



Biogeographic patterns in sea pens (Octocorallia: Pennatulacea)

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Abstract

Pennatulaceans (Octocorallia: Pennatulacea) are among the most dominant octocoral species living in soft bottom communities. Some of them are cosmopolitan and have been recorded in all seas and oceans of the world, from shallow waters up to about 6260 m deep. In the present study, we try to find answers to questions about the biogeographical distribution of sea pens including most recently described species. We also evaluate the diversity and faunistic affinities among pennatulaceans of the world's oceans, and determine the degree of faunistic isolation of the Mediterranean Sea from the Atlantic. Finally, we return to the old debate about the hypothetical oldest diversification center of sea pen lineages.

Keywords Zoogeographic composition · Bathymetry · Ecoregions · Mediterranean Sea · Endemism · Cosmopolitanism

Introduction

The unexplored portions of the deeper ocean zones are so vast that the description of their faunas, such as those constituted by benthic suspension feeders, is far from being completed (Fabricius and Alderslade 2001; Emig and Geistdoerfer 2004; UNEP 2006). Nevertheless, current knowledge about the distribution patterns of some of their faunistic groupings is sufficient to sketch their biogeographic affinities (Soto Ángel and Peña Cantero 2017).

The pattern of deep cold-water movement is largely determined by the sea floor topography (Smith and Sandwell 1997; Gille et al. 2004). The circulation of deep-water currents is driven by differences in density related to temperature and salinity (Rudels and Quadfasel 1991; Rahmstorf 2002; Jungclaus et al. 2005). Most of the north Atlantic deep water originally come from the northern seas and flow toward the south (Rudels and Quadfasel 1991; Bersch 1995; Davies et al. 2001). This continuous flow from north to south (as occurs in

the NE Atlantic or NE Pacific) or vice versa (as with the West Australian current) (Cenedese and Gordon 2021) could be behind certain faunistic relationships between areas affected by these currents.

In this scenario, the topographical isolation of certain marine areas such as the Mediterranean Sea, derived from the bottleneck imposed by the Strait of Gibraltar or the closure of Trans-Tethyan corridor (Rögl 1997), could act as a dead end of these large currents, giving rise faunistic isolation (Almaça 1985; Almada et al. 2001).

Other isolated marine areas, such as the Arctic and Antarctic regions could hypothetically also function as biogeographic “islands,” since they are partially isolated by the Arctic current and the Antarctic Circumpolar Current, respectively (Cenedese and Gordon 2021). Equally, large oceanic areas affected by the same large currents, such as the Indo-Pacific or the South Atlantic regions, could result in a high degree of relationship between the species that inhabit them (Vinogradova 1979; Potts 1983; Bachraty et al. 2009). Some studies based on extinct faunistic affinities have documented the colonization of the Mediterranean deep-sea beds by benthic organisms through the Strait of Gibraltar from deep waters of the NE Atlantic Ocean, supporting the relationship between these two contiguous marine areas (Chimienti et al. 2019b).

In some cases, the study of faunistic affinities can be biased by the consideration of wide distribution patterns attributed to some taxa that are often considered cosmopolitan (Pérez et al. 2016), which may depend on the distribution of only one species belonging to such taxa (Darwin 1872). In other words,

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this concept of cosmopolitanism should be revisited, since morphospecies previously considered as widely distributed, such as *Pennatula phosphorea*, have been suggested to be species complexes by recent molecular studies (García-Cárdenas et al. 2019). Thus, a cosmopolitan genus should be understood by the presence of its species in different biogeographic areas worldwide, including in most cases at least one polar region (Klautau et al. 1999; Zeppilli et al. 2011).

A given wide distribution (e.g., cosmopolitan) could be a consequence of physical factors resulting from changes in past environmental processes, such as the movements of continents that enabled or isolated certain seas and oceans (Valentine and Moores 1972; Rögl 1997; Barnes et al. 2006; van Baak et al. 2016), or the formation of large deep currents (Steele et al. 1962; Hamilton 1990). But it could also be enhanced by biological traits exhibited by the species themselves, especially those related to locomotion or mobility (Hickson 1909; Musgrave 1909; Kastendiek 1976). On the other hand, the wide distribution attributed to certain species or genera could also be an artefact resulting from misidentifications, including species that are morphologically similar but phylogenetically different. These cases could appear to be more common than expected based on recent molecular phylogenetic analyses (García-Cárdenas et al. 2019; López-González and Drewery 2022).

On the contrary, a restricted distribution (e.g., endemism) may be the result of a specific adaptation, a drastic reduction of populations (relict species), or a biased sampling effort (Leão and Kikuchi 2005; Pérez et al. 2016). Regarding the octocoral fauna, for example, there are several areas that show a high level of endemism, such as Antarctica, South Africa, Brazil, and the Gulf of Mexico (Williams 2011; Pérez et al. 2016).

Most of the few putative cosmopolitan octocoral species have been found in the order Pennatulacea (Pérez et al. 2016). They may occur in a wide bathymetrical range, from shallow waters up to about 6260 m deep (Williams 2011, 2021; Williams et al. 2014). Among sea pens, the best-known genera are currently considered to have a circumglobal distribution, such as *Anthoptilum*, *Distichoptilum*, *Funiculina*, *Balticina*, *Kophobelemnion*, *Pennatula*, *Umbellula*, and *Virgularia* (Williams 2011).

Nowadays, the Order Pennatulacea contains more than 200 accepted species, distributed over 41 genera and 16 families (Williams 2015, 2017; García-Cárdenas et al. 2019; López-González and Drewery 2022). Pennatulacean species have colonized many benthic marine environments (such as intertidal sand, mud flats, and sandy areas) and present a unique muscular peduncle for anchoring in these soft sediments. One of the characteristics of having this peduncle is the primary establishment of a weak attachment to the substrate, enabling these colonies to detach later on and to remain adrift for some time (Hickson 1909; Musgrave 1909). The combination of initial attachment in juvenile stage and mobility in an adult

free-living stage is also seen in some free-living mushroom corals that can inflate soft body parts (Abe 1939; Hubbard 1972; Bongaerts et al. 2012; Hoeksema and Bongaerts 2016). This is perhaps also the case in inflatable solitary deep-sea corals, such as some species of Micrabaciidae (Williams 1986; Cairns 2002). This non-common biological trait along with the production of lecithotrophic larvae capable of surviving up to 30 days and travelling long distances helped by dominant current systems (Chia and Crawford 1973; Tyler et al. 1995) might favor dispersal and range expansion of these species. In addition to these biological traits, a recently published analysis of divergence time suggested that despite the fact that pennatulaceans are one of the most specialized octocoral groups, they have an early origin since the Lower Cretaceous, ~144 Ma ago (García-Cárdenas et al. 2020; Goedert et al. 2022). This long period of existence (coupled with the mobility outlined above) could be interpreted as a sufficiently long period of time to achieve an extensive diversification and wide biogeographical distribution ranges. As suggested by Williams (2011), this dispersal potential is undoubtedly of fundamental importance regarding patterns of restricted vs. widespread geographic ranges.

Despite the fact that pennatulaceans are well-known (Ellis 1764; Kölliker 1869; Kükenthal 1915), only few contributions have dealt with their global distribution patterns around the world by highlighting previous attempts to understand the geographic distribution of sea pens (Williams 1992) and localized biogeographic contributions (Murillo et al. 2016; Ruiz-Pico et al. 2017; Bastari et al. 2018). Williams (2011) reviewed the global diversity and distribution of the Order Pennatulacea, summarizing the knowledge that has emerged in past decades.

The architecture of the colonies and the form of their anchorage within the substrate mean that pennatulaceans are directly affected by deep oceanic currents (Williams 2011). As result, associating dispersal capabilities of these species with the nature of environmental changes (such as currents) could provide relevant information on the distribution of these benthic communities.

The aim of the present study is (1) to offer an update of the global biogeographic distribution of the Order Pennatulacea, including the most recently described genera and species; (2) to explore the faunistic composition of pennatulaceans across various marine ecoregions; and (3) to identify diversity hot spots, also considering bathymetric zonation. Finally, some observations have been made on where the oldest centre of diversification of the Pennatulacea lineage, could be located.

Materials and methods

A comprehensive review of the literature concerning records of the current pennatulacean species at a global level

(including original descriptions and other documents that provided useful taxonomic reviews, comments, and additional information on the distribution of the species, as well databases such as WoRMS portal (2022)) has been carried out in order to create a complete sea pen species presence/absence data matrix of marine ecoregions of the world (see below).

The criteria employed for the elaboration of this matrix aim to minimize the bias inherent in the comparison of results from different sources (Carver 1991). We excluded from the matrix all materials not identified at species level, as well as those concerning doubtful identifications or specimens tentatively assigned to a species without strong confidence by the author (see Discussion). Additionally, we updated the distributional information of each taxon based on the most recent findings (e.g., Li et al. 2021; López-González and Drewery 2022).

Ecoregions and bathymetric zonation

The delimitation of the ecoregions was provided by Spalding et al. (2007), as Marine Ecoregions of the World (MEoW) with some modifications (Fig. 1): the area corresponding to the North Atlantic was subdivided into western, eastern, temperate, and tropical regions in order to more clearly reflect the degree of relationship or isolation, as it is one of the areas more intensively studied since the 18th century. Therefore, mainly according to Spalding et al. (2007), the following 16 ecoregions were considered (Fig. 1): AR, Arctic region; NES,

Northern European Seas; LU, Lusitanian; ME, Mediterranean Sea (including the Black Sea); NWA, Northwest Atlantic (including cold and warm temperate Northwest Atlantic); NP, Temperate North Pacific (including cold and warm temperate Northwest and Northeast Pacific); TWA, Tropical Western Atlantic (including tropical Northwestern Atlantic and North Brazil Shelf); TEA, Tropical Eastern Atlantic; TSAM, Temperate South America; TEP, Tropical Eastern Pacific; EIP, East Indo-Pacific; TSA, Temperate Southern Africa; WIP, Indo-Western Pacific; CIP, Indo-Central Pacific; TA, Temperate Australasia; and SO, Southern Ocean (including the Antarctic region).

In this study, the bathymetric comparisons used the bathymetric zonation proposed for sea pens by Williams (2011). These bathymetric zones were 0–400 m (shelf, S), 400–2000 m (bathyal, B), and 2000–6000 m (abyssal, A). Additional comparisons according to the number of species from each bathymetric zonation were also explored.

Richness and distribution of sea pen genera and species

As a preliminary approach, the richness of genera and species for each ecoregion and bathymetric zone was calculated (Clarke and Warwick 1998; Magurran 2004), followed by a comparative approach between ecoregions (and bathymetric zones) covering larger geographical areas.

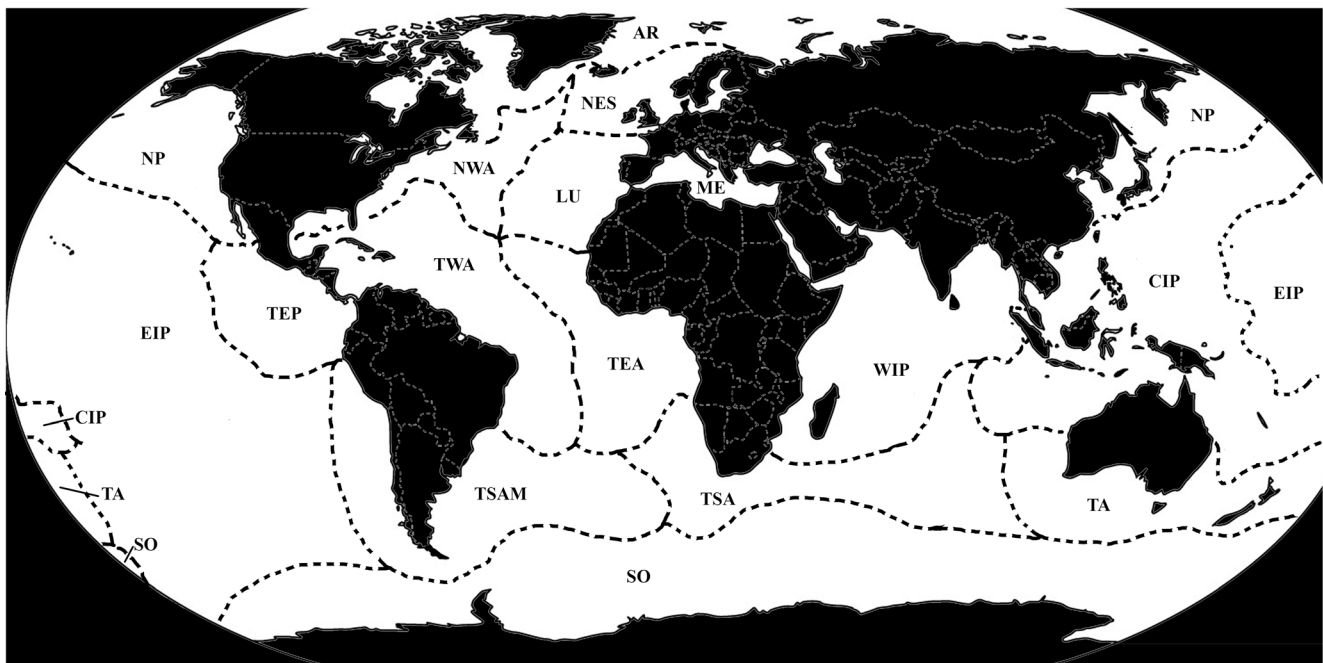


Fig. 1 Biogeographic ecoregions considered in this study: AR, arctic region; NES, Northern Seas of Europe; LU, Lusitania; ME, Mediterranean Sea; NWA, Northwest Atlantic; NP, Temperate North Pacific; TWA, Tropical Western Atlantic; TEA, Tropical Eastern Atlantic; TSAM, Temperate South America; TEP, Tropical Eastern

Pacific; EIP, East Indo-Pacific; TSA, Temperate Southern Africa; WIP, Indo-Western Pacific; CIP, Indo-Central Pacific; TA, Temperate Australasia; and SO, Southern Ocean. The black dashed lines represent the theoretical boundaries between regions. Adapted from Spalding et al. (2007)

In this study, two comparative perspectives were considered: the faunistic composition analysis for each ecoregion considering the zoogeographic distribution category assigned to each sea pen species according to its known geographical distribution (Medel and López-González 1996, 1998); and the analysis of the faunistic affinity between ecoregions based on the geographic and bathymetric known distribution of pennatulacean species.

Faunistic composition

The faunistic composition study (or zoogeographic affinities) was based on assigning a zoogeographic category to each sea pen species according to the ecoregions in which it has been reported (Medel and López-González 1996, 1998), and these are grouped into four large classes (Table S1), following some considerations summarized by Williams (2011): (1) endemism, when the species is only present in a single ecoregion (e.g., if a species is only recorded from the Mediterranean Sea, this endemism was abbreviated as ME); (2) wide distribution (WD), when the species is present in two or more ecoregions within one or more oceans (e.g., a wide distribution in the Atlantic ocean, abbreviated as WDA, could include combinations of the ecoregions such as NES, LU, ME, TEA, and TSA); (3) cosmopolitanism (CO), when the putative species is recorded in all or almost all oceans including in most cases at least one polar region (for example, a species mentioned in a combination of the distant ecoregions such as NES, LU, ME, NWA, NP, TSA, WIP, and TA, was considered cosmopolitan); (4) other Distribution, a species was considered within the category “other distribution” when, while being present in more than one ecoregion, it has not been included in any of the previous categories (Table S1). The zoogeographic categories were linked to the ecoregions in a new matrix, whose analysis determined the number and percentage of endemism, wide distribution, cosmopolitanism, and other distributions for each ecoregion.

Faunistic affinity

The presence/absence data matrix (Table S2) was used to obtain a similarity matrix (triangular matrix) between ecoregion + bathymetry using the Sørensen similarity index (Sørensen 1948; Demey et al. 2011; Soto Ángel and Peña Cantero 2017). A cluster analysis (hierarchical agglomerative linkage by group average) was performed in order to determine possible groupings among ecoregions. The following Simprof parameters were used: 10000 permutations for mean profile, 10000 simulation permutations, and 5% significance level (Clarke and Warwick 1994). The resulting relationships were represented by a dendrogram.

Affinity between genera based on geographic and bathymetric distribution

Finally, a distribution data matrix was condensed at genus level and transposed in order to reflect the genera as variable parameters. The analyses between variables using the Sørensen similarity index resulted in a triangular matrix that was clustered to try to detect groups of genera with similar geographic and bathymetric distributions. Statistical analyses were performed using the software packages PRIMER 6 (v.6.1.6) (Clarke and Gorley 2006) and PAST (v 3.21) (Hammer et al. 2001).

Results

A total of 220 pennatulacean species distributed over 41 genera and 16 families were used in the present biogeographic study over the above listed ecoregions (Table S2). It is necessary to point out that the description of geographic and bathymetric patterns at the family level will not be considered, since the systematics of sea pens is currently under review and our possible comments or conclusions would be of little use in this regard (see also the “Discussion” section).

Richness and distribution of sea pens

The most speciose genus was *Pteroeides* (29 spp.), followed by *Virgularia* (18 spp.), *Cavernularia* (15 spp.), *Stylatula* (11 spp.), *Lituaria* (10 spp.), and *Pennatula* (10 spp.) (Table S3). A quite unequal species richness between genera is recognized when half of the known genera (in this case 20 out of 41 or 48%) included just 36 species (~16%, a mean 1.8 spp. per genus), while only six genera (~15% of the total) included almost half of the described species (~43%, a mean of 15.6 spp. per genus) (Table S3). This unequal distribution of species in the different genera necessitates the treatment of geographical and bathymetric data distributions from both perspectives.

Ecoregions and bathymetric distribution of genera

Sea pen genera were present in all ecoregions considered (see Fig. 2, Table S2). The ecoregions with the highest number of genera observed (>20 genera) were CIP (22 genera), NP (22 genera), and WIP (21 genera), while those with the lowest values (<10 genera) were TSAM (4 genera), AR (6 genera), TEP (6 genera), SO (6 genera), EIP (7 genera), and ME (9 genera) (Fig. 2a). Considering the bathymetric distribution within each ecoregion (as a percentage of the total), we observed that ecoregions with the highest number of genera mainly showed a shallow

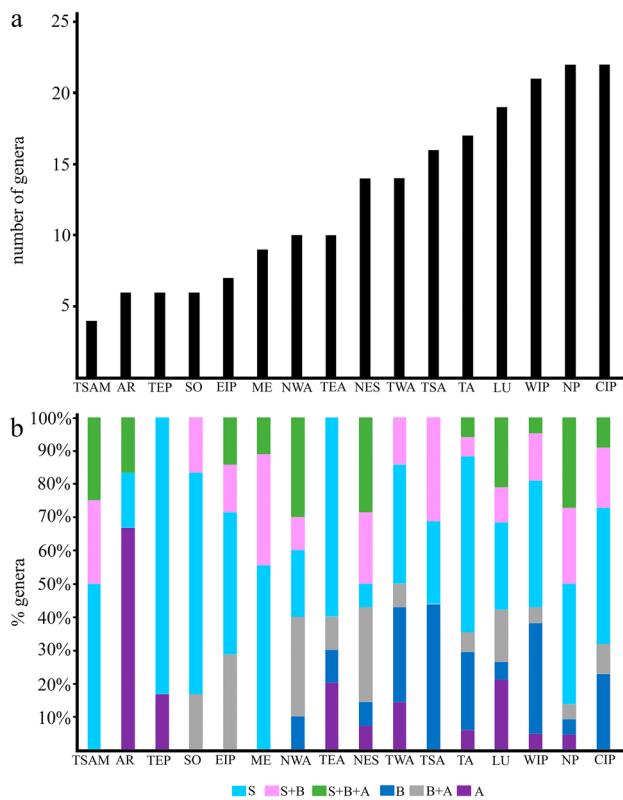


Fig. 2 Ecoregions and bathymetry distribution of sea pen genera, **a** ecoregions ordered according to the number of genera they contain; **b** comparative proportion of genera abundance (in percentages) over bathymetric categories in each ecoregion. Categories: S shelf (<400 m), B bathyal (400–2000 m), A abyssal (2000–6000 m). Abbreviation as in Fig. 1

water distribution (S), followed by bathyal (B) and bathyal+abyssal (B+A) distributions. Ecoregions with the lowest values also predominantly showed a shallow water (S) distribution (Fig. 2b).

The comparisons within each bathymetric range showed that the ecoregions with the highest values of shallow-water genera (<400 m) were NP (19 genera) and CIP (15 genera), while those with the lowest values (< 5 genera) were TSAM and AR with four and two genera, respectively (Fig. 3a). At bathyal depths (400–2000 m), ecoregions CIP and NP had the highest values (>12 genera), while ecoregions with the lowest values were AR, TSAM, SO, and TEA (<4 genera) (Fig. 3b). The only ecoregion without any bathyal genus was TEP. Finally, the ecoregions with the highest values in abyssal bathymetry (2000–6000 m) were LU and NES (>8 genera), while TSAM, TEP, SO, and ME were the ecoregions with the lowest values (one genus each). The only ecoregion without any abyssal genus was the TSA (Fig. 3c).

Regarding the global bathymetric distribution of the different genera (Table S3), in the three most speciose genera, the shallow water component is dominant. In *Pteroeides*, 100% of the species have an exclusive shelf distribution, as do species of *Virgularia* and *Cavernularia* with 94%

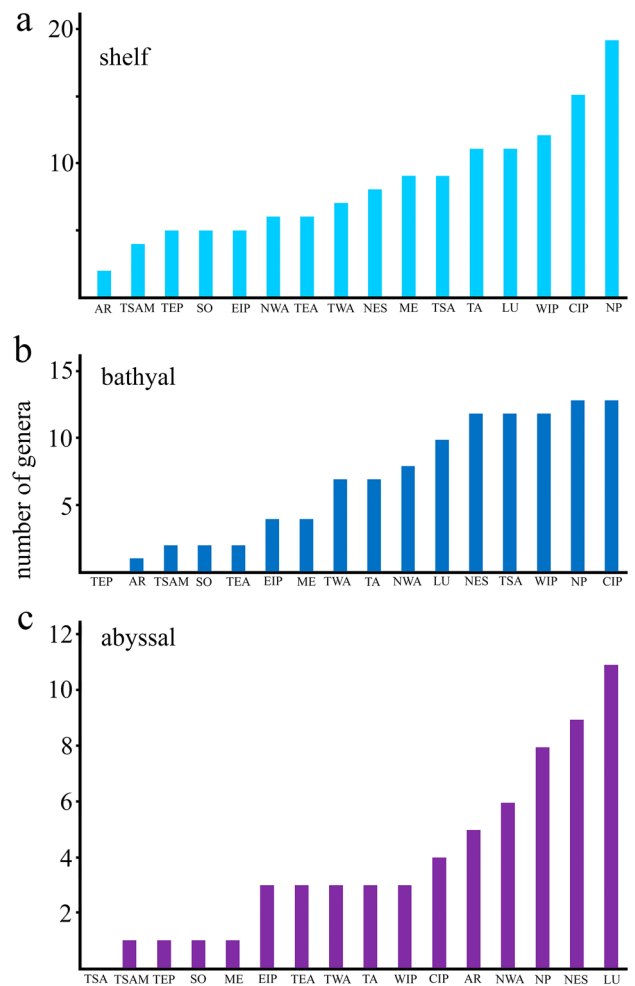


Fig. 3 Genus diversity in each ecoregion and bathymetric level, **a** shelf; **b** bathyal; and **c** abyssal. Ecoregions are ordered according to their genera richness. Abbreviation as in Fig. 1

and 100%, respectively. The genera *Lituarina* (10 spp.), *Veretillum* (6 spp.), *Sarcoptilus* (5 spp.), *Cavernulina* (3 spp.), *Crassophyllum* (2 spp.), *Grasshoffia* (2 spp.), *Malacobelemnion* (2 spp.) *Actinoptilum* (1 sp.), *Amphibelemnion* (1 sp.), and *Gilibelemnion* (1 sp.) show a distribution that is restricted to the continental shelf. Four genera (of just one or two species) have exclusively been reported from the bathyal zones: *Alloptilella*, *Amphiacme*, *Chunella* and *Scytaliopsis*. The genera *Porcupinella* (2 spp.) and *Scleroptilum* (1 sp.) are exclusively abyssal. The genera *Pennatula*, *Kophobelemnion*, *Umbellula*, *Protoptilum*, *Balticina*, *Anthoptilum*, *Ptilella*, *Funiculina*, and *Gyrophyllum* include at least one species reported from the complete bathymetric distribution (S+B+A).

Ecoregions and bathymetric distribution of species

Sea pen species were present in all ecoregions (see Fig. 4, Table S2). The ecoregions with the highest number of

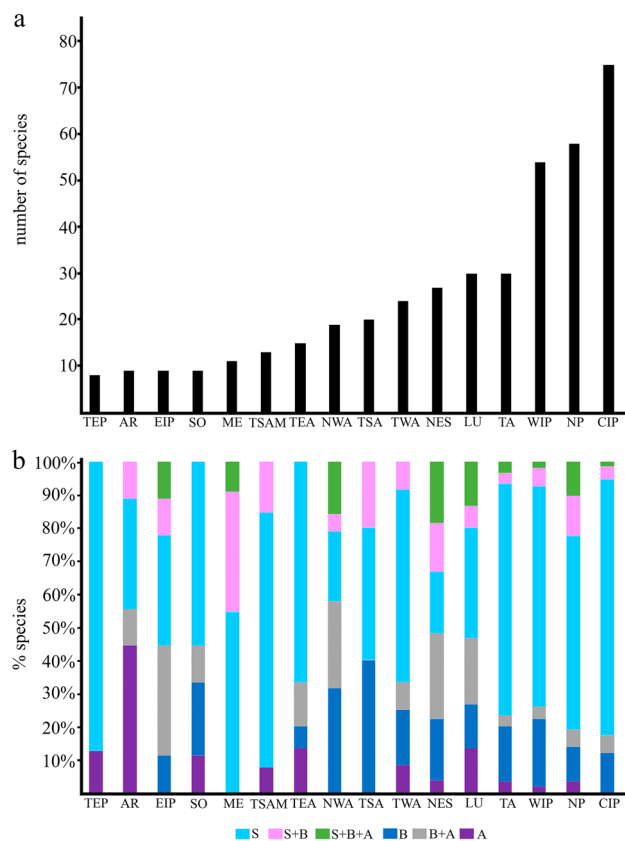


Fig. 4 Ecoregions and bathymetry distribution of sea pen species, **a** ecoregions ordered according to the number of species they contain; **b** comparative proportion of species abundance (in percentages) over bathymetric categories in each ecoregion. Categories: S shelf (<400 m), B bathyal (400–2000 m), A abyssal (2000–6000 m). Abbreviation as in Fig. 1

species (>50 spp. each) were CIP (75 spp.), NP (58 spp.), and WIP (54 spp.), while those with the lowest values (<10 spp.) were TEP (8 spp.), AR (9 spp.), EIP (9 spp.), and SO (9 spp.) (Fig. 4a). Among the three most speciose ecoregions of these, the commonest bathymetric range was shelf-exclusive (S), followed distantly by bathyal (B) and bathyal-abyssal (B+A) (Fig. 4b), while less speciose ecoregions showed their species distributed in a lower number of bathymetric zones [either exclusive (S, B, A) or concatenated (e.g. S+B or B+A)], being mainly dominated by shelf-dwelling species (S) (Fig. 4b).

Comparisons between ecoregions within the same bathymetric range (Fig. 5) revealed that 1) the three most speciose ecoregions at shelf zone (>35 spp.) are CIP (62 spp.), NP (47 spp.), and WIP (40 spp.), contrary to what was observed in AR, EIP, and SO (<6 spp.) (Fig. 5a); 2) considering only the bathyal zone, the ecoregions with the highest number of species (>20 spp.) were NP (22 spp.) and NES (21 spp.), while AR, TSAM, SO, and TEA are those with the lowest values (<5 spp.) (Fig. 5b), only TEP

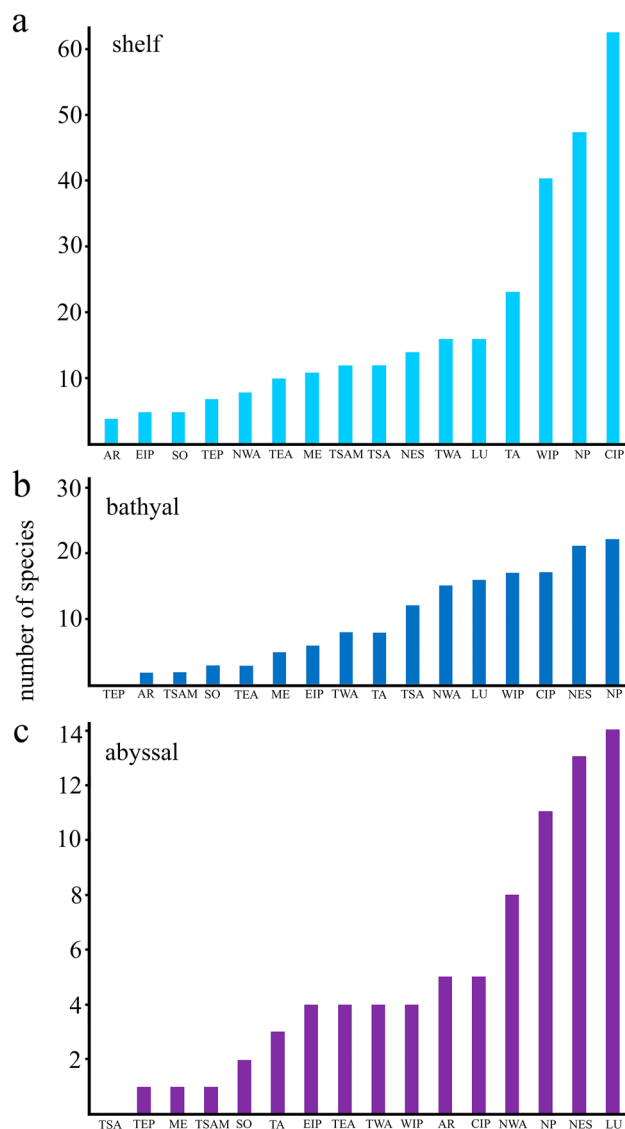


Fig. 5 Species richness in each ecoregion and bathymetric level, **a** shelf; **b** bathyal; **c** abyssal. Note that ecoregions are ordered according to their species richness. Abbreviation as in Fig. 1

did not have bathyal species; and 3) finally, in the abyssal zone, the three more speciose ecoregions (>10 spp.) are LU (14 spp.), NES (13 spp.), and NP (11 spp.), only TSA did not have abyssal species, while TEP, ME, and TSAM had just one species each (Fig. 5c).

Overall, the number of pennatulacean species was clearly higher on the continental shelf (179 spp., 148 of them exclusive) than bathyal (64 spp., 25 exclusive) and abyssal (29 spp., 8 exclusive). Regarding wider bathymetric distributions, 18 spp. showed a wide bathymetric range at 0–2000 m (S+B); 8 spp. was recorded between 400–6000 m (B+A); and 13 species have been recorded from all bathymetric zones (S+B+A) (Tables S2, S3).

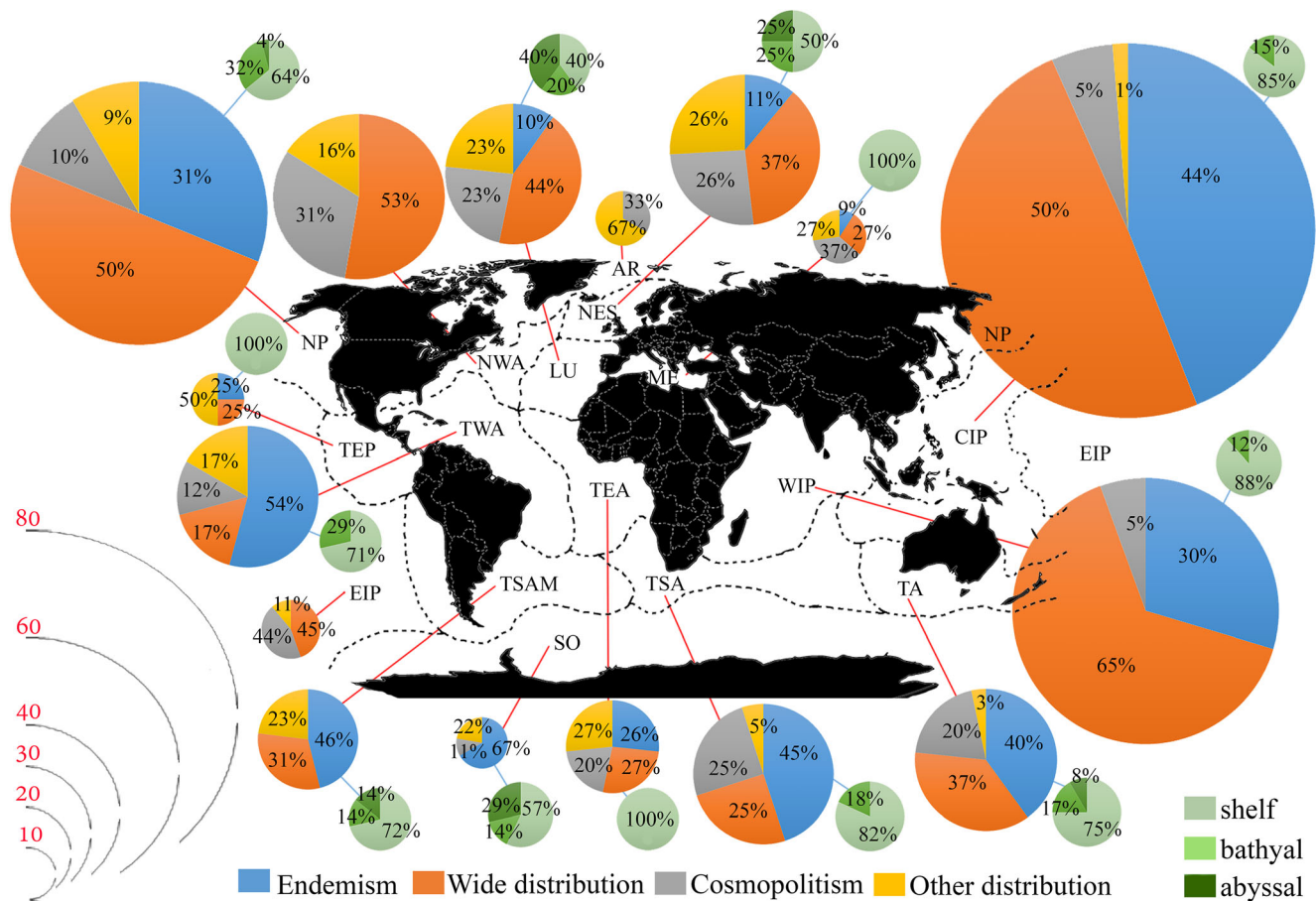


Fig. 6 Faunistic composition in the ecoregions considered in this study. The diagrams represent the percentage of endemics (blue), wide distribution (orange), cosmopolitanism (gray), and other distribution (yellow) of each ecoregion. The size of each chart is proportional to the number of species in each ecoregion. For each endemism sector, the percentage for each bathymetric zone is indicated in a separate chart (in this last case the size of the chart is not proportional to the number of species)

Biogeographic analyses

Fauna composition

A total of 30 zoogeographic categories was considered according to possible geographic distribution of sea pen species over the a priori considered ecoregions, isolated or combined (Tables S1, S2).

Most ecoregions showed some endemic species (Fig. 6) except for Eastern Indo-Pacific (EIP), Northwestern Atlantic (NWA) and Arctic (AR). The highest percentage of endemism was found in Southern Oceans (SO, 67%), followed by Tropical Western Atlantic (TWA, 54%), Temperate South America (TSAM, 46%), Temperate Southern Africa (TSA, 45%), and Central Indo-Pacific (CIP, 44%). Semi-closed seas like the Mediterranean showed 9%, similar to the neighbouring Lusitanian (LU, 10%) and Northern European Seas (NES, 11%) ecoregions. Among most ecoregions with endemic species (12 out of 13) >50% of endemism inhabit the continental shelf, with 100% in TEA, TEP and ME (Fig. 6, Table S5).

All ecoregions except the Arctic and Southern Ocean had some species with wide distribution (Fig. 6). The highest percentages of wide distributions were found in Western Indo-Pacific (WIP, 65%), followed by Northwestern Atlantic (NWA, 53%), and North and Central Indo-Pacific (NP and CIP with, 50%). Neither the Arctic (AR) nor the Southern Ocean (SO) showed widely distributed species as defined here.

Most of the ecoregions showed some cases of cosmopolitanism (Fig. 6), except for Tropical Eastern Pacific (TEP) and Temperate South America (TSAM). The highest percentages of cosmopolitanism were found in the Eastern Indo-Pacific (EIP, 44%), followed by the Mediterranean Sea (ME, 37%),

Faunistic affinity among ecoregions

Overall, the cluster analysis on the species distribution over ecoregions using the Sørensen index (Fig. 7) showed

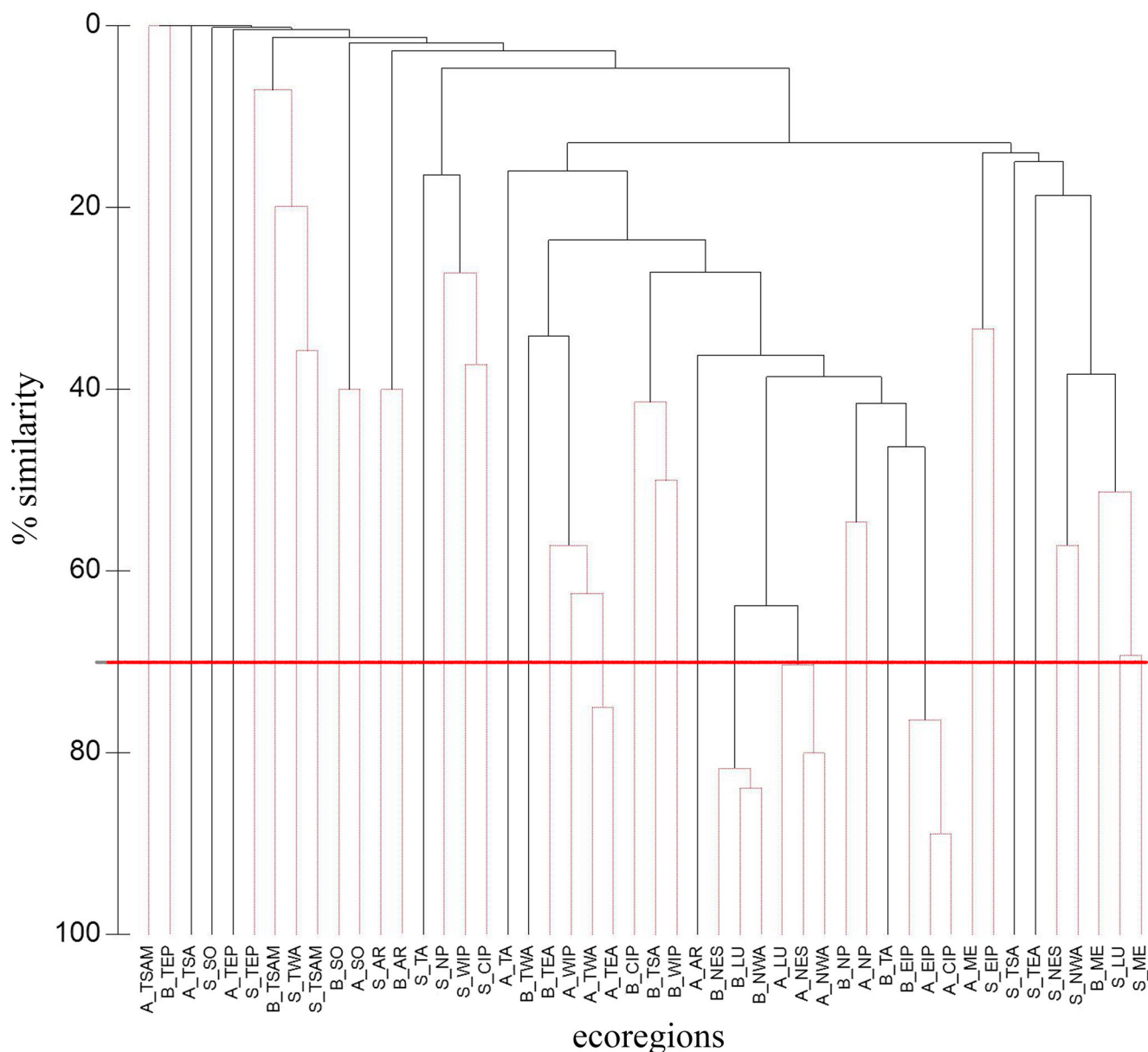


Fig. 7 Cluster analysis of the a priori considered ecoregions based on sea pen species distribution (Table S2) and Sørensen Similarity Index. Categories: S shelf (<400 m), B bathyal (400–2000 m), A abyssal (2000–6000 m). Abbreviation for ecoregions as in Fig. 1. The 70% of similarity is indicated

relatively poor grouping patterns (most relationships between 20% and 70% of similarity).

Under a similarity value of ~70%, some combinations of ecoregion-bathymetric zones were highlighted: (1) the Mediterranean (S_ME) and Lusitanian (S_LU) shelves (close to B_ME) sea pen faunas are quite similar, while their abyssal fauna (A_ME and A_LU) are shown to be different (see Discussion); (2) the shelves of Lusitanian, Mediterranean, Northwest Atlantic, and Northern European Seas (S_LU+S_ME and S_NWA+S_NES). For polar regions, the Arctic shelf (S_AR) and bathyal (B_AR), and the Southern Ocean bathyal (B_SO) and

abyssal (A_SO) faunas are grouped only under ~40% of similarity. The abyssal Arctic (A_AR) is widely separated from its shelf and bathyal zones, but close to the bathyal and abyssal zones of Northeastern ecoregions (NWA, LU and NES), while Southern Ocean deeper bathymetric zones (B_SO+A_SO) are grouped only under ~40% of similarity, far to the shelf zone (S_SO) (see the “Discussion” section) (Fig. 7).

On the other hand, the bathyal and abyssal zones of several ecoregions are shown to have a remarkable similarity, such as the deep zones of the Eastern and Central Indo-Pacific (A_EIP+A_CIP and B_EIP, >70% in

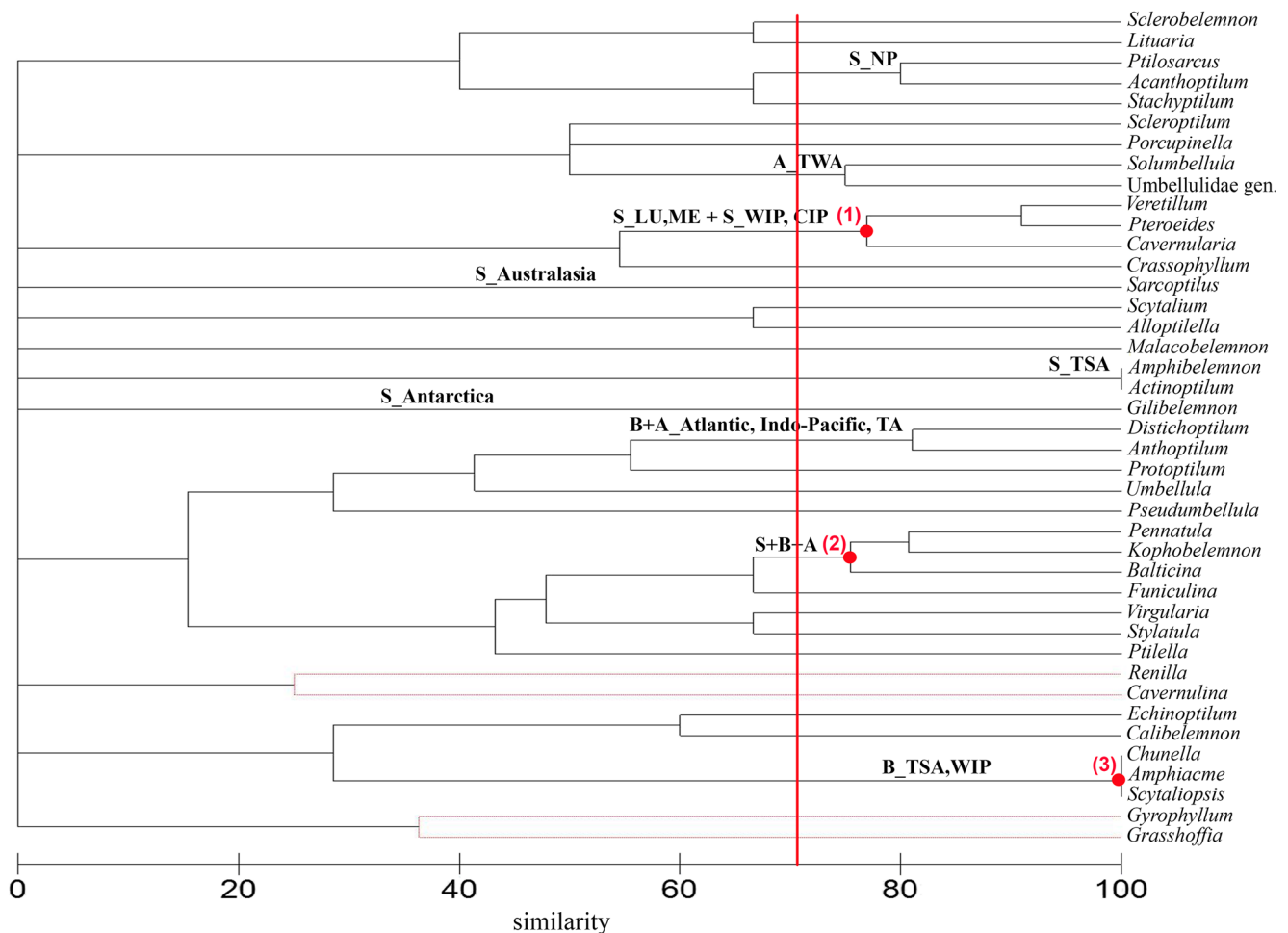


Fig. 8 Cluster analysis of sea pen genera according to their bathymetric distribution (Table S2) and Sørensen Similarity index and using all genera described. S shelf (<400 m), B bathyal (400–2000 m), A abyssal (2000–6000 m). Abbreviation for ecoregions as in Fig. 1. The 70% of similarity is indicated

similarity); the bathyal zones of the Northwestern Atlantic, the Lusitanian, and the Northern European Seas (B_NWA+B_LU+B_NES, >80% in similarity), close to their respective abyssal zones (A_NWA+A_LU+A_NES); the abyssal zones of the Tropical Eastern Atlantic and the Tropical Western Atlantic (A_TEA+A_TWA), close to the abyssal zone of the Western Indo-Pacific (A_WIP) and the bathyal zone of the Tropical Eastern Atlantic (B_TEA) (Fig. 7). These relationships observed in the dendrogram may be affected by a combination of regional or bathymetric originalities and identification of putative widely distributed taxa.

Affinity among genera based on geographic and bathymetric distribution

In a similar treatment as developed for the faunistic affinities, when geographic and bathymetric distributions of genera (based on the condensed species matrix) are

analysed, most of the groupings also showed low similarity (Fig. 8). However, to be in agreement with previous comparisons (see above), using a similarity cut-off of ~70%, the following groupings (> 2 genera) were highlighted: (1) *Veretillum*-*Pteroeides*-*Cavernularia* (sharing shelf of the Mediterranean and Lusitanian (S_ME+S_LU) and the Western and Central Indo-Pacific (S_WIP+S_CIP)); (2) *Pennatula*-*Kophobelemnon*-*Balticina* and *Funiculina* (sharing a wide bathymetric range in the North Atlantic (NES, LU, NWA), Pacific (NP) and Australasia (TA)); and (3) *Chunella*-*Amphiacme*-*Scytaliopsis* (sharing bathyal zones of the Tropical South Atlantic (TSA) and the Western Indo-Pacific (WIP)). In contrast, some genera were isolated (i.e., low affinity), corresponding in most cases to a restricted distribution of their species or monotypic genera (see Discussion). For example, the monospecific genus *Gilibelemnon* endemic to Antarctica, or *Sarcoptilus* endemic to Australasia.

Discussion

Biogeographic patterns

Biogeographic studies on sea pens involve a series of limitations when obtaining reliable datasets. These may be due to incomplete sampling efforts (geography or bathymetric limitations) (Marshall 1979; Williams 1992), or/and even some biological features inherent to these species, such as a patchy distribution (Birkeland 1974; Lopes et al. 2012; Ruiz-Pico et al. 2017) or a burial capacity under conditions of physical stress, such as the proximity of sampling gears (Pavans de Ceccatty and Buisson 1965; Levin et al. 1994; Chimienti et al. 2018; Ambroso et al. 2013, 2021). Another impediment for biogeographical studies arises from incomplete or imprecise source of information, especially noticeable in old described and reported materials (particularly those before the 1950s). At the time some species were erected based on a single specimen (e.g., Kölliker 1872; Broch 1910), and general terms used for locality data (e.g., “Atlantic,” “Pacific,” or “deep”) are relatively frequent (Kölliker 1869, 1872; Broch 1910; Kükenthal and Broch 1911; Kükenthal 1915).

Despite these limitations, the information obtained from biogeographic studies offers a wide approach concerning the distribution pattern, expanding our previous knowledge in detecting local to regional diversity hot-spots involving evolutionary or environmental management implications, or possible misidentifications for which specific studies should be addressed: [Allen and Sanders 1996 (protobranchs); Sibuet 1979 and Price et al. 1999 (asteroids); Monniot 1979 (tunicates); Watling and Auster 2005 (octocorals), Cairns and Chapman 2001 (scleractinians); Henry et al. 2008 (hydroids)].

Pennatulaceans have been found in all oceans, from polar to equatorial zones, and from shallow to great abyssal depths (Broch 1910; Kükenthal 1915; Williams 1995, 2011). Williams (2011) using a total of 35 genera and at least 203 valid species, suggested that approximately 54% of these genera have a widespread geographic distribution, the remaining 46% being geographically restricted (e.g., *Ptilosarcus* (W America, Pacific), *Gilibelemon* (Antarctica), *Porcupinella* (N Atlantic), *Sarcoptilus* (S Australia, Indo-Pacific), *Crassophyllum* (E Africa, N Atlantic-Mediterranean), *Amphibelemon* and *Actinoptilum* (S Africa, Atlantic-Indian), *Scytaliopsis* and *Amphiacme* (E Africa, Indo-Pacific)).

In the present study, the term “endemism” is considered in a more restrictive sense (only present in a single ecoregion) than the “geographically restricted” category used by Williams (2011). Despite this, some endemic genera in our study are in agreement with those geographically restricted genera considered by Williams (2011, Fig. 2). These were *Sarcoptilus* (5 spp., Australasia), the monotypic genera

Actinoptilum and *Amphibelemon* (Temperate Southern Africa), *Gilibelemon* (Southern Oceans, Antarctica), and *Ptilosarcus* (North Pacific) (Table S4). However, and according to the ecoregions here defined, the following genera would not fit our definition of endemism: the genus *Porcupinella* (2 spp.), its status having been modified because a new species has been recently described in the abyssal zone of the Tasman Sea (Australia) (see *P. tasmanica* in Williams 2021) adding the Tropical Eastern Atlantic to its previously known distribution in the abyssal zones of the North Atlantic (LU, NES) (see *Porcupinella profunda* in López-González and Williams 2011), and the genus *Crassophyllum*, because it has an endemic Mediterranean species (see *C. thessalonicae* in Vafidis and Koukouras 1991) but also another endemic species in the Tropical Eastern Atlantic ecoregion (see *Crassophyllum cristatum* in Tixier-Durivault 1961); the two monotypic genera *Scytaliopsis* and *Amphiacme*, because they are recorded in the Western Indo-Pacific (*Scytaliopsis djiboutiensis* and *Amphiacme abyssorum* see original descriptions) but also both species have been reported in the Temperate Southern Africa (see Williams 1995). As a result, the percentage of endemism would be ~12% of genera (5 endemic genera) and would occur mainly on the continental shelf (12 endemic spp., 11 on shelf, ~91%) (see below).

On the other hand, in our study, the percentage of cosmopolitan genera increased up to ~76% (61% wide distribution plus 15% cosmopolitan). In agreement with Williams (2011), the genera *Anthoptilum*, *Distichoptilum*, *Funiculina*, *Kophobelemon*, and *Pennatula* should still be considered cosmopolitan, adding also to *Virgularia* (since *V. mirabilis* is recorded from Arctic waters to Atlantic and Indo-Pacific waters and Australasia, see López-González et al. 2001, and Table S2). However, the assignment of the cosmopolitan category to a given genus because it has numerous species (each of which could be endemic to a given ecoregion) present in many of the ecoregions considered here is not the same as those cases in which the assignment of cosmopolitan status is derived from the presence of a species nowadays considered cosmopolitan. The latter type of cosmopolitanism occurs within the above listed genera (see *A. grandiflorum*, *D. gracile*, *K. stelliferum*, *F. quadrangularis*, *P. phosphorea*, and *V. mirabilis*). In this sense, it is likely that multiple records of a given species name (often type species of its respective genus) reported around the world could just be supported by morphological similarities rather than reliable genetic homogeneity, as was suggested, for example, for *Pennatula phosphorea* (García-Cárdenas et al. 2019).

Bathymetric zonation in sea pens

Regarding the vertical distribution, Williams (2011) represented the bathymetric distributions of pennatulacean genera according to an arbitrary demarcation between bathymetric

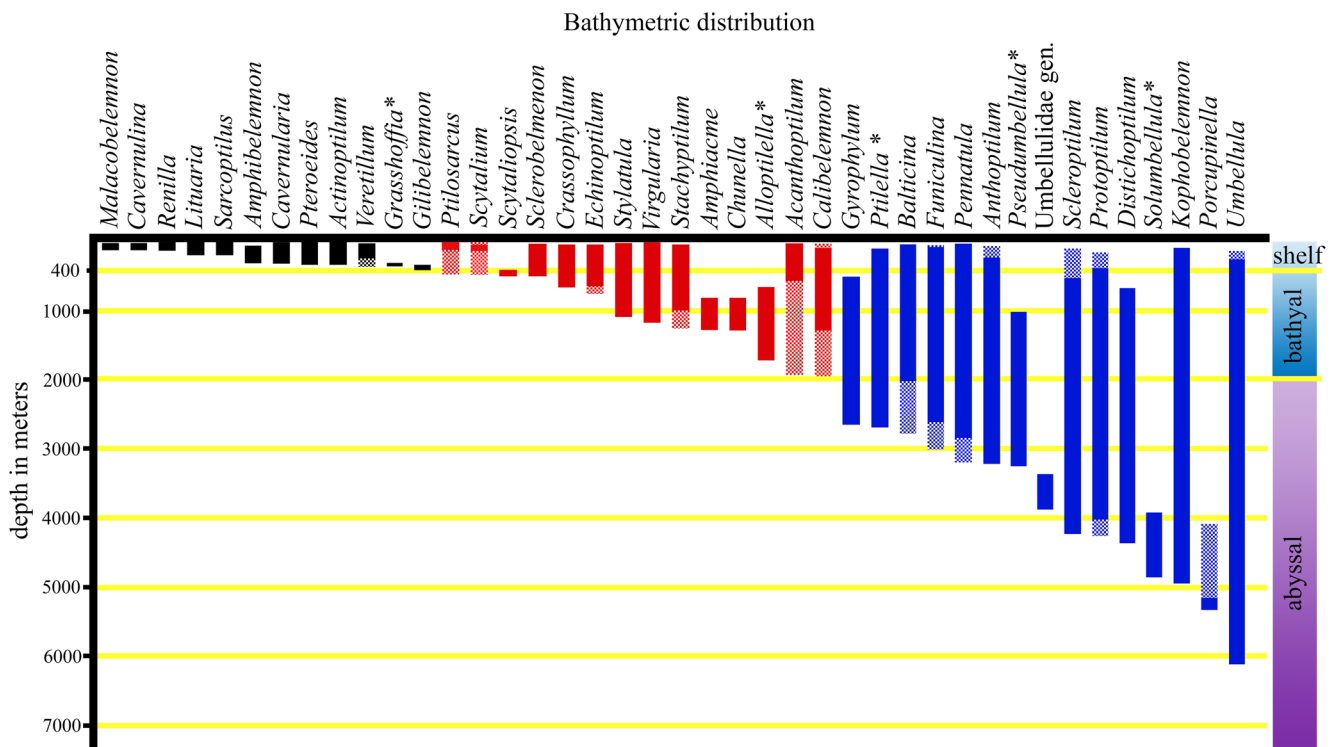


Fig. 9 Bathymetric distributions of known pennatulacean genera. shelf 0–400 m, bathyal 400–2000 m, and abyssal 2000–6000 m. * indicates genera described after Williams 2011. The dotted bar area represents a further improvement in the knowledge of genera distribution based on new records during the last decade

groups, such as shallow (<400 m), mid-range (400–1300m), and deep (>2000 m) (Williams 2011: Fig. 4). Following this bathymetric zonation, in the present contribution, we have updated this bathymetric information including the new species and genera described after Williams (2011) (Fig. 9).

Among the shallow-water sea pens (Fig. 9) shown by Williams (Williams 2011: Fig. 4), the following genera expanded their bathymetric range: the genus *Veretillum*, although most of its species are found <200 m depth on soft sediments (Gili and Pagès 1987; Williams 1990, 2011; López-González et al. 2001; Sardá et al. 2012), its type-species *V. cynomorium* was detected at an unusual depth of 372 m (Ruiz-Pico et al. 2017). Among the mid-depth range taxa (Fig. 9), the genus *Ptilosarcus* has expanded its range to between 16 and 475 m (Whitmire et al. 2017); *Scytalium* between 18 and 489 m (Li et al. 2021; López-González 2021); *Echinoptilum* between 50 and 750 m (Williams et al. 2014); *Stachyptilum* between 388 and 1244 m (Whitmire et al. 2017); *Acanthoptilum* between 5 and 1981 m (Whitmire et al. 2017); and *Calibelemon* between 30 and 1969 m (Kushida and Reimer 2020). Finally, the group of deeper species (Fig. 9) that have expanded their bathymetric range is the genus *Balticina* to between 46 and 2780 m (Whitmire et al. 2017); *Funiculina* between 20 and 3000 m (Williams et al. 2014; Ruiz-Pico et al. 2017; Whitmire et al. 2017); the genus *Pennatula* is found from shallow water to 3208 m according to the last records attributable to *P. murrayi* (see Dolan et al.

2013; Kushida and Reimer 2019); the genus *Anthoptilum* between 72 and 3651 m (Whitmire et al. 2017); the genus *Scleroptilum* has recently been found in shallow water to about 109 m (Whitmire et al. 2017); the genus *Protoptilum* between 150 and 4270 m (Mastrototaro et al. 2015; Whitmire et al. 2017); the distribution of the abyssal genus *Porcupinella* is corrected and expanded according to Williams (2021); the genus *Umbellula* slightly extends its bathymetric range when considering the shallowest bathymetric distribution of *U. encrinus* recently reported (Neves et al. 2015; Hamel et al. 2020). It is necessary to mention that the genera *Pennatula* and *Umbellula* require extensive revision work, so it will be necessary to update their species and bathymetric ranges.

Among the new pennatulacean genera described or resurrected (Fig. 9) since Williams (2011), the genus *Grasshoffia* is here included with a range of 318–333 m (see *G. profundica* in Williams 2017); the genus *Alloptilella* between 559 and 1733 m (Li et al. 2021; López-González 2022); the genus *Ptilella* has a bathymetric range between 90 and 2700 m, mainly due to the wide bathymetric distribution of *Ptilella grandis* (García-Cárdenas et al. 2019); *Pseudumbellula* between 1033 and 3282 m (Risaro et al. 2020; López-González and Drewery 2022); and, finally, the genus *Solumbellula* between 3910 and 4851 m.

Studies for other invertebrate taxa groups (e.g., isopods in Svavarsson et al. 1993; or hexacorals in Riemann-Zürneck

1998; among others) suggested bathymetric boundaries reflecting general faunistic changes from the edge of the shelf (200 m) to the abyssal zone (≥ 6000 m), with an intermediate limit around 3000 m, below which the appearance of species was more similar to deep (abyssal) species, with a pronounced decline in the number of species (Hansen 1975; Sibuet 1979; Billet 1991). However, as mentioned earlier, Williams (2011) used two intermediate limits (400 m and 2000 m) to define their bathymetric groups, showing a total of 27, 21, and 11 genera in each bathymetric range, respectively (Williams 2011: Fig. 4). In agreement with Williams (1992, 2011), the bathymetric distribution shown here fits better with this last bathymetric zonation (0–400m, 400–2000, 2000–6000 m depth) and supports a reduction in sea-pen diversity with increasing depth (Williams 1992, 2011; present study).

The absence of a global consistency in faunistic patterns would suggest that the processes that structure diversity with respect to bathymetry are probably different (Olabarria 2006). As a result, the processes that structure sea pen diversity at various depths can be different and may depend on the environmental particularities of each ecoregion. The current systems and environmental conditions of the continental shelves could be responsible for their isolation from their respective deep-sea bottoms, as well as for the little similarity found between the shelf zones of neighbouring ecoregions (Almada et al. 2001; Gille et al. 2004; Mortensen et al. 2008). This lack of connectivity could be behind the high degree of endemism that occurs on the continental shelf.

In our study, only in certain ecoregions (such as the Arctic Ocean and the Mediterranean Sea) an association between shelf and bathyal fauna (range 0–2000 m) can be observed. The Arctic abyssal zone (A_AR) was close to the Northeastern deeper ecoregions by the presence of two supposed cosmopolitan species (*Distichoptilum gracile* and *Kophobelemnon stelliferum*) and *Protoptilum denticulatum*; and the far position of the Mediterranean abyssal zone (A_ME) is characterized by the presence of the supposed cosmopolitan species *Kophobelemnon stelliferum*, reported in many different ecoregions and over the entire bathymetric range (Mastrototaro et al. 2013; Bastari et al. 2018; Pierdomenico et al. 2018; Chimienti et al. 2019a, b).

Tethys and Mediterranean sea-pen forms

The Mediterranean Sea is a young ecoregion, initially formed about 5.3 million years ago when a narrow strait opened to the Atlantic, flooding the Western basin, which was almost dry (Garcia-Castellanos et al. 2009; Sutton et al. 2017; Real et al. 2021). It can be considered that the colonization of the Mediterranean basin by Atlantic elements once the Strait of Gibraltar was opened after the Messiniense crisis (Loget and Van Den Driessche 2006) can be observed in the isolation of temperate-tropical elements today

considered endemic, such as the scleractinian *Astroides calycularis*, a monotypic scleractinian genus closely related to other tropical African genera of Dendrophylliidae (Zibrowius 1995; Goffredo et al. 2010) or the eastern Mediterranean sea pen *Crassophyllum thessalonicae* whose only existing congener, *Crassophyllum cristatum*, inhabits shallow-water bottoms of Guinea to Angola (Tixier-Durivault 1961; Vafidis and Koukouras 1991, Vafidis et al. 1994; Fryganiotis et al. 2011).

The biogeographic distribution of the three shallow-water genera *Veretillum*, *Pteroeides*, and *Cavernularia* appears to have relatively high similarity (Fig. 8). This relationship may be discussed in a hypothetical framework involving the ancient sea of Tethys (Rögl 1997; Hrbek and Meyer 2003; Bialik et al. 2019). Species of these three genera are present in the Mediterranean, Lusitanian, and the Tropical Eastern Atlantic from one side, as well as in the Central and Western Indo-Pacific (Williams 1989, 1995; Fu et al. 1999; Williams et al. 2012). These two water masses were connected by the Tethys until the “Trans-Tethyan-Trench-Corridor” was closed (~13 Ma ago) (Rögl 1997; Hrbek and Meyer 2003; Bialik et al. 2019). Thus, it is reasonable to assume that these genera (at least the morphological characters today recognized as these genera) were already present before the closure of Tethys, and subsequently evolved independently and diversified in different species in both main water bodies. Furthermore, as commented above, the closure of the Strait of Gibraltar and desiccation of the Mediterranean would potentially have eliminated these Tethys pennatulacean elements in the Mediterranean basin. The subsequent opening of the Strait of Gibraltar would give rise to the close relationship between the sea pen fauna of Mediterranean and nearby Atlantic regions (Sampaio et al. 2019; Chimienti et al. 2019a). However, the existence of related cnidarian taxa between the Northwestern Mediterranean (Gulf of Lion canyons) and the Southeastern Cantabrian Sea (Gulf of Biscay) may suggest that influence of the Paratethys connexions (throughout the north of the Iberian Peninsula) are still present, and that the possible Tethys relic fauna could have survived the Messiniense crisis near to main contributions associated with the most important rivers (Rögl 1997; Gili et al. 1998, 2000; Bitner et al. 2013; van Baak et al. 2016).

The oldest diversification centre of sea pen lineages

The first relevant studies considered the pennatulaceans as a group originating in deep waters, because most of the described species at the time were from the deep sea and structurally simpler, such as Funiculinidae and Kophobelemnidae, found in the European and North Atlantic seas (Kölliker 1869, 1872; Wilson 1883). Later authors, however, suggested a shallow-water origin (Koch 1878; Kükenthal and Broch 1911) and a posterior diversification to the depths (Hickson

1916, 1937). Their argument was mainly based on the fact that the structurally simpler (and supposedly more primitive) pennatulaceans (traditionally included in the family Veretillidae) were shallow-water species, constituting the earliest diverging taxa. Hickson (1916) stated that knowledge of the global pennatulacean fauna was still too imperfect to advance with certitude in the resolution of the possible origin of this particular octocoral group, although he suggested the Malay Archipelago as a potential candidate region.

Several decades later, following the suppositions expressed by Koch (1878), Kükenthal and Broch (1911), and Hickson (1916), a preliminary biogeographic and phylogenetic assessment of the shallow water Indo-Pacific pennatulacean fauna carried out by Williams (1992, 1994) postulated that the sea pens as a group initially differentiated in the shallow waters of tropical oceans (Indo-Pacific) and have subsequently diversified and dispersed to all depths of the temperate and polar regions, as well as the tropics. These shallow water pennatulaceans include veretillids (*Veretillum*, *Lituarina*, *Cavernularia*, and *Cavernulina*) and echinoptilids (*Echinoptilum* and *Actinoptilum*). However, over a decade later, the first molecular analyses (McFadden et al. 2006; Dolan et al. 2013) although without Veretillidae and Echinoptilidae, demonstrated that those structurally simplest morphologies needed to be analyzed. Then, Kushida and Reimer (2019) detected this matter in their phylogenetic analyses using those taxa for the first time. Later studies, in agreement with Kushida and Reimer (2019), discarded the traditional arguments that considered the structurally simplest morphologies (exemplified as veretillids) as the first diverging taxa, the available veretillid sequences being in a well-supported group, within the molecular clade I, close to *Pteroeides*, *Virgularia* or *Umbellula* species (García-Cardenas et al. 2020; López-González and Drewery 2022).

Today, after more than a century of expeditions and descriptions of dozens of new taxa, the geographic and bathymetric origin of sea pens remains an open question. However, our analyses of diversity and bathymetric distribution are consistent in suggesting the Central Indo-Pacific continental shelf (the ecoregion with the highest number of sea pen genera, species, and endemics) as one of the best possibilities to place the oldest diversification centre of sea pen lineages, where one of the most important hot-spots of biodiversity, the coral triangle, is commonly recognized (Hoeksema 2007; Veron et al. 2009, 2011).

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Sampling and field studies Not applicable.

Data availability The data generated and analyzed during this study are included in the supplementary information files.

Author contribution FJ and PJ conceived and designed research, analyzed data, and wrote the manuscript. Both authors read and approved the manuscript.

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