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Taxonomy of Oncaeidae (Copepoda, Poecilostomatoida) from the Red Sea. VI. Morphology and zoogeography of *Oncaea bispinosa* sp. nov., a sistertaxon of *O. zernovi* Shmeleva

RUTH BÖTTGER-SCHNACK

MARINE ZOOLOGIE (FB2), UNIVERSITÄT BREMEN (NW2), POSTFACH 330440, D-28334 BREMEN, GERMANY

POSTAL ADDRESS: MOORSEHDENER WEG 8, D-24211 RASTORF-ROSENFELD, GERMANY E-MAIL: dschnack@ifm.uni-kiel.de

A new small species of oncaeid copepods, Oncaea bispinosa, is described from the Red Sea. It is closely related to O. zernovi Shmeleva, which is known from the Atlantic and the Mediterranean. The two species can be separated mainly by the outer spine count on the distal exopod segment of the second swimming leg, which shows two spines in O. bispinosa, but three spines in O. zernovi. A neotype of O. zernovi, for which type material is no longer extant, was designated. Oncaea tenella sensu Malt et al. and O. tenella var. pacifica Olson are regarded as junior subjective synonyms of O. zernovi. First data on the zoogeographical distribution of the two species, which seem to be geographically separated, are provided by examination of material from the northeastern Atlantic, the Indian Ocean and the Pacific. The ecological importance of species of the zernovi-type, which appear to be one of the most numerous microcopepod species in tropical/subtropical areas, is emphasized.

INTRODUCTION

Small oncaeid species of the *zernovi*-type have recently been found to be one of the most numerous members of the oceanic microcopepod communities in low latitudes, such as the Red and Arabian Seas (Böttger-Schnack, 1990a, b, 1995, 1996), the Mediterranean [(Böttger-Schnack, 1997; Kršinić, 1998) and Kršinić unpublished data] and the upwelling area off northwest Africa (D. Schnack and S. Grau, unpublished data). In the Red Sea and in the eastern Mediterranean they account for up to 20% of the total copepod numbers (excluding nauplii) in the upper mesopelagic zone, between 100 and 450 m depth (Böttger-Schnack, 1995, 1997), and even higher values have been found in the Adriatic Sea (F. Kršinić, unpublished data). In the epipelagic zone, between the surface and about 100 m depth, *zernovi*-type oncaeids are also present in high numbers, but their relative abundance in this zone can be lower due to high concentrations of epipelagic copepod species, among which calanoid and cyclopoid taxa as well as oncaeid species of the *ivlevi*-group dominate (Böttger-Schnack, 1995, 1996; Kršinić, 1998). Due to their small size, about 0.3 mm in the adult stage, and the resulting difficulties in taxonomic identification, oncaeid species of the *zernovi*-type have not yet been identified and/or reported quantitatively outside these areas.

The *zernovi*-group, as defined in the preliminary version of an ongoing phylogenetic study of Oncaeidae (Böttger-Schnack and Huys, 1998), presently includes three species, *Oncaea tenella*, Sars, 1916, *O. zernovi* Shmeleva 1966, and *O. tenella sensu* Malt *et al.*, 1989. The taxonomy and zoogeography of *zernovi*-type oncaeids is not well known. *Oncaea tenella* was originally described from the western Mediterranean, near the Moroccoan coast (Sars, 1916) and was recorded also from the eastern Mediterranean (Malt *et al.*, 1989). However, a detailed comparison of the two descriptions during the present study confirmed earlier assumptions that Malt's description was based on a different species. Her specimens appear to be more similar to *O. zernovi*, as will be discussed in the present paper. The female of *O. zernovi* was originally described from the Adriatic Sea by Shmeleva (Shmeleva, 1966). Later, the author published a French version of the original Russian description, including additional material from the tropical Atlantic (Shmeleva, 1969). In both accounts, the morphological descriptions of the species are deficient and type material is no longer extant (Shmeleva, personal communication). Kršinić provided a detailed redescription of *O. zernovi* based on material from the type locality (Kršinić, 1988). He was the first to include data on the mouthparts and to describe the male.

Within the frame of a current taxonomic study of Red Sea Oncaeidae, first results of which have already been published (Böttger-Schnack, 1999, 2000, 2001), the species previously reported as *O. zernovi* from this area was found to represent a distinct yet closely related species. The new species, which will be described in the present account, differs from *O. zernovi* mainly in the leg armature of the second swimming leg. A detailed morphological comparison with its sister taxon *O. zernovi* will be provided upon re-examination of topotype material from the Adriatic Sea kindly made available by F. Kršinić, thereby complementing Kršinić's previous re-description of the species in 1988. A female of *O. zernovi* from the Adriatic Sea was designated as the neotype. Preliminary information on the zoogeographical distribution of the two species are provided by examination of material from the northeastern Atlantic, the Indian Ocean and the Pacific. The distributional records of *O. tenella*, for which no material was available, are reviewed from the literature. The vertical distribution pattern of the new species in the various regions of the Red Sea is presented, supplementing earlier ecological data from this area (Böttger-Schnack, 1995) and the few published quantitative data of *zernovi*-type oncaeids are summarized, thereby emphasizing their ecological importance within the microcopepod communities of tropical and subtropical areas.

METHOD

Oncaeids were collected with a multiple opening-closing net (MSN) (Weikert and John, 1981) with a mesh size of 0.055 mm during the RV 'Meteor' cruise 44/2 in 1999 in the Gulf of Aqaba, northernmost Red Sea (Figure 1A, B). The sampling programme was part of an ongoing ecological and taxonomic study on the microcopepod fauna in the Gulf of Aqaba (Böttger-Schnack *et al.*, 2001), conducted within the frame of a multidisciplinary research programme concerned with the impact of biological processes during early spring in the Gulf (Pätzold *et al.*, 2000; Sommer *et al.*, in press). Pre-sorted specimens from fine-mesh net samples taken with the same equipment during cruise 5 of RV 'Meteor' in 1987 in the northern and southern Red Sea, the eastern Mediterranean and the northern Arabian Sea were also included in the taxonomic study (Figure 1, Table I). Data on vertical distribution presented herein are based on earlier ecological investigations of the microcopepod community in the various regions of the Red Sea, 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 a 4% formaldehyde–sea water solution buffered with hexamethylene tetramine, and transferred after approximately 2 years into a preservation fluid of 5% propylene glycol, 0.5% propylene phenoxetol and 94.5% filtered sea water (Steedman, 1976). Zooplankton samples from the Adriatic Sea, which were kindly made available by Frano Kršinić (Dubrovnik), were used for the designation of the neotype of *O. zernovi*. Additional zooplankton material collected with fine-mesh nets in the northeastern Atlantic, upwelling area off northwest Africa, during cruise 64 of RV 'Meteor' (Siedler *et al.*, 1983), in the eastern Indian Ocean during cruise 76-5 of RV 'Hakuho Maru' with a Motoda net, mesh size 0.10 mm (material by S. Nishida), in the southeastern Indian Ocean, near the northwest Cape of Australia (material by D. McKinnon), and in the northeastern Pacific, near Monterey, California (material by R. Hopcroft) as well as unpublished taxonomic data on *zernovi*-type specimens collected in the northwestern Pacific, around Japan, which were kindly made available by H. Itoh, were used for the examination of zoogeographical distribution of *zernovi*-type oncaeids.

Specimens were dissected in lactic acid, mounted on slides in lactophenol, and sealed with high-quality nail-varnish. All the 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 mid-dorsal 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 the 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). The following abbreviations are used in the text: ae, aesthetasc; enp, endopod; exp, exopod; exp(or enp) –1, –2, –3, denote the proximal, middle, distal segments of a

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 and adjacent areas

Station	Date	Geographic position	Time	Sampling depth (m)	Total water depth (m)
R/V 'Meteor' Cruise 5					
Eastern Mediterranean Sea, near Crete					
35	20.1.1987	34°25.3′N 26°14.8′E	N	250–300	3400
Central-northern Red Sea					
663	20.7.1987	22°58.4′N 37°19.4′E	D	150–200	1200
Southern Red Sea, Strait of Bab al Mandab					
641	12.7.1987	12°39.5′N 42°14.5′E	D	100–120	245
Northern Arabian Sea					
496	12.5.1987	18°00.1′N 66°25.5′E	N	50–100	3035
R/V 'Meteor' Cruise 44/2					
Gulf of Aqaba, northern Red Sea					
151	01.03.1999	29°29.41′N 34°57.02′E	D/N	250–300	596
164	06.03.1999	29°51.03′N 34°04.98′E	N	0–50	824

D, day; N, night; D/N, dusk.

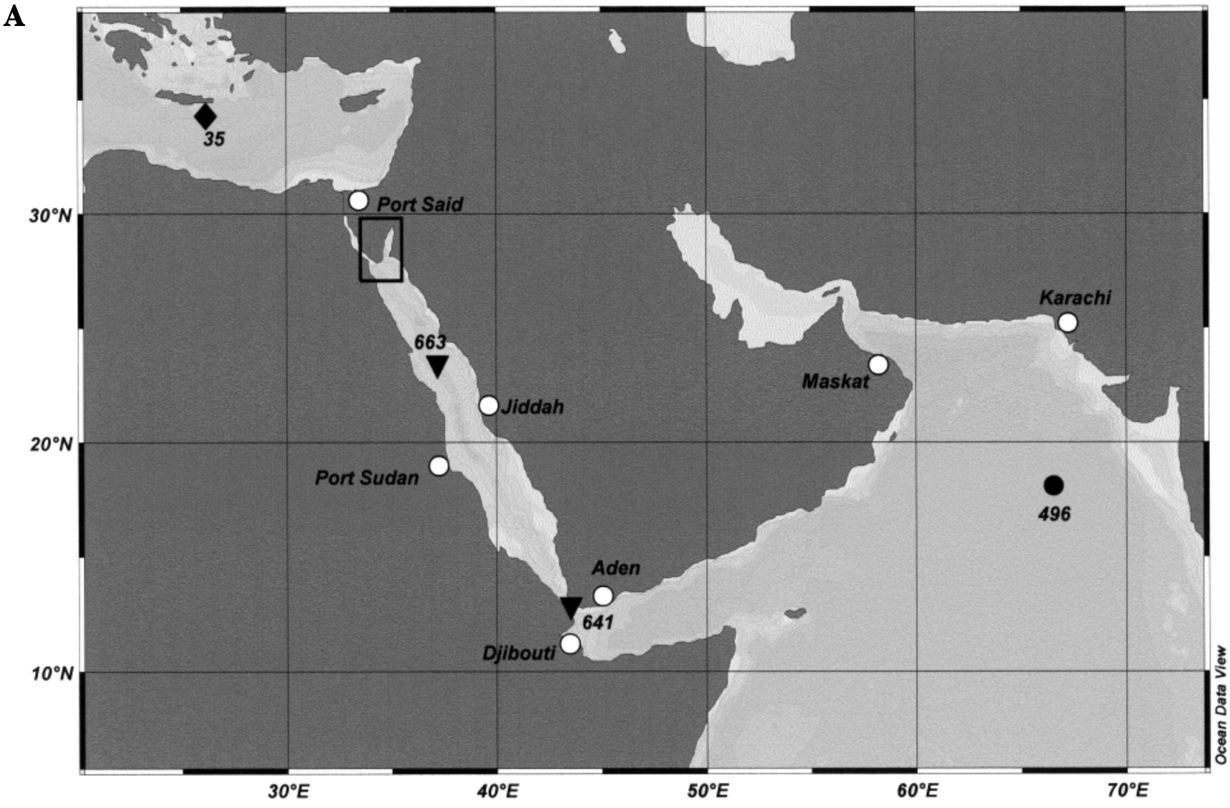

Fig. 1. Location of sampling stations. (**A**) Red Sea and adjacent areas (**B**) Gulf of Aqaba, northern Red Sea. ◆ = METEOR-Cruise 5/1, January 1987; ● = METEOR-Cruise 5/3b, May 1987; ▼ = METEOR-Cruise 5/5, July/August 1987; ■ = METEOR-Cruise 44/2, March 1999.

B

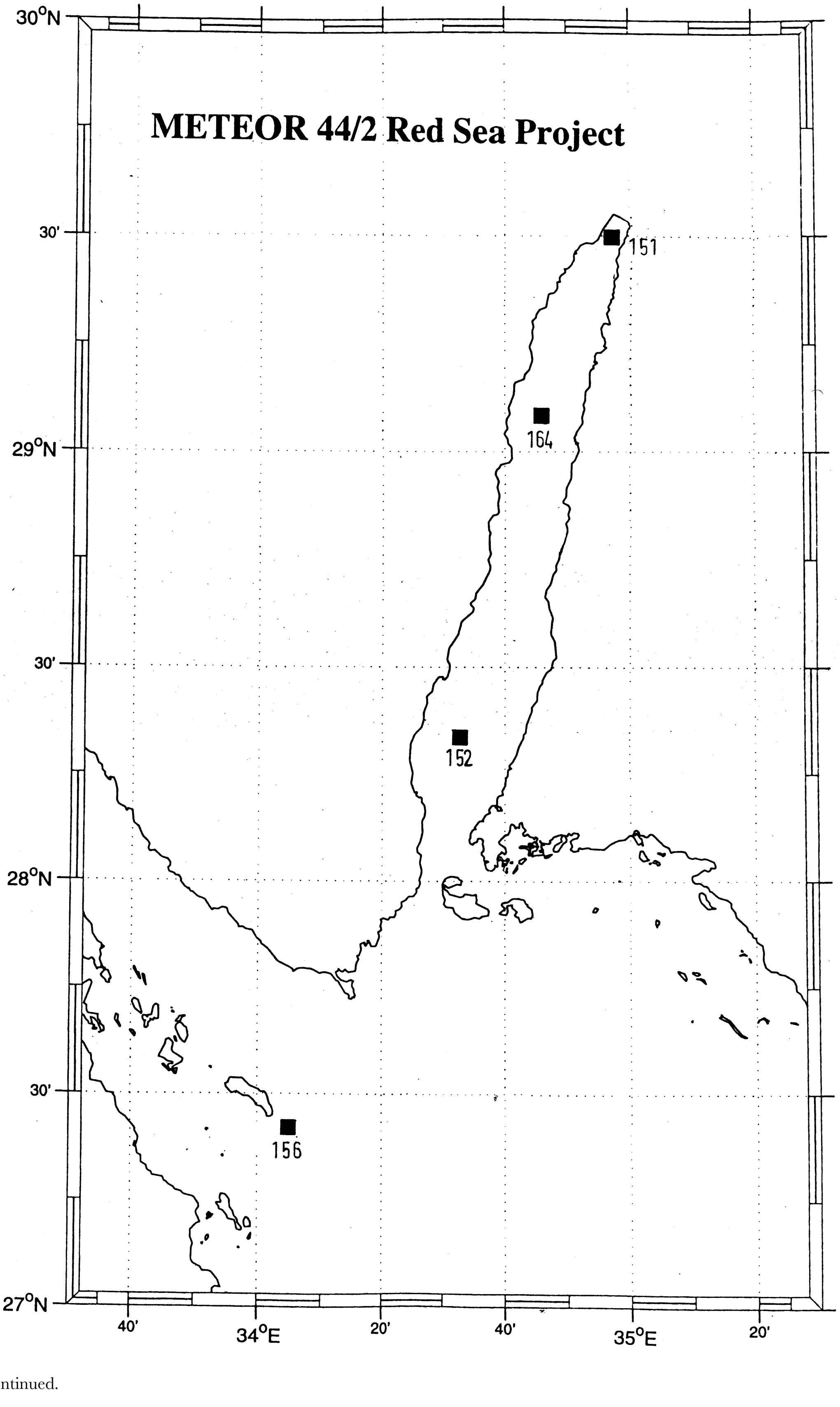

Fig. 1. Continued.

ramus; P1–P6, the first to sixth thoracopods. Oncaeidae typically exhibit pores and other integumental structures (e.g. pits, scales) on the body surface, but these were hardly discernible with a light microscope in *zernovi*-type specimens due to the weak sclerotization of the exoskeleton. Type, neotype 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). Paratypes or other material retained in the personal collection of R. Böttger-Schnack are designated RBS.

DESCRIPTION OF *ONCAEA BISPINOSA* SP. NOV.

Type locality

Gulf of Aqaba, Red Sea, 29°E 51.03′N, 34°E 45.99′E: Station 164; RV 'Meteor' leg 44/2: collected March 6, 1999 with MSN 0.055 mm net (Haul 11/5); depth 0–50 m; total water depth 824 m.

Material examined

(1) Gulf of Aqaba, Red Sea, 29°E 51.03′N, 34°E 45.99′E: Station 164; RV 'Meteor' leg 44/2: collected March 6, 1999 with multiple opening-closing net (MSN) with 0.05 mm mesh size (Haul 11/5); depth 0–50 m; total water depth 824 m.
  (a) Holotype ♀, in alcohol (ZMH reg.no. K-40093). Paratypes, two ♀♀, three ♂♂ in alcohol (ZMH reg.no. K-40094).
  (b) two ♀♀, three ♂♂ in alcohol (NHM reg.no. 2001.6769–6773).
  (c) one ♂ dissected on slides, two ♀♀, two ♂♂ partly dissected, antennula, antenna and mouthparts on slides, remaining specimens in alcohol, four ♀♀, two ♂♂ on slides, two ♀♀, three ♂♂ in alcohol (RBS).

Additional paratypes

(2) Gulf of Aqaba, Red Sea, 29°E 29.41′N, 34°E 57.02′E: Station 151; RV 'Meteor' leg 44/2: collected March 1, 1999 with MSN 0.055 mm net (Haul 2/4); depth 250–300 m; total water depth 596 m: one ♀ (typical form), one ♀ (expanded prosome) on slide (RBS).
(3) Northern Red Sea, 22°E 58.4′N, 37°E 19.4′E: Station 663; RV 'Meteor' leg 5/5: collected July 20, 1987 with MSN 0.05 mm net (Haul 17/2); depth 150–200 m; total water depth 1200 m: two ♀♀, one ♂ dissected on slides (RBS).
(4) Southern Red Sea, Strait of Bab al Mandab, 12°E 39.5′N, 42°E 14.5′E: Station 641; RV 'Meteor' leg 5/5: collected July 12, 1987 with MSN 0.055 mm net (Haul 6/4); depth 100–120 m; total water depth 245 m: one ♀ dissected on slides, two ♀♀ on slides (RBS).
(5) Northern Arabian Sea, 18°E 00.1′N, 66°E 25.5′E: Station 496; RV 'Meteor' leg 5/3b: collected May 12, 1987 with MSN 0.055 mm net (Haul 4/2); depth 50–100 m; total water depth 3035 m: two ♀♀ on slide (RBS).
(6) Equatorial Indian Ocean, 04°E 47.7′S, 87°E 14.4′E: Station 11; RV 'Hakuho Maru' leg 76–5: collected January 24, 1977 with Motoda 0.10 mm net; depth 75 m, horizontal haul; total water depth 3035 m (leg. S. Nishida): one ♀, one ♂ on slide (RBS).

Description

Adult female (Figures 2–4)

Body length (measured in lateral aspect; from anterior margin of rostral area to posterior margin of caudal rami, calculated as sum of individual somites): 423 μm [traditional method: (a) 333 μm, range 320–340 μm, based on three specimens from the Red Sea measured during present study; (b) 310 μm, range 310–320 μm, based on 25 Red Sea specimens (Böttger-Schnack *et al.*, 1989); these values are probably underestimated, because the caudal ramus, which is very weakly sclerotized, may have been excluded from the earlier length measurements].

Exoskeleton weakly chitinized. Rostral area gradually tapering in dorsal view (Figure 2A). Prosome 2.2 times length of urosome, excluding caudal rami, 2.0 times urosome length including caudal rami. P2-bearing somite without conspicuous dorso-posterior projection in lateral aspect (Figure 2B). Integumental pores on prosome as indicated in Figure 2A,B, probably not fully discerned. Pleural areas of P4-bearing somite with rounded postero-lateral corners. Expanded prosome of some specimens from the northernmost Gulf area as shown in Figure 2G.

Proportional lengths (%) of urosomites are 8.1 : 70.9 : 4.5 : 4.0 : 12.5. Proportional lengths (%) of urosomites and caudal rami are 7.3 : 63.4 : 4.0 : 3.6 : 1.2 : 10.5.

Genital double-somite twice as long as maximum width (measured in dorsal aspect) and about eight times as long as postgenital somites combined; largest width measured at anterior third, posterior part tapering gradually. Paired genital apertures located dorsally at about one-third distance from anterior margin of genital double-somite; armature represented by one long spine, spinous process(es) absent. Pore pattern on dorsal surface as indicated in Figure 2C, other surface ornamentation absent.

Anal somite1.3 times wider than long; 1.4 times longer than caudal rami (Figure 2C). Two pairs of secretory pores present dorsally, one pair on either side of anal opening, the second near the posterior margin. Paired dorsal sensillae anterior to anal operculum not found,

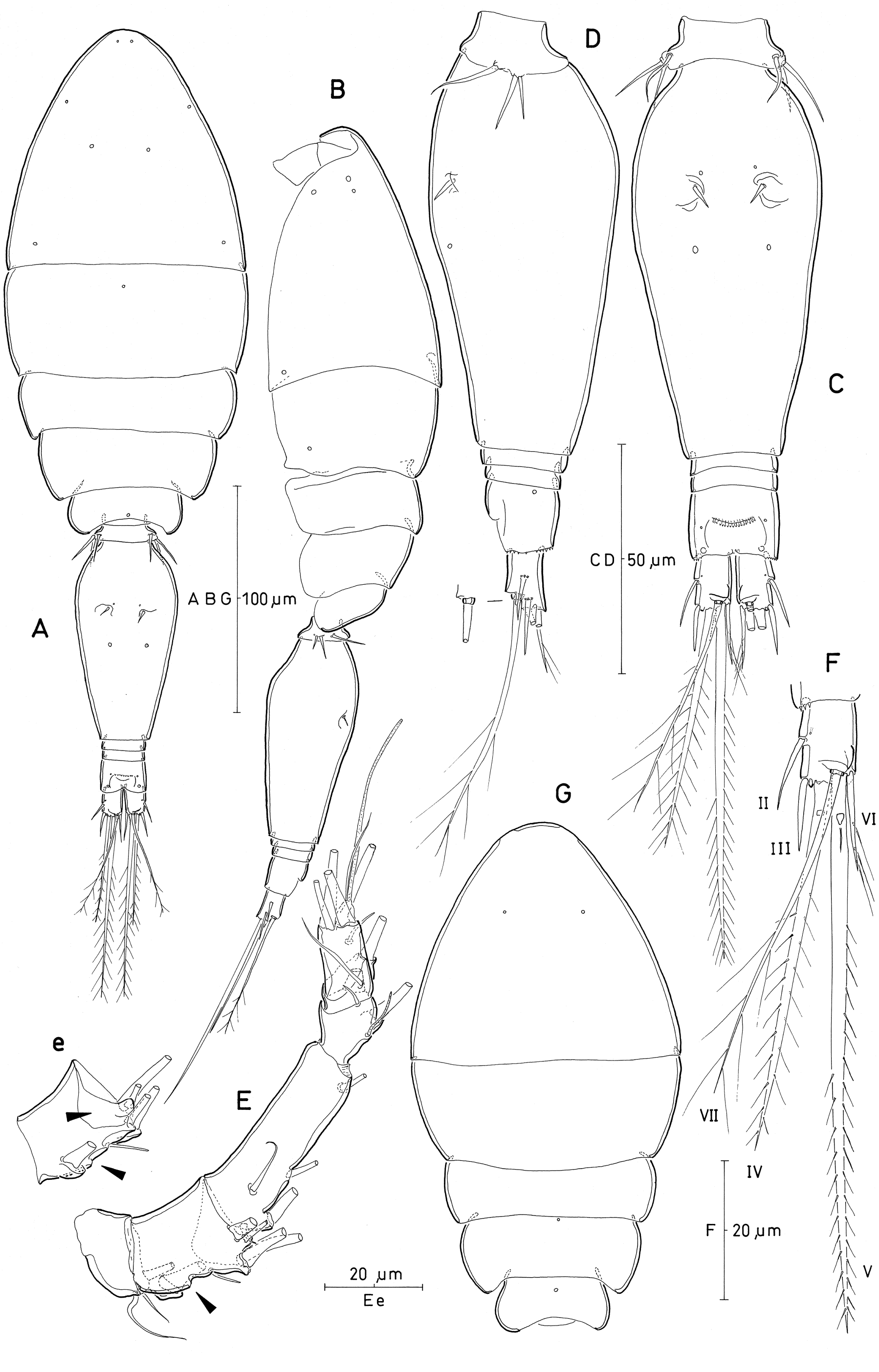

Fig. 2. *Oncaea bispinosa* sp. nov., female (Red Sea) (**A**) Habitus, typical form, dorsal, pore pattern on prosome not fully discerned; (**B**) same, lateral (appendages omitted); (**C**) urosome, dorsal, setae IV, V and VII on left side omitted; (**D**) urosome, lateral, bi-articulation at base of seta VII figured separately; (**E**) antennule, [e, segment 2]; arrows indicating the position at which additional setae are present in most other oncaeid species, which are not found in *O. bispinosa* (see text); (**F**) caudal ramus, dorsal; (**G**) expanded prosome, dorsal, pore pattern not discerned.

probably absent. Anterior margin of anal opening (vestigial anal opening) with transverse row of minute spinules (?). Ventral surface with paired pore near posterior margin as figured for male (cf. Figure 5E). Posterior margin of somite finely serrate ventrally and laterally (Figure 2D).

Caudal ramus (Figure 2F) 1.3 times longer than wide.

Small expansion on dorsal surface surrounding insertion of seta VII. Armature consisting of six elements: setae II and III spiniform and bare; seta IV long and plumose; seta V longest and plumose; seta VI short, slightly longer than seta III and ornamented with few setules along inner margin, slightly longer than caudal ramus; seta VII about as long as seta IV, sparsely plumose and bi-articulate at base (Figure 2D). Inner margin of caudal ramus unornamented, posterior margin finely serrate ventrally; dorsal and ventral surface unornamented, except for dorsal anterior surface with secretory pore near insertion of seta II (Figure 2F).

Antennule six-segmented (Figure 2E), relative lengths (%) of segments measured along posterior non-setiferous margin 7.9 : 19.1 : 40.4 : 10.7 : 6.2 : 15.7. Armature formula: 1-[3], 2-[6], 3-[5], 4-[3+ae], 5-[2], 6-[5+(1+ae)]. Seta on anterior margin of segment 2 with rounded tip, probably representing sensory element. Small sensory element on segment 6 not discernible. Aesthetasc on segment 4 very small, aesthetasc on segment 5 absent; apical aesthetasc well developed and fused basally to adjacent seta.

Antenna three-segmented, distinctly reflexed (Figure 3A). Coxobasis with row of long, fine spinules along outer margin; with short seta at inner distal corner, ornamented with spinules bilaterally. Endopod segments unequal in length; proximal endopod segment moderately subtriangular forming outer lobate outgrowth bearing three strong spinules or denticles, with short row of three very strong denticles extending from posterior surface to posterior inner margin. Distal endopod segment slightly longer than proximal segment, with narrow cylindrical base articulating with the proximal endopod segment; posterior surface with two rows of spinules along outer margin, which are short (distal row) or of varying length (proximal row); lateral armature consisting of two bare setae, with seta I shorter than seta II, 1 strong, spiniform seta (III), ornamented with spinules bilaterally at distal part, and one minute seta (IV), which is difficult to discern; distal armature consisting of four long, spiniform setae (A–D), ornamented with spinules bilaterally at distal part, and one short, bare seta (E); seta F and G absent.

Labrum (Figure 3B,C) distinctly bilobed. Distal (ventral) margin of each lobe with one strong marginal tooth medially, and one or two teeth adjacent to it, which are smaller, short row of denticles at outer ventral margin and row of broad spinules or denticles along inner margin. Median concavity covered anteriorly by several overlapping rows of spatulated setules. Anterior surface (Figure 3B) unornamented, except for large secretory pore posterior to median swelling. Posterior wall of medial concavity with two chitinized spinous teeth and patch of setules, flanked by row of broad spinules or denticles (Figure 3C). Posterior face with two secretory pores located distally on each lobe.

Mandible (Figure 3D) gnathobase with five elements: three setae and two blades. Ventral element (A) as long as as ventral blade (B), with long fine setules along dorsal side; ventral blade strong and spiniform, with row of minute spinules on posterior side; dorsal blade (C) strong and very broad, spinulose along distal half of dorsal margin; seta D with double row of setules along dorsal margin; dorsal element (E) setiform and bipinnate.

Maxillule (Figure 3E) indistinctly bilobed, surface ornamentation not discernible. Inner lobe (praecoxal arthrite) with three elements: outermost element spiniform, swollen at base, ornamented with spinules unilaterally; middle element setiform and bare; innermost element located along concave inner margin close to other elements, bipinnate at distal half. Outer lobe with three setiform elements [innermost element absent], which are bare or sparsely unipinnate.

Maxilla (Figure 3F) two-segmented, allobasis almost as long as syncoxa. Syncoxa unarmed, surface ornamented short row of 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 extending to tip of allobasal claw, ornamented with two long spinules bilaterally at distal part, tip of seta without tubular extension; inner margin with short naked seta and strong basally swollen spine with double row of strong spinules along the medial margin and two shorter spinules along outer margin.

Maxilliped (Figure 3G) four-segmented, comprised of syncoxa, basis and two-segmented endopod. Syncoxa unarmed, without surface ornamentation. Basis elongate and slender, palmar margin with two spiniform bi- or unipectinate elements, proximal element about three-fifths the length of distal element; short row of small spinules between half the distance of distal seta and articulation with endopod; anterior surface with two spinular rows along palmar margin, distalmost spinule of first row very long, as illustrated in Figure 3G. 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 minute, naked seta on outer proximal margin and unipectinate spine fused basally to inner proximal corner of claw.

Swimming legs 1–4 biramous (Figure 4A–D), with three-segmented rami. Armature as shown in Table II. Intercoxal sclerites well developed, without ornamentation. Coxae and bases of P1–P4 with sparse surface ornamentation as shown in Figure 4A–D. Bases with short naked outer seta; with anterior secretory pore near

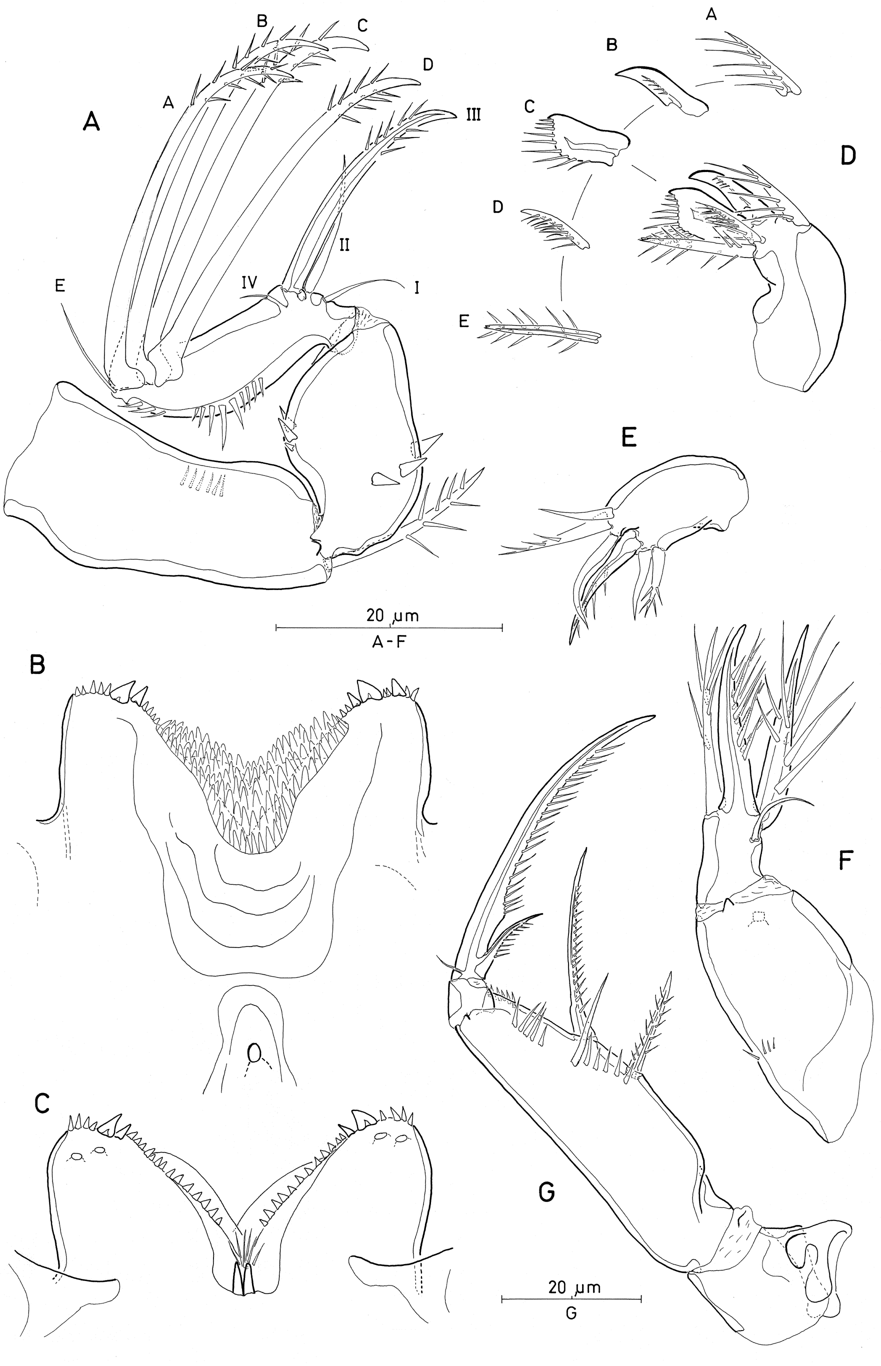

Fig. 3. *Oncaea bispinosa* sp. nov., female (Red Sea) (**A**) Antenna; (**B**) labrum, anterior; (**C**) same, posterior; (**D**) mandible, showing individual elements; (**E**) maxillule; (**F**) maxilla; (**G**) maxilliped.

outer proximal corner; inner portion slightly produced adaxially into rounded (P1) or pointed (P2–P4) process (Figure 4B–D); inner margin of basis with two short spinules in P1 (Figure 4A,a). Inner basal seta on P1 spiniform and naked. Respective legs without distinct length differences between exopod and endopod. Bases of spines on exopodal and endopodal segments anteriorly surrounded by small spinules, most obvious around terminal

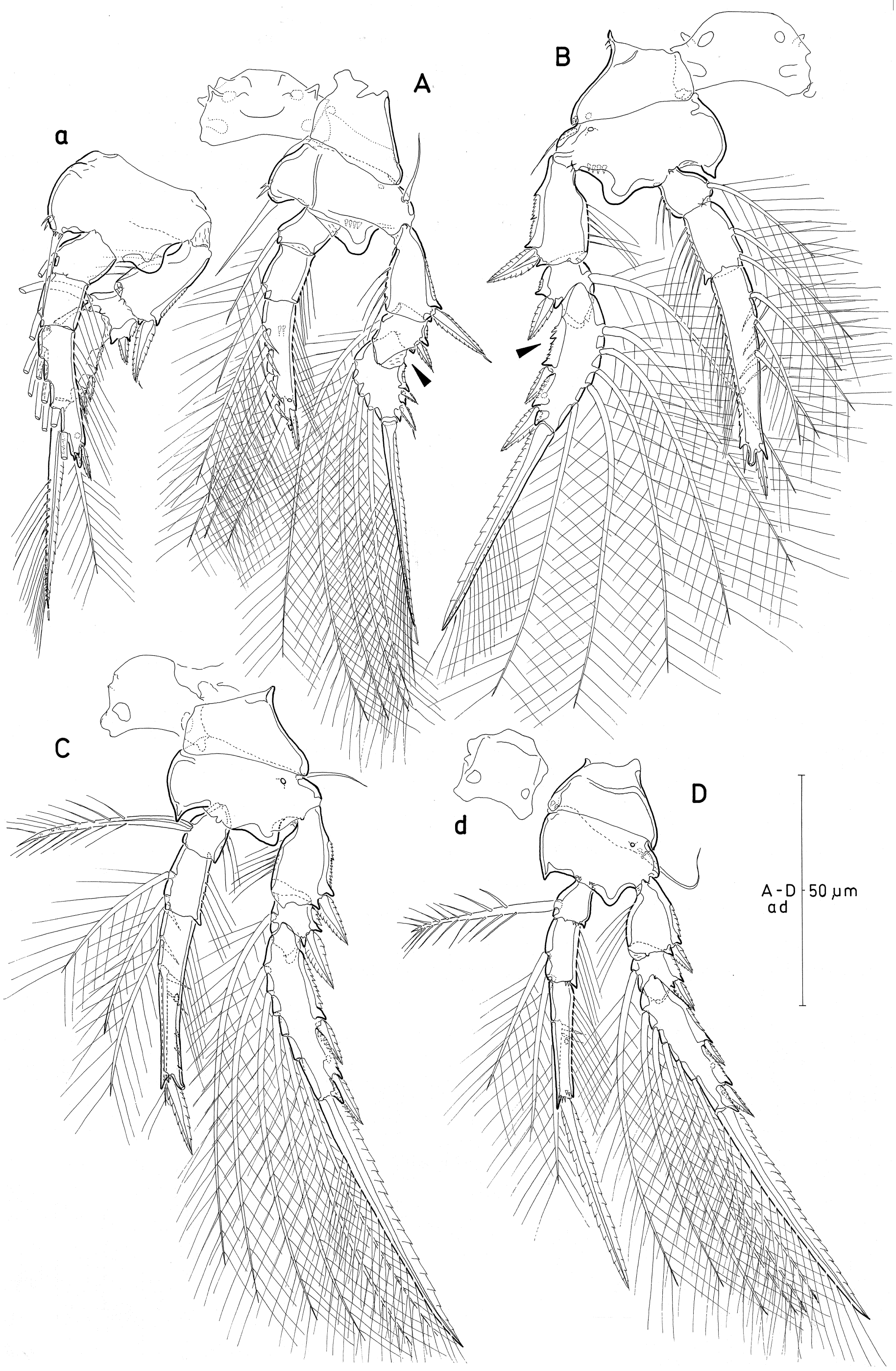

Fig. 4. *Oncaea bispinosa* sp. nov., female (Red Sea) (**A**) P1, posterior, arrow indicating broad membrane between exopod segment 2 and 3 [*a*, same, anterior, showing typical position of inwardly folded exopod; coxa and intercoxal sclerite omitted]; (**B**) P2, anterior, arrow indicating small gap in serrated hyaline lamella on outer margin (see text); (**C**) P3, anterior, intercoxal sclerite slightly damaged; (**D**) P4, anterior [d, intercoxal sclerite].

Table II: Oncaea bispinosa sp. nov., armature of swimming legs

	Coxa	Basis	Endopod	Exopod
Leg 1	0–0	1-I	0–1; 0–1; 0,I,5	I-0; I-1; II,I,4
Leg 2	0–0	1–0	0–1; 0–2; I,I,3	I-0; I-1; **II**,I,5
Leg 3	0–0	1–0	0–1; 0–2; 0,I,2	I-0; I-1; II,1,5
Leg 4	0–0	1–0	0–1; 0–2; 0,I,1	I-0; I-1; II,I,5

Roman numerals indicate spines, arabic numerals represent setae. Exopodal spine count differing from *O. zernovi* marked in bold.

endopod spines of P3 and P4 (Figure 4C,D). Surface ornamentation of all segments sparse.

Exopods, P1 with distal exopod segment greatly reduced in length; typical position of inwards folded exopod shown in Figure 4a; broad membrane on posterior outer margin between exp-2 and -3 arrowed in Figure 4A. Outer margin of exopod segments with well-developed serrated hyaline lamella, which has a small gap on proximal third of P2 exp-3 (arrowed in Figure 4B), possibly indicating the position at which an additional spine is found in the sister taxon *O. zernovi* (see Figure 7C, arrowed); inner margin of proximal exopod segments with long setules. Secretory pore present on posterior surface of distal segments in P2–-P4. Hyaline lamellae on outer spines well developed, narrow hyaline lamella on terminal spine in P1; outer and terminal spines of P1 with subapical tubular extension, except for spine on exp-2 and proximal spine of exp-3, which are also reduced in length. Outer spines well developed (P2+P3) or reduced in length (P4); spines on P1 differing in size, with spine on exp-1 very long, those on exp-2 and -3 considerably reduced in length. Terminal spines much longer than distal exopod segments, almost as long as entire exopod in P1 and P3–P4. Ornamentation of terminal spines of P1 and P2 not fully discernible, probably ornamented with small denticles in addition to long setules.

Endopods, outer margin of endopod segments with fringe of long setules, except for proximal segment of P1 and P4; fringe on distal segment extending along entire length (P1 + P4) or along proximal half as far as position of posterior pore (P2 + P3) with distal half ornamented with denticles on posterior face (Figure 4B,C). Distal segment of P3 and P4 tapering at distal half. Inner seta of proximal endopod segment reduced in length in P1–P4; this seta slightly swollen and spiniform in P3 and P4, ornamented with strong spinules bilaterally. Distal endopod segments with single secretory pore on posterior surface; distal margin of P2 and P3 produced into conical process with apical pore (Figure 4B,C). Terminal spine increasing in length from P1 to P4: very short in P1 and P2, about half the length of distal endopod segment in P3, and almost as long as entire endopod in P4. Outer subdistal spine shorter than distal spine in P2. Outer margin of distal segment of P1 terminating in a long process obscuring insertion of distalmost inner seta (Figure 4a). Spinular comb on proximal inner margin of inner setae of distal endopod segments of P1–4 reduced to one or two strong spinules, proximal spinule strongest and swollen at base; single strong spinule also present on distal inner seta of middle endopod segment in P3.

P5 (Figure 2G) comprising short outer basal seta, which is bare, and small exopod segment fused to somite. Exopodal setae short, spiniform and naked, dorsal element slightly longer than ventral element.

P6 (Figure 2C) represented by operculum closing off each genital aperture; armed with a long spine, spinous process(es) absent.

Egg-sacs not found.

Adult male (Figure 5)

Body length: 350 μm [traditional method: 305 μm, range 280–320 μm, based on four specimens.] Pore pattern on prosome not discerned. Sexual dimorphism in antennule, maxilliped, P6, and in genital segmentation, slight modification in setal length of P5.

Proportional lengths (%) of urosomites (excluding caudal rami) 8.4 : 67.4 : 4.7 : 3.7 : 3.7 : 12.1; proportional lengths (%) of urosomites (caudal rami included) 7.5 : 59.9 : 4.1 : 3.3 : 3.3 : 10.7 : 11.2. Length to width of caudal rami and proportional lengths of caudal setae as in female. Dorsal surface of genital somite without pores. Surface of genital flaps unornamented except for single denticle at outer posterior corner (Figure 5E,F).

Antennule (Figure 5B) four-segmented; distal segment corresponding to fused segments 4–6 of female; relative lengths (%) of segments measured along posterior non-setiferous margin 9.8 : 20.2 : 44.8 : 25.2. Armature formula: 1-[3], 2-[6], 3-[4], 4-[10+(1+ae)].

Maxilliped (Figure 5C) three-segmented, comprising syncoxa, basis and one-segmented endopod. Syncoxa unarmed and without surface ornamentation. Basis elongate, moderately inflated in proximal half forming

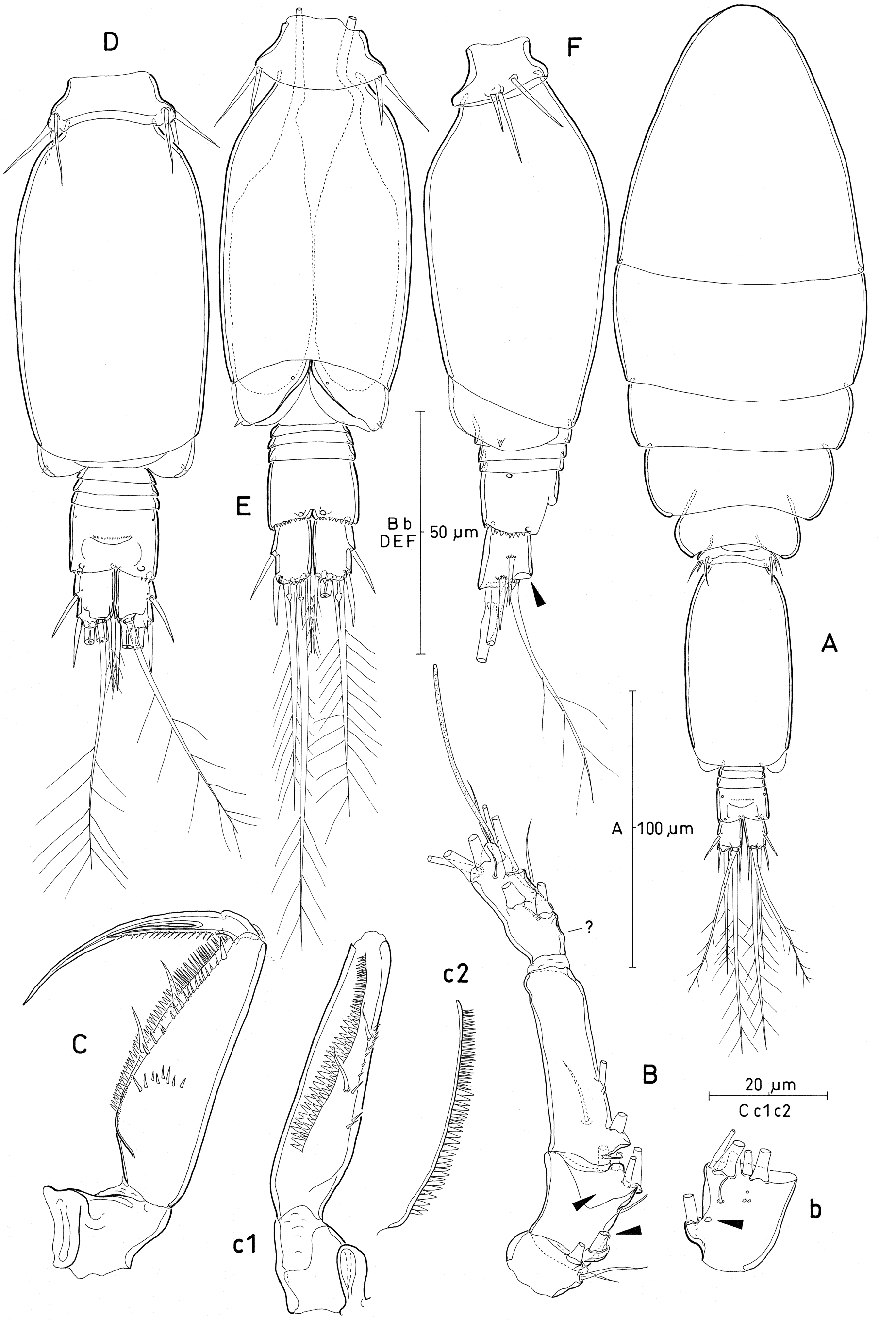

Fig. 5. *Oncaea bispinosa* sp. nov., male (Red Sea) (**A**) Habitus, dorsal; (**B**) antennule, [**b**, segment 2], arrows indicating the position at which additional setae are present in most other oncaeid species, which are not found in *O. bispinosa* (see text); question mark indicating the position at which an aesthetasc is present in the female (cf. Figure 2E), which was not found in the male; (**C**) maxilliped, anterior [**c1**, same, medial view, claw omitted; **c2**, inner margin of basis, posterior]; (**D**) urosome, dorsal, caudal ramus seta IV and V omitted; (**E**) urosome, ventral, left caudal ramus seta V omitted (spermatophores not fully developed); (**F**) same, lateral, arrow indicating dorsal expansion on caudal ramus.

indistinct bulbous swelling; anterior surface with one transverse spinular row in addition to row of short spinules along inner margin (Figure 5C); posterior surface with one or two rows of short spatulated spinules of graduated length along palmar margin (Figure 5c1), decreasing in width distally (Figure 5c2); with two small naked setae within the longitudinal cleft, which are about equal in length. Endopod drawn out into long curved claw, concave margin unornamented; accessory armature consisting of long, unipectinate spine basally fused to inner proximal corner of claw; tip of claw without hyaline apex (Figure 5C).

P1–P4 with armature and ornamentation as in female.

P5 (Figure 5D,F) exopod not delimited from somite, general shape and armature as in female, except for exopodal setae being slightly shorter than in female; outer basal seta as in female.

P6 (Figure 5E) represented by posterolateral flap closing off genital aperture on either side; ornamented with single denticle as shown in Figure 5E; posterolateral corners not protruding laterally and not well discernible in dorsal aspect (Figure 5D).

Spermatophore oval, of variable size according to state of maturity (Figure 5E); swelling of spermatophore during development not affecting shape and relative size of genital somite.

Etymology

The specific name is derived from the Latin prefix *bi*-, meaning two, and *spinosus*, meaning carrying spines, and refers to the outer spine count on the distal exopod segment of P2.

Taxonomy

Oncaea bispinosa is a sistertaxon of *Oncaea zernovi* Shmeleva, with which it has been confounded during earlier ecological studies in the Red and Arabian Seas (Böttger-Schnack, 1990a, b, 1995, 1996). It can readily be distinguished from *O. zernovi* by the outer spine count on P2 exopod-3, showing two spines, whereas the typical number of three spines is found in *O. zernovi* (Table III). Females of the two species differ slightly in size, with *O. bispinosa* being smaller than *O. zernovi*, and in the form of the genital double-somite, which is less slender in *O. bispinosa*. A further difference is found in the length of the distal endopod spine in P3, which is about half the length of the distal segment in *O. bispinosa* but about two-thirds the length in *O. zernovi*. Males of the two species are similar in length and do not exhibit any further morphological differences, except for the endopodal spine length mentioned above. The general habitus of both species is very similar, and no differences in ornamentation details were found between the two species upon detailed re-examination of *O. zernovi* from the type locality in the Adriatic Sea (see below). Thus, an unequivocal identification of the two species requires microscopic examination of the swimming legs.

The antennule of *O. bispinosa* and *O. zernovi* displays a setal formula differing from that of most other oncaeids as will be discussed in the discussion section. The position at which two additional setae on segment 2 are usually found in oncaeid species (but are not present in species of the *zernovi*-type) are indicated by arrows in Figure 2E, e and Figure 5B, in order to ease the identification of elements on this segment. In the male, the lateral seta on segment 2 seems to be replaced by a deep pit, which is marked by an arrow in Figure 5b.

Form variants

In the northernmost part of the Gulf of Aqaba, several females of *O. bispinosa* were found, which exhibited a conspicuous expansion of the anterior prosome (Figure 2G). The same phenomenon was observed in its sister taxon *O. zernovi* in the Adriatic Sea and it occurred regularly in *O. zernovi* populations from the northeastern Atlantic (see below). Heron reported specimens with an abnormal expansion of the prosome for several oncaeid species (e.g. *O. setosa*, *O. pumilis*) in the Pacific and related this deformation to internal cystic growth under tergite (Heron, 1977; Heron *et al.*, 1984). [The same author reported a propensity for developing a tumorous growth on the mid-dorsal surface of the prosome for *Triconia derivata*, which appeared to be associated with pores (Heron and Bradford-Grieve, 1995).] In the case of *O. bispinosa* and *O. zernovi*, no internal cysts could be observed, rather the expansion of the prosome seemed to be related to the development of eggs (?) in the body.

Ecological notes

Geographical distribution

Oncaea bispinosa is distributed throughout the Red Sea, including its northernmost extension, the Gulf of Aqaba [(Böttger-Schnack, 1988), as *Oncaea* sp. P, (Böttger-Schnack, 1990a, b, 1995), Böttger-Schnack *et al.*, 2001 as *Oncaea zernovi*)]. No information is available on its occurrence in the Gulf of Suez. The species was also recorded from the northern Arabian Sea and the Equatorial Indian Ocean during the present study. In the samples from the southeastern Indian Ocean, off the northwest Cape of Australia, however, specimens of the *zernovi*-type were found to belong to the closely related *O. zernovi* (Table V).

Vertical distribution and vertical migration

In the Red Sea, *Oncaea bispinosa* exhibits a wide vertical distribution range, extending from the epipelagic to the

Table III: Oncaea zernovi, armature of swimming legs

	Coxa	Basis	Endopod	Exopod
Leg 1	0–0	1-I	0–1; 0–1; 0,I,5	I-0; I-1; II,I,4
Leg 2	0–0	1–0	0–1; 0–2; I,I,3	I-0; I-1; **III**,I,5
Leg 3	0–0	1–0	0–1; 0–2; 0,I,2	I-0; I-1; II,I,5
Leg 4	0–0	1–0	0–1; 0–2; 0,I,1	I-0; I-1; II,I,5

Roman numerals indicate spines, arabic numerals represent setae. Exopodal spine count differing from O. bispinosa marked in bold.

Table IV: Oncaea tenella, armature of swimming legs [after (Sars, 1916), Plate V]

	Coxa	Basis	Endopod	Exopod
Leg 1	0–0	1-I	0–1; 0–1; 0,I,5	I-0; I-1; II,I,4
Leg 2	0–0	1–0	0–1; 0–2; I,II,3	I-0; I-1; III,I,5
Leg 3	no information		0–1; 0–2; I,II,2	no information
Leg 4	no information		0–1; 0–2; 0,II,1	no information

mesopelagic zone, with a few individuals found as deep as 1650 m [(Böttger-Schnack, 1990a, b, 1995), and unpublished data from summer 1987]. The main bulk of the population was found in the upper 450–600 m. Within this depth range, females exhibited a bimodal distribution pattern in the epi- and upper mesopelagic zone in the central area during the autumn: the epipelagic population was concentrated in the 20–40 m depth layer during the day and shifted upwards into the surface zone during the night, while the mesopelagic population occurred mainly between 200 and –300 m without diurnal differences (Böttger-Schnack, 1990a). No consistent seasonal and/or regional differences from this distribution pattern were apparent during winter and/or in the northern Red Sea (Böttger-Schnack, 1990b). During the summer, this bimodal pattern again became apparent for both sexes in the central Red Sea (Figure 6D), but differed in the other areas between uni-, bi-, or even plurimodal patterns and was also different between sexes. This was most conspicuous in the Gulf of Aden and the Strait of Bab al Mandab, where females had a bimodal vertical distribution in the upper 250 m (or bottom), while males were mainly concentrated in the upper 50 m (Figure 6).

The actual abundance of *O. bispinosa* was underestimated considerably in the earlier ecological studies in the Red Sea (Böttger-Schnack, 1988, 1990a, b), because a net of 0.1 mm mesh had been used, which does not sample the adults quantitatively (Böttger, 1985). Subsequent zooplankton studies, which were conducted with a finer net, of 0.055 mm mesh size, during the summer yielded two to five times more adults in the central Red Sea (Böttger-Schnack, 1995). However, as the samples were taken during a different season, the differences might also reflect a considerable seasonal variation in abundance in this area. The proportion of males differed considerably between the two surveys: they made up 2–10% of the adults in the 0.1 mm net samples (Böttger-Schnack *et al.*, 1989), but comprised about 25% of the adults in the 0.055 mm net samples. Besides some seasonal variation in sex ratio this might also indicate a more efficient catch of the somewhat smaller and more slender males by the smaller mesh nets.

In the 0.055 mm mesh nets, *O. bispinosa* was among the three most numerous oncaeid species, the adults of which contributed 10–17% to the total standing stock of oncaeids in the upper 1050 m of the water column in the Red Sea (Böttger-Schnack, 1995). These values might have been even greater if all juvenile stages of the species had been identified. The relative abundance of the species was greatest in the upper mesopelagic zone, between 100 and 450 m depth, where it represented between 20 and 30% of total oncaeids. In the epipelagic zone, between the surface and 100 m depth, they were also present in high concentrations (Figure 6), however, their relative

Table V: Zoogeographical distribution of Oncaea zernovi Shmeleva and O. bispinosa sp. nov., identified by the outer spine count on distal exopod segment of P2

Region	No. of spines	Species identification
Atlantic Ocean		
Northeastern Atlantic, upwelling off northwest Africa	3	*O. zernovi*
Adriatic Sea [type locality]	3	*O. zernovi*
Eastern Mediterranean	3	*O. zernovi*
Red Sea and Indian Ocean		
Red Sea [type locality]	2	*O. bispinosa* sp. nov.
Northern Arabian Sea	2	*O. bispinosa* sp. nov.
Equatorial Indian Ocean	2	*O. bispinosa* sp. nov.
Southeastern Indian Ocean, off northwest Cape Australia	3	*O. zernovi*
Pacific Ocean		
Northwest Pacific, neighbouring waters of Japan[a]	3	*O. zernovi*
Northeast Pacific, off Monterey, California	3	*O. zernovi*

[a] Based on unpublished data by H. Itoh.

abundance in this layer was lower (10–20%) due to high concentrations of epipelagic oncaeid species, such as *Spinoncaea ivlevi* and its congeners (Böttger-Schnack, 1995, 2002), *Triconia dentipes* and related forms (Böttger-Schnack, 1995, 1999), *Oncaea scottodicarloi* (Böttger-Schnack, 1995, 2001) and *Monothula subtilis* (Böttger-Schnack, 1995, Böttger-Schnack and Huys, 2001).

Reproduction

Eggs or egg-sacs have not yet been observed for *O. bispinosa*, but may possibly be similar to those of *O. ivlevi*, which carry only two to four large eggs (Böttger-Schnack *et al.*, 1989; Böttger-Schnack, 2002). Females of *O. bispinosa* with spermatophores attached to the genital double-somite were frequently observed in the Red Sea, indicating continuous reproduction in this area (Böttger-Schnack *et al.*, 1989).

DESCRIPTION OF *ONCAEA ZERNOVI* SHMELEVA, 1966

Synonyms. *Oncaea tenella* var. *pacifica*, Olson, 1949 [MS]; *Oncaea tenella sensu* Malt *et al.*, 1989.

Original description. (Shmeleva, 1966): pp.934, 935, Figures 3.1–3.9 (♀ only).

Other descriptions. (Olson, 1949) [MS]: pp.9, 97–101, Plate XXII, Figures 1–9 (♀), Plate XXIII, Figures 1–10 (♂) [as *O. tenella* var. *pacifica*]; (Shmeleva, 1969): pp.10–11, 27, Figure 7a–i (♀ only); (Kršinić, 1988): pp.543–550, Figures 1,2 (♀), Figures 3,4 (♂); (Malt *et al.*, 1989): pp.953–957, Figure 3A–I (♀), Figure 4A,B (♂) [as *O. tenella*].

Type locality (Neotype)

Adriatic Sea, 42°E 38.5′N, 18°E 02.0′E: Station 'Lokrum', about 1 nautical mile south of Island Lokrum near Dubrovnik; collected December 3, 1996 with Nansen type plankton net, diameter 45 cm, mesh size 0.053 mm, depth 25–50 m, vertical haul (leg. F. Kršinić).

Material examined

(1) Adriatic Sea, 42°E 38.5′N, 18°E 02.0′E: Station 'Lokrum', about 1 nautical mile south of Island Lokrum near Dubrovnik; collected December 3, 1996 with Nansen type plankton net, diameter 45 cm, mesh size 0.053 mm, depth 25–50 m, vertical haul (leg. F. Kršinić):
  (a) Neotype ♀ in alcohol (ZMH reg.no. K-40087), five ♀♀, two ♂♂ in alcohol (ZMH reg.no. K-40088)
  (b) five ♀♀, two ♂♂ in alcohol (NHM reg. no. 2001.6774–6780)

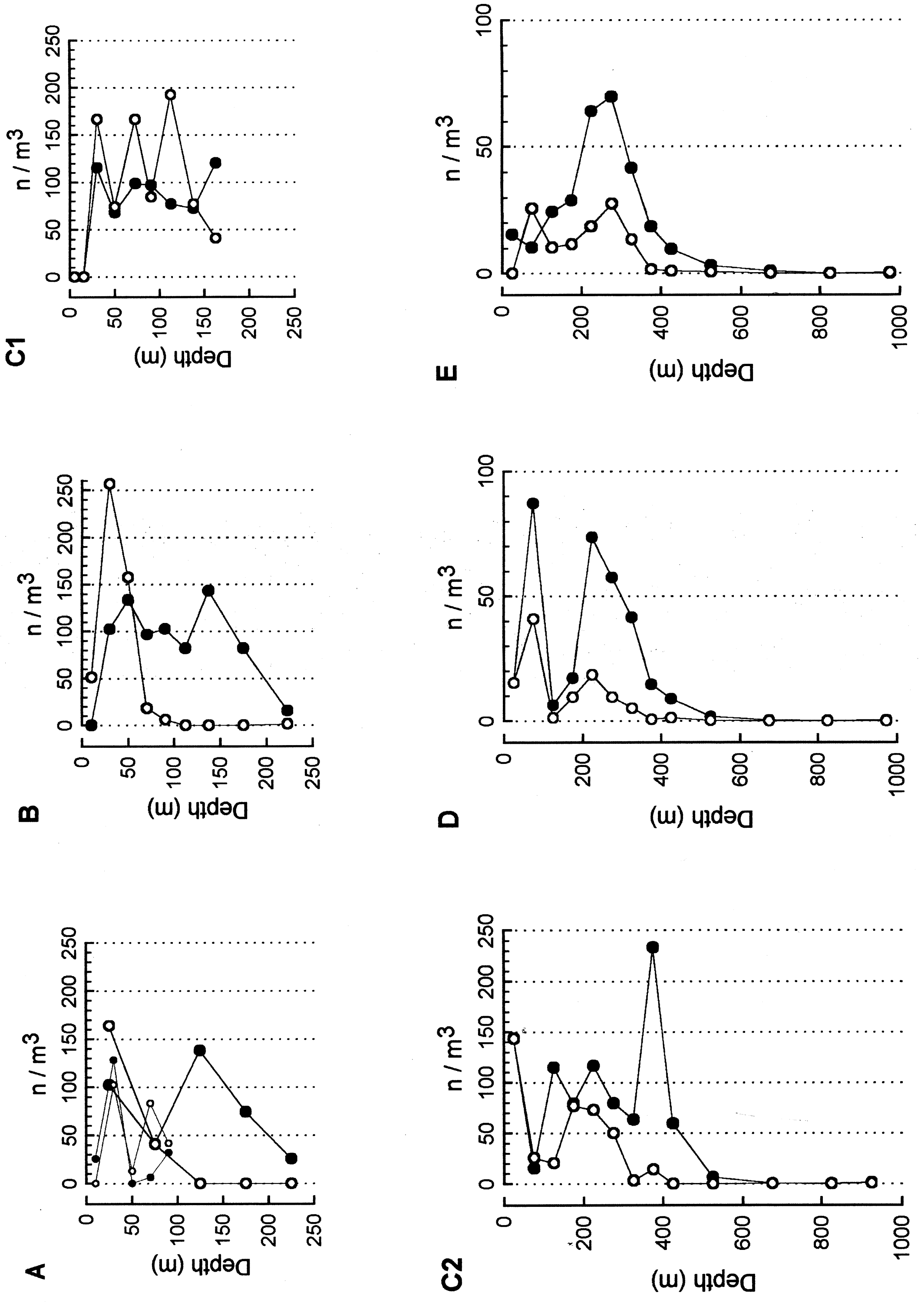

Fig. 6. Vertical distribution of *O. bispinosa* sp. nov. in the upper 200/250 m (A–C1) and in the upper 1000 m (C2–E) along a transect from the Gulf of Aden to the northern Red Sea during summer 1987. (● = females, ○ = males). (**A**) Gulf of Aden, small symbols indicate fine-scale distribution in the upper 100 m (total water depth (TWD) = 1400 m); (**B**) Bab al Mandab (TWD = 250 m); (**C**) southern Red Sea [**C1**: shallow (TWD = 190 m); **C2**: deep (TWD = 970m)]; (**D**) central Red Sea (TWD = 1890 m); (**E**) northern Red Sea (TWD = 1200 m). All data are from daytime samples, except for the 250 m profile in the Gulf of Aden, which was taken during the night.

(c) one ♀ dissected on slides, two ♀♀, two ♂♂ undissected on slides, 22 ♀♀, eight ♂♂ in formaldehyde (RBS).

(2) Eastern Mediterranean Sea, 34°E 25.3′N, 26°E 14.8′E: Station 35; RV 'Meteor' leg 5/1: collected January 20, 1987 with MSN 0.055 mm net (Haul 25/4); depth 250–300 m; total water depth 3400 m: one ♀ dissected on a slide in polyvinyl-lactophenol (RBS)

(3) Northeastern Atlantic, upwelling area off northwest Africa, 18°E 42′N, 20°E 06′W: Station 237 (DII); RV 'Meteor' leg 64: collected March 11–12, 1983 with Messhai [= multiple opening-closing modified Gulf III type sampler, (Pommeranz *et al.*, 1979; Pommeranz and Moser, 1987)] mesh size 0.05 mm; total water depth 3172 m

(3.1) Haul no. 28/2/50; depth 145–30 m, step oblique haul, main step 120 m: one ♀ dissected on a slide in polyvinyl-lactophenol (RBS)

(3.2) Haul no. 32/5/50; depth 325–300 m, horizontal haul, main depth 325 m: one ♀ dissected on a slide in polyvinyl-lactophenol (RBS)

(4) Northeastern Atlantic, upwelling area off northwest Africa, 18°E 42′N, 20°E 08′W: Station 237 (DII); RV 'Meteor' leg 64: collected March 12, 1983 with multiple opening-closing net (Weikert and John, 1981) mesh size 0.05 mm; haul 507/1/50; one ♀ (expanded prosome) dissected on a slide in polyvinyl-lactophenol (RBS)

(5) Northeastern Atlantic, upwelling area off north-west-Africa, 17°E 34′–32′N, 17°E 40′–47′W: Station 248 (DIII); RV 'Meteor' leg 64: collected March 15–16, 1983 with Messhai [cf. (3)] mesh size 0.05 mm; total water depth 2550 m

(5.1) Haul no. 34/2/50; depth 60–50 m, horizontal haul, main step 50 m: one ♀ dissected on a slide in polyvinyl-lactophenol (RBS)

(5.2) Haul no. 46/4/50; depth 275–250 m, horizontal haul, main depth 250 m: one ♀ dissected on a slide in polyvinyl-lactophenol (RBS)

(6) Northeastern Atlantic, upwelling area off northwest Africa, 17°E 37′N, 16°E 26′W: Station 262 (DIV); RV 'Meteor' leg 64: collected March 19, 1983 with Messhai [cf. (3)] mesh size 0.05 mm; total water depth 100 m

(6.1) Haul no. 58/5, depth 40 m, horizontal haul; one ♀, one ♂ undissected on a slide each in polyvinyl-lactophenol (RBS).

(6.2) Haul no. 58/3; depth 80 m, horizontal haul; one ♀, one ♂ dissected on a slide each in polyvinyl-lactophenol (RBS).

(7) Southeastern Indian Ocean, off northwest Cape Australia, 21°E 37.28′S, 114°E 09.54′E: Station E; NWC 011/1; RV 'Lady Basten' leg 1630; collected October 27, 1997 with 0.5 m WP-2 net with 0.073 mm mesh, vertical haul; depth 0–60 m (leg. D. McKinnon): two ♀♀, one ♂ undissected on slides, six ♀♀, 12 ♂♂ in formaldehyde (RBS).

(8) Northeast Pacific, off Monterey Bay, California, 36°42′N, 122°23.6′W: Station M2; collected October 5, 1999 with cylinder-cone net (~ stretched WP2, 30 cm mouth, 1 m cone length followed by 1.6 m cone length) with 0.064 mm mesh, vertical haul; depth 0–300 m; total water depth >1000 m (leg. R. Hopcroft): two ♀♀ undissected on slides, 13 ♀♀, two ♂♂ in formaldehyde (RBS).

Redescription

Illustrations are based on specimens from the new type locality in the Adriatic Sea, except for Figure 7D, which is based on a specimen from the northeastern Atlantic.

Adult female (Figure 7A–D)

Body length (measured in lateral aspect; from anterior margin of rostral area to posterior margin of caudal rami, calculated as sum of individual somites): 435 μm [traditional method: 367 μm, range 360–380 μm, based on nine specimens from the Adriatic Sea].

Exoskeleton weakly chitinized. Proportional length of prosome to urosome as in *O. bispinosa*. Rostral area flattened in dorsal view (Figure 7B), integumental pores on prosome not fully discerned. Expanded prosome observed in specimens from the northeastern Atlantic and Indian Ocean similar to *O. bispinosa* (cf. Figure 2G).

Proportional lengths (%) of urosomites are 7.8 : 70.3 : 5.1 : 4.3 : 12.5. Proportional lengths (%) of urosomites and caudal rami are 7.1 : 64.1 : 4.6 : 3.9 : 11.4 : 8.9, almost identical to *O. bispinosa*.

Genital double-somite with lateral margins somewhat more rounded at anterior third than in *O. bispinosa*, length to width ratio 1.8 : 1 (measured in dorsal aspect); anal somite and caudal ramus (Figure 7B) as in *O. bispinosa*.

Caudal ramus with length to width ratio and proportional length of caudal setae similar to *O. bispinosa*.

Antennule with armature formula as in *O. bispinosa*, small element on segment 3 and aesthetascs on segments 4 and 6 missing in Kršinić's redescription [(Kršinić, 1988): p.545, Figure 1c].

Antenna as in *O. bispinosa*, minute seta IV on second endopod segment not described by Kršinić [(Kršinić, 1988): p.545, Figure 1d]. He also missed some ornamentation details, such as the row of long, fine setules on the coxobasis, the strong denticles on the outer and inner margin of the first endopod segment and the distal row of setules on the second endopod segment.

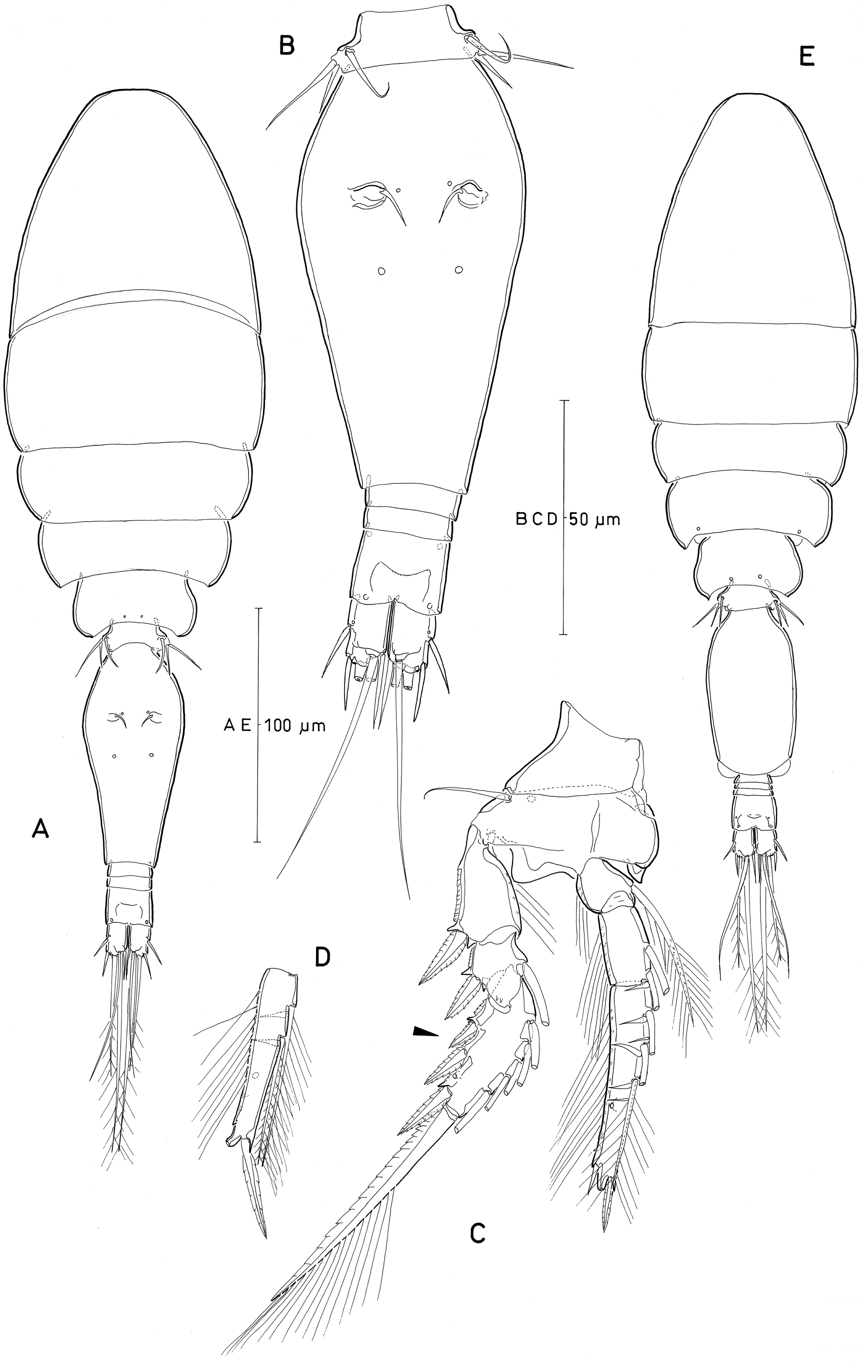

Fig. 7. *Oncaea zernovi*, female (Adriatic Sea) (**A**) Habitus, typical form, dorsal, pore pattern on prosome not fully discerned; (**B**) urosome, dorsal, setae IV and V omitted; (**C**) P2, posterior, proximal-most outer spine on distal exopod segment arrowed, intercoxal sclerite not figured, inner exopodal and endopodal setae partly omitted. *Oncaea zernovi*, female (northeastern Atlantic) (**D**) P3, endopod-3, anterior. *Oncaea zernovi*, male (Adriatic Sea) (**E**) Habitus, dorsal, pore pattern on prosome not fully discerned.

Labrum as in *O. bispinosa*; number of pores on posterior face not discerned.

Mandible gnathobase with five elements as in *O. bispinosa*, not only four as reported by Kršinić [(Kršinić, 1988): p.545, Figure 1f]. Relative lengths and ornamentation of elements as in *O. bispinosa*.

Maxillule with six elements, three elements each on inner and outer lobe (as in *O. bispinosa*), not seven as reported by Kršinić [(Kršinić, 1988): p.545, Figure 1g]: he described an innermost element on the outer lobe, which was not confirmed upon re-examination of specimens from the Adriatic.

Maxilla as in *O. bispinosa*, short, naked seta on inner margin of allobasis missing in Kršinić's redescription [(Kršinić, 1988): p.545, Figure 1h] [he also misinterpreted the number of elements by regarding the allobasal claw as an extra element].

Maxilliped as in *O. bispinosa*.

Swimming legs with armature as shown in Table III, differing from *O. bispinosa* in outer spine count on P2 exp-3, showing the typical number of three spines (Figure 7C, arrowed). Ornamentation of exopodal and endopodal segments, as well as proportional lengths of setae and spines similar to *O. bispinosa*, except for distal spine of P3 endopod, measuring about two-thirds the length of the distal endopod segment (Figure 7D), whereas this spine is only about half the length of the segment in *O. bispinosa* (cf. Figure 4C).

P5 similar to *O. bispinosa*, except for outer exopodal seta being slightly longer, about twice as long as inner seta (Figure 7B).

P6 (Figure 7B) with spine longer and more slender than in *O. bispinosa*.

Egg-sacs not found.

Adult male (Figure 7E)

Body length: 385 µm [traditional method: 320 µm, based on two specimens from the Adriatic Sea]. Pore pattern on prosome not discerned. Sexual dimorphism in antennule, maxilliped, P6, and in genital segmentation.

Proportional lengths (%) of urosomites (excluding caudal rami) 9.9 : 62.6 : 4.4 : 4.4 : 3.3 : 15.4; proportional lengths (%) of urosomites (caudal rami included) 8.8 : 55.9 : 3.9 : 3.9 : 3.0 : 13.7 : 10.8, slightly different from *O. bispinosa*. Length to width of caudal rami and proportional lengths of caudal setae as in female. Dorsal surface of genital somite without pores. Surface ornamentation of genital flaps not discerned.

Antennule and maxilliped as in *O. bispinosa*.

P1–P4 with armature and ornamentation as in female; sexual dimorphism in length of distal spine on P2 enp-3 reported by Kršinić [(Kršinić, 1988): Figure 4c] not confirmed.

P5 (Figure 7E) and P6 as in *O. bispinosa*, ornamentation on genital flaps not discerned.

Taxonomy

In the original description of *O. zernovi* from the southern Adriatic Sea, Shmeleva (Shmeleva, 1966, 1969) figured the female habitus, urosome, antennule, antenna, maxilliped and the swimming legs. In both accounts, she described the distal endopod segment of P3 with two outer spines [(Shmeleva, 1966): Figure 3.8; (Shmeleva, 1969): Figure 7h], which was not confirmed in Kršinić's redescription of the species from the type locality [(Kršinić, 1988): p.547, Figure 2d] and in the present account. Shmeleva also missed the inner seta on the distal endopod segment of P4, which had already been noted by Kršinić before [(Kršinić, 1988): p.547, erroneously called a 'spine'). This seta can easily be overlooked, because it is located on the posterior face of the segment, as in *O. bispinosa* (cf. Figure 4D). Furthermore, the inner seta on the middle exopod segment of P4 was not figured by Shmeleva [(Shmeleva, 1966): Figure 3.9; (Shmeleva, 1969): Figure 7i], but was recorded in Kršinić's redescription [(Kršinić, 1988): Figure 2e] and in the present account. Shmeleva erroneously recorded three elements on the palmar margin of the maxillipedal basis in the female [(Shmeleva, 1966): p. 934; (Shmeleva, 1969): p.11], which was not confirmed by Kršinić (Kršinić, 1988) and in the present account. [She possibly misinterpreted the distalmost, long spinule of the first row on the anterior face (cf. Figure 3G) as being a spine.] Several other elements are missing or inadequately illustrated in Shmeleva's figures, such as the basal seta of P5 and the number of elements on the antennule.

In his detailed redescription of *O. zernovi*, Kršinić (Kršinić, 1988) included the first data on the mouthparts and described the male for the first time. Most of his observations were confirmed during the present study upon re-examination of presorted copepod material collected from the type locality by Kršinić. Several corrections and amendments to Kršinić's morphological data, in particular with regard to the number of elements on the mandible and maxillule, which are very difficult to discern, have been included in the present account (see above). Like Shmeleva, Kršinić misinterpreted the distalmost seta on the endopod of P1 and reported it as a spine in the leg armature given in a text table. The insertion of this seta is hidden beneath a short spinous outgrowth of the distal segment, as in *O. bispinosa* (cf. Figure 4A, a).

Careful re-examination of *O. zernovi* specimens from the type locality in the Adriatic Sea confirmed that all details of ornamentation described for *O. bispinosa* are also shared by the former species. Thus, the only morphological discrepancies between both species are (1) the different spine count on P2 exopod-3, (2) the different proportional length of the distal spine on P3 exopod, (3) the slight difference in the form of the female genital double-somite, and (4) the small size difference in the females (but not in the males).

Oncaea zernovi was recorded from a wide range of localities during the present study, including the Atlantic, the southeastern Indian Ocean, off the northwest Cape of Australia, and the eastern Pacific (Table V); it also occurred in the the western Pacific, in the neighbouring waters of Japan (H. Itoh, unpublished data). These identifications, however, were based on a limited number of characters, such as the exopodal spine count of P2 (Table V), the size and general habitus of the females as well as details of the mouthparts that could be examined without dissecting the specimens. More detailed examination of the populations in the Indo-Pacific are necessary in order to confirm their identification. In view of the great number of undescribed species found in the family Oncaeidae [cf. (Böttger-Schnack, 1996)] and the great morphological similarity of species within the species groups (= new genera) (Böttger-Schnack, 1999), closer examination may probably reveal them to be different form variants or even closely related species.

Other records of *O. zernovi*

Olson (Olson, 1949), in an unpublished thesis, described a new form variant of *O. tenella* Sars, var. *pacifica*, from the Pacific Ocean, off Oregon, and included figures of the habitus, antenna, maxilliped and swimming legs for both sexes, as well as the antennule of the male. Although he noted several distinct morphological differences between his specimens and the original description of *O. tenella* by Sars (Sars, 1916), he did not 'create a new . . . species' for the reason that it would not have been identifiable without dissection, which he regarded as too difficult in these small-sized specimens [(Olson, 1949), p.100: 'the very small size of the copepod itself not only seems to minimize these differences but renders them diagnostically useless . . . Without attempting the difficult task of dissecting this, the smallest known copepod, these differences would not be apparent.']. *Oncaea tenella* var. *pacifica* displays all the morphological characters typical for *O. zernovi* and the two species are here regarded as synonymous, based on the following characters: (1) endopods of P2 and P3 with outer spine absent, as noted by Olson [(Olson, 1949): p.100, erroneously named 'exopod', Plate XXII, Figures 7,8, Plate XXIII, Figures 9,10), while they are present in *O. tenella* Sars (Table IV), (2) endopod of P4 with terminal spine as long as distal segment, while the spine is much shorter than this segment in *O. tenella*, (3) maxillipedal basis with distal palmar seta twice the length of proximal seta, while the proximal seta is longer than the distal seta in *O. tenella*. The identity of Olson's species with *O. zernovi* can furthermore be supported by the outer spine count on the distal exopod segment of P2, which was figured as having three outer spines in Olson's specimens [(Olson, 1949): Plate XXII, Figure 9 (♀), Plate XXXIII, Figure 6 (♂)], and not two spines as in the sister taxon *O. bispinosa* from the Red Sea and the Indian Ocean. Also, the morphological examination of specimens from the northeastern Pacific during the present study, which were collected near Olson's research area and are regarded as being conspecific with *O. zernovi*, corroborate the above conclusions.

Olson (Olson, 1949) assumed that the Pacific records of *O. tenella sensu* Wilson, who recorded the species from a wide range of localities in the world ocean (Wilson, 1942), might be identical to his new form variant *O. tenella* var. *pacifica* (and thus might assigned to *O. zernovi*, based on the above assumption that the two species are conspecific). However, Wilson did not provide figures or a description that positively identified the species (Wilson, 1942).

In a taxonomic study on oncaeid copepods from the eastern Mediterranean Sea, near the Lebanese coast, Malt *et al.* described a species of the *zernovi*-type and identified it as *O. tenella* Sars (Malt *et al.*, 1989). Their description, however, which included figures of the female habitus and postgenital somites, swimming legs, antennule, antenna and maxilliped as well as the male urosome and maxilliped, differs substantially from the original account of *O. tenella* by Sars (Sars, 1916). Most morphological characters of *O. tenella sensu* Malt *et al.* (Malt *et al.*, 1989) correspond well with those described for *O. zernovi*. Thus, *O. tenella sensu* Malt *et al.* is here regarded as a synonym of *O. zernovi*, based on the following characters: (1) distal endopod segment in P2 showing one outer spine (as in *O. zernovi*), not two as in *O. tenella* (Table IV), (2) distal endopod segment of P3 with spine absent (as in *O. zernovi*), not with two spines as in *O. tenella* (Table IV), (3) distal endopod segment of P4 with spine absent (as in *O. zernovi*), not with one spine as in *O. tenella* (Table IV), (4) palmar setae on maxillipedal basis with distal element longer than proximal seta, not *vice versa* as figured by Sars for *O. tenella*, (5) first endopodal segment of antenna with strong denticles (as in *O. zernovi*), which were not figured for *O. tenella* by Sars. Despite the fact, that Malt's specimens were not re-examined in detail during the present study, the above mentioned arguments were regarded sufficient to place her specimens as being synonymous with *O. zernovi*, because it is one of the most abundant oncaeid species in the eastern Mediterranean (Böttger-Schnack, 1997), but was not mentioned in their account.

An unusual character reported by Malt *et al.* for *O. tenella* is a long distal seta on the endopod segment of P1 (their Figure 3F) in addition to a short distal spine and five inner setae, which leads to an unusual leg armature of I, I, 5 in their text table [(Malt *et al.*, 1989): p.955]. An armature like this has not yet been observed in any oncaeid species. [It may be possible that the authors misinterpreted one of the exopodal setae, which are lying underneath or above the endopodal setae, when the exopod is found in its typically inwardly bent position (as in *O. bispinosa*, cf Figure

3a).] An inconsistency between text and figure in the description by Malt *et al.* is found in the leg armature of the endopod-3 of P4, which is figured as having one inner seta and one distal spine [(Malt *et al.*, 1989): Figure 3I), whereas in the text table the leg armature of P4 endopod is listed with two distal spines in addition to the inner seta [(Malt *et al.*, 1989): p.955; 0, II, 1]. Also, the basal seta of P4 is figured on the inner margin (their Figure 3I), not on the outer margin, as usually found in oncaeids (and correctly listed in their text table on p.955).

Ecological notes

In the Adriatic Sea, *O. zernovi* is supposed to have a wide distribution range, since it had recently been reported in the estuarine waters of the South Adriatic [(Kršinić and Viličić, 1989); cited after (Hure and Kršinić, 1998)]. It is the most numerous oncaeid species in this area, contributing 80% to the adult stages in the upper 50 m depth layer and between 40 and 65% to the adult oncaeids in the layers from 50 to 400 m depth on a yearly average [(Kršinić, 1998) and unpublished data, based on samples retained by 0.053 mm mesh net]. In the depth layers below 400 m, relative abundances of the species decrease to values of 20% or less of the adult population. The species is also known as a dominant oncaeid in the microcopepod community of the eastern Mediterranean Sea, accounting on average for 12% of total poecilostomatoid numbers in the 1850 m water column (Böttger-Schnack, 1997). These values would have been even greater if all the juvenile stages of *O. zernovi* had been identified. When considering only the adult population of oncaeids, the proportion of *O. zernovi* in the eastern Mediterranean increases to 21% for the 1850 m water column [calculated from (Böttger-Schnack, 1997), based on net samples with 0.055 mm mesh size]. Greatest relative abundances of about 40% of all adult oncaeids occur in the epipelagic zone, at 0–100 m, whereas in the depth layers from 100 m to 450 m they were found to contribute between 20 and 30% to all adult oncaeids, which is considerably lower than in the Adriatic Sea. In summary, the numerical importance of *O. zernovi* within the microcopepod fauna of Mediterranean waters appears to be of the same magnitude as (eastern Mediterranean) or is even greater than (Adriatic Sea) that of its sister taxon *O. bispinosa* in the Red Sea, which accounted for about 10–40% of adult oncaeid copepods in the upper 100 m and for 20–40% of all adult oncaeids between 100 and 450 m depth [calculated from (Böttger-Schnack, 1995) and unpublished data, based on net samples with 0.055 mm mesh size].

Vertical distribution and vertical migration

Similar to its sister taxon *O. bispinosa* in the Red Sea (see above), *O. zernovi* occurs over an extended vertical depth range of more than 1850 m in the water column, with highest concentrations in the upper 400–600 m. In the eastern Mediterranean, the highest concentrations, of about 50–150 individuals m^{-3} were reported from the epipelagic zone, decreasing more or less constantly with depth [(Böttger-Schnack, 1997), Figure 5]. Below 500 m depth, concentrations rarely exceeded 1 individuals m^{-3}. In the Adriatic Sea, Shmeleva (Shmeleva, 1966) recorded the species from 0 to 700 m depth, with maximum concentrations of 95 individuals m^{-3} at 50–100 m, while Kršinić (unpublished data) found highest concentrations of adults in the upper 50 m, averaging 200 individuals m^{-3} on a yearly basis, and decreasing insignificantly to values between 87 and 146 individuals m^{-3} down to 400 m depth. Below 600 m, values between 1 and 10 individuals m^{-3} were found, which is in the same order of magnitude as, or even higher than, in the eastern Mediterranean.

DISCUSSION

Taxonomy

In *O. bispinosa* the length of the spine fused basally to the inner proximal corner of the maxillipedal claw is sexually dimorphic, being much longer in the male than in the female. This sexually dimorphic character is also present in *O. zernovi* [(Kršinić, 1988) and present study], but it is not found in the closely related *Epicalymma* (Heron, 1977; Heron *et al.*, 1984; Heron and Frost, 2000), or in any other oncaeid species known so far. Thus, it may serve as an additional character to distinguish the species of the *zernovi*-complex. *Oncaea tenella* differs from the other two species of this group mainly by the outer spine count of the distal endopod segment in P2–P3. Other slight differences can be found in the length of the palmar setae of the maxilliped and in the length of the terminal spine on the endopod of P4. Sars' (Sars, 1916) original material of *O. tenella* could not be investigated during the present study. Further morphological differences might become apparent when the species is examined in more detail.

The antennule of *O. bispinosa* and *O. zernovi* displays a setal formula differing from that of most other oncaeids. An unpublished survey of the various species of Oncaeidae revealed that antennary armature is remarkably conservative in the family, with the majority of species sharing the following setal formula in the female: 1-[3], 2-[8], 3-[5], 4-[3+ae], 5-[2+ae], 6-[6+(1+ae)] [but see (Böttger-Schnack and Huys, 1997) for an exception in the recently discovered primitive oncaeid genus *Archioncaea*, which displays additional setae on segments 2, 3 and 4]. In *O. bispinosa* and *O. zernovi*, the number of elements is reduced, exhibiting two setae less on segment 2, no aesthetasc on segment 4 and no small sensory element on segment 6. While the reduction in number of aesthetascs or small elements (which are difficult to discern) has recently been observed in other oncaeid lineages as well (*ivlevi*-group, Böttger-Schnack, 2002), the reduced number of six setae on segment 2 has not been observed in any other oncaeid species so far. In order to ease the identification of elements on this segment in future studies of oncaeids, the position at which the two setae are usually found in oncaeid species (but are not present in species of the *zernovi*-type) are indicated by arrows in Figure 2E, e and Figure 5B. In the male, the lateral seta on segment seems to be replaced by a deep pit, which is arrowed in Figure 5b.

Phylogenetic relationships

Within the Oncaeidae, *O. zernovi* and *O. bispinosa* are closely related to *Oncaea tenella* Sars and *O. tenella sensu* Malt *et al.* (Malt *et al.*, 1989), which was assigned to *O. zernovi* during the present study. Common characters shared by the members of this group are the reduced distal exopod segment of P1, armed with two outer spines, and the very elongate genital double-somite of the female. A first assessment of the phylogenetic relationships of the *zernovi*-complex within the Oncaeidae was given by Böttger-Schnack and Huys [(Böttger-Schnack and Huys, 1998): species group 1 in their Figure 1]. According to their results, the *zernovi*-complex is a sister group of the genus *Epicalymma* Heron. 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. The species of the *zernovi*-complex will eventually be placed in a new genus.

Zoogeography

The zoogeographical distribution of the newly described *O. bispinosa* was limited to the Red and Arabian Seas and the equatorial waters of the Indian Ocean. Its sister taxon *O. zernovi*, on the other hand, was recorded from a wide range of localities during the present study, including the northeastern Atlantic, the eastern Mediterranean, the southeastern Indian Ocean (off Australia) and the northwest and northeast Pacific. Thus, the two species differ considerably in zoogeographical distribution, with *O. zernovi* being circumglobal in tropical and subtropical areas, whereas *O. bispinosa* seems to be provincial to the northern and equatorial Indian Ocean. Within the range of their habitat, the two species did not co-occur at any station. Among the cyclopoid family Oithonidae, Nishida found a similar pattern of distribution for the two closely related inlet water species *Oithona oculata* and *O. rigida* (Nishida, 1985). *Oncaea rigida*, which initially had been reported from the Red Sea (Giesbrecht, 1896), was restricted to the indo-west Pacific region, while its sister taxon *O. oculata* was considered to have a circumglobal distribution. However, the author pointed to the neccessity of more detailed morphological comparisons for such widely distributed species ['It is not unlikely that the populations in these regions have already speciated into . . . allied species which are distinguished only by a close examination.' (Nishida, 1985), p.145], which has also been stressed for oncaeid species of the *zernovi*-type in the present paper.

No reliable zoogeographical data are yet available for *O. tenella*, representing the third species of the *zernovi*-complex, due to uncertainties in the taxonomic identification of the species. The only two previous records that include a description of the species appear to be based on specimens of *O. zernovi* (see above under *O. zernovi*, above). To date, no reliable morphological description of *O. tenella* other than the initial record from the western Mediterranean Sea, near the Moroccan coast (Sars, 1916) has been published and its zoogeographical distribution is unknown. Further investigations on *zernovi*-type oncaeids in the Mediterranean are needed, to demonstrate their zoogeographical distribution in this area and to confirm morphological differences/similarities of this species within the *zernovi*-group.

A distinct zoogeographical separation between the Red Sea and the Eastern Mediterranean became apparent for the two species of the *zernovi*-group examined in detail herein. This is the first group of oncaeids for which such a separation of closely related species has been confirmed. For other closely related species-groups of oncaeids occurring in the Red Sea, distributional results indicate their co-occurrence in both zoogeographical provinces [e.g. *Spinoncaea ivlevi-tenuis-humesi*, (Böttger-Schnack, in press)] or a restriction to one province only [e.g. *Oncaea clevei-paraclevei*, indo-west Pacific, (Böttger-Schnack, 2001)]. For several newly described species of oncaeids in the Red Sea, however, corresponding results from the eastern Mediterranean are not yet available [e.g. *Triconia hawii-recta* or *T. dentipes-elongata-giesbrechti*, (Böttger-Schnack, 1999)].

Ecological notes

The compilation of the few available data on the abundance of *O. zernovi* and *O. bispinosa* in the Mediterranean, Red and Arabian Seas in the present paper indicates their high ranking among the oncaeid fauna in tropical and subtropical marine areas. They occur over an extended vertical depth range of more than 400 m, covering the epipelagic as well as the mesopelagic depth zones. *Oncaea bispinosa* also occurred in fairly large numbers in the samples from the equatorial Indian Ocean examined during the present study (unpublished data, based on material by S. Nishida), and its sister taxon *O. zernovi* was found in large numbers in the western Pacific, in the neighbouring waters off Japan (H. Itoh, unpublished data). In the northeastern Pacific, *O. zernovi* appeared to be the most abundant oncaeid in fine-mesh net samples collected off Monterey, California, that were examined during the present study (unpublished data, based on material by R. Hopcroft). In fine-mesh net samples collected in the northeastern Atlantic (upwelling area off northwest Africa), *O. zernovi* was recorded as one of the most numerous microcopepod species (D. Schnack and S. Grau, unpublished data). In conclusion, it can be stated that species of the *zernovi*-complex so far have been found to represent one of the most numerous oncaeid species in the oceanic microcopepod community of tropical and subtropical areas. Future investigations on the community structure of oncaeids in these areas, such as the western Pacific, are in progress (H. Itoh, personal communication), which will help to elucidate further their quantitative role in the marine copepod community.

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