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Heterochrony in *Haplomesus* (Crustacea: Isopoda: Ischnomesidae): revision of two species and description of two new species

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Abstract

Two new species of Ischnomesidae, *Haplomesus celticensis* sp. nov. and *Haplomesus hanseni* sp. nov. are described from the southwest of Ireland and the Argentine Basin respectively. Both species lack the expression of pereopod VII, a characteristic that we argue is produced by progenesis, not neoteny as suggested by Brökeland & Brandt (2004). *Haplomesus angustus* Hansen, 1916 and *Haplomesus tropicalis* Menzies, 1962, also lack pereopod VII and are revised from the type material. The original description of *Haplomesus angustus* Hansen, 1916 describes the adult type specimen as a juvenile; the original description of *Haplomesus tropicalis* Menzies, 1962 fails to mention the lack of pereopod VII. Progenesis is discussed for the above species and within the family Ischnomesidae as a whole.

Key words: Isopoda, Asellota, Ischnomesidae, *Haplomesus*, heterochrony, progenesis

Introduction

The Ischnomesidae is a family of marine benthic asellote isopods found mostly at bathyal and abyssal depths, with records from about 250–7000 m (Wolff 1962; Kussakin 1988). To date, 99 species have been described in five genera. The known diversity of this family, however, is increasing owing to recent reports of several new species (e.g. Merrin & Poore 2003). In this paper, we report two new species of *Haplomesus* from the Atlantic Ocean, *Haplomesus celticensis* sp. nov. from the Celtic Sea off southwestern Ireland, and *Haplomesus hanseni* sp. nov. from the Argentine Basin. These species are unusual because they lack pereopod VII. Two other ischnomesid species with the same condition have been described recently by Brökeland & Brandt (2004): *Haplomesus corniculatus* and

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Stylomesus hexapodus, from the deep Southern Ocean. *Haplomesus angustus* Hansen, 1916, that we revise from the type material, is a fifth species of this family that also exhibits this character. The original description of *Haplomesus angustus* was based on a specimen identified as being juvenile (that had yet to develop the last leg) when in fact it is an adult male. The description of *Haplomesus tropicalis* Menzies, 1962 is also revised, using the literature and the allotype. Although the adult specimens of this species clearly lack pereopod VII, Menzies does not mention this feature in his description. Brökeland & Brandt (2004) suggested that the changes observed in the species above are due to neoteny, i.e. becoming sexually mature in a juvenile state. Here we demonstrate that the primary process involved in the absence of pereopod VII is progenesis, a different type of heterochrony. Progenesis describes an earlier offset of development in a particular trait. We discuss this process in relation to the above species and to the family Ischnomesidae as a whole.

Methods

Haplomesus celticensis sp. nov. and *Haplomesus hanseni* sp. nov. were collected in epibenthic sled samples by H. Sanders, F. Grassle and party on several Woods Hole Oceanographic Institute (WHOI) transects in the Atlantic Ocean in 1972 and 1976 (see Fig. 1).

A female was designated holotype in each case. Our experience has shown that females are more difficult to separate than males, so identifications using our descriptions should work on both sexes. An adult male paratype was also described in each case. Where possible, manca and juvenile specimens were illustrated and described. Mouthparts and pleopods were dissected and drawn from male specimens. Due to the brittle nature of the individuals, few intact pereopods remained so we have not illustrated complete limbs in most cases. Pencil illustrations were prepared using a camera lucida on a Nikon microscope, and then inked by tracing onto translucent vellum. Temporary mounts were made using glycerin. Museum mounts were prepared using glycerin jelly.

Descriptions were generated using the taxonomic database system DELTA (Dallwitz 1980; Dallwitz *et al.* 2000) and diagnoses were constructed from the INTKEY output of the DELTA programme. Measurements were made from drawings, using a stage micrometer for calibration. In general, character measurements are presented as ratios to normalise differences in body size, and where several specimens were available for measurement, ranges are displayed. Anterior body length is defined as the length of the head and the first 4 pereonites, altogether.

Females are described, with male characters which differ from females described separately. The descriptions make use of "implicit characters", which are characters that are common to the genus *Haplomesus* or more generally to the Ischnomesidae. If a species does not have a character state described explicitly, then it will have the state mentioned in the implicit characters. For example, absence of spines on a particular pereonite is not mentioned, although the database has options for such characters in case they are present. Unless indicated otherwise, the following attributes are implicit throughout the descriptions, except where the characters concerned are inapplicable.

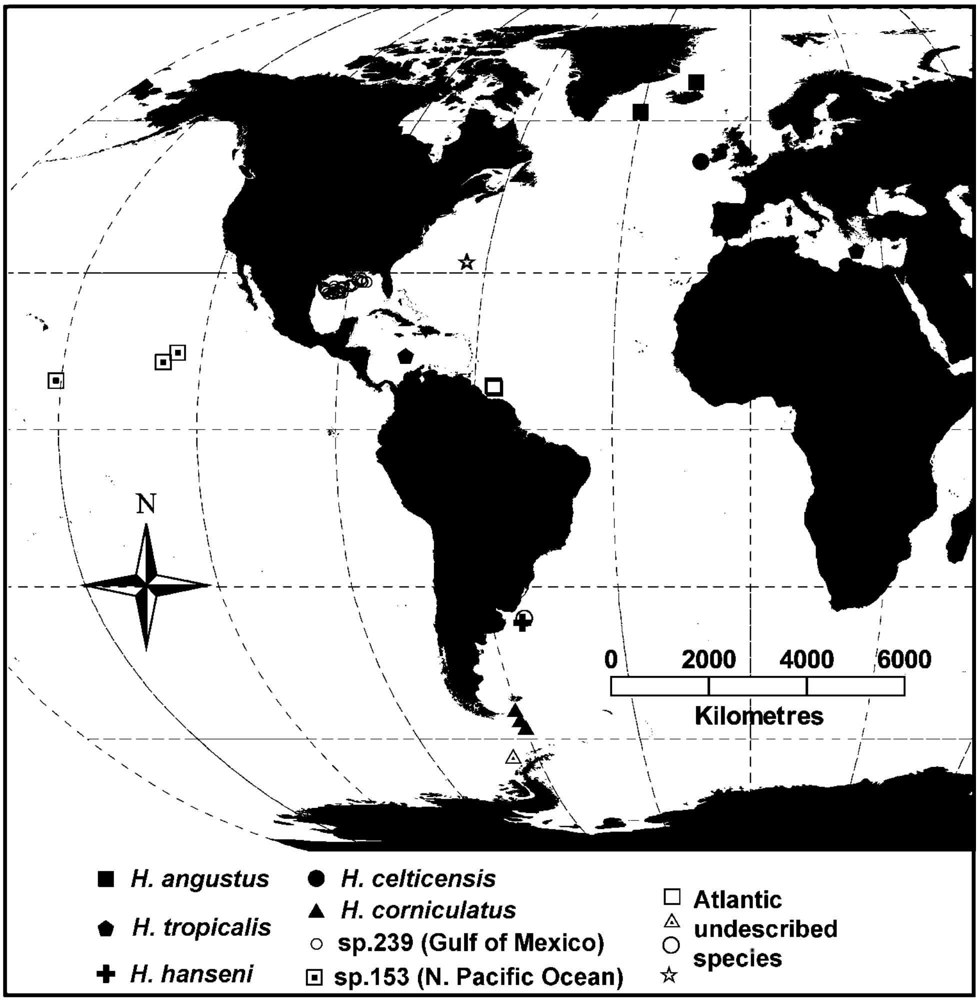

FIGURE 1. Distribution of Haplomesus species that lack pereopod VII, data from this paper, or from Thistle & Wilson (1996), Wilson (1998) or Rowe (2003). Dashed lines indicate 30° lines of latitude or longitude.

Implicit Characters

Female

Body granulate; with only scattered setae; pereonite 7 length not reduced, similar to pereonite 6; tergites not projecting. Head dorsal surface without bulges or protuberances;

antennae emerging directly from head; without spines or tubercles. Pereonites 1–7 without spines or tubercles. Pleonite 1 region of pleotelson without spines or tubercles. Pleotelson posterolateral margin adjacent to uropods convex; without spines or tubercles; posterolateral margin anterior to uropods without spines or tubercles; terminal margin without spines or tubercles.

Antennula and antenna. Antennae emerging directly from head, not on projections. Antennula article 1 squat and globular; without spines; article 2 length greater than 3 article 1 length, article 2 straight, not curved at proximal insertion, inserting on article 1 dorsally, projecting anteriorly, with long ventromedial setae; terminated with aesthetasc. Antenna article 2 without lateral spines, ventromedial spines; article 3 length at least twice article 4 length, article 3 cuticle granulate, without spines.

Mouthparts. Mandible palp absent. Maxilliped palp shorter than basis, articles 2 and 3 width subequal, epipod setae absent.

Pereopods. Pereopod bases with conspicuous neck connecting shaft to coxal articulation, without dorsal projection on proximal part of shaft. Pereopod I weakly carposubchelate; carpus palm without pectinate setae, carpus palm with 1 elongate robust seta; with 1 dactylar claw. Pereopod VII present, as long as pereopod VI. Pereopods II–VII bases smooth, with no spines; ischia without spines.

Pleopods and uropods. Pleopod II operculum with narrow proximal neck, almost circular posteriorly, with plumose setae on lateral and distal margins. Pleopod III exopod length more than half endopod length. Pleopod IV without exopod; V absent.

Male

Antenna. Antenna flagellum decreasing in width distally, tubular, longer than wide. *Pleopods and uropods*. Pleopod I length more than twice proximal width, lateral margins indented midway along length, without simple setae on lateral margins, without setae on distal margins. Pleopod II protopod with setae on lateral and distal margin, tapering and pointed, not heavily calcified.

Taxonomy

Ischnomesidae Hansen, 1916

Ischnomesini Hansen, 1916: 54; Wolff, 1956: 86.
Ischnomesidae.—Gurjanova, 1932: 40; Menzies, 1962: 111; Wolff, 1962: 71–73; Birstein, 1971: 198–199; Menzies & George, 1972: 971; Chardy, 1974: 1537; Kussakin, 1988: 418.

Diagnosis. Head deeply embedded in and fused with pereonite 1, without intersegmental articulation, without eyes or rostrum, dorsal surface sloping into frons and clypeus. Pereon thin, elongate, pereonites 4 and 5 elongate, subcylindrical, produced backwards and forwards, respectively, pereonite 5 longest; female spermathecal duct pores near dorsal midline of pereonite 5, not covered by posterior margin of pereonite 4; pereonites 5–7 narrowing posteriorly. Pleotelson shorter than pereonites 5–7; anus subterminal (at obtuse angle to ventral surface), external to pleopodal chamber and separated from it by broad cuticular bar, anal region projecting from anterior pleotelson. Antennula with 2 to 6 articles; article 1 short and rounded; article 2 tubular, much longer than wide; article 3 flagellar. Antenna much longer than anterior portion of body, article 3 without scale. Mandibles with distinct incisor and molar processes, dorsal condyle elongate and smoothly curled on posterior margin of mandibular body. Maxilliped basis broader than palp, endite shorter than palp, palp positioned in distal third of basis, articles 4–5 narrower than articles 1–3. Pereopod I prehensile between carpus and propodus; carpus with robust setae on ventral margin. Pereopods II–VII long, thin, paucisetose; dorsal (anterior) dactylar claw longer than posterior (ventral) claw, robust; posterior dactylar claw flattened, slightly curled. Pleopod III exopod shorter than endopod, thin, pointed, with 1 distal plumose seta; endopod quadrate, with 3 distal plumose setae. Uropod paucisetose, uniramous, inserting terminally lateral to anus. Sexual dimorphism common in non-sexual features: pereonites longer and thinner in males, spination of pereon and pleotelson more developed in males; antenna male flagellum more robust, with more setae and articles than in female; uropods longer in male than in female.

Remarks. The family Ischnomesidae is easily distinguished by an elongate fifth pereonite, which occurs uncommonly in other families, and certainly not as pronounced as seen in this family. Ischnomesids have other unique combination of characters such as cephalon embedded in the first pereonite with an unexpressed articulation, completely dorsal and exposed spermathecal duct pores in the female, a subterminal anus, subcylindrical pereonites 4 and 5, short and highly modified antennulae and uniramous uropods. Although the mandibles are relatively normal for Janiroidea, they have an unusual curled dorsal condylar region that is confluent with the posteromedial margin of the mandibular body, and the mandibular palp is generally absent (although a few species have a palp, such as *Ischnomesus roseus* Wolff, 1962). Although we don't have sufficient data on all described species, most species have a brittle calcified cuticle, which contributes to their fragmentation in deep-sea samples.

Haplomesus Richardson, 1908

Haplomesus Richardson, 1908: 81; Hansen, 1916: 59; Gurjanova, 1932: 42; Birstein, 1960: 6; 1963: 59; 1971: 209; Menzies, 1962: 117; Wolff, 1962: 86; Menzies & George, 1972: 973; Kussakin, 1988: 445.
Not *Haplomesus*. Merrin & Poore, 2003: 286.
Type species: *Haplomesus quadrispinosus* (Sars, 1879).

Species included: *Haplomesus angustus* Hansen, 1916; *H. bifurcatus* Menzies, 1962; *H.*

biscayensis Chardy, 1975; *H. brevispinis* Birstein, 1960; *H. concinnus* Birstein, 1971; *H. consanguensis* Mezhov, 1980; *H. corniculatus* Brökeland & Brandt, 2004; *H. cornutus* Birstein, 1960; *H. formosus* Mezhov, 1981; *H. gigas* Birstein, 1960; *H. gorbunovi* Gurjanova, 1946; *H. insignis* Hansen, 1916; *H. orientalis* Birstein, 1960; *H. modestatenuis* Menzies & George, 1972; *H. modestus* Hansen, 1916; *H. ornatus* Menzies, 1962; *H. profundicola* Birstein, 1971; *H. quadrispinosus* (Sars, 1879); "*H. quadrispinosus*" sensu Brandt, 1992; *H. robustus* Birstein, 1960; *H. scabriusculus* Birstein, 1960; *H. tenuispinis* Hansen, 1916; *H. thomsoni* (Beddard, 1886); *H. tropicalis* Menzies, 1962; *H. zuluensis* Kensley, 1984. Excluded species: *H. franklini* Merrin & Poore, 2003 (incertae sedis).

Diagnosis. Pereonites 5–7, pleonite 1 and pleotelson lacking intersomite articulations. Pereonites 5–7 narrowing posteriorly. Antennulae with 5 or 6 articles, distal flagellar articles at least twice as long as wide. Pereopod I carpus without ventral expansion of palm. Maxilliped palp narrower than basal endite, articles 2 and 3 expanded. Uropods uniramous, single segmented, distally tapering. Mandible palp absent.

Remarks. Many *Haplomesus* species have thin, attenuated bodies, although a few species such as *H. robustus* Birstein, 1960 are rather more heavy bodied and *Heteromesus*-like. Species in the genus exhibit a great variety of spination, and none is completely lacking spines anywhere on the body. A few other characters may be characteristic of the genus but are not illustrated in most species. For example, the species that we have examined have a distinct thin neck between the pereopodal articulation of the basis and coxa and the shaft of the basis, with the basis neck and shaft forming an approximate right angle. This character, but with an added spinose shoulder, is also found in several species of *Heteromesus* (Cunha & Wilson personal communication). We exclude *H. franklini* Merrin & Poore, 2003 from the genus because its uropod does not match the current diagnosis, in being elongate and biarticulate. Merrin & Poore (2003) state that the presence of biarticulate uropods is treated as a specific autapomorphic character, but this view argues for an ad hoc reversal of a more general character. The uropod is more parsimoniously interpreted as plesiomorphically biarticulate, with the transition to the uniarticulate conical form as a synapomorphy of the genus *Haplomesus.* The inclusion of *H. franklini* into the genus, therefore, substantially weakens its definition. They also indicate that the fusion of pereonites 5–7 with the pleonites and pleotelson, and the stylet of male pleopod II not extending beyond the sympod are key synapomorphies for the genus. The stylet character is not likely to be apomorphic, given the variation seen in the other species of the family (both long and short forms can be found). Ultimately a cladistic analysis could arbitrate the apomorphic status of these characters, but none is published to support these assertions. On the pleotelson of *H. franklini*, the uropods project from a raised part of the posterolateral margin, whereas the uropods of all *Haplomesus* species sit in a concavity, and the pleonite 1–2 region of *H. franklini* is longer and somewhat more inflated than seen in *Haplomesus.* In the absence of an empirical test of these assertions, *H. franklini* should be not included. Nevertheless, we use a broad definition of *Haplomesus;*

the missing last pereonite alone is not sufficient evidence or justification for creating a new genus (see discussion below).

A few *Haplomesus* species have been given broad distributions by some authors, despite most species being known from fairly narrow ranges. Notably Menzies (1962) ascribed a Mediterranean-Caribbean distribution to his species *H. tropicalis* (discussed below). More recently, *H. quadrispinosus* was reported in the South Atlantic near Antarctica, but Brandt's (1992) illustrations show that this is a different species from Sars' species. The Brandt species should be compared with *H. bifurcatus* Menzies, 1962 and other species with an indented pleotelson axis. Although most ocean basins have insufficient sampling, our experience (e.g. the undescribed species shown in Fig. 1) shows that each species have distributions limited to basins or smaller regions.

Haplomesus hanseni sp. nov. (Figs 2–7)

Etymology. Named for H.J. Hansen who described the first species of Ischnomesidae without pereopod VII, *Haplomesus angustus* Hansen, 1916.

Material examined. *Holotype* female, 4.7 mm, AM P68182, *Atlantis II* cruise 60, Howard Sanders & party, WHOI stn 245 (subsample B), 14 March 1971, Argentine Basin, 36°55.7S, 53°01.4'W, depth 2707 m, epibenthic sled. *Paratypes*, same subsample: adult male 3.7 mm and slide of pereopod I AM P71668; juvenile male 3.6 mm, AM P71669 manca male 2.7 mm, AM P71670; paratype adult male pleopods on slide AM P.71711; paratype adult male mouthparts slide P.71712. Additional paratypes from same sample (218 ind., WHOI 245B): 2 males & 2 females P.71671, adults P.71672, juveniles P.71673, paratype mancas P.71674; (227 ind., WHOI 245A): 1 male fragment AM P.71771, 207 ind. AM P.64981.

Diagnosis. Male and female with subequal spines on pereonites 1 and 4. Male spines elongate, length near width of pereonite 1, female spines short, length near length of pereonite 1. Pleotelson posterolateral margin anterior to pereopods with pedestal spines, in female shorter than uropoda, not reaching pleotelson posterior margin; in male longer than uropoda and extending past pleotelson posterior margin. Antennula with 4 distal flagellar articles. Pereopod I carpus ventral margin with 2 proximal robust setae and 1 distal robust seta on palm. Pleopod I of male with simple setae on distal and lateral margins. Female pleopod II operculum with plumose setae.

Description of female. Body length 4.5–4.7 mm; pereonite 7 reduced. Head length 0.7 width; lobe on ventrolateral margin absent in lateral view; dorsal cuticle densely covered with fine granules. Pereonite 1 width 0.16 total body length. Pereonites 1 and 4 anterolateral simple spines conical shape. Pereonite 5 length 2.9 width, 0.4 total body length. Pleotelson length 1.3 width.

Antenna and antennula. Antennula with 6 articles altogether; article 1 with 1 penicillate seta, article 2 length 1.3 head width, with 2 elongate ventromedial setae, distal articles altogether small, shorter than article 2; article 3 length similar to article 4; article 3 elongate and tubular, much longer than wide; terminal article shorter than penultimate article; aesthetascs absent. Antenna article 3 length 0.2 anterior body length, length 3.9 width, cuticle smooth.

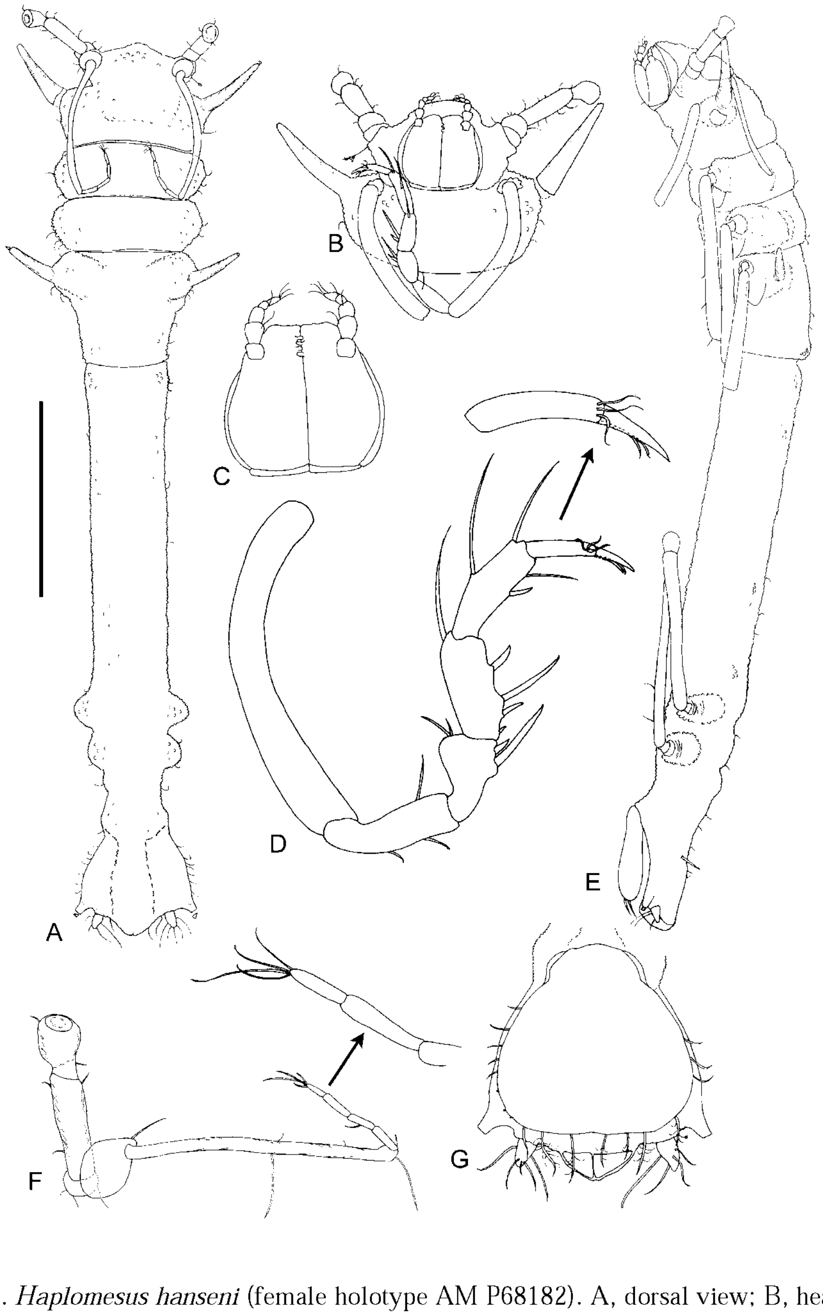

FIGURE 2. *Haplomesus hanseni* (female holotype AM P68182). A, dorsal view; B, head ventral; C, maxilliped; D, pereopod I; E, lateral view; F, antenna and antennula; G, pleotelson ventral (scale bar 1 mm).

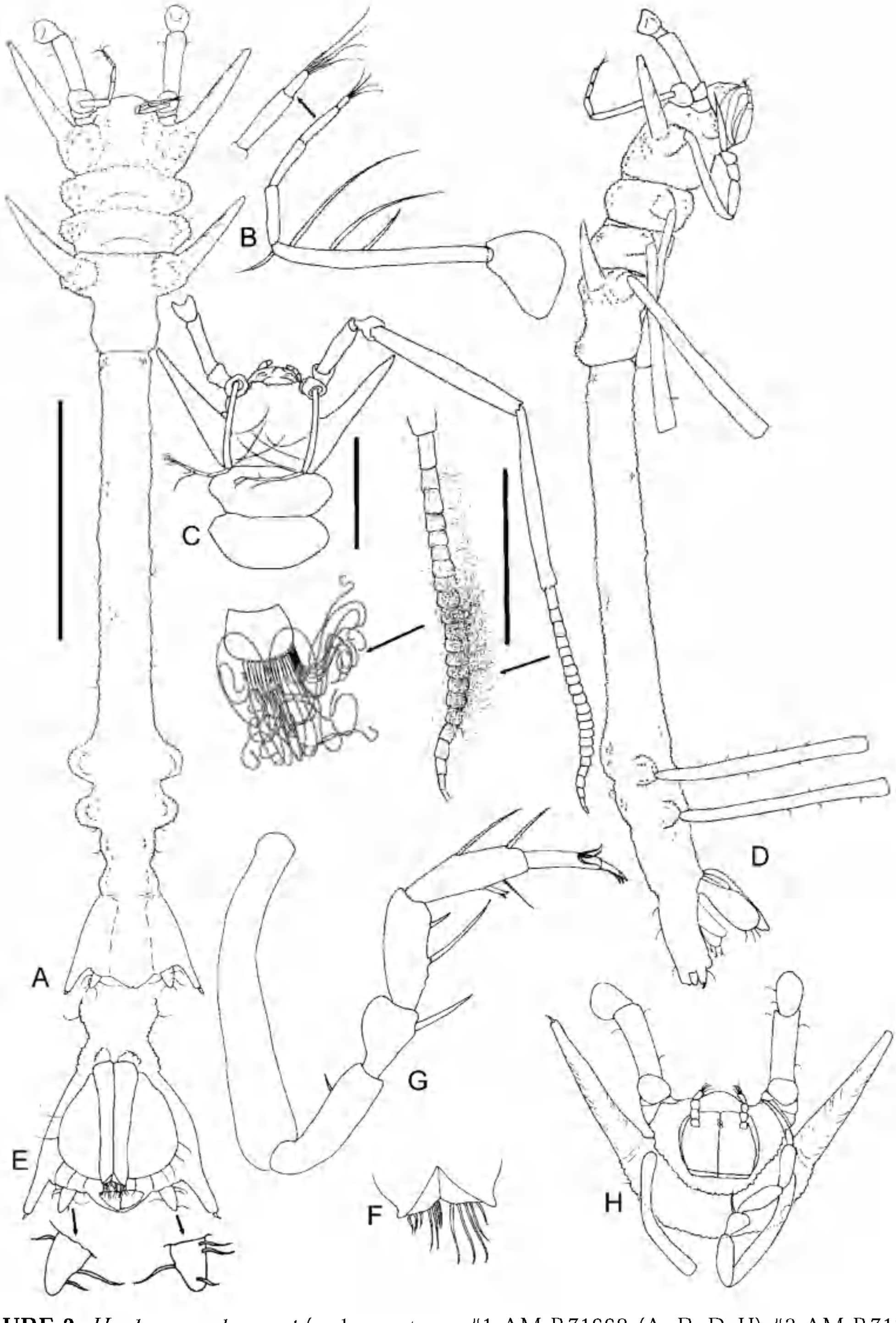

FIGURE 3. *Haplomesus hanseni* (male paratypes #1 AM P.71668 (A, B, D–H) #2 AM P.71771 (C)). A, dorsal view; B, antenna; C, head with antenna, flagellum detail; D, lateral view; E, pleotelson ventral; F, pleopod I ventral; G, pereopod I; H, head ,ventral (scale bars A, B, D–H. 1 mm; C. 0.5 mm).

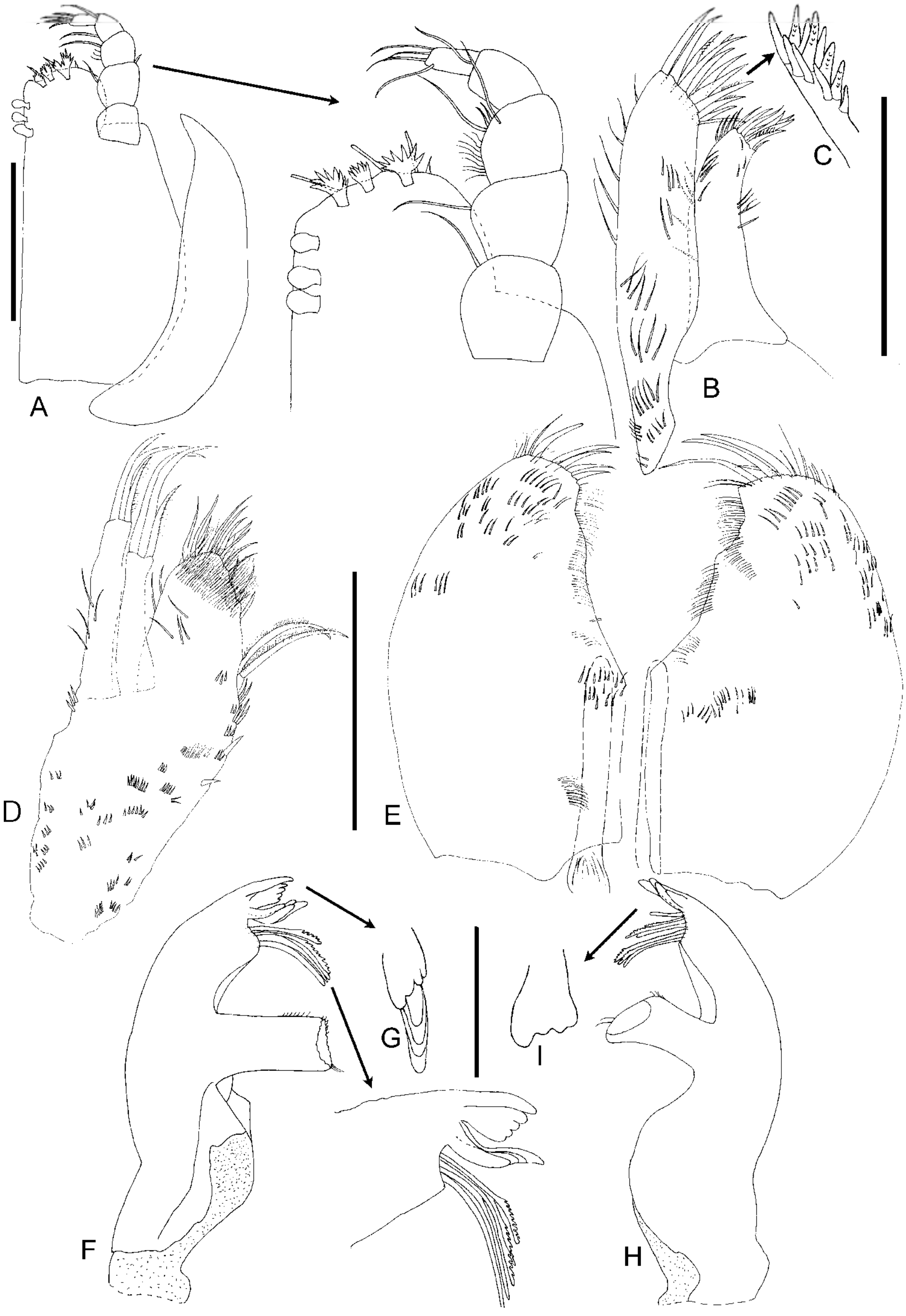

FIGURE 4. *Haplomesus hanseni* (male paratype mouthparts AM P.71712). A, maxilliped; B, maxillula; C, maxillula detail; D, maxilla; E, paragnaths; F, left mandible; G, left mandible detail; H, right mandible (scale bars 0.1 mm).

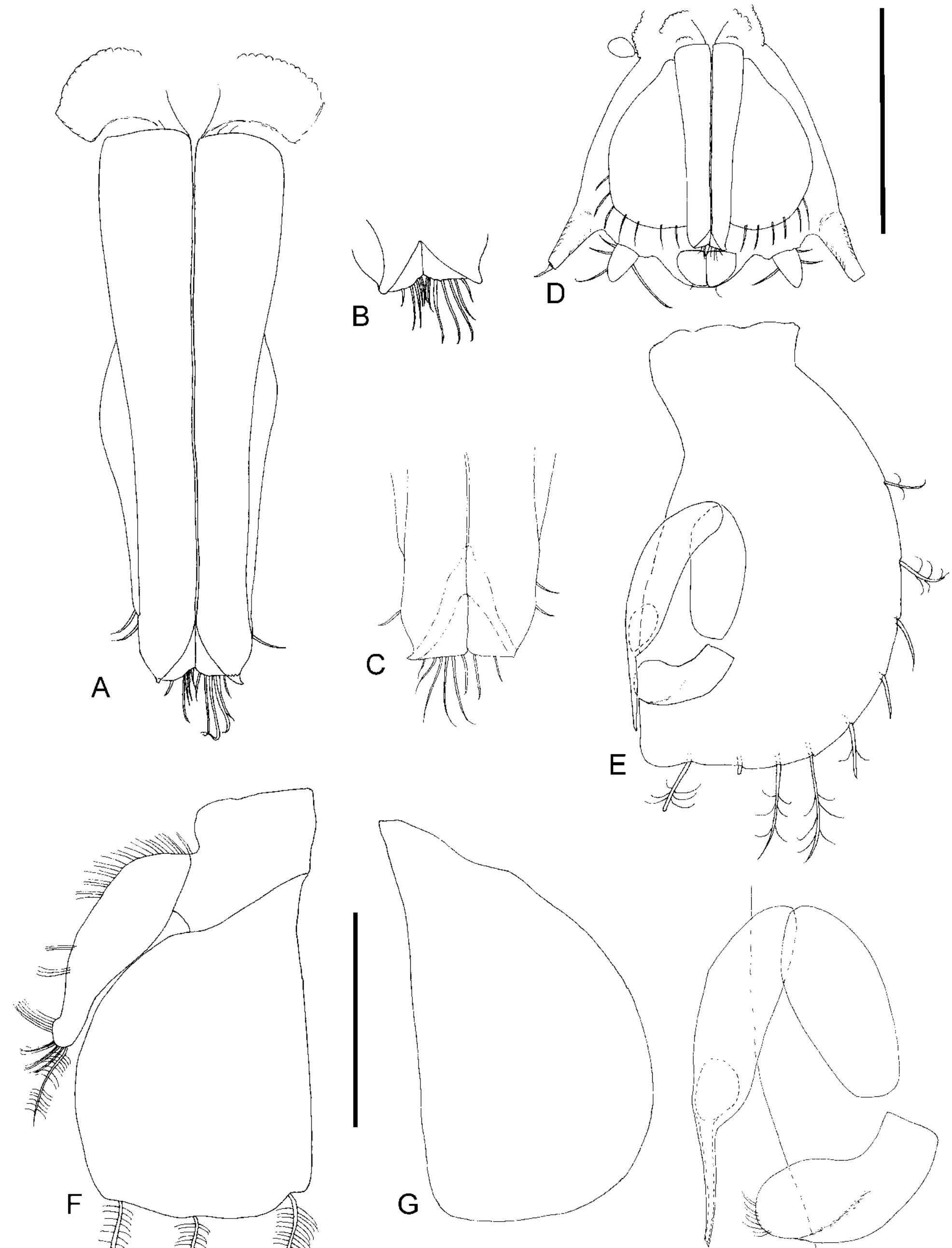

FIGURE 5. *Haplomesus hanseni* (male paratype pleopods AM P. 71711). A, pleopod I, ventral; B, pleopod I ventral detail; C, pleopod I dorsal detail; D, pleotelson ventral; E, pleopod II; F, pleopod III; G, pleopod IV; H, pleopod II stylet (scale bars D. 0.5 mm; A, E–G. 0.1 mm).

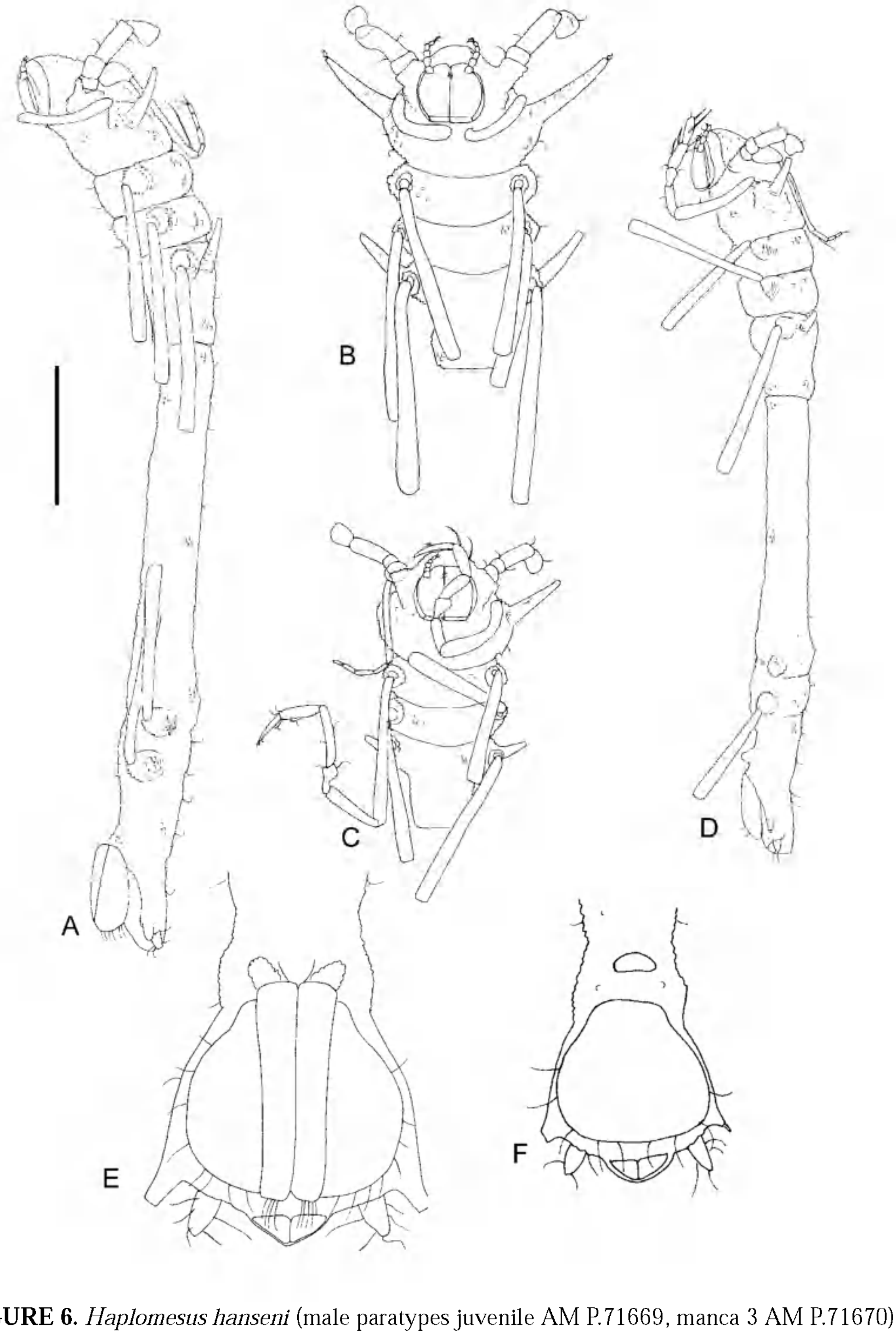

FIGURE 6. *Haplomesus hanseni* (male paratypes juvenile AM P.71669, manca 3 AM P.71670). A, juvenile lateral; B, juvenile ventral; C, manca 3 ventral; D, manca 3 lateral; E, juvenile pleotelson ventral; F, manca 3 pleotelson ventral (scale bar 0.5 mm).

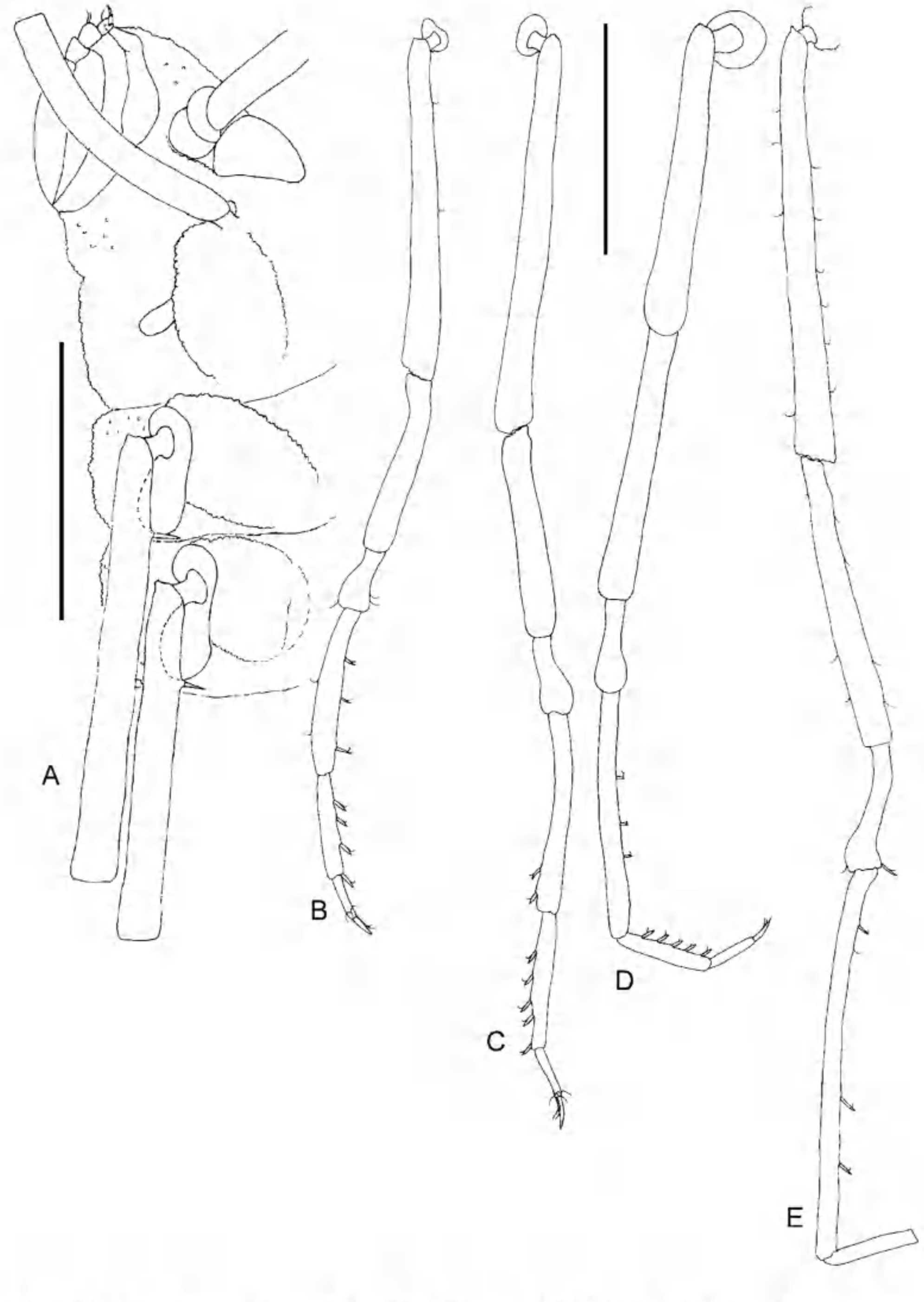

FIGURE 7. *Haplomesus hanseni* (female holotype AM P.68182 (A,B), male paratypes AM P.71671 (C,D, E) A, lateral view; B, pereopod II; C, pereopod III; D, pereopod IV; E, pereopod V (scale bar 0.5 mm).

Mouthparts. Maxillula with 11 robust setae on lateral lobe; medial lobe with 1 robust medially-projecting dentate seta. Maxilla with 2 long (approximately as long as lateral lobes) medially-projecting pectinate seta on medial lobe. Maxilliped palp article 2 wider than 3.

Pereopods. Pereopod I propodus ventral margin with 1 robust seta. Pereopod VII absent in adults.

Pleopods and uropods. Pleopod II operculum with narrow proximal neck, laterally convex, broadening posteriorly to rounded angles, posterior margin weakly convex. Uropods extending near posterior margin of pleotelson; length 0.1 length of pleotelson.

Description of male.

Body length 3.7–4.9 mm. Head length 0.5 width. Head cuticular structure granulated. Pereonite 1 width 0.16 total body length. Pereonite 5 length 3.8 width, 0.48 total body length. Pleotelson length 1.1 width; posterolateral margin simple spines approximately twice as long as spines in female.

Antennula and antenna. Antennula article 2 length 1.3 head width. Antenna length 0.2 anterior body length. Antenna article 3 length 2.5 width; flagellum with some segments expanded, wider than long, with more setae on distal margins than female or juvenile.

Pleopods and uropods. Pleopod I distal tip with lateral horns. Pleopod II protopod apex rounded, stylet not extending to distal margin of protopod. Pleopod III exopod with plumose seta on distal margin, with fringe of fine setae on lateral margin. Uropods extending near posterior margin of pleotelson, length 0.1 length of pleotelson.

Distribution. South Atlantic Ocean: Argentine Basin, 2440–2707 m.

Remarks. The females of *Haplomesus hanseni* sp. nov. (Fig. 2) and *H. celticensis* sp. nov (Fig. 8) are easily distinguished from one another by a different spination pattern, *Haplomesus hanseni* has anterolateral spines on pereonites 1 and 4, *Haplomesus celticensis* has spines on pereonite 1 only. The males share the same spination pattern. Both sexes are easily distinguished by the number of articles in the antennular flagellum: three articles in *H. celticensis*, and *Haplomesus hanseni* with four articles. The males also differ in the setation of the first pleopod: *H. hanseni* males have distal setae on the first pleopod (Fig. 5A) and *H. celticensis* males do not (Fig. 11A).

Haplomesus celticensis sp. nov. (Figs 8–12)

Etymology. Named from the type locality of the Celtic Sea, Ireland.

Material examined. Holotype female, 4.1 mm, AM P64985, RV *Chain* cruise 106, J.F. Grassle and party, WHOI stn 313, 17 August 1972, Celtic Sea, off west coast of Ireland 51°32.2'N, 12°35.9'W, 1491–1500 m, epibenthic sled. Paratypes: male 4 mm, AM P.71659; juvenile male, 3.7 mm, AM P.71660 manca male 3 mm, AM P.71661, paratype male mouthparts slide and carcass AM P.71667, paratype male pleopods slide and carcass AM P.71666, same station; additional paratypes 49 ind., paratype adults, 2 males, 2 females, AM P.71662, paratype adults AM P.71663, paratype juveniles AM P.71664, paratype mancas AM P.71665, same locality as holotype.

Diagnosis. Male with spines on pereonites 1 and 4. Female with anterolateral spines on pereonite 1 only, shorter than spines observed on pereonite 1 of males. Pleotelson posterolateral margin anterior to uropods with pedestal spines: in female length approximately half uropod length, in male subequal to uropod length. Antennula with 3 distal flagellar articles. Pereopod I carpus ventral margin with 1 proximal robust seta and 1 distal robust seta on palm. Pleopod I of male without setae. Pleopod II female operculum without plumose setae.

Description of female. Body length 4.0–4.4 mm; pereonite 7 reduced. Head length 0.7 width; lobe on ventrolateral margin absent in lateral view; dorsal cuticle densely covered with fine granules. Pereonite 1 width 0.16 total body length. Pereonite 1 anterolateral simple spines, short, length projecting dorsally, somewhat anteriorly curved. Pereonite 5 length 3.2 width, 0.4 total body length. Pleotelson length 1.3 width; dorsal surface axial ridge weakly vaulted, separated from lateral fields only by shallow elongate concavities; posterolateral margin adjacent to uropods convex.

Antennula and antenna. Antennula with 5 articles altogether, article 2 length 0.7 head width, inserting on article 1 dorsally, with 2 elongate ventromedial setae; distal articles short, in total shorter than article 2; article 3 length similar to article 4; article 3 elongate and tubular, much longer than wide; terminal article longer than penultimate article; aesthetascs absent. Antenna article 3 length 0.2 anterior body length, length 3 width, cuticle smooth.

Mouthparts. Maxillula with 10 robust setae on lateral lobe; medial lobe with 1 robust medially-projecting dentate seta. Maxilla with 2 long (approximately as long as lateral lobes) medially-projecting pectinate setae on medial lobe. Maxilliped palp article 2 wider than 3.

Pereopods. Pereopod I propodus ventral margin with 1 robust seta. Pereopod VII absent in adults.

Pleopods and uropods. Pleopod II female operculum with narrow proximal neck, laterally convex, broadening posteriorly to rounded angles, posterior margin weakly convex. Uropods extending near posterior margin of pleotelson; length 0.1 length of pleotelson.

Description of male. Body length 3.9–4.0 mm. Head length 0.7 width. Pereonite 1 width 0.15 total body length. Pereonite 1 spines projecting dorsally, elongate, length near width of pereonite 1. Pereonite 4 anterolateral simple spines, projecting dorsally, short, length near pereonite 1 length. Pereonite 5 length 3.9 width, 0.47 total body length. Pleotelson length 1.2 width.

Antennula and antenna. Antennula article 2 length 0.6 head width. Antenna article 3 length 3.1 width.

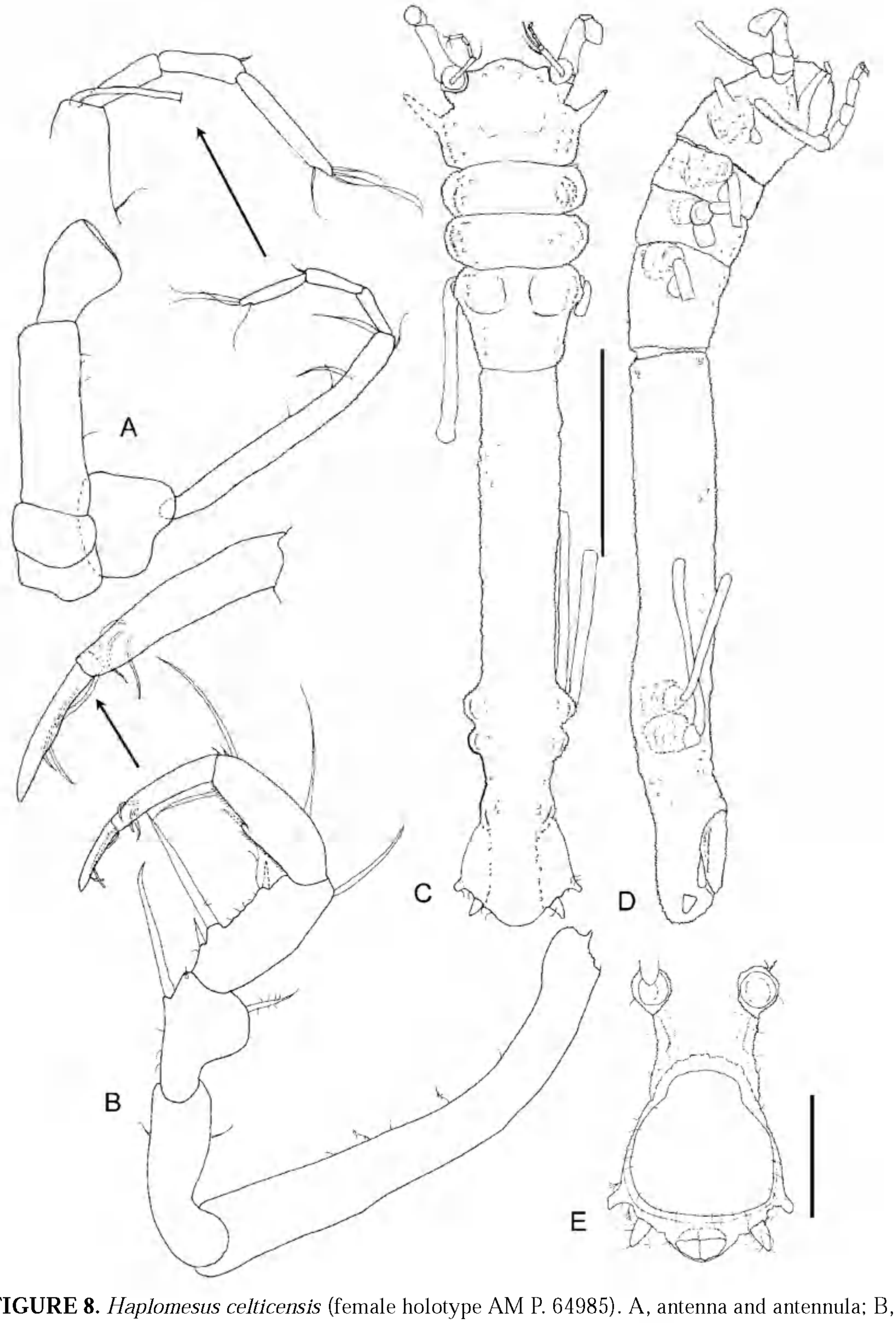

FIGURE 8. *Haplomesus celticensis* (female holotype AM P. 64985). A, antenna and antennula; B, pereopod I; C, D, body dorsal and lateral; E, pleotelson ventral (scale bars C, D, 1 mm; E, 0.5 mm).

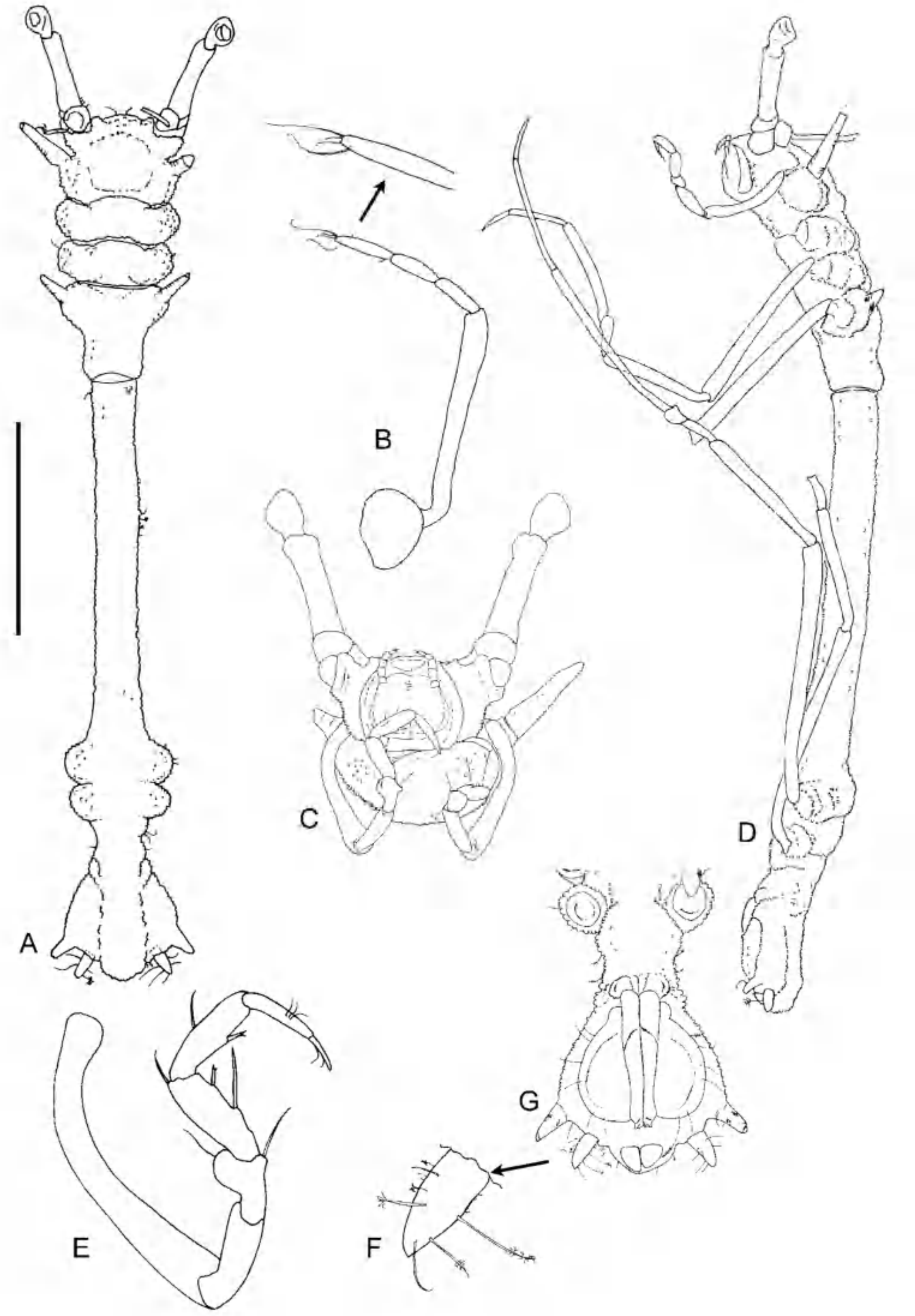

FIGURE 9. *Haplomesus celticensis* (male paratype AM P.71659). A, dorsal view; B, antennula; C, head ventral; D, lateral view E, pereopod I; F, uropod; G, pleotelson ventral (scale bar 1 mm).

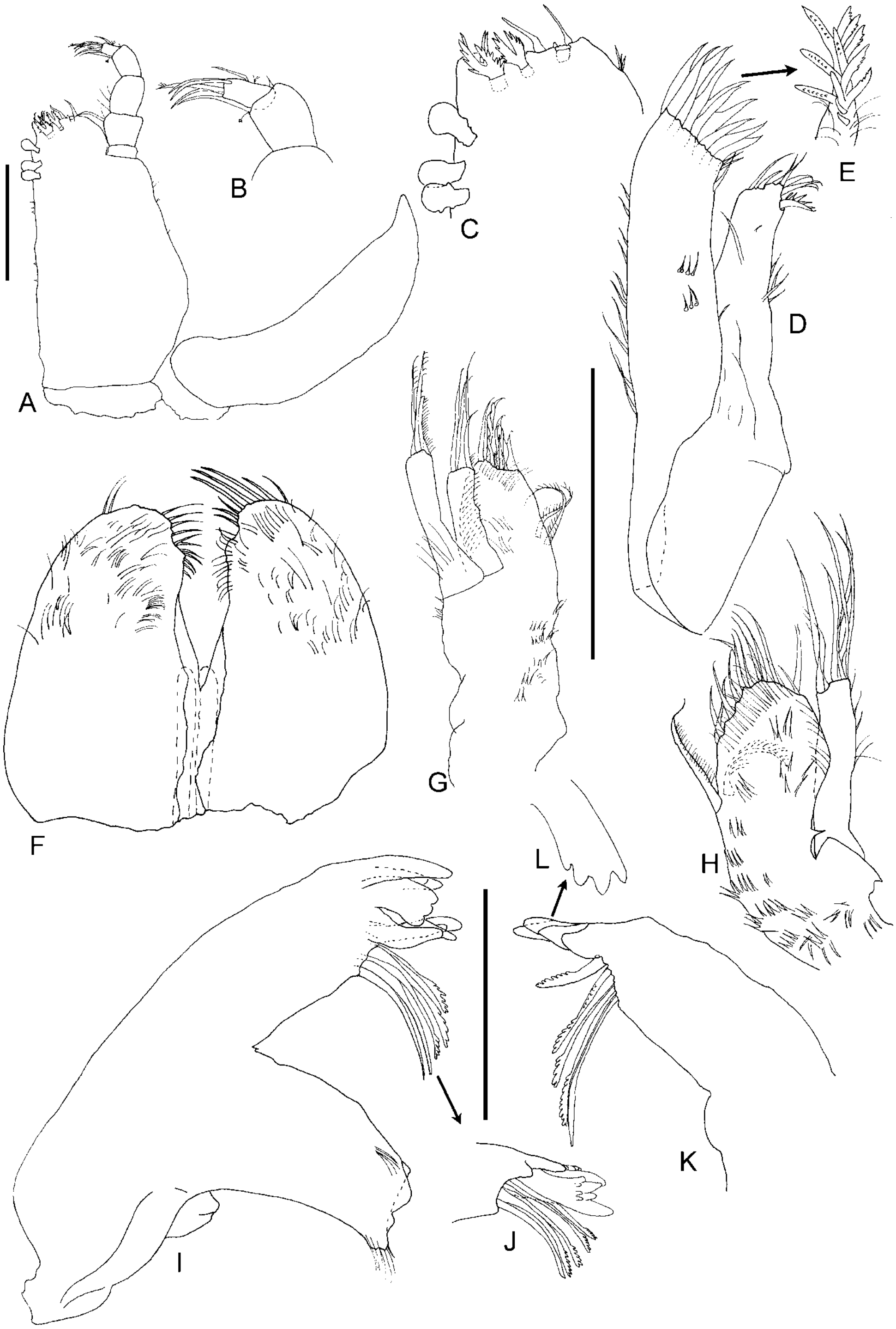

FIGURE 10. *Haplomesus celticensis* (male paratype mouthparts AM P.71667). A, maxilliped; B, maxilliped palp; C, maxilliped endite; D, maxillula; E, maxillula detail; F, paragnaths; G, H, maxillae; I, left mandible, J, left mandible detail; K, right mandible; L, right mandible detail (scale bars 0.1 mm).

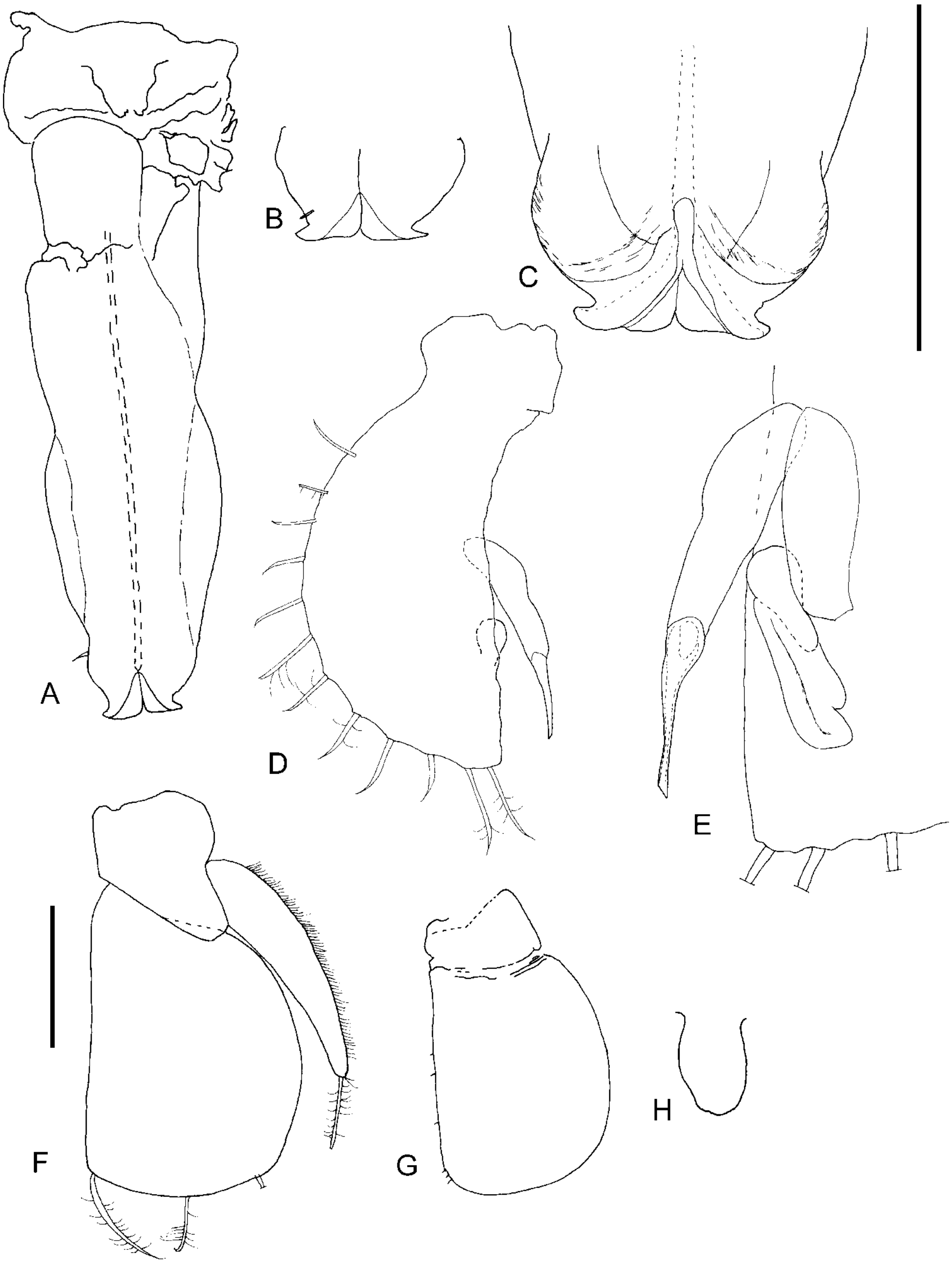

FIGURE 11. *Haplomesus celticensis* (paratype male pleopods AM P.71666). A, pleopod I ventral; B, pleopod I ventral detail; C, pleopod I dorsal; D, pleopod II; E, pleopod II stylet; F, pleopod III; G, pleopod IV; H, pleopod V (scale bar 0.1 mm).

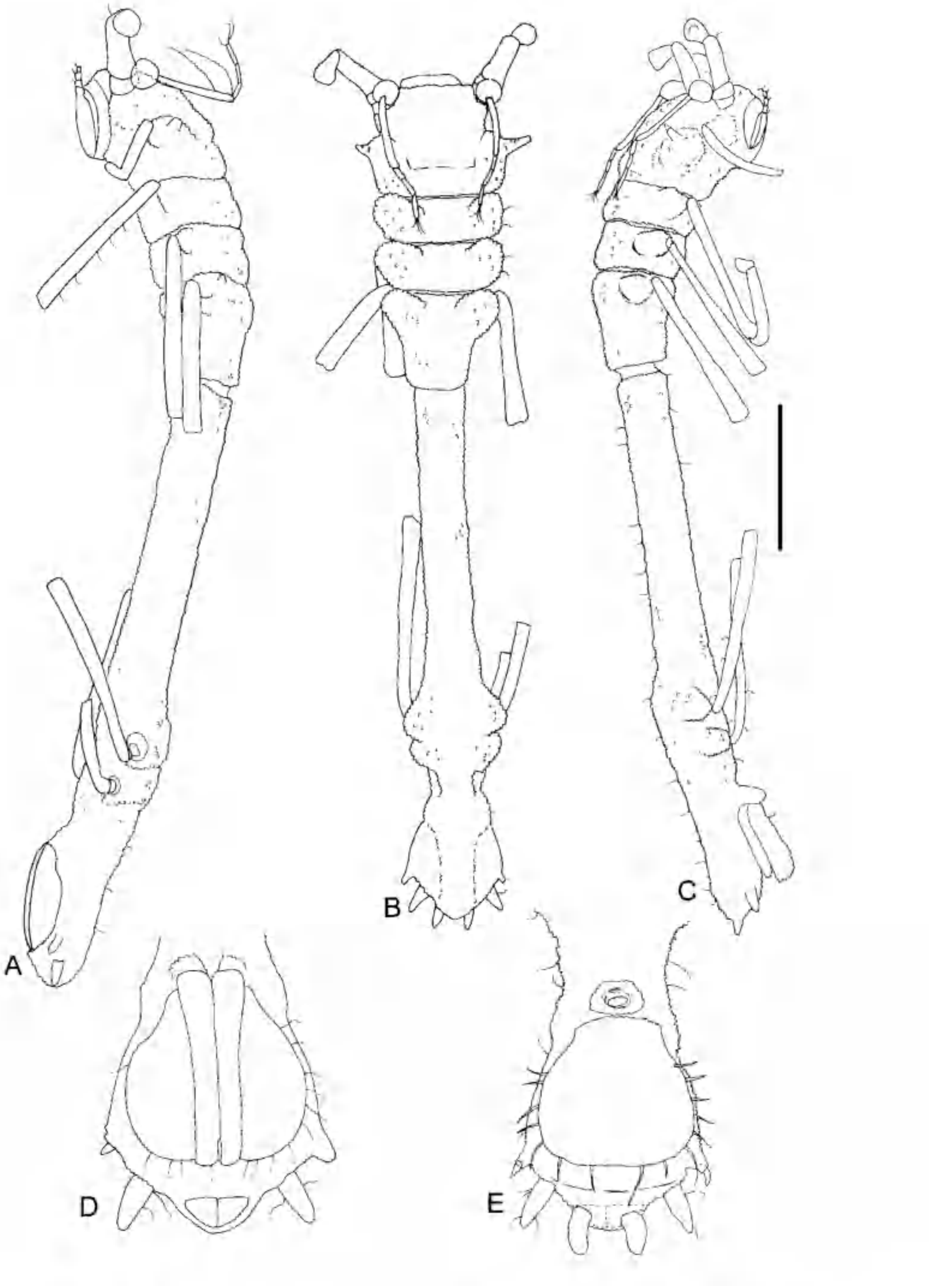

FIGURE 12. *Haplomesus celticensis* (male paratypes juvenile AM P.71660, manca 3 AM P.71661). A, juvenile male body lateral; B, manca 3 male dorsal view; C, manca 3 male lateral view; D, juvenile male pleotelson ventral; E, manca 3 male pleotelson ventral (scale bar 0.5 mm).

Pleopods and uropods. Pleopod I distal tip with lateral horns. Pleopod II stylet not extending to distal margin of protopod. Pleopod III exopod with plumose setae, with fringe of fine setae on lateral margin. Pleopod V present. Uropods extending near posterior margin of pleotelson, length 0.1 length of pleotelson.

Distribution. North Atlantic Ocean: Celtic Sea, South West of Ireland, 1491–1500 m.

Remarks. *H. celticensis* sp. nov. can be immediately identified by the combination of spination pattern: male with spines on pereonites 1 & 4, female with spines on pereonite 1 only, 3 articled antennular flagellum and the lack of distal setae on male pleopod I, as discussed in the remarks for *H. hanseni*.

Haplomesus angustus Hansen, 1916 (Figs 13–14)

Haplomesus angustus Hansen, 1916: 61–62, pl. V, fig. 2a–e; Gurjanova, 1932: 43, tabl. XIV, 50; 1933: 410; Gorbunov, 1946: 76–77; Menzies, 1962: 119, fig. 20A–D; Wolff, 1962: 86, 217, 262, 289; Gurjanova, 1964: 259; Kussakin, 1988: 454–456, fig. 375.

Remarks on Type Material. The holotype male is in relatively good condition. The spines on pereonite 1, however, have been broken off since Hansen's original illustration. Hansen also designated a male paratype that he illustrated but did not describe. The paratype specimen is missing the head and anterior pereonites 1 and 2, but otherwise is in good condition. Pereonite 5 of the paratype is 4 times as long as wide, whereas the holotype has a ratio of five times as long as wide; this may be due to the smaller size of the paratype. A small difference in the posterolateral spines of the pleotelson may be attributed to slight damage of both specimens.

Material examined. Holotype male 4.8 mm, ZMUC CRU-5338, *Ingolf* Station 18, south of Denmark Strait, 61°44'N, 30°29'W, 1135 Danish fathoms (2137 m). Paratype male 4 mm (estimated), ZMUC CRU-5338, *Ingolf* Station 125, 68°08'N, 16°02'W, 729 Danish fathoms (1373 m).

Diagnosis. Male with anterolateral spines on pereonite 1 only. Pereonite 7 length reduced, less than pereonite 6. Pleotelson posterolateral margin anterior to uropods with simple spines, length subequal to uropods. Antennula with 3 distal flagellar articles. Pereopod I carpus ventral margin with 1 proximal robust seta and 1 robust seta on palm. Pleopod I of male without simple setae on lateral or distal margins.

Description of male (female unknown). Body length 4.8 mm. Head length 0.9 width. Head cuticular structure granulated; pereonite 7 length reduced, less than pereonite 6. Head lobe on ventrolateral margin absent in lateral view. Pereonite 1 width 0.1 total body length, anterolateral simple spines, short, length near pereonite 1 length, acutely pointed. Pereonite 5 length 5 width, 0.5 total body length. Pleotelson dorsal surface axial ridge weakly vaulted, separated from lateral fields only by shallow elongate concavities; Pleotelson length 1.4 width; posterolateral margin adjacent to uropods convex.

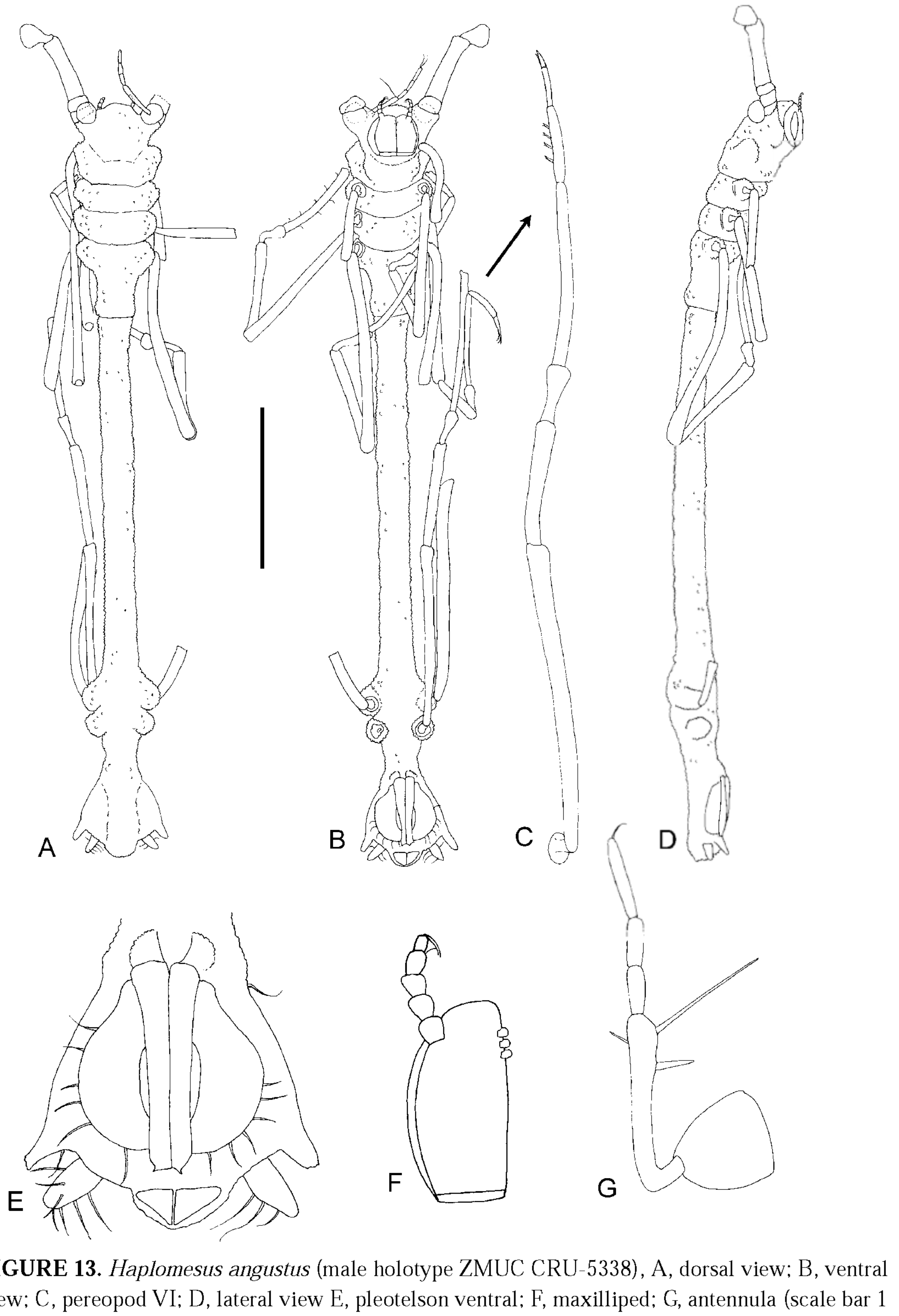

FIGURE 13. *Haplomesus angustus* (male holotype ZMUC CRU-5338), A, dorsal view; B, ventral view; C, pereopod VI; D, lateral view E, pleotelson ventral; F, maxilliped; G, antennula (scale bar 1 mm).

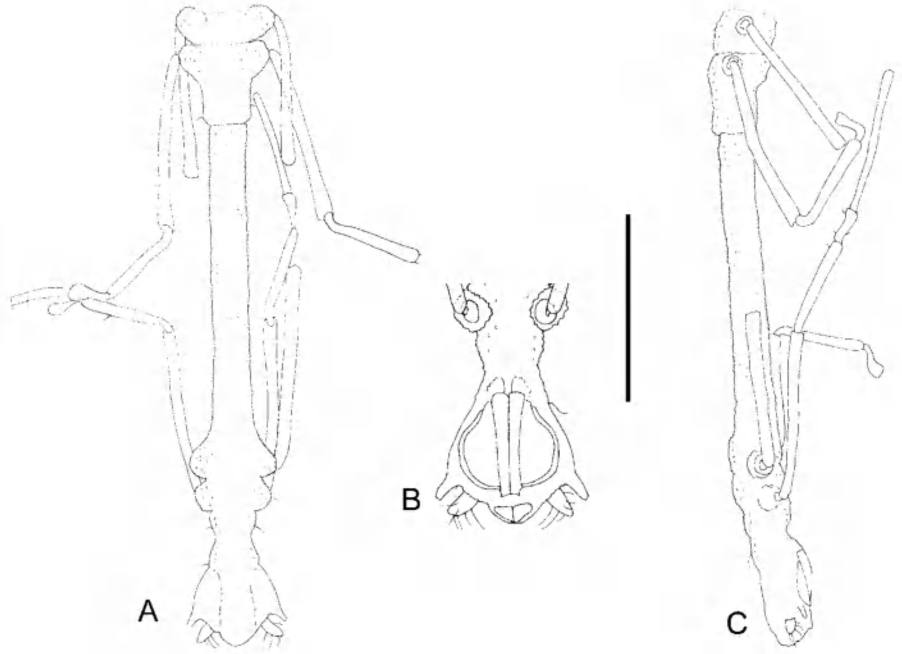

FIGURE 14. *Haplomesus angustus* (male paratype ZMUC CRU-5338). A, dorsal view; B, pleotelson ventral; C, lateral view (scale bar 1 mm).

Antennula and antenna. Antennula with 5 articles; article 2 length 0.6 head width, with 2 elongate ventromedial setae; distal articles in total small, shorter than article 2; article 3 cuticle smooth, length similar to article 4, elongate and tubular, much longer than wide; terminal article longer than penultimate article; aesthetascs absent, length 3.9 width.

Mouthparts. Maxilliped palp article 3 wider than article 2.

Pereopods. Pereopod I propodus ventral margin with 1 robust seta (see Hansen, 1916: pl. V, fig. 2C). Pereopod VII absent in adults.

Pleopods and uropods. Pleopod I distal tip with lateral horns. Uropods extending near posterior margin of pleotelson, length 0.2 length of pleotelson.

Distribution. Northeast Atlantic Ocean, south of Denmark Strait; Arctic Ocean east of Greenland, 1333–2076 m.

Remarks. The holotype of *Haplomesus angustus* Hansen, 1916 was considered by Hansen to be a juvenile male, due to the lack of pereopod VII. Hansen (1916: 64) estimated that a fully grown male of *H. angustus* would measure about 9–12 mm. This would be an unusually large specimen for a *Haplomesus* species, although *H. gigas* Birstein, 1960 is in this size range. Species described from the North East Atlantic generally range from 4–5 mm, similar to the holotype of *H. angustus* (4.3 mm, fig. 13A).

The type specimen is sexually mature. The first pleopods (Fig. 13E) are fully developed, with lateral horns on the distal tips, in contrast to the rounded tips that would be expected in a juvenile specimen (Fig. 6E). The seventh pereonite is also much reduced, as noted by Hansen, a feature seen in most species that lack a pereopod VII as adults. We can conclude that the holotype is not a juvenile but rather is an adult without expression of the seventh pereopod.

H. angustus males are distinct from those of other '6 pereopod' group species by having only short (approximately as long as width basally) anterolateral spines on pereonite 1 only. *H. corniculatus* males have long (much longer than wide) anteriorly-curving robust anterolateral spines on pereonite 1. Other species also have anterolateral spines on pereonite 4, which are absent in *H. angustus*.

Haplomesus corniculatus Brökeland & Brandt, 2004

Haplomesus corniculatus Brökeland & Brandt, 2004: 1777–1784, figs 6–10.

Holotype (ZMH-K40638) (not examined).

Type locality. 59°40.30'–40°.32'S, 57°35.42'–35.64'W, 3689 m, off Elephant Island, Drake Passage, Scotia Sea.

Material examined. None, description based on Brökeland & Brandt (2004) for the males.

Diagnosis. Male with anterolateral spines on pereonite 1 only. Pereonite 7 length not reduced, similar to pereonite 6; pleotelson posterolateral margin anterior to uropods with pedestal spines, longer than uropods. Antennula with 4 distal flagellar articles. Pereopod I carpus ventral margin with 1 distal robust seta on palm. Pereopods II–VI bases with simple spines on dorsal and ventral margin. Pleopod I of male with simple setae on lateral and distal margins; pleopod II stylet extending beyond distal margin of protopod.

Description of male (female unknown). Body length 4.2 mm. Head length 0.6 width. Head cuticular structure granulated. Head lobe on ventrolateral margin absent in lateral view. Pereonite 1 width 0.14 total body length. Pereonite 1 anterolateral simple spines, elongate, length near width of pereonite 1. Male pereonite 1 anterolateral spines robust and anteriorly curved. Pereonite 5 length 3.9 width, 0.5 total body length. Pleotelson length 1.1 width; posterolateral margin anterior to uropods with pedestal spines. Pleotelson dorsal surface axial ridge weakly vaulted, separated from lateral fields only by shallow elongate concavities; posterolateral margin adjacent to uropods convex.

Antennula and antenna. Antennula with 6 articles altogether; article 2 length 0.6 head width, with 2 elongate ventromedial setae; distal articles altogether small, shorter than article 2; article 3 length similar to article 4; article 3 elongate and tubular, much longer than wide; terminal article shorter than penultimate article. Antenna length 2.5 anterior body length; article 3 cuticle smooth, length 7.5 width; article 5 length 0.6 anterior body length; article 6 length 0.7 anterior body length; flagellum length 0.3 total antennal length, flagellum with 20 articles, flagellum some segments expanded, wider than long.

Mouthparts. Maxillula with 12 robust setae on lateral lobe; medial lobe with 1 robust medially-projecting dentate seta. Maxilla medial lobe with 2 long (approximately as long as lateral lobes) medially-projecting pectinate seta. Maxilliped palp article 2 wider than 3.

Pereopods. Pereopod I propodus ventral margin with 1 robust seta. Pereopod VII absent in adults. Pereopods II–VI bases with simple spines in random pattern.

Pleopods and uropods. Pleopod I distal tip with lateral horns. Pleopod II protopod apex rounded. Pleopod 3 exopod with plumose setae, with fringe of fine setae. Uropods not extending near posterior margin of pleotelson, length 0.1 length of pleotelson.

Distribution. South Atlantic Ocean, Drake Passage and Scotia Sea, depth 3689–3962 m.

Remarks. *H. corniculatus* males lack lateral or anterolateral spines on pereonite 4, whereas these spines are present on males of other species. This species differs from *H. angustus* in that the first pereonite spines are especially robust and anteriorly curving. This species also retains a distinct segment at pereonite 7 whereas the segment is largely reduced or undeveloped in other species that lack the last pereopod. Brökeland & Brandt (2004) illustrate the antennular second article ventromedial setae as having setules, while these setae are almost certainly the long curved simple seta that occur in other species.

Haplomesus tropicalis Menzies, 1962 (Fig. 15)

Haplomesus tropicalis Menzies, 1962: 120–121, fig. 20K–M.

Type fixation. Holotype male AMNH 12062; paratype ("allotype") AMNH 12063.

Type locality. Mediterranean Sea, 34°14'N, 24°10'E, 2526 m.

Remarks on type material. Paratype ("allotype") female is decalcified, with antennae and several pereopods broken. Although the container received from the American Museum contained labels for both "Holotype" and "Allotype," the male holotype specimen described by Menzies (1962) was not in the jar. Menzies (1962) also reports another specimen from a different locality that was not examined here: AMNH 12206, LGO Biotrawl no. 95, Vema 15–10, 7 November 1958, 4071 m, 14°05'N, 75°25'W, central part of Columbia Abyssal Plain.

Material examined. Paratype female, AMNH 12063, Lamont Geological Observatory Biotrawl no. 76, Mediterranean Sea, Vema 14–32, 9 July 1958, 2526 m. Holotype male not examined, data taken from illustration.

Diagnosis. Male with small spines on pereonites 1 and 4 only; female with spines on pereonite 1 only, spines short (length distinctly less than pereonite 1 lateral margin) and acutely pointed. Male pereonite 1 with 3 pairs of low spines on posterolateral margin, minute, acute (see Menzies 1962: 120, fig. 20K–M). Pleotelson posterolateral margin anterior to uropods with simple spines, less than half uropoda length. Pereopod I carpus ventral margin with 1 proximal robust seta and with 2 distal robust setae on palm. Pleopod I of male with simple setae on distal margins.

Description of female. Body length 4.1 mm; pereonite 7 undeveloped. Head length 0.8 width; lobe on ventrolateral margin absent in lateral view. Pereonite 1 width 0.15 total body length. Pereonite 5 length 3.5 width, 0.4 total body length. Pleotelson length 1.6 width; dorsal surface axial ridge weakly vaulted, separated from lateral fields only by shallow elongate concavities; posterolateral margin adjacent to uropods convex.

Antennula and antenna. Antennula article 2 length 0.9 head width, with 2 elongate ventromedial setae. Antenna article 3 length 0.1 anterior body length, length 3.2 width.

Mouthparts. Maxilliped palp article 2 wider than 3.

Pereopods. Pereopod I propodus ventral margin with 1 robust seta. Pereopod VII absent in adults.

Pleopods and uropods. Pleopod II operculum with narrow proximal neck, laterally convex, broadening posteriorly to rounded angles, posterior margin weakly convex, without plumose setae. Uropods extending near posterior margin of pleotelson; length 0.2 length of pleotelson.

Description of male. Body length 3.1mm. Head length 0.8 width. Pereonite 1 width 0.14 total body length. Pereonite 4 anterolateral simple spines, minute, length distinctly less than pereonite 1 length. Pereonite 5 length 3.7 width, 0.4 total body length. Pleotelson length 1.5 width;

Antennula and antenna. Antennula article 2 length 1.1 head width. Antenna article 3 length 1.5 width.

Pleopods and uropods. Uropods extending near posterior margin of pleotelson, length 0.2 length of pleotelson.

Distribution. Mediterranean Sea, 2526m; ?North Atlantic Ocean, Caribbean Sea, Columbia Abyssal Plain, 4071 m.

Remarks. *H. tropicalis* is easily distinguished from other species without pereopod VII by having the shortest spines on pereonites 1 and 4 (Fig. 15A). It is also distinguished in males by the group of posterolateral minute spines on pereonite 1. The holotype of *H. tropicalis* Menzies, 1962 is an immature male specimen, based on our inspection of the original description (Menzies 1962: 120–121). A fully grown male would be expected to have lateral horns on pleopod I, and well developed spines both on the pleotelson and pereonites 1 and 4. Although the holotype was not examined because it has been apparently lost (see above remarks on the type material), the dorsal illustration by Menzies (1962, fig. 20K) shows the lack of development of pereonite 7, which implies that pereopod VII is also absent. The "allotype" is a preparatory female with oostegites. This specimen also lacks pereopod VII and the seventh pereonite is undeveloped, a fact overlooked by Menzies (1962).

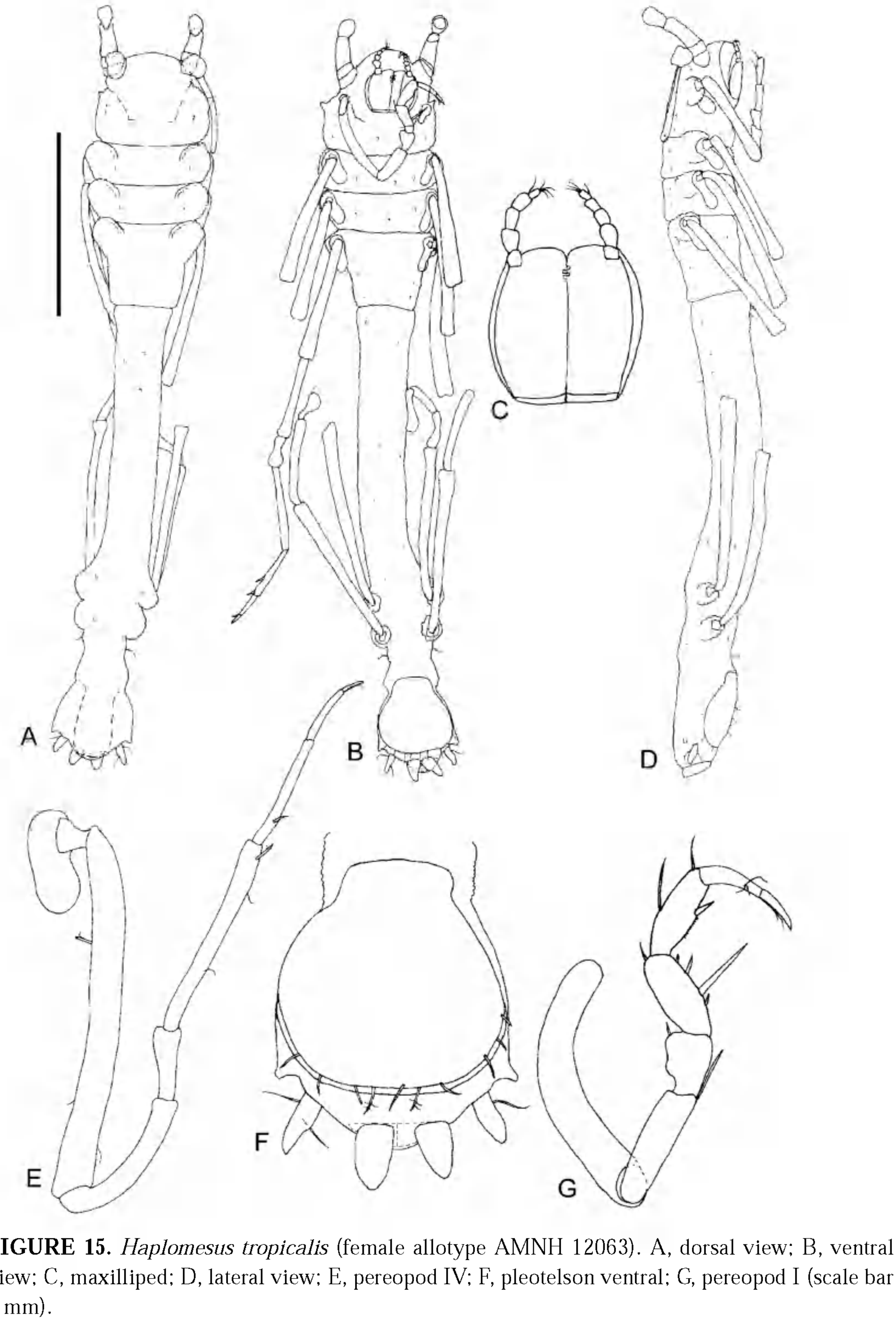

FIGURE 15. *Haplomesus tropicalis* (female allotype AMNH 12063). A, dorsal view; B, ventral view; C, maxilliped; D, lateral view; E, pereopod IV; F, pleotelson ventral; G, pereopod I (scale bar 1 mm).

Distribution of species lacking the seventh pereopod

Species without the seventh pereopod exist throughout the Atlantic Ocean (see fig. 1), with species collected as far north as the Arctic circle (*H. angustus*), and as far south as the Southern Ocean, just north of the Antarctic circle (*H. corniculatus*), at depths from 1333–4071 m. All species, however, have limited distributions thus far confined to small regions. The exception is *H. tropicalis*, with specimens recorded by Menzies from both the type location in the Mediterranean, and from the Columbia abyssal plain. An undescribed species similar to *H. tropicalis* is known (Wilson, unpublished data) from the Gulf of Mexico [DGoMB stns (see Rowe 2003), sp. 239], that has short spines on pereonites 1 and 4, but lacks the lateral group of short sharp denticles on pereonite 1. The specimen from the Columbia Abyssal Plain reported by Menzies should be examined in relation to this Gulf of Mexico material. At least 1 other unidentified species has also been collected, from the Pacific Ocean (Clipperton Clarion Fracture Zone, sp. 153; see Thistle & Wilson 1996). Species of this group may have been collected elsewhere but may have been considered as manca specimens or the missing last pereopod has not been noted. Therefore, we suspect that this species group has a cosmopolitan deep-sea distribution and may be an older clade than *Heteromesus*, which is restricted to the North Atlantic (Cunha & Wilson, personal communication)

Key to described *Haplomesus* species that lack the last pereopod

1. Pereonite 4 of male without anterolateral spines 2
   Pereonite 4 of male with anterolateral spines 3
2. Pereonite 7 length not reduced, similar to pereonite 6; antennula with 4 distal flagellar articles; pleotelson posterolateral margin with pedestal spines (with small robust seta on tip); male pereonite 1 with elongate anterolateral spine, length near width of pereonite 1 .... *Haplomesus corniculatus*
   Pereonite 7 length reduced, less than pereonite 6; antennula with 3 distal flagellar articles; pleotelson posterolateral margin with simple spine; male pereonite 1 with short anterolateral spine, length near pereonite 1 length....................... *Haplomesus angustus*
3. Pereonite 4 of female with short anterolateral spine, length near that of pereonite 1 length; Pereonite 4 of male with elongate anterolateral spine, length near that of width of pereonite 1; pereopod I carpus palm with 2 smaller proximal robust seta .... *Haplomesus hanseni*
   Pereonite 4 of female without anterolateral spine 4
4. Pereonite 4 of male with short anterolateral spine, length near that of pereonite 1 length; pereopod I carpus palm with 1 proximal robust setae.. .... *Haplomesus celticensis*
   Pereonite 4 of male with tiny anterolateral spine, length distinctly less than pereonite 1 length; pereopod I carpus palm with 2 smaller distal robust setae................................. .... *Haplomesus tropicalis*

Discussion

In this section, we discuss the unusual feature of lack of pereopod VII, described above, and also observed in numerous deep sea isopods (see also Wilson 1976; 1989). The ontogenetic trajectory of the Ischnomesidae, as is seen in the Asellota generally (Zimmer 1926; Hessler 1970; Wilson 1981), consists of three postmarsupial manca stages prior to the juvenile instars. The last leg is absent in mancas 1 and 2. In the third manca, pereopod VII is present but is rudimentary. By the fourth instar, pereopod VII is well developed, although it may be smaller than preceding legs (e.g. in the Munnopsidae: Wilson 1981). Over any period of evolutionary time, the prevailing ontogenetic trajectory within a lineage may either recur unchanged from generation to generation or alter (Arthur 2001). In the case of the species described above, the ontogenetic trajectory has become altered resulting in the lack of expression of pereopod VII.

Research has shown that the *Distal-less* (*Dll*) gene is responsible for limb growth in various arthropods (Vachon *et al.* 1992; Warren *et al.* 1994). Although how *Dll* is regulated in most Crustacea, and especially in Isopoda, is not certain, the research to date suggests that a mechanism involving Hox genes may be operating in the Ischnomesidae as well as in other deep-sea isopod species (Pangiban *et al.* 1995; Shiga *et al.* 2002; Deutsch & Mouchel-Vielh 2003). Specifically, the genetic mechanism for the seventh pereopod has not been lost, but it is being repressed in some way that results in its lack of expression (see also Boxshall 2004). A change in the timing or amount of expression of *Dll* could occur as a result of a mutation in the genes regulating its expression. Such mutations could change the rate at which the limbs develop, and thus give rise to morphological heterochronies. Gould (1977) defined heterochrony as the "changes in relative time of appearance and rate of development of characters already present in ancestors". In the case of the species listed above, the ancestral juvenile character of six pereopods is retained in preference to the adult complement of seven, resulting in paedomorphic species (see also Alberch *et al.* 1979; McNamara 1986; Klingenberg 1998). The species still continue to develop into adults through the normal instars, but one trait simply stops during the developmental trajectory. This indicates that progenesis is the primary process involved rather than neoteny; i.e. these species are not sexually-active juveniles, but have an earlier offset of development of pereopod VII. Because the seventh pereopod appears only during the postmarsupial instars, an interruption in its development at this stage would result in the animal reaching sexual maturity without the limb, thus resulting in the complete lack of expression of the leg rather than a reduced limb.

Regardless of the precise genetic process involved, the loss of the last limb is a phylogenetic trend within the Ischnomesidae, and it may not have arisen by a single mutation event. Most species of *Ischnomesus* have a seventh pereonite and pereopod that are similar in size to the preceding one. For many Ischnomesidae, however, the last pereonite is reduced, and the last leg is normally smaller than the preceding one. A reduced pereonite 7 can be observed for example in *Heteromesus granulatus* Richardson, 1908 and *Stylomesus wolffi* Birstein, 1960. This trend is more widespread amongst *Haplomesus*, with five species exhibiting a reduced pereonite 7, e.g. *Haplomesus brevispinis* Birstein, 1960; Unfortunately, pereopod VII is undescribed for many *Haplomesus* species. All pereopods are illustrated for *Haplomesus cornutus* Birstein, 1960, however, and in this case pereopod VII is approximately two-thirds the length of pereopod VI. Pereonite 7 is also reduced in this species. Species without pereopod VII also occur in several other asellote groups including the Haplomunnidae, Dendrotionidae, Eurycopinae and Lipomerinae (Wilson 1976). Indeed, other non-asellote groups such as the Gnathiidae (Monod 1926), and some Anthuridea (Poore 1984), also have this trait. The independent evolution of this attribute suggests that, while a similar mechanism may be involved in each case, a common explanation as to why this feature has evolved (i.e. homology) is unlikely. Wilson (1976) suggested that, in Haplomunnidae at least, this feature may relate to the long-legged ambulatory habits of these animals, by serving to make the body more compact. Hessler & Stromberg (1989), concluded from behavioural experiments on *Ischnomesus bispinosus,* that Ischnomesidae were predominantly infaunal. This lifestyle might also benefit from a more compact body.

A similar trend to that observed in the Ischnomesidae occurs in the Lipomerinae, where some taxa have a normal seventh pereopod, while others have it variously reduced e.g. *Limpomera (Lipomera) lamellata* Tattersall, 1905; or absent e.g. *Lipomera (Paralipomera) knorrae* Wilson, 1989. This trend continues so that in the genus *Mimocopelates*, even pereonite VI is reduced. Clearly, the evolutionary patterns are quite different in Lipomerinae from the Ischnomesidae, but a single pattern is beginning to emerge within the Ischnomesidae. If the lack of expression of pereopod VII is considered to be an evolutionary feature within the Ischnomesidae, then the reduced pereonite 7 in most *Haplomesus* species (*sensu lato*) might be interpreted as a cessation of development at instar 4. In the first juvenile instar, the last leg is present and functional, but much reduced in comparison to the anterior pereopods. So progenesis may be an evolutionary trend within the Ischnomesidae affecting the expression of the last leg to varying degrees. For this reason, we find several distinct clades lacking the last leg (*Stylomesus* and *Haplomesus)*, but many taxa with reduced legs. Further research is required to understand whether this occurred within the Ischnomesidae at a particular point in their evolution (i.e. a single synapomorphy of some but not all species) or whether the trend has occurred in parallel in several distinct lineages of the family. Therefore we conclude that the current diversity at the higher level of the crustaceans is related to their developmental plasticity, so much so, that the heterochronies seen in the deep-sea isopods may be a fundamental evolutionary trend within this group.

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