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Taxonomy of Oncaeidae (Copepoda, Poecilostomatoida) from the Red Sea. III. Morphology and phylogenetic position of *Oncaea subtilis* Giesbrecht, 1892

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Abstract

Both sexes of *Oncaea subtilis* Giesbrecht, 1892, a small oncaeid species commonly occurring in temperate and tropical regions, are redescribed on the basis of material from the Red Sea. It is placed in a new monotypic genus, *Monothula*, on the basis of the loss of the outer spine on the third segment of the endopod of legs 2–4, and the presence of a single dorsal egg-sac, which is attached medially to the genital double-somite. The latter character is unique among oncaeids. The geographical distribution of *M. subtilis* comb. nov. is reviewed, and additional taxonomic data based on material from the eastern Mediterranean, the Arabian Sea and the eastern Indian Ocean are presented. The phylogenetic relationships of *M. subtilis* within the Oncaeidae are discussed.

Introduction

Small copepod species of the family Oncaeidae are common members of marine planktonic communities, occurring in all depth zones of the world's oceans from the epipelagic to the bathypelagic. Their great ecological importance, which is reflected both in high numerical abundance (e.g. Paffenhöfer, 1983; Böttger, 1987; Cowles et al., 1987) and species diversity (e.g. Böttger-Schnack, 1988, 1994; Kršinić, 1998), has been increasingly recognized during the past 2–3 decades [for review of relevant literature see Böttger-Schnack (1999)].

Because of their great morphological similarity, oncaeid species are very hard to distinguish, and detailed morphological descriptions, including mouthparts and labrum, are often required for unequivocal identification. While many of the larger species have recently been described or redescribed in great detail (Heron, 1977; Heron et al., 1984; Heron & Bradford-Grieve, 1995; Böttger-Schnack & Huys, 1997), the taxonomy of smaller oncaeid species, about 0.5 mm (or less) in length is still inadequate. Many important morphological characters, such as the armature and ornamentation of the mandible and the labrum, which proved to be essential in resolving phylogenetic relationships among oncaeids (Böttger-Schnack & Huys, 1998), are as yet unknown for species belonging to this size category.

The phylogenetic relationships of the Oncaeidae s.str. as defined by Huys & Böttger-Schnack (1997), are currently under review. Preliminary results of a phylogenetic analysis of the 3 genera retained in the family, i.e. *Oncaea* Philippi, 1843, *Conaea* Giesbrecht, 1891, and *Epicalymma* Heron, 1977, identified about 20 monophyletic lineages, to each of which may be attributed generic status (Böttger-Schnack & Huys, 1998). A comprehensive study of the phylogeny of the Oncaeidae is currently in progress and will be published elsewhere.

This paper focuses on one of the monotypic lineages (group 18) recognized by Böttger-Schnack & Huys (1998). Its sole representative, *Oncaea subtilis* Giesbrecht, 1892, is a small species commonly found at lower latitudes (Malt, 1983a). Both sexes are redescribed in detail on the basis of material from the Red Sea, eastern Mediterranean, Arabian Sea and eastern Indian Ocean. *Oncaea subtilis* is transferred to a new genus, *Monothula*, on account of the loss of the outer spine on the third segment of the endopod of legs 2–4 and the unique presence of a dorsal median egg-sac. The phylogenetic relationships of *Monothula* with other Oncaeidae are discussed.

Materials and methods

Monothula subtilis was collected using a multiple opening-closing net (Weikert & John, 1981) with a mesh size of 0.055 mm during cruise 5 of R/V *Meteor* in various locations of the Red Sea, the eastern Mediterranean and the northern Arabian Sea (cf. Fig. 1 of Böttger-Schnack, 1994). Samples collected in the eastern Indian Ocean during cruise 76-5 of *R/V Hakuho Maru* with a Motoda net, mesh size 0.10 mm, were also examined. The plankton was initially fixed in 4% formaldehyde-seawater solution buffered with hexamethylene tetramine, and transferred after ca 2 years into a preservation fluid of 5% propylene glycol, 0.5% propylene phenoxetol and 94.5% filtered seawater (Steedman, 1976). Specimens were dissected in lactic acid, mounted on slides in lactophenol and sealed with high-quality nail-varnish. All figures have been prepared using a camera lucida on a Leitz Dialux differential interference contrast microscope.

Total body length and the ratio of prosome–urosome (excluding caudal rami) were calculated as the sum of the middorsal lengths of individual somites measured in lateral view. In the case of telescoping somites, these lengths were measured from the anterior to the posterior margin. This approach differs from that traditionally used in oncaeid taxonomy, where the telescoping of somites is not considered in length measurements. In order to make measurements of the species in this paper comparable to those of previous descriptions, length data were obtained by the traditional method as well (i.e. measured dorsally from the tip of prosome to the distal end of the caudal ramus), and are given in square brackets.

Descriptive terminology for body and appendages follows that of Huys & Boxshall (1991). Abbreviations used in the text are: ae – aesthetasc; CR – caudal rami; enp – endopod; exp – exopod; exp(enp)-1(-2, -3) – to denote the proximal (middle, distal) segment of a ramus; P1–P6 – first to sixth thoracopods. Oncaeidae typically exhibit pores and other integumental structures (e.g. pits, scales) on the body surface, but only those discernible with a light microscope were figured or mentioned.

Reference material is deposited in the collections of The Natural History Museum, London (NHM), and the Zoologisches Institut und Museum der Universität Hamburg (ZMH).

The phylogenetic software package PAUP 3.1.1, written by David Swofford of the Laboratory of Molecular Systematics, Smithsonian Institution (Swofford, 1993), was used to analyse phylogenetic relationships within the Oncaeidae. It has been assumed for the majority of characters that oligomerization is the principal trend of evolutionary transformation within the Copepoda (Huys & Boxshall, 1991). Hence, most characters were set irreversible which suppresses reversals at the expense of introducing extra convergences and consequently increasing tree length. The BRANCH AND BOUND search procedure was used with accelerated character transformation (ACCTRAN) and tree-bisection-reconnection (TBR) branch swapping.

Systematics

Order Poecilostomatoida Thorell, 1859
Family Oncaeidae Giesbrecht, 1892
Genus *Monothula* gen. nov.

Diagnosis: Oncaeidae. Body cyclopiform, prosome elongate. P2-bearing somite without dorsoposterior projection in female. Cephalosome without lateral lobate extensions. Genital double-somite in female showing distinct bilateral swelling in middle part, not swollen dorsally; with several transverse spinule rows ventrally in midregion. First and second postgenital somites large, longer than anal somite. Anal somite with wide anal opening; vestigial operculum with minute spinules. Exoskeleton moderately chitinized.

Sexual dimorphism in antennule segmentation and armature, maxilliped, genital segmentation and ornamentation, P5, and P6; slight modifications also present in P1–P3 endopods and caudal rami.

Antennule 6-segmented in female, with armature formula 1-[3], 2-[8], 3-[5], 4-[3+ae], 5-[2+ae], 6-[6+(1+ae)]; 4-segmented in male, with formula 1-[3], 2-[8], 3-[4], 4-[11+2ae+(1+ae)]. Distalmost seta of female segment 3 absent in male. Proximal aesthetascs short and delicate.

Antenna prehensile. Enp-1 without projection on outer margin; inner margin with denticular row. Enp-2 longer than enp-1; posterior surface with double row of spinules; lateral armature consisting of 3 bare setae (IV reduced) and 1 long spiniform seta with long spinules (III); distal armature consisting of 4 strong setae

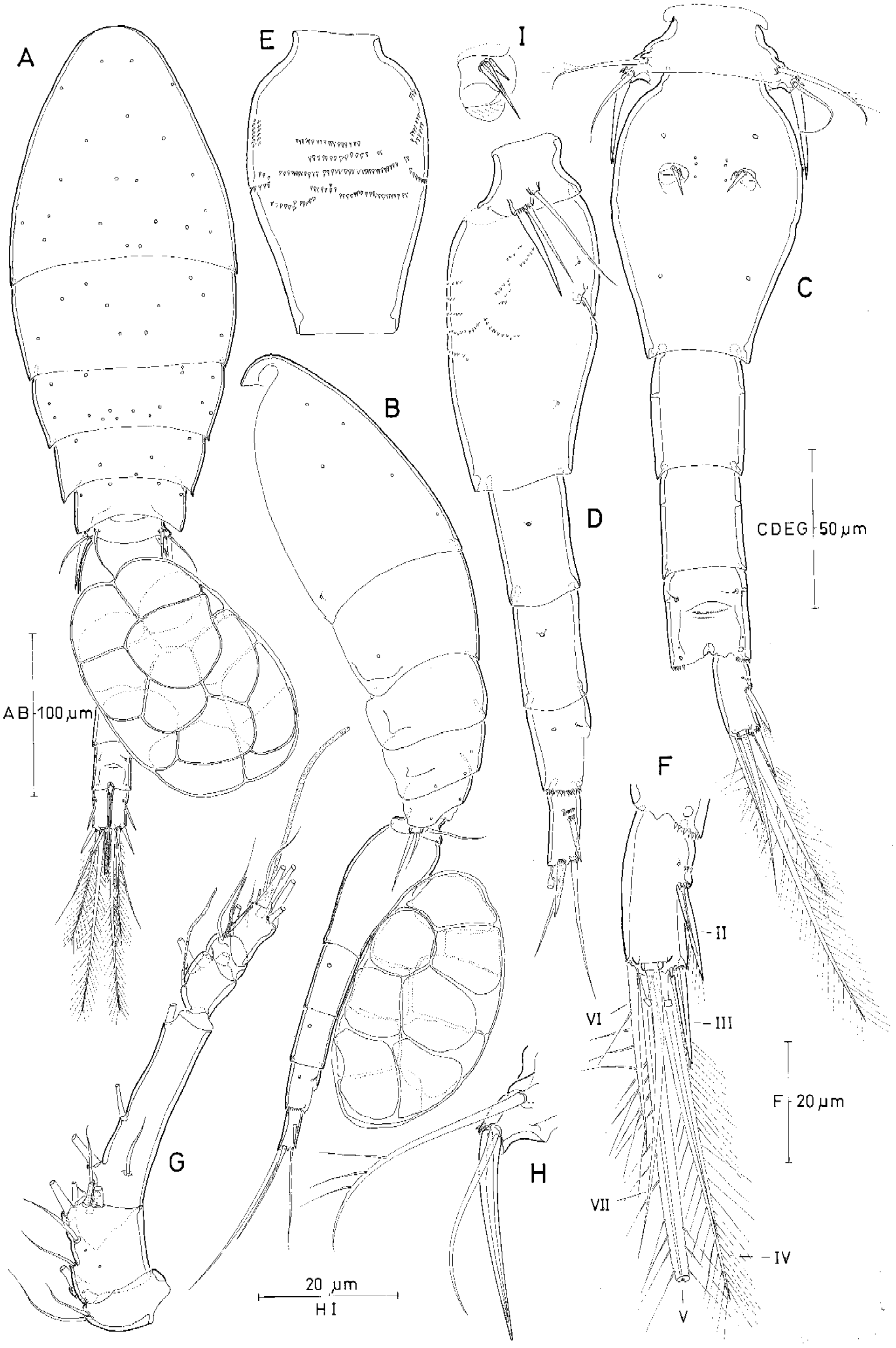

Figure 1. *Monothula subtilis* (Giesbrecht, 1892) comb. nov. Female. (A) Habitus, dorsal; (B) same, lateral (appendages omitted); (C) urosome, dorsal; (D) urosome, lateral, ventro-anterior margin slightly damaged; (E) genital double-somite, ventral; (F) caudal ramus, dorsal, setae are numbered using Roman numerals; (G) antennule; (H) P5, dorsal; (I) P6.

(A–D), ornamented with long spinules bilaterally, and 3 short, bare setae (E–G), much shorter in length than setae A–D.

Labrum distinctly bilobate. Lobes with 3–4 marginal teeth apically flanked by row of setules (outer) or small spinules (inner). Median concavity membranous, with anterior patch of overlapping spinules. Posterior face with group of 3 large pores near apical margin of each lobe; with 2 sclerotized teeth medially. Anterior face without paired integumental pockets or slit-like pores; spinular rows present.

Mandible with 2 blades and 3 setae. Seta A as long as blade B. Blades fused basally along posterior surface; dorsal concavity of B cupping ventral basal process of C. Blade C spinulose along entire dorsal margin and with few surface setules near ventral margin. Element D well developed and setiform. Element E very long, spiniform and multipinnate.

Maxillule weakly bilobate; inner lobe (=praecoxal arthrite) with innermost element not distinctly displaced and outermost element spiniform and naked.

Maxilla with allobasis equal in length to syncoxa.

Maxilliped ♀ ovoid-elongate. Basis without ornamentation on posterior surface; anterior surface with double row of widely dispersed large spinules along palmar margin; both palmar elements setiform and very long, proximal one ornamented with long spinules bilaterally, distal one bipinnate along inner margin; both setae about equally long. Enp-1 completely separated. Enp-2 with long, pinnate claw, rudimentary outer setule and fused unipinnate inner spine.

Maxilliped ♂. Palmar margin forming shallow longitudinal cleft bordered by anterior spinular fringe, developed into small distal flap and posterior multiple rows of coarse, blunt spinules. Anterior surface of basis with transverse spinular row. Proximal palmar seta very long, minutely pinnate. Endopodal claw curved, naked, with hyaline apex.

P1 exopod: Outer and terminal spines with subapical tubular extension, which is lacking on proximalmost spine of exp-3; lateral spines on exp-3 increasing in size distally.

P1 endopod: Enp-2 with long spinules along inner margin. Enp-3 outer spine stout, with broad serrate hyaline flanges; base of distal inner seta concealed beneath long anterior spinous outgrowth of segment.

P2–P4 exopods: Outer spines stout, with broad serrate hyaline flanges; lateral spines on P2 exp-3 (not on P3–P4) slightly increasing in size distally.

P2–P4 endopods 3-segmented: Enp-3 longer than enp-1 and -2 combined; with small conical processes on P2–P3. Enp-3 inner distal spine short in P2–P3, much longer in P4, with broad serrate hyaline flanges; outer distal spines small, with narrow serrate hyaline flanges; outer spines absent.

The swimming leg armature formula is shown on Table 1.

P5 represented by outer basal seta and small exopod fused to somite; outer exopodal seta setiform, inner seta spiniform, both elements naked. Sexual dimorphism in length of exopodal setae.

Genital apertures of ♀ large, located in proximal half of dorsal surface of genital double-somite; each operculum with spine and small spinule.

Male P6 membranous flaps produced posterolaterally into spinous process; without armature.

Caudal ramus about two to three times as long as wide; without conspicuous dorsal expansion surrounding base of seta VII. Seta I absent; setae II and III unipinnate; setae IV and V relatively rigid and bipinnate; seta VI short, spiniform and unipinnate along inner margin; seta VII long and naked. No seta displaced.

Etymology: The generic name is derived from the Greek *monos*, meaning single, and *thylax*, genit. *thylakos*, meaning sac, and refers to the unpaired egg-sac of the type species. Gender: feminine.

Type and sole species: Oncaea subtilis Giesbrecht, 1892=*Monothula subtilis* (Giesbrecht, 1892) comb. nov.

Monothula subtilis (Giesbrecht, 1892) comb. nov.
Synonymy. Oncaea subtilis Giesbrecht, 1892
Original description: Giesbrecht (1892): 593–599, 603–604, 756, 774, Plate 47, Figures 14, 18, 25, 43 and 60 (♀) [as *Oncaea subtilis*].
Other descriptions: Olson (1949): 94–97, Plate XXI, Figures 1–11 (♀), Plate XXV, Figures 8–10 (♂) [as *Oncaea subtilis*]; Razouls (1974): 239, Figure 9A–E [as *Oncaea subtilis*]; Gallo (1976): 275–280, Planche 1a+b, Figure 1A–I (♂) [as *Oncaea subtilis*]; Malt (1982): 129–130, 134–141, Figures 6a–g, 7a–n, 8a–z and 9a–p [as *Oncaea subtilis*].
Type locality: Gulf of Naples, Mediterranean Sea

Material examined

(1) Southern Red Sea, shallow area, 13° 40.0′ N, 42° 37.4′ E, St. 708, *R/V Meteor* leg 5/5: collected on 5 August 1987 with a MSN 0.055 mm net (Haul 46/2); depth 125–150 m; total water depth 190 m: (a) 2 ♀♀,

Table 1. Swimming leg armature formula for *Monothula* gen. nov.

Leg	Coxa	Basis	Exopod	Endopod
P1	0-0	1-I	I-0; I-1; III,I,4	0-1; 0-1; 0,I,5
P2	0-0	1-0	I-0; I-1; III,I,5	0-1; 0-2; 0,II[a],3
P3	0-0	1-0	I-0; I-1; II,I,5	0-1; 0-2; 0,II[a],2
P4	0-0	1-0	I-0; I-1; II,I,5	0-1; 0-2; 0,II[a],1

[a] Indicates the position of the subdistal pore on outer margin.

2 ♂♂ in alcohol (NHM reg. no. 2000.414–417); 2 ♀♀, 2 ♂♂ in alcohol (ZMH reg. no. K-39572); (c) 4 ♀♀, 5 ♂♂ in alcohol retained in personal collection of R. Böttger-Schnack.

(2) Southern Red Sea, shallow area, 13° 40.0′ N, 42° 37.4′ E, St. 708, *R/V Meteor* leg 5/5: collected on 05 August 1987 with a MSN 0.055 mm net (Haul 46/4); depth 80–100 m; total water depth 190 m: 1 ♂ dissected on 9 slides, retained in personal collection of R. Böttger-Schnack.

(3) Southern Red Sea, Strait of Bab al Mandab, 12° 32.0′ N, 43° 24.5′ E, St. 717, *R/V Meteor* leg 5/5: collected on 06 August 1987 with a MSN 0.055 mm net (Haul 49/3); depth 40–60 m; total water depth 245 m: 1 ♀ (ovigerous) dissected on 11 slides, 1 ♀ (ovigerous) in alcohol, retained in personal collection of R. Böttger-Schnack.

(4) Eastern Mediterranean, near Crete, 34° 25.3′ N, 26° 14.8′ E, St. 35, *R/V Meteor* leg 5/1: collected on 20 January 1987 with a MSN 0.05 mm net (Haul 24/5); depth 0–50 m; total water depth 3400 m: (a) 2 ♀♀ in alcohol (NHM reg. no. 2000.418–419); (b) 2 ♀♀ in alcohol (ZHM reg. no. K-39573); (c) 1 ♀ dissected on 10 slides, 2 ♀♀ in alcohol, retained in personal collection of R. Böttger-Schnack.

(5) Northern Arabian Sea, 18° 00.1′ N, 66° 25.5′ E, St. 496, *R/V Meteor* leg 5/3b: collected on 20 January 1987 with a MSN 0.05 mm net (Haul 2/2); depth 450–600 m; total water depth 3035 m: 1 ♀ dissected on 10 slides, 2 ♀♀ in alcohol, retained in personal collection of R. Böttger-Schnack.

(6) Eastern Indian Ocean, 04° 47.7′ S, 87° 14.4′ E, St. 11, *R/V Hakuho Maru* leg 76-5: collected on 24 January 1977 with a Motoda 0.10 mm net; depth 500 m, horizontal haul; total water depth 3035 m; leg S. Nishida: 1 ♀ in alcohol, retained in personal collection of R. Böttger-Schnack.

Redescription

Female (Figs 1–3, illustrations are based on specimens from the southern Red Sea, Strait of Bab al Mandab). Body length (measured in lateral aspect; from anterior margin of rostral area to posterior margin of caudal rami, calculated as sum of individual somites): 607 μm [traditional method: 490 μm (range: 440–520 μm), based on 5 specimens].

Exoskeleton well chitinized. Prosome about twice the length of urosome, excluding caudal rami, 1.7 times urosome length including caudal rami. P2-bearing somite without dorso-posterior projection in lateral aspect (Fig. 1B). Integumental pores on prosome as indicated in Figure 1A,B. Pleural areas of P4-bearing somite with rounded posterolateral corners.

Proportional lengths (%) of urosomites are 8.3:41.2:19.0:17.2:14.3. Proportional lengths (%) of urosomites and caudal rami are 7.4:36.7:16.9:15.3: 12.8:10.9.

Genital double-somite 1.5 times as long as maximum width (measured in dorsal aspect) and 4/5 length of postgenital somites combined; lateral margins rounded, largest width measured at anterior half, posterior part tapering gradually. Pore pattern on dorsal surface as in Figure 1C; ventral surface with several rows of minute spinules medially and laterally (Fig. 1E), position of lateral spinules indicated by small lateral constriction at dorsal view (Fig. 1C). Paired genital apertures located dorsally at about 1/3 distance from anterior margin of genital double-somite; armature represented by 1 long spine and 1 spinule (Fig. 1I).

Anal somite slightly longer than wide and somewhat longer than caudal rami (Fig. 1C). Paired dorsal sensillae present anterior to anal operculum. Two pairs of secretory pores present dorsally near posterior margin and 1 pair laterally in anterior third of somite. Anterior margin of anal opening (vestigial anal operculum) with minute spinules. Posterior margin of somite finely serrate ventrally and laterally (Fig. 1D).

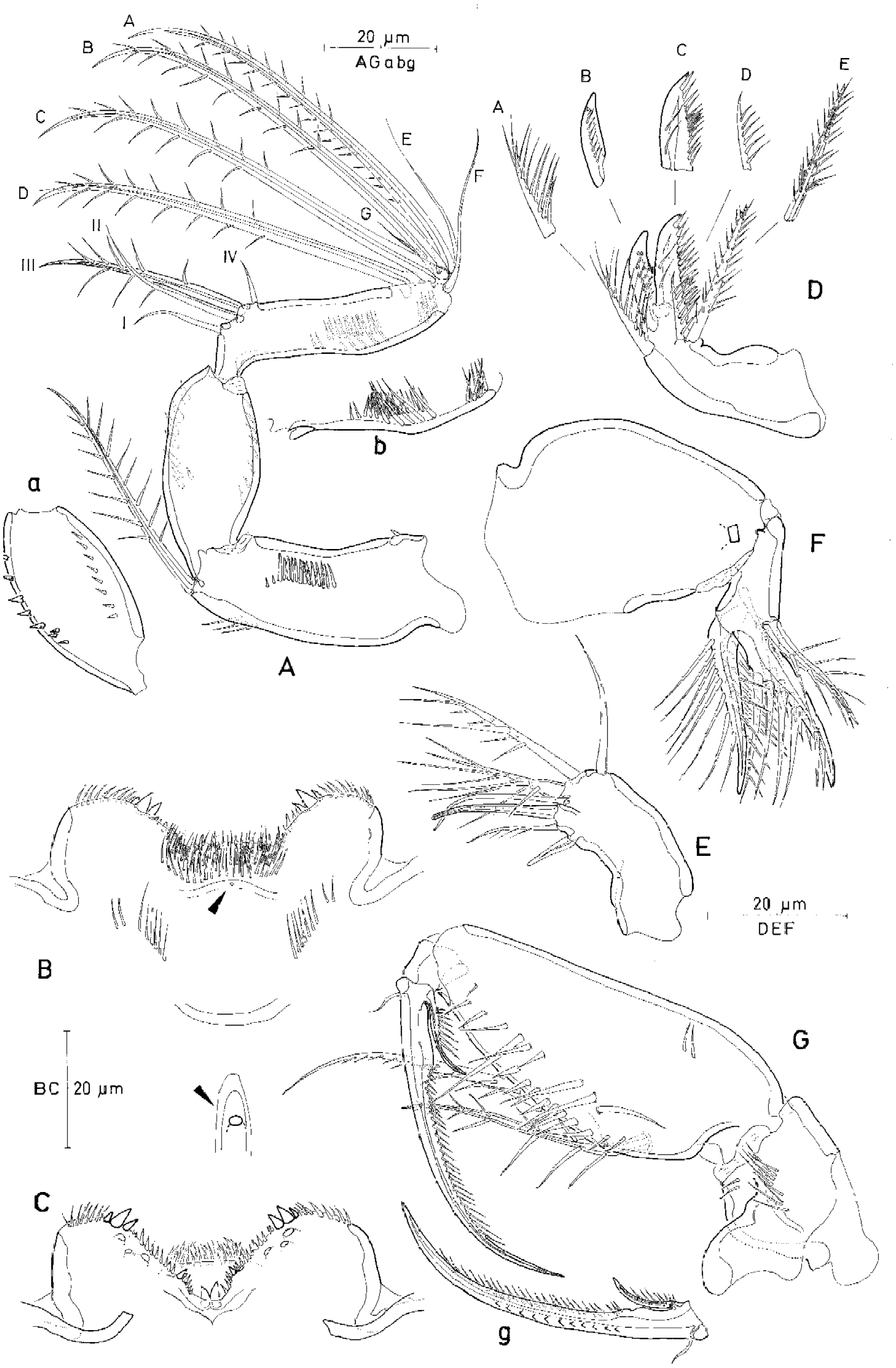

Figure 2. Monothula subtilis (Giesbrecht, 1892) comb. nov. Female. (A) Antenna, anterior, lateral elements are numbered using Roman numerals, distal elements numbered using capital letters [a: proximal endopod segment, posterior; b: outer margin of distal endopod segment, posterior]; (B) labrum, anterior, arrows indicating secretory pores; (C) same, posterior; (D) mandible, showing individual elements, which are numbered using capital letters; (E) maxillule; (F) maxilla; (G) maxilliped, anterior [g: claw, posterior, showing ornamentation along outer margin].

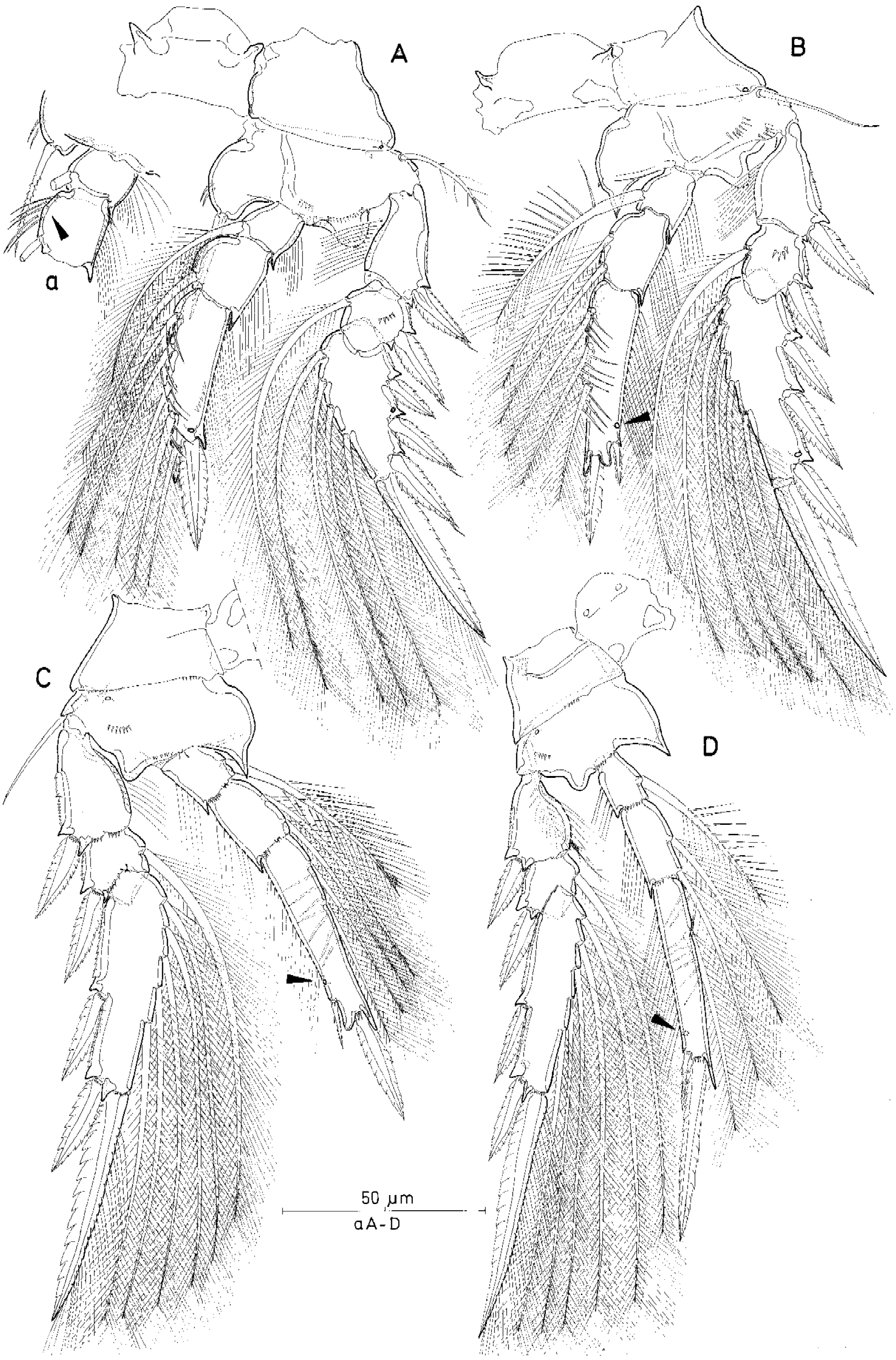

Figure 3. Monothula subtilis (Giesbrecht, 1892) comb. nov. Female. (A) P1, posterior [a: first 2 endopod segments and inner part of basis, arrow indicating ornamentation of endopod-2]; (B) P2, posterior; (C) P3, anterior, intercoxal sclerite partly omitted; (D) P4, anterior; [arrows in (B)–(D) indicating pore on inner margin of endopod-3].

Caudal ramus (Fig. 1F) 2.2 times as long as wide [2.7: 1 in specimens from the eastern Mediterranean Sea]. Armature consisting of 6 elements: setae II and III well developed, spiniform and unipinnate along medial margin; seta IV long and plumose; seta V longest, unipinnate along inner margin at proximal part, plumose at distal part; seta VI half the length of seta IV and slightly longer than caudal ramus, unipinnate along inner margin; seta VII slightly shorter than seta IV, bare and bi-articulate at base. Ornamentation on inner margin of somite not discernible. Dorsolateral surface (Fig. 1F) with secretory pore and minute spinules near insertion of seta II.

Antennule 6-segmented (Fig. 1G), relative lengths (%) of segments measured along posterior non-setiferous margin 4.4:19.0:48.7:11.4:4.5:12.0. Armature formula: 1-[3], 2-[8], 3-[5], 4-[3+ae], 5-[2+ae], 6-[6+(1+ae)]. Aesthetascs on segments 4 and 5 short and slender; apical aesthetasc well developed and fused basally to adjacent seta.

Antenna 3-segmented, distinctly reflexed (Fig. 2A). Coxobasis with row of blunt spinules along outer margin and few long spinules on inner margin, minute denticle on proximal part of outer (exopodal) margin; with long seta at inner distal corner, ornamented with strong spinules bilaterally. Endopod segments unequal in length. Proximal endopod segment elongate-oval, expanded outer margin bearing spinular row; posterior surface with row of short, strong denticles along inner margin (Fig. 2a). Distal endopod segment about 4 times longer than wide, slightly longer than proximal endopod segment, with narrow cylindrical base articulating with the proximal endopod segment; posterior surface with 2 rows of spinules of different length along outer margin (Fig. 2b) and additional patch of setules distally; lateral armature consisting of 3 bare seta of different length, with seta IV shortest, and 1 long spiniform seta (III), ornamented with strong spinules bilaterally; distal armature consisting of 4 spiniform setae (A–D), ornamented with strong spinules bilaterally, and 3 short naked setae (E–G); seta E and F similar in length, posterior seta (G) shortest.

Labrum (Fig. 2B,C) distinctly bilobed. Distal (ventral) margin of each lobe with 3–4 marginal teeth of different size medially (usually 1 or 2 large and 2 small), long row of fine spinules at outer ventral margin, and row of small spinules or denticles along inner margin. Median concavity covered anteriorly by overlapping rows of long spinules. Anterior surface (Fig. 2B) with paired rows of long setules; median swelling weakly developed, with minute pore distally near medial concavity and large secretory pore proximally (both arrowed in Fig. 2B). Posterior wall of medial concavity with two chitinized spinous teeth, flanked by row of minute denticles or spinules and 1 small dentiform process. Posterior face (Fig. 2C) with 3 secretory pores located distally on each lobe.

Mandible (Fig. 2D) gnathobase with 5 elements: 3 setae and 2 blades. Blades fused basally along posterior surface. Ventral element (A) as long as ventral blade (B), with long, fine setules along dorsal side; blade B strong and spiniform, with row of setules on posterior side; dorsal blade (C) strong and broad, spinulose along entire dorsal margin and with few setules near ventral margin; dorsal elements setiform, the shorter (D) unipinnate, the longer (E) multipinnate.

Maxillule (Fig. 2E) indistinctly bilobed, surface ornamentation not discernible. Inner lobe (praecoxal arthrite) with 3 elements: outermost element spiniform and naked, tip with tubular extension; middle element setiform and unipinnate; innermost element smallest, located along concave inner margin close to other elements, unornamented and with rounded tip. Outer lobe with 4 setiform elements; outermost element curved and bare, shorter than the following; element next outermost longest, unipinnate, and with 2 long setules along inner margin; element next innermost swollen at base, with long setules bilaterally; innermost seta bare.

Maxilla (Fig. 2F) 2-segmented, allobasis nearly as long as syncoxa. Syncoxa unarmed, surface ornamentation not discerned, except for 1 large secretory pore. Allobasis produced distally into slightly curved claw bearing 2 rows of very strong spinules along medial margin: spinules of inner row shorter, proximal group of 4 spinules on outer row longer; outer margin with strong seta shorter than allobasal claw, ornamented with long setules bilaterally; inner margin with slender pinnate seta and strong basally swollen spine with double row of long spinules along medial margin, and single row of shorter spinules along outer margin.

Maxilliped (Fig. 2G) 4-segmented, comprised of syncoxa, basis, and 2-segmented endopod. Syncoxa unarmed, anterior surface ornamented with row of long spinules. Basis elongate, palmar margin with 2 long spiniform elements equal in length, proximal element ornamented with strong spinules bilaterally, distal element bipinnate along inner margin; anterior surface with double row of strong spinules of varying length along palmar margin, few additional spinules on outer margin. Proximal endopod segment unarmed. Distal endopod segment drawn out into long curved claw, with pinnules along proximal 4/5 of concave margin, and row of denticle-like structures on posterior outer margin (Fig. 2g); accessory armature consisting of minute, naked seta on outer proximal margin and unipectinate spine fused basally to inner proximal corner of claw.

Swimming legs 1–4 biramous (Fig. 3A–D), with 3-segmented rami. Spine and setae formula as for genus. Intercoxal sclerites well developed, without ornamentation. Coxae and bases with sparse surface ornamentation as figured. Bases with plumose (P1 and P4) or naked (P2–P3) outer seta, arising from posterior surface; inner portion of basis slightly produced adaxially into rounded (P1) or pointed process (P2–P4) bearing short spinule(s) along inner margin in P1–P2 (Fig. 3A,B). Inner basal seta on P1 spiniform and minutely pinnate (Fig. 3a). Respective legs without distinct length differences between exopod and endopod. Bases of spines on exopodal and endopodal segments surrounded anteriorly by small spinules. Surface ornamentation of all segments sparse.

Exopods: Outer margin of exopod segments with well developed serrated hyaline lamella; inner margin of proximal exopod segments with long setules. Secretory pore present on posterior surface of distal segments, small denticles on P1–P2 exp-2. Serrate hyaline lamellae on outer spines well developed; outer and terminal spines of P1 with subapical tubular extension, except for proximalmost spine on exp-3. Spines on P1 exp-3 increasing in size distally. Terminal spine about equal in length to (P2–P3) or slightly longer than (P1 and P4) distal exopod segment.

Endopods: Outer margin of endopod segments with fringe of long setules. Inner seta of proximal endopod segments slightly swollen (e.g. Fig. 3B). Posterior surface of distal endopod segments with large secretory pore, located distally on P1 and subdistally at position of absent outer subdistal spine in P2–P4 (arrowed in Fig. 3B–D). Inner margin of P1 enp-2 ornamented with long spinules (arrowed in Fig. 3a). P1 enp-3 ornamented with longitudinal row of denticles on anterior surface; outer margin terminating in long process obscuring insertion of distalmost inner seta. Distal margin of P2–P3 produced into conical process ornamented with apical pore. P2 enp-3 with variable length of outer distal spine, being more than half length of distal spine in Red Sea specimens, but less than half its length in specimens from the Arabian Sea and eastern Mediterranean. Incomplete fusion of P2 enp-2 and -3 as reported by Böttger-Schnack & Huys (1997) not confirmed upon re-examination. Inner setae of distal endopod segments in P1–P4 with spinule comb along proximal inner margin. Distal spine on P4 as long as distal segment.

P5 (Fig. 1H) comprised of long unipinnate seta arising from lateral surface of somite, and small segment fused to somite representing exopod. Exopod about as long as wide, bearing stout spiniform seta and slender seta similar in length; posterior margin ornamented with minute spinules laterally (Fig. 1D).

P6 (Fig. 1I) represented by operculum closing off each genital aperture; armed with a long spine and a short spinule.

Egg-sac unpaired, elongate-oval, containing approximately 16 eggs (diameter 45–55 μm).

Male (Figs 4 and 5, illustrations are based on specimens from the southern Red Sea, shallow area). Body length: 446 μm [traditional method: 340–380 μm, based on several specimens]. Pore pattern on prosome as in Figure 4A. Sexual dimorphism in antennule, P5–P6, endopods of P1–P3, caudal ramus, and in genital segmentation.

Proportional lengths (%) of urosomites (excluding caudal rami) 9.4:59.9:4.25:4.25:5.2:17.0; proportional lengths (%) of urosomites (caudal rami included) 8.1:51.6:3.7:3.7:4.5:14.6:13.8. Posterior margin of leg 5-bearing somite with paired row of denticles ventrally (Fig. 4E).

Caudal rami 1.8 times longer than wide, shorter than in female. Caudal seta IV and VII relatively longer than in female: seta IV more than 2/3 the length of seta V, seta VII longer than seta IV and 4/5 the length of seta V; other setae with proportional lengths as in female. Seta III with weak transverse constriction at about midlength (Figs 4E,F and 5A). Seta V bipinnate on distal half, unornamented on proximal half, and distinctly constricted at base (Fig. 5A). Dorsal surface lacking spinular row near insertion of seta II (Fig. 5A).

Dorsal surface of genital somite with pore pattern as in Figure 4D. Surface of genital flaps ornamented with several rows of small spinules (Fig. 4E).

Antennule (Fig. 4G) 4-segmented; distal segment corresponding to fused segments 4–6 of female; relative lengths (%) of segments measured along posterior non-setiferous margin 5.3:20.0:47.0:27.7. Armature formula: 1-[3], 2-[8], 3-[4], 4-[11+2ae+(1+ae)]. Apical aesthetasc well developed and fused basally to adjacent seta.

Maxilliped (Fig. 4B,C) 3-segmented, comprised of syncoxa, basis and 1-segmented endopod. Syncoxa with several rows of spinules on posterior surface, un-

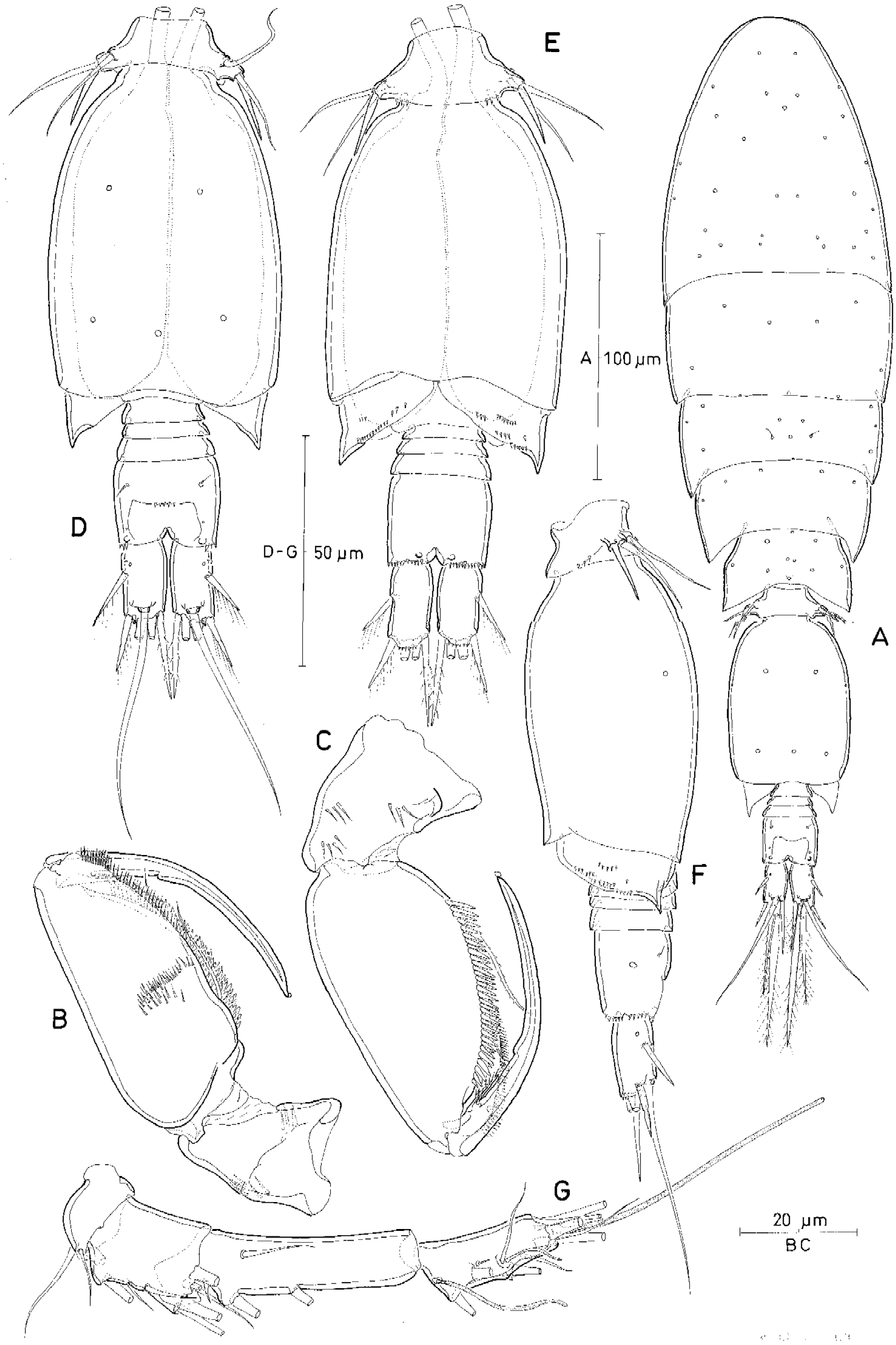

Figure 4. Monothula subtilis (Giesbrecht, 1892) comb. nov. Male. (A) Habitus, dorsal; (B) maxilliped, anterior; (C) same, posterior; (D) urosome, dorsal (spermatophores well developed); (E) urosome, ventral; (F) same, lateral; (G) antennule.

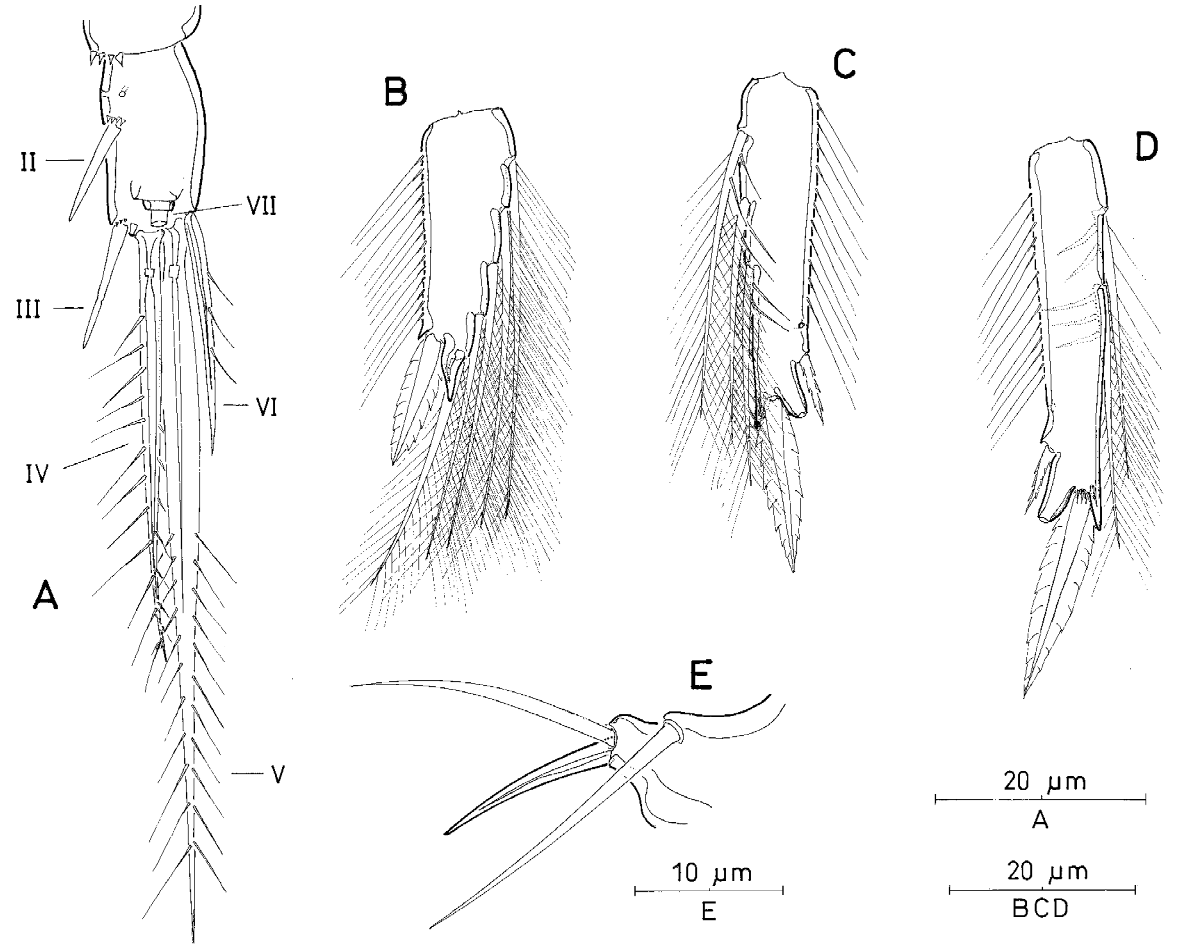

Figure 5. Monothula subtilis (Giesbrecht, 1892) comb. nov. Male. (A) Caudal ramus, dorsal, setae are numbered using Roman numerals, dorsal seta (VII) omitted; (B) P1, endopod-3, anterior; (C) P2, endopod-3, posterior; (D) P3, endopod-3, anterior; (E) P5, dorsal.

armed. Basis robust, moderately inflated in proximal half, forming small bulbous swelling; anterior surface with row of short spinules along palmar margin, developed into small distal flap, in addition to 2–3 transverse spinular rows (Fig. 5B); posterior surface with 3 rows of short spatulated spinules of graduated length along palmar margin (Fig. 4C); with 2 minutely pinnate setae within longitudinal cleft, proximal seta almost twice length of distal seta. Endopod drawn out into long curved claw, concave margin unornamented, showing notch on inner margin; accessory armature consisting of short, unipinnate spine basally fused to inner proximal corner of claw; tip of claw with minute hyaline apex.

Distal endopod spine of P1 (Fig. 5B) shorter than in female. Outer subdistal spines on distal endopod segment in P2–P3 (Fig. 5C,D) shorter than in female, almost as long as conical process.

P5 (Fig. 5E) exopod with general shape and armature as in female, except for outer slender setae longer than spiniform inner seta; posterior margin ornamented with single spinule laterally (Fig. 4F); long seta arising from lateral surface of somite unornamented.

P6 (Fig. 4E) represented by posterolateral flap closing off genital aperture on either side; covered by pattern of denticles as in Figure 4E; posterolateral corners protruding laterally so that they are discernible in dorsal aspect (Fig. 4D).

Spermatophore oval, of variable size according to state of maturity (Fig. 4D,E); swelling of spermatophore during development not affecting shape and relative size of genital somite.

Discussion

Taxonomic notes

Females of *Monothula subtilis* from the Red Sea and adjacent areas agree closely with Giesbrecht's (1892) original description, except for the following minor characters: (1a) antenna: seta II of the lateral armature being much longer than described by Giesbrecht (1892: 596, Fig. 18); however, since this seta is located very closely to the strong spiniform seta III (cf. Fig. 2A), he may not have been able to observe the correct length, (1b) antenna: setae E and F of the distal armature are similar in length and about half the length of setae A–D in Red Sea specimens, whereas they were drawn unequal in length and one of them nearly as long as setae A–D by Giesbrecht (1892: Taf. 47, Fig. 18); (2) maxilliped: ornamentation of the distal endopodal segment (claw) extending along almost entire inner margin in our material, but drawn as being restricted to the proximal third of the claw by Giesbrecht (1892: Taf. 47, Fig. 43); (3) P4 enp-3: distal spine about as long as the segment in Red Sea specimens, whereas Giesbrecht (1892: 599 and Taf. 47, Fig. 60) described it as being slightly longer than the segment. Giesbrecht's type material deposited in the Stazione Zoologica "A. Dohrn" in Naples is currently inaccessible for study, however, A. Ianora and M.G. Mazzocchi (in litt.) confirmed that the deficient condition of the original syntype material of *O. subtilis* (consisting of a single female on slide) would not permit confirmation of the minor differences listed above.

The male of *M. subtilis* was first recorded by Olson (1949) and subsequently described by Gallo (1976), who was not aware of Olson's study. In Gallo's account, several armature elements are either missing (e.g. setal counts of P1–P3 are incomplete) or illustrated incorrectly (ornamentation of distal endopodal spines). Sexual dimorphism in endopodal spine length was not recorded by Gallo. The distal endopodal spine in P1 and P2 was somewhat longer in his specimens than in males from the Red Sea, the latter spine being even longer than in females from this area. The body length of Gallo's specimens (0.45 mm) was somewhat larger than in the present study (0.34–0.38 mm), however, body size reduction is a common feature in Red Sea specimens (Böttger-Schnack et al., 1989), and both measurements fall into the size range of males as reported by Olson (0.38–0.47 mm).

Monothula subtilis is most closely related to *Oncaea curvata* Giesbrecht, 1902 and to species of the *ivlevi*-complex (see 'Phylogenetic relationships'). It can be distinguished from its sistertaxon *O. curvata* mainly by (1) loss of the outer subdistal spine on P2–P4 enp-3; (2) nature of outer exopodal seta on P5, being strong and spiniform, while this seta is slender and setiform in *O. curvata*; and (3) presence of an unpaired median dorsal egg-sac. Other minor differences between the two species are found in (1) the length of the outer distal spine on P2–P3 enp-3 in the females, being longer than the distal conical process in *M. subtilis* but shorter than this process in *O. curvata* (cf. Heron & Bradford-Grieve, 1995: their Figs 21n,o); (2) the length of the anterolateral seta on the caudal ramus, reaching to the insertion of the posterolateral seta in *M. subtilis*, but being distinctly shorter in *O. curvata*; (3) the ornamentation of the coxobasal seta and setae A–D plus III on the distal endopodal segment of the antenna, as well as of the proximal element on the maxillipedal basis, with their setules generally being longer and much stronger than in *O. curvata*; (4) the length of the outermost seta of the outer maxillulary lobe, being longer in *M. subtilis*. The two species also appear to be geographically isolated: *O. curvata* is typically restricted to high latitude cold waters, being distributed in the Antarctic sectors of the Atlantic, Pacific and Indian Ocean (see Heron & Bradford-Grieve, 1995 for distributional records), whereas *M. subtilis* tends to occur in equatorial and subtemperate regions (see below).

Other records of Monothula subtilis

Monothula subtilis exhibits a moderately wide to wide distribution in the northern and southern hemisphere, between 60° N and 40° S (Malt, 1983a,b), but only those records including figures or a description that positively identified the species are considered here.

Olson (1949) reported the species from the coastal waters of Oregon and Lower California in the Pacific. His description differs from the present account by the greater length to width ratio of the caudal ramus (3:1 as compared to only 2.2–2.7:1), and the differences in length of the distal spine on P1 enp-3 (shorter than in Red Sea specimens) and P2 enp-3 (longer than in Red Sea specimens). The distal spine in P4 enp-3 is drawn as being longer than the distal segment, which is similar to Giesbrecht's original description, but differs from the present account. Like some other authors, Olson overlooked seta II on the antenna (see above) and his figures of the mouthparts are incomplete.

Razouls (1974) illustrated the female of *M. subtilis* from the region of Banyuls-sur-mer (Golfe du Lion) and summarized previous records from the Mediterranean. He gave no textual description, and many morphological details and several armature elements are lacking in his figures. A positive identification of his specimens can nevertheless be made on the basis of the length ratio of the urosomites, which is not found in any other known species of *Oncaea* s.l. (except *O. curvata*). Additionally, the armature and ornamentation of the antenna and maxillipedal basis in Razouls' figures also serve to distinguish this species.

Malt (1982) described the developmental stages of *M. subtilis*, based on individuals reared in the laboratory (NI–NVI) and collected at sea (CII–CVI ♀ and ♂). She described the female CV with a 4-segmented urosome (1 somite between the genital double-somite and anal somite), which is very unusual in copepods exhibiting the full complement of urosomites in the adult. Typically, in females, the total number of urosomites remains constant during the final moult from CV to adult, since the addition of the penultimate abdominal somite (by fission of the last somite) is compensated by the simultaneous fusion of the genital and first abdominal somite, forming a genital double-somite (e.g. Itoh & Nishida, 1995). Thus, female CV stages and adult females can only be separated confidently by the absence/presence of functional genital apertures. Remarkably, the only other report of oncaeid copepodid stages by Björnberg (1972), also describes the female CV of an unidentified *Oncaea* sp. with a 4-segmented urosome. Both descriptions, however, contradict our own unpublished observations of female oncaeid copepodid stages displaying a 5-segmented urosome but lacking genital apertures. According to the general pattern of somite, the latter stages should be regarded as the typical female CV and the juveniles described by Malt (1982) and Björnberg (1972) as CIV. A detailed re-examination of developmental stages of various oncaeid species is currently in progress (Böttger-Schnack, 2001) in order to confirm these contradictory observations.

Phylogenetic relationships

Phylogenetic analysis of the Oncaeidae executed at species level, to be published in detail elsewhere, identified a robust clade of 5 species, including *M. subtilis*, *O. curvata*, *O. tregoubovi*, Shmeleva, 1968, *O. ivlevi* Shmeleva, 1966, and *Oncaea* sp. K (undescribed species, see Böttger-Schnack, 1992). The relationships between these species are depicted in Figure 6. The topology of this clade and the position of *M. subtilis* is significantly different from the preliminary consensus tree presented by Böttger-Schnack & Huys (1998), who anticipated changes and further resolution as additional information on the smaller species became available. The discrepancies in topology of the clade considered here can be attributed to refinement of the data set by recent examination of the small species and the addition of characters which had previously been ignored or neglected.

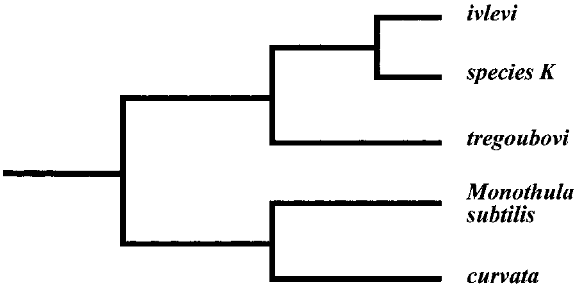

Figure 6. Cladogram depicting relationships between *Monothula subtilis* (Giesbrecht) comb. nov. and related oncaeid species (*Oncaea* sp. K, according to Böttger-Schnack, 1992).

All 5 species of the clade illustrated in Figure 6 show a prehensile antenna in which the distal endopodal segment is elongate and slender, typically articulating with the proximal endopodal segment by means of a narrow base, and being distinctly longer than this segment. An additional antennary character shared by these species is the reduction of element IV. Prehensile antennae have undoubtedly evolved independently in other oncaeid lineages such as *Conaea* and *Epicalymma*, but we have regarded them as the product of convergence. All 5 species show a close resemblance in labral structure, particularly the presence of 2 medial teeth on the posterior face of the concavity. The monophyly of the clade is further supported by two unique characters: (1) the proximal palmar seta on the male maxilliped is secondarily enlarged, being much longer than the distal seta, while in all other oncaeids both setae are about equally long or the distal seta is markedly longer than the proximal seta; (2) the presence of a spinular row along the inner margin of P1 enp-2; this row is somewhat reduced in *O. ivlevi* and *Oncaea* sp. K but still represented by a few long spinules, while in other Oncaeidae the margin of this segment is naked. The latter character illustrates the phylogenetic significance of ornamentation and the level of detail and scale of observation required for the study of oncaeid taxonomy and phylogeny.

Two lineages can be defined within the clade, *subtilis-curvata* and *tregoubovi-ivlevi*-sp. K, both of which are well supported. *Monothula subtilis* and *O. curvata* cluster together on the basis of the following synapomorphies: (1) the presence of marginal teeth apically on each lobe of the labrum, (2) the fusion of the P5 exopod to the supporting somite (but retaining its full complement of setae), and (3) the secondarily enlarged postgenital somites in the female, which are as long as or even longer than the anal somite. The sister-group of the *subtilis-curvata* clade is supported by: (1) the presence of midventral spinous processes on the P5-bearing somite; (2) the reduction of the P5 exopod, being represented by a small free segment but retaining only 1 seta (and 1 spinule); and (3) the dilated caudal rami setae IV and (particularly) V. Within this clade, *O. tregoubovi* occupies the most primitive position. The monophyly of the *ivlevi*-sp. K group is substantiated by at least two synapomorphies: (1) hyaline frill of urosomites undulate or lobate; and (2) modification of caudal ramus seta III into a strong spiniform element. Our faunistic studies provide strong indications that both *O. tregoubovi* and the *ivlevi*-sp. K group represent species complexes which may be attributed generic rank in the future.

Monothula shares the same swimming leg armature formula as the *O. englishi* group. In both the outer spine on P2–P4 enp-3 is lost, however the scoring for non-swimming leg setation characters suggests that this loss has happened convergently. Within the 5-taxon clade (Fig. 6), this reduction happened only in *M. subtilis* and serves to distinguish the latter from its sister-group *O. curvata* which has retained the ancestral armature pattern on all swimming legs. *Monothula subtilis* also differs from *O. curvata* in the presence of a median dorsal egg-sac and the spiniform nature of the outer seta of the P5 exopod.

Ecological notes

Geographical distribution in the Red Sea and adjacent areas. *Monothula subtilis* occurs in the Gulf of Aden and the southernmost part of the Red Sea, but does not penetrate further north into the central or northern regions (Böttger-Schnack, 1990, 1995). The species was not reported from the Red Sea before (see compilation of previous records by Halim, 1969), which is possibly due to its limited spatial distribution or to observational errors caused by the small size. It also occurred in the eastern Mediterranean and in the northern Arabian Sea (Böttger-Schnack, 1994).

Vertical distribution

Monothula subtilis is generally regarded as an epipelagic species (Malt, 1983b). Maximum concentrations have been reported from the upper 50 or 100 m in the eastern Mediterranean and the Adriatic Sea (Böttger-Schnack, 1997; Kršinić, 1998). In the Strait of Bab al Mandab, at the southern entrance of the Red Sea, *M. subtilis* was a dominant epipelagic species with highest densities of up to 300 ind. m^{-3} (only females considered) in the 20–60 m layers; the population showed a downward shift in the shallow southern Red Sea, where it was found mainly in the 100–150 m layer (Böttger-Schnack, 1995). No data on diurnal vertical migration are available. In the northern Arabian Sea, the species showed a further marked downward shift of its population centre, which was found in the 100–250 m layer in the coastal area near Oman, but much deeper, at 450–600 m depth, in the central Arabian Sea (Böttger-Schnack, 1996). Specimens in the central Arabian Sea showed an increased proportion of empty exoskeletons (carcasses), which may indicate that the population was moribund. Samples from the eastern Indian Ocean collected at a different season and by different sampling methods, however, indicated a correspondingly deep occurrence of *M. subtilis* in this area, with individuals being mainly found at the 500 m depth layer. In conclusion, *M. subtilis* is not exclusively epipelagic in zonation but can frequently migrate into the mesopelagic zone.

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