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Taxonomic position of and generic distinction between *Parepactophanes* Kunz, 1935 and *Taurocletodes* Kunz, 1975 (Copepoda, Canthocamptidae *incertae sedis*), with description of a new species from the Black Sea

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Both sexes of a new species of *Taurocletodes* Kunz, 1975 (Copepoda, Harpacticoida, Canthocamptidae *incertae sedis*) are described from sandy beaches along the Black Sea coast of Turkey. The genus *Taurocletodes* is removed from its synonymy with *Parepactophanes* Kunz, 1935 and re-instated as a valid genus, accommodating the type species *T. dubius* (Noodt, 1958) **comb. nov.** and *T. tumenae* **sp. nov.** Both genera can be differentiated by major differences in the segmentation of P1–P3 endopods, the absence/presence of penicillate setae on P1 endopod, the number of outer spines on P2–P4 exp-3, the armature of P2–P4 endopods and the sexual dimorphism of P2 endopod and P3 exopod. *T. tumenae* **sp. nov.** and *T. dubius* are morphologically very similar, differing in morphometric characters related to the endopodal segmentation of P1 and P4, and armature of the male P5. The controversial taxonomic status of *Parepactophanes* and *Taurocletodes* within the family Canthocamptidae is discussed. © 2004 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2004, 140, 469–486.

ADDITIONAL KEYWORDS: Harpacticoida – intertidal – *Taurocletodes dubius* **comb. nov.** – *T. tumenae* **sp. nov.** – Turkey.

INTRODUCTION

As part of an ecological review of the copepods from Schleswig-Holstein and Kiel Bay (Germany), Kunz (1935) described three new species of harpacticoids: *Horsiwella trisetosa*, *Pseudectinosoma minor* and *Parepactophanes minuta*. The latter was collected from brackish water in Bottsand (Kieler Bucht) and has since then been recorded from other low salinity habitats along both the eastern shores (Noodt, 1956, 1957) and North Sea coast (Lorenzen, 1969) of Schleswig-Holstein. The species appears to be endemic to northern Germany where it is a typical representative of the impoverished meiofaunal communities of salt-marshes ('Salzwiesen') and the supralittoral zone (Schäfer, 1936; Noodt, 1957, 1958a). It has thus far not been recorded from similar habitats in the Baltic proper (e.g. Noodt, 1970) or elsewhere in north-western Europe.

Noodt (1958b) described a second species from a sandy beach in Tenerife, which he preferred to cite as *Parepactophanes? dubia*. In the absence of males he expressed strong reservations about its familial and generic affinities. Although he recognized certain similarities with *P. minuta* in body shape, antennule, antenna, P5 and caudal rami, Noodt stated that there was no unequivocal support for common ancestry and that the generic assignment of *P.? dubia* had to be treated as provisional. Kunz (1975) created the genus *Taurocletodes* for a new species *T. gallicus*, based on a single male from Banyuls-sur-Mer. He did not mention possible relationships with *Parepactophanes*, recognizing instead morphological similarity with a number of other taxonomic 'oddballs' in the Cletodidae such as *Hemimesochra* Sars, *Heteropsyllus* T. Scott, *Mesopsyllus* Por and *Corallicletodes* Soyer. During a later study, Kunz (1983) found both sexes of *P. dubia* in the Azores and concluded that the male, previously described as *T. gallicus*, was conspecific with Noodt's (1958b) female. He relegated *Taurocletodes* to a junior

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synonym of *Parepactophanes*, a course of action he had already suggested to Wells (1981) and which Por (1986) adopted.

Kunz (1935) assigned *Parepactophanes* to the family Canthocamptidae on account of the overall similarity with *Epactophanes* Mrázek in the segmentation of the antennule and swimming legs, the structure of the antennary exopod, and the morphology of the caudal rami and anal operculum. His justification for treating it as sufficiently distinct from the latter was based on the 1-segmented nature of the P2–P3 endopods and the fusion of the baseopod and exopod in the fifth pair of legs. After re-examination of *P. minuta*, Lang (*in litt.* to Kunz) refuted a relationship with the Canthocamptidae in general and *Epactophanes* in particular. Instead, he suggested placing *P. minuta* in the Cletodidae and, based on the confluent fifth legs and incomplete fusion of the genital double-somite, considered it to be most closely related to the genus *Cletocamptus* Shmankevich, a view subsequently accepted by Kunz (1937) and re-iterated by Lang (1948). Por's (1986) controversial review of the Cletodidae resulted in the recognition of four new families and the removal of some genera to a new subfamily Hemimesochrinae within the Canthocamptidae. The remaining cletodid taxa, which did not fit any of his new family concepts, were merely reallocated to the Canthocamptidae as *incertae sedis*, i.e. *Parepactophanes*, *Cletocamptus*, *Leimia* Willey, *Hemimesochra rapiens* Becker (now *Perucamptus*; see Huys & Thistle, 1989) and *Heteropsyllus serratus* Schriever. Bodin (1997) listed *Parepactophanes* under the Hemimesochrinae but did not comment on this re-assignment.

During the course of a survey along the Turkish Black Sea coast numerous specimens of a new species related to *P. dubia* were encountered, the description of which is given below. In this paper we also re-evaluate the generic distinctiveness of *Parepactophanes* and *Taurocletodes* and reconsider their floating taxonomic position within the family Canthocamptidae.

MATERIAL AND METHODS

Harpacticoids were collected using the Karaman–Chappuis method (Delamare Deboutteville, 1954). Specimens were dissected in lactic acid and the parts mounted on slides in lactophenol mounting medium. Glass fibres were added to prevent the animal and appendages from being compressed by the coverslip and to facilitate rotation and manipulation, allowing observation from all angles. Preparations were sealed with transparent nail varnish. All drawings have been prepared using a camera lucida on an Olympus BX-50 differential interference contrast microscope. Measurements were made with an ocular micrometer.

Scale bars in illustrations and SEM micrographs are in μm .

Males and females of *Taurocletodes tumenae* sp. nov. were examined with a Philips XL30 scanning electron microscope. Specimens were prepared by dehydration through graded acetone, critical point dried, mounted on stubs and sputter-coated with gold-palladium alloy.

The descriptive terminology is adopted from Huys *et al.* (1996). Abbreviations used in the text are: ae, aesthetasc; P1–P6, first to sixth thoracopod; exp (enp)-1 (2, 3) to denote the proximal (middle, distal) segment of a ramus.

Attempts to trace the types of *Parepactophanes minuta*, *P. dubia* and *Taurocletodes gallicus* failed. The male holotype of the latter was deposited by Kunz (1975) in the Zoologisches Museum in Hamburg, but inspection of the vial (reg. no. K-30348) proved it to be empty (A. Brandt, pers. comm.). The type material of *P. minuta* as well as the remainder of Kunz' earlier collections were destroyed during World War II when the Institut für Meereskunde was heavily bombed in 1944 (Schriever, 1984). The personal collections of the late Drs Wolfram Noodt (types of *P. dubia*) and Helmut Kunz (Azorian material of *T. gallicus*) have as yet not been deposited in a museum and proved impossible to locate. Type material of *Taurocletodes tumenae* is deposited in the collections of the Natural History Museum, London (NHM) and Balıkesir University (BU).

RESULTS

FAMILY CANTHOCAMPTIDAE BRADY, 1880

GENUS *TAUROCLETODES* KUNZ, 1975

TAUROCLETODES TUMENAE SP. NOV.

Type locality: Sandy beach 10 km west of Akçaabat, Trabzon province (station 39) (Turkey).

Type material: Holotype ♀ in alcohol (reg. no. NHM 2003.704). Paratypes preserved in alcohol are 20 ♀♀ and 30 ♂♂ (deposited in NHM under reg. nos NHM 2003.705–754), and ten ♀♀ and ten ♂♂ (deposited in BU). Additional paratypes dissected on slides deposited in BU. Collected on 11 July 2001 from type locality; leg. S. Karaytug and S. Sak.

Other material. Numerous specimens of both sexes (in alcohol) collected from sandy beach in Beşikdüzü, Trabzon province (station 38a), deposited in BU. Leg. S. Karaytug and S. Sak, 11 July 2001.

Description (based on dissected paratypes)

Female: Total body length from tip of rostrum to posterior margin of caudal rami: 290–370 μm (mean = 336 μm ; $n = 10$). Body (Fig. 1C) more or less

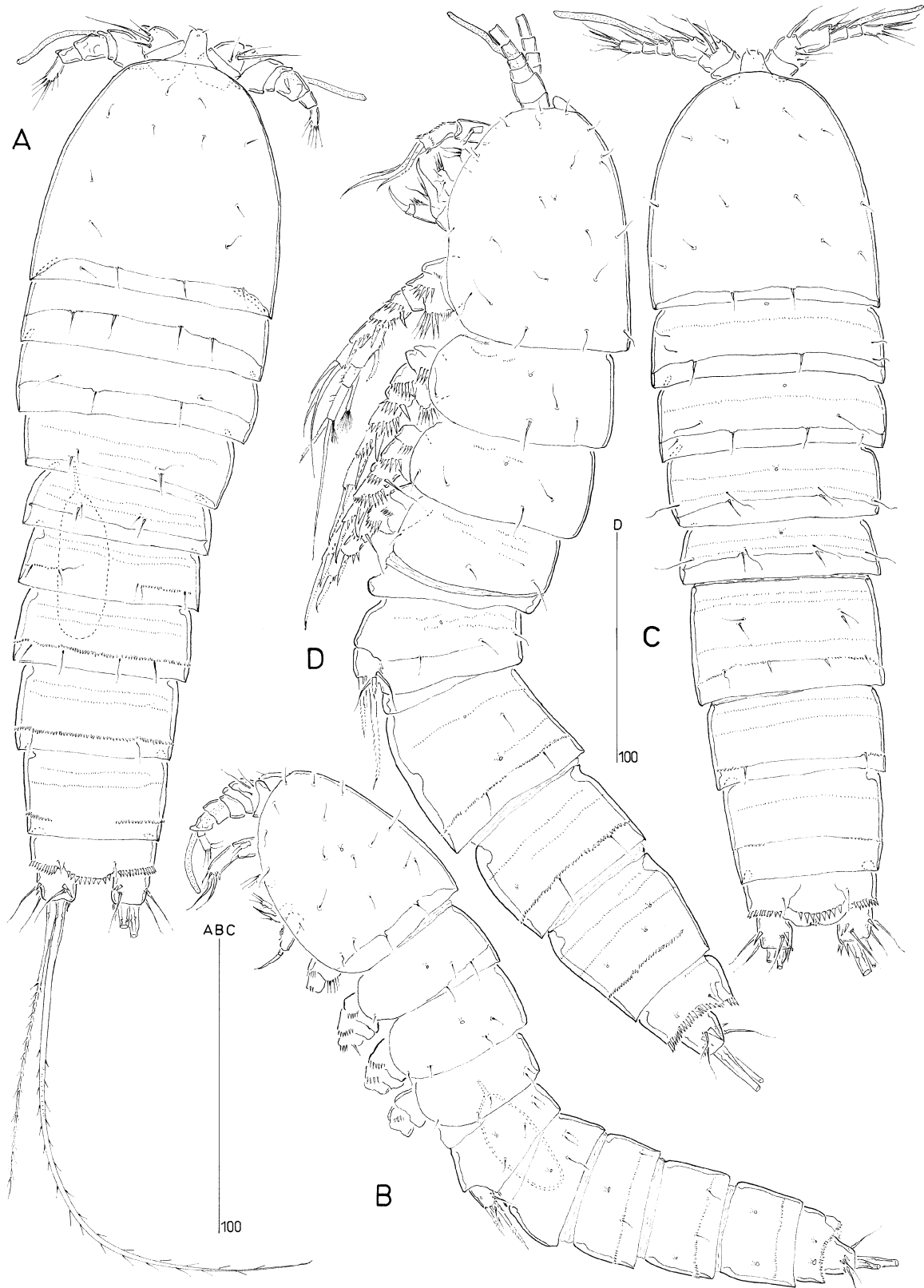


Figure 1. *Taurocletodes tumenae* sp. nov. A, habitus ♂, dorsal. B, habitus ♂, lateral. C, habitus ♀, dorsal. D, habitus ♀, lateral.

cylindrical, gradually tapering posteriorly; maximum width measured at posterior margin of cephalothorax. Integument of somites with transverse rows of minute spinules as figured (Figs 1C,D, 2A). Sensillar pattern as figured; somites bearing P4–P5 and genital half of double-somite with pairs of closely set sensillae dorsally (Figs 1C, 2A). Posterior margin of body somites with plain hyaline frill (Fig. 1C).

Rostrum (Figs 3A, 8B) elongate, demarcated and widest at base; with two delicate sensillae and mid-dorsal pore; rounded at tip; base surrounded by membranous areas.

Genital double-somite (Fig. 2A,B) wider than long; without indication of original segmentation except for sensillar pattern and paired cuticular reinforcements ventrally (attachment sites of longitudinal trunk muscles; Fig. 2B). Double rows of tiny spinules present on either lateral side of genital field; midventral row posterior to copulatory pore; larger spinules forming transverse row around posterior margin (interrupted middorsally). Genital field located far anteriorly (Fig. 2B). Genital apertures paired (Fig. 6G), each closed off by operculum derived from vestigial sixth legs, and bearing three nonarticulating, short pinnate spines; copulatory pore large, leading to short and wide copulatory duct; seminal receptacles unconfirmed.

Free abdominal somites with tiny spinules anteriorly and larger spinules around posterior margin (except middorsally). Anal somite with row of minute spinules between dorsal sensillate tubercles (Fig. 2A); operculum multispinose with 8–10 spike-like projections (Fig. 4D). Anus large, positioned terminally between caudal rami; anal fringe deeply incised forming setular lappets (partly concealed by anal operculum in Fig. 4D).

Caudal rami (Fig. 4D) short and about as long as width; with six setae, seta I absent; spinules present around ventral posterior margin, inner margin and around base of seta II; with two pores dorsally; setae II–III bare; setae IV–V strongly developed and bipinnate (Fig. 2A); seta VI shorter than caudal ramus; seta VII tri-articulate at base.

Antennule (Fig. 3B) short, 6-segmented; segmental membranes well developed; with outer sclerite at base of segment 1 (Fig. 3A). Segment 1 short and wide; with tiny seta and spinules near anterodistal margin. Posteriormost seta on segment 2 plumose. Segment 3 largest with long aesthetasc (L: 35 µm) fused at base to short seta. Armature formula: 1-[1], 2-[7 + 1 plumose], 3-[6 + (1 + ae)], 4-[1], 5-[2], 6-[7 + acrothek]. Apical acrothek consisting of short aesthetasc (L: 10 µm) and two slender setae. Setae arising from minute socles present on segments 3 (2), 4 (1) and 6 (5).

Antenna (Fig. 3C, D) comprising coxa, allobasis and 1-segmented rami. Coxa small and naked. Allobasis

with spinular row near base of exopod; abexopodal seta unipinnate (probably basal in origin). Exopod an elongate segment with one apical and one subapical unipinnate seta; with transverse spinule row halfway along the segment length. Free endopod with two rows of coarse spinules near inner margin and finer spinules at outer distal corner; lateral armature consisting of two unipinnate spines and one fine seta; apical armature consisting of two unipinnate spines and three geniculate setae (largest spiniform, with large spinules proximal to geniculation, and subapical tubular extension).

Mandible (Fig. 3E). Coxa elongate, forming narrow gnathobase provided with series of multicuspitate teeth distally and unipinnate seta at dorsal corner (Fig. 3F); with spinule row near implantation of palp. Palp 1-segmented with four setae arising from subdistal outer margin; with spinule row apically.

Maxillule (Fig. 3G). Praecoxa with few spinules around proximal outer margin; arthrite delimited at base by transverse surface suture, with two tube-setae on anterior surface and four anterior plus four posterior elements around distal margin. Coxal endite surrounded at base by membranous area, cylindrical; with one seta and one unipinnate curved spine. Palp represented by single segment; with tiny spinule row on posterior surface; armature consisting of four setae along outer margin, one seta arising from anterior surface, and two setae plus one unipinnate claw apically.

Maxilla (Fig. 4C) comprising syncoxa and allobasis. Syncoxa with numerous spinule rows as figured; with two cylindrical endites; each endite with two naked setae and drawn out into spine with very long, medially directed setules. Allobasis forming acutely recurved spinous endite with spinules along medial margin; accessory armature represented by two naked setae; endopod completely incorporated into allobasis, represented by three naked setae arising from membranous area.

Maxilliped (Fig. 3H) subchelate, comprising syncoxa, basis and 1-segmented endopod. Syncoxa with few spinules at base and strong pinnate spine at distal inner corner. Basis unarmed, with surface spinule row, long spinules along palmar margin and few spinules near distal outer corner. Area between basis and endopod with small sclerite surrounded by membrane. Endopod with one small accessory seta and drawn out into long acutely curved, naked claw.

P1 (Fig. 5A). Intercoxal sclerite wide, without ornamentation. Praecoxa well developed, with anterior spinule row. Coxa very wide, forming lobate outer expansion; with large spinules near outer margin and minute spinule rows on both anterior and posterior surfaces. Basis much narrower than coxa, anterior surface with secretory pore and various spinule rows

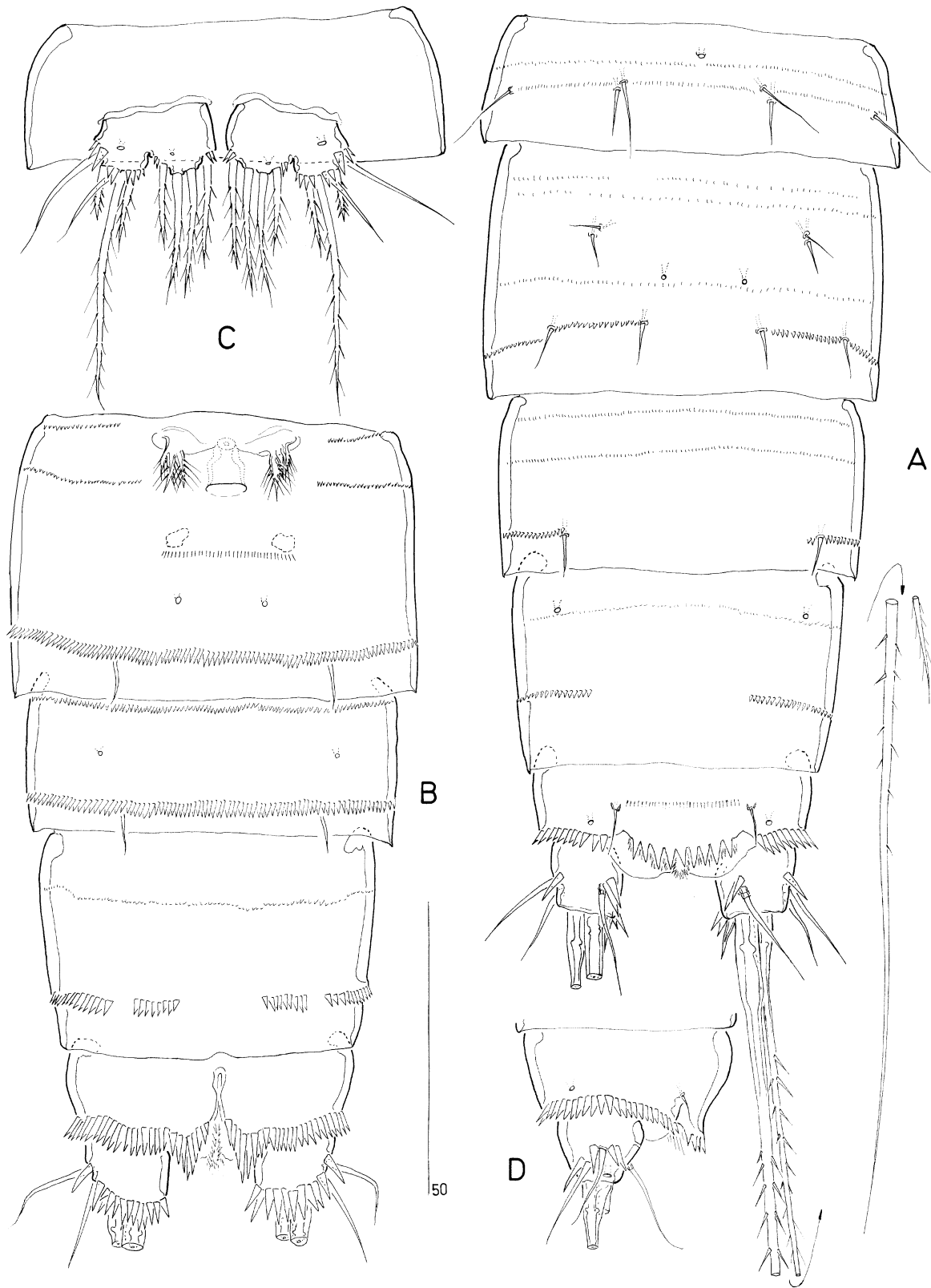


Figure 2. *Taurocletodes tumenae* sp. nov. Female. A, urosome, dorsal. B, urosome (excluding P5-bearing somite), ventral. C, fifth pair of legs, anterior. D, anal somite and left caudal ramus, lateral.

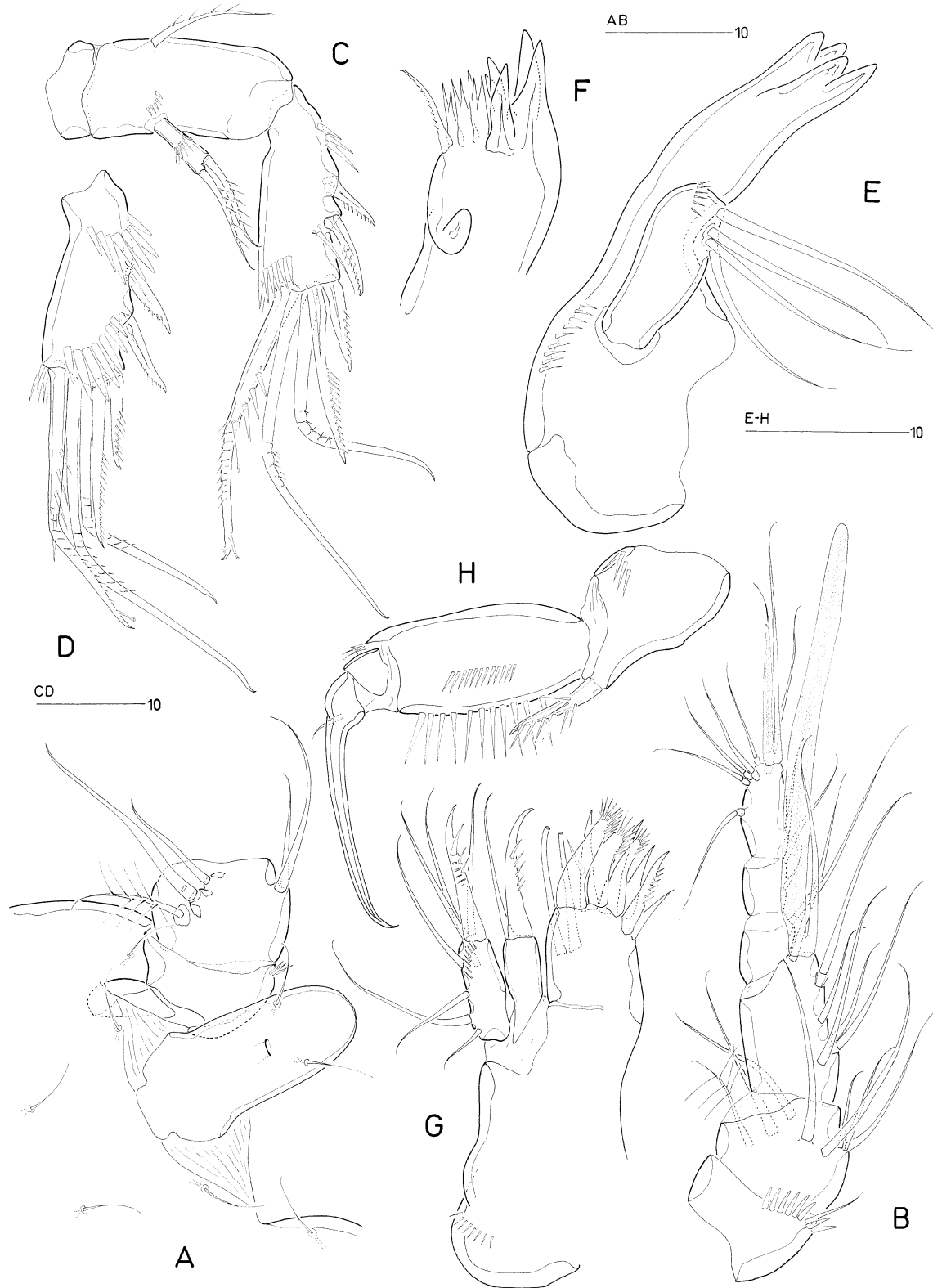


Figure 3. *Taurocletodes tumenae* sp. nov. Female. A, rostrum and proximal segments of left antennule, dorsal. B, antennule, anterior. C, antenna, outer lateral. D, antennary endopod, medial. E, mandible. F, mandibular gnathobase. G, maxillule, posterior. H, maxilliped.

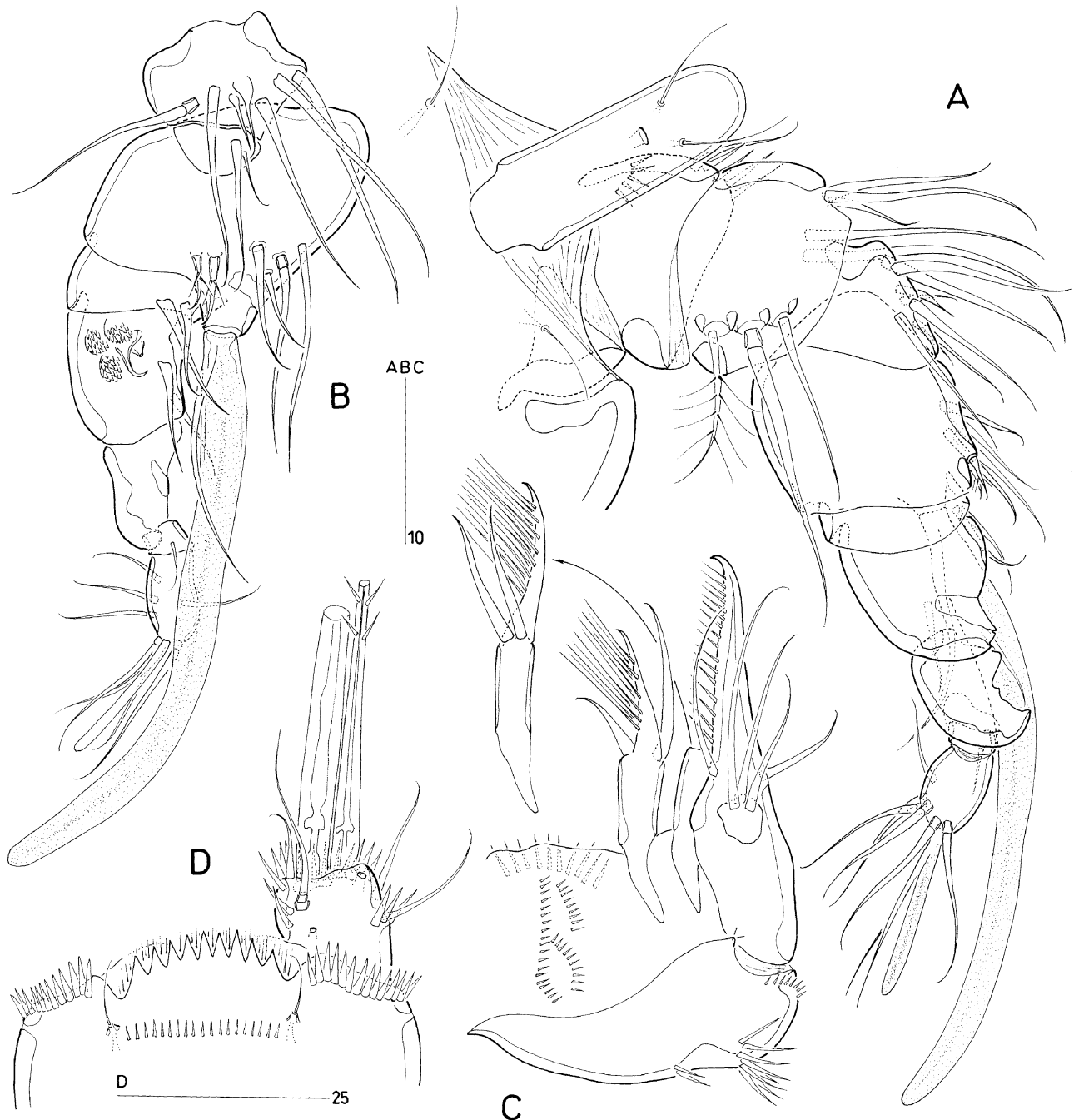


Figure 4. *Taurocletodes tumenae* sp. nov. A, rostrum and right antennule ♂, dorsal (for complete armature of segments 3–4 see B). B, antennule ♂, segments 3–10, ventral. C, maxilla (inset showing distal syncoxal endite). D, anal somite and left caudal ramus.

as figured; outer spine naked, inner spine pinnate. Rami 3-segmented. Exopod segments with coarse spinules along outer and distal margins, inner margins naked; inner seta of exp-2 minute and easily overlooked; outer spine of exp-1 and -2 unipinnate and with subapical tubular extension; exp-3 with two unipinnate spines and two slender, weakly geniculate

setae bearing fine spinules near apex. Endopod (Fig. 5B) much longer than exopod, prehensile; tapering distally, with large arthroal membranes between segments; enp-1 with spinules along outer margin and bipinnate inner seta; enp-2 much shorter than proximal and distal segments, with spinules along outer margin and large, penicillate inner seta arising from

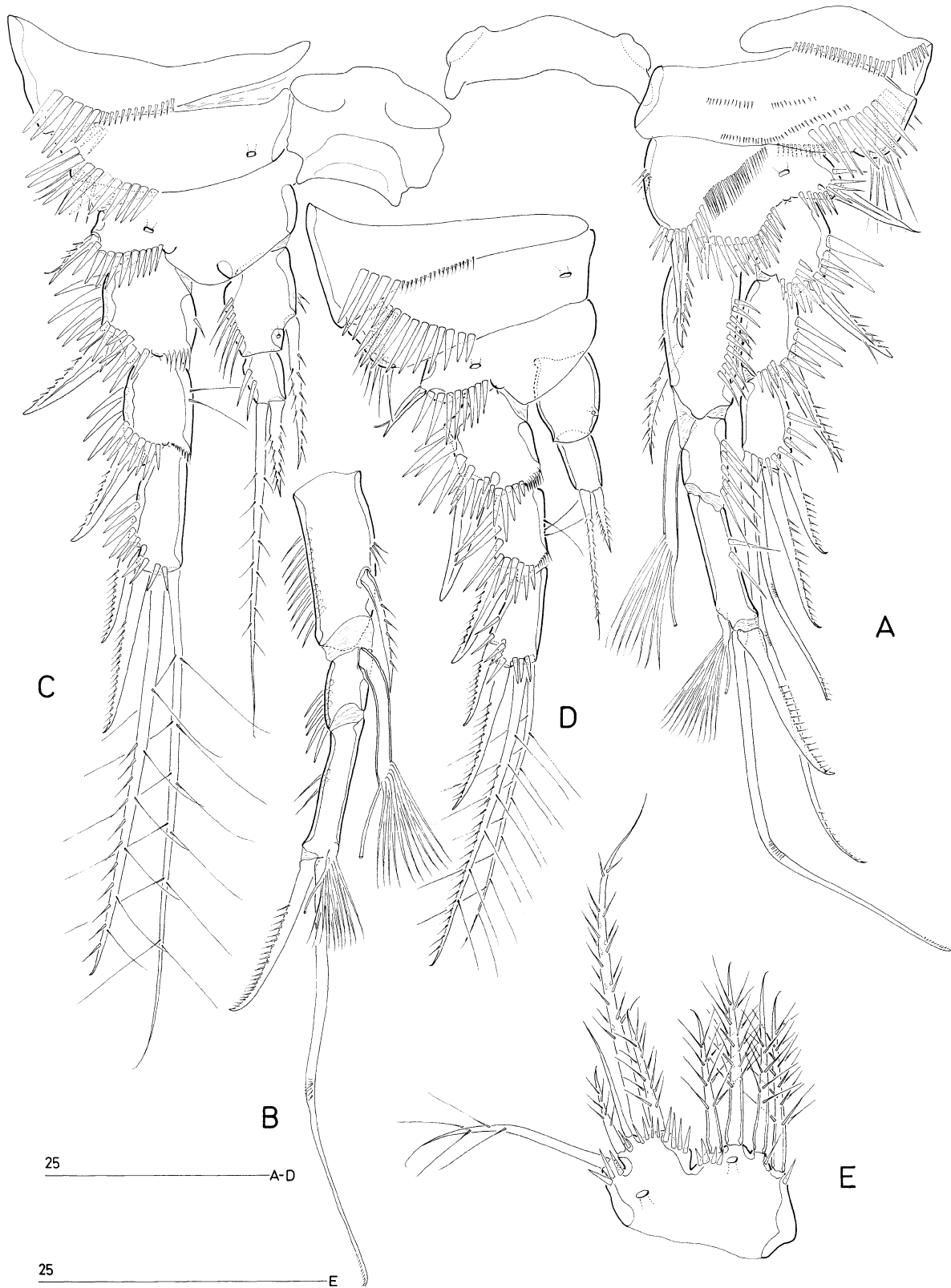


Figure 5. *Taurocletodes tumenae* sp. nov. A, P1 ♀, anterior. B, P1 endopod ♀, posterior. C, P2 ♀, anterior. D, P2 ♂, anterior. E, left P5 ♀, anterior.

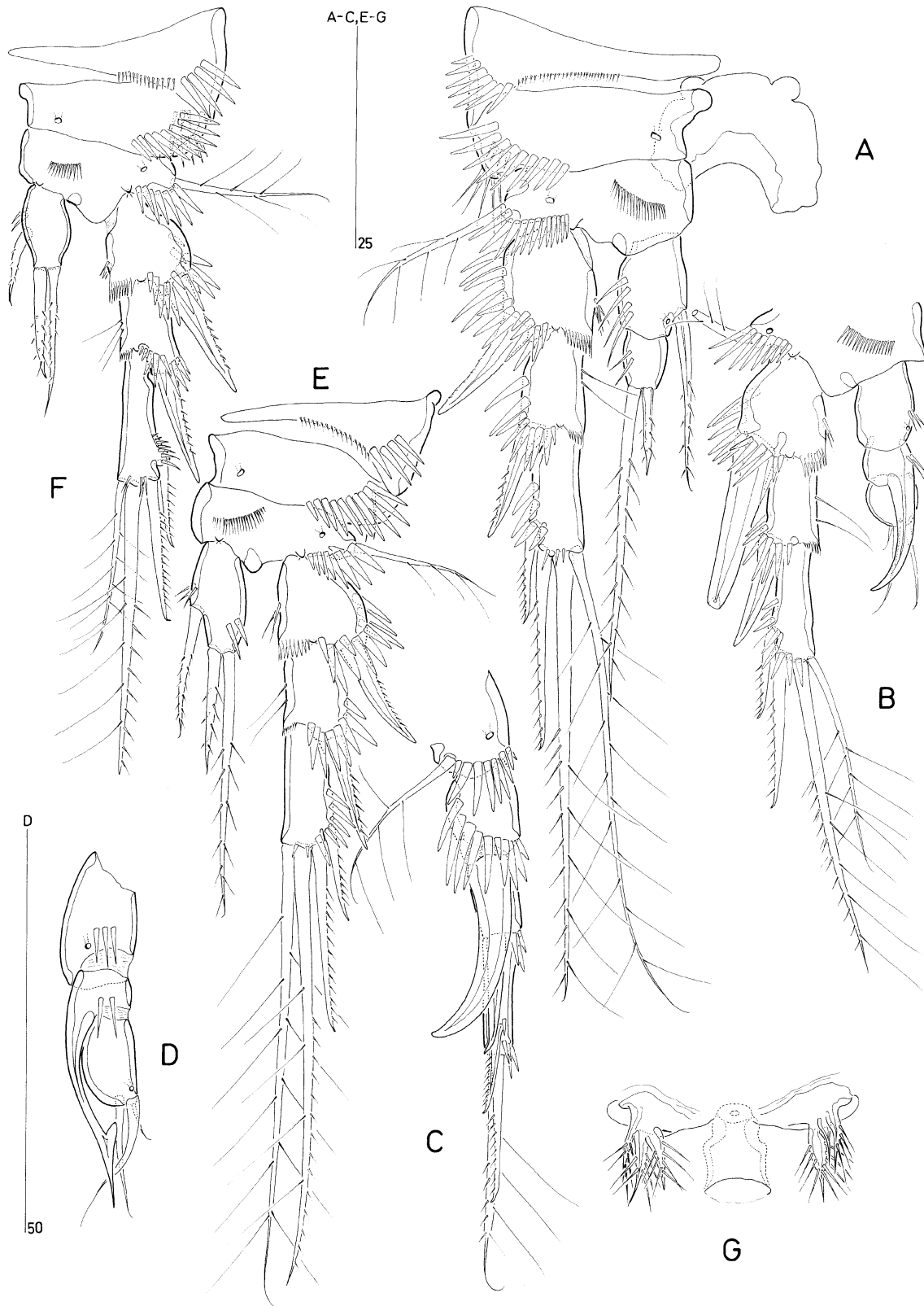


Figure 6. *Taurocletodes tumenae* sp. nov. A, P3 ♀, anterior. B, P3 ♂ (excluding praecoxa and coxa), anterior. C, P3 exopod ♂, outer lateral. D, P3 endopod ♂, medial. E, P4 ♀, anterior. F, P4 ♂, anterior. G, ♀ genital field.

posterior surface; enp-3 with two spinules along outer margin, a small, penicillate inner seta subdistally, and one unipinnate spine plus one long geniculate seta with serrate tip distally. Penicillate setae on enp-2 and -3 with tubular extension apically (arrowed in Fig. 9A) and subapical tuft of flat setules; seta on enp-2 with swollen shaft, that on enp-3 fused at base to segment.

P2–P4 (Figs 5C, 6A,E). Intercoxal sclerites with concave free margin and without ornamentation. Praecoxae with coarse spinules near outer margin and fine spinules around distal margin. Coxae with anterior pore near inner margin and spinule rows on both anterior and posterior surfaces as figured. Bases with outer unipinnate spine (with subapical tubular extension; P2) or plumose seta (P3–P4); anterior surface with secretory pore and setular row (not in P2; Fig. 5C) and with coarse spinules around distal margin near insertion of exopod. Exopods 3-segmented, endopods 1- (P4) or 2-segmented (P2–P3). All exopod segments with coarse spinules around outer margin; exp-1 and -2 typically with few spinules or setules along inner margin; hyaline frills incised; outer portion of exp-1 expanded; outer spines of exp-1 and -2 stout and unipinnate. Endopods small; with outer marginal spinules on all segments; P2–P3 enp-1 with anterior surface pore; inner distal element on enp-2 (P2–P3) or enp-1 (P4) short and spiniform, outer distal element long and setiform. Spine and seta formula as follows (apo = apophysis):

	Exopod	Endopod
P1	0.1.022	1.1.111
P2	0.0.022	1.020 [0.020 in ♂]
P3	0.0.022	1.020 [0.apo.030 in ♂]
P4	0.0.022	120

Fifth legs closely set together (Fig. 2C), without intercoxal sclerite. Baseoendopod and exopod fused forming bilobate plate (Fig. 5E); inner lobe with four multipinnate setae; outer lobe with one very long and two short (multi)pinnate setae plus one naked seta; both lobes with few spinules around distal margin and one anterior surface pore; outer basal seta sparsely plumose, arising from very short setophore surrounded by spinules.

Male: Total body length from tip of rostrum to posterior margin of caudal rami: 260–340 µm (mean = 300 µm; $n = 10$). Sexual dimorphism in rostrum, antennule, P2–P6, and in genital segmentation. Ornamentation of body (Figs 1A,B, 7A,B) generally as in female except for some small differences in spinulation, particularly on urosome. First abdominal somite with paired rounded internal reinforcements midventrally (attachment sites of longitudinal trunk

muscles; Fig. 7B). Rostrum (Fig. 4A) distinctly longer and narrower than in ♀.

Antennule (Figs 4A,B, 8A–D, 9B) 10-segmented, haplocer with geniculation between segments 7 and 8. Segment 1 with small sclerite at proximal posterior corner. Segment 3 U-shaped, with five articulating setae and two setae fused to segment. Segment 4 a small sclerite with two setae (Fig. 4A). Segment 5 swollen, forming lobate expansion anteriorly (Figs 4B, 8A); with large aesthetasc arising from pedestal and fused basally to short slender seta. Segment 7 with three modified elements (arrowed in Figs 8C, 9B), one basally fused element, two naked setae and one raised tube-pore. Segment 8 with anterior distal corner forming recurved dentate process (possibly representing modified element; arrowed in Fig. 8C,D), concealing three raised tube-pores. Segment 9 minute, with one tiny seta. Armature formula 1-[1], 2-[7 + 1 plumose], 3-[5 + 2 basally fused], 4-[2], 5-[4 + 2 pinnate + (1 + ae)], 6-[2], 7-[2 + 1 basally fused + 3 modified], 8-[1 dentate process], 9-[1], 10-[6 + acrothek]. Acrothek consisting of short aesthetasc fused basally to two bare setae. Scaled setae present on segments 2 (1), 3(1), 5(1) and 10(5). Many setae with terminal pore (Fig. 8B,C).

P2 (Fig. 5D) as in female except for (1) exopod relatively shorter; (2) exp-1 with outer spine naked instead of pinnate; (3) exp-3 with distal elements relatively shorter, inner distal seta shorter than outer one; (4) endopodal segments without spinules along outer margin; (5) enp-1 smaller and without inner element; (6) enp-2 outer distal seta much shorter.

P3 (Fig. 6B–D) strongly sexually dimorphic. Protopod as in female. Outer spine of exp-1 enlarged, naked, reaching to middle of exp-3 and backwardly recurved (Fig. 6C). Outer spine of exp-2 naked instead of unipinnate (Fig. 6B). Distal elements of exp-3 reduced in size with inner distal seta markedly shorter than outer seta (instead of equally long). Endopod 3-segmented; enp-1 unarmed, with anterior surface pore and few spinules around inner margin (Fig. 6D); enp-2 forming anterior apophysis with barbed apical part (Fig. 6D), with two spinules along inner margin; enp-3 round, with surface pore, one vestigial and two naked setae.

P4 (Fig. 6F). Protopod as in female. Exp-2 with smaller spinules around outer distal corner. Exp-3 constricted in proximal half; distal outer spine and apical setae shorter than in female; inner distal seta much shorter than outer one. Endopod 1-segmented, smaller than in female; inner seta and outer distal seta reduced in size.

Fifth legs (Fig. 7B) medially fused. Exopod and baseoendopod fused, forming bilobate plate with two anterior surface pores (Fig. 9C). Endopodal lobe with two spines, exopodal lobe with two pinnate spines, one naked and two plumose setae.

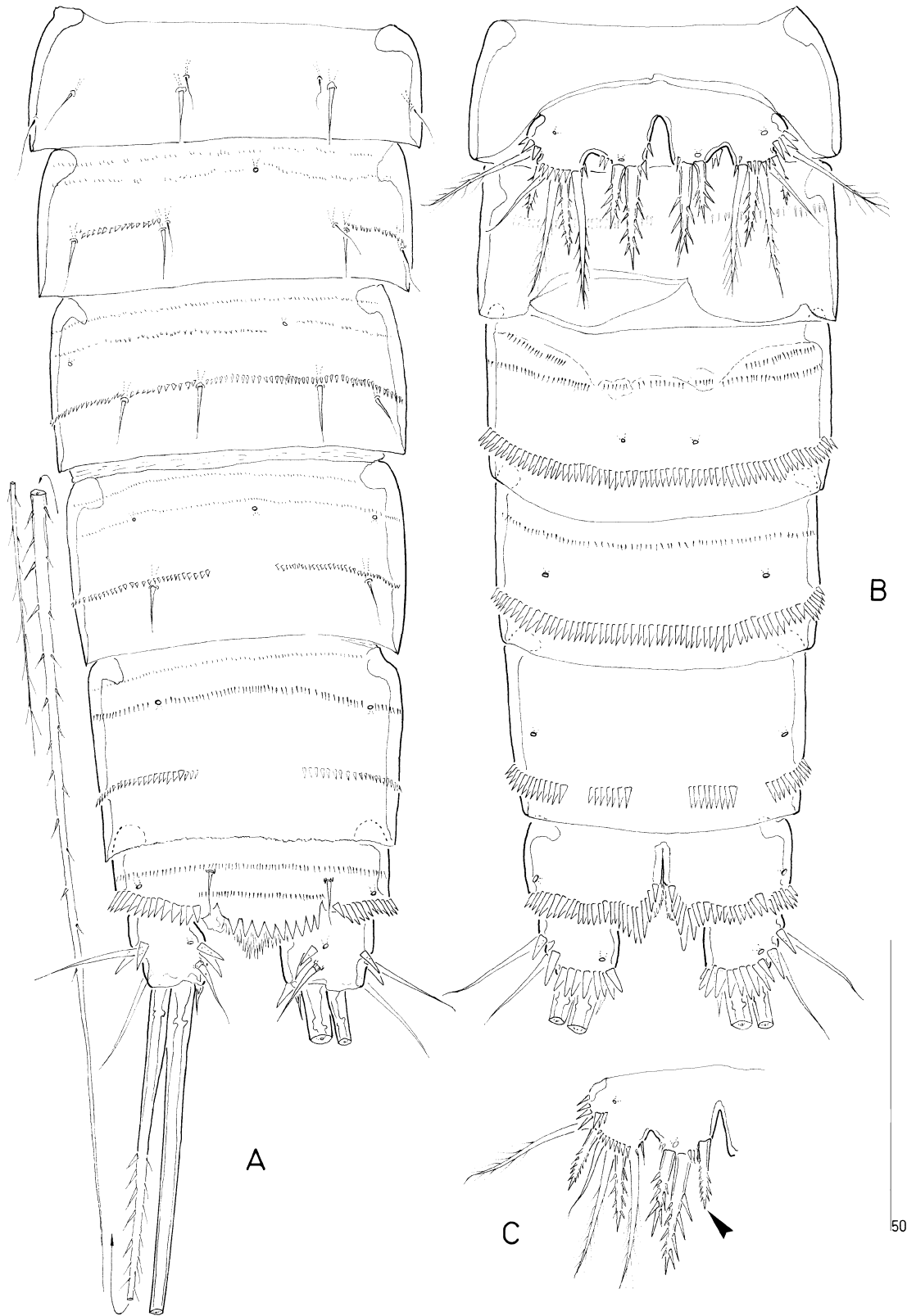


Figure 7. *Taurocletodes tumenae* sp. nov. Male. A, urosome, dorsal. B, urosome, ventral. C, aberrant P5 (supernumerary inner spine arrowed).

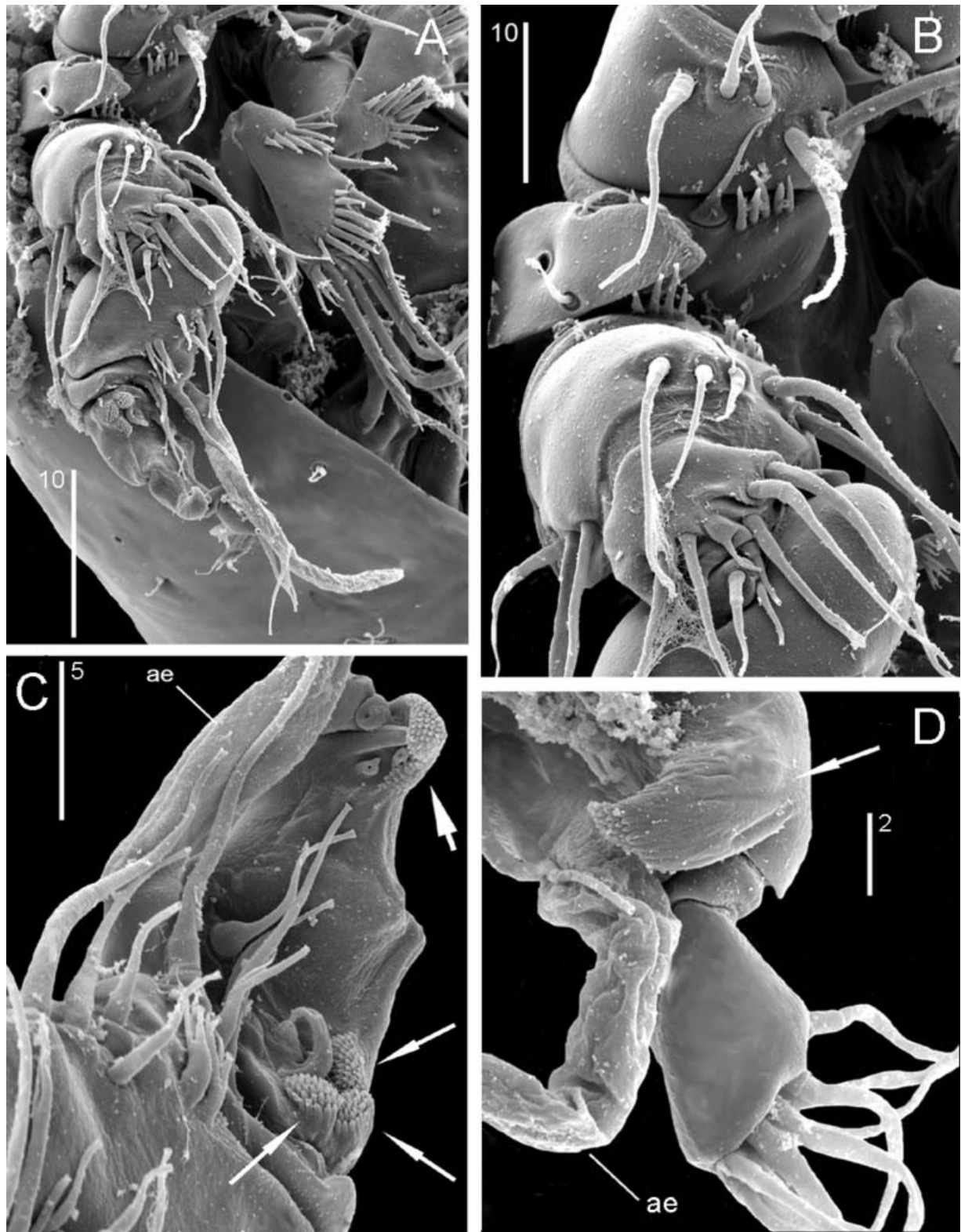


Figure 8. *Taurocletodes tumenae* sp. nov. SEM micrographs, male. A, cephalothorax, ventral, showing rostrum, antennule and antenna. B, rostrum and proximal segments of antennules. C, antennule, segments around geniculation (slender arrows: modified elements on segment 7; large arrow: recurved dentate process on segment 8). D, antennule, segments 8–10 (recurved dentate process on segment 8 arrowed) ae = aesthetasc.

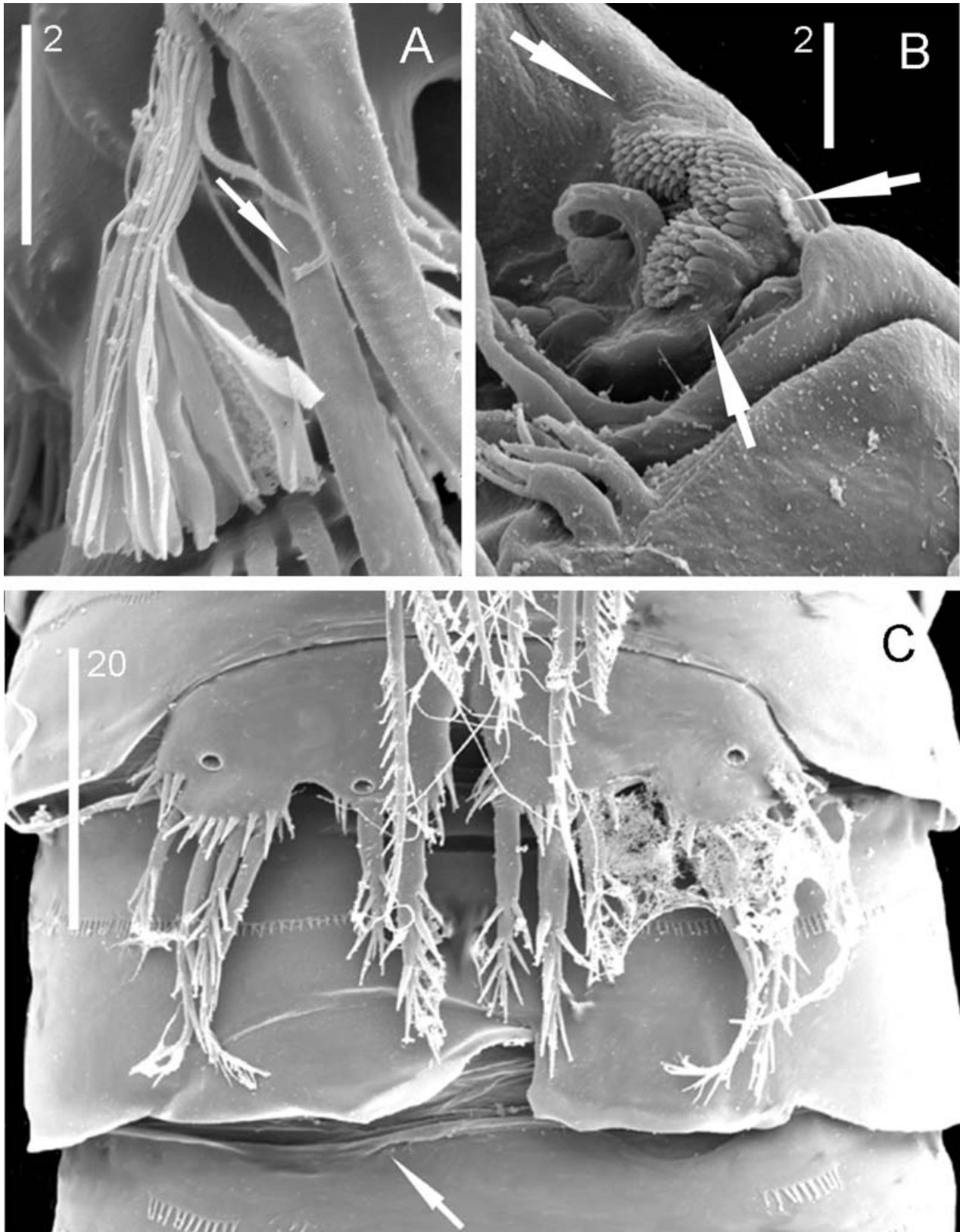


Figure 9. *Taurocletodes tumenae* sp. nov. A, P1 endopod ♀, penicillate seta on enp-3 (tubular extension arrowed). B, antennule ♂, segments 5–7, anterior (modified elements arrowed). C, fifth and sixth legs ♂, ventral (functional gonopore arrowed).

Sixth legs (Figs 7B, 9C) asymmetrical, fused to somite. Operculum closing off functional gonopore (arrowed in Fig. 9C) delimited by surface suture.

Variability. Slight differences in size and ornamentation were observed in the setae of the female sixth legs (Fig. 6G). Three paratypic males displayed a supernumerary inner spine on the endopodal lobe of the P5 (arrowed in Fig. 7C). The male sixth legs show either dextral or sinistral arrangements depending on whether the right or left testes, vas deferens and gonopore are functional.

Etymology. The species is dedicated to Prof. Dr Gülen-dam Tümen, Manager of the School of Nursery at the University of Balıkesir, in recognition of her continuous support and encouragement to the senior author.

DISCUSSION

VALIDITY OF *TAUROCLETODES* AND GENERIC DIAGNOSES

Proper comparison between the type species *P. minuta* and the material variously identified or named as *P. dubia*, *T. gallicus* or *P. dubia* has until now been hampered by the fragmentary nature of the corresponding (re)descriptions or the unavailability of either males (Noodt, 1958b) or females (Kunz, 1975). Consequently, the issue whether the respective type species of *Parepactophanes* and *Taurocletodes* are congeneric (Kunz, 1983), has not been satisfactorily addressed. The description of both sexes of *T. tumenae* now enables us to subject the proposed synonymy of *Parepactophanes* and *Taurocletodes* to more scrutiny. Although Noodt (1958b) identified *Parepactophanes* as the closest match for *P. dubia*, it is obvious that he intended only provisional generic assignment. Amongst other, less significant, features he recognized the 3-segmented P1 endopod in the Tenerife material as the major stumbling block to its inclusion in *Parepactophanes*, since both the type species *P. minuta* and the allegedly most closely related genera (*Cletocampus*, *Limnocletodes* Borutzky) exhibit the 2-segmented condition.

Parepactophanes minuta has not been redescribed since Kunz' (1935) original description, which omitted illustrations of the mouthparts but was otherwise sufficiently informative by contemporary standards. Using Kunz' (1935) illustrations as the basis for comparison with *T. tumenae* we believe that there are sufficient grounds to maintain the generic distinction between *Parepactophanes* and *Taurocletodes*. Most diagnostic characters readily emerge from a comparison of the swimming legs. We have no reason to doubt the accuracy of Kunz' observations of the swimming legs since Noodt, who was generally more detailed in

his approach and identified *P. minuta* on more than one occasion (Noodt, 1956, 1957, 1958a), would undoubtedly have reported oversights or ambiguities in the original description when attempting to overcome the difficulties in placing *P. dubia*.

The P1 endopod in *Parepactophanes* is as long as the exopod, 2-segmented, displays a [1.111] armature formula and lacks penicillate setae on the distal segment. In *Taurocletodes* it is distinctly longer than the exopod, 3-segmented, exhibiting a formula [1.1.111] with the inner seta on the middle and distal segments clearly penicillate in nature (Figs 5A,B, 9A) (for absence of these setae in Kunz' (1975) description of *T. gallicus*, see below). The distal exopod segment of P2–P4 has two outer spines in *Taurocletodes* but this number is reduced to one in *Parepactophanes*. In addition, *P. minuta* possesses an inner seta on P4 exp-3, which is lacking in all *Taurocletodes* species. Males of both genera can be readily distinguished by the sexual dimorphism on the P2–P3 exopods, being completely absent in *Parepactophanes*, but clearly expressed in the outer spine of the proximal segment in *Taurocletodes*. This modification is moderate in P2, involving modest size increase of the spine and loss of surface ornamentation (Fig. 5C, D). It attains extreme proportions on the proximal exopod segment of P3 where the massive spine arises from a distinct pedestal, formed by the outer portion of the segment, and reaches to halfway along the distal segment (Fig. 6B,C).

Both genera also differ in the segmentation and sexual dimorphism of the P2–P3 endopods. In *P. minuta* the endopods are 1-segmented and that of the P2 not sexually dimorphic. In *Taurocletodes* both endopods are 2-segmented but the inner seta on enp-1 found in the female P2 (and corresponding to the inner seta of the 1-segmented endopod of *Parepactophanes*) is absent in males. The sexual dimorphism of the P3 endopod is similar in both genera although the fine details of segmentation and ornamentation are not discernible in Kunz' drawings of *P. minuta*. The distal portion of the male P3 endopod appears to extend into an apophysis and the inner seta present in the female is lost in the male (as in *Taurocletodes*; Fig. 6B,D).

Finally, in *Parepactophanes* the rostrum is short and blunt, and the female P5 baseopod bears two spines and two setae. In *Taurocletodes*, the rostrum is long and spatulate (Figs 3A, 4A) and the endopodal lobe of the female P5 carries four setiform elements (Fig. 5E).

On the basis of the suite of generic diagnostics identified above we refute Kunz' (1983) course of action to relegate *Taurocletodes* to a junior synonym of *Parepactophanes*, and instead re-instate the former as a valid genus, with *T. dubius* (Noodt, 1958) comb. nov. as its type species. Amended generic diagnoses for both genera are given below.

GENUS PAREPACTOPHANES KUNZ, 1935

Diagnosis: Canthocamptidae. Small-sized (<0.5 mm). Body cylindrical, prosome hardly wider than urosome. Anal operculum multispinose (bare in ♂?). Nauplius eye present. Rostrum short and blunt. Antennule 6-segmented in ♀, with aesthetasc on segment 3 (and most likely as part of acrothek on segment 6); all elements setiform and bare; subchirocer in ♂. Antenna with allobasis bearing one abexopodal seta; exopod 1-segmented, bisetose. Mandible with 1-segmented palp bearing four setae. Maxillule and maxilla unconfirmed. Maxilliped subchelate, syncoxa with seta, basis unarmed, endopod drawn out into claw. P1 with 3-segmented exopod and 2-segmented endopod; exp-2 without inner seta; enp-2 with unmodified setae; endopod as long as exopod. P2–P4 ♀ short and robust, with 3-segmented exopods and 1-segmented endopods. Exopods with one outer spine on exp-3; without sexual dimorphism; P4 exp-3 inner seta present. Endopods P2 and P4 not sexually dimorphic; ♂ P3 endopod (in)completely 2-segmented; drawn out into slender apophysis, without inner seta on enp-1. P1–P4 armature formula as follows:

	Exopod	Endopod
P1	0.0.022	1.111
P2	0.0.021	120
P3	0.0.021	120 [modified in ♂]
P4	0.0.121	020

Fifth pair of legs medially free in ♀, presumably fused in ♂. Exopod and baseoendopod fused in both sexes. Exopodal lobe with four elements in ♀, five in ♂. Endopodal lobe with two spines and two setae in ♀, with two setae in ♂. Genital field in ♀ and sixth legs in ♂ unconfirmed. Caudal rami about as long as wide; setae IV–V well developed.

Type and only species: *Parepactophanes minuta* Kunz, 1935 (by monotypy).

Remarks: Kunz (1935) noted sexual dimorphism in the anal operculum, being multispinose in the female and bare in the male. He also suggested that eggs were laid freely in sediment (as in the Darcythompsoniidae) since no egg-sacs were observed despite the ovaries being fully mature. Both observations require confirmation.

GENUS TAUROCLETODES KUNZ, 1975

Diagnosis: Canthocamptidae. Small-sized (<0.5 mm). Body robust, more or less cylindrical with prosome slightly wider than urosome. Anal operculum multispinose. Nauplius eye present. Rostrum long, elongate and hyaline. Antennule 6-segmented in ♀, with aes-

thetasc on segment 3 and as part of acrothek on segment 6; all elements setiform and bare except for posteriormost seta on segment 2; 10-segmented in ♂, with geniculation between segments 7–8. Antenna with allobasis bearing one abexopodal seta; exopod 1-segmented, bisetose. Mandible with 1-segmented palp bearing four setae. Maxillule with two elements on coxa, four on basis; endopod and exopod represented by one and three setae, respectively. Maxilla with three endites. Maxilliped subchelate, syncoxa with strong spine, basis unarmed, endopod drawn out into claw. P1 with 3-segmented rami; exp-2 with small inner seta; enp-2 with long penicillate seta near boundary with enp-1, enp-3 with short penicillate seta near inner distal corner; endopod much longer than exopod. P2–P4 ♀ short and robust; with 3-segmented exopods and 2-segmented (P2–P3) or 1-segmented (P4) endopods. Exopods with two outer spines on exp-3; P4 exp-3 inner seta absent. Outer spines of P2–P4 exp-1 and –2 enlarged in ♂, that of P3 exp-1 very large. Endopods P2–P3 sexually dimorphic; inner seta of P2 enp-1 absent in ♂; ♂ P3 endopod 3-segmented; drawn out into short apophysis, without inner seta on enp-1. P1–P4 armature formula as follows (apo = apophysis):

	Exopod	Endopod
P1	0.1.022	1.1.111
P2	0.0.022	1.020 [0.020 in ♂]
P3	0.0.022	1.020 [0.apo. 030 in ♂]
P4	0.0.022	120

The inner seta on P1 exp-2 is minute in *T. tumenae*. Noodt (1958b) states explicitly that this segment is unarmed in *T. dubius* but his figure indicates that the inner seta is present.

Fifth pair of legs medially free in ♀, fused in ♂. Exopod and baseoendopod fused in both sexes. Exopodal lobe with four elements in ♀, five in ♂. Endopodal lobe with four setae in ♀, with two spines in ♂. Genital field of ♀ comprising separate gonopores covered by opercula bearing three pinnate spines; sixth legs asymmetrical in ♂, represented by unarmed opercula. Caudal rami about as long as wide; with six setae, setae IV–V well developed.

Type species: *Taurocletodes gallicus* Kunz, 1975 = *Parepactophanes? dubia* Noodt, 1958b = *Taurocletodes dubius* (Noodt, 1958b) comb. nov.

Other species: *T. tumenae* sp. nov.

SPECIES DIFFERENTIATION

It is clear that some of the differences between the type species *T. dubius* and *T. tumenae* can be attributed to Kunz' (1975) imperfect description of the

former (as *T. gallicus*), which was conceivably based on a damaged specimen. For example, Kunz did not figure the penicillate setae on the P1 endopod nor did he mention them in his supplementary description based on the Azorian material (Kunz, 1983). His illustration (Abb. 128) shows instead a long plumose seta arising from the distal inner corner of enp-1 whereas in Noodt's (1958b) description the inner seta is markedly shorter and originating from the middle third of the segment (as in *T. tumenae*). The origin of the penicillate seta on enp-2 is difficult to determine when viewed in anterior aspect (Fig. 5A) since it is positioned posteriorly near the proximal margin (Fig. 5B). We therefore assume that Kunz (1975) figured the penicillate seta on enp-2 but had misinterpreted its insertion site and ornamentation. The seta on enp-1 and the penicillate element on enp-3 were overlooked, presumably because they were either missing or concealed by the endopodal segments. Kunz' (1975) illustration of the male P6 does not refer to that structure but represents the paired cuticular insertion sites of the ventral longitudinal trunk muscles, typically found on the first abdominal somite, posterior to the sixth legs (Fig. 7B).

The available descriptions (Noodt, 1958b; Kunz, 1975, 1983) do not provide any morphological evidence contradicting the conspecificity of *P. dubia* and *T. gallicus*. Kunz (1983) remarked that the Azorian females lacked the dorsal spinule row found on the caudal rami of the Mediterranean specimens. However, since he drew the innermost spinule on both rami it is more likely that he has overlooked the remaining surface spinules. A second difference noted between both populations concerns the structure of the male P3 endopod but this can be attributed to observation under different angles (cf. Fig. 6B,D).

T. tumenae and *T. dubius* are morphologically very similar, displaying identical armature formulae on the swimming legs and ornamentation patterns on the urosome of both sexes. They can be differentiated by the following characters: (1) relative length of endopodal segments of P1, enp-2 being only half the length of enp-3 in *T. tumenae* (equally long in *T. dubius*); (2) P4 endopod ♂ shorter than exp-1, with rounded lateral margins, and inner seta shorter than apical elements in *T. tumenae* (as long as exp-1, with straight lateral margins and inner seta distinctly longer than apical elements in *T. dubius*); Kunz (1975) remains vague about the segmentation of the P4 endopod, stating that it is either indistinctly 2-segmented (his Abb. 131 shows a faint suture) or 1-segmented; in the female (Noodt, 1958b) the endopod is clearly 1-segmented as in both sexes of *T. tumenae*; (3) P5 endopodal lobe ♂ with inner spine twice as long as outer one in *T. tumenae* (outer spine slightly longer than inner one in *T. dubius*); (4) P5 exopodal lobe ♂ with second

innermost element spiniform and distinctly shorter than adjacent setae in *T. tumenae* (innermost three elements all setiform and equally long).

PHYLOGENETIC CONSIDERATIONS

Por (1986), in his revision of the family Cletodidae (*sensu* Lang, 1948), removed *Parepactophanes* without giving any specific reasons and placed it *incertae sedis* in the Canthocamptidae. Recent studies have significantly refined the concept of the Cletodidae (Gee, 1994, 1998, 1999; Gee & Huys, 1996), resulting in the recognition of 17 valid genera: *Cletodes* Brady, *Enhydrosoma* Boeck, *Limnocletodes*, *Enhydrosomella* Monard, *Stylicletodes* Lang, *Acrenhydrosoma* Lang, *Monocletodes* Lang, *Interpletodes* Fiers, *Kollerua* Gee, *Schizacron* Gee & Huys, *Strongylacron* Gee & Huys, *Triathrix* Gee & Burgess, *Sphingothrix* Fiers, *Spinapecurris* Gee, *Dyacrenhydrosoma* Gee, *Paracrenhydrosoma* Gee, and *Neoacrenhydrosoma* Gee & Mu.

Neither *Parepactophanes* nor *Taurocletodes* fit the revised family diagnosis since: (1) the rostrum is clearly defined at the base (always fused to the cephalothorax in Cletodidae); (2) the ♀ antennule is 6-segmented (at most 5-segmented in Cletodidae); (3) the body somites are not separated by constrictions and lack sensillate integumental socles around the posterior margins (always present in Cletodidae); (4) the distal endopod segment of P1 in *Parepactophanes* has an inner lateral seta (= homologue of inner seta on enp-2 in *Taurocletodes*) (inner margin of enp-2 without lateral seta in Cletodidae).

Additional characters excluding *Taurocletodes* from the Cletodidae include: (1) the 3-segmented P1 endopod with [1.1.111] formula (at most 2-segmented in Cletodidae with primitively [1.111] formula); (2) presence of an inner seta on P1 exp-2 (and possibly also in *Parepactophanes*; absent in Cletodidae), and (3) the presence of an inner seta on P2–P3 enp-1 in the female (always absent in both sexes of Cletodidae, enp-1 also being distinctly shorter than enp-2). Finally, the inner seta on P1 enp-1 of both *Taurocletodes* and *Parepactophanes* is within the Cletodidae only found in the genus *Limnocletodes* whose current placement in the family is provisional (Gee, 1998).

Gómez Noguera & Fiers (1997) recently expressed an urgent need for revision of the Canthocamptidae, suggesting that this will eventually lead to the exclusion of the genera *Mesochra* Boeck and *Amphibiperita* Fiers & Rutledge from that family. Although the authors do not present specific arguments for their statement, it is conceivable that it was partly based on the detailed morphology of the male P3 endopod which they regarded as particularly distinctive because of the distad displacement of the vestigial inner setae. Such a character has potential phyloge-

netic significance but, as for many other sexually dimorphic character states, its utility is limited since some taxa have secondarily lost the inner setae on P3 enp-2 in the female (and concomitant with this the sexual dimorphism in the male), thereby obscuring phylogenetic relatedness. This limitation is illustrated in both *Taurocletodes* and *Parepactophanes* where the inner margin of P3 enp-2 is unarmed in the female.

Within the primarily freshwater Canthocamptidae there is a core group of genera confined to marine and brackish water habitats, comprising *Mesochra*, *Amphibiperita*, *Psammocamptus* Mielke, *Bathycamptus* Huys & Thistle (synonymized with the former by Mielke (1997) but reinstated by George & Schminke (2003)), *Mesopsyllus* and *Isthmiocaris* George & Schminke. Members of this group share the reduced morphology of the male sixth legs, being represented by membranous flaps completely lacking in armature elements. In the females the sixth legs closing off the genital apertures bear 1–3 setae, indicating a different ontogenetic trajectory between the sexes. The same sexual dimorphism is also encountered in *Taurocletodes* (Fig. 9C) and most likely (although unconfirmed at present) also in *Parepactophanes*. In most freshwater canthocamptids the male sixth legs typically bear two or three well developed setae (e.g. Dussart, 1967; Hamond, 1987).

The genera *Hemimesochra*, *Poria* Lang, *Perucamptus* Huys & Thistle and *Pusillargillus* Huys & Thistle are known from females only but show close similarity in mouthpart morphology with *Bathycamptus*, *Mesopsyllus* and *Psammocamptus*, and by inference, are also regarded as representatives of the group above (named here the *Mesochra*-group for practical, but not necessarily phylogenetic reasons). Other marine genera such as *Pholetiscus* Humes, *Ophirion* Por, *Itunella* Brady, *Dahlakia* Por, *Heteropsyllus*, *Nannomesochra* Gurney and *Cletocamptus* have well developed sixth legs in the males, show numerous additional discrepancies in the mouthparts and swimming legs, and almost certainly represent at least two different evolutionary lineages, not directly related to the *Mesochra*-group. Within the latter, *Taurocletodes* and *Parepactophanes* appear to be most closely related to *Mesochra*, but precise phylogenetic inferences cannot be drawn at present because the genus is not a natural unit (Gómez Noguera & Fiers, 1997) and possibly polyphyletic.

One character that is potentially indicative of phylogenetic affinity between *Parepactophanes*/*Taurocletodes* and the *Mesochra* complex is the peculiar arrangement of the dorsal sensillae on the thoracic somites bearing legs 4–6. In both sexes of *T. tumenae* the two dorsal sensillar pairs are very closely set together with typically one in a slightly

more anterior position (Figs 2A, 7A). A similar displacement of the dorsal sensillae was also illustrated by Gómez Noguera & Fiers (1997) in two species of *Mesochra*; however, the level of detail contained in most other species descriptions does not enable us to extrapolate this to the whole genus (but confirmed in *M. rapiens* (Schmeil, 1894), *M. pygmaea* (Claus, 1863), *M. lilljeborgi* Boeck, 1865 and *M. heldti* Monard, 1935; pers. observ. by RH).

The close relationship between *Parepactophanes* and *Taurocletodes* is indicated by the following derived character states: (1) antennule ♀ 6-segmented with aesthetasc on segment 3; (2) antennary exopod 1-segmented and bisetose; (3) mandibular palp 1-segmented with four setae, all arising subapically; (4) robust and short P2–P4; (5) absence of inner exopodal setae on P2–P4 (except for P4 exp-3 in *P. minuta*); (6) P5 with fused exopod and baseendopod in both sexes, and possibly (7) P6 ♂ without armature elements. Some of these, such as the antennular segmentation and the condition of the male P6, may be synapomorphies diagnosing a wider group of taxa, but the remaining characters leave little doubt about their sistergroup relationship.

Parepactophanes displays a number of autapomorphies distinguishing it from *Taurocletodes*: (1) P1 endopod 2-segmented (fusion of enp-2 and -3); (2) P1 exp-2 without inner seta (although this would require confirmation considering its minute size in *Taurocletodes*); (3) P2–P4 exp-3 with only one outer spine; (4) endopod P2–P3 1-segmented. Unique autapomorphies defining *Taurocletodes* include the penicillate setae on the P1 endopod (and the extreme proximad displacement of the inner seta on enp-2) and the marked sexual dimorphism on the swimming leg exopods (in particular P3 exp-1). The enlarged spine on P3 exp-1 in the male bears a remarkable similarity to the massive outer spine reported in the male of *Amphibiperita tropica* (Jakobi, 1956); however, in the latter it is found on P4 exp-1 (Fiers & Rutledge, 1990) and consequently is not serially homologous.

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