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SYSTEMATICS AND PHYLOGENY OF THE ANCORABOLIDAE (COPEPODA: HARPACTICOIDA). II. POLYPHYLY OF *POLYASCOPHORUS* AND DESCRIPTION OF *ARTHURICORNUA*, NEW GENUS

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A B S T R A C T

Both sexes of a new genus and species of Ancorabolidae are described from the San Diego Trough in the Northeastern Pacific. *Arthuricornua anendopodia*, new genus, new species, is placed in the newly defined *Ceratonotus*-group which includes the genera *Ceratonotus* Sars, *Dorsiceratus* Drzycimski, and *Polyascophorus* George. Members of this group are characterized by the cylindrical body shape, presence of dorsal processes on somites bearing P2–P4, rostral shape, proximal antennular elongation, 3-segmented condition of ♂ P3 endopod, and absorption of P5 endopodal lobe in both sexes. The major evolutionary transformations within the *Ceratonotus*-group are discussed and polarized by outgroup comparison with the Cletodidae. Parsimony analysis confirmed *Dorsiceratus* and *Ceratonotus* as monophyletic genera, but demonstrated the polyphyletic status of *Polyascophorus*. *Polyascophorus schminkei* George is identified as the earliest offshoot within the *Ceratonotus*-group and is transferred to a new genus *Touphapleura*. The common ancestry of *Arthuricornua* and *Dorsiceratus*, and the sistergroup relationship between *Ceratonotus* and *Polyascophorus*, are strongly supported. A basal dichotomy divides the genus *Ceratonotus* into two geographically separated clades. The genus *Polyascophorus* is redefined to include only *P. martinezi* George and *P. gorbunovi* (Smirnov).

The harpacticoid family Ancorabolidae Sars comprises two subfamilies, the Ancorabolinae and the Laophontodinae (Lang, 1944), and currently contains 46 species and subspecies in 16 genera. In the visually striking Ancorabolinae, the number of species has almost quadrupled since Lang's (1948) review of the family, unveiling an unexpected wide distribution in both northern and southern hemispheres (see Conroy-Dalton and Huys, 2000). The majority inhabit the coastal zone and muddy sediments in the deep sea, with a few exceptions including reports from brackish waters (Kunz, 1935), sandy sediments (Drzycimski, 1969; Moore *et al.*, 1987), and polar pack ice tow net samples (Brady, 1918). Recent discoveries include new taxa from the Arctic (George, 1998a) and (sub-) Antarctic waters (George, 1998b; George and Schminke, 1998) and the first record of the subfamily from a deep-sea hydrothermal vent in the northeastern Pacific Ocean (Conroy-Dalton and Huys, 2000). Although members of the Ancorabolinae are generally found in low numbers, with males typically scarcer than females, their previ-

ously accepted rarity and currently underestimated diversity can be regarded merely as a reflection of logistic problems related to sampling the deep sea and other remote environments.

In the early 1970s the benthos of the San Diego Trough was extensively sampled during the Expedition Quagmire (Thiel and Hessler, 1974), an American integrated-sampling programme designed to investigate the entire benthic community at a single deep-sea locality. Thistle (1978) examined the harpacticoid fauna and identified a total of 140 putative harpacticoid species from these samples. Species were arbitrarily allocated to three functional groups according to presumed habitat utilization which he inferred from their basic morphology (Thistle, 1982). Species which typically had sediment particles attached to the dorsal surface of the body were assigned to the "sediment-covered" group and included the Argestidae, Ancorabolidae, and members of *Malacopsyllus* Sars (Ameiridae). Thistle (1982) discriminated four species of Ancorabolinae at the Quagmire site, belonging to the genera *Dor-*

siceratus Drzycimski, *Echinopsyllus* Sars, and *Ceratonotus* Sars. Examination of this material, kindly placed at my disposal by Dr. David Thistle, revealed the presence of a new genus and species described herein. The discovery of *Arthuricornua anendopodia* new genus, new species, also provided the impetus for an analysis of the phylogenetic relationships between the related genera *Polyascophorus* George, *Dorsiceratus*, and *Ceratonotus*.

MATERIALS AND METHODS

Ekman grab (20 × 20 cm) sediment samples were collected in the San Diego Trough (Expedition Quagmire; 1973–74) 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 a 1-mm and 62- μ m mesh diameter sieve. Both sieve fractions were stained with rose bengal and the harpacticoids sorted under a dissecting microscope. For detailed sampling procedures see Thistle (1978).

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

Additional material examined in this study includes the type material of *Dorsiceratus octocornis* Drzycimski, *D. triarticulatus* Coull, and *Ceratonotus pectinatus elaphus* Por, and unregistered specimens of *C. pectinatus pectinatus* Sars (coll. R. Huys) and *D. triarticulatus* (coll. D. Thistle).

The descriptive terminology is adopted from Huys and Boxshall (1991). 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. The term acrothek is used to denote the trifid seta complement found apically on the distal antennular segment.

The phylogenetic software package PAUP 3.1.1, written by David Swofford of the Laboratory of Molecular Systematics, Smithsonian Institution (Swofford, 1993), was used to analyse phylogenetic relationships within the *Ceratonotus*-group.

Type material is deposited in the Natural History Museum (NHM), London, U.K.

Scale bars in all figures are indicated in μ m.

SYSTEMATICS

Family Ancorabolidae Sars, 1909

Subfamily Ancorabolinae Sars, 1909

Arthuricornua, new genus

Diagnosis.—Ancorabolinae. Body cylindrical, tapering slightly posteriorly, without clear demarcation between prosome and urosome. Urosomites without paired processes or tu-

bercles. Cephalothorax with large, conical frontolateral horns; posterior margin with paired laterodorsal processes; lateroventral margin forming setulose lobate outgrowth. Somites bearing P2–P4 each with paired dorsal processes; none of thoracic processes dendroid. Hind margins of urosomites often with very fine setular extensions. Body somites and caudal rami with conspicuous tube-pores dorsally and laterally. Anal operculum with fine spinules. Caudal rami elongate and cylindrical with 7 setae; seta III pinnate. Sexual dimorphism in body size, antennule, P3 endopod, P5, P6, genital segmentation, and degree of development of dorsal body processes.

Rostrum small, discernible in dorsal aspect; fused to cephalic shield; with paired plumose sensillae, membranous projections and long distinctive midventral tube-pore subapically. Antennule 4-segmented in ♀, 6-segmented and subchirocer in ♂ (with one segment distal to geniculation); aesthetasc arising from segments 3 and 4 in ♀, segments 5 and 6 in ♂; segment 1 elongate and with long setules along anterior margin. Antenna with allobasis showing partial suture along exopodal margin, abexopodal margin with 2 setae of which basal one reduced; exopod entirely absent; endopod with 3 lateral and 6 distal elements. Mandible with robust coxa; palp 1-segmented, uniramous with 5 setae (3 endopodal, 1 basal, and 1 exopodal). Maxillule with 2 elements on coxal endite; basis with 4 elements on proximal and 1 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 basal constriction and 3 accessory elements; endopod minute, with 2 setae. Maxilliped subchelate, slender and elongate; syncoxa with 1 reduced seta; endopod drawn out into long narrow, curved claw with 1 accessory seta.

P1–P4. Intercoxal sclerites wide and narrow; praecoxae well developed; coxae small, trapezoid; bases extremely transversely elongate. P1 endopod absent, original position indicated by slightly membranous area with small nodule; exopod 2-segmented, exp-2 with 4 geniculate setae and 1 outer spine. P2–P4 exopods 3-segmented; endopods absent (P2) or 2-segmented (P3–P4, except ♂ P3 endopod); without inner setae on exp-1 and

endopodal segments; exp-3 with only 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	I-0; I + 4	absent
P2	I-0; I-1; II,2,1	absent
P3	I-0; I-1; II,2,2	0-0; 0,2,0 (♀) 0-0; 0-0; 0,2,0 (♂)
P4	I-0; I-1; II,2,1	0-0; 0,2,0

P5 uniramous in both sexes; basal setophore reduced to short cylindrical outgrowth; endopodal lobe vestigial, represented by 2 setae and 2 conspicuous tube-pores; exopod elongate with 1 inner, 1 apical and 3 outer elements (middle outer spine reduced and displaced to posterior surface), fused with baseopod in ♀, distinct in ♂. Female genital field located anteriorly, with moderately large copulatory pore; gonopores covered by common genital operculum derived from medially fused P6 with 1 pinnate seta on either side. Male P6 asymmetrical; without armature; functional member represented by small membranous flap.

Type Species.—*Arthricornua anendopodia*, new species.

Etymology.—The generic name is derived from the Latin *cornu*, horn, referring to the dorsal and lateral horn-like projections on the cephalothorax and pedigerous somites. The genus is named in memory of Dr. Arthur G. Humes, founding editor of *Journal of Crustacean Biology* and the most prolific copepod systematist of all time.

Gender.—Feminine.

Arthricornua anendopodia, 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 48Y) in alcohol (NHM reg. no. 2000.1036); paratypes are 1 ♀ (E 47Z) dissected on 11 slides (NHM

reg. no. 2000.1037) and 3 ♂♂ (E 11X, E 48Y, E 48X) (NHM reg. no. 2000.1038–1040) in alcohol (right antennule of 1 ♀ (E 11X) dissected and mounted separately on slide); donated by David Thistle.

Description of Female (Figs. 1, 3, 4A–B, 5A–C, 6A–B, E, 7).—Total body length 705–783 μm (\bar{x} = 744 μm; n = 2) measured from anterior tip of rostrum to posterior margin of caudal rami. Body (Fig. 1) cylindrical, tapering slightly posteriorly, without clear demarcation between prosome and urosome; integument moderately chitinized, prosome with series of produced processes. Processes with fine spinules and unmodified sensillae; absent on urosomites (Fig. 1); additional sensillae covering body surface plumose. Somatic hyaline frills weakly developed and smooth (Figs. 1, 7C); somatic margins often with very fine setular extensions (Figs. 1, 7C). Cephalothorax (Fig. 1) with pair of elongate processes at anterior outer corners, furnished with long, fine spinules; posterior margin with pair of laterodorsal (Fig. 1) sensilla-bearing processes. Free prosomites (Fig. 1) with paired backwardly produced dorsal processes. All body somites and caudal rami with conspicuous tube-pores dorsally and laterally (Figs. 1, 7C, E, F). Original segmentation of genital double-somite indicated by dorsal surface ridge with few spinules and by lateral bulbous projections ornamented with long spinules, tube-pores and sensillae (Figs. 1, 7C, D); posterior half with lateral and dorsal spinule rows around hind margin. Second abdominal somite with similar spinular pattern around posterior margin. Third abdominal somite with almost continuous row of fine spinules dorsally and laterally and with some spinules ventrally (Figs. 1, 7C). Anal somite partly cleft medially (Fig. 7C); 2 tube-pores and small spinules present around ventral hind margin (Fig. 7C); anal operculum rounded, furnished with long fine spinules (Fig. 7E).

Caudal rami elongate, divergent and slightly bent inwards, cylindrical (Figs. 1, 7C, E); outer lateral margin with spinular patches around insertion sites of setae I–III, VI, and VII; with 3 tube-pores and 7 setae (Fig. 7C, E). Seta I minute, positioned ventral to seta II (see insert Fig. 7E); seta IV (Fig. 7C, E) shortest; seta V well developed, pinnate (Fig. 1B); seta VII triarticulate at base and arising from minute dorsal pedestal, near posterior margin (Fig. 7E).

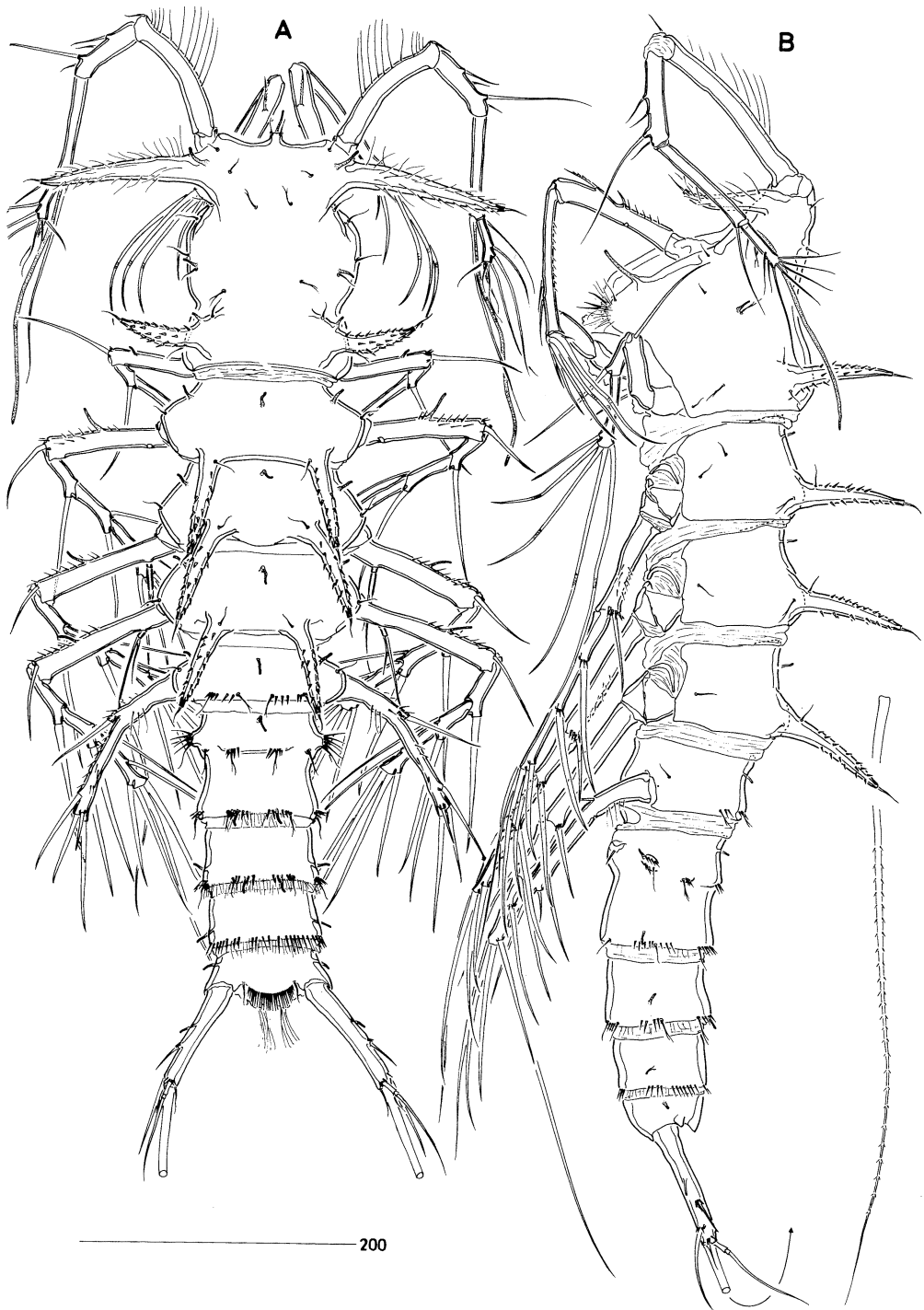


Fig. 1. *Arthuricornua anendopodia*, new genus, new species (♀): A, habitus, dorsal; B, habitus, lateral.

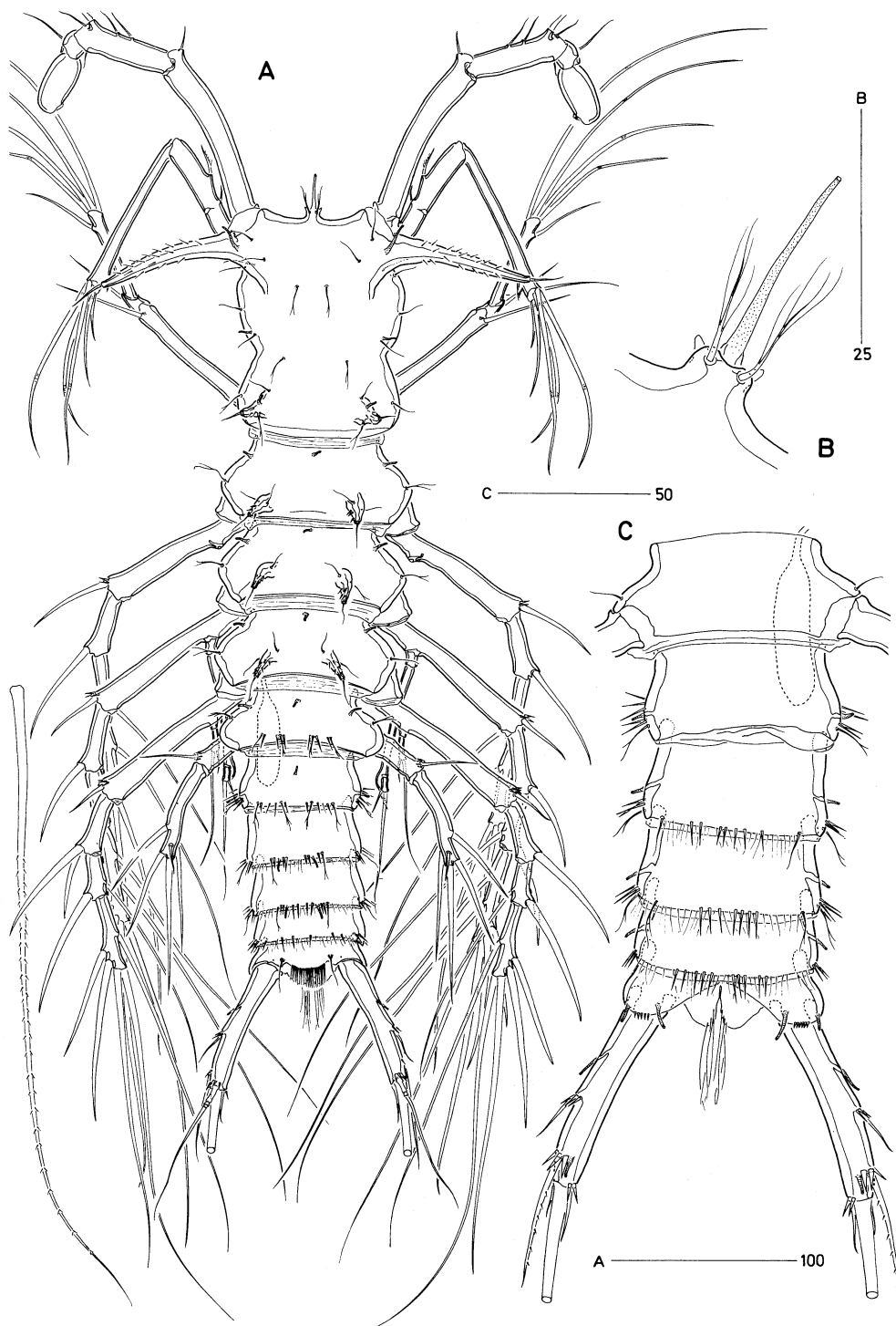


Fig. 2. *Arthuricornua anendopodia*, new genus, new species (δ): A, habitus, dorsal; B, rostrum, dorsal; C, urosome (P5 omitted), ventral.

Rostrum fused to cephalic shield (Figs. 1A, 6E); small, trapezoid in shape; paired sensillae arising from tiny pedestals forming vaguely bifid apical margin; with paired pointed membranous projections laterally (arrow in Fig. 6E) just proximal to sensillae; midventral tube-pore subapically, well developed and reinforced proximally.

Antennule (Figs. 1, 3A) 4-segmented. Segments 1 and 2 covered with fine setules. Segment 1 longest, with long fine spinules along anterior margin; with reduced pinnate seta subapically. Segment 3 second longest, with aesthetasc (length 180 μm). Segment 4 with apical acrothek consisting of aesthetasc and 2 slender setae. Armature formula: 1-[1 pinnate], 2-[5 + 2 pinnate], 3-[6 + (1 + ae)], 4-[9 + acrothek].

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

Labrum well developed; with lappet-like ornamentation along distal margin as in Fig. 4A; anterior face with large median tube-pore and fine setules.

Mandible (Fig. 4B). Coxa robust, recurved (see Fig. 4A for *in situ* view showing representative orientation, shape and length); expanding distally to gnathobase bearing 2 multicuspidate teeth and several thin, incised blades; 1 pinnate seta at dorsal corner. Palp well developed, 1-segmented, with some spinules and fine setules; with 1 unipinnate seta along inner margin (representing basal element), 3 apical setae (representing incorporated endopod) and outer margin with 1 pinnate seta (representing exopod).

Paragnaths moderately developed, trilobate (Fig. 4A); lateral lobes with few spinule and setule patches, mostly around outer margins; median lobe with paired dense setular patches posteriorly.

Maxillule (Fig. 3C). Praecoxal arthrite subrectangular with 2 setae on anterior surface; distal armature consisting of 2 pinnate, 4 pectinate, 2 bare, and 2 apically serrate spines; few tiny spinules along inner margin. Transverse membranous zones present around base of praecoxal arthrite and coxa allowing for additional flexure. Coxal endite with 1 pinnate spine and 1 bare seta; few spinules apically; outer margin with tuft of fine spinules. Basis with 2 spinule rows; proximal endite with 4 elements; distal endite with 1 bare seta. Rami completely incorporated into basis; exopod represented by 2 setae; endopod represented by 1 plumose and 2 naked setae.

Maxilla (Fig. 3D). Syncoxa with 3 spinule patches as figured; with 2 endites, arising from membranous area; proximal endite with short spinule row, 1 strong pinnate spine basally fused to endite, and 2 setae; distal endite with 2 pectinate spines and 1 naked seta. Allobasis drawn out into claw with spinules subdistally; accessory armature consisting of 2 bare setae and 1 pinnate spine. Endopod minute, with 2 naked setae.

Maxilliped (Fig. 3E). Subchelate, slender and elongate. Syncoxa with 1 reduced seta surrounded with few spinules. Basis with spinules along outer margin. Endopod drawn out into long, narrow, curved claw; claw smooth, with 1 accessory seta at base.

P1 (Fig. 5A). Intercoxal sclerite wide and narrow. Praecoxa well developed. Coxa small, trapezoid. Basis transversely elongate, with conspicuous anterior tube-pore; with pinnate outer spine and naked inner seta; anterior spinule pattern as indicated in Fig. 5A. Exopod 2-segmented, with fine setules along inner margin; exp-1 outer spine long, pinnate; exp-2 with 4 geniculate setae and 1 pinnate outer spine. Endopod absent; original position represented by slightly membranous area with small nodule (Fig. 5A, B).

P2-P4 (Figs. 5C, 6A, B) with wide, narrow intercoxal sclerites without ornamentation. Praecoxae (Figs. 5C, 6A, B) very well developed, with fine setular extensions. Coxae (Figs. 5C, 6A, B) trapezoid, with 2 (P2-P3) or 3 (P4) large spinules anteriorly. Bases transversely elongate; outer margin with spinule row (Figs. 5C, 6A, B) and anterior tube-pore in distal half; additional patches of fine setules on anterior surface; outer distal seta bipinnate, arising from tiny, posteriorly displaced setophore. Exopods 3-segmented,

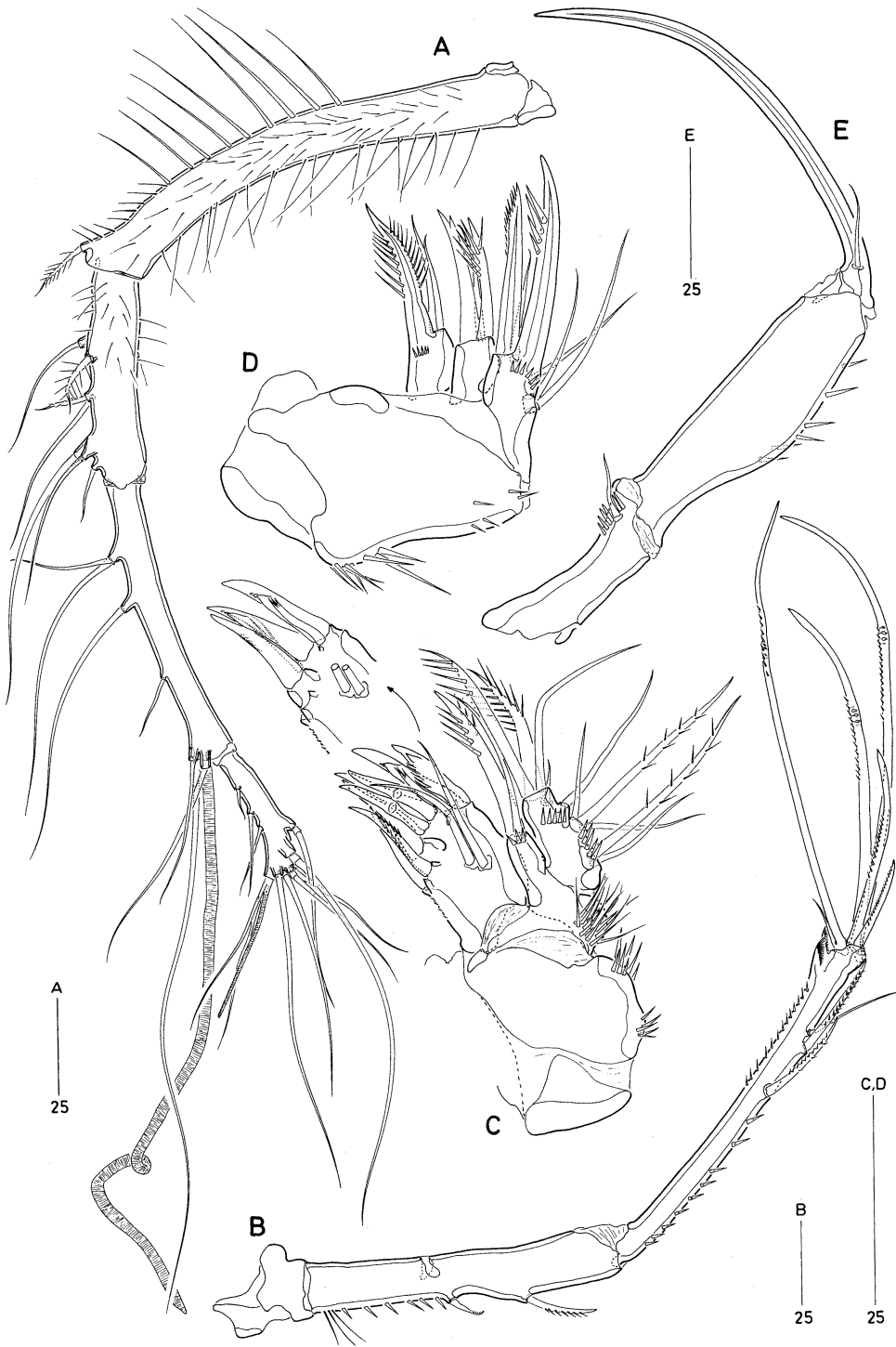


Fig. 3. *Arthricornua anendopodia*, new genus, new species (♀): A, antennule, dorsal; B, antenna; C, maxillule, anterior (inset showing distal portion of arthrite with five posteriormost elements only); D, maxilla.

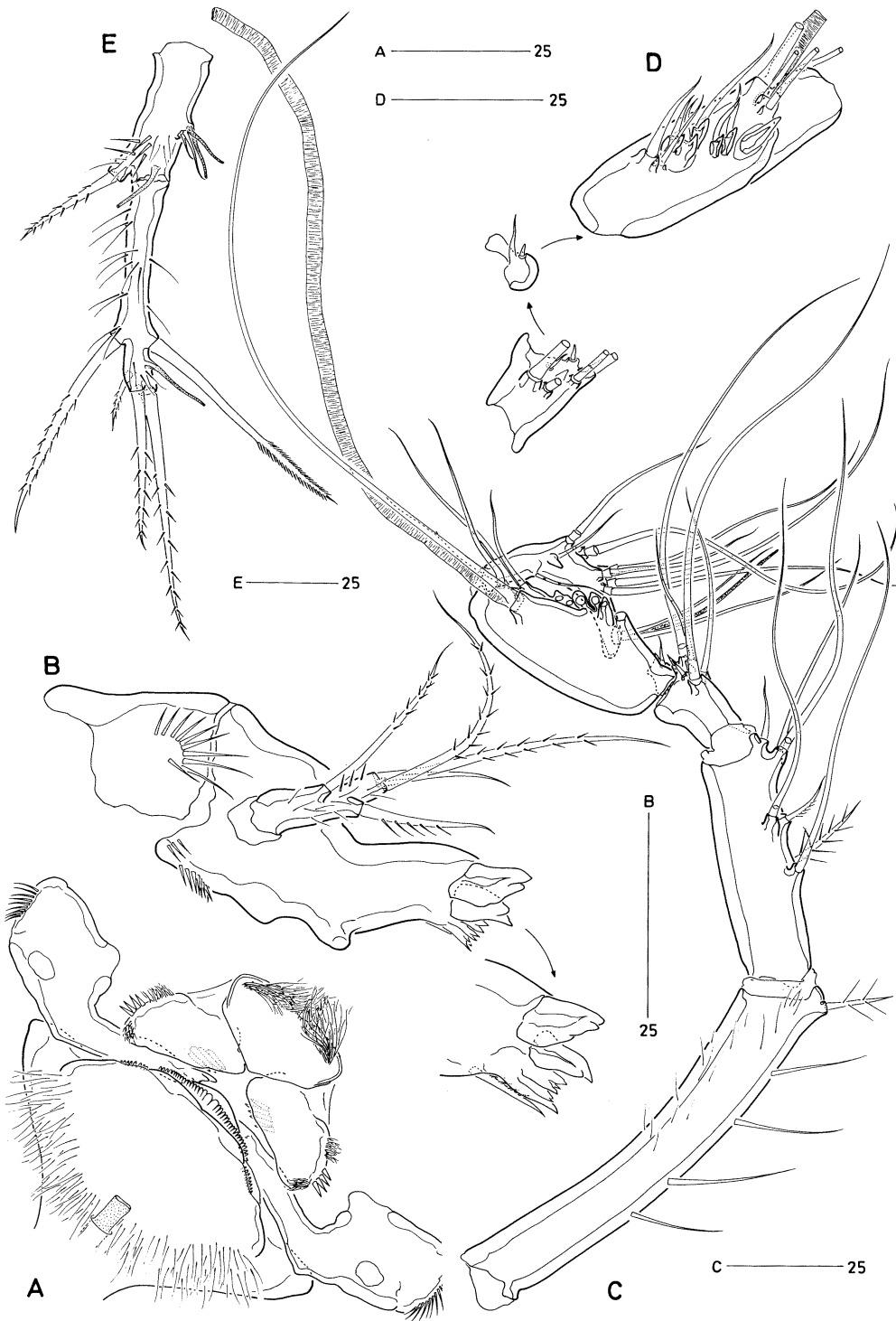


Fig. 4. *Arthuricornua anendopodia*, new genus, new species: A, oral area (♀) showing position of labrum, mandibles (palps omitted) and paragnaths, ventral; B, mandible (♀) (inset showing distal armature of gnathobase); C, antennule (♂), (ventral anterior armature of segment 5 omitted); D, antennular segments 3–5 (♂) disarticulated, anterior; E, P5 (♂) anterior.

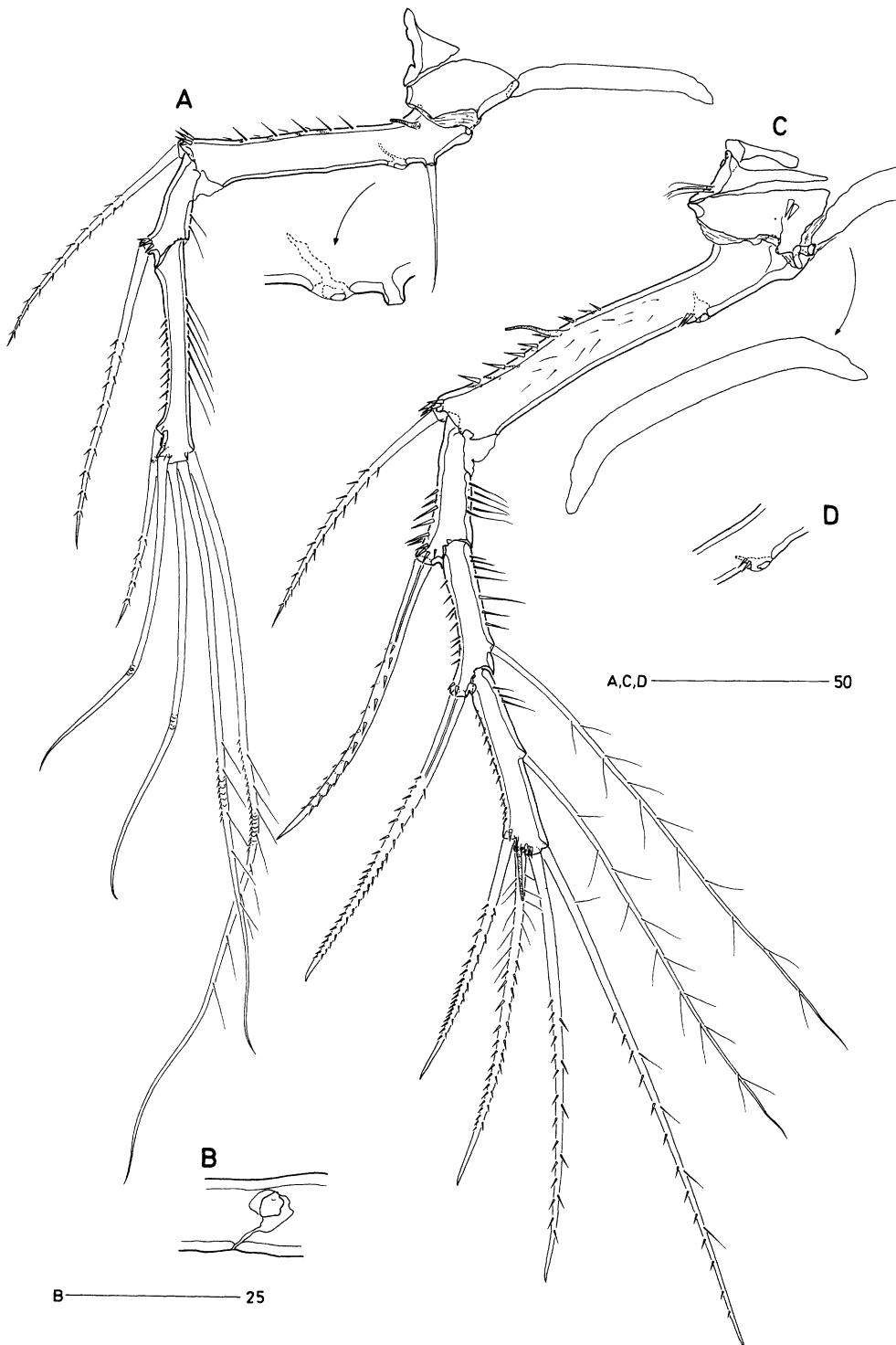


Fig. 5. *Arthuricornua anendopodia*, new genus, new species: A, P1 (♀), anterior (inset showing small nodule representing original position of endopod); B, P1 (♀) proximal basal area representing position of endopod, medial; C, P2 (♀), anterior (inset showing intercoxal sclerite at full size); D, P2 (♂) proximal basal area indicating original position of endopod.

spines elongate. P2 endopod absent, position represented by slightly membranous area, with small nodule and few spinules (Fig. 5C). P3–P4 endopod (Fig. 6A, B) reduced and 2-segmented; enp-1 tiny, unarmed; enp-2 slightly longer, with 2 apical setae. Armature formula as for genus.

P5 (Fig. 7A, B) uniramous. Baseoendopod and exopod fused, with minute membranous area marking original segmentation (arrow in Fig. 7B). Baseoendopod with large, subdistal tube-pore; setophore reduced, fused to baseoendopod, bearing pinnate outer basal seta. Endopodal lobe absorbed, represented by tiny raised pedestal (Fig. 7B), with 2 conspicuous tube-pores, 1 pinnate and 1 naked seta. Exopod long, slender; with fine setules on anterior surface; with finely serrate inner spine, tube-pore along inner margin subdistally, 1 pinnate spine distally, and 3 pinnate outer setae (middle one reduced and displaced posteriorly).

Genital field (Fig. 7C, D) with fused gonopores opening via common midventral slit covered by genital operculum derived from vestigial sixth legs. P6 (Fig. 7D) each with 1 pinnate seta. Copulatory pore moderately large (arrow in Fig. 7D), flanked by paired tube-pore triplet, just posterior to each gonopore. Area posterior to copulatory pore slightly membranous.

Description of Male (Figs. 2, 4C–E, 5D, 6C, D).—Smaller than ♀ (Fig. 2A); total body length 474–495 µm (\bar{x} = 483 µm; n = 3) measured from tip of rostrum to posterior margin of caudal rami. Sexual dimorphism in body size, degree of development of body processes, antennule, P3 endopod, P5, P6 and in genital segmentation.

Body processes (Fig. 2A) relatively smaller than in ♀ (except those at anterior corners of cephalothorax). Ornamentation pattern of processes and sensillae as in ♀ (Fig. 2A, C).

Rostrum (Fig. 2B) as in ♀.

Antennule (Fig. 4C) 6-segmented and subchirocer, geniculation between segments 5 and 6; segment 4 represented by a U-shaped sclerite (Fig. 4D); segment 1 longest; aesthetasc present on segment 5 and as part of apical acrothek on segment 6. Segment 1 with few long spinules along anterior margin. Segments 3, 4, and 5 with 3, 2, and 1 vestigial elements, respectively. Segments 5 and 6 with several elements (5 and 1 respectively) each

arising from small spinous tubercle. Armature formula: 1–[1 pinnate], 2–[2 pinnate + 5], 3–[4 + 3 vestigial], 4–[2 vestigial], 5–[10 + 1 reduced + (1 + ae)], 6–[8 + acrothek]. Apical acrothek consisting of 2 setae and aesthetasc.

P1 and P2 (see Fig. 5D for P2 endopodal region) as in ♀.

P3 endopod (Fig. 6C) 3-segmented; enp-2 elongate, with spinules along inner margin, anterior distal surface produced into small, recurved apophysis; enp-3 with 2 apical setae, outermost seta proportionally longer than in ♀.

P4 as in ♀, enp-2 (Fig. 6D) outermost seta proportionally longer than in ♀.

P5 (Fig. 4E) uniramous. Baseoendopod with large distal tube-pore; setophore reduced, fused to baseoendopod, bearing pinnate outer basal seta. Endopodal lobe absorbed, represented by slightly raised area (Fig. 4E) bearing 2 conspicuous tube-pores and 2 setae. Exopod distinct and elongate, with fine setules on anterior surface; with finely serrate inner spine, long tube-pore along inner margin subdistally; 1 pinnate spine distally and 3 pinnate outer setae (middle one reduced and displaced posteriorly).

Sixth pair of legs asymmetrical (Fig. 2C), with only 1 functional member, represented by reduced membranous flap; other member fused to somite P6 without armature.

Spermatophore elongate, 58 µm.

Variability.—One female (E 47Z) displayed size variation in the caudal rami (Fig. 7F).

Etymology.—The species is derived from the Greek prefix *ἀν-* (not, without), and refers to the complete absence of the P1–P2 endopod (Greek: *ἐντός*, within; *πόδι*, foot).

PHYLOGENETIC ANALYSIS OF *CERATONOTUS*-GROUP

Monophyly of Ingroup

Conroy-Dalton and Huys (2000) recognized a coherent group of five genera within the Ancorabolinae, characterized by antennular segmentation, rostral morphology, cephalothoracic sensillar patterns, presence of lateral body processes, elongation of P1 endopod, segmentation of male P3 endopod, and P5 morphology and armature in both sexes. Comparison of the remaining taxa reveals a second lineage comprising nine species (and one subspecies) contained within

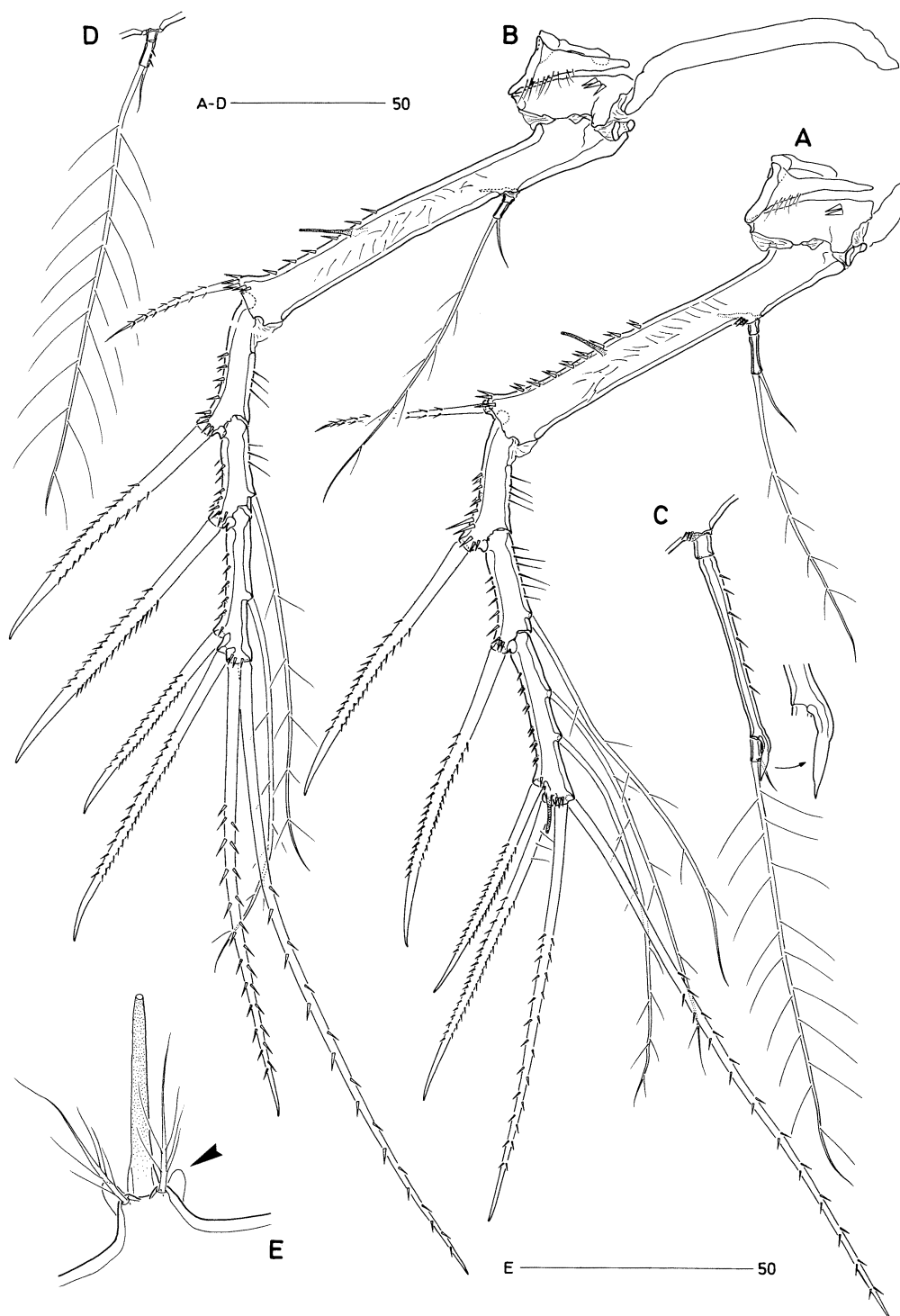


Fig. 6. *Arthricornua anendopodia*, new genus, new species: A, P3 (♀), anterior; B, P4 (♀), anterior; C, P3 (♂) right endopod, anterior (inset showing apophysis); D, P4 (♂) right endopod, anterior; E, rostrum (♀), dorsal (lateral membranous projection, arrow).

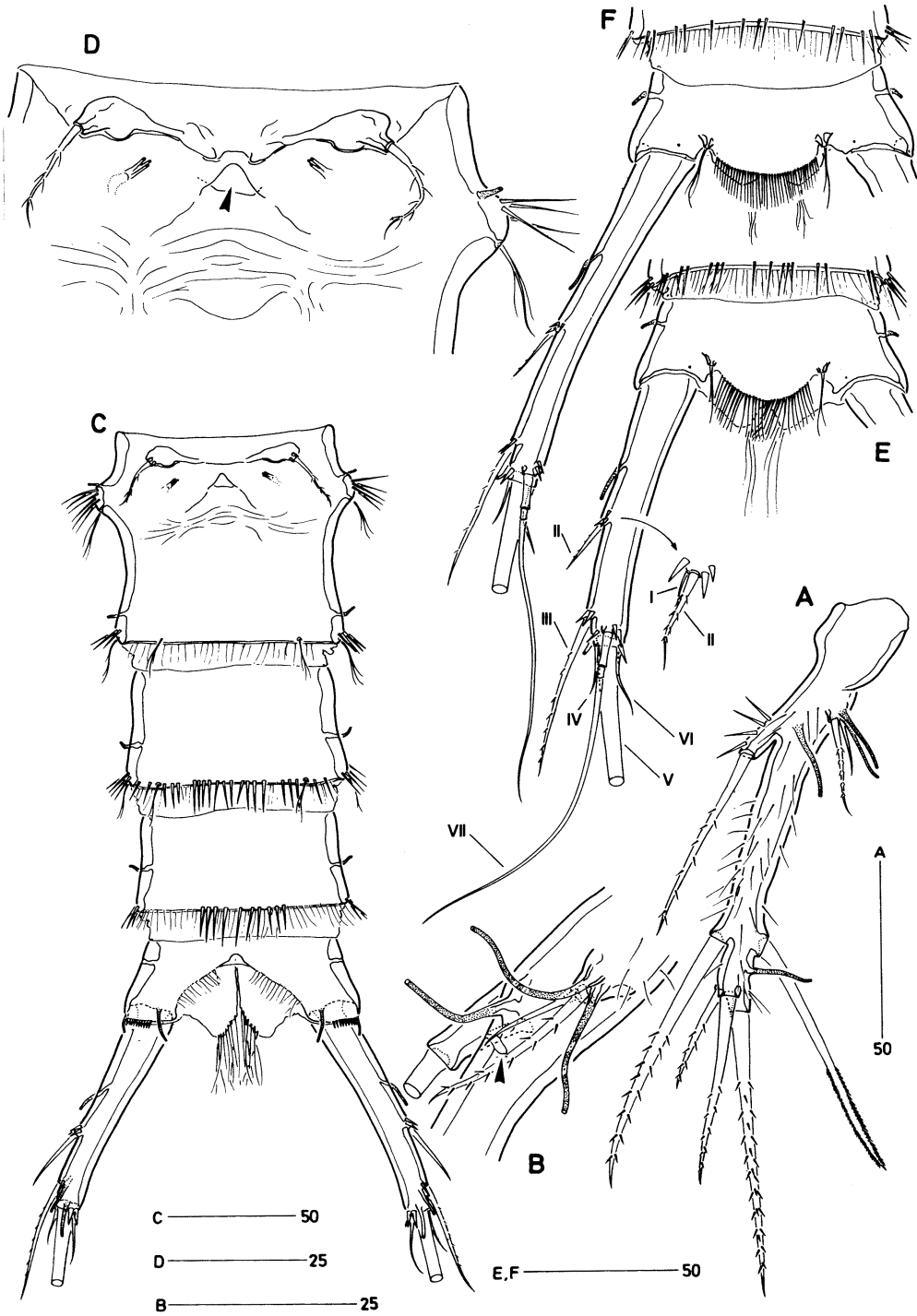


Fig. 7. *Arthuricornua anendopodia*, new genus, new species (♀): A, P5, anterior; B, P5 baseendopod, medial (membranous area marking original segmentation, arrow); C, urosome (excluding P5-bearing somite), ventral; D, genital field, ventral (copulatory pore, arrow); E, anal somite and right caudal ramus, dorsal (inset showing position of setae I and II, lateral); F, same, example of variability.

Table 1. Morphological characters used in the phylogenetic analysis. Apomorphic states are referred to in square brackets.

1. Rostrum protruding, discernible in dorsal aspect [anterior displacement and partial absorption into anteroventral surface of cephalothorax].
2. Cephalothorax without conspicuous setular/spinular ornamentation [with setular tufts along lateral margins].
3. Anterolateral corners of cephalothorax not produced [1: forming small projections; 2: produced into long frontolateral horns].
4. Lateroventral margins of cephalothorax produced into lobate or slightly conical extension [produced into large laterally directed processes].
5. Cephalothorax without posterior pair of processes [1: with dorsal pair of conical processes; 2: processes bifurcate and laterally displaced].
6. Thoracic processes (when present) on cephalothorax (P1) and somites bearing P2–P4 conical and spinulose [dendroid].
7. Thoracic processes on somites bearing P2–P4 small in ♀ [large, dorsally directed horns].
8. Size of thoracic processes not sexually dimorphic [distinctly smaller in ♂].
9. Thoracic processes on somites bearing P2–P4 arising dorsally [laterally displaced].
10. P5-bearing somite without processes [paired dorsal processes present].
11. First abdominal somite in ♂ (abdominal half of genital double-somite in ♀) without paired tubercles or processes [1: with dorsal pair of tubercles; 2: secondarily enlarged forming dendroid processes].
12. Second abdominal somite without tubercles [paired dorsal tubercles present].
13. Antennular segments 1 and 2 free in both sexes [fused, forming elongate compound segment].
14. Anterior margin of antennular segment 1 with long spinules [bare].
15. Antennule ♂ with 2 segments distal to geniculation [single segment and no subdivision expressed].
16. Antennary allobasis with 2 abexopodal setae [basal seta lost].
17. Antennary allobasis with both abexopodal setae (when present) basis well developed [basal seta reduced].
18. P1 exopod 3-segmented [2-segmented; exp-2 and -3 failed to separate].
19. Distal segment P1 exopod with 1 (when 3-segmented) or 2 outer spines and 3 geniculate setae [distal outer spine transformed into geniculate seta].
20. P1 endopod well developed [significantly reduced in size; at most scarcely longer than exp-1].
21. P1 endopod (when present) with 2 terminal setae/spines [1 seta/spine].
22. P2 endopod present [completely absent].
23. P2 exp-2 with 2 apical setae [1 apical seta].
24. P3 exp-3 with 2 inner setae [1 inner seta].
25. P3 exp-2 with outer spine [without].
26. P4 exp-3 with inner seta [without].
27. P4 exp-2 with 2 apical setae [1 apical seta].
28. P4 endopod not sexually dimorphic [with additional outer spine in ♂].
29. P5 protopod with long articulating setophore bearing basal seta [reduced to short tubular outgrowth].
30. P5 protopod with basal setophore [absent].
31. P5 exopod with all outer spines arising from marginal position [middle outer spine displaced to posterior surface and reduced in size].
32. P5 exopod with 3 outer elements [proximal and middle elements lost].

three genera: *Ceratonotus pectinatus pectinatus* Sars, 1909; *C. pectinatus elaphus* Por, 1965; *C. coineau* Soyer, 1965; *C. magellanicus* George and Schminke, 1998; *C. antarcticus* George and Schminke, 1998; *Dorsicercatus octocornis* Drzycimski, 1967; *D. triarticulatus* Coull, 1973; *Polyascophorus gorbunovi* (Smirnov, 1946); *P. martinezi* George, 1998b; and *P. schminkei* George, 1998b. The common ancestry of this lineage, named hereafter the *Ceratonotus*-group, is supported by the following synapomorphies: (1) body somites virtually cylindrical; (2) somites bearing P2–P4 with paired backwardly produced (latero)dorsal processes; (3) rostrum small, without apical elongation posterior to insertion

point of sensillae; no sexual dimorphism where males are known; (4) antennular segment 1 elongate (fused to segment 2 in *Ceratonotus* but equivalent portion also elongate); (5) P1–P4 endopods reduced, with armature elements always arranged around apex of terminal segment; (6) P3 male with 3-segmented endopod; apophysis arising from middle segment; (7) P5 endopodal lobe in both sexes absorbed into protopod; with reduced armature, represented by at most two setae.

The *Ceratonotus*-group differs significantly from the *Ancorabobolus*-group in the cephalothoracic sensillar pattern and the complete absence of lateral wing-like processes on the body somites.

Taxa and Characters

Table 2. Character data matrix [0 = ancestral (plesiomorphic) state, 1-2 = derived (apomorphic) states, ? = missing data]. Characters 3, 5, and 11 are multistate characters.

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32					
<i>Arthuricornua anedopodia</i>	0	0	2	0	1	0	1	1	0	0	0	0	0	0	1	0	1	1	1	1	?	1	?	0	1	0	0	0	1	0	0	1	0				
<i>Ceratonotus antarcticus</i>	?	0	2	0	1	1	1	?	1	1	1	1	1	1	?	1	0	1	1	0	0	1	?	?	1	1	1	?	0	1	0	1	0	1			
<i>Ceratonotus coineai</i>	?	0	2	0	1	1	1	?	1	1	2	?	1	1	?	1	0	1	0	0	1	?	?	1	1	?	0	1	0	1	0	1	0	1			
<i>Ceratonotus magellanicus</i>	1	0	2	1	1	1	1	?	1	1	1	1	1	1	?	1	0	1	1	0	1	?	?	1	1	1	?	0	1	0	1	0	1	0	1		
<i>Ceratonotus pectinatus pectinatus</i>	1	0	2	0	1	1	1	?	1	1	2	1	1	1	?	1	0	1	0	0	0	0	0	0	0	1	0	1	0	1	0	1	0	1	0	1	
<i>Ceratonotus pectinatus elaphus</i>	1	0	2	0	1	1	1	?	1	1	2	1	1	1	?	1	0	1	0	0	0	0	0	0	0	1	0	1	0	1	0	1	0	1	0	1	
<i>Dorsiceratus octocornis</i>	0	1	1	0	1	0	1	1	0	0	0	0	0	0	1	0	1	1	1	0	0	0	1	1	1	0	0	1	0	1	0	1	0	1	0	0	1
<i>Dorsiceratus triarticulatus</i>	0	1	1	0	1	0	1	1	0	0	0	0	0	0	1	0	1	1	0	0	0	0	1	1	1	0	0	1	0	1	0	1	0	1	0	0	1
<i>Polyascophorus gorbunovi</i>	0	0	2	0	2	0	1	?	1	1	0	0	0	0	?	0	0	1	1	1	1	1	?	1	0	1	0	1	0	0	0	0	0	0	0	0	0
<i>Polyascophorus marinezzi</i>	0	0	2	0	2	0	1	0	1	1	0	0	0	0	0	0	0	1	1	1	1	1	?	1	0	1	0	1	0	0	0	0	0	0	0	0	0
<i>Polyascophorus schminkei</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

The phylogenetic analysis was executed at species level in order to test the monophyly of the genera *Ceratonotus*, *Dorsiceratus*, and *Polyascophorus*, and to determine the position of *Arthuricornua*. Examination of the morphological data revealed 32 phylogenetically informative characters which were polarized by outgroup-comparison with the Cletoidea *sensu* Por (1986). Apomorphic character states are denoted inside square brackets using the multistate coding system (Table 1). Character state scores for each taxon are compiled in matrix format in Table 2. A question mark indicates missing entries, either because the appendage or the ramus is unknown in that species (certain sexually dimorphic characters could not be scored in taxa where only one sex was known), or because it was impossible to assign scores confidently due to the lack of morphological detail in the original description. It has been assumed for the majority of characters that oligomerization is the principal trend of evolutionary transformation within the Copepoda (Huys and Boxshall, 1991). Hence, all characters (except character 3) were set irreversible, which suppresses reversals at the expense of introducing extra convergences and consequently increasing tree-length. The BRANCH AND BOUND search procedure was used with accelerated character transformation (ACCTRAN) and tree-bisection-reconnection (TBR) branch swapping.

Although being potentially informative in other ancorabolid lineages (Conroy-Dalton and Huys, 2000), mouthpart characters have not been considered in the present analysis because descriptions of several species are deficient in this respect (e.g., Smirnov, 1946) and no material was available for re-examination. There is also circumstantial evidence that antennular setation patterns and P5 segmentation may provide phylogenetically significant information; however, for analogous reasons these characters have been excluded from this study. Additional notes are provided for the following characters:

Rostrum.—The rostrum is small to minute in all members of the *Ceratonotus*-group. In *Polyascophorus*, *Dorsiceratus*, and *Arthuricornua*, the rostrum is represented by a small blunt or slightly bifid outgrowth located along

the concave anterior margin of the cephalic shield. This rostral position is considered as the plesiomorphic state. In species of *Ceratonotus* the rostrum has migrated further anteriorly and is no longer discernible in dorsal aspect (personal observation). It has become largely integrated in the anteroventral surface of the cephalothorax, a position that is scored as the apomorphic state (Table 1; *character 1*). In all species the rostrum bears a long median, anteriorly directed tube-pore, paired sensillae, and two membranous projections (Fig. 2B). George (1998b) mistakenly regarded these hyaline bulb-like "appendages" as an autapomorphy for *Polyascophorus*. Conroy-Dalton and Huys (2000) demonstrated their presence in all members of the *Ancorabolus*-group, and unpublished observations of *Ceratonotus* and *Dorsiceratus* revealed that they are characteristic for a wider group of taxa. It has been suggested that these structures are raised pores, possibly homologous with the fourth unit of the organ of Bellonci (Conroy-Dalton and Huys, 2000). George (1998b) regarded the presence of long spinules on the rostrum as a generic diagnostic for *Polyascophorus* and used it as supporting evidence to place *Ceratonotus gorbunovi* in this genus. We have tentatively refrained from scoring this as a separate character because the plumose nature of the rostral sensillae recorded in other species (Figs. 2B, 6E) may have caused observational errors in earlier descriptions. There is no evidence of rostrum sexual dimorphism in the *Ceratonotus*-group.

Processes on Cephalic Shield.—Because processes can differ in number, shape, position, and origin, general cephalic ornamentation has been disintegrated into a number of discrete characters (*characters 3–5*). Congruence with non-cephalic characters suggests that the *Ceratonotus*-group is derived from an ancestor that lacked processes on the cephalic shield. This condition is retained only in *P. schminkei*. In all other members of the group the anterolateral corners of the cephalothorax have produced, laterally directed processes which take the shape of frontolateral horns in *Arthricornua*, *Ceratonotus*, and the remaining species of *Polyascophorus*. The short anterolateral projections found in *Dorsiceratus* are positionally homologous to the frontolateral horns, but it is

unclear whether they represent a precursor state or merely secondarily reduced processes. Conroy-Dalton and Huys (2000) showed that reductions in the sensillar array can lead to secondary loss of body processes in the *Ancorabolus*-group. Pending a detailed examination of the sensillar patterns across genera, this multistate character (3) is therefore scored as unordered rather than irreversible.

Members of the *Ceratonotus*-group have a propensity for developing an extension of the free lateroventral pleural margins of the cephalothorax. In *Arthricornua* and *Dorsiceratus* this is represented by a lobate expansion which typically bears a tuft of setules (Fig. 1B). Further elongation has occurred in *C. pectinatus*; both subspecies show a similar lobate outgrowth but bear a terminal conical process. This process is laterally directed and has undergone extreme development in both Southern Hemisphere species of *Ceratonotus* (George, 1998b) (*character 4*). In *C. antarcticus* these lateroventral processes are spinous and bare, whereas in *C. magellanicus* they have become dendroid, resembling the paired dorsal body processes.

With the exception of *P. schminkei*, all species of the *Ceratonotus*-group bear a posterior pair of processes on the cephalothorax (*character 5*). These processes are conceivably thoracic in origin, being derived from the incorporated P1-bearing somite. In *Arthricornua* and *Dorsiceratus*, the processes are conical, spinulose and distinctly shorter than the frontolateral horns, whereas in *Ceratonotus* they are much longer and dendroid. In the two Arctic *Polyascophorus* species, the processes have migrated from their ancestral laterodorsal position to a lateroventral location. They have also become apically bifurcate with a short anterior and a long posterior branch, and have undergone excessive growth, becoming the largest pair of body processes.

Processes on Pedigerous Somites.—All members of the *Ceratonotus*-group possess paired dorsal processes on the pedigerous somites bearing P2–P4; however, in *P. schminkei* their development has remained modest. The short conical processes in this species can be considered as the precursors of the large, dorsally directed horns found in *Arthricornua*, *Dorsiceratus*, *Ceratonotus*, and the remaining

Polyasophorus species (character 7). In *A. anendopodia* (Figs. 1A, 2A) and both species of *Dorsiceratus* (personal observation), the dorsal processes (including those derived from the incorporated P1-bearing somite) are sexually dimorphic in size, being distinctly smaller in males and attaining only the size of those in *P. schminkei* (character 8). Another transformation affecting all four pairs of processes is secondary branching, forming dendroid horns in the genus *Ceratonotus* (character 6). In this genus the horns are displaced from their original dorsal position and arise dorsolaterally instead. This is an apomorphic state shared with the two Arctic species of *Polyasophorus* (character 9).

Processes on Urosome.—*P. schminkei*, and the genera *Arthuricornua* and *Dorsiceratus*, lack dorsal processes on the P5-bearing somite. Paired dorsal processes are present in all other members, and are either short and conical (*Polyasophorus* part.) or large and dendroid (*Ceratonotus*) (character 10). Additional urosomal processes are found only in the genus *Ceratonotus* where the abdominal half of the female genital double-somite (and first abdominal somite in males?) possesses paired dendroid processes in the three European (sub)species (character 11). In *C. magellanicus* and *C. antarcticus* these processes have remained in the tuberculate precursor state (George, 1998b). Finally, all *Ceratonotus* species appear to have paired dorsal tubercles on the second abdominal somite (character 12). It is conceivable that Soyer (1965) overlooked these in his description of *C. coineau*.

Antennules.—Except for *Ceratonotus*, where they have failed to separate and form an elongate compound segment, antennular segments 1 and 2 are completely separated in both sexes (Figs. 3A, 4C) (character 13). Similarly, the anterior margin of antennular segment 1 typically has long stiff spinules that are secondarily lost in *Ceratonotus* (Fig. 3A) (character 14). The male antennular segmentation pattern in *Polyasophorus* suggests that, ancestrally, there were two free segments distal to the geniculation. Soyer's (1965) description of the male of *C. coineau* indicates that this state is also retained in the genus *Ceratonotus*. In *Arthuricornua* and *Dorsiceratus* these distal segments have

failed to separate, leaving only one segment distal to the geniculation (Fig. 4C) (character 15).

Antennae.—The antennary allobasis primitively has two abexopodal setae. In all species of *Ceratonotus* the basal seta is lost (character 16). Coull (1973) illustrated only one seta in *D. triarticulatus* but re-examination of the types revealed that the basal seta was overlooked and that its position coincides with the marked notch indicated in his Fig. 31. Both abexopodal setae are equally long in the ancestral state; however, in *Arthuricornua* and *Dorsiceratus* the basal seta has undergone size reduction (Fig. 3B) (character 17).

P1 Segmentation and Armature.—*Dorsiceratus triarticulatus* is the only species that has retained a three-segmented P1 exopod. Re-examination of Coull's (1973) type material and of additional specimens discovered in the San Diego Trough samples confirmed the presence of a well-defined articulation between exp-2 and exp-3. In all other species of the *Ceratonotus*-group these segments have failed to separate during ontogeny (character 18). Confusion exists over the correct armature of the exp-2 (exp-3 when three-segmented) in some species. Soyer (1965) figured only four setae on P1 exp-2 of *C. coineau* but mentioned five elements in the text. The latter is probably correct (by analogy with its congeners), and it is conceivable that Soyer (1965) missed one of the geniculate setae. Coull (1973) gave the correct armature formula for *D. triarticulatus*, but his illustration (Fig. 36) shows that the distal exopod segment had accidentally rotated during mounting. This inadvertent error was also made for the P5 exopod (his Fig. 40). The ancestral armature of the distal exopod segment consists of three geniculate setae and two outer spines (only one if exopod three-segmented). This configuration is retained only in *P. schminkei* and in the European species of *Ceratonotus*. In all other taxa the distal outer spine is transformed into an additional geniculate seta (Fig. 5A) (character 19).

The P1 endopod displays reductions in various taxa and it is entirely lost in *Arthuricornua*. The endopod is significantly reduced in size in the Arctic species of *Polyasophorus*, retaining its two-segmented condition in *P. martinezi* but further reduced to a minute

segment in *P. gorbunovi* (character 20). In both species the endopod carries only one element. Although this character is shared with the Antarctic *Ceratonotus* species, it is not necessarily indicative of common ancestry (character 21: see below). Outgroup comparison with the Cletodidae (e.g., Gee, 1994; Fiers, 1996) suggests that the ancestral setation of P1 enp-2 in the *Ceratonotus*-group comprises two distal elements, the outer one being spiniform and the inner one setiform and geniculate. This pattern is still displayed by *P. schminkei* and *D. triarticulatus* (the variability claimed by Coull (1973) being unreal and based on a damaged specimen). In Arctic *Polyascopephorus* species only the geniculate seta is retained, whereas in Antarctic *Ceratonotus* species the element is a bipinnate spine according to George's (1998b) descriptions, suggesting that a different element (the inner one) was lost in these species. Finally, some species deviate from the ancestral pattern by the possession of two geniculate setae. This implies the transformation of the outer spine and is found in members of two genera, i.e., *D. octocornis* in *Dorsiceratus*, and the European species of *Ceratonotus*.

P3 Armature.—All species of the *Ceratonotus*-group possess two inner setae on P3 exp-3, except for *C. magellanicus* which has only one (character 24). The P3 exopod is unknown in the closely related *C. antarcticus*, but it is conceivable that a similar reduction has occurred because the P4 exopod follows an analogous pattern in both species (character 26). On the basis of this assumption, character 24 was retained in the data matrix and scored as a missing entry for *C. antarcticus*, despite being a potential autapomorphy for its sister taxon *C. magellanicus*.

The outer spine on the female P3 enp-2 is found only in *P. schminkei*. The state for *C. coineaui* was scored as a missing entry because the female is unknown (character 25).

P4 Sexual Dimorphism.—The sexual dimorphism displayed on the P4 endopod in both species of *Dorsiceratus* and in *P. martinezi* is difficult to interpret. In the males of these species, the distal endopod segment gains an outer spine which is not found in any female members of the *Ceratonotus*-group. This dimorphism was first reported by Drzycimski (1967) for *D. octocornis* and initially over-

looked (Coull, 1973) but subsequently confirmed in *D. triarticulatus* (personal observation). The outer spine is present (both sexes) in all members of the *Ancorabolus*-group (Conroy-Dalton and Huys, 2000) and appears to be commonly present in the Cletodidae. In the latter, the P4 endopod is first recognizable as a discrete segment at CIII stage, bearing two apical setae. At the next moult, both the two-segmented condition and the outer spine are expressed (Fiers, 1996). This condition persists in adult cletodids (both sexes) and corresponds to that found in the males of *Dorsiceratus* and *P. martinezi* (in the latter, however, only one apical seta is left). From this it is inferred that the expression of sexual dimorphism is caused by a heterochronic change in the female development. The developmental constraint is clearly progenetic (early offset of development at CIII) and suppresses the expression of the outer spine at CIV and subsequent moults. This local progenesis, affecting the female developmental sequence only, is regarded as the apomorphic state (character 28).

P5 Protopod.—All species of *Polyascopephorus* possess a long articulating setophore bearing the outer basal seta. George (1998b) regarded this character as diagnostic for the genus. It is scored here as the plesiomorphic state because it is widespread in the cletodid outgroup (e.g., Gee, 1994; Fiers, 1996) and characteristic for the *Ancorabolus*-group (Conroy-Dalton and Huys, 2000). In both sexes of *Arthuricornua* and *Dorsiceratus*, the setophore is significantly reduced to a short, non-articulating, tubular outgrowth (Figs. 4E, 7A), and in *Ceratonotus* it is completely lost. During cletodid development the setophore is expressed at CIV when the exopodal and endopodal lobes first become apparent (Fiers, 1996). Because the setophore typically increases in length during successive moults, the condition in *Arthuricornua* and *Dorsiceratus* may be considered as paedomorphic (character 29). The complete absence of the setophore in *Ceratonotus* is not regarded as a further derived state because it is caused by a different developmental process. Examination of late copepodids of *C. p. pectinatus* revealed that the outer basal seta is not expressed until the final moult, speculating that the loss of the setophore is related to the late appearance of this seta (character 30).

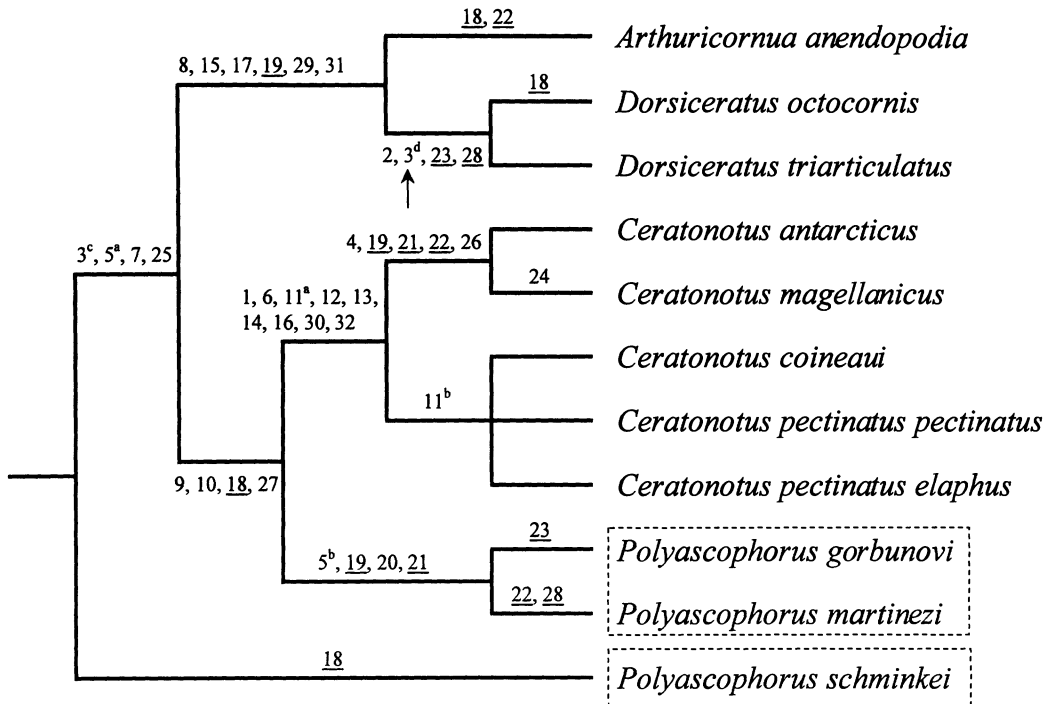


Fig. 8. Phylogenetic tree depicting relationships between species of the *Ceratonotus*-group. Superscript letters refer to multistate character changes [^a: 0→1; ^b: 1→2; ^c: 0→2; ^d: 2→1]. Reversal (character 3) at arrow. Polyphyletic group enclosed in dashed rectangles. Underlined numbers refer to convergences. For explanation, see Tables 1, 2 and text.

P5 Exopod.—In its most primitive condition the P5 exopod bears three equally long spines along the outer margin. This pattern is displayed in the three species of *Polyascopephorus*. In *Arthuricornua* and *Dorsiceratus*, the middle outer spine is displaced to the posterior surface of the exopod and markedly reduced in size (character 31). Setal reduction from five to three elements has occurred in the genus *Ceratonotus*, possibly as a result of the loss of the proximal and middle outer spines (character 32).

Results and Discussion

Parsimony analysis identified a single most parsimonious tree with a tree length of 45 steps and consistency index 0.778 (Fig. 8). Most state changes are concentrated on internal nodes, which is reflected in the high retention index (0.916). The presence of the small anterolateral projections in both *Dorsiceratus* species is treated as a reversal (arrow in Fig. 8). Setting this character irreversible rather than unordered increases the tree length by one step, results in a slightly

lower consistency index (0.761), but does not affect the topology of the tree.

The cladogram depicted in Fig. 8 unequivocally demonstrates the polyphyletic status of *Polyascopephorus*, with *P. schminkei* representing the first offshoot, and the remaining species showing a sistergroup relationship with *Ceratonotus*. The unnatural status of the genus was already reflected in George's (1998b) inexplicit generic diagnosis which allowed for variation in important characters such as the number of thoracic processes and the segmentation of the P2 endopod and which did not include the pattern of cephalic processes, P1 endopod morphology, and P4 sexual dimorphism. The basal position of *P. schminkei* is substantiated by the complete absence of processes on the cephalothorax, the modest size of the dorsal processes on the free pedigerous somites, and the presence of the outer spine on P3 enp-2. Additional plesiomorphic states include the large P1 endopod, the long articulating basal setophore on leg 5, and the primitive segmentation and setal formula on the swimming

legs. The fact that *P. schminkei* cannot be regarded as a pedomorphic form lends weight to the hypothesis that the *Ceratonotus*-group, like the *Ancorabolus*-group (Conroy-Dalton and Huys, 2000), is derived from an ancestor that lacked pronounced body processes. The independent evolution of both major lineages from unadorned ancestors makes a sistergroup relationship less conceivable and may indicate that their roots should be sought in the Cletodidae. *Polyascophorus schminkei*, which is placed in a separate genus below, is readily identifiable by the lateral setular tufts on the cephalothorax and free body somites. It also shares the apomorphic two-segmented P1 exopod with most species of the *Ceratonotus*-group. The cladogram supports the geographical segregation between *P. gorbunovi* and *P. martinezi*, which occur in the Arctic, and *P. schminkei*, which is known only from the Antarctic Weddell Sea.

A basal dichotomy divides the residual species into two clades. *Arthuricornua* is identified as the sistergroup of *Dorsiceratus*, which together stand in apposition to the *Ceratonotus-Polyascophorus* clade. The monophyletic status of the genus *Dorsiceratus* is confirmed despite the marked difference in P1 exopodal segmentation between *D. octocornis* and *D. triarticulatus*. Both species display sexual dimorphism on the P4 endopod, have only one apical seta on P2 enp-2, and possess lateroventral setular tufts on the cephalothorax. The reduction of the frontolateral horns (*character 3*), treated as a reversal in Fig. 8, may be the result of an underlying heterochronic mechanism. Testing this hypothesis would require examination of early copepodid stages of *Arthuricornua*. The sistergroup relationship between *A. anendopodia* and the ancestor of *Dorsiceratus* is particularly robust. Common ancestry is supported by the sexual dimorphism in the thoracic processes, male antennary segmentation, size reduction in antennary allobasal setation, reduction of the P5 basal setophore, and the displacement of the middle outer spine of the P5 exopod. In addition, this clade is also defined by the presence of four geniculate setae on the distal exopod segment of P1; however, this character has less weight because the transformation of the proximal outer spine has occurred convergently in the genus *Polyascophorus*. The genus *Arthuricornua*

is defined by the following autapomorphies: (1) reduction of syncoxal seta of maxilliped; (2) loss P1 endopod; and (3) loss P2 endopod.

Lateral displacement of the thoracic processes, development of processes on the P5-bearing somite, and the reduction of the armature on P4 enp-2 to a single seta are the major synapomorphies supporting the *Ceratonotus-Polyascophorus* clade. The generic assignment of *Echinopsyllus gorbunovi* Smirnov, 1946, proposed by George (1998b) is confirmed by the analysis. Its relationship to *P. martinezi* is indicated by the lateral displacement and bifurcate nature of the posterior cephalothoracic processes, the presence of four geniculate setae on the distal exopod segment of P1, and the size reduction displayed by the P1 endopod. The parallel loss of one apical element on the latter ramus (*character 21*) in both *Polyascophorus* and a subgroup of *Ceratonotus* is a clear convergence based on non-homologous character states (see above).

There is overwhelming evidence for the monophyly of *Ceratonotus*, provided by rostral morphology, dendroid nature of body processes, pattern of urosomal projections/tubercles, antennary segmentation and ornamentation, antennary armature, and P5 morphology and setation. The genus is divided into two geographically separated clades, the *antarcticus-magellanicus* pair which is restricted to (sub)antarctic waters, and a European group represented by an unresolved trichotomy. The former group is readily defined by the large, laterally directed processes on the cephalic shield, the presence of only one element on P1 endopod, the loss of P2 endopod, and the absence of the inner seta on P4 (and possibly also P3) exp-3. The latter clade is characterized by the presence of dorsal dendroid processes on the first abdominal somite (abdominal half of genital double-somite in the female).

DEFINITIONS OF *POLYASCOPHORUS* AND *TOUPHAPLEURA*, NEW GENUS

Polyascophorus George, 1998b

Diagnosis.—Ancorabolinae. Body cylindrical, tapering slightly posteriorly, without clear demarcation between prosome and urosome.

Cephalothorax with large, conical frontolateral horns; posterior margin with paired bifurcate, laterally displaced processes; lateroventral margin unconfirmed. Somites bearing P2–P5 each with paired processes; none of thoracic processes dendroid, but those of somites bearing P2–P4 laterally displaced. Body somites and caudal rami with conspicuous tube-pores dorsally and laterally. Anal operculum with fine spinules. Caudal rami elongate and cylindrical with 7 setae; seta III pinnate. Sexual dimorphism in body size, antennule, P3–P4 endopod, P6, and genital segmentation.

Rostrum small, discernible in dorsal aspect; fused to cephalic shield; with paired sensillae, membranous projections, and long distinctive midventral tube-pore subapically. Antennule 4-segmented in ♀, 7-segmented and subchirocer in ♂ (with 2 segments distal to geniculation); aesthetasc arising from segments 3 and 4 in ♀, segments 5 and 7 in ♂; segment 1 elongate, with long setules along anterior margin. Antenna with allobasis showing partial suture along exopodal margin, abexopodal margin with 2 setae of equal length; exopod entirely absent; endopod with 3 lateral and 6 distal elements. Mandible with robust coxa; palp 1-segmented, uniramous, with 5 setae (3 endopodal, 1 basal, and 1 exopodal). Maxillule with 2 elements on coxal endite; detailed setation on palp unconfirmed. Maxillary syncoxa with 2 well-developed endites, each with 3 elements; allobasis drawn out into claw with basal constriction and 3 accessory elements; endopod minute, with 2 setae. Maxilliped subchelate, robust; syncoxa with 1 plumose seta; endopod drawn out into long, narrow, curved claw with 1 accessory seta.

P1–P4. Intercoxal sclerites and praecoxae unconfirmed; coxae small, trapezoid; bases extremely transversely elongate. P1 endopod small, 1- or 2-segmented, with 1 geniculate seta on enp-2; exopod 2-segmented, exp-2 with 4 geniculate setae and 1 outer spine. P2–P4 exopods 3-segmented; endopods minute (1- or 2-segmented) or absent (except ♂ P3 endopod); without inner setae on exp-1 and endopodal segments; exp-3 with only 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	I-0; I+4	0-0; 0,1,0 or 0,1,0
P2	I-0; I-1; II,2,1	0,1,0 or absent
P3	I-0; I-1; II,2,2	0-0; 0,2,0 or 0,1,0 (♀) 0-0; 0-0; 0,2,0 (♂)
P4	I-0; I-1; II,2,1	0-0; 0,1,0 or 0,1,0 (♀) 0-0; I,1,0 (♂)

P5 uniramous in both sexes; basal setophore very long, articulating; endopodal lobe vestigial, represented by 1 seta and 2 conspicuous tube-pores; exopod elongate, with 1 inner, 1 apical, and 3 outer elements (middle outer spine not reduced or displaced to posterior surface), fused with baseoendopod in both sexes. Female genital field located anteriorly, with moderately large copulatory pore; gonopores covered by common genital operculum derived from medially fused P6 with 1 seta on either side. Male P6 presumably asymmetrical; without armature.

Type Species.—*Polyascophorus martinezi* George, 1998b (by designation).

Other Species.—*Polyascophorus gorbunovi* (Smirnov, 1946).

Touphapleura, new genus

Diagnosis.—Ancorabolinae. Body short, cylindrical, tapering slightly posteriorly, without clear demarcation between prosome and urosome. Pleural areas laterally produced forming lobate setulose expansions. Cephalothorax without paired dorsal horns or processes; lateroventral margin unconfirmed. Somites bearing P2–P4 each with small, paired dorsal processes; none of thoracic processes dendroid. Body somites and caudal rami with conspicuous tube-pores dorsally and laterally. Anal operculum with fine spinules. Caudal rami elongate, cylindrical, with 7 setae; seta III pinnate. Sexual dimorphism in body size, antennule, P3 endopod, P6, and genital segmentation.

Rostrum small, discernible in dorsal aspect; fused to cephalic shield; with paired sensillae, membranous projections, and long distinctive midventral tube-pore subapically. Antennule 4-segmented in ♀, 7-segmented and subchirocer in ♂ (with 2 segments distal to geniculation); aesthetasc arising from segments 3 and 4 in ♀, segments 5 and 7 in ♂;

segment 1 elongate, with long setules along anterior margin. Antenna with allobasis showing partial suture along exopodal margin, abexopodal margin with 2 setae of equal length; exopod entirely absent; endopod with 3 lateral and 6 distal elements. Mandible with robust coxa; palp 1-segmented, uniramous, with 5 setae (3 endopodal, 1 basal, and 1 exopodal). Maxillule with 2 elements on coxal endite; detailed setation on palp unconfirmed. Maxillary syncoxa with 2 well-developed endites, with 2 and 3 elements respectively; allobasis drawn out into claw with basal constriction and 3 accessory elements; endopod represented by 2 setae. Maxilliped subchelate, robust; syncoxa with 1 plumose seta; endopod drawn out into long, narrow, curved claw with 1 accessory seta.

P1–P4. Intercoxal sclerites wide and narrow; praecoxae unconfirmed; coxae small, trapezoid; bases extremely transversely elongate. P1 endopod well developed, 2-segmented, with 1 geniculate seta and 1 spine on enp-2; exopod 2-segmented, exp-2 with 3 geniculate setae and 2 outer spines. P2–P4 exopods 3-segmented; endopods 2-segmented (except ♂ P3 endopod); without inner setae on exp-1 and endopodal segments; exp-3 with only 2 outer spines. P3 endopod ♂ 3-segmented; enp-2 elongate, anterior surface produced distally into recurved apophysis; setation of enp-3 unknown. Armature formula as follows:

	Exopod	Endopod
P1	I-0; II+3	0-0; 0,I+1,0
P2	I-0; I-1; II,2,1	0-0; 0,2,0
P3	I-0; I-1; II,2,2	0-0; I,2,0 (♀) 0-0; 0-0; 0,?,0 (♂)
P4	I-0; I-1; II,2,1	0-0; 0,2,0

P5 uniramous in both sexes; basal setophore very long and articulating; endopodal lobe vestigial, represented by 1 seta and 1 (?) conspicuous tube-pore; exopod elongate with 1 inner, 1 apical, and 3 outer elements (middle outer spine not reduced or displaced to posterior surface), free at base in both sexes. Female genital field located anteriorly, with moderately large copulatory pore; gonopores covered by common genital operculum derived from medially fused P6 with 1 seta on either side. Male P6 presumably asymmetrical; without armature.

Type Species.—*Polyascophorus schminkei* George, 1998b = *Touphapleura schminkei* (George, 1998b), new combination.

Etymology.—The generic name is derived from the Greek *τόψα*, meaning tuft, and *πλευρά*, meaning side, and refers to the presence of setular tufts on the pleural areas of the cephalothorax and free body somites.

Gender.—Feminine.

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