

Taxonomy of Oncaeidae (Copepoda, Cyclopoida s.l.) from the Red Sea. IX. *Epicalymma bulbosa* sp. nov., first record of the genus in the Red Sea

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The oncaeid genus Epicalymma comprises small copepod species usually living at meso- and bathypelagic depth layers in oceanic areas. The genus had previously been assumed to be absent from the Red Sea, due to the unusually high deep-sea temperatures and salinities in this area. In the present account a new species, Epicalymma bulbosa, is described from the Red Sea, which appears to be the only representative of the genus in the region. The new species is the smallest Epicalymma species so far recorded, with a total body length of ~0.32 and ~0.29 mm in the female and male, respectively. Apart from its small size, it differs from all known Epicalymma species by an extremely long exopodal seta on P5 in both sexes, and by a free exopod segment of P5 and a very long and basally swollen spinule on the syncoxa of the maxilliped in the female. In contrast to other Epicalymma species, which are distributed between 500 and >2500 m depth, the new species occurred much shallower (100–750 m) in the Red Sea, which may be interpreted as an avoidance mechanism of the unfavourable environmental conditions in the deep Red Sea. The taxonomic status of the new species within the genus Epicalymma is discussed and the few available ecological data on Epicalymma species in the world ocean are summarized.

INTRODUCTION

The genus *Epicalymma* was established by Heron (Heron, 1977) in order to accommodate species of the family Oncaeidae characterized by an outer spine count of II; III; III; I on the third exopod segments of the first to fourth swimming leg. Six species have been described to date from various parts of the world ocean, including the temperate and tropical Atlantic (Farran, 1908; Gordeyeva, 1973), Arctic and Antarctic regions (Heron, 1977; Heron *et al.*, 1984; Heron and Bradford-Grieve, 1995) and the open NE Pacific as well as Washington inland waters (Heron and Frost, 2000). *Epicalymma* species are small-sized, with a female total body length ranging between 0.47 and 0.88 mm for the six known species. Males have so far been described for four

species and are somewhat smaller than females, measuring between 0.43 and 0.67 mm in total body length. Copepods of the genus *Epicalymma* are usually found at depths >500 m and even down to >2500 m, though a single record from shallow inland waters (~200 m depth) is also known (Heron and Frost, 2000). Unlike many other oncaeid microcopepods, whose morphological characteristics are inadequately known (Böttger-Schnack *et al.*, 2004), the morphology of most *Epicalymma* species has been described and/or (re)described in sufficient detail by previous authors (Heron, 1977; Heron *et al.*, 1984; Heron and Bradford-Grieve, 1995), including the antennule, the antenna and the mouthparts. The detailed knowledge of these morphological characters has been recognized as indispensable

for the identification of oncaeid species, which otherwise are very similar in morphology and include many sibling species [e.g. (Heron and Bradford-Grieve, 1995; Böttger-Schnack, 1999, 2002, 2005)].

The taxonomic diversity of oncaeid microcopepods smaller than 0.5 mm in length is still insufficiently known, and quantitative ecological data on these small copepods are scarce, due to the inadequate sampling methods and the difficulties in identifying the small species (Kršinić, 1998; Böttger-Schnack *et al.*, 2004; Nishibe and Ikeda, 2004). In particular, the deep-dwelling oncaeids of this size range have rarely been investigated both taxonomically and ecologically. The few quantitative data available on the community structure of oncaeid microcopepods in mesopelagic and deep-sea layers point to a great numerical importance of the genus *Epicalymma* Heron, 1977 in these habitats (Kršinić, 1998; Kršinić and Grbec, 2002), accounting for up to 30% of the adult oncaeid population (Nishibe and Ikeda, 2004; Nishibe, 2005; F. Kršinić, unpublished data) and up to 5% of the total numbers of oncaeids, including juvenile stages (Böttger-Schnack, 1996, 1997).

In a comparative study of the oncaeid microcopepod fauna from the Red Sea and adjacent areas, the genus *Epicalymma* had previously been assumed to be absent from the Red Sea [(Böttger-Schnack, 1994) as *Oncaea* sp. 5]. Improvement of the taxonomic resolution of Red Sea Oncaeidae lead to the detection of a very small as yet undescribed species belonging to this genus [(Böttger-Schnack *et al.*, 2001, 2004) as *Epicalymma* sp.], which will be described in the present paper. The vertical distribution of the new species in the various regions of the Red Sea is presented, supplementing earlier ecological data from this area (Böttger-Schnack, 1995; Böttger-Schnack *et al.*, 2008), and the results are

compared with published data on *Epicalymma* species from other areas of the world ocean.

METHOD

Epicalymma-type oncaeids were collected with a multiple opening–closing net (Weikert and John, 1981) with a mesh size of 0.055 mm during R/V “Meteor” cruise 44/2 in 1999 in the northernmost Red Sea and the Gulf of Aqaba (Table I). The sampling programme was part of an ecological and taxonomic study of the microcopepod fauna in the Gulf of Aqaba (Böttger-Schnack *et al.*, 2001, 2008), conducted within the frame of a multidisciplinary research programme on the impact of biological processes during early spring in the Gulf (Pätzold *et al.*, 2000; Hempel and Richter, 2002). Presorted specimens from fine mesh net samples collected with the same equipment during cruise 5 of R/V “Meteor” in 1987 in the central and southern Red Sea were also included in the taxonomic study (Table I). The vertical distribution pattern of *Epicalymma bulbosa* in the central and southern Red Sea was analysed by the re-examination of material collected during earlier ecological investigations of the microcopepod community in these areas, and the methods of sampling and details of the quantitative enumeration have been described by Böttger-Schnack (Böttger-Schnack, 1995). The plankton was initially fixed in 4% formaldehyde-seawater solution buffered with borax (R/V “Meteor” cruise 44/2) or hexamethylene tetramine (R/V “Meteor” cruise 5). For sorting, the samples were transferred into a preservation fluid of 5% propylene glycol, 0.5% propylene phenoxetol and 94.5% filtered seawater (Steedman, 1976); after analysis they were returned into a 4% formaldehyde-

Table I: Station list for sampling conducted with multiple opening–closing net with 0.055 mm mesh size during R/V “Meteor” Cruises 5 and 44 in the Red Sea

Stn	Date	Geographic position	Time, D=Day, N=Night	Sampling, depth (m)	Total water, depth (m)
R/V “Meteor” Cruise 5					
Central Red Sea					
682	25.07.1987	21°13.9'N 38°05.7'E	D	300–350	1880
Southern Red Sea, oceanic area					
703	02.08.1987	15°34.8'N 41°54.9'E	D	450–600	970
R/V “Meteor” Cruise 44/2					
Northern Red Sea, main basin					
156	04.03.1999	27°25.00'N 34°04.96'E	D	300–350 500–550 550–650	798
Gulf of Aqaba					
164	06.03.1999	29°04.98'N 34°45.96'E	N	450–50	822

seawater solution. Long-term storage in Steedman's fluid proved to be detrimental, as samples become partly infected with fungi after > 10 years of preservation time (R. Böttger-Schnack, unpublished data). 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 to 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 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 and Boxshall (Huys and 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 and scales) on the body surface, but these were not fully discernible with a light microscope in *Epicalymma*-type specimens due to the weak sclerotization of the exoskeleton. Type and reference material is deposited in the collections of the Zoologisches Institut und Museum der Universität Hamburg (ZMH) and The Natural History Museum, London (NHM). Dissected specimens and some other material are retained in the personal collection of R. Böttger-Schnack (R.B.S.).

The family Oncaeidae was established by Wilhelm Giesbrecht in his comprehensive monograph on the pelagic copepods of the Gulf of Naples (Giesbrecht 1893 ["1892"]). Following the arguments given by Holthuis and Vervoort (Holthuis and Vervoort, 2006), the actual date of publication of Giesbrecht's monograph appears to be different (1893) from the date specified in the work (1892). According to Article 22A.2.3. of the International Code of Zoological Nomenclature, it is recommended to cite both dates with the actual date cited first, followed by the imprint date for information and enclosed in parentheses or other brackets and quotation marks.

The family Oncaeidae has traditionally been placed in the order Poecilostomatoida. Following Huys *et al.* (Huys *et al.*, 2002) and Boxshall and Halsey (Boxshall and Halsey, 2004), the latter and its constituent families are now subsumed under the order Cyclopoida based on morphological grounds. Although this course of action has not universally been accepted yet [e.g. (Ho *et al.*, 2006)], recent molecular analyses using small subunit rDNA (18S) sequences have provided additional evidence for a close relationship between the cyclopoid and poecilostomatoid families (Huys *et al.*, 2006, 2007) and increased taxon sampling among the Cyclopoida rendered the latter paraphyletic at the exclusion of the Poecilostomatoida (R. Huys, unpublished results).

RESULTS

Taxonomy

Family Oncaeidae Giesbrecht, 1893 ["1892"]

Genus *Epicalymma* Heron, 1977

Epicalymma bulbosa **sp. nov.**

Synonym. *Epicalymma* sp. *sensu* Böttger-Schnack *et al.*, 2004: 1130 (Table I, group X.).

Type locality

Northern Red Sea, main basin, 27°25.00'N, 34°04.96'E. Stn. 156; R/V "Meteor" leg 44/2; depth 300–350 m; total water depth 798 m.

Material examined

(1) Type locality: collected 04 March 1999 with MSN 0.055 mm net.

(1.1) Haul 9/3; depth 300–350 m:

(a) Holotype ♀, in alcohol (total body length 345 µm, measured in traditional way) (ZMH reg. no. K- 42151). *Paratypes.* 1♂ in alcohol (ZMH reg. no. K- 42152).

(b) 1♀ dissected on slides, 2♂♂ *in toto* on slides (RBS).

Additional paratypes

(1.2) Haul 10/3; depth 500–550 m: 2♂♂ males dissected on slides, 1♂ *in toto* on slide, 2♀♀ in formaldehyde (RBS);

(1.3) Haul 10/2; depth 550–650 m:

(a) 3♀♀, 2♂♂ in alcohol (ZMH reg. no. K- 42153)

(b) 2 ♀♀ in alcohol (NHM reg. no. 2009.22–23)

(2) Northern Red Sea, Gulf of Aqaba, 29°04.98'N, 34°45.96'E: Stn. 164; R/V "Meteor" leg 44/2:

collected 06 March 1999 with MSN 0.055 mm net (Haul 13/4); depth 450–500 m; total water depth 822 m.

- (a) 2♀♀, 2♂♂ in alcohol (ZMH reg. no. K- 42154)
 - (b) 2♀♀, 2♂♂ in alcohol (NHM reg. no. 2009.24-27)
 - (c) 2♀♀ *in toto* on slides, 2♀♀, 2♀♀ (empty exoskeletons), 1♂ in formaldehyde (RBS)
- (3) Central Red Sea, 21°13.9'N, 38°05.7'E: Stn. 682; R/V "Meteor" leg 5/5: collected 25 July 1987 with MSN 0.055 mm net (Haul 27/4); depth 300–350 m; total water depth 1880 m: 1♀ dissected on slides, 2♀♀ *in toto* on slides (RBS).
- (4) Southern Red Sea, oceanic area, 15°34.8'N, 41°54.9'E: Stn. 703; R/V *Meteor* leg 5/5: collected 2 August 1987 with MSN 0.055 mm net (Haul 37/4); depth 450–600 m; total water depth 970 m: 1♀ (typical form), 1♀ (elongate form) *in toto* on slides (RBS).

Description of female

Body length (measured in lateral aspect; from anterior margin of rostral area to posterior margin of caudal rami, calculated as sum of individual somites): 390 µm [traditional method: 318 µm, range: 302–347 µm, based on six specimens].

Exoskeleton weakly chitinized. Prosome 2.3 times length of urosome, excluding caudal rami, 1.9 times urosome length including caudal rami. P2-bearing somite without conspicuous dorso-posterior projection in lateral aspect (Fig. 1B). Integumental pores on prosome as indicated in Fig. 1A and B. Pleural areas of P4-bearing somite with rounded posterolateral corners, minute pointed tip or process inserting on inner (ventral) margin of corner (Fig. 1C).

Proportional lengths (%) of urosomites are 8.8:67.1:4.9:4.6:14.6. Proportional lengths (%) of urosomites and caudal rami are 7.5:57.5:4.1:4.0:12.5:14.4.

P5-bearing somite usually with two paired midventral spinous processes as figured for male (cf. Fig. 4E), sometimes aberrant number of only three processes found (Fig. 1E).

Genital double-somite elongate, 2.1 times as long as maximum width (measured in dorsal aspect) and 2.8 times as long as postgenital somites combined; lateral margins almost straight, largest width measured along midregion from one-fourth distance of anterior margin to one-fourth distance of posterior margin. Paired genital apertures located dorsally at about one-fourth distance from anterior margin of genital double-somite; armature hardly discernible, possibly 1 or 2 diminutive spinules (stippled in Fig. 1I). Pore pattern on dorsal surface as indicated in Fig. 1C; large paired pore on lateral surface near posterior margin (Fig. 1D). Ventral

surface ornamented with group of granules near anterior midventral margin (Fig. 1E).

Anal somite 1.8 times wider than long; slightly shorter than caudal rami (Fig. 1C). Dorsal surface with paired dorsal sensillae anterior to anal opening, pair of secretory pores at midregion of somite and patch of small middorsal spinules near posterior margin (Fig. 1C and F). Anterior margin of anal opening (vestigial anal opening) without ornamentation. Posterior margin of somite finely serrate ventrally and laterally (Fig. 1D).

Caudal ramus (Fig. 1F) about 1.3 times as long as wide measured along outer margin, with conspicuous expansion on dorsal surface surrounding insertion of seta VII. Armature consisting of six elements, numbered by Roman numerals in Fig. 1F: seta II and III small and slender, spiniform and unornamented; seta IV and V very long and resilient, almost equal in length, bulbous ventricle on the inner cavity of both setae absent; seta IV displaced to midregion of distal margin and slightly bent near base, ornamented with short spinules along outer margin and long, fine pinnules along inner margin; seta V with outer margin unornamented, inner margin ornamented with few short spinules anteriorly and long, fine pinnules at posterior part; seta VI about same length as seta III, spiniform and unipinnate; seta VII unornamented and very long, almost as long as seta IV and V, bi-articulation at base not discernible, probably absent. Inner margin of CR unornamented. Dorsal anterior surface with minute secretory pore near insertion of seta II (Fig. 1F).

Antennule six-segmented (Fig. 1G), relative lengths (%) of segments measured along posterior non-setiferous margin 7.7:17.5:44.3:11.4:4.7:14.4. Armature formula: 1-[3], 2-[8], 3-[5], 4-[2+ae], 5-[2+ae], 6-[5+(1+ae)]; small seta on posterior margin of segment 4 and small sensory element on distal part of segment 6 not discerned. Aesthetasc on segment 4 very small and slender. Segment 1 ornamented with short row of spinules.

Antenna three-segmented, not distinctly reflexed (Fig. 2A). Coxobasis with row of long spinules along outer margin and few long, fine spinules at inner margin; posterior surface with few additional short denticles; with long bipinnate seta at inner distal corner. Endopod segments unequal in length, distal segment about 1.5 times longer than proximal one; proximal endopod segment oval-elongate with row of strong denticles along inner margin and row of spinules (possibly representing branched tubular extensions) along entire outer margin. Distal endopod segment very long and slender, with narrow cylindrical base articulating with proximal endopod segment; posterior surface with two

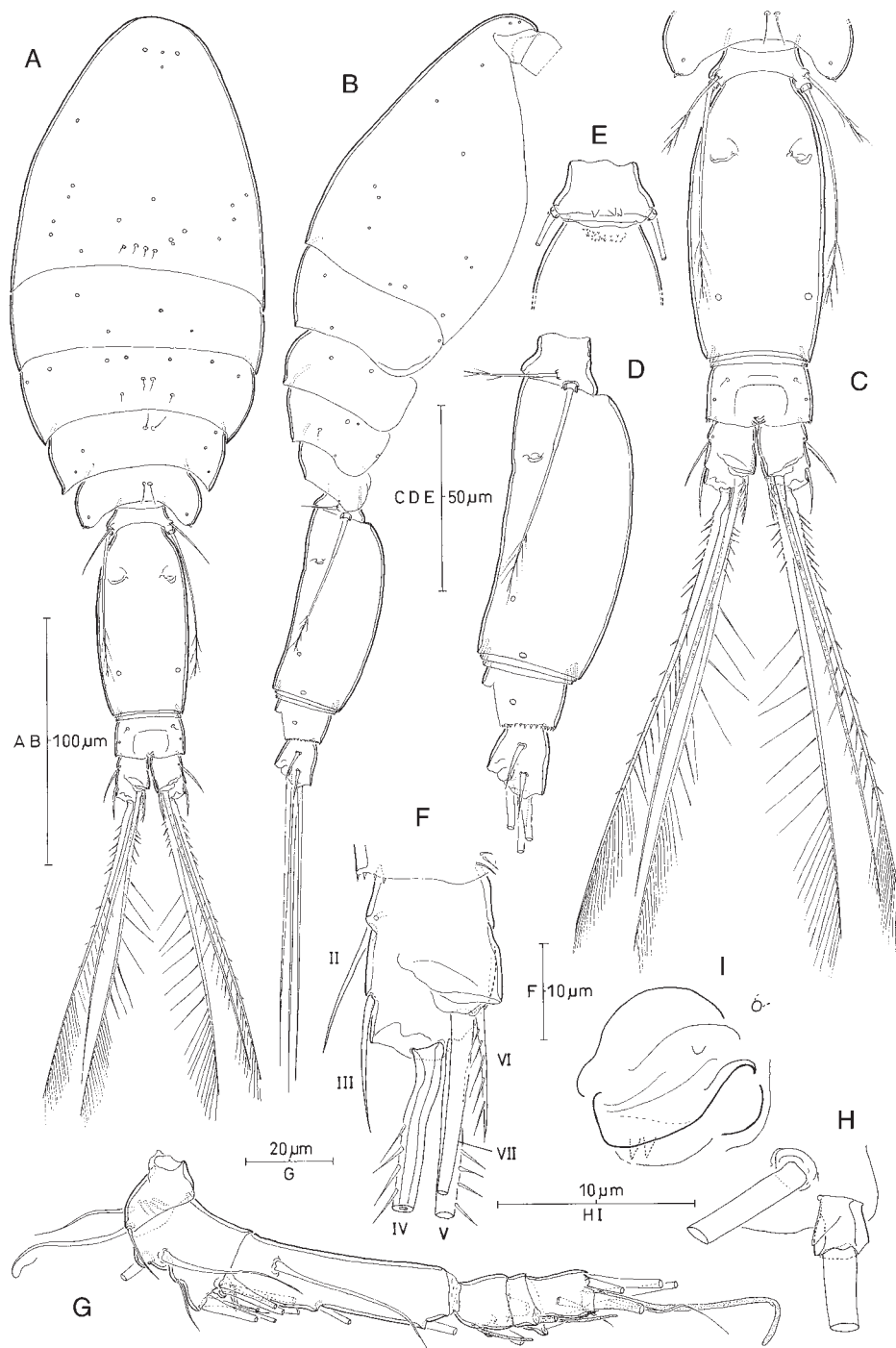


Fig. 1. *Epicalymma bulbosa* sp. nov., female (Red Sea): (A) Habitus, dorsal; (B) same, lateral (appendages omitted); (C) posterior part of P4-bearing somite and urosome, dorsal; (D) urosome, lateral; (E) P5-bearing somite and anterior part of genital double-somite, ventral; (F) caudal ramus, dorsal, individual elements numbered using Roman numerals; (G) antennule; (H) leg 5, lateral; (I) leg 6, armature not clearly discerned (stippled).

rows of spinules along outer margin, short distal row with small spinules, long proximal row with two overlapping rows of spinules, which are short (inner row) or very long and thin (outer row) (Fig. 2A); lateral

armature consisting of two bare setae (I+II) of equal length, one strong, spiniform seta (III), ornamented with strong, curved spinules bilaterally and one small bare seta (IV); distal armature consisting of four long,

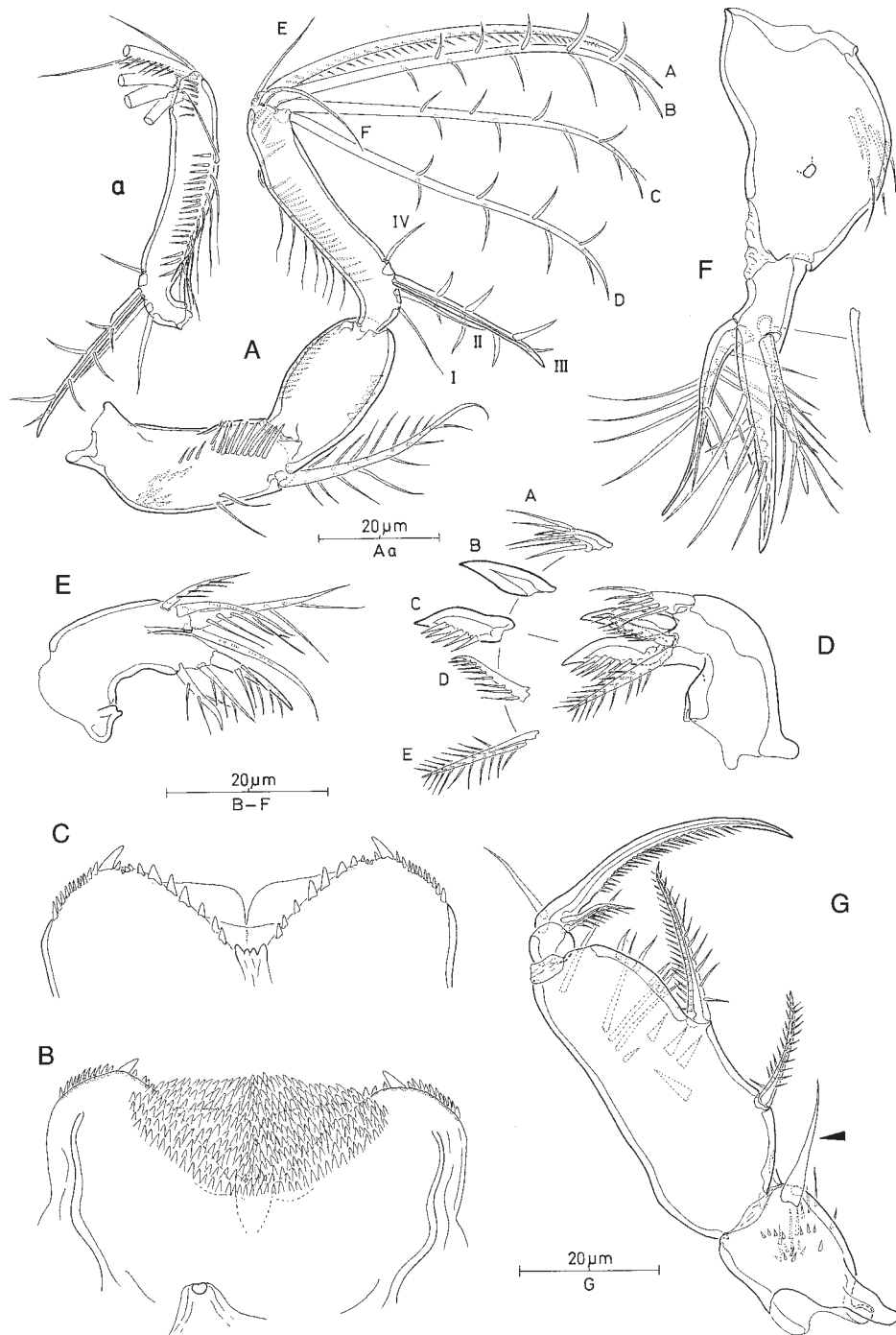


Fig. 2. *Epicalymma bulbosa* sp. nov., female (Red Sea): **(A)** Antenna, anterior, lateral elements numbered using Roman numerals, distal elements numbered using capital letters [a, distal endopod segment, posterior; setae A–D omitted]; **(B)** labrum, anterior; **(C)** same, posterior; **(D)** mandible, showing individual elements numbered using capital letters; **(E)** maxillule; **(F)** maxilla, seta on inner margin of allobasis figured separately; **(G)** maxilliped, posterior, arrow indicating long, basally swollen spinule on syncoxa.

spiniform setae (A–D) of equal length, ornamented with dense row of fine spinules unilaterally (A) or with few strong, curved spinules bilaterally (B–D), and two short, bare setae (E+F); seta G absent.

Labrum (Fig. 2B and C) bilobed. Distal (ventral) margin of each lobe with one strong marginal tooth medially, long row of small spinules or denticles at outer ventral margin and row of 7–8 large, strong denticles

along inner margin, all ornamentation elements inserting posteriorly. Median concavity covered anteriorly by several overlapping rows of hyaline spatulated setules. Anterior surface (Fig. 2B) unornamented, except for large secretory pore posterior to weakly developed median bulge. Posterior wall of medial concavity with one large chitinized spinous tooth, showing 4-fold upper edge (Fig. 2C). Ornamentation on posterior surface not discerned.

Mandible (Fig. 2D) gnathobase with five elements: three setae and two blades. Ventral element (A) slightly shorter than ventral blade (B), with long fine setules along dorsal side; ventral blade strong and spiniform, unornamented; dorsal blade (C) strong and broad, spinulose along dorsal margin; seta D almost as long as blades B and C, spinulose along dorsal margin; dorsal element (E) longest, setiform and bipinnate.

Maxillule (Fig. 2E) weakly bilobed, no surface ornamentation discernible. Inner lobe (praecoxal arthrite) with three elements: outermost element spiniform, slightly swollen at base, ornamented with spinules unilaterally and two coarse spinules, middle element setiform and unipinnate; innermost element located along concave inner margin close to other elements, sparsely bipinnate. Outer lobe with four setiform elements, which are bare or unipinnate, element next to innermost seta longest and swollen at base, outermost element shortest.

Maxilla (Fig. 2F) two-segmented, allobasis slightly longer than syncoxa. Syncoxa unarmed, surface ornamented with cluster of long spinules and one large secretory pore. Allobasis produced distally into slightly curved claw bearing two rows of strong spinules along medial margin; outer margin with strong seta not extending to tip of allobasal claw, ornamented with long spinules bilaterally, tubular extension on tip of seta not discernible; inner margin with long naked seta (figured separately in Fig. 2F) and strong basally swollen spine with double row of long, fine spinules along the medial margin and two spinules along outer margin.

Maxilliped (Fig. 2G) four-segmented, comprised of syncoxa, basis and two-segmented endopod. Syncoxa unarmed, posterior surface ornamented with small denticles and one long, basally swollen spinule at inner margin (arrowed in Fig. 2G); anterior surface with additional rows of spinules. Basis elongate, anterior surface ornamented with row of up to four very long, stiff setules and short row of strong denticles, and with row of spinules along the palmar margin between distal seta and articulation with endopod; palmar margin with two strong spiniform bipectinate elements, proximal element about three-fourth length of distal element; posterior surface unornamented. Proximal endopod

segment unarmed. Distal endopod segment drawn out into long-curved claw, with pinnules along entire length of concave margin; accessory armature consisting of long, 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 three-segmented rami, endopodal segments 2 and 3 indistinctly (P1) or completely (P2–P4) fused. Armature as shown in Table II. Intercostal sclerites well developed, sparsely ornamented in P2 + P3 as figured (Fig. 3b1 and c1). Coxae and bases of P1–P4 with surface ornamentation as shown in Fig. 3A–D, coxa of P4 with patch of long, fine setules on posterior face. Bases with outer seta, which is long and sparsely plumose (P1, P3, P4) or short and naked (P2); with anterior secretory pore near outer proximal corner; inner portion produced adaxially into rounded (P1) or pointed (P2–P4) process; inner margin of basis with two spinules (P1) or with large marginal pore on posterior face near pointed process (P2–P4) (arrowed in Fig. 3b2). Inner basal seta on P1 very strong and spiniform, ornamented with small spinules bilaterally. Endopods equal in length to exopod (P1) or shorter than exopods of respective legs (P2–P4). Basis of terminal endopod spine of P2 surrounded by small spinules (Fig. 3B), not discernible on other spines and/or legs. Surface ornamentation of all segments sparse, region of fusion between enp-2 and enp-3 in P2–P4 indicated by transverse spinular row on anterior surface (cf. Fig. 3B and D), representing the remnant of ornamentation on distal margin of enp-2.

Exopods. P1 with distal exopod segment greatly reduced in length. Outer margin of exopod segments with hyaline lamella, which is finely (proximal segments) or coarsely (middle and distal segments) serrated, outer margin of P1 with small gap at position of absent spine (arrowed in Fig. 3A); inner margin of proximal exopod segments with long setules. Large secretory pore present on posterior surface of distal segment, located close to middle spine (P2–P4), and indicating position of absent middle spine in P1. Hyaline lamellae on outer spines of proximal and middle segment of P1–P3 well developed, narrow hyaline lamella on outer spines of distal exopod segments in P1–P3 and of all segments in P4; outer spines of P1 with subapical tubular extension, hardly discernible on small proximalmost spine of distal exopod segment. Outer spines differing in size within the respective legs, with spine on proximal segment being largest and proximalmost spine on distal segment being smallest; outer spines on distal segments in P1–P3 increasing in length distally. Terminal spines much longer than distal exopod segments, even longer than entire exopod in all legs; hyaline lamella on terminal spines very narrow, in particular in P1.

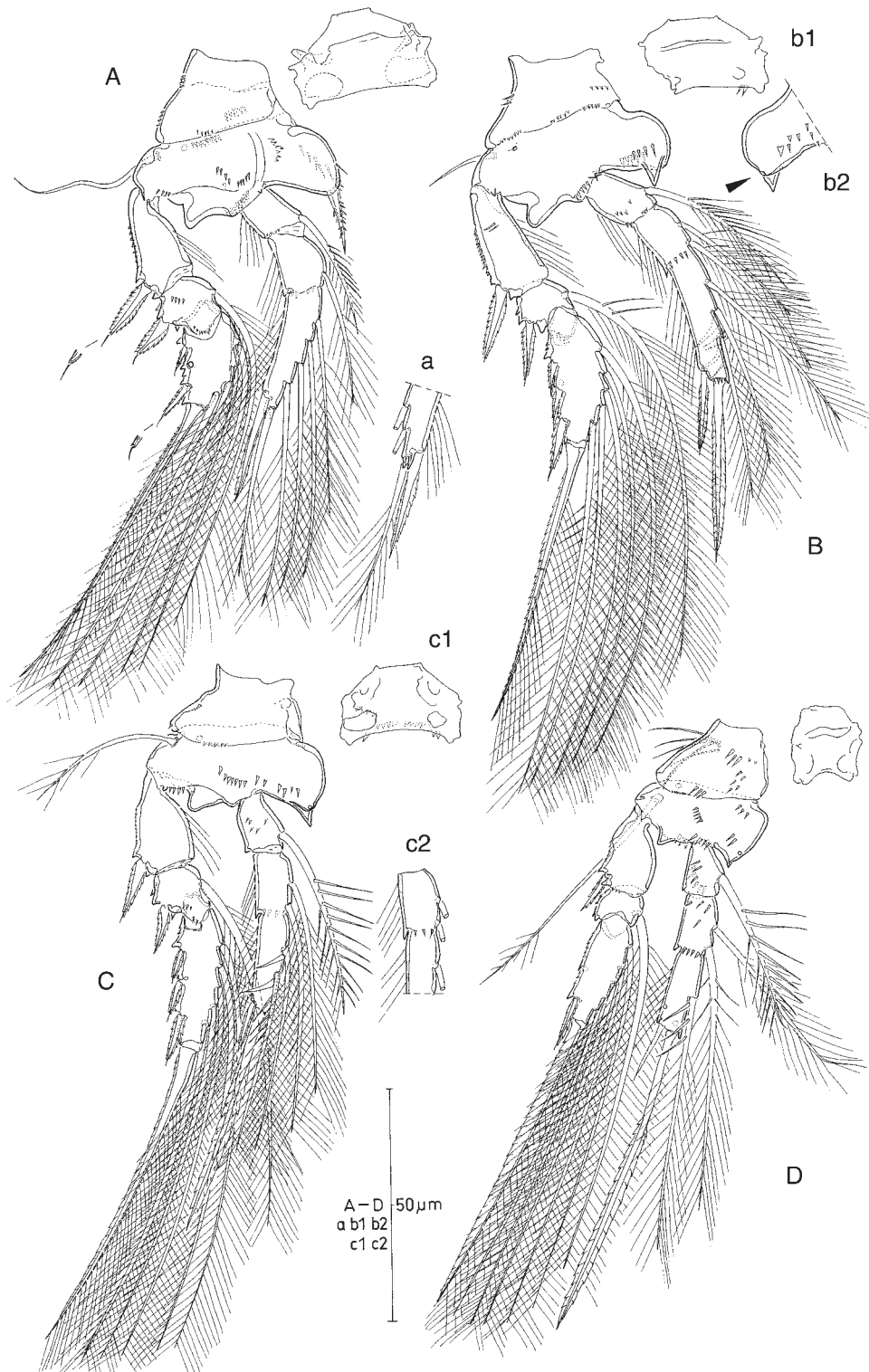


Fig. 3. *Epicalymma bulbosa* sp. nov., female (Red Sea): **(A)** P1, posterior, intercoxal sclerite figured separately, tubular extensions on outer exopodal spines exemplarily enlarged on exopod-1 and -3 [a, terminal part of endopod, anterior, showing apical processes]; **(B)** P2, anterior [b1, intercoxal sclerite, posterior, slightly damaged; b2, inner basal margin, posterior, arrow indicating pore]; **(C)** P3, posterior [c1, intercoxal sclerite, anterior; c2, endopod-2 and proximal part of endopod-3, anterior, showing spinular row indicating region of fusion of segments]; **(D)** P4, anterior, intercoxal sclerite figured separately.

Table II: *Epicalymma bulbosa* sp. nov.
Armature of swimming legs

	Coxa	Basis	Endopod	Exopod
Leg 1	0-0	1-1	0-1; 0-1 ^a ; 0,1,5	1-0; 1-1; II,1,4
Leg 2	0-0	1-0	0-1;1,1,5	1-0; 1-1; III,1,5
Leg 3	0-0	1-0	0-1;1,1,4	1-0; 1-1; III,1,5
Leg 4	0-0	1-0	0-1;1,1,3	1-0; 0-1; 1,1,5

Roman numerals indicate spines, Arabic numerals represent setae. Footnote 'a' indicating incomplete fusion of second and third endopodal segment.

Endopods: Distal endopod segments reduced in length in all legs. Outer margin of endopod segments with fringe of long setules, except for proximal segments of P3 + P4 and proximal part of fused middle and distal segments of P4. Inner seta of proximal endopod segments slightly spiniform and reduced in length in P1–P4, this seta plumose (P1–P2) or ornamented with long spinules bilaterally (P3–P4). Distal endopod segments with single secretory pore on anterior surface in P1 + P4; distal margin of P2–P4 without conical process and/or apical pore; outer and distal margin of distal segment of P1 terminating anteriorly in two small processes obscuring insertion of distalmost inner seta (Fig. 3A). Terminal spine on P1 inserting subdistally. Terminal spine increasing in length from P1 to P4: about 4/5 length of distal endopod segment in P1, about as long as distal and fused middle segment combined in P2, and longer than entire endopod in P3 + P4. Spinular comb on proximal inner margin of inner setae of distal endopod segments of P2–P4 reduced to one to two strong spinules, proximal spinule strongest and swollen at base.

P5 (Fig. 1H) comprised of short outer basal seta, reaching almost as far as genital apertures and being sparsely plumose, and small exopod segment delimited from somite. Exopod about as long as wide, ornamented with a small spinous process laterally (Fig. 1H) and armed with single very long, plumose seta, reaching about 4/5 length of genital double-somite, almost as far as paired pore on dorsal surface.

P6 (Fig. 1I) represented by operculum closing off each genital aperture; armature not clearly discernible, possibly represented by 1–2 minute spinules (stippled in Fig. 1I).

Egg-sacs not found.

Description of male

Body length (measured in lateral aspect; from anterior margin of rostral area to posterior margin of caudal rami, calculated as sum of individual somites): 358 μm

[traditional method: 293 μm , range: 292–294 μm , based on three specimens]. Pore pattern on prosome probably not fully discerned. Sexual dimorphism in antennule, maxilliped, P1, P5 and P6, and in genital segmentation, slight modification in proportional lengths of endopodal spines in P2.

Proportional lengths (%) of urosomites (excluding caudal rami) 10.4 : 63.2 : 4.1 : 4.7 : 5.2 : 12.4; proportional lengths (%) of urosomites (caudal rami included) 8.8 : 53.5 : 3.5 : 3.9 : 4.4 : 10.5 : 15.4. Length to width of caudal rami (Fig. 4H) and proportional lengths of caudal setae as in female. Dorsal surface of genital somite without pores (Fig. 4D), ventral surface ornamented with short row of large denticles near anterior midventral margin (Fig. 4E). Surface of genital flaps unornamented. Anal somite with length to width as in female, pore pattern as in female.

P5-bearing somite with two paired midventral spinous processes (Fig. 4E).

Antennule (Fig. 4B) four-segmented; distal segment corresponding to fused segments 4–6 of female; relative lengths (%) of segments measured along posterior non-setiferous margin 8.5 : 19.5 : 46.4 : 25.6. Armature formula: 1-[3], 2-[8], 3-[4], 4-[9 + 2ae + (1 + ae)]. Small seta on posterior margin of segment 4 and small sensory element on distal part of this segment not discerned. Proximalmost aesthetasc very small and slender, hardly discernible. Segment 1 ornamented with short row of spinules as in female.

Maxilliped (Fig. 4C, c1 and c2) three-segmented, comprising syncoxa, basis and one-segmented endopod. Syncoxa unarmed, ornamented with spinules on posterior face and one strong spinule at inner margin, which is shorter than in female and not swollen at base. Basis elongate, moderately inflated in proximal half forming indistinct bulbous swelling; anterior surface with one transverse spinular row, varying greatly in length, in addition to row of minute spinules along inner margin (Fig. 4C); posterior surface with two rows of spatulated spinules of graduated length along palmar margin (Fig. 4c1), decreasing in width distally (Fig. 4c2); with one small naked setae within the longitudinal cleft (arrowed in Fig. 4c2). Endopod drawn out into long curved claw, concave margin unornamented; accessory armature consisting of short naked spine basally fused to inner proximal corner of claw (figured separately in Fig. 4C); tip of claw without hyaline apex (Fig. 4C, c1).

P1–P4 with armature and ornamentation as in female. Endopod of P1 with distalmost inner seta greatly reduced in length, being about half the length of distal spine (Fig. 5A). Distal spine relatively longer than in female, being longer than distal endopod segment and ornamented with spinules bilaterally, hyaline lamella absent.

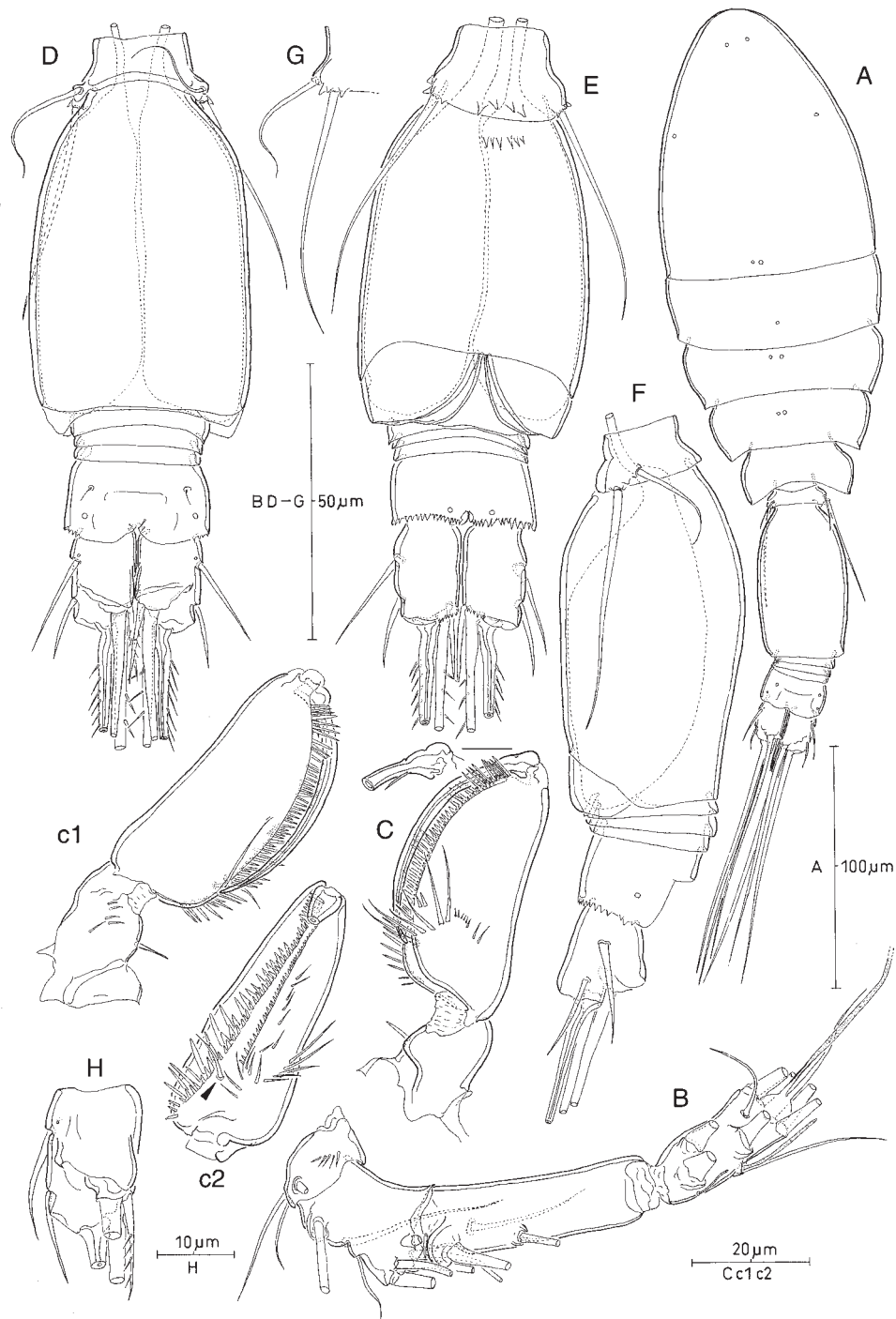


Fig. 4. *Epicalymma bulbosa* sp. nov., male (Red Sea): (A) Habitus, dorsal, ornamentation of caudal setae not shown; (B) antennule, length of distal aesthetasc not fully discerned; (C) maxilliped, anterior, small spine basally fused to inner proximal corner of claw figured separately [c1, same, posterior; c2, maxillipedal basis, medial view, claw omitted, arrow indicating seta within longitudinal cleft]; (D) urosome, dorsal, caudal ramus setae IV, V and VII not fully shown; (E) same, ventral; (F) urosome, lateral; (G) leg 5, dorsolateral; (H) caudal ramus, dorsal, showing dorsal expansion, setae IV, V and VII omitted.

Proportional spine lengths on distal endopod segment of P2 slightly different from female with outer distal spine being relatively shorter than in female (Fig. 5B).

P5 (Fig. 4G) exopod not delimited from somite, located latero-ventrally, armature as in female; outer basal seta as in female.

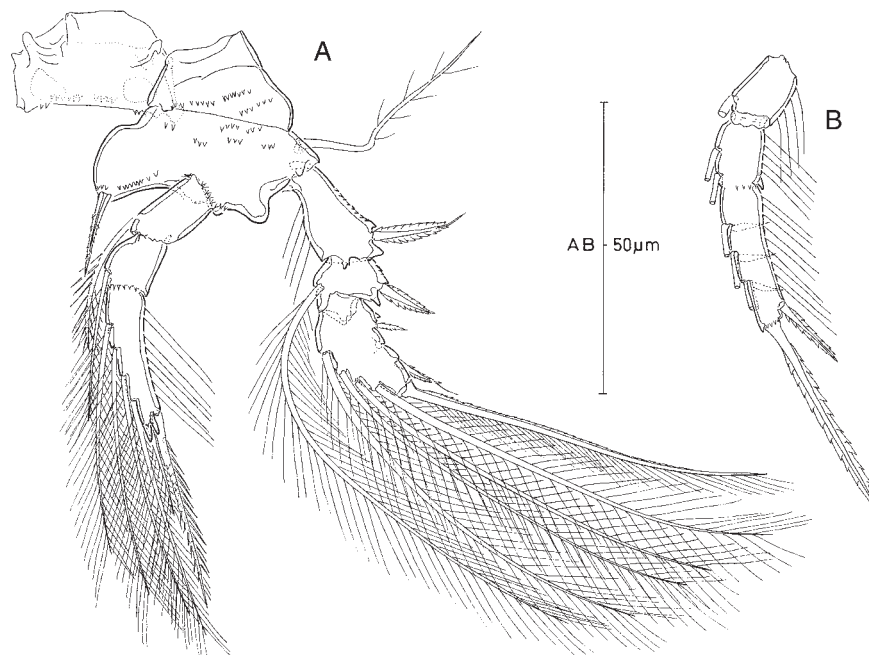


Fig. 5. *Epicalymma bulbosa* sp. nov., male (Red Sea): (A) P1, anterior; (B) P2, endopod, anterior, inner setae omitted.

P6 (Fig. 4E) represented by posterolateral flap closing off genital aperture on either side, unornamented; posterolateral corners not protruding laterally and not well discernible in dorsal aspect (Fig. 4D).

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

Etymology

The specific name is derived from the Latin *bulbosus*, meaning bulbous, and refers to the form of the long, basally swollen spinule on the syncoxa of the female maxilliped.

Form variants

Female *Epicalymma bulbosa* exhibited some variability in the length-to-width ratio of the genital double-somite, with the typical form exhibiting a smaller length-to-width ratio (1.8:1) than the elongate form (2.3:1). All other morphological characters, including the delimited exopod segment on P5, the length of the exopodal seta on P5 and the conspicuous ornamentation on the syncoxa of the maxilliped (long basally swollen spinule) were similar between the two forms. The elongate form of *E. bulbosa* was found only in the southern Red Sea, but may not be restricted to this

area. The typical form of *E. bulbosa* was found in the entire Red Sea, including the Gulf of Aqaba, the northernmost extension of the Red Sea. Potential differences in zoogeographical distribution of the two forms in the Red Sea could not be clarified during the present study due to difficulties in distinguishing the specimens without microscopic examination.

Distribution and abundance

Epicalymma bulbosa is distributed throughout the Red Sea, including its northernmost extension, the Gulf of Aqaba [(Böttger-Schnack *et al.*, 2001) and (Böttger-Schnack *et al.*, 2004) as *Epicalymma* sp.]. No information is available on its occurrence in the Gulf of Suez. In the northernmost Red Sea and the Gulf of Aqaba, abundances of *Epicalymma bulbosa* in the entire water column ranged between 600 and >2000 ind. m⁻² during spring, with abundance values increasing from the northern Red Sea towards the central or northern Gulf (Böttger-Schnack *et al.*, 2008). The species accounted for 0.3–0.7% of the total number of oncaeid copepods (excl. nauplii) in the entire water column, and for maximum values of up to ~5% in single midwater layers between 350 and 650 m. During earlier ecological investigations in the Red Sea (summer), the species/genus had not yet been positively identified and the pre-identified adult and late juvenile specimens had been summarized together with the numerous unidentified juvenile oncaeids under “*Oncaea*

spp.” (Böttger-Schnack, 1995). Re-examination of the presorted *Epicalymma*-type oncaecids from the earlier survey during the present study verified the occurrence of *E. bulbosa* in the deep oceanic area of the southern Red Sea, where it occurred in similar abundances than in the Gulf of Aqaba (~ 2500 ind. m^{-2}). In the shallow neritic area of the southern Red Sea and in the Strait of Bab el Mandab, at the southern entrance of the Red Sea, a few specimens of *Epicalymma*-type oncaecids were found in the deepest depth stratum sampled (150–175 and 200–245 m, respectively), which were not examined further.

No information is available on the seasonal variation in abundance in the central Red Sea, as during the earlier investigations in autumn and winter a mesh size of 0.1 mm was used (Böttger-Schnack, 1990a, b), which cannot sample the species quantitatively.

The vertical distribution of *Epicalymma bulbosa* differed between the regions studied: in the northern Red Sea and the Gulf of Aqaba, the species was generally distributed in mesopelagic layers below 200 m depth, with maximum concentrations of 2–26 ind. m^{-3} occurring between 200 and 400 m (northern Red Sea and southern Gulf) or 350 and 650 m (central and northern Gulf) (Böttger-Schnack *et al.*, 2008, their fig. 6). In the southern Red Sea, on the other hand, the species was distributed somewhat shallower, between 100 and 750 m depth, with maximum concentrations of up to 10 ind. m^{-3} in the lower epipelagic zone, at 150–200 m depth, and in the mesopelagic zone, at 450–600 m depth (Böttger-Schnack, unpublished results).

DISCUSSION

Taxonomy

Epicalymma bulbosa is the smallest *Epicalymma* species described so far. Apart from its small size, it differs from all congeners in the nature of the P5 exopod, being delimited from the somite (female), and in the length of the exopodal seta on P5, measuring more than half the length of the genital double-somite (both sexes). Note that for females of *E. ancora* (Gordeyeva), the separation of the P5 exopod cannot be discerned clearly from the figure presented by the author [(Gordeyeva, 1973), her fig. 20] (fused to somite?), and in the text she described it as follows: “. . . shape of a small spherical tubercle with an apical seta. . .” [translated from (Gordeyeva, 1973)], which does not give clear evidence whether the P5 exopod is delimited or not. Another distinctive feature of *E. bulbosa* is the very strong and basally swollen spinule on the syncoxa of the female maxilliped. In

other *Epicalymma* species, this spinule is very slender (*E. brittoni* Heron, English and Damkaer) and much shorter [*E. vervoorti* Heron, English and Damkaer; *E. exigua* (Farran)] or even absent [*E. schmitti* Heron; *E. umbonata* Heron; *E. ancora*] (Gordeyeva, 1973; Heron, 1977; Heron *et al.*, 1984).

Among the known species of *Epicalymma*, *E. bulbosa* is closely related to *E. vervoorti*, which has been described from the central Arctic Ocean and the Norwegian Sea at depths below 1000 m (Heron *et al.*, 1984). In addition to the differences in morphological characters stated above, females of the two species differ in (i) the form of the genital double-somite, with lateral margins being almost straight in *E. bulbosa* (rounded in *E. vervoorti*); (ii) the length of the outer basal seta on P5, reaching as far as the genital apertures in *E. bulbosa* (not reaching the genital apertures in *E. vervoorti*), and (iii) the complete fusion of endopod-2 and -3 in P2–P4 in *E. bulbosa* [incompletely fused (P2, P4) or separated (P3) in *E. vervoorti*]. The fusion of segments may be obscured when viewed from the anterior face, because the distal margin of endopod-2 in P2–P4 in *E. bulbosa* is ornamented with a spinular row on the anterior surface, which remains after the fusion of endopod-2 and -3 (cf. Fig. 3B and D). The fusion of segments can be recognized more easily when viewed from the posterior face, where the spinular row is absent (Fig. 3C). Thus, to overcome difficulties in the examination of endopod segmentation, as previously stated also for some other *Epicalymma* species (Heron *et al.*, 1984), an appropriate orientation of the legs is necessary. Further morphological differences between *E. bulbosa* and *E. vervoorti* are found in (iv) the nature of the inner basal seta on P1 being stout and ornamented in *E. bulbosa* (slender and naked in *E. vervoorti*), (v) the length of distal spine on endopod-3 in P1, being as long as the distal segment and measuring more than half the length of the distal seta in *E. bulbosa* (shorter than distal segment and about same length as distal seta in *E. vervoorti*), (vi) the length of the coxobasal seta in the antenna, being longer than the first endopod segment in *E. bulbosa* (shorter than this segment in *E. vervoorti*), and (vii) the relative lengths of the (short) distal setae E and F on the second endopod segment of the antenna, being similar in lengths in *E. bulbosa* (differing in length in *E. vervoorti*). The latter two characters are similar to *E. exigua* as redescribed by Heron *et al.* (Heron *et al.*, 1984), which is a sibling species of *E. vervoorti*. However, *E. bulbosa* can readily be differentiated from *E. exigua* by the nature of the anal opening, with the distal margin being straight, while the margin is distended in *E. exigua*. This character is regarded as the most important character separating *E. exigua* from related species (Heron *et al.*, 1984).

The antennule of *Epicalymma bulbosa* appears to have a reduced setal formula compared with that found in the majority of oncaeid species (Huys and Böttger-Schnack, 1996–1997; Böttger-Schnack and Huys, 1997), lacking the small seta on posterior margin of segment 4 and the small sensory element on distal part of segment 6. The existence of the small element on segment 4 had been described and figured for the type species of *Epicalymma*, *E. schmitti* [(Heron, 1977) her fig. 28d], and was recorded also for *E. brittoni* [(Heron *et al.*, 1984) their fig. 15j]. For other *Epicalymma* species (re)described by these authors, a similar setal formula was stated in the text, but figures were not provided, and the antennular armature of *E. ancora* as described by Gordeyeva (Gordeyeva, 1973) is completely unknown. As the present new species is the smallest *Epicalymma* species yet described, it cannot be excluded that the missing antennular element(s) may be too small to be discerned under a light microscope. However, in the related species *Oncaea bispinosa*, which is similar in size, the small seta on the distal margin of segment 4 was clearly discernible with the same technical equipment (Böttger-Schnack, 2002), thus disproving a methodical bias. Apart from its different setal armature, the antennule of *E. bulbosa* exhibits some surface ornamentation on the first segment. The existence of such ornamentation details for other *Epicalymma* species still needs to be determined. Usually, the antennular elements of oncaeid copepods are unornamented, but some species of *Spinoncaea* have recently been found to exhibit a spinular row along the inner non-setiferous margin of the second and third segment (Böttger-Schnack, 2003), indicating that ornamentation details on the antennule may be more widespread among oncaeids than previously known.

The maxillipedal basis of male *E. bulbosa* is armed with only one (proximal) seta within the longitudinal cleft, which appears to differ from all *Epicalymma* males described thus far. The males of *E. schmitti* and *E. umbonata* exhibit two setae within the longitudinal cleft of the maxillipedal basis (Heron, 1977), whereas in the males of *E. vervoorti* and *E. exigua* the maxillipedal basis is unarmed (Heron *et al.*, 1984). The males of *E. brittoni* and *E. ancora* are unknown. Thus, it cannot be judged whether the reduced maxillipedal armature found in *E. bulbosa* is unique or may probably be found in other *Epicalymma* species as well. Usually, the maxillipedal basis of male oncaeids is armed with two elements, except for species of *Spinoncaea* which have only one large (proximal) seta (Böttger-Schnack, 2003). Furthermore, the ornamentation of the maxillipedal claw in the male appears to differ between *Epicalymma* species, being naked in *E. bulbosa*, while it was found to

be pinnate along the proximal half of the concave margin in *E. schmitti* (Heron, 1977, her fig. 29d). However, for the males of *E. vervoorti* and *E. exigua* (Heron *et al.*, 1984), and for those of *E. umbonata* (Heron and Frost, 2000), the discrepancies between text and figures do not allow a justification of whether the concave margin of the claw is pinnate (as stated in the text) or naked (as figured by the authors).

The caudal setae IV, V and VII of *Epicalymma bulbosa* are very long and resilient, which is a distinctive feature of this genus (Heron, 1977; Heron *et al.*, 1984). Remarkably, these long setae were never found to be broken off in the specimens examined during the present study, in contrast to other oncaeid taxa, which often lose their long terminal caudal setae during the sampling procedure and/or the handling of the specimens [e.g. (Huys and Böttger-Schnack, 2007)]. The inner cavity of caudal rami setae IV and V in oncaeid copepods usually have a bulbous ventricle, resulting in a reduced wall thickness near the base of the seta [examples are given by Böttger-Schnack (Böttger-Schnack, 2001), her fig. 11E, and Böttger-Schnack (Böttger-Schnack, 2003), her fig. 6F]. At this “predetermined breaking point” the setae may break off easily. The detailed analysis of the internal structure of caudal setae IV and V of *E. bulbosa* proved the absence of a bulbous ventricle and corresponding reduced wall thickness near the base of the seta (cf. Fig. 1F). Due to the absence of such “predetermined breaking point” the setae apparently are much more resistant to breakage (and loss). It needs to be clarified by future analyses whether or not this morphological characteristic may be typically found in *Epicalymma* species as previous authors did not examine the internal structure of the caudal rami.

In earlier descriptions of *Epicalymma* species, the armature of the distal endopod segment on P1 was given as I;I;4 (Heron, 1977; Heron *et al.*, 1984), which should better read 0;I;5 (cf. Table II), because the distal-most inner element of endopod-3 on P1 in all *Epicalymma* species is a seta and not a spine as can readily be confirmed from the figures published by Heron and her co-workers.

Biodiversity

Epicalymma bulbosa appears to be the only representative of the genus in the Red Sea main basin, thereby confirming a reduced species diversity of the deep-sea fauna in this area, which also has been demonstrated for various other zooplankton taxa (Halim, 1969; Weikert, 1987; Böttger-Schnack *et al.*, 2004). In the adjacent Arabian Sea, seven as yet unidentified species of *Epicalymma* in the size range between 0.34 and 0.66 mm

(adult females) have been recorded in the upper 1850 m depth layer (Böttger-Schnack, 1996). In the deep Arctic Ocean and the Norwegian Sea, five *Epicalymma* species have been recorded (Heron *et al.*, 1984), and up to four species of this genus have been found to date in the deep NE Pacific (Heron and Frost, 2000), all of which have a female body length larger than ~ 0.5 mm. Thus, the diversity of *Epicalymma* species in these areas may be even higher when the smaller species of less than 0.5 mm would have been considered.

In the Mediterranean Sea, however, the species diversity of *Epicalymma* appears to be as low as in the Red Sea, as only one *Epicalymma* species has so far been recorded in the upper 1850 m of the water column (Shmeleva, 1973; Böttger-Schnack, 1997; Kršinić, 1998). In both areas, the deep-sea temperatures are unusually high, resulting in a correspondingly high remineralization and causing an extremely limited downward transport of organic matter, which has been regarded as the reason for the lack of a special deep-sea fauna (Wishner, 1980; Weikert, 1982). On the other hand, it may as well be possible that the diversity of the *Epicalymma* fauna in the Mediterranean has been underestimated so far due to their small size and the apparent taxonomic uncertainties in species identification. Recent investigations on the deep-sea benthopelagic fauna in the eastern Mediterranean Sea at 4200 m depth showed at least two as yet unidentified species of *Epicalymma* of very small size (0.3–0.4 mm) (R. Böttger-Schnack, unpublished results), and preliminary results of a survey of Mediterranean oncaeids in the upper 1000 m water column (Böttger-Schnack and Schnack, 2009) pointed to the existence of even more than five different *Epicalymma* morphs, which need to be investigated further.

Distribution and abundance

Outside the Red Sea, *Epicalymma* species are usually found at depths below 500 m and down to >2500 m (Farran, 1908; Gordeyeva, 1973; Heron, 1977; Heron *et al.*, 1984), whereas the Red Sea species was distributed much shallower, occurring already at depths below 200 m or even below 100 m (southern Red Sea). A similarly shallow distribution of *Epicalymma* species than noted in the Red Sea has also been recorded for a small, as yet unidentified species of *Epicalymma* in the Mediterranean Sea (Böttger-Schnack, 1997; Kršinić, 1998). Whether or not the observed shallow distribution pattern in these areas is an avoidance mechanism of the unfavourable environmental conditions in the deep-sea layers (see above) or whether it is a general phenomenon in the smaller-sized

Epicalymma species cannot be answered at present, because the depth distributions of species less than 0.5 mm in body length have not yet been investigated in subtropical and/or tropical areas with more typical (cold) deep-sea layers.

The numerical abundance of the genus *Epicalymma* in the Red Sea appears to be in the same order of magnitude than in the adjacent eastern Mediterranean Sea (Table III) and the proportion of this genus within the adult population of oncaeid copepods appears to be similar in both areas (Table III). In the adjacent Arabian Sea, on the other hand, the absolute and relative abundances of *Epicalymma* spp. were much lower (Table III). In particular, the vertically extended oxygen minimum zone between 100 and 1000 m depth, which is a characteristic feature in this area (Wyrki, 1973), appears to be avoided by the copepods. Below the oxygen depleted layer, abundance values of the genus increased in this area. In the subarctic NW Pacific (Nishibe and Ikeda, 2004; Nishibe, 2005), however, the absolute and relative abundances of *Epicalymma* spp. in midwater and deep-sea layers appear to be considerably higher than those recorded from the Red Sea and adjacent areas (Table III), possibly indicating a preference of this copepod genus for cold-water habitats. For a better understanding of the vertical, regional and zoogeographical distribution of *Epicalymma* species in different climates, plankton sampling with very fine mesh nets are required, particularly in subtropical/tropical oceanic areas with typical (cold) deep-sea layers. It remains to be clarified whether the observed geographical differences in the abundances of *Epicalymma* species and their proportion within the oncaeid community are caused by a methodological bias (small species not yet sampled) or in fact due to a preference of these copepods for cold-water habitats. Also, the allegedly amphitropical distributions of some *Epicalymma* species stated by Heron and Frost (Heron and Frost, 2000) will have to be re-examined, as the conclusions drawn by Heron and Frost were not supported by the data presented in their study, which were merely based on samples collected in polar and subpolar areas of both hemispheres.

Morphology and phylogenetic relationships of *Epicalymma* species

The genus *Epicalymma* was established by Heron (Heron, 1977) on the basis of the leg armature, showing an outer spine count of II;III;III;I on the third exopod segments of the first to fourth swimming leg. Common morphological characters of *Epicalymma* species are found in the nature and armature of the caudal ramus,

Table III: *Epicalymma* spp.—Standing stock ($N = \text{ind.}/1 \text{ m}^2$ in the given depth layer) and relative abundance (% = percentage of total number of adult oncaeid copepods) in different climates

	Warm temperate/tropical						Subarctic	
	Red Sea ^{a,b} ($n = 3-4$)		Eastern Mediterranean ^c ($n = 4$)		Northern Arabian Sea ^d ($n = 1/1$)		NW Pacific ^e ($n = 4$)	
TWD (m)	Max. 950		~4000		2500–3000		3050–6700	
Depth range (m)	N	%	N	%	N	%	N	%
0–100	0–4	<0.1	0	0	0	0	ng	<2.0
100–250	0–770	0–1.4	220	0.6	0/72	<0.1	ng	Max.2.1
250–450	0–610	0–64	1100	5.8	0/32	<0.1	ng	<2.0
450–1050 (or bottom)	260–1300	1.2–2.0	1200	3.6	32/0	<0.1	1700–4500	2.8–6.5
1050–1850 (or 2000 m)	–	–	100	4.3	220/520	2.1/1.6	2600–9500	10–26

n , number of sampling series; TWD, total water depth; ng, data not given (low abundance).

^aBöttger-Schnack *et al.*, 2008.

^bBöttger-Schnack, unpublished data from southern Red Sea.

^cBöttger-Schnack, 1997.

^dBöttger-Schnack, 1996.

^eAfter Nishibe, 2005.

the armature and ornamentation of the maxilliped and the antenna, and in the nature of the labrum. Heron (Heron, 1977) placed *E. umbonata* in the genus on the basis of the leg armature. However, *E. umbonata* differs in several morphological characters from the type species *E. schmitti* and all other species in the genus, including the newly described Red Sea species. The most important differences separating *E. umbonata* from all known *Epicalymma* species are (i) the nature of the two setae within the longitudinal cleft of the maxillipedal basis, being short and unornamented (long and bipinnate in typical *Epicalymma* species); (ii) the ornamentation of the maxillipedal basis with two long rows of spinules (few long, stiff setules in typical *Epicalymma*); (iii) the labrum exhibiting a central, vertical bifurcation (not found in other *Epicalymma* species); (iv) the antenna with distal seta D being very short (long in other *Epicalymma* species); (v) antennary distal setae B–D and antennary lateral seta III indistinctly pectinate (only a few long and strong spinules bilaterally in all other *Epicalymma* species). Further differences are found in the lack of fusion of endopodal segments in P2–P4 and the ornamentation of the mandibular element E. Altogether, the combination of morphological characters found in *E. umbonata* indicate that the species may not be congeneric with *Epicalymma*.

The generic level classification of the family Oncaeidae, as defined by Huys and Böttger-Schnack (Huys and Böttger-Schnack, 1996–1997), is currently under review by Böttger-Schnack and Huys (Böttger-Schnack and Huys, 1998), who identified 20 species groups within the genus *Oncaea*, many of which may eventually be accorded generic status. According

to results of a first assessment of the phylogenetic relationships of species groups within the Oncaeidae (Böttger-Schnack and Huys, 1998), the genus *Epicalymma* Heron is a sistergroup of the *zernovi*-complex (Böttger-Schnack, 2002). Together they form a monophyletic group, which represents the most primitive offshoot in the early evolution of the Oncaeidae (Böttger-Schnack and Huys, 1998). More detailed information on the phylogenetic relationships within the Oncaeidae will be published after completion of the phylogenetic study, which is still in progress. By then, the species of the *umbonata*-group will eventually be placed in a new genus.

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