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Capturing the moment: a snapshot of Mediterranean bryozoan diversity in the early 2023

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Abstract

This paper provides an update on Mediterranean bryozoan diversity since the annotated checklist of Rosso & Di Martino (2016), following the publication of numerous papers describing new taxa and new species, and the addition of new records of non-indigenous species. Some of the 32 new species described after the previous checklist (plus one only figured) replace records of cosmopolitan or widespread species, while others are the result of the dismantling of species complexes. New records include mainly species and genera previously known from the near-Atlantic and subordinately from the Pacific. In addition to replacements, removal of species/genera is also linked to formalized synonymies. These changes also reflect modifications in the composition and representation of families. The updated bryozoan fauna consists of 588 species, 220 genera and 99 families. The proportions at order level remain largely unchanged with cheilostomatids (*ca* 77%) dominating over cyclostomatids (*ca* 13%) and ctenostomatids (*ca* 10%). Ten families account for about half of the total species diversity. The newly available information is the result of investigations of habitats and localities previously overlooked, the examination of historical collections in museums, as well as the more routine use of Scanning Electron Microscopy, with increasing support from molecular sequencing. Regularly updated species checklists represent a unique, simple tool to monitor biodiversity in agreement with the Kunming-Montreal Global Biodiversity Framework adopted by the United Nations.

Keywords: Bryozoa; Cheilostomatida; Cyclostomatida; Ctenostomatida; Taxonomy.

Introduction

The Kunming-Montreal Global Biodiversity Framework was adopted by the United Nations during the Convention on Biological Diversity CBD/COP/DEC14/4 held on the 7–19 December 2022. It assesses that “biodiversity is fundamental to human well-being, a healthy planet, and economic prosperity for all people”. One of its main purposes is to halt and reverse biodiversity loss, implementing “broad-based actions in line with the 2030 Agenda for Sustainable Development and its Sustainable Development Goals, and ensure that, by 2050, the shared vision of living in harmony with nature is fulfilled”.

Indeed, biodiversity – the diversity within species, among species and of ecosystems – is declining faster than at any other time in human history (e.g., Butchart *et al.*, 2010). The Kunming-Montreal Global Biodiversity Framework actions include: 1) *Collective effort* towards the targets, mobilizing a broad public support; 2) *Science and innovation* with implementation of the framework itself, based on scientific evidence and traditional knowledge and practices, to achieve conservation and a sustain-

able use of biodiversity; and 3) *Biodiversity and health* acknowledging their interlinkage, and aiming to sustainably balance and optimization of “the health of people, animals, plants and ecosystems, recognizing the need for equitable access to tools and technologies and highlighting the urgent need to reduce pressures on biodiversity and decrease environmental degradation”.

However, high disparity exists in global conservation research capacity between countries and geographical areas (e.g., Zhang *et al.*, 2023), and between land and marine environments. For marine organisms, although efforts have been made to identify habitats and species at risk, we still lack information about the status of most species (usually reported as data deficient), and the possible future scenarios caused by the spread of non-indigenous species (e.g., Roura-Pascual *et al.*, 2021). Furthermore, our knowledge about biodiversity (even at the simplest species level) is still fragmentary (Bouchet *et al.*, 2023), especially for some taxonomic groups such as bryozoans (Appeltans *et al.*, 2012; Rosso & Di Martino, 2016) that are generally less conspicuous and/or unexploited for human needs, except for a few species providing bioac-

tive compounds with medical potential (see reviews of Figuerola & Avila, 2019; Ciavatta *et al.*, 2020). However, bryozoans are an important component of benthic marine biodiversity and key ecological players. First, they are part of the food web with many species of several groups of organisms preying on them primarily or exclusively (e.g., nudibranchs, pycnogonids, turbellarians, certain polychaetes, small arthropods, and nematodes) (Lidgard, 2008). Second, they are important habitat constructors with several species building colonies with a complex 3D structure that provide home to other groups of invertebrates and act as nursery ground for many juvenile fish species, thus enhancing biodiversity (Wood *et al.*, 2012; Lombardi *et al.*, 2021).

Regularly updated species checklists and compilation of large datasets represent a unique, simple tool to understand and monitor biodiversity, especially in the present-day rapidly changing world, involving not only the natural and artificial (human-driven and/or human-mediated) variation in the distribution, but also our notion of species as resulting from new awareness and technological advances, including routine use of Scanning Electron Microscopy (SEM) and the support of molecular analyses.

The most recent checklist for Mediterranean bryozoans was published by Rosso & Di Martino in 2016. Since then, 19 taxonomic papers have been published on the group, adding a considerable knowledge including the description of new taxa and new species, and new records of non-indigenous species. In this context, the present paper aims to guide both bryozoan experts and other researchers interested in the biodiversity of the Mediterranean Sea through changes in the composition of the bryozoan fauna, providing an updated checklist of species as well as all relevant references. Unpublished new name combinations are also suggested for the first time for some species.

Materials and Methods

For the present compilation, the list of the Mediterranean bryozoans provided by Rosso & Di Martino (2016) was revised and updated based on the bryozoan literature produced in the last six years (up to May 2023). The primary sources of data were: 1) taxonomic reviews of families and genera from the Mediterranean; 2) surveys describing new species and higher taxa from the whole basin and/or including new species records for specific areas; 3) taxonomic papers introducing changes in the allocation of taxa affecting Mediterranean species. The list of papers already available to the authors was cross-checked with the annual list of references and taxa of the Bryozoa Home Page edited by P. Bock (available at bryozoa.net).

All papers dealing with Cenozoic to present-day bryozoans were examined, using the search utility with the term Mediterranean, to locate the description of new taxa and new records from this area and/or changes and discussions related to extant Mediterranean taxa. New records were included only if figured and described; names

of species only listed were excluded. Caution was exercised on the origin of the material to discard records derived from nearby localities. For instance, this is the case of *Biflustra arborescens* (Canu & Bassler, 1928), repeatedly reported as occurring in the Mediterranean Sea (Cook, 1985; Alvarez, 1992, recently followed by Almeida *et al.*, 2017). This species was omitted from the present list because the specimens of Canu & Bassler (1928), as well as the colony photographed by O. Reverter-Gil and available in WoRMS (World Register of Marine Species, accessed 26.04.2023), are from the Gulf of Cadiz (Atlantic Ocean).

All additions and changes to the list provided by Rosso & Di Martino (2016) are shown in Appendix 1. Updates are indicated in Tables 1–4. Tables 1 and 2 include newly added and removed taxa, respectively, with comments on the nature and reasons for the changes and related references; Table 3 reports changes in taxonomic status as well as genus/family displacements with related references; Table 4 shows the new distribution of families, genera and species in higher taxa compared to Rosso & Di Martino (2016).

In all tables and Appendix 1, taxa were listed using the systematic order reported in the Bryozoa Home Page and WoRMS compiled by Bock & Gordon (2013).

Scanning Electron Microscopy was performed on uncoated specimens of selected species housed in the Rosso Collection at the Paleontological Museum of the University of Catania (PMC), using a TESCAN VEGA 2 LMU at the Microscopical Laboratory (Department of Biological, Geological and Environmental Sciences, University of Catania) in backscattered-electron/low-vacuum mode.

The assignment of the status of non-indigenous bryozoan species (NIB) follows the criteria suggested by Marchini *et al.* (2015) based on the European Environmental Agency (2012) definition, which includes three categories of uncertainty, i.e., taxonomic identification of the species, actual occurrence of the species in the area, and its status as an alien. All listed species meet the first two criteria. For some species, however, there is no consensus about their non-indigenous status. These species are indicated with NIB * in Appendix 1. Species are indicated as cryptogenic (CRY) when they are part of species complexes as indicated by molecular analyses but not yet disentangled, or when their origin is uncertain, i.e., they are neither clearly native nor exotic (e.g., Minchin, 2009).

Results

Changes to the species list provided by Rosso & Di Martino (2016)

In the investigated six year-long period (2017 to May 2023), a total of 33 new species were described from the Mediterranean (Abdel-Salam *et al.*, 2017: 1 species; Cáceres-Chamizo *et al.*, 2017: 1 sp.; Ullman *et al.*, 2017: 1 sp.; Souto *et al.*, 2018: 1 sp.; Berning *et al.*, 2019: 1 sp.; Harmelin *et al.*, 2019: 3 spp.; Schwaha *et al.*, 2019: 1 sp.; Di Martino *et al.*, 2020: 1 sp.; Harmelin, 2020: 1 sp.;

Haugen *et al.*, 2020: 1 sp.; Ramalho *et al.*, 2020: 1 sp.; Rosso *et al.*, 2020a: 3 spp.; Berning *et al.*, 2021: 1 sp.; Decker *et al.*, 2021: 1 sp.; Di Martino & Rosso, 2021: 3 spp.; Reverter-Gil & Souto, 2021: 1 sp.; Pica *et al.*, 2022: 6 spp.; Ramalho *et al.*, 2022: 2 spp.; Harmelin & Rosso, 2023: 3 spp.) (see Table 1, Figs 1, 2). Some of these replace known Mediterranean records of previously widely distributed species due to the re-description of the type or topo-typical material using SEM (see Table 1). This is the case for: 1) *Hornera mediterranea* which replaced *H. lichenoides*, a species from the northern Atlantic and Arctic seas to which Mediterranean colonies were repeatedly referred (see Rosso, 2009; Harmelin, 2020); 2) *Pherusella minima* which replaced the Pacific species *P. brevittuba*, erroneously reported based on colonies collected on *Posidonia oceanica* leaves at 10–28 m depth near Ustica (southern Tyrrhenian Sea), and considered as an alien species in the Mediterranean by Chimenz Gusso & d’Hondt (2005) (see also Decker *et al.*, 2021); 3) *Hincksina synchysia* which replaced *H. flustroides crassispinata*, a subspecies with a very complex history whose colonies, collected by Calvet from near Cete (Corse), were characterized by thick, flattened spines and might be an ecomorph (see Berning *et al.*, 2021); 4) *Exechonella harmelini* erected for Mediterranean specimens from the Aegean and Levantine seas, previously recorded as *E. antillea*, a very distinctive species now considered restricted to the Caribbean (Cáceres-Chamizo *et al.*, 2017); 5) *Metroporiella mesogeia* which replaced *M. lepralioides*, now restricted to the Azores Archipelago in the Atlantic Ocean (Berning *et al.*, 2019); 6) *Schizomavella (Calvetomavella) biancae* which replaced *S. (C.) discoidea*, a species from Madeira, Atlantic (Pica *et al.*, 2022); 7) three new species of *Hemicyclopora* replacing *H. multispinata* (Busk, 1861), which is restricted to the Atlantic and possibly to Madeira (Harmelin & Rosso, 2023); and 8) three species of *Schizoretepora* that were previously attributed to *S. imperati* (Madurell *et al.*, 2019).

New species often resulted from the dismantling of species complexes whose nominal species are still considered present in the Mediterranean, such as *Microporella ciliata* and *Collarina balzaci*. Following the selection of a neotype for *M. ciliata* by Kukliński & Taylor (2008) and the reexamination of historical and modern Mediterranean collections, Di Martino *et al.* (2020) and Di Martino & Rosso (2021) proved that the Mediterranean records of this taxon consist of at least five different species (Table 1). Harmelin *et al.* (2019) recognized three different species in the material previously reported as *C. balzaci* (Table 1).

Further additions shown in Table 1 include first records of species previously known from the near-Atlantic and recently found in the Alboran Sea, such as *Chartella elongata*, *Hincksina longispinosa*, *Terminoflustra barleei*, *Marguetta pulchra* and *Schizomavella (Schizomavella) linearis profunda* (Ramalho *et al.*, 2022). *Juxtacribrilina mutabilis*, originally from Japan, has been recently found in several European sites including the Mediterranean (Crete and Piran) (Martaeng *et al.*, 2023). *Tretosina arcuifera*, only known from Hawaii, was sur-

prisingly discovered in submarine caves of Lesvos Island (Rosso *et al.*, 2020b). A formally still undescribed species, *Hippopodina* sp. A, has been found in several localities of the eastern Mediterranean (Ullman *et al.*, 2017; Ferrario *et al.*, 2018).

Patinella distincta, overlooked in the previous checklist, is now included. This species was described based on a few colonies from the Alboran Sea and the Gibraltar Strait by Alvarez (1993) and, seemingly, never found again.

Species removed from the previous checklist are shown in Table 2, including those that were replaced (see above) and a few others that were synonymized. *Smittina colletti* was synonymized with *S. cervicornis* (Souto & Reverter-Gil, 2019) and *Schizoretepora longisetae* with *S. pungens*, which in turn replaced *S. imperati* (Madurell *et al.*, 2019). Colonies and fragments reported as *S. imperati* by Rosso (1989, 1996; AR unpublished personal observations) from offshore SE Sicily (Gulf of Noto: alive at 74–83 m depth, and dead at 33 m and again at 74–83 m in the Biocoenosis of Detritic Bottoms, and at 86–128 m in the Biocoenosis of Offshore Bottoms) and from the Sicily Strait (dead at 118–128 m depth in the Biocoenosis of Offshore Bottoms), and by Chimenz Gusso *et al.* (2014: fig. 151a–g) from the Tyrrhenian and the Aegean seas (30–40 m) also belong to *S. pungens*.

Overall, eleven genera were added (Table 1) and two were removed (Table 2). *Terminoflustra*, *Juxtacribrilina*, *Marguetta* and *Tretosina* were included based on new records of species previously unknown from the Mediterranean. Two new genera, *Scutocyclopora* and *Terwasipora*, were introduced to place “*Hemicyclopora*” *dentata* and “*Watersipora*” *complanata* as suggested by Harmelin & Rosso (2023) and Reverter-Gil & Souto (2019), respectively. Both *Hemicyclopora* and *Watersipora* persist in the basin as they are represented by other species. Rosso *et al.* (2018) suggested elevation of *Cribrilaria* and *Glabrilaria* to genus level, both taxa previously being considered as subgenera of *Puellina*. A new genus and species of ctenostomatid, *Aethozooides uraniae*, was found in Mediterranean deep waters (Schwaha *et al.*, 2019). *Ascorhyza* is included for *A. mawatari*, a species overlooked in the previous checklist. The two genera removed are *Diporula* and *Smittipora*. *Diporula* was synonymized with *Microporella* (Di Martino & Rosso, 2021) based on morphological characters, later supported by molecular sequencing showing *Diporula* to be nested within *Microporella* (Orr *et al.*, 2022). The only species of *Smittipora* recorded in the Mediterranean “*Smittipora disjuncta*” was placed in the new genus *Bryobifallax* (Rosso *et al.*, 2020b).

Six families were added to the updated checklist. Aethozooidae was introduced for the new species *A. uraniae*. Calescharidae, previously represented in the Mediterranean by *Coronellina fagei* subsequently placed in Microporidae, is reintroduced following the new record of *Tretosina arcuifera*. Ellisinidae and Fenestulinidae are also reintroduced. Ellisinidae includes *Ellisina* and *Retevirgula* previously placed in Calloporidae (Gordon, 2018), and Fenestulinidae includes *Fenestulina* previously placed in Microporellidae (Orr *et al.*, 2018).

Table 1. Taxa added to the checklist of Rosso & Di Martino (2016). For each taxon, the reason of its addition and the related reference is provided.

Taxa	Comments	References
Myolaemata	New taxon	Schwaha <i>et al.</i> , 2020
<i>Hornera mediterranea</i>	New species, replaces <i>H. lichenoides</i> Auctt. not (Linnaeus, 1758)	Harmelin, 2020
<i>Patinella distincta</i>	Overlooked in Rosso & Di Martino, 2016	This paper
Aethozoidae	New family and genus to allocate <i>Aethozooides uraniae</i>	Schwaha <i>et al.</i> , 2019
<i>Aethozooides</i>		
<i>Aethozooides uraniae</i>	New species	
<i>Ascorhyza</i>	Overlooked in Rosso & Di Martino, 2016	Harmelin & d'Hondt, 1992
<i>Ascorhyza mawatari</i>		
<i>Pherusella minima</i>	New species, replaces <i>P. brevituba</i> Soule, 1951	Decker <i>et al.</i> , 2021
<i>Crassimarginatella matildae</i>	New species, partly replaces <i>C. crassimarginata</i> (Hincks, 1880)	Pica <i>et al.</i> , 2022
Ellisinidae	Introduced for <i>Ellisina</i> and <i>Retevirgula</i> displaced from the Calloporidae	Gordon, 2018
<i>Chartella elongata</i>	New record	Ramalho <i>et al.</i> , 2022
<i>Hincksina longispinosa</i>		
<i>Hincksina synchysia</i>	New species, replaces <i>H. flustroides crassispinata</i> Gautier, 1962	Berning <i>et al.</i> , 2021
<i>Terminoflustra</i>	Introduced for the new record <i>T. barleei</i>	Ramalho <i>et al.</i> , 2020
<i>Terminoflustra barleei</i>	New record	
<i>Beania mediterranea</i>	New species, largely replaces <i>B. magellanica</i> (Busk, 1852)	Souto <i>et al.</i> , 2018
<i>Cradoscrupocellaria severoi</i>	New species	Reverter Gil & Souto, 2021
<i>Bryobifallax</i>	Introduced for <i>Smittipora disjuncta</i> (Canu & Bassler, 1930)	Rosso <i>et al.</i> , 2020a
<i>Micropora biopesiula</i>	New species, partly replaces <i>M. coriacea</i> (Johnston, 1847)	Pica <i>et al.</i> , 2022
<i>Setosella alfoi</i>	New species, partly replaces <i>S. folini</i> Jullien, 1882	Rosso <i>et al.</i> , 2020a
<i>Setosella cycloensis</i>	New species, partly replaces <i>S. vulnerata</i> (Busk, 1860)	
<i>Setosella rossanae</i>	New species	
Calescharidae	Introduced to allocate <i>Tretosina arculifera</i>	Rosso <i>et al.</i> , 2020b
<i>Tretosina</i>		
<i>Tretosina arculifera</i>	New record	
<i>Collarina denticulata</i>	New species from the <i>C. balzaci</i> (Audouin, 1826)-complex	Harmelin <i>et al.</i> , 2019
<i>Collarina gautieri</i>		
<i>Collarina spelunca</i>		
<i>Cribrilaria</i>	Subgenus elevated to genus-rank	Rosso <i>et al.</i> , 2018
<i>Glabrilaria</i>		
<i>Juxtacribrilina</i>	New record, non-indigenous	Martaeng <i>et al.</i> , 2023
<i>Juxtacribrilina mutabilis</i>		
<i>Haplopoma celeste</i>	New species	Pica <i>et al.</i> , 2022
<i>Exechonella harmelini</i>	New species, replaces <i>E. antillea</i> (Osnum, 1927)	Cáceres-Chamizo <i>et al.</i> , 2017

Continued

Table 1 continued

Taxa	Comments	References
<i>Adeonellopsis</i> aff. <i>multiporosa</i>	New record	Ramalho <i>et al.</i> , 2022
<i>Reptadeonella zabalai</i>	New species, partly replaces <i>R. violacea</i> (Johnston, 1847)	Haugen <i>et al.</i> , 2019
<i>Marguetta</i>	New record	Ramalho <i>et al.</i> , 2020
<i>Marguetta pulchra</i>		
Exochellidae	Acceptance of Hayward & Ryland (1999) proposal, accordingly to the re-introduction of Escharellidae (see below)	this paper
Escharellidae	Acceptance of <i>Hemicyclopora</i> and <i>Escharella</i> in this family rather than in Romancheinidae	Harmelin & Rosso, 2023
<i>Escharella similis</i>	New species	Ramalho <i>et al.</i> , 2022
“ <i>Escharella</i> ” <i>massiliana</i>	New species	Harmelin & Rosso, 2023
<i>Hemicyclopora admirabilis</i>	New species	Ramalho <i>et al.</i> , 2022
<i>Hemicyclopora hexaspinae</i>	New species, partly replaces <i>H. multispinata</i> (Busk, 1861)	Harmelin & Rosso, 2023
<i>Hemicyclopora neatonensis</i>		
<i>Scutocyclopora</i>	Introduced for <i>Hemicyclopora dentata</i>	
<i>Metroperiella mesogeia</i>	New species replaces <i>M. lepralioides</i> (Calvet, 1903)	Berning <i>et al.</i> , 2019
<i>Schizomavella</i> (<i>S.</i>) <i>cerranoi</i>	New species	Pica <i>et al.</i> , 2022
<i>Schizomavella</i> (<i>S.</i>) <i>linearis profunda</i>	New record	Ramalho <i>et al.</i> , 2020
<i>Schizomavella</i> (<i>Calvetomavella</i>) <i>biancae</i>	New species, replaces <i>S. (Calvetomavella) discoidea</i> (Busk, 1859)	Pica <i>et al.</i> , 2022
<i>Calyptotheca alexandriensis</i>	New species, considered as non-indigenous	Abdelsalam <i>et al.</i> , 2017
<i>Terwasipora</i>	Introduced for <i>Watersipora complanata</i> (Norman, 1864)	Reverter-Gil & Souto, 2019
<i>Schizoporella adelaide</i>	New species	Pica <i>et al.</i> , 2022
<i>Hippopodina</i> sp. A	New, illustrated but still formally undescribed species	Ulman <i>et al.</i> , 2017
<i>Microporella bicollaris</i>	New species, from the <i>M. ciliata</i> -complex	Di Martino & Rosso, 2021
<i>Microporella funbio</i>	New record	Ramalho <i>et al.</i> , 2022
<i>Microporella ichnusae</i>	New species, from the <i>M. ciliata</i> -complex	Di Martino & Rosso, 2021
<i>Microporella modesta</i>	New species, largely replaces <i>M. ciliata</i>	Di Martino <i>et al.</i> , 2020
<i>Microporella pachyspina</i>	New species, from the <i>M. ciliata</i> -complex	Di Martino & Rosso, 2021
Fenestrulinidae	Separated from Microporellidae	Orr <i>et al.</i> , 2018
<i>Buskea medwaves</i>	New species	Ramalho <i>et al.</i> , 2020
<i>Turbicellepora incrassata</i>	Senior synonym replaces <i>T. avicularis</i> (Hinks, 1860)	Rosso <i>et al.</i> , 2020b
<i>Schizoretepora pungens</i>	Replaces <i>S. imperati</i> and is synonym of <i>S. longisetae</i> (Canu & Bassler, 1928)	Madurell <i>et al.</i> , 2019
<i>Schizoretepora aviculifera</i>	Previously largely considered as synonym of <i>S. imperati</i> (Busk, 1884)	Madurell <i>et al.</i> , 2019
<i>Schizoretepora</i> sp. = <i>S. imperati</i> <i>sensu</i> O’Donoghue & de Watterville, 1939	Previously included in <i>S. imperati</i> (Busk, 1884)	Madurell <i>et al.</i> , 2019

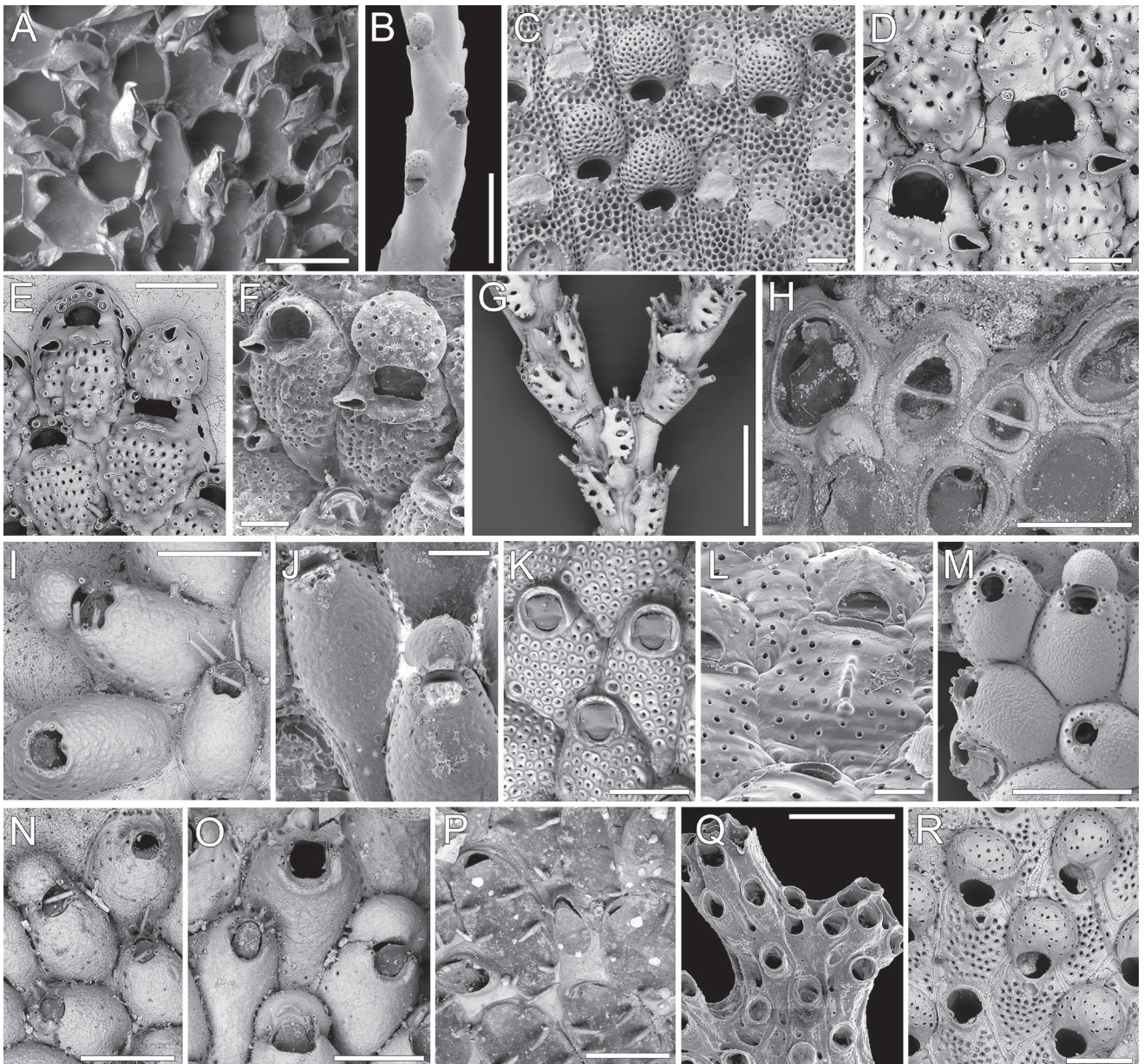


Fig. 1: SEM micrographs of the new bryozoan species described from the Mediterranean Sea since the latest review of Rosso & Di Martino (2016). Species are presented in alphabetical order. A. *Beania mediterranea* Souto, Nascimento, Reverter-Gil & Vieira, 2018 (photo by J. Souto), paratype MHNUSC 10105, Croatia. B. *Buskea medwaves* Ramalho, Caballero-Herrera, Urra & Rueda, 2020 (photo by L. Ramalho), unregistered specimen, Spain. C. *Calyptotheca alexandriensis* Abdel-Salam, Taylor, & Dorgham, 2017 (photo by P.D. Taylor), paratype NHMUK 2016.12.22.1, Egypt. D. *Collarina denticulata* Harmelin in Harmelin *et al.* (2019) (photo by J.-G. Harmelin), unregistered specimen, France. E. *Collarina gautieri* Harmelin in Harmelin *et al.* (2019) (photo by J.-G. Harmelin), paratype MNHN-IB-2014-1923, France. F. *Collarina spelunca*, Harmelin in Harmelin *et al.* (2019) (photo by J.-G. Harmelin), paratype MNHN-IB-2014-1915, France. G. *Cradoscrupocellaria severoi* Reverter-Gil & Souto, 2021 (photo by J. Souto), paratype MNCN 25.03/4234, Spain. H. *Crassimarginatella matildae* Pica & Berning, 2022 in Pica *et al.* (2022) (photo by A. Rosso), PMC Rosso-Collection I. Ps. B.94a, Italy. I. “*Escharella*” *massiliana* Harmelin & Rosso, 2023, paratype PMC Rosso-Collection B36. 5.5.2021, Corse. J. *Escharella similis* Ramalho, Rodríguez-Aporta & Gofas, 2022 (photo by L. Ramalho), unregistered specimen, Spain. K. *Exechonella harmelini* Cáceres-Chamizo, Sanner, Tilbrook & Ostrovsky, 2017 (photo by A.N. Ostrovsky), paratype DPUV 2016-0002-0002, Lebanon. L. *Haplopoma celeste* Pica & Berning, 2022 in Pica *et al.* (2022) (photo by D. Pica), unregistered specimen, Italy. M. *Hemicyclopora admirabilis* Ramalho, Rodríguez-Aporta & Gofas, 2022 (photo by L. Ramalho), holotype MNCN 25.03/4307, Spain. N. *Hemicyclopora hexaspinae* Harmelin & Rosso, 2023 (photo by A. Rosso), paratype PMC Rosso-Collection B29.8.11.2020, Italy. O. *Hemicyclopora neatonensis* Harmelin & Rosso, 2023 (photo by A. Rosso), holotype PMC Rosso-Collection B34.1.4.2021a, Italy. P. *Hincksina synchysia* Berning, Spencer Jones & Vieira, 2021 (photo by B. Berning), holotype MNHN-IB-2017-782, Italy. Q. *Hornera mediterranea* Harmelin, 2020 (photo by J.-G. Harmelin), unregistered specimen, France. R. *Metroperiella mesogeia* Berning, Achilleos & Wisshak, 2019 (photo by A. Rosso), PMC Rosso-Collection I. Ps. B.95a, Italy. Scale bars: A, G, H, I, K, N, O, Q, 500 µm; B, M, 700 µm; C, E, J, 200 µm; D, F, L, 100 µm; P, R, 250 µm.

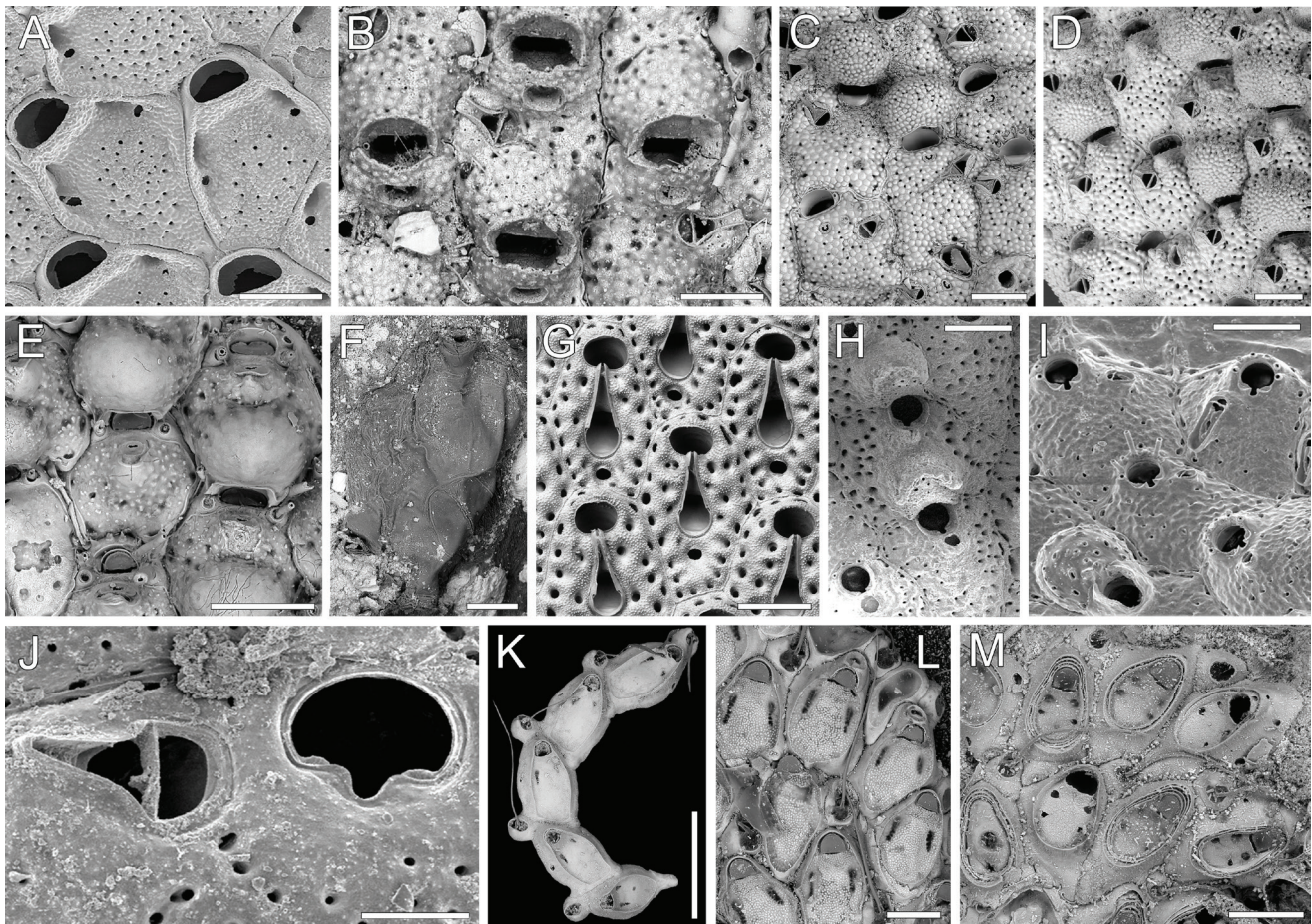


Fig. 2: SEM micrographs of the new bryozoan species described from the Mediterranean Sea since the latest review of Rosso & Di Martino (2016). Species are presented in alphabetical order. A. *Micropora biopesiula*, Pica & Berning, 2022 in Pica *et al.* (2022) (photo by D. Pica), unregistered specimen, Italy. B. *Microporella bicollaris* Di Martino & Rosso, 2021 (photo by A. Rosso), PMC Rosso-Collection I. Ps. B.96a, Italy. C. *Microporella ichnusae* Di Martino & Rosso, 2021 (photo by A. Rosso), Rosso Collection, holotype PMC. B30a. 20.11.2020, Italy. D. *Microporella modesta* Di Martino, Taylor & Gordon, 2020 (photo by P.D. Taylor), paratype NHMUK 1869.10.6.6d, Algeria. E. *Microporella pachyspina* Di Martino & Rosso, 2021 (photo by A. Rosso), PMC Rosso Collection I. H. B.87a, Italy. F. *Pherusella minima* Decker, Gordon, Spencer Jones, & Schwaha, 2021 (photo by A. Rosso), PMC Rosso-Collection I. Ps. B.97a, Italy. G. *Reptadeonella zabalai* Haugen, Novosel, Wisshak & Berning, 2020 (photo by E. Di Martino), holotype NHMO H 1431, Croatia. H. *Schizomavella (Schizomavella) cerranoi* Pica & Berning, 2022 in Pica *et al.* (2022) (photo by D. Pica), unregistered specimen, Italy. I. *Schizomavella (Calvetomavella) biancae* Pica & Berning, 2022 in Pica *et al.* (2022) (photo by D. Pica), holotype MSNG 62428, Italy. J. *Schizoporella adelaide* Pica & Berning, 2022 in Pica *et al.* (2022) (photo by D. Pica), unregistered specimen, Italy. K. *Setosella alfoi* Rosso, Di Martino & Gerovasileiou, 2020 (photo by A. Rosso), PMC. Rosso Collection I.H. B-45a, Italy. L. *Setosella cycloensis* Rosso, Di Martino & Gerovasileiou, 2020 (photo by A. Rosso), Rosso Collection, paratype PMC. B24. 8.3.2018b, Italy. M. *Setosella rossanae* Rosso, Di Martino & Gerovasileiou, 2020 (photo by A. Rosso), Rosso collection, holotype PMC. B25. 30.6.2018a, Italy. Scale bars: A–I, L, M, 200 μ m; J, 100 μ m; K, 500 μ m.

Following Harmelin & Rosso (2023), Escharellidae is reintroduced for *Escharella* and *Hemicyclopora*, and Exochellidae for *Escharoides*, all three genera now removed from Romancheinidae. This change is also consistent with the suggestion made by Hayward & Ryland (1999) about the family attribution of these genera.

Finally, following Schwaha *et al.* (2020) Myolaemata is introduced as the new clade grouping all present-day Mediterranean bryozoans.

In this paper we also suggest new combinations for some cribrilid species, and the extension of trinomens for some species in the genus *Schizomavella* based on the work of Rosso *et al.* (2018) and Reverter-Gil *et al.* (2015), respectively. In the case of *Schizomavella*, subgeneric attribution of some species was not possible because of the

absence of diagnostic characters, such as ovicells in *S. rossanae*, and the presence of ambiguous features (seemingly unrelated to both *Schizomavella* and *Calvetomavella*) in *S. adriatica*. The new combination *Celleporaria mickeli* is suggested for *Trematooecia mickeli*, a species reported by Sokolover *et al.* (2016), from Israel, based on the morphology of the globose ooecium, characterized by a wide arched opening, partly obscuring the primary orifice. All newly suggested changes are summarized in Table 3.

Updated composition of the Mediterranean bryozoan fauna

Taking into consideration all taxon additions (Table 1)

Table 2. Taxa deleted from the checklist of Rosso & Di Martino (2016). For each taxon, the reason for its deletion and the related reference is provided.

Taxa	Comments	References
<i>Hornera lichenoides</i>	Replaced by <i>H. mediterranea</i>	Harmelin, 2020
<i>Pherusella brevituba</i>	Replaced by <i>P. minima</i>	Decker <i>et al.</i> , 2021
<i>Hincksina flustroides crassispinata</i>	Replaced by <i>H. synchysia</i>	Berning <i>et al.</i> , 2021
<i>Smittipora</i>	<i>S. disjuncta</i> now in <i>Bryobifallax</i>	Rosso <i>et al.</i> , 2020a
<i>Onychocella angulosa</i> Reuss, 1847	Specimens considered as belonging to <i>O. marioni</i>	Rosso <i>et al.</i> , 2020b; Di Martino <i>et al.</i> , 2022
<i>Hemicyclopora collarina</i> Canu & Lecointre, 1930	Only fossil, present-day specimens now in <i>S. dentata</i>	Harmelin & Rosso, 2023
<i>Diporula</i>	Synonymized with <i>Microporella</i>	Di Martino & Rosso, 2021
<i>Turbicellepora avicularis</i>	Replaced by <i>T. incrassata</i>	Rosso <i>et al.</i> , 2020c
<i>Metroperiella lepralioides</i>	Endemic of Azores	Berning <i>et al.</i> , 2019
<i>Smittina colletti</i>	Synonymized with <i>S. cervicornis</i>	Souto & Reverter-Gil, 2019
<i>Exechonella antillea</i>	Replaced by <i>E. harmelini</i>	Cáceres-Chamizo <i>et al.</i> , 2017
<i>Hagiosynodos hadros</i>	Synonymised with <i>H. latus</i>	Pica <i>et al.</i> , 2022
<i>Schizomavella discoidea</i>	Replaced by <i>S. (Calvetomavella) biancae</i>	Pica <i>et al.</i> , 2022
<i>Schizoretepora imperati</i>	Replaced by <i>S. pungens</i>	Madurell <i>et al.</i> , 2019
<i>Schizoretepora longisetae</i>	Synonymised with <i>S. pungens</i>	Madurell <i>et al.</i> , 2019

Table 3. List of changes in ranking, taxonomic status and genus/family displacements in relation to the checklist of Rosso & Di Martino (2016). For each taxon, the type of change and the related reference are reported.

Taxon	Change	Reference
<i>Ellisina</i>	Displaced from Calloporidae to Ellisinida	Gordon, 2018
<i>Retevirgula</i>		
<i>Bryobifallax disjuncta</i>	Recognised as a Microporidae rather than an Onychocellidae	Rosso <i>et al.</i> , 2020b
<i>Cribrilaria arrecta</i>		
<i>Cribrilaria cassidainsis</i>	Displaced from <i>Puellina</i> , following the elevation of <i>Cribrilaria</i> to genus rank	Rosso <i>et al.</i> , 2018
<i>Cribrilaria hincksi</i>		
<i>Cribrilaria innominata</i>		
<i>Cribrilaria mikelae</i>		Rosso <i>et al.</i> , 2021
<i>Cribrilaria minima</i>	Placed in <i>Cribrilaria</i> , first used by Harmelin	this paper
<i>Cribrilaria picardi</i>	New combination	
<i>Cribrilaria p. pseudoradiata</i>		
<i>Cribrilaria radiata</i>		
<i>Cribrilaria scripta</i>	Displaced from <i>Puellina</i> , following the elevation of <i>Cribrilaria</i> to genus rank	Rosso <i>et al.</i> , 2018
<i>Cribrilaria setiformis romana</i>		
<i>Cribrilaria venusta</i>		

Continued

Table 3 continued

Taxon	Change	Reference
<i>Glabrilaria pedunculata</i>		
<i>Glabrilaria corbula</i>	Displaced from <i>Puellina</i> , following the elevation of <i>Glabrilaria</i> to genus rank	Rosso <i>et al.</i> , 2018
<i>Glabrilaria o. orientalis</i>		
<i>Glabrilaria orientalis lusitanica</i>		
<i>Puellina gattya</i>	The mention of the subgenus <i>Puellina</i> is deleted	this paper
<i>Puellina setosa</i>		
<i>Celleporaria mikeli</i>	Displaced from the genus <i>Trematoeocia</i>	this paper
<i>Hippomenella</i>	Displaced from Escharinidae to Romancheinida	Berning, 2013
<i>Scutocyclopora dentata</i>	Displaced from the genus <i>Hemicyclopora</i> , and the family Romancheinidae, temporarily to Escharellidae	
<i>Escharoides</i>		Harmelin & Rosso, 2023
<i>Escharella</i>	Displaced from Romancheinidae to Exochellidae	
<i>Hemicyclopora</i>		
<i>Schizomavella (S.) mystacea</i>		Achilleos <i>et al.</i> , 2020
<i>Schizomavella (S.) stanislavi</i>	Introduced in the subgenus <i>Schizomavella</i>	this paper
<i>Schizomavella (S.) tubulata</i>		
<i>Escharina protecta</i>	Previously a subspecies in <i>Escharina dutertrei</i>	Pica <i>et al.</i> , 2022
<i>Microporella joannae</i>	Displaced from the genus <i>Fenestulina</i>	Di Martino & Rosso, 2021

and removals (Table 2), as well as newly suggested changes (Table 3), the Mediterranean bryozoan fauna (Appendix 1, Table 4) to date (May 2023) consists of 99 families (11 cyclostomatids, 19 ctenostomatids and 69 cheilostomatids), 220 genera (26 cyclostomatids, 28 ctenostomatids and 166 cheilostomatids) and 588 species (76 cyclostomatids, 58 ctenostomatids and 454 cheilostomatids). Cheilostomatids are the most diverse, representing 69.7%, 75.5% and 77.2% at family, genus and species level, respectively. Cyclostomatids (11.1%, 11.8% and 12.9% of families, genera and species) and ctenostomatids (19.2%, 12.7% and 9.9%) are subordinate.

The net increase in species is largely due to cheilostomatids, which increased from 424 to 454 species, thus including 30 additional species. A single species is added for cyclostomatids and two for ctenostomatids. Several of the added species belong to already species-rich genera/families. This is the case for the family Cribrilinidae, now represented by 29 species following the inclusion of three new species of *Collarina* (Harmelin *et al.*, 2019) and one of *Juxtacribrilina* (Martaeng *et al.*, 2023). Four newly described species and the transfer of *Diporula verrucosa* and *Fenestulina joannae* into *Microporella* (Di Martino *et al.*, 2020; Di Martino & Rosso, 2021), as well as the record of a new species from the Alboran Sea (Ramalho *et al.*, 2022), nearly doubles the diversity of this genus from 8 to 15 species. However, the total number of species in the family Microporellidae in-

creased only by two (now 16 species) due to the re-attribution of the genus *Fenestulina*, with its three remaining species, to Fenestulinidae following Orr *et al.* (2018). Flustridae increased from 9 to 12 species due to new records from the Alboran Sea (Ramalho *et al.*, 2020, 2022); Bitectiporidae increased by two species after the revision of the genus *Schizomavella* (Pica *et al.*, 2022). Several families such as Phidoloporidae, Celleporidae, Candidae, Schizoporellidae and Bryocryptellidae increased by one species. Calloporidae decreased by one species, while Romancheinidae decreased from five to two genera and from 19 to two species following the inclusion of the genus *Hippomenella* (Berning, 2013) and the exclusion of the genera *Escharella*, *Hemicyclopora* and *Neolagenipora* (see Harmelin & Rosso, 2023). The greatest diversity change occurred in the family Escharellidae, which now includes three genera and temporarily the new genus *Scutocyclopora*. Among less diverse families, Setosellidae, with only the genus *Setosella*, doubled the number of species increasing to six (Rosso *et al.*, 2020a), and Adeonidae increased to 10 species following a new record (Ramalho *et al.*, 2022), and the description of a new species (Haugen *et al.*, 2020).

Excepting Crisiidae, the most species-rich families belong to the cheilostomatids, with only 10 families (10.1%), representing 251 species and accounting for 42.8% of the total diversity. These families are: Phidoloporidae (38 species), Celleporidae (35 spp.), Bitectiporidae (31 spp.),

Table 4. Present-day bryozoan diversity in the Mediterranean Sea (present paper) in comparison with previous figures provided in Rosso & Di Martino (2016). For each family, the number of genera and species is reported. Total values for orders, classes the clade and the phylum are given in bold.

	R & DM, 2016			This paper		
	F	G	Sp	F	G	Sp
BRYOZOA	93	212	556	99	220	588
MYOLAEMATA	93	212	556	99	220	588
STENOLAEMATA	11	26	75	11	26	76
Cyclostomatida	11	26	75	11	26	76
Stomatoporidae		1	2		1	2
Oncousoeciidae		5	7		5	7
Tubuliporidae		3	10		3	10
Plagioeciidae		4	9		4	9
Terviidae		1	1		1	1
Annectocymidae		3	9		3	9
Entalophoridae		1	1		1	1
Fronciporidae		1	1		1	1
Crisiidae		4	19		4	19
Horneridae		1	2		1	2
Lichenoporidae		2	14		2	15
GYMNOLAEMATA	82	186	481	88	194	512
Ctenostomatida	18	27	57	19	28	58
Benedeniporidae		1	2		1	2
Alcyonidiidae		3	10		3	10
Clavoporidae		2	3		2	3
Pherusellidae		1	2		1	2
Victorellidae		3	3		3	3
Nolellidae		1	2		1	2
Aethozoidae		–	–		1	1
Immergentiidae		1	1		1	1
Oncousoeciidae		2	14		2	14
Buskiidae		1	2		1	2
Triticellidae		2	3		2	3
Aeverilliidae		1	1		1	1
Farrellidae		1	1		1	1
Walkeriiidae		1	3		1	3
Mimosellidae		2	3		2	3
Hypophorellidae		1	1		1	1
Arachnidiidae		2	3		2	3
Spathiporidae		1	2		1	2
Penetrantiidae		1	1		1	1
Cheilostomatida	64	159	424	69	166	454
Aeteidae		1	5		1	5
Scrupariidae		1	2		1	2
Eucrateidae		1	1		1	1
Membraniporidae		2	3		2	3
Electridae		5	12		5	12
Tendridae		1	1		1	1
Thalamoporellidae		1	4		1	4

Continued

Table 4 continued

	R & DM, 2016			This paper		
	F	G	Sp	F	G	Sp
Calloporidae		12	23		10	22
Ellisinidae		–	–		2	2
Antroporidae		2	2		2	2
Cymuloporidae		1	1		1	1
Chaperiidae		1	2		1	2
Heliodomidae		1	2		1	2
Cupuladriidae		2	4		2	4
Flustridae		5	9		6	12
Bugulidae		6	19		6	19
Beaniidae		1	4		1	5
Epistomiidae		2	2		2	2
Candidae		6	18		6	19
Microporidae		5	8		6	9
Setosellidae		1	3		1	6
Onychozellidae		2	4		1	2
Chlidoniidae		1	1		1	1
Calescharidae		–	–		1	1
Cellariidae		2	5		2	5
Monoporellidae		1	1		1	1
Cribrilinidae		6	25		9	29
Catenicellidae		1	1		1	1
Savignyellidae		1	1		1	1
Hippothoidae		2	4		2	4
Chorizoporidae		1	1		1	1
Trypostegidae		1	2		1	2
Haplopomidae		1	6		1	7
Pasytheidae		1	1		1	1
Exechonellidae		1	1		1	1
Adeonidae		4	8		4	10
Lepraliellidae		2	8		2	9
Bryocryptellidae		4	9		5	10
Romancheinidae		5	19		2	2
Exochellidae		–	–		1	3
Escharellidae		–	–		4	17
Umbonulidae		1	1		1	1
Tessaradomidae		1	1		1	1
Jaculinidae		1	3		1	3
Smittinidae		5	22		5	22
Bitectiporidae		4	29		4	31
Lanceoporidae		2	8		2	9
Watersiporidae		1	5		2	5
Schizoporellidae		3	12		3	13
Margarettidae		1	1		1	1
Myriaporidae		1	1		1	1
Hippopodinidae		1	3		1	4
Escharinidae		4	7		3	6

Continued

Table 4 continued

	R & DM, 2016			This paper		
	F	G	Sp	F	G	Sp
Cryptosulidae		1	1		1	1
Cheiloporinidae		1	1		1	1
Teuchoporidae		1	1		1	1
Phoceanidae		2	3		2	3
Hippaliosinidae		1	2		1	2
Fenestrulinidae		–	–		1	3
Microporellidae		4	14		2	16
Robertsonidridae		1	1		1	1
Petraliellidae		1	1		1	1
Lacernidae		2	3		2	3
Crepidacanthidae		1	1		1	1
Cleidochasmatidae		2	3		2	3
Colatooeiidae		1	2		1	1
Celleporidae		9	34		9	35
Hippoporidridae		3	5		3	4
Phidoloporidae		11	37		11	38

Cribrilinidae (29 spp.), Calloporidae and Smittinidae (22 spp. each), Bugulidae, Candidae, Crisiidae (19 spp. each), and Escharellidae (17 spp.). Fifteen families (nine cheilostomatids, four cyclostomatids and two ctenostomatids) each including 9 to 16 species account for 167 species, representing a further 28.4% of the total diversity. In contrast, 31 families (32%; three cyclostomatids, six ctenostomatids and 22 cheilostomatids) are mono-specific, representing only 5.3% of the total diversity.

Several species-rich families are also rich in the number of genera, such as Phidoloporidae (11 genera), Calloporidae (10 gen.), Celleporidae and Cribrilinidae (9 gen. each), Bugulidae and Candidae (6 gen. each). Fewer genera belong to Smittinidae (5 gen.), Crisiidae and Escharellidae (4 gen. each). Six genera belong to the relatively less species-rich families Flustridae (12 spp.) and Microporidae (9 spp.).

Similarly, a few genera, mostly within the Cheilostomatida, contribute most to species diversity. The most species-rich cheilostomatid genera are *Schizomavella* (24 spp.), *Reteporella* and *Microporella* (15 spp. each), *Cribrilaria* (12 spp.), *Schizoporella* (11 spp.), *Escharella*, *Celleporina* and *Turbicellepora* (10 spp. each), *Bugulina* (9 spp.), *Cradoscrupocellaria*, *Celleporaria* and *Parasmittina* (8 spp. each), *Haplopoma* and *Rhynchozoon* (7 spp. each). Only two genera per group are species-rich within Cyclostomatida (*Crisia* and *Disporella* with 15 and 9 spp., respectively) and Ctenostomatida (*Amathia* and *Alcyonidium* with 13 and 8 spp., respectively). Almost half of the genera (109 out of 220) are monospecific with 13 cyclostomatids, 16 ctenostomatids and 80 cheilostomatids, representing only 18.6% of all species.

Discussion

This updated checklist reports on changes in the Mediterranean bryozoan diversity introduced between 2016 and May 2023 and derived from both new records and newly described species (Figs 1, 2), discovered following the re-examination of historical and recent collections, as well as from the analysis of material obtained during recent surveys in relatively understudied areas and habitats.

Introduced changes

The case of *Aethozooides uraniae*, which was collected in 2011 at about 3500 m depth in the extreme habitat provided by superficial sediments at the upper edge of the halocline of a hypersaline anoxic brine lake (Urania Basin, central Ionian Sea), is a prime example of new species described from previously understudied areas and habitats (Bernhard *et al.*, 2015; Schwaha *et al.*, 2019). *Setosella alfoi* was collected in bathyal sectors (513–1521 m depth) of the southern Tyrrhenian Sea and the northeastern Ionian Sea (Rosso *et al.*, 2020a). Three species have comparably shallower distributions in the Alboran Sea. These are *Buskea medwaves*, recorded on soft bottoms ranging from the outer shelf to the upper slope (Chella Bank: 95–322 m), and *Escharella similis* and *Hemicyclopora admirabilis*, collected on gravelly grounds of the shelf break, at 95–120 m and 112–120 m, respectively (Ramalho *et al.*, 2020, 2022). “*Escharella*” *massiliana*, a species only recorded from the French part of the Mediterranean Sea between Marseille and Calvi (Corsica), has a similar depth distribution, ranging from 110 to 150 m. *Hemicyclopora hexaspinae* also has a deep core of records in the outer shelf at 60–150 m, in addition to shallower records (5–40 m) in submarine caves of the

western Mediterranean (Harmelin & Rosso, 2023).

Several newly described species originate from shallower, generally more easily accessible habitats located on the continental shelf. This is the case for six species (i.e., *Crassimarginatella matildae*, *Micropora biopesiula*, *Haplopoma celeste*, *Schizomavella* (*Schizomavella*) *cerranoi*, *Schizomavella* (*Calvetomavella*) *biancae*, and *Schizoporella adelaide*), associated with coralligenous bottoms at 60 m depth in the northern Ionian Sea (Pica *et al.*, 2022).

Some species thrive in shelf soft bottoms and extend deeper toward and beyond the shelf break. These include *Setosella cycloensis*, found from about 30 m down to 162 m in the northwestern Mediterranean and the Ionian Sea (Rosso *et al.*, 2020a); *Hemicyclopora neatonensis*, reported from open shelf bottoms between 27 and 120 m depth in the central-western Mediterranean (Harmelin & Rosso, 2023); *Metroperiella mesogeia*, associated with several substrata and habitats and widespread in the Mediterranean from the surface to about 60 m depth and reported also from deeper waters (70–120 m) in Cyprus (Berning *et al.*, 2019); and *Beania mediterranea*, widely distributed in the Mediterranean, from the Ibero-Balearic Basin to the south Tyrrhenian Sea, the north Adriatic and the Aegean Sea at less than 40–45 m and also down to about 100 m in the Balearic and Columbretes archipelagos (Souto *et al.*, 2018).

Collarina gautieri is widespread in the NE Atlantic and the Mediterranean Sea, recorded from the Faeroes to the southern Iberian coasts and down to 130 m off Brittany. It is found at shallower depths (5–88 m) in the Mediterranean where it has been reported from several localities in the Gulf of Leon, Tyrrhenian and Adriatic seas, typically encrusting small substrata in soft bottoms (Harmelin *et al.*, 2019). The distribution of this species is seemingly more extensive in the Mediterranean because of its misidentification as *C. balzaci*, as also suggested by the identification of *C. gautieri* colonies encrusting volcanic ashes collected at 5–26 m depth in photophilic algae assemblages in the Ionian Sea (Rosso *et al.*, 2019).

Microporella modesta is another shallow shelf species mostly reported shallower than 40 m, although occasionally found deeper (*ca* 60 m) where it is often associated with vegetate bottoms. Though first described from a single locality of the northern African coast (Di Martino *et al.*, 2020), Di Martino & Rosso (2021) proved that it is common and widespread in the Mediterranean, representing most of the previous records of *M. ciliata*.

Some other species are also found in shallow waters of the inner-mid shelf, in the infralittoral, or in infralittoral-to-shallow circalittoral habitats. *Microporella pachyspina*, is presently known only from the type locality in the Egadi Islands (W Sicily) at less than 20 m depth, associated with vegetate bottoms, both in the infralittoral algae biocoenosis and *Posidonia* meadows (Di Martino & Rosso, 2021). *Microporella bicollaris*, originally reported alive associated with algae of the coralligenous biocoenosis in the northern Ionian Sea (Gulf of Taranto) at 5–15 m depth, and dead in a semidark cave (23 m) in the western Ionian Sea (Di Martino & Rosso, 2021), was later collect-

ed alive also on coralligenous build-ups at *ca* 36 m depth in the same area (AR, unpublished personal observation). *Collarina denticulata*, seemingly endemic to the Catalonia-Provence-Corse area, was found in less than 25 m depth on natural and artificial substrata, including plastic and asbestos tiles (Harmelin *et al.*, 2019). *Reptadeonella zabalai*, presumably widespread in the Mediterranean, and likely representing previous records of *R. violacea*, is presently reported only from the SE Adriatic and the W Ionian (Sicily) seas, between 4 and 45 m on a variety of substrata (Haugen *et al.*, 2020). *Hincksina synchysis* from Yves Gautier's collection was collected at 30–40 m near Portofino (Ligurian Sea) (Berning *et al.*, 2021). *Cradoscrupocellaria severoi*, is currently only known from the type locality at Columbretes Islands, between 3 and 42 m (Reverter-Gil & Souto, 2021). Finally, *Pherusella minima*, described based on colonies collected at 2.5 m depth in Istria (Croatia), is possibly widespread in the Mediterranean (Decker *et al.*, 2021). Indeed, some specimens of this species from the Tyrrhenian Sea were first misidentified as *P. brevituba* (Soule, 1951) by Chimenz Gusso & d'Hondt (2005), and a pair of colonies collected off Capo Rizzuto (Calabria, southern Italy, North Ionian Sea) occur in the collection of one of us (AR, PMC). The species seems infralittoral in distribution and is invariably associated with *P. oceanica* meadows.

Further, new species with apparent shallow bathymetric distribution originate from semidark to dark submarine caves that tend to have high bryozoan diversity (e.g., Harmelin, 1969, 1997; Rosso *et al.*, 2013a, 2021a, Gerovasileiou & Bianchi, 2021, and references therein). Such new species include: the Atlantic-Mediterranean *Collarina speluncola* found in the dark sectors of several caves in the Marseille area, mostly at 3–4 m depth, but also down to 18 m (Harmelin *et al.*, 2019); *Microporella ichmusae*, collected in 2009 in semidark caves from NW Sardinia mostly at about 8 m depth (Di Martino & Rosso, 2021); and *Setosella rossanae* collected in the dark parts of caves in SE Sicily and Lesvos Island between 17 and 30 m depth during extensive surveys in 2009 and 2010 and studied in subsequent years (Rosso *et al.*, 2020a). It is expected that most, if not all, these species will be discovered in other cryptic and/or deep circalittoral to bathyal habitats, as is the case for most species typical of submarine caves (e.g., Harmelin, 1997; Rosso *et al.*, 2013b). Samples from caves of Lesvos Island (Aegean Sea), collected between 17 and 27 m, also have a few colonies of *Tretosina arcuifera*, a species never reported after its first description from Hawaii more than a century ago (Rosso *et al.*, 2020b). Finally, *Calypsotheca alexandriensis* was described from red-coloured open-honeycomb spherical colonies, formed by bilaminar anastomosing fronds and growing in dense clusters, discovered in the port of Alexandria (Egypt) in December 2015 from the sea level to 1 m depth. It has been described and interpreted as a non-indigenous species for the Mediterranean with a possible Indo-Pacific origin (Abdel-Salam *et al.*, 2017). *Juxtacribrilina mutabilis* is also of Pacific origin and it was first recorded through DNA barcoding, and subsequently found encrusting Autonomous Reef Monitoring

Structures (ARMS) in two Mediterranean sites, Crete and Piran, at 4–21 and 9 m depth, respectively (Martaeng *et al.*, 2023). *Hippopodina* sp. A, although still formally undescribed, has been reported by Ullman *et al.* (2017) and Ullman (2018), from marinas in Rhodes and Turkey, also encrusting boat-hulls. It was later listed as an alien species in Turkey (Çinar *et al.*, 2021) and the Mediterranean (Ferrario *et al.*, 2018; Zenetos & Galanidi, 2020).

Some other species additions derive from the examination of type specimens that nowadays are becoming more accessible due to increasing digitalization efforts, thus leading to the re-evaluation/resurrection of synonyms. This is the case for *Turbicellepora incrassata* which proved to be a senior synonym of *T. avicularis* after its type specimens kept in the Lamarck collection at the Muséum national d'Histoire naturelle in Paris were digitalized (see Rosso *et al.*, 2020c). Madurell *et al.* (2019) disentangled a very intricate history of synonymies regarding the Mediterranean species of the genus *Schizoretepora*: *S. imperati* was synonymized with *S. longisetae* and *S. pungens* (the latter now suggested as the valid name), while *S. avicularis* previously considered as a synonym of *S. imperati* is now re-evaluated as a distinct valid species.

It is worth noting that several species additions derive from the dismantlement of already known or newly identified species complexes and/or the separation as distinct species of the Mediterranean populations from presumed widely distributed taxa. In some instances, long-standing issues related to misinterpretations/misidentifications have been solved, such as in *Microporella*, *Hornera* and *Escharella* and *Hemicyclopora*. The selection of a neotype for *M. ciliata* by Kukliński & Taylor (2008) led to the revision of previous Mediterranean records of the species resulting to species reassignment and the description of new species. The case of *Hornera* is even more relevant because *H. lichenoides* is paradoxically the only bryozoan species included in the list of endangered or threatened species (Annex II) of the Barcelona Convention (UNEP/MAP-SPA/RAC, 2018; see Rosso, 2009; Rosso *et al.*, 2010; Harmelin, 2020) and hence considered in need of protection, though no investigation is known assessing any threat. After the formal description of *H. mediterranea* by Harmelin (2020) and comments about the possible main threat to which the conspecific *H. frondiculata* is exposed, emendation in the Annex II is to be expected. Examination by Harmelin & Rosso (2023) of Mediterranean and Atlantic material traditionally assigned to *Hemicyclopora multispinata* led to the identification of several species, including at least three new from the Mediterranean; *H. neatonensis* and *H. hexaspinata*, and a third species temporarily assigned to *Escharella*, “*E. massiliensis*”.

Unresolved issues - equivocal species and records

Problems relating to equivocal records and records of species of doubtful taxonomic status already remarked in Rosso & Di Martino (2016, table 3) persist. Historical

collections should be revisited to locate the type specimens of species that were described a long time ago but often never reported again after their first description, most of which are not included in Mediterranean bryozoan checklists (Harmelin, 1992; Rosso, 2003; Rosso & Di Martino 2016; this paper). It is essential to trace, image the type specimens using SEM and redescribe the species when necessary to clarify their morphological identity and assess their status. This would also avoid anomalous records, even in modern/contemporary literature, e.g., *Adeonella lichenoides* (Lamarck, 1816) in Albayrak & Balkis (2016). Some suggestions have already been given in recent papers but further investigation is needed to confirm proposed synonymies. Di Martino & Rosso (2021) suggested the synonymy of *Microporella flabelligera* Levinsen, 1909 described from off SE Sicily and *M. appendiculata*. *Scrupocellaria capreolus* Heller, 1867, is likely to represent a species close to but distinct from *Cradoscrupocellaria bertholletii* (Vieira *et al.*, 2013). “*Reptoporina*” *aspera* d’Orbigny 1852, described from off Algiers in the SW Mediterranean is possibly a *Schizomavella* species based on the images of the type specimen kept at the Muséum national d’Histoire naturelle in Paris and available at <https://science.mnhn.fr/institution/mnhn/collection/f/item/r64295?listindex=34&listCount=6769> (accessed 26.04.2023). However, we avoided the inclusion of such undefined species in this update pending further revision demonstrating either their validity or establishing formal synonymies.

Mollia planata (Moll, 1803) and *M. folineae* (delle Chiaje, 1828), described from the Mediterranean and reported as *taxa inquirenda* in bryozoa.net (<http://bryozoa.net/cheilostomata/microporidae/mollia.html>, accessed 26.04.2023) and WoRMS but never included in any Mediterranean faunal list of species, would need to be located and examined in order to clarify their status. The same applies to *Conopeum fluviatilis* (Canu, 1928) and *C. spiculata* (Canu, 1928) described from Tunisia and considered as valid species in WoRMS but confirmed to be synonyms of *C. seurati* in Gordon *et al.* (2020).

Future challenges relating to improved technologies, global change and anthropogenic impact

Recently published taxonomic revisions have recognized several species complexes thanks to the observation of relevant, although subtle, diagnostic morphological differences. It is likely that further species still reported in the present list need to be revised because they could represent species complexes when they have apparent high variabilities as well as wide geographical (usually in the Atlantic-Mediterranean region) and/or stratigraphical distributions. This is particularly true for species whose type specimens originate from extra-Mediterranean localities or from fossil assemblages, and for those that have never been illustrated using SEM or other modern techniques such as 3D scans of internal skeletal features. There are numerous examples based on our personal experience and observations. This issue is corroborated

by the relatively high number of species reported as cf. or aff. in modern literature (e.g., Harmelin, 2014; Rosso *et al.*, 2019; Achilleos *et al.*, 2020; Pica *et al.*, 2022). In recent taxonomic papers, this has led to synonymy lists including only selected papers that provide figures useful for species identification and therefore reliable (see Pica *et al.*, 2022).

Well-known examples of species complexes remaining to be dismantled include the *Candidae* colonies from the Catalan coasts that were first reported as *Scrupocellaria macrorhyncha* by Zabala (1986) but later assigned to *S. reptans* by Zabala & Maluquer (1988) even though the material presented different features, as also suggested by Vieira *et al.* (2013). These differences were also noted by Reverter-Gil & Souto (2021) who introduced the new species *Cradoscrupocellaria severoi* for some of the colonies while leaving others unassigned. The colonies of *Arthropoma ceciliae* (the only species of this genus known from the Mediterranean) reported from the Tyrrhenian Sea by Chimenz Gusso *et al.* (2014) possibly belong to a different species, as suggested by Min *et al.* (2017). Another example is *Bugula neritina* consisting of three cryptogenic species only recognizable through molecular analyses (Fehlauer-Ale *et al.*, 2014), two of which presumably occur in the Mediterranean (Tanduo *et al.*, 2021).

An increase in molecular studies on bryozoans is helping with the identification of species complexes, often prompting the detection of new morphological traits that are useful for species recognition. On the other hand, synonymy of species with distinct morphology and distribution has also been suggested by molecular analyses. This is the case for two *Adeonella* species, *A. calveti* and *A. pallasii*, that seem genetically identical (Orr *et al.*, 2019). The two species have similar ecological requirements but differ in the shape, size, position, and orientation of the peristomial adventitious avicularia. These species also have distinct geographical distributions in the western and eastern parts of the Mediterranean, respectively, only with a limited overlap (Rosso & Novosel, 2010). Both have been maintained in the present list.

More changes are expected in the future, following the increasing arrival of non-indigenous species mostly in the Levantine Basin, largely affected by the presence of the Suez Canal and its marine traffic connecting the Mediterranean to the Red Sea and the Indo-Pacific. In addition to *Calypsotheca alexandriensis*, *Hippopodina* sp. A and *Juxtacribrilina mutabilis* (see above: Abdel-Salam *et al.*, 2017; Ullman *et al.*, 2017; Martaeng *et al.*, 2023), more species will probably need to be added in future lists.

Many changes, including formalized new species and synonymies, have also resulted from the inspection of historical collections in museums. This highlights the tremendous relevance of museum collections in preserving material for future generations of researchers.

In addition to the validity of some species and species records, open issues include the validity of some genera and the correct allocation of some species at genus-level. A few examples are: 1) the distinction between the genera *Hemicyclopora* and *Escharella* needs to be test-

ed using molecular analyses given that the diagnostic morphological characters currently used represent the extreme aspects of traits showing a series of continuous variations documented in several species (Harmelin & Rosso, 2023); 2) the controversial synonymy of *Biflustra* d'Orbigny (1852) and *Acanthodesia* Canu and Bassler, 1919, although widely addressed (see Grischenko *et al.*, 2002; Taylor & Tan, 2015; Cook *et al.*, 2018), is still unresolved; 3) the status of the genus *Fron dipora* and of its type species *Millepora reticulata* Linnaeus, 1758 considered as a *taxon inquirendum* in WoRMS (accessed, 17.03.2023) and of *F. gracilis* Canu & Bassler, 1930 with both species described from the Mediterranean and often synonymized with *F. verrucosa* (see Harmelin, 1976, and references therein).

Conclusions

Since 2016, the Mediterranean bryozoan fauna has shown an increase in the number of families (93 to 99), genera (212 to 219) and species (556 to 588) owing to the description of new species, the dismantle of species complexes, the re-examination of previous records of widespread species, and first records including non-indigenous species. With 588 species, the Mediterranean bryozoan diversity is equivalent to 63%, 45%, and 46% of Europe, Greater Australia, and Zealandian bryozoan diversities, respectively, as reported in Gordon *et al.* (2019, table 2), which also include species undescribed or of uncertain status. Compared to the present-day global bryozoan diversity, from data provided in bryozoa.net (accessed 24.03.2023) and Bock & Gordon (2013), Mediterranean bryozoan diversity accounts for slightly more than 9.1%, revealing a slight decline when compared with previous figures of ca 9.4–9.6% (see Rosso & Di Martino, 2016). This change could be relevant to the total number of bryozoan species described from the Mediterranean and globally in the last years. Focusing on the years 2015–2023, 39 new species were described from the basin, representing only 8.1% of the species described globally in the same time span. This decline in the descriptions of species from the Mediterranean compared with other geographical areas (Fig. 3) might be related to the knowledge already obtained for this basin due to past investigation efforts and its limited and well-defined boundaries. However, artifacts deriving from the limited period of time under consideration and the low number of bryozoan taxonomists cannot be ruled out.

The increase in the number of newly described species from the Mediterranean and globally is, however, decidedly higher than those expected after the predictions by Pagès-Escollà *et al.* (2020). Based on the marine bryozoan data obtained by 2014, these authors estimated a global increase of 780 and 1350 species by 2050 and 2100, respectively. Data obtained by early 2023 (extracted from bryozoa.net) indicate that in a very restricted time span (ca 8 years), 443 new species have been described globally, accounting for about 57% of the number of new species expected by 2050 and 33% of new species expected

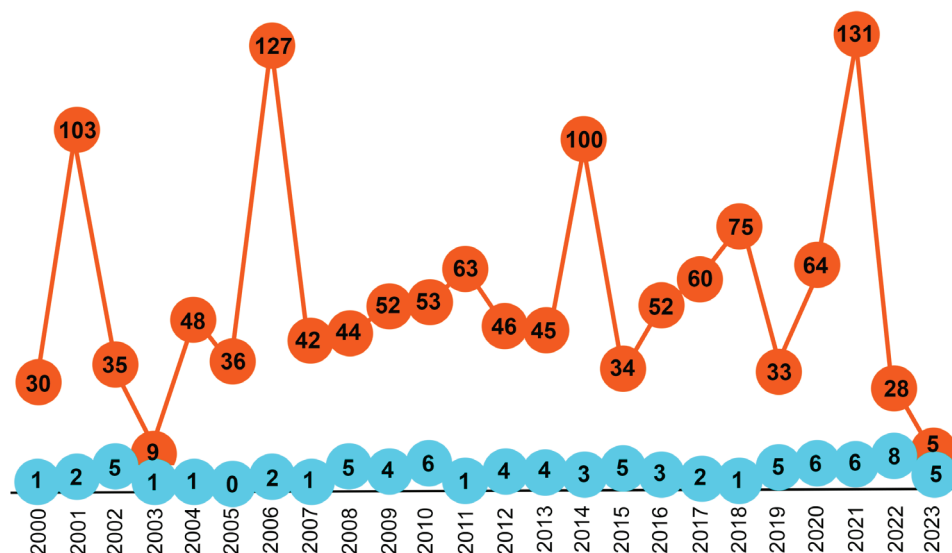


Fig. 3: Plot showing the number of new bryozoan species described per year from the Mediterranean only (blue dots) and globally (red dots), including the Mediterranean, since 2000.

by 2100. Considering that Mediterranean bryozoans represent *ca* 9% of the global biodiversity, the 39 newly described species since 2015 represent a large amount of the expected increase of *ca* 70 and 121 species for 2050 and 2100, respectively. Consequently, the reported data might be underestimated. Assuming that the rate of the description of new species will remain unchanged for some time and may even reduce over the years, we need to revise the projections taking into consideration the possible range of 8,700–11,100 extant bryozoan species postulated by Appeltans *et al.* (2012).

A possible increase in research effort might also be necessary to improve our biodiversity knowledge at local and global scale. This necessity was indicated by a number of recent publications providing first and/or updated lists of species from several geographical areas worldwide, such as the Falklands and South Georgia Islands (Figuerola *et al.*, 2017), Scotland (Rouse *et al.*, 2018), Ireland (Kelso-Maguire, 2020), Greenland (Denisenko & Blicher, 2021), and deep-water environments of New Zealand (Gordon, 2021). In fact, regularly updated faunal checklists are essential tools to monitor biodiversity changes, identify the mechanisms driving variations, including ecological and biogeographical patterns, and plan suitable conservation.

In this respect, modern and historical museum collections, the latter preserving historical biodiversity, as well as taxonomic expertise, are fundamental to raising the awareness of bryozoan biodiversity among the general public as well as governmental agencies and stakeholders involved in the management of natural resources.

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Supplementary Material

The following supplementary information is available online for the article:

Appendix 1

List of bryozoan species reported as living in the Mediterranean Sea (updated at 24.05.2023). As in Rosso & Di Martino (2016), we maintained taxa that were described/figured though not formalized when clearly distinct from established species (e.g., *Stomatopora* sp. *sensu* Harmelin, 1976; *Hippopodina* sp. A in Ullman *et al.*, 2017), and stipulated genera but undetermined species (e.g., *Annectocyma* sp.) when the taxon represented the unique occurrence of the genus. In the column "Status" it is indicated if the species is considered as being non-indigenous for the Mediterranean (NIB) or cryptogenic (CRY). An asterisk is added for some species, reported as NIB in Rosso & Di Martino (2016) and references therein, but not included in Ferrario *et al.* (2018), which follows more restrictive criteria for NIB status assessment (see also Materials and Methods). ? = species for which the NIB status is uncertain.