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# SYSTEMATICS AND PHYLOGENY OF THE ANCORABOLIDAE (COPEPODA: HARPACTICOIDA). III. DESCRIPTION OF TWO NEW SPECIES OF *CERATONOTUS* SARS AND *DENDROPSYLLUS*, NEW GENUS

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ABSTRACT

*Ceratonotus pectinatus* Sars, 1909, the type species of *Ceratonotus* Sars, 1909 (Copepoda: Harpacticoida: Ancorabolidae), is redescribed on the basis of females collected from southern Norway and by re-examination of extant material from the collections of Sars (Oslo, Norway), Lang (Stockholm, Sweden), and Drzycimski (Bergen, Norway). Some morphological characteristics of *C. pectinatus* males are provided from direct observations of the male copepodid V stage. Re-examination of Por's (1965) material from Raunefjord, Norway, did not provide any conclusive evidence to maintain *C. pectinatus elaphus* as a valid subspecies; it is considered here a junior subjective synonym of *C. pectinatus*. The validity of *C. coineaui* Soyer, 1964, is confirmed. Two new species of *Ceratonotus* are described, each based on a single sex, *C. thistlei* (♀) from the San Diego Trough (northeastern Pacific) and *C. concavus* (♂) from the eastern Mediterranean. An updated generic diagnosis for *Ceratonotus* is provided and intergeneric relationships discussed. *Dendropsyllus thomasi*, new genus, new species, is described from the San Diego Trough, northeastern Pacific. The new genus is characterised by the distinctive pattern of dendroid body processes (lacking on abdominal somites), lateroventral margins of cephalothorax with well-developed conical process, P1 exp-2 with 4 geniculate setae, P1 enp-2 with 1 apical seta, complete absence of P2 endopod, P3 exp-3 with 1 inner seta, and loss of the inner seta on P4 exp-3. *Ceratonotus magellanicus* and *C. antarcticus*, previously isolated as a distinct clade through parsimony analysis by Conroy-Dalton (2001), are both transferred to *Dendropsyllus* because they deviate significantly from the revised diagnosis for *Ceratonotus*. *Ceratonotus* and *Dendropsyllus* share a close sister-group relationship strongly supported by eight synapomorphies. The general phylogenetic relationships within the *Ceratonotus*-group are reinforced.

The subfamily Ancorabolinae Sars, 1909 (Harpacticoida, Ancorabolidae) currently contains 31 species and subspecies in 12 genera, and has recently been the subject of several phylogenetic investigations (Conroy-Dalton and Huys, 2000; Conroy-Dalton, 2001; Gómez and Conroy-Dalton, 2002). At least two distinct lineages within the subfamily can be recognized (Conroy-Dalton and Huys, 2000; Conroy-Dalton, 2001). The *Ancorabolus*-group comprises the genera *Ancorabolus* Norman, 1903; *Arthropsyllus* Sars, 1909; *Juxtaramia* Conroy-Dalton and Huys, 2000; *Breviconia* Conroy-Dalton and Huys, 2000; and *Uptionyx* Conroy-Dalton and Huys, 2000. The *Ceratonotus*-group includes the genera *Ceratonotus* Sars, 1909; *Dorsiceratus* Drzycimski, 1967; *Polyascophorus* George, 1998; *Arthuricornua* Conroy-Dalton, 2001; and *Touphapleura* Conroy-Dalton, 2001.

The highly distinctive but rare genus *Ceratonotus* was originally created by Sars (1909) to accommodate a single new species, *C. pectinatus*. Soyer (1964) added *C. coineaui* based on a single male from off Banyuls and also transferred *Echinopsyllus gorbunovi* Smirnov, 1946, to this genus. The latter was subsequently placed in *Polyascophorus* by George (1998), and this generic assignment has recently been confirmed by cladistic analysis (Conroy-Dalton, 2001). Por (1965) recognized a subspecies *C. pectinatus elaphus* on the basis of a single female from Bergen (Norway). Recently, two closely related species were added to the genus, *C. magellanicus* George and Schminke, 1998, and *C. antarcticus* George and Schminke, 1998, which were shown to form a distinct, geographically separated clade within *Ceratonotus* (Conroy-Dalton, 2001). Because the genus *Ceratonotus* had previously been reported only from Scandinavian waters (Sars, 1909; Lang, 1936, 1948; Por, 1965; Drzycimski, 1969) and the western Mediterranean (Soyer, 1964), the discovery of *C. magellanicus* and *C. antarcticus* significantly increased the distribution range for the genus, extending it now to the (sub)polar waters of the Southern Hemisphere.

The discovery in the northeastern Pacific and the eastern Mediterranean of three new ancorabolids with dendroid body processes supports the basal dichotomy previously identified within *Ceratonotus* (Conroy-Dalton, 2001) and provides further evidence that the two clades in fact warrant generic distinction. The genus *Ceratonotus* is herein restricted to the European species *C. pectinatus* and *C. coineaui*, and two new species, *C. concavus* (Israel) and *C. thistlei* (California). A new genus, *Dendropsyllus*, is proposed to accommodate the type *D. thomasi*, new species from the San Diego Trough, and the two (sub-) Antarctic species *C. magellanicus* and *C. antarcticus*. The intra- and intergeneric phylogenetic relationships of *Ceratonotus* and *Dendropsyllus* are discussed.

## Materials and Methods

Pacific material: Sediment samples were collected in the San Diego Trough (Expedition Quagmire; 1973–74) with Ekman grab (20 × 20 cm) by Remote Underwater Manipulator (RUM), an unmanned, tractor-like vehicle cable-connected to its surface support vessel (Thiel and Hessler, 1974). Each grab was divided into four 10 × 10 cm subunits. The overlying water and upper 1 cm layer of the green muddy sediment was extracted from a random selection of subsamples and passed through 1-mm and 62-μm mesh diameter sieves. Both sieve fractions were stained with rose bengal, and the harpacticoids were sorted under a dissecting microscope. For detailed sampling procedures see Thistle (1978).

Mediterranean material: Deepwater samples, from coal fly ash dumping site off the coast of Hadera, northern Israel, were collected using a 0.5 mm plankton net secured on top of a Marinovich-type deep water trawl during cruises from December 1998 to January 1999 as part of pollution monitoring surveys (1994–1999) conducted by the Israel Oceanographic and Limnological Research (IOLR). Samples were initially preserved in 10% buffered Formalin on board ship, then passed through a 180 μm sieve, stained with rose bengal, preserved in 70% alcohol, and the copepods were picked out (at IOLR).

Norwegian material: Meiofaunal core samples were collected from Frierfjord/Langesundfjord, Norway, as part of the Groups of Experts for Effects (biological) of Pollutants (GEEP) surveys during the Spring of 1985, and the harpacticoid copepods were picked out and preserved in alcohol.

Specimens were cleared and dissected in lactic acid, and the dissected parts were mounted in lactophenol. Preparations were sealed with transparent nail varnish. All drawings have been prepared using a *camera lucida* on a Leitz Diaplan microscope equipped with differential interference contrast.

The descriptive terminology for body and appendage morphology is adopted from Huys and Boxshall (1991). Abbreviations used in the text and figures are: ae, aesthetasc; P1–P6, first to sixth thoracopod; exp(enp)-1(2, 3) to denote the proximal (middle, distal) segment of a ramus. The term acrothek is used to denote the trifid seta complement found apically on the distal antennulary segment.

Type material was deposited in the Natural History Museum, London, UK (NHM). Additional material examined in this study includes the type material of *Ceratonotus pectinatus elaphus* from the collections in the Zoologisk Museum, Universitetet i Bergen, Norway (ZMUB), and specimens of *C. pectinatus* from the collections of G. O. Sars at the Zoologisk Museum, Oslo, Norway (ZMO), and K. Lang at the Naturhistoriska Riksmuseet, Stockholm, Sweden (SMNH).

Scale bars in figures are indicated in μm.

## Systematics

### Family Ancorabolidae Sars, 1909

### Subfamily Ancorabolinae Sars, 1909

### *Ceratonotus* Sars, 1909

*Diagnosis*.—Ancorabolinae. Body cylindrical, tapering slightly posteriorly, without clear demarcation between prosome and urosome; body ornate with series of produced dendroid processes, each bearing unmodified sensillum terminally. Cephalothorax with bilateral constriction in anterior half; anterior corners with sensory triplet consisting of 2 sensilla and tube-pore; with curved conical frontolateral horns; posterior margin with paired laterodorsal dendroid processes; lateroventral margin with small conical process and basally reinforced tube-pore. Thoracic somites bearing P2–P5 each with paired laterodorsal dendroid processes; P6-bearing somite in ♂ or genital half of double-somite in ♀, without produced processes. First abdominal somite in ♂ or abdominal half of double-somite in ♀, with paired laterodorsal dendroid processes; second abdominal somite with paired sensillate dorsal tubercles. Somatic hyaline frills weakly developed and smooth. Body somites, swimming legs, P5 and caudal rami with conspicuous tube-pores. Anal operculum smooth. Caudal rami elongate, divergent and cylindrical, with 7 setae; seta I minute; setae I and II inserted in proximal third of ramus, seta III inserted in median third. Seta V longest, well developed; seta VI reduced; seta VII triarticulate at base. Sexual dimorphism in antennule, P3 endopod, P6, and genital segmentation.

Rostrum not discernible in dorsal aspect; fused to cephalic shield; anteriorly displaced and partially absorbed into anteroventral surface of cephalothorax; with paired sensilla and bulbous membranous projections displaced laterally to bases of antennules; with long, distinctive median tube-pore. Antennule 3-segmented in ♀, 6-segmented and subchirocer in ♂ (with two segments distal to geniculation); aesthetasc arising from segments 2 and 3 in ♀, segments 4 and 6 in ♂; first segment compound and elongate in both sexes, with 1 subapical anterior seta arising from distinctive spinous projection. Antenna with allobasis showing partial suture along exopodal margin, abexopodal margin with 1 well-developed seta in distal (endopodal) half; exopod entirely absent; endopod with 3 lateral and 6 distal elements (2 spines and 3 geniculate setae, longest one fused basally to tiny naked seta). Mandible with robust coxa bearing slender dorsal seta; palp 1-segmented, uniramous with 5 setae (3 endopodal and 2 basal). Maxillule with 2 elements on coxal endite; basis with 4 elements on proximal and 2 elements on distal endite; exopod and endopod completely incorporated into basis, represented by 2 and 3 setae respectively. Maxillary syncoxa with 2 well developed endites, each with 3 elements; allobasis drawn out into claw with 3 accessory elements; endopod not defined, represented by 2 setae. Maxilliped subchelate, slender, elongate; syncoxa with 1 seta; endopod drawn out into long, narrow curved claw with 1 reduced accessory seta.

P1–P4. Intercoxal sclerites wide and narrow; praecoxae weakly developed; coxae small, trapezoid, bases extremely transversely elongate. P1 rami 2-segmented; endopod longer than exopod, enp-1 reduced, enp-2 with 2 geniculate setae distally; exp-2 with 3 geniculate setae and 2 outer spines. P2–P4 coxae with spinulose lobate process; exopods 3-segmented; endopods 1- or 2-segmented; without inner setae on exp-1 and endopodal segments; exp-3 with 2 outer spines. P3 endopod ♂ 3-segmented; enp-2 elongate, anterior surface produced distally into recurved apophysis; enp-3 with 2 apical setae. Armature formula as follows:

| | Exopod | Endopod |
|---|---|---|
| P1 | 0.023 | 0.020 |
| P2 | 0.1.122 | 0.020 or 020 |
| P3 | 0.1.222 | 0.020 or 020(♀) |
| | 0.1.222 | 0.0.020(♂) |
| P4 | 0.1.122 | 0.0[1-2]0 or 0[1-2]0 |

P5 basal setophore absent; endopodal lobe vestigial, represented by 1 seta and 1 conspicuous tube-pore; exopod distinct in both sexes and elongate with 1 inner, 1 apical and 1 outer element. Female genital field located anteriorly; gonopores covered by common, unarmed genital operculum derived from medially fused P6. Male P6 asymmetrical; without armature; functional member represented by small membranous flap.

*Type Species*.—*Ceratonotus pectinatus* Sars, 1909 (by monotypy).

*Other Species*.—*C. coineaui* Soyer, 1964; *C. thistlei*, new species; *C. concavus*, new species.

*Remarks*.—Soyer (1964) described the male antennule of *C. coineaui* as 5-segmented. For members of the *Ceratonotus*-group, where males are known (*Arthuricornua anendopodia* Conroy-Dalton, 2001; *Dorsiceratus octocornis* Drzycimski, 1967; *D. triarticulatus* Coull, 1973), there is typically a tiny, U-shaped sclerite proximal to the geniculation, representing segment 4 (latter two species, personal observation). As this segment was repeatedly overlooked in previous descriptions, it is assumed here that *Ceratonotus* males also possess 6-segmented antennules, with two segments distal to geniculation.

### ***Ceratonotus pectinatus*** Sars, 1909

*Synonym*.—*Ceratonotus pectinatus elaphus* Por, 1965, new synonym.

*Type Locality*.—Frierfjord/Langesundfjord, Norway; 99 m depth, muddy sediment.

*Material Examined*.—Type material. The single female found by Sars from Flekkerö could not be traced.

*Other Material*.—(a) Zoologisk Museum, Oslo, Norway: 1 ♀ in alcohol (ZMO reg. no. F20335) from Risør, Norway; coll. and det. G. O. Sars; (b) Naturhistoriska Riksmuseet, Stockholm, Sweden: 3 ♀♀ in alcohol (SMNH reg. no. 15354 [old no. 497]) from Gullmarfjord, Sweden; 40 m, mud; coll. K. Lang, 14.03.1937; (c) Zoologisk Museum, Universitetet i Bergen, Norway; 1 ♀ mounted on 1 slide (ZMUB reg. no. 47975) labelled as *Ceratonotus pectinatus elaphus* "TYPUS"; coll. and det. F. D. Por. Slide restored and specimen remounted on seven slides; (d) The Natural History Museum, London, UK: 1 ♀ dissected on 12 slides and designated as neotype (NHM reg. no. 2002.372; 4 ♀♀ and 8 copepodids (1 ♂ and 1 ♀ CV, 4 CIV stages and 2 CII stages) in alcohol (NHM reg. no. 2002.373–384); all from meiofauna samples collected at Frierfjord/Langesundfjord, Norway; 99 m deep mud; coll. R. Huys, Spring 1985.

Examination of the G. O. Sars collections held in the Zoologisk Museum, Oslo, Norway, proved that the type material of *C. pectinatus* is no longer extant. The single damaged female specimen deposited by Sars and listed under (a) was neither designated as type material, nor comes from the type locality given by Sars (1909). Individuals listed under (d) came as nearly as practicable from the original type locality, were in far better condition, cleaner and less damaged, and are used for the redescription below. In the confirmed absence of a name-bearing type and in the light of the ambiguous recognition of taxa of subspecific rank within *C. pectinatus* (Por, 1965; see below), a female specimen from this locality was selected and formally designated here as the neotype, in accordance with the Code (ICZN Art. 75.3). The new type locality for *C. pectinatus*, consequently, becomes Frierfjord/Langesundfjord (ICZN Art. 76.3).

*Redescription of Female* (Figs. 1, 2, 3, 4A, C, D, F–H).—Total body length 633 μm ($\bar{x} = 619$ μm; $n = 5$) measured from anterior outer corner of cephalothorax to posterior margin of caudal rami. Body (Fig. 1) cylindrical, tapering slightly posteriorly, without clear demarcation between prosome and urosome; integument moderately chitinized, ornate with series of produced dendroid processes; processes with fine denticles and unmodified sensilla (Figs. 1, 4C). Somatic hyaline frills weakly developed, smooth (Figs. 1, 4F). Cephalothorax (Fig. 1) bilaterally constricted in anterior half; anterior corners with sensory triplet consisting of sensillum with closely associated tube-pore and additional sensillum anteriorly (Fig. 1A); with pattern of produced sensillate processes as follows: pair of strongly dentate conical processes at anterior outer corners (Fig. 1A, B); posterior margin with pair of laterodorsal dendroid processes, with dorsal tube-pore halfway along process length (Fig. 1A); and lateroventral margin with small conical process (Fig. 1C) and conspicuous tube-pore slightly anteriorly. Free thoracic somites bearing P2–P5 (Fig. 1) and abdominal half of genital double-somite (= first abdominal somite) with paired laterodorsal dendroid processes, processes of P2–P4-bearing somites with basal sensilla ventrally (see Fig. 4B, C); genital half of double-somite without produced processes; second abdominal somite with pair of simple dorsal tubercles, each bearing sensillum. Urosomites and caudal rami with conspicuous tube-pores (Figs. 1, 4F–H). Transverse intersomitic sclerite present ventrally between P5-bearing and genital double-somites (Fig. 4F, G). Original segmentation of genital double-somite indicated by bilateral constriction (Figs. 1, 4F, G). Second abdominal somite (Fig. 4F) with ventral median spinule row around posterior margin. Third abdominal somite with slightly longer ventral median spinule row around posterior margin (Fig. 4F). Anal somite partly cleft medially (Fig. 4F); tube-pore and small spinules present around ventral hind margin (Fig. 4F); anal operculum rounded, smooth (Fig. 4H); anal frill finely setulose.

Caudal rami elongate, divergent, cylindrical (Figs. 1, 4F, H), with fine denticles; outer lateral margin with few spinule patches around insertion sites of setae (Fig. 4F, H). Seta I minute, positioned ventral to seta II (arrowed in Fig. 4F); setae II and III bipinnate; seta V well developed, pinnate and fused basally to seta IV (Fig. 4H); setae IV and VI (Fig. 4H) shorter; seta VII triarticulate at base and arising from minute dorsal pedestal, near posterior margin (Fig. 4H).

Rostrum (Fig. 4A) fused to cephalic shield; anteriorly displaced and partially absorbed into anteroventral surface of cephalothorax; with paired branched sensilla and paired bulbous membranous projections (arrowed in Fig. 4A), laterally displaced to bases of antennules; midventral tube-pore, well developed and reinforced proximally.

Antennule (Figs. 1A, 2A) 3-segmented. Segment 1 compound, longest; 1 dorsal subapical seta arising from spinous projection (arrowed in Fig. 2A). Segment 2 with aesthetasc (length 138 μm). Segment 3 with apical acrothek consisting of aesthetasc and 2 slender setae. Armature formula: 1-[8 + 1 pinnate], 2-[6 + (1 + ae)], 3-[9 + acrothek].

Antenna (Fig. 2B). Coxa represented by well-developed sclerite (Fig. 1B, C; arrowed in Fig. 1C). Basis and proximal endopod segment fused, forming allobasis; membranous insert along exopodal margin marking original position of exopod; exopod completely absent; abexopodal margin with spinules in basal half and 1 pinnate seta in endopodal half. Endopod with 2 distal surface frills; spinules along medial margin; lateral armature consisting of 2 pinnate spines and 1 bare seta; distal armature consisting of 2 pinnate spines and 3 geniculate setae, longest one with spinules around geniculation and fused basally to vestigial seta.

Labrum well developed (Fig. 1B).

Mandible (Fig. 2C). Coxa robust, expanding distally to gnathobase bearing several incised blades; 1 sparsely pinnate seta at dorsal corner. Palp well developed, 1-segmented; with 2 plumose setae along inner margin (representing basal elements), 3 apical plumose setae (representing incorporated endopod), and outer margin without armature.

Maxillule (Fig. 2D). Praecoxal arthrite subrectangular, with 2 setae on anterior surface and few long spinules on posterior surface; distal armature consisting of 6 bare and 3 spinulose spines. Coxal endite with 1 pinnate spine and 1 bare seta; few spinules apically. Basis with 4 elements on proximal and 2 pinnate setae on

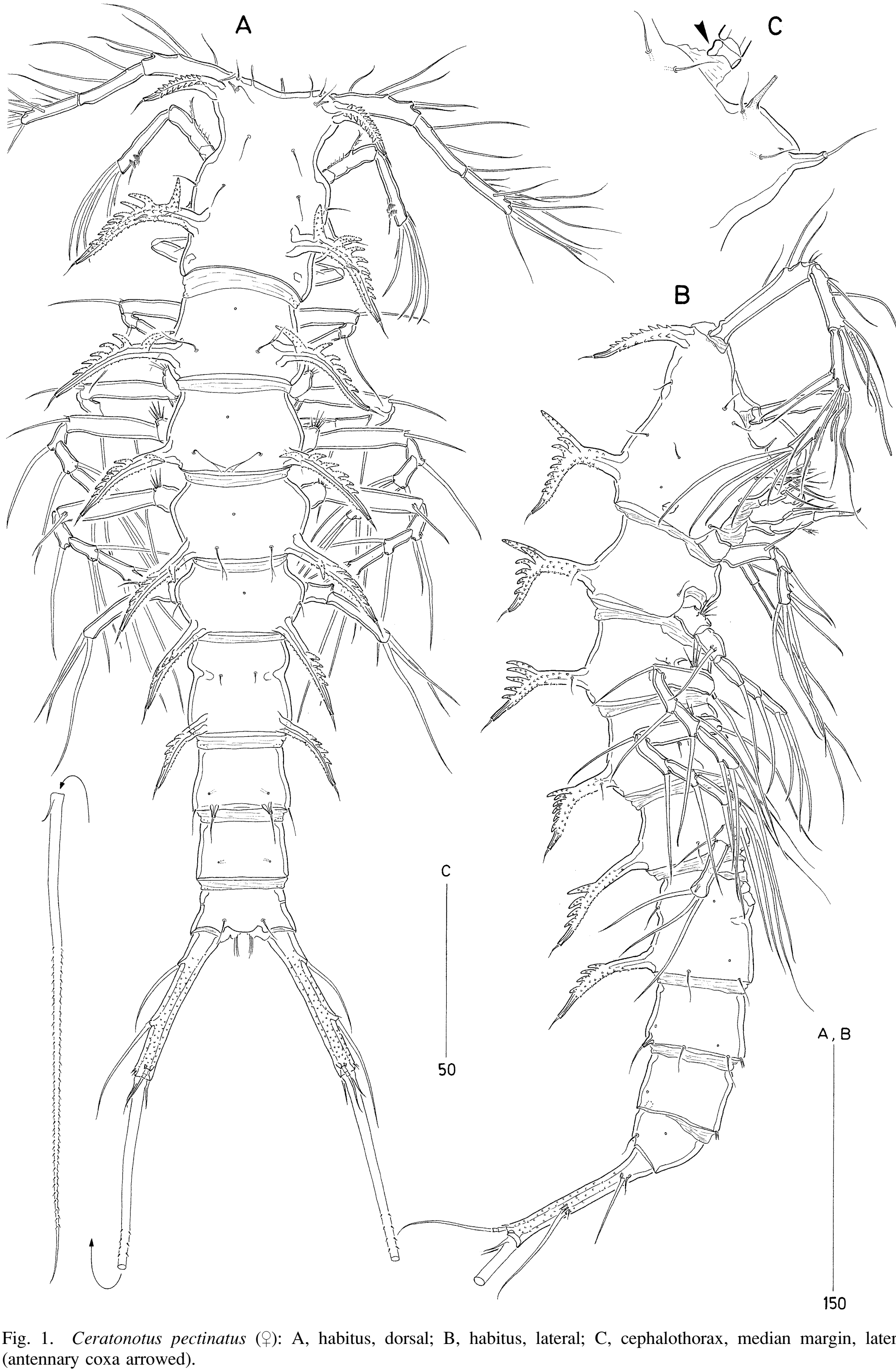



Fig. 1. *Ceratonotus pectinatus* (♀): A, habitus, dorsal; B, habitus, lateral; C, cephalothorax, median margin, lateral (antennary coxa arrowed).


Fig. 2. *Ceratonotus pectinatus* (♀): A, antennule, ventral (spinous projection bearing anterior seta arrowed); B, antenna; C, mandible; D, maxillule (inset showing distal portion of arthrite with 6 posteriormost elements only); E, maxilla (inset showing proximal endite); F, maxilliped.

distal endite. Rami completely incorporated into basis; exopod represented by 1 tiny and 1 pinnate seta; endopod represented by 3 pinnate setae.

Maxilla (Fig. 2E). Syncoxa with 3 spinule patches as figured; with 2 coxal endites, arising from membranous area; proximal endite with 1 strong pinnate spine basally fused to endite and 2 spinulose spines; distal endite with 3 spinulose spines. Allobasis drawn out into claw with spinules subdistally; accessory armature consisting of 1 bare seta, 1 spinulose and 1 pinnate spines. Endopod represented by 2 plumose setae.

Maxilliped (Fig. 2F). Subchelate, slender. Syncoxa with 1 pinnate seta. Basis with short spinules along outer margin and long, strong spinules along palmar margin. Endopod drawn out into long, narrow curved claw; claw finely pinnate with 1 accessory seta at base.

P1 (Fig. 3A). Intercoxal sclerite wide, narrow. Praecoxa weakly developed. Coxa trapezoid. Basis transversely elongate, with conspicuous anterior tube-pore; with pinnate outer spine and plumose inner seta; anterior spinule pattern as indicated in Fig. 3A. Both rami 2-segmented; exp-1 outer spine pinnate; exp-2 with spinules along inner margin, with 3 geniculate setae and 2 pinnate outer spines. Enp-2 1.9 times longer than enp-1, with 2 geniculate setae apically.

P2–P4 (Fig. 3B–D) with wide intercoxal sclerites lacking ornamentation (see Fig. 3B as for P2). Praecoxae (Fig. 3B, C) weakly developed. Coxae (Fig. 3B, C) trapezoid, with spinulose lobate process on outer margin. Bases transversely elongate; with anterior tube-pore in distal half; additional patches of fine setules on anterior surface; outer distal seta bipinnate (P2) or bare (P3–P4). Exopods 3-segmented, spines elongate. Endopods (Fig. 3B–D) reduced (P2–P3) or minute (P4). Armature formula as follows:

| | Exopod | Endopod |
|---|---|---|
| P2 | 0.1.122 | 020 |
| P3 | 0.1.222 | 020 |
| P4 | 0.1.122 | 010 |

P5 (Fig. 4D). Baseoendopodal setophore absent, outer basal seta bare with large tube-pore at base. Endopodal lobe absorbed, represented by tiny raised pedestal (Fig. 4D), with conspicuous tube-pore and 1 naked seta. Exopod distinct, long, slender; with 1 inner, 1 distal, and 1 outer bipinnate setae.

Genital field (Fig. 4G) with fused gonopores opening via common midventral slit covered by genital operculum derived from vestigial sixth legs. P6 (Fig. 4G) unarmed. Copulatory pore moderately large (arrowed in Fig. 4G), flanked by paired tube-pore triplet, just posterior to each gonopore.

*Male CV* (Fig. 4I J).—Pattern of body processes as in ♀, but less well developed and processes of first abdominal somite only weakly dendroid. First and second abdominal somites with spinule row along ventral hind margin. Terminal urosomite with 2 ventral spinule rows medially.

General morphology and armature formula of antenna, mandible, maxillule, maxilla, maxilliped, P1–P2, P3 exopod, and P4 as in ♀.

Antennule (not figured) 3-segmented.

P3 exopod as in ♀; endopod (Fig. 4I) indistinctly 2-segmented; enp-2 with apophysis arising subdistally, with 2 setae apically.

P5 (Fig. 4J). Baseoendopod, outer basal and endopodal setae not expressed; exopod distinct, with 1 inner, 1 outer, and 1 apical pinnate setae.

*Variability*.—Some slight differences in degree of development and in the number of branches per process were observed between specimens and between right and left sides of the same individual. Por's (1965) specimen differed in the length/width ratio of the ♀ P5 exopod (see Fig. 4E).

*Remarks*.—Sars (1909) based the description of *C. pectinatus* on a single female from the southern coast of Norway. The species has subsequently been reported only occasionally and always in low numbers, with all records from Scandinavia (Lang, 1936, 1948; Por, 1965; Drzycimski, 1969; present study). Both Lang (1948) and Drzycimski (1969) reported a single male specimen of *C. pectinatus*; however, only the former author provided some cursory morphological information. In a footnote, Lang (1936) stated that the male is smaller and more slender than the female, differing only in the structure of the antennule and the P3 endopod, which is 3-segmented, with an inner projection on segment 2. Lang (1948) did not provide any illustrations of the male although he alluded in the text to a figure of the anterior margin of the cephalothorax and antennule of the male; the only relevant illustration given is the one copied from Sars (1909), which was based on a female. He also stated that processes are absent on the first abdominal but present on

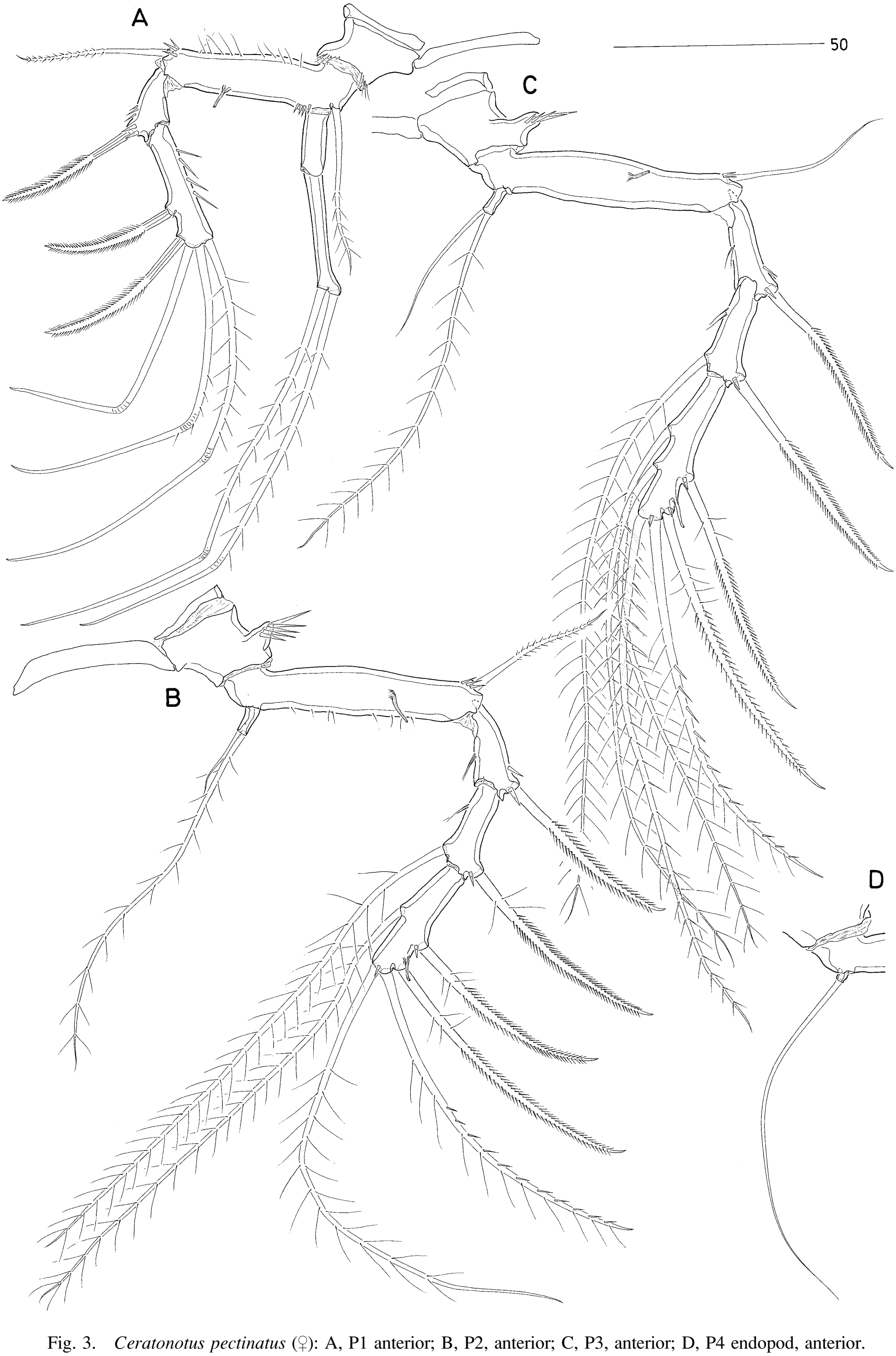



Fig. 3. *Ceratonotus pectinatus* (♀): A, P1 anterior; B, P2, anterior; C, P3, anterior; D, P4 endopod, anterior.

the second abdominal somite, that the P3 endopod is modified in the "usual" way, and that the P5 is identical to that of the female, although being somewhat smaller.

Drzycimski (1969) was the first to address some of the diagnostic anomalies persisting in the literature with regard to antennulary segmentation and both endopodal armature and segmentation in P4. Sars (1909) described the female antennule of *C. pectinatus* as 4-segmented, with a small segment 2 (probably misinterpreting the apical part of segment 1). Both Lang (1948) and Soyer (1964) adopted the 4-segmented condition in their updated generic diagnoses, but Por (1965) described the antennule of *C. pectinatus elaphus* as 3-segmented. Drzycimski (1969) showed that aberrant conditions can occur in female antennulary segmentation, having found some specimens with 3-segmented, some with 4-segmented antennules, and one asymmetrical specimen exhibiting both conditions. No such variability was detected in the material under study, and the 3-segmented condition of the female antennule is considered the normal state for this genus.

Sars (1909) described the P2–P4 endopods of *C. pectinatus* as 1-segmented, bearing two setae in P2–P3 and being "rudimentary" in P4, but he mislabeled P3 as P4 in his plate CCXIII, creating some ensuing confusion. Lang's (1948) statement that the P4 endopod is "ganz rückgebildet" is equally vague. Drzycimski (1969) pointed out that this ramus is represented by a minute segment with one apical seta, an observation confirmed in the present account. The latter author also remarked on some intraspecific variability in the size/length of produced body processes. Although Drzycimski speculated that the differences between *C. coineaui* and the type species could merely reflect such variability, he did not formally synonymise the former with the latter.

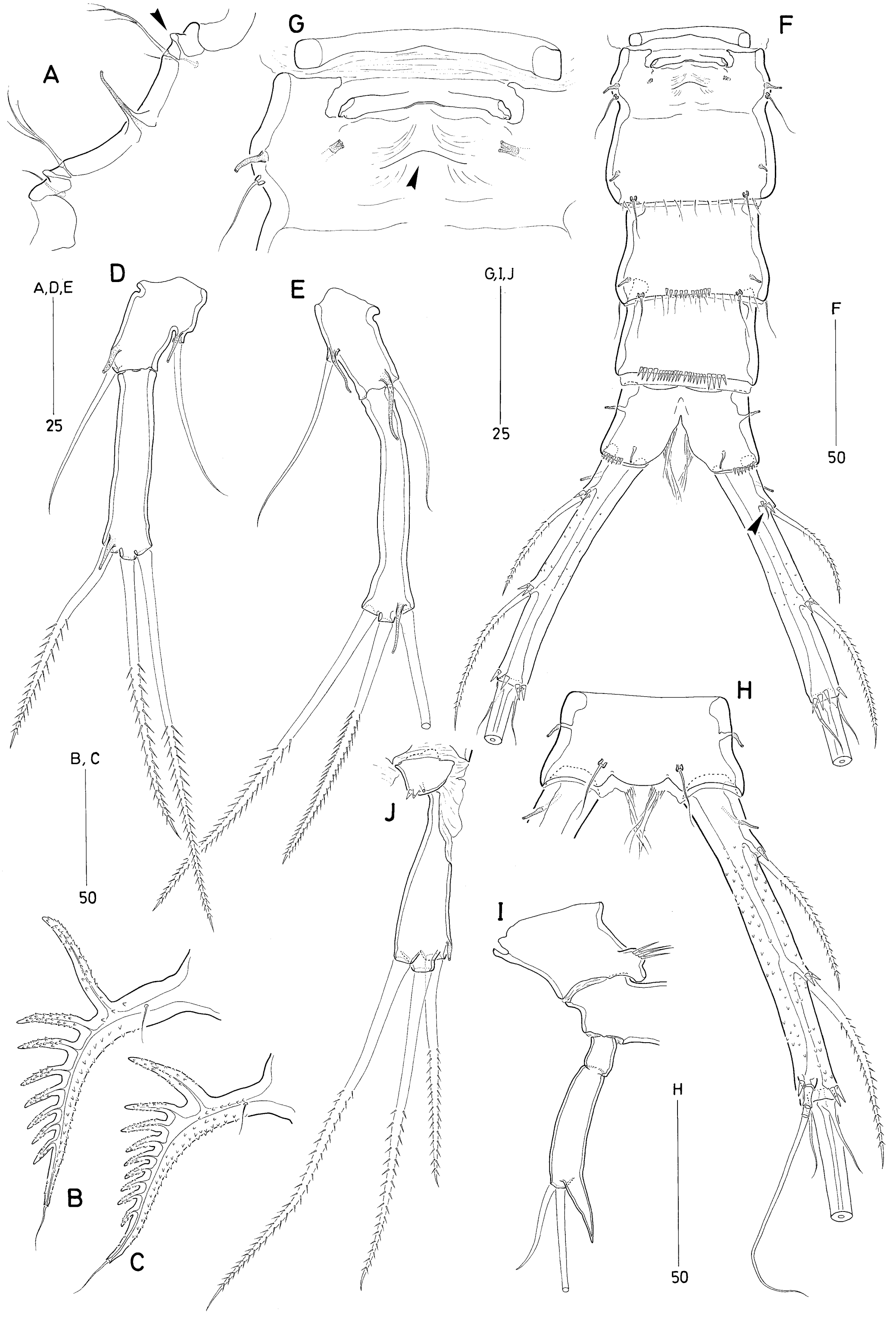
Por (1965) described the subspecies *C. pectinatus elaphus* from southern Norway (Raunefjord) based on a single female specimen. The characters he used to differentiate his specimen from the nominotypical subspecies are summarised as follows: (a) third abdominal somite longer, more than half the length of the abdomen; (b) antennule 3-segmented; (c) P4 endopod 1-segmented with 1 apical seta; (d) P4 exopod outer spines serrate subdistally; (e) P5 exopod elongate, 10 times as long as wide; (f) caudal rami longer; (g) degree of development of dendroid processes; (h) presence of small dorsal tubercles on third abdominal somite. Detailed comparative analysis of the type material of *C. pectinatus elaphus* with *C. pectinatus pectinatus* proved that (b), (c), and (h) can be disregarded because the same condition is displayed in *C. pectinatus pectinatus* but was overlooked in Sars' (1909) original description (note for (h) that Por was actually referring to the second abdominal somite). For characters (f) and (g), the differences in size/length are not as marked as claimed by Por (1965). Only very slight differences in the size of the dendroid processes (see Fig. 4B, C), and no differences in the proportional length of the caudal rami, were observed. Character (d) is an optical illusion created by the plane at which this appendage was mounted. The outer spines of the P4 exopod are finely pinnate and identical in form to those on other swimming legs or to those of *C. pectinatus pectinatus*. It has been impossible to decipher what Por (1965) meant by character (a). The only discernible difference was found in the length of the P5 exopod (character (e)), which is proportionally longer in Por's specimen (see Fig. 4D, E), 4.5 times as long as the greatest width, but not 10 times as long as stated by Por (1965). No morphological discrepancies in the (oral and swimming) appendages and abdominal ornamentation could be detected between both subspecies. In the absence of any discriminating characters, *C. pectinatus elaphus* is therefore formally synonymised with *C. pectinatus*.

*Distribution*.—Norway: Flekkerö (Sars, 1909); Raunefjord (Por, 1965: as *C. pectinatus elaphus*); Korsfjord, Fanafjord and Husnesfjord (Drzycimski, 1969); Frierfjord/Langesundfjord and Risør (present account). Sweden: Gullmarfjord (Lang, 1936, 1948).

## ***Ceratonotus thistlei***, new species

*Type Locality*.—Quagmire site; near the base of the Coronado Escarpment, San Diego Trough, north Pacific Ocean; 32°35.75′N, 117°29.00′W; depth 1,220 m; hemipelagic green mud.

*Material Examined*.—Type series collected from 500-m equilateral triangular sampling site. Individual subcore units of each grab allocated a specific sample number (E ***), referred to in parentheses. For detailed locality data and subcore sampling strategy, see Thistle (1978). Holotype ♀ (E 14Y) in alcohol (NHM reg. no. 2002.385); paratypes are 1 ♀ (E 48Y) dissected on 9 slides (NHM reg. no. 2002.386) and 2 ♀♀ (E 12W, E 46Y) (NHM reg. no. 2002.387–388) in alcohol; donated by Dr David Thistle.


A
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H
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*Description of Female* (Figs. 5, 6).—Total body length 636 μm ($\bar{x}$ = 677 μm; $n$ = 3) measured from anterior outer corner of cephalothorax to posterior margin of caudal rami. Body (Fig. 5A) cylindrical, tapering slightly posteriorly, without clear demarcation between prosome and urosome; integument moderately chitinized, ornate with series of produced dendroid processes. Pattern (Fig. 5A, B) identical to that of type species, except all modified body processes significantly more elongate and well developed; dorsal tubercles on second abdominal somite smaller than in type species. Cephalothorax with bilateral constriction in anterior half; anterior corners with sensory triplet consisting of sensillum with closely associated tube-pore and additional sensillum anteriorly; pattern of processes (Fig. 5A, B) identical to that of type species. Body somites and caudal rami with conspicuous tube-pores (Fig. 5A, C). Original segmentation of genital double-somite indicated by bilateral constriction (Fig. 5A, C). Abdominal somites (Fig. 5A, C) with ornamentation pattern as for type species. Anal somite partly cleft medially (Fig. 5C); tube-pore and small spinules present around ventral hind margin (Fig. 5C); anal operculum rounded, smooth (Fig. 5A).

Caudal rami (Fig. 5A, C) elongate, divergent, cylindrical; outer lateral margin with few spinule patches around insertion sites of setae. Seta I minute, positioned ventral to seta II (arrowed in Fig. 5C); setae II and III bipinnate; seta V well developed, pinnate, fused at base to seta IV (Fig. 5A); setae IV and VI (Fig. 5C) shorter; seta VII triarticulate at base and arising from minute dorsal pedestal, near posterior margin (Fig. 5A). [Note: caudal rami foreshortened in Fig. 5A due to flexure of body; for real length see Fig. 5C].

Rostrum (Fig. 5A, B) as for type species; fused to cephalic shield; anteriorly displaced and partially absorbed into anteroventral surface of cephalothorax; with paired bulbous membranous projections proximal to paired, unmodified sensilla, laterally displaced to bases of antennule; midventral tube-pore well developed, reinforced proximally.

Antennule (Figs. 6A) segmentation and armature as for type species except segments more slender and elongate (Fig. 6A). Armature formula: 1-[9], 2-[6 + (1 + ae)], 3-[9 + acrothek].

Antenna (Fig. 6B) as for type species; generally segments more elongate; lateral endopodal seta longer.

Labrum, mandible, maxillule, maxilla, maxilliped (not figured) as for type species.

P1 (Fig. 6C) as for type species except: coxa with spinule on raised notch as figured; outer basal seta pinnate and well developed, inner seta strongly plumose. Enp-2, 1.83 times as long as enp-1.

P2–P4 (Fig. 6D–G). Intercoxal sclerites wide, crescent-shaped, without ornamentation (see Fig. 6F as for P4); coxae trapezoid, with spinulose lobate process on outer margin (see Fig. 6 E, F as for P3 and P4). Exopods as for type species. Endopods (Fig. 6D–G) 2-segmented, enp-1 reduced; both segments reduced in P4 (Fig. 4G). Armature formula as follows:

| | Exopod | Endopod |
|---|---|---|
| P2 | 0.1.122 | 0.020 |
| P3 | 0.1.222 | 0.020 |
| P4 | 0.1.122 | 0.010 |

P5 (Fig. 5C) as in type species except outer basal seta plumose.

Genital field (Fig. 5C) as for type species except copulatory pore wider.

*Male*.—Unknown.

*Etymology*.—The species is named after Dr David Thistle, who made available for study and donated all the ancorabolid material collected during Expedition Quagmire (1973–1974) in the San Diego Trough, northeastern Pacific.

## ***Ceratonotus concavus***, new species

*Type Locality*.—Eastern Mediterranean Sea, off the coast of Hadera, Israel; 32°39′N, 34°14′E; depth 1,416 m; Station number P14.

*Material Examined*.—Holotype ♂ dissected on seven slides (NHM reg. no. 2002.389); donated by Dr Bella Galil.

⟵

Fig. 4. *Ceratonotus pectinatus* A–H (adult ♀), I, J (CV ♂): A, (♀) rostrum, ventral (bulbous membranous projection arrowed); B, (♀) dendroid process of P2-bearing somite, outer lateral view, Por's slide material (ZMUB reg. no. 47975); C, (♀) same, Huys' material (NHM reg. no. 2002.372); D, (♀) P5, anterior, Huys' material (NHM reg. no. 2002.372); E, (♀) same, anterior, Por's slide material (ZMUB reg. no. 47975); F, (♀) urosome (excluding P5-bearing somite), ventral (caudal seta I arrowed); G, (♀) genital field, ventral (copulatory pore arrowed); H, (♀) anal somite and right caudal ramus; I, (CV ♂) P3 endopod; J, (CV ♂) P5 anterior.

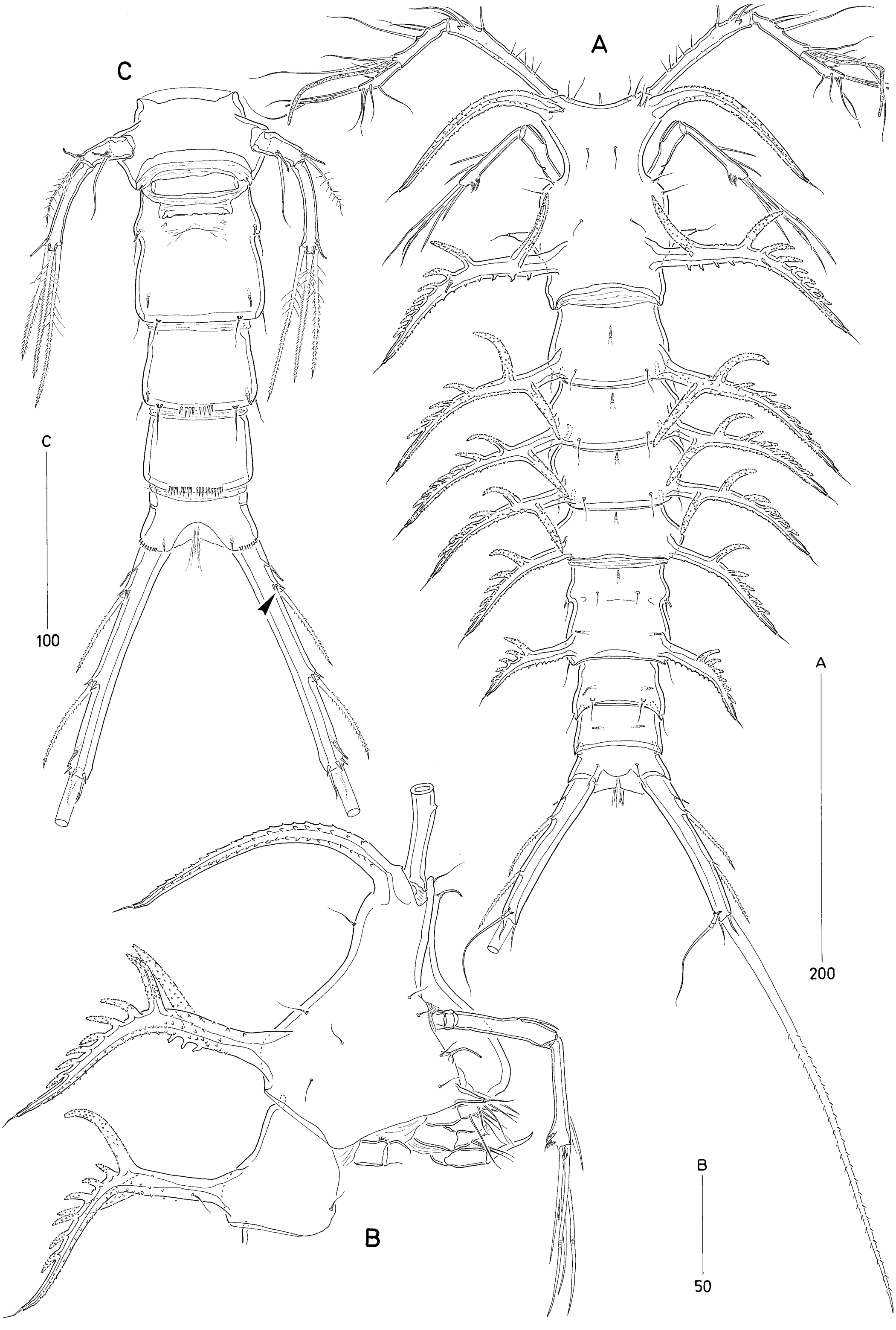


Fig. 5. *Ceratonotus thistlei*, new species (♀): A, habitus, dorsal; B, cephalothorax and P2-bearing somite, lateral; C, urosome, ventral (caudal seta I arrowed).

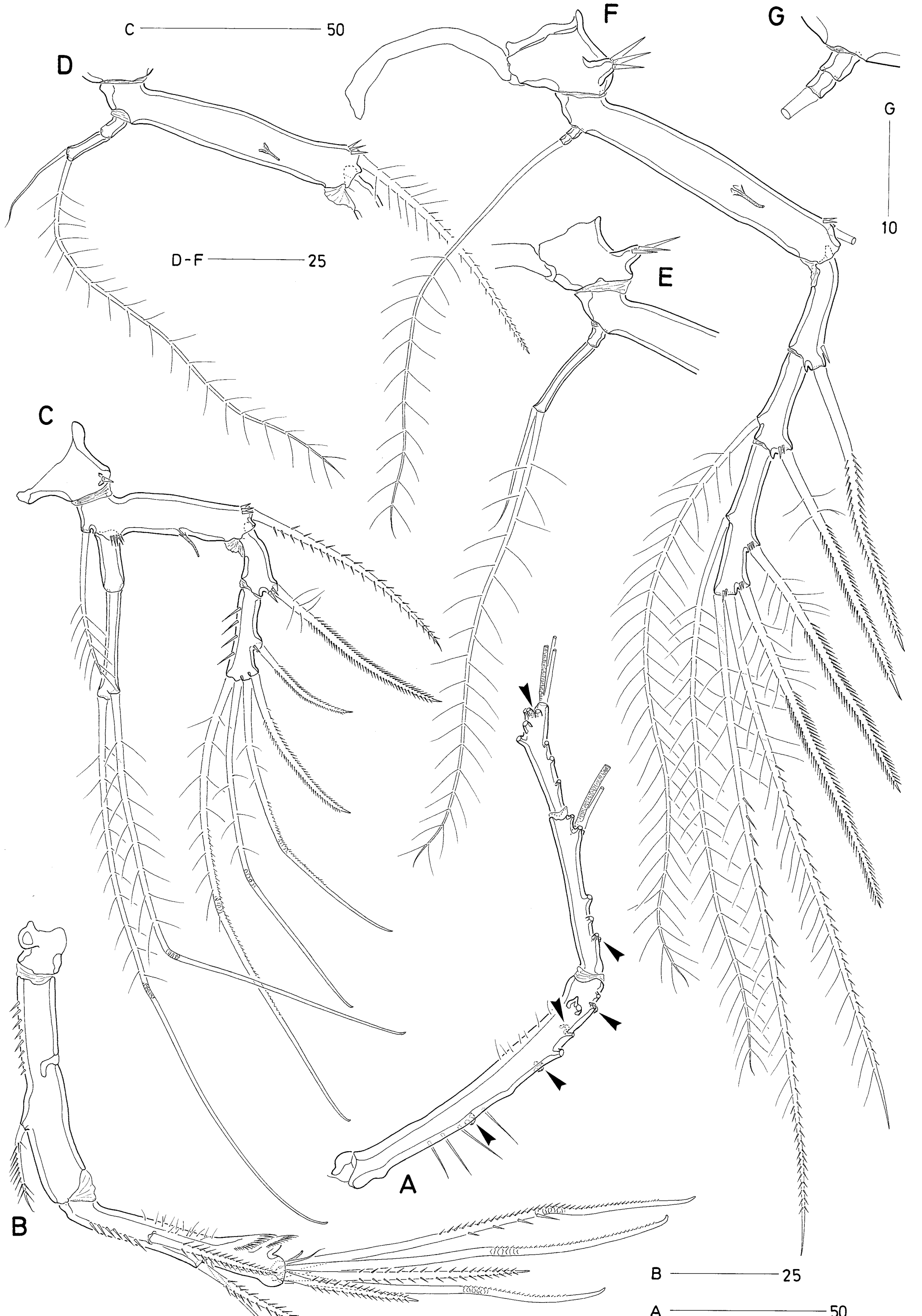


Fig. 6. *Ceratonotus thistlei*, new species (♀): A, antennule, dorsal (armature omitted; insertion sites of ventral setae arrowed); B, antenna; C, P1, anterior; D, P2 (exopod omitted), anterior; E, P3 endopod; F, P4, anterior; G, P4 endopod, anterior.

*Description of Male*.—(Figs. 7, 8).—Total body length 370 μm measured from anterior outer corner of cephalothorax to posterior margin of caudal rami. Body (Fig. 7A) cylindrical, tapering slightly posteriorly, without clear demarcation between prosome and urosome; integument moderately chitinized, ornate with series of produced dendroid processes. Pattern (Fig. 7A) identical to type species except: all modified body processes significantly more elongate and well developed [processes on P4-bearing somite broken off, but basal part still discernible]; dorsal tubercles on second abdominal somite (Fig. 7A) longer than in type species. Cephalothorax (Fig. 7A) with bilateral constriction in anterior half; anterior margin distinctly concave (Fig. 7A, B); anterior corners with sensory triplet consisting of two sensilla and anteriorly displaced tube-pore; pattern of processes (Fig. 7C) identical to that of type species except: lateroventral conical process moderate in size and with additional small, conical sensillate process anterior to conspicuous marginal tube-pore. Body somites and caudal rami with conspicuous tube-pores (Fig. 7A, D). First, second, and third abdominal somites (Fig. 7D) with median spinule row ventrally. Anal somite partly cleft medially (Fig. 7D); tube-pore present near ventral hind margin (Fig. 7D); anal operculum rounded, smooth (Fig. 7A).

Caudal rami (Fig. 7A, D) elongate, divergent, cylindrical. All setae missing, broken off. Setae I and II inserting in proximal half of ramus, seta III in distal half.

Rostrum (Fig. 7B) fused to cephalic shield; anteriorly displaced and partially absorbed into anteroventral surface of cephalothorax; with paired sensilla arising from distinct processes (broken, true size unknown) and paired bulbous membranous projections (arrowed in Fig. 7B) laterally displaced to bases of antennules.

Antennule unknown, broken off.

Antenna, mandible, maxillule, maxilla, maxilliped (spinules along basal palmar margin more slender and numerous), and P1 (not figured) as for type species.

P2–P4 (Fig. 8A–C). Intercoxal sclerites wide; coxae with spinulose lobate process on outer margin (see Fig. 8B as for P3); bases transversely elongate. Exopods as for type species. Endopods P2 and P4 2-segmented; enp-2 with 2 apical setae. P3 (Fig. 8B) endopod 3-segmented; enp-2 elongate, with few fine spinules along inner margin, anterior distal surface produced into small, recurved apophysis; enp-3 with 2 apical setae. Armature formula as follows:

| | Exopod | Endopod |
|---|---|---|
| P2 | 0.1.122 | 0.020 |
| P3 | 0.1.222 | 0.0.020 |
| P4 | 0.1.122 | 0.020 |

P5 (Fig. 8D) baseoendopod without setophore; with large tube-pore proximal to outer basal seta. Endopodal lobe absorbed, with conspicuous tube-pore and 1 naked seta. Exopod distinct; with 1 inner, 1 distal, and 1 outer bipinnate setae.

Sixth pair of legs asymmetrical (Fig. 7D), with only 1 functional member, represented by a membranous flap; other member fused to somite; P6 without armature. Spermatophore small, 29 μm.

*Female*.—Unknown.

*Etymology*.—The specific name refers to the distinctly concave shape of the anterior margin of the cephalothorax.

*Remarks*.—Unfortunately, the single male specimen was in very poor condition, with the antennules and several body processes having been broken off and with only one member of each pair of legs (P1–P5) and caudal rami present. Despite this unsatisfactory situation, the decision to describe this new species was taken, because (a) it provides information on male characters as yet unknown for the genus (the only other male known being the holotype of *C. coineaui*, and Soyer's (1964) type-material is lost to Science (A. Dinet, personal communication)); (b) it exhibits an increased elaboration of cephalothoracic processes previously unknown in *Ceratonotus*; and (c) the endopodal segmentation and armature of P4 is unique within the genus. These data are relevant to the generic diagnosis given above.

## ***Dendropsyllus***, new genus

*Diagnosis* [based on ♀♀ only].—Ancorabolinae. Body cylindrical, tapering slightly posteriorly, without clear demarcation between prosome and urosome; body ornate with series of produced dendroid processes, each bearing unmodified sensillum terminally. Cephalothorax with bilateral constriction in anterior half; anterior corners with sensory triplet consisting of two sensilla and tube-pore; with conical frontolateral horns; posterior margin with paired laterodorsal dendroid processes; lateroventral margin with

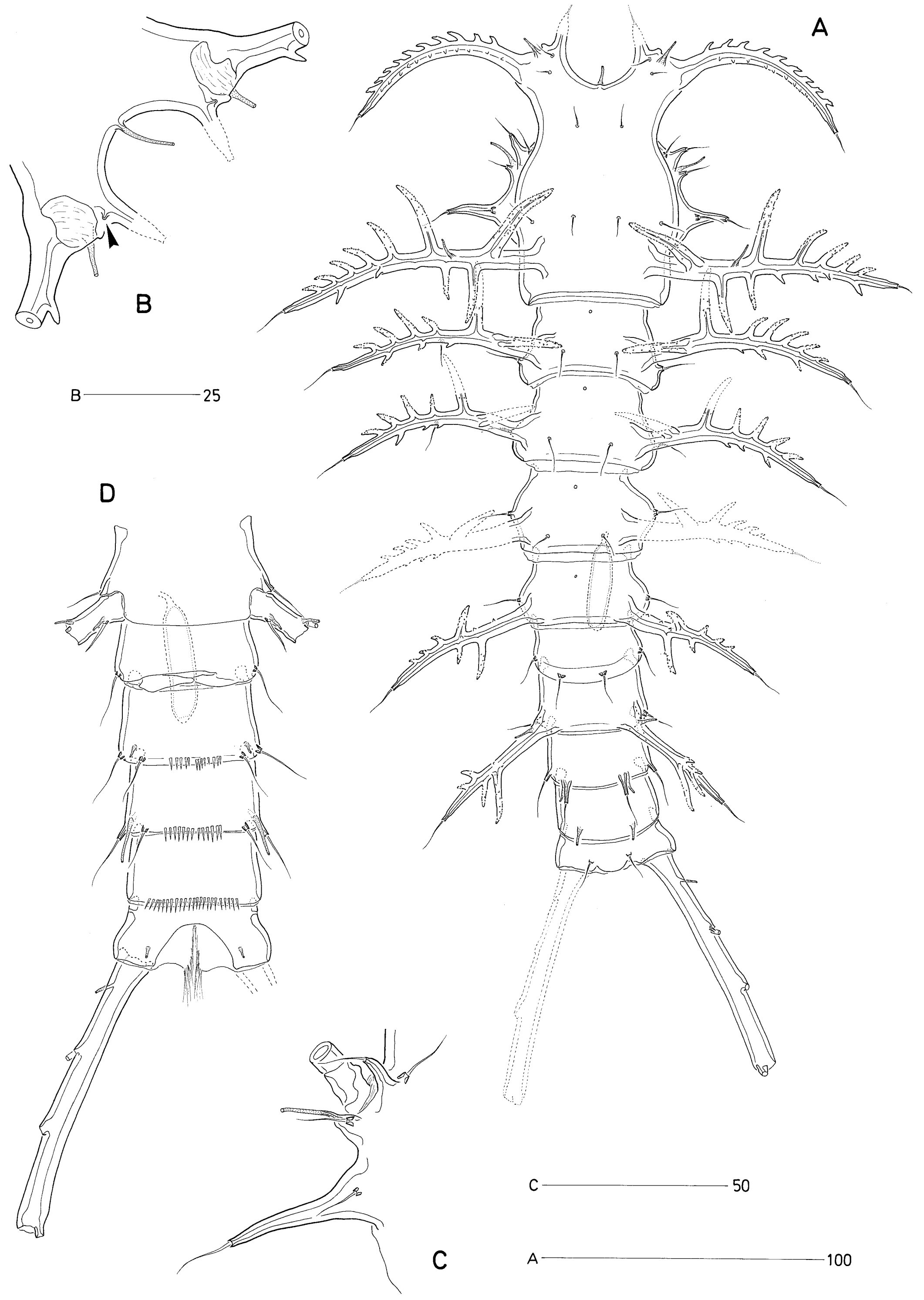


Fig. 7. *Ceratonotus concavus*, new species (♂): A, habitus, dorsal; B, rostrum, ventral (bulbous membranous projection arrowed); C, cephalothorax, median margin, lateral; D, urosome (P5 right exopod omitted, left exopod missing), ventral. Stippled lines indicate missing/broken body parts.

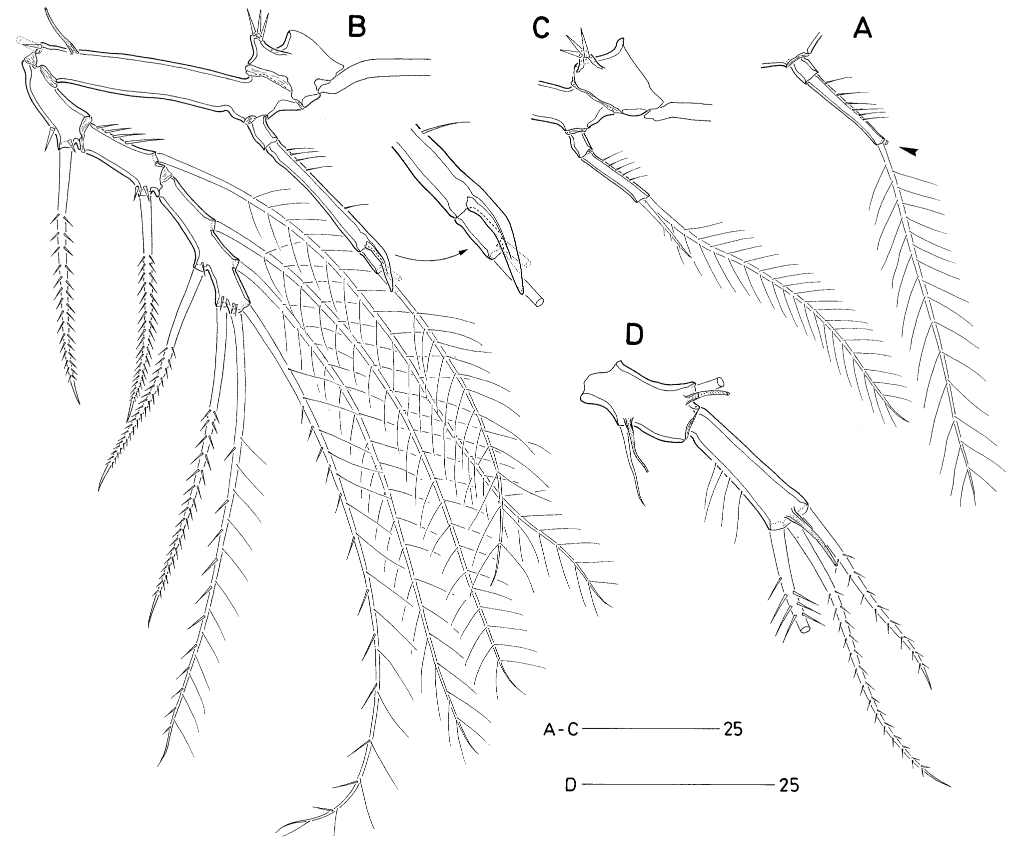


Fig. 8. *Ceratonotus concavus*, new species (♂): A, P2 endopod, anterior (broken seta arrowed); B, P3, anterior (insert showing enlargement of apophysis); C, P4 endopod, anterior; D, P5 anterior.

large, well-developed conical process, often strongly dentate, and additional small conical process bearing sensillum slightly dorsal to conspicuous marginal tube-pore (both proximal to large process). Free thoracic somites bearing P2–P5 each with paired laterodorsal dendroid processes. Abdominal half of genital double-somite (= first abdominal somite) and second abdominal somite with dorsal pair of sensillate tubercles. Somatic hyaline frills weakly developed, smooth. Body somites, swimming legs, P5, and caudal rami with conspicuous tube-pores. Anal operculum smooth. Caudal rami elongate, cylindrical, with 7 setae; seta I minute and positioned ventral to seta II; setae I and II inserted in median third of ramus; seta III inserted in distal third; seta IV reduced and basally fused to well developed seta V; seta VI reduced; seta VII triarticulate at base.

Rostrum not discernible in dorsal aspect; fused to cephalic shield; anteriorly displaced and partially absorbed into anteroventral surface of cephalothorax; with paired sensilla and paired bulbous membranous projections displaced laterally to bases of antennules; with long, distinctive median tube-pore. Antennule 3-segmented in ♀; aesthetasc arising from segments 2 and 3 in ♀; first segment compound, elongate, with 1 subapical anterior seta arising from distinctive spinous projection. Antenna with allobasis showing partial suture along exopodal margin, abexopodal margin with 1 reduced element in distal (endopodal) half; exopod entirely absent; endopod with 2 lateral spines and 6 distal elements (with 2 spines and 3 geniculate setae, longest one fused basally to tiny naked seta). Mandible with robust coxa; palp 1-segmented, uniramous, with 5 setae (3 endopodal and 2 basal). Maxillule with 2 elements on coxal endite; basis with 4 elements on proximal and 2 elements on distal endite; exopod and endopod completely incorporated into basis, represented by 2 and 3 setae respectively. Maxillary syncoxa with 2 well-developed endites; allobasis drawn out into claw; endopod minute, with 2 setae. Maxilliped subchelate, slender, elongate; syncoxa with 1 seta; endopod drawn out into long, narrow curved claw with 1 reduced accessory seta.

P1–P4. Intercoxal sclerites wide and narrow; praecoxae weakly developed; coxae small, trapezoid; bases extremely transversely elongate. P1 rami 2-segmented; endopod shorter than exopod, enp-1 reduced, enp-2 with 1 distal seta; exp-2 with 4 geniculate setae and 1 outer spine. P2–P4 coxae with spinulose lobate process; exopods 3-segmented; without inner setae on exp-1 and endopodal segments; exp-3 with only 2 outer spines; exp-3 with 1 inner seta (P3) and without inner setae (P4); P2 endopod absent; P3 endopod 2-segmented; P4 endopod 1- or 2-segmented. Armature formula as follows (♀♀ only):

| | Exopod | Endopod |
|---|---|---|
| P1 | 0.023 | 0.010 |
| P2 | 0.1.[0 – 1]22 | absent |
| P3 | 0.1.122 | 0.020 |
| P4 | 0.1.022 | 0.010 or 010 |

P5 baseoendopodal setophore absent; endopodal lobe vestigial, represented by 1 tiny seta and 1 conspicuous tube-pore; exopod long, slender, with 1 inner, 1 apical, and 1 outer elements. Female genital field located anteriorly; gonopores covered by common, unarmed genital operculum derived from medially fused P6.

*Type Species.*—*Dendropsyllus thomasi*, new species

*Other Species.*—***D. magellanicus*** (George and Schminke, 1998), new combination; ***D. antarcticus*** (George and Schminke, 1998), new combination.

*Etymology.*—The generic name is derived from the Greek *dendron* (tree) and *psulla* (flea), and refers to the branched processes present on the cephalothorax and free thoracic somites.

*Gender.*—Masculine.

### ***Dendropsyllus thomasi***, new species

*Type Locality.*—Quagmire site; near the base of the Coronado Escarpment, San Diego Trough, north Pacific Ocean; 32°35.75′N, 117°29.00′W; depth 1,220 m; hemipelagic green mud.

*Material Examined.*—Type series collected from 500-m equilateral triangular sampling site. Individual subcore units of each grab allocated a specific sample number (E ***), referred to in parentheses. For detailed locality data and subcore sampling strategy, see Thistle (1978). Holotype ♀ (E 11X) dissected on 12 slides (NHM reg. no. 2002.390); paratype is 1 ♀ (E 47W) in alcohol (NHM reg. no. 2002.391); donated by Dr David Thistle.

*Description of Female.*—(Figs. 9, 10, 11, 12).—Total body length 550 μm ($\bar{x}$ = 620 μm; $n$ = 2) measured from anterior outer corner of cephalothorax to posterior margin of caudal rami. Body (Fig. 9A) cylindrical, tapering slightly posteriorly, without clear demarcation between prosome and urosome; integument moderately chitinized, ornate with series of large dendroid processes; processes with fine denticles and unmodified sensilla (Figs. 9A, B). Somatic hyaline frills weakly developed, smooth (Fig. 9A). Cephalothorax (Fig. 9A) bilaterally constricted in anterior half; anterior corners with sensory triplet consisting of two sensilla and closely associated tube-pore; with pattern of produced sensillate processes as follows: pair of strongly dentate conical processes at anterior outer corners (Fig. 9A, B); posterior margin with pair of laterodorsal dendroid processes, with dorsal tube-pore in proximal half (Fig. 9A), and lateroventral margin with well-developed, conical, strongly dentate process (Fig. 9 A, B), additional small conical process bearing sensillum proximal to large process and slightly dorsal to conspicuous marginal tube-pore. Free thoracic somites bearing P2–P5 each with paired laterodorsal dendroid processes (Fig.9A); processes of somites bearing P2–P4 (Fig. 9A) with anterior sensillum halfway along length of process; genital half of double-somite with paired dorsal sensilla arising from tiny tubercle; abdominal half of double-somite and second abdominal somite with paired sensillate tubercles bearing dorsally (Fig. 9A), laterally, and ventrally (Fig. 9C, latter two smaller than dorsal pair). Body somites and caudal rami with conspicuous tube-pores (Figs. 9, 10E). Original segmentation of genital double-somite indicated by bilateral constriction (Figs. 9A, C). Second and third abdominal somites (Fig. 9C) ventrally with few median spinules around posterior margin. Anal somite partly cleft medially (Fig. 9C); with few small spinules around ventral hind margin (Fig. 9C); anal operculum rounded, smooth (Fig. 10E).

Caudal rami extremely elongate, divergent, cylindrical (Figs. 9A, 10E); 12.8 times as long as maximum width (taken at proximal end); with conspicuous outer tube-pore in proximal third of ramus. Seta I minute, positioned ventral

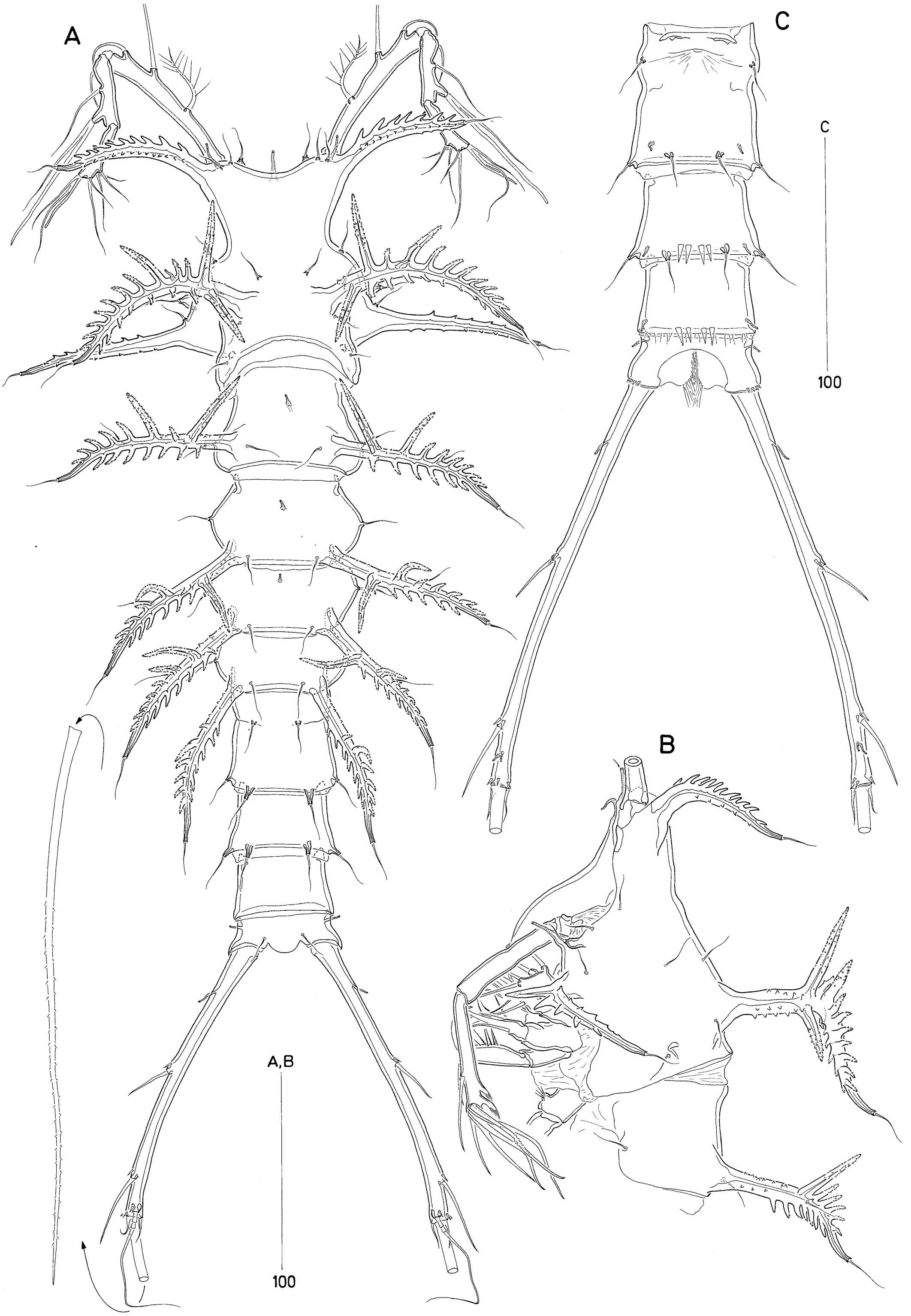


Fig. 9. *Dendropsyllus thomasi*, new genus, new species (♀): A, habitus, dorsal; B, cephalothorax and P2-bearing somite, lateral; C, urosome (excluding P5-bearing somite), ventral.

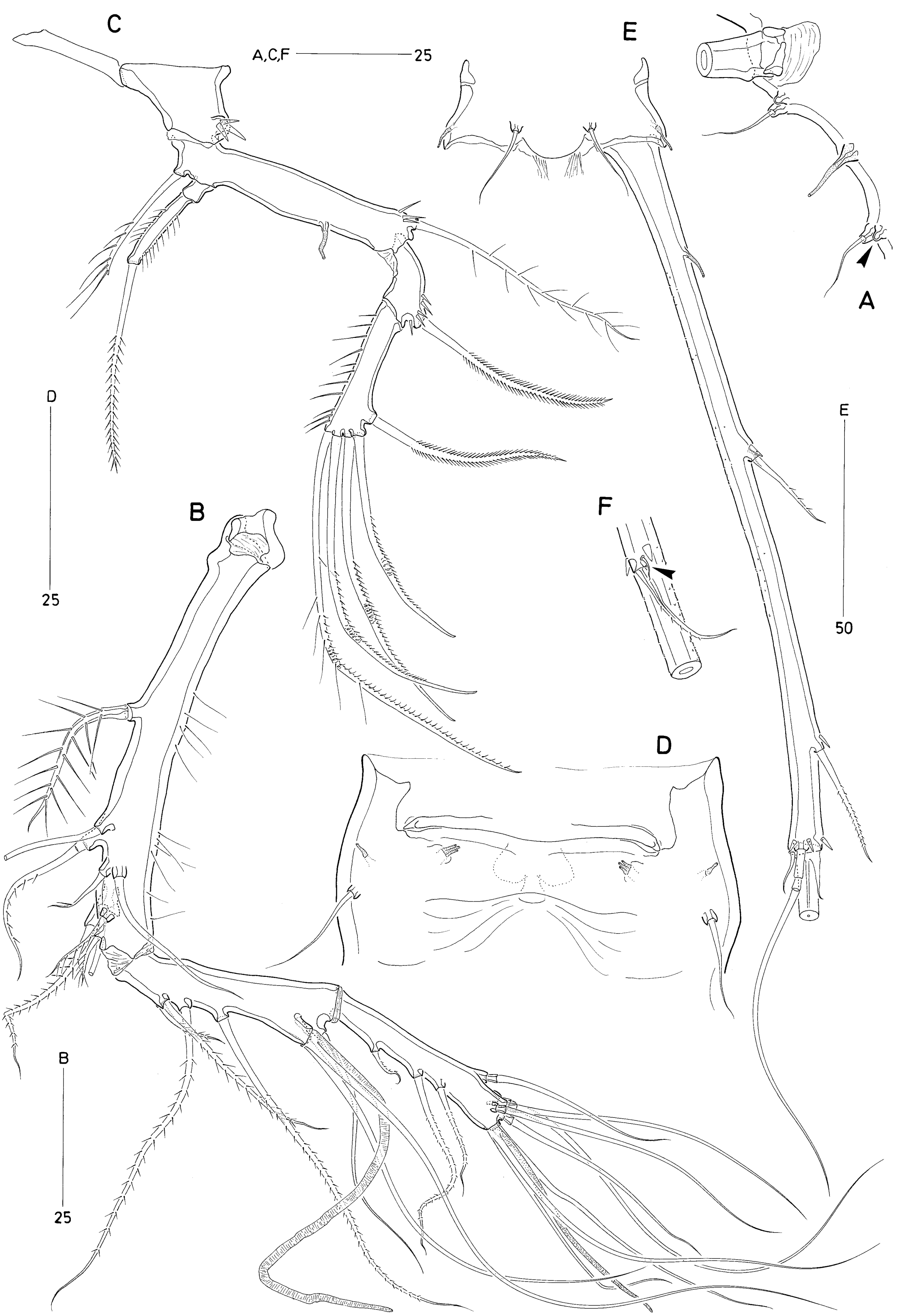


Fig. 10. *Dendropsyllus thomasi*, new genus, new species (♀): A, rostrum, ventral (bulbous membranous projection arrowed); B, antennule, ventral; C, P1 anterior; D, genital field, ventral; E, anal somite and right caudal ramus, dorsal; F, caudal setae I and II, lateral (minute seta I arrowed).

to seta II (arrowed in Fig. 10F); setae II and III bipinnate; seta V well developed, pinnate, fused at base to seta IV (Fig. 9A); setae IV and VI (Fig. 10E) shorter; seta VII triarticulate at base and arising from minute dorsal pedestal, near posterior margin (Fig. 10E).

Rostrum fused to cephalic shield (Fig. 10A); anteriorly displaced and partially absorbed into anteroventral surface of cephalothorax; with paired sensilla arising from small pedestal and paired bulbous membranous projections (arrowed in Fig. 10A), both laterally displaced to bases of antennules; midventral tube-pore well developed, reinforced proximally.

Antennule (Fig 10B) 3-segmented. Segment 1 compound, longest; proximal anterior (inner) element spinous, pinnate; 1 dorsal subapical seta arising from spinous projection. Segment 2 with aesthetasc (length 117 μm). Segment 3 with apical acrothek consisting of aesthetasc (length 60 μm) and 2 slender setae. Armature formula: 1-[3 + 6 pinnate], 2-[2 + 4 pinnate + (1 + ae)], 3-[6 + 3 pinnate + acrothek].

Antenna (Fig. 11A). Coxa represented by well-developed sclerite (Fig. 11A). Basis and proximal endopod segment fused, forming allobasis; membranous insert along exopodal margin marking original position of exopod; exopod completely absent; abexopodal margin with 2 spinule rows, with 1 reduced pinnate seta in endopodal half. Endopod surface with few fine setules, with 2 distal surface frills; spinules along medial margin; lateral armature consisting of 2 bipinnate spines; distal armature consisting of 2 pinnate spines and 3 geniculate setae, longest one with spinules around geniculation and fused basally to vestigial seta.

Mandible (Fig. 11B). Coxa robust, expanding distally to gnathobase bearing several incised blades; 1 bifid seta at dorsal corner. Palp well developed, 1-segmented, with few spinules as figured; with 2 plumose setae along inner margin (representing basal elements) and 3 apical plumose setae (representing incorporated endopod); outer margin without armature.

Maxillule (Fig. 11C). Praecoxal arthrite quadrate, with 2 setae on anterior surface; distal armature consisting of 5 bare and 4 pinnate spines. Coxal endite with 1 pinnate spine and 1 naked seta; few spinules apically. Basis with 4 elements and few spinules apically on proximal endite; with 1 pinnate and 1 bare setae on distal endite. Rami completely incorporated into basis; exopod represented by 1 pinnate and 1 tiny setae; endopod represented by 3 pinnate setae.

Maxilla (Fig. 11D). Syncoxa with spinule patches as figured; with 2 coxal endites; proximal endite with 1 strong pinnate spine basally fused to endite and 2 spinulose spines; distal endite with 3 spinulose spines. Allobasis drawn out into claw with spinules subdistally; accessory armature consisting of 3 bare setae (2 outer) and 1 spinulose spine. Endopod tiny, 1-segmented, with 2 pinnate setae.

Maxilliped (Fig. 11E). Subchelate, slender. Syncoxa with 1 pinnate seta; with few strong spinules. Basis with robust long, spinules along palmar margin. Endopod drawn out into long, narrow curved claw; claw strongly bipinnate, with 1 accessory seta at base.

P1 (Fig. 10C). Intercoxal sclerite moderately wide and narrow. Praecoxa weakly developed. Coxa trapezoid, with small, spinulose lobate process. Basis transversely elongate, with conspicuous anterior tube-pore; with plumose outer seta and setulose inner seta. Both rami 2-segmented; exp-1 outer spine pinnate; exp-2 with spinules along inner margin, with 4 geniculate setae and 1 pinnate outer spine. Enp-1 small, unarmed; enp-2, 3.9 times as long as enp-1, with 1 spinulose seta apically.

P2–P4 (Fig. 12A–C) with wide intercoxal sclerites without ornamentation (as for P2 see Fig. 12A). Praecoxae weakly developed (as for P2 see Fig. 12A). Coxae (Fig. 12A, C) trapezoid, with small, spinulose lobate process on outer margin. Bases (Fig. 12A–C) transversely elongate; with anterior tube-pore in distal half; outer distal seta bipinnate (P2) or bare (P3–P4). Exopods 3-segmented, outer spines elongate (see Fig. 12A, C for P2 and P4). Endopods (Fig. 12A–C) absent (P2) or reduced and 2-segmented (P3–P4); when 2-segmented, enp-1 minute. Armature formula as follows:

| | Exopod | Endopod |
|---|---|---|
| P1 | 0.023 | 0.010 |
| P2 | 0.1.122 | absent |
| P3 | 0.1.122 | 0.020 |
| P4 | 0.1.022 | 0.010 |

P5 (Fig. 12D) baseoendopod and exopod fused, with membranous area marking original segmentation, setophore completely absent, outer basal seta bare, with large tube-pore at base. Endopodal lobe absorbed, represented by tiny pedestal (Fig. 12E), with conspicuous tube-pore and 1 minute seta. Exopod slender and elongate; with 1 outer, 1 distal, and 1 (finely pinnate) inner setae.

Genital field (Fig. 10D) with fused gonopores opening via common midventral slit covered by

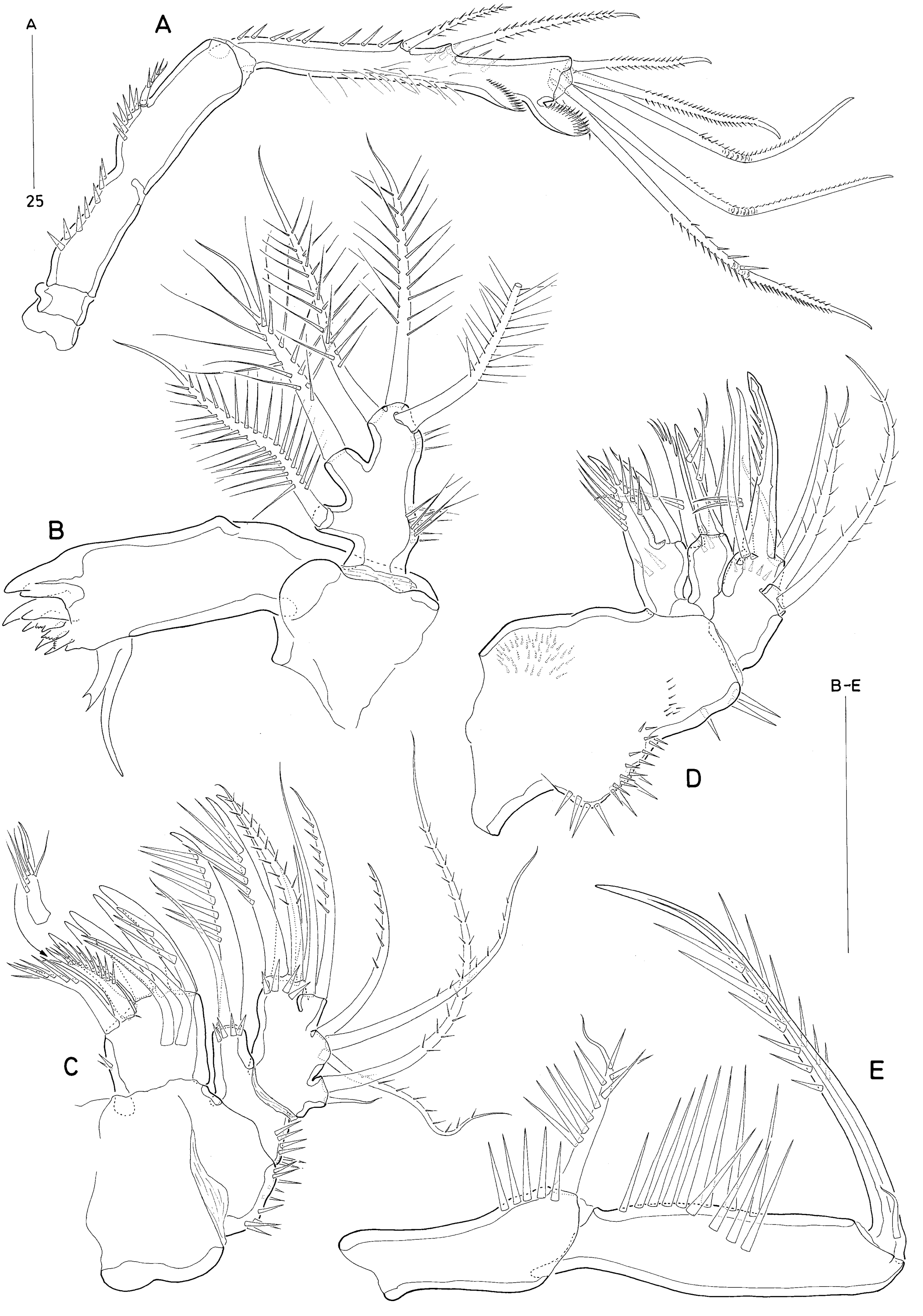


Fig. 11. *Dendropsyllus thomasi*, new genus, new species (♀): A, antenna; B, mandible; C, maxillule (insert showing posteriormost element of arthrite); D, maxilla; E, maxilliped.

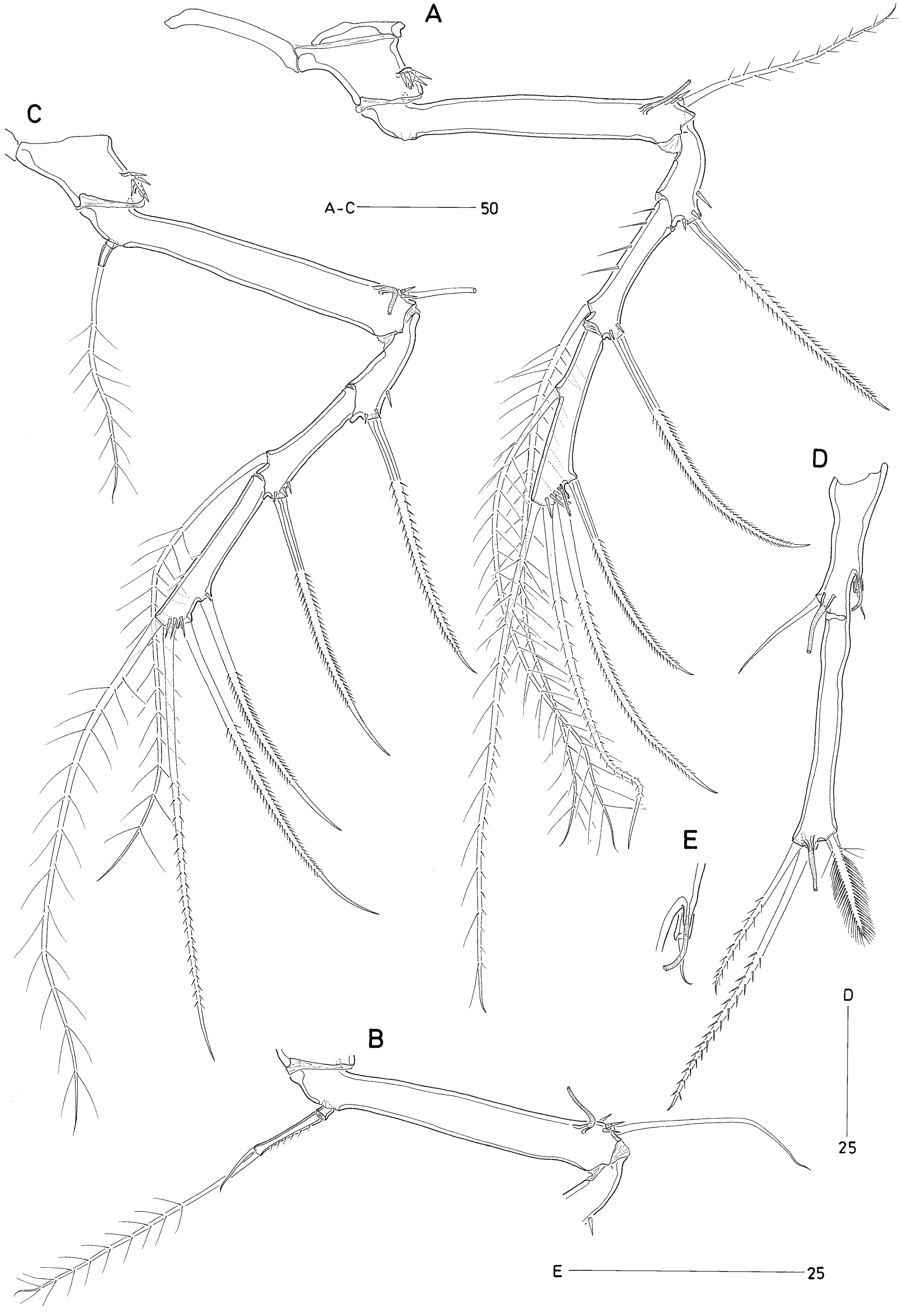


Fig. 12. *Dendropsyllus thomasi*, new genus, new species (♀): A, P2, anterior; B, P3 (exopod omitted), anterior; C, P4, anterior; D, P5, anterior; E, P5 endopodal lobe, anterior.

genital operculum derived from vestigial sixth legs. P6 (Fig. 9C, 10D) flimsy, unarmed. Copulatory pore flanked by paired tube-pore triplet, just posterior to each gonopore.

*Male*.—Unknown.

*Variability*.—Number of branches on dendroid processes may vary slightly between right and left members.

*Etymology*.—The species is named in fond memory of my father, Thomas Conroy-Dalton.

## Discussion

Members of *Ceratonotus* are usually encountered in low numbers, and males are particularly rare. Each of the currently valid *Ceratonotus* species are known from a single sex, although the male of *C. pectinatus* has been reported twice in the literature (Lang, 1948; Drzycimski, 1969) but not described in any detail. Despite this lack of any diagnostic morphological information on the male of *C. pectinatus*, Soyer (1964) substantiated the specific distinction of his new species *C. coineaui* on the basis of (1) the degree of development and proportional lengths of produced dendroid body processes, P1 inner basal seta, caudal rami, and caudal seta V; (2) the 2-segmented P2 endopod; and (3) the 1-segmented P4 endopod.

Comparison of the males of *C. coineaui* and *C. pectinatus* revealed several additional differentiating characters for the former species as follows: (a) the size/degree of development of produced dendroid processes; (b) P1 proportional lengths of: basis, exopodal and endopodal segments, exopodal outer spines [note: Soyer (1964) erroneously figured only two geniculate setae on P1 exp-2, but described it as having three geniculate elements]; (c) P2 basis more elongate; (d) P2 endopod 2-segmented; and (e) proportional length of caudal seta V. Extending the specific boundaries of *C. pectinatus* to include *C. coineaui*, as suggested by Drzycimski (1969), seems unjustified. With particular reference to character (d), there is at present no evidence suggesting that sexual dimorphism in swimming leg endopodal segmentation (except P3) occurs in the genus *Ceratonotus*. The male copepodid V stage (CV) of *C. pectinatus* observed here displayed the same segmentation and full complement of armature on both rami of the swimming legs as in the adult female (except for P3 endopod; see Fig. 4I). It is concluded that for *C. pectinatus* (1) no further changes in swimming leg segmentation and/or armature occur at the final moult from CV to adult, except for segmental differentiation in the male P3 endopod (by analogy with adult male P3 endopodal condition in *C. coineaui* and *C. concavus*); and (2) except for P3 endopod, swimming leg armature formula and segmentation are identical in both sexes. This general swimming leg developmental pattern is supported by ontogenetic patterns observed in *Ancorabolus* (Gómez and Conroy-Dalton, 2002).

Both new species, *C. thistlei* and *C. concavus*, are placed in *Ceratonotus* on account of the following suite of characters: (a) body highly ornate with distinctive dendroid processes on posterior margin of cephalothorax, thoracic somites bearing P2–P5 and first abdominal somite (abdominal half double-somite in ♀), but never on P6- bearing somite (genital half of double-somite in ♀); (b) lateroventral margin of cephalothorax produced into simple conical process; (c) rostrum anteriorly displaced and partially absorbed into anteroventral surface; (d) P1 exp-2 with three geniculate setae; (e) P2 endopod 1- or 2-segmented, with two setae terminally; (f) P3 exp-3 with two inner setae; (g) P5 exopods discrete; and (h) caudal setae I and II inserted in proximal third of caudal ramus.

*Ceratonotus thistlei* can be readily differentiated from its congeners on the basis of the following characters: (1) elongate and slender nature of antennule; (2) antennary segments slender and elongate; (3) P1 with long outer basal spine; (4) P4 endopod 2-segmented with both segments reduced and about equal in size; and (5) P4 enp-2 with one apical seta. *Ceratonotus thistlei* appears most closely related to the Mediterranean species *C. concavus* because of the similar degree of development and length of the dendroid processes, the elongate and slender nature of the caudal rami, and the 2-segmented condition of the P4 endopods.

The most plesiomorphic condition in P2–P4 endopodal segmentation and armature within the genus is displayed by *C. concavus*. It can be readily differentiated from its congeners by the following characters: (1) cephalothoracic anterior margin distinctly concave; (2) rostral sensillae arising from distinct pedestals; (3) cephalothoracic lateroventral conical process well developed; (4) lateroventral margin of cephalothorax with additional small conical process anterior to conspicuous tube-pore; and

(5) degree of development of paired lateral and dorsal tubercles on second abdominal somite.

The proposal of a new genus *Dendropsyllus* for *D. thomasi*, new species, is justified by the following combination of apomorphies: (a) cephalothoracic lateroventral margin with elongate, well-developed processes; (b) antennary allobasal seta reduced; (c) P1 exp-2 with four geniculate setae; (d) P1 enp-2 with one apical seta; (e) P2 endopod completely absent; (f) P3 exp-3 with one inner seta; and (g) P4 exp-3 without inner setae. In addition, the genus exhibits the following diagnostic plesiomorphies: (h) first abdominal somite with paired sensillate tubercles dorsally; and (i) maxilla, allobasal accessory armature consisting of four elements. Based on this suite of characters, the two (sub-) Antarctic *Ceratonotus* species, *C. magellanicus* and *C. antarcticus*, recently described by George and Schminke (1998), can be unequivocally transferred to *Dendropsyllus*. Several of the generic characters used by George and Schminke (1998) to place these species in *Ceratonotus* are common to a larger group of genera as shown by Conroy-Dalton (2001). Although George and Schminke pointed out some discrepancies in the generic diagnosis given by Soyer (1964) (principally as a result of his inclusion of *Echinopsyllus gorbunovi* Smirnov, 1946), they provided no clarification or update themselves that would have justified maintaining the two (sub-) Antarctic species in the genus. *Ceratonotus magellanicus* and *C. antarcticus* share the combination of apomorphic and plesiomorphic diagnostics (a)-(i) listed above for *Dendropsyllus*, with two exceptions: the plesiomorphic condition of the maxillary allobasal setation (i) could not be verified for either *D. magellanicus* and *D. antarcticus* (George and Schminke's (1998) drawings and text are inconclusive), nor could the P3 exopodal armature for *D. antarcticus* (f), which was damaged in the only specimen at hand.

Within the genus, *D. thomasi* and *D. magellanicus* are the most closely related on account of the nature of cephalothoracic processes anterolaterally and along the lateroventral margin, spinulose nature of the maxilliped, P4 endopodal segmentation, and P5 morphology. *Dendropsyllus thomasi* can be differentiated from its congeners on the basis of the elongate dendroid body processes, A1 segment-1 slender and elongate, and the extreme elongation of the caudal rami.

The basic topology of the phylogenetic tree depicting the relationships for the *Ceratonotus*-group presented by Conroy-Dalton (2001) remains unchanged as a result of the generic redefinition of *Ceratonotus* and the establishment of *Dendropsyllus*. The two genera share a close sister-group relationship, unambiguously supported by the following synapomorphies: (1) absorption of the rostrum into the anteroventral margin of the cephalothorax; (2) dendroid nature of body processes; (3) first abdominal somite (abdominal half of genital double-somite in female) with produced body processes, dorsally (multistate character: Conroy-Dalton, 2001); (4) second abdominal somite with paired dorsal tubercles; (5) 3-segmented female antennule; (6) antennary allobasis with one abexopodal seta (endopodal in origin); (7) P5, basal setophore absent; and (8) P5 exopod with only one outer element. The monophyletic status of *Dendropsyllus* is strongly supported by seven apomorphic characters (a)-(g), listed above. *Ceratonotus* is characterized by the dorsal processes on the first abdominal somite, character (3) being dendroid in nature (cf. *Dendropsyllus* with paired dorsal tubercles).

That both *Ceratonotus thistlei* and *Dendropsyllus thomasi* co-occur in the San Diego Trough is remarkable. In view of the disjunct records of their respective congeners (Antarctic, Scandinavia, Mediterranean), this may indicate that both *Ceratonotus* and *Dendropsyllus* assume a worldwide distribution. This would reinforce the assumption that only a fraction of the species diversity has been uncovered and that any zoogeographical inferences based on the currently available data on the family Ancorabolidae are premature if not speculative.

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