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MONOGRAPH

The Mediterranean Sepiolidae (Mollusca Cephalopoda) diversity

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ABSTRACT Sepiolidae (Mollusca Cephalopoda) is the most diverse cephalopod family in the Mediterranean Sea, where 17 species of this taxon have been identified. In the present review, the updated list of the Mediterranean sepiolids is given along with the species type locality, the first documented record in this basin and the present geographical distribution. The exclusion of *Sepiola atlantica* and *Heteroteuthis atlantis* - species that have been reported in the Mediterranean but whose presence is not warranted - from the list is also explained. Moreover, patently erroneous information about the bathymetric and geographical distributions of *Sepiola rondeletii* is revised. The extreme rarity of *Sepiola aurantiaca* and the comparatively recent entrance into the Mediterranean and establishment of *Stoloteuthis leucoptera* are discussed. The genesis of the Mediterranean sepiolid-fauna, in relation to the NE Atlantic fauna, is dealt with and, in particular, the reasons that determined its comparatively broad diversity are examined. They are to be traced back to both the mode of life and reproductive biology of these small-sized cephalopods. In connection with the latter matter, the high degree of endemism in the subfamily Sepiolinae is also explained.

KEY WORDS Cephalopoda; biogeography; biodiversity; Mediterranean; NE Atlantic Ocean.

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To Adolf Naef (1883-1949)
and George Evelyn Hutchinson (1903-1991),
perennial sources of inspiration

INTRODUCTION

Sepiolidae is the most diverse cephalopod family in the Mediterranean Sea, which represents a hot-spot for this taxon since its maximum worldwide richness value was recorded just in this ecoregion (Rui et al., 2019). In all, 17 sepiolid species have been identified in the Mediterranean (Bello, 2008, 2017); all of them are small-sized. They are assigned to three subfamilies, namely Sepiolinae, Rossiinae and Heteroteuthinae, which are distributed worldwide. Members of a fourth, undescribed subfamily were discovered in the Pacific Ocean (Young, 2007).

The present review aims, firstly, at establishing the critical systematic list of the Mediterranean members in this family; secondly, at discussing its biogeography in the north-eastern Atlantic and Mediterranean districts.

To the former aim, the first documented record in this sea is reported for each species and the un-

warranted, questionable records, both geographically- and depth-wise, are discussed. In fact, the members of Sepiolinae are not promptly identifiable to the species level, especially before their sexual maturation, hence the literature, chiefly the old one, is crowded with many determination mistakes. In this respect, we have to mention that the first scholar to understand the systematics of Sepiolidae, was Adolf Naef (1883-1949). He, when working at the Stazione Zoologica in Naples, revised the whole Mediterranean teuthofauna (Naef, 1923) and described two new genera and seven new species of Sepiolinae (Naef, 1912a, 1912b, 1912c, 1916).

Identification tools for the Mediterranean Sepiolidae are Naef (1923) (a monograph of paramount importance), Mangold & Boletzky (1987), Guerra (1992) (this also includes NE Atlantic taxa), Bello (1995), Reid & Jereb (2005) (this is a reference worldwide review that includes the Atlantic species), Bello (2013) (this only relates to the Atlantic-Mediterranean *Sepiola atlantica* group).

As for the latter aim, the biogeography of the Mediterranean Sepiolidae was discussed by Bello (2003). In the present paper, it is further considered in relation to the NE Atlantic sepiolid-fauna in order to explain the genesis of the Mediterranean sepiolid diversity.

MATERIAL AND METHODS

This review is based on the relevant literature. In particular, I referred to the "Checklist of the flora and fauna in Italian seas" (Bello, 2008, 2017) for the systematic inventory of the Mediterranean Sepiolidae species, Bello (2015) for their updated nomenclature, and Reid & Jereb (2005) for their general distribution in both the Mediterranean Sea and the Atlantic Ocean.

Following the critical systematic list of the Mediterranean Sepiolidae, each specific entity is reported with its type locality, first documented Mediterranean record and general distribution. Next, peculiar cases are dealt with: the unwarranted Mediterranean and Atlantic records, the recent entrance into the Mediterranean, and the occurrence in this sea of rare sepiolid species.

RESULTS

Systematic list of Mediterranean Sepiolidae

In each subfamily and genus, the type genus and type species, respectively, are reported first, followed by the remaining genera and species arranged in alphabetical order.

Familia SEPIOLIDAE Leach, 1817
Subfamilia SEPIOLINAE Leach, 1817

Sepiola Leach, 1817
- *Sepiola rondeletii* Leach, 1817
- *Sepiola affinis* Naef, 1912
- *Sepiola aurantiaca* Jatta, 1896
- *Sepiola boletzkyi* Bello et Salman, 2015
- *Sepiola bursadhaesa* Bello, 2013
- *Sepiola intermedia* Naef, 1912
- *Sepiola ligulata* Naef, 1912
- *Sepiola robusta* Naef, 1912
- *Sepiola steenstrupiana* Levy, 1912

Rondeletiola Naef, 1921
- *Rondeletiola minor* (Naef, 1912)

Sepietta Naef, 1912
- *Sepietta oweniana* (d'Orbigny in Férussac et d'Orbigny, 1841)
- *Sepietta neglecta* Naef, 1916
- *Sepietta obscura* Naef, 1916

Subfamilia HETEROTEUTHINAE Appellöf, 1898

Heteroteuthis Gray, 1849
- *Heteroteuthis dispar* (Rüppell, 1844)

Stoloteuthis Verrill, 1881
- *Stoloteuthis leucoptera* (Verrill, 1878)

Subfamilia ROSSIINAE Appellöf, 1898

Rossia Owen, 1835
- *Rossia macrosoma* (delle Chiaje, 1830)

Neorossia Boletzky, 1971
- *Neorossia caroli* (Joubin, 1902)

The Mediterranean Sepiolidae

Sepiolinae

The nominotypical subfamily, Sepiolinae, is the best-defined taxon in this family. In addition to

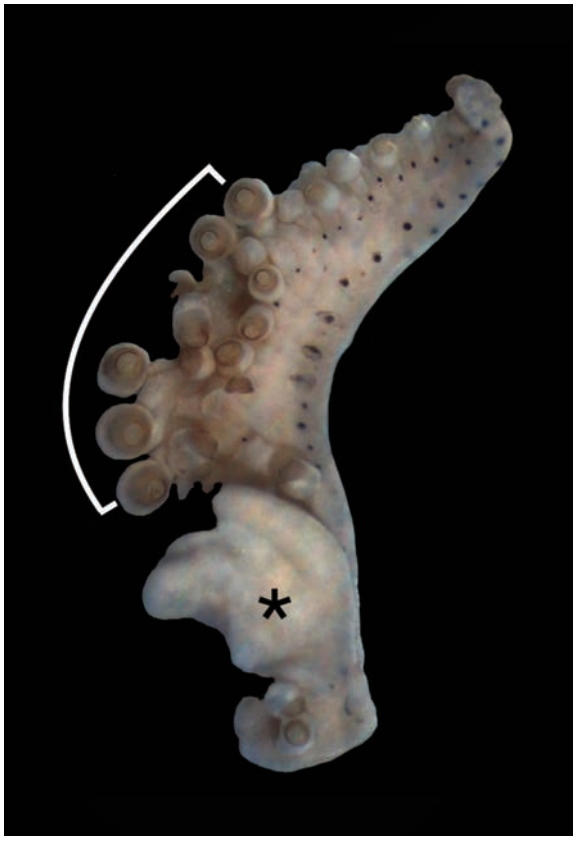

Figure 1. Hectocotylus of *Sepiola boletzkyi*. The left dorsal arm of Sepiolinae bears modified suckers: the asterisk * marks a group of suckerless lengthened stalks, the white line points out several enlarged suckers in the dorsal row.

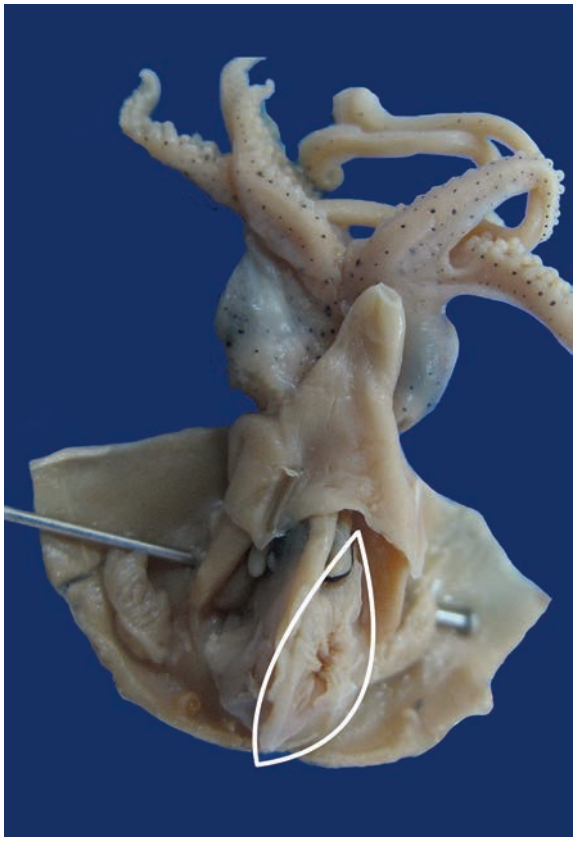

Figure 2. Visceral organs of a female *Sepiola boletzky*. The white line encompasses the bursa copulatrix, which is the terminal part of the gonoduct; on it the male implants its spermatophores during copulation.

other features, it is characterized by peculiar copulatory organs: the hectocotylus in males, i.e. the left dorsal arm modified to transfer spermatophores to females (Fig. 1) and the bursa copulatrix in females, placed in the left ventral mantle cavity (Fig. 2). The latter is an apomorphic character, a unique feature of Sepiolinae. This taxon contains the genera *Sepiola* (type genus), *Euprymna, Inioteuthis*, *Rondeletiola* and *Sepietta*. *Euprymna* and *Inioteuthis* are exclusively Indo-Pacific. Members of this taxon are mainly benthic.

Sepiola rondeletii

Type locality. "European sea" (Leach, 1817); corrected type locality: Mediterranean Sea (Sweeney, 2001; Bello, 2015). First Mediterranean documented record: Naef (1912a). Note that almost all European sepioline species were ascribed to the nominal species *Sepiola rondeletii* before the revision by Naef (1912a) (see further), so that it is virtually impossible to validate all records of this sepioline published before Naef's works (1912a, 1912b, 1923), unless supported by museum specimens and/or well-defined illustrations. Naef (1912a) was the first author to accurately define this species, hence, the first trustworthy identifications are to be credited to him (Bello, 2015).

Distribution and Ecology. It is a quasi-endemic Mediterranean sepioline, which is distributed all over the Mediterranean Sea (Reid & Jereb, 2005) and in the Atlantic Ocean close to the Strait of Gibraltar, e.g. in the Gulf of Cadiz (Guerra, 1982) (quasi-endemic sensu Bello (2003) is a Mediterranean species that is also found in the Atlantic Ocean in the vicinities of Gibraltar). Although *Sepiola rondeletii* has been reported in the northeast-

ern Atlantic Ocean from the North Sea to Senegal (see review by Reid and Jereb, 2005), the northern Atlantic records are inaccurate according to Groenenberg et al. (2009). The typical habitat of this sepioline is "*sandy and muddy substrates, common in* Posidonia *seagrass beds down to 35 m*" (Reid & Jereb, 2005: 168), however deeper finds, down to 450 m depth, are reported in the literature (cf. Reid & Jereb, 2005). In the Gulf of Cadiz, two specimens were collected from a muddy bottom 190 m deep (Guerra, 1982). See the next chapter "Unwarranted sepiolid records" for geographically- or depth-wise improbable records of *Sepiola rondeletii.*

Sepiola affinis

TYPE LOCALITY. Gulf of Naples, Tyrrhenian Sea, western Mediterranean. First Mediterranean documented record: Naef (1912b). It proceeds from the original description.

DISTRIBUTION AND ECOLOGY. A Mediterranean endemic species. It is a shallow water sepioline that has been reported from the whole coastal belt of the western basin and from the northern coasts of the eastern basin (Reid & Jereb, 2005), but most probably it also lives along the northern African and Asia Minor shores.

Sepiola aurantiaca

TYPE LOCALITY. Gulf of Naples, Tyrrhenian Sea, western Mediterranean. First Mediterranean documented record: Jatta (1896). It proceeds from the original description.

DISTRIBUTION AND ECOLOGY. The only known specimens were collected in the Amontatura (or Ammontatura) channel (100 to 140 m deep) in the Gulf of Naples.

Sepiola boletzkyi

TYPE LOCALITY. Gulf of Ildir (Turkey), Aegean Sea, eastern Mediterranean. First Mediterranean documented record: Bello & Salman (2015). It proceeds from the original description.

DISTRIBUTION AND ECOLOGY. A shallow water species only known from its type locality.

Sepiola bursadhaesa

TYPE LOCALITY. Catalan Sea, western Mediterranean. First Mediterranean documented record: Bello (2013). It proceeds from the original description.

DISTRIBUTION AND ECOLOGY. It is only known from its type locality. It is most probably a shallow water species.

Sepiola intermedia

TYPE LOCALITY. Gulf of Naples, Tyrrhenian Sea, western Mediterranean. First documented record: Naef (1912a). It proceeds from the original description.

DISTRIBUTION AND ECOLOGY. *Sepiola intermedia* is a Mediterranean quasi-endemic, since it was also collected in the Gulf of Cadiz (West of Gibraltar) by Guerra (1982). Reid & Jereb (2005) refer that it is distributed, between 60 and 200 m of depth, in the whole Mediterranean except the Libyan, Egyptian and Asia Minor coasts. Anyway, most probably it also lives there.

Sepiola ligulata

TYPE LOCALITY. Gulf of Naples, Tyrrhenian Sea, western Mediterranean. First Mediterranean documented record: Naef (1912a). It proceeds from the original description.

DISTRIBUTION AND ECOLOGY. This is a comparatively deep water sepioline, living on muddy bottoms from a few tens of metres down to the upper slope (ca. 350 m). It was deemed a Mediterranean quasi-endemic (Bello, 2003) because the northernmost record was that by Guerra (1986) in the Ría de Vigo (NW Spain). The presence of a *Sepiola ligulata* population in that district was recently corroborated by the collection of paralarvae (Olmos-Pérez et al., 2017). Indeed, in addition to the whole Mediterranean Sea, it inhabits a wide portion of the NE Atlantic Ocean (de Heij et al., 2017), hence it cannot any longer be termed quasi-endemic.

Sepiola robusta

TYPE LOCALITY. Gulf of Naples, Tyrrhenian Sea, western Mediterranean. First Mediterranean docu-

mented record: Naef (1912a). It proceeds from the original description.

Distribution and Ecology. An endemic Mediterranean found all over the basin, from a few tens of metres down to 500 m.

Sepiola steenstrupiana

Type locality. Off Villefranche (Alpes Maritimes, France), Gulf of Lions, western Mediterranean. First Mediterranean documented record: Levy (1912). It proceeds from the original description.

Distribution and Ecology. It has been recorded in the northern part of the Mediterranean Sea and in the Levant Sea (Reid & Jereb, 2005). Outside the Mediterranean, it was collected in the Red Sea (Adam, 1973) and off the eastern Somali coast (Indian Ocean) (Rocha et al., 1998). Accordingly, *Sepiola steenstrupiana* is an endemic Mediterranean sepioline that seemingly crossed the Suez Canal in a counter-Lessepsian migration.

Rondeletiola minor

Type locality. Gulf of Naples, Tyrrhenian Sea, western Mediterranean. First Mediterranean documented record: Naef (1912a). It proceeds from the original description.

Distribution and Ecology. This is a deep-water East Atlantic-Mediterranean sepioline. Reid & Jereb (2005) report that it is found from 76 to 496 m of depth all over the Mediterranean Sea, including the Sea of Marmara, and off the West African and West Iberian coasts, from Namibia to the Gulf of Biscay. A recent survey collected very many specimens farther North to the West of Ireland, and few scattered ones off Scotland and Norway, in a wider depth range, from 25 to 800 m (de Heij et al., 2017. *Rondeletiola minor* is one of the most frequently netted sepiolines in the Mediterranean Sea.

Sepietta oweniana

Type locality. Unknown. This species occurs in both the Mediterranean Sea and the NE Atlantic Ocean. First Mediterranean documented record: Jatta (1896). This author lumped in his description of "*Sepiola rondeletii*" several sepioline species from the Gulf of Naples, comprising *Sepietta* spp. too. The pictured elements of the purported *Sepiola rondeletii* include a hectocotylus (Jatta, 1896: pl. 14 fig. 28) (Fig. 3), which is unmistakably *Sepietta oweniana*'s (compare Jatta's figure to Naef, 1912b: fig. 1, shown in figure 6 of present paper).

Distribution and Ecology. A NE Atlantic-Mediterranean species from Mauritania to North Norway (Reid & Jereb, 2005). The occurrence of a specimen farther North, in the SW Barents Sea, is possibly due to the ocean waters warming (Golikov et al., 2014). *Sepietta oweniana* is distributed over a wide depth range, from few tens of metres to over 1,000 m (Reid & Jereb, 2005), and is the most abundantly collected Mediterranean sepioline.

Sepietta neglecta

Type locality. Gulf of Naples, Tyrrhenian Sea, western Mediterranean. First Mediterranean documented record: Naef (1916). It proceeds from the original description.

Distribution and Ecology. Reid & Jereb (2005) refer that *Sepietta neglecta* is found from 25 to 475 m of depth, in the whole Mediterranean, including the Sea of Marmara, and in the NE Atlantic Ocean from Marocco to the Orkney Islands and South Norway. De Heij et al. (2017) extended its distribution to the waters West of England, Wales and Ireland.

Sepietta obscura

Type locality. Gulf of Naples, Tyrrhenian Sea, western Mediterranean. First Mediterranean documented record: Naef (1916). It proceeds from the original description.

Distribution and Ecology. A quasi-endemic Mediterranean sepioline that was found in most of the Mediterranean littoral waters and off the West Iberian coast (Reid & Jereb, 2005). According to the literature data referred by the same Authors, *Sepietta obscura* depth range is 27 to 376 m. In my opinion, this is a shallow water species that dwells on littoral grounds only, from few metres of depth on (personal observations).

HETEROTEUTHINAE

The taxon Heteroteuthinae is indeed polyphyletic (Allcock et al., 2014) and needs a thorough revision. Its members are characterized by a broad web between arms and a comparatively large mantle with extended ventral shield, which characters are indicative of their pelagic mode of life. Some of them display an occipital band, i.e. a dorsal commissure between mantle and head, a feature shared with Sepiolinae, e.g. *Heteroteuthis*, and others do not, which is typical of Rossiinae, e.g. *Stoloteuthis*. In addition to the type genus, *Heteroteuthis*, this subfamily includes *Amphorateuthis*, *Nectoteuthis*, *Iridoteuthis*, *Sepiolina*, and *Stoloteuthis* (Young et al., 2015).

Heteroteuthis dispar

TYPE LOCALITY. Off Messina, Strait of Messina, Mediterranean. First Mediterranean documented record: Rüppell (1844). It proceeds from the original description.

DISTRIBUTION AND ECOLOGY. A mesopelagic species that lives in the whole Mediterranean and the North Atlantic Ocean, down to about 1,600 m of depth (Reid & Jereb, 2005). It is very abundant and, despite its diminutive size, is a key item in food webs (e.g. Bello, 1999).

Stoloteuthis leucoptera

TYPE LOCALITY. Gulf of Maine, NW Atlantic Ocean. First Mediterranean documented record: Orsi Relini & Massi (1991), in the Ligurian Sea, western Mediterranean.

DISTRIBUTION AND ECOLOGY. Jereb & Reid (2005) refer that it is an amphi-Atlantic species living in the northern West Atlantic Ocean, from Canada to Florida, and from the Bay of Biscay to Namibia in the East Atlantic Ocean; depth range: 160-700 m. It entered the western Mediterranean Sea in recent times and established there a viable population (see further).

ROSSIINAE

The subfamily Rossiinae contains the largest-sized members of the Sepiolidae (up to 10 cm mantle length), which are characterized by the absence of both the occipital band and the ventral mantle shield. This subfamily includes the genera *Rossia* (type genus), *Austrorossia*, *Neorossia*, and *Semirossia*. All rossiines are benthic (Young & Vecchione, 2014).

Rossia macrosoma

TYPE LOCALITY. In the surroundings of Naples, Tyrrhenian Sea, western Mediterranean (Bello, 2015). First Mediterranean documented record: delle Chiaje (1830). It proceeds from the original description.

DISTRIBUTION AND ECOLOGY. A North Atlantic-Mediterranean sepiolid living on comparatively deep grounds, from 25 to 900 m (Reid & Jereb, 2005; de Heij et al., 2017). It dwells in the whole Mediterranean basin and in the Atlantic Ocean from Greenland to Norway and far south to Senegal (Reid & Jereb, 2005).

Neorossia caroli

TYPE LOCALITY. The Azores, North Atlantic Ocean. First Mediterranean documented record: Dieuzeide (1959), off the Aguelli island (Algeria), south-western Mediterranean.

DISTRIBUTION AND ECOLOGY. *Neorossia caroli* is found in the eastern Atlantic Ocean from Namibia to Iceland (Reid & Jereb, 2005). According to the review of these Authors, it is a typical upper slope benthic sepiolid recorded down to 1744 m; it has been recorded from neritic grounds as shallow as 40 m, although, in the Mediterranean Sea, the preferred upper limit is at about 400 m of depth.

Unwarranted sepiolid records

Adolf Naef, who may be rightly termed the father of modern Teuthology, revised several cephalopod taxa during his stay at the Stazione Zoologica of Naples. He did a most accurate study of Sepiolidae, whose taxonomic situation was quite muddy at that time, and described two new genera and seven new species (Naef, 1912a; 1912b; 1916; 1921; 1923). Before Naef's revision, all or almost all European sepioline species were ascribed to the nominal species *Sepiola rondeletii*

(cf. Bello, 2015). Hence, all records of "*Sepiola rondeletii*" prior to 1912 are to be regarded as unwarranted and should not be taken into account. For instance, the drawing of the purported hectocotylus of "*Sepiola Rondeleti*" presented by Joubin (1902: fig. 2) is evidently copied from Jatta (1896: pl. 14 fig. 28), whose figure, as reported above, depicts the hectocotylus of *Sepietta oweniana*, a species well established at that time (Fig. 4) (compare Joubin's figure to Jatta, loc. cit.). Also, the arm crown of "*Sepiola rondeletii*" depicted by Pfeffer (1908: fig. 56) is in fact misidentified: it belongs indeed to *Sepiola intermedia,* as Naef (1923) already showed; in Pfeffer's partial defence one may say that *Sepiola intermedia* had not yet been described when he wrote his paper. Sadly enough, even after Naef disclosed and described the Atlantic-Mediterranean diversity in Sepiolinae, many misidentifications have occurred (Bello, 2015). As reported above, in the current literature, the *Sepiola rondeletii* distribution is reported to cover, in addition to the Mediterranean Sea, the north-eastern Atlantic Ocean from the North Sea to Senegal (see review by Reid & Jereb, 2005). However, later on, Groenenberg et al. (2009) suggested that the northern Atlantic records are inaccurate. Also, some depth records, as deep as 450 m (cf. Reid & Jereb, 2005), are questionable since this sepioline is typically a coastal cephalopod.

As for comparatively recent implausible records, Würtz et al. (1995) reported a finding of *Sepiola atlantica* in the South Tyrrhenian Sea, which was not warranted in any way, i.e. no textual description, no photograph, no deposit in any institutional collection. A search for the specimen from

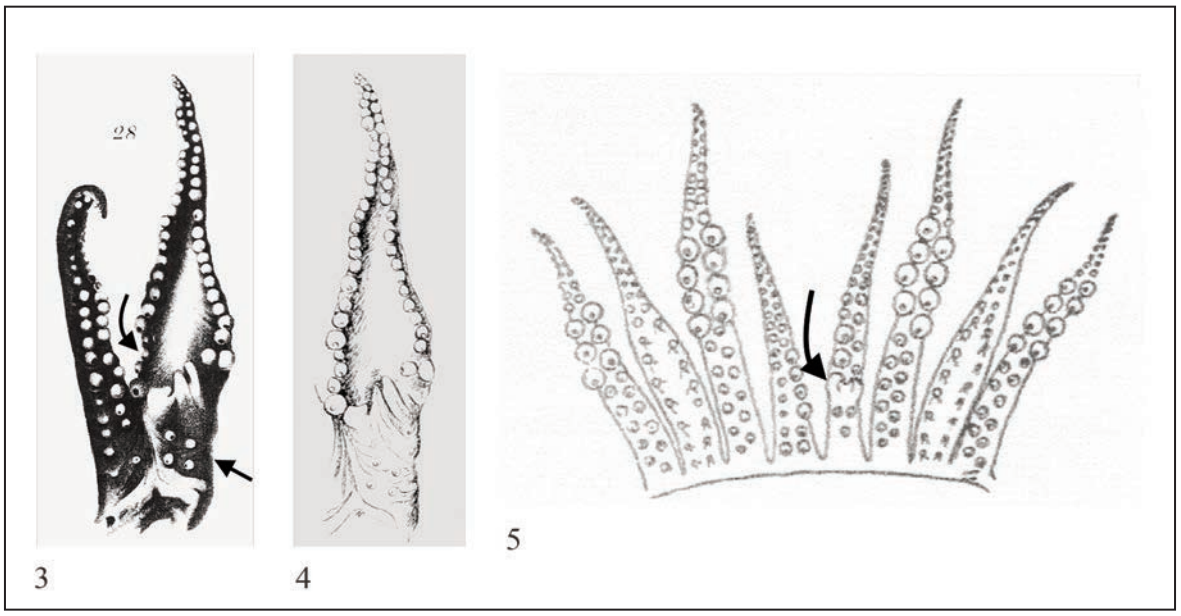

Figure 3. Drawing of the dorsal arms of purported *Sepiola rondeletii* from Jatta (1896: pl. 14 fig. 28). In fact, the depicted hectocotylus (arm on the right) is typically *Sepietta oweniana*'s according to the four basal suckers (straight arrow) (three in *S. rondeletii*) and the distribution of the enlarged suckers in two groups parted by few smaller suckers (curved arrow) in the dorsal row; the copulatory apparatus is not very indicative of any specific taxon. Compare Jatta's figure to Naef (1912b: fig. 1) (Fig. 6 of present paper), where the actual *S. rondeletii* and *S. oweniana* are labelled c and e, respectively.

Figure 4. Drawing of the hectocotylus of purported *Sepiola rondeletii* from Joubin (1902: fig. 2). This is a copy of a part of Jatta's figure (1896: pl. 14 fig. 28) (see Fig. 3 of present paper) and therefore depicts indeed the hectocotylus of *Sepietta oweniana*.

Figure 5. Arm crown of "*Sepiola rondeletii*" depicted by Pfeffer (1908: fig. 56). Naef (1923) stated that this belongs to *Sepiola intermedia*, according to the distribution of enlarged suckers and despite the fact that the copulatory apparatus (arrow) was inadequately delineated.

the Tyrrhenian Sea by the present author was unsuccessful. A further negative evidence is the list by Giordano & Carbonara (1999) which did not report this species among the cephalopods collected in 13 extensive bottom trawl surveys in that sea. In my opinion Würtz et al.'s (1995) record is not be taken into consideration. It was also doubted by Reid & Jereb (2005) by a question mark in the relevant distribution map.

A Mediterranean finding of *Heteroteuthis atlantis* was reported in a note of the paper describing the new species (Voss, 1955). Though this binomen was placed into synonymy with *Heteroteuthis dispar* by Nesis (1987), *Heteroteuthis atlantis* was subsequently cited, doubtfully yet, among the Mediterranean Sepiolidae (e.g. Bello, 1995). Nesis' (1987) opinion is shared by MolluscaBase (2018). Reid & Jereb (2005) state that until the taxonomy of the genus is studied, the validity of this heteroteuthine remains questionable.

Recent sepiolid Mediterranean entrance

Stoloteuthis leucoptera is the only extra-Mediterranean sepiolid that entered this basin in comparatively recent times. It is an amphi-Atlantic species (Reid & Jereb, 2005) that was first recorded in the Ligurian Sea thanks to three specimens collected there in 1988 (Orsi Relini & Massi, 1991) and afterwards was found in other western Mediterranean districts (Volpi et al., 1995; Würtz et al., 1995; Sánchez et al., 1998; Cuccu et al., 2010; Quetglas et al., 2013). The report by Quetglas et al. (2013), who netted 25 specimens mostly in the Alboran Sea, is particularly interesting because they started to capture this sepiolid only in 2001, while no one had been caught in previous surveys, from 1994 to 2010. In my opinion, the many Mediterranean occurrences of this cephalopod from the late '80s on, coupled with the lack of previous records from areas well surveyed in the past, soundly support the hypothesis that *Sepiola leucoptera* naturally entered the Mediterranean Sea from the Atlantic Ocean through the Straits of Gibraltar, extended its range within the western basin and succeeded in generating a self-sustained population (Battaglia et al., 2011). As for the Alboran Sea, the reported presence of *Sepiola leucoptera* since 2001 only (Quetglas et al., 2013) may be either due to a further immigration bout or to the westward expansion of the recent Mediterranean population. Lastly, heteroteuthines are known to lay their eggs on the sea floor (Nesis, 1993), hence the crossing of the Gibraltar Strait for sure involved juveniles and/or adults rather than early juveniles of this pelagic species.

The *Sepiola leucoptera* case makes a good example of the way the Mediterranean Sea has become naturally populated by Atlantic species after its re-connection to the ocean following the Messinian salinity crisis till the present.

Rare species

Three *Sepiola* species can be regarded as very rare, since each of them was only found in a very limited site, which coincides with its type locality. They are *Sepiola aurantiaca*, *Sepiola bursadhaesa* and *Sepiola boletzkyi*. The rarity of the latter two species may be just apparent because they were only recently described, hence they might have been overlooked if found in other district samples; in this respect, let us mention once more that members of Sepiolinae are the most difficult to identify species among the Mediterranean cephalopods especially when sexually immature.

As for *Sepiola aurantiaca*, the only known specimens were collected about one century ago exclusively in the spot called Amontatura, in the Gulf of Naples (Jatta, 1896). Until a few years ago, this sepioline had been reported in the eastern Atlantic Ocean as well, but Goud & de Heij (2012) showed that the Atlantic specimens belong indeed to *Sepiola pfefferi* Grimpe, 1921, a sister species of *Sepiola aurantiaca*. The Mediterranean rarity of the latter sepioline is quite puzzling especially when one takes into account that the Gulf of Naples is possibly the best explored place in the Mediterranean Sea thanks to the workers at the Stazione Zoologica, including Giuseppe Jatta, the species discoverer, and Adolf Naef, the Sepiolidae reviser, both of them keen cephalopod collectors.

Among the comparatively rare species, one may mention *Sepiola steenstrupiana*. In fact, this sepioline has been found in all Mediterranean districts (Mangold & Boletzky, 1987; Reid & Jereb, 2005). Its deceptive rarity depends on the fact that it lives in coastal areas only, at very shallow depths which are poorly explored with the customary trawl nets. Moreover, strangely enough, *Sepiola steenstrupi-*

ana has been reported from the Red Sea (Adam, 1973) and the western Indian Ocean (coasts of Somalia) (Rocha et al., 1998). This might be a rare case of counter-Lessepsian migration, from the Mediterranean to the Red Sea.

GENERAL REMARKS

In summary, updates for the Mediterranean Sepiolidae with respect to an earlier review of the Mediterranean teuthofauna (Bello, 2003) consist in: (a) the addition of the newly described species *Sepiola bursadhaesa* and *Sepiola boletzkyi*, one century after the mentioned discoveries by Naef (1912a, 1912b, 1912c; 1916); (b) evidence that *Sepiola aurantiaca* is endemic to this sea; (c) disclosure that *Sepiola rondeletii* is not widely distributed in the NE Atlantic Ocean but just close to the Gibraltar Strait, hence it is a quasi-endemic species; (d) evidence that *Sepiola ligulata* lives also in the NE Atlantic Ocean (it was deemed quasi-endemic by Bello, 2003; see also Reid & Jereb, 2005); (e) confirmation that *Stoloteuthis leucoptera* has established a viable population in the western basin. As for the Atlantic sepiolid diversity, in addition to the just conveyed news on *Sepiola rondeletii* and *Sepiola ligulata*: (f) a new species was described, namely *Sepiola tridens;* (g) *Sepiola pfefferi* was found to be the NE Atlantic sibling of the Mediterranean *Sepiola aurantiaca*.

As stated in Introduction, Sepiolidae is the most speciose cephalopod family in the Mediterranean (17 species) as well as in the NE Atlantic district (16 species); the overall NE Atlantic-Mediterranean

Figure 6. The hectocotylus diversity in many sepioline species (after Naef, 1912b: fig. 1). The drawings show the pair of dorsal arms - the hectocotylus is that on the right side – of *Sepiola steenstrupiana*, *S. robusta*, *S. rondeletii*, *S. aurantiaca*, *Sepietta oweniana*, *S. atlantica*, *S. ligulata*, *S. intermedia*, and *Rondeletiola minor* (left to right, starting from upper row).

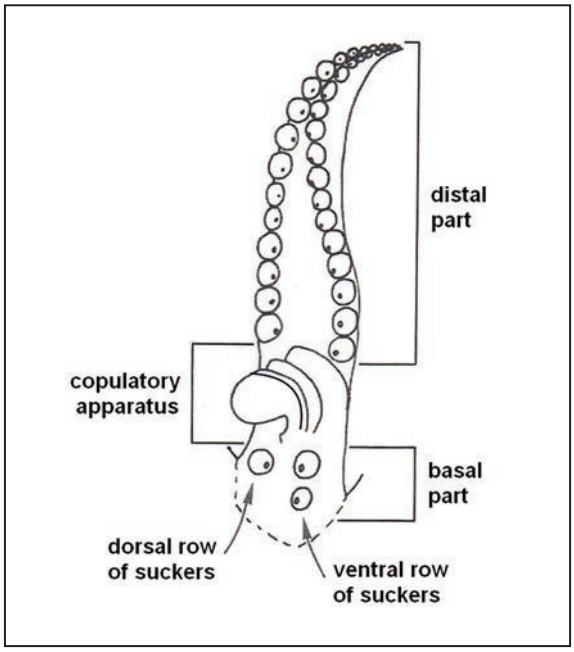

Figure 7. The hectocotylus basic type of the *Sepiola atlantica* group (sensu Naef, 1923). The copulatory apparatus is formed by four suckerless, elongate stalks fused with each other throughout their length into a structure apically directed and curled inwards; in some species the two dorsal suckers are not readily perceivable because of their strict fusion into a single tubercle.

sepiolid diversity includes 22 specific entities, 12 of which are shared by both districts (Table 1). The most speciose subfamily is Sepiolinae, which amounts to 13 specific entities in the Mediterranean, 10 in the NE Atlantic Ocean and overall 16, seven of which are found in both districts; in other words, this subfamily includes a fairly high fraction of endemic and quasi-endemic species: 69% in the Mediterranean Sea and 30% in the NE Atlantic. On the contrary, the few Mediterranean species belonging to Rossiinae and Heteroteuthinae live also in the North Atlantic Ocean; the only two endemic species in the latter district, namely *Rossia palpebrosa* and *Rossia moelleri*, live in high latitudes, well north of the Strait of Gibraltar.

The NE Atlantic-Mediterranean Sepiolinae form a fairly compact clade, where *Sepietta* and *Rondeletiola* are sister genera, that is synthetically (*Sepiola*, *Sepietta, Rondeletiola*)) (Bello, 1998). The males in this clade are characterized by a peculiar hectocotylus - the male left dorsal arm modified into a copulatory organ - where the copulatory apparatus is made of four modified suckers, two ventral and two dorsal (additional modified dorsal suckers may occur in some species) (Naef, 1923; Bello, 1995); the modification consists in the loss of the sucker proper and lengthening and/or widening of the stalk (Fig. 6) (Naef, 1923; Bello, 1995). The females bear a unique feature, that is an apomorphic character: the bursa copulatrix (Fig. 2).

A closer look at Sepiolinae reveals a fairly high number of twin- and sister-species (the former species displaying a closer affinity with each other than the latter) (Table 2). The majority of the *Sepiola* species, both Mediterranean and Atlantic, are gathered in the "*atlantica* group" sensu Naef (1923) because of their similarity (see also Bello, 2013) (Table 2). This group is characterized by the lengthening, fusion throughout their length, and inwards curling of the four modified sucker stalks of the copulatory apparatus (Fig. 7) (Naef, 1923; Bello, 2013). All of them are either Mediterranean endemics/quasi-endemics or NE Atlantic endemics, seven and two species respectively. Outside the "*atlantica* group", *Sepiola aurantiaca* and *Sepiola pfefferi* are twins and are endemic of the Mediterranean and the Atlantic Ocean respectively. The genus *Sepietta* contains fewer specific entities: a Mediterranean quasi-endemic, i.e. *Sepiola obscura*, and two widely distributed twin species, i.e. *Sepiola oweniana* and *Sepiola neglecta.*

GENESIS OF THE MEDITERRANEAN SEPIOLIDAE DIVERSITY

The Mediterranean Sea is generally deemed a sub-region of the Atlantic Ocean because its biodiversity originated with the Zanclean flood (5.3 MYA) following the Messinian salinity crisis (Blanc, 2002), which allowed the colonization by Atlantic organisms. The latter phenomenon has gone on since and is still at work; as for cephalopods, see for instance the above reported recent entrance and establishment of *S. leucoptera* in the western Mediterranean basin. One must point out that not all species entering the Mediterranean succeed in establishing a viable population here because the environmental conditions may be neither suitable for their survival nor for their reproduction (Bouchet & Taviani, 1992).

GENERA	SPECIES	NE ATLANTIC	MEDITERRANEAN	NOTES
Sepiola (*atlantica* group)	*affinis*		E	1
	atlantica	E		2
	boletzkyi		E	
	bursadhaesa		E	
	intermedia	(+)	QE	
	robusta		E	
	rondeletii	(+)	QE	
	steenstrupiana		E	
	tridens	E		2
Sepiola (others)	*aurantiaca*		E	3
	ligulata	+	+	
	pfefferi	E		3
Rondeletiola	*minor*	+	+	
Sepietta	*neglecta*	+	+	4
	obscura	(+)	QE	
	oweniana	+	+	4
Heteroteuthis	*dispar*	+	+	
Stoloteuthis	*leucoptera*	+	+	5
Rossia	*macrosoma*	+	+	
	moelleri	E		
	palpebrosa	E		
Neorossia	*caroli*	+	+	

Table 1. Composition of the north-eastern Atlantic and Mediterranean sepiolid-faunas. E: endemic species; QE: quasi-endemic species (see text); +: occurring in large part of district; (+): occurring close to Gibraltar Strait. NOTES: (1) The species of *Sepiola* in the "*atlantica* group" are phylogenetically closely connected with each other, hence they are sister species (Naef, 1923; Bello, 2013); (2) *atlantica* and *tridens* are twin species (de Heij & Goud, 2010); (3) *pfefferi* and *aurantiaca* are twin species (Goud & de Heij, 2012); (4) *oweniana* and *neglecta* are sibling species (Bello, 1998); (5) non-indigenous species recently established in the western Mediterranean (Battaglia et al., 2011).

MEDITERRANEAN SEA	NE ATLANTIC OCEAN
Sepiola aurantiaca	*Sepiola pfefferi*
Sepiola atlantica group (*affinis, boletzkyi, bursadhaesa, intermedia, robusta, rondeletii, steenstrupiana*)	*Sepiola atlantica* group (*atlantica, tridens*)

Table 2. Closely related NE Atlantic-Mediterranean pairs of *Sepiola* species.

Incidentally, additional, albeit unnatural, comparatively recent sources for the Mediterranean colonization are the opening of the Suez Canal, on 17 November 1869 and living creatures carrying in ship ballast water. In consequence of the former, some 500 Red Sea organisms have crossed the canal to reach the Levant Sea and, in several instances, spread out across most Mediterranean waters (Galil et al., 2017); they include some cephalopods too, e.g. *Sepioteuthis lessoniana* (Teuthida Loliginidae) (Salman, 2002). The latter source, i.e. ballast water, was invoked by Orsi Relini (2009) to explain the Mediterranean occurrences of the Indo-Pacific *Tremoctopus gracilis* (Octopoda Tremoctopodidae).

The natural colonization of the Mediterranean, a medium-latitude sea, by Atlantic organisms was heavily shaped by the sequence of Pleistocene glaciations and interglaciations that brought into the Mediterranean cold and warm elements respectively (Taviani, 2003). This phenomenon is typified by the rossiines: *Rossia macrosoma* and *Neorossia caroli* are respectively of Mauretanic (i.e. warm) and Lusitanic (i.e. cold) affinity (classification according to Ekman,1953). Parenthetically, Bello (2003) suggested that in a pair of akin species the cold-water one inhabits deeper layers than the warm-water one; this supposition is backed up by the distributions of the above-mentioned pair of rossiines.

The above paragraph implies that the two species of Mediterranean Rossiinae came from the near Atlantic Ocean. The same is true for the two species of Mediterranean Heteroteuthinae, whose entrance was further favoured by their mode of life, pelagic for *Heteroteuthis* dispar and bentho-pelagic for *Stoloteuthis leucoptera* (Reid & Jereb, 2005). The only NE Atlantic endemic species belonging to these two subfamilies live at high latitudes and most probably never moved southward to the level of the Strait of Gibraltar: *Rossia palpebrosa* is strictly temperate and *Rossia moelleri* is arctic (Reid & Jereb, 2005).

In addition to the species coming from the Atlantic Ocean, many new entities originated in the Mediterranean by in situ speciation after its re-colonization by Atlantic organisms. This statement concerns all marine taxa and, as for cephalopods, is particularly true for Sepiolinae, which, differently from the co-familiar subfamilies, display a high degree of endemism especially in the genus *Sepiola*.

Endemic members of this genus are also found in the Atlantic Ocean, namely *Sepiola atlantica*, *Sepiola tridens* and *Sepiola pfefferi* (Table 1). Mediterranean *Sepiola* species have their twin or sister counterparts in the ocean (Table 2), with the only exception of *Sepiola ligulata*, which occurs in both districts. This peculiar distribution is robust evidence to corroborate the close affinity between Mediterranean and Atlantic sepiolines and to support the hypothesis that both the Atlantic and Mediterranean *Sepiola* species originated from Atlantic common ancestors - possibly one for *pfefferi-aurantiaca*, which are twin species (Goud & de Heij, 2012), and another one for the "*atlantica* group" - that entered the Mediterranean and produced separate populations, which evolved independently to give rise to the present-day species. Moreover, some of the species that evolved in the Mediterranean basin went back through the Strait of Gibraltar and spread in its Atlantic vicinities, which species I termed quasi-endemic (Bello, 2003), namely *Sepiola intermedia* and *Sepiola rondeletii*. In particular, the situation of the "*atlantica* group" is quite interesting. As reported above, the members of this group share a peculiar hectocotylus, different from all other sepiolines. The examination and comparison of the hectocotylus of the "*atlantica* group" members show that its variations are just different expressions of a common proto-hectocotylus (proto- with respect to this group, not to the whole Sepiolinae) (Fig. 7).

As for the other genera in Sepiolinae, the species of *Rondeletiola* and *Sepietta* are found in both districts, although *Sepiola obscura* is a Mediterranean quasi-endemic, as reported above.

Two features appear of paramount importance in characterizing high-dispersal sepiolines (i.e. occurring in both the Atlantic Ocean and the Mediterranean) vs. low-dispersal species (endemic or quasi-endemic of either district): relative egg size (sensu Boletzky, 1974 and 1977) and, to a lesser extent, habitat depth. As shown by Boletzky (1974 and 1977), the egg relative size is responsible for the hatchling mode of life: the larger it is the shorter the planktonic life, hence less wide the spreading. In fact, the *Sepiola* species - all of which, with one exception, are endemic or quasi-endemic of either district - reproduce by comparatively large eggs (Gabel-Deickert, 1995) and live

mostly in shallow waters. The exception, namely *Sepiola ligulata*, though reproducing by large eggs, has been collected as deep as 350 m. The other comparatively deep water *Sepiola* species, i.e. *intermedia* and *robusta*, are quasi-endemic. *Rondeletiola* and *Sepietta*, on the contrary, include comparatively small-egged, deep-living species, with the exception of *Sepiola obscura,* which is large-egged and lives in shallow waters (Gabel-Deickert, 1995). Accordingly *R. minor*, *S. owenia-ana*, and *S. neglecta* are widely spread in both the Atlantic Ocean and the Mediterranean Sea, whereas *S. obscura*, as stated above, is a Mediterranean quasi-endemic.

According to Bello (2003), the high rate speciation in Sepiolinae is due to the following features: small body size; short life cycle (less than a year); reduced number of eggs, hence reduced fecundity, with respect to other Mediterranean cephalopods (Gabel-Deickert, 1996); reproduction by large eggs, which give birth to benthic early juveniles (Boletzky, 1974 and 1977); nekto-benthic mode of life (Bello & Biagi, 1995); mostly living in shallow coastal waters; fairly diverse hectocotylus, in males, and bursa copulatrix, in females (Naef, 1923; Bello, 1995). All these characteristics greatly favour speciation. For instance, the comparatively low-dispersal capabilities of both early juveniles and adults in shallow water habitats facilitates the establishment of small, marginal populations where the process of speciation may occur more efficiently (Eldredge & Gould, 1972). In fact, a few Mediterranean *Sepiola* species seemingly have a restricted distribution, e.g. *Sepiola aurantiaca* and *Sepiola bursadhaesa*. Bello (2003) also stated that sepiolines living in littoral environments appear to fit fairly well the statement of Hutchinson (1959) in his Homage to Santa Rosalia: "*... small size, by permitting animals to become specialized to the conditions offered by small diversified elements of the environmental mosaic, clearly makes possible a degree of diversity quite unknown among groups of larger organisms.*" (see Bello, 2003, for further comments). Moreover, a role in speciation is most probably also played by the species-specific lock-and-key copulatory organs, i.e. the male hectocotylus and the female bursa copulatrix, which preventing hybridization among allied sympatric species reinforces reproduction isolation (Hutchinson, 1959). In recent times, the lock-and-key mechanisms have been subjected to criticism and are no longer believed to depend on natural selection exclusively but rather on a combination of natural and sexual selection (Masly, 2012; Brennan & Prum, 2015). Whatever the evolutionary driving forces behind this selection, we can at least safely state that the species-specific hectocotylus-bursa copulatrix pairs in the Sepiolinae are the result of co-evolutionary processes.

CONCLUSIONS

We presently have at our disposal a fairly satisfactory picture of the systematics and biogeography of Mediterranean Sepiolidae, but there is still much to learn.

First of all, it must be stressed that, sadly enough, the literature is still crowded with misidentifications of sepioline specimens, including those used in genetic research (Groenenberg et al., 2009), which hinders the understanding of both their phylogenetic relationships and distribution, geographical as well as bathymetrical. Therefore, a prudent approach is suggested to workers dealing with sepiolid identification; on this respect a fair solution is the deposit of voucher specimens in official collections.

For a worldwide view, the phylogenetic relationships of the Atlantic-Mediterranean Sepiolidae with co-familiar members from the other oceans need to be studied on the basis of both morphological and genetic accounts. In turn, the ocean-wide biogeography of the family should be analyzed. This way, further light would also be shed on the Mediterranean situation of Sepiolidae.

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