Pergamon

Zoologica Scripta, Vol. 27, No. 1, pp. 1–15, 1998
Elsevier Science Ltd

PII: S0300–3256(97)00018–4
0300–3256/98 $19.00 + 0.00

Novocriniidae, a new family of harpacticoid copepods from anchihaline caves in Belize

RONY HUYS and THOMAS M. ILIFFE

Accepted 7 August 1997

Huys, R. & Iliffe, T. M. 1998. Novocriniidae, a new family of harpacticoid copepods from anchihaline caves in Belize.—*Zool. Scr. 27*: 1–15.

A new family of fusiform, semi-planktonic harpacticoid copepods is described from two anchihaline caves, Caye Chapel Cave and Columbus Caye Blue Hole, on the Belize Barrier Reef. The Novocriniidae fam. n. is proposed to accommodate *Novocrinia trifida* gen. et sp. n. and is placed in the tisbidimorph complex of families (Tisboidea) by virtue of its maxilliped morphology. The new genus shares several characters with other tisbidimorph families but cannot be placed in any of them without an unnatural extension of their diagnoses. The Novocriniidae display a suite of plesiomorphic character states in most appendages from the antennules to the P5, indicating their basal position on the tisbidimorph phylogenetic tree. They exhibit a unique sexually dimorphic modification of the antennae, involving the transformation of two setal elements into filamentous sensory tufts. The unusual presence of supernumerary elements on the male P5 baseoendopod is briefly discussed as well as the presence of a genuine but incipient oral cone derived from the labrum and medially fused paragnaths. © 1998 The Norwegian Academy of Science and Letters

Zoology Department, The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.
Department of Marine Biology, Texas A & M University at Galveston, Galveston, Texas 77553, U.S.A.

Introduction

Harpacticoid copepods are an important constituent of the marine fauna inhabiting anchihaline caves and submerged lava tubes. Recent exploration of these unusual habitats has resulted in the discovery of two highly distinctive families of harpacticoids (Huys, 1988*a*, 1996). The Rotundiclipeidae is a monotypic family described from Cueva del Agua, a shallow cave on Tenerife, Canary Islands (Huys 1988*a*). The Superornatiremidae comprises three genera *Superornatiremis* Huys, *Neoechinophora* Huys and *Intercrusia* Huys, all described from North Atlantic caves on Bermuda and the Canary Islands (Huys 1996). The recent discovery of these genera in the Balearic Islands (Jaume, 1997) provides evidence that the family assumes an Amphi-Atlantic/Mediterranean distribution pattern. Other records of harpacticoid copepods in anchihaline caves are listed by Huys (1996).

The Belize Barrier Reef is the largest reef system in the Western Hemisphere and second only to the Great Barrier Reef of Australia. It consists of a rimmed shelf with a series of barrier reefs fronting a 20–40 km wide lagoon. An almost continuous line of low sand islands, called 'cayes', extends along almost the entire length (250 km) of the barrier reef. Numerous, now submerged, karst features of impressive size are present, both immediately behind the barrier reef and on the offshore atolls. The most famous of these is the Lighthouse Reef Blue Hole, a submarine sinkhole explored by Jacques Cousteau using a submersible and found to be over 100 m deep (Cousteau 1973). The Giant Cave at Caye Caulker is one of the world's largest submarine caves. Although exploration of this cave is still ongoing, over 3 km have thus far been surveyed. Giant Cave is the type locality of the ridgewayiid calanoid *Brattstromia longicaudata* Fosshagen, which is probably the most abundant copepod inhabiting the Belize Caves (Fosshagen & Iliffe 1991). Examination of a number of samples from three different caves on the Belize Barrier Reef resulted in the discovery of two new species of Superornatiremidae and an as yet unknown family of harpacticoids with tisbidimorph affinities described herein. The Superornatiremidae will be dealt with in a separate paper (Huys & Iliffe, in prep.).

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, Poole, UK). All drawings were prepared with a camera lucida on a Zeiss Axioskop differential interference contrast microscope.

The descriptive terminology is adopted from Huys & Boxshall (1991). The term 'acrothek' is introduced for the trifid setal structure found on the apical margin of the distal antennulary segment. Abbreviations used in the text are: ae, aesthetasc; P1–P6, first to sixth thoracopod; exp(enp)-1(2, 3) to denote the proximal (middle, distal) segment of a ramus. The type series is deposited in the collections of the Zoology Department, The Natural History Museum, London.

Description of caves

Caye Chapel Cave is located 0.5 km east (seaward) of the

northern tip of Caye Chapel. The entrance consists of two vertical shafts located about 15 m apart on a seagrass bed in 3 m depth. At a depth of 8 m in the cave, the two entrance shafts join in a low room from where a sandy restriction under a ledge leads to a large descending rift, well decorated with stalactites and floored with white sandy sediments. At 35 m depth, the rift levels off and begins to ascend to a point at which the cave ends in collapse 150 m from the entrance. The water is clear with visibility about 20–30 m. The deeper waters of the cave appear relatively more sterile in comparison with regions closer to the entrance where encrusting sponges, orange mysids, and red shrimps are conspicuous. Representatives of the primitive calanoid genera *Ridgewayia* Thompson & A. Scott, *Enantiosis* Barr, and *Pseudocyclops* Brady have been recorded from this cave (Fosshagen, pers. comm.).

Columbus Caye Blue Hole is located about 2 km northwest of Columbus Caye and 3 km from the outer edge of the barrier reef. The entrance is a 10 m long by 3 m wide slit at the bottom of a 10 m deep sand funnel. Inside, the cave immediately widens into a single circular chamber, 90 m in diameter, with a maximum depth of 50 m. Light from the overhead skylight entrance penetrates to all corners of this spacious cavern. Directly beneath the entrance, a barren sand mound at 27 m depth appears to have been formed by sand deposited in the cave during storms. From the mound, the bottom slopes away to maximum depths nearest the walls where the sediment changes to a fine silt. Walls in the upper sections of the cave are completely covered with serpulid worm tubes, which have formed pseudo-stalactites, all pointing toward the entrance. Visibility is uniform throughout the cavern at about 10 m. Fosshagen (pers. comm.) recorded small numbers of the calanoids *B. longicaudata*, *Ridgewayia* sp. and *Epacteriscus* sp. A new species of the superornatiremid genus *Neoechinophora* was discovered in sections close to the entrance of the cave; a second undescribed species was collected in the northern section of Giant Cave at Caye Caulker (Huys & Iliffe, in prep.).

NOVOCRINIIDAE fam. n.

Diagnosis. Harpacticoida. Body fusiform. First pedigerous somite fused to cephalosome forming cephalothorax. Rostrum strongly developed, ventrally deflected, fused to cephalic shield, trifid. Female genital double-somite with complete transverse, internal chitinous rib marking original segmentation. Anal operculum weakly developed, rounded, bare; pseudoperculum semicircular, denticulate. Caudal rami shorter than wide, with 6 setae (seta I absent; setae IV–V well developed, spinulose). Sexual dimorphism in antennule, antenna, P5, P6, abdominal ornamentation, and in genital segmentation.

Antennule slender, with projection and spinular comb on segment 1; 9-segmented; modified spines present on proximal segments; with aesthetasc on segment 4 and acrothek on segment 9 in ♀; haplocer in ♂, none of segments swollen (geniculation between segments 7 and 8; 2 segments distal to geniculation), with aesthetasc on segments 2, 3, 5 and acrothek on segment 9; acrothek consisting of aesthetasc and 1 seta; homology of male antennulary segmentation: I, II–VIII, IX–XII, XIII, XIV–XVII, XVIII, XIX–XX, XXI–XXIII, XXIV–XXVIII. Antenna with unisetose basis; exopod 4-segmented with formula [1,1,1,3]; enp-1 with abexopodal seta; enp-2 with 2 setae + setoid tuft laterally, and distal armature consisting of 6 (4 geniculate) setae (in ♀) or 5 (3 geniculate) setae + setoid tuft (in ♂). Labrum strongly developed triangular lobe, partly fused to labium (derived by median fusion of paragnaths) forming distinct oral cone. Mandible with elongate gnathobase; biramous palp consisting of bisetose basis, 2-segmented endopod with formula [1,4] and 4-segmented exopod with formula [1,1,1,2]. Maxillule with elongate arthrite (1 element spiniform); coxal endite with 6 elements; exopod cylindrical with 2 setae; endopod membranous, largely incorporated in basis, with 4 setae; basis bearing 2 distinct endites with 3 and 4 elements. Maxillary syncoxa with 1 trisetose endite; endopod 2-segmented with formula [4,4]. Maxilliped subchelate with unarmed syncoxa; basis with 1 seta; endopod an elongate segment drawn out into long subdistal claw bearing 2 accessory elements and forming apical pedestal with 2 geniculate setae.

P1 exopod 3-segmented; exp-1 without inner seta; exp-3 with total of 6 elements. P1 endopod 3-segmented, not prehensile. P2–P4 with outer seta/spine on basis and 3-segmented rami. Spine- and seta formulae as for type-species.

P5 with separate exopod and baseoendopod; exopod with 5 spines/setae, endopodal lobe with 4 spines; baseoendopods fused medially in ♂.

Female gonopores fused forming transverse common genital slit; covered by fused vestigial P6 each bearing 3 short setae; midventral copulatory pore single, small; short copulatory duct leading to paired seminal receptacles. Number of egg-sacs unconfirmed.

Male sixth pair of legs symmetrical, with 3 setae each.

Anchihaline caves, freeliving.

Type and only genus: Novocrinia gen. n.

Genus *Novocrinia* gen. n.

Diagnosis. As for family.

Type and only species: Novocrinia trifida gen. et sp. n.

Etymology. The generic name is derived from the Latin *novus*, meaning new, and *crinis*, tuft of hair, and refers to the presence of setoid tufts on the antenna of both sexes. Gender: feminine. The species name *trifida*, derived from the Latin *trifidus*, three-forked, alludes to the shape of the rostrum.

Novocrinia trifida sp. n.

Type material and locality. Holotype ♀ (reg. no. 1996.1284) dissected on 9 slides; paratypes are 1 ♂ dissected on 8 slides and 2 ♂♂ in alcohol (reg. nos 1996.1285–1287); collected at Stn. 89/20, Caye Chapel Cave, Caye Chapel, Belize; collected with plankton net in 8–10 m depths in sections close to the entrance at 40–60 m penetration; 18 February 1989; leg. T. M. Iliffe and S. Sarbu.

Other specimens. (a) 1 ♂ in alcohol (reg. no. 1996.1288); collected at Stn. 89/19, Caye Chapel Cave, Caye Chapel, Belize; collected with plankton net in 20–35 m depths in more hydrologically isolated sections at a penetration to 150 m; 18 February 1989; leg. T. M. Iliffe and S. Sarbu; (b) 1 ♀ and 1 ♂ in alcohol (reg. nos 1996.1289–1290); collected at Stn. 89/26, Columbus Caye Blue Hole, Columbus Caye, Belize; collected with plankton net in 30–45 m depths from near the surface of silty sediments on ledges on the cave floor; 28 February 1989; leg. T. M. Iliffe and S. Sarbu.

Description

Female. (Figs 1–3, 4A–B, 5, 6A–B, 7A,C,D). Total body length 590–600 μm ($n = 2$; $\bar{x} = 595$ μm), measured from anterior margin of rostrum to posterior margin of caudal rami. Largest width (190 μm) measured at posterior margin of cephalothorax.

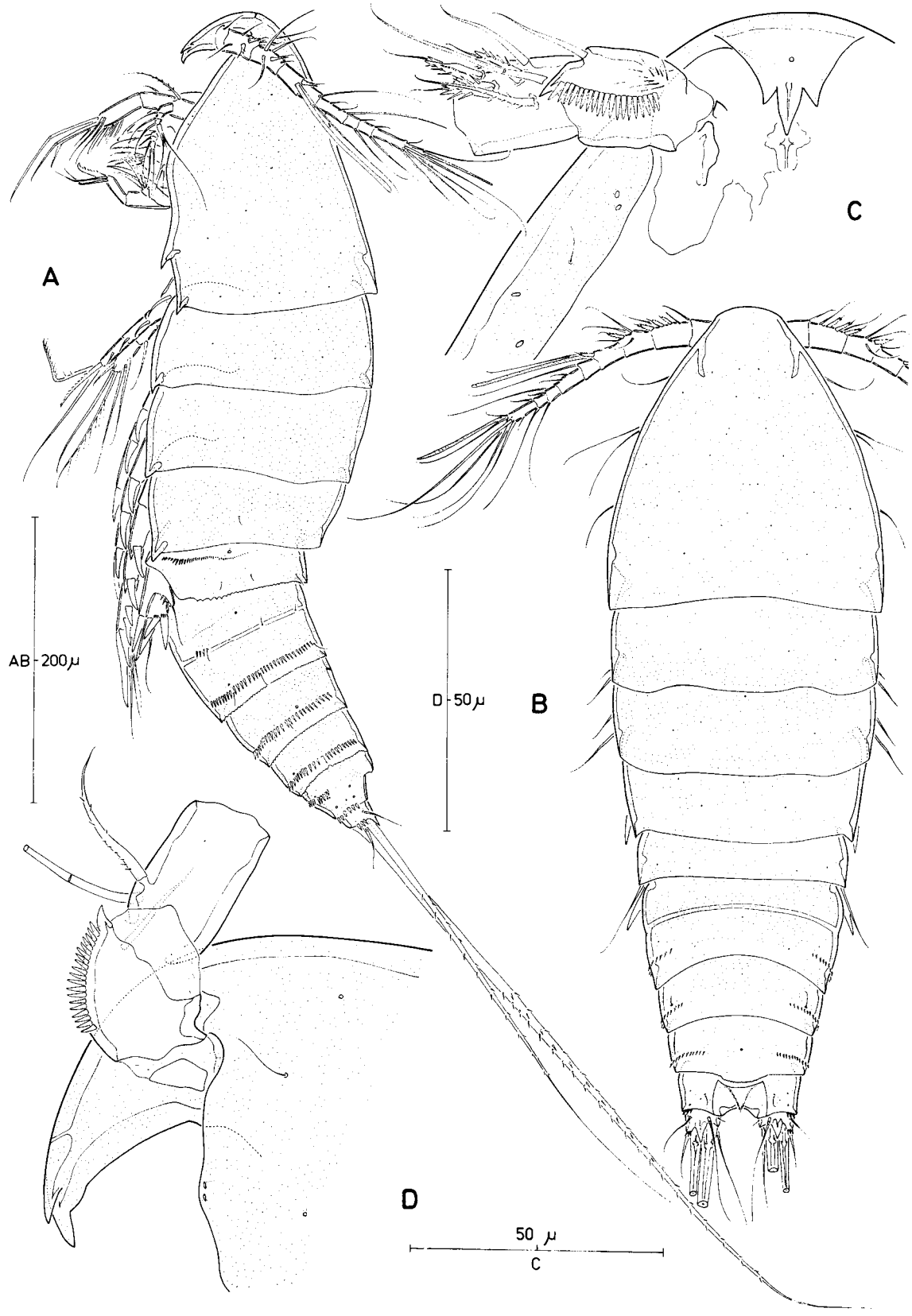

Fig. 1. Novocrinia trifida gen. et sp. n.—*A*. Habitus ♀, lateral.—*B*. Habitus ♀, dorsal.—*C*. Rostrum and proximal segments of right antennule, frontal.—*D*. Rostrum and proximal segments of left antennule, lateral.

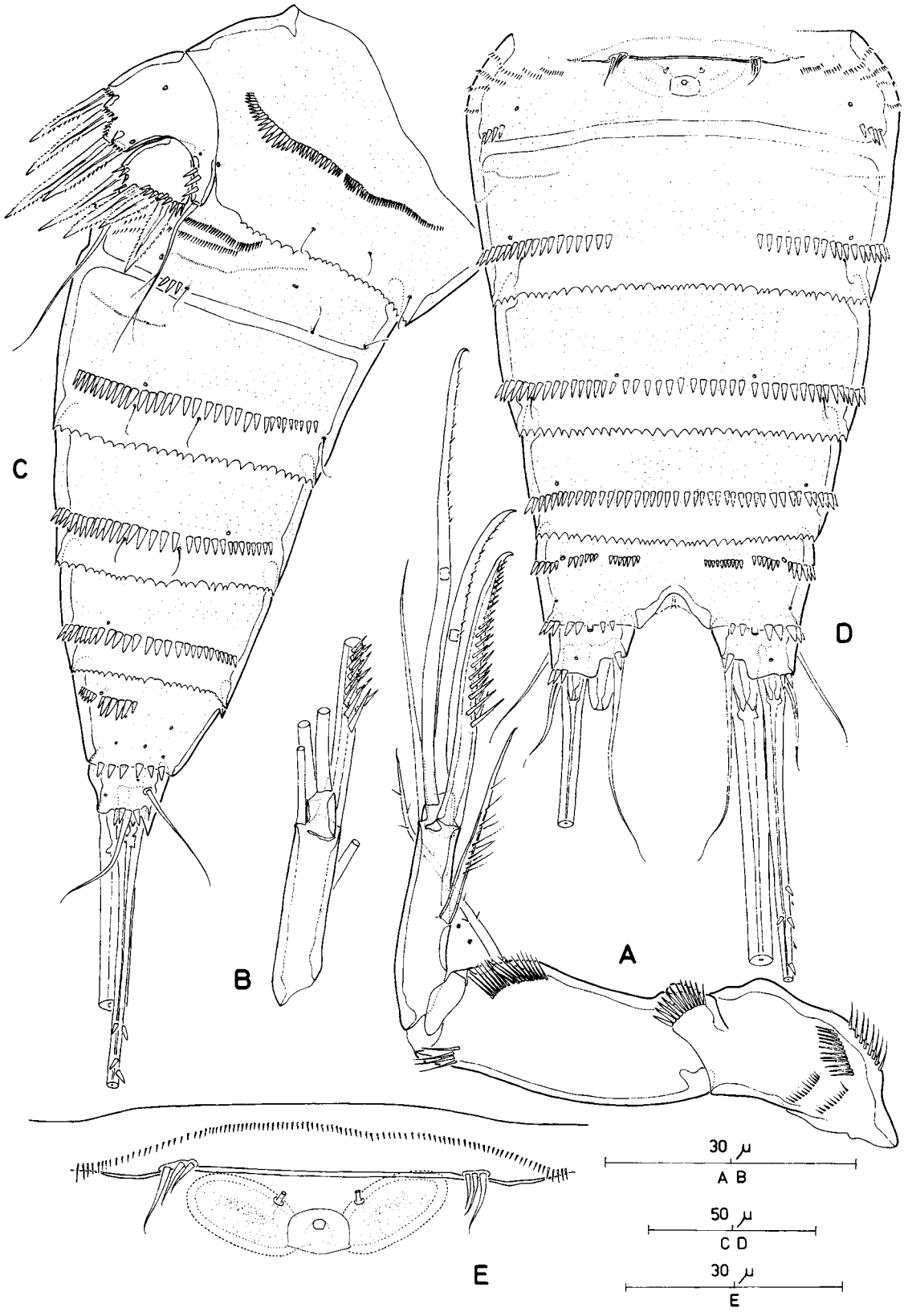

Fig. 2. Novocrinia trifida gen. et sp. n.—*A*. Maxilliped, anterior.—*B*. Endopod of maxilliped, posterior.—*C*. Urosome ♀, lateral.—*D*. Urosome (excluding P5-bearing somite), ventral.—*E*. Genital field ♀, ventral.

Body fusiform (Fig. 1A–B), without clear demarcation between prosome and urosome; somites gradually tapering posteriorly. Integument of rostral area, cephalic shield and body somites pitted, strongly chitinized. Body surface with numerous pores interspersed with few sensilla. P1-bearing somite completely incorporated into cephalosome to form cephalothorax. Hyaline frills smooth and plain on cephalothorax and somites bearing P2–P4; minutely denticulate on other somites (Figs 1A–B, 2C–D, 7C). Cephalic shield distinctly increasing in width posteriorly; ventral margins with paired pointed processes near posterior corners (Fig. 1A). Posterolateral corners of somites bearing P2–P4 also produced into spinous process (Fig. 1A). Pleural areas of thoracic somites strongly developed

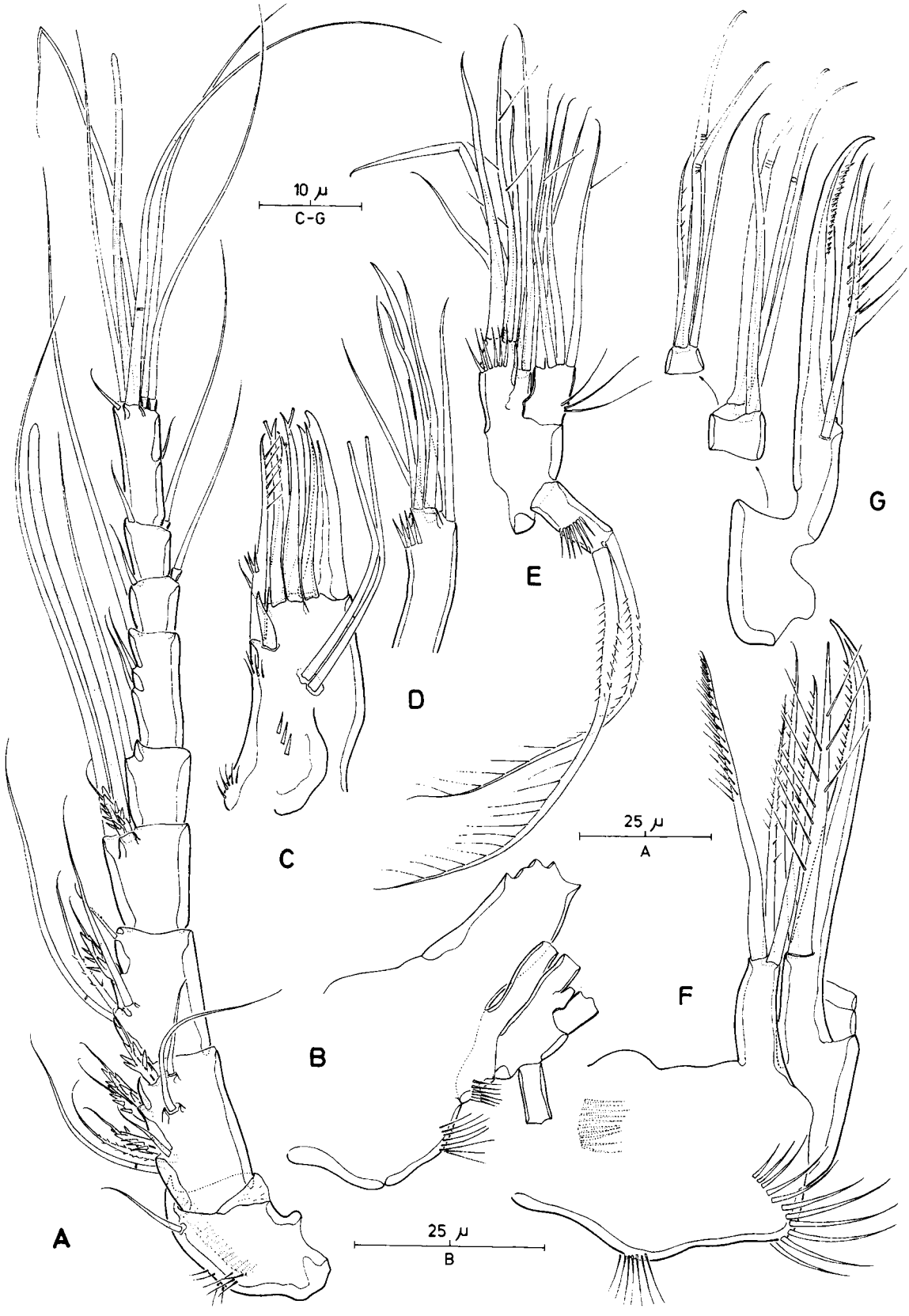

Fig. 3. Novocrinia trifida gen. et sp. n.—*A*. Antennule ♀, dorsal.—*B*. Contours of maxillule.—*C*. Maxillulary arthrite.—*D*. Maxillulary coxal endite.—*E*. Maxillulary palp.—*F*. Maxilla, anterior [armature of endopod omitted].—*G*. Maxillary allobasis with disarticulated endopod, posterior.

and largely overlapping; completely concealing protopods of swimming legs (Fig. 6A). No distinct intersomitic membranes discernible. Posterior margin of thoracic somites without, of abdominal somites with transverse row of spinules which is interrupted only dorsally (Figs 1A–B, 2C–D), except for the genital double-somite where it is also interrupted ventrally (Fig. 2D). P5-bearing somite with lateral spinule rows as figured (Fig. 2C). Genital double-somite wider than long; original segmentation marked by continuous internal chitinous rib (Figs 1B, 2C–D). Anal somite with paired spinular rows ventrally (Fig. 2D); anal operculum weakly developed,

Fig. 4. Novocrinia trifida gen. et sp. n.—*A*. Antenna ♀, setoid tuft omitted.—*B*. Distal endopod segment of ♀ antenna showing proximal setoid tuft (arrowed).—*C*. Antenna ♂, setoid tufts omitted.—*D*. Distal endopod segment of ♂ antenna showing proximal and distal setoid tufts. [Homologies between distal setal elements of both sexes indicated by letters a–f; perforated areas in *A* and *C* indicating position of omitted setoid tufts.]

rounded (Fig. 7C); pseudoperculum a moderately developed rounded extension of penultimate somite, denticulate (Fig. 7C).

Caudal rami (Figs 2C–D, 7C) short, wider than long; dorsal rear margin produced into backwardly directed spinous process (Fig. 7C), ventral rear margin stepped and hyaline (Fig. 2D); with 6 setae (seta I absent). Setae II, III and VI slender and bare, setae IV and V long and pinnate (Fig. 1A) with distinct fracture planes, seta VII triarticulate at base and slender. Inner margin with long dorsal hair-like setule.

Rostrum (Fig. 1A–D) large, completely fused tc

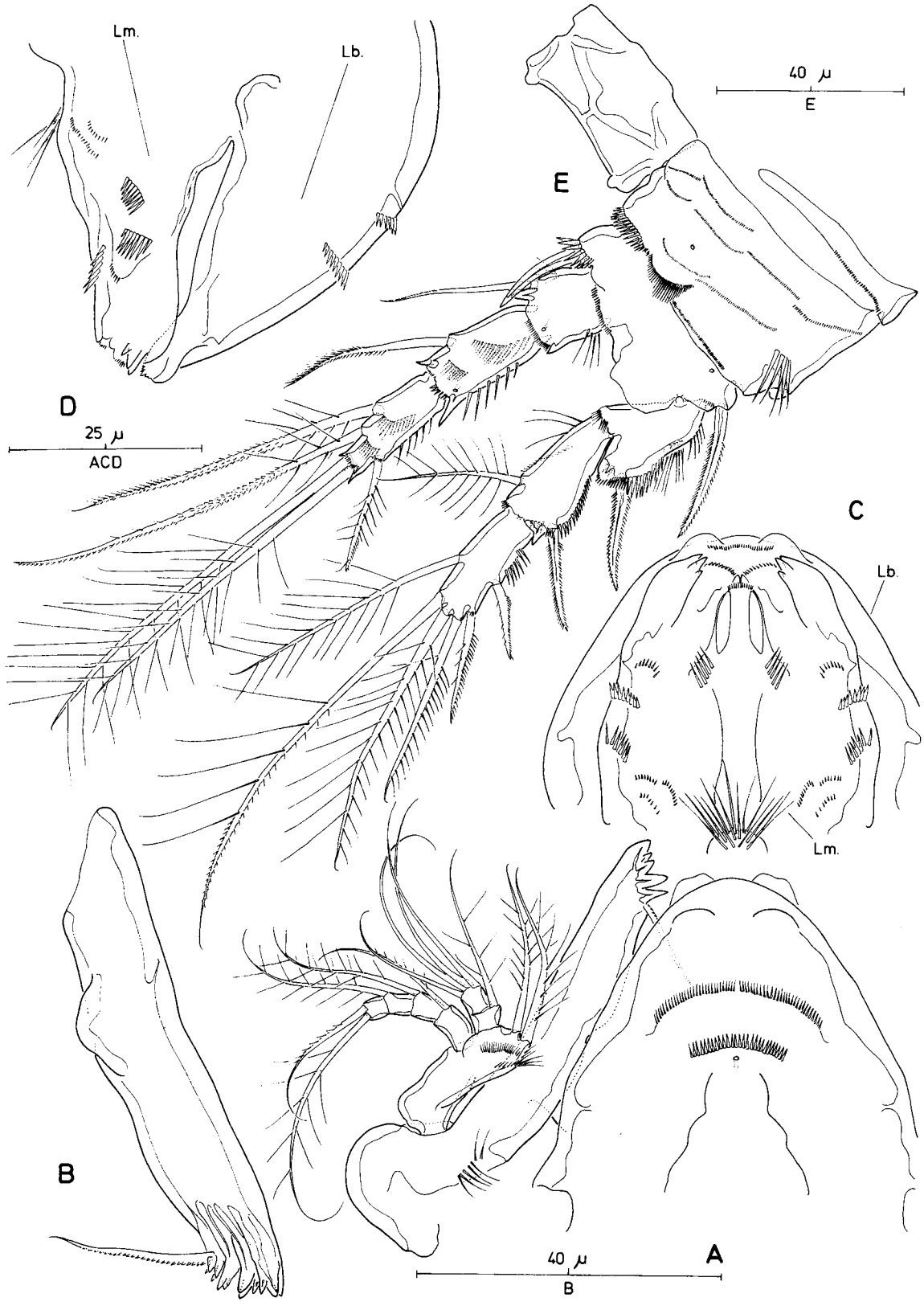

Fig. 5. Novocrinia trifida gen. et sp. n.—*A*. Labrum and left mandible, anterior.—*B*. Mandibular gnathobase.—*C*. Labium (Lm.) superimposed on labrum (Lb.), posterior.—*D*. Labrum (Lb.) and labium (Lm.), lateral.—*E*. P1, anterior.

cephalic shield; rounded in dorsal aspect (Fig. 1C) but distinctly recurved ventrally and backwardly in lateral aspect (Fig. 1A, D); with trifid tip (Fig. 1C); strongly chitinized; with middorsal integumental pore; sensilla not observed.

Antennule (Fig. 1C–D, 3A) 9-segmented, slender; small sclerite discernible at base (Fig. 1D), well developed intersegmental membranes present between cephalic shield and segments 1–2 (Fig. 1D). Segment 1 short; anterior margin with ventral spinule comb and produced into small spinous process; dorsal surface with tuft of setules. Segment 2 longest. Segment 4 with long aesthetasc (80 µm) fused basally to slender seta. All setae bare and slender except for stubby modified spines on segments 2–4

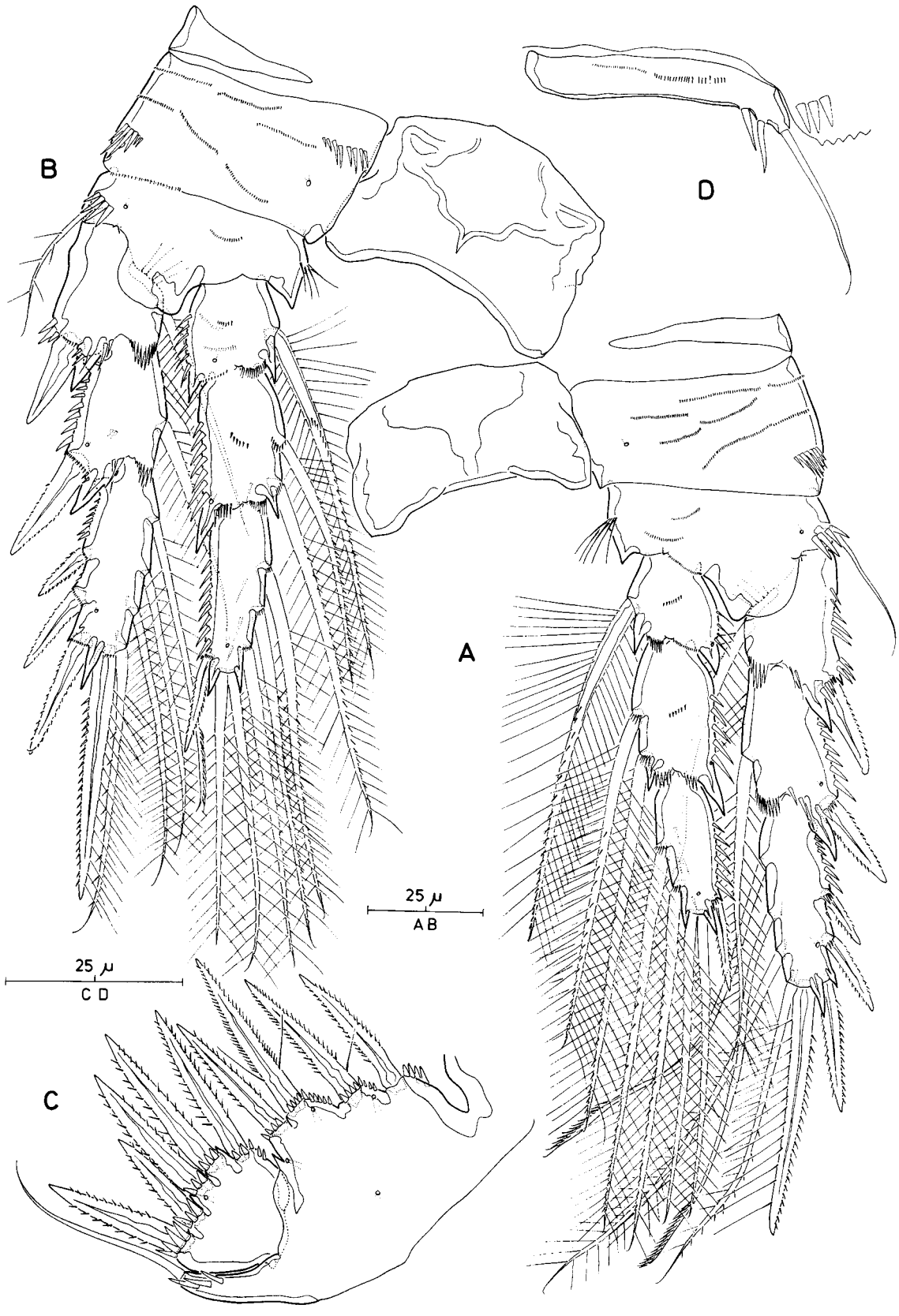

Fig. 6. Novocrinia trifida gen. et sp. n.—*A*. P4, anterior.—*B*. P3, anterior.—*C*. P5 ♂, anterior.—*D*. Left P6 ♂, anterior.

and few pinnate setae on segments 2–3. Armature formula: 1–[1], 2–[4 bare + 1 pinnate + 4 spines], 3–[2 bare + 2 pinnate + 1 spine], 4–[(1 + ae) + 1 spine], 5–[1], 6–[3], 7–[2], 8–[2], 9–[6 + acrothek]. Acrothek consisting of aesthetasc (65 µm) fused basally to slender seta.

Antenna (Fig. 4A–B). Coxa small, with spinule row. Basis with rows of tiny spinules as figured; completely separate from endopod; with long abexopodal seta, plumose in proximal half, pinnate in distal half. Exopod large, 4-segmented; segments 1–3 with 1 pinnate seta; segment 4 with 2 long, sparsely plumose setae flanking minute bare seta; segment 1 with small bump along inner margin; segment 4 constricted. Endopod 2-segmented; enp-1 with tiny spinules as figured and pinnate abexopodal

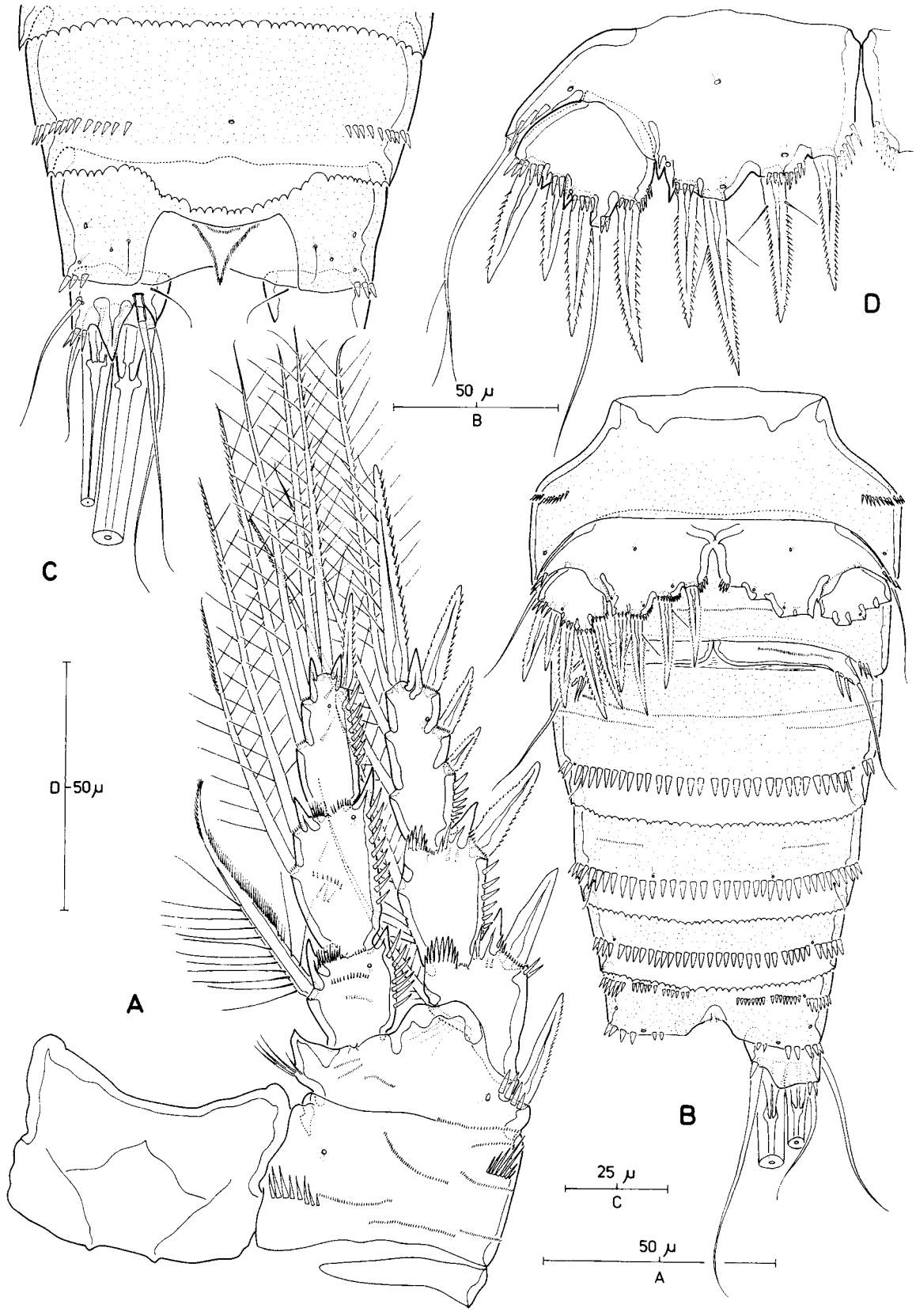

Fig. 7. Novocrinia trifida gen. et sp. n.—*A*. P2, anterior.—*B*. Urosome ♂, ventral [spines of left P5 omitted to show ornamentation of somite].—*C*. Penultimate somite, anal somite and left caudal ramus, dorsal.—*D*. P5 ♀, anterior.

seta; enp-2 long, with 2 hyaline surface frills, lateral armature consisting of setoid tuft and 2 unipinnate setae (accompanied by large spinule), distal armature consisting of 4 geniculate setae (labelled a–c, f in Fig. 4A) and 2 slender setae (labelled d–e). Setoid tuft (arrowed in Fig. 4B) consisting of about 35 filiform elements, each with apical pore (not figured).

Labrum (Fig. 5A, C–D). Large; anterior surface with 2 spinular rows (distal one interrupted in middle), and median secretory pore; posterior surface with paired lappets distally and patch of minute spinules.

Mandible (Fig. 5A–B). Coxa elongate, gnathobase with 1 unipinnate spine at dorsal corner and several multicuspidate teeth around distal margin. Palp biramous. Basis

with 2 spinule rows and 2 plumose setae. Endopod incompletely 2-segmented, segments fused along outer margin; enp-1 with 1 lateral, sparsely plumose seta; enp-2 with 4 naked setae apically. Exopod 4-segmented; exp-1 with 1 unipinnate seta, exp-2 and -3 with 1 plumose seta, exp-4 with 1 plumose seta and 1 unipinnate seta.

Paragnaths fused forming large median labium (Fig. 5C); original separation indicated by medially incised distal margin; posterior surface with complex pattern of spinules as figured; median tuft of long spinules present at base of labium. Labrum and labium closely adpressed forming oral cone (Fig. 5D).

Maxillule (Fig. 3B–E). Praecoxa and coxa partly fused. Praecoxal arthrite cylindrical, with 2 tube-setae on anterior surface and 9 elements around distal margin; distalmost element strongly developed and claw-like (Fig. 3C). Coxa without epipodite; endite cylindrical with 1 claw and 5 slender setae. Basis with 2 separate endites; proximal endite with 1 plumose and 3 slender setae; distal endite with 3 slender setae. Endopod largely incorporated into basis, represented by rectangular membranous segment with 4 slender setae apically and few long spinules along outer margin. Exopod represented by a posteriorly directed elongate segment bearing 1 spinule row and 2 very long, pinnate setae.

Maxilla (Fig. 3F–G). Syncoxa with 3 spinule rows and 1 cylindrical endite; endite closely adpressed to allobasis, with 3 pinnate setae. Allobasis drawn out into pinnate claw; accessory armature comprising strong spine and pinnate seta on proximal margin. Endopod 2-segmented; enp-1 with 2 slender and 2 geniculate setae; enp-2 with 1 naked, 1 pinnate ad 2 geniculate setae.

Maxilliped (Fig. 2A–B). Subchelate, well developed, elongate. Syncoxa with spinular pattern as figured, without setae. Basis with 2 spinule rows and pinnate seta on palmar margin near articulation with endopod. Endopod an elongate segment with 1 claw and a pinnate seta along inner margin, a naked seta along outer margin and 2 geniculate setae apically. Geniculate setae derived from separate minute segment which is demarcated by posterior surface suture (Fig. 2B).

Swimming legs (Figs 5E, 6A–B, 7A) with 3-segmented rami. Intercoxal sclerites rectangular, bare. Praecoxae represented by well developed U-shaped sclerites. Coxae with distinctive pattern of both long and minute spinules as figured. Bases with outer pinnate spine (P1–P2), plumose seta (P3) or bare seta (P4); inner distal corner with curved bare spine (P1) or produced into spinous process (P2–P4). Exopods at least slightly longer than endopods.

P1 (Fig. 5E) more slender than following swimming legs. Praecoxa with tiny spinules. Outer basal spine long and slender, bipinnate. Inner basal spine bare and slightly curved. Enp-2 with spinous inner and outer distal corners; inner seta serrate. Posterior surface of enp-2 and -3 with spinule rows. Enp-3 with distinctly stepped inner margin; bearing 2 multipinnate inner setae, 2 plumose distal setae and 1 slender outer spine. Exp-1 with outer portion expanded into lobe overlapping proximal part of exp-2 in lateral aspect. Intersegmental joint between exp-1 and -2 modified, directing distal portion of exopod outwardly. Exp-3 with 6 elements.

P2–P4 (Figs 6A–B, 7A). Praecoxae without spinules. Bases forming large, partly hyaline outgrowth between insertion sites of rami. Outer exopodal spines strongly developed (particularly in P2 and P3). Outer distal corners of all segments forming spinous processes. Hyaline frills between exopod segments well developed. Outer spine of P2 exp-1 bare. Inner seta of P2 enp-1 distinctive (Fig. 7A). Spine- and seta formula as follows:

	Exopod	Endopod
P1	0.1.222	1.1.221
P2	1.1.223	1.2.221
P3	1.1.323	1.2.321
P4	1.1.323	1.2.221

Fifth pair of legs (Figs 2C, 7D) not fused medially; biramous with separate exopod and baseoendopod. Baseoendopod wide; with outer sparsely plumose seta arising from cylindrical setophore. Endopodal lobe with paired spinous processes along outer margin and spinules along distal inner margin; apical margin stepped, with 4 pinnate spines (2 of which typically with long setules proximally); anterior surface with 5 secretory pores. Exopod oval; distal margin stepped, with 4 pinnate spines and 1 long slender seta arising from small cylindrical process.

Genital field positioned near anterior margin of genital double-somite (Fig. 2D–E). Gonopores fused medially forming common transverse genital slit; slit closed off by fused opercula derived from vestigial P6, each bearing 3 short setae; row of tiny spinules present anterior to genital slit. Copulatory pore small; located in semicircular, shallow depression; leading via very short duct to paired seminal receptacles; flanked by 2 secretory tube pores.

Egg-sac(s) not observed.

Male. (Figs 4C–D, 6C–D, 7B, 8). Total body length 505–515 μm ($n=3$; $\bar{x}=510$ μm), measured from anterior margin of rostrum to posterior margin of caudal rami. Largest width (165 μm) measured at posterior margin of cephalothorax. Sexual dimorphism in antennule, antenna, P5, P6, abdominal spinulation and genital segmentation.

Posterior margin of thoracic somites without, of abdominal somites with transverse row of spinules which is interrupted only dorsally (Figs 7B, 8A). Genital (P6-bearing) somite and first two abdominal somites with transverse rows of minute spinules as figured (Fig. 7B). Spinule pattern on anal somite as in ♀.

Antennule (Fig. 8A–D) 9-segmented, slender; haplocer with geniculation between segments 7 and 8; small sclerite discernible at base, well developed intersegmental membranes present between cephalic shield and segments 1–2. Segment 1 short; anterior margin with ventral spinule comb and produced into small spinous process; dorsal surface with tuft of setules. Aesthetasc present on segments 2 (40 μm), 3 (80 μm), 5 (100 μm) and as part of acrothek on segment 9 (50 μm); all aesthetascs arising from ventral surface, that of segment 5 fused basally to slender seta. All setae bare except for stubby modified spines on segments 2–5 and single pinnate seta on segment 3 (Fig. 8B–D). Armature formula: 1–[1], 2–[5 + 5 spines + ae], 3–[4

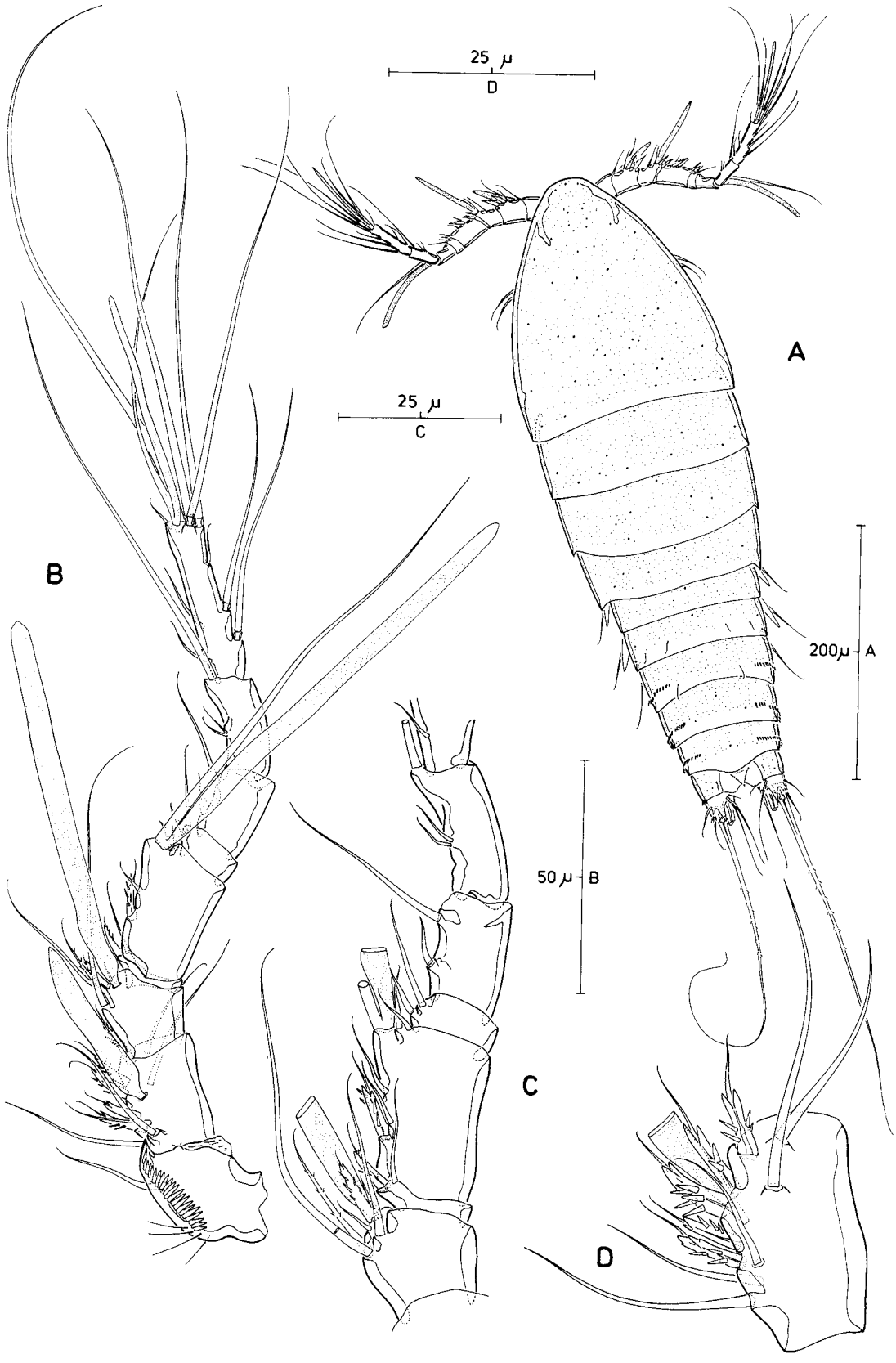

Fig. 8. Novocrinia trifida gen. et sp. n.—*A*. Habitus ♂, dorsal.—*B*. Antennule ♂, ventral.—*C*. Antennulary segments 3–8 of ♂, dorsal.—*D*. Antennulary segment 2 of ♂, dorsal.

bare + 1 pinnate + 1 spine + ae], 4–[(1 + 1 spine], 5–[4 + 1 spine + (1 + ae)], 6–[2], 7–[2], 8–[3], 9–[10 + acrothek]. Acrothek consisting of aesthetasc fused basally to slender seta.

Antenna (Fig. 4C–D). Protopod, exopod and enp-1 essentially as in ♀ except for small differences in spinule patterns. Enp-2 without spinules in proximal half; hyaline surface frills and lateral armature (including setoid tuft) as in ♀. Distal armature of enp-2 consisting of 3 geniculate setae (labelled a–c in Fig. 4C) and 2 slender setae (labelled d–e); homologue of sixth seta (labelled f in Fig. 4A) replaced by distal setoid tuft (arrowed in Fig. 4d) consisting of about 25 filiform elements.

Fifth pair of legs (Figs 6C, 7B) fused medially; biramous

with separate exopod and baseoendopod. Baseoendopods forming wide, medially incised plate across ventral surface of somite; armature as in ♀; endopodal lobe with single spinous processes along outer margin and spinules along distal inner margin; apical margin stepped; anterior surface with 4 secretory pores. Exopod oval; distal margin stepped, with 5 strong pinnate spines.

Sixth pair of legs (Figs 6D, 7B) symmetrical, defined at base; each P6 with 2 transverse rows of minute spinules on anterior surface, armature consisting of long outer and 2 short setae.

Discussion

The Novocriniidae and Ectinosomatidae show a remarkable similarity in general body shape. The characteristically fusiform habitus of *Novocrinia trifida* is reminiscent of most ectinosomatid genera (with the exception of some interstitial taxa and the dorso-ventrally flattened *Peltobradya* Médioni & Soyer) but is regarded here as the result of convergent evolution. Whilst in the Ectinosomatidae this body shape can be viewed as the morphological impact of adopting a burrowing (endobenthic) life-style, it is difficult to speculate on the possible advantages offered by a fusiform, strongly chitinized body in the planktonic or epibenthic environment.

The new family is placed in the tisbidimorph complex of families (Tisboidea) by virtue of the morphology of its maxilliped. *Tachidiopsis cyclopoides* Sars, currently assigned to the subfamily Idyanthinae in the Tisbidae, displays the most primitive state of the maxilliped and provides a useful reference for comparison with other families of the Tisboidea. In this species the maxilliped is 4-segmented, comprising a syncoxa with 6 elements, a bisetose basis and a 2-segmented endopod (Huys & Boxshall 1991: fig. 2.4.15D). The ancestral setation of the endopod consists of 6 elements. The proximal segment bears 1 inner and 1 outer seta, and a strong, usually pinnate claw subdistally. The distal segment is partly concealed under the claw of the proximal segment and carries 1 lateral seta and 2 long, typically juxtaposed, geniculate setae apically. This highly distinctive pattern is found in all tisbidimorph families and the presence of paired geniculate setae on the distal segment serves as a robust synapomorphy linking the Tisbidae, Superornatiremidae, Novocriniidae, Porcellidiidae and Paramesochridae in a monophyletic group. Secondary fusion of segments or reduction and loss of armature elements can obscure the pattern such as in the Superornatiremidae where all elements are retained but the segments have fused forming a 1-segmented endopod. In the Paramesochridae both endopodal segments are usually discrete but a variable number of elements can be lost. In the Novocriniidae the endopod has lost one of the outer lateral elements, however since the suture between both segments is incomplete, it is impossible to decide whether it is the distal or proximal outer seta that is retained.

The Chappuisiidae also possess a 2-segmented endopod with 1 spine on the proximal and 2 parallel setae on the distal segment. Earlier workers invariably described these distal elements as simple setae but re-examination has proven them to be distinctly geniculate as illustrated by Glatzel's (1989) SEM observation (Glatzel 1989; his Fig. 44; but not his line drawing Fig. 12). It is conceivable that the Chappuisiidae represent a specialized lineage of relicts that has diverged very early in the evolution of the Tisboidea and subsequently radiated in groundwater habitats in Central Europe. The relationships within the Tisboidea are intricate and due to the numerous deficient descriptions they cannot be resolved solely on the basis of data available in the literature. A detailed phylogenetic analysis therefore is beyond the scope of this paper but will be the subject of a forthcoming study.

The new family displays a number of plesiomorphic character states reflecting its primitive position within the Tisboidea:

—*Antennules*. *Novocrinia trifida* males display the maximum number of aesthetascs found in the Harpacticoida. Aesthetascs are present on segments 2, 3, 5 and 9 which corresponds to the pattern found in the Cerviniidae (e.g. Itô 1982) and the Rotundiclipeidae (Huys 1988*a*). The Clytemnestridae have 6 aesthetascs expressed which are arranged in three pairs on segments 3, 4 and 7 (in *Clytemnestra scutellata* Dana) or 6 (in *C. rostrata* (Brady)), respectively. However, this duplication in aesthetasc number is caused by the morphological transformation of setae into aesthetascs and is clearly secondary as a result of colonizing the open pelagic environment.

—*Antennae*. The exopod is distinctly 4-segmented and both abexopodal setae (on basis and proximal endopod segment) are retained.

—*Mandibles*. Both rami display the maximum number of segments. The 2-segmented endopod is further only found in the two polyarthran families Canuellidae and Longipediidae and in a number of Paramesochridae.

—*Maxillules*. The coxal endite has 6 elements, which is the maximum recorded in harpacticoids.

—*Maxillae*. The endopod is well developed, 2-segmented and carries 4 setae on each segment.

—*P1*. The endopodal armature with 5 setae on the distal segment is the most ancestral type found in the Harpacticoida. Within the tisbidimorph complex this number is further only found in some genera of the Idyanthinae (e.g. *Idyanthe* Sars). The Superornatiremidae which bear 7 setae on this segment are not considered here since a secondary increase in the number of elements has obscured the original condition (Huys 1996). The unmodified, non-prehensile endopod and the presence of 6 elements on P1 exp-3 are also primitive features.

—*Swimming legs P2–P4*. The complete absence of sexual dimorphism on the swimming legs (including on the P2 endopod which is frequently modified in tisbidimorph copepods) is another primitive character.

The fifth legs are sexually dimorphic in the majority of the harpacticoids. Sexual dimorphism can be expressed at different levels and the collective transformation in the male is usually the result of more than one developmental process. Differences between sexes can be found in the basic segmentation pattern of the exopod (and exceptionally the protopod), the separation and shape or form of the endopodal lobe, the number of armature elements on the

exopod and the endopodal lobe of the baseoendopod, and size. With very few exceptions male harpacticoids have a maximum of three setae on the endopodal lobe whereas the maximum number in females is six as in *Mesochra lilljeborgi* Boeck and species of *Cletocamptus* Shmankevich (Canthocamptidae). As a rule, males have fewer setae/spines on the endopodal lobe of the baseoendopod when the number in the female is higher than three. Typically the fifth legs appear at the third copepodid in harpacticoid development and attain the definitive state in the adult (see e.g. *Orthopsyllus* sp.; Huys 1990*a*). Addition of setae on the endopodal lobe in the male is completed at copepodid IV. In the female, additional elements are typically added during the following moult and in some species the full complement of setae and spines does not appear until the adult. The sexual difference in endopodal setal numbers is almost universal in those harpacticoids with four or more setae in the female and can be explained by two alternate developmental scenarios. A first scenario is based on heterochronic postdisplacement of the appearance of the additional setae in the male. This would imply that the appearance in ontogeny of these setae has been delayed beyond the definitive moult, and they have been effectively lost. A second scenario is that the loss of particular setae in the male is caused by repression of a gene function controlling the expression of setae at copepodid V. Phenotypic evidence of this kind of genotypic repression can be inferred from the very few male harpacticoids that have more than three elements on the endopodal lobe. Four setae are found in the male of *N. trifida* and in a representative of an as yet undescribed new family from the Great Barrier Reef, illustrated by Huys & Boxshall (1991 fig. 2.4.21C). The maximum setation is found in the ameirid *Nitokra hibernica* (Brady), which possesses 5 endopodal elements in both sexes (Gurney 1932). In all three examples the number of setae is identical in both sexes, suggesting that no gene repression has taken place. These exceptions belong to three genera placed in three different families that are phylogenetically advanced and are not closely related. There is no evidence that the presence of supernumerary setae in the male represents the ancestral harpacticoid condition, which is retained only in the genera above and has been lost in all other lineages. A more parsimonious hypothesis would be that the appearance of these elements was repressed historically very early in the evolution of the Harpacticoida, if not in the harpacticoid ancestor, and expression happened erratically in different lineages later in evolution. From ontogenetic sequences there is a substantial body of evidence that the setation of the endopodal lobe in the male harpacticoid P5 is under inhibitory control. The fifth pair of legs is probably more 'labile' since the functional constraints imposed on the morphology of genuine swimming legs are no longer present. It is not unlikely that under specific environmental conditions gene repression can be lifted resulting in convergent redevelopment of the ancestral state. Such conditions can be found in the brackish water habitat (*Nitokra hibernica*) or anchihaline caves (*Novocrinia trifida*).

The Novocriniidae can be readily distinguished by the presence of filamentous tufts on the antenna, the number of which is sexually dimorphic. Sexually dimorphic antennae have been described for a wide range of genera, however many of these reports are erroneous and stem from inadequate observations and descriptions. This is particularly the case for *Macrosetella* A. Scott (Miraciidae; Boxshall 1979), *Stenhelia* Boeck (Diosaccidae; Schriever 1982), *Metahuntemannia* Smirnov (Huntemanniidae; Schriever 1983), *Mesocletodes* Sars (Argestidae; Schriever, 1985) and *Heterolaophonte* Lang (Laophontidae; Hamond 1973). In others the differences between sexes are subtle such as in *Balaenophilus unisetosus* Aurivillius (Balaenophilidae; Vervoort & Tranter 1961) and some species of *Pontostratiotes* Brady (Cerviniidae; Itô 1982), *Harpacticella* Sars (Harpacticidae; Itô & Kikuchi 1977) and *Harpacticus* Milne Edwards (Harpacticidae; e.g. Itô 1976, 1979). In the family Paramesochridae, distinct antennary sexual dimorphism can be displayed on the endopod (*Diarthrodella neotropica* Mielke) or the exopod (*Rossopsyllus* Soyer, *Diarthrodella chilensis* Mielke, *D. galapagoensis* Mielke) (Mielke 1984, 1985). Males of the harpacticid genera *Tigriopus* Norman and *Paratigriopus* Itô possess sexually dimorphic features on the allobasis (e.g. Itô 1969, 1977). In all other cases both the endopod and exopod are modified in the males. In various species of *Karllangia* Noodt, sexual dimorphism is expressed on the exopod and the proximal endopod segment (Wells 1967; Mielke 1994). *Euterpina acutifrons* (Dana) represents a special case since males are known to be dimorphic. The antenna of the small morph resembles that of the female in all aspects, however, the large size morph is characterized by distinct modifications on both the exopod and distal endopod segment (Huys *et al.* 1996). Finally, the bathypelagic Aegisthidae, which possess atrophied mouthparts in the males, display strong sexual dimorphism in the antennae (Huys 1988*b*).

Novocriniidae display a unique sexual dimorphism on the distal endopod segment of the antenna. In the female, a tuft of filamentous structures is situated in the proximal half of this segment (arrowed in Fig. 4B). Males differ in the presence of a second tuft arising from the subapical portion of the segment. The distal armature in the female (Fig. 4A) consists of 4 geniculate setae (labelled *a–c* and *f*) and 2 simple setae (*d–e*). The male carries only 5 setae around the distal margin (Fig. 4C), which by virtue of their form and position can be homologized with setae *a–e* of the female. The distal filamentous tuft of the male is regarded here as a transformed setal element homologous with the missing geniculate seta *f* found in this position in the female. A similar transformation process can be invoked to explain the presence of the proximal tuft in both sexes. In other tisbidimorph families such as the Superornatiremidae (Huys 1996), the lateral armature consists of 3 setae, one of which is placed in a slightly more proximal position corresponding to the insertion site of the tuft. The positional homologues of the other two setae are retained in the Novocriniidae, and consequently it is conceivable that the proximal filamentous tuft represents the missing third element.

The presence of similar filamentous tufts has been recorded on the male antennules of representatives of two thalestridimorph families. Masunari (1988) described a group of filamentous elements arising from the third antennulary segment in *Parathalestris mourei* Masunari

(Thalestridae). In males of both genera of the family Ambunguipedidae an antennulary tuft is found on the sixth segment. Huys (1990*b*) rejected a setal origin for these tufts and coined the term 'setoid elements' to describe the filaments since they did not insert into a hole through the integument and apparently lacked an axial core. Examination of the ontogeny of the antennules in both sexes of *Ambunguipes rufocincta* (Brady) provided unequivocal evidence that at least in the Ambunguipedidae the antennulary tuft is homologous with a seta found on the fourth segment in the female and therefore represents a transformed armature element. Comparative evidence for this homology is also provided by the presence of this seta in both sexes of the Hamondiidae, the sistergroup of the Ambunguipedidae. The filamentous elements in *Ambunguipes* proved upon re-examination to be distinctly hollow at the tip and to possess an axial core connected through the segment wall with the underlying tissue. Although the nature of the filaments is similar in both Novocriniidae and Ambunguipedidae, it is unlikely that they perform the same role. In species of *Ambunguipes* Huys and *Lucayostratiotes* Huys, the antennulary tuft is only present in the male and appears late during the ontogeny at the copepodid V stage as an incipient but not yet functional cluster of blunt processes. This suggests a chemosensory role in connection with mate location for the sensory tuft as it is only up and running when the last moult is completed, it is only present in the male, and it is located on the antennule, the primary appendage involved in mate location. In the Novocriniidae the tufts are located on the antennae and one of them is present in both sexes suggesting a possible role in food location or selection. A similar function has been postulated for the sensory aesthetascs present on the oral appendages of some paranannopid genera (Gee & Huys, 1991; Huys & Gee 1992, 1996) since these structures were found to be present throughout copepodid development in both sexes. Unfortunately no information is available on the ontogeny of *Novocrinia* and thus any statement about their possible function would be speculative. The possibility that these tufts may be involved in food selection rather than mate location is also demonstrated by the bathypelagic calanoid *Augaptilina scopifera* Sars. This advanced augaptiloid is known from a single female only and shows dense brushes of fine, serrated setae on the basis and four endopodal segments of the maxilla, and on the five endopodal segments of the maxilliped (Huys & Boxshall 1991: Fig. 3.16.2). The tubular nature of the individual elements and their arrangement suggests that in this species also the tufts arose from a secondary multiplication of original setae.

Novocrinia trifida differs from most other harpacticoids by the possession of a well developed labium derived by medial fusion of the paired paragnaths. The labium is closely adpressed and fused basally and laterally to the labrum forming a bulbous oral cone. This conical structure can be regarded as an incipient siphon or mouth cone as found in the Siphonostomatoida, although it is clear that there is no close fit between the anterior and posterior lips. The large slits between the labrum and labium strongly suggest that the mandibular gnathobases can move freely in and out of the oral cone. The only previously known example of an oral cone in harpacticoids is that of the Superornatiremidae, coincidentally also a family of cavernicolous copepods (Huys 1996). In all three superornatiremid genera, the mouthcone is of the simplified siphonostomatoid type as found in the primitive families Asterocheridae and Dirivultidae (Boxshall 1990). In the Superornatiremidae, the paired origin of the labium is no longer discernible externally. In the Novocriniidae, the original bipartite structure of the labium is still reflected in the symmetrical spinulation patterns on its posterior face and in the medially concave ventral (distal) margin forming two weakly developed dentate lobes (Fig. 5C).

Acknowledgements

This research was supported by a grant from the Smithsonian Institution's Caribbean Coral Reef Ecosystems Program awarded to Thomas Iliffe. Serban Sarbu served as a research assistant on the expedition and assisted with cave diving collections and sorting of specimens. Invaluable logistic and cave diving support was provided by Frank Bounting of the Belize Diving Services at Caye Caulker. We gratefully acknowledge the Belize Department of Archaeology and Commissioner Harriot W. Topsey for granting us permission to carry out these cave investigations. Logan McNatt also provided assistance with the studies. Dr Audun Fosshagen (University of Bergen) kindly made unpublished data available.

References

Boxshall, G. A. (1979). The planktonic copepods of the northeastern Atlantic Ocean: Harpacticoida, Siphonostomatoida and Mormonilloida. *Bulletin of the British Museum of Natural History, Zoology 35*, 201–264.

Boxshall, G. A. (1990). The skeletomusculature of siphonostomatoid copepods, with an analysis of adaptive radiation in structure of the oral cone. *Philosophical Transactions of the Royal Society, London B328*, 167–212.

Cousteau, J. Y. (1973). *Three adventures: Galapagos, Titicaca, the Blue Holes*. New York: A&W Visual Library.

Fosshagen, A. & Iliffe, T. M. (1991). A new genus of calanoid copepod from an anchihaline cave in Belize. *Bulletin of the Plankton Society of Japan, Special Volume (1991)*, 339–346.

Gee, J. M. & Huys, R. (1991). A review of Paranannopidae (Copepoda: Harpacticoida) with claviform aesthetascs on oral appendages. *Journal of Natural History 25*, 1135–1169.

Glatzel, T. (1989). Comparative morphology of *Chappuissius inopinus* Kiefer and *C. singeri* Chappuis (Copepoda, Harpacticoida). *Zoologica Scripta 18*, 411–422.

Gurney, R. (1932). *British fresh-water Copepoda, 2*. London: The Ray Society.

Hamond, R. (1973). Some Laophontidae (Crustacea: Harpacticoida) from off North Carolina. *Transactions of the American Microscopical Society 92*, 44–59.

Huys, R. (1988*a*). Rotundiclipeidae fam. nov. (Copepoda, Harpacticoida) from an anchihaline cave on Tenerife, Canary Islands. Stygofauna of the Canary Islands, 10. *Stygologia 4*, 42–63.

Huys, R. (1988*b*). Sexual dimorphism in aegisthid cephalosomic appendages (Copepoda, Harpacticoida): a reappraisal. *Bijdragen tot de Dierkunde 58*, 114–136.

Huys, R. (1990*a*). Amsterdam Expeditions to the West Indian Islands, Report 64. A new family of harpacticoid copepods and an analysis of the phylogenetic relationships within the Laophontoidea T. Scott. *Bijdragen tot de Dierkunde 60*, 79–120.

Huys, R. (1990*b*). A new harpacticoid copepod family collected from Australian sponges and the status of the subfamily Rhynchothalestrinae Lang. *Zoological Journal of the Linnean Society 99*, 51–115.

Huys, R. (1996). Superornatiremidae fam. nov. (Copepoda: Harpacticoida): an enigmatic family from North Atlantic anchihaline caves. *Scientia Marina 60*, 497–542.

Huys, R. & Boxshall, G. A. (1991). *Copepod evolution*. London: The Ray Society.

Huys, R. & Gee, J. M. (1992). Revision of *Danielssenia perezi* Monard, *D. paraperezi* Soyer, *D. eastwardae* Coull (Harpacticoida; Paranannopidae) and their transfer to a new genus. *Zoological Journal of the Linnean Society 104*, 31–56.

Huys, R. & Gee, J. M. (1996). *Sentiropsis, Peltisenia* and *Afrosenia*: Three new genera of Paranannopidae (Copepoda, Harpacticoida). *Cahiers de Biologie marine 37*, 49–75.

Huys, R., Gee, J. M., Moore, C. G. & Hamond, R. (1996). Marine and brackish water harpacticoids. Part 1. *Synopses of the British Fauna (New Series) 51*, i–vii, 1–352.

Itô, T. (1969). Descriptions and records of marine harpacticoid copepods from Hokkaido. II. *Journal of the Faculty of Science, Hokkaido University, Zoology 17*, 58–77.

Itô, T. (1976). Descriptions and records of marine harpacticoid copepods from Hokkaido, VI. *Journal of the Faculty of Science, Hokkaido University, Zoology 20*, 448–567.

Itô, T. (1977). New species of marine harpacticoid copepods of the genera *Harpacticella* and *Tigriopus* from the Bonin Islands, with reference to the morphology of copepodid stages. *Journal of the Faculty of Science, Hokkaido University, Zoology 21*, 61–91.

Itô, T. (1979). Descriptions and records of marine harpacticoid copepods from Hokkaido, VII. *Journal of the Faculty of Science, Hokkaido University, Zoology 22*, 42–68.

Itô, T. (1982). Harpacticoid copepods from the Pacific abyssal off Mindanao. I. Cerviniidae. *Journal of the Faculty of Science, Hokkaido University, Zoology 23*, 63–127.

Itô, T. & Kikuchi, Y. (1977). On the occurrence of *Harpacticella paradoxa* (Brehm) in Japan; a fresh-water harpacticoid copepod originally described from a Chinese lake. *Annotationes zoologicae japonenses 50*, 40–56.

Jaume, D. (1997). First record of Superornatiremidae (Copepoda: Harpacticoida) from Mediterranean waters, with description of three new species from Balearic anchihaline caves. *Scientia Marina*.

Masunari, S. 1988. *Parathalestris mourei*, a new species of seaweed-dwelling copepod (Harpacticoida, Thalestridae) from Santos Bay, Brazil. *Crustaceana 54*, 104–112.

Mielke, W. (1984). Interstitielle Fauna von Galapagos. XXXI. Parame-sochridae (Harpacticoida). *Microfauna Marina 1*, 63–147.

Mielke, W. (1985). *Diarthrodella chilensis* sp. n. und *Rossopsyllus kerguelensis quellonensis* subsp. n. (Copepoda, Paramesochridae) von Chile. *Zoologica Scripta 14*, 45–53.

Mielke, W. (1994). Two co-occurring new *Karllangia* species (Copepoda: Ameridae) from the Caribbean coast of Costa Rica. *Revista de Biologia Tropical 42*, 141–153.

Schriever, G. (1982). Neue Harpacticoidea (Crustacea, Copepoda) aus dem Nordatlantik II. Vier neue Arten der Familien Diosaccidae und Ameiridae. *Meteor Forschungs-Ergebnisse (D) 35*, 27–34.

Schriever, G. (1983). New Harpacticoidea (Crustacea, Copepoda) from the North Atlantic Ocean. III. New species of the family Cletodidae. *Meteor Forschungs-Ergebnisse 36*, 65–83.

Schriever, G. (1985). New Harpacticoida from the North Atlantic Ocean. VII. The description of five new species of the genus *Mesocletodes* Sars (Cletodidae). *Mitteilungen aus dem Zoologischen Museum in Kiel 23*, 1–12.

Vervoort, W. & Tranter, D. (1961). *Balaenophilus unisetus* P.O.C. Aurivillius (Copepoda Harpacticoida) from the southern Hemisphere. *Crustaceana 3*, 70–84.

Wells, J. B. J. (1967). The littoral Copepoda (Crustacea) of Inhaca Island, Mozambique. *Transactions of the Royal Society of Edinburgh 677*, 189–358.