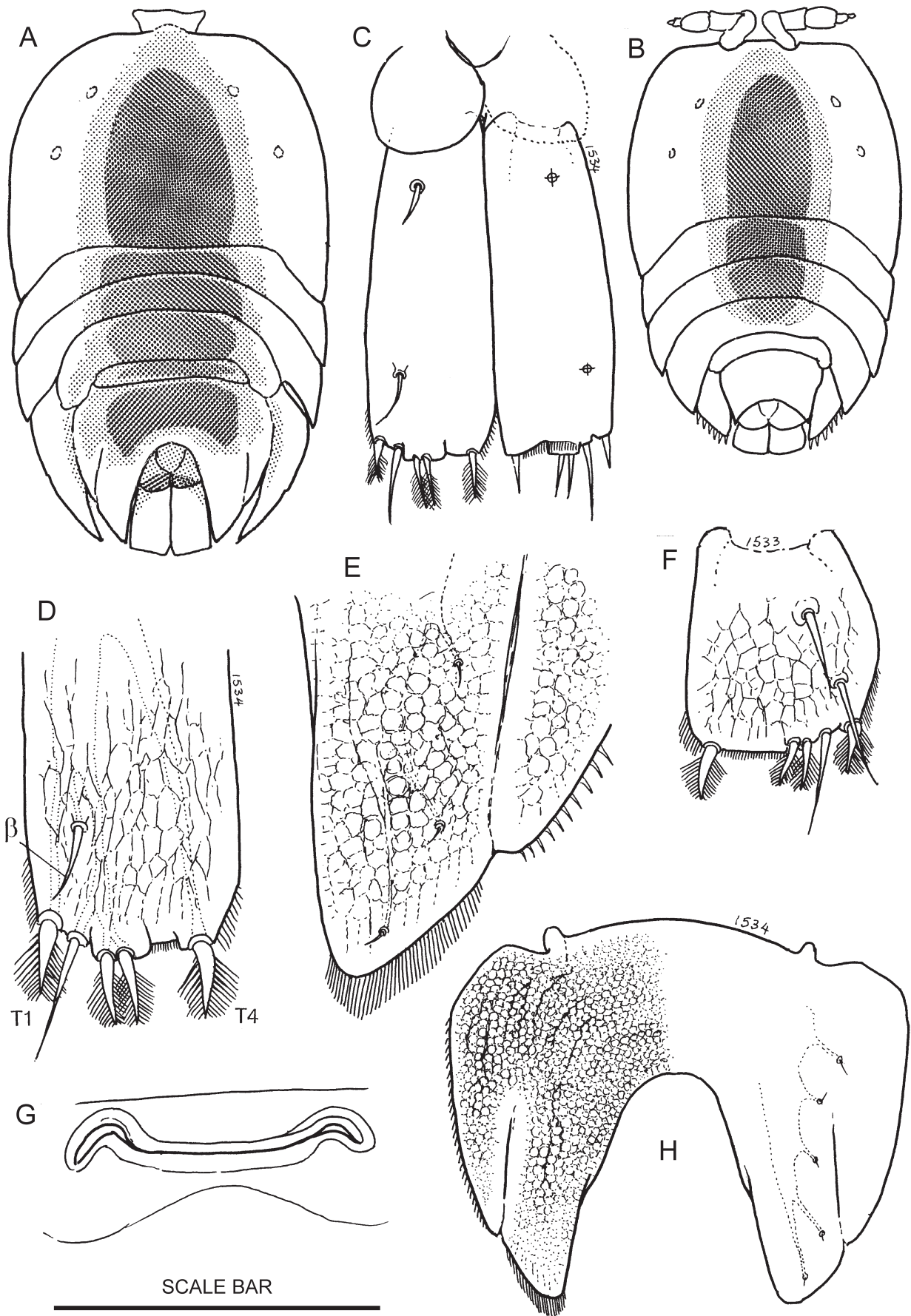


Figure 9. *Porcellidium fimbriatum* Claus, 1863. Female: (A) adult showing colour pattern; (C) caudal rami (left dorsal, right ventral); (D) detail of caudal ramus; (E, H) genital double-somite, detail of posterior lobe; (G) genital opening. Male: (B) adult; (F) caudal ramus. Drawings of specimens from Scotland. Scale bar: A, B = 0.45 mm. C = 0.13 mm. D, E, F, G = 0.08 mm. H = 0.23 mm.

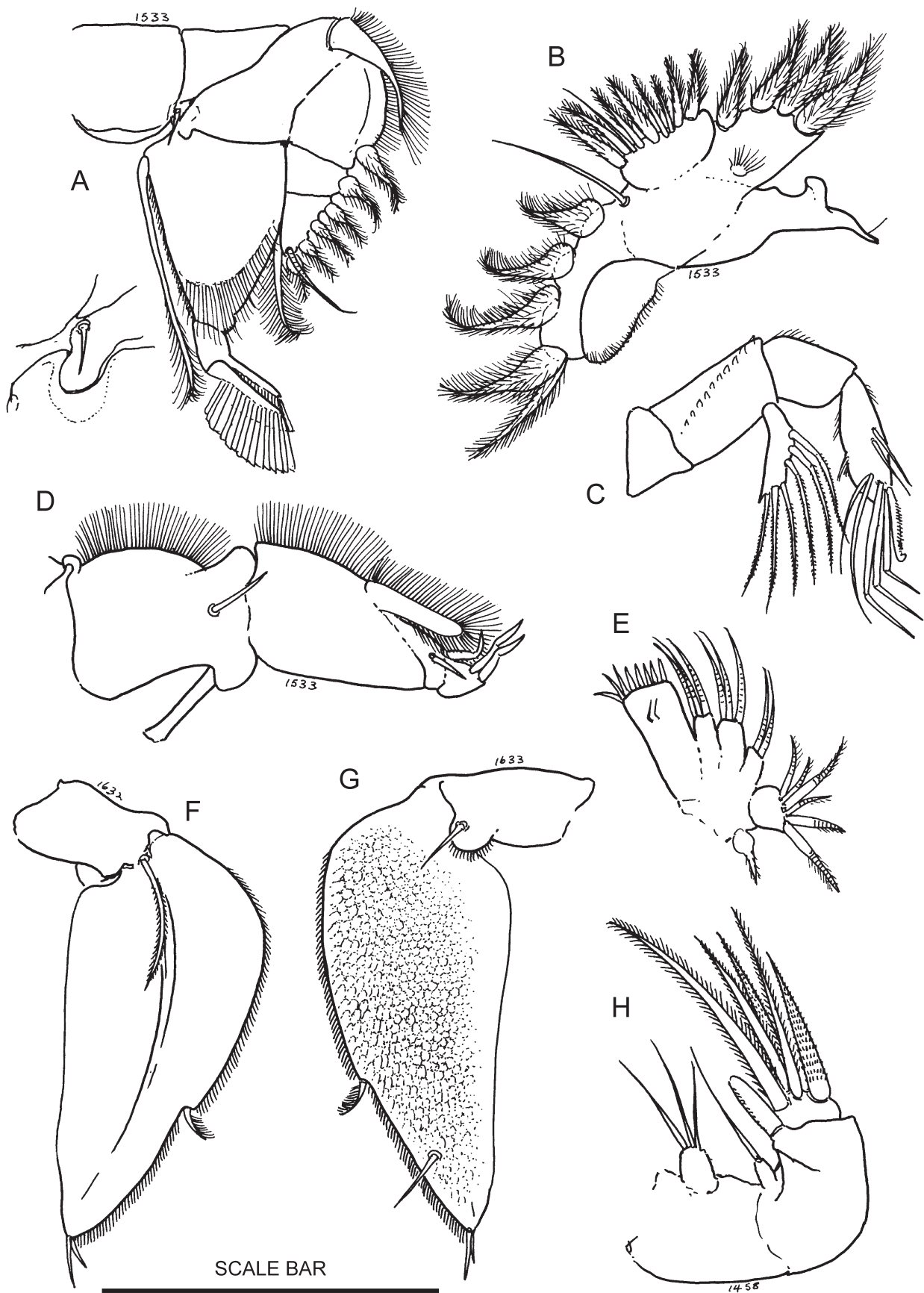


Figure 10. *Porcellidium fimbriatum* Claus, 1863. Female: (A) P1 inset showing seta on coxa; (B) mandible; (C) antenna; (D) maxilliped; (E) maxillule; (F, G) P5 (ventral and dorsal); (H) maxilla. Scale bar: A, C = 0.13 mm. B = 0.15 mm. D, E, H = 0.08 mm. F, G = 0.18 mm.

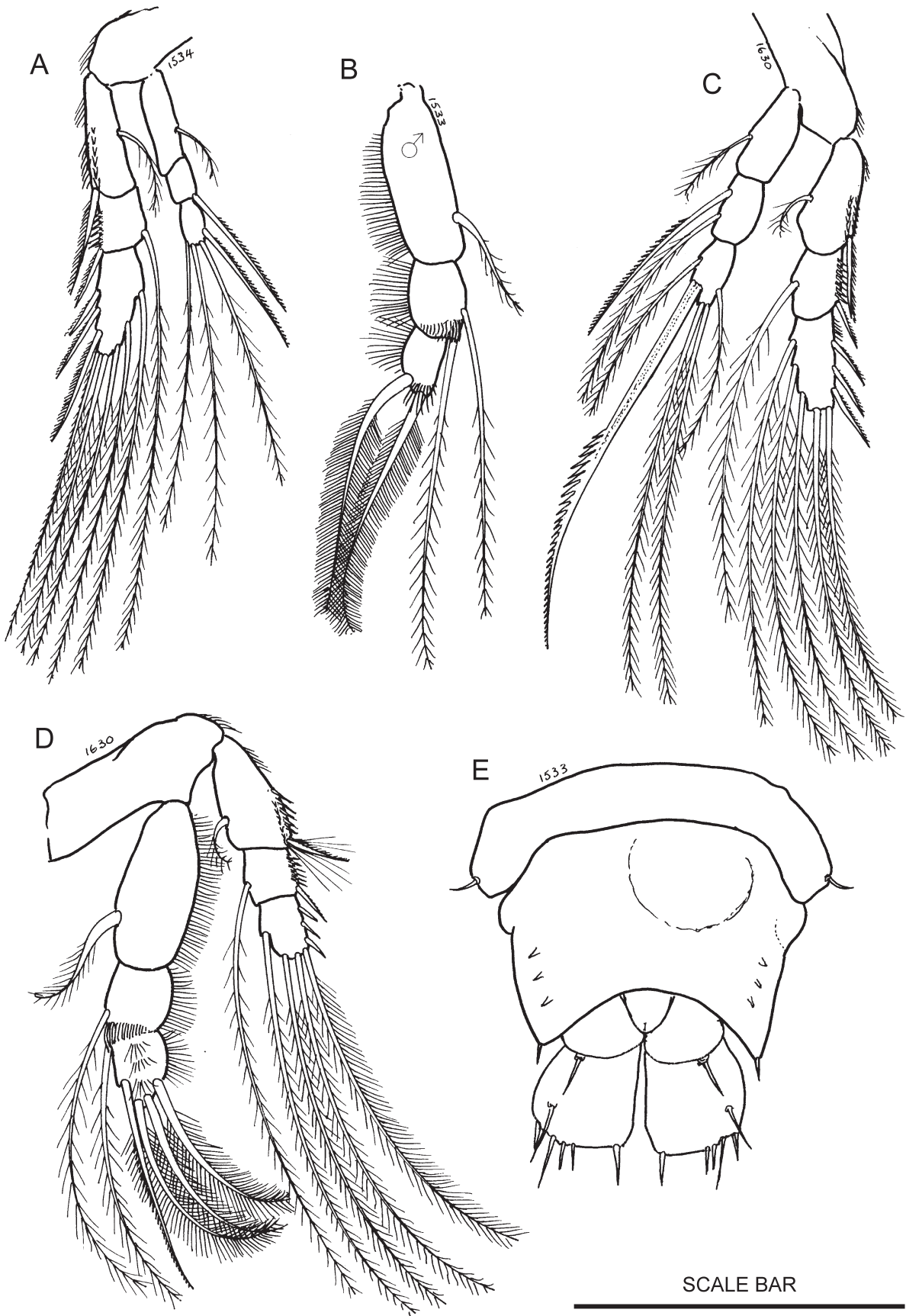


Figure 11. *Porcellidium fimbriatum* Claus, 1863. Female: (A) P4; (C) P3; (D) P2. Male: (B) P2 endopod; (E) genital somite (dorsal). Scale bar: A, C, D, E = 0.15 mm. B = 0.13 mm.

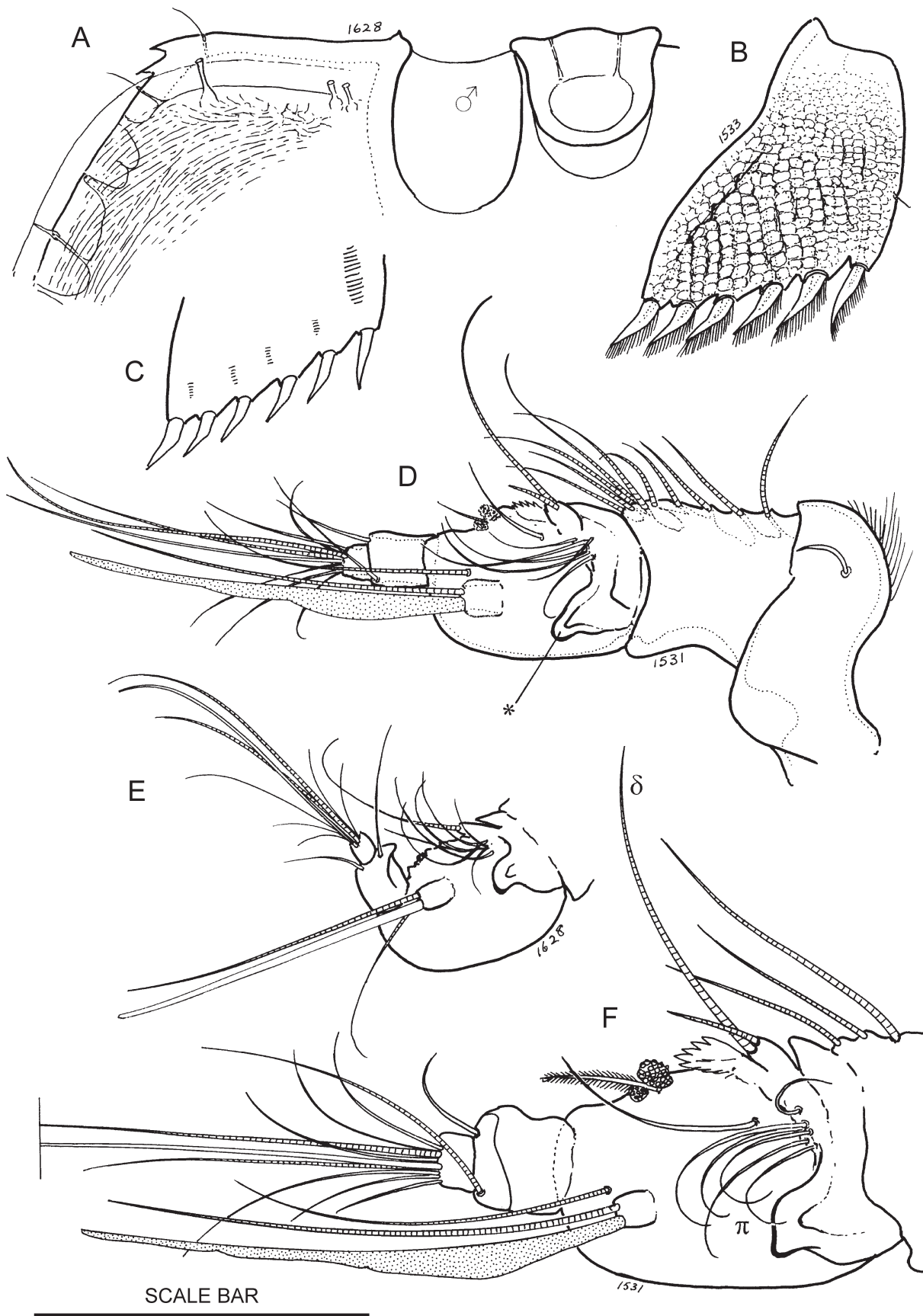


Figure 12. *Porcellidium fimbriatum* Claus, 1863. Male: (A) rostrum and shoulder (ventral); (B, C) P5 (dorsal, ventral); (D, E, F) antennule (* ventral process). Scale bar: A, B, D, E = 0.08 mm. F = 0.06 mm.

Adult males (Fig. 9B; Plate 1E, p. 67). Colouration as for female except that in a few specimens the violet blue colour is absent from posterior region of body. Heavily sclerotized parts of the antennules and antennule sockets are orange on most males. Cephalosome truncated, anterior edge straight (not convex in mid-line), shoulders rounded. Rostrum not wrinkled ventrally, ventral surface of cephalosome with fine wrinkles (Fig. 12A). Dorsal surface with pits as for female. Genital somite with dorsal pits, lateral row of three dorsal sensilla on each side (Fig. 11E). Caudal rami slightly longer than wide ($l/w = 1.1$), dorsal surface with reticulate markings, medial edge straight, lateral edge convex (Fig. 9F). Beta seta $\frac{2}{3}$ down ramus, terminal setae conspicuously pinnate, space between T3 and T4 wider than in female (almost $\frac{1}{2}$ width of ramus) with fringe of fine setules. Antennule (Figs 12D, F) with first seta on segment 2 not longer than 1.5 times length of second seta, segment 3 with short blade-like ventral process, segment 4 with three coupling denticles (proximal with serrated edge, middle and distal denticles small with botryoidal surface, no denticulate pad), dactylus very short, cylindrical ($< \frac{1}{3}$ length of segments 3+4), distinctly two segmented, without pronounced terminal hook. P2 endopod with two plumose terminal setae (Fig. 11B), Setae on segments 2 and 3 of P4 endopod all plumose. P5 exopod with dorsal pits (Fig. 12B), ventral setules at base of each terminal seta (Fig. 12C), apical angle of P5 50° .

Remarks. Claus did not explain why he called this species *fimbriatum*, but he must have been impressed by the marked difference between the narrow pointed caudal rami of his *Porcellidium tenuicauda* and the posterior border fringed with bristles of his new 1863 species, (*L. fimbriatum* = separated into shreds or filaments, fringed). Claus redescribed the species in 1889 showing several species specific characters that allowed animals from Scotland to be identified as *Porcellidium fimbriatum*. The species is commonly found with *P. viride* on *Laminaria* in samples from Scotland.

Collection data. *Porcellidium fimbriatum* has been collected from the following algae. *Laminaria* sp., Plymouth, Devonshire, 1970. *Alaria esculenta* and *Gigartina stellata* at Skokholm Island, Pembrokeshire, 1970. *Hymanthalia elongata* at Great Castle Rocks, Dale, Pembrokeshire, Wales, V. A. Harris 1970, 1974. *Chondrus crispus* at Clachan, Seil Sound, Oban Scotland ES2.9/74, 18 ♀♀, 25 ♂♂ and ES18b.11/74, 38 ♀♀, 5 ♂♂ + 13 ♂♂ coupled to juveniles; *C. crispus* and *G. stellata* ES18a.11.74, 72 ♀♀, 28 ♂♂; *Lithothamnion* encrusted stones and boulders ES14.9/74, 3 ♀♀, 1 ♂; *Laminaria saccharina* ES17.9/74, 7 ♀♀, 1 ♂; *C. crispus* and *L. saccharina* ES20.9/97, 76 ♀♀, 16 ♂♂ + 11 ♂♂ coupled with juveniles; *Laminaria digitata* ES19.9/97, 5 ♀♀, 1 ♂, V. A. Harris 1970, 1974, 1987, 1997.

Porcellidium roscoffensis (Bocquet) comb. nov.

Figs 13–16

Porcellidium lecanoides var. *roscoffensis* Bocquet, 1948: 250, fig. IX.

P. lecanoides.—Huys, *et al.* (1996): 308; Wells (2007): 79.

P. viride.—Bodin (1997):64.

Material examined. Specimens collected from mixed seaweeds, Castle Head, Dale, Pembrokeshire, Wales (3 ♀♀, 2 ♂♂) ($51^\circ42'N$ $50^\circ10'W$), V. A. Harris, 1970, 1974. Three slide-mounted dissections deposited in NHM, London.

The following account is based on Bocquet's (1948) descriptions of the caudal ramus and genital double-somite of *P. lecanoides* var. *roscoffensis*.

Diagnosis. Male antennule with knob or peg-like ventral process on segment 3, large proximal pad of fine denticles on segment 4, distal denticle with fine comb-like edge, dactylus not broad, concave on one side, hooked terminally, segment 6 inconspicuous, fused to segment 5; ventral surface of male rostrum with U-shaped ridges or wrinkles; indentation (without border setules) marks boundary between anterior and posterior lobes of female genital double-somite, posterior lobe with two sensilla at edge; dorsal surface of male genital somite with five sensilla on each side; dorsal surface of female caudal ramus with pits, β seta close to γ seta.

Biometric data. *Females* (N = 1): body length (L_{urs}) 0.85 mm; cephalosome width (W) 0.60 mm; rostrum width (R) 0.15 mm; genital double-somite width 0.39 mm, length 0.28 mm; caudal ramus length 0.12 mm, width 0.05 mm.

Ratios: L_{urs}/W 1.42; W/R 4.0; genital double-somite width 65% of cephalosome width, w/l 1.4; caudal ramus 14% of L_{urs} , l/w 2.4, Hicks' index for β seta 16%.

Males (N = 1): body length L_{urs} 0.70 mm; body width 0.51 mm.

Ratios: L_{urs}/W 1.4; caudal ramus l/w 0.8; antennule 46% of cephalosome width, segments 3+4 40%, and dactylus 32% of antennule length.

Description. *Adult females* (Fig. 13A): colour (see under *Remarks*). Anterior of cephalosome broadly rounded, rostrum prominent. Dorsal surface ornamented with circular pits 3 μ m diameter, no obvious ridges but numerous pit and collared sensilla present on cephalosome, metasome and genital double-somite (see Fig. 13D). Ventral surface of cephalosome smooth, but ventral surface of rostrum has transverse ridges or wrinkles. Hyaline border without striations, 12 μ m wide. Labrum without ridge plates or setules. Genital double-somite (Fig. 13D) broad, semicircular in outline, slight lateral notch without setules at that point, two small sensilla at edge of posterior lobe (Fig. 13E), posterior arch deep, encloses most of the caudal rami. Genital opening (Fig. 13F). Caudal ramus (Fig. 13C) rectangular, dorsal surface ornamented with small pits, medial edge straight, medial corner slightly bevelled, lateral edge slightly convex. Terminal setae pinnate, T1 and γ setae recessed at lateral corner, β seta close to γ and posterior edge of ramus, T2 and T3 very close, T4 at medial corner, gap between T3 and T4 less than $\frac{1}{2}$ width of ramus, fringed with fine setules. No finely plumulose setae on segment 2 of antennule, first seta on segment 2 less than $1\frac{1}{2}$ times length of setae 2 or 3. Structure and setation of mouthparts and ambulatory limbs

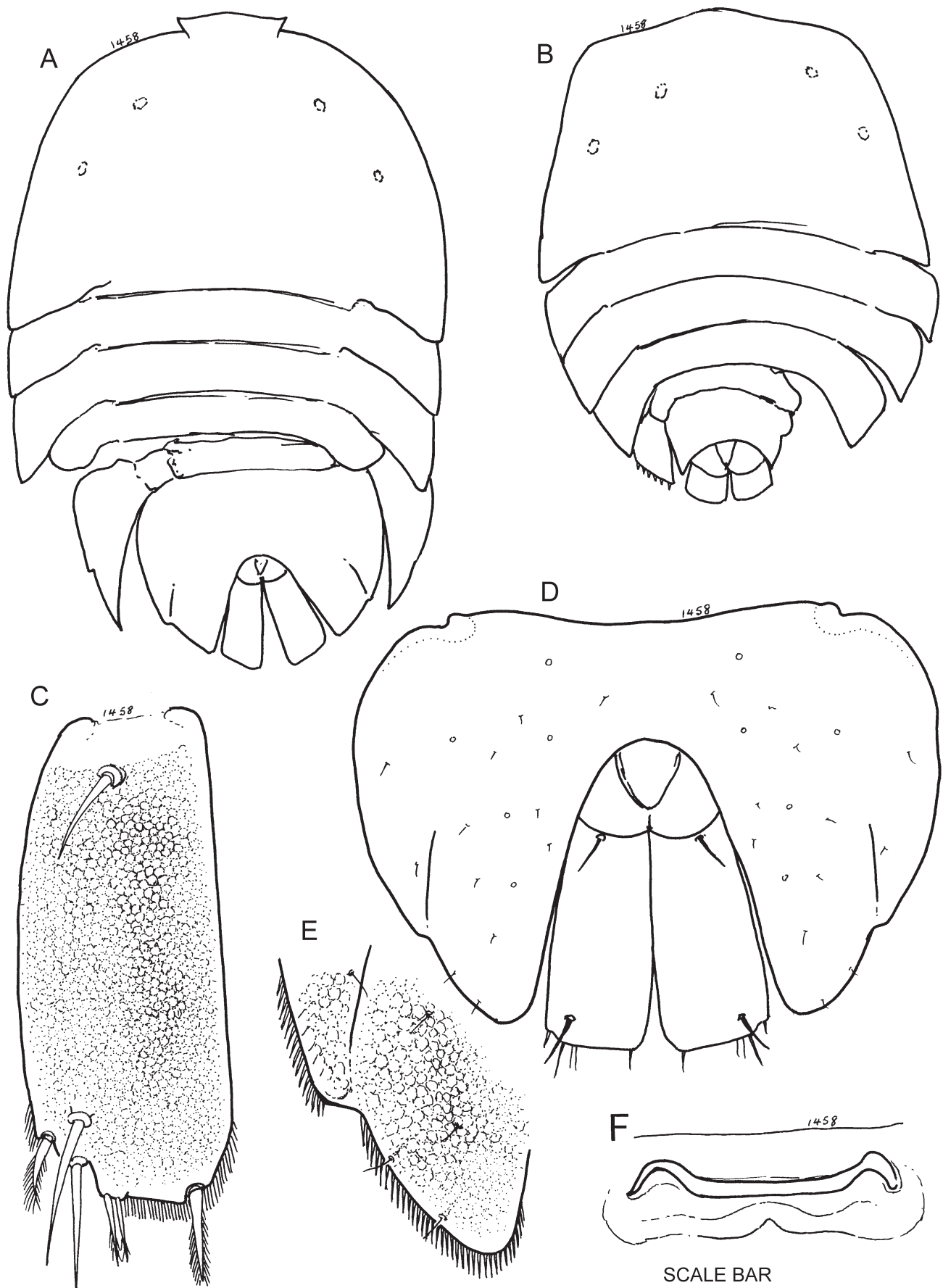


Figure 13. *Porcellidium roscoffensis* (Bocquet, 1948) comb. nov. Female: (A) adult; (C) caudal ramus; (D, E) genital double-somite (E, posterior lobe detail); (F) genital opening. Male: (B) adult. Drawings of specimens from Pembrokeshire. Scale bar: A = 0.48 mm. C, F = 0.08 mm. D = 0.23 mm.

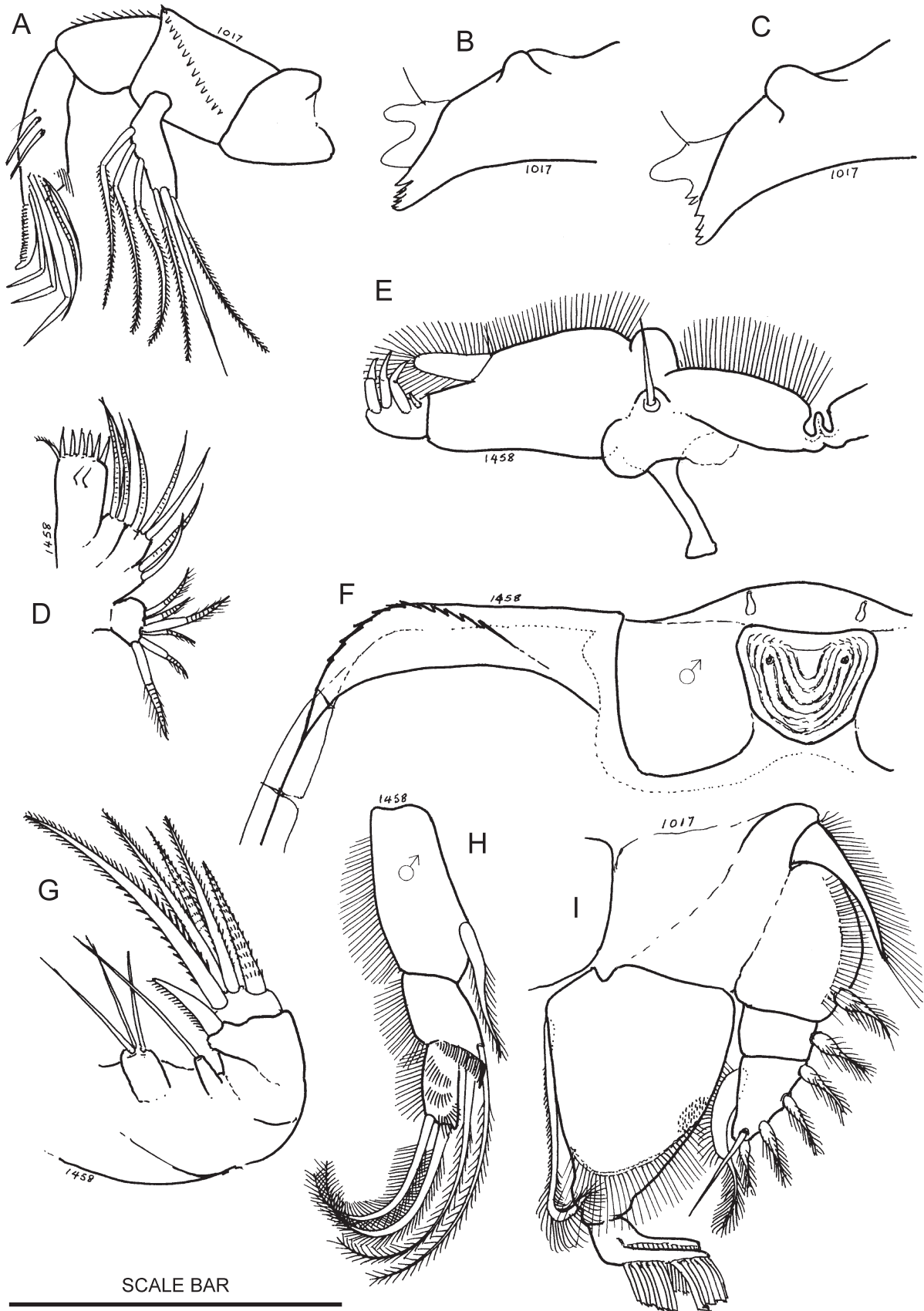


Figure 14. *Porcellidium roscoffensis* (Bocquet, 1948) comb. nov. Female: (A) antenna; (B, C) molar process of mandible; (D) maxillule (exopod seta missing); (E) maxilliped; (G) maxilla. Male: (F) rostrum and shoulder (ventral); (H) P2 endopod; (I) P1. Scale bar: A, F = 0.13 mm. B, C, D, E, G = 0.08 mm. H, I = 0.15 mm.

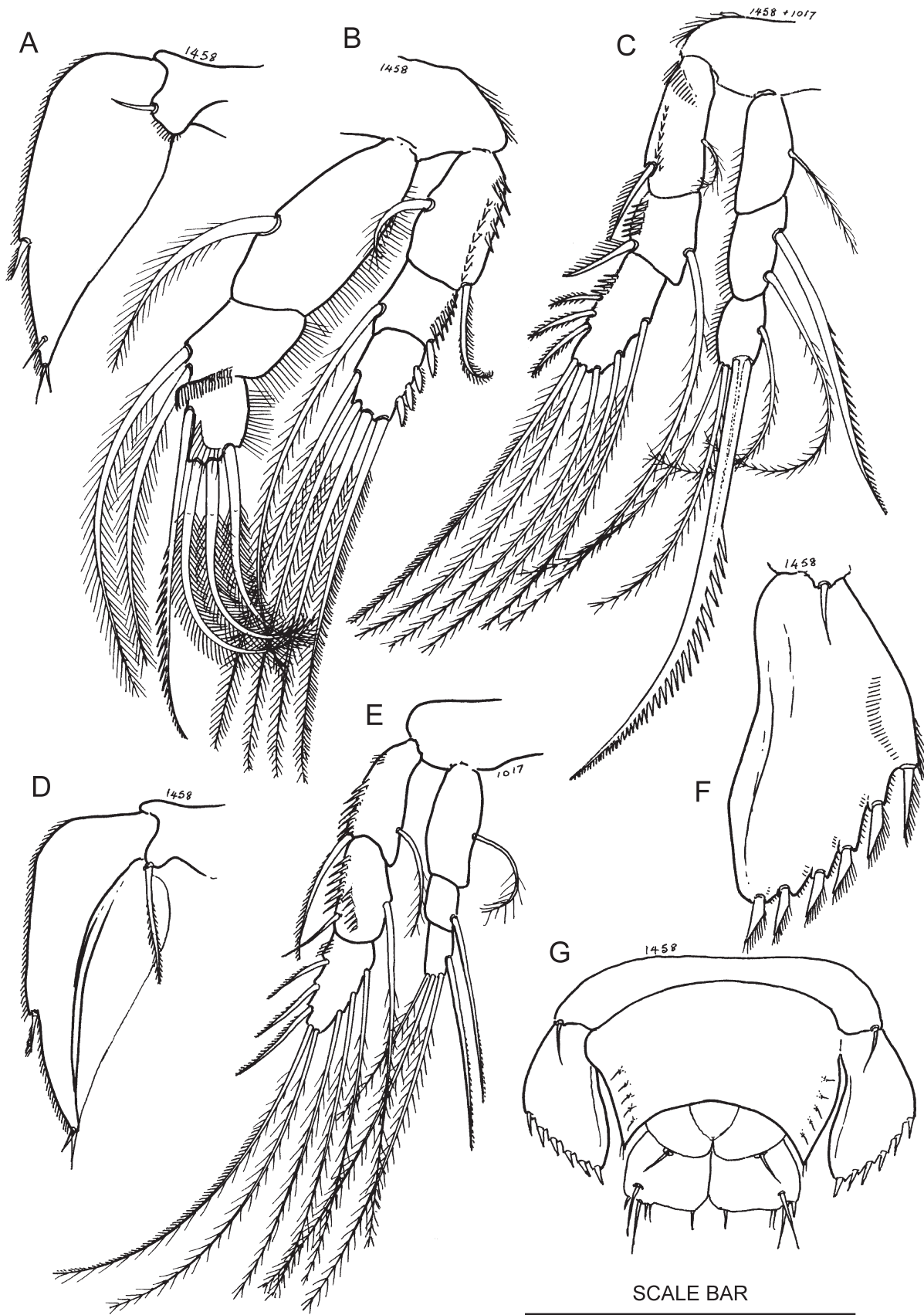


Figure 15. *Porcellidium roscoffensis* (Bocquet, 1948) comb. nov. Female: (A, D) P5 (dorsal, ventral); (B) P2; (C) P3; (E) P4. Male: (F) P5 (ventral); (G) genital somite (dorsal). Scale bar: A, D, G = 0.23 mm. B, C, E = 0.15 mm. F = 0.08 mm.

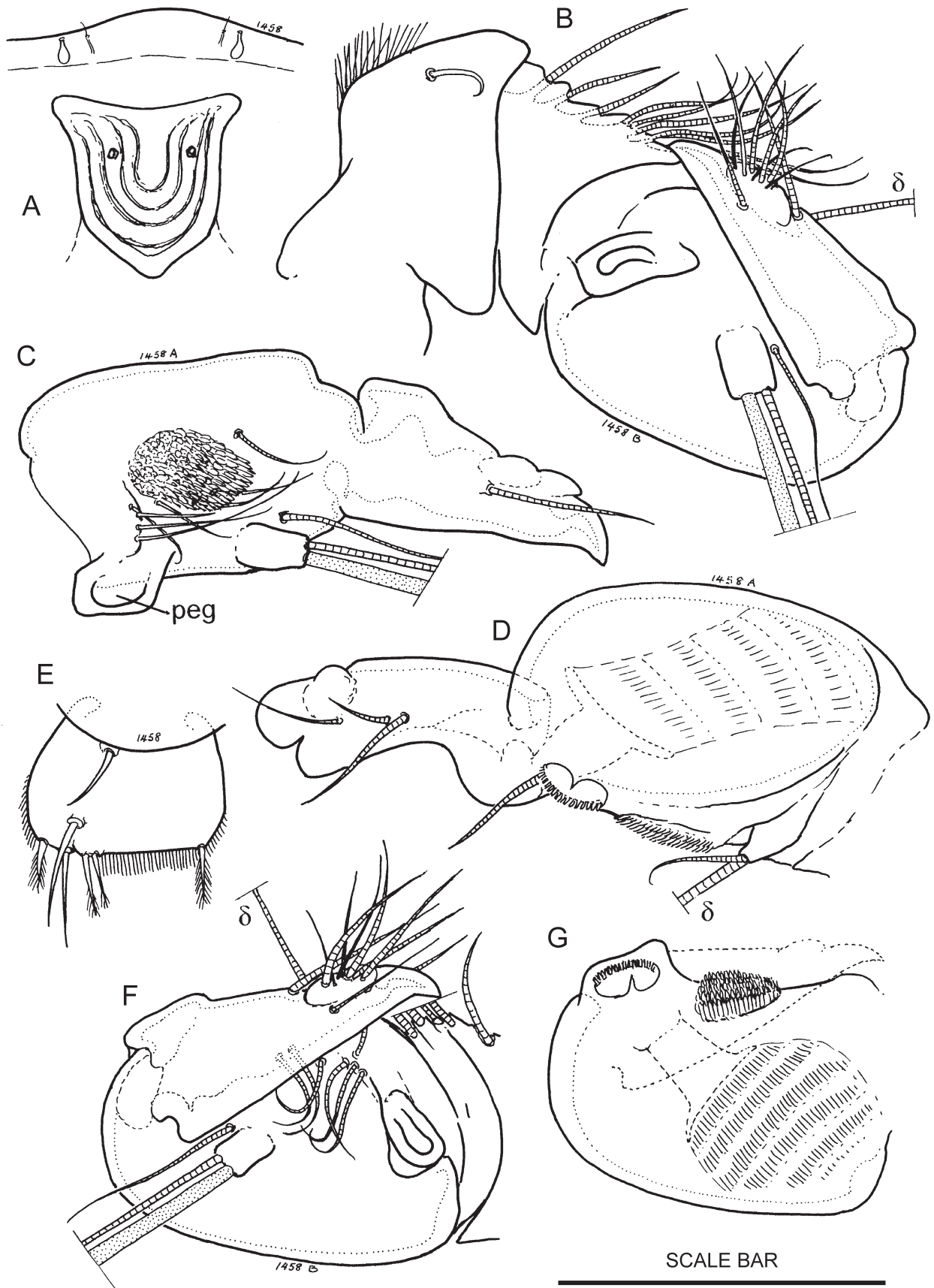


Figure 16. *Porcellidium roscoffensis* (Bocquet, 1948) comb. nov. Male: (A) rostrum (ventral); (B) antennule; (C, D, F, G) details of antennule dactylus and coupling denticles; (E) caudal ramus. Scale bar: A-G = 0.08 mm.

typical of family. Antenna (Fig. 14A) with row of triangular setules on basis, three lateral setae on endopod segment 2, end part of geniculate setae plain, terminal claw comb-like about $\frac{1}{3}$ length of endopod segment 2. Tips of molar process on mandible (Fig. 14B, C), maxillule (Fig. 11D, exopod not shown), maxilla (Fig. 14G) and maxilliped (Fig. 14E) as described for *Porcellidium viride*. Triangular first segment of P1 endopod narrow ($l/w = 1.3$), very small peg field at lateral corner of fimbriate crescent (Fig. 14I). Serrate spinous seta on segment 3 of P2 endopod almost as long as endopod (Fig. 15B). Serrate spinous seta on P3 endopod segment 2 (Fig. 15C) as long as endopod, large serrate spinous seta on segment 3 longer than endopod (1.45:1). Seta on P4 endopod segment 2 and internal seta on segment 3 spinous, very finely serrulate (Fig. 15E). Internal seta on baseoendopod of P5 $\frac{1}{3}$ length of exopod, exopod lanceolate, dorsal surface with small pits, one subterminal and two apical setae present (Fig. 15A, D). Number of eggs not known, none of the females is ovigerous.

Adult males (Fig. 13B). Cephalosome truncated with rounded shoulders, anterior edge folded ventrally (Fig. 14F). Hyaline border and dorsal ornamentation as described for female. Ventral surface of cephalosome not wrinkled, but ventral surface of rostrum with U-shaped ridges or wrinkles (Figs 14F, 16A). Genital somite with dorsal pits and row of five sensilla on either side (Fig. 15G). Caudal ramus subquadrate ($l/w = 0.8$), lateral edge convex, medial edge straight, ends in slight bevel with T4 at corner, posterior border straight, T1 and γ setae not recessed, β seta subterminal, fringe of fine border setules between T3 and T4 (Fig. 16E). Antennule (Fig. 16B). No finely plumulose setae on segment 2, first seta less than 1.5 times length of second seta, segment 3 with knob or peg-like ventral process, no spine close to δ seta, proximal coupling denticle on segment 4 large finely denticulate pad, distal denticle with fine comb-like edge (Fig. 16B, C, D, F, G), segment 5 of dactylus almost as long as segments 3+4, concave on one side (Fig. 16D), hooked distally (Fig. 16C), segment 6 inconspicuous. P2 endopod terminates in two plumose setae (Fig. 14H). P5 with short row of small setules at base of each terminal seta (Fig. 15F).

Remarks. Bocquet (1948) describes two colour forms of *P. lecanoides* from Roscoff, Brittany, France. The first is uniform golden yellow, the second is golden yellow with narrow dark violet median stripe down back and caudal rami. Because of their colouration, shape of the caudal rami and statistical difference in size, the second form was considered a variety of Claus' *P. lecanoides* and named *P. lecanoides* var. *roscoffensis*. Bocquet did not give a complete description of the new variety, but the specimens collected from Pembrokeshire conform precisely to Bocquet's illustrations of the caudal rami plus genital double-somite and are considered to be the same species. However, *P. lecanoides* is a synonym for *P. viride* and the Pembrokeshire animals do not resemble *P. viride*. It is considered that Bocquet's variety should be raised to specific rank as *Porcellidium roscoffensis* (Bocquet, 1948) comb. nov.

The antennae of the two male specimens used in this description are either closed or in a position where critical observation of the coupling denticles is difficult. What can be seen is illustrated in Fig. 16.

Distribution. Bocquet (1948) records the species as abundant on *Bifurcaria tuberculata* in tidal pools at Roscoff. It is also abundant in the Bay of Morlaix. Bocquet describes their colour as yellow with a band of violet down the back, but the colour of living animals from Pembrokeshire is not known. They were found among *Porcellidium viride* washed from a mixture of seaweeds many years after collection and were colourless.

Genus *Porcelloides* gen. nov.

Type species. *Porcelloides tenuicaudus* (Claus, 1860) comb. nov.

Porcellidium tenuicauda.—Claus, 1860: 6–8.

Diagnosis. Spermatophore of male reniform (kidney-shaped) with recurrent duct (Fig. 17A, 18C) deposited on dorsal side of female P5, firmly attached on its side by adhesive material, remains attached to female long after egg laying has started (semi-permanent), deposition of more than one spermatophore on female common; male antennule without denticle or ventral process on segment 3, segment 4 with three coupling denticles, proximal denticle triangular with serrated edge, medial denticle large denticulate pad, distal denticle variable (brush-pad absent); outline of male and female body ovoid (egg-shape), anterior of male cephalosome not obviously truncated; hyaline border surrounds edge of cephalosome; female caudal ramus trapezoid or rhomboid; six setae on maxillule endopod, maxilliped coxae touch in midline; dorsal setae of female P5 pinnate, no ventral expansion to P5; male P5 trapezoid with one lateral and five terminal setae.

Species composition. *Porcelloides tenuicaudus* (Claus, 1860) comb. nov.; *Porcelloides scutatus* (Claus, 1889) comb. nov.

Distribution. Genus known from Sicily, Mediterranean Sea; Roscoff, France; Scilly Islands; Ireland; Pembrokeshire, Wales; Scotland.

Remarks. The animals named *Porcellidium tenuicauda* by Claus (1860) are excluded from the diagnosis for *Porcellidium* by apomorphic characters not possessed by *P. viride*. They must be moved to a new genus. The name *Porcelloides* (treated as masculine) is proposed for this new genus. Claus (1860) did not say why he chose the diminutive *Porcellidium* for the name of his new animal, but he might have been impressed by the way they conglobate just like *Porcellio* (the sow bug or woodlouse).

Key to the species of *Porcelloides*

- 1 Female caudal rami excluded from arch of genital double-somite. T3 absent from caudal ramus, γ seta $\frac{1}{2}$ way down bevelled edge of ramus. Hyaline border of cephalosome not striated. Male rostrum keeled. Terminal setae on male P5 short ($< \frac{1}{3}$ length of lateral edge of P5). Colour brown. Europe. (Plate 1G, p. 67)
 *Porcelloides tenuicaudus* (Claus, 1860) comb. nov.
- Half female caudal rami included in arch of genital double-somite. T3 present on caudal ramus, γ seta at lateral corner of bevelled edge. Hyaline border of cephalosome striated. Male rostrum not keeled. Terminal setae on male P5 long ($\frac{2}{3}$ length of lateral edge of P5). Dorsal patch of red/brown on cephalosome. Europe. (Plate 1E, p. 67) *Porcelloides scutatus* (Claus, 1860) comb. nov.

***Porcelloides tenuicaudus* (Claus, 1860)
 comb. nov.**

Figs 17–20

Porcellidium tenuicauda Claus, 1860: 6–8, taf., II, abb., 10–18.

P. tenuicauda.—Brady, 1880: 166; Claus, 1863: 149; Claus, 1889: 32; Norman & Scott, 1906: 182; Pesta, 1935: 374; Bocquet, 1948: 239–242; Lang, 1948: 422; Bartsch, 1987: 139–143; Huys *et al.*, 1996: 307; Bodin, 1997: 65; Walker-Smith, 2001: 656; Wells, 2007: 79.

Porcellidium dentatum.—Claus, 1860.

Porcellidium ovatum.—Haller, 1879; Haller, 1880: 58.

Material examined. Specimens in NHM, London and NMI, Dublin (see Appendix 1 and 2). Living material was collected for dissection and measurement from the sublittoral at Castle Head, Dale, Pembrokeshire, Wales (51°42'N 5°10'W) and Clachan, Shiel Sound, Oban, Scotland (56°19'N 5°35'W), V. A. Harris, 1974, 1987.

Specimens deposited in NHM, London (1 ♂, 4 ♀♀ and three slide mounted dissections).

The following re-description is based on specimens from Clachan identified from Claus (1860, 1863, 1889) and Bocquet's (1948) description of *Porcellidium tenuicauda* and *P. dentatum*.

Diagnosis. Hyaline border plain (no striations); male rostrum with ventral keel (Fig. 20C); female caudal rami excluded from arch of genital double-somite, ramus acutely trapezoid, apical angle 25°, bevelled edge long (4 × length of lateral edge), marginal setules down whole length of medial and bevelled edge, T1 and γ seta half-way down bevelled edge, T3 absent (Fig. 17D); spinous setae on female P4 endopod segments 2 and 3 slender, finely serrulate; falciform ridge of female P5 a smooth curve (compare Fig. 22E), apical seta not pinnate; terminal setae on male P5 short ($\frac{1}{3}$ length of exopod lateral edge).

Biometric data. Because animals are not as dorsoventrally flattened as other species and tend to conglobate (roll into a ball) when preserved, some distortion takes place when specimens are mounted flat on a slide. This leads to uncertainty in some of the measurements. There is a wide difference in body length measured to posterior of genital double-somite (L_{urs}) and the total length measured to the extremity of the caudal rami (L_{max}). Both measurements are given. Claus (1860) gives female length as $1\frac{1}{3}$ mm and

Brady (1880) gives $1/23$ rd inch (1.1 mm). The following measurements were made on specimens from Scotland and Pembrokeshire, Wales.

Females (N = 6): maximum length (L_{max}) 1.04 mm (range 0.99–1.10 mm), body length (L_{urs}) 0.89 mm (range 0.87–0.92 mm); cephalosome width (W) 0.74 mm (range 0.71–0.80 mm); rostrum width (R) 0.16 mm (range 0.15–0.18 mm); genital double-somite width 0.35 mm, length 0.29 mm; caudal ramus length 0.19 mm, width 0.07 mm; apical angle of ramus 25–30°.

Ratios: L_{max}/W 1.4 (range 1.22–1.42), L_{urs}/W 1.2 (range 1.13–1.24); W/R 4.5; genital double-somite width 45% of cephalosome width, w/l 1.2, length of posterior lobe 15% of lateral border, arch 24% of genital double-somite length; caudal ramus 21% of L_{urs} , w/l 2.7, Hicks' index for α seta 93%, for β seta 81%.

Males (N = 2): maximum length (L_{max}) 1.0, 1.02 mm, body length (L_{urs}) 0.95 mm; cephalosome width (W) 0.80 mm; apical angle of caudal ramus 25°; antennule fully extended 0.22 mm; spermatophore (N = 4 measured on females) 0.29 × 0.08 mm.

Ratios: L_{max}/W 1.27, L_{urs}/W 1.2; male antennule (fully extended) 28% of cephalosome width, segment 2 32%, segment 3+4 34%, dactylus 18% of antennule length; spermatophore 30% of body length L_{urs} .

Description. *Adult females* (Fig. 17A; Plate 1G, p. 67): colour red-brown partly due to orange oil droplets in body, middle of cephalosome darker in some animals. Body oviform (egg-shape) in outline, cephalosome semicircular, wider (relative to body length) than any other species in the family, body not dorsoventrally flattened to the same extent as most other species (height approximately $\frac{1}{4}$ cephalosome width). Animals can conglobate. Rostrum projects $\frac{1}{3}$ of its width. Hyaline border clear (no striations) with eight sensilla in plane of membrane, width 15 μm . Ducts of marginal glands open dorsal to hyaline membrane. Dorsal surface with small pits 4–5 μm in diameter, medial portion of P5 and dorsal surface of caudal rami ornamented with network of ridges (Figs 17D, 19D, 20B). Genital double-somite (Fig. 17B) narrow, $\frac{1}{2}$ cephalosome width, length about $\frac{1}{3}$ body length, posterior lobe short ($\frac{1}{3}$ lateral border), not expanded laterally, bordered with a few filiform setules, posterior arch houses anal somite only, caudal rami completely excluded from arch. Genital aperture simple (Fig. 17C). Caudal ramus trapezoid, elongate, acute pointed, ($l/w = 2.6$). Seta T4 large

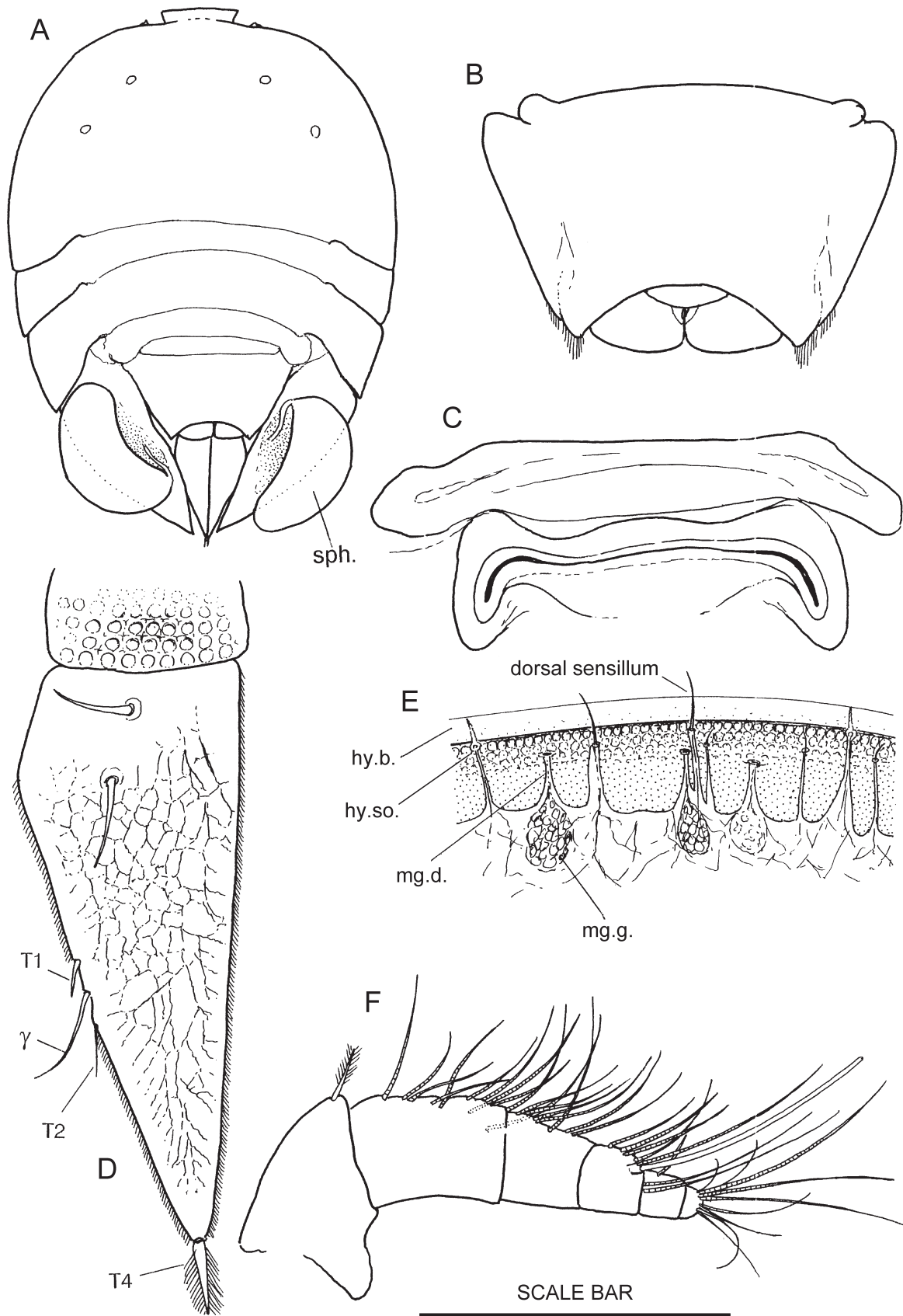


Figure 17. *Porcelloides tenuicaudus* (Claus, 1860) comb. nov. Female: (A) adult (carrying two empty spermatophores on dorsal surface of P5s); (B) genital double-somite; (C) genital opening; (D) caudal ramus (dorsal); (E) border of cephalosome (*hy.b.* hyaline membrane; *hy.so.* hyaline sense organ; *mg.d.* duct; *mg.g.* marginal gland); (F) antennule. Scale bar: A = 0.65 mm. B = 0.25 mm. C, D = 0.1 mm. E = 0.2 mm. F = 0.14 mm.



Figure 18. *Porcelloides tenuicaudus* (Claus, 1860) comb. nov. Female: (A) antenna; (B) maxillule; (C) empty spermatophore attached to P5; (D) maxilliped; (E) mandible; (F, G) right and left molar process; (H) maxilla. Scale bar: A, D, H = 0.1 mm. B = 0.08 mm. C = 0.4 mm. E = 0.19 mm. F, G = 0.14 mm.

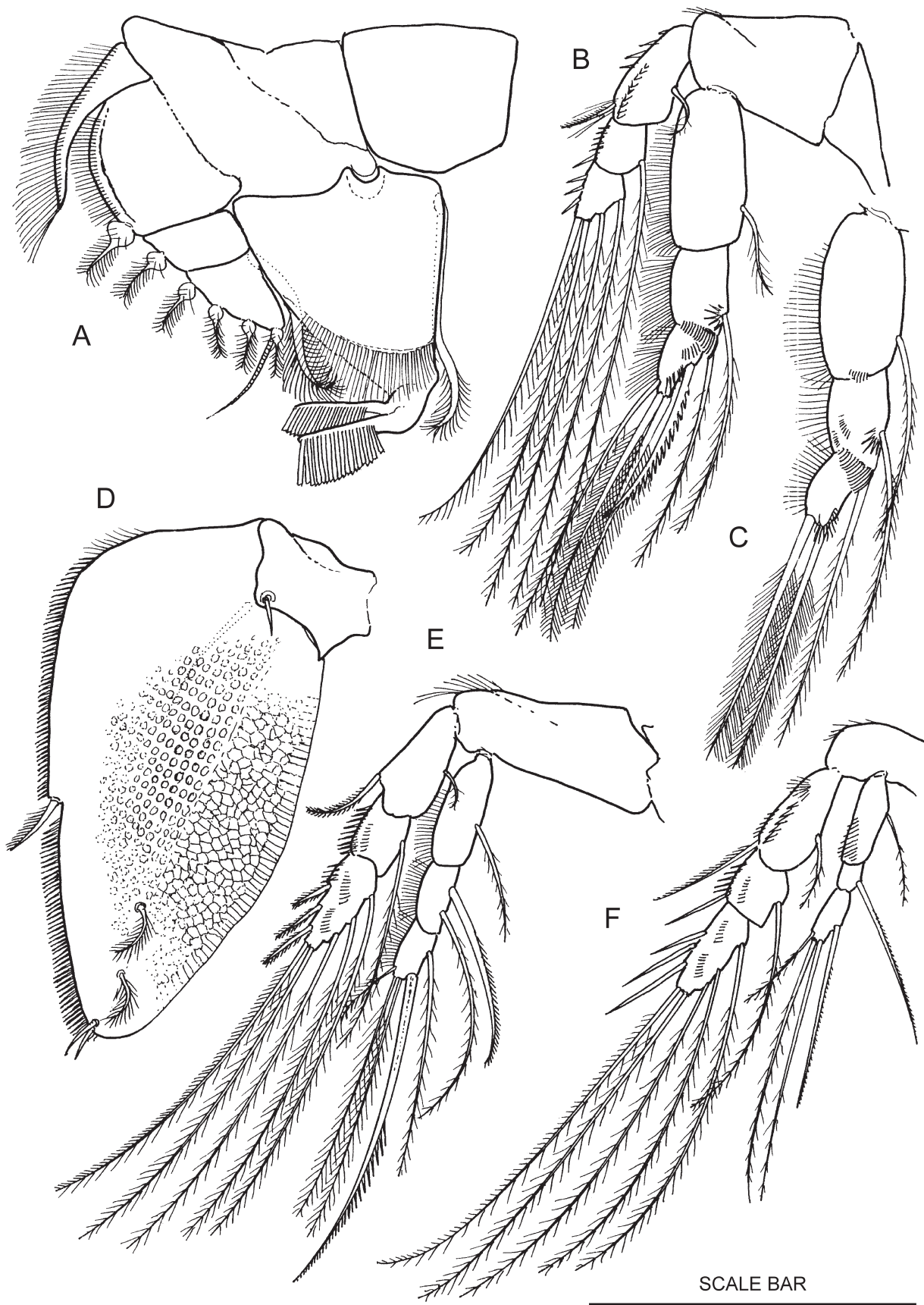


Figure 19. *Porcelloides tenuicaudus* (Claus, 1860) comb. nov. Female: (A) P1; (B) P2; (D) P5 (dorsal); (E) P3; (F) P4. Male: (C) P2 endopod. Scale bar: A = 0.16 mm. B, C, E, F = 0.22 mm. D = 0.25 mm.

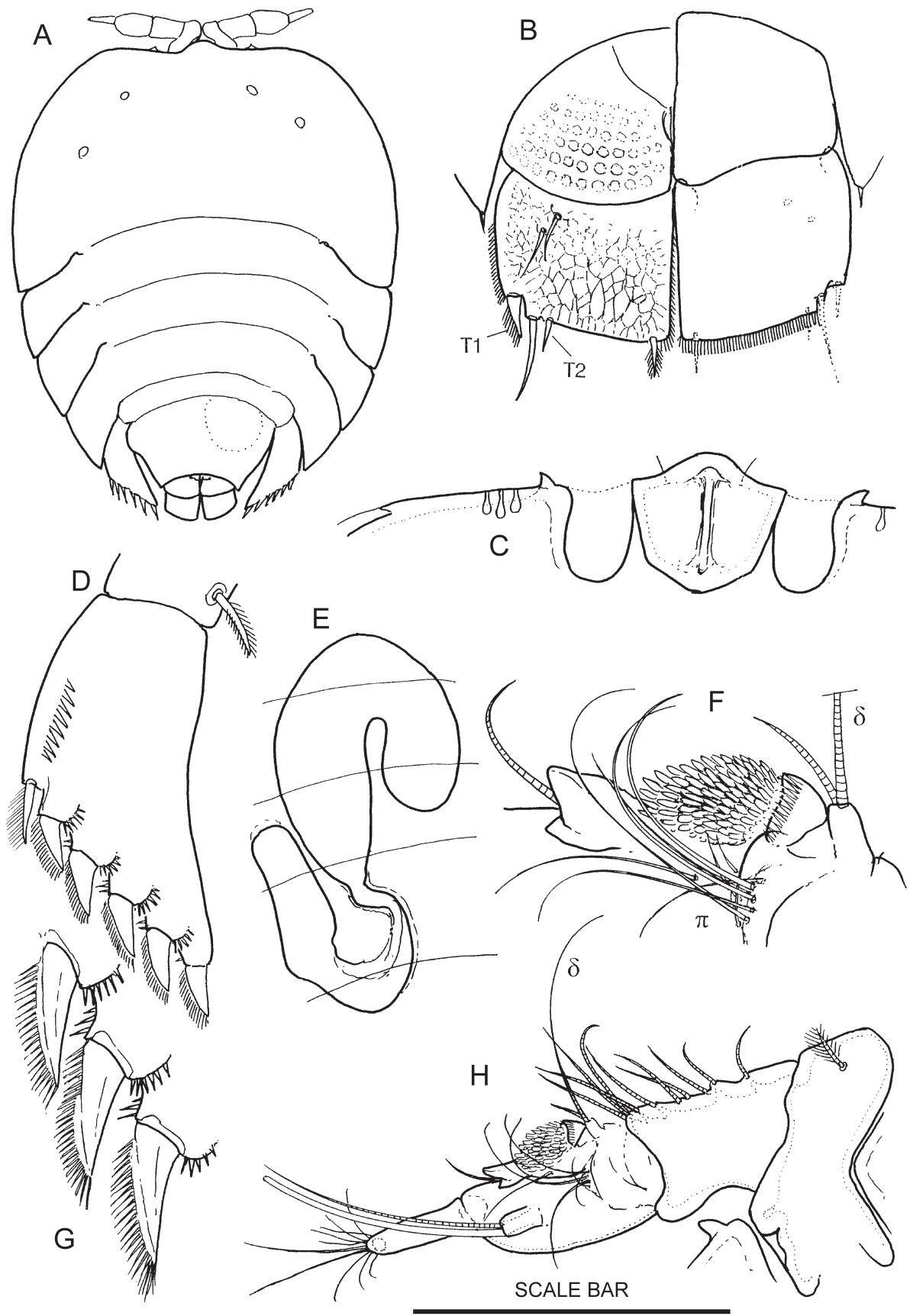


Figure 20. *Porcelloides tenuicaudus* (Claus, 1860) comb. nov. Male: (A) adult; (B) caudal rami (left dorsal, right ventral); (C) rostrum (ventral); (D, G) P5 (ventral, detail of terminal setae); (E) developing spermatophore; (F) coupling denticles on antennule; (H) antennule. Scale bar: A = 0.65 mm. B = 0.14 mm. C, D = 0.15 mm. E = 0.3 mm. F = 0.06 mm. G = 0.08 mm. H = 0.12 mm.

pinnate at posterior apex (Fig. 17D), medial edge straight, bordered with fine setules along entire length, lateral edge divergent, without setules, extends as far as level of β seta, bevelled edge $4 \times$ length of medial edge, bordered with fine setules, α and β setae inserted proximally, terminal seta T1 small inserted about $\frac{1}{3}$ down bevelled edge, γ and T2 about $\frac{1}{2}$ way down bevelled edge, T3 absent. Antennule, segment 1 seta pinnate (Fig. 17F), no plumulose setae on segment 2. Setation of mouthparts and ambulatory limbs typical of family. Basis and segment 1 of antenna endopod with setules along medial border, exopod with five plumulose setae and one plain spinous seta, segment 2 of endopod with one small and two longer lateral setae (1 pinnate), geniculate setae with distal part plain, claw comb-like (Fig. 18A). Anterior lobe of mandibular palp with small patch of ventral setules (Fig. 18E). Gnathobase of maxillule pre-coxa (Fig. 18B) with five plain and three pinnate setae plus two lateral geniculate setae, endite on coxa and two endites on basis with four setae each, endopod with six setae, exopod with one plain and one bulbous seta. Proximal endite on syncoxa of maxilla (Fig. 18H) with four setae, distal endite with one seta, spatulate seta on basis with comb-like edge, endopod with three biserrulate and two multi-serrulate setae. Maxilliped coxae touch in midline, basis with fimbriate border and fimbriate process (Fig. 18D). No peg area on P1 endopod, endopod $l/w = 1.05$, terminal claws of endopod lamellate (Fig. 19A). P2 endopod $1\frac{1}{2}$ times length of exopod (Fig. 19B), external seta on exopod segment 1 short, terminal segment of endopod with strong, serrate spinous seta plus three plumose setae. P3 (Fig. 19E) spinous seta on segment 2 of endopod finely serrulate, shorter than endopod (0.75:1), large spinous seta on terminal segment slender, serrate, longer than endopod (1.4:1). P4 endopod $\frac{2}{3}$ length of exopod (Fig. 19F), external seta on segment 1 of exopod as long as segment 1, spinous seta on endopod segment 2 and first (internal) spinous seta on segment 3 both long, thin and finely serrulate. P5 (Fig. 19D) baseoendopod with small plain external and serrulate internal seta, exopod broad, ovate ($*w/l = 0.45$), bordered along external edge with short setules, dorsal surface with pits except for medial edge which has a reticulate pattern, two large pinnate dorsal setae plus two plain setae at apex. P5s reach to posterior extremity of caudal rami. (* Width of P5 at level of lateral seta).

Adult males (Fig. 20A). Colour, body shape, hyaline border and dorsal pits as for female. Anterior edge of cephalosome rounded, slightly truncated, rostrum with ventral keel, only visible from ventral view, projects as convex bulge in midline (Fig. 20C), lateral angle of antennule socket with conical projection. Caudal ramus short, almost quadrate (Fig. 20B), lateral edge convex with setules down posterior $\frac{2}{3}$, medial edge straight with fine setules down length, α and β setae short ($\frac{1}{4}$ width of ramus), T1 pinnate, short, slightly recessed, T2 very short, plain, T3 absent, T4 pinnate, close to medial corner, posterior border with fine setules, dorsal surface of rami with fine reticulate pattern. Antennule short, 28% of cephalosome width with dactylus fully extended, (Fig. 20A, H), segment 1 expanded medially to touch its fellow in front of rostrum, segment 3 with anterior process bearing δ and δ' setae, and π series, segment 4 with proximal triangular coupling denticle, large denticulate pad and bicuspid distal denticle (Fig. 20F), dactylus (segment 5) cylindrical ($\frac{1}{2}$ length of segment 3+4), hooked distally, segment 6 small, fused to segment 5. Ambulatory limbs differ

from female as follows. Endopod of P2 with two plumose terminal setae (Fig. 19C). P5 exopod trapezoid (Fig. 20D), length of terminal setae $< \frac{1}{3}$ of P5 lateral edge, first (lateral) seta narrower than rest of terminal setae, ventral row of six or seven setules at base of each terminal seta (Fig. 20G). Developing spermatophore S-shaped (Fig. 20E), reniform (kidney or bean-shaped) with recurrent duct when fully formed and deposited on female P5 (Fig. 18C).

Remarks. Only a few isolated specimens of *Porcelloides tenuicaudus* have been found after extensive sampling on the West coast of Scotland and Pembrokeshire, Wales, which suggests the animal's preferred habitat was not sampled. The typical dorsoventral flattened body of most porcellidiid species is correlated with life in fast flowing or turbulent waters of the littoral zone where the shape of their body enables them to hold on tenaciously to the substratum. When *P. tenuicaudus* is subjected to fast flowing water (i.e., a jet from a pipette) it rolls into a ball and detaches from the substratum (personal observation). This suggests that its normal habitat may be in deeper water away from fast flowing currents. Haller (1879) dredged his *Porcellidium ovatum* (= *Porcelloides tenuicaudus*) from 80–150 metres and Brady dredged it from 10 fathoms near the Scilly Islands.

Distribution. In the present study specimens were collected from the following algae. *Himantalia elongata* at Castle Bay, Dale, Pembrokeshire (51°42'N 5°10'W), (4 ♀♀), V. A. Harris, 1974. From *Chondrus crispus*, holdfasts of *Laminaria saccharina*, and stones covered with pink *Lithothamnion*, in the sublittoral at Clachan, Shiel Sound, Oban, Scotland (56°19'N 5°35'W), (4 ♀♀, 2 ♂♂), V. A. Harris, 1974, 1987.

In literature (cf. Lang, 1948) it is reported from Shetland Islands, Ireland, Scilly Islands, W coast of France and Mediterranean Sea.

Porcelloides scutatus (Claus, 1889) comb. nov.

Figs 21–24

Porcellidium scutatum Claus, 1889: 34, taf., VIII, abb., 9–18.
Porcellidium ovatum.—Lang, 1948: 442; Geddes, 1968: 14;
 Holmes & O'Conner, 1990: 66; Huys *et al.*, 1996: 307,
 123; Wells (2007): 79.

Material examined. Spirit material and prepared slides in NMI, Dublin, collected by D. Minchin and J.M.C. Holmes from Loch Hyne (Ine), Co. Cork, Ireland (9°15'W 51°30'N), (see Appendix 2). Living material, used for measurements and the following description, was collected from red alga (?*Gelidium* sp.) Loch Hyne, Co. Cork, Ireland and identified from species specific characters in Claus' 1889 description of *Porcellidium scutatum*.

Specimens of *Porcelloides scutatus* (4 ♀♀, 5 ♂♂ and five dissections mounted on slides) have been deposited at NHM, London, V. A. Harris, 1997.

Diagnosis. Hyaline border appears striated; about $\frac{1}{2}$ female caudal ramus lies in arch of genital double-somite; female caudal ramus trapezoid, apical angle 50°, bevelled edge almost equal in length to lateral edge, T1 and γ setae at lateral corner of bevelled edge, T2 normal, T3 very thin, inconspicuous, no setules along medial edge (Fig. 22H); female P4 with massive serrated spinous setae on segments 2 and 3 of endopod (Fig. 23B); ventral falciform ridge on female P5 undulating (wavy), apical seta pinnate (Fig. 22D,

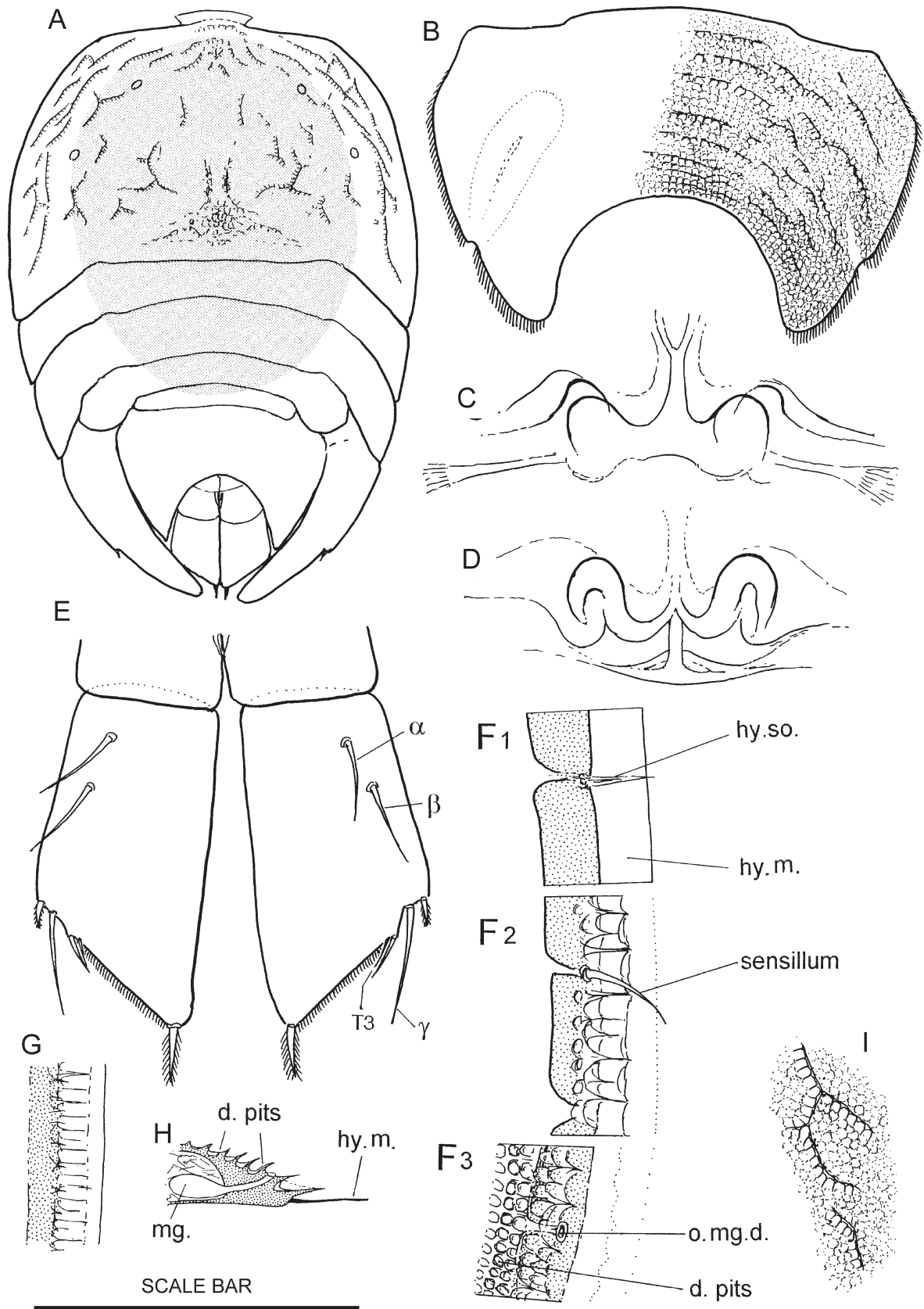


Figure 21. *Porcelloides scutatus* (Claus, 1889) comb. nov. Female: (A) adult*; (B) genital double-somite; (C, D) genital opening, superficial and deep focus; (E) caudal rami; (F) cephalosome border; F_1 focus in plane of hyaline membrane; F_2 focus above membrane showing cuticular ridges; F_3 dorsal focus showing dorsal pits (*d. pits*, *hy.m.* hyaline membrane; *hy.so.* hyaline sense organ; *o.mg.d.* opening of marginal gland duct); (G) appearance of border showing false striations; (H) diagrammatic section through cephalosome border (*mg.* marginal gland); (I) dorsal cuticular ridges on cephalosome. *Drawing of specimen from Ireland. Scale bar: A = 0.45 mm. B = 0.23 mm. C, D = 0.1 mm. E = 0.14 mm. F = 0.07 mm.

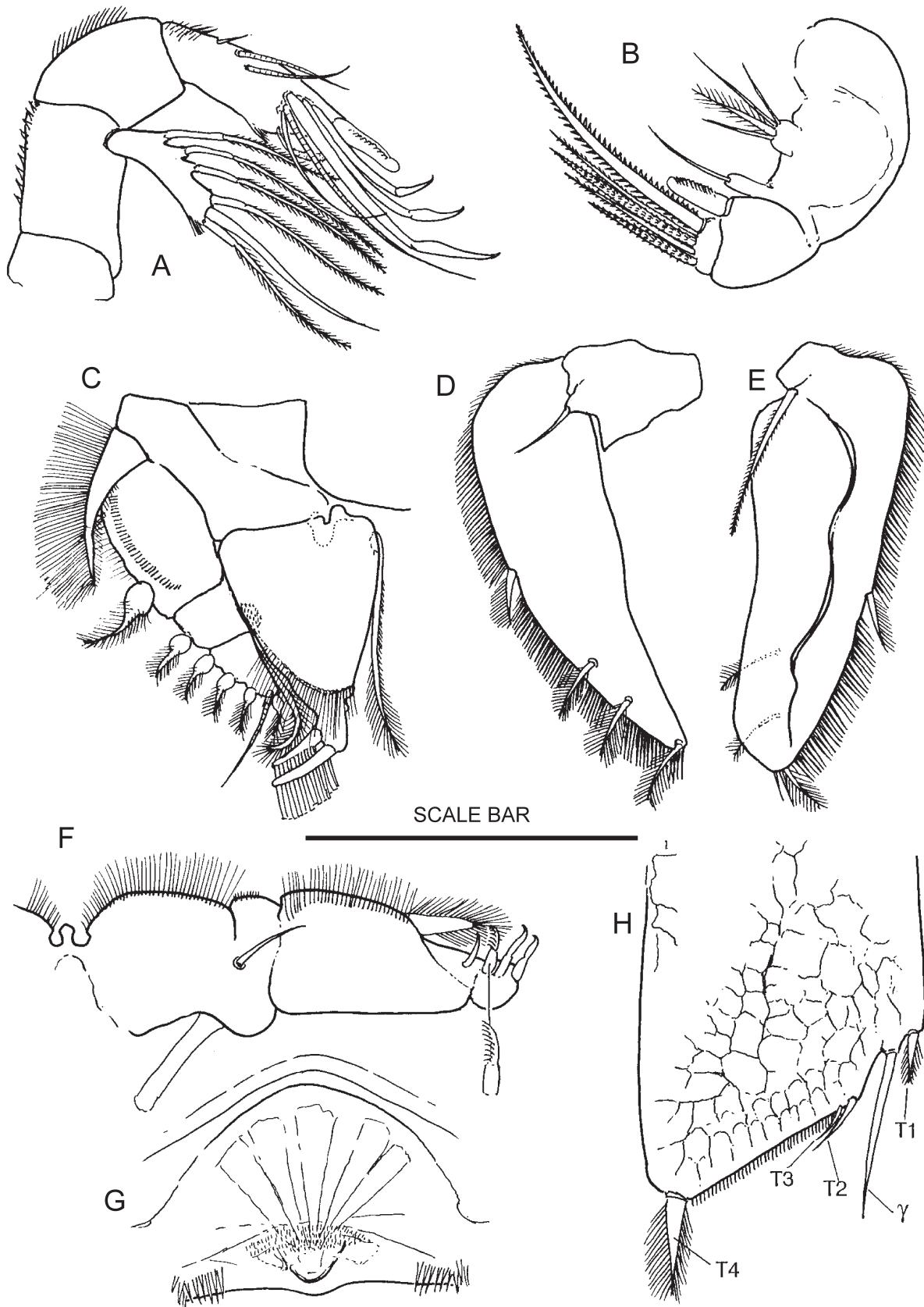


Figure 22. *Porcelloides scutatus* (Claus, 1889) comb. nov. Female: (A) antenna; (B) maxilla; (C) P1; (D, E) P5 (dorsal and ventral, showing pinnate dorsal setae and undulating ventral falciform ridge); (F) maxilliped; (G) labrum; (H) caudal ramus (detail). Scale bar: A, B, F, G = 0.1 mm. C = 0.19 mm. D, E = 0.25 mm. H = 0.08 mm.

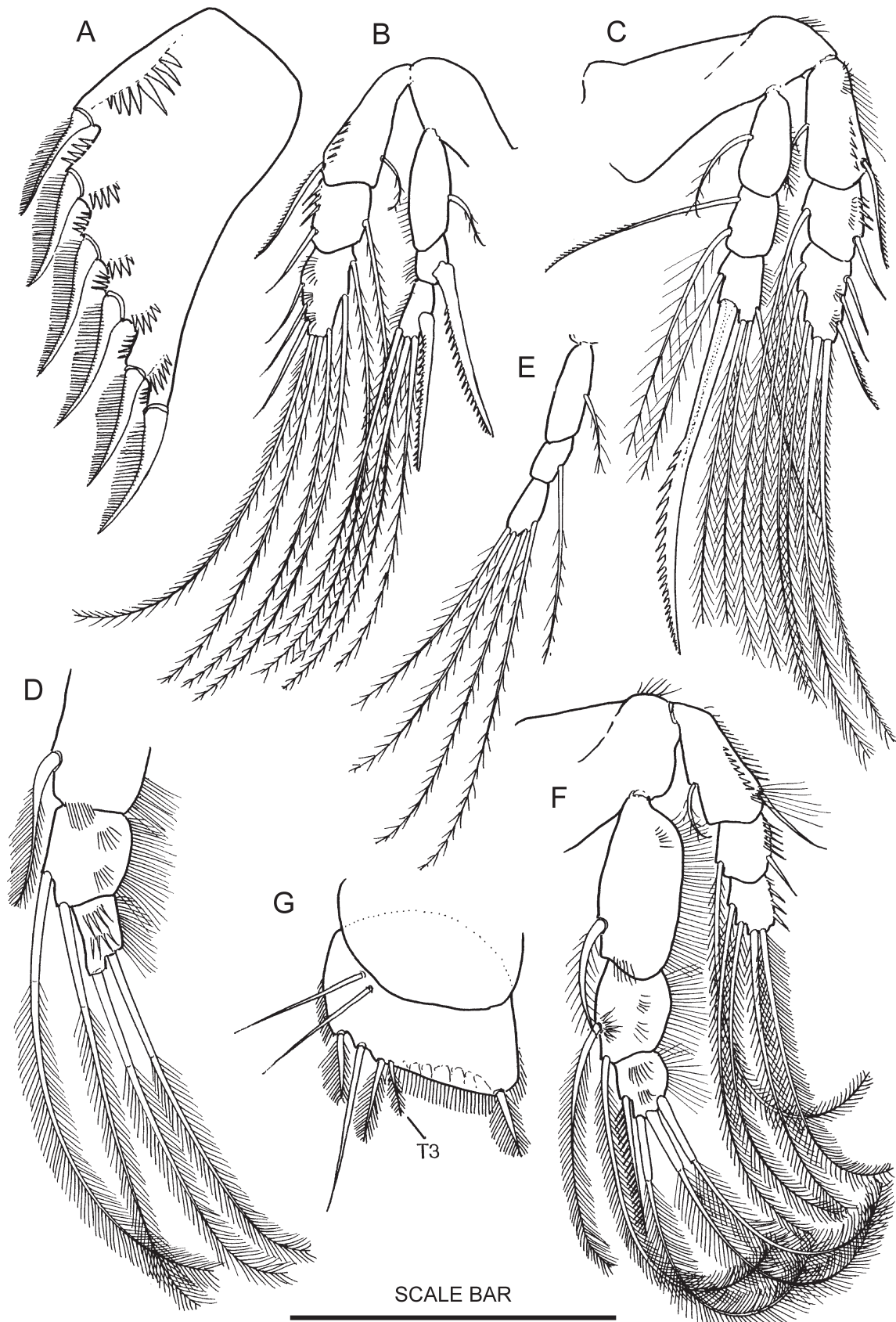


Figure 23. *Porcelloides scutatus* (Claus, 1889) comb. nov. Male: (A) P5 (ventral); (D) P2 endopod; (E) P4 endopod; (G) caudal ramus. Female: (B) P4; (C) P3; (F) P2. Drawing of specimen from Ireland. Scale bar: A, G = 0.1 mm. B, C, E, F = 0.15 mm. D = 0.14 mm.

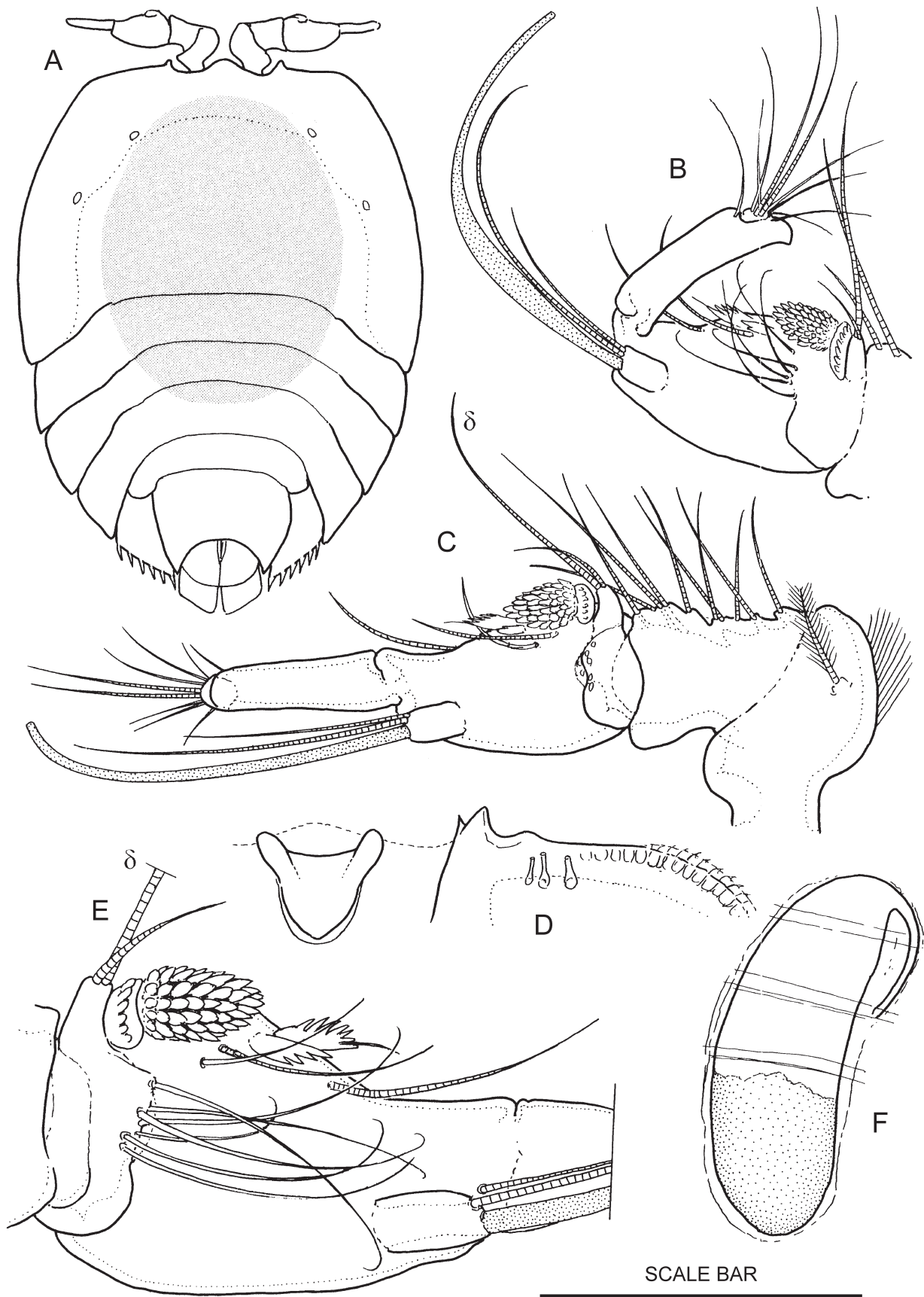


Figure 24. *Porcelloides scutatus* (Claus, 1860) comb. nov. Male: (A) adult; (B, C) antennule (ventral, π setae omitted in C); (D) rostrum and anterior border of cephalosome (ventral); (E) detail of coupling denticles on antennule; (F) spermatophore. Scale bar: A = 0.45 mm. B, C = 0.11 mm. D = 0.15 mm. E = 0.06 mm. F = 0.23 mm.

E); terminal setae on male P5 exopod long ($>1/2$ length of lateral edge).

Biometric data. *Females* (N = 11): maximum length (L_{\max}) 0.84 mm, body length (L_{urs}) 0.78 mm (range 0.74–0.83 mm) [female body length from literature 0.75–0.80 mm, Claus (1889)]; cephalosome width (W) 0.56 mm; rostrum width (R) 0.11 mm; genital double-somite width 0.38 mm, length 24.5 mm; caudal ramus length 0.135 mm, width 0.075 mm; apical angle of ramus 50° .

Ratios: L_{\max}/W 1.52, L_{urs}/W 1.4; W/R 5.1; genital double-somite width 68% of cephalosome width, w/l 1.54, length of posterior lobe 30% of lateral border, arch 40% of genital double-somite length; caudal ramus 17% of L_{urs} , l/w 1.8, Hicks' index for α seta 88%, for β seta 72%.

Males (N = 8): maximum length (L_{\max}) 0.78 mm, body length (L_{urs}) 0.70 mm; cephalosome width (W) 0.53 mm; apical angle of caudal ramus 70° ; antennule fully extended 0.23 mm; spermatophore 0.25×0.087 mm (measured on female P5).

Ratios: L_{\max}/W 1.47, L_{urs}/W 1.3; antennule 43% of cephalosome width, segment 2 26%, segment 3+4 39%, dactylus 28% of antennule length; spermatophore 36% of body length (L_{urs}).

Description. *Adult females* (Fig. 21A; Plate 1F, p. 67): central area of cephalosome and metasome reddish-brown, rest of body colourless. Body ovoid in outline, dorsoventrally depressed, anterior slightly truncated, rostrum prominent with hyaline border, not obscured by anterior bulge of cephalosome. Animals do not conglobate. Dorsal pits conspicuous, 3–5 μm , area round pits slightly thickened to form cuticular network (Fig. 21I), very few dorsal sensilla. Hyaline border appears to have striations perpendicular to edge (Fig. 21G). Striations due to network of ridges expanding out above hyaline border (Fig. 21F₂, H), hyaline border itself is without striations (Fig. 21F₁). Cuticular striations 7–9 μm wide, hyaline border 11–13 μm wide (Fig. 21F₂). Labrum with central patch of very short setules plus group of about eight setules on either side of posterior edge (Fig. 22G). Sternum of metasome segment 4 with fimbriate setules along posterior border. Genital double-somite short, broad (Fig. 21B), small lateral notch and area devoid of pits or setules marks boundary between anterior and posterior lobes, posterior lobe short ($1/3$ of lateral edge), both lobes fringed with fine setules. Posterior arch almost half length of genital double-somite, accommodates anal segment and $2/3$ of caudal rami (as far as lateral corner of the bevelled edge). Genital opening (Fig. 21C, D). Caudal ramus trapezoid (Fig. 21E), widens slightly posteriorly (maximum width $2/3$ down ramus where bevelled edge starts), medial edge without setules, T1 pinnate close to γ at lateral corner of bevelled edge, T2 tends to lie almost parallel to bevelled edge, T3 very thin, inconspicuous, about $3 \times$ length of terminal setules (difficult to see on some animals, Fig. 22H), T4 pinnate at apex of ramus, fine setules along bevelled edge between T3 and T4. Dorsal surface of ramus with network of ridges. Seta on first segment of antennule pinnate. Setation of mouthparts and ambulatory limbs typical of family. Antenna (Fig. 22A) with filiform setules on basis and segment 1 of endopod, exopod with five plumulose setae and one spinous seta, segment 2 of endopod with proximal setules, one small and two larger lateral setae, one plain and one annulate terminal seta, three

geniculate setae with plain distal portion, terminal claw with blunt serrations. Mandible without setules on anterior lobe of palp. Maxillule similar to *P. tenuicaudus*, maxilla (Fig. 22B), maxilliped (Fig. 22F). P1 (Fig. 22C) exopod segment 1 with single crescentic row of denticles parallel to border, endopod with small triangular area of denticles at lateral end of fimbriate crescent, endopod $l/w = 1.25$. Serrulate spinous seta on segment 2 of P3 endopod thin, almost equal to length of endopod, large, serrate, spinous seta on segment 3 longer than endopod (1.5:1), (Fig. 23C). P4 endopod with massive, short, serrate, spinous seta on segment 2 and a similar serrate seta on segment 3 (Fig. 23B). P5 (Fig. 22D, E), dorsal (external) seta on baseoendopod long (40 μm), exopod lanceolate with blunt apex ($w/l = 0.26$ at level of lateral seta), ventral falciform ridge undulating, two pinnate dorsal setae, seta at apex pinnate, border setules filiform, long (25–30 μm), dorsal surface with network of ridges. Females carry 12 eggs in brood chamber (N = 7).

Adult males (Fig. 24A). Colouration, pits, network and striated hyaline border as described for female. Anterior outline of cephalosome rounded, slightly truncated with small convex projection in midline, lateral angle of antennule sockets with conical projection, rostrum V-shaped without ventral keel (Fig. 24D). Caudal ramus trapezoid (Fig. 23G), width greater than length ($l/w = 0.9$), medial edge straight, lateral edge slightly convex, posterior $1/3$ of both edges with setules, α and β setae long ($3/4$ width of ramus), terminal setae T1–T4 long, all pinnate, T3 larger than on female ramus, fringe of fine setules between T3 and T4. Antennule 43% of cephalosome width (Fig. 24A), segment 1 with pinnate seta, no ventral process on segment 3, segment 4 with small serrated triangular proximal denticle, medial large denticulate pad, distal denticle with double serrated edge (Fig. 24E), segment 5 of dactylus slender, cylindrical, $3/4$ length of segment 3+4, hooked distally (Fig. 24B), segment 6 small and fused with segment 5. Ambulatory limbs as for female except for following. P2 endopod with two plumulose setae on terminal segment (Fig. 23D). P4 endopod segments 2 and 3 with long plumulose setae (Fig. 23E). P5 acutely pointed trapezoid, setae long ($2/3$ length of lateral edge, first (lateral) seta pinnate with row of 7–8 ventral setules, remaining setae with 3–5 ventral setules (Fig. 23A). Spermatophore reinform with recurrent neck (Fig. 24F).

Remarks. The animals from Loch Hyne, Ireland, correspond to Claus' description of *Porcellidium scutatatum*. For example, they are the same size and colour, the caudal rami are the same shape and have the same setation (Claus does not show T2, but as pointed out above this is hard to see on some specimens) and both have a long cylindrical dactylus on the male antennule. But the most compelling reason for regarding the two animals to be the same species is the unique hyaline border to the cephalosome. Claus states "...surface at the edge of the cephalothorax with a clear outer margin set through with little rods" (taf.VIII, abb.18). Figure 21F, G, H show the striated border of *Porcelloides scutatus*. Only two other species are known with a striated hyaline border, *Porcellidium akashimum* Harris and Iwasaki (1996a) and an undescribed Australian species of *Kushia*. The false border of *Tectacingulum tumidum* Harris, (1994) is striated, but the true hyaline border, which lies on the ventral side of the cephalosome, is not striated.

Superficially, the female of Claus' *Porcellidium scutatatum*

looks very different from *Porcelloide tenuicaudus*. The caudal rami are not acutely pointed or excluded from the arch of the genital double-somite. However, two features show that Claus' *P. scutatatum* belongs to the genus *Porcelloides*. The arrangement of denticles on the male antennule closely resembles that of *Porcelloides tenuicaudatus*, but differs from all other known species in the family. This together with the fact that two females from Loch Hyne carry eggs and an empty spermatophore on their P5 limb shows that Claus' *P. scutatatum* should be assigned to the new genus as *Porcelloides scutatatus* (Claus, 1889), comb. nov.

Distribution. Living specimens of this species were collected from a red alga (?*Gelidium*) in shallow water (10 to 40 cm) on the west side of Loch Hyne, Co. Cork, Ireland, in deep shade from overhanging trees, LH4.9.97, 11 ♀♀, 12 ♂♂, V. A. Harris 1997.

Claus (1889) collected this species from rocks and *Laminaria* in Trieste Harbour, Adriatic Sea, but it has not been recorded anywhere else since. It is not found on the coast of Ireland, or the west coast of England and Scotland. Its presence in Loch Hyne is surprising for it implies two widely separated isolated occurrences.

Loch Hyne (Ine) in County Cork, Ireland, is a deep tidal marine loch, about one square kilometre in area, situated about one kilometre inland. It is connected to the sea by a very narrow channel and rapids through which sea water flows at high tide on the coast. Tidal swing in the Loch is only a few centimetres. It supports an extremely rich marine fauna that includes many Mediterranean (Lusitanian) species not found elsewhere round the coast of Ireland, England or Scotland. The inland location of the Loch would protect it from the extreme weather of the open coast and this suggests it may contain a relic fauna from a period when the climate was warmer. The Loch's origin is uncertain but may represent a glacial lake that was replaced by sea water when sea-levels rose above the level of the rapids, due to changes in land or sea level. It is possible that *Porcelloides scutatatus* represents a relic Lusitanian species that was once more widely distributed.

Animals belonging to *Porcelloides* have not been recorded from the Pacific region (Australia or Japan).

Discussion

The absence of a precise diagnosis for *Porcellidium viride* until now stems from the inadequacy of published descriptions and figures that has resulted in significant taxonomic confusion. This has led to wide difference of opinion among authors as to where the boundaries of the genus *Porcellidium* should be drawn.

There are two aspects to this problem. First there is the disagreement as to the synonymy of the species. Lang (1948) lumped together *P. fimbriatum* and *P. lecanoides* under the one name *P. viride* Philippi. Vervoort (1964) followed Lang and included *P. sarsi* under *Thyone viridis*. Bocquet (1948) recognized *P. lecanoides*, but renamed *P. fimbriatum* (*sensu* Sars 1904) as *P. sarsi*. Other authors recognize *P. fimbriatum* as a valid species. Harris & Robertson (1994) recognized *P. viride*, *fimbriatum* and *sarsi*, while Huys *et al.* (1996) recognized *P. fimbriatum*, *sarsi* and *lecanoides*. Walker-Smith (2001) and Wells (2007) recognize *P. viride*, *fimbriatum* and *lecanoides*. However, the detailed

descriptions given above for *P. viride*, *P. fimbriatum* and *P. roscoffensis* clears up this uncertainty and shows that *P. sarsi* and *P. lecanoides* are synonyms for *P. viride*.

The second problem relates to the validity of new genera. Huys *et al.* (1996) reject five new genera proposed by Harris & Robertson (1994) and Harris (1994) on the grounds that new genera should not be erected until the genus *Porcellidium* had been settled, but they maintain that the family has only one genus *Porcellidium*. However, a number of their characters for the family are seriously inaccurate; for example, they maintain that the male antennule has five segments and is haplocer—features that would exclude all known species from the family.

Walker-Smith (2001) accepts that the family has more than one genus, but does not recognize five of the new genera and places them in *Porcellidium*. This move is recognized by Wells (2007). However, by doing this new characters are introduced into the diagnosis of *Porcellidium* that are not found in the type species, *P. viride*. Walker-Smith correctly asserts that new genera should be based on apomorphic characters and not unique combinations of characters.

In 1840 Philippi gave a diagnosis for a new genus, *Thyone*, for three new species, one of which he named *Thyone viridis*. From his drawing this appears to be a male stage IV copepodid belonging to the Porcellidiidae, but its shape is very strange and cannot be identified with any other known copepodid or adult within the family. Claus (1860) pointed out that *Thyone* was preoccupied and introduced the replacement generic name *Porcellidium* for his two new species, but he does not appear to recognize Philippi's *Thyone viridis* for he does not mention the name in any of his works.

However, Brady (1880) thought that one of his specimens was the same species as Philippi's animal and corrected the name to *Porcellidium viride* (Philippi, 1840). He gave a written description of a copepodid which he thought was the adult female of *P. viride*, but his illustration shows that it was a male copepodid.

Neither Claus nor Brady understood the significance of "mate guarding behaviour", where an adult male clasps a stage III, IV or V female copepodid with his antennules until the copepodid undergoes metamorphosis to an adult female. At that moment the male places his spermatophore on the nubile female. Adult males do not couple with male copepodids, consequently their P5s are easily seen—they terminate with six clearly visible setae. In contrast, the shape and setation of juvenile female P5s cannot be seen during the time they are clasped by the guarding male. As nearly all female copepodids are coupled to a male, the majority of free copepodids are males. Both Claus and Brady appear to have thought that P5s with six setae was a common feature of male and female animals and wrongly assumed that all copepodids, whether coupled or free, were adult females of the same species as the guarding male. Claus (1860), for example, labelled a male copepodid as the adult female of his *Porcellidium dentatum*; the true adult female, which is much larger and has differently shaped P5 limbs and caudal furca, he considered to be another species and named it *Porcellidium tenuicauda*. Similarly, Brady (1880) labelled a male copepodid "adult female", but the true adult female he incorrectly identified as another species—*Porcellidium fimbriatum*.

This confusion caused by sexual differences was further

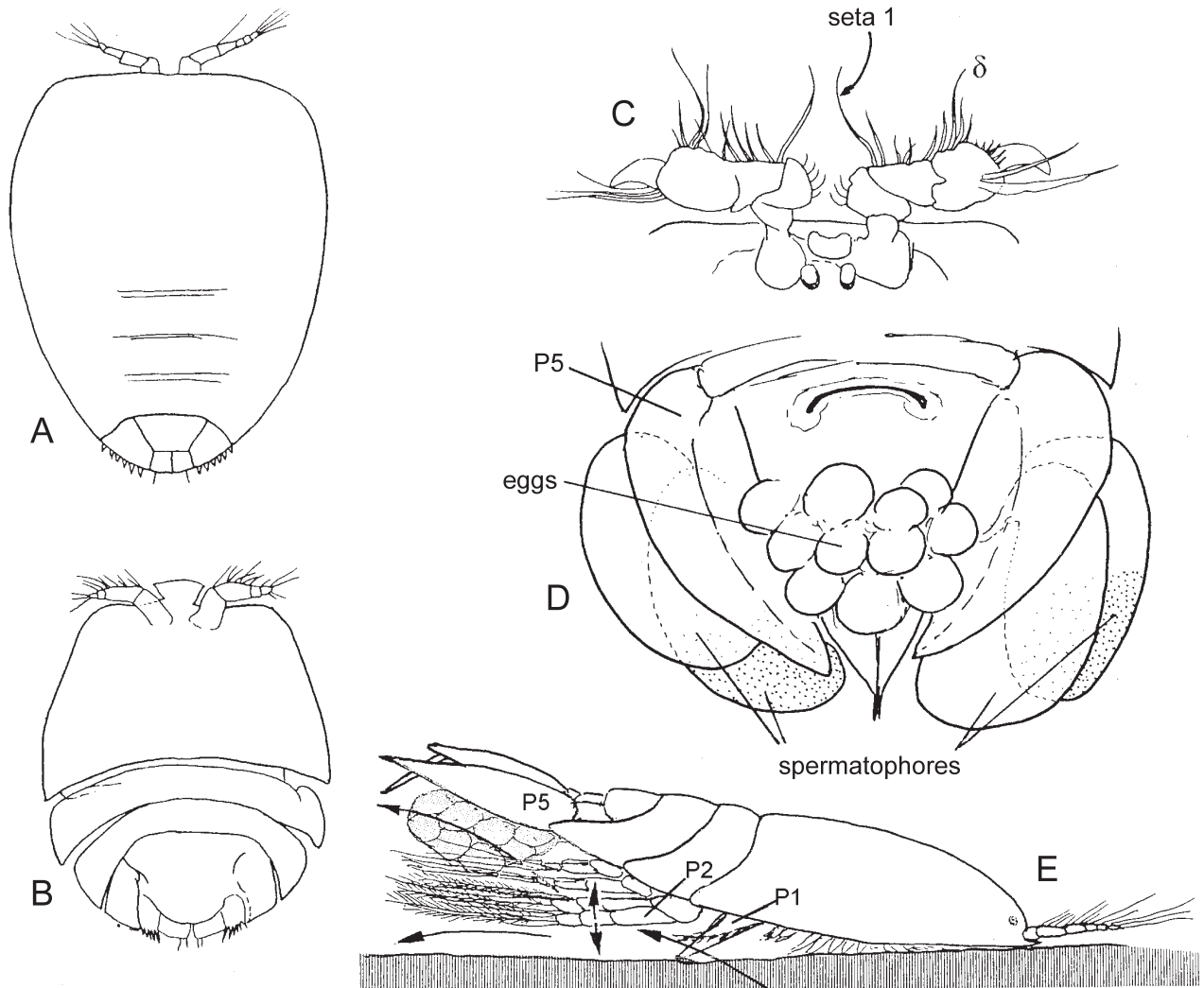


Figure 25. (A) Philippi's 1840 drawing of *Thyone viridis*. (B) Male copepodid labelled "female *Porcellidium viride*" (incorrectly identified as an adult female) Brady (1880). (C) *Porcellidium viride* male antennules (showing very long first seta on segment 2), Brady (1880). (D) *Porcelloides tenuicaudus* (Claus, 1860). Adult female with eggs and four spermatophores attached (freehand sketch of specimen in the NHM collection, V. A. Harris). (E) Female lifting body with P1 limbs to irrigate eggs.

complicated by wrong identification of animals. Claus (1889) acknowledges that his *P. dentatum* is really the male of *P. tenuicauda*, but his (1860) drawing of male *P. dentatum* is of a male *P. fimbriatum*. Similarly, Brady's 1880 drawing of *P. fimbriatum* is clearly the adult female of *P. viride*.

From this confusion and the absence of accurate description it is not surprising that later authors disagree on the true identity of *P. viride* and the diagnostic characters of the genus *Porcellidium*.

The confusion between "viride", "fimbriatum", "lecanoides" and "sarsi"

Brady thought that the large females in his collection were a different species to his *P. viride* and identified them as *P. fimbriatum* Claus, 1863, but Claus' description is not very clear and his illustrations do not show a single species specific character that would have enabled Brady to identify his animals correctly. The most obvious difference between the two species is the placement of the β caudal seta, but this is not shown by either Brady or Claus. A revised description of *P. fimbriatum* was given by Claus (1889) in which at least

eight specific characters are mentioned or illustrated. This showed clearly that Brady's female was the adult female of *P. viride* and not *P. fimbriatum*. Paradoxically, Claus makes the mistake of stating that both Brady's *P. fimbriatum* and *P. viride* are synonymous with his *P. fimbriatum* 1863.

In the present study, samples collected from *Laminaria digitata* at Clachan, Seil Sound Oban, Scotland were found to have two distinct species living on the same seaweed, [Brady (1880) collected some of his specimens of *P. viride* at Loch Fyne, near Oban, Scotland]. They are easily distinguished by their colouration and size. Adult males of the larger species have an unusually long first seta on segment 2 of the antennule (it is about $2\frac{1}{2}$ times the length of seta 2 and 3, Fig. 7G). This is a unique species specific character that has not been found on any other known member of the Porcellidiidae. Brady's illustration of the antennules of his adult male *P. viride* shows the same long first seta (Fig. 25C), therefore, the larger male animals from Scotland must be *P. viride*. The corresponding larger females clearly resemble Brady's illustration of *P. fimbriatum* which must be the adult female of *P. viride*. It is of interest to note that animals from Norway identified by Sars (1904) as *P. fimbriatum* (and

renamed *P. sarsi* by Bocquet in 1948) have the same long first seta on segment 2 of the male antennule and must be *P. viride*. Claus' (1889) description of *Porcellidium lecanoides* does not show the male antennule, but he illustrates five other species specific characters which show his animals are *P. viride*, thus, *P. lecanoides* and *P. sarsi* are junior synonyms for *Porcellidium viride*.

The second species found in the samples from Clachan, Scotland, is smaller and distinguished by a dark blue stripe down the back (Plate 1C,E, p. 67). Comparison of these with *P. viride* from the same locality show that the first seta on segment 2 of the male antennule (Figs 12D) is not much longer than the second or third seta, moreover, details of the female genital double-somite (Fig. 6E) and caudal rami (Fig. 6D) are very different and conform to Claus' (1889) description of *Porcellidium fimbriatum*.

The “*ovatum*” problem

Porcellidium ovatum Haller, 1879 and *P. scutatum* Claus, 1889 have caused problems even to this day because of Haller's poor description. Lang (1948) and Wells (2007) consider them synonymous, but Bodin 1997 does not list either (presumably because he considers both synonymous with Claus' *Porcellidium tenuicauda*). The illustration Haller (1880) gives of *Porcellidium ovatum* Haller, 1879 shows a remarkable resemblance to *Porcelloides tenuicaudus*. It is not clear why Haller (1879) regarded his animal as a separate species, but the body proportions of Claus' (1860) original drawing appear distorted and not obviously egg-shaped. This, together with the apparent difference in shape of the caudal rami, may have led Haller (1879) to regard them as different species. The caudal rami on most preserved specimens of *Porcelloides tenuicaudus* are depressed and appear short in dorsal view, just as Haller (1880) shows in his illustration, but when dissected and laid flat the rami are elongate as shown by Claus (1860).

Monard (1935) states *Porcellidium ovatum* is identical to *Porcellidium tenuicauda*, but gives no evidence for this. There are, however, good reasons for accepting his opinion. Both Claus (1863) and Haller (1879) record a length of 1.3 mm. This is unusually large for members of the Porcellidiidae and is only exceeded by two other species: *Dilatatiocauda bipartita* (Kim & Kim, 1997), 1.45 mm and *Murramia magna* Harris, 1994, 1.38 mm. Haller (1880) describes his animal as “egg-shaped” in outline (hence the trivial name *ovatum*), but *Porcelloides tenuicaudus* is also “egg-shaped” or ovoid, although this is not obvious from Claus' (1860) drawing (the “egg shape” is more obvious when the animal conglobates).

Most members of the Porcellidiidae are coloured or have a colour pattern, due to the colour of the chitinous exoskeleton and/or pigment localized immediately under the cuticular exoskeleton, but *Porcelloides tenuicaudus* shows a marked departure from this arrangement. Specimens from Scotland contained a large number of dark orange or brown oil droplets in the haemocoel that gave the animals an orange or reddish-brown colouration (these are lost in spirit preserved specimens). In his description of *Porcellidium ovatum*, Haller (1880) states that the animals are coloured due to the presence of red and yellow fat globules in the body that glitter through the colourless cuticle. It should be noted that *Porcelloides scutatus*, the only other egg-shaped

European species, does not have oil droplets and its dorsal red patch is due to sub-cuticular pigment. However, by far the most compelling reason for regarding *Porcellidium ovatum* synonymous with *Porcelloides tenuicaudus* is the presence of two reniform spermatophores on the female's P5 limbs shown in Haller's (1880) illustration. Claus (1860) and Bartsch (1987) both show two reniform spermatophores in their illustrations of *Porcellidium tenuicauda*. This is in contrast to the rest of the Porcellidiidae where only one spermatophore is deposited on a female and this only stays attached for a matter of hours.

Lang (1948) treats *Porcellidium scutatum* Claus, 1889 and *Porcellidium acuticaudatum* Thompson & Scott, 1903 as synonyms for *P. ovatum* Haller, 1879, thus, anyone using Lang's key will misidentify *Porcelloides scutatus* as *Porcellidium ovatum*. Three other species have been misidentified through Lang's key. Geddes (1968) referred animals from Barbados to *P. ovatum*, but they do not show any of the characteristics of *Porcelloides tenuicaudus* and probably belong to *Acutiramus*. Holmes & O'Connor (1990) referred specimens in the NMI of *Porcelloides scutatus* collected from Loch Hyne by D. Minchin (July 1982) to *Porcellidium ovatum*. Animals from Oshoro Bay, Hokkaido, Japan (Kito 1977) and Guandong Province, China (Zhang & Li 1976) both referred to as *P. ovatum* are unlikely to belong to that species. The porcellidiid fauna of Japan is reasonably well known but the genus *Porcelloides* has not been recorded from that region. It is probable that the animals from Hokkaido and Guandong are a species of *Kensakia* because the caudal rami of *Porcelloides* and *Kensakia* are superficially similar. Anyone using Lang's (1948) key for identification would misidentify species of *Kensakia* as *P. ovatum*. *Porcellidium acuticaudatum* almost certainly belongs to *Kensakia*.

Haller (1879) described another species, *Porcellidium parvulum*, also from Messina, which he illustrated the following year, Haller (1880). One of his animals appears to be a stage III or IV female copepodid (it does not have typical stage V P5 limbs and is only 0.55 mm). The other animal is a male but its antennules are not transformed and therefore it is not an adult. With a body length of 0.71 mm, it is likely to be a stage IV or possibly stage V male copepodid. The large size of these juveniles suggests they belong to *Porcelloides tenuicaudus*, but their identity cannot be established with certainty from Haller's (1880) description.

Reproductive biology of Porcellidiidae

Perhaps the most significant fact revealed through study of the European species is a fundamental difference in the reproductive biology between *Porcelloides tenuicaudus* and all other members of the Porcellidiidae.

From observations on living animals in Scotland and Australia it was found that shortly after metamorphosis an adult male will seek and couple with a juvenile female copepodid (usually stage II or III) by clasping the posterior region with his antennules. This coupling has been referred to as mate guarding behaviour, Huys & Boxshall (1991). Each time the female copepodid moults to the next stage the guarding male re-couples with it until stage V is reached. About this time the spermatophore develops in the male. The spermatophore of *Porcellidium viride* is typical of nearly all members of the family. It is a long tubular sac (sausage-

shape) with a narrow neck. About $\frac{3}{4}$ of its volume is occupied by the sperm mass, the remainder is a clear fluid. The guarding male re-couples with the newly metamorphosed female, as she emerges from the final moult, to deposit his spermatophore on her body. Usually it is placed on the ventral side of the females genital double-somite, but it may be placed anywhere on the dorsal or ventral part of the posterior body. Only part of this activity has been observed on one occasion with *P. hormosirii* (personal observation). Whilst clasping the female in the usual manner, the male pushed the hind region of its body forward under the female that appeared to be lifting her body as she does when irrigating eggs (Fig. 25E). The spermatophore, when deposited, adheres by its neck end (presumably by the congealed clear fluid) and remains attached for a relatively short period, an hour or so, before the empty case is lost. During that time the spermatozoa migrate to the spermathecae. When filled with sperm the spermathecae can usually be seen through the transparent cuticle of the nubile female before it hardens and colouration develops. The empty spermatophore case is lost long before egg-laying starts. Females receive only one spermatophore during their life span.

Although the reproductive behaviour of *Porcelloides tenuicaudus* has not been observed and no coupled specimens were found in the very small sample available for study, there is a striking difference in the pattern of insemination between this genus and that outlined above. Mature males have typical antennules modified for clasping and, like all other members of the family, carry only one spermatophore. But the shape of the spermatophore and its placement on the female is quite different. It is common to see female *P. tenuicaudus* carrying two or more spermatophores. This must indicate that more than one male has deposited a spermatophore on the same female.

The spermatophore, when deposited on the female is a large bean-seed or kidney-shaped (reniform) sack with a recurrent neck or duct running along the concave side. It is firmly attached to the dorsal surface of the female's P5 lying on its side, (on some animals the recurrent duct can be seen lying in the gap between P5 and genital double-somite). The original drawing by Claus (1860) is ambiguous: he shows two spermatophores connected by ducts to the spermatheca, but it is not clear whether they are dorsal or ventral to the P5 limb.

Perhaps the most significant feature in the reproductive biology of *P. tenuicaudus* is multiple deposition of spermatophores on the female. Claus (1860), Haller (1880) and Bartsch (1987) all show two spermatophores, one on each P5, but Bocquet (1948) states that there may be two, three or four. The female shown in Fig. 17A and Plate 1G (p. 67) has two spermatophores attached to the P5s, but a specimen of *Porcelloides tenuicaudus* in the NHM, London carrying eggs has four spermatophores attached (Fig. 25D), (personal observation). Because a male only produces one spermatophore, the presence of more than one on a female implies that the female has received them from more than one male. The fact that a female of other species only receives one spermatophore during her life time (immediately after metamorphosis) and males never couple with adult (egg bearing) females implies that the normal mate guarding behaviour and the stimulus inducing release of the spermatophore is different in *Porcelloides* to all other species.

Spermatophores remain attached for a long period. This is indicated by two facts. First empty spermatophore cases are sometimes covered in the same epizoic micro-organisms (diatoms, suctorian protozoa etc.) found on the female's body and second, empty cases are still present on females carrying eggs.

These reproductive peculiarities appear to be of more fundamental significance than normal apomorphic differences and set *Porcelloides* apart from all other genera. This might be considered grounds for splitting the family into two sub-families, but a far more detailed study of the reproductive biology of *Porcelloides* is necessary before such a step is taken. Except for its own apomorphies, *Porcelloides* shares all the characteristics of the Porcellidiidae.

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Appendices

Appendix 1. Identity of specimens in the Norman slide collection Natural History Museum, London (339 Porcellidiidae).

Twenty microscope slides of specimens collected by A. M. Norman over a period from 1861 to 1906 are of interest because they contain type specimens of his *Porcellidium subrotundum* and reflect the nomenclature of that period. Unfortunately identification is difficult because the slides are in very poor condition, but several of the specimens can be positively identified. Norman based his identifications on Claus' 1863 description of *P. fimbriatum*. The following criteria have been used to separate the species

Porcellidium viride

body shape $L/W \leq 1.5$

caudal ramus $l/w \leq 2.2$

$M_1/M_2 < 0.9$ (where $M_1 = \alpha$ to β , $M_2 = \beta$ to γ); diatoms usually present

Porcellidium fimbriatum

body shape $L/W > 1.7$

caudal ramus $l/w \geq 2.7$

$M_1/M_2 > 2.5$

reg. number	label	identification
1951.8.10.892	<i>Porcellidium tenuicauda</i> . Washed off dredged weed, Ventry Bay. 1 ♂ <i>P. fimbriatum</i> 1 ♂.	<i>Porcelloides tenuicaudus</i> . <i>Porcellidium viride</i> . CR. $l/w = 1.9$.
1951.8.10.894	<i>P. tenuicauda</i> Claus. In bulb of <i>Laminaria bulbosa</i> Roundstone, 1865.	<i>Porcelloides tenuicaudus</i> .
M2609	<i>P. tenuicauda</i> Claus. Gurnsey.	<i>Porcelloides tenuicaudus</i> .
M2566	<i>P. lecanoides</i> Claus. Plymouth, 1889.	<i>Porcellidium fimbriatum</i> . CR. $l/w = 2.7$: terminal setae pinnate, genital double-somite cleft.
1900.3.6.706	<i>P. fimbriatum</i> Claus. = <i>viride</i> Phil? Shetland, 1861.	<i>Porcellidium viride</i> , 3 ♀♀. Covered in diatoms. $L/W 1.3$; $l/w 1.6$; $M_1/M_2 = 0.8$.
M2565	<i>P. fimbriatum</i> Claus. Hillswick, Shetland, 1867.	Poor slide. Diatoms++. Probably <i>Porcellidium viride</i> .
M2613	<i>P. fimbriatum</i> Claus. Hillswick, Shetland, 1867.	<i>Porcellidium viride</i> (males). Male with purple patch on cephalosome. Many male copepodids.
M2614	<i>P. fimbriatum</i> Claus. Male <i>dentatum</i> + junior; Hillswick, Shetland, 1867.	<i>Porcellidium viride</i> (copepodids).
1900.3.6.707	<i>P. fimbriatum</i> Claus. 1 ♂ and 3 ♀♀ Tide marks. Oban, 1877.	<i>Porcellidium viride</i> . Poor slide, diatoms ++
M2611	<i>P. fimbriatum</i> Claus. Male <i>P. dentatum</i> Cl. Oban, 1877.	<i>Porcellidium viride</i> . (5 poor ♀♀ and copepodids). Diatoms++, $M_1/M_2 = 0.88$, CR. $l/w = 2.0$.
M2612	<i>P. fimbriatum</i> Claus. Oban, 1877.	Males. Poor slide, probably <i>Porcellidium viride</i> .
M2564	<i>P. fimbriatum</i> Claus. Firth of Clyde, 1862.	<i>Porcellidium viride</i> . Diatoms ++, $M_1/M_2 = 0.57, 0.68$.
M2610	<i>P. fimbriatum</i> Claus = ? <i>viride</i> . Catwater, Plymouth, 1889.	Probably <i>Porcellidium viride</i> . Male covered in diatoms.
M2615	<i>P. fimbriatum</i> Claus. Rock pools, Plymouth, 1889.	Two females, poor specimens with diatoms. Probably <i>Porcellidium viride</i> .
1900.3.6.708	<i>P. fimbriatum</i> Claus. Males and females. Tobermory, Mull, 1866.	All <i>Porcellidium viride</i> . Diatoms ++
1900.3.6.709	<i>P. fimbriatum</i> Claus. Males. Florö, Norway, 1882.	Poor slide. Mostly copepodids of <i>Porcellidium viride</i> .
M2608	<i>P. lecanoides</i> Claus. Guernsey, 1906.	<i>Porcellidium viride</i> .
M2607	<i>P. subrotundum</i> . Norman types = <i>P. fimbriatum</i> junior. Hillswick, Shetland, 1867.	Seven copepodids, some with patch of purple on posterior cephalosome. All appear to be <i>Porcellidium viride</i> .
1951.8.10.893	<i>P. subrotundum</i> and <i>P. dentatum</i> . On <i>Laminaria</i> . Hillswick, Shetland.	All copepodids of <i>Porcellidium viride</i> .

Appendix 2. Identity of specimens of Porcellidiidae in the National Museum of Ireland, Dublin.

catalogue description	locality where found	identification
<i>Porcellidium fimbriatum</i>	Discovery Bay, Jamaica	Unidentified, but not <i>P. fimbriatum</i> Claus 1863
<i>P. lecanoides</i> Claus	Achill, Co. Mayo	<i>Porcellidium viride</i>
<i>P. ovatum</i> Haller	Loch Hyne, Co. Cork,	<i>Porcelloides scutatus</i> (Claus, 1889) comb. nov.
<i>P. ovatum</i> , sensu Geddes	Discovery Bay, Jamaica	<i>Acutiramus geddesi</i> (Geddes, 1968) comb. nov.
<i>P. sarsi</i> Bocquet	Loch Hyne, Co. Cork; Co. Dublin; Co. Galway	<i>Porcellidium viride</i>
<i>P. tenuicauda</i>	Loch Hyne, Co. Cork	<i>Porcelloides tenuicaudus</i> (Claus, 1860) comb. nov.

Note. Slide and spirit specimens in the NMI collection do not have individual registration numbers to identify them.