

Taxonomic diversity and identification problems of oncaeid microcopepods in the Mediterranean Sea

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Abstract The species diversity of the pelagic microcopepod family Oncaeidae collected with nets of 0.1-mm mesh size was studied at 6 stations along a west-to-east transect in the Mediterranean Sea down to a maximum depth of 1,000 m. A total of 27 species and two form variants have been identified, including three new records for the Mediterranean. In addition, about 20, as yet undescribed, new morphospecies were found (mainly from the genera *Epicalymma* and *Triconia*) which need to be examined further. The total number of identified oncaeid species was similar in the Western and Eastern Basins, but for some co-occurring sibling species, the estimated numerical dominance changed. The deep-sea fauna of Oncaeidae, studied at selected depth layers between 400 m and the near-bottom layer at >4,200 m depth in the eastern Mediterranean (Levantine Sea), showed rather constant species numbers down to ~3,000 m depth. In the near-bottom layers, the diversity of oncaeids declined and species of *Epicalymma* strongly increased in numerical importance. The taxonomic status of all oncaeid species recorded earlier in the Mediterranean Sea is evaluated: 19 out of the 46 known valid oncaeid species are insufficiently described, and most of the taxonomically unresolved species (13 species) have originally been described from this area (*type locality*). The deficiencies in the species identification of oncaeids cast into doubt the allegedly cosmopolitan distribution of some

species, in particular those of Mediterranean origin. The existing identification problems even of well-described oncaeid species are exemplified for the *Oncaea media*-complex, including *O. media* Giesbrecht, *O. scottodicarloi* Heron & Bradford-Grieve, and *O. waldemari* Bersano & Boxshall, which are often erroneously identified as a single species (*O. media*). The inadequacy in the species identification of Oncaeidae, in particular those from the Atlantic and Mediterranean, is mainly due to the lack of reliable identification keys for Oncaeidae in warm-temperate and/or tropical seas. Future efforts should be directed to the construction of identification keys that can be updated according to the latest taxonomic findings, which can be used by the non-expert as well as by the specialist. The adequate consideration of the numerous, as yet undescribed, microcopepod species in the world oceans, in particular the Oncaeidae, is a challenge for the study of the structure and function of plankton communities as well as for global biodiversity estimates.

Keywords Copepoda · Oncaeidae · Mediterranean Sea · Species diversity · Deep-sea · *Oncaea media*-complex

Introduction

Marine microcopepods of the family Oncaeidae are important components of the pelagic copepod community due to their high numerical abundance and taxonomic diversity (e.g., Heron 1977; Malt 1983; Paffenhöfer 1993; Böttger-Schnack 1994). Over 100 oncaeid species are known to date (cf. Razouls et al. 2005–2009) and the vast majority of the species has been described in the last 30 years (see Böttger-Schnack et al. 2004 for a review). Since the rate of discovery shows no tendency to decline, it

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is probable that the actual number of extant species is in the hundreds. In contrast to most other holozooplankton taxa, the size of oncaeid species is negatively correlated with depth (Gibbons et al. 2005), indicating that in particular the little studied microcopepod communities of meso- and bathypelagic layers of the oceans may represent “hotspots” for the biodiversity of this copepod family.

Taxonomic identification of oncaeid species is often hampered by their small size and the lack of adequate taxonomic descriptions. Oncaeid copepods are known for their high morphological similarity and include many sibling species. Many of the allegedly cosmopolitan species, such as *Triconia confiera* (Giesbrecht), *Oncaea notopus* Giesbrecht, or *O. media* Giesbrecht, have in fact been shown to include a number of distinct species, which are closely related (e.g., Heron 1977; Heron and Bradford-Grieve 1995; Böttger-Schnack 2001). Although the knowledge of oncaeid morphology and phylogenetic relationships has been improved greatly by detailed taxonomic studies in the past three decades (e.g., Boxshall 1977; Heron 1977; Heron and Bradford-Grieve 1995; Böttger-Schnack 1999, 2001; Huys and Böttger-Schnack 1996/1997; Böttger-Schnack and Huys 1998), the new taxonomic findings are not yet consistently considered in ecological and/or biodiversity studies. For example, the three species of the *media*-complex, *O. media* Giesbrecht, *O. scottodicarloi* Heron and Bradford-Grieve, and *O. waldemari* Bersano and Boxshall are often not recognized or considered as different species in recent ecological studies, but are summarized under the name of the species-complex (e.g., Zervoudaki et al. 2006, 2007), thereby disregarding potential distinctions in the spatial and temporal occurrence and numerical abundance of the different species of this complex.

The Mediterranean Sea includes a highly diverse oncaeid fauna. Almost half the total number of all known oncaeid species have been recorded from this area (cf. Razouls et al. 2005–2009) and many of them (26 species) were originally described from the Mediterranean as their *type locality*. Some oncaeid species of Mediterranean origin have subsequently been reported as dominant or “key” taxa in very distant oceanic regions (e.g., Webber and Roff 1995; Böttger-Schnack 2002; Nishibe and Ikeda 2004; Rezai et al. 2004). However, due to the insufficient taxonomic descriptions, at least some of the allegedly cosmopolitan species may in reality represent a complex of distinct, though closely related, species. In order to resolve the taxonomic confusion that currently exists for many of the oncaeids in the Mediterranean Sea, a research project was recently started, applying novel molecular techniques in combination with traditional morphological methods. First results of the genetic analyses of a selection of morphologically pre-identified oncaeid species and forms from the Mediterranean Sea showed that detailed morphological characters used to

differentiate between the species and even form variants of Oncaidae were supported by clear genetic distances with regard to the COI and 12S genes (Böttger-Schnack and Machida 2008). The present paper provides the complete list of oncaeid morphospecies, sampled during this study along a west–east-transect in the Mediterranean Sea down to 1,000 m depth, thereby considering potential regional differences in the species richness between the western and eastern areas. The Mediterranean Sea is separated into a Western and Eastern Basin by the Sicilian–Tunisian rise, constituting a geographical, hydrological and even climatic frontier between the western and eastern parts (Furnestin 1979). From the western to the eastern Mediterranean, a more or less strong decline in the species richness has been observed for some zooplankton taxa (see Furnestin 1979 for a review of the earlier literature; Dolan et al. 2002), while other taxa show a more homogeneous distribution in the whole Mediterranean (Furnestin 1979).

The deep-sea in the Mediterranean is characterized by a homogeneous water mass of constant and relatively high temperatures and salinities (Wüst 1960). Due to the unfavorable environmental conditions, the zooplankton fauna is generally known to be impoverished and inhabited by few deep-living mesopelagic species, while a typical deep-sea fauna is not found (e.g., Furnestin 1979; Scotto di Carlo et al. 1991). However, the species community of Oncaidae below 1,000–2,000 m depth is hardly known in the Mediterranean Sea. Greze (1963) found only two oncaeid species (*Oncaea media*, *Triconia dentipes*) in the deep Ionian Sea below 1,000 m depth and Scotto di Carlo et al. (1975) recorded only one species (*O. ornata*) in the deep Tyrrhenian Sea, while Vaissière and Seguin (1980) identified six species in that area. During an extended deep-sea study in different parts of the Mediterranean Sea, Scotto di Carlo et al. (1991) found three oncaeid species (*O. ornata*, *O. mediterranea*, *T. confiera*) and more recently, Lapernat and Razouls (2001) identified these three oncaeid species as well as a fourth one (*O. englishi*) in the deep oceanic area off Malta. Except for the study of Greze, all these studies were based on net samples taken with mesh sizes of 0.2 mm or larger, which are not adequate for sampling the small species of Oncaidae. Furthermore, the species diversity of oncaeids may have been underestimated in these studies due to the existence of similar-looking species, which were not recognized or differentiated (see above). By using small mesh nets of 0.055-mm mesh size, Böttger-Schnack (1997) recorded about 20 oncaeid species in the deep eastern Mediterranean Sea between 1,000 and 1,850 m. Several of these species, such as *Oncaea ovalis*, *Spinoncaea ivlevi*, *Triconia dentipes*, *T. confiera* and *O. media*, were found to include two or even three different species upon more detailed taxonomic analyses (Böttger-Schnack 1999, 2001, 2005).

In the present study, the qualitative analysis of samples on the west–east transect for regional comparison of species richness, mentioned above, is complemented by quantitative analysis of samples taken on a fixed station in the eastern Mediterranean to examine the species diversity and community structure of deep-sea Oncaeidae at selected depth layers down to 4,200 m. For a comprehensive overview of the taxonomic status of all known oncaeid species in the Mediterranean Sea (including those not found in the present study), the available taxonomic literature is evaluated critically and the existing identification problems of oncaeid copepods are exemplified for the species of the *media*-complex.

Materials and methods

Plankton sampling

Samples were taken during RV “Meteor Cruise” 51/2 between October 19 and November 10, 2001, at six stations along a transect from the western to the eastern Mediterranean Sea (Fig. 1). A multiple opening-closing net (Weikert and John 1981) with a mouth area of 0.25 m² equipped with five nets of 0.1 mm mesh size was used. Samples were taken at vertical hauls mostly at the following depth intervals: 0–50 m, 50–100 m, 100–300 m, 300–600 m, and 600–1,000 m (Table 1). Details of the sampling procedure are given by Elvers (2003) in a cruise report edited by Hemleben et al. (2003). Plankton samples were concentrated using a 0.055-mm mesh net, transferred to 250-ml Kautex bottles and preserved in 100% undegraded ethanol. The Kautex bottles were sealed with

parafilm and stored in the dark at room temperature. After the cruise, they were stored in a refrigerator at a temperature of ~5°C.

Additional deep-sea plankton samples were taken during the same cruise between October 26 and 29, 2008 at a fixed station in the eastern Mediterranean (Levantine Sea), above the Ierapetra Deep (Fig. 1). Mesozooplankton samples were taken by oblique or horizontal hauls (towing speed: 2 knots) with the use of a 1 m²-Double MOCNESS (Multiple Opening and Closing Net and Environmental Sensing System; Wiebe et al. 1985) equipped with 18 nets of 0.333 mm mesh aperture (large mesozooplankton) and 2 nets of 0.1 mm mesh size (small mesozooplankton), which can be sequentially opened and closed at defined depths. Filtered volumes ranged from 300 m³ in the upper 450 m to 900 m³ at all depths below 1050 m. The system is equipped with conductivity (Seabird SBE 4), temperature (Seabird SBE 3S) and depth sensors to obtain the abiotic parameters. Details of the sampling procedure and the hydrographical conditions during the sampling period are given by Koppelman et al. (2009). In the present paper, only results of the 0.1 mm mesh nets are presented, which were taken at the following depth strata: 400–450 m, 1250 m, 2750–3000 m, 4200 m and 10 meters above the bottom (Table 2). Upon recovery of the MOCNESS, the nets were rinsed with seawater and half of the samples was preserved in a 4% formaldehyde-seawater solution buffered with sodium tetraborate (Steedman 1976) for taxonomical analyses.

Morphology

Adult female oncaeids were qualitatively sorted from the complete plankton samples of the west-to-east-transect

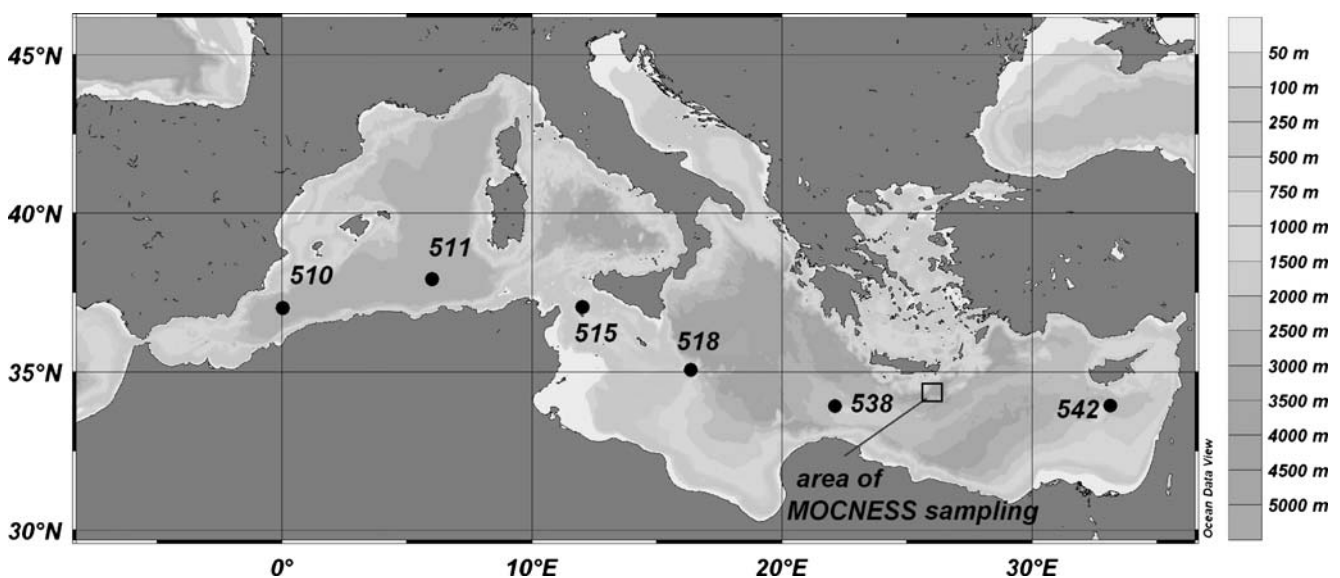


Fig. 1 Sampling locations in the Mediterranean Sea

Table 1 METEOR-cruise 51/2. Sampling data of 0.1-mm mesh multiple opening–closing plankton nets along a west-to east Ttransect in the Mediterranean Sea

| Station no. | Date 2001 | Position | | Time | Depth range sampled (m) | Total water depth (m) |
|-----------------------------------|-----------|------------|------------|-------|-------------------------|-----------------------|
| | | Latitude | Longitude | | | |
| Western Basin | | | | | | |
| 510 | 19.10 | 36°59.82'N | 00°00.45'E | Day | 0–600 | 2,666 |
| 511 | 20.10 | 37°59.85'N | 05°59.93'E | Day | 0–1,000 | 2,807 |
| Strait between Sicily and Tunisia | | | | | | |
| 515 | 22.10 | 36°54.17'N | 12°00.16'E | Day | 0–600 | 624 |
| Ionian Sea | | | | | | |
| 518 | 23.10 | 35°00.27'N | 16°22.8'E | Day | 0–1,000 | 2,095 |
| Eastern Basin | | | | | | |
| 538 | 01.11 | 34°00.04'N | 22°05.20'E | Day | 0–1,000 | 2,951 |
| 542 | 03.11 | 34°04.97'N | 32°59.97'E | Night | 0–1,000 | 2,521 |

under a dissection microscope and identified to genera, species and/or morphological units (form variants) using the taxonomic literature of Shmeleva (1969), Gordeyeva (1972, 1975), Heron (1977), Heron et al. (1984), Heron and Bradford-Grieve (1995), Heron and Frost (2000); Böttger-Schnack (1999, 2001), Böttger-Schnack and Huys (1997), and recent taxonomic descriptions and revisions of Mediterranean Oncaidae [Böttger-Schnack 2002, 2003, 2005; Böttger-Schnack and Huys 2001; Huys and Böttger-Schnack 2008 (“2007”)]. The two form variants of *Oncaea venusta*, f. *venella* and f. *typica*, which represent different genetic lineages (Elvers et al. 2006), were separated morphologically by their size and the presence/absence of the small dorsal swelling on the P2-bearing somite (cf.

Böttger-Schnack and Huys 2004) and are treated as separate species herein. Similarly, the slender and the broad form variant of *O. mediterranea* (cf. Böttger-Schnack and Huys 1997), which have recently been shown to be genetically distinct (Böttger-Schnack and Machida 2008), are regarded as separate species in this study. Morphological details of closely related and/or small-sized species were examined under a Leitz Dialux differential interference contrast microscope using dissected and/or undissected reference specimens. Descriptive terminology for body and appendages follows that of Huys and Boxshall (1991). Abbreviations used in the text are: P1–P6 = first to sixth thoracopods. Not all species of the Oncaidae from the samples have yet been identified and many of them are

Table 2 METEOR-cruise 51/2. Sampling data of 0.1-mm mesh MOCNESS-nets in the eastern Mediterranean Sea, above the Ierapetra Deep

| Station no. | Haul no. | Net no. | Date 2001 | Position | | Time | Depth range sampled (m) | Total water depth (m) |
|-------------|----------|----------|-----------|------------|------------|-------|-------------------------|-----------------------|
| | | | | Latitude | Longitude | | | |
| 528-1 | MOC-D-01 | L2 L9 | 26.10 | 34°22.45'N | 25°55.73'E | Night | 1,250 400–450 | 4,285 |
| 528-2 | MOC-D-02 | L2 L9 | 27.10 | 34°19.91'N | 26°08.47'E | Day | 4,200 2,750–3,000 | 4,241 |
| 528-3 | MOC-D-03 | L2 L9 | | 34°18.81'N | 26°08.49'E | Night | 4,200 2,750–3,000 | 4,270 |
| 528-4 | MOC-D-04 | L2 L9 | 28.10 | 34°18.88'N | 26°08.34'E | Night | 1,250 400–450 | 4,264 |
| 528-5 | MOC-D-05 | L2 L9 | | 34°19.34'N | 26°08.28'E | Day | 1,250 400–450 | 4,263 |
| 528-6 | MOC-D-06 | L2 L9 | | 34°19.33'N | 26°08.25'E | Day | 1,250 400–450 | 4,261 |
| 528-7 | MOC-D-07 | L2 L9 | | 34°19.52'N | 26°03.04'E | Night | 10 mab 2,750–3,000 | 4,261 |
| 528-8 | MOC-D-08 | L2 | 29.10 | 34°18.97'N | 26°05.66'E | Day | 10 mab 2,750–3,000 | 4,285 |

mab Meters above bottom

probably new. Unidentified morphotypes, which could be clearly separated by morphological characters, were classified as “putative species”. Dissected specimens are being kept in the personal collection of R. Böttger-Schnack.

Deep-sea Oncaeidae

The species diversity and numerical abundance of Oncaeidae at selected depth layers in the eastern Mediterranean Sea was quantitatively evaluated from the formaldehyde-preserved samples (1/2 of the original net sample). Samples were split into two fractions over a 0.3-mm mesh gauze. All oncaeid specimens in the large fraction were identified and counted, while in the smaller size fractions only subsamples of between 500–1,000 individuals were counted. For details of the subsampling procedure, see Böttger-Schnack (1997). The taxonomic literature used for species identification is given above.

Taxonomic status of mediterranean Oncaeidae

For evaluating the taxonomic status of species of Oncaeidae recorded in the Mediterranean Sea, the original taxonomic description of each species as well as reliable redescriptions were examined. A complete reference list of the taxonomic literature used can be obtained from the senior author. The grouping of species into taxonomically “resolved” and “unresolved” species was chosen to differentiate between species which have been fully (re-)described and can be clearly identified, and those which are insufficiently described and need further taxonomic (morphological) examination for unequivocal identification. The latter category also includes species showing different form variants (e.g., *Oncaea venusta* f. *typica* and f. *venella*).

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

Results

Species diversity

A total of 27 oncaeid species and two form variants were identified during the present study (Table 3). Three of the

identified species are new records for the Mediterranean Sea (*Triconia elongata*, *T. furcula* and *Oncaea memorata*). In addition, 6 putative species and 14 unidentified morphotypes were found, most of which belong to the genera *Epicalymma* (6 morphotypes) and *Triconia* (2 putative species and 6 morphotypes). The unidentified morphospecies of *Epicalymma* spp. do not match any of the six described species of the genus (Farran 1908; Heron 1977; Heron et al. 1984), and differ also from a new *Epicalymma* species found in the Red Sea, whose description is in progress (Böttger-Schnack, *in press*). Similarly, the 2 putative species and 6 unidentified morphotypes of *Triconia*, all of which belong to the *similis*-subgroup of the genus (Table 3), could not be assigned to any of the 7 described species of this subgroup (cf. Böttger-Schnack 1999). Two putative species, *Triconia* sp. 8 and *Oncaea* sp. 7, were especially abundant. *Triconia* sp. 8 regularly co-occurred with the closely related *T. umerus* and *T. minuta* in the same depth layers. The species differs from its two congeners by the form of the genital double-somite, proportional lengths of setae on the exopod of P5, and proportional spine lengths on the endopods of P2 and P3. *Oncaea* sp. 7 belongs to the *notopus*-group of Oncaeidae, which is characterized by an elongated exopod segment of P5 (cf. Heron 1977; Böttger-Schnack and Huys 1998; as species group 7). It was the only representative of this group in the material examined and differed from all described species of the *notopus*-group (6 species) by its much smaller size, measuring only about 0.55 mm in the adult female and by a combination of morphological characters, including urosome segmentation, P5 and caudal setae. A complete morphological description of *Triconia* sp. 8 and *Oncaea* sp. 7 is in progress.

Regional distribution

Between the western and eastern regions, no consistent trend was noted in the total numbers of identified oncaeid species (Table 3). Some species, such as *Triconia elongata*, *T. furcula*, and the slender form of *Oncaea mediterranea*, were rare or even absent in the Western Basin, while others, e.g., *Oncaea tenuimana*, *Monothula subtilis* and both forms of *O. venusta*, were not found in the eastern part. For some very small species, such as the *vodjanitskii*-group and *O. memorata*, the distributional records are inconclusive, as the species were not quantitatively sampled by the 0.1 mm mesh nets used.

Deep-sea Oncaeidae (Eastern Mediterranean Sea)

The community structure of oncaeid copepods in the deep-sea samples of the eastern Mediterranean Sea is shown in Table 4. While the numerical abundance decreased consid-

Table 3 Species of Oncaidae recorded during the present study sorted by current taxonomic status

| Species/taxon | Mediterranean Sea | | | | | | |
|--|--------------------------------------|-------------|---------------------------------|-----------|-----------------|-----------------|-----|
| | Western | | Central | | Eastern | | |
| | Alboran B. | Balearic B. | Strait between Tunisia & Sicily | Ionian B. | Levantine B. | | |
| Station no. | 510 | 511 | 515 | 518 | SE of Crete 538 | S of Cyprus 542 | |
| A. Identified species | | | | | | | |
| a. Taxonomic status resolved | | | | | | | |
| * <i>Monothula subtilis</i> | (Giesbrecht 1893 [“1892”]) | + | + | + | + | – | – |
| * <i>Oncaea</i> s.l. <i>crypta</i> | Böttger-Schnack 2005 | + | + | + | + | + | + |
| <i>Oncaea</i> s.l. <i>englishi</i> | Heron 1977 | – | + | + | + | + | + |
| <i>Oncaea</i> s.l. <i>ornata</i> | Giesbrecht 1891 | + | + | + | + | + | + |
| * <i>Oncaea</i> s.l. <i>ovalis</i> | Shmeleva 1966 ^a | + | – | – | – | – | + |
| * <i>Oncaea</i> s.l. <i>parabathyalis</i> | Böttger-Schnack 2005 | + | + | + | + | + | + |
| * <i>Oncaea</i> s.l. <i>prendeli</i> | Shmeleva 1966 | + | + | + | + | + | + |
| <i>Oncaea</i> s.l. <i>tenuimana</i> | Giesbrecht 1891 | + | + | – | – | – | – |
| * <i>Oncaea</i> s.l. <i>tregoubovi</i> | Shmeleva 1968 | + | + | + | + | + | + |
| * <i>Oncaea</i> s.l. <i>zernovi</i> | Shmeleva 1966 | + | + | + | + | + | + |
| <i>Oncaea</i> s.str. <i>media</i> | Giesbrecht 1891 | + | + | + | + | + | + |
| * <i>Oncaea</i> s.str. <i>scottodicarloi</i> | Heron and Bradford-Grieve 1995 | + | + | + | + | + | + |
| <i>Oncaea</i> s.str. <i>waldemari</i> | Bersano and Boxshall 1994 | + | + | + | + | + | (+) |
| <i>Spinoncaea humesi</i> | Böttger-Schnack 2003 | + | + | – | + | + | + |
| * <i>Spinoncaea ivlevi</i> | (Shmeleva 1966) | + | + | + | + | + | + |
| <i>Spinoncaea tenuis</i> | Böttger-Schnack 2003 | + | (+) | – | + | + | – |
| <i>Triconia conifera</i> | (Giesbrecht 1891) | + | + | + | + | + | + |
| <i>Triconia dentipes</i> | (Giesbrecht 1891) | + | + | + | + | (+) | – |
| # <i>Triconia elongata</i> | Böttger-Schnack 1999 | – | (+) | + | + | + | + |
| # <i>Triconia furcula</i> | (Heron and Bradford-Grieve 1995) | – | – | (+) | + | + | + |
| * <i>Triconia minuta</i> | (Giesbrecht 1892) | + | + | + | + | + | + |
| <i>Triconia umerus</i> | (Böttger-Schnack and Boxshall 1990) | (+) | – | + | + | + | + |
| b. Taxonomic status unresolved | | | | | | | |
| # <i>Oncaea</i> s.l. <i>memorata</i> | Gordeyeva 1973 | – | (+) | – | – | – | – |
| <i>Oncaea</i> s.l. <i>shmelevi</i> | Gordeyeva 1972 | + | + | + | + | + | + |
| * <i>Oncaea</i> s.l. <i>vodjanitskii</i> | Shmeleva and Delalo 1965 | – | – | – | – | (+) | (+) |
| * <i>Oncaea</i> s.str. <i>mediterranea</i> | (Claus 1863) Slender form | – | – | + | + | + | + |
| | Broad form ^b | + | + | + | + | + | + |
| * <i>Oncaea</i> s.str. <i>venusta</i> | Philippi 1843 f. <i>typica</i> | + | – | + | + | – | – |
| | Farran 1929 | – | + | + | + | – | – |
| | f. <i>venella</i> Farran 1929 | – | + | + | + | – | – |
| Total number of identified species | | 22 | 23 | 23 | 25 | 23 | 22 |
| B. Unidentified morphospecies | | | | | | | |
| <i>Epicalymma</i> spp. | 6 unidentified morphospecies | + | + | + | + | + | + |
| <i>Oncaea</i> s.l. sp. 7 | <i>notopus</i> -group ^{c,d} | + | + | + | + | + | + |
| <i>Oncaea</i> s.l. sp. A | Unidentified morphospecies | – | – | – | (+) | – | – |
| <i>Oncaea</i> s.l. sp. B | Unidentified morphospecies | – | (+) | – | – | – | – |
| <i>Oncaea</i> s.l. sp. | <i>atlantica/vodjanitskii</i> -group | – | – | – | – | (+) | (+) |

Table 3 (continued)

| Species/taxon | | | Mediterranean Sea | | | | | |
|--|-------|--|-------------------|-------------|---------------------------------------|-----------|-----------------------|-----------------------|
| | | | Western | | Central | Eastern | | |
| Station no. | | | Alboran B. | Balearic B. | Strait between Tunisia & Sicily | Ionian B. | Levantine B. | |
| | | | 510 | 511 | 515 | 518 | SE of Crete 538 | S of Cyprus 542 |
| <i>Oncaea</i> s.l. | spp. | 2 morphospecies, <i>tregoubovi</i> -group | – | (+) | – | – | – | (+) |
| <i>Triconia</i> | sp. 8 | <i>similis</i> -subgroup ^{c,d} | + | + | + | + | + | + |
| <i>Triconia</i> | sp. | cf. <i>T. gonopleura</i> Böttger-Schnack 1999 | – | – | – | – | – | (+) |
| <i>Triconia</i> | spp. | 6 morphospecies, <i>similis</i> -subgroup | + | + | + | + | + | + |
| Estimated maximum number of unidentified species | | | 14 | 17 | 14 | 15 | 15 | 18 |

*Species originally described from the Mediterranean (type locality)

New record for Mediterranean Sea

+ = present, (+) = isolated finds, – = not found

^aNot *O. ovalis* Shmeleva 1969 (cf. Böttger-Schnack 2005)

^b*Sensu* Böttger-Schnack and Huys (1997)

^cCf. Böttger-Schnack (1997: Table 10)

^dNew species, description in progress

B Basin

erably by about one order of magnitude when comparing the mesopelagic (400–450 m) and the bathypelagic (2750–3000 m) zone, the total number of species was similar, amounting on average to 26 and 28 species or taxa, respectively, at these depths. Dominant species were *Oncaea zernovi*, two species of the *ovalis*-group (*O. crypta* and *O. ovalis*), *Triconia* sp. 8, *O. tregoubovi*, and *Epicalymma* spp.. In-between, at 1250 m, oncaeid species numbers were lower (17 species), with few species (*Oncaea* sp. 7, *O. zernovi*, females of *O. crypta*) dominating, however, at highly variable abundance values. In the near-bottom area, at and below 4200 m depth, the abundance values and species numbers of oncaeids were considerably lower than above (5–7 species) and the community was strongly dominated by species of *Epicalymma* (Table 4).

Taxonomic status of mediterranean Oncaeidae

Table 5 lists mediterranean species of Oncaeidae which were not found during the present study, grouped according to their current state of taxonomic knowledge. Three species names are regarded as invalid, because their description was based on juvenile stages (cf. Malt 1982). Two species represent new, as yet undescribed, morphospecies (Table 5d). For most of the remaining 22 species, the taxonomic knowledge is regarded as insufficient. In

summary, from the total number of 46 oncaeid species that had previously been recorded in the Mediterranean Sea (Table 3, 5), 19 species were found to be inadequately described and most of these had their *type locality* in the Mediterranean Sea (14 species).

Discussion

Species diversity

The species diversity of Oncaeidae in the Mediterranean Sea appears so far to have been underestimated to a great extent. In addition to the 46 valid species and two form variants previously reported from this area (cf. Tables 3, 5), more than 20 putative species and/or morphotypes were found during the present study, thereby increasing the number of species by ~50%. Even when taking into account some doubtful earlier records (*O. pumilis* Heron 1977, *Triconia rufa* (Boxshall and Böttger), and *Oncaea notopus* Giesbrecht), and facing the fact that some rare and/or taxonomically unresolved species, i.e., those not yet having been described in sufficient detail (cf. Table 5), may have been overlooked in the present study, the data presented here indicate that the actual number of species of Mediterranean Oncaeidae may well be about 70. An

Table 4 Abundance (ind./1000 m³) of oncaeid microcopepods at four selected depth layers in the deep eastern Mediterranean Sea, SE of Crete

| Species/taxon | Sex/stage | 400–450m | | 1,250m | | 2,750–3,000m | | 4,200m | 10 mab | |
|---------------|--|----------|--------|---------------|--------|--------------|--------|-----------|---------|---------|
| | | X4 | R4 | X4 | R4 | X4 | R4 | R2 | R2 | |
| 1 | <i>Epicalymma</i> spp. | 300 | 0–770 | 89 | 64–220 | 150 | 88–200 | 35/25 | 120/120 | |
| 2 | <i>Monothula subtilis</i> | FM | 0 | 0 | | 1.1 | 0–4.4 | 0/0 | 0/0 | |
| | <i>Oncaea</i> s.l., total | | 36,000 | 26,500–47,000 | 2,900 | 1,100–6,050 | 1,050 | 450–1,400 | 15/2.6 | 43/11 |
| 3 | <i>Oncaea crypta</i> | F | 7,900 | 5,700–10,000 | 310 | 0–1,200 | 32 | 0–80 | 4.3/0 | 1.3/0 |
| 4 | <i>Oncaea</i> sp. 7 | FM | 320 | 190–450 | 1,350 | 380–2,900 | 120 | 55–220 | 0/0 | 0/0 |
| 5 | <i>O. ornata</i> | FMJ | 350 | 0–1,150 | 67.5 | 39–82 | 12 | 0–49 | 0/0 | 0/0 |
| 6 | <i>O. ovalis</i> | F | 550 | 0–860 | 11 | 0–45 | 40 | 0–68 | 0/0 | 0/0 |
| | <i>O. ovalis</i> –group | MJ | 5,300 | 3,000–8,850 | 4,200 | 0–1,700 | 500 | 2.3–150 | 0/0 | 5.2/0 |
| 7 | <i>O. parabathyalis</i> | F | 350 | 0–770 | 20 | 0–82 | 9.7 | 0–22 | 0/0 | 0/0 |
| 8 | <i>O. prendeli</i> | F | 440 | 220–770 | 10 | 0–40 | 30 | 0–72 | 0/0 | 0/0 |
| 9 | <i>O. shmelevi</i> | FM | 1,300 | 0–3,100 | 10 | 0–40 | 9.5 | 0–38 | 2.1/0 | 0/0 |
| 10 | <i>O. tregoubovi</i> | FM | 2,150 | 860–3,500 | 40 | 0–160 | 62 | 0–110 | 0/1.3 | 0/0 |
| 11 | <i>O. zernovi</i> | FM | 15,000 | 8,500–20,000 | 530 | 0–2,100 | 450 | 300–520 | 0/1.3 | 16/11 |
| 12 | <i>Oncaea</i> s.l. spp. | (F)MJ | 3,200 | 1,300–5,000 | 85 | 0–280 | 240 | 93–440 | 8.6/0 | 21/0 |
| | <i>Oncaea</i> s.str., total | | 640 | 43.5–1,300 | 14 | 4.6–34 | 105 | 30–180 | 2.1/0 | 0/0 |
| 13 | <i>O. media</i> | F | 8.7 | 0–24 | 0 | | 18 | 0–44 | 0/0 | 0/0 |
| 14 | <i>O. mediterranea</i> , slender form | F | 24 | 9.0–40 | 3.2 | 0–5.0 | 13 | 3.0–38 | 2.1/0 | 0/0 |
| 15 | <i>O. mediterranea</i> , broad form | F | 24 | 9.0–36 | 1.5 | 0–3.1 | 7.3 | 0–24.5 | 0/0 | 0/0 |
| | <i>O. mediterranea</i> | M | 110 | 0–410 | 4.7 | 0–14 | 22 | 0–44 | 0/0 | 0/0 |
| 16 | <i>O. scottodicarloi</i> | FMJ | 360 | 0–780 | 0.60 | 0–2.5 | 19.5 | 7.0–46 | 0/0 | 0/0 |
| 17 | <i>O. venusta</i> f. <i>typica</i> | F | 0 | | 0 | | 0.70 | 0–2.7 | 0/0 | 0/0 |
| 18 | <i>O. venusta</i> f. <i>venella</i> | F | 0 | | 3.1 | 0–12.5 | 0 | | 0/0 | 0/0 |
| | <i>Oncaea</i> s.str. spp. | M | 0 | | 0 | | 21 | 0–85 | 0/0 | 0/0 |
| 19 | <i>O. waldemari</i> | FM | 120 | 3.0–445 | 0.60 | 0–2.5 | 4.9 | 0–17 | 0/0 | 0/0 |
| | <i>Spinoncaea</i> , total | | 48 | 0–190 | 3.0 | 0–12 | 12 | 0–25 | 0/0 | 0/0 |
| 20 | <i>S. ivlevi</i> | F | 48 | 0–190 | 0 | | 12 | 0–25 | 0/0 | 0/0 |
| | <i>Spinoncaea</i> spp. | (FM)J | 0 | | 3.0 | 0–12 | 0 | | 0/0 | 0/0 |
| | <i>Triconia</i> , total | | 5,300 | 1,900–8,700 | 58 | 0–205 | 210 | 130–260 | 0/0 | 0/0 |
| 21 | <i>Triconia</i> cf. <i>similis</i> (2 species) | F | 330 | 0–760 | 0 | | 4.9 | 0–17 | 0/0 | 0/0 |
| 22 | <i>T. conifera</i> | FM | 35 | 9.0–60 | 3.1 | 0–12.5 | 3.3 | 0–8.2 | 0/0 | 0/0 |
| 23 | <i>T. elongata</i> | F | 270 | 7.0–500 | 0 | | 44 | 3.0–100 | 0/0 | 0/0 |
| | <i>T. elongata</i> | M | 190 | 0–390 | 10 | 0–40 | 27 | 0–44 | 0/0 | 0/0 |
| 24 | <i>T. furcula</i> | FM | 230 | 24–780 | 0 | | 1.1 | 0–4.2 | 0/0 | 0/0 |
| 25 | <i>Triconia</i> cf. <i>minuta/umerus</i> | F | 200 | 0–570 | 3.1 | 0–12.5 | 5.5 | 0–22 | 0/0 | 0/0 |
| 26 | <i>T. minuta</i> | F | 58 | 7.0–200 | 0.60 | 0–2.5 | 7.4 | 0–25 | 0/0 | 0/0 |
| 27 | <i>Triconia</i> sp. | F | 100 | 0–210 | 0 | | 0 | | 0/0 | 0/0 |
| 28 | <i>Triconia</i> sp. 8 | F | 2,900 | 1,100–5,800 | 40 | 0–160 | 73.5 | 39.5–100 | 0/0 | 0/0 |
| 29 | <i>T. umerus</i> | F | 840 | 0–1,800 | 1.2 | 0–5.0 | 20 | 0–38 | 0/0 | 0/0 |
| | <i>Triconia</i> spp. | M | 57 | 0–225 | 0 | | 22 | 17–25 | 0/0 | 0/0 |
| | Total Oncaeidae | | 43,000 | 31,000–54,000 | 3,000 | 1,200–6,300 | 1,500 | 750–2,000 | 52/28 | 160/135 |
| | Total no. of species/taxa | | 26 | | 17 | | 28 | | 7 | 5 |

Xn Average of *n* samples, *Rn* range from *n* samples, *F* female, *M* male, *J* juveniles, *mab* Meters above bottom

Table 5 Species of Oncaeidae from the Mediterranean not found during the present study and sorted by current taxonomic status

| Species/taxon | | |
|---|-------------------|--|
| a. Taxonomic status resolved | | |
| <i>Conaea</i> | <i>rapax</i> | Giesbrecht 1891 |
| <i>Epicalymma</i> | <i>exigua</i> | (Farran 1908) |
| * <i>Oncaea</i> s.l. | <i>bathyalis</i> | Shmeleva 1968 ^a |
| ? <i>Oncaea</i> s.l. | <i>pumilis</i> | Heron 1977 |
| <i>Oncaea</i> s.str. | <i>clevei</i> | Früchtl 1923 |
| <i>Triconia</i> | <i>borealis</i> | (Sars 1918) |
| ? <i>Triconia</i> | <i>rufa</i> | (Boxshall and Böttger 1987) |
| <i>Triconia</i> | <i>similis</i> | (Sars 1918) |
| b. Taxonomic status unresolved | | |
| * <i>Oncaea</i> s.l. | <i>africana</i> | Shmeleva 1979 |
| * <i>Oncaea</i> s.l. | <i>alboranica</i> | Shmeleva 1979 |
| <i>Oncaea</i> s.l. | <i>atlantica</i> | Shmeleva 1967 |
| * <i>Oncaea</i> s.l. | <i>brodskii</i> | Shmeleva 1968 |
| * <i>Oncaea</i> s.l. | <i>furnestini</i> | Shmeleva 1979 |
| * <i>Oncaea</i> s.l. | <i>longipes</i> | Shmeleva 1968 |
| * <i>Oncaea</i> s.l. | <i>longiseta</i> | Shmeleva 1968 |
| * <i>Oncaea</i> s.l. | <i>minima</i> | Shmeleva 1968 |
| * <i>Oncaea</i> s.l. | <i>minor</i> | Shmeleva 1979 |
| <i>Oncaea</i> s.l. | <i>mollicula</i> | Gordeyeva 1975 |
| ? <i>Oncaea</i> s.l. | <i>notopus</i> | Giesbrecht 1891 |
| <i>Oncaea</i> s.l. | <i>oceanica</i> | Gordeyeva 1972 |
| * <i>Oncaea</i> s.l. | <i>tenella</i> | Sars 1916 |
| * <i>Oncaea</i> s.str. | <i>curta</i> | Sars 1916 |
| c. Invalid species (juvenile stages, cf. Malt 1982) | | |
| <i>Oncaea</i> | <i>obscura</i> | Farran 1908 |
| * <i>Oncaea</i> | <i>neobscura</i> | Razouls 1969 |
| * <i>Oncaea</i> | <i>parobscura</i> | Shmeleva 1979 |
| d. Undescribed new morphospecies | | |
| <i>Oncaea</i> s.l. | sp. 4 | <i>atlantica</i> - group ^b |
| <i>Oncaea</i> s.l. | sp. 6 | taxonomic group uncertain ^b |

^a Species inquirenda (cf. Böttger-Schnack 2005)

^b cf. Böttger-Schnack (1997: Table 10)

*Species originally described from the Mediterranean (type locality)

? Record questioned (see text)

interoceanic comparison of the biodiversity of Oncaeidae in the Mediterranean Sea with corresponding data from other oceanic areas, such as the Red Sea (Böttger-Schnack 1994; Böttger-Schnack et al. 2004), the Arabian Sea (Böttger-Schnack 1996), and the NW Pacific (Nishibe 2005), however, can only be given after the taxonomic status of the various unidentified oncaeid morphs in the Mediterranean has been clarified.

Two of the newly recorded oncaeid species are sister or sibling taxa of species that had previously been recorded in the Mediterranean Sea: *Triconia furcula* belongs to the

conifera-subgroup, which includes morphologically very closely related species (Heron and Bradford-Grieve 1995), and *T. elongata* is a sibling of *T. dentipes* (cf. Böttger-Schnack 1999). The Mediterranean occurrence of another sister species, *Oncaea englishi*, which is closely related to *O. ornata*, was only reported recently by Lapernat and Razouls (2001) and was substantiated in the present study. It may be assumed that all these newly recorded species had erroneously been included under the name of their corresponding sibling or sister species during earlier studies in this area (e.g., Scotto di Carlo et al. 1991; Böttger-Schnack 1997). The co-occurrence of sibling species among oncaeid copepods has frequently been observed in the sea. Nishibe (2005) identified several co-occurring siblings of the *conifera*-complex in the NW Pacific area. Heron and Frost (2000) found two species of the *ornata*-group, *Oncaea ornata* and *O. englishi*, to co-occur regularly in the open NE Pacific, and Nishibe et al. (2009) recorded both species from the NW Pacific, off southern Japan. In the Red Sea, the three sibling species of the *dentipes*-subgroup are known to co-occur widely, though regional differences may be found (Böttger-Schnack 1999; Böttger-Schnack et al. 2008). As for the Mediterranean Sea, the regional and/or seasonal extension of the co-occurrence of newly recorded sister or sibling species among oncaeids still needs to be examined in more detail.

The genus *Triconia* appears to be exceptionally speciose in the Mediterranean Sea: In addition to the seven species so far known from this area (Tables 3, 5), two identified species and eight as yet unidentified morphotypes and/or putative species were newly recorded during the present study. As yet unidentified and probably new *Triconia* species have also been found in other areas of the world ocean, such as the NE Indian Ocean, off the NW Cape of Australia (McKinnon et al. 2008), and in the NW Pacific (Nishibe et al. 2009), thus pointing to an unresolved—and probably high—diversity of the genus in these areas, too. In particular, the diversity of the *similis*-subgroup of *Triconia* appears so far to have been underestimated to a great extent. Eight of the newly recorded morphotypes or putative species in the Mediterranean Sea belong to this subgroup, so that the number of species so far known in this group (7 species; cf. Böttger-Schnack 1999) is more than doubled. It seems that the *similis*-subgroup may be even more diverse than the *conifera*-subgroup of *Triconia*, which presently contains 11 species (Heron and Bradford-Grieve 1995; Böttger-Schnack 1999).

Several oncaeid species reported earlier from the Mediterranean Sea were not found during the present study (Table 5). These include *Conaea rapax*, *Oncaea brodskii* and a number of very small species, such as *O. longipes*, *O. minor* and *O. minima*. For the first two species mentioned, their absence may be explained by their rare occurrence, as

they were also not found previously during extended regional (e.g., Scotto di Carlo et al. 1991) or temporal (e.g., Kršinić 1998; Kršinić and Grbec 2002) quantitative plankton sampling in the Mediterranean Sea. However, the fact that *Conaea rapax*, known as a deep-living species (e.g., Boxshall 1977; Heron 1977), has not been reported in quantitative deep sea studies in the Mediterranean Sea (e.g., Scotto di Carlo et al. 1991; Böttger-Schnack 1997) raises some doubt as to whether the occurrence of the species in this area can be verified. The species was originally described by Giesbrecht (1891) from the tropical East Pacific Ocean and subsequently redescribed by the same author in his comprehensive taxonomic study on copepods from the Gulf of Naples [Giesbrecht 1893 (“1892”)]. However, in the Naples study, Giesbrecht explicitly stated that *C. rapax* was an “auswärtige Species” [1893 (“1892”): 605], not occurring in the Mediterranean Sea [1893 (“1892”): 771]. Subsequent morphological redescriptions of *C. rapax* by Heron (1977) and Boxshall (1977) were based on copepod material from the Pacific Antarctic area and the NE Atlantic Ocean, respectively. Thus, it may be possible that in the Mediterranean Sea the species had been confounded with similar-looking species by authors who might have been unaware of Giesbrecht’s remarks in 1893. In the Mediterranean study of deep sea copepods by Vaissière and Seguin (1980), for example, the occurrence of *Conaea rapax* was listed while the ubiquitous *O. ornata* was not mentioned. As long as no taxonomic description of *C. rapax* from the Mediterranean is provided, the geographical record should be regarded as doubtful.

For the very small species with a female body length less than 0.25 mm mentioned above, it is reasonable to assume that, due to their small size, they had not been sampled in the 0.1-mm mesh nets used during our study. However, the total absence of the small *O. longipes* at all stations sampled along the west-to-east transect during October 2001 is quite unexpected, as this species had previously been recorded as a numerically abundant taxon in the midwater community of oncaeids in the eastern and western regions (Böttger-Schnack 1997; Kršinić 1998; Kršinić and Grbec 2002). Thus, it should have been caught at least occasionally during our study, as other species of similar size (e.g., species of the *atlantica*- and the *vodjanitskii*-group) have been recorded during the present study, even though only in very small numbers. At present, no convincing explanation can be given for this absence of *O. longipes* in our material.

The Mediterranean records of three oncaeid species are regarded as doubtful (Table 5). The record of *Oncaea pumilis* by Malt et al. (1989) was based on a single male specimen collected in the eastern Mediterranean. The species had previously been recorded only from the deep Arctic and Antarctic sectors of the Pacific (Heron 1977; Heron et al. 1984). The description of *O. pumilis sensu*

Malt et al. (1989) includes inconsistencies between text and figures (e.g., proportional spine lengths of swimming legs) and their identification arguments appear to be inconclusive. The species they described might belong to the *ovalis*-group of oncaeids, which have a very complicated taxonomic history and have been redescribed in detail by Böttger-Schnack (2005). However, a positive identification of *O. pumilis sensu* Malt et al. (1989) cannot be given without examination of their specimen. *Triconia rufa* as recorded by Malt et al. (1989) may have been confounded with the very similar new morphospecies *Triconia* sp. 8 as separated by Böttger-Schnack (1997). Similarly, in the earlier records of *Oncaea notopus* (e.g., Vaissière and Seguin 1980; Kovalev and Shmeleva 1982; Uysal et al. 2002) the species may have been confounded with the new, as yet undescribed, morphospecies *Oncaea* sp. 7, which appears to be the only representative of the *notopus*-group in the Mediterranean Sea (Böttger-Schnack 1997; this study). A possible explanation for the erroneous earlier records of *O. notopus* in the Mediterranean Sea may be the same as given above for *Conaea rapax*: *O. notopus* was originally described by Giesbrecht (1891) based on copepod material from the Pacific and redescribed as an “auswärtige Species” in the Naples study of Giesbrecht (1893 [“1892”]), but was not recorded in the Mediterranean Sea by this author [1893 (“1892”): 774]. No representative of the *notopus*-group was recorded by Malt et al. (1989), Kršinić (1998), and Kršinić and Grbec (2002), although their fine mesh net sampling included depth layers down to 650 m or even 800 m, where the species is usually found.

Regional distribution

During the present study, regional differences in the total numbers of identified species between the Western and Eastern Basins appeared to be minor, but some species were restricted either to the western or the eastern parts, thereby counterbalancing the changes in total numbers. This impression may change when all the unidentified morphospecies have been clearly described. Also, the temporal and spatial restrictions of the sampling strategy during the present study do not allow for a more detailed comparison of the regional differences in species diversity. Species of Indo-Pacific origin may have entered the eastern Mediterranean by the way of the Suez canal (Furnestin 1979), such as anticipated for *Oncaea clevei* which was recorded only recently in the Eastern Basin by Uysal et al. (2002). However, the great morphological similarity of oncaeid species requires careful taxonomic examination of any species new to this area, in order to exclude erroneous identifications, as demonstrated above for *Triconia rufa*.

Apart from the observed differences in species diversity, a considerable change in the numerical dominance of co-

occurring siblings was indicated among oncaeid copepods along the west-to-east-axis, though no quantitative data can be given. For example, the numerical proportion of the two siblings of the *dentipes*-group, *T. dentipes* and *T. elongata*, clearly differed between the regions, with *T. dentipes* dominating in the western area and *T. elongata* being more numerous in the eastern parts. A similar observation of a regional change in the numerical abundances of these two species has recently been observed in the Red Sea, where both species are present in similar abundances in the main basin, whereas *T. elongata* is highly dominant in the northern extension, the Gulf of Aqaba (Böttger-Schnack et al. 2008). In the Mediterranean, other closely related species also appeared to differ in numerical importance between the west and the east, such as the two siblings of the *conifera*-group, *T. conifera* and *T. furcula* (the latter being more abundant in the east) and the species of the *media*-group, with *O. waldemari* being less abundant in the eastern part.

Deep-sea Oncaeidae (>1,000 m depth)

The limited dataset on the species diversity of bathypelagic oncaeid copepods in the Mediterranean Sea obtained during the present study, being restricted both temporally (one season) and spatially (Eastern Basin), does not allow for a detailed discussion of this topic. Nevertheless, the data give first insights into the species richness and community structure of this important microcopepod family in the deep Mediterranean Sea, which is little known. Compared to results from other oceanic regions, such as the Red and the Arabian Seas, the oncaeid fauna in the deep Mediterranean Sea had previously been presumed to hold an intermediate position with regard to its species richness (Böttger-Schnack 1994). In the adjacent Red Sea, only fewer than 10 oncaeid species or taxa inhabit the depth layers below 1,000 m (Böttger-Schnack 1994), and several oncaeid genera or groups typical for deep-sea layers, such as *Conaea* and the *notopus*- or the *ornata*-group, are absent in this area. The reduced species diversity and the lack of typical deep-sea forms of pelagic copepods in the Red Sea has been explained by the elevated temperatures, which cause a comparably low vertical flux of particulate organic matter into the deep-sea by increasing the bacterial degradation in the mesopelagic zone (e.g., Wishner 1980; Weikert 1982, 1987). A similar explanation had been given for the impoverished deep-sea fauna in the Mediterranean Sea (Scotto di Carlo et al. 1984, 1991; Weikert and Trinkaus 1990), which likewise is characterized by a homogeneous, relatively warm, deep water mass (Wüst 1960, 1961). However, subsequent studies (Böttger-Schnack 1994, 1997; present study) now indicate that the deep-sea community of eastern Mediterranean Oncaeidae appears to have a much higher species richness as compared to the Red Sea. The

present observation of up to 28 species in the depth range below 1,000 m even appears to be an underestimation, as several taxa, such as *Epicalymma* and the *similis*-group of *Triconia*, included a high number of yet unidentified morphospecies, thereby supporting the earlier mentioned hypothesis (see “Introduction”), that these depth layers of the ocean may in fact be regarded as “hotspots” of microcopepod diversity. The size range of the newly detected *Epicalymma* morphospecies (0.28–0.42 mm) cannot be sampled by the conventionally used nets of 0.2-mm mesh size. By taking into account these unidentified morphospecies, the total number of deep-sea oncaeids in the Mediterranean may be well above 30 species. This diversity in the oncaeid fauna appears to be similar to that observed in oceanic habitats and climates with more typical (cold) deep sea waters, such as the Arabian Sea and the subarctic NW Pacific. In the Arabian Sea, 18 identified species and 7 groups of provisionally classified species of Oncaeidae [including approx. 44 morphospecies] were found between 1,000 and 1,850 m depth (Böttger-Schnack 1994, 1996), and in the subarctic NW Pacific, between 17–21 species of oncaeids were present in the 1,000–2,000 m depth layer (Nishibe and Ikeda 2004; Nishibe 2005, Table 2.4).

In contrast to the bathypelagic depth layers discussed above, the near-bottom layers in the Mediterranean Sea showed a very reduced abundance and species diversity of Oncaeidae (mainly *Epicalymma* spp.), and small calanoids (mainly Discoidae and unidentified juvenile stages) dominated the microcopepod community in the benthopelagic zone (Koppelman et al. 2009). However, in other years and seasons, high abundances of *Epicalymma* spp. in the near-bottom layers of the eastern Mediterranean Sea have been found (Böttger-Schnack, unpublished data), thus underlining the observed high variability in this habitat (Koppelman et al. 2009). So far, no comparable data from other benthopelagic habitats are available for the size spectrum of microcopepods. The high variability in the community structure of small zooplankton taxa observed at these depths requires more extended and rather demanding further investigation. Calanoid and non-calanoid copepod taxa are supposed to have different life strategies (feeding requirements) and the few available data cannot give any convincing answer to the observed differences in the community structure of benthopelagic microcopepods.

Identification problems of Oncaeidae

For many oncaeid species, the taxonomic status is unresolved because the original descriptions are insufficient and many sister or sibling species have been detected, putting into question the apparently worldwide distribution of allegedly cosmopolitan species. Regarding the Mediterranean Sea, the earlier records of several oncaeid species,

such as *Triconia conifera*, *T. dentipes*, *Oncaea ornata* and *O. media*, have to be revised, because they were found to include two (*conifera*-group, *dentipes*-group) or even three (*ornata*-group, *media*-group) different species upon detailed re-examination (see above). Apart from zoogeographical questions, the unequivocal differentiation of species is crucial for the study of population biology, ecological relations and community functions. However, it appears to be difficult to transfer progress in taxonomy into the field of ecological studies, as shall be exemplified below for the species of the *media*-complex:

Oncaea media was originally described by Giesbrecht (1891) from the tropical Pacific, and was redescribed by the same author in a subsequent study including additional copepod material from the Gulf of Naples (Giesbrecht 1893 [“1892”]). Note that in this case the presence of the species in the Mediterranean was explicitly stated by the author, in contrast to the species of the *notopus*-group and *Conaea rapax* discussed above. In 1995, Heron and Bradford-Grieve concisely redescribed *O. media* based on material from the Pacific and from the Gulf of Naples. They clarified some taxonomic confusion of Giesbrecht’s redescription of *O. media* in 1893 [“1892”] by describing a new species, *O. scottodicarloi*, which they found to be partly conspecific with *O. media sensu* Giesbrecht (1893 [“1892”]: figure 11 only). The third species of the *media*-complex, *O. waldemari*, was described by Bersano and Boxshall [1996 (“1994”)] and redescribed by Böttger-Schnack (2001) based on material from various localities and the type material, thereby clarifying some taxonomic inconsistencies between the text and the figures of Bersano and Boxshall’s original description. The developmental stages of *O. media* as described by Malt (1982) were assigned to *O. waldemari* upon re-examination of the adult specimens of Malt’s material from Plymouth Sound (Böttger-Schnack 2001). The taxonomic characters separating the species of the *media*-complex were summarized (Böttger-Schnack 2001: Table 6), and the complicated taxonomic history and status of *O. curta* Sars (originally described from the western Mediterranean Sea) was outlined, which belongs to the *media*-group, but cannot be positively identified due to the lack of type material.

The relevance of the species differentiation within the *media*-complex for ecological studies in the Mediterranean Sea has recently been demonstrated by Kršinić et al. (2007). By incorporating the latest taxonomic findings in a comprehensive study on the copepod assemblages in the Adriatic Sea, a succession was found for *O. waldemari* (1993–1996) and *O. media* (1997), thereby updating previous studies from this area, which recorded “*O. media*” as the dominant form (e.g., Wiryawan 1997; Lučić and Kršinić 1998; Riccardi and Mariotto 2000). In many other ecological studies, however, the overarching name “*O. media*” is still used, without

differentiating the species of this complex. In the Aegean Sea, for example, recent comprehensive studies on zooplankton distribution (Zervoudaki et al. 2006) and copepod reproduction (Zervoudaki et al. 2007) listed “*O. media*” as the dominant oncaeid, although previous examination of their plankton material had shown all three species of the *media*-complex to be present in this area and a seasonal succession between the species was indicated (R. Böttger-Schnack, unpublished data). In the same area, Sever et al. (2005) reported “*O. media*” as the main food organism for the European pilchard, *Sardina pilchardus* Walbaum, being dominant “for six months of the year”, but it remains open, whether the absence of any seasonal differences in the relative importance of the species observed by the authors may in fact have been obscured not recognizing seasonal potential successions of species within this complex. For the North Atlantic, an identification tool of developmental stages of 26 copepod species, including “*O. media*”, was recently provided by Conway (2006) as a revised version of an earlier paper by Conway and Minton (1975). Unfortunately, the species name *O. media* has not been revised according to the state of knowledge. The earlier data of Conway and Minton (1975) had been based on *O. media* f. *minor sensu* Malt (1982), which intermittently had been recognized to be conspecific with *O. waldemari* (see above). By referring to Conway’s length data of “*O. media*”, an error was introduced by Irigoien and Harris (2006) into their study on the comparative population structure, abundance and vertical distribution of six copepod species in the Atlantic, including unidentified *Oncaea* spp., for which they took “*O. media*” as the reference species. The data provided by Irigoien and Harris may well include several species of the *media*-complex.

The main reason for the inadequate consideration of taxonomic findings in marine ecological studies appears to be a gap in the flow of information from taxonomists to ecologists; identification keys that can easily be used by (non expert)-scientists are rare or lacking for the small copepods. Original taxonomic papers, usually including many morphological details, are often difficult to read by non-experts and are, thus, not adequately considered by ecologists. The few reliable identification keys of Oncaeiidae in the world ocean are restricted to particular geographic provinces and do not include all size groups of the family (e.g., Heron 1977; Heron and Frost 2000). Identification keys including very small oncaeid species (e.g., Shmeleva 1969), on the other hand, are insufficient for the purpose of modern taxonomic findings. Regional identification keys, restricted in the considered size range, may lead to erroneous results when applied to copepod material sampled with mesh sizes different from the one used by the taxonomist who established the key: For example, most keys of Heron and co-workers do not

include the smaller oncaeid species less than 0.5 mm in length. To overcome the present restrictions in the species identification of Oncaidae, it would be desirable to construct identification keys that can be easily updated according to the latest taxonomic findings. Such keys, which should include traditional morphological data as well as novel molecular traits (cf. Elvers et al. 2006; Böttger-Schnack and Machida 2008) should be made available to the scientific community via a data-delivery system, which can be used by the non-expert as well as by the specialist. The adequate consideration of the numerous, as yet undescribed, microcopepod species in the world ocean, in particular the Oncaidae, appears to be a challenge for ecological studies as well as global biodiversity estimates.

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