

A new genus of Canuellidae (Copepoda, Harpacticoida) associated with Atlantic bathyal sea-urchins

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Both sexes of *Echinosunaristes bathyalis* gen. et sp. n. are described from the rectum of a deepwater spatangoid sea-urchin *Palaeopneustes* sp. taken off San Salvador Island, Bahamas. The new genus displays strong sexual dimorphism in body form, size, antennules and caudal rami. *E. bathyalis* can also be readily distinguished from the other members of the family by the specialized geniculation mechanism of the male antennule, the atypical reductions in the mouthparts and the unusual facies of the swimming legs. On the basis of the structure of the genital field in both sexes, *Echinosunaristes* is placed in the *Sunaristes* lineage which groups species that are primarily associated with crustacean hosts. A new genus *Intersunaristes* is established to accommodate *Sunaristes curticaudata* Thompson & A. Scott, 1903 and *S. dardani* Humes & Ho, 1969. *Canuella paenelanitica* Fiers, 1992 is formally transferred to the genus *Elanella* Por, 1984. Records of Canuellidae associated with other invertebrates are compiled and a key to the 17 genera of the family is presented.

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Introduction

Only two species of harpacticoid copepods have been reported as genuine ecto-associates of sea-urchins. Humes & Gelerman (1962) described *Porcellidium echinophilum* (Porcellidiidae) from washings of the body surface of *Echinometra mathaei* (de Blainville) collected at Nosy Bé, Madagascar. High numbers of adults, copepodids and nauplii and several pairs *in amplexus* were found on the echinoid host, suggesting that the association was not accidental and the entire life cycle takes place on the host. The second species *Discoharpacticus mirabilis* (Harpacticidae), found between the spines of *Loxechinus albus* (Molina), was described from material collected along the Chilean coast (Noodt 1954). Interestingly, both genera developed independently a ventral sucking-disc, facilitating adherence to the host.

Various authors (Willey 1930; Noodt 1954; Volkmann 1979) have reported on other harpacticoids that were found on echinoids, but all these species are better known as free-living forms and their association seems to be of little or obscure ecological significance. Bell & McClintock (1982) found six harpacticoid families associated with two species of sea-urchins in Florida, and stated that the copepod species composition overlapped considerably between hosts. The species found on *Lytechinus variegatus* (Lamarck) and *Arbacia punctulata* (Lamarck) were generally representatives of groups residing in a

variety of environments such as phytal habitats, tide-pools, coarse shelly substrates and fine sandy sediments.

The majority of other copepods associated with echinoderms were described from shallow-water hosts, with most hosts coming from the tropical intertidal and subtidal. Very few deepwater echinoderms have been examined for copepods. In fact, only three species, all on holothurians, have been reported from greater depths. Humes (1974) described two new species, the siphonostomatoid *Brychiopontius falcatus* and the cyclopoid *Gomphopodarion byssoicum*, from *Oneirophanta mutabilis* Théel collected at about 4430 m depth on the abyssal plain west of Ireland. Another siphonostomatoid *Nanaspis ninae* Bresciani & Lützen, 1962, was recovered from *Parastichopus tremulus* (Gunnerus) in 479–485 m, also west of Ireland (Humes 1980).

This paper describes a new genus of Canuellidae from the rectum of bathyal irregular sea-urchins collected in the North Atlantic. The host is an undescribed species of *Palaeopneustes* found approximately 530 m off San Salvador Island, Bahamas.

Material and methods

Specimens were dissected in lactic acid and the dissected parts were placed in lactophenol mounting medium. Preparations were sealed with glyceel (Gurr[®], BDH Chemicals Ltd, Poole, U.K.). All drawings have been prepared using a camera lucida on a Leitz Diaplan differential interference contrast microscope. Females and males were examined with a Hitachi S-800 scanning electron microscope. Specimens were prepared by dehydration through graded acetone, critical point dried, mounted on stubs and sputter-coated with palladium.

The descriptive terminology is adopted from Huys & Boxshall (1991). Abbreviations used in the text are: P1–P6, first to sixth thoracopod; exp(enp)-1(2, 3) to denote the proximal (middle, distal) segment of a ramus. The type series is deposited in the collections of the Zoology Department, The Natural History Museum, London.

Family CANUELLIDAE Lang, 1944

Genus *Echinosunaristes* gen. n.

Diagnosis. Canuellidae. P1-bearing somite completely fused to cephalosome. Cephalothorax distinctly wider than rest of body. Female genital and first abdominal somites completely fused to form genital double-somite. Penultimate and anal somites almost coalescent in ♀. Sexual dimorphism in body shape, size, antennule, P6, caudal rami and in genital segmentation.

Rostrum bell-shaped. Antennule set on well-developed pedestal; 4-segmented with 2 aesthetascs on segment 2 in ♀; indistinctly 6-segmented with 2 aesthetascs on segment 2 and conspicuous clasping apparatus on swollen segment 5 in ♂. Antenna with exopod larger than endopod; exopod 8-segmented with armature formula [1,0,1,1,1,1,1,4]; endopod 3-segmented with armature formula [1,4,7]. Mandible with small 2-segmented endopod (formula [1,4] and large, indistinctly 5-segmented exopod (formula [1,1,1,1,2]); basis without setae. Maxillule with reduced, tetraspinoe praecoxal arthrite: coxa without epipodite and with small bisetose endite; endopod 2-segmented; exopod foliaceous, with 9 setae. Maxilla small; syncoxa with 3 endites (formula [1,2,3]); allobasis with 1 seta and 1-segmented trisetose endopod. Maxilliped 2-segmented comprising undivided protopod and slightly subdivided endopod.

Swimming legs with flattened rami; inner coxal seta present on P1–P2; endopodal segments without distinct apophyses; armature elements typically multipinnate. Spine- and seta formulae:

	Exopod	Endopod
P1	0.1.223	1.1.222
P2	0.1.223	1.1.122
P3	0.1.122	1.1.121
P4	0.1.122	1.0.121

P5 not sexually dimorphic, with 4 setae. Female genital field simple; genital apertures closely set together; gonopores and copulatory pores covered by common genital operculum with outer seta and inner spinulose process. Male P6 with outer seta and 2 minute spinous processes; first abdominal somite with midventral spinular patch in ♂.

Caudal ramus with 7 setae in both sexes; in ♀ shorter than maximum width, produced ventrally and adaxially, with 2 spinulose, modified setae near proximal inner corner; in ♂ conical, longer than wide, without modified setae.

Males clasping entire female caudal ramus during mate guarding.

Found in rectum of bathyal sea-urchins.

Monotypic.

Type species: *Echinosunaristes bathyalis* gen. et sp. n.

Etymology. The generic name is derived from the Greek *echinos*, meaning sea-urchin, and *Sunaristes*, and refers to the host association of the new genus and its close relationship to *Sunaristes*. Gender: masculine.

Echinosunaristes bathyalis sp. n.

Material examined and type locality. 16 ♀♀ and 9 ♂♂ obtained by dissection of several specimens of *Palaeopneustes* sp., collected during various dives of the submersible DSRV *Johnson-Sea-Link-I* brought on board the RV *Seward Johnson*, from a depth of approximately 530 m in French Bay off San Salvador Island, Bahamas Archipelago, North Atlantic; 31 October 1990. Holotype ♀ dissected on 8 slides (reg. No. 1995.165), paratypes (reg. No. 1995.166–189) are 12 ♀♀ and 7 ♂♂ (in alcohol; antennule of 1 ♂ dissected on slide), and 3 ♀♀ and 2 ♂♂ (on SEM stub).

Etymology. The trivial name is derived from the Greek *bathys*, meaning deep, and refers to the deepwater habitat of the species.

Description

Female (Figs 1A, 2A–C, 3–6, 8A, 9, 10D). Total body length 1800–1950 µm ($n = 8$; $\bar{x} = 1880$ µm), measured from tip of rostrum to posterior margin of caudal rami. Largest width (535 µm) measured at posterior margin of cephalothorax.

Body cylindrical, slender (Figs 1A, 6A). Integument smooth, not strongly chitinized. P1-bearing somite completely incorporated into cephalosome to form cephalothorax. Cephalic shield increasing in width posteriorly, with slightly produced posterolateral corners. Free thoracic and abdominal somites distinctly narrower than cephalothorax; pleural areas of thoracic somites minute (Fig. 6A). Intersomitic membranes strongly developed except between penultimate and anal somites (Fig. 6A). Posterior margin of thoracic somites with continuous row of tiny spinules except for the P5-bearing somite where it is interrupted dorsally (Figs 1A, 6B). Genital double-somite and abdominal somites also with spinular row dorsally and laterally but not ventrally (Fig. 2A). Genital double-somite elongate; original segmentation marked by internal chitinous rib dorsally and laterally (Figs 1A, 6B). Penultimate and anal somites almost coalescent (Figs 1A, 2A, 6B). Anal somite with paired spinular rows ventrally (Fig. 2A); anal operculum weakly developed (Fig. 6D); anus terminal (Fig. 10A).

Caudal rami short, modified; basal part produced ventrally (Fig. 6E) and adaxially (Figs 2A; 6D); with 7 setae. Inner margin with 2 stubby, spinulose setae proximally (presumably setae I and II). Outer margin with pinnate seta (seta III). Distal margin with 3 multipinnate setae (Fig. 6D–E). Dorsal seta VII short and bi-articulate at base.

Rostrum (Figs 1A, 3A–B) large, bell-shaped; with 2 tiny sensilla dorsally and a ventral integumental pore subapically.

Cephalic appendages and maxillipeds located in anterior half of cephalothorax (Fig. 3A).

Antennule (Fig. 2B–C) 4-segmented, articulating with well-developed pedestal bearing 2 spinular rows. Segment 1 short, connected with pedestal by well-developed intersegmental membrane; partly fused with segment 2;

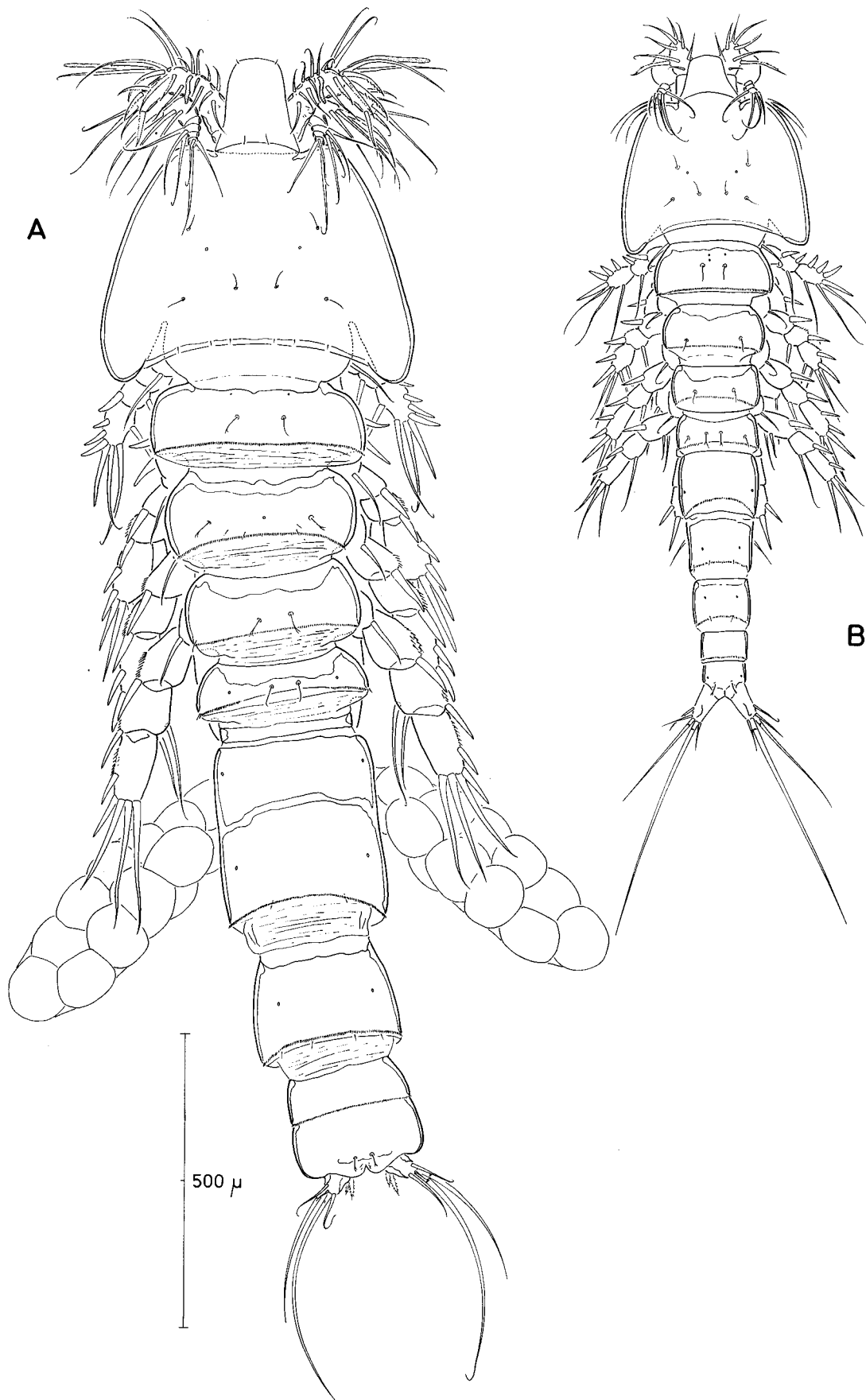


Fig. 1. *Echinosunaristes bathyalis* gen. et sp. n.—A. Habitus ovigerous ♀, dorsal.—B. Habitus ♂, dorsal.

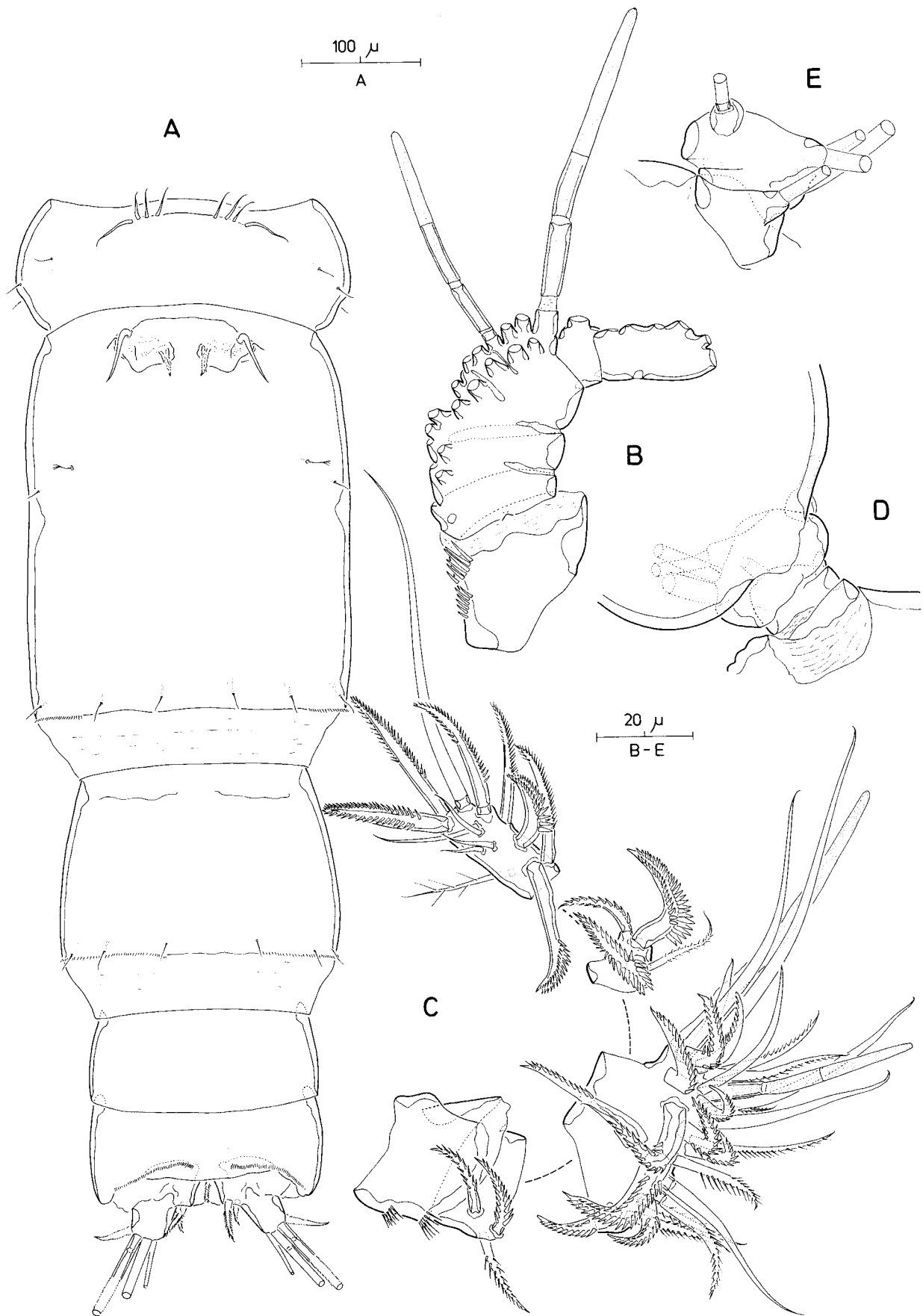


Fig. 2. *Echinosunaristes bathyalis* gen. et sp. n.—A. Urosome ♀, ventral.—B. Antennule ♀, armature omitted.—C. Same, disarticulated, showing complete armature.—D. Antennule ♂, segments 3–4, dorsal,—E. Same, ventral.

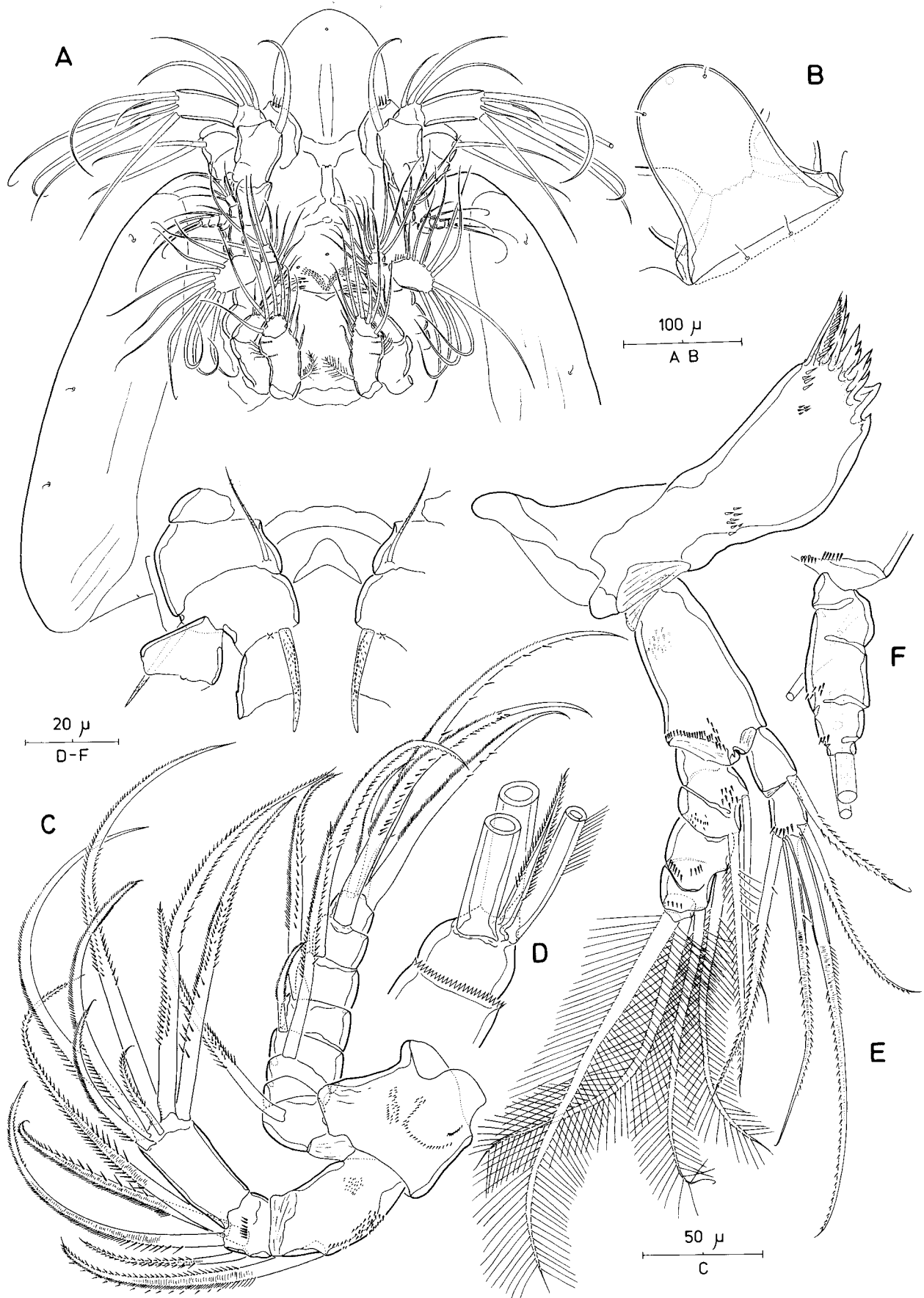


Fig. 3. *Echinosunaristes bathyalis* gen. et sp. n.—A. Cephalothorax, ventral.—B. Rostrum, dorsal.—C. Antenna, posterior.—D. Distal segment of antennary exopod, anterior.—E. Mandible, anterior.—F. Mandibular exopod, posterior.

with 3 pinnate setae. Segment 2 longest, indistinctly subdivided posteriorly by transverse surface furrow; with 26 setae (all pinnate) and 2 jointed aesthetascs, distal one being longer (135 μm) than proximal (115 μm). Segment 3 with 2 pinnate and 2 strongly spinulose setae. Segment 4 with 1 long naked seta apically, 4 short naked setae, 1 plumose seta and 7 pinnate or spinulose setae/spines.

Antenna (Fig. 3C). Coxa and basis fused to form short coxo-basis; laterally produced into cylindrical pedestal for exopods; with rows of tiny spinules on posterior surface. Exopod large, equal in size to endopod; characteristically recurved anteriorly and discernible in dorsal aspect (Figs 1A, 3A); 8-segmented; segments 1, 3, 5–7 with long pinnate seta; segment 2 without seta; segment 4 with short pinnate seta; segment 8 (Fig. 3D) with 1 short, 1 medium-sized and 2 long, pinnate setae; anterior margins of segments with incised hyaline frill (Fig. 3D). Endopod 3-segmented; enp-1 with tiny spinules on posterior surface, and 1 seta laterally; enp-2 short, with 1 short and 3 long setae; enp-3 with 1 short and 6 long setae around distal margin, all of them being discrete at base; all endopodal setae pinnate, none geniculate.

Labrum (Figs 8A, 10D). Large; anterior surface with 2 spinular patches, 2 lateral and 2 median secretory pores.

Mandible (Fig. 3E–F). Coxa elongate, gnathobase with 1 pinnate spine at dorsal corner and several multicuspitate teeth around distal margin. Palp biramous, with small endopod and large exopod. Basis without setae but with 2 patches of tiny spinules. Endopod 2-segmented; enp-1 with 1 lateral seta; enp-2 with 4 setae. Exopod indistinctly 5-segmented (Fig. 3F); exp-1 with 1 naked seta, exp-2 with 1 pinnate seta, exp-3 and -4 with 1 plumose seta each, exp-5 with 2 plumose setae distally.

Maxillule (Fig. 4A). Praecoxa and coxa partly fused. Praecoxal arthrite cylindrical, markedly reduced, with 4 pinnate spines distally (Fig. 10D). Coxa without epipodite; endite a vestigial, cylindrical process with 2 naked setae. Basis without separate endites; enditic armature consisting of 1 short, pinnate and 3 long, plumose setae. Exopod very large, foliaceous; with 3 pinnate setae along inner margin and 6 plumose setae around distal margin. Endopod 2-segmented; enp-1 with 2 lateral setae; enp-2 small, with 4 setae; endopodal setae plumose.

Maxilla (Fig. 4B–C) small. Syncoxa elongate, with 3 endites; proximal endite a small knob with 1 pinnate spine; middle and distal endites cylindrical, with 2 and 3 pinnate spines, respectively. Allobasis drawn out into pinnate claw; accessory armature very reduced, consisting of single pinnate seta on proximal margin. Endopod a trisetose segment.

Maxilliped (Fig. 4D). Phyllopodial, reduced. Two-segmented, comprising undivided protopod (derived by fusion of syncoxa and basis) and 1-segmented endopod. Inner margin of protopod with plumose seta proximally and 3 pinnate spines in distal half; outer margin with long setules distally. Endopod with external trace of original subdivision near outer margin; with 2 pinnate setae on inner margin, 3 plumose setae apically and 1 densely plumose seta near the outer proximal corner.

P1 (Fig. 5A) smaller than following swimming legs. Praecoxa a small sclerite. Coxa with inner pinnate seta, anterior surface with minute denticles. Basis with long

outer seta and inner spine, both multipinnate. Rami 3-segmented. Outer margins of exopodal and endopodal segments spinulose anteriorly; rest of anterior surface largely covered with tiny setules.

P2–P4 (Fig. 5B–D). Praecoxae well developed. Coxae finely spinulose in outer half of anterior surface; with long inner seta in P2; without inner seta in P3–P4. Bases with pattern of fine spinules anteriorly; outer seta present. Exopods and endopods with flattened segments lacking distinct processes. Exp-1 without inner seta. Outer margins of exopodal and endopodal segments spinulose anteriorly; rest of anterior surface with characteristic pattern of tiny setules as illustrated in Fig. 5B–D. All armature elements typically with multiple rows of fine pinnules (Fig. 9C). Spine and seta formula as for genus.

P5 (Fig. 9B) vestigial, incorporated into somite; with 4 pinnate setae, outermost longest.

Genital field positioned on bulbous elevation near anterior margin of genital double-somite (Figs 2A, 6B, 9A). Gonopore and copulatory pore on either side covered by common genital operculum derived from P6 (Figs 6C, 9A). Genital apertures closely set together but separate. Genital operculum covered with patches of minute spinules (Fig. 9D); inner corner with spinulose process; outer margin with smooth outer seta and 2 modified armature elements involved in subsurface locking mechanism.

Egg-sacs paired, elongate; each sac containing 25–30 eggs (Fig. 6A).

Colour of live specimens a bright orange (Campos-Creasy, pers. commun.).

Male (Figs 1B, 2D–E, 7, 8B–F, 10A–C). Much smaller than female (Fig. 1). Total body length 1120–1210 μm ($n = 6$; $x = 1165 \mu\text{m}$), measured from tip of rostrum to posterior margin of caudal rami. Largest width (320 μm) measured at posterior margin of cephalothorax. Sexual dimorphism in habitus, antennule, P6, genital segmentation and caudal rami.

Body (Fig. 1B) more slender than in female; post-cephalothoracic trunk gradually tapering posteriorly. Genital and first abdominal somites distinct. Penultimate and anal somites also clearly defined.

Antennule (Fig. 7) arising from well-developed cylindrical pedestal bearing 2 spinular rows (Fig. 7A–B); indistinctly 6-segmented; geniculation between segments 5 and 6. Segment 1 partly fused to segment 2 (Fig. 7B), with 1 spinulose and 2 pinnate setae. Segment 2 densely armed along the anterior margin with most setae arising from small cylindrical processes (Fig. 7B); with 2 jointed aesthetascs, and 6 naked, 3 pinnate and 9 spinulose setae; proximal aesthetasc (38 μm) distinctly shorter than distal one (88 μm). Segment 3 partly annulated; with 1 naked seta (Figs 2D–E, 7B). Segment 4 partly subdivided; with 1 plumose (on articulate process: Figs 2E, 7A–B) and 3 spinulose setae. Segment 5 (Figs 7A, C–D, 10A–C) largest, swollen and anteriorly expanded; with 8 simple setae and conspicuous clasping apparatus consisting of 2 large, modified spines (stippled in Fig. 7A, C–D); clasping spines with series of transverse lamellae on the inner surface (Fig. 7D), ventral spine largest and flattened, dorsal spine narrower and recurved. Segment 6 only



Fig. 4. *Echinosunaristes bathyalis* gen. et sp. n.—A. Maxillule, anterior.—B. Maxilla, posterior.—C. Same, anterior.—D. Maxilliped.

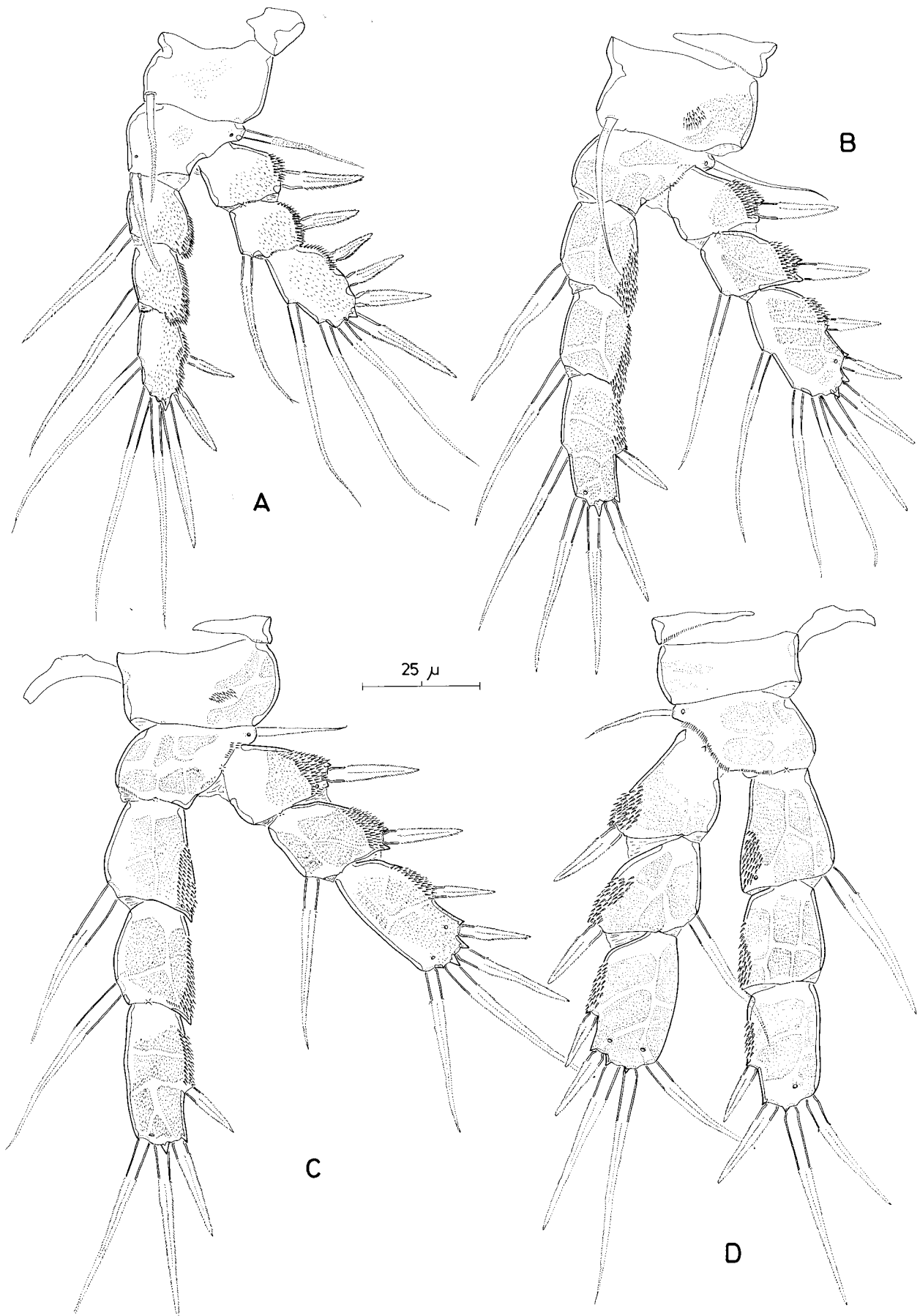


Fig. 5. *Echinosunaristes bathyalis* gen. et sp. n.—A. P1, anterior—B. P2, anterior.—C. P3, anterior.—D. P4, anterior.

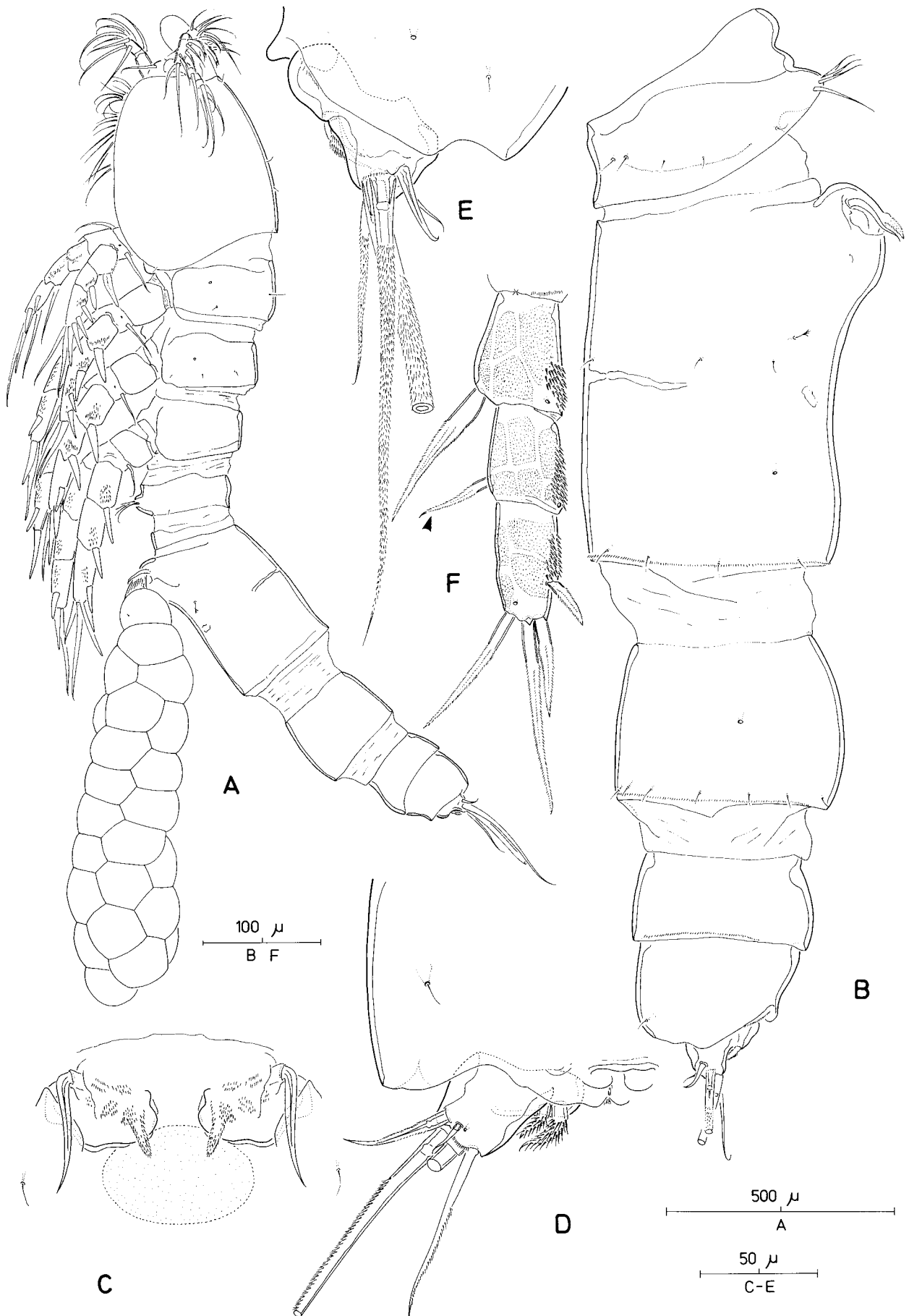


Fig. 6. *Echinosunaristes bathyalis* gen. et sp. n.—A. Habitus ovigerous ♀, lateral.—B. Urosome ♀, lateral.—C. Genital field ♀.—D. Caudal ramus ♀, dorsal.—E. Same, lateral.—F. Aberrant P4 endopod ♀ (extra seta arrowed).

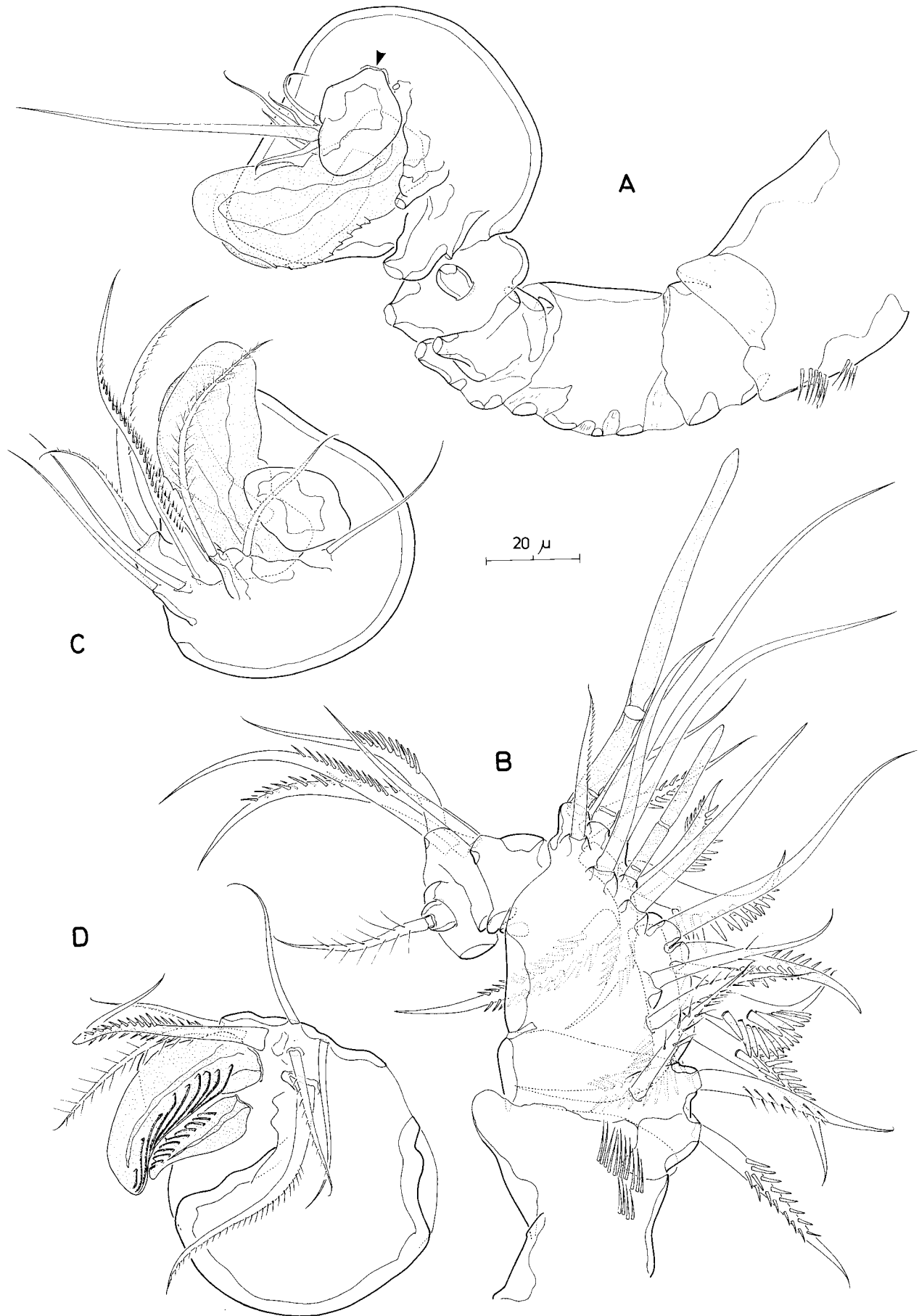


Fig. 7. *Echinosunaristes bathyalis* gen. et sp. n. (Antennule ♂).—A. Ventral view (geniculation arrowed; armature proximal to geniculation omitted).—B. Portion proximal to swollen segment showing complete armature.—C. Segments around geniculation (armature of apical segment omitted).—D. Segment proximal to geniculation, anterior view. (Specialized clasp spines on penultimate segment stippled in A, C, D.)

segment distal to geniculation, small; with 1 long and 5 short naked setae (Fig. 7A).

P5 (Fig. 8G) as in female; with 4 setae.

Urosome (Fig. 8B) slender; abdominal somites with continuous row of tiny spinules. P6-bearing somite with midventral chitinous reinforcement. P6 symmetrical, simple (Fig. 8B, D); inner distal and proximal corners attenuated; outer corner with pinnate seta; surface with several rows of tiny spinules and 2 spinous processes (probably derived from armature elements). First abdominal somite (Fig. 8C–D) with symmetrical spinular patch on midventral swelling. Anal somite with median spinular row ventrally (Fig. 8F).

Caudal rami (Fig. 8B, E–F) elongate, conical, about 1.9 times as long as maximum width; with 7 setae; setae IV and V longest and multipinnate.

Variability. In one female the left P4 endopod had an inner seta on the middle segment (arrowed in Fig. 6F).

Status of *Parasunaristes* Fiers, 1982

Fiers (1982) reviewed the taxonomy of *Sunaristes* Hesse and on the basis of the P4 endopodal segmentation transferred *S. curticaudata* Thompson & A. Scott, 1903 and *S. dardani* Humes & Ho, 1969 to a new genus *Parasunaristes*. *Ellucana chelicerata* Por & Marcus, 1973 and a new species *P. cucullaris* Fiers, 1982, were also referred to this genus. Re-examination of these four species reveals significant differences in the shape of the cephalothorax and the structure of the antennule, maxilla, maxilliped, P1, male P2 and caudal ramus. On the base of this suite of characters the genus *Parasunaristes* is redefined below to accommodate only *P. cucullaris* and *P. chelicerata*, and the other species, *S. dardani* and *S. curticaudata*, are referred to a new genus *Intersunaristes*.

Genus *Parasunaristes* Fiers, 1982

Diagnosis (amended). Canuellidae. P1-bearing somite completely fused to cephalosome. Cephalothorax laterally compressed; posterolateral pleural areas backwardly extended into angular process. Female genital and first abdominal somites completely fused to form genital double-somite; original segmentation marked by dorso-lateral internal ribs. Sexual dimorphism in size, antennule, maxilla, P2 endopod, P6 and in genital segmentation.

Rostrum elongate bell-shaped. Antennule set on well-developed pedestal; 4-segmented with 2 aesthetascs on segment 2 in ♀; indistinctly 5-segmented in ♂, with 2 aesthetascs on segment 2, segment 4 extremely large and swollen, with distinct spinous process arising from proximal half of segment forming subchela with chitinized terminal segment. Antenna with exopod shorter than endopod; exopod 8-segmented with armature formula [1,0,1,1,1,1,1,4]; endopod 3-segmented with armature formula [1,4,7]. Mandible with small 2-segmented endopod (formula [3,8]) and indistinctly 4-segmented exopod (formula [1,1,1,3]); basis with 2 setae. Maxillule with well-developed praecoxal arthrite; coxa with bisetose

epipodite and with 6 setae on endite; endopod 2-segmented (formula [5,6]); exopod foliaceous, with 7 setae. Maxilla sexually dimorphic; syncoxa with 4 endites (formula [5,2,3,3]); allobasis in ♀ drawn out into very large, strongly chitinized, brownish, recurved claw, in ♂ whole limb much smaller and claw shorter, straight and provided with blunt teeth in distal half; endopod well developed. Maxilliped 3-segmented comprising syncoxa, basis and slightly subdivided endopod; syncoxa without seta near proximal margin.

Swimming legs with inner coxal seta present on P1 only; P1 endopodal segments elongated; endopodal segments with distinct apophyses in P2–P3. P4 endopod 2-segmented. Spine and seta formulae as follows:

	Exopod	Endopod
P1	0.1.223	1.1.222
P2	0.1.223	1.1.122
P3	0.1.122	1.1.111
P4	0.1.121	1.111

P2 endopod modified in ♂; with spinous apophyses on outer margins of enp-2 and enp-3; apophysis of enp-2 short, not extending to insertion site of proximal inner seta of enp-3.

P5 not sexually dimorphic, with 4 setae. Female genital field simple; genital apertures closely set together; gonopores and copulatory pores covered by common genital operculum with outer seta and inner spinous process. Male P6 with outer seta and 2 modified spines along the inner margin; first abdominal somite without midventral spinular patch in ♂.

Caudal ramus conical and with 7 setae in both sexes, not sexually dimorphic; seta VI short and bare, located at inner distal corner.

Type species: *Parasunaristes cucullaris* Fiers, 1982 (by original designation).

Other species: *Ellucana chelicerata* Por & Marcus, 1973 = *P. cheliceratus* (Por & Marcus 1973) Fiers, 1982.

Remarks. One of the characters used by Fiers (1982) to distinguish *P. cucullaris* from the other species of the genus is the mid-dorsal cap-like extension of the cephalothoracic shield in the male. Re-examination of this shield in the types of *E. chelicerata* revealed that the dorsal sensilla shown in Fiers' drawings (pl. XIV6 and pl. XV5) are positioned on short, longitudinal, cuticular reinforcements along the posterior margin. These paired structures might easily be misinterpreted as somite contours and it is therefore assumed here that the shape and form of the cephalothoracic shield are identical in both sexes, i.e. as illustrated for the female by Fiers (1982; pl. XIV5).

Genus *Intersunaristes* gen. n.

Diagnosis. Canuellidae. P1-bearing somite completely fused to cephalosome. Cephalothorax laterally com-

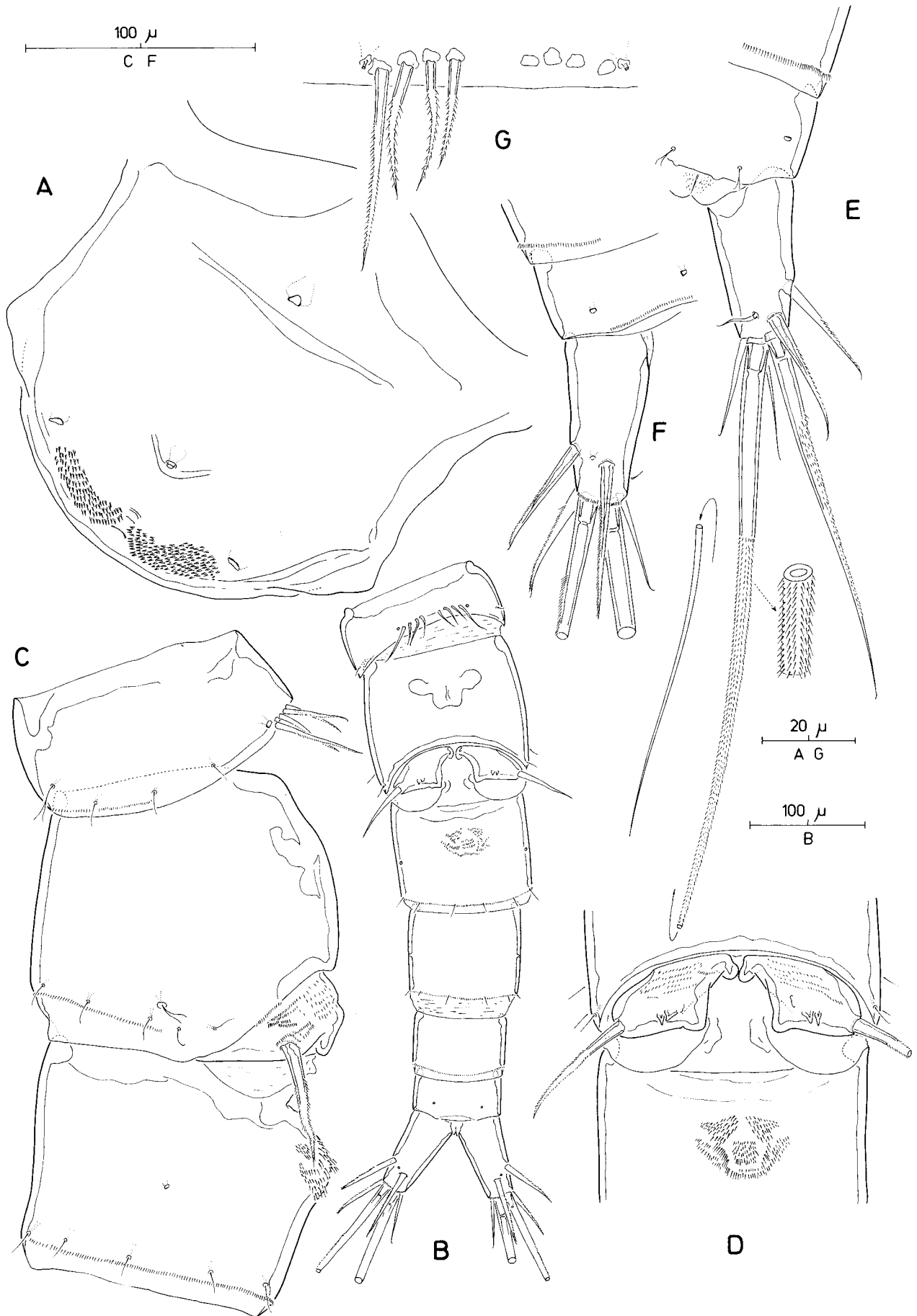


Fig. 8. *Echinosunaristes bathyalis* gen. et sp. n.—A. Labrum, anterior.—B. Urosome ♂, ventral.—C. First three somites of urosome ♂, lateral.—D. P6 ♂ and ornamentation on first abdominal somite.—E. Anal somite and right caudal ramus ♂, dorsal.—F. Same, ventral.—G. P5 ♂.

pressed; posterolateral pleural areas rounded. Female genital and first abdominal somites completely fused to form genital double-somite. Sexual dimorphism in size, antennule, P2 endopod, P6, and in genital segmentation.

Rostrum elongate bell-shaped. Antennule set on well-developed pedestal; 4-segmented with 2 aesthetascs on segment 2 in ♀; indistinctly 5-segmented in ♂, with 2 aesthetascs on segment 2, segment 4 distinctly swollen, forming subchela with terminal segment. Antenna with exopod shorter than endopod; exopod 8-segmented with armature formula [1,0,1,1,1,1,4]; endopod 3-segmented with armature formula [1,4,7]. Mandible with small 2-segmented endopod (formula [3,8]) and indistinctly 4-segmented exopod (formula [1,1,1,3]); basis with 2 setae. Maxillule with well-developed praecoxal arthritis; coxa with bisetose epipodite and with 6 setae on endite; endopod 2-segmented (formula [5,6]); exopod foliaceous, with 7 setae. Maxilla not sexually dimorphic; syncoxa with 4 endites (formula [5,2,3,3]); allobasis drawn out into short claw accompanied by 4 setae; endopod well developed. Maxilliped 3-segmented comprising syncoxa, basis and slightly subdivided endopod; syncoxa with seta near proximal margin.

Swimming legs with inner coxal seta present on P1 only; P1 endopodal segments not elongated; endopodal segments with distinct apophyses in P2–P3, P4 endopod 2-segmented. Spine and seta formulae as for *Parasunaristes*. P2 endopod modified in ♂; with spinous apophyses on outer margins of enp-2 and enp-3; apophysis of enp-2 extending to distal margin of enp-3.

P5 not sexually dimorphic, with 4 setae. Female genital field simple; genital apertures closely set together; gonopores and copulatory pores covered by common genital operculum with outer seta and inner spinous process. Male P6 with outer seta and 1 modified inner spine; first abdominal somite without midventral spinular patch in ♂.

Caudal ramus conical and with 7 setae in both sexes, not sexually dimorphic; seta VI long and plumose, located at inner distal corner.

Type species: Sunaristes dardani Humes & Ho, 1969

Other species: Sunaristes curticaudata Thompson & A. Scott, 1903 = *I. curticaudatus* (Thompson & Scott 1903) comb. n.

Etymology. The generic name is derived from the Latin *inter*, meaning between, and *Sunaristes*, and refers to the intermediate phylogenetic position of the new genus, i.e. between *Parasunaristes* and *Sunaristes*. Gender: masculine.

Discussion

With the discovery of *Echinosunaristes* and the establishment of *Intersunaristes* the family Canuellidae currently encompasses 17 genera. Four other genera are known to live in relatively close association with invertebrates—all being crustacean hosts (Table I). The most speciose and best documented genus is *Sunaristes* Hesse whose four species (Hesse 1867; Humes & Ho 1969; Hamond 1973; Ho 1986) are known to reside in gastropod shells utilized

by two families of hermit crabs, Paguridae and Diogenidae. The genus is widespread in the Indo-Pacific, assumes a boreo-Mediterranean distribution in Europe, but is notably absent from the American continent and the Atlantic seaboard of Africa. The free-living *S. inopinata* Thompson & A. Scott, 1903 is regarded here as *incertae sedis* in the family and should be allocated to the *Scotto-lana* complex.

Intersunaristes dardani (Humes & Ho 1969) has been repeatedly recorded as an associate of an extensive spectrum of hermit crab hosts on both sides of the Indo-Pacific (Table I). The other species, *I. curticaudatus* is known from a single female found in '... general washings of Ceylon Invertebrates ...' (Thompson & Scott 1903).

Parasunaristes cheliceratus, originally described from sediment samples taken in the Suez Canal (Por & Marcus 1973), was found in about half of the domiciles constructed by the tubicolous corophioid amphipod *Siphonocetes* sp. in shallow water in the northern Red Sea (Falck & Bowman 1994). Domiciles were composed of a secreted tube with embedded sediment particles, extending into the opening of usually a gastropod shell, or less frequently a polychaete tube.

Finally, Hamond (1973) found three species of *Briannola* Monard to 'co-occur' with the hermit crab *Diogenes senex* in the swimming pool of the C.S.I.R.O., Sydney. These species, as well as many other harpacticoids, were found in washings of a bulk sample containing about 1000 specimens of *D. senex*. No attempt had been made to prove the association by individual dissection of hermit crabs (Hamond pers. commun.). The fact that these species have been reported in the literature as free-living in intertidal sediment pools and among seaweeds (Hamond 1973; Fiers 1982; Wells & Rao 1987) also suggests that this relationship is more apparent than real. All three species have recently also been found in coralline sand samples from the Great Barrier Reef (Huys unpubl.).

Examination of the canuellid material held in the collections of the Institute of Taxonomic Zoology, University of Amsterdam, revealed the presence of four vials containing *Canuella perplexa* T. & A. Scott, 1893, collected from *Buccinum* shells inhabited by *Pagurus bernhardus*. The specimens (ZMA Co. 100.042 [7 ♀♀], 100.043 [13 ♀♀], 100.044 [3 damaged ♀♀] and 100.054 [2 ♀♀, 6 ♂♂]) were collected in the Dutch Waddensea and identified by J. H. Stock. This case and Jakubisiak's (1932) record on *Maia squinado*, however, almost certainly represent chance associations or contaminations since species of *Canuella* T. & A. Scott are good swimmers living near or in the upper few cm of sandy deposits (Băcescu *et al.*, 1957; Vincx & Heip 1979).

Echinosunaristes can be readily distinguished from other canuellid genera by the unusual body shape of the female, several atypical reductions in the mouthparts and the remarkable sexual dimorphism in body form, size (i.e. ♀ and ♂ are drawn at the same scale in Fig. 1) and caudal ramus structure. Gross disparity in size between sexes clearly imposes certain constraints on the body posture that is assumed during mate guarding. In the majority of the Canuellidae, males typically grasp the female caudal rami as described for two species of *Canuella* by Glatzel

(1988). Close examination of pairs in amplexus of various genera has revealed that this grasp can be achieved in a number of ways, i.e. by holding onto very specific setae or by grasping the entire ramus. Either the left or the right caudal ramus can be involved in this process, however, it was found that grasping both rami is the prevailing con-

dition. Caudal rami are typically long, conical and divergent in Canuellidae, whereas their antennules, though sometimes being strongly modified (e.g. *Parasunaristes*; Fiers 1982; Por & Marcus 1973), are generally short in the males. A dual linkage between the female caudal rami and the male antennules therefore can only be achieved if

Table 1. Records of Canuellidae associated with other invertebrates

Associate	Host	Distribution	References
<i>Sunaristes paguri</i>	<i>Pagurus bernhardus</i>	Hvalør, Norway	Sars (1903, 1919)
		Gullmar Fjord, Sweden	Lang (1948)
		Sylt, Germany	W. Müller (1884)
		Cromarty Firth, Scotland	T. Scott (1906), T. & A. Scott (1894, 1897)
		Devon coast, Liverpool Bay and Mersey, England	A. Scott (1896), Thompson (1896), Norman & T. Scott (1906)
		Clare Island, Ireland	Farran (1913)
		Roscoff and Grandcamp, France	Hesse (1867), Chevreux (1908), Monard (1935)
		The Netherlands	Vervoort (1950), Leenhouts (1950a, b), Stock (1952), Stock in Humes & Ho (1969)
		Locality unknown	Bresciani & Lützen (1962)
			Bourdon in Hamond (1973)
<i>Sunaristes inaequalis</i>	<i>Pagurus cuanensis</i> <i>Diogenes pugilator</i>	Roscoff, France	Codreanu & Mack-Fira (1961), Hamond (1973)
		Saint-Efflam and Marseille, France	Codreanu & Mack-Fira (1961)
	<i>Clibanarius erythropus</i> washings of invertebrates washings of dredged invertebrates <i>Dardanus megistos</i>	Agigea and Mangalia, Roumania	Codreanu & Mack-Fira (1961)
		Banyuls-sur-Mer, France	Stock (1960)
		Muttuvaratu, Sri Lanka	Thompson & A. Scott (1903) [doubtful]
		near New Guinea	A. Scott (1909) [doubtful]
		Nosy Bé region, Madagascar	Humes & Ho (1969)
		Nouméa region, New Caledonia	Humes (1972)
		Nouméa region, New Caledonia	Humes (1972)
		Nouméa region, New Caledonia	Humes (1972)
<i>Sunaristes tranteri</i>	<i>Clibanarius carnifex</i> <i>Clibanarius virescens</i> [washings of several unidentified small hermit crabs]	Entedebir, Dahlak Archipelago	Humes & Ho (1969)
		Nouméa region, New Caledonia	Humes (1972)
		Nosy Bé region, Madagascar	Humes & Ho (1969)
		Sydney area, Australia	Hamond (1973)
		Ceram and Halmahera, Moluccas	Humes (1981)
		Ceram and Banda, Moluccas	Humes (1981)
		Banda, Moluccas	Humes (1981)
		Banda, Moluccas	Humes (1981)
		Banda, Moluccas	Humes (1981)
		Banda, Moluccas	Humes (1981)
Banda, Moluccas	Humes (1981)		
<i>Sunaristes japonicus</i>	<i>Trizopagurus strigatus</i> <i>Pagurus geminus</i> <i>Pagurus similis</i> <i>Pagurus japonicus</i> <i>Clibanarius bimaculatus</i>	Sado Island and Shirahama, Japan	Ho (1986)
		Sado Island and Noto-ogi, Japan	Ho (1986)
		Noto-ogi, Japan	Ho (1986)
		Shirahama, Japan	Ho (1986)
		Auckland, New Zealand	Hamond (1973)
<i>Sunaristes</i> sp. <i>Intersunaristes dardani</i>	<i>Pagurus novaezealandiae</i> <i>Dardanus megistos</i>	Nosy Bé region, Madagascar	Humes & Ho (1969)
		Eniwetok Atoll, Marshall Islands	Humes (1971)
		Nouméa region, New Caledonia	Humes (1972)
		Nosy Bé region, Madagascar	Humes & Ho (1969)
		Mauritius	Humes & Ho (1969)
		Nosy Bé region, Madagascar	Humes & Ho (1969)
		Eniwetok Atoll, Marshall Islands	Humes (1971)
		Nosy Bé region, Madagascar	Humes & Ho (1969)
		Mauritius	Humes & Ho (1969)
		Eniwetok Atoll, Marshall Islands	Humes (1971)
Nouméa region, New Caledonia	Humes (1972)		
<i>Intersunaristes curticaudatus</i> <i>Parasunaristes cheliceratus</i> <i>Brianola elegans</i> <i>Brianola sydneyensis</i> <i>Brianola pori</i> <i>Canuella perplexa</i>	<i>Dardanus deformis</i> <i>Dardanus guttatus</i> <i>Dardanus lagopodes</i>	Eniwetok Atoll, Marshall Islands	Humes (1971)
		Nouméa region, New Caledonia	Humes (1972)
		Eniwetok Atoll, Marshall Islands	Humes (1971)
		Nosy Bé region, Madagascar	Humes & Ho (1969)
		Eniwetok Atoll, Marshall Islands	Humes (1971)
		Nosy Bé region, Madagascar	Humes & Ho (1969)
		Eniwetok Atoll, Marshall Islands	Humes (1971)
		Nouméa region, New Caledonia	Humes (1972)
		Eniwetok Atoll, Marshall Islands	Humes (1971)
		Nosy Bé region, Madagascar	Humes & Ho (1969)
Eniwetok Atoll, Marshall Islands	Humes (1971)		
<i>Scottolana longipes</i> <i>Scottolana inopinata</i> <i>Echinusunaristes bathyalis</i>	<i>Clibanarius virescens</i> <i>Dardanus setifer</i> / <i>D. lagopodes</i> / <i>Calcinus elegans</i> (mixed at time of collection)	Nosy Bé region, Madagascar	Humes & Ho (1969)
		Eniwetok Atoll, Marshall Islands	Humes (1971)
		Nouméa region, New Caledonia	Humes (1972)
		Mauritius	Humes & Ho (1969)
		Muttuvaratu, Sri Lanka	Thompson & A. Scott (1903) (doubtful)
		Northern Red Sea	Falck & Bowman (1993)
		Sydney area, Australia	Hamond (1973)
		Sydney area, Australia	Hamond (1973)
		Sydney area, Australia	Hamond (1973)
		Wadden Sea, The Netherlands	J. H. Stock (unpubl.)
Roscoff, France	Jakubisiak (1932)		
<i>Scottolana longipes</i> <i>Scottolana inopinata</i> <i>Echinusunaristes bathyalis</i>	<i>Maia squinado</i> Washings of invertebrates Washings of invertebrates	Muttuvaratu, Sri Lanka	Thompson & A. Scott (1903) (doubtful)
		Muttuvaratu, Sri Lanka	Thompson & A. Scott (1903) (doubtful)
		Bahamas	Present account

both sexes do not differ greatly in size as in *Canuella* and the related genera of the *Scottolana* complex. In the case of gross size disparity between females and males it seems that the functional constraints and requirements lie different since a 'dwarf' male can only achieve such a double grip by either assuming a proportionally much wider grasp with its antennules, or through reduction and shortening of the divergent caudal rami in the female as in *Echinosunaristes*.

The geniculation mechanism in male *E. bathyalis* is unique. The major geniculation is located between segments 5 and 6 as in other Canuellidae; however, the size of the terminal segment does not permit the male to clasp anything larger than a seta (Fig. 7A). Claspings the entire caudal ramus is achieved by an indirect mechanism involving a modified spine (stippled in Fig. 7A, C–D) on the penultimate segment which through its size and curvature is capable to hold onto larger cylindrical structures. Flexure at the geniculation directs the terminal segment anteromedially and closely adpresses the modified flat spine onto another modified spine and the remainder of the anterior surface of the fifth segment. Since the ramus is 'passively' grasped by a single armature element, it is assumed that no muscles operate other than those already involved in the geniculation mechanism. The transverse ridges on the clasping spines function as a ratchet mechanism strengthening the grasp and preventing the caudal ramus from sliding out.

It is noteworthy that gross disparity in size between sexes is also displayed by *Coullana canadensis* (Willey 1923) (cf. Coull 1972); however, in this species an alternative clasping posture was observed whereby the male attaches to the female genital double-somite or P5-bearing somite in a ventral to ventral surface orientation (Huys pers. obs.).

The habitat shift towards a sheltered micro-environment inside the echinoid host, and consequently the alteration in food supply and diet, must undoubtedly have changed the feeding mode of the harpacticoid. In contrast to *Sunaristes* and *Intersunaristes* which inhabit hermit crab shells, this habitat shift had a significant impact on the morphology of the feeding appendages. With the exception of the antenna which has retained its primitive facies, all other postantennular appendages of the cephalosome have undergone strong reductions, in particular the endites. The mandible has lost its 4 setae on the basis, and the rich armature present on the endopod of other Canuellidae is also strongly reduced. The maxillules lack an epipodite, and the praecoxal arthrite and distal endites of coxa and basis are only represented by vestigial lobes. The maxilla and maxilliped are most strongly reduced in size (Fig. 3A), and their setation stands in marked contrast to the elaborate armature found, for example, in *Canuella* (Huys & Boxshall 1991: figs 2.4.13C and 2.4.15A).

Kohlhage (1993) analysed the movement patterns of the mouth appendages in *Canuella perplexa* using high-frequency cinematographic techniques and concluded that the antennae perform an important function in the feeding and cleaning processes. It is conceivable that the antenna in *Echinosunaristes* is involved in a similar grooming mechanism since it is the only cephalic append-

age that has retained the ancestral complement of segments and armature (8-segmented exopod, ground pattern of endopodal armature).

The thoracopods P1–P4 of *E. bathyalis* are unique in two aspects. First, the segments of both rami are unusually flattened, transversely expanded, and the P2–P3 lack the distinct attenuations of the proximal and middle endopodal segments typically found in other Canuellidae. Second, *E. bathyalis* is the only member of the family that lacks the plumosity of the inner setae, the ornamentation being replaced by multiple longitudinal rows of fine spinules (as on the outer and distal spines: see Fig. 9C). The armature formula of the swimming legs is remarkably primitive and identical to that of *Canuella*. Within the Canuellidae only the two species of *Elanella* are more plesiomorphic in this respect since they have retained the full complement of setae and spines, i.e. also the inner spine on P4 enp-2. This element, however, was found in a single aberrant female of *E. bathyalis* and is illustrated in Fig. 6F.

The combination of autapomorphies related to the sexual dimorphism and reductions in the mouthparts, and plesiomorphies retained from the ancestral canuellid stock (e.g. setation of P1–P4) does not provide much phylogenetically useful information and consequently hinders the assessment of the evolutionary relationships of *Echinosunaristes*. However, examination of the detailed structure and complexity of the genital field in both sexes has proven this character to be of paramount importance in the analysis of the evolutionary relationships in the Canuellidae. It is primarily on the basis of this information that *Echinosunaristes* is placed in the *Sunaristes* lineage, containing *Sunaristes*, *Parasunaristes* and *Intersunaristes*. In all 4 genera the female genital field is positioned far anteriorly near the boundary with the P5-bearing somite. On each side of the ventral midline the genital aperture comprises a gonopore (the oviduct opening) and a copulatory pore, both covered by a common operculum derived from the sixth legs. In *E. bathyalis* the copulatory pore is concealed beneath a spinulose-pointed process that might possibly represent 1 of the 3 armature elements of the 6th legs. A clearly homologous, spinous structure is present in all species of *Sunaristes* [e.g. *S. inaequalis*; Humes & Ho (1969: fig. 34)] and *Intersunaristes* [e.g. *I. dardani*; Huys & Boxshall (1991: fig. 2.4.25C)]. In other genera this spinous process is absent as in *Ellucana* and *Canuellina* or the copulatory pores have undergone posterior migration as in *Canuella* and *Scottolana*. The 4 genera of the *Sunaristes* group are also very similar in the structure of the male genital field. The 6th legs closely resemble the typical pattern found in other harpacticoid families and are not elaborated as in *Canuella*, *Canuellopsis* and *Scottolana*.

Within the *Sunaristes* lineage, *Parasunaristes* and *Intersunaristes* share a sistergroup relationship on the basis of the 2-segmented nature of the P4 endopod. The immediate outgroup of this clade is formed by *Sunaristes* which has retained the 3-segmented condition. The monophyletic status of this group of 3 genera is supported by the absence of the inner seta on the P2 coxa, the presence of 3 elements on P3 enp-3 (i.e. outer spine absent), 4 elements on P4 exp-3 (i.e. only 1 outer spine), 3 elements on P4

enp-3 (or enp-2 when endopod 2-segmented), and the sexual dimorphism of the P2 endopod involving the formation of outer apophyses on enp-2 and enp-3 in the male. The plesiomorphic alternatives for these characters are displayed by *Echinosunaristes* which is regarded here as the most primitive genus of the *Sunaristes* lineage: P2 coxa with inner seta, P3 enp-3 with outer spine, P4 exp-3 with 5 elements (2 outer spines), P4 enp-3 with 4 elements, and the complete absence of sexual dimorphism on the swimming legs. Pending confirmation of the doubtful associations recorded for some Australian *Brianola* species (Hamond 1973), the current phylogeny of the family Canuellidae suggests that all genuine associations

with three different host categories—hermit crabs, corophioid amphipods and spatangoid echinoids—have evolved within the same lineage.

The associated lifestyle of *E. bathyalis* shows some resemblance with that of the amphinomid polychaete *Benthoscolex cubanus* Hartman, which was found in the intestine of another spatangoid sea-urchin, *Archaeopneustes hystrix* (A. Agassiz), and at similar depths in the Bahamas Archipelago (Emson *et al.* 1993). The polychaete lacked obvious adaptations for life inside the gut of the echinoid host; however, Emson *et al.* pointed out that the cuticle was thicker than in most polychaetes. As for the amphinomid, there is no evidence to suggest that *E.*

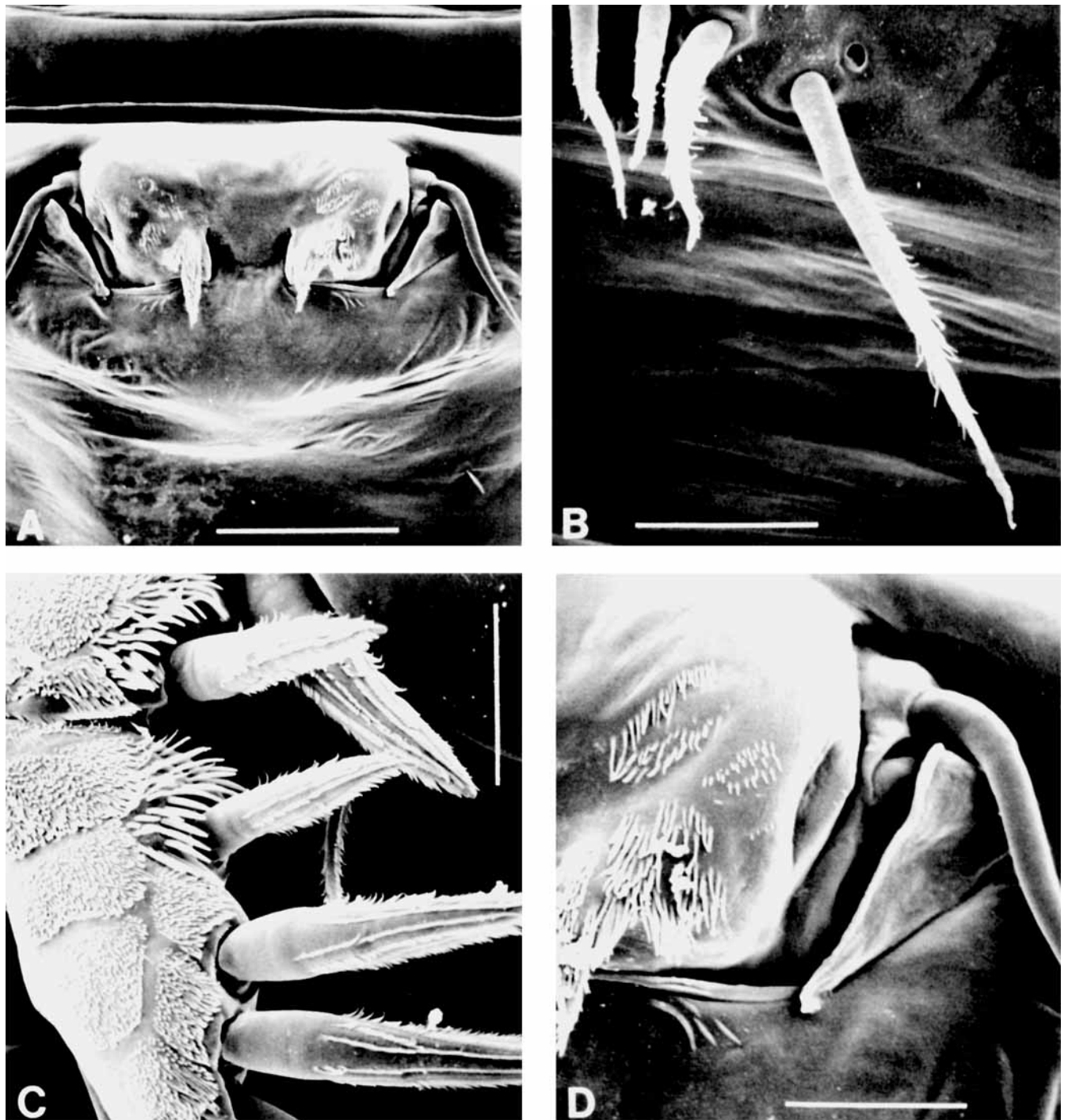


Fig. 9. *Echinosunaristes bathyalis* gen. et sp. n.: SEM micrographs.—A. Genital field ♀.—B. P5 ♀.—C. P1 exopodal spines.—D. Genital aperture ♀. (Scale bars in μm : A. 50 μm ; B. 15 μm ; C. 30 μm ; D. 17.6 μm .)

bathyalis temporarily leaves the host to feed on or in the sediment and, even more so than in *B. cubanus*, it is restricted to the part of the alimentary tract where enzyme secretion is virtually non-existent. Consequently, the integument in *E. bathyalis* is clearly thinner and less chitinized than in free-living Canuellidae, probably because concealment inside the host protects it from external mechanical stress, and the copepod does not require special cuticular adaptations to prevent digestion by the host. The presence of numerous ovigerous females and several pairs *in amplexus* suggests that both copulation and reproduction take place inside the host. Nauplii

seemed to be entirely absent from the rectum content which is in accordance with the life-style of hermit crab associated *Sunaristes* species where the nauplius stages represent the infective dispersal phase (Ho 1988).

Canuellidae inhabit a wide variety of sediments ranging in grain size from flocculent muds to coralline debris, and they are primarily found in the intertidal and shallow subtidal areas of the continental shelves. Some genera such as *Canuella* and *Canuellopsis* have been reported from deeper muds (e.g. Lang 1936; Por 1964); however these are exceptions. Despite its long phylogenetic history (Por 1984) the family has been virtually unsuccessful

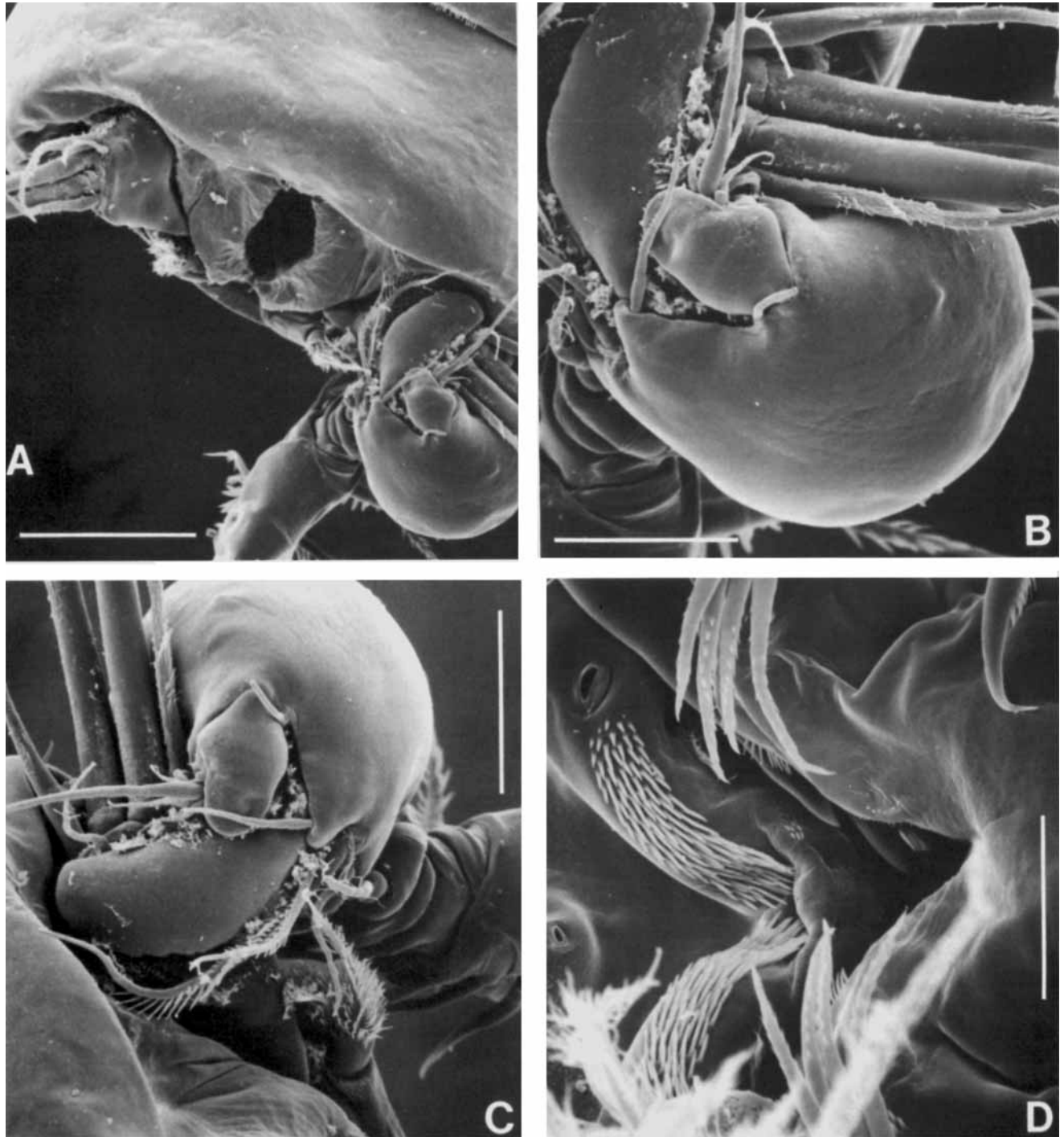


Fig. 10. *Echinosenaristes bathyalis* gen. et sp. n.: SEM micrographs.—A. Male antennule clasp on right female caudal ramus.—B. and C. Area around geniculation showing minute distal segment and massive clasp on penultimate segment.—D. Oral area, showing maxillary arthrites and labral ornamentation and pores. (Scale bars in μm : A. 60 μm ; B. 25 μm ; C. 30 μm ; D. 15 μm .)

in invading the deep-sea environment. Apart from *E. bathyalis* only one other species has been recorded from depths greater than 500 m. *Intercanuella lima* Becker & Schriever was described from a single female collected at 2000 m in the Peru Trench; however, it is not related to the *Sunaristes* lineage.

Key to genera

A worldwide revision of the family is currently in progress (Huys, in prep.) and will almost double the number of species described. The latest and only key to genera was provided by Lang (1948) and included only the genera *Canuella* T. & A. Scott, *Canuellopsis* Lang, *Canuellina* Gurney, *Sunaristes* Hesse and *Brianola* Monard. Twelve genera, including *Echinosunaristes* and *Intersunaristes*, have been added since (Becker & Schriever 1979; Fiers 1982; Mielke 1979, 1994; Por 1967, 1984; Sewell 1940; Vervoort 1964). The following key is applicable to both sexes.

1. P4 endopod distal segment with 4 setae/spines 7
P4 endopod distal segment with 3 setae/spines 2
P4 endopod distal segment with 2 setae/spines
..... *Microcanuella* Mielke, 1994
- 2(1). P4 endopod 2-segmented 3
P4 endopod 3-segmented 5
- 3(2). Distal segments of both rami of P3 with 4 setae/spines; P4 exp-2 without inner seta *Ellucana* Sewell, 1940*
P3 exp-3 and enp-3 with 5 and 3 setae/spines, respectively; P4 exp-2 with inner seta 4
- 4(3). Maxilla sexually dimorphic, allobasal claw strongly chitinized, dark brown and recurved in ♀, much smaller, straight and with blunt teeth in ♂; antennule with enormous subchela in ♂ *Parasunaristes* Fiers, 1982
Maxilla not sexually dimorphic, allobasal claw short and accompanied at base by 4 accessory setae; antennule with moderately developed subchela *Intersunaristes* gen. n.
- 5(2). P1 exp-3 and enp-3 with 6 and 4 setae/spines, respectively *Galapacanuella* Mielke, 1979.
P1 exp-3 and enp-3 with 7 and 5-6 setae/spines, respectively 6
- 6(5). Distal segment of both rami of P3 with 4 setae/spines; P4 exp-2 without inner seta *Canuellina* Gurney, 1927
P3 exp-3 and enp-3 with 5 and 3 setae, respectively; P4 exp-2 with inner seta *Sunaristes* Hesse, 1867
- 7(1). P1 exopod 2-segmented *Canuellopsis* Lang, 1936
P1 exopod 3-segmented 8
- 8(7). P3 exp-3 with 4 setae/spines 9
P3 exp-3 with 5 setae/spines 10
- 9(8). P2 exp-3 with 4 setae/spines *Brianola* Monard, 1927†
P2 exp-3 with 5 setae/spines *Nathaniella* Por, 1984‡
P2 exp-3 with 6 setae/spines *Ifanella* Vervoort, 1964
P2 exp-3 with 7 setae/spines
..... *Intercanuella* Becker & Schriever, 1979
- 10(8). P4 exp-3 with 4 setae/spines 11
P4 exp-3 with 5 setae/spines 12
- 11(10). P1-bearing somite fused to cephalosome; P4 exp-3 without inner seta *Coullana* Por, 1984
P1-bearing somite not fused to cephalosome; P4 exp-3 with inner seta *Scottolana* Por, 1967
- 12(10). P4 enp-2 without inner seta 13
P4 enp-2 with inner seta *Elanella* Por, 1984§
- 13(12). Female caudal rami distinctly longer than wide; P3-P4 coxa with inner seta; free-living *Canuella* T. & A. Scott, 1893
Female caudal rami not longer than wide; P3-P4 coxa without inner seta; endo-associates of sea-urchins
..... *Echinosunaristes* gen. n.

Notes

**Canuellina nicobaris* Wells & Rao, 1987, whose taxonomic status is unresolved, keys out to the genus *Ellucana*.

†*Brianola pori* Hamond, 1972, keys out to the genus *Coullana*. Por (1984) suggested that this species does not belong to the genus *Brianola* and should probably be placed in a separate genus. Re-examination of *B. pori* and *C. canadensis* revealed close similarities indicating that the former should be removed to the genus *Coullana* (Huys in prep.).

‡Re-examination of the types of *Nathaniella reichi* (Por 1964) revealed 5 setae/spines instead of 4.

§*Canuella paenelanitica* Fiers, 1982, closely related to *C. elanitica* Por, 1967 (now the type-species of *Elanella*: cf. Por 1984), is formally transferred here to the genus *Elanella* as *E. paenelanitica* (Fiers 1982) comb. n.

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