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Taxonomy of Oncaeidae (Copepoda: Cyclopoida) from the Red Sea. VII. *Oncaea cristata*, a new species related to the *ovalis*–complex, and a revision of *O. ovalis* Shmeleva and *O. bathyalis* Shmeleva from the Mediterranean

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Abstract: A new small species of oncaeid copepod, *Oncaea cristata*, is described from the mesopelagic zone of the Red Sea. The species is characterized by a very small outer distal spine on the endopods of swimming legs 2 and 3, being shorter than the terminal conical projection on the distal segment. Females of an oncaeid species sharing this distinct morphological character were described by Shmeleva (1969) from the Adriatic Sea under the name *O. ovalis*. However, the original description of *O. ovalis* by Shmeleva (1966), based on male specimens from the same area, exhibits distinct differences in the proportional spine lengths on swimming legs 2 and 3, suggesting that two different species may have been described under this name. Since the type material of *O. ovalis* is no longer extant, new material from the mesopelagic zone in the southern Adriatic Sea was examined during the present study in an attempt to clarify the taxonomic confusion surrounding *ovalis*-type oncaeids. Both sexes of three different *ovalis*-type oncaeids were found in the Adriatic, which are distinguished by distinct differences in endopodal spine lengths on legs 2 and 3: *ovalis*-type 1 is assigned to *O. ovalis* Shmeleva, 1966, based on (1) outer distal spine longer than the terminal conical projection on legs 2 and 3, and (2) outer distal spine equal in length to the distal spine on leg 2; *ovalis*-type 2 is characterized by very short outer distal spines on the endopods of leg 2 and 3, being shorter than the terminal conical projection in both legs and is described here as a new species, *O. crypta* sp. nov. being conspecific with *O. ovalis sensu* Shmeleva (1969) (female only); *ovalis*-type 3 is similar to the male of *O. bathyalis sensu* Shmeleva (1969), however, differences in the endopodal spine lengths between the two sexes in Shmeleva´s (1968) original description of the female and her subsequent redescription of both sexes in 1969 render it virtually impossible to make any positive statement as to the identity of genuine *O. bathyalis* or the potential conspecificity of the two sets of specimens she examined. Pending the discovery of material showing the same combination of characters figured by Shmeleva (1968) for female *O. bathyalis*, the species should be regarded as *species inquirenda*. The *ovalis*-type 3 from the Adriatic Sea is here described as a new species, *O. parabathyalis* sp. nov. and is conspecific with *O. bathyalis sensu* Shmeleva (1969) (male only). The newly described *O. cristata*, which is the sole representative of the *ovalis*-complex in the Red Sea, is a sibling species of *O. crypta* sp. nov. from the Mediterranean. The two siblings differ only in very few characters, such as the proportional spine lengths on the exopods of swimming legs 3 and 4 or the setal lengths on leg 5. Together they form a distinct group within the Oncaeidae which is not as closely related to the *ovalis-parabathyalis*-subgroup as previously assumed. *O. minia sensu* Olson (1949) and *O. ovalis sensu* Heron & Frost (2000) belong to the *crypta-cristata*-group and their taxonomic status is discussed. *O. ovalis sensu* Malt et al. (1989) and *O. bathyalis sensu* Malt et al. (1989) are placed in the *ovalis-parabathyalis*-group, but cannot unequivocally be designated to one of these two species. Preliminary zoogeographical data of the two newly recognized species groups within the *ovalis*-complex, the *ovalis*-

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parabathyalis-subgroup and the *crypta-cristata*-subgroup, are presented based on examination of *ovalis*-type copepods from the Atlantic, the Indian Ocean and the Pacific. The few ecological data known for *ovalis*-type oncaeids are summarized and the results point to a high numerical importance of this group in the mesopelagic microcopepod community of tropical and warm-temperate regions.

Résumé : *Taxinomie des Oncaeidae (Copepoda: Cyclopoida) de la Mer Rouge. VII.* Oncaea cristata*, une nouvelle espèce apparentée au complexe* ovalis*, et une révision de* O. ovalis *Shmeleva et* O. bathyalis *Shmeleva de Méditérranée.* Une petite espèce nouvelle d'Oncaeidae (Copepoda), *Oncaea cristata*, est décrite pour la zone mésopélagique de la Mer Rouge. L'espèce se caractérise par une très petite épine extérieure distale sur les endopodites des pattes natatoires 2 et 3, plus courte que la saillie terminale conique sur le segment distal. Des femelles ayant ce caractère morphologique distinctif ont été décrites par Shmeleva (1969) sous le nom de *O. ovalis* en Mer Adriatique. Toutefois, la description originale de *O. ovalis* (Shmeleva, 1966), basée sur des spécimens mâles de la même région, montre des différences concernant les longueurs relatives de l'épine extérieure distale sur les pattes natatoires 2 et 3, indiquant que deux espèces différentes peuvent avoir été décrites sous ce nom. Comme le matériel type d'*O. ovalis* n'existe plus, de nouveaux spécimens venant de la zone mésopélagique du sud de la Mer Adriatique ont été examinés, afin de tenter de supprimer la confusion taxinomique relative aux Oncaeidae de type *ovalis*. Les deux sexes de trois Oncaeidae différentes de type *ovalis* ont été trouvés en Mer Adriatique ; ces Oncaeidae se distinguent par la longueur de l'épine extérieure distale sur les endopodites des pattes 2 et 3: le type 1 *ovalis* est attribué à *O. ovalis* Shmeleva, 1966, basé sur une épine extérieure distale qui est (1) plus longue que la saillie terminale conique sur les pattes 2 et 3 et en même temps (2) aussi longue que l'épine distale sur la patte 2; le type 2 *ovalis* se caractérise par de très courtes épines extérieures distales sur les endopodites des pattes 2 et 3 lesquelles sont plus courtes que les saillies terminales coniques sur les deux pattes; il est décrit ici comme une espèce nouvelle, *O. crypta* sp. nov., conspécifique de *O. ovalis sensu* Shmeleva (1969) (seulement des femelles); le type 3 *ovalis* ressemble au mâle d'*O. bathyalis sensu* Shmeleva (1969); néanmoins, des différences entre les deux sexes concernant les longueurs de l´épine sur les endopodites mentionnées par Shmeleva (1968) dans la description originale de la femelle et affirmées de nouveau dans la description suivante des deux sexes en 1969, rendent pratiquement impossible d'affirmer l´identité d'*O. bathyalis* originale ou la conspecificité potentielle des deux séries de spécimens qu'elle a examinées. Jusqu´à la découverte de matériel montrant la même combinaison de caractères figurés par Shmeleva (1968) pour *O. bathyalis* femelle, l'espèce devrait être considérée comme une *espèce inquirenda*. Le type 3 *ovalis* de la Mer Adriatique est décrit ici comme une espèce nouvelle, *O. parabathyalis* sp. nov., et il est conspécifique de *O. bathyalis sensu* Shmeleva (1969) (seulement des mâles). L'espèce nouvelle, *O. cristata*, est le seul représentant du complexe *ovalis* en Mer Rouge et une espèce jumelle de *O. crypta* sp. nov. de Méditerranée. Elles ne diffèrent qu'en très peu de caractères spécifiques comme la longueur proportionnelle de l´épine extérieure distale sur les exopodites des pattes natatoires 3 et 4 et la longueur des soies sur la patte 5. Elles forment ensemble un groupe spécifique parmi les Oncaeidae, lequel n'est pas aussi étroitement lié au sous-groupe *ovalis-parabathyalis* qu'il était supposé. *O. minia sensu* Olson (1949) et *O. ovalis sensu* Heron & Frost (2000) appartiennent au groupe *crypta-cristata*, leur appartenance taxinomique est discutée. *O. ovalis sensu* Malt et al. (1989) et *O. bathyalis sensu* Malt et al. (1989) sont placées dans le groupe *ovalis-parabathyalis*, mais elles ne peuvent pas être attribuées incontestablement à l'une de ces deux espèces. Des données zoogéographiques préliminaires des deux groupes d'espèces nouvellement identifiés dans le complexe *ovalis*, le sous-groupe *ovalis-parabathyalis* et le sous-groupe *crypta-cristata*, sont présentées ici en les basant sur l'examen des individus de type *ovalis* de l'Atlantique, de l'Océan Indien et de l'Océan Pacifique. Le peu de données écologiques connu pour les Oncaeidae de type *ovalis* est résumé ici, les résultats indiquent l'importance numérique de ce groupe dans la communauté des microcopépodes des couches mésopélagiques.

Keywords : Copepoda, Oncaeidae, *ovalis*-type, *Oncaea cristata* sp. nov., *O. crypta* sp. nov, *O. parabathyalis* sp. nov., Taxonomy, Red Sea, Mediterranean Sea, Plankton

INTRODUCTION

Oncaeid microcopepods are important members of oceanic copepod communities, occurring from low to high latitudes (e.g. Judkins, 1980; Star & Mullin, 1981; Cowles et al., 1987; Richter, 1994; Metz, 1995; see also Paffenhöfer, 1993) and from epi- to bathypelagic zones (e.g. Boxshall, 1977a; Wishner, 1979; Roman et al., 1985; Yamaguchi et al., 2002). In contrast to other microcopepod taxa, such as calanoids and the cyclopoid family Oithonidae, which are most abundant in the epipelagic zone, maximum concentrations of oncaeid copepods have been found to occur over extended depth ranges, resulting in a strong increase of their relative abundance with increasing depth. In midwater layers between 100 m and 1000 m or deeper, oncaeids

usually account for more than 50% and up to 90% of all copepods sampled with fine mesh nets (e.g. Böttger-Schnack, 1994; Kršinic, 1998; Kršinic & Grbec, 2002; Yamaguchi et al., 2002).

The taxonomic diversity of the family Oncaeidae, as defined by Huys & Böttger-Schnack (1996/1997), has been increasingly recognized during the past years (e.g. Boxshall, 1977;, Heron, 1977; Heron et al., 1984; Heron & Bradford-Grieve, 1995; Böttger-Schnack, 1999, 2001; Heron & Frost, 2000), including the importance of sibling species within the family (Böttger-Schnack et al., 2004). Due to their great morphological similarity, recognition of oncaeid species requires detailed knowledge of all their taxonomic characters, including mouthparts and ornamentation structures, which are difficult to examine in these small-sized copepods. Detailed taxonomic investigation (Heron & Bradford-Grieve, 1995; Heron & Frost, 2000; Böttger-Schnack, 2001) recently demonstrated that many of the allegedly well known species, such as *Triconia conifera* (Giesbrecht, 1891) and *Oncaea media* Giesbrecht, 1891, in reality represent a complex of distinct, yet closely related, species.

Literature data suggest that among the numerous mesopelagic oncaeid species known (e.g. Heron, 1977; Heron et al., 1984; see also Malt, 1983) small specimens of the *ovalis*-type (size range of 0.35-0.5 mm) have a wide zoogeographical and vertical distribution. They have been recorded from very distant localities in the world ocean, such as the Mediterranean (e.g. Shmeleva, 1966, 1968, 1969; Malt et al., 1989; Böttger-Schnack, 1997; Kršinic, 1998), the Red and Arabian Seas (Böttger-Schnack, 1990a, b, 1995, 1996), the NW and NE Pacific (Heron & Frost, 2000; Nishibe & Ikeda, 2004) and the Antarctic (cf. Metz, 1993, as *Oncaea* "mini", R. Böttger-Schnack, unpubl.). The depth distribution of *ovalis*-type oncaeids extends over a vertical range from the upper 180 m (Heron & Frost, 2000) down to a maximum depth of 3800 m (Sargasso Sea; R. Böttger-Schnack, unpubl. data). However, as the level of species identification is still unsatisfactory, it is highly probable that different oncaeid species have been recorded under the name *O. ovalis* in the literature.

As part of an ongoing taxonomic study of the oncaeid fauna of the Red Sea (see Böttger-Schnack et al., 2004 for review), the *ovalis*-type oncaeid occurring in this area was examined in detail. The species was characterized by very short outer distal spines on the endopods of P2 and P3, being shorter than the terminal conical projection, which is similar to the female of *Oncaea ovalis* described by Shmeleva (1969), but differs from the original description of *O. ovalis* Shmeleva (1966), which was based on male specimens (see below). Thus, the Red Sea *ovalis*-type oncaeid could not unequivocally be identified due to the apparent discrepancies in Shmeleva´s description.

Oncaea ovalis was originally described by Shmeleva (1966) based on male specimens collected in the southern Adriatic Sea. In a subsequent account, Shmeleva (1969) redescribed the species from the same area and included a description of the female. The two sexes of *O. ovalis sensu* Shmeleva (1969) differ considerably in proportional spine lengths on the endopods of the second and third swimming leg (referred to as P2 and P3 hereafter), with the outer distal spine being distinctly longer than the terminal conical projection in the male (1969: fig. 9g, h), while they are shorter than (or about as long as) the projection in the female (1969: fig. 8g, h). Since oncaeid copepods usually do not exhibit any significant sexual dimorphism in proportional length of endopodal spines [for exceptions see Heron et al., 1984 (their text p. 476, fig. 14D: male *O. delicata* Heron, English & Damkaer, 1984, terminal spines on P2 endopods shorter than in female) and Böttger-Schnack, 2001 (her text p. 37, 46, figs. 7A-F: male *O.venusta* forma *typica* and f. *venella*, distal process on P1 and terminal conical projection on P2 and P3 longer than in female)], it seems likely that the female described by Shmeleva (1969) is not conspecific with the original male of *O. ovalis* (cf. Shmeleva 1966). Other taxonomic characters described by Shmeleva (1969) cannot be used for comparison between the two sexes, because they are either sexually dimorphic (maxilliped, urosomites) or were incompletely described by the author (antenna, antennule). The type material of *O. ovalis* is no longer extant.

In order to clarify the taxonomic confusion surrounding *ovalis*-type oncaeids, new material from the type locality of *O. ovalis* in the southern Adriatic Sea, kindly made available by F. Kršinic (Plankton Lab. Dubrovnik, Croatia), was examined during the present study. Three different species of the *ovalis*-type were found which - apart from many other morphological differences - differed distinctly in proportional spine length on the endopods of P2 and P3. *Ovalis*-type 1 was similar to the male described by Shmeleva (1966), showing a unique combination of two endopodal characters: (1) the outer distal spine on P2 and P3 is longer than the terminal conical projection, and (2) the outer distal spine is as long as the distal spine on P2 (Shmeleva, 1966, fig. 9g). This species is here regarded as conspecific with *O. ovalis* s. str. *Ovalis*-type 2 exhibited reduced outer distal spines on the endopods of P2 and P3, being shorter than the conical projection, and is here described as a new species, *O. crypta* sp. nov. This species is here regarded as conspecific with Shmeleva´s (1969) female erroneously described under the name of *O. ovalis*.

Ovalis-type 3 from the Adriatic Sea was similar to *ovalis*-type 1 in showing the outer distal spine on P2 and P3 to be longer than the terminal conical projection, but differed in the second endopodal character because it exhibited an outer distal spine on P2 being only about half the

length of the distal spine. The same combination of endopodal characters is found in Shmeleva´s (1969) male of *Oncaea bathyalis*, but differs from the original description of female *O. bathyalis* Shmeleva (1968) which was designated as the holotype. In her original account, Shmeleva (1968) described both sexes of *O. bathyalis* from the southern Adriatic Sea, providing figures of the general habitus and some appendages (maxilliped, antennule, antenna) for both sexes, but including figures of the swimming legs for the female only (1968: figs 2.6-2.9). In her subsequent redescription of the species, Shmeleva (1969) figured the leg armature for both sexes. The male of *O. bathyalis sensu* Shmeleva (1969) differs from the female in the proportional length of the outer distal spine on the endopod of P2, being longer than the terminal conical projection (1969: fig. 13g), while this spine is only about as long as the conical projection in the female (1968: fig. 2.7, 1969: fig. 12g). The endopodal spine lengths on P3, on the other hand, showed the outer distal spine to be longer than the projection and were figured similarly for both sexes (1968: fig. 2.8, 1969: figs 12h, 13h). The discrepancies between the two sexes in Shmeleva´s (1968) original description of the female and her subsequent redescription of both sexes in 1969 render it virtually impossible to make any positive statement as to the identity of genuine *O. bathyalis* or the potential conspecificity of the two sets of specimens she examined. A species showing the combination of endopodal characters described for female *O. bathyalis sensu* Shmeleva (1968) was not found in the Adriatic Sea during the present study, but may well be present upon examination of oncaeid copepod material from different depth layers and/or seasons. Pending the discovery of material showing the combination of characters described by Shmeleva (1968) for female *O. bathyalis*, the species should be regarded as *species inquirenda*. The *ovalis*-type 3 from the Adriatic Sea, is described here as a new species, *O. parabathyalis* sp. nov., and regarded as conspecific with *O. bathyalis sensu* Shmeleva (1969) (male only).

Neotype and type material of the three *ovalis*-type species from the Mediterranean (re)described here were designated by using specimens from the type locality of *O. bathyalis* and *O. ovalis* in the southern Adriatic Sea. Presorted specimens from the eastern Mediterranean collected during earlier ecological studies (Böttger-Schnack, 1997) were also used as reference material. The taxonomic descriptions presented here included all mouthparts and details of ornamentation, thus enabling unequivocal identification of the three mediterranean species and their future separation from other representatives of the *ovalis*-complex occurring elsewhere in the world.

The *ovalis*-type oncaeid from the Red Sea represents a sibling species of *O. crypta* sp. nov. from the Mediterranean and is described as a new species, *O. cristata* sp. nov., herein. The two siblings differ in very few morphological characters, such as the proportional lengths of exopodal spines on P3 and P4 or the lengths of P5 setae, and microscopical examination is required for their unequivocal species identification. Together the two species form a distinct subgroup within the *ovalis*-complex, the *crypta-cristata*-subgroup, which resembles the *ovalis-parabathyalis*-subgroup merely in general habitus but is morphologically not as closely related to this group as previously assumed. Preliminary considerations about the phylogenetic relationships of the *ovalis-parabathyalis*-subgroup within the Oncaeidae had been presented during an earlier phylogenetical study (Böttger-Schnack & Huys, 1998). The phylogenetic relationships of the *crypta-cristata*-subgroup, on the other hand, still need to be investigated, as they had not been included in the study of Böttger-Schnack & Huys (1998). *O. ovalis sensu* Malt et al. (1989) and *O. bathyalis sensu* Malt et al. (1989) are placed in the *ovalis-parabathyalis*-subgroup, but cannot unequivocally be designated to one of these two species. *O. minia sensu* Olson (1949) [Ms] and *O. ovalis sensu* Heron & Frost (2000) belong to the *crypta-cristata*-subgroup and their taxonomic status is discussed. First zoogeographical data of the two newly recognized species groups within the *ovalis*-complex, the *ovalis-parabathyalis*-subgroup and the *crypta-cristata*-subgroup, are presented by examination of *ovalis*-type copepods from various localities in the Atlantic, the Indian Ocean and the Pacific. The few ecological data known for *ovalis*-type oncaeids are summarized.

Material and Methods

Oncaeid microcopepods were collected with a multiple opening-closing net (Weikert & John, 1981) with a mesh size of 0.055 mm during *R/V Meteor* cruise 44/2 (March/April 1999) in the northernmost Red Sea and the Gulf of Aqaba (Fig. 1). The sampling programme was part of an ecological and taxonomic study on the microcopepod fauna in the Gulf of Aqaba (Böttger-Schnack et al., 2001), conducted within the frame of a multidisciplinary research programme directed towards the impact of biological processes during early spring in the Gulf (Pätzold et al., 2000; Sommer et al., 2002). Presorted oncaeid specimens collected with the same equipment during cruise 5 of *R/V Meteor* in 1987 along a north to south transect in the Red Sea proper (Böttger-Schnack, 1995), in the eastern Mediterranean (Böttger-Schnack, 1997) and the northern Arabian Sea (Böttger-Schnack, 1996) were also included in the taxonomic study (Fig. 1, Table 1a). Data on the vertical distribution of *ovalis*-type oncaeids summarized here are based on earlier ecological investigations of the microcopepod communities in the various regions of the Red Sea, the eastern Mediterranean and the northern Arabian Seas, and

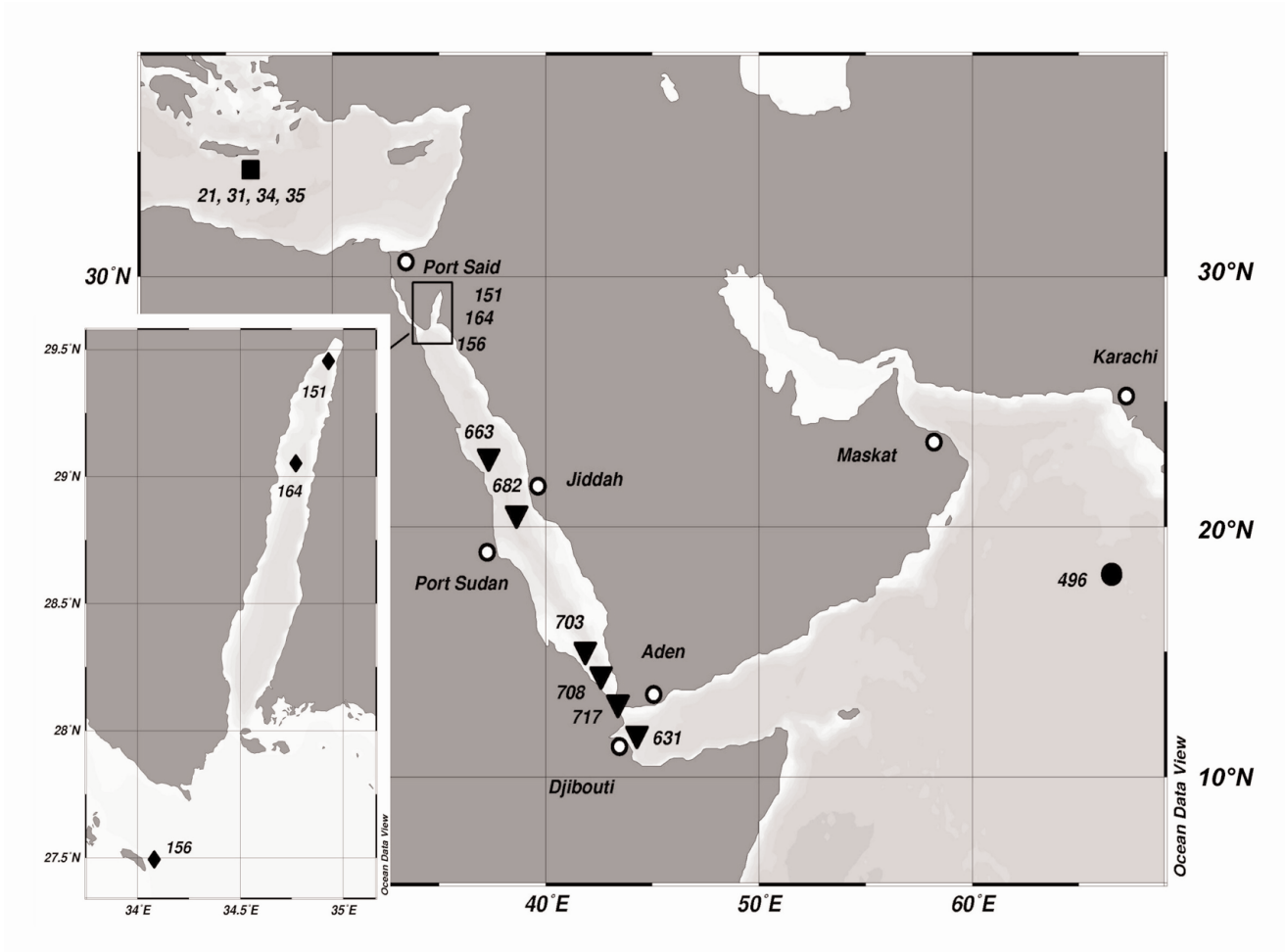

Figure 1. Location of stations in the Red Sea and adjacent areas: ▼ = METEOR-Cruise 5/5, July/August 1987; ◆ = METEOR-Cruise 44/2, March 1999; ● = METEOR-Cruise 5/3b, May 1987; ■ = METEOR-Cruise 5/1, January 1987.

Figure 1. Positions des stations en Mer Rouge et dans les régions adjacentes: ▼ = METEOR-Cruise 5/5, juillet/août 1987; ◆ = METEOR-Cruise 44/2, mars 1999; ● =METEOR-Cruise 5/3b, mai 1987; ■ = METEOR-Cruise 5/1, janvier 1987.

the methods of sampling and details of the quantitative enumeration have been described by Böttger-Schnack (1995, 1996, 1997). The plankton was initially fixed in 4% formaldehyde-seawater solution buffered with hexamethylene tetramine, and transferred after ca 2 years to a preservation fluid of 5% propylene glycol, 0.5% propylene phenoxetol, and 94.5% filtered seawater (Steedman, 1976).

Ovalis-type oncaeids from the southern Adriatic Sea, the type locality of *O. ovalis* and *O. bathyalis*, were used to verify the taxonomic identity of these species and to designate type and neotype material, as Shmeleva´s type material is no longer extant. The Adriatic specimens, which were presorted and kindly made available by Dr Frano Kršinic (Dubrovnik), were collected in the South Adriatic Pit in 1998 with a Nansen net, 50 cm in diameter, equipped with a closing system, mesh size 0.053 mm at a sampling depth of 260-400 m (Table 1b).

Additional zooplankton material collected with fine mesh nets in the Sargasso Sea during cruise 200 of *R/V Poseidon* (Schnack et al., 1994), in Sognefjorden, Norway (material collected by A. Fosshagen; for sample location cf. Swanberg & Bjørklund 1987, fig. 1), in the Antarctic, Weddell Sea, during cruise Ant V-3 of *R/V Polarstern* (material collected by C. Metz; cf. Metz 1993), in the Eastern Equatorial Indian Ocean during cruise 76-5 of *R/V Hakuho Maru* (material collected by S. Nishida; cf. Nishida & Marumo, 1982), in the northwestern subarctic Pacific, Oyashio region (material collected and presorted by Y. Nishibe; cf. Nishibe & Ikeda, 2004) and in the northeastern Pacific, off Monterey Bay, California (material collected by R. Hopcroft; cf. Hopcroft et al. 2002, fig. 1) were used for the examination of zoogeographical distribution of *ovalis*-type oncaeids (Table 1b).

Specimens were dissected in lactic acid, mounted on

Table 1a. Sample locations for oncaeid species of the *ovalis*-type in the Red Sea and adjacent areas. MSN = multiple opening-closing net, vertical hauling.

Tableau 1a. Localisation des prélèvements d'oncaéidés du type *ovalis* en Mer Rouge, et dans les zones adjacentes. MSN = filet à ouvertures successives, trait vertical.

Stn	Date	Geographic position	Time D = Day N = Night	Sampling gear [mesh size]	Sampling depth (m)	Total water depth (m)
Red Sea and Gulf of Aden						
R/V Meteor Cruise 5/5						
663	20 Jul 1987	22°58.4'N 37°19.4'E	D	MSN [0.055 mm]	750-900 900-1050	1200
682	25 Jul 1987	21°13.9'N 38°05.7'E	D	MSN [0.055 mm]	300-350	1880
703	2 Aug 1987	15°34.8'N 41°54.9'E	D	MSN [0.055 mm]	200-250	970
708	5 Aug 1987	13°40.0'N 42°37.4'E	D	MSN [0.055 mm]	150-175	190
717	5 Aug 1987	12° 32.0'N 43° 24.5'E	D	MSN [0.055 mm]	150-200	250
631	11 Jul 1987	11°55.5'N 43°37.9'E	N	MSN [0.055 mm]	200-250	1400
R/V Meteor Cruise 44/2						
156	4 March 1999	27°25.00'N 34°04.98'E	D	MSN [0.055 mm]	500-550	798
164	6 March 1999	29°04.98'N 34°45.96'E		MSN [0.055 mm]	500-600 700-800	822
151	1 March 1999	29°29.41'N 34°57.02'E	D/N	MSN [0.055 mm]	200-250 400-450	596
Northern Arabian Sea						
R/V Meteor Cruise 5/3b						
496	12 May 1987	18°00.1'N 66°25.5'E	N	MSN [0.055 mm]	100-150	3035
Eastern Mediterranean Sea						
R/V Meteor Cruise 5/1						
21	17 Jan 1987	34°26.64'N 26°15.99'E	D	MSN [0.055 mm]	450-600 750-900	3500
31	20 Jan 1987	34°26.73'N 26°15.39'E	D	MSN [0.055 mm]	400-450	3400
34	20 Jan 1987	34°23.9'N 26°11.2'E	N	MSN [0.055 mm]	450-600	3400
35	20 Jan 1987	34°25.3'N 26°14.8'E	N	MSN [0.055 mm]	350-400 400-450	3400

slides in lactophenol, and sealed with high-quality nail-varnish. For some specimens polyvinyllactophenol was used as a mounting medium. All figures have been prepared using a camera lucida on a Leitz Dialux differential interference contrast microscope.

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

Descriptive terminology for body and appendages follows that of Huys & Boxshall (1991). Abbreviations used in the text are: A1 = antennule; A2 = antenna; ae = aesthetasc; CR = caudal rami; enp = endopod; exp = exopod; exp(enp)-1(-2, -3) = to denote the proximal (middle, distal) segment of a ramus; P1-P6 = first to sixth thoracopods. Oncaeidae typi-

Table 1b. Sample locations for oncaeid species of the *ovalis*-type in various localities of the Mediterranean Sea, and in the Atlantic, Indian and Pacific Oceans. MSN = multiple opening-closing net, vertical hauling.

Tableau 1b. Localisation des prélèvements d'oncaéidés de type *ovalis* en différents endroits de Méditerranée, Atlantique, Océan Indien et Océan Pacifique. MSN = filet à ouvertures successives, trait vertical.

Station	Date	Geographic position	Sampling gear [mesh size]	Sampling depth (m)	Total water depth (m)
Adriatic and western Mediterranean Sea					
South Adriatic Pit, Dubrovnik area (*R/V Bios*; leg. F. Kršinic)					
"P1000"	28 Mar 1998	42°20.0'N 17°42.5'E	Nansen type [0.053 mm]	260-400 vertical	~1000
Western Mediterranean (*R/V Meteor* Cruise 51/2; leg. D. Elvers)					
511	20 Oct 2001	37°59.85'N 05°59.93'E	MSN [0.1 mm]	300-600 vertical	2800
Atlantic Ocean					
Sargasso Sea (*R/V Poseidon* Cruise 200/1; leg. D. Schnack)					
210	13 Mar 1993	24°29.4'N 62°00.2'W	MSN [0.055 mm]	3300-3800 vertical	~5000
Sognefjorden, Norway (leg. A. Fosshagen; cf. Swanberg & Bjørklund 1987, fig. 1))					
1	2 Dec 1982	off Bekken ~61°06'N 05°10'E	Juday net [0.063 mm]	500-1000 vertical	?
Antarctic					
Weddell Sea (*R/V Polarstern* Cruise AntV-3; leg. C. Metz)					
604	17 Nov 1986	72°40'S ~20°47'W	MSN [0.1 mm]	500-1000 vertical	3253
Indian Ocean					
Equatorial Indian Ocean (*R/V Hakuho Maru* Cruise 76-5; leg. S. Nishida)					
11	24 Jan 1977	04°47.7'S 87°14.4'E	Motoda net [0.1 mm]	300 horizontal	3035
Pacific Ocean					
NW Pacific, subarctic (*TS Hokusei Maru* leg 76; leg. Y. Nishibe)					
HO9743 HO9744	5 Oct 1996	41°30'N 145°47'E	Norpac net, modified [0.1 mm]	250-500 500-1000 vertical	6670
NE Pacific, off Monterey, California (leg. R. Hopcroft)					
M1	11 May 1999	~36° 45'N ~122°01'W	~WP-2, stretched [0.064 mm]	0-200 vertical	1000

cally exhibit pores and other integumental structures (e.g. pits, scales) on the body surface, but only those discernible with a light microscope were included in the description. Type, neotype and reference material is deposited in the collections of the Zoologisches Institut und Museum der Universität Hamburg (ZMH) and The Natural History Museum, London (NHM). Additional paratypes or other material are retained in the personal collection of R. Böttger-Schnack (RBS).

The ordinal classification of Copepoda as a whole has changed recently and Cyclopoida and Poecilostomatoida are no longer regarded as separate orders (Huys et al., 2002; Boxshall & Halsey, 2004). According to the new classification concept, the family Oncaeidae, previously attributed to the Poecilostomatoida (Huys & Boxshall, 1991), now is placed in the Cyclopoida, which comprises all those families previously attributed to both the Cyclopoida and the Poecilostomatoida (Boxshall & Halsey, 2004).

Species Descriptions

Order CYCLOPOIDA
Family Oncaeidae
Oncaea cristata sp. nov.

Type locality

Northern Red Sea, main basin, 27°25.00'N, 34°04.96'E. Stn. 156; *R/V Meteor* leg 44/2; depth 500-550 m; total

water depth 798 m.

Material examined

(1) Type locality: collected 04 March 1999 with MSN 0.55 mm net.

(a) Holotype ♀ in alcohol (total body length 420 µm, measured in traditional way) (ZMH reg. no. K-40799). *Paratypes.* 5 ♀♀, 2 ♂♂ in alcohol (ZMH reg. no. K-40800).

Other paratypes.

(b) 5 ♀♀, 2 ♂♂ in alcohol (NHM reg. no. 2004.3094-3100).

(c) 5 ♀♀, 1 ♂, 1 juvenile in alcohol (RBS).

(2) Northern Red Sea, Gulf of Aqaba, 29°29.41'N, 34°57.02'E: Stn. 151; *R/V Meteor* leg 44/2: collected 01 March 1999 with MSN 0.055 mm net; total water depth 596 m:

(2.1) Haul 2/1; depth 400-450 m:

(a) 1 ♀ in alcohol (ZMH reg. no. K-40801); 4 ♀♀, 3 ♂♂ in alcohol (ZMH reg. no. K-40802).

(b) 5 ♀♀, 3 ♂♂ in alcohol (NHM reg. no. 2004. 3101-3108).

(c) 1 ♀ partly dissected (urosome on slide, prosome in alcohol), 1 ♂ partly dissected [antennules, antenna (1 side) on slides, rest of specimen in alcohol], 1 ♀ (with expanded prosome), 1 ♂ in toto on slides, 4 ♀♀, 1 ♂ in alcohol (RBS).

(2.2) Haul 3/1; depth 200-250 m: 2 ♀♀ in formaldehyde (RBS).

(3) Northern Red Sea, Gulf of Aqaba, 29°04.98'N, 34°45.96'E: Stn. 164; *R/V Meteor* leg 44/2: collected 06 March 1999 with MSN 0.055 mm net; total water depth 822 m:

(3.1) Haul 13/1; depth 700-800 m: 1 ♀ (ovigerous) in toto on slide, several detached egg-sacs on slide (RBS).

(3.2) Haul 13/3; depth 500-600 m: 1 ♀, 1 ♀ (with expanded prosome) mounted in toto on slides (RBS).

(4) 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 0.055 mm net; total water depth 1200 m:

(4.1) Haul 15/1; depth 900-1050 m: 1 ♀ dissected on slides, 2 ♀♀ in toto on slides, 1 ♂ dissected on slides, 1 ♂ partly dissected (antennules, right antenna on slides, rest of specimen in alcohol), 3 ♂♂ in toto on slides (RBS)

(4.2) Haul 15/2; depth 750-900 m:

(a) 3 ♀♀ in alcohol (ZMH reg.no. K-40803).

(b) 2 ♀♀ in alcohol (NHM reg. no. 2004.3109-3110).

(c) 3 ♀♀ in alcohol (RBS).

(5) Central Red Sea, 21°13.9'N, 38°05.7'E: Stn. 682; *R/V Meteor* leg 5/5: collected 25 July 1987 with MSN 0.055 mm net (Haul 27/3); depth 300-350 m; total water depth 1880 m: 2 ♀♀, 6 ♂♂ in formaldehyde (RBS).

(6) Southern Red Sea, oceanic area, 15°34.8'N, 41°54.9'E: Stn. 703; *R/V Meteor* leg 5/5: collected 2 August 1987 with MSN 0.055 mm net (Haul 39/1); depth 200-250 m; total water depth 950 m: 1 ♀ dissected on 1 slide in polyvinyl-lactophenol (RBS).

Other material examined

(7) Southern Red Sea, shallow area, 13°40.0'N, 42°37.4'E: Stn. 708; *R/V Meteor* leg 5/5: collected 5 August 1987 with MSN 0.055 mm net (Haul 46/1); depth 150-175 m; total water depth ~175 m: 1 ♀ [provisionally assigned to *O. cristata*], 1 ♂ in toto on slides (RBS).

Description

Adult female (Figs. 2-4, 6). Body length: 536 µm [444 µm, range: 420-460 µm, based on 10 specimens from the Red Sea, including the Gulf of Aqaba].

Exoskeleton weakly chitinized. Prosome 2.7 times length of urosome, excluding caudal rami, 2.4 times urosome length including caudal rami. P2-bearing somite without conspicuous dorso-posterior projection in lateral aspect (Fig. 2B). Integumental pores on prosome as indicated in Fig. 2A, B. Pleural areas of P4-bearing somite with rounded posterolateral corners. Numerous specimens found which exhibited an extremely expanded prosome as depicted in Fig. 2G, 5A.

Proportional lengths (%) of urosomites are 10.6 : 53.9 : 12.3 : 9.5 : 13.7. Proportional lengths (%) of urosomites and caudal rami are 9.4 : 48.1 : 11.0 : 8.5 : 12.3 : 10.7.

P5-bearing somite with 3 paired midventral spinous processes (Fig. 2D), dorsoposterior pores absent (Fig. 2C).

Genital double-somite oval-elongate, usually 1.8 times as long as maximum width measured in dorsal aspect (range: 1.7-1.9:1, n = 5) and 1.6 times as long as postgenital somites combined; largest width measured almost at midregion, lateral margins more or less rounded (Fig. 2A), posterior part tapering gradually. Paired genital apertures located dorsally at about 2/5 the distance from anterior margin of genital double-somite; armature represented by 1 long spine, spinous process(es) absent (Fig. 2C). Dorsal surface ornamented with paired pore near posterior margin and several rows of minute denticles dorso-laterally and posterior to genital apertures (Fig. 2C).

Anal somite 1.3 times wider than long; slightly longer than caudal rami (Fig. 2C). Two pairs of secretory pores present dorsally on either side of anal opening, located near posterior margin. Paired dorsal sensillae anterior to anal operculum absent. Paired lateral pore present (Fig. 2C, D). Anterior margin of anal opening (vestigial anal opening) smooth. Ventral surface with paired pore near posterior margin as figured for male (cf. Fig. 6E). Posterior margin of somite finely serrate ventrally and laterally (Fig. 2D).

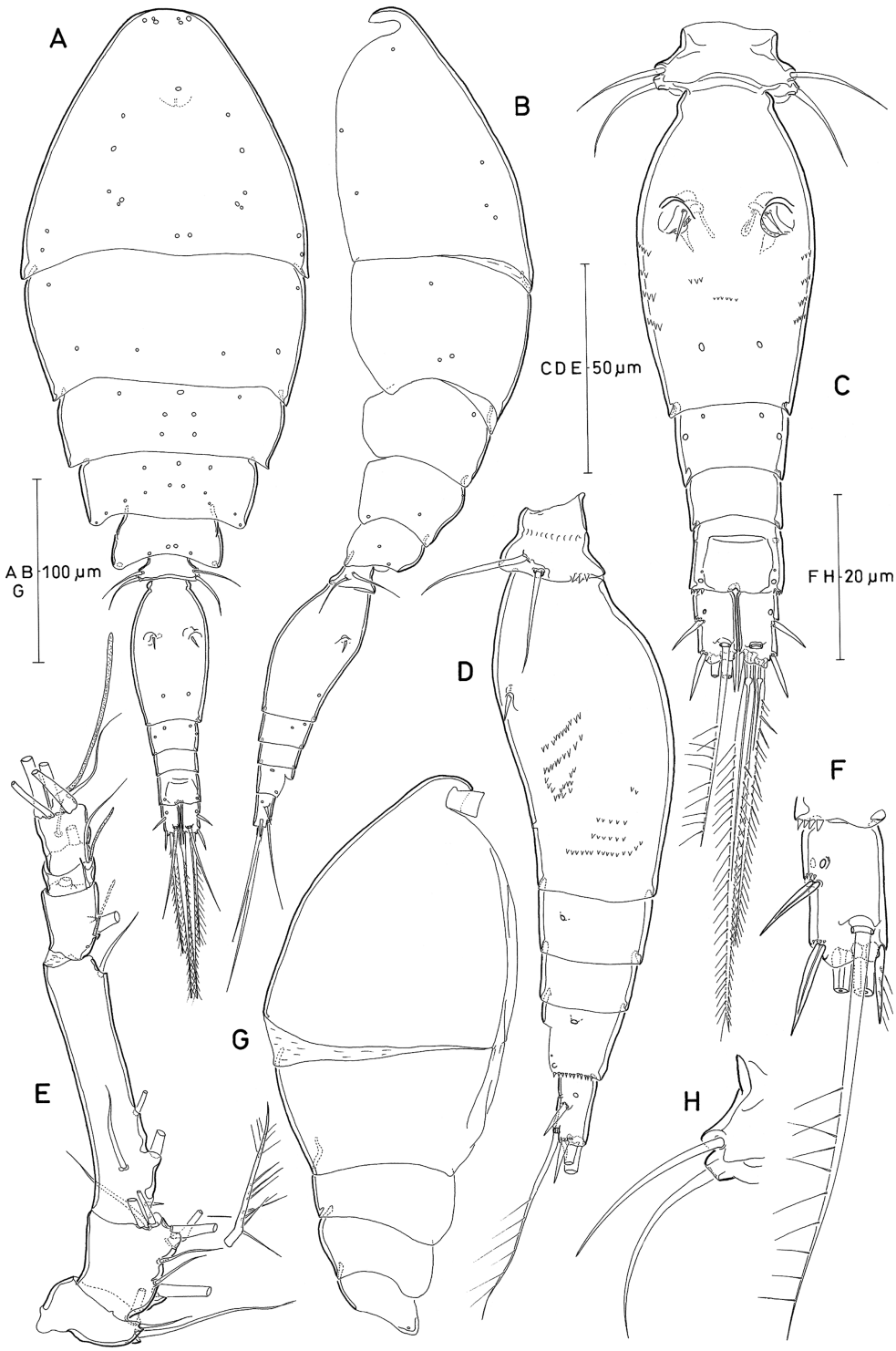

Figure 2. *Oncaea cristata* sp. nov., female (Red Sea, main basin). **A.** Habitus, dorsal. **B.** Same, lateral (appendages omitted). **C.** Urosome, dorsal. **D.** Urosome, lateral. **E.** Antennule, comb-like seta on segment 2 figured separately, aesthetasc on segment 4 not well discerned, stippled. **F.** Caudal ramus, dorsal. **G.** Specimen showing expanded prosome, lateral. **H.** Leg 5, dorsal.

Figure 2. *Oncaea cristata* sp. nov., femelle (Mer Rouge, bassin central). **A.** Habitus, vue dorsale. **B.** Habitus, vue latérale (appendices omis). **C.** Urosome, dorsal. **D.** Urosome, latéral. **E.** Antennule, soie modifiée en forme de peigne sur le segment 2, figurée séparément, esthetasque sur le segment 4 peu discernable, pointillé. **F.** Palette furcale, dorsale. **G.** Spécimen montrant le prosome gonflé, vue latérale; (H) patte 5, vue dorsale.

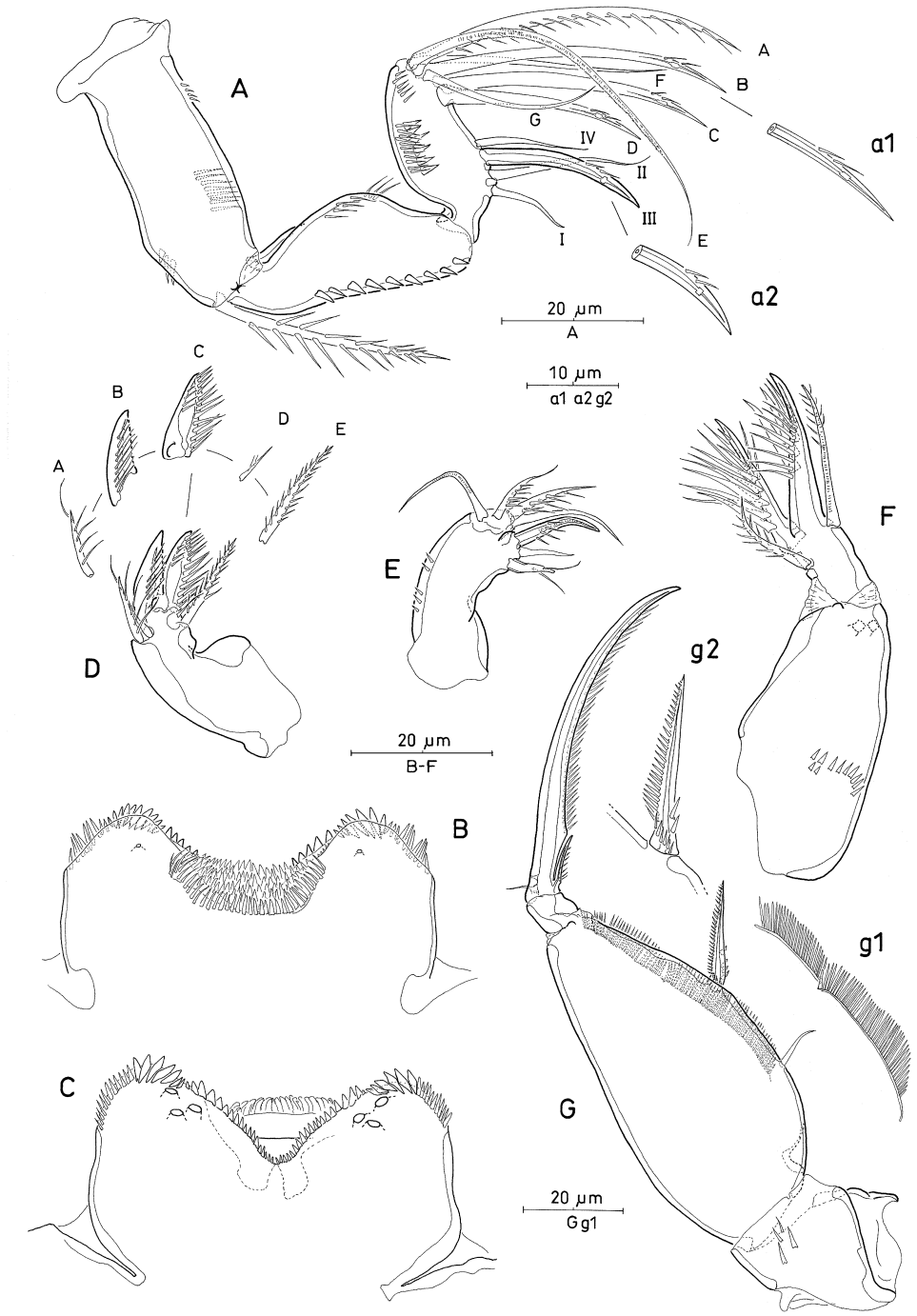

Figure 3. *Oncaea cristata* sp. nov., female (Red Sea, main basin). **A.** Antenna, lateral elements are numbered using Roman numerals, distal elements are identified by capital letters (**a1**, distal part of element B; **a2**, distal part of element III). **B.** Labrum, anterior. **C**. Same, posterior. **D.** Mandible, showing individual elements. **E.** Maxillule. **F.** Maxilla. **G.** Maxilliped, anterior (**g1**, inner margin of basis, posterior; **g2**, distal element on basis, posterior, showing ornamentation).

Figure 3. *Oncaea cristata* sp. nov., femelle (Mer Rouge, bassin central). **A.** Antenne, les éléments latéraux sont numerotés par des chiffres romains, les éléments distaux sont identifiés par des capitales (**a1**, partie distale d´élément B; **a2**, partie distale d'élément III). **B.** Labre, antérieur. **C.** Labre, postérieur. **D.** Mandibule, montrant des éléments individuels. **E.** Maxillule. **F.** Maxille. **G.** Maxillipède, antérieur (**g1**, bord intérieur de la base, postérieur; **g2**, élément distal sur la base, postérieur, montrant de l'ornementation).

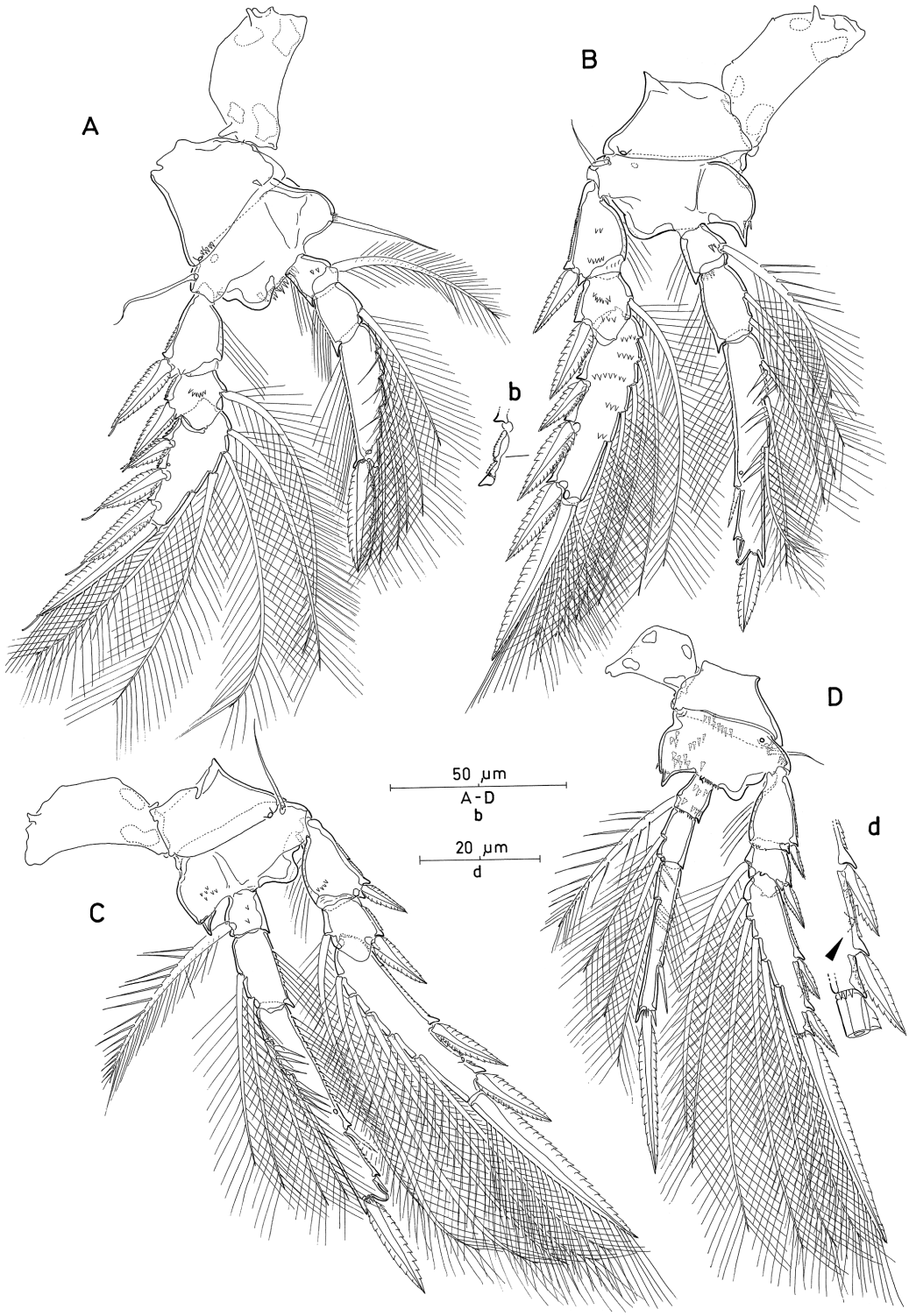

Figure 4. *Oncaea cristata* sp. nov., female (Red Sea, main basin). **A.** P1, posterior. **B.** P2, posterior (**b**, lateral margin of exp-3, showing pore between outer subdistal and outer distal spine, spines not figured). **C.** P3, posterior. **D.** P4, anterior (**d**, outer margin of exp-3, arrow indicating pore between outer subdistal and outer distal spine).

Figure 4. *Oncaea cristata* sp. nov., femelle (Mer Rouge, bassin central). **A.** P1, postérieur. **B.** P2, postérieur (**b**, bord latéral de exp-3, montrant un pore entre l'épine extérieure sousdistale et l'épine extérieure distale, épines non figurées). **C.** P3, postérieur. **D.** P4, antérieur (**d**, bord extérieur de exp-3, flèche indiquant un pore entre l´épine extérieure sousdistale et l'épine extérieure distale).

Caudal ramus (Fig. 2C,F) about 1.5 times longer than wide. Armature consisting of 6 elements (for numbering of elements see Fig. 7F): seta II and III short, spiniform and bare; seta IV long and plumose; seta V longest and plumose; seta VI slightly shorter than seta III, ornamented with few setules along inner margin (Fig. 2F); seta VII about 1/2 length of seta V, unipinnate and bi-articulate at base. Inner margin of CR naked; anterior surface with two pores near insertion of seta II, one located dorsally and the second ventro-laterally (Fig. 2F, D); posterior ventral margin finely serrate as in male (cf. Fig. 6E).

Antennule 6-segmented (Fig. 2E), relative lengths (%) of segments measured along posterior non-setiferous margin 8.2 : 14.3 : 49.0 : 11.8 : 5.3 : 11.4. Armature formula: 1-[3], 2-[8], 3-[5], 4-[3+ae?], 5-[2+ae], 6-[5+(1+ae)]. Segment 2 with modified comb-like seta (figured separately in Fig. 2E) showing sharply bent basal part and ornamented with single row of strong spinules along proximal half of outer margin, distal part bipinnate. Small sensory element on segment 6 not found. Aesthetasc on segment 4 not fully discerned (stippled in Fig. 2E), aesthetasc on segment 5 very slender, apical aesthetasc well developed and fused basally to adjacent seta.

Antenna 3-segmented, distinctly reflexed (Fig. 3A). Coxobasis with row of long, fine setules along outer margin, short row of spinules on proximal part of outer (exopodal) margin and few spinules on distal part of inner margin; with bipinnate seta at inner distal corner, being slightly shorter than proximal endopod segment. Endopod segments unequal in length; proximal endopod segment moderately subtriangular forming outer lobate outgrowth bearing spinular row, with row of strong denticles along posterior inner margin. Distal endopod segment slightly shorter than proximal endopod segment, with narrow cylindrical base articulating with the proximal endopod segment; posterior surface with two patches of short spinules along outer margin, proximal patch consisting of double row of spinules, with lower spinular row dentiform and broader than upper spinular row; lateral armature consisting of 3 bare seta (I, II and IV), with seta I shortest, and 1 curved spiniform element (III) ornamented with few spinules unilaterally at distal part (Fig. 3a2); distal armature consisting of 4 long setae (A-D), ornamented with pinnules along entire inner margin (A) or with few spinules unilaterally at distal part (B-D, Fig. 3a1), and 3 bare setae (E-G), with seta E longest and setae F+G shorter than setae A-D.

Labrum (Fig. 3B,C) distinctly bilobed. Distal (ventral) margin of each lobe medially with 6 large rhombic dentiform processes of varying length, row of long blunt setules at outer ventral margin and row of broad spinules or denticles along inner margin. Median concavity covered anteriorly by several overlapping rows of spatulated setules. Anterior surface unornamented, except for small pore located distally on each lobe, median swelling not distinct. Posterior part of medial concavity without chitinized teeth (Fig. 3C), with paired row of broad spinules or denticles, which are increasing in size distally. Posterior face with group of 3 secretory pores located distally on each lobe.

Mandible (Fig. 3D) without surface ornamentation on coxa, gnathobase with 5 elements: 3 setae and 2 blades. Ventral element (A) shorter than ventral blade (B), with long fine setules along dorsal side; ventral blade strong and spiniform, with row of minute spinules on posterior side; dorsal blade (C) strong and broad, spinulose along entire dorsal margin and additional spinular row on distal half of posterior side; seta D very short and difficult to discern, ornamented with sparse setules; dorsal element (E) longest, setiform and bipinnate.

Maxillule (Fig. 3E) indistinctly bilobed, surface with row of spinules along outer margin. Inner lobe (praecoxal arthrite) with 3 elements: outermost element spiniform and curved, fringed with few coarse spinules, tubular extension at tip of element not well discernible, middle element setiform and bare, innermost element setiform with rounded tip and few long spinules at distal half, located along concave inner margin close to other elements. Outer lobe with 4 setiform elements, which are bare (outermost and innermost element) or unipinnate (middle elements). Innermost element longer than spinous outermost element of inner lobe.

Maxilla (Fig. 3F) 2-segmented, allobasis slightly shorter than syncoxa. Syncoxa unarmed, surface ornamented with spinular row 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 to tip of allobasal claw, ornamented with few spinules bilaterally at distal part, tip of seta with tubular extension; inner margin with long pinnate seta and strong basally swollen spine with double row of very strong spinules along the medial margin and 2 shorter spinules along outer margin.

Maxilliped (Fig. 3G) 4-segmented, comprised of syncoxa, basis and 2-segmented endopod. Syncoxa unarmed, surface ornamented with few spinules. Basis oblong-robust, inner margin with 2 elements unequal in length: proximal element setiform and bare, about half the length of distal element, which is spiniform and ornamented with spinular row along entire outer posterior margin and curved row of few strong spinules basally (Fig. 3g2); fringe of long pinnules between proximal seta and articulation with endopod, interrupted at about half the distance between distal element and articulation with endopod (Fig. 3g1); anterior surface without ornamentation. Proximal endopod segment unarmed. Distal endopod segment drawn out into long curved claw, with pinnules along entire length of concave margin; accessory armature consisting of minute, naked seta on outer proximal margin and unipectinate spine fused

Table 2. *Oncaea cristata* sp. nov. Armature of swimming legs. Roman numerals indicate spines, Arabic numerals represent setae.

Tableau 2. *Oncaea cristata* sp. nov. Armature des pattes natatoires. Les chiffres latins indiquent les épines, les chiffres arabes les soies.

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

basally to inner proximal corner of claw: minute pore near seta on outer margin.

Swimming legs 1-4 biramous (Fig. 4A-D), with 3-segmented rami. Armature as shown in Table 2. Intercoxal sclerites well developed, without ornamentation. Coxae and bases of P1-P4 with sparse surface ornamentation as figured, most obvious on basis of P4 (Fig. 4D). Coxae of P1-P4 with posterior raised secretory pore near outer distal corner. Bases with short, naked outer seta; with anterior secretory pore near outer proximal corner (not figured for P3); inner portion produced adaxially into pointed process in P2-P4 (Fig. 4B-D). Inner basal seta on P1 spiniform and naked. Respective legs without distinct length differences between exopod and endopod. Bases of spines on exopodal and endopodal segments anteriorly surrounded by small spinules, as examplified on terminal exopod spine of P4 (Fig. 4d). Surface ornamentation of all segments sparse.

Exopods. Outer margin of exopod segments with narrow serrated hyaline lamella; inner margin of proximal exopod segments with long setules. Posterior surface of distal segments with one (P3 and P4) or 2 (P2) marginal pore(s), located between outer subdistal and outer distal spine (arrowed in Fig. 4b, d). Hyaline lamellae on outer spines well developed. Outer and terminal spines of P1 with long subapical tubular extensions, except for proximalmost spine on distal segment. Outer spines on distal exopod segment in P1 increasing in length distally. Terminal spine longer than (P1 + P4) or about equal in length to (P2 + P3) distal exopod segment; length of terminal spine on P3 slightly variable between individual specimens, equal in length to or slightly longer than the distal segment. Outer subdistal spine of P3 reaching beyond insertion of outer distal spine (Fig. 4C), outer subdistal spine of P4 reaching beyond marginal pore (arrowed in Fig. 4d).

Endopods. Outer margin of endopod segments with fringe of long setules, except for proximal segments of P3 + P4 and middle segment of P4. Inner seta of proximal endopod segment slightly swollen, plumose (P1 + P2) or spiniform and ornamented with long, fine spinules bilaterally (P3+P4). Distal endopod segments with single pore on posterior surface; distal margin of P2 and P3 produced into conical process with apical pore (Fig. 4B,C). Distal endopod segment of P4 tapering gradually. Terminal spine slightly shorter than (P1), less than 1/2 length of (P2 + P3) or about as long as (P4) distal endopod segment. Outer distal spines very short in P2-P4, shorter than conical process in P2 and P3. Outer subdistal spine short, not reaching insertion of outer distal spine, with hyaline lamellae reduced to small denticles (P2 + P3), or longer and bare, almost reaching insertion of subdistal spine or even beyond (P4, Fig. 4D). Outer margin of distal segment of P1 terminating in a small process obscuring insertion of distalmost inner seta. Inner setae of distal endopod segments of P2-P4 with spinule comb along proximal inner margin; this comb less obvious in P1; also present on distal inner seta of middle endopod segment in P4.

P5 (Fig. 2C, D) comprising short outer basal seta and small exopod segment fused to somite, armed with single short seta, not reaching as far as genital apertures. Both elements spiniform and bare.

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

Egg-sacs paired, oval (Fig. 5B), each sac containing 4 eggs with a diameter of 40-50 µm (Fig. 5b).

Adult male (Fig. 6). Body length: 460 µm [395 µm, range: 380-400 µm, based on 4 specimens from northern Red Sea]. Sexual dimorphism in antennule, maxilliped, P6, and in genital segmentation, slight modification in length of P5 setae.

Proportional lengths (%) of urosomites (excluding caudal rami) 9.8 : 64.5 : 4.5 : 4.5 : 4.1 : 12.6; proportional lengths (%) of urosomites (caudal rami included) 8.6 : 56.8 : 4.0 : 4.0 : 3.6 : 11.1 : 11.9. P5-bearing somite with 4 paired midventral spinous processes (Fig. 6E), not 3 as in female, dorsoposterior pores absent (Fig. 6D) as in female. Length to width ratio of caudal rami and proportional lengths of caudal setae as in female. Dorsal surface of genital somite with two pairs of pores as figured. Surface of genital flaps sparsely ornamented with small spinules (Fig. 6E). Anal somite with length to width ratio and pore pattern as in female, dorsal posterior pore dislocated on left side of specimen figured (arrowed in Fig. 6D).

Antennule (Fig. 6B) 4-segmented; distal segment corresponding to fused segments 4-6 of female, indicated by suture line in Fig. 6B (stippled); relative lengths (%) of segments measured along posterior non-setiferous margin 5.4 : 16.2 : 51.4 : 27.0. Armature formula: 1-[3], 2-[8], 3-[4], 4-[10+2ae+(1+ae)]. Modified comb-like seta on segment 2 figured separately in Fig. 5B. Small apical sensory element not discerned. Proximal aesthetasc very short, but well discernible (arrowed in Fig. 6B)

Maxilliped (Fig. 6C) 3-segmented, comprised of syncoxa, basis and 1-segmented endopod. Syncoxa unarmed, surface ornamented with few spinules. Basis oblong-robust, inflated in proximal half forming bulbous swelling; anterior surface with 2 transverse spinular rows in addition to row of short spinules along inner margin (Fig. 6C); posterior surface with 2 rows of short spatulated spinules of graduated length along palmar margin (Fig. 6c); with 2

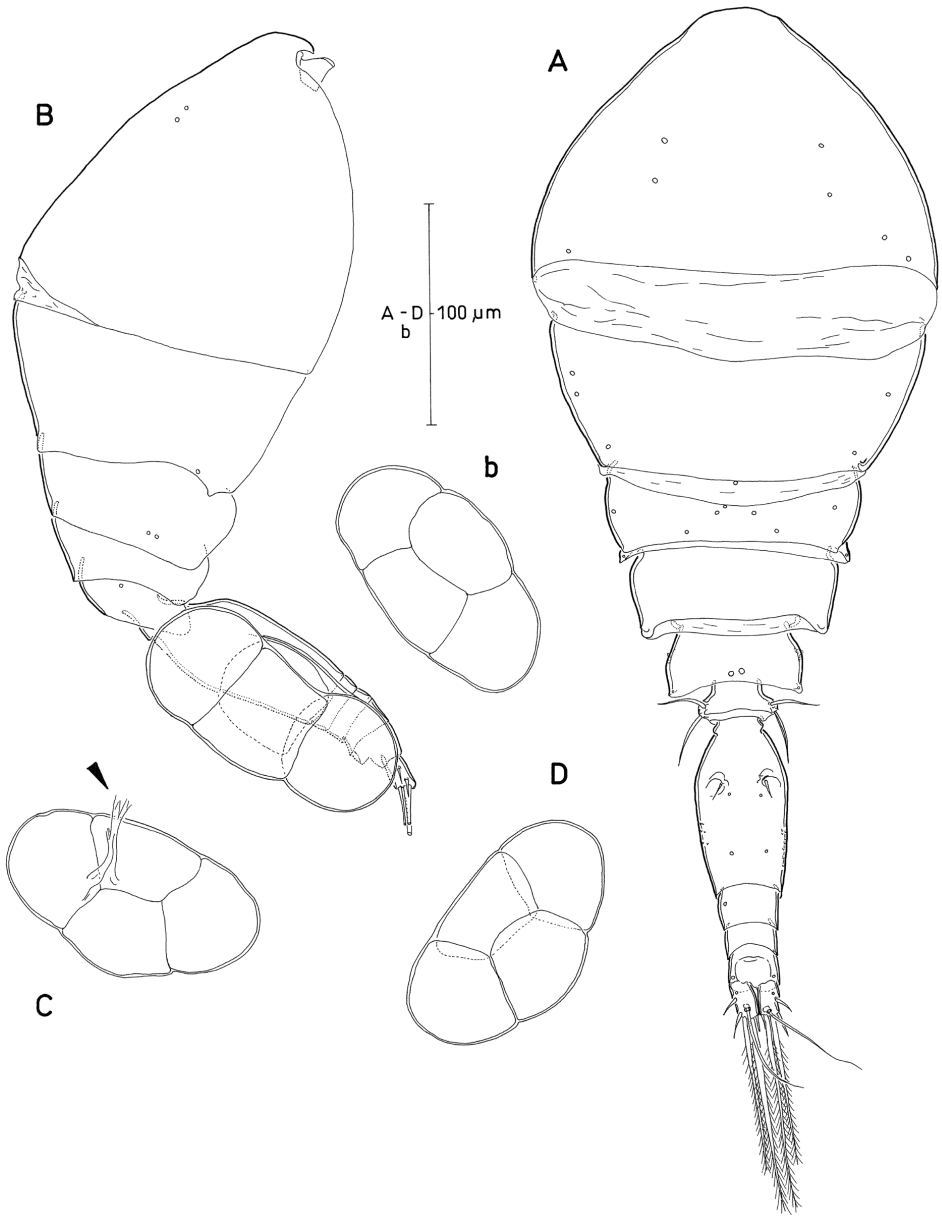

Figure 5. *Oncaea cristata* sp. nov., female (Gulf of Aqaba, northern Red Sea). **A.** Dorsal aspect of specimen showing expanded prosome and slight variation in form of genital double-somite (elongate form). **B.** Ovigerous female, lateral, caudal setae partly omitted [**b**, egg sac of same specimen, dorsal]. **C.** Detached egg sac (provisionally assigned to *O. cristata*), inner view, showing egg-sac string (arrowed). **D.** same, outer view.

Figure 5. *Oncaea cristata* sp. nov., femelle (Golfe d'Aqaba, partie septentrionale de la Mer Rouge). **A.** Aspect dorsal du spécimen montrant le prosome gonflé et une petite variation en forme de double segment génital (forme longue). **B.** Femelle ovigère, vue latérale, soies caudales en partie omises (**b**, sac d'oeufs du même spécimen, dorsal). **C.** Sac d'oeufs détaché (provisoirement attribué à *O. cristata*), vue intérieure montrant le filament du sac d'oeufs (marqué par des flèches). **D.** Sac d'oeufs détaché, vue extérieure.

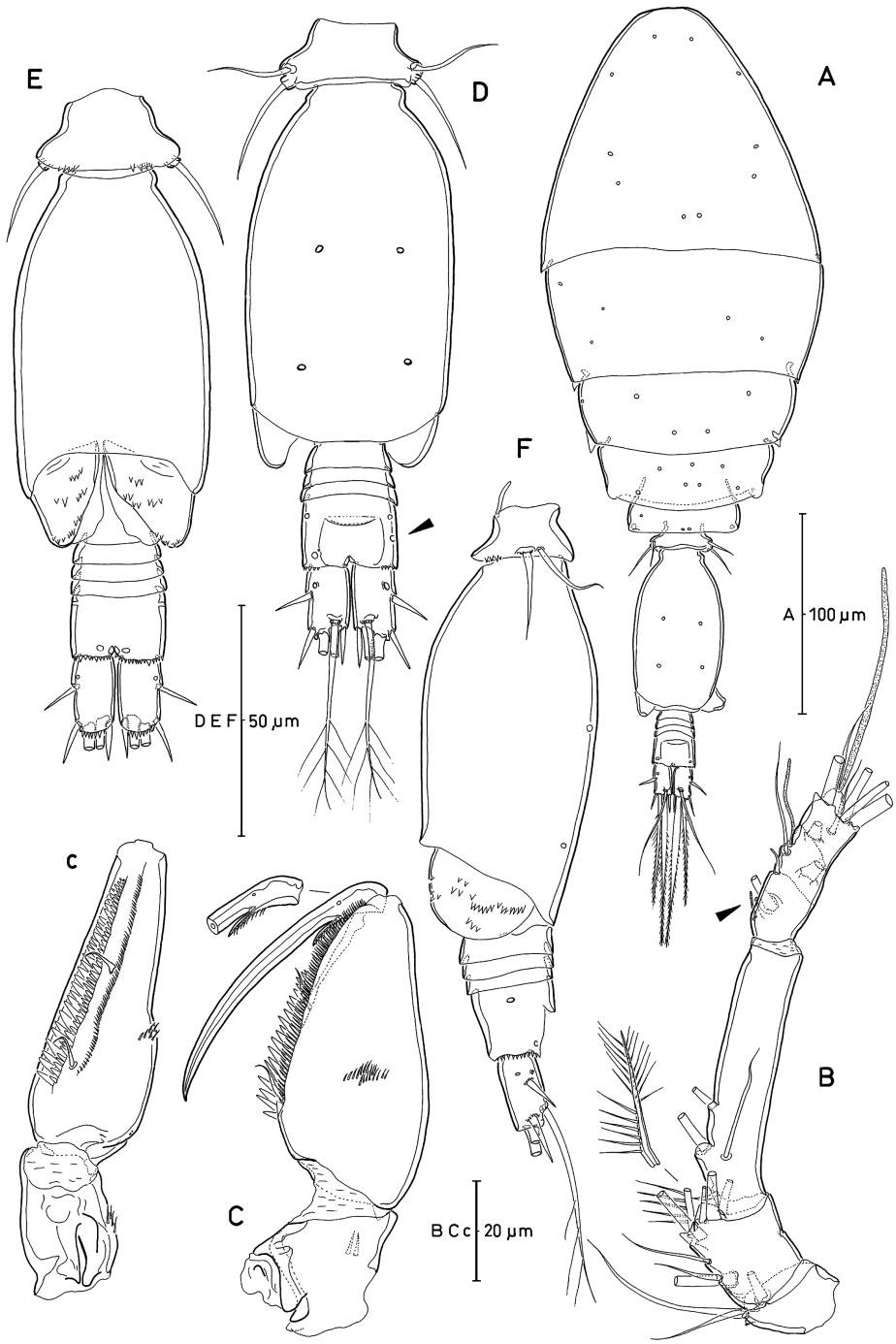

Figure 6. *Oncaea cristata* sp. nov., male (Red Sea, main basin). **A.** Habitus, dorsal. **B.** Antennule, comb-like seta on segment 2 figured separately, arrow indicating proximal small aesthetasc. **C.** Maxilliped, anterior, proximal part of endopodal claw, showing fused pectinate spine (**c**, medial view, claw not figured). **D.** Urosome, dorsal, dislocated pore on anal somite arrowed. **E.** Urosome, ventral. **F**. Same, lateral.

Figure 6. *Oncaea cristata* sp. nov. mâle (Mer Rouge, bassin central). **A.** Habitus, vue dorsale. **B.** Antennule, soie en forme de peigne sur le segment 2, figurée séparément, flèche indiquant le petit esthétasque proximal. **C.** Maxillipède, antérieur, partie proximale de la griffe sur l'endopodite, montrant l´épine fusionnée en forme de peigne (**c**, vue centrale, griffe non figurée). **D.** Urosome, dorsal, pore disloqué sur le segment anal, marquée par des flèches. **E.** Urosome, ventral. **F.** Urosome, latéral.

small naked setae within the longitudinal cleft, which are 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; minute pore on outer proximal margin of claw, tip of claw without hyaline apex.

P1-P4 with armature and ornamentation as in female.

P5 (Fig. 6D, F) exopod not delimited from somite, general shape and armature as in female; outer basal seta and exopodal seta somewhat shorter than in female.

P6 (Fig. 6E) represented by posterolateral flap closing off genital aperture on either side; covered by pattern of denticles as shown in Fig. 6E; posterolateral corners rounded and not protruding laterally so that they are hardly discernible in dorsal aspect (Fig. 6D).

Spermatophore not figured.

Etymology

The specific name is derived from the Latin *cristatus*, meaning comb-like, and refers to the modified seta on the second segment of the antennule.

Remarks

Taxonomy. Oncaea cristata is a sibling species of *O. crypta* sp. nov., the latter being conspecific with *O. ovalis sensu* Shmeleva (1969) (female only). *O. cristata* has been recorded under the name *O. ovalis* during earlier ecological studies in the Red Sea (Böttger-Schnack, 1988, 1990a, b, 1995; Böttger-Schnack et al., 2001). Apart from their different size (*O. cristata* is somewhat larger than *O. crypta*), the two siblings differ in the proportional lengths of exopodal spines on P3 and P4: (1) the outer subdistal spine on P3 exp-3 reaches beyond the insertion of the outer distal spine in *O. cristata*, while this spine does not reach as far as the insertion of the succeeding spine in *O. crypta* (cf. Fig. 9C); (2) the outer subdistal spine on P4 exp-3 reaches beyond the marginal pore between the outer subdistal and the outer distal spine and almost as far as the insertion of the outer distal spine in *O. cristata*, while this spine is shorter in *O. crypta*, not reaching beyond the marginal pore between the two spines (cf. Fig. 9D). Further differences between the two siblings are found in the length of the outer basal seta and the exopodal seta on P5 in both sexes, both being shorter in *O. cristata* than in *O. crypta*, and in the proportional lengths of the caudal setae with (1) seta IV being 3/4 length of seta V in *O. cristata*, but less than 3/5 this length in *O. crypta*, (2) spiniform seta VI being slightly shorter than seta III in *O. cristata*, whereas in *O. crypta* the two setae are equal in length, and (3) seta VII being 1/2 length of seta V in *O. cristata*, but only 2/5 its length in *O. crypta*. Differences in the length to width ratio (L:W) and the form of the genital double-somite observed between the typical form of *O. cristata* (L:W <2:1, rounded lateral margins) and *O. crypta* (L:W > 2:1, straight lateral margins), cannot be used for species identification, because this character was found to be variable in both species (see under *Variability.*). Males of the two siblings are morphologically very similar and can be separated merely by their size differences, by the lengths of outer exopodal spine on P3 and P4, by the lengths of setae on P5, as well as the proportional length of caudal seta VI. Potential differences in the lengths of caudal setae IV and V between males of the two species could not be determined during the present study, because these setae were broken off in all male specimens of *O. crypta* examined (eastern Mediterranean).

The common characteristic of *O. cristata* and *O. crypta* is the extremely small size of the outer distal spine on the endopods of P2 and P3, being shorter than the terminal conical projection in both legs. In most other oncaeid species (or -groups) the outer distal spines on the endopods are longer than the projections and thus, the character can be used to separate species of the *crypta-cristata*-subgroup from other oncaeid species, such as *O. bathyalis* and related forms [*O. setosa* Heron, 1977; *O. delicata* Heron, English & Damkaer, 1984; and *O. petila* Heron, 1977 (cf. Böttger-Schnack & Huys, 1998, their species group 12)] or the *lacinia*-group [including *O. lacinia* Heron, English & Damkaer, 1984; *O. pumilis* Heron, 1977; and *O. oceanica* Gordeyeva, 1972 (cf. Böttger-Schnack & Huys, 1998, their species group 11)], all of which are very similar in general habitus (see below under "*Geographical distribution*"). The only other species exhibiting very small outer distal spines on the endopods of P2 and P3 are *O. tenuimana* Giesbrecht, 1891 and *O. macilenta* Heron, 1977, which belong to a different species group within the Oncaeidae (Böttger-Schnack & Huys, 1998, their species group 9). However, in this species group the form of the distal endopod segment is much broader and the relative position of the endopodal spines is quite different from those of *O. cristata* and *O. crypta* and they can further be separated by differences in other morphological characters, in particular in the mouthparts (maxilliped, mandible, labrum).

The modified comb-like seta on the second segment of the antennule in *O. cristata* can also be found in its sibling *O. crypta* (cf. Fig. 7E, arrowed), but has not been reported for any other oncaeid species so far, suggesting that it is unique for species of the *crypta-cristata*-subgroup. Usually the armature and ornamentation of the antennule is very conservative in oncaeid copepods (Huys & Böttger-Schnack, unpubl. data) and thus has not been used as a diagnostic character before. However, recent detailed examinations of various oncaeid species indicated that differences in setal formula and modification of elements on the antennule occur more often within the family than previously assumed. Examples are the flattened setae on the

second segment of the antennule in *O. platysetosa* Boxshall & Böttger, 1987, which have also been found in *O. atlantica* Shmeleva, 1967 and *O. vodjanitskii* Shmeleva & Delalo, 1965, or related forms (R. Böttger-Schnack, unpubl. data), the additional setae on segments 2, 3 and 4 in the recently discovered primitive genus *Archioncaea* Böttger-Schnack & Huys, 1997, the reduced setal formula in the *zernovi*-group (Böttger-Schnack, 2002) or the ornamentation along the inner non-setiferous margin of segments 2 and 3 in some species of *Spinoncaea* (Böttger-Schnack, 2003).

Variability. Female *O. cristata* exhibited some variability in the form (dorsal aspect) and in the length to width ratio of the genital double-somite (GDS). The GDS of the typical form exhibited rounded lateral margins (Fig. 2C) and a smaller length to width ratio (1.85:1) than the elongate form, which showed more or less straight lateral margins (Fig. 5A) and a length to width ratio of 1.95:1 (range 1.9-2.0:1, n = 3). All other morphological characters, including the outer exopodal spine lengths of P3 and P4, the proportional length of setae on the caudal ramus and on P5, were similar in the two forms. The elongate form of *O. cristata* was found mainly in the Gulf of Aqaba, the northernmost extension of the Red Sea, but may not be restricted to this area. The typical form of *O. cristata* was distributed in the entire Red Sea, including the Gulf of Aqaba. Potential differences in zoogeographical distribution of the two forms in the Red Sea could not be clarified during the present study due to difficulties in distinguishing the specimens without microscopic examination.

In the shallow neritic area of the southernmost Red Sea, a single female specimen was collected, which exhibited several characters intermediate between those of the typical *O. cristata* and *O. crypta* sp. nov., i.e. the proportional lengths of outer spines on the distal exopod segments of P3 and P4, the length of the outer subdistal spine on the distal endopod segment in P4, and the form of the GDS. The proportional lengths of setae on CR and P5 of this specimen were similar to *O. cristata* and it was provisionally assigned to this species. A single male examined from the same sample matched all characters typical for *O. cristata*.

Ecological notes

Geographical distribution. Oncaea cristata is distributed in the entire Red Sea (Böttger-Schnack 1988 as *Oncaea* sp. M, Böttger-Schnack 1990a, b, 1995, as *O. ovalis*), including its northernmost extension, the Gulf of Aqaba (Böttger-Schnack et al., 2001, as *O. ovalis*). It has thus far not been found outside the Red Sea. During earlier ecological studies, several *ovalis*-type oncaeids had been recorded in the Strait of Bab al Mandab and the Gulf of Aden (Böttger-Schnack, 1995, as *O. ovalis*) and in the adjacent northern Arabian Sea (Böttger-Schnack, 1996, as *Oncaea* sp. A and *Oncaea* sp. C), which were re-examined during the present study. Upon closer examination they were found to consist of a number of different species, none of which belonged to the *cristata-crypta*-subgroup as defined in the present study. Specimens from the Strait and the Gulf of Aden were close to *O. parabathyalis* sp. nov. (see below), but differed in exopodal spine lengths and probably belong to an as yet undescribed species. *Oncaea* sp. A from the Arabian Sea was close to *O. infantula* Gordeyeva, 1972 in leg armature, showing the unusual outer spine formula I, I, 0 on the distal endopod segments of P2-P4. [A single specimen of this oncaeid type was recently also found in the southernmost Red Sea, shallow area.] *Oncaea* sp. C from the Arabian Sea was similar in morphology to the *lacinia*-group of oncaeids (cf. Böttger-Schnack & Huys 1998, their species group 11).

Abundance and vertical distribution. O. cristata is among the most numerous oncaeid species in the Red Sea, the adults of which contributed 3-7% to the total standing stock of oncaeids (including juvenile copepodids) in the upper 450 m sampled by 0.1 mm mesh nets (Böttger-Schnack, 1988, 1990b) and in the upper 1050 m of the water column sampled by 0.055 mm mesh nets (Böttger-Schnack, 1995). The relative abundance of the species was highest in the mesopelagic zone, between 250 and 1050 m depth, where it usually represented 10-22% of total oncaeids (Böttger-Schnack, 1990b, 1995 and unpubl. data), with maxima of more than 30% in single depth layers (Gulf of Aqaba, central part, 500-600 m, spring 1999, unpubl. data). These values may even have been higher if the juvenile copepodid stages of the species would have been identified. Recent investigations in the northern Red Sea and the Gulf of Aqaba indicated that larger juvenile stages (>CIII/IV) already would add 50% to the standing stock of adults sampled by 0.055 mm mesh nets in the entire water column. Seasonal variation in abundance in the central Red Sea were found to be insignificant (Böttger-Schnack, 1990b, 1995) and *O. cristata* thus can be regarded as a dominant species in mesopelagic layers throughout the year.

The vertical distribution of *O. cristata* reaches from the meso- to the bathypelagic zones of the Red Sea, occurring regularly below 200 m and down to the deepest layer of 1650 m sampled (Böttger-Schnack, 1990a, b, 1995 and unpubl. data). In the central-northern part of the Red Sea proper, maximum concentrations of females were found between 250-600 m depth, within the oxygen-minimum-zone or slightly above it. Males were always distributed shallower than females, showing concentration peaks between 200-350 m depth (O_2-gradient). No consistent seasonal difference between autumn and winter became apparent (Böttger-Schnack, 1990b). In the deep southern Red Sea, both sexes were more or less evenly distributed below 200 m down to the bottom at ~970 m depth (R. Böttger-

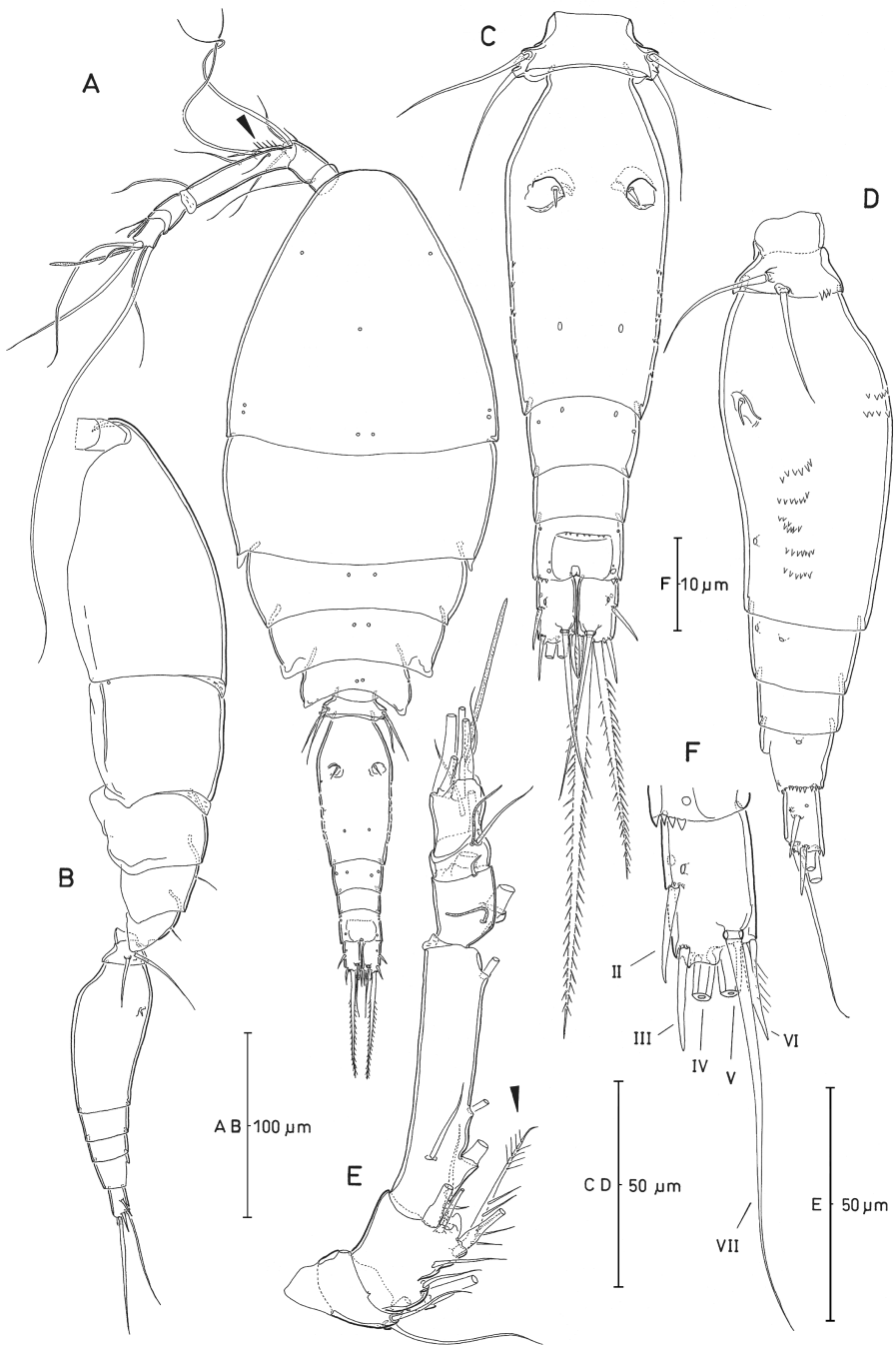

Figure 7. *Oncaea crypta* sp. nov., female (holotype, Adriatic Sea). **A.** Habitus, dorsal, caudal rami seta V missing, arrow indicating "comb-like" seta on antennule. **B.** Same, lateral (appendages omitted). *O. crypta* sp. nov., female (Eastern Mediterranean Sea). **C.** Urosome, dorsal, left caudal setae IV and V omitted. **D.** Urosome, lateral, caudal setae IV and V omitted. **E.** Antennule (modified "comb-like" seta on segment 2 arrowed). **F.** Caudal ramus, dorsal, setae IV and V omitted, individual elements numbered using Roman numerals.

Figure 7. *Oncaea crypta* sp. nov., femelle (holotype, Mer Adriatique). **A.** Habitus, vue dorsale, soie caudale V manquante (soie en forme de peigne sur l'antennule, marquée par des flèches). **B.** Habitus, vue latérale (appendices omis). *O. crypta* sp. nov., femelle (partie orientale de la Méditerranée). **C.** Urosome, dorsal, soies caudales gauches IV et V omises. **D.** Urosome, latéral, soies caudales IV et V omises. **E.** Antennule (soie modifiée en forme de peigne sur le segment 2, marquée par des flèches). **F.** Palette furcale, dorsale, soies caudales IV et V omises, éléments individuels numérotés par des chiffres romains.

Schnack, unpubl. data). In the Gulf of Aqaba, where no oxygen-minimum-zone is found (Reiss & Hottinger, 1984), the population of *O. cristata* was distributed deeper in the water column during spring (e.g. central Gulf: females at 500-700 m, males at 400-500 m) than in the main basin of the Red Sea (females: 450-550 m, males 300-450 m), thus indicating that the lower distribution range of the species was limited by the low oxygen values (Böttger-Schnack, Hagen & Schnack, in prep.).

Reproduction. Information on egg size and egg number for *O. cristata* presented in this study are based on a single ovigerous female, which was collected in the Gulf of Aqaba at a depth of 700-800 m. During earlier ecological studies in the Red Sea main basin, ovigerous females of *O. cristata* had not been found and no specimens carrying spermatophores attached to the genital apertures were observed (Böttger-Schnack et al., 1989), although males and juveniles occurred regularly. The egg-sacs of *O. cristata* seem to get detached from the females easily during collection and sample processing, which is similar to another small oncaeid species, *O. bispinosa*, the egg-sacs of which have been identified only recently (Böttger-Schnack & Schnack, in press). A number of different types of detached egg-sacs were noted in the sample from the Gulf of Aqaba containing the ovigerous *O. cristata* female. Among these, one type of egg sacs resembled the typical egg-sac of *O. cristata*: it contained 4 eggs per sac with a diameter between 44-52 µm (Fig. 5C, D).

The proportion of males sampled by 0.1 mm mesh nets in the upper 450 m water column during autumn and winter ranged between 55-70% of the adult standing stock and did not show any apparent seasonal variation (Böttger-Schnack, et al. 1989, as *O. ovalis*). In samples collected in the upper 1050 m with a somewhat smaller mesh size of 0.055 mm during summer, a correspondingly higher proportion of males was found, ranging between 51-53% of the adult standing stock (Böttger-Schnack, 1995, and unpubl. data). Recent investigations in the northernmost Red Sea and the Gulf of Aqaba gave similar proportions of 45-70% in the adult population sampled by 0.055 mm mesh nets in the entire water column (800 m depth). Thus continuous reproduction of the species in the area can be assumed.

Oncaea crypta sp. nov.

Synonymy

Oncaea ovalis Shmeleva, 1969 (♀ only)

Other description

Shmeleva (1969): 11-13, Fig. 8a-i (♀) [not Fig. 9a-i (♂)] (as *O. ovalis*)

Doubtful descriptions

Olson (1949 [MS]): 84-85, Plate XV 1.-8. (as *Oncaea minia*); Heron & Frost (2000): 1052, 1056 (key), Fig. 20G-R (♀), 21A (♂) (as *O. ovalis*).

Type locality

Adriatic Sea, 42°20.0'N, 17°42.5'E: Stn. "P1000", South Adriatic Pit, Dubrovnik area, sampling depth 260-400 m, total water depth ca 1000 m.

Material examined

(1) Type locality: *R/V Bios*, collected 28 March 1998 with Nansen net, 50 cm in diameter, equipped with a closing system, mesh size 0.053 mm, vertical haul (leg. F. Kršinic).

(a) Holotype ♀ [CR seta V missing] in alcohol (ZHM reg. no. K-40794). 1 paratype ♀ [CR seta V missing] in alcohol (ZHM reg. no. K-40795)

Other paratypes.

(b) 1 ♀ [CR seta V missing] in alcohol (NHM reg. no. 2004.3084a)

(c) 1 ♀ [CR seta V missing] in toto on slide (RBS).

(2) Western Mediterranean Sea, 37°59.85'N, 05°59.93'E: Stn. 511; *R/V Meteor* leg 51/2: collected 20 October 2001 with MSN 0.1 mm net (Haul 1/2); depth 300-600 m; total water depth 2800 m: 2 ♀♀ in toto on slides (RBS).

(3) 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 25/1); depth 400-450 m; total water depth 3400 m.

(a) 5 ♀♀ in alcohol (ZHM reg. no. K-40796), 1 ♂ [CR seta IV+V missing] in alcohol (ZHM reg. no. K-40797)

(b) 5 ♀♀ in alcohol (NHM reg. no. 2004.3084b-3088), 1 ♀ [CR seta IV+V missing] in alcohol (NHM reg. no. 2004.3089)

(c) 2 ♀♀ dissected on slides, 2 ♀♀ in toto on slides, 1 ♂ dissected on slides [CR seta V missing], 2 ♀♀, 2 ♂♂ (1 partly damaged) in formaldehyde (RBS).

(4) Eastern Mediterranean Sea, 34°26.64'N, 26°15.99'E: Stn. 21; *R/V Meteor* leg 5/1: collected 17 January 1987 with MSN 0.055 mm net (Haul 12/4); depth 450-600 m; total water depth ca 3500 m.

(a) 4 ♂♂ in alcohol (ZMH reg. no. K-40798)

(b) 4 ♂♂ in alcohol (NHM reg. no. 2004.3090-3093)

(c) 1 ♂ in toto on slide (RBS)

(5) Eastern Mediterranean Sea, 34°23.9'N, 26°11.2'E: Stn. 34; *R/V Meteor* leg 5/1: collected 20 January 1987 with MSN 0.055 mm net (Haul 23/4); depth 450-600 m; total water depth 3400 m: 1 ♀ dissected on 1 slide in polyvinyl-lactophenol (RBS).

Other material examined

(6) Sargasso Sea, 24°29.4'N, 62°00.2'W: Stn. 210; R/V

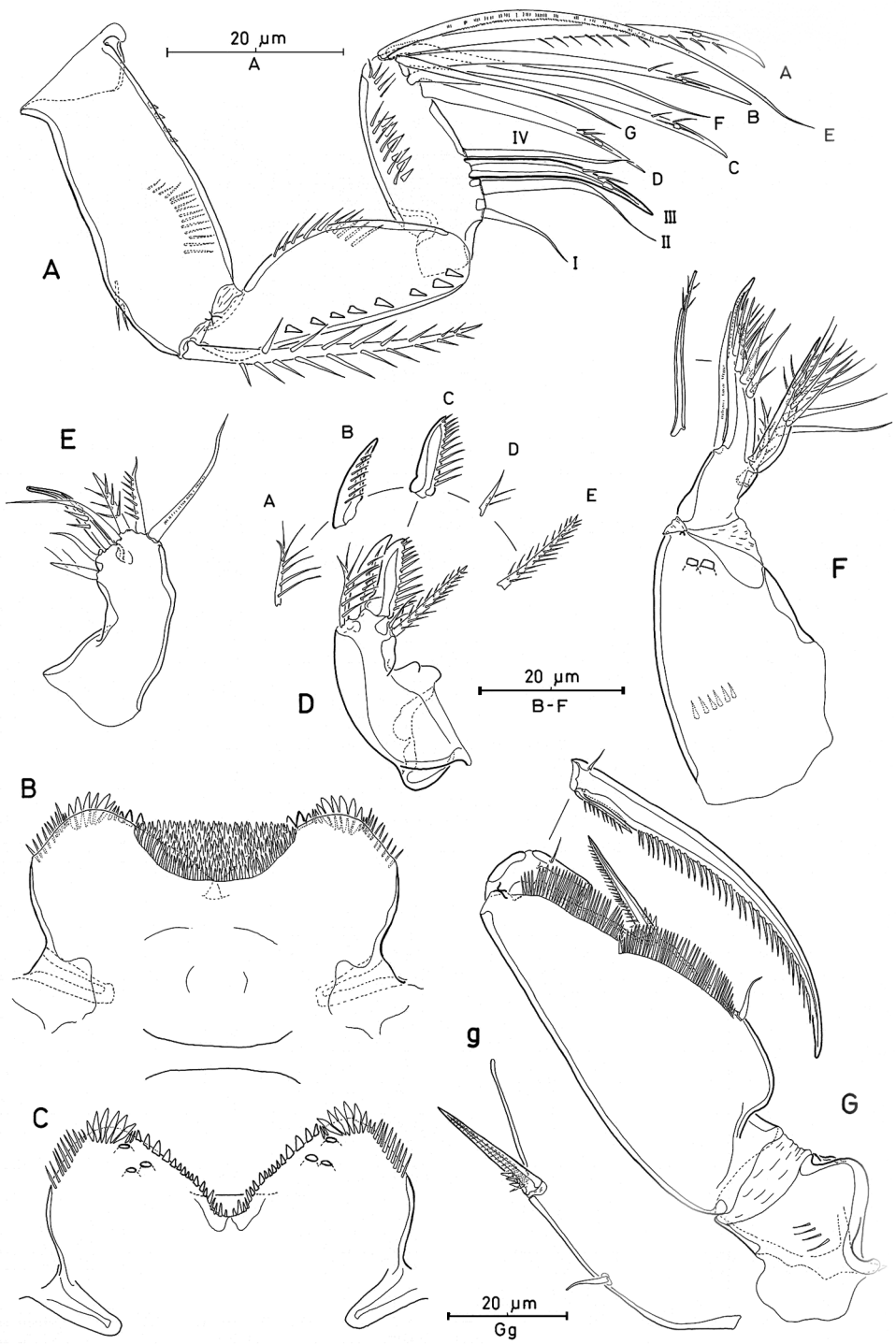

Figure 8. *Oncaea crypta* sp. nov., female (Eastern Mediterranean Sea). **A.** Antenna, lateral elements are numbered using Roman numerals, distal elements are identified by capital letters. **B.** Labrum, anterior. **C.** Same, posterior. **D.** Mandible, showing individual elements. **E.** Maxillule. **F.** Maxilla, seta on outer margin figured separately. **G.** Maxilliped, anterior, claw figured separately (**g**, palmar margin, posterior, showing ornamentation details of distal element).

Figure 8. *Oncaea crypta* sp. nov., femelle (Méditerranée orientale). **A.** Antenne, les éléments latéraux sont numérotés par des chiffres romains, les éléments distaux sont identifiés par des capitales. **B.** Labre, antérieur. **C.** Labre, postérieur. **D.** Mandibule, montrant des éléments individuels. **E.** Maxillule. **F.** Maxille, soie sur le bord extérieur, figurée séparément. **G.** Maxillipède, antérieur, griffe figurée séparément (**g**, bord palmaire, postérieur, montrant des détails d'ornementation de l'élément distal).

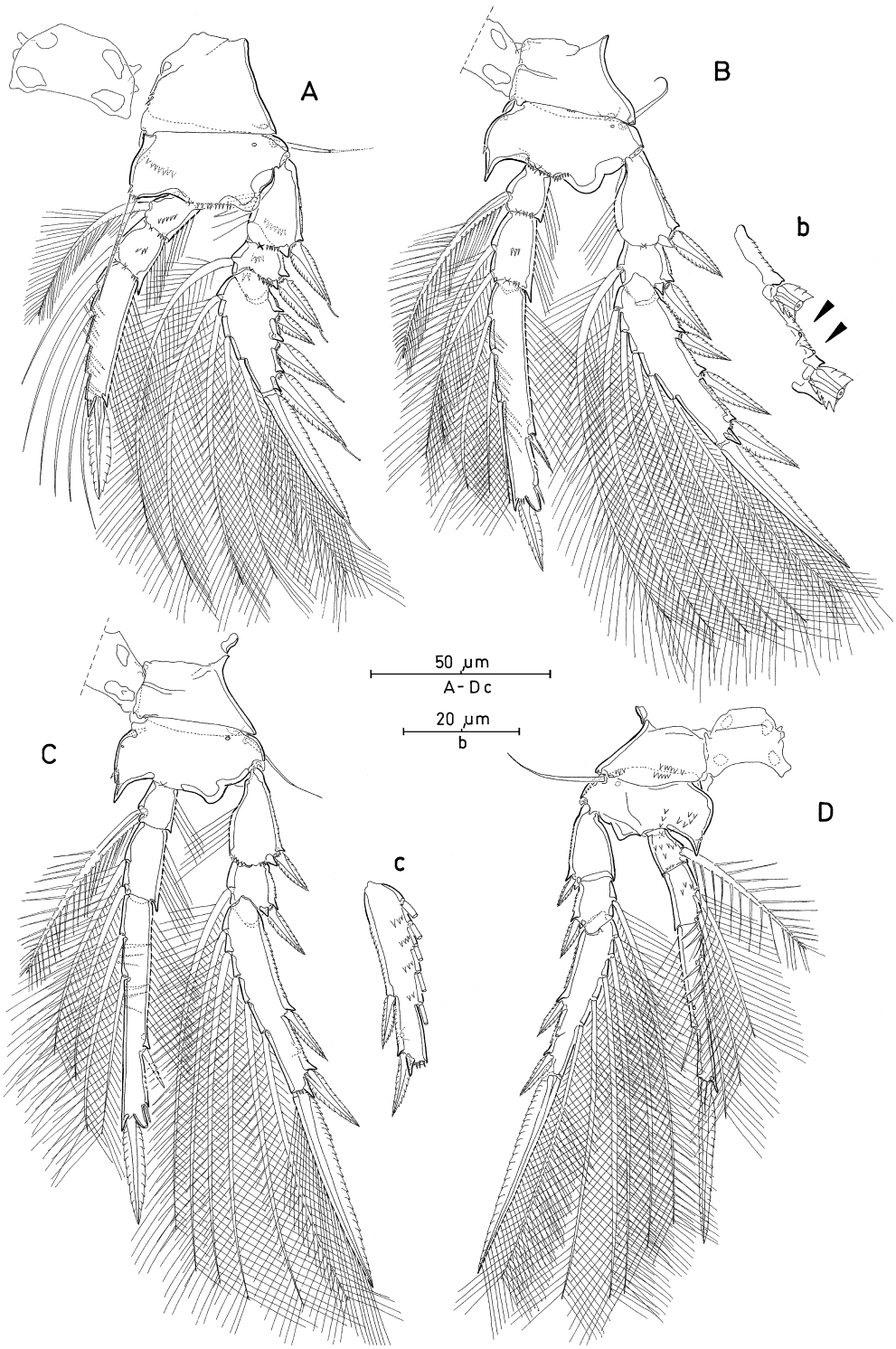

Figure 9. *Oncaea crypta* sp. nov., female (Eastern Mediterranean Sea). **A.** P1, anterior. **B.** P2, anterior (**b**, distal outer margin of exopod-3, posterior, arrows indicating position of pores). **C.** P3, anterior (**c**, exopod-3 of another specimen, showing variation in length of outer subdistal spine). **D.** P4, posterior.

Figure 9. *Oncaea crypta* sp. nov., femelle (Méditerranée orientale). **A.** P1, antérieur. **B.** P2, antérieur (**b**, bord extérieur distal de l'exopodite-3, postérieur, flèches indiquant la position des pores). **C.** P3, antérieur(**c**, exopodite-3 d'un autre spécimen, montrant une variation de la longueur de l'épine extérieure sousdistale). **D.** P4, postérieur.

Poseidon leg 200/1-2: collected 13 March 1993 with MSN 0.055 mm net (Haul 1/1); depth 3300-3800 m; total water depth ca. 5000 m (leg. D. Schnack): 1 ♀ in toto on slide [tentatively assigned to *O. crypta*] (RBS).
(7) Equatorial Eastern Indian Ocean, 04°47.7'S, 87°14.4'E: Stn. 11; *R/V Hakuho Maru* leg 76-5: collected 24 January 1977 with a Motoda net, 0.1 mm mesh size; depth layer 300 m, horizontal haul; total water depth 3035 m (leg. S. Nishida): 4 ♀♀ in toto on slides, 2 ♀♀, 1 juvenile in formaldehyde [tentatively assigned to *O. crypta*] (RBS)
(8) NW Pacific, subarctic, Oyashio region, 41°30'N, 145°47'E: Site H; *TS Hokusei Maru* leg 76: collected 5 October 1997 with a closing type net (Kawamura, 1989), 0.1 mm mesh size; total water depth 6670 m (leg. Y. Nishibe):

(8.1) Sample no. HO9743; depth 250-500 m: 1 ♀ in toto on slide [tentatively assigned to *O. crypta*] (RBS)

(8.2) Sample no. HO9744; depth 500-1000 m: 2 ♀♀ in formaldehyde [tentatively assigned to *O. crypta*] (RBS)

(9) NE Pacific, off Monterey, California , ~36°45'N, ~122°01'W: Stn. M1; collected 11 May 1999 with stretched WP-2 net, 30 cm diameter, 0.064 mm mesh size, vertical haul, depth 0-200 m; total water depth ~1000 m (leg. R. Hopcroft): 2 ♀♀ in toto in slides [tentatively assigned to *O. crypta*] (RBS)

Description

Adult female (Figs. 7-9; illustrations of female dorsal and lateral habitus are based on the holotype, other illustrations are based on specimens from the eastern Mediterranean Sea). Body length (calculated as sum of individual somites, not including extended dorsal hyaline membrane on first and second somite): 499 µm (Holotype) [(a) 430 µm, range: 420-440 µm based on 4 specimens from the Adriatic Sea; (b) 390 µm, range: 380-400 µm based on 2 specimens from the eastern Mediterranean].

Exoskeleton weakly chitinized. Prosome 2.5 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. 7B). Integumental pores on prosome as indicated in Fig. 7A,B, possibly not fully discerned. Pleural areas of P4-bearing somite with rounded posterolateral corners. Specimens with heavily expanded prosome observed regularly, similar to *O. cristata* (cf. Figs. 2G, 5A).

Proportional lengths (%) of urosomites are 9.3 : 56.6 : 12.4 : 10.0 : 11.7. Proportional lengths (%) of urosomites and caudal rami are 8.3 : 50.4 : 11.1 : 8.9 : 10.5 : 10.8.

P5-bearing somite with number of midventral spinous processes (Fig. 7D) and absence of dorsoposterior pores similar to *O. cristata*.

Genital double-somite 2.0-2.1 times as long as maximum width (measured in dorsal aspect), relatively longer than in the typical form of *O. cristata*, and 1.7 times longer than postgenital somites combined; largest width measured at anterior third, lateral margins straight with posterior part tapering slightly. Paired genital apertures located at 1/3 distance from anterior margin of genital double-somite; armature represented by 1 spine (Fig. 7C). Surface ornamentation and pore pattern as indicated in Fig. 7C, D.

Anal somite 1.3 times wider than long; about same length as caudal rami (Fig. 7C). Pore pattern on dorsal and ventral surface as in *O. cristata*. Anterior margin of anal opening (vestigial anal opening) with transverse row of minute denticles.

Caudal ramus (Fig. 7C, F) about 1.4 times as long as wide. Armature and ornamentation generally similar to *O. cristata*, proportional length of caudal setae slightly different, with seta IV being 3/5 length of seta V, seta VI being about as long as seta III, and seta VII being 2/5 length of seta V.

Antennule 6-segmented (Fig. 7E), relative lengths (%) of segments measured along posterior non-setiferous margin 4.8 : 15.3 : 50.7 : 12.0 : 4.8 : 12.4. Armature formula: 1-[3], 2-[8], 3-[5], 4-[3+ae], 5-[2+ae], 6-[**5?**+(1+ae)]. Modified comb-like seta on segment 2 (arrowed in Fig. 7A, E) as in *O. cristata*. Small sensory element on distal segment not found. Aesthetasc on segments 4 and 5 small and very slender, but clearly discerned.

Antenna (Fig. 8A) as in *O. cristata*, except for seta on coxobasis slightly longer, being as long as proximal endopod segment. Labrum (Fig. 8B,C), maxillule (Fig. 8E), and maxilliped (Fig. 8G) as in *O. cristata*. Maxilla (Fig. 8F) and mandible (Fig. 8D) similar to *O. cristata*, except for minor differences in the ornamentation of mandibular blade C and length of seta E, and slight difference in the ornamentation on the outer seta of the maxilla. Tubular extension at tip of outermost element on praecoxal arthrite of maxillule well discerned. Fringe of long pinnules along palmar margin of maxillipedal basis (Fig. 8G) and ornamentation of distal spiniform element (Fig. 8g) similar to *O. cristata*.

Swimming legs (Fig. 9A-D) with armature and ornamentation similar to *O. cristata* (Table 2). Outer subdistal spine on P3 exp-3 shorter than in *O. cristata*, hardly reaching insertion of outer distal spine (Fig. 9C, c), and outer subdistal spine on P4 exp-3 shorter than in *O. cristata*, reaching as far as posterior marginal pore, but not beyond (Fig. 9D). Paired pore on outer margin between subdistal and distal outer spine of P2 exp-3 arrowed in Fig. 9b. Proportional lengths of distal exopodal spines similar to *O. cristata*; variability in length of distal exopodal spine on P3 as in *O. cristata*.

P5 (Fig. 7G) similar to *O. cristata*, except for length of exopodal and outer basal seta being distinctly longer, the former reaching as far as genital apertures.

P6 (Fig. 7C) represented by operculum closing off each genital aperture; armed with 1 spine, spinous process(es) absent.

Egg-sacs not found.

Adult male (Fig. 10). Body length: 421 µm [347 µm, range: 330-360 µm, based on 4 specimens from the eastern Mediterranean]. Sexual dimorphism in antennule, maxilliped, P6, and in genital segmentation.

Proportional lengths (%) of urosomites (excluding caudal rami) 9.2 : 66.0 : 3.9 : 3.9 : 3.9 : 13.1; proportional lengths (%) of urosomites (caudal rami included) 8.1 : 58.3 : 3.5 : 3.5 : 3.5 : 11.6 : 11.6. P5-bearing somite with 3 paired midventral spinous processes (Fig. 10E) as in female. Caudal rami 1.4 times longer than wide. Caudal setae IV and V broken off in all specimens examined, proportional lengths of other caudal setae as in female. Dorsal surface of genital somite with two pairs of pores as figured. Surface of genital flaps with several rows of small spinules (Fig. 10E).

Antennule (Fig. 10B) 4-segmented; distal segment corresponding to fused segments 4-6 of female; relative lengths (%) of segments measured along posterior non-setiferous margin 7.8 : 15.5 : 48.7 : 28.0. Armature formula: 1-[3], 2-[8], 3-[4], 4-[10+2ae+(1+ae)]. Modified comb-like seta on segment 2 as figured (Fig. 10b). Small apical sensory element not discerned. Proximalmost aesthetasc not discernible, position indicated by small pit (Fig. 10B).

Maxilliped (Fig. 10C) mainly as in *O. cristata*, except for slight differences in ornamentation with anterior surface showing 2-3 transverse spinular rows in addition to row of short flat spinules along inner margin (Fig. 10c1) and posterior surface showing 3 rows of short spatulated spinules of graduated length along palmar margin (Fig. 10c1, c2); the 2 small naked setae within the longitudinal cleft unequal in length, with the proximal one being slightly longer than the distal one.

P1-P4 with armature as in female.

P5 (Fig. 10D, F) as in female, i.e. lacking sexual dimorphism in proportional length of setae observed in *O. cristata*.

P6 (Fig. 10E) represented by posterolateral flap closing off genital aperture on either side; covered by pattern of denticles as shown in Fig. 10E; posterolateral corners rounded and not protruding laterally so that they are hardly visible in dorsal aspect (Fig. 10D).

Spermatophore oval (Fig. 10D); swelling of spermatophore during development not affecting shape and relative size of genital somite.

Remarks

Taxonomy. The female of *Oncaea crypta* sp. nov. was erroneously described under the name *O. ovalis* by Shmeleva (1969). The original description of *O. ovalis* by Shmeleva (1966) was based on male specimens only and in her subsequent (re)description of both sexes the author apparently confounded the two species, as has been demonstrated by a careful comparison of Shmeleva´s figures during the present study (cf. *Remarks.* of *O. ovalis*). The most important morphological character separating the two species figured by Shmeleva (1969) is the proportional length of the outer distal spines on the endopod of P2 and P3, which is distinctly longer than the terminal conical projection in the male (= *O. ovalis* s. str.), while these spines are shorter than or about as long as the projection in the female (= *O. crypta* sp. nov.). The complete description of both sexes of the two species in the present account allows for a more detailed comparison of the two species, including mouthparts and ornamentation details which had not been described before. The main diagnostic characters separating *O. crypta* from *O. ovalis* s. str. are (1) its smaller size, (2) the smaller length to width ratio of the CR, (3) P5 exopod fused to somite (free in *O. ovalis* s.str.) and ornamented with single long seta (2 setae in *O. ovalis* s. str.), (4) antennule with comb-like seta on segment 2, being visible in dorsal aspect (this seta not modified in *O. ovalis* s.str.), (5) outer distal spines on endopods of P2 and P3 shorter than terminal conical projection (distinctly longer than projection in *O. ovalis* s.str.), (6) terminal exopod spines of swimming legs longer than or about equal in length to the respective terminal segment (these spines always shorter than their respective segments in *O. ovalis* s. str.), and (7) genital lappets with rounded posterolateral corners in the male (corners are constricted in *O. ovalis* s.str.). Further morphological differences in mouthparts and details of ornamentation are: (8) form and ornamentation of proximal endopod segment of the antenna, being less elongate in *O. crypta* than in *O. ovalis* s.str. and the length of the coxobasal seta, being shorter in *O. crypta*, (9) ornamentation details of labral lobes, (10) surface ornamentation of maxillipedal basis and ornamentation of its distal spine.

Oncaea crypta is a sibling species of *O. cristata*, which thus far occurs exclusively in the Red Sea. The two species differ only in some minor characters (see under *Remarks.* of *O. cristata*), as for instance the proportional length of the outer exopodal spines, the length to width ratio of the genital double-somite, proportional lengths of CR setae, and the length of exopodal and outer basal seta on P5. However, the form of the genital double-somite of *O. crypta* is similar to that of an elongate form variant of its sibling *O. cristata* occurring in the northern Red Sea (Gulf of Aqaba). Separation of the two species merely by their general habitus is difficult and consequently microscopic examination of the exopodal spine lengths and other details is required to separate them.

The species described by Heron & Frost (2000) as *O. ovalis* from the open NE Pacific (2 females) and Washington Inland waters (Dabob Bay, 0-180 m depth, 5 females, 1 male) can be assigned to the *crypta-cristata*-subgroup based on the distinct character of very short outer distal spines on the endopods of P2 and P3, being shorter than the terminal conical projections (their figs. 2J, 20P+Q)

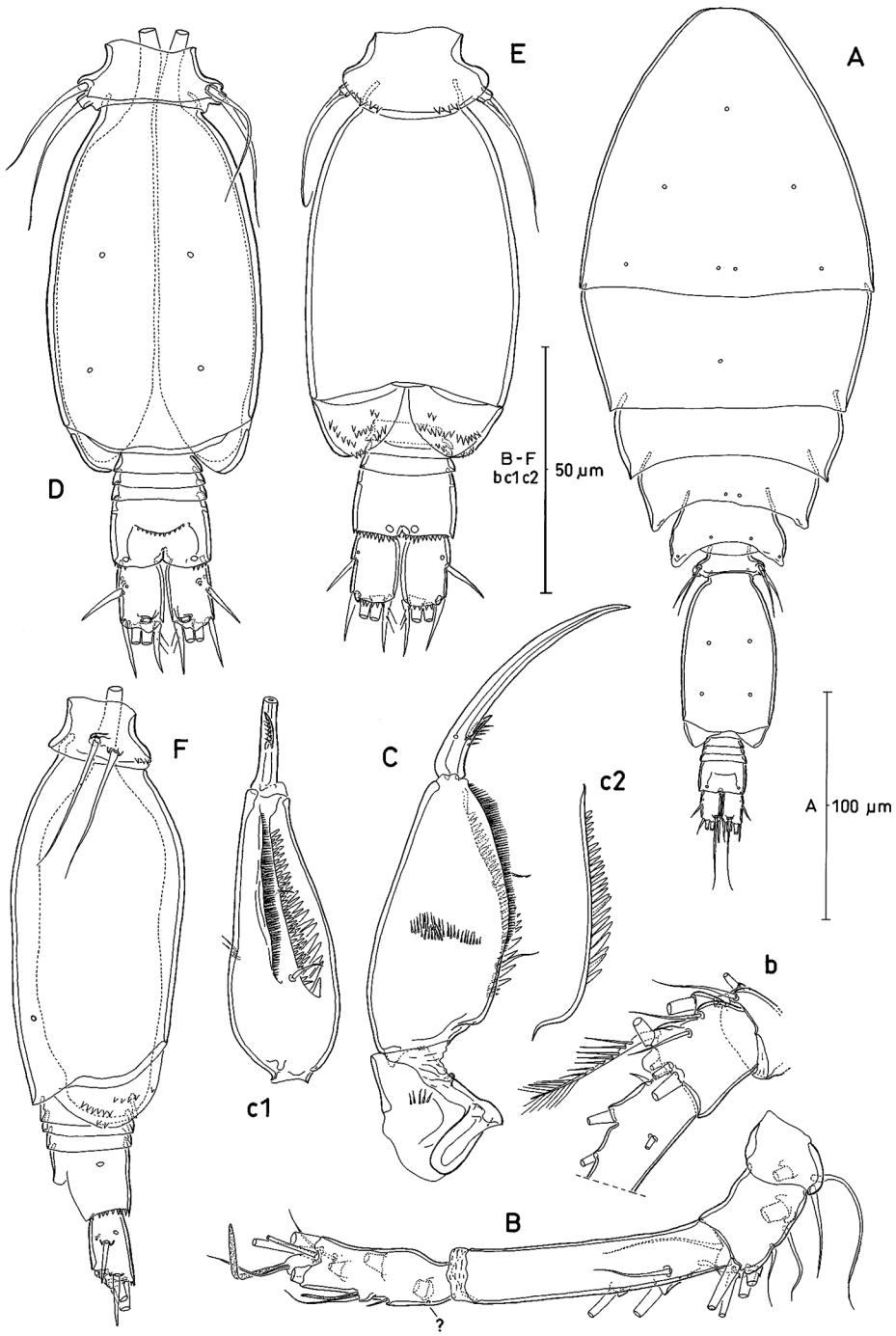

Figure 10. *Oncaea crypta* sp. nov., male (Eastern Mediterranean Sea). **A.** Habitus, dorsal, caudal setae IV and V missing. **B.** Antennule, question mark on segment 4 indicating position of proximalmost aesthetasc (small pit) (**b:** segment 1(partly), 2 and 3 (proximal half), showing comb-like seta on segment 2). **C.** Maxilliped, anterior (**c1:** medial view, syncoxa and distal part of claw omitted; **c2:** palmar margin, posterior view). **D.** Urosome, dorsal. **E.** Urosome, ventral. **F.** Same, lateral (spermatophores not fully developed).

Figure 10. *Oncaea crypta* sp.nov., mâle (Méditerranée orientale). **A.** Habitus, vue dorsale, soies caudales IV et V manquantes. **B.** Antennule, point d'interrogation sur le segment 4 indiquant la position de l'esthétasque le plus proximal (petite fosse) (**b**: segment 1 (à part), 2 et 3 (moitié proximale), montrant la soie en forme de peigne sur le segment 2). **C.** Maxillipède, antérieur (**c1**: vue centrale, syncoxa et partie distale de la griffe omises; **c2**: bord palmaire, vue postérieure). **D.** Urosome, dorsal. **E.** Urosome, ventral. **F.** Urosome, latéral (spermatophores non entièrement développés).

and the single long seta on P5 exopod (their fig. 20H). Their description of the female, which included all mouthparts except for the antennule, resembles *O. crypta* in certain characters, such as the length to width ratio of the genital double-somite and the length of the outer subdistal spine on P4 exp-3, not reaching the insertion of the outer distal spine. The length of the exopodal and outer basal seta on P5, on the other hand, appears to be more similar to *O. cristata*, not reaching as far as the genital apertures. However, some characters of *O. ovalis sensu* Heron & Frost (2000) differ from both *O. cristata* and *O. crypta*, such as (1) the length to width ratio of caudal rami, being about 1.8 times longer than wide [1.5 and 1.6 times longer than wide in *O. crypta* and *O. cristata*, respectively], (2) the proportional lengths of exopodal spines on P3, with the outer subdistal spine not reaching as far as the insertion of outer distal spine [this spine reaching as far as the insertion (*O. crypta*) or even beyond (*O. cristata*)], and (3) the ornamentation of the distal element on the maxillipedal basis, being naked [unipectinate in *O. cristata* and *O. crypta*]. Several elements are missing or not clearly discernible from Heron and Frost´s figures, such as the proportional lengths of CR setae, the ornamentation of the antenna and of the maxillipedal basis (fringe of setules ?). The male was not illustrated in detail by the authors. Given the wide geographical distance between both „populations" and the small morphological differences found in sibling species of the *crypta-cristata*-subgroup, a positive identification of Heron & Frost´s specimens can only be made after a careful re-examination of their specimens, paying particular attention to the CR setae and details of the swimming legs.

Ecological notes

Geographical distribution. O. crypta is distributed in the entire Mediterranean Sea, including its easternmost parts (Böttger-Schnack, 1997, as *O. ovalis*; present study). Outside the Mediterranean, species of the *crypta-cristata*-subgroup are found in very distant localities in the world ocean, including the NE and NW Pacific, the Indian Ocean and the Sargasso Sea (Table 4), but accurate species identification requires more detailed taxonomic analyses and will be done in subsequent studies. The occurrence of the *crypta-cristata*-subgroup in the subarctic NW Pacific, Oyashio region, was restricted to the seasons of importing waters from the (warm) Kuroshio current (April, October) (Nishibe & Ikeda, 2004, and pers. comm.).

Vertical distribution.

O. crypta is assumed to be a mesopelagic species, as it was mainly recorded from depth layers between 100-1000 m, with only scattered occurrence in the upper 100 m (Shmeleva, 1969 [500-700 m], Kršinic, 1998 [50-1000 m], Böttger-Schnack, 1997 [mainly 50-1050 m, few records between 1050-1850 m]). Nishibe & Ikeda (2004) found species of the c*rypta-cristata*-subgroup at depths between 250 - 1000 m in the NW Pacific. In the NE Pacific, species of this group occurred in the upper 200 m layer (Hopcroft material; see Table 4). The actual depth distribution of *O. crypta* remains uncertain, since the species has not yet been differentiated from other species of the *ovalis*-complex during quantitative analyses. In view of the many morphologically similar *ovalis*-type oncaeids occurring in the meso- and bathypelagic zone of the oceans (e.g. Böttger-Schnack, 1996, table VI; see also under "*Concluding Remarks.*") further taxonomic investigations of this species complex are required.

Oncaea ovalis Shmeleva, 1966

Original description

Shmeleva (1966): 935, Fig. 4.1-4.9 (♂ only)

Other description

Shmeleva (1969): 11-13, Fig. 9a-i (♂) [not Fig. 8a-i (♀)]

Doubtful description

Malt et al. (1989): 959-962, Fig. 5I, 6A-J (♂ only)

Type locality

Southern Adriatic Sea, 40°40.8'N, 18°50'E (Stn. 46), 500-700 m.

New type locality (Neotype)

Adriatic Sea, 42°20.0'N, 17°42.5'E: Stn. "P1000", South Adriatic Pit, Dubrovnik area, sampling depth 260-400 m, total water depth ca 1000 m.

Material examined

(1) New type locality: *R/V Bios*, collected 28 March 1998 with Nansen net, 50 cm in diameter, equipped with a closing system, mesh size 0.053 mm, vertical haul (leg. F. Kršinic).

(a) Neotype ♀ in alcohol (ZMH reg. no. K-40804), 3 ♀♀ in alcohol (ZMH reg. no. K-40805), 1 ♂ in alcohol (ZMH reg. no. K-40806).

(b) 3 ♀♀ in alcohol (NHM reg. no. 2004.3078-3080).

(c) 1 ♀ dissected on 10 slides, 1 ♀ in toto on slide, 1 ♂ [partly damaged, most swimming legs missing, except for P1 (left) and P2 endopod (left), provisionally assigned to *O. ovalis*] in toto on slide, 4 ♀♀ (1 with expanded prosome, 1 damaged, urosome and parts of swimming legs missing) in alcohol (RBS).

(2) 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; total water depth 3400 m:
(2.1) Haul 25/1; depth 400-450 m: (a) 2 ♀♀ in alcohol (ZMH reg. no. K-40807)
(b) 1 ♂ in alcohol (NHM reg. no. 2004.3081), 1 ♀ (CR setae IV and V missing) in alcohol (NHM reg. no. 2004.3082)
(c) 1 ♂ in alcohol, 1 ♀ (empty exoskeleton, provisionally assigned to *O. ovalis*) in toto on slide, 1 ♂ dissected on 10 slides, 1 ♂ in alcohol (RBS)
(2.2) Haul 25/2; depth 350-400 m: 2 ♀♀ in alcohol (RBS).
(3) Eastern Mediterranean Sea, 34°26.73'N, 26°15.39'E: Stn. 31; *R/V Meteor* leg 5/1: collected 20 January 1987 with MSN 0.055 mm net (Haul 20/1); depth 400-450 m; total water depth ca 3400 m.
(a) 1 ♂ in alcohol (ZMH reg. no. K-40808)
(b) 1 ♀ in alcohol (NHM reg. no. 2004.3083)
(c) 1 ♀ in alcohol, 1 ♂ in toto on slide (RBS)
(4) Sargasso Sea, 24°29.4'N, 62°00.2'W: Stn. 210; *R/V Poseidon* leg 200/1-2: collected 13 March 1993 with MSN 0.055 mm net (Haul 1/1); depth 3300-3800 m; total water depth ca. 5000 m (leg. D. Schnack): 1 ♀ in toto on slide (RBS).

Description

Adult female (Figs. 11-13; figures are based on specimens from the new type locality in the Adriatic Sea). Body length: 541 µm [(a) 486 µm, range: 470-500 µm, based on 4 specimens from the Adriatic Sea; (b) 450 µm, range: 440-460 µm, based on 4 specimens from the eastern Mediterranean].

Exoskeleton moderately chitinized. Prosome 2.4 times length of urosome, excluding caudal rami, 2.1 times urosome length including caudal rami. P2-bearing somite without dorso-posterior projection in lateral aspect (Fig. 11B). Integumental pores on prosome as indicated in Fig. 11A, B. Pleural areas of P4-bearing somite with rounded posterolateral corners. Single specimen with expanded prosome observed.

Proportional lengths (%) of urosomites are 9.0 : 54.7 : 11.9 : 9.9 : 14.5. Proportional lengths (%) of urosomites and caudal rami are 7.9 : 48.0 : 10.5 : 8.7 : 12.7 : 12.2.

P5-bearing somite with 4 paired midventral spinous processes (Fig. 11D), dorsoposterior pores absent (Fig. 11C).

Genital double-somite oval, twice as long as maximum width (measured in dorsal aspect) and 1.5 times longer than postgenital somites combined; largest width measured slightly anterior to midregion, lateral margins rounded with posterior part tapering gradually. Paired genital apertures located dorsally slightly anterior to midregion of genital double-somite; armature represented by 1 long spine, spinous process(es) absent (Fig. 11C). Dorsal surface without ornamentation except for paired pore at posterior third of genital double-somite (Fig. 11C), ventral surface with single transverse row of spinules anterior to midregion (Fig. 11D).

Anal somite about as wide as long; slightly longer than caudal rami (Fig. 11C). Single pair of secretory pores on either side of anal opening, located dorsally near posterior margin, additional pair of pores anterolaterally to anal operculum (Fig. 11C, D). Anterior margin of anal opening (vestigial anal opening) smooth. Ventral surface with paired pore near posterior margin as in male (cf. Fig. 14E). Posterior margin of somite finely serrate ventrally and laterally (Fig. 11D).

Caudal ramus (Fig. 11F, for numbering of elements cf. Fig. 7F) 1.9 times longer than wide. Armature consisting of 6 elements: seta II and III short, spiniform and unipinnate along medial margin; seta IV long and bipinnate, about half the length of seta V; seta V longest and bipinnale; seta VI very short, slightly longer than seta III, ornamented with few setules along inner margin (Fig. 11F); seta VII about 3/4 length of seta IV, bipinnate and bi-articulate at base. Inner margin of CR naked; anterior surface with 1 dorsal and 1 ventrolateral secretory pore near insertion of seta II (Fig. 11D, F); posterior ventral margin finely serrate as in male (cf. Fig. 14E).

Antennule 6-segmented (Fig. 11E), relative lengths (%) of segments measured along posterior non-setiferous margin 5.5 : 19.6 : 48.0 : 11.4 : 4.4 : 11.1. Armature formula: 1-[3], 2-[8], 3-[5], 4-[3+ae?], 5-[2+ae], 6-[6+(1+ae)]. Seta on segment 2 unipinnate along proximal half (Fig. 11E), but not modified to "comb-like" element as in *O. cristata* or *O. crypta*. Aesthetasc on segment 4 not discerned (pit at position of ae in question marked in Fig. 11E), aesthetasc on segment 5 very slender, apical aesthetasc well developed and fused basally to adjacent seta. Small sensory element on distal segment well discernible.

Antenna 3-segmented, distinctly reflexed (Fig. 12A). Coxobasis with row of long, fine setules along outer margin, row of small spinules along entire outer (exopodal) margin and few long spinules on distal part of inner margin (Fig. 12a), posterior face with row(s) of strong denticles at distal half (Fig. 12A); with bipinnate seta at inner distal corner, being slightly longer than proximal endopod segment (Fig. 12a). Endopod segments unequal in length; proximal endopod segment elongate, moderately subtriangular forming insignificant outer lobate outgrowth bearing long spinular row, with scattered row(s) of small strong denticles along posterior inner margin. Distal endopod segment much shorter than proximal endopod segment (about 3/4 length of proximal endopod segment), with narrow cylindrical base articulating with the proximal endopod segment; posterior surface with two patches of short spinules

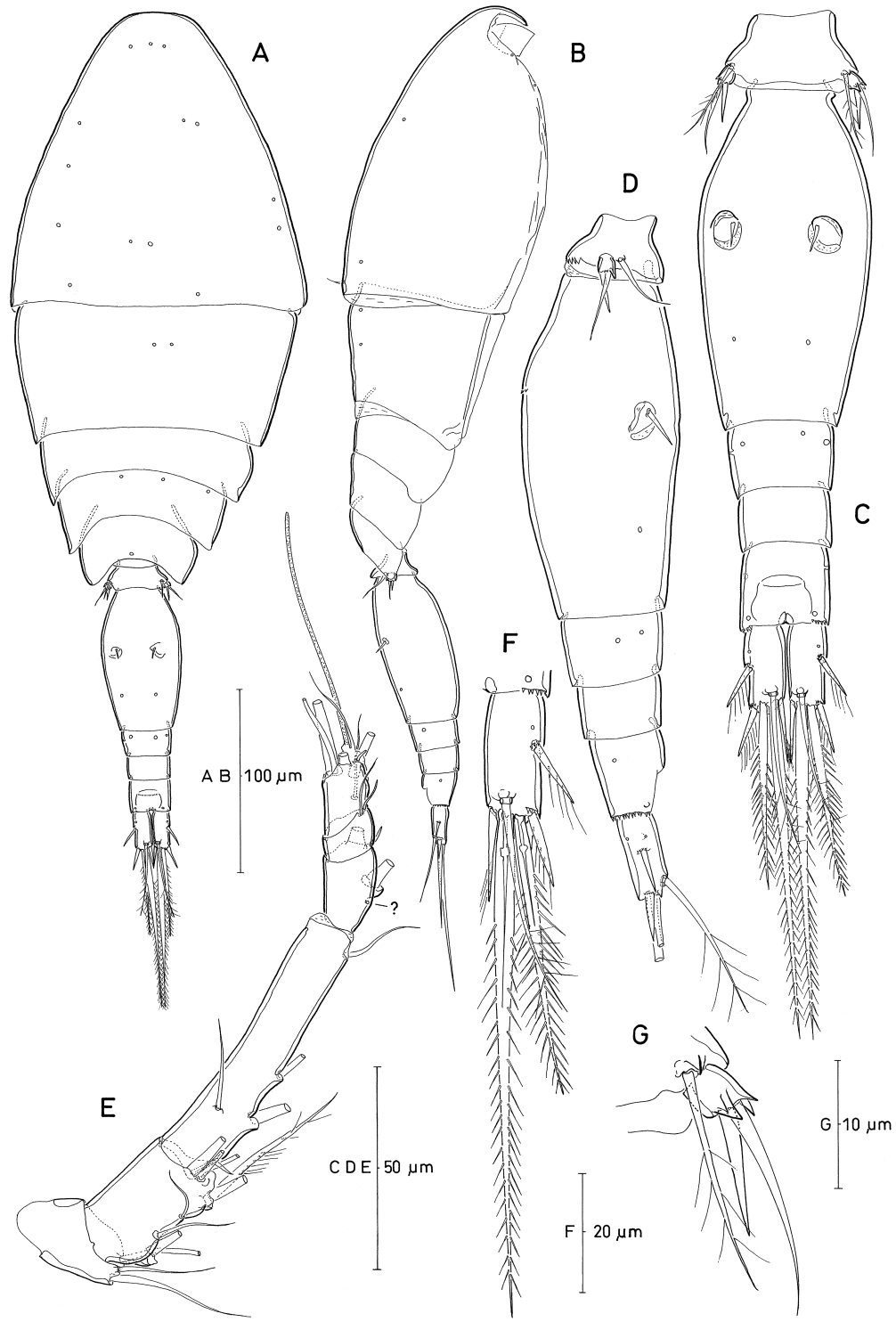

Figure 11. *Oncaea ovalis* Shmeleva 1966, female (Adriatic Sea). **A.** Habitus, dorsal. **B.** Same, lateral (appendages omitted). **C.** Urosome, dorsal. **D.** Urosome, lateral, caudal setae IV and V omitted. **E.** Antennule, question mark on segment 4 indicating position of aethetasc in question (small pit). **F.** Caudal ramus, dorsal. **G.** P5, dorsal.

Figure 11. *Oncaea ovalis* Shmeleva 1966, femelle (Mer Adriatique). **A.** Habitus, vue dorsale. **B.** Habitus, vue latérale (appendices omis). **C.** Urosome, dorsal. **D.** Urosome, latéral, soies caudales IV et V omises. **E.** Antennule, point d'interrogation surle segment 4 indiquant la position de l'esthetasque en question (petite fosse). **F.** Palette furcale, dorsale. **G.** P5, dorsal.

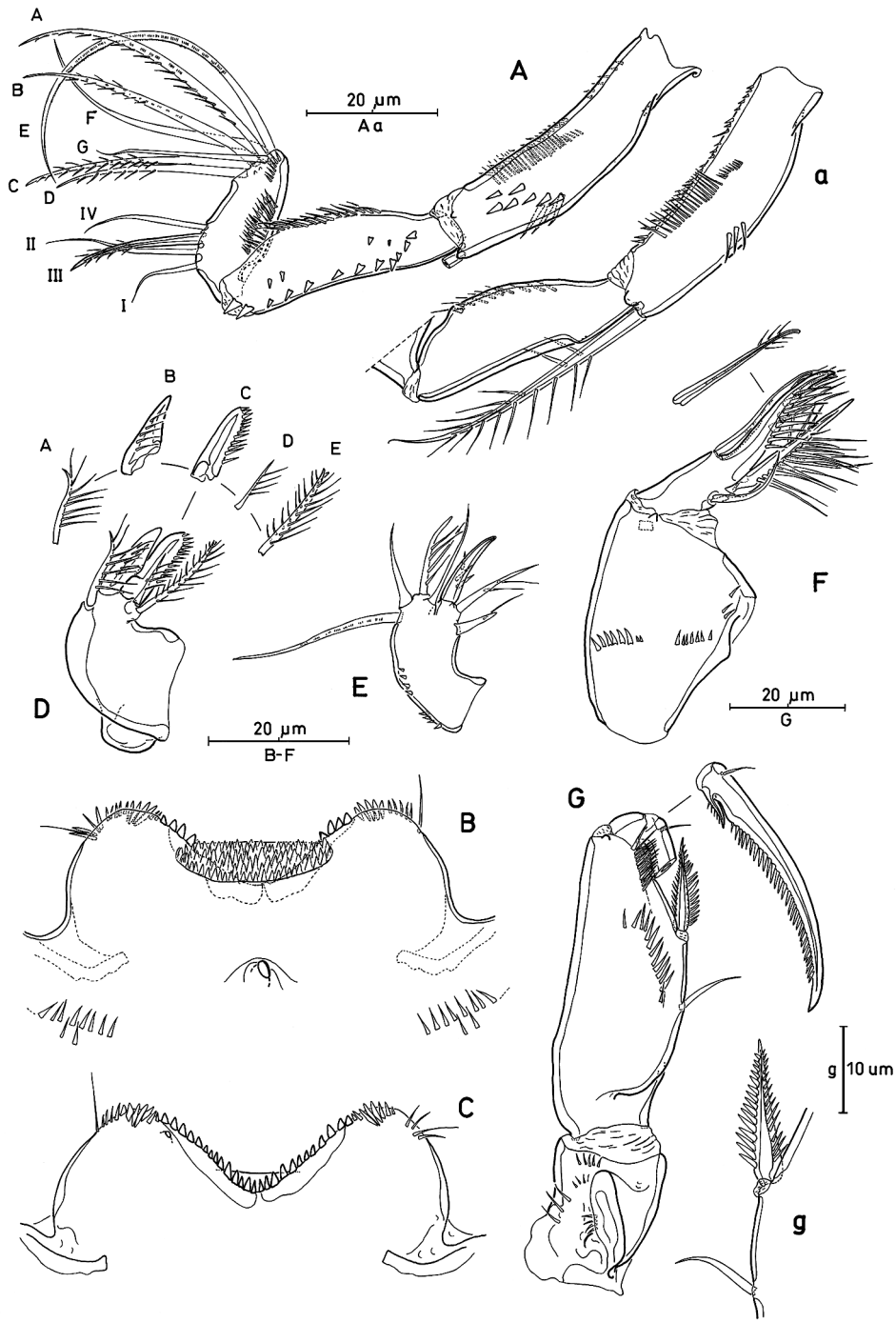

Figure 12. *Oncaea ovalis* Shmeleva 1966, female (Adriatic Sea). **A.** Antenna, posterior, lateral elements are numbered using Roman numerals, distal elements are identified by capital letters, coxobasal seta omitted (**a**, coxobasis and proximal endopod segment, anterior, showing armature and ornamentation details). **B.** Labrum, anterior. **C.** Same, posterior. **D.** Mandible, showing individual elements. **E.** Maxillule. **F.** Maxilla, seta on outer margin figured separately. **G.** Maxilliped, anterior, claw figured separately (**g**, elements on palmar margin, posterior view, showing ornamentation details).

Figure 12. *Oncaea ovalis* Shmeleva 1966, femelle (Mer Adriatique). **A.** Antenne, postérieure, les éléments latéraux sont numérotés par des chiffres romains, les éléments distaux sont identifiés par des capitales, soie coxobasale omise (**a**, coxobase et segment proximal de l'endopodite, antérieurs, montrant l´élément et des détails d'ornementation). **B.** Labre, antérieur. **C.** Labre, postérieur. **D.** Mandibule, montrant des éléments individuels. **E.** Maxillule. **F.** Maxille, soie sur le bord extérieur, figurée séparément. **G.** Maxillipède, antérieur, griffe figurée séparément (**g**, éléments sur le bord palmaire, vue postérieure, montrant des détails d´ornementation).

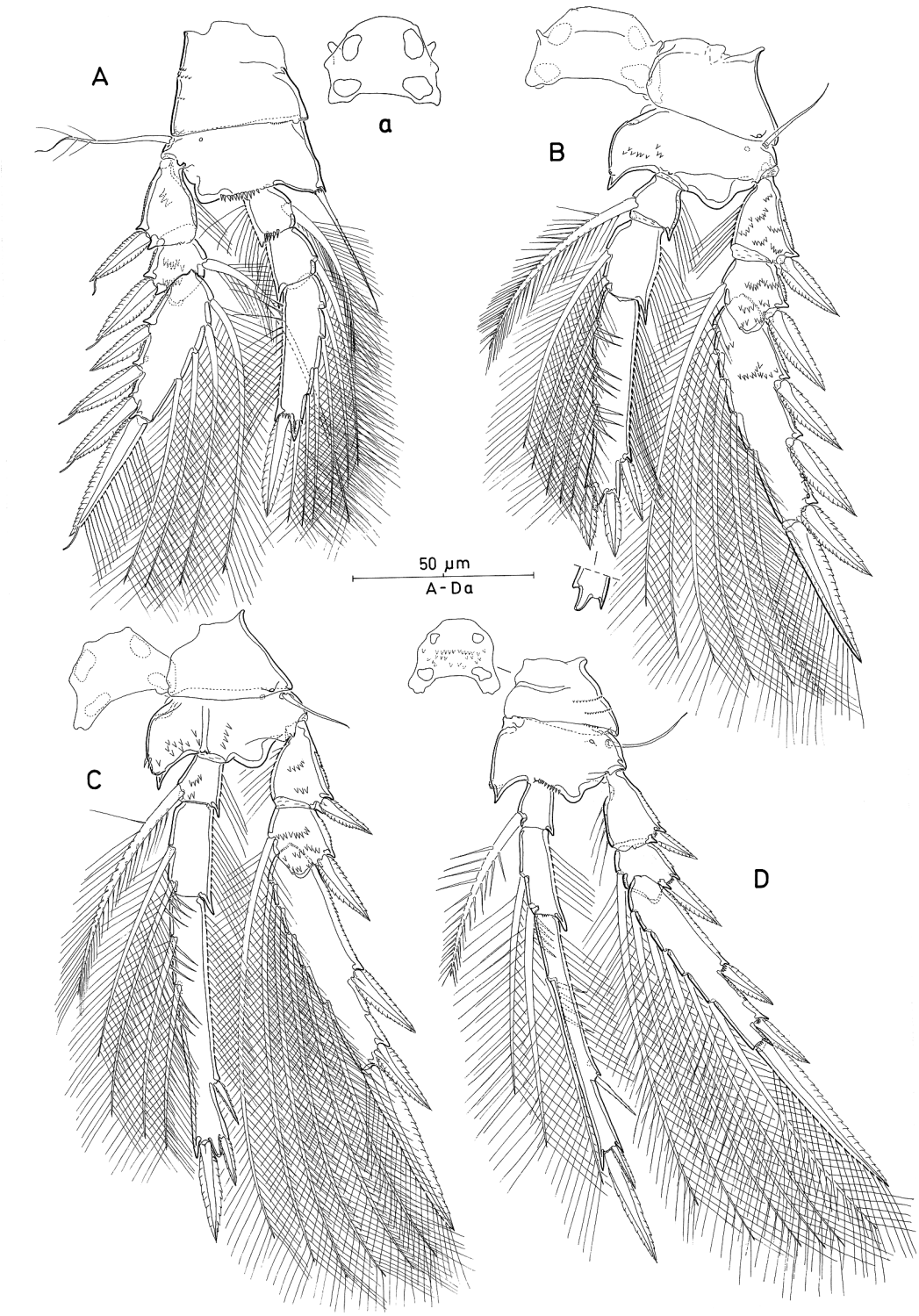

Figure 13. *Oncaea ovalis* Shmeleva 1966, female (Adriatic Sea). **A.** P1, posterior (**a**, intercoxal sclerite, anterior). **B.** P2, posterior. **C.** P3, posterior. **D.** P4, anterior, intercoxal sclerite figured separately.

Figure 13. *Oncaea ovalis* Shmeleva 1966, femelle (Mer Adriatique). **A.** P1, postérieur (**a**, sclérite intercoxal, antérieur). **B.** P2, postérieur. **C.** P3, postérieur. **D.** P4, antérieur, sclérite intercoxal, figuré séparément.

along outer margin, proximal patch consisting of double row of spinules equal in length and form; lateral armature consisting of 3 bare seta (I, II and IV) with seta I shortest, and 1 curved spiniform element (III) ornamented with few spinules bilaterally at distal half (Fig. 12A); distal armature consisting of 4 long setae (A-D), ornamented with pinnules along entire inner margin (A) or bipinnate at distal half (B-D), and 3 bare setae (E-G), with seta E longest and seta G shorter than setae A-D and F.

Labrum (Fig. 12B, C) distinctly bilobed. Distal (ventral) margin of each lobe with 4-6 small rhombic dentiform processes of varying length medially, row of long fine setules at outer ventral margin and row of broad denticles along inner margin. Median concavity covered anteriorly by several overlapping rows of setules. Anterior surface median swelling ornamented with large secretory pore posteriorly, paired row of long setules either side of, but posterior to median swelling (Fig. 12B). Posterior part of medial concavity lacking chitinized teeth (Fig. 12C), with paired row of broad denticles of similar length. Secretory pore(s) on posterior face on distal part of lobes as figured (Fig. 12C), possibly not fully discerned.

Mandible (Fig. 12D) without surface ornamentation on coxa, gnathobase with 5 elements: 3 setae and 2 blades. Ventral element (A) about as long as ventral blade (B), with long fine setules along dorsal side; ventral blade (B) strong and spiniform, with row of minute spinules on posterior side; dorsal blade (C) strong and broad, spinulose along entire dorsal margin; seta D short and and unipinnate; dorsal element (E) longest, setiform and bipinnate.

Maxillule (Fig. 12E) indistinctly bilobed, surface with row of spinules along outer margin. Inner lobe (praecoxal arthrite) with 3 elements: outermost element spiniform and curved, fringed with few coarse spinules, tip of element with tubular extension, middle element setiform and ornamented with few long setules, innermost element setiform with rounded tip and single long spinule at distal half, located along concave inner margin close to other elements. Outer lobe with 4 setiform elements, which are unipinnate (element next to innermost one) or bare. Innermost element slightly longer than spinous outermost element of inner lobe.

Maxilla (Fig. 12F) 2-segmented, allobasis about as long as syncoxa. Syncoxa unarmed, surface ornamented with 2 spinular rows, few additional spinules and 1 large secretory pore. Allobasis produced distally into slightly curved claw bearing 2 rows of very strong spinules along medial margin; outer margin with strong seta extending to tip of allobasal claw, bipinnate at distal part, tip of seta with tubular extension; inner margin with long bare seta and strong basally swollen spine with double row of very strong spinules along the medial margin and 3 spinules along outer margin.

Maxilliped (Fig. 12G) 4-segmented, comprised of syncoxa, basis and 2-segmented endopod. Syncoxa unarmed, surface ornamented with several short rows of spinules. Basis oblong-robust, inner margin with 2 elements unequal in length: proximal element setiform and bare, about 2/3 length of distal element, which is spiniform and ornamented with row of broad spinules along outer posterior margin and smaller spinules along inner margin (Fig. 12g); anterior surface with fringe of long pinnules between half the distance of distal seta and articulation with endopod (Fig. 12G) and row of strong spinules along palmar margin between proximal and distal seta. Proximal endopod segment unarmed. Distal endopod segment drawn out into long curved claw, with pinnules along entire length of concave margin; accessory armature consisting of minute, naked seta on outer proximal margin and unipectinate spine fused basally to inner proximal corner of claw.

Swimming legs 1-4 biramous (Fig. 13A-D), with 3-segmented rami. Armature as in *O. cristata* (Table 2). Intercoxal sclerites well developed, without ornamentation (P1-P3) or with several rows of denticles on posterior face (P4) (Fig. 13D). Coxae and bases of P1-P4 with sparse surface ornamentation as figured. Coxae of P1-P4 with posterior raised secretory pore near outer distal corner. Bases with short outer seta, which is pinnate (P1) or naked (P2-P4); with anterior secretory pore near outer proximal corner; inner portion produced adaxially into pointed process in P2-P4 (Fig. 13B-D), ornamented with raised pore and few spinules at base of process. Inner basal seta on P1 spiniform and naked. Respective legs without distinct length differences between exopod and endopod (P1 + P2) or endopod slightly longer than exopod (P3 + P4). Bases of spines on exopodal and endopodal segments anteriorly surrounded by small spinules, as examplified on terminal exopod spine of P4 (Fig. 13D). Surface ornamentation of all segments sparse.

Exopods. Outer margin of exopod segments with narrow (P1) or well (P2-P4) serrated hyaline lamella; inner margin of proximal exopod segments with long setules. One or 2 secretory pore(s) present on posterior surface of distal segment in P1-P4, located laterally close to outer margin between outer subdistal and outer distal spine in P2-P4 (Fig. 13B-D). Hyaline lamellae on outer spines well developed. Outer and terminal spines of P1 with long subapical tubular extensions, except for proximalmost spine on distal segment. Outer spines on distal exopod segment in P1 increasing in length distally. Terminal spines shorter than distal exopod segments in all legs. Outer subdistal spine of P3 + P4 reaching as far as insertion of outer distal spine (Fig. 13C, D).

Endopods. Outer margin of endopod segments with fringe of long setules, except for proximal segment of P4. Inner seta of proximal endopod segment slightly swollen and plumose (P1-P3) or spiniform and ornamented with long, fine spinules bilaterally (P4). Distal endopod segments of P2 and P3 with distal margin produced into coni-

cal process, showing apical pore (Fig. 13B, C). Distal endopod segment of P4 tapering gradually, posterior surface with single secretory pore. Terminal spine much shorter than distal endopod segment in all legs, less than 1/2 length of this segment in P4. Outer distal spines well developed in P2-P4, much longer than conical process in P2 + P3, as long as distal spine (P2) or about half the length of distal spine (P3 + P4). Outer subdistal spine relatively short in P3 + P4, not reaching insertion of outer distal spine, hyaline lamella reduced. Outer margin of distal segment of P1 terminating in a small process obscuring insertion of distalmost inner seta (Fig. 13A). Inner setae of distal endopod segments of P2-P4 with spinule comb along proximal inner margin; this comb not obvious in P1; also present on distal inner seta of middle endopod segment in P3 + P4.

P5 (Fig. 11G) comprising short outer basal seta, which is pinnate, and small exopod segment delimited from somite. Exopod about as long as wide, ornamented with spinous processes dorsally and laterally at posterior margin and armed with 2 unequal elements: inner seta strong and spiniform, about half the length of setiform outer seta. None of elements reaching as far as genital apertures.

P6 (Fig. 11C, D) represented by operculum closing off each genital aperture; armed with a long spine, spinous process(s) absent or not discernible.

Egg-sacs not observed.

Adult male (Fig. 14, 15A; figures are based on specimens from the eastern Mediterranean Sea, except for Fig. 15A, which is based on a specimen from the new type locality in the Adriatic Sea). Body length (a) 505 µm [440 µm, based on 2 specimens from Adriatic Sea]; (b) 540 µm [400 µm, based on 2 specimens from eastern Mediterranean Sea]. Sexual dimorphism in antennule, maxilliped, P6, and in genital segmentation, slight modification in anal somite and in proportional lengths of endopodal spines on P4.

Proportional lengths (%) of urosomites (excluding caudal rami) 9.3 : 59.5 : 5.9 : 5.1 : 5.4 : 14.8; proportional lengths (%) of urosomites (caudal rami included) 8.1 : 51.9 : 5.1 : 4.4 : 4.7 : 12.9 : 12.9. P5-bearing somite with 3 paired midventral spinous processes (Fig. 14E), not 4 as in female. Length to width ratio of caudal rami and proportional lengths of caudal setae similar to female. Dorsal surface of genital somite with two pairs of pores as figured (Fig. 14D). Surface of genital flaps densely ornamented with several rows of small spinules or denticles, short spinular row on midventral inner margin stronger than those on surface (Fig. 14E). Anal somite 1.2 times wider than long, different from female, pore pattern as in female.

Antennule (Fig. 14B) 4-segmented; distal segment corresponding to fused segments 4-6 of female; relative lengths (%) of segments measured along posterior nonsetiferous margin 7.8 : 17.3 : 48.6 : 26.3. Armature formula: 1-[3], 2-[8], 3-[4], 4-[11+1ae+(1+ae)]. No modified comb-like seta on segment 2. Small apical sensory element well discernible. Proximalmost aesthetasc not discerned (position indicated by question mark in Fig. 14B)

Maxilliped (Fig. 14C) 3-segmented, comprised of syncoxa, basis and 1-segmented endopod. Syncoxa unarmed, surface ornamented with few spinules and medial pore (Fig. 14c1). Basis oblong-robust, inflated in proximal half forming bulbous swelling; anterior surface with 2 transverse spinular rows, fringe of pinnules along inner margin between proximal seta and articulation with endopod (Fig. 14C); posterior surface with 2-3 rows of spatulated spinules of graduated length along palmar margin, proximal elements much longer than distal ones (Fig. 14C) making them well discernible in anterior view (Fig. 14c2); with 2 small naked setae within the longitudinal cleft, proximal seta slightly longer than distal one. 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 without hyaline apex.

P1-P4 with armature and ornamentation mainly as in female, except for P4 enp-3 with outer subdistal and outer distal spine slightly longer than in female, the latter reaching about half the length of distal spine (Fig. 14H).

P5 (Fig. 14D, F) exopod delimited from somite, general shape and armature as in female.

P6 (Fig. 14E) represented by posterolateral flap closing off genital aperture on either side; covered by pattern of denticles as shown in Fig. 14E, G; posterolateral corners constricted and protruding laterally so that they are discernible in dorsal aspect (Fig. 14A, 15A), with receptor (pore) at inner edge of corners (Fig. 14D).

Spermatophore oval (Fig. 14E), of variable size according to state of maturity; swelling of spermatophore during development not affecting shape and relative size of genital somite.

Remarks

Taxonomy. The original description of *Oncaea ovalis* was based on male specimens collected in the southern Adriatic Sea (Shmeleva, 1966). Later, the author published a French version of the original Russian description including figures of the general habitus, urosome, swimming legs, antennule, antenna and maxilliped of both sexes (Shmeleva, 1969). The female described in her subsequent account (1969: 11-12, fig. 8a-i) differs distinctly from the male in the proportional lengths of the spines on the distal segments of the swimming legs: (1) the outer distal spine on the endopods of P2 and P3 are shorter than (P2) or about as long as (P3) the terminal conical projection in the female (1969: fig. 8g, h), while they are distinctly longer than the projection in the male (1966: fig.4.7, 4.8; 1969: fig. 9g, h), (2) the distal endopodal

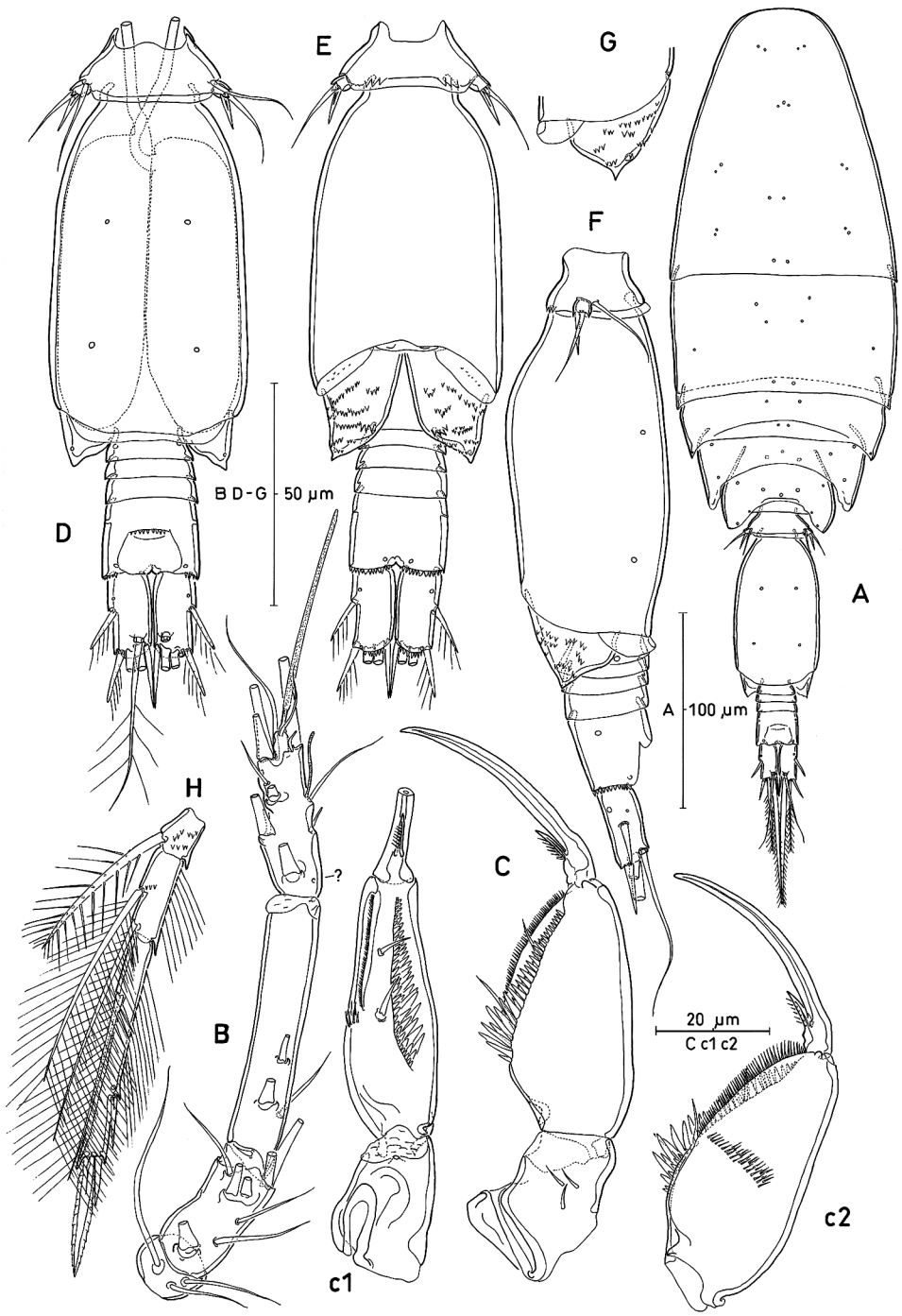

Figure 14. *Oncaea ovalis* Shmeleva 1966, male (Eastern Mediterranean Sea). **A.** Habitus, dorsal. **B.** Antennule, question mark on segment 4 indicating position of proximalmost aesthetasc (small pit). **C.** Maxilliped, posterior (**c1**, medial view, distal part of claw omitted; **c2**, anterior view, syncoxa omitted). **D.** Urosome, dorsal, spermatophores almost fully developed. **E.** Urosome, ventral. **F.** Same, lateral. **G.** Genital lappets, lateral. **H.** P4 endopod, posterior.

Figure 14. *Oncaea ovalis* Shmeleva 1966, mâle (Méditerranée orientale). **A.** Habitus, vue dorsale. **B.** Antennule, point d´interrogation sur le segment 4 indiquant la position de l'esthétasque le plus proximal (petite fosse). **C.** Maxillipède, postérieur (**c1**, vue centrale, partie distale de la griffe omise; **c2**, vue antérieure, syncoxa omise). **D.** Urosome, dorsal, spermatophores presque entièrement développés. **E.** Urosome, ventral. **F.** Urosome, latéral. **G.** Lobes génitaux, latéraux. **H.** Endopodite P4, postérieur.

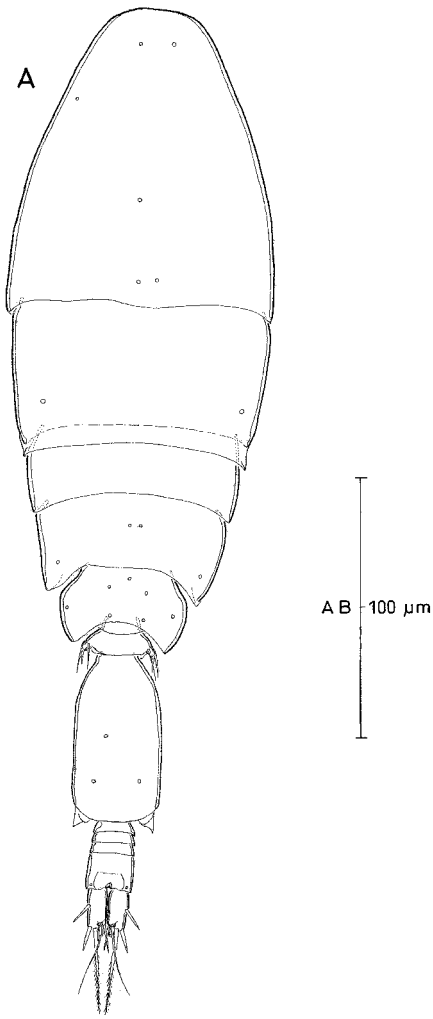

Figure 15. *Oncaea ovalis* Shmeleva 1966, male (Adriatic Sea). Habitus, dorsal, caudal seta V missing.

Figure 15. *Oncaea ovalis* Shmeleva 1966, mâle (Mer Adriatique). Habitus, vue dorsale, soie caudale V manquante.

spines on P1-P3 are longer in the female than figured for the male, (3) the terminal exopodal spine on P3 is longer than the terminal exopod segment in the female, while this spine is about equal in length to the segment in the male. Based on these differences - and substantiated by the recent discovery of both sexes of a species in the Adriatic Sea exhibiting the same proportional spine lengths as in the original description of *O. ovalis* by Shmeleva (1966) - the two sexes described in Shmeleva´s subsequent account cannot be regarded as conspecific. The species described in the present paper is regarded as conspecific with *O. ovalis* s. str., of which only the male had been described (Shmeleva, 1966), while the female of *O. ovalis sensu* Shmeleva (1969) belongs to *O. crypta* sp. nov. (see above). The morphological characters separating the two species are summarized under "*Remarks"* of *O. crypta*.

The male *O. ovalis sensu* Shmeleva (1966) was here identified based on the proportional spine lengths on the endopod of P2, with the outer distal spine being about as long as the distal spine. This is the only reliable character described by Shmeleva that can be used to unequivocally separate the species from the closely related *O. parabathyalis*, where this outer distal spine is shorter than the distal spine (cf. Fig. 18B). Several other characters described in the present redescription of *O. ovalis* differ from Shmeleva´s original account, such as the genital lappets, which are constricted and visible in the dorsal aspect, and not rounded and invisible as in Shmeleva´s record (1966, fig. 4.1). She also described the terminal spine on the exopods of P1, P3 and P4 as being longer than the distal segment, whereas all terminal spines were found to be shorter than their respective segment in the new type material. The size of Shmeleva´s (1966) male is smaller (310 µm) than reported here, which has also been observed for other species of the *ovalis*-group examined during the present study (potential reasons for this discrepancy are discussed under *O. parabathyalis*). Shmeleva´s original (1966) and subsequent (1969) descriptions of the male of *O. ovalis* are incomplete with regard to the armature of the swimming legs. She did not observe the inner seta on the distal endopod segment of P4, which can easily be overlooked, because it is located on the posterior face of the segment (cf. Fig. 13D). Also, the small outer distal spine of P4 enp-3 cannot be identified clearly from Shmeleva´s figure (1966: Fig. 4g; 1969: Figs. 8i, 9i), instead she obviously misinterpreted the long spinous outgrowth on the outer margin as a spine. Several other elements are missing or inadequately illustrated in Shmeleva´s figures, as for instance the number of elements on the antennule, the antenna, and the elements on the maxillipedal basis, but these inconsistencies can be attributed to difficulties in dissecting and observing these small copepods. The remaining mouthparts were not investigated by the author.

Malt et al. (1989) described the male of *O. ovalis* based on a single specimen collected in the eastern Mediterranean Sea near the Lebanese coast. They figured the outer distal spine on the endopod of P2 as being shorter than the distal spine (their fig.6G), which is different from Shmeleva´s original description, but appears to be similar to *O. parabathyalis* sp. nov. described below. On the other hand, Malt et al. (1989) reported the terminal spine lengths on the exopods of P1, P3 and P4 as being equal in length or even longer than the distal segment in their specimen, and the constricted corners of the genital lappets not being visible in dorsal aspect (their fig. 5I), which is similar to Shmeleva´s description of *O. ovalis*, but different from *O. parabathyalis*. [Note, that in their figure 5I illustrating the

dorsal aspect of the urosome, the (dorsal) CR seta VII is not shown; it may be possible that they erroneously figured the ventral side, explaining why the corners were not visible]. Several elements are missing or inadequately figured in Malt´s description, as for instance (1) the antenna, which is figured with 5 lateral elements on the second endopod segment (their fig 6C), but described with 4 elements in the text (p. 960); (2) the armature of the antennule, which is incomplete (their text p. 960); (3) CR seta VII is missing (their fig. 5I) and seta VI is figured as being distinctly longer than seta III, not equal in length as found in the present study for *O. ovalis* s.str.; (4) in the maxilla, the position of the seta on the inner margin is erroneously figured close to the outer seta (their fig. 6D) and ornamentation details are missing; (5) the maxilliped is described as having the unusual number of four segments (their p. 960, fig. 6E), which was not confirmed during the present study [and is atypical for male oncaeids]; (6) the small outer distal spine on the distal endopod segment of P4 was not recorded by Malt et al. (their table on p. 960, fig. 6J); (7) a discrepancy between text and figures is also found in the proportional length of terminal spine of P1 exp-3, which is described as being equal in length to the distal segment in the text (p. 960), while it is figured being shorter than this segment (their fig. 6F). In summary, the male described by Malt et al. (1989) can be placed in the *ovalis-parabathyalis*-subgroup but the combination of characters decribed by Malt et al. (1989) is found in neither of the two species described herein. Thus, positive identification of *O. ovalis sensu* Malt et al. (1989) cannot be given without examination of their specimen.

O. minia sensu Olson [MS] (1949) was provisionally assigned to *O. ovalis* by Malt (1983), but the presence of extremely short outer distal spines on the endopods of P2 and P3, being shorter than the conical projection (1949: plate XV, 6.+7.) clearly indicate that the species belongs to the *crypta-cristata*-subgroup.

Boxshall (1977b) synonymized *O. ovalis* with *O. curta* Sars, 1916, but this course of action was not followed by Malt et al. (1989) nor in the present account for grounds that have been discussed by Böttger-Schnack (2001, p. 29).

Heron & Frost (2000) recorded *O. ovalis* from the open NE Pacific and Washington Inland waters. Their species can unequivocally be assigned to the *crypta-cristata*-subgroup based on the distinct character of very short outer distal spines on the endopods of P2 and P3 (their fig. 20P+Q). Their taxonomic status is discussed in detail under *O. crypta* (see above).

Ecological notes

Geographical distribution. The geographical distribution of *O. ovalis* s. str. is not well known. The species has been recorded from various localities in the Mediterranean during the present study, but records outside this area appear to be doubtful and/or need to be confirmed as most *ovalis*-type specimens recorded from other localities [e.g. NE Pacific (Heron & Frost, 2000), Monterey, California (Hopcroft material), off California/Oregon, (Olson, 1949 [MS]) and NW Pacific (Nishibe material)] were assigned to the *crypta-cristata*-subgroup or other oncaeid species (or -groups) (cf. Table 4). However, the positive identification of *O. ovalis* s.str. from the deep Sargasso Sea during the present study (Table 4) indicates that the species appears to be widely distributed in the subtropical Atlantic.

Abundance and vertical distribution. Kršinic (1998) reported on the vertical distribution of *O. ovalis* in the south Adriatic Pit, where it shared rank 3 among the most numerous oncaeid species in the mesopelagic layers between (100) 200-600 m depth on a yearly average (Kršinic, pers. comm.). Re-examination of copepod material from this area during the present study showed, however, that the hitherto unknown *O. crypta* sp. nov. co-occurs with *O. ovalis* s.str. in that area and thus the actual abundances and distribution patterns of the two species remain unknown. In the eastern Mediterranean, Böttger-Schnack (1997) investigated the vertical distribution patterns of oncaeid microcopepods down to 1850 m depth and found maximum abundances of *ovalis*-type oncaeids (as "*O. ovalis*" + "*O. bathyalis*") at depths between 100-1000 m. [The species *O. ovalis sensu* Böttger-Schnack (1997) is identical with *O. crypta* sp. nov., while both *O. ovalis* s. str. and the newly described *O. parabathyalis* were grouped together under the name "*O. bathyalis*" by Böttger-Schnack (1997).]

Oncaea parabathyalis sp. nov.

Synonymy

Oncaea bathyalis Shmeleva, 1968: 1785-1786, fig. 2.10-2.12 (♂) [not Fig. 2.1-2.9 (♀)].

Other description

Shmeleva (1969): 16-18, Fig. 13a-i (♂) [not Fig. 12a-i (♀)].

Doubtful description

Malt et al. (1989): 962-964, Fig. 7A-J (♂ only).

Type locality

Adriatic Sea, 42°20.0'N, 17°42.5'E: Stn. "P1000", South Adriatic Pit, Dubrovnik area, sampling depth 260-400 m, total water depth ca 1000 m.

Material examined

(1) Type locality: *R/V Bios*, collected 28 March 1998 with

Nansen net, 50 cm in diameter, equipped with closing system, mesh size 0.053 mm, vertical haul (leg. F. Kršinic).

(a) Holotype ♀ in alcohol (ZMH reg. no. K-40786), 1 paratype ♂ in alcohol (ZMH reg. no. K-40787).

Other paratypes. (2) Eastern Mediterranean Sea, 34°25.26'N, 26°14.99'E: Stn. 35; *R/V Meteor* leg 5/1: collected 20 January 1987 with MSN 0.055 mm net; total water depth ca 3400 m:

(2.1) Haul 25/1; depth 400-450 m: (a) 1 ♂ in alcohol (ZMH reg. no. K-40788), 1♂ in alcohol (ZMH reg. no. K-40789)

(b) 1 ♂ in alcohol (NHM reg. no. 2004.3072)

(b) 1 ♀ in alcohol (RBS)

(2.2) Haul 25/2; depth 350-400 m: 2 ♀♀ in alcohol, 1 ♂ in toto on 1 slide (A1 and A2 missing), 1 ♂ dissected on 10 slides (RBS)

(3) Eastern Mediterranean Sea, 34°23.90'N, 26°11.19'E: Stn. 34; *R/V Meteor* leg 5/1: collected 20 January 1987 with MSN 0.055 mm net (Haul 23/4); depth 450-600 m; total water depth 3570 m.

(a) 1 ♀ in alcohol (CR setae complete) (ZMH reg. no. K-40790), 2 ♀♀ in alcohol (CR setae IV and V missing) (ZMH reg. no. K-40791)

(b) 2 ♀♀ in alcohol (CR setae IV and V missing) (NHM reg. no. 2004.3073-3074)

(c) 1 ♀ dissected on 1 slide in polyvinyllactophenol, 1 ♀ on 1 slide in lactophenol (P4 and P5 partly missing), 1 ♀ partly dissected (P1-P4, urosome, A1 and A2 on 8 slides, remaining mouthparts in alcohol), 1 ♀ dissected on 12 slides, 1 ♀ in alcohol (CR setae IV and V missing, prosome moderately expanded) (RBS)

(4) Eastern Mediterranean Sea, 34°26.64'N, 26°15.99'E: Stn. 21; *R/V Meteor* leg 5/1: collected 17 January 1987 with MSN 0.055 mm net (Haul 12/2); depth 750-900 m; total water depth ca 3500 m.

(a) 1 ♀ in alcohol (ZMH reg. no. K-40792)

(b) 2 ♀♀ in alcohol (NHM reg. no. 2004.3075-3076)

(5) Eastern Mediterranean Sea, 34°26.73'N, 26°15.39'E: Stn. 31; *R/V Meteor* leg 5/1: collected 20 January 1987 with MSN 0.055 mm net (Haul 20/1); depth 400-450 m; total water depth ca 3400 m.

(a) 1 ♂ in alcohol (ZMH reg. no. K-40793)

(b) 1 ♂ in alcohol (NHM reg. no. 2004.3077)

(c) 2 ♀♀ in alcohol, 1 ♂ in toto on 1 slide (RBS)

Other material examined. (6) Northern Arabian Sea, 20°44'N, 59°40'E: Stn. 347; *R/V Meteor* leg 5/3a: collected 5 April 1987 with MSN 0.055 mm; total water depth 2500 m:

(6.1) Haul 7/2; depth 250-300 m: 1 ♀ dissected on 1 slide in polyvinyllactophenol (RBS)

(6.2) Haul 5/4; depth 1450-1650 m: 1 ♀ dissected on 1 slide in polyvinyllactophenol (RBS).

(7) Equatorial Indian Ocean, 04°47.7'S, 87°14.4'E: Stn. 11; *R/V Hakuho Maru* leg 76-5: collected 24 January 1977 with a Motoda net, 0.1 mm mesh size; depth layer 300 m, horizontal haul; total water depth 3035 m (leg. S. Nishida): 3 ♀♀ in toto on slides, 2 ♀♀, 1 juvenile in formaldehyde [tentatively assigned to *O. parabathyalis*] (RBS)

Description

Adult female (Figs. 16-18, figures are based on specimens from the eastern Mediterranean). Body length: 635 µm [(a) 500 µm, based on 1 specimen from the Adriatic Sea; (b) 470µm, range: 460-510 µm, based on 7 specimens from the eastern Mediterranean Sea].

Exoskeleton well chitinized. Prosome 2.6 times length of urosome, excluding caudal rami, 2.3 times urosome length including caudal rami. P2-bearing somite without dorso-posterior projection in lateral aspect (Fig. 16B). Integumental pores on prosome as indicated in Fig. 16A, B. Pleural areas of P4-bearing somite with rounded posterolateral corners. Few specimens with moderately expanded prosome.

Proportional lengths (%) of urosomites are 11.7 : 57.8 : 9.7 : 7.3 : 13.5. Proportional lengths (%) of urosomites and caudal rami are 10.2 : 50.4 : 8.4 : 6.4 : 11.8 : 12.8.

P5-bearing somite with 3 paired midventral spinous processes (Fig. 16E), paired dorsoposterior pore present (Fig. 16C).

Genital double-somite oval, 1.8 times as long as maximum width (measured in dorsal aspect) and about 2 times longer than postgenital somites combined; largest width measured anterior to midlevel at 2/5 distance from anterior margin, lateral margins rounded with posterior part tapering gradually. Paired genital apertures located dorsally slightly anterior to midregion of genital double-somite; armature represented by 1 short spine, spinous process(es) absent (Fig. 16C). Dorsal surface with paired pore at posterior quarter of genital double-somite (Fig. 16C), ventral surface ornamented with 4 tranverse rows of small denticles (Fig. 16E).

Anal somite 1.2 times wider than long; about as long as caudal rami (Fig. 16C). Single pair of secretory pores on either side of anal opening, located dorsally near posterior margin, additional pair of pores anterolaterally to anal operculum (Fig. 16D). Anterior margin of anal opening (vestigial anal opening) smooth. Ventral surface with paired pore near posterior margin as in male (cf. Fig. 19E). Posterior margin of somite finely serrate ventrally and laterally (Fig.16D).

Caudal ramus (Fig. 16F) 1.9 times longer than wide. Armature consisting of 6 elements (for numbering of elements cf. Fig. 6F: seta II and III short, spiniform and bare (?); seta IV long and bipinnate, almost 2/3 the length of seta V; seta V longest and bipinnate, both setae with short strong pinnules along proximal third of seta and longer pinnules

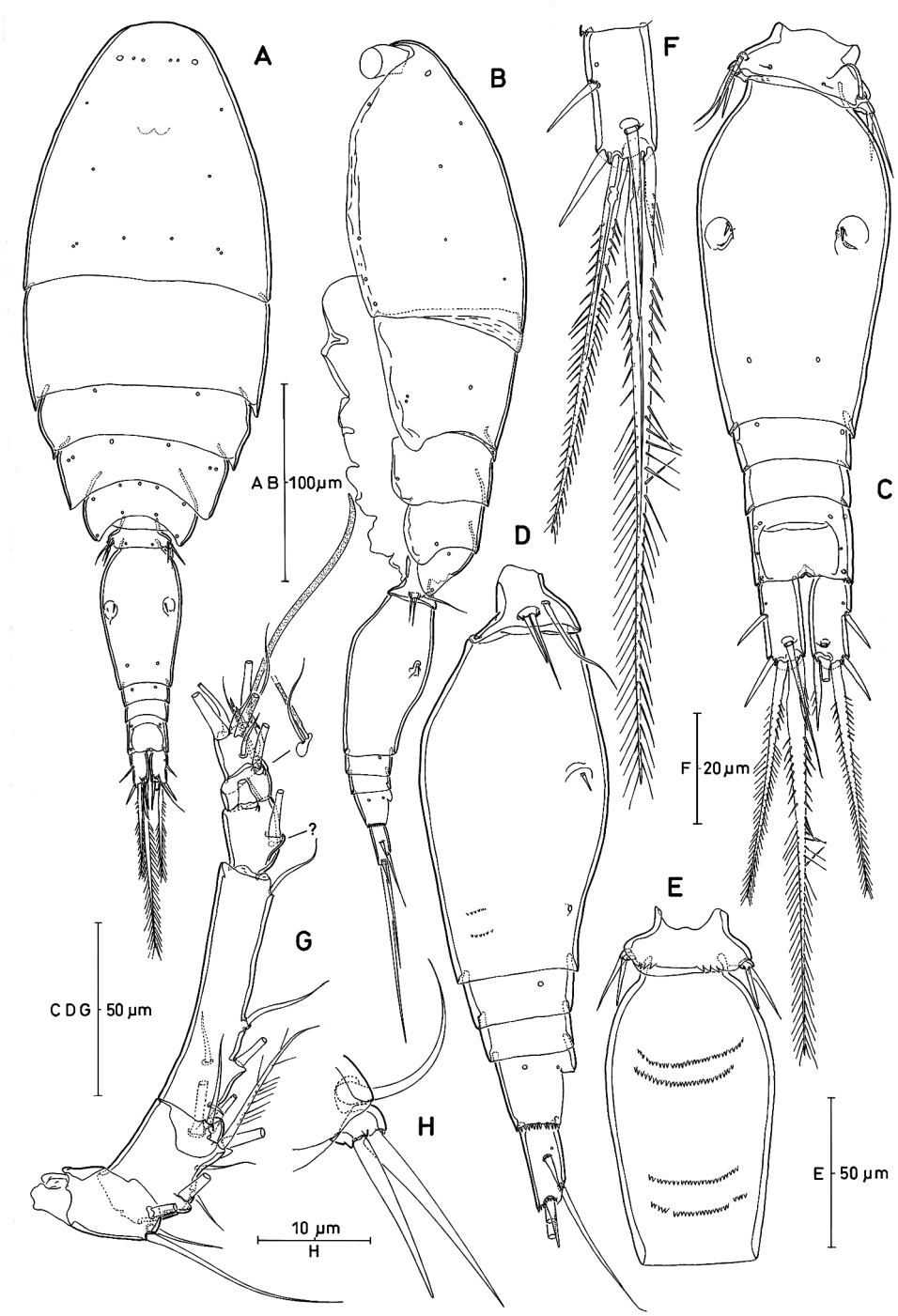

Figure 16. *Oncaea parabathyalis* sp. nov., female (Eastern Mediterranean Sea). **A.** Habitus, dorsal, left caudal seta V missing. **B.** Same, lateral (appendages omitted). **C.** Urosome, dorsal, left caudal setae V missing. **D.** Urosome, lateral, caudal setae IV and V omitted. **E.** P5-bearing somite and genital-double somite, ventral. **F.** Caudal ramus, dorsal. **G.** Antennule, question mark on segment 4 indicating position of aesthetasc in question (small pit).

Figure 16. *Oncaea parabathyalis* sp. nov., femelle (Méditerranée orientale). **A.** Habitus, vue dorsale, soie caudale gauche V manquante. **B.** Habitus, vue latérale (appendices omis). **C.** Urosome, dorsal, soie caudale gauche V manquant. **D.** Urosome, latéral, soies caudales gauches IV et V omises. **E.** Segment portant P5 et double segment génital, ventraux. **F.** Palette furcale, dorsale. G. Antennule, point d´interrogation sur le segment 4 indiquant la position de l´esthétasque en question (petite fosse).

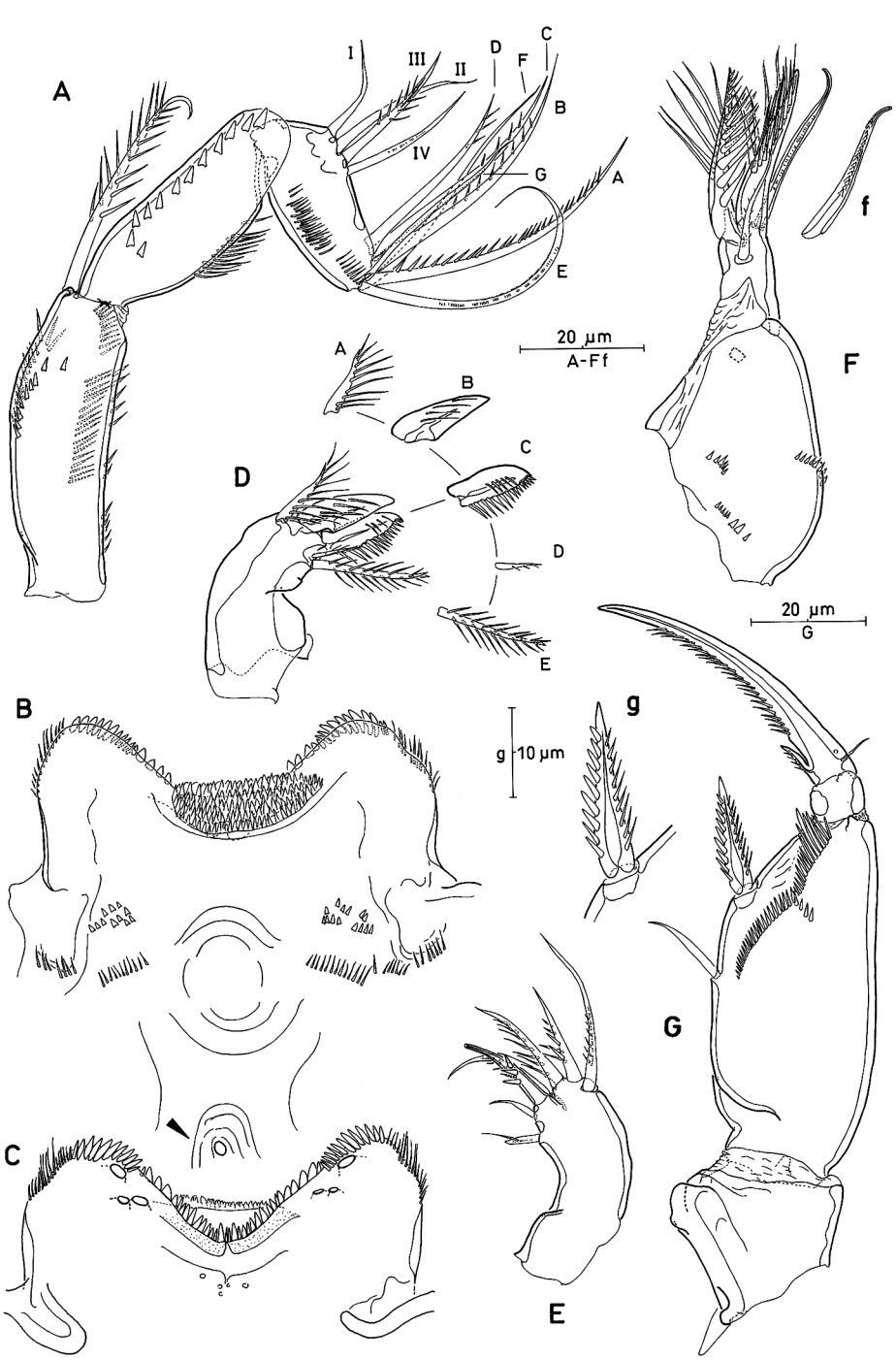

Figure 17. *Oncaea parabathyalis* sp. nov., female (Eastern Mediterranean Sea) **A** Antenna, lateral elements are numbered using Roman numerals, distal elements are identified by capital letters. **B.** Labrum, anterior, large secretory pore on posterior part of median swelling arrowed. **C.** Same, posterior. **D.** Mandible, showing individual elements, numbered by capital letters. **E.** Maxillule. **F.** Maxilla, (**f**, seta on outer margin, showing ornamentation details). **G.** Maxilliped, anterior (**g**, distal element on palmar margin, anterior, showing ornamentation details).

Figure 17. *Oncaea parabathyalis* sp. nov., femelle (Méditerranée orientale). **A.** Antenna, les éléments latéraux sont numérotés par des chiffres romains, les éléments distaux sont identifiés par des capitales. **B.** Labre, antérieur, grand pore secrétant, se trouvant sur la partie postérieure de l'élément central gonflé, marquée par des flèches. **C.** Labre, postérieur. **D.** Mandibule, montrant des éléments individuels, numérotés par des capitales. **E.** Maxillule. **F.** Maxille (**f**, soie sur le bord extérieur, montrant des détails d'ornementation). **G.** Maxillipède, antérieur (**g**, élément distal sur le bord palmaire, antérieur, montrant des détails d'ornementation).

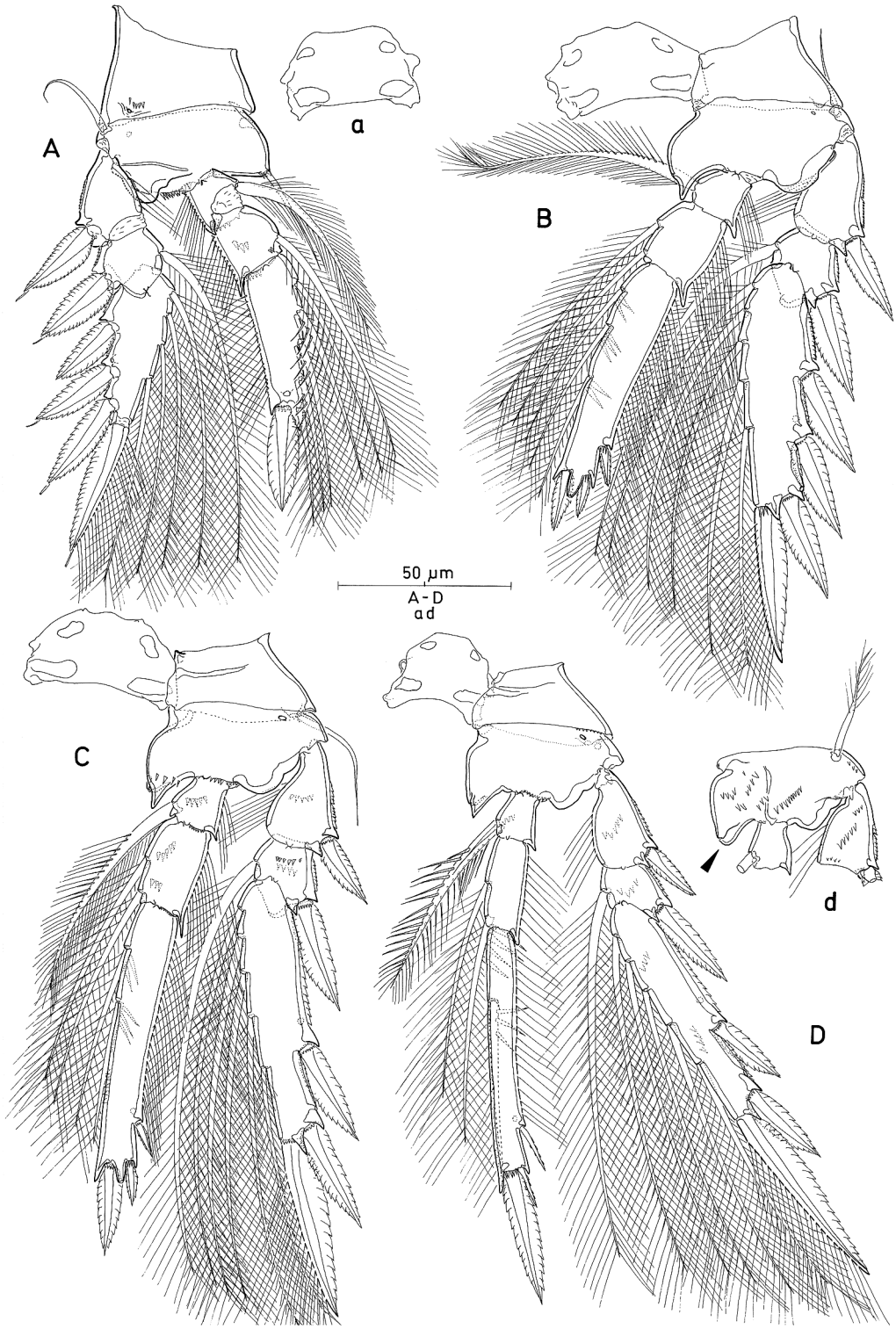

Figure 18. *Oncaea parabathyalis* sp. nov., female (Eastern Mediterranean Sea). **A.** P1, posterior. **B.** P2, anterior. **C.** P3, anterior. **D.** P4, anterior, basal seta missing (**d**, basis of another specimen, posterior, showing basal seta, arrow indicating aberrant (rounded) process on outer proximal corner).

Figure 18. *Oncaea parabathyalis* sp. nov., femelle (Méditerranée orientale). **A.** P1, postérieur. **B.** P2, antérieur. **C.** P3, antérieur. **D.** P4, antérieur, soie basale manquante (**d**, base d'un autre spécimen, postérieur, montrant la soie basale, flèche indiquant un élément atypique sur le coin extérieur proximal).

along distal half; seta VI short and swollen at proximal half, somewhat longer than seta III, ornamented with few setules along inner margin (Fig. 16F); seta VII about half the length of seta IV, bi-articulate at base and bare (?). Inner margin of CR naked; anterior surface with 1 dorsal pore near insertion of seta II (Fig. 16F); posterior ventral margin finely serrate as in male (cf. Fig. 19E).

Antennule 6-segmented (Fig. 16E), relative lengths (%) of segments measured along posterior non-setiferous margin 8.3 : 18.9 : 48.3 : 11.0 : 4.5 : 9.0. Armature formula: 1-[3], 2-[8], 3-[5], 4-[3+ae?], 5-[2+ae], 6-[6+(1+ae)]. Seta on segment 2 (Fig. 16G) unipinnate along proximal half, but not modified into "comb-like" element. Aesthetasc on segment 4 not discerned (pit at position of ae in question marked in Fig. 16E), aesthetasc on segment 5 very slender, apical aesthetasc well developed and fused basally to adjacent seta. Small sensory element on distal segment well discernible.

Antenna 3-segmented, distinctly reflexed (Fig. 17A). Coxobasis with row of long, fine setules near outer and inner margins, row of spinules along entire outer (exopodal) margin and few long spinules on distal part of inner margin, posterior face with curved row of strong denticles at distal half; with bipinnate seta at inner distal corner, being as long as proximal endopod segment (Fig. 17A). Endopod segments unequal in length; proximal endopod segment elongate, outer lobate outgrowth insignificant, with long spinular row along outer margin, curved row of very strong denticles along posterior inner margin. Distal endopod segment shorter than proximal endopod segment (about 2/3 length of proximal endopod segment), with narrow cylindrical base articulating with the proximal endopod segment; posterior surface with 1 patch and 1 row of short spinules along outer margin; lateral armature consisting of 3 bare seta (I, II and IV), with seta I slightly shorter and seta II somewhat longer than seta IV, and 1 curved spiniform element (III) ornamented with few spinules bilaterally at distal half (Fig. 17A); distal armature consisting of 4 long setae (A-D), ornamented with pinnules along entire inner margin (A) or at distal half (B-D), and 3 bare setae (E-G), with seta E longest and seta G shorter than setae A-D and F.

Labrum (Fig. 17B, C) distinctly bilobed. Distal (ventral) margin of each lobe with 10-12 rhombic dentiform processes of graduated length medially, row of long fine setules at outer ventral margin and row of broad denticles along inner margin. Median concavity covered anteriorly by several overlapping rows of spatulated hyaline setules. Anterior surface with paired row(s) of setules and patch of small denticles either side of median swelling; large secretory pore located posteriorly at some distance (arrowed in Fig. 17B). Posterior part of medial concavity lacking chitinized teeth (Fig. 17C), with paired row of more or less broad denticles of similar length. Posterior face with 3 secretory pores located distally on each lobe (Fig. 17C).

Mandible (Fig. 17D) without surface ornamentation on coxa, gnathobase with 5 elements: 3 setae and 2 blades. Ventral element (A) about as long as ventral blade (B), with long fine setules along dorsal side; ventral blade (B) strong and spiniform, with row of minute spinules on posterior side; dorsal blade (C) strong and broad, spinulose along entire dorsal margin and with additional row of spinules on distal half of posterior face; seta D short and and unipinnate; dorsal element (E) longest, setiform and bipinnate.

Maxillule (Fig. 17E) indistinctly bilobed, surface unornamented. Inner lobe (praecoxal arthrite) with 3 elements: outermost element spiniform and curved, fringed with 3 coarse spinules and additional row of setules along inner margin, tip of element with tubular extension, middle element setiform and bare, innermost element small and setiform with rounded tip, located along concave inner margin at small distance from other elements and ornamented with 1 long spinule distally. Outer lobe with 4 setiform elements, which are uni- or bipinnate or bare (innermost element). Outermost element longest, the 2 inner elements longer than spinous outermost element of inner lobe.

Maxilla (Fig. 17F) 2-segmented, allobasis about as long as syncoxa. Syncoxa unarmed, surface ornamented with 3 spinular rows and 1 large secretory pore. Allobasis produced distally into slightly curved claw bearing 2 rows of very strong spinules along medial margin; outer margin with strong seta extending to tip of allobasal claw, ornamented with overlapping row of minute denticles along one side (Fig. 17f), tip of seta with tubular extension; inner margin with long sparsely pinnate seta and strong basally swollen spine with double row of very strong spinules along the medial margin and 3 spinules along outer margin.

Maxilliped (Fig. 17G) 4-segmented, comprised of syncoxa, basis and 2-segmented endopod. Syncoxa unarmed, surface ornamentation not discerned. Basis oblong-robust, inner margin with 2 elements unequal in length: proximal element setiform and bare, about 3/4 length of distal element, which is spiniform and ornamented with row of broad spinules along outer posterior margin and more slender spinules of similar length along inner margin (Fig.17g); anterior surface with 2 rows of blunt pinnules merging one into another along palmar margin, proximal row between proximal and distal seta slightly curved, with pinnules similar in length, distal row between distal seta and articulation with endopod showing pinnules of graduated length (Fig. 17G). Proximal endopod segment unarmed. Distal endopod segment drawn out into long curved claw, with pinnules along entire length of concave margin; accessory armature consisting of minute, naked seta on outer proximal margin and unipectinate spine fused basally to inner proximal corner of claw.

Swimming legs 1-4 biramous (Fig. 18A-D), with 3-seg-

mented rami. Armature as in *O. cristata* (Table 2). Intercoxal sclerites well developed, without ornamentation. Coxae and bases of P1-P4 with sparse surface ornamentation as figured. Coxae of P1-P4 with posterior raised secretory pore near outer distal corner. Bases with short outer seta, which is naked (P1-P3) or pinnate (P4); with anterior secretory pore near outer proximal corner; inner portion usually produced adaxially into pointed process in P2-P4 (Fig. 18B-D, aberrant form of process arrowed in Fig. 18d), ornamented with raised pore and few spinules at base of process. Inner basal seta on P1 spiniform and naked. Respective legs without distinct length differences between exopod and endopod. Bases of spines on exopodal and endopodal segments anteriorly surrounded by small spinules. Surface ornamentation of all segments sparse.

Exopods. Outer margin of exopod segments with narrow (P1) or well (P2-P4) serrated hyaline lamella; inner margin of proximal exopod segments with long setules. One or 2 secretory pore(s) present on posterior surface of distal segment in P1-P4, distal one located laterally close to outer margin between outer subdistal and outer distal spine in P2-P4 (Fig. 18B-D). Hyaline lamellae on outer spines well developed. Outer and terminal spines of P1 with long subapical tubular extensions, except for proximalmost spine on distal segment. Outer spines on distal exopod segment in P1 slightly increasing in length distally. Terminal spine shorter than distal exopod segment in all legs. Outer subdistal spine reaching well beyond insertion of outer distal spine (P2 + P3) or as far as insertion of outer distal spine (P4) (Fig. 18B-D).

Endopods. Outer margin of endopod segments with fringe of long setules, except for proximal segment of P4. Inner seta of proximal endopod segment slightly swollen and plumose (P1-P3) or spiniform and ornamented with long, fine spinules bilaterally (P4). Distal endopod segments of P2 and P3 with distal margin produced into conical process, showing apical pore (Fig. 18B,C). Distal endopod segment of P4 with single secretory pore on posterior surface. Terminal spine much shorter than distal endopod segment in all legs, about 1/2 length of this segment in P4. Outer distal spines well developed in P2-P4 and much longer than conical process in P2 + P3; shorter than terminal spines in P2-P4, reaching about 2/3 the length (P2), about 1/2 the length (P3) or about 1/3 the length (P4) of distal spine. Outer subdistal spine short in P3 + P4, not reaching insertion of (P3) or slightly beyond (P4) outer distal spine, hyaline lamella reduced especially in P4. Outer margin of distal segment of P1 terminating in a small process obscuring insertion of distalmost inner seta (Fig. 18A). Inner setae of distal endopod segments of P1-P4 with spinule comb along proximal inner margin; also present on distal inner seta of middle endopod segment in P4.

P5 (Fig. 16H) comprising outer basal seta, which is naked, and small exopod segment delimited from somite. Exopod slightly wider than long, unornamented and armed with 2 setiform elements unequal in length: inner (ventral) seta about 4/5 the length of outer (dorsal) seta. None of the elements reaching as far as genital apertures.

P6 (Fig. 16C, D) represented by operculum closing off each genital aperture; armed with a single spine, spinuous process(es) absent.

Egg-sacs not observed.

Adult male (Fig. 19, figures are based on specimens from the eastern Mediterranean Sea, except for Fig. 19A, which is based on a specimen from the type locality). Body length: 540 µm [(a) 440 µm, based on a single specimen from Adriatic Sea; (b) 403 µm, range: 400-410 µm, based on 6 specimens from eastern Mediterranean Sea]. Sexual dimorphism in antennule, maxilliped, P6, and in genital segmentation, slight modification in proportional lengths of endopodal spines on P2 and in number of midventral spinous processes on P5-bearing somite.

Integumental pores on prosome and urosome as figured (Fig. 19A); surface of exoskeleton on prosome and genital somite densely covered with numerous small pits as examplified for genital somite in Figs. 19D, E (pits not figured in Fig. 19A).

Proportional lengths (%) of urosomites (excluding caudal rami) 11.7 : 60.0 : 5.2 : 4.5 : 4.1 : 14.5; proportional lengths (%) of urosomites (caudal rami included) 10.7 : 51.8 : 4.4 : 3.9 : 3.6 : 12.5 : 13.7.

P5-bearing somite with number of midventral spinous processes (Fig. 19E) and dorsoposterior pores as in female.

Length to width ratio of caudal rami and proportional lengths of caudal setae similar to female. Dorsal surface of genital somite with two pairs of pores and densely covered with numerous small pits (Fig. 19D), ventral surface less pitted (Fig. 19E). Surface of genital flaps ornamented with several rows of small spinules or denticles (Fig. 19E). Anal somite about 1.3 times wider than long, similar to female, pore pattern as in female.

Antennule (Fig. 19G) 4-segmented; distal segment corresponding to fused segments 4-6 of female; relative lengths (%) of segments measured along posterior nonsetiferous margin 8.0 : 19.6 : 48.4 : 24.0. Armature formula: 1-[3], 2-[8], 3-[4], 4-[11+2ae+(1+ae)]. Seta on segment 2 similar to female. Small sensory element on apical segment not well discernible. Proximalmost aesthetasc difficult to discern (shown separately in Fig. 19G).

Maxilliped (Fig. 19B, C) 3-segmented, comprised of syncoxa, basis and 1-segmented endopod. Syncoxa unarmed, surface ornamented with few spinules (Fig. 19C), medial pore not discerned. Basis oblong-robust, inflated in proximal half forming bulbous swelling; anterior surface with spinular patch and curved spinular row, inner margin

with fringe of pinnules between half the distance between proximal and distal element and articulation with endopod (Fig. 19C), minute pore at (below?) distal part of fringe; posterior surface with 2-3 rows of spatulated spinules of graduated length along palmar margin, size of elements decreasing gradually from proximal to distal elements; with 2 small naked setae within the longitudinal cleft, proximal seta longer than distal one and distinctly curved (Fig. 19c). Endopod drawn out into long curved claw, concave inner margin unornamented, proximal outer margin with 3 minute pits or pores; accessory armature consisting of short, unipectinate spine basally fused to inner proximal corner of claw; tip of claw without hyaline apex.

P1-P4 with armature and ornamentation as in female, except for outer subdistal spine on P2 enp-3 slightly longer than in female, reaching beyond the insertion of outer distal spine (Fig. 19H, arrowed).

P5 (Fig. 19D, F) exopod delimited from somite, general shape and armature as in female.

P6 (Fig. 19E) represented by posterolateral flap closing off genital aperture on either side; covered by pattern of denticles as shown in Fig. 19E; posterolateral corners constricted and protruding laterally so that they are discernible in dorsal aspect (Fig. 19D), receptor (pore) at inner edge of corners not discerned.

Spermatophore oval, of variable size according to state of maturity (Fig. 19D); swelling of spermatophore during development not affecting shape and relative size of genital somite.

Etymology

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

Remarks

Taxonomy. Oncaea parabathyalis sp. nov. is closely related to *O. bathyalis*, but differs in the proportional spine length on the endopod of P2, with the outer distal spine being longer than the conical projection (Fig. 18B), while this spine is only about as long as the projection in *O. bathyalis* (Shmeleva, 1968, her fig. 2.7). Shmeleva´s (1968) original Russian description of *O. bathyalis* from the southern Adriatic Sea included a description of both sexes, but the swimming legs were figured for the female (holotype) only. In a subsequent French version of her taxonomic study, Shmeleva (1969) redescribed *O. bathyalis* from the same area and included figures of the swimming legs for both sexes. The male of *O. bathyalis sensu* Shmeleva (1969) differs from the female in the proportional spine length on the endopod of P2, with the outer distal spine being longer than the conical projection (her fig. 13g), which is similar to the *bathyalis*-type species found in the Adriatic during the present study. As both sexes of the latter show the same combination of characters figured for the male of *O. bathyalis sensu* Shmeleva (1969), it may be assumed that the two sexes of *O. bathyalis* described by Shmeleva (1969) are not conspecific. Specimens showing the combination of endopodal characters described for *O. bathyalis sensu* Shmeleva (1968) [i.e. (a) the outer distal spine on P2 being about as long as the terminal conical projection, and (b) the outer distal spine on P3 being longer than conical projection] were not found in the Adriatic Sea during the present study, however, as only copepod material from a single sample representing a limited depth range (260-400 m) was examined, it may well be that *O. bathyalis sensu* Shmeleva (1968) is present in different layers and/or during other seasons than examined here. Pending the discovery of a species showing the combination of endopodal spine lengths originally described for *O. bathyalis* Shmeleva, the species should be regarded as *species inquirenda*. The newly described *O. parabathyalis* is regarded conspecific with the male of *O. bathyalis sensu* Shmeleva (1969) based on the similarity in the proportional spine lengths on the endopods of P2-P4. The total length of Shmeleva´s (1969) males (340-400 µm) was smaller than those reported during the present study (Adriatic Sea: 440 µm; eastern Mediterranean: 400-410 µm). This difference may be due to some seasonal size variation, as Shmeleva´s samples were collected in July, while the specimens of the present study were obntained during March. However, the difference may also be caused by different methods of size measurements between the two studies.

Shmeleva´s (1968, 1969) descriptions of female *O. bathyalis* differ furthermore in the setal count of the distal exopod segment of female P1, showing the unusual number of only 3 inner setae in the original record (1968: fig. 2.6), but 4 setae in the subsequent account (1969: fig. 12f). The mouthparts were not included in Shmeleva´s description.

O. parabathyalis is a sister species of *O. ovalis*, which is redescribed in the present account. The two species are extremely similar in size and general habitus, in leg armature and ornamentation, in proportional lengths of terminal spines of the exopods (being shorter than the terminal exopod segment in all P1-P4) and in proportional spine lengths on the distal endopod segments of P3-P4, as well as in the armature of the mouthparts (in particular the labrum) and the maxilliped. They can be separated from each other most easily by the following distinct characters: (1) the proportional lengths of urosomites, with the 2 postgenital somites being relatively shorter in *O. parabathyalis* than in *O. ovalis*; (2) the proportional length of outer subdistal endopod spine on P2, being about 2/3 the length of the distal spine in *O. parabathyalis*, while the two spines are equal in length in *O. ovalis*; (3) the proportional lengths of exopodal setae on P5, with the inner element being almost as long as

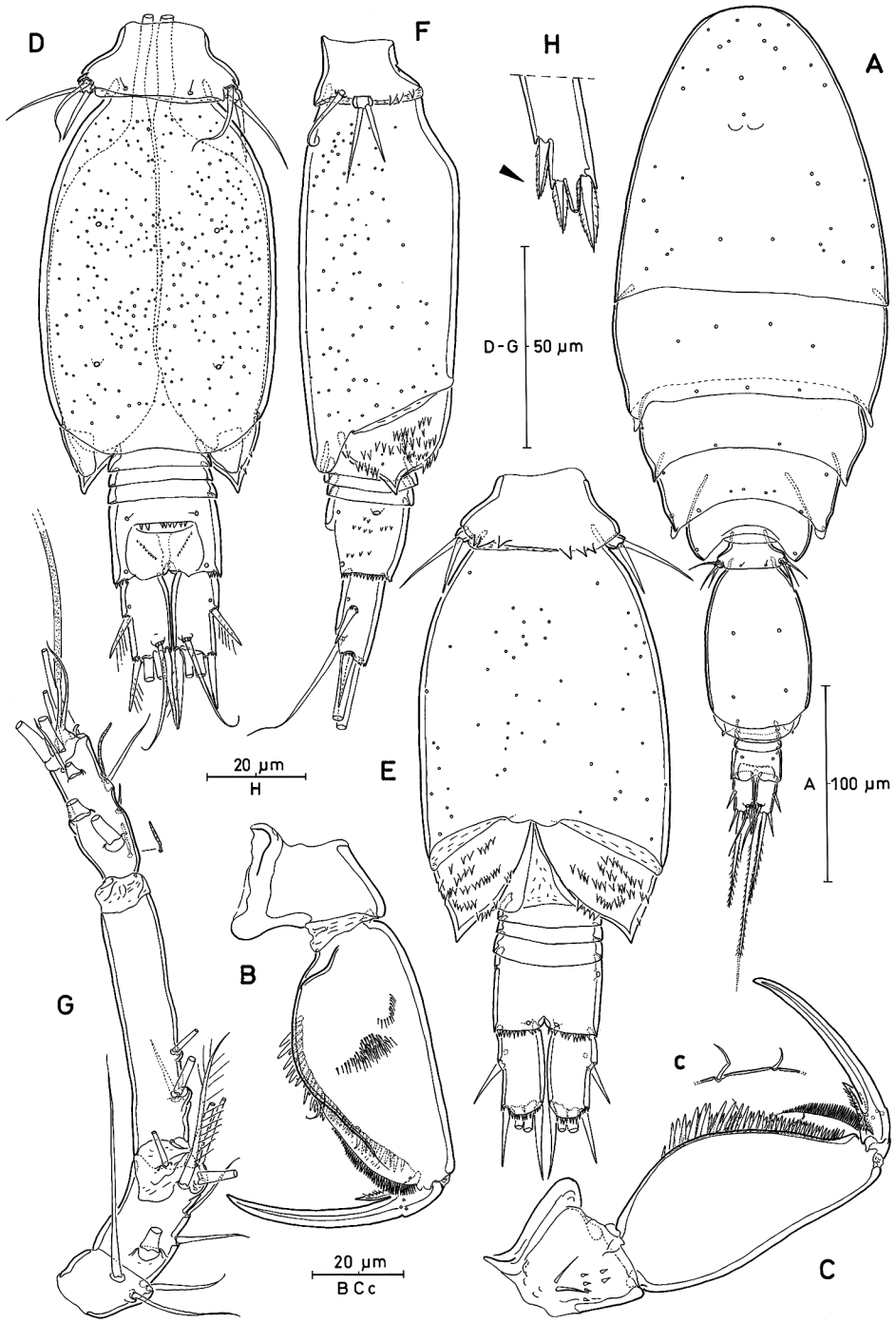

Figure 19. *Oncaea parabathyalis* sp. nov., male (Adriatic Sea). **A.** Habitus, dorsal, left caudal seta V missing. *O. parabathyalis* sp. nov., male (Eastern Mediterranean Sea. **B.** Maxilliped, anterior. **C.** Maxilliped, posterior (**c:** elements within longitudinal cleft of basis). **D.** Urosome, dorsal (spermatophores almost fully developped). **E.** Urosome, ventral. **F.** Same, lateral. **G.** Antennule, proximal aesthetasc on fused segments 4-6 shown separately, length of distal aesthetasc not fully discerned. **H.** P2, tip of endopod, arrow indicating sexually dimorphic spine.

Figure 19. *Oncaea parabathyalis* sp. nov., mâle (Mer Adriatique). **A.** Habitus, vue dorsale, soie caudale gauche V manquant. *O. parabathyalis* sp.nov. mâle (Méditerranée orientale. **B.** Maxillipède, antérieur. **C.** Maxillipède, postérieur (**c**: éléments dans la fente longitudinale de la base). **D.** Urosome, dorsal (spermatophores presque entièrement développés). **E.** Urosome, ventral. **F.** Urosome, latéral. **G.** Antennule, esthétasque proximal sur les segments fusionnés 4-6, montrés séparément, longueur de l'esthétasque distal non entièrement discernée. **H.** P2, bout de l'endopodite, flèche indiquant l'épine sexuellement dimorphe.

the outer element in *O. parabathyalis*, while this element is much shorter and spiniform in *O. ovalis*; (4) proportional lengths of caudal rami, with seta III being longer than seta IV in *O. parabathyalis*, whereas the two setae are equal in length in *O. ovalis*, and seta VII, which is shorter in *O. parabathyalis* than in *O. ovalis*. These characters allow for a separation of the two species without dissection during routine counts. Numerous other minor differences between the two species can be found, such as the number of mid-ventral processes on the P5-bearing somite, the length to width ratio of the genital double-somite and the anal somite, the length of the coxobasal seta on the antenna, the size and ornamentation of the exopodal segment P5, the proportional length of the outer subdistal spine on the endopod of P4, and a variety of ornamentation details on the mouthparts as figured above for the two species. The sexual dimorphism expressed in endopodal spine lengths of P4 in *O. ovalis*, however, is not found in *O. parabathyalis*; instead a slight difference between the sexes is found in proportional endopodal spine lengths of P2.

Malt et al. (1989) redescribed the male of *O. bathyalis* based on a single specimen collected in the eastern Mediterranean Sea, near the Lebanese coast. Their description, which included figures of the body in dorsal aspect, urosome, swimming legs, antennule, antenna, maxilliped and maxilla, resembles *O. parabathyalis* in the length of exopodal setae on P5 (being almost equal in length), the spine length of outer subdistal spine on P2 enp-3 (not reaching the insertion of outer distal spine), and the length of outer subdistal spine on P4 enp-3 (reaching beyond the insertion of outer distal spine). However, the proportional spine lengths on P2 enp-3 of Malt et al.´s specimen were more similar to *O. ovalis*, with the outer distal spine on P2 enp-3 being almost as long as the distal spine (their fig. 7H). Some morphological characters figured by Malt et al. (1989) are not found in either of the two species, such as the length of terminal exopod spine on P4, being as long as the terminal segment in their description (their text p. 962, fig. 7J), while they are shorter than the segment in both *O. ovalis* and *O. parabathyalis*, or the length of caudal rami, being shorter than the anal somite (their fig. 7B), while they are longer than (*O. parabathyalis*) or equal in length to (*O. ovalis*) the anal somite. In summary, the combination of characters decribed by Malt et al. is found in neither of the two species described herein and *O. bathyalis sensu* Malt et al. (1989) cannot be unequivocally identified without re-examination of the specimen. Several characters are missing or inadequately figured by Malt et al. (1989), such as the coxobasal seta and the distal armature on the distal endopod on the antenna, the armature of the antennule, the 2 palmar elements on the palmar margin of the maxillipeds, the armature of the maxilla, and the inner seta on P1 enp-1 (their fig. 7G, table on p. 962).

Ecological notes

Geographical distribution. The zoogeographical distribution of *Oncaea parabathyalis* outside the Mediterranean is not well known. Specimens of the *bathyalis*-type recorded from the Northern Arabian Sea by Böttger-Schnack (1996, her table IV + V) were re-examined during the present study and were provisionally assigned to *O. parabathyalis*. The species was also recorded from the Equatorial Indian Ocean (Table 4). Specimens from the Gulf of Aden and the Strait of Bab al Mandab, on the other hand, were found to belong to a closely related, as yet undescribed, species of the *ovalis-bathyalis*-subgroup (Table 4), which differed in the proportional spine lengths on the endopods of P2 and P3, the terminal spines being distinctly longer than in *O. parabathyalis*. More detailed studies of *bathyalis*-type copepods in the Arabian Sea and adjacent areas are required.

Vertical distribution. O. parabathyalis is a mesopelagic species, occurring between 260-400 m in the Adriatic Sea (present study). In the Northern Arabian Sea it was found between 100-450 m depth, with few specimens occurring as deep as 1850 m (Böttger-Schnack, 1996, as *O. bathyalis*). In a year-round quantitative survey of the oncaeid fauna in the southern Adriatic Sea, Kršinic (1998) recorded *bathyalis*-type oncaeids as solitary finds from 400 m down to the maximum depth of 1000 m sampled. The sample from Kršinic´s study area, which was examined during the present study, originated from 260-400 m depth, thus pointing to a somewhat shallower distribution of the species. In the eastern Mediterranean, *O. parabathyalis* was not separated from the closely related *O. ovalis* s.str. in the ecological study by Böttger-Schnack (1997), and both species combined occurred in maximum abundances between 100 m to 1000 m depth. No data on diurnal vertical migration are available.

Conclusions

Taxonomy and Phylogeny of ovalis*-type oncaeids*

The four species of the *ovalis*-complex described in the present study display great similarity in general habitus and in leg armature, and have been confounded with each other in earlier taxonomic and ecological studies due to the inadequate knowledge of their morphological structures. This is not unexpected and has been shown to occur quite often in marine planktonic taxa assuming a supposedly “cosmopolitan” distribution (Huys & Conroy-Dalton, 2000). The present taxonomic results show that species of the *ovalis*-complex resemble each other in the morphology of the mouthparts, in particular the labrum (absence of

medial teeth on the posterior side) and the mandible (element C spinulose along entire dorsal margin), and thus may belong to the same lineage within the Oncaeidae. However, the four species are not as closely related as might be assumed, because they differ in distinct morphological characters, such as the proportional spine lengths on the endopods of P2 and P3, the proportional length of terminal exopodal spines on P1-P4, the armature of P5, the ornamentation of elements on the antennule and the maxilliped as well as the form of the genital lappets in the male, and thus can be separated into two subgroups, the *ovalis-parabathyalis*-subgroup and the *crypta-cristata*-subgroup (Table 3).

Within the Oncaeidae, species of the *ovalis-parabathyalis*-subgroup belong to the *setosa*-group as defined in a preliminary phylogenetic study of Böttger-Schnack & Huys (1998: their species group 12), including *O. setosa*, *O. delicata* and *O. petila*. They are also related to the *lacinia*-group, including *O. lacinia*, *O. pumilis* and *O. oceanica* (cf. Böttger-Schnack & Huys, 1998, their species group 11), but differences in labral structure separate the two groups: *lacinica*-type oncaeids exhibit two strong medial teeth on the posterior side of the labrum (R. Böttger-Schnack, unpubl. data) and thus are different from the *ovalis*-complex, which lack medial teeth (cf. Table 4). [Recently, Heron & Frost (2000) recorded two new oncaeid species from the eastern subarctic Pacific, *O. rimula* and *O. glabra*, which resemble the *setosa*- and *lacinia*-groups and thus can be placed in either groups as well.] The phylogenetic relationships of the newly described *crypta-cristata*-subgroup, on the other hand, are still unresolved, because the species were not included in the earlier phylogenetic study by Böttger-Schnack & Huys (1998). The common characteristic of the *crypta-cristata*-subgroup are the greatly reduced length of the outer distal spine on the endopods of P2 and P3, being almost hidden by the terminal conical projection, which separates them from most other oncaeid species (or -groups), where the outer distal spines on the endopods are

Table 3. Major morphological characters separating the 2 species groups recognized within the *ovalis*-complex of Oncaeidae
Tableau 3. Caractères morphologiques majeurs séparant les 2 groupes d'espèces reconnus à l'intérieur du complexe *ovalis* d'Oncaeidae.

P1-P5 = thoracopds 1-5 | TCP = terminal conical projection | ODS = outer distal spine
exp-3 = third exopod segment | DS = distal spine | l. = length
orn. = ornamentation

Character	*ovalis-parabathyalis*-subgroup	*crypta-cristata*-subgroup
FEMALE		
Total body length [1]	440-510 µm	380-460 µm
P2+P3 endopod - l.ratio of ODS : TCP	longer	shorter
P1-P4 exopod - l.ratio of DS : exp-3	shorter	about equal or longer
P5 exopod - segment	delimited from somite	fused to somite
no. of setae	2	1
Antennule - segment 2 with "comb-like" seta	no	yes
Maxilliped - orn. of distal basal spine	bispinulose	unispinulose + curved spinular row at base
MALE		
Total body length [1]	400-440 µm	330-400 µm
Genital lappets - posterolateral corners	constricted	rounded

[1] traditional method, see text

Table 4. Taxonomic status of *ovalis*-type oncaeids from various locations in the world ocean examined during the present study, identified by the proportional length of outer distal spine (ODS) on P2 and P3 and by the number of strong medial teeth on the labrum (posterior view): L = ODS longer than terminal conical projection; S = ODS shorter than terminal conical projection .

Tableau 4. Situation taxonomique des Oncaeides, type *ovalis* de localisation diverses de l'Océan mondial, examinés durant cette étude, identifié par la longueur proportionnelle de l'épine dorsale extérieure (ODS) sur P2 et P3 et par le nombre de fortes dents médiales sur le labre : L = ODS plus longue que la projection conique terminale ; S = ODS plus courte que la projection conique terminale .

Character/Synonyms		***O. ovalis* s.str. Shmeleva, 1966**	***O. parabathyalis* sp. nov.**	***O. ovalis-parabathyalis*-subgroup**	***O. crypta* sp. nov.**	***O. cristata* sp. nov.**	***O. crypta-cristata*-subgroup**	***O. lacinia*-complex, unidentified**	**Other groups**
Region	**Sampling depth [m]**								
ODS on P2 + P3		L	L	L	S	S	S	L	L
Labrum, medial teeth		0	0	0	0	0	0	2	2
Synonymies [1]		*O. ovalis sensu* Shmeleva (1969) (male only)	*O. bathyalis sensu* Shmeleva (1968) (male only) [2] *O. bathyalis sensu* Shmeleva (1969) (male only) [2]	*O. ovalis sensu* Malt et al.(1989) *O. bathyalis sensu* Malt et al. (1989)	*O. ovalis sensu* Shmeleva (1969) (female only)		*O. minia sensu* Olson (1949) [MS] *O. ovalis sensu* Heron & Frost (2000)		
NORTH ATLANTIC + MEDITERRANEAN SEA									
Mediterranean Sea	200->1000	+	+		+				
Sargasso Sea	3300-3800	+					+		
Sognefjorden, Norway	500-1000							+	
ANTARCTIC									
Weddell Sea	500-1000							+	
RED SEA + INDIAN OCEAN									
Red Sea	200-1650					+			
Gulf of Aden +	200-250			+					
Strait of Bab al Mandab	150-200			+					
Northern Arabian Sea									
- *O. bathyalis sensu*	100-1850		+						
Böttger-Schnack 1996 (table IV+V)									
- *Oncaea* sp. A *sensu*	0-100								related to
Böttger-Schnack 1996 (table VI) [3]									*infantula*
Gordeyeva									
- *Oncaea* sp. C *sensu*	250-1850							+	
Böttger-Schnack 1996 (table VI) [4]									
Equatorial Indian Ocean	300		+				+		
NORTH PACIFIC OCEAN									
NW Pacific, subarctic	0-80							+	
	250-1000						+		
NE Pacific, off Monterey	0-200						+		

[1] only taxonomic records considered

[2] female of *O. bathyalis sensu* Shmeleva (1968) and Shmeleva (1969) regarded as *species inquirenda* herein (see text)

[3] syn. with *Oncaea* sp. AB *sensu* Böttger-Schnack 1994, table 2

[4] syn. with *Oncaea* sp. AV *sensu* Böttger-Schnack 1994, table 2

equal to or longer than the conical projections. The only other two oncaeid species known to exhibit very short outer endopodal spines on P2-P4 are *O. tenuimana* Giesbrecht, 1891 and *O. macilenta* Heron, 1977. However, in these two species, which belong to a different species group within the Oncaeidae (Böttger-Schnack & Huys, 1998, their species group 9), the form of the distal endopod segment is much broader and the relative position of the endopodal spines is quite different from those of *O. cristata* and *O. crypta*. They are furthermore separated from the *crypta-cristata*-subgroup by distinct differences in the maxilliped and the mouthparts (mandible, labrum). Thus, it may be assumed that a reduction of endopodal spines may have evolved convergently in the Oncaeidae.

Gordeyeva (1972) described a new species, *Oncaea infantula*, from the tropical Atlantic and stated that it was close to *O. ovalis*. However, *O. infantula* displays several characters not found in species of the *ovalis-parabathyalis*-subgroup and/or the newly recognized *crypta-cristata*-subgroup, in particular the reduced distal endopod segment on P4 and very short terminal spines on the endopods of P2 and P4 (terminal spine of P3 endopod was not figured by the author). The combination of both characters indicates that *O. infantula* may be closely related to *O. rotunda* Heron, 1977 and *O. rotundata* Boxshall, 1977, which are morphologically similar (Böttger-Schnack & Huys, 1998, their species group 10).

Zoogeographical distribution of ovalis-type oncaeids

Both subgroups recognized within the *ovalis*-complex during the present study occur at very distant localities in the world ocean, including the Atlantic, the Indian Ocean and the Pacific (Table 4). The occurrence of the *ovalis-parabathyalis*-subgroup was verified for the Atlantic and the Indian Ocean, but representatives of this group have not been found in the Pacific so far (Table 4). However, the apparent absence of the *ovalis-parabathyalis*-subgroup from the Pacific might not reflect their actual distribution limit, but is more likely due to the limited number of Pacific specimens examined during the present study. According to unpublished taxonomic data by Itoh from the northwestern Pacific (Kuroshio extension), the *ovalis*-type oncaeids collected in that area included a species similar to the *(para)bathyalis*-type (H. Itoh, pers. commn.). Future examination of Itoh´s specimens might help to verify the absence or presence of this species group in the Pacific Ocean.

The occurrence of *O. parabathyalis* in the Northern Arabian Sea, at far distance from the type locality in the Mediterranean, was verified during the present study (Table 4). The species had been recorded as *O. bathyalis* in earlier ecological studies from the Arabian Sea (Böttger-Schnack, 1996, table IV + V). In the same account, two unidentified Arabian Sea oncaeids, *Oncaea* sp. A and *Oncaea* sp. C, had provisionally been assigned to the *ovalis*-complex by Böttger-Schnack (1996, table VI). However, re-examination of specimens of both taxa during the present study confirmed that they are different from all 4 species of the *ovalis*-type described in the present account, with regard to urosome segmentation, armature and ornamentation of swimming legs, P5 and setae on caudal rami. *Oncaea* sp. A, which is synonymous with *Oncaea* sp. AB *sensu* Böttger-Schnack 1994 (1994: table 2), was similar in leg armature to *O. infantula* Gordeyeva, 1972, showing the unusual outer spine formula I, I, 0 on the distal endopod segments of P2-P4. The terminal spine on the reduced P4 endopod, however, was much longer than described for *O. infantula*. *Oncaea* sp. C, which is identical with *Oncaea* sp. AV *sensu* Böttger-Schnack 1994 (1994: table 2), was similar to the *ovalis-parabathyalis*-subgroup in leg armature, but differed considerably in urosome segmentation and in P5, both of which resembled the *lacinia*-group of oncaeids (Böttger-Schnack 1998, species group 11). The two Arabian Sea taxa will be examined in more detail in a subsequent study.

In the Gulf of Aden, an oncaeid species of the *ovalis*-type occurred at a depth of 200-250 m (R. Böttger-Schnack, unpubl. data, 1 female dissected on 1 slide in polyvinyllactophenol), which greatly resembled *O. parabathyalis* sp. nov. in morphological characters. However, it differed from *O. parabathyalis* in the proportional endopodal spine lengths on P2 and P3, with the distal spine being much longer than in *O. parabathyalis* from the Mediterranean. Another specimen of the same type was found in the Strait of Bab al Mandab, at the southern entrance of the Red Sea, at a depth of 150-200 m (R. Böttger-Schnack, unpubl. data, 1 female undissected on slide), indicating that the *ovalis-parabathyalis*-subgroup in that area may be represented by an as yet undescribed species closely related to *O. parabathyalis*.

In the Equatorial Indian Ocean, one representative each of the *ovalis-parabathyalis*-subgroup and the *crypta-cristata*-subgroup were found during the present study (Table 4). In addition, small mesh net samples from this area (material by S. Nishida; cf. Nishida & Marumo, 1982) yielded a variety of *ovalis*-type oncaeids related to the *ovalis-parabathyalis*-subgroup (R. Böttger-Schnack, unpubl. data), all of which require further taxonomic examination.

The *crypta-cristata*-subgroup was found in all great oceans, including the North Atlantic (Sargasso Sea), the equatorial Indian Ocean and the eastern and western side of the Pacific (Table 4). The occurrence of the *crypta-cristata*-subgroup in the subarctic NW Pacific, Oyashio region, was restricted to the seasons of importing waters from the (warm) Kuroshio current (April, October) (Nishibe & Ikeda, 2004, and pers. comm.). Specimens from the Indo-

Pacific region outside the Red Sea appeared to be more close to *O. crypta* than to the sibling *O. cristata* from the Red Sea, based on the proportional lengths of outer exopodal spines on P3 and P4. However, they could not be positively identified, because they differed in terminal exopodal spine length on P3, being relatively longer than in *O. crypta*. Specimens from the eastern side of the North Pacific exhibited further differences in the proportinal lengths (1) of the outer subdistal spine on P3 exopod (not reaching the insertion of outer distal spine), (2) the distal spine on P4 endopod (being shorter than the distal segment) and (3) the seta on the somite near P5 (reaching beyond the genital apertures). In view of the great morphological similarity of siblings within the *crypta-cristata*-subgroup, more detailed taxonomic analyses of their Indo-Pacific representatives, including the mouthparts and ornamentation details, are neccessary to clarify the species identity.

The *ovalis*-type oncaeid from the Antarctic (Weddell Sea, cf. Metz, 1993, as *Oncaea* "mini") was tentatively assigned to *O. lacinia*, based on the proportional lengths of urosomites and the endopodal spines on P2-P4. However, slight differences in the proportional lengths of exopodal setae on P5 were noted in the specimens examined, with the inner seta being shorter and much stronger than figured by Heron et al. (1984, their fig. 14G).

The *ovalis*-type specimen from the Norwegian fjord was similar in morphology to *O. lacinia* (P5, labrum), but differed in the proportional endopodal spine lengths on P2-P4 and might represent an as yet undescribed species of the *lacinia*-group.

Summarized, the data compiled in Table 4 indicate that species of the *ovalis*-complex are widely distributed in tropical and warm-temperate regions of the ocean, but thus far have not been recorded from cold-temperate and/or polar areas.

Abundance and vertical distribution of ovalis*-type oncaeids*

All four species described in the present paper are inhabitants of midwater layers occurring from the lower epipelagic to bathypelagic zones (Table 4). The combined group of *ovalis*-type oncaeids has been found to occur in almost equal concentrations of about 10-100 individuals m^{-3} over extended depth layers, as for instance in in the Adriatic (100-600 m: 17-25 ind m^{-3} as a yearly average; Kršinic, pers. comm.) or in the eastern Mediterranean (100-1000 m: 10-50 ind m^{-3}; Böttger-Schnack, 1997). In the Red Sea, concentrations of *O. cristata*, the sole representative of the *ovalis*-complex in that area, ranged between 20-70 ind m^{-3} in the depth layer 200->1000 m (Böttger-Schnack, 1995, and unpubl. data). In a study on the vertical distribution of oncaeid microcopepods in the upper 200 m of the Kuroshio extension, Itoh and co-workers found maximum concentrations of up to 20 ind m^{-3} (*O. "ovalis"*) or 60-80 ind m^{-3} (*O. "bathyalis"*), respectively, in the subsurface layers, at 150-200 m depth (H. Itoh, pers. comm.). With the exception of *O. cristata*, the actual species specific depth distributions of *ovalis*-type oncaeids are unknown, however, because they were not counted separately during quantitative investigations (e.g. Böttger-Schnack, 1997) or their taxonomic identity remains uncertain (e.g. Kršinic, 1998). The taxonomic revision of the *ovalis*-complex presented in this paper will help to unravel spatio-temporal differences in distribution of these important oncaeid species in future ecological investigations on oceanic microcopepods.

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