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Diversity and ecology of Corallimorpharians and Zoantharians in the Maldive's central atolls

Diversità ed ecologia dei corallimorfari e degli zoantari negli atolli centrali delle Maldive

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to all the roads that we are yet to pave
to all the dreams that stillness entertains and slays

to the wilders

RIASSUNTO

Le scogliere coralline rappresentano uno degli ecosistemi marini più complessi e biodiversi del pianeta, nonché uno degli ambienti più produttivi negli oceani tropicali, svolgendo funzioni ecosistemiche fondamentali. In questi ecosistemi, oltre ai coralli costruttori (Scleractinia), tra le specie sessili si trovano organismi appartenenti agli ordini Corallimorpharia e Zoantharia. Tali ordini mostrano strategie ecologiche distintive, quali la crescita clonale e un'elevata competitività per lo spazio, che ne favoriscono l'espansione a discapito di altri organismi (in particolare i coralli costruttori), specialmente in scenari di disturbo ambientale. In queste circostanze, la proliferazione di corallimorfari e zoantari altera significativamente la struttura e la dinamica delle popolazioni locali, determinando cambiamenti nella composizione delle comunità con profonde implicazioni per la resilienza e la capacità di recupero degli ecosistemi corallini.

Nonostante la crescente importanza ecologica attribuita a livello globale a questi organismi, la conoscenza della loro diversità e della loro distribuzione nelle Maldive rimane limitata, frammentata e molte volte errata. Lo scopo di questa tesi è stato analizzare la diversità, la distribuzione e le associazioni ecologiche di corallimorfari e zoantari negli atolli centrali delle Maldive, con particolare riferimento a quelli di Malé Sud e Felidhoo. A tal fine, lo studio si è posto i seguenti obiettivi: sviluppare un catalogo dei caratteri morfologici di identificazione sulla base della letteratura esistente e chiavi dicotomiche per l'identificazione delle specie; censire le specie presenti nell'arcipelago maldiviano e analizzarne i pattern di distribuzione in relazione a variabili ambientali quali profondità, tipologia di scogliera e composizione del substrato.

Le attività di campo sono state condotte durante la 24ª Crociera Scientifica alle Maldive, durante la quale sono stati effettuati campionamenti in diversi siti nei due atolli sopracitati.

I dati ecologici sono stati raccolti mediante lo scatto di 200 fotoquadrati lungo transetti a tempo (time limited) a diverse profondità (30 m, 20 m, 10 m e *reef flat*). Contestualmente, sono stati raccolti 36 campioni per procedere ad indagini tassonomiche, che hanno portato all'identificazione di 8 specie appartenenti ai generi *Amplexidiscus*, *Rhodactis*, *Palythoa* e *Zoanthus*. Questo studio conferma la presenza di 2 specie già precedentemente note alle Maldive e attesta la presenza di 6 specie mai osservate in questo ambiente ma solo nelle aree limitrofe; 1 specie segnalata nelle vicinanze non è trovata.

Le immagini scattate sono state successivamente analizzate tramite il software ImageJ, consentendo di stimare la copertura percentuale del substrato e l'abbondanza delle diverse specie. Le analisi statistiche sono state effettuate mediante approcci multivariati, tra cui Indicator Species Analysis

(ISA) e Outlier Mean Index (OMI), al fine di identificare eventuali associazioni tra specie e variabili ambientali.

Le analisi di distribuzione hanno mostrato una significativa eterogeneità spaziale tra i siti e tra le diverse tipologie di reef; in particolare, alcune specie hanno mostrato associazioni specifiche con determinati habitat o gradienti ambientali. Questi risultati indicano come la distribuzione di Corallimorpharia e Zoantharia nei reef maldiviani sia influenzata da una combinazione di fattori ambientali, tra cui profondità, tipologia di substrato e tipologia di reef (oceanico o lagunare).

Questo studio rappresenta il primo del suo genere alle Maldive ed i risultati ottenuti contribuiscono a colmare questa lacuna conoscitiva e fornire nuove informazioni utili per comprendere il ruolo di questi organismi nelle dinamiche ecologiche delle comunità dei reef tropicali.

La ricerca è stata svolta presso i laboratori di Ecologia Marina e di Zoologia Marina del Dipartimento di Scienze della Terra, dell'Ambiente e della Vita (DISTAV) dell'Università degli Studi di Genova, nell'ambito del corso di Laurea Magistrale in Biologia ed Ecologia Marina.

ABSTRACT

Coral reefs represent one of the most complex and biodiverse marine ecosystems on the entire planet, as well as one of the most productive environments in tropical oceans, performing essential ecosystem functions. In addition to builder corals (Scleractinia), sessile species in these ecosystems include organisms belonging to the orders Corallimorpharia and Zoantharia. These orders exhibit distinctive ecological strategies, such as clonal growth and high competition for space, which favor their expansion at the expense of other organisms (particularly builder corals), especially in environments of environmental disturbance. Under these circumstances, the proliferation of Corallimorpharia and Zoantharia significantly alters the structure and dynamics of local populations, leading to changes in community composition with profound implications for the resilience and recovery capacity of coral ecosystems.

Despite the growing ecological importance attributed to these organisms globally, knowledge of their diversity and distribution in the Maldives remains limited, fragmented, and often inaccurate. The aim of this thesis was to analyze the diversity, distribution, and ecological associations of corallimorpharians and zoantharians in the central atolls of the Maldives, with particular reference to those of South Malé and Felidhoo. To this end, the study set the following objectives: to develop a catalog of morphological identification characters based on existing literature and dichotomous keys for species identification; to survey the species present in the Maldivian archipelago and analyze their distribution patterns in relation to environmental variables such as depth, reef type, and substrate composition.

The fieldwork was conducted during the 24th Scientific Cruise to the Maldives, during which sampling was carried out at various sites in the two aforementioned atolls.

Ecological data were collected by taking 200 photo-quadra along time-limited transects at various depths (30 m, 20 m, 10 m, and reef flat). At the same time, 36 samples were collected for taxonomic investigations, which led to the identification of eight species belonging to the genera *Amplexidiscus*, *Rhodactis*, *Palythoa*, and *Zoanthus*. This study confirms the presence of 2 species previously reported in the Maldives and attests to the presence of 6 species never observed in the Maldives but only in the surrounding areas; 1 species previously reported in the surroundings was not found.

The images were then analyzed using ImageJ software, allowing us to estimate the percentage of substrate cover and the abundance of the different species. Statistical analyses were performed using multivariate approaches, including Indicator Species Analysis (ISA) and Outlier Mean Index (OMI), to identify any associations between species and environmental variables.

Distribution analyses showed significant spatial heterogeneity between sites and across different reef types; in particular, some species exhibited specific associations with certain habitats or environmental gradients. These results indicate that the distribution of Corallimorpharia and Zoantharia on Maldivian reefs is influenced by a combination of environmental factors, including depth, substrate type, and reef type (oceanic or lagoon).

This study represents the first of its kind in the Maldives, and the results obtained help fill this knowledge gap and provide new insights into the role of these organisms in the ecological dynamics of tropical reef communities.

The research was carried out at the Marine Ecology and Marine Zoology laboratories of the Department of Earth, Environmental and Life Sciences (DISTAV) of the University of Genoa, as part of the Master's Degree in Marine Biology and Ecology.

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1 INTRODUCTION

1.1 Coral reefs

Coral reefs are one of the most complex and biologically diverse marine ecosystems on Earth and represent the dominant ecosystem characterizing tropical seas (Sheppard et al., 2018), with a distribution extending approximately between 30°N and 30°S (Kleypas et al., 1999).
These systems consist of biogenic, three-dimensional carbonate structures resistant to hydrodynamic forces, and develop in shallow, warm, and well-illuminated waters (Hoegh-Guldberg, 2011); this environmental characteristic, restricts the reefs' distribution to relatively shallow depths and waters with high transparency. At higher latitudes, calcification rates drop below erosion rates, resulting in negative reef growth and the disappearance of carbonate coral reefs. Conversely, at lower latitudes, the rate of calcium carbonate ($CaCO_3$) deposition greatly exceeds physical and biological erosion, leading to the accumulation of the reef's three-dimensional framework (Hoegh-Guldberg, 2011).
Three main biogeographic regions host these ecosystems: the Indo-Pacific region, the Western Atlantic region, and the Red Sea region. The Indo-Pacific region supports the largest and most rich ensemble of coral reefs in terms of coral species and fish diversity. Coral reefs are estimated to cover approximately 284,300 km^2, of which about 91% occurs in this region.

Tropical reefs are primarily constructed by scleractinian corals, colonial organisms belonging to the phylum Cnidaria, class Anthozoa. Each colony is composed of interconnected polyps, allowing them to share nutrients and metabolites; each polyp has a central gastrovascular cavity and tentacles equipped with cnidocytes, which are used for prey capture and defence (in addition to autotrophic nutrition mediated by symbionts).
The growth capacity of these corals is closely linked to their mutualistic symbiosis with photosynthetic dinoflagellates (zooxanthellae) belonging to the *Symbiodinium* genus (LaJeunesse et al., 2018). These symbionts live in large numbers in the endodermal tissues of the coral host, where they perform an intensive photosynthetic carbon fixation that is transferred to the coral, concurring to 90–95% of the host's energetic requirements (Muscatine & Porter, 1977).
The polyp uses calcium ions (Ca^{2+}) and bicarbonate ions (HCO_3^-) from seawater to build a hard protective skeleton made of calcium carbonate ($CaCO_3$) (Wooldridge, 2017). Skeleton deposition happens in the subcalicoblastic compartment, where the calicoblastic tissue actively regulates ionic transport and the local chemistry of the calcifying fluid (Edmunds et al., 2007); this process is

metabolically expansive and strongly dependent on the energetic supply coming from photosynthetic symbiosis.
Concurrently with the calcification, bioerosion by boring sponges, echinoderms, molluscs, and microorganisms contributes to the continuous remodelling of reefs structures.
Coral reefs have a long evolution history dating back to the Palaeozoic era, modern reefs dominated by Scleractinia instead, became established mostly during the Mesozoic era, in conjunction with the evolutionary radiation of Scleractinia and climatic conditions positive for carbonate deposition (Glynn & Manzello, 2015).
Sea-level fluctuations during the Quaternary era have profoundly influenced the present-day morphology of the reefs; during glacial periods, sea-level regression exposed extensive carbonate platforms to subaerial erosion, contrariwise during the interglacial phase's sea levels rising, promoted the vertical growth of carbonate structures.
The alternation of sea-level regressions and transgressions has played a fundamental role in the formation of modern coral reefs.

There is a general scientific consensus about the classification of coral reefs in four main categories:

- Fringing reefs: reefs in continuity to the shoreline of the islands. They may have a minimum length of about 10 m and depths reaching 100 m. They typically develop near the surface and are separated from the coast by narrow, shallow lagoons. This is the most widespread reef type (Edmunds et al., 2007).
- Barrier reefs: reefs that extend parallel to the coastline but are separated from it by wider and deeper lagoons. They may develop at some distance from the shore in areas where coral growth has compensated the gradual subsidence of the sea floor (Cesar, 2002).
- Atolls: are circular coral formations that enclose lagoons, often located in the open ocean. They typically form when islands surrounded by fringing reefs subside or become submerged due to the sea-level rising (Edmunds et al., 2007).
- Patch reefs: isolated coral formations that rise from the seabed of island or continental shelves. They exhibit considerable variability in size and generally develop in calm and sheltered waters (Coral Reef Alliance, 2024).

Despite an estimated covering of 260,000–284,300 km² (Spalding et al., 2001; Roberts et al., 2002), coral reefs host over 25% of all known marine species, making them one of the most important global biodiversity hotspots (Burke et al., 2011; Lee et al., 2024). A total of 34 different animal phyla are represented in reef ecosystems, more than any other habitat on Earth.

Coral reefs support highly complex trophic networks, in which primary producers, herbivores, carnivores, and apex predators interact through intricate ecological relationships.
The estimates number of plant and animal species living in coral reefs vary widely, ranging from 600,000 to more than 9 million species globally. However, the true diversity remains unknown, and just only about 10% of the species have been formally identified (Sheppard et al., 2018).
A balance exists between reefs building corals and macroalgae; this is strongly influenced by the presence of herbivores, whose grazing activity limits algal proliferation and maintains available space for corals recruitment.
From an ecosystem perspective, coral reefs provide essential ecosystem services, including: food security for tropical coastal populations (Teh & Sumaila, 2013), coastal protection through wave-energy dissipation (Ferrario et al., 2014) and major contributions to the global biogeochemical cycles of carbon and nitrogen. The global economic value linked to these services exceeds one trillion of US dollars annually (Heron et al., 2017), although coral reefs occupy less than 1% of the seafloor, they are widely regarded as the most diverse and productive ecosystems in the oceans (Elliff & Kikuchi, 2017).

1.2 Pressures on coral reefs

In recent decades, the integrity of natural ecosystems has been progressively compromised by the intensification of human activities and the acceleration of global climate change (Obura, 2022). In this scenario, coral reefs emerge as one of the most sensitive and representative systems of the contemporary ecological crisis.
Coral reefs are not static ecosystems in permanent equilibrium; on the contrary, they experience periods of expansion and growth that can alternate to phases of regression or mass mortality.
Under relatively stable environmental conditions, the distribution of coral communities is regulated by the availability of fundamental primary resources, such as: space, light, and nutrients; by the interaction between abiotic factors, such as hydrodynamics and thermal regime; as well as by biotic factors, including intra- and interspecific competition, predation, mutualisms, and the availability of protective microhabitats.
The persistence of these non-equilibrium ecosystems relies on their resilience; recovery, if successful, ensures the maintenance of species composition and the respective ecological functions that they perform. (Vercelloni, 2019). However, the combined actions of local pressures and global climate change, has progressively eroded this resilience, reducing the natural recovery capacity of coral reefs communities (Chan, 2023).

The most recent estimates show that up to 50% of the world's coral reefs are degraded, with a 14% loss in the last decade. (Eddy et al., 2021).
This trend is not attributable to a single cause, but rather to a combination of local stressors (such as fishing, pollution, coastal development, coral disease, and cyclones) as well as global stressors (such as warming and acidification), and their cumulative and synergistic interactions (Obura, 2022; Pancrazi et al., 2020).

Rising of the sea surface temperatures represent the most immediate and widespread threat, directly affecting the metabolism, growth rates, reproduction, and geographic distribution of species.
In addition to the global temperatures rising, carbon dioxide (CO_2) and other major greenhouse gases have increased worldwide; these gases have been emitted into the atmosphere at an ever-increasing rate since the Industrial Revolution in the second half of the 19th century.
During the 20th century, this process resulted in an average increase of the ocean temperature approximately around 0.74°C, a sea level rise around 17 cm, and a decrease in surface pH around 0.1 units (Guldberg, 2011). Reefs are therefore exposed to environmental conditions that combine high temperatures, changes in carbonate ion availability, and pH variations. The most critical note is not only the extent of the change, but its speed: changes that under natural conditions would have taken thousands of years, occurred in the span of a single century.

The mass bleaching is the most obvious manifestation of thermal stress; the first widely studied event occurred in 1998, during which, over the course of weeks, corals around the world bleached across vast areas of reefs.
During bleaching events, coral tissue turns white due to pigment loss as the corals expel their symbiotic dinoflagellate algae, resulting in the loss of these symbionts and a reduction in energy supply (Guldberg, 2011).
Coral bleaching is generally caused by anomalous seawater temperatures that often interact with high levels of sun light/irradiance. The frequency and intensity of these events have increased steadily over the past three decades, and the frequency of extreme thermal events is expected to increase further (Morri et al., 2015; Montefalcone et al., 2018).
The consequences of this trend on the coral community may include widespread mortality, reduction in coral cover, and functional reorganization of the benthic communities; however, the impact is not uniform, as the response depends on numerous factors, such as specific community composition, colony morphology, environmental conditions, etc.

Massive and sub-massive forms generally tend to show greater resistance than branched forms, which are more sensitive to thermal anomalies (Ateweberhan et al., 2013).

The composition of symbionts communities plays a key role in the response to stress, as many corals appear to host a single dominant clade; however, genetically distinct symbionts have been identified within coral colonies; symbiont mixing represents a crucial mechanism through which some coral species can increase their thermal tolerance. However, this mechanism alone may not be enough to keep up with the increasingly marked increase of the sea temperatures due to global warming (Oppen et al., 2008). Post-bleaching recovery is strictly dependent on local environmental conditions and community structure; it can be significantly delayed in the presence of additional stressors, such as those of anthropogenic origin, while it may take less time in the absence of additional impacts (Ateweberhan et al., 2013).

Along with warming, ocean acidification represents a stressor that threatens the health of corals (Ateweberhan et al., 2013); this is due to the increase in atmospheric carbon dioxide (CO_2), which, once it enters the ocean, reacts with water molecules to form carbonic acid (H_2CO_3). The latter subsequently dissociates, releasing a proton (H^+), which reacts with carbonate ions (CO_3^{2-}), converting them to bicarbonate ions (HCO_3^-). Carbonate ion concentrations are commonly quantified in relation to the saturation state of seawater with respect to aragonite, the main crystalline form of calcium carbonate deposited by corals and many other calcifying marine organisms, such as bivalves and gastropods. With increasing atmospheric carbon dioxide levels, aragonite saturation in the world's oceans has decreased (Guldberg, 2011).

Furthermore, larvae are thought to be more vulnerable to bleaching during the early stages of their life cycle; this implies that both acidification and bleaching can negatively impact coral recruitment and competitive ability (Ateweberhan et al., 2013).

Regarding sea level rise, coral reefs are generally unaffected if coral growth remains sustained. However, drastic changes in sea level due to the disintegration of ice shelf can cause damage that reduces sunlight levels in the deeper portions of the reef, resulting in coral discoloration and death (Guldberg, 2011). Other factors can sometimes interact with coral reefs and influence their growth, such as storm activity, changes in ocean circulation, and the increase in some reef fish species that feed directly on corals (Guldberg, 2011). But as we will see shortly, there are also other organisms that can lead profound reorganizations of communities, with implications for their resilience, conservation and management (Aeby & Maragos, 2008)

1.3 Corallimorpharia and Zoantharia in coral reefs

Coral reefs are often described as ecosystems dominated by scleractinian corals; however, reef functionality, defined as competition for space, food webs, successional dynamics, and post-disturbance resilience, also depends mostly on numerous non-skeletal benthic cnidarians, including corallimorpharians and zoantharians specimens.

Both groups belong to the subclass Hexacorallia (class Anthozoa) and the order Corallimorpharia share some important morphoanatomical traits with scleractinian corals, such as the presence of mesenteries, a cnidome, and polyp organization. However, both orders possess unique ecological strategies that can make them dominant under specific environmental conditions or following disturbances (Sinniger et al., 2013).

Ecologically, Corallimorpharia and Zoantharia are important within a coral community because:

- they compete for space with corals and other sessile benthic organisms (such as sponges, cnidarians, algae, etc.), showing a highly competitive efficiency, as they are capable of lateral growth, showing a high level of contact aggression (Cha, 2006);
- they can expand rapidly through clonal strategies and lateral growth, forming mats or extremely dense aggregations, allowing them to establish a stable situation of local dominance (Furman & Spiegel, 2000); under stressful conditions, they can increase coverage and contribute to phase shifts, moving from reefs dominated by scleractinian corals to reefs dominated by non-calcifying organisms (Work et al., 2008).
- they often host symbionts (such as Zooxanthellae) or grow on living substrates such as sponges, hydrozoans, octocorals, etc., contributing to complex ecological networks (Irei, Sinniger & Reimer, 2015).

The presence of documented cases of corallimorpharian-dominated reefs suggests that these organisms are not simply "accessory components" of reefs, but can drive deep community reorganizations, with implications for their resilience, conservation, and management. This is also demonstrated at Palmyra, where the dominance of corallimorpharians in community composition has caused a true phase shift in the coral community itself, with significant consequences for coral reef dynamics (Aeby & Maragos, 2008). For the zoantharians, however, their ability to grow by forming patches (as in the case of some species of the genus *Palythoa*) and to colonize cryptic microhabitats (as in the case of some species of the genus *Zoanthus*) or living substrates (as in some species of the genus *Epizoanthus*) suggests that their importance is not measured solely in percentage coverage of the substrate, but it is clear that these also influence: recruitment and succession (as they compete for space); symbiotic networks and epibiotic associations; biodiversity and functional complexity (Sinniger, Ocaña & Baco, 2013).

1.3.1 Corallimorpharians

Corallimorpharians are "soft" anthozoans lacking a calcareous skeleton; most of the species are photosymbionts (typically disc-shaped forms found in shallow waters), while other species lack zooxanthellae and can live in a wide bathymetric gradient. They show a broad geographic distribution (from the tropics to the poles, and from the surface to deep environments) and great morphological/biological plasticity (Cha, 2006).
Several cloning mechanisms are known for these organisms, including longitudinal fission, inverse budding, and especially marginal budding, the latter reported as a particularly significant and rare modality compared to other cnidarians. Numerous studies have also documented the ability of some species to perform a clonal replication all year-round (as demonstrated, for example, by some species of the genus *Rhodactis*, which exhibit seasonal growth peaks) (Furman & Spiegel, 2000).
The ability of corallimorpharians to compete with scleractinian corals derives not only from clonal growth but also from agonistic mechanisms; some species (such as *Rhodactis rhodostoma*) have been described as having marginal tentacles capable of increasing in numbers as needed, thus enhancing competitive effectiveness, with prolonged effects on near-sessile organisms (such as building corals) (Furman & Spiegel, 2000).
In terms of community dynamics, this means that overgrowth or contact pressure can reduce the performance of adjacent corals; furthermore, clonal growth amplifies the competitive advantage by increasing the chance of establishing large-scale contacts; the overall effect of these capabilities, can contribute to reducing reef resilience following global or local pressures. One study also shows how the iron availability (coming from the skeleton of a near wreck) and therefore the modification of local conditions helped the proliferation of corallimorpharians and the relative regression of builder corals (Aeby & Maragos, 2008).

The mechanisms described so far allow us to understand how, under certain conditions, these organisms can transition from being "one competitor among many others" to being "a community dominator organism" especially where disturbances, chemical-physical alterations, or reductions in coral cover allow colonization of free spatial niches.
These characteristics are ecologically crucial because they link corallimorpharians: to potentially stable (or difficult to reverse) state transitions; to reduced coral recruitment (if the substrate is monopolized); and consequently, to the loss of three-dimensional complexity of the reef.
A lesser considered, but ecologically interesting, aspect is the fact that some corallimorpharian species can enter food webs as food or specialized predators, indirectly contributing to reef dynamics. A recent study found that *Paracorynactis hoplites* helps exert some control over populations of *Acanthaster* sp. (crown-of-thorns starfish), a known predator of scleractinian corals. Although this type of interaction requires further scientific confirmation, it is evident that corallimorpharians may play not only competitive but also trophic roles, with potential implications for the stability of coral communities (Ocaña, den Hartog, Brito & Bos, 2010).

1.3.2 Zoantharians

Zoantharians are common on reefs as colonial or solitary benthic organisms, capable of forming mats or colonies (in some species, particularly large) on hard substrates, crevices, and even in cryptic microhabitats. Their abundance and variety of ecological strategies make them one of the most versatile groups among the Hexacorallia, with important roles ranging from primary production (in photosymbionts) to epizoic relationships with other invertebrates (Irei, Sinniger, & Reimer, 2015).
Most zoantharians typical of shallow reefs are zooxanthellate and can obtain a significant portion of their energy budget from photosynthesis, supplementing it with feeding on particulate matter and/or zooplankton; this mixed trophic pattern increases energetic resilience in oligotrophic environments, making zoantharians competitive in illuminated areas of the reef (Trench, 1974).
At the same time, the existence of azooxanthellate species demonstrates remarkable plasticity (such as, for example, *Palythoa mizigama* and *Palythoa umbrosa* in southern Japan); these live in shaded environments (cavities, crevices, recesses, etc.) and appear to depend predominantly or exclusively on planktonic food resources, displaying adaptations to environments with limited nutritional and energy resources (Irei, Sinniger & Reimer, 2015).

Competition for space is a key ecological issue for zoantharians as well (especially when dealing with species that form very large mats/colonies), which can therefore limit the recruitment of corals and other benthic organisms.
This type of strategy (like: rapid lateral growth, dense colonies of individuals, tolerance to variability of environmental conditions) can also make some zoantharian species particularly competitive in contexts where coral mortality creates free surfaces and/or natural or anthropogenic pressure reduces the efficiency of building corals (Suchanek & Green, 1981).

A significant portion of zoantharian biodiversity and ecology involves associations with living substrates; in the Parazoanthidae family and beyond, the substrate can play a fundamental evolutionary and functional role, influencing distribution, growth pattern, and potential impact on the host, with taxonomic significance as well (Sinniger, Ocaña, & Baco, 2013).
Some zoantharian species (such as *Corallizoanthus tsukaharai*, associated with the Japanese red coral *Paracorallium japonicum*, which lives at depths between 125 and 250 m) can live stably even in the deepest coral ecosystems, contributing to the biological complexity of the environment and potentially influencing the fitness and integrity of the hosts. The nature of these relationships, likely symbiotic/commensal (with the theoretical possibility of parasitism), requires further study to determine their mechanisms and nature (Reimer, Nonaka, Sinniger, & Iwase, 2008).

1.4 Morphological traits of the two orders

Inside the Class Hexacorallia, the orders Corallimorpharia and Zoantharia share a basic organization: a polyp with an oral disc, column, and gastrovascular cavity divided by mesenteries.

This divergence is reflected in a set of external (tentacled pattern, oral disc morphology, presence of coenenchyma, particle incorporation) and internal (arrangement of mesenteries, development of the sphincter and marginal musculature) characteristics, which assume diagnostic value only when interpreted considering the phenotypic plasticity and state of contraction of the polyp (Swain et al., 2015).

Morphological analyses remain very important because they allow preliminary identification in the field and allow setting an appropriate sampling strategy; furthermore, a morphological analysis allows the interpretation of the ecological functions of various organisms (such as spatial competition, predation, etc.).

However, especially for the order Zoantharia, numerous studies have highlighted that the traditional approach based on a few macroscopic traits is insufficient as many "classic" anatomical characters are subject to convergence and require integration with microanatomy and, when available, molecular phylogeny (Swain et al., 2015; Sinniger, Ocaña & Baco, 2013; Reimer et al., 2017).

1.4.1 Corallimorpharia

- **Growth forms**

A first distinction within Corallimorpharia is based on their different growth patterns: they can be solitary organisms (a single polyp) or colonial organisms (aggregates, resulting from asexual reproduction), with considerable variability in the proportions between column length and oral disc diameter.

A frequent descriptive distinction is also based on the distinction between more cylindrical forms (with a relatively high column) and more discoidal forms (with a very expanded oral disc and a relatively low column). These initial differences obviously have functional implications and are frequently used in systematic analyses of the order (Cha, 2006; Wallace, 2008).

The most accredited analyses for Corallimorpharia require particular attention to specific anatomical characteristics such as: tentacle pattern, presence of acrospheres and cnidome, precisely because the general shape of the polyp can change following the environment conditions and the degree of expansion/contraction (den Hartog, 1980).

- **Oral disc**

The oral disc is frequently the most dominant morphological feature in many Corallimorpharia species; it houses the mouth opening and represents the main surface used for capturing and ingesting

particulate matter and prey.The mouth (indicated by the letter M in Figure 1) can appear as a more or less elongated slit; the actinopharynx then connects the mouth to the gastrovascular cavity and represent an internal region where, in several taxa, characteristic cnidae are observed (den Hartog, 1980; Cha, 2006).
Although in many descriptions the oral disc is treated primarily in relation to the tentacles, it is important to underline that the morphology of the disc (width, margin, any raised areas/folds) contributes to determining the animal's external "signature," useful for in situ identification.
In discoidal forms, the disc can extend well beyond the column, increasing the percentage of substrate coverage (Laird, 2013).

- **Tentacles**

One of the most informative traits in the order Corallimorpharia is the organization of the tentacle system. In several taxa, discal tentacles and marginal tentacles are distinguished, which may or may not be retractile; in some organisms, the marginal tentacles may be reduced or completely absent, while the discal tentacles, in these cases, are organized in radial rows or more complex patterns (also very branched). In several studies, these traits are used in systematics as diagnostic criteria between families and genera (den Hartog, 1980).
The combination of tentacle arrangement and cnidome constitutes one of the few relatively stable sets of characters for the group's systematics, in a context where other traits, such as polyp shape, can be more variable (Cha, 2006).
A particularly relevant morphological feature is also the presence and position, in some Corallimorpharia, of a tentacle-free zone between the perioral area and the discal tentacle crown (Figure 1); this type of organization is very useful for distinguishing different related/similar species (Cha, 2006). Another characteristic used in the literature for morphological identification is the combination of the number, arrangement, and type of tentacles (marginal or discal), and the position of the tentacle-free zone.

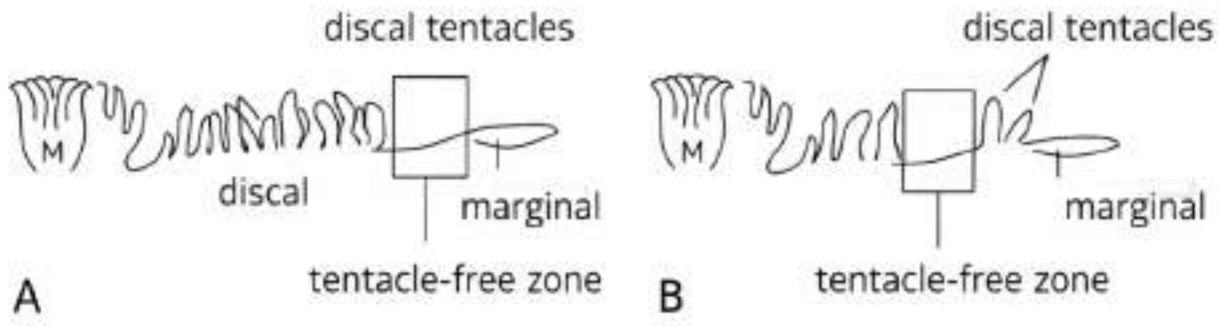


Figure 1: types of tentacle-free zones on oral disc: A: between discal and marginal tentacles; B: among discal tentacles.

Obviously, these characteristics cannot be used in field observations, as they can be influenced by polyp contraction and microhabitat (Laird, 2013).

- **Column and pedal disc**

The column of corallimorpharians is generally free of encrustations or sediment, a characteristic that differentiates them from many zoantharians; the pedal disc can be more or less broad, generally with a smaller diameter than the oral disc to allow stable adhesion to the substrate.
It is known in the literature that some taxa can produce clones that originate beneath the pedal disc and then grow autonomously on the sides of the parent organism; this strategy serves to increase spatial coverage, with competitive effects on other surrounding benthic organisms. (Wallace, 2008; Laird, 2013).

- **Internal anatomy: mesenteries, muscles and sphincter**

Regarding internal anatomy, corallimorpharians are characterized by a compartmentalized gastrovascular cavity with numerous mesenteries, often described as relatively irregular in number and arrangement; this irregularity reduces the usefulness of this trait at the taxonomic level (Cha, 2006).
The overall musculature is often considered less "specialized" than in zoantharians, and the sphincter is frequently described as weak and diffuse in many forms (Cha, 2006; Swain et al., 2015).

- **Cnidome**

The cnidome represents one of the most used characters in the identification of corallimorpharians, especially when the external characters are variable or not very informative; several studies highlight how the classification and identification of nematocysts are difficult but extremely effective, highlighting how the different body districts of the organism (tentacles, column, actinopharynx, mesenteries, etc.) can present characteristic combinations of cnidae (Figure 2) (Cha, 2006; Wallace, 2008; Swain et al., 2015).

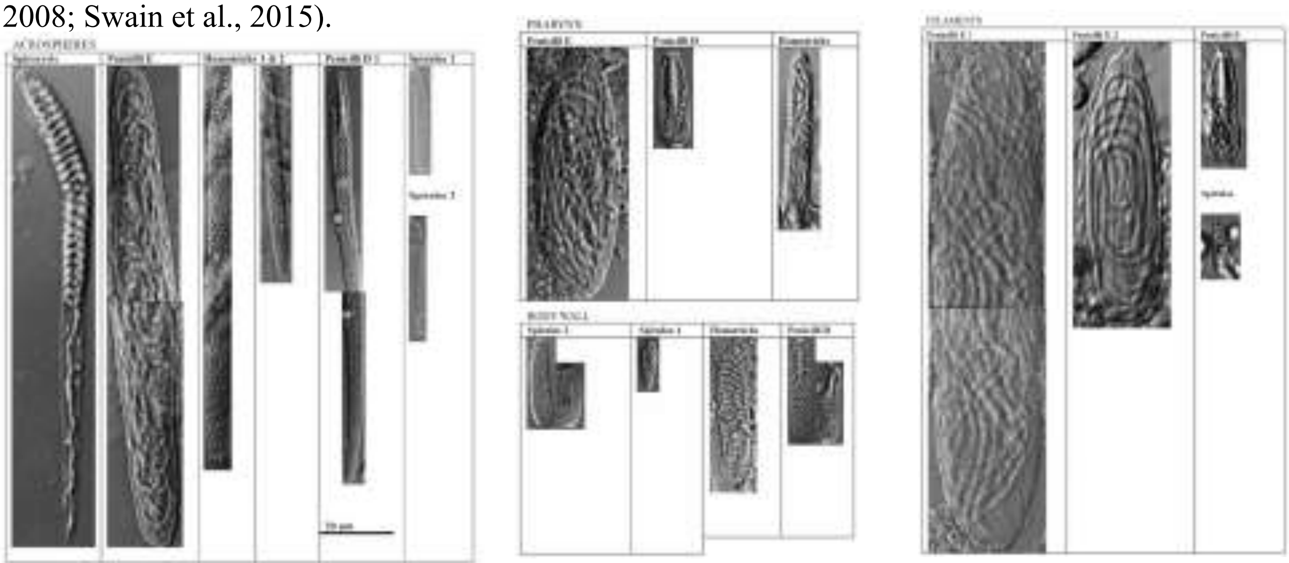


Figure 2: example of cnidome from *Corynactis globulifera* divided in the body part that came from: acrospheres, pharynx, body wall and filaments. Different kind of cnidae observed in this species: spirocysts; penicilli E (E1 ed E2) e D; spirulae 1 e 2; homotrics.

1.4.2 Zoantharia

- **Growth form**

Unlike many corallimorpharians, most zoantharians are colonial; the polyps are connected by stolons or a coenenchyma that can cover the substrate, allowing for lateral expansion. This trait has been highlighted in descriptions of both surface- and deep-sea zoantharians, including those associated with seamounts (Sinniger, Ocaña & Baco, 2013; Carreiro-Silva et al., 2017).

Functionally, zoantharian coloniality increases local resilience, facilitates substrate conquest, and supports spatial distribution of resource capture; in coral reefs, this strategy can translate into the ability to form extensive mats, detrimental to other surrounding benthic organisms (Wallace, 2008; Reimer et al., 2017).

- **Oral disc and tentacles**

The zoantharians' oral disc is a central structure not only for its trophic functions but also for morphological identification at the genus and species level (Figure 3); it constitutes the apical portion of the polyp and houses the mouth and the tentacular crown, marking the transition between the capitulum and the column. In colonial taxa, the oral disc emerges from the common coenenchyma and maintains a certain functional autonomy while being structurally connected to the other polyps of the colony (Sinniger, Ocaña & Baco, 2013; Carreiro-Silva et al., 2017).

One of the most characteristic features of Zoantharia is the presence of two concentric ranks of tentacles (Figure 3), a trait traditionally considered distinctive of the order. This tentacular organization manifests as a double crown surrounding the mouth, with tentacles generally thin, cylindrical, and radially arranged. This arrangement directly reflects the internal organization of the mesenteries, since each tentacle is associated with an intermesenterial space (endocoel or exocoel), highlighting a close relationship between internal architecture and external morphological expression (Reimer et al., 2017; Sinniger, Ocaña & Baco, 2013).

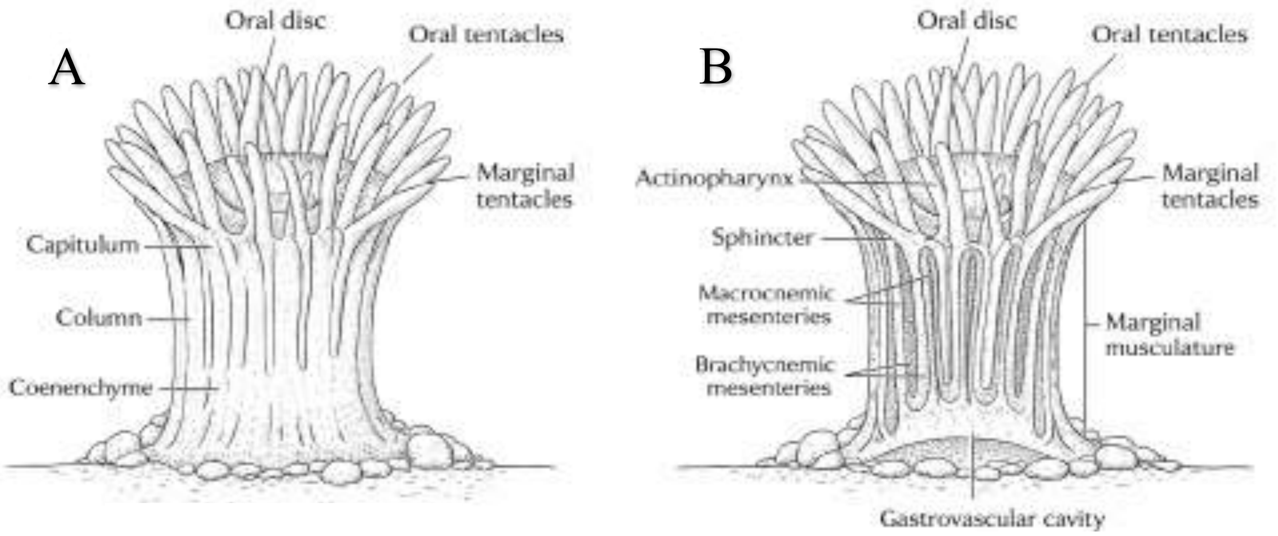


Figure 3: external (A) and internal (B) morphology from a single zoantharian polyp.

Anatomically, the double tentacle crown is often associated with a morphological distinction between the capitulum and the column. The capitulum may be delimited by a groove or a variation in tissue consistency, and in encrusting or epizoic taxa, it may appear more flexible than the column, which is frequently strengthened by the incorporation of sand particles. This regional difference has functional implications, as it allows the polyp to maintain greater mobility of the tentacle region while retaining a stable and protected base (Carreiro-Silva et al., 2017).
Another important aspect concerns the variability in the total number of tentacles, which can represent a useful diagnostic trait at the specific or generic level. Although the presence of two ranks is a common feature, the absolute number of tentacles, their relative length, and their density along the margin of the oral disc can vary significantly between taxa. This variability reflects differences in mesenteric organization and may be related to several ecological factors, such as food availability, hydrodynamism and depth (Sinniger, Ocaña & Baco, 2013).

- **Sand encrustation**

Many zoantharians incorporate mineral particles (sand, detritus, biogenic fragments) into their external tissues (Figure 4), giving the column and coenenchyma a more rigid and "armoured" look. This trait is often mentioned as a distinctive characteristic, and it's particularly evident in epizoic taxa and deep-sea organisms (Carreiro-Silva et al., 2017). Even in coral reef contexts, sand-encrustation is commonly discussed as a recognition trait and a possible adaptation to high-sedimentation or high-stress microhabitats (Reimer et al., 2017; Wallace, 2008).

Figure 4: sand encrustation of the external tissues of *Antipathozoanthus cavernus*.

- **Mesenteries (Macrocnemina vs Brachycnemina)**

In the zoantharians' systematics, a widely used anatomical character is the structure of the fifth pair of mesenteries; this character is used to distinguish the two different suborders of the order Zoantharia, namely Macrocnemina and Brachycnemina. Macrocnemina are described as zoantharians with a complete fifth pair of mesenteries (unlike Brachycnemina which have an incomplete one) (Haddon & Shackleton, 1891).

- **Marginal musculature and retraction**

Marginal musculature is a key component of polyp retraction mechanisms; it can be divided into endodermal and mesogleal.

Marginal musculatures include a variety of morphological states (at least a dozen), with diverse architectures and distributions that can converge under similar selective pressures; several studies also highlight allometric relationships between polyp size and musculature development, linking muscle shape to retraction performance and oral disc protection (Swain et al., 2015).

- **Cnidome**

The cnidome (Figure 5) is also used as a diagnostic aid in zoantharians, but its interpretation can be more complex in some contexts, especially deep-sea, where cases of "atypical" compositions or those difficult to interpret without rigorous standardization of the tissue districts sampled (Sinniger, Ocaña & Baco, 2013; Carreiro-Silva et al., 2017).

In shallow-sea zooxanthellate groups, the cnidome is a particularly useful trait, especially given the high external similarity between species and the phenotypic plasticity associated with environmental conditions and microhabitat (Reimer et al., 2017).

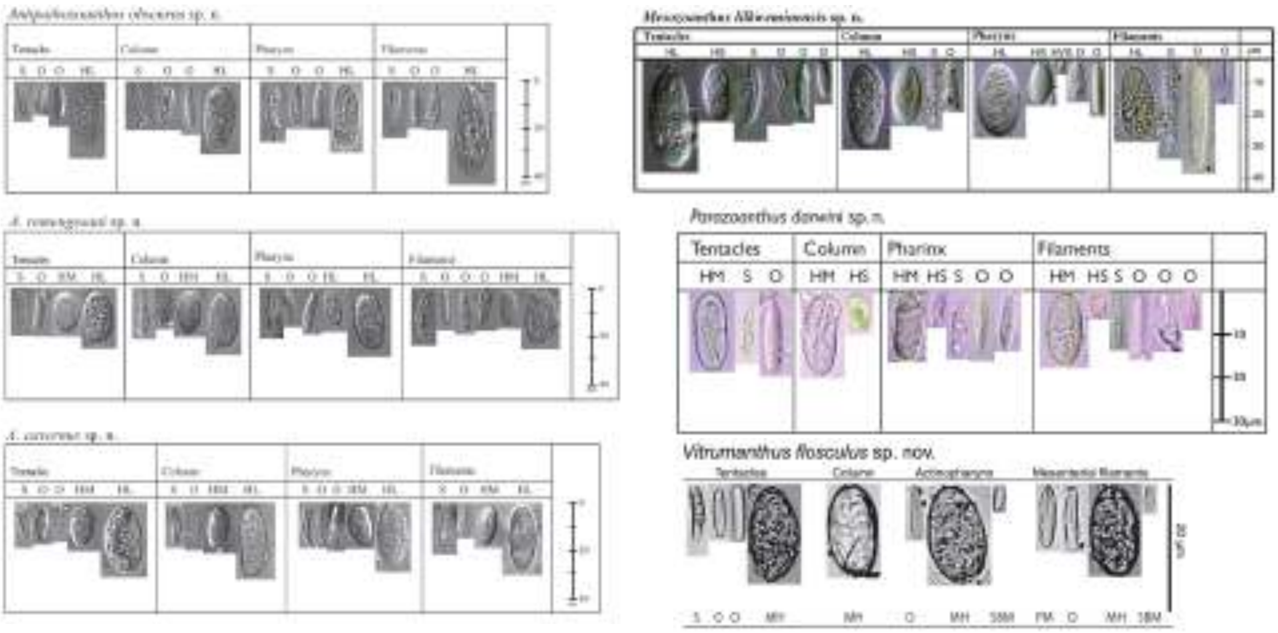


Figure 5: example of Zoantharians' cnidome divided in different body part: tentacles; column; Pharynx and filaments. Different kind of cnidae observed in this species: S: spirocysts; O: basitrics or mastigophorous; H: holotrics (medium holotrichs M and large holotrics L); SBM: special microbasics.

1.5 Global distribution of the two orders

1.5.1 Corallimorpharia

Corallimorpharia exhibit a wide distribution (Figure 6), occurring from the tropics to nearly the poles and from shallow waters to the deep sea. This is largely due to their high ecological plasticity (Cha, 2006).

The apparent discontinuous distribution in some areas is mainly due to the lack of information, which is evident in some regions (such as the Maldives, where Corallimorpharia have not been recorded since 1980), underscoring the importance of studies of this type.

Figure 6: distribution of Corallimorpharia all over the world (Worms, 2026): green dots indicate known distribution of corallimorpharians; red dot le Maldives.

1.5.2 Zoantharia

Among the Zoantharia, Brachycnemina include many zooxanthellate taxa typical of tropical and subtropical reefs; in these environments, they are dominant and widely distributed, especially following extreme disturbances, such as bleaching (Wallace, 2008).

Many Macrocnemina, on the other hand, are epizoic (or epibiont), associating with sponges, hydrozoans, antipatharians, octocorals, and other invertebrates. In this context, a surprisingly high diversity is evident in deep environments, comparable in quality to that observed in shallow tropical reefs (Sinniger, Ocaña & Baco, 2013).

Deep environments associated with cold-water corals and coral gardens represent epifaunal biodiversity hotspots, where Zoanthidea can be common.

The perceived global distribution (Figure 7) is inevitably influenced by historically more studied regions (such as the Caribbean) and by the difficulties in sampling and identifying the various deep-sea taxa (very cryptic diversity requiring markers and revisions).

These factors explain why recent studies in less explored contexts (such as the Maldives) often report new species and new associations, rapidly restructuring the biogeography of the entire group (Carreiro-Silva et al., 2017).

Figure 7: distribution of Zoantharia around the world (Worms, 2026): green dots indicate known distribution of zoantharians; red dot le Maldives.

1.6 Maldives

The Maldives (Figure 8) are an archipelagic nation located in the north-central Indian Ocean that extends for approximately 90,000 km^2 between latitude 7° 06' 30'' N and 0° 42' 30'' S, and longitude 72° 32' 30'' E and 73° 46' 15'' E (Godfrey, 2023).

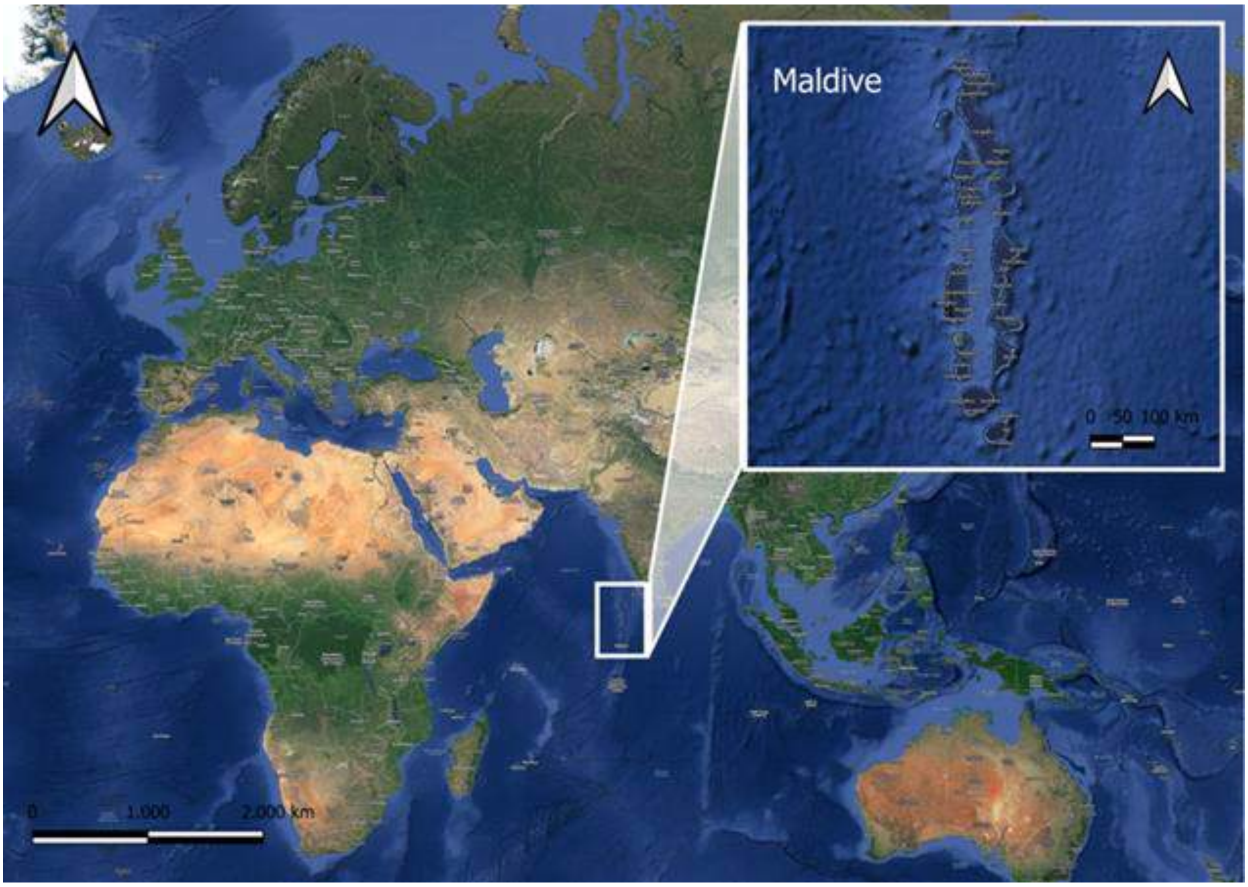


Figure 8: map focusing on the Maldives position (references: created by Daniel Pietrocola).

The Maldivian archipelago is in the central part of the Chagos-Maldives-Laccadive Ridge (Lasagna et al., 2010) and is surrounded to the west by the Arabian Basin and to the east by the Central Indian Basin. Its coral islands are assembled in a double row of atolls separated by an inland sea, forming the largest community of coral reefs and atolls in the Indian Ocean (Kunnummal & Anand, 2022).

The archipelago is composed of 26 atolls and approximately 1,190 islands, of which 991 are uninhabited and 199 are inhabited (the number varies based on the definition of an island; those mentioned are islands with some form of vegetation, be it grass, shrubs, or trees) (Kundur, 2012).

The Maldives' atolls exhibit a wide diversity of geomorphological settings: they range from more open formations, with numerous islands and patches and pinnacles distributed both in the lagoon and along the atoll margin, to almost closed configurations, where the number of internal lagoons, pinnacles, and patches is more limited.

Faros, in particular, are annular reef structures that emerge at low tide; each has its own sandy lagoon and is separated from adjacent units by deep channels; the edges of these reefs are typically occupied by live corals, with both branching and massive components. Patch reefs can rise up to about 40 m from the lagoon floor and are often crowned by remarkably robust breakwater corals. Knolls that do not emerge to the surface tend to have high coral cover, similar to what is observed in reefs associated with multiple islands (Jaleel, 2013).
The Maldives' coral reef ecosystem is extensive, covering approximately 4,513 km² and comprising 2,041 individual reefs (Naseer and Hatcher, 2004). The Maldivian archipelago's coral reef system represents nearly 5% of the world's coral reefs, ranking it the seventh largest in the world in terms of total area covered (Spalding et al., 2001).

In the Maldivian context, it is possible to distinguish two main types of reefs based on the degree of exposition to the open ocean, specifically:

2 oceanic (or external) reefs are characterized by extensive shallow terraces and relatively uniform, vertical slopes; being directly exposed to oceanic conditions, they generally show higher oxygen concentrations and lower salinity values than lagoonal reefs (Lasagna et al., 2010).
3 lagoon (or inside) reefs, on the other hand, are associated with lagoons with greater morphological diversity, where sandy slides, slopes, and accumulations of coral debris are frequent; these reefs communicate with the ocean by numerous channels that interrupt the reef edge in several location. This conformation offers greater protection but also makes these environments more susceptible to episodes of increased temperature (Semprucci et al., 2018).

The archipelago's diverse landforms are shaped by oceanographic and climatic gradients, which vary between the northern and southern sectors of the Maldives.
In general, the northern atolls are more open and shallower, with lagoons typically reaching 40–50 m depth; the southern atolls, on the other hand, are more often enclosed, with deeper lagoons ranging from 70–80 m depth and a greater concentration of islands along the atoll's perimeter. Consistently, wave energy tends to be significantly higher in the southern atolls than in the northern ones, and precipitation progressively increases southward (East, 2017).
Waves and currents are key drivers in shaping reefs and ecological processes. Wave and current energy can, in fact, propagate through wide, deep passages in the atoll margin, penetrating the lagoon without significant energy dissipation (Lasagna et al., 2010). In addition to their physical erosion effects, these hydrodynamic processes perform crucial ecosystem functions, including nutrient

transport, larval dispersal and recruitment, and the provision of water and oxygen to reef-associated marine communities (Semprucci et al., 2018).

The Maldives' climate is classified as tropical, meaning it is generally humid, with relative humidity around 80%; in tropical areas, rainfall is often torrential and intense, though short-lived (Chaudhuri, 2021).

Temperatures remain moderate throughout the year, but are influenced by monsoon winds, which play a crucial role in shaping the structure of the country's atolls and coral reefs (Kench and Brander, 2006), as well as determining the weather conditions of the various islands in the archipelago (Chaudhuri, 2021).

The months from April to September are characterized by the southwest monsoon (*Hulangu*), or northern summer monsoon, with winds averaging 5.0 m/s, higher humidity, and more frequent rainfall; this phenomenon is more intense in the northern islands than in the other islands. The northeast monsoon (*Iruvaa*), or northern winter monsoon, from October to April, brings favourable weather and sunny days; this period is generally calmer, occasionally interrupted by strong raindrops and thunderstorms, with an average wind speed of 4.8 m/s (Wyrtki, 1973; Kench et al., 2006).

Maldives reefs are subject to numerous environmental and anthropogenic pressures, including coral mining, dredging, improper waste disposal, overfishing, and tourism. It should be noted that coral has long been mined for construction, lime production, and coastal protection; since the 1970's, the construction boom has made this a critical issue (Jaleel, 2013). In 1990's, the government banned coral mining from all reefs (Naylor, 2015).

Dredging and the construction of jetties, ports, or airports generate turbidity and sedimentation, resulting in silt deposits that are harmful to corals (Cowburn et al., 2018); waste management is also a problem: many islands have unmanaged coastal sites, from which waste can reach the sea during high tides and storm surges, becoming trapped in corals or threatening organisms such as turtles.

The entire Maldivian population lives on coral islands and depends directly on the ecosystem services of the reefs, such as fishing and tourism. Unsustainable fishing practices can alter the ecological balance and contribute to biodiversity loss. Fishing for giant clams has been forbidden since 1990; sea cucumber fishing is regulated, and export bans are in place for several ornamental species (Jaleel, 2013). The Maldivian economy is heavily influenced by international marine tourism, which accounts for approximately a quarter of GDP, with approximately one million visitors annually in recent years. Since the early 1970s, resorts have been concentrated in the central atolls (North Malé, South Malé, and Ari), with annual growth between 5% and 20% (Cowburn et al., 2018).

Environmental pressures include storms, coral bleaching events, tsunamis, and proliferations of predators such as the starfish *Acanthaster planci* (Jaleel, 2013).

Between April 4 and 7, 1987, a severe storm occurred in the southern Indian Ocean, causing long-period waves to travel a 4,500 km circular path to the central Maldives. On April 10, waves 5 m above sea level were recorded in Malé, causing extensive flooding for two days. After this event, the damaged area was filled, and barriers were installed around the entire island; these measures proved effective during the 2004 Indian Ocean tsunami, preventing a reiteration of the 1987 effects (Naylor, 2015). Although Maldivian reefs have historically adapted to sea level fluctuations, they are currently weakened by rising sea surface temperatures (SSTs) and ocean acidification, both of which increase coral mortality (Naylor, 2015).

Historically, the Maldives has been affected by two major global bleaching events, in 1998 and 2016; bleaching often occurs when sea temperatures rise approximately 1°C above the seasonal average maximum, depending on marine and meteorological conditions (Montefalcone et al., 2020). The 1997–1998 event was linked to an increase in *El Niño* frequency, which altered the thermal characteristics of the Indian Ocean, causing 95% mortality in shallow-water coral communities (Jaleel, 2013; Bianchi et al., 2017). After this event, reefs were dominated by coralline algae and herbaceous algae (68%), with an increase in erect fleshy algae and sponges compared to the past. Branching species were the most affected, with the genera *Porites* and *Astreopora* becoming dominant in 1998 (McClanahan, 2000). Mortality did not show significant differences between atolls with different levels of human pressure (Montefalcone et al., 2020). Complete recovery of pre-bleaching hard coral cover took approximately 16 years (Morri et al., 2015). The 2016 heat wave was considered by NOAA to be the largest and potentially most severe bleaching event ever recorded. Over 70% of the world's coral reefs experienced catastrophic mortality. In the Maldives, mortality was highest in atolls with higher human pressure. Furthermore, exposed reefs (oceanic reefs) showed lower mortality than more sheltered reefs (lagoonal reefs). The adaptive bleaching hypothesis (ABH) may be strengthened in shallow reefs in the Maldives, given that mortality was lower in 2016 than in 1998. Hard coral cover dropped from approximately 70% to less than 8% after 1998; in 2015, it had again exceeded 70%, only to decline to approximately 20% after 2016 (Montefalcone et al., 2020). The deep refuges hypothesis (DRH) has also been discussed: due to the low cover of surviving corals on mesophotic reefs, their role as a refuge or recruitment reservoir for shallow-water recovery may be limited in the Maldives (Bongaerts, 2010; Morri et al., 2017).

By the end of the century, coral reefs are expected to collapse due to the increased frequency and intensity of bleaching events globally (Montefalcone et al., 2020).

In this context, it emerges that tsunamis can also have significant impacts on coral communities in the Maldives; for example, the 2004 tsunami caused damage not only to beaches and coastlines, but to all Maldivian marine ecosystems (Jaleel, 2013); Indeed, a study conducted between 2003 and 2004 at Dega Thila (Ari Atoll) showed that corallimorpharians almost completely covered the coral detritus, particularly down to 15 m deep, while algae (including encrusting corallines and *Halimeda*), the bleach-resistant coral *Goniopora* (McClanahan et al., 2004), and other organisms (including sponges) were far less abundant. Organisms that settle on coral detritus are thought to play a key role in reef regeneration, as they are presumed to act as precursors to rigid cementation (Rasser and Riegl, 2002). Corallimorpharians, however, are known for their ability to monopolize the substrate surface to the detriment of other potential colonizers, including calcifying organisms and coral recruits (Langmead and Chadwick-Furman, 1999).
Therefore, despite a possible role in the recovery of reef structure, the "soft cementation" performed by corallimorpharians may have actually hindered the establishment of "true cementers," preventing or slowing the recovery process. The December 2004 tsunami, however, removed this unconsolidated debris, and corallimorpharians almost completely disappeared from Maldivian reefs (Morri et al., 2015).

1.6.1 Current knowledge in the Maldives

The Maldives has been the subject of scientific study since the mid 19th century and continues to serve as a "natural laboratory" for testing models of reef response to oceanic and climatic changes. In the case of the Maldives, however, comparing to other charismatic groups (scleractinian corals, reef fishes, etc.), general and systematic knowledge about Corallimorpharia and Zoantharia orders is inexistent or extremely dated, fragmented, incomplete, or wrong; this leads to undersampling and an underestimation of true diversity, a problem that has been noticed in other contexts, where intensified taxonomic and molecular studies have revealed cryptic lineages and unexpected diversity.
Taxonomic studies, in fact, constitute a preliminary and operational approach for any ecological and management assessment of reefs, as without an accurate characterization of the biological organisms present, it is difficult to correctly interpret distribution patterns, temporal trends, and response to disturbance. This is particularly true in rapidly changing systems like the Maldives, where acute events (such as repeated bleaching) and anthropogenic pressures (coastal development, tourism, etc.) can favour phase shifts toward more opportunistic or more tolerant taxa (such as corallimorpharians and zoantharians), thus altering the functionality of the reef ecosystem itself.

Evidence from recent monitoring conducted in the Maldives indicates that in some sites, following environmental disturbances, dominance transitions from hard coral toward opportunistic or more resistant taxa, including corallimorpharians (of the genus *Rhodactis*), may occur, with potential implications for habitat structure and reef recovery trajectories (Morri et al., 2015).
As demonstrated in a recent study conducted at Dhega Thila (3°50.405'N 72°45.010'E) (Ari Atoll), this phase shift became particularly evident after the 2016 bleaching event, although signs of this transition were already observable at depths greater than 7 m in the years following the 1998 bleaching event, when the site was first explored by dive (Pancrazi et al., 2025). This study also highlights how a reef fails to recover the communities of scleractinian corals, fish, and macroinvertebrates, but can instead favour the maintenance of opportunistic species such as those belonging to the order Corallimorpharia.
These studies therefore represent a valuable model for understanding the long-term consequences of cumulative disturbances (such as bleaching events) and human activities (such as tourism), as well as for identifying thresholds beyond which passive recovery becomes unlikely.
In the Maldivian context, by the way, understanding the diversity and ecology of organisms living on coral reefs is a fundamental key for correctly understand and interpretate reef response to global and local pressures, promptly detecting community changes, and designing management and restoration measures.
The integration of standardized monitoring (such as the Reef Check protocol), comprehensive taxonomic revisions (morphological, cnidome, and genetic analyses), and spatial datasets (such as remote sensing, etc.) therefore constitutes the most robust path to filling knowledge gaps and improving the conservation of Maldivian coral reefs.

2 AIM OF THE THESIS

The primary objective of this thesis is to characterize the diversity, distribution, and ecological associations of the orders Corallimorpharia and Zoantharia within the central Maldivian atolls (specifically South Malé and Felidhoo). Surveys conducted in the area in recent years have revealed a high diversity and abundance of these groups. Nevertheless, during visual censuses, they are often treated as generic Operative Taxonomic Units (OTUs), and are frequently even grouped together, due to the difficulty of identifying species, genera and even orders *in situ*. This taxonomic knowledge gap has not only limited diversity censuses but has also consequently restricted the collection of ecological information on these taxa.

Since these identification difficulties are often due to outdated descriptions based exclusively on fixed material, it was first necessary to conduct a comprehensive literature review to determine characters suitable for the morphological identification of both preserved and living specimens. Secondly, it was necessary to obtain an extensive collection of *in situ* pictures and preserved material in order to perform the most comprehensive diversity assessment for both taxa.

With regards to ecological aspects, the study aims to quantify how environmental drivers, such as bathymetry, reef typology (lagoonal vs. oceanic), and substrate composition, shape the community structure of these organisms. By utilizing high-resolution photosquare analysis (via ImageJ), this work establishes a baseline for understanding the resilience and success of these often-overlooked anthozoans in the face of environmental disturbance.

3 MATERIALS AND METHODS

3.1 STUDY AREA

This study was conducted from May 13 2024 to May 17 2024 during the 24th Scientific Cruise, which took place in two different atolls of the Maldives archipelago: South Malé (03° 57' 00'' N; 73° 25' 00'' E) and Felidhoo (03° 28' 00'' N; 73° 32' 00'' E) (Figure 9).

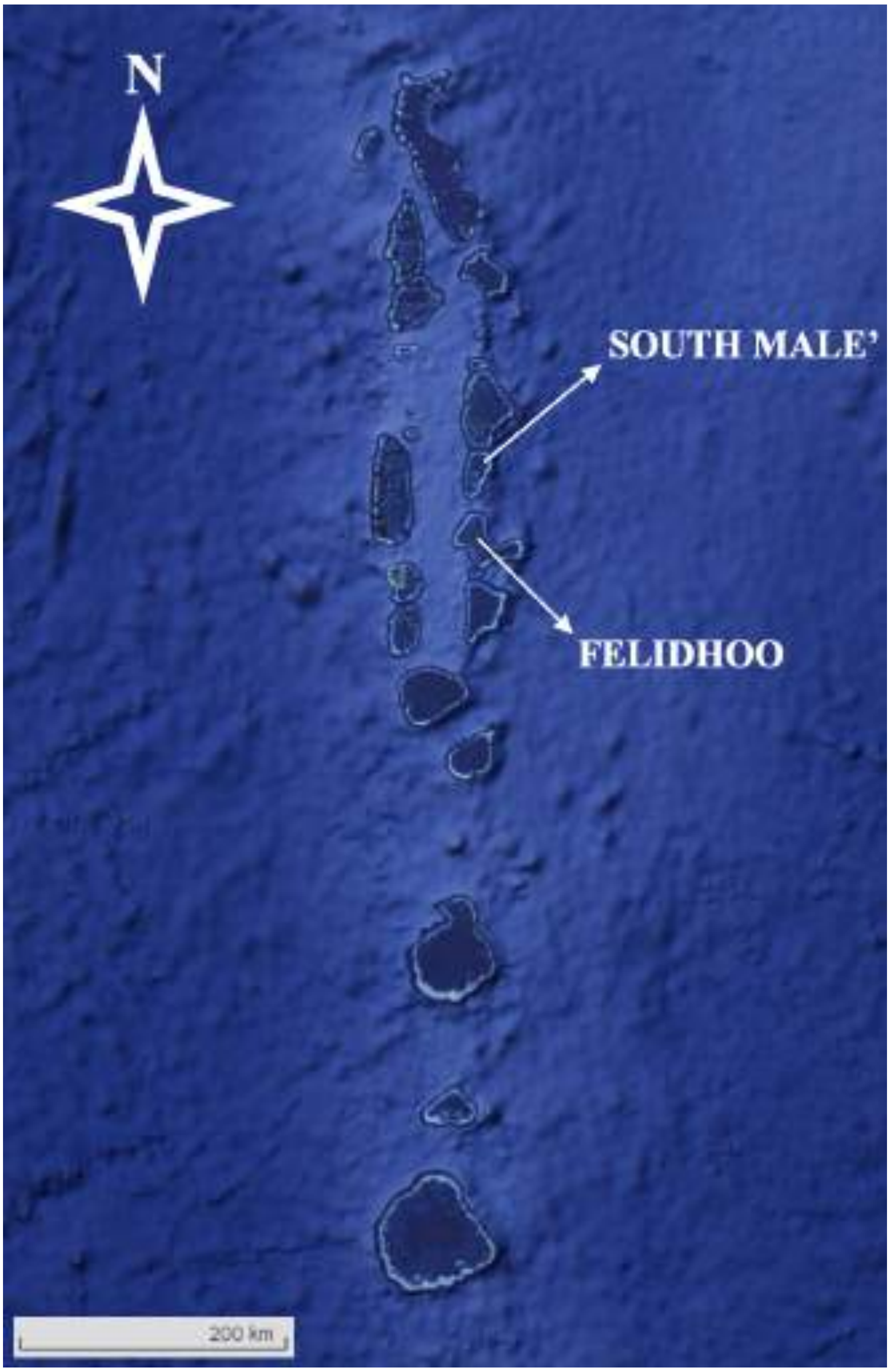


Figure 9: the Maldives Archipelago; the two white arrows point out the atolls considered in this study.

South Malé and North Malé atolls form the Malé atoll, an administrative unit of the Maldivian archipelago located on the northeastern side of the double atoll chain (Rasheed et al., 2021). South

Malé atoll is separated from North Malé atoll by a channel called Vaadhoo Kandu, approximately 5 km wide and nearly 400 m deep (in its central areas). This atoll covers an area of approximately 558.31 km² and includes 112 identified coral reefs, for a total surface area of approximately 175.60 km² (Naseer & Hatcher, 2004). Unlike North Malé atoll, the outer margin of South Malé atoll is more continuous and features fewer channels interrupting the atoll's edge.
Both North and South Malé have undergone coastal modifications and land reclamation projects, largely related to the development of the tourism industry, with nearly half of the currently existing islands having been reclaimed. This scenario makes these atolls ideal environments for studying human impacts and changes in coral reefs (Rasheed et al., 2021).
Felidhoo Atoll (03° 27' 00" N; 73° 27' 00" E) is located south of South Malé atoll, separated from it by a large channel approximately 10 km wide called Fulidhoo Kandu. This atoll has a maximum length of approximately 42 km and a maximum width of approximately 68 km, with an irregular morphology of the fringing reef (Naseer & Hatcher, 2004; Godfrey, 2004). It is composed of approximately 21 islands, distributed mainly along the eastern margin of the atoll.
The atoll's structure is characterized by an almost continuous reef in the eastern portion, interspersed with narrow passages and an internal lagoon with few emerging reefs; lagoons depths generally reach about 60–70 m (Naseer & Hatcher, 2004; Godfrey, 2004).

During this study, a total of 10 sites were sampled; specifically: 4 in the South Malé Atoll and 6 in the Felidhoo Atoll. Among the 10 sampled sites, 4 sites (Bhajia giri and Villivaru kuda giri in South Malé; Bodumohora giri and Rakeedhoo inside reef in Felidhoo atoll) belong to the "lagoonal" type (marked with orange dots in Figure 10), while 6 sites (Miyaru faru, Miyaru kandu, Kandooma beyru, Fulidhoo beyru, Fotteyo beyru and Rakeedhoo oceanic reef) belong to the "oceanic" type (marked with dark blue dots in Figure 10).
All the information regarding: atolls, sites, latitude, longitude, sampling date, and habitat (oceanic reef or lagoon reef) are summarized in Table 1.

Atoll	Site	Lat.	Long.	Data	Habitat
South Male	Miyaru faru	3°59.573' N	73°31.479' E	13/05/24	O
South Male	Bhajia giri	3°55.942' N	73°27.895' E	17/05/24	L
South Male	Kandooma beyru	3°55.388' N	74°28.293' E	18/05/24	O
South Male	Villivaru kuda giri	3°54.234' N	73°26.663' E	17/05/24	L
Felidhoo	Fulidhoo beyru	3°41.010' N	73°24.966' E	13/05/24	O
Felidhoo	Fotteyo beyru	3°30.313'N	73°44.569'E	14/05/24	O
Felidhoo	Bodumohora giri	3°19.563' N	73°29.175' E	15/05/24	L
Felidhoo	Turtle giri	3°31.462' N	72°55.214'	17/05/24	L
Felidhoo	Rakeedhoo inside reef	3°19.057' N	73°28.151' E	15/05/24	L
Felidhoo	Rakeedhoo oceanic reef	3°18.702' N	73°27.931' E	16/05/24	O

Table 1: summary table of all the sites monitored in this study, divided by: atolls, sites, latitude, longitude, date of sampling and habitat (O: oceanic reef; L: lagoon reef).

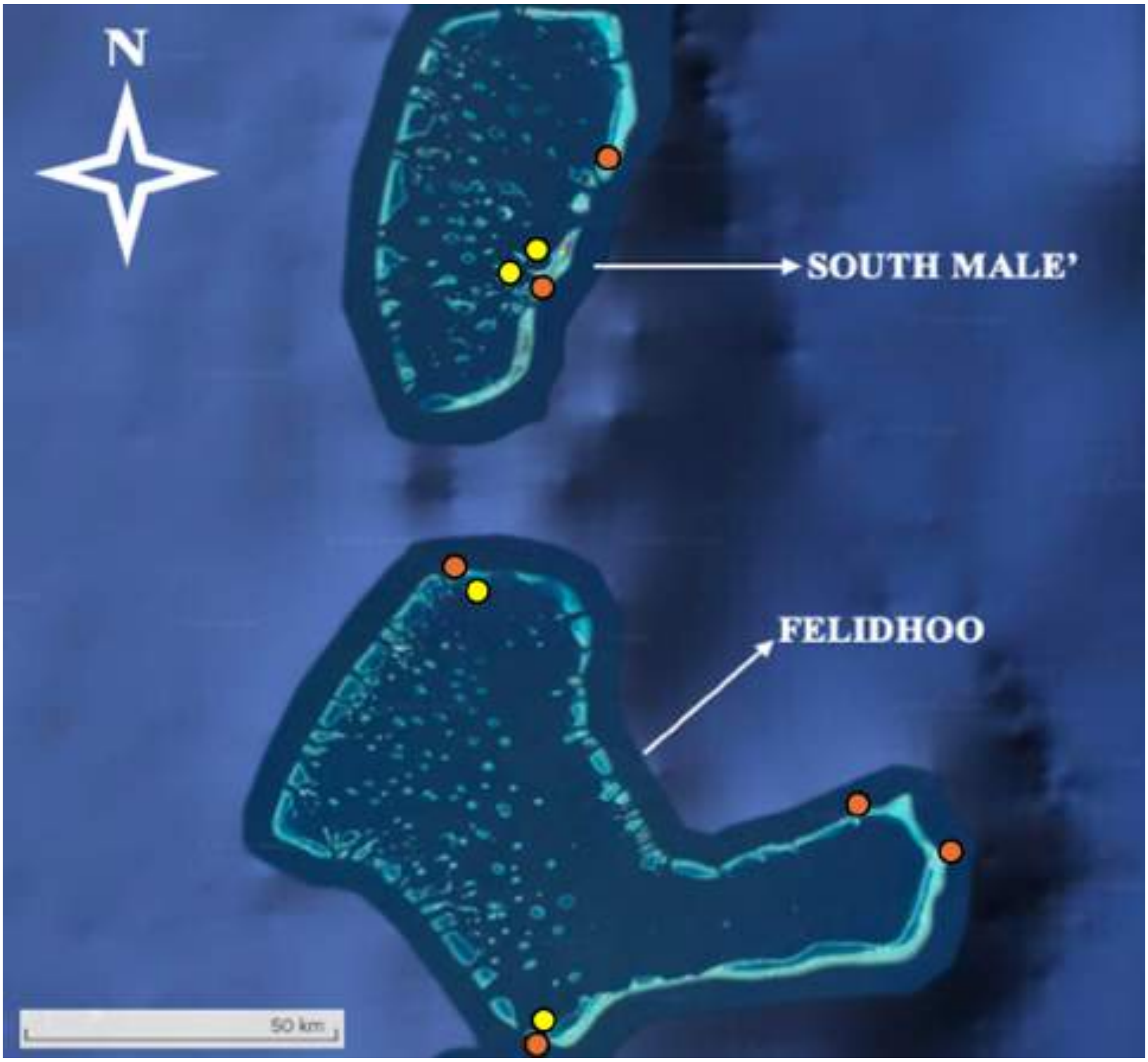


Figure 10: details of South Malé atoll and Felidhoo atoll; the white arrows point out the three atolls considered in this study. On this figure is also marked by: orange dots all the inside/lagoon reefs and yellow dots all the oceanic reefs considered in this study.

3.2 Literature overview of Corallimorpharia and Zoantharia around the Maldives

An extensive bibliographic research was conducted on the Indo-Pacific Corallimorpharia and Zoantharia to determine characters suitable for the morphological identification of both preserved and living specimens of families, genera and species. Below is a summary of all the species found in the area around the Maldives; the table (Table 2) lists the: authority, documented distribution, habitat, and bathymetric range for each genus. This information is provided for each family, each genus, and each species of the two orders documented in the area.

Order	Family	Genus	Species	Authority	Documented distribution	Habitat	Bathymetric range
Corallimorpharia				Carlgreen, 1943	Almost ubiquitarius	Various	0-1000 m
	Discosomidae			Verril, 1869	Tropical	Reef	50-60 m
		Amplexidiscus		Dunn & Hamner, 1980	Australia, Indonesia, Maldives, Japan, Papua New Guinea	Reef	Intertidal and subtidal
			A. fenestrafer	Dunn & Hamner, 1980	Australia, Indonesia, Maldives, Giappone, Papua Nuova Guinea	Reef	3-25 m
		Rhodactis		Milne Edwards & Haime, 1851	Only indopacific	Reef and rock	Intertidal and subtidal
			R. howesii	Saville-Kent, 1893	All Indopacific	Reef	5-20 m
			R. indosinensis	Carlgren, 1943	Cambodia, Vietnam, Japan (Indopacific)	Rock	0-20 m
			R. rhodostoma	Hemprich & Ehrenberg in Ehrenberg, 1834	Red Sea, East Africa (Indopacific)	Reef	0-20 m

Order	Suborder	Family	Genus	Species	Authority	Documented distribution	Habitat	Bathymetric range
Zoantharia					Rafinesque, 1815			
	Brachycnemina				Haddon & Shackleton, 1891	Atlantic and Indopacific	Various	0-100 m
		Sphenopidae			Hertwig, 1882	Atlantic and Indopacific	Reef and rock	Intertidal and subtidal
			Palythoa		Lamouroux, 1816	Tropical/sub-tropical	Reef and rock	Intertidal and subtidal
				Palythoa caesia	Dana, 1846	Tropical/sub-tropical	Reef and rock	Intertidal and subtidal
				Palythoa tuberculosa	Esper, 1805	Tropical/sub-tropical	Reef and rock	Intertidal and subtidal
				Palythoa heliodiscus	Ryland & Lancaster, 2003	Tropical/sub-tropical	Reef and rock	Intertidal and subtidal
				Palythoa grandis	Verrill, 1900	Tropical/sub-tropical	Reef and rock	Intertidal and subtidal
		Zoanthidae			Lamarck, 1801	Tropical/sub-tropical	Reef and rock	Intertidal and subtidal
			Zoanthus		Lamarck, 1801	Tropical/sub-tropical	Reef and rock	Intertidal and subtidal
				Zoanthus coppingeri	Haddon & Shackleton, 1891	Tropical/sub-tropical	Reef and rock	Intertidal and subtidal
	Macrocnemina				Haddon & Shackleton, 1891	Atlantic and Indopacific	Various	0-1000 m
		Parazoanthidae			Delage & Hérouard, 1901	Atlantic and Indopacific	Various	0-100 m
			Antipathozoanthus		Sinniger, Reimer & Pawlowski, 2010	Atlantic and Indopacific	Mostly on antipatharians but also on polychaete tubes and reef	5-330 m
				Antipathozoanthus cavernus	Kise, Fujii, Masucci, Biondi & Reimer, 2017	Maldives, Palau, Kagoshima (Japan)	Only on antipatharians from the genus Myriopathes	18-38 m
				Antipathozoanthus remengesaui	Kise, Fujii, Masucci, Biondi & Reimer, 2017	Maldives, Red Sea, Palau, Okinawa e Kagoshima (Japan)	Only on antipathes	9-40 m

Table 2: summary of all the species of Corallimorpharia and Zoantharia documented in the area around the Maldives. Only *Amplexidiscus* and *Antipathozoanthus* were previously recorded here.

3.3 Field activities

The data and samples analysed in this study were collected during the "Scientific Cruise" from May 12, 2024, to May 17, 2024. This annual cruise is organized by ISSD (International School for Scientific Divers) in collaboration with the University of Genoa and the tour operator Albatross Top Boat. During SCUBA dives on the scientific cruise, photo-squares images were taken at various depths to collect in vivo morphological and ecological data. Inside these photo-squares, few organisms were collected for subsequent taxonomic identification. Additional equipment was used (Figure 11), specifically: an underwater chronometer (integrated into a MARES® Genius dive computer system), a SONY® RX100 MKVII camera equipped with an ISOTTA® diving case, two WeeFine® headlights, 4,500 lumens each, a folding wooden ruler, a specially designed PVC slate, a stainless-steel screwdriver with a rubber handle, Falcon® tubes, and plastic zip-lock bags.

Figure 11: equipment used by diver A in the upper line: from the left: SONY® RX100 MKVII; ISOTTA® diving case; WeeFine® headlight; folding wooden ruler.
Equipment used by diver B in the lower line: from the left: scientific PVC slate; Falcon® tubes; plastic zip-lock bags.

At each of the 10 dive sites covered in this study, four timed transects were conducted, each at four different depths: 30 m; 20 m; 10 m; and the reef flat (from 1 m to 6 m deep) (Figure 12 A).
At each depth, five random photosquares measuring 40 cm x 40 cm were taken (using a wooden folding ruler), for a total of 20 photo-squares per dive and 200 photo-squares in total. The photos were taken using the automatic mode of the camera.
The time spent monitoring at each depth was approximately 9–10 minutes of linear swimming, not including the time spent: taking photographs; recording the data on the underwater slate; collecting any samples; and communicating with the working group members. The time for each transects was determined by considering the average time required by a diver (equipped with all standard equipment plus specific equipment for this purpose) to traverse 100 m of reef in stable current and visibility conditions. The diving activities were carried out in a buddy system: one diver (diver B) took the

photographs, and another (diver A) collected the data using an underwater slate and, if necessary, collecting samples (using a screwdriver to eradicate the organisms to be collected from the reef substrate, if necessary) (Figure 12 B). The data recorded on the underwater slates included: water temperature at each of the four different depths; for each of the five replicates (for each bathymetry), the following were also recorded: substrate type, abundance of corallimorpharians and/or zoantharians, any coloniality/gregarious habitus, and the code of any sample collected (in addition to the date and time of the dive, weather conditions, and atoll).

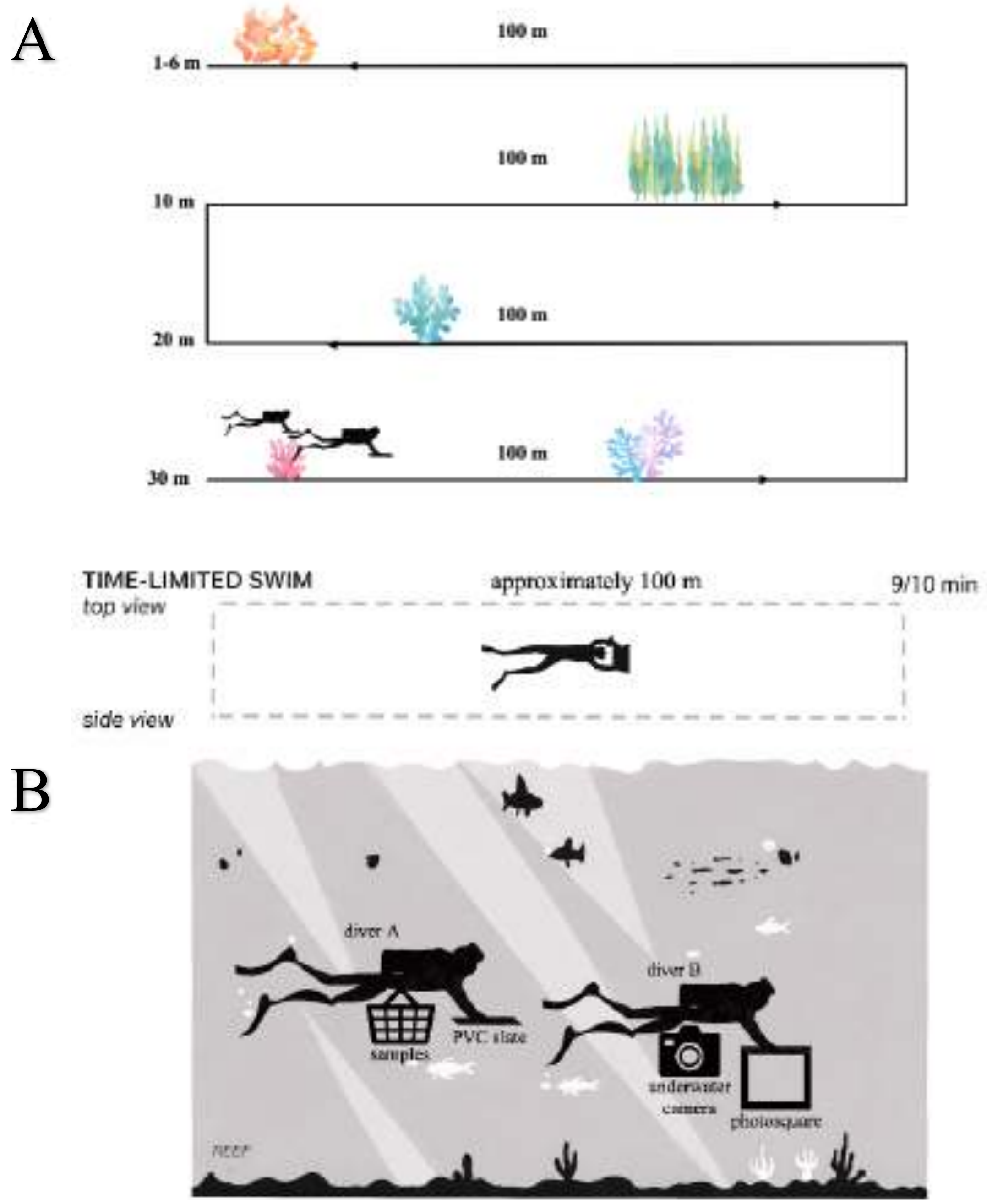


Figure 12: figure A: sampling technique using a time limited swim transect; figure B: the two operators' equipment on field activities, divided in: diver A and diver B.

3.4 Laboratory's morphological analyses

The 36 samples collected as described above were preserved in 95% ethanol immediately after collection and brought to the surface, following commonly used protocols described in the literature for similar purposes (Cha, 2007). The samples were subsequently packaged, shipped, and transported to the University of Genova for taxonomic identification.

Samples were prepared by replacing the ethanol when excessively cloudy with "fresh" 95% ethanol and labelling the samples as follows: CORMAL1_24 (Corallimorpharia sample no° 1 collected in 2024) and ZOAMAL1_24 (Zoantharia sample no° 1 collected in 2024) (Figure 13).

Figure 13: the photo on the left show the 36 samples just arrived at the University's laboratory. The photo on the right shows the labelling process on corallimorpharians and zoantharians samples.

Morpho-anatomical analyses were conducted using a binocular optical microscope equipped with a millimetre bar in the right lens.

For each of the 10 specimens previously attributed to the order Corallimorpharia, the following characteristics were considered: habitus (gregarious or colonial); the size in cm of the living individual in situ; the shape, colour, and diameter of the fixed pedal disc; the type, shape, colour, length, number, and retractability of the marginal tentacles; the type, shape, colour, length, number, and retractability of the discal tentacles; the morphology of the mouth; the presence/absence of the naked area and the presence/absence of the acrospheres.

The morphological characteristics observed for each of the 26 specimens previously attributed to the order Zoantharia are: the habitus (colonial or solitary); the dimensions in cm of the living and fixed individual, the diameter of the polyp, and the total height of the organism; its roughness, its colour, and the height of the column when fixed; the shape and colour of the oral disc, both living and fixed; the morphology of the mouth; the type, shape, colour, length, and number of tentacles present, and any ecological notes (e.g., epibiont host).

3.5 Photographic analysis

The 200 photo-squares taken were analysed with the free ImageJ software, obtaining the percentage coverage (%) and abundance of different categories and subcategories referring to both benthic organisms and the abiotic substrate (Figure 55).

- For the corallimorpharian category, the subcategories are: *Amplexidiscus fenestrafer*; *Rhodactis* cf. *howesii*; *Rhodactis* cf. *indosinensis*; and other corallimorpharians.
- For the zoantharian category, the subcategories are: *Palythoa heliodiscus*; *Palythoa caesia* or *tuberculosa* complex; *Palythoa* cf. *grandis*; *Zoanthus* cf. *coppingeri*; and other zoantharians.
- The green algal component was divided into: turf, filamentous green algae, encrusting green algae, erect green algae, and algae of the genus *Halimeda*.
- The sponge category was further subdivided based on growth forms into: massive sponges, encrusting sponges, and erect sponges.
- Soft corals were considered a single category given the limited information available in the literature for the Maldivian environment.
- Building hard corals were subdivided into: *Acropora*, *Pocillopora*, massive corals, encrusting corals, and solitary corals.
- Ascidians were considered separately.
- The "other" category includes all organisms that do not fall into the other categories (such as: vagile benthic organisms; stony corals of the genus *Tubastrea*, *Porytes*; tridacna, etc.).
- Abiotic categories include bare rock, coral rubble (or debris), and sand (or fine sediment).

Excluding the categories referring to the two genera of organisms studied in this study, all other categories considered were chosen because they have historically been used in the Maldives for ecological analyses (Montefalcone et al., 2020). Each category was associated with a specific colour to facilitate visual identification during analysis using ImageJ software (Figure 14):

- Corallimorpharia: dark black.
- Zoantharia: light black.
- Green algae: green (in decreasing order of shading, starting from the turf category and ending with the *Halimeda* algae).
- Sponges: red (darker for massive sponges, intermediate for encrusting sponges, and very light for erect sponges).
- Soft corals: light blue.
- Hard corals: from dark yellow for Acropora, progressively lighter in hue until solitary corals.
- Ascidians: metallic blue.
- Other: fuchsia.
- Bare rock: brownish
- Coral rubble: grey.
- Fine sand: white.

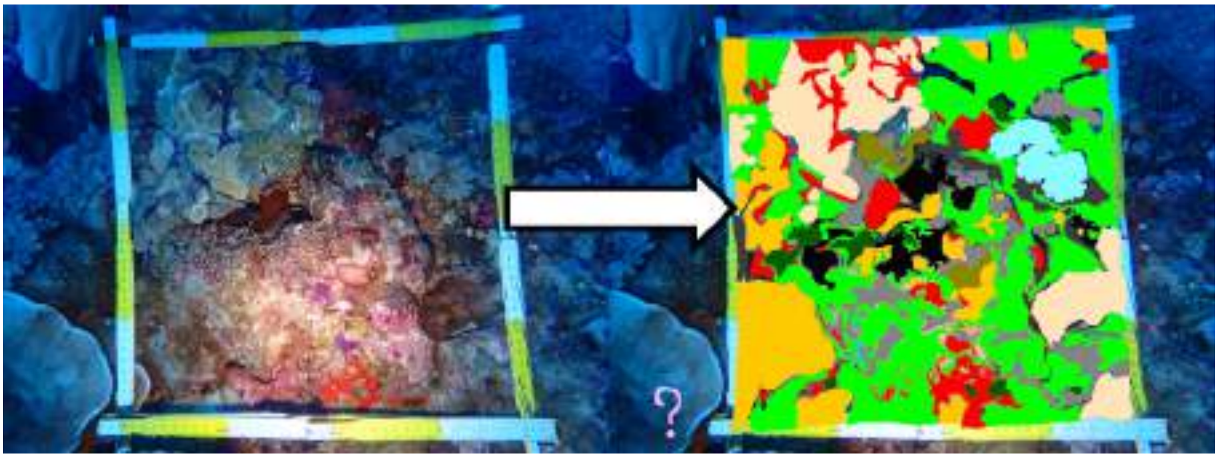


Figure 14: on the left is possible to see a photo-square taken as previously reported. On the right the same photo-square after being analysed using ImageJ software.

The total sum of all the coverages of each category mentioned above (when present) for each photo square always turned out to be equal to 1600 cm2 (consequently to the size of the photo square itself: 40 cm x 40 cm).

3.6 Data analysis

All data obtained from photographic analyses on the cm^2 coverage and abundance of corallimorpharians and zoantharians, as well as all other categories, were organized into Excel spreadsheets and subsequently used for statistical analyses using the R programs (R Core Team, 2025) and Excel (p-value significance threshold = 0.05).

The Indicator Species Analysis (ISA; Dufrene & Legendre, 1997) was used to identify corallimorpharians and zoantharian species statistically associated with one or more environmental factors, namely different depths (reef flat ~ 2-5 m, 10, 20, and 30 m), atoll, and location. This statistical analysis was performed using the "multipatt" function of the R package "indicspecies" (De Caceres et al., 2016).

To better analyse the ecological preferences/niches of the various taxa, the OMI (Outlier Mean Index) analysis was performed. This type of analysis allowed us to identify the preferred environmental conditions of individual taxa based on their abundance (Doledec et al., 2000; Dray & Dufour, 2007). This analysis is based on two parameters: marginality (OMI) describes the distance between the preferred environmental conditions of a given species and the most frequent and recurring ones measured across all sampling sites in the entire study.

Species with high OMI values have marginal niches, meaning they prefer "atypical" environments compared to those most frequently surveyed in the study.

Tolerance (Tol), on the other hand, described and quantified the breadth of the ecological niche. Low values indicate that a species is distributed in a limited range of environmental conditions (specialist species), while high values indicate that the species is distributed across a broad gradient (generalist species) (Bo et al., 2017).

4 RESULTS

4.1 Identified species

The morpho-anatomical analyses allowed the identification of 3 species of Corallimorpharia and 5 species of Zoantharia.

4.1.1 Corallimorpharia (Stephenson, 1937)

- **Species 1: *Amplexidiscus fenestrafer* (Dunn & Hamner, 1980) (Table 3)**

We analyse the collected specimens labelled as: CORMAL4_24; CORMAL5_24; CORMAL6_24; CORMAL7_24, and CORMAL9_24 (Table 3 D and 3 E).

CORMAL4_24 (1 specimen), CORMAL5_24 (2 specimens), CORMAL6_24 (1 specimen), and CORMAL9_24 (6 specimens) were sampled on May 17, 2024, at Villivaru kuda giri (3°54.234' N 73°26.663' E, South Male) at depths of 30 m (colony of 4 individuals), 20 m, 27 m, and 27 m (all part of a single large colony) on a sub-vertical inner reef. CORMAL7_24 (1 specimen) was also sampled on May 17, 2024, but in Kandooma beyru, 3°55.388' N 74°28.293' E (South Male), at a depth of 28 m from a colony of approximately 24 individuals on an outer wall reef.

Diagnosis: live dimensions range from 2.5 cm to 16 cm in width of the oral disc, while when attached, they range from 1.2 cm to 5.65 cm; the diameter of the pedal disc ranges from 0.5 cm to 4.4 cm when attached; the height of the column ranges from 0.1 cm to 0.6 cm when attached.
The pedal disc appears circular in shape; the column appears smooth with a flattened columnar shape; the oral disc has a circular oval shape with a ribbed underside; the oral cone is flattened. The colour of the individual when fixed in each of these portions is uniformly pale yellow/brownish; in life, the oral disc is a dull brownish-greenish-brownish colour, paler towards the margin (Table 3 A and 3 B). The column is a similar colour to the oral disc, while at the base (in the pedal disc) the colour decreasing slightly (Table 3 F and 3 G).
The marginal tentacles (sparser than the discal tentacles) are flattened, triangular in shape (Table 3 C), 0.1 cm to 0.25 cm long (shorter than the marginal tentacles) and 0.1 cm to 0.3 cm wide; these tentacles are spaced widely apart (0.1 cm to 0.4 cm); they are present in numbers ranging from 30 to 50 and are not retractable. In live field conditions, it has been noted that they become finger-shaped when the oral disc is folded, while they are slightly shorter when the oral disc is expanded.

The discal tentacles (between 40 and 400) are longer than the marginal ones, are always papilliform, never dendritic; they are 0.1 cm to 0.3 cm long and 0.1 cm to 0.15 cm wide; the marginal window ranges from 0.3 cm to 0.8 cm with a number of tentacles equal to 1-4 tentacles per row; the central fenestra contains 2-13 tentacles per row. The marginal window is separated from the central window by a tentacle-free zone present in all specimens; in this zone, in some rare cases (1 specimen in 5), tentacles identical to the discal tentacles but isolated have been noted.

The area immediately around the mouth in these specimens (Table 3 H) is devoid of tentacles (less densely present in the vicinity). No external body area is encrusted with sand.

From an ecological perspective, these specimens all display a gregarious habitus; the least populated colony contained four individuals and was located on the seabed in the immediate proximity of the reef on a small rock, while the largest colony contained 24 individuals and was scattered along a reef wall, almost completely covering the substrate (much less densely and with space between each individual, compared to other observed corallimorpharians such as *Rhodactis* cf. *howesii* / *rhodostoma* complex).

Considering the morphological and ecological details (Figure 15), it was concluded that these specimens definitely belong to the species *Amplexidiscus fenestrafer* (Dunn & Hamner, 1980).

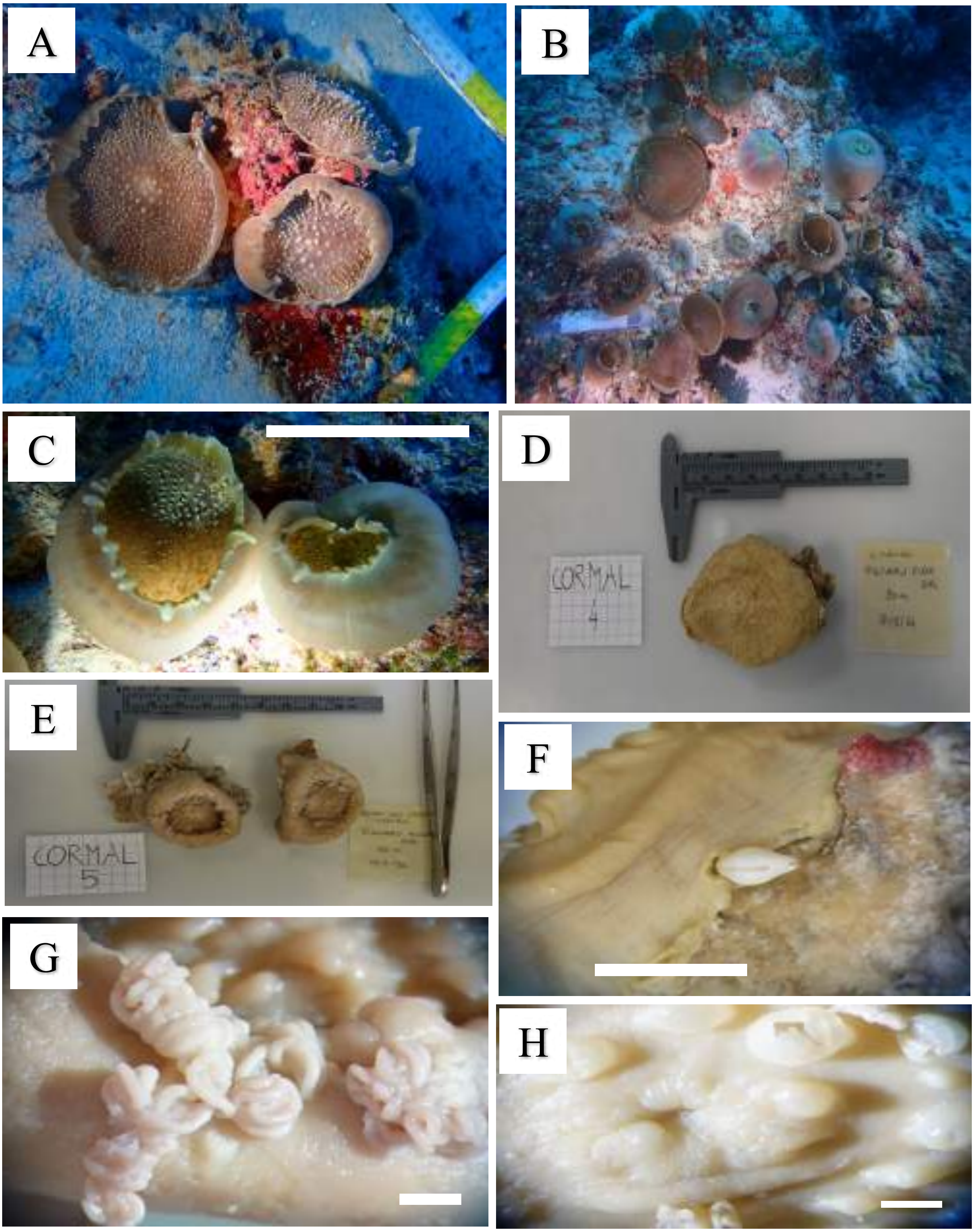


Table 3: A and B represent different aggregations of specimens; C: focus on the triangular shape of the marginal tentacles; D and E are two of the collected samples; F and G are examples of column and colour of the external body when preserved (in G you can notice the acontia filaments); H is the mouth (scale bar C around 10 cm; scale bar G and H 0,2 cm).

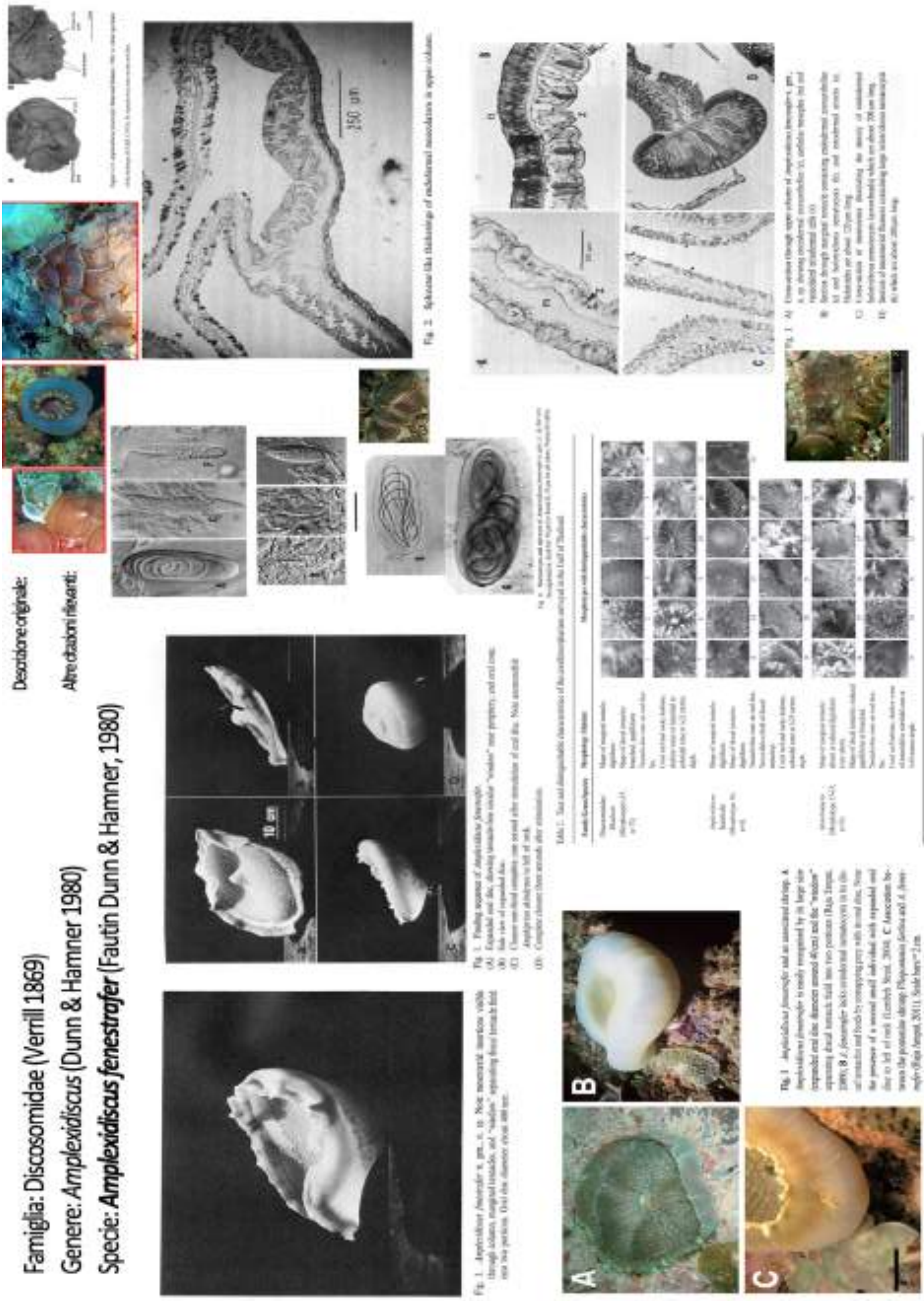


Figure 15: extract from the morphological catalogue (from: Chapter 7: Appendix) relating to species *Amplexidiscus fenestrafer*.

- **Species 2: *Rhodactis indosinensis* (Carlgren, 1943) (Table 4)**

We analyse the collected specimens labelled as: CORMAL8_24 (Table 4 E).

CORMAL8_24 is a sample consisting of four specimens collected on May 17, 2024, at Bajya giri (3°55.942' N 73°27.895' E) at a depth of 11.3 m on the subvertical wall of an inner reef.

Diagnosis: the oral disc width ranges from 8 cm to 12 cm when alive, and from 3 cm to 4.7 cm when attached. The diameter of the pedal disc ranges from 2.4 cm to 3.8 cm when attached; the column height ranges from 0.2 cm to 0.3 cm when attached.

The pedal disc is circular in shape; the column is smooth and flattened; the oral disc is circular, oval in shape (lobed when alive); the oral cone is bright pink (Table 4 F). The colour (Table 4 A) of the entire live specimens is grey-beige (when viewed against the light, the oral disc is highly transparent); on the oral disc, both live and fixed, longitudinal beige lines are visible (yellow when fixed) with light brown tentacles (less transparent). When fixed, it is a fairly uniform pale yellow/brownish colour; longitudinal beige lines are visible on the oral disc when alive.

The marginal tentacles (less full than the discal tentacles) are both papilliform and dendritic, averaging 0.3 cm long and 0.1 cm wide; these tentacles are present in numbers ranging from 70 to 90 and are non-retractable.

The discal tentacles (between 100 and 120) are longer than the marginal tentacles and can be highly dendritic (Table 4 B and 4 G); they range from 0.3 cm to 0.5 cm long and 0.1 cm to 0.15 cm wide. It is noteworthy that in life, when the organism was disturbed, it took on a curled appearance (Table 4 D).

The specimens do not have a tentacle-free zone or acrospheres.

No external body area is encrusted with sand (Table 4 C).

From an ecological perspective, these specimens all display a gregarious habit (the colony consisted of more than 40 adult individuals), completely covering the reef area at that specific bathymetry (8-12 m). The patch of these individuals completely overhangs the existing hard corals (most of which are dead or clearly suffering from spatial competition with these organisms).

Considering the morphological and ecological details (Figure 16), it was concluded that these specimens most likely belong to the species *Rhodactis indosinensis* (Carlgren, 1943).

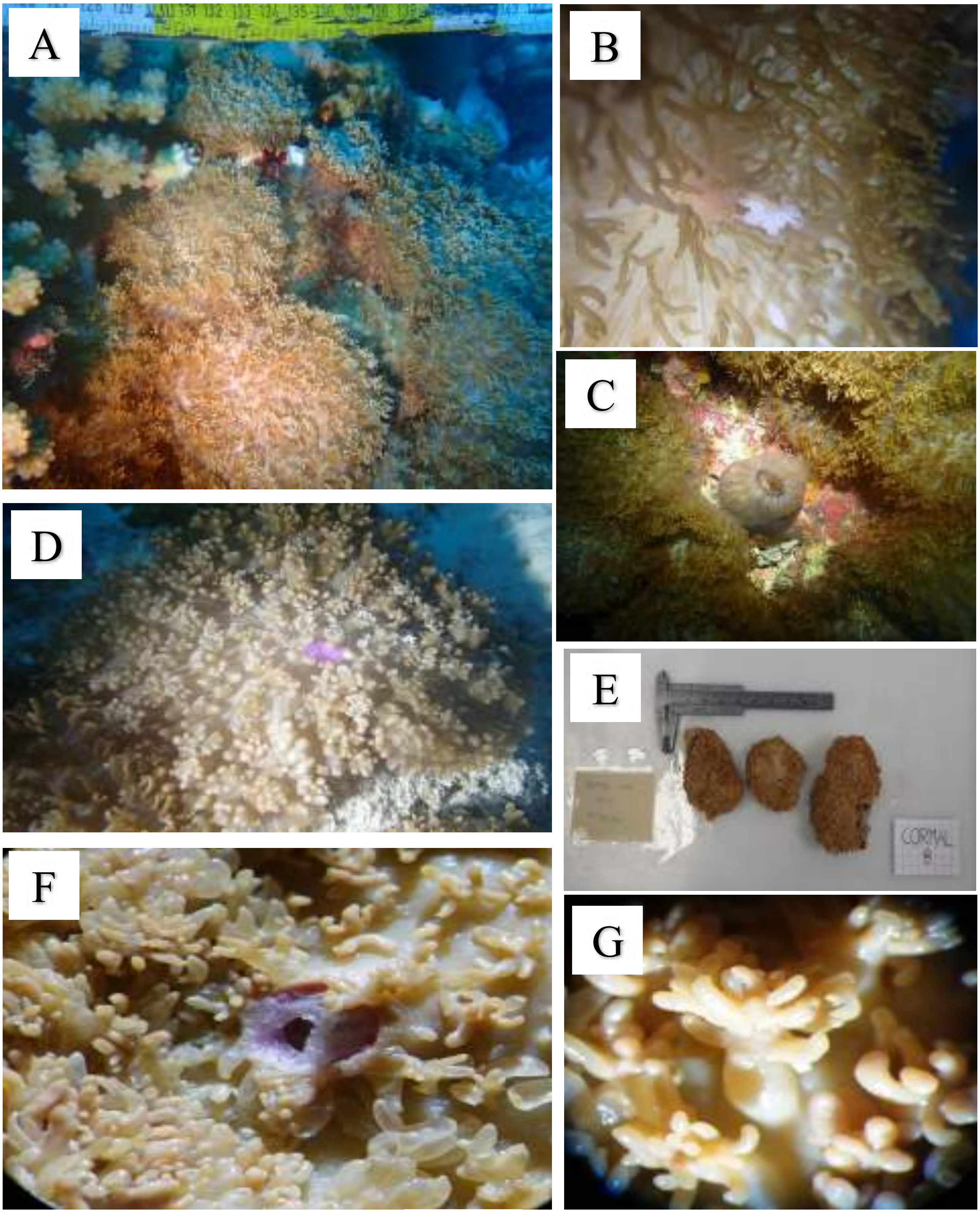


Table 4: A: group of specimens with grey-beige colour; B and G show the discal tentacles; C: closed specimen, as it's noticeable there is no encrustation on the external body; D: curled appearance of the discal tentacle when contracted; E: the only sample collected of this species; F: pink oral cone (scale bar F and scale bar G are 0,4 cm).

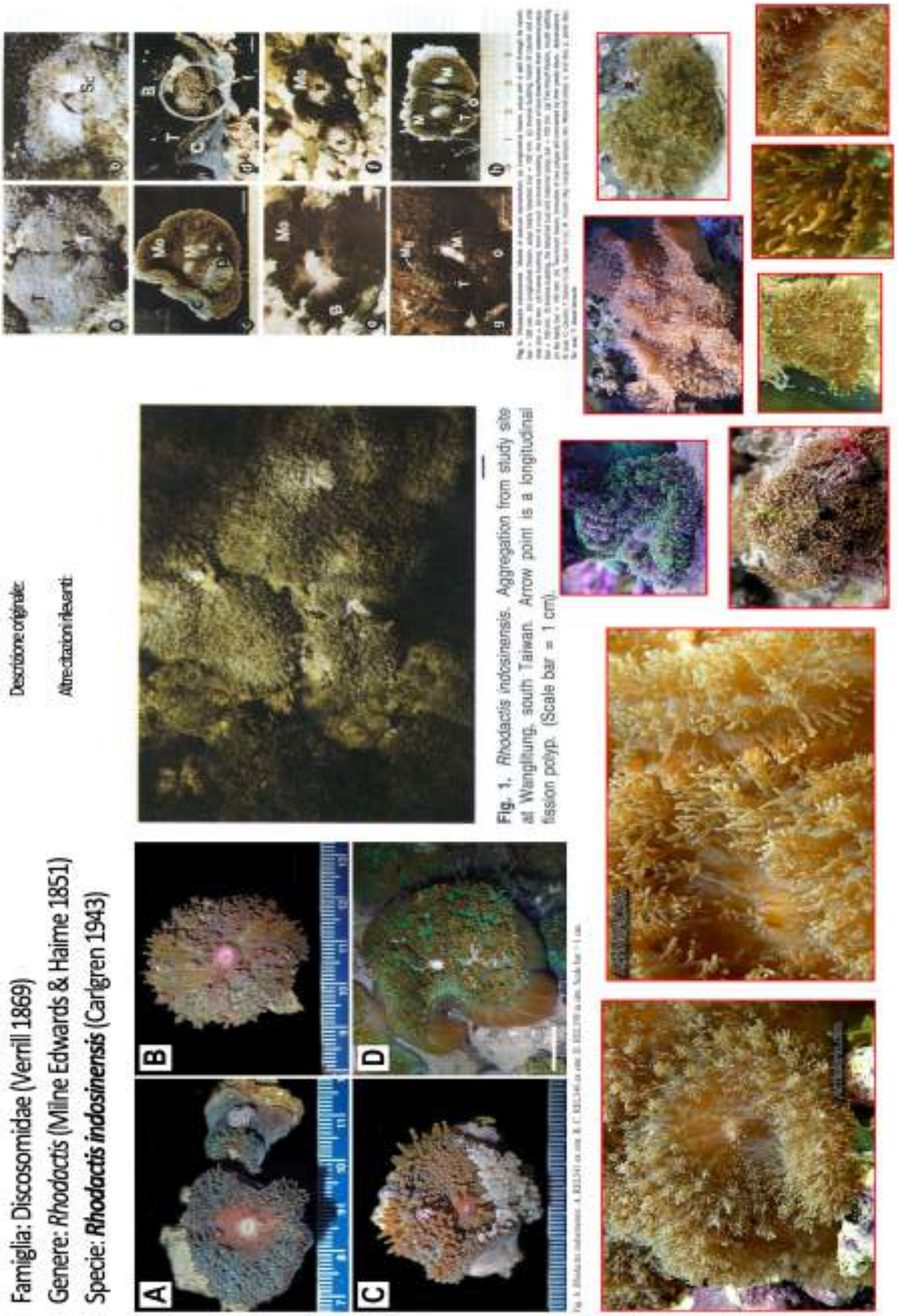


Figure 16: extract from the morphological catalogue (from: Chapter 7: Appendix) relating to species *Rhodactis indosinensis*.

- **Species 3: *Rhodactis* cf. *howesii* (Saville-Kent, 1893) / *rhodostoma* (Hemprich & Ehrenberg in Ehrenberg, 1834) complex (Table 5)**

We analyse the collected samples labelled as: CORMAL1_24; CORMAL2_24; CORMAL3_24, and CORMAL10_24 (Table 5 D).

CORMAL1_24 (6 specimens), CORMAL2_24 (8 specimens), CORMAL3_24 (4 specimens), and CORMAL10_24 (1 specimen) were sampled on May 22, 2024, at Turtle Giri, 3°31.462' N 72°55.214' E (South Ari), at depths of 30 m, 20 m, 10 m, and 20 m, respectively, on an inner reef. CORMAL1_24, CORMAL2_24, and CORMAL10_24 come from the subvertical walls of this reef, while CORMAL3_24 comes from the Giri drop-off. These samples were not collected during the scientific cruise, but from a sampling plan of the same name conducted independently in South Ari Atoll.

Diagnosis: the oral disc measures 2 cm to 3.5 cm in width when alive, and 0.9 cm to 2.2 cm when attached; the diameter of the pedal disc ranges from 0.2 cm to 2.3 cm when attached; the column height ranges from 0.01 cm to 0.3 cm when attached.
The pedal disc is circular in shape; the column is smooth and flattened in shape; the oral disc is circular-oval in shape. The colour of the attached individual in each of these areas is fairly uniformly pale yellow/brownish; in life, the colour is brown-beige, and the column is a similar colour to the oral disc (Table 5 C). The oral cone is pinkish, with a fuchsia-purple edge; The acontia are pink, like the oral cone, and display scattered purple pigmentation (Table 5 F).
The marginal tentacles are all papilliform, ranging from 0.05 cm to 0.1 cm long and averaging 0.1 cm wide; they range in number from 50 to 100 and are non-retractable.
The discal tentacles (between 40 and 160) are dendritic but papilliform toward the inside (Table 5 E); they range from 0.1 cm to 0.25 cm long and average 0.1 cm wide. The area immediately around the oral cone in these specimens has sparse tentacles (less dense than the surrounding area).
Ecologically, these specimens all exhibit a gregarious habit (Table 5 B); the site from which they originated (Turtle giri) is 70-80% covered (up to 95% in some areas of the reef); the percentage of cover progressively decreases with depth, reaching zero around 34-35 m (toward the reef bottom). They were found on: rock, coral rubble, sponges, and live hard corals (Table 5 A). They were found in both well-lit environments and more shade-loving microhabitats, but were not found in the completely dark parts of the reef (deeper portions of cracks etc.) or at depths greater than 34 m.
Their coloration, if found in day light, appears paler to faded; completely white individuals were found under some rocks (still viable given the retractability of their tentacles in situ).

Overall, these organisms have shown great plasticity in colonizing the substrate at this site; the reef's coral cover appears almost completely absent, particularly in the shallower sections, revealing a few rare and scattered patches of Acropora. This reef is notable for its scattered colourful anemones and a high presence of turtles (not green ones, the others) (hence the site's name), which show particular interest in these organisms, which they were observed feeding on during sampling.
It was concluded that these samples (Figures 17 and 18) belong to *Rhodactis* cf. *howesii* (Saville-Kent, 1893) or *Rhodactis* cf. *rhodostoma* (Hemprich & Ehrenberg in Ehrenberg, 1834); these two species are indistinguishable without further analysis (cnidome and genetic); recent studies show that they are probably the same species (Cha, 2006).

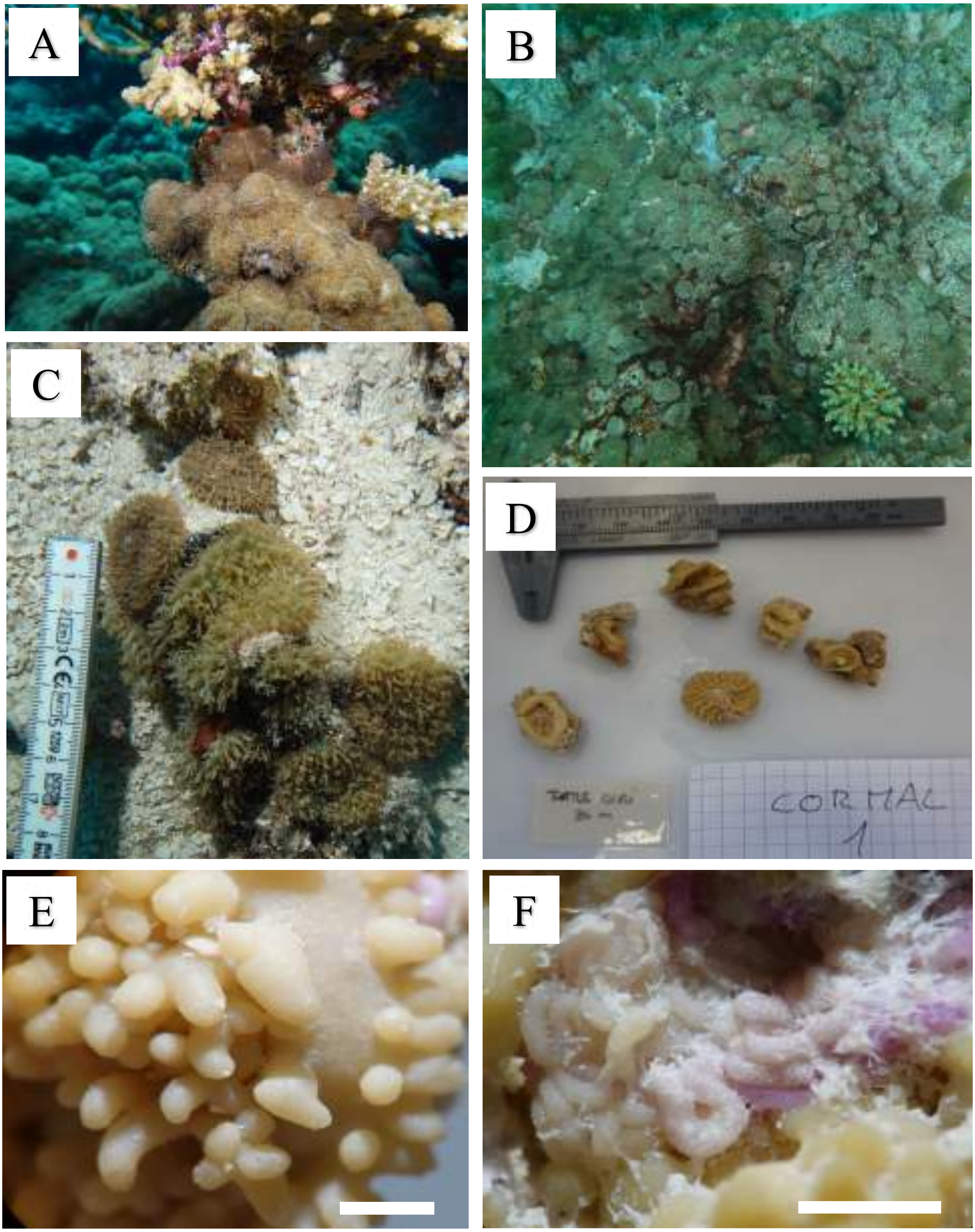


Table 5: A: specimens growing on hard corals, sponges and algee; B: large patch of specimens showing a gregarious habitus; C: different colour variation in the same patch of organism; D: examples of the collected samples; E: examples of dendritic and papilliform discal tentacles; F: pink colour variation of the acontia and the oral cone (scale bar E and scale bar F 0,2 cm).

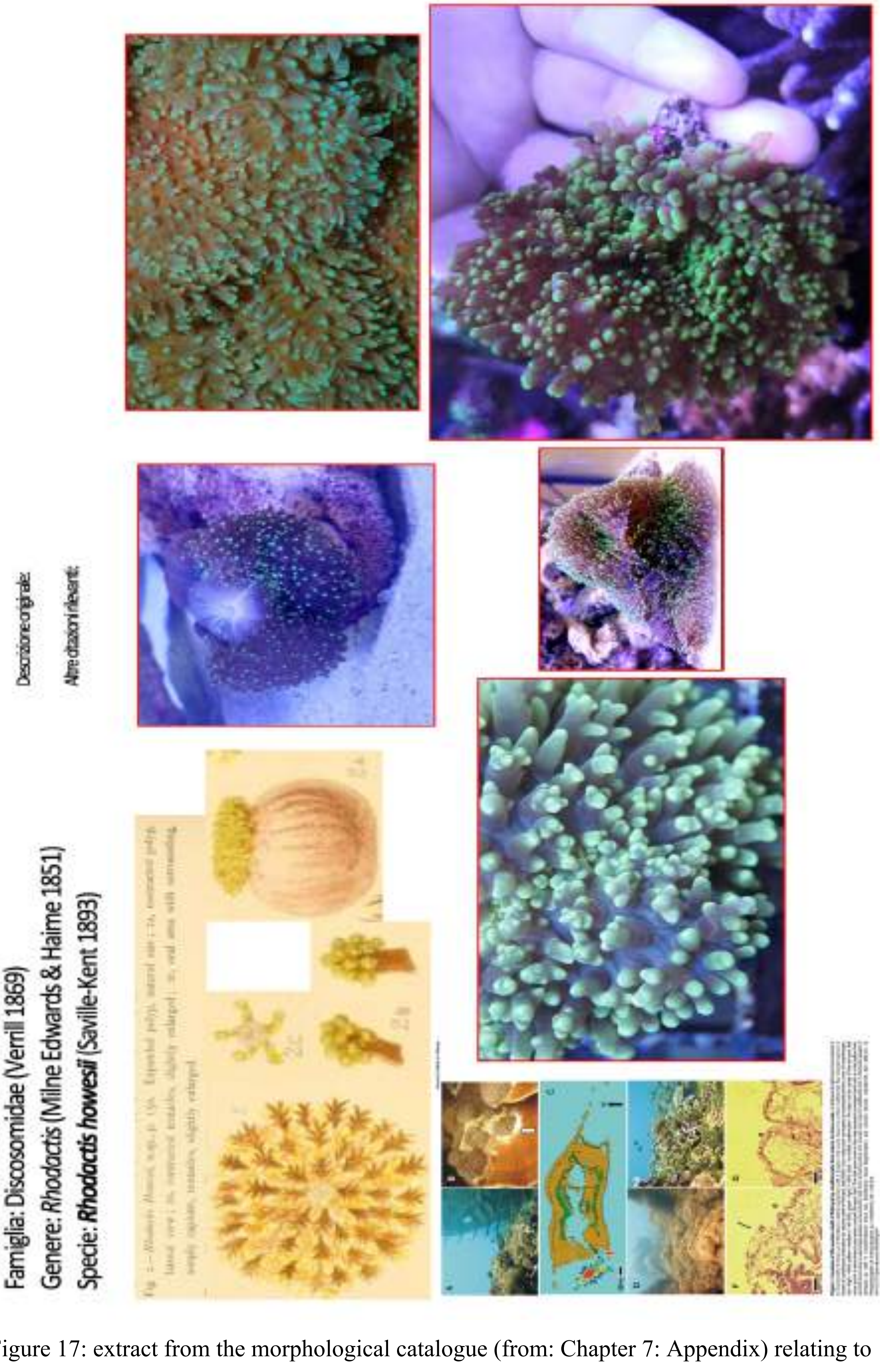


Figure 17: extract from the morphological catalogue (from: Chapter 7: Appendix) relating to species *Rhodactis howesii*.

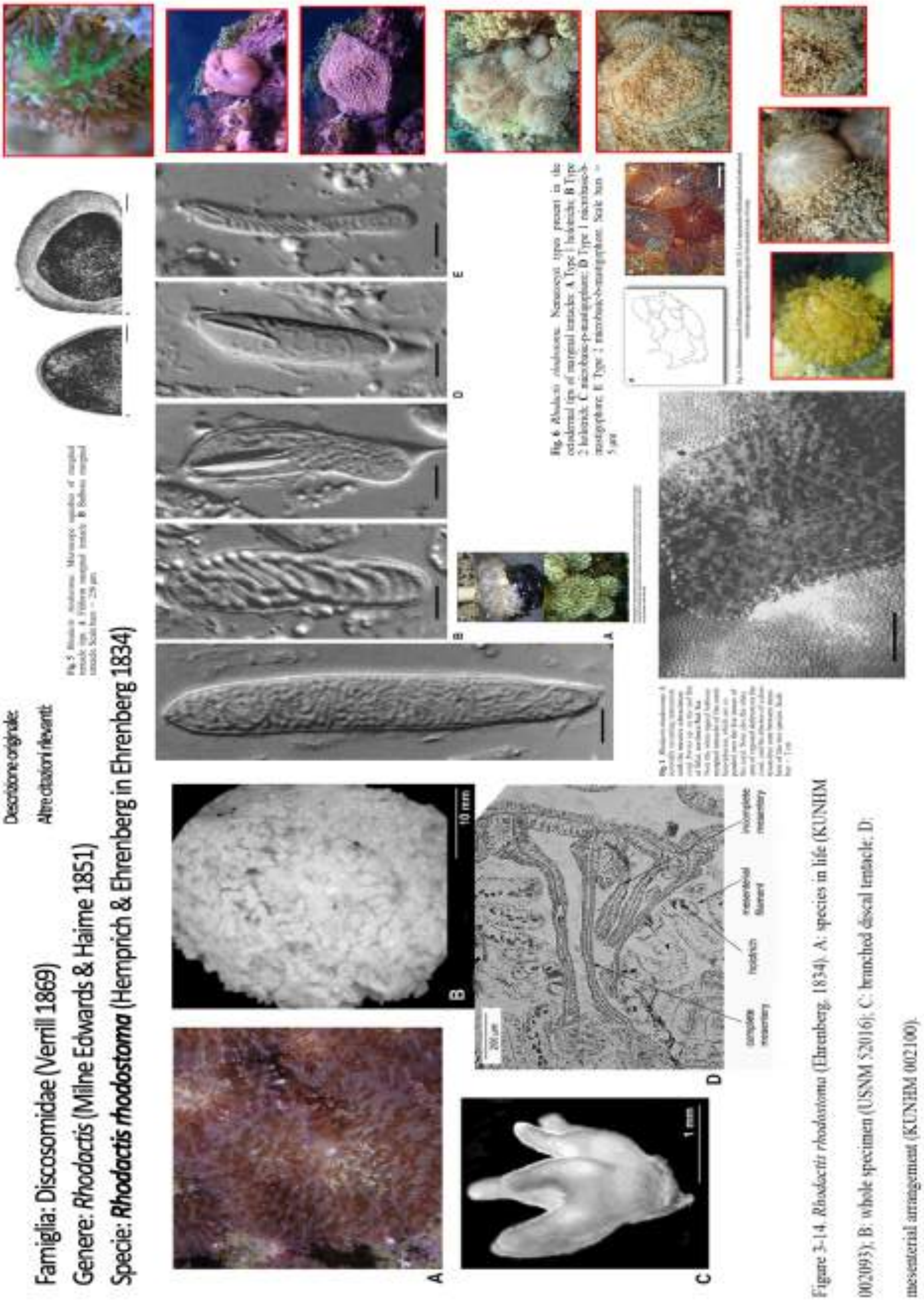


Figure 18: extract from the morphological catalogue (from: Chapter 7: Appendix) relating to species *Rhodactis rhodostoma*.

4.1.2 Zoantharia (Gray, 1832)

- **Species 1: *Palythoa caesia* (Dana, 1846) / *tuberculosa* (Esper, 1805) complex (Table 6)**

We analyse the collected samples labelled as: ZOAMAL15_24; ZOAMAL17_24; and ZOAMAL21_24 (Table 6 C, 6 D and 6 E).

ZOAMAL15_24 and ZOAMAL17_24 were sampled on May 14, 2024, at Fotteyo beyru, 3°30.313'N 73°44.569'E (Felidhoo), at a depth of 10 m on the horizontal reef and on the reef flat (around 3-4 m), respectively. ZOAMAL21_24 was sampled on May 15, 2024, but at Bodumoheraa giri, 3°19.563'N 73°29.175'E (Felidhoo), at a depth of 20 m on the sub-vertical wall of an outer reef.

Diagnosis: All samples appear as a mat/colony of individuals (absence of a true column); live colonies range in size from 1 cm x 1.5 cm wide to 4.5 cm x 5 cm wide, with an average colony height of 0.4 cm; while fixed colonies range in size from 0.5 cm x 0.6 cm wide to 3.65 cm x 3.8 cm wide, with an average height of 0.3 cm. Live colonies appear flattened and wrinkled, with an irregular oval oral disc (Table 6 A). Live colonies are cream-colored (off-white), with yellowish-brown polyps, tentacles, and oral discs. Fixed colonies maintain the same texture (Table 6 F) but display a uniform, light yellow-cream colour (Table 6 E).
The polyps are separated from one another and have an oral disc diameter of between 0.2 cm and 0.6 cm when alive, and between 0.15 cm and 0.35 cm when fixed.
The tentacles of the various live polyps appear retractable, cylindrical, and squat, and are arranged in two rows of 15-40 tentacles (10-20 tentacles per row). The tentacles in the two rows appear to be of different types: the largest, located further out on the oral disc, have a length ranging from 0.08 cm to 0.1 cm; the others are smaller (the size was not measured due to the extreme retractability of the tentacles, which retracted as soon as the individual was eradicated from the substrate). The colonies in all their external body portions appear lightly or moderately concretioned/encrusted with sediment in a homogeneous manner.
Ecologically, these specimens all exhibit a colonial habitus and were found on the reef in different microhabitats: ZOAMAL15_24 was collected from beneath a bleached juvenile Pocillopora, near an encrusting coral; ZOAMAL17_24 comes from the reef flat, therefore exposed to particularly extreme conditions of hydrodynamics and light irradiation; ZOAMAL21_24 on corallinaceous red algae, in the perimeter of a large massive coral (Table 6 B). Considering the morphological and ecological details (Figure 19 and Figure 20), it was concluded that these specimens belong to *Palythoa caesia*

(Saville-Kent, 1893) or *Palythoa tuberculosa* (Hemprich & Ehrenberg in Ehrenberg, 1834). These two species are indistinguishable without further analysis (cnidome and genetics). Recent genetic analyses show that *Palythoa tuberculosa* and *Palythoa caesia* are a single large clade, with mixing between the specimens attributed to the two names. (Hibino et al., 2014).

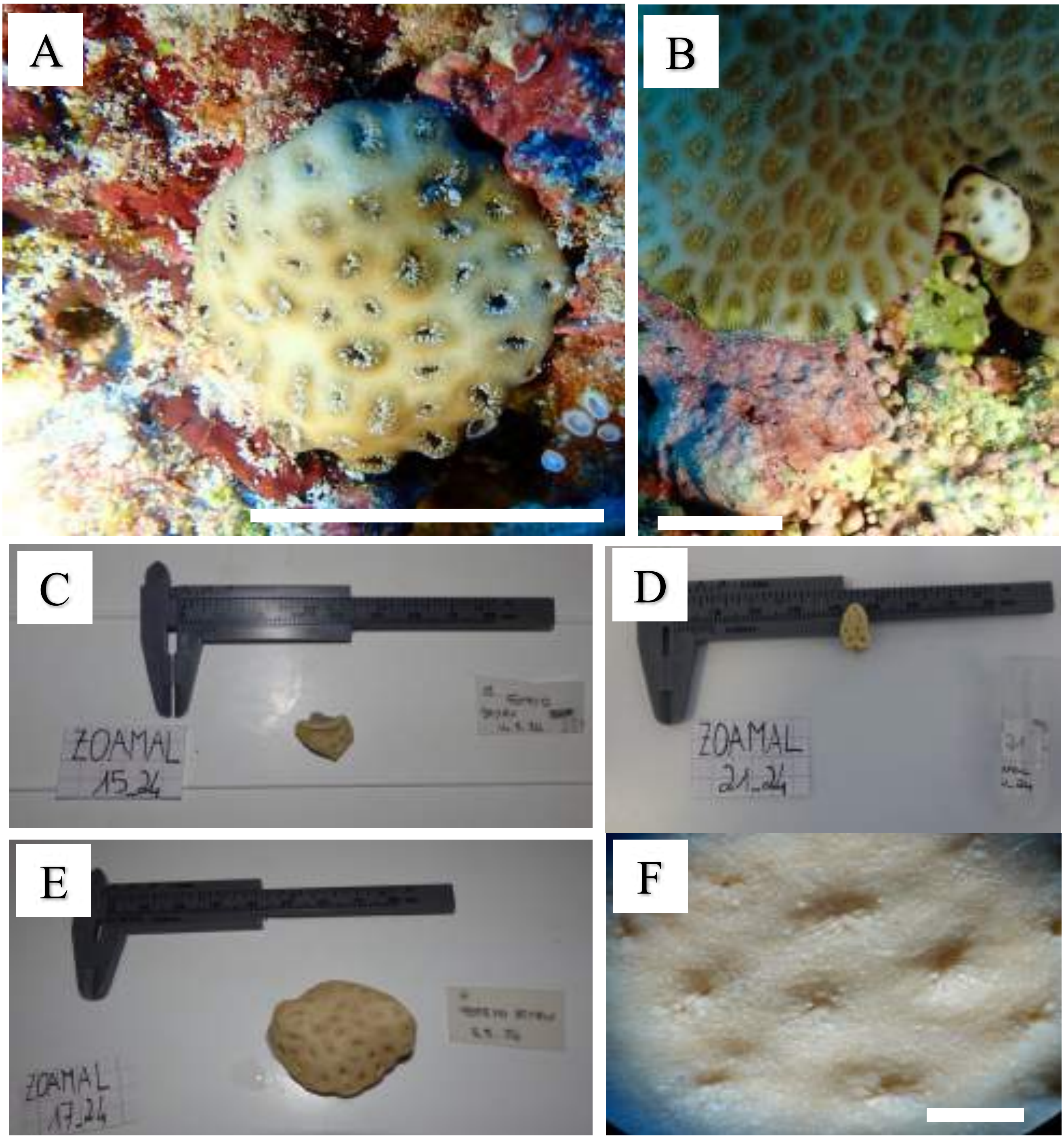


Table 6: photo A shows detail of the irregular and oval oral disc; photo B shows how this species can grow in very different context and near different organisms (like covering the perimeter of a big massive coral in this case); C, D and E are the samples collected; F: detail of the concretioned external body (scale bar A 5 cm; scale bar B 1,5 cm; scale bar F 0,4 cm).

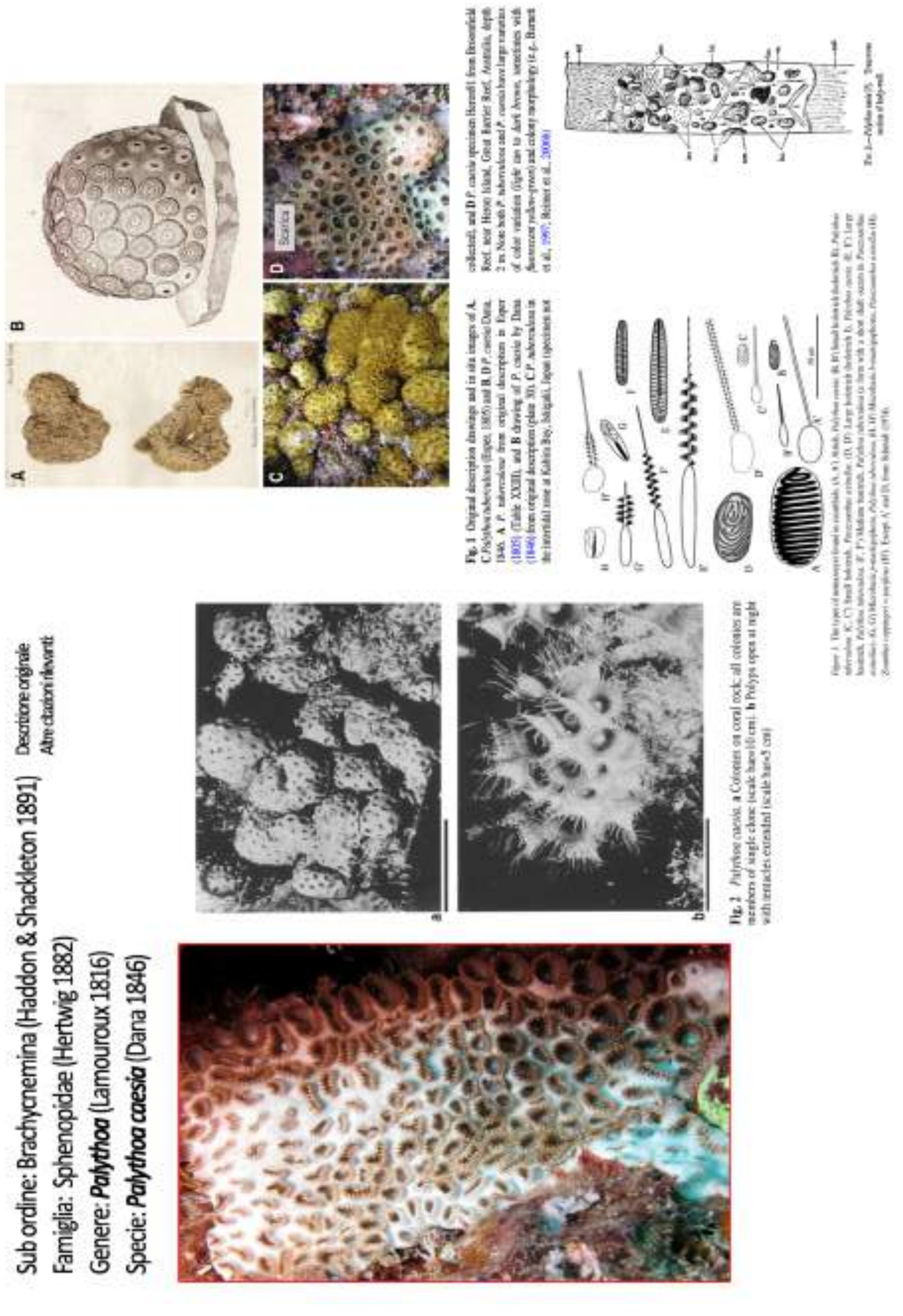


Figure 19: extract from the morphological catalogue (from: Chapter 7: Appendix) relating to species *Palythoa caesia*.

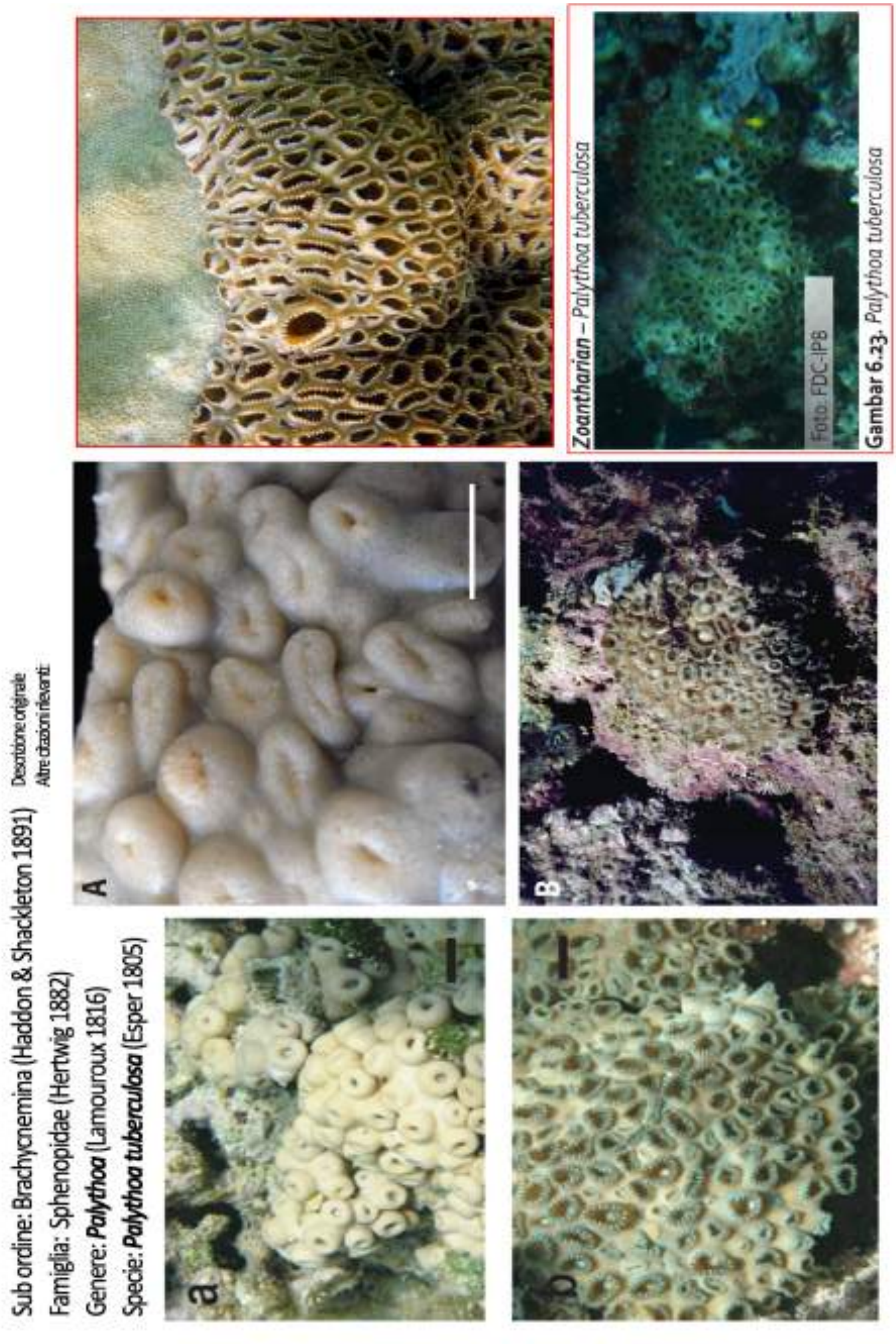


Figure 20: extract from the morphological catalogue (from: Chapter 7: Appendix) to species *Palythoa tuberculosa*.

- **Species 2: *Palythoa* cf. *heliodiscus* (Ryland & Lancaster, 2003) (Table 7)**

We analyse the collected samples labelled as: ZOAMAL1_24; ZOAMAL2_24; ZOAMAL3_24; ZOAMAL4_24; ZOAMAL5_24; ZOAMAL7_24; ZOAMAL8_24; ZOAMAL9_24; ZOAMAL13_24; ZOAMAL19_24; ZOAMAL20_24; ZOAMAL23_24; ZOAMAL24_24, and ZOAMAL26_24 (Table 7 C).

ZOAMAL1_24 (1 specimen), ZOAMAL2_24 (1 specimen); ZOAMAL3_24 (2 specimens) and ZOAMAL4_24 (1 specimen) were sampled on May 12, 2024, at the Kuda Giri Wreck, 3°58.257'N 73°29.277'E (South Male), and were collected during a fun dive at depths of 10 m (on coral rubble on a sub-vertical reef), 20 m (on a sub-vertical reef), 11.2 m (on a sub-horizontal reef), and on the flat reef, respectively. ZOAMAL5_24 (1 specimen), ZOAMAL7_24 (4 specimens); ZOAMAL8_24 (2 specimens), ZOAMAL9_24 (7 specimens) were sampled on May 12, 2024, at Myaru faru, 3°59.573'N 73°31.479'E (South Male); The first two samples came from a depth of 20 m (the first collected on the sub-horizontal reef, the second on the sub-vertical reef), while the other two were taken at a depth of 30 m (the first of these on the sub-horizontal reef, the second on the sub-vertical reef). ZOAMAL13_24 (1 specimen) was collected on May 14, 2024, at Fotteyo beyru 3°30.313'N 73°44.569'E (Felidhoo) from a depth of 30 m on the sub-horizontal reef. ZOAMAL19_24 (11 specimens), ZOAMAL20_24 (8 specimens), ZOAMAL23_24 (this specimen is a fragment of specimen ZOAMAL20_24) were sampled on May 15, 2024, at Bodumoheraa giri, 3°19.563' N 73°29.175' E (Felidhoo), at 20 m (on the sub-vertical reef) and 34.4 m (on the sub-horizontal reef), respectively. ZOAMAL24_24 (5 specimens) was collected on May 17, 2024, at Villivaru kuda giri, 3°54.234' N 73°26.663' E (South Male), at 30 m depth on the sub-vertical reef. ZOAMAL26_24 (4 specimens) was sampled on 15 May 2024 at Rakedhoo inside reef 3°19.057' N 73°28.151' E (Felidhoo) at 20 m depth on the sub-horizontal reef.

Diagnosis: all specimens appear like a colony of individuals joined by collenchyma; the colonies differ greatly in size (from a few polyps to colonies of more than 500-600 polyps) and are difficult to identify in terms of shape and size, as the polyps themselves retract extremely easily and the collenchyma is either under the sand, in carbonate rock, or submerged under algal turf (so the precise perimeter of the colony is not visible).
The polyps of live colonies appear like a “garden of flowers”(Table 7 A and 7 B); the coloration of the oral disc changes greatly in live specimens, ranging from a white-grey (especially in external reefs and at greater depths) to various shades of green and brown, some of which are very bright (especially in shallower, shady environments). In live specimens, the oral disc also displays streaks of different

colours (white, dark green), arranged radially or in two concentric circles of different colours. There are two types of marginal tentacles on the oral disc, and both can appear on various colours in the wild: white, almost transparent, green, or brownish (sometimes the colours of the two types are the same, other times they are different). When fixed, the polyps, however, display a more uniform colour, like a brownish-cream colour; the mouth is white in fixed specimens (Table 7 D).

The polyps are separated from each other and have an oral disc diameter ranging from 0.2 cm to 1.4 cm when alive and between 0.08 cm and 0.55 cm when fixed. The height of individual polyps ranges from 0.1 cm to 1 cm when alive; while when fixed, they range from 0.01 cm to 0.3 cm.

The fixed polyp column (when measurable) ranges from 0.08 cm to 0.75 cm (the individual live column was not measured due to the retractability of the polyps) and is rough and heavily concretioned in all specimens (Table 7 E).

The oral disc is irregularly oval in shape in all specimens (Table 7 F).

The tentacles of the various live polyps appear retractable, arranged in two marginal rows with a number ranging from 20 to 46 tentacles (10 to 20 tentacles per row). The tentacles in the two rows appear to be of different types: the tentacles defined as "thick" are located further out on the oral disc and range in length from 0.05 cm to 0.15 cm; immediately behind a thick tentacle is a tentacle of the second type, designated as "thin," which are slightly shorter and wider than the others (if only slightly).

Ecologically, these specimens all exhibit a colonial habitus and were found on the reef in various microhabitats. Many were collected on encrusting corallines, but with differences: ZOAMAL2_24 was collected near massive coral; ZOAMAL3_24 was near a massive sponge and a juvenile *Pocillopora*; ZOAMAL5_24 was near erect green algae (genus *Halimeda*); ZOAMAL9_24 was also located on corallines but among a lot of fine sand. The other specimens originate from similar ecological situations, but with different environmental variables, for example: ZOAMAL7_24 was sampled in a semi-sciaphilous environment; ZOAMAL24_24 was completely covered in turf.

Considering the morphological and ecological details (Figure 21), it was concluded that these specimens belong to *Palythoa* cf. *heliodiscus* (Ryland & Lancaster, 2003).

Considering the morphological and ecological details, we concluded that ZOAMAL4_24 is instead a juvenile anemone.

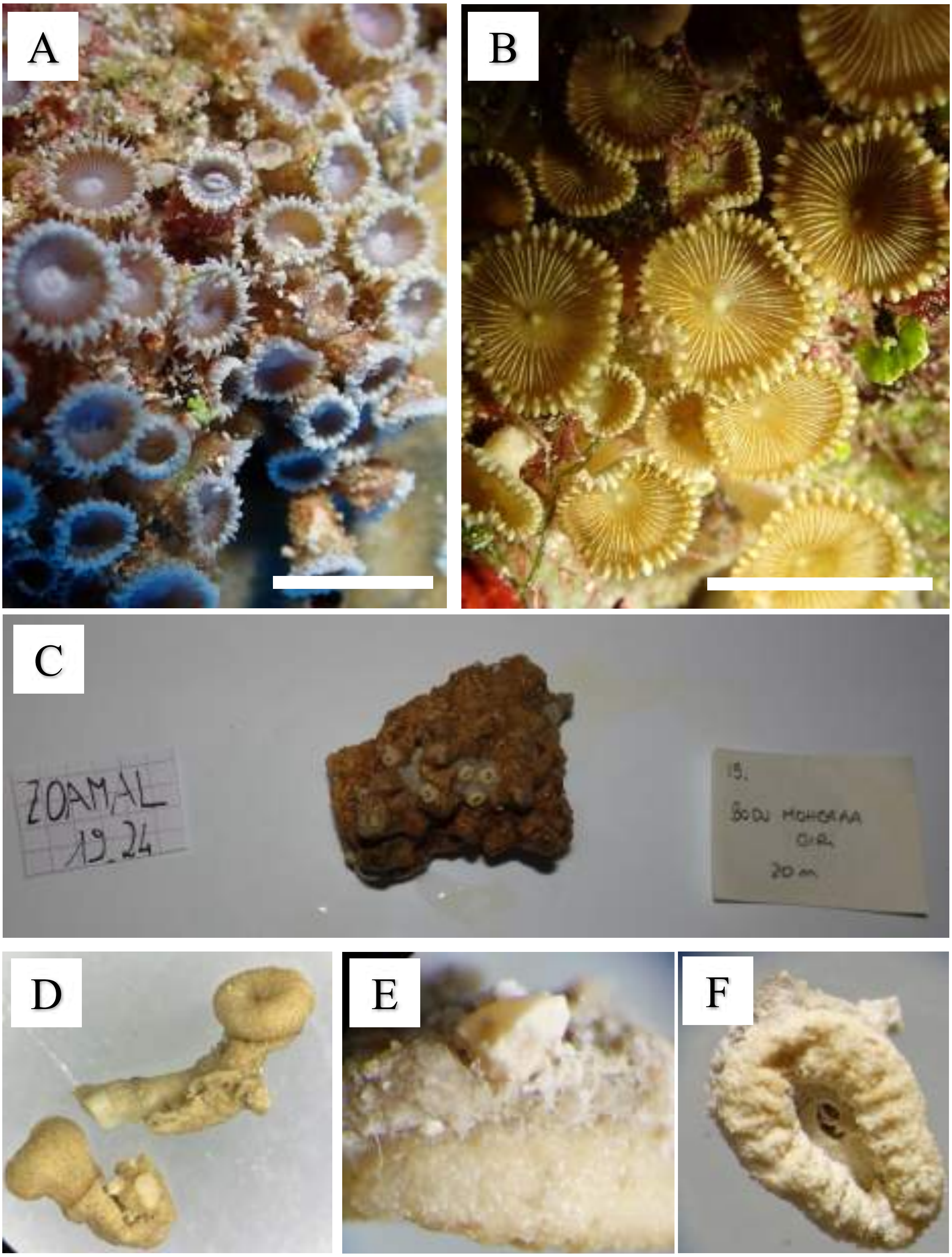


Table 7: photos A and B show how the species con look like a “garden of flowers” with different colour variations; C: example of the samples collected; D: colour and shape of the speciem while preserved; E: concretioned external body; F: shape of the oral disc and the oral cone (scale bar A 0,5 cm; scale bar B 1 cm).

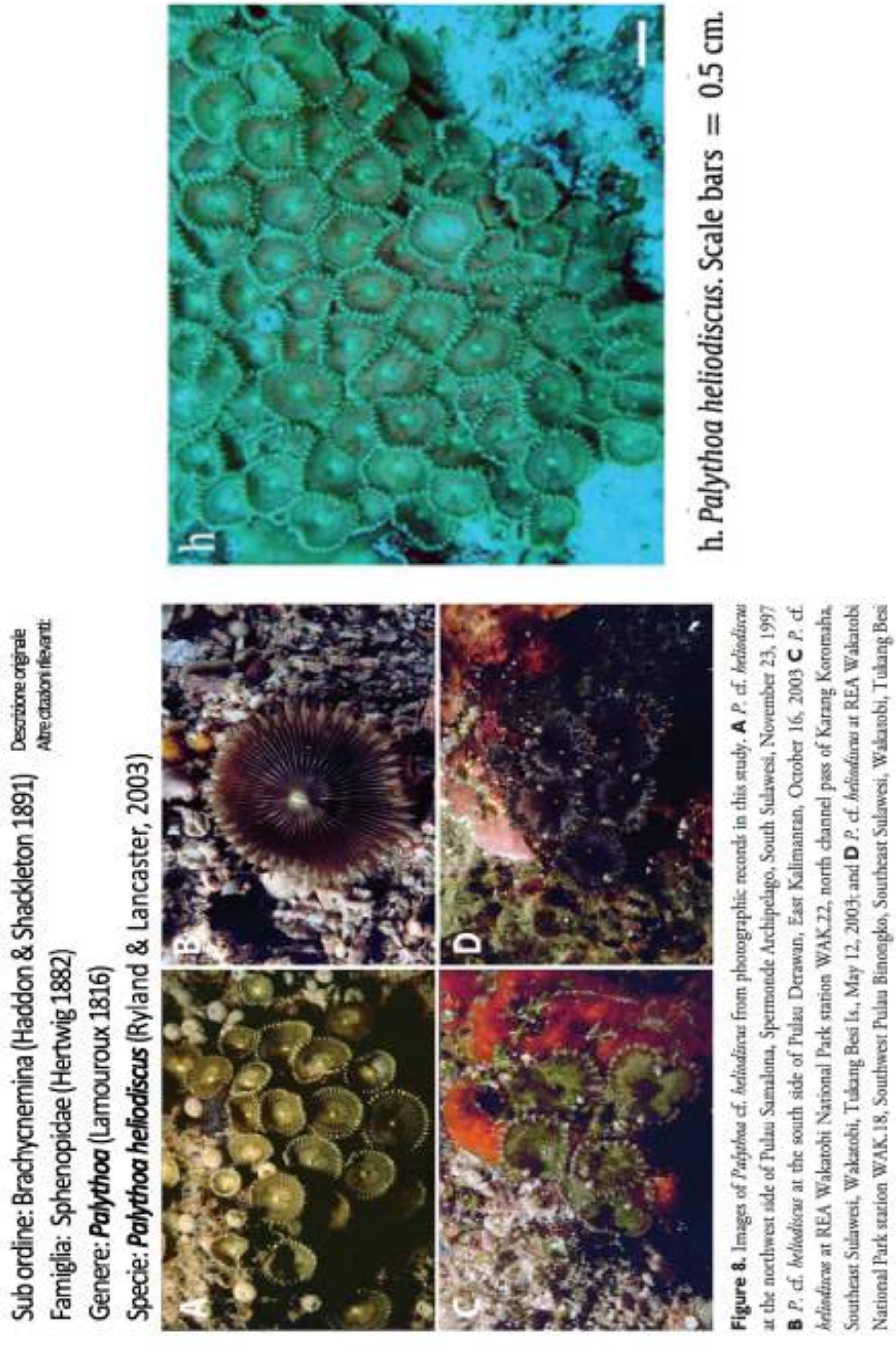


Figure 21: extract from the morphological catalogue (from: Chapter 7: Appendix) relating to species *Palythoa heliodiscus*.

- **Species 3: *Palythoa* cf. *grandis* (Verrill, 1900) (Table 8)**

We analyse the collected samples labelled as: ZOAMAL6_24, ZOAMAL10_24; ZOAMAL16_24 and ZOAMAL22_24 (Table 8 C).

ZOAMAL6_24, ZOAMAL10_24 and ZOAMAL16_24 were sampled on May 13, 2024, at Fulidhoo beyru 3°41.010' N 73°24.966' E (Felidhoo) at depths of 20 m (on the sub-vertical reef wall), 30 m (on a vertical reef wall), and on the reef flat (around 5-6 m on the sub-horizontal reef). ZOAMAL22_24 was sampled on May 16, 2024, at Rakedhoo Oceanic Reef (3°18.702' N 73°27.931' E) (Felidhoo) at a depth of 5-6 m on the reef flat.

Diagnosis: ZOAMAL10_24 and ZOAMAL16_24 appear as single, non-colonial polyps/specimens Table 8 B); ZOAMAL6_24 and ZOAMAL22_24, on the other hand, are two tightly attached polyps (Table 8 A). Live polyps are very cryptic, with oral disc colorations ranging from light brown (when the polyp is closed) to a darker ochre-brown to a greenish-yellowish (when the polyp has its oral disc opened/expanded). These samples also contain two types of tentacles, ranging in colour from light brown to dark ochre-brown in the live state (sometimes the colours of the two types are the same, other times they are different). When fixed, the polyps, however, show a more uniform colour, paler to a yellow hue.
The diameter of the oral disc of the polyps ranges from 0.2 cm to 1.2 cm in the when alive, and from 0.15 cm to 0.7 cm in the fixed state. The height of individual polyps ranges from 0.5 cm to 0.6 cm in when alive; while when fixed, they range from 0.35 cm to 0.5 cm.
The column of the fixed polyps ranges from 0.1 cm to 0.26 cm (the individual live column was not measured as the polyps were deeply embedded in the carbonate rock) and is extremely rough and heavily concretioned in all samples (Table 8 E). The oral disc is pseudo-oval in shape, with a plump perimeter, lighter in colour, and abundant sand grains (Table 8 D).
The tentacles of the various live polyps appear retractable, finger-like (when extended), and arranged in two marginal rows of 30-60 tentacles (an average of 30 tentacles per row/type). The tentacles in the two rows appear to be of different types: the tentacles defined as "thick" are located further out on the oral disc, range in length from 0.05 cm to 0.06 cm, and average 0.1 cm thick. Immediately behind a thick tentacle is a tentacle of the second type, designated as "thin," which is slightly shorter and narrower than the other type of tentacles (albeit only slightly).
Ecologically, these specimens exhibit both colonial and solitary habitats and were found on the reef, always on rock, but in various microhabitats, all characterized by moderate sun light (small crevices,

cracks, etc.). ZOAMAL10_24 was collected among a lot of sand and some erect green algae; ZOAMAL22_24 was instead located on the reef among a lot of turf.

Considering the morphological and ecological details (Figure 22), it was concluded that these specimens belong to *Palythoa* cf. *grandis* (Verrill, 1900); without further analysis (cnidome and genetics), it is impossible to be completely certain, therefore the term "cf." is reported.

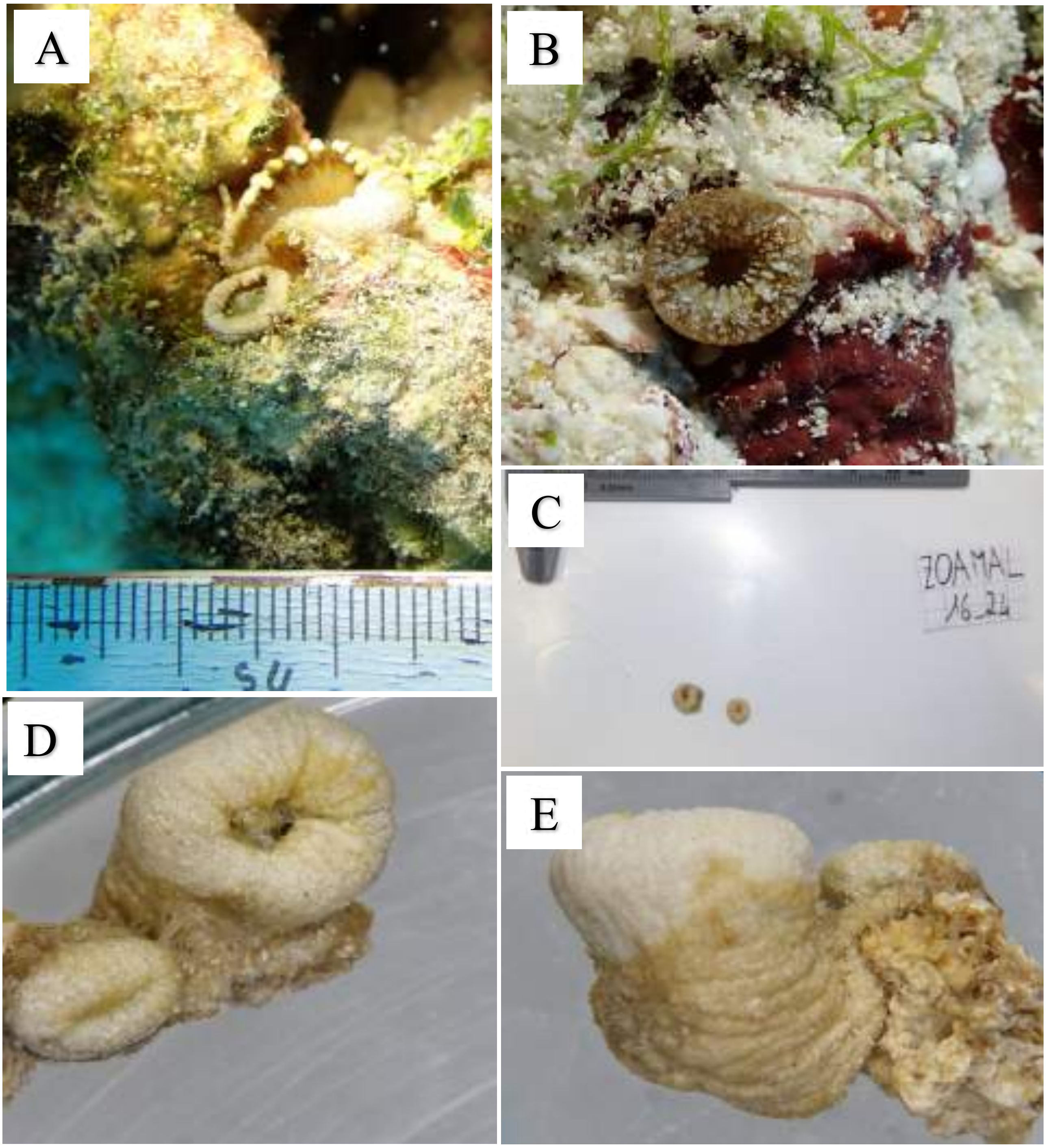


Table 8: A: colony composed by two attached polyps; B: non-colonial single polyp; C: example of the samples collected; D: plump perimeter of the oral disc; E: external look of the sample, the concretioned external body here is very noticeable.

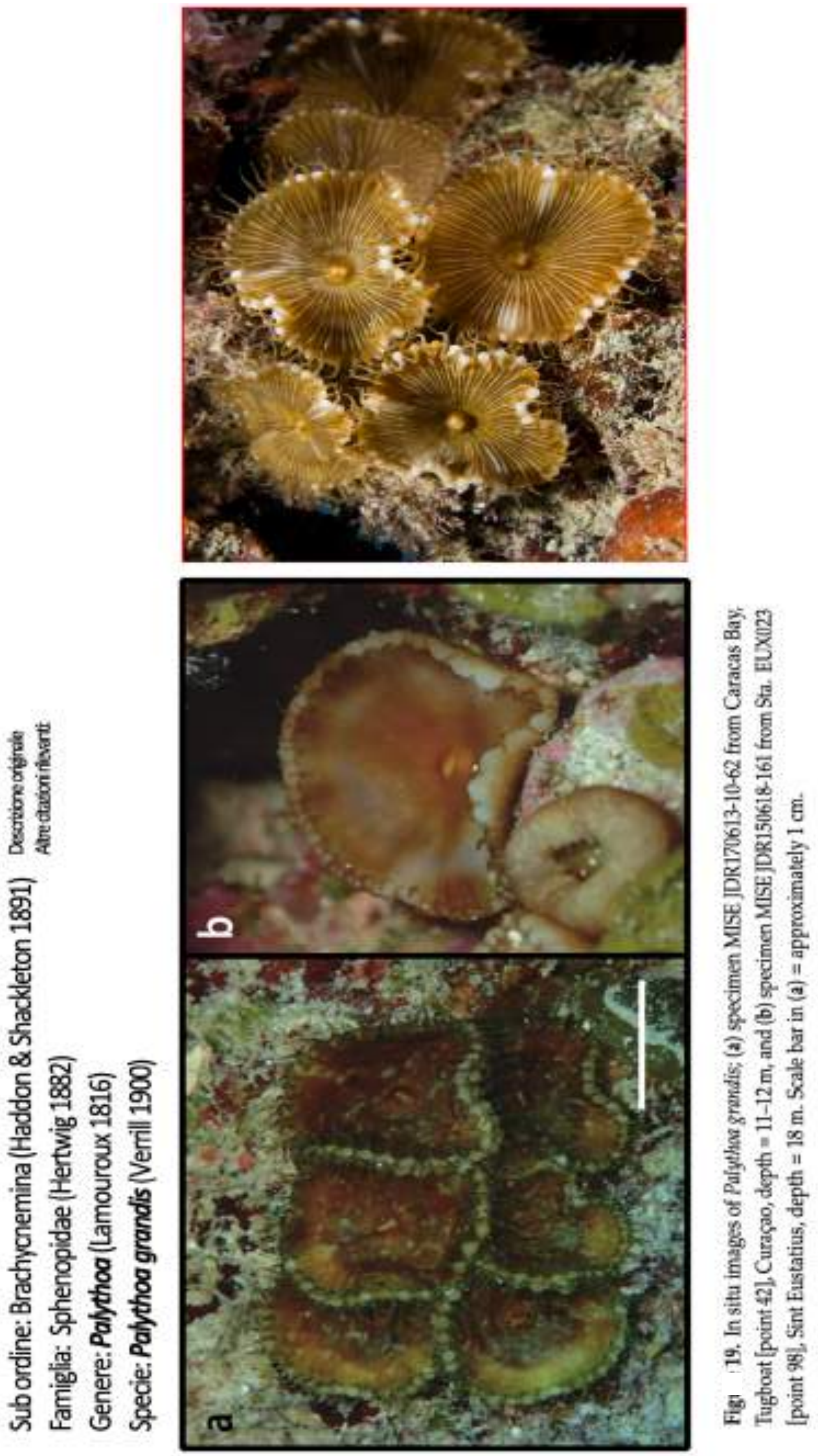


Figure 22: extract from the morphological catalogue (from: Chapter 7: Appendix) to species *Palythoa grandis*.

- **Species 4: *Zoanthus* cf. *coppingeri* (Haddon & Shackleton, 1891) (Table 9)**

We analyse the collected specimens labelled as: ZOAMAL11_24, ZOAMAL12_24, and ZOAMAL25_24 (Table 9 C and 9 D).

ZOAMAL11_24 (3 specimens), ZOAMAL12_24 (1 specimen), and ZOAMAL25_24 (6 specimens) were sampled on May 13, 2024, at Fulidhoo beyru, 3°41.010' N 73°24.966' E (Felidhoo), respectively, at a depth of: 30 m (on the sub-vertical reef wall) and on the reef flat (around 5-6 m on the sub-horizontal reef).
ZOAMAL25_24 (6 specimens) was sampled on May 15, 2024, at Rakedhoo Inside Reef (3°19.057' N 73°28.151' E) (Felidhoo) at a depth of 30 m on a sub-horizontal reef wall.

Diagnosis: all specimens appear to be a colony of individuals joined by collenchyma; the colonies from which the specimens originate change a lot in size (from a dozen polyps to colonies of more than 90-100 polyps) and their shape and size are difficult to identify (Table 9 A), as the polyps themselves retract extremely easily and the collenchyma is either under the sand or in the carbonate rock (therefore, the precise perimeter of the colony is not visible) (Table 9 B).
Polyps in live colonies appear like a garden of flowers (like *Palythoa* cf. *Heliodiscus*, but deeper into the substrate, with smaller polyps and generally present in more sciophilous environments). The outer wall of the oral disc in live specimens ranges from white-grey to brownish-brown, the two rows/types of marginal tentacles present take on the same coloration as this portion of the oral disc (in some cases the coloration is the same but slightly lighter-transparent). The inside of the oral disc in live specimens, however, appears brownish-brown (purple in some cases), with a ring of varying colours (from orange to green to black, with very bright hues) surrounding the mouth cone (generally light green) at 0.1 cm. When fixed, the polyps instead display a more uniform colour, lighter to a brownish-cream hue; the mouth is whitish in fixed specimens and the ring surrounding it is pink (Table 8 E and 9 F)..
The polyps are separated from one another (Table 9 G) and have an oral disc diameter ranging from 0.3 cm to 1.2 cm when alive and between 0.05 cm and 0.55 cm when attached. The height of individual polyps ranges from 0.1 cm to 0.26 cm when attached (the height of the individual in vivo was not measured due to the extreme depth of the organisms in the substrate).
The fixed polyp column ranges from 0.08 cm to 0.1 cm (the individual live column was not measured due to the retractability of the polyps) and is moderately wrinkled and concretioned in all specimens. The oral disc is oval in shape in all specimens.

The tentacles of the various live polyps appear retractable and arranged in two marginal rows, one facing outward from the oral disc and the other facing inward (alternating: 1 inside, 1 outside). The number of tentacles ranges from 50-60 (25-30 tentacles per row) and the dimensions range from 0.05 cm to 0.1 cm.

From an ecological perspective, these specimens all exhibit a colonial habitus; ZOAMAL11_24 and ZOAMAL25_24 were collected on encrusting corallines, while ZOAMAL12_24 grew on carbonate rock; ZOAMAL25_24 was also close to large erect sponges.

Considering the morphological and ecological details (Figure 23), it was concluded that these specimens belong to *Zoanthus* cf. *coppingeri* (Haddon & Shackleton, 1891). Without further analysis (cnidome and genetics), it is impossible to be completely certain which species they are, therefore the term "cf." is used.

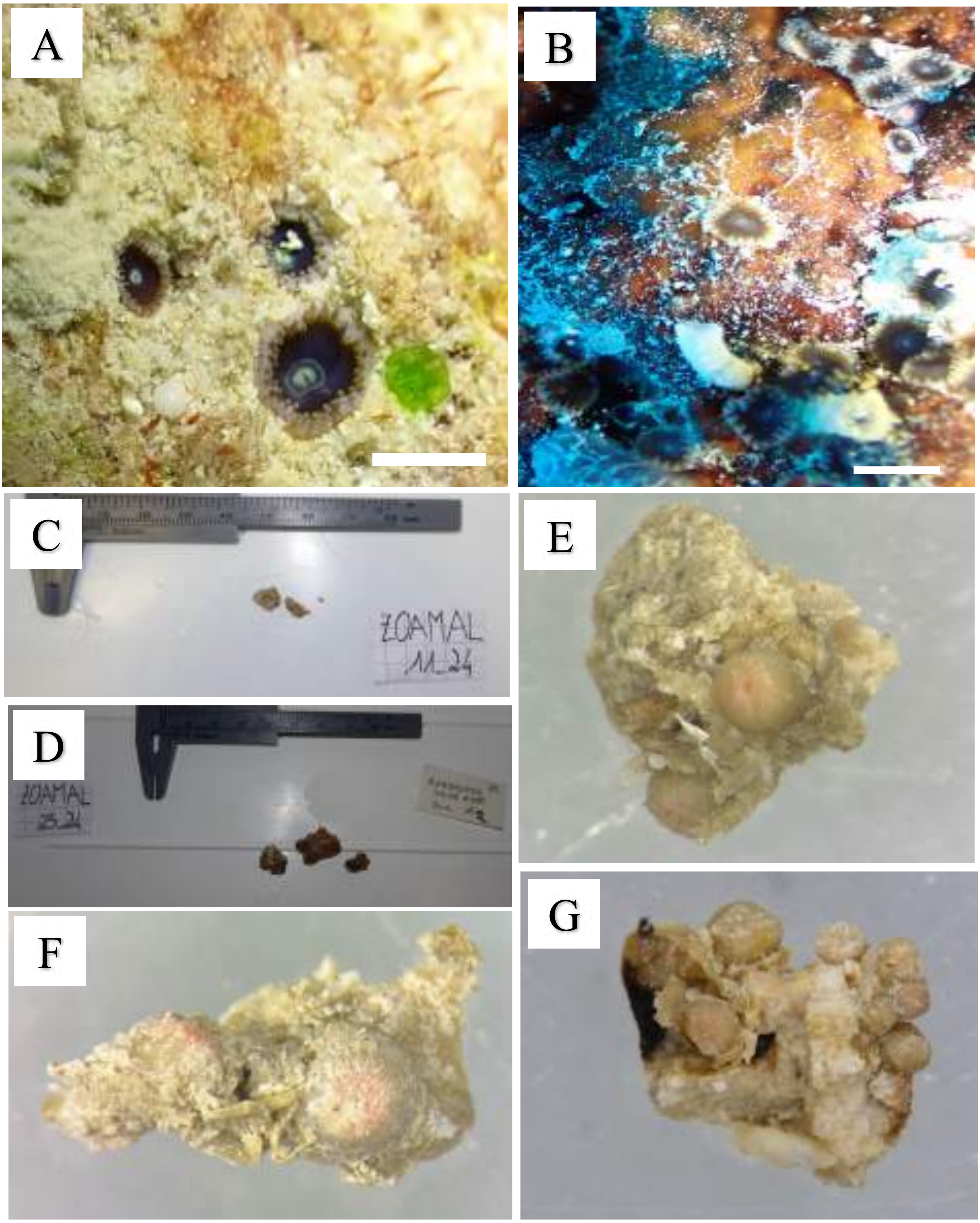


Table 9: in the photo A is noticeable how some specimens can grow inside the carbonate rock; in the photo B is possible to see a colour variation of the species (always with the collenchyma under the carbonate rock); C and D are examples of the collected samples; E and F show the ring surrounding the mouth, that is pink in colour; G is possible to see the collenchyma that connects all the polyps of the colony (all scale bar 0,6 cm).

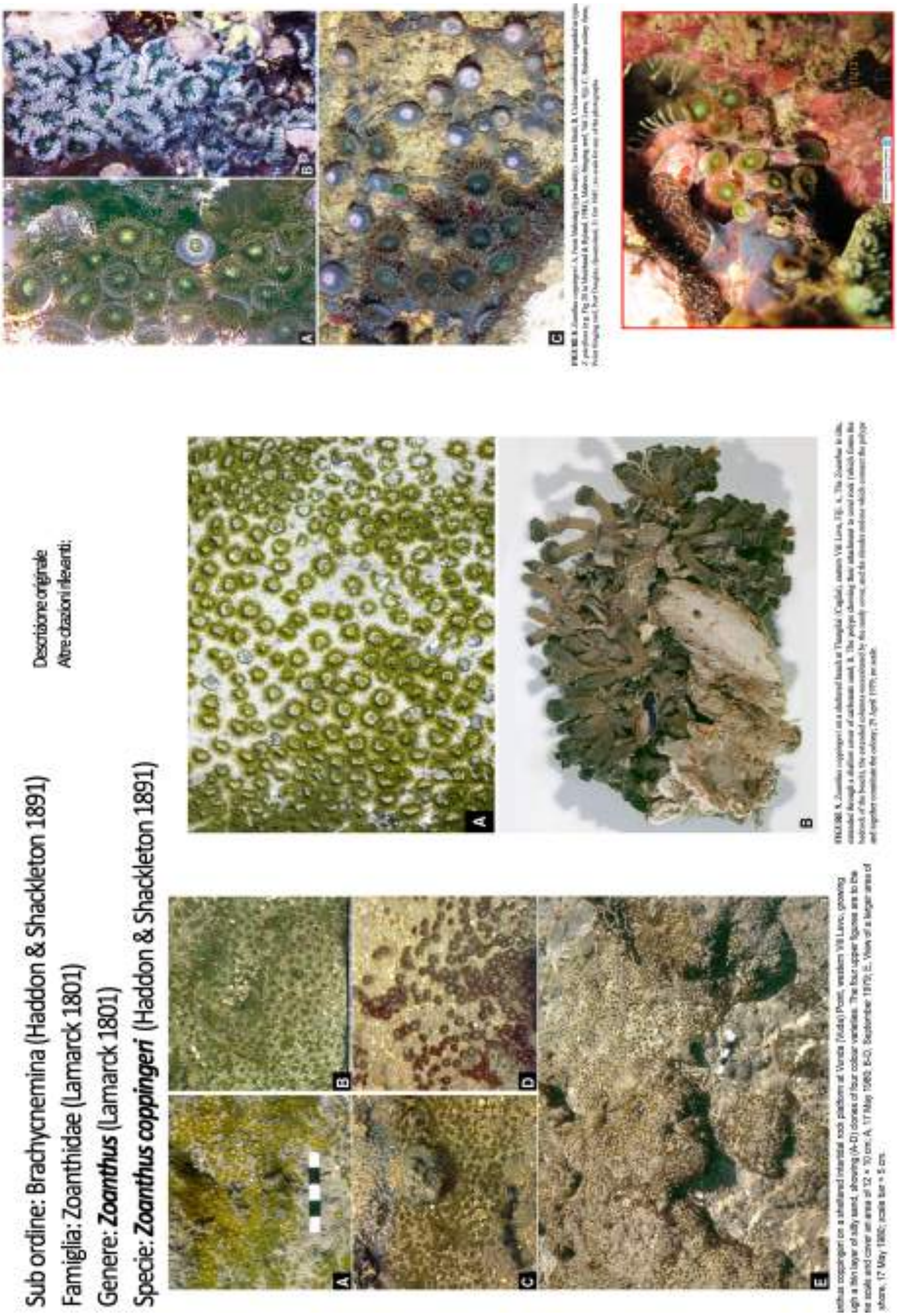


Figure 23: extract from the morphological catalogue (from: Chapter 7: Appendix) relating to species *Zoanthus coppingeri*.

- **Species 5: *Antipathozoanthus* cf. *cavernus* (Kise, Fujii, Masucci, Biondi & Reimer, 2017) (Table 10)**

We analyse the collected specimens labelled as: ZOAMAL14_24 and ZOAMAL18_24 (Table 10 D and 10 E).

Both of these two specimens consist in several antipatharians branches, colonized on various degrees by these colonial zoantharians (Table 10 A and 10 B). Both specimens were collected on May 14, 2024, at Fotteyo kandu (3°29.174' N 73°41.550 E) (Felidhoo), more precisely from a cave entrance at a depth of 34–34.4 m and were found on 50–60% of the branches of two different antipatharians of the genus *Myripathes* (family Myripathidae).

Diagnosis: all specimens appear like a colony of individuals joined by highly developed collenchyma surrounding the branches of the antipatharian host (Table 10 C).
The outer wall of the oral disc is orange/pink or yellow in colour with various hues when alive; the other external and internal body portions are difficult to observe when alive due to the polyps' extreme sensitivity (even from meters away, they feel the presence of operators and closed), therefore the internal colour of the oral disc or tentacles when alive is unknown. However, when fixed, the marginal tentacles appear to be the same colour as the polyps, displaying a uniform ochre-cream colour (Table 10 G and 10 H). The oral cone could not be observed (neither when alive or when fixed).
The polyps' oral disc diameter ranges from 0.2 cm to 0.3 cm in vivo and from 0.15 cm to 0.2 cm in fixed condition. The height of individual polyps ranges from 0.2 cm to 0.35 cm in vivo; when fixed, however, the height ranges from 0.1 cm to 0.2 cm.
The column of fixed polyps ranges from 0.1 cm to 0.25 cm (the individual column was not measured in live conditions due to the polyps' retractability).
All polyps in all specimens are heavily concretioned on all external body portions (Table 10 F). The oral disc is oval in shape in all specimens.
The tentacles of the various polyps, when attached, appear retractable, ranging from 20 to 25 in number and measuring from 0.05 cm to 0.1 cm.
From an ecological perspective, these specimens all have a colonial habit and as previously mentioned, live in obligate symbiotic associations with antipatharians of the genus *Myripathes*.
Considering both morphological and ecological details (Figure 24), it was concluded that these specimens belong to *Antipathozoanthus* cf. *cavernus* (Kise, Fujii, Masucci, Biondi & Reimer, 2017). Without further analysis (cnidome and genetic), it is impossible to be completely certain of the species, therefore the term "cf." is reported.

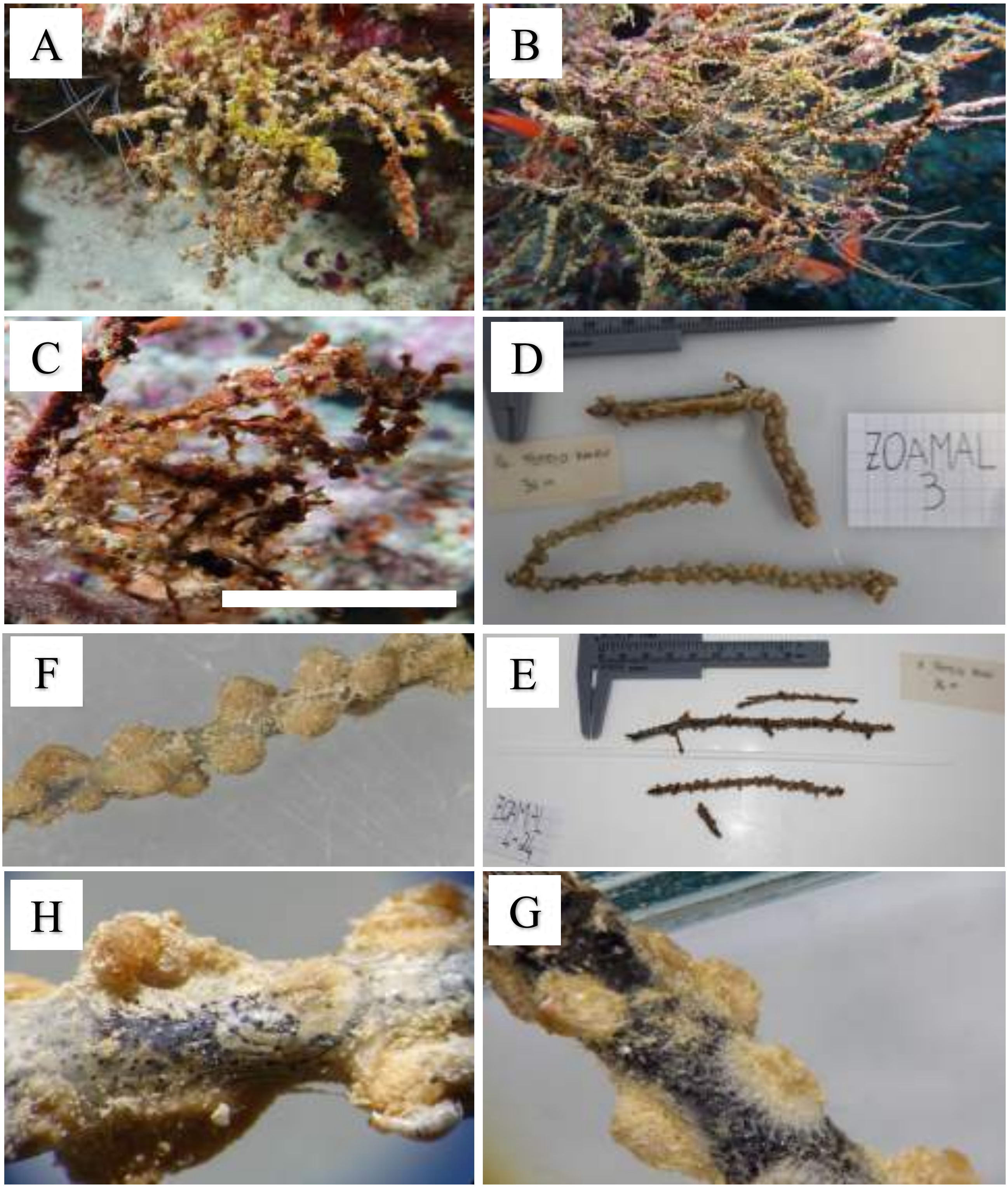


Table 10: photos A and B show how this zoantharian can colonize the antipatharians hosts; C: colony of individuals joined by highly developed collenchyma surrounding the branches of the antipatharian host; photos D and E are the samples collected on two differents antipatharians hosts; F: heavily concretioned external body; photos G and H show the external colour of the colony and the different colour of the antipatharian host (completely balck) (scale bar C is around 4 cm).

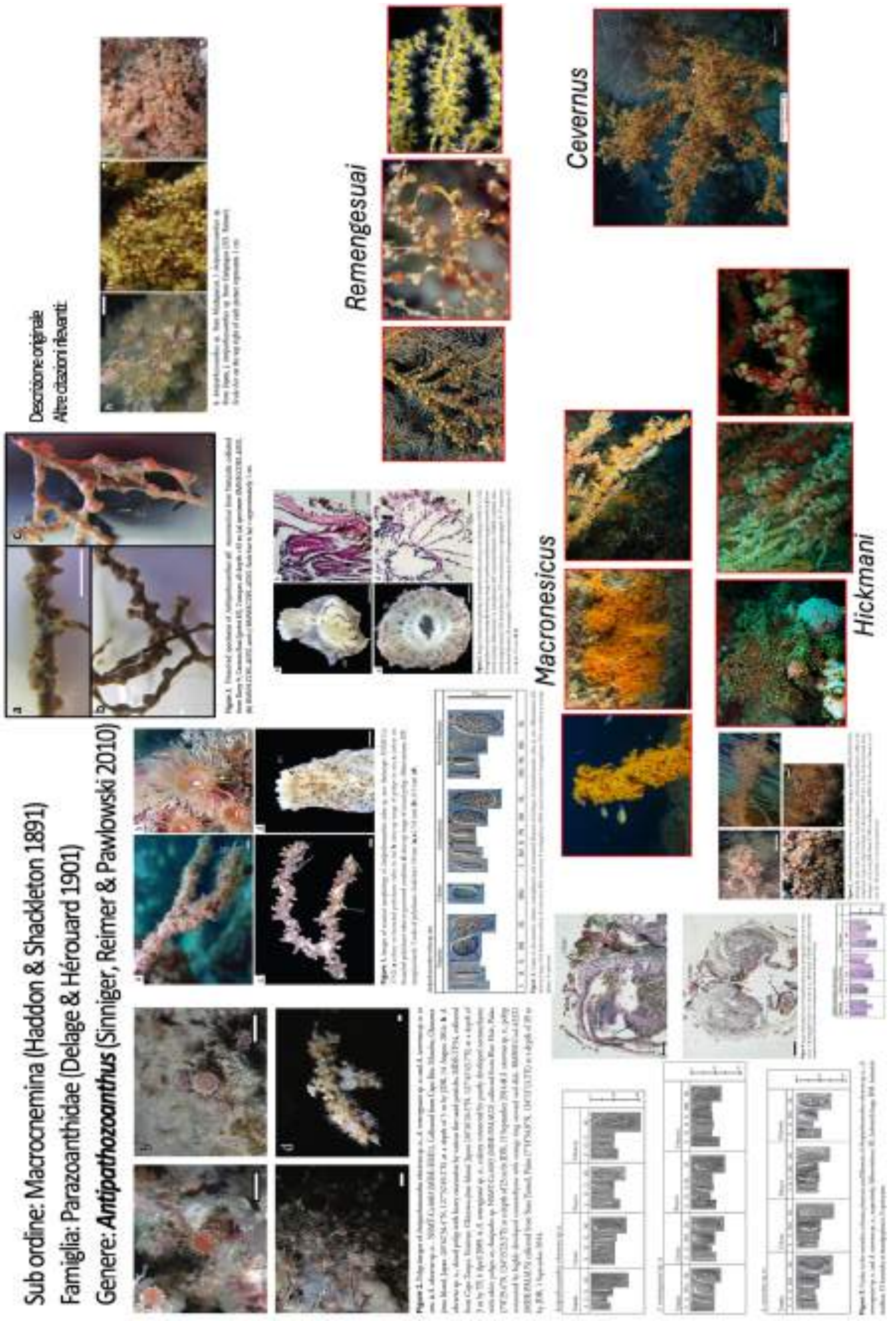


Figure 24: extract from the morphological catalogue (from: Chapter 7: Appendix) relating to genus *Antipathozoanthus*.

4.2 Analysis of photo-squares (distributions and abundances)

The Indicator Species Analysis (ISA) was used to identify species significantly associated with specific environmental categories (depth, atoll, site, reef type), combining frequency and relative abundance. The Ind. Val value ranges from 0 to 1 and indicates the strength of the association; p-values indicate the statistical significance of the association (Table 11).

Category		Species	Ind. Val	p-value
Depth	20 + 30 m	*Palythoa cf. Heliodiscus*	0.7010	< 0.001
Depth	0 + 10 + 20 m	*Palythoa caesia / tuberculosa* complex	0.5660	0.0230
Atoll	South Malé	*Amplexidiscus fenestrafer*	0.2240	0.0490
Site	Fulidhoo beyru	*Palythoa* cf. *grandis*	0.4230	0.0020
Site	Villivaru kuda giri	*Amplexidiscus fenestrafer*	0.3870	0.0170
Sites	Foththeyo beyru + Fulidhoo beyru + Miyaru faru + Rakeedhoo oceanic reef	*Palythoa caesia / tuberculosa* complex	0.6970	< 0.001
Sites		Palythoa cf. heliodiscus	0.6960	< 0.001
Type	Reef esterno/oceanico	*Palythoa caesia / tuberculosa* complex	0.6970	< 0.001
Type		*Palythoa* cf. *heliodiscus*	0.6960	< 0.001

Table 11: value of Ind. Val and p-value for each of the following categories: depth (20 + 30 m or 0 + 10 + 20 m), atoll (South Malé or Felidhoo), site/sites (Fulidhoo beyru or Villivaru kuda giri or a complex of sites) and type (reef type: lagoon or oceanic). This has been done for each of the following species: *Palythoa* cf. *heliodiscus*; *Palythoa caesia* / *tuberculosa* complex; *Amplexidiscus fenestrafer* and *Palythoa* cf. *grandis*.

The analyses performed showed that the species *Palythoa* cf. *heliodiscus* was significantly associated with depths of 20 and 30 m, with an indication value IndVal = 0.7010 and $p < 0.001$.
Conversely, the *Palythoa caesia* / *tuberculosa* complex was significantly associated with depths of 0, 10, and 20 m, with IndVal = 0.5660 and $p = 0.0230$.
The species *Amplexidiscus fenestrafer* was significantly associated with the South Malé Atoll, with an IndVal value = 0.2240 and $p = 0.0490$, and with the Villivaru Kuda Giri site, with an IndVal value = 0.3870 and $p = 0.0170$.
The species *Palythoa* cf. *grandis* was significantly associated with the Fulidhoo Beyru site, with IndVal = 0.4230 and $p = 0.0020$.
A different pattern emerged for *Palythoa caesia* / *tuberculosa* complex and *Palythoa* cf. *heliodiscus*, which were significantly associated with a group of sites consisting of: Foththeyo Beyru, Fulidhoo Beyru, Miyaru Faru, and Rakheedhoo Oceanic Reef. Very high indication values were recorded for

these associations (IndVal = 0.6970 for *Palythoa caesia* / *tuberculosa* complex; IndVal = 0.6960 for *Palythoa* cf. *heliodiscus*; $p < 0.001$ in both cases).
Regarding reef type, the ISA highlighted a clear association between some species and external/ocean reefs; In particular, the species *Palythoa caesia* / *tuberculosa* complex and the species *Palythoa* cf. *heliodiscus* were significantly associated with external reefs, with very high indication values (IndVal = 0.6970 and 0.6960, respectively; $p < 0.001$).

An OMI (Outlier Mean Index) analysis, shown in (Table 12), was also performed to reconstruct the taxa's ecological preferences/niches based on their abundance relative to the environmental categories measured in the photosquares (Figures 25 A and 25 B); the key parameters were marginality (OMI), tolerance (Tol), and residual tolerance (Rtol). This multivariate analysis was applied to the entire database (N = 160 objects) and transformed the initial data using the Hellinger transformation. In this study, three species/taxa were found to be statistically significant: *Palythoa* cf. *heliodiscus*, *Palythoa caesia* / *tuberculosa*, and *Zoanthus coppingeri* (highlighted in yellow in Table 11).

Species	**Inertia**	**% OMI**	**% Tol**	**% Rtol**	**% omi**	**% tol**	**% rtol**
Amplexidiscus fenestrafer	5.15	2.95	0.02	2.19	57.20	0.40	42.40
Rhodactis indosinensis	4.65	4.65	0.00	0.00	100.00	0.00	0.00
Palythoa cf. *heliodiscus*	12.84	1.68	0.62	10.54	13.10	4.80	82.10
Palythoa caesia or *tuberculosa* complex	13.69	0.94	1.23	11.53	6.80	9.00	84.20
Zoanthus coppingeri	26.87	3.57	1.99	21.31	13.30	7.40	79.30
Palythoa cf. *grandis*	7.88	1.94	0.63	5.31	24.70	8.00	67.40

Specie	**% Obs**	**% Std. Obs**	***p*-value**
Amplexidiscus fenestrafer	2.95	-0.73	0.8120
Rhodactis indosinensis	4.65	-0.65	0.9090
Palythoa cf. *heliodiscus*	1.68	11.89	0.0010
Palythoa caesia / *tuberculosa* complex	3.57	3.59	0.0010
Zoanthus cf. *coppingeri*	1.94	-0.72	0.0040
Palythoa cf. *grandis*	2.62	-0.70	0.8630

Table 12: all these two tables show the value of marginality (OMI), tolerance (Tol), and residual tolerance (Rtol) used in the OMI index; these were calculated for all the following species: *Amplexidiscus fenestrafer*; *Rhodactis indosinensis*; *Palythoa* cf. *heliodiscus*; *Palythoa caesia* / *tuberculosa* complex; *Zoanthus* cf. *coppingeri* and *Palythoa* cf. *grandis* Highlighted in green are the significant values for the species *Palythoa* cf. *heliodiscus*, *Palythoa caesia* / *tuberculosa* complex and *Zoanthus* cf. *coppingeri*.

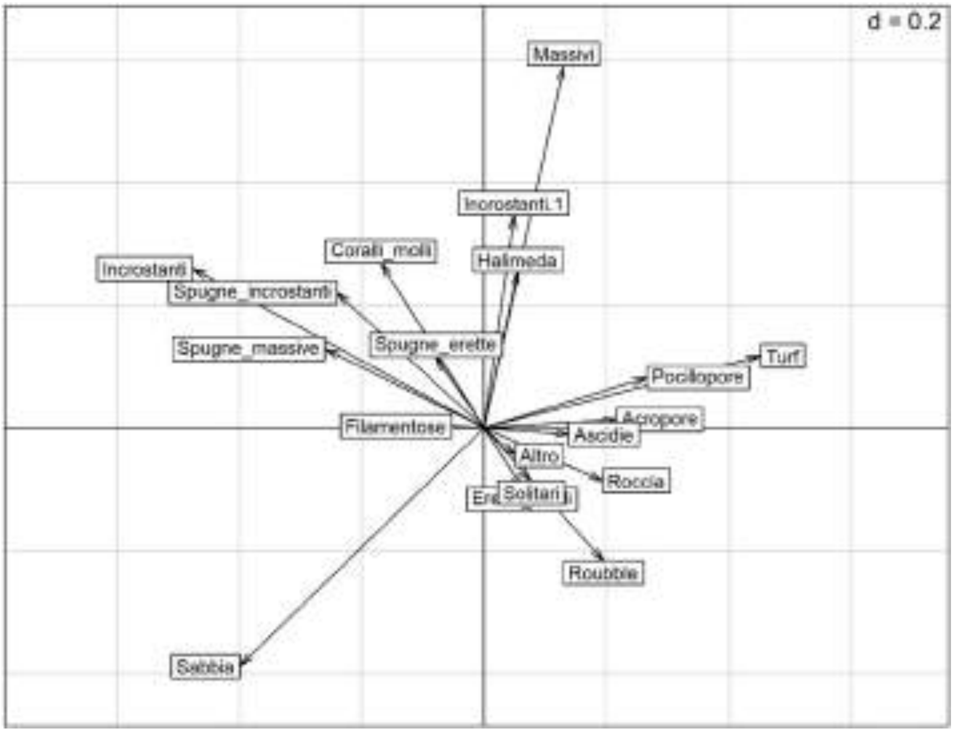


Figure 25 A: this figure shows the vectors of environmental variables: taxa placed in the same direction as an arrow are associated with relatively higher values of that coverage category.

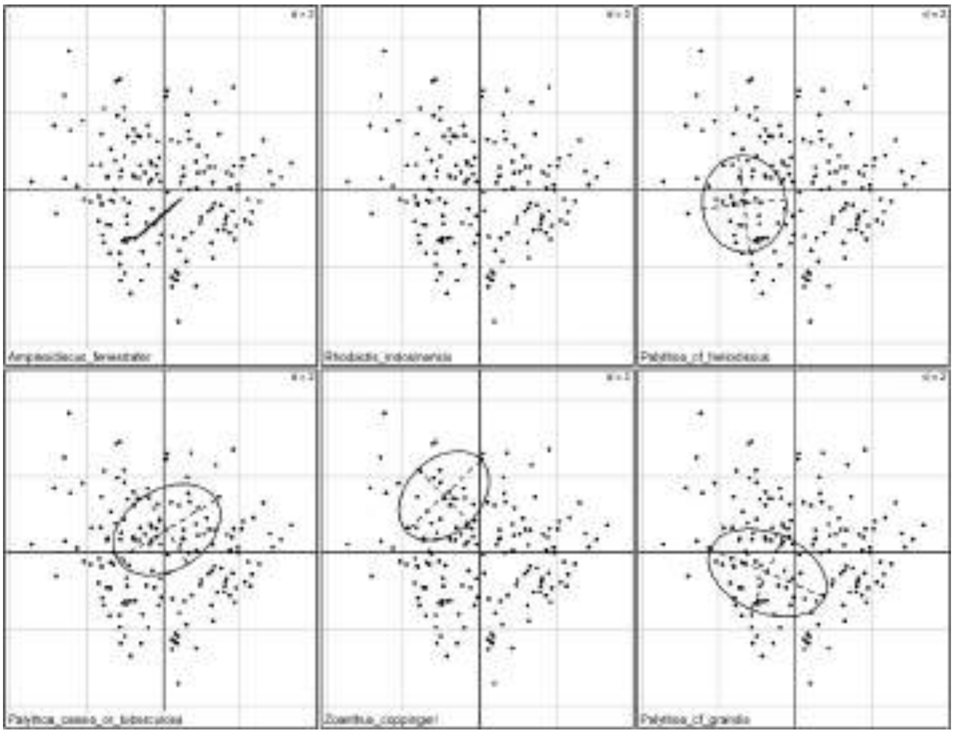


Figure 25 B: this figure shows, for each species, the centre of the niche and the elliptical dispersion around it: small ellipses indicate a narrower niche; large ellipses indicate greater variability in association. Ecological preferences can be read and interpreted depending on how the ellipse is oriented with respect to the environmental variables (arrows) illustrated in the first graph above (Figure 25 A).

Analysis shows that *Amplexidiscus fenestrafer* falls in the lower left quadrant, clearly oriented toward the "sand" category: the species shows a tendency to associate with environments with a higher sedimentary component. The ellipse is small, but the marginality test is not significant.
The species *Rhodactis indosinensis* is located practically at the origin of the axes, with no clear deviation toward any variable, thus indicating the absence of a strong association with a particular substrate cover category.
The species *Palythoa* cf. *heliodiscus* occupies the upper left quadrant, thus orienting itself toward green algae of the genus *Halimeda*, encrusting/massive corals, and, more generally, a live and consolidated benthic substrate, rather than toward sand or rubble. Its ellipse is relatively small and centered in a position distinct from the origin.
Palythoa caesia / *tuberculosa* complex is also located to the left of the origin, but lower than *Palythoa* cf. *heliodiscus*. This highlights a preference for environments less directly associated with massive corals/*Halimeda* and closer to a mixed component, with lower affinity for the substrates on the right side of the graph (builder corals). The species, however, maintains a distinct positioning from the origin, and for it too, the OMI shows significant marginality.
Zoanthus cf. *coppingeri* is located in the upper left quadrant, even higher and wider than *Palythoa* cf. *heliodiscus*. This places it closer to the arrows of massive corals, encrusting corals, and, in part, the green algae of the genus Halimeda. However, the ellipse appears wider, indicating that the species exhibits greater ecological variability in the dataset.
Palythoa cf. *grandis* falls in the lower right quadrant, toward the "rock" and "rubble" categories, and closer to the right-sided variable group than the other zoantharians considered. The ellipse is relatively small, but the marginality is not significant.

The same multivariate analyses were also applied to the entire database (N = 160 subjects) and the initial data were transformed using the Hellinger transformation; in this case, however, the following variables were grouped:

- All algae categories were added together (= algae).
- All corals categories were added together (= hard corals).
- All sponges' categories were added together (= sponges).
- All sediments categories were added together (= sediment).

From the statistical relevance point of view, nothing changes compared to the analysis performed above (Table 13 and Figure 26 A and 26 B); this second attempt give the same statistic results that were obtained in the previous test, meaning that all the same three species (*Palythoa* cf. *heliodiscus*, *Palythoa caesia* / *tuberculosa* complex and *Zoanthus* cf. *coppingeri*) were statistically significant also by grouping all the variables.

Specie	Inertia	% OMI	% Tol	% Rtol	% omi	% tol	% rtol
Amplexidiscus fenestrafer	3.20	1.93	0.00	1.26	60.40	0.20	39.50
Rhodactis indosinensis	4.11	4.11	0.00	0.00	100.00	0.00	0.00
Palythoa cf. heliodiscus	5.12	0.42	0.65	4.05	8.20	12.80	79.00
Palythoa caesia or tuberculosa	4.14	0.44	0.80	2.90	10.60	19.40	70.10
Zoanthus coppingeri	11.33	1.63	2.60	7.09	14.40	23.00	62.60
Palythoa cf. grandis	3.03	0.67	0.11	2.26	22.00	3.60	74.40

Specie	% Obs	% Std. Obs	*p*-value
Amplexidiscus fenestrafer	1.93	-0.08	0.3220
Rhodactis indosinensis	4.11	-0.19	0.4090
Palythoa cf. heliodiscus	0.42	4.47	0.0050
Palythoa caesia or tuberculosa	1.63	3.08	0.0080
Zoanthus coppingeri	0.67	-0.43	0.0170
Palythoa cf. grandis	1.53	-0.15	0.3960

Table 13: all these two tables show the value of marginality (OMI), tolerance (Tol), and residual tolerance (Rtol) used in the OMI index; these were calculated for all the following species: *Amplexidiscus fenestrafer*; *Rhodactis indosinensis*; *Palythoa* cf. *heliodiscus*; *Palythoa caesia / tuberculosa* complex; *Zoanthus* cf. *coppingeri* and *Palythoa* cf. *grandis* Highlighted in green are the significant values for the species *Palythoa* cf. *heliodiscus*, *Palythoa caesia / tuberculosa* complex and *Zoanthus* cf. *coppingeri*.

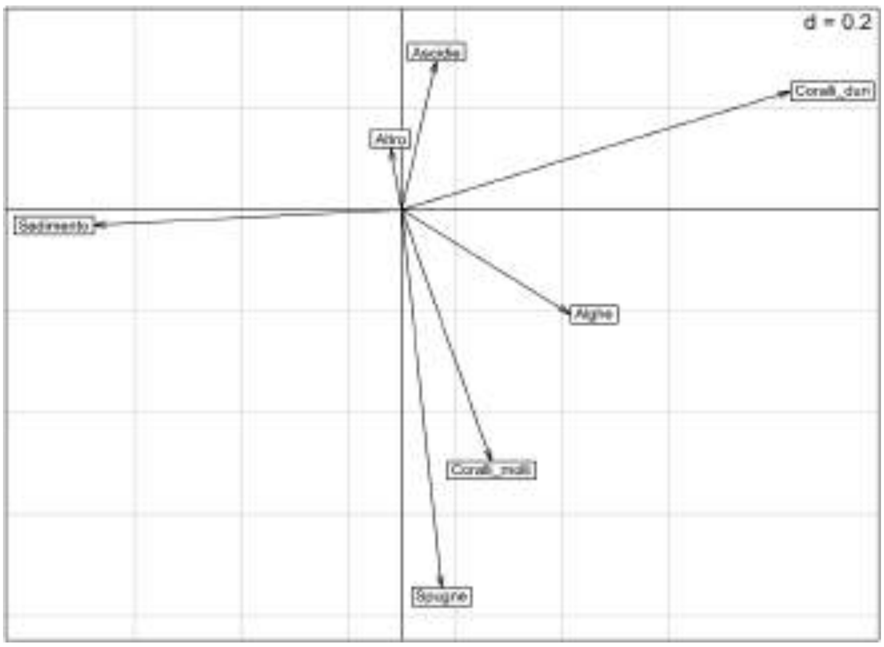


Figure 26 A: this figure shows the vectors of environmental variables: taxa placed in the same direction as an arrow are associated with relatively higher values of that coverage category.

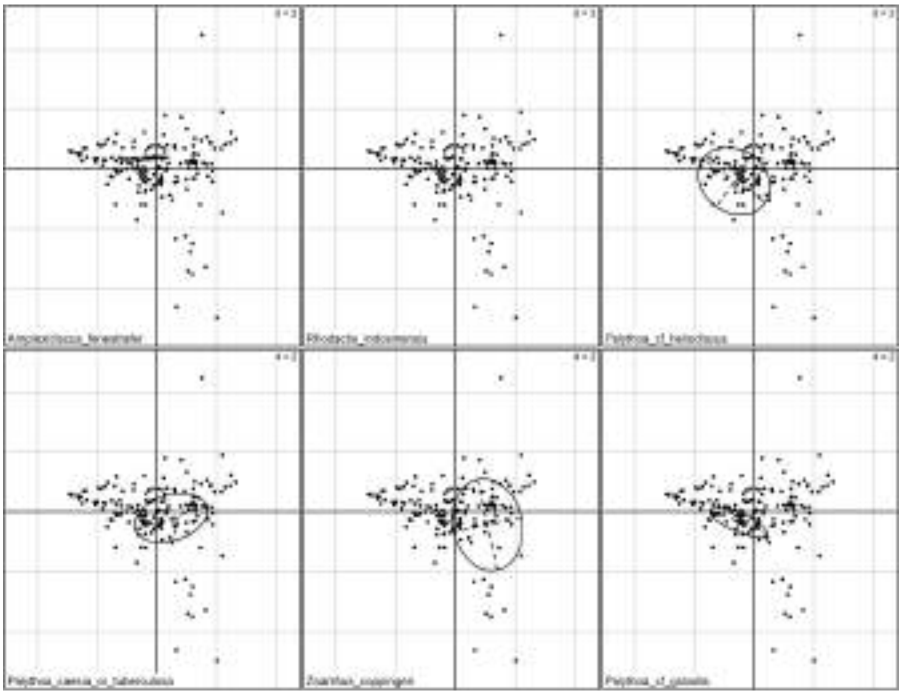


Figure 26 B: this figure shows, for each species, the centre of the niche and the elliptical dispersion around it: small ellipses indicate a narrower niche; large ellipses indicate greater variability in association. Ecological preferences can be read and interpreted depending on how the ellipse is oriented with respect to the environmental variables (arrows) illustrated in the first graph above (Figure 26 A).

5 DISCUSSION

Data on diversity, abundance, distribution and ecology of Corallimorpharia and Zoantharia are often hampered by the current difficulties in taxonomic identification at species, genera and even order levels. The present study identified a total of eight species, 3 belonging to the order Corallimorpharia and 5 to the order Zoantharia, in the central atolls of the Maldives, revealing a good level of diversity among these groups. The study confirmed the occurrence of 2 out of the 9 species previously reported in the Maldivian area, providing a precious and significant enlargement and documentation of the morphological traits of the taxa.

Numerous ecological studies have demonstrated that the distribution of benthic invertebrates is strongly influenced by microenvironmental factors such as depth, current speed, and substrate characteristics, which contribute to defining the ecological niche of the species (Bo et al., 2016). The present results confirm that Corallimorpharia and Zoantharia distribution is influenced by a combination of environmental factors,suggesting a non-random distribution of taxa in the analysed area. For instance, *Palythoa* cf. *heliodiscus* was significantly associated with depths of 20 m and 30, indicating a strong preference of the species for deeper environments compared to the other species considered. The analyses suggest that it has a fairly well-defined ecological niche; this is consistent with the OMI values, which show that this species is one of the few that show significant marginality compared to the average environmental conditions of the sampling. These aspects indicate that *P.* cf. *heliodiscus* not only occupies a peculiar sector of the environmental space but also does so in a specific geomorphological and bathymetric context. Opposite, *Palythoa caesia* / *tuberculosa* complex was found to be more characteristic of the superficial and intermediate bathymetric zones, showing a broader distribution along the bathymetric gradient, but still showing a statistically significant preference for shallower levels. This finding is also supported by the literature (Reimer et al., 2006), where these two species are described as more superficial and typical of more illuminated (and in some cases impacted) environments. Many tropical Anthozoa host symbiotic dinoflagellates belonging to the genus *Symbiodinium*, which contribute significantly to the host's energy metabolism through photosynthesis. The distribution of symbiotic organisms and their hosts is therefore strongly influenced by the availability of light and the environmental conditions associated with depth (Daugherty, 2014). Finally, *Palythoa* cf. *grandis* has a relatively localized spatial distribution compared to the other species. This ecological differentiation among species of the same genus suggests possible niche partitioning mechanisms that allow the coexistence of similar species within the same ecosystem (Chadwick-Furman et al., 2000).

Amplexidiscus fenestrafer is statistically more frequent in South Malé Atoll than in the other species included in the sample. This pattern suggests that its distribution could be influenced by local environmental conditions characteristic, such as the geomorphological configuration of the reef, environmental conditions, or anthropogenic impacts. The tendency of this species toward

environments with a higher sedimentary component is plausible but it finds no support in the scientific papers, so it should not be observed or considered a statistically demonstrated ecological preference. *Zoanthus* cf. *coppingeri* is not strictly confined to a single microhabitat. The species appears to have an associative tendency, but not strong enough to define it as a distinctly marginal species in the set of conditions examined.
Zoantharians tend to colonize hard substrates or pre-existing benthic organisms (such as sponges or building corals), while some species of corallimorpharians (such as *Rhodactis* cf. *howesii* and *A. fenestrafer*) can also settle on more unstable substrates (such as coral rubble) or seafloors rich in sediment. Several studies have demonstrated that some corallimorpharians possess physiological strategies that allow them to tolerate extreme environmental conditions better than scleractinian corals, such as high temperatures and high levels of irradiance (Kuguru et al., 2007). For example, the genus *Rhodactis* is able to temporarily survive even after bleaching episodes and subsequently re-establish symbiosis with zooxanthellae, demonstrating remarkable resilience to thermal stress (Kuguru et al., 2007; Pancrazi et al., 2025).
Finally, species distribution may also be influenced by other environmental factors not considered in this study, such as current dynamics, nutrient availability, biotic interactions with other organisms and direct anthropic impact (such as divers, who, through direct contact with multiple specimens of these organisms, may favour their spread, especially in sites already undergoing a dominance shift).

The observed distribution is consistent to the literature reports, where Corallimorpharia and Zoantharia are often described as opportunistic organisms capable of colonizing various available substrates and, in some cases, even rapidly forming large aggregations in tropical reef communities (Chadwick-Furman et al., 2000; Reimer, Davis, Fujii, Takuma, 2010). The presence of indicator species (such as the genus *Rhodactis*) in specific sites (such as Turtle giri or Dhega thila) may also reflect environmental conditions particularly favourable to the growth and reproduction of these species (Pancrazi et al., 2025). In many cases, corallimorpharians and zoantharians can rapidly colonize open spaces on the substrate thanks to asexual reproduction and clonal expansion (Cha, 2006). These characteristics suggest that Corallimorpharians and Zoantharians may play an important role in the ecological successional dynamics in the reefs, contributing to the recolonization of habitats after disturbance events, as confirmed by other studies in the Maldives (Morri et al. 2015; Pancrazi et al. 2025).

6 CONCLUSIONS

In conclusion, this study has contributed to a deeper understanding of the diversity, distribution, and ecology of Corallimorpharia and Zoantharia orders in the central atolls of the Maldives (an area that represents one of the main marine biodiversity hotspots in the Indo-Pacific), also providing new insights into the structure of the benthic communities associated with these Anthozoan groups. Although these organisms are generally less studied in reefs than the building-bearing scleractinian corals (particularly in the Maldives), the results highlight their importance as a component of benthic communities in tropical reefs and may play a significant role in the dynamics of Maldivian reefs.

It should be noted that in recent decades, tropical coral reefs have been subject to increasing disturbances related to climate change and anthropogenic pressures; the Maldives, in particular, represent one of the marine environments most vulnerable to the effects of rising sea surface temperatures, which have caused numerous bleaching events in recent decades (Montefalcone et al., 2018; 2020; Pancrazi et al., 2025). In this context, opportunistic organisms such as corallimorpharians and zoantharians could play an increasingly important role in the structure of benthic communities, especially in scenarios of coral reef degradation, where these organisms could increase in abundance, contributing to changes in the structure and functioning of reef ecosystems.
These findings highlight the importance of considering ecological variability and complexity, as well as environmental variability, in the management and conservation of Maldivian coral reefs, especially considering the increasing pressures from climate change and human activities.

This study also highlights the importance of including these organisms in broader studies on coral reef biodiversity and conservation.
Future studies could integrate molecular genetic approaches, studies of the entire cnidome, and zooxanthellae to determine with absolute certainty the species present (permanently removing the epithet "cf." for some of the species under study), their evolutionary relationships, and verify the presence of any cryptic species, a phenomenon already documented in several groups of Corallimorpharia and Zoantharia (Cha, 2006; Kise, Obuchi, & Reimer, 2021).

7 APPENDIX

The chapters/tools in this paragraph were fundamental in resolving the morphologic uncertainty encountered during the sampling phase and for the morpho-anatomic identification during the laboratory analysis.

7.1 Complete literature overview

A primary outcome of this research was a literature overview of the orders Corallimorpharia and Zoantharia (focused in the Indopacific area).Corallimorpharia and Zoantharia represent two lineages of "anemone-like" Hexacorallia, particularly relevant due to the absence of skeletal features and the complexity of their ecological and anatomical characteristics (coloniality, occasional symbiosis with dinoflagellates, epizoism, and substrate specialization) (Cha, 2006; Daly et al., 2007). Recent reviews agree on the fact that an integrated approach is needed for taxonomic analyses, as no single character among external morphology, sphincter, cnidome, or host ecology can be conclusive if analysed individually. To make an accurate and robust diagnosis, therefore, the different characteristics must be combined and, preferably, integrated with phylogenetic analyses (Cha, 2006).

7.1.1 Corallimorpharia (Carlgren, 1943)

Corallimorpharia are hexacorals with polyps and no calcareous skeleton. They can be solitary or colonial (habitus), often with a morphology intermediate between sea anemones and madrepore corals. The absence of a skeleton alone is not a sufficient character; from a phylogenetic and comparative standpoint, the order has been interpreted as related to the Scleractinia.

A key element in the diagnosis (in a phylogenetic sense) is the presence of multiple tentacles per endocoel and a partially "scleractinian-like" cnidome (Daly, Dunn & Cappola, 2003).

Molecular evidence and combined datasets support the monophyly of Corallimorpharia and a sister-taxon relationship with the Scleractinia, with direct consequences for the evolutionary interpretation of skeletal characterization (Daly, Dunn & Cappola, 2003).

1) Family Corallimorphidae (Hertwig, 1882)

This family primarily includes relatively columnar forms, frequently azooxanthellate and therefore potentially present beyond the photic zone. They have a solitary or colonial habitus and numerous nematocyst types in various body regions (therefore, the cnidome remains one of the diagnostic pillars of the group). It’s often noticeable a zooxanthellae absence’s tendency (a useful trait, but not absolute, characteristic for distinguishing them from many photophilous Discosomatidae); tentacles frequently are capitate or with acrospheres (present in several genera), often retractile (multiple tentacles may exist per endocoel); cnidome is with common/numerous nematocysts in the tentacles; holotrics, mastigophorous, and microbasics are often present (with useful variability at the generic and specific levels). Regarding internal anatomy, numerous mesenteries are noted; the presence/absence of incomplete mesenteries and the configuration of the directives are informative at the genus level. The family includes the genera: *Corynactis, Pseudocorynactis, Corallimorphus, Nectactis, Sideractis and Paracorynactis*.

I. Genus *Corynactis* (Allman, 1846)

This genus has a purely colonial habitus (Figure 27), as it is known to divide through asexual fission, with a tendency to form rather large aggregations. The tentacles are retractile, often bearing acrospheres; the presence of multiple tentacles emerging from the endocoel is noted, following with the order diagnosis (Cha, 2006). The cnidome contains spirocysts, holotrics, and microbasics mastigophores; this characteristic is used for precise species identification.

The presence of complete and incomplete mesenteries is noted, with the absence of directing mesenteries; the configuration of the mesenteries is one of the points emphasized in the revision to avoid confusion with related genera (Cha, 2006).

Figure 27: from the left: group of *Corynactis* sp.; mats of *Corynactis australis* covering the reef substrate; colour variation in a group of *Corynactis australis*.

II. Genus *Pseudocorynactis* (den Hartog, 1980)

They are solitary organisms and are generally larger than the *Corynactis* genus (Figure 28).

The tentacles are retractile, with multiple tentacles per endocoel; this, combined with the internal characteristics, supports their separation from *Corynactis*. Regarding the cnidome, we have long spirocysts, including: holotrichs; mastigophores and microbasics p present in normal and hoplotelic forms (a very useful detail since variations in the type of mastigophores and their distribution can be more informative than oral disc size alone).

The mesenteries are all complete, with two directive mesenteries also noted (Cha, 2006).

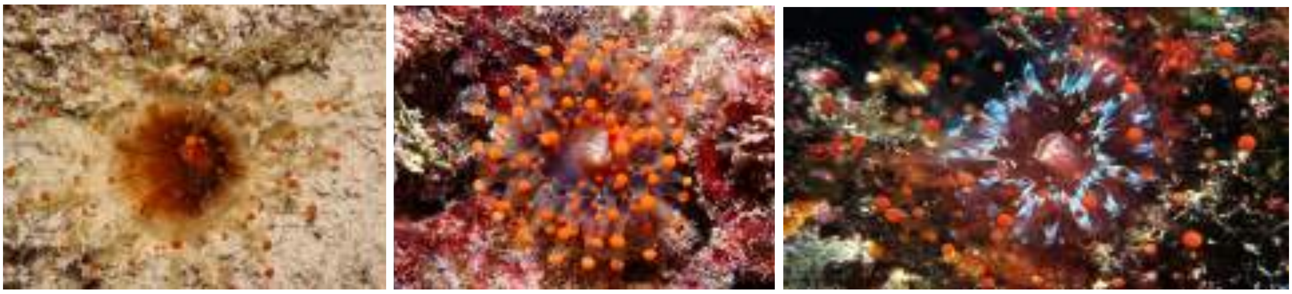


Figure 28: from the left: opened oral disc of *Pseudocorynactis caribbeorum*; contracted specimen of *Pseudocorynactis caribbeorum*; specimen of *Pseudocorynactis tuberculata*.

III. Genus *Paracorynactis* (Ocaña, den Hartog, Brito & Bos, 2009)

This genus has partially retractable tentacles, with three or four marginal radial rows (figure 29); there is also a differentiation between more developed tentacles and smaller ones; this tentacular architecture is one of the most immediate criteria for quickly distinguishing the genus.

Regarding cnidoma: the spirocysts are very large and present in the acrospheres; this condition constitutes a highly useful diagnostic feature (Ocaña, Brito & Bos, 2009).

Figure 29: from the left: different colour variation of different specimen of *Paracorynactis hoplites*.

2) Family Discosomatidae (Verrill, 1869)

The Discosomatidae family predominantly includes discoid growth forms; these corallimorpharians, often zooxanthellate, have a generally gregarious habitus. Spirocysts are rare or completely absent; the tentacles are often non-capitate and can be classified as discal (branched or papilliform) or marginal. Regarding internal anatomy, the mesenteries may be complete or incomplete, and the sphincter can be extremely variable. Regarding body shape, however, they generally have a very large oral disc and a reduced or barely visible column; in some genera, a bare area appears on the oral disc. They tend to grow attached to hard substrates. The cnidome shows spirocysts that are generally rare or completely absent from the tentacles (unlike Corallimorphidae). Furthermore, the mastigophores types and their distribution can separate morphologically similar genera.

The family includes the genera *Amplexidiscus, Discosoma, Rhodactis, Actinotryx, Metarhodactis*.

I. Genus *Amplexidiscus* (Dunn & Hamner, 1980)

Amplexidiscus (Figure 30) is represented by the only species *Amplexidiscus fenestrafer*, the largest corallimorpharian, reaching an oral disc diameter of up to approximately 40 cm. It is also recognizable by a combination of characteristics rare among discoidal corallimorpharians (Dunn & Hamner, 1980; Cha, 2006).

▪ Species *Amplexidiscus fenestrafer* (Dunn & Hamner, 1980)

Amplexidiscus fenestrafer (Figure 30) is the type species of the *Amplexidiscus* genus (Dunn & Hamner, 1980) and has been described as the largest corallimorpharian currently known; it is distinguished mainly by its tentacular structure and its feeding behaviour based on the enfolding of the oral disc (Dunn & Hamner, 1980). The diagnosis proposed in the original description highlights that *A. fenestrafer* is distinct from other corallimorpharians:

1. for its much larger size than any other solitary or gregarious corallimorphs known to date;
2. due to the presence of a tentacle free zone that separates the field of discal tentacles from the perioral/marginal region (observable only in adult and not juvenile individuals);
3. for a peculiar histological arrangement of the margin, with differences between the tentacular margin and the non-tentacular margin;
4. for a circular endodermal musculature in the upper column described as a "sphincter-like" thickening but without a true sphincter (Dunn & Hamner, 1980).

Living specimens display greenish-brown colorations attributed to the presence of zooxanthellae, while fixation produces chromatic lightening; the genus is included in the photophilous discoidal corallimorpharians typical of the superficial zone of coral reefs (Dunn & Hamner, 1980; Cha, 2006). Regarding the oral disc and column, the species is described as "immovably attached" to the hard substrate, with an irregular but roughly circular oral disc. The diameter of the expanded oral disc can reach approximately 45 cm, although it normally measures around 20–25 cm. The column can reach 5 cm in height and is smooth; its coloration varies depending on the density of zooxanthellae (Dunn & Hamner, 1980). The pedal disc is smaller than the oral disc, with an average diameter of approximately 18 cm and appears smooth; mesenteric attachments are noted, visible due to transparency (Dunn & Hamner, 1980). The tentacles are described as two types: simple, small, and numerous tentacles on the oral disc, and fewer but larger finger-like tentacles on the margin of the oral disc (the latter giving the margin a crenulated appearance). The tentacle-free zone separates the field of numerous discal tentacles from the marginal/perioral zone; under contractions, this distinction between marginal and discal tentacles may blur (Dunn & Hamner, 1980). The coloration may appear dark gray-green or brownish, tending to darken toward the margin of the oral disc; the coloration is probably attributed entirely to the presence of endodermal zooxanthellae (Dunn & Hamner, 1980). A very high mesentery number is reported on the order of 500 pairs in an adult individual, with thin mesenteries. The retractor muscles are described as very weak, and the mesenteries lack strong muscles (gonads have been observed in only one specimen in the literature) (Dunn & Hamner, 1980). Circular endodermal musculature is present in the upper column with a sphincter-like thickening, but overall, the absence of a true sphincter is reiterated (Dunn & Hamner, 1980). Overall, the cnidome includes: atrics, holotrichs, microbasics p-mastigophores (including hoplotelic forms), and spirocysts, with tissue-specific distribution (Dunn & Hamner, 1980). *A. fenestrafer* is considered a typical tropical reef species; it has been found primarily in shallow waters (maximum depth 30 m), often on rocks and near hard corals. Clusters of individuals interpreted as clones, derived asexually from a founder, have also been reported in the literature (Dunn & Hamner, 1980).

Figure 30: from the left: open oral disc of *Amplexidiscus fenestrafer* with the naked zone exposed and visible; half-closed specimens of *A. fenestrafer*; gregarious habitus shown by *A.fenestrafer*.

II. Genus *Discosoma* (Rüppell & Leuckart, 1828)

This genus is typically disc-shaped (Figure 31), often with very short tentacles on the disc (less than 1 mm), making it difficult to separate from other related genera. Cnidome contain: holotrichs; microbasics p mastigophores are present in various body regions but are absent from the mesenteries. The mesenteries can be complete or incomplete, and the sphincter is also present but of variable shape (Cha, 2006).

Figure 31: from the left: specimen of *Discosoma dawydoffi;* group of *Discosoma fungiforme*; specimens of *Discosoma* sp.

III. Genus *Rhodactis* (Milne Edwards & Haime, 1851)

Species of this genus are often gregarious. The tentacles are indicated as non-retractile (or poorly retractile), a useful feature to distinguish it from other genera with markedly retractile tentacles.
Individuals of the genus *Rhodactis* have a typically dish-shaped body, with a broad, flattened, and often wavy oral disc, adapted to adhesion to hard substrates in coral reefs (Figure 32). The oral disc is generally completely covered with tentacles, without a true tentacle-free zone (Cha, 2006).
The tentacles are often highly variable in shape (finger-shaped, lobed, etc.) and are distributed relatively uniformly across the oral disc; this characteristic contrasts with the more organized or differentiated distribution of tentacles observed in other discoid genera and represents a useful characteristic in comparative diagnosis (Cha, 2006). As in other Discosomatidae, the marginal musculature in *Rhodactis* is generally poorly developed and does not form a robust sphincter; this characteristic is consistent with its habitus and the limited retraction capacity of the oral disc compared to other corallimorpharians (more cylindrical and less discoidal) (Cha, 2006). The mesenteries are numerous and radially organized, with high numerical variability. The cnidome is composed of holotrichs, microbasics p-mastigophores, microbasics b-mastigophores, and spirocysts. Like other members of the family, this genus commonly hosts symbiotic zooxanthellae; this characteristic is consistent with its prevalent distribution on flat reefs, where these corallimorpharians can form dense aggregations and dominate disturbed benthic substrates (Cha, 2006).

Figure 32: from the left: specimen of *Rhodactis bryoides*; colour variation of *Rhodactis bryoides*; group of *Rhodactis inchoata*.

- ***Rhodactis indosinensiis* (Carlgren, 1943)**

Rhodactis indosinensis is a zooxanthellate corallimorpharian.
Its external diagnosis is based primarily on: the organization of the oral disc, the morphology and development of the discal and marginal tentacles and color and surface characteristics related to the mesenteric attachments (Figure 33). It has a very short column and margins that tend to expand, giving it a "resting" appearance on the substrate; the column is very thin; while the mesenteric attachments on the oral disc may be visible as radial lines (Oh et al., 2019).

The oral disc features irregular grooves or furrows radiating from the center toward the margin; the mesenteric attachments on the oral disc may be visible as radial lines extending from the perioral region to the margin of the disc (Oh et al., 2019). The mouth can be round or oval, often slightly elevated; in some cases, the mouth is brightly colored (Oh et al., 2019).
The discal tentacles are well developed and highly branched; when not fully everted, they can also appear as curly hairs or bumps; these tentacles are arranged in radial rows (Oh et al., 2019). The marginal tentacles, on the other hand, are thin, dense and often bulbous; they can visually connect to the radial lines of the disc associated with the mesenterial attachments (Oh et al., 2019).
The mesenteries are described as complete (Oh et al., 2019); acontia (mesenterial filaments rich in nematocysts) can protrude through the discal tentacles, a feature observed only in living individuals in situ (Oh et al., 2019).
Coloration is variable (from greenish to reddish-brown), with tentacle tips sometimes lighter or of a different color (like green), consistent with phenotypic plasticity and environmental conditions (Oh et al., 2019). The cnidome reported in the literature includes: atrichs, holotrichs, microbasics b-mastigophores, microbasics p-mastigophores, and spirocysts (Oh et al., 2019). The species is reported as typically tropical, primarily found in the Indo-Western Pacific and East Asia.

Figure 33: different photos of *Rhodactis indosinensis* with his branched discal tentacles.

- ***Rhodactis howesii* (Saville-Kent, 1893)**

The species has a: small to medium size, slightly and elevated oral disc. When contracted, it can assume an almost spheroidal shape. The structure of the tentacles is the most distinctive feature, as the discal tentacles can be simple or complex; they consist of a short, cylindrical central axis; the marginal tentacles are simple (generally 5 to 30 are present, depending on the size of the individual). The discal tentacles appear elongated and subcylindrical when expanded, while when contracted, they lean against the central axis and take a capitate or spheroidal appearance. These discal tentacles can be simple (single tentacle) or complex/compound (with a few bumps/protuberances along the axis of the main tentacle) but never branched (as in *R. indosinensis*). Another characteristic is that the tentacles around the mouth (generally 4/5) are all simple; this organization differs from the tentacle arrangement of *Rhodactis rhodostoma* (in which the simple tentacles are marginal, and the complex ones are perioral; here, however, the few simple tentacles are immediately perioral). Coloration can be quite variable; typically, we have brown polyps with sometimes the tips of the tentacles being bright green or in any case a very bright colour that differs from the rest of the tentacle. This species is famous for its capacity to create dense aggregations and for having strong competition skills that can lead to a drastic shift in the benthic community of the reef (Figure 34). The original description does not include analysis of the cnidome or details on the types of nematocysts, the number of mesenteries, the presence/absence of a sphincter, or the muscular structure. In the absence of this data, a thorough analysis would require molecular testing (using 16sRNA as a molecular marker). Recent studies in fact highlight the possibility that this species is simply a variant of *Rhodactis rhodostoma*.

Figure 34: different photos from different location in the atoll of Palmyra (USA, Northern Pacific Ocean), well known for its shift to a *Rhodactis howesii* / *rhodostoma* complex carpet.
From the left: carpet of *Rhodactis howesii* / *rhodostoma* complex close to a wreck; detail of some *Rhodactis howesii* / *rhodostoma* complex specimens; view of the reef covered in a carpet of *Rhodactis howesii* / *rhodostoma* complex.

- ***Rhodactis rhodostoma* (Hemprich & Ehrenberg in Ehrenberg, 1834)**

Rhodactis rhodostoma is typically disc-shaped, often gregarious, and associated with zooxanthellae; the column is generally smaller and hidden compared to the expanded oral disc, matching the habitus of the Discosomatidae (Figure 35). A key element in the is the presence of two tentacle categories: the discal tentacles are frequently papilliform or branched; often arranged in radial rows, with a higher density in the central area of the disc and a lower density towards the margin and perioral region (Cha, 2007), the marginal tentacles are finger-shaped and often reduced (in some cases, they may even be extremely reduced or completely absent) (Cha, 2007). The species also has numerous mesenteries, which may be complete and/or incomplete, often with an irregular arrangement. The overall musculature is very weak; the sphincter is also very weak or completely absent (the retractor muscles are weak) (Cha, 2007). The cnidome is dominated by holotrichs (some of large size, particularly in disc tentacles and mesenteric filaments) and by microbasics p and b mastigophores, with spirocysts reported as rare/absent (the absence/rarity may depend on the tissue sampled and the methodological approach) (Cha, 2007). The species is associated with tropical/subtropical environments in the Indo-Western Pacific, typically in shallow waters (a few meters to about 12 m in literature samples). (Cha, 2007).

They are historically known to form dense aggregations that dominate the substrate and frequently cover other sessile organisms (Langmead & Chadwick-Furman, 1999).

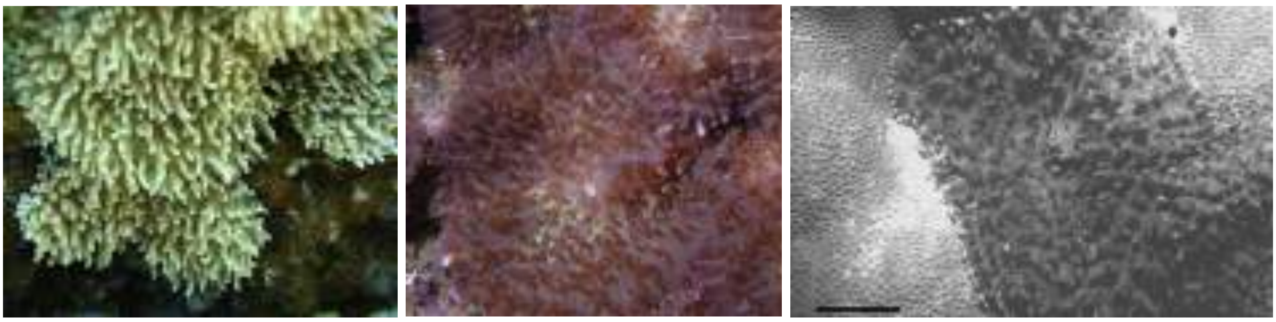


Figure 35: all available photos found in scientific papers about *Rhodactis rhodostoma* (the last photo scale bar is 2 cm).

IV. Genus *Metarhodactis* (Carlgren, 1943)

Genus separated from *Discosoma* and *Rhodactis* by cnidome characteristics (like the presence and type of nematocysts in the mesenteric filaments). The oral disc is generally quite large, with non-capitate tentacles and a relatively uniform distribution (Figure 36). The mesenteries may be complete or incomplete; a sphincter is present. The cnidome is composed of: microbasics and mastigophores in the mesenteries (Cha, 2006). This genus only has one species: *Metarhodactis boninensis* (Carlgren, 1943).

Figure 36: different photos of *Metarhodactis boninensis* (the only species of this genus); from the left: group of *Metarhodactis boninensis* with a crenulated oral disc perimeter; huge group of *Metarhodactis boninensis* specimens; detail on the retracted tentacles in a group of *Metarhodactis boninensis.*

3) Family Ricordeidae (Watzl, 1922)

The Ricordeidae are often distinguishable from other families primarily by a combination of tentacle and cnidome characteristics. This family contains only one genus.

I. Genus *Ricordea* (Duchassaing & Michelotti, 1860)

Often a photophilous and zooxanthellate genus, a correct diagnosis for this genus (Figure 37) must integrate the morphology of the disc with the characteristics of the cnidome (spirocysts in the tentacles are frequently reported).

Figure 37: from the left: specimen of *Ricordea Yuma*; colour variation of *Ricordea Yuma*; carpet of *Ricordea florida* (all the scale bars in the first two photos are 1 cm).

7.1.2 Order Zoantharia (Gray, 1832)

Zoantharia have polyps that are often colonial (more rarely solitary) and almost always have two rows of tentacles; these organisms display distinctive internal characteristics, such as the arrangement of the mesenteries in dimorphic pairs and the almost constant presence of encrustations (sand/debris) on the external body surface.

Systematically, the order is supported by molecular analyses, but the distinction between the various families/genera has been repeatedly reorganized, especially due to the high homoplasy of muscular characteristics (Daly et al., 2007).

The modern revision of the genus highlights that the position of the sphincter (mesogleal or endodermal; continuous or discontinuous; single or double) is not always sufficient to determine the various genera (this is because the muscular architecture can evolve as a convergent adaptation for polyp retraction and defence) (Swain et al., 2015).

On the other hand, cnidome can provide diagnostic information, but require significant time and resources, and require standardized methods (because the classes and sizes of nematocysts vary between tissues and individuals).

The literature shows that integrating these anatomical characteristics with a genetic-based strategy is often the most robust way to delimit species and genera (Sinniger, Ocaña & Baco, 2013).

In the order Zoantharia, two suborders are distinguished: Brachycnemina and Macrocnemina. These are distinguishable because Brachycnemina mostly live in symbiosis with zooxanthellae, while Macrocnemina resort to epizoic associations and generally live at greater depths.

In phylogenetic terms, some works indicate that the suborder Macrocnemina may be paraphyletic, but the distinction remains useful for descriptive and diagnostic purposes when applied with caution and integrated with molecular evidence (Daly et al., 2007).

A. Suborder Brachycnemina (Haddon & Shackleton, 1891)

1) Family Neozoanthidae (Herberts, 1972)

Specimens of this family appear partially encrusted with sand only at the base of the column; this represents an intermediate condition between heavily encrusted families (like Sphenopidae) and families with minimal encrustation (such as many Zoanthidae). This is of both functional (wall rigidity) and diagnostic importance. The combination of the presence of partial encrustation and an endodermal sphincter contributes to the identification of the family.

I. Genus *Neozoanthus* (Herberts, 1972)

Organisms of this genus (Figure 38) show partial encrustation at the base of the column and an endodermal sphincter; therefore, in this case too, the diagnosis depends on a combination of characteristics such as encrustation, musculature, and, of course, if possible, genetic analysis.

Figure 38: from the left: colonies of *Neozoanthus uchina*; colour variation in a colony of Neozoanthus *uchina*; colony of *Neozoanthus uchina* with two colour variation (all scale bars 1 cm).

2) Family Sphenopidae (Hertwig, 1882)

They have a distinctive feature: sand encrustations in the ectoderm and mesoglea. Numerous zooxanthellate lineages are also present. (Reimer et al., 2017).

I. Genus *Palythoa* (Lamouroux, 1816)

They typically have heavily encrusted epidermis and mesoglea; this characteristic confers rigidity and protection to the organism and represents a central diagnostic trait of the genus. They are typically colonial with polyps completely immersed in the coenenchyma, indicating an often massive coloniality and a morphology that can make it difficult to distinguish them from related taxa (Figure 39). In some ecological conditions and/or in some taxa, isolated polyps or more free-form may also occur (Irei, Sinniger & Reimer, 2015; Ryland & Lancaster, 2003). Phenotypic plasticity is one of the main factors complicating the taxonomy of *Palythoa*; this variability often responds to environmental gradients (hydrodynamics, available sediment, light, microhabitat, etc.).

These peculiarities of the genus can give rise to divergent morphotypes that have historically been described as distinct species (Reimer et al., 2006). Within the genus *Palythoa*, recent studies have shown that cnidocyst size can show statistically significant differences between closely related species, despite extensive overlap that makes it, alone, inconclusive for diagnosis (Irei, Sinniger & Reimer, 2015). A feature of great biological significance is the frequent association of the genus *Palythoa* with palytoxin (PTX). The literature highlights how PTX may have ecological functions that facilitate spatial competition with other sessile invertebrates (Ryland & Lancaster, 2003); the presence of palytoxin must also be considered in relation to the significant biological risk it poses (manipulation in the field and in the laboratory) (Reimer et al., 2006).

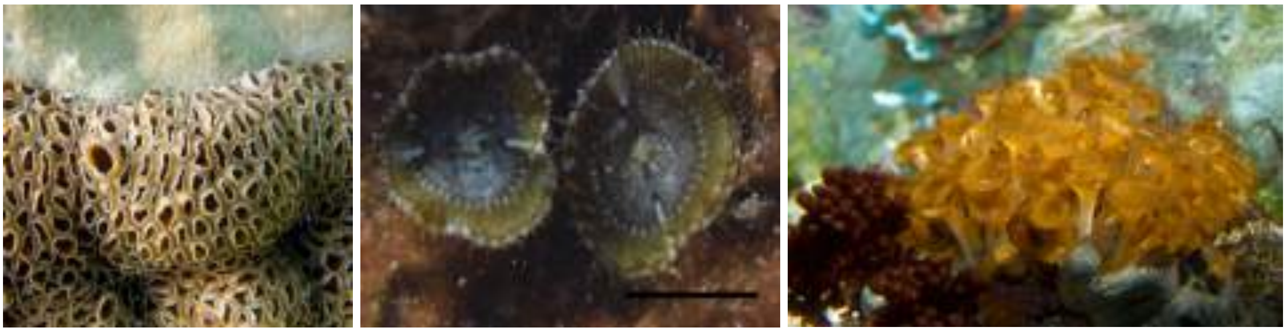


Figure 39: from the left: colony of *Palythoa tuberculosa*; two polyps of *Palythoa variabilis* (scale bar 5 mm); colony of *Palythoa* sp.

- ***Palythoa heliodiscus* (Ryland & Lancaster, 2003)**

Within the Indo-Pacific zooxanthellate Sphenopidae, *Palythoa heliodiscus* (Figure 40) is distinguished primarily by a combination of traits, such as the relatively large and highly conspicuous oral disc, with extremely small tentacles compared to other similar intertidal species (such as, for example, *Palythoa mutuki*). This characteristic makes the colony observable in situ as "gardens of discs" rather than as aggregates of tentacled polyps (Ryland & Lancaster, 2003); the polyps are more recognizable individually, and the coenenchyma does not completely enclose them as in "carpet" *Palythoa* (Ryland & Lancaster, 2003; Reimer et al., 2006).

The cnidome of *P. heliodiscus* shows a lack of basitrics in key areas (such as the tentacles), a condition generally associated with reduced predation (Ryland & Lancaster, 2003).

A distinctive ecological trait (which, however, is somewhat in odds with what was previously stated) is this species' preference for low light conditions compared to other *Palythoa* genera, as it is reported to occur under overhangs, under stony corals, or in other areas sheltered from direct light (Ryland & Lancaster, 2003; Reimer et al., 2006).

Figure 40: different colour variation of *Palythoa heliodiscus* (from light green to dark brown).

▪ ***Palythoa caesia* (Dana, 1846)**

It is a zooxanthellate, colonial zoantharian, characterized by polyps heavily encrusted with sand and debris and a marked tendency for the polyps to be deeply immersed in well-developed coenenchyma. (Pax, 1910; Hibino et al., 2014). However, current literature highlights that these characteristics are not sufficient to clearly separate it from *Palythoa tuberculosa* (Esper, 1805), with which *P. caesia* (Figure 41) has frequently been confused and alternatively identified in different Indo-Pacific regions (Hibino et al., 2014).

Encrustation is not a marginal aspect, as in the genus *Palythoa* it can represent a very significant fraction of the body weight (Haywick & Mueller, 1997; Hibino et al., 2014).

The coloration reported for *P. caesia* (light to dark brown, sometimes with yellow-green hues or fluorescence) largely overlaps with that observed for *P. tuberculosa* and shows wide variability among different populations; this greatly reduces the reliability of colour as a specific trait.

Comparative syntheses indicate polyp sizes in the range of a few millimetres up to approximately 1–1.5 cm (depending on contraction and specimen conditions) (Hibino et al., 2014).

A trait frequently used to distinguish *P. caesia* from *P. tuberculosa* is the number of tentacles: *P. caesia* shows higher average values than *P. tuberculosa* (41–44 versus 35–39), but with a wide range and overlap between populations, individuals, and localities (Hibino et al., 2014). Furthermore, in Zoantharia, the number of tentacles increases with age/polyp size, making it difficult to define when an individual is mature and therefore comparable (Hibino et al., 2014). Regarding cnidome, there are several categories, including spirocysts, basitrics, and microbasics mastigophores, as well as holotrichs. In a direct comparison between *P. caesia* and *P. tuberculosa*, analysis of multiple tissues (tentacles, actinopharynx, mesenteric filaments) shows that there are no clear and reproducible differences between the two species based on type and size (Hibino et al., 2014).

A molecular approach has been performed in the literature using mitochondrial (COI, 16S) and nuclear (ITS-rDNA) markers; the results show sequence identity or near-identity between samples attributed to the two pairs across a broad geographic spectrum, with clade mixing and no consistent segregation (Hibino et al., 2014). Therefore, *Palythoa caesia* most likely corresponds to *Palythoa tuberculosa* (Esper, 1805) (Hibino et al., 2014).

Figure 41: different polyps' appearance and colour variation in different *Palythoa caesia* colonies.

- ***Palythoa tuberculosa* (Esper, 1805)**

Historically, the species (Figure 42) has often been confused with other morphologically similar taxa, particularly with *Palythoa caesia* (Dana, 1846). Analyses based on COI, 16s RNA ITS-RNA, etc., show that *Palythoa tuberculosa* and *Palythoa caesia* are probably a single large clade, with intermixing between the specimens attributed to the two names. (Hibino et al., 2014).

Figure 42: different polyps' appearance and colour variation in different colonies of *Palythoa tuberculosa* (last photo scale bar is 1 cm).

- ***Palythoa grandis* (Verrill, 1900)**

Palythoa grandis (Figure 43) is described with distinctive colour and tentacle features, along with a distinctive contraction behaviour. The polyps are described as citrus yellow colour, with 30–32 tentacles that are pointed distally and wider at the base; when contracted, the polyps do not assume the "mammillary" shape typical of many *Palythoa*, but instead form an apical depression (Montenegro et al., 2020). For *P. grandis*, the primary source relies primarily on external diagnosis and distribution, while cnidome and histology analyses are lacking.

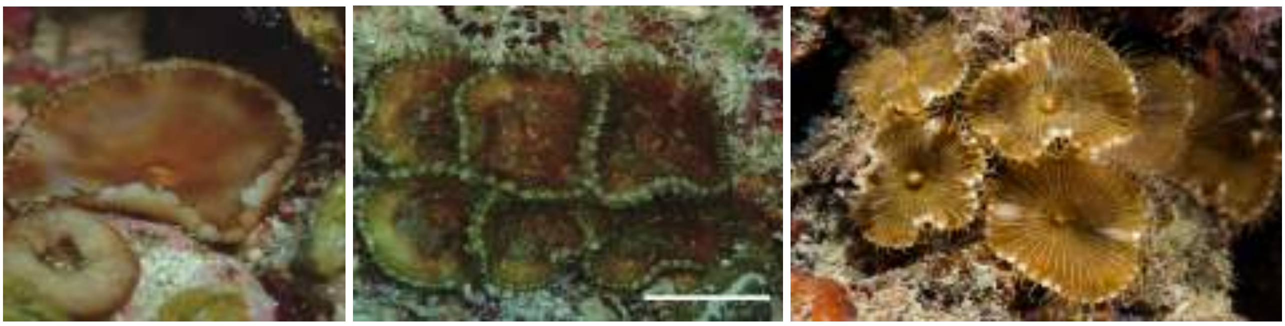


Figure 43: from the left: individual specimen of *Palythoa grandis*; colony of six *Palythoa grandis* with green colour variation (scale bar 1 cm); colony of *Palythoa grandis* with extended tentacles.

II. Genus *Sphenopus* (Steenstrup, 1856)

It is a typically azooxanthellate genus, typical of loose bottoms (sandy/muddy) and with a solitary habitus (Figure 44). Cannot be confused with any other genus by his morphological and size appearance.

Figure 44: from the left: closed individual of *Sphenopus marsupialis* (scale bar approximately 1 cm); specimens of *Sphenopus marsupialis* with opened oral disc (scale bar approximately 1 cm); single specimen of *Sphenopus edulis*.

3) Family Zoanthidae (Lamarck, 1801)

This family exhibits little or no sand/debris encrustation on the external body surface; this characteristic, combined with the frequent presence of zooxanthellae, makes these organisms extremely competitive on reefs, especially in light-rich environments.

The marginal musculature can be continuous or discontinuous, highlighting their variability and thus the need for phylogenetic analysis (Swain et al., 2015).

I. Genus *Acrozoanthus* (Saville-Kent, 1893)

These are zooxanthellate organisms free of any encrustation (Figure 45). Regarding their internal anatomy, they have a double sphincter, a potentially useful feature but one that should be interpreted with caution given the risk of muscular convergence (Swain et al., 2015). The only species of this genus is *Acrozoanthus australiae* (Saville-Kent, 1893)

Figure 45: different photos with different colour variation of *Acrozoanthus australiae* specimens.

II. Genus *Isaurus* (Gray, 1828)

Generally recognizable by their robust polyps and the frequent presence of longitudinal grooves/ridges on the body surface (Figure 46); the literature shows that this genus is sparsely encrusted. Historically, marginal musculature has been discussed as a comparative trait among tropical genera, but always within a phylogenetic framework (Swain et al., 2015).

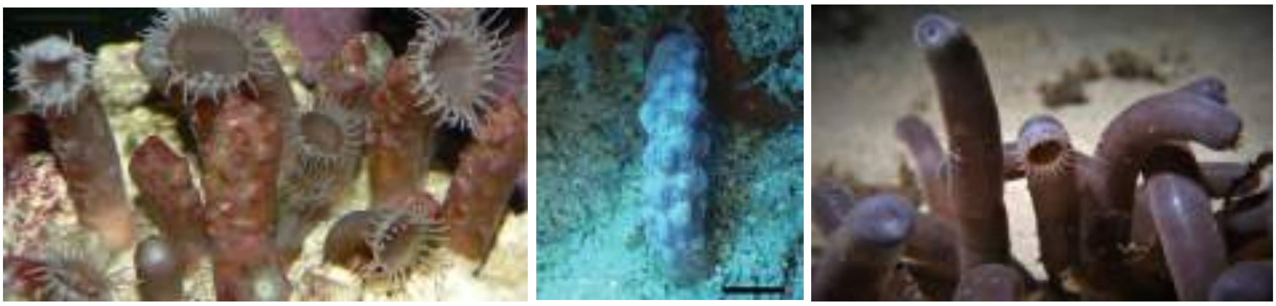


Figure 46: from the left: live colony of *Isaurus tuberculatos* specimens; single polyp of *Isaurus tuberculatos* (scale bar 1 cm); colony of *Isurus Cliftoni*.

III. Genus *Zoanthus* (Cuvier, 1800)

Typically known for their scattered columnar and coenenchyma encrustation and their symbiotic relationship with zooxanthellae, they have a smooth column (typically erect) and non-obvious endodermal invaginations. They possess a mesogleal sphincter with a clear distinction between the distal and proximal portions (a sphincter defined as double) as well as a system of mesogleal canals devoid of true sinuses.

In a modern taxonomic review, the genus *Zoanthus* demonstrates the limitations of diagnosis based solely on external morphology, as many species exhibit high phenotypic plasticity (defined as great variability in polyp size, colony shape, oral disc colour, number of tentacles, etc.), resulting in a risk of overestimating the true number of species if a purely morphological approach is adopted (Reimer et al., 2006).

The genus *Zoanthus* (Figure 47) is typically colonial and forms encrusting aggregates on hard substrates (rocks, coral reefs, etc.), often in areas with wave motion or strong currents. However, it does not necessarily dominate over other sessile organisms (in undisturbed conditions).

Colonies may have closely spaced polyps and relatively thin or moderately developed coenenchyma. Plasticity in *Zoanthus* is not an accessory trait, as demonstrated by an experiment (conducted on *Zoanthus sansibaricus*); in this study, several individuals of the species were transplanted into dimly lit environments. After 87 days of "shading," it was observed that the colonies developed polyps that were on average larger than the "control" individuals (placed in brighter environments), with measurable variations in several morphometric traits (Reimer & Todd, 2013).

From a taxonomic perspective, these findings have two implications: the size of the polyp and sometimes the number of tentacles can vary depending on microhabitats and local conditions; furthermore, the external morphology must be interpreted taking into account environmental

variables (light, flow, depth, exposure), and ideally documented in vivo with a standardized set (photographs + measurements) before fixation (Reimer & Todd, 2013).
Historically, the cnidome has been proposed as a valid alternative in the identification of different *Zoanthus* species; however, the review highlights that the morphology of the nematocysts can depend on the age of the polyp, the size of the colony and the sampling position within the polyp itself, at the same time increasing the risk of incurring experimental errors (Reimer et al., 2006).

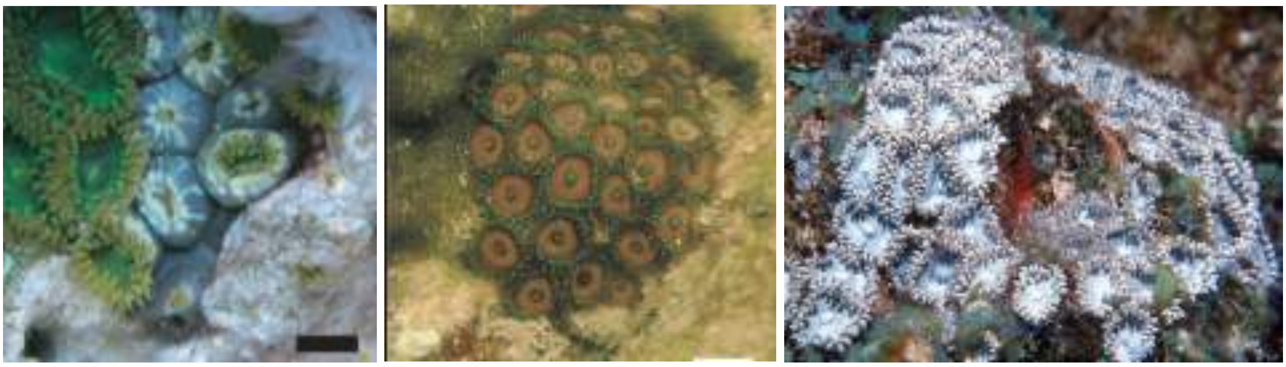


Figure 47: from the left, different colony of: *Zoanthus gigantus* (scale bar 0,4 cm); *Zoanthus Erythochlora*; *Zoanthus Gigantus*.

- ***Zoanthus coppingeri* (Haddon & Shackleton 1891)**

The original description defines *Zoanthus coppingeri* (Figure 48) as a species with a smooth body, papilliform when contracted and more elongated when extended; the polyps are arranged in clusters, with a thin, encrusting coenenchyma. The tentacles are arranged in two rows and without marked differences between the internal and external tentacles (Haddon & Shackleton, 1891).
Regarding colour, the original diagnosis is very detailed: the external portion of the oral disc is described as pink, the internal portion as greenish or bright green with brown spots; the mouth margin is noted as brown; while the tentacles are grey with a black spot between each tentacle (Haddon & Shackleton, 1891).
The measurements reported for the fixed type of material are: length of the contracted polyp around 0,15 cm and diameter of the upper portion around 0,5 cm (Haddon & Shackleton, 1891).
A distinct external cuticle is described, and between the cuticle and the ectoderm is a thin peripheral layer of mesoglea (called subcuticula).
The ectoderm forms an almost continuous layer but is traversed by numerous mesogleal filaments that join in a peripheral layer. Branching canals are also reported originating from the ectoderm and traversing the mesoglea, often in a radial direction, with variable size and no observed connection with the endoderm. Many canals enter the mesenteries and form large sinuses, containing nematocysts like those found in the ectoderm.

The mesoglea constitutes the main thickness of the wall and is described as homogeneous and light (Haddon & Shackleton, 1891).
This species tends to occupy subtidal or intertidal environments, extending into deeper areas or even those covered by sediment (as it can grow through a thin layer of sand) (Ryland, 2015).
One of the most recent point of the taxonomic review concerns the possible equivalence between *Z. coppingeri, Zoanthus sansibaricus, Zoanthos mantoni*, and other Indo-Pacific species; gene frequencies have identified a few species, but they are described under a multitude of different names (Ryland, 2015). *Zoanthus coppingeri* is likely the same named species as *Zoanthus sansibaricus*, with a conflict over nomenclatural priority (Haddon & Shackleton, 189); recent studies propose retaining the most commonly used name for taxonomic stability (*Zoanthus sansibaricus*) but emphasize the need for direct genetic comparisons between the northern and southern hemispheres of the Indo-Pacific (Ryland, 2015).

Figure 48: different colonies and colour variation of *Zoanthus coppingeri*.

B. Suborder Macrocnemina (Haddon & Shackleton, 1891)

1) Family Epizoanthidae (Delage & Hérouard, 1901)

This family typically has many epizoic forms and grows predominantly on mobile or biogenic substrates.
It has a simple mesogleal muscle. For an effective diagnosis of this genus, it is preferable to identify the host's genus (substrate) rather than relying on individual external traits (Sinniger, Ocaña & Baco, 2013).

I. Genus *Epizoanthus* (Gray, 1867)

Typically, an epizoic genus, like the family it belongs to (Figure 49); it has a simple mesogleal muscle; diagnosis often requires, in addition to the host's genus, when possible, also molecular data, because the habitus can vary depending on the host (Sinniger, Ocaña & Baco, 2013).

Figure 49: from the left: unidentified *Epizoantus* sp. on *Stylocidaris lineata*; colony of *Epizoanthus loricatus*; colony of *Epizoanthus papillosus* on a hermit crab.

II. Genus *Thoricactis* (Gravier, 1918)

Thoracactis (Figure 50) is a zoantharian associated with glass sponges (*Hexasterophora*), particularly *Sarostegia oculata* (Topsent, 1904), with its polyps often completely embedded in the sponge.
The genus includes only the species *Thoracactis topsenti* (Gravier, 1918), found in deep environments (between 550 and 1,311 m) (Kise et al., 2024).

Figure 50: different *Thoricactis topsenti* colonies photos (all scale bars are 10 mm).

2) Family Hydrozoanthidae (Sinniger, Reimer & Pawlowski, 2010)

In this family, most species appear to be associated with hydrozoans; this represents a highly distinctive ecological character (Sinniger, Ocaña & Baco, 2013).

I. II. e III. Genus: *Aenigmanthus* (Sinniger, Reimer & Pawlowski, 2010), *Hydrozoanthus* (Sinniger, Reimer & Pawlowski, 2010), *Terrazoanthus* (Reimer & Fujii, 2010)

Each of these genera (Figure 51) has a preferred substrate/host (this is a distinctive trait of high systematic value because it links morphology and ecological niche and is often congruent with molecular clades) (Sinniger, Ocaña & Baco, 2013).

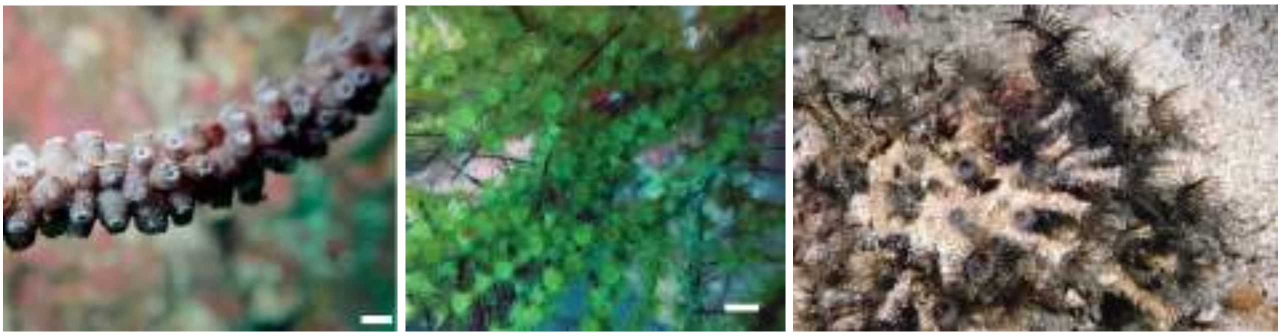


Figure 51: from the left, colonies of: *Aenigmanthus segoi* (scale bar 10 mm); *Hydrozoanthus gracilis* (scale bar 10 mm); *Terrazoanthus* sp. on sandy bottom.

3) Family Microzoanthidae (Fujii & Reimer, 2011)

A typically azooxanthellate family with abundant sand encrustations along the entire base, but not along the entire column.

Species often cryptic (often found on coral rubble, stones, and in reef crevices), with characteristic encrustations (Figure 35) (Fujii & Reimer, 2011).

I. Genus *Microzoanthus* (Fujii & Reimer, 2011)

Very little information is available for this genus (Figure 52), because of small sizes and limited habitat accessibility (Fujii & Reimer, 2011).

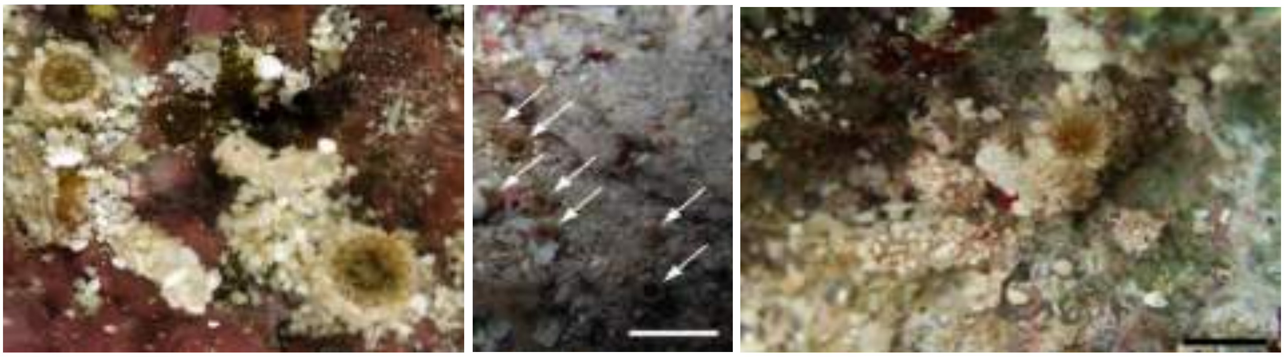


Figure 52: different colonies of: *Microzoanthus occultus* (all scale bars are 2 mm).

4) Family Nanozoanthidae (Fujii & Reimer, 2013)

A recently described family exhibiting encrustations along the entire spine and a mesogleal sphincter; the absence of lacunae/spaces in some internal body segments is noted.

This combination of anatomical features supports a clear familial diagnosis, although confirmation on large samples and phylogenies remains necessary (Fujii & Reimer, 2013).

I. Genus *Nanozoanthus* (Fujii & Reimer, 2013)

A genus (Figure 53) associated with encrustations along the entire column and featuring a mesogleal sphincter (typical of the family). Morphological diagnosis requires great care, as the small size increases the difficulty in describing the above-mentioned characteristics.

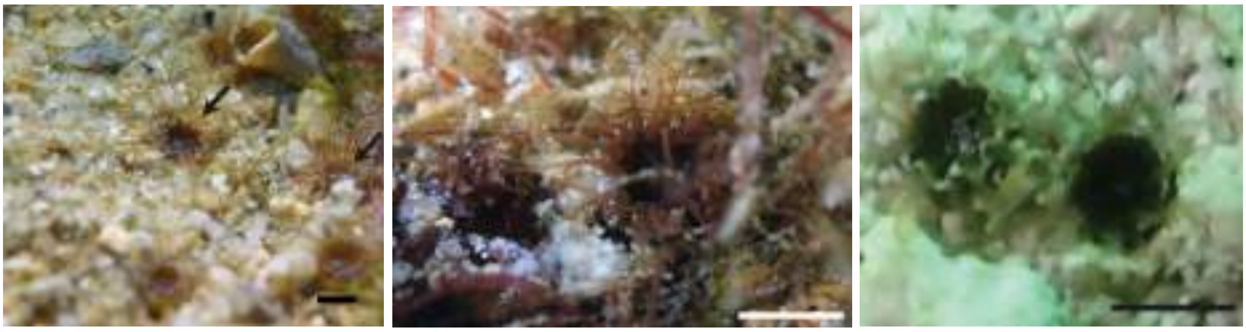


Figure 53: different colonies of *Nanozoanthus arenaceus* (all scale bars are 3 mm).

5) Family Parazoanthidae (Delage & Hérouard, 1901)

They are known for their frequent association with other organisms. Recent literature shows high diversity in this family and highlights previously unseen associations, indicating that revising the Parazoanthidae family requires diverse data, such as host identification, bathymetric range, and, above all, genetic analysis (Sinniger, Ocaña, & Baco, 2013; Carreiro-Silva et al., 2017).

In the Parazoanthidae, substrate association is used as a trait with evolutionary value.

I. Genus *Antipathozoanthus* (Sinniger, Reimer & Pawlowski, 2010)

Species (Figure 54) typically colonial, with polyps joined by a coelom that can often cover the host's body surface. They are primarily (though not exclusively) associated with Antipatharia. In comparative diagnoses between different species, polyp size, number of tentacles, and coloration are often used (Sinniger, Reimer & Pawlowski, 2010).

The column and coelom are frequently heavily encrusted with mineral particles; in some species, the encrustation is so severe that it makes histological analysis difficult (Kise et al. 2017).

For cnidome, the following are reported: basitrics, microbasics b-mastigophores, microbasics p-mastigophores, holotrics, and spirocysts (Kise, Obuchi, & Reimer, 2021).

Available data show a broad distribution with Indo-Pacific as an hotspots and Atlantic/Mediterranean presences for some related lineages.

The genus *Antipathozoanthus* was established as part of the DNA-based reorganization of the Parazoanthidae (Sinniger, Reimer, & Pawlowski, 2010) and is divided into "antipatharian-associated species" and "non-antipatharian-associated species."

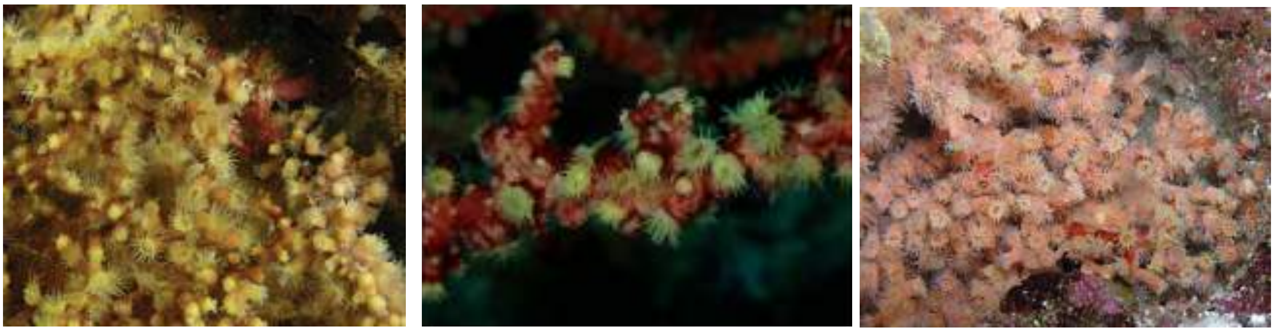


Figura 54: from the left, colonies of: *Antipathozoanthus* sp.; *Antipathozoanthus hickmani*; *Antipathozoanthus* sp.

- ***Antipathozoanthus cavernus* (Kise, Fujii, Masucci, Biondi & Reimer, 2017)**

Antipathozoanthus cavernus (Figure 55) was described as a new species in a recent study conducted in the Indo-Pacific; it was identified and described using a combination of external morphological traits, cnidome analysis, ecological traits, and molecular analyses.

A colonial habitus is described, with polyps connected by a highly developed coenenchyma covering the host axis; specifically, it is found exclusively associated with antipatharians of the genus *Myriopathes* (family Myriopathidae) (Kise et al., 2017). Overall, it appears heavily encrusted with visible sandy particles.

In situ, the polyps are reported to have a diameter of approximately 4–15 mm when the oral disc is expanded and a height of approximately 3–10 mm from the coenenchyma surface. The tentacles (ranging from 32 to 40) are translucent and relatively short (1–5 mm long), with lengths comparable to the diameter of the oral disc or slightly shorter (the tentacle/disc ratio is useful in comparison with species with proportionally longer tentacles) (Kise et al., 2017).

The presence of approximately 16–20 capitular ridges is noted, visible when the polyp is closed (Kise et al., 2017).

Regarding coloration (tendentially light orange), this is treated in the literature by the authors as a distinguishing trait from *Antipathozoanthus hickmani* (which instead includes red or cream-colored phenotypes) and *Antipathozoanthus macaronesicus* (more yellowish in comparison) (Kise et al., 2017).

The species is reported to be typical of low-light environments, such as the sides and/or floors of cave entrances or steep slopes (consistent with the species name and the availability of *Myripathes* host colonies in such contexts) (Kise et al., 2017). The bathymetric range is from 19 to 39 m, i.e., the shallow sublittoral/mesophotic zone (Kise et al., 2017).

It has been reported to be present in the Maldives, Palau, and Japan (Kagoshima) (Kise et al., 2017).

The cnidome includes spirocysts, holotrichs (medium and large), basitrics, and microbasics p-mastigophores (often difficult to distinguish from basitrics). A useful detail in intra-genus comparison is the fact that several species of the genus, including *Antipathozoanthus cavernus*, show holotrichs in the column, while some newly described species (for example, *A. tubus*) do not show them (Kise et al., 2017).

The internal anatomy includes a comb-like marginal endodermal muscle, observed in longitudinal section, and the absence of zooxanthellae (Kise et al., 2017).

Genetic studies on the genus (particularly on new species and on diversity in Japan) consistently place *Antipathozoanthus cavernus* in the associated group, along with *A. macaronesicus, A. hickmani*, and *A. remengesaui* (Kise, Hirok, Obuchi, Reimer, 2021).

Comparing *Antipathozoanthus cavernus* with *Antipathozoanthus remengesaui*, it is noted that both can occupy similar environments, but *Antipathozoanthus remengesaui* is associated with *Antipathes* (family Antipathidae) and is covered by a poorly developed coenenchyma, while *A. cavernus* is associated with *Myriopathes* (family Myriopathidae) and has a highly developed coenenchyma (Kise et al., 2017).

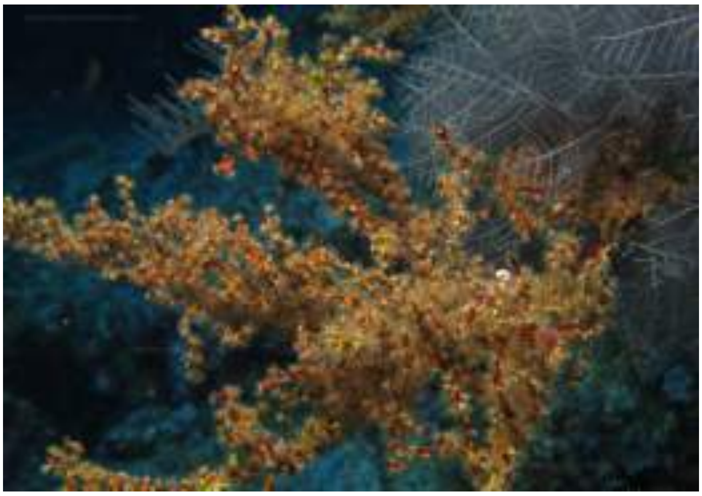


Figure 55: colony of *Antipathozoanthus cavernus* on *Myriopathes*.

- ***Antipathozoanthus hickmani* (Reimer & Fujii, 2010)**

This species (Figure 56) has been described as epibiotic on *Antipathes galapagensis* (in the Galápagos) (Reimer, Davis, Fujii, Takuma, 2010). The original description defines *Antipathozoanthus hickmani* as a colony on the branches of *Antipathes galapagensis* (Diechmann, 1941), with polyps lining the host's branches and connected by a well-developed coenenchyma covering the axis of the antipatharian. The colony generally comprises about 40 polyps, with reported diameters (when fixed) of about 1.5–4.0 mm and heights from the coenenchyma surface of about 1.0–6.0 mm. In the literature, they have a bathymetric range from 10 to 45 m in depth; They have been described so far only in the Galapagos Islands, in subtidal areas of the archipelago, generally on rocky cliffs and ridges (Reimer, Davis, Fujii, Takuma, 2010).

This species exhibits polyps clearly emerging from the coenenchyma, with an elongated and often very visible column (Reimer, Davis, Fujii, Takuma, 2010).

The tentacles are almost always longer than the diameter of the expanded oral disc, a useful trait for discriminating the species in the field from taxa with longer tentacles (Reimer, Davis, Fujii, Takuma, 2010). Diagnosis of cnidome includes: spirocysts (typical of the tentacles and regions involved in adhesion/contact); basitrics and microbasics p-mastigophores (often difficult to separate with certainty, especially in rapid preparations) and medium and large sized holotrics, consistent with other *Antipathozoanthus* associated with antipatharians (Reimer, Davis, Fujii, Takuma, 2010).

In the 2017 Indo-Pacific revision, *Antipathozoanthus hickmani* falls firmly within the monophyletic clade of *Antipathozoanthus*, within the family Parazoanthidae and, more specifically, within the subclade of antipatharian-associated species, resulting in it being the sister species of *Antipathozoanthus cavernus* (Kise et al., 2017).

In comparisons, *Antipathozoanthus hickmani* is distinguished from *Antipathozoanthus cavernus* by its different coloration (absence of the typical red/cream hues described on *hickmani*) and by differences in host association (Kise et al., 2017). More generally, *hickmani* is distinguished from other non-antipatharian-associated Parazoanthidae by: substrate (antipatharian versus sponges/rocks); the architecture of the colony and the coenenchyma (*hickmani* has more emergent polyps) and, in profile, the number of tentacles (Reimer, Davis, Fujii, Takuma, 2010).

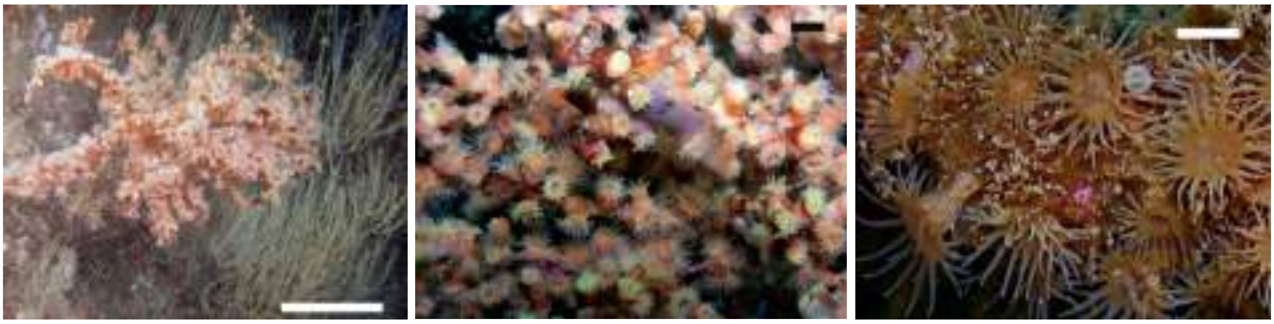


Figure 56: different photos of different colonies of *Antipathozoanthus hickmani* on *Antipathes galapagensis* (first scale bar 10 cm; second and third one are 1 cm).

- ***Antipathozoanthus macronesicus* (Ocana & Brito, 2003)**

Antipathozoanthus macaronesicus (Figure 57) originated as *Gerardia macaronesicus* (Ocaña & Brito, 2003) and was later transferred to *Antipathozoanthus* (Sinniger, Reimer, Pawlowski, 2009).

It appears as a colonial zoantharian, with polyps connected by a basal coenenchyma that typically covers the entire axis of the antipatharian; the specimens present in the literature and examined are all associated with antipatharians. The polyps often protrude from the coenenchyma, but partially submerged polyps may also coexist (Montenegro et al., 2020). A much more discussed trait known in the literature for this species is the ability to develop a skeleton even as the colony grows freely, forming lateral branches (Ocaña & Brito, 2003; Montenegro et al., 2020). The skeletal secretion reported for *Antipathozoanthus macaronesicus* has not been observed in any other species of the genus (including new species), indicating that this trait requires further comparative verification in additional populations (Kise, Obuchi & Reimer, 2021). The literature reports 42 tentacles, pointed and almost always arranged in two circles; their dimensions when fixed are highly variable (with a height between 0.2 cm and 1 cm and a diameter of 0.2–0.5 cm), while in life they range from 2 cm to 3 cm (Montenegro et al., 2020). Noteworthy features include: encrustation of the column up to the external mesoglea; the absence of mesogleal canals; approximately 26 tentacles; and the presence of a cteniform endodermal muscle (Kise, Obuchi, Reimer, 2021). Individuals have been reported from Cape Verde (around 18 m deep) and Príncipe (around 45 m deep) (Sinniger, Reimer, & Pawlowski, 2009). In the Caribbean Sea, it is reported as the only *Antipathozoanthus* species, however, western specimens are often treated as *Antipathozoanthus* aff. *macaronesicus* due to its distance from scientifically accepted areas of occurrence in the Eastern Atlantic (Montenegro et al., 2020). In comparison, *Antipathozoanthus macronesicus* differs from *Antipathozoanthus hickmani* because *hickmani* is associated with *Antipathes galapagensis*; and also the ability of *hickmani* to deposit a skeleton is not known (Reimer & Fujii, 2010; Kise, Obuchi Reimer, 2021). *Antipathozoanthus cavernus*, on the other hand, is associated with *Myriopathes*, often in cave environments, while *Antipathozoanthus macaronesicus* is associated with *Antipathes* (Kise et al. 2017).

Figure 57: different colonies of *Antipathozoanthus macronesicus*; on the last photo is noticeable how this species can grow not only on antipatharian host but can produce his own skeleton.

- ***Antipathozoanthus obscurus* (Kise, Fujii, Masucci, Biondi & Reimer, 2017)**

This species constitutes a crucial exception in the genus *Antipathozoanthus*, as it is not associated with Antipatharia, but lives almost exclusively on carbonate substrates (Figure 58) in low-light environments (such as overhangs, caves, etc.). The external morphology (in vivo) shows an oral disc

5–10 mm in diameter when open, and a polyp height of approximately 5–10 mm when open. Polyps in a single colony are connected by a stolon that forms a network. Furthermore, the polyps and coenenchyma are heavily encrusted with numerous sandy particles of highly variable size. There is an average number of 26–32 brown/orange tentacles, as long as or longer than the diameter of the oral disc (Kise et al., 2017). The species is described as azooxanthellate, but heavy sand and silica encrustation in the ectoderm and mesoglea has historically prevented clear cross-sections and images from being obtained in the literature to fully describe the arrangement of the mesenteries, the marginal muscle (Kise et al., 2017); in *Antipathozoanthus obscurus* traditional internal diagnosis is limited, consequently, the description of the species relies more heavily on external characters, the cnidome, ecology and phylogeny (Kise et al., 2017; Low et al., 2016). The cnidome described for *Antipathozoanthus obscurus* includes spirocysts, basitrics and microbasics p-mastigophores (often difficult to distinguish from each other), and large holotrics (Kise et al., 2017). The key feature of the cnidome of *Antipathozoanthus obscurus* is the absence of medium-sized holotrics in all tissues; only large holotrics are present in all areas analysed (Kise et al., 2017). Molecular analyses (COI, 16s-RNA, and ITs-RNA) firmly place *Antipathozoanthus obscurus* within the genus *Antipathozoanthus* (Kise et al., 2017). Interestingly, although not associated with antipatharians, *Antipathozoanthus obscurus* is genetically very close to antipatharian-associated species and presents COI and 16S-rDNA sequences almost identical to those of *Antipathozoanthus macaronesicus* (Kise et al., 2017); subsequent genetic analyses show a subclade composed of *Antipathozoanthus tubus* and *Antipathozoanthus obscurus* (Kise et al., 2021). Phylogeny indicates that the loss (or failure to evolve) of the association with antipatharians may have occurred without leaving the genus, and that the evolution of settlement strategies in shaly microhabitats on carbonate substrates is compatible with the evolutionary history of *Antipathozoanthus* (Kise et al., 2017; Kise et al., 2021). The distribution confirmed in the original description includes Okinawa (Japan), the Red Sea and Saudi Arabia, with individuals reported from 3 to 15 m depth and associated with shady microhabitats (Kise et al., 2017).

Figure 58: different colonies of *Antipathozoanthus obscurus*; from the left: colony on an antipatharian host; in the last two photos is noticeable how this species can also grow on carbonate substrates (all scale bars are 5 mm).

- ***Antipathozoanthus remengesaui* (Kise, Fujii, Masucci, Biondi & Reimer, 2017)**

Antipathozoanthus remengesaui (Figure 59) is a species associated with Antipatharia and appears to be azooxanthellate.

In vivo, polyps are 4–8 mm in diameter (when the oral disc is expanded) and 3–8 mm in height; the colony's polyps (white/off-white in colour) may be solitary or connected by coenenchyma (which, however, is generally poorly developed).

40–42 tentacles (pink and/or translucent) are present, generally as long as the diameter of the open oral disc; the latter is generally pink (or bright brown).

It is described as having sandy encrustations visible on the coenenchyma and ectodermal tissue (Kise et al., 2017). This combination is particularly useful because it separates *Antipathozoanthus remengesaui* from *Antipathozoanthus cavernus* (which has *Myripathes* as its host and a highly developed coenenchyma) and from *Antipathozoanthus hickmani* (which has on average larger polyps and a well-developed coenenchyma) (Kise et al., 2017).

In the literature, *Antipathozoanthus remengesaui* is described with internal characteristics considered informative, including the presence of a cteniform endodermal marginal muscle (observed in longitudinal section) and the presence of large, scattered lacunae in the ectoderm and mesoglea, attributed to the heavy degree of encrustation (Kise et al., 2017).

The cnidome reported for *Antipathozoanthus remengesaui* includes holotrichs (large and medium-sized), basitrics, and microbasics p-mastigophores (often difficult to distinguish from each other), and spirocysts (Kise et al., 2017). Compared to *Antipathozoanthus hickmani*, the latter lacks spirocysts in the column, while *Antipathozoanthus remengesaui* does (Kise et al., 2017).

Phylogenetically, *Antipathozoanthus remengesaui* also displays unique ITs-RNA sequences (Kise et al., 2017). Studies conducted on *Antipathozoanthus remengesaui* show its presence in multiple regions of the Indo-Pacific and the Red Sea (Palau, Kagoshima, Japan, and the Maldives). It is generally described with a bathymetric range from 9 m to 40 m in depth (Kise et al., 2017); specifically, it is reported to be present: in the Maldives between 9 m and 24 m; in Palau between 22 m and 37 m; in Kagoshima between 20 m and 40 m; and in Saudi Arabia and the Red Sea between 11 m and 12 m (Kise et al., 2017). Regarding intra-genus comparisons, when we compare *Antipathozoanthus remengesaui* with *Antipathozoanthus cavernus*, both can occur in comparable environments, but *remengesaui* is associated with Antipathes and is characterized by a poorly developed coenenchyma, while *cavernus* is associated with *Myripathes* and has a highly developed coenenchyma (Kise et al., 2017).

If we compare *Antipathozoanthus remengesaui* with *Antipathozoanthus hickmani*, we note that *hickmani* has on average larger polyps (about 4–12 mm in diameter and about 4–15 mm in height) connected by well-developed coenenchyma, while *remengesaui* has slightly smaller in situ polyps (about 4–8 mm in diameter and about 3–8 mm in height), often solitary or with a reduced coenenchyma. It also differs from cnidoma because it has spirocysts in the column (Kise et al., 2017).

Figure 59: different colonies of *Antipathozoanthus remengesaui* always on *Antipathes* species.

- ***Antipathozoanthus tubus* (Kise, Obuchi & Reimer, 2021)**

It is the first species of the genus *Antipathozoanthus* reported as an epibiont on polychaete tubes (Figure 60); the second species of the genus not to be associated exclusively with antipatharians (after *Antipathozoanthus obscurus*) (Kise, Obuchi, Reimer, 2021).

Typically azooxanthellate; the host has not been identified with certainty, but an affinity with the genus *Eunice* (family Eunicidae) is suggested (Kise, Obuchi, Reimer, 2021).

From the point of view of external morphology, the following are notable: polyps (in vivo) with a height greater than 8 mm; a column diameter less than 10 mm; and a 5–8 mm oral disc with a light orange coloration (Kise, Obuchi & Reimer, 2021). There are 30–34 transparent tentacles arranged in two rows (specifically: 15–17 internal endocoel tentacles and 15–17 external exocoel tentacles), as long as the diameter of the oral disc (when expanded); the tips of the tentacles are frequently described as cream-colored (Kise, Obuchi, Reimer, 2021).

The number of oral grooves is equals to the number of tentacles, and at the centre of the oral disc is a circular protrusion (typically cream-colored) with a mouth at its tip (Kise, Obuchi, Reimer, 2021).

The literature shows a fairly complete internal characterization for this species: a number of mesenteries ranging from 30 to 34, with 15–17 complete mesenteries and 15–17 incomplete mesenteries; the presence of mesenterial filaments. Must be noted the presence of a cteniform endodermal marginal muscle (supported by comb-like mesogleal folds along the entire length of the muscle). The basal canals of the mesenteries are absent. The possible presence of gametes has also been described in some longitudinal sections (Kise, Obuchi, Reimer, 2021).

The cnidome includes: basitrics, microbasics b-mastigophores, microbasics p-mastigophores, holotrics, and spirocysts (Kise, Obuchi & Reimer, 2021).

A useful data for comparison is given by the distribution in the tissues, this is because *Antipathozoanthus tubus* shows the absence of holotrics in the column, while *Antipathozoanthus macaronesicus, Antipathozoanthus remengesaui, Antipathozoanthus cavernus, Antipathozoanthus hickmani and Antipathozoanthus obscurus* present holotrichs in the column (Kise, Obuchi, Reimer, 2021). The COI, 16S-rDNA, and ITS-rDNA sequences reported for *Antipathozoanthus tubus* are all unique, with reported genetic distances between *tubus* and *obscurus* (the two species that may not be associated with Antipatharia) of 0.009 (COI), 0.03 (16S), and 0.12 (ITS) (Kise, Obuchi, Reimer, 2021). Its historically confirmed distribution in the literature includes the Northwest Pacific and Sagami Bay (in Kanagawa, Japan); it is described as typical of shallow waters, at depths less than 14 m, tending to live in light-exposed environments (Kise, Obuchi, Reimer, 2021).

Figure 60: different colonies of *Antipathozoanthus tubus*; in the last photo, marked with the with arrow, is noticeable how this species can grow also on polychaete tubes (T) (the first and the last photos' scale bar are 10 cm; the middle photo scale bar is 5 mm).

II. III. IV. V. VI. VII. Genus: *Bergia* (Duchassaing & Michelotti, 1860), *Bullagummizoanthus* (Sinniger, Ocaña & Baco, 2013), *Churabana* (Kise, Montenegro & Reimer, 2021), *Parachurabana* (Kise, 2023), *Kauluzoanthus* (Sinniger, Ocaña & Baco, 2013), *Kulamanamana* (Sinniger, Ocaña & Baco, 2013)

They represent the most recently described genera in the Zoantharia (Figure 61 A and Figure 61 B); these derive from modern phylogenetic revisions (Sinniger, Ocaña, Baco, 2013). What differentiates them most is the nature of their preferred hosts (sponges for the genus *Bergia*, etc.).

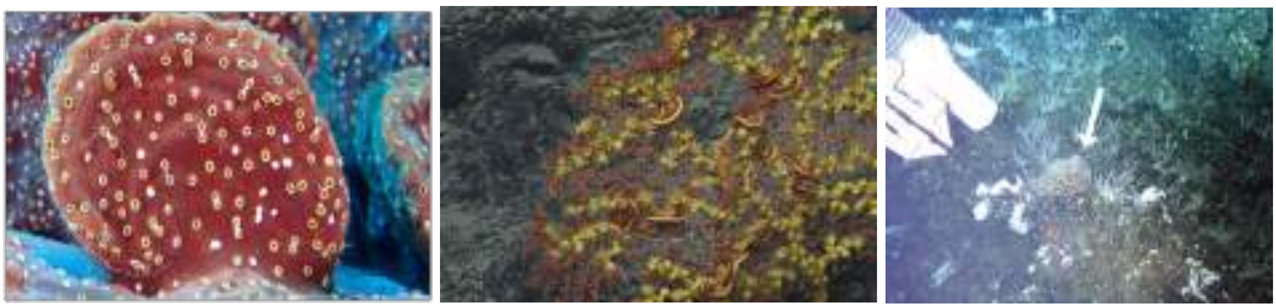


Figure 61 A: from the left, colonies of: *Bergia* sp.; *Bullagummizoanthus* sp.; *Churabana* sp.

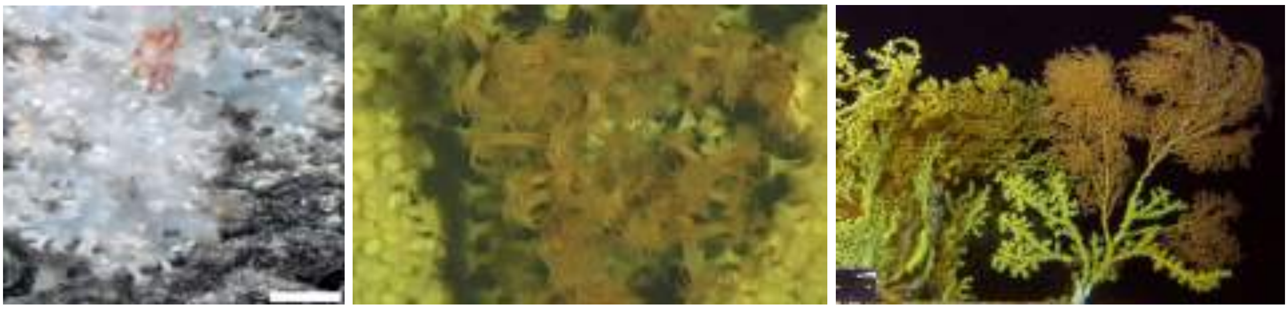


Figure 61 B: from the left, different colonies of: Parachurabana sp. (scale bar D 20 mm); Kauluzoanthus sp.; Kulamanamana sp.

VIII. IX. X. Genus: *Corallizoanthus* (Reimer in Reimer Nonaka Sinniger & Iwase, 2008), *Zibrowius* (Sinniger, Ocaña & Baco, 2013), *Mesozoanthus* (Sinniger, Ocaña & Baco, 2009)

These genera are frequently discussed in different contexts, such as deep-sea and cold-water corals (figure 62); recent studies highlight the presence of new species/associations, confirming that the taxonomy of the group remains expanding and requires further integration (Silva et al., 2017).

Figure 62: from the left, colonies of: *Corallizoanthus* sp. (scale bar 0,5 cm); Zibrowius sp.; Mesozoanthus sp. (scale bar 1 cm).

XI. Genus *Isozoanthus* (Carlgren in Chun, 1903)

The genus (Figure 63) presents limitations regarding its identification using only criteria based on sphincter and external morphology; therefore, molecular analysis is often necessary for confirmation.

Figure 63: different colonies and species of *Isozoanthus* genus; from the left: *Isozoanthus Sulcatus*; *Isozoanthus antumbrosus*; *Isozoanthus canapesi*.

XII. Genus *Parazoanthus* (Haddon & Shackleton, 1891)

Genus (Figure 64) now restructured; modern diagnosis uses host and genetics (Ocaña, Baco, 2013).

Figure 64: from the left, different colonies of *Parazoanthus*: *axinellae*, *swiftii* and *Anguicumus*.

XIII. Genus *Savalia* (Nardo, 1844)

These organisms (Figure 65) are often associated with specific substrates (gorgonians/octocorals or biogenic structures); they also have a great ecological importance (as they can give birth to particularly long-lived structures).

Figure 65: from the left, different colonies of *Savalia*: *lucifica*; *savalia*; *lucifica*.

XIV. XV. Genus: *Umimayanthus* (Montenegro, Sinniger & Reimer, 2015) e *Vitrumanthus* (Kise, Montenegro & Reimer, 2022)

Both distinct genera (Figure 66) emerged from phylogenetic rearrangements of complexes historically attributed to *Zoanthus/Palythoa*. The distinction requires morphological and genetic integration, as external traits (colour, tentacle density) are highly plastic (Daly et al., 2007).

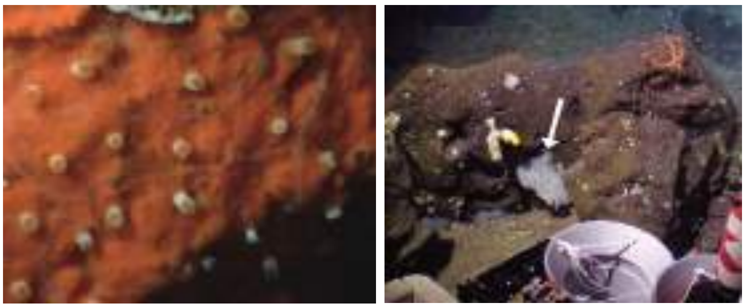


Figure 66: from the left: *Umimayanthus* sp. and *Vitrumanthus* sp. colonies.

7.2 Complete morphological catalogue

After the literature review, the primary aim was to develop two morphological catalogue that was used as a comprehensive reference database featuring high-resolution diagnostic imagery and descriptions for field-based identification. These two catalogues are divided in one page for each genus and one page for each species reported in literature as present in the Indopacific area (from Table X to Table X; inside these, all the photos contorted in red, aren't coming from scientific sources).

7.2.1 Corallimorpharia (Carlgren, 1943)

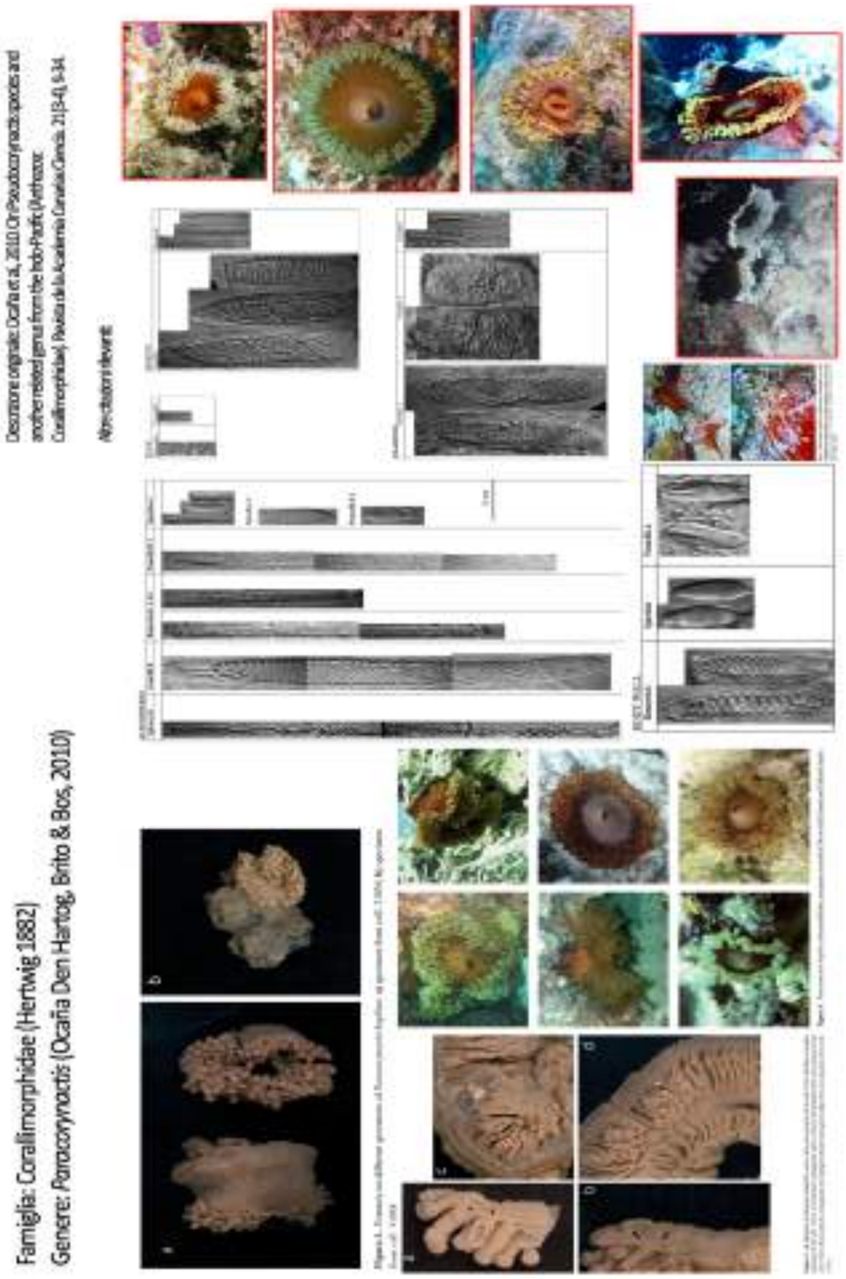


Table 14: all the images in the table refer to the genus *Paracorynactis*.

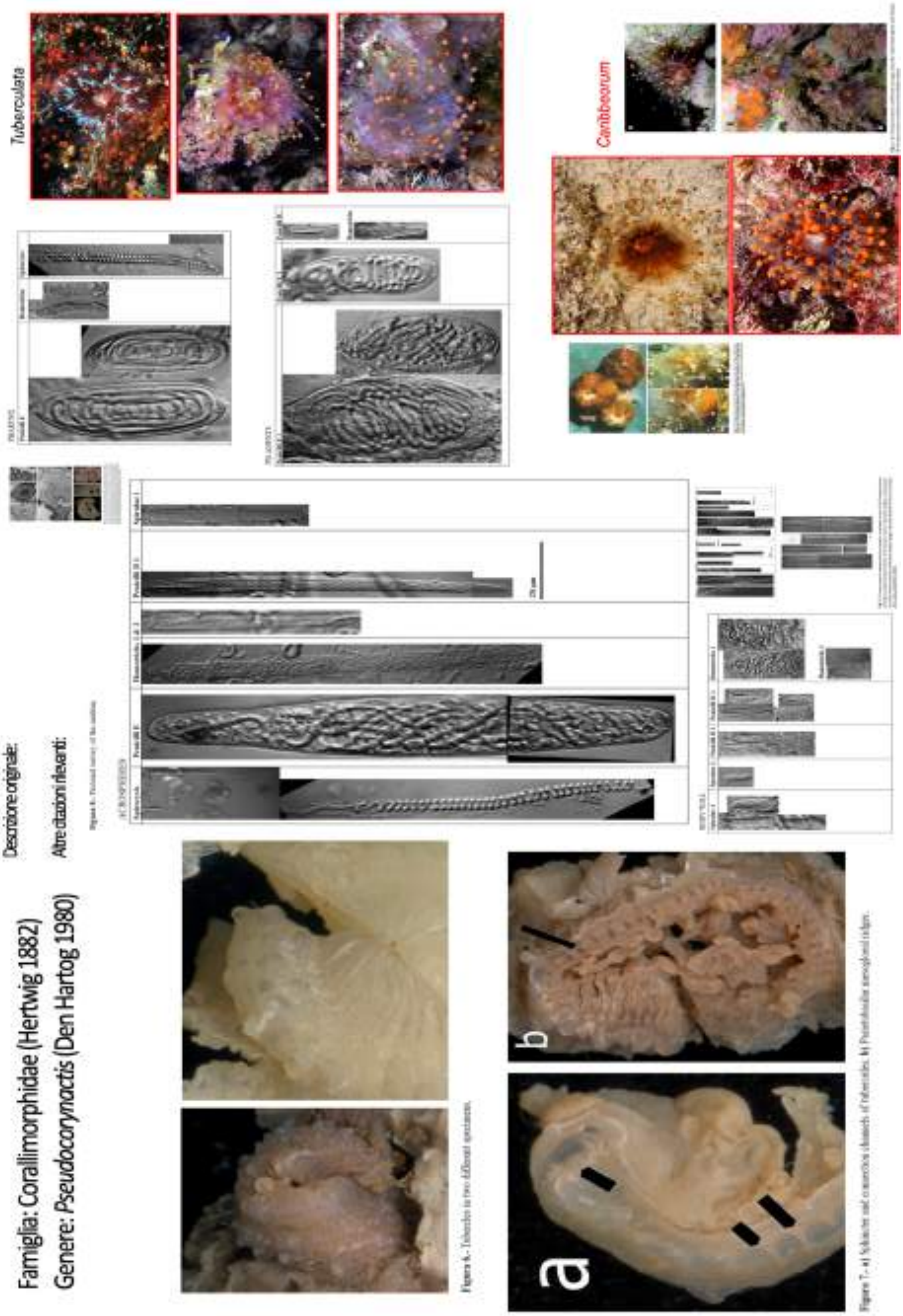


Table 15: all the images in the table refer to the genus *Pseudocaracorynactis*.

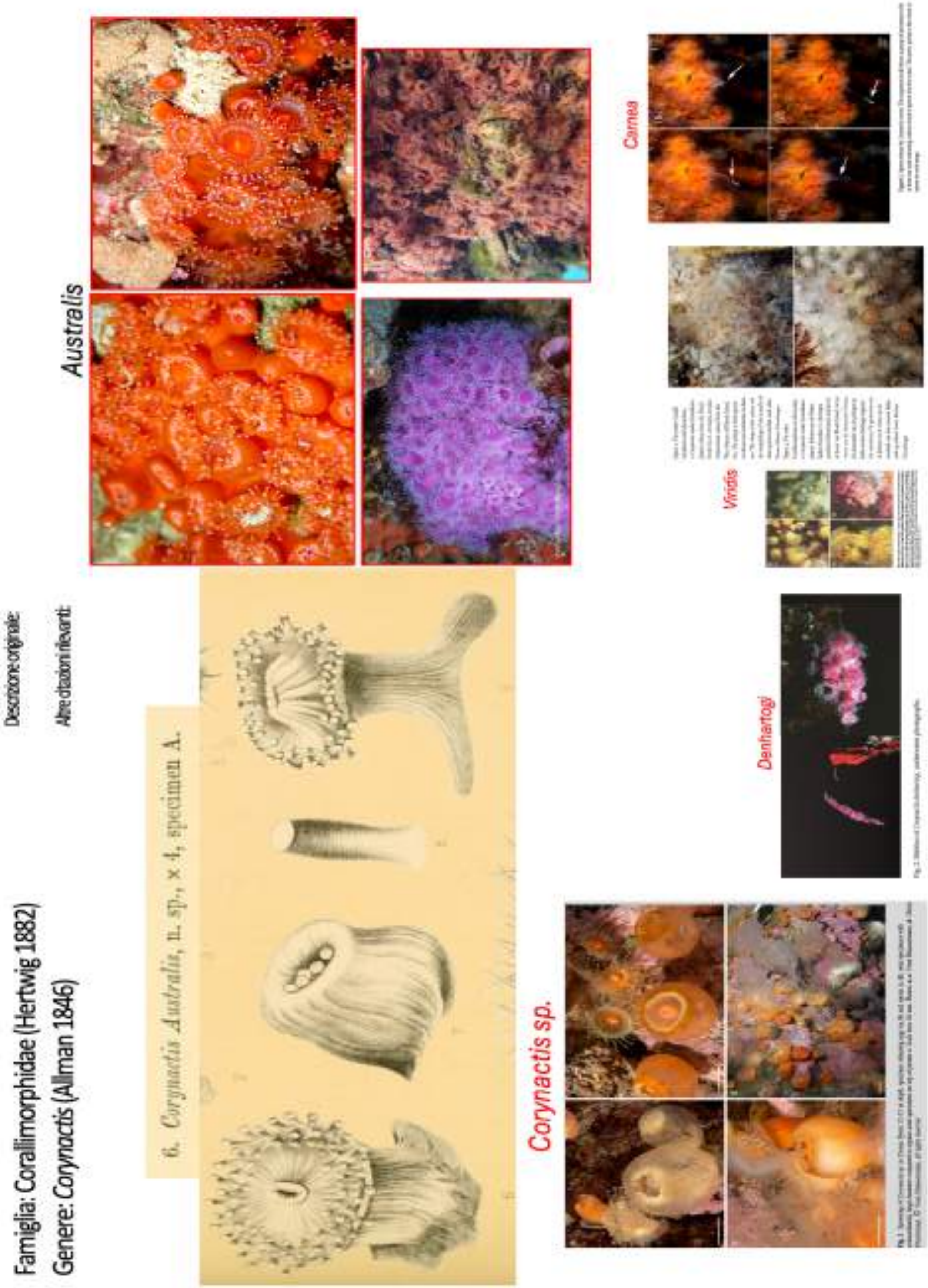


Table 16: all the images in the table refer to the genus *Corynactis*.

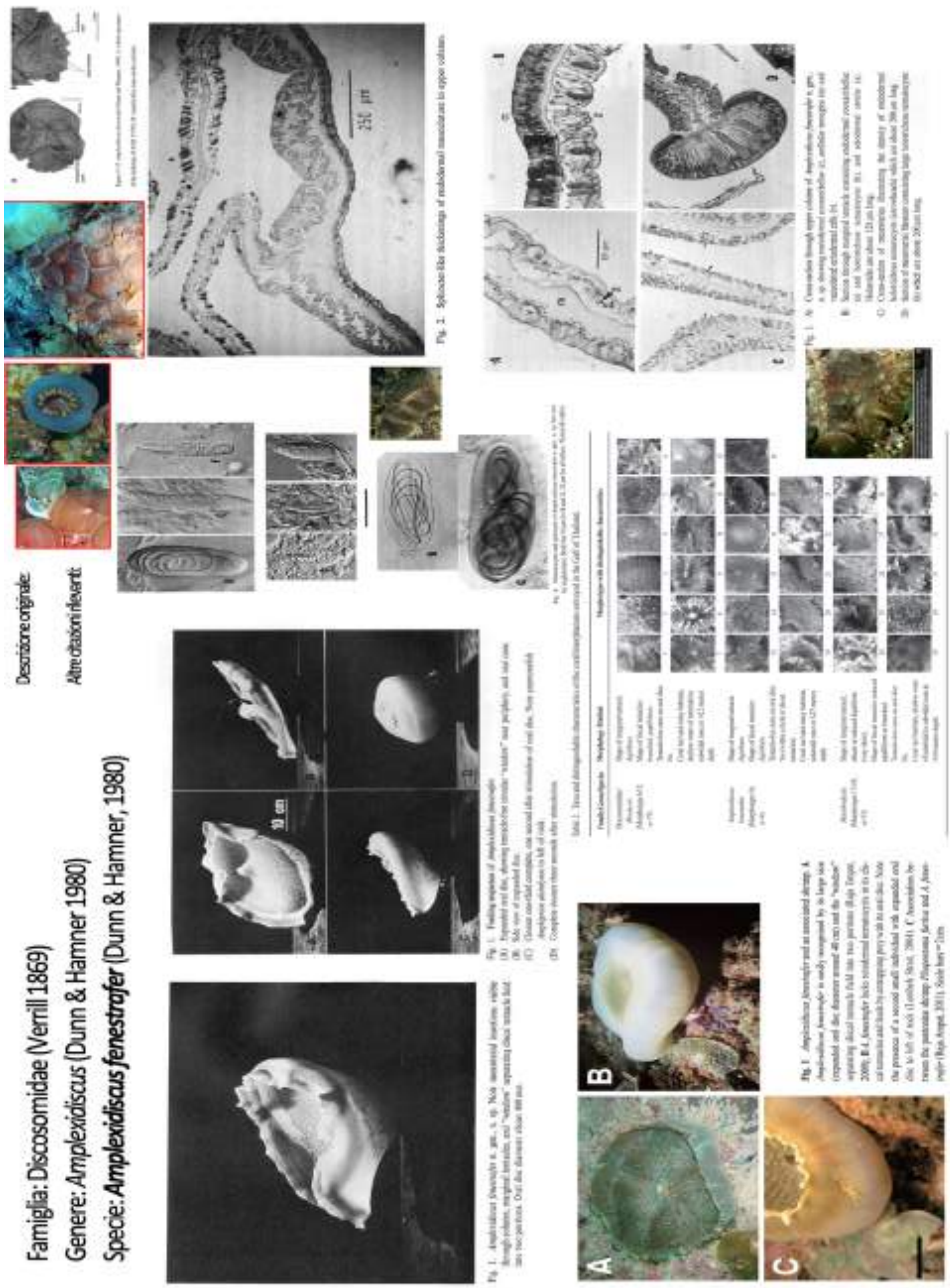


Table 17: all the images in the table refer to the species *Amplexidiscus fenestrafer* (the only species which belongs to this genus).

Famiglia: Discosomidae (Verrill 1869)
Genere: *Discosoma* (Rüppell & Leuckart 1828)

Descrizione originale:

Altre citazioni rilevanti:

Table 18: all the images in the table refer to the genus *Discosoma*.

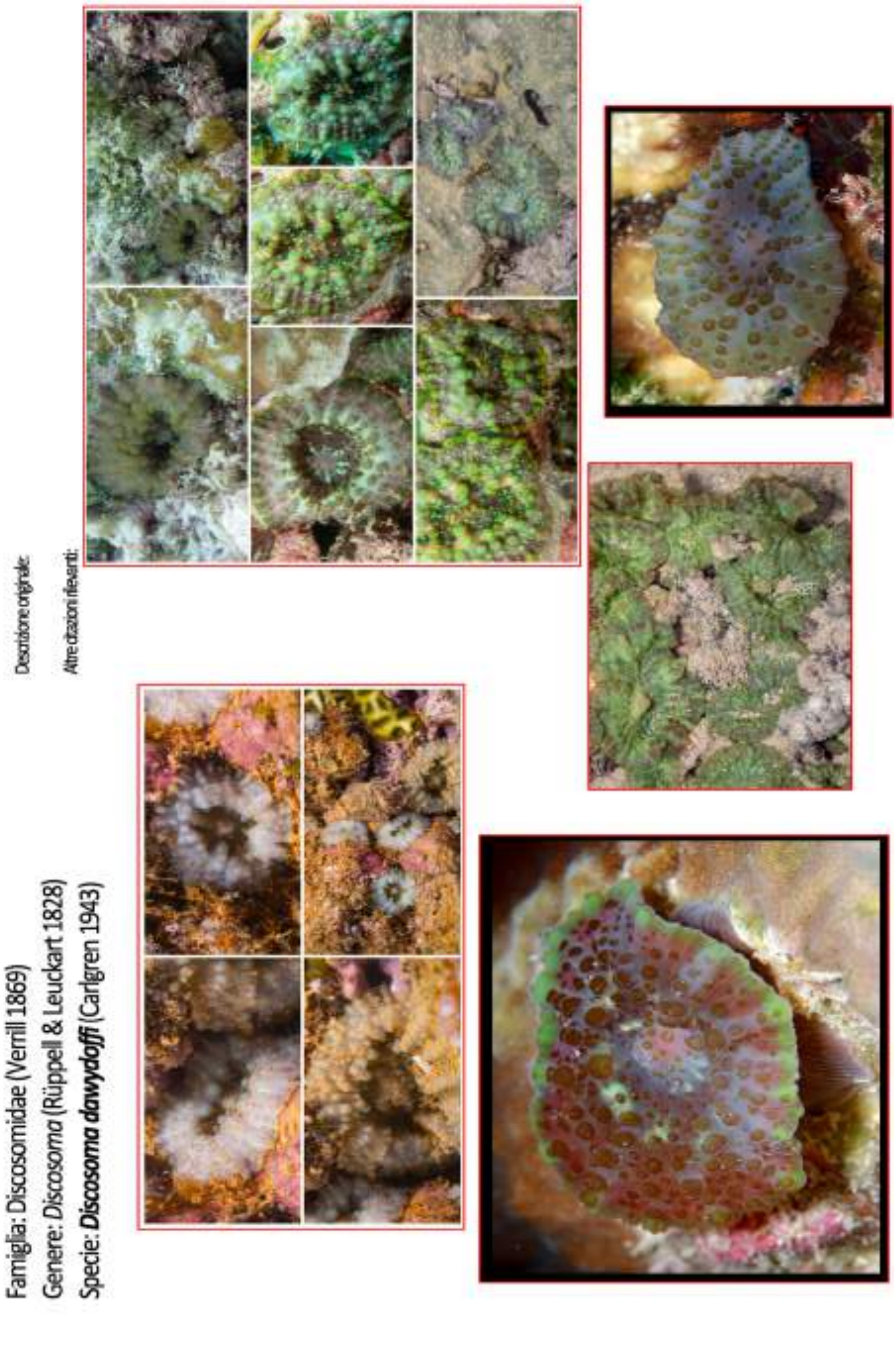


Table 19: all the images in the table refer to the species *Discosoma dawydoffi*.

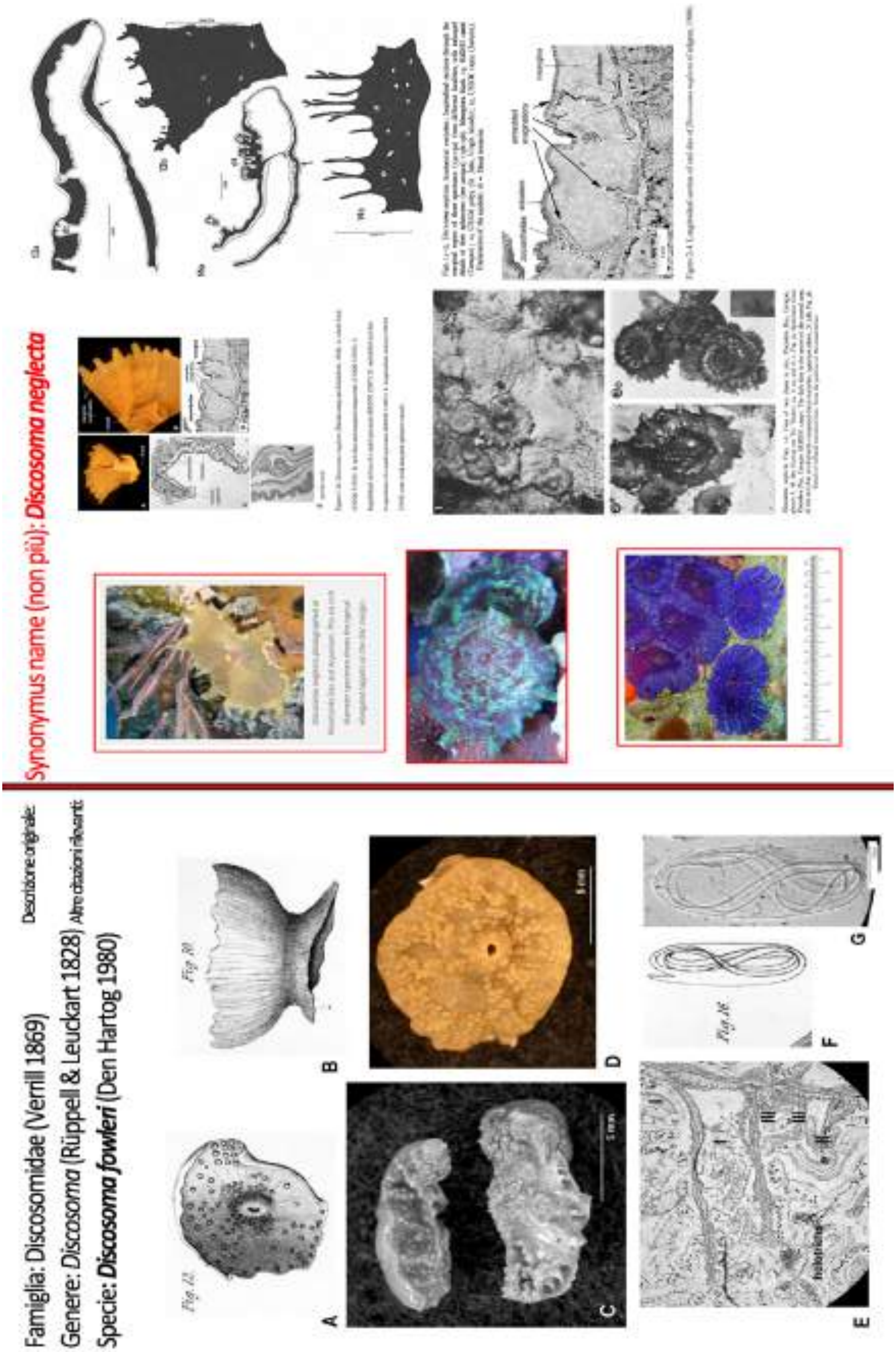


Table 20: all the images in the table refer to the species *Discosoma fowleri*.

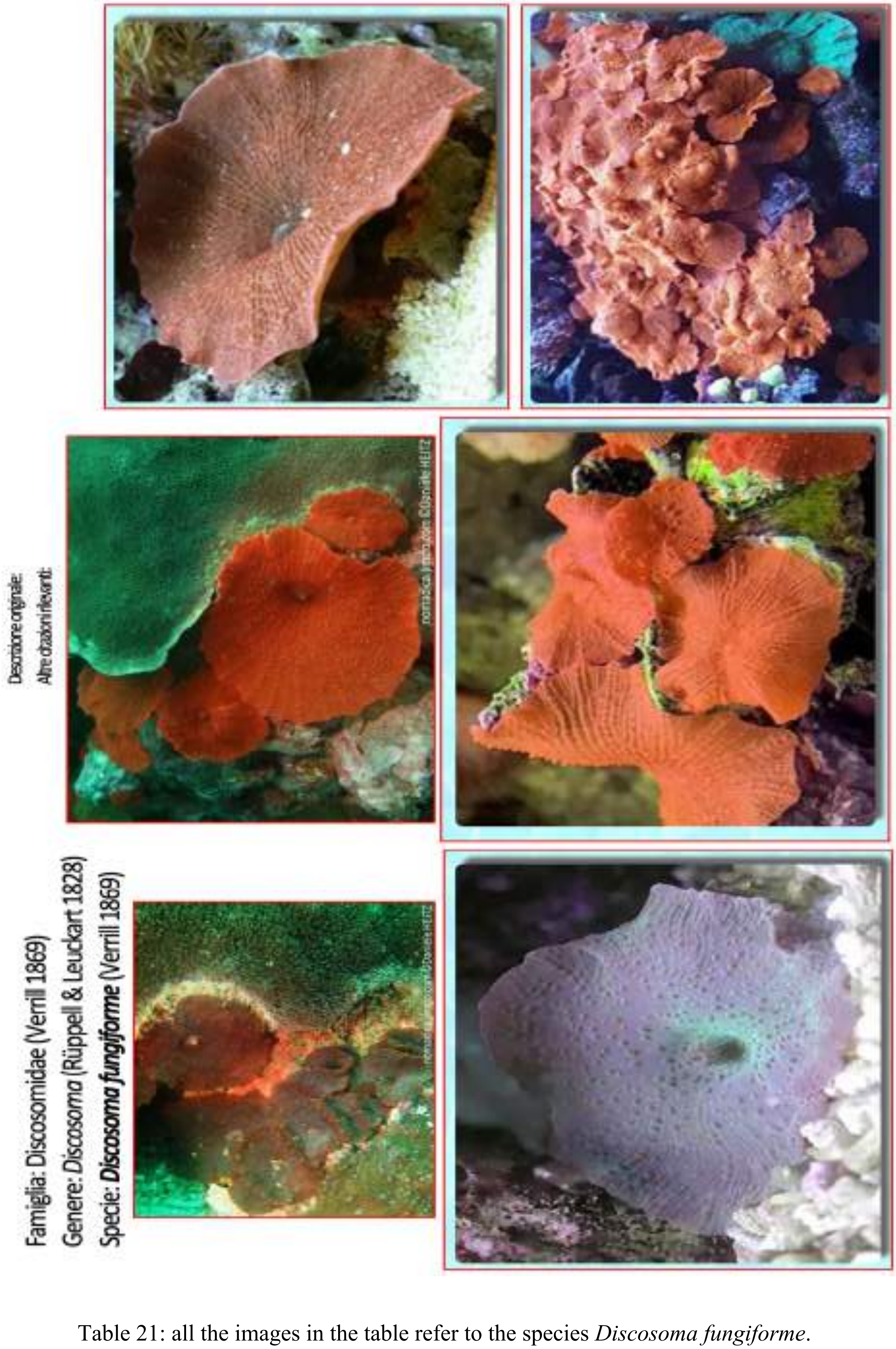
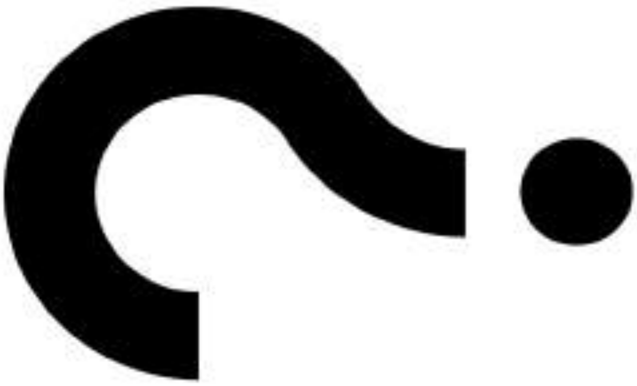


Table 21: all the images in the table refer to the species *Discosoma fungiforme*.

Famiglia: Discosomidae (Verrill 1869)
Genere: *Discosoma* (Rüppell & Leuckart 1828)
Specie: ***Discosoma molle*** (Couthouy in Dana 1846)



Descrizione originale:

Altre citazioni rilevanti:

Table 22: about the species *D*iscosoma *molle* not one single photos/images were found.

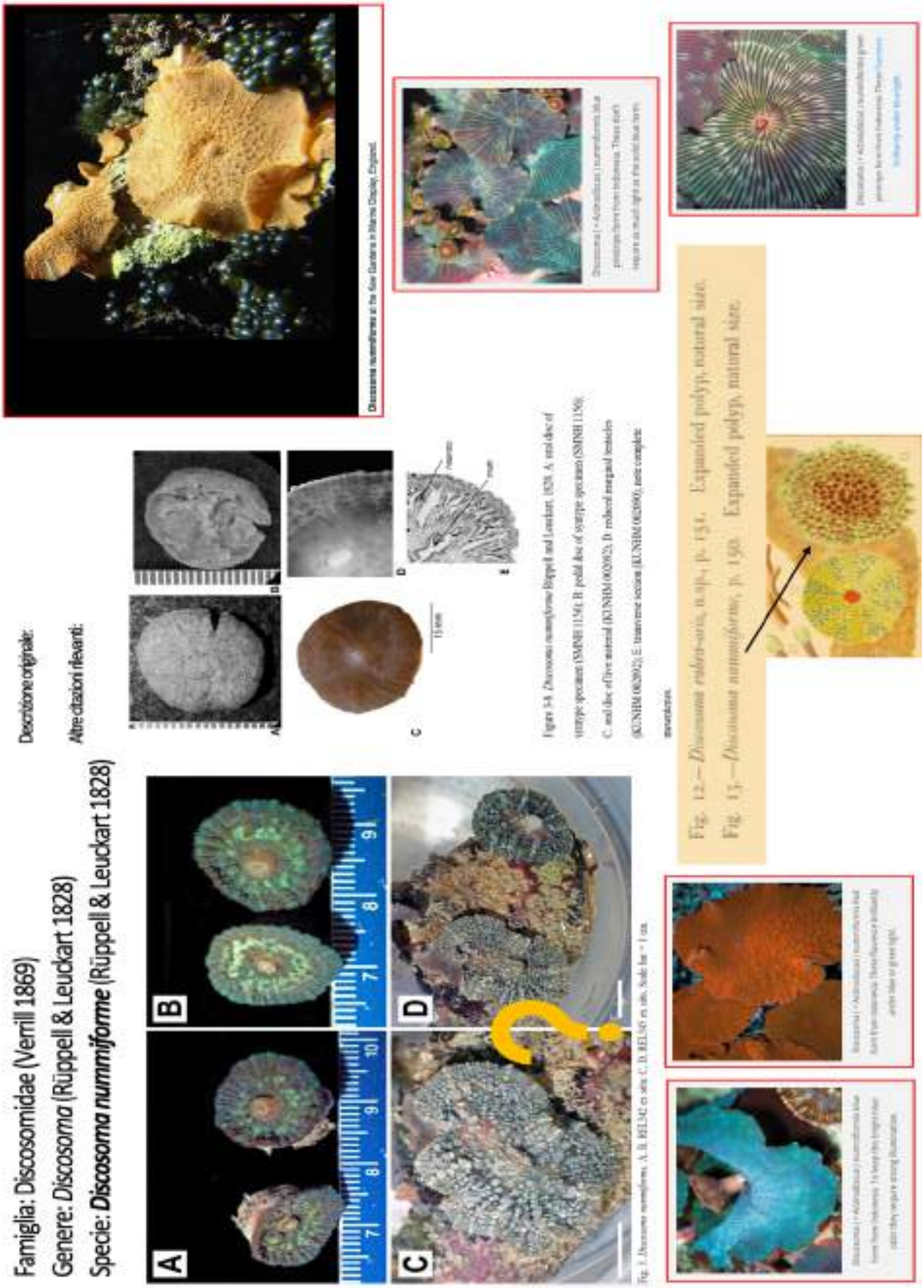


Table 23: all the images in the table refer to the species *Discosoma nummiforme*.

Famiglia: Discosomidae (Verrill 1869)

Genere: *Discosoma* (Rüppell & Leuckart 1828)

Specie: ***Discosoma rubraoris*** (Saville-Kent 1893)

Descrizione originale:

Altre citazioni rilevanti:

Fig. 12.—*Discosoma rubra-oris*, n.sp., p. 151. Expanded polyp, natural size.

Fig. 13.—*Discosoma nummiforme*, p. 150. Expanded polyp, natural size.

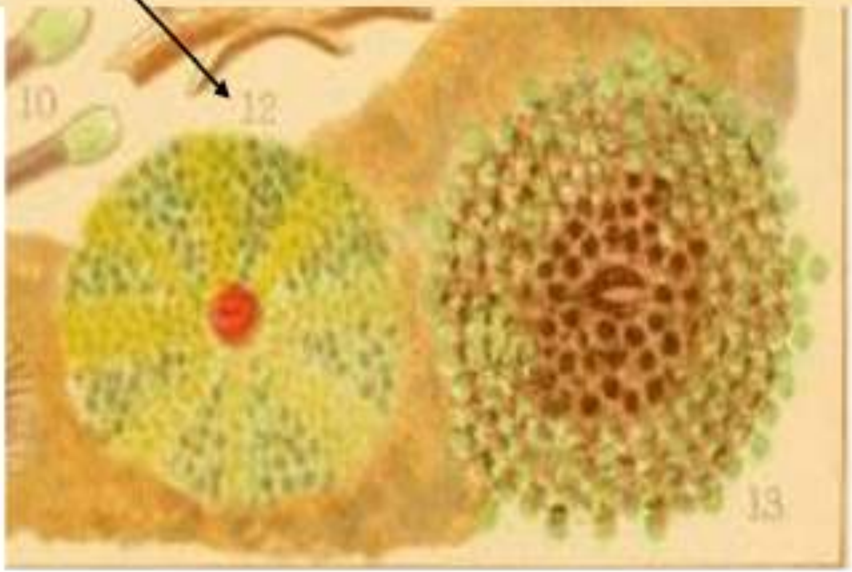


Table 24: all the images in the table refer to the species *Discosoma rubraoris*.

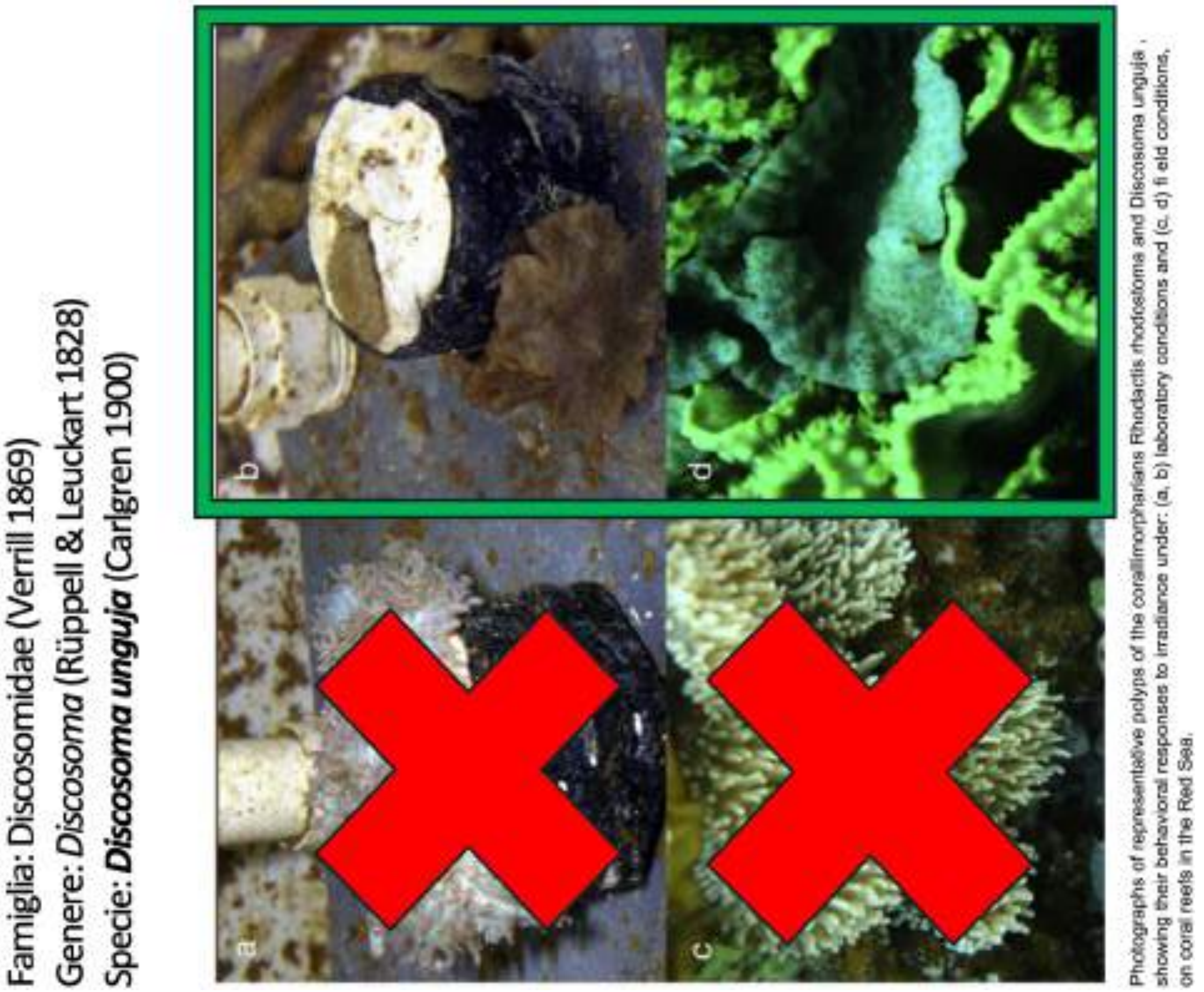


Table 25: all the images in the table refer to the species *Discosoma unguja*.

Famiglia: Discosomidae (Verrill 1869)
Genere: *Discosoma* (Rüppell & Leuckart 1828)
Specie: ***Discosoma viridescens*** (Quoy & Gaimard 1833)

Table 26: all the images in the table refer to the species *Discosoma viridescens*.

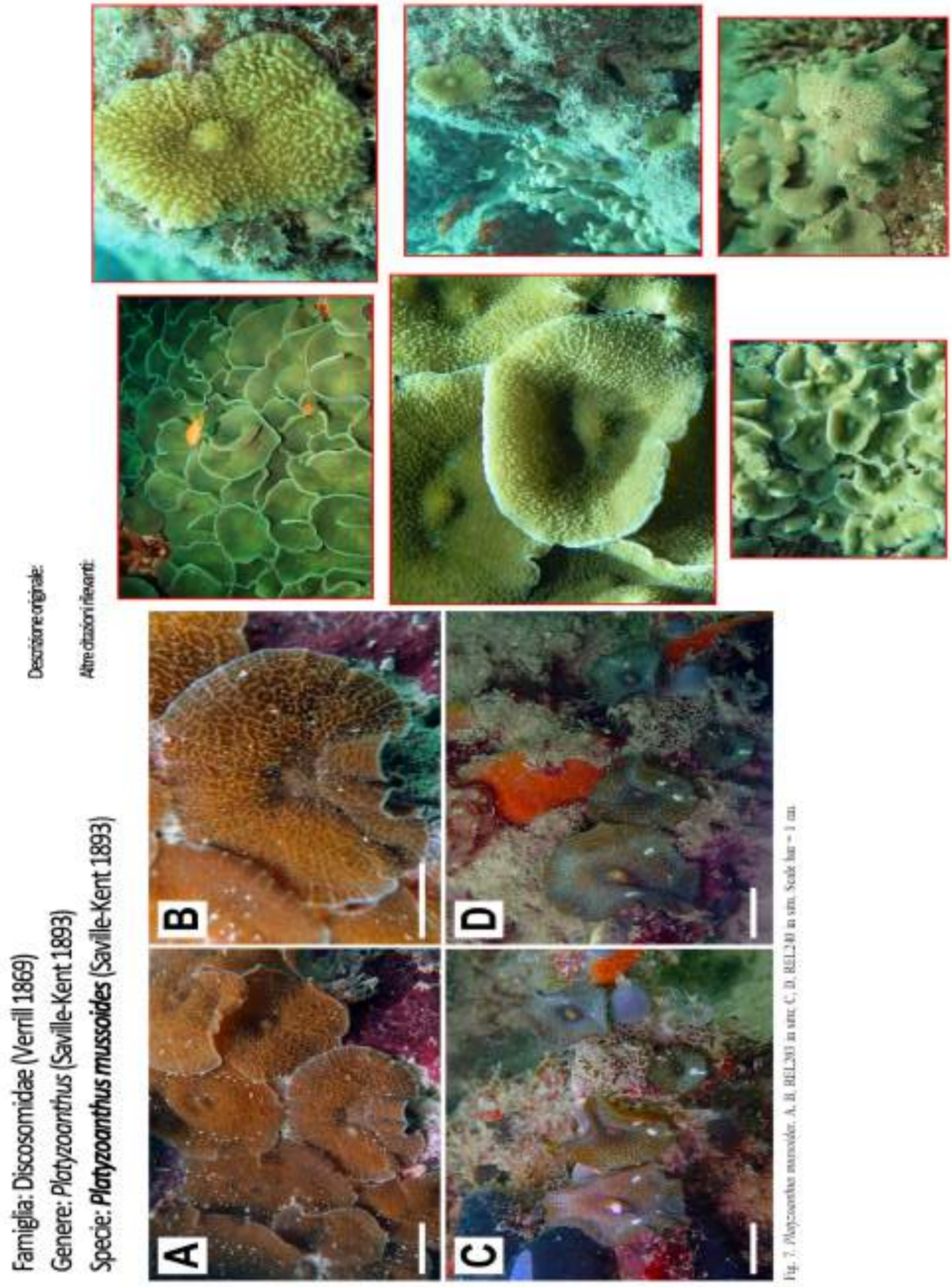


Table 27: all the images in the table refer to the species *Platyzoanthus mussoides* (the only species which belongs to this genus).

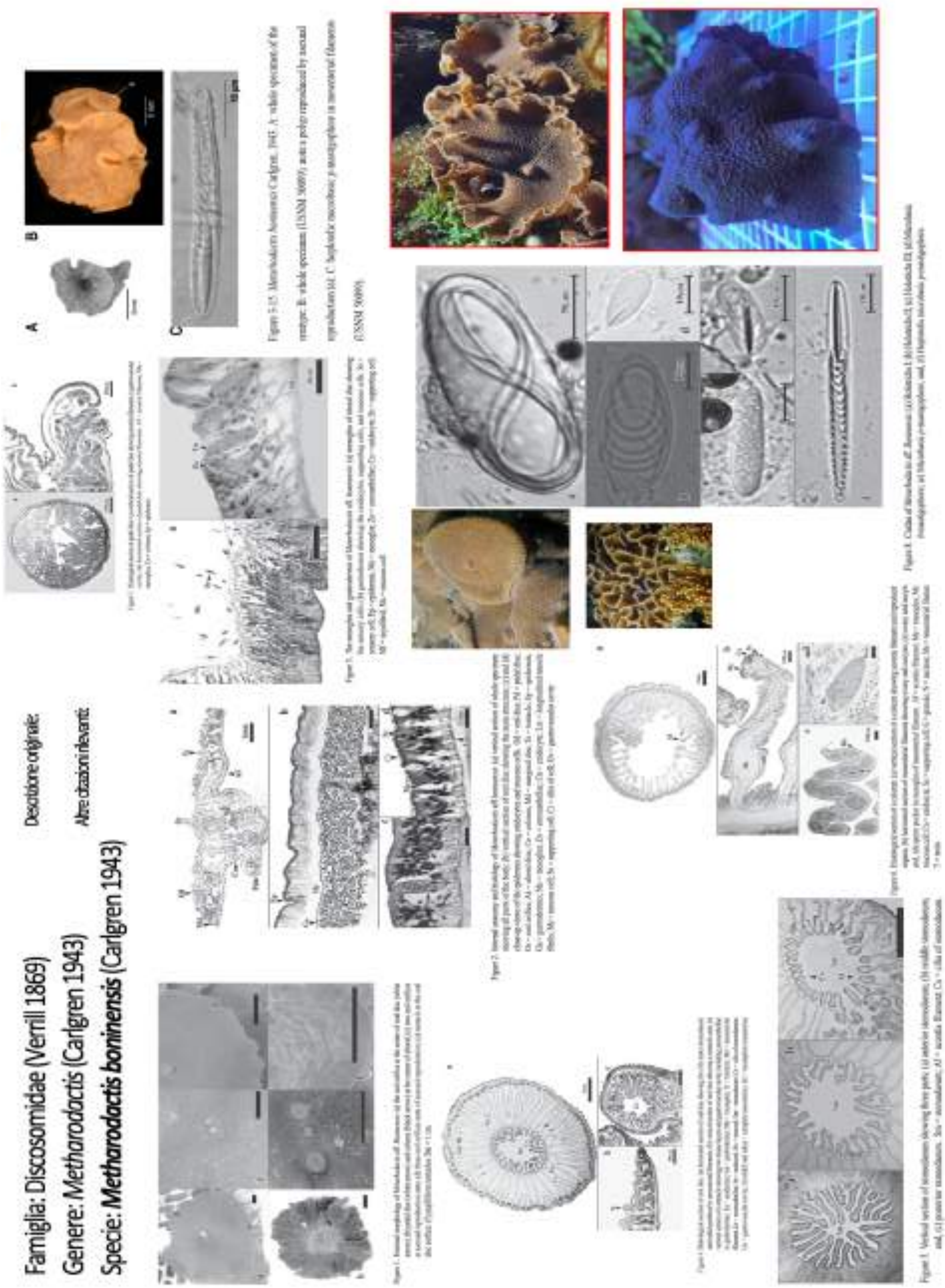


Table 28: all the images in the table refer to the species *Metharodactis boninensis* (the only species which belongs to this genus).

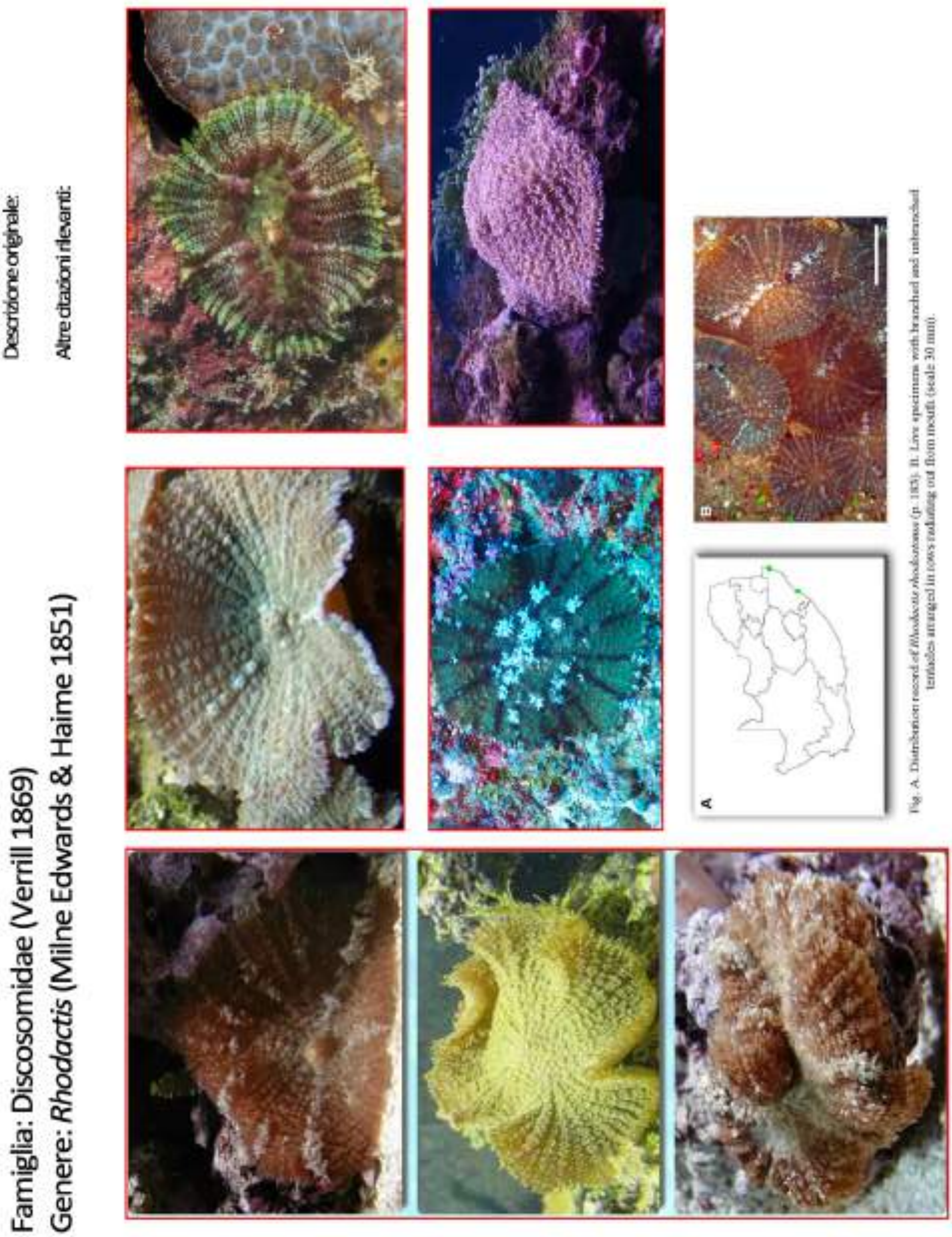


Table 29: all the images in the table refer to the genus *Rhodactis*.

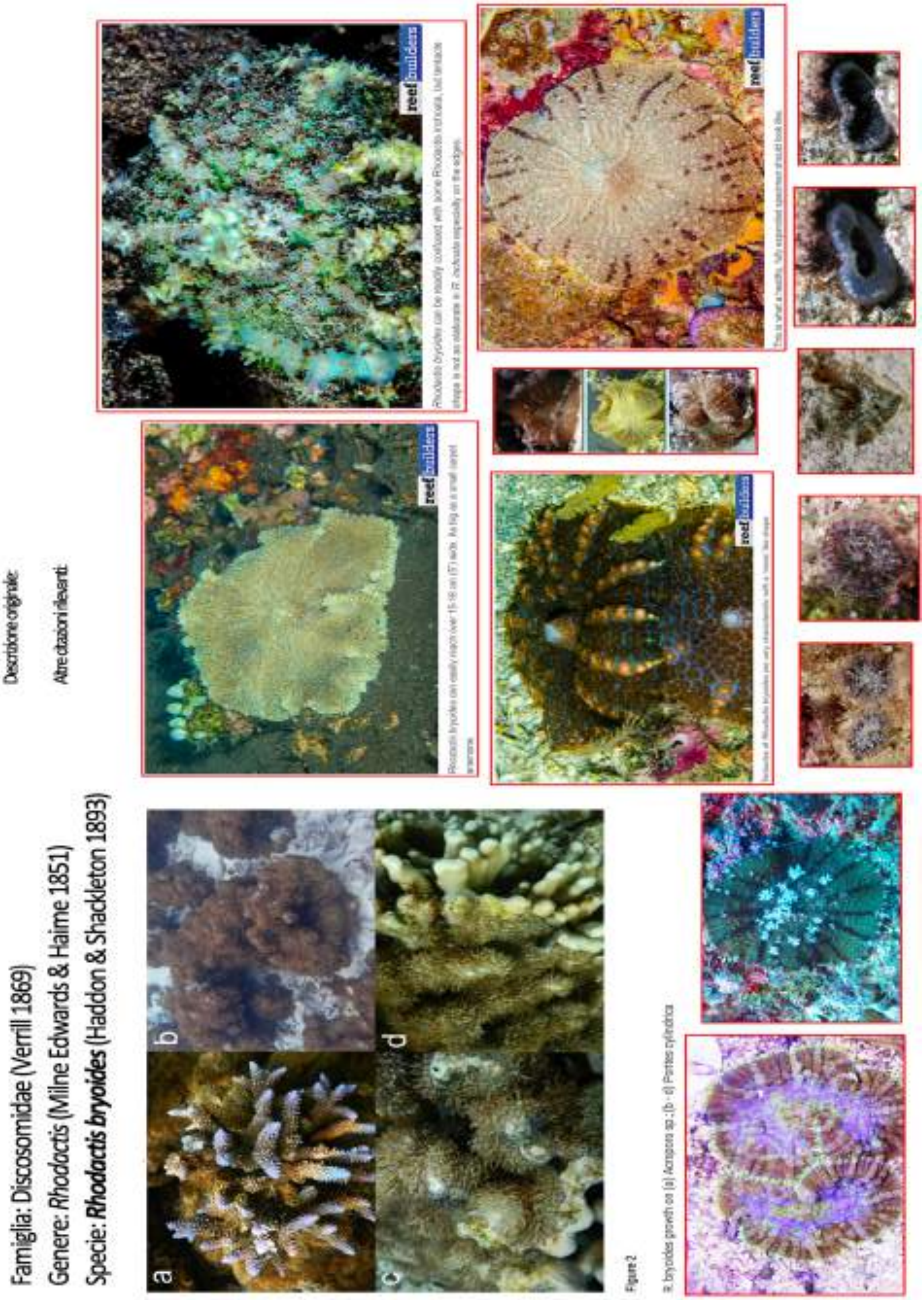
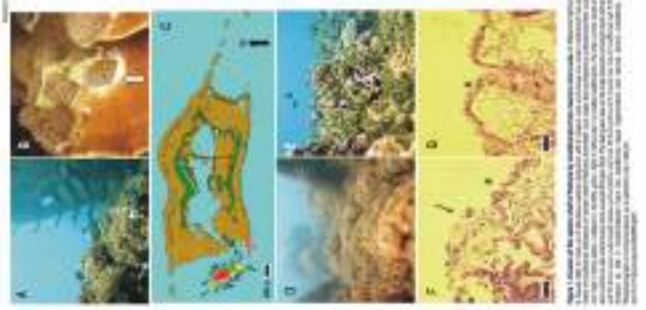


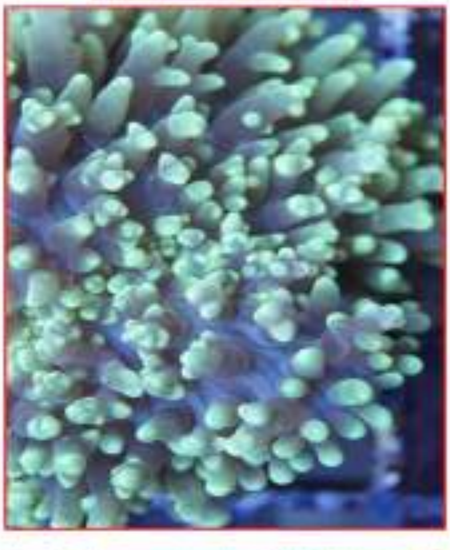
Table 30: all the images in the table refer to the species *Rhodactis bryoides*.

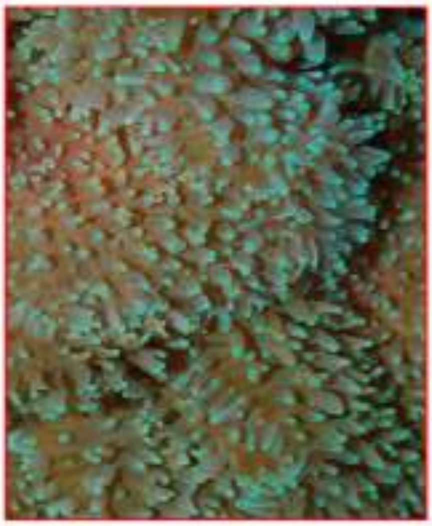
Famiglia: Discosomidae (Verrill 1869)
Genere: *Rhodactis* (Milne Edwards & Haime 1851)
Specie: ***Rhodactis howesii*** (Saville-Kent 1893)



Descrizione originale:

Altre citazioni rilevanti:





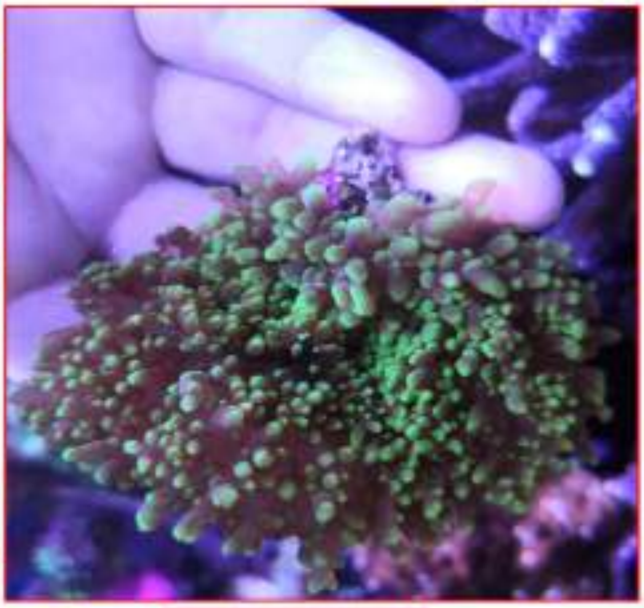


Table 31: all the images in the table refer to the species *Rhodactis howesii*.

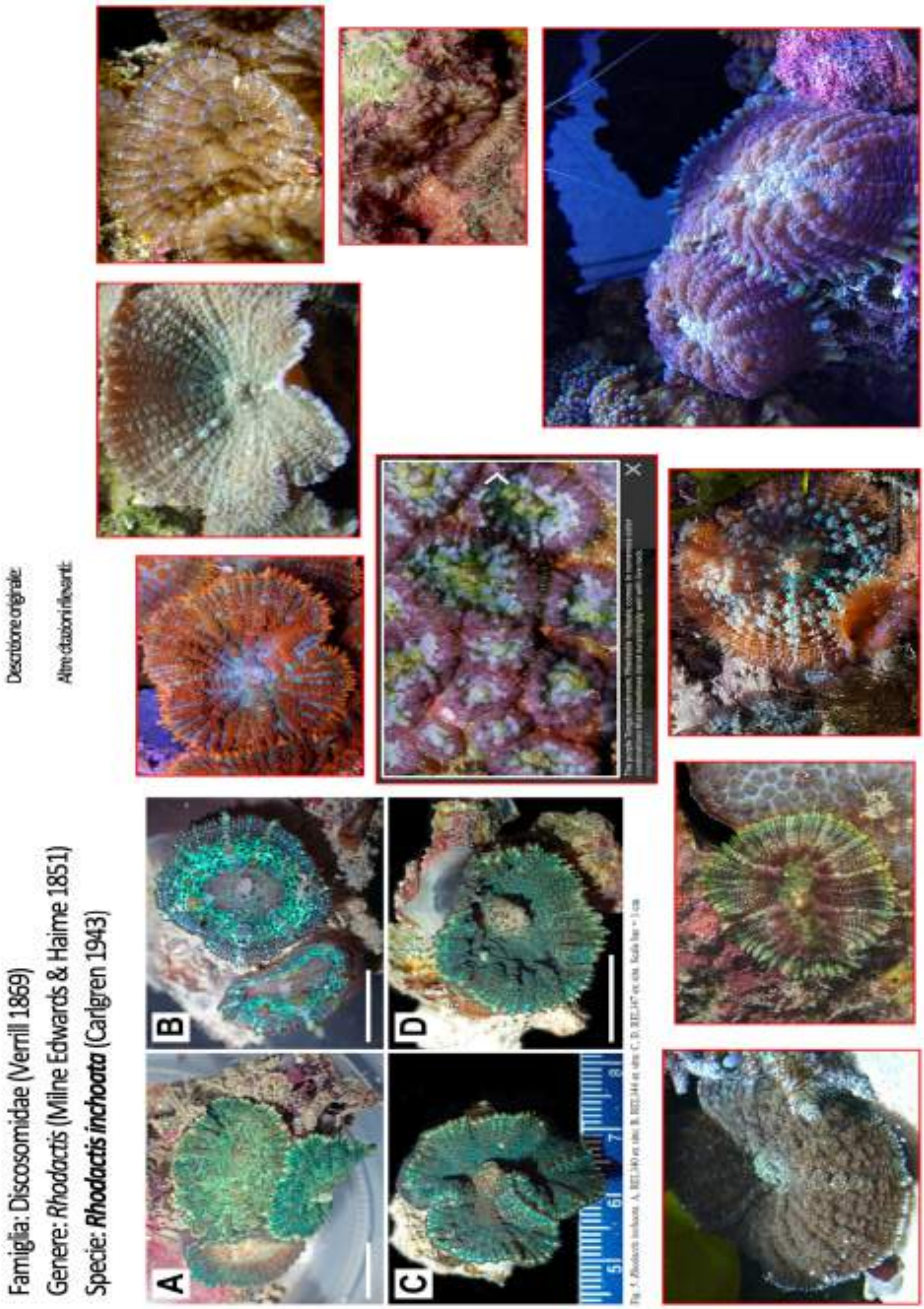


Table 32: all the images in the table refer to the species *Rhodactis inchoata*.

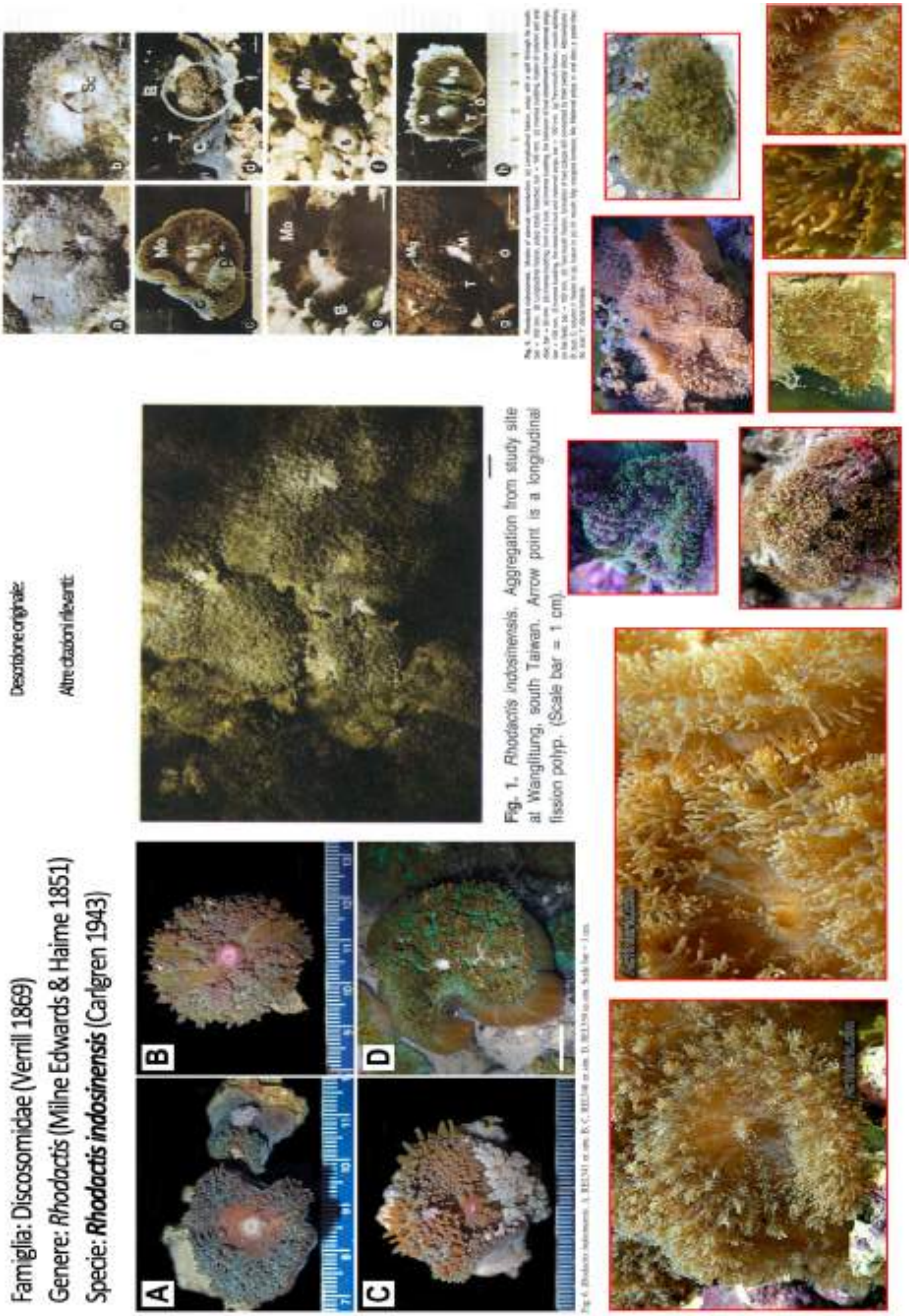


Table 33: all the images in the table refer to the species *Rhodactis indosinensis*.

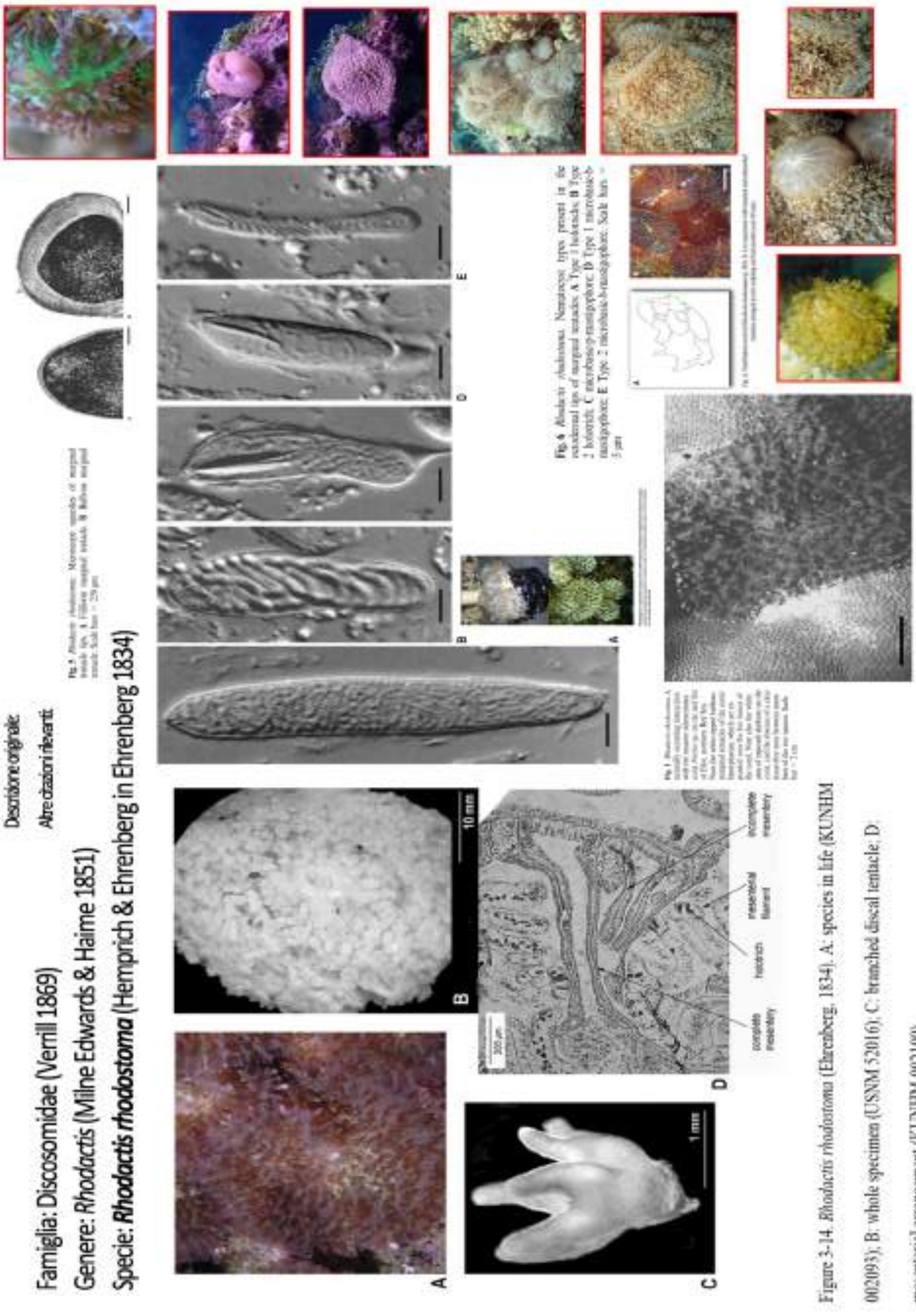


Table 34: all the images in the table refer to the species *Rhodactis rhodostoma*.

7.2.2 Zoantharia (Gray, 1832)

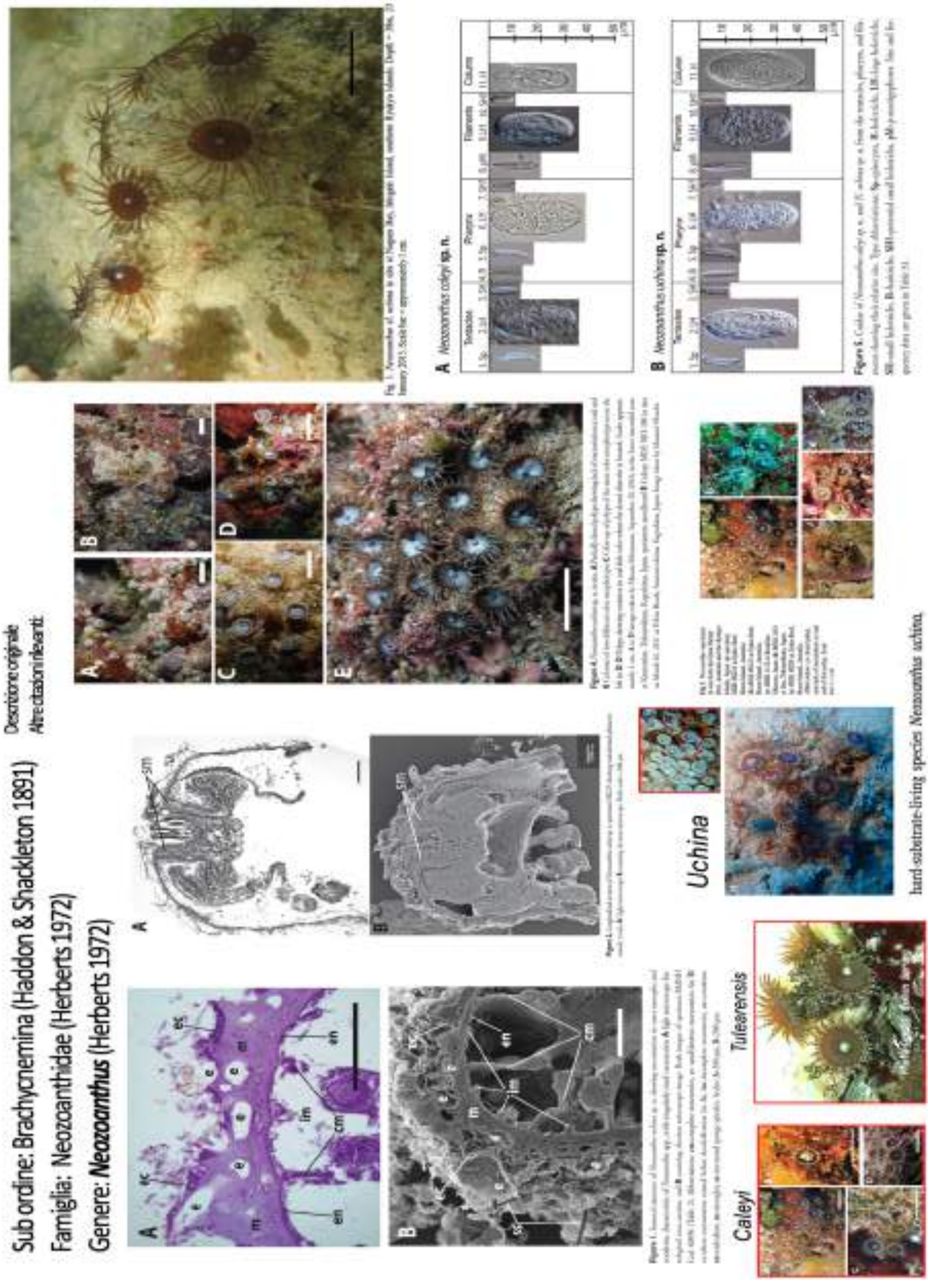


Table 35: all the images in the table refer to the genus *Neozoanthus*.

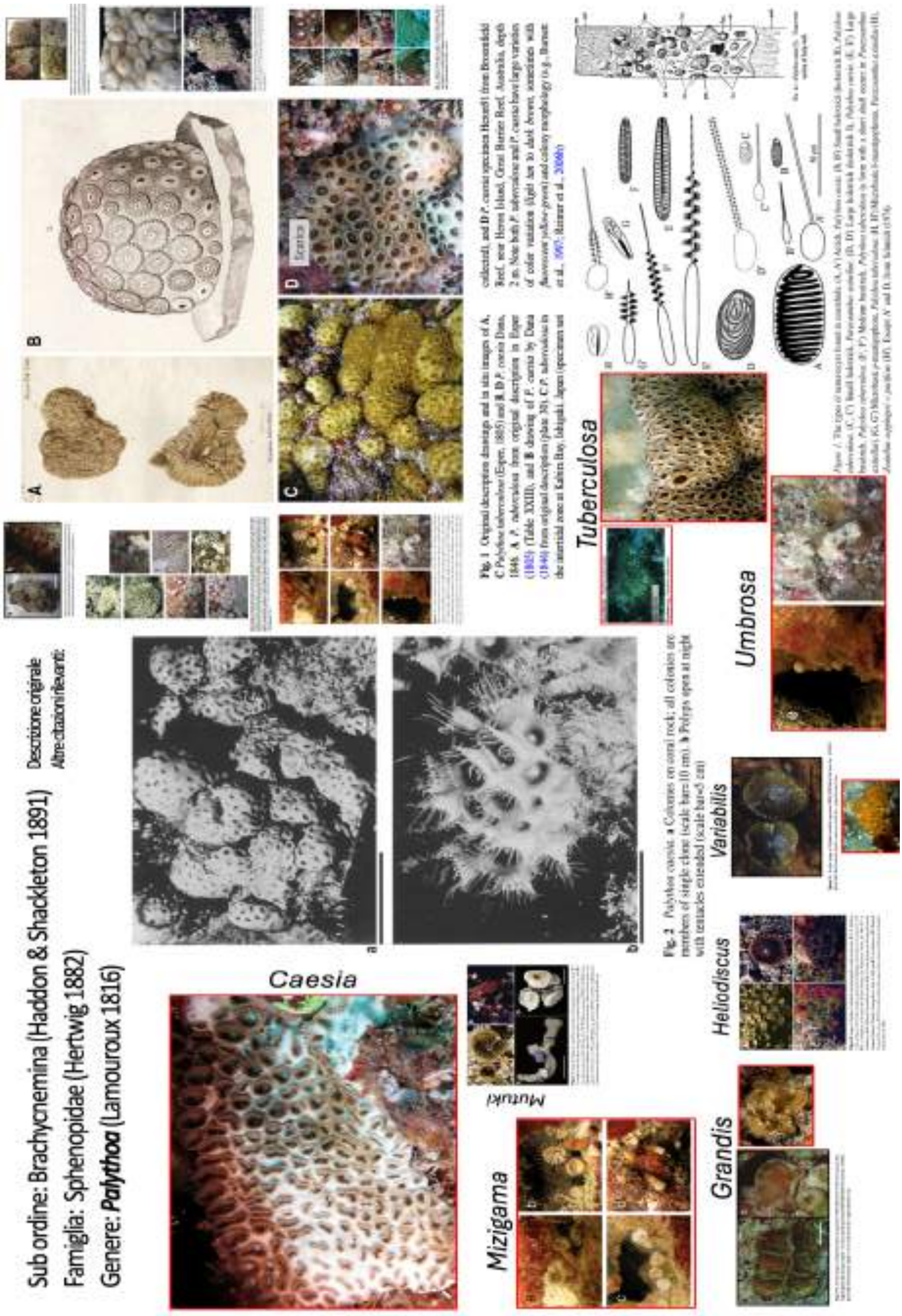


Table 36: all the images in the table refer to the genus *Palythoa*.

Sub ordine: Brachycnemina (Haddon & Shackleton 1891)
Famiglia: Sphenopidae (Hertwig 1882)
Genere: ***Palythoa*** (Lamouroux 1816)
Specie: ***Palythoa caesia*** (Dana 1846)

Descrizione originale
Altre citazioni rilevanti:

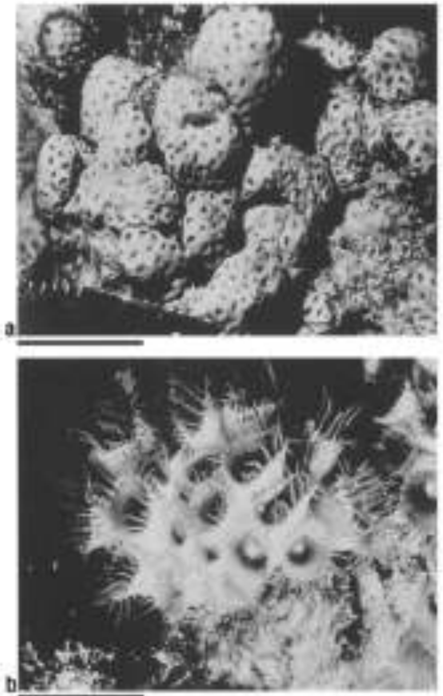


Fig. 2 *Palythoa caesia*. **a** Colonies on coral rock; all colonies are members of single clone (scale bar=10 cm). **b** Polyps open at night with tentacles extended (scale bar=5 cm)

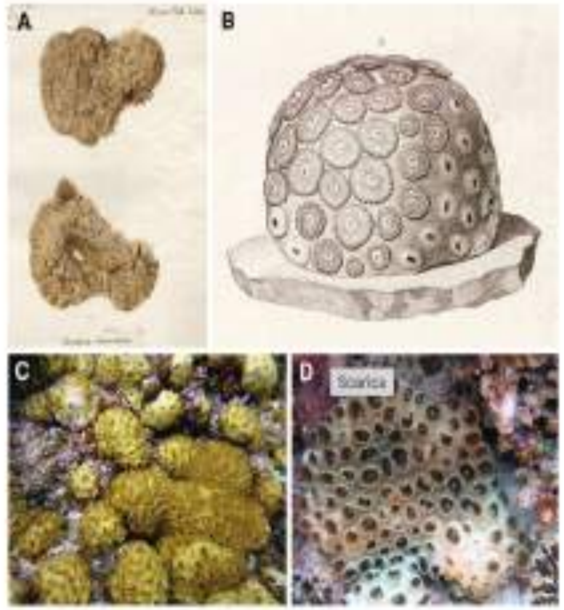


Fig. 1 Original description drawings and in situ images of **A**, **C** *Palythoa tuberculosa* (Esper, 1805) and **B**, **D** *P. caesia* Dana, 1846. **A** *P. tuberculosa* from original description in Esper (1805) (Table XXIII), and **B** drawing of *P. caesia* by Dana (1846) from original description (plate 30). **C** *P. tuberculosa* in the intertidal zone at Kabira Bay, Ishigaki, Japan (specimen not collected), and **D** *P. caesia* specimen Heron91 from Broomfield Reef, near Heron Island, Great Barrier Reef, Australia, depth 2 m. Note both *P. tuberculosa* and *P. caesia* have large varieties of color variation (light tan to dark brown, sometimes with fluorescent yellow-green) and colony morphology (e.g., Burnett et al., 1997; Reimer et al., 2006b)

Table 37: all the images in the table refer to the species *Palythoa caesia*.

Sub ordine: Brachycnemina (Haddon & Shackleton 1891)

Famiglia: Sphenopidae (Hertwig 1882)

Genere: *Palythoa* (Lamouroux 1816)

Specie: *Palythoa heliodiscus* (Ryland & Lancaster, 2003)

Descrizione originale

Altre citazioni rilevanti:

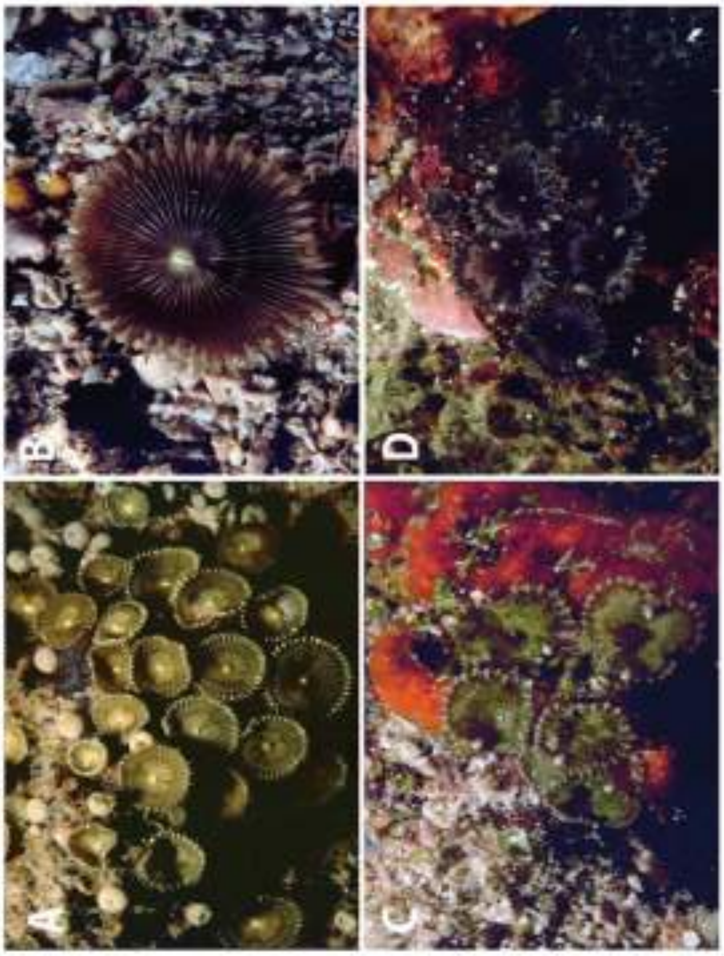
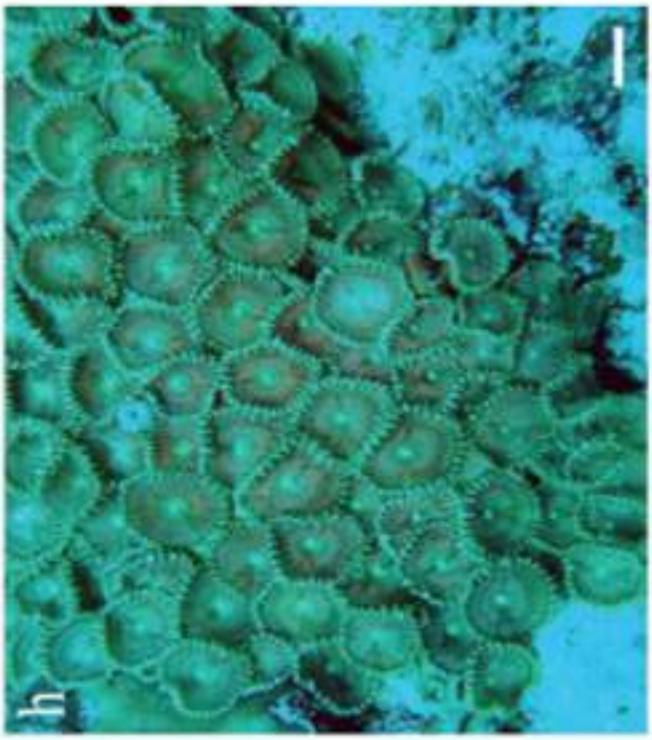


Figure 8. Images of *Palythoa* cf. *heliodiscus* from photographic records in this study. **A** *P.* cf. *heliodiscus* at the northwest side of Pulau Samalona, Spermonde Archipelago, South Sulawesi, November 23, 1997 **B** *P.* cf. *heliodiscus* at the south side of Pulau Derawan, East Kalimantan, October 16, 2003 **C** *P.* cf. *heliodiscus* at REA Wakatobi National Park station WAK.22, north channel pass of Karang Koromaha, Southeast Sulawesi, Wakatobi, Tukang Besi Is., May 12, 2003; and **D** *P.* cf. *heliodiscus* at REA Wakatobi National Park station WAK.18, Southwest Pulau Binongko, Southeast Sulawesi, Wakatobi, Tukang Besi Islands, May 10, 2003.



h. *Palythoa heliodiscus*. Scale bars = 0.5 cm.

Table 38: all the images in the table refer to the species *Palythoa heliodiscus*.

Table 39: all the images in the table refer to the species *Palythoa grandis*.

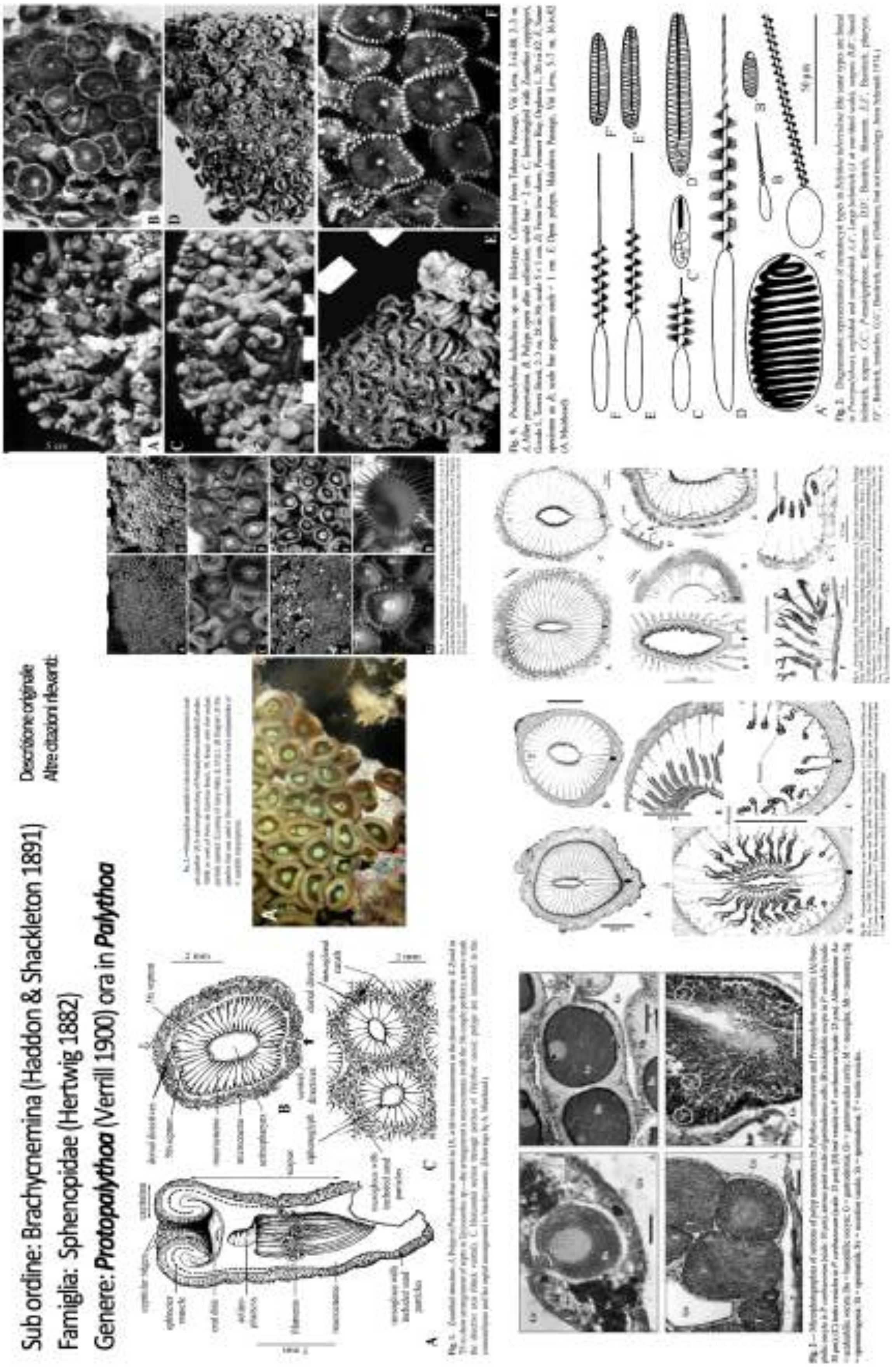


Table 40: all the images in the table refer to the genus *Protopalythoa* (now in the genus Palythoa).

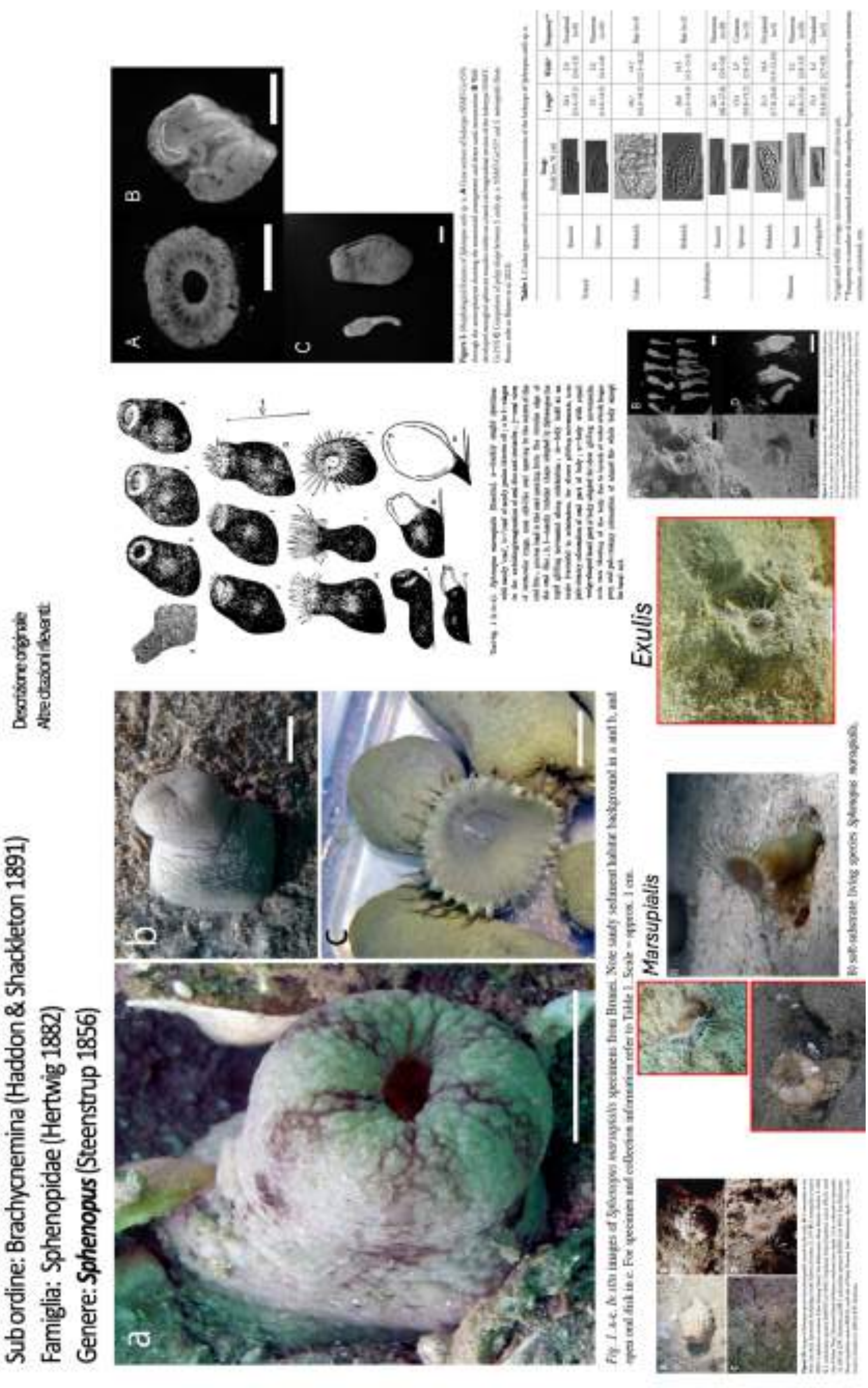


Table 41: all the images in the table refer to the genus *Sphenopus*.

Table 42: all the images in the table refer to the genus *Acrozoanthus* and his only one species *Acrozoanthus australiae*.

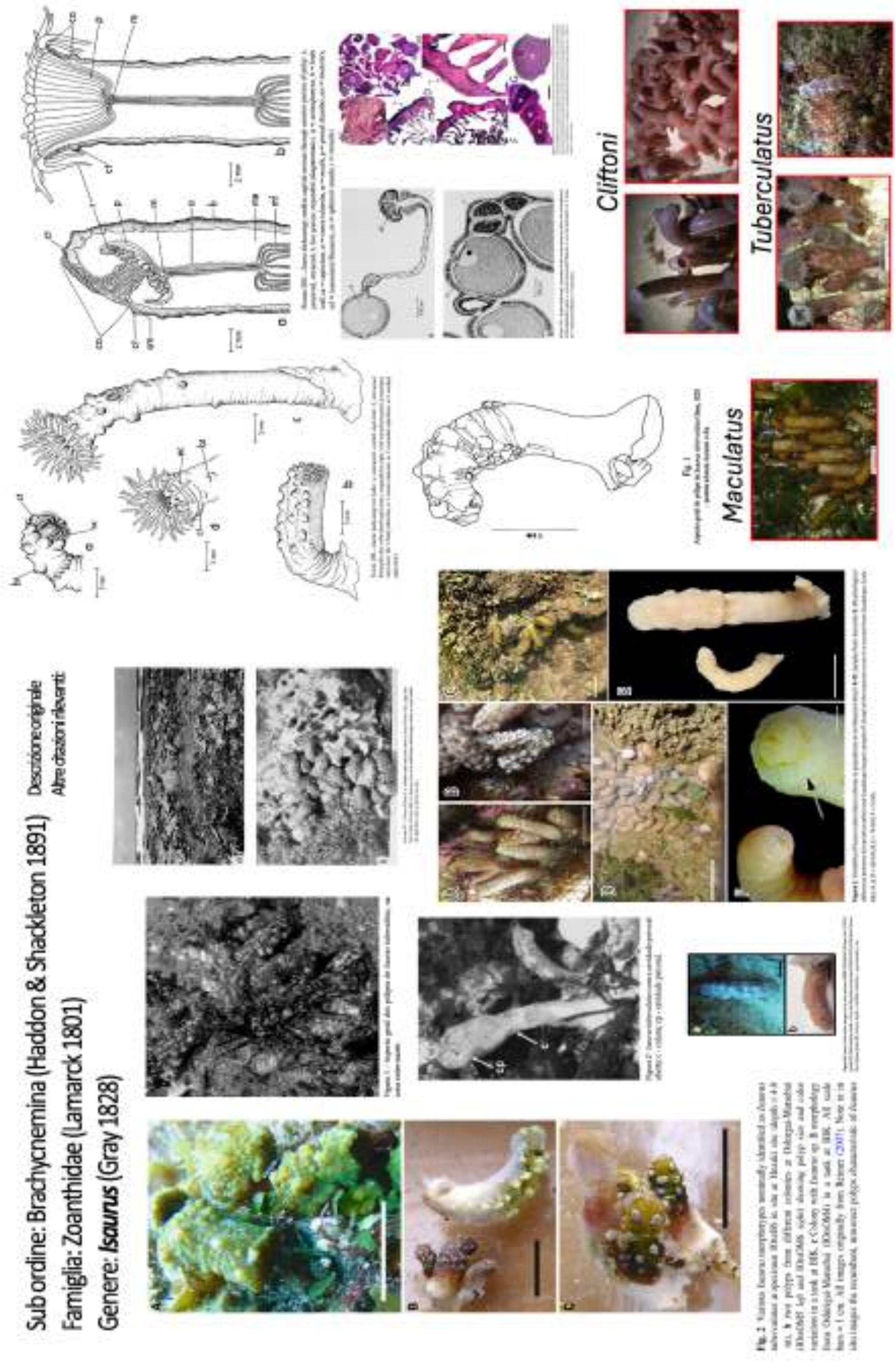


Table 43: all the images in the table refer to the genus *Isaurus*.

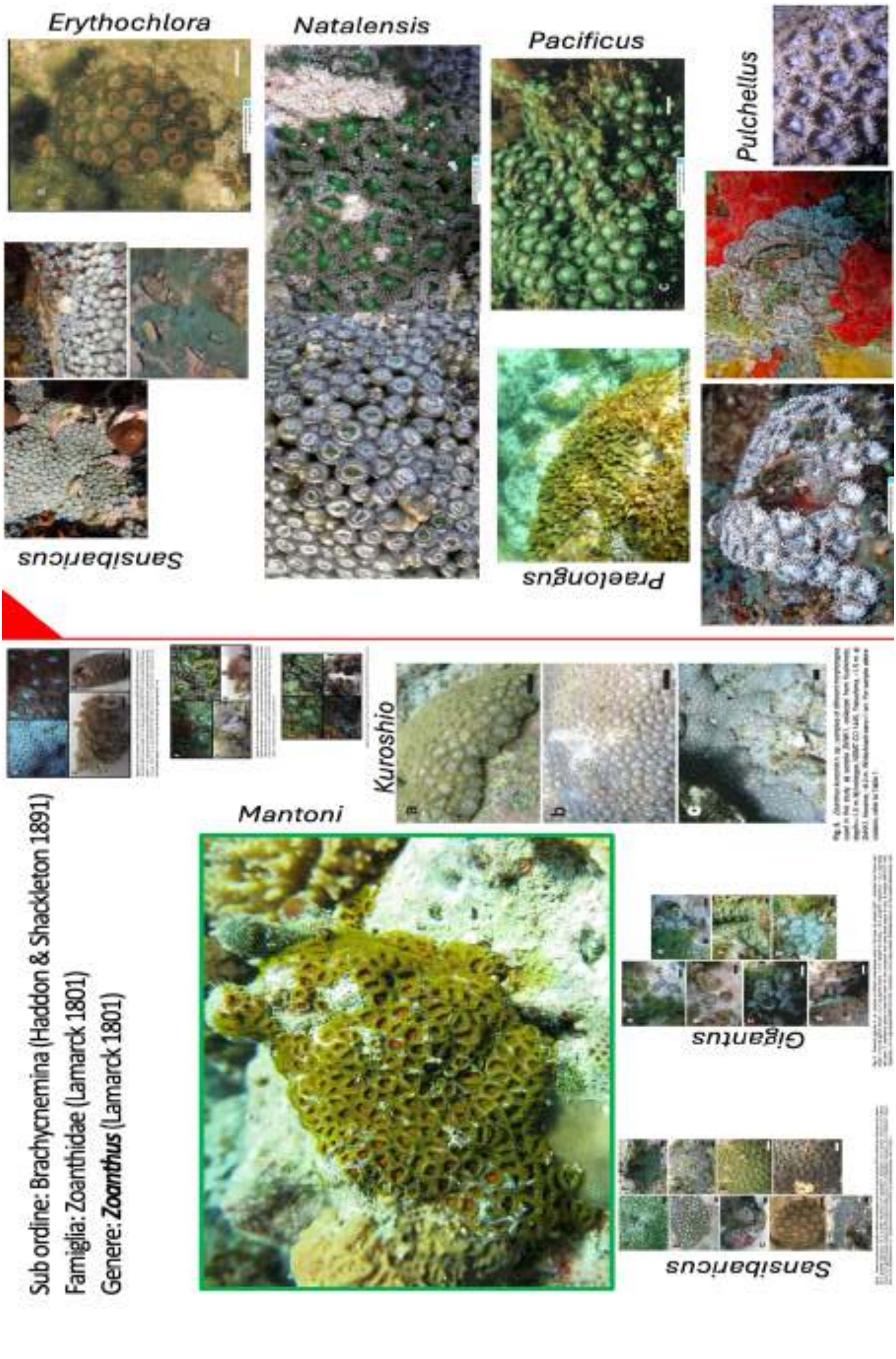


Table 44: all the images in the table refer to the genus *Zoanthus*.

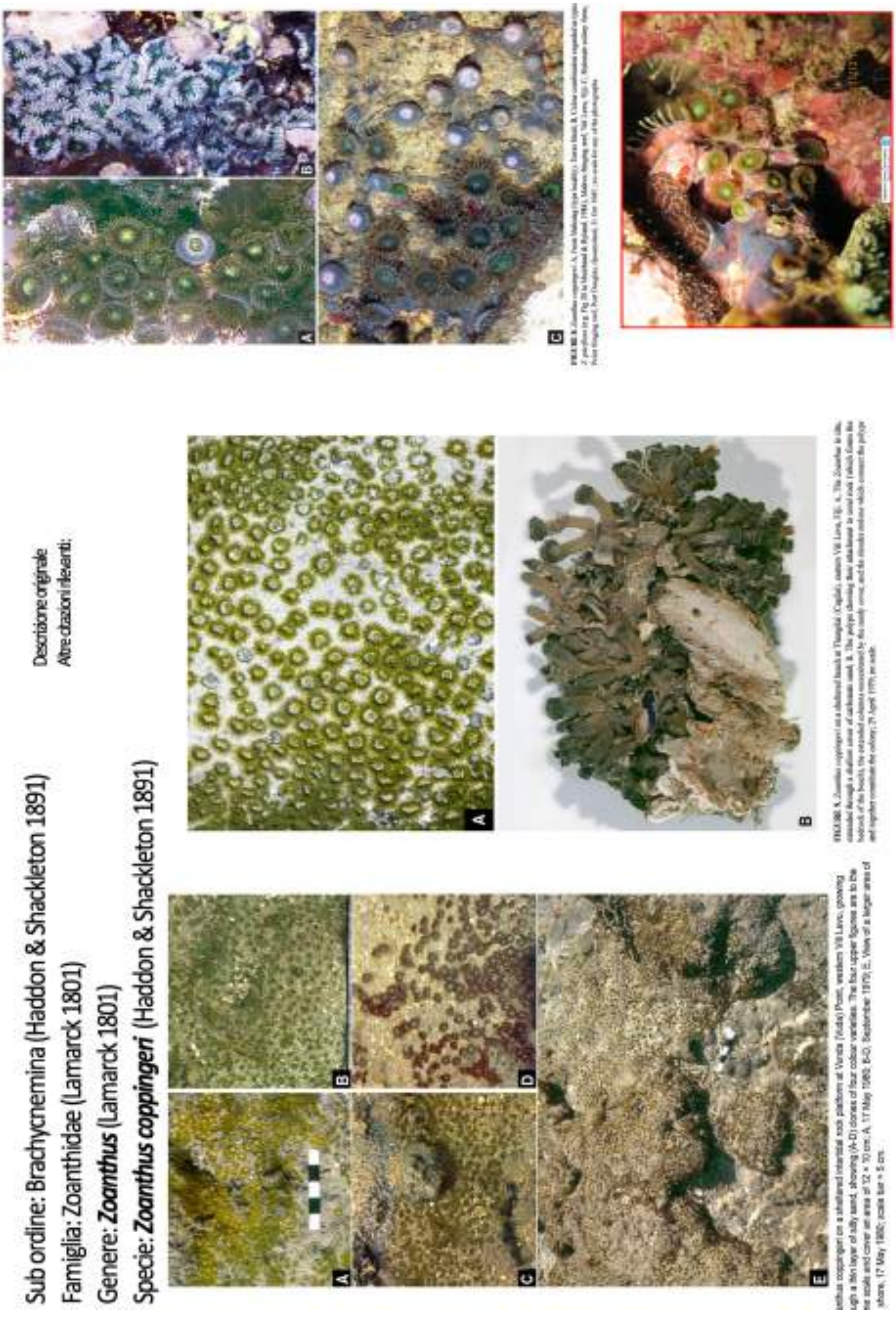


Table 45: all the images in the table refer to the species *Zoanthus coppingeri*.

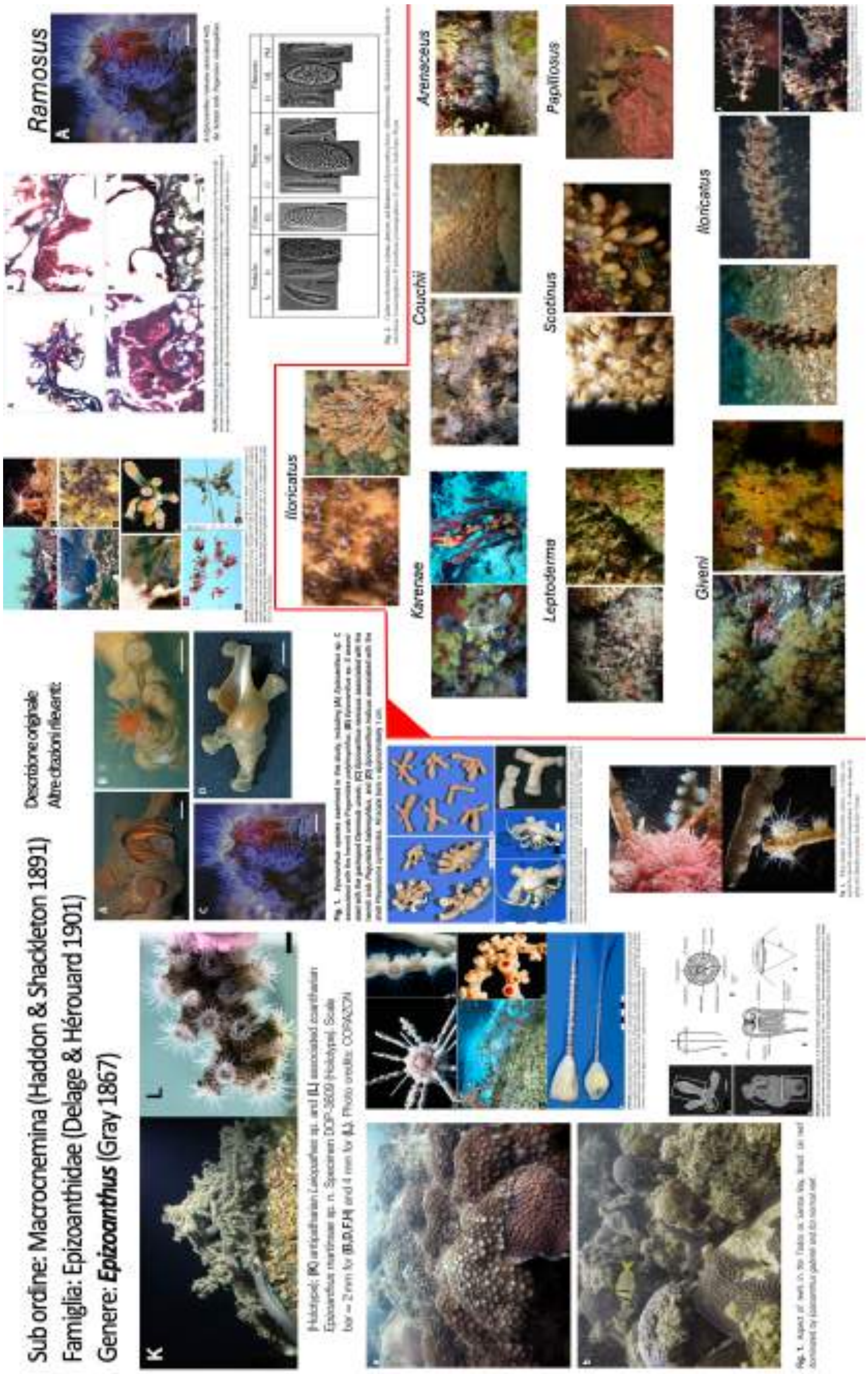
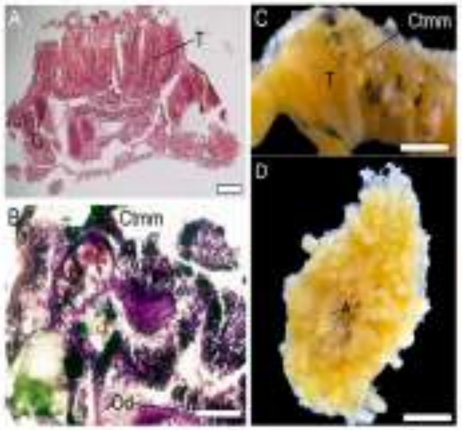


Table 46: all the images in the table refer to the genus *Epizoanthus*.

Sub ordine: Macrocnemina (Haddon & Shackleton 1891)
Famiglia: Epizoanthidae (Delage & Hérouard 1901)
Genere: ***Thoracactis*** (Gravier 1918)

Descrizione originale
Altre citazioni rilevanti:

FIGURE 2 Images of external morphology of topotype of *Thoracactis topsenti*. (a) preserved topotypic specimen (RMNH.COEL.45636). (b) close-up image of a single preserved polyp (RMNH.COEL.45636). (c) image of museum specimen taken by Michèle Bruni (MOM INV-0017721). (d) living polyps on a hexactinellid sponge *Sarostegia oculata*. Scale bars: 10 mm



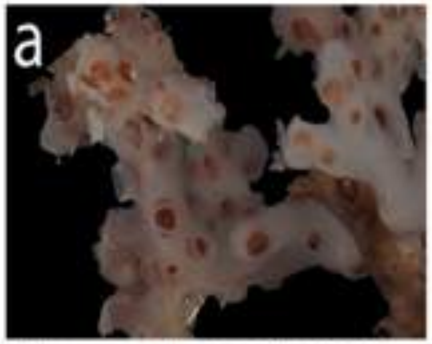
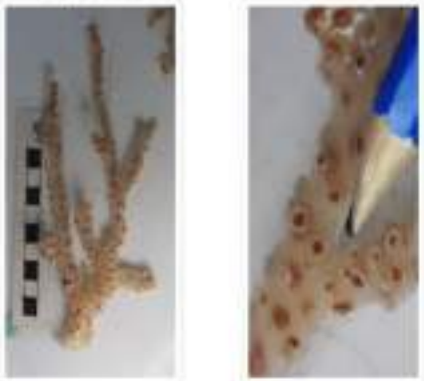


Figure 6. Corals, sponges and associated macrofauna collected during Project BIOIL Cruise I in November 2019 at Santos Basin. a branch of the glass sponge *Sarostegia oculata* with the symbiotic zoanthid *Thoracactis topsenti*.



A colony of Sarostegia oculata obtained from a dredge (left). Detail of the sponge and its associated Thoracactis topsenti polyps (right).

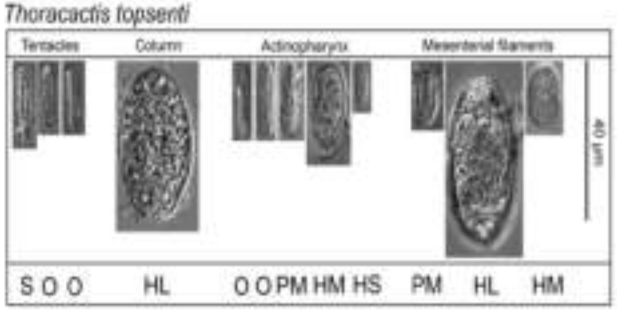


Table 47: all the images in the table refer to the genus *Thoracactis*.

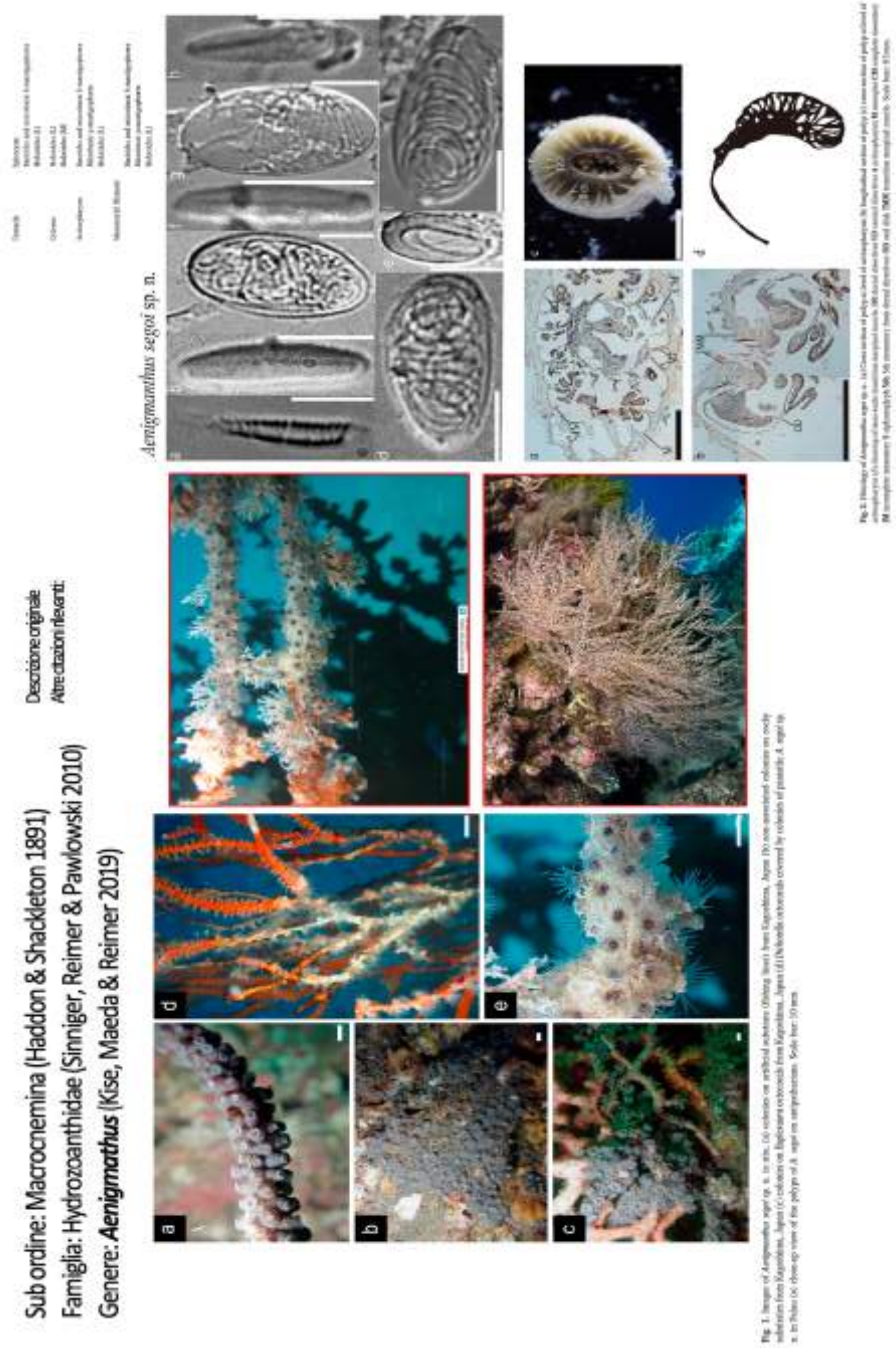


Table 48: all the images in the table refer to the genus *Aenigmanthus*.

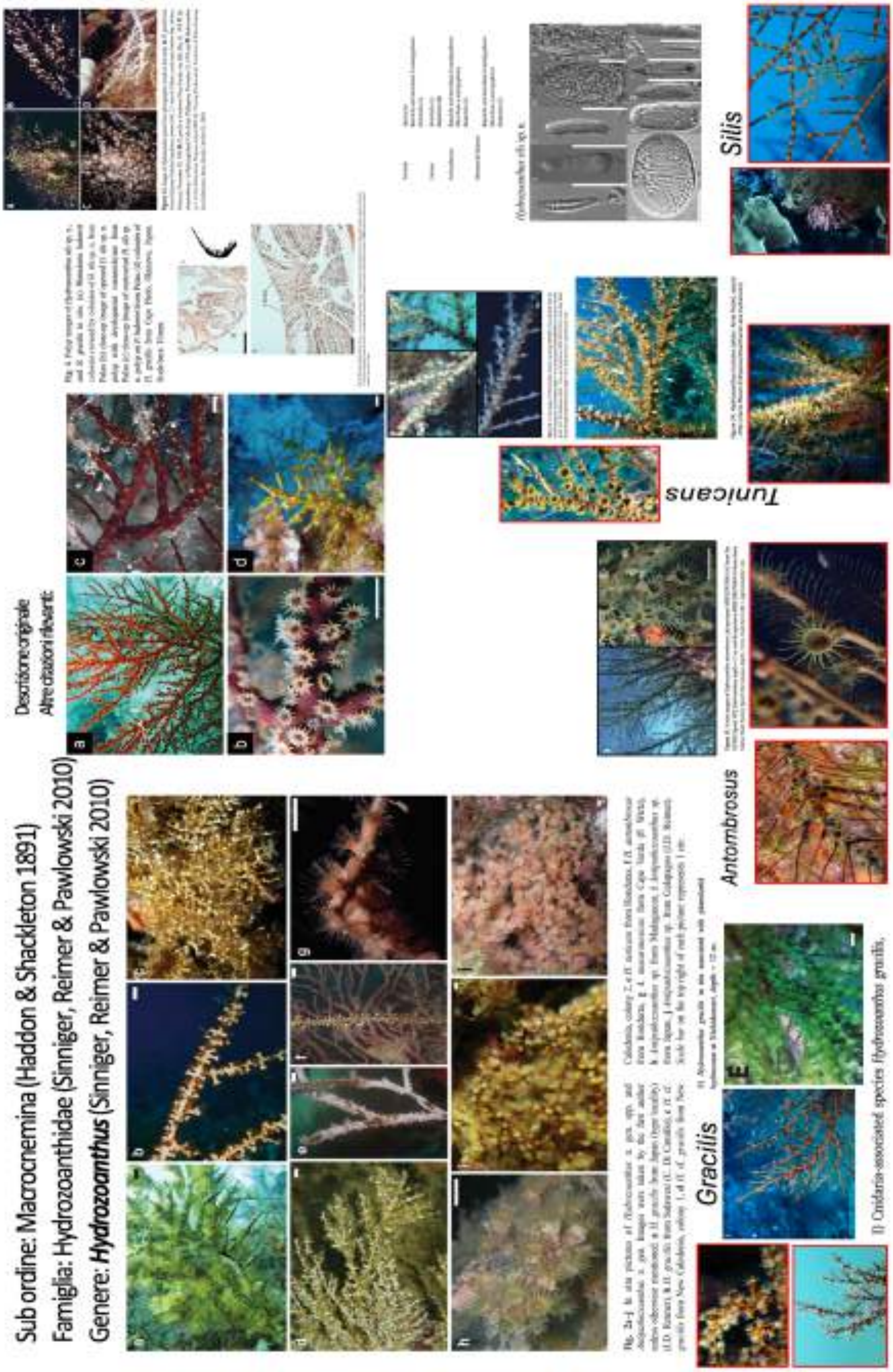


Table 49: all the images in the table refer to the genus *Hydrozoanthus*.

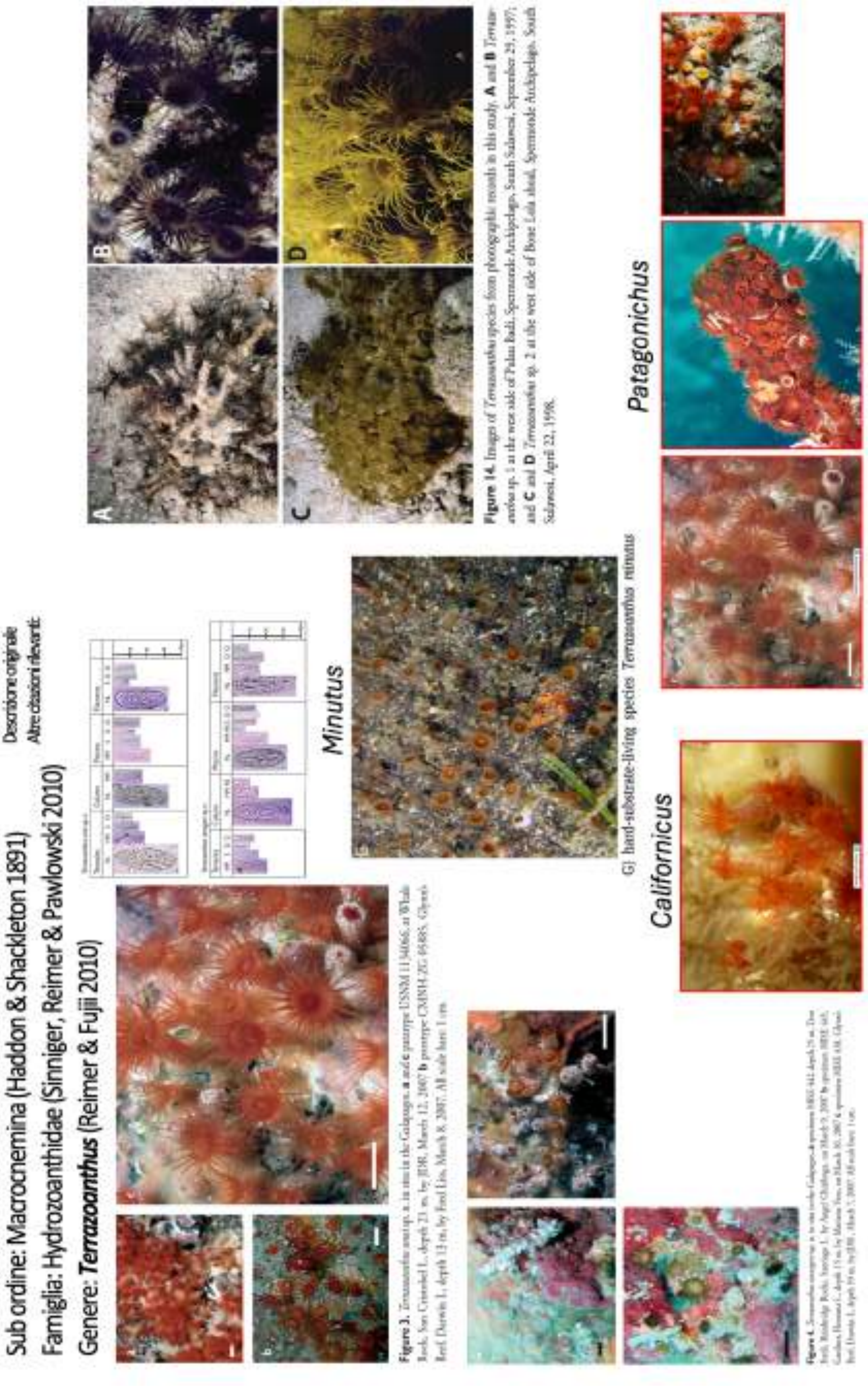


Table 50: all the images in the table refer to the genus *Terrazoanthus*.

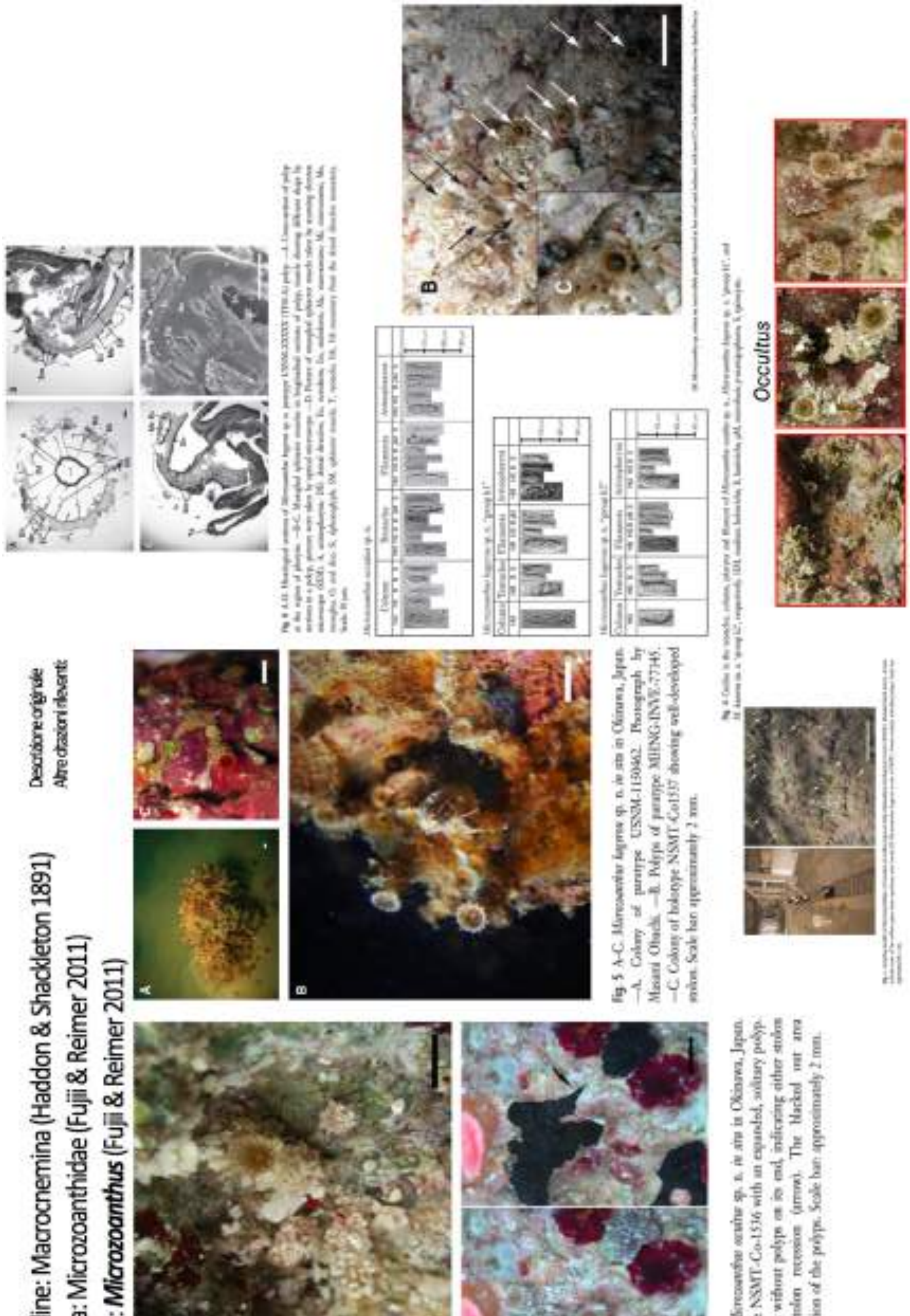


Table 51: all the images in the table refer to the genus *Microzoanthus*.

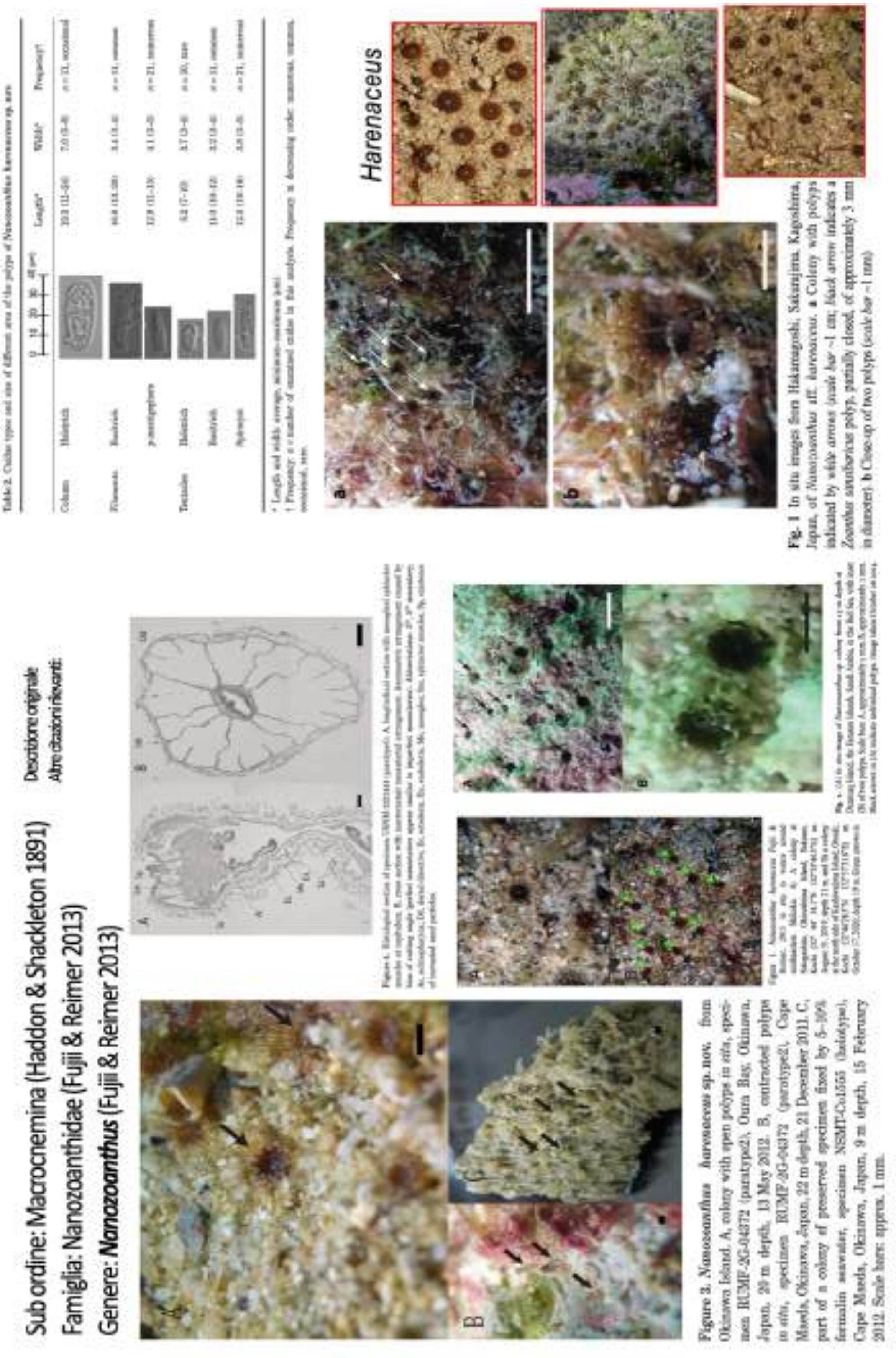


Table 52: all the images in the table refer to the genus *Nanozoanthus*.

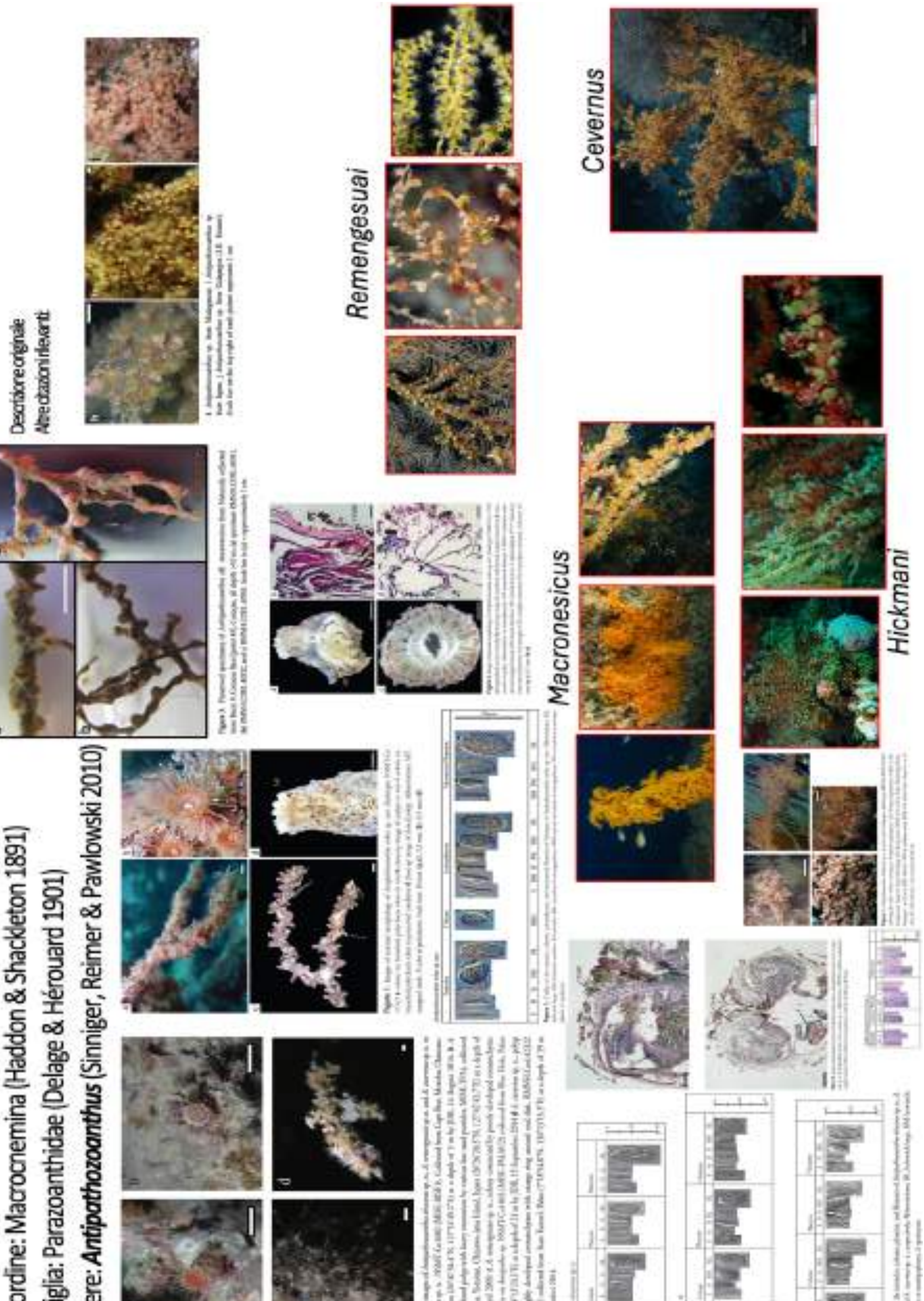


Table 53: all the images in the table refer to the genus *Antipathozoanthus*.

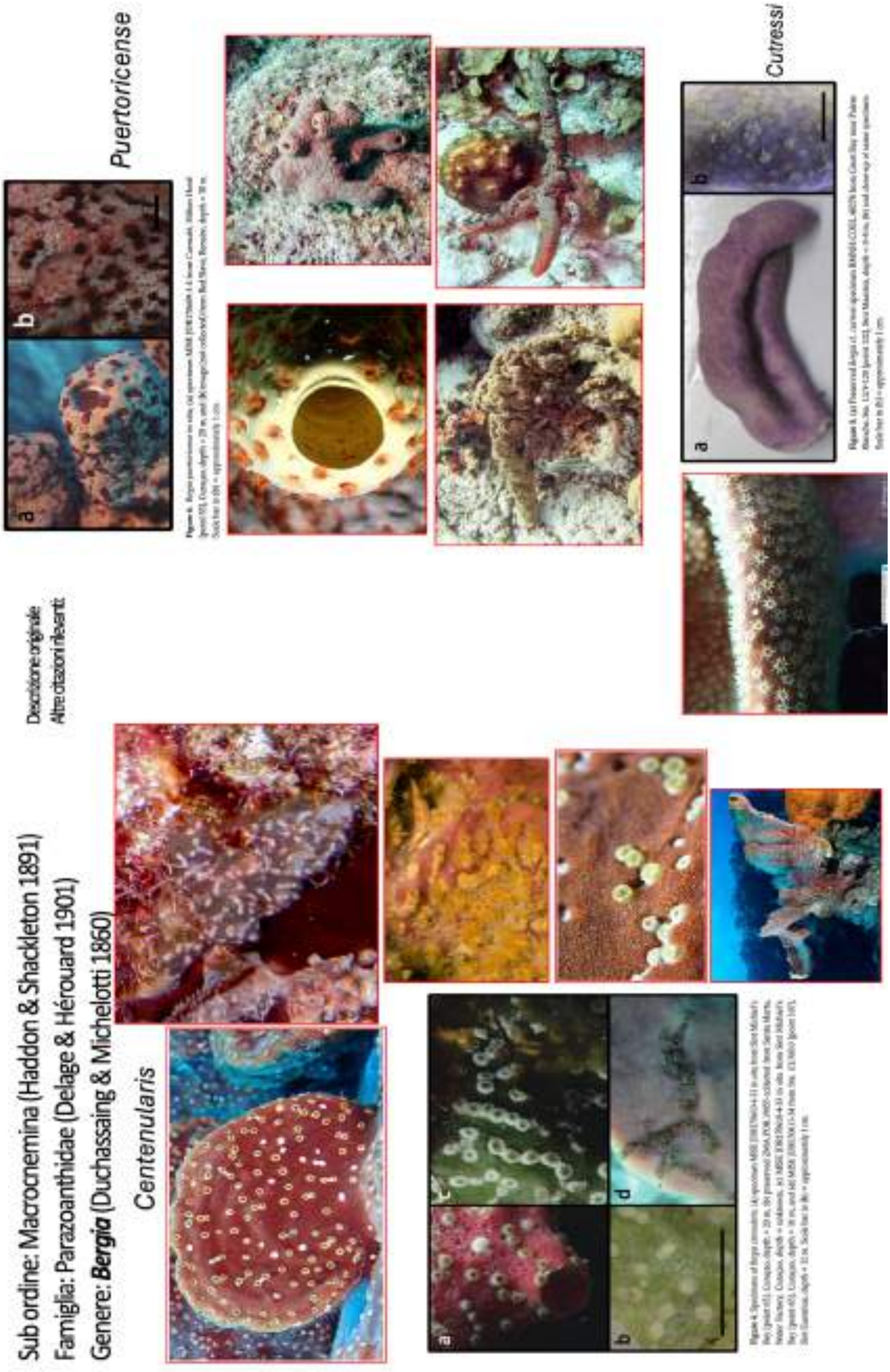


Table 54: all the images in the table refer to the genus *Bergia*.

Sub ordine: Macrocnemina (Haddon & Shackleton 1891)
Famiglia: Parazoanthidae (Delage & Hérouard 1901)
Genere: ***Bullagummizoanthus*** (Sinniger, Ocaña & Baco 2013)

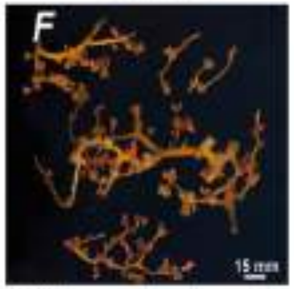
Descrizione originale
Altre citazioni rilevanti:

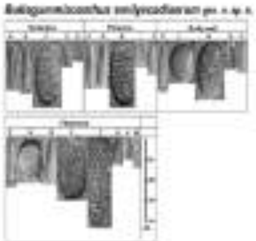
Emilyacadiaarum

Cnidaria – Zoanthidea (Frederic Sinniger, University of Ryukyus, Japan)

Schnabel et al. (2019) reported for the first time the zoanthid genus *Bullagummizoanthus* in the New Zealand region with two samples identified from the EEZ by expert Frederic Sinniger. One further sample (NIWA 65950) from the Lord Howe Rise (ET) was newly identified by Dr. Sinniger based on a photograph and is included in this report. Figure 9 shows the pale pink/yellow zoanthids growing on the bright pink host bubblegum coral *Paragorgia coralloides* that so far appears to be the exclusive host of this associated zoanthid (Sinniger et al. 2013). Only one species is currently contained within the genus *Bullagummizoanthus* and taxonomic work (using morphology and DNA) by Sinniger and colleagues is underway to determine whether the New Zealand specimens belong to an undescribed species.

Figure 9: *Bullagummizoanthus* (NIWA 65950, Trip 3177/37) zoanthid, attached to the bubblegum coral host (NIWA 65949).





F) *Bullagummizoanthus emilyacadiaarum* gen. n. sp. n. fixed sample.

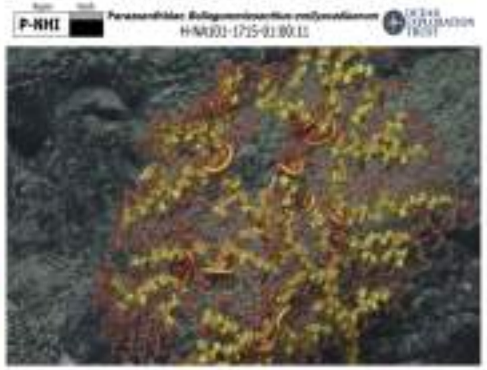


Table 55: all the images in the table refer to the genus *Bullagummizoanthus*.

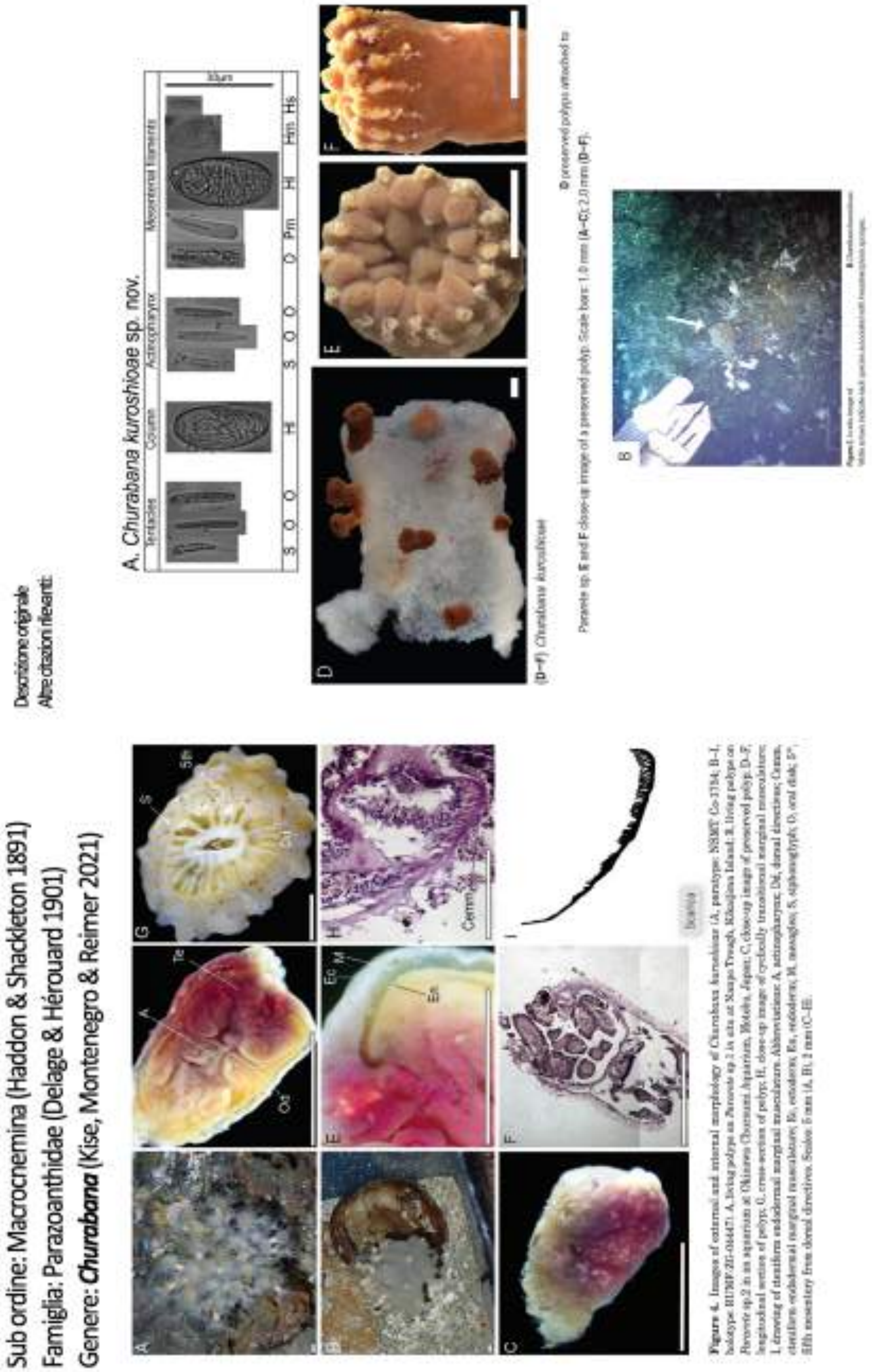


Table 56: all the images in the table refer to the genus *Churabana*.

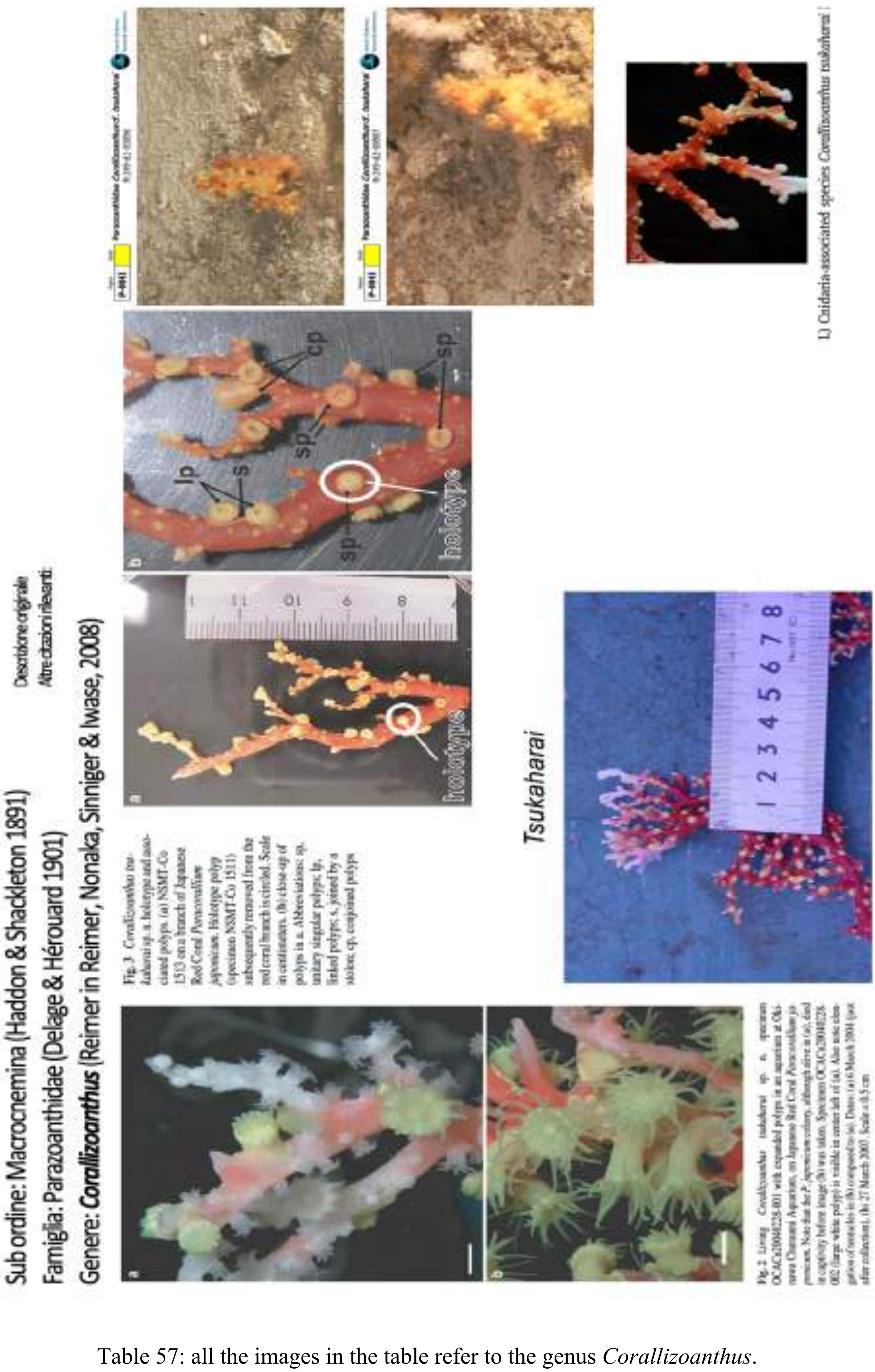


Table 57: all the images in the table refer to the genus *Corallizoanthus*.

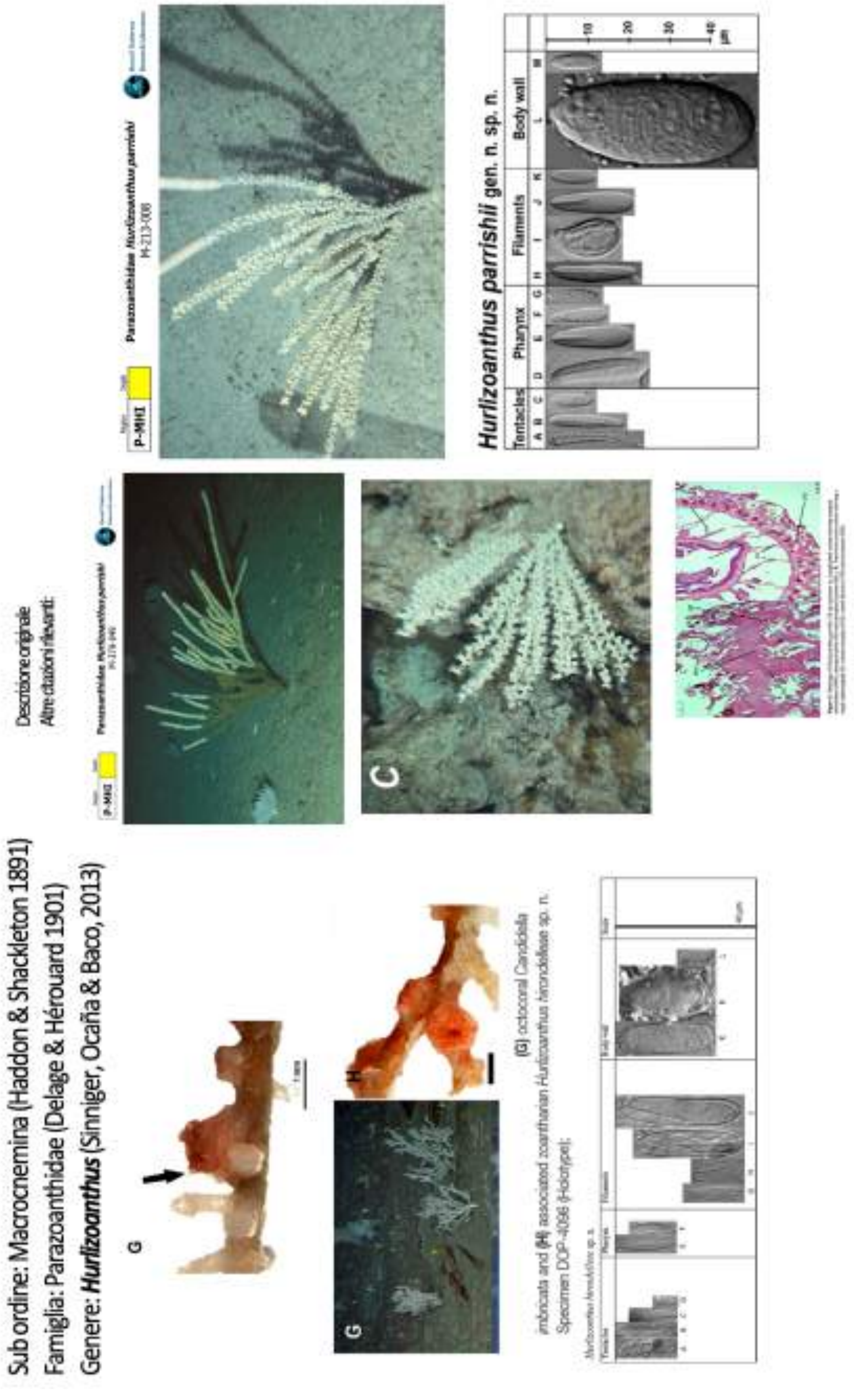


Table 58: all the images in the table refer to the genus *Hurlizoanthus*.

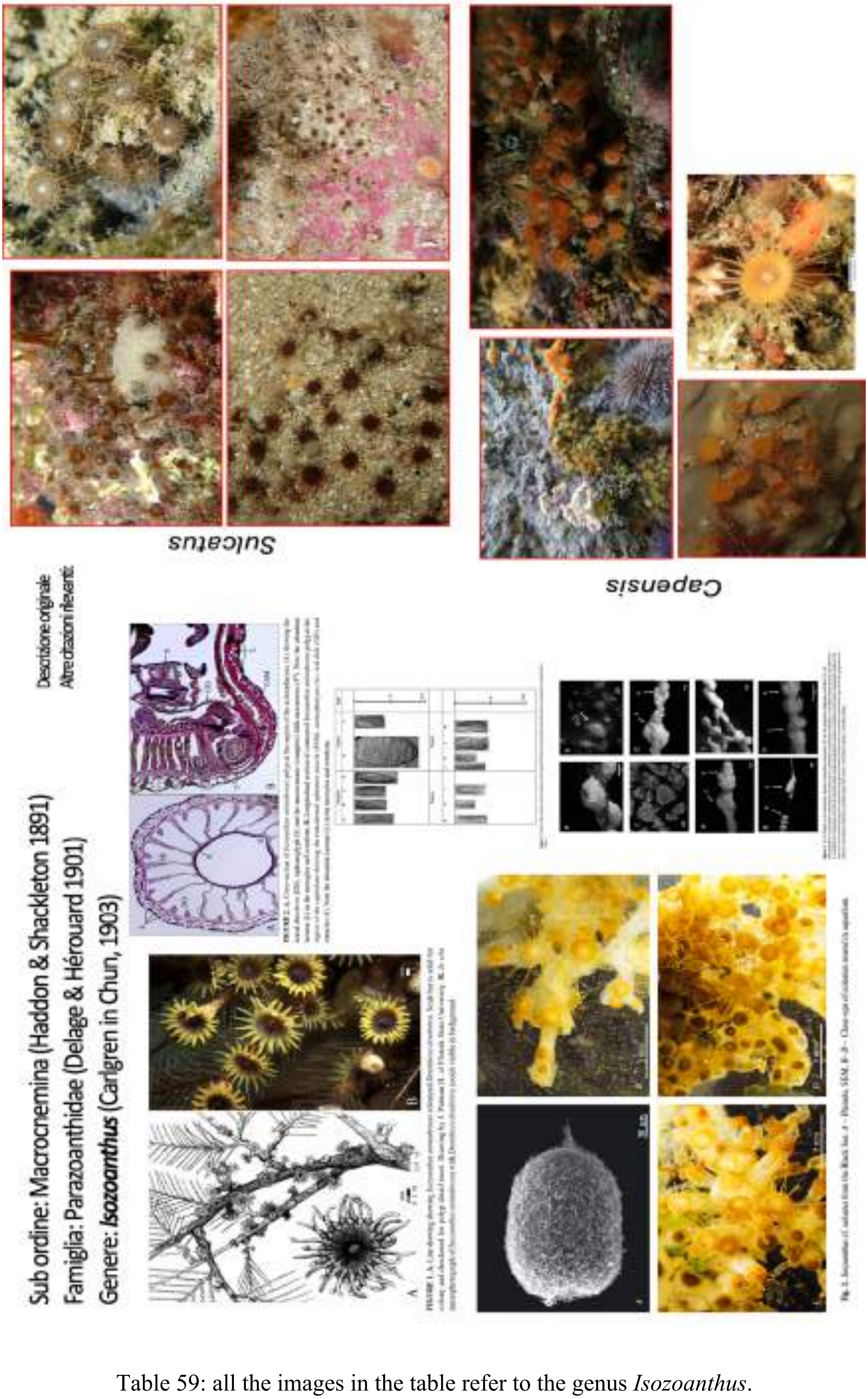
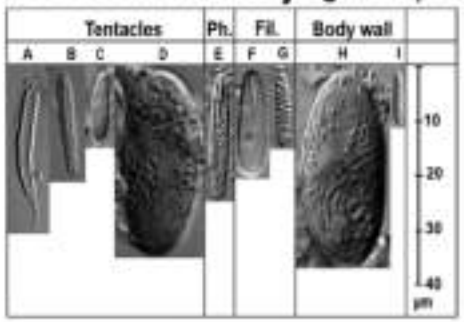


Table 59: all the images in the table refer to the genus *Isozoanthus*.

Sub ordine: Macrocnemina (Haddon & Shackleton 1891)
Famiglia: Parazoanthidae (Delage & Hérouard 1901)
Genere: ***Kauluzoanthus*** (Sinniger, Ocaña & Baco, 2013)

Descrizione originale
Altre citazioni rilevanti:

Kauluzoanthus kerbyii gen. n. sp. n.



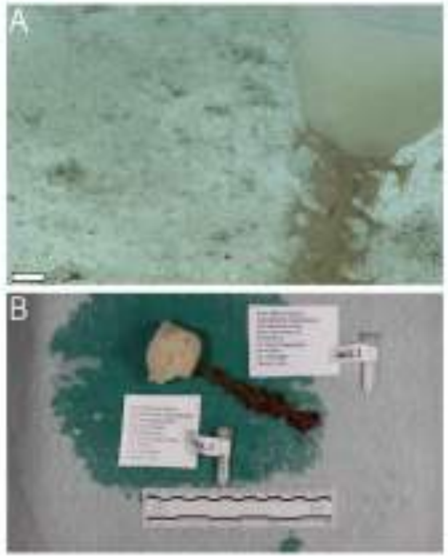


Figure 9. Images of *Kauluzoanthus* sp.: A, *in situ* image of *Kauluzoanthus* sp. on stalks of *Hyalonema* sp.; B, preserved colony. Scale: 10 mm (A). Images credits: Okeanos/NOAA.

Table 60: all the images in the table refer to the genus *Kaulozoanthus*.

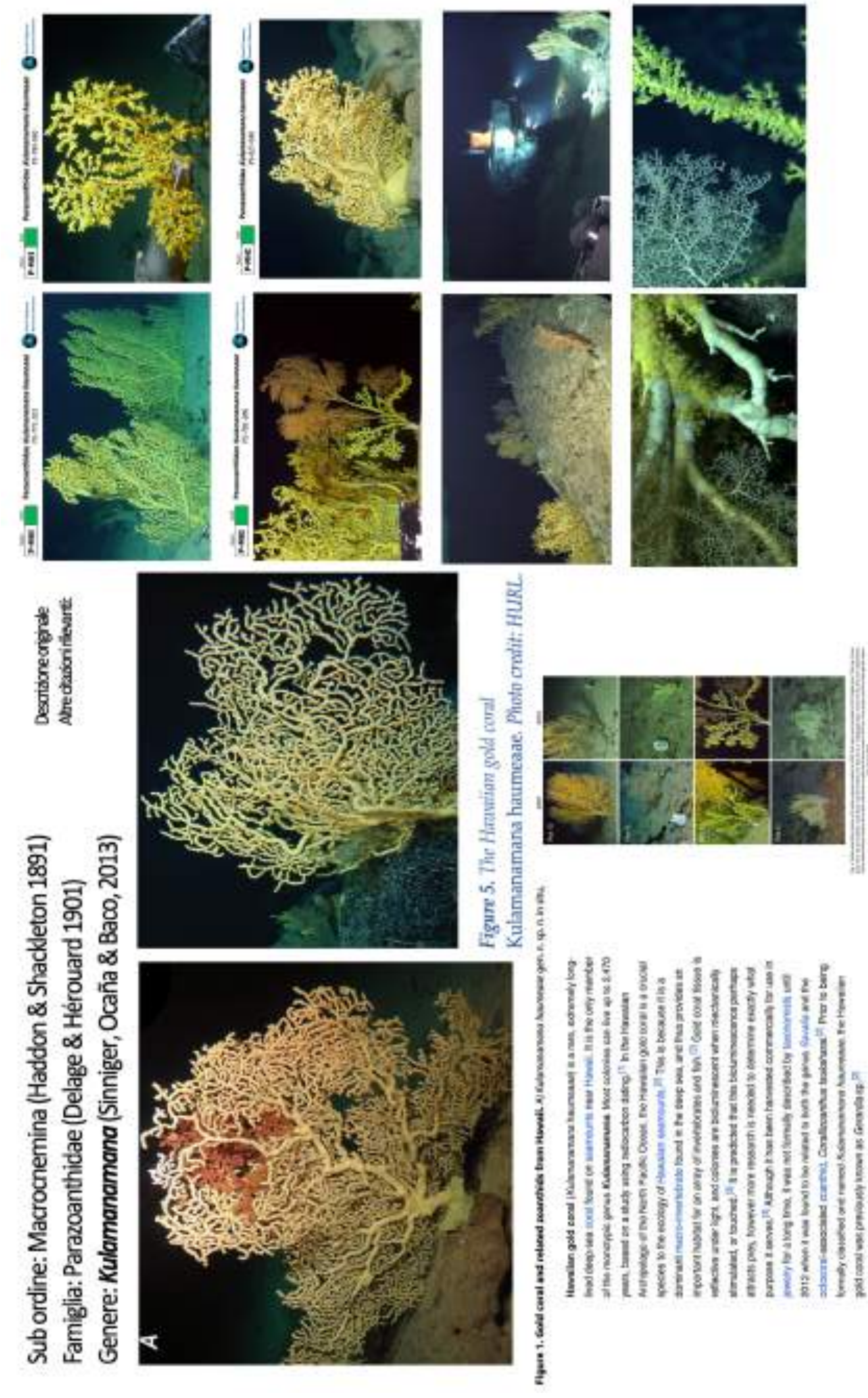


Table 61: all the images in the table refer to the genus *Kulamanamana*.

Sub ordine: Macrocnemina (Haddon & Shackleton 1891)
Famiglia: Parazoanthidae (Delage & Hérouard 1901)
Genere: ***Mesozoanthus*** (Sinniger & Haussermann, 2009)

Descrizione originale
Altre citazioni rilevanti:

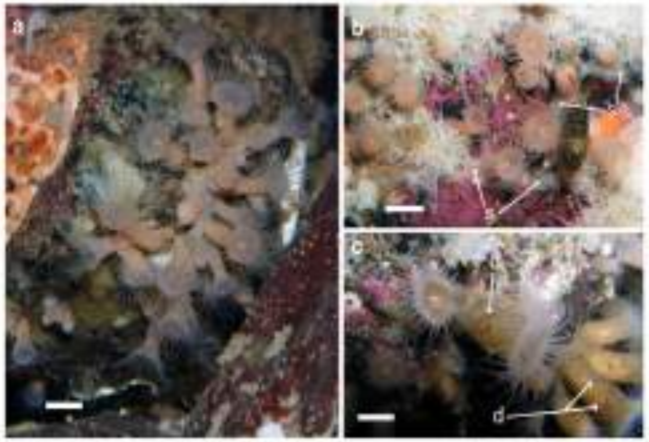


Fig. 2 *Mesozoanthus lillkweminensis* n. sp. in aquarium at VA. Holotype polyps were taken from this colony. Note the cream-pink coloration in both a and b and reduced or stoloniferous coenenchyme (c) in b. c *Epizoanthus scotinus* from Jesse Island, Nanaimo, British Columbia (12.7–17.2 m) shown for comparison. Note higher sedimentation/detritus (d) on outer surface of polyps as well as different coloration, particularly of polyp column's outer surface. Additionally, *E. scotinus* has more (44–52) tentacles than *M. lillkweminensis* (34–38). All scale bars=1 cm

Mesozoanthus lillkweminensis sp. n.

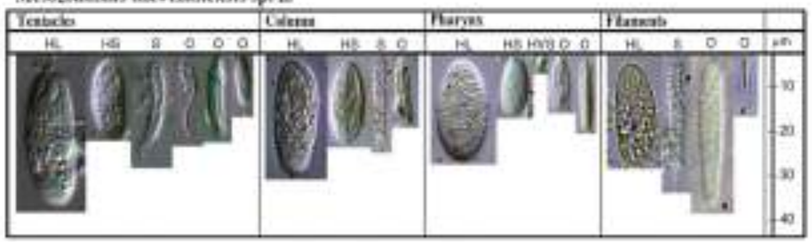


Fig. 3 Cnidae in the tentacles, column, pharynx and filament of *Mesozoanthus lillkweminensis* n. sp. *HL* large holotrich, *HS* small holotrich, *HVS* very small holotrich, *O* basitrichs or mastigophores, *S* spirocysts

Fossii

Mesozoanthus sp.

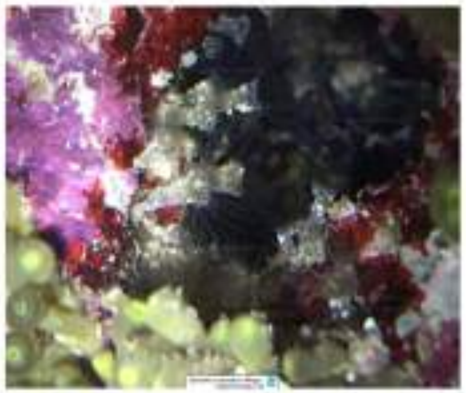


Table 62: all the images in the table refer to the genus *Mesozoanthus*.

Sub ordine: Macrocnemina (Haddon & Shackleton 1891)
Famiglia: Parazoanthidae (Delage & Hérouard 1901)
Genere: ***Parachurabana*** (Kise, 2023)

Descrizione originale
Altre citazioni rilevanti:

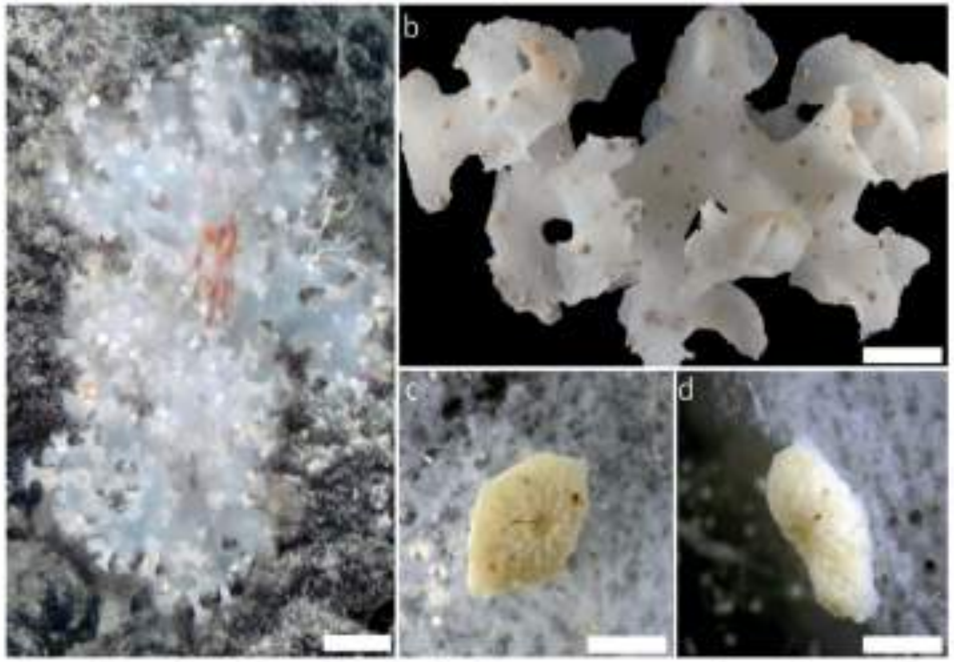


Figure 1. External morphology of *Parachurabana shinseimaruae* sp. nov. **a** photographic record from Takuyo-Daigo Seamount off southwestern Minami-Torishima Island **b–d** NSMT-Co 1819 **a** living polyps on a hexactinellid sponge *Farrea* sp. **b** preserved specimen **c** close-up image of a single preserved polyp **d** close-up, side-view image of a single preserved polyp attached to a hexactinellid sponge *Farrea* sp. Scale bars: 20 mm (**a, b**); 1 mm (**c, d**).

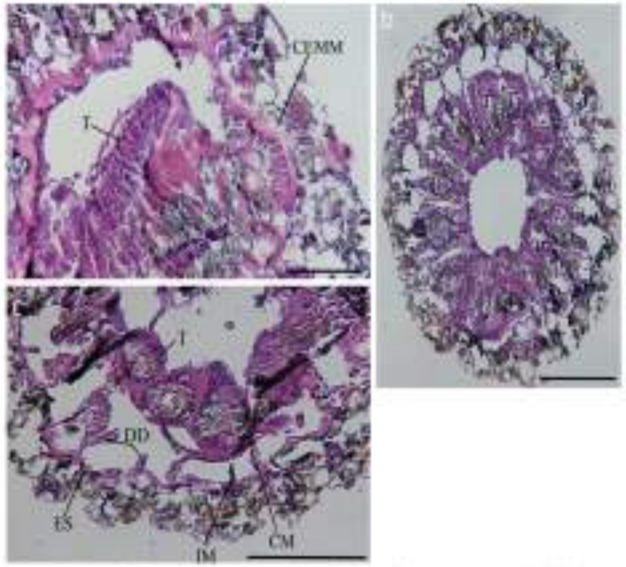


Figure 2. Images of the internal morphology of *Parachurabana shinseimaruae* sp. nov. NSMT-Co 1819 **a** close-up image of cteniform endodermal marginal muscle in a longitudinal polyp section **b** cross-section at the height of tentacles **c** cross-section at the height of the actinopharynx. Abbreviations: CEMM, cteniform endodermal marginal muscle; CM, complete mesentery; CW, column wall; DD, dorsal directives; ES, encircling sinus; IM, incomplete mesentery; T, tentacles. Scale bars: 200 µm (**a**); 500 µm (**b, c**).

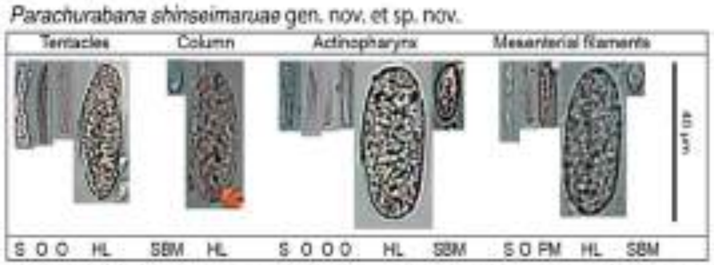


Figure 3. Cnidae in the tentacles, column, actinopharynx, and mesenterial filaments of the holotype of *Parachurabana shinseimaruae* sp. nov. Abbreviations: HL, holotrich large; O, basitrichs and microbasic b-mastigophores; SBM, special microbasic b-mastigophores; PM, microbasic p-mastigophores; S, spirocysts.

Table 63: all the images in the table refer to the genus *Parachurabana*.

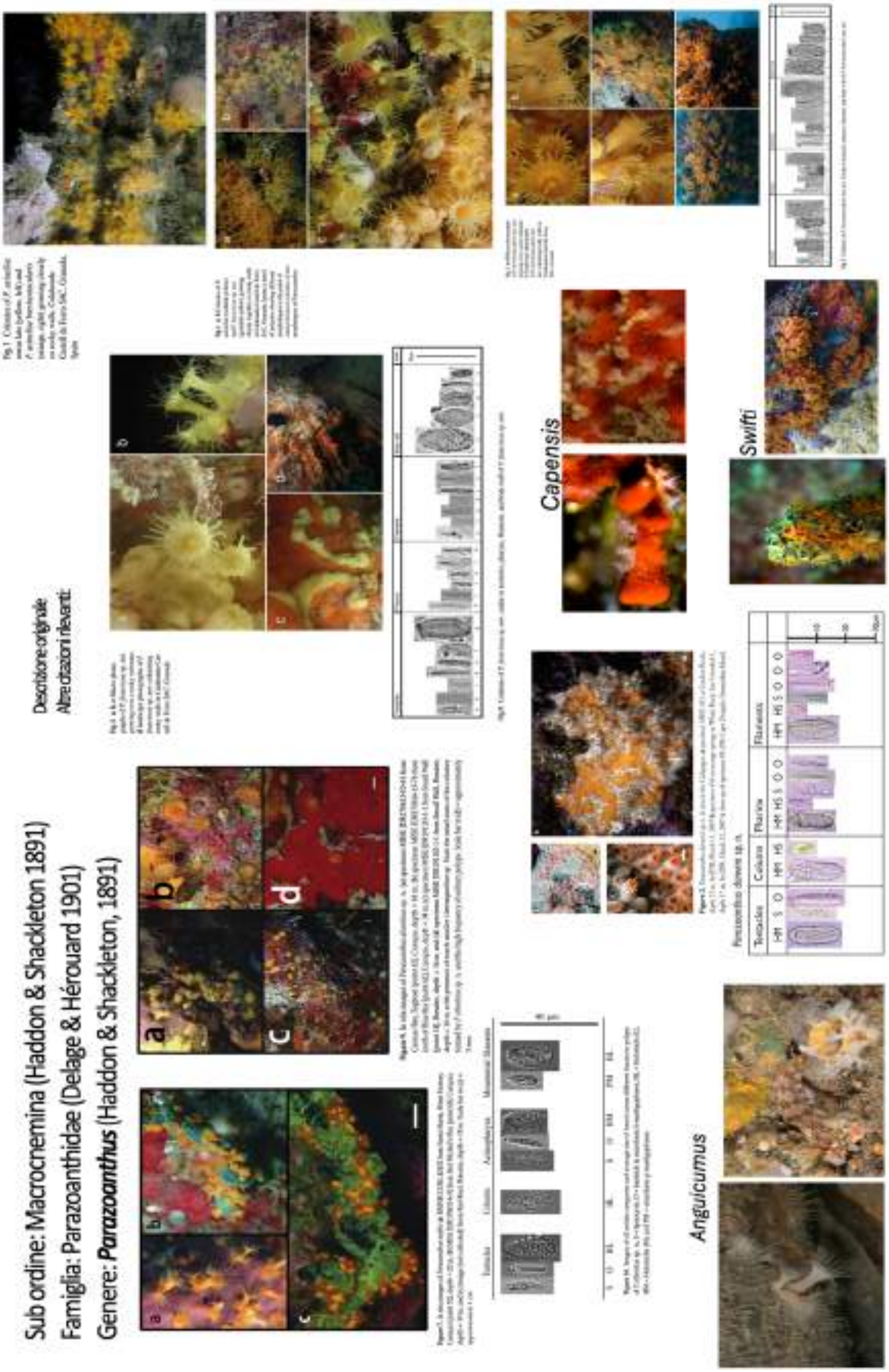


Table 64: all the images in the table refer to the genus *Parazoanthus*.

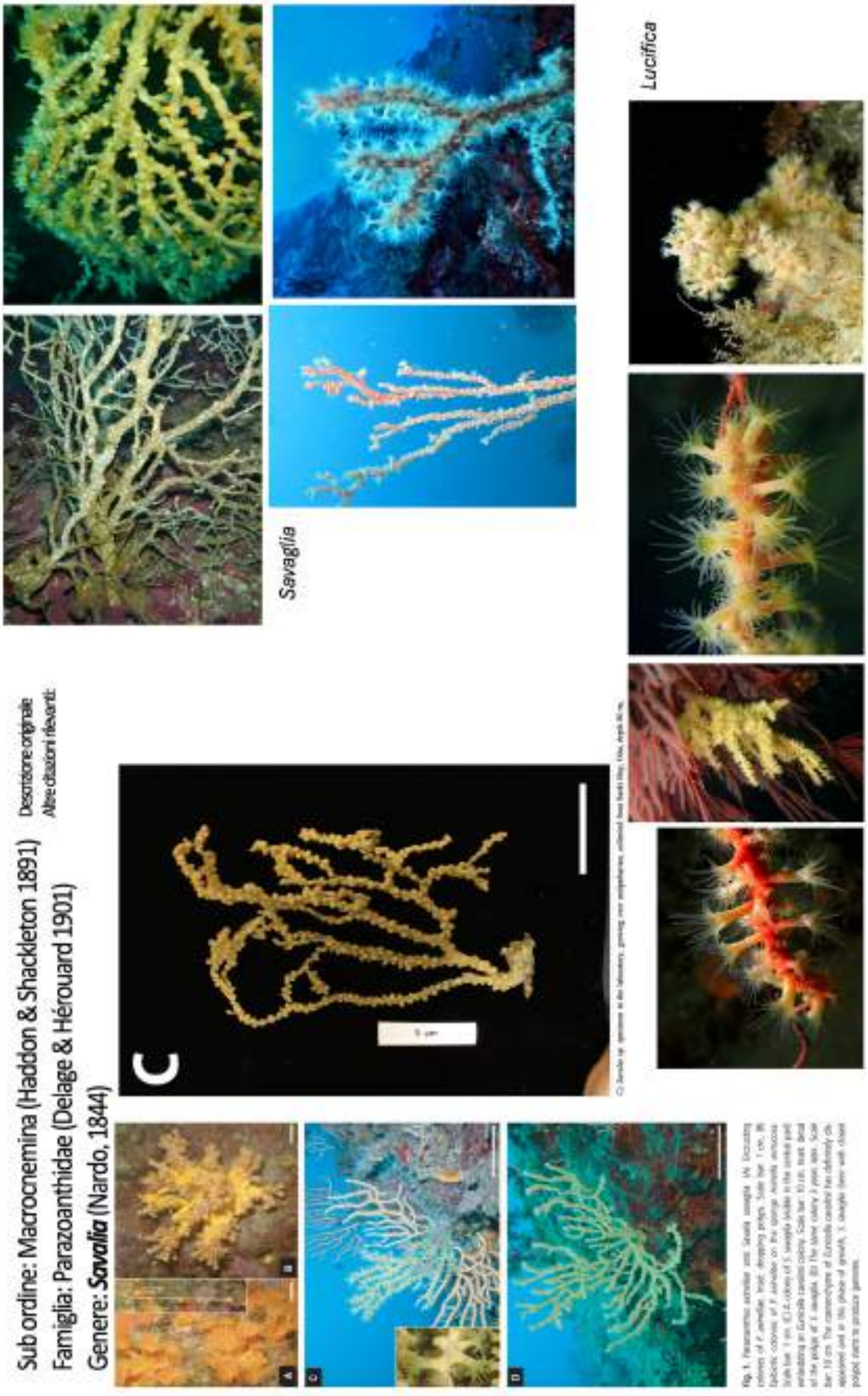


Table 65: all the images in the table refer to the genus *Savalia*.

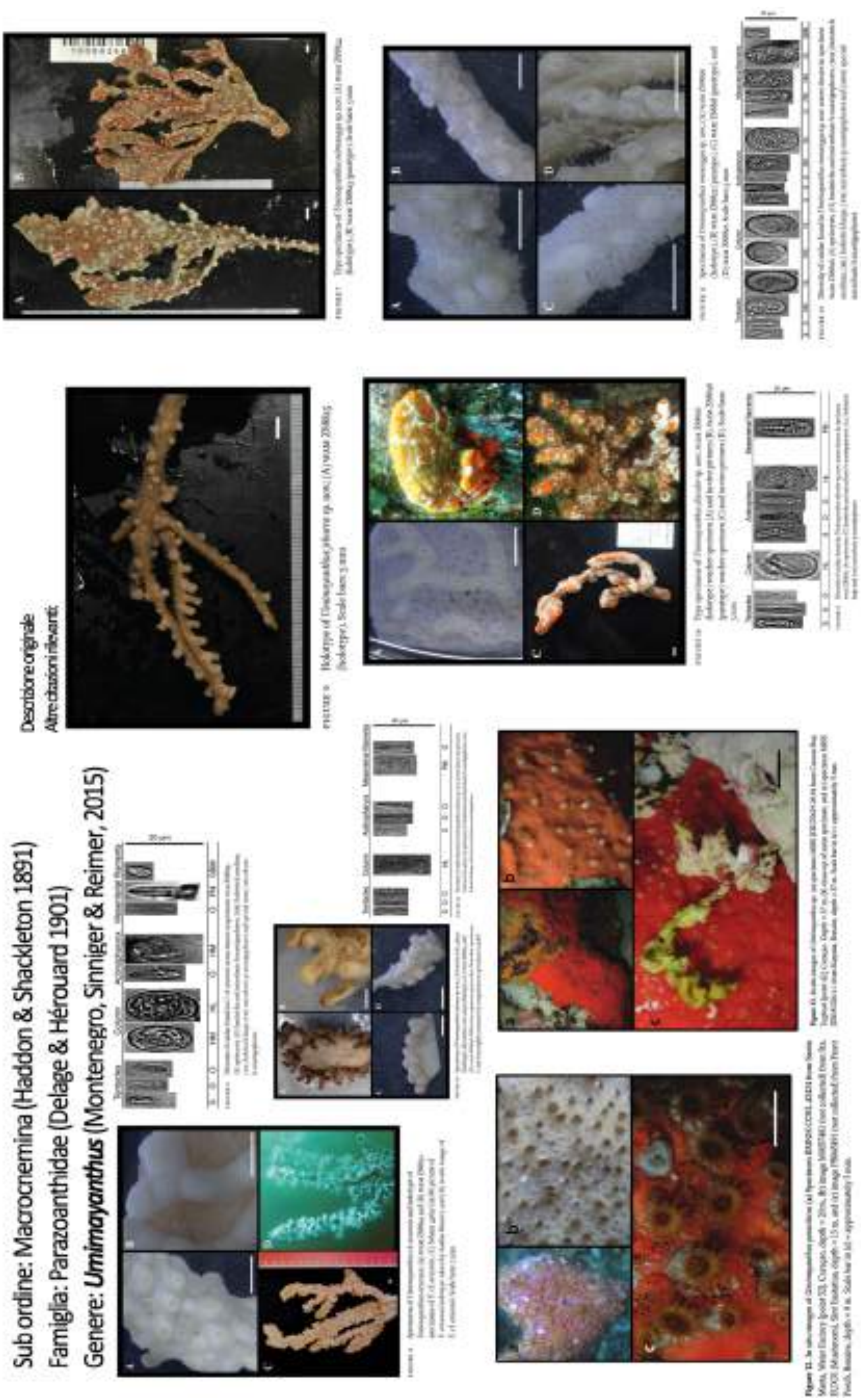


Table 66: all the images in the table refer to the genus *Umimayanthus*.

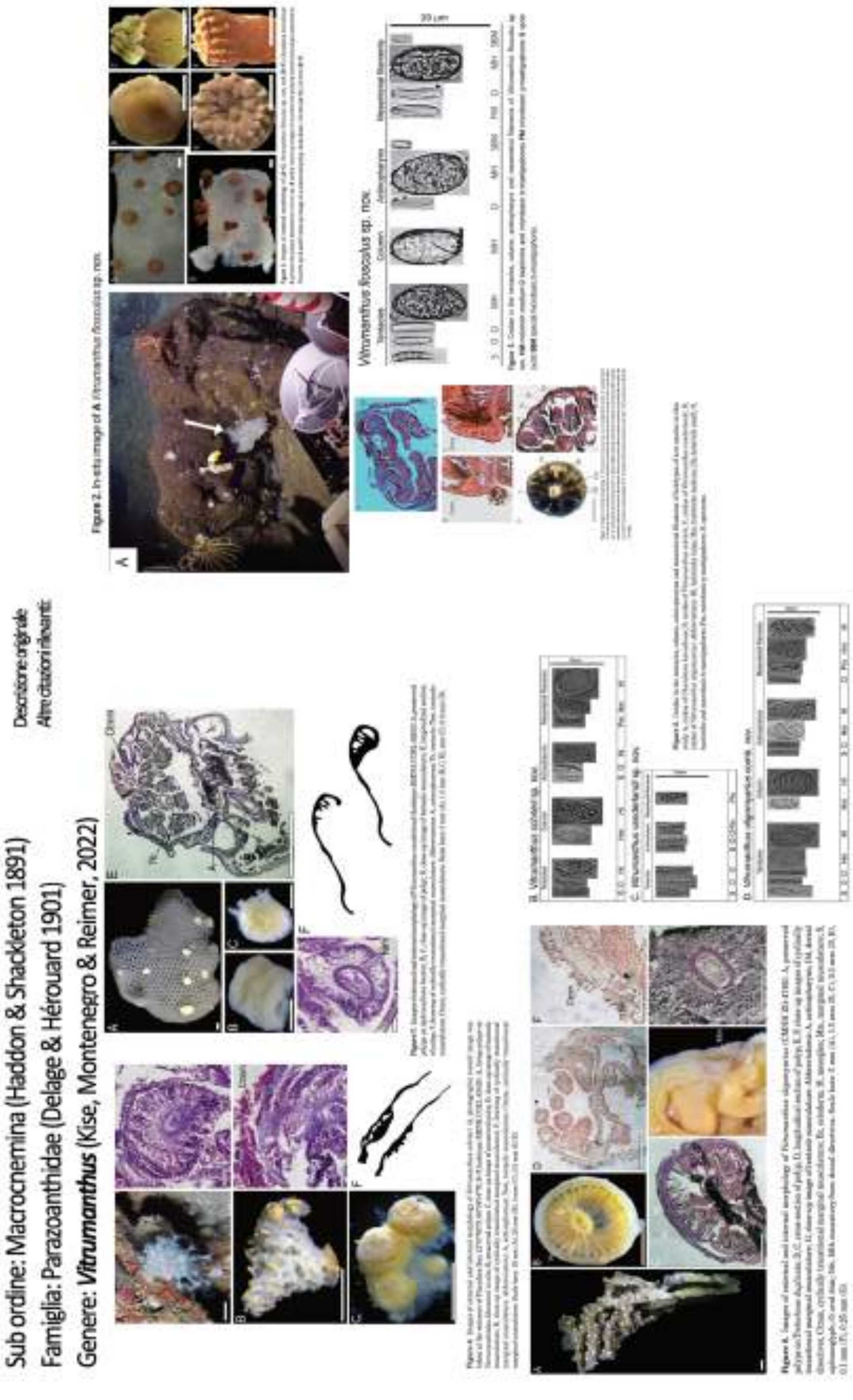


Table 67: all the images in the table refer to the genus *Vitrumanthus*.

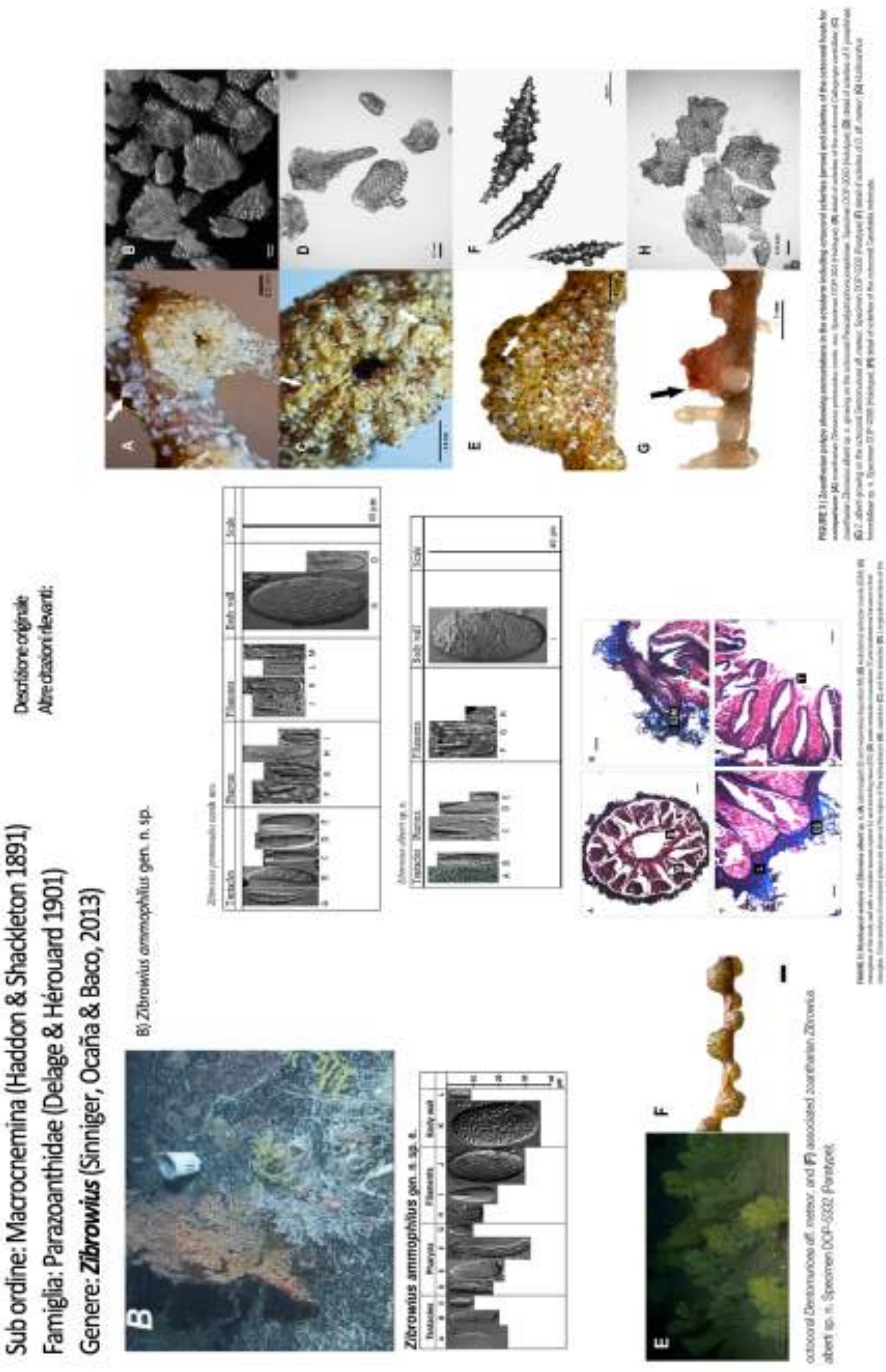


Table 68: all the images in the table refer to the genus *Zibrowius*.

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Fiu Fiu