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Contribution of soft-bodied meiofaunal taxa to Italian marine biodiversity

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Abstract
Meiofauna includes an astonishing diversity of organisms, whose census is far from being complete. Most classic ecological studies have focused on hard-bodied Ecdysozoan taxa (notably Copepoda and Nematoda), whose cuticle allows determination at species-level after fixation, rather than soft-bodied, Spiralian taxa, which most often lose any diagnostic feature in fixed samples. Yet, metabarcoding studies have recently revealed a species-richness of soft-bodied taxa comparable, and in cases superior, to that of Copepoda and Nematoda together. However, given objective difficulties inherent to their study, which necessarily has to be performed on living individuals, and their limited utilisation for ecological and applicative research, taxonomic expertise on soft-bodied organisms has declined over the years, and diversity of these phyla in most areas of the world is presently completely unknown. Here we present an expert-based survey of current knowledge on the composition and distribution of soft-bodied meiofaunal taxa in Italy, with special references to the predominantly or exclusively meiobenthic phyla Gastrotricha, Gnathostomulida, Platyhelminthes, Rotifera, Xenacoelomorpha, and macrofaunal taxa with conspicuous meiofaunal representatives (Annelida, Mollusca and Nemertea). A total of 638 described species have been reported from Italian coasts; furthermore, the existence of a large number of undescribed species is mentioned. Knowledge of Annelida, Gastrotricha, and Rotifera appears particularly detailed, placing Italy among the best-known country worldwide. In contrast, knowledge of Platyhelminthes and Xenacoelomorpha appears patchy, and limited to few areas. Sampling effort has been uneven, with most species recorded from the Tyrrhenian Sea, while large sections of the Adriatic and Ionian seas have been poorly explored. Results highlight the role that Marine Biological Stations, notably the Zoological Station "Anton Dohrn" in Naples, have had in promoting the study of soft-bodied taxa in Italy.

Keywords: *Meiobenthos, mesopsammon, microscopic biodiversity, Italy*

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Introduction

Out of 34 metazoan phyla, at least 23 have some representatives in the meiofauna (Cerca et al. 2018), operationally defined as the fraction of fauna passing through sieves with 500 (or 1000, depending on the definition) μm mesh width and being retained by sieves with 31 (or 63) μm mesh width (see, i.e., Giere 2009). Studies on size spectra of marine benthic fauna have proved that meiofauna, far from being just an arbitrarily defined size-class, represents a distinct ecological and biological unit, and an important link between micro- and macrobenthos (Warwick 1984).

Marine meiofauna is known for its extremely high diversity: not only, in fact, a number of phyla (among which Gastrotricha, Gnathostomulida, Kinorhyncha, Loricifera, and Rotifera) are exclusively meiofaunal (Higgins & Thiel 1988), but the exact figure of meiofaunal species worldwide is still very far from having been assessed (Appeltans et al. 2012). Based on the numbers of site-restricted OTUs in sites a mere 20 km far apart along coasts of the United Kingdom and on the proportion of the few OTUs that can be attributed to known species, Fonseca et al. (2014) suggested that at least one million meiofaunal species have yet to be described – and this considering littoral habitats only.

While minute body size, rapid turn-over, and restricted dispersal capability are common traits of meiofaunal organisms, others, such as filiform or flattened body shapes, adhesive structures and static organs are particularly crafted features that allow these organisms to live interstitially among sand grains (see Giere 2009). Most classic ecological studies on the astonishingly diverse interstitial meiofauna have focussed on the so-called "hard-bodied meiofauna" (notably Copepoda and Nematoda), whose thick cuticle allows retrieval of specimens from fixed samples, in conditions suitable for identification at the species level (Kennedy & Jacoby 1999), and even allowed descriptions of species from Late Cambrian fossils (Harvey & Butterfield 2017). This is not the case for the "soft-bodied" taxa, which most often lose any diagnostic character after fixation (Garraffoni & Freitas 2017). As an arguable result, ecological studies on meiofauna, largely based upon fixed samples, have emphasised the role of Nematoda and Copepoda in terms of biomass and diversity, as well as their relevance for monitoring pollution, to the exclusion of any other meiofaunal taxa (Raffaelli & Mason 1981; Warwick 1981). This widely accepted view was to change in later decades. With its high diversity and challenging taxonomic resolutions, meiofauna became in fact an ideal field for the application of innovative techniques such as metabarcoding on environmental DNA, which revealed a comparable, if not higher, diversity of soft-bodied taxa with respect to hard-bodied taxa (Fonseca et al. 2010). However, the vast majority of the retrieved sequences of soft-bodied taxa could not be assigned to known species, due to lack of correspondence in GenBank (Leasi et al. 2018).

The taxonomic bias affecting meiofaunal studies in general is particularly felt in soft-bodied taxa, whose diagnostic features need to be observed on living material (Higgins & Thiel 1988), making quick examination of samples necessary, ideally on facilities close to the coast, such as Marine Biological Stations. Given these operative difficulties, and the limited utilisation of soft-bodied taxa for ecological studies and applicative research, which nowadays attract most of the funds, it is not surprising that taxonomic expertise on soft-bodied organisms has declined over the years, leading to the current situation where there are few taxonomic experts worldwide, if any. Taxonomic knowledge of these taxa is consequently patchy and limited to the areas where the few experts have operated. Several workshops held in the past decades, focussing on biodiversity of meiofauna, including soft-bodied taxa, resulted in few, restricted zones comparatively very well known, in particular parts of the North Sea, the Swedish West coast, South Brazil, Galapagos islands, and Lanzarote (Canary Islands) (Westheide 1991; Armonies & Reise 2000; Willems et al. 2009; Fonseca et al. 2014; Martínez et al. 2019, and references therein). These areas contrast sharply with large part of the planet, from which nothing is known.

In Italy, soft-bodied taxa have been the focus of two workshops held in the National Parks "Arcipelago di La Maddalena" and "Isola dell'Asinara". There, in a 10-day-period, 203 and 191 species, respectively, were found, more than 1/3 of which new to science (Curini-Galletti et al. 2012; Martínez et al. 2020). The only partial overlap in species composition of the two close-by sites suggests that, given the length and complexity of the Italian coastline, the heterogeneity of physical and chemical parameters of its seas (Berline et al. 2014), and the potential for allopatric speciation and restricted ranges of interstitial meiofauna (Giere 2009, but see Cerca et al. 2018), soft-bodied meiofaunal taxa may contribute significantly to Italian biodiversity.

During the LXXX congress of the "Unione Zoologica Italiana", held in Rome in September 2019, one session, organised by the "Comitato Scientifico per la Fauna d'Italia", was specifically devoted to presentation of the state of knowledge of Italian biodiversity. This prompted worldwide experts on interstitial meiofauna to join efforts in order to summarise the present

knowledge about diversity and distribution of main soft-bodied metazoan meiofaunal taxa along the Italian coasts. The results are presented here.

Material and methods

Information on species occurrence and distribution given is mainly based on existing literature. The backbone data derive from the comprehensive checklist of the Italian marine fauna sponsored by the Società Italiana di Biologia Marina (S.I.B.M.) (Relini 2008, 2010), updated with information published in the timeframe 2010–2019, whose citations may be found below, in sections devoted to single taxa. Most recent data on Platyhelminthes and Xenacoelomorpha have been acquired from websites devoted to these organisms (i.e., http://acoela.myspecies.info/en; http://marinespecies.org/turbellarians/index.php; http://turbellaria.umaine.edu/) and maintained/edited by authors of the present paper. When unpublished information is provided, this is properly detailed. Information concerning new, still unpublished species is also given in the following sections. Distribution maps are based on the biogeographical sectors of the Italian seas, as proposed by Bianchi (2004).

Xenacoelomorpha

Xenacoelomorpha includes two phyla: Xenoturbellida and Acoelomorpha (Philippe et al. 2011). Only this latter is represented in the Mediterranean, by the two taxa – traditionally considered at the order-level – Acoela and Nemertodermatida (Hejnol et al. 2009). Xenacoelomorpha is a clade of paramount phylogenetic interest for its position as the sister group of the remaining Bilateria (the Nephrozoa), although alternative hypotheses have been advanced, placing it with the Deuterostomes (see Jondelius et al. 2019 for critical analysis). The basally splitting branch occupied by Xenacoelomorpha has enhanced studies on their character states and molecular organisation, as a key to a better understanding of the origin and diversification of the Bilateria (Jondelius et al. 2011).

In contrast to Xenoturbellida, which may attain a large size (to more than 20 cm) (Rouse et al. 2016), the vast majority of Acoela and Nemertodermatida are typical representatives of soft-bodied, interstitial meiofauna (Figure 2(b,c)) – although a few larger, epibenthic species exist, as well as very few planktonic and symbiotic species. Acoela is by far the most diverse group, with about 440 nominal species described worldwide (Jondelius & Jondelius 2020). They are abundant in marine coastal and deep habitats, from clean sand to mud, with some species occurring in the sulphide biome (Jondelius & Jondelius 2020). In many habitats, they can be among the dominant organisms: in particular, the algal-symbiont bearer convolutids, such as *Symsagittifera roscoffensis* (von Graff 1891), can be so numerous that, when exposing the photosynthetic partners to light at low tide, they may give the sand a bright green colour (Schmidt-Rhaesa 2020). In the Ligurian Sea, the abundance of acoels was observed to rise in conjunction with the settlement of larvae of macrobenthic organisms. Predation of acoels on these larvae, and especially on Polychaeta may thus ultimately contribute in shaping macrofaunal communities (Danovaro et al. 1995).

A total of 41 species have been so far reported for Italy, with a larger number (62) of new, still undescribed species, which have been collected in recent years (U.J. own unpubl. data; http://acoela.myspecies.info/en). Most species have been found in the comparatively intensely studied sectors 2, 3 and 9, with 29, 18 and 13 species, respectively, where specific research by one of the authors (U.J.) was undertaken. In sharp contrast, very few species or none are known from the severely understudied sectors 5, 6, 7. Given the long tradition of studies on Acoela in Italy –the oldest record dates from mid-nineteenth century: *Symsagittifera schultzei* (Schmidt, 1852), from Lesina – it is not surprising that numerous species were described in the XIX and early XX centuries for Naples, Messina, and the Gulf of Trieste, where existing commodities allowed research to foreign students.

In contrast to Acoela, Nemertodermatida are much rarer animals, known in some instances for few specimens only (Jondelius & Jondelius 2020). Eighteen nemertodermatid species are currently known worldwide. However, the lack of easily diagnosable characters, and the slight morphological differentiation among species, if any, make often necessary to rely on molecular data for species identification, and numerous cryptic species remain to be formally described (Meyer-Wachsmuth et al. 2014; Jondelius & Jondelius 2020). Italy has been comparatively well studied, and a total of 9 species has been reported (http://acoela.myspecies.info/en). Contrary to most areas of the world, nemertodermatids in Italy may be common in suitable habitats (medium-coarse, clean sand) (U.J. & M.C.G., pers. obs.).

The distribution of described species of Acoelomorpha in the Italian biogeographical sectors is given in Figure 1(a). Occurrence of most species of Acoela appears limited to a single sector, with

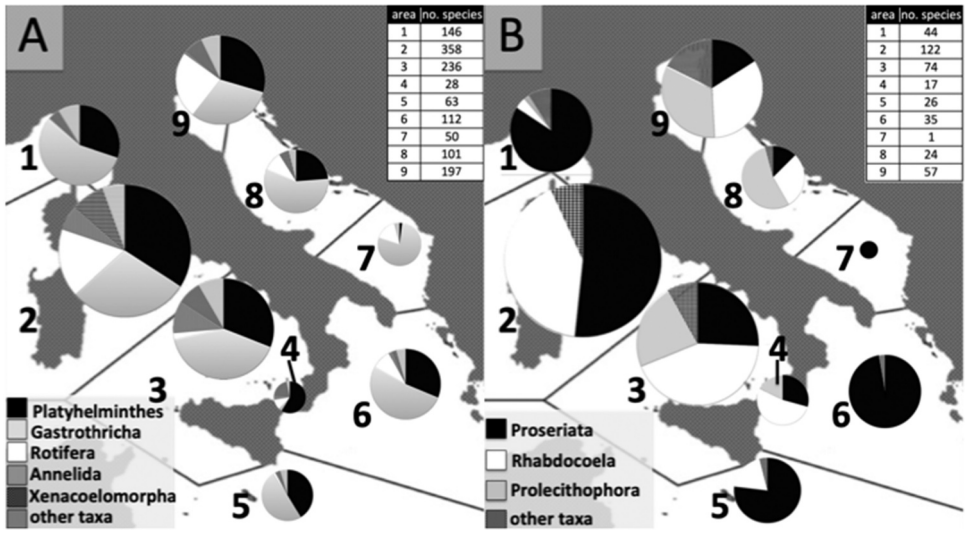

Figure 1. Composition of soft-bodied meiofaunal phyla (a) and major platyhelminth orders (b) in the nine biogeographical sectors of the Italian seas (see text for details). The size of the pie charts is related to the number of species in the areas.

very limited overlap among sectors. Moreover, even distribution of species within single sectors may not be homogenous. In particular, within sector 2, relatively close-by areas such as Southern Tuscany and Northern Sardinia have only 13% of the species in common (U.J., own data). Available information does not allow discerning whether this patchy distribution is due to unrepresentative sampling, or indeed reflects restricted species ranges. In any case, present knowledge of composition and distribution of Acoela in Italian waters has to be considered particularly poor.

Platyhelminthes

The vast majority of marine free-living Platyhelminthes pertain to the meiofauna size class, with the only exceptions of most Polycladida and few representatives of Tricladida Maricola (Cannon 1986). Apart from some members of Prolecithophora and Rhabdocoela, which may occur preferentially or exclusively in epibenthic habitats, such as the periphyton, all other taxa are almost exclusively found interstitially, and are among the dominant meiofaunal groups, both in terms of biomass and species number, in sandy and brackish-water habitats (Martens & Schockaert 1986; Fonseca et al. 2010). About 2700 species of free-living marine flatworms have been described worldwide, and this figure may represent less than one-tenth of the existing species (Appeltans et al. 2012). Of these, about 1700 described species are meiofaunal and marine (Smith et al. 2020). So far, 235 species of meiofaunal Platyhelminthes have been reported for the Italian coasts (Tyler et al. 2006–2018, MCG, own data). However, only a fraction of the coastline has been sampled for most major taxa, and this number may represent just a fraction of the actual diversity of the group in Italy. It is noteworthy that a number of species have been reported from the Croatian coast (Rovinj), and may also occur in the Gulf of Trieste. Exemplary of the poor knowledge on most platyhelminth taxa is the case of Prolecithophora, with 30 Italian species, found during past research in the Gulf of Naples (Riedl 1954, 1959) and in Northern Adriatic (mainly von Graff 1891), with no recent studies on the taxon whatsoever. Similarly, knowledge on Rhabdocoela – the most diverse and species-rich taxon of free-living Platyhelminthes, with at least 1000 marine species described worldwide (Tyler et al. 2006–2018), and which counts 97 marine species reported for Italy (Figure 2(f,g)) – is mostly based on material collected by the leading taxonomic expert of the group (T.A.) during workshops held in Sardinia, whereas most previous records date back especially to von Graff (1891). However, the actual number of rhabdocoels that occur along the Italian coasts is probably at least an order of magnitude higher, as each sampling campaign in the recent past yielded a high number of species new for Italy, or even new to science (Curini-Galletti et al. 2012; T.A. unpublished data). Even unexpected areas, such as the channels in the middle of the city of Venice, can harbour species of rhabdocoels new to science (Artois et al. 2013), and several new species await formal description, including members of the peculiar genera *Lurus* Marcus, 1950, Dalythyphloplanida with complex statocyst, and *Bertiliella* Rieger & Sterrer, 1975 (Kalyptorhynchia),

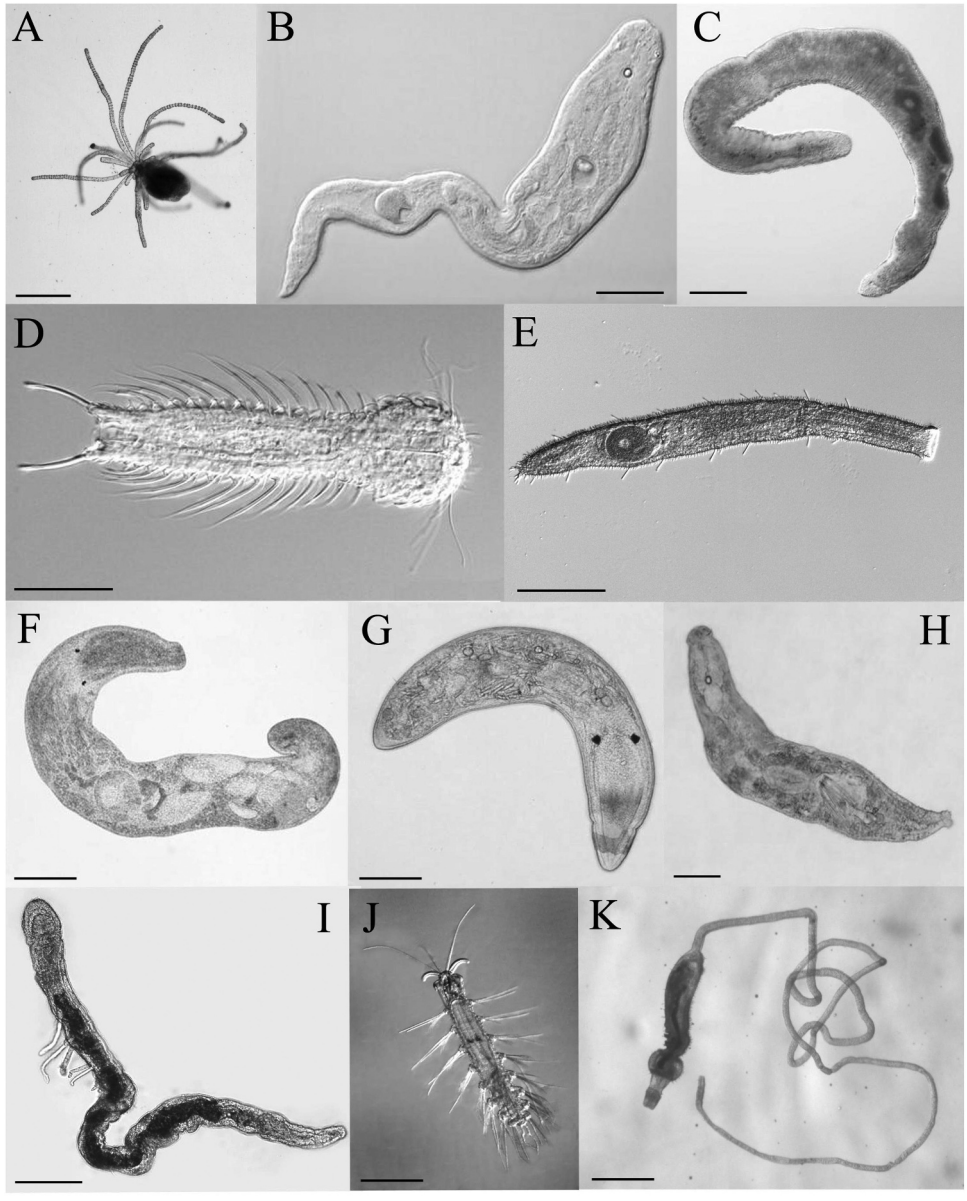

Figure 2. Representatives of Italian soft-bodied meiofauna. (a): *Halammohydra* cf *schulzei* Remane, 1927 (Cnidaria,), Meloria Shoals, Tuscany. (b, c): Acoelomorpha ((b): *Mecynostomum filiferum* Ax, 1963 (Acoela), Asinara Is., Sardinia); (c): *Sterreria rubra* (Faubel, 1976) (Nemertodermatida), Castiglione della Pescaia, Tuscany. (d, e): Gastrotricha ((d): *Halichaetonotus aculifer* (Gerlach 1953), Siracusa, Sicily; (e): *Acanthodasys aculeatus* Remane, 1927, Castiglione della Pescaia, Tuscany) (f-h): Platyhelminthes ((f): *Ceratopera gracilis* (von Graff 1891) (Rhabdocoela), Asinara Is., Sardinia; (g): *Progyrator mamertinus* (Graff, 1874) (Rhabdocoela), Asinara Is., Sardinia; *Parotoplana procerostyla* Ax, 1956 (Proseriata), Arbatax, Sardinia). (i, j): Annelida ((i): *Psammodrilus curinigallettii* Worsaae et al. 2015, Budelli Is., Sardinia; (j): *Leptonerilla* n. sp., Nereo Cave, Sardinia). (k): *Tubiluchus troglodytes* Todaro & Shirley, 2003 (Priapulida), il Ciolo Cave, Apulia. Scale bar: (a, j, k) = 250 μm; (b, c, e-i) = 100 μm; (d): 25 μm.

with a calcareous "skeleton" (see Rieger & Sterrer 1975) (W.S., pers. comm.). The 17 species of marine Macrostomorpha reported for Italy largely derive from research in limited areas of Tyrrhenian and Ligurian seas, and in Northern Adriatic (Rieger 1971; Janssen et al. 2015, and references therein). One of the Adriatic species, *Macrostomum lignano* Ladurner et al., 2005, only known from the lagoon of Grado (Ladurner et al. 2005), is easily kept in culture and has received particular attention, as a model species in research fields ranging from stem-cell biology, reproduction, ageing, and chromosome evolution (Mouton et al. 2018).

Proseriata (Figure 2(h)) is the second most diverse taxon of interstitial Platyhelminthes, and usually outnumbers any other flatworm group in term of number of individuals, especially in clean, medium to coarse-sand (Curini-Galletti 2001). Proseriata may be so abundant in the swash zone of exposed beaches that they characterise the entire interstitial community, known, after the dominant genus in the Mediterranean, as the "*Otoplana*-zone" (Remane 1933; Brown & McLachlan 2006). It is somehow paradoxical that, while the term is used worldwide, the genus *Otoplana* is endemic to the Mediterranean-Lusitanian Region (Scarpa et al. 2017). Of the about 430 species of Proseriata known worldwide, 93 have been reported from Italy (Tyler et al. 2006–2018). However, there is a high number of new species (over 130) that still awaits formal description (M. C.G, unpubl data). Proseriates are large for meiofaunal organisms, particularly sticky, and without any means for dispersal (Curini-Galletti 2001). These biological traits have in many instances resulted in complexes of species with restricted ranges, parapatrically distributed along the Italian coastline (Martens & Curini-Galletti 1994; Delogu & Curini-Galletti 2009; Casu et al. 2014). Extreme at this regard is the case of five species of the genus *Otoplana* Du Plessis, 1889, which occur in a narrow stretch of coast in the Ligurian Sea (Meini 2013). The taxonomy of the genus, however, needs a thorough revision with the contribution of molecular data, in order to evaluate the extent of interpopulational variability (Scarpa et al. 2017). A few species of Proseriata seem to present extremely restricted ranges. *Monocelis exquisita* Curini-Galletti & Casu, 2016, the sister taxon of boreal, Northern Atlantic *Monocelis fusca* Örsted, 1843, was found in a single brackish-water lagoon in Sardinia, and, notwithstanding extensive research in similar habitats, so far has not been found elsewhere (Scarpa et al. 2016). Similarly, two large and comparatively very obvious species are known from their type locality only. *Meidiama etrusca* Curini-Galletti, Casu & Scarpa, 2017, the only representative known of the genus *Meidiama* outside South America, has been found in one single spot in Tuscany (Scarpa et al. 2017); *Digenobothrium inerme* Palombi, 1926, a distinctive member of Calviriidae, whose closest relatives are species of *Diskeria* Schockaert, Curini-Galletti, De Ridder & Artois, 2011 from Southern Hemisphere (Tasmania and Kerguelen), appears limited to the Strait of Messina (Palombi 1926). Finally, an important area of endemism for proseriates, and possibly for other meiofaunal taxa, is the Northern Adriatic Sea, where numerous species not found elsewhere occur, only partly published so far (Meixner 1943, M.C.G. unpubl. data).

Other taxa (Catenulida, Gnosonesimida, Tricladida, Polycladida) have few representatives in marine meiofauna. Marine Catenulida (Retronectidae) have been reported so far from only a few localities worldwide (Sterrer & Rieger 1974), including the Ligurian coast. Interstitial Polycladida – a taxon best known for its macrobenthic representatives – mainly occur in tropical areas, and are represented in Italy by a single species, *Theama mediterranea* Curini-Galletti et al., 2008. This is one of the largest mesopsammic organisms, over 2 cm long, filiform in shape, widely distributed in almost any locality sampled in the Mediterranean and adjacent Atlantic, in suitable habitats (coarse clean sand), where it can be abundant (Curini-Galletti et al. 2008). The fact that, notwithstanding its size and abundance, the species has only been described recently, may be taken as exemplary of the overall poor level of knowledge of meiofauna.

The distribution map of described species in the nine Italian biogeographical sectors (Figure 1(b)) reveals a strong author's bias, with the highest number of species, especially Proseriata and Rhabdocoela, reported from the most intensely studied Sector 2. Conversely, most Adriatic species known belong to the Prolecithophora and Macrostomorpha. Knowledge of Sector 3 is mainly based on old records for the Gulf of Naples, with large, potentially highly diverse areas, such as Sicily, which have never been sampled. The same is true for Sector 6. Knowledge for the highly species-rich Rhabdocoela is particularly spotty. It is therefore reasonable to conclude that the 235 species of Platyhelminthes presently known may represent just a small fraction of the diversity of the group in Italy.

Gastrotricha

Gastrotricha is a phylum of minute, acoelomate worms, phylogenetically allied with Platyhelminthes, with which they form the clade Rouphozoa, nested within the bilaterian Spiralia (Egger et al. 2015). Of the about 860 gastrotrich species known to date, 510 species have been described from marine ecosystems; these marine taxa are distributed in 46 genera and 14 families within the two recognised orders Macrodasyida and Chaetonotida (Todaro et al. 2019a; WoRMS, 2020). Many of these species are from the coast of the Mediterranean Sea, and of Italy in particular (Todaro & Shirley 2003). In this regard, the Italian coastline is the best-known long coastline worldwide, with 164 nominal species of marine Gastrotricha (101 Macrodasyida and 63 Chaetonotida) recorded from over 250 investigated localities as of this writing (Hummon & Todaro 2009; Todaro et al. 2001, 2008, 2019b; Curini-Galletti et al. 2012; Martínez et al., 2020). Beside hosting 32% of all known marine gastrotrich species, the Italian waters house 76% (N = 35) of the marine genera and 71% (N = 10) of the marine families known to date from all over the world. Currently, 60 species and one genus (*Dendropodola* Hummon, Todaro & Tongiorgi, 1993) are considered endemic to Italy. For completeness, it is worth mentioning that at least 25–30 species and one genus found along the Italian coasts during the last two decades are still waiting to the be described (M.A.T., unpubl. data). Most records of Italian marine Gastrotricha come from the western seas, and the Tyrrhenian Sea in particular, where the microhabitat preferred by Gastrotricha (e.g., crystalline water and sublittoral medium to fine sand, especially if organogenous) is particularly well represented. About 140 species have been recorded from over 160 investigated localities along coasts of the Ligurian and Tyrrhenian Seas. The highest number of species has been recorded from area 2 (N = 105), followed by area 3 (N = 97) and area 1 (N = 81), all of which are on the western Italian shores. A single species has been documented from the micro-sector 4, while 31 species have been found in the relatively restricted area 5, which, however, includes the highly diverse island of Lampedusa. The Jonian Sector 6 hosts 58 species, similarly to the Adriatic Sectors 8 and 9 (59 and 60 species, respectively). It should be highlighted that most records of the Ionian area 6 come from Apulian localities, whereas Basilicata and Calabria coasts have been poorly investigated. Most of the species found in area 8 have been recorded from the Gargano and Tremiti islands, whereas most species from the upper Adriatic Sea, area 9, have been recorded in spotty locations along the coasts of Veneto and Friuli Venezia Giulia regions (e.g., Isola della Cona, at the mouth of the Isonzo river), being the coastal sediment of this sector, and in particular of Emilia-Romagna and part of the Marche coast, made up of fine to very fine sand, and consequently not suitable for most gastrotrich species.

While some species seem restricted to one or two biogeographic sectors, most others exhibit a wide geographic range along the Italian coastline, with five Macrodasyida and five Chaetonotida having been recorded in all the biogeographic areas, except micro-sector 4; among these are the macrodasyidan *Acanthodasys aculeatus* Remane, 1927 (Macrodasyida, Thaumastodermatidae) and the chaetonotidan *Halichaetonotus aculifer* (Gerlach 1953) the most frequently sampled species (Figure 2(d)). Notwithstanding the relatively high number of marine gastrotrich species found along the Italian coast and the high number of investigated localities, there are indications that a comprehensive knowledge of the Italian gastrotrich fauna is not completed. Future research should focus primarily on portion of the coastline poorly of never investigated (e.g., the Tyrrhenian and Ionian cost of Calabria) and on deeper sandy sediments (e.g., below 10 m depth).

Rotifera

All rotifers (Bdelloidea, Monogononta, and Seisonacea, with the exclusion of Acanthocephala) belong to meiofauna as they are minute in size, usually between 0.05 and 1 mm (Fontaneto & De Smet 2015); some species can be found in the meiobenthos, others in the zooplankton, and also as epibionts or in the periphyton (Wallace et al. 2006). They are mostly freshwater and limno-terrestrial organisms, but several species can be found in haline habitats: out of more than 2000 known rotifer species, about 450 have been found in marine waters (Fontaneto et al. 2006; Leasi & De Smet 2020). Of these, 90 are known to occur along the Italian coasts, including seven bdelloids, 81 monogononts, and two seisonaceans (De Smet et al. 2015). Some of the species found in Italy have been previously reported from other continents as cosmopolitan, such as members of the *Brachionus plicatilis* Muller, 1786 species complex (Mills et al. 2017), *Colurella colurus* (Ehrenberg, 1830), *Proales similis* de Beauchamp, 1907, and *Synchaeta cecilia* Rousselet, 1902; other species seem to have a much narrower distribution, being known only from the type locality, such as *Lecane insulaconae* Fontaneto, Segers & Melone, 2008 or *Lindia aequorea* De Smet, 2015. Some species seem to be very common and abundant in some areas and rare or absent in others, such as *Rotaria laticeps*

Wulfert, 1942 commonly occurring in any marine habitat in the Northern Adriatic but rare elsewhere.

The richest areas in the Italian coasts are the Tyrrhenian (area 2) and the Northern Adriatic (area 9), with more than 60 species each. Yet, no inference can be considered reliable on rotifer distribution, given the extremely small number of faunistic studies in marine habitats. This is a common and known problem in rotifer biodiversity, for which the known species richness of a region is a function of sampling effort and not of biological reality (Fontaneto et al. 2012). Only a fraction of the coastline has ever been sampled, and the number of known species, as well as their records, surely represents just a fraction of the actual diversity of the group in Italy.

Annelida

Annelida include more than 17,000 described species, exhibiting a vast morphological disparity and ecological ubiquity (Weigert & Bleidorn 2016). Meiofaunal forms are common and spread across the annelid tree, represented by more than 400 species classified into 25 families (Worsaae 2020). While most of these families include both macrofaunal and meiofaunal representatives, 11 of them are considered as entirely meiofaunal (Worsaae 2020). Members of these entirely meiofaunal families typically consist of small and comparatively simple forms, grouped in three main lineages: Psammodrilidae, basally branching; Protodriliformia, sister to the remaining Errantia; and meiofaunal Orbinida, nested within Sedentaria (Laumer et al. 2015; Struck et al. 2015). A total of nine exclusively meiofaunal families have been reported from Italy, accounting for 44 species. This high diversity is linked to a historically intense sampling effort, which already started in the XIX century and continues nowadays, favoured by the presence of important Marine Biological Stations in the country. Notably, Italy hosts the type locality of one family (Hatschek 1888) and 11 nominal species, most of them described around the Zoological Station "Anton Dohrn" in Naples. Indeed, most Italian species are known from Sector 3 (25 species), where the Zoological Station is located, and from Sector 2 (22 species), where workshops on meiofauna have been organised (Curini-Galletti et al. 2012; Martínez et al. 2020). In contrast, southern Italy and most of the Italian Adriatic coast remain unexplored to this day.

Nerillidae is the most species-rich family in Italy with 16 species, including 4 unequivocally new, still undescribed species (Martínez and Worsaae, unpubl. data). Nerillids are commonly found subtidally in coarse or medium well-sorted sediments. *Mesonerilla intermedia* Wilke, 1953 and *Nerillidium mediterraneum* Remane, 1928 are the most common species, recorded from Sardinia, Tuscany, Campania, and Sicily, typically in coarse sandy patches amongst rocks or in *Posidonia oceanica* meadows (Worsaae et al. 2015, 2019). *Nerillia antennata* O. Schmidt, 1848 is also widely distributed, but prefers coarse or gravelly sediments often along the high-tide (Gelder 1974). In contrast, the four undescribed nerillids, belonging to the genera *Leptonerilla* Westheide & Günter, 1996 (Figure 2(j)), *Micronerilla* Jouin, 1970, and *Trochonerilla* Tzetlin & Saphonov, 1992, are exclusively known from single marine caves in Capo Caccia (Sardinia) and around Salerno (Curini-Galletti et al. 2012). The mud-specialised *Paranerilla limicola* Jouin & Swedmark, 1965 has been recorded at a depth of 25 m in the Northern Adriatic (Sterrer 1968).

Protodrilidae is a very diverse family as well, with 14 species recorded in Italy (Martínez et al. 2019). The family has been originally described based on specimens found near Messina (Hatschek 1888). Most of the early studies on Protodrilidae rely on the work of Piero Pierantoni from the Zoological Station "Anton Dohrn", who described five new species (three of them considered as valid) and performed very detailed studies on the morphology and development of the group (Pierantoni 1906, 1907, 1908). Amongst the Italian protodrilids, *Claudrilus hypoleucus* (Armenante, 1903) is the most ubiquitous, and it has been found in nearly every published survey of the Italian interstitial fauna (e.g., Pierantoni 1908; Boaden 1965; Magagnini 1980; Curini-Galletti et al. 2012; Martínez et al. 2015), although it seems to prefer coarse sediments ranging from 2 to 20 m depth. In contrast, *Lindrilus flavocapitatus* (Uljanin, 1877) and the three species of *Meiodrilus* Martínez et al., 2015, are more common in sandy beaches (Martínez et al. 2019). *Lindrilus flavocapitatus* has been exclusively found in the upper layers of exposed gravelly areas at the swash zone, while *Meiodrilus* species are more common in medium to coarse sediments, where they tend to penetrate deeper in the sediments to avoid wave disturbance. The species of *Protodrilus* Hatschek, 1882 and *Megadrilus* Martínez et al., (2015) are very common in subtidal shell gravel, with a single record of *Megadrilus schneideri* (Langerhans, 1881) in a marine cave (Curini-Galletti et al. 2012).

Saccocirridae is represented by four species. Species of the genus *Saccocirrus* Bobretzky, 1871 are an important component of the interstitial communities in many exposed marine environments such as sandy beaches, where they feed on suspended particles drifting along

with the sand grains moved by the wave action (Di Domenico et al. 2014a). They are non-selective feeders, and they have even been found with ingested microfiber particles in several beaches of the world, including those at the Asinara National Park (Gusmão et al. 2016). Three species are found in Italy, exhibiting a strong variation in size, which has been correlated to different habitat preferences in terms of grain size, with *S. parvus* Gerlach, 1953 in medium sand, *S. papillocercus* Bobretzky, 1871 in coarse sand, and the (comparatively) enormous *Saccocirrus major* Pierantoni, 1907 amongst pebbles in Naples and Tuscany (Pierantoni 1907). In contrast, species of *Pharyngocirrus* prefer protected subtidal environments (Di Domenico et al. 2014b). They are represented in Italy by *Pharyngocirrus goodrichi* Jouin-Toulmond & Gambi, 2007, which is exclusively known from subtidal shell gravel in the Gulf of Naples (Jouin-Toulmond & Gambi 2007). This ecological segregation between species of *Saccocirrus* and *Pharyngocirrus* has been found in other regions of the world, such as Brazil or the Canary Islands (Di Domenico et al. 2019).

The remaining families are less diverse. Psammodrilidae is represented by *Psammodrilus curinigallettii* Worsaae et al., (2015) (Figure 2(i)) and *Psammodrilus didomenicoi* Worsaae & Martínez, 2018, respectively, described from Sardinia and Campania (Worsaae et al. 2015, 2018). Diurodrilidae is also represented by two species, *Diurodrilus benazzi* Gerlach, 1952 and *D. dohrni* Gerlach, 1953, both originally described from Italy, but while *D. benazzi* has been found in sandy beaches near Pisa, *D. dohrni* is exclusively known from subtidal areas of the Gulf of Naples (Gerlach 1952, 1953). Dinophilidae is only known for *Dimorphodrilus gyrociliatus* (O.Schmidt, 1857), described from the Gulf of Naples and thereafter recorded in Liguria and Ravenna, in sediments with algae at the swash-zone. Finally, an unidentified specimen of the elusive family Lobatocerebridae has been reported from Elba Island (Tuscany) (Kerbl et al. 2015).

Although the pioneering studies of the last century and the descriptions of several interstitial annelid species date more than 100 years ago, recent surveys performed in the Gulf of Naples allowed the recovery of the species described by Pierantoni, in the same type localities. Other species, possibly new to science, were also found (A. M. & M.D.D., unpubl. data). Despite the time gap since Pierantoni studies, the interstitial environment in Naples, even intensely modified over the last century as it is, still provides the potential for studies on systematics, evolution, and the ecology of meiofaunal annelids.

Gnathostomulida

The phylogenetic position of Gnathostomulida has long been enigmatic (Sterrer et al. 1985). First described as an order of primitive turbellarians (Ax 1956), they were later recognised as a separate phylum, with debated phylogenetic affinities (Riedl 1969). Nowadays, they appear firmly nested within Gnathifera, which also includes Rotifera and Micrognathozoa (Kristensen & Funch 2000), and possibly Chaetognatha (Fröbius & Funch 2017).

Gnathostomulida is a small phylum, with exclusively meiobenthic representatives. There are about 25 genera and 101 species known globally (Sørensen & Sterrer 2020). The group, however, is severely understudied, and the finding of new species may be expected, especially in the peculiar habitat where many Gnathostomulida thrive, the thiobenthos, under anoxic conditions (Sørensen & Sterrer 2020). Furthermore, given the presence of similar morphotypes worldwide, the occurrence of cryptic species in the group is highly suspected. Indeed, Gnathostomulida is one of the taxa on which the hypothesis of morphological stasis of meiofaunal organism, possibly resulting from stabilising selection on morphotypes due to the constraints of the interstitial environment, was largely based (see Sterrer 1973). The phylum is poorly represented in the Mediterranean, with 11 species described for the whole basin. Of these, nine have been found in Italy, mostly from sectors 2 and 9, where research has been more intensive – however, seven additional species still await formal description (W.S., unpubl. data).

Other Phyla

A number of predominantly macrobenthic phyla have representatives in the soft-bodied meiofauna. However, the meiofaunal component in these phyla is reduced to very few species. This is the case of Cnidaria, with more than 12000 species currently known, and only about 25 interstitial species described worldwide (Schmidt-Rhaesa et al. 2020). Seven species of Cnidaria belong to the Italian fauna, pertaining to the genera *Otohydra* Swedmark & Teissier, 1958, *Halammohydra* Remane, 1927, *Psammohydra* Schulz, 1950, *Siphonohydra* Slawini-Plawen, 1966, *Armorhydra* Swedmark & Teissier, 1958 (Hydrozoa), and *Stylocoronella* Salwini-Plawen, 1966 (Staurozoa) (Bouillon et al. 2004; Avian 2008; Schmidt-Rhaesa et al. 2020). Members of the genus *Halammohydra* (Figure 2

(a)), in particular, may be occasionally common in coarse sand, where they are actively preyed by members of the platyhelminth genus *Archimonocelis* (Karling 1966). Among Chaetognatha, the largely benthic genus *Spadella* Langerhans, 1880 has few very small species that belong to the meiofauna. Recently, a meiobenthic *Spadella* (*S. interstitialis* Kapp & Giere 2005) has been described from Elba Is. (Kapp & Giere 2005). Furthermore, *Spadella ledoyeri* Casanova, 1986, found interstitially in a few marine caves close to Marseille (France) (Casanova et al. 2006), may be present in Italian waters. Indeed, the presence of undetermined, interstitial specimens of *Spadella* in Italian caves has been noticed on several occasions (M.C.G.; MA.T., pers. obs.), but never formally reported, and the group is a common component of the meiobenthos of other caves around the world (Gerovasileiou et al. 2016). Similarly, Ascidiacea has a number of miniaturised, free-living members, crawling among sand grains, mainly pertaining to the genera *Heterostigma* Ärnbäck-Christie-Linde, 1924, *Psammostyela* Weinstein, 1961, *Polycarpa* Heller, 1877, and occurring in European waters, but none of them has been so far reported (or accurately searched) in Italy (Brunetti & Mastrototaro 2017). Priapulida, Ecdysozoan that may be nonetheless considered among the soft-bodied taxa, comprises two truly meiofaunal species in Italy: the cave-dwelling *Tubiluchus troglodytes* Todaro e Shirley, 2003 (Figure 2(k)), and *Maccabeus tentaculatus* Por, 1973 (Todaro & Shirley 2003; Todaro et al. 2020).

Two phyla, however, deserve special mention. Nemertea, with more than 1300 species known, displays by far the widest size span of any animal phylum, ranging from about 1 mm to more than 50 m (Strand & Sundberg 2010). About 50 meiofaunal-sized species are known worldwide, occurring interstitially in coarse-sand sediments. All are predators on other meiofauna, though at least some littoral forms can be collected by baiting with fresh fish meat (Andrade et al. 2011). While there are many nemertean species that qualify as meiofaunal in size as adults, most of these are not tightly associated with sediments. The most characteristic interstitial nemerteans belong to the statocyst-bearing genus *Ototyphlonemertes* Diesing, 1863, with at least 33 nominal species known worldwide (Norenburg et al. 2020). Interstitial nemerteans have been assumed to have direct or lecithotrophic development; in both instances, planktonic dispersal may be present (Norenburg & Stricker 2002). A presumed short (few days) planktonic direct-developing larva is known for only two species of *Ototyphlonemertes* but presumed as likely present in the remaining species (J.L.N., pers. obs.). The large number of discrete but difficult to diagnose morphotypes (about 90, mostly from the northern hemisphere (J.L.N., own unpubl. obs.)) recognised within the genus *Ototyphlonemertes* is highly suggestive of the presence of cryptic species, which has been corroborated by molecular study, with some genetically defined species having very wide distributions (up to 9000 Km) whereas others appear quite restricted, with one strong connection between the Canary Islands and areas of the Mediterranean (Leasi et al. 2016). Seven species of meiofaunal Nemertea have been reported so far for Italy, belonging to the genera *Cephalothrix* Oersted, 1843 (two species) and *Ototyphlonemertes* (five species) (J.L.N., own unpubl. data). Members of *Ototyphlonemertes* can be very abundant in coarse, intertidal sand (J.L.N.; M.C.G., pers. obs.). *Ototyphlonemertes* commonly co-occur with proseriates and annelids that favour coarse intertidal and subtidal sediments and shell hash but these habitats are effectively unsampled in Italy with respect to Nemertea, with the only exception of Sardinia's northern coast (J.L.N., M.C.G., own unpubl. obs.). Interstitial cephalothricids almost always occur in subtidal coarse sediments and are rarely abundant (J.L.N., own unpubl. obs.). The Gulf of Naples is the type locality for five species (*Cephalothrix bipunctata* Bürger, 1892, *C. buergeri* Wijnhoff, 1913 *Ototyphlonemertes brunnea* Bürger, 1895, *O. duplex* Bürger, 1895, *O. macintoshi* Bürger, 1895), resulting mostly from Bürger's prolific work as a guest researcher at the Zoological Station "Anton Dohrn". Surprisingly, whereas *Ototyphlonemertes* cf. *duplex* and *O.* cf. *pallida* have been found at multiple sites on the Sardinian coast, *O. macintoshi* has not been found there despite being relatively common along the French Mediterranean coast (J.L.N., own unpubl. obs.). In the wake of a molecular reassessment of the taxonomy of the interstitial nemerteans, the finding of specimens of nominal species in their type locality – if still existing – may be crucial for the taxonomic resolution of species-complexes. Increasing sampling along the Italian coasts will undoubtedly yield many additional meiofaunal non-*Ototyphlonemertes* Nemertea species but most will be rare, as is evidenced elsewhere in the world (J.L.N., own unpubl. obs.).

Mollusca is the most species-rich phylum in the marine environment, but similarly to Nemertea is largely macrofaunal. While some bivalves are minute in size, representatives of soft-bodied meiofaunal organisms may be found among

Gastropoda, and aplacophoran Solenogastres and Caudofoveata. The two latter are worm-shaped molluscs, lacking a shell but bearing a cuticle with layers of different types of sclerites (scales and spicules). Most of the approximately 300 species of Solenogastres and 125 species of Caudofoveata worldwide occur in the deep sea (i.e., beyond the 200 m shelf area) and many are meiofaunal in size, ranging between 1 and 4 mm (Bergmeier & Jörger 2020). Some Solenogastres live epizooic on their cnidarian prey, others inhabit the interstices among sandy sediments. Representatives of Caudofoveata burrow in soft and muddy sediments. Knowledge of the Italian solenogaster fauna is scarce and largely focused on epibenthic species, which usually exceed a body size of 10 mm. Of the 15 species of Solenogastres known from Italian waters (Salvini-Plawen 2008a), mostly from the Gulf of Naples, only three species (simrothiellid *Kruppomenia minima* Nierstrasz, 1903 and lepidominiid *Tegulaherpia stimulosa* Salvini-Plawen, 1983 and *Tegulaherpia myodoryata* Salvini-Plawen, 1988) do not exceed 3 mm in size and are traditionally recognised as meiofauna. Among Caudofoveata, only species within the family Prochaetodermatidae are known to belong to the permanent meiofauna. Of the six known species of Caudofoveata in Italian waters (Salvini-Plawen 2008b), three prochaetodermatids are reported: *Prochaetoderma alleni* (Scheltema & Ivanov 2000), *P. boucheti* Scheltema & Ivanov, 2000 and *P. raduliferum* (Kowalevsky, 1901). All these meiofaunal prochaetodermatids show broad distribution ranges through the Mediterranean and partially large bathymetric ranges (i.e., 50–2600 m in *P. alleni*, see Scheltema & Ivanov 2000). Among gastropods, numerous taxa are sufficiently small to be identified as meiofaunal. In the context of this paper, we only consider the shell-less, properly "soft-bodied" representatives, which show a series of convergent adaptation to the interstitial life, previously termed as "meiofauna syndrome", e.g., vermiform body, reduction of appendages and colouration, presence of adhesive mechanisms, and, often of spiculae (Jörger et al. 2020). Representatives of meiofaunal slugs in Italian waters are known among the Acochlidimorpha, Sacoglossa, Cephalaspidea, Nudibranchia and the still enigmatic Rhodopemorpha. The most common meiofaunal slugs in shallow-water, coarse sediments of the Mediterranean are the acochlidimorphs *Pontohedyle milaschewitchii* (Kowalevsky, 1901), *Microhedyle glandulifera* (Kowalevsky, 1901) and *Hedylopsis spiculifera* (Kowalevsky, 1901) with wide distribution ranges along the European coastline. Two additional species of acochlidimorphs are known from Italy (*Parhedyle cryptophthalma* (Westheide & Wawra, 1974) and *Asperspina rhopalotecta* (Salvini-Plawen, 1973)) but are comparably rare; a sixth acochlidimorph species should occur along the Italian coastline, based on its reported distribution range: *Parhedyle tyrtowii* (Kowalevsky, 1901) (see Eder et al. 2011). Sacoglossan *Platyhedyle denudata* Salvini-Plawen, 1973, as well as the cephalaspidean *Philinoglossa praelongata* Salvini-Plawen, 1973 and *Abavopsis latosoleata* (Salvini-Plawen, 1973) are also described from Italian waters and probably distributed throughout the Mediterranean. Among the enigmatic rhodopemorphs, which have puzzled zoologists for nearly a century until their systematic placement could be settled among gastropods, *Rhodope veranii* Kölliker, 1847 is described from Italy and at least three undescribed species of *Helminthope* Salvini-Plawen, 1991 and *Rhodope* Koelliker, 1847 occur in the Mediterranean (K.J., own unpubl. data). Among Nudibranchia, only two families, Embletoniidae and Pseudovermidae, have (permanently) meiofaunal representatives, with one species of *Embletonia* Alder & Hancock, 1851 which probably lives epibenthic on shell gravel, and four species of *Pseudovermis* Perejaslavtzeva, 1891 (all truly mesopsammic) known from Italy (Cattaneo-Vietti & Giovine 2008).

Concluding remarks

With 638 described species, and more than 250 additional species known to be present, but yet awaiting formal description, the contribution of soft-bodied taxa of interstitial meiofauna to Italian marine biodiversity appears relevant. The scenario is however strongly uneven. Knowledge of some taxa, such as Annelida, Gastrotricha, and Rotifera appears particularly detailed, placing Italy among the best-known countries worldwide. By no means, however, does this imply that further species additions should not be expected, since only parts of the Italian coastline have been sampled, and mostly in littoral to shallow sublittoral habitats. In sharp contrast is the situation in other large, particularly species-rich groups, notably Platyhelminthes, where knowledge appears patchy, strongly limited to few sampled areas, and, especially for some taxa of Platyhelminthes, suffering for lack of

recent research. Therefore, the census of most groups of meiofauna in Italian waters should be considered far from being complete. Furthermore, distribution of species in the nine biogeographical sectors is particularly uneven and clearly reflects both the size of the sectors and the efforts of sampling done, with the largest and more thoroughly sampled Sectors 2 and 3 by far richer than the others (Figure 1(a)). By contrast, Sector 6, which includes most of the Ionian Sea, appears severely under-sampled, and the number of species known is taken as not representative of the potential diversity of the area. This may also apply to the similarly under-sampled Sectors 7 and 8. Sector 5 includes the extreme South-Eastern corner of Sicily, and the Pelagie islands, a highly biodiverse area, but whose knowledge is so far limited to Gastrotricha and Proseriata. The potentially interesting Sector 4 also appears to be poorly investigated.

The results also highlight the role that Marine Biological Stations played, especially in the past. Most records from Sector 3 in fact derive from research performed at the Zoological Station "Anton Dohrn" in Naples, which, for a time, was among the major marine research centres, attracting researchers from around the world for its position and facilities. It is interesting to note that most of the reports from Naples date up to the '50 s of last century, reflecting either a subsequent availability of Marine Biological Stations elsewhere in the world, and a change of attitude towards taxonomic studies at the Zoological Station itself. Similarly, data from Sector 4, a micro-sector limited to the Strait of Messina, which presents unique ecological conditions (Bianchi 2004), derive from researchers who, in the past, have worked there, then at the forefront of the zoological interest for the frequent stranding of deep-water organisms in the area (Genovese et al. 1971). Indeed, the remarkable platyhelminth *Digenobothrium inerme* was first picked by ichthyologists, as it was feeding on abyssal fish stranded on the beach (Palombi 1926).

Given the lack of deposited holotypes, or, if present, their limited usefulness (see Garraffoni & Freitas 2017), the finding of these species in their type localities would offer precious details on morphology, not included in the original descriptions, as well as the possibility to place these species into the framework of molecular phylogenies. In this regard, it is comforting to note that in the Gulf of Naples, possibly the area in Italy with the highest number of type localities for marine species, sandy-shore habitats still maintain the original interstitial annelid fauna (see above), raising hopes for the rest of meiofauna.

Finally, it should be mentioned that the authors of the present paper include retired and close-to- retirement researchers. In the wake of the crisis of taxonomy worldwide (Costello et al. 2013), and the general obscurity and difficulties of the study of soft-bodied meiofauna, future recruitment in the field may be foreseen as limited at best, and the national and global census of the numerous species of these minute, inconspicuous taxa will take a long time to be completed, if ever.

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