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The Cnidaria, Past, Present and Future

The world of Medusa and her sisters

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Abstract

Octocorals are a group of striking presence in marine benthic communities. With approximately 3400 valid species the taxonomy of the group is still not resolved, mainly because of the variability of morphological characters and lack of optimization of molecular markers. Octocorals are distributed in all seas and oceans of the world, from shallow waters up to 6400 m deep, but with few cosmopolitan species (principally pennatulaceans). The Indo-Pacific is the region that holds the greatest diversity of octocorals, showing the highest level of endemism. However, endemism in octocorals as we know might be the reflex of a biased sampling effort, as several punctual sites present high level of endemism (e.g. Alaska, Antarctica, South Africa, Brazil, Gulf of Mexico). Since around 75 % of described octocoral species are found in waters deeper than 50 m, increasing knowledge on octocoral diversity and distribution is still limited by the availability of resources and technologies to access these environments. Furthermore, the limited number of octocoral taxonomists limits progress in this field. Integrative taxonomy (i.e. morphology, molecular biology, ecology and biogeography) appears to be the best way to try to better understand the taxonomy of such a diverse and important group in marine benthic communities.

Keywords

Octocoral • Soft coral • Anthozoa • Worldwide distribution • Deep sea

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8.1 Diversity in Octocorals of the World: Number of Valid Species, New Trends in the Classification of Octocorals

Cnidarians in the subclass Octocorallia constitute a faunistic group with significant presence in benthic communities, made remarkable by their beauty, diversity, abundance and interspecific relationships. This group is represented by a number of growth forms, varying from encrusting, filiform and membranous, to complex and elaborate arborescent architectures. Octocorals are distributed in all marine environments, but are generally conspicuous and diverse in shal-

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low tropical reefs and in deep-sea habitats (e.g. seamounts), where they are important structural components of the community (Williams and Cairns 2013).

To this day there are over 3400 valid species of octocorals (Williams and Cairns 2015), whose taxonomy is far from being resolved. As an example, 3490 octocoral nominal species in >370 genera are listed in the World Register of Marine Species, but from these only 3103 species are considered valid names (van Ofwegen 2015).

Attempts to understand the taxonomy and phylogenetic relationships in this group have been hampered by a shortage of useful morphological characters, widespread homoplasy (parallelisms, convergences, and reversals) and pronounced intraspecific variation in characters such as colony growth form and morphology of sclerites (Williams 1997). Recent molecular phylogenies have shown how branching patterns can evolve independently several times from unbranched hypothetical ancestors involving different axial materials (Sánchez et al. 2003a, b; Etnoyer et al. 2006). Added to this, as pointed out by Daly et al. (2007), numerous species remain either undescribed or simply unidentifiable; lost type specimens and the poor quality of most nineteenth and early twentieth centuries species descriptions preclude species-level identifications in many groups.

To estimate the precise number of described species in Octocorallia is a very difficult task, as most genera have never been revised, and several regions of the world are still to be explored. Furthermore, the number of octocoral taxonomists is very limited, and the literature is quite dispersed (Bayer 1981a; Cairns 2007a). Efforts to condense and compile information on Octocorallia have started with a series of studies by Dr. Frederick M. Bayer (Bayer 1981a and Bayer et al. 1983).

Until the 1990s, octocoral systematics was mainly based on alpha-taxonomy (Kölliker 1880; Hickson 1916; Bayer 1955, 1956; Williams 1992a, b, 1997). However, the limitation of octocorals in the fossil record made it more difficult to polarize taxonomic characters in phylogenetic reconstructions (Bayer 1956).

The current classification of octocoral orders and families is mainly based on the studies by Kükenthal (1906, 1915, 1919, 1921, 1924, 1925), Hickson (1906, 1916, 1930), and Bayer (1956, 1981b) who created a classification system that is still in use, with few modifications (Tables 8.1 and 8.2).

Among the orders, Helioporacea (blue corals) and Pennatulacea (sea pens) are the only ones with well-defined synapomorphies. The blue corals because of their massive aragonite skeleton, and the sea pens because of their proximal peduncle used for anchorage in the soft substrate. Although the other orders also have well-defined stereotypes, they also have intermediate forms.

Bayer (1981b) suggested that increased research on octocorals slowly approximated the orders originally established by Hickson, Kükenthal, and others. According to Bayer, based on colonial organization and skeletal structure, the only distinguishable taxa were Pennatulacea, Helioporacea

Table 8.1 Octocoral classification by Kükenthal (1925)

Orders	Suborders	Families (n)	Genera (n)
Alcyonaria		9	37
Gorgonaria	Scleraxonia	4	24
	Holaxonia	8	85
Pennatularia	Sessiliflorae	11	18
	Subselliflorae	3	10
Total		35	174

Table 8.2 Octocoral classification by Hickson (1930)

Orders	Suborders	Families (n)	Genera (n)
Stolonifera		3	16
Telestacea		1	4
Alcyonacea		5	29+
Gorgonacea	Scleraxonia	4	11+
	Holaxonia	8	53+
Coenothecalia		1	1
Pennatulacea		13	31
Total		35	145+

Table 8.3 Octocoral classification by Bayer (1981b)

Orders	Sub-ordinal groups	Families (n)	Genera (n)
Helioporacea		2	2
Alcyonacea	Protoalcyonaria	1	1
	Stolonifera	5	19
	Alcyoniina	6	48
	Scleraxonia	7	23
	Medullate Holaxonia	4	40
	Restricted Holaxonia	5	67
Pennatulacea		14	28
Total		44	228

and the “restricted” Holaxonia that lack a chambered axis medulla (families Ellisellidae, Ifalukellidae, Chrysogorgiidae, Primnoidae, and Isididae). On the other hand, Stolonifera, Telestacea, Gastraxonacea, Alcyonacea, Scleraxonia, and the “medullate” Holaxonia (with chambered axial medulla) should be united by intermediate forms, and be included in the order Alcyonacea. Therefore, Bayer suggested that the traditional subdivisions (suborders) should be kept in a quasi-subordinal grade level, only as convenient levels, not taxa (Table 8.3).

The system proposed by Bayer (1981b) was well accepted by the scientific community, and it is still in use. Based on skeletal apomorphies, Grasshoff (1999) subdivided the order Alcyonacea in: Holaxonia sensu stricto (the medullate Holaxonia of Bayer) and Calcaxonia (the “restricted” Holaxonia of Bayer). Calcaxonia was created to include gorgonians with an axis lacking a cross-chambered hollow core, but having large amounts of calcareous material, either calcite or aragonite. The remnant four groups in the order (Alcyoniina, Protoalcyonaria, Scleraxonia, Stolonifera) can be maintained for convenience, as suggest by Bayer (1981b),

Table 8.4 Current octocoral classification system (Bayer 1981b; Grasshoff 1999; Daly et al. 2007). Records of valid names based on World Register of Marine Species (van Ofwegen 2015)

Orders	Sub-ordinal groups	Families (n)	Genera (n)	Species (n)
Helioporacea		2	2	4
Alcyonacea	Protoalcyonaria	1	1	1
	Stolonifera	7	27	165
	Alcyoniina	6	86	1235
	Scleraxonia	7	28	249
	Holaxonia	4	74	541
	Calcaxonia	6	111	685
Pennatulacea		14	37	223
Total		47	364	3103

however they do not represent actual clades and should be seen only as grades of colony architecture (Fabricius and Alderslade 2001) (Table 8.4).

In the 1990s the use of molecular techniques started to be employed in the study of octocorals. Molecular phylogenetic studies support the monophyly of Octocorallia, but there is no consensus yet regarding the relationships among groups below the subclass level (McFadden et al. 2010). Apparently, the major problem is in the optimization of molecular markers, as well as the lack of available material for molecular use, since many studies have analyzed the molecular phylogeny using a scarce number of taxa samples.

The rapid development of new molecular markers has helped to improve the resolution of molecular techniques in the taxonomy of octocorals. For instance, the first molecular markers used in the phylogeny of octocorals (mt 16 s and nuclear 18 s) were only able to resolve individuals at the genus or family level (Berntson et al. 2001; France 2007), whereas more recently developed mt markers such as *msh1* and *ND2* have a better resolution than these original markers (McFadden et al. 2006a, b, 2010).

The most complete phylogeny published for Octocorallia is that by McFadden et al. (2006a, b) who sequenced two mitochondrial protein-coding regions, *msh1* and *ND2*, for 115 genera representing 29 of 47 families. The phylogenetic analysis resulted in two major clades: one clade (Pennatulacea-Calcaxonia) comprised Calcaxonia plus Pennatulacea, with Helioporacea included in some analyses; another clade (Holaxonia-Alcyoniina) included all members of Holaxonia, a majority of Alcyoniina, and representatives of Scleraxonia and Stolonifera; and a third small clade (*Anthomastus-Corallium*) included deep-water Scleraxonia and several taxa of Alcyoniina. Although this study agreed with the previous findings using 16 s and 18 s genes (France et al. 1996; Berntson et al. 2001), none agreed with the traditional taxonomic divisions placed within the Octocorallia (McFadden et al. 2006a, b). The addition of cytochrome oxidase I (COI) and complete 28S rDNA sequences to existing 16S, 18S, and mtDNA datasets continues to support the two major clades of Octocorallia (Holaxonia-Alcyoniina and

Calcaxonia-Pennatulacea), but provides no further insights into relationships within the unresolved Holaxonia-Alcyoniina clade (McFadden et al. 2010). In addition, incongruence between mitochondrial and nuclear gene trees suggests that hybrid speciation and reticulate evolution may be an important mechanism of diversification in some genera (McFadden et al. 2010).

The proposed molecular phylogenetic resolutions for the order Alcyonacea are consistent with those proposed by Bayer (1981b), and they support the idea that the previous orders created by Kükenthal and Hickson cannot be supported by traditional taxonomy or molecular phylogenetics. The molecular phylogenetic studies published to date support the monophyly of Pennatulacea (McFadden et al. 2010) although the phylogeny of this order is not yet resolved. Molecular analyses do not support its traditional classification, as the suborder Sessiliflorae is paraphyletic, and Subselliiflorae is polyphyletic. Apparently, the high frequency of morphological homoplasy in pennatulaceans has led to many misinterpretations in the systematics of the group (Dolan et al. 2013).

The solution for the taxonomy of Octocorallia seems to be in the reconciliation of morphology and molecular data, as suggested by McFadden et al. (2010). The current octocoral classification is based on morphological characters, some of which are highly plastic or present a high convergence, often influenced by the environment. In these cases, molecular phylogenies do not agree with the groups suggested by the traditional classification. For instance, certain characters including polyp sclerites, sclerite ornaments, and mineralization of the axis in Plexauridae and Gorgoniidae are consistent with molecular phylogenies. On the other hand, mineralization, surface sclerites and length of sclerites are highly homoplasious (Sánchez et al. 2003b). The opposite can also be observed, as molecular analyses have revealed the taxonomic importance of certain morphological characters not frequently used to classify certain groups. For instance, in the soft corals *Sinularia*, *Sarcophyton*, and *Lobophytum* the presence, arrangement, and form of sclerites in the polyps are not frequently considered in the taxonomy of these genera. However, molecular analyses have

shown that these characters are actually congruent with the major molecular clades (McFadden et al. 2006b, 2009). Although the use of character mapping has been shown to be useful at differentiating octocoral genera and families, additional molecular studies are necessary before this approach can be successfully applied at subordinal levels (McFadden et al. 2010).

The main issue in the current taxonomy of octocorals is to understand the taxonomic relevance of the intraspecific variation, since the lack of understanding of morphological variation and the absence of variation in the molecular markers at the species level make difficult the establishment of limits between taxa, and consequently of a suitable classification. As pointed out by McFadden et al. (2010), the development of molecular markers, new tools and approaches to the study of morphological variations are needed to deepen the knowledge of species and speciation processes in octocorals.

8.2 Current Patterns of World Distribution of Octocorals: Regions of Endemism and Hotspots

Octocorals can be found from the intertidal zone to depths up to 6400 m, inhabiting both reef environments and soft bottoms (Williams 2011). The deepest octocoral record is 6400 m *Thouarella vityaz*, by Zapata-Guardiola and Lopez-Gonzalez (2012). Although common in all oceans, they have peculiarities on their local distribution, which is directly influenced by factors such as presence/absence of strong currents, suspended organic matter, and distance from coast (Fabricius and Alderslade 2001). Globally, they can be found from tropical to polar environments. Few species are cosmopolitan, with most of them being found in the order Pennatulacea (Williams 2011). Species with wide depth ranges – such as pennatulaceans – tend to occupy more areas, which is the case of several abyssal species that are cosmopolitan, while species usually inhabiting continental margins are more geographically restricted (Williams 2011).

The actual diversity in the deep-sea is not always evident. The distinction of limits between species and morphologic plasticity sometimes can only be detected with the use of molecular techniques (Baco and Cairns 2012; McFadden and Ofwegen 2013; Quattrini et al. 2013). Furthermore, biogeographic barriers can be subtle and identification complex.

Examples of deep-water octocoral endemism include *Callogorgia delta* Cairns and Bayer, 2002, which is only known from the Gulf of Mexico (Quattrini et al. 2013); and *Primnoella delicatissima* Kükenthal, 1908 and *Primnoella polita* Deichmann, 1936, which are restricted to tropical latitudes in South America (Cairns 2006). Endemism in the deep-sea is a complex subject, and several studies have been

trying to better understand it. Some of these have discussed the role of seamounts as hotspots, refuges or centers of endemism (Thoma et al. 2009; Rowden et al. 2010). However, because knowledge on the organisms living in the deep sea is still scarce and fragmented, what we consider now an endemic species might also be the result of a biased sampling effort. Reproduction mechanisms and recruitment events are also not well known, limiting information on dispersion and colonization (Rogers et al. 2007).

Understanding the distribution of deep-water octocorals is very challenging, considering the important logistics associated with accessing the deep sea. In this context, the field of marine habitat mapping has come to fill an important gap. For instance, habitat suitability models have been increasingly used to map the distribution of cold-water octocorals at both large (e.g. Yesson et al. 2012) and local scales (e.g. Bryan and Metaxas 2007). Based on known information on environmental requirements of different species, these studies allow one to further predict species distribution. In a global suitability model on cold-water octocorals, Yesson et al. (2012) estimated that salinity, temperature, broad scale slope, productivity, and oxygen and calcite saturation states are important factors influencing the distribution of cold-water octocorals. According to this study, the suborder Sessiliflorae (Pennatulacea) has the widest potential habitat range, whereas all octocoral suborders suggest a habitat preference for continental shelves and margins, particularly in the Northwest Atlantic and Western Pacific Rim.

As for scleractinian corals (Cairns 2007a), the world region that supports the highest diversity of octocorals is certainly the Indo-Pacific (Fig. 8.1), where a great number of endemic species is found. As an example, in Australia 457 deep-water octocoral species have already been documented (~21 % or 94 of the identified species are Australian endemics) (Alderslade et al. 2014). Some sub-regions considered as possible centers of origin and potentially highly diverse include the Philippines, Southeast Australia, New Caledonia, and New Zealand (McCoy and Heck 1976).

In 1981, Bayer (1981a) indicated several areas in the Indo-Pacific and Pacific coast of the Americas south of Panama as “poorly known” (Fig. 8.1 – areas 13 and 18), the latter with only two studies (Philippi 1892; Hickson 1928). More than 20 years later, Bayer (2002) reaffirmed the paucity of knowledge on gorgonians from the Indo-West Pacific areas. In the same document, he emphasized that knowledge on octocorals of the eastern Pacific, Indo-west Pacific and Southern Ocean presented a “greater problem” (Bayer 2002) when compared with the Atlantic, for example. The knowledge of octocorals from the Indo-Pacific region has greatly improved since then. To date, more than 100 genera of shallow-water octocorals from the Indo-Pacific have been described (Fabricius and Alderslade 2001; Paulay et al. 2003; Fabricius and McCorry 2006). However, there are still major

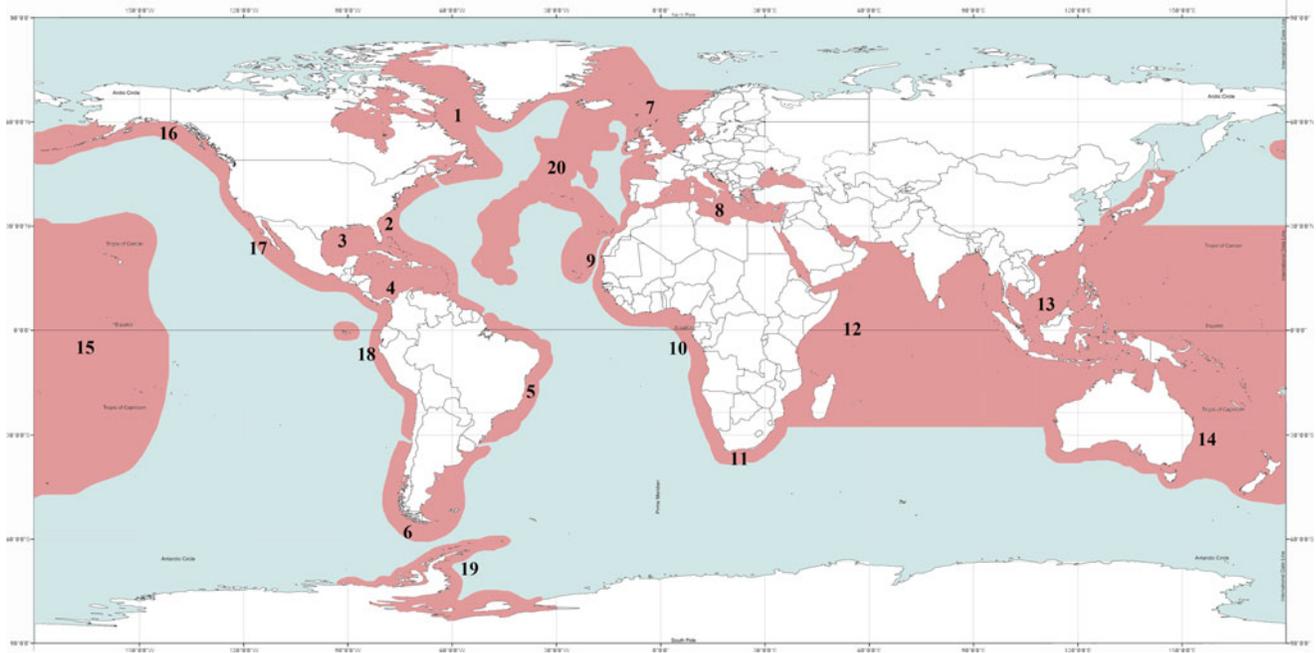


Fig. 8.1 Map of geographical areas and richness estimates of known species by region, based on local surveys. 1 Atlantic Canada (~40 spp.), 2 Atlantic USA (~140 spp.), 3 Gulf of Mexico (~170 spp.), 4 Caribbean (~156 spp.), 5 Brazil (~100 spp.), 6 Subantarctic (~55 spp.), 7 Northeast Atlantic (>80 spp.), 8 Mediterranean (~54 spp.), 9 Macaronesia (~60 spp.), 10 Western Africa (~24 Pennatulacea), 11 Southern Africa (~170

spp.), 12 Red sea and Western Indian (~208), 13 Western Pacific (~890), 14 Australia (~460 spp.), 15 Central Pacific (~70), 16 Alaska (~98 spp.), 17 Pacific coast of North America (~76 spp.), 18 Pacific coast of Central and South America (~69 spp.), 19 Antarctic (~30 spp.), 20 Northern mid-Atlantic ridge (~30 spp.)

gaps in the knowledge of octocoral distribution in this region, mainly because past inventories described the octocoral fauna at the family level or in terms of colony shape patterns, such as “soft coral” or “sea fans”, which can make identification inaccurate (Fabricius et al. 2007).

A series of studies has been published since the 1980s, including descriptions of species (Alderslade 1983, 1986, 1991, 2003; Bayer 1990; Williams 1990; Bayer and Stefani 1988; Ofwegen and Benayahu 2006; Alderslade and McFadden 2007; Ofwegen and Alderslade 2007), reviews of several taxa (Alderslade 1985; Williams 1992; Cairns 2010; Namin and Ofwegen 2010; Ofwegen et al. 2013) and regional surveys (Grasshoff 2007; Benayahu et al. 2004; Benayahu and Chou 2010; Benayahu and Fabricius 2010; Benayahu and Ofwegen 2012; Benayahu 2013; Alderslade et al. 2014). And yet, it is unlikely that we are getting closer of knowing the total octocoral diversity in these regions.

The Indo-Pacific is a very large region that covers a tropical range of Indian and Pacific oceans, including the Red Sea, Oceania, and the islands of the Pacific (Melanesia, Micronesia and Polynesia). This area is very heterogeneous and it is treated uniformly in several works of taxonomic inventories, which makes it difficult to study. Local surveys are the best way to improve the understanding of the octocoral diversity in the Indo-Pacific (Fig. 8.1 – areas 11–15)

and in many other areas in the world. Thus, here we present a quick overview of some sub-areas of this region.

A series of studies performed by Williams since 1980s revealed a richness of ~170 species in the southern Africa region (Fig. 8.1 – area 11). South Africa is one of the most important centers of endemism for Octocorallia. From the described species, ~50% are endemic with at least seven endemic genera (Williams 1989a, b, 1992, 2000; 2003; Williams and Little 2001). From the north-western region of Madagascar, Tixier-Durivault (1966) and Verseveldt (1969, 1971) listed 63 species. The octocoral fauna of the Red Sea is composed of approximately 60 shallow-water species (Verseveldt and Benayahu 1978; Benayahu 1990; Benayahu et al. 2002; Halász et al. 2014) and around 85 shallow-water species for India (Kumar et al. 2015).

In the Western Pacific the reports are generally for islands or archipelagos (Fig. 8.1 – area 13). For instance, the region of Taiwan has around 70 species listed, mostly from shallow waters (Benayahu et al. 2004). Fabricius et al. (2007) made an octocoral inventory of the archipelago of Palau and they found a great diversity containing at least 76 genera in 24 families (~150 spp.), with the family Nephtheidae being the dominant taxon with tall colonies and high abundance; alcyoniid species of the genera *Sinularia*, *Sarcophyton* and *Lobophytum* were also conspicuous at many places. Also in Micronesia, Paulay et al. (2003) inventoried the octocoral

fauna of Guam (Mariana Islands) and recorded 79 species (32 genera) with a great predominance of the soft coral *Sinularia*. They pointed out that the diversity and abundance of gorgonians (*Acabaria*, *Suberogorgia*, *Junceella*) increases strikingly with depth. The available knowledge on octocorals from China's Exclusive Economic Zone is the result of a few studies, mainly focusing on gorgonians (Stiasny 1938; Ren-Lin et al. 1991) and alcyonaceans (Li 1982a, b, 1984, 1986, 1993; Zou et al. 1991; Malyutin 1993) from the southern China. These studies, which have been published since the 1980s, indicate the presence of about 40 shallow-water species in the region. There are no recent reviews in addition to species descriptions given by Benayahu and Ofwegen (2009) and Benayahu and Fabricius (2010). The region of New Caledonia has an estimated richness of 266 species, but the accuracy of this number is questionable. Ofwegen (2007) and Grasshoff (2007) cited respectively 173 and 93 species for this area. Ofwegen (2007) pointed out, however, that the list was based mainly on data from Tixier-Durivault (1970) and as many of her identifications are frequently challenged, an intense working revision is necessary. Of the 280 species known from the New Zealand EEZ (Cairns et al. 2009; Cairns in press), only 12 occur in shallow waters (Grange and Brook 2010). In Japan 260 species of octocorals are known (144 gorgonians and 36 pennatulaceans), of which 120 can be found in the upper bathyal to abyssal depths (Matsumoto et al. 2007). The shallow water epicentre of marine diversity, the Coral Triangle (tropical marine waters of Indonesia, Malaysia, Papua New Guinea, Philippines, Solomon Islands and Timor-Leste), is poorly known but the deep waters of this region might house a great octocoral diversity. For example, the Malay Archipelago contains about 25 species of *Chrysogorgia* (Chrysogorgiidae), which is more than 40% of the current species richness of this genus (Watling et al. 2011).

The region of Australia (Fig. 8.1 – area 14) is probably the largest, both in terms of diversity and number of published studies on octocorals. In 2005, an expedition on the shelf and slope of Western Australia (100–1000 m) detected 141 species of soft corals, 80% of which have been estimated to be new to science (Butler et al. 2010). Then, Alderslade et al. (2014) published the most comprehensive study on octocorals in the region, listing, as stated previously, 457 species, belonging to 131 genera and 28 families. Of this total, more than 45% occur at depths >500 m, and 69 are probably new species.

The Hawaiian Archipelago (Fig. 8.1 – area 15) has a pattern different from other shallow-water reefs of the world, with few octocoral species described (only four). However, the diversity of deep-water octocoral is very high, with at least 70 confirmed species (Grigg and Bayer 1976; Cairns and Bayer 2008; Cairns 2009, 2010).

The coast of North Pacific of the Aleutian Archipelago and Alaska (Fig. 8.1 – area 16) has around 300 seamounts, representing a vast area of hard substrate for populations of octocorals that forming dense gardens with big colonies (Stone and Shotwell 2007). Heifetz et al. 2005 suggested that this region may be a possible center of origin for some octocoral families. Gorgonians are the most diverse group with more than 60 species that making dense assemblages of *Primnoa* spp and big colonies of *Paragorgia arborea* and bamboo corals. True soft corals and pennatulaceans are not a rich group (nine and ten species respectively) but they are very abundant, as species of *Clavularia* with densities of 1.7 colonies m² and with giant colonies as the sea pen *Halipteris willemoesi* which can reach up to 3 m high (Stone 2006; Stone and Shotwell 2007).

In the Pacific coast of North America (Fig. 8.1 – area 17) seems to repeat the same pattern of octocoral diversity of Alaska. More richness of gorgonians (36 species from 10 families) with dense “forest” of the bubblegum coral *Paragorgia arborea* and isidids, few species of true soft corals (8) and a high abundance of sea pens (28 species) principally of *Stylatula* spp., *Anthoptilum grandiflorum* and *Umbellula* spp. which are found coast wide (Stone and Shotwell 2007).

In the region that includes the Pacific coast of Central and South America (south Panama) (Fig. 8.1 – area 18) an increasing number of species has been revealed since the 1980s (Bayer 1986; Williams and Breedy 2004; Breedy and Guzman 2005, 2012; Guzman and Breedy 2012; Breedy and Cortés 2011; Breedy and Williams 2013; Cairns 2007b; Ofwegen et al. 2009). The octocoral fauna in the Galapagos Islands was virtually unknown until a few years ago, when Breedy et al. (2009) recorded 15 gorgonian (mainly *Pacifigorgia* and *Muricea*) and 3 pennatulacean species (*Virgularia galapagensis*, *Ptilosarcus undulatus*, and *Cavernulina darwini*), most of which were considered endemic to the archipelago.

The region between Antarctica and surroundings (Subantarctic) – including the southern South American continent – (Fig. 8.1 – area 6 and 19) has received special attention in the recent years. Octocorals living in this area are limited to cold and dark environments (as deep-water octocorals), where so far species richness has been considered low. However, it seems to be a potential center of endemism, with some genera and over a dozen species being described only in the last decade (Zamponi and Pérez 1995; López-González and Gili 2000; Pérez and Zamponi 2000; López-González and Williams 2002; López-González et al. 2002; Williams and López-González 2005; López-González 2006; Häussermann and Försterra 2007; Ofwegen et al. 2006, 2007; Zapata-Guardiola and López-González 2010; McFadden and Ofwegen 2013).

Most of the known species in the Arctic were studied in more than 30 manuscripts written by Dr. Hjalmar Broch between the years 1910 and 1965 (e.g. Broch 1929), and it is difficult to assume a number of species, since no further reviews or checklists of octocoral species have been developed for this region. Nephtheids and sea pens such as *Umbellula* spp. are some of the most common octocorals reported in Arctic waters (e.g. Broch 1956; Bluhm et al. 2005). Broch (1956) also reported *Acanella arbuscula* and *Virgularia*. Bamboo corals (e.g. *A. arbuscula*, *Keratoisis* sp.) and sea pens have been frequently caught as fishing bycatch in the Baffin Bay area (Eastern Arctic) (e.g. Neves et al. 2014), and a bamboo coral identified as *Isidella lofotensis* has also been found in high densities in East Greenland (Mayer and Piepenburg 1996).

In contrast to the Indo-Pacific, where communities of reef octocorals are mainly composed of soft corals (Xeniidae, Nephtheidae, Alcyoniidae) (Benayahu and Loya 1981) (Fig. 8.2a), in the Western Atlantic (Fig. 8.1 – areas 2, 3, 4 and 5) Gorgoniidae and Plexauriidae (Fig. 8.2b) are the most representative families (Bayer 1953, 1961).

In the Western Atlantic, the highest diversity is concentrated in the Caribbean and Gulf of Mexico. Around 10% of the octocoral species found in the Gulf of Mexico are endemic (Cairns and Bayer 2009). This region is considered the probable center of origin for tropical species in the Southwestern Atlantic (Brazil) (Rocha 2003), where diversity is lower but endemism is higher (~24% of endemism and at least two endemic genera) (Castro et al. 2010). Cairns and Bayer have published a series of eight manuscripts on the 59 deep-water calceonian species found in this region (Cairns 2001, 2006, 2007a, c; Cairns and Bayer 2002, 2003, 2004a, b).

In the Mediterranean (Fig. 8.1 – area 8) only 54 octocoral species have been recorded (Vafidis et al. 1994; Pastor 2006; Sartoretto 2012), although it presents an important endemism (18.5%). In the Azores (Fig. 8.1 – area 9), about 41 species have been recorded, with most of these being known to live near continental margins, near islands and seamounts (Tixier-Durivault and d'Hondt 1973; Braga-Henriques et al. 2013), its octocoral fauna, however has been little studied. Further south, according to Raddatz et al. (2011), cold-water corals occur in abundance in the archipelago of Cape Verde, but few publications include descriptions of specimens in the region. In the Canary Islands, the situation is not much different, however, at least two species were described in the 1990s (Ocaña et al. 1992; López-González et al. 1995) and one genus and species in the 2000s (Ocaña and Ofwegen 2003). The African Atlantic coast is much less studied. López-González et al. (2001) revealed that – at the time of their study – only 15 studies had reported on Pennatulacea for that region. These authors recorded 24 species of pennatulaceans for the African Atlantic coast, from depths ranging 0–6200 m (Fig. 8.1 – area 10).

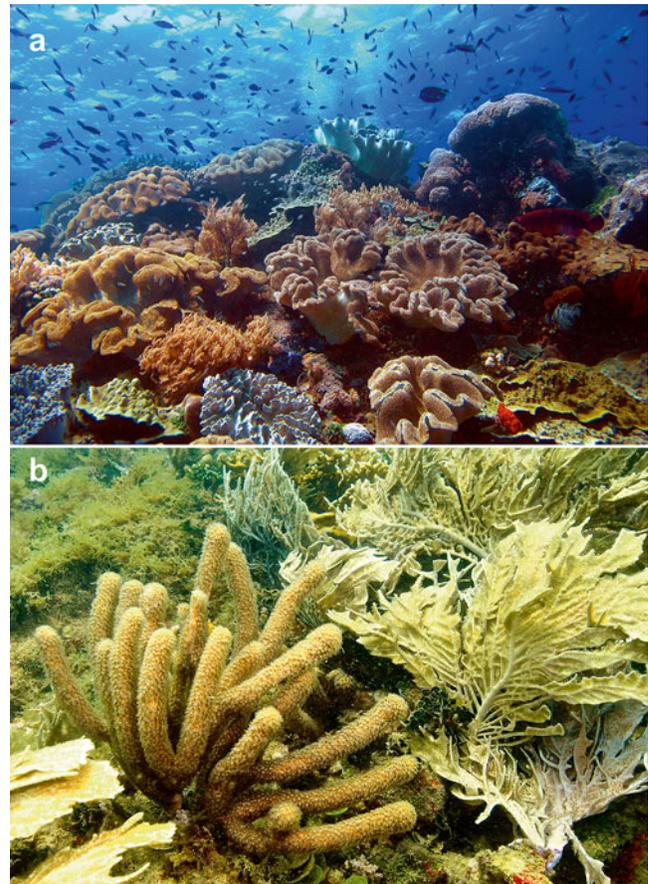


Fig. 8.2 Comparison between octocoral reef communities in the Indo-Pacific and Western Atlantic. (a) Alcyoniids from Komodo Island (Photo: Henrique Maranhão). (b) Gorgonids and plexaurids in a Brazilian reef (Bahia State) (Photo: Clovis B. Castro)

Finally, the deep-sea fauna of the mid-Atlantic ridge is particularly important in terms of understanding dispersion and connectivity patterns between eastern and western Atlantic populations. In the recent years there was an increase in the knowledge of this particular octocoral fauna, mainly in the northern mid-Atlantic ridge, where recent reports indicate an approximate number of 30 species (Watling 2007; López-González and Gili 2008; Mortensen and Buhl-Mortensen 2008; Watling et al. 2011; Molodtsova 2013). The octocoral fauna of the southern mid-Atlantic remains largely unknown, although recent efforts MAR-ECO (Patterns and processes of the ecosystems of the northern mid-Atlantic) have started to be made in order to explore the region (Pérez et al. 2012).

8.2.1 Richness According to Depth

It is a common perception that due to a dependence on light, shallow-water zooxanthellate octocorals have a more limited distribution than their azooxanthellate counterparts. Shallow-water species living in coastal environments are exposed to

river runoff and large variations in temperature and salinity. These factors can expose organisms living in such environments to speciation and a higher endemism, by creating geographic barriers. In the deep sea, speciation is as frequent as in shallow water environments, as evidenced by the high diversity found in the deep-sea (>75% of octocoral species are found in waters >50 m; Cairns 2007a, b). However, the endemism observed in shallow waters is more easily detected (see Thoma et al. 2009; Quattrini et al. 2013).

The Gulf of Mexico (Fig. 8.1 – area 3) is a good example of how octocoral richness varies with depth. In this region, about 80 species are known from environments up to 50 m, while there is an increase in the number of species at >50 m (Cairns and Bayer 2009) (Fig. 8.3).

Even though the octocoral fauna in the Gulf of Mexico region has been classified as “poorly known”, richness in waters >50 m is almost 40% higher than in shallower waters. Richness, however, is not homogeneously distributed and tends to decrease with depth (Cairns and Bayer 2009). Another example is the New Zealand EEZ, from which of its 281 known species (Cairns et al. 2009; Cairns 2012), only 12 (3.6%) occur in shallow water (Grange and Brook 2010). A higher octocoral diversification in deeper environments is also notable in the continental shelf and seamounts, where an increasing slope gradient with depth leads to more diverse habitats, despite geographic proximity (Quattrini et al. 2013). These habitats are influenced by different ranges of temperature, pressure, dissolved oxygen, which promote speciation. Towards the abyssal plain, richness tends to decrease and species are more adapted to more extreme life conditions.

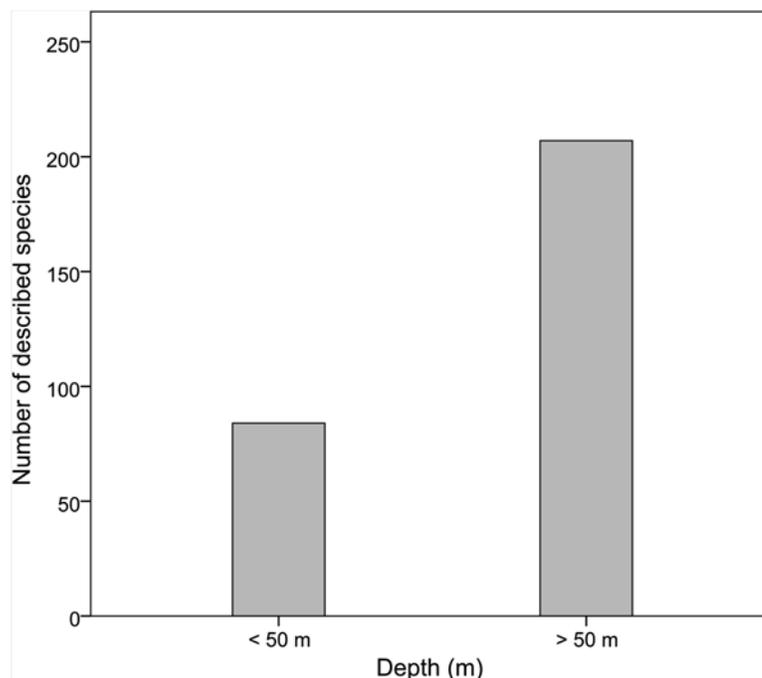
Similarly to how certain families are more common in shallow/tropical environments (e.g. Gorgoniidae and Clavulariidae), certain taxa also tend to occupy deep rather than shallow-water environments (see section on deep-sea octocorals).

8.3 Deep-Sea Octocorals

8.3.1 History, Families and More Representative Genera

The deep sea is generally defined as the zone that begins at the end of the shelf edge (Gage and Tyler 1991). By this definition, deep-water octocorals are those species usually found at depths below 200 m; although corals living at depths >50 m have also been considered deep-water corals (Cairns 2007a; Roberts et al. 2009). The terms deep-water and cold-water corals have commonly been used interchangeably, since most findings and observations of these organisms come from cold and deep-water environments. However, certain primarily deep-water species can eventually be observed in much shallower environments, a phenomenon known as deep-water emergence. In Tracey Arm – a fjord in Alaska – the red-tree coral *Primnoa pacifica* (a primarily deep-water octocoral) can be found at depths as shallow as 10 m (Cairns 2010; Waller et al. 2014). The opposite pattern can also occur, with cases of primarily shallow-water species being eventually found in deeper waters. In the Red Sea, shallow-water soft corals have been observed at depths of

Fig. 8.3 Richness of octocorals in the Gulf of Mexico in two bathymetric classes: 0–50 m and ≥ 50 m (Data from Cairns and Bayer 2009)



360–720 m, where the temperature can be as high as 20 °C (Qurban et al. 2014). Both cases indicate that factors other than depth alone influence the distribution and growth of these octocorals (Freiwald et al. 2004; Roberts et al. 2009).

Deep-water octocorals – as other corals – have been known for centuries. At least since the eighteenth century, these organisms have been caught in fishing gear, as bycatch. They were particularly familiar to fishermen, who did not know the nature of these structures and fragments that came in their nets and lines (Roberts et al. 2006). The first known mention of the sea pen *Umbellula* in the literature came from the description of a colony caught in a fishing line, during a whale fishery near Greenland (Ellis 1753).

Knowledge of deep-water octocorals started to increase with results from early oceanographic expeditions, such as the *HMS Challenger* (1872–1876) (Wright and Studer 1889). In the nineteenth and twentieth centuries, important octocoral taxonomic and anatomical studies were published, based on descriptions of a number of deep-water specimens collected during such expeditions (e.g. Kölliker 1880; Versluys 1906; Kükenthal and Broch 1911; Kükenthal 1915, 1919, 1924; Jungersen 1904; Hickson 1916; Verrill 1922; Deichmann 1936). It was with the advent of novel underwater technologies – including remotely operated vehicles (ROVs), automated underwater vehicles (AUVs), sonar technologies, etc. – that the understanding of the ecology and distribution of deep-sea corals has considerably improved (Roberts et al. 2009). These technologies allow the direct sampling, in situ observation and monitoring in a way not possible before.

All three Octocorallia orders (i.e. Alcyonacea, Pennatulacea and Helioporacea) have representatives in the deep-sea. As already mentioned, around 75 % of the described octocoral species are known to be found in waters deeper than 50 m (Cairns 2007a), with around 67 % of octocoral families being found deeper than 200 m (Watling et al. 2011). Although most species are found in the continental shelf and shelf break (Watling et al. 2011), many species extend their ranges to much deeper waters. The primnoid *Convexella krampi* and the sea pen *Umbellula* sp. for example, are some of the deepest known octocorals, with records from 5850 m to >6000 m, respectively (Williams 1995, 2011; Madsen 1956).

Primnoidae, Chrysogorgiidae and Isididae are considered the three major deep-sea octocoral families. Primnoidae is a primarily deep-water family (Cairns and Bayer 2009), as is Chrysogorgiidae (Pante et al. 2012). In Isididae, some taxa are exclusive of deep-water environments, such as species in the subfamily Keratoisidinae (Alderslade 1998). Paragorgiidae and Parisididae are examples of families exclusively found in waters >200 m (Sánchez 2005; Watling et al. 2011).

Families of soft corals such as Nephtheidae and Alcyoniidae also have some genera exclusive to cold-water

(but not necessarily deep) environments. *Gersemia* is an example of temperate-polar nephtheid with an eurybathic distribution (Williams and Lundsten 2009). These soft corals are commonly reported in North Atlantic waters (Mortensen and Buhl-Mortensen 2005a, b; Wareham and Edinger 2007). The mushroom soft corals *Anthomastus* and *Heteropolypus* are some of the common alcyoniids found in deep-water environments (Molodtsova 2013). Colonies of the recently described octocoral family Aquaumbridae are also found in deep-waters (Breedy et al. 2012).

In Pennatulacea most families can be found in both shallow and deep waters. The three deepest pennatulacean genera are *Umbellula*, *Kophobelemonn*, and *Porcupinella* (Williams 2011). Although *Umbellula* and *Kophobelemonn* can also be found at much shallower depths (<200 m), *Porcupinella* is only known from its type location and depth (5300 m) (López-González and Williams 2011). In Helioporacea only the genus *Epiphaxum* is found in deep-water environments (Bayer 1992).

8.3.2 Adaptations and Environmental Requirements

Some of the features that characterize deep-water octocorals and differentiate them from their shallow-water counterparts include the absence of association with zooxanthellae, high longevities, slow growth rates, tolerance to low water temperatures and limited food availability. Cold-water corals are usually found in environments where temperature ranges 4–12 °C, although there are species that support even colder temperatures (Roberts et al. 2009; Baker et al. 2012; Neves et al. 2014).

Many deep-water octocorals have a suspension feeding habit and depend upon currents to have access to food. The flabellate colonies of some gorgonians such as *Primnoa* and *Paragorgia* have a concave shape in response to strong and unidirectional currents, characteristic of deep-water environments (Grigg 1972; Mortensen and Buhl-Mortensen 2005b; Tong et al. 2012). This shape is usually associated to adjusting position in relation to currents to maximize prey capture (Grigg 1972).

In Pennatulacea, morphological adaptations to deep-water environments can be identified in taxa living at great depths (e.g. >3000 m), and include reduction in the number of feeding polyps (with an increase in their size), and absence of polyp leaves (Williams 2011). The alcyoniid genus *Anthomastus* also shows a reduction in the number but increase in size of polyps, which are much larger than polyps of other soft coral species (Bayer 1993; Molodtsova 2013); this character has not been explicitly referred to as an adaptation to deep-water environments in this taxon.

8.3.3 Substrate Requirements

The distribution and growth of deep-water octocorals depends on substrate availability. Most deep-water sea pens (Pennatulacea) are found inhabiting soft bottoms, with only two genera (*Anthoptilum* and *Calibelemnon*) known to have species adapted to colonize hard substrates (Williams and Alderslade 2011). Conversely, most soft corals and gorgonians require hard substrates for larval attachment and subsequent growth. Large gorgonians such as *Primnoa*, *Paragorgia*, *Paramuricea* and *Keratoisis* are frequently observed attached to bedrock, boulders and cobbles (Edinger et al. 2011). However, certain bamboo corals (Isididae) and chrysogorgiids can also be found in soft bottoms, as many species have root-like branches (holdfasts) to anchor in the soft substrate (Deichmann 1936). For instance, the bamboo coral *Keratoisis* sp. was observed forming dense forests on a soft bottom environment in West Greenland (Neves et al. 2014).

8.3.4 Longevity and Growth Rates

Most of the studies on growth rates and longevity of deep-water octocorals have focused on gorgonians, whereas growth in soft corals and sea pens has rarely been addressed. Several species of deep-water gorgonians lay down growth rings in their skeletons (Cairns 2002; Sherwood et al. 2005; Roark et al. 2009; Sherwood and Edinger 2009), and in certain taxa (e.g. *Primnoa*, *Acanella* and *Keratoisis*) ring formation periodicity has been shown to be annual (Sherwood and Edinger 2009). Longevity in these octocorals can reach hundreds of years, with linear growth rates being as slow as $<1 \text{ cm}\cdot\text{year}^{-1}$ (Sherwood and Edinger 2009). The high longevities presented by some deep-water octocorals suggest they can be archives of environmental change, being of particular interest in palaeoceanography (e.g. Thresher et al. 2004; Roark et al. 2005; Hill et al. 2012). The analysis of the internal axis of deep-water sea pens suggest they are also slow growing organisms ($2\text{--}5 \text{ cm}\cdot\text{year}^{-1}$), but with a decadal longevity (Wilson et al. 2002; Neves et al. 2015).

8.3.5 Vulnerability and Conservation

Deep-water octocorals are important components of Vulnerable Marine Ecosystems (VME) (Roberts et al. 2009) for several reasons. They are highly vulnerable to anthropogenic activities such as bottom fisheries, as contact with fishing gear can damage, dislodge, and kill colonies (Jones 1992; Watling and Norse 1998; Pauly et al. 2003; Troffe et al. 2005; Heifetz et al. 2009; Althaus et al. 2009). They have slow growth rates and high longevities (as outlined above), which suggest that full

recovery from damage can take from decades to centuries, depending on the species. They also make structure and habitat for a number of other species (e.g. Auster 2005; Buhl-Mortensen and Mortensen 2004; Buhl-Mortensen et al. 2010).

In some locations, deep-water octocorals can form large assemblages commonly referred to as forests or gardens (Auster et al. 2013; Bullimore et al. 2013; Neves et al. 2014). These gardens are usually reported as being dense aggregations of gorgonians and other arborescent corals. Deep-water sea pens too, can be found forming dense fields up to 1 km in length (Baker et al. 2012; Kenchington et al. 2014), and possess a rich invertebrate associated fauna (Baillon et al. 2014). The finding of redfish larvae associated with different species of deep-water sea pens in the Northwest Atlantic highlighted their importance as habitat for these commercially important fish species, in an otherwise flat environment (Baillon et al. 2012).

Deep-water octocorals are diverse, abundant and widespread. New taxa are often being described and new hotspots of octocoral diversity being discovered. Concomitantly, threats, such as commercial fisheries, tend to expand to deeper environments (e.g. Paulay et al. 2003), with pristine areas becoming rarer. A better understanding of deep-water octocoral distribution and the taking of measures to protect and better know them is therefore essential for the maintenance of these populations. On the bright side, as underwater technologies become more accessible and logistics less constrained, an increase in the knowledge of deep-water octocorals will hopefully be witnessed in the next years, helping to increase protection and conservation of these organisms.

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