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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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ABSTRACT

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 antennulary elongation, 3-segmented condition of \( \delta \) 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 previously 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-

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 9, 6-segmented and subchirocer in $\delta$ (with one segment distal to geniculation); aesthetasc arising from segments 3 and 4 in $\varphi$, segments 5 and 6 in $\delta$; segment 1 elongate and with long setules along anterior margin. Antenna with allosasis showing partial suture along exopodal margin, abepodopodal 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; allosasis 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 $\delta$ 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; exp-3 with 2 apical setae. Armature formula as follows:

<table>
<thead>
<tr>
<th>Exopod</th>
<th>Endopod</th>
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<tbody>
<tr>
<td>P1</td>
<td>I-0; I+ 4</td>
</tr>
<tr>
<td>P2</td>
<td>I-0; I-1; II,2,1</td>
</tr>
<tr>
<td>P3</td>
<td>I-0; I-1; II,2,2</td>
</tr>
<tr>
<td>P4</td>
<td>I-0; I-1; II,2,1</td>
</tr>
</tbody>
</table>

P5 uniramous in both sexes; basal setophore reduced to short cylindrical outgrowth; endopod elongate with 1 inner, 1 apical and 3 outer elements (middle outer spine reduced and displaced to posterior surface), fused to baseoendopod 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.**—Arthuricornua 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.

**Arthuricornua 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 (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 spines 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 (♂): A, habitus, dorsal; B, rostrum, dorsal; C, urosome (P5 omitted), ventral.
Rostrum fused to cephalic shield (Figs. 1A, 6E); small, trapezoid in shape; paired sensilla arising from tiny pedestals forming vaguely bifid apical margin; with paired pointed membranous projections laterally (arrow in Fig. 6E) just proximal to sensilla; 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 spines 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 spine row along outer margin; 1 spine 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 spines 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 spine and setule patches, mostly around outer margins; median lobe with paired dense setular patches posteriorly.

Maxillule (Fig. 3C). Praecoxal arthrite sub-rectangular with 2 setae on anterior surface; distal armature consisting of 2 pinnate, 4 pectinate, 2 bare, and 2 apically serrate spines; few tiny spines 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 spines apically; outer margin with tuft of fine spines. Basis with 2 spine 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 spine patches as figured; with 2 endites, arising from membranous area; proximal endite with short spine 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 spines 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 spines. Basis with spines 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 spine 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 spines anteriorly. Bases transversely elongate; outer margin with spine 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 9 (Fig. 2A); total body length 474–495 μm (μ = 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 9 (except those at anterior corners of cephalothorax). Ornamentation pattern of processes and sensillae as in 9 (Fig. 2A, C).

Rostrum (Fig. 2B) as in 9.

Antennule (Fig. 4C) 6-segmented and sub-chirocer, 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 9.

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 9.

P4 as in 9, enp-2 (Fig. 6D) outermost seta proportionally longer than in 9.

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 αϊν (not, without), and refers to the complete absence of the P1–P2 endopod (Greek: εντός, 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 antennulary 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. *Arthuricornua 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 baseoendopod, 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.

<table>
<thead>
<tr>
<th>Character Description</th>
<th>Apomorphic States</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rostrum protruding, discernible in dorsal aspect [anterior displacement and partial absorption into anteroventral surface of cephalothorax].</td>
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<tr>
<td>Cephalothorax without conspicuous setular/spinular ornamentation [with setular tufts along lateral margins].</td>
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<tr>
<td>Anterolateral corners of cephalothorax not produced [1: forming small projections; 2: produced into long frontolateral horns].</td>
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<tr>
<td>Lateroventral margins of cephalothorax produced into lobate or slightly conical extension [produced into large laterally directed processes].</td>
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<tr>
<td>Cephalothorax without posterior pair of processes [1: with dorsal pair of conical processes; 2: processes bifurcate and laterally displaced].</td>
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<tr>
<td>Thoracic processes (when present) on cephalothorax (P1) and somites bearing P2–P4 conical and spinulose [dendroid].</td>
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<tr>
<td>Size of thoracic processes not sexually dimorphic [distinctly smaller in ♀].</td>
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</tr>
<tr>
<td>Thoracic processes on somites bearing P2–P4 arising dorsally [laterally displaced].</td>
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<tr>
<td>P5-bearing somite without processes [paired dorsal processes present].</td>
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<tr>
<td>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].</td>
<td></td>
</tr>
<tr>
<td>Second abdominal somite without tubercles [paired dorsal tubercles present].</td>
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</tr>
<tr>
<td>Antennulary segments 1 and 2 free in both sexes [fused, forming elongate compound segment].</td>
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<tr>
<td>Anterior margin of antennulary segment 1 with long spinules [bare].</td>
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</tr>
<tr>
<td>Antennule ♀ with 2 segments distal to geniculation [single segment and no subdivision expressed].</td>
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<tr>
<td>Antennary allabasis with 2 abexopodal setae [basal seta lost].</td>
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<tr>
<td>Antennary allabasis with both abexopodal setae (when present) basis well developed [basal seta reduced].</td>
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<tr>
<td>P1 expod 3-segmented [2-segmented; exp-2 and -3 failed to separate].</td>
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<tr>
<td>Distal segment P1 expod with 1 (when 3-segmented) or 2 outer spines and 3 geniculate setae [distal outer spine transformed into geniculate setae].</td>
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</tr>
<tr>
<td>P1 endopod well developed [significantly reduced in size; at most scarcely longer than exp-1].</td>
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<tr>
<td>P1 endopod (when present) with 2 terminal setae/spines [1 seta/spine].</td>
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<tr>
<td>P2 endopod present [completely absent].</td>
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<tr>
<td>P2 exp-2 with 2 apical setae [1 apical seta].</td>
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<td>P2 exp-3 with 2 inner setae [1 inner seta].</td>
<td></td>
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<tr>
<td>P3 exp-2 with outer spine [without].</td>
<td></td>
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<tr>
<td>P4 exp-3 with inner seta [without].</td>
<td></td>
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<tr>
<td>P7 exp-2 with 2 apical setae [1 apical seta].</td>
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<tr>
<td>P8 endopod not sexually dimorphic [with additional outer spine in ♀].</td>
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<tr>
<td>P9 protopod with long articulating setophore bearing basal seta [reduced to short tubular outgrowth].</td>
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<td>P5 protopod with basal setophore [absent].</td>
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<tr>
<td>P5 exopod with all outer spines arising from marginal position [middle outer spine displaced to posterior surface and reduced in size].</td>
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<td>P5 exopod with 3 outer elements [proximal and middle elements lost].</td>
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three genera: *Ceratonotus pectinatus pectinatus* Sars, 1909; *C. pectinatus elaphus* Por, 1965; *C. coineaui* Soyer, 1965; *C. magellanicus* George and Schminke, 1998; *C. antarcticus* George and Schminke, 1998; *Dorsiceratus 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 (lateral)dorsal processes; (3) rostrum small, without apical elongation posterior to insertion point of sensillae; no sexual dimorphism where males are known; (4) antennulary 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 Ancorabolus-group in the cephalothoracic sensillar pattern and the complete absence of lateral wing-like processes on the body somites.
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 Clerotidae 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 (ACC-TRAN) 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 antennulary 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 Belloci (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 cephalothorax. 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 Arthuricornua, 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 Arthuricornua 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 PI-bearing somite. In Arthuricornua 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 Arthuricornua, Dorsiceratus, Ceratonotus, and the remaining...
Polyascophorus 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 Polyascophorus (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 (Polyascophorus 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. coineaui.

Antennules.—Except for Ceratonotus, where they have failed to separate and form an elongate compound segment, antennulary segments 1 and 2 are completely separated in both sexes (Figs. 3A, 4C) (character 13). Similarly, the anterior margin of antennulary segment 1 typically has long stiff spinules that are secondarily lost in Ceratonotus (Fig. 3A) (character 14). The male antennulary segmentation pattern in Polyascophorus suggests that, ancestrally, there were two free segments distal to the geniculation. Soyer’s (1965) description of the male of C. coineaui 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. coineaui 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 Polyascophorus, retaining its two-segmented condition in P. martinezi but further reduced to a minute.
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 Polyascophorus 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 overlooked (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 molts. This local progenesis, affecting the female developmental sequence only, is regarded as the apomorphic state (character 28).

P5 Protopod.—All species of Polyascophorus 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 molts, 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).
**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 *Polyascophorus*. 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 *Polyascophorus*, 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 endopod. 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 paedomorphic 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 undorned 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 fronthocentral 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 antennulary 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 maxillipeds; (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, antennulary 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 \( \delta \), 7-segmented and subchirocer in \( \varphi \) (with 2 segments distal to geniculation); aesthetasc arising from segments 3 and 4 in \( \varphi \), segments 5 and 7 in \( \delta \); 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 \( \delta \) P3 endopod); without inner setae on exp-1 and endopodal segments; exp-3 with only 2 outer spines. P3 endopod \( \delta \) 3-segmented; enp-2 elongate, anterior surface produced distally into recurved apophysis; enp-3 with 2 apical setae. Armature formula as follows:

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<td>P1</td>
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<td>P2</td>
<td>I-0; I-1; II,2,1</td>
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<tr>
<td>P3</td>
<td>I-0; I-1; II,2,2</td>
<td>0-0; 0,2,0 or 0,1,0 (( \varphi ))</td>
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<tr>
<td>P4</td>
<td>I-0; I-1; II,2,1</td>
<td>0-0; 0,1,0 or 0,1,0 (( \varphi ))</td>
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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


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 \( \varphi \), 7-segmented and subchirocer in \( \delta \) (with 2 segments distal to geniculation); aesthetasc arising from segments 3 and 4 in \( \varphi \), segments 5 and 7 in \( \delta \);
segment 1 elongate, with long setules along anterior margin. Antenna with allobasis showing partial suture along exopodal margin, abepodal margin with 2 setae of equal length; exopod entirely absent; endopod with 3 lateral and 6 distal mandibles. Mandible with robust coxa; palp 1-segmented, uniramous, with 5 setae (3 endopodal, 1 basal, and 1 exopodal). Maxillulate 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; endop-2 elongate, anterior surface produced distally into recurved apophysis; setation of enp-3 unknown. Armature formula as follows:

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<td>P1</td>
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<td>I-0; I-1; II,2</td>
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<td>P4</td>
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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 τόνυσα, meaning tuft, and πλέυρα, 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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Dr. David Thistle (Florida State University, Tallahassee, U.S.A.) made available for study the harpacticoid copepods from the San Diego Trough, northeastern Pacific. Chad Walter (Smithsonian Institution), Prof. Bruce Coull (University of South Carolina), and Endre Willassen (Bergen Museum) provided type and other material of Ceratonotus and Doriscercus species. Dr. N. N. Smirnov (Moscow) is gratefully acknowledged for his help in translating the description of P. gorbunovi. Special thanks are also due to Dr. Rony Huys for his constant encouragement and guidance, and for his valuable comments and criticism on early drafts of the manuscript.

**Literature Cited**


Drzymalski, I. 1969. Harpacticoida (Copepoda) wód morskich Bergen (Zachodnie Wybrzeże Norwegii) I ich ekołogia. [Harpacticoida (Copepoda) of sea waters in Bergen region (West Coast of Norway) and their ecology.].—Wyższa Szkoła Rolnicza w Szczecinie 17: 1–72.

Fiers, F. 1996. Redescription of Enhydrosoma lacunae Jakubiak, 1933 (Copepoda, Harpacticoida); with comments on the Enhydrosoma species reported from west Atlantic localities, and a discussion of cletodid development.—Sarsia 81: 1–27.


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