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Aquilastacus gen. nov. from the southern North Sea and the taxonomic position of *Leptastacus operculatus* Masry, 1970 (Copepoda: Harpacticoida: Leptastacidae)

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Abstract: A new genus of Leptastacidae (Copepoda: Harpacticoida) is described from subtidal sandy sediments in the Southern Bight of the North Sea. *Aquilastacus serratus* gen. nov. sp. nov. is most closely related to *Arenocaris* Nicholls with which it shares the unique sexual dimorphism on the P4 endopod, the distally constricted caudal rami and the loss of the subdistal spine on the P3 endopod in the female (and hence of the sexual dimorphism in the male). The genus *Aquilastacus* is more plesiomorphic than *Arenocaris* in most character states, except for the confluent fifth legs, the absence of the outer basal seta on P1 and the presence of only two setae on the female P6. The genus can be readily distinguished by the strong serrate plate arising from the anal operculum and the form of the fifth legs in both sexes. The type material of *Leptastacus operculatus* Masry, 1970, previously considered *species incertae sedis* in the Leptastacidae, is re-examined. The only paratype slide labelled as the male proved to contain a female, casting doubts on Masry's (1970) illustrations of the male. Based on a detailed redescription of the female, *L. operculatus* is removed from *Leptastacus* T. Scott and designated as the type species of a new genus, *Stereoxiphos*. The new genus holds a transitionary position between *Belemnopontia* Huys and a clade comprising *Cerconeotes* Huys and *Psammastacus* Nicholls. It can be distinguished from other Leptastacidae by the combination of (1) loss of inner seta on P1 enp-1, (2) pedigerous somites with internal pattern of plate-like reinforcements, and (3) anal operculum with very large middorsal projection.

Résumé : Aquilastacus *gen. nov. du sud de la Mer du Nord et situation taxonomique de* Leptastacus operculatus *Masry, 1970 (Copepoda: Harpacticoida: Leptastacidae).* Un nouveau genre de Leptastacidae (Copepoda: Harpacticoida) est décrit, provenant des sables subtidaux du sud de la Mer du Nord. *Aquilastacus serratus* gen. nov. sp. nov. est très proche du genre *Arenocaris* Nicholls avec lequel il partage l'unique dimorphisme sexuel sur l'endopode du P4, la rame caudale rétrécie distalement et la perte de l'épine sous-distale sur l'endopode du P3 de la femelle (et par conséquent du dimorphisme sexuel chez le mâle). Le genre *Aquilastacus* est davantage plésiomorphe que *Arenocaris* pour la plupart des caractères sauf pour les cinquièmes pattes confluentes, l'absence de soies basales externes sur le P1 et la présence de seulement deux soies sur le P6 de la femelle. Le genre se distingue par la longue plaque partant de l'opercule anal et la forme des cinquièmes pattes chez les deux sexes. Le matériel type de *Leptastacus operculatus* Masry, 1970, considéré précédemment *species incertae sedis* chez les Leptastacidae, est réexaminé. La seule lame du paratype désigné comme mâle s'avère être une femelle, amenant des doutes sur les représentations de mâle de Masry (1970). Sur la base d'une redescription détaillée de la femelle, *L. operculatus* est retirée du genre *Leptastacus* T. Scott et proposée comme l'espèce type d'un nouveau genre, *Stereoxiphos*. Le nouveau genre occupe une position intermédiaire entre *Belemnopontia* Huys et un clade comprenant *Cercoceotes* Huys et *Psammastacus* Nicholls. Il peut être distingué des autres Leptastacidae par la combinaison de (1) la

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perte de la soie interne sur P1 enp-1, (2) des somites pédigères avec un patron interne de renforts en forme de plaques et (3) un opercule anal muni d'une très grande projection médiodorsale.

Keywords: Copepoda, Harpacticoida, Leptastacidae, *Aquilastacus* gen. nov., *Stereoxiphos* gen. nov., Phylogeny.

Introduction

Leptastacid harpacticoids are important faunal elements of sandy beaches and shallow subtidal habitats (Hicks & Coull, 1983). The family Leptastacidae currently contains 55 valid species in 16 genera (Huys, 1992; Huys et al., 1996*a*; Huys & Todaro, 1997) and another 19 species have been assigned the status of *species inquirenda* or *species incertae sedis*. This high number of problematic taxa testifies to the difficulties encountered in the study of these harpacticoids, which are further exacerbated by the presence of sibling species. Their abundance reflects both inadequate study of morphological features (pseudo-sibling species) and divergence in habitat, life history and chemical recognition systems without parallel divergence in morphology (sibling species) (Knowlton, 1993). One example in the Leptastacidae is the genus *Cerconeotes* Huys which contains four valid and three problematic species. Species discrimination within the genus is notoriously difficult and the key to species constructed by Huys (1992) illustrates the level of subtle morphological distinction that is required. In contrast to *Leptastacus nichollsi* Krishnaswamy, 1951, *L. euryhalinus* Krishnaswamy, 1955 and *L. waltairensis* Rao & Ganapati, 1969, all of which clearly belong to *Cerconeotes* but cannot unequivocally be discriminated from their congeners at present, Huys (1992) only reluctantly included *L. operculatus* Masry, 1970 as *species inquirenda* in the genus because the taxonomic uncertainty surrounding this species did not stem from morphological similarity with its congeners but from failure to use or consider potentially available characters.

Due to security measures imposed during the Persian Gulf War (1991), the specimen loan policy at the Hebrew University of Jerusalem (HUJ) was reviewed, resulting in the suspension of all outgoing loans. The type material of *L. operculatus* held in the collections of the HUJ, only became available for re-examination after Huys' (1992) manuscript had already gone to press. In a note added in proof (p. 194), revising his earlier claim that it should be ranked as *species inquirenda* in the newly proposed genus *Cerconeotes* (pp. 162-163), Huys (1992) suggested to tentatively consider Masry's species a *species incertae sedis* in the Leptastacidae since several characters had been overlooked in the original description and the paratype female had been mistaken for a male. Huys & Todaro (1997) asserted that *L. operculatus* should be placed in a separate genus. In this paper the female of this species is redescribed in more detail, providing arguments for its designation as type species of a new genus, *Stereoxiphos*, which is most closely related to *Cerconeotes* and *Psammastacus* Nicholls.

Members of the genera *Leptastacus* T. Scott (4 species), *Paraleptastacus* Wilson (5 species) and *Arenocaris* Nicholls (2 species) often co-occur in sediment samples in the southern North Sea. Occasionally, unnamed species of *Schizothrix* Huys and *Minervella* Cottarelli & Venanzetti can also be found in coarser substrata (Huys, unpublished data). The phylogenetic relationships of these genera are well understood (Huys, 1992) with the possible exception of *Arenocaris* which appears to hold a transitionary position between the more primitive genera and the leptastacid crowngroup. Huys (1992) hinted at a sistergroup relationship with the genus *Psamathea* Cottarelli & Venanzetti, based on similarities in P1 exopodal segmentation and setation. He also pointed out that both genera display sexual dimorphism on the P4 endopod, but admitted that the quality of Cottarelli & Venanzetti's (1989) description of *Psamathea nautarum* did not enable a rigorous homology assessment. Huys *et al.* (1996*a*) redescribed this species, added *P. brittanica* to the genus and, based on the resemblance in caudal ramus morphology and P4 sexual dimorphism, favoured a sistergroup relationship between *Psamathea* and *Paraleptastacus*.

A subtidal survey during the summer of 1987 in the Southern Bight of the North Sea resulted in the discovery of an as yet unknown leptastacid which cannot be accommodated in any existing genus. In this paper we set out (1) to describe both sexes of the new species and designate it as the type of a new genus, *Aquilastacus* and (2) to provide substantiated evidence for its sistergroup relationship with *Arenocaris*.

Material and methods

Before dissection the habitus of *Aquilastacus serratus* was drawn from a whole specimen temporarily mounted in lactophenol. Specimens were dissected in lactic acid and the parts individually mounted in lactophenol under coverslips which were subsequently sealed with transparent nail varnish. The holotype ♀ of *Leptastacus operculatus* was originally mounted *in toto* in glycerin. After extended soaking in acetone and lactic acid the specimen was successfully restored and cleared; after completion of the habitus drawing the specimen was dissected on 6 slides. All drawings were-

prepared using a camera lucida on a Leica Diaplan or Leica DMR differential interference contrast microscope. The terminology for body and appendage morphology follows that of Huys & Boxshall (1991), Huys (1992) and Huys et al. (1996b). Abbreviations used: *P1 - P6* for swimming legs 1-6; *exp(enp)-1(-2-3)* to denote the proximal (middle, distal) segment of a ramus; and *ae* for aesthetasc. Body length was measured along the dorsal curvature in lateral aspect, from the anterior margin of the rostrum to the posterior margin of the caudal rami.

Type material of *Aquilastacus serratus* gen. nov. sp. nov. has been deposited in the Natural History Museum, London (NHM).

Systematics

Order Harpacticoida Sars, 1903
Family Leptastacidae Lang, 1948
Aquilastacus gen. nov.

Diagnosis

Leptastacidae. Integument smooth. Hyaline frill of urosomites minutely serrate. Anal operculum a well developed pectinate lobe. Caudal ramus with distal constriction, seta I minute, none of setae modified. Sexual dimorphism in antennule, P3 endopod, P4 endopod, P5, P6, and genital segmentation. Slight dimorphism in anal operculum and caudal ramus (seta VII).

Rostrum elongate-triangular. Antennule 7-segmented in ♀, with aesthetasc on segment 4 and as part of acrothek on segment 7; haplocer and 9-segmented in ♂, with geniculation between segments 7 and 8 and aesthetascs on segment 5 and as part of acrothek on segment 9. Antenna with allobasis and exopod with 2 distal setae. Labrum without frontal recurved process, not distinctly tri-lobate. Mandibular gnathobase with series of strong spinules; palp 2-segmented; basis with 1 seta, endopod with 4 setae. Maxillule with exopod and endopod represented by 1 and 2 setae, respectively; arthrite rotated relative to coxa and basis. Maxilla with 2 cylindrical endites on syncoxa; endopod elongate, indistinctly 2-segmented. Maxilliped with syncoxal seta; accessory seta on endopod long.

P1 basis without inner or outer seta. P1 exopod 3-segmented; exp-3 with 3 setae/spines. P1 endopod 2-segmented, not prehensile, longer than exopod; enp-1 with inner seta. P2-P4 bases with outer seta; endopods 2-segmented. Outer spine of P4 exp-1 not elongate or curved. Inner subdistal spine of P4 enp-2 short. Armature formula of swimming legs:

P3 endopod ♂ with additional spinule row on enp-2; distal spine not modified. P4 endopod ♂ modified; with special joint enabling medial flexure of enp-2; enp-2 with blunt distal spine, inner subdistal spine modified into claw with flagellate tip. P5 uniramous in both sexes, with distinct lobes; exopodal lobe with 3 small setae and large, distally flagellate, spine; endopodal lobe with 2 short setae. Female P6 with long inner and short outer seta. Male P6 with 3 setae.

	Exopod	Endopod
P1	0.0.021	1.011
P2	0.0.021	1.010
P3	0.0.121	1.010
P4	0.1.221	0.110

Type and only species. Aquilastacus serratus gen. nov. sp. nov.

Etymology

The generic name is derived from the Latin *aquilonis* (the north wind, the north) and the Greek αστακοσ (lobster), and refers to its type locality in the North Sea. Gender: masculine.

Aquilastacus serratus gen. nov. sp. nov.

Type locality

Southern Bight of North Sea; 52°02'30"N, 3°25'00"E; 37.2 m depth.

Material examined

Holotype ♀, dissected on 7 slides (NHM reg. no. 2005.205); paratype ♂, dissected on 6 slides (NHM reg. no. 2005.206); coll. R. Huys, 24 June 1987.

Description

Female (Figs 1A-C, G; 2A, C-H; 3A, C; 4A-E). Total body length: 425 µm.

Body slender, cylindrical (Fig. 1A), almost colourless; intersomitic boundaries well developed. Integument smooth, moderately chitinised. Hyaline frills of cephalothorax and somites bearing P2-P4 plain, those of urosomites finely serrate (Figs 1A, C; 3A, C). Cephalothorax tapering anteriorly, no distinct difference in width between cephalothorax and free body somites; no distinct separation between prosome and urosome. Genital-double somite longer than wide (Figs 1A, C; 3A, C), original subdivision marked dorsally by paired submedian sensillae and small round chitinous reinforcements (Fig. 3A); with genital apertures located in anterior half (Fig. 1C). Anal somite

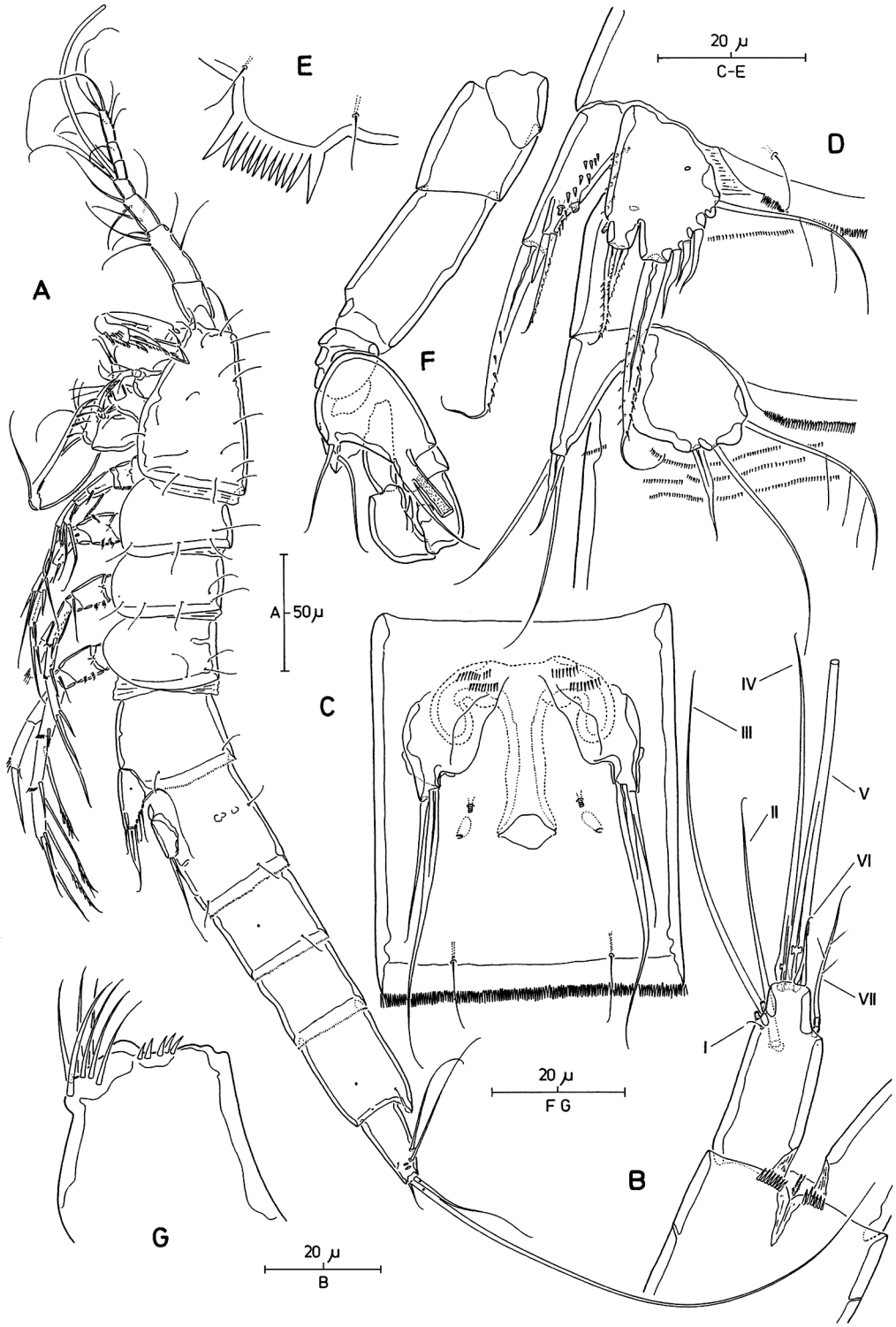

Figure 1. *Aquilastacus serratus* gen. nov. sp. nov. **A.** Habitus ♀, lateral. **B.** Left caudal ramus ♀, ventral. **C.** Genital double-somite ♀. **D.** P5 and P6 ♂, ventrolateral. **E.** Anal operculum ♂. **F.** Antennule ♂ [armature omitted]. **G.** Labrum ♀, lateral.

Figure 1. *Aquilastacus serratus* gen. nov. sp. nov. **A.** Habitus ♀, vue latérale. **B.** Rame caudale gauche ♀, vue ventrale. **C.** Somite double génital ♀. **D.** P5 et P6 ♂, vue ventro-latérale. **E.** Opercule anal ♂. **F.** Antennule ♂ [armature omise]. **G.** Labre ♀, vue latérale.

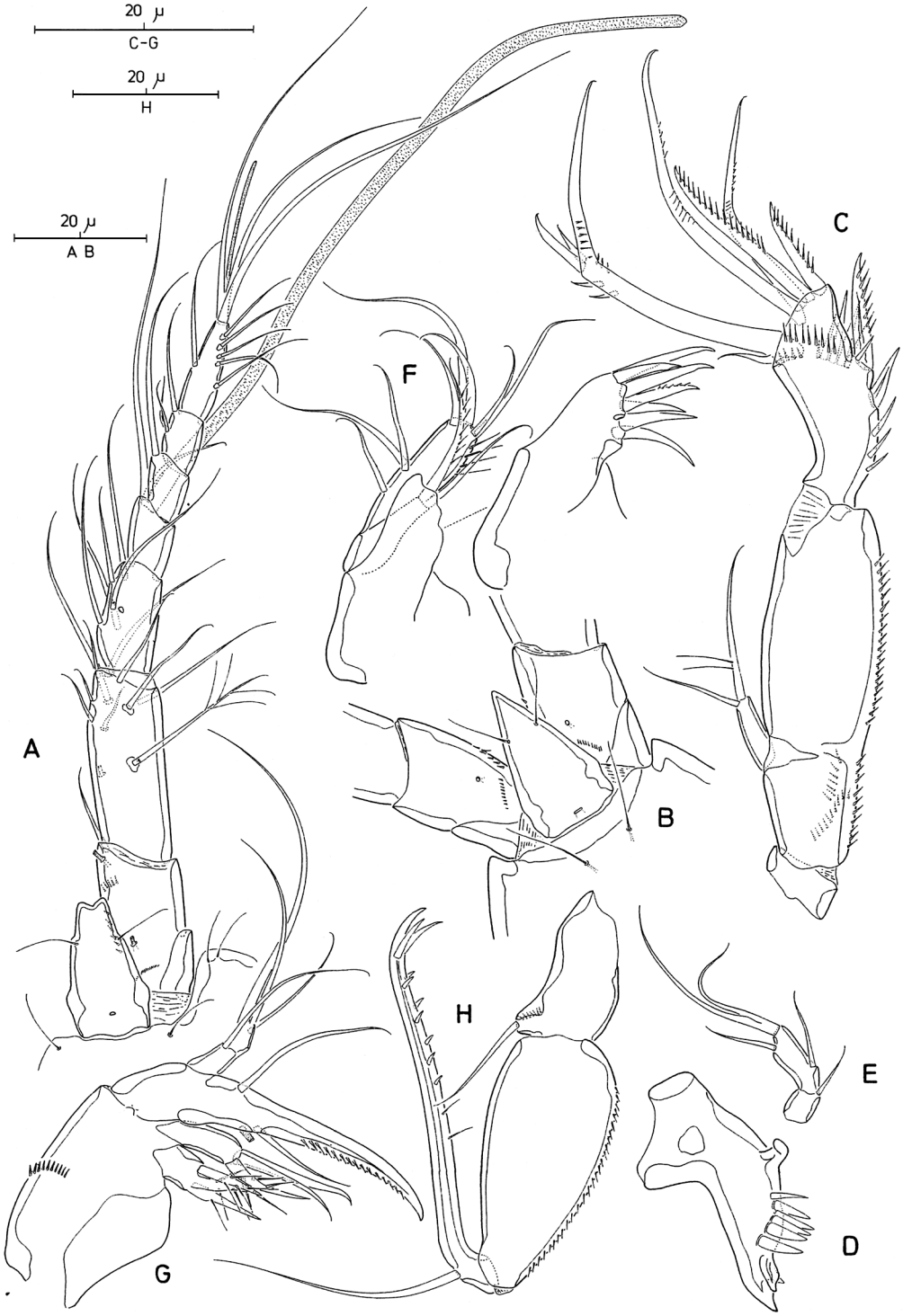

Figure 2. *Aquilastacus serratus* gen. nov. sp. nov. **A.** Rostrum and antennule ♀, dorsal. **B.** Rostrum and first antennulary segments ♂, dorsal. **C.** Antenna. **D.** Mandibular gnathobase. **E.** Mandibular palp. **F.** Maxillule [praecoxa shown in inset]. **G.** Maxilla. **H.** Maxilliped.

Figure 2. *Aquilastacus serratus* gen. nov. sp. nov. **A.** Rostre et antennule ♀, vue dorsale. **B.** Rostre et premiers articles antennulaires ♂, vue dorsale. **C.** Antenne. **D.** Gnathobase mandibulaire. **E.** Palpe mandibulaire. **F.** Maxillule [praecoxa illustrée en encart]. **G.** Maxille. **H.** Maxillipède.

about 1.4 times as long as wide (Fig. 3A), with well developed anal operculum drawn out into conspicuous transversely pectinate plate (Fig. 3A) overlying anal opening (Fig. 3C); ventral rear margin with spinules medially (Fig. 1B).

Caudal rami slightly divergent (Figs 1B & 3A), about 2.4 times as long as maximum width; distal quarter bilaterally constricted (Fig. 1B). Armature consisting of 7 setae: seta I vestigial; setae II and III long and naked; seta IV well developed, not fused basally to seta V; seta V strongly developed, as long as half the body length; setae IV and V both with fracture planes; seta VI short and swollen at base, displaced ventrally; seta VII located at constriction of inner margin, tri-articulated at base, sparsely plumose. Lateral surface of ramus with 2 tubular pores; no oblique spinular row on dorsal surface.

Rostrum (Fig. 2A) well developed, elongate triangular, not reaching to distal margin of first antennulary segment, free at base; apex with concave anterior margin [probably aberrant condition; see ♂: Fig. 2B]; with two long sensillae at two-thirds length of rostrum and middorsal pore near proximal margin.

Antennule 7-segmented, slender (Figs 1A; 2A). Segment 1 surrounded at base by small sclerite along posterior margin; with tiny spinule rows as figured in Fig. 2A; dorsal surface with 2 secretory tube-pores; segment 2 longest, with tube-pore on ventral surface; segment 3 with dorsal pore; segment 4 with very long aesthetasc (105 µm); segment 7 with apical acrothek consisting of 2 long setae fused basally to short aesthetasc (25 µm). Armature formula: 1-[1], 2-[9 + 1 plumose], 3-[5], 4-[1 + (1+ae)], 5-[1], 6-[3], 7-[7+acrothek].

Antenna (Fig. 2C). Coxa small, without ornamentation. Allobasis about 3.1 times as long as maximum width; original segmentation marked by transverse membranous area around base of exopod; with numerous small spinules as illustrated. Exopod 1-segmented, small; with 2 apical setae, one of which with stiff lateral setules. Distal endopodal margin with 2 geniculate setae, 2 pinnate spines and a large geniculate spine which is swollen at the base, fused with a vestigial seta and ornamented with spinules around the geniculation; lateral endopodal margin with 1 smooth and 1 unipinnate spine; with spinulation pattern as figures.

Mandibular palp 2-segmented (Fig. 2E); basis with 1 seta; endopod with 1 proximal inner seta, 1 subapical outer seta and 2 confluent apical setae; all armature elements bare. Gnathobase (Fig. 2D) small with conspicuous row of coarse spinules around cutting edge.

Labrum strongly developed but not distinctly tri-lobate (Fig. 1G); without spinous process on anterior surface; covered with long spinules anteriorly and medially, and flanked by lobes with few smaller spinules laterally.

Maxillule (Fig. 2F) with arthrite rotated at right angle relative to main axis. Praecoxal arthrite with 7 spines around distal margin; without anterior surface setae. Coxal endite with 1 bare and 1 pinnate seta. Basis with 5 setae around distal margin and long setules along inner margin. Rami completely incorporated into basis; exopod represented by 1, endopod by 2 setae.

Maxilla (Fig. 2G). Syncoxa with 1 spinule row and 2 cylindrical endites closely adpressed to allobasis; proximal endite with 1 discrete and 2 basally fused pinnate spines; distal endite with 3 free elements (1 pinnate, 2 bare). Allobasis drawn out into long unipinnate claw; with 2 accessory setae and 1 secretory tube-pore. Endopod indistinctly 2-segmented; with 1 seta on enp-1; enp-2 with 2 basally fused apical setae and 1 discrete lateral seta.

Maxilliped (Fig. 2H) with long naked seta and minute spinular row on syncoxa. Basis transversally expanded, with convex outer and inner margins; with spinules along outer margin. Endopod with sigmoid pinnate claw and long, slender accessory seta.

P1-P4 (Fig. 4A-D) with 3-segmented exopods and 2-segmented endopods; endopods always shorter than exopods except for P1 endopod. Successive legs increasing in length.

P1 (Fig. 4A). Praecoxa a well developed bare sclerite. Coxa with 2 spinule rows on posterior surface. Basis with spinules around anterior distal margin but without inner or outer seta. Exopod 3-segmented; outer margin of segments spinulose; outer spines unipinnate, pinnules long and stiff; exp-3 with 1 unipinnate spine and 2 geniculate setae, innermost of which longest. Endopod 2-segmented, longer than exopod but not prehensile; enp-1 1.5 times as long as enp-2, with short serrate inner seta and 2 spinular rows along outer margin; enp-2 with continuous spinular rows along outer margin and 2 geniculate setae distally, inner one twice as long as outer.

P2-P4 (Fig. 4B-D) with anterior spinule row on praecoxae; with strongly developed coxae ornamented with spinular rows on both anterior and posterior surfaces as illustrated. Bases with outer seta which is very long in P3; anterior surface with distinct secretory tube-pore and spinules around distal margin. Exopodal segments with distinct hyaline frills, those of P2 with minute spinules along inner margins. Outer spine of P4 exp-1 and exp-2 neither elongate nor recurved at tip. Inner setae of P4 exp-2 and P3-P4 exp-3 distinctly pectinate. Inner setae of P2-P3 enp-1 serrate. P2-P3 enp-2 with 1 distal bipinnate seta. P4 enp-2 with apical bipinnate spine, and short inner spine with flagellate tip; posterior surface with pore. Armature formula of swimming legs as for genus.

P5 (Fig. 4E) with exopod and baseoendopod confluent, forming distinctly bilobate plate; Endopodal lobe cylindrical, with posterior spinular row near inner margin; with 2 spiniform setae, inner one of which fused to segment. Exopodal lobe with very large apical spine with flagellate

tip and 3 short setae along the outer margin. Outer basal seta sparsely plumose. Secretory pores present on anterior and posterior surfaces and along inner margin at transition between short and long spinules.

Sixth legs (P6) represented by a small non-articulating plate on either side, closing off the genital apertures and armed with 1 long distal seta and very long, basally swollen seta subapically (Fig. 1C); anterior surface with 2 rows of tiny spinules. Two secretory tube-pores and 2 blind-ending sac-like structures discernible on either side of the ventral midline. Copulatory pore large, located posterior to genital apertures; paired anterior extensions of copulatory duct well chitinized.

Male (Figs 1D-F; 2B; 3B; 4F-G). Total body length: 415 µm.

Urosomites with pattern of fine spinule rows as shown in Figs. 1D and 3B. Anal operculum (Fig. 1E) more chitinized and pronounced than in ♀. Caudal ramus seta VII apparently not plumose, slightly longer than in ♀ (Fig. 3B).

Rostrum (Fig. 2B) elongate-triangular, with middorsal slit-like pore near proximal margin.

Antennule (Fig. 1F) indistinctly 9-segmented, slender and haplocer; geniculation located between segments 7 and 8; segment 5 with large spinous outgrowth anteriorly, with long aesthetasc on segment 6 and as part of acrothek on segment 9.

P3 (Fig. 4F). Protopod and exopod as in ♀. Endopod 2-segmented; enp-1 slightly more slender than in ♀; enp-2 with additional spinule row on posterior surface; no processes present, apical spine not modified.

P4 (Fig. 4G). Protopod, exopod and enp-1 as in ♀. Joint between endopodal segments modified, allowing for enp-2 to swing medially. Enp-2 with inner spine larger than in ♀, modified into curved claw with flagellate tip; distal spine blunt and slightly shorter than in ♀; posterior surface with tube-pore.

P5 (Figs 1D; 3B) with exopod and baseoendopod confluent, forming bilobate plate as in ♀. Endopodal lobe with 1 short and 1 long pinnate seta; both elements discrete at base; spinules along distal inner margin distinctly shorter. Exopodal lobe with large, pinnate apical spine with flagellate tip, and 3 short setae along outer margin. Outer basal seta long and slender, sparsely plumose. Pore pattern as in ♀.

Sixth legs (Figs 1D; 3B) asymmetrical. One member represented by large articulating plate bearing inner spine, middle naked seta and outer plumose seta; other member with same armature but smaller.

Etymology

The species name is derived from the Latin *serra*, meaning saw, and refers to the serrate anal operculum.

Distribution

Known only from the type locality.

Remark

The sexual dimorphism encountered in the rostrum of both sexes is probably not real and merely the result of an aberration in the holotype ♀.

Stereoxiphos gen. nov.

Synonym

Leptastacus T. Scott, 1906 [partim]: Masry (1970).

Remark

Huys (1992) pointed out various deficiencies in Masry's (1970) description of *Leptastacus operculatus*. In addition to the anal operculum, body size and P5 shape, Masry (1970) attached considerable importance to minor characters such as the absence of sensillae on the rostrum and the slenderness of the antennules in order to differentiate it from *L.* (= now *Cerconeotes*) *constrictus* Lang, 1965. Since he failed to provide adequate illustrations of the male P3 endopod, the anal operculum and the caudal rami in dorsal aspect, the relationships of *L. operculatus* could not unequivocally be resolved by Huys (1992). Having originally assigned it as *species inquirenda* to the genus *Cerconeotes* on the basis of the setation on the P1 exopod, the shape of the fifth leg and the setation of the male P6 (p. 163), Huys (1992) subsequently relegated it to a *species incertae sedis* in the Leptastacidae in a note added in proof (p. 194). Re-examination of the type material revealed that *L. operculatus* should be designated the type species of a new genus *Stereoxiphos*, which shows a close relationship to *Cerconeotes*. The diagnosis below is largely based on our re-examination of the female holotype and paratype; additional information on the male is based on Masry's (1970) illustrations.

Diagnosis

Leptastacidae. Thoracic somites with integumental pattern of cuticular thickenings. Hyaline frill of abdominal somites moderately developed, multilobate and striated. Anal operculum drawn out into long, attenuated, median process. Caudal ramus slightly produced distally, with 3 large spinules at ventral posterior margin; seta IV vestigial and fused to long seta V. Sexual dimorphism in antennule, P3 endopod, P5, P6, and genital segmentation.

Rostrum elongate. Antennule 7-segmented in ♀, with aesthetasc on segment 4 and as part of acrothek on segment 7; unconfirmed in ♂ but probably haplocer and 9-segmented

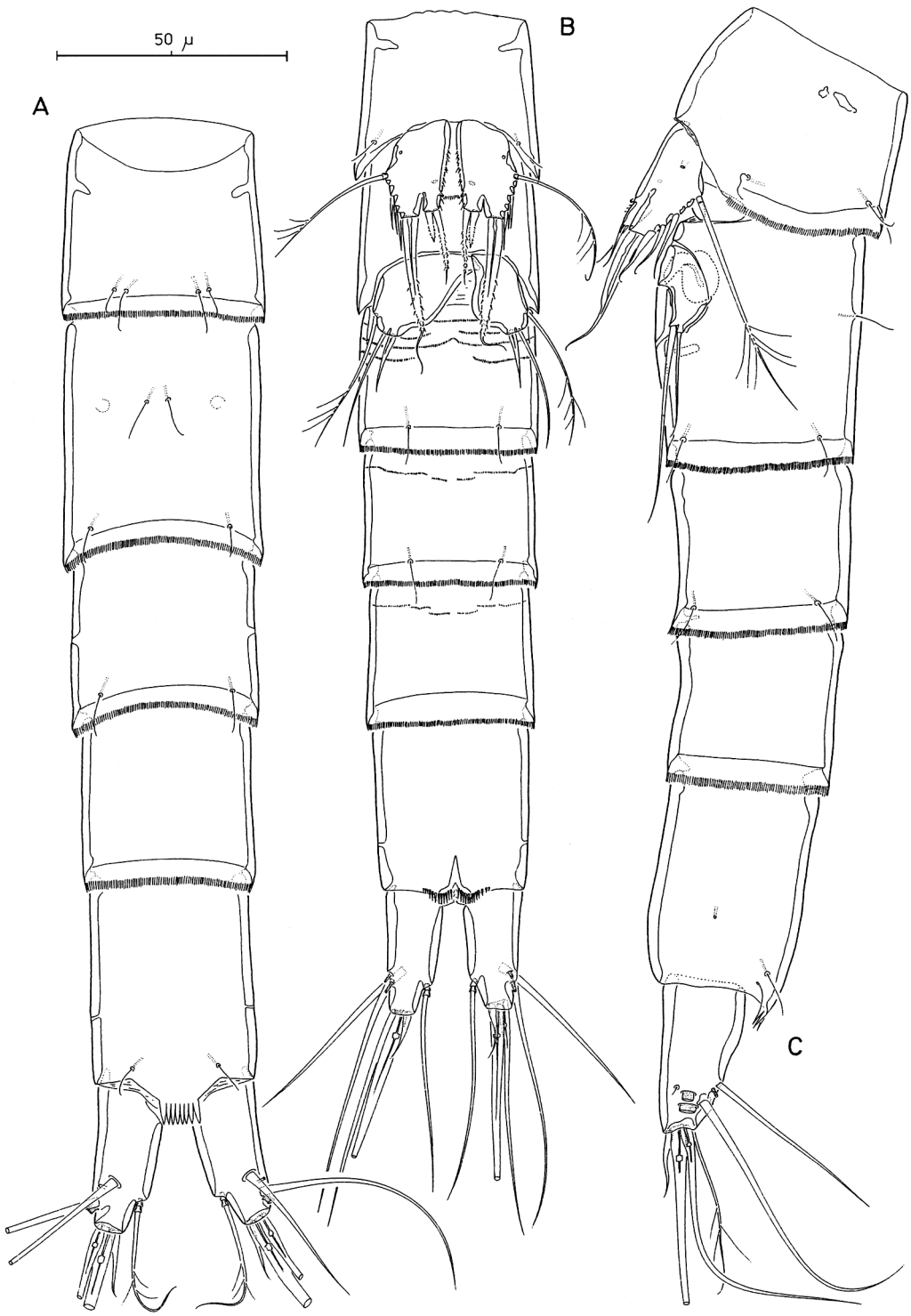

Figure 3. *Aquilastacus serratus* gen. nov. sp. nov. **A.** Urosome ♀, dorsal. **B.** Urosome ♂, ventral. **C.** Urosome ♀, lateral.

Figure 3. *Aquilastacus serratus* gen. nov. sp. nov. **A.** Urosome ♀, vue dorsale. **B.** Urosome ♂, vue ventrale. **C.** Urosome ♀, vue latérale.

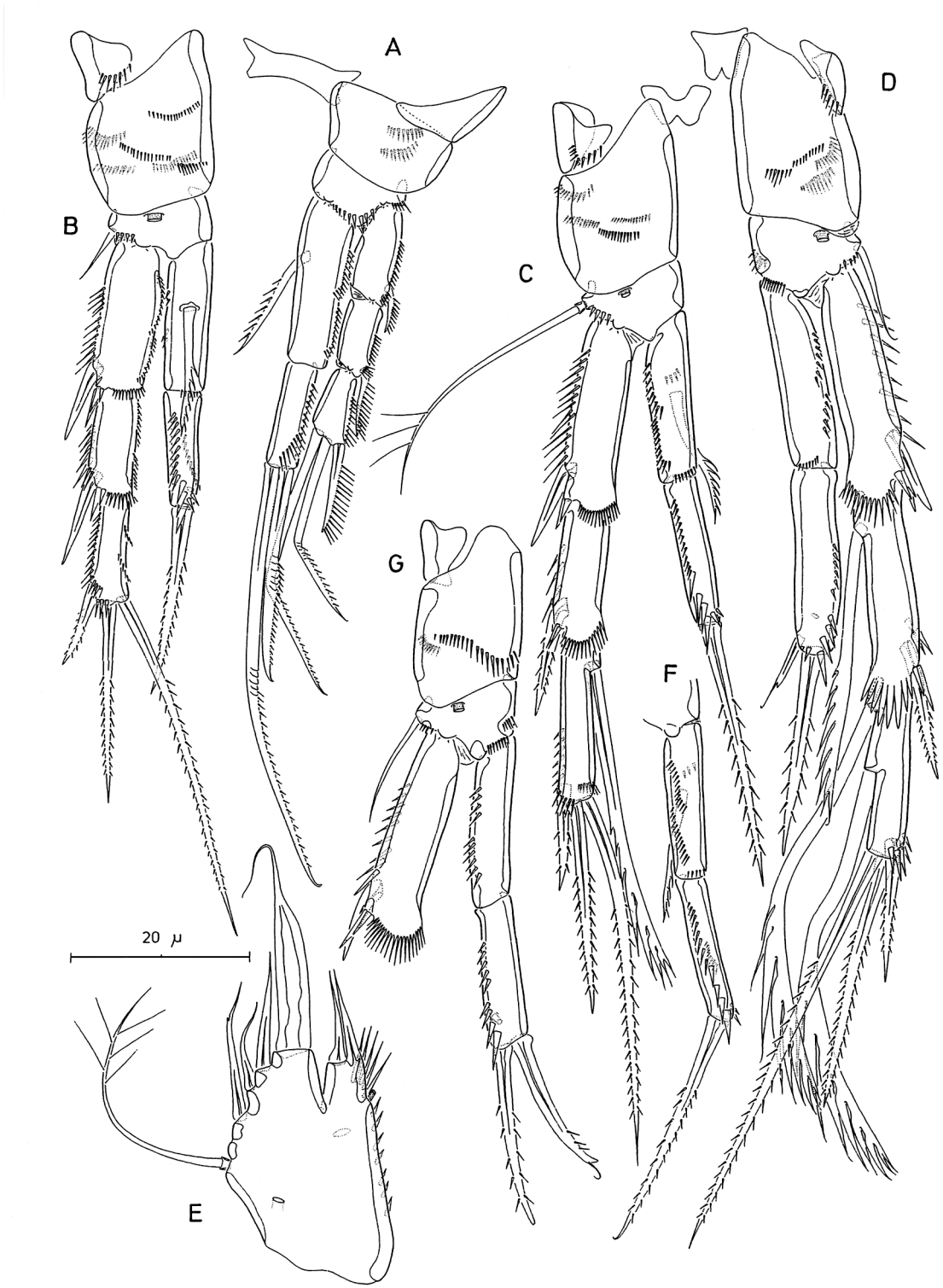

Figure 4. *Aquilastacus serratus* gen. nov. sp. nov. **A.** P1 ♀, anterior. **B.** P2 ♀, anterior. **C.** P3 ♀, anterior. **D.** P4 ♀, anterior. **E.** P5 ♀, anterior. **F.** P3 endopod ♂, anterior. **G.** P4 ♂, anterior [exp-2 and -3 omitted].

Figure 4. *Aquilastacus serratus* gen. nov. sp. nov. **A.** P1 ♀, vue antérieure. **B.** P2 ♀, vue antérieure. **C.** P3 ♀, vue antérieure. **D.** P4 ♀, vue antérieure. **E.** P5 ♀, vue antérieure. **F.** Endopodite de P3 ♂, vue antérieure. **G.** P4 ♂, vue antérieure [exp-2 et -3 omises].

with geniculation between segments 7 and 8. Antenna with allobasis and exopod with 2 distal setae. Labrum without frontal recurved process, not distinctly tri-lobate. Mandibular palp 2-segmented; basis without seta, endopod with 5 setae. Antennary exopod with 2 distal setae. Labrum without frontal dorsally projected spinous process. Maxillipedal syncoxa without seta. Maxillule with exopod and endopod represented by 1 and 2 setae, respectively; arthrite rotated relative to coxa and basis. Maxilla with 2 cylindrical endites on syncoxa; endopod elongate, indistinctly 2-segmented. Maxilliped without syncoxal seta; accessory seta on endopod long.

P1 basis without inner seta. P1 exopod 3-segmented; exp-3 with 3 setae/spines. P1 endopod 2-segmented, not prehensile, longer than exopod; enp-1 without inner seta. Bases of P1-P2 without outer seta. P2-P4 endopods 2-segmented. P3 enp-2 with anterior serrate spine fused to segment. Outer spine of P4 exp-1 elongated and curved. Armature formula of swimming legs:

	Exopod	Endopod
P1	0.0.021	0.011
P2	0.0.021	0.010
P3	0.0.121	0.011
P4	0.1.121	0.110

P3 endopod ♂ with reduced distal spine (possibly fused to enp-2). P5 uniramous, triangular and produced distally; with 4 well developed setae in ♀, 3 in ♂. Female P6 with 1 long, 1 short and 1 vestigial seta. Male P6 with 2 setae.

Type and only species

Leptastacus operculatus Masry, 1970 = *Stereoxiphos operculatus* (Masry, 1970) comb. nov.

Etymology

The generic name is derived from the Greek στερεος meaning solid, and ξιφος, meaning sword, and refers to the robust, spinous middorsal projection of the anal operculum. Gender: masculine.

Stereoxiphos operculatus (Masry, 1970) comb. nov.

Synonyms

Leptastacus operculatus Masry, 1970; *Cerconeotes operculatus* (Masry, 1970) Huys (1992).

Type locality

North Israel, Akhziv (mediterranean coast); intertidal, well sorted sand.

Material examined

Holotype ♀ dissected on 6 slides; paratype ♀ (erroneously labelled ♂) mounted *in toto*; collected at type locality (station 9) by D. Masry, 31 October 1968. The precise history of the type material is puzzling. Masry (1970) claimed to have found one female and one male. His illustrations (Fig. 11-51, 53, 54) of the P3 endopod, P5 and P6 appear to substantiate that he had a male but inspection of the only male paratype slide proved it to contain a female instead. Except for the body length measurement all observations below are based on the holotype which was restored from its original slide and subsequently dissected.

Redescription

Female (Figures 5A-E; 6A-F; 7A-C). Total body length: 365 µm (based on paratype).

Body slender, cylindrical (Fig. 5A), yellowish; intersomitic boundaries well developed. Integument smooth; on P2- to P5-bearing somites moderately chitinised only in delimited areas interspersed with membranous inserts. Hyaline frill of cephalothorax and somites bearing P2-P4 reduced, of abdominal somites moderately developed, multilobate and finely striated (Figs 5A & 7A-C). Cephalothorax tapering anteriorly, no distinct difference in width between cephalothorax and free body somites; no distinct separation between prosome and urosome. Genital-double somite about as long as wide (Figs 5A, E & 7B), without traces of original subdivision; with genital apertures located in anterior half (Fig. 5E). Anal somite short, about 0.8 times as long as wide (Fig. 7B), with strongly developed anal operculum drawn out into long, attenuated middorsal extension which is slightly longer than the anal somite length (Figs 5A & 7B, C); ventral posterior margin with spinules medially (Fig. 7A).

Caudal rami slightly divergent (Fig. 7A-B), about 2.9 times as long as maximum width; tapering in distal quarter (Fig. 7A). Armature consisting of 7 setae: seta I vestigial; setae II and III long and naked; seta IV vestigial, fused basally to seta V; seta V strongly developed, as long as one-third the body length, with fracture plane; seta VI vestigial; seta VII tri-articulated at base, sparsely plumose. Distal portion of ramus slightly produced posteriorly so that fused setae IV and V arise from dorsal surface; ventral posterior margin with 3 large spinules. Lateral surface with 2 tube-pores; no oblique spinular row on dorsal surface.

Rostrum (Fig. 5B-C) well developed, elongate, lanceolate, about as long as first antennulary segment, free at base; with 2 sensilla; no median pore discernible.

Antennule 7-segmented, slender (Fig. 5A); with long aesthetasc (80 µm) on segment 4; segment 7 with apical acrothek consisting of 2 long setae fused basally to short aesthetasc (22 µm). Armature formula: 1-[1], 2-[9+1 plu-

mose], 3-[5], 4-[1+(1+ae)], 5-[1], 6-[3], 7-[7+acrothek]. Tube-pores present on segments 1 (Fig. 5C) and 2.

Antenna (Fig. 5B). Coxa small, without ornamentation. Allobasis about 3 times as long as maximum width; without traces of original segmentation. Exopod 1-segmented, small; with 2 short apical setae. Distal endopodal margin with 2 geniculate setae, 2 pinnate spines and a large geniculate spine which is swollen at the base, fused to a dwarfed seta and ornamented with spinules around the geniculation; inner endopodal margin with 2 spines and covered by a few spinules.

Mandibular palp 2-segmented (Fig. 5B); basis without seta; endopod with 1 proximal inner seta, 2 short outer setae and 2 confluent apical setae.

Labrum strongly developed (Fig. 5B); without spinous process on anterior surface; covered with long spinules anteriorly and medially, and flanked by lobes with smaller spinules laterally.

Maxillule with arthrite rotated at right angle relative to main axis. Praecoxal arthrite with 7 spines around distal margin; without anterior surface setae. Coxal endite with 1 bare and 1 pinnate seta. Basis with 5 setae around distal margin. Rami completely incorporated into basis; exopod represented by 1, endopod by 2 setae.

Maxilla. Syncoxa with 2 cylindrical endites closely adpressed to allobasis; proximal endite with 1 discrete and 2 basally fused pinnate spines; distal endite with 3 free elements. Allobasis drawn out into long unipinnate claw; with 2 accessory setae and 1 secretory tube-pore. Endopod indistinctly 2-segmented; with 1 seta on enp-1; enp-2 with 3 basally fused apical setae.

Maxilliped (Fig. 5D) with few spinules but without seta on syncoxa. Basis elongate, with spinules along outer and inner margins. Endopod with sigmoid pinnate claw and long, slender accessory seta.

P1-P4 (Fig. 6A-E) with 3-segmented exopods and 2-segmented endopods; endopods shorter than exopods except for P1 endopod. Successive legs increasing in length.

P1 (Fig. 6A). Praecoxa represented by a bare sclerite. Coxa strongly developed, with 2 spinular rows on posterior and 1 spinular row on anterior surface. Basis distinctly shorter than coxa; inner and outer setae absent; with spinules around anterior distal margin, and large pore on anterior surface. Exopod 3-segmented; outer margin of segments spinulose; outer spines of exp-1 and exp-2 unipinnate; exp-3 with outer unipinnate spine (with long stiff pinnules) and 2 geniculate setae distally, innermost of which longest. Enp-1 1.15 times as long as enp-2; without inner seta; with spinular row along inner margin and few spinules along outer margin. Enp-2 with spinular row along outer margin and 2 geniculate setae distally, inner one longest.

P2 - P4 (Fig. 6B-E) with strongly developed coxae ornamented with spinular rows as illustrated. Bases of P2 without, of P3-P4 with outer seta; all with large pore on anterior surface and along inner margin; with few spinules near outer distal corner and around articulation with endopod. Inner setae of P4 exp-2 and P3-P4 exp-3 pectinate [pectines present but not shown for P4 exp-3 due to different orientation: Fig. 6E]. Hyaline frills between exopodal segments well developed. Outer spine of P4 exp-1 elongate and recurved at tip. P3 enp-2 with long, distal bipinnate seta and shorter, subdistal, anteriorly displaced, pectinate spine fused to segment (Fig. 6D). P2 and P4 endopods with outer lateral pore on enp-2 (arrowed in Fig. 6B, E). P4 enp-2 with apical bipinnate spine, and short inner spine. Armature formula of swimming legs as for genus.

P5 (Figs 6F; 7A, C) with exopod and baseoendopod confluent, forming triangular, distally produced plate; with 2 long setae along inner margin, 1 short and 1 sparsely plumose seta along outer margin; with 3 pores on anterior surface and 1 at apex; distal part of outer margin with membranous flange.

P6 represented by a triangular non-articulating plate on either side, closing off the genital apertures and armed with 1 long outer seta, 1 middle setule and 1 short inner seta (Fig. 5E). Two secretory tube-pores and 2 blind-ending sac-like structures discernible on either side of the ventral midline. Copulatory pore large, located slightly posterior to genital apertures; paired anterior extensions of copulatory duct relatively small.

Male. Masry's (1970) description is brief and his illustrations contain several ambiguities, possibly because some of them were not based on a male specimen. For example, the antennule is clearly not geniculate, which could indicate that he either mislabelled the figure or had based it on the female paratype that was inadvertently labelled as the male (see above). His statement that the anal operculum is larger than in the female and reaching past the halfway line of the caudal rami also requires confirmation. Our observation of the two females showed that the opercular extension is much longer than figured by Masry (1970: Fig. 10-48) and, consequently, that this structure is probably not sexually dimorphic. Another difference attributed to the male concerns the presence of only "... two long dorsal sub-terminal setae..." on the caudal ramus but this is contradicted by his own illustrations (Fig. 11-59, 59') which show three dorsally directed elements (II, III, VII) as in the female.

Masry (1970) described the distal setae on the male P3 endopod as "... much shorter than their equivalent in the female." It appears from his illustration (Fig. 11-51) that the inner seta is radically reduced. This element is almost certainly the equivalent of the anteriorly displaced subdistal seta in the female which forms a short, barbed apophysis in males of the genera *Belemnopontia* Huys, *Schizothrix*,

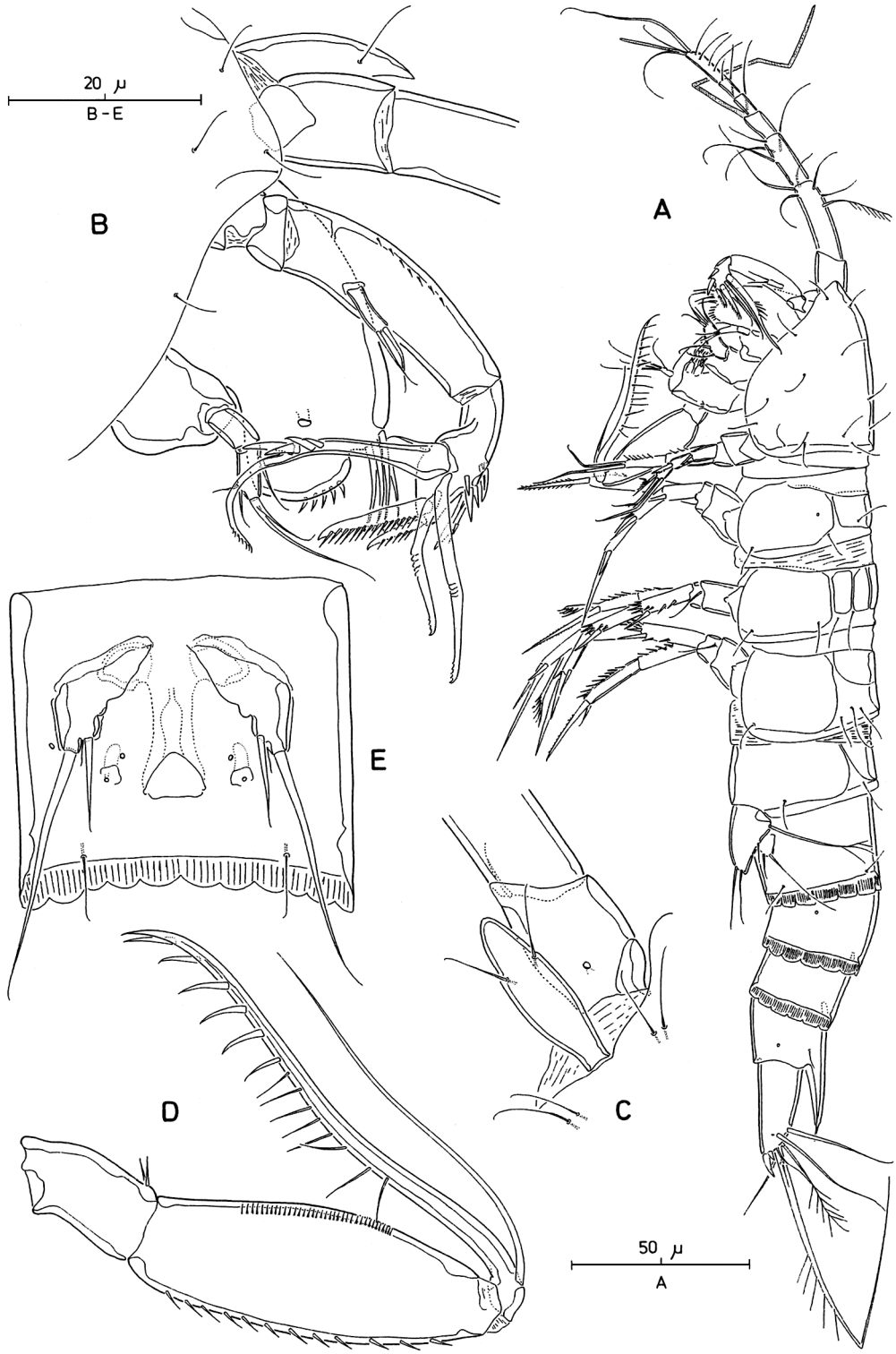

Figure 5. *Stereoxiphos operculatus* (Masry, 1970) comb. nov. (♀). **A.** Habitus, lateral. **B.** Rostrum, antennulary base, antenna, labrum and mandible, lateral. **C.** Rostrum and first antennulary segment, dorsal. **D.** Maxilliped. **E.** Genital double-somite, ventral.

Figure 5. *Stereoxiphos operculatus* (Masry, 1970) comb. nov. (♀). **A.** Habitus, vue latérale. **B.** Rostre, base antennulaire, antenne, labre et mandibule, vue latérale. **C.** Rostre et premiers articles antennulaires, vue dorsale. **D.** Maxillipède. **E.** Somite double génital, vue ventrale.

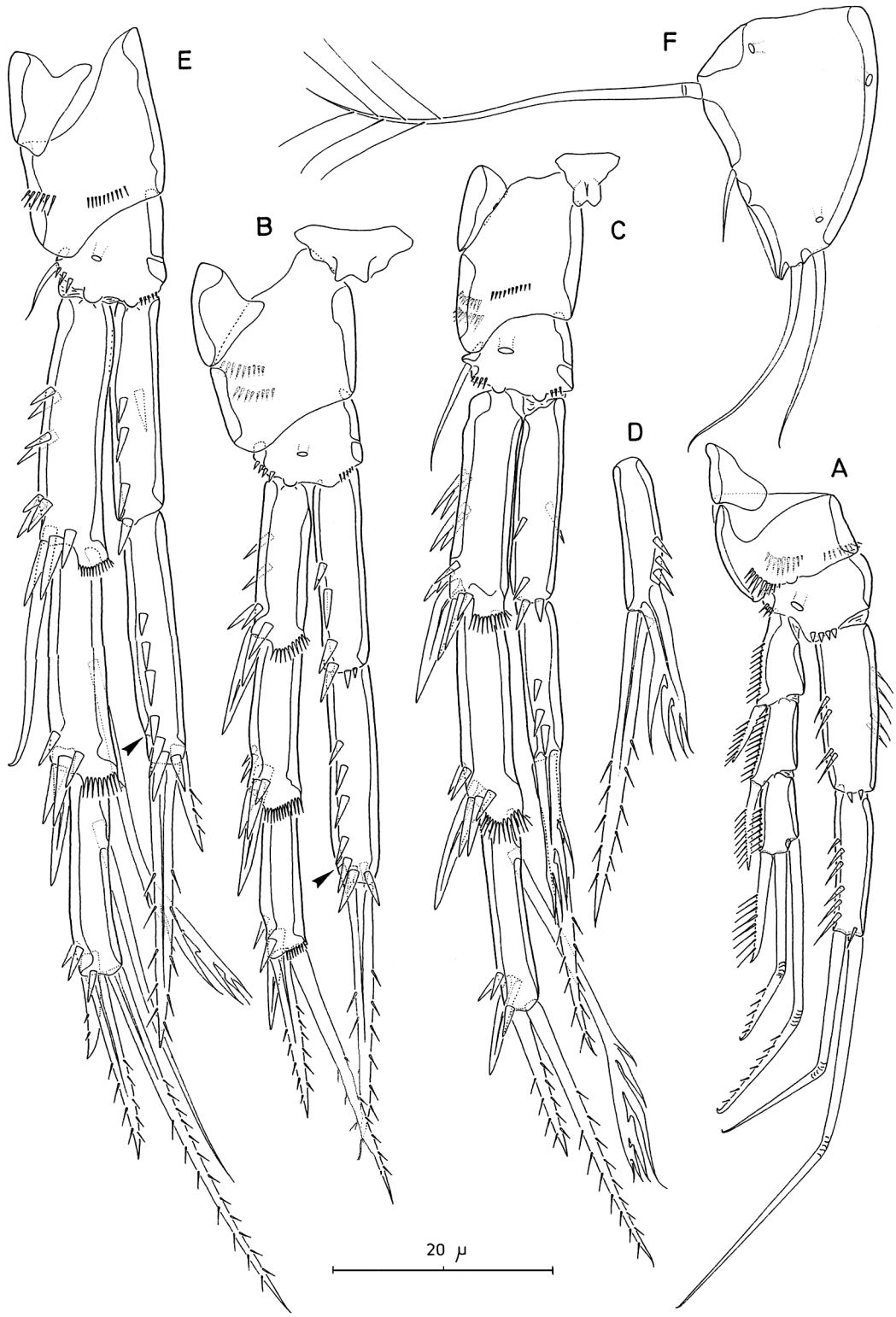

Figure 6. *Stereoxiphos operculatus* (Masry, 1970) comb. nov. (♀). **A.** P1, anterior. **B.** P2, anterior. **C.** P3, anterior. **D.** P3 endopod, lateral. **E.** P4, anterior. **F.** P5, anterior. [Arrows indicating lateral pores on endopods].

Figure 6. *Stereoxiphos operculatus* (Masry, 1970) comb. nov. (♀). **A.** P1, vue antérieure. **B.** P2, vue antérieure. **C.** P3, vue antérieure. **D.** Endopodite de P3, vue antérieure. **E.** P4, vue antérieure. **F.** P5, vue antérieure. [Les flèches indiquent les pores latéraux sur les endopodites].

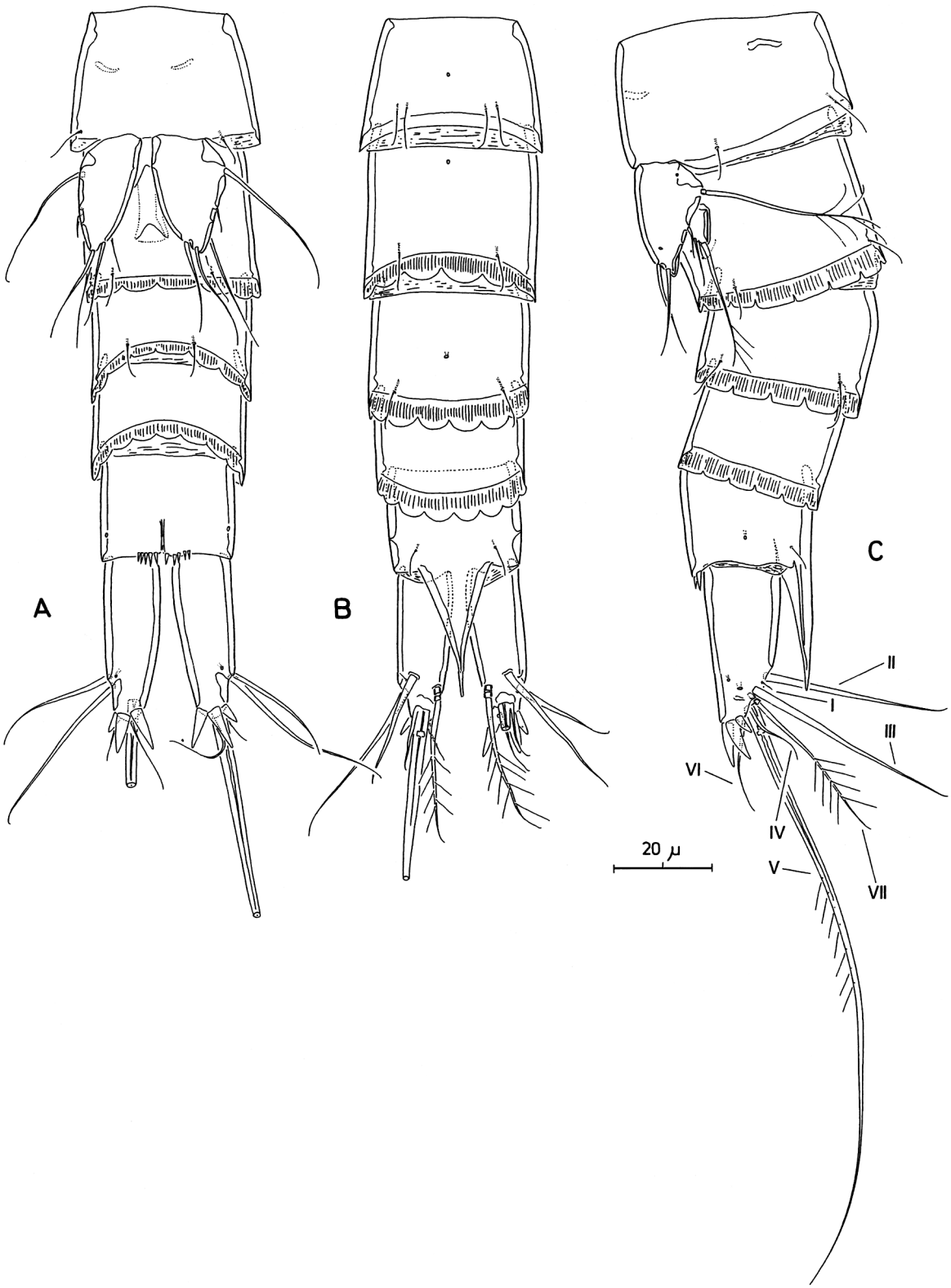

Figure 7. *Stereoxiphos operculatus* (Masry, 1970) comb. nov. (♀). **A.** Urosome, ventral. **B.** Urosome, dorsal. **C.** Urosome, lateral.

Figure 7. *Stereoxiphos operculatus* (Masry, 1970) comb. nov. (♀). **A.** Urosome, vue ventrale. **B.** Urosome, vue dorsale. **C.** Urosome, vue latérale.

Cerconeotes and *Psammastacus* (Mielke, 1982, 1983; Huys, 1992). The only problem with this interpretation is that in these genera the subdistal modified element is typically positioned near the outer distal corner, adjacent to the longer distal spine, whereas in *S. operculatus* it appears to arise from the inner distal corner. Since the subdistal apophysis is usually fused to the anterior surface of the segment (e.g. Huys, 1992: Fig. 34D; note that the figures, not the legends, of Figs 33-34 were inadvertently transposed in this publication), slight changes in the angle of mounting and/or observation may account for this positional discrepancy. It is also possible that the endopod was accidentally rotated but this is less likely since Masry did not dissect his specimens; however, this seems to be the only plausible explanation for his erroneous observation of the ♂ P4 endopod (see below).

The male P5 illustrated by Masry is similar in shape to that of the female but possesses only 3 setae instead of 4. Masry maintained that it is the terminal seta that is lost in the male but comparison with the sexually dimorphic pattern encountered in other related genera it appears more likely that the inner one is absent (= seta *b* according to Huys' (1992: Fig. 21) terminology). The male P6 has 2 setae and resembles the condition found in *Psammastacus* and *Cerconeotes*. Masry's (1970) illustration lacks the detail to confirm whether the middle vestigial element (as found in *Belemnopontia* and *Schizothrix*) is present or not.

Distribution

Known from type locality only.

Remarks

There are some significant discrepancies between our redescription and Masry's (1970) text and illustrations, all of which can be attributed to observational errors in the original description: (1) the abdominal somites do not bear a "... tight band of fine hair along their posterior margin"; Masry was obviously referring to the striated multilobate hyaline frills (Fig. 7); (2) the antennary exopod bears 2 apical setae, not 1 as originally illustrated (his Fig. 11-58); (3) Masry figured a long outer basal seta on the P2 of both sexes but according to our observations this seta is absent, as in the majority of Leptastacidae; (4) the outer spine on P4 exp-1 in the female is much shorter in the original description; surprisingly, Masry figured the correct length for the right male P4 (his Fig. 11-52') but not for the left one (his Fig. 11-52); (5) Masry illustrated P4 enp-2 with a short outer spine and a long distal spine; this mirrored orientation (which was consistently figured for both sexes) indicates that he had accidentally rotated the endopod (or at least enp-2) by 180° in his mount (cf. Fig. 6E for correct orientation).

Discussion

Relationships of Aquilastacus gen. nov.

The close affinity between *Arenocaris* and *Aquilastacus* is undeniable. The strongest evidence for this sistergroup relationship is provided by the unique sexual dimorphism expressed in the P4 endopod (Fig. 4D, G). In both genera the joint between the proximal and distal segment is modified [although not always clearly visible externally; but see *Arenocaris reducta* Huys, 1992 (Huys, 1992: Fig. 30D)] so that the distal part of the ramus can swing medially. The distal armature elements of P4 enp-2 are modified in a similar way with the inner one, which is short and bare in the female, being transformed into a curved flagellate claw in the male.

A similar, but not homologous, medially directed endopod is found in the genus *Arenotopa* Chappuis & Rouch (e.g. Wells & Rao, 1987: Fig. 131g). *Arenotopa* males also have a modified hinge between the elongated proximal segment and the modified distal segment, however allometric growth of the terminal part has altered the original insertion sites of the two distal setae. The outer distal seta is positioned along the outer margin at about 1/3 distance from the tip, while the inner distal seta inserts along the inner margin near the apex of the segment. No allometric growth has occurred in *Arenocaris* or *Aquilastacus* so the distal setae have not moved away from their original position. Based on Cottarelli & Venanzetti's (1989) drawings of *Psamathea nautarum*, Huys (1992) suggested the possibility of a similar modification in *Psamathea*. Examination of the type species and *P. brittanica* shows the modification to be of another kind, involving the size reduction of the distal segment and the inner seta (Huys et al., 1996*a*). This sexual dimorphism is also found in males of *Paraleptastacus* where the subdistal element can be considerably reduced in length.

A second synapomorphy shared by *Arenocaris* and *Aquilastacus* is displayed in the P3 endopod. Females of both genera lack the outer subdistal seta. As a result of this secondary absence, there is also no sexual dimorphism on the endopod in the male since it is this element that is modified in most Leptastacidae.

Finally, both genera also share a similar caudal ramus type although some important setal differences occur. The ramus is typically constricted in its distal quarter at the level where the dorsal seta VII inserts. In *Arenocaris*, however, seta III is modified into a tubular element, seta IV is extremely reduced, and both setae IV and V have lost their fracture planes (Table 1).

In general, *Aquilastacus* is more plesiomorphic than *Arenocaris* in most character states (Table 1). Notable exceptions are the loss of the outer basal seta of P1, the

Table 1. Comparison between *Arenocaris* and *Aquilastacus* gen. nov.
Tableau 1. Comparaison entre *Arenocaris* and *Aquilastacus* gen. nov.

		Arenocaris	*Aquilastacus* gen. nov.
Rostrum shape		elongate	triangular
Hyaline frill urosomites		rectangular lappets	finely serrate
Genital field ♀ P6		3 setae, outermost longest	2 setae, innermost longest
Anal operculum		weakly developed, smooth	with strong pectinate plate
Caudal ramus	seta III	swollen, tubular	normally developed
	seta IV	vestigial	well developed
	setae IV-V	without fracture planes	with fracture planes
Mandibular palp		1-segmented	2-segmented
P1 outer basal seta		present	absent
P1 exopod		2-segmented	3-segmented
P2-P3 endopods	segmentation	1-segmented	2-segmented
	armature	010	1.010
P5 baseoendopod and exopod ♀/♂		free	fused

confluent fifth legs and the reduction in the number of setal elements on the female P6. Both genera can be distinguished on the basis of the characters listed in Table 1.

Relationships of Stereoxiphos gen. nov.

Based on similarities in swimming leg armature (except P4 endopod) and shape of P5, Masry (1970) recognized a relationship between *L. operculatus* and *L. constrictus*, which was originally described from the Californian coast (Lang, 1965) but subsequently also recorded from San Juan Island, Washington State (Gray, 1968) and Malaysia (Renaud-Mornant & Serène, 1967). Differentiating characters employed by Masry (1970) to justify the proposal of his new species included body length, the detailed morphology of the male P5, slenderness of the antennule, absence/presence of rostral sensillae, shape and size of anal operculum, and armature of caudal rami. Although some of these characters are unreliable and others debatable, the present redescription leaves no doubt about the validity of *L. operculatus* but calls into question its current position in the Leptastacidae.

Huys (1992) removed *L. constrictus* and three other species from the genus *Leptastacus* and assigned them to a new genus, *Cerconeotes*. In addition, he also placed four inadequately described taxa as *species inquirendae* in the genus: *L. nichollsi*, *L. euryhalinus*, *L. waltairensis* and *L. operculatus*. Huys (1992) questioned the absence of the inner seta on P1 enp-1 in Masry's description but our re-examination has proven this suspicion to be unfounded. The loss of this element has evolved convergently in the genus *Psamathea* which has no relationship with *L. operculatus*, but which is most likely the sistergroup of *Paraleptastacus* Wilson (Huys et al., 1996*a*). Despite other, more significant, obstacles, Huys (1992) placed the species in *Cerconeotes* based on the setation of the P1 exopod, the shape of the P5 and the presence of only 2 setae on the male P6. However, after a cursory examination of the type material at the galley proof stage, Huys (1992: 194) revised his earlier opinion and ranked *L. operculatus* as *species incertae sedis* in the family.

Leptastacus operculatus shares three apomorphies with a well supported clade accommodating *Schizothrix*, *Belemnopontia*, *Cerconeotes* and *Psammastacus* (Huys, 1992): (1) the subdistal serrate spine of P3 enp-2 is fused to the anterior surface of the segment in the female (Fig. 6C-D) and forms a barbed apophysis in the male [although Masry's (1970) description of the male provides insufficient detail to verify the latter part of the apomorphy, the reduced size of this element is here interpreted as circumstantial evidence]; (2) the outer spine of P4 exp-1 is secondarily elongated and acutely recurved at the tip in both sexes (Fig. 6E) [Huys (1992) postulated that this spine had the same shape and size before it was secondarily lost in *Psammastacus*]; and (3) the rear margin of the caudal ramus forms a posteriorly directed spinous process so that setae IV-VI arise from a dorsal rather than a terminal position (Fig. 7C). The caudal ramus in *L. operculatus* supports Huys' (1992) earlier assumption that this appendage is in a state of reduction in *Cerconeotes*, forming an intermediate stage between the strongly produced caudal ramus type in *Schizothrix* and *Belemnopontia*, and the short caudal ramus without distal process in *Psammastacus*. *L. operculatus* represents yet another transitionary stage in this evolutionary series by showing limited extension of the distal part of the ramus.

The three species of *Schizothrix* occupy the most basal position in this clade. The common ancestry of *Leptastacus operculatus* and the three residual genera is supported by:

(1) the loss of the inner basal seta on the mandibular palp; (2) the loss of the inner seta on P2-P3 enp-1; (3) the loss of the proximal inner seta on P4 exp-3; and (4) the loss of seta *c* in the female P5 and seta *b* in the male P5 [see Huys (1992: Fig. 21) for setal coding]. Within this group the genus *Belemnopontia* is the only taxon that has retained the ancestral armature pattern on the P1 exopod. In species of *Cerconeotes* and *Psammastacus*, as well as in *L. operculatus* (Fig. 6A), the proximal outer spine of the distal segment is lost, resulting in a [021] pattern. These taxa have also a more reduced P5 in the female as a result of the loss of setae *a* and *e* which are retained in *Belemnopontia*, albeit in a state of reduction. Huys (1992) showed that *Cerconeotes* and *Psammastacus* are sistertaxa, their common ancestry being supported by the presence of only one spine on P4 enp-2 and the modification of caudal ramus seta V which is tubular, short and ending in an apical opening. *Leptastacus operculatus* does not share either of these synapomorphies, showing 2 elements on P4 enp-2 (Fig. 6E) and a normally developed seta V (Fig. 7C) instead. The species can readily be identified by the very large middorsal projection arising from the anal operculum which is a unique autapomorphy in the family. Another unusual character is the absence of the inner seta on P1 enp-1. This element is present in all other genera with the exception of *Psamathea*, but in this genus the P1 endopod is prehensile. The latter genus also shows a complex internal pattern of chitinous plate-like reinforcements on all body somites (Huys et al., 1996*a*), however in *L. operculatus* these integumental structures are restricted to the thoracic somites bearing P2-P5. On the basis of the arguments presented above we designate *L. operculatus* as the type and only species of a new genus *Stereoxiphos*, which holds a transitionary position between *Belemnopontia* and the *Cerconeotes-Psammastacus* clade.

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