Zoological Journal of the Linnean Society, 2006, **148**, 169–208. With 29 figures

A new genus from the continental slope off Brazil and the discovery of the first males in the Hirsutiidae (Crustacea: Peracarida: Bochusacea)

DAMIÀ JAUME[1]*, GEOFF A. BOXSHALL[2] and ROGER N. BAMBER[2]

[1]*IMEDEA (CSIC-UIB), Instituto Mediterráneo de Estudios Avanzados, c/Miquel Marquès 21, 07190-Esporles (Illes Balears), Spain*
[2]*Department of Zoology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK*

Received July 2005; accepted for publication December 2005

***Montucaris distincta* gen. nov. sp. nov.**, a new genus and species of hirsutiid, is described from the bathyal floor of the northern South Atlantic, off Brazil. It is easily distinguished from other members of the family by the reduced, one-segmented exopods of pereopods 5 and 6 and the array of stout triangular spines present on the anterior margin of the basis and proximal endopodal segments of the third pereopod. This discovery is notable as it includes the first record of males in the family, demonstrating that hirsutiids are gonochoristic. Developmental stages including mancas, preparatory females and juvenile males were recovered, in addition to numerous brooding females and two morphs of adult males. We infer that the new genus has a life cycle involving non-feeding terminal males with regressed mouthparts. These males display a bizarre cephalic configuration, with a clearly defined transverse dorsal suture on the dorsal cephalothoracic shield just behind the articulation of mandibles, a feature present also in syncarida and in some Thermosbaenacea and that we interpret as secondary. The peracaridan affinities of the Hirsutiidae are firmly established here after settling definitively the oostegitic nature of the setose plates present on the posteromedial margin of the pereopodal coxae of brooding females. The separate ordinal rank for hirsutiids – as the Bochusacea – with respect to the Mictacea, within which they had been previously classified, is favoured here. In addition, we highlight similarities between hirustiids and tanaidaceans that warrant further investigation.
© 2006 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2006, **148**, 169–208.

ADDITIONAL KEYWORDS: deep sea – limb musculature – Mictacea – *Montucaris* – South Atlantic – taxonomy.

INTRODUCTION

In 1985 a new order of peracaridan crustaceans, the Mictacea, was established to accommodate two newly discovered genera and families (Bowman *et al*., 1985): the family Mictocarididae comprising a single species *Mictocaris halope* Bowman & Iliffe, 1985, from anchialine caves on Bermuda (Bowman & Iliffe, 1985), and the Hirsutiidae, also comprising a single species, *Hirsutia bathyalis* Sanders, Hessler & Garner, 1985, from a depth of 1000 m in the tropical Atlantic (Sanders, Hessler & Garner 1985). No further mictocaridids have been discovered since 1985, but one new genus and three new species have been assigned to the Hirsutiidae. In 1988, a second species of *Hirsutia*, *H. sandersetalia* Just & Poore, 1988, was discovered from a depth of 1500 m in the South Pacific, off southeastern Australia (Just & Poore, 1988). Then a decade later, the new genus *Thetispelecaris* Gutu & Iliffe, 1998 was established to accommodate a single species, *Thetispelecaris remex* Gutu & Iliffe, 1998, found in anchialine and marine caves in the Exuma Cays, Bahamas (Gutu & Iliffe, 1998): this was the first hirsutiid to be reported from caves. A second species, *Thetispelecaris yurikago* Ohtsuka, Hanamura & Kase, 2002, was recently described from a submarine cave on Grand Cayman Island (Ohtsuka, Hanamura & Kase, 2002). All four species of Hirsutiidae are known only from females, leading Ohtsuka *et al*. (2002) to speculate that members of this family might be parthenogenetic.

*Corresponding author. E-mail: vieadjl@uib.es

Despite the apparent similarity between the Mictocarididae and Hirsutiidae, the relationship between these two families and their higher classification are controversial. Some authors (e.g. Sanders *et al*., 1985; Gutu & Iliffe, 1998; Hessler & Watling, 1999) suggested that the Hirsutiidae could not be peracarids as the homology of the setose process carried posteriorly on the pereopodal coxa with the typical peracaridan oostegite was equivocal. Gutu & Iliffe (1998) created a new order, the Bochusacea, to accommodate the Hirsutiidae, and Gutu (1998) also treated the Mictacea, as represented by the monotypic family Mictocarididae, together with the Speleogriphacea, as suborders of a new order, the Cosinzeneacea. Acceptance of these new taxa has varied: Ohtsuka *et al*. (2002) adopted the Bochusacea as the ordinal placement for their new species of *Thetispelecaris*, whereas Martin & Davis (2001) and Richter & Scholtz (2001) considered the new classification of these taxa to be problematic and elected not to follow it, maintaining the Mictacea in its original form.

During February and March 2001 an extensive baseline survey of the seabed on the continental slope about 300 km east of Brazil revealed a rich sample of a hitherto undescribed genus of hirsutiid, including some developing stages, two male morphs and brooding females. This material is described and has provided the opportunity for a more comprehensive study of the Hirsutiidae and further comments on the validity of the Bochusacea.

MATERIAL AND METHODS

Material was collected during February and March 2001 in the northern part of the South Atlantic Ocean off Brazil. A total of 184 samples taken by box corer (0.25 m^2) was collected from 77 stations and from which two 0.1-m^2 faunistic samples were extracted. Samples were sieved across a 0.5-mm mesh on board and fixed in 4% formalin. Hirsutiids were found from depths of 619–778 m. The material is deposited in the Crustacea collections of the Museum of Zoology, University of Sao Paulo (MZUSP) and of the Department of Zoology, The Natural History Museum, London (BMNH).

Morphological observations were made on intact and dissected specimens. Some specimens were treated in the laboratory with hot lactic acid to remove internal tissue. Specimens examined for musculature were observed as temporary preparations in lactophenol. Drawings were prepared using a camera lucida on an Olympus BH-2 microscope equipped with differential interference contrast. Body measurements were calculated from the sum of the maximum dorsal dimensions of the carapace (rostrum included), free somites and telson, including telescoped portions (visible by transparency in lactic acid digested specimens). Material for scanning electron microscopy was washed in distilled water, dehydrated through a graded acetone series, critical-point dried using liquid carbon dioxide as the exchange medium, mounted on aluminium stubs and sputter coated with palladium. Coated material was examined on a Phillips XL30 scanning electron microscope. Pereopods and pleopods are abbreviated as P and PL, respectively, in the text. Pappose setae are referred in the descriptions to those setae having setules radiating or spiralling around the central shaft, whereas penicillate setae are sensory and have a distinct articulated pedestal, and bear two distal rows of long, extremely thin setules.

HABITAT AND ACCOMPANYING FAUNA

The bottom sediments throughout the survey area were fine silts, with extensive areas of mounds and debris of the deep-water ahermatypic coral *Lophelia pertusa* (Linnaeus, 1758). The hirsutiids were found in sediments composed of fine silts (5–17% sand), the median diameter of grains ranging from 10.6 to 18.6 μm (mean diameter 14 μm). They were present across the sampling area, at 48 of the 77 stations sampled, at a mean density of 13 individuals m^{-2} (maximum 90 individuals m^{-2}). Correlations between their density and the full range of sediment granulometry and chemistry did not show any significant relationships. There was an indication that the hirsutiids preferred the deeper parts of the survey area: in the shallowest sampling zone (613–639 m, mean depth 627 m), they were only found at three of 19 stations (15.8%) at a mean density of 0.1 per sample (0.1 m^2); by contrast, in the depth range 680–781 m, higher densities with a mean of 1.8 per sample were encountered and hirsutiids were present in 80% of the samples.

The benthos across the survey area was generally sparse but extremely diverse, with a total of 405 infaunal taxa identified: 178 species of annelids, 159 arthropod taxa, 17 echinoderm species, 48 mollusc species and three species of sipunculids (R.N.B., pers. obs.). The number of taxa per station ranged between 33 and 109, yet total abundance of individuals per sample was only in the range 55–191. The community at the sample sites was generally uniform. The dominant species were an opheliid and a cirratulid polychaete, three species of tanaidacean, and four (two urothoids, one phoxocephalid and one ampeliscid) amphipods. Subsidiary characteristic species included glycerid, amphinomid, spionid, oweniid and paraonid polychaetes, sipunculans, and the hirsutiids. Only 35 species occurred at an average density greater than one individual per station (0.2 m^2). There was a clear trend with depth in this community, with peracarids becoming increasingly dominant with depth.

TAXONOMY

Superorder Peracarida Calman, 1904
Order Bochusacea Gutu & Iliffe, 1998

Emended diagnosis

Body comprising cephalothorax incorporating only first thoracomere (bearing maxillipeds), pereon composed of seven somites, pleon of five somites, and pleotelson comprising sixth pleonite plus telson. Anus opening terminally on pleotelson. Dorsal cephalothoracic shield with post-mandibular area of lateral margin produced ventrally on each side into paired rounded lappets covering bases of maxillules through maxillipeds; lappets apparently articulating with cephalothoracic shield; mandibular gnathobase completely exposed. Posterior carapace fold lacking. Eyes and eyestalks lacking.

Antennule with three-segmented peduncle and two flagella. Antenna located on well-defined pedestal, biramous, with two-segmented protopod, four-segmented endopod with terminal segment annulated forming flagellum, and marginally setose exopodal scale on second protopodal segment (basis). Lacinia mobilis present on left mandible only. Paragnaths drawn out distally into long, filiform extension. Maxillule bilobate, with lobes representing coxa and basis; rami lacking. Maxilla retaining vestige of endopod as non-articulated process carrying long seta; maxillary gland present, opening posterolaterally on basal pedestal of maxilla. Maxilliped lacking both coxal endite and epipodite.

Pereopods all with monocondylic articulation between coxa–basis, and with basis–endopodal intersegmental articulations all dicondylic with hinge lines perpendicular to limb plane except articulation between merus and carpus, which lies parallel to it. Distal endopodal segments lacking annulations. Pereopods 1–6 biramous, with plumose, locomotory exopods originating anterolaterally on proximal part of basis. Pereopod 1 unspecialized, non-chelate, probably assisting in manipulation of food. Pereopod 2 stouter than rest, apparently fossorial. Oostegites on female pereopods 2–6, located posteromedially on coxa, fringed with long plumose setae; oostegites apparently permanent once developed. Male penes paired, tubular.

Pleopods vestigial in female; well developed, locomotory in male, comprising protopod and one-segmented stenopodial rami except modified pleopod 2, with two-segmented exopod and inflated, one-segmented endopod. Uropods biramous, with undivided protopod and stenopodial, non-foliaceous rami; exopod two-segmented, endopod annulated, apparently five-segmented, but lack of intrinsic musculature suggesting one-segmented condition.

Life cycle including manca stage. Reproductive strategy involving non-feeding terminal males.

Composition

The order comprises three genera from two very different habitats: the oceanic bathyal floor, and marine and anchialine caves. *Hirsutia*, with two species, is a bathyal form reported from the South Pacific off Australia and the western Atlantic off Guayana. *Thetispelecaris*, with also two species, is known only from caves in the Bahamas and the Cayman Islands. *Montucaris* gen. nov. lives in the northern South Atlantic on the continental slope, off Brazil.

Remarks

Gutu (2001) emended his original diagnosis of the Bochusacea after noticing that *Thetispelecaris remex* has the second thoracomere incorporated into the cephalothorax. We have confirmed this in the three adult female and one juvenile paratypes deposited in the National Museum of Natural History (Smithsonian Institution, Washington; Reg. No. USNM 291178). Nevertheless, we interpret this feature as an autapomorphy of the species as this somite is completely separated from the cephalothorax in *T. yurikago* and in all members of the other genera.

All previous descriptions of hirsutiid species have reported the presence of a free telson. Just & Poore (1988) showed what appears to be a well-defined ventral articulation between the sixth pleonite and telson, but other authors figured only a faint line in the homologous position. Ohtsuka *et al*. (2002: fig. 6a–d) and Gutu (2001: fig. 2a,b) show scanning electron micrographs of that part of the body, but these photographs are inconclusive and do not confirm the presence of a ventral articulation. The new taxon described herein possesses a pleotelson: there is no suture line marking the plane of articulation between sixth pleonite and telson on the ventral body surface and there is no indication of an articulation reflected in the ventral longitudinal trunk musculature. In addition the mid-dorsal suture line separating the sixth pleonite from the telson is non-functional, lacking any arthrodial membrane. A similar situation has been described for some anthurid isopods, which have traditionally been considered to be the exception within the Isopoda with regard to the presence of a pleotelson (Brusca & Wilson, 1991).

Family Hirsutiidae Sanders, Hessler & Garner, 1985

Emended diagnosis

As for order.

MONTUCARIS GEN. NOV.

Diagnosis

Hirsutiidae with anterior (= lateral) margin of basis and ischium to carpus of endopod of pereopod 3 bearing stout triangular spines; exopod present on pereopod 1; exopods on pereopods 5 and 6 reduced, one-segmented. Filiform extension of paragnaths naked distally. Female with medial margin of proximal segment of uropodal endopod bearing row of spinules; female pleopods 4 and 5 not articulated proximally to body. Male with dorsal cephalothoracic shield as in female, or with dorsal transverse suture located just behind insertion of mandibles; mouthparts normally developed as in female or regressed; medial armature of proximal segment of uropodal endopod as in female or lacking row of spinules. Male pleopods as for the order.

Type species

Montucaris distincta sp. nov. by original designation.

Etymology

The genus is named after the late Mónica Montú (Universidade Federal do Rio Grande do Sul, Brazil) and is combined with the termination *karis*, derived from the Greek name for shrimp. Gender feminine.

MONTUCARIS DISTINCTA SP. NOV. (FIGS 1–29)

Material examined

South Atlantic Ocean off Brazil, between 22°38′S/40°27′W and 22°40′S/40°24′W; fine silt bottoms, 619–778 m depth; February–March 2001.

Holotype: Brooding female (oostegites fully developed, setose), body length (BL) 5.30 mm (MSUSP Reg. no. 17045).

Female paratypes: Fifty-four brooding specimens, of which 18 measured: BL 4.63, 5.95, 5.70 and 5.23 mm [MSUSP Reg. no. 17046] and 5.51, 5.45, 4.60, 5.26, 4.80, 5.04, 4.60, 4.75, 5.43, 5.17, 5.03, 5.10, 5.08 and 5.43 mm (BMNH Reg. nos. 2005.401–410]. Two preparatory specimens (with oostegite buds), of which one measured, BL 3.81 mm (BMNH Reg. nos. 2005.411–412]. Seven preparatory specimens (oostegites with setation not fully developed), of which two measured: BL 4.45 and 4.49 mm (BMNH Reg. nos. 2005.413–419]. Two brooding specimens prepared for SEM and one dissected for study of musculature.

Male morph-I paratypes (see description below): Seven specimens, of which one measured, BL 3.70 mm with P1 and P3–P4 missing, P2 and uropods both with distal part of endopod missing (MSUSP Reg. no. 17047). One specimen with PL1–PL5 dissected, rest of body in vial; body size not determined owing to damage to specimen. One specimen used for SEM observations.

Male morph-II paratypes (see description below): One specimen BL 3.88 mm with well-preserved P7, pleopods, uropods and telson; P1–P4 with distal portion of endopod missing; P5–P6 missing except coxa and proximal part of basis. One specimen partially dissected with pleopods 3–5 loose in vial, PL1–2 accidentally lost; P1, P5, PL1–5 and uropods well preserved; P2–P4 and P6 with distal portion missing; P7 missing; body size not determined due to damage to specimen, not measured, well preserved, dissected for study of musculature (BMNH reg. nos. 2005.430–432).

Juvenile male paratypes (pleopods not fully developed): Specimen BL 3.64 mm, with P1–P3 with distal parts missing, P4 and P6 missing, and exopods of uropods missing. One damaged specimen (body anterior to 5th pereonite – bearing P4 – missing), not measured; retaining P5, pleopods and uropods except exopod (BMNH Reg. nos. 2005.420–427).

Manca paratypes: One damaged manca stage-III (pereopod 7 not fully developed, and exopods on rest of pereopods more developed than in adult, and inserted laterally on basis), with anterior part of body (in front of 4th pereonite, bearing P3) missing; one manca stage-IV (exopods of pereopods as in adult in development and insertion; pereopod 7 not fully developed), 3.10 mm (BMNH Reg. nos. 2005.428–429).

Description

Brooding female (Figs 1A, 2–7, 9–17)

Body vermiform, subcylindrical (Fig. 1A), with surface ornamented with numerous fine setules and comb rows (Figs 2A, 4, 5B, 6A). Proportional lengths of cephalothorax : pereon : pleon (including telson) 0.11 : 0.43 : 0.46, respectively. Cephalothorax incorporating maxilliped-bearing first thoracomere only; broad in dorsal view (Fig. 2A), slightly wider than long, excluding rostrum; dorsal cephalothoracic shield produced frontally into small anteroventrally curving rostrum, acutely pointed at tip. Paired lateral folds of dorsal shield ellipsoid in outline, longer than wide, defined basally by complete suture line (Figs 3, 7A). Dorsal shield without transverse groove and lacking posterodorsal extension (= carapace fold).

Pereonites becoming successively larger posteriorly; pereonite 1 much shorter than rest (Figs 1A, 2A, 4A); vestigial pleurae present anterolaterally on pereonites 4–7 (Fig. 4A). Pleonites 1–5 free, becoming successively longer towards posterior, slightly depressed dorsoventrally, with vestigial pleurae on pleonites 1–4

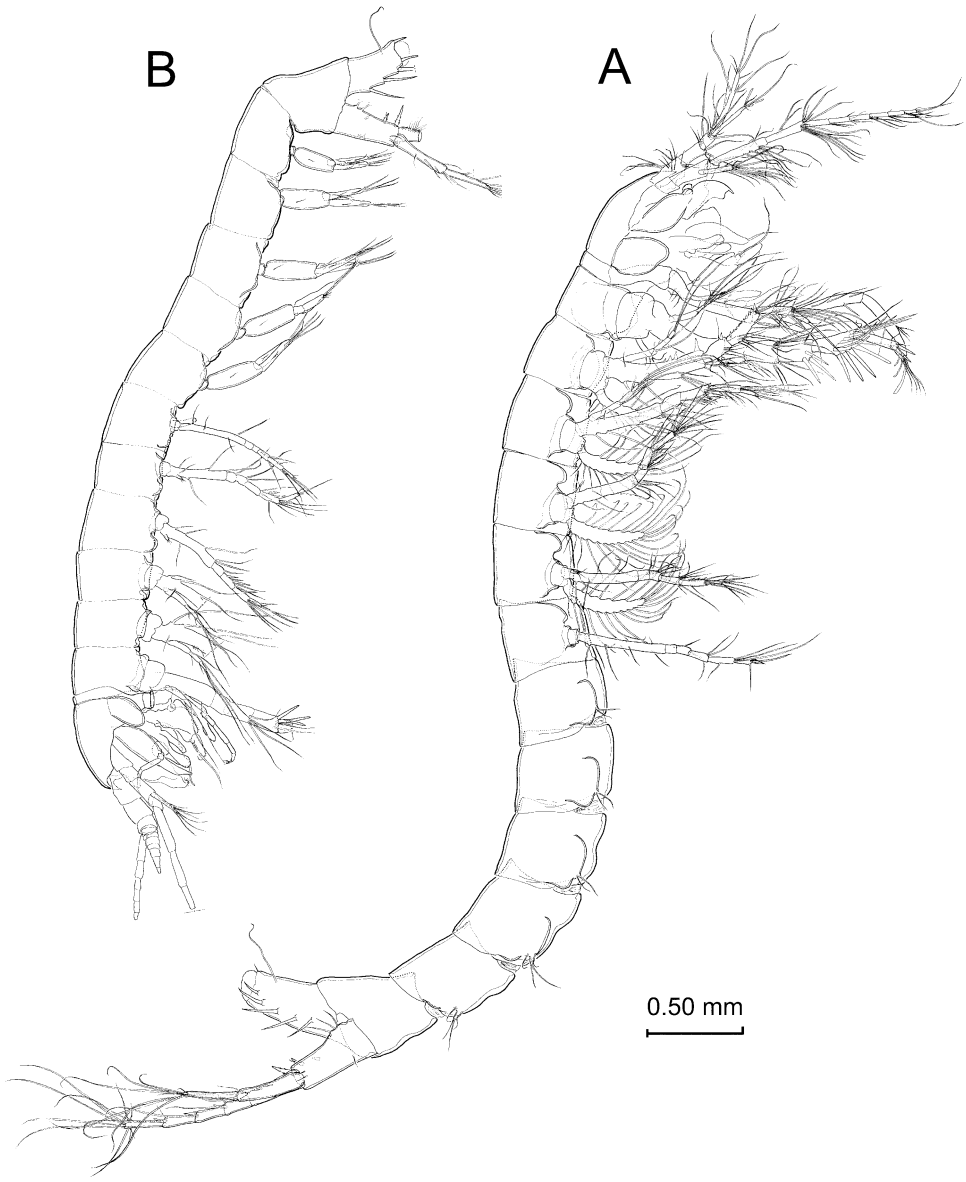

Figure 1. ***Montucaris distincta*** **gen. et sp. nov**. A, brooding female; B, male morph-I.

(Figs 1A, 4B, 5B, 6A). Sixth pleonite similar to preceding somites and apparently distinct from telson in dorsal view, but mid-dorsal suture line between sixth pleonite and telson non-functional, lacking arthrodial membrane; pleotelson present: ventral suture line marking plane of articulation between sixth pleonite and telson absent; no interruption in ventral longitudinal trunk muscles.

Rear part of pleotelson representing telson (Figs 5B, 6C) longer than wide, tapering gradually towards posterior; cylindrical in section; anus opening ventroterminally, closed off by paired anal valves projecting beyond rear margin; valves ornamented with fine hair-like setules. Armature comprising five stout spinulate spines along lateral margins, long slender seta arising dorsolaterally and short, smooth spine located dorsally on posterior margin (Fig. 5B). Entire surface of telson ornamented with short crescentic spinule rows.

Antennule (Fig. 2A, C) with short, unequal flagella; surfaces of peduncular segments and both flagella densely ornamented with crescent-shaped scales with setular fringes or with crescentic rows of setules. Peduncular segments provided with intrinsic muscles inserting on proximal rim of primary and accessory flagellar branches. Segment 1 longest. Some setae on segments 1 and 2 penicillate. Segment 3 shortest, produced dorsally into terminal setiferous process armed

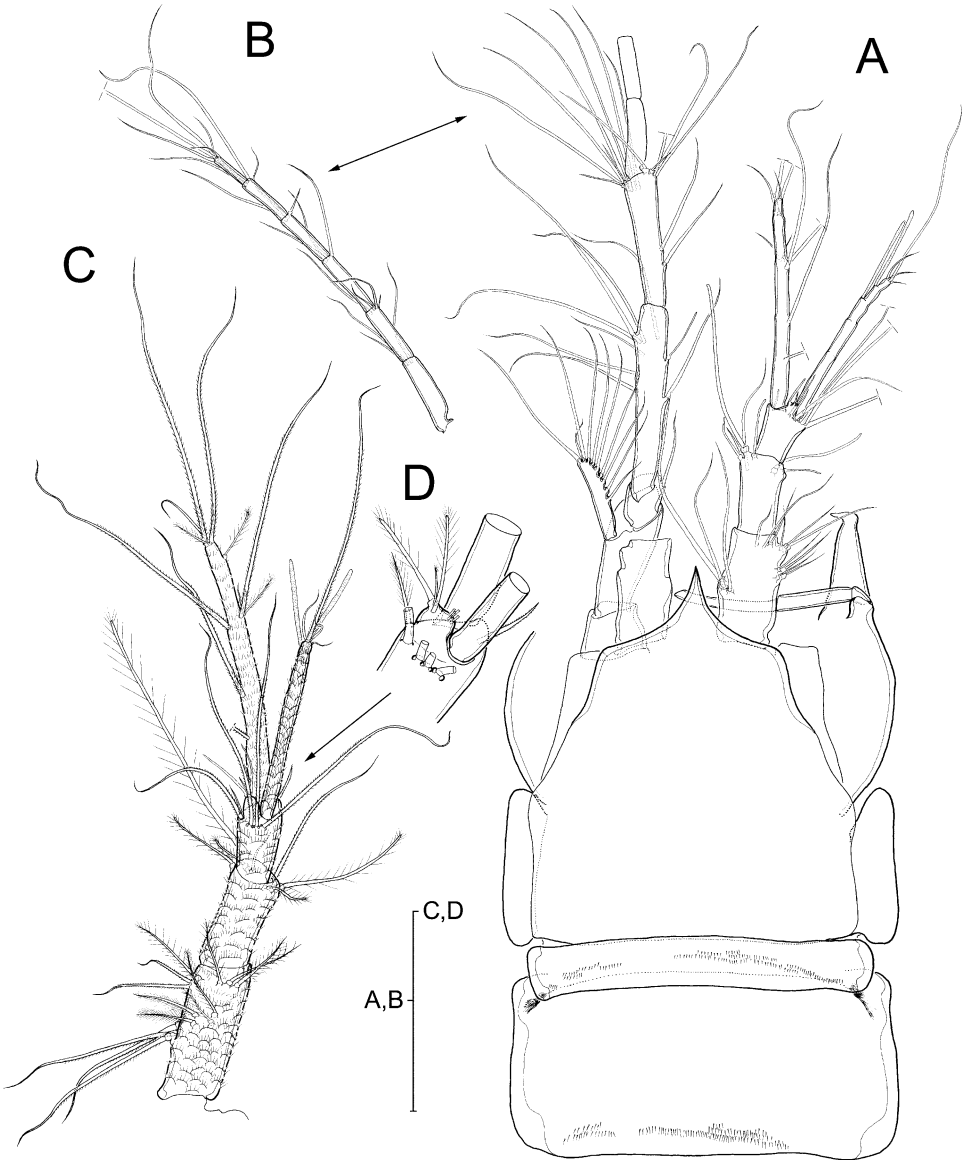

Figure 2. ***Montucaris distincta*** **gen. et sp. nov.**, brooding female. A, cephalothorax with right antennule, left antenna and right mandible attached, plus two first pereonites, dorsal view; B, detail of flagellum (fourth endopodal segment) of left antenna, dorsal; C, right antennule with full complement of integumental ornamentation, lateral; D, detail of distal part of third peduncular segment of antennule, lateral. Scale bars: 0.25 mm (A–C); 0.125 mm (D).

with three setae and several short, apparently tubular elements (Fig. 2D). Accessory flagellum located dorsomedially on distal margin of third peduncular segment, indistinctly five-articulate. Primary flagellum shorter than accessory flagellum, located ventrolaterally on distal margin of third peduncular segment, bearing two subapical aesthetascs and four unequal, apical setae.

Antenna (Figs 2A, B, 5A) with protopodal segments characterized by presence of intrinsic musculature (Fig. 8B): segment 1 (coxa) with short intrinsic muscle inserting on proximal rim of segment 2 (basis), long second muscle originating in coxa passing through basis and inserting on proximal rim of first endopodal segment; long intrinsic muscle originating in basis and inserting on rim of first endopodal segment, short intrinsic muscle originating midway along basis inserting on proximal rim of exopodal scale. First to third endopodal segments each with pair of opposing intrinsic muscles inserting on rim of adjacent distal segment. Fourth endopodal segment annulated, forming flagellum; six component articles not defined by intrinsic musculature. Coxa short, unarmed; basis almost three times longer than maximum width, with

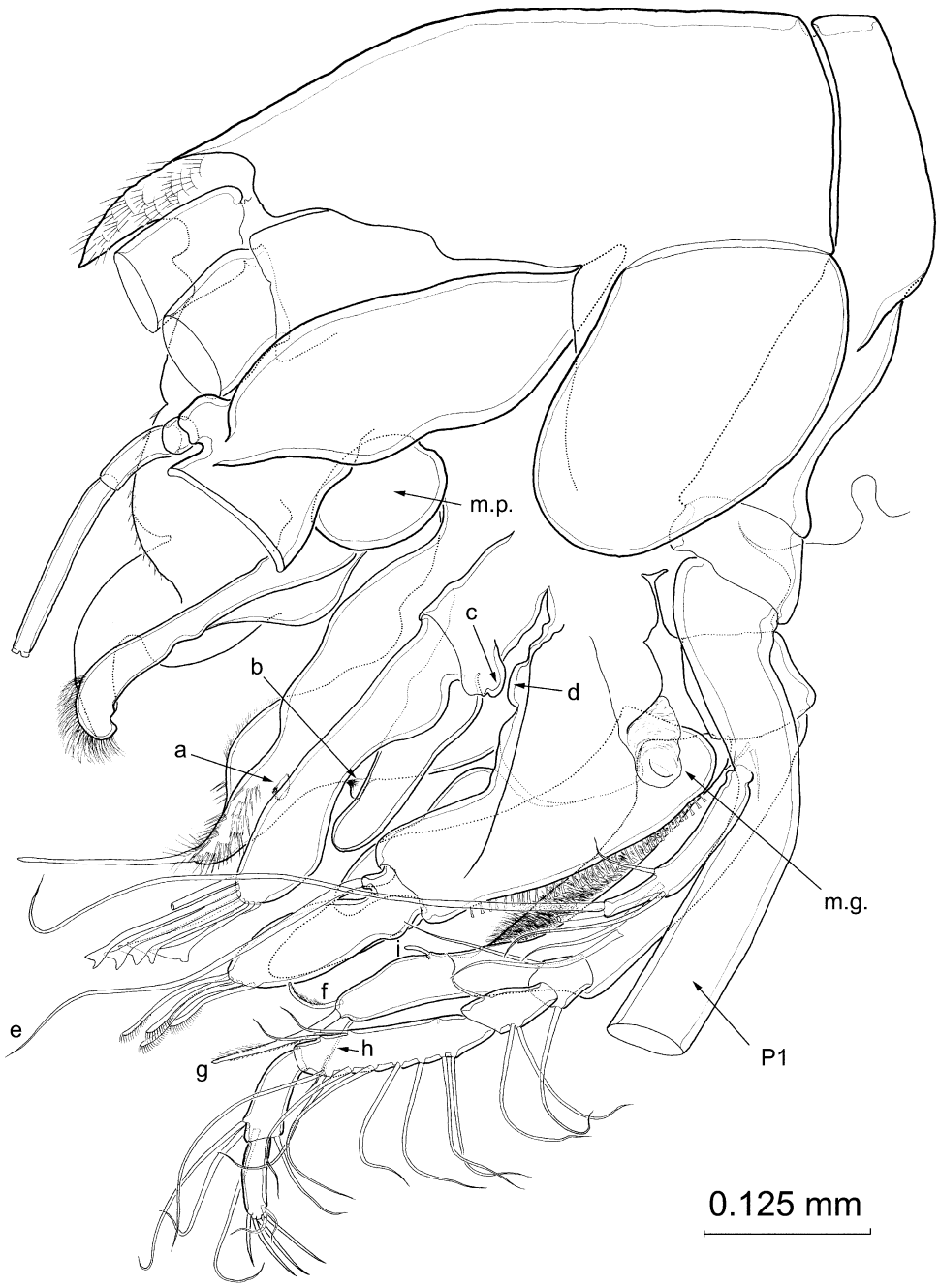

Figure 3. ***Montucaris distincta*** **gen. et sp. nov.**, brooding female. Cephalothorax and first pereonite with appendages in place, lateral. Note the distal portions of both the mandible and the endopod of the first pereopod (P1) are omitted. a, b: processes on posterior surface of paragnath as also labelled in Fig. 14A; c: process on posterolateral surface of maxillule as labelled in Fig. 10E; d: process on anterolateral surface of pedestal of maxilla as labelled in Fig. 11A; e: maxillary endopodal seta, as in Fig. 11A, B; f–i: armature elements of basal endite of maxilliped as also labelled in Fig. 12; m.p.: molar process of mandible; m.g.: opening of maxillary gland.

oblique distal surface bearing rami, unarmed. Antennal scale cylindrical, with array of ten setae along inner and distal margins. First endopodal segment short, articulating with second segment at oblique joint; segments 3 and 4 elongate.

Labrum large, trapezoidal in posterior aspect, with distal margin produced into evenly rounded lappet folded backwards (Figs 3, 9A). Anterior surface with rows of thick spinules; surface with transverse constriction about midway (Fig. 3). Posterior surface

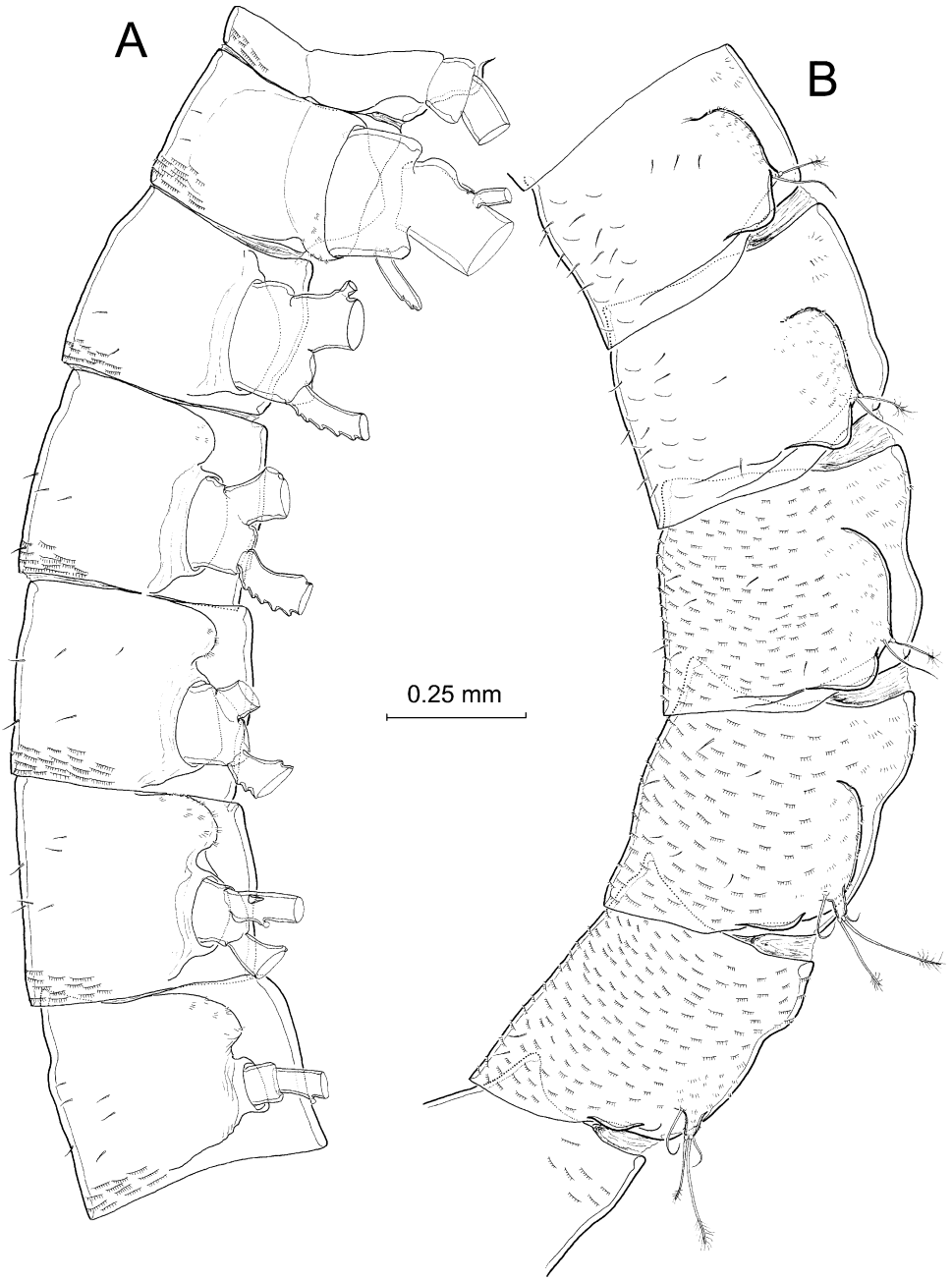

Figure 4. ***Montucaris distincta*** **gen. et sp. nov.**, brooding female. A, lateral view of pereonites; B, lateral view of pleonites 1–5.

globose, but becoming deeply concave subdistally. Ornamented with short setules on margins and dense array of setules on posterior surface (Fig. 7E).

Labium (Figs 3, 14A, B) formed by paired paragnaths; each paragnath lobate, tapering abruptly to elongate, terminal process ornamented with scattered hair-like setules with expanded tip basally, process naked distally; inner surface irregular, forming small bilobed process at inner distal angle densely ornamented with fine hair-like setules; bilobed process with striated sclerotized plate along inner margin (Fig. 14B: *c*); row of three spines present on distal margin adjacent to process, innermost spine simple, curved with blunt tip, middle and outer spines with angled tips and with denticles along oblique inner distal margin. Surface of paragnath lobe ornamented with numerous rows of slender spinules, becoming stouter closer to margin. Posterior surface of lobe

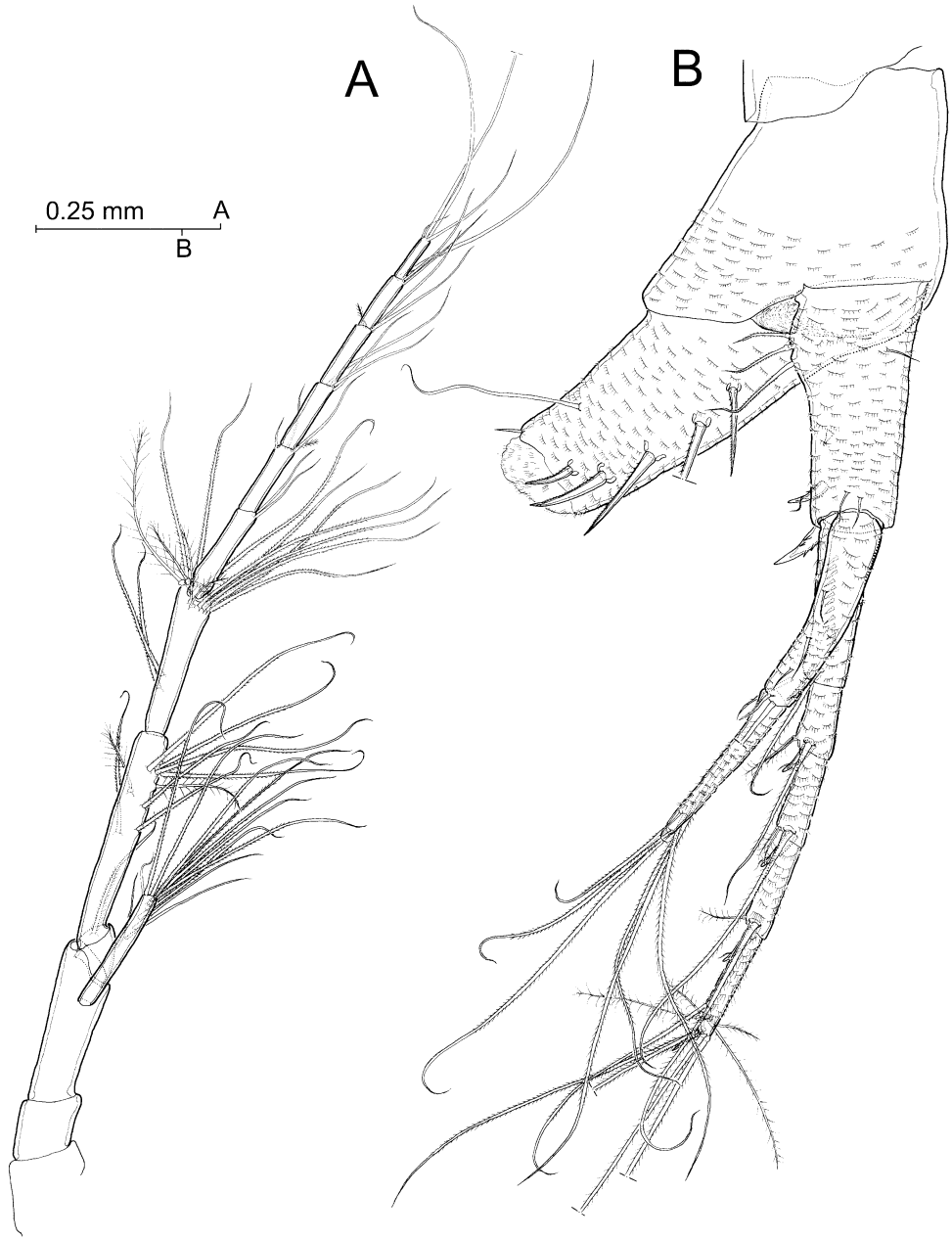

Figure 5. ***Montucaris distincta*** **gen. et sp. nov.**, brooding female. A, right antenna, lateral; B, pleotelson and right uropod, lateral.

with two small processes (labelled *a* and *b* in Figs 3, 14A).

Mandibles (Fig. 9B–F) comprising coxa with well-developed gnathobase and three-segmented palp. Coxal gnathobase with flattened and concave distal portion (see cutaway section in Fig. 3), with widely separated incisor and molar processes; ventral surface of gnathobase irregular in outline with numerous small spinous projections; with scattered spinule rows ventrally and fine hair-like setules dorsally near bases of elements composing setal row between incisor and molar. Right mandible (Fig. 9D) incisor orientated at about right angle to remaining edge of mandible, with three larger and three smaller cusps (Fig. 9E), separated by concave gap from rounded expansion on dorsal margin of gnathobase, armed with row of about 31 spines; distalmost spine short, bifid and blade-like, next three spines also bifid and blade-like, but more slender and with pectinate tips (Fig. 9F); remaining spines simple, becoming progressively more slender,

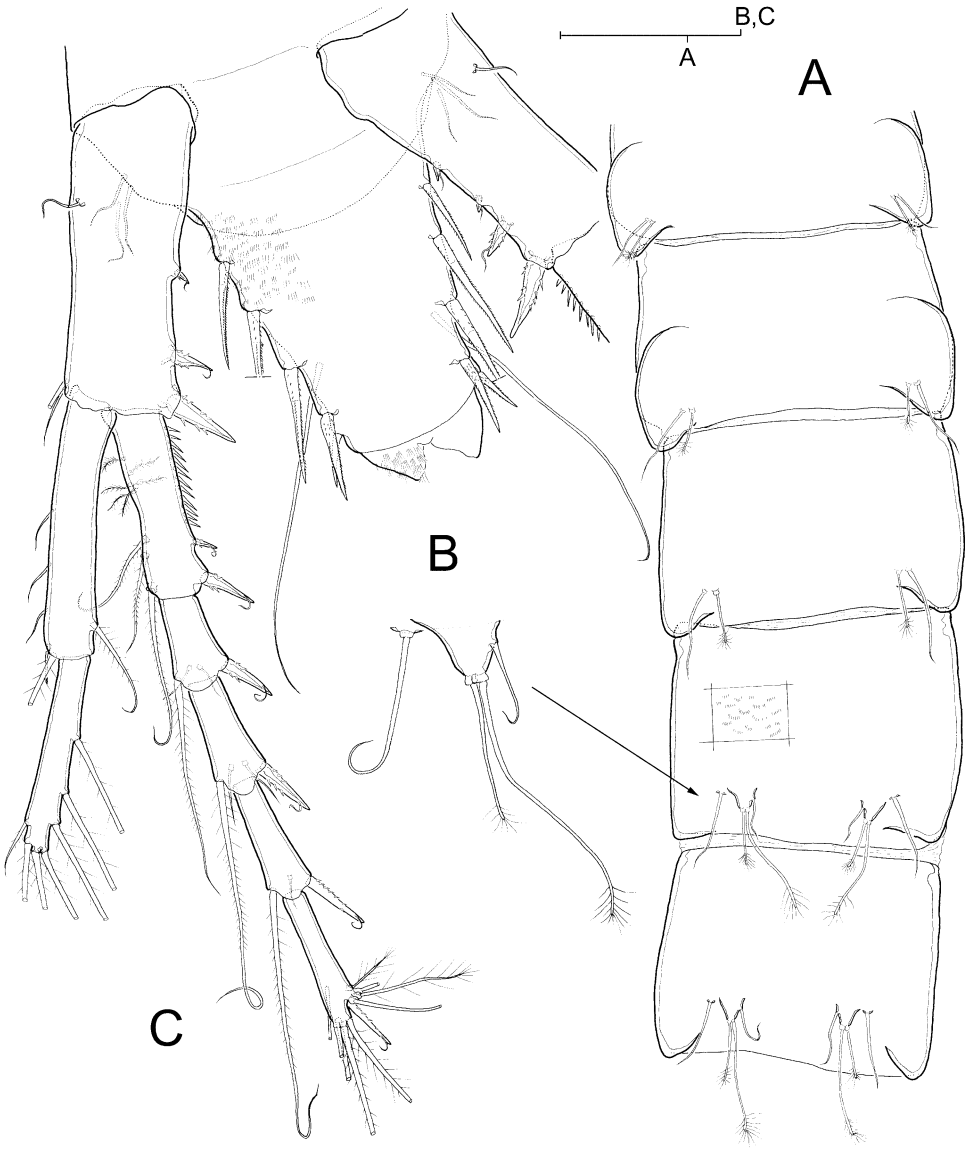

Figure 6. ***Montucaris distincta*** **gen. et sp. nov.**, brooding female, integumentary ornamentation of somites and segments omitted. A, pleonites 1–5 with corresponding pleopods attached, ventral; B, detail of right fourth pleopod; C, Right uropod and telson, ventral. Scale bars: 0.25 mm (A, C); 0.125 mm (B).

longer and setiform; 5–6 spines at proximal end of row becoming progressively shorter. Molar process columnar, directed medio-ventrally (see Fig. 3: *m.p.*), with grinding surface sclerotized and smooth; series of faintly striated, imbricating scales distributed along proximal margin of grinding surface, descreasing in size towards proximo-dorsal angle. Left mandible with four-cusped incisor inserted at about right angle to remaining edge of mandible (Fig. 9C); lacinia mobilis five-cusped, with appearance similar to incisor and orientated parallel to it; three spines placed adjacent to lacinia, most proximal bifid and hirsute, remaining two spines simple, hirsute, blade-like. Dorsal margin of gnathobase with swelling bearing spine row, separated by distinct gap from distal cluster of three spines terminating in lacinia mobilis; this proximal row comprising 18 setiform spines, more distal spine with strongly defined basal swelling, swelling less well defined in innermost spines. Mandibular palp three-segmented; first segment short, unarmed; middle segment unarmed; distal segment slightly bowed, with three apical setae; palp inserted on clearly defined dorsolateral pedestal on gnathobase (see Figs 3, 9D); relative lengths of segments: 0.13 : 0.40 : 0.47.

Maxillule (Fig. 10E) lacking palp, comprising two segments, coxa and basis, each produced into well-

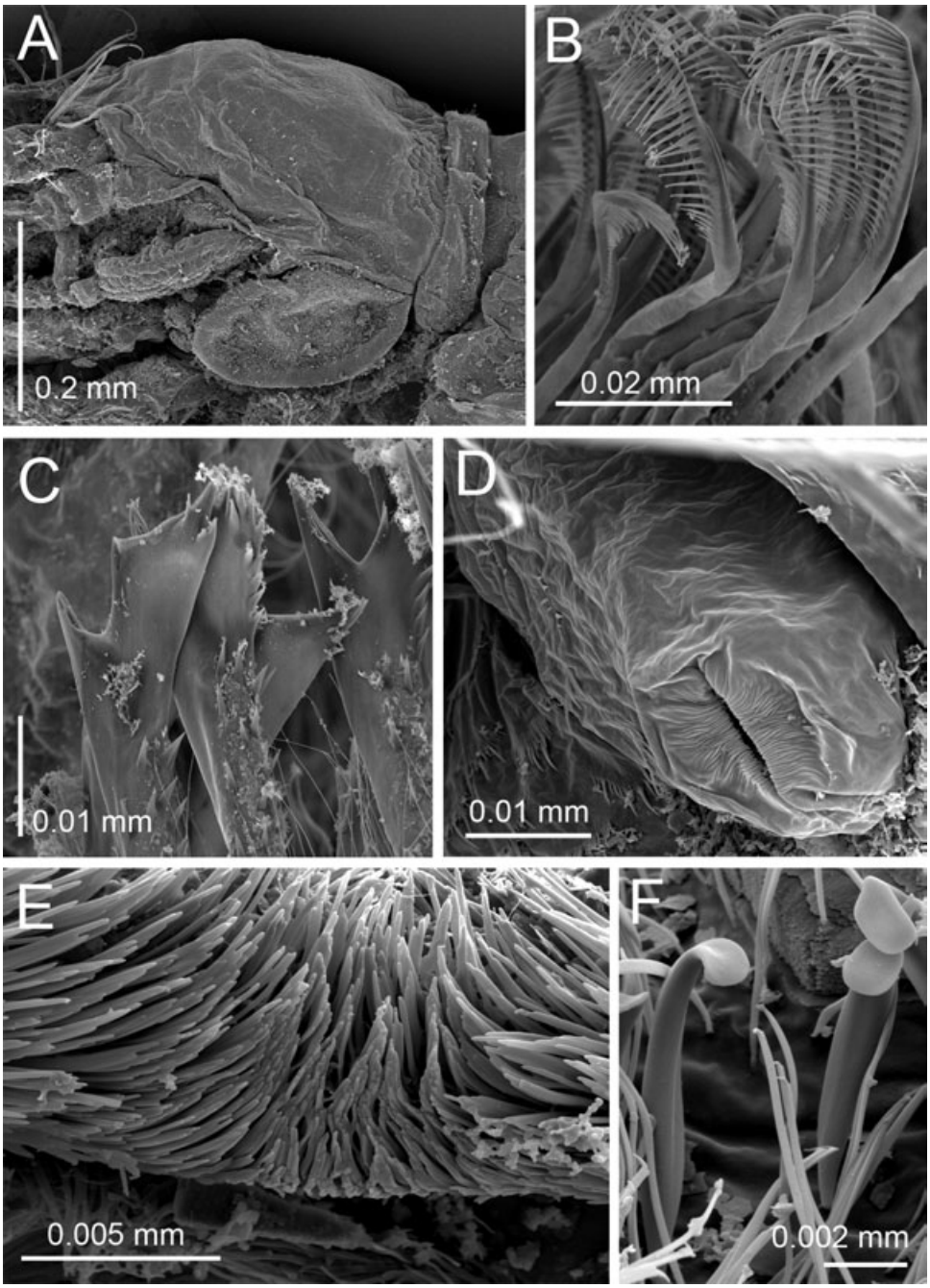

Figure 7. ***Montucaris distincta*** **gen. et sp. nov.**, brooding female, scanning electron micrographs. A, lateral view of cephalothorax showing lateral lappet on dorsal shield and its separation from shield by proximal suture; B, rake-like setae on distal endite of maxillary basis; C, tips of setae on posterolateral lobe of endite on basis of maxillule; D, opening of maxillary gland; E, setular ornamentation on frontal surface of labrum; F, spatulate spinules on posteromedial surface of maxilla.

developed endite; surfaces of both segments ornamented with crescentic rows of setules. Coxa with distinct, unarmed lobe distally on postero-lateral surface, near articulation with basis (cf. Fig. 10E: *c* and Fig. 3: *c*); coxal endite (= inner lobe) with distal armature of five setae: dorsal two setae bipinnate in distal half, middle seta smooth with multicuspid tip, next seta ornamented with single row of denticles on one side and pinnate on other, ventral seta pappose. Surface of endite ornamented with stout spinules

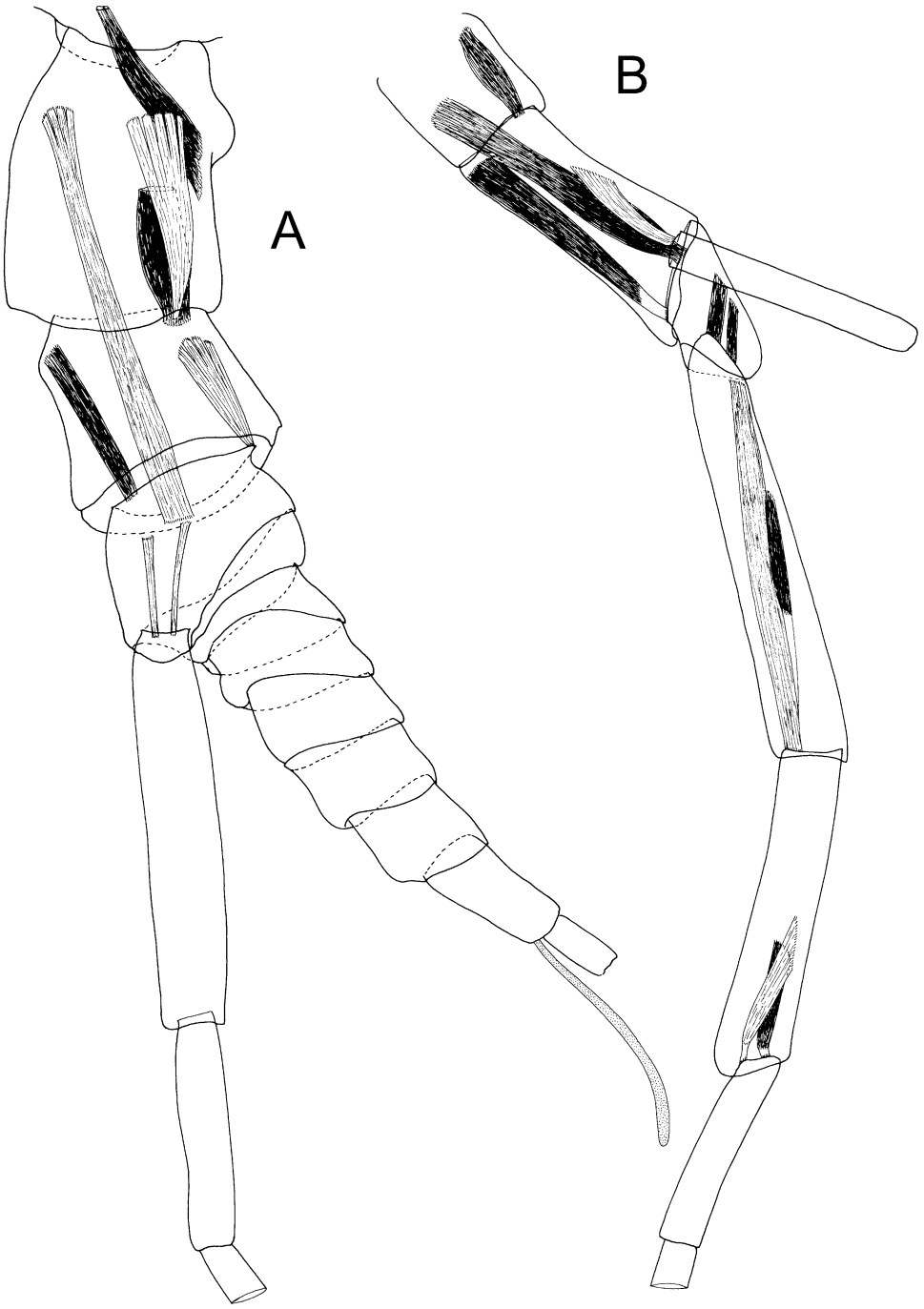

Figure 8. ***Montucaris distincta*** **gen. et sp. nov.** A, male morph-II antennule showing segmentation pattern and intrinsic musculature; B, brooding female antenna showing intrinsic musculature within peduncular segments and distal flagellar section of endopod lacking intrinsic muscles.

dorsally, and with fine hair-like setules around ventral convex margin. Basal endite (= outer lobe) slightly bilobed at tip, each lobe armed with distinctive setal elements; plus two isolated pappose setae located subdistally on posterior surface (Fig. 10F). Posterolateral lobe bearing complete linear array of 17 setae, becoming progressively shorter from outer to inner end of row, structure and ornamentation of expanded bifid tips of setae also changing gradually along row as in Figures 10E and 7C. Anteromedial lobe armed with 12 setae arranged in double row (Fig. 10G); setae typically stout, blade-like, armed

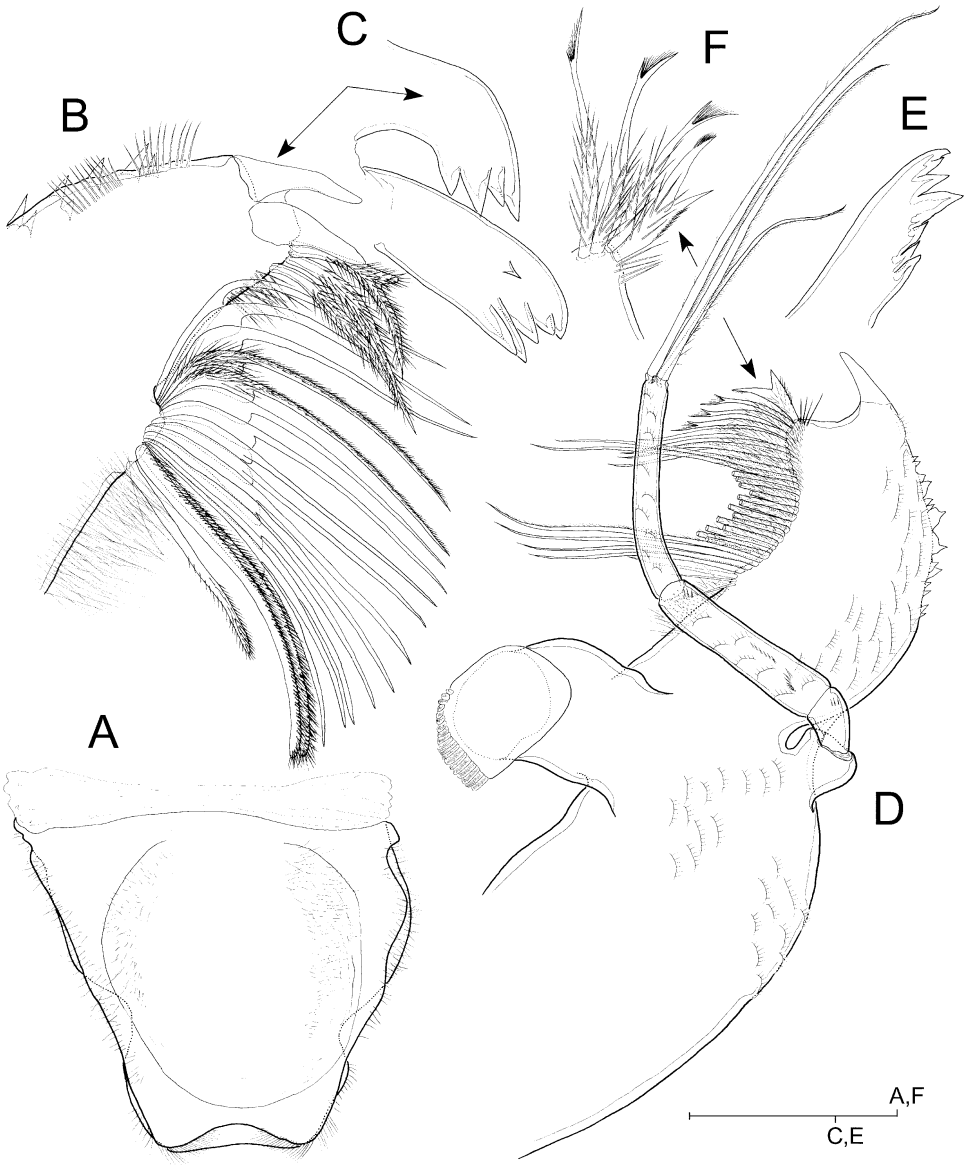

Figure 9. ***Montucaris distincta*** **gen. et sp. nov.**, brooding female. A, labrum, posterior; B, left mandible, medial; C, detail of incisor and lacinia; D, right mandible, medial; E, detail of incisor of latter; F, detail of four distalmost elements of spine row. Scale bars: 0.125 mm (A, D); 0.05 mm (B, F); C and E not to scale.

with row of short spinules, one seta longer and with bifid tip.

Maxilla (Fig. 11A, B) two-segmented; proximal segment representing coxa with inner margin produced distally into indistinctly bipartite endite; distal segment produced into two distally directed lobes, and bearing small, non-articulated process with long, apical pappose seta, tentatively interpreted here as representing vestigial endopod (cf. Fig. 11A, B: *e* and Fig. 3: *e*). Structure located proximal to limb interpreted as pedestal with posterolateral conical process carrying opening of maxillary gland (cf. Fig. 11A: *m.g.*, Fig. 3: *m.g.* and Fig. 7D), and with anterolateral process (Fig. 11A: *d*) positioned opposing posterolateral lobe on coxa of maxillule (see Fig. 3: *c* and *d*). Coxal medial margin elongate, with double row of marginal setae; 12 setae composing posterior row slightly shorter than setae of anterior row, pappose proximally with strong pinnules all around but becoming bipinnate distally; tips of setae stout and denticulate, as in Fig. 11G; 13 setae composing anterior row slender, ornamented unilaterally with short spinules distally. Coxal endite indistinctly bipartite, divided into proximal and distal parts defined by change in setation.

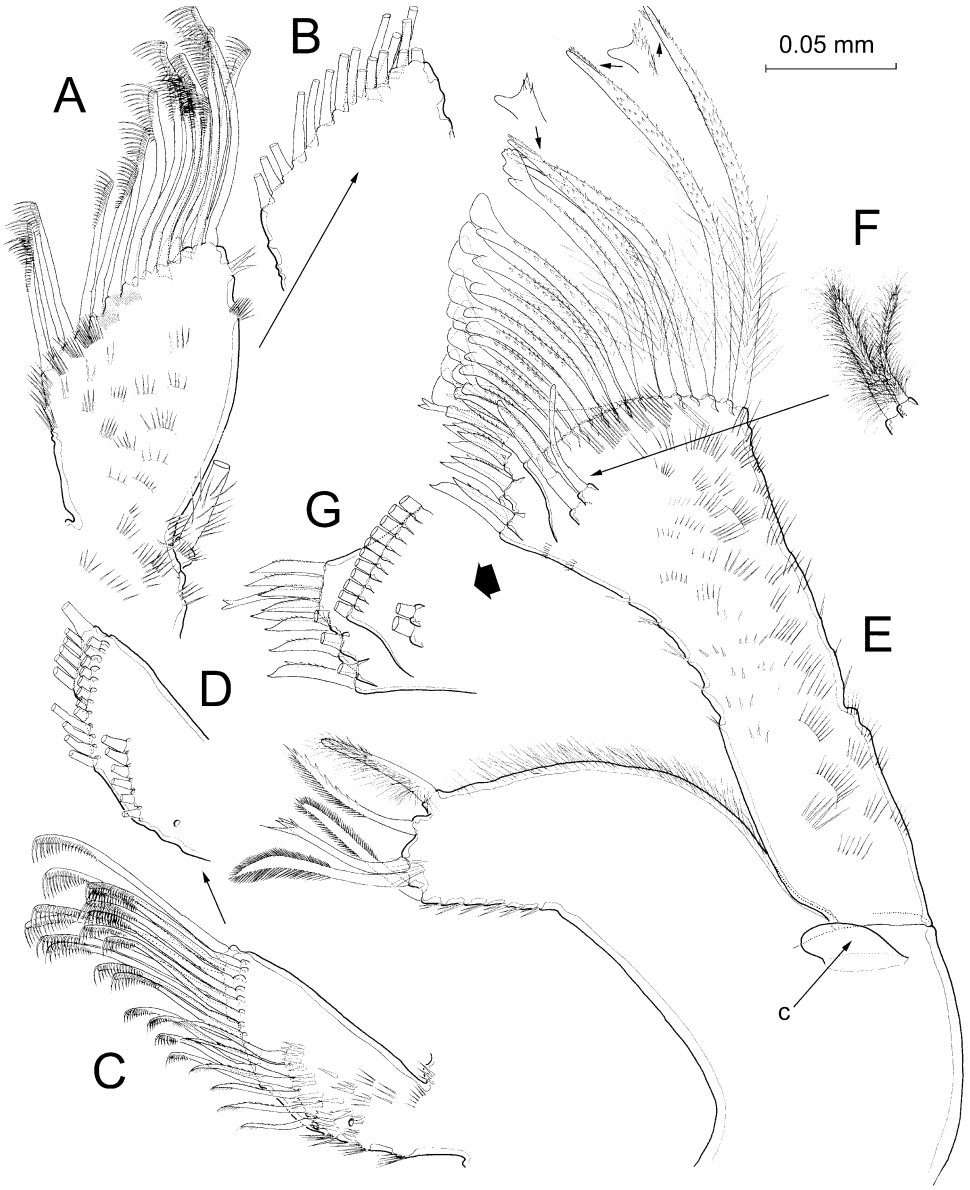

Figure 10. ***Montucaris distincta*** **gen. et sp. nov.**, brooding female. A, detail of distal basal endite and tentative endopod of maxilla; B, inset showing distribution of marginal setae on endite; C, detail of proximal basal endite of maxilla; D, inset showing distribution of setae on latter. E, left maxillule, posterior (c: same process as in Fig. 3); F, detail of two short pappose setae on posterior surface of basal endite (= outer lobe); G, detail of armature of anteromedial lobe.

Distal part displaying row of ten marginal setae becoming progressively shorter from distal to proximal end of row; proximal two of these setae pappose with tuft of hair-like setules proximally and unilaterally denticulate distally (Fig. 11D), rest unilaterally ornamented with distal brush of hair-like setules and proximal row of denticles; proximal three of these brush-like setae with subapical sensilla, giving tip bifid appearance (Fig. 11F); two additional setae implanted subdistally close to each other on posterior surface of distal part of coxal endite (Fig. 11C), proximal seta pappose with unilateral tuft of setules proximally, distal seta with series of transverse lamellar structures proximally. Proximal part of coxal endite with six unequal setae (Fig. 11B, D) heterogeneously ornamented, as follows from proximal to distal end of row: one uniformly bipinnate, next thick and pappose, next slender and smooth with tricuspidate tip, next with distal brush and subapical sensilla (Fig. 11E), next stout and smooth, and finally next similar to preceding seta but with bicuspid tip (see Fig. 11B). Two pappose setae with smooth distal portion positioned

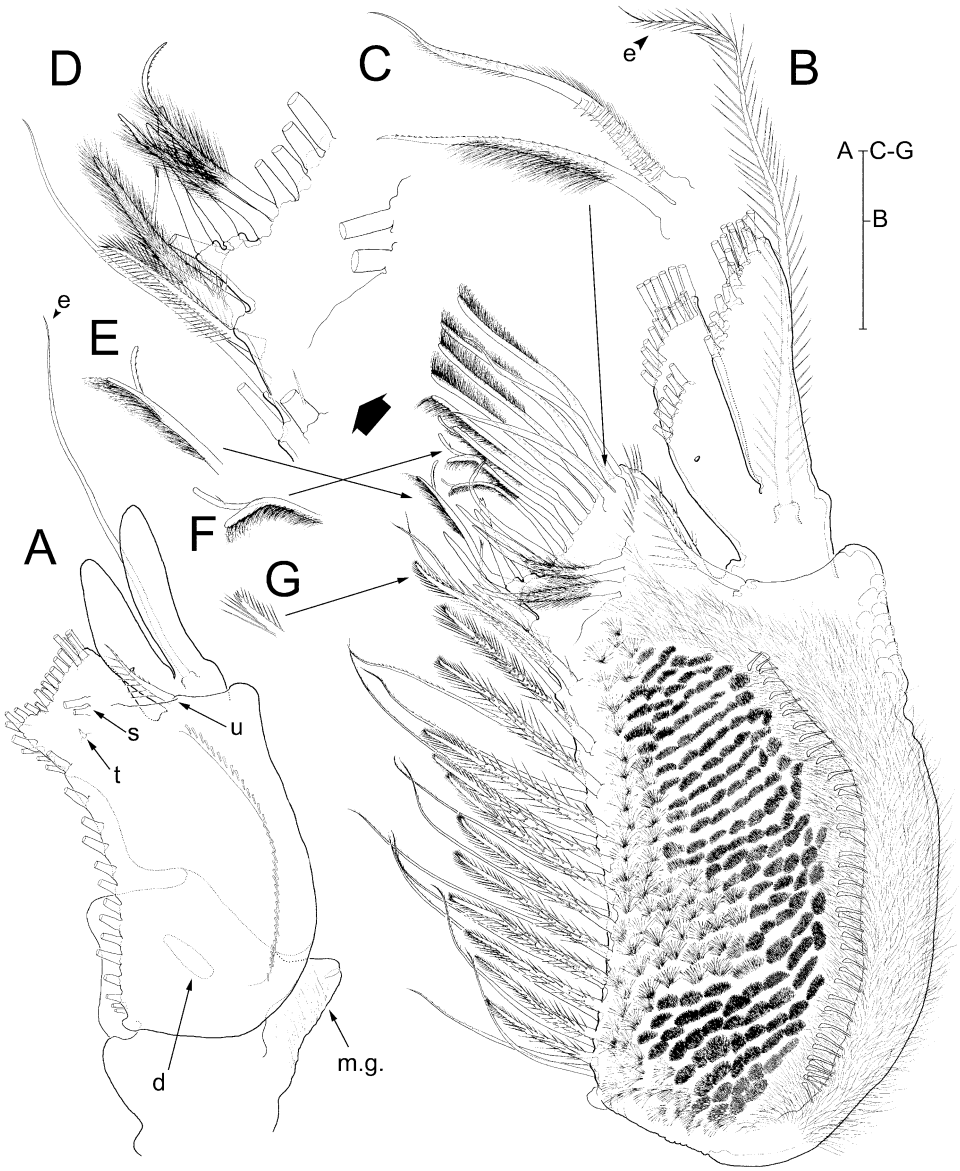

Figure 11. ***Montucaris distincta*** **gen. et sp. nov.**, brooding female. A, sketch of left maxilla, posterior (note pedestal with conical process carrying opening of maxillary gland (m.g.) and anterolateral process (d) disposed proximally to limb; e: seta interpreted as armature of vestigial endopod; s: pair of pappose setae on posterior surface of coxal endite; t: thorn-like seta on anterior surface of coxal endite; u: stout spinulate seta adjacent to coxa–basis joint; B, detail of maxilla displaying full ornamentation of basis (e: same as in preceding figure); C, detail of two subdistal setae on posterior surface of indistinct distal lobe of coxal endite; D, inset showing insertion of setae on distal angle of indistinct proximal lobe of coxal endite; E–G, detail of different types of setae on coxal endite. Scale bars: 0.125 mm (A); 0.05 mm (B–G).

proximally on integumental fold on posterior surface of coxal endite (Fig. 11A: *s*), plus tiny thorn-like seta proximally on anterior surface (Fig. 11A: *t*). Posterior surface of coxa with stout isolated spinulate seta situated adjacent to coxa–basis joint (Fig. 11A: *u*); spinules along one side of seta longer than counterparts on other side. Entire posteromedial surface of coxa densely ornamented with tufts of short spinules, tufts located closer to anteromedial margin with spinules somewhat longer and finer; tufts area delimited laterally by single row of spatulate spinular elements (Figs 7F, 11A, B).

Proximal endite of maxillary basis (Figs 10C, D, 11B) about three times longer than wide, with oblique distal margin armed with three parallel rows of setae; most proximal row, located subdistally on posterior surface, consisting of six setae, each unilaterally pectinate distally and with row of denticles proximally on

other side; apical surface of lobe occupied by distal row of six and adjacent subdistal row of 12 similar, unilaterally pectinate in distal part, rake-like blunt setae. Surface of endite ornamented with irregular, short rows of spinules, as in Figure 10C; wide pore visible proximally on posterior surface of endite. Distal endite (Figs 7B, 10A, B, 11B) with oblique distal margin armed with row of 13 rake-like, blunt setae plus additional row of four similar setae near outer apical angle of lobe. Lobe with short rows of spinules irregularly scattered over surface as figured.

Maxilliped (Fig. 12) uniramous, comprising short coxa, elongate basis produced into distal enditic lobe and five-segmented endopod; exopod absent. Coxa short, ornamented with fine hair-like setules laterally and with irregular spinule rows medially. Basis elongate, with complex setal armature and ornamentation. Lateral margin of basis with two short setae close to coxa–basis articulation, longer seta also positioned proximally and long pappose seta with bluntly rounded tip located just proximal to origin of endopod. Medial margin of basis mostly unarmed except for

Figure 12. ***Montucaris distincta*** **gen. et sp. nov.**, brooding female. A, right maxilliped, antero-medial view (f–i identify same armature elements as in Fig. 3); B, detail of endopod, anterior.

short, blunt proximal seta. Linear array of 18 setae with increasingly modified and elaborate ornamentation towards distal end of row placed postero-medially on segment; more distal setae ornamented with lamellar hyaline elements; seta 17 with slightly expanded distal section bearing serrate flange; all setae except 18 with tiny sensilla subdistally. Surface of basis with tufts of long spinules located marginally near setal row, and longer setules providing dense covering anteriorly.

Maxillipedal basal endite with isolated plumose seta proximally and three rows of setae along oblique distal margin; anteriormost row comprising nine pappose setae with bluntly rounded tips (cf. Fig. 12A: *f* and Fig. 3: *f*); middle row with most proximal element pappose on along one side only, then six long, robust setae, each ornamented with two rows of denticles in middle to distal region and single row of setules in distal third (cf. Fig. 12A: *g* and Fig. 3: *g*), distalmost five of these six setae each with apical pore; posterior row comprising three bipinnate setae (cf. Fig. 12A: *h* and Fig. 3: *h*). Short, modified seta with bluntly, rounded tip with tiny spinules placed midway of lateral margin of endite (cf. Fig. 12A: *i* and Fig. 3: *i*). Surface of endite with scattered spinules and spinule rows, and with patches of integumental scales proximally.

Maxillipedal endopod (Figs 3, 12B) implanted posterolaterally to basal endite, five-segmented; all segments ornamented with spinule rows. Segmental setation formula: 2, 3, 10–11, 4–5, 5–6; either three or four apical setae modified as claw-like elements; setae ornamented as figured.

Pereopods of typical peracarid type (cf. Hessler, 1982), i.e. all displaying monocondylic articulation between coxa–basis, and dicondylic articulation between rest of podomeres; hinge line of articulations perpendicular to limb plane except that between merus–carpus, which is parallel to it. Junction between body and coxa ovoid, with long axis orientated more or less parallel to main body axis (Fig. 4A); hinge points of articulation between coxa and body not observed, but: (i) (limited) abduction/adduction possible at this plane (demonstrated by manipulation with probe) suggesting hinge line runs about parallel to main axis of junction between coxa and body in pereopods 2–7; whereas (ii) limited promotion-remotion at this level in pereopod 1 suggests hinge line running about perpendicular to main axis of body. Invaginated condyle of coxa–basis articulation projecting inward posterolaterally from distal end of coxa in pereopods 6–7 (see Fig. 18C), and turning progressively more lateral from pereopod 5 to 1. Coxa–basis joint defined by insertion of one intrinsic and six extrinsic muscles (Fig. 13A) around proximal rim of basis; one anteriorly located extrinsic muscle inserting at coxa–body joint.

Pereopods (P1 to P7) biramous except P7, each with short annular coxa well delimited and clearly separate from corresponding sternite; P1 extended forward under mouthparts. Basis of P1 conspicuously bowed at insertion of exopod; rest of bases of pereopods roughly straight. Exopods inserted anterolaterally on proximal part of basis, those of P1 and P2 indistinctly two-segmented, setal formula 1 + 1, 2; exopods of P3 and P4 indistinctly three-segmented, setal formula 1 + 1, 1 + 1, 2; exopods of P5 and P6 vestigial, reduced to single segment with three terminal setae. Oostegites present on P2 to P6, inserted on posteromedial surface of coxa, becoming successively larger from P3 to P6; that of P2 somewhat reduced; oostegites falcate, with numerous long setae along margins; setae pappose proximally, plumose along rest of shaft. Endopods of P1, P2, P6 and P7 each five-segmented, segments corresponding to ischium, merus, carpus, propodus and dactylus, bearing unguis (but note that articulation between basis and ischium of endopod of P6 is not completely expressed; see Fig. 15C; and that articulation between ischium and merus of P2 is not completely expressed in some specimens). Free endopod of P3, P4 and P5 four-segmented due to complete (although vestiges of articulation expressed in P5; see Fig. 17C) failure of separation of ischium from basis as indicated also by musculature signature (see Fig. 13B), with intrinsic muscles actuating ischium–merus joint originating just distal to level of non-expressed basis–ischium joint.

Dactylus of P1 (Fig. 14C, D) with two inner spines with rounded, expanded tip; unguis spatulate. P2 endopod heavily built, with unguis apparently absent (Fig. 15A); three stout barbed spines on distomedial angle of carpus; two parallel rows, each comprising six barbed spines, along distomedial margin of propodus; two shorter barbed spines terminally on dactylus; one short denticulate spine positioned distolaterally on propodus (Fig. 15B). P3 (Figs 13A, B, 16A) with four stout triangular spines on anterior margin of compound basis–ischium, isolated spine on anterodistal margin of merus, and row of up to 12 spines along anterior margin of carpus; one slender barbed spine subdistally on posterior margin of carpus, plus two similar slender barbed spines subdistally on posterior margin of propodus. P4 (Fig. 17A) with one hyaline triangular spine distally on anterior margin of carpus, and six barbed spines on posterior margin of segment (Fig. 17B); propodus with two slender barbed spines on posterior margin (Fig. 17B). P5 (Fig. 17C) with five and one slender barbed spines on posterior margin of carpus and propodus, respectively. Propodus of P6 with six slender barbed spines on posterior margin (Fig. 15C). Endopod of P7 slender, lacking marginal spines; dactylus with stout penicillate seta subterminally on lateral margin, as in P6 (Fig. 15D, E and

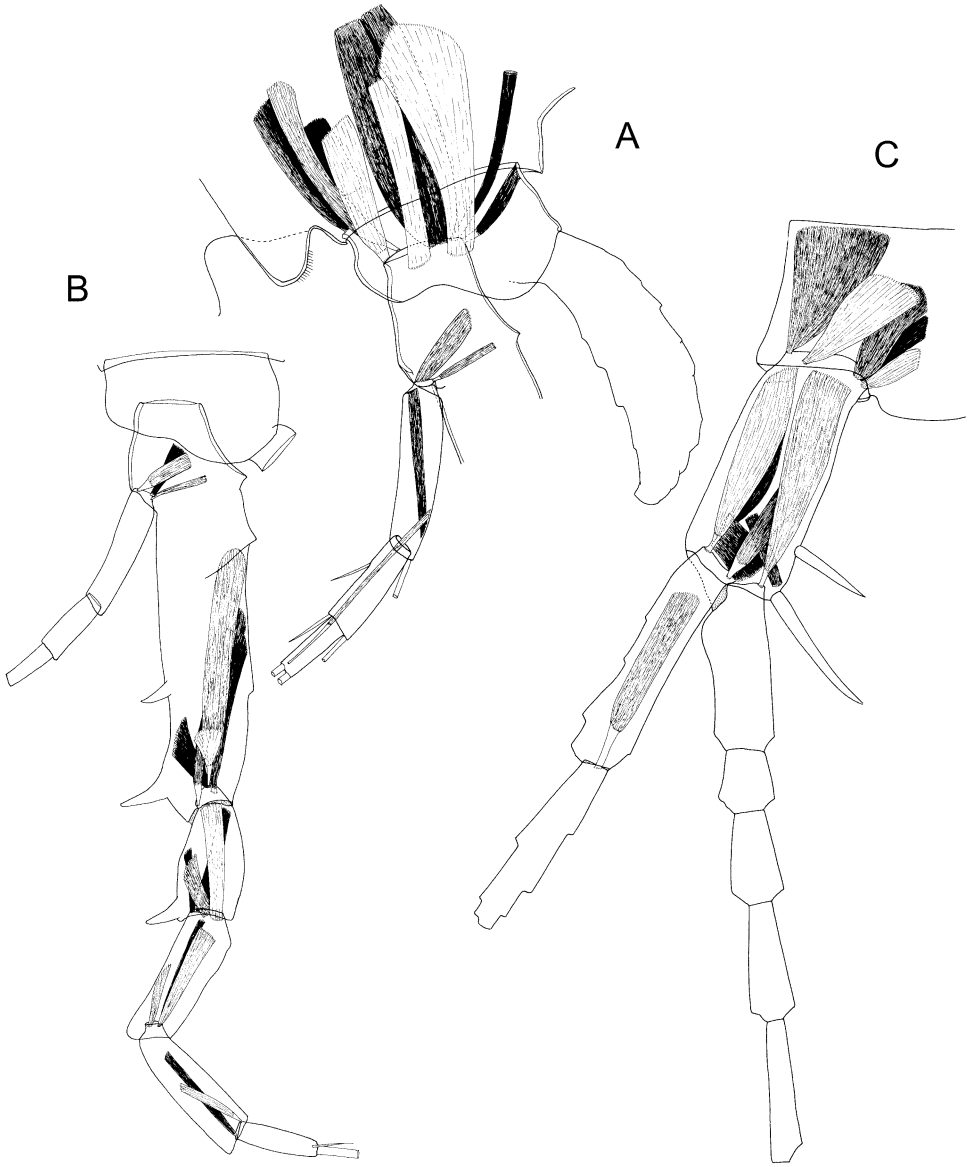

Figure 13. ***Montucaris distincta*** **gen. et sp. nov.**, brooding female. A, proximal articulation of left P3 on body, showing extrinsic muscles inserting in protopodal part of limb and intrinsic musculature of exopod; B, left P3 showing intrinsic muscles affecting movement of the exopod and the intrinsic musculature within the endopod; C, uropod and part of pleotelson corresponding to sixth pleonite showing uropodal musculature.

Fig. 15C, respectively). Unguis of P3–P7 elongate, acicular. Propodus of latter limbs with transverse row of long setae (extending beyond tip of corresponding unguis) distally on anterior margin of segment.

Pleopods reduced. PL1 to PL3 each represented by pair of setae inserted directly onto ventral surface of body (Figs 4B, 6A); outer seta naked, inner seta penicillate. PL4–5 (Figs 4B, 6A, B) each represented by isolated outer seta arising directly from body surface and inner tapering non-articulated process bearing short inner seta and two unequal penicillate setae distally.

Uropod (Figs 5B, 6C) protopod with powerful extrinsic muscles inserting around proximal rim (Fig. 13C); intrinsic muscles mostly inserting on proximal rim of rami; one oblique intrinsic muscle inserting near base of large spine at inner distal angle. Endopod 'segments' lacking any intrinsic musculature, corresponding to superficial annulations in internal structure.

Protopod armed with 3–4 stout spines along inner margin, proximal spine shortest, distal spine longest, proximal and middle spines with subdistal sensilla on tip; spines denticulate with few, sparsely set strong denticles placed proximally; proximal swelling on dor-

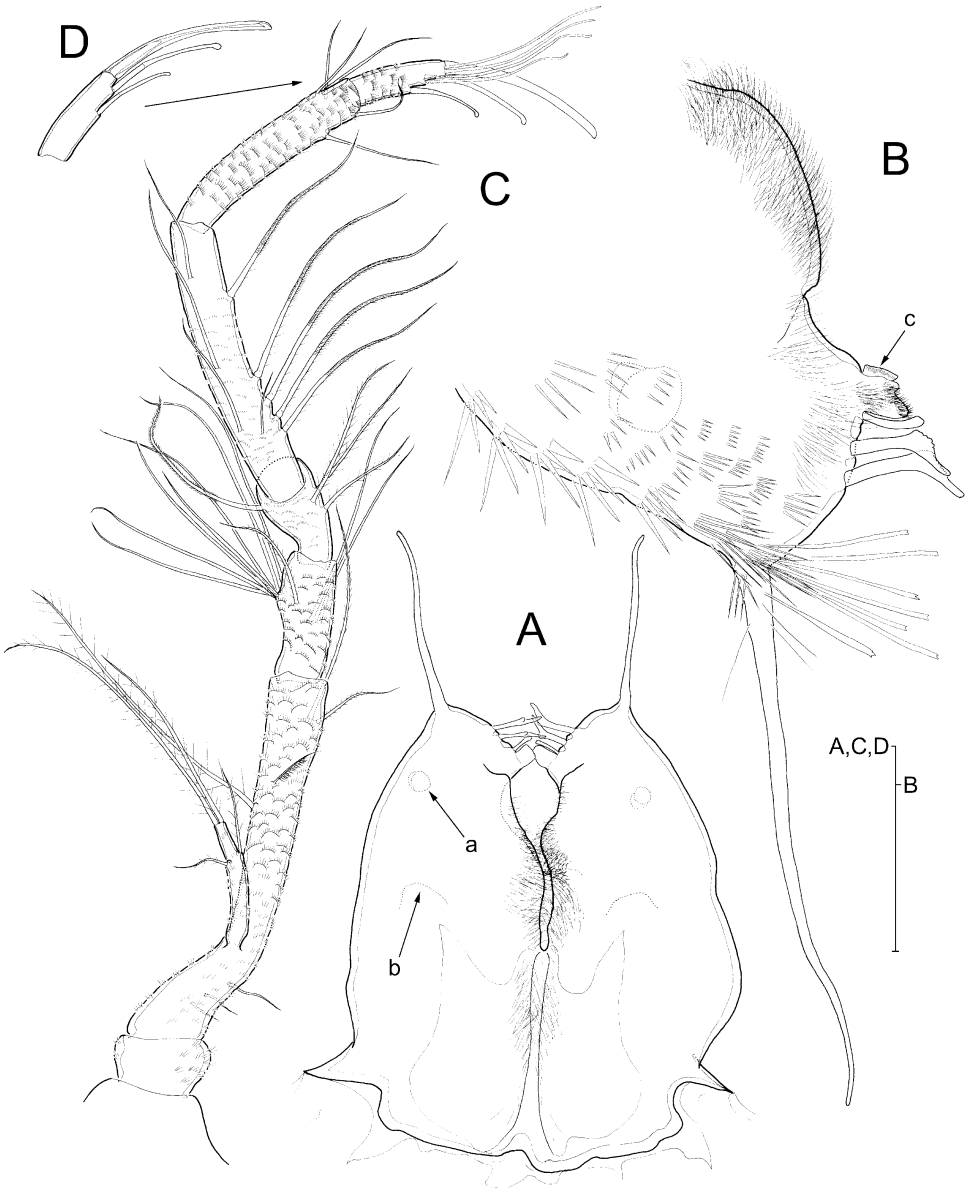

Figure 14. ***Montucaris distincta*** **gen. et sp. nov.**, brooding female. A, paragnaths with most integumental ornamentation omitted, anterior (a, b: processes on posterior surface labelled as in Fig. 3); B, detail of right paragnath, anterior (c: striated sclerotized plate along inner margin of bilobed process); C, right first pereopod, lateral; D, detail of dactylus with setae omitted. Scale bars: 0.25 mm (C, D); 0.125 mm (A); 0.05 mm (B).

sal surface of segment with three setae. Exopodal segment 1 bearing one inner and five outer setae, four proximal setae on outer margin reduced; segment 2 with three long outer setae, two long distal setae, and two unequal setae subdistally on outer margin. Endopodal annuli 1–5 with, respectively, two, one, one, one and one inner spines with subdistal sensilla on tip similar to those on protopod; additional setation comprising nine, three, three, two and setae, respectively, several penicillate; setal ornamentation as figured; first article with row of about 12 strong triangular spinules along inner margin. Surface of limb ornamented with short crescentic spinule rows.

Male morph-I (Figs 1B, 18–21, 22A)

Similar to female (with well-developed mouthparts) except for display of penes and absence of oostegites, smaller body size (Fig. 1B, 3.70 mm vs. 4.60–5.95 mm in brooding females), morphology of rostrum, antennules and pleopods, and some aspects of armature of P3, uropods and telson. Rostrum short, directed downwards (Fig. 18B). Telson (Fig. 18D) displaying only

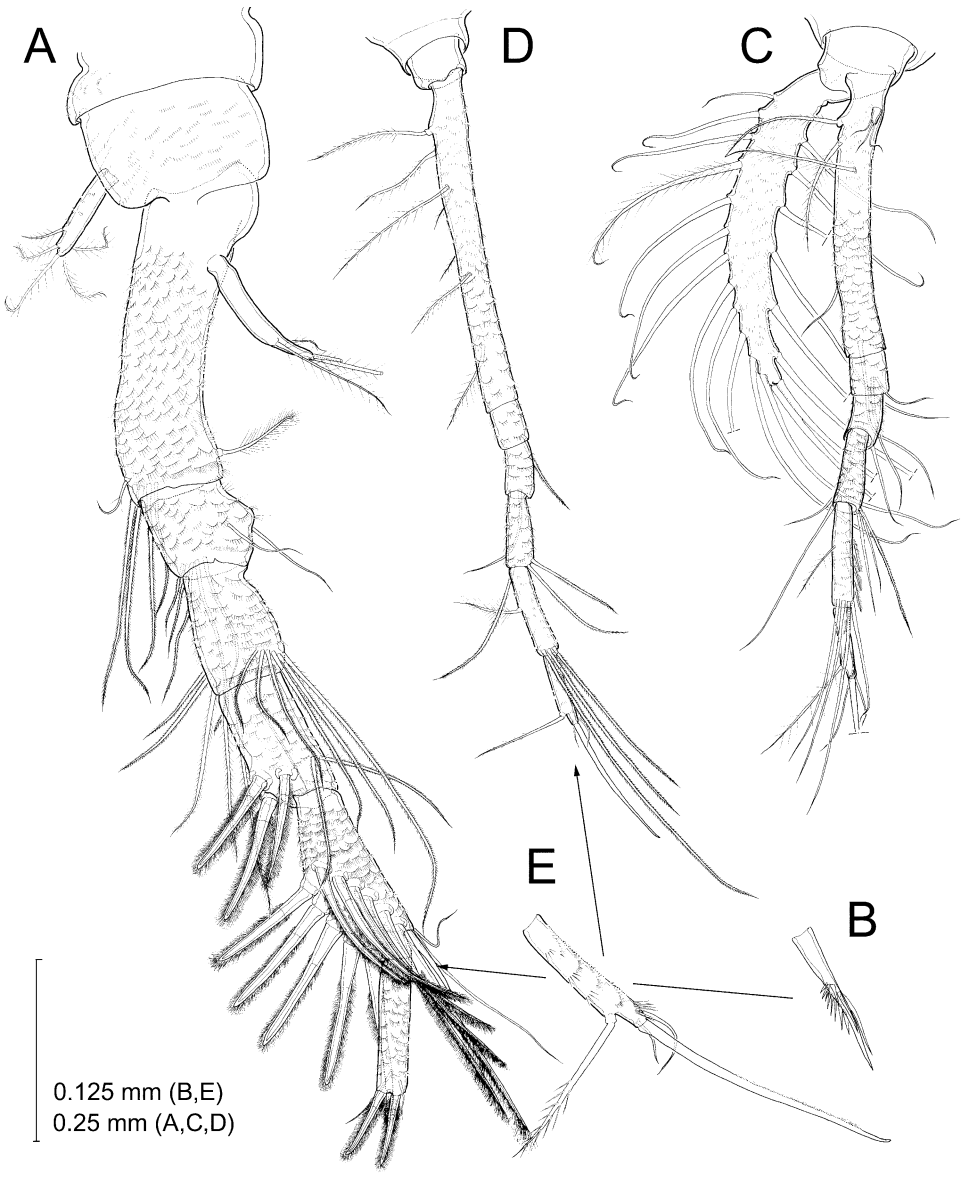

Figure 15. ***Montucaris distincta*** **gen. et sp. nov.**, brooding female. A, right second pereopod, lateral; B, detail of short spine on distolateral angle of propodus; C, right sixth pereopod, lateral (note basis–ischium intersegmental articulation not fully expressed medially); D, right seventh pereopod, lateral; E, detail of dactylus–unguis.

four marginal spinulate spines (five in female), and with dorso-distal stout spinulate spine instead of tiny smooth spine present in homologous position in female (cf. Figs 5B, 18D).

Antennule (Figs 18A, B, 19A) with armature not fully resolved owing to specimen damage. Peduncular segment 3 produced dorsally into setiferous process with at least three penicillate setae (armature of process probably not fully resolved). Primary flagellum inserted ventrolaterally on distal margin of third peduncular segment, comprising seven flagellar articles; articles wider than long except distal two; armature of articles missing except isolated aesthetasc on distomedial angle of articles 5–6, and five unequal setae on tip of distal article; nevertheless flagellum packed full of conspicuous nerves, dividing off from dense central nerve bundle at base of antennule and with longitudinal fibres inserting at distomedial angle of each article, possibly innervating clusters of aesthetascs lost during sampling and/or sorting (see condition in proximal article of main flagellum in male morph-II; Fig. 23B, C). Accessory flagellum originating dorsomedially on distal margin of third peduncular segment, comprising six articles; articles becoming

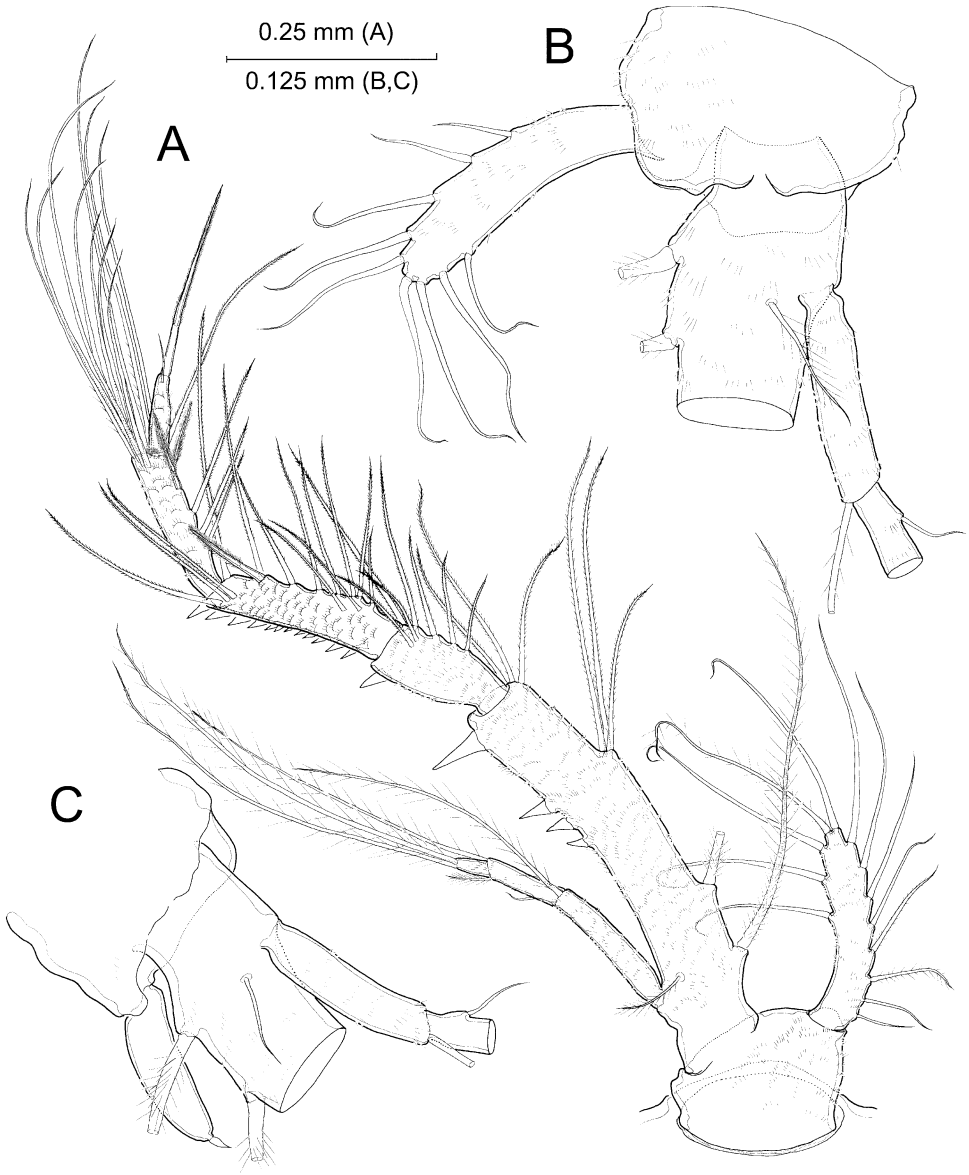

Figure 16. ***Montucaris distincta*** **gen. et sp. nov.** A, right third pereopod of brooding female 5.30 mm long (number and arrangement of triangular spines on basis and endopod as in juvenile male); B, detail of proximal part of same pereopod for preparatory female 4.45 mm long; C, same for preparatory female 3.81 mm long. Note variation in development of oostegite with body size.

successively shorter towards tip, proximal article elongate, with distal margin reaching that of article 4 of main flagellum.

Third pereopod with triangular spines on anterior margin of basis–ischium differing from female by transformation of most proximal spine into two more slender elements (cf. Figs 16A and 22A). Penes tubular, smooth, located on sternite of eighth thoracomere close to seventh pereopods (Figs 1B, 18C).

Pleopods well developed on all pleonites, natatory (Fig. 1B). Protopods with distinct lateral cuticular outgrowth proximally, subcylindrical, somewhat depressed antero-posteriorly, becoming successively shorter from first to fifth pleopod; short smooth lateral seta at one-third of distance along margin, plus seta submarginally at two-thirds of distance along medial margin; patch of stout spinules between insertion of latter seta and distomedial angle of segment. PL1 (Fig. 20A) and PL3 (Fig. 21A) similar, with partially annulated, apparently multisegmented rami, although muscle signature suggests one-segmented condition; hardly developed digitiform lobe crowned

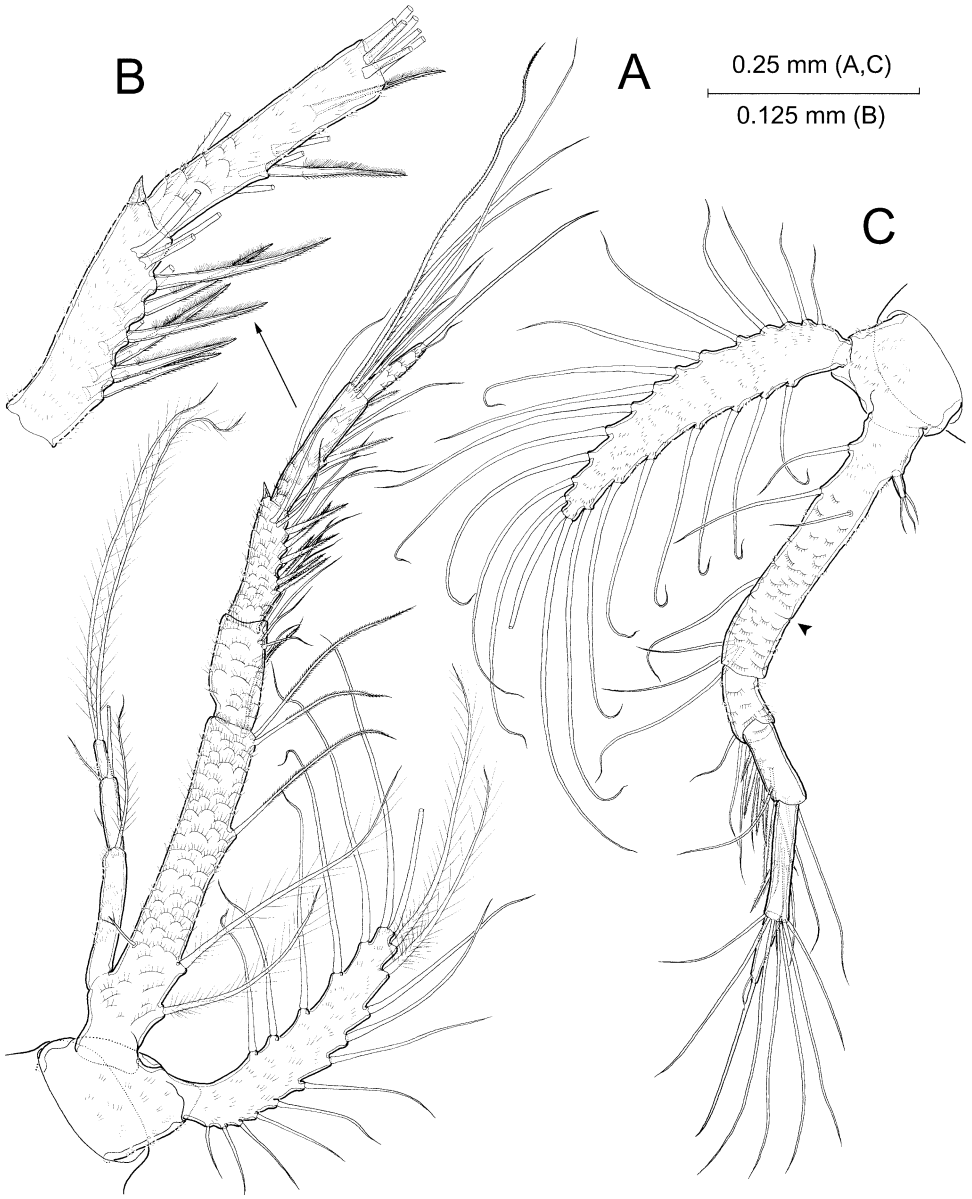

Figure 17. ***Montucaris distincta*** **gen. et sp. nov.**, brooding female. A, right fourth pereopod, lateral; B, inset of carpus–propodus; C, right fifth pereopod, lateral (arrowhead indicates vestige of basis–ischium intersegmental articulation, partially expressed laterally).

with one penicillate seta on postero-lateral margin of endopods; arrangement of setae on rami as figured. PL4 (Fig. 21B) and PL5 (Fig. 21C) with rami similar to PL1 and PL3 except digitiform lobe of endopod now powerfully developed and crowned with two penicillate setae instead of one. PL2 (Fig. 20B, C) with both rami modified: exopod apparently two-segmented and shorter than endopod, proximal segment naked, distal segment elongate with three distal setae, innermost long and plumose, other two short and smooth; additional short seta subdistally on lateral margin of segment; endopod one-segmented, with four plumose setae distally; proximal portion of segment slightly expanded, with hardly developed digitiform process crowned with penicillate seta on posterolateral surface; anterior surface of segment with rounded outgrowth at about two-thirds of distance of segment; tiny rounded process placed on same surface just above outgrowth (see Fig. 20C).

Uropod (Fig. 19B) differing from female as follows: (i) annulations on endopod not expressed dorsally and intersegmental articulation on exopod incompletely expressed medially (articulation fully expressed in female); (ii) middle of five setae on outer margin of

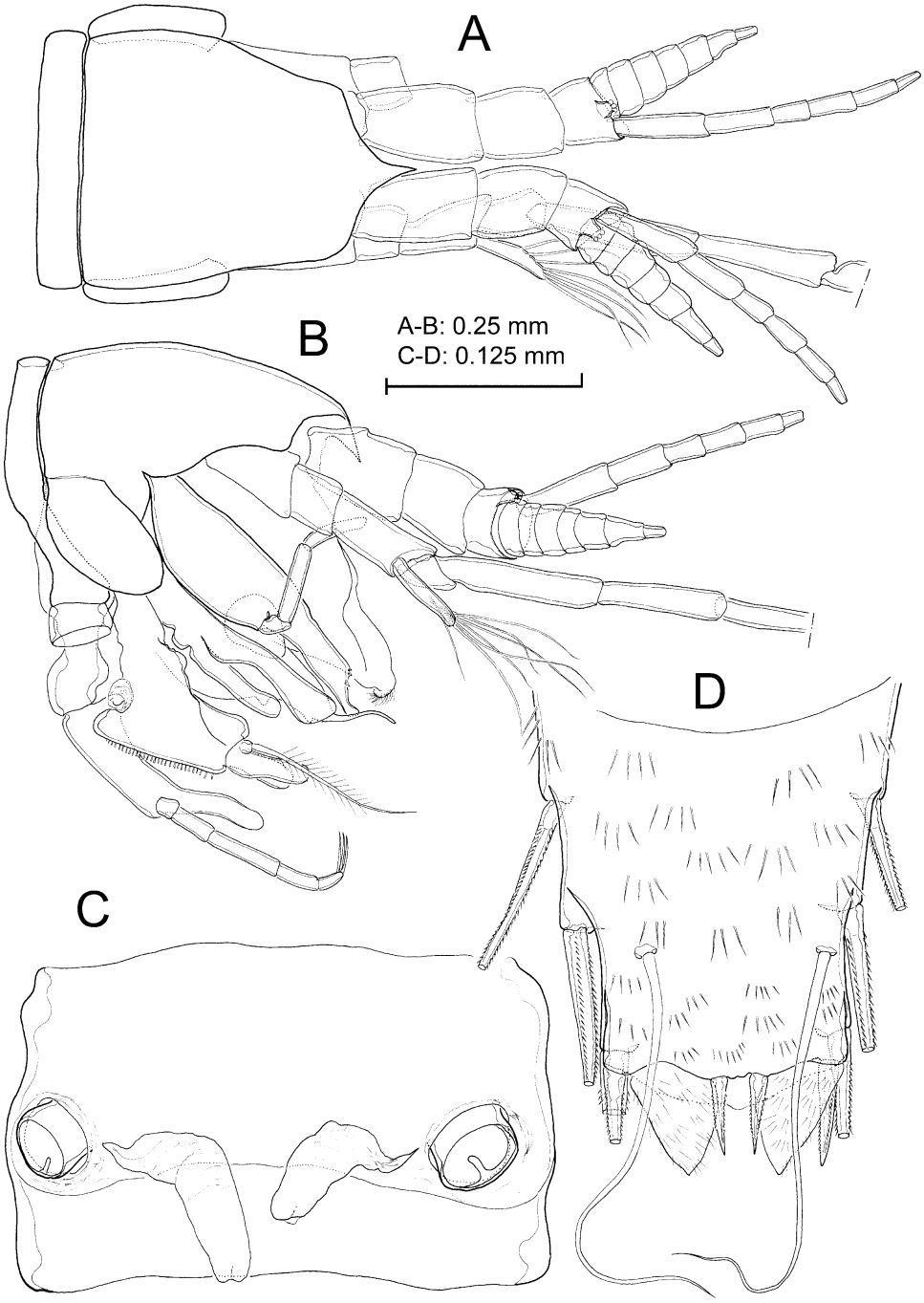

Figure 18. ***Montucaris distincta*** **gen. et sp. nov.**, male morph-I. A, cephalothorax and first pereonite, dorsal; B, same, lateral (with ornamentation of A1, A2 and of mouthparts omitted); C, seventh pereonite with (stretched) penes and coxae of P7, ventral (note coxo-basal condyle located posterolaterally on coxa); D, portion of pleotelson corresponding to telson, dorsal.

exopodal segment 1 short and spiniform (vs. all setae normal in female; cf. Figs 6C and 19B); (iii) second exopodal segment with three marginal setae on each side and two distal setae (only two setae, located subdistally, on outer margin of segment in female). Endopod differing from female in: (iv) presence of additional long spine terminally on distal article; (v) ornamentation of all spines, uniformly serrate and lacking subapical sensilla (except short subdistal spine), with serrations formed by hyaline lamellae (all

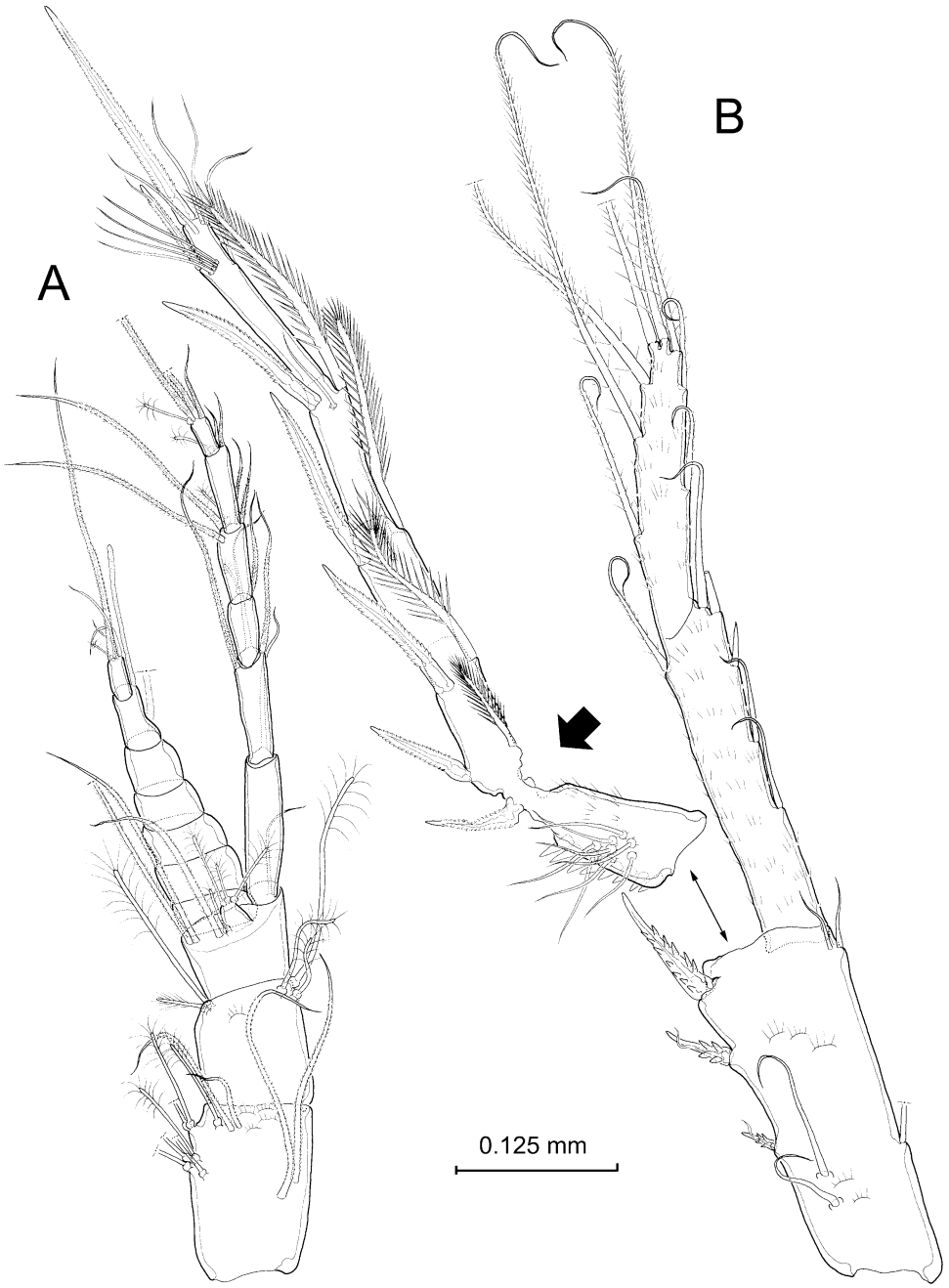

Figure 19. ***Montucaris distincta*** **gen. et sp. nov.**, male morph-I. A, left antennule, dorsal (integumental ornamentation of segments mostly omitted; armature of main flagellum not fully resolved); B, left uropod, dorsal (= posterior; arrow points to damaged proximal region of endopod; integumental ornamentation of protopod mostly omitted).

spines sparsely denticulate proximally and with subapical sensilla in female); (vi) greater number of penicillate setae on dorsal surface of proximal article; (vii) length of spines on articles longer than in female (cf. Figs 6C and 19B); and (viii) condition of outer bipinnate setae on endopodal articles 1–4, shorter and stouter than in female, with stronger pinnules reaching stout tips of setae (distal portion of setae smooth in female; cf. Figs 6C and 16B).

In addition, male morph-I does not express basis–ischium articulation on P5 (expressed laterally only in female), whereas on P6 this articulation is fully expressed (again expressed laterally only in female).

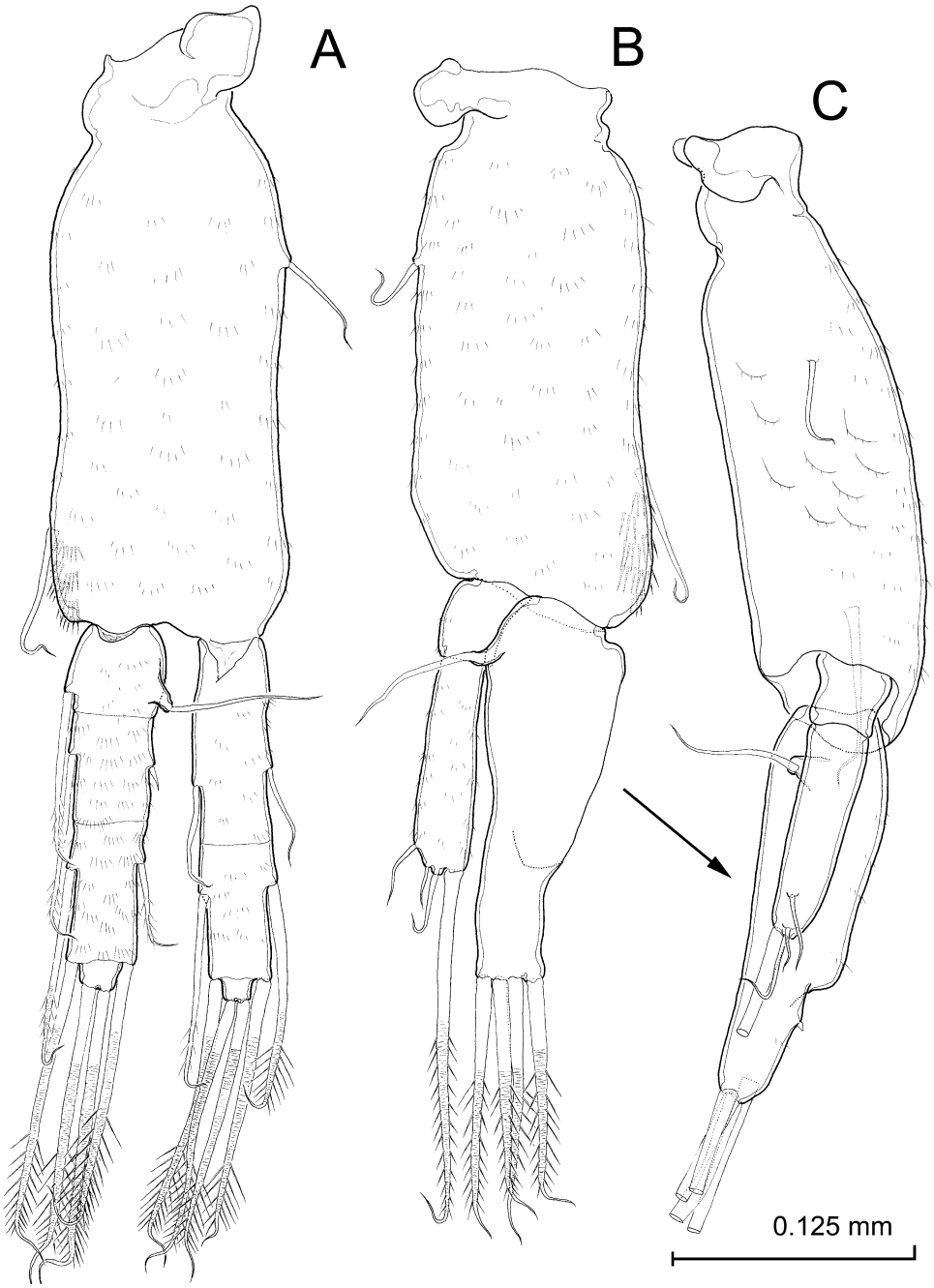

Figure 20. ***Montucaris distincta*** **gen. et sp. nov.**, male morph-I. A, right pleopod 1, posterior; B, left pleopod 2, posterior; C, same, lateral.

Male morph-II (Figs 8, 23–29)

Body aspect (Fig. 23A) similar in most major features to male morph-I, but with strikingly different integumental ornamentation of pereonites and pleonites, in particular in honeycombed pattern of hyaline frill extensions (see Fig. 24C; and Fig. 23A). Body size (3.88 mm) slightly greater than male morph-I (3.70 mm). Cephalothoracic structure differing, with transverse suture line present on dorsal cephalothoracic shield just behind plane of articulation of mandibles; line clearly visible in all three specimens available (Figs 23B, 24A). Telson (Fig. 24B) with spines longer than in male morph-I (cf. Figs 18D, 24B); spines differing in ornamentation also, being serrate with hyaline lamellae rather than spinulate; two small scars on dorsal surface could correspond to

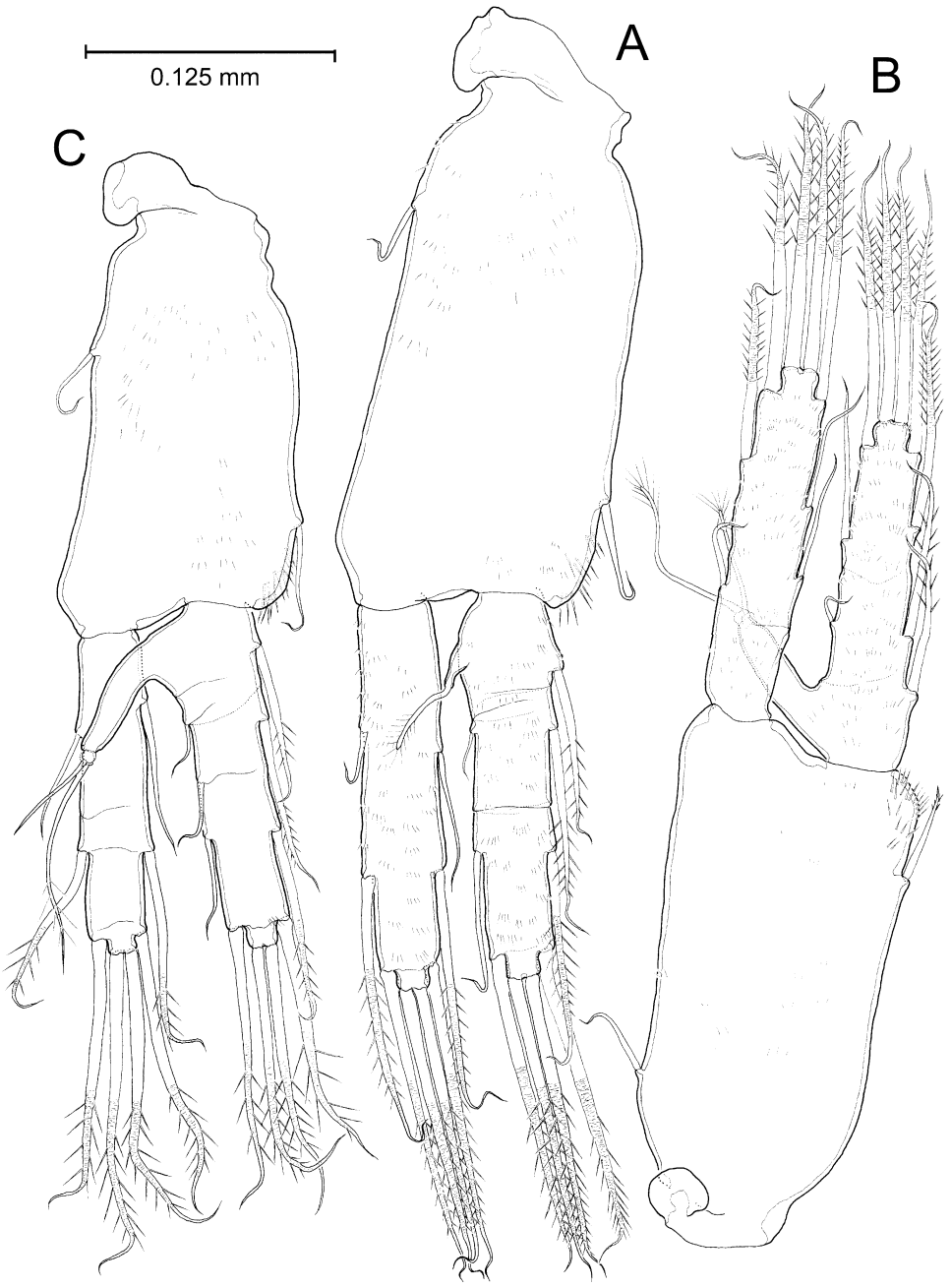

Figure 21. ***Montucaris distincta*** **gen. et sp. nov.**, male morph-I. A, left pleopod 3, posterior; B, left pleopod 4, anterior; C, left pleopod 5, posterior.

insertion of (missing?) setae; integument displaying honeycombed pattern of hyaline frills (Fig. 24C).

Antennule (Figs 8A, 23B, C) sharing basic structure with male morph-I; robust peduncular segments defined by presence of intrinsic muscles (Fig. 8A); one pair of intrinsic muscles originating in segment 1 and inserting proximally in segment 2; long unpaired muscle originating in segment 1 passing without intermediate attachment to insert in segment 3; intrinsic muscle pair originating in segment 2 inserting in segment 3; pair arising in segment 3 inserting at base of accessory flagellum. Putative differences in ornamentation not evaluated as many elements missing in available specimens of both morphs; peduncular segment 3 with dorsal setiferous process armed with at least eight short spiniform setae plus three penicillate setae (only socles of latter preserved in specimen illustrated in Fig. 23B, C); segment displaying oblique

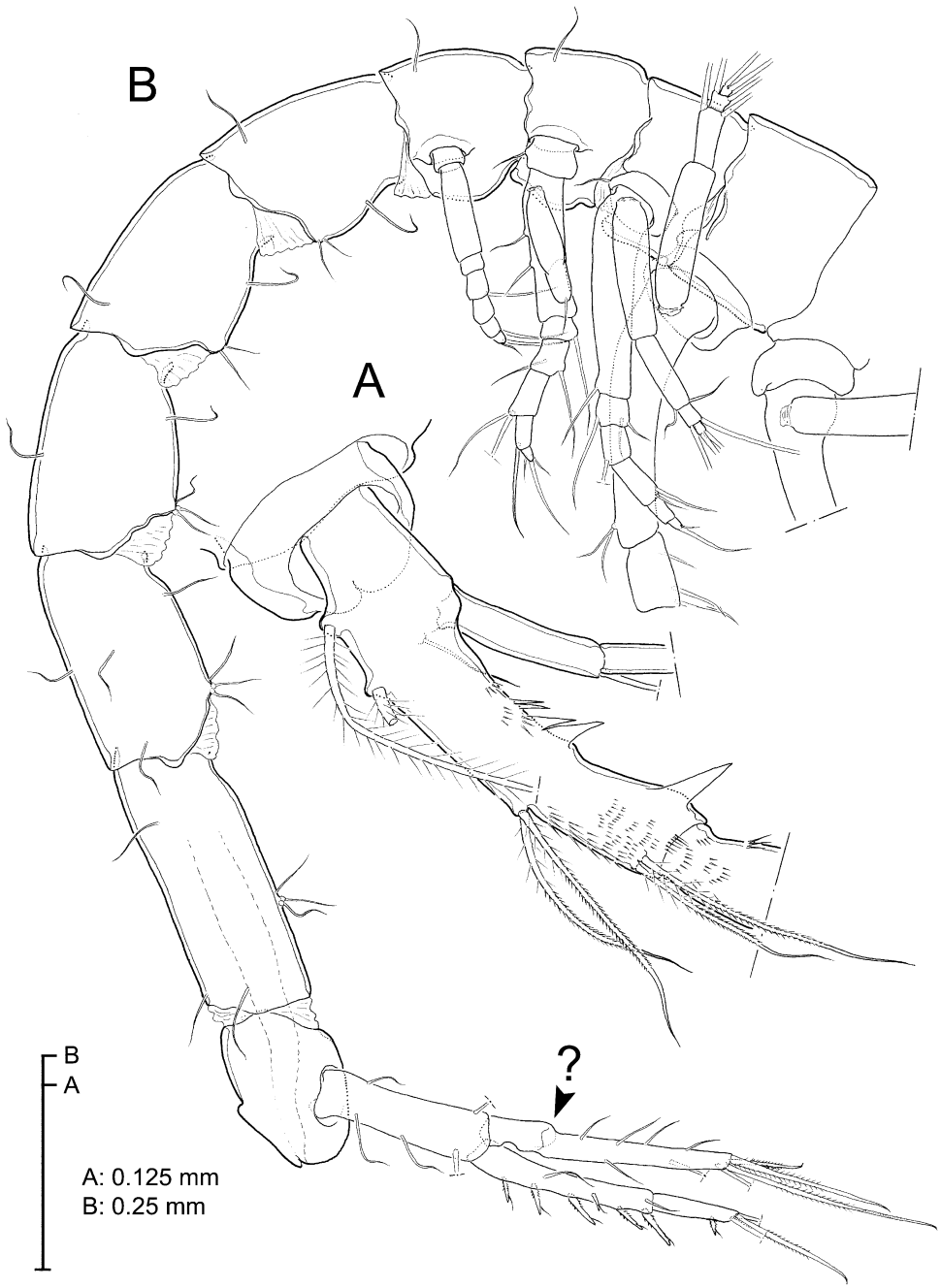

Figure 22. ***Montucaris distincta*** **gen. et sp. nov.** A, proximal portion of male morph-I left P3, medial; B, manca stage-III, lateral (arrowhead points to apparently distorted proximal portion of exopod of uropod).

suture line subdistally on dorsal surface, just behind setiferous process. Primary flagellum comprising at least six articles (antennules broken off beyond this article); articles wider than long except distalmost; armature of articles not preserved except cluster of four aesthetascs on dorsodistal angle of proximal article. Accessory flagellum comprising six articles; proximal article elongate, with distal margin extending beyond article 5 of main flagellum (article shorter in male morph-I, its distal margin reaching only distal margin of article 4 of main flagellum; cf. Figs 19A, 23B); two simple setae per article arranged as in Figure 23A, B.

Antenna (Fig. 23D) longer than antennule (cf. Fig. 23A), similar to male morph-I; armature of segments unresolved (missing in all specimens), as well

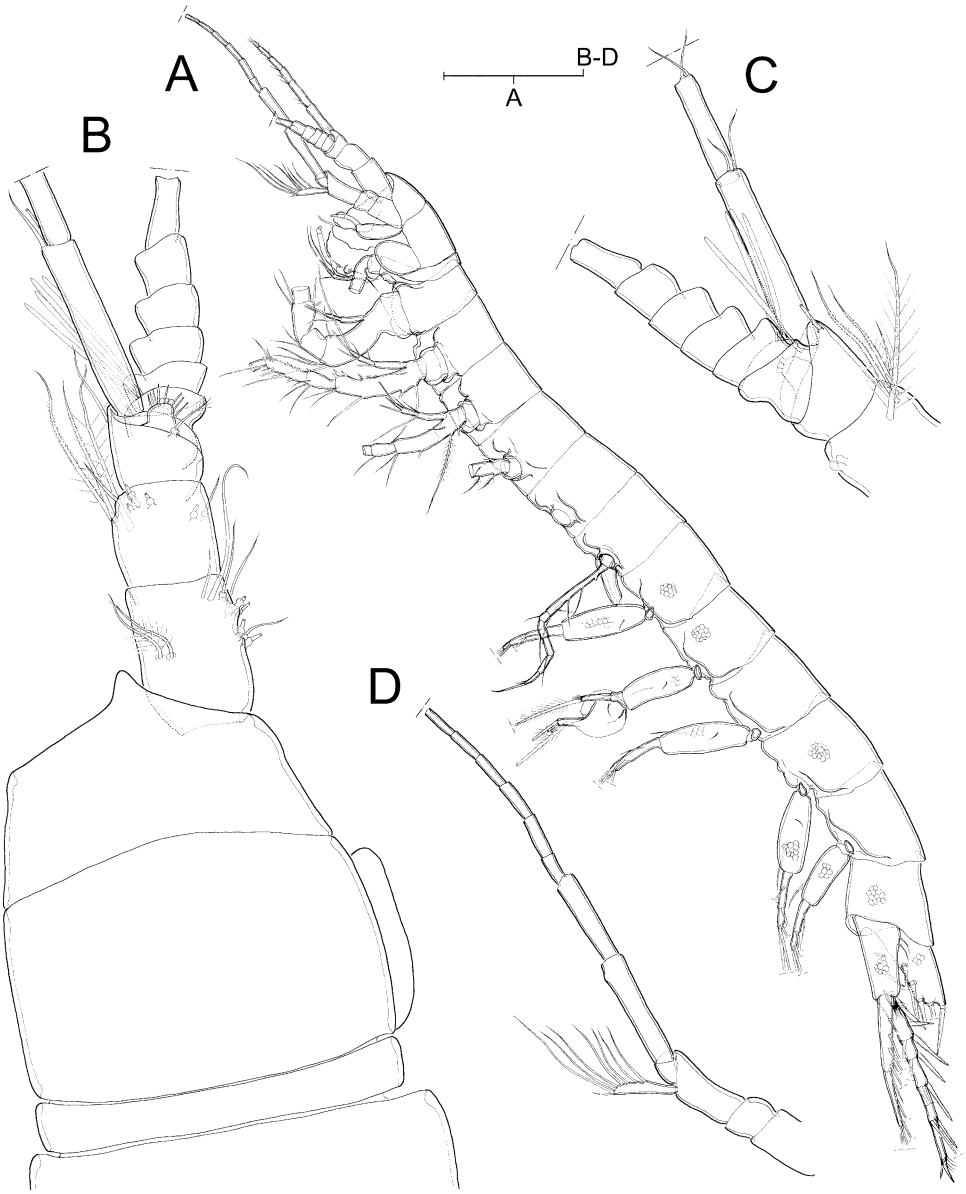

Figure 23. ***Montucaris distincta*** **gen. et sp. nov.**, male morph-II. A, habitus, lateral; B, right antennule, cephalothorax and first pereonite, dorsal; C, detail of right antennule, ventral; D, left antenna, lateral. Most armature elements on segments of antennule and antenna missing. Scale bars: 0.25 mm (A, D); 0.125 mm (B, C).

as number of articles comprising flagellum (distal portion missing from all specimens).

Mouthparts regressed, almost devoid of armature elements but still displaying diagnostic filiform extension of paragnaths, three-segmented mandibular palp, outlet of maxillary gland, and maxillipedal palp (Figs 23A, 24A).

Pereopod 1 (Fig. 25A) similar to male morph-I. P2–P4 and P6 with distal part of endopod missing. P2 (Fig. 26A) with three strong barbed spines on carpus, as in morph-I. P3 differing from morph-I in number, size and arrangement of triangular spines on anterior margin of basis–ischium, with up to ten unequal spines, vs. only four present in morph-I (cf. Figs 22A, 26B); in addition, merus and carpus (missing in morph-I) differing also from condition displayed in female in number of triangular spines on anterior margin (five and 17 spines on merus and carpus of male morph-II, vs. one and 13 in female; cf. Figs 16A, 26B). P4 (Fig. 26C) differing from morph-I (Fig. 17A) in retaining lateral vestige of intersegmental articulation between basis and ischium (vs. complete failure

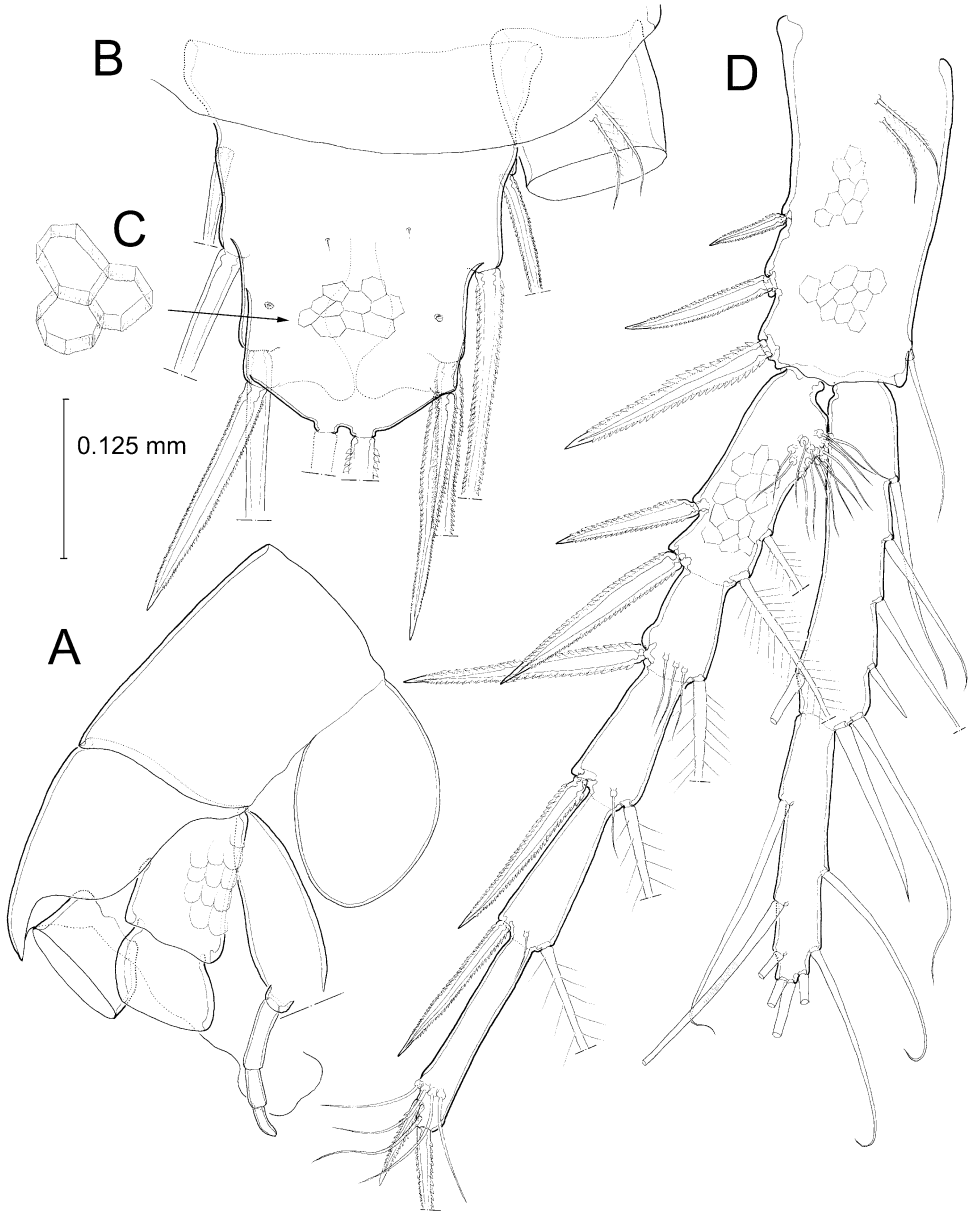

Figure 24. ***Montucaris distincta*** **gen. et sp. nov.**, male morph-II. A, cephalothorax, lateral; B, portion of pleotelson corresponding to telson, dorsal; C, detail of honeycombed integumental ornamentation; D, right uropod, dorsal (= posterior). [C not to scale.]

to separate segments), and by the structure of proximal seta on posterior (= medial) margin of basis, which is comparatively shorter, with an expanded tip. P5 and P6 (Fig. 25B, C) similar to morph-I but with three proximal setae on basis comparatively shorter and with expanded tips; apart from this, P5 and P6 differing also in retaining lateral vestige of intersegmental articulation between basis and ischium (segments completely merged in P5, and fully articulated in P6 of morph-I). P7 (Fig. 25D) similar to morph-I except for two proximal setae on basis, with expanded tips, and by absence of long penicillate seta on outer margin of propodus. Exopods on P2 to P6 similar in segmentation, armature and relative dimensions to those of morph-I.

Pleopods differing from morph-I in squamose integument of protopod, with tightly set crescentic hyaline frills, and longer and less stiff distal setae on both rami. Pleopodal musculature as in morph-I: extrinsic muscles (Fig. 29B) short, originating on lateral body wall and inserting proximally in protopodal part; protopods with pair of powerful intrinsic muscles anteri-

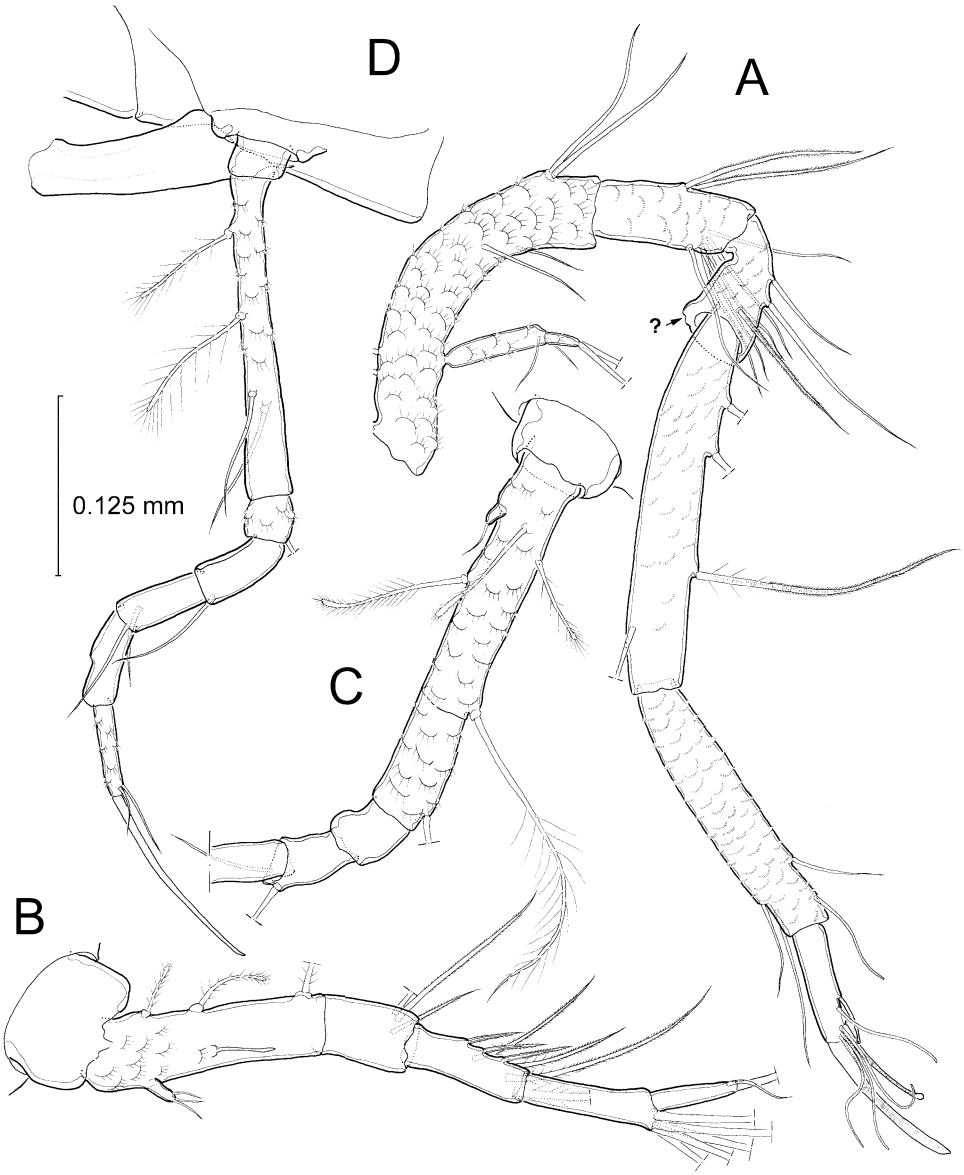

Figure 25. ***Montucaris distincta*** **gen. et sp. nov.**, male morph-II. A, left first pereopod, lateral; B, left fifth pereopod, lateral; C, left sixth pereopod, lateral; D, right seventh pereopod and right penis, lateral. Integumental ornamentation of pereopods not fully resolved except for first pereopod.

orly and three shorter muscles (two exopodal and one endopodal); long muscle extending from base to near tip of both exopod and endopod and short oblique muscle present within proximal endopodal segment (Fig. 29A–D). PL1 (Figs 27A, 29A) and PL3 (Fig. 28A) lacking postero-lateral digitiform process present proximally on margin of endopod in morph-I. PL4 (Figs 28B, 29D) and PL5 (Fig. 28C) as in morph-I in major features. PL2 (Figs 27B, C, 29B, C) with exopod as in morph-I; but endopod much more inflated, with three long plumose setae distally and another seta subdistally on inner margin (four distal setae at this position in morph-I); proximo-lateral margin of segment evenly rounded, lacking digitiform process (present in morph-I), with short seta; anterior and posteromedial surface of segment hardly sclerotized, inflated, bilobed anteriorly, evenly rounded posteromedially; anterior surface lacking tiny rounded process present at this location in morph-I.

Uropod (Fig. 24D) biramous, with basic structure similar to morph-I (Fig. 19B); but differing in: (i) condition of three spines on inner margin of protopod, long and serrate, with hyaline serrations and lacking subapical sensilla; (ii) outer margin of segment with

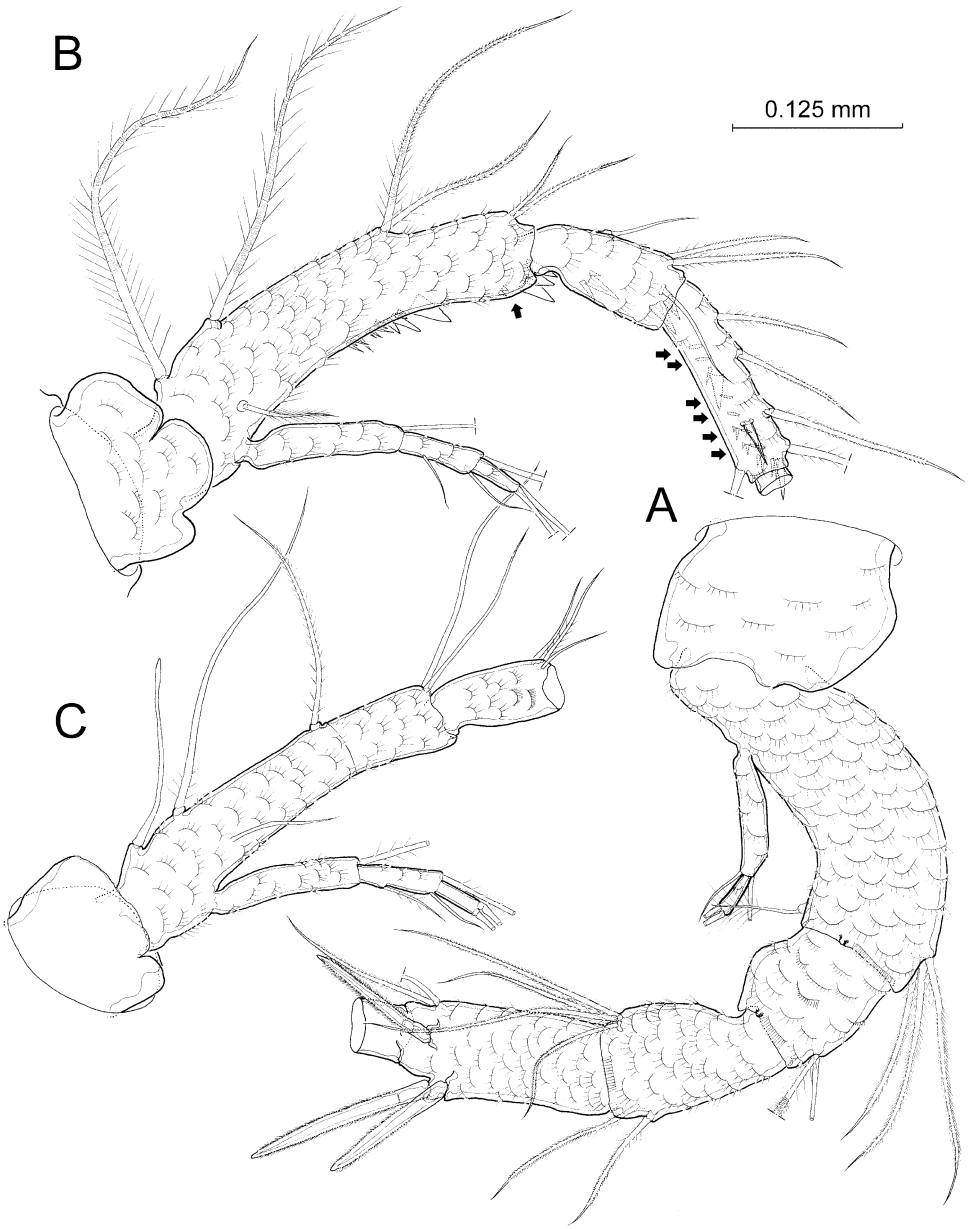

Figure 26. ***Montucaris distincta*** **gen. et sp. nov.**, male morph-II. A, left second pereopod, lateral; B, left third pereopod, lateral (arrows point to missing triangular spines on surface of ischium and carpus, with their origins indicated by ellipsoid scars); C, left fourth pereopod, lateral (ornamentation of setae not fully resolved; note faint basis–ischium intersegmental articulation expressed on lateral surface only).

naked seta at outer distal angle (two setae in morph-I); (iii) exopodal segment 1 with five outer setae (six setae in morph-I); (iv) endopodal proximal article lacking row of spinules along inner margin (row present in morph-I); (v) setae on outer distal angle of endopodal articles 2–4 plumose and slender (stout and pinnate in morph-I). Extrinsic musculature (Fig. 13C) originating within sixth pleonite and inserting around proximal rim of undivided protopods; intrinsic musculature (Fig. 13C) well developed, with large muscles originating proximally within protopod and inserting on the proximal rims of both rami; additional short muscles lying obliquely in distal part of segment, inserting near base of inner angle spine. Exopod with single intrinsic muscle. Endopod lacking intrinsic muscles (Fig. 13C). Surface of limb ornamented with honeycombed pattern of hyaline frill extensions (as in Fig. 24C).

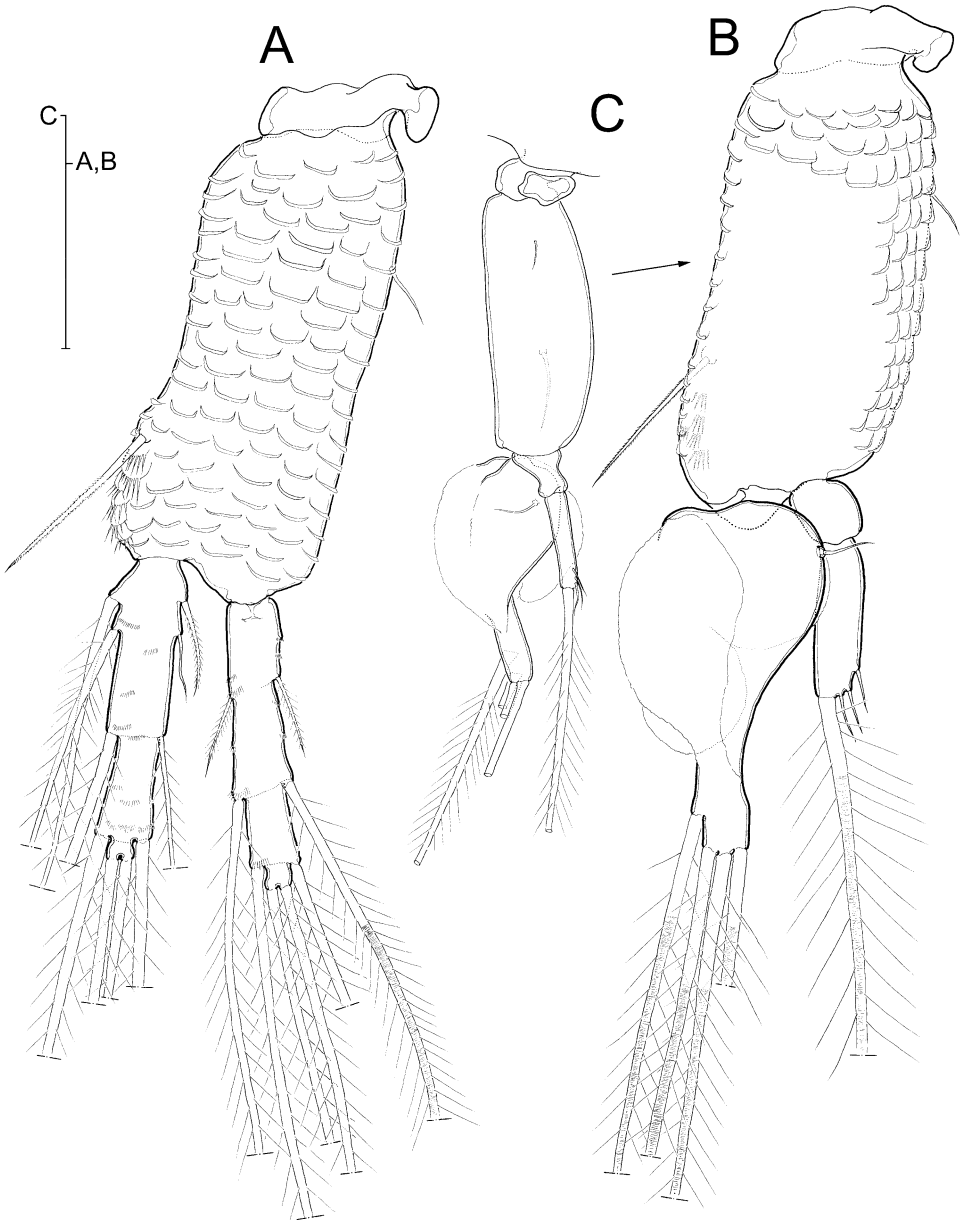

Figure 27. ***Montucaris distincta*** **gen. et sp. nov.**, male morph-II. A, left first pleopod, anterior; B, right second pleopod, anterior (integumental ornamentation on protopod partially omitted); C, same, lateral. Scale bars: 0.125 mm (A, B); 0.25 mm (C).

Juvenile male

Not figured. Body 3.64 mm long. As male morph-I in most major features, but with pleopods not fully developed. Pleopods with well-developed protopod but with both rami represented by buds; no armature developed on rami except setae on posterolateral digitiform process of endopod, fully developed already at this stage; pleopod 2 as rest of pleopods, not modified as in adult. Additional differences from male morph-I in armature of endopod of uropod, as follows: (i) distal annulus lacking long terminal spine; (ii) spines on all annuli ornamented as in female, i.e. sparsely denticulate proximally and with subapical sensilla (spines uniformly serrate and lacking sensilla, with serrations formed by hyaline lamellae in male morph-I); and (iii) outer bipinnate setae on articles 1–4 as in female, i.e. longer and more slender than in male morph-I, with distal portion smooth; condition of exopod unknown as ramus missing in both available specimens. Penes hardly developed, less than half length of those of adult.

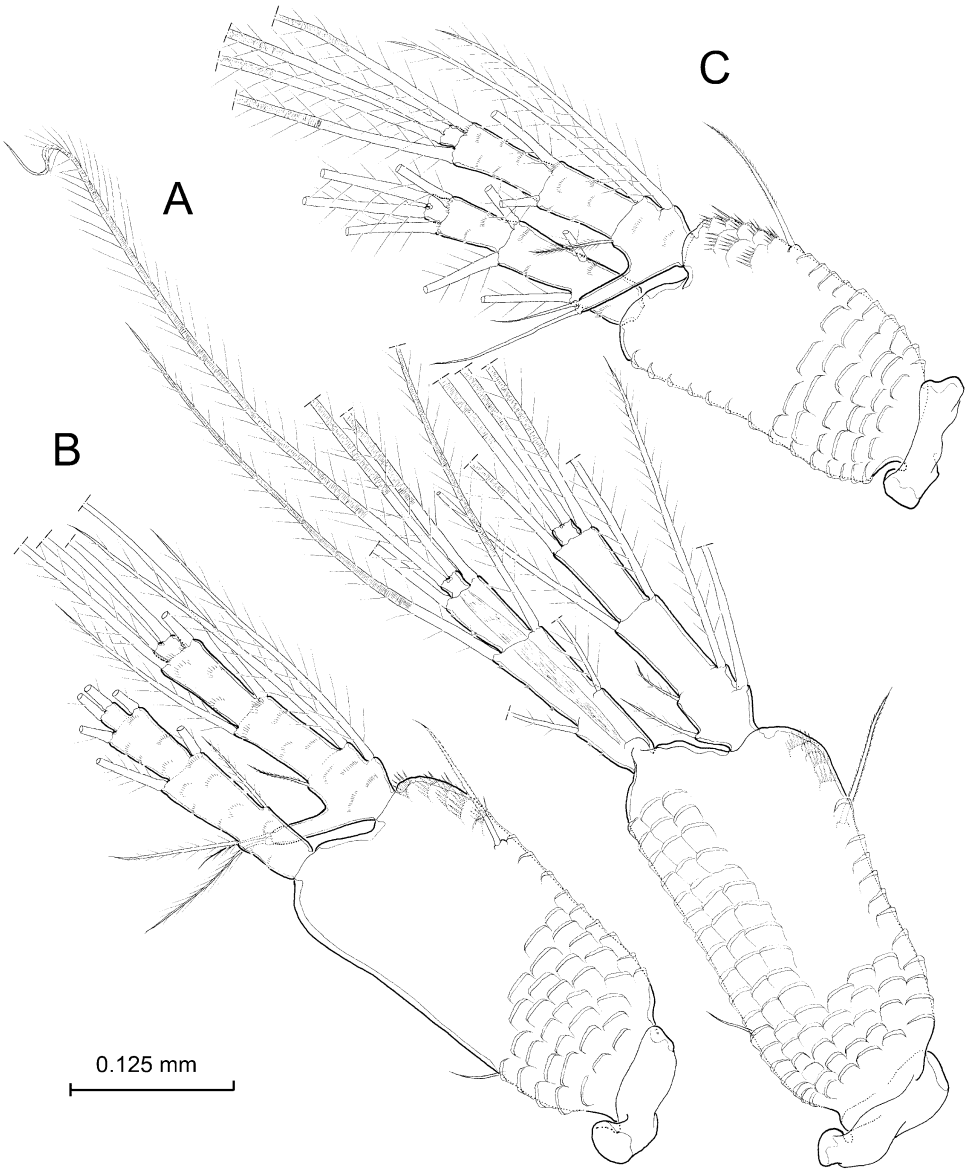

Figure 28. ***Montucaris distincta*** **gen. et sp. nov.**, male morph-II. A, right third pleopod, posterior; B, left fourth pleopod, anterior; C, right fifth pleopod, anterior. All pleopods with integumental ornamentation on basis partially omitted.

Manca stages (Fig. 22B)

Two specimens identified as manca stages *sensu lato* as P7 not fully developed, representing different stages, referred to as stage III and stage IV. Single damaged specimen with portion of body anterior to third pereonite missing considered manca stage-III (Fig. 22B). Pereopods of this specimen recognized as P3 to P7 based on display of buds of diagnostic triangular spines of P3 on anterior margin of basis–ischium of anteriormost pereopod (although segments were damaged and are not figured). Pereopods differing from adult in lateral – but not anterolateral – insertion of exopod on proximal part of basis. Exopods on P5 powerfully developed compared with adult; P6 displaying indistinctly two-segmented exopodal bud. Pleon with pleopods not developed, but paired rudiments present in form of two, two, three, three and three setae located posteriorly (midway, on pleonite 5) on each side of ventral surface of pleonites 1–5, respectively. Fifth pleonite distinctly more elongate than rest. Pleonite 6 with biramous uropods attached ventrolaterally midway along segment; posterior margin of segment apparently rounded, probably damaged, with terminal anal opening. Telson indistinct, apparently fully incorporated into last pleonite. Uropods biramous with elongate protopod, two-articulated

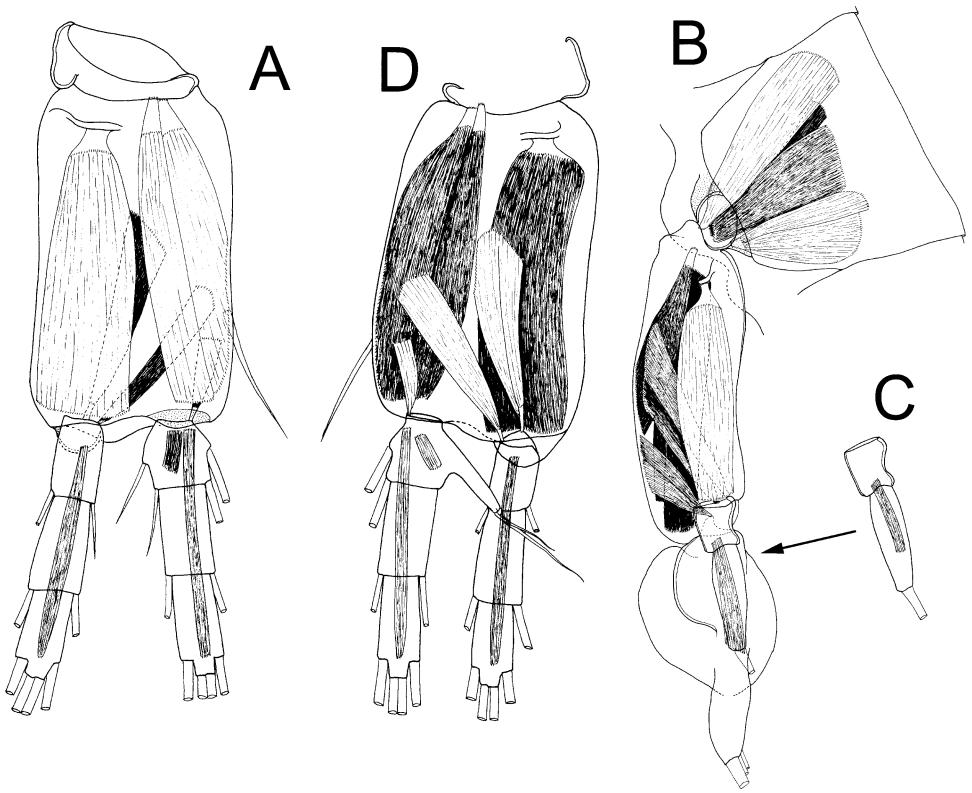

Figure 29. ***Montucaris distincta*** **gen. et sp. nov.**, male morph-II. A, first pleopod showing intrinsic musculature; B, second pleopod, lateral view showing extrinsic and intrinsic musculature; C, inset showing detail of intrinsic muscles within exopod; D, fourth pleopod showing intrinsic musculature.

endopod and one-segmented exopod (probably distorted proximally in Fig. 22B); armature as figured; note ornamentation of stout spines on inner margin of endopod, resembling male morph-I rather than morph-II.

Manca stage-IV (not figured) 3.10 mm long, as brooding female in all respects except in incomplete development of P7 and absence of oostegites.

Remarks

The new genus differs from *Hirsutia* and *Thetispelecaris*, the two other hirsutiid genera, currently known only from females, in the presence of a series of stout triangular spines along the anterior (= lateral) margin of the basis–ischium, merus and carpus of P3. These processes are absent in the other two genera. In addition, *Montucaris* carries a proximal row of about 12 strong triangular spinules along the medial margin of the proximal endopodal article of the uropod, in addition to two stout spines each with a subdistal sensilla. In both other genera the medial armature of this article comprises only stout spines with subdistal sensillae; the row of spinules is absent. Finally, the new genus has vestigial exopods on P5 and P6, whereas the exopods of these limbs are well developed in the other two genera.

Additional differences from *Hirsutia* include the biramous condition of the first pereopod (exopod absent in *Hirsutia*); the medial armature of the carpus of P2 comprising only three barbed spines (5–6 barbed spines in *Hirsutia*); and the armature of telson, which lacks the two stout dorso-distal serrate spines at this position in *Hirsutia*. In addition, *Montucaris* gen. nov. does not express the intersegmental articulation between basis and ischium in P3, P4 and P5. The articulation is expressed in both P3 and P4 in *H. bathyalis*; but P3 and P4 are unknown in *H. sandersetalia*.

Additional differences from *Thetispelecaris* include the filiform extension of the paragnaths, which are smooth in *Montucaris* but setulose in *Thetispelecaris*; and the condition of female PL4–5, which are not articulated proximally to the body in *Montucaris* whereas they are articulated in *Thetispelecaris*.

LIFE CYCLE AND REPRODUCTIVE MODE IN HIRSUTIIDS

All four existing species of Hirsutiidae are known only from females, a statistic that led Ohtsuka *et al*. (2002)

to speculate that members of this family might be parthenogenetic. The discovery of males with paired tubular penes and modified second pleopods indicates that hirsutiids are gonochoristic.

The life cycle of hirsutiids is not yet fully resolved. Gutu & Iliffe (1998) demonstrated that in *Thetispelecaris remex* it includes at least three different manca stages *sensu lato* (i.e. stages with no trace of P7 or with this limb not completely developed) in stating 'smallest specimens (0.80–0.87 mm long) lack last pair of locomotor pereopods . . . In four specimens, pair of tubercles on the last pereonite corresponding to last pair of pereopod. In slightly larger specimen (measuring 0.95 mm) last pair of pereopods formed almost entirely'. These three stages correspond to: (i) specimens with no trace of exopod on P7 (we term manca-I here); (ii) specimens with only buds of P7 (manca-II); and (iii) a single specimen with P7 almost entirely formed. Gutu & Iliffe (1998) could go no further in distinguishing additional stages within the 'P7-almost-entirely formed' category as only a single specimen was available. In the new hirsutiid two different stages with P7 in an intermediate degree of development can be distinguished. Assuming that the new taxon passes through the same early stages as *Thetispelecaris*, this totals at least four different manca stages in the life cycle of hirsutiids. On this basis, we have tentatively termed the two stages found in *Montucaris* manca-III and manca-IV. Future discoveries may further refine the life cycle of these animals and may result in modification of this terminology. Manca stage-III is characterized by having the pereopodal exopods of P5 and P6 more developed than in the adult, and inserted laterally on the basis; manca stage-IV has the exopods and other features as in adult in development and insertion. Both stages have P7 not fully developed.

The three male morph-II specimens described above fit well into the genus *Montucaris* based on the presence of stout triangular spines on the anterior margin of the basis and endopod of P3, the presence of an exopod on P1, and the reduction of the exopods of P5 and P6. They differ from the male morph-I, which unquestionably corresponds to *Montucaris distincta* in: (i) the unusual structure of the dorsal cephalothoracic shield, which has a clearly defined transverse suture just behind the insertion of mandibles; (ii) the regressed condition of the mouthparts; (iii) the size, number and arrangement of triangular spines on the basis and endopod of P3; (iv) the absence of the row of spinules on the inner margin of the proximal article of the uropodal endopod; and (v) the honeycombed integumental ornamentation of body somites. Additional differences include the relatively longer proximal article of the accessory flagellum of antennule in the male morph-II; the absence of the digitiform process on the posterolateral margin of the endopod of pleopods 1–3; the larger and serrate spines of the telson; the absence of the lateral penicillate seta on the propodus of P7; and the armature of uropods, with the spines on the inner margin of the protopod serrate, not denticulate, the presence of only five instead of six outer setae on exopodal segment 1, and the form of the setae on the outer distal angle of endopodal articles 2–4, plumose and slender instead of stout and pinnate as in male morph-I.

These specimens were found together with 64 females, nine morph-I males and two mancas of *Montucaris distincta*, where the male–female assignment is based on the following shared diagnostic morphological features: (i) the similar dorsal cephalothoracic shield, lacking transverse suture line mid-dorsally; (ii) the ordinary, non-regressed condition of the mouthparts; (iii) the similar integumental ornamentation of the body; (iv) the similar ornamentation of the spines of the telson (all spinulate); (v) the common display of a row of spinules on the medial margin of the proximal article of the endopod of the uropod; (vi) the similar ornamentation of the spines on the medial margin of the protopod of the uropod, all denticulate proximally; (v) the almost identical pattern of triangular spines on P3, etc. No females were identified within the available specimen pool that corresponded to the three morph-II males based on the common display of apparently non-sexually dimorphic features such as those listed above, i.e. females with a transverse mid-dorsal suture on the cephalothoracic shield and/or absence of the medial spinule row on the proximal segment of the uropodal endopod. The question arises therefore whether these three so-called male morph-II specimens correspond to the adult terminal stage of *M. distincta* which, as in tanaidaceans, would be non–feeding and devoted solely to reproduction (Larsen, 2001), or they represent a new species of *Montucaris* for which the female remains unknown. Neither of these two possibilities can be absolutely refuted given the current paucity of knowledge of the life cycle of hirsutiids. Our current working hypothesis is that the *Montucaris* male morph-II is the adult terminal stage in the life cycle of *Montucaris distincta*, and that male morph-I corresponds to a subadult male in the process of maturation.

This interpretation is supported by the larger body size of morph-II males compared with morph-I (3.88 vs. 3.70 mm long, respectively). The progressive transformation of the ornamentation of the spines of the uropod with increasing body size is readily explained by this interpretation. The spines on the inner margin of the protopod and endopod of the uropod are all sparsely denticulate proximally and smooth apically in adult females (Fig. 6C) and juvenile males (3.64 mm), and bear a subapical sensilla. In morph-I

males (3.70 mm), the spines on the protopod remain as in the juvenile, but those on the endopod become serrate (Fig. 19B); none has a subdistal sensilla except for the subdistal spine. In the morph-II male (3.88 mm) all spines, either protopodal or endopodal, are uniformly serrate and lack a subdistal sensilla (Fig. 24D).

The increase in body size could also explain the progressive transformation in number and arrangement of triangular spines on the anterior margin of the basis and endopod of P3 [cf. the state of this character in Fig. 16A (juvenile male), Fig. 22A (morph-I male) and Fig. 26B (morph-II male)]. The more inflated aspect of the endopod of PL2 in the morph-II male might be similarly explained (complete maturation).

The statement by Messing (1983) that all tanaidaceans in which the males bear strongly reduced mouthparts will prove to be potential protogynous hermaphrodites raises the possibility that the *Montucaris* morph-I males (3.70 mm in length) are derived by metamorphosis from a female (4.60–5.95 mm long). This seems highly improbable given the relatively huge decrease in body size, but we cannot completely exclude this possibility given the current paucity of knowledge of the life cycle of the hirsutiids.

The second possibility is that the morph-II males represent a different species (also new), with a sex-ratio extremely biased toward males. The putative lack of males in all other species of the family, even though each is known only from a few specimens, tends to refute this hypothesis, despite the striking morphological differences between the two male morphs. These differences include major characters such as: (i) the condition of the dorsal cephalothoracic shield; (ii) the presence or absence of the spinule row from the medial margin of the proximal endopodal article of the uropod; (iii) the presence or absence of the digitiform process on the posterolateral margin of the endopod of PL2; or (iv) the plumose condition of the outer setae displayed on the uropodal endopod of morph-II male, whereas in the smaller morph-I male these setae have a stout spinulose aspect (after having first been plumose in the juvenile).

FEEDING HABITS IN HIRSUTIIDS

All specimens of the new species except the males with regressed mouthparts showed the digestive tract full of fine-grained, amorphous material from end to end. No trace of animal prey could be discerned, and consequently the suggestion of a predatory or scavenging diet (as made elsewhere for hirsutiids; see Sanders *et al*., 1985) can be confidently discarded, as numerous specimens were available for study.

Gutu & Iliffe (1998: 97) considered hirsutiids to be swimmers and filter-feeders. According to these authors, the first pereopod would play a feeding role by generating a water current towards the mouthparts, which would then retain the particles of food transported by the current. When the animal was not swimming, the first pereopod would draw food particles from the substratum, either by generating water currents or by detaching particles and directing them to the mouth. We do not share this interpretation of the feeding system as none of the mouthparts is equipped with a filter.

We follow Just & Poore (1988) in considering hirsutiids as essentially small particle scrapers. Their feeding mode would be similar in general terms to that described by Fryer (1964) for thermosbaenaceans, with occasional involvement of the first pereopods in gripping and transferring large food items directly to the mandibles. The long endopodal seta of the maxilla and the exopod of the first pereopod would also assist in pushing suspended material towards the mouthparts (see Fig. 3). Indeed, the structure of the mouthparts of hirsutiids fits completely with what Fryer (1964: 76) considered to be the general pattern in aquatic arthropods that scrape food particles from a substrate. Namely, there is a series of scrapers, and the first scraper in the functional series (here the basal endite of the maxillule) is the coarsest, followed by longer sweeping spines or setae (on the basal endites of the maxilla). Contrary to what is found in the thermosbaenaceans, the maxilliped seems to play a more active role in feeding, as suggested by its hirsute anterior surface and the extraordinary arrangement of coarse setae, provided with putative chemosensory aesthetascs, arrayed submarginally adjacent to the medial margin of the basis, on the posterior surface of the segment (see below). We conclude that these structures on the maxilliped serve to retain and capture stray particles lost posteriorly from the maxillules and maxillae.

The extraordinary degree of ornamentation of hirsutiid mouthparts leads us to conclude that collecting food must be a selective process rather than an indiscriminate process of particle gathering. We do not know how this feeding process proceeds, but the system does not constitute an adaptation to collect particles only from fine oozes in the deep sea or in caves, as hirsutiids have also been captured with hand-held nets on the rocky ceiling of tunnels subject to strong currents in the Bahamas (T. M. Iliffe, pers. comm.). Several features of the mouthparts are unusual and suggest specialized functions, such as the filiform distal extension of the paragnaths (for probing into soft sediments?) or the teeth present on their medial margin. Also noteworthy is the similarity between the tiny spatulate spinules (Fig. 7F) forming a ventro-lateral row on the maxillary coxa and the structures recently described by Langer, Ruppersberg & Gorb (2004) on

the attachment pads of the legs of a fly. These structures enable the fly to adhere to surfaces via attractive capillary forces mediated by a pad secretion. In hirsutiids they could either attach to the antero-lateral margin of the basis of the maxilliped, thereby closing off laterally the hirsute chamber formed by the posterior surface of the maxilla and the anterior surface of the maxilliped, or they could comb the hirsute anterior surface of the maxilliped to resuspend retained food particles prior to their being gathered by the coxal endite of the maxilla.

Further evidence that the feeding mechanism is neither automatic nor indiscriminate is the presence of aesthetasc-like hyaline structures proximally on the stout setae arrayed posteromedially on the maxilliped basis. Somewhat similar aesthetascs are present on the antennules of copepods, and are allegedly chemosensory in function (Boxshall & Huys, 1998). They could play a role in selecting the stray particles dislodged by the maxillules and maxillae, prior to their recovery by the coxal endite of the maxilla.

OOSTEGITES AND EPIPODITES IN HIRSUTIIDS

Oostegites are outgrowths of the pereopodal coxa which form the ventral marsupium or brood pouch in adult female peracarids. The presence of oostegites on the pereopods is a key synapomorphy of the superorder Peracarida: present in the ground pattern of the orders Lophogastrida, Mysida, Cumacea, Tanaidacea, Mictacea, Spelaeogriphacea, Isopoda and Amphipoda. Oostegites are absent in the order Thermosbaenacea, which has commonly been placed in a distinct superorder, the Pancarida (e.g. Siewing, 1956; Richter & Scholtz, 2001), but is here included in the Peracarida.

Oostegites are typically located medially on the coxa and it is widely accepted that oostegites represent modified epipodites (Claus, 1885; Siewing, 1956; Dahl, 1983) despite developmental heterogeneity within the Peracarida (e.g. Watling, 1999). The atypical position of the oostegites on the posterior surface of the coxa in adult female Hirsutiidae has generated considerable debate concerning their homology. Sanders *et al*. (1985) interpreted the posterior position of the oostegites of *H. bathyalis* as a result of a change in alignment of the limb, with the typical linear arrangement of exopod–endopod–oostegite being rotated from lateral–medial to anterior–posterior. Just & Poore (1988) adopted this interpretation in their description of *H. sandersetalia*. When describing *Thetispelecaris*, Gutu & Iliffe (1998) offered a different interpretation. They distinguished between the typical peracaridan oostegite as a membranous structure devoid of setae ('with few exceptions'), which are temporary, developing to form the marsupium in concert with the egg-laying cycle, and the hirsutiid 'oostegite', which they interpret as a permanent structure functioning to retain eggs and also to assist in respiration and the flow of water currents. Gutu & Iliffe (1998), Gutu (2001) and Ohtsuka *et al*. (2002) refer to the 'oostegite' of hirsutiids as epipodites. Given the accepted interpretation of the oostegite as a homologue of the coxal epipodite, the argument of Gutu & Iliffe (1998) and Gutu (2001) seems superfluous. Gutu (2001: 53) speculated that these structures, to which he assigned a primarily respiratory function, would probably be present in males too. Hirsutiids possess pereopodal epipodites which function to retain developing eggs in a ventral marsupium; by definition these should be referred to as oostegites. In their highly setose form, the oostegites of hirsutiids resemble those of gammaridean amphipods (e.g. Jaume & Christenson, 2001).

The interpretation of hirsutiid oostegites as homologues of the oostegites in other peracaridans is also supported by their absence in males, and by their presence in brooding females only, with preparatory females showing an intermediate degree of development (Fig. 16A–C) while they are absent from manca stages. Their unusual posteromedial placement on the coxa (not posterior as assumed by other authors) is easily explicable by Sanders *et al*.'s (1985) hypothesis that a change in alignment of the limb occurs, a hypothesis which finds support in our observations that the exopod migrates from a lateral origin in manca stage-III to become anterolateral in position in manca stage-IV.

COMMENTS ON RELATIONSHIPS OF THE HIRSUTIIDAE

Hirsutiids are placed within the Peracarida, which is a relatively robust taxon although there is some uncertainty regarding its boundaries. This uncertainty is centred on the inclusion of the Thermosbaenacea and, to a lesser extent, of the Mysidacea (comprising Lophogastrida plus Mysida) (see Richter & Scholtz, 2001; Spears *et al*., 2005).

The Hirsutiidae share a basic, unspecialized appearance with two taxa that are also represented by few species and remain relictual in cave environments, namely the Mictacea (considered here to comprise only *Mictocaris* Bowman & Iliffe, 1985) and the Spelaeogriphacea. Their roughly cylindrical body is almost featureless, comprising a cephalothorax incorporating only the first thoracic somite and lacking a carapace, a pereon comprising seven free somites, and a pleon of apparently six free somites plus telson. In addition, the pereopods are all similar and look rather undifferentiated, with basically ambulatory endopods and natatory exopods; no epipodites are exhibited on

these limbs other than the female oostegites. The structure of the mouthparts is also roughly similar in these groups, and corresponds to a feeding mode based on scraping food particles from the substrate (Fryer, 1964). This rather featureless pattern contrasts strikingly with the characteristic body plans of other peracaridan orders.

Establishing whether this common pattern is symplesiomorphic, homoplasic (as recent molecular analyses might suggest; see Spears *et al*., 2005) or reflects the close phylogenetic affinity of these orders is a difficult task. Characterizing these groups on the basis of autapomorphies is inconclusive: not even a single diagnostic synapomorphy can be listed for the Mictacea, while only the filiform extension of the paragnaths, the antero-posterior orientation of the pereopods and the annulate endopod of the uropods could be considered as such for the Hirsutiidae. The Spelaeogriphacea show the exopods of pereopods IV–V transformed into non-setose respiratory paddles, but the posterior extension of the dorsal cephalothoracic shield partially covering the second thoracomere, a feature considered to be unique to the group, is apparently inconsistently displayed in *Mangkurtu mityula* (cf. Poore & Humphreys, 1998), which resembles the hirsutiids and mictaceans in this respect. Even the non-setose, paddle-like condition of the exopods of the rear pereopods of spelaeogriphaceans is approached by some monodellid thermosbaenaceans (Fryer, 1964; Wagner, 1994).

Determining whether the extraordinary mouthparts of the hirsutiids are only specializations for an unusual food regime in a peculiar habitat, or should be considered as part of the groundplan of the group, is seemingly difficult. Nevertheless, the observation of hirsutiids on the rocky walls and ceilings of submarine tunnels subject to strong tidal currents invites caution in the uncritical acceptance of their feeding apparatus solely as an adaptation to collect food from the deep sea or cave ooze.

Detailed study of the maxilla has revealed a new and potentially informative character: the long plumose seta carried on a small papilla-like process on the basis, immediately proximal to the basal endites. We interpret this seta as representing a vestigial ramus. Within the Peracarida, the maxillary endopod is present as a well-developed, two-segmented ramus only in the Mysida, Lophogastrida and Thermosbaenacea. A well-developed exopod is also present in Mysida, Lophogastrida and Thermosbaenacea (e.g. *Tulumella* Bowman & Iliffe, 1988), and we accept the interpretation of the isolated seta located on a small papilla in thermosbaenid and monodellid thermosbaenaceans as representing the vestigial exopod (cf. Wagner, 1994; Monod & Cals, 1999). Apart from these, no other peracaridans retain any vestige of the maxillary rami, except for the papillate seta present on the maxillary basis in the Hirsutiidae. It is possible to interpret this as representing a vestige of either the exopod or the endopod. The dorsal origin of this seta on the basis does not provide conclusive evidence of its homology. Comparative analysis indicates that within the Crustacea every uniramous maxilla is uniramous by virtue of loss of the exopod. We found no examples of uniramous maxillae in which the endopod is lost and the exopod retained. On this comparative basis we tentatively interpret this seta as representing the endopod in the Hirsutiidae. This endopodal seta is absent in *Mictocaris* and in Spelaeogriphacea. The presence of a vestige of the endopod is a phylogenetically informative character that has not previously been used in analyses of relationships between peracaridan taxa.

The discovery of the adult males of the Hirsutiidae has provided important new data concerning the state of the pleopods. Well-developed, biramous, natatory pleopods of the form exhibited in the new genus are also present in male Mysidacea (in both lophogastrids and mysids), Amphipoda, Cumacea, Tanaidacea and Spelaeogriphacea. Such natatory pleopods are biramous and are characterized by their large, muscular protopods. Pleopods are well developed, but are modified, typically lamellate in form and have a respiratory function in male isopods. In *Mictocaris* and Thermosbaenacea males the pleopods are reduced.

The new data on hirsutiids highlight the heterogeneity of the Mictacea as formerly constituted. However, the character states used by Gutu & Iliffe (1998) to distinguish between the Hirsutiidae, as the Bochusacea, and the Mictocarididae, as the suborder Mictacea within the order Cosinzeneacea, are flawed. Data provided here indicate that the posteromedially located lobes on the pereopods referred to as epipodites by Gutu & Iliffe (1998) are only present in females and develop progressively towards maturity, as typical for peracaridan oostegites. Evidence also exists of a change in alignment of the exopod–endopod–oostegite axis during development, as postulated by Sanders *et al*. (1985). On this evidence we identify these lobes as homologues of peracaridan oostegites, a conclusion that removes the key character from the diagnosis of the Bochusacea as constructed by Gutu & Iliffe (1998).

We thus consider that there could have been unwarranted inflation in the level of separation of these three taxa. On the basis of currently observed synapomorphies and autapomorphies their separation at the ordinal or subordinal level is difficult to justify. The relationships between these three taxa, and between them and other peracaridans, are in urgent need of re-assessment. The provision of detailed descriptions of both sexes of Mictacea and Spelaeo-

KEY TO SPECIES OF HIRSUTIIDAE (FEMALES ONLY)

1. Pereopods 5–6 with exopods reduced, one-segmented; P3 with anterior margin of basis and proximal segments of endopod bearing stout triangular spines; proximal segment of uropodal endopod with row of spinules along medial margin (*Montucaris*) ..... *M. distincta*
   Pereopods 5–6 with well-developed, multisegmented exopods; P3 without stout triangular spines; proximal segment of uropodal endopod without medial row of spinules 2
2. Pereopod 1 with exopod; P2 carpus with three barbed spines on distomedial angle; filiform extension of paragnaths setulose from base to tip; pleopods 4–5 articulated proximally to body (*Thetispelecaris*) 3
   Pereopod 1 lacking exopod; P2 carpus with 5–6 barbed spines on distomedial angle; filiform extension of paragnaths smooth distally; pleopods 4–5 not articulated proximally to body (*Hirsutia*) 4
3. Distal segment of maxillipedal endopod with three spines plus two slender setae; pleopods 4–5 with two setae terminally ..... *T. yurikago*
   Only three setae on distal segment of maxillipedal endopod; pleopods 4–5 with three setae terminally ..... *T. remex*
4. Rostrum absent ..... *H. bathyalis*
   Downward-curving rostrum present ..... *H. sandersetalia*

griphacea is necessary before such a study can be undertaken. Meanwhile, we prefer to retain the Hirsutiidae – as the Bochusacea – as a separate order. The evidence on which this decision is based is several differences between hirsutiids and *Mictocaris*, including the male pleopodal arrangement, the telson structure and its incorporation into the sixth pleonite to form a pleotelson, the retention of the maxillary endopod, the posteromedial insertion of the female oostegites on the pereopodal coxae, the multiarticulated endopod of uropod, and the location of the male penile papillae (on the sternite of the eighth thoracomere instead of on the coxae of the seventh pereopod). Nevertheless, we are aware that some of these features show intraordinal variation in other peracaridan orders [for example: penile papillae may be coxal or on the sternite in isopods (see Brusca & Wilson, 1991); the uropodal endopod may be multiarticulate or one-segmented in tanaids (Gutu & Sieg, 1999); the oostegites may be inserted medially or posteromedially in Amphipoda (Just & Poore, 1988); and the telson may be free or incorporated into a pleotelson in Thermosbaenacea and Cumacea (Wagner, 1994; Băcescu & Petrescu, 1999)].

Irrespective of whether or not they reflect the close phylogenetic relationship between both groups, we want to stress here striking similarities between hirsutiids and some tanaidaceans. In addition to the common possession of (i) maxillary gland, (ii) multiarticulated uropodal endopod, and the morphology of adult males, with (iii) regressed mouthparts, (iv) same general pleopod morphology and (v) similar position of the penile papillae, it is noteworthy that (vi) the tanaidacean paragnaths display a variety of extensions some of which resemble the filiform condition found in hirsutiids (see Gutu & Sieg, 1999: figs 44, 45). In addition (vii) the well-developed exopods on pereopods 5–6 of the so-called manca stage-IV of hirsutiids, which regress in the adult into a setose bud, is reminiscent of the developmental pattern described for the tanaidacean families Kalliapseudidae and some Sphyrapidae (see Gutu & Sieg, 1999: 366 and Fig. 9.96). Finally, (viii) the incorporation of the second thoracomere of some hirsutiids (i.e. *Thetispelecaris remex*) into the cephalothorax, as well as (ix) the presence of a pleotelson incorporating the sixth pleonite in hirsutiids are features that approach the condition shown in some living tanaidaceans.

ACKNOWLEDGEMENTS

This is a contribution to Spanish MEC project REN2001-0580. We are grateful to Gardline Environmental Ltd and Enterprise Oil for providing the material for study and the accompanying environmental data. We would also like to thank Ben Williamson of the Electron Microscope Unit at the NHM for his assistance with scanning electron microscopy and Kevin Webb of the Photo Studio at the NHM for producing Figure 7.

REFERENCES

Băcescu M, Petrescu I. 1999. Ordre des Cumacés (Cumacea Krøyer, 1846). In: Forest, J, ed. *Traité de Zoologie. Anatomie, Systématique, Biologie. Tome VII (Fascicule III a), Crustacés Péracarides. Mémoires de l'Institut Océanographique Fondation Albert I^er^ Monaco* **19:** 391–428.

Bowman TE, Garner SP, Hessler RR, Iliffe TM, Sanders HL. 1985. Mictacea, a new order of Crustacea Peracarida. *Journal of Crustacean Biology* **5:** 74–78.

Bowman TE, Iliffe TM. 1985. *Mictocaris halope*, a new unusual peracaridan crustacean from marine caves of Bermuda. *Journal of Crustacean Biology* **5:** 58–73.

Boxshall GA, Huys R. 1998. The ontogeny and phylogeny of copepod antennules. *Philosophical Transactions of the Royal Society of London, Biological Sciences* **353:** 765–786.

Brusca RC, Wilson GDF. 1991. A phylogenetic analysis of the Isopoda with some classificatory recommendations. *Memoirs of the Queensland Museum* **31:** 143–204.

Claus C. 1885. Neue Beiträge zur Morphologie der Crustaceen. *Arbeiten aus dem Zoologischen Instituten der Universität Wien und der Zoologischen Station in Trieste* **6:** 1–108.

Dahl E. 1983. Malacostracan phylogeny and evolution. In: Schram, FR, ed. *Crustacean Phylogeny*, Crustacean Issues, Bd. 1. Rotterdam: A.A. Balkema, 189–212.

Fryer G. 1964. Studies on the functional morphology and feeding mechanism of *Monodella argentarii* Stella (Crustacea: Thermosbaenacea). *Transactions of the Royal Society of Edinburgh* **66:** 49–90.

Gutu M. 1998. Spelaeogriphacea and Mictacea (Partim) suborders of a new order, Cosinzeneacea (Crustacea, Peracarida). *Travaux du Muséum National d'Histoire Naturelle 'Grigore Antipa'* **40:** 121–129.

Gutu M. 2001. Emendations of the description of *Thetispelecaris remex* Gutu and Iliffe, 1998 and the diagnosis of the order Bochusacea (Crustacea: Peracarida). *Travaux du Muséum National d'Histoire Naturelle 'Grigore Antipa'* **43:** 47–57.

Gutu M, Iliffe TM. 1998. Description of a new hirsutiid (n. g., n. sp.) and reassignement of this family from order Mictacea to the new order, Bochusacea (Crustacea, Peracarida). *Travaux du Muséum National d'Histoire Naturelle 'Grigore Antipa'* **40:** 93–120.

Gutu M, Sieg J. 1999. Ordre des Tanaïdacés (Tanaidacea Hansen, 1895). In: Forest, J, ed.*Traité de Zoologie. Anatomie, Systématique, Biologie. Tome VII (Fascicule III a), Crustacés Péracarides*. *Mémoires de l'Institut Océanographique Fondation Albert I^er^ Monaco* 19: 353–389.

Hessler RR. 1982. The structural morphology of walking mechanisms in eumalacostracan crustaceans. *Philosophical Transactions of the Royal Society of London, Series B* **296:** 245–298.

Hessler RR, Watling L. 1999. Ordre des Mictacés. In: Forest, J, ed. *Traité de Zoologie. Anatomie, Systématique, Biologie. Tome VII (Fascicule III a), Crustacés Péracarides*. *Mémoires de l'Institut Océanographique Fondation Albert I^er^ Monaco* **19:** 85–91.

Jaume D, Christenson K. 2001. Amphi-Atlantic distribution of the subterranean amphipod family Metacrangonyctidae (Gammaridea). *Contributions to Zoology* **70:** 99–125.

Just J, Poore GCB. 1988. Second record of Hirsutiidae (Peracarida: Mictacea): *Hirsutia sandersetalia*, new species, from southeastern Australia. *Journal of Crustacean Biology* **8:** 483–488.

Langer M, Ruppersberg JP, Gorb S. 2004. Adhesion forces measured at the level of a terminal plate of the fly's seta. *Proceedings of the Royal Society of London, Series B* **271:** 2209–2215.

Larsen K. 2001. Morphological and molecular investigation of polymorphism and cryptic species in tanaid crustaceans: implications for tanaid systematics and biodiversity estimates. *Zoological Journal of the Linnean Society* **131:** 353–379.

Martin JW, Davis GE. 2001. An updated classification of the Recent Crustacea. *Natural History Museum of Los Angeles County Science Series* **39:** 1–124.

Messing CG. 1983. Postmarsupial development and growth of *Pagurapseudes largoensis* McSweeny (Crustacea, Tanaidacea). *Journal of Crustacean Biology* **3:** 380–408.

Monod T, Cals P. 1999. Ordre des Thermosbaenacés. In: Forest, J, ed. *Traité de Zoologie. Anatomie, Systématique, Biologie. Tome VII (Fascicule III a), Crustacés Péracarides*. *Mémoires de l'Institut Océanographique Fondation Albert I^er^ Monaco* **19:** 11–34.

Ohtsuka S, Hanamura Y, Kase T. 2002. A new species of *Thetispelecaris* (Crustacea: Peracarida) from submarine cave on Grand Cayman Island. *Zoological Science* **19:** 611–624.

Poore GCB, Humphreys WF. 1998. First record of Spelaeogriphacea from Australasia: a new genus and species from an aquifer in the arid Pilbara of Western Australia. *Crustaceana* **71:** 721–742.

Richter S, Scholtz G. 2001. Phylogenetic analysis of the Malacostraca (Crustacea). *Journal of Zoological Systematics and Evolutionary Research* **39:** 113–136.

Sanders HL, Hessler RR, Garner SP. 1985. *Hirsutia bathyalis*, a new unusual deep-sea benthic peracaridan crustacean from the tropical Atlantic. *Journal of Crustacean Biology* **5:** 30–57.

Siewing R. 1956. Untersuchungen zur Morphologie der Malacostraca (Crustacea). *Zoologische Jahrbücher (Anatomie)* **75:** 39–176.

Spears T, DeBry RW, Abele LG, Chodyla K. 2005. Peracarid monophyly and interordinal phylogeny inferred from nuclear small-subunit ribosomal DNA sequences (Crustacea: Malacostraca: Peracarida). *Proceedings of the Biological Society of Washington* **118:** 117–157.

Wagner HP. 1994. A monographic review of the Thermosbaenacea (Crustacea: Peracarida). *Zoologische Verhandelingen* **291:** 1–338.

Watling L. 1999. Towards understanding the relationship of the peracaridan orders: the necessity of determining exact homologies. In: Schram, FR, von Vaupel Klein, JC, eds. *Crustaceans and the Biodiversity Crisis. Proceedings of the Fourth International Crustacean Congress*, Vol. I. Leiden: NV Brill, pp. 73–89.