Coral Reefs
https://doi.org/10.1007/s00338-025-02744-4

RESEARCH

Deep-sea octocorals from bathyal canyons and seamounts of the Ligurian Sea (NW Mediterranean Sea)

Francesco Enrichetti[1,2,3] · **Giorgio Bavestrello**[1,2,3] · **Marzia Bo**[1,2,3]

Received: 31 January 2025 / Accepted: 27 August 2025

Abstract In recent decades, our understanding of deep-sea ecosystems has significantly improved, yet the taxonomic identity of associated species often remains understudied and this is particularly true for octocorals. This study describes the octocoral fauna inhabiting cold-water coral habitats on seamounts, canyons, and the continental slope of the Ligurian Sea (NW Mediterranean Sea), ranging from 400 to 822 m. Eighteen specimens were photographed in situ and collected using a remotely operated vehicle during two campaigns conducted in 2017 and 2021.

Taxonomic analyses, based on the features of the colony, polyps, and sclerites, led to the identification of ten species. Among these, common Mediterranean bathyal species were identified, including *Muriceides lepida*, *Villogorgia bebrycoides*, *Bebryce mollis*, and *Callogorgia verticillata*. In addition, other less common species were identified, such as *Acanthogorgia armata*, *Placogorgia coronata*, and *Placogorgia massiliensis*. More problematic taxa included *Rolandia* cf. *coralloides, Acanthogorgia* sp., and *Acanella* cf. *arbuscula*. Each specimen is described in detail, with morphological observations complemented by high-definition images of live specimens and anatomical details. Novel insights into anatomical features, distribution patterns, and ecological preferences are presented, contributing to a more comprehensive delineation of these species. Finally, the study addresses major taxonomic challenges (including plasticity of the key anatomical characters, access to deep-sea multi-samples, and descriptions supported by high-quality images) and discusses zoogeographical and bathymetrical affinities of the Ligurian bathyal octocoral fauna.

Résumé Au cours des dernières décennies, la compréhension des écosystèmes profonds s'est améliorée, mais l'identité taxonomique des espèces associées reste souvent méconnue, notamment chez les octocoralliaires. Cette étude décrit la faune d'octocoraux des habitats coralliens d'eaux froides de la mer Ligure (Méditerranée nord-occidentale), entre 400 et 822 m de profondeur. Dix espèces ont été identifiées à partir de spécimens photographiés et collectés par véhicule sous-marin téléguidé en 2017 et 2021. Outre des espèces bathyales communes (*Muriceides lepida, Villogorgia bebrycoides, Bebryce mollis, Callogorgia verticillata*), des espèces moins fréquentes ont été signalées, comme *Acanthogorgia armata, Placogorgia coronata* et *Placogorgia massiliensis*. Des observations morphologiques et iconographiques apportent de nouvelles informations sur l'anatomie, la distribution et les affinités écologiques, contribuant à une meilleure caractérisation de la faune bathyale d'octocoraux en Méditerranée.

Resumen En las últimas décadas ha mejorado notablemente el conocimiento de los ecosistemas profundos, aunque la identidad taxonómica de muchas especies asociadas sigue poco estudiada, especialmente en los octocorales. Este trabajo describe la fauna de octocorales de hábitats coralinos de aguas frías en el mar de Liguria (Mediterráneo noroccidental), entre 400 y 822 m de profundidad. Se identificaron diez especies a partir de ejemplares fotogra-

---

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00338-025-02744-4.

✉ Francesco Enrichetti
francesco.enrichetti@edu.unige.it

[1] Dipartimento di Scienze della Terra, dell'Ambiente e della Vita (DISTAV), Università di Genova, Genoa, Italy

[2] National Biodiversity Future Centre (NBFC), Palermo, Italy

[3] Consorzio Nazionale Interuniversitario per le Scienze del Mare (CONISMA), Rome, Italy

fiados y recolectados con un vehículo operado a distancia durante campañas en 2017 y 2021. Además de especies batiales comunes (*Muriceides lepida, Villogorgia bebrycoides, Bebryce mollis, Callogorgia verticillata*), se registraron especies menos frecuentes como *Acanthogorgia armata, Placogorgia coronata y Placogorgia massiliensis*. Las descripciones morfológicas, apoyadas por imágenes de alta calidad, aportan información novedosa sobre anatomía, distribución y afinidades ecológicas, contribuyendo a una visión más completa de la fauna de octocorales batiales en el Mediterráneo.

Keywords Gorgonians · *Acanella* · *Acanthogorgia* · *Muriceides* · *Placogorgia* · *Rolandia*

Introduction

Octocorals are anthozoans characterized by an octamerous symmetry. Mostly colonial, they exhibit diverse growth forms, ranging from encrusting stolonal webs to complex arborescent structures. They are exclusive marine and inhabit a wide range of environments, from shallow tropical waters to polar and abyssal zones, occurring on both soft and hard substrates (Bayer 1973; Ruppert et al. 1994; Williams 2011; Zapata-Guardiola and Lopez-Gonzalez 2012; Perez et al. 2016; Bryce et al. 2018). While important in shallow reefs (Lasker et al. 2020; Rodriguez et al. 2020), their highest diversity occurs in the deep sea, with around three-quarters of the over 3600 known species (McFadden et al. 2024) found below 50 m depth (Cairns 2007; Yesson et al. 2012; Perez et al. 2016). At these depths, gorgonians, soft corals, and pennatulaceans often form mono- or multi-specific assemblages. These create structurally complex habitats known as coral meadows, gardens, or forests, which support a rich associated fauna (Buhl-Mortensen and Mortensen 2004; Freiwald et al. 2004; Stone 2006; Edinger et al. 2007; Söffker et al. 2011; Bo et al. 2014a, 2015; Bullimore et al. 2013; Neves et al. 2015; Rossi et al. 2017; Li and Wang 2019). These habitats suffer from the mechanical impact of demersal fishing practices: octocorals are frequently caught as bycatch and lost fishing gear frequently entangles in their structures (Watling and Norse 1998; Hall-Spencer et al. 2002; Freiwald et al. 2004; Stone 2006; Aguilar et al. 2017). Due to their slow growth and longevity, many species show low resilience, with limited recovery even decades after disturbance (Freiwald et al. 2004; Althaus et al. 2009).

Despite the adoption of international resolutions, conservation efforts targeting octocorals are often hampered by taxonomical uncertainties. Environment-driven variability of key diagnostic characters make many octocoral species difficult to identify (Fabricius and Alderslade 2001; Altuna and Poliseno 2019; McFadden et al. 2022). Furthermore, several taxonomic descriptions often lack detailed information and illustrations, and type material is often missing or poorly preserved. These issues limit the ability to distinguish among closely related species and hinder accurate assessments of biodiversity (Giangrande 2003; Mace 2004; Ely et al. 2017).

Octocorals classification is traditionally based on colony morphology and sclerite features (Bayer 1961). Colony traits are typically used for higher-level classification, while sclerites are essential for genus- and species-level identification (Kükenthal 1919; Madsen 1944; Bayer 1981; Daly et al. 2007). Molecular studies have recently reshaped octocoral systematics, showing that traditional classifications based on colony form and axis structure relied on homoplastic traits (McFadden et al. 2006, 2022). However, while phylogenomic approaches have significantly improved the resolution of higher taxonomic ranks—such as families and orders—molecular markers currently available often lack the sensitivity to distinguish closely related genera and species. As a result, at finer taxonomic scales, many morphologically similar taxa remain unresolved (Altuna and Poliseno 2019).

Mediterranean octocorals were re-examined in the second half of the twentieth century by Carpine and Grasshoff (1975), Grasshoff (1972, 1973, 1977, 1992), Weinberg (1976, 1977, 1978), and Weinberg and Grasshoff (2003). More recently, ROV-based explorations revealed areas of high octocoral diversity and abundance, offering new insights into their diversity, distribution, and ecology (Bo et al. 2012, 2015; Grinyó et al. 2016; Chimienti et al. 2019; Enrichetti et al. 2019; Dominguez-Carrió et al. 2022; Toma et al. 2022). The latest review by Altuna and Poliseno (2019) reports 40 alcyonaceans and 10 pennatulaceans in the deep Mediterranean Sea. ROV manipulators have greatly improved sample collection for taxonomic studies: unlike material obtained by dredging or as fishing bycatch, ROV-collected specimens are generally well preserved and accompanied by high-resolution in situ images, enabling more accurate identification and providing a better understanding of these organisms (e.g., López-Gonzalez et al. 2012, 2015; Mastrototaro et al. 2015; Saucier et al. 2017; Grinyó et al. 2018).

This study presents a detailed taxonomic examination of the deep-sea octocoral specimens collected during a series of ROV explorations conducted in the Ligurian Sea (NW Mediterranean Sea) between 2017 and 2021, at depths ranging from 400 to 822 m. Specimens were collected from a variety of bathyal environmental settings, including muddy plains, sparse coral rubble, coral thanatocoenoses, living coral mounds, and outcropping rocks, all located along the eastern continental slope and the "Di Levante" Canyon, or associated with three off-shore seamounts, namely Ulisse, Penelope, and Janua. Accurate morphological descriptions of the collected specimens are presented, accompanied by high-definition images of living colonies and anatomical features, including polyps and sclerite architecture. The main aim is to create a baseline for the morphological identifications of the species. Finally, the zoogeographic relationships and the major taxonomic issues hindering the identification of Mediterranean and NE Atlantic octocorals are discussed.

Materials and methods

Study area

The Ligurian Sea lies in the northern sector of the western Mediterranean Sea (Fig. 1), bordered to the North by the Apennines and the Ligurian Arc, to the Southeast by the Tuscan Archipelago and Corsica, and to the Southwest by the Gulf of Lions and the Algero-Provençal Basin (Cattaneo-Vietti et al. 2010). Its heterogeneous topography reflects a relatively recent origin (approximately 30 Ma) caused by the rifting of the Liguro-Provençal Basin and the rotation of the Corsica-Sardinia block (Stanley and Mutti 1968; Rollet et al. 2002; Rosenbaum et al. 2002). The eastern basin features an extended shelf and gentle, rugged slopes, whereas the western basin has a narrow shelf, a steep slope, and a broad bathyal plain at approximately 2600 m depth (Fanucci et al. 1989; Cattaneo-Vietti et al. 2010; Würtz 2012).

While submarine canyons are abundant in the West, only three major canyon systems shape the eastern slope: Bisagno and Polcevera canyons, perpendicular to the coast near Genoa, and the Levante Canyon, which runs almost parallel to the coast for about 70 km before merging into the Bisagno system (Cattaneo-Vietti et al. 2010; Harris and Whiteway 2011; Würtz 2012; Soulet et al. 2016) (Fig. 1). The steep Levante Canyon is fed by several tributaries (Entella, Deiva Marina, Punta Mesco, and Monterosso) and host a lush cold-water coral province with living reefs, complex thanatocoenoses, and extended areas of sparse coral rubble (Delbono et al. 2014; Fanelli et al. 2017; Enrichetti et al. 2018; Bo et al. 2023).

Off-shore, six major volcanic seamounts shape the seafloor (Fanucci and Nicolich 1984; Rollet et al. 2002; Réhault et al. 2012; Bo et al. 2014b; Würtz and Rovere 2015). Three of them, namely Ulisse, Penelope, and Janua, arise from 700 to 1300 m depth in the central portion of the Ligurian

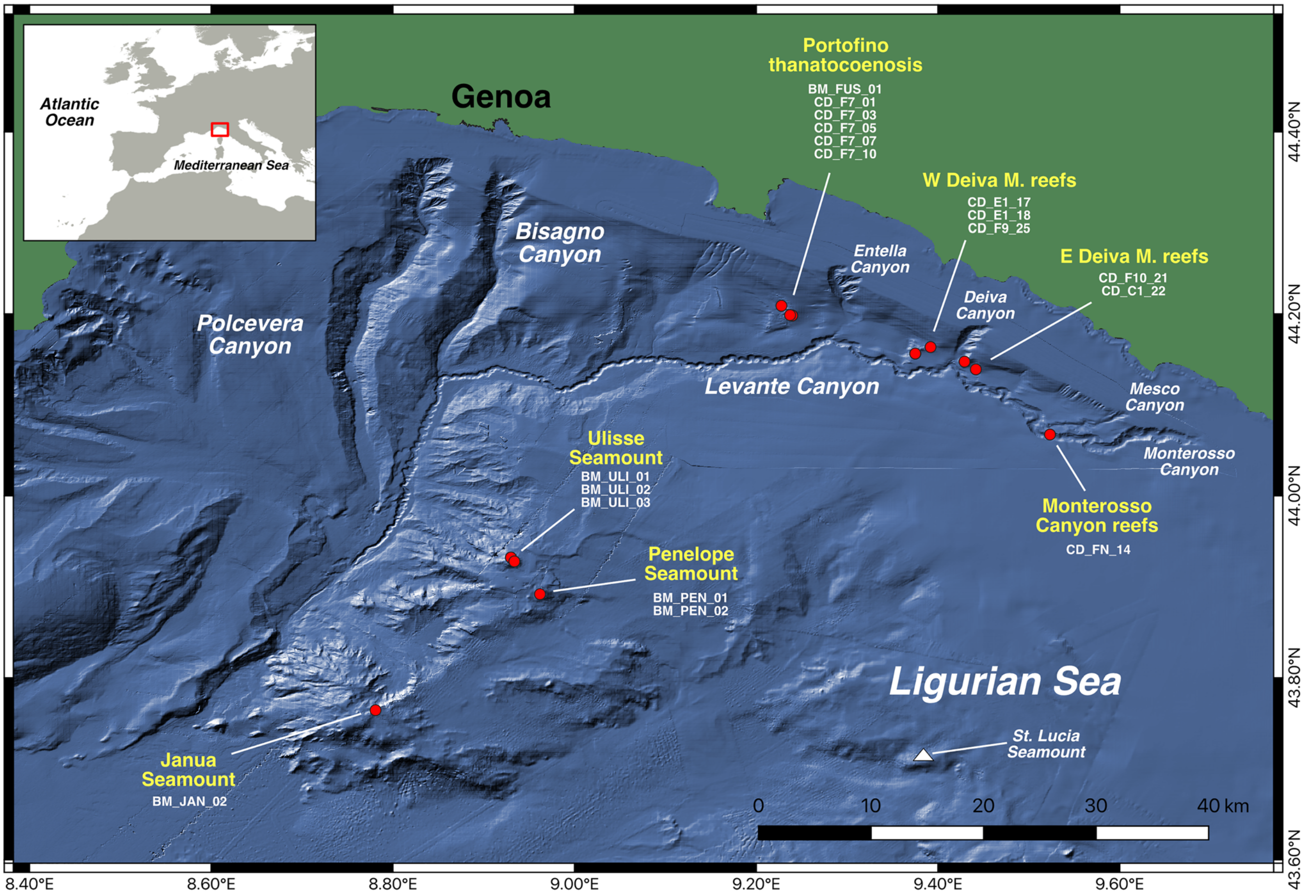


Fig. 1 Map of the study area and its position within the NE Atlantic region and the western Mediterranean basin (inset). The major topographic structures of the seabed are indicated. Red dots indicate the site where samples were collected through ROV

Sea. Ulisse and Penelope are part of the same large volcanic complex, with peaks at 397 and 447 m, while Janua reaches 810 m. Bo et al. (2020a, 2021) recently investigated the deep-sea fauna associated with these structures.

The Ligurian basin receives runoffs drained from the Alps and Apennines, with the Arno and, to a minor extent, the Magra River (both located in the easternmost sector) providing the largest discharges (Astraldi et al. 1994; Bassano et al. 2000). The water circulation in the basin follows a clear cyclonic pattern, with well-defined water masses flowing at different depths. Among them, the Levantine Intermediate Water (LIW), originating in the eastern Mediterranean Sea and flowing westward at 300–700 m depth, is considered particularly important in sustaining bathyal communities dominated by cnidarians along the central and western Mediterranean slopes (Millot 1999; Taviani et al. 2017; Chimienti et al. 2019; Vertino et al. 2019; Prieur et al. 2020; Weinberg et al. 2022).

ROV surveys

The octocoral specimens investigated in this study were collected by the ROV MultiPluto (GayMarine) during two oceanographic campaigns conducted on board the *Daedalus* catamaran (Fondazione AzioneMare). The first campaign (BIOMOUNT project—SIR-MIUR) was conducted between 2017 and 2018: Twenty-four dives were performed to explore the megabenthic communities inhabiting the Ligurian seamounts and nearby bathyal areas between 135 and 1826 m. The second campaign (Curiosity Driven Project—University of Genova) took place in 2021. It aimed to investigate the cold-water coral areas located along the Levante Canyon in the eastern Ligurian Sea through 14 ROV dives performed at depths ranging from 445 to 797 m. The ROV was equipped with two strobe lights, a high-definition video camera (Sony RX100 II), a depth sensor, a compass, and an acoustic tracking position system (USBL HDR Gaymarine). A three-jaw grabber mounted on a manipulative arm was dedicated to collecting specimens for taxonomical analyses. Additional information on the two ROV campaigns, including the complete lists of explored sites and results, can be found in Enrichetti et al. (2018) and Bo et al. (2020a, 2021; 2023).

Sample collection

Eighteen octocoral specimens were photographed in situ between 400 and 822 m and collected using the MultiPluto three-jaw grabber. The collected material was preserved either dry or in 96% ethanol and transferred to the laboratory for taxonomic analysis. Although the present study is limited to morphological characters, subsamples of most specimens were preserved in absolute ethanol to enable potential future molecular analyses. Samples obtained from deep trawl fishing bycatch in the eastern Ligurian Sea were included in the study. Table 1 presents the complete list of specimens, along with their associated metadata. All the collected material has been deposited in the DISTAV deep-sea zoological collection, University of Genoa.

Morphological analysis

Colony architecture and polyp arrangement were initially examined under a stereomicroscope and photographed for documentation. Dissociated sclerites were obtained by immersing small branches (< 1 cm) in a sodium hypochlorite solution. After the complete dissolution of the organic matter, the sclerites were rinsed with water. Dissociated sclerites and cleaned polyp material (obtained through brief rinses in sodium hypochlorite solution followed by washing with water) were dried and then mounted on stubs coated with a carbon layer and sputtered with a 50-nm-thick gold layer. The arrangement, morphology, size, and ornamentation of sclerites were observed and measured using a Vega 3 TESCAN microscope (type LMU). Measurements were taken using ImageJ software (version 1.53).

Species distribution

The geographical ranges and bathymetric distributions of the identified species were analyzed based on the available scientific literature, allowing for the classification of the Ligurian bathyal octocorals into key chorological and bathymetric categories. Furthermore, the geographical coordinates associated with the collected samples and the annotations collected during ROV video analysis (see Bo et al. 2020a, 2021, 2023) were plotted using QGIS software (version 3.22.12-Bialowieza) on a map of the Ligurian Sea to investigate the basin-scale distribution of the considered species. To provide a more comprehensive overview of the deep-sea octocoral fauna of the Ligurian Sea, all records previously reported from the area were included in the geographical and bathymetrical distribution analysis.

Systematics

Subphylum ANTHOZOA Ehrenberg, 1834.

Class OCTOCORALLIA Haeckel, 1866.

Order Octocorallia *incertae sedis.*

Family Clavulariidae Hickson, 1894 (Note: family assigned following Ocaña and Çinar (2018), although the current phylogenetic position remains uncertain due to lack of molecular data as stated in McFadden et al. 2022).

Genus *Rolandia* de Lacaze-Duthiers, 1900.

***Rolandia* cf. *coralloides* de Lacaze-Duthiers, 1900**

Table 1 List of the octocoral samples analyzed with associated information. Date: dd.mm.yyyy. BM: SIR-MIUR_BIOMOUNT Project "Biodiversity Patterns of the Tyrrhenian Seamounts" (2017–2018). CD: University of Genoa Curiosity-Driven Project "Lost coral reefs: ancient deep-sea bioherms in a modern world" (2021–2022). * Not analyzed in the present study (see Bo et al. 2020a). ** Sample under investigation

Sample ID	ROV DIVE code	Date	Site	x	y	Depth (m)	Substrate	Species
BM_ULI_01	BM_01	30.05.2017	Ulisse Seamount	8.92983	43.93200	448	Outcropping rock	*Callogorgia verticillata*
BM_ULI_02	BM_01	30.05.2017	Ulisse Seamount	8.92983	43.93200	448	Outcropping rock	*Bebryce mollis*
BM_ULI_03	BM_02	30.05.2017	Ulisse Seamount	8.93367	43.92767	400	Outcropping rock	*Villogorgia bebrycoides*
BM_JAN_02	BM_05	31.05.2017	Janua Seamount	8.78083	43.76433	822	Biogenic conglomerate	*Chelidonisis aurantiaca**
BM_FUS_01	BM_FUS_01	15.06.2017	Portofino thanatocoenosis	9.22767	44.20900	737	Coral rubble	*Acanthogorgia* sp.
BM_PEN_01	BM_07	14.08.2017	Penelope Seamount	8.96367	43.89267	457	Mud and biogenic detritus	cf. *Daniela koreni***
BM_PEN_02	BM_08	14.08.2017	Penelope Seamount	8.96183	43.89167	497	Coral rubble	*Muriceides lepida*
CD_F7_01	CD_03	15.06.2021	Portofino thanatocoenosis	9.23952	44.19824	724	Coral framework	*Placogorgia coronata*
CD_F7_03	CD_03	15.06.2021	Portofino thanatocoenosis	9.23952	44.19824	724	Plastic sheet	*Acanthogorgia armata*
CD_F7_05	CD_03	15.06.2021	Portofino thanatocoenosis	9.23952	44.19824	724	Plastic sheet	*Muriceides lepida*
CD_F7_07	CD_03	15.06.2021	Portofino thanatocoenosis	9.23952	44.19824	724	Plastic sheet	*Rolandia* cf. *coralloides*
CD_F7_10	CD_04	16.06.2021	Portofino thanatocoenosis	9.23718	44.19877	712	Coral framework	*Muriceides lepida*
CD_FN_14	CD_08	10.09.2021	Monterosso Canyon reefs	9.52330	44.06730	549	Mud	*Acanella* cfr. *arbuscola*
CD_E1_17	CD_10	11.09.2021	W Deiva Marina reefs	9.37500	44.15633	675	Coral rubble	*Acanthogorgia armata*
CD_E1_18	CD_10	11.09.2021	W Deiva Marina reefs	9.37500	44.15633	675	Coral rubble	*Muriceides lepida*
CD_F10_21	CD_11	13.09.2021	E Deiva Marina reefs	9.44170	44.13900	541	Coral rubble	*Placogorgia massiliensis*
CD_C1_22	CD_12	13.09.2021	E Deiva Marina reefs	9.42920	44.14750	474	Coral rubble	*Rolandia* cf. *coralloides*
CD_F9_25	CD_13	12.11.2021	W Deiva Marina reefs	9.39180	44.16350	567	*M. oculata*	*Muriceides lepida*
DISTAV1 20,230,522	Bycatch (M/P Teresa Madre)	22.05.2022	Off Portofino	9.24098	44.22289	350–450	Plastic debris	*Rolandia* cf. *coralloides*

(Figs. 2, 3, Table S1).

Examined material. CD_F7_07 Portofino thanatocoenosis, 724 m, on plastic debris; CD_C1_22 eastern Deiva Marina Canyon, 474 m, on dead *Madrepora oculata* fragment; DISTAV1_20230522 collected on May 22, 2023, by M/P Teresa Madre in the trawling ground nearby the Portofino thanatocoenosis (indicatively: 44.22289°N 9.24098°E), 350–450 m, on plastic debris.

Description. Colonies small, formed by six (CD_F7_07) to about 200 polyps (DISTAV1_20230522) arising in rows at irregular intervals from ribbon-like stolons (Fig. 2a) or embedded at short distances in a common coenenchyme formed by fused stolons (Fig. 2b, c). Stolons are circular or flattened in cross section, with 4 to 6 internal canals (Fig. 2d). Calyx width ranges from 1 to 4 mm (Fig. 2a-d). The color ranges from reddish and light red to deep orange (Fig. 2 a-d).

Sclerites types include: i) irregular plates (Fig. 3a), ranging from 74 to 140 µm in length; ii) shuttles (Fig. 3b), ranging from 65 to 92 µm in length; iii) six radiates (Fig. 3c), ranging from 56 to 84 µm in length; iv) fused quadruplets (Fig. 3d), ranging from 45 to 105 µm in length; and v) flat rods, ranging from 39 to 70 µm in length. Irregular plates and fused quadruplets are widely distributed within the

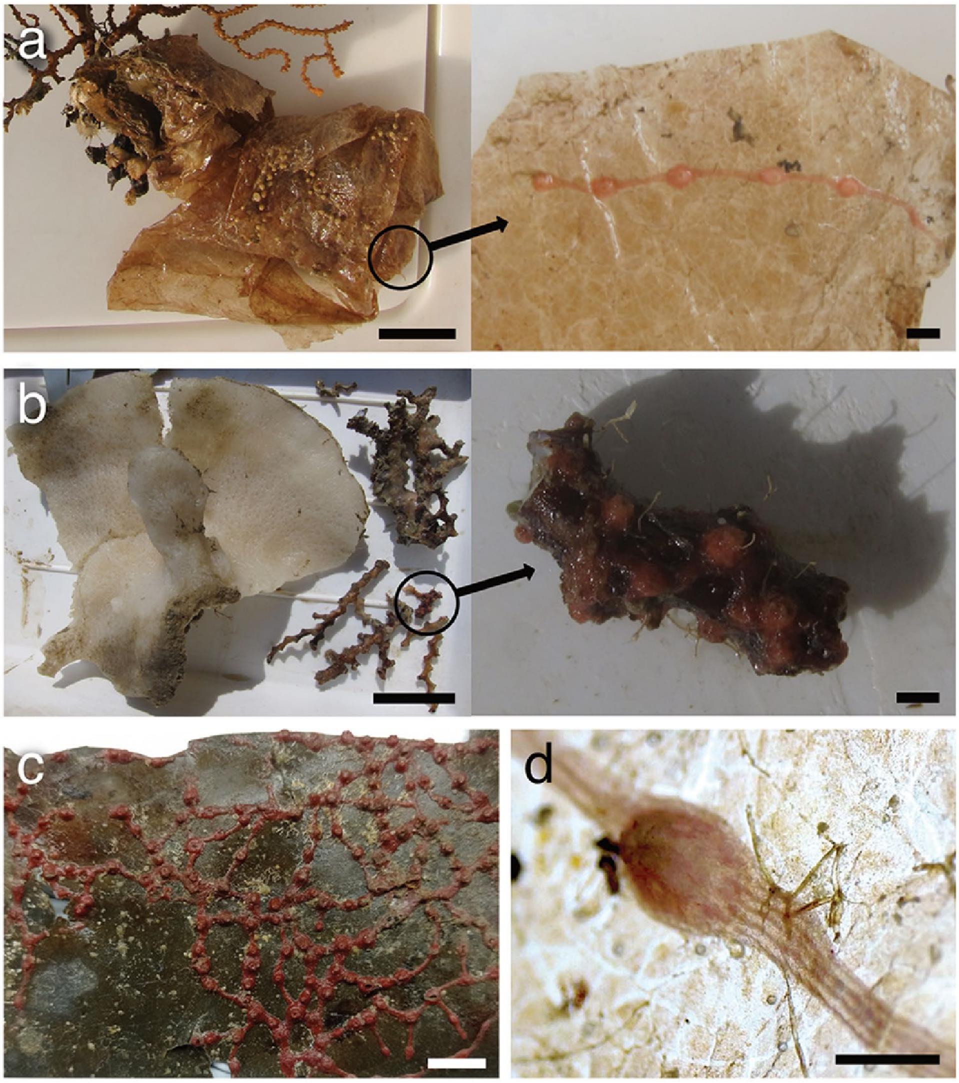


Fig. 2 *Rolandia* cf. *coralloides*. **a** The plastic sheet entangled on the coral fragment at the base of a large colony of *Placogorgia coronata* hosts living zoanthids, small *Muriceides lepida* colonies, and the specimen CD_F7_07 (inset). **b** The *Madrepora oculata* rubble colonized by encrusting sponges, a large *Pachastrella monilifera* specimen, and the specimen CD_C1_22 (inset). **c** Specimen DISTAV1_20230522. **d** Details of the polyp and stolon at the stereomicroscope (CD_F7_07). The ribbon-like structure crossed by 4–6 internal canals is evident. Scale bars: a = 4 cm (inset = 2 mm); b = 4 cm (inset = 2 mm); c = 10 mm; d = 1 mm

colony, whereas six radiates are located in the stolon and shuttles in the calyx. Flat rods are probably situated in the anthocodium.

Taxonomic remarks. *Rolandia coralloides* has been long considered a synonym of *Sarcodictyon catenatum* Forbes in Johnston, 1847. However, Ocaña et al. (2000a) separated the two species, identifying the presence of fused quadruplets as a distinctive feature of *R. coralloides*. Following Ocaña et al. (2000a), other characteristics support this separation: *S. catenatum* typically displays smaller colonies, stolons with 2–4 canals, larger calyces (3–6 mm), smaller sclerites (< 0.07 mm), and is generally found at shallower depths (0–100 m depth) (Table S1).

The samples analyzed in the present study show fused quadruplets as in *R. coralloides*; however, the sclerome shows some affinities with the sclerites types described for *S. catenatum* by Ocaña et al. (2000a) (see Fig. 1, page 417), including a possible fifth type of sclerite. This additional type, probably located in the tentacles, is characterized by reduced size and flattened shape. At the same time, i) the number of polyps is more variable than previously reported for *R. coralloides* (10 to more than 50) (Ocaña et al. 2000a), ranging from 6 in sample CD_F7_07 to more than 200 in sample DISTAV1_20230522, and ii) the stolon can be flattened in cross section with 4–6 internal canals, rather than exclusively circular with 9–12 canals as reported by Ocaña et al. (2000a).

The degree of variability in morphological characters, along with the influence of environmental gradients, remains unresolved in these two species. A larger number of samples along with phylogenetic analyses are required to disentangle these two taxa. Therefore, a conservative approach is adopted in this study and the identification is *Rolandia* cf. *coralloides*.

Ecological remarks. *R. coralloides* occupies a wide bathymetrical range, extending from littoral to 800 m depth,

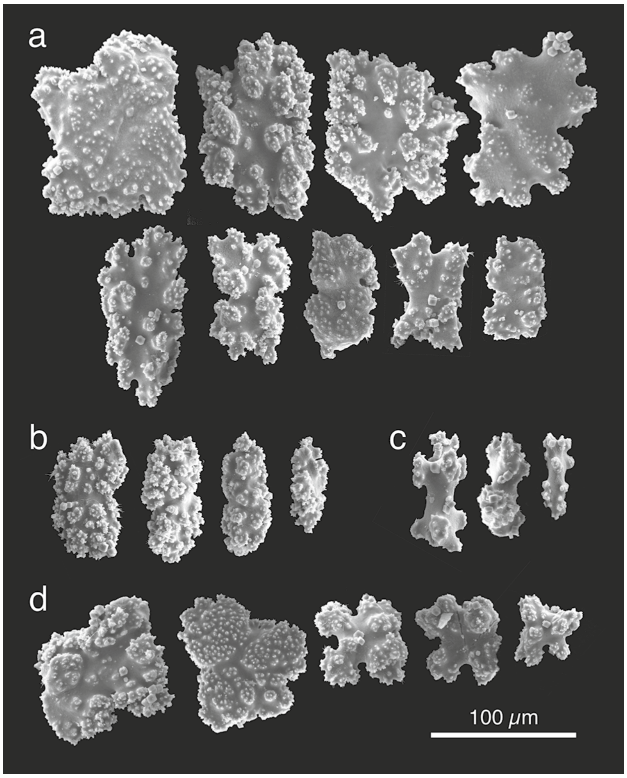


Fig. 3 SEM images of *Rolandia* cf. *coralloides* sclerites (sample CD_ C1_22): **a** irregular plates, **b** shuttles, **c** six radiates, and **d** fused quadruplets

and is often reported associated with circalittoral coralligenous communities. It has been reported to grow on several substrates, including stones, shells, coral rubble, *Posidonia oceanica* rhizomes, and epibiont on sponges, gorgonians, scleractinians, bryozoans, barnacles, and ascidians (Weinberg 1978; Gili 1982; Ocaña et al. 2000a; Ocaña and Çinar 2018). The samples presented in the present study were found between 400 and 724 m on *Madrepora oculata* rubble and plastic debris. If the identification of samples CD_F7_07 and DISTAV1_20230522 as *R. coralloides* is confirmed, it would represent the first evidence of this species settling on plastic.

Distribution. *R. coralloides* is reported from the NE Atlantic (Azores) and the Mediterranean Sea (Gibraltar, Algeria, Spain, Gulf of Lions, Ligurian Sea, Gulf of Naples, Adriatic Sea, Sea of Marmara) (Rossi 1958; Weinberg 1978; Ocaña et al. 2000a; Ocaña and Çinar 2018).

The presence of this species in the eastern Ligurian Sea was documented by Rossi (1958). In the present study, all examined samples were collected from the same area investigated by Rossi (1958), located on the continental slope near the Portofino thanatocoenosis. Additionally, two unidentified stoloniferans were observed in ROV footage from the Ulisse, Penelope, and Janua Seamounts (Bo et al. 2020a, 2021) (Fig. 22); however, their taxonomic identity remains unresolved.

Order Malacalcyonacea McFadden, van Ofwegen & Quattrini, 2022.

Family Acanthogorgiidae Gray, 1859.

Genus *Acanthogorgia* Gray, 1857.

Acanthogorgia armata Verrill, 1878

(Figs. 4, 5, Table S2).

Examined material. CD_F7_03 Portofino thanatocoenosis, 724 m, on a plastic sheet, juvenile; CD_E1_17 Deiva Marina Canyon, 675 m, on coral rubble.

Description. Colonies planar and relatively small, with sample CD_E1_17 measuring 18 cm and sample CD_F7_03, a juvenile colony, measuring 4 cm. Color ranges from yellow to pale yellow both in vivo and in preserved material (Fig. 4a-c). Stem thickness at the base about 2 mm in diameter (0.5 mm in the juvenile colony). The polyps are mainly arranged in two rows; they are not particularly dense in the basal and central portions of the colony (Fig. 4d) but become crowded and oriented in all directions toward the tips of the branches (Fig. 4b, e). Polyps are tall (up to 3.2 mm in CD_F7_03 and up to 5 mm in CD_E1_17), slender and thin, narrower in the central area of the column and thicker in the basal and collar regions (Fig. 4d, f). This characteristic shape is less evident in juvenile colonies (CD_F7_03) (Fig. 4c, e) and young/small polyps. The neck area is not constricted (Fig. 4f).

In the polyp, at the base of each tentacle, there are several differently sized crown spines (Figs. 4f, 5a), the longest of which are up to 2 mm. The basal part of these sclerites is covered with tubercules, but the free-standing part is smooth (Fig. 5a). Small tentacle sclerites (Fig. 5b) and thin long sclerites from the neck area (Fig. 5c) are also present. Polyp's wall is smooth, with eight rows of flattened, obliquely opposed sclerites (Figs. 4f, 5d). Coenenchyme with simple and branched sclerites (Figs. 4g, 5e, f) do not project from the surface. Thornstars are not present.

Taxonomic remarks. At present, records of *A. armata* within the Mediterranean Sea are scarce and limited to the Alboran Sea (Ocaña et al. 2000b; Pardo et al. 2011), with *A. hirsuta* being considered the only *Acanthogorgia* species inhabiting the basin (Grasshoff 1973, 1986; Carpine and Grasshoff 1975; Altuna and Poliseno 2019). However, the specimens examined in this study do not display the thornstars of the coenenchyme that are characteristic of *A. hirsuta*. These specimens are identified as *A. armata* also based on the morphology and size of the polyps, the size of the crown spines, and the presence of several branched sclerites in the coenenchyme (Table S2). ROV analysis of the *A. armata* population along the Levante Canyon, where the samples were collected, revealed an average colony height of 9.5 ± 4.8 cm (n = 244), with maximum heights reaching up to 30 cm (unpublished), fitting the size range known in the literature for this species (Table S2).

In the Mediterranean region, most *Acanthogorgia* records are attributed to *A. hirsuta* by default, often without thorough species-level verification, therefore possibly resulting in an underestimation of the occurrence of *A. armata*. None of the other NE Atlantic species, including *Acanthogorgia pico* Grassohoff, 1973, matches the diagnosis of the Ligurian samples examined here.

Ecological remarks. In the Atlantic Ocean, *A. armata* has been recorded at depths ranging from 171 to 2137 m on hard substrates, including rocks and biogenic detritus (Verrill 1883; Grasshoff 1973, 1981, 1989; Buhl-Mortensen et al. 2015). Two samples settled on *Keratoisis grayi* Wright, 1869 colonies are reported from the Newfoundland and Labrador regions (Wareham and Edinger 2007). Slightly different depth ranges have been observed along the opposite coasts of the N Atlantic Ocean: 171–1445 m in the NW sector (Wareham and Edinger 2007; Jørgensen et al. 2013; Buhl-Mortensen et al. 2015) and 557–1237 m in the NE sector. The associated fauna includes juvenile gooseneck barnacles (*Lepas* sp.) and the Iceland scallop *Chlamys islandica* (O. F. Müller, 1776) (Wareham and Edinger 2007). In the Alboran Sea, *A. armata* has been reported growing on rocks and dead corals between 315 and 460 m depth (Pardo et al. 2011).

In the Ligurian Sea, *A. armata* occurs at depths between 445 and 779 m, reaching densities of up to 6.5 colonies m^{-2} (Bo et al. 2023) on hard bottoms, mainly represented by dead corals. The record on plastic debris is the first documentation for this species. Overall, *A. hirsuta* is primarily a mesophotic species (70–200 m), while *A. armata* is predominantly bathyal.

Distribution. NW Atlantic (off Massachusetts, Maine, Nova Scotia, Newfoundland, Labrador, Davis Strait, W

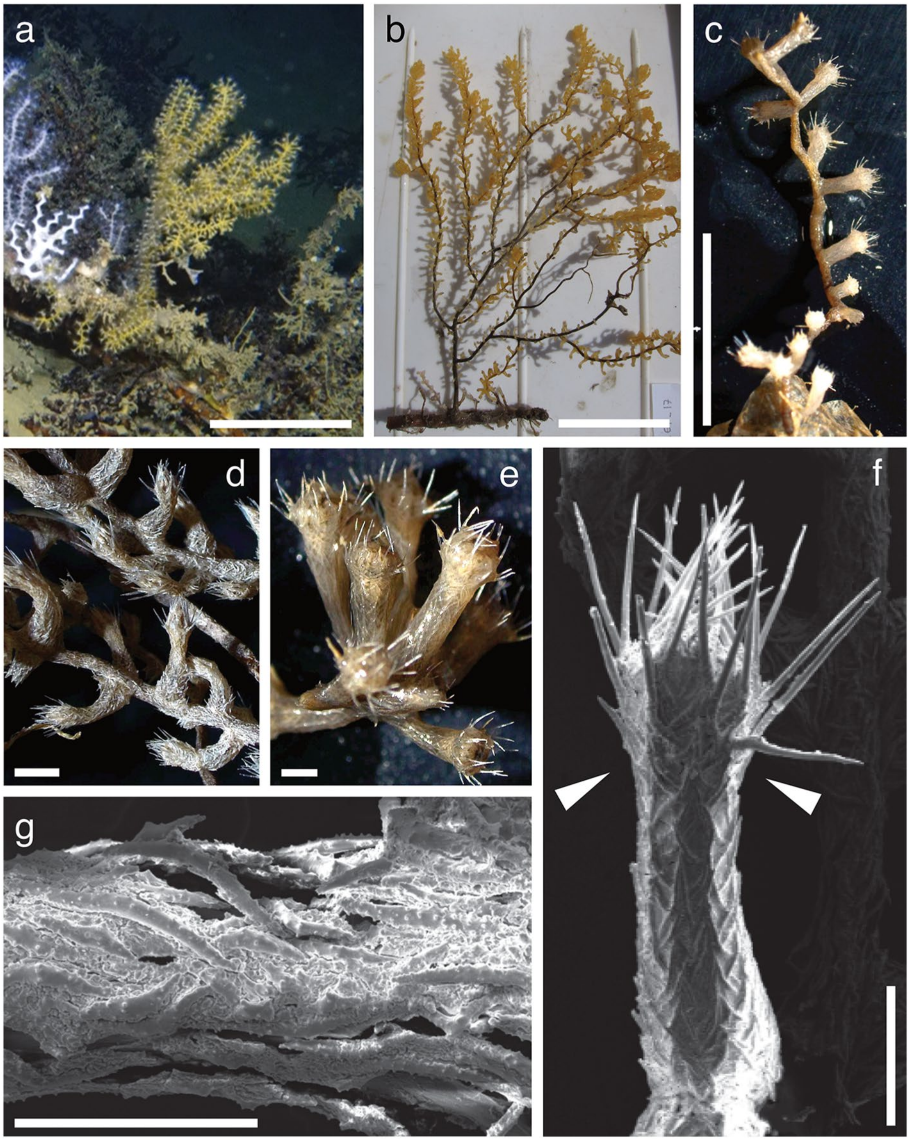


Fig. 4 *Acanthogorgia armata*. **a** ROV image of living *A. armata* from Deiva Marina Canyon at 675 m (CD_E1_17). *Madrepora oculata* and *Muriceides lepida* colonies colonize the same coral rubble. **b** Sample CD_E1_17 freshly collected. **c** A juvenile colony settled on a plastic sheet (CD_F7_03). Polyps density and distribution vary from the central area of the colony **d** (CD_E1_17) to the arm tip **e** (CD_F7_03). SEM image of a polyp **f** and the coenenchyme **g** (CD_E1_17). White arrows indicate the neck area. Scale bars: a = 10 cm; b = 5 cm; c = 1 cm; d = 2 mm; f = 1 mm; g = 0.5 mm

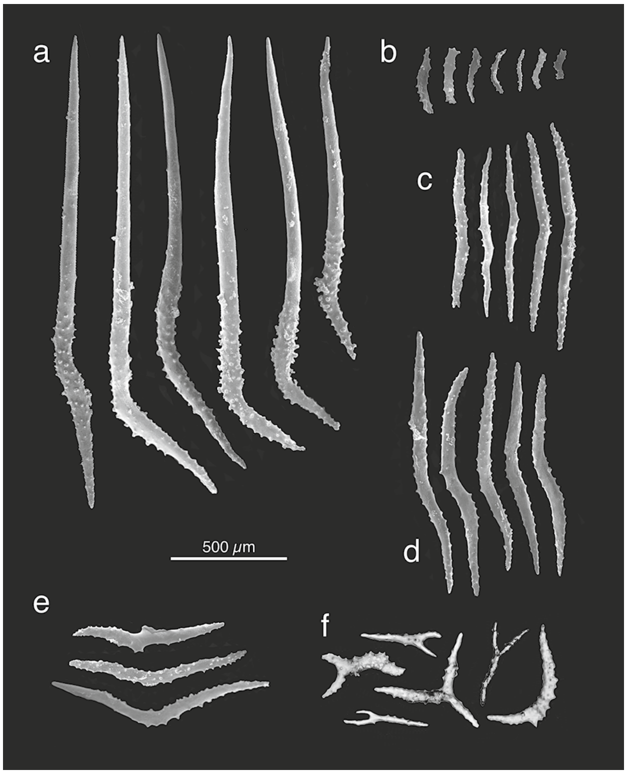


Fig. 5 SEM images of *Acanthogorgia armata* sclerites (sample CD_E1_17). **a** Crown spines. **b** Tentacle sclerites. **c** Sclerites of the neck area. **d** Sclerites of the body wall. **e** Sclerites of the outer layer of the coenenchyme. **f** Branched sclerites of the coenenchyme

Greenland) and NE Atlantic (SW Iceland, SW Ireland, Bay of Biscay, Portugal, Morocco, Acores, Mid-Atlantic Ridge) (Verrill 1883; Grasshoff 1973, 1981, 1989; Buhl-Mortensen et al. 2015). In the Mediterranean Sea, *A. armata* was previously known only from the Alboran Sea (Cabliers and El Algarrobo 250–500 m) (Pardo et al. 2011); therefore, this represents the first documented record of this species for the western Mediterranean basin. In the Ligurian Sea, *A. armata* has been observed exclusively on the continental shelf, along the path of the Levante Canyon (Fig. 22).

***Acanthogorgia* sp.**

(Figs. 6, 7, Table S2).

Examined material. BM_FUS_01 Portofino thanatocoenosis, 737 m, on a subfossil coral framework.

Description. Small colony (5 cm), planar, slender, and yellow (Fig. 6a, b). Stem diameter at the base 0.8 mm. Polyps mainly arranged in two rows: scarce in the basal and central portions of the colony, but more crowded and oriented in all directions toward the tips of the branches (Fig. 6b). Polyps' height up to 3 mm, thick, with a peculiar constriction in the neck area (Fig. 6c-e). In the body wall, the tips of the obliquely opposed sclerites moderately protrude (Fig. 6c-e).

Crown spines short, generally not exceeding 0.9–1.0 mm (Fig. 7a). Their basal part is covered with tubercules, and the free-standing portion is smooth. Tentacle sclerites (Fig. 7b) and neck sclerites (Fig. 7c) also present. Coenenchyme with curved simple sclerites (Fig. 7d). Thornstars not present.

Taxonomic remarks. The reduced colony size of sample BM_FUS_01 may suggest that some morphological characters are not fully developed, complicating species identification. However, several features observed in this specimen strongly support its assignment to *Acanthogorgia pico* Grasshoff 1973 (Table S2). In other NE Atlantic *Acanthogorgia* species, crown spines are longer (1.7–2.1 mm), and polyps are considerably larger (3–8 mm long). Polyps of *A. armata* are slender and lack a constriction in the neck region, with the narrowest point located roughly at the midsection of the body. Additionally, *A. armata* possesses branched sclerites in the coenenchyme, while *A. hirsuta* is characterized by thornstars, neither of which is present in sample BM_FUS_01. Phylogenetic analyses, ideally including type materials, may help determine whether *A. armata* and *A. pico* represent distinct taxa or age-related morphotypes of the same species. In this study, we adopted a conservative approach and identified the specimens as *Acanthogorgia* sp.

Ecological remarks. *A. pico* is known from hard bottoms, including coral rubble, at depths ranging from 550 to 930 m. Therefore, this Mediterranean finding fits perfectly in the known ecological setting of the taxon.

Distribution. If the identification of specimen BM_FUS_01 as *Acanthogorgia pico* is confirmed, it would represent the first record of this species in the Mediterranean Sea. To date, the species is known only from the NE Atlantic Ocean (Azores, Ireland) (Grasshoff 1973).

Genus *Placogorgia* Wright & Studer 1889

Placogorgia coronata Carpine & Grasshoff 1975

(Figs. 8, 9, Table S3).

Examined material. CD_F7_01 Portofino thanatocoenosis, 724 m, on a subfossil coral framework.

Description. Fan-shaped colony, approximately 44 cm tall and 46 cm wide, dark yellow (brown when dried) (Fig. 8a-c). Irregularly branched, with thick basal ramifications (about 4 mm in diameter) developing in more slender, thin branches (1–1.8 mm), usually slightly thicker at the tips. Anastomoses between branches not observed. Basal diameter of the stem 10.4 mm, growing on a dead *M. oculata* skeleton entangled in a plastic sheet. Polyps well-spaced and irregularly distributed on the basal part of the colony (Fig. 8d), becoming denser and mainly arranged on the lateral sides of the branches in the central and distal areas (Fig. 8e). Polyps particularly crowded and irregularly distributed on the branch tips. Contracted polyps range from 0.8

to 2.1 mm (Fig. 8d-e, g; Table S3); expanded polyps measure up to 3 mm in height (Fig. 8f).

Calyx formed by thornscales, characterized by a large apical spine and a flat portion bearing several downward root-like projections (Figs. 8f-g, 9a). Apical spine generally thicker in the median region, a distinctive characteristic of this species. Size and complexity of the thornscales vary considerably within the same specimen, ranging from slender sclerites with a large apical spine (up to 2 mm) to thick sclerites with a short spine and large and more branched basal plates (0.4–0.9 mm). Anthocodium presenting: i) an operculum, formed by 2–5 curved rods (0.4–1.2 mm) located at the base of each tentacle (Figs. 8f, 9b); ii) a collaret of 5–7 rings of slender and curved sclerites (0.4–0.8 mm) (Figs. 8f, 9c); iii) small tentacles sclerites (0.2–0.4 mm) (Fig. 9d). Coenenchyme with simple and branched spindles (0.4–0.6 mm) in the inner layer (Fig. 9e) and thornspindles (0.6–1.1 mm) in the outer layer (Fig. 9f). Thornspindles have a flattened and widened spindle-like basal part with root-like projections and one (occasionally two) upward thorn. Thornstars not present.

Taxonomic remarks. A detailed morphological description of *P. coronata* was recently provided by Enrichetti et al. (2018), based on 13 samples collected as bycatch from trawling grounds in the eastern Ligurian Sea. The study addressed the main taxonomic challenges related to this species, particularly its distinction from the closely related genera *Paramuricea* and *Spinimuricea*. In particular, the separation between *Paramuricea* and *Placogorgia* is very subtle, as confirmed also by the phylogenomic analyses (McFadden

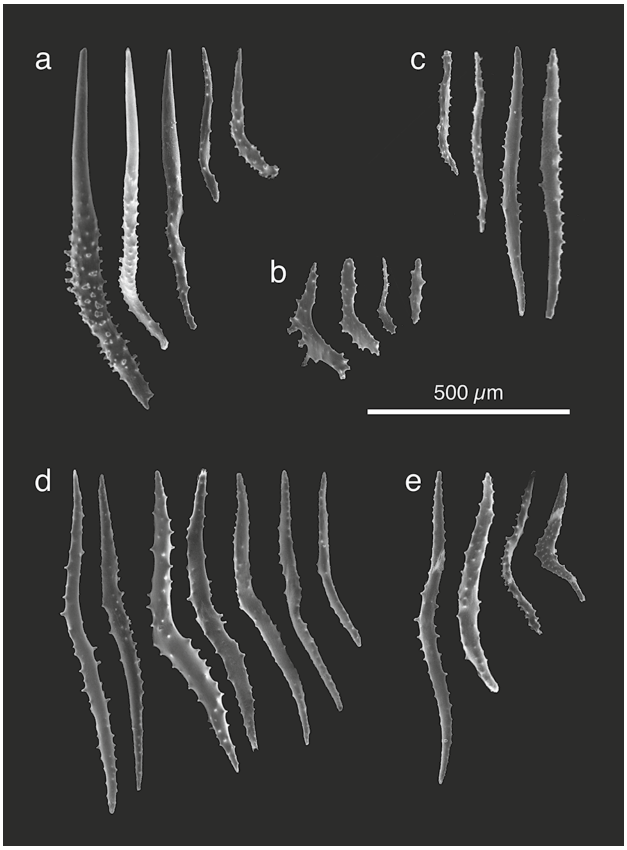
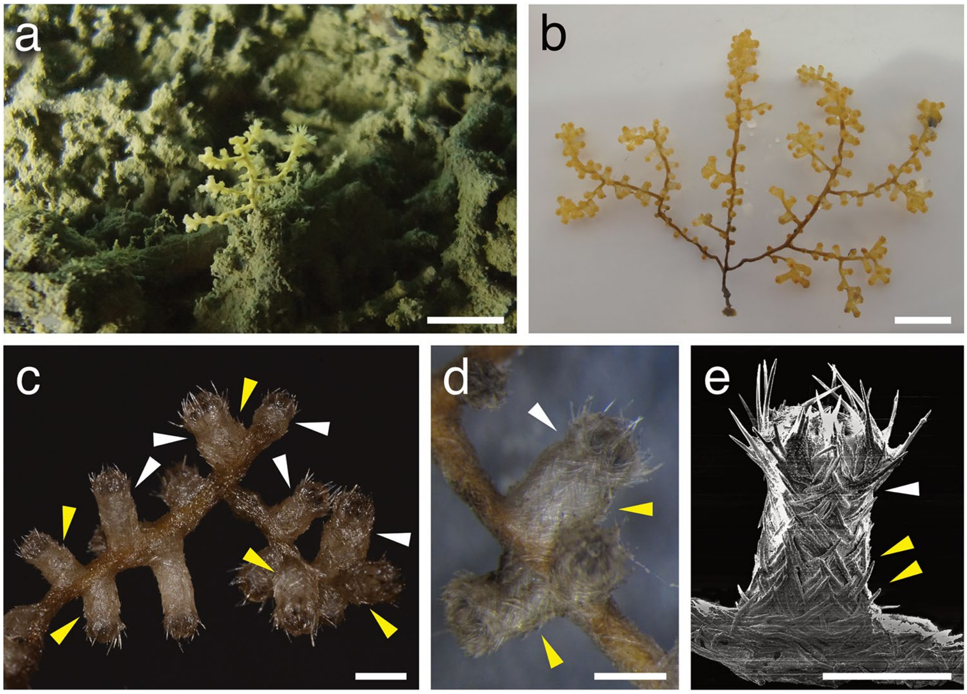


Fig. 7 SEM images of *Acanthogorgia* sp. sclerites (sample BM_FUS_01). **a** Crown spines. **b** Tentacle sclerites. **c** Sclerites of the neck area. **d** Sclerites of the polyp wall. **e** Sclerites of the coenenchyme

Fig. 6 *Acanthogorgia* sp. (BM_FUS_01). **a** Living colony from the Portofino thanatocoenosis, at 737 m. **b** The same colony freshly collected. Images of polyps at the stereomicroscope **c**, **d** and SEM **e**. The restriction under the neck area (white arrows) and the moderately protruding sclerites of the body wall (yellow arrows) are indicated. Scale bars: a-b = 1 cm; c-e = 1 mm



et al. 2022). The key distinguishing character is the presence, in *Placogorgia*, of spiny sclerites in the coenenchyma, specifically thornspindles and thornstars, which give the colony its characteristic thorny appearance (Bayer 1959; Grasshoff 1977). Conversely, the coenenchyme of *Paramuricea* contains only simple or branched spindles, lacking any spines, resulting in a smoother surface.

However, spiny sclerites in the coenenchyme are not observed in all *Placogorgia* species, including *Placogorgia becena* Grasshoff 1977 and the type species *Placogorgia atlantica* Wright & Studer 1889. This raises the possibility of either a taxonomic misidentification or a more fluid boundary between *Placogorgia* and *Paramuricea*. Notably, the type species of *Paramuricea*, *Paramuricea placomus* (Linnaeus, 1758), has occasionally been reported to exhibit coenenchymal sclerites with spines (Grasshoff 1977). In *Placogorgia*, there appears to be a morphological continuum between the thornscales of the calyx wall and the thornspindles of the coenenchyma. The thornscales at the base of the calyx gradually show shorter thorns and broader, branched basal plates (Fig. 9a), closely resembling the thornspindles found in the coenenchyme (Fig. 9f). This continuity may lead to confusion in species or genus identification.

Another trait often used to distinguish the two genera is the shape of the thornscales. In *Placogorgia*, these structures typically have a broad, flat plate, less evident, or absent in *Paramuricea*. In specimen CD_F7_01, both the well-developed basal plates of the calyx wall thornscales (Fig. 9a) and the prominent spine on the coenenchymal sclerites (Fig. 9f) support its attribution to the genus *Placogorgia*.

Six *Placogorgia* species are known in the eastern Atlantic Ocean, two of which occur in the Mediterranean Sea. These species have been grouped based on colony morphology and presumed genera affinity (Enrichetti et al. 2018).

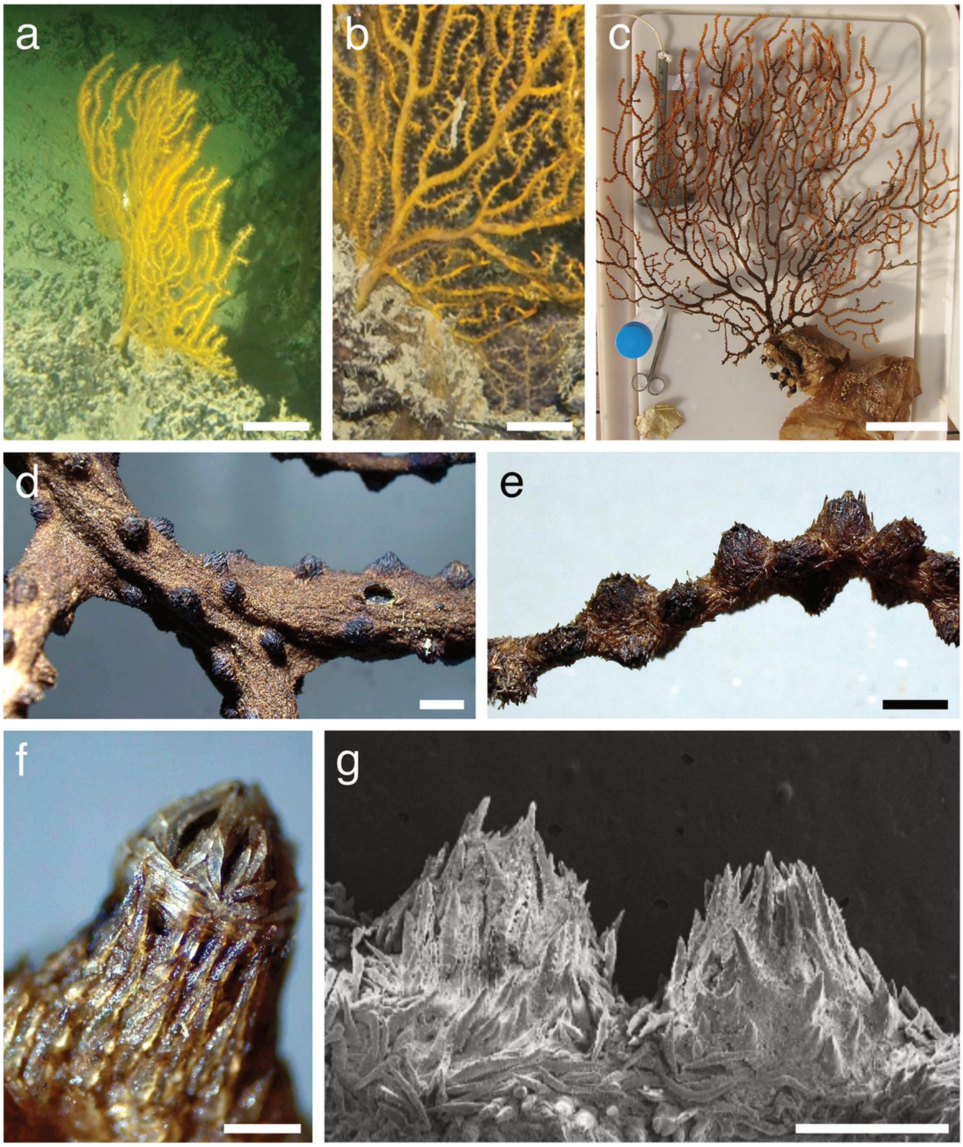


Fig. 8 *Placogorgia coronata* (CD_F7_01). **a**, **b** Living colony of *P. coronata* from the Portofino thanatocoenosis, at 724 m. **c** The same colony freshly collected. Note the darkening of the color and the plastic sheet entangled on the colony base. **d**, **e** Differences in polyp distribution and abundance between the basal part of the colony (**d**) and a distal ramification (**e**). **f** Stereomicroscope image of a polyp showing the architecture of the sclerites of the anthostele (thornscales) and the anthocodium (collaret sclerites and points/opercular sclerites). **g** SEM image of two retracted polyps. Scale bars: a, c = 10 cm; b = 5 cm; d, e = 2 mm; f = 0.5 mm; g = 1 mm

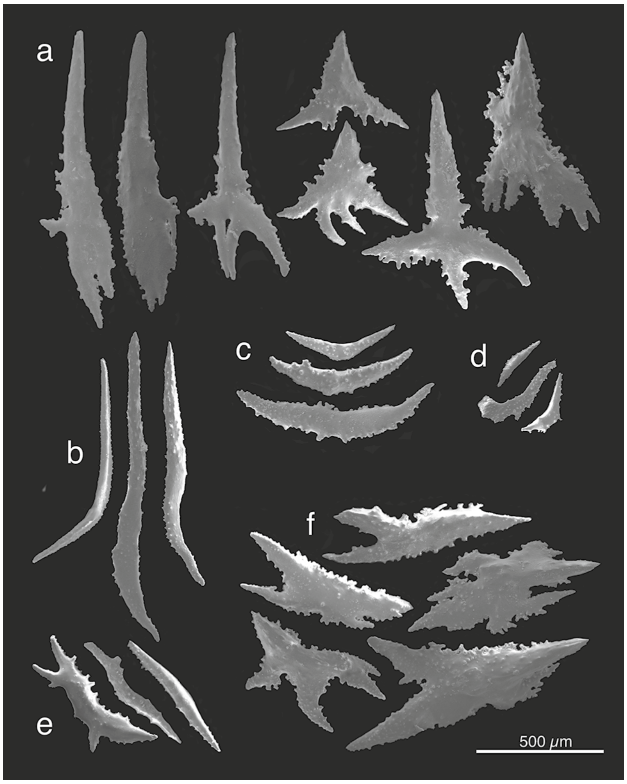


Fig. 9 SEM images of *Placogorgia coronata* sclerites (sample CD_F7_01). **a** Thornscales of the calyx. **b** Points or opercular sclerites. **c** Spindles of the collaret. **d** Small rods from the tentacles. **e** Branched and unbranched spindles of the inner layer of the coenenchyme. **f** Thornspindles of the outer layer of the coenenchyme

The *Paramuricea*/*Echinomuricea*-like group includes species with large colonies (up to 45 cm), thick branches, and densely packed polyps: *P. graciosa* (Tixier-Durivault & d'Hondt, 1974), *P. intermedia* (Thomson 1927), and *P. terceira* Grasshoff 1977. In contrast, the *Placogorgia*-like group comprises smaller (up to 15 cm), slender, fragile colonies with sparse polyps arranged mostly in a single plane: *P. becena* Grasshoff 1977, *P. coronata*, and *P. massiliensis* Carpine & Grasshoff 1975. However, new observation on colony size, polyp arrangement, and sclerite morphology blurs the distinction between these two groups. In particular, *P. graciosa* (found only off Brittany and Ireland) shows affinities with *P. coronata* and *P. massiliensis* from the NE Atlantic and the Mediterranean Sea. Based on the complex basal plates of the thornscales, the median enlargement of their spines (Fig. 9a), and the morphology of the coenenchymal thornspindles (Fig. 9f), specimen CD_F7_01 is identified as *P. coronata*.

In this sample, the collar spindles and the thornscales are slightly smaller than those reported by Carpine and Grasshoff (1975) and Grasshoff (1977), but comparable to specimens previously collected from the Ligurian Sea (Enrichetti et al. 2018) (Table S3). More notable features include the large colony size (the largest recorded to date), the thickness of the branches, and the locally high polyp density. ROV analysis of the *P. coronata* population in the Levante Canyon revealed an average colony height of 15.7 ± 0.5 cm (n = 316), with a maximum of 46 cm (unpublished), considerably larger than the 10 cm known from the literature (Table S3). Morphological features may likely be influenced by environmental conditions and colony age.

Ecological remarks. Literature records indicate that *P. coronata* inhabits hard substrates (rocks, stones, and biogenic debris) at depths ranging from 585 to 2200 m (Carpine and Grasshoff 1975; Grasshoff 1977, 1981, 1985a, 1986, 1989; Brito and Ocaña 2004; Sampaio et al. 2019; Bo et al. 2020b). The record on coralligenous rock (51 m) from Cape Blanc, Morocco (Grasshoff 1977), should be considered with caution. As Grasshoff himself suggested, this unusual occurrence may be explained by the strong upwelling currents in the region, which could allow larvae of deep-water species to settle in shallower habitats that still offer suitable conditions for growth. Similar patterns have been observed in other typically deep-water gorgonians, such as *Paramuricea gray* and *Muriceides sceptrum*, which have also been reported at coralligenous depths in the same area (Grasshoff 1977).

In the eastern Ligurian Sea, an extensive population of *P. coronata* colonies was documented between 445 and 750 m, growing on subfossil coral frameworks and coral rubble, as revealed by ROV exploration conducted in this study (Bo et al. 2023). Sample CD_F7_01 was found settled on a dead *M. oculata* skeleton at 724 m, which also hosted polyps of *Desmophyllum dianthus* (Esper, 1794) and encrusting sponges. ROV analysis of the *P. coronata* population along the Levante Canyon, where sample CD_F7_01 was collected, recorded a maximum density of 4.9 col. m^{-2} (Bo et al. 2023). These observations, together with data on colony size, suggest that *P. coronata* specimens often collected as bycatch in this part of the Ligurian Sea (Enrichetti et al. 2018) may be smaller specimens that settle on coral rubble near the main coral frameworks. In contrast, the largest colonies appear to aggregate directly on the frameworks themselves, where the structural complexity may offer protection from bottom trawling. This preliminary hypothesis has relevant implications for conservation strategies (Davies et al. 2007).

Distribution. In the present study, the examined sample and all the ROV observations were collected from the same area, located along the Levante Canyon in the eastern Ligurian continental slope (Fig. 22). The presence of *P. coronata* in the trawling ground of the eastern Ligurian Sea, located along the Levante Canyon, was documented by Enrichetti et al. (2018). Unidentified *Placogorgia* species have been reported from the Ligurian offshore seamounts based on

ROV footage (Bo et al. 2020a, 2021). However, the presence of *P. coronata* on the Ulisse Seamount has been recently confirmed by the latest exploration (Bo, pers. comm.). Additional records from the western Mediterranean Sea include the Cassidaigne Canyon (Marseille) and the Blanes Canyon (Catalan margin) (Carpine and Grasshoff 1975; Bo et al. 2020b). Additional records from the Alboran Sea are currently only image-based (Aguilar et al. 2009). In the NE Atlantic Ocean, *P. coronata* has been reported from the Bay of Biscay, Morocco, Mauritania, Madeira, the Canary Islands, and the Mid-Atlantic Ridge (Grasshoff 1977, 1981, 1985a, 1986, 1989; Brito and Ocaña 2004; Sampaio et al. 2019).

Placogorgia massiliensis Carpine & Grasshoff 1975
(Figs. 10, 11, Table S3).

Examined material. CD_F10_21 Deiva Marina Canyon, 541 m, on sub-outcropping coral rubble. Few apical fragments, the stem and most of the colony are missing.

Description. Colony small, approximately 4 cm tall and 2.5 cm wide (Fig. 10a). Yellow in color, becoming brown when dried (Fig. 10a-c). Colony irregularly branched and bushy, with slender and delicate ramifications (about 0.5–0.7 mm wide) (Fig. 10c-d). Polyps well-spaced and irregularly distributed, occasionally arranged in two rows (Fig. 10a-c). Contracted polyps range from 0.5 to 0.8 mm in height; expanded polyps reach 2.1 mm (Fig. 10c-f).

Thornscales from the calyx wall relatively slender and 0.4–0.6 mm in height (Figs. 10d-f, 11a). Operculum in the anthocodium formed by eight groups of 2 (rarely 3) curved rods (0.6–0.9 mm) (Figs. 10e-f, 11b) with the collaret presenting 2–4 rings of sclerites (each about 0.6–0.9 mm) (Figs. 10e-f, 11c). Tentacle sclerites 0.1–0.3 mm long (Fig. 11d). Coenenchyme characterized by simple and branched spindles (0.2–0.4 mm) in the inner layer (Fig. 11e) and thornstars (0.2–0.4 mm) in the outer layer (Figs. 10d-f, 11f).

Taxonomic remarks. The assignment of sample CD_F10_21 to the genus *Placogorgia* is supported by the spiny appearance of the coenenchyme, due to the presence of thornstars in the outer layer. This type of sclerite, along with the slender shape of the thornscales and the absence of multi-spined sclerites, allows for a confident identification as *Placogorgia massiliensis* (Carpine & Grasshoff 1975). Some differences from the original description are noted: i) The colony is slender and bushy, rather than relatively robust and planar; ii) polyps are mostly irregularly distributed, while in the type material they are typically arranged in two rows; iii) both the polyps and thornscales are slightly smaller (Table S3). However, only a few specimens of this species have been studied to date, and no information is available on intraspecific morphological variability, particularly in relation to environmental conditions or colony age. Additionally, the present description is based solely on a few apical branch fragments (Fig. 10b), and no information is available for the rest of the colony. ROV analysis of the *P. massiliensis* population in the Levante Canyon, from which the sample was collected, revealed an average colony height of 7.2 ± 0.1 cm ($n = 425$), with maximum heights reaching 20 cm (unpublished), hence much larger than literature data (Table S3).

Ecological remarks. The limited records available for this species indicate that it inhabits bathyal rocky bottoms, cold-water coral frameworks, and coral rubble, at depths ranging from 350 to 1850 m (Sartoretto and Zibrowius 2018). The only known Atlantic occurrence is from 488 to 510 m (Grasshoff 1985a). In the Ligurian Sea, dense aggregations of *P. massiliensis* on coral rubble (up to 10 colonies m^{-2}) were reported from the areas of Portofino and Deiva Marina coral structures along the Levante Canyon (Bo et al. 2023), where the specimen analyzed in this study was collected.

Distribution. This species is considered endemic to the Mediterranean Sea; however, a record from Galicia (Grasshoff 1985a) raises doubts about this possibility. In the Mediterranean Sea, *P. massiliensis* has been reported from Gibraltar and the Cassidaigne Canyon (Carpine and Grasshoff 1975; Grasshoff 1977; Sartoretto and Zibrowius 2018). Unverified records have been reported from the Ionian Sea, the Strait of Sicily, and the Gulf of Cadiz (Freiwald et al. 2011; Díaz del Rio et al. 2014). This study provides the first record of *P. massiliensis* for the Ligurian Sea.

Genus *Muriceides* Wright & Studer 1889
Muriceides lepida Carpine & Grasshoff 1975
(Figs. 12, 13, Table S4).

Examined material. BM_PEN_02 Penelope Seamount, 497 m, on coral rubble; CD_F7_05 Portofino thanatocoenosis, 724 m, on a plastic sheet; CD_F7_10 Portofino thanatocoenosis, 712 m, on a subfossil coral framework; CD_E1_18 Deiva Marina Canyon, 675 m, on coral rubble; CD_F9_25 Deiva Marina Canyon, 567 m, on a dead colony of *M. oculata*.

Description. Colonies planar, irregularly ramified, white (both in vivo and when fixed), and relatively small, on average 8.2 cm tall, with one (CD_F7_10) reaching 19.3 cm in height (Fig. 12a-b, f-g, j, l-n; Table S4). Ramifications slender and delicate, ranging from 0.4 to 2 mm in diameter (Fig. 12b-c, g-h, j-k, m, o). Basal portion of the stems and major ramifications often denuded, with the dark-brown organic axis being exposed and sometimes colonized by sessile organisms such as the barnacle *Metaverrucaria* sp. (CD_F7_10) (Fig. 12b). Polyps from crowded (CD_F7_10) (Fig. 12c) to scattered and irregularly distributed (CD_E1_18, CD_F7_05, BM_PEN_02) (Fig. 12h, k, o). Calyxes generally wider than high, showing the typical Fujiyama

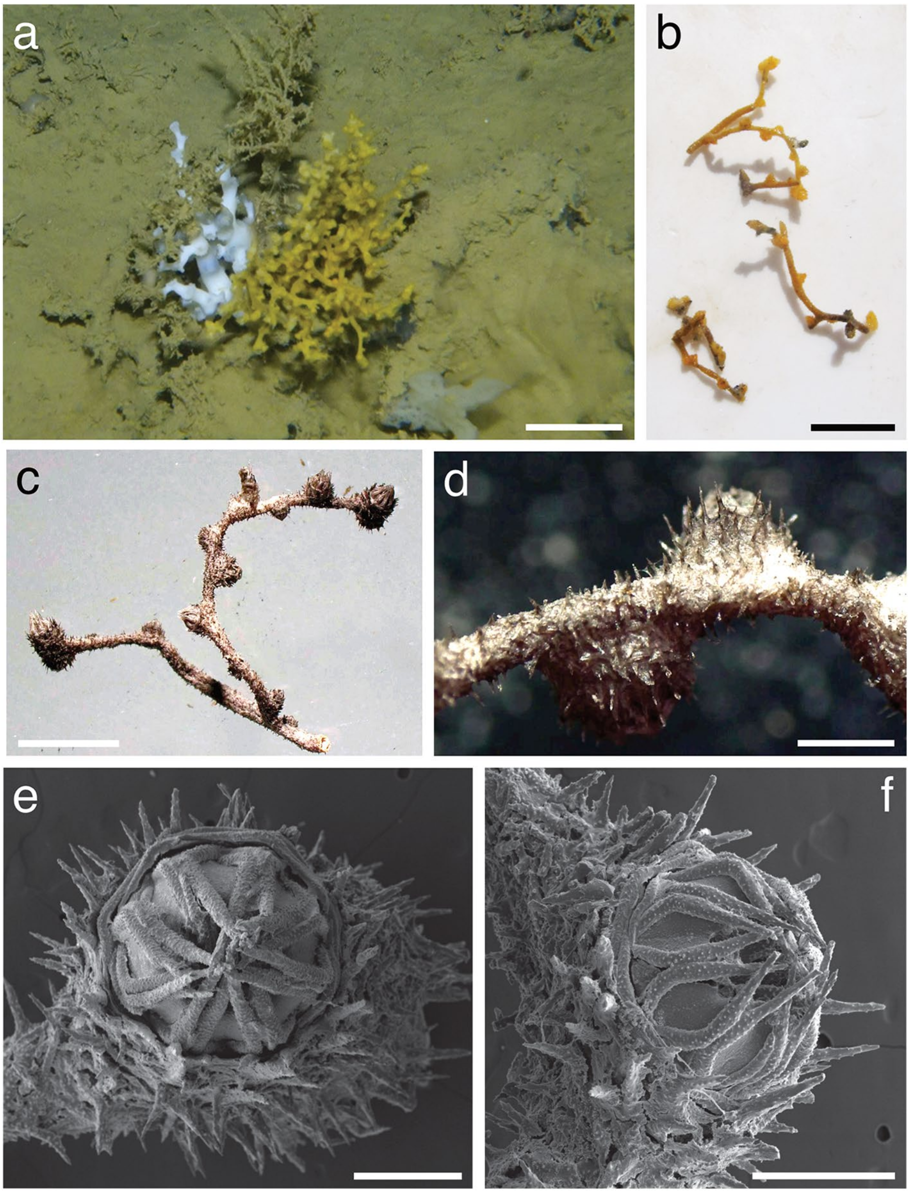


Fig. 10 *Placogorgia massiliensis* (CD_F10_21). **a** The living colony collected from the Deiva Marina Canyon at 541 m, on sub-outcropping coral rubble with a small *M. oculata* colony. **b** A few apical branches freshly collected from the colony. **c** Detail of branch tips, showing the distribution and the different size of the polyps. Note the progressive darkening of the color from (**a**) to (**b**) and (**c**). **d** Stereomicroscope close-up of polyps, showing the characteristic spiny aspect of the calyx and coenenchyme owed to the presence of thornscales and thornspindles. **e**–**f** SEM images of *P. massiliensis* expanded polyps. The architecture of the thornscales forming the calyx and the sclerites of the anthocodium (collaret sclerites and points/opercular sclerites) is shown. Scale bars: a-b = 1 cm; c = 0.5 cm; d = 1 mm; e–f = 0.5 mm

form (Fig. 12d-e, h-i, k, o-p); their height ranging from 0.3 mm (CD_F7_05) to 1.6 mm (BM_PEN_02) (Table S4).

All specimens with numerous thornspindles oriented longitudinally, forming the calyx wall (Fig. 12d-e, p); oblique projection directed upward placed more or less toward the end of the spindle (Fig. 13a). In the calyx wall, thornspindles aligned vertically along their length with tips projecting upward (Fig. 12d-e, p). Anthocodium characterized by i) a collaret of 5 to 10 rings of spindles (Figs. 12d, h-i, k; 13d), ii) 4 to 9 opercular sclerites at the base of each tentacle (Figs. 12d, h-i, k, o-p; 13e), and iii) tentacle sclerites (Fig. 13f). Outer layer of the coenenchyme containing thornspindles with one (occasionally two) thick central projection turned upward (Figs. 12e; 13b). Inner layer of the coenenchyme containing simple spindles (Fig. 13c); only in one sample (CD_F7_05), two branched spindles were observed (Fig. 12k inset).

Taxonomic remarks. The assignment of the analyzed specimens to the genus *Muriceides* Wright & Studer 1889 is strongly supported by the presence of large, conical calyxes (commonly referred to as "Fujiyama" shape) as well as by the occurrence of thornspindles in both the coenenchyme and the calyx wall (Carpine and Grasshoff 1975; Grasshoff 1977).

M. lepida is the only species of the genus known from the Mediterranean Sea, with a distribution that extends into the NE Atlantic Ocean. Alongside *M. lepida*, two other species are currently recognized in the NE Atlantic: *Muriceides sceptrum* (Studer, 1891) and *Muriceides kuekenthali* (Broch, 1912) (Table S4). A fourth species, *Muriceides*

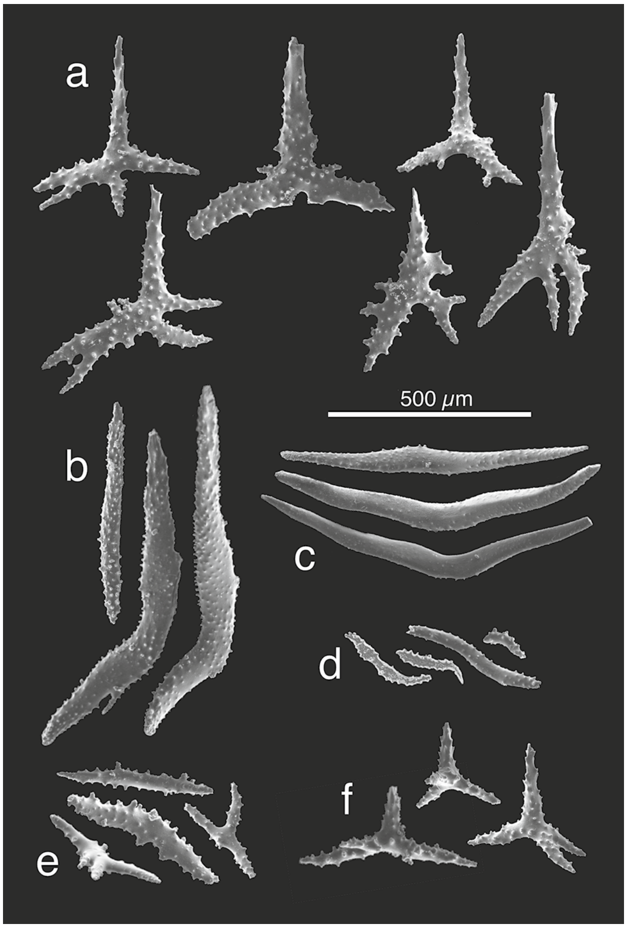


Fig. 11 SEM images of *Placogorgia massiliensis* sclerites (sample CD_F10_21). **a** Thornscales of the calyx. **b** Points or opercular sclerites. **c** Sclerites of the collaret. **d** Small sclerites of the tentacles. **e** Branched and unbranched sclerites of the inner layer of the coenenchyme. **f** Thornstars of the outer layer of the coenenchyme

echinata Thomson 1927, was poorly described based on a single small fragment collected during the *Campagnes Scientifique du Prince Albert I^{er} de Monaco*. It was not considered in subsequent taxonomic works on Atlantic gorgonians (Deichman 1936; Grasshoff 1977). *M. kuekenthali* differs clearly from *M. lepida* in branch thickness (1.5–2.8 mm), pink coloration, and the high number of sclerite rings in the collaret (10–15) (Table S4). It also has a distinct distribution, being confined to the boreal eastern Atlantic Ocean. Differences between *M. lepida* and *M. sceptrum* are mainly related to colony size and branch thickness (Table S4). According to Grasshoff (1977), *M. lepida* typically does not exceed 10 cm in height. In this regard, specimen CD_F7_10 and CD_F9_25 (19.3 and 14.7 cm high, respectively) (Fig. 12a-b, l-m) represent a significant extension of the known size range. In fact, ROV surveys in the Levante Canyon, where most samples were collected, documented an average colony height of 8.5 ± 0.1 cm (n = 1199 colonies), with a maximum size of approximately 34 cm (unpublished). Grasshoff (1977) also reported that *M. lepida* branches are about 1 mm thick, while those of *M. sceptrum* reach ~ 2 mm. Sample CD_F7_10 (Fig. 12a-c), though overall slender, shows ramifications up to 2.1 mm thick in some areas. This trait likely correlates with colony size and possibly local hydrodynamic conditions and does not appear to be a reliable character for distinguishing between the two species. Additional characters used to differentiate the two species include the number of spines on the coenenchyme thornspindles and the presence of branched spindles in the inner layer (Table S4). *M. lepida* typically has only one spine in its thornspindles, while *M. sceptrum* can have one, occasionally two, and rarely more than two (Grasshoff 1977). Branched spindles in the inner coenenchyma layer are exclusive to *M. sceptrum* and *M. kuekenthali*, whereas *M. lepida* has only simple spindles (Grasshoff 1977). However, our data reveal some variability in these traits, blurring the distinction between *M. lepida* and *M. sceptrum* (Table S4). For instance, thornspindles with two spines were observed in samples CD_F7_10 and BM_PEN_02 (Fig. 13b), and two branched sclerites from the inner coenenchyme layer were found in sample CD_F7_05 (Fig. 12k inset). Both species also share a similar, mainly Lusitanic, geographical range (Table S4). In this study, considering the large number of colonies analyzed (> 5), their overall slender appearance, reduced polyp size, and the rarity of two-spined thornspindles and branched coenenchyme sclerites, all specimens were identified as *M. lepida*. Further research, especially molecular analyses, could clarify the confusing taxonomy of these species.

Ecological remarks. Ligurian records of *M. lepida* align well with previous observations, showing the species occurs at depths of 90–1350 m in the Atlantic Ocean and 80–1014 m in the Mediterranean Sea, always on hard substrates such as rocks, stones, and dead corals (Table S4) (Carpine and Grasshoff 1975; Grasshoff 1977, 1981; Maldonado et al. 2015; Sampaio et al. 2019; Angeletti et al. 2020; Bilan et al. 2023). Carpine and Grasshoff (1975) noted a preference for steep areas, cliffs, or drop-offs between 80 and 250 m. However, recent ROV video surveys reveal *M. lepida* is more frequently found at bathyal depths (e.g., Maldonado et al. 2015; Sampaio et al. 2019; Angeletti et al. 2020; Bilan et al. 2023) than in mesophotic zones (e.g., Würtz and Rovere 2015). In the Ligurian Sea, despite extensive ROV surveys (> 100 dives) between 40 and 200 m, *M. lepida* has not been detected on the deep continental shelf and shelf break (Enrichetti et al. 2019). Conversely, dense meadows of *M. lepida* (up to 19.7 colonies m^{-2}) have been found at bathyal depths, associated with canyon habitats along the continental shelf and offshore seamounts (Bo et al. 2020a, 2021, 2023). Notably, the Ligurian record of

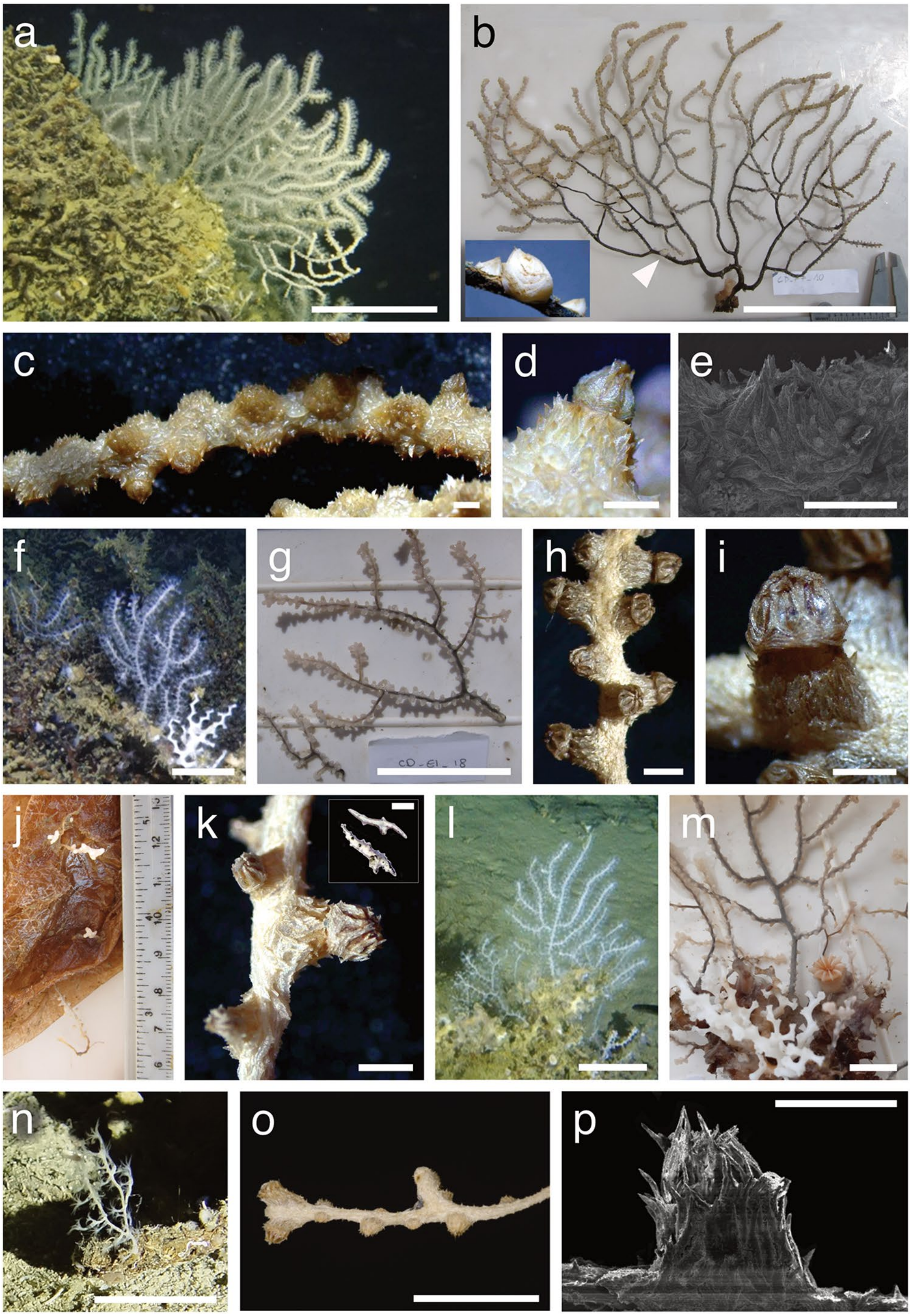


Fig. 12 *Muriceides lepida*. Images of living (**a**, **f**, **l**, **n**) and freshly collected (**b**, **g**, **j**, **m**) colonies. The different substrates are shown: coral framework (**a**), coral rubble (**f**, **l**, **n**), and plastic sheet (**j**). In b, the arrow and the inset indicate the barnacle *Metaverrucaria* sp. on the denuded axis. In m, encrusting sponges and the scleractinians *Madrepora oculata* and *Desmophyllum dianthus* grow on the coral rubble with *M. lepida* colonies. Details of the branches and polyp distribution (**c**, **h**, **k**, **o**). Colony CD_F7_10 presents thick branches with crowded polyps (**c**), while the other specimens have slender branches with more spaced polyps (**h**, **k**, **o**). Details of the calyx sclerite armature, photographed at the stereomicroscope (**d**, **j**). The arrangement of the opercular sclerites, thornscales of the calyx wall, and thornscales of the outer layer of the coenenchyme is shown in e and q. a-e: sample CD_F7_10; f-i: sample CD_E1_18; j-k: sample CD_F7_05; l-m: sample CD_F9_25; n-p: sample BM_PEN_02. Scale bars: a-b = 10 cm; f-g, l, n = 5 cm; m = 2 cm; o = 1 cm; c, h = 2 mm; d-e, i, k, p = 1 mm; k inset = 0.1 mm

M. lepida on plastic debris is the first documented case for this species.

Distribution. NE Atlantic (Bay of Biscay, Josephine Bank, Azores, Madeira, Canary Islands, Cape Verde) and the Mediterranean Sea (Gibraltar, Alboran, Balearic Sea, Marseille, Ligurian Sea, Corsica Channel) (Carpine and Grasshoff 1975; Grasshoff 1977, 1981; Maldonado et al. 2015; Sampaio et al. 2019; Angeletti et al. 2020; Bilan et al. 2023). In the Ligurian Sea, this species inhabits the continental shelf and off-shore seamounts (Fig. 22) (Bo et al. 2020a 2021, 2023).

Genus *Villogorgia* Duchassaing & Michelotti, 1860.
Villogorgia bebrycoides (von Koch 1887).
(Figs. 14, 15).

Examined material. BM_ULI_03 Ulisse Seamount, 400 m, on outcropping rock. Colony broken, the stem is missing.

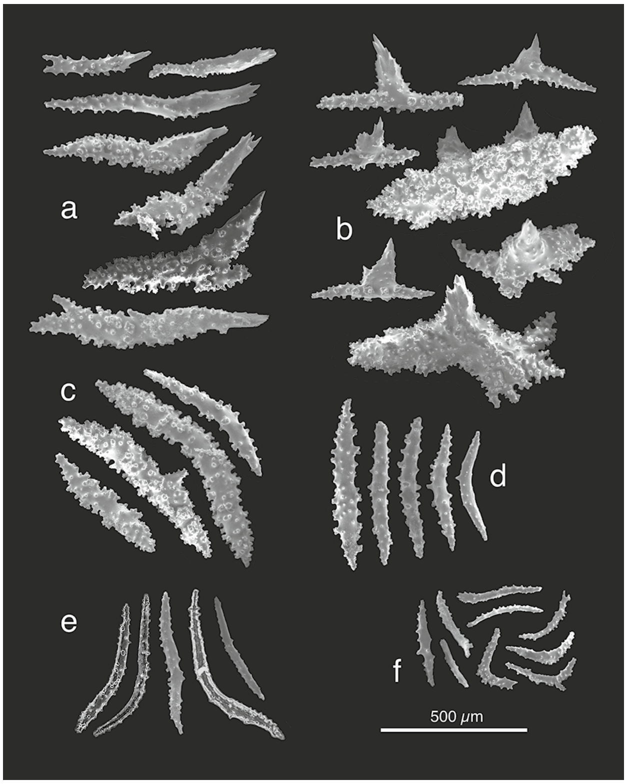


Fig. 13 SEM images of *Muriceides lepida* sclerites (sample CD_F7_10). **a** Thornspindles from the calyx wall. **b** Thornspindles from the outer layer of the coenenchyme. A large thornspindle with two spines is visible in the lower left. **c** Simple spindles from the inner layer of the coenenchyme. **d** Curved spindles from the collaret of the anthocodium. **e** Points or opercular sclerites. **f** Small rods from the tentacles

Description. Colony white, small (about 4 cm) and delicate, irregularly ramified on a single plane (Fig. 14a, b). Dark brown axis below the white coenenchyme evident in the freshly collected material (Fig. 14b). Branches slender, ranging from 0.3 to 0.5 mm in diameter, with polyps scattered and irregularly distributed; both branches and calyces with tiny processes giving a general spiny aspect to the colony (Fig. 14b-e). Calyx cylindrical, about as wide as it is tall (Fig. 14c-g); generally, about 1 mm wide and 1 mm high, but the terminal polyp at the branch apex can grow particularly larger (Fig. 14d).

Calyx built by a heavy armature of thornscales (Fig. 14f-g), characterized by a wide basal part with flat root projections an upright central spine formed by leaf-like ridges (Fig. 15a). The anthocodium has an operculum composed of few robust sclerites (Fig. 15b), two collaret rings (Fig. 15c), and tentacles sclerites (Fig. 15d). The coenenchyme has a compact layer of thornspindles with a central vertical spine similar to that of the thornscales (Fig. 15e).

Taxonomic remarks. A vertical leafy projection in the thornscales of the calyx and the thornspindles of the coenenchyme supports assigning sample BM_ULI_03 to the genus *Villogorgia*. The presence of massive opercular sclerites is another characteristic feature of this genus. *V. bebrycoides* is the only species of this genus recorded in the NE Atlantic and Mediterranean regions. Another species, *Villogorgia nigrescens* Duchassaing & Michelotti, 1860, is known from the western Atlantic Ocean. It closely resembles *V. bebrycoides* but differs by having 4–5 collaret rings in the anthocodium collaret (compared to just one ring of large sclerites in *V. bebrycoides*, sometimes followed by a single row of smaller sclerites). Additionally, *V. nigrescens* grows much larger, with type specimens reaching about 40 cm tall and 50 cm width (Carpine and Grasshoff 1975).

Ecological remarks. This species is known from the hard bottoms of the NE Atlantic Ocean seamounts and offshore islands, between 56 and 845 m (Grasshoff 1977; Brito and Ocaña 2004; Sampaio et al. 2019). In the Mediterranean Sea, this species has been reported on outcropping rocks and deep corals from 70 to 500 m, often forming mixed assemblages with other gorgonians (Fig. 14a) (Carpine and Grasshoff 1975; Aguilar et al. 2018; Bo et al. 2012, 2020a). Therefore, the specimen BM_ULI_03 analyzed here, coming from a bathyal seamount summit, is consistent with previous observations.

Distribution. In the NE Atlantic Ocean, this species occurs in the Azores, Madeira, Josephine Bank, Gorringe Seamount, Canary Islands (Grasshoff 1977, 1985b; Brito and Ocaña 2004; Sampaio et al. 2019). In the Mediterranean Sea, *V. bebrycoides* occurs in the Sicily Channel, the Tyrrhenian Sea, the Gulf of Naples, the Corsica Channel, and the Ligurian Sea (Koch 1887; Rossi 1958; Carpine and Grasshoff 1975; Aguilar et al. 2018; Bo et al. 2012, 2014a, b, 2020a). In the study area, this species has been observed exclusively on offshore seamounts (Fig. 22) (Bo et al. 2014b, 2020a, 2021).

Genus *Bebryce* Philippi, 1842.

***Bebryce mollis* Philippi, 1842.**

(Figs. 16, 17).

Examined material. BM_ULI_02 Ulisse Seamount, 448 m, on outcropping rock.

Description. Colony small and delicate, about 5 cm high (Fig. 16a-b). Colony with few, long and slender branches, ranging commonly from 0.6 to 0.8 mm in diameter, with the proximal portion being slightly thicker than the distal one (Fig. 16b). Polyps scattered and irregularly distributed, with cylindrical, highly protruding calyces (Fig, 16c), approximatively 1.3 mm wide and 0.8 mm high (Fig. 16d-e).

Calyx and coenenchyme covered by an outer layer of tightly packed cup-shaped sclerites, distinctive of the genus (Figs. 16e-f; 17a). Coenenchyme with an inner layer composed of distinctive flattened sclerites, showing a multilobate base and only a slight indication of a central spine pointing

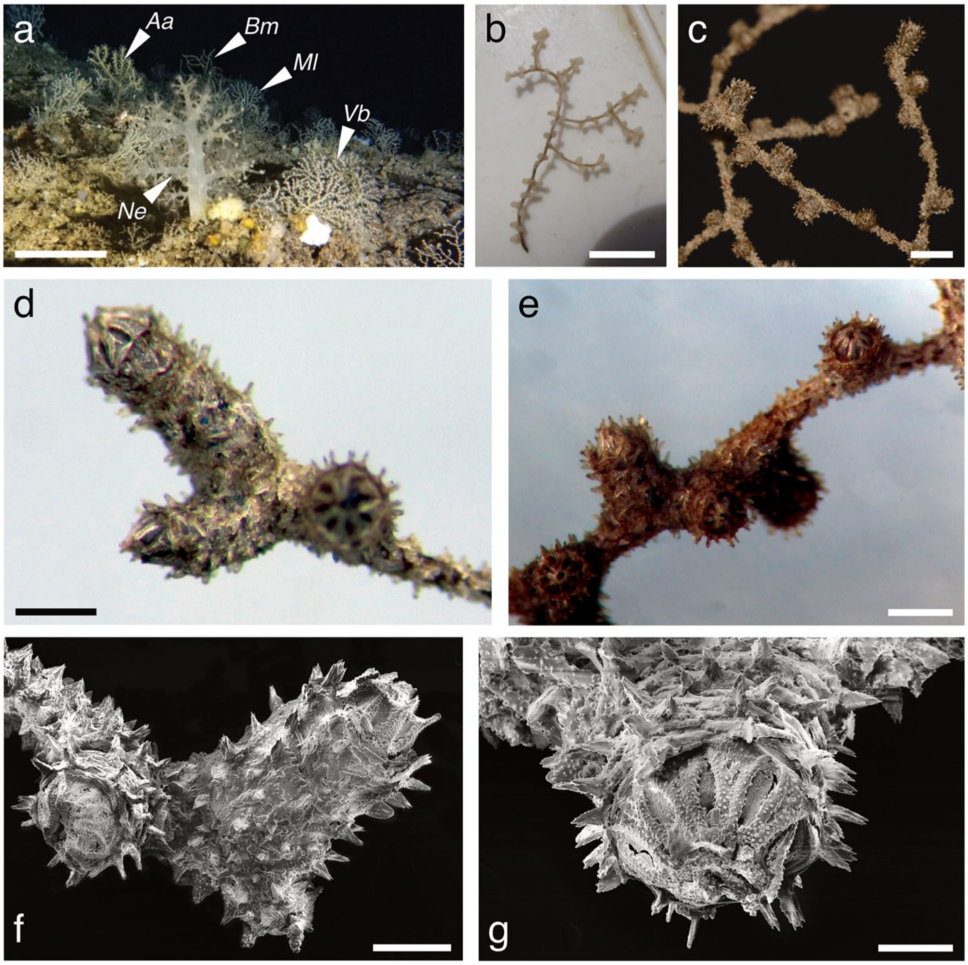


Fig. 14 *Villogorgia bebrycoides*. **a** A pluri-specific gorgonian garden dominated by *V. bebrycoides* (*Vb*) colonies from the Ulisse seamount summit. Specimens of *Muriceides lepida* (*Ml*), *Acanthogorgia armata* (*Aa*), *Bebryce mollis* (*Bm*), and a large Nephtheidae (cf. *Daniela koreni*) (*Ne*) also contribute to the assemblage. **b** A freshly collected fragment of the sample BM_ULI_03. Details of branches (**c**) and polyps (**d**-**e**). The spiny aspect of the calyx and coenenchyme is evident. In (**d**), a particularly large polyp from an arm tip is shown. **f**-**g** SEM images of polyps showing the arrangement of the sclerites in the calyx and anthocodium. Scale bars: a = 10 cm; b = 1 cm; c = . 2 mm; d-e = 1 mm; f = 0.5 mm; g = 0.25 mm

upward (Fig. 17b). In the most apical part of the calyces, cup-shaped sclerites replaced by spindles with leafy projections protruding upward (Fig. 17c). Anthocodium with an operculum composed of curved large sclerites (Fig. 17d), a collaret of sclerites (Fig. 17e) arranged in 4 or 5 rings, and rod-like sclerites of the tentacles (Fig. 17f).

Taxonomic remarks. *B. mollis* is the only species known so far for this genus in the eastern Atlantic Ocean and the Mediterranean Sea. Occasionally, larger and thicker colonies, reaching up to 20 cm in height, are reported from the study area.

Ecological remarks. This species is known from hard substrates of the continental shelf edge and the upper part of the continental slope, from 97 to 1250 m in the NE Atlantic Ocean and from 100 to 400 m in the Mediterranean Sea (Carpine and Grasshoff 1975; Grasshoff 1977, 1989; Fourt et al. 2017; Sampaio et al. 2019). It adapts to rocky surfaces and biogenic substrates, including deep-sea corals, coral rubble, and mollusc shells on detritic bottoms. Therefore, this Mediterranean finding fits perfectly in the known ecological setting of the taxon.

Distribution. In the eastern Atlantic Ocean, *B. mollis* is reported from Portugal, Gibraltar Gulf, Josephine Bank, Great Meteor Bank, Azores, Canary Islands, and Cape Verde; in the Mediterranean Sea this species is reported from the Alboran Sea, Gulf of Lions, Ligurian Sea, Corse Island, Tyrrhenian Sea, Sicily Channel, Ionian Sea, S Adriatic Sea (Rossi 1958; Carpine and Grasshoff 1975; Grasshoff 1977, 1989; Brito and Ocaña 2004; Bo et al. 2014b; Bayer and Van Ofwegen 2016; Fourt et al. 2017; Sampaio et al. 2019). In the Ligurian basin, *B. mollis* is reported exclusively from offshore seamounts (Fig. 22) (Bo et al. 2014b, 2020a, 2021).

Order SCLERALCYONACEA McFadden, van Ofwegen & Quattrini, 2022.

Family PRIMNOIDAE Milne Edwards, 1857.

Genus *Callogorgia* Gray, 1858.

***Callogorgia verticillata* (Pallas, 1766).**

(Figs. 18, 19).

Examined material. BM_ULI_01 Ulisse Seamount, 448 m, on outcropping rock.

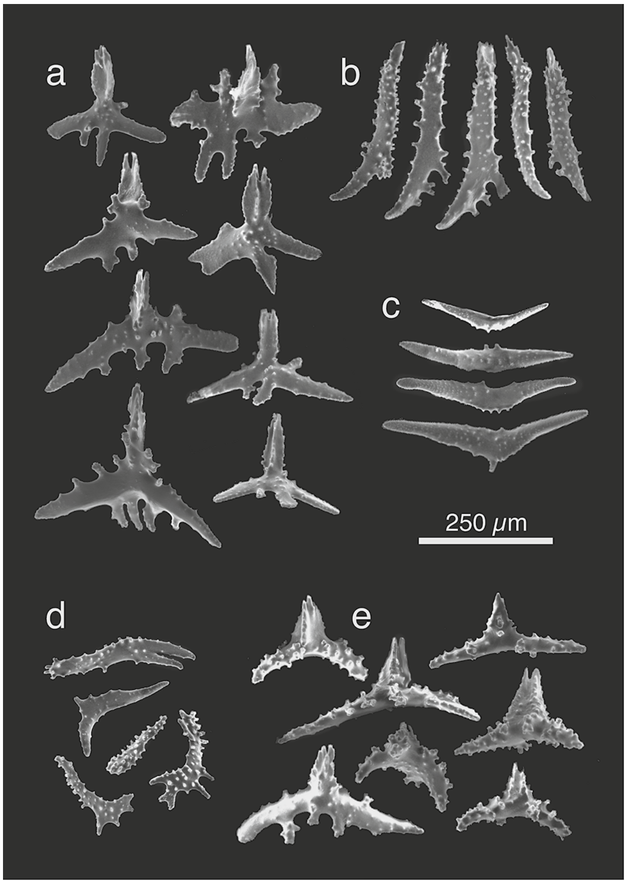


Fig. 15 SEM images of *Villogorgia bebrycoides* sclerites (sample BM_ULI_03). **a** Thornspindles from the calyx wall. **b** Points or opercular sclerites. **c** Curved spindles from the collaret. **d** Small rods from the tentacles. **e** Thornspindles from the outer layer of the coenenchyme

Description. Fan-like yellowish colony (Fig. 18a-e), with axial skeleton rich in calcium carbonate. Branches organized in multiple orders on a single plane, resembling large feathers. Polyps turned toward the axis and arranged in whorls of two or rarely one (Fig. 18d, e).

Sclerites in the form of scales, with the inner surface covered in large warts and the outer surface smooth with ridges (Fig. 19a-c). Eight apical scales large, triangular and elongated, forming the operculum (Figs. 18f, g; 19a). Walls of the polyps with scales arranged in eight vertical rows (Figs. 18f, g; 19b). Opercular scales can open, while marginal scales remain fixed. Coenenchyme with large and small plates whose surface resembles that of the polyps' sclerites (Figs. 18f, g; 19c).

Taxonomic remarks. *C. verticillata* colonies can grow up to 150 cm in height (Fig. 18b), and the color ranges from bright white to yellowish or light pink. Furthermore, the number of polyps arranged in a whorl varies from one to more than four, depending on the branch diameter. Despite this variability, *C. verticillata* is the only species of its genus present in the Mediterranean Sea and eastern Atlantic Ocean (Carpine and Grasshoff 1975). It is easily recognizable by its feather-like planar branching and its polyps, curved upward and arranged in whorls.

Ecological remarks. Found on hard bottoms, generally with high sedimentation, at similar depth in the eastern Atlantic Ocean (130–1300 m) and the Mediterranean Sea (90–1000 m) (Carpine and Grasshoff 1975; Grasshoff 1985b; Fourt et al. 2017; Chimienti et al. 2019 and references therein). Carpine and Grasshoff (1975) suggested that *C. verticillata* may be too large and fragile to withstand the

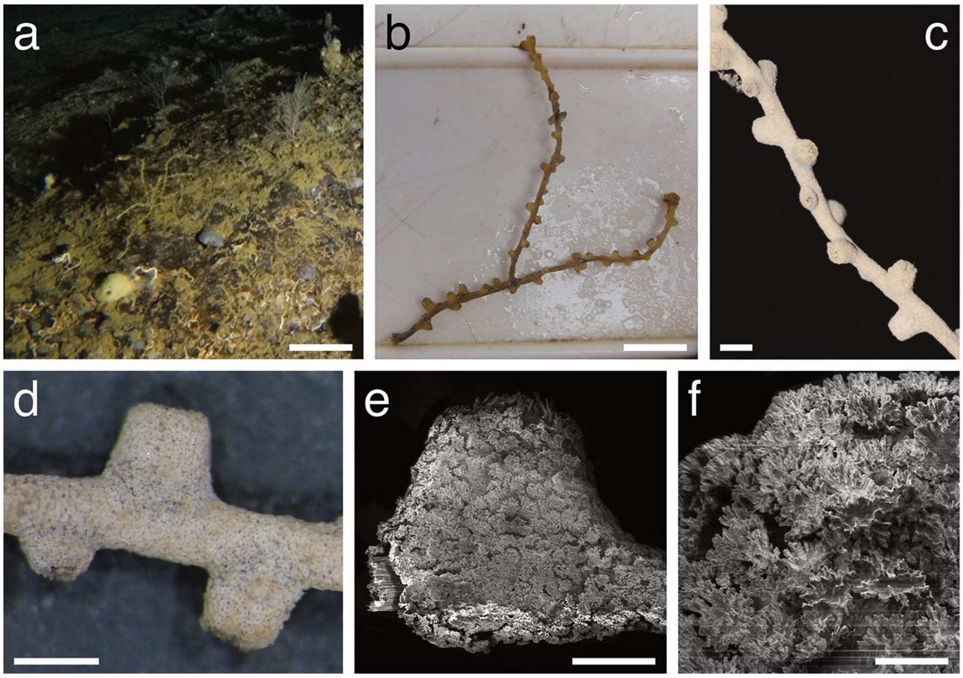


Fig. 16 *Bebryce mollis*. **a** Colony of *B. mollis* on the summit of the Ulisse Seamount (448 m) before being collected by the ROV. *Callogorgia verticillata*, encrusting sponges, and serpulids are also visible. **b** Image of sample BM_ULI_02 immediately after collection. **c** Branch of *B. mollis* at the stereomicroscope with **d** detail of the polyps. **e**, **f** SEM images of *B. mollis* polyps showing the external layer of cup-like sclerites covering the calyx and the axis (**e**, **f**) and the sclerite from the apical part of the calyx wall (**e**). Scale bars: a = 5 cm; b = 1 cm; c, d = 1 mm; e = 0.5 mm; f = 0.1 mm

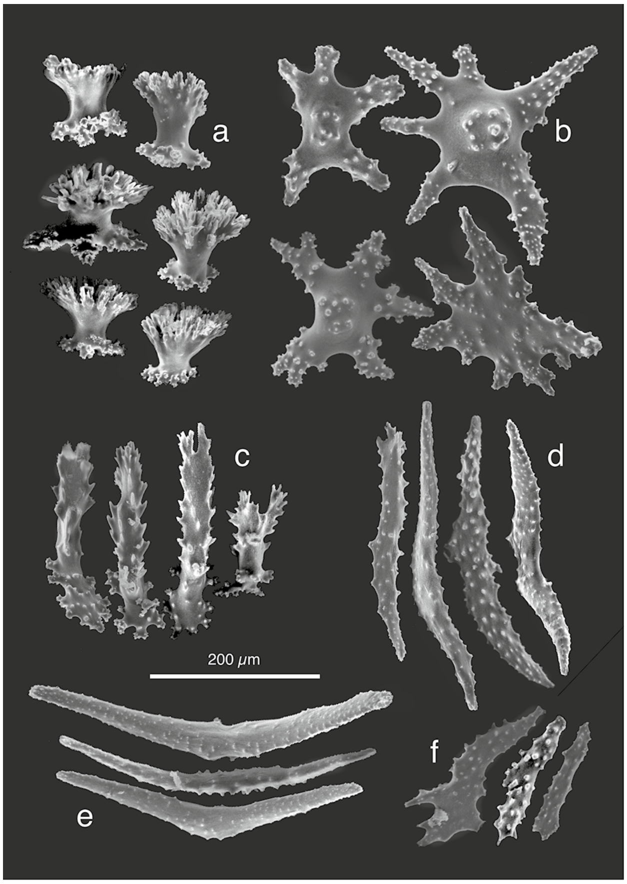


Fig. 17 SEM images of *Bebryce mollis* sclerites (sample BM_ULI_02). **a** Cuplike sclerites from the superficial layer of the calyx wall and coenenchyme. **b** Thornstars from the inner layer of the coenenchyme. **c** Sclerites from the apical edge of the calyx wall. **d** Points or opercular sclerites. **e** Curved spindles from the collaret. **e** Small rods from the tentacles

relatively strong currents of the slope break; this observation is consistent with the occurrence of this species in areas characterized by high sedimentation levels. *C. verticillata* host a rich associated fauna, including the parasitic zoanthid *Zibrowius primnoidus* Carreiro-Silva, Braga-Henriques, Sampaio, de Matos, Porteiro and Ocaña, 2010, the sea slug *Tritonia callogorgiae* Chimienti, Furfaro & Taviani, 2020, the crinoid *Leptometra phalangium* (Müller, 1841), and the cusk-eels *Benthocometes robustus* (Goode & Bean, 1886) (Carreiro-Silva et al. 2011; Bo et al. 2014a; Fabri et al. 2014; Chimienti et al. 2020).

The dense forests of *C. verticillata* on the Ulisse Seamount summit, from which the sample analyzed here originates, were recently described by Bo et al. (2021). These forests reach a density of up to 3.4 colonies m^{-2}. They are dominated by juvenile colonies (Fig. 18a), often mixed with other small gorgonians (Fig. 16a). Large colonies of *C. verticillata* form aggregations (Fig. 18b) only on flat or gently sloping hardgrounds of the western sector of the seamount summit (Bo et al. 2021).

Distribution. Eastern Atlantic Ocean (Azores, Great Meteor Bank, Madeira, Josephine Bank, Bay of Biscay, Morocco, Mauritania, Cape Verde) and the Mediterranean Sea (Alboran Sea, Balearic Sea, Gulf of Lions, Ligurian Sea, Sardinia, Tyrrhenian Sea, Sicily Channel, Ionian Sea, S Adriatic Sea, Aegean Sea) (Carpine and Grasshoff 1975; Grasshoff 1986; Aguilar et al. 2013; Bo et al. 2011; Fourt et al. 2017; De la Torriente et al. 2018; Fabri et al. 2014; Ramos et al. 2016; Chimienti et al. 2019 and references therein). In the Ligurian Sea, *C. verticillata* is reported exclusively from the Ulisse and Penelope seamounts (Bo et al. 2021).

Family KERATOISIDIDAE Gray 1870
Subfamily KERATOISIDINAE Gray 1870
Genus *Acanella* Gray 1870
Acanella* cf. *arbuscula (Johnson 1862).
(Figs. 20, 21, Table S5).

Examined material. CD_FN_14 Monterosso Canyon, 549 m, on mud. Basal plate missing.

Description. Fan-shaped colony, 13 cm high. Color dark yellow in vivo (Fig. 20a, b), bright orange soon after collection (Fig. 20c), and brown when dried (Fig. 20g-i). Branching occurring at node level dichotomously or, more rarely, trichotomously. Ramifications not occurring exactly on the same plane, but overall aspect of the colony planar. Axial skeleton organized in horny nodes and calcareous internodes (Fig. 20d). Organic nodes brown with concave margins (Fig. 20e), more scattered and thinner toward the apical part of the colony. Internodes white and smooth, with delicate longitudinal groves, noticeable only along basal internodes (Fig. 20d). Internodes ranging in length from 8 to 19 mm and hollow, with central canal about 15% of the axis diameter (Fig. 20f). Basal plate missing, but calcareous, lobate, root-like bases reported from other samples collected by trawlers in the study area (Enrichetti, pers. comm.). Non-retractile polyps arranged quite regularly, primarily (but not exclusively) in two opposite rows, opposite or alternate (Fig. 20b-c, g, h). Polyps emerging almost vertically from the branches, being densely packed (6–12 polyps per cm), and with two to three polyps at the tip ends (Fig. 20i). Size ranges from 1.3 to 5.4 mm in height and from 0.8 to 1.9 mm in width (Fig. 20g-n). Polyps generally funnel-shaped, with proximal end being smaller than distal end (Fig. 20g, j, m); when dried, closed polyps with cylindrical to conical shape (Fig. 20k, l, m).

Long slender sclerites (from 0.6 to 3.6 mm long) arranged longitudinally and obliquely along polyp wall (Figs. 20g-n; 21a), giving the polyp a twisted aspect. Some polyp body sclerites (generally the longest) projecting beyond the base of the contracted tentacles, creating

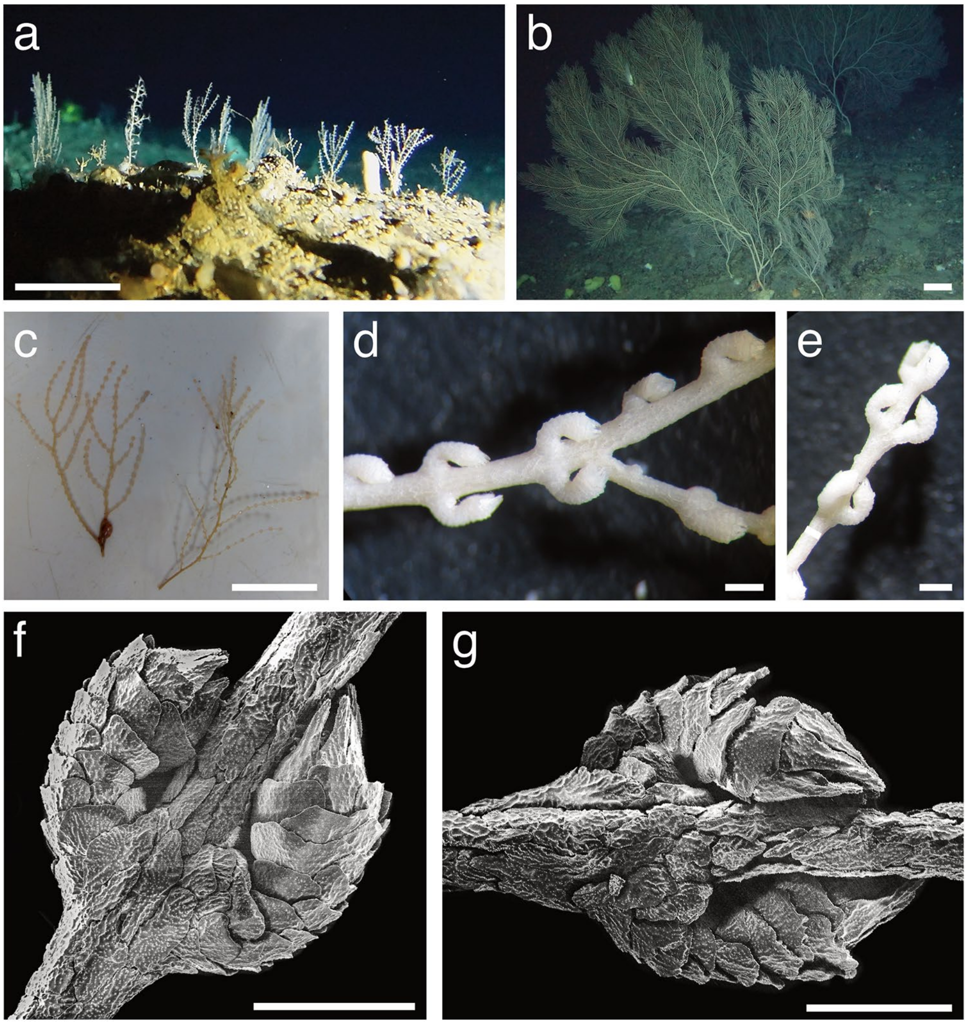


Fig. 18 *Callogorgia verticillata*. **a** A dense aggregation of juvenile colonies of *C. verticillata* from the summit of the Ulisse Seamount (448 m). **b** A forest of large colonies from the same site. **c** Two fragments collected by ROV (BM_ULI_01). **d** Branch of *C. verticillata* observed at the stereomicroscope; note the organization of the polyps in verticils. **e** Detail of a branch tip. **f**, **g** SEM images showing the complex armature of sclerites covering *C. verticillata* polyps and coenenchyme. Scale bars: a, b = 10 cm; c = 2.5 cm; d, e = 1 mm; f, g = 0.5 mm

a crown of about 0.5–1.5 mm (Fig. 20g-n). Distal end of these sclerites with a sharp point, whereas proximal end often enlarged and, in some cases, bifurcate (Figs. 20k; 21a). Small tentacle sclerites also present (Fig. 21b). Thin coenenchyme containing needle-like sclerites ranging from 0.1 to 1.8 mm in length (Fig. 20g-n, 21c). All sclerite types presenting fine ornamentations uniformly distributed on the surface (Fig. 21, inset).

Taxonomic remarks. Several species historically attributed to *Acanella* have been reported from the Mediterranean Sea, including *Acanella eburnea* (Pourtalès, 1868), *Acanella furcata* Thomson 1929, *Acanella gigliolii* Cecchini 1914, and *Acanella mediterranea* Cecchini 1914 (Cecchini 1914; Thomson 1929; Carpine 1963). However, these species have lately been synonymized with *Isidella elongata* (Esper, 1788), which Carpine and Grasshoff (1975) recognized as the only member of the family Keratoisididae in the Mediterranean Sea. Consequently, all Mediterranean records of bamboo corals have been assigned to *I. elongata* by default, based solely on their collection location (Saucier et al. 2017). Notably, the original description of *I. elongata* focused exclusively on the axial skeleton, without accounting for polyps or sclerites (Esper 1791). Despite subsequent redescriptions (Koch 1887; Bayer 1990), distinctions between *Isidella* and closely related genera such as *Acanella* remain unresolved. Recent phylogenetic analyses have further shown that *Isidella* is not monophyletic, complicating its classification (France 2007; Dueñas et al. 2014; Waitling et al. 2022).

The genus *Isidella* shows a strong affinity with *Acanella*, as both exhibit branching from the nodes. Traditionally, the two genera have been distinguished based on branching pattern, with *Isidella* being planar and *Acanella* bushy and tridimensional (Kükenthal 1924; Bayer 1990), and the polyp crown structure, with *Isidella* lacking the protruding apical end of the polyp wall sclerites among the tentacle bases, which is typical of *Acanella* (Koch 1887). However, both characters have proven unreliable: Dichotomous and planar branching patterns have been repeatedly observed in *Acanella* (Kükenthal 1915; Thomson 1927; Aurivillius

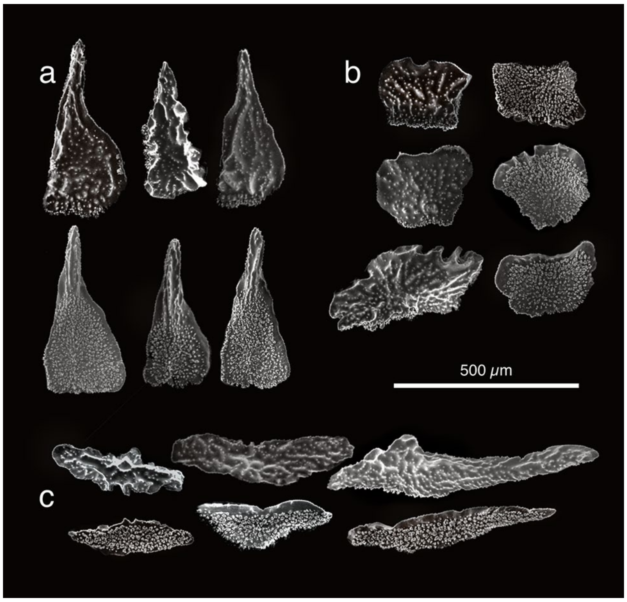


Fig. 19 SEM images of *Callogorgia verticillata* sclerites (sample BM_ULI_01). **a** Scales from the operculum (lower line: inner side). **b** Scales from the polyp wall (right column: inner side). **c** Scales from the coenenchyme (lower line: inner side)

1931; Bayer 1990; Saucier et al. 2017), and the structure of the polyp crown is highly dependent on the degree of contraction and therefore on fixation methods (Wright and Studer 1889; Kükenthal 1924; Carpine and Grasshoff 1975; Saucier et al. 2017). Morphological and molecular analyses of samples from various geographical regions have shown that traits commonly used to distinguish *A. arbuscula*, *A. eburnea*, and *I. elongata* (i.e., branching pattern, polyp size, and sclerite length) (Table S5) fall within an intraspecific continuum (Saucier et al. 2017). Notably, Saucier et al., (2017) revealed the presence of two *Acanella* species in the Mediterranean Sea, *A. arbuscola* and *A. furcata*, inhabiting the same muddy environment and depth range (300–800 m) typically attributed to *I. elongata*. These findings cast doubt on the validity of previous Mediterranean records of *I. elongata*. Moreover, recent phylogenetic studies indicate that genera within the family Keratoisididae, including *Acanella* and *Isidella*, are polyphyletic and require taxonomic revision (Morrissey et al. 2023).

In the present study, sample CD_FN_14 is attributed to the genus *Acanella* based on i) the length of the internodes, ii) the trumpet-shaped polyps, and iii) the presence of curved sclerites twisted around the polyp wall. At the species level, the assignment of this specimen to *Acanella* cf. *arbuscola* is supported by the taxonomical comparison presented in Table S5. The ROV analysis of the Ligurian population from which sample CD_FN_14 originates revealed an average colony height of 16.8 ± 0.7 cm (n = 254) (unpublished), which is consistent with literature data for *A. arbuscola*. However, it is noteworthy that the maximum colony height observed is considerably greater, reaching up to 52 cm (unpublished). Furthermore, the colony habitus is never bushy, in contrast to what is typically observed in Atlantic populations, and the axis of the analyzed specimen is hollow. Additionally, the presence of large bilobate polyp wall sclerites, described here for the first time, may indicate either a new species or an unrecognized variant within the known morphological continuum. Further morphological and phylogenetic analyses are currently underway to clarify this issue.

Ecological remarks. *Acanella arbuscula* inhabits both hard and soft bottoms between 350 and 2035 m, with the few confirmed Mediterranean records occurring exclusively on soft bottoms, approximately from 300 to 1082 m (Mytilineou et al. 2016; Saucier et al. 2017). In the Ligurian Sea, two distinct populations of *Acanella* sp. have been recently reported from muddy plains in the proximity of the Deiva Marina Canyon (670–730 m) and Monterosso Canyon (500–560 m), with a maximum density of 3.3 colonies m^{-2} (Bo et al. 2023). In the basin, the occurrence of keratoisidids has been considered a good indicator of pristine environments (Bo et al. 2015; Carbonara et al. 2020; Angiolillo et al. 2024).

Distribution. *Acanella arbuscula* has a circumglobal distribution, with sparse records reported from the Pacific and Indian oceans and a distribution center in the North Atlantic Ocean. In the latter basin, the species is widely distributed between the equator to the South and the Davis Strait and the submarine ridges connecting Greenland, Iceland, and Scotland to the North (Grasshoff 1986, 1989; Buhl-Mortensen et al. 2015; Saucier et al. 2017). The presence of *A. arbuscula* in the Mediterranean Sea has been confirmed through molecular analysis in the eastern Ionian and Balearic Seas (Mytilineou et al. 2016; Saucier et al. 2017).

Geographical and bathymetrical distribution

At the regional scale, the ten species analyzed in this study, along with the three additional species reported by Bo et al. (2020a, 2021, 2023), show distinct distribution patterns between coastal habitats (5–8 NM) and offshore sites (50–75 NM) (Fig. 22). Four species, namely *Acanthogorgia armata*, *Acanthogorgia* sp., *Placogorgia massiliensis*, and *Acanella* cf. *arbuscula*, occur exclusively on the continental slope and the Levante Canyon. The identity of the stoloniferans observed on the offshore seamounts (Bo et al. 2020a, 2021) remains unclear. They may belong to *Rolandia* cf. *coralloides*, a species found along the Ligurian continental slope. A similar situation is seen in the genus *Placogorgia*: *P. coronata* and *P. massiliensis* are found on the continental slope, while an unidentified *Placogorgia* sp. was observed on the

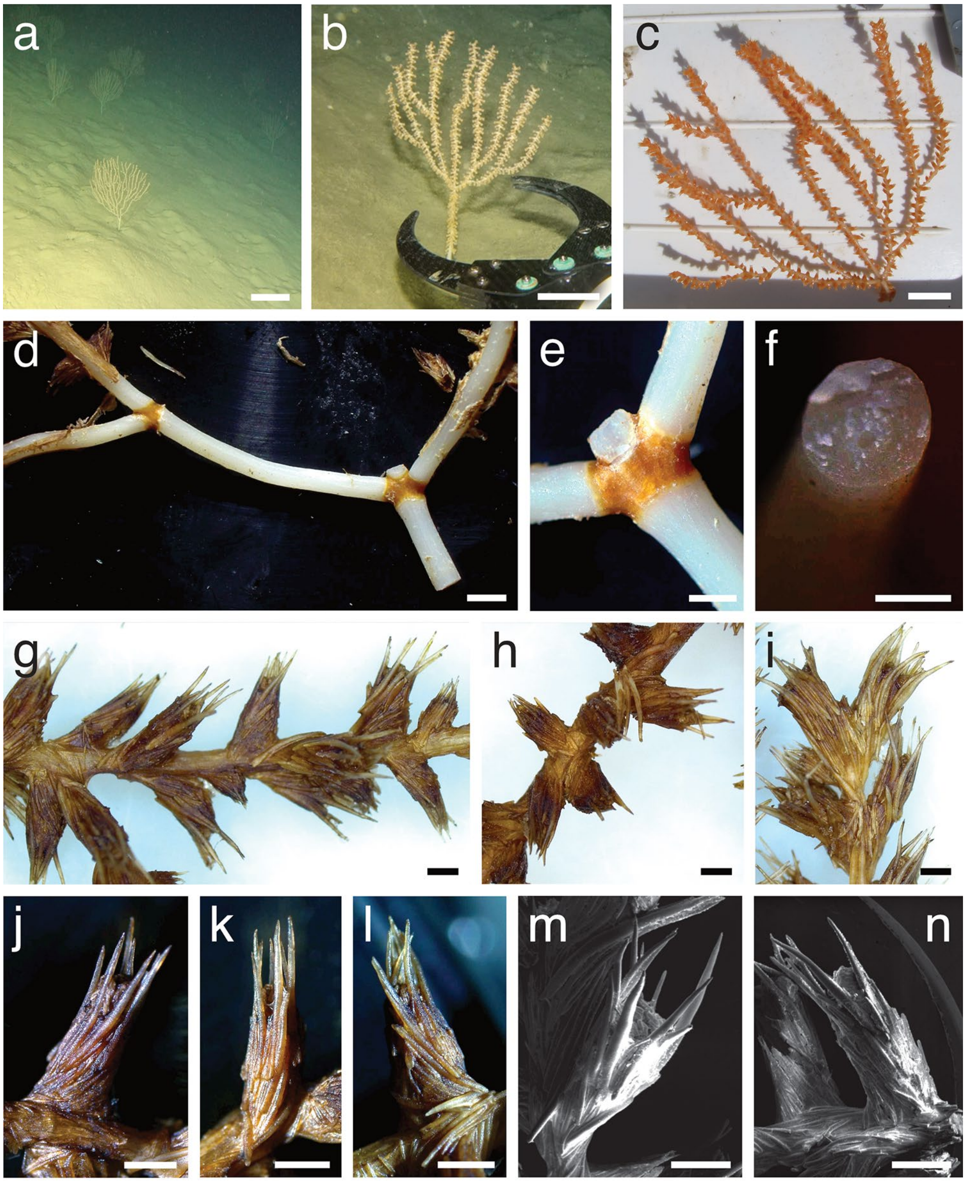


Fig. 20 *Acanella* cf. *arbuscola*. **a** Aggregation on the muddy flanks of the Monterosso Canyon, at 459 m. **b** Sample CD_FN_14 photographed immediately before (**b**) and after (**c**) collection. Note the bright orange color in (**c**). **d** The basal portion of the axial skeleton deprived of coenenchyme after chlorite hypochlorite cleansing. The organization in nodes and internodes is clearly depicted. **e** Close-up of the basal node of the colony. **f** Detail of a broken internode showing the allow central core. **g-i** Stereomicroscope images of *Acanella* branches from the central (**g**), basal (**h**), and apical (**i**) part of the colony. **j-l** Polyps with different status of contraction: opened (**j**), closed (**k**), and highly contracted (**l**). **m–n** SEM images of *Acanella* polyps. Scale bar: a = 10 cm; b = 5 cm; c = 2 cm; d = 2 mm; e, g-k = 1 mm; f = 0.5 mm

offshore seamounts (Bo et al. 2020a, 2021). In this case, however, the occurrence of *P. coronata* on the Ulisse Seamount has been recently confirmed (Bo, pers. comm.). The pennatulacean *Kophobelemnon stelliferum* (Müller, 1776) is herein reported only from the Penelope Seamount. However, this species is commonly encountered along the French continental slope and canyons (Fourt et al. 2017). A single colony has also been observed at mesophotic depth (70 m) along the western Ligurian coast (Enrichetti et al. 2019), further confirming its broad bathymetric range. Given that most of the ROV surveys conducted in this area targeted hard bottoms, it is plausible that records of *K. stelliferum*, as well as other pennatulaceans, are partially biased. *Muriceides lepida* and *Swiftia dubia* have been reported both inshore and offshore (Fig. 22). Among the species recorded exclusively offshore, *Bebryce mollis* and *Dendrobrachia bonsai* are the most widespread, occurring in all three seamounts. Conversely, *Villogorgia bebrycoides* and *Callogorgia verticillata* are reported only for the Ulisse and Penelope seamounts (upper bathyal tops) and *Chelidonisis aurantiaca* exclusively from the Janua Seamount (lower bathyal top). The faunal similarities among the three seamounts are unsurprising, since they are part of the same volcanic complex (Fanucci and Nicolich 1984). The Janua Seamount lies about 15 km southwest of the others, and the Penelope summit rises as a secondary peak of the Ulisse Seamount. Curiously, *V. bebrycoides* and *B. mollis* are also reported from the St. Lucia Seamount (mesophotic top), approximately located 25 NM East (Bo et al. 2014b) (Fig. 1).

Following the zoogeographical regionalization of the North Atlantic Ocean for deep-sea corals (Cairns and Chapman 2001; Watling et al. 2011), the Ligurian bathyal

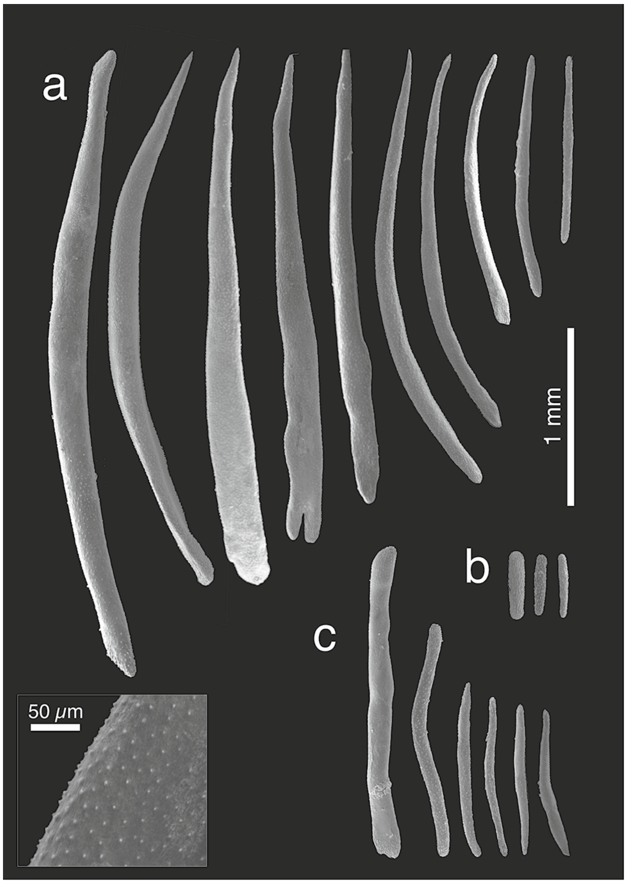


Fig. 21 SEM images of sclerites from sample CD_FN_14, identified as *Acanella* cf. *arbuscula*. **a** Polyp body sclerites. **b** Coenenchyme sclerites. **c** Tentacle sclerites. Inset: detail of polyp body sclerite tuberculation

octocoral fauna has been classified into five chorological categories (Fig. 23). Most species (62%) are distributed across both the Mediterranean Sea and the eastern Atlantic coast, corresponding to the Mediterranean Sea and Lusitanian provinces (Spalding et al. 2007). The geographical boundaries of the Lusitanian Province extend northward through the Bay of Biscay, SW England, and W Ireland, and southward along the Moroccan and Mauritanian coasts, including the Macaronesian Archipelago (Cape Verde, Canary Islands, Madeira, Azores). The whole province falls within the limits of the warm-temperate latitudinal belt. The gorgonian fauna of this area is distinguishable due to its richness in endemisms (Grasshoff 1977; Watling et al. 2011; Braga-Henriques et al. 2013). The dominance of warm-temperate NE Atlantic-Mediterranean species among the Ligurian bathyal octocorals—over half of the total—is unsurprising. This reflects the Mediterranean's biogeographic history, shaped by its connection to the Atlantic Ocean and strongly influenced by Quaternary climatic events (Bianchi et al. 2012).

Two species (15%), namely *A. armata* and *C. aurantiaca*, are known to occur exclusively in the North Atlantic Ocean. If specimen BM_FUS_01 is confirmed as *Acanthogorgia pico*, a third species would fall into this chorological category. *A. pico* has been recorded only along the eastern Atlantic Ocean, specifically the Azores and Ireland, while *A. armata* and *C. aurantiaca* are considered amphi-Atlantic. *A. pico* and *C. aurantiaca* are warm-temperate species, whereas *A. armata* is cold-temperate. It occurs from Newfoundland, Labrador, Greenland, and Iceland, extending southward into the warm-temperate belt only in the eastern North Atlantic. *A. armata* has also been reported from the Mediterranean Sea, though only in the Alboran region (Pardo et al. 2011).

Two species exhibit a widespread, circumglobal distribution. The pennatulacean *K. stelliferum* is broadly distributed throughout the temperate waters of both the Atlantic and Pacific Oceans (Rice et al. 1992; López-González et al. 2001; Mastrototaro et al. 2013). Similarly, *A. arbuscula* has been reported from the SW Pacific Ocean, the Aleutian Islands, the Indian Ocean, and the northern to equatorial Atlantic Ocean, including the Mediterranean Sea and the Gulf of Mexico (Saucier et al. 2017). However, the Ligurian population may represent a distinct *Acanella* species with a more restricted distribution. If so, the proportion of widespread species would decrease to 7%.

Among the Ligurian bathyal octocorals, *P. massiliensis* is currently the only species considered endemic to the Mediterranean Sea, although it has been recorded once off the coast of Galicia (Grasshoff 1985a). Due to its small size and delicate appearance, this species is likely often difficult to distinguish from the background, especially when scattered on coral rubble and sand. For this reason, the few records from both the Mediterranean (Sartoretto and Zibrowius 2018) and the Atlantic (Grasshoff 1985a) are likely underestimated, suggesting a wider distribution range for this species. A low level of endemism is plausible considering i) the relatively recent origin of the Mediterranean deep-sea fauna (Bianchi et al. 2012) and ii) the tendency for octocoral taxa with limited geographical ranges to inhabit coastal shallow waters, whereas species with widespread or cosmopolitan distributions are more common in deeper waters (Grasshoff 1977; Williams 1992). Notably, some species formerly regarded as Mediterranean endemics, but with vicariant counterparts in the Atlantic Ocean, are now considered synonyms, as exemplified by *K. stelliferum* and *K. leukarti* (Mastrototaro et al. 2013). However, it should be noted that *D. bonsai* is primarily reported from the Mediterranean basin, with only a single record in the NE Atlantic Ocean, from the Gulf of Cadiz (Díaz del Río et al. 2014), possibly indicating a quasi-endemic distribution.

Regarding bathymetric distribution, three main categories are identified for the Ligurian bathyal octocoral fauna (Fig. 23). The "highly eurybathic" species extend

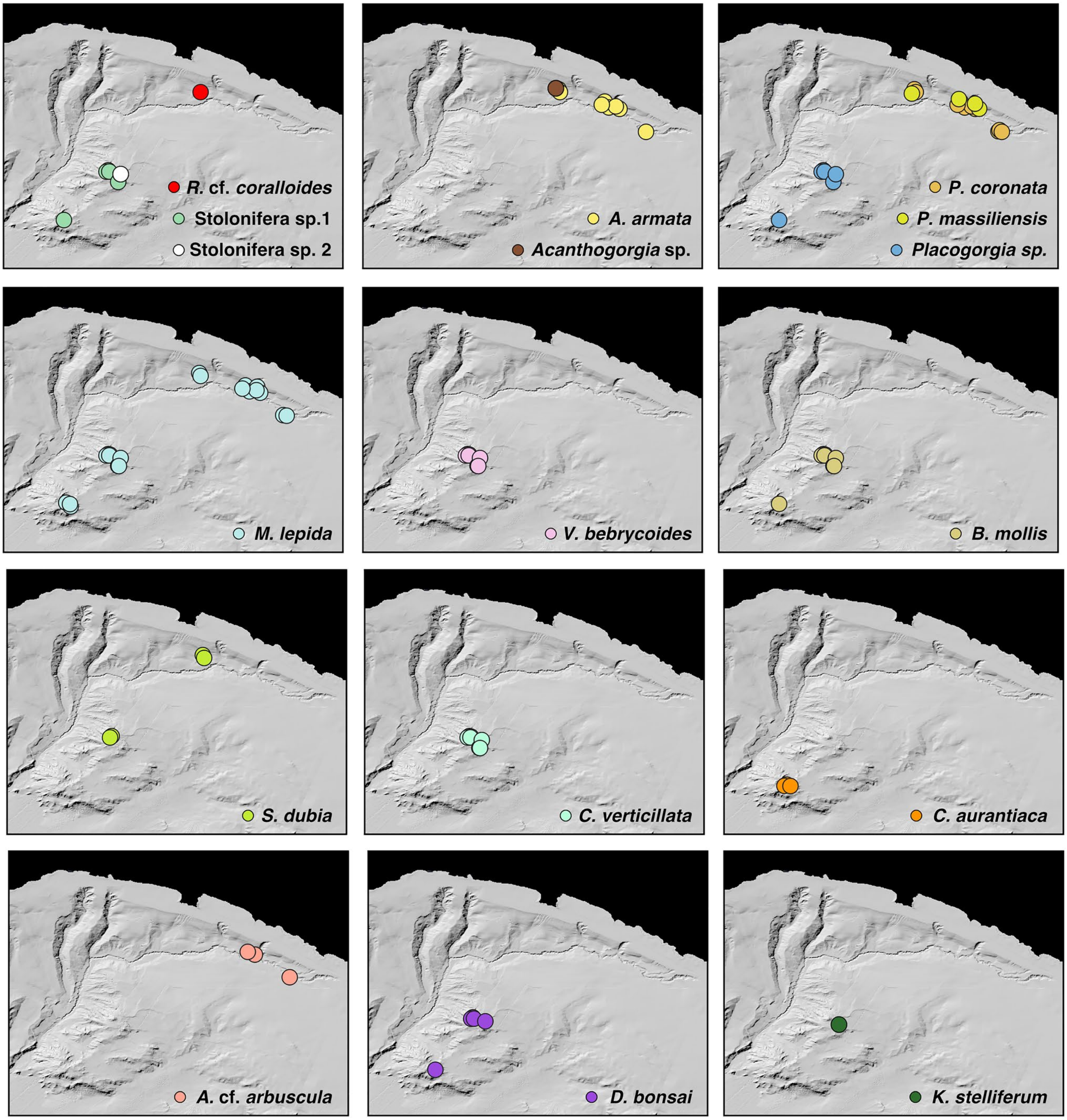


Fig. 22 Geographical distribution of the Ligurian bathyal octocorals based on recent ROV investigations. Data from Bo et al. (2020a, 2021, 2023)

their distribution from littoral depths down to the lower bathyal, reaching at least 2000 m (i.e., *S. dubia* and *K. stelliferum*). The "eurybathic" species extend from littoral depths to the lower bathyal but generally do not occur below 1000–1500 m. Some eurybathic species (i.e., *M. lepida*, *B. mollis*, and *C. verticillata*) show a stronger affinity for the lower bathyal zone compared to other taxa that tend to prefer mesophotic or upper bathyal depths (i.e., *V. bebrycoides*, *R. coralloides*). Finally, the true "bathyal" species are distributed below 200 m depth. Some of these species (namely *D. bonsai* and *C. aurantiaca*) are mainly found within the first 1000 m. In contrast, others (i.e., *A. armata*, *Placogorgia* spp., and *A. arbuscula*) generally inhabit greater depths.

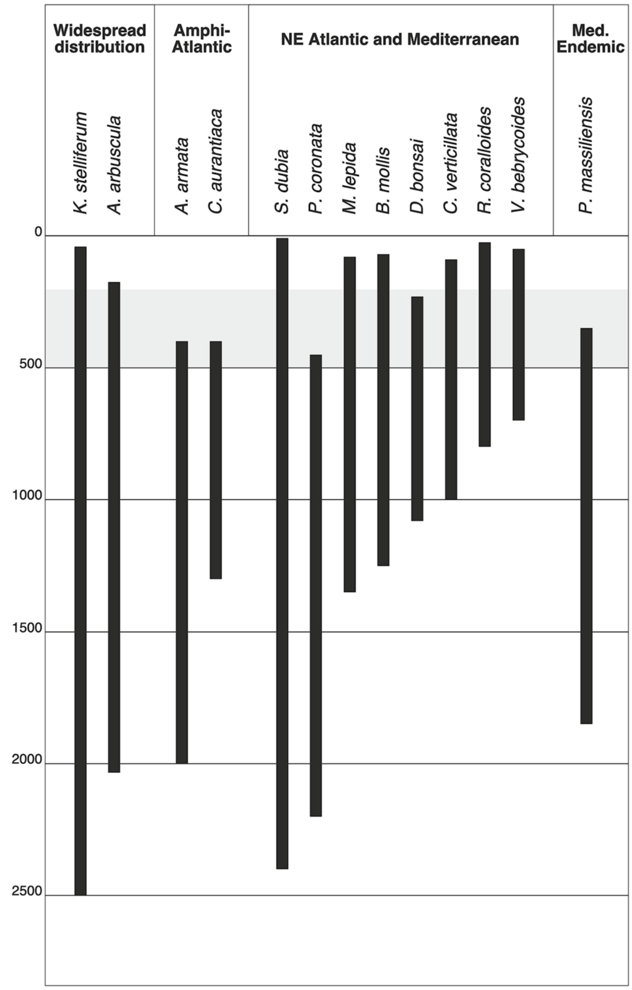


Fig. 23 Chorological categories and depth ranges of the Ligurian bathyal octocorals investigated in the present study. The shaded area indicates the upper bathyal belt (200–500 m) according to the most recent marine habitat classification for the Mediterranean Sea (Montefalcone et al. 2021)

Discussion

This study provides a detailed morphological description of the bathyal octocoral fauna from the Ligurian Sea, along with comprehensive anatomical, ecological data and imagery for taxa that are generally poorly documented. Ten species were sampled using an ROV and accurately examined (Table 1). Some of the identified species are considered widespread in the Mediterranean bathyal ecosystems. *Callogorgia verticillata*, for example, appears to be the most frequently recorded species, having been reported in eight out of the nine Mediterranean cold-water coral provinces (Rueda et al. 2019; Angeletti et al. 2020; Bo et al. 2023). Similarly, *Bebryce mollis*, *Muriceides lepida*, and *Villogorgia bebrycoides* were reported in five, four, and three cold-water coral provinces, respectively (Taviani et al. 2017; Moccia et al. 2019; Angeletti et al. 2020; Bo et al. 2023). Some of these species, along with the stoloniferan *Rolandia coralloides*, have also been recorded at shallower depths (Bo et al. 2012; Gori et al. 2017; Ocaña and Çinar 2018), confirming a wide geographical distribution.

This study contributed to expanding the known distribution of five species considered rare in the Mediterranean Sea. The inconspicuous habitus and the reduced size of some of these species limit their detection during deep-sea explorations. As new data from deep-sea studies become available, their occurrence and distribution may be significantly revised. Along with *P. massiliensis*, a small and rarely reported species currently considered endemic to the Mediterranean Sea, two other species are here reported for the first time in the Ligurian Sea. These include *Acanthogorgia armata*, previously recorded only in the Alboran Sea (Pardo et al. 2011), and *Acanella* cf. *arbuscula*, identified through molecular markers in the Ionian and Balearic Seas (Mytilineou et al. 2016; Saucier et al. 2017). Finally, the Atlantic species *Chelidonisis aurantiaca* represents a new record for the entire Mediterranean basin (Bo et al. 2020a), possibly along with *Acanthogorgia* cf. *pico*.

Three species were not physically collected but were identified from ROV footage in previous studies: *Swiftia dubia*, *Dendrobrachia bonsai*, and *Kophobelemnon stelliferum* (Bo et al. 2020a, 2021, 2023). An additional soft coral (sample BM_PEN_01) was collected on the Penelope Seamount on mud and biogenic detritus at 457 m (Bo et al. 2021) (Table 1). The taxonomic identity of this specimen, probably belonging to the genus *Daniela* von Koch, 1891, is still under investigation.

Additional information on octocoral diversity in the study area is available from historical studies mainly based on bycatch monitoring from bathyal trawling grounds in the eastern Ligurian Sea (Brian 1931; Issel 1932; Rossi 1958; Relini-Orsi and Relini 1972; Relini et al. 1986; Relini 2007). Rossi (1958) focused extensively on the cnidarians collected between 200 and 700 m in the Ligurian Sea. She analyzed both discarded material and the anthozoans collected by J.M. Pérès and J. Picard during the *Calypso* cruise in November 1957 (Blanc 1959). Her significant contribution led to the identification of twelve octocoral species, including: *Rolandia coralloides*, *Telestula* sp., *Alcyonium palmatum* Pallas, 1766, *Paramuricea macrospina* (Koch, 1882), *Villogorgia bebrycoides*, *Bebryce mollis*, *Isidella elongata*, and the pennatulaceans *Kophobelemnon stelliferum*, *Funiculina quadrangularis* (Pallas, 1766), *Virgularia mirabilis* (Müller, 1776), *Pennatula rubra* Ellis, 1764, *Pennatula phosphorea* Linnaeus, 1758, and *Pteroeides griseum* (Bohadsch, 1761). Among these, six were new records for the Ligurian Sea, and one species (*Telestula* sp.) was a new record for the entire Mediterranean Sea. Since Rossi's report, the genus *Telestula* has not been observed again in the Mediterranean

Sea, likely due to its small size and cryptic habitus. The record of *P. macrospina* is problematic, as the only currently known population in the Ligurian Sea is found at shallower depths (75–105 m) in the western sector (Enrichetti et al. 2019). Considering i) the morphological similarity between the genus *Paramuricea* and *Placogorgia*, and ii) that the first record and description of *Placogorgia* species in the Mediterranean occurred only in 1975, it is possible that the specimen observed by Rossi (1958) actually belonged to *Placogorgia*. A re-examination of Rossi's original material would be valuable to verify those records in light of current taxonomic knowledge.

Recent explorations in the study area include three dives carried out in 1994 with the bathyscaphe *Cyana*, off the Portofino Promontory and the nearby Entella Canyon, at depths between 125 and 520 m (Tunesi and Diviacco 1997; Tunesi et al. 2001). Additional ROV surveys were conducted in 2013–2014 in the Mesco and Monterosso Canyons, at depths of 378–580 m, by the Marine Environment Research Centre ENEA of La Spezia and the Marine Hydrographic Institute (Fanelli et al. 2017). These investigations reported living and dead scleractinians, as well as soft-bottom octocoral species, including *A. palmatum*, *F. quadrangularis*, and *I. elongata*.

Including historical data, the octocoral diversity in the bathyal Ligurian Sea now totals 24 species. This represents nearly half (48%) of the entire bathyal Mediterranean octocoral fauna, which comprises 50 species in total (Altuna and Poliseno 2019). Several factors likely contribute to the high octocoral diversity in the bathyal Ligurian Sea. First, the complex seabed topography (featuring steep slopes, canyons, and seamounts) offers firm substrates for larval settlement and a variety of exposure condition (Fanucci et al. 1989; Cattaneo-Vietti et al. 2010; Würtz 2012). Second, the area is influenced by the Levantine Intermediate Water (LIW), a cold, well-oxygenated current that plays a crucial role in sustaining Mediterranean bathyal communities dominated by cnidarians (Taviani et al. 2017; Chimienti et al. 2019; Vertino et al. 2019; Wienberg et al. 2022). Furthermore, the Ligurian Sea is the northernmost and coldest sector of the western Mediterranean Sea, offering optimal oceanographic conditions for deep-sea fauna, which is mainly composed of elements with Boreo-Atlantic affinity (Fredj and Laubier 1985; Bianchi et al. 2012). Finally, the octocoral diversity of the bathyal Ligurian Sea represents about 22% of the group's total diversity in the NE Atlantic Ocean (Watling et al. 2011; García-Cárdenas et al. 2023). This finding supports the general view that the Mediterranean deep-sea coral fauna is less diverse than that of the adjacent NE Atlantic Ocean (Altuna and Poliseno 2019).

Another aim of this study was to identify the main taxonomic shortcomings affecting the identification of Mediterranean deep-sea octocorals. Some octocoral genera in the Mediterranean are monospecific and characterized by a distinct sclerite type. In these cases, species identification is relatively straightforward, as seen in *V. bebrycoides*, *B. mollis*, and *C. verticillata*. However, in most genera, the high morphological plasticity complicates the identification (Altuna and Poliseno 2019). In such cases, accurate identification should rely on multiple features, including the sclerome, polyps, colony structure, and axial skeleton. Our analysis of the Ligurian specimens revealed that some traits are particularly prone to variability, making them less reliable in certain taxa. For example, colony size and branch thickness vary considerably in *Placogorgia* and *Muriceides*. Similarly, the presence of branched or unbranched sclerites in the inner layer of the coenenchyme shows significant variability in *Acanthogorgia*, *Placogorgia*, and *Muriceides*.

The present study highlights the difficulty in separating some closely related genera, such as the pairs *Rolandia*/*Sarcodictyon*, *Paramuricea*/*Placogorgia*, and *Acanella*/*Isidella*. These difficulties often reflect the confusion affecting the entire taxonomic group, as seen in the family Keratoisididae (Watling et al. 2022; Morrissey et al. 2023). In the case of *Paramuricea* and *Placogorgia*, the two genera represent a continuum of different forms without clear boundaries. In all these situations, a major systematic revision supported by morphological and phylogenetic evidence is needed (Altuna and Poliseno 2019).

Some taxonomic aspects highlighted in the present study suggest that the diversity of certain groups of Mediterranean octocorals may be higher than currently known. Deep-sea octocorals identification in the Mediterranean Sea is largely based on Carpine and Grasshoff (1975), who described several monospecific genera, including *Acanthogorgia*. In the present study, however, three species of the genus *Acanthogorgia* are reported for the Mediterranean, namely *A. armata*, *A. hirsuta*, and *Acanthogorgia* sp. A similar situation is described for the Mediterranean keratoisidids. Three species, namely *A. arbuscula*, *A. furcata*, and *I. elongata,* are known from bathyal muds (Saucier et al. 2017), compared to only one reported by Carpine and Grasshoff (1975). This study also considers the possibility that *Acanella* cf. *arbuscula* and *Rolandia* cf. *coralloides* represent undescribed species. Conversely, it highlights the unclear morphological distinctions between *M. lepida* and *M. sceptrum*.

Finally, this study provided some new ecological insights into the identified species. Substrate preference, for example, has been expanded for three species documented growing on plastic debris, namely *A. armata*, *M. lepida*, and, if confirmed, *R.* cf. *coralloides*.

The contrasting distribution patterns between inshore and offshore habitats displayed by the species analyzed in the present study remain difficult to explain (Fig. 22). One possible explanation is that the stable conditions and unique trophic environment of offshore seamounts favor some deep-sea octocoral species, accounting for the high observed diversity. In contrast, the oceanographic conditions of the Ligurian continental shelf may vary greatly due to the seabed topography, river inputs, and coastal urbanization (Cattaneo-Vietti et al. 2010). Additionally, the influence of the LIW, together with upwelling and downwelling along the continental slope, likely contributes to the high abundances of species forming dense forests along the Levante Canyon, namely *A. armata*, *P. coronata*, *P. massiliensis*, *M. lepida*, and *Acanella* cf. *arbuscula*.

The bathymetric distributions identified here are consistent with the information available in the literature (Fig. 23). For some closely related species pairs, the analysis of literature records suggests a possible bathymetric separation between mainly mesophotic and mainly bathyal species. For example, *A. hirsuta* and *V. bebrycoides* are probably more common at mesophotic depths, while *A. armata* and *M. lepida* can be considered true bathyal species.

Establishing a solid morphological reference framework is essential for advancing octocoral taxonomic knowledge, including molecular analyses. While recent advances in phylogenomic have significantly improved our understanding of higher-level relationships among octocoral orders and families (McFadden et al. 2022), the resolution at genus and species level remains limited. Molecular markers often yield ambiguous or even erroneous results, especially when not supported by robust morphological verification (Altuna & Poliseno 2019). The present study focused on establishing a solid morphological framework as a necessary baseline for future integrative approaches. Continued improvements in molecular techniques, combined with robust morphological verification, are expected to provide a more accurate picture of generic and species-level diversity in the coming years.

Taxonomic studies on deep-sea marine organisms are also crucial for supporting ROV-based surveys and refining biodiversity estimates. In particular, gorgonians play a key ecological role in structuring deep-sea habitats. A clearer and more consistent taxonomic framework allows for better assessment of species richness and distribution, ultimately contributing to more informed conservation strategies and the effective protection of these vulnerable ecosystems.

Acknowledgements The authors would like to thank the crew of the *Daedalus* catamaran (Fondazione AzioneMare) for their invaluable support and assistance during the research activities. Authors also thank Federico Betti for his assistance with improving the figure quality.

Author contributions FE and MB helped in conceptualization, methodology, investigation. MB and GB contributed to funding acquisition, resources, supervision, writing—review and editing. FE helped in data curation, writing—original draft preparation, visualization. All authors reviewed the manuscript.

Funding Open access funding provided by Università degli Studi di Genova within the CRUI-CARE Agreement. This research was supported by 1) Università degli Studi di Genova, Curiosity-Driven Project "Lost coral reefs: ancient deep-sea bioherms in a modern world" (2021–2022), 2) SIR-MIUR_BIOMOUNT Project "Biodiversity Patterns of the Tyrrhenian Seamounts" [grant number RBSI14HC9O], and 3) National Biodiversity Future Center—NBFC project, code [CN_00000033], Concession Decree No. 1034 of June 17, 2022, adopted by the Italian Ministry of University and Research [CUP D31B21008270007].

Data Availability No datasets were generated or analyzed during the current study.

Declarations

Conflict of interest The authors declare no competing interests.

References

Aguilar R, Pastor X, Garcia S, Marin P, Ubero J (2013) Importance of seamounts-like features for Mediterranean marine habitats and threatened species. Rapports De La Comm Int Pour La Mer Méditerranée 40:716

Aguilar R, Perry AL, López J (2017) Conservation and management of vulnerable marine benthic ecosystems. In: Bramanti L, Gori A, Orejas C (eds) Rossi S. Springer International Publishing, Marine animal forests. The Ecology of Benthic Biodiversity Hotspots. Cham, pp 1165–1207

Aguilar R, Pastor X, De la Torriente A, García S (2009) Deep-sea coralligenous beds observed with ROV on four seamounts in the Western Mediterranean. In: UNEP-MAP-RAC/SPA, Proceedings of the 1st Mediterranean symposium on the conservation of the coralligenous and others calcareous bio-concretions. Tabarka, Tunis: CAR/ASP publishing, pp 147–149

Aguilar R, Garcia S, Perry AL, Alvarez H, Blanco J, Chimienti G, Montesanto F, Mastrototaro F (2018) Deep-sea habitats and communities in the Aeolian Islands (north Sicily). In: 2nd Mediterranean Symposium on the conservation of Dark Habitats. 2018. pp 27

Althaus F, Williams A, Schlacher TA, Kloser RJ, Green MA, Barker BA, Schlacher-Hoenlinger MA (2009) Impacts of bottom trawling on deep-coral ecosystems of seamounts are long-lasting. Mar Ecol Prog Ser 397:279–294

Altuna A, Poliseno A (2019) Taxonomy, genetics and biodiversity of mediterranean deep-sea corals and cold-water corals. In: Orejas C, Jiménez C (ed) Mediterranean cold-water corals: past, present and future. Coral Reefs of the World, vol 9. Springer, Cham.

Angeletti L, Castellan G, Montagna P, Remia A, Taviani M (2020) The "Corsica channel cold-water coral province" (Mediterranean Sea). Front Mar Sci 7:661

Angiolillo M, Di Lorenzo B, Izzi A, Giusti M, Nonnis O, Pazzini A, Trabucco B, Tunesi L (2024) Healthy assemblages of *Isidella elongata* unintentionally protected from trawling offshore of Asinara Island (northwestern Sardinia, NW Mediterranean Sea). Sci Rep 14:12813

Astraldi M, Gasparini GP, Sparnocchia S (1994) The seasonal and interannual variability in the Ligurian-Provencal basin. In: La Viollette PE (ed) Seasonal and interannual variability of the Western Mediterranean Sea. American Geophysical Union, Washington, DC, pp 93–113. https://doi.org/10.1029/CE046p0093

Aurivillius M (1931) The Gorgonarians from Dr. Sixten Bock's expedition to Japan and Bonin Islands 1914

Bassano E, Boniforti R, Pezzani A (2000) Parametri meteorologici e idrologici. In: Peroni C (ed) Sistema informativo e di monitoraggio marino costiero della provincia della Spezia. La Spezia, Italy, ENEA, pp 17–55

Bayer FM (1959) A review of the gorgonacean genus *Placogorgia* Studer, with a description of *Placogorgia tribuloides*, a new species from the Straits of Florida. J Wash Acad Sci 49:54–61

Bayer FM (1961) The shallow-water Octocorallia of the West Indian region. Stud Fauna Curacao Other Caribb Isl 12:1–373

Bayer FM (1981) Key to the genera of Octocorallia exclusive of Pennatulacea (Coelenterata: Anthozoa), with diagnosis of new taxa. Proc Biol Soc Wash 94:902–947

Bayer FM (1990) A new isidid octocoral (Anthozoa: Gorgonacea) from New Caledonia, with descriptions of other new species from elsewhere in the Pacific Ocean. Proc Biol Soc Wash 103:205–228

Bayer FM, van Ofwegen L (2016) The type specimens of *Bebryce* (Cnidaria, Octocorallia, Plexauridae) re-examined, with emphasis on the sclerites. Zootaxa 4083(3):301–358

Bayer FM (1973) Colonial organization in octocorals. In: Boardman, Cheetham, Oliver (ed) Animal colonies. Dowden, Hutchinson & Ross, Inc., Stroudsburg, Pa

Bianchi CN, Morri C, Chiantore M, Montefalcone M, Parravicini V, Rovere A (2012) Mediterranean Sea biodiversity between the legacy from the past and a future of change. Life in the Mediterranean Sea: a Look at Habitat Changes 1:55

Bilan M, Gori A, Grinyó J, Biel-Cabanelas M, Puigcerver-Segarra X, Santín A, Piraino S, Rossi S, Puig P (2023) Vulnerability of six cold-water corals to sediment resuspension from bottom trawling fishing. Mar Pollut Bull 196:115423

Blanc JJ (1959) Recherches sur les vases du Golfe de Génes (Région de Portofino). Ann Inst Oceanogr 37:274–287

Bo M, Bertolino M, Borghini M, Castellano M, Covazzi Harriague A, Camillo CG, Bavestrello G (2011) Characteristics of the mesophotic megabenthic assemblages of the Vercelli seamount (North Tyrrhenian Sea). PLoS ONE 6:e16357. https://doi.org/10.1371/journal.pone.0016357

Bo M, Canese S, Spaggiari C, Pusceddu A, Bertolino M, Angiolillo M, Giusti M, Loreto MF, Salvati E, Greco S, Bavestrello G (2012) Deep coral oases in the South Tyrrhenian Sea. PLoS ONE 7:e49870

Bo M, Cerrano C, Canese S, Salvati E, Angiolillo M, Santangelo G, Bavestrello G (2014a) The coral assemblages of an offshore deep Mediterranean rocky bank (NW Sicily, Italy). Mar Ecol 35:332–342

Bo M, Bava S, Canese S, Angiolillo M, Cattaneo-Vietti R, Bavestrello G (2014b) Fishing impact on deep Mediterranean rocky habitats as revealed by ROV investigation. Biol Conserv 171:167–176

Bo M, Bavestrello G, Angiolillo M, Calcagnile L, Canese S, Cannas R, D'Elia M, D'Oriano F, Follesa MC, Quarta G, Cau A (2015) Persistence of pristine deep-sea coral gardens in the Mediterranean Sea (SW Sardinia). PLoS ONE 10:e0119393

Bo M, Coppari M, Betti F, Massa F, Gay G, Cattaneo-Vietti R, Bavestrello G (2020a) Unveiling the deep biodiversity of the Janua Seamount (Ligurian Sea): first Mediterranean sighting of the rare Atlantic bamboo coral *Chelidonisis aurantiaca* Studer, 1890. Deep Sea Res I 156:103186

Bo M, Al Mabruk SA, Balistreri P, Bariche M, Batjakas IE, Betti F, Gerovasileiou V (2020b) New records of rare species in the Mediterranean Sea. Med Mar Sci 21:608–630. https://doi.org/10.12681/mms.23674

Bo M, Coppari M, Betti F, Enrichetti F, Bertolino M, Massa F, Bava S, Gay G, Cattaneo-Vietti R, Bavestrello G (2021) The high biodiversity and vulnerability of two Mediterranean bathyal seamounts support the need for creating offshore protected areas. Aquat Conserv Mar Freshw Ecosyst 31:543–566

Bo M, Enrichetti F, Betti F, Gay G, Quarta G, Calcagnile L, Bavestrello G (2023) The cold-water coral province of the eastern Ligurian Sea (NW Mediterranean Sea): historical and novel evidences. Front Mar Sci 10:1114417

Braga-Henriques A, Porteiro FM, Ribeiro PA, De Matos V, Sampaio Í, Ocaña O, Santos RS (2013) Diversity, distribution and spatial structure of the cold-water coral fauna of the Azores (NE Atlantic). Biogeosciences 10:4009–4036

Brian A (1931) La biologia del fondo a Scampi nel Mare Ligure. V. Aristeomorpha, Aristeus ed altri macruri natanti. Boll Mus Zool Anatom Comp Reg Univ Genova 11(2):1–6

Brito A, Ocaña B (2004) Corales de las Islas Canarias: antozoos con esqueleto de los fondos litorales y profundos. Francisco Lemus, Editor

Bryce M, Radford B, Fabricius K (2018) Soft coral and sea fan (Octocorallia) biodiversity and distribution from a multitaxon survey (2009–2014) of the shallow tropical Kimberley, Western Australia. Rec West Aust Mus 85:45–73

Buhl-Mortensen L, Mortensen PB (2004) Crustaceans associated with the deep-water gorgonian corals *Paragorgia arborea* (L., 1758) and *Primnoa resedaeformis* (Gunn., 1763). J Nat Hist 38(10):1233–1247

Buhl-Mortensen L, Olafsdottir SH, Buhl-Mortensen P, Burgos JM, Ragnarsson SA (2015) Distribution of nine cold-water coral species (Scleractinia and Gorgonacea) in the cold temperate North Atlantic: effects of bathymetry and hydrography. Hydrobiologia 759:39–61

Bullimore RD, Foster NL, Howell KL (2013) Coral-characterized benthic assemblages of the deep Northeast Atlantic: defining "Coral Gardens" to support future habitat mapping efforts. ICES J Mar Sci 70(3):511–522

Cairns SD (2007) Deep-water corals: an overview with special reference to diversity and distribution of deep-water scleractinian corals. Bull Mar Sci 81(3):311–322

Cairns SD, Chapman RE (2001) Biogeographic affinities of the North Atlantic deep-water Scleractinia. In: Proceedings of the First International Symposium on Deep-Sea Corals, Ecology Action Centre and Nova Scotia Museum, Halifax, Nova Scotia, Canada

Carbonara P, Zupa W, Follesa MC, Cau A, Capezzuto F, Chimienti G, D'Onghia G, Lembo G, Pesci P, Porcu C, Bitetto I, Spedicato MT, Maiorano P (2020) Exploring a deep-sea vulnerable marine ecosystem: *Isidella elongata* (Esper, 1788) species assemblages in the Western and Central Mediterranean. Deep Sea Res Part I: Oceanogr Res Pap 166:103406

Carpine C (1963) Contribution à la connaissance des Gorgones Holaxonia de la Mediterranean occidentale. Bull Inst Oceanogr Monaco 60(1270):1–52

Carpine C, Grasshoff M (1975) Les Gorgonaries de la Mediterranee. Bull Musee Oceanogr Monaco 71:1–140

Carreiro-Silva M, Braga-Henriques A, Sampaio I, de Matos V, Porteiro FM, Ocaña O (2011) *Isozoanthus primnoidus*, a new species of zoanthid (Cnidaria: Zoantharia) associated with the gorgonian *Callogorgia verticillata* (Cnidaria: Alcyonacea). ICES J Mar Sci 68(2):408–415

Cattaneo-Vietti R, Albertelli G, Aliani S, Bava S, Bavestrello G, Cecchi LB, Wurtz M (2010) The Ligurian Sea: present status, problems and perspectives. Chem Ecol 26(S1):319–340

Cecchini C (1914) Su due nuovi Isidae nel Mediterraneo. Monit Zool Ital 25:49–52

Chimienti G, Bo M, Taviani M, Mastrototaro F (2019) Occurrence and biogeography of Mediterranean cold-water corals. In: Orejas C, Jiménez C (eds) Mediterranean Cold-water corals: past, present and future. Springer, Cham, pp 213–243

Chimienti G, Angeletti L, Furfaro G, Canese S, Taviani M (2020) Habitat, morphology and trophism of *Tritonia callogorgiae* sp. nov., a large nudibranch inhabiting *Callogorgia verticillata* forests in the Mediterranean Sea. Deep Sea Res Part I: Oceanogr Res Pap 165:103364

Daly M, Brugler MR, Cartwright P, Collins AG, Dawson MN, Fautin DG, France SC, McFadden CS, Opresko MN, Rodriguez E, Romano SL, Stake JL (2007) The phylum Cnidaria: a review of phylogenetic patterns and diversity 300 years after Linnaeus. In: Shear WA (ed) Zhang ZQ. Linnaeus Tercentenary: Progress in Invertebrate Taxonomy, Zootaxa, pp 1–766

Davies AJ, Roberts JM, Hall-Spencer J (2007) Preserving deep-sea natural heritage: emerging issues in offshore conservation and management. Biol Conserv 138(3–4):299–312

De la Torriente A, Serrano A, Fernández-Salas LM, García M, Aguilar R (2018) Identifying epibenthic habitats on the Seco de los Olivos Seamount: species assemblages and environmental characteristics. Deep Sea Res Part I: Oceanogr Res Pap 135:9–22. https://doi.org/10.1016/j.dsr.2018.03.015

Deichmann E (1936) The Alcyonaria of the western part of the Atlantic Ocean. Mem Mus Comp Zool 53:1–317

Delbono I, Ivaldi R, Pratellesi M, Fanelli E, Peirano A, Cocito S, et al. (2014) Seafloor morphology: nature of the seabed and the cold-water corals of the Levante canyon (eastern Ligurian Sea, NW Mediterranean). EGU General Assembly Conference Abstracts 14732

Díaz-del-Río-Español V, Bruque-Carmona G, Fernández-Salas LM, Rueda JL, González-García E, López-González N, Arcos JM (2014) Volcanes de Fango del Golfo de Cádiz. Areas de Estudio del proyecto LIFE+ INDEMARES

Dominguez-Carrió C, Riera JL, Robert K, Zabala M, Requena S, Gori A, Orejas C, Lo Iacono C, Estournel C, Corbera G, Ambroso S, Uriz MJ, López-González PJ, Sardá R, Gili JM (2022) Diversity, structure and spatial distribution of megabenthic communities in Cap de Creus continental shelf and submarine canyon (NW Mediterranean). Prog Oceanogr 208:102877

Dueñas LF, Alderslade P, Sánchez JA (2014) Molecular systematics of the deep-sea bamboo corals (Octocorallia: Isididae: Keratoisidinae) from New Zealand with descriptions of two new species of *Keratoisis*. Mol Phylogenet Evol 74:15–28

Edinger EN, Wareham VE, Haedrich RL (2007) Patterns of groundfish diversity and abundance in relation to deep-sea coral distributions in Newfoundland and Labrador waters. Bull Mar Sci 81(3):101–122

Ely CV, de Loreto Bordignon SA, Trevisan R, Boldrini II (2017) Implications of poor taxonomy in conservation. J Nat Cons 36:10–13

Enrichetti F, Bavestrello G, Coppari M, Betti F, Bo M (2018) *Placogorgia coronata* first documented record in Italian waters: Use of trawl bycatch to unveil vulnerable deep-sea ecosystems. Aquat Conserv Mar Freshw Ecosyst 28(5):1123–1138

Enrichetti F, Dominguez-Carrió C, Toma M, Bavestrello G, Betti F, Canese S, Bo M (2019) Megabenthic communities of the Ligurian deep continental shelf and shelf break (NW Mediterranean Sea). PLoS ONE 14(10):e0223949

Esper EJC (1791) Die Pflanzenthiere in Abbildungen nach der Natur mit Farben erleuchtet, nebst Beschreibungen, vol 1. Raspischen Buchhandlung, Nurnberg, pp 1–320

Fabri MC, Pedel L, Beuck L, Galgani F, Hebbeln D, Freiwald A (2014) Megafauna of vulnerable marine ecosystems in French Mediterranean submarine canyons: spatial distribution and anthropogenic impacts. Deep Sea Res Part II Top Stud Oceanogr 104:184–207. https://doi.org/10.1016/j.dsr2.2013.06.016

Fabricius KE, Alderslade P (2001) Soft corals and sea fans: a comprehensive guide to the tropical shallow water genera of the central-west Pacific, the Indian Ocean and the Red Sea

Verrill AE (1883) Report on the Anthozoa, and on some additional species dredged by the "Blake" in 1877–1879, and by the US Fish Commission steamer "Fish Hawk" in 1880–82. Museum of Comparative Zoology at Harvard College

Fanelli E, Delbono I, Ivaldi R, Pratellesi M, Cocito S, Peirano A (2017) Cold-water coral *Madrepora oculata* in the eastern Ligurian Sea (NW Mediterranean): historical and recent findings. Aquat Conserv Mar Freshw Ecosyst 27(5):965–975

Fanucci F, Nicolich R (1984) Il Mar Ligure: nuove acquisizioni sulla natura, genesi ed evoluzione di un “bacino marginale.” Mem Soc Geol It 27:97–110

Fanucci F, Eva C, Cattaneo M, Firpo M, Piccazzo M (1989) Tettonica e morfogenesi olocenica in Mar Ligure. Mem Soc Geol Ital 42:221–227

Fourt M, Goujard A, Pérez T, Chevaldonné P (2017) Guide de la faune profonde de la mer Méditerranée: Explorations des roches et canyons sous-marins des côtes françaises. Muséum national d’Histoire naturelle, Paris, 184 p. Patrimoines Naturels 75

France SC (2007) Genetic analysis of bamboo corals (Cnidaria: Octocorallia: Isididae): does lack of colony branching distinguish *Lepidisis* from *Keratoisis*? Bull Mar Sci 81(3):323–333

Fredj G, Laubier L (1985) The deep Mediterranean benthos. Mediterranean marine ecosystems. Springer, Boston, MA, pp 109–145

Freiwald A, Fossâ JH, Grehan A, Koslow T, Roberts JM (2004) Cold-water coral reefs: out of sight-no longer out of mind. UNEP-WCMC

Freiwald A, Boetius A, Bohrmann G (2011) Deep water ecosystems of the eastern Mediterranean – cruise no. M70 – September 24–December 8, 2006 – La Valletta (Malta)–Heraklion (Greece). METEOR-Berichte, M70. Bremen, Germany: DFG-Senatskommission für Ozeanographie

García-Cárdenas FJ, López-González PJ (2023) Biogeographic patterns in sea pens (Octocorallia: Pennatulacea). Mar Biodivers 53(1):18

Giangrande A (2003) Biodiversity, conservation, and the ‘Taxonomic impediment.’ Aquat Conserv Mar Freshw Ecosyst 13(5):451–459

Gili JM (1982) Fauna de cnidaris de las Illes Medes. Treb Inst Catalana Hist Nat 10:1–175

Gori A, Bavestrello G, Grinyó J, Dominguez-Carrió C, Ambroso S, Bo M (2017) Animal forests in deep coastal bottoms and continental shelf of the Mediterranean Sea. In: Bramanti L, Gori A, Orejas C (eds) Rossi S. Springer International Publishing, Marine animal forests. The Ecology of Benthic Biodiversity Hotspots. Cham, pp 1–27

Grasshoff M (1972) Die Gorgonaria des östlichen Nordatlantik und des Mittelmeeres, I. Die Familie Ellisellidae (Cnidaria: Anthozoa): Auswertung der "Atlantischen Kuppenfahrten 1967" von FS "Meteor." Meteor Forschungsergebnisse: Reihe D, Biologie 10:73–87

Grasshoff M (1973) Die Gorgonaria des östlichen Nordatlantik und des Mittelmeeres, II. Die Gattung *Acanthogorgia* (Cnidaria: Anthozoa): Auswertung der "Atlantischen Kuppenfahrten 1967" von FS "Meteor." Meteor Forschungsergebnisse: Reihe D, Biologie 13:1–10

Grasshoff M (1981) Gorgonaria und Pennatularia (Cnidaria: Anthozoa) vom Mittelatlantischen Rücken SW der Azoren. Steenstrupia 7(9):213–230

Grasshoff M (1985b) Die Gorgonaria und Antipatharia der Großen Meteor-Bank und der Josephine-Bank. (Cnidaria: Anthozoa). Senckenb Biol 17:65–87

Grasshoff M (1986) Die Gorgonaria der expeditionen von "Travailleur" 1880–1882 und "Talisman" 1883 (Cnidaria, Anthozoa). Bull Mus Natl Hist Nat Paris A Zool Biol Ecologie Anim 8(1):9–38

Grasshoff M (1989) Die Meerenge von Gibraltar als Faunen-Barriere: Die Gorgonaria, Pennatularia und Antipatharia der Balgim-Expedition (Cnidaria: Anthozoa). Senckenb Marit 20:201–223

Grasshoff M (1992) Die Flachwasser-Gorgonarien von Europa und Westafrika (Cnidaria, Anthozoa). Cour Forsch Inst Senckenb 149:1–135

Grasshoff M (1977) Die Gorgonarien des östlichen Nordatlantik und des Mittelmeeres: III. Die Familie Paramuriceidae (Cnidaria: Anthozoa). "Meteor" – Forschungs – Ergebnisse D27: 5–76

Grasshoff M (1985a) Die Gorgonaria, Pennatularia und Antipatharia des Tiefwassers der Biscaya (Cnidaria: Anthozoa). III. Ergänzungen. In: Laubier L, Monniot C (Eds.), Peuplements profonds du Golfe de Gascogne. Campagnes BIOGAS. IFREMER, Brest, pp. 99–310

Gray JE (1870) Catalogue of lithophytes or stony corals in the collection of the British Museum. order of the Trustees

Grinyó J, Gori A, Ambroso S, Purroy A, Calatayud C, Dominguez-Carrió C, Coppari M, Lo Iacono C, López-González PJ, Gili JM (2016) Diversity, distribution and population size structure of deep Mediterranean gorgonian assemblages (Menorca Channel, Western Mediterranean Sea). Prog Oceanogr 145:42–56

Grinyó J, Gori A, López-González PJ, Santín A, Baena P, Gili JM (2018) Morphological features of the gorgonian *Paramuricea macrospina* on the continental shelf and shelf edge (Menorca Channel, Western Mediterranean Sea). Mar Biol Res 14(1):30–40

Hall-Spencer J, Allain V, Fosså JH (2002) Trawling damage to Northeast Atlantic ancient coral reefs. Proc R Soc Lond B Biol Sci 269(1490):507–511

Harris PT, Whiteway T (2011) Global distribution of large submarine canyons: geomorphic differences between active and passive continental margins. Mar Geol 285(1–4):69–86

Issel R (1932) La fauna profonda del golfo di Genova dal punto di vista ecologico e pratico. Boll Zool 3:15–21

Johnson JY (1862) Descriptions of some new corals from Madeira. Proc Zool Soc Lond 30(1):194–197

Jørgensen OA, Tendal OS, Arboe NH (2013) Preliminary mapping of the distribution of corals observed off West Greenland as inferred from bottom trawl surveys 2010–2012. NAFO SCR Doc 13/007, Northwest Atlantic Fisheries Organization, Serial No. N6156: 1–10

Koch G (1887) Die Gorgoniden des Golfes von Neapel und der angrenzenden meeresabschnitte: Erster theil einer monographie der Anthozoa Alcyonaria (Vol 9). R Friedlander & Sohn

Kükenthal W (1915) System und stammesgeschichte der isididae. Zool Anz 46:116–126

Kükenthal W (1919) Gorgonaria. Wiss Ergebn Deutsch Tiefsee-Exped "Valdivia" 1898–1899 13: 1–946, pls 30–89

Kükenthal WG (1924) Das Tierreich: Eine Zusammenstellung und Kennzeichnung der rezenten Tierformen. Lfg. 47 Coelenterata: Gorgonaria (Vol 47). de Gruyter

Lasker HR, Bramanti L, Tsounis G, Edmunds PJ (2020) The rise of octocoral forests on Caribbean reefs. Adv Mar Biol 87:361–410

Li J, Wang P (2019) Discovery of deep-water bamboo coral forest in the South China Sea. Sci Rep 9(1):15453

López-González PJ, Gili JM, Williams GC (2001) New records of Pennatulacea (Anthozoa: Octocorallia) from the African Atlantic coast, with description of a new species and a zoogeographic analysis. Sci Mar 65(1):59–74

López-González PJ, Grinyó J, Gili JM (2012) Rediscovery of *Cereopsis studeri* Koch, 1891, a forgotten Mediterranean soft coral species, and its inclusion in the genus *Nidalia* Gray, 1835 (Octocorallia, Alcyonacea, Nidaliidae). Mar Biol Res 8(7):594–604

López-González PJ, Grinyó J, Gili JM (2015) *Chironephthya mediterranea* n. sp. (Octocorallia, Alcyonacea, Nidaliidae), the first species of the genus discovered in the Mediterranean Sea. Mar Biodivers 45:667–688

Mace GM (2004) The role of taxonomy in species conservation. Philos Trans R Soc Lond B: Biol Sci 359(1444):711–719

Madsen FJ (1944) Octocorallia. Danish Ingolf-Expedition 5:1–65

Maldonado M, Aguilar R, Blanco J, Garcia S, Serrano A, Punzon A (2015) Aggregated clumps of lithistid sponges: a singular, reef-like bathyal habitat with relevant paleontological connections. PLoS ONE 10(5):e0125378

Mastrototaro F, Maiorano P, Vertino A, Battista D, Indennidate A, Savini A, Tursi A, D'Onghia G (2013) A facies of *Kophobelemnon* (Cnidaria, Octocorallia) from Santa Maria di Leuca coral province (Mediterranean Sea). Mar Ecol 34(3):313–320

Mastrototaro F, Chimienti G, Capezzuto F, Carlucci R, Williams G (2015) First record of *Protoptilum carpenteri* (cnidaria: octocorallia: pennatulacea) in the Mediterranean Sea. Ital J Zool 82(1):61–68

McFadden CS, France SC, Sánchez JA, Alderslade P (2006) A molecular phylogenetic analysis of the Octocorallia (Cnidaria: Anthozoa) based on mitochondrial protein-coding sequences. Mol Phylogenet Evol 41(3):513–527

McFadden CS, Van Ofwegen LP, Quattrini AM (2022) Revisionary systematics of Octocorallia (Cnidaria: Anthozoa) guided by phylogenomics. Bull Soc Syst Biol 1(3)

McFadden C, Cordeiro R, Williams G, van Ofwegen L (2024) World List of Octocorallia. In O Bánki, Y Roskov, M Döring, G Ower, DR Hernández Robles, CA Plata Corredor, T Stjernegaard Jeppesen, A Örn, L Vandepitte, D Hobern, P Schalk, RE DeWalt, K Ma, J Miller, T Orrell, R Aalbu, J Abbott, R Adlard, CAedo, et al., Catalogue of Life Checklist (ver. 05/2024). https://doi.org/10.48580/dg6lk-3d2

Millot C (1999) Circulation in the western Mediterranean Sea. J Mar Syst 20(1–4):423–442

Moccia D, Cau A, Alvito A, Canese S, Cannas R, Bo M et al (2019) New sites expanding the "Sardinian cold-water coral province" extension: a new potential cold-water coral network? Aquat Conserv 29:153–160. https://doi.org/10.1002/aqc.2975

Montefalcone M, Tunesi L, Ouerghi A (2021) A review of the classification systems for marine benthic habitats and the new updated Barcelona Convention classification for the Mediterranean. Mar Environ Res 169:105387

Morrissey D, Gordon JD, Saso E, Bilewitch JP, Taylor ML, Hayes V, McFadden CS, Quattrini AM, Allcock AL (2023) Bamboozled! Resolving deep evolutionary nodes within the phylogeny of bamboo corals (Octocorallia: Scleralcyonacea: Keratoisididae). Mol Phylogenet Evol 188:107910

Mytilineou C, Akel EH, Babali N, Balistreri P, Bariche M, Boyaci YO, Çelik M (2016) New mediterranean biodiversity records (November, 2016)

Neves BDM, Edinger E, Hillaire-Marcel C, Saucier EH, France SC, Treble MA, Wareham VE (2015) Deep-water bamboo coral forests in a muddy Arctic environment. Mar Biodivers 45:867–871

Ocaña O, Çinar ME (2018) Descriptions of two new genera, six new species and three new records of Anthozoa (Cnidaria) from the Sea of Marmara. J Nat Hist 52(35–36):2243–2282

Ocaña O, López-González PJ, Núñez J, García-Gómez JC (2000a) A survey of the genera *Sarcodictyon* Forbes, 1847, and *Rolandia* Lacaze-Duthiers, 1900, (Anthozoa: Octocorallia) in the North-eastern Atlantic and the Mediterranean. Zool Meded 73:413–426

Ocaña A, Tocino LS, López-González PJ (2000b) Consideraciones faunística y biogeográficas de los antozoos (Cnidaria: Anthozoa) de la costa de Granada (Mar de Alborán). Zool Baetica 11:51–65

Pardo E, Rubio RA, García S, de la Torriente DA, Ubero J (2011) Documentación de arrecifes de corales de agua fría en el Mediterráneo occidental (Mar de Alborán). Chronica Naturae 1:20–34

Pérez CD, de Moura NB, Cordeiro RT, Williams GC, Cairns SD (2016) Diversity and distribution of Octocorallia. In: Goffredo S, Dubinsky Z (eds) The Cnidaria, Past, Present and Future. Springer, Cham, pp 109–123. https://doi.org/10.1007/978-3-319-31305-4_8

Prieur L, D'Ortenzio F, Taillandier V, Testor P (2020) Physical oceanography of the Ligurian Sea. In: Migon C, Nival P, Sciandra A (eds) The Mediterranean Sea in the era of global change 1: 30 years of multidisciplinary study of the Ligurian Sea. Wiley, London, pp 49–78. https://doi.org/10.1002/9781119706960.ch3

Ramos M, Bertocci I, Tempera F, Calado G, Albuquerque M, Duarte P (2016) Patterns in megabenthic assemblages on a seamount summit (Ormonde Peak, Gorringe Bank, Northeast Atlantic). Mar Ecol 37:1057–1072. https://doi.org/10.1111/maec.12353

Réhault JP, Honthaas C, Guennoc P, Bellon H, Ruffet G, Cotten J, Maury RC (2012) Offshore oligo-Miocene volcanic fields within the Corsica-Liguria Basin: magmatic diversity and slab evolution in the western Mediterranean Sea. J Geodyn 58:73–95

Relini G (2007) La pesca batiale in Liguria. Biol Mar Mediterr 14(2):190–244

Relini G, Peirano A, Tunesi L (1986) Osservazioni sulle comunità dei fondi strascicatoli del Mar Ligure Centro-Orientale. Boll Mus Ist Biol Univ Genova 52:139–216

Relini-Orsi L, Relini G (1972) Note sui crostacei decapodi batiali del Mar Ligure. Boll Mus Ist Biol Univ Genova 40:47–73

Rice AL, Tyler PA, Paterson GJL (1992) The pennatulid *Kophobelemnon stelliferum* (Cnidaria: Octocorallia) in the Porcupine Seabight (northeast Atlantic Ocean). J Mar Biol Assoc UK 72(2):417–434

Rodriguez MVB, Segumalian CS, Lalas JAA, Maningas JM (2020) Octocorals outcompete scleractinian corals in a degraded reef. IOP Conf Ser Earth Environ Sci 420(1):012027

Rollet N, Déverchère J, Beslier MO, Guennoc P, Réhault JP, Sosson M, Truffert C (2002) Back arc extension, tectonic inheritance, and volcanism in the Ligurian Sea, Western Mediterranean. Tectonics 21(3):6–1

Rosenbaum G, Lister GS, Duboz C (2002) Reconstruction of the tectonic evolution of the western Mediterranean since the Oligocene. J Virtual Explorer 8:(10.3809)

Rossi S, Bramanti L, Gori A, Orejas C (2017) Marine animal forests. The ecology of benthic biodiversity hotspots. Springer International Publishing, Cham

Rossi L (1958) Contributo allo studio della fauna di profondità vivente presso la Riviera ligure di Levante. Doriana

Rueda JL, Urra J, Aguilar R, Angeletti L, Bo M, García-Ruiz C, Taviani M (2019) Cold-water coral associated fauna in the Mediterranean Sea and adjacent areas. In: Orejas C, Jiménez C (eds) Mediterranean Cold-Water Corals: Past, Present and Future. Springer, Cham, pp 295–333

Ruppert EE, Barnes RD, Fox RS (1994) Invertebrate zoology, vol 6. Saunders College Publishing, Fort Worth, pp 950–966

Sampaio Í, Carreiro-Silva M, Freiwald A, Menezes G, Grasshoff M (2019) Natural history collections as a basis for sound biodiversity assessments: Plexauridae (Octocorallia, Holaxonia) of the Naturalis CANCAP and Tyro Mauritania II expeditions. ZooKeys 870:1

Sartoretto S, Zibrowius H (2018) Note on new records of living Scleractinia and Gorgonaria between 1700 and 2200 m depth in the western Mediterranean Sea. Mar Biodiv 48:689–694

Saucier EH, Sajjadi A, France SC (2017) A taxonomic review of the genus *Acanella* (Cnidaria: Octocorallia: Isididae) in the North Atlantic Ocean, with descriptions of two new species. Zootaxa 4323(3):359–390

Söffker M, Sloman KA, Hall-Spencer JM (2011) In situ observations of fish associated with coral reefs off Ireland. Deep Sea Res Part I: Oceanogr Res Pap 58(8):818–825

Soulet Q, Migeon S, Gorini C, Rubino JL, Raisson F, Bourges P (2016) Erosional versus aggradational canyons along a tectonically-active margin: the northeastern Ligurian margin (western Mediterranean Sea). Mar Geol 382:17–36

Spalding MD, Fox HE, Allen GR, Davidson N, Ferdana ZA, Finlayson C, Robertson J (2007) Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. Bioscience 57(7):573–583

Stanley DJ, Mutti E (1968) Sedimentological evidence for an emerged land mass in the Ligurian Sea during the Palaeogene. Nature 218(5136):32–36

Stone RP (2006) Coral habitat in the Aleutian Islands of Alaska: depth distribution, fine-scale species associations, and fisheries interactions. Coral Reefs 25(2):229–238

Taviani M, Angeletti L, Canese S, Cannas R, Cardone F, Cau A et al (2017) The "Sardinian cold-water coral province" in the context of the Mediterranean coral ecosystems. Deep Sea Res Part II 145:61–78. https://doi.org/10.1016/j.dsr2.2015.12.008

Thomson JA (1927) Alcyonaires provenant des campagnes scientifiques du Prince Albert Ier de Monaco. Résultats des Campagnes Scientifiques Accomplies Sur Son Yacht Par Albert Ier Prince Soverain De Monaco 73:1–77

Thomson JA (1929) Alcyonaires des environs de Monaco et de localités diverses. Bull Inst Oceanogr Monaco 534:1–10

Toma M, Bo M, Cattaneo-Vietti R, Canese S, Canessa M, Cannas R, Bavestrello G (2022) Basin-scale occurrence and distribution of mesophotic and upper bathyal red coral forests along the Italian coasts. Mediterr Mar Sci 23(3):484–498

Tunesi L, Diviacco G (1997) Observations by submersible on the bottoms off shore Portofino promontory (Ligurian Sea). Atti del 12° congresso AIOL. Ed. M. Piccazzo (Italy: Genova). 61–74

Tunesi L, Diviacco G, Mo G (2001) Observations by submersible on the biocoenosis of the deep-sea corals off Portofino promontory (northwestern Mediterranean Sea). In: Proceedings of the first international symposium on deep-sea corals. Ed. JHM Willison, et al. (Canada: Halifax). 76–87

Vertino A, Taviani M, Corselli C (2019) Spatio-temporal distribution of Mediterranean cold-water corals. In: Orejas C, Jiménez C (eds) Mediterranean Cold-water Corals: Past, Present and Future. Springer, Cham, pp 67–83. https://doi.org/10.1007/978-3-319-91608-8_9

Wareham VE, Edinger EN (2007) Distribution of deep-sea corals in the Newfoundland and Labrador region, Northwest Atlantic Ocean. Bull Mar Sci 81(3):289–313

Watling L, Norse EA (1998) Disturbance of the seabed by mobile fishing gear: a comparison to forest clearcutting. Conserv Biol 12(6):1180–1197

Watling L, France SC, Pante E, Simpson A (2011) Biology of deep-water octocorals. Adv Mar Biol 60:41–122

Watling L, Saucier EH, France SC (2022) Towards a revision of the bamboo corals (Octocorallia): Part 4, delineating the family Keratoisididae. Zootaxa 5093(3):337–375

Weinberg S (1976) Revision of the common Octocorallia of the Mediterranean circalittoral. I. Gorgonacea. Beaufortia 24(313):63–104

Weinberg S (1977) Revision of the common Octocorallia of the Mediterranean circalittoral part II. Alcyonacea. Beaufortia 25(326):131–166

Weinberg S (1978) Revision of the common Octocorallia of the Mediterranean circalittoral. III. Stolonifera. Beaufortia 27(338):139–176

Weinberg S, Grasshoff M (2003) Gorgonias. El Mar Mediterraneo. Fauna, Flora, Ecologia. II/1. Guia Sistematica y de Identificacion. Ediciones Omega, 428–443

Wienberg C, Krengel T, Frank N, Wang H, Van Rooij D, Hebbeln D (2022) Cold-water coral mounds in the western Mediterranean Sea: new insights into their initiation and development since the mid-Pleistocene in response to changes of African hydroclimate. Quat Sci Rev 293:107723. https://doi.org/10.1016/j.quascirev.2022.107723

Williams GC (1992) Biotic diversity, biogeography, and phylogeny of pennatulacean octocorals associated with coral reefs in the Indo-Pacific. Proceedings of the Seventh International Coral Reef Symposium, Guam 2:729–736

Williams GC, Alderslade P (2011) Three new species of pennatulacean octocorals with the ability to attach to rocky substrata (Cnidaria: Anthozoa: Pennatulacea). Zootaxa 3001(1):33–48

Wright EP, Studer T (1889) Report on the Alcyonaria collected by HMS "Challenger" during the years 1873–1876. Rep Sci Results Expl Voyage HMS Challenger 1873–76, Zool 31: pls-1

Würtz M, Rovere M (2015) Atlas of the Mediterranean seamounts and seamount-like structures. IUCN, Gland, Switzerland, p 276

Würtz M (2012) Mediterranean submarine canyons: Ecology and governance. IUCN

Yesson C, Taylor ML, Tittensor DP, Davies AJ, Guinotte J, Baco A, Rogers AD (2012) Global habitat suitability of cold-water octocorals. J Biogeogr 39(7):1278–1292

Zapata Guardiola R, López González PJ (2012) Revision and redescription of the species previously included in the genus Amphilaphis Studer and Wright in Studer, 1887 (Octocorallia: Primnoidae). Sci Mar 76(2):357–380

Terms and Conditions

Springer Nature journal content, brought to you courtesy of Springer Nature Customer Service Center GmbH (“Springer Nature”).

Springer Nature supports a reasonable amount of sharing of research papers by authors, subscribers and authorised users (“Users”), for small-scale personal, non-commercial use provided that all copyright, trade and service marks and other proprietary notices are maintained. By accessing, sharing, receiving or otherwise using the Springer Nature journal content you agree to these terms of use (“Terms”). For these purposes, Springer Nature considers academic use (by researchers and students) to be non-commercial.

These Terms are supplementary and will apply in addition to any applicable website terms and conditions, a relevant site licence or a personal subscription. These Terms will prevail over any conflict or ambiguity with regards to the relevant terms, a site licence or a personal subscription (to the extent of the conflict or ambiguity only). For Creative Commons-licensed articles, the terms of the Creative Commons license used will apply.

We collect and use personal data to provide access to the Springer Nature journal content. We may also use these personal data internally within ResearchGate and Springer Nature and as agreed share it, in an anonymised way, for purposes of tracking, analysis and reporting. We will not otherwise disclose your personal data outside the ResearchGate or the Springer Nature group of companies unless we have your permission as detailed in the Privacy Policy.

While Users may use the Springer Nature journal content for small scale, personal non-commercial use, it is important to note that Users may not:

1. use such content for the purpose of providing other users with access on a regular or large scale basis or as a means to circumvent access control;
2. use such content where to do so would be considered a criminal or statutory offence in any jurisdiction, or gives rise to civil liability, or is otherwise unlawful;
3. falsely or misleadingly imply or suggest endorsement, approval , sponsorship, or association unless explicitly agreed to by Springer Nature in writing;
4. use bots or other automated methods to access the content or redirect messages
5. override any security feature or exclusionary protocol; or
6. share the content in order to create substitute for Springer Nature products or services or a systematic database of Springer Nature journal content.

In line with the restriction against commercial use, Springer Nature does not permit the creation of a product or service that creates revenue, royalties, rent or income from our content or its inclusion as part of a paid for service or for other commercial gain. Springer Nature journal content cannot be used for inter-library loans and librarians may not upload Springer Nature journal content on a large scale into their, or any other, institutional repository.

These terms of use are reviewed regularly and may be amended at any time. Springer Nature is not obligated to publish any information or content on this website and may remove it or features or functionality at our sole discretion, at any time with or without notice. Springer Nature may revoke this licence to you at any time and remove access to any copies of the Springer Nature journal content which have been saved.

To the fullest extent permitted by law, Springer Nature makes no warranties, representations or guarantees to Users, either express or implied with respect to the Springer nature journal content and all parties disclaim and waive any implied warranties or warranties imposed by law, including merchantability or fitness for any particular purpose.

Please note that these rights do not automatically extend to content, data or other material published by Springer Nature that may be licensed from third parties.

If you would like to use or distribute our Springer Nature journal content to a wider audience or on a regular basis or in any other manner not expressly permitted by these Terms, please contact Springer Nature at

onlineservice@springernature.com