

Taxonomy of Oncaeidae (Copepoda, Poecilostomatoida) from the Red Sea.

II. Seven species of *Oncaea* s.str.

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SYNOPSIS. Seven species of Oncaeidae (one of which is new to science) are described from the Red Sea, including a description of the hitherto unknown male of *Oncaea clevei* Früchtl. They all belong to *Oncaea sensu stricto* as defined in a phylogenetic study of oncaeid species by Böttger-Schnack and Huys in 1998. The genus is defined by a combination of characters including the absence of a conical process on the distal margin of the endopod of swimming leg 4, ornamentation of the labrum and mandibular blade and sexual dimorphism in antennary setae and in endopods of swimming legs. *Oncaea* s. str. includes two subgroups, the *venusta*-subgroup and the *clevei*-subgroup, females of which can be separated by the absence or presence of a dorso-posterior projection on the P2-bearing somite. Species of the *venusta*-subgroup in the Red Sea include *O. venusta* Philippi, *O. mediterranea* (Claus), *O. media* Giesbrecht, *O. scottodicarloi* Heron & Bradford-Grieve and *O. waldemari* Bersano & Boxshall; the *clevei*-subgroup consists of *O. clevei* Früchtl and *O. paraclevei* sp. nov. *Oncaea praeclara* Humes is a junior subjective synonym of *O. venusta*. *O. philippinensis* (Kazatchenko & Avdeev) as well as *Oncaea* sp. 1 and sp. 2 sensu Ferrari are regarded as *species inquirendae* in *Oncaea* s.str. The type species of the genus, *O. venusta*, has two form variants, *forma typica* and *forma venella* Farran, which can be distinguished by differences in size and in a few minor morphological characters. Their spatio-temporal distribution differs considerably in the Red Sea, which may indicate reproductive isolation. The world-wide records of *O. venusta* forms are reviewed and discussed.

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INTRODUCTION

Small copepod species of the family Oncaeidae are widely distributed in marine pelagic areas, extending from the epipelagic zone (e.g. Boxshall, 1977a; Dessier & Donguy, 1985; Cowles *et al.*, 1987) to the deep-sea (Wishner, 1979; Humes, 1988) and from tropical (Tsalkina, 1970; Deevey & Brooks, 1977) to polar regions (Hopkins, 1985; Richter, 1994; Metz, 1995). Due to their small size, oncaeid copepods are often neglected or under represented in marine plankton investigations, which are usually conducted with conventional nets of 0.3 or 0.5 mm mesh sizes. In recent years, increasing attention has been paid to the study of smaller mesozooplankton organisms sampled with fine mesh nets of 0.1 mm mesh size or less. In particular, small oncaeid copepods were sampled in high abundance by these nets (e.g. Böttger, 1982; Paffenhöfer, 1983; Schnack

et al., 1985; Cowles *et al.*, 1987; Böttger-Schnack, 1987) and subsequent research topics have focussed on their community structure and biology [see Böttger-Schnack (1999) for a review of the literature], thereby providing new insights into the largely unknown ecological importance of this copepod group.

Apart from ecological issues, the taxonomy of oncaeid species has been the subject of increasingly detailed studies over the past two decades (e.g. Boxshall, 1977b; Heron, 1977; Malt, 1982a, b, 1983a, b, c, d; Heron *et al.*, 1984; Kršinić & Malt, 1985; Boxshall & Böttger, 1987; Kršinić, 1988; Böttger-Schnack & Boxshall, 1990; Heron & Bradford-Grieve, 1995; Böttger-Schnack & Huys, 1997a, b, in press; Itoh [in: Chihara & Murano (1997)]). Despite these efforts, however, the taxonomy of many oncaeid species is still inadequate and particularly those species that are smaller than 0.5 mm have not been described in sufficient detail. Moreover, many oncaeid species are morphologically very similar, and thus can be

distinguished only by a few characters, including microstructure of the mouthparts and on the exoskeleton, which require a level of detail not generally adopted in most taxonomic descriptions. Such integumental microstructures have been used to differentiate between closely related species of cyclopoid (Ueda *et al.*, 1996; Rocha, 1998) and oncaeid (Böttger-Schnack, 1999; Böttger-Schnack & Huys, in press) copepods.

The phylogenetic relationships of the Oncaeidae are not well understood. The diphyletic status of the family has recently been recognized by Huys & Böttger-Schnack (1996/97), who proposed the new family Lubbockiidae to accommodate *Lubbockia* Claus, 1862 and related genera, retaining only *Oncaea* Philippi, 1843, *Conaea* Giesbrecht, 1891 and *Epicalymma* Heron, 1977 in the Oncaeidae. The large type genus *Oncaea sensu lato*, which currently contains over 70 validly described species (Heron & Bradford-Grieve, 1995), has been recognized as a paraphyletic assemblage (Huys & Böttger-Schnack, 1996/97). A detailed phylogenetic analysis of the three oncaeid genera at the species level is currently in progress and will result in the recognition of numerous new genera. Some preliminary results of the phylogenetic study were briefly presented by Böttger-Schnack & Huys (1998).

The Red Sea is an extreme environment, with constant and unusually high deep-sea temperatures (21.7°C) and salinities (40.5 PSU) (Edwards, 1987). Due to these unique environmental conditions an impoverished zooplankton fauna is found in the Red Sea, which is characterized by the absence of true deep sea species (Weikert, 1982, 1987). This phenomenon was also reported for oncaeid copepods (Böttger-Schnack, 1994, 1999) and their estimated species number in the Red Sea (about 26) appears to be low in comparison to the adjacent Arabian Sea, where the vast majority of the about 70 recorded oncaeid species and forms is made up by deep-living representatives (Böttger-Schnack, 1994). The surface waters in the Red Sea show a considerable increase in salinity from the southern entrance to the central-northern areas (Morcos, 1970). Due to the less favourable environmental conditions in the north, species numbers of planktonic taxa generally decrease from south to north (e.g. Halim, 1969; Kimor, 1973; Almeida Prado-Por, 1983; Böttger-Schnack, 1995). For oncaeid copepods, however, a corresponding regional decrease in species number from south to north is less pronounced (Böttger-Schnack, 1995). This unexpected result was assumed to be at least partly attributable to the taxonomic difficulties encountered in the identification of oncaeids, since the proportion of unidentified form variants recorded in the south was much higher than in the north. In a subsequent taxonomic study five new species of oncaeids were described, four of which occurred mainly or exclusively in the southern area (Böttger-Schnack, 1999), thereby indicating some latitudinal difference in species numbers for this copepod group.

The ecology of oncaeid copepods in the Red Sea has been investigated intensively during the past years within the framework of multidisciplinary environmental research programmes (Thiel *et al.*, 1986; Weikert, 1988). The species diversity, vertical distribution and diurnal vertical migration, as well as some biological parameters, such as variation in body length and breeding activity or feeding of oncaeid copepods were studied on the basis of routine sampling with fine nets of 0.1 mm or 0.05 mm mesh size in the upper 500 m or 1000 m of the water column during different seasons and in various regions [see Böttger-Schnack (1999) for a review of the literature]. The taxonomy of Red Sea Oncaeidae is less well known, however. Boxshall & Böttger (1987) and Böttger-Schnack & Boxshall (1990) described four new oncaeid species from the central Red Sea, and provided a redescription of *Oncaea atlantica* Shmeleva. More recently, *O. mediterranea* (Claus) was redescribed from this

area, including a thorough review of the taxonomic history of this allegedly cosmopolitan species (Böttger-Schnack & Huys, 1997). In a recent taxonomic study, 11 species of Oncaeidae were described or redescribed from the Red Sea, which belong to the *conifera/similis*-group as defined in the phylogenetic study of Böttger-Schnack & Huys (1998). A new genus, *Triconia*, was proposed to accommodate all oncaeid species belonging to this group (Böttger-Schnack, 1999).

As part of an ongoing taxonomic study of Red Sea Oncaeidae, the present paper describes seven species, which belong to the *venusta*-group as defined by Böttger-Schnack & Huys (1998). In their cladogram of oncaeid species it is equivalent to species group 2. This core-group includes *Oncaea venusta* Philippi, the type species of the genus, and is considered here as *Oncaea sensu stricto*. *Oncaea* s.str. is defined by a combination of characters including the absence of a conical projection on the distal margin of P4 endopod, ornamentation of the labrum and of the dorsal blade of the mandible, sexual dimorphism in the antenna and in the endopods of the swimming legs. *Oncaea* s. str. is considered as the sister-group of *Triconia* Böttger-Schnack, 1999, and the establishment of the revised genus is briefly substantiated in the present paper. A detailed discussion of phylogenetic relationships of *Oncaea* s.str. within the Oncaeidae will be published separately (Huys & Böttger-Schnack, in prep.).

Oncaea s.str. currently includes 8 species, 6 of which had previously been reported from the Red Sea (Böttger-Schnack, 1994) and are redescribed in the present account. For *O. mediterranea*, redescribed recently by Böttger-Schnack & Huys (1997b), some short corrective notes will be given. A new species similar to *O. clevei* Früchtl will be described. The taxonomic status of *O. curta* Sars, for which no material was available, will be discussed on the basis of literature data.

The type species of *Oncaea* s.str., *O. venusta*, was recently redescribed in detail by Heron & Bradford-Grieve (1995), based on specimens collected in the Gulf of Naples, near the type locality in the Mediterranean Sea. Their account does not contain information about the two size variants of the species, forma *typica* and forma *venella* (Farran, 1929), which are generally known to occur in tropical and temperate areas (Malt, 1983b), but are poorly documented morphologically. Apart from a distinct size difference, only few minor differences in body morphology have been reported for the two forms so far (Farran, 1929; Sewell, 1947; Ferrari, 1975; Boxshall, 1977a). In the Red Sea, both size variants of *O. venusta* occur. They differ considerably in spatio-temporal distribution (Böttger-Schnack, 1990b, 1995), which may indicate reproductive isolation. Both forms of *O. venusta* will be redescribed in detail in the present account, including observations with scanning electron microscope (SEM). Particular attention is paid to microstructures in the mouthparts and on the exoskeleton, which might provide new and helpful information for the separation of the two forms. The relationship of the two Red Sea forms with the species occurring in the Mediterranean Sea is defined upon re-examination of specimens from Heron & Bradford-Grieve's material. The present knowledge on the world-wide distribution of the two *venusta* forms is reviewed.

The two size variants of *O. media* as defined by Sewell (1947) have recently been recognized as distinct species by Heron & Bradford-Grieve (1995). They assigned forma *major* to *O. media* Giesbrecht (except for his Plate 47, Fig. 11), and described forma *minor* as a new species, *O. scottodicarloi*. Both species occur in the Red Sea and are briefly redescribed in the present paper, including some important morphological details not noted by these authors. *O. waldemari*, which is very similar to *O. media* and *O. scottodicarloi*, had recently been described from Brazilian waters by Bersano & Boxshall (1994). Due to some descriptive errors, however, the authors did not notice the close relationship of *O. waldemari* with

species of *Oncaea* s.str. and erroneously placed it in a group containing *O. petila* Heron, *O. ovalis* Shmeleva and others. In the present account, *O. waldemari* is completely redescribed based on Red Sea specimens (figures) and the type material from Brazilian waters, with additional comparisons on specimens from different localities in the Atlantic and Pacific Ocean.

MATERIAL AND METHODS

Oncaeids were collected using a multiple opening-closing net with a mesh size of 0.05 mm during cruise 5/5 of R/V *Meteor* (Weikert, 1988) in various locations of the Red Sea (Fig. 1). Samples collected during cruise 29 of R/V *Valdivia* with the same sampling gear, but

equipped with nets of 0.1 mm mesh, were also examined. A station list and sampling data are given in Table I. The plankton was initially fixed in a 4% formaldehyde-seawater solution buffered with hexamethylene tetramine and transferred after ca 2 years into a preservation fluid of 5% propylene glycol, 0.5% propylene phenoxetol, and 94.5% filtered seawater (Steedman, 1976). Specimens were dissected in lactic acid, mounted on slides in lactophenol and sealed with transparent 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 are measured from the anterior to the

Table 1 Sampling data of multiple opening-closing net in the Red Sea and adjacent areas (D = Day, N = Night).

Stn. No.	Date	Time	Total water depth (m)	Mesh size (mm)	Geographic position (°N, °E)
Red Sea + Gulf of Aden					
<i>R/V Valdivia</i> Cruise 29					
130	28.10.1980	D	1960	0.1	21°25.5', 38°01.9'
664	21. 2.1981	D	2000	0.1	21°22.1', 38°05.1'
<i>R/V Meteor</i> Cruise 5/5					
631a	11.7.1987	N	1400	0.05	11°55.5', 43°37.9'
663	20.7.1987	D	1200	0.05	22°58.4', 37°19.4'
703	3.8.1987	D	970	0.05	15°34.8', 41°54.9'
708	5.8.1987	D	190	0.05	13°40.0', 42°37.4'
Northern Arabian Sea					
<i>R/V Meteor</i> Cruise 32/3					
247	14. 5.1995	D	3000	0.05	ca 19°, ca 65°
Eastern Mediterranean Sea					
<i>R/V Meteor</i> Cruise 5/1					
35	20. 1.1987	N	3400	0.05	34°25.3', 26°14.8'

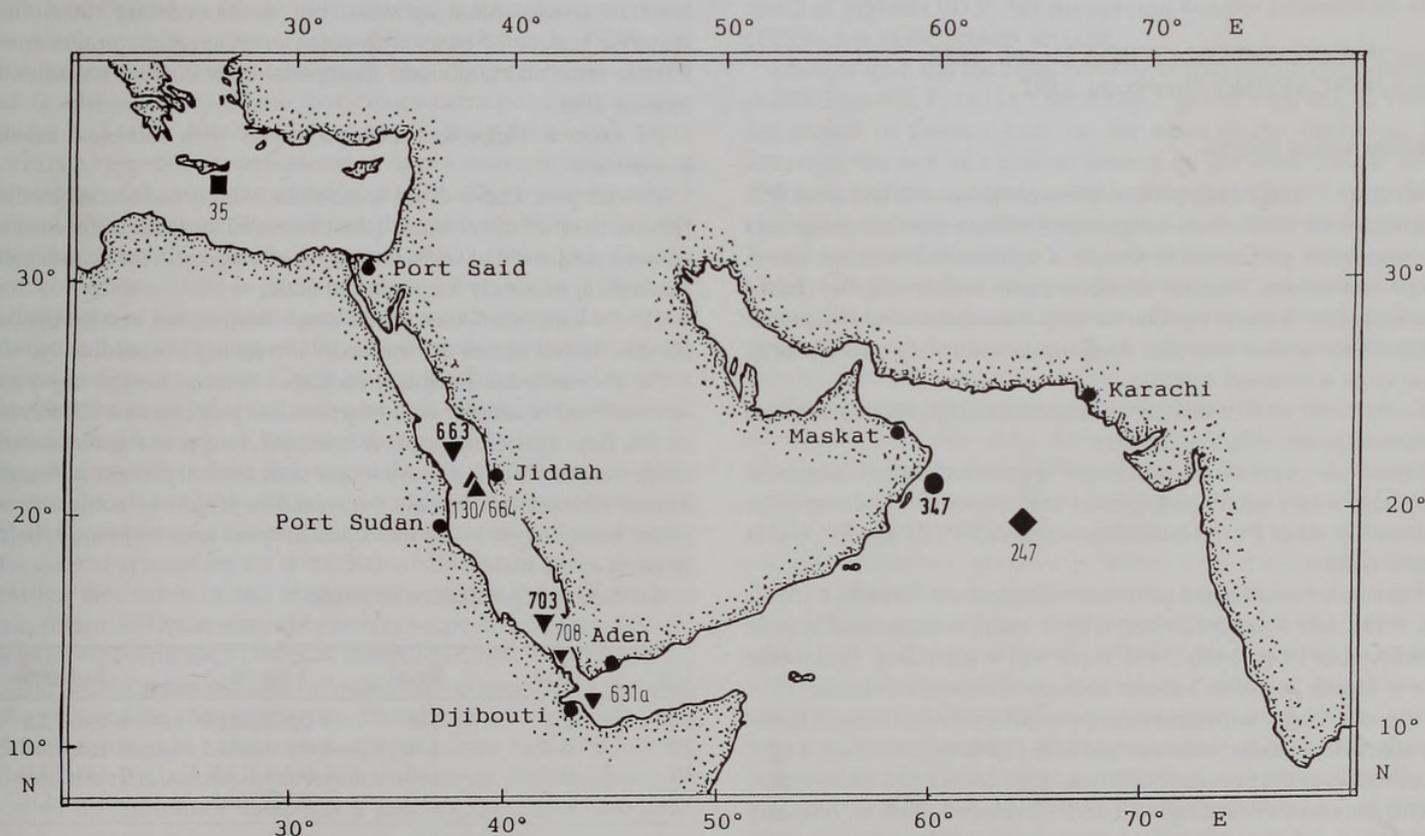


Fig. 1 Location of stations in the Red Sea and adjacent areas. ▲ = *Valdivia*-Cruise 29, October 1980, February 1981; ■ = *Meteor*-Cruise 5/1, January 1987; ● = *Meteor*-Cruise 5/3a, April 1987; ▼ = *Meteor*-Cruise 5/5, July/August 1987; ◆ = *Meteor*-Cruise 32/3, May 1995.

posterior margin. This approach differs from that traditionally used in oncaeid taxonomy, where the telescoping of somites is not considered in length measurements. Traditional length data of Red Sea oncaeids as given by Böttger-Schnack *et al.* (1989) are only up to 70% of the sizes presented in this paper, due to the excessive telescoping of somites in the sorting medium. In order to make sizes of the species in this paper comparable to those of previous taxonomic descriptions (e.g. Heron & Bradford-Grieve, 1995; Bersano & Boxshall, 1994), length data of each species were obtained by the traditional method as well (i.e. measured dorsally from the tip of prosome to the distal end of caudal ramus) and are given in square brackets.

Descriptive terminology for body and appendages follows that of 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–P4 = swimming legs 1–4. Species of Oncaeidae have a number of pores and other integumental structures (e.g. pits, scales) on body surfaces, but only those discernible with a light microscope were figured or mentioned.

O. venusta was examined with a Philips XL30 scanning electron microscope. Specimens were prepared by dehydration through graded ethanol, critical point dried, mounted on stubs and sputter-coated with palladium.

Type and other material is deposited in the collections of The Natural History Museum, London (BMNH), Smithsonian Institution (USNM) and the Zoologisches Institut und Museum der Universität Hamburg (ZMH). Paratypes or other material retained in personal collection, R. Böttger-Schnack designated (RBS).

GENERIC DIAGNOSIS

Order **POECILOSTOMATOIDA** Thorell, 1859
Family **ONCAEIDAE** Giesbrecht, 1892

Oncaea sensu stricto

DIAGNOSIS. *Body* cycloform, prosome stout or broad-oval. P2-bearing somite with (*clevei*-subgroup) or without (*venusta*-subgroup) dorsoposterior projection in female. Cephalosome without lateral lobate extensions. Genital double-somite female slightly flask-shaped, not particularly swollen dorsally. First and second postgenital somites shorter than anal one. Anal somite with wide anal opening; operculum with small spinules.

Exoskeleton well or heavily chitinized, usually ornamented with numerous pores, ridges and scales.

Sexual dimorphism in antennule segmentation and armature, antennary setae, maxilliped, genital segmentation and ornamentation, endopods of P1–P3 (sometimes also in P4), P5 and P6, and in caudal ramus.

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

Antenna. Enp-1 with triangular projection on outer margin forming concavity distally; inner margin with 1–2 denticular rows. Enp-2 shorter than enp-1; posterior surface with double row of spinules; lateral armature consisting of 3 well developed, bare or minutely pinnate setae (I, II and IV) and 1 pinnate spine (III) in female; distal armature consisting of 4 pinnate setae, 1 long bare or minutely pinnate seta, and 2 bare setae; posterior seta well developed. Sexual

dimorphism in lateral armature of enp-2, with seta III much stouter and seta IV spiniform and curved in male, both elements shorter than in female; often also expressed in coxobasal seta, being short and naked in male.

Labrum distinctly bilobate, forming paired semi-circular posteroventral lobes. Lobes without marginal teeth but with row of minute denticles around outer ventral margin, with row of long fine setules latero-distally (except for *clevei*-subgroup) and dentiform processes converging and decreasing in size medially. Lobes separated by semicircular vertex covered anteriorly by overlapping rows of small hyaline petaloid flaps, flanked by slit-like pores located on proximal part of each lobe; posterior face with median sclerotized teeth and usually with paired patches of long fine setules (absent in *media*). Anterior face with paired spinular patches or denticulate rows (except for *venusta*); paired integumental pockets usually well developed, free margin of pockets serrated or ornamented with denticle row.

Mandible with 2 blades, 2 setae and 1 spine. Dorsal blade with 3 dentiform processes along distal margin and up to 2 additional processes along dorsal margin.

Maxillule weakly bilobate; praecoxal arthrite with innermost element proximally displaced and outermost element spiniform and bearing transverse row of spinules.

Maxilla. Allobasis shorter than syncoxa.

Maxilliped (female). Large, moderately ovoid. Basis without ornamentation on posterior surface; anterior surface with spinular row and spinular fringe along palmar margin half the distance between distal seta and endopod; both palmar elements long, spiniform and spinulose, similar in length. Enp-1 completely separated. Enp-2 with long, minutely pectinate claw, rudimentary outer setule and fused unipinnate inner spine.

Maxilliped (male). Palmar margin forming shallow longitudinal cleft bordered by anterior denticulate fringe and posterior multiple rows of coarse, blunt spinules; not developed into distal flap. Anterior surface of basis with patch of transverse spinular rows. Palmar setae short, smooth. Endopodal claw curved, naked, with hyaline apex.

P1 exopod. Outer and terminal spines with subapical tubular extensions.

P1 endopod. Enp-3 distal spine stout, with broad serrate hyaline flange; base of distal inner seta concealed beneath long anterior spinous outgrowth of segment; length of outgrowth (often) sexually dimorphic, relatively longer in the male.

P2–P4 exopods. Outer spines stout, with broad, serrate hyaline flanges; lateral spines not markedly increasing in size distally.

P2–P4 endopods 3-segmented. Enp-3 twice as long as enp-1 and -2 combined or longer; with large conical processes on P2–P3, not on P4. Enp-3 distal spine short in P2–P3, longer in P4; distal outer spine small in P2–P3, always longer than conical process in female. Sexual dimorphism usually expressed in length of conical processes, being longer in the male, and in spine length of enp-3, being reduced in the male.

Swimming leg armature formula:

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

P5 small; represented by outer basal seta and small exopod with 2 spiniform setae; exopod delimited at base in females, fused to

somite in males; sometimes additional sexual dimorphism in shape and length of exopodal setae. Genital apertures of female large; located near midregion of dorsal surface of genital double-somite but usually in proximal half; each operculum with small spine and 2 minute spinules or spinous processes.

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

Caudal ramus about 3–4 times as long as wide or shorter, without conspicuous dorsal expansion surrounding base of seta VII. Seta I absent; setae II and III unipinnate; setae IV and V not resilient, relatively rigid and bipinnate; seta VII plumose and distinctly shorter than V; seta VI spiniform and sparsely pinnate. None of setae displaced. Sexual dimorphism expressed in length to width ratio of CR, being smaller in male, and in proportional lengths of caudal setae.

TYPE SPECIES. *Oncaea venusta* Philippi, 1843 (by monotypy)

OTHER SPECIES

O. mediterranea (Claus, 1863)

O. media Giesbrecht, 1891

O. curta Sars, 1916 [not *O. curta* sensu Boxshall, 1977b]

**O. clevei* Früchtl, 1923

[*O. praeclara* Humes, 1988] syn. of *O. venusta*

O. waldemari Bersano & Boxshall, 1994

O. scottodicalroi Heron & Bradford-Grieve, 1995

**O. paraclevei* sp. nov.

SPECIES INQUIRENDAE

Oncaea sp. 1 Ferrari, 1975

Oncaea sp. 2 Ferrari, 1975

O. philippinensis (Kazatchenko & Avdeev, 1977)

[Species marked with an asterisk (*) belong to the *clevei*-subgroup, remaining species belong to *venusta*-subgroup.]

REMARKS

Within the Oncaeidae *Oncaea* s.str. belongs to a lineage comprising the *conifera/similis*-group (*Triconia* Böttger-Schnack, 1999), the *notopus*-group and the *brocha*-group (including *O. brocha* Heron and *O. olsoni* Heron). These four groups correspond with species groups 2, 3+4, 6 and 7 recognized by Böttger-Schnack & Huys (1998) and together are considered to form a monophyletic lineage on account of the structure of the labrum (median concavity with 4 posterior dentiform processes) and the male maxilliped (palmar margin with multiple overlapping rows of blunt spinules). *Oncaea* s.str. is considered here as the sistergroup of *Triconia* on the basis of the presence of integumental pockets on the anterior surface of the labrum and the formation of the dorsoposterior projection on the second pedigerous somite. The fact that the latter character is not expressed in all members of both genera is interpreted as the result of secondary loss which happened convergently in each genus. *Oncaea* s.str. differs from *Triconia* in the sexual dimorphism of the antenna (seta II and IV modified in the male), the presence of paired slit-like pores on the anterior surface of the labrum and the absence of a conical process on the distal endopod segment of P4. A more detailed discussion of the phylogenetic relationships of *Oncaea* s.str. within the Oncaeidae is beyond the scope of this paper and will be published separately (Huys & Böttger-Schnack, in prep.).

The revised genus includes two subgroups of species, the *venusta*-subgroup and the *clevei*-subgroup. Females of the *clevei*-subgroup are characterized by a dorso-posterior projection on the P2-bearing somite, which is lacking in the *venusta*-subgroup. The dorsal projection on the prosome ('hump') is a sexually dimorphic character, which is absent in males. Thus males of both subgroups are very hard to distinguish. A further morphological character separating the 2 subgroups is found in the ornamentation of the labrum, the row

of long setules on the latero-distal margin of the lobes being absent in the *clevei*-subgroup.

Oncaea curta Sars, 1916 (p. 228, Plate IV, as *Oncaea curta*) was originally described from the western Mediterranean, near the Moroccan coast. The species has also been widely recorded at low latitudes in the Atlantic and Pacific [as compiled by Malt (1983a) and Razouls (1996)]. Recently, Heron & Bradford-Grieve (1995, p.41) recorded the species from the Gulf of Naples, but at the same time noted in their samples several as yet undescribed species close to *O. media*, *O. scottodicalroi* and *O. curta* indicating that a complex of species close to *O. curta* exists within *Oncaea* s.str. Thus, a number of different species might have been recorded in the literature under the wrong name *curta* (e.g. Boxshall 1977b, see remarks below) and the geographical records of *O. curta* appear to be doubtful. Due to the identification problems, the species had erroneously been placed into the *bowmani*-group in the preliminary cladogram of Böttger-Schnack & Huys (1998). The species could not be re-examined during the present study, since no material was available. Therefore, Sars' description was taken as a basis to compare the morphology of *O. curta* with the closely related *O. media*, *O. scottodicalroi* and *O. waldemari* (see under *O. scottodicalroi*, Remarks). A thorough revision of *O. curta* is needed to clarify the taxonomic confusion surrounding this species.

Oncaea curta sensu Boxshall (1977b: p.141–143, Table 1–2, Fig. 21a–k) does not belong to *Oncaea* s. str. Malt (1983a) has already pointed out the similarity of the species with *O. illgi* Heron, which belongs to the *bowmani*-group as defined in the phylogenetic study of Böttger-Schnack & Huys (1998; their species group 5). Common characteristics of this group are very elongate conical processes on the distal endopod margins in P2–P3 and a very robust maxillipedal basis, armed with 2 relatively short setae. Boxshall (1977b) synonymized *O. curta* with *O. ovalis* Shmeleva, *O. longiseta* Shmeleva and *O. latimana* Gordeyeva, as well as with *Oncaea* sp. 1 and 2 of Ferrari (1975), but his opinion was not followed by Malt (1983a) nor in the present account.

Oncaea sp. 1 and sp. 2 described by Ferrari (1975; *Oncaea* sp. 1: p. 228, Figs. 6E, F, 7A–D; *Oncaea* sp.2: p.228, Figs. 6G, H, 7E–H) are placed in *Oncaea* s.str. on the basis of the swimming leg armature, the lack of a conical process on the distal margin of P4 endopod, and the size and position of the maxillipedal setae. Malt (1983a) tentatively assigned *Oncaea* sp. 1 to *O. media* Giesbrecht forma *minor* and *Oncaea* sp. 2 to both *O. curta* Sars and *O. venusta* Giesbrecht f. *venella*, reflecting the author's undecisiveness on this matter. Since the original description of both species lacks sufficient detail necessary for unequivocal identification, they are regarded here as *species inquirendae* in *Oncaea* s.str.

Myuspictosum philippinensis Kazatchenko & Avdeev, 1977 (p. 44–47, Fig. 9a–i, 10a–g) has been synonymized with *Oncaea* s.l. by Malt (1982a; erroneously spelled *Myctospictosum* by Malt) and her opinion was followed by Huys & Böttger-Schnack (1996/97). The single male of *O. philippinensis* was found on the gills of the deep-sea fish *Myctophum spinosum* collected in the Philippine Trench at 7255 m, which is the deepest record of an oncaeid species so far. The unusually deep record has been regarded as accidental rather than real (Huys & Böttger-Schnack, 1996/97). *O. philippinensis* might well belong to *Oncaea* s.str., based on the modified seta IV on the antenna, which is hook-like as in most other species of the genus. However, the leg armature in Kazatchenko & Avdeev's description is incomplete in P2 (endopod missing) and very unusual in P1, the endopod showing 4 inner setae and 3 outer and distal spines, with a conical process at the distal margin. This combination of armature elements is not found in any oncaeid species known thus far and the species is regarded here as *species inquirenda* in *Oncaea* s.str.

Oncaea praeclara Humes is regarded as a synonym of *O. venusta*, on grounds that will be discussed below under *O. venusta*, Remarks.

DESCRIPTION OF SPECIES

Oncaea venusta Philippi, 1843

Oncaea venusta Philippi (1843): 62–63, Tafel III, Fig. 2a–d.

Oncäa venusta Giesbrecht, 1892

Oncaea venusta Farran, 1929

Oncaea praeclara Humes, 1988

RELIABLE DESCRIPTIONS. Giesbrecht (1892): 590–604, 755, 756, 774, 789, Plate 2, Fig. 5, Plate 3, Fig. 7, Plate 47, Fig. 2, 5, 13, 19, 39, 44, 48, 50, 54, 58 [as *Oncäa venusta*]; Farran (1929): 284–285, Fig. 33 [as *Oncaea venusta*]; Wilson (1932): 353–354, Fig. 213a–d; Mori (1937, reprinted 1964): 119–120, Plate 66 Figs. 1–9; Dakin & Colefax (1940): 116, Fig. 205A a–f; Sewell (1947): 263–264; Olson [MS] (1949): 101–104, Plate XXIV Figs. 1–8 (♀), Plate XXV Figs. 11–13 (♂); Tanaka (1960): 71–72; Corral Estrada (1970): 216–217; Chen *et al.* (1974): 40–41, Plate 6 Figs. 1–5; Ferrari (1975): 225–228, Figs. 5I–K, 6A–D; Boxshall (1977b): 124–128 Figs. 11a–k (♀), 12a–d (♂); Ho (1984): 41–44, Figs. 12–14; Humes (1988): 475–485, Figs. 1a, b, d [not Fig. 1c, e], 2a–i, 3a–g (♀), 4a–g (♂) [as *Oncaea praeclara*]; Huys & Boxshall (1991): 286, 289, 445 Figs. 2.10.8.B, 2.10.10.A, 2.10.21.B, 2.10.21.D, 2.10.24.A; Heron & Bradford-Grieve (1995): 33, 36, Figs. 14e–l, 15a–j, 27b, 28; Itoh [in: Chihara & Murano 1997]: 981–982, Plate 223 Figs. 371(left) a–b (f. *venella*), 371(right) a–e (f. *typica*).

DOUBTFUL DESCRIPTIONS. Razouls (1974): 236–237, Figs. 1A–H (♀), 2A–C (♂); Humes (1988): only Fig. 1c, e (as *Oncaea praeclara*).

TYPE LOCALITY. Western Mediterranean Sea, near Palermo.

MATERIAL EXAMINED.

Red Sea: see below under *O. venusta* f. *typica* and f. *venella*

Other areas:

- (1) Gulf of Naples, Italy; collected 1 February 1967; depth 0–100 m; leg. B. Scotto di Carlo; identified by G.A. Heron: 1 ♀, 1 ♂ in alcohol (RBS).
- (2) Pacific Ocean, off Tanega Islands; R/V *Toyoshio-maru*; collected 5 November 1994 with ORI-plankton net, mesh size 0.33 mm; oblique haul, depth 1600 m; leg. S. Ohtsuka: several ♀♀ and ♂♂ (RBS).
- (3) Sea of Japan, Tassha Bay, Sado Island; collected 1978 from colonies of *Solandria secunda* (Inaba), a hydroid; depth 10 m; leg. and identified by J.-s. Ho; 4 ♀♀ in alcohol (RBS).
- (4) (a) North Pacific Ocean, Galapagos Rift, 00° 48.0'N, 086° 13.0'W; collected 7 December 1979; DSRV *Alvin* dive no. 990; depth 2451 m; 1 specimen in alcohol, labelled *Oncaea praeclara*, Humes, 1988, holotype ♀ (National Museum of Natural History, Smithsonian Institution, Washington, DC, reg. no. USNM 234 109): this vial contains *Oncaea venusta* (1 ♀); parts of the specimen broke off during re-examination and are mounted on slides in lactophenol [right antennule (segment 4–6), left antenna (endopod segments 1 and 2), right maxilliped (claw)].
(b) North Pacific Ocean, Galapagos Rift; further sampling data not specified; 1 specimen in alcohol labelled: Acc.no. 37 66 47; *O. praeclara*, 13 August 1987 (USNM 234 111): this vial contains *Oncaea venusta* (1 ♀).
(c) North Pacific Ocean, Galapagos Rift, 00° 48.0'N, 086°

13.0'W; collected 5 December 1979; DSRV *Alvin* dive no. 998; depth 2450 m; 1 specimen in alcohol labelled *Oncaea praeclara*, Humes, 1988, 1 ♂ (USNM 234 112): this vial contains *Oncaea venusta* (1 ♂, possibly f. *typica*).

- (d) North Pacific Ocean, Galapagos Rift, 00° 47'N, 086° 08'W; collected 24 January 1979; DSRV *Alvin* dive no. 883; depth 2493 m; 4 specimens in alcohol labelled *Oncaea praeclara*, 3 ♂♂, 1 ♀ (USNM 234114): this vial contains a mixture of *O. venusta* (1 ovigerous ♀, 1 ♂), *Oncaea* sp. (1 ♂, possibly *venusta* f. *venella*), *Triconia* sp. (1 ♂).
- (e) North Pacific Ocean, Galapagos Rift, 00° 48.25'N, 086° 13.48'W; collected 30 November 1979; DSRV *Alvin* dive no. 983; (material donated to R. Böttger-Schnack by A. Humes); 11 specimens in alcohol labelled *Oncaea praeclara*, Humes 1988, 4 ♀♀, 7 ♂♂: this vial contains a mixture of *O. venusta* (2 ♀♀, 3 ♂♂), *O. media* (2 ♀♀), *O. clevei* (1 ♂), Oncaeidae indet. (2 ♂♂), Corycaeidae indet. (1 juvenile); (RBS).
- (f) East Pacific Rise, 12° 48.52'N, 56° 48'W; collected 22 November 1987, *Hydronaut* Cruise, *Nautila* dive 221; depth 2630 m (material donated to R. Huys, NHM, by A. Humes); 9 specimens in alcohol labelled *O. praeclara*, Humes, 5 ♀♀, 5 ♂♂: this vial contains 5 ♀♀ (1 ♀ ovigerous) and 4 ♂♂ of *O. venusta* (all specimens empty exoskeletons with no internal tissue).
- (5) Sargasso Sea, near Bermuda, 31° 37.94'N, 64° 09.45'W; collected 9 July 1998 with 1 m net, mesh size 0.15 mm; depth 210 m; leg. D. Steinberg: several ♀♀ (ovigerous and non-ovigerous), 3 ♂♂ in alcohol, for molecular analysis (A. Bucklin, Durham, New Hampshire); 2 ♀♀, 2 CV ♀♀ in alcohol (RBS).

Philippi's (1843) description of *O. venusta* was the first account of an oncaeid species. It was based on a single male specimen collected in the western Mediterranean, near Palermo. Unfortunately, the specimen was lost by accident before the author could complete the description. Giesbrecht (1892) redescribed *O. venusta* in more detail from the Gulf of Naples and recently, Heron & Bradford-Grieve (1995) provided an excellent redescription of the species based on material from the Gulf of Naples as well as from other localities in the Atlantic and Pacific Ocean. Both authors do not mention the existence of different size variants among *O. venusta*, although the range of size variation was quite large in Giesbrecht's specimens from the Pacific. In 1929, Farran described two distinct size morphs of *O. venusta*, forma *typica* and forma *venella*, from various Atlantic and Pacific locations, which were separated mainly by their size and some minor morphological characters. The two forms were distinguished in some of the subsequent taxonomic descriptions (e.g. Tanaka, 1960; Ferrari, 1975; Boxshall, 1977b) and a third, 'robust' form was added by Boxshall (1977b). In the Red Sea, both form variants of *O. venusta* sensu Farran occur. They differ considerably in temporal and spatial distribution (Böttger-Schnack, 1990b, 1995), thus indicating the existence of reproductively isolated populations. A detailed morphological examination of both size variants was undertaken during the present study, including microstructures on the appendages and on the exoskeleton (pores, scales), partly by using SEM analyses. The results pointed out several morphological differences between the two forms not noted in the literature before, but these were not regarded as sufficient to warrant recognition of the two forms as separate species. In order to provide the morphological basis required for future taxonomic analyses on *O. venusta*, both forms are redescribed. A further approach to differentiate the two forms using alternative methods, e.g. molecular analysis, is currently in progress.

Oncaea venusta Philippi, 1843 forma *typica* Farran, 1929*Oncaea venusta* Farran (1929): 284 [as *Oncaea venusta* forma *typica*]*Oncaea venusta* forma *typica* Farran, 1929

TYPE LOCALITY. Not specified, various locations in the temperate and tropical Atlantic, as well as south of New Zealand.

MATERIAL EXAMINED.

Central Red Sea, 21° 22.09'N, 38° 05.09'E: Stn. 664; *R/V Valdivia* leg 29: collected 21 February 1981 with MSN 0.1 mm net (Haul 218/5); depth 0–50 m; total water depth ca 2000 m.

(a) 5 ♀♀, 5 ♂♂ in alcohol (BMNH 1998.2777–2786).

(b) 5 ♀♀, 5 ♂♂ in alcohol (ZMH K-39586).

(c) 2 ♀♀ dissected on slides, 1 ♀ in alcohol; 3 ♂♂ dissected on slides, 1 ♂ in alcohol; 1 ♀, 1 ♂ in mating position in alcohol (RBS).

DESCRIPTION. Note illustrations are based on (c).

ADULT FEMALE (Figs. 2–5, 8A–E, 9A–F).

Body length (measured in lateral aspect; from anterior margin of rostral area to posterior margin of caudal rami, calculated as sum of individual somites): 1615 µm [traditional method 1130 µm, range: 1000–1230 µm, based on 14 specimens (Böttger-Schnack *et al.*, 1989)].

Exoskeleton heavily chitinized, covered with numerous granules, forming long raised structures (lines), especially along lateral part of cephalic shield (Fig. 8A). Prosome 2.1 times length of urosome, excluding caudal rami, 1.7 times urosome length including caudal rami. P2-bearing somite without dorso-posterior projection in lateral aspect (Fig. 2B). P3-bearing somite with conspicuous raised pore protruding laterally (Fig. 2A). Other integumental pores on prosome as indicated in Fig. 2A, B. Pleural areas of P4-bearing somite with rounded posterolateral corners.

Proportional lengths (%) of urosomites 12.2 : 57.7 : 8.5 : 9.1 : 12.5. Proportional lengths (%) of urosomites and caudal rami 10.0 : 47.0 : 6.9 : 7.3 : 10.2 : 18.6.

Genital double-somite 1.5 times as long as maximum width (measured in dorsal aspect) and 1.9 times as long as postgenital somites combined (Fig. 2C); largest width measured at anterior two-thirds, lateral margins of genital double-somite rounded, posterior part tapering gradually. Paired genital apertures located at about 2/5 the distance from anterior margin of genital double-somite; armature represented by 1 spine and 2 minute spinous processes (Fig. 8B), only 1 of which discernible under light microscope (Fig. 2G). Double-curved sclerotization between, but slightly anterior to, genital apertures, pore pattern on dorsal surface as indicated in Fig. 2C.

Anal somite 1.6 times wider than long; about half the length of caudal rami (Fig. 2C). Secretory pore discernible on either side of anal opening and additional one near posterior margin. Anterior margin of anal opening (vestigial anal opening) with transverse row of minute denticles. Posterior margin of somite finely serrate ventrally and laterally (Fig. 2D). Ventral face with paired secretory pore near posterior margin (Fig. 2C, cf. also Fig. 6E).

Caudal ramus (Fig. 2F) about 3.5 times as long as wide. Armature consisting of 6 elements: antero- and posterolateral setae (II+III) long, spiniform and unipinnate along medial margin; outer terminal seta (IV) long and plumose; inner terminal seta (V) longest and plumose; terminal accessory seta (VI) more than 2/3 the length of outer terminal seta and 1.4 times longer than caudal ramus; dorsal seta (VII) about same length as posterolateral seta (III) and less than half the length of terminal accessory seta, plumose and bi-articulate at base. Inner margin of somite with fringe of long setules. Dorsal anterior surface (Fig. 2F) with secretory pore near insertion of seta II. Dorsal surface covered with numerous small scales (Fig. 2F).

Antennule 6-segmented (Fig. 2E), relative lengths (%) of segments measured along posterior non-setiferous margin 8.4 : 27.6 : 39.3 : 10.7 : 4.7 : 9.3. Armature formula: 1-[3], 2-[8], 3-[5], 4-[3+ae], 5-[2+ae], 6-[6+(1+ae)]. Small element on segment 4 ornamented with row of scales along entire length, tip with tubular extension (SEM observation, not figured). Small element on segment 6 (arrowed in Fig. 2E) with tubular extensions (Fig. 8C), indicating sensory function.

Antenna 3-segmented, distinctly reflexed (Fig. 3A). Coxobasis with row of long, fine spinules or setules near outer margin and with few additional denticles on proximal and distal part of outer (exopodal) margin, curved row of denticles on posterior face; with bipinnate seta at inner distal corner. Endopod segments unequal in length; proximal endopod segment subtriangular forming outer lobate outgrowth bearing patch of branched tubular extensions (Fig. 8D, E), with row of denticles along posterior inner margin. Distal endopod segment distinctly shorter than proximal endopod segment, with narrow cylindrical base articulating; with two patches of branched tubular extensions along outer margin (Fig. 8D); lateral armature with 4 elements, numbered using Roman numerals in Fig. 3A: 1 unipinnate spiniform seta (III) and 3 curved setae (I, II, IV), setae I and II sparsely pinnate, seta I shortest; distal armature consisting of 7 elements: 1 long curved unipinnate seta (E), 4 slightly curved unipinnate setae of graduated length (A–D), seta D being shortest, and 2 slender naked setae (F and G), similar in length and shorter than seta D; none of armature elements spiniform or geniculate.

Labrum (Fig. 3B,C) distinctly bilobed. Each lobe with row of minute denticles around outer ventral margin, row of long fine setules latero-distally and dentiform processes converging and decreasing in size medially. Lobes separated by median concavity covered anteriorly by overlapping rows of broad hyaline petaloid flaps, flanked by paired slit-like pores on proximal part of each lobe (Fig. 9A, B; position of pore arrowed in Fig. 3B). Anterior surface with well developed integumental pockets (Fig. 9C) either side of median swelling, free margin of pockets serrate (Fig. 9D); median swelling with large secretory pore posteriorly. Posterior part of medial incision ornamented with four rounded integumental thickenings (Fig. 3C). Posterior surface with paired patch of very long fine setules and 2 large secretory pores located on proximal part of each lobe.

Paragnaths (Fig. 5, 9C) with small lateral extensions, anterior margin densely covered with several rows of long setules, median bulge unornamented.

Mandible (Fig. 3D) with few minute setules on surface of coxa; gnathobase with 5 elements, indicated by capital letters in Fig. 3D: 1 at subdistal ventral -corner, 2 along distal margin and 2 along subdistal dorsal margin; ventral element (A) shorter than ventral blade, with long, fine setules along dorsal side; ventral blade (B) strong and spiniform, with row of setules on posterior side; dorsal blade (C) strong and broad, with 3 dentiform processes along distal margin; dorsal elements setiform, the shorter (D) hyaline, flat and densely setose, the longer (E) multipinnate.

Maxillule (Fig. 3E) indistinctly bilobed, with numerous spinules on anterior and posterior surfaces. Inner lobe subcylindrical, with 3 elements: outermost one spiniform, swollen at base, fringed with coarse spinules, others setiform and bipinnate; innermost one located along concave inner margin at some distance from other elements. Outer lobe with 4 elements; outermost element spiniform, curved and bipinnate along inner proximal margin, unipinnate along distal margin, longer than the following; other elements bipinnate or naked, element next to the innermost shortest.

Maxilla (Fig. 3F) 2-segmented, comprising syncoxa and allobasis.

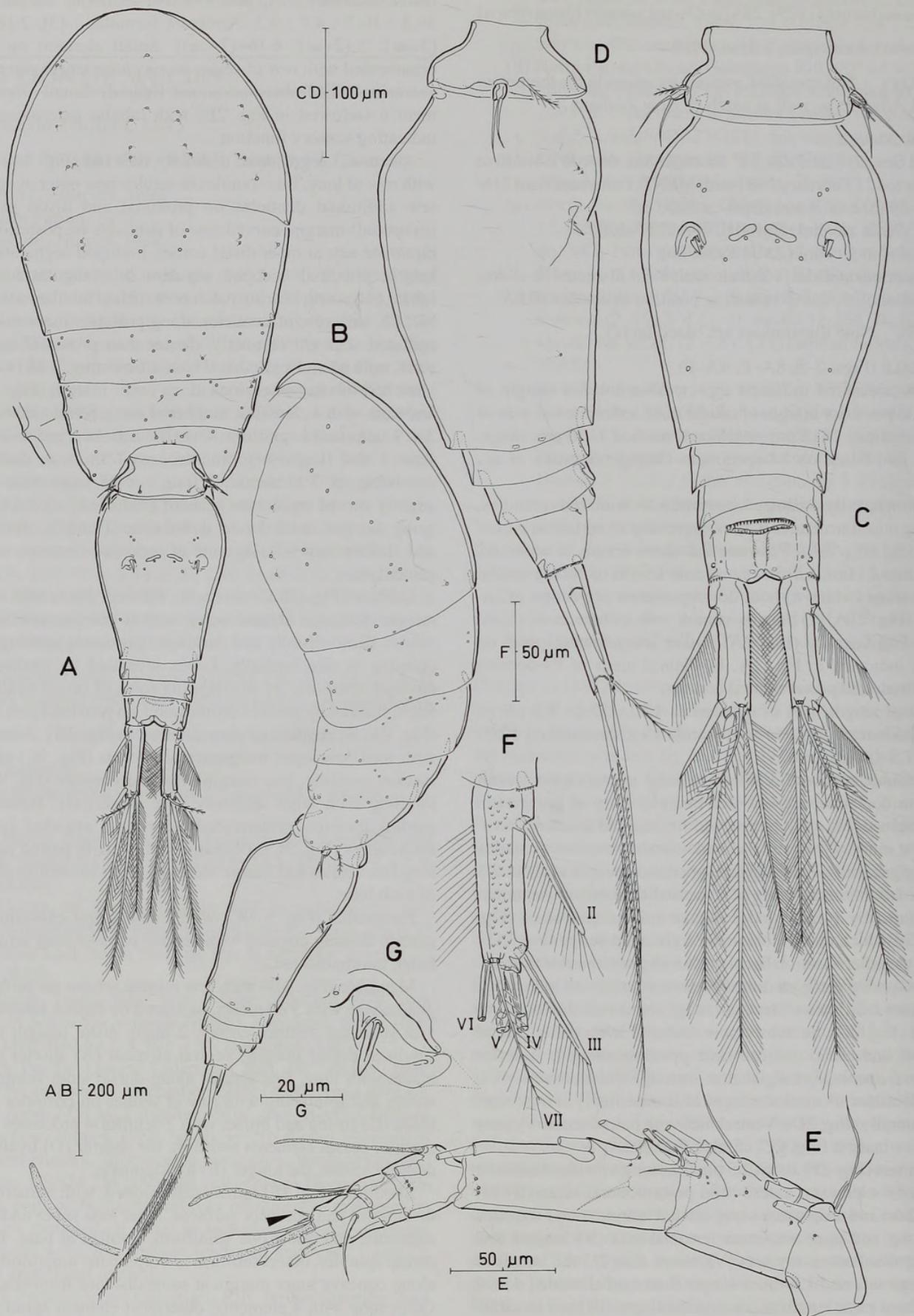


Fig. 2 *Oncaea venusta* f. *typica*, female (Red Sea) (A) Habitus, dorsal (lateral raised pore enlarged); (B) same, lateral (appendages omitted); (C) urosome, dorsal; (D) urosome, lateral; (E) antennule, small sensory element arrowed; (F) caudal ramus, dorsal, setae are numbered using Roman numerals; (G) P6.

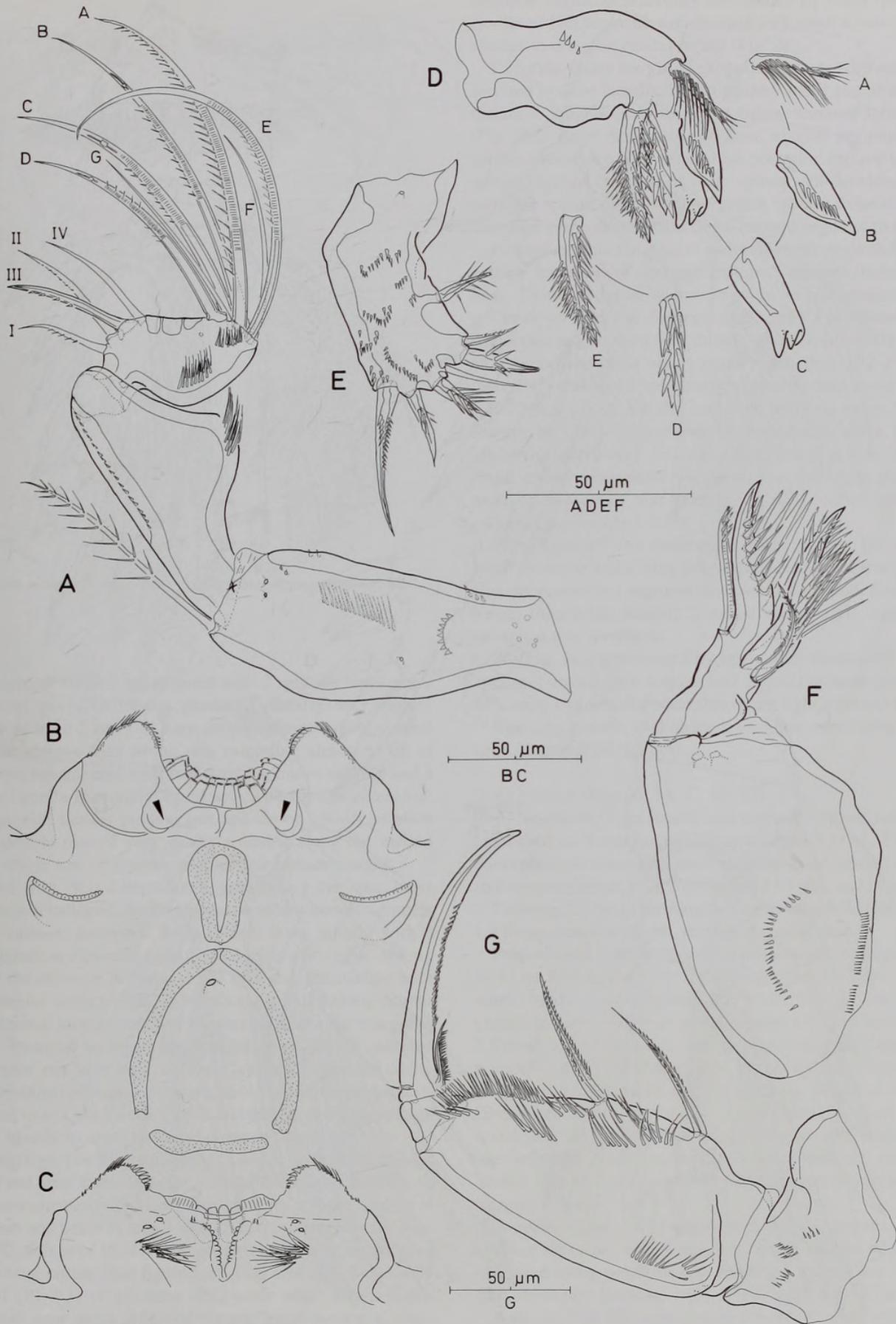


Fig. 3 *Oncaea venusta* f. *typica*, female (Red Sea) (A) Antenna, posterior, lateral elements are numbered using Roman numerals, distal elements indicated by capital letters; (B) labrum, anterior, slit-like pores arrowed; (C) same, posterior; (D) mandible, showing individual elements, identified using capital letters; (E) maxillule; (F) maxilla; (G) maxilliped.

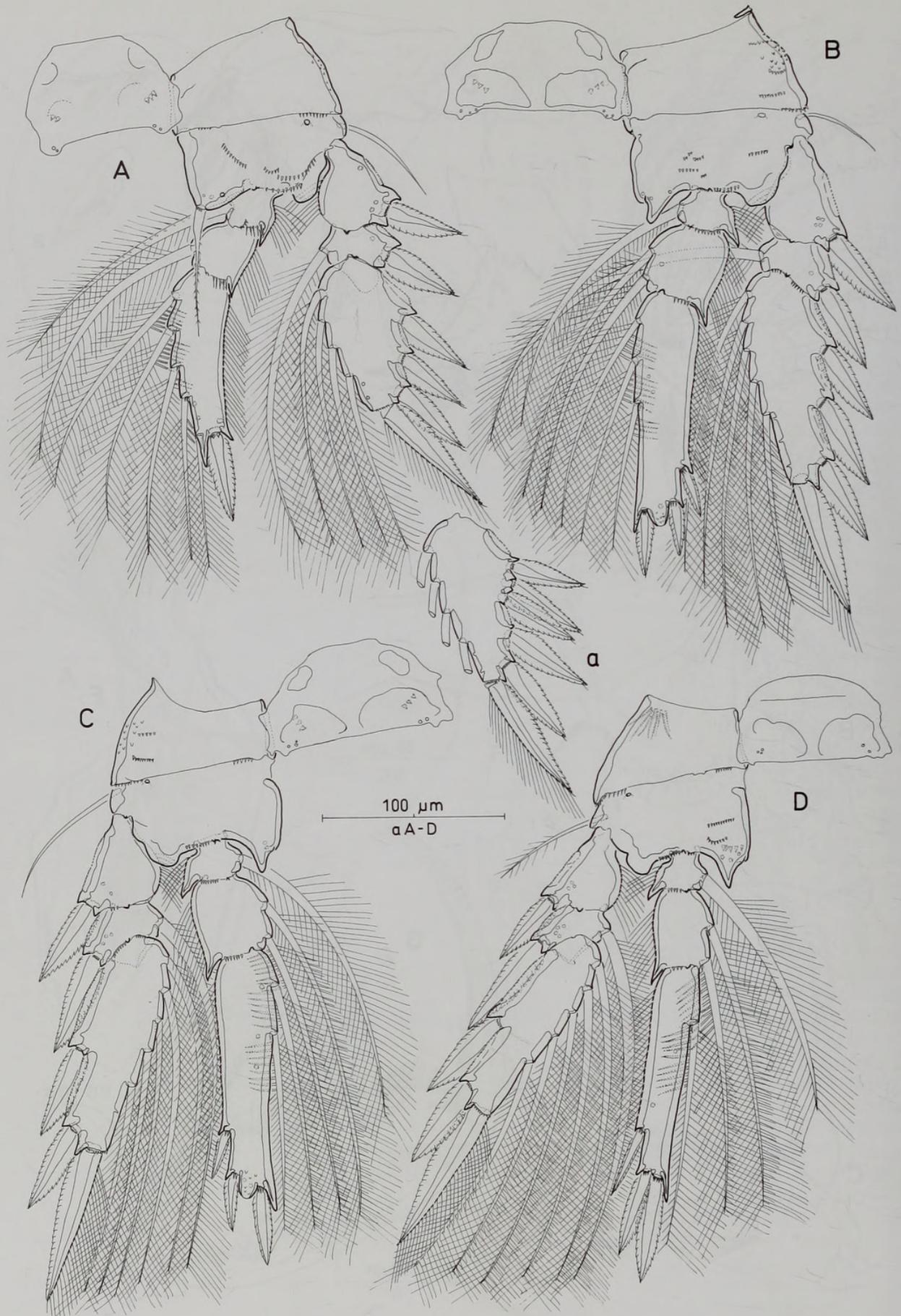


Fig. 4 *Oncaea venusta f. typica*, female (Red Sea) (A) P1, anterior [a, third endopod segment, showing aberrant spine number]; (B) P2, anterior; (C) P3, anterior; (D) P4, anterior.

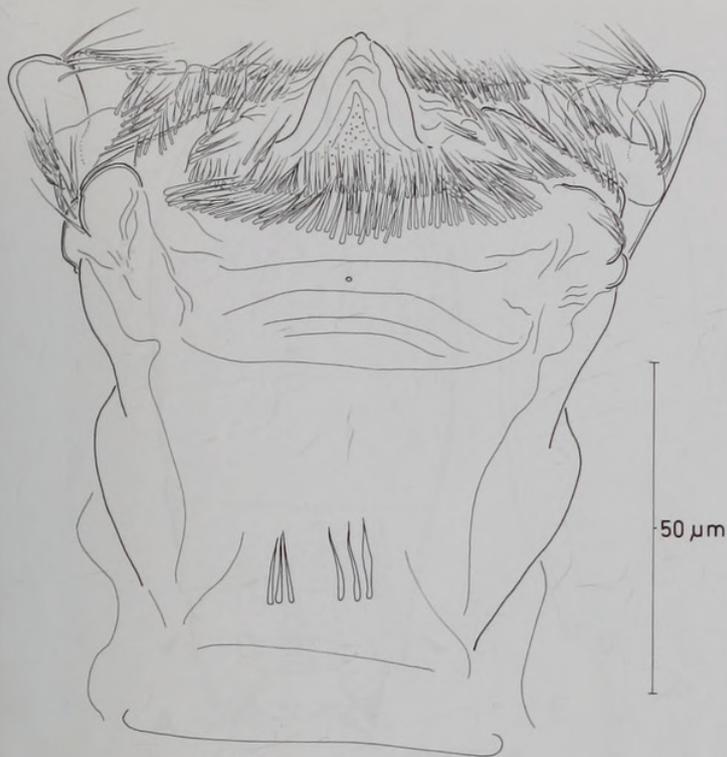


Fig. 5 *Oncaea venusta* f. *typica*, female (Red Sea) Paragnaths, ventral view.

Syncoxa unarmed, surface ornamented with 2 spinular rows and 2 large secretory pores. Allobasis produced distally into slightly curved claw bearing 2 rows of very strong spinules along medial margin; outer margin with strong seta extending almost to tip of allobasal claw, ornamented with few strong spinules distally and a thin hyaline lamella bilaterally, tip of seta with tubular extension; inner margin with slender pinnate seta and strong basally swollen spine with double row of very strong spinules along the medial margin and single row of shorter spinules along outer margin.

Maxilliped (Fig. 3G) 4-segmented, comprising syncoxa, basis and 2-segmented endopod. Syncoxa ornamented with few spinules on anterior surface, unarmed. Basis robust, inner margin with 2 spiniform spinulose elements nearly equal in length; fringe of long setules half the distance between distal seta and articulation with endopod; anterior surface with 2 rows of long spinules along palmar margin, additional longitudinal row of spinules near outer margin as in Fig. 3G. Proximal endopod segment unarmed. Distal endopod segment drawn out into long curved claw, with pinnules along proximal two-thirds 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 (Fig. 4A–D), with 3-segmented rami. Spine and setae formula as for genus. Intercoxal sclerites well developed, ornamented with 3 posterior denticles at distal corners in P1–P3. Coxae and bases of legs 1–4 with surface ornamentation as in Fig. 4A–D. Coxae of P1–P4 with posterior raised secretory pore near outer distal corner (not figured, cf. Fig. 13A–D). Bases with short naked (P1–P3) or plumose (P4) outer seta; with anterior secretory pore near outer proximal corner; inner portion slightly produced medially in P2–P4 (Fig. 4B–D). Inner basal seta on P1 spiniform and minutely pinnate. Respective legs without distinct length differences between exopod and endopod (P1) or with endopod slightly longer than exopod (P2–P4). Bases of spines on exopod and

endopod segments anteriorly surrounded by small spinules. Anterior face of all segments ornamented with small scales (not figured), similar to those on caudal ramus (Fig. 2F).

Exopods. Outer margin of exopod segments with well developed serrated hyaline lamella, interrupted by small gap at about half the distance, longitudinal concavity below serrated lamellar margin (Fig. 9E); inner margin of proximal exopod segments with long setules. Secretory pore present on posterior surface of distal segments. Hyaline lamellae on outer spines well developed; outer and terminal spines of P1 with subapical tubular extension (Fig. 9F). Terminal spine shorter than distal exopod segment in all legs.

Endopods. Outer margin of endopod segments with fringe of long setules. Inner seta of proximal endopod segment slightly swollen at base. Distal endopod segments with several secretory pores on posterior surface; distal margin of P2 and P3 produced into conical projection ornamented with minute spinules anteriorly (Fig. 4B,C). Outer subdistal spine nearly equal in length to (P2–P3) or shorter than (P4) outer distal spine, always shorter than distal spine. Outer distal spine about 3/4 the length of terminal spine in P4. Outer margin of distal segment of P1 terminating in a long process obscuring insertion of distalmost inner seta (Fig. 4A). Inner setae of distal endopod segments with spinule comb along proximal inner margin; this comb also present on distal inner seta of middle endopod segment in P3–P4.

P5 as figured for *O. venusta* f. *venella* (cf. Fig. 11G), comprising small plumose seta arising from lateral surface of somite, and small free unornamented segment representing exopod. Exopod slightly longer than wide, bearing 2 naked setae nearly equal in length, subapical one spiniform.

P6 (Fig. 2G) represented by operculum closing off each genital aperture; armed with a spine and 2 small spinous processes (Fig. 8B), only 1 of which discernible under light microscope (Fig. 2G).

Egg-sacs paired, oval-shaped; each sac containing appr. 30–40 eggs (diameter 50–60 μ m).

ADULT MALE (Figs. 6, 7A–C, 8F, 10).

Body length: 1158 μ m [traditional method: 910 μ m, range: 880–950 μ m, based on 9 specimens (Böttger-Schnack *et al.*, 1989)]. Sexual dimorphism in antennule, antenna, maxilliped, genital segmentation and ornamentation, P1–P3 (endopod), P5–P6, and in caudal ramus.

Prosoma 2.0 times the length of urosome, excluding caudal rami, 1.7 times urosome length, including caudal rami.

Proportional lengths (%) of urosomites (excluding caudal rami) 10.1 : 64.5 : 6.0 : 4.4 : 5.0 : 10.1; proportional lengths (%) of urosomites (caudal rami included) 8.6 : 55.0 : 5.1 : 3.7 : 4.3 : 8.6 : 14.7. Length to width ration of genital somite 1.5 : 1. Caudal rami about 2.5 times longer than wide, shorter than in female. Caudal setae with proportional lengths as in female, except for seta VI, which is about 2/3 the length of seta IV and 2.2 times the length of caudal ramus. Dorsal and ventral surface of caudal ramus covered with minute scales as in female. Surface of genital flaps and ventral surface of anal segment ornamented with several rows of small spinules. Ventral face of anal somite with paired secretory pore near posterior margin (Fig. 6E).

Antennule (Fig. 6B) 4-segmented; distal segment corresponding to fused segments 4–6 of female; relative lengths (%) of segments measured along posterior non-setiferous margin 8.0 : 27.1 : 43.3 : 23.6. Armature formula: 1-[3], 2-[8], 3-[4], 4-[11+2ae+(1+ae)].

Antenna (Fig. 6H) with seta on coxobasis naked and shorter than in female. Distal endopod segment with seta III much stouter than in female, seta IV spiniform and curved, both elements shorter than in female (Fig. 8F).

Maxilliped (Fig. 6C) 3-segmented, comprising syncoxa, basis

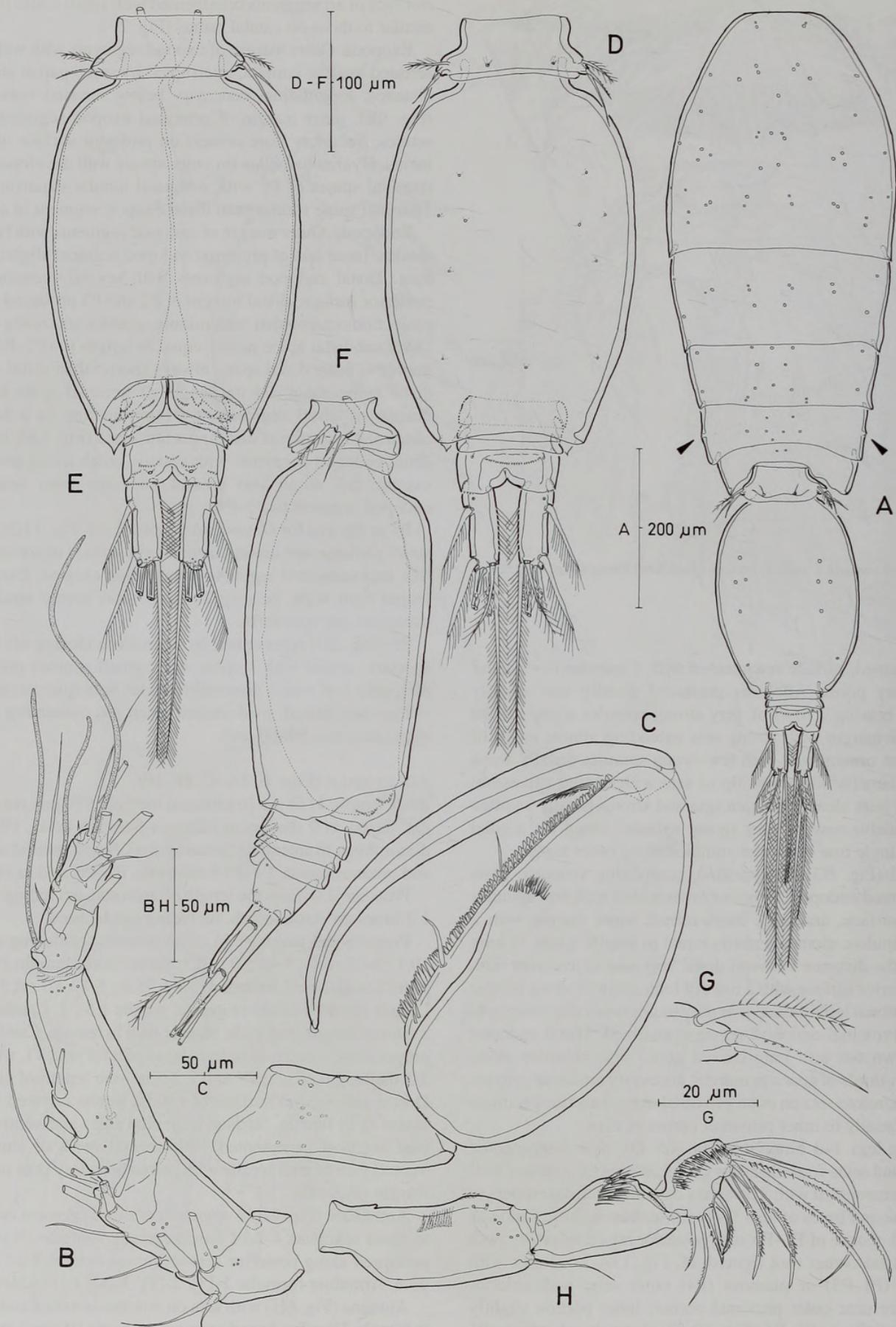


Fig. 6 *Oncaea venusta* f. *typica*, male (Red Sea) (A) Habitus, dorsal, arrows indicating position of lateral raised pores; (B) antennule; (C) maxilliped, anterior; (D) urosome, dorsal; (E) urosome, ventral; (F) same, lateral (spermatophores fully developed); (G) P5, dorsal; (H) antenna, posterior.

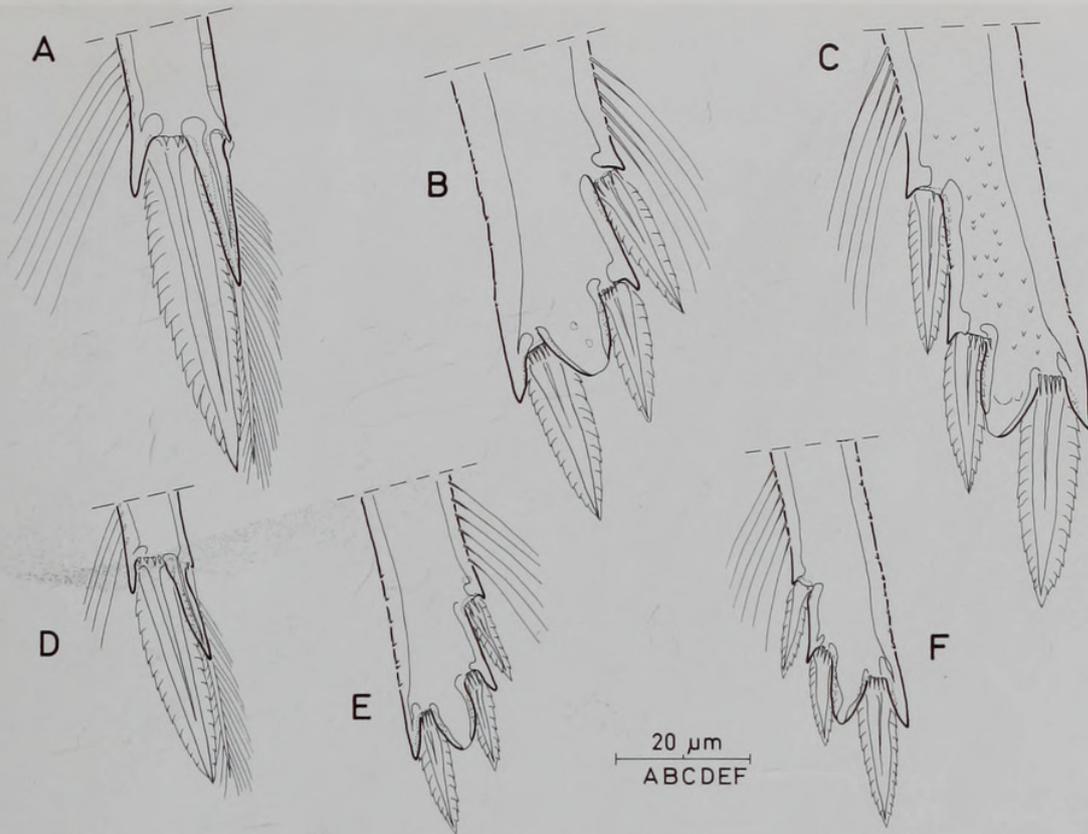


Fig. 7 *Oncaea venusta f. typica*, male (Red Sea) (A) P1, distal part of endopod; (B) P2, distal part of endopod; (C) P3, distal part of endopod. – *Oncaea venusta f. venella*, male (Red Sea) (D) P1, distal part of endopod; (E) P2, distal part of endopod; (F) P3, distal part of endopod.

and 1-segmented endopod. Syncoxa without surface ornamentation, except for several secretory pores, unarmed. Basis robust, particularly inflated in proximal half forming bulbous swelling; anterior surface with 2–3 transverse spinular rows in addition to row of short flat spinules along inner margin (Fig. 6C); posterior surface with 3 rows of short spatulated spinules of graduated length along palmar margin (Fig. 6C); with 2 small naked setae within the longitudinal cleft, nearly equal in length. Endopod drawn out into long curved claw, concave margin unornamented; accessory armature consisting of short, unipectinate spine basally fused to inner proximal corner of claw; tip of claw with minute hyaline apex.

Swimming legs 1–4 with armature and ornamentation as in female; sexual dimorphism expressed in terminal process on P1 enp-3, being longer than in female, reaching half the length of distal spine (Fig. 7A) and in conical projections on distal endopod segment of P2–P3, being longer than in female, reaching half the length of outer distal spine (Fig. 7B, C).

P5 (Fig. 6G) exopod not delimited from somite, general shape and armature as in female, except for subapical seta spiniform and shorter than in female, ornamented with row of minute spinules along outer margin.

P6 (Fig. 6E) represented by posterolateral flap closing off genital aperture on either side; covered by pattern of denticles as shown in Fig. 6E and 10A; with receptor (pores) at inner edge of posterolateral corners (Fig. 10B); these corners not protruding laterally so that they are hardly discernible in dorsal aspect (Fig. 6D).

Spermatophore oval (Fig. 6F), of variable size according to state of maturity; swelling of spermatophore during development not affecting shape and relative size of genital somite.

***Oncaea venusta* Philippi, 1843 forma *venella* Farran, 1929**

Oncaea venusta Farran (1929): 284–285, Fig. 33 (female only) [as *Oncaea venusta* forma *venella*].

Oncaea venusta forma *venella* Farran, 1929

TYPE LOCALITY. Not specified, various locations in the temperate and tropical Atlantic, as well as south of New Zealand (Farran, 1929).

MATERIAL EXAMINED

- (1) Central Red Sea, 21° 22.09'N, 38° 05.09'E: Stn. 664; *R/V Valdivia* leg 29: collected 21 February 1981 with MSN 0.1 mm net (Haul 218/5); depth 0–50 m; total water depth ca 2000 m.
 - (a) 5 ♀♀, 5 ♂♂ in alcohol (BMNH 1998.2787–2796)
 - (b) 5 ♀♀, 5 ♂♂ in alcohol (ZMH K-39587)
 - (c) numerous ♀♀ and ♂♂ (RBS).
- (2) Southern Red Sea, 15° 34.8'N, 41° 54.9'E: Stn. 703; *R/V Meteor* leg 5/5: collected 03 August 1987 with MSN 0.05 mm net (Haul 39/5); depth 0–50 m; total water depth 970 m: 1 ♂ in alcohol (RBS).
- (3) Southern Red Sea, 15° 34.8'N, 41° 54.9'E: Stn. 703; *R/V Meteor* leg 5/5: collected 03 August 1987 with MSN 0.05 mm net (Haul 39/4); depth 50–100 m; total water depth 970 m: 2 ♀♀, 2 ♂♂ dissected on slides, 1 ♀, 1 ♂ in alcohol (RBS).

DESCRIPTION. Note illustrations are based on (3).

ADULT FEMALE (Figs. 11–13)

Body length (measured in lateral aspect; from anterior margin of

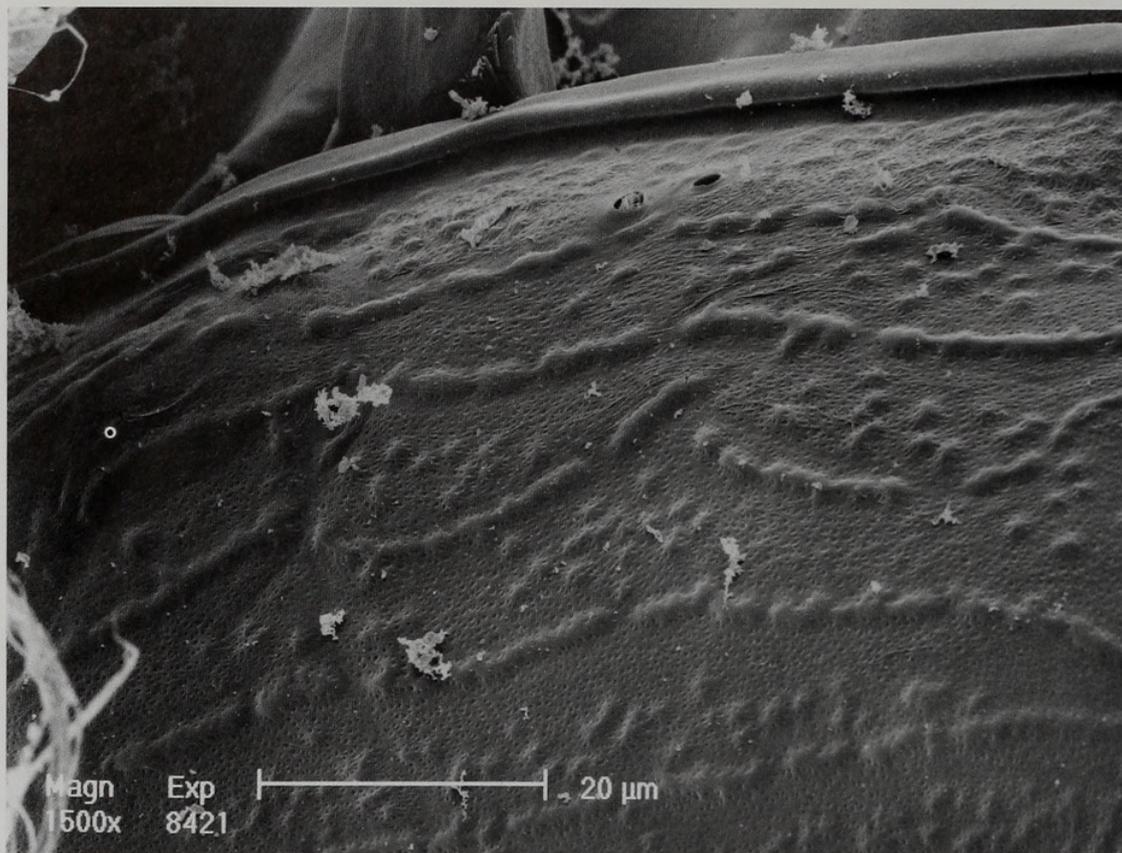


Fig. 8A *Oncaea venusta* f. *typica*, female (Red Sea) Cephalic shield, lateral, showing surface ornamentation.

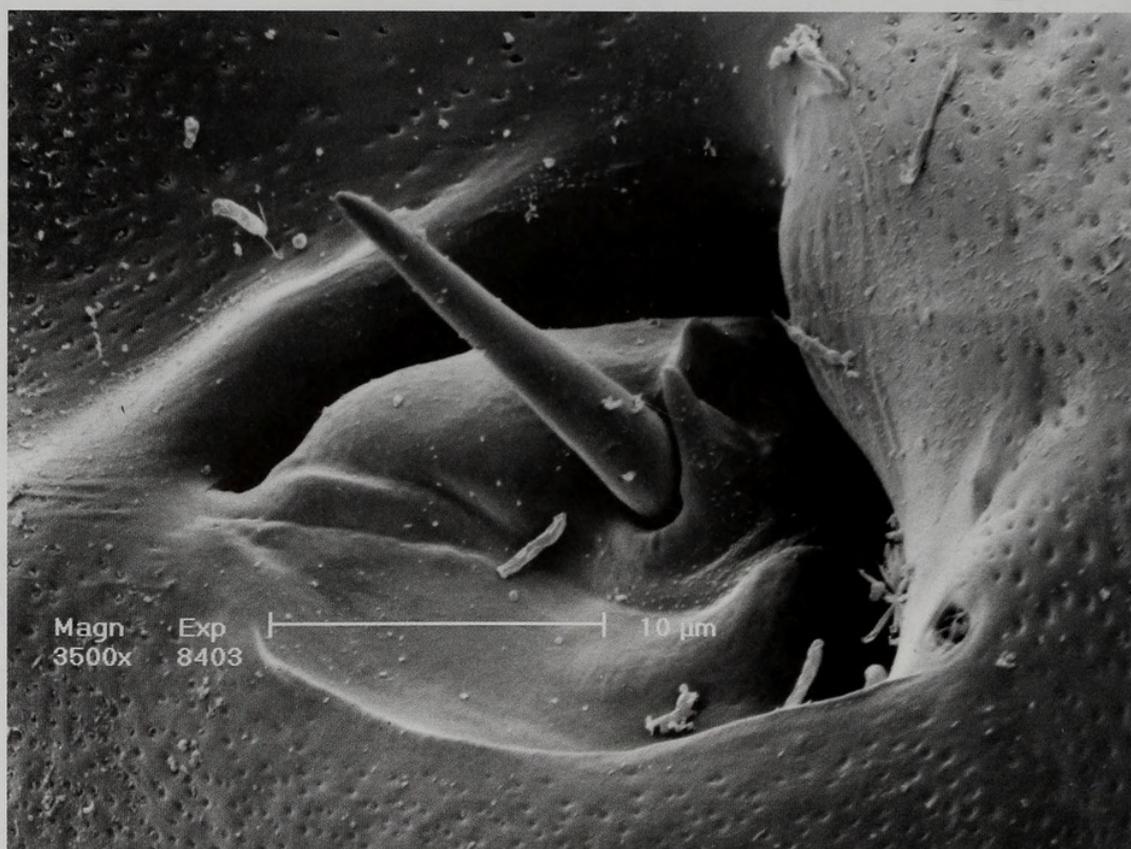


Fig. 8B *Oncaea venusta* f. *typica*, female (Red Sea) Genital aperture, right;



Fig. 8C *Oncaea venusta* f. *typica*, female (Red Sea) Antennule, 6th segment, short sensory element.

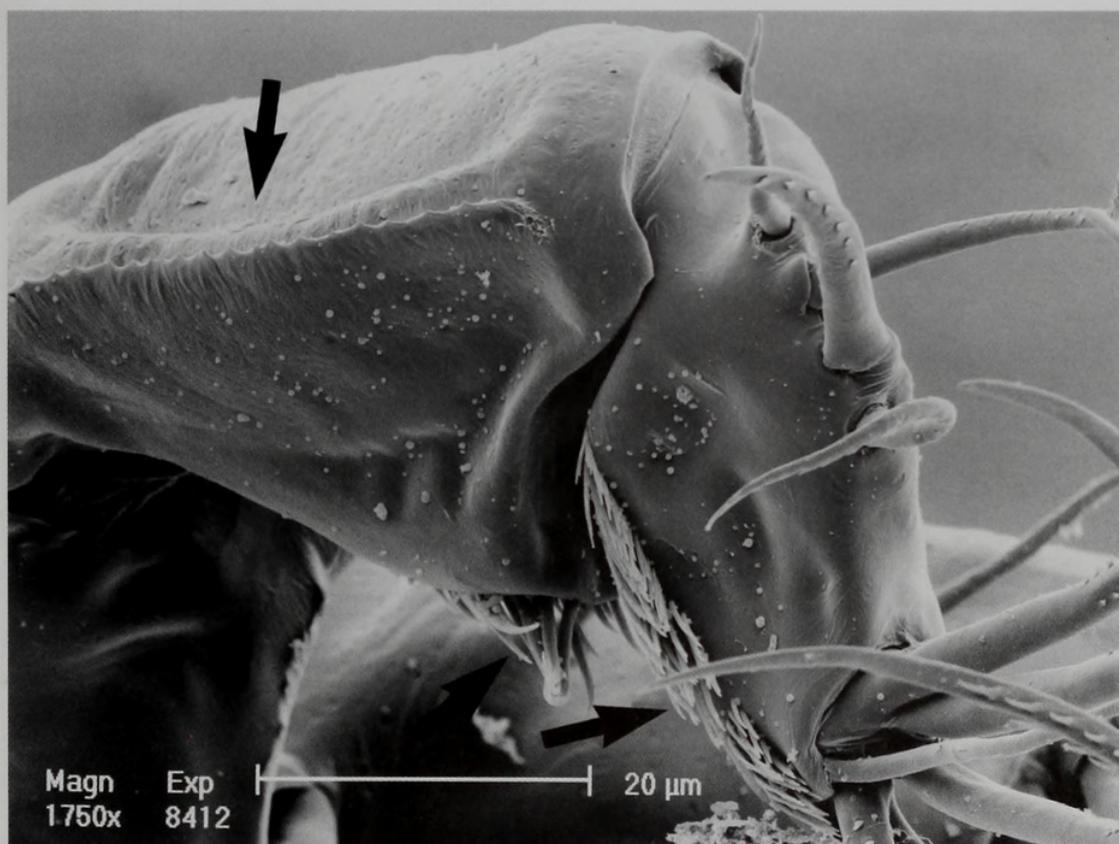


Fig. 8D *Oncaea venusta* f. *typica*, female (Red Sea) Antenna, endopod segment 1 + 2, concavity and patches of tubular extensions arrowed.

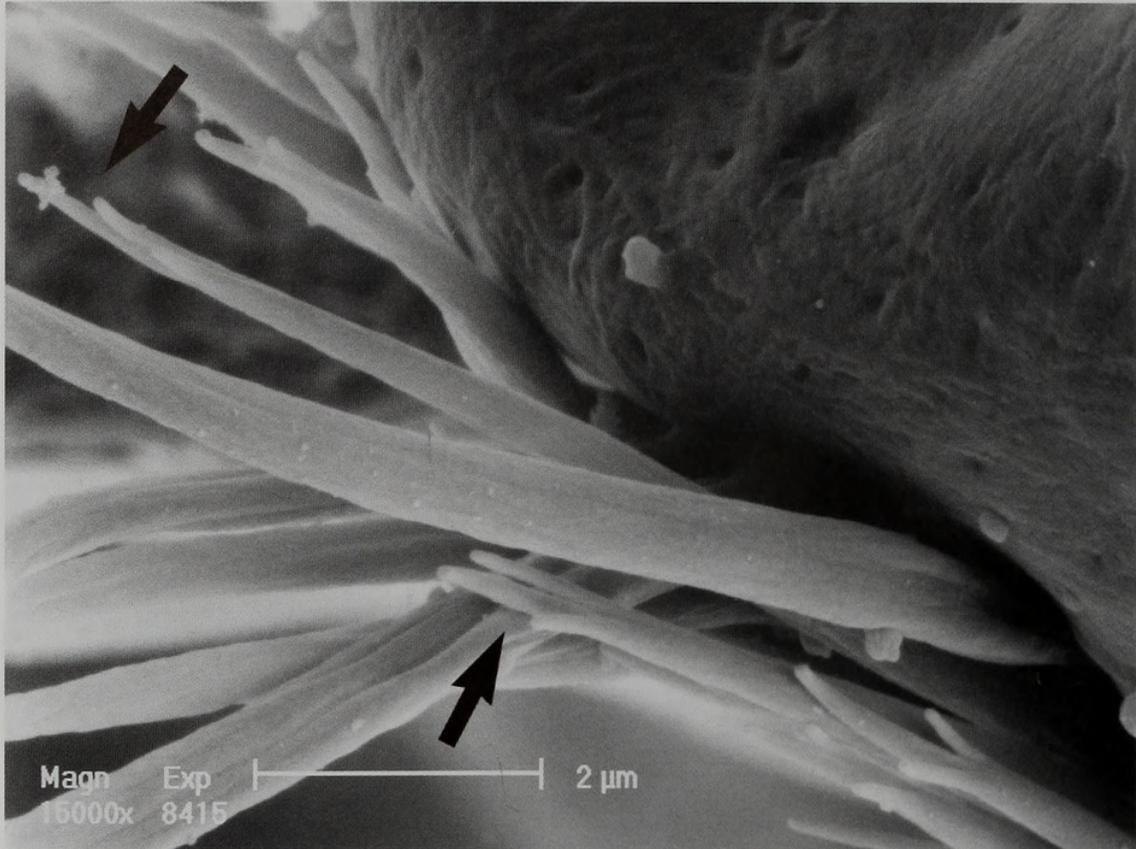


Fig. 8E *Oncaea venusta f. typica*, female (Red Sea) Antenna, endopod segment 2, branched tubular extensions (arrowed).

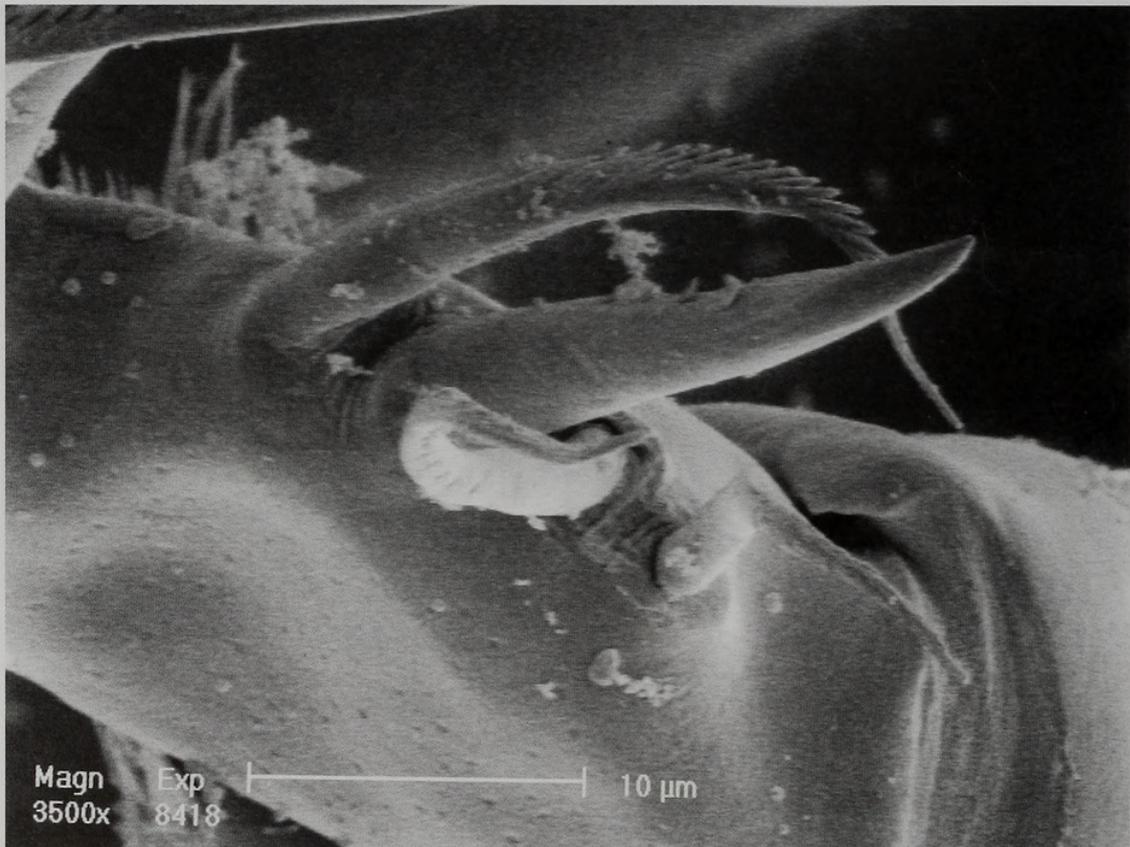


Fig. 8F *Oncaea venusta f. typica*, male (Red Sea) Antenna, endopod segment 2, lateral armature.

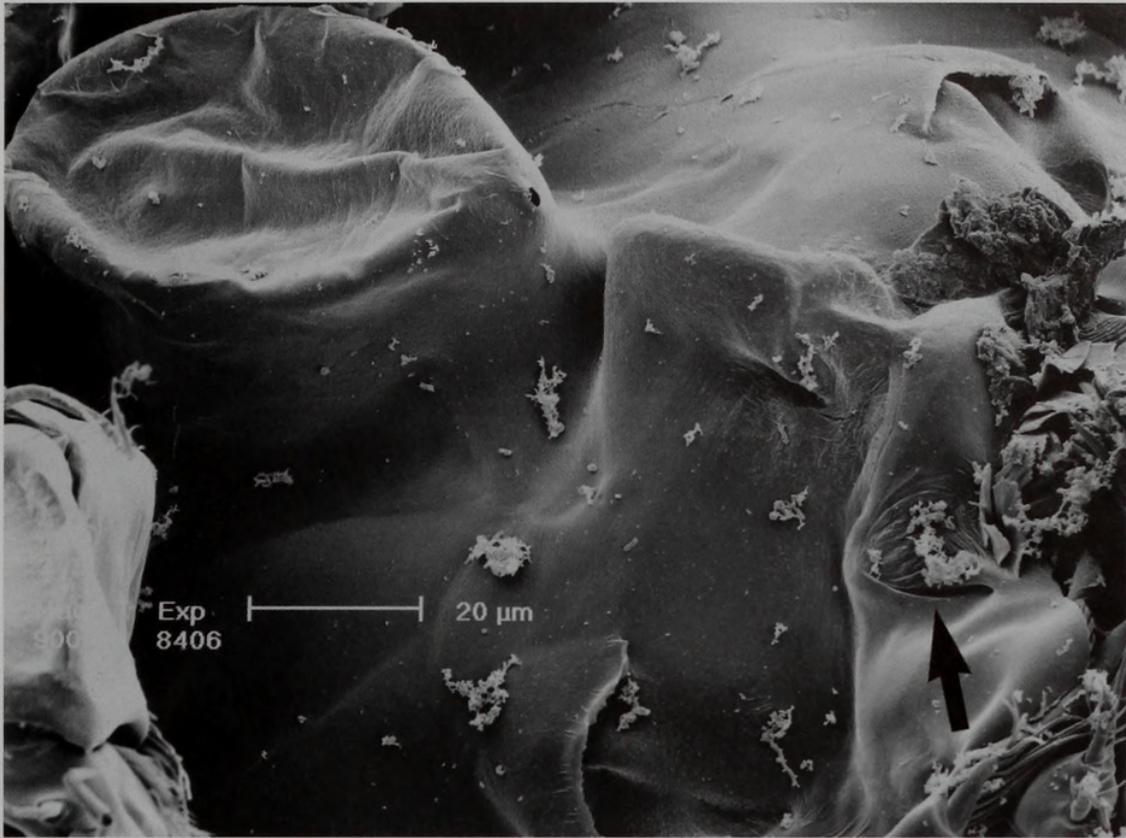


Fig. 9A *Oncaea venusta* f. *typica*, female (Red Sea) Labrum, anterior, showing integumental pockets either side of median swelling and right slit-like pore (arrowed).

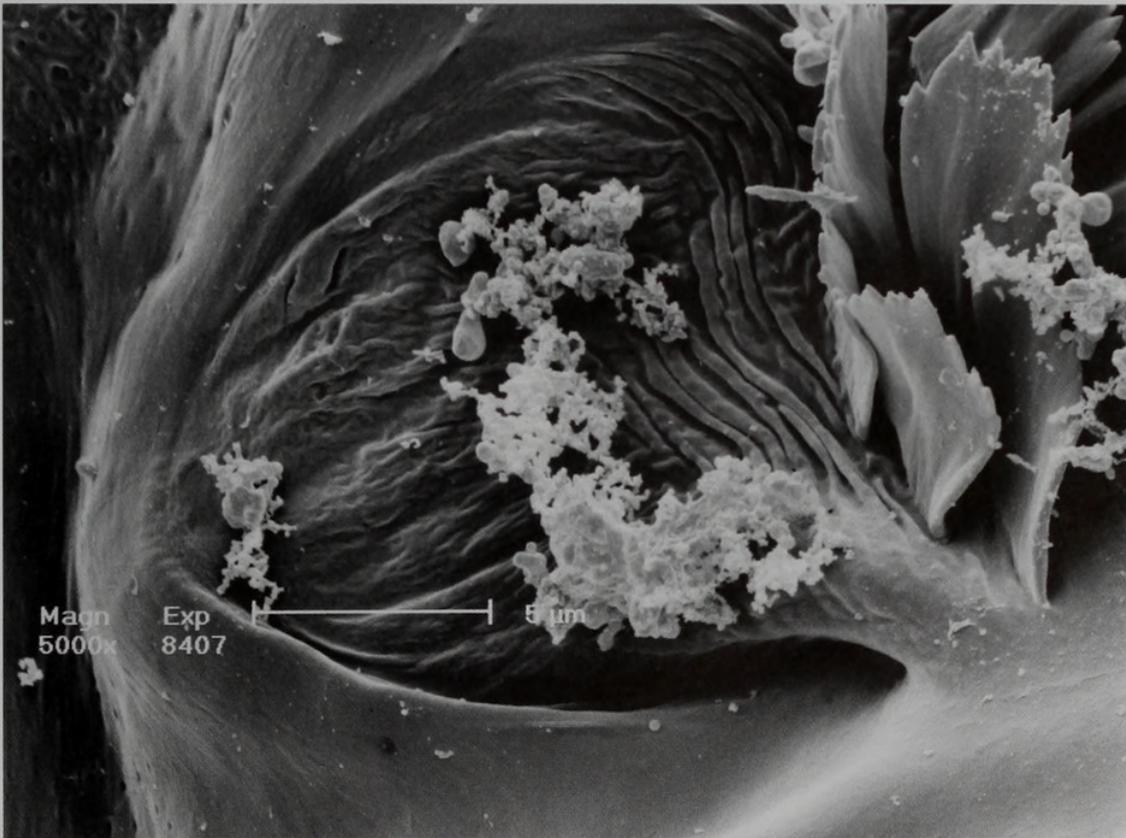


Fig. 9B *Oncaea venusta* f. *typica*, female (Red Sea) Labrum, anterior, slit-like pore, right.

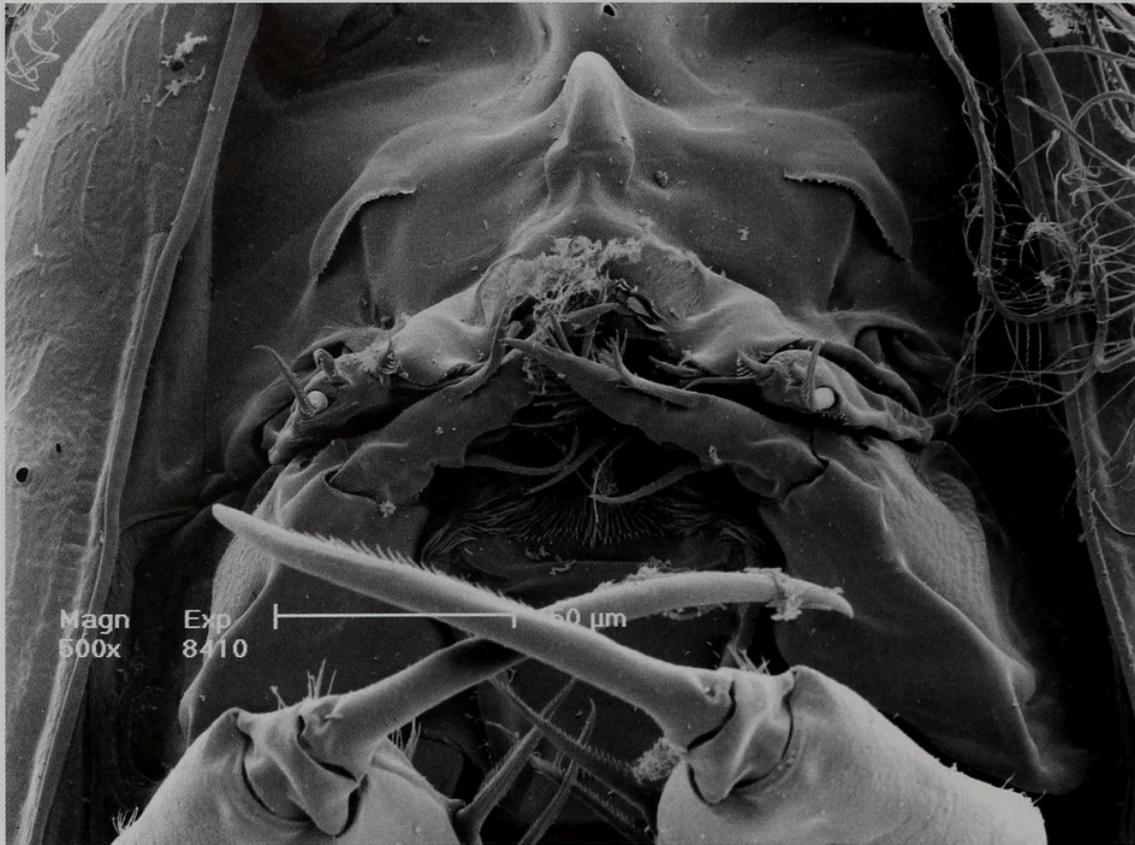


Fig. 9C *Oncaea venusta f. typica*, female (Red Sea) Oral area, ventral.

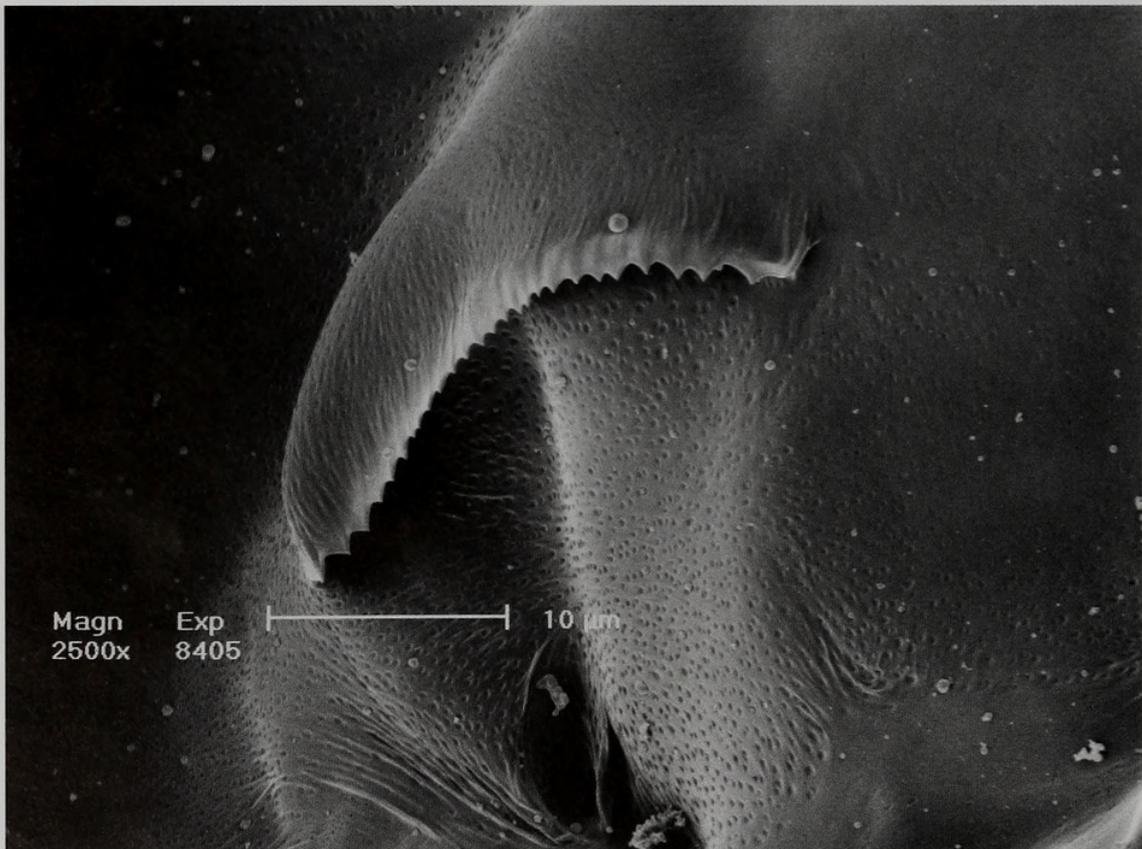


Fig. 9D *Oncaea venusta f. typica*, female (Red Sea) Labrum, anterior, integumental pocket, right.

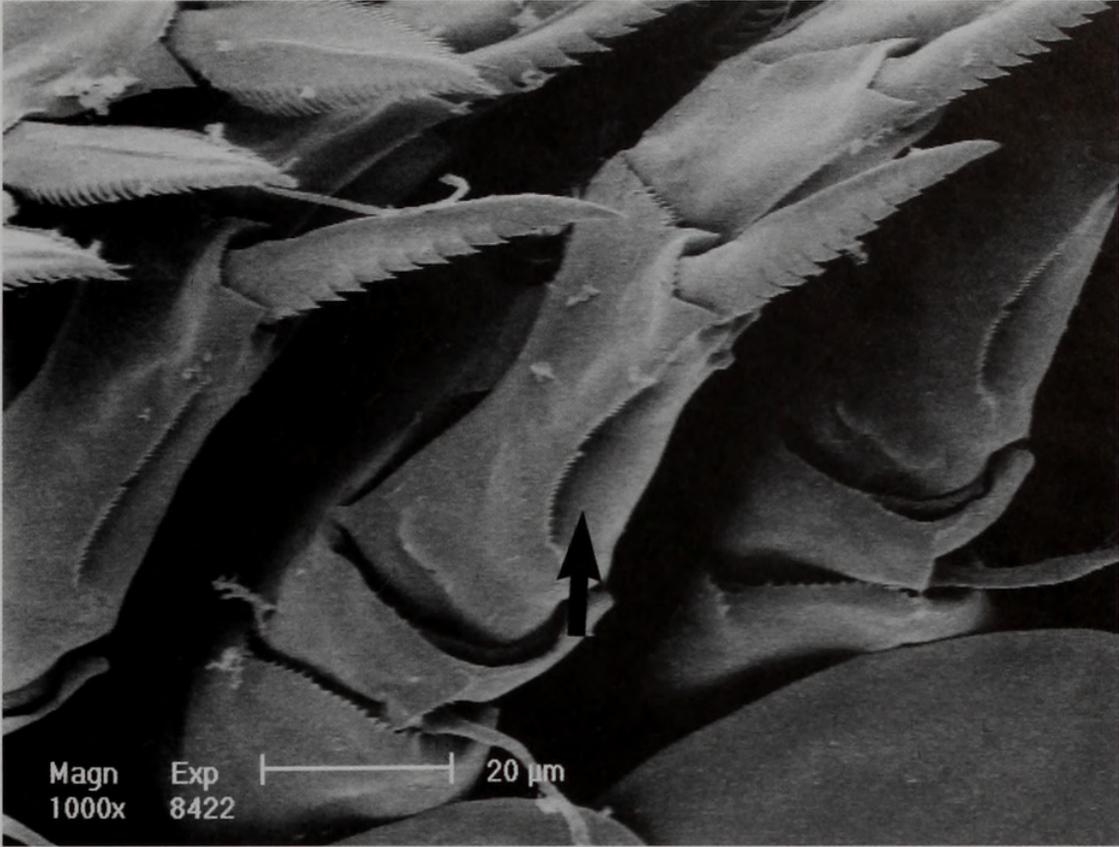


Fig. 9E *Oncaea venusta* f. *typica*, female (Red Sea) P2-P4, exopod-1, showing lateral concavity (arrowed).

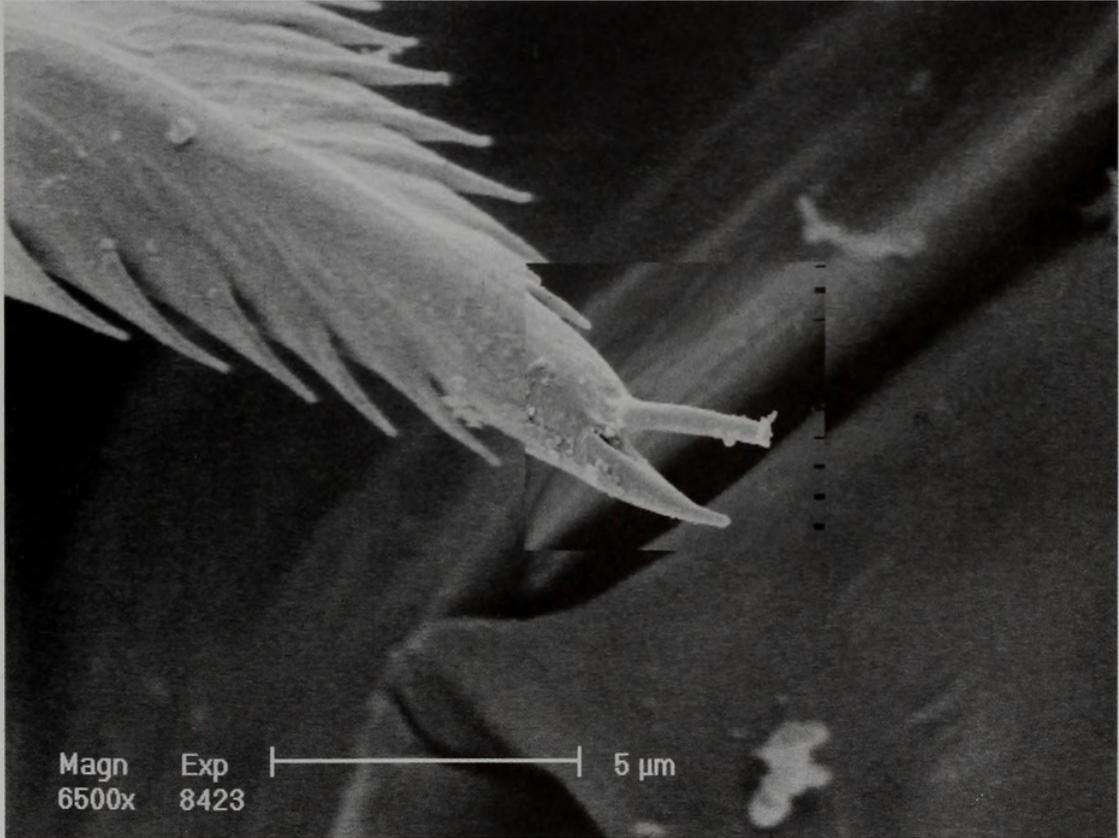


Fig. 9F *Oncaea venusta* f. *typica*, female (Red Sea) P1, exopod-1, tip of spine, showing tubular extension.

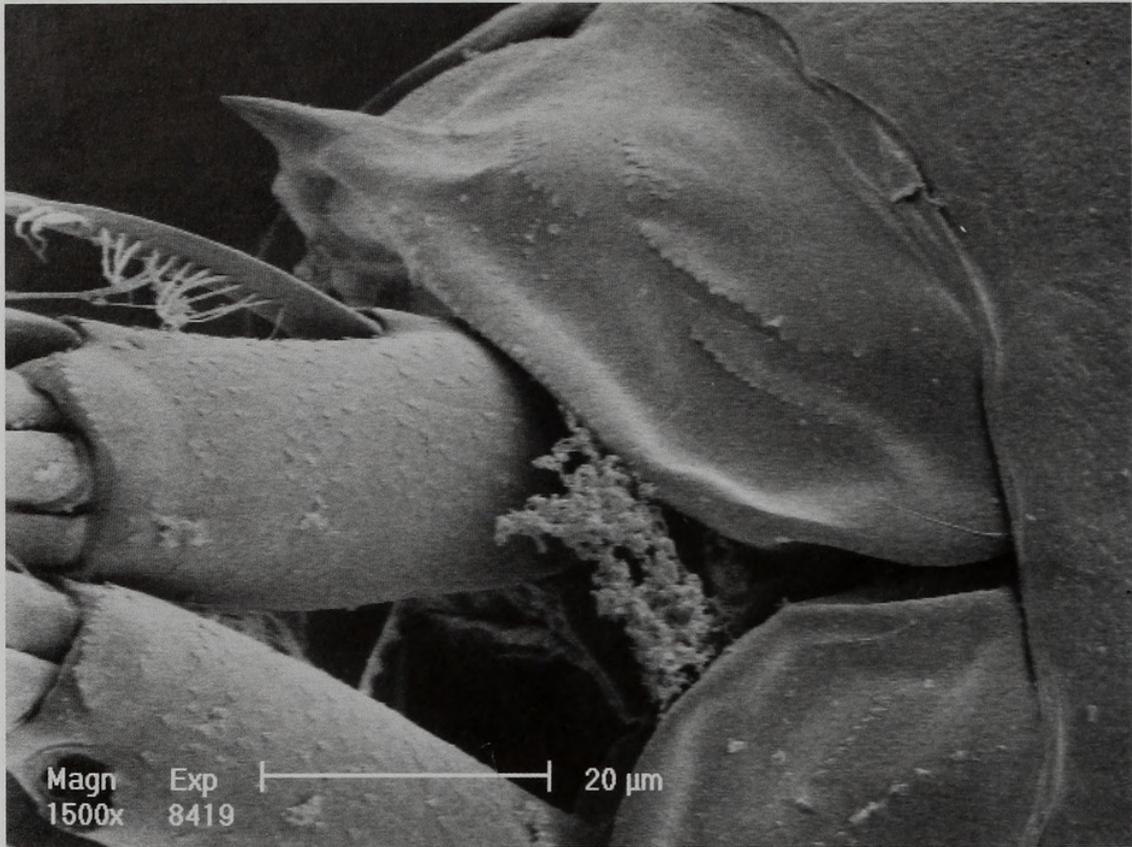


Fig. 10A *Oncaea venusta* f. *typica*, male (Red Sea) Caudal ramus and P6, ventral.

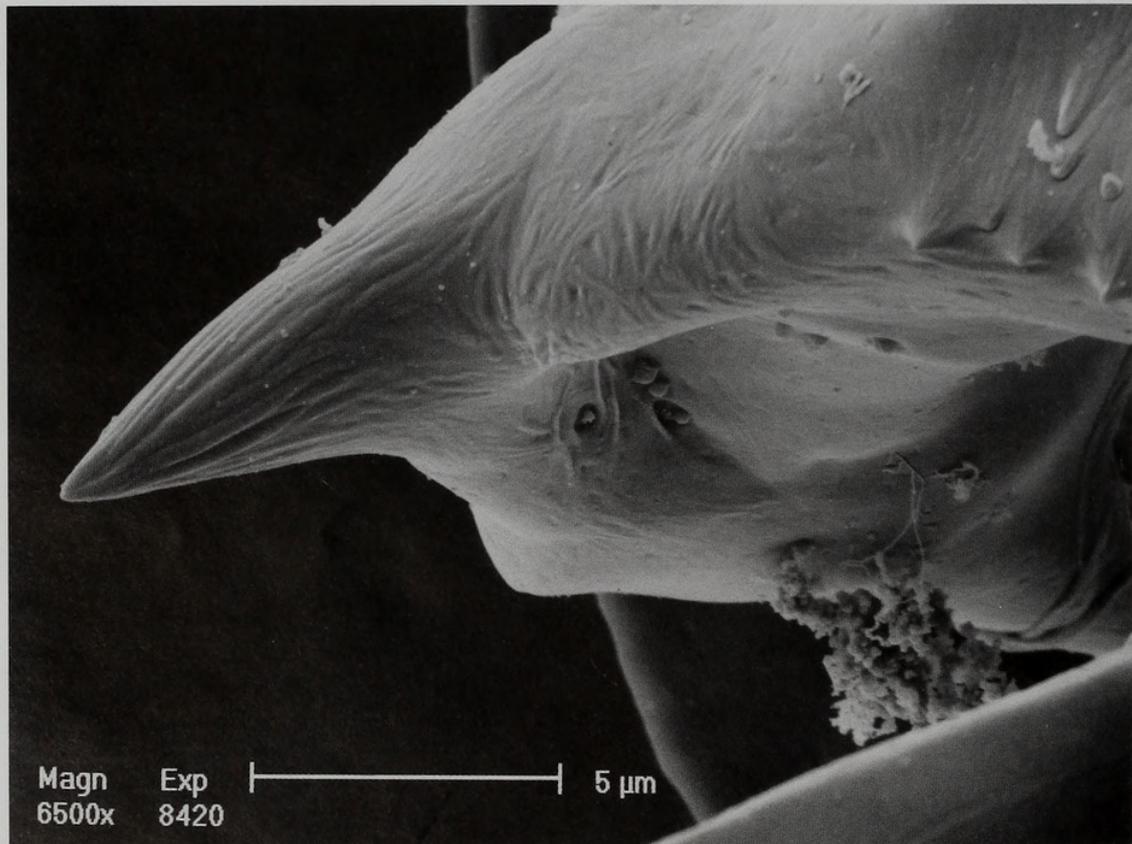


Fig. 10B *Oncaea venusta* f. *typica*, male (Red Sea) P6, posterolateral corners, showing receptor pores at inner edge.

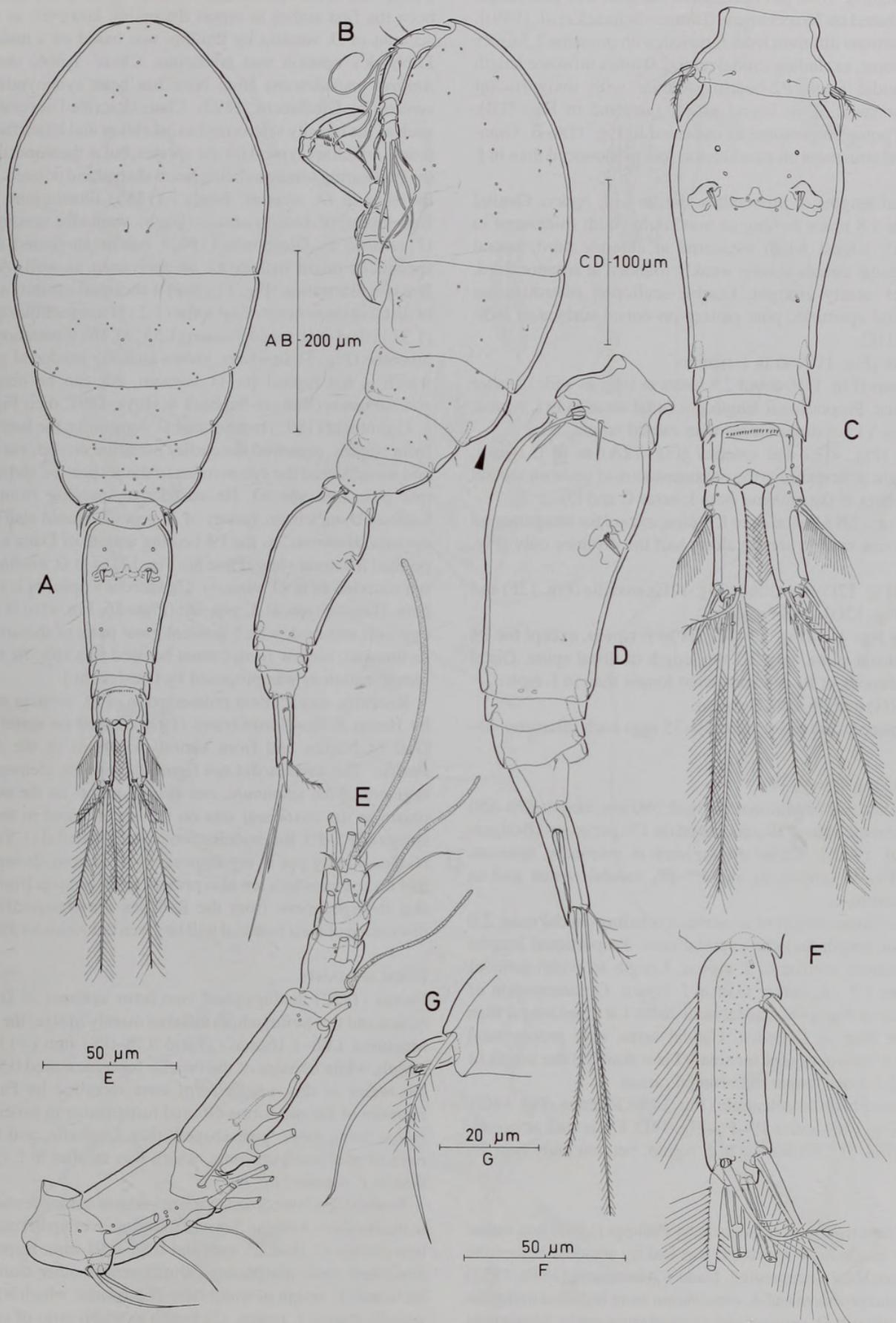


Fig. 11 *Oncaea venusta* f. *venella*, female (Red Sea) (A) Habitus, dorsal; (B) same, lateral (appendages omitted; dorsoposterior swelling on P2-bearing somite arrowed); (C) urosome, dorsal; (D) urosome, lateral; (E) antennule; (F) caudal ramus, dorsal; (G) P5, dorsal.

rostral area to posterior margin of caudal rami, calculated as sum of individual somites): 1096 μm [traditional method: 800 μm , range: 750–880 μm , based on 36 specimens (Böttger-Schnack *et al.* 1989)].

Body proportions different from *f. typica*, with prosome 2.5 times length of urosome, excluding caudal rami, 2.0 times urosome length including caudal rami. P2-bearing somite with insignificant dorsoposterior swelling in lateral aspect (arrowed in Fig. 11B). Integumental pores on prosome as indicated in Fig. 11A, B. Granules and raised structures on exoskeleton less pronounced than in *f. typica*.

Proportional lengths of urosomites similar to *f. typica*. Genital double-somite 1.8 times as long as maximum width (measured in dorsal aspect); largest width measured at anterior third, lateral margins of genital double-somite weakly rounded at anterior third, posterior part nearly straight. Double-scalloped sclerotization between genital apertures, pore pattern on dorsal surface as indicated in Fig. 11C.

Anal somite (Fig. 11C) as in *f. typica*.

Caudal ramus (Fig. 11F) about 2.8 times as long as wide, shorter than in *f. typica*. Proportional length of caudal setae as in *f. typica*, except for seta VI 1.6 times longer than caudal ramus.

Antennule (Fig. 11E) and antenna (Fig. 12A) as in *f. typica*, except for slight differences in the ornamentation of setae on second endopod segment in the antenna (seta I; setae C and D).

Labrum (Fig. 12B, C) similar to *f. typica*, except for integumental pockets with free margin serrate along half the distance only (Fig. 12B).

Mandible (Fig. 12D), maxillule (Fig. 12E), maxilla (Fig. 12F) and maxilliped (Fig. 12G) as in *f. typica*.

Swimming legs 1–4 (Fig. 13A–D) as in *f. typica*, except for P4 enp-3 outer distal spine only 2/3 the length of distal spine. Distal spines on endopods of P1–P4 somewhat longer than in *f. typica*.

P5 (Fig. 11G) and P6 as in *f. typica*.

Egg-sacs paired, containing appr. 30–35 eggs each (diameter 40–50 μm).

ADULT MALE (Fig. 7D–F, 14).

Body length: 985 μm [traditional method: 590 μm , range: 550–650 μm (single extreme value 730 μm), based on 17 specimens (Böttger-Schnack *et al.* 1989)]. Sexual dimorphism in antennule, antenna, maxilliped, P1–P3 (endopod) and P5–P6, caudal ramus and in genital segmentation.

Prosome 2.3 times length of urosome, excluding caudal rami, 2.0 times urosome length including caudal rami. Proportional lengths (%) of urosomites similar to *f. typica*. Length to width ratio of genital somite 1.7 : 1, longer than in *f. typica*. Ornamentation of genital flaps as in Fig. 14E. Caudal rami about 1.9 times longer than wide, shorter than in *f. typica*. Caudal setae with proportional lengths as in *f. typica*, except for seta VI less than 2/3 the length of seta IV and 2.4 times longer than caudal ramus.

Sexual dimorphism in antennule (Fig. 14B), antenna (Fig. 14G), maxilliped (Fig. 14C) and in P5–P6 (Fig. 14D, E), as well as in enp-3 of P1–P3 (Fig. 7C, D) similar to *f. typica*. Seta on body near P5 naked.

TAXONOMY

The original description of *O. venusta* by Philippi (1843) was rather poor and the single male specimen was lost by accident before the mouthparts could be documented. Dana's subsequent (1849, 1852) records of *Antaria obtusa* and *A. crassimana* were included under the synonymies of both *O. venusta* and *O. mediterranea* by Giesbrecht (1892), reflecting the author's undecisiveness on this matter. Lubbock (1860) described the species (as *Oncæa pyriformis*) from the equatorial Atlantic and the southern Indian Ocean, and synonymized it with

Dana's *A. obtusa*. He was the first to record male-female pairs ('couples') of the species and erroneously believed that he had also been the first author to report the males; however, as the original account of *O. venusta* by Philippi was based on a male specimen, Lubbock's opinion was erroneous. Claus' (1866) description of *Antaria coerulescens* from Nice has been synonymized with *O. venusta* by Giesbrecht (1892). Claus described several characters, such as the heavily sclerotized exoskeleton and its surface ornamentation, which are typical for the species, but at the same time recorded the P4-bearing somite as being heart-shaped and pointed, which is not the case in *O. venusta*. Brady's (1883) illustrations [Challenger Expedition] of *Antaria obtusa* (Dana), were also synonymized with *O. venusta* by Giesbrecht (1892), but he suspected that Brady's specimens might include *O. mediterranea* as well. According to Brady's illustration (Fig. 11), the P4 endopod exhibits a length ratio of distal spine to outer distal spine (1.2 : 1) more similar to *O. venusta* (1.3 : 1) than to *O. mediterranea* (1.55 : 1). His illustration of the male urosome (Fig. 3), however, shows laterally produced genital flaps, which is not typical for *O. venusta*, but can be observed in *O. mediterranea* (Böttger-Schnack & Huys, 1997, their Fig. 4A, D).

Giesbrecht (1892) redescribed *O. venusta* on the basis of material from Naples, reviewed the earlier literature on *Antaria* and *Oncæa* and summarized the synonymies of the respective species known at that time (see above). He stated that, judging from its general habitus, Dana's form variety of *A. gracilis* would also resemble *O. venusta*. However, as the P4-bearing somite of Dana's specimen is pointed in lateral view (Plate 86, Fig. 12) as in *O. mediterranea*, and not rounded as in *O. venusta*, Giesbrecht's opinion is not followed here. [Dana's typical *A. gracilis* (Plate 86, Fig. 11b) is figured with egg-sacs attached, which conceal great parts of the urosome. Thus its unusual, narrow form cannot be used as a specific character for identification as was proposed by Giesbrecht.]

Recently, an excellent redescription of *O. venusta* was provided by Heron & Bradford-Grieve (1995), based on material from the Gulf of Naples and from various locations in the Atlantic and Pacific. The authors did not figure the minute element on the 6th segment of the antennule, and did not report on the sexual dimorphism in the coxobasal seta on the antenna and in the endopodal spines of P1–P3. Re-examination of their material (1 ♀ and 1 ♂ from Naples, kindly put at my disposal by G. Heron) showed, however, that these characters are also present in *O. venusta* from Naples and that the specimens from the Red Sea are conspecific. A further discussion of their material will be given below under *Form variants*.

FORM VARIANTS

Farran (1929) distinguished two form variants of *O. venusta*, *f. typica* and *f. venella*, which differed mainly in size: the typical form measured 1.08–1.16 mm (♀) and 0.78–0.81 mm (♂) in total body length, while females of the *venella* form measured 0.91–1.07 mm. No males of the *venella* form were recorded by Farran (1929). Females of the two forms differed furthermore in general habitus, *f. typica* being more 'pear-shaped' than *f. venella*, and in the length ratio of prosome : urosome, which was smaller in *f. typica* (1.3:1) than in *f. venella* (1.5:1).

Sewell (1947) recorded two size variants among female *O. venusta* in the northern Arabian Sea and found no overlap in size between the two groups (1.18–1.25 mm and 0.85–0.91 mm, respectively). He described some morphological differences other than size, which included (1) length to width ratio of prosome, which was larger in *f. venella* than in *f. typica*, (2) length to width ratio of caudal ramus, which was larger in *f. typica* than in *f. venella* and (3) slight differences in the proportions of urosomites and caudal ramus between the two forms.

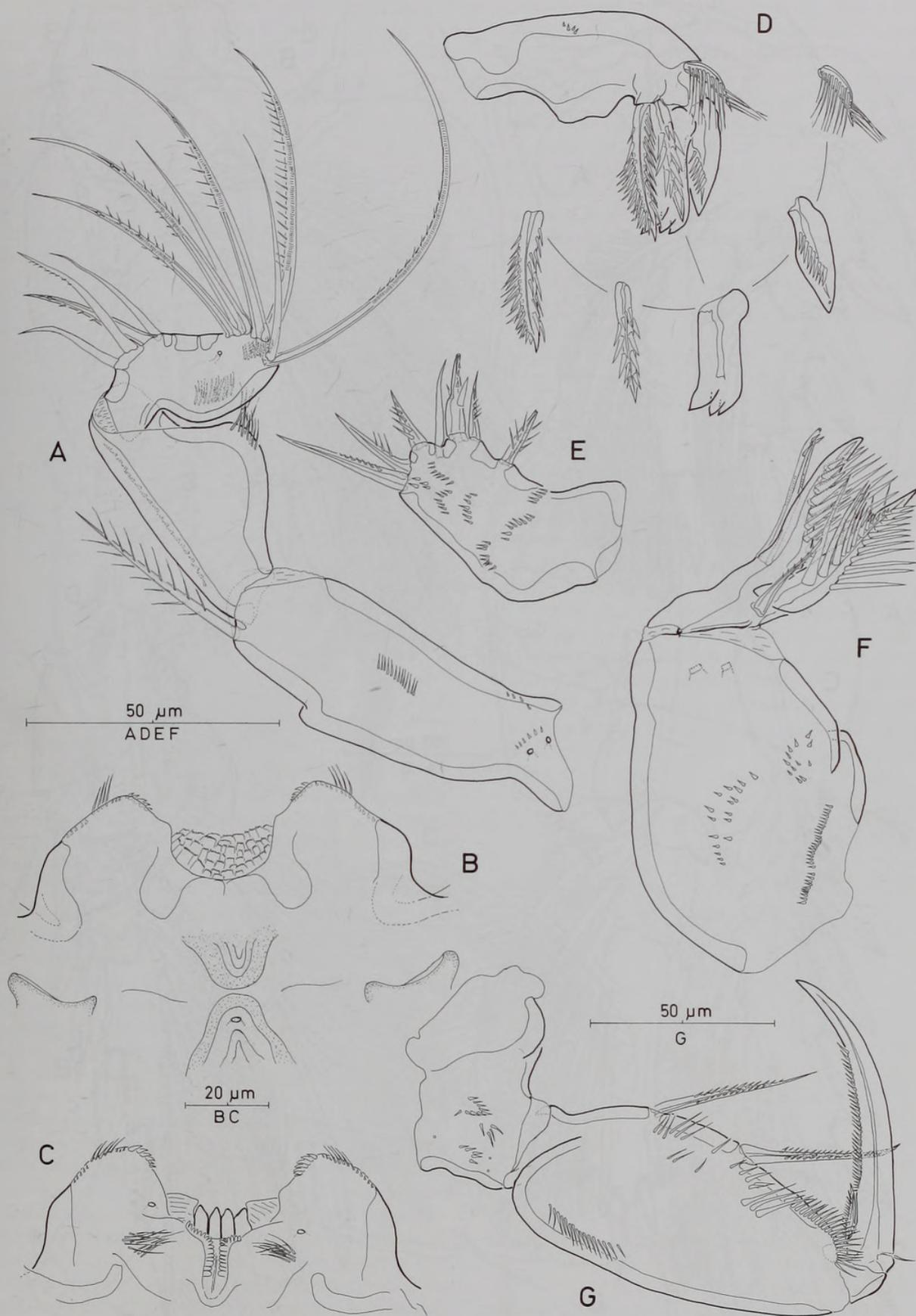


Fig. 12 *Oncaea venusta* f. *venella*, female (Red Sea) (A) Antenna, anterior; (B) labrum, anterior; (C) same, posterior; (D) mandible, showing individual elements; (E) maxillule; (F) maxilla; (G) maxilliped.

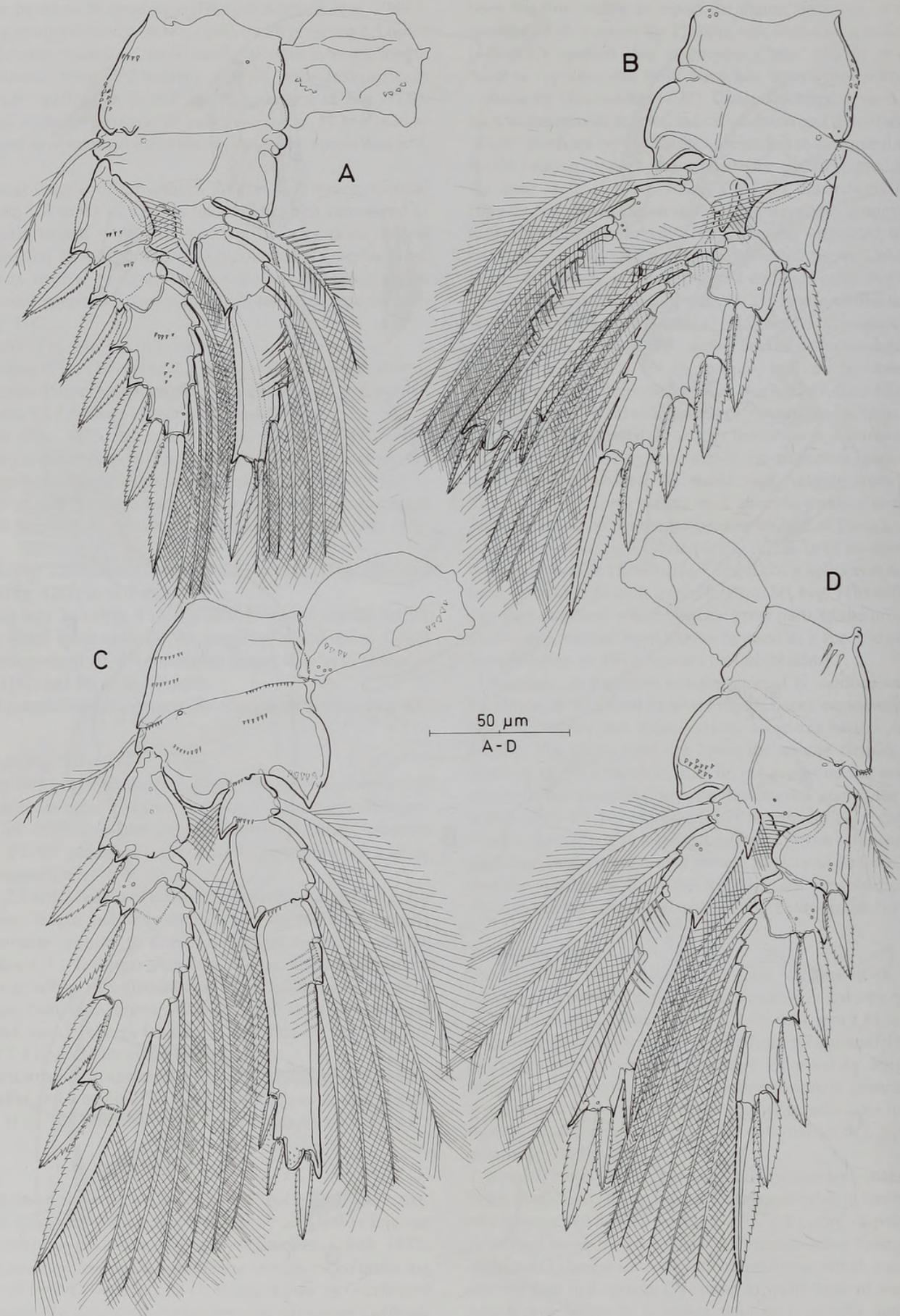


Fig. 13 *Oncaea venusta* f. *venella*, female (Red Sea) (A) P1, posterior; (B) P2, posterior, intercoxal sclerite omitted; (C) P3, anterior; (D) P4, posterior.

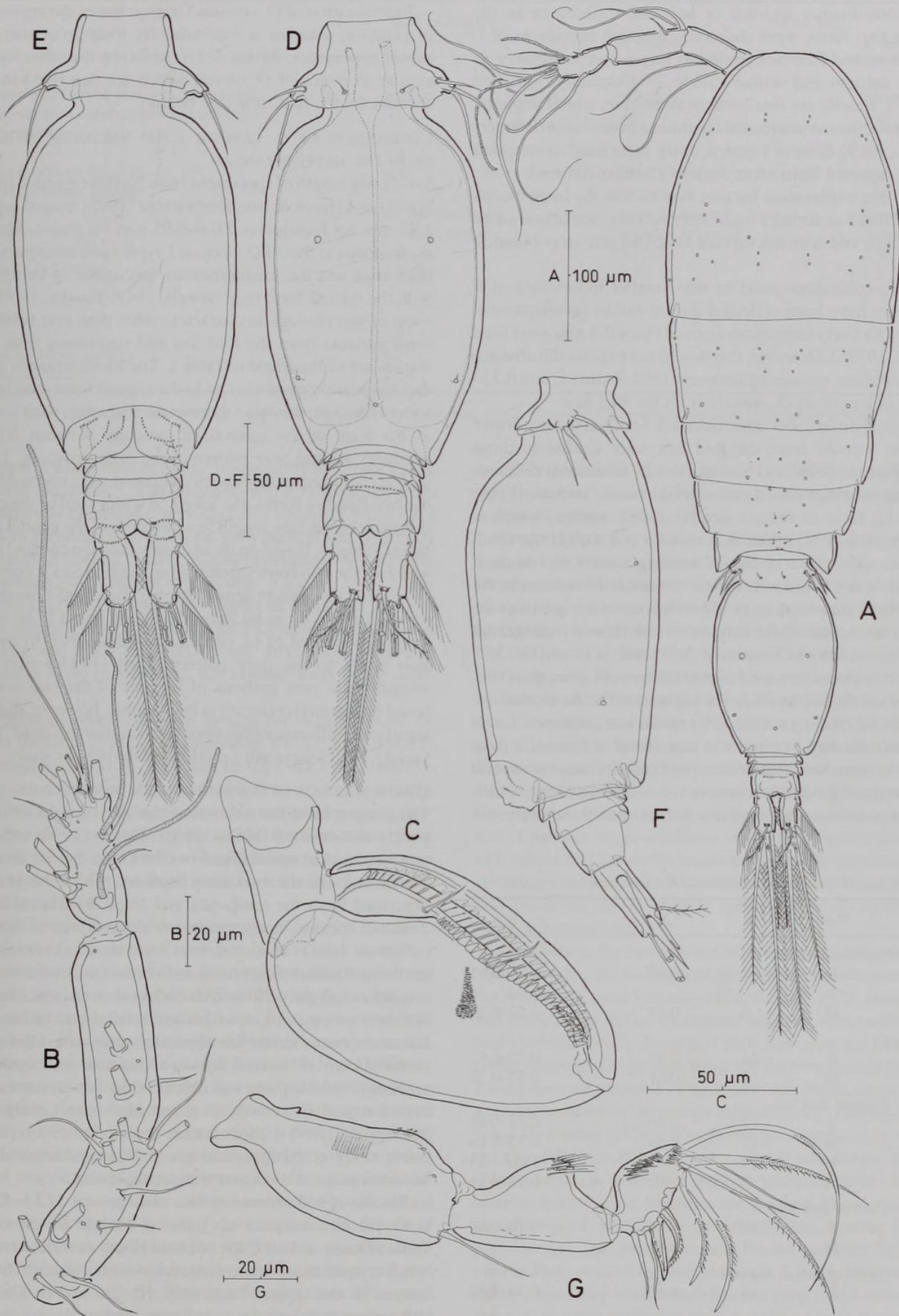


Fig. 14 *Oncaea venusta* f. *venella*, male (Red Sea) (A) Habitus, dorsal; (B) antennule; (C) maxilliped, anterior; (D) urosome, dorsal (spermatophores not fully developed); (E) urosome, ventral; (F) same, lateral; (G) antenna, posterior.

Specimens of *O. venusta* from the Red Sea exhibited a corresponding difference in size (Table 2) with no overlap between the two groups. No distinct regional or seasonal differences in the lengths of the two forms were observed, although specimens of *f. venella* in the central Red Sea tended to be smaller in summer as compared to autumn and winter (Table 2). Generally, Red Sea specimens of *f. venella* are smaller than elsewhere, which might be related to the extreme environmental conditions in this basin (Böttger-Schnack *et al.*, 1989). Sizes of *f. typica*, on the other hand, correspond well to those reported from other regions (Böttger-Schnack *et al.*, 1989). A possible explanation for this may be that the large morph penetrates the Red Sea during a limited period only (see below under *Ecological notes*) and does not survive as an indigenous population in this area.

Alternative explanation could be that smaller individuals of *f. venella* may not have been collected during earlier investigations, because nets with fairly large mesh sizes of about 0.3 mm were used (e.g. Boxshall, 1977b). However, this would not explain the absence of intermediate sizes, measuring between 0.9–1.0 mm (♀) and 0.75–0.85 mm (♂) in length, in *O. venusta* from the Red Sea.

Morphological differences other than size between the two forms of *O. venusta* females from the Red Sea were similar to those recorded by Farran (1929) and Sewell (1947). Additional differences in body morphology found in the present study include (1) the length to width ratio of female genital double-somite, which is smaller in *f. typica* (1.5:1) than in *f. venella* (1.8:1), (2) the small dorso-posterior protrusion of the P2-bearing somite in female *f. venella*, which is not found in *f. typica*, (3) small differences in the relative lengths of distal spines on P4 endopod, which are likewise found in both sexes, and (4) the length to width ratio of male genital somite, which is smaller in *f. typica* (1.5 : 1) than in *f. venella* (1.7 : 1). The latter two characters are the only differences other than size, by which males of the two forms can be separated. The dorsoposterior swelling on the P2-bearing somite in *f. venella* was consistent for all specimens from the Red Sea and was also found in *f. venella* from the northern Arabian Sea. Altogether, the results pointed to several additional morphological differences between the two forms, which had not been noted in the literature before, but these were not

regarded as sufficient to warrant distinction of the two forms as separate species.

Identification of *O. venusta f. typica* males during routine counts in plankton samples is facilitated by their great size and overall robust appearance. Males of *f. venella*, on the other hand, are very similar to males of *O. clevei*, which are described in the present account for the first time (see below).

COMPARISON OF *O. VENUSTA* FORM VARIANTS WITH SPECIMENS FROM THE MEDITERRANEAN

Total body length of specimens from Naples recorded by Giesbrecht (1892) and Heron & Bradford-Grieve (1995) ranged between 1.09–1.27 mm for females, and 0.8–0.95 mm for males. This size range corresponds to that of *O. venusta f. typica* and most previous authors have regarded the mediterranean specimens as being conspecific with the typical form (e.g. Sewell, 1947; Tanaka, 1960). A comparison of morphological characters other than size between the two form variants from the Red Sea and specimens from the Gulf of Naples are summarized in Table 2. The Mediterranean specimens in fact seem to be more similar to the typical form than to the *venella* form. However, they also share some characters with *f. venella*, such as the form of the sclerotized structure between female genital apertures and the pore pattern of the male urosome. Two morphological characters of the Naples specimens were intermediate between the two Red Sea forms, the length to width ratio of the caudal ramus in both sexes and the length to width ratio of the genital somite in the male (Table 2). Based on these observations, it cannot be confirmed, which of the two form variants from the Red Sea is conspecific with *O. venusta* Giesbrecht sensu Heron & Bradford-Grieve. The length to width ratio of caudal ramus has been found to be very variable among specimens of *O. venusta* (Boxshall, 1977b) and this might also apply to the pore pattern. Malt (1983c) investigated the integumental pore patterns of females of the two *venusta* forms, based on material collected in the Atlantic, however, did not find any significant differences between them and/or the third 'robust' form variety. Males were not investigated during her study.

OTHER RECORDS OF *O. VENUSTA* FORM VARIANTS

The geographical distribution of the size morphs of *O. venusta* is poorly documented (Malt, 1983a). Farran (1936) reported a great size variation in specimens from the Great Barrier Reef, but could not distinguish the two form variants, which he previously had described from the temperate and tropical Atlantic and off New Zealand, because many specimens intermediate in size occurred.

Sewell (1947) recorded two variants of *O. venusta* from the northern Arabian Sea (discussed above), and concluded that they might have slightly different breeding seasons, since both exhibited different proportions of ovigerous females and of females bearing spermatophores in the samples. He summarized the geographical distribution of *O. venusta* known at that time and concluded that the smaller *f. venella* form was absent in the Mediterranean. However, both forms of *O. venusta* were recorded from Lebanese waters by Malt *et al.* (1989) without further descriptive details. In the quantitative study of Böttger-Schnack (1996) conducted in the Eastern Mediterranean, *O. venusta* was totally absent.

Tanaka (1960) recorded two size groups (1.13–1.39 mm and 0.90–1.0 mm, respectively) among female *O. venusta* from the Indian Ocean and off Cape of Good Hope, as well as from Antarctic waters; specimens from Japanese waters (South China Sea) belonged to the typical form only. He did not find any structural differences between the two forms, except for a somewhat more slender prosome in *f. venella* as compared to *f. typica*. The caudal rami were four times longer than wide in both forms, irrespective of sex; this is unusual for species of *Oncaea* s. str., which typically have

Table 2 Body length (mm) of *O. venusta* in the Red Sea.

Form variant	Sex	n	X	R
AUTUMN	<i>Northern Red Sea</i>			
<i>f. venella</i>	F	15	0.80	0.75–0.85
	M	6	0.58	0.57–0.59
	<i>Central Red Sea</i>			
<i>f. venella</i>	F	24	0.80	0.75–0.85
	M	4	0.61	0.57–0.73
WINTER	<i>Central Red Sea</i>			
<i>f. venella</i>	F	12	0.80	0.75–0.88
	M	16	0.59	0.55–0.65
<i>f. typica</i>	F	14	1.11	1.00–1.23
	M	7	0.92	0.88–0.95
SUMMER	<i>Central Red Sea</i>			
<i>f. venella</i>	F	10	0.76	0.70–0.80
	M	1	0.56	
	<i>Gulf of Aden + Strait of Bab al Mandab</i>			
<i>f. venella</i>	F	14	0.83	0.74–0.92
	M	3	0.60	0.58–0.63
<i>f. typica</i>	F	5	1.15	1.10–1.22

n = no. of individuals measured; X = mean; R = range

Table 3 Comparison of morphological characters of *Oncaea venusta* Giesbrecht from the Gulf of Naples with two forms, *f. typica* and *f. venella*, from the Red Sea.

Species/form	Gulf of Naples	<i>f. typica</i>	Red Sea	<i>f. venella</i>
	Female			
Ornamentation on surface of prosome (ridges, etc)	very strong	strong		present, less strong
P2-bearing somite with dorso-posterior swelling	no	no		yes
<i>Genital double-somite</i>				
l : w ratio	1.4 : 1	1.5 : 1		1.8 : 1
anterior part produced dorsally	yes	yes		no
sclerotization between gen.ap.				
– form	double-scalloped	paired s-shaped		double-scalloped
– location	between gen.ap.	anterior to gen.ap.		between gen.ap.
Caudal ramus, l : w ratio	3.0 : 1	3.5 : 1		2.8 : 1
P4 enp-3, ratio of DS:ODS	1.5 : 1	1.3 : 1		1.5 : 1
Male				
<i>Genital segment</i>				
l : w ratio	1.7 : 1	1.5 : 1		1.7 : 1
no. of pores on dorsal surface	5	11		5
Caudal ramus, l : w ratio	2.2 : 1	2.5 : 1		1.9 : 1

DS = distal spine; ODS = outer distal spine; gen.ap. = genital apertures; P2, P4 = swimming legs 2, 4; enp-3 = third endopod segment; l = length; w = width; no. = number

a smaller length to width ratio of caudal ramus in the male (see above under 'Generic diagnosis'). The length to width ratio of the male genital segment was greater in *f. venella* (1.6 : 1) than in *f. typica* (1.3 : 1), which is in accordance with results from the Red Sea. The body lengths of males in Tanaka's study ranged between 0.74–1.07 mm, with no separation given for the two groups.

Corral Estrada (1970) recorded two forms of female *O. venusta* from the NE Atlantic, near Tenerife, which differed mainly in size (1.05–1.25 mm and 0.87–0.95 mm). Small differences were also found in overall body proportions, the *venella* form being more slender.

Ferrari (1975) recorded two size groups for both sexes of *O. venusta* from the Gulf of Mexico, measuring 1.1–1.2 mm or 0.92–0.99 mm (females) and 0.76–0.86 mm or 0.57–0.63 mm (males). Both groups occurred over the entire period (4 yrs) of his study, without exhibiting any overlap in size. No morphological differences other than size were noted by the author. His illustration of the male antenna of the typical form (his Fig. 6D) shows a long, plumose seta on the coxobasis, not the small naked one usually found in *O. venusta* (cf. Fig. 6H, 14G).

Boxshall (1977b) reported both size morphs of female *O. venusta* from the NE Atlantic, near the Cap Verde Islands, and in another report gave detailed information on their vertical distribution and diurnal vertical migration (Boxshall 1977a). The two forms differed only in size, with a mode length of 1.13 mm for *f. typica* and 0.98 mm for *f. venella*. No other detectable differences were recorded. The length frequency distribution of both forms (his Fig. 13) shows very little overlap in size between the two groups. Males were not distinguished into size groups during his study, their length ranged between 0.96–1.08 mm with a mean of 1.01 mm. Both sexual dimorphic characters of the male antenna (naked seta on coxobasis and modified seta on lateral armature) were illustrated by Boxshall (his Fig. 12b). The terminal accessory seta on the male caudal ramus, however, was figured as being less than twice the length of CR, whereas it is more than twice the length in *O. venusta* from Naples and the Red Sea. In addition to the two forms known at that time, Boxshall also recorded a few female specimens of a third 'robust form', which was more squat in general appearance and differed in the length to width ratio of the caudal ramus. The length of the specimens ranged between 0.88–1.4 mm, thus covering the length range of both other varieties of *O. venusta*. The 'robust form',

however, seemed to have a limited distribution range, because it was not discovered again in subsequent collections from other North Atlantic localities (Malt 1983c).

Recently, Itoh [in: Chihara & Murano (1997)] recorded both size morphs of *O. venusta* from Japanese waters. His descriptions of female and male habitus exhibit the same differences in overall body morphology between the two morphs as recorded here for Red Sea specimens. Also, Itoh's illustration of the male antenna [Plate 223, Fig. 371(right) c] shows the two sexual dimorphic characters typical for the species. No overlap in size between the two groups was noted by Itoh, females measured 1.09–1.23 mm (*f. typica*) or 0.86–0.94 mm (*f. venella*) and males 0.89–0.98 mm (*f. typica*) or 0.62–0.65 mm (*f. venella*). Specimens of female *O. venusta* from the Sea of Japan examined during the present study, however, covered a wide size range from 0.80–1.3 mm, and many specimens intermediate in size (about 0.96 mm) occurred. Specimens at the upper and lower end of the size range exhibited nearly all morphological characters of *f. typica* and *f. venella*, respectively, while specimens intermediate in size could be assigned to neither morph. [The same phenomenon was observed in *O. venusta* specimens from Australian waters (McKinnon material).]

In summary, the two distinct size morphs of *O. venusta*, *f. typica* and *f. venella*, are widespread in tropical and temperate regions of the Atlantic (Corral Estrada, 1970; Ferrari, 1975; Boxshall, 1977b) and the western Indian Ocean and adjacent seas, including the Red Sea (Sewell, 1947; Tanaka, 1960; this report). Records of two corresponding size groups from the Eastern Indian Ocean and the Pacific are rare, because intermediate size forms occur, which make a clear separation of the groups more difficult. This had already been noted by Farran (1936), who found specimens of *O. venusta* from the Great Barrier Reef covering a wide size range, without being able to separate them into the two groups. Further studies on *O. venusta* from Pacific localities are required in order to define their morphological relationship to Atlantic and western Indian Ocean populations. The present results, based on both light and SEM microscopy, pointed to several morphological differences between the two *venusta* forms, which had not been noted before. However, these were not regarded as sufficient to warrant recognition of the two forms as separate species. Alternative taxonomic techniques, such as molecular analysis, may permit examination of any genetic differentiation between the forms of this ubiquitous species. A study

on the molecular genetics of *O. venusta* size variants from the Atlantic is in progress and future morphological studies in other areas are recommended.

OTHER RECORDS OF *O. VENUSTA*

O. venusta is widely distributed at mid- and low latitudes, between approximately 50°S and 65°N (Malt, 1983a, b). Due to its relatively large size and the characteristic habitus of the female, it is one of the best documented oncaeid species in the world.

Halim (1969) listed *O. venusta* as one of the 'perennial-indigenous' species of the Red Sea, being distributed throughout the main basin and the Gulf of Suez all year round. His compilation of earlier records did not differentiate between the two forms of the species, which were found to exhibit considerable differences in regional and seasonal distribution in the Red Sea (see below under *Ecological notes*).

Wilson (1932) recorded *O. venusta* as the most abundant species of the genus in the Woods Hole region. The length range of his specimens (♀♀: 1.1–1.27 mm, ♂♂: 0.8–0.95 mm) indicates that he had collected the typical form, however, his illustration of dorsal aspect of the female (Fig. 213A; from W.M. Wheeler) shows the form of genital double-somite to be more similar to *f. venella*.

In the Western Pacific area, Mori (1937, reprinted 1964) figured *O. venusta* from Japanese waters and Dakin & Colefax (1940) recorded it as the commonest species in the coastal waters of Australia (New South Wales). Chen *et al.* (1974) described the species from the Yellow Sea and the East China Sea. Their illustration of P4 endopod (Plate 6, Fig. 3) shows 2 inner setae on distal segment which is not found in any species of *Oncaea* s. str. This requires confirmation. The length range reported by Mori (♀♀: 1.0–1.28 mm, ♂♂: 0.8–1.0 mm) was smaller than the sizes reported by Chen *et al.* (♀♀: 1.2–1.35 mm, ♂♂: 0.9–1.1 mm), but the dorsal habitus of females illustrated by these authors indicate that both were dealing with *f. typica*.

Olson (1949) recorded *O. venusta* from the East Pacific, off Oregon, which according to its size (♀♀: 1.25 mm, ♂♂: 0.9 mm) and female habitus might belong to the typical form. The author did not note any sexual dimorphism on the antenna or on the swimming legs.

Razouls (1974) figured *O. venusta* from the region of Banyuls-sur-mer (Golfe du Lion) and summarized previous records from the Mediterranean Sea. His illustrations lack many details, such as the genital apertures on the female genital double-somite, several elements on the antennule, antenna, P5 and the basal seta on P2–P4; moreover, the distal endopod spines in P2–P4 of his specimens are figured much longer than usually found in *O. venusta* (especially in P4). Further differences between his specimens and typical characters of *O. venusta* are found in the female caudal ramus, which is less than 3 times longer than wide and the length of caudal seta VI, which is unusually short in both sexes. The coxobasal seta on the male antenna was figured as long and plumose by Razouls, which is not the case in *O. venusta*. In summary, positive identification of his specimens can only be given after re-examination of his material.

Ho (1984) redescribed *O. venusta* based on several females collected from colonies of *Solandria secunda* (Inaba), a hydroid found at 10 m depth in Tassha Bay, Sado Island (Japan). His description differs from the present account in the setal formula of P1 endopod (4 instead of 5 setae on distal segment), in the armature of the antennule (some elements missing on segment 4 and 5), and in the armature of P6 (2 minute spinous processes not mentioned). Four females from his collection were kindly made available by J.-s. Ho. Re-examination showed that all specimens from Sado Island exhibit the typical setal formula on P1 enp-3 (5 setae). The insertion

of the distalmost seta is hidden beneath the long terminal process (cf. Fig. 4A) and thus can easily be overlooked. Also, the armature of the antennule and on P6 is the same as described here. Due to their large size, Ho ascribed his specimens to *f. typica* and his opinion is followed here, although some characters, such as proportional spine lengths on P4 enp-3 were inconclusive in the two smaller specimens (0.92–0.96 mm) examined.

Humes (1988) described both sexes of a new species of *Oncaea* s.str., *O. praeclara*, collected with slurp guns or box corers during deep dives by manned deep-sea submersibles from the vicinity of deep-sea hydrothermal vents in the eastern Pacific. The main characters for the new species as summarized by Humes are: (1) its relatively large size [1.01–1.3 mm in the female], (2) extremely long caudal rami, about twice longer than anal somite and exhibiting a length to width ratio between 4.96–6.7 : 1 (measured halfway down the CR length), (3) sexual dimorphism on third segment of male antenna (not on fourth segment, as erroneously stated in his abstract), (4) labrum with nearly straight posteroventral margins. The female holotype as well as female and male paratypes of *O. praeclara* from the collection of the National Museum of Natural History, Smithsonian Institution, were re-examined, in addition to several samples of the species kindly made available by A.G. Humes. The following measurements taken of the female holotype gave strong evidence that *O. praeclara* is conspecific with *Oncaea venusta*: (1) length to width ratio of CR 4.2 : 1 (measured halfway down the CR length), 3.5 : 1 (measured proximally) [as reported in the present account], (2) maxillipedal basis with spinular row along palmar margin (not smooth as described by Humes, his Fig. 2h), (3) labrum bilobate [ornamentation on lobes not discernible without dissection of specimen], integumental pockets and slit-like pores on anterior face present. The male paratype of *O. praeclara* can be assigned to *O. venusta* on the basis of (1) the sexual dimorphism of antenna, with coxobasal seta short and naked (not noted by Humes), seta I on second endopod segment curved, and (2) the pore pattern on dorsal surface of genital segment (11 pores).

Humes' account of *O. praeclara* may have been based on two different species: the form of the genital double-somite and the position of the genital apertures differ considerably between his Fig. 1a (habitus, dorsal) and Fig. 1c (urosome, dorsal). The extremely elongate CR noted by Humes (his Fig. 1c, e) was found neither in the female holotype nor in any of the specimens re-examined, but may have been present in other specimens. Fig. 1c and 1e (caudal ramus) as well as Fig. 2h (maxilliped) of Humes (1988) are regarded here as belonging to a different species, which, however, could not be traced in his material, although some of the samples contained a mixture of oncaeid species (see 'Material examined' above). The remaining figures of Humes seem to be identical with *O. venusta*. Like Ho (1984), Humes erroneously figured the distal endopod segment of P1 with 4 outer setae, instead of 5. He also missed one seta on the distal armature in the male antenna.

Huys & Boxshall (1991) illustrated several appendages and a dorsal view of the female urosome of *O. venusta*, based on specimens from the North Atlantic. Their Fig. 2.10.10.A of the mandible shows 4 dentiform processes along the distal margin, whereas only 3 processes are found in specimens from the Red Sea (Fig. 3D, 7D) and in those from the Gulf of Naples (Heron & Bradford-Grieve 1995, their Fig. 14J). The authors erroneously figured the female P5 with 1 exopodal seta only (their Fig. 2.10.21.B), not with 2 setae as usually found in *O. venusta*.

Many more records of *O. venusta* from different localities of the world ocean are known [see Malt (1983a) for a review], but are not considered here, because they did not include figures or a description that positively identified the species.

ECOLOGICAL NOTES

O. venusta f. *venella* is much more abundant than f. *typica* in the Red Sea, exceeding the population densities of the latter by a factor of between 3 to 100, when both forms co-occur (Böttger-Schnack, 1990b, 1995).

GEOGRAPHICAL DISTRIBUTION

In the Red Sea, *O. venusta* f. *venella* is more widespread than *O. venusta* f. *typica*, it occurs throughout the main basin (Böttger-Schnack, 1990a, b, 1995) and was also found in samples from the northernmost part of the Gulf of Aqaba (unpubl. data). *O. venusta* f. *typica* is mainly restricted to the southernmost Red Sea and the Gulf of Aden, reaching the central Red Sea only during the winter months, when a strong seasonal inflow of southern Red Sea waters influences the plankton fauna in the central area (Böttger-Schnack, 1990b; see also Weikert, 1987; Beckmann, 1996).

VERTICAL DISTRIBUTION AND VERTICAL MIGRATION

O. venusta is mainly distributed in the epipelagic zone in the Red Sea, with maximum abundances in the 0–100 (150) m depth layer (Böttger-Schnack, 1990 a, b). Occasional finds of the species in the bathypelagic zone (unpubl. data, see also Beckmann, 1996) were usually regarded as moribund specimens or may be due to contamination of the nets.

When co-occurring, the two forms of *O. venusta* tend to be vertically separated: Both sexes of *O. venusta* f. *typica* were concentrated in the upper epipelagic zone at 0–20 m (Strait of Bab al Mandab) or at 0–40 m (Gulf of Aden) during summer, whereas female f. *venella* occurred deeper in the water column, with maximum concentrations at 20–60 m (Bab al Mandab) and (20)80–100 m (Gulf of Aden), respectively. Male f. *venella* occurred at the same depth horizon as females in the Gulf, but were concentrated somewhat shallower than females (0–40 m) in the Strait, thereby extending into the depth horizon where f. *typica* dominates. No corresponding vertical separation of the two forms became obvious in the central Red Sea during winter, when both forms stayed in the upper 50 m during day and night (Böttger-Schnack, 1990b). However, the sampled depth strata in the epipelagic zone were broader during winter (50 m-intervals) than during summer (20 m-intervals) and thus a vertical segregation may not have been detected due to the limitations in the sampling strategy.

In the central and northern Red Sea, *O. venusta* f. *venella* was mainly concentrated in the lower epipelagic zone, within and below the strong seasonal thermocline, during autumn (Böttger-Schnack, 1990a). Diurnal vertical migration of moderate intensity was observed during this season, with specimens showing a stronger tendency to concentrate within the depth range of maximum temperature gradients during the night than during the day. From autumn to winter, a conspicuous shift of the population centre from the lower epipelagic zone (40–100 m) to shallower depths (0–50 m) was observed, which coincided with the weakening of the thermocline during the winter season (Böttger-Schnack, 1990b). Males of *O. venusta* f. *venella* generally exhibited the same depth distribution as females, but were evaluated semi-quantitatively during the autumn survey only.

SEASONAL VARIATION IN ABUNDANCE (CENTRAL RED SEA)

Seasonal variation in abundance in the central Red Sea was most conspicuous for *O. venusta* f. *typica*, which occurred in the central area only during winter, but was absent during summer and autumn (Böttger-Schnack, 1990b, 1995). By this, a strong inflow of southern Red Sea populations into the central area was indicated, and the species has been regarded as an indicator species of southern Red Sea waters, similar to other copepod species, such as species of

Eucalanus (Beckmann, 1984, 1996). Abundances of *O. venusta* f. *venella* in the central Red Sea were highest during winter, but moderately high densities were also found during autumn, thereby indicating a lesser influence of the southern inflow than was observed for f. *typica*.

Oncaea mediterranea (Claus, 1863)

Antaria mediterranea Claus (1863): 159-160, Tafel XXX, Fig. 1–6 (♀, 7 ♂).

Oncaea mediterranea (Claus, 1863); *Oncäa mediterranea* (Claus, 1863).

OTHER DESCRIPTIONS. Giesbrecht (1892) [as *Oncäa mediterranea*]; Heron (1977); Heron & Bradford-Grieve (1995); for further details see Böttger-Schnack & Huys (1997b).

TYPE LOCALITY. Tyrrhenian Sea; Messina.

PRELIMINARY NOTE. A detailed redescription of *O. mediterranea*, based on material from the Red Sea and the Eastern Mediterranean, has recently been published by Böttger-Schnack & Huys (1997b), including a review of the taxonomic history of the species. The following corrective note describes additional morphological details, which were not mentioned in the previous account, but might be of importance for constructing phylogenetic relationships within the genus *Oncaea* s. str.

CORRECTIVE NOTE

- (1) The labrum of *O. mediterranea* exhibits an additional patch of long spinules on posterior face at posterior part of each lobe, similar to *O. venusta* (cf. Fig. 3C), which was not figured by Böttger-Schnack & Huys.
- (2) The endopodal spines of P1 exhibit a subapical tubular extension, similar to *O. venusta* (cf. Fig. 4A). These extensions seem to be widespread among oncaeids as they have been found in distantly related species, such as *Archioncaea arabica* (Böttger-Schnack & Huys, 1997a), species of *Triconia* (Böttger-Schnack, 1999), *O. subtilis* (Böttger-Schnack & Huys, in press) and species of the *atlantica*-group (unpubl. data).
- (3) The coxa of P4 is ornamented with a patch of long setules on posterior face, similar to *O. venusta* (cf. Fig. 4D).
- (4) The female P6 is ornamented with 1 spine and 2 spinous processes, as in all other species of *Oncaea* s.str., not only 1 spinous process as erroneously figured by Böttger-Schnack & Huys.
- (5) In addition to the sexually dimorphic characters described by Böttger-Schnack & Huys, sexual dimorphism is expressed in the endopods of P1–P3, in the ornamentation of P5, and in the length of caudal setae: (1) in P1, the spinous outgrowth at the distal margin of the endopod is relatively longer in the male, reaching half the length of the distal spine, (2) in P2–P3, the conical projections on enp-3 are relatively longer in the male as compared to the female, similar to *O. venusta* (cf. Fig. 7B, C, E, F), (3) the outer long seta on P5 exopod is ornamented with triplicate row of minute spinules along entire length, not naked as in female, (4) caudal setae VI and IV are relatively shorter in the male as compared to the female, which was correctly figured by Böttger-Schnack & Huys (their Fig. 4A), but erroneously described as being equal in length to the female in the text.

Oncaea media Giesbrecht, 1891*Oncaea media* Giesbrecht (1891): 477.*Oncäa media* Giesbrecht (1892)

RELIABLE DESCRIPTIONS. Giesbrecht (1892): 591–600, 602, 603, 756, 757, 774, Plate 47, Fig. 1 (not Fig. 11), 29–33, 40 [as *Oncäa media*]; Tanaka (1960): 69, 70, Plate XXXI, Figs. 4–9; Heron & Bradford-Grieve (1995): 36, 39, Figs. 15k, 16a–k, 17a–i, 26b; Itoh [in: Chihara & Murano 1997]: 980, Fig. 365a–f.

DOUBTFUL DESCRIPTIONS. Dakin & Colefax (1940): 117, Fig. 205C a [♀ only]; Chen *et al.* (1974): 41–42, Plate 6, Figs. 12–15; Mori (1937; reprinted 1964): 120–121, Plate 66, Figs. 14–18.

TYPE LOCALITY. not specified; original description based on material from various locations near the equator in the tropical Pacific.

PRELIMINARY NOTE. Giesbrecht's original material of *O. media* was not available for study, because it is not allowed to be sent out on loan (A. Ianora, Zoological Station Naples, pers. comm.). Heron & Bradford-Grieve (1995) gave an excellent redescription of *O. media* based on specimens from the Gulf of Naples and provided a summary of its distribution in the Pacific Ocean and other areas. They pointed to the great similarity between *O. media* and *O. scottodicarloi*, which they described as a new species, and cleared up the confusion in Giesbrecht's (1892) redescription with regard to these two species. Specimens from the Red Sea agreed in almost every detail with the redescription of Heron & Bradford-Grieve (1995). However, some morphological characters are described below, which were not noted by Heron & Bradford-Grieve and/or appeared to differ between the two areas. Also, the body dimensions of the species from the Red Sea calculated by the different methods used throughout this study are provided.

MATERIAL EXAMINED.

- (1) Northern Red Sea, 22° 58.4'N, 37° 19.4'E: Stn. 663; *R/V Meteor* leg 5/5: collected 20 July 1987 with MSN 0.05 mm net (Haul 17/4); depth 50–100 m; total water depth ca 1200 m.
 - (a) 2 ♀♀ in alcohol (BMNH 1998.2797–2798).
 - (b) 1 ♂ in alcohol (ZMH K-39584).
 - (c) 1 ♀ dissected on slides, 2 ♀♀ in alcohol; 1 ♂ dissected on slides, 2 ♂♂ in alcohol (RBS).
- (2) Gulf of Aden, 11° 55.5'N, 43° 37.9'E: Stn. 631; *R/V Meteor* leg 5/5: collected 11 July 1987 with MSN 0.05 mm net (Haul 3/5); depth 0–50 m; total water depth ca 1400 m.
 - (a) 2 ♀♀, 2 ♂♂ in alcohol (BMNH 1998.2799–2802).
 - (b) 2 ♀♀, 2 ♂♂ in alcohol (ZMH K-39585).
 - (c) 2 ♀♀ (1 ovigerous), 2 ♂♂ in alcohol, (RBS).

DESCRIPTION. Note illustrations are based on 1 (c).

ADULT FEMALE (Fig. 15).

Body length: 884 µm [traditional method: 710 µm, range: 650–770 µm, based on 22 specimens (Böttger-Schnack *et al.*, 1989)].

Exoskeleton moderately chitinized. Prosome 2.6 times length of urosome, excluding caudal rami, 2.2 times urosome length including caudal rami. P2-bearing somite without conspicuous dorso-posterior projection visible in lateral aspect (Fig. 15B). Integumental pores on prosome as indicated in Fig. 15A, B. Pleural areas of P4-bearing somite with rounded posterolateral corners.

Proportional lengths (%) of urosomites 13.0 : 62.7 : 8.5 : 6.1 : 9.7. Proportional lengths (%) of urosomites and caudal rami 11.4 : 55.2 : 7.5 : 5.3 : 8.5 : 12.1.

Genital double-somite 1.9 times as long as maximum width

(measured in dorsal aspect) and 2.6 times as long as postgenital somites combined (Fig. 15C). Genital apertures with armature represented by 1 spine and 2 minute spinous processes (Fig. 15I) [the latter 2 not mentioned by Heron & Bradford-Grieve]. Double-curved sclerotization between genital apertures, pore pattern on dorsal surface as indicated in Fig. 15C.

Anal somite 2.0 times wider than long; about 2/3 length of caudal rami (Fig. 15C). Ornamentation as in *O. venusta*.

Antennule with armature as for genus, small element on 6th segment (arrowed in Fig. 15 D) not mentioned by Heron & Bradford-Grieve.

Antenna as figured by Heron & Bradford-Grieve (their Fig. 16c), except for seta I of lateral armature on first endopod segment slightly longer than figured by these authors; additional surface ornamentation on coxobasis as in *O. waldemari* (cf. Fig. 25A).

Labrum (Fig. 15E, F) as for *O. venusta*, but lacking patch of setules on posterior face at posterior part of each lobe. [*O. media* is the only species of *Oncaea* s.str. that misses these setules.]

Mandible mainly as figured by Heron & Bradford-Grieve (their Fig. 16e), except for dorsal blade (C) ornamented with 4 dentiform processes at distal margin, 1 of them inserted subdistally, and 1 minute process halfway at dorsal margin (Fig. 16E). Maxillule, maxilla and maxilliped mainly as figured by Heron & Bradford-Grieve (their Figs. 16f–h), but with additional surface ornamentations and microstructures, such as 2 large secretory pores (not 1) on surface of maxilla and third single row of shorter spinules along outer margin of strong maxillary spine (similar to *O. waldemari*, cf. Fig. 25F). [Complete pattern of microstructures on surface of exoskeleton not additionally figured in present account, but generally similar to those observed for *O. venusta* and *O. waldemari*.]

Swimming legs with armature as for genus and surface ornamentation similar to *O. waldemari* (cf. Figs. 26A–D). P1–P4 with spines on exp-1 longer than figured by Heron & Bradford-Grieve (their Figs. 16i–k, 17a), reaching beyond half length of spine on exp-2. P1 with inner basal element minutely pinnate (Fig. 15G), not naked as figured by Heron & Bradford-Grieve; distal margin of exp-1 and -2 ornamented with long spinules anteriorly as in *O. scottodicarloi* (cf. Fig. 23C).

P5 (Fig. 15H) with exopod longer than wide, length to width ratio 1.7 : 1.

P6 (Fig. 15I) armed with a spine and 2 small spinous processes [the latter 2 not mentioned by Heron & Bradford-Grieve].

Egg-sacs not observed.

ADULT MALE (Fig. 16).

Body length: 672 µm [traditional method: 560 µm, 1 specimen]. Sexual dimorphism in antennule, antennary setae, maxilliped, P1–P3 (endopod) and P5–P6, caudal ramus and in genital segmentation.

Prosome 2.2 times the length of urosome, excluding caudal rami, 1.9 times urosome length, including caudal rami.

Proportional lengths (%) of urosomites (excluding caudal rami) 12.3 : 66.4 : 4.3 : 3.7 : 4.3 : 8.6; proportional lengths (%) of urosomites (caudal rami included) 10.9 : 58.7 : 3.8 : 3.3 : 3.8 : 7.6 : 11.9. Caudal rami about as long as wide, much shorter than in female. Caudal setae with proportional lengths as in female, except for seta VI, which is about 2/3 the length of seta IV and 3 times the length of caudal ramus (Fig. 16A).

Antennule with armature as for genus.

Antenna (Fig. 16D) as in female, except for seta on coxobasis naked and shorter than in female [not mentioned by Heron & Bradford-Grieve]; lateral armature on distal endopod segment differing from female, with spiniform seta III much stouter and seta IV spiniform and curved, with row of dentiform processes along outer distal margin; both elements shorter than in female.

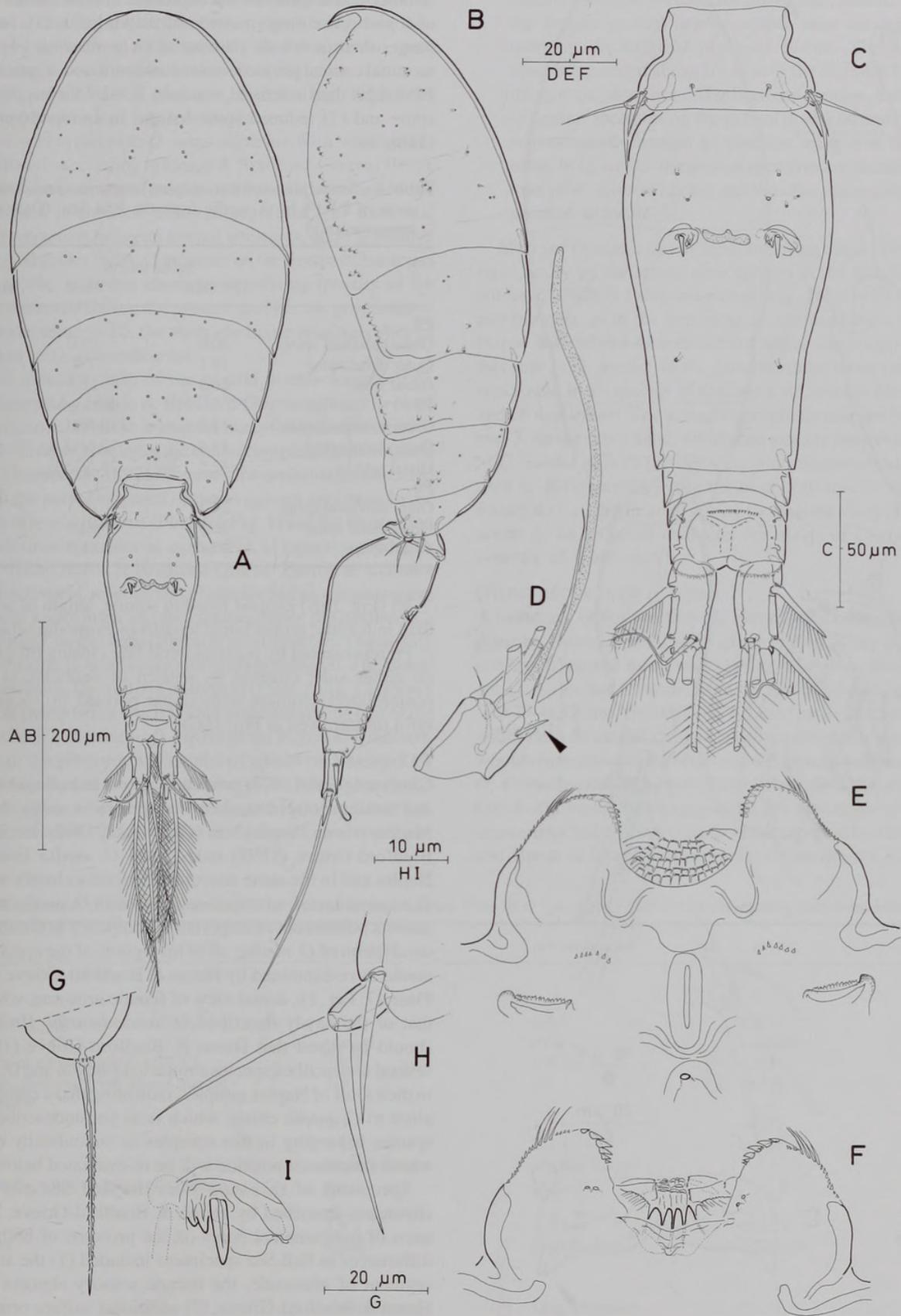


Fig. 15 *Oncaea media*, female (Red Sea) (A) Habitus, dorsal; (B) same, lateral (appendages omitted); (C) urosome, dorsal; (D) antennule, 6th segment, small sensory element arrowed; (E) labrum, anterior; (F) same, posterior; (G) inner basal seta of P1; (H) P5, dorsal; (I) P6.

Maxilliped as figured by Heron & Bradford-Grieve (their Fig. 17f).

Swimming legs 1–4 with armature and ornamentation as in female; sexual dimorphism expressed in (1) terminal process on P1 endopod (obscuring insertion of distalmost seta), being relatively longer than in female (similar to *O. scottodicarloi*, Fig. 23I), (2) terminal conical projections on distal endopod segment of P3 (not on P2) longer than in female, reaching 2/3–3/4 the length of outer distal spine and (3) reduced spine lengths in endopod spines of P2–P4 (Table 4).

Table 4 Sexual dimorphism in spine length (μm) on distal endopod segment of P2–P4 in *O. media* from the Red Sea. (Data represent single measurements).

	Spine length		
	Female	Male	Male : female (%)
P2			
Outer subdistal spine	20.0	10.0	50
Outer distal spine	18.1	7.5	41
Distal spine	26.3	11.3	43
P3			
		left/right	
Outer subdistal spine	18.8	10.6/11.3	57/60
Outer distal spine	19.4	10.6/13.8	55/71
Distal spine	32.5	25.6/25.6	79
P4			
Outer subdistal spine	24.3	16.3	67
Outer distal spine	26.3	20.6	78
Distal spine	43.8	31.3	72

P5 (Fig. 16B) exopod fused to somite, length of segment shorter than in female; proportional lengths of exopodal setae as in female.

P6 represented by posterolateral flap closing off genital aperture on either side; covered by pattern of denticles as in Fig. 16C; posterolateral corners with single pointed tip, occasionally with bifid tip (arrowed in Fig. 16C).

TAXONOMY

Giesbrecht (1891: 477) presented a short latin diagnosis of *O. media* and subsequently described the species in more detail from the Mediterranean, Naples area (Giesbrecht, 1892). Recently, Heron & Bradford-Grieve (1995) redescribed *O. media* from the Gulf of Naples and in the same account described a closely related species, *O. scottodicarloi*, which co-occurred with *O. media* in the Gulf. The authors pointed out an important discrepancy in Giesbrecht's (1892) description of *O. media*: all of his figures of the species matched *O. media* as re-examined by Heron & Bradford-Grieve, except for his Plate 47, Fig. 11, dorsal view of female urosome, which resembled that of the newly described *O. scottodicarloi*. [In this context it should be noted that Heron & Bradford-Grieve (1995) recorded several undescribed species similar to *O. media* and *O. scottodicarloi* in their Gulf of Naples samples, indicating that a complex of species close to *O. media* exists, which is as yet undescribed. One of the species belonging to this complex is undoubtedly *O. waldemari*, whose taxonomic position will be re-evaluated below.]

Specimens of *O. media* from the Red Sea met all important characters described by Heron & Bradford-Grieve, including patterns of integumental pores on the prosome of both sexes. Slight differences in Red Sea specimens included (1) the armature on 6th segment of antennule, the minute sensory element not noted by Heron & Bradford-Grieve, (2) additional surface ornamentation on coxobasis of female antenna and (3) spine lengths on P2–P4 enp-3 in the male. The first two characters are difficult to discern and may have been overlooked in the previous description. The reduction of spine lengths on P2–P4 enp-3 in male *O. media* was less pronounced

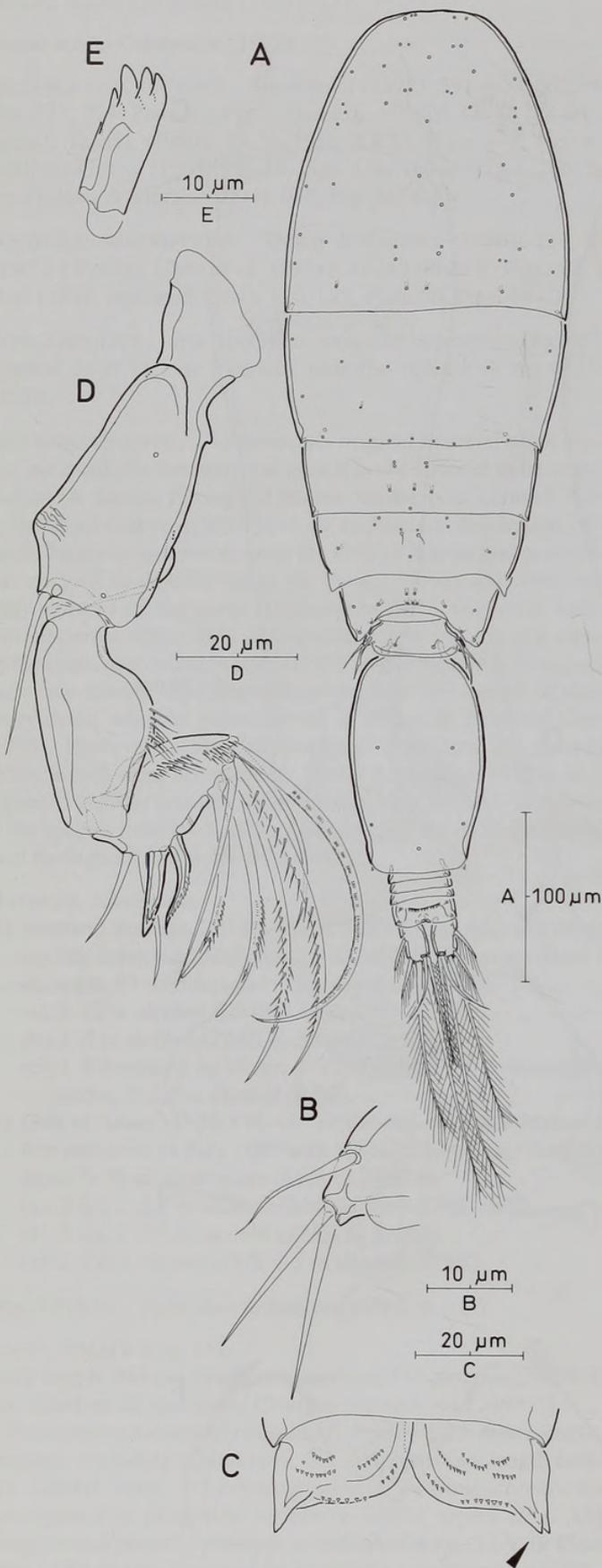


Fig. 16 *Oncaea media*, male (Red Sea) (A) Habitus, dorsal; (B) P5, dorsal; (C) P6, aberrant posterolateral corner arrowed. (D) antenna, anterior; (E) mandible, blade C.

in specimens from the Red Sea than had been reported by Giesbrecht (1892, Pl. 47, Figs. 32, 33) and Heron & Bradford-Grieve (their Fig. 17g-i). In particular the outer distal spine on P2 enp-3 was longer in Red Sea specimens, measuring about 3/4 the length of the outer subdistal spine (cf. Table 4), whereas it was figured being only 1/3–1/2 that length by the authors mentioned above. Proportional spine lengths on P2 enp-3 of *O. media* males from Japanese waters as recorded by Itoh (in: Chihara & Murano, 1997: his Fig. 365f) were similar to those found in Red Sea specimens.

O. media is closely related to *O. scottodiarloii*, with which it has often been confused. According to Heron & Bradford-Grieve (1995), important distinctions between females of the two species are found in (1) proportional lengths of urosome segments, (2) form and location of sclerotization between genital apertures, and (3) relative lengths of endopod spines of P4. Comments on the first two characters will be given below. A further character separating females of the two species as observed during the present study is the proportional length of exopodal setae on P5, the outer one being relatively shorter in *O. media* than in *O. scottodiarloii*.

(1) The typical elongate form of the genital double-somite of *O. media* as figured by Heron & Bradford-Grieve appears to be of great significance, because it enables unequivocal separation of *O. media* from other species of the *media* complex. In the original account of Giesbrecht (1892), however, the urosome is concealed underneath the paired egg-sacs of the ovigerous specimen in the illustration of female habitus (Plate 47, Fig. 1) and his illustration of the female urosome in dorsal aspect (Fig. 11) was assigned to *O. scottodiarloii* by Heron & Bradford-Grieve. Therefore it cannot be decided definitely, whether this character had also been present in Giesbrecht's specimen and the conspecificity of Giesbrecht's *O. media* with *O. media* sensu Heron & Bradford-Grieve can only be confirmed after re-examination of his type material. The lateral view of *O. media* as figured by Giesbrecht (Plate 2, Fig. 12) shows the genital segment being twice as long as the remaining part of the urosome, which is similar to *O. media* sensu Heron & Bradford-Grieve; also, the proportional lengths of spines on P4 enp-3 P4 figured by Giesbrecht are more similar to *O. media* than to *O. scottodiarloii*. Since both characters support Heron & Bradford-Grieve's conclusion, their opinion is followed in the present account.

(2) The integumental sclerotization located between the genital apertures is a reinforced attachment site for the insertion of the dorsal longitudinal trunk muscles (R. Huys, pers. commn.). These usually insert on the anterior rim of each somite, or in the case of the female genital double-somite near the genital apertures, marking the original plane of fusion. The sclerotization is always located at about 1/3 to 40% the distance from the anterior margin and does not differ between species, but as the position of genital apertures on the genital double-somite is different, the sclerotization changes its position relative to the genital apertures. In *O. media*, the genital apertures are located more laterally than in *O. scottodiarloii*, and thus the sclerotization changes its position accordingly.

Males of *O. media* can be separated from those of *O. scottodiarloii* most easily by the sexual dimorphism in the coxobasal seta of the antenna, which is short and naked (Fig. 16D) in *O. media*, but long and plumose as in the female in *O. scottodiarloii*. Giesbrecht and Heron & Bradford-Grieve did not notice the sexual dimorphism of this seta in *O. media*. In the present study, however, this character was found in all species of *Oncaea* s.str., except for *O. scottodiarloii* and *O. waldemari*. The sexual dimorphism in spine lengths of P2–P4 enp-3, on the other hand, which had already been reported for males of *O. media* in both previous account mentioned above, cannot be used to distinguish between males of both species, since it was also found in *O. scottodiarloii* during the present study (Fig. 23J, M) and seems to be a typical character for males of *Oncaea* s.str. (cf. *O. venusta*, *O. waldemari*).

OTHER RECORDS OF *O. MEDIA*

A summary of the world-wide records of *O. media* has been compiled by Heron & Bradford-Grieve (1995). They point to the great confusion caused by Sewell (1947), who described two size variants, f. *major* and f. *minor*, from the Arabian Sea. The *major* form (♀: 0.73–0.82 mm, ♂♂: 0.53–0.62 mm) exhibited a smaller length to width ratio of caudal ramus (2:1) than the *minor* form (3:1), which would correspond to the observed differences between *O. media* and *O. scottodiarloii*. However, Sewell described the distal spine on P4 enp-3 of f. *major* measuring about 2/3 the length of distal endopod segment (p.261), which is longer than reported by Giesbrecht (1892) and Heron & Bradford-Grieve for *O. media*, the spine being only

Table 5 List of important characters separating *O. media* and related species. Data of *O. curta* after Sars (1918), remaining data from present study.

Species	<i>media</i>	<i>scottodiarloii</i>	<i>curta</i>	<i>waldemari</i>
Female				
<i>GDS</i>				
– l:w ratio	1.9:1	1.5:1	1.5:1	1.7:1
– Form	very el.	oval-el.	squarish	elongate
– ratio GDS : rest of urosomites ¹ (excl.CR)	3.9:1	2.5:1	1.5:1	1.9:1
– position gen.ap., distance from lateral margin	1/4	1/3	ca 1/5	1/4
<i>L. ratio caudal setae</i>				
– seta VI:IV	2/3	1/2	ca 1/2	3/4
– seta VI:CR	3.8:1	2.2:1	ca 1:1	1.6:1
– seta VII:III	slightly longer	slightly longer	?	longer
Labrum, anterior face, paired patch of setules	no	yes	?	yes
<i>P5 exopod</i>				
– l:w ratio	1.9:1	1.7:1	ca 1.5:1	1.3:1
– outer:inner seta	equal	slightly longer	1/2length	equal
Male				
<i>Antenna</i>				
– coxobasal seta	short naked	long, plumose	?	long, plumose
– endopod 2, element IV	strong-curved	curved	?	slightly curved
l. ratio caudal seta VI:VII	longer	longer	?	equal

GDS = genital double-somite; CR = caudal ramus; gen.ap.= genital apertures; el. = elongate; l = length; w = width

¹Calculated by traditional method (i.e. telescoping of segments not considered)

1/2 length of the segment. Confusingly, Sewell refers to his figures of swimming legs, but these are not given in his account. A relatively long distal spine on P4 enp-3 is found in *O. scottodicarloi*, and it might be that Sewell had mixed up the characters of both species in his report. Since all three species of the *O. media*-complex (*O. media*, *O. scottodicarloi* and *O. waldemari* are found in the Arabian Sea (Böttger-Schnack, 1996, as *O. media* f. *major*, *O. media* f. *minor* and *Oncaea* sp. B, respectively), it is conceivable that he included the latter species in the lower size range of females as well.

Mori (1937, reprinted 1964) described the species from Japanese waters and Chen *et al.* (1974) recorded two size groups of *O. media* from the East China Sea and the Yellow Sea. In both accounts, the female genital double-somite is much shorter than in *O. media* sensu Heron & Bradford-Grieve and also seta VI on caudal ramus is too short. The same argument applies for the record of Dakin & Colefax (1940) from Australian waters. Although the illustration of the male antenna by Mori (his Plate 66, Fig. 17) shows a naked coxobasal seta, positive identification cannot be made without a closer examination of the specimens, especially in view of the extremely wide size range that was recorded for females (0.5–0.92 mm) in his account. However, the occurrence of *O. media* in the marine plankton of Japan has been confirmed in a recent excellent account by Itoh [in Chihara & Murano, 1997].

Tanaka (1960) recorded *O. media* from various locations in the East China Sea, Indian Ocean and south of Cape of Good Hope. He mentions the occurrence of two size groups, f. *major* and f. *minor*, which covered an overall size range of 0.55–0.79 mm. Sizes of the two groups were not recorded separately. His Plate XXXI, Fig. 4 clearly shows the dorsal view of female *O. media* sensu Heron & Bradford-Grieve, although he identified them as f. 'minor'. The different length ratio between subdistal and distal spines on P4 enp-3, which according to Heron & Bradford-Grieve (1995) separate *O. media* from *O. scottodicarloi*, is not apparent between Tanaka's f. *major* and f. *minor* (his Figs. 5 and 6). So it cannot be judged whether his small sized specimens are identical to *O. scottodicarloi* or probably belong to another closely related species, such as *O. waldemari*.

O. media f. *minor* sensu Malt (1982b) was assigned to *O. waldemari* during the present study and will be discussed below. In the identification key of oncaeids (Malt, 1983b) the separation between males of *O. media* and *O. venusta* needs to be revised, since the sexual dimorphism on antenna is found in both species, not only in *O. venusta*, as was erroneously stated by Malt.

GEOGRAPHICAL DISTRIBUTION

Oncaea media had been reported as *O. media* f. *major* in the previous quantitative accounts of Böttger-Schnack (1990b, 1994, 1995, 1996, 1997). The species is distributed throughout the Red Sea, but exhibits very variable abundances both seasonally and regionally. During summer, the species occurred in minimal numbers in the southern Red Sea, but exhibited higher values to the north, in the central-northern Red Sea, as well as to the south, in the Gulf of Aden and Bab al Mandab area (Böttger-Schnack, 1995).

In the northern Arabian Sea, *O. media* was found in appreciable numbers, with abundances being one to two orders of magnitude higher than in the Gulf of Aden and/or in the central Red Sea (Böttger-Schnack, 1996). The species also occurred in the Eastern Mediterranean Sea (Böttger-Schnack, 1997) in comparably low numbers.

SEASONAL VARIATION IN ABUNDANCE (CENTRAL RED SEA)

O. media was recorded from the central-northern Red Sea during winter (Böttger-Schnack, 1990b) and summer (Böttger-Schnack, 1995), but not during autumn, when it was completely absent or occurred as solitary finds only (Böttger-Schnack, 1990a, b). Due to

its seasonality, the species had previously been assumed to be of southern origin (Böttger-Schnack, 1990b), but subsequent data from the summer season did not point to a consistent seasonal variation in the central Red Sea (Böttger-Schnack, 1995).

VERTICAL DISTRIBUTION AND VERTICAL MIGRATION

O. media was generally confined to the epipelagic zone (0–150 m) in the Red Sea, with few, isolated finds down to 900 m. The species had a unimodal distribution pattern with maximum densities in the upper epipelagic (0–50 m) and was classified as non-migratory during winter in the central Red Sea (Böttger-Schnack, 1990b). In the Gulf of Aden and Strait of Bab al Mandab, maximum densities were found at a depth of 0–20 m and 0–60 m, respectively, during summer (unpubl. data). By this, the species tended to be vertically separated from the two related species, *O. scottodicarloi* and *O. waldemari*, which generally occurred deeper and over a much wider depth range in that area.

Oncaea clevei Früchtl, 1923

Oncaea clevei Früchtl (1923): 455, Tafel 26, Figs. 19–22 (♀ only).

Oncaea conifera Cleve, 1901

RELIABLE DESCRIPTIONS. Früchtl (1924): 22–23, 89–91, Figs. 14, 15, 60–70 (♀ only); Itoh [in: Chihara & Murano (1997)]: 979, Fig. 361a, d, f (♀ only).

DOUBTFUL DESCRIPTIONS. Sewell (1947): 258 [as *Oncaea clevei*]; Tanaka (1960): 66, Plate XXVIII, Figs. 7–13; Chen *et al.* (1974): 42, Plate 7, Figs. 4–7.

TYPE LOCALITY. Aru Archipelago, Indo-Pacific area.

PRELIMINARY NOTE. The original description of Früchtl (1923, 1924) lacks many details, particularly in the mouthparts, of which he described only the maxilliped. A detailed redescription of *O. clevei* from the Red Sea is given below, including a description of the hitherto unknown males. During the course of the study a closely related species was found, which is described as a new species, *O. paraclevei* sp. nov. A comparison of morphological characters separating the two species is included under *O. paraclevei* see *Remarks*.

MATERIAL EXAMINED.

- (1) Central Red Sea, 21° 25.53'N, 38° 01.91'E: Stn. 130; *R/V Valdivia* leg 29: collected 28 October 1980 with MSN 0.1 mm net (Haul 117/5); depth 0–20 m; total water depth 1960 m.
 - (a) 2 ♀♀ in alcohol (BMNH 1998.2803–2804).
 - (b) 2 ♀♀ in alcohol (ZMH K-39574).
 - (c) 1 ♀ partly dissected (maxilliped and maxilla on slides), 1 ♀ in alcohol (RBS).
- (2) Southern Red Sea, 15° 34.8'N, 41° 54.9'E: Stn. 703; *R/V Meteor* leg 5/5: collected 03 August 1987 with MSN 0.05 mm net (Haul 39/5); depth 0–50 m; total water depth 970 m.
 - (a) 1 ♂ partly dissected (urosome on slide), remaining specimen in alcohol (BMNH 1998.2805), 3 ♂♂ in alcohol (BMNH 1998.2806–2808).
 - (b) 1 ♂ dissected on 10 slides (ZMH K-39575a–i), 1 ♀, 3 ♂♂ in alcohol (ZMH K-39576).
 - (c) 2 ♀♀, 3 ♂♂ in alcohol (RBS).
- (3) Gulf of Aden, 11° 55.5'N, 43° 37.9'E: Stn. 631a; *R/V Meteor* leg 5/5: collected 11 July 1987 with MSN 0.05 mm net (Haul 3/5); depth 0–50m; total water depth 1400 m.
 - (a) 1 ♀, 1 ♂ (mating position, ♂ lacking urosome) in alcohol (BMNH 1998.2809–2810).
 - (b) 1 ♀, 1 ♂ (mating position) in alcohol (ZMH K-39577).

- (c) 1 ♂ (from mating pair) dissected on 9 slides, 1 ♀ (ovigerous, from mating pair) in alcohol, 1 ♀, 1 ♂ (mating position) in alcohol (RBS).
- (4) Northern Arabian Sea, 19° N, 65° E: Stn. 247; R/V Meteor leg 32/3: collected 14 May 1995 with MSN 0.05 mm net (coll. L. Postel); depth 0–50m; total water depth ca 3000 m: 1 ♀ dissected on 11 slides, 1 ♀ in alcohol (RBS).
- (5) Northern Arabian Sea, near Oman, 20° 44.3'N, 59° 40.5'E: Stn. 347; R/V Meteor leg 5/3a: collected 05 April 1987 with MSN 0.05 mm net (Haul 8/1); depth 0–50 m; total water depth ca 2500 m: 6 ♀♀ in alcohol (RBS).
- (6) Pacific Ocean, Great Barrier Reef; further sampling data not specified; leg G.P. Farran, 1928–1929, cf. Farran (1936); 10 specimens in alcohol, labelled *Oncaea clevei* (BMNH 1949.12.31.516): this vial contains 5 ♀♀ of *O. clevei*, 1 prosome with dorsal hump and 4 damaged prosomes; 2 urosomes (1 of *O. clevei*, 1 possibly of *O. paraclevei* sp. nov.), and 2 bits of calanoid copepods).
- (7) Pacific Ocean, Great Barrier Reef; further sampling data not specified; leg G.P. Farran, 1928–1929, cf. Farran (1936); more than 10 specimens in alcohol, labelled *Oncaea clevei* (BMNH 1948.4.28.140): this vial contains 22 ♀♀ of *O. clevei*, 1 ♂ Corycaeidae indet., 1 calanoid copepod.

DESCRIPTION. Note illustrations are based on (2a–2c) and (4).

ADULT FEMALE (Figs. 17–19, 21A).

Body length: 810 µm [traditional method: 640 µm, range: 620–680 µm, based on 4 specimens].

Exoskeleton well chitinized. Prosome 2.4 times length of urosome, excluding caudal rami, 2.1 times urosome length including caudal rami. P2-bearing somite with conspicuous dorso-posterior projection in lateral aspect (Fig. 17B), not varying in size between specimens examined. Integumental pores on prosome as indicated in Fig. 17A, B. Pleural areas of P4-bearing somite with rounded posterolateral corners.

Proportional lengths (%) of urosomites 11.4 : 55.3 : 10.1 : 10.1 : 13.1. Proportional lengths (%) of urosomites and caudal rami 9.6 : 46.5 : 8.5 : 8.5 : 11.0 : 16.0.

Genital double-somite almost rectangular in dorsal aspect, 1.4 times as long as maximum width (measured in dorsal aspect) and 1.6 times as long as postgenital somites combined (Fig. 17C); largest width measured near anterior margin, lateral margins of genital double-somite rounded at anterior quarter, posterior part tapering slightly. Paired genital apertures located very close to dorsolateral margin at about 2/5 the distance from anterior margin of genital double-somite; armature represented by 1 spine and 2 minute spinous processes (Fig. 17H). Sickle-shaped sclerotization between, but slightly posterior to genital apertures, pore pattern on dorsal surface as indicated in Fig. 17C.

Anal somite 1.4 times wider than long; slightly shorter than caudal rami (Fig. 17C). Surface ornamentation mainly as in *O. venusta*.

Caudal ramus (Fig. 17F) about 2.3 times as long as wide. Seta VI more than 4/5 length of seta IV and 2.5 times longer than caudal ramus; seta VII about half length of seta VI and longer than seta III (Fig. 17C, F). Inner margin of somite with few long setules.

Antennule (Fig. 17E) with relative lengths (%) of segments measured along posterior non-setiferous margin 6.7 : 26.1 : 38.3 : 11.1 : 4.4 : 13.3. Armature as for genus.

Antenna (Fig. 18A) similar to *O. venusta*, except for coxobasis with fewer surface ornamentation and seta III on second endopod segment bipinnate.

Labrum (Fig. 18B,C) as in *O. venusta*, except for long fine setules missing latero-distally on outer margins of lobes. Anterior surface (Fig. 18B) with row of stout denticles on proximal part of each lobe, which are not found in *O. venusta*.

Mandible (Fig. 18D) as in *O. venusta*, except for blade C ornamented with 1 additional dentiform process halfway on dorsal margin. Maxillule (Fig. 18E), maxilla (Fig. 18F), and maxilliped (Fig. 18G) mainly as in *O. venusta*.

Swimming legs (Fig. 19A–D) with armature as for genus and surface ornamentation similar to *O. venusta*, except for less surface ornamentation on coxae and bases, most obvious in P4 coxa, lacking patch of long setules on posterior surface. Endopodal and exopodal spine lengths mainly as in *O. venusta*, except for terminal spines on endopods of P1, P2 and P4 relatively longer, particularly in P4, reaching more than half the length of distal endopod segment. P2 with outer subdistal spine reaching insertion of outer distal spine; P4 with outer distal spine shorter than in *O. venusta*, about 1/2 length of distal spine. Inner basal seta on P1 naked; outer basal seta on P3 plumose.

P5 (Fig. 17G) comprising small naked seta arising from lateral surface of somite, and free unornamented segment representing exopod. Exopod twice as long as wide, bearing 2 spiniform, naked setae equal in length, which are straight.

P6 (Fig. 17H) represented by operculum closing off each genital aperture; armed with a spine and 2 small spinous processes.

Egg-sacs paired, oval-shaped; each sac containing appr. 15–20 eggs (diameter 40–48 µm) (Böttger-Schnack *et al.*, 1989).

ADULT MALE (Fig. 20, 21A–C).

Body length: 630 µm [traditional method: 540 µm, range: 490–570 µm, based on 4 specimens]. Sexual dimorphism in antennule, antenna, maxilliped, P2–P3 (endopod) and P5–P6, caudal ramus and in genital segmentation.

Prosome 2.5 times the length of urosome, excluding caudal rami, 2.2 times urosome length, including caudal rami.

Proportional lengths (%) of urosomites (excluding caudal rami) 12.5 : 66.9 : 4.3 : 4.3 : 4.3 : 7.6; proportional lengths (%) of urosomites (caudal rami included) 11.0 : 58.9 : 3.8 : 3.8 : 3.8 : 6.7 : 12.0. Caudal rami about 1.8 times longer than wide, shorter than in female. Caudal setae with proportional lengths as in female, except for seta VI, which is about 3/5 the length of seta IV and 2.2 times length of caudal ramus; seta VII longer than in female, reaching about 2/3 length of seta VI (Fig. 20A).

Antennule (Fig. 20B) relative lengths (%) of segments measured along posterior non-setiferous margin 10.0 : 24.1 : 38.2 : 27.6. Armature formula as for genus.

Antenna (Fig. 20H) as in female, except for seta on coxobasis naked and shorter than in female; lateral armature on distal endopod segment differing from female, with element III being much stouter and element IV spiniform and distinctly curved; both elements shorter than in female.

Maxilliped (Fig. 20C) similar to *O. venusta*.

Swimming legs 1–4 with armature and ornamentation as in female; terminal process on P1 endopod as in female; P4 with outer distal spine half length of distal spine as in female; sexual dimorphism expressed in size of terminal conical projections on distal endopod segment of P2–P3, being relatively longer than in female, reaching 2/3 length (P2) or almost same length (P3) of outer distal spine (Fig. 21B1, B2, C). Variation in spine length as shown in Fig. 21B1, B2.

P5 (Fig. 20G) exopod not delimited from somite, general shape and armature as in female, except for exopodal setae shorter than in female.

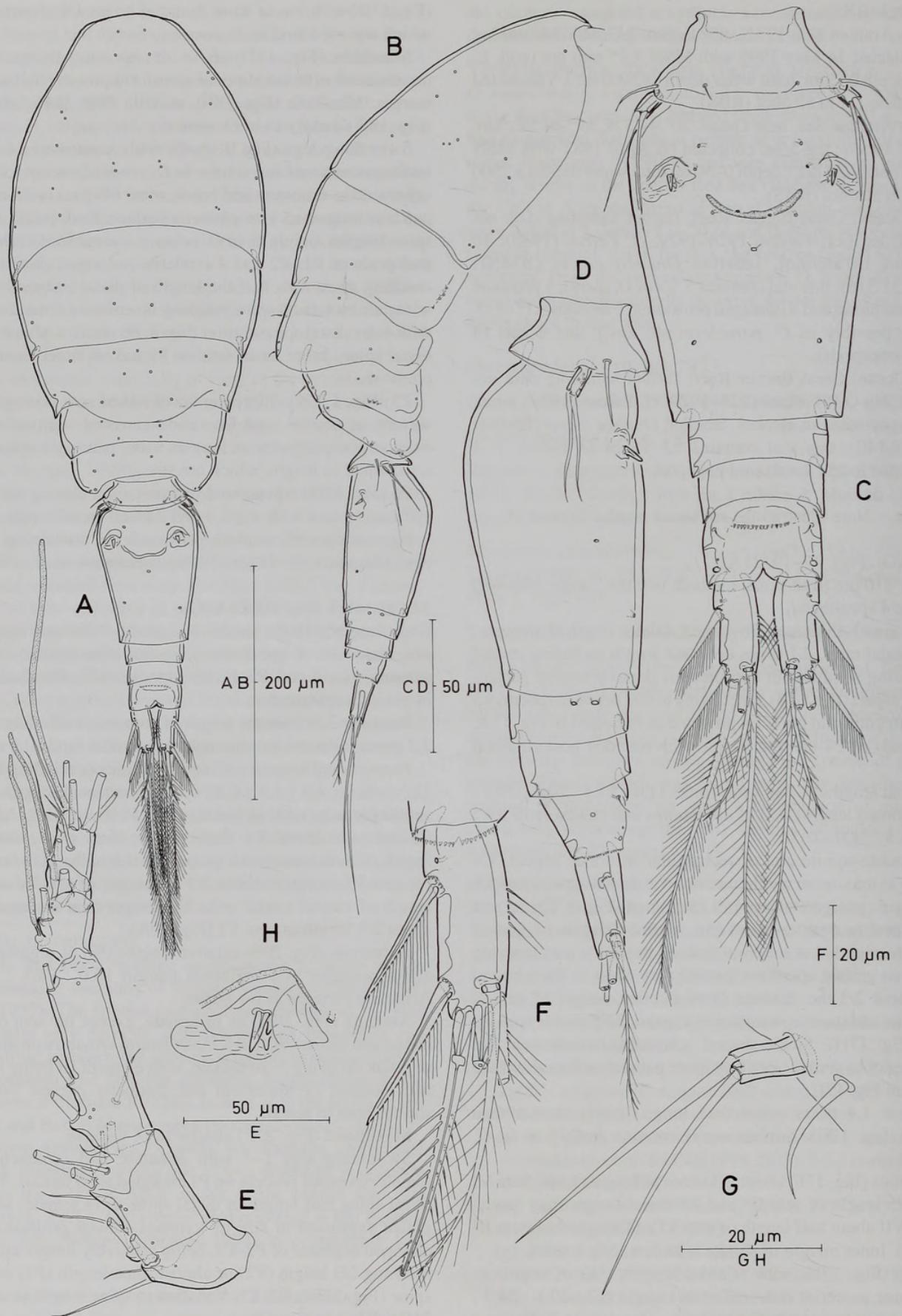


Fig. 17 *Oncaea clevei*, female (Red Sea) (A) Habitus, dorsal; (B) same, lateral (appendages omitted); (C) urosome, dorsal; (D) urosome, lateral; (E) antennule; (F) caudal ramus, dorsal; (G) P5, dorso-lateral; (H) P6.

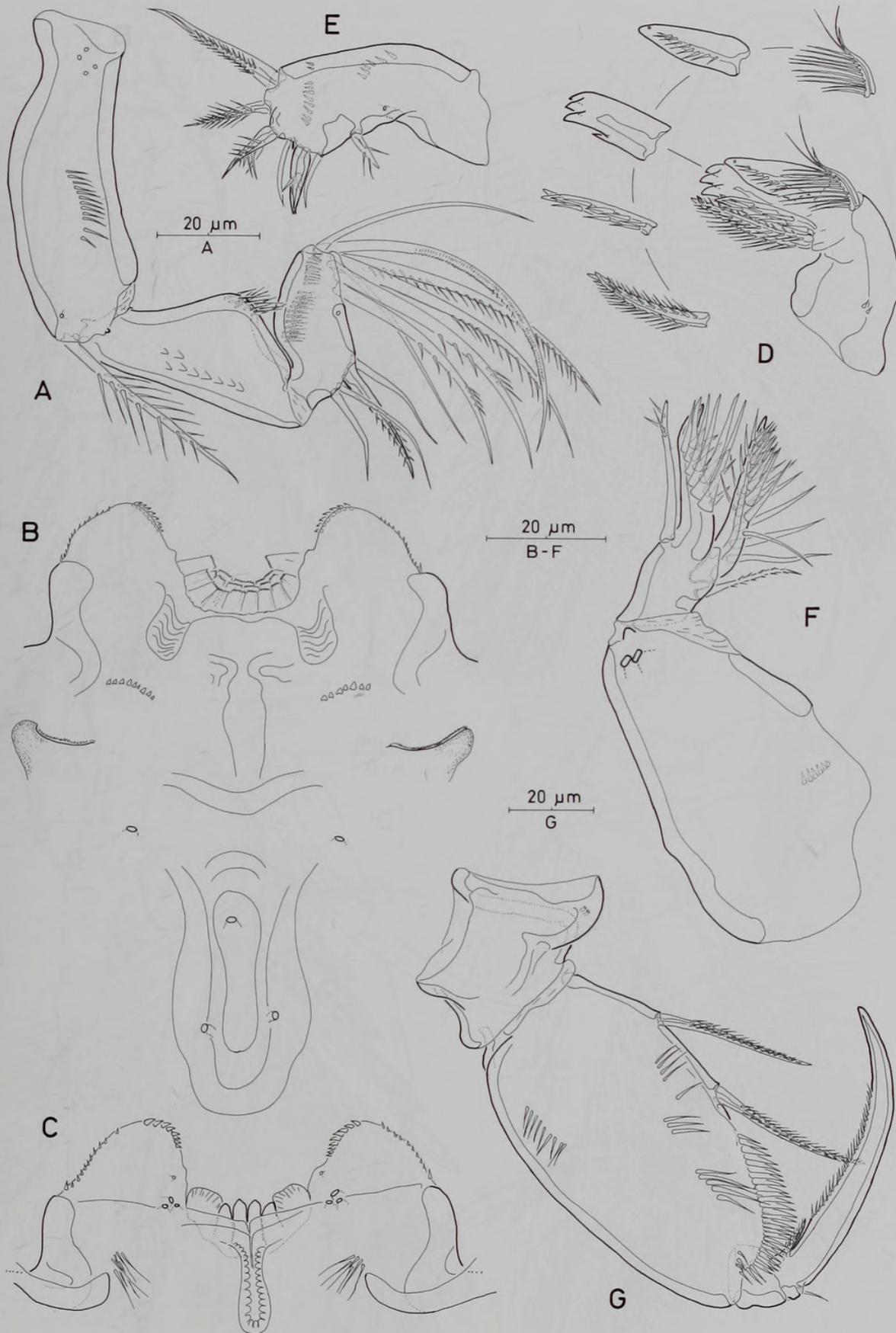


Fig. 18 *Oncaea clevei*, female (Red Sea) (A) Antenna; (B) labrum, anterior; (C) same, posterior; (D) mandible, showing individual elements; (E) maxillule; (F) maxilla; (G) maxilliped.

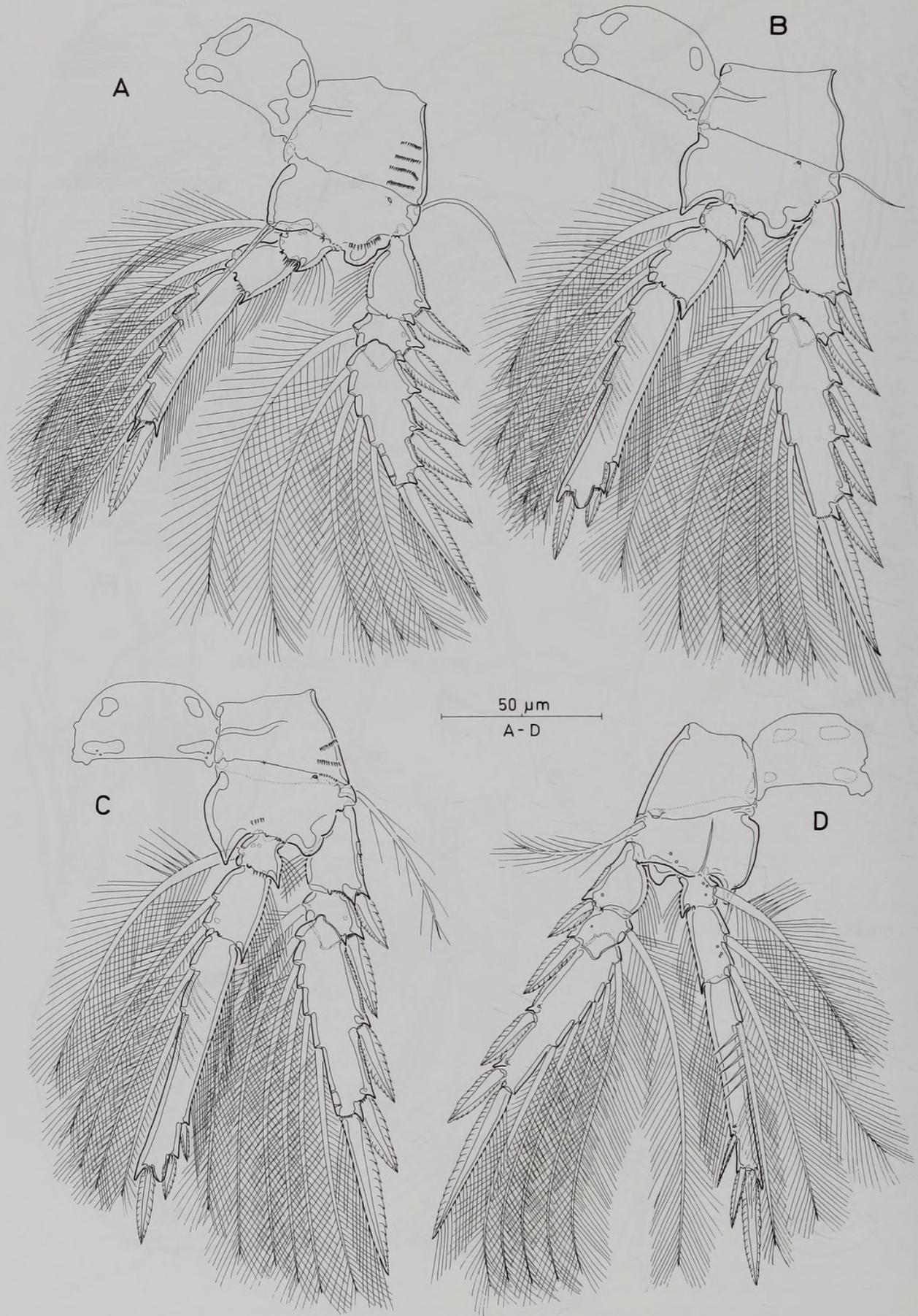


Fig. 19 *Oncaea clevei*, female (Red Sea) (A) P1, anterior; (B) P2, anterior; (C) P3, anterior; (D) P4, posterior.

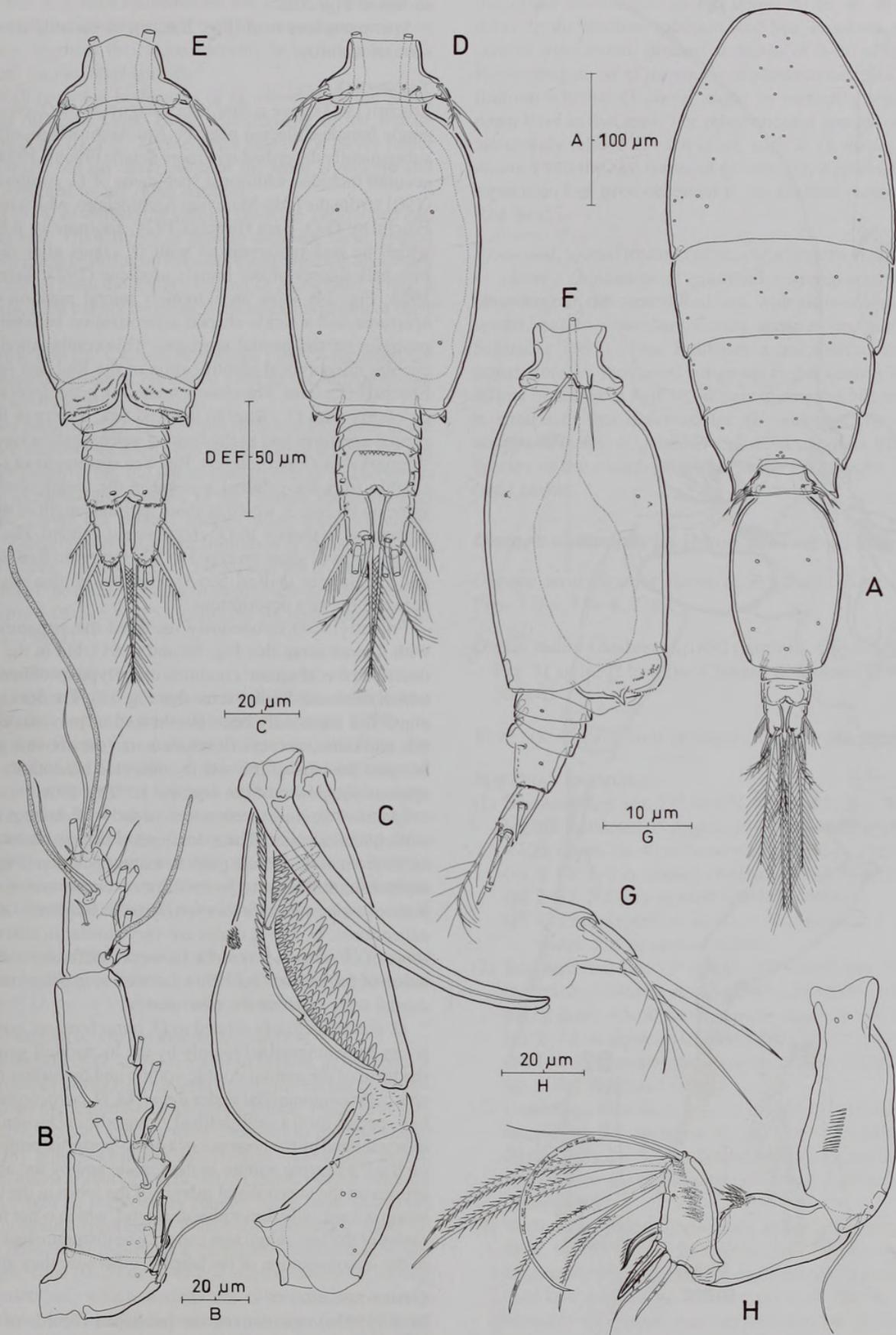


Fig. 20 *Oncaea clevei*, male (Red Sea) (A) Habitus, dorsal; (B) antennule; (C) maxilliped, medial; (D) urosome, dorsal (spermatophores immature); (E) urosome, ventral; (F) same, lateral; (G) P5, dorsal; (H) antenna, anterior.

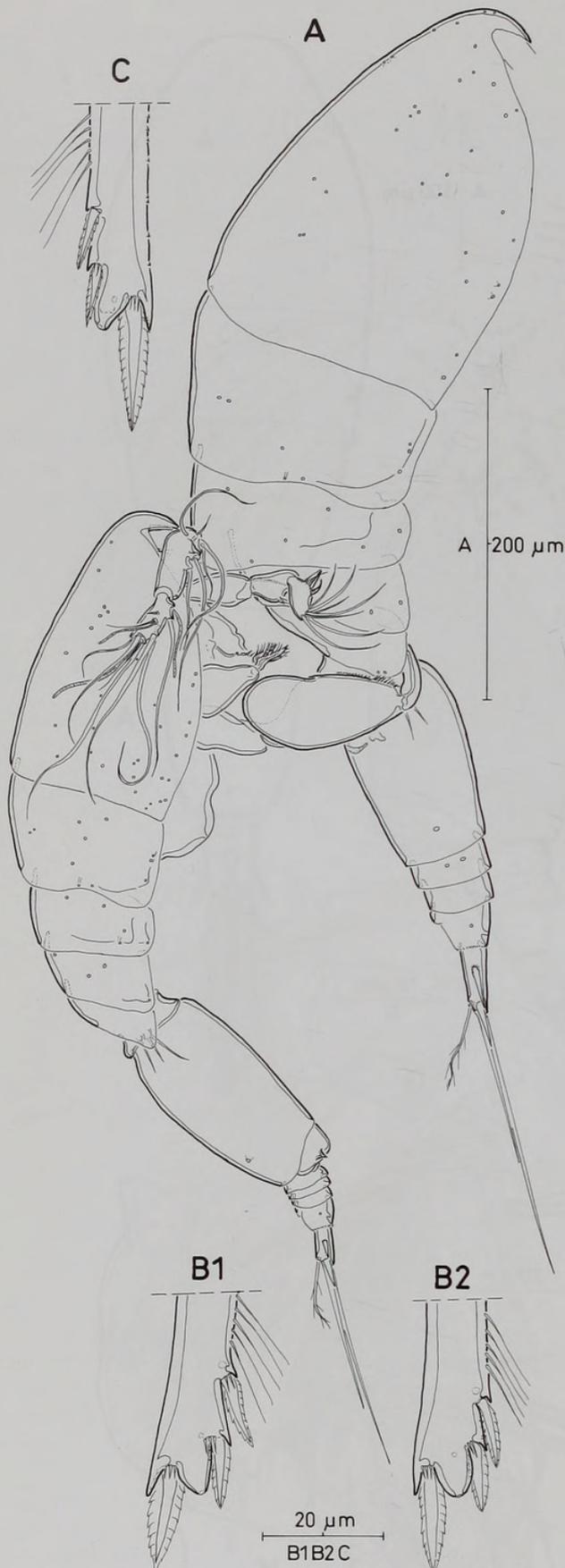


Fig. 21 *Oncaea clevei* (Red Sea) (A) Female and male, mating position, lateral, appendages of female and swimming legs of male omitted. *Oncaea clevei*, male (Red Sea) (B1, B2) P2, distal part of endopod, showing variation in spine length. (C) P3, distal part of endopod.

P6 (Fig. 20E) represented by posterolateral flap closing off genital aperture on either side; covered by pattern of denticles as shown in Fig. 20E.

Spermatophore oval (Fig. 20E, F), of variable size according to state of maturity.

TAXONOMY

Früchtl (1923) gave a first short diagnosis of *O. clevei* based on a single female collected near the Aru Archipelago, off Wokam, and subsequently described it in more detail (Früchtl, 1924). The second account included additional specimens of *O. conifera* sensu Cleve (1901) from the Indo-Malayan Archipelago, which had been sent to Früchtl by G.O. Sars (Früchtl, 1924, footnote to p. 89 (111)), and which he had synonymized with *O. clevei* after re-examination. Früchtl's figures of the female urosome (1923: Tafel 26, Fig. 19; 1924: Fig. 24) show an extremely lateral position of the genital apertures and a sickle-shaped sclerotization between, but slightly posterior to, the genital apertures. This combination of characters enables unequivocal identification of the Red Sea specimens with Früchtl's *O. clevei*. The closely related *O. paraclevei* sp. nov., which co-occurs with *O. clevei* in the Red Sea, differs in the location of genital apertures and in the form of sclerotization (see below under 'Remarks' of *O. paraclevei*). Red Sea specimens of *O. clevei* differ slightly from the original account in the length of the outer distal spine on P4 enp-3, which is about half the length of the distal spine, whereas it is shorter in *O. clevei* sensu Früchtl. The length of the outer subdistal spine on enp-3 in P2 (shorter in Red Sea specimens) and P3 (longer in Red Sea specimens) is also slightly different between the two descriptions.

Früchtl (1924) erroneously recorded the armature of P1 enp-3 with 4 inner setae (his Fig. 66 and p. 91), but in the same account described the 'aberrant' condition of the type specimen from Wokam, which exhibited 5 inner setae (his Fig. 15). The 5th inner seta on P1 enp-3 has repeatedly been overlooked in previous descriptions of this and other species of *Oncaea* s.str. (see above e.g. *O. venusta*), because the base of the seta is concealed beneath the long anterior spinous outgrowth of the segment (cf. Fig. 19A).

Males of *O. clevei* were not recorded by Früchtl in any reliable subsequent account. Their description here is based on specimens taken from male-female pairs in mating position (Fig. 21A), which represents the highest probability of encountering a conspecific male of a given species (but see Heron & Bradford-Grieve, 1995 for exceptions). *O. clevei* males are very similar in size and habitus to those of *O. venusta* f. *venella*. However, differences in the ornamentation of the labrum (see below) as well as in proportional lengths of caudal setae separate the two species.

O. clevei is closely related to *O. paraclevei* sp. nov., from which it can be distinguished mainly by the location of genital apertures, the form of the genital double-somite and by further morphological characters summarized under *Remarks, O. paraclevei*. Together, the two species form a well-defined group within *Oncaea* s.str., which is characterized by the presence of a dorso-posterior projection ('hump') on the P2-bearing somite in the female and by the absence of long setules on the latero-distal margin of the lobes in the labrum. As the hump is a sexually dimorphic character, which is not found in males, males of the two subgroups can only be distinguished by differences in the ornamentation of the labrum, otherwise they are very similar.

OTHER RECORDS OF *O. CLEVEI*

Malt (1983a) summarized the published records of *O. clevei* and found it restricted to surface waters in low latitudes of the western Pacific and Indian Ocean. In view of the existence of a hitherto undescribed species, which is extremely close to *O. clevei*, it may be assumed that both *O. clevei* and *O. paraclevei* may have been

recorded under the name *O. clevei* in previous records.

Sewell (1947, p. 258) recorded the species from the northern Arabian Sea, but it is not clear whether his material included *O. paraclevei* as well, because he stated that 'the dorsal projection on the 2nd thoracic segment varies considerably in its development', which is typical for the latter species.

Tanaka (1960) recorded both sexes of *O. clevei* from the South China Sea and off Cape Good Hope. His drawing of the female urosome (Plate XXVIII, Fig. 7) resembles that of *O. clevei* rather than *O. paraclevei*, but his description of the male is meagre and could also be assigned to any other oncaeid.

Chen *et al.* (1974) described the species from the Yellow Sea and the East China Sea. Their figure of female urosome lacks genital apertures and/or the sclerotization between them, which is necessary to separate *O. clevei* from the closely related *O. paraclevei*. Thus, a positive identification cannot be given without examination of their specimens.

More recently, Itoh [in: Chihara & Murano (1997)] recorded the species from Japanese waters; his dorsal view of the female shows the two characters typical for *O. clevei*.

Several other records of *O. clevei* from different localities in the Indo-Pacific are known [see Malt (1983a) for a review], but are not considered here because they did not include figures or a description that positively identified the species. In the Eastern Mediterranean Sea, neither *O. clevei* nor related species were found (Böttger-Schnack, 1997), thus corroborating the limitation of this subgroup to the Indo-Pacific area. The fact that *O. clevei* was not recorded in the detailed account of the oncaeid fauna from the New Zealand area by Heron & Bradford-Grieve (1995), confirms its restriction to low latitudes (Malt, 1983a).

GEOGRAPHICAL DISTRIBUTION

Oncaea clevei is distributed throughout the Red Sea, with lowest abundances in the northern area (Böttger-Schnack, 1990a, b, 1995). It was not found in small mesh net samples from the northernmost part of the Red Sea, in the Gulf of Aqaba (unpubl. data). In the southernmost Red Sea and at Bab al Mandab, abundances of the species were up to two orders of magnitude higher than in the central part (Böttger-Schnack, 1995). The data from both areas include an unknown number of *O. paraclevei* sp.nov., however, which was not separated from *O. clevei* during the quantitative counts. Thus, the actual regional difference in abundance remains uncertain.

In the northern Arabian Sea, *O. clevei* was recorded from the epipelagic zone by Böttger-Schnack (1996), however, the potential co-occurrence of *O. paraclevei* was not investigated.

VERTICAL DISTRIBUTION AND VERTICAL MIGRATION

The depth distribution of *O. clevei* remains uncertain, as the species was counted together with *O. paraclevei* during the earlier quantitative investigations in the Red Sea (Böttger-Schnack, 1988, 1990a, b, 1995). Generally, the two species were confined to the epipelagic zone (0–100 m) with occasional occurrences below that depth. Individual specimens found down to 950 m depth during summer (unpubl. data) might be regarded as contaminants from shallower depths or as moribund specimens. Within the epipelagic zone, *O. clevei* and *O. paraclevei* exhibited a unimodal distribution in the upper epipelagic zone (0–20 or 0–40 m), staying above the strong seasonal thermocline, which usually develops during autumn (Böttger-Schnack, 1990a). No indication of a significant diurnal vertical movement became apparent and also no seasonal variation in the depth distribution of the two species was noted in the central Red Sea (Böttger-Schnack, 1990b).

In the deep southern Red Sea and in the Strait of Bab al

Mandab/Gulf of Aden area, the depth distribution of the two species was similar to that observed in the central area, with maximum abundances in the upper 20 to 40 m layer (unpubl. data). In the shallow southern Red Sea, however, two population centres were found, situated at depths of 0–20 m and 100–125 m. Re-investigations of the southern plankton samples are required to find out whether *O. clevei* might be vertically separated from *O. paraclevei* in that area. For other oncaeid species or forms, which are closely related to each other, such as *O. media* and *O. scottodicarloi* and the two forms of *O. venusta*, a corresponding vertical separation had been observed in the shallow parts of the southern Red Sea.

SEASONAL VARIATION IN ABUNDANCE (CENTRAL RED SEA)

O. clevei / *O. paraclevei* exhibited a strong seasonal variation in abundance in the central Red Sea, with highest abundances during winter, but low numbers during summer and autumn (Böttger-Schnack, 1995). This indicates a substantial recruitment for populations of the *clevei*-subgroup in the central area due to the inflow of southern Red Sea waters during the NE monsoon, which is similar to that observed for *O. venusta* f. *typica*. It remains uncertain, however, whether this effect applies likewise for both species of the *clevei*-subgroup, as the two species were not separated earlier.

Oncaea scottodicarloi Heron & Bradford-Grieve, 1995

Oncaea scottodicarloi Heron & Bradford-Grieve (1995): 39–41, Figs. 17j–r, 18a–k, 27a.

Oncäa media Giesbrecht, 1892 (partim); Giesbrecht 1892, Pl. 47, Fig. 11 only; H.Itoh [in: Chihara & Murano (1997)]: 981, Fig. 369a–f.

TYPE LOCALITY. Gulf of Naples, western Mediterranean Sea.

MATERIAL EXAMINED

- (1) Southern Red Sea, 13° 40.0'N, 42° 37.4'E: Stn. 708; *R/V Meteor* leg 5/5: collected 05 August 1987 with MSN 0.05 mm net (Haul 47/3); depth 20–40 m; total water depth ca 190 m.
 - (a) 2 ♀♀, 1 ♂ in alcohol (BMNH 1998.2811–2813).
 - (b) 2 ♀♀, 2 ♂♂ in alcohol (ZMH K-39581).
 - (c) 2 ♀♀ dissected on slides, 1 ♀ in alcohol; 1 ♂ dissected on slides, 1 ♂ in alcohol (RBS).
- (2) Southern Red Sea, 13° 40.0'N, 42° 37.4'E: Stn. 708; *R/V Meteor* leg 5/5: collected 05 August 1987 with MSN 0.05 mm net (Haul 47/2); depth 40–60 m; total water depth ca 190 m.
 - (a) 2 ♂♂ in alcohol (BMNH 1998.2814–2815).
 - (b) 1 ♀, 1 ♂ (mating position) in alcohol (ZMH K-39582).
 - (c) 2 ♂♂ in alcohol (RBS).
- (3) Central-northern Red Sea, 22° 58.4'N, 37° 19.4'E: Stn. 663; *R/V Meteor* leg 5/5: collected 20 July 1987 with MSN 0.05 mm net (Haul 17/2); depth 150–200 m; total water depth 1200 m: 1 ♀ on slide in lactophenol, numerous ♀♀ and ♂♂ for length measurements (RBS).
- (4) North-East Atlantic, upwelling area off Northwest-Africa, 17° 36'N, 16° 26'W: Stn. 262 (DIV); *R/V Meteor* leg 64: collected March 1983 with Messhai [= multiple opening-closing modified Gulf III type sampler, Pommeranz *et al.* (1979), Pommeranz & Moser (1987)] mesh size 0.05 mm; depth 80 m; total water depth 100 m: 1 ♀ dissected on 1 slide in polyvinyl-lactophenol (RBS).
- (5) North-East Atlantic, upwelling area off Northwest-Africa, 16° 09'N, 16° 48'W: Stn. 284 (DV); *R/V Meteor* leg 64: collected 27 March 1983 with Messhai [cf. (4)], mesh size 0.05 mm; depth

10–20–40 m; total water depth 100 m: 1 ♀ dissected on 1 slide in polyvinyl-lactophenol (RBS).

- (6) Eastern Indian Ocean, NW Cape Australia, 21° 49.86'S, 114° 30.3'E: Stn. B; NWC 005/2; RV 'Lady Basten' leg 1630; collected 26 October 1997 with 0.5 m WP-2 net with 0.073 mm mesh, vertical haul; depth 0–20 m (leg. D. McKinnon): 4 ♀♀ (RBS).

DESCRIPTION. Note illustrations are based on 1(c).

ADULT FEMALE (Figs. 22, 23A–E).

Body length (measured in lateral aspect; from anterior margin of rostral area to posterior margin of caudal rami, calculated as sum of individual somites): 803 µm [traditional method: (a) 600 µm, range: 540–610 µm, based on numerous specimens from southern Red Sea and Gulf of Aden; (b) 510 µm, range: 480–520 µm, based on 12 specimens from central Red Sea (Böttger-Schnack *et al.* (1989))].

Exoskeleton moderately chitinized. Prosome 2.8 times length of urosome, excluding caudal rami, 2.4 times urosome length including caudal rami. Integumental pores on prosome as indicated in Fig. 22A, B.

Proportional lengths (%) of urosomites 10.6 : 63.8 : 7.7 : 7.2 : 10.6. Proportional lengths (%) of urosomites and caudal rami 9.2 : 55.3 : 6.7 : 6.3 : 9.2 : 13.4.

Genital double-somite 1.5 times as long as maximum width (measured in dorsal aspect) and 2.5 times as long as postgenital somites combined (Fig. 22C); straight sclerotization between genital apertures, pore pattern on dorsal surface as indicated in Fig. 22C. Armature of genital apertures represented by 1 spine and 2 minute spinous processes (Fig. 22G).

Anal somite 1.8 times wider than long; about 3/4 length of caudal rami (Fig. 22C). Ornamentation as for *O. venusta*.

Caudal ramus (Fig. 22F) about 2.3 times as long as wide, shorter than reported by Heron & Bradford-Grieve. Dorsal seta (VII) half the length of terminal accessory seta (VI), not 2/3 the length as reported by Heron & Bradford-Grieve, plumose and bi-articulate at base.

Antennule with minute element on 6th segment (arrowed in Fig. 22E), which was not mentioned in the original account.

Antenna as figured by Heron & Bradford-Grieve (their Fig. 17m), except for additional surface ornamentation on coxobasis similar to *O. waldemari* (cf. Fig. 25A) and 2 patches of spinules (not only 1) on anterior surface of distal endopod segment.

Labrum (Fig. 23A, B) similar to *O. waldemari*, but fewer dentiform processes medially on each lobe and free margin of integumental pockets distinctly serrate (Fig. 23A).

Mandible generally as figured by Heron & Bradford-Grieve, dorsal blade ornamented with 1 additional minute dentiform process at dorsal margin (Fig. 22H). Maxillule, maxilla and maxilliped similar to *O. waldemari*, some ornamentation elements on syncoxa of maxilla and on basis of maxilliped missing in the account of Heron & Bradford-Grieve.

Swimming legs 1–4 with armature as for genus and surface ornamentation similar to *O. waldemari* (Fig. 26A–D), except for anterior face of P1 enp-1 and -2 with stronger spinules on distal margin (Fig. 23C). P1 exp-3 with outer distal spine slightly longer than figured by Heron & Bradford-Grieve. P4 exp-3 and enp-3 (Fig. 23E) with outer distal spines somewhat longer than in original account, outer endopodal spine reaching almost 1/2 length of distal spine.

P5 (Fig. 22F) with exopodal segment longer than figured by Heron & Bradford-Grieve, ornamented with 3 spinules ventrally; inner one of exopodal setae stouter and slightly shorter than outer one.

P6 (Fig. 22G) represented by operculum closing off each genital

aperture; armed with a spine and 2 small spinous processes.

Egg-sacs paired, oblong-oval; each sac containing 6 eggs (diameter 40–45 µm) (Böttger-Schnack, 1989, as *O. media* f. *minor*).

ADULT MALE (Fig. 23F–M).

Body length: 607 µm [(a) 440–480 µm, based on several specimens from southern Red Sea and Gulf of Aden; (b) 410 µm, range: 410–440 µm, based on 7 specimens from central Red Sea (Böttger-Schnack *et al.* (1989))]. Sexual dimorphism in antennule, antenna, maxilliped, endopods of P2–P4, P5–P6, caudal ramus and in genital segmentation.

Prosome 2.5 times length of urosome, excluding caudal rami, 2.2 times urosome length, including caudal rami.

Proportional lengths (%) of urosomites (excluding caudal rami) 11.2 : 69.2 : 3.8 : 3.8 : 3.8 : 8.3; proportional lengths (%) of urosomites (caudal rami included) 10.0 : 61.1 : 3.3 : 3.3 : 3.3 : 7.3 : 11.6. Caudal rami about 1.6 times longer than wide, shorter than in female. Caudal setae with proportional lengths as in female, except for seta VI 2.6 times the length of caudal ramus, and dorsal seta VII 2/3 the length of seta VI.

Antennule with armature as for genus.

Antenna with seta on coxobasis long and plumose as in female; lateral armature on distal endopod segment differing from female, element III much stouter and element IV spiniform and curved, ornamented with dentiform processes along distal margin (arrowed in Fig. 23H); both elements shorter than in female.

Maxilliped as figured by Heron & Bradford-Grieve, except for endopodal segment (claw) with concave margin naked, not ornamented with short spinules pinnate as figured in their Fig. 18j.

Swimming legs 1–4 with armature and ornamentation as in female; terminal conical projections on P2–P3 enp-3 as in female. Sexual dimorphism expressed in reduced spine lengths on enp-3, most obvious in P3 (Fig. 23D, J) and in outer subdistal spine of P4 (Fig. 23E, M). Spine lengths on P2 enp-3 less reduced.

P5 (Fig. 23K) exopod not delimited from somite, shape and armature as in female, except for exopodal setae more spiniform and shorter than in female; small plumose seta arising from lateral surface of somite shorter than in female.

P6 represented by posterolateral flap closing off genital aperture on either side; covered by pattern of denticles as shown in Fig. 23L.

Spermatophore not observed.

TAXONOMY

O. scottodicarloi is the species previously referred to as *O. media* f. *minor* in the quantitative studies of Böttger-Schnack (1990a, b, 1994, 1995). Specimens from the Red Sea agreed in almost every detail with the original account of Heron & Bradford-Grieve (1995) from the Mediterranean, except for their smaller size, which is discussed below under 'Size variation'. The only other remarkable difference in female morphology between the two regions was the length to width ratio of caudal ramus, which was smaller in Red Sea specimens (2.3:1) than in the original account (about 3:1). [In the closely related *O. waldemari*, the length to width ratio of the caudal ramus turned out to be a variable character at closer examination (see below), which might also apply to *O. scottodicarloi*]. Other slight differences between the two descriptions, such as the surface ornamentation on mouthparts and antenna, as well as the minute element on 6th segment of antennule, which was not mentioned by Heron & Bradford-Grieve, are not regarded as substantial and/or might have been overlooked in the original account.

Males of *O. scottodicarloi* from the Red Sea differed from the original account in the ornamentation of maxillipedal claw, which was naked, while it had been described as having short spinules along the concave margin by Heron & Bradford-Grieve (1995, p. 40,

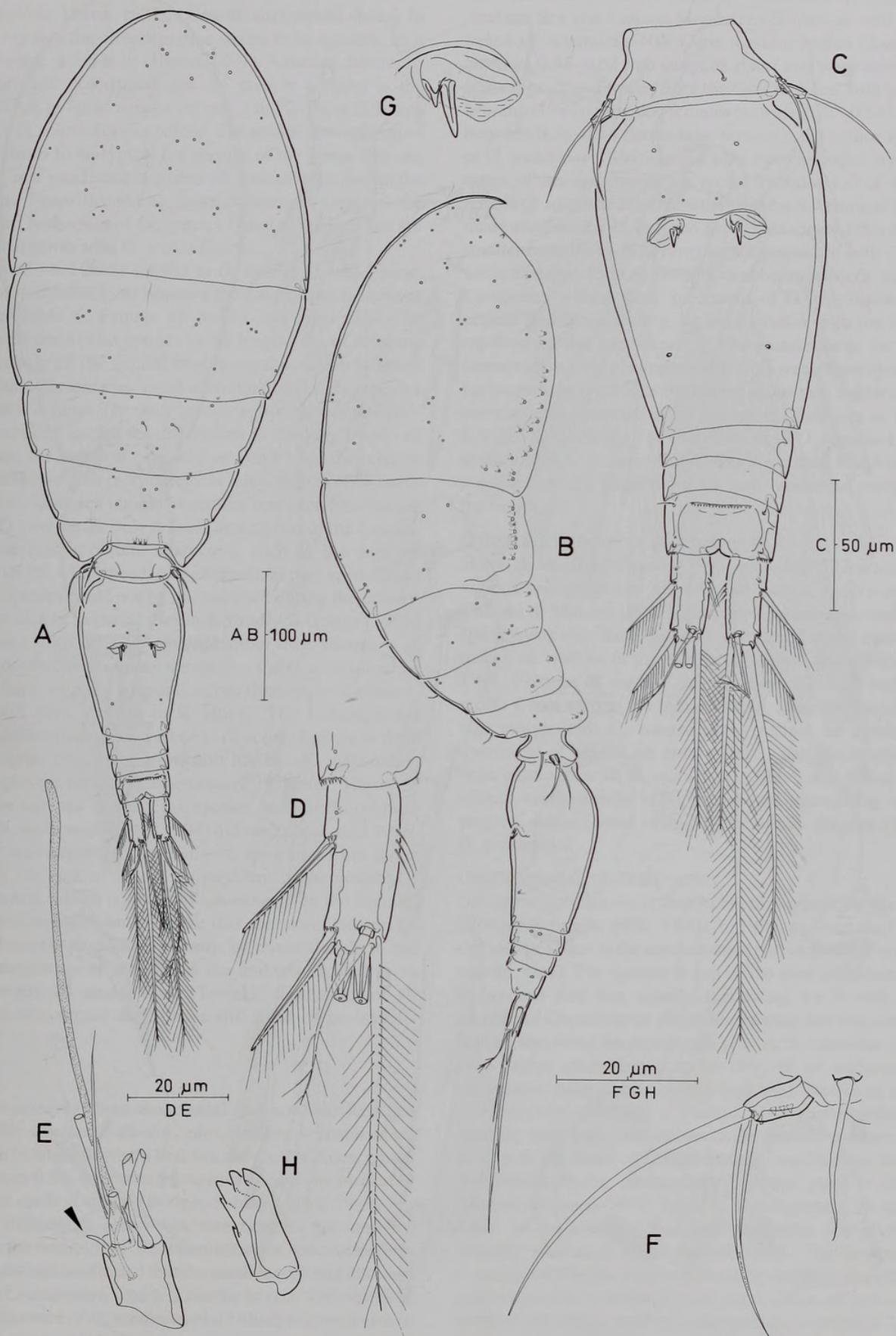


Fig. 22 *Oncaea scottodicarloi*, female (Red Sea) (A) Habitus, dorsal; (B) same, lateral (appendages omitted); (C) urosome, dorsal; (D) caudal ramus, dorsal; (E) antennule, 6th segment (short sensory element arrowed); (F) P5, dorsal; (G) P6; (H) mandible, blade C.

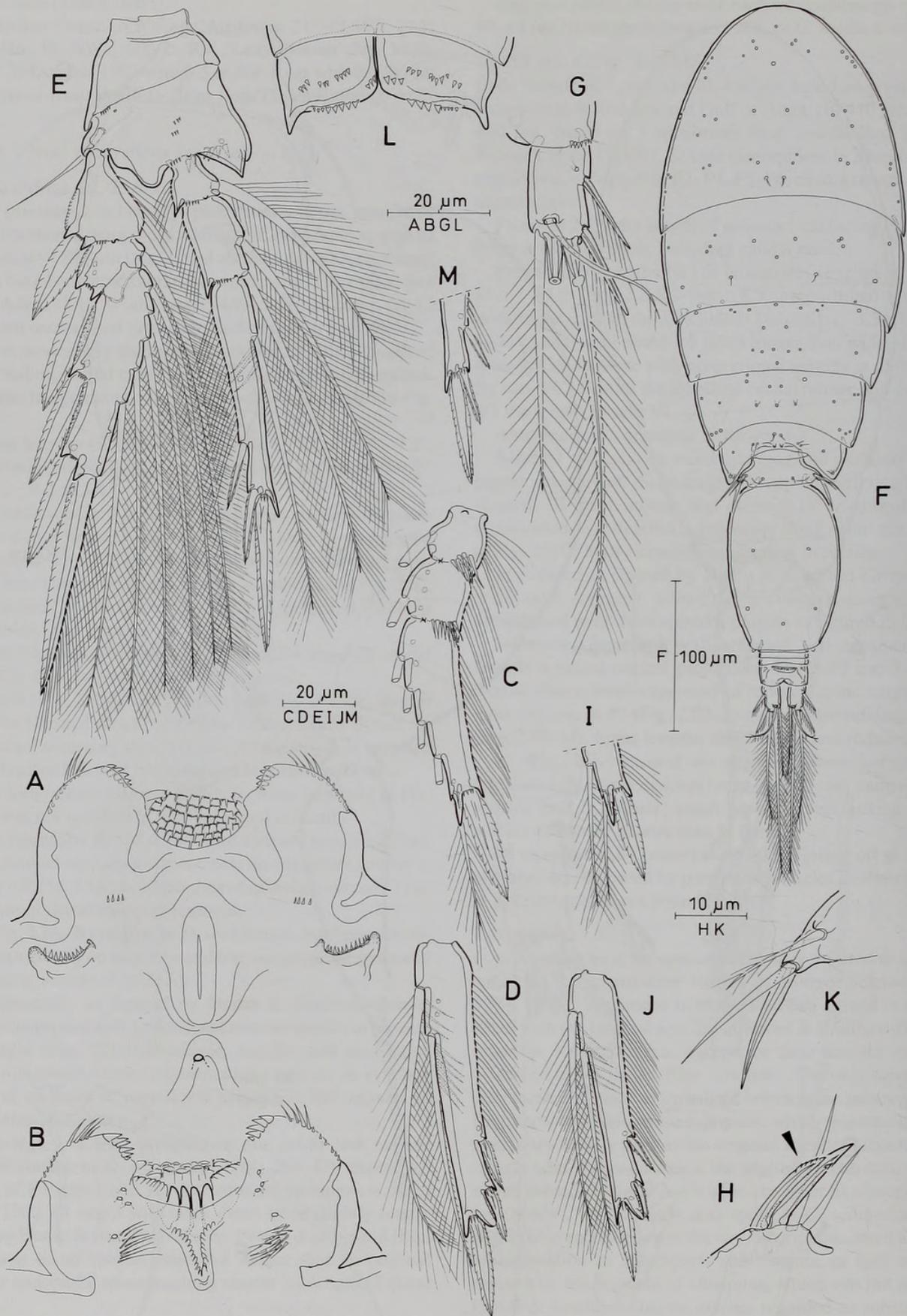


Fig. 23 *Oncaea scottodicarloi*, female (Red Sea) (A) Labrum, anterior; (B) same, posterior; (C) P1, endopod, anterior; (D) P3, distal endopod segment, anterior; (E) P4, anterior. – *Oncaea scottodicarloi*, male (Red Sea) (F) Habitus, dorsal; (G) caudal, ramus, dorsal (seta V not drawn); (H) antenna, lateral armature of second endopod segment (ornamentation of seta IV arrowed); (I) P1, distal part of endopod; (J) P3, distal endopod segment; (K) P5, dorsal; (L) P6; (M) P4, distal part of endopod.

Fig. 18j). Males of oncaeid species usually exhibit a naked maxillipedal claw, with few exceptions only [*Epicalymma schmitti* and *Oncaea englishi* (Heron, 1977); *O. mollicula* (unpubl. data)]. In the case of *O. englishi* the ornamentation seems to be variable, as it was lacking in some individuals (Heron, 1977). A further difference between the original description and the present account is the sexual dimorphism in spine lengths on enp-3 in P2–P4, which was not reported for *O. scottodicarloi* before. The sexual dimorphism of this character seems to be typical for species of the genus *Oncaea* s.str., however, as it was found in almost all species described in the present account. Notwithstanding these differences between the two descriptions, both sexes of the species found in the Red Sea are regarded as conspecific with *O. scottodicarloi*.

O. scottodicarloi is closely related to *O. media*, *O. waldemari*, and *O. curta*. Major distinctions between the four species have been summarized in Table 5. Female *O. media* can most easily be separated from the three other species by the length ratio of urosome somites, particularly of the genital double-somite, which is much longer. This character enables rapid identification of the species during quantitative counts. The three remaining species are morphologically very similar, except for differences in the length ratio of urosome somites, the length of exopodal seta on P5 and the relative lengths of caudal setae. The morphological relationships of *O. curta* within this species complex remain uncertain, however. Sars' original account of *O. curta* is the only reliable description of the species. He described several important characters, such as the unequal exopodal setae on P5, which need to be affirmed, as they are difficult to discern. The species could not be re-examined during the present study due to the lack of material. Heron & Bradford-Grieve (1995) recorded *O. curta* from the Gulf of Naples, but their summary of morphological distinctions between the species and *O. scottodicarloi* was based on Sars' original account, rather than on own observations (G. Heron, pers. comm. to R. Huys). The authors noted several as yet undescribed species close to *O. scottodicarloi* in their samples from Naples, one of which probably had been *O. waldemari*, which is also present in the Mediterranean. However, Heron & Bradford-Grieve were not aware of this species, because the original description of *O. waldemari* (dated 1994) did not appear until 1996.

Males of *O. scottodicarloi* can easily be separated from those of *O. media* by the lack of sexual dimorphism in the coxobasal seta on the antenna, which is long and plumose as in the female. Males of *O. waldemari*, however, share this character and can be distinguished from *O. scottodicarloi* only by minor details in the form and ornamentation of seta IV on the antenna as well as in proportional lengths of caudal setae (Table 5). For males of *O. curta* corresponding sexual differences still need to be investigated.

SIZE VARIATION

Female *O. scottodicarloi* from the central and northern Red Sea were considerably smaller (0.48–0.52 mm, Böttger-Schnack *et al.*, 1989) than those from the southern Red Sea and Gulf of Aden, which measured between 0.54–0.61 mm (numerous specimens measured by the traditional method used by Böttger-Schnack *et al.*, 1989). No morphological differences other than size became apparent for specimens from the two regions. Re-examination of specimens from the central populations confirmed that the small morph had not been confused with *O. waldemari*, which is similar in size. The observed regional size difference of *O. scottodicarloi* (which occurred also in the males) does not seem to be a temporary phenomenon, as the lengths of specimens in the central Red Sea did not vary during different seasons. Generally, *O. scottodicarloi* seems to exhibit a wide range in body length: Heron & Bradford-Grieve reported

females between 0.59–0.72 mm, with distinct differences between different oceanic areas. Female *O. scottodicarloi* from the northern Arabian Sea and Eastern Mediterranean Sea as well as those collected of Australia's NW Cape (eastern Indian Ocean) measured between 0.58–0.62 mm (unpubl. data) and were thus in the upper size range of specimens from the Gulf of Aden. Itoh [in: Chihara & Murano (1997)] recorded females between 0.50–0.64 mm and males between 0.38–0.54 mm in size, however, the author was not aware of *O. waldemari*, which might have been included in the lower size range of his specimens. [A recent examination of two forms of female *O. scottodicarloi* from the Western Subtropical Pacific kindly made available by H. Itoh and S. Nishida showed that females of the smaller form (0.49–0.62 mm) were conspecific with *O. waldemari*, while the larger form (0.58–0.71 mm) belonged to *O. scottodicarloi*.] Compared to these data, specimens of *O. scottodicarloi* from the central Red Sea appear to be even smaller than the lowest values reported for this species so far. The occurrence of the small morph seems to be a local phenomenon for this area. A possible explanation for the reduced size of central populations may be the more extreme environmental conditions in the central Red Sea as discussed by Böttger-Schnack *et al.* (1989). Similar to *O. venusta* f. *venella*, the small morph of *O. scottodicarloi* in the central Red Sea seems to be a self-sustaining population, with no substantial recruitment from the South.

OTHER RECORDS OF *O. SCOTTODICARLOI*

Heron & Bradford-Grieve (1995) recorded *O. scottodicarloi* from various regions in the Atlantic and Pacific and recently Itoh [in: Chihara & Murano (1997)] described it from Japanese waters. The species was also found in great abundance in the Eastern Mediterranean as well as in the northern Arabian Sea (Böttger-Schnack, 1994, 1996, as *O. media* f. *minor*). Sewell (1947) had reported *O. media* f. *minor* from the Indian Ocean, however, the identity of his size morph with *O. scottodicarloi* cannot be confirmed as the specimens of Sewell are not available. The specimens might have been confused with *O. waldemari*, which was found to co-occur with *O. scottodicarloi* in both areas (see below). The identity of *O. media* f. *minor* (*sensu* Malt, 1982b) will be discussed below under *O. waldemari*.

GEOGRAPHICAL DISTRIBUTION

Oncaea scottodicarloi is distributed throughout the Red Sea proper (Böttger-Schnack, 1988, 1990a, b, 1995, as *O. media* f. *minor*) and can also be found in the northernmost part of the Gulf of Aqaba (own unpubl. data). The species is one of the most abundant oncaeids in the central Red Sea, usually accounting for 2–10% of the total number of Oncaeidae in the water column down to 450 or 1050 m depth, depending on region and season. In narrower depth layers, even higher percentages, up to 15%, of all oncaeids are found (epipelagic zone, winter, central Red Sea). Similar to *O. media*, *O. scottodicarloi* exhibited a 2-tailed horizontal distribution during summer, with high abundances in the central-northern Red Sea as well as in the Strait of Bab al Mandab and Gulf of Aden, but low abundances in the intermediate southern parts of the Red Sea (Böttger-Schnack, 1995: Table 6). Consequently, its relative abundance in the southern Red Sea was rather low (0.4/1.6%), but strongly increased again further south. The proportion of *O. scottodicarloi* in the Gulf was possibly underestimated, since samples in that area covered only the upper 250 m of the water column, thereby excluding a potential mesopelagic population. In Table 8 of Böttger-Schnack (1995), the abundance values of *O. scottodicarloi* in the uppermost depth zone (0–100 m) were inadvertently changed between stations. The correct data for *O. scottodicarloi* are given in Table 6 of the present account.

Table 6 Abundance (individuals beneath 0.25m²) of *O. scottodicaloi* adults in the Gulf of Aden and different regions of the Red Sea during summer 1987.

	Gulf of Aden		Bab al Mandab	South, shallow	South, deep	Red Sea Main Basin	
	631	633	717	708	703	Central	North
Stn.						682	663
Sampling Time	N	D	D	D	D	D	D
Total water depth (m)	1400	1300	250	190	970	1890	1200
Depth layer (m)							
0–100	2800	2000	5000	380	300	770	850
100–250	160	–	330	620*	81	220	380
250–450	–	–	–	–	91	350	620
450–1050	–	–	–	–	7**	28	130

Corrected data of Table 8 in Böttger-Schnack (1995)

D = Day; N = Night; – = no data; Stn. = Station number

* = Depth range 100–175m

** = Depth range 450–950m

VERTICAL DISTRIBUTION AND VERTICAL MIGRATION

In the Red Sea, *O. scottodicaloi* had an epi- and mesopelagic distribution mainly between the surface and 600 m depth in the Red Sea; individual finds occurred down to 1250 m. Females exhibited a bimodal vertical distribution pattern, with maximum abundances in the epipelagic zone (0–100m) and in the mesopelagic zone, at 200–400(450) m depth (Böttger-Schnack, 1990a, b and unpubl. data from summer 1987). The depth horizon of the two population centres varied seasonally, with the epipelagic mode shifting to shallower depth during winter, due to absence of a strong thermocline, as well as regionally, with the mesopelagic mode shifting to shallower depth in the South as compared to the central-northern area. In general, however, the bimodal pattern was consistent. Diurnal vertical migration of moderate intensity was observed only for the epipelagic part of the female population during autumn, which migrated upwards at night. During winter, the vertical migration behaviour of the species was not investigated.

In contrast to females, males of *O. scottodicaloi* exhibited a unimodal distribution pattern in the epipelagic zone, with highest densities in the upper 50 m (winter, summer) or in the 50–100 m zone (autumn). Within this depth zone, their diurnal vertical migration was stronger than in the females.

The mesopelagic population centre of *O. scottodicaloi* did not show a regional downward shift between the central and northern Red Sea in relation to the regional differences in oxygen profiles, as had been observed for other oncaeid exhibiting bimodal distribution patterns in the area, such as *O. mediterranea* and *Lubbockia squillimana* (Böttger-Schnack, 1990b). During summer, however, the lower part of the population occurred somewhat shallower in the southern Red Sea (200–300 m) than in the central-northern area (250–400/450 m) (own unpubl. data). This might be related to a corresponding regional shift in the depth of the oxygen minimum (Böttger-Schnack, 1995). However, as the sampling variability within each area was not investigated during the summer, the data are inconclusive.

In the shallow part of the southern Red Sea (SRS) and in the Strait of Bab al Mandab (BaM), both sexes of *O. scottodicaloi* were found more or less evenly distributed between 40 m and the near-bottom layer at 175 m (SRS) or occurred in maximum concentrations between 20–60 m depth (BaM) during summer (unpubl. data). In this area, the population occurred at the same depth as *O. waldemari*, but the two species were vertically separated from *O. media*, which was concentrated much shallower, at 0–20 m (BaM).

SEASONAL VARIATION IN ABUNDANCE (CENTRAL RED SEA)

O. scottodicaloi exhibited no consistent seasonal variation in

abundance in the central Red Sea, indicating that the species is not markedly influenced by seasonal inflow of southern Red Sea waters (Böttger-Schnack, 1995, see also above under 'Size variation').

Oncaea waldemari Bersano & Boxshall, 1994

Oncaea waldemari Bersano & Boxshall (1994): 29–41, Figs. 1–6.

Oncaea media f. *minor* Malt (1982b): 130–133, Figs. 1a–i, 2a–j, 3a–z', 4a–o, 5a–h.

TYPELOCALITY. Southern Brazilian shelf (31°40'–33°45'S, 51°00'–52°20'W).

PRELIMINARY NOTE. The type description by Bersano & Boxshall (1994) includes some inconsistencies between text and figures, in particular with regard to P5 exopod, that severely hampers a positive identification of the species. Re-examination of the type material of *O. waldemari* during the present study gave unequivocal evidence that specimens from the Red Sea are conspecific. The species is redescribed based on Red Sea specimens (figures) and the type material. It includes several morphological details which were not mentioned in the original account (e.g. labrum). Also, body dimensions of specimens from the Red Sea, calculated by the different methods used throughout this study, are provided. The urosome segmentation of a typical female Copepodid Stage V, which has been incorrectly described for oncaeid copepods in the literature before, is described and briefly discussed.

MATERIAL EXAMINED.

- (1) Southern Red Sea, 13° 40.0'N, 42° 37.4'E: Stn. 708; *R/V Meteor* leg 5/5: collected 05 August 1987 with MSN 0.05 mm net (Haul 47/3); depth 20–40 m; total water depth 190 m.
 - (a) 2 ♀♀ in alcohol (BMNH 1998.2816–2817).
 - (b) 2 ♀♀, 1 ♂ in alcohol (ZMH K-39583).
 - (c) 2 ♀♀, 3 ♂♂ dissected on slides; 2 ♀♀, 1 ♂ in alcohol (RBS).
- (2) Southern Red Sea, 13° 40.0'N, 42° 37.4'E: Stn. 708; *R/V Meteor* leg 5/5: collected 05 August 1987 with MSN 0.05 mm net (Haul 47/2); depth 40–60 m; total water depth 190 m.
 - (a) 2 ♂♂ in alcohol (BMNH 1998.2818–2819).
 - (b) 3 ♀♀, 3 ♂♂ (RBS).
- (3) Southern Brazilian shelf, 31° 40'–33° 45'S, 51° 00'–52° 20'W, collected between 1988–1991 with cylindrical-conical closing net (mesh size 0.15 mm); depth 0–25m: holotype ♀ (Stn. 319, BMNH 1994.6213), 2 ♀♀ paratypes (Stn. 309), 2 ♂♂ paratypes (Stn. 319) (BMNH 1994.6214–6223).
- (4) Eastern Mediterranean Sea, 34° 25.3'N, 26° 14.8'E, Stn. 35; *R/V Meteor* leg 5/1: collected 20 January 1987 with MSN 0.055 mm

- net (Haul 24/5); depth 0–50 m; total water depth 3400 m: 1 ♀ in alcohol (RBS).
- (5) Northern Arabian Sea, near Oman, 20° 44.3'N, 59° 40.5'E: Stn. 347; *RV Meteor* leg 5/3a: collected 05 April 1987 with MSN 0.05 mm net (Haul 8/1); depth 0–50 m; total water depth ca 2500 m: 5 ♀♀, 2 ♂♂ for length measurements (RBS).
- (6) Plymouth Sound, BMNH 1981.229, labelled *Oncaea media* (*sensu* Malt, 1982): 3 ♀♀, 2 ♂♂ in alcohol.
- (7) Adriatic Sea, 42° 38.5'N, 18° 02.0'E: Stn. 'Lokrum 100'; collected 26 September 1996 with 0.053 mm Nansen type net; depth 0–25 m, vertical haul (leg. F. Kršinić): 2 ♀♀ (1 ovigerous), 1 CV ♀, 1 ♂ in alcohol (RBS).
- (8) Eastern Indian Ocean, NW Cape Australia, 21° 49.86'S, 114° 30.3'E: Stn. B; NWC 005/2; *RV 'Lady Basten'* leg 1630; collected 26 October 1997 with 0.5 m WP-2 net with 0.073 mm mesh, vertical haul; depth 0–20 m (leg. D. McKinnon): 2 ♀♀ in alcohol (RBS).
- (9) Western Subtropical Pacific, off Sagami Bay (Japan), 34° 15.0'N, 139° 45.0'E: Stn. 1; *RV Tansei-Maru* leg KT-00-5; collected 09 May 2000 with Norpac net with 0.1 mm mesh; depth 0–200 m, vertical haul (leg. S. Nishida; H. Itoh): > 30 ♀♀ in alcohol for molecular analysis (RBS)

REDESCRIPTION. Note illustrations are based on 1 (c) and (7) (CV ♀).

ADULT FEMALE (Figs. 24–26).

Body length: 637 µm [Traditional method: 420–500 µm, based on 21 specimens].

Exoskeleton well chitinized. Prosome 2.7 times length of urosome, excluding caudal rami, 2.3 times urosome length including caudal rami. P2-bearing somite without conspicuous dorso-posterior projection in lateral aspect (Fig. 24B). Integumental pores on prosome as in Fig. 24A, B.

Proportional lengths (%) of urosomites 10.3 : 56.6 : 10.7 : 8.7 : 12.6. Proportional lengths (%) of urosomites and caudal rami 8.8 : 48.1 : 9.1 : 7.4 : 11.6 : 15.1.

Genital double-somite (GDS) of Red Sea specimens 1.7 times as long as maximum width (measured in dorsal aspect) and 1.7 times as long as postgenital somites combined (Fig. 24C); GDS length to width ratio of three female paratypes from Brazilian waters ranging between 1.6–1.7 : 1, larger than reported by Bersano & Boxshall (1.4:1). Armature of genital apertures represented by 1 spine and 2 small spinous processes, as figured by SEM-micrograph by Bersano & Boxshall (their Fig. 5D), the second minute one hardly discernible with light microscope in Red Sea specimens (Fig. 24H).

Anal somite shorter than caudal rami (Fig. 24C), 3/4 the length of caudal rami in Red Sea specimens; variable in paratype specimens due to differences in length of caudal rami (see below).

Caudal ramus (Fig. 24F) about 2.3 times as long as wide in Red Sea specimens, longer in paratypes, varying between 2.4–2.8 : 1. Seta VI longer than dorsal seta VII and less than twice the length of caudal ramus; seta VII distinctly longer than seta III.

Antennule (Fig. 24E) with armature formula as for genus, some elements missing in original account of Bersano & Boxshall (their Fig. 2A); pore pattern as figured (Fig. 24E).

Antenna 3-segmented (Fig. 25A). Coxobasis with row of long, fine spinules or setules near outer margin and with few additional denticles on proximal part of outer (exopodal) margin, not figured in the original account of Bersano & Boxshall.

Labrum (Fig. 25B, C) as for *O. venusta*, except for additional surface ornamentation (paired row of denticles) on anterior face, and integumental pockets either side of median swelling more pronounced (Fig. 25B).

Paragnaths (not figured) as in *O. venusta*.

Mandible (Fig. 25D) with surface of coxa unornamented; armature elements as for *O. venusta*, but dorsal blade with 2 additional dentiform processes along dorsal margin (not only one as figured by Bersano & Boxshall).

Maxillule (Fig. 25E) as for *O. venusta*, with the 3 innermost elements on outer lobe similar in length, not innermost one shortest, as erroneously figured by Bersano & Boxshall (their Fig. 3C).

Maxilla (Fig. 25F) and maxilliped (Fig. 25G) similar to *O. venusta*. Proximal basal seta of maxilliped slightly longer than distal one (Fig. 25G), not shorter, as erroneously figured by Bersano & Boxshall (their Fig. 3E).

Swimming legs 1–4 with armature as for genus, surface ornamentation as shown in Fig. 26A–D. Exopods and endopods with ornamentation and spine lengths similar to *O. venusta*, except for terminal spine on P4 endopod relatively longer and hyaline lamella more narrow (Fig. 26D).

P5 with small exopodal segment clearly delimited from somite (Fig. 24G), not fused as stated by Bersano & Boxshall (p. 35). Exopod slightly longer than wide, ornamented with minute subapical pore and bearing 2 naked setae nearly equal in length, inner one spiniform. Small naked seta arising from lateral surface of somite.

P6 (Fig. 24H) represented by operculum closing off each genital aperture; armed with a spine and 2 small spinous processes, smaller one hardly discernible in Red Sea specimens.

Egg-sacs paired, oval-shaped; each sac containing appr. 10–12 eggs (diameter ca 50 µm).

ADULT MALE (Fig. 27).

Body length: 454 µm [Traditional method: 340–360 µm, based on 6 specimens]. Sexual dimorphism in antennule, antenna, maxilliped, P1 and P3 (endopod), P5–P6, caudal ramus and in genital segmentation.

Proportional lengths (%) of urosomites (excluding caudal rami) 9.3 : 66.8 : 3.3 : 4.7 : 4.2 : 11.5; proportional lengths (%) of urosomites (caudal rami included) 8.3 : 59.6 : 3.3 : 4.2 : 3.8 : 10.0 : 10.8. Caudal rami about 1.4 times longer than wide, shorter than in female. Caudal setae with proportional lengths as in female, except for seta VI shorter than in female, about same length as seta VII and 2.0 times length of caudal ramus. The extreme shortness of seta VI recorded by Bersano and Boxshall (about half the length of seta VII, according to their Fig. 1D) could not be confirmed upon re-examination of male paratypes. Surface of genital flaps ornamented with several rows of small spinules and area of minute pits as in Fig. 27E.

Antennule (Fig. 27B) with armature as for genus, pore pattern as figured [distalmost element on segment 2 erroneously figured as belonging to segment 3 in original account, Fig. 2B of Bersano & Boxshall].

Antenna as in female, except for third spiniform element on lateral armature being somewhat stouter than in female and fourth element curved and ornamented with vestigial dentiform processes along distal margin (arrowed in Fig. 27H). Seta on coxobasis long and plumose as in female.

Maxilliped (Fig. 27C) similar to *O. venusta*.

Swimming legs 1–4 with armature and ornamentation as in female; sexual dimorphism expressed in terminal process on P1 enp-3, being relatively longer than in female (Fig. 27J), and in longer terminal conical projection on P3 enp-3, reaching 2/3 the length of outer distal spine (Fig. 27K).

P5 (Fig. 27G) exopod not delimited from somite, general shape and armature as in female, except for setae slightly shorter than in female; small naked seta arising from lateral surface of somite as in female.

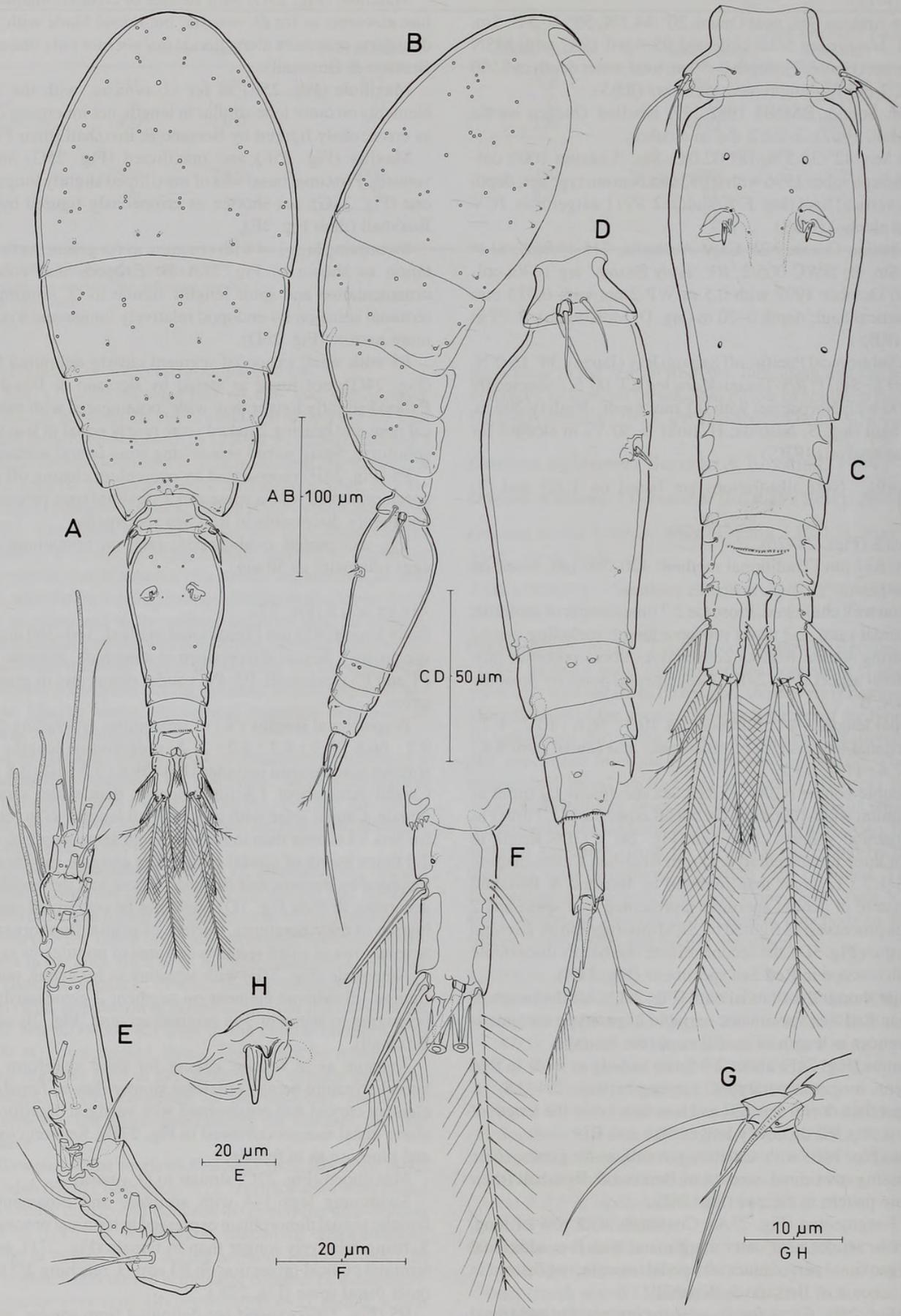


Fig. 24 *Oncaea waldemari*, female (Red Sea) (A) Habitus, dorsal; (B) same, lateral (appendages omitted); (C) urosome, dorsal; (D) urosome, lateral; (E) antennule; (F) caudal ramus, dorsal; (G) P5, dorsal; (H) P6.

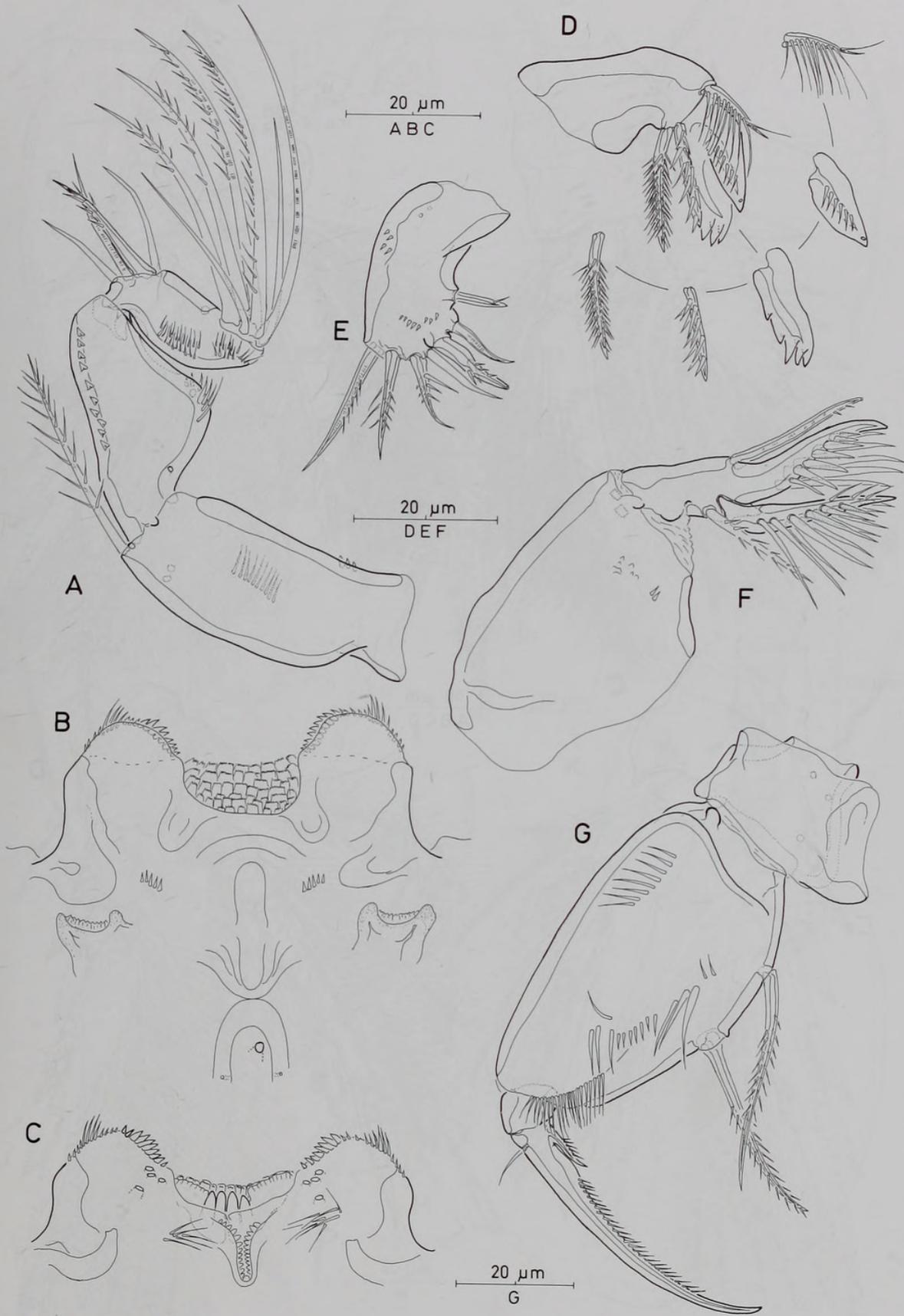


Fig. 25 *Oncaea waldemari*, female (Red Sea) (A) Antenna, posterior; (B) labrum, anterior; (C) same, posterior; (D) mandible, showing individual elements; (E) maxillule; (F) maxilla; (G) maxilliped.

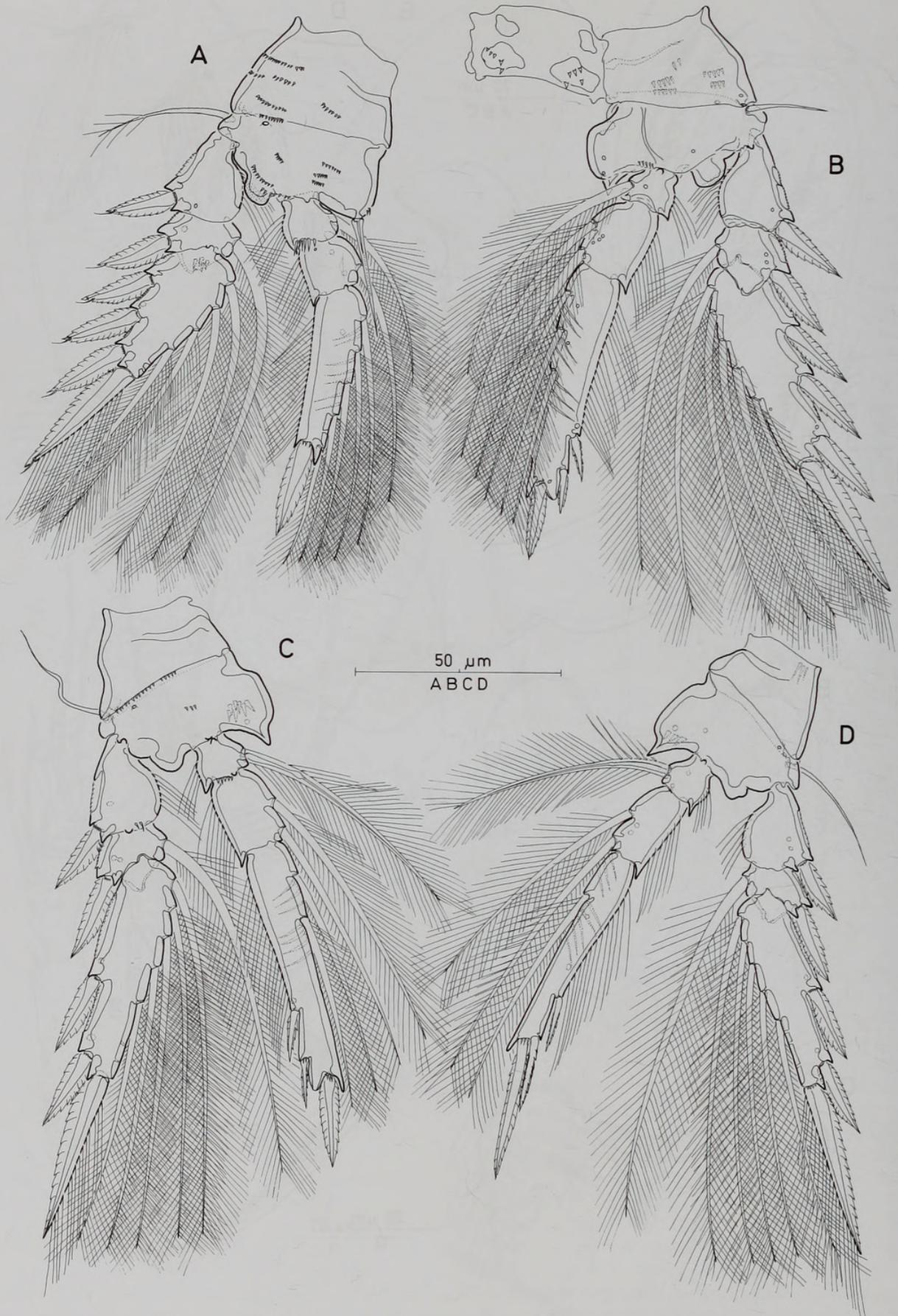


Fig. 26 *Oncaea waldemari*, female (Red Sea) (A) P1, anterior; (B) P2, posterior; (C) P3, anterior; (D) P4, anterior.

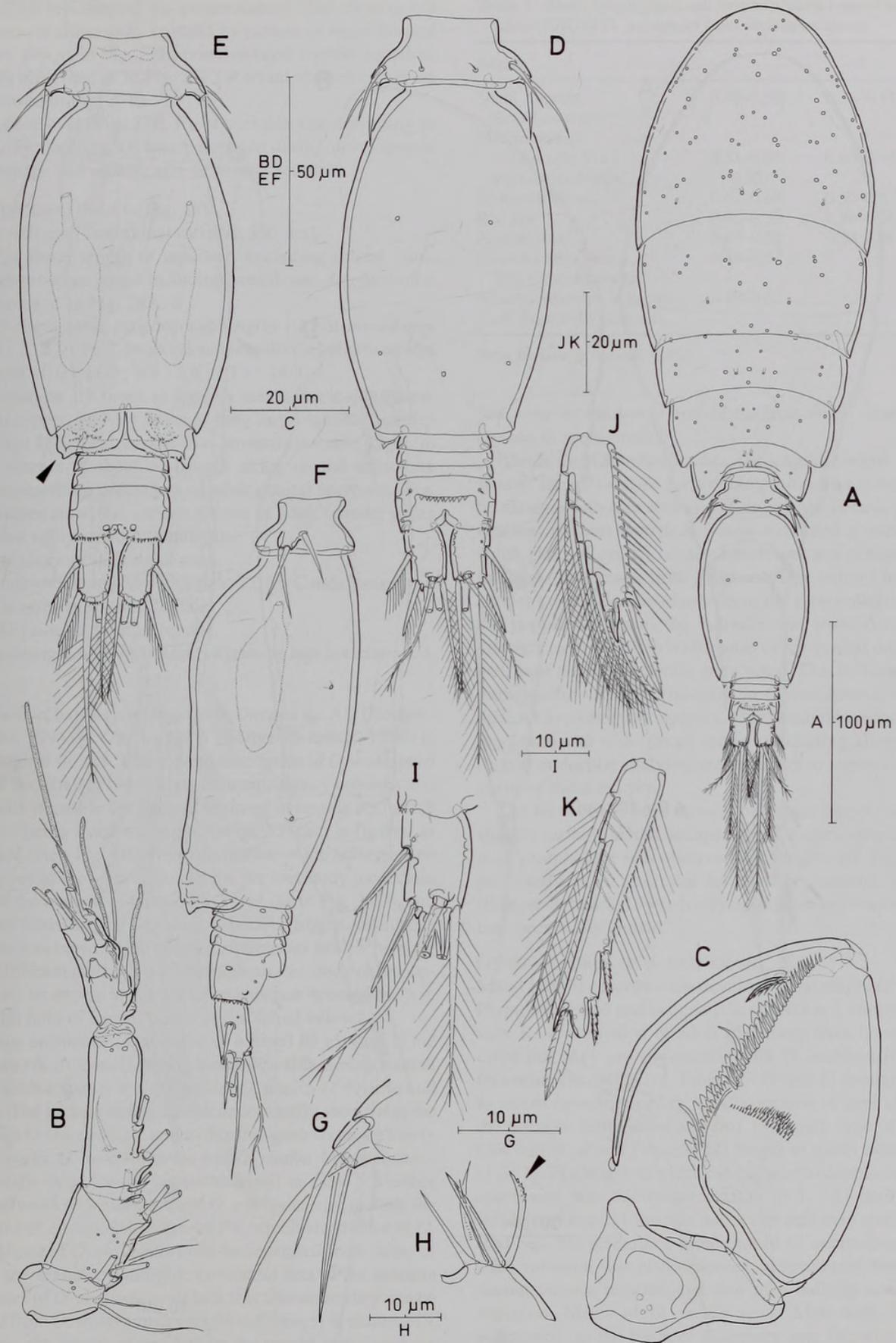


Fig. 27 *Oncaea waldemari*, male (Red Sea) (A) Habitus, dorsal; (B) antennule; (C) maxilliped, anterior; (D) urosome, dorsal; (E) urosome, ventral (spermatophores immature), modified tip of posterolateral corner on P6 arrowed; (F) same, lateral; (G) P5, dorsal; (H) antenna, lateral armature of distal endopod segment (ornamentation of seta IV arrowed); (I) caudal ramus, dorsal; (J) P1, distal endopod segment, anterior; (K) P3, distal endopod segment, anterior.

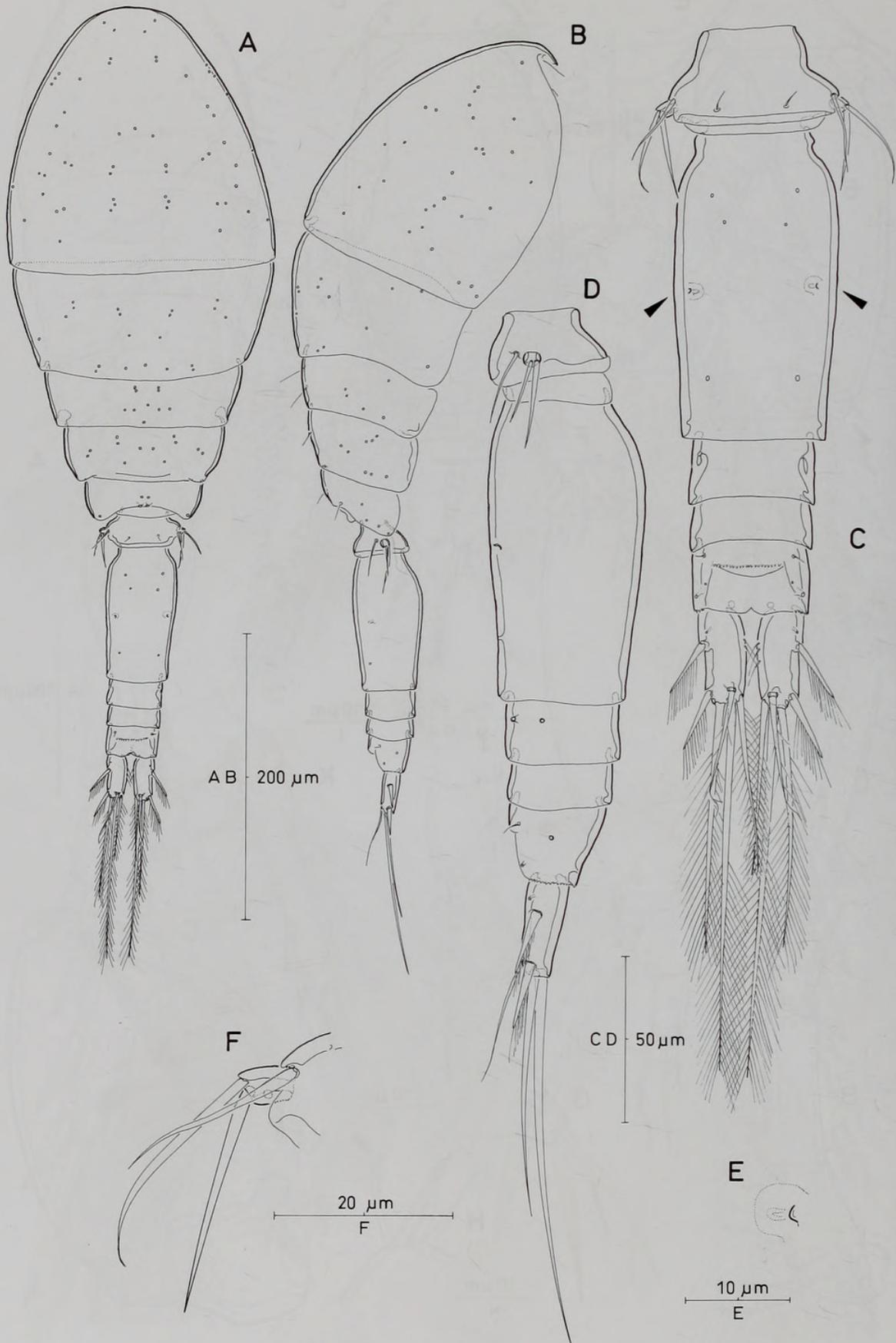


Fig. 28 *Oncaea waldemari*, female copepodid stage V (Adriatic Sea) (A) Habitus, dorsal; (B) same, lateral (appendages omitted); (C) urosome, dorsal, slit-like structures arrowed; (D) urosome, lateral; (E) slit-like structure; (F) P5, dorsal.

P6 (Fig. 27E) represented by posterolateral flap closing off genital aperture on either side; covered by pattern of denticles and area of minute pits as in Fig. 27E; posterolateral corners rounded, generally with bifid tips, as in Fig. 27F (aberrant stunted corner on right side arrowed in Fig. 27E).

Spermatophore oval (Fig. 27E, F), of variable size according to state of maturity; swelling of spermatophore during development not affecting shape and relative size of genital somite.

FEMALE COPEPODID STAGE V (Fig. 28).

Body length: 640 μ m [Traditional method: 550 μ m].

Prosoma 2.4 times length of urosome, excluding caudal rami, about 2.1 times urosome length including caudal rami. Integumental pores on prosoma as in Fig. 28A, B.

Urosome 5-segmented; proportional lengths (%) of urosomites 11.7 : 51.7 : 11.5 : 8.9 : 16.2. Proportional lengths (%) of urosomites and caudal rami 10.0 : 44.0 : 9.8 : 7.6 : 13.8 : 14.8.

Second urosomite 1.8 times as long as maximum width (measured in dorsal aspect) and 1.4 times as long as postgenital somites combined (Fig. 28C). Paired slit-like structure located close to dorso-lateral margin at about midlength along second urosomite (Fig. 28C), representing precursors of adult genital apertures (Fig. 28E). Pore pattern on dorsal surface similar to adult female; entire surface covered with numerous small pits.

Anal somite shorter than caudal rami.

Caudal ramus with length to width ratio 2.0 : 1. Caudal setae with proportional lengths as in adult female.

P5 (Fig. 28F) similar to adult female.

Antennule, antenna, mouthparts and swimming legs not examined.

TAXONOMY

Oncaea waldemari has been referred to as *Oncaea* sp. AD (Böttger-Schnack, 1994, 1995) or *Oncaea* sp. B (Böttger-Schnack, 1996) in previous ecological studies. The original description of *O. waldemari* by Bersano & Boxshall (1994) shows an inconsistency between text and figures with regard to the exopod segment of female P5, which is described as being fused to the somite (p. 35), but is figured as being delimited (their Fig. 1B). Re-examination of the holotype and female paratypes of the species during the present study gave clear evidence, that the exopod of female P5 is free (as in Fig. 24G), and that specimens from the Red Sea are conspecific. Slight differences in body dimensions between the two descriptions are mainly brought about by the different methods used throughout this study (telescoping of somites) or appear to be variable between specimens (e.g. length to width ratio of caudal ramus as discussed below).

Based on the erroneous assumption of a fused P5 exopod in the female, Bersano & Boxshall (1994) placed *O. waldemari* in a small group of oncaeids together with *O. petila*, *O. ovalis*, *O. brocha* and *O. compacta*. The present redescription undoubtedly shows that the species belongs to *Oncaea* s.str. and within this genus is most closely related to *O. curta*, *O. scottodicaloi* and *O. media*. Major distinctions between the three species are summarized in Table 5. Further differences between *O. waldemari* and *O. scottodicaloi* include the relative lengths of endopodal spines on P4, which are shorter in *O. waldemari*. Males of *O. waldemari* can be separated from those of *O. media* by the sexually dimorphic coxobasal seta of the antenna (Table 5). Males of *O. scottodicaloi* lack this character; they can be distinguished from *O. waldemari* by slight differences in element IV on the antenna, the length of seta VII on the caudal ramus and the ornamentation of the P6.

SIZE VARIATION

The body length of *O. waldemari* varies considerably in different geographic regions (Table 7). Lengths of specimens from the Red

Table 7 Body length (mm) and length to width ratio of female caudal ramus (CR) of *O. waldemari* from various locations.

Region	♀	♂	CR
South Atlantic, Brazilian waters*	0.49–0.58	0.36–0.41	2.4–2.8 : 1
Mediterranean			
(a) Adriatic Sea	0.51–0.60	0.40–0.46	2.4 : 1
(b) Eastern Medit.	0.50		
Plymouth Sound	0.62–0.69	0.50–0.52	2.5 : 1
Red Sea	0.42–0.50	0.34–0.36	2.3 : 1
Arabian Sea	0.47–0.52	0.34;0.38	no data
Eastern Indian Ocean, NW Cape Australia	0.48–0.54	–	2.2–2.4 : 1
Western Subtropical Pacific, off Sagami Bay (Japan)	0.49–0.62	–	no data

*after Bersano & Boxshall (1994)

Sea were in the lower end of the size range observed for other regions or were smaller.

Beside the difference in size, the length to width ratio of caudal ramus (Table 7) and the form of the genital double-somite seemed to be variable within an area as well as outside. Female paratypes of *O. waldemari* from Brazilian waters exhibited a variable length to width ratio of caudal ramus, which was not noticed the Red Sea material. Specimens from Plymouth (see below) had a somewhat shorter genital double-somite than the type collection, and within the populations from the Adriatic and from Australian waters, differences in length to width ratio of the genital double-somite, as well as of the caudal ramus, were noted. This indicates considerable intraspecific variation (morphs) in *O. waldemari*, which makes it difficult to identify the species. More detailed taxonomic studies on this small and widespread species, including alternative methods such as molecular analyses, are necessary to ascertain the taxonomic status of these morphs.

The form of the bifid corners of genital lappets on male P6 was slightly variable in Red Sea specimens. A corresponding variation in male morphology was observed in *O. media* (cf. Fig. 16C) and had previously been observed for another oncaeid, *Triconia hawaii* (Böttger-Schnack, 1999). It may be more widespread among oncaeids than previously known.

OTHER RECORDS OF *O. WALDEMARI*

Malt (1982b) described the developmental stages of *O. media* from Plymouth Sound and assigned the species to f. *minor* on the basis of size. Re-examination of adult specimens from her collection indicated that they are conspecific with *O. waldemari*, based on the following characters (cf. Table 5): (1) ratio of genital double-somite to rest of urosomites (2.0 : 1), (2) position of genital apertures (1/4 the distance from lateral margin), (3) length ratio of seta VI on CR (3/4 length of seta IV), and (4) length to width ratio of P5 exopod (1.3 : 1). The length to width ratio of genital double-somite of Malt's specimens was somewhat smaller (1.5 : 1) than in typical *O. waldemari* and its form was not as elongate as in specimens from the Red Sea, but resembled more that of *O. scottodicaloi*. However, such variation was also observed in specimens from the Adriatic during various seasons, and thus may indicate some intraspecific variation. Males of *O. media* sensu Malt were assigned to *O. waldemari* on the basis of antennary seta IV, which was slightly curved and setiform (cf. Fig. 27H), rather than being spiniform as in *O. scottodicaloi*.

The records of *O. waldemari* from very distant localities in tropical and temperate regions of the three great oceans indicate a world-wide distribution of the species. However, some morphological

differences were observed between these morphs, which need to be clarified.

DEVELOPMENTAL STAGE CV ♀ OF *O. WALDEMARI*

The developmental stages (NI–NVI, CI–CVI ♀ and ♂) of *O. waldemari* were described by Malt (1982b, as *O. media* f. *minor*), based on individuals reared in the laboratory and collected at sea. According to her report, the female CV exhibits a 4-segmented urosome (1 segment between genital double-somite and anal somite), which is very unusual among copepods exhibiting the full complement of urosomites in the adult. Typically, the number of somites between female CV and CVI does not change in female copepods possessing a genital double-somite because the addition of one abdominal somite from CV to CVI is compensated for by the fusion of the genital somite and the first abdominal somite in the female (e.g. Itoh & Nishida, 1995). Remarkably, the only other taxonomic report of copepodid stages of oncaeids by Björnberg (1972) also describes the female CV of an unidentified *Oncaea* sp. with a 4-segmented urosome. So both Malt and Björnberg must in fact have been dealing with a CIV. In the present study, late female copepodid stages of *O. waldemari* and related species, such as *O. venusta*, *O. mediterranea*, and *O. scottodicaloi*, were found with a 5-segmented urosome, which exhibited no genital apertures (cf. Fig. 28C, E). According to the general rule mentioned above, these stages should be regarded as the typical female CV. A more detailed re-examination of developmental stages of *O. waldemari* and other oncaeid species is in progress.

GEOGRAPHICAL DISTRIBUTION

O. waldemari was confined to the Gulf of Aden / Strait of Bab al Mandab area and the southernmost, shallow parts of the Red Sea. It was not found in the deep oceanic area of the southern Red Sea or further north in the central/northern regions (Böttger-Schnack, 1995, as *Oncaea* sp. AD). Thus, it cannot be regarded as a typical Red Sea species. In the Arabian Sea, it was present in somewhat greater numbers near Oman than in the central Arabian Sea (Böttger-Schnack, 1996, as *Oncaea* sp. B). The species is also present in the Eastern Mediterranean, but was not separated from the closely related *O. scottodicaloi* during earlier quantitative counts in that area (Böttger-Schnack, 1997, as *O. media* f. *minor*).

VERTICAL DISTRIBUTION

Both sexes of *O. waldemari* occurred in the lower epipelagic zone, with maximum concentrations between 20–60 m in the Gulf of Aden and the Strait of Bab al Mandab. In the southern, shallow region of the Red Sea (total water depth 190 m), the populations showed a strong tendency to submerge: they were generally found between 20–175 m, with maximum concentrations between 125–175 m (females) or 100–150 m (males).

Oncaea paraclevei sp. nov.

TYPE LOCALITY. Southern Red Sea, oceanic area, 15° 34.8'N, 41° 54.9'E, at 0–50 m; total water depth 970 m.

MATERIAL EXAMINED.

- (1) Southern Red Sea, 15° 34.8'N, 41° 54.9'E: Stn. 703; *R/V Meteor* leg 5/5: collected 03 August 1987 with MSN 0.05 mm net (Haul 39/5); depth 0–50 m; total water depth 970 m.
 - (a) holotype ♀ dissected on 11 slides (urosome partly damaged after documentation (ZMH K-39578a–j); paratypes: 6 ♀♀ in alcohol, some ovigerous (ZMH K-39579).
 - (b) additional paratypes: 1 ♀ dissected on 10 slides (BMNH 1998.2820), 5 ♀♀ in alcohol (BMNH 1998.2821–2825).
 - (c) additional paratypes: 1 ♂ dissected on 10 slides, 1 ♀ dis-

sected on 11 slides, 6 ♀♀ (1 ovigerous, 2 with spermatophores, 1 with small dorsal projection, 1 without dorsal projection) in alcohol (RBS).

- (2) Central Red Sea, 21° 25.53'N, 38° 01.91'E: Stn. 130; *R/V Valdivia* leg 29: collected 28 October 1980 with MSN 0.1 mm net (Haul 117/5); depth 0–20 m; total water depth ca 1960 m.
 - (a) 1 paratype ♀ in alcohol (BMNH 1998.2826).
 - (b) 2 paratype ♀♀ in alcohol (ZMH K-39580).
 - (c) 1 paratype ♀ dissected on 10 slides (RBS).
- (3) Northern Arabian Sea, near Oman, 20° 44.3'N, 59° 40.5'E: Stn. 347; *R/V Meteor* leg 5/3a: collected 05 April 1987 with MSN 0.05 mm net (Haul 8/1); depth 0–50 m; total water depth ca 2500 m: 2 ♀♀ in alcohol (RBS).

DESCRIPTION. Note illustrations are based on the holotype, except for habitus, maxilliped and labrum.

ADULT FEMALE (Figs. 29–31).

Body length (measured in lateral aspect; from anterior margin of rostral area to posterior margin of caudal rami, calculated as sum of individual somites): 770 µm [traditional method: 650–660 µm, based on 2 specimens].

Exoskeleton well chitinized. Prosome 2.1 times length of urosome, excluding caudal rami, 1.8 times urosome length including caudal rami. P2-bearing somite with dorso-posterior projection in lateral aspect (Fig. 29B), variable in conspicuousness according to degree of telescoping of somites (Fig. 29a–c). Integumental pores on prosome as indicated in Fig. 29A, B. Pleural areas of P4-bearing somite elongate and with rounded posterolateral corners.

Proportional lengths (%) of urosomites 9.4 : 58.5 : 9.9 : 10.4 : 11.8. Proportional lengths (%) of urosomites and caudal rami 7.9 : 49.2 : 8.3 : 8.7 : 9.9 : 15.9.

Genital double-somite oval-elongate, 1.6 times as long as maximum width (measured in dorsal aspect) and 1.9 times as long as postgenital somites combined (Fig. 29C); largest width measured at anterior third, lateral margins of genital double-somite rounded anteriorly, tapering posteriorly. Paired genital apertures located near dorsolateral margin at about 1/3 distance from anterior margin of genital double-somite; armature represented by 1 spine and 2 minute spinous processes (Fig. 29H). Double-curved sclerotization between genital apertures, varying in form as in Fig. 28d, e; pore pattern on dorsal surface as in Fig. 29C.

Anal somite 1.3 times wider than long; about 3/4 length of caudal rami (Fig. 29C). Anterior margin of anal opening (vestigial anal opening) with transverse row of minute denticles, which are variable in number, ranging between 4 (holotype) and 10. Other surface ornamentation as in *O. venusta*.

Caudal ramus (Fig. 29F) about 2.3 times as long as wide, variation within (Fig. 29F) and between specimens ranging between 2.1–2.4 : 1 (4 specimens). Surface ornamentation and length ratios of caudal setae as in *O. clevei*, except for longer outer terminal seta (IV), reaching 4/5 the length of inner terminal seta (V).

Antennule (Fig. 29E) with relative lengths (%) of segments measured along posterior non-setiferous margin 6.0 : 24.5 : 42.9 : 10.9 : 4.3 : 11.4. Armature formula as for genus.

Antenna (Fig. 30A) as in *O. clevei*, except for seta III on second endopod segment unipinnate.

Labrum (Fig. 30B,C) as in *O. clevei*, except for anterior surface lacking row of denticles on proximal part of each lobe.

Mandible (Fig. 30D) similar to *O. clevei*, except for number of dentiform processes along distal margin of blade C varying between 3 or 4 (Fig. 30D, d).

Maxillule (Fig. 30E), maxilla (Fig. 30F), and maxilliped (Fig. 30G) as in *O. clevei*.

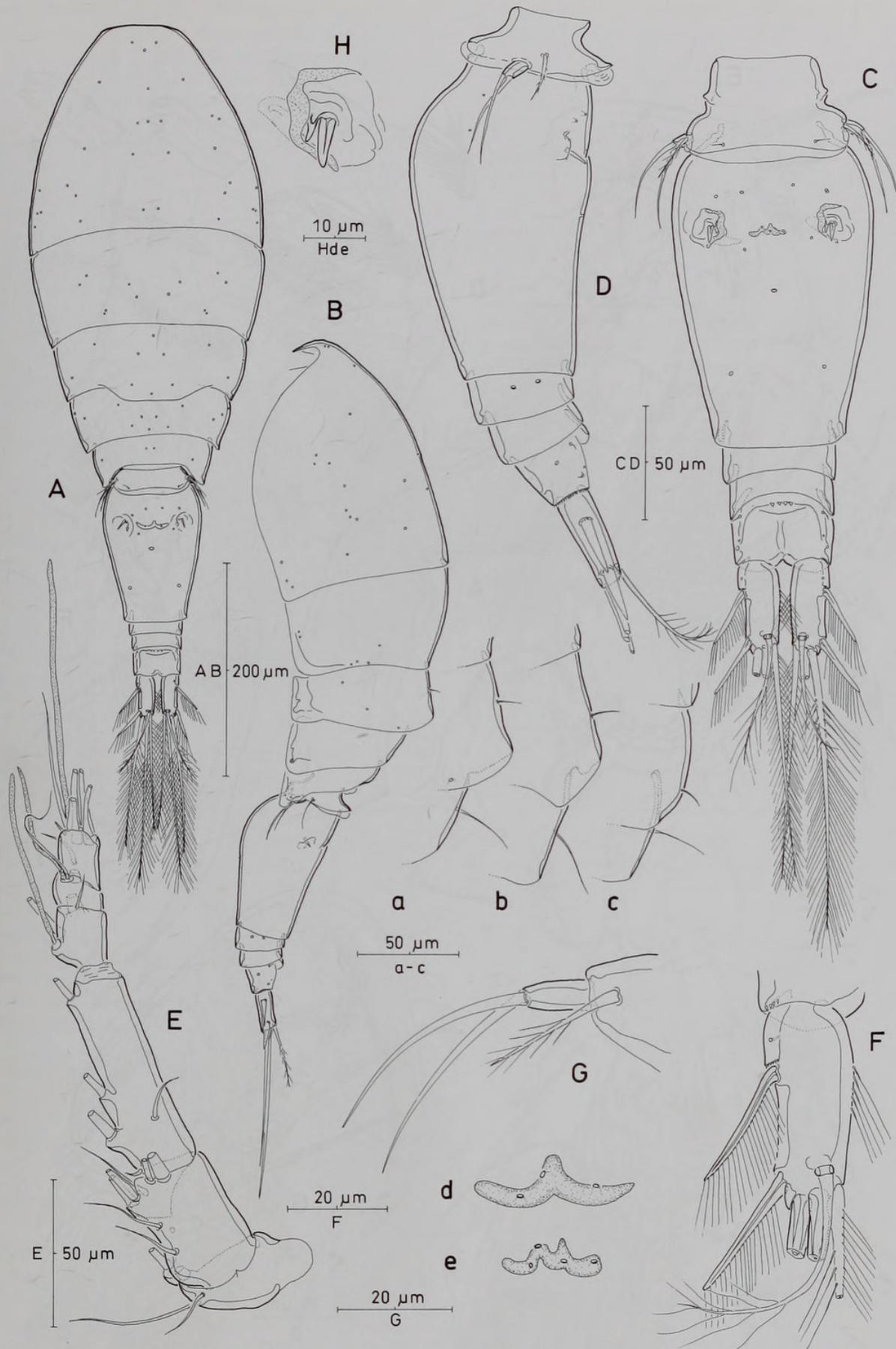


Fig. 29 *Oncaea paraclevei* sp. nov., female (Red Sea) (A) Habitus, dorsal; (B) same, lateral (appendages omitted) [a-c: different degrees of telescoping of somites, causing variation in conspicuousness of dorso-posterior projection on P2-bearing somite]; (C) urosome, dorsal, setae V and VI (right) not figured [d, e: variation in form of sclerotization between genital apertures]; (D) urosome, lateral; (E) antennule; (F) caudal ramus, dorsal; (G) P5; (H) P6.

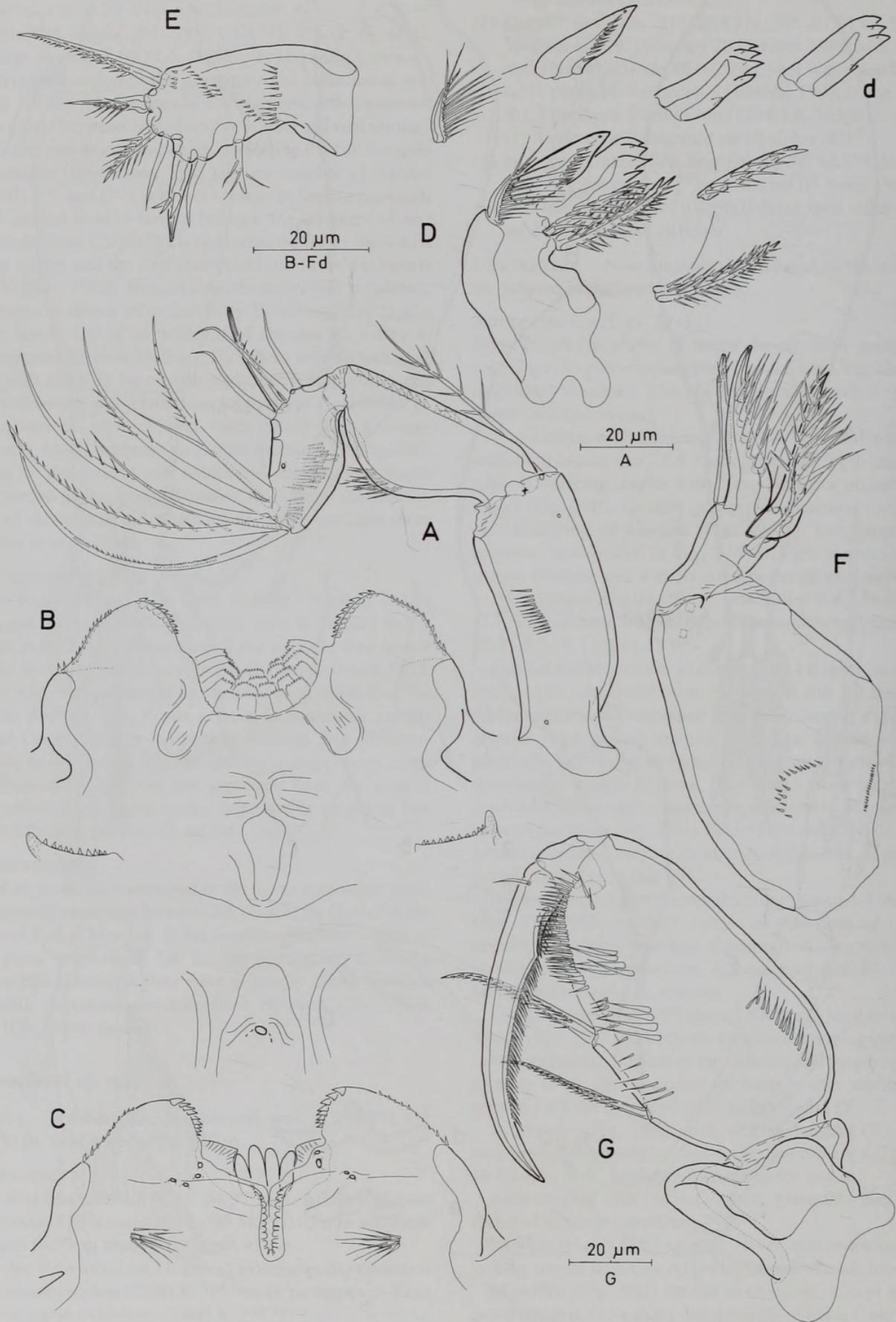


Fig. 30 *Oncaea paraclevei* sp. nov., female (Red Sea) (A) Antenna, anterior; (B) labrum, anterior; (C) same, posterior; (D) mandible, showing individual elements [d: blade C, showing variation in number of dentiform processes]; (E) maxillule; (F) maxilla; (G) maxilliped.

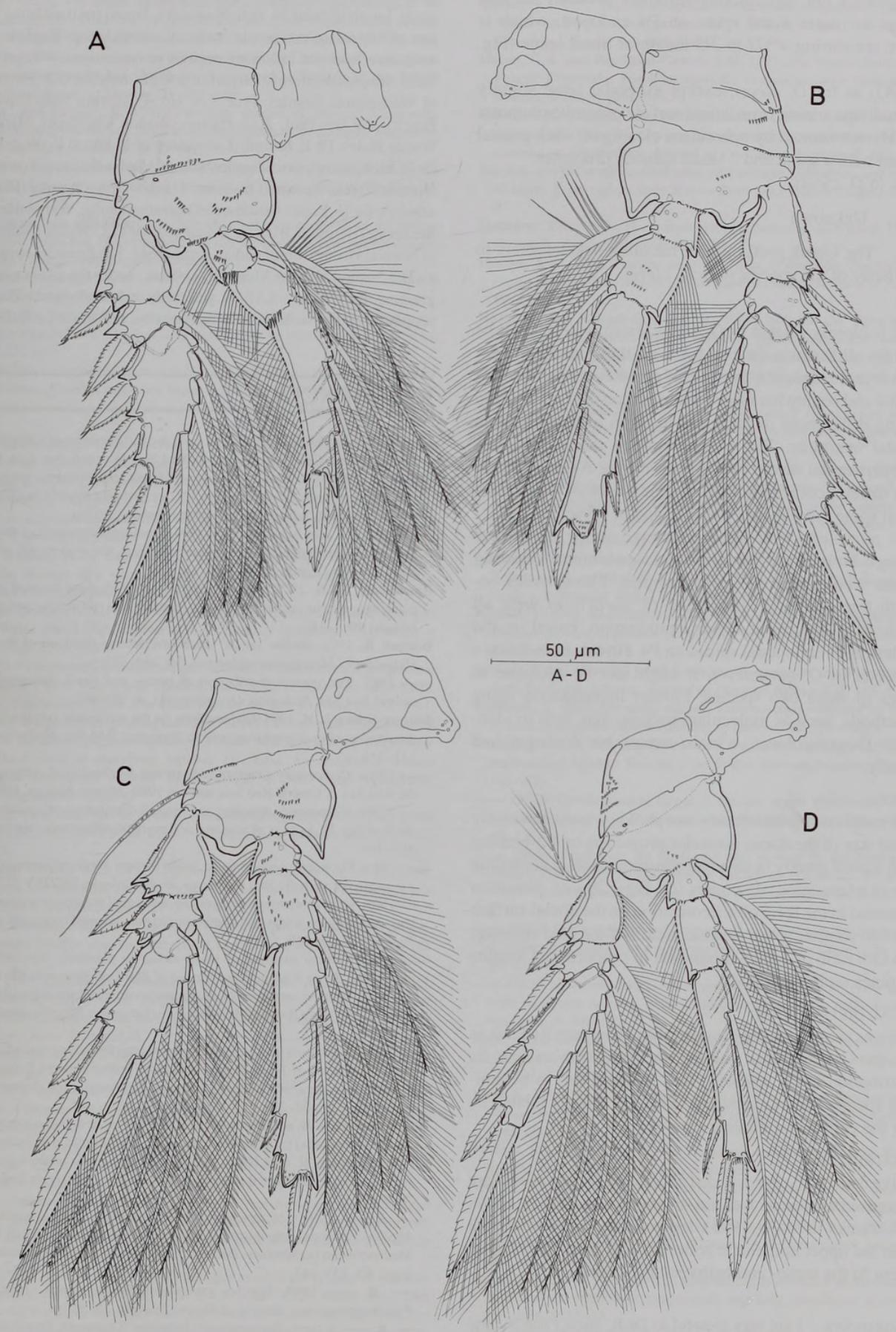


Fig. 31 *Oncaea paraclevei* sp. nov., female (Red Sea) (A) P1, anterior; (B) P2, anterior; (C) P3, anterior; (D) P4, anterior.

Swimming legs 1–4 (Fig. 30A–D) with armature as for genus and surface ornamentation as in *O. clevei*. Spine length of exopodal and endopodal segments not substantially different between the two species, except for outer distal spine on P4 endopod, which is slightly longer, measuring $> 1/2$ to $3/5$ length of distal spine (Fig. 30D).

P5 (Fig. 29G) as for *O. clevei*, except exopodal setae slightly curved, and small seta arising from lateral surface of somite plumose.

P6 (Fig. 29H) represented by operculum closing off each genital aperture; armed with a spine and 2 small spinous processes.

Egg-sacs as in *O. clevei*.

ADULT MALE. Unknown.

ETYMOLOGY. The Greek prefix *para-*, meaning beside, refers to the great similarity of the species with *O. clevei*.

TAXONOMY

O. paraclevei is closely related to *O. clevei*, from which it can be distinguished by differences in the form of the genital double-somite, which is more elongate, location of genital apertures, which are more medial and somewhat more posterior than in *O. clevei*, and by the resulting differences in form and location of sclerotization between genital apertures. The combination of these characters enables rapid separation of the two species during routine counts. Further minor differences are found in ornamentation of the labrum, in proportional spine lengths on P4 enp-3, and in P5 setae.

Males of *O. paraclevei* were not encountered during the present study, although ovigerous females and specimens carrying spermatophores were observed in the samples. Those males co-occurring with females of *O. clevei* and *O. paraclevei* were all assigned to the first species at closer examination, based on the proportional length of endopodal spines on P4. However, as this is a variable character in *O. paraclevei*, it might not be adequate to separate males of these two species. Further investigation using alternative methods, such as molecular analysis, may help to identify males of *O. paraclevei*, which cannot be distinguished morphologically.

SIZE VARIATION

O. paraclevei exhibited variable body morphology, most obviously in the form and size of the dorso-posterior projection on P2-bearing somite, which varied greatly in size and conspicuousness according to the degree of telescoping of somites (cf. Figs. 29a–c). Variation was also expressed in the form of sclerotization on the dorsal surface of genital double-somite, in the ornamentation of the anal opening, in length to width ratio of caudal ramus and in proportional lengths of terminal spines on P4 endopod.

GEOGRAPHICAL DISTRIBUTION

O. paraclevei was recorded from the central and southern Red Sea as well as from the Gulf of Aden and the northern Arabian Sea. Its potential distribution in the northern Red Sea still has to be confirmed, as the species was not separated from the closely related *O. clevei* during the earlier quantitative counts.

VERTICAL DISTRIBUTION

No quantitative data on the vertical distribution of *O. paraclevei* are available, because the species was not distinguished from *O. clevei* by Böttger-Schnack (1990a, b, 1995). It generally co-occurred with this species in the upper epipelagic zone, at 0–20 or 0–50 m depth, and was absent in the meso- and bathypelagic zones.

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