

A REVIEW OF GORGONIAN CORAL SPECIES (CNIDARIA, OCTOCORALLIA, ALCYONACEA) HELD IN THE SANTA BARBARA MUSEUM OF NATURAL HISTORY RESEARCH COLLECTION: FOCUS ON SPECIES FROM SCLERAXONIA, HOLAXONIA, AND CALCAXONIA

> BY Elizabeth Anne Horvath



Acanthogorgia gracillima var. typica Kükenthal, 1909

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# A review of gorgonian coral species (Cnidaria, Octocorallia, Alcyonacea) held in the Santa Barbara Museum of Natural History research collection: focus on species from Scleraxonia, Holaxonia, and Calcaxonia

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MONOGRAPH



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## Abstract

Gorgonian specimens collected from the California Bight (northeastern Pacific Ocean) and adjacent areas held in the collection of the Santa Barbara Museum of Natural History (SBMNH) were reviewed and evaluated for species identification; much of this material is of historic significance as a large percentage of the specimens were collected by the Allan Hancock Foundation (AHF) 'Velero' Expeditions of 1931–1941 and 1948–1985. Examination and reorganization of this collection began early in 2002; initially, it was estimated that at most, twelve to fifteen species of gorgonian could be found within the Bight. Following collection evaluation, it was determined that at a minimum, approximately twenty three genera, encompassing some forty-plus species, of gorgonian coral have been found living within the California Bight region, often extending some distance into adjacent geographical areas both north and south. All species from the California Bight in the collection are discussed to some degree (in three separate parts, this being Part I), with digital images of both colony form and sclerite composition provided for most. Collection specimens from the suborders and families covered in Part I are not extensive, but several genera are featured that have not been previously reported for the California Bight region. Additionally, a potential

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new species (genus Sibogagorgia Stiasny, 1937) from the Paragorgiidae is described in Part I. Overall, the collection displays an emphasis on species belonging to the Holaxonia, particularly the plexaurids. A brief discussion of a California Bight grouping, referred to as the "red whips," is presented in Part II; this grouping encompasses several species with very similar colony appearance across a number of genera. A new species (a whip or thread-like form) in the genus Eugorgia Verrill, 1868, belonging to the Gorgoniidae, is described in Part II. The genus Swiftia Duchassaing & Michelotti, 1864 is one of the most challenging taxon groups represented; those species in the genus Swiftia collected within the California Bight are discussed fully, based on SBMNH (and other) specimens in Part III. Scanning electron microscopy images for species of Swiftia from the California coast have rarely, if ever, been published and are included, with a discussion of the geographic range of the genus in the eastern Pacific, from the southern boundary of the California Bight to the Bering Sea, Alaska. Finally, specimens of the genus Thesea Duchassaing & Michelotti, 1860, displaying a whip or thread-like body form, are discussed at a preliminary level in Part III; they also presented challenges to a clear understanding of their taxonomy. While Part I focuses on species of Scleraxonia and those of the Holaxonia in the Acanthogorgiidae family held in the SBMNH collection, all three parts taken together represent the first comprehensive work that reviews the research collection of SBMNH, which focuses on species of gorgonian coral known to inhabit the California Bight.

#### Keywords

Allan Hancock Foundation (AHF) – 'Velero' Expeditions, museum collection, new species, "red whips", soft corals, *Swiftia*, "thread-like" forms

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# Introduction

The trawl seemed to have gone over a regular field of a delicate, simple Gorgonid . . . . the stems, which were from eighteen inches to two feet in length, were coiled in great hanks around the beam-trawl and engaged in masses in the net; and as they showed a most vivid phosphorescence of a pale lilac colour, their immense number suggested a wonderful slate of things beneath – animated cornfields waving gently in a slow tidal current and glowing with a soft diffused light, scintillating and sparkling on the slightest touch, and now and again breaking into long avenues of vivid light indicating the paths of fishes or other wandering denizens of their enchanted region. Wyville Thomson (during the voyage of the 'Challenger')

With an extensive collection of California gorgonians housed at Scripps Institute of Oceanography (Univ. of California, San Diego) to the south and a large gorgonian collection housed to the north (California Academy of Sciences, San Francisco), the Santa Barbara Museum of Natural History (SBMNH) research collection would seem to be a small and redundant collection. However, SBMNH is the repository for the bulk of the Allan Hancock Foundation (AHF) cnidarian collection, amassed from the 'Velero' Expeditions (1931–1941, 1948–1985). Thus, the SBMNH research collection includes many gorgonian specimens of historical interest. It is a significant resource for those studying this cnidarian group as it may best illustrate the diversity of gorgonian species that can be found in California waters. This is the first part of a comprehensive work that reviews the research collection of SBMNH, which focuses on species of gorgonian coral known to inhabit the California Bight. Brief taxonomic reviews of previously described species (with representation in the collection), and additional information on species recorded from the Bight, regarding distribution, biology/ecology and noteworthy observations are presented in all three parts. Also included are more extensive descriptions for genera and species not previously reported for the California Bight, as are fuller descriptions for several potentially new species. It is apparent from the SBMNH research collection that gorgonian coral diversity within the California Bight is far greater than previously thought, pointing to a geographic location that needs further extensive exploration throughout, both geographically and with depth.

For the purposes of understanding what is meant by a "gorgonian," as discussed in all three parts of this work, the term "gorgonian" is used in reference to members of the Subclass Octocorallia, Order Alcyonacea, specifically the scleraxonians, holaxonians, and calcaxonians. Defining features (based on Bayer 1981c, Fabricius and Alderslade 2001, Brusca et al. 2016) include: 1) modular colonies, either encrusting or erect, often massive in size, usually colorful, 2) with colonies generally branched and tree-like, often forming flat, fan-like shapes, 3) stems and branches with a stiff, supporting, organic (horny), centrally internal skeletal axis (whether or not enclosed by a specialized secretory epithelium), comprised of calcite and scleroproteinous gorgonin, producing a relatively solid central support (scleraxonians with axis of fused sclerites, holaxonians with axis having no free sclerites but with hollow, cross-chambered central core and calcaxonians without hollow, cross-chambered central core but with large amounts of nonscleritic CaCo<sub>3</sub> forming internodes), with 4) polyps each supported by a portion of the central axis and having 5) all portions of central axis covered with a fleshy and flexible, somewhat thin coenenchyme, filled with embedded and surface sclerites. The gorgonian octocorals of the California Bight discussed herein (and subsequent parts) are those commonly referred to as sea fans and sea whips.

The subclass is composed of 50 families (Williams and Cairns 2014), with the gorgonians themselves encompassing 16–19 of those families, comprising more than 3,400 species (Daly et al. 2007, McFadden and Ofwegen 2013, Williams and Cairns 2014). Gorgonian corals can be found in all oceans (McFadden and Ofwegen 2013) from low inter-tidal to extreme depth (Williams 1990, 2013), varying widely in size, color and branch pattern. While gorgonian corals are known in a general sense by many who snorkel or scuba-dive, these organisms often do not readily identify to species based on the field identifiers of size, color, or branch morphology. Taxonomic revisions of numerous genera (such as Breedy and Guzmán 2007, 2011, 2016; Breedy et al. 2009) are necessary before many species can be recognized as valid and correctly identified, due to lack of clarity in many of the older original descriptions.

While seemingly fragile and delicate in overall appearance, gorgonians are remarkably "plastic" (Bayer 1958, 1961, Grigg 1972, Muzik 1979, Fabricius and Alderslade 2001, Horvath 2011). They exhibit an array of body forms and a rather hardy lifestyle, either living at great depth (a hostile environment of intense cold and pressure with no light) (Freiwald and Roberts 2005, Watling et al. 2011) or in shallow, sunlit climes, in areas with slow, constant current, or in areas of marked current flow, literally assuming a stance that allows them maximum exposure to that current (Wainwright and Dillon 1969, Grigg 1970, 1972, Leversee 1976, DeVogelaere et al. 2005). Some deep-water species achieve great size (Heifetz 2002, DeVogelaere et al. 2005) and longevity (Grigg 1974, 1975, Griffen and Druffel 1989, Druffel et al. 1990, 1995, Risk et al. 2002, Andrews et al. 2005, Sherwood et al. 2005), all produce an interesting array of organic compounds used for defense, some of which may prove to be pharmaceutical in nature (Fenical et al. 1981, Rodriquez et al. 1994, Deghrigue et al. 2013, Almeida et al. 2014), and some exhibit an amazingly wide range of geographic distribution. Many seem to function as a sheltering, protective, three-dimensional "tree," harboring many other forms of organism, in or under their branches (Buhl-Mortensen and Mortensen 2004a, 2004b, Auster 2005, Devogelaere et al. 2005, Etnoyer and Morgan 2005, Brancato et al. 2007, Buhl-Mortensen et al. 2010, Rossi et al. 2017). Those species that prefer warm water are often the conspicuous fan-like forms noted in context with stony, reef-building corals, adding a brilliant array of color to the reef. Others, preferring temperate water, may be only generally known in some areas (particularly true of those species with representation in the SBMNH collection seen in the California Bight, which are usually identified by eye, and seemingly not very diverse with regards to number of species), and still others, preferring extreme cold and often seen at great depth, are species that are surprising researchers with their level of diversity, abundance and color. The focus here is on temperate water species found in the research collection at SBMNH from the California Bight (and immediately adjacent areas). Initially, the collection appeared to be composed of a fairly consistent group of gorgonian corals, represented by a dozen or so species that many working within the Bight seemed to know. A primary goal was to assess the SBMNH research collection, and while conducting the reorganization of the collection, to confirm or refute the assertion of such a small number of species in a region that is known for its high degree of biodiversity (McGinnis 2006).

The primary method used for identification of a gorgonian coral species is examination of the skeletal structures embedded in the gorgonian's soft tissue; identification in this group has always required microscopic examination of the skeletal elements, the sclerites (Valenciennes 1855, Grasshoff and Bargibant 2001). The importance of the sclerite to species identification was first recognized by Valenciennes in 1855, although he often neglected to put his observations into practice. Kölliker (1865) put this means of identification on stronger footing and gorgonian taxonomists following in his stead (Verrill 1868, Kükenthal 1924) adopted, expanded and improved the system further; this system was finally emended by Hickson in 1930 (Hickson 1930). Further work by Bayer, dating from the late 1940s firmly established this practice and continues to be the best morphological method for determining species identification. While branch pattern, size of colony, and its color can be useful features in the identification of a gorgonian octocoral, particularly when working in the field or when doing a first examination of a collected specimen, these characters only provide limited identification. With these characters only, determination to a genus might be possible, but ultimately, the single most important character in octocoral identification is the microscopic calcareous

sclerite. Sclerites, formerly known as spicules (Bayer et al. 1983), are found in nearly all species of octocoral (Fabricius and Alderslade 2001). Found in large number in every colony, "ten's of thousands (would) not (be) unusual in a modest-sized colony. Even a small fragment may contain thousands of sclerites" (Cairns, in Etnoyer et al. 2006). These structures, composed of calcitic calcium carbonate, range in size from twenty µm to five mm and are found in both polyps and the coenenchymal tissue between the polyps (Cairns, in Etnoyer et al. 2006). These skeletal structures provide a small measure of support and structure to polyps and their tissue (Lewis and von Wallis 1991). As can be seen in the illustrated trilingual glossary, published in 1983, edited by Bayer, Grasshoff, and Verseveldt, sclerites themselves show an amazing range of diversity in both size and shape. At first, the variety of sclerite shapes can seem overwhelming, and the names given for sclerite forms rather fanciful (torch vs. leaf-scale vs. caterpillar vs. opera glass) (Bayer et al. 1983). This glossary, a first attempt at classifying all the possible forms of sclerite seen in octocorals, ultimately defined, synonymized, and illustrated 57 different sclerite forms. Correct identification of specimens in the SBMNH collection, using sclerite characters, was a key component of the reorganization undertaken.

Other tools that are currently being explored and utilized, with varying degrees of success, for potential identification of organisms are genetic methods and molecular analysis (Etnoyer et al. 2006). Various octocorals, including alcyonacean gorgonians, have been examined by this means (Berntson et al. 2001, France and Hoover 2001, Sánchez et al. 2003a, 2003b, McFadden et al. 2006, Sánchez et al. 2007, Herrera et al. 2010, McFadden et al. 2014, Figueroa and Baco 2014a). These efforts, while still in their infancy, may add valuable insight into the relationships between, and evolutionary development of, gorgonian octocorals, with their taxonomic standing, but will not supplant the need for direct examination of colonies and their sclerites.

As study and reorganization of the SBMNH collection began, it was suggested that identification of gorgonians from a study of their defensive nematocysts might be possible; some work had been conducted that illustrated possible mechanisms for nematocyst function (Mariscal and Bigger 1976, Sebens and Miles 1988), but no published taxonomic work using nematocysts as characters for identification could be found. Successful identification efforts were best achieved through microscopic examination of the sclerites. Sclerites, however, are affected by current flow (both its direction and speed), and other environmental conditions, evidenced by their placement, numbers, thickness, shape variation and degree of ornamentation. This was confirmed through a number of sources (e.g., Gori et al. 2012).

A further area of study that needs to be more extensively undertaken is that regarding gorgonian coral ecology; studies that necessarily focus on the ways in which these organisms deal with the physical features of their environment, as well as the biological issues of finding food, defending themselves from predators and successfully mating. Fabricius and Alderslade (2001) provide a short but comprehensive overview of the physical and biological challenges that all octocorals must address. What we currently know about gorgonian ecology will certainly be affected in the future by the destruction of habitats (Brancato et al. 2007), changes in temperature, water pH (acidifica-

tion), as discussed in a number of published articles (Orr et al. 2005, Wood et al. 2008, Yilmaz et al. 2008; Ziveri 2012, Bramanti et al. 2013), and nutrient levels resulting from global climate change, the alteration in geographic distribution of other organisms stemming from that same climatic change (and how the shifts in other animal and plant populations may affect the substrate-restricted gorgonian corals) and the on-going interest that biochemists and pharmacologists have in the gorgonians (and other invertebrate organisms). Of particular interest with regards to gorgonian ecology are the many obligate symbiont associations that gorgonians have, particularly with other species of cnidarians, cirripede barnacles, amphipods, copepods, and ophiuroids (Patton 1972, Laubitz and Lewbel 1974, Lewbel 1976, Humes and Lewbel 1977, Buhl-Mortensen and Mortensen 2004a, b), to name but a few, as well as what appear to be more symbiotic commensal relationships that exist between gorgonians and various species of fish, who may seek shelter in or under the colonies (Etnoyer and Morgan 2005, Brancato et al. 2007). There are also issues associated with predator-prey interactions for gorgonians (Gomez 1973, Grasshoff and Bargibant 2001) as well as relationships that appear to be more parasitic in nature (McLean and Yoshioka 2007) that provide opportunities for further investigation.

Available literature on gorgonian species of the California Bight was, on one hand, somewhat abundant, but often not very accessible, being spread over so many different publications. The earliest works on California gorgonians date to those published by Verrill (1864, 1865, 1868, 1869) and Nutting (early 1900s). These older works are primarily species descriptions (many of which were designated as new species by Verrill or Nutting). Additionally, work by Kükenthal (1920s), Wright and Studer (late 1880s), Aurvillius (1930s), etc., are still available, although many of these works are in a language other than English, requiring careful translation in order to clearly determine the subtle nuances that distinguish one species from another. Unfortunately, in many of these instances, the authors were working with very small samples of very few specimens and had no context for the larger colony's location in situ. Bayer described a large number of new species, dating from the 1950s to the present (Cairns 2009), but predominantly from geographic areas other than the California Bight. Generally, very little further taxonomic work had been published on many species from California (Hardee and Wicksten 1996); some work was carried out on the ecology and physiology of a few of the California Bight species by Grigg (1970, 1972), Lissner and Dorsey (1986), and Satterlie and Case (1978, 1979), to name the few. More recently, Williams (2013) proposed a new genus (Chromoplexaura) designation for a "red whip" species often found in California waters. While there have been recent reviews done by Cairns and Bayer (2005, 2009) and Cairns (2007) on the Primnoidae, Sánchez (2005) on Paragorgia/ Sibogagorgia, and Breedy and Guzmán on Pacifigorgia (2002), Leptogorgia (2007), Eugorgia (2009), Heterogorgia (2011), and Muricea (2015, 2016), several of which include species from the California Bight, there was no single, comprehensive work on all gorgonian species found within the California Bight (and areas extending slightly either north or south of it), a region that is defined by Cabo Colnett, Baja, Mexico to the south and Point Arguello, California, to the north. This review of the SBMNH research

collection is an attempt to fill that void. New species are likely to be described from this region in the future, and certainly, the number of possible new species that are being documented at greater depth north of the Bight, in Monterey Bay for instance, could well have implications for what potentially may still be discovered within the Bight.

The systematics of eastern Pacific coast octocorals, particularly with regards to the alcyonacean gorgonian corals from Baja, Mexico to the California, Oregon and Washington coasts, seemed sporadic and at times, unreliable. Part of the confusion generated was likely due to the cosmopolitan distribution of a number of species which, when first collected off California, were described as new species (but had actually already been described based on collection events undertaken elsewhere). As stated previously, taxonomists were often working with a very small (and not always stellar) sample from a larger colony, or did not take into account (perhaps because it was not known at the time) the environmental plasticity of these organisms; thus they would describe a species as always branching in one plane, when current flow, we now know (Wainwright and Dillon 1969, Grigg 1970, 1972, Leversee 1976) is often the reason for a colony being in more than one plane. Conversely, some specimens which appeared superficially to be the same species, had all been allocated one name when, in reality, those included in the group were actually several separate species.

A second problem related to the lack of types for some of the taxa described from the California coast. There are excellent reviews by Bayer (1956a, 1981a, 1981c) which have helped to resolve some of the generic confusion surrounding many species names that potentially represented synonyms, but there are those that still need to be resolved (Dunn, 1982). Finally, based on species being noted and/or collected off northern California (survey work being done by NOAA or the research institute associated with the Monterey Bay Aquarium, MBARI), as well as several species that independent researchers have sent to SBMNH (staff from both Los Angeles, LACSD, and Orange County OCSD, Sanitation Districts, Milton Love at University of California, Santa Barbara, etc.), some have not been described at all and it has been revealed that there are previously described species of gorgonian living in the California Bight region that have not been collected and recorded in this locality simply because they have not been looked for. Variously, these are inconspicuous colonies mistaken for some other organism, which have not been examined at the level of the sclerites, or live at depths that have only recently become accessible.

## Materials and methods

Nearly all of the specimens examined (housed currently as part of the Santa Barbara Museum of Natural History's permanent research collection, Invertebrate Laboratory), were collected over a period of years dating from the 1930s to the present in either dry or wet condition. The collection of gorgonians housed at SBMNH, while of moderate size, is a fairly diverse one. The collection displayed diversity due to the activities of many independent collectors over the years who chose to donate their material to the museum, but the collection achieved substantial value when, in 1998, the SBMNH

became the official recipient of the diverse 10,000-lot cnidarian collection, a portion of the Allan Hancock Foundation (AHF) collection built upon the historic 'Velero' expeditions of 1931-1941 and 1948-1985. Thus, the SBMNH cnidarian collection has become a collection of great historical significance, particularly with regards to species that live, or have lived, along northeastern Pacific shores. Of particular note were the extensive lots of material (both wet and dry) encompassing alcyonacean gorgonians, with hydroids and sea pens; these physically arrived at the museum in 2002. The SBMNH now houses approximately 515 lots (many composed of multiple specimens within a single lot) of gorgonian coral. The number of lots indicated does not include numerous lots housed elsewhere in the collection; gorgonian coral fragments are housed in the museum's mollusk collection (the mollusks in question were found on, and collected with, a species of gorgonian, for instance), or in other sections of the museum's cnidarian collection (such as zoanthid anemones collected on gorgonian corals). Also scattered throughout other portions of the museum's invertebrate collection are bryozoans, barnacles, or brittle stars that were collected from within or on gorgonian coral colonies and were preserved with the gorgonian they were living with. To aid in the identification of the museum's specimens, critical to this reorganization, examinations of specimens of known species from or collected in the Bight were also performed on material found in the collections of the National Museum of Natural History, Smithsonian (USNM = NMNH), the California Academy of Sciences, San Francisco (CAS), the Los Angeles County Museum of Natural History (LACoMNH), Scripps Institute of Oceanography (SIO), the Monterey Bay Aquarium Research Institute (MBARI), Moss Landing Marine Laboratories (MLML) and the small museum which is a part of the Cabrillo Marine Aquarium in San Pedro, California (CMA) (see Appendix 1: List of material examined). These were compared to SBMNH specimens, to identify species represented in the collection. Additionally, specimens collected by the Olympic Coast National Marine Sanctuary (OCNMS) on several expeditions (2006, 2008) were examined, as were specimens from various National Oceanographic and Atmospheric Administration (NOAA) offices from both the western and eastern United States. However, extensive collecting of gorgonians was not generally required for this collection reorganization and review; in future, collecting of further specimens may be needed.

Any new material that may have come in was supplied through standard collection procedures that are employed by others (NOAA, LACSD, OCSD) in their on-going, survey-based collection events. A succinct yet comprehensive overview of collection procedures can be found in Etnoyer et al. (2006). The initial part of the study required that material in the collection be checked for correct storage conditions; if they were not so stored, preparation for long-term storage was undertaken.

Approximately two-thirds of the SBMNH collection is stored wet, in 70% ethanol; the other third of the collection is dry stored. When the cnidarian material from AHF came into the SBMNH's possession, all of the wet material had to be properly stored, then original hand-written labels with collection data had to be preserved for both wet and dry specimens and the museum's official institutional labels had to be printed and stored with the original label. All specimens discussed in this publication, housed at SBMNH, were cataloged as voucher specimens and data for these specimens were entered into the Museum's online database.

All colonies were examined for gross morphology; records of height and width of a colony, length of main and secondary branches, diameter of those branches, color of the axis (if visible), and color of the colony were made. No molecular taxonomic work was undertaken with specimens received from AHF. As no formalin should come in contact with the samples, and there was no certainty that any of the material in the SBMNH collection had not encountered formalin, molecular extraction was not considered. A fuller discussion on methods for preserving and handling tissue for molecular study (DNA or RNA analysis) can be found in Etnoyer et al. (2006).

For this review, examination of the calcareous sclerites, present in different parts of the colony, was conducted for nearly all specimens. Two specimens lying side by side, and appearing similar in color and overall colony form could have very different sclerites, thus establishing them as potentially different species (however, as sclerites themselves can be environmentally "plastic," which can complicate species identification). This was a common theme regarding certain genera present in the California Bight as reflected in the SBMNH collection. Geographic location of the specimen or sample collected, as well as details/specifics (depth, degree of current flow, etc.), aided in identifications. Following sclerite preparation, using the standard method for sclerite extraction (tissue sample in common household bleach), light microscopy via a compound Olympus (CH) microscope, was used initially to determine the genus to which a specimen belonged; careful examination of sclerite details then allowed for identification to species. Sclerites were then photographed using a digital camera system (Olympus BH2 microscope with an Olympus Q Color 5 digital camera) able to record a millimeter scale on each image. Scanning Electron Microscopy (SEM) of the sclerites was then undertaken. All samples were coated with gold, using a Cressington Sputter Coater Unit, 108auto. Samples were examined and digital images taken, using a Zeiss Scanning Electron Microscope EVO 40, at 10 kV. Sclerites were chosen from stub arrays that best displayed the key features of variety, size, shape, or ornamentation; despite bits of organic debris or some damage, if a sclerite, overall, was a good representation of a "key" sclerite shape, it was used. Images were both stored on computer hard-drive and cataloged on external drives, for permanent, backup archival storage. SEM stubs were housed in plastic stub boxes; stubs were numbered with Museum Catalog numbers and each box bears a paper label, listing all species with their museum number, contained in that particular box. This SEM information was then entered into the Museum's on-line database, supplementing all other key information known for each specimen. SEM was used to confirm identification in all species, through comparison against SEM images found in published literature of species with verified identification. In the end, some 40-plus species of gorgonian, from approximately 23 genera, were identified, cataloged, and appropriately housed. This first part covers a dozen species, those classified as scleraxonians as well as those from the family Acanthogorgiidae (Holaxonia). A summative overview of species housed in the SBMNH research collection, from these specific

• •	
# of specimens analyzed with sclerite preparations	32
# of specimens examined without sclerite preparation	1
Breakdown of specimens examined:	
# of specimens analyzed from SBMNH collection	13
# of specimens analyzed from USNM-Smithsonian	13
# of specimens analyzed from CAS	2
# of specimens analyzed from other institutions	4
Total # of species that received sclerite observations	12
# of new species described	1
Breakdown of species examined:	
# of species from the SBMNH collection	6
# of species from USNM-Smithsonian	11
# of species from CAS	1
# of species from other sources	4
# of species shown in Figures (colony)	5
# of species shown in Figures (either light microscopy and/or SEM of sclerites)	4

Part I: Collective specimen and species data.

	SBMNH	Other institutions	Colony figure	Sclerite figure
Anthothela pacifica	Yes	Yes	Yes	Yes
Paragorgia arborea	Yes	Yes	Yes	No
Paragorgia regalis	No	Yes	No	No
Paragorgia stephencairnsi	No	Yes	No	No
Paragorgia yutlinux	No	Yes	No	No
Sibogagorgia californica sp. nov.	Yes	Yes	Yes	Yes
Hemicorallium ducale	Yes	Yes	No	No
Hemicorallium imperiale	No	Yes	No	No
Hemicorallium regale	No	Yes	No	No
Acanthogorgia gracillima	Yes	?	Yes	Yes
Acanthogorgia sp. A	Yes	?	Yes	Yes
Muricella complanata	No	?	No	No

Species covered in this part.

groups, is included above. As further exploratory work is undertaken in the CA Bight, and adjacent areas, likely more species will be added to the list, and (hopefully), new specimens will find their way into the SBMNH research collection.

This information regarding species and lots of specimens, examined for Part I, both for colony morphology and sclerites (either through light microscopy or SEM) is a summation of the more detailed information to be found in the Appendix 1: List of material examined – Part I. It is evident from this summative overview that the SBM-NH research collection (while illustrative of species considered part of the scleraxonian group or the holaxonian Acanthogorgiidae found within or near the California Bight) is not extensive, nor likely fully representative of all species of scleraxonian and Acanthogorgiidae that could potentially exist in the California Bight region.

# Systematic accounts

(Classification used throughout this paper conforms to that of Bayer 1981c)

# Diagnosis of the order Alcyonacea Lamouroux, 1816

(Gorgonian corals, as defined previously)

Octocorals with uniformly short gastrovascular cavities; colonies typically arborescent, rarely lobate or incrusting, producing more or less specialized three-dimensional axial skeletal structures: either a distinct central axis of horny (gorgonin) or calcareous material (or both), or a central medullar zone of calcareous sclerites which are loosely or inseparably bound together by horny or calcareous matter.

# Scleraxonia Studer, 1887

Octocorals with central axis, medullar zone or inner layer containing sclerites bound together more or less solidly either by horny or calcareous material; outer layer of coenenchyme containing proximal portions of gastrovascular chambers of polyps, endodermal canals and solenia; cortical sclerites free, commonly appearing different from those in medullar region; axial cylinder/medulla may contain canals and solenia but polyp cavities do not penetrate; cross-chambered central chord absent; sclerites always present.

# Key to Families represented in SBMNH collection (Scleraxonia)

1	Axis with spongy, horny nodes, filled with sclerites alternating with longer calcareous internodes composed of cemented sclerites
	(not discussed in this publication)
_	Axis not composed of alternating horny nodes and calcareous internodes2
2	Axis a medullar region composed of completely fused calcareous sclerites
	forming a central cylinder of solid calcium carbonateFamily Coralliidae
_	Axis a medullar region composed of multiple, separate, sclerites held together
	by a horny material
3	Axis with a cross-chambered central chord (not discussed in this publication)
_	Axis without a chambered central chord, but often with numerous gastroder-
	mal canals
4	Cortex set off from medulla by a ring of boundary canals; polyps monomor-
	phic and protruding
_	Cortex not set off from medulla by a ring of boundary canals; medulla formed
	only by unfused sclerites, penetrated throughout by longitudinal canals; pol-
	yps retractile, not protruding Family Paragorgiidae

# List of species of Scleraxonia Studer, 1887

Class Anthozoa Subclass Octocorallia Haeckel, 1866 Order Alcyonacea Lamouroux, 1816 Suborder Scleraxonia Studer, 1887 Family Anthothelidae Broch, 1916 Anthothela pacifica (Kükenthal, 1913) Family Paragorgiidae Kükenthal, 1916 Paragorgia arborea var. pacifica (Verrill, 1922) Paragorgia regalis Nutting, 1912 Paragorgia stephencairnsi Sánchez, 2005 Paragorgia yutlinux Sánchez, 2005 Sibogagorgia californica sp. nov. Family Coralliidae Lamouroux, 1812 Hemicorallium ducale (Bayer, 1955) Hemicorallium imperiale (Bayer, 1955) Hemicorallium regale (Bayer, 1956)

## Descriptions of species of Scleraxonia Studer, 1887

# Family Anthothelidae Broch, 1916

**Diagnosis.** Branches of colonies slender. Polyps monomorphic, with prominent calyces, anthocodiae usually exsert. Axis not jointed, without a cross-chambered central core. Medulla surrounded by longitudinal boundary canals (of roughly equal size) separating it from cortex; medulla only rarely perforated by gastrodermal solenia in smaller branches and even then, not as extensively as in lower parts of colony; in larger branches, medulla perforated by solenia. Generally, medulla with separable sclerites; medullar sclerites stout spindles (not needle-like), thorny, ornamented with warts, spines or branching processes, that may link sclerites together. Sclerites of coenenchyme longer fusiform spindles, sometimes clavate or bent, occasionally with radiate bodies and capstans (rarely).

**Discussion.** Within the Subclass Octocorallia, taxonomic placement of this family reflects the changeable history the Order Alcyonacea has experienced since its inception. Currently, Alcyonacea is one of three orders in the subclass (Williams and Cairns 2014). The current Order Alcyonacea was, however, originally divided into four orders (Alcyonacea, Gorgonacea, Stolonifera, and Telestacea). Current coral taxonomy now divides Order Alcyonacea into five nominal groups: Calcaxonia, Holaxonia, Scleraxonia, Alcyoniina and Stolonifera (Bayer 1981c, Fabricius and Alderslade 2001). While the Family Anthothelidae is today recognized as valid in the Order Alcyonacea [Scleraxonia], a number of species in the family were originally placed in the older Order Stolonifera, often within the Family Clavulariidae. A few researchers may still group some of the families

of soft corals in an Order Stolonifera, but since then, a number of genera and several species have been moved out of Stolonifera. Fabricius and Alderslade (2001) noted that the "decision whether to categorize a particular genus as a stoloniferan becomes so subjective that the name plainly has limited classificatory value . . . ." Use of the Order Stolonifera, and placement of the Family Anthothelidae in it, or the nominal group, Scleraxonia (as opposed to Stolonifera), has had a continued, tumultuous history (Hickson 1915, Molander 1918, Kükenthal 1919, 1924, Madsen 1944, Bayer 1961, Bayer 1981a, b, c, Hochberg 1979). Currently, the classification of species in the family is determined by the presence of a membranous colony form, presence, or absence of coenenchyme layers surrounding an axis, and the way in which polyps arise from the membranous base.

Any membranous octocoral colony currently held in the SBMNH collection (few in number, small in size, deteriorated due to early formalin storage) could be a member of either the genus *Clavularia* or the genus *Anthothela* (the latter, a genus within the Order Alcyonacea, Scleraxonia). A detailed examination of the few colonies held in the SBMNH collection, in comparison with material housed elsewhere is needed; that necessitates a separate project, to be undertaken at some future date. Most of the material in the SBMNH collection with membranous colony form is present in a very fragile state; a more detailed description for each will not be easy, in some instances, not possible at all. It is likely that even with a more thorough examination of the material held at SBMNH, the results will necessarily be inconclusive. A complete revision of the genus *Anthothela* was recently completed by Moore et al. (2017), utilized here.

#### Genus Anthothela Verrill, 1879

#### Briareum Sars, 1856b: 63 [pars].

? Gymnosarca Kent, 1870a: 397. Stephens, 1909: 7.

Anthothela Verrill, 1879a: 199; 1883: 40. Studer (and Wright) 1887: 28. Grieg 1891: 3. Broch 1913: 4. Kükenthal 1919: 43; 1924: 14. Thomson and Dean 1931: ?

11-20. Stiasny 1937: 20. Verseveldt 1940: 37. Bayer 1961: 57-58 (key), 65 (key),

67-68, 70. Arantes and de Medeiros 2006: 2. Moore et al. 2017: 19.

? Stereogorgia Kükenthal, 1916: 178.

Suberia Nutting, 1911: 15.

## Type species. Briareum grandiflorum Sars, 1856b (by subsequent designation).

**Diagnosis.** With slender, rounded, tortuous, commonly upright, abundant anastomosing branches producing tangled colonies. Branches always solid; no main stems developed, branches grading upwards from broadened membranous base. Polyps present on base as well as on branches, widely scattered on all sides, sometimes clustered into large masses. Polyps elongated in expansion arising from distinctly projecting, short yet elevated cylindrical calyces. Polyps partially retractile, seldom entirely retractile; large anthocodiae commonly preserved exsert, arising from either extended, rather thin, slightly sharp, spiculose, but spongy, basal membrane (encrusting) or from slender irregular stems (branched). Axis spiculose, well differentiated, not firm. Long, strongly warted, often irregular spindles and short, girdled rods in coenenchyme. Sclerites of axis more irregular; bear fewer, larger warts, knobs or lobes. Spongy base filled with thin spindles and rods, permeating tissue. Bright rosy-red or brownish in life, but other color forms likely.

## Anthothela pacifica (Kükenthal, 1913)

Figures 1A, B, 2

- Anthothela pacifica (Kükenthal, 1913a): 237–239; text figs E–G. Bayer 1961: 336. Moore et al. 2017: 34–40.
- (?) Clavularia pacifica Nutting, 1909: 686. Kükenthal 1913a: 237–239. Hickson 1915: 548.
- (?) Sympodium armatum Wright & Studer, 1889: 272. Nutting 1909: 686.
- (?) Anthothela argentea Studer, 1894: 60. Kükenthal 1919: 45; 1924: 16. (No longer valid; see WoRMS Data Base, Cordeiro et al. 2018a, Anthothela)

**Type locality.** USA, California, China Point, (?) San Clemente Island, SW tip, 50 fm (91 m).

**Type specimen.** Location of type unknown.

**Material examined.** One specimen in SBMNH collection was identified as this species (see Appendix 1: List of material examined).

Description. Colony (Figure 1A) of thin, flattened branches, crooked, tortuous, somewhat anastomosed; no large main stem development. Rather low-lying, prostrate form; height 0.5 mm-7.0 mm; "stolon" thin, membranous; arrangement of medulla and "cortex" as described for family. Calyces (Figure 1B) prominent, projecting cylinders up to 2.5–3.0 mm tall; polyps stout, with highly retractile portion up to 2.5 mm in length; total calyx/polyp size 5.0 mm tall by 2.0 mm wide. Calyces monomorphic, with eight deep, longitudinal grooves, delineating eight ridges or ribs with sharp edges. Distal part of polyp usually exsert, bearing eight double-rows of spindles. Polyps large, rather widely spaced. Color of living colony described as light yellow or straw-colored to grayish white; in alcohol, creamy white. Sclerites (Figure 2) of coenenchyme large, elongate, thin, pointed spindles, often with prominent projections on edges; generally, fusiform (0.25-0.3 mm long), not capstans; often appearing bent. Older descriptions indicate that sometimes these are strongly clavate at terminal end, appearing as clubbed spindles; this condition not seen in material examined. Anthocodial armature strong spindles, often clavate or bent, only rarely as radiate bodies and capstans. Spindles at base of tentacles (collaret), 0.18 mm long, those of calyx 0.22 mm long, none of these club-shaped. Sclerites widely spaced, showing transverse disposition at base of tentacles; sclerites of medulla strong thorny spindles. Colony surface rough to the touch due to projecting sclerites.

Etymology. Presumably named for type locality, northern Pacific Ocean.

**Common Name.** Dwarf white gorgonian.

**Distribution.** Not definitively known at this time for coastal western United States; potentially from southern California: USA, California, San Diego, Point Loma,



**Figure 1.** *Anthothela pacifica*, SBMNH 265939. **A** Large portion of colony fragment; several rocks accompanied specimen (presumed substrate); colony unattached, ~7.0 cm in length **B** close-up of polyps, each polyp ~0.5 mm tall.

200 m (Nutting 1909) and China Point, (?) San Clemente Island, SW tip, 91 m, to at least northern California, Monterey Bay, 900 m (Nutting 1909); possibly as far north as southern British Columbia, Canada (Lamb and Hanby 2005).

**Biology.** According to Kozloff (1987), a shallow subtidal form. Lamb and Hanby (2005) state it as "subtidal, below 40 m (133 ft)."



**Figure 2.** *Anthothela pacifica*, SBMNH 265939, SEM image. Coenenchymal sclerites, colored a very pale yellow to white. Length of largest sclerites examined ~400 µm.

Remarks. Kükenthal (1913a) indicated species is not equal to Sympodium armatum Wright and Studer as cited in Nutting (1909). However, an interesting aspect presented itself through an unexpected source. A letter, found in SBMNH archives, dated 1978, from Dr Frederick Bayer to Dr Eric Hochberg, indicated the suggestion of a possible synonymy between Anthothela argentea Studer, 1894 and Anthothela pacifica. In that letter Dr Bayer made two significant statements, the first being that the two lots reported and identified (and misidentified) by Nutting (1909: 686) as "Sympodium armatum Wright & Studer, 1889," subsequently identified by Kükenthal (1913) as Clavularia pacifica, are in actuality gorgonians of the genus Anthothela. Bayer (1961) made mention of this in relation to the Atlantic Ocean species Anthothela tropicalis Bayer, 1961. Secondly (key point of the letter), Bayer believed that it was "possible that 'Clavularia' pacifica is identical with Anthothela argentea Studer, in which case Studer's name takes precedence." Further reading in Bayer (1961) showed that there was indeed a genus name change. Bayer, discussing family Anthothelidae, genus Anthothela, made the following statement: "A distinctly different species has now been recorded from the Gulf of Mexico, also in deep water, which proves to be a new species closely related to the eastern Pacific Anthothela pacifica (Kükenthal), forming with it an eastern Pacific-western Atlantic twin-pair of species." Note the change in genus name (from Clavularia to Anthothela). Regarding the distributional range for A. argentea, location records noted on distribution maps posted on the Encyclopedia Of Life website showed it occurring throughout the southeastern Pacific Ocean, extending into the northeastern Pacific, to at least central California (USA; USNM 94428 was collected in proximity of the western edge of the Bight). This indicated a possible geographic overlap with (or the possibility that it was synonymous with) A. pacifica. However, the work of Moore et al. (2017) puts the suggested synonymy of Bayer in question, having reassigned Anthothela argentea to the genus Victorgorgia López-González & Briand, 2002 and the new family Victorgorgiidae, as they indicated that there are clear morphological and genetic differences from the genus Anthothela.

From the World List of Octocorallia, the World Register of Marine Species (WoRMS), *Anthothela pacifica* is an accepted scientific name, while *Anthothela argentea* has been accepted as *Victorgorgia argentea*, and from that listing it is clear that these two are considered separate species (Cordeiro et al. 2018a).

Identification of specimen relied on notes made by Dr Hochberg, with a description given by Kükenthal; fragility of specimen did not permit an extensive examination, but as far as it could be done, one was done with the specimen to hand.

Hickson (1915) lamented: the "widely distributed and very variable genus *Clavularia* is badly in need of revision. It is probable that such a revision would lead to a considerable reduction in the numbers of species, many of which have been founded on very in-adequate characters." He went on to say that the genus *Clavularia* is well represented in the North Pacific Ocean; how many other species belong in the genus *Clavularia*, and how many may be members of the genus *Anthothela*, or some other genus, remains to be seen. Bayer (1961:70) affirmed that Nutting's and Kükenthal's specimens are gorgonians of the genus *Anthothela*. Hochberg (1979) stated, "comparison with the type is needed to identify what has been called *Clavularia pacifica* from this area in the past. The generic change (to *Anthothela*) is an obscure reference, being only a few lines in Bayer's work (1961) on Caribbean octocorals."

Location of type is at issue; someone (unknown) noted: "China Point, 'San Clemente Island (SW tip).' " There was no way to confirm this statement, and there is the added problem of a China Point on Santa Catalina Island (SW side of island), as well. There was no means to identify which "China Point" was the correct collection location.

## Family Paragorgiidae Kükenthal, 1916

**Diagnosis.** Robust, profusely branched colonies with dimorphic polyps (feeding autozooids, reproductive siphonozooids). Axial skeletal structure solely a continuous medulla, containing separable sclerites. Medulla perforated by gastrodermal canals all the way to branch tips, not separated from cortex by a ring of boundary canals.

#### Genus Paragorgia Milne Edwards & Haime, 1857

Paragorgia Milne Edwards & Haime, 1857: 190. Verrill 1878b: 476. Kükenthal 1919:
77 [synonymy]; 1924: 28 [synonymy]. Verseveldt 1940: 137. Bayer 1956a: F197;
1993: 2. Sánchez 2005: 15.

**Type species.** *Alcyonium arboreum* Linné, 1758; [= by subsequent designation, *Para-gorgia arborea* (Linnaeus, 1758), by monotypy].

**Diagnosis.** Massive, tree-like colonies with thick branches, measuring up to 7.0 meters tall, perhaps as much as 6.0–7.0 meters wide. Sclerites in axial medulla, long,

ornate rods (spindles) with branching processes, derived from capstan type, up to 0.6–0.8 mm in length, colorless or pink; elsewhere (coenenchyme, tentacles, etc.) sclerites small (less than 0.15 mm in length), differing shapes, commonly pink or red. Surface sclerites six-, seven-, and eight-radiate capstans, always less than 0.1 mm long, with globular, smooth, grooved or lobulated ornamentation. Sclerites in subsurface/outer medulla of intermediate form, ranging between radiates and spindles. Autozooid polyp tentacles have distinctively blunt, stubby rods or ovals, less than 0.1 mm.

# Paragorgia arborea var. pacifica (Verrill, 1922)

Figure 3

Paragorgia pacifica (Verrill, 1922): G16–G18; plate VIII, figs 3, 4b.

Alcyonium arboreum Linnaeus, 1758: 803. Pallas, 1787: 164.

*Paragorgia arborea* (Linnaeus, 1758): 803. Milne Edwards 1857: 190. Broch 1912: 6. Hickson 1915: 548–549. Grasshoff 1979: 117 [and references therein]. Sánchez 2005: 15–20.

Paragorgia nodosa Koren & Danielsson, 1883: 19 [sensu Bayer 1956b: 70].

(?) Paragorgia nodosa Nutting, 1912: 99.

(?) Paragorgia regalis Nutting, 1912: 100.

Type locality. Canada, British Columbia, Vancouver Island, Jervis Inlet, ~20 m. Type specimens. Holotype YPM-5373 [dry].

Material examined. ~1–2 lots (see Appendix 1: List of material examined).

**Description.** Collection lot studied contains one branch fragment (Figure 3); in most respects, examination of fragment revealed characters that align with the description given in Sánchez (2005, pages 15–20). The branch is distinctive in its knobby aspect, but sclerites fall well within the parameters of morphology as discussed and shown in Sánchez (2005).

**Etymology.** The variety name *pacifica* was presumably proposed in reference to the location/distribution of the species in the Pacific Ocean.

**Common name.** Referred to frequently as "Bubblegum coral." Cairns et al. (2003) referred to Breeze et al. (1997) where this genus/species is also listed as "Rubber Trees" and "Strawberry Plants." Specifically, it could be called the "Pacific bubblegum tree."

**Distribution.** Recorded from Alaskan waters, Bering Sea, 'Albatross', 54°02'40"N, 166°42'00"W, at a depth of 504 m; USNM 3315. Also, recorded from Unalaska to Kodiak, 'Albatross', 54°19'00"N, 159°40'00"W, taken by dredge, 114 m; USNM 3338. Bayer indicated (unpublished ms 2, Cairns 2009) that known distribution of this species was from the Bering Sea south to Vancouver Island (specimen collected by Mr Wm Spreadborough, at Ucluelet, Vancouver Island, BC, at a depth of 16 m, June, 1909. [Col. No. 51, Coelenterates, Victoria Memorial Museum, Ottawa]) on the east side of the Pacific, and likely over to Japan on the west; southern limit (at the time Bayer was writing) was unknown. Based on more recent work, including the review of systematics for the family by Sánchez (2005), this species, in the Pacific Ocean (a pos-



Figure 3. *Paragorgia arborea* var. *pacifica*, SBMNH 422977. Single branch fragment, ~5.0 cm long, displaying knobby condition of branches seen in some specimens.

sible variant of *P. arborea*), extends to at least the northern limit of the California Bight on the eastern side (at question, further south, at depth), and down into New Zealand waters on the Pacific Ocean's western side.

Biology. Specimens collected or photographed in the Monterey Bay Marine Sanctuary have harbored polychaete worms, purple in color (species identification not determined), with the worms wound around the branches of the colony (Langstroth and Langstroth 2000). On a specimen examined from Mexico, Gulf of California, Baja, Bahia de Los Angeles, there was a complete over-covering of what may be some sort of grey colonial or zoanthid-type organism (the specimen was not included in the list of material examined, as the overgrowth of the zoanthids precluded any clear examination of the host gorgonian itself). A MBARI video clip, viewed on a visit to MBARI, had an excellent segment of this species heavily colonized by numerous basket stars, so many in fact, that the entire, large tree-like colony displayed a heavy growth of "hair." According to Langstroth and Langstroth (2000), on a Paragorgia specimen, a feather star, Florometra serratissima, was seen clutching the gorgonian with its leg-like cirri. While this was seen in a lab setting, the feather star likely may have come with the gorgonian during the collection process. If so, other filter-feeding echinoderms might be seen living on/with these gorgonians in situ. Evidence from recent OCNMS expeditions, as well as numerous MBARI and NOAA video clips support this. Colonies living in deeper water grow very slowly in some areas and could be several hundred years old (Andrews et al. 2005, Sherwood et al. 2005), reaching heights of several meters (DeVogelaere et al. 2005). It is speculated (Brancato et al. 2007) that these large, aged colonies provide critical habitat for such organisms as Northern Rockfish, Pacific Ocean Perch, species of King Crab, and Pacific Cod. An expedition undertaken by Olympic Coast NMS (May 2006) lent credence to this speculation.

**Remarks.** Sclerite examination of the sample shown in Figure 3 agreed with those seen in Sánchez (2005: fig 9); the six-radiates distinctive of this species were confirmed. Verrill (1922), reporting on specimens of *Paragorgia arborea*, discussed the possibility of the existence of this variant. Bayer stated in his unpublished manuscript (ms 2, Cairns 2009)) that "*P. arborea* seems limited to latitudes of 40° or higher . . . . *P. arborea* seems to be truly bipolar, since no reliable finds have been made south of British Co-

lumbia in the Pacific. It is impossible to be sure that the species does not show equatorial submergence." Thus, "it appears that the genus *Paragorgia*, an inhabitant of cold waters, . . . whose various species occur at moderate depths in boreal and anti-boreal regions, follow the cool water to greater depths in low latitudes." Bayer additionally stated that a specimen obtained in British Columbia, as *P. pacifica* could be a variety of *P. arborea*. Kozloff et al. (1987) stated that *Paragorgia pacifica* is "the most commonly encountered gorgonian of" the Pacific Northwest region; "it has been called *Paragorgia arborea* Linnaeus, 1758." The final word comes from Sánchez (2005); he stated that a comprehensive review of North Pacific populations of *P. arborea*, "including type material and genetics is needed before reaching conclusions on *P. pacifica* and the differentiation of south vs. north *P. arborea* populations."

The California Academy of Sciences has approximately 30 lots of this, or other species, attributed to this genus; most specimens are from Alaska; as well, two are from the USSR, one is from Norway, and one is from Oregon. Nine of the remaining lots are specimens collected from California; most are from Monterey Bay, with one from the Davidson Seamount. Of these nine, only three have been identified as being this particular species. MBARI has extensive video records of this species from Monterey Canyon, as well as the Davidson Seamount. In the Moss Landing Marine Labs collection there is a small specimen of what may well be this species, collected in Monterey Bay, ~36°27'12"N, 122°04'02"W, ~450 meters; coll. G McDonald, 13 March 1974; C0067 [wet]. As well, there is an impressive, tree-sized dry specimen on display in the hallway near the museum door. (Collection data may be available for this specimen, but collection data could not be located.)

Based on multiple examinations of possible *Paragorgia* material in the SBMNH research collection, none (one exception) were examples of *P. arborea* var. *pacifica*; numerous sclerite preparations never revealed the six-radiate sclerite form that is characteristic of this species; only a very few displayed eight-radiates. As well, no polyp sclerites were ever obtained. As most of the SBMNH specimens examined clearly lacked the "key" identifying sclerites, no request was made to obtain the holotype specimen from Yale Peabody Museum. *P. arborea* (though not the variety *pacifica* suggested by Verrill) is an accepted species in the WoRMS listings (Cordeiro et al. 2018b). As well, the three following species are also accepted species in the WoRMS registry. These are included as they have been collected in very close proximity to the California Bight region. None however, are represented in the SBMNH collection and research indicated that they were never collected on any of the 'Velero' expeditions. In point of fact, there were no records of any specimens in the genus *Paragorgia* having been collected.

# Paragorgia regalis Nutting, 1912

Paragorgia regalis Nutting, 1912: 100. Sánchez 2005: 25–29. Paragorgia dendroides Bayer, 1956b: 69 [sensu Bayer 1964a: 526]. Grasshoff 1979: 120.

**Material examined.** No material in SBMNH collection (see Appendix 1: List of material examined).

**Remarks.** Inclusion of *P. regalis* is based on USNM 1027063, which was collected just west of the California Channel Islands, in proximity to western boundary edge of Bight. Moss Landing Marine Labs may have a representative sample of this species in their collection, from Monterey Bay Canyon, 36°25'54"N, 122°00'03"W, ~900 m; coll. D Rold and H King, December 1978; C0074 [wet]. It is possible that some of the *Paragorgia* seen in MBARI video segments could be this species; this species may have been seen when examination of samples of gorgonian collected by J Barry (MBARI) was done, made available for examination by Lonny Lundsten. Distribution ranges across the Pacific Ocean (based on collection records for specimens in NMNH). Collection depths in Hawaii and Japan range from 452–1840 m (Sánchez 2005), and as noted from NMNH collection. For a common name, this species might be called the "Regal bubblegum tree."

### Paragorgia stephencairnsi Sánchez, 2005

Paragorgia stephencairnsi Sánchez, 2005: 57-60; figs 39-41.

**Material examined.** No material in SBMNH collection (see Appendix 1: List of material examined).

**Remarks.** A paratype specimen at NMNH (USNM 94437), identified as this species, was collected in proximity of the southern California Channel Islands, in an area lying close to the western boundary of the California Bight; range seems to extend northward to an area off British Columbia, Canada (location data for USNM 57982, the holotype; discussed in Sánchez 2005). As this species was named in honor of Dr Stephen Cairns of the National Museum of Natural History, Smithsonian, it would be fitting to call this "Stephen's bubblegum tree." Any similarities between this and other species in the genus were thoroughly discussed in Sánchez (2005).

#### Paragorgia yutlinux Sánchez, 2005

Paragorgia yutlinux Sánchez, 2005: 53-57; figs 36-38.

**Material examined.** No material in SBMNH collection (see Appendix 1: List of material examined).

**Remarks.** A specimen at NMNH (USNM 90345), identified as this species, was collected west of the southern California Channel Islands in an area that lies near the western boundary of the California Bight. A MBARI sample taken from Monterey Canyon, near Point Sur, on 7 April 2008 could also be this species. A number of other samples, examined cursorily, housed at MBARI, could be this species.

# Genus Sibogagorgia Stiasny, 1937

Sibogagorgia Stiasny, 1937b: 80. Sánchez 2005: 60. Herrera et al. 2010: 132.

**Type species.** *Sibogagorgia weberi* Stiasny, 1937b: 80 [= *Suberia köllikeri* Nutting, 1911: 13, nec Studer 1879].

**Diagnosis.** A genus in the family Paragorgiidae with scleritic medulla showing no (or very few, one to two) large penetration canals; main solenia around subsurface/ outer medulla as boundary canals, forming reticulate network; network of canals observable with light microscopy as a regularly reticulate and uniform mesh just beneath surface. Polyps without tentacular sclerites, outer surface with radiate sclerites; generally, medullary sclerites nearly bare of ornamentation. Autozooid polyps uniformly to randomly distributed along branches, throughout colony. Branching colonies often in one plane (but not always); main branches usually thicker than terminals; terminals clavate. Coloration either of uniform beige or bright orange-red to a beige coloring with slightly projected pinkish orange polyp apertures.

#### Sibogagorgia californica sp. nov.

http://zoobank.org/5B485BEF-92D9-4A35-923F-BC491076AC72 Figures 4, 5A–C, 6A, B, 7A–C

**Type locality. Holotype** USA, California, Los Angeles County, West end, Santa Catalina Island, 300 meters. **Paratype** USA, California, Los Angeles County, NE × E of Long Point, Santa Catalina Island, 415–486 meters.

Type specimens. Holotype SBMNH 422974; Paratype SBMNH 422973.

Material examined. ~8 lots (see Appendix 1: List of material examined).

**Diagnosis.** Specimens rarely displayed growth in one plane. Sclerites of medulla with blunt tips, bearing minimal ornamentation, smooth in areas between widely spaced spiny processes; sclerites of colony surface and coenenchymal tissue intermediate between surface and medulla 7-radiates, but never 8-radiates. Thick, compact branches with color variation from pinkish orange to pale pink.

**Description.** *Colony* (Figure 4, 6) fragments robust, tree-like, with thick, conspicuous branches. Specimen of Figure 4 approximately 18 cm tall, that of Figure 6 roughly 36 cm long (when gently stretched out). Coenenchyme is thick and tough (like cutting through raw carrot). Branches moderately smooth in appearance, although lumpy in many spots, with small calyces evident; appear somewhat moderately spaced, scattered irregularly, on all sides of branches; distal or lateral branch tips each end with round, swollen knob. Color of branch coenenchyme (Figure 4) bright reddish orange; specimen shown in Figure 6 creamy beige with orange polyp apertures (this could be normal color or could have bleached out due to earlier storage solutions); in both specimens, polyps of same orange hue, with tentacles white (more visible in



**Figure 4.** *Sibogagorgia californica* sp. nov., SBMNH 422974 (Holotype). Large fragment, ~18 cm long, showing branching pattern; intertwined tendrils from shark egg case are visible.

specimen of Figure 4). Cross section samples of both colonies revealed obvious boundary canals, and both colonies have very few, but rather large penetration canals in the medulla. No blunt, stubby, ornate polyp tentacular sclerites (rods) were ever found in any of numerous tissue samples examined; outer surface sclerites are radiate (Figures 5C, 7C), most closely matching a 7-radiate configuration, with ornamentation often jagged and extensive; color of these sclerites a pale pinkish orange; medullary sclerites (Figures 5A, 7A) are spindles, with moderate ornamentation, not as bare as seen in most other species of the genus; these spindles are more or less white, but may often have a very pale yellow color.

**Etymology.** Nearly all specimens examined, with the exception of two, are from locations within the vicinity of the California Channel Islands, thus a reference to the state of California, where most of the specimens were collected.

Common name. Proposed, "California orange bubblegum" coral.

**Distribution.** Based on the specimens in the SBMNH collection, ranges from at least Lincoln County, Oregon through southern California waters.

**Remarks.** Preliminary examinations led to identification of this small group of specimens as *Sibogagorgia cauliflora* Herrera et al., 2010. The two colony morphs shown in their description matched well with that seen in the SBMNH specimens: either a vibrant orange-pink (Figure 4) or a more dull cream color with orange polyp apertures (Figure 6). Unfortunately, the paler-colored specimens at SBMNH had been stored in less than desirable conditions for a lengthy period of time; still, the resemblance was strong. However, the SBMNH specimens were decidedly different in the appearance of their radiate sclerites, taken from the surface cortex. In the species described here, surface radiates were not oval, with 8-radiate origination; this form of sclerite was never seen in examined specimens, despite numerous tissue/sclerite preparations, and is the key distinguishing feature



**Figure 5.** *Sibogagorgia californica* sp. nov., SBMNH 422974, SEM image. Sclerites either bright salmon in color, or pale yellow to white. **A** Sclerites from colony medulla **B** sclerites from colony surface and possible intermediates toward the medulla **C** 7-radiate sclerites from colony surface.

of *S. cauliflora*. Several possibilities emerged: 1) that the SBMNH specimens were an endemic subspecies of *S. cauliflora*, or (because of their strictly southern California location), 2) a very similar, but different species, or 3) the specimens collected were an isolated group of *S. cauliflora* that just happened to be found in a location where, for some environmental reason, the distinctive 8-radiates that normally would form in development



**Figure 6.** *Sibogagorgia californica* sp. nov., SBMNH 422978. **A** Large, ~36 cm long colony fragment **B** close-up view of polyps, illustrating color and position on branch; note contrast color between polyps and surrounding coenenchyme, characteristic of species in the genus. This may however, be a partially bleached specimen, rather than one exhibiting true coloring.

and growth, did not. Because of their collection location, and differences in sclerite forms, a new species designation is proposed for what may be a very closely-related, species.

From a taxonomic perspective, in their most recent molecular work Figueroa and Baco (2014) recommended that family Sibogagorgiidae be reinstated. According to WoRMS, the genus *Sibogagorgia* is still retained in the family Paragorgiidae (Cordeiro et al. 2018c).

The museum collection at Moss Landing Marine Labs held a specimen that might be this species, collected in Monterey Bay, 36°26'42"N, 122°01'56"W, ~684 m; coll. G McDonald, 14 August 1974; C0071 [wet]. Coloring of this specimen showed either a slightly bleached condition (storage artifact) or the beige coloring with orange pimples, a slightly brighter condition than that seen in SBMNH 422978.

The SBMNH holotype specimen has, tightly wound around/across its branches, the attachment tendrils from the ends of a swell shark's mermaid's purse. The tree-like nature of species not only in this genus, but also in the genus *Paragorgia*, likely provides anchorage and hiding places for a number of organisms, ranging from brittle stars to fish.

## Family Coralliidae Lamouroux, 1812

**Diagnosis.** Axis an unjointed medullar region composed of completely fused calcareous sclerodermites (solid calcium carbonate) derived from sclerites; Grillo et al. (1993)



**Figure 7.** *Sibogagorgia californica* sp. nov., SBMNH 422978, SEM image. Color of sclerites from this colony very pale pinkish orange or white. **A** Sclerites from colony medulla **B** intermediate form between surface and internal medulla **C** 7-radiates from the surface. Compare this plate with that of Figure 5; these two appear extremely similar, indicating that SBMNH 422978 is likely a color variant (or very bleached) colony of that species represented by SBMNH 422974.

indicated calcium carbonate axis of family is not derived from the fusion of sclerites, but rather that there are two different origins for the sclerites and the axial skeleton (concentric addition of  $CaCO_3$ ). Sclerites present as numerous regular capstans, or as rods, plates, and irregular forms without capstans.

### Genus Hemicorallium Gray, 1867

Madrepora (pars) Linnaeus, 1758: 797.

*Corallium* [ächte rothe Steincoralle] Müller in Knorr, 1766: Delic. Nat. 1: 7, pl A I, figs 1, 2; 23, pl A VII, fig 1; 24, pl A VIII, figs 2–4; 127 (pars); nec. pp 9–13, 25, 128. *Isis* (pars) Linnaeus, 1767: 1288.

Nec Isis Linnaeus, 1758: 799.

Nec Corallium Burman, 1769: [3] (= Isis Linnaeus, 1758).

Corallium Cuvier, 1798[1797]: 673. Lamarck 1801: 378. Dana 1846: 640–641. Gray 1860: 393; 1867: 126. Ridley 1882a: 221–222, 225. Kishinouye 1903: 626; 1904; 28; 1905: 27. Hickson 1905a: 268; 1907b: 13c1, 2. Kükenthal 1919: 743, 828, 902. Aurivillius 1931: 22. Bayer 1950: 61; 1956b: 70, 73; 1964b: 466–467; ? 1993: 17; 1996b: 206, 213. Bayer and Cairns 2003: 222, 224. Tu et al. 2016: 1006.

Pleurocorallium Gray, 1867: 126. Ridley 1882a: 221–222. Johnson 1898: 421; 1899: 59.
Kükenthal 1924: 47, 52. Bayer 1956b: 74; 1964b: 467. Bayer and Cairns 2003: 222.
Figueroa and Baco 2014b: 83. Tu et al. 2015a: 302; 2015b: 173; 2016: 1022–1023.

Hemicorallium Gray, 1867: 126. Ridley 1882a: 221–222. Johnson 1899: 59. Kü-kenthal 1924: 47, 52. Bayer 1956b: 74; 1964b: 467. Bayer and Cairns 2003: 222. Ardila et al. 2012: 254. Figueroa and Baco 2014b: 83. Tu et al. 2015a: 302; 2015b: 173; 2016; 1010–1011.

**Type species.** *Madrepora rubra* Linnaeus, 1758 (by subsequent monotypy, the first species being assigned by Lamarck 1801).

**Diagnosis.** Sclerites of cortex numerous, regular capstans, often modified with six, seven or eight radii; or as double clubs (only some species), crosses and opera glasses; long spindles present in tentacles. Without axial pits bearing beaded rims beneath autozooids. Autozooids prominent, non-retractile (when contracted cannot fully retract into cortex) and ovate-cylindrical, usually distributed on one side of colony.

**Etymology.** Bayer (1956b) stated that the name *Corallium* "is an old name of dubious origin, going back to the ancient Greeks, classically applied to the red coral of commerce, the 'true red stony coral'."

**Remarks**. An interesting genus; its connection to human enterprise and profit make it so. Collectively, "pink coral, red coral, noble coral, angel skin coral, Sardinia coral, midway coral" (CITES proposal, Convention of the Parties, CoP14 Prop. 21, June 2007) has had a long history, with the primary focus on harvesting of the coral for profit. At least one proposal, and multiple CITES conferences over the years (2007, 2010, 2013), have made this genus a focus of discussion. Numerous articles have been published concerning the impact of harvesting, management issues, etc. (Tsounis et al. 2010, 2013, to name but a couple).

Because all species of coral in this genus tend to form tall, tree-like colonies, they likely increase three-dimensional complexity of the habitats they are found in and consequently, increase biodiversity where they occur. These colonies could easily provide valuable microhabitat for sessile, associated commensal invertebrates (Baco and Shirley 2005, Baco 2007), protecting them from strong currents and predators. With regards to species occurring in the Pacific Ocean, "one of the more notable commensal relationships is the association of polynoid polychaetes with species in (this genus). Each *Corallium* species appears to have its own species of polynoid polychaete, which can reach high densities within individual colonies" (Baco 2007). They would also provide structural relief that fishes and mobile invertebrates could use as feeding, spawning and resting grounds (CITES proposal, Convention of the Parties, June 2007). Thus, they contribute far more to their natural living situation than perhaps had been considered when commercial harvesting for species in this genus was first instituted.

A number of species in the genus *Corallium* have recently been transferred to the genus *Hemicorallium* (encompassing species discussed here; Cordeiro et al. 2019); this is based on the work of Tu et al. (2015a, b, 2016). Species in the genus *Hemicorallium* are represented in the SBMNH collection by a single specimen, SBMNH 471940 (likely *Hemicorallium ducale*; see Appendix 1: List of material examined), but three species have been recorded (collected west of the California Channel Islands), in proximity to the western boundary edge of the Bight (location data for specimens housed at NMNH). The California Academy of Sciences has seven separate lots of specimens in this genus. Generally, all are from the Hawaiian Islands, with the exception of one. That one, identified only to genus, is from California, Davidson Seamount, 128 km SW of Monterey, taken at a depth of 1481 m, 21 May 2002. Further documentation of the presence of *Hemicorallium* in or near the California Bight is needed; in consideration of their rarity and commercial value, their presence would need to be very carefully monitored.

# Hemicorallium ducale (Bayer, 1955)

Corallium ducale Bayer, 1955: 210-211, plate 1. Bayer and Cairns 2003: 224.

**Material examined.** One lot, 2 specimens + fragments (recent addition) in SBMNH collection, most likely this species (see Appendix 1: List of material examined).

**Remarks.** Distribution extends in Eastern Pacific from Mexico (Bayer, 1955), northern Baja Mexico (USNM 50111 (type locality) to at least California Channel Islands (USNM 94459). SEM images on file (Bayer's personal collection): SEM #2284, for USNM 94459 and SEM #s 2483 and 2484 for USNM 50111. Specimen USNM 50111 represented one of the first finds of the genus *Hemicorallium* in North American waters.

The specimen in question does not easily identify to a species; in color it appeared more like that of *Hemicorallium imperiale*, but the polyps' appearance and scleritic spindles were more like those seen in *H. ducale*. While all type material for this species

(and the other two that follow) at NMNH were examined some years ago, this one specimen, recently received into the SBMNH collection, requires further study.

WoRMS Data Base (Cordeiro et al. 2019) verifies that *H. ducale*, with the other two listed below, are accepted species. They are included, with brief comments, due to their collection locations and proximity to the region of the California Bight. It should be noted that there are no specimens that came into the SBMNH collection from the 'Velero' expeditions.

## Hemicorallium imperiale (Bayer, 1955)

Corallium imperiale Bayer, 1955: 209–210, plate 2, c-h. Bayer and Cairns 2003: 224.

**Material examined.** No material in SBMNH collection (see Appendix 1: List of material examined).

**Remarks.** Distribution in the Eastern Pacific, northern Baja, California (Bayer 1955), as seen for the **holotype** (USNM 50110) to California Channel Islands, in proximity of western boundary edge of Bight (USNM 85082). No SEM images for this species were found in Bayer's personal collection at NMNH. Could be called "Imperial red coral."

## Hemicorallium regale (Bayer, 1956)

Corallium regale Bayer, 1956b: 70, 73-76; 77-78; figs 5c; 7e-g. Bayer and Cairns 2003: 224.

Synonyms. (see Remarks section below.)

**Material examined.** No material in SBMNH collection (see Appendix 1: List of material examined).

**Remarks.** Around the Pacific, from Hawaii (holotype, USNM 49520) to offshore seamounts some miles west of California coast (outer edge of Bight western boundary, USNM 94460), certainly at substantial depth (based on specimens housed in NMNH collection). Not enough specimens examined (or collected with attention to specific collection locations) to determine extent of north-south range. Bayer commented (1956b), "of all the Hawaiian precious corals, *C. regale* has the best color and might be of commercial value if it could be fished in quantity." Thin, calcareous extensions of axis extending outward to thick coenenchyme can support expansion of coenenchyme near sides of branches as recurved flaps, a distinctive feature. These can form tunnels inhabited by polychaete commensals (Baco and Shirley 2005, Baco 2007). Could be given the common name "Regal red coral."

Several species in the now updated genus *Hemicorallium*, including this one, found within the Hawaiian archipelago (and elsewhere in the western Pacific, in-
cluding international waters) have been the focus of commercial exploitation (then recognized as species in the genus Corallium). Based on reports made public by CITES, regarding "consideration of proposals for amendment of Appendices I and II" (2007, 2010) and Bruckner (2009), there was much discussion, and confusion, as to whether this species (using older genus designation) was valid and/or whether it could be synonymous with *Corallium laauense* (misspelled as *C. lauuense*). Grigg and Bayer (1976: 169) and Grigg (2002: 17-19) specifically mentioned C. regale and/or C. laauense as separate species. CoP14 Prop. 21 (CITES, 2007) listed this species as a potential synonym for *C. laauense*; this based on Baco and Shank (2005: 664). However, Baco and Shank (2005) did not treat this species as a synonym of C. lauuense (note the misspelling), but a comment they made regarding the work of Grigg (2002) may have inadvertently lead some to assume that was the case. Cairns (CITES, 2007) did not consider these two taxa to be synonymous and Bruckner (2009: 321) also discussed these taxa as two separate species. Bruckner indicated that although he discussed them as two separate species, "these 2 species may be synonymous." In the document, Proposal, CoP15 Prop. 21 (CITES 2010), C. regale was still shown as a synonym of C. lauuense (sic); note the following statement: "C. lauuense and C. regale are listed as separate species in the US Precious Coral Fishery Management plan, but these species are usually considered synonymous (Parrish 2007)". Again, C. laauense and C. regale were treated as synonymous; however, regarding C. regale, Baco and Shank (2005) stated: "C. lauuense was previously misidentified and referred to as C. regale which is not an indication of synonymy. There may still be some unresolved taxonomic problems concerning these two species." Additionally, "Bayer and Cairns (2003) differs from the SS species list in a number of ways: C. boshuense, C. niveum, C. porcellanum, C. pusillum, C. vanderbilti, and C. variabile are not mentioned; C. regale is treated as valid." (CITES 2010); of these species, C. boshuense and C. variabile have been moved to the genus Hemicorallium (Cordeiro et al. 2019) in the WoRMS Database. The final implication was that Corallium sp. was found throughout "the Hawaiian archipelago and into the Emperor Seamount Chain" (Baco 2007), but that the certainty of species identification was still in question.

In studying Bayer's original 1956 description of *C. laauense* (correctly spelled) and *C. regale*, no determination could be made as to why these two were linked as synonymous. The now recognized species *Hemicorallium regale* has many double club sclerites, while *H. laauense* has none. As well, the entire colony of *H. regale*, as well as the axis, is pink, while the colony color of *H. laauense* is white or very faintly pink with a white axis. SEM images are on file (Bayer's personal collection), SEM #2283, USNM 94460.

The work by Tu et al. (2015a, b; 2016) resulted in most species of *Corallium* being placed in the genus *Hemicorallium*. WoRMS (Cordeiro et al. 2019) confirms the placement of the species discussed here: *H. ducale*, *H. imperiale*, *H. regale* (as well as *H. laauense*); all are listed as accepted, separate species.

## Holaxonia Studer, 1887

With distinct central axis composed of horny material alone or of horny material more or less heavily permeated with calcareous substance, continuous or with alternating horny and calcareous joints. In center of axis is a relatively narrow, largely hollow, tubular space partitioned into series of small chambers, referred to as the cross-chambered central chord. Calcareous material of the peripheral zone of axis is in nonscleritic form (single exception in Keroeididae).

### Key to Families represented in SBMNH collection (Holaxonia)

1	Axis horny, with a chambered, hollow, soft central chord2
_	Axis not horny, but is a solid axis, with no soft, central, hollow core
	Suborder Calcaxonia, Part III
2	Axis purely horny, composed of scleroprotein, without any calcareous depos-
	its
_	Axis horny, but some calcareous material may be present in some forms; hol-
	low, horny, soft-chambered central chord is wide; there is a peripheral zone
	of hollow horny spaces containing calcareous material; cortex is thick, with
	an inner and outer layer, formed by systematic longitudinal canals; polyps
	retractile into prominent calyces
3	Axis perforated by a wide, cross-chambered central chord; cortex thin; polyps
	not retractile; sclerites spikey and conspicuous
	Family Acanthogorgiidae, this part
_	Distinct hollow, horny, soft-chambered central chord that perforates axis is
	narrow; axial cortex surrounding the core is very dense; polyps fully retractile,
	into calyces

## List of species of Holaxonia Studer, 1887

Class Anthozoa Subclass Octocorallia Haeckel, 1866 Order Alcyonacea Lamouroux, 1816 **Suborder Holaxonia Studer, 1887** Family Acanthogorgiidae Gray, 1859 *Acanthogorgia gracillima* var. *typica* Kükenthal, 1909; (? *A. gracillima* var. *lata* Kükenthal, 1909) *Acanthogorgia* species A *Muricella* cf. *complanata* Wright & Studer, 1889

# Descriptions of species of Holaxonia Studer, 1887

## Family Acanthogorgiidae Gray, 1859

**Diagnosis.** Axis purely horny (scleroprotein without calcareous deposits), dark-colored, predominantly black; very difficult to cut, with wide, hollow, cross-chambered central core. Coenenchyme very thin, polyps conspicuous, contractile, not retractile, completely covered with both straight and curved fusiform sclerites (forming, in appearance only, cylindrical calyces; no calyces actually present). Sclerites arranged in eight double rows, forming eight en chevron fields; no well-defined operculum; sclerites instead arranged as transverse ring and eight points of converging spindles on tentacle bases; thus, sclerites of polyps continuous with those of tentacular crown, latter being sharp spines arrayed conspicuously around top of polyp, with no intervening sclerite-free neck zone or transverse collaret. Consequently, no clear division between anthocodia and anthostele. Tentacles fold inward over oral disk. Predominant sclerites colorless, in form of prickly or warty spindles; sometimes, presence of three- and fourarmed radiates.

## Genus Acanthogorgia Gray, 1857

Acanthogorgia Gray, 1857a: 128, pl 3, fig 2 [1851]. (pars) Johnson 1861: 297; 1862a: 195. (nec) Verrill 1866a: 152. Pourtales 1867: 113. (nec) Studer 1879: 652 (vide Kükenthal 1919: 911). Verrill 1883: 30. Studer (and Wright) 1887: 54. Wright and Studer 1889: 93 + pl. Hedlund 1890: 8. Studer 1901: 43. Thomson and Henderson 1906a: 50. Kükenthal and Gorzawsky 1908a: 626; 1908b: 52. Kükenthal 1909: 71. Nutting 1910: 12. Kükenthal 1919: 298, 762, 846; 1924: 239. Aurivillius 1931: 53. Stiasny 1943b: 129; 1947: 31. Bayer 1996a: 1–2. Grasshoff 1999: 20; 2000: 40. Fabricius and Alderslade 2001: 184.

Blepharogorgia (pars) Duchassaing & Michelotti, 1864: 15.

Paracanthogorgia Stiasny, 1943b: 130; 1947: 11, 53. Grasshoff 1973: 1; 1992: 89. (Type species: Paracanthogorgia paratruncata Stiasny, 1943b; species designation by Bayer 1996a: 2).

**Type species.** *Acanthogorgia hirsuta* Gray, by monotypy (? = *A. aspera* Pourtalès, 1867).

**Diagnosis.** Colonies generally flattened (flabellate); commonly reticulate, or developed into dense bushy shrubs. Branches appear thin and delicate. Polyps tall, cylindrical, topped with thorny crown of strongly projecting spinous sclerites, embedded at tentacle bases. They lie, collectively, over infolded tentacles, protruding end of sclerites smooth. Polyps on all sides of branches, or roughly biserial; arise vertically at right angle to branch surface, acalycinous, not retractile. Coenenchyme between branches usually thin, axis visible through it. Sclerites in polyps slender spindles slightly bent, arranged en chevron in eight longitudinal double rows. Back of tentacles with only

numerous small, flat, bent sclerites; stem coenenchyme with slender, generally bent or sinuous spindles sculptured by prickles or simple tubercles; in deeper layers of coenenchyme (some species), with radiates (tri-radiates and crosses, often with a projecting central spine). Axis dark, but coenenchyme usually colored; sclerites always colorless.

**Remarks.** Only one collected specimen from the genus appeared in the 'Velero' material; it does not match any of the described species it has been compared it to, thus far. It was collected in Mexican waters, beyond the geographic range covered in this work; description of this specimen is in progress.

### Acanthogorgia gracillima var. typica Kükenthal, 1909

Figures 8, 9A, B, 10, 11, 12A-D

*Acanthogorgia gracillima* var. *typica* Kükenthal, 1909: 73–76; pl 6, fig 33; (syn.) 1919: 763. Aurivillius 1931: 67–72.

? A. gracillima var. lata Kükenthal, 1909: 71, 73, 75.

Type locality. (?) Okinawa, Japan; 400 fathoms.

**Type specimens.** Zoological Museum of the University of Hamburg, Germany (formerly, Naturhistorisches Museum, Hamburg); Catalog Number 3298, with Catalog Number 3297. (Not labeled as type.)

Material examined. 1 lot (see Appendix 1: List of material examined).

Description. Colony (Figures 8, 9A) richly branched, not entirely in one plane, forming bushy fan or tree no more than 10 cm at widest point. Colony appeared fragile and delicate, but actually a tough, spiky bush/fan, branches reminiscent of those in a bottlebrush (Figure 9B); not greatly flexible. Colony height (dictated by main, central, generally straight stem), base to tip, 15–16 cm; 7.0 cm broad; holdfast remnant present. If any regularity to branching pattern, slightly dichotomous to pinnate, usually in one plane; all lateral branches, of differing lengths, project at nearly right angles, extending/ curving quickly upward, even those with more lateral placement. Branch diameter averages 2.0–3.0 mm. Polyps distributed over entire surface (not so much on lower portion of main stem, just above base), nearly in rings around branches, closely placed but not crowded (Figure 10); sometimes two with bases contiguous, generally separated by 1.0 mm, perhaps more; terminal twigs rounded, almost clavate in appearance; numerous polyps at apex, completely covered with straight and curved spindle-shaped sclerites. Polyps not retractile; very conspicuous, decidedly slender, columnar in shape, height between ~4.0–7.0 mm (most average 5.0–6.0 mm tall); diameter generally 1.0 mm for most of polyp length, narrowing slightly, then increasing to ~1.5 mm wide at the crown. Easily recognized by crown of sharp spines encircling top of polyp. Coenenchyme very thin and translucent, with axis color showing through. Color of freshly collected specimen bright lemon yellow (M Love, pers. comm.; Figure 8); on being placed in alcohol quickly turned, generally, light olive-green towards base, becoming slightly darker grey-green at uppermost branch tips. (While species in family are described as having a



**Figure 8.** *Acanthogorgia gracillima* var. *typica*. In situ, living colonies, illustrating vibrant yellow color, as seen in Santa Barbara Channel, photograph by D Schroeder; image courtesy of M Love, UCSB.

predominantly black, purely horny axis, color of axis showing through extremely thin coenenchyme appeared to account for overall olive-green color. Having now sat in 70% ETOH for some time, the colony has turned more yellowish brown.) Sclerites (Figures 11, 12A, B) mainly spindle-shaped; straight or curved, showing arrangement of eight double rows, forming longitudinally-placed chevrons (obliquely angled double-rows) characteristic of genus. A very few oddly branched; some, more a tripod shape. Sclerites appear mostly tuberculate, with distinct boomerang bend (Figure 12A), easily removed from surface of colony. The longest sclerites, with distinct bend roughly a third of the way along their length, range from 1.0-2.0 mm in length (average 1.6 mm L × 0.17 mm W); one third of surface of sclerite bears tubercles, while other two-thirds is generally smooth; this smooth section, thin, rounded, somewhat beveled, is the distal, prominent spike that projects from the thorny basal portion embedded in the mesoglea of the body wall, in nearly longitudinal direction; lower, embedded portion, ~0.5 mm long, appears to cross over into the neighboring angled rows, these basal portions not much different one from another. These sclerites form the crown of thorns seen around top of polyp. Two very long spines project upwards to form the points of the crown at distal end of each of the eight double-rows. Smooth portion of these sclerites sit with approximately 1.0 mm of their length free of polyp. Numerous, slightly smaller, flatter sclerites have bend more centrally located, their entire surface covered with tubercles



**Figure 9.** Acanthogorgia gracillima var. typica, SBMNH 423074. **A** Whole colony preserved in 70% ETOH. Maximum height of colony 15–16 cm,  $\leq$  10 cm at widest point **B** magnified view of several branches; pronounced, rather spikey appearance of polyps is evident.

(average 1.0 mm L × ~0.08 mm W). These primarily cover outside surface of polyp (Figure 11), illustrating chevron pattern (eight longitudinal double rows) in placement. Sclerites of coenenchyme similar to those seen on polyps' surface (~0.8 mm long), perhaps slightly thicker in width and slightly more fully covered with tubercles; tentacular sclerites smaller still, bent, flattened (up to ~0.18 mm long), completely covered with tubercles; more prominent, dense, on dorsal side of tentacles. If present, a few smaller (0.1 mm long) radiate or cross-shaped sclerites may be seen. In the coenenchyme covering the base, exclusively, are 0.25 mm long, bent, strongly spined spindles. All sclerites completely colorless, reminiscent of thin, bent shards of glass.

**Etymology.** For designation *gracillima*, the Latin *gracili*- means slender; this may reference the conspicuous, very slender polyps and very slender points in the crown of this species. Kükenthal (1909) gave no explanation for the derivation of the species name.

**Common name.** None specifically designated; the Slender glass-shard gorgonian would be appropriate. Worth considering is whether or not this is the species that, predominantly, MBARI and NOAA researchers are seeing and calling the "Gold gorgonian."

**Distribution.** For genus in general, "species. . . inhabit moderate to considerable depths; various species of *Acanthogorgia* occur in all seas, some thriving in very cold waters" (Bayer, penciled personal annotations in Kükenthal 1924). Examinations of the



**Figure 10.** *Acanthogorgia gracillima* var. *typica*, greater magnification of SBMNH 423074. Shows position of polyps on branches. Note prominent crown of sclerites at distal end of each polyp, polyp height averages 5.0–6.0 mm.



**Figure 11.** Acanthogorgia gracillima var. typica (light microscopy image), SBMNH 423074. 4X magnification, demonstrating position of long, boomerang-shaped sclerites, arranged longitudinally on surface of polyp, mid-section to distal end.

literature revealed numerous species in the Indo-Pacific region. Recent MBARI on-line postings indicated this genus is found in northern California waters, often at great depth. Milton Love (description based on specimen he collected) indicated (pers. comm.) that the color of this gorgonian is very vibrant, thus easily seen; it is quite abundant in certain areas, such as the Footprint, a feature outside the Anacapa/Santa Cruz Island Passage. Thus, for this species, range seems to extend around the Pacific Ocean from Japan (Kü-kenthal's specimen) to eastern Pacific waters of California; further study will be required to determine whether, and how far, it extends north and south of California.

**Biology.** On this particular specimen, there were at least two scale worms wrapped around the base of polyps in two separate areas within the colony.

**Remarks.** To handle the specimen during examination, although colony fairly hardy, gloves were necessary. Generally, all the long sclerites were very sharp, comparable to small shards of thin glass; those that got into the skin under the fingernail were rather painful. Given the delicate, and somewhat brittle/fragile nature of the longer boomerang-type sclerites, these sclerites are easily broken. It was often difficult to ascertain whether radiates and crosses really existed as such, or whether they were bits that had broken off from the longer spindle forms; this could account for some of the odder-shaped sclerites that previous description (Kükenthal 1909) made mention of. Microscopic examinations were always done without a cover glass, when possible, so that sclerites were not crushed.

This description (and original description for the species) was based on the specimen used by Kükenthal (1909). In initial comparisons of known, and described species, using characteristics of the colony (lying more or less in one plane, with polyps generally more than 4.0 mm in length), the key that Kükenthal (1924) provided in his overview of the genus was relied upon, but it took some time to rule possibilities out. Bayer (1996b) stated that all the sclerites are so similar in form within all members of the genus, that distinguishing species is difficult; this was confirmed. As well, there are very few recent descriptions of any Acanthogorgia species that are truly adequate to use for comparative purposes. Few specimens had been collected from California waters; thus, not a lot of material to compare against. In examinations of collections at other institutions, only two/three specimens were found at NMNH that approximated the appearance of this colony (USNM 1071429, dry and USNM 1072361, wet, in two lots). The dry specimen is from Cross Seamount, Hawaii, USA and the wet lots are from a seamount east of Necker Island, Hawaii, USA. Both are identified to genus, but not to species; in color, branch pattern, pattern of sclerite positioning on polyps and sclerite morphology, specimen USNM1071429 appeared most similar. If NMNH specimens can be accurately identified to species, they could confirm (or negate) the notion of trans-Pacific distribution. In any event, this discussion/description represents one of the first published reports for this particular species in southern to central California waters; overall the genus needs further work, not only on those specimens being frequently noted in underwater explorations (cruises and surveys being done by MBARI and NOAA), but also on those that have already been collected, perhaps described or need description, currently housed in other museum collections. With greater access to locations of depth, and the use of ROV, AUV, digital imaging and improved ability to collect specimens at depth, many currently described species can be confirmed and many new species are likely to come to light. As well, with careful attention to locations where specimens are found, it should be possible to develop a far more accurate picture of the distribution of these deep-water forms.

While the original specimen does indeed still exist, no opportunity to travel to Hamburg, Germany occurred and no request that the specimen be sent was made. The species is an accepted species in the WoRMS Data Base (Cordeiro et al. 2018e).

[*Acanthogorgia* (= ? *Acalycigorgia*) Grey, 1857)]; not accepted, WoRMS (Cordeiro et al. 2018e).



**Figure 12.** *Acanthogorgia gracillima* var. *typica*, SBMNH 423074, SEM image. These sclerites are colorless. **A** Sclerites from crown **B** sclerites from polyp surface **C** small sclerites from coenenchyme **D** odd coronal or polyp surface sclerite.

# Genus *Acalycigorgia* (= ? *Acanthogorgia*) Kükenthal, 1908; not accepted, WoRMS (Cordeiro et al. 2018e)

*Acalycigorgia* Kükenthal, 1908b: 38; 1919: 298; 1924: 237–239. Kükenthal and Gorzawsky 1908a: 629; 1908b: 38. Kükenthal 1919: 764, 846. Aurivillius 1931: 40. Bayer 1956a: F203; 1981c: 920.

? = *Acanthogorgia* Gray, 1857a: 128, pl 3, fig 2 [1851]. (pars) Hedlund 1890: 3, 6. (pars) Thomson and Russell 1910: 145. Fabricius and Alderslade 2001: 184.

? Paramuricea Moroff, 1902: 407.

**Type species.** *A. grandiflora* Kükenthal & Gorzawsky, 1908a; subsequent designation by Kükenthal and Gorzawsky (1908b).

**Diagnosis.** Polyps not functionally differentiated into anthocodia and anthostele; contractile but not retractile within common coenenchyme; tentacles fold over oral disk in contraction. Polyps similar to those of *Acanthogorgia* (without crown of strongly projecting spines, however), but polyps can be short and verruciform to prominent, tall and cylindrical, not clavate. Sclerites of polyp walls large spindles, very conspicuous; commonly arranged more or less distinctly en chevron in eight long, longitudinal double rows, but distal ones project little or not at all. Distal ends of sclerites around tentacle bases not specifically differentiated as spines, though the tips may project somewhat around polyps' apex. Polyps are without suture separating tentacular/anthocodial from subtentacular sclerites. Sclerites of polyp body gradually merge with those of tentacle bases, which are not abruptly smaller; coenenchymal sclerites with tubercles of inner and outer sides similarly developed; inner layer of coenenchyme with more or less abundant radiates.

Acanthogorgia species A

Figures 13, 14A, B, 15A–C

Type locality. Cannot be indicated at this time.

Type specimens. Cannot be indicated at this time.

Material examined. 1 lot (see Appendix 1: List of material examined).

**Description.** Colonies (two) generally in one plane; one measures 7.0 cm × 5.5 cm (length to width); second (Figure 13) measures 9.0 cm × 4.5 cm, at widest, halfway up colony. Thin, delicate-looking branches (round to slightly square in shape); branching more or less dichotomous; closely monopodial. No flattening at branch origins. Base 2.0 mm wide, main branch 1.0 mm wide; branchlets vary between 0.5-0.75 mm wide and tips of branchlets very thin, thread-like; all branches quite stiff. Coenenchyme very thin (very little still present in these specimens); axis predominantly exposed, yellow-gold to rusty-brown. Of the few polyps present on a few branches, most located near branch tips (Figure 14A); coenenchyme and polyps creamy-white. Polyps primarily sit lateral to branch, at distance of ~1.0 mm or less from each other; closer to branch tip sitting literally side by side; some few branches indicate that polyps can be found on all sides. There are marked, longitudinal grooves/ridges at distal ends of polyps; there is barely apparent a very short little spiny crown at their very tip (Figure 14B). The ridges, eight in number, are each formed by a parallel collection of two or three bent spindle-type sclerites. Polyp surface densely covered with sclerites; no calyx apparent. Polyp height 3.0 mm, 2.0 mm from base to area of longitudinal grooves with another 1.0 mm of height when area of grooves/ridges included. All approximately 1.0 mm wide, distal end



Figure 13. Acanthogorgia species A, SBMNH 423075. Of tissue present, polyps readily visible, colony measuring ~ 9.0 cm in height.

slightly wider, somewhat obvious, ~1.5 mm wide. No expanded tentacles readily visible (contracted over mouth); all heavily covered or encased by sclerites. Sclerites (Figures 15, A particularly) predominantly bent spindles; all tuberculated across entire surface, averaging 0.5 mm long by 0.08 mm wide. The largest (~0.7 mm × ~0.1 mm), decidedly bent spindles; these form the eight ridges mentioned above; others appear to lie in longitudinal direction up to and beyond upper edge of polyp, barely showing as short points of a crown. Bent spindles, somewhat smaller, almost tend to the formation of the en chevron, double-row pattern at the proximal end of ridges and down on to lower end of polyp. Also, less bent ones, seemingly very narrow spindles (0.6 mm × 0.05 mm); few appear slightly club-shaped (average 0.4 mm × 0.06 mm), primarily from lower polyp wall and coenenchyme. Sclerites with boomerang shape scarce or not present. From initial light microscopy examination, apparent that many of these spindles can be broken; many odd-shaped bits seen in arrays, with some of the spindles having oddly truncated ends, where some aspect of the sclerites likely had broken off. All forms quite densely arrayed on specimen's surface, giving polyp and branch coenenchyme a distinct white to glassy appearance; all sclerites colorless. Inner coenenchyme radiates not found.



**Figure 14.** *Acanthogorgia* species A, SBMNH 423075. **A** Closer view of polyps present at tips of several branches; polyp height 3.0 mm tall, 1.0 mm broad **B** further magnification of polyps. Barely visible at distal end of several polyps, the weakly developed crown of sclerites can be seen.

**Remarks.** It is possible that these specimens, and several others in the collections either at CAS or NMNH, Smithsonian (not yet identified to species), could be first records of appearance for this species in, or near boundaries of, the California Bight.



Figure 15. *Acanthogorgia* species A, SBMNH 423075, SEM image. Sclerites from these colonies are white, rather than clear. A Coronal sclerites **B**, **C** smaller coenenchymal sclerites.

Description here is based on two specimens, which in overall colony appearance superficially look very similar to Nutting's photographs (1912: pl 11, fig 1, 1a), shown for *Muriceides cylindrica*, which Nutting established as a new species. However, the sclerites illustrated in Nutting (1912: pl 20, fig 3), while of comparable size to that indicated for the species described here, do not match. In considering overall appearance of polyps on the branches, and the manner in which sclerites covered the surface of the polyps from distal to proximal ends, a generic best fit occurred working from an illustration that was given in Bayer (1956a) for *Acalycigorgia*. However, Fabricius and Alderslade (2001) have stated that "(m)any species of *Acanthogorgia*, in which the polyp sclerites are so short that there is little or no projecting crown, erroneously appear in the literature under the name *Acalycigorgia* Kükenthal, 1919. *Acalycigorgia* is actually a synonym of *Acanthogorgia* and most species referred to the former should be called *Acanthogorgia*." This is supported in the WoRMS Data Base (Cordeiro et al. 2018e) for taxon information regarding status of the genus *Acalycigorgia*. It now remains to be seen if the species described here is indeed one of the 61 species listed as accepted by the Data Base.

# Genus Muricella Verrill, 1869

Lissogorgia (pars) Verrill, 1865: 187.

- Muricea (pars) Verrill, 1868c: 411-416.
- Muricella Verrill, 1869a: 450 (= ? Anthogorgia Fabricius & Alderslade, 2001). Studer 1879: 650. Ridley 1882b: 128; [= ? Muricea Ridley 1884: 335, 579]. Studer 1887: 58. Wright and Studer 1889: 123 + plate. Germanos 1896: 181. Brundin 1896: 17. Whitelegge 1897: 315. Hiles 1899: 49. Hargitt and Rogers 1900–1902: 282. Hickson 1905b: 815. Thomson and Henderson 1905a: 301; 1905b: 178; 1906a: 78. Nutting 1908: 586; 1909: 717. Thomson and Simpson 1909: 241. [= ? Versluysia Nutting 1910: 29, 35]. Thomson and Russell 1910: 158. Nutting 1912: 78. Kükenthal 1913b: 28. Schimbke 1915: 26. Kükenthal 1919: 75, 838, 909. Molander 1921: 11. Aurivillius 1931: 123. Bayer 1956a: F206. Grasshoff 1999: 33. Fabricius and Alderslade 2001: 188.
- ? Anthogorgia Verrill, 1868 (=?Acalycigorgia Kükenthal, 1908b). Grasshoff 1999: 33. Fabricius and Alderslade 2001: 186.
- ? *Acalycigorgia* Kükenthal, 1908b (= ? *Acanthogorgia* or *Astrogorgia* [see Fabricius and Alderslade 2001] as proposed by Cairns and Bayer, unpublished synonymy).

? Astrogorgia Verrill, 1868c: 413. Fabricius and Alderslade 2001: 210.

? Acanthogorgia Gray, 1857a: 128 [1851]. Fabricius and Alderslade 2001: 184.

Type species. *Lissogorgia flexuosa* Verrill, 1865; [subsequent diagnosis by Nutting 1910].

**Diagnosis.** Colonies fan-shaped, branching in one plane, some anastomosing. Larger branches with axis often tending to be flattened at right angles to plane of fan; in older colonies, smaller branches can bend and grow perpendicular from the fan. Polyps prominent, low, wart-like, non-retractile; coenenchyme thick between polyps. Sclerites of polyp tentacles small rods; below anthocodiae, sclerites large and bow-shaped, in angled double rows (chevrons), forming eight marginal points, forming strong collaret; tentacular operculum distinct. Sclerites of coenenchyme in two distinct layers, mostly spindles (coarse or densely warted), small capstans, with some clubs or discoidal forms.

**Remarks.** Kükenthal (1924) articulated the characteristics of this genus, which include: condition of the branch ends, position, orientation, height, and form of polyps, presence of an operculum, and arrangement of sclerites in the coenencyme. Fabricius and Alderslade (2001) discussed aspects of comparison/contrast between this genus and others; it was stated, "not much separates this genus from *Anthogorgia*, and a study of a large suite of specimens could see the two synonymized." Additionally, a characteristic feature pertinent to the genus diagnosis came from the Octocoral Taxonomy Laboratory Manual (2007): There are no calyces in the genus *Muricella*; "almost 90% of the species attributed to this genus do not belong there. A major revision is needed." In reviewing older literature there were references to calyces in this genus; Bayer (1956a) comments on the "truncated cones" or "rounded, low verrucae." In descriptions given by Verrill (1869a), reference is made to calyces, as well. The concept of how to define a calyx may need revisiting, notably with regards to this genus.

## Muricella complanata Wright & Studer, 1889

Muricella complanata Wright & Studer, 1889: 125–126. Thomson and Henderson 1905a: 303. Nutting 1909: 717–718. Thomson and Simpson 1909: 250. Nutting 1910: 31. Thomson and Russell 1910: 158. Kükenthal 1924: 172.

**Material examined.** No material identified as this species in collection at SBMNH (see Appendix 1: List of material examined).

**Remarks.** Included here briefly, as there was a California collection location for a specimen that was identified as this species.

Based on Kükenthal (1924), the species ranges from coastal to abyssal depths; likely can be found in a wide and diverse number of locations around the world. The type was collected off Japan, but present location of the type specimen could not be determined. The specimen upon which Nutting's 1909 description was based, taken by the Fisheries Steamer 'Albatross', Station 4461, Point Loma Lighthouse, S 3, E 9.3 miles, 285 fathoms, was said to have differed slightly from the type, particularly in having a well-marked collaret and in the arrangement of the calycular sclerites. Kükenthal (1924) indicated that the California location (at an approximate depth of 250 m) is questionable. There is no certainty that any specimens found in the California Bight will be specimens of Muricella complanata, or whether the species actually exists. Harden (unpublished dissertation, 1979) suggested that Muricella complanata was synonymous with Swiftia torreyi. Both were stated to display anastomosing (S. torreyi is always anastomosed; was unable to determine if that is always case with Muricella complanata, as thus far no confirmed specimen of this species has been located). As well, I would disagree with a comment found in an unpublished Bayer annotation: "Muricella complanata = a Swiftia?" in that S. torreyi is a plexaurid, while Muricella is a recognized genus within the family Acanthogorgiidae (Bayer 1981c, Fabricius and Alderslade 2001, Cordeiro et al. 2018f) with no mention of any species of Muricella being synonymized with any Swiftia species.

## Conclusions

It is clear from this first part of the systematic review of alcyonacean gorgonian species in the SBMNH collection that the Scleraxonia and the family Acanthogorgiidae (Holaxonia) are found within the California Bight but are not well-represented within the collection; as well, very few of the species examined for this first part came to the museum via the Allan Hancock Foundation 'Velero' Expeditions. This is not surprising; many of the species in question would be/are fairly deep water forms, and the technology for achieving the required depths was not available at the time of those expeditions. As well, much of the 'Velero' material came from locations located closer to shore, geographic areas that the 'Velero' expeditions primarily focused on and worked in; many species of scleraxonian, as well as those of the holaxonian Acanthogorgiidae, generally exist in deeper water further off of mainland California, particularly in canyons and basins associated with the California Channel Islands. Despite visiting several institutions where these groups were better represented, there was simply not enough material in the SBMNH collection to make good comparisons. As well, there were not enough specimens in the SBMNH collection to adequately display the variation within and across species within the discussed families. Based on survey work done by NOAA in the recent past as part of their Deep Sea Coral Research and Technology Program, West Coast Research Initiative (supported by the Magnuson-Stevens Fisheries Conservation and Management Act of 2006), with field research programs undertaken off California, Oregon and Washington in 2010–2012, and during the years 2016 and 2017, more and more material from the groups covered in this first part is being photographed, mapped and collected. From these two major west coast research events, it is clear that there are many more species in the groups discussed here, and thus a far greater degree of octocoral biodiversity appearing off the California coast, at greater depths, than is evidenced by the SBMNH collection. Additionally, the West Coast Deep-Sea Coral Initiative for fiscal years 2018–2021, which is just beginning to establish priority collecting sites in preparation for this segment of exploratory research, will reveal much more, as the goal is to explore even greater depths at strategic sites that have not yet been extensively studied. As more of this exploratory and survey work is undertaken within, or near, the region of the California Bight, primarily by NOAA and its collaborators, there will be a need for taxonomic work, and through that work (some of which will be conducted by myself, in collaboration with staff at several NOAA field offices), the museum may be able to increase its specimen holdings to better illustrate these taxonomic groups as they relate to gorgonian diversity in the California Bight.

## References

Almeida MTR, Moritz MIG, Capel KCC, Pérez CD, Schenka EP (2014) Chemical and biological aspects of octocorals from the Brazilian coast. Revista Brasileira de Farmacognosia 24(4): 446–467. https://doi.org/10.1016/j.bjp.2014.05.002

- Andrews AH, Cailliet GM, Kerr LA, Coale KH, Lundstrom C, DeVogelaere AP (2005) Investigations of age and growth for three deep-sea corals from the Davidson Seamount off central California. In: Freiwald A, Roberts, JM (Eds) Cold-water Corals and Ecosystems. Springer-Verlag, Berlin-Heidelberg, 1021–1038. https://doi.org/10.1007/3-540-27673-4\_51
- Arantes RCM, de Medeiros MS (2006) First Record of Anthothela grandiflora (Sars, 1856) (Cnidaria, Octocorallia, Anthothelidae) in Brazil. Arquivios do Museu Nacional, Rio de Janeiro 64(1): 11–17.
- Ardila NE, Giribet G, Sánchez JA (2012) A time-calibrated molecular phylogeny of the precious corals: reconciling discrepancies in the taxonomic classification and insights into their evolutionary history. BMC Evolutionary Biology 12: 246, 11 pp. https://doi. org/10.1186/1471-2148-12-246
- Aurivillius M (1931) The gorgonians from Dr. Sixten Bock's expedition to Japan and the Bonin Islands, 1914. Kungliga Svenska Vetenskapsakademiens Handlingar (ser. 3) 9(4): 1–337.
- Auster PJ (2005) Are deep-water corals important habitats for fishes? In: Freiwald A, Roberts JM (Eds) Cold-water Corals and Ecosystems. Springer-Verlag, Berlin-Heidelberg, 747– 760. https://doi.org/10.1007/3-540-27673-4\_33
- Baco AR (2007) Exploration for Deep-Sea Corals on North Pacific Seamounts and Islands. Oceanography 20(4): 108–117. https://doi.org/10.5670/oceanog.2007.11
- Baco AR, Shank TM (2005) Population genetic structure of the Hawaiian precious coral *Corallium lauuense* (Octocorallia: Coralliidae) using microsatellites. In: Freiwald A, Roberts JM (Eds) Cold-water Corals and Ecosystems. Springer-Verlag, Berlin-Heidelberg, 663–678. https://doi.org/10.1007/3-540-27673-4\_33
- Baco AR, Shirley TC (2005) Habitat association of macroinvertebrates with deep-sea corals in Hawaii. Proceedings of the Third International Symposium on Deep-Sea Corals Science and Management, November 28-December 2, 2005, University of Florida, IFAS, Miami-Florida, Abstract, 210.
- Bayer FM (1950) A new precious coral from North Borneo. Journal of the Washington Academy of Sciences 40(2): 59–61. [1 fig.] https://repository.si.edu/handle/10088/863
- Bayer FM (1955) Contributions to the Nomenclature, Systematics, and Morphology of the Octocorallia, #3357. Proceedings of the United States National Museum 105(3357): 207– 220. [8 pls.] https://doi.org/10.5479/si.00963801.105-3357.207
- Bayer FM (1956a) Octocorallia, Part F. Coelenterata. In: Moore RC (Ed.) Treatise on Invertebrate Paleontology. Geological Society of America and University of Kansas Press, Lawrence-Kansas, F166–F231.
- Bayer FM (1956b) Descriptions and Redescriptions of the Hawaiian Octocorals Collected by the U.S. Fish Commission Steamer 'Albatross' (2. Gorgonacea: Scleraxonia). Pacific Science 10: 67–95. https://repository.si.edu/handle/10088/879
- Bayer FM (1958) Les Octocoralliaires plexaurides des cótes occidentals d'Amérique. Mémoires du Muséum national d'Histoire naturelle (nouvelle série; série A, Zoologie) 16(2): 41–56. https://repository.si.edu/handle/10088/891
- Bayer FM (1961) The shallow-water Octocorallia of the West Indian Region: (A manual for marine biologists). In: Hummelinck W (Ed.) Studies on the Fauna of Curacao and other Caribbean Islands 12(55): 1–373. [Martinus Nijhoff, The Hague]

- Bayer FM (1964a) A new species of the octocorallian genus *Paragorgia* trawled in Florida waters by R/V 'Gerda.' Zoologische Mededelingen 39: 526–532. [figs 1–3] https://repository. naturalis.nl/document/150534
- Bayer FM (1964b) The genus *Corallium* (Gorgonacea: Scleraxonia) in the western North Atlantic Ocean. Bulletin of Marine Science of the Gulf and Caribbean 14(3): 465–478. [figs 1–7] https://repository.si.edu/handle/10088/884
- Bayer FM (1981a) Status of Knowledge of Octocorals of World Seas. Seminários de Biologia Marinha, São Paulo, 9–15 Fevereiro de 1980. Academia Brasileira de Cieñcia, Rio de Janeiro, 102 pp. https://repository.si.edu/handle/10088/1237
- Bayer FM (1981b) On some genera of stoloniferous Octocorals (Coelenterata: Anthozoa), with descriptions of new taxa. Proceedings of the Biological Society of Washington 94(3): 878–901. https://repository.si.edu/handle/10088/971
- Bayer FM (1981c) Key to the genera of Octocorallia exclusive of Pennatulacea (Coelenterata: Anthozoa) with diagnoses of new taxa. Proceedings of the Biological Society of Washington 94(3): 902–947. https://repository.si.edu/handle/10088/978
- Bayer FM (1993) Two New Species of the Gorgonacean Genus *Paragorgia* (Coelenterata: Octocorallia). Precious Corals & Octocoral Research 2: 1–10. https://repository.si.edu/handle. net/10088/2391
- Bayer FM (1996a) A New Species of the Gorgonacean Genus Acanthogorgia (Anthozoa: Octocorallia) from Aldabra Atoll. Precious Corals & Octocoral Research 4(5): 1–16. https:// repository.si.edu/handle/10088/1000
- Bayer FM (1996b) Three new species of precious coral (Anthozoa: Gorgonacea, genus Corallium) from Pacific waters. Proceedings of the Biological Society of Washington 109(2): 205–228. [figs 1–19] https://repository.si.edu/handle/10088/998
- Bayer FM (unpublished manuscript 2) A review of the octocorallian genus *Paragorgia* [32 pp and numerous unfinished plates, several new species]. In Literature Cited: Cairns S (2009) Influence of Frederick (Ted) M. Bayer on deep-water octocoral research. Marine Ecology progressive Series 397(Suppl. 1): 7–10. https://doi.org/10.3354/meps08066
- Bayer FM, Cairns SD (2003) A new genus of the scleraxonian family Coralliidae (Octocorallia: Gorgonacea). Proceedings of the Biological Society of Washington 116(1): 222–228. https://repository.si.edu/handle/10088/1240
- Bayer FM, Grasshoff M, Verseveldt J (1983) Illustrated Trilingual Glossary of Morphological and Anatomical Terms Applied to Octocorallia. EJ Brill/Dr W Backhuys, Leiden-the Netherlands, 75 pp. https://repository.si.edu/handle//10088/6237
- Berntson EA, Bayer FM, McArthur AG, France SC (2001) Phylogenetic relationships within the Octocorallia (Cnidaria: Anthozoa) based on nuclear 18S rRNA sequences. Marine Biology 138: 235–246. https://doi.org/10.1007/s002270000457
- Bramanti L, Movilla J, Guron M, Calvo E, Gori A, Dominguez-Carrio C, Giny OJ, Lopez-Sanz A, Martinez-Quintana A, Pelejero C, Ziveri P, Rossi S (2013) Detrimental effects of ocean acidification on the economically important Mediterranean red coral (*Corallium rubrum*). Global Change Biology (2013): 1–12. https://doi.org/10.1111/gcb.12171
- Brancato MS, Bowlby CE, Hyland J, Intelmann SS, Brenkman K (2007) Observations of Deep Coral and Sponge Assemblages in Olympic Coast National Marine Sanctuary, Washing-

ton. Cruise Report: NOAA Ship *McArthur II* Cruise AR06-06/07. Marine Sanctuaries Conservation Series NMSP-07-04. Joint publication of U.S. Department of Commerce, National Oceanographic and Atmospheric Administration, and National Marine Sanctuary Program, Silver Spring, Maryland, 48 pp. https://aquaticcommons.org/2278/1/bowlby3.pdf

- Breedy O, Guzmán HM (2002) A revision of the genus *Pacifigorgia* (Coelenterata: Octocorallia: Gorgoniidae). Proceedings of the Biological Society of Washington 115(4): 782–839. https://biodiversitylibrary.org/page/35519153
- Breedy O, Guzmán HM (2007) A revision of the genus *Leptogorgia* Milne Edwards and Haime, 1857 (Coelenterata: Octocorallia: Gorgoniidae) in the eastern Pacific. Zootaxa 1419: 1–90. https://doi.org/10.11646/zootaxa.1419.1.1
- Breedy O, Guzmán HM (2011) A revision of the genus *Heterogorgia* Verrill, 1868 (Anthozoa: Octocorallia: Plexauridae). Zootaxa 2995: 27–44. https://doi.org/10.11646/ zootaxa.2995.1.2
- Breedy O, Guzmán HM (2015) A revision of the genus *Muricea* Lamouroux, 1821 (Anthozoa, Octocorallia) in the eastern Pacific. Part I: Eumuricea Verrill, 1869 revisited. ZooKeys 537: 1–32. https://doi.org/10.3897/zookeys.537.6025
- Breedy O, Guzmán HM (2016) A revision of the genus *Muricea* Lamouroux, 1821 (Anthozoa, Octocorallia) in the eastern Pacific. Part II. ZooKeys 581: 1–69. https://doi.org/10.3897/ zookeys.581.7910
- Breedy O, Guzmán HM, Vargas S (2009) A revision of the genus *Eugorgia* Verrill, 1868 (Coelenterata: Octocorallia: Gorgoniidae). Zootaxa 2151: 1–46. https://repository.si.edu/handle/10088/11792
- Breeze H, Derek DS, Butler M, Valdimir K (1997) Distribution and status of deep sea corals off Nova Scotia. Marine Issues Committee Special Publication Number 1, Ecology Action Center, 34 pp.
- Broch Hj (1912) Die Alcyonarien des Trondhjemsfjordes II. Gorgonacea. Kongelige Danske Videnskabernes Selskabs Skrifter 1912(2): 1–48. [figs 1–29]
- Broch Hj (1916) Alcyonarien. In: Results of Dr. E. Mjobergs Swedish Scientific Expeditions to Australia 1910–1913. XI. Kungliga Svenska Vetenskapsakademiens Handlingar 52(11): 1–48. [figs 1–62, pls 1–4]
- Bruckner A (2009) II. Global Perspective of Coral Disease: The Global Perspective of Incidence and Prevalence of Coral Diseases. Global Reef Expedition. Khaled bin Sultan Living Ocean Foundation, 36 pp. https://www.livingoceansfoundation.org/wpcontent/uploads/2013/08/Bruckner\_DiseasePrevalence.pdf
- Brundin JAZ (1896) Alcyonarien aus der Sammlung des Zoologischen Museum in Uppsala. Bihang till Kungliga Svenska Vetenskapsakademiens Handlingar 22(4) (No. 3): 1–22. [pls 1, 2]
- Brusca RC, Moore W, Shuster SM (2016) Invertebrates (3<sup>rd</sup> edn). Sinauer Associates Inc., Publishers, Sunderland, 1104 pp.
- Buhl-Mortensen L, Mortensen PB (2004a) Symbiosis in deep-water corals. Symbiosis 37: 33-61.
- Buhl-Mortensen L, Mortensen PB (2004b) Crustacean fauna associated with the deep-water corals *Paragorgia arborea* and *Primnoa resedaeformis*. Journal of Natural History 38: 1233– 1247. https://doi.org/10.1080/0022293031000155205

- Buhl-Mortensen L, Vanreusei A, Gooday AJ, Levin LA, Priede IG, Buhl-Moretensen P, Gheerardyn H, King NJ, Raes M (2010) Biological structures as a source of habitat heterogeneity and biodiversity on the deep ocean margins. Marine Ecology 31: 21–50. https:// doi.org/10.1111/j.1439-0485.2010.00359.x
- Burmannus J (1769) Index alter in omnes tomos Herbarii Amboinensis Cl. Georgii Everhardi Rumphii, quem de novo recensuit, auxit, et emendavit. Lugduni Batavorum apud Cornelium Haak; Amstelaedami apud Iohannem Schreuderum, 22 pp.
- Cairns S (2007) Calcaxonian Octocorals (Cnidaria; Anthozoa) from Eastern Pacific Seamounts. Proceedings of the California Academy of Sciences 58(25): 511–541. https://repository. si.edu/handle/10088/7491
- Cairns S (2009) Influence of Frederick (Ted) M. Bayer on deep-water octocoral research. Marine Ecology progressive Series 397(Suppl. 1): 7–10. https://doi.org/10.3354/meps08066
- Cairns S, Bayer FM (2005) A Review of the Genus *Primnoa* (Octocorallia: Gorgonacea: Primnoidae), with the Description of Two New Species. Bulletin of Marine Science 77(2): 225–256. https://repository.si.edu/handle/10088/124
- Cairns S, Bayer FM (2009) A generic revision and phylogenetic analysis of the Primnoidae (Cnidaria: Octocorallia). Smithsonian Contributions to Zoology 629: 1–79. https://doi.org/10.5479/si.00810282.629
- Center for the International Trade in Endangered Species (2007) Consideration of Proposals for Amendment of Appendices I and II (CoP14 Prop. xx). Report from the Fourteenth meeting of the Conference of the Parties, The Hague (Netherlands), 3–15 June 2007, 1–23.
- Committee on Common Names of Cnidaria and Ctenophora (American Fisheries Society), Cairns S (2003) Common and Scientific Names of Aquatic Invertebrates from the United States and Canada: Cnidaria and Ctenophora, Revised 2<sup>nd</sup> Edition. American Fisheries Society, Bethesda, Maryland, 126 pp.
- Convention on International Trade in Endangered Species and Wild Fauna and Flora (2010) Consideration of Proposals for Amendment of Appendices I and II (CoP15 Prop. 21). Report from the Fifteenth meeting of the Conference of the Parties, Doha (Qatar), 13–25 March 2010, 1–35.
- Convention on International Trade in Endangered Species and Wild Fauna and Flora (2013) Taxonomic checklist of all CITES listed coral species (CoP16 Doc. 43.1 [Rev. 1], Annex 5.1, pp 1–9) and Taxonomic checklist of CITES listed coral species (CoP16 Doc. 43.1 [Rev. 1], Annex 5.2, pp 1–117). Report from the Sixteenth meeting of the Conference of the Parties, Bangkok, Thailand, 3–14 March 2013.
- Cordeiro R, van Ofwegen L, Williams G (2018a) World List of Octocorallia. *Anthothela* Verrill, 1879. http://www.marinespecies.org/aphia.php?p=taxdetails&id=125324
- Cordeiro R, van Ofwegen L, Williams G (2018b) World List of Octocorallia. *Paragorgia* Milne Edwards, 1857. http://www.marinespecies.org/aphia.php?p=taxdetails&id=125326
- Cordeiro R, van Ofwegen L, Williams G (2018c) World List of Octocorallia. *Sibogagorgia* Stiasny, 1937. http://www.marinespecies.org/aphia.php?p=taxdetails&id=267835
- Cordeiro R, van Ofwegen L, Williams G (2018d) World List of Octocorallia. *Corallium* Cuvier, 1798. http://www.marinespecies.org/aphia.php?p=taxdetails&id=125325

- Cordeiro R, van Ofwegen L, Williams G (2018e) World List of Octocorallia. *Acanthogorgia* Gray, 1857. http://www.marinespecies.org/aphia.php?p=taxdetails&id=125293
- Cordeiro R, van Ofwegen L, Williams G (2018f) World List of Octocorallia. *Muricella* Verrill, 1868. http://www.marinespecies.org/aphia.php?p=taxdetails&id=267602
- Cordeiro R, van Ofwegen L, Williams G (2019) World List of Octocorallia. *Hemicorallium* Gray, 1867. http://www.marinespecies.org/aphia.php?p=taxdetails&id=718773
- Cuvier G (1797[1798]) Tableau élémentaire de l'histoire naturelle des animaux. Boudouin, Paris, 710 pp. [14 pls] https://doi.org/10.5962/bhl.title.45918
- Daly M, Brugler MR, Cartwright P, Collins AG, Dawson MN, Fautin DG, France SC, McFadden CS, Opresko DM, Rodriquez E, Roman SL, Stake, JL (2007) The phylum Cnidaria: A review of phylogenetic patterns and diversity, 300 years after Linnaeus. Zootaxa 1668: 127–182. http://www.mapress.com/zootaxa/2007f/zt01668p182.pdf
- Dana JD (1846) Zoophytes. United States Exploring Expedition during the years 1838, 1839, 1840, 1841, 1842, under the command of Charles Wilkes, USN vol. 7. Lea and Blanchard, Philadelphia, 740 pp. [45 text figs. Atlas, Zoophytes, 61 pls, 1849; See nos. 21, 22, 25, and 26 in Haskell DC: The United States Exploring Expedition, 1838–1842 and its publications 1844–1874. Greenwood Press, New York, 1968.] https://sil.si.edu/DigitalCollections/ usexex/follow-01.htm
- Deghrigue M, Dellai A, Bouraoui A (2013) In vitro antiproliferative and antioxidant activities of the organic extract and its semi-purified fractions from the Mediterranean gorgonian *Eunicella singularis*. International Journal of Pharmacy and Pharmaceutical Sciences 5(2): 432–439. http://www.ijppsjournal.com/Vol5Suppl2/6869.pdf
- DeVogelaere AP, Burton EJ, Trejo T, King CE, Clague DA, Tamburri MN, Cailliet GM, Kochevar RE, Douros WJ (2005) Deep-sea corals and resource protection at the Davidson Seamount, California, U.S.A. In: Freiwald A, Roberts JM (Eds) Cold-water Corals and Ecosystems. Springer-Verlag, Berlin-Heidelberg, 1189–1198. https://doi.org/10.1007/3-540-27673-4\_61
- Druffel ERM, King LL, Belastock RA, Buessler KO (1990) Growth rate of a deep-sea coral using <sup>210</sup>Pb and other isotopes. Geochimica Cosmochimica Acta 54: 1493–1499. https:// doi.org/10.1016/0016-7037(90)90174-J
- Druffel ERM, Griffen S, Witter A, Nelson E, Southon J, Kashgarian M, Vogel J (1995) Gerardia: Bristlecone pine of the deep-sea? Geochimica Cosmochimica Acta 59: 5031–5036. https://doi.org/10.1016/0016-7037(95)00373-8
- Duchassaing P, Michelotti G (1864) Supplement au mémoire sur les Coralliaires des Antilles. Memorie della Reale Accademia delle Scienze di Torino (ser. 2) 23: 97–206. [Reprint paged 1–112].
- Dunn DF (1982) Cnidaria. In: Parker SA (Ed.) Synopsis and Classification of Living Organisms. Vol. I. McGraw-Hill Book Company, New York, 669–706.
- Etnoyer PJ, Morgan LE (2005) Habitat-forming deep-sea corals in the Northeast Pacific Ocean. In: Freiwald A, Roberts, JM (Eds) Cold-water Corals and Ecosystems. Springer-Verlag, Berlin-Heidelberg, 331–343. https://doi.org/10.1007/3-540-27673-4\_16
- Etnoyer PJ, Cairns SD, Sánchez JA, Reed JK, Brooke S, Watling L, Baco-Taylor A, Lopez JV, Schroeder WW, McDonough J, Morgan LE, Bruckner AW, Shepard AN, Lindner A, Williams G, France SC, Barr B (2006) Deep-Sea Coral Collection Protocols. A synthesis of

field experience from deep-sea coral researchers, designed to build our national capacity to document deep-sea coral diversity. NOAA Technical Memorandum NMFS-OPR-28, Silver Spring, Maryland, October 25, 45 pp. https://repository.si.edu/handle/10088/18821

- Fabricius KE, Alderslade P (2001) Soft Corals and Sea Fans: A Comprehensive Guide to the tropical shallow-water genera of the Central-West Pacific, the Indian Ocean and the Red Sea. Australian Institute of Marine Science, Queensland, Australia, 264 pp.
- Fenical W, Okuda RK, Bandurraga MM, Culver P, Jacobs RS (1981) Lophotoxin: a novel neuromuscular toxin from Pacific sea whips of the genus *Lophogorgia*. Science 212: 1512– 1514. https://doi.org/10.1126/science.6112796
- Figueroa DF, Baco AR (2014a) Octocoral Mitochondrial Genomes Provide Insights into the Phylogenetic History of Gene Order Rearrangements, Order Reversals, and Cnidarian Phylogenetics. Genome Biology and Evolution 7(1): 391–409. https://doi.org/10.1093/gbe/evu286
- Figueroa DF, Baco AR (2014b) Complete mitochondrial genomes elucidate phylogenetic relationships of the deep-sea octocoral families Coralliidae and Paragorgiidae. Deep Sea Research II 99: 83–91. https://doi.org/10.1016/j.dsr2.2013.06.001
- France SC, Hoover LL (2001) Analysis of variation in mitochondrial DNA sequences (ND3, ND4L, MSH) among Octocorallia (=Alcyonaria) (Cnidaria: Anthozoa). Bulletin of the Biological Society of Washington 10: 110–118 on the USGS. https://www.sciencebase. gov/catalog/item/50578025e4b01ad7e027f439
- Fraser CM (1943) General account of the scientific work of the *Velero III* in the Eastern Pacific, 1931–41. Allan Hancock Pacific Expeditions, Volume 1, Parts I, II, and III with Appendix (1942). Allan Hancock Foundation publications of the University of Southern California, University of Southern California Press, 445 pp.
- Freiwald A, Roberts JM (2005) Cold-water Corals and Ecosystems. Springer-Verlag, Berlin, 1243 pp. https://doi.org/10.1007/3-540-27673-4
- Germanos NK (1896) Gorgonaceen von Ternate. In: Kükenthal W (Ed.) Ergebnisse einer zoologischen Forschungsreise in den Molukken und Borneo, im Auftrage der Senckenbergischen naturforschenden Gesellschaft ausgefuhrt von Dr. Willy Kükenthal, Teil 2, Band 1. Abhandlungen der Senckenbergischen naturforschenden Gesellschaft 23(1): 145–187. [pls 9–12]
- Gomez ED (1973) Observations on feeding and prey specificity of *Tritonia festiva* (Stearns) with comments on other tritoniids (Mollusca: Opisthobranchia). The Veliger 16: 163–165.
- Gori A, Bramanti L, López-González P, Thoma JN, Gili J-M, Grinyo J, Uceira V, Rossi S (2012) Characterization of the zooxanthellate and azooxanthellate morphotypes of the Mediterranean gorgonian *Eunicella singularis*. Marine Biology 159: 1485–1496. https:// doi.org/10.1007/s00227-012-1928-3
- Grasshoff M (1973) Die Gorgonaria des östlichen Nordatlantik und des Mittelmeeres.II. Die Gattung *Acanthogorgia* (Cnidaria: Anthozoa). Auswertung der "Atlantischen Kuppenfahrten 1967" von FS 'Meteor.' 'Meteor' Forschungs-Ergebnisse D13: 1–10. [figs 1–12]
- Grasshoff M (1979) Zur bipolaren Verbreitung der Oktokoralle *Paragorgia arborea* (Cnidaria: Anthozoa: Scleraxonia). Senckenberg Marit 11: 115–137.
- Grasshoff M (1992) Die Flachwasser-Gorgonarien von Europa und Westafrika (Cnidaria, Anthozoa). Courier Forschungsinstitut Senckenberg 149: 1–135. [figs 1–155, tabs 1–4, pls 1–7]
- Grasshoff M (1999) The shallow water gorgonians of New Caledonia and adjacent islands (Coelenterata: Octocorallia). Senckenbergiana Biolologica 78(1/2): 1–245.

- Grasshoff M (2000) The gorgonians of the Sinai coast and the Strait of Gobal, Red Sea (Coelenterata: Octocorallia). Courier Forschunginstitut Senckenberg 224: 1–125.
- Grasshoff M, Bargibant G (2001) Coral Reef Gorgonians of New Caledonia. Institut de Recherche pour le Développement, Collection Faune et Flore tropicales, Paris, 38, 335 pp.
- Gray JE (1857) Description of a new genus of Gorgoniadae. Proceedings of the Zoological Society of London 1857: 128–129.
- Gray JE (1859) On the arrangement of zoophytes with pinnated tentacles. Annals and Magazine of Natural History (3)4: 439–444. https://doi.org/10.1080/00222935908697159
- Gray JE (1860) Description of a new coral (*Corallium johnsoni*) from Madeira. Proceedings of the Zoological Society of London 1860: 393–394. [pl 18]
- Gray JE (1867) Additional note on *Corallium johnsoni*. Proceedings of the Zoological Society of London 1867: 125–127.
- Grieg JA (1891) Tre nordiske Alcyonarier. Bergens Museum Aarsberetning for 1890(2): 1–13. [1 pl]
- Griffen S, Druffel ERM (1989) Sources of carbon to deep-sea corals. Radiocarbon 31: 533–543. https://doi.org/10.1017/S0033822200012121
- Grigg RW (1970) Ecology and Population Dynamics of the Gorgonians, *Muricea californica* and *Muricea fruticosa* (Coelenterate: Anthozoa). PhD Dissertation, University of California, San Diego. [Abstracts International, 31B: 2153]
- Grigg RW (1972) Orientation and growth form of the sea fans. Limnology and Oceanography 17(2): 185–192. https://doi.org/10.4319/lo.1972.17.2.0185
- Grigg RW (1974) Growth rings: annual periodicity in two gorgonian corals. Ecology 55: 876–881. https://doi.org/10.2307/1934424
- Grigg RW (1975) Age structure of a longevous coral: a relative index of habitat suitability and stability. American Naturalist 109: 647–657. https://doi.org/10.1086/283035
- Grigg RW (2002) Precious corals in Hawaii: discovery of a new bed and revised management measures for existing beds. Marine Fisheries Review 64: 13–20.
- Grigg, RW, Bayer FM (1976) Present knowledge of the systematics and zoogeography of the order Gorgonacea in Hawaii. Pacific Science 30(2): 167–175.
- Grillo M-C, Goldberg WM, Allemand D (1993) Skeleton and sclerite formation in the precious red coral *Corallium rubrum*. Marine Biology 117: 119–128. https://doi.org/10.1007/ BF00346433
- Hardee M, Wicksten MK (1996) Redescription and taxonomic comparison of three eastern Pacific species of *Muricea* (Cnidaria: Anthozoa). Bulletin of the Southern California Academ of Sciences 95(3): 127–140. http://biodiversitylibrary.org/page/39810558; http://scholar. oxy.edu/scas/vol95/iss3/1
- Harden DG (1979) Intuitive and Numerical Classification of East Pacific Gorgonacea (Octocorallia). PhD Dissertation, Illinois State University, Illinois, 214 pp.
- Hargitt CW, Rogers CG (1901) The Alcyonaria of Porto Rico. Bulletin of the United States Fish Commission 20(2): 265–287. [figs A–K, pls 1–4]
- Hedlund T (1890) Einige Muriceiden der Gattungen Acanthogorgia, Paramuricea und Echinomuricea im zoologischen Museum der Universität, Upsala. Stockholm. Kongliga Svenska Vetenskaps-Akademiens, Bihang till Handlingar Vol. 16, Avd. 4, No. 6: 1–19.
- Heifetz J (2002) Coral in Alaska: Distribution, abundance, and species associations. Hydrobiologia 471: 19–28. https://doi.org/10.1023/A:1016528631593

- Herrera S, Baco A, Sánchez JA (2010) Molecular systematics of the bubblegum coral genera (Paragorgiidae, Octocorallia) and description of a new deep-sea species. Molecular Phylogenetics and Evolution 55(1): 123–135. https://doi.org/10.1016/j.ympev.2009.12.007
- Hickson SJ (1905a) On a new species of *Corallium* from Timor. Koninklijke Akademie Wetenschappen Amsterdam, Proceedings in Section on Science 8: 268–271.
- Hickson SJ (1905b) The Alcyonaria of the Maldives. Part III. The families Muriceidae, Gorgonellidae, Melitodidae, and the genera Pennatula, Eunephthya. In: Gardiner, JS (Ed.) The Fauna and Geography of the Maldive and Laccadive Archipelagoes 2(4): 807–826. [pl 67]
- Hickson SJ (1907) Die Alcyoniden der Siboga-Expedition I. Coralliidae. Siboga-Expeditie Monographie 13c: 1–8. [pl 1]
- Hickson SJ (1915) Some Alcyonaria and a *Stylaster* from the west coast of North America. Proceedings of the Zoological Society London 37: 541–557. https://doi.org/10.1111/j.1469-7998.1915.00541.x
- Hickson SJ (1930) On the classification of the Alcyonaria. Proceedings of the Zoological Society of London 15: 229–252. https://doi.org/10.1111/j.1096-3642.1930.tb00975.x
- Hiles IL (1899) Report on the gorgonacean corals collected by Mr J Stanley Gardiner at Funafuti. Proceedings of the Zoological Society of London 1899: 46–54. [pls 1–4] https:// doi.org/10.1111/j.1469-7998.1899.tb06843.x
- Hochberg FG (1979) Southern California Stoloniferans, Telestaceans, Alcyonaceans. Proceedings of the Southern California Coastal Water Research Project (SCCWRP) Taxonomic Standardization Program 7(1): 17–29.
- Horvath EA (2011) An unusual new "sea fan" from the northeastern Pacific Ocean (Cnidaria: Octocorallia: Gorgoniidae). Proceedings of the Biological Society of Washington 124(1): 45–52. https://doi.org/10.2988/10-27.1
- Humes AG, Lewbel GS (1977) Cyclopoid copepods of the genus Acanthomolgus (Lichomolgidae) associated with a gorgonian in California. Transactions of the American Microscopical Society 96(1): 1–12. https://doi.org/10.2307/3225957
- Janes MP, Wah LM (2007) Octocoral Taxonomy Laboratory Manual. Results of the International Workshop on the Taxonomy of Octocorals, March 20–26, 2005. University of Kerala, India, 1–91. https://searchworks.stanford.edu/view/9269618
- Johnson JY (1861) Description of a second species of *Acanthogorgia* from Madeira. Proceedings of the Zoological Society of London 1861: 296–298.[2 figs]
- Johnson JY (1862) Descriptions of some new corals from Madeira. Proceedings of the Zoological Society of London 1862: 194–197. [14 figs] [Also in Annals and Magazine of Natural History (3)11: 140–143, 14 figs (1863)] https://doi.org/10.1111/j.1469-7998.1862. tb06497.x
- Johnson JY (1898) Short diagnoses of two new species of Coralliidae from Madeira. Annals and Magazine of Natural History (7)2: 421–422. [Full descriptions with illustrations published in Proceedings of the Zoological Society of London 1899: 57–63, June 1, 1899.] https:// doi.org/10.1080/00222939808678066
- Johnson JY (1899) Notes on the Coralliidae of Madeira, with descriptions of two new species. Proceedings of the Zoological Society of London 1899: 57–63. [pls 5–7]

- Kent WS (1870) On two genera of alcyonid corals, taken in the recent expedition of the yacht 'Norma' off the coast of Spain and Portugal. Quarterly Journal of Microscopic Science (NS) 10: 397–399.
- Kishinouye K (1903) Preliminary note on the Coralliidae of Japan. Zoologischer Anzeiger 26(705): 623–626. www.biodiversitylibrary.org/part/68752#/summary
- Kishinouye K (1904) Sango no kenkyu. Suisan chosa hokoku 14(1): 1-31. [pls 1-9]
- Kishinouye K (1905) Notes on the natural history of corals. Journal of the Imperial Fisheries Bureau 14(1): 1–32. [pls 1–9]
- Knorr GW (1766–67) Deliciae Naturae Selectae; oder auserlesense Naturalien-Cabinet, welches aus den drey Reichen der Natur zeiget was von... Liebhabern aufbehalten und gesammlet zu werden verdienet. Ehemals heraus gegeben von GW Knorr...fortgesetzt von dessen Erben, beschrieben von PLS Muller, und in das Franzosische ubersetzt von MV de la Blaquiere. Knorr (Erben), Nurnberg, 144 pp. [91 pls] https://doi.org/10.5962/bhl.title.149936
- Kölliker RA von (1865) Icones histiologicae oder Atlas der vergleichenden Gewebelehre. Zweite Abtheilung. Der feinere Bau der hoheren Thiere. Erstes Heft. Die Bindesubstanz der Coelenteraten. Verlag von Wilhelm Engelmann, Leipzig, 87–181. [pls 10–19, 13 text figs] https://doi.org/10.5962/bhl.title.82233
- Koren J, Danielssen DC (1883) Nye Alcyonider, Gorgonider og Pennatulider tilhorende Norges Fauna. Bergens Museum. John Griegs Bogtrykkeri, Bergen, 1–38. [pls 1–13] https:// doi.org/10.5962/bhl.title.60111
- Kozloff E, Price LH et al. (1996) Marine Invertebrates of the Pacific Northwest. University of Washington Press, Seattle, 512 pp.
- Kükenthal W (1909) Japanische Gorgoniden. II. Teil: Die Familien der Plexauriden, Chrysogorgiiiden und Melitodiden. In: Beitrage zur Naturgeschichte Ostasiens. Abhandlungen der mathematische-physics. Klasse der K. Bayer. Akademie der Wissenschaften. Supplement-Band 1(5): 1–78. [7 pls]
- Kükenthal W (1913a) Über die Alcyonarienfauna Californiens und ihre tiergeo-graphischen Beziehungen. Zoologische Jahrbucher Abteilung fur Systematik 35(2): 219–270. https:// doi.org/10.5962/bhl.part.16718
- Kükenthal W (1913b) Alcyonaria des Roten Meeres. In: Expeditionen SM Schiff 'Pola' in das Rote Meer. Zoologische Ergebnisse 29. Denkschrift mathematische-naturwissenschaftlich Klasse der K Bayer. Akademie der Wissenschaften 89: 1–31. [pls 1–3]
- Kükenthal W (1916) System und Stammesgeschichte der Scleraxonier und der Ursprung der Holaxonier. Zoologischer Anzeiger 47(6): 170–183. https://biodiversitylibrary.org/ page/972892
- Kükenthal W (1919) Gorgonaria. Wissenschaftliche Ergebnisse der deutsche Tiefsee Expeditionen 'Valdivia' 1898–99, 13(2): 1–946. [pls 30–89]
- Kükenthal W (1924) Gorgonaria. Das Tierreich, Vol. 47. Walter de Gruyter & Company, Berlin, 478 pp.
- Kükenthal W, Gorzawsky H (1908a) Diagnosen neuer japanischer Gorgoniden (Reise Doflein 1904/05). Zoologischer Anzeiger 32(20/21): 621–631. https://biodiversitylibrary.org/ page/9895336

- Kükenthal W, Gorzawsky H (1908b) Japanische Gorgoniden. I. Teil: Die Familien der Primnoiden, Muriceiden und Acanthogorgiiden. In: Beitrage zur Naturgeschichte Ostasiens.
  Abhandlungen der mathematische-physics. Klasse der K. Bayer. Akademie der Wissenschaften. Supplement-Band 1(3): 1–71. [+ pls 1–4]
- Lamarck JB de (1801) Systeme des animaux sans vertebras, ou tableau general des classes, des ordres, et des genres de ces animaux. Chez l'auteur, au Muséum d'Histoire Naturelle, Paris, 432 pp.
- Lamb A, Hanby BP (2005) Marine Life of the Pacific Northwest: A Photographic Encyclopedia of Invertebrates, Seaweeds and Selected Fishes. Harbour Publishing, Madeira Park-British Columbia, 398 pp.
- Lamouroux JVF (1816) Histoire des polypiers coralligènes flexibles, vulgairement nommés Zoophytes. A Caen, De l'Imprimerie du F Poisson, 560 pp. [pls 1–19] https://doi. org/10.5962/bhl.title.11172
- Langstroth L, Langstroth L (2000) A Living Bay: The Underwater World of Monterey Bay. Series in Marine Conservation, 2. University of California and Monterey Bay Aquarium, Berkeley, 287 pp.
- Laubitz DR, Lewbel GS (1974) A new species of caprellid (Crustacean: Amphipoda) associated with gorgonian octocorals. Canadian Journal of Zoology 52: 549–551. https://doi. org/10.1139/z74-070
- Leversee Jr GR (1976) Flow and feeding in fan-shaped colonies of the octocoral, *Lep-togorgia virgulata*. Biological Bulletin (Woods Hole) 151(2): 344–356. https://doi.org/10.2307/1540667
- Lewbel GS (1976) Sex ratios in *Caprella gorgonia* (Crustacea: Amphipoda: Caprellidae. PhD Dissertation, University of California, San Diego.
- Lewis JC, von Wallis E (1991) The Function of Surface Sclerites in Gorgonians (Coelenterata, Octocorallia). Biological Bulletin 181(2): 275–288. https://doi.org/10.2307/1542099
- Linnaeus C (1758) Systema naturae. Editio decima, reformata. Holmiae: Impensis Direct. Laurentii Salvii, 1, 824 pp. https://biodiversitylibrary.org/page/726886
- Linnaeus C (1767) Systema naturae. Editio duodecima, reformata. Holmiae 1(2): 533–1327. [+ 18 lvs] https://biodiversitylibrary.org/page/461997
- Lissner AL, Dorsey JH (1986) Deep-water biological assemblages of a hard-bottom bank-ridge complex of the Southern California Continental Borderland. Bulletin of the Southern California Academy of Sciences 85(2): 87–101.
- López-González PJ, Briand P (2002) A new scleraxonian genus from Josephine Bank, northeastern Atlantic (Cnidaria, Octocorallia). Hydrobiologia 482(1–3): 97–105. https://doi. org/10.1023/A:1021256230344
- McFadden CS, France SC, Sánchez JA, Alderslade P (2006) A molecular phylogenetic analysis of the Octocorallia (Cnidaria: Anthozoa) based on mitochondrial protein-coding sequences. Molecular Phylogenetics and Evolution 41: 513–527. https://doi.org/10.1016/j. ympev.2006.06.010
- McFadden CS, Benayahu Y, Pante E, Thoma JN, Nevarez PA, France SC (2011) Limitations of mitochondrial gene barcoding in Octocorallia. Molecular Ecology Resources 11: 19–31. https://doi.org/10.1111/j.1755-0998.2010.02875.x

- McFadden CS, Ofwegen LP van (2013) Molecular phylogenetic evidence supports a new family of octocorals and a new genus of Alcyoniidae (Octocorallia, Alcyonacea). ZooKeys 20(3): (346)59–83. https://doi.org/10.3897/zookeys.346.6270
- McGinnis MV (2006) Negotiating ecology: Marine bioregions and the destruction of the Southern California Bight. Futures 38(4): 382–405. https://doi.org/10.1016/j.futures.2005.07.016
- McLean EL, Yoshioka PM (2007) Associations and interactions between gorgonians and sponges. In: Custódio MR, Lôbo-Hajdu G, Hajdu E, Muricy G (Eds) Porifera Research: Biodiversity, Innovation and Sustainability. Rio de Janeiro-Museu Nacional, 443–448.
- Madsen FJ (1944) Octocorallia. Danish Ingolf-Expedition 5(13): 1-65. [53 figs, 1 pl]
- Mariscal RN, Bigger CH (1976) A Comparison of Putative Sensory Receptors Associated with Nematocysts in an Anthozoan and a Scyphozoan. In: Mackie GO (Ed.) Coelenterate Ecology and Behavior. Springer-Verlag, Berlin-Heidelberg, 559–568. https://doi. org/10.1007/978-1-4757-9724-4\_58
- Milne Edwards H, Haime J (1857) Histoire naturelle des coralliaires ou polypes proprement dits, Vol. I. Libraire Encyclopédique de Roret, Paris, i–xxxiv + 326 pp. [8 pls, numbered A1–6, B1–2] https://doi.org/10.5962/bhl.title.11911
- Molander AR (1918) Der Kelch als systematischer Charakter bei den Alcyonaceen. Arkiv for Zoologi 11(22): 1–12.
- Molander AR (1921) Alcyonarien von Madagaskar. Arkiv for Zoologi 14(2): 1–13. https://doi. org/10.5962/bhl.part.20150
- Moroff T (1902) Studien über Octocorallien. II. Über einige neue Gorgonaceen aus Japan. Zoologische Jahrbucher Abteilong für Systematik, Geographie und Biologie 17: 363–410. [pls 14–17]
- Moore KM, Alderslade P, Miller KJ (2017) A taxonomic revision of Anthothela (Octocorallia: Scleraxonia: Anthothelidae) and related genera, with the addition of new taxa, using morphological and molecular data. Zootaxa 4304(1): 1. https://doi.org/10.11646/ zootaxa.4304.1.1
- Muzik KM (1979) A systematic revision of the Hawaiian Paramuriciidae and Plexauridae (Coelenterata: Octocorallia). PhD Dissertation, University of Miami, Coral Gables.
- Nutting CC (1908) Descriptions of the Alcyonaria collected by the U.S. Bureau of Fisheries steamer 'Albatross' in the vicinity of the Hawaiian Islands in 1902. Proceedings of the United States National Museum 34: 543–601. [pls 41–51] https://doi.org/10.5962/bhl. title.49592
- Nutting CC (1909) Alcyonaria of the California coast. Proceedings of the United States National Museum 35: 681–727. https://doi.org/10.5479/si.00963801.35-1658.681
- Nutting CC (1910) The Gorgonacea of the Siboga Expedition. III. The Muriceidae Siboga Expedition Monograph, 13b: 1–108. [22 pls]
- Nutting CC (1911) The Gorgonacea of the Siboga Expedition VIII. The Scleraxonia. Siboga-Expedition Monograph, 13b5: 1–62. [pls 1–12]
- Nutting CC (1912) Descriptions of the Alcyonaria collected by the US Fisheries Steamer 'Albatross' primarily in Japanese waters during 1906. Proceedings of the United States National Museum 43(1923): 1–104. [21 pls] https://doi.org/10.5479/si.00963801.43-1923.1

- Orr JC, Fabry VJ, Aumont O (2005) Anthropogenic ocean acidification over the twentyfirst century and its impact on calcifying organisms. Nature 437: 681–686. https://doi. org/10.1038/nature04095
- Pallas PS (1787) Charakteristik der Thierpflanzen...aus dem Lateinischen ubersetzt, und mit Anmerkungen versehen, von CF Wilkens, und nach seinem Tode herausgegeben von Johann Wilhelm Herbst. Verlegt von der Raspischen Buchhandlung, Nurnberg, 2 vols.
- Paoli C, Montefalcone M, Morri C, Vassallo P, Bianchi CN (2017) Ecosystem Functions and Services of the Marine Animal Forests, Chapter 44. [pages 1271–1312] In: Rossi S, Bramanti L, Gori A, Orejas C (Eds) The Ecology of Benthic Biodiversity Hotspots. Springer International Publishing, 1366 pp.
- Parrish FA (2007) Density and habitat of three deep-sea corals in the lower Hawaiian chain. In: George RY, Cairns SD (Eds) Conservation and adaptive management of seamount and deep-sea coral ecosystems. Bulletin of Marine Science 81(Supplement 1): 1–324. http:// www.pifsc.noaa.gov/library/pubs/Parrish\_5477\_2007.pdf
- Patton WK (1972) Studies on the animal symbionts of the gorgonian coral, *Leptogorgia virgulata*. Bulletin Marine Science 22(2): 419–431. https://www.ingentaconnect.com/content/umrsmas/bullmar/1972/00000022/00000002/art00009?crawler=true
- Pourtales LF de (1867) Contributions to the Fauna of the Gulf Stream at great depths. Bulletin of the Museum of Comparative Zoology, Harvard 1(6): 103–142.
- Quattrini A, Etnoyer PJ, Doughty C, English L, Falco R, Remon N, Rittinghouse M, Cordes EE (2014) A phylogenetic approach to octocoral community structure in the deep Gulf of Mexico. Deep Sea Research Part II: Topical Studies in Oceanography 99: 92–102. https:// doi.org/10.1016/j.dsr2.2013.05.027
- Ridley SO (1882a) On the arrangement of the Coralliidae, with descriptions of new or rare species. Proceedings of the Zoological Society of London 1882: 221–233. [pl 9]
- Ridley SO (1882b) Contributions to the knowledge of the Alcyonaria II. Including descriptions of new species from Mauritius. Annals and Magazine of Natural History (5) 10: 125–133. https://doi.org/10.1080/00222938209459682
- Ridley SO (1884) Alcyonaria. In: Report on the Zoological Collections made in the Indo-Pacific Ocean during the Voyage of HMS 'Alert' 1881–1882. British Museum, London, 327–365. [pls 36–38]
- Risk MJ, Heikoop JM, Snow MG, Beukens R (2002) Lifespans and Growth Patterns of Two Deep-Sea Corals: *Primnoa resedaeformis* and *Desmophyllum cristagalli*. Hydrobiologia 471: 125–131. https://doi.org/10.1023/A:1016557405185
- Rodriquez AD, Cóbar OM, Martinez N (1994) Isolation and structures of sixteen Asbestinin Diterpenes from the Caribbean Gorgonian *Briareum asbestinum*. Journal of Natural Products 57(12): 1638–1655. https://doi.org/10.1021/np50114a005
- Sánchez JA (2005) Systematics of the bubblegum corals (Cnidaria: Octocorallia: Paragorgiidae) with description of new species from New Zealand and the Eastern Pacific. Zootaxa 1014: 1–72. https://doi.org/10.11646/zootaxa.1014.1.1
- Sánchez JA, Lasker HR, Taylor DJ (2003a) Phylogenetic analyses among octocorals (Cnidaria): mitochondrial and nuclear DNA sequences (Isu-rRNA, 16S and ssu-rRNA, 18S) support two convergent clades of branching gorgonians. Molecular Phylogenetics and Evolution 29: 31–42. https://doi.org/10.1016/S1055-7903(03)00090-3

- Sánchez JA, McFadden CS, France SC, Lasker HR (2003b) Molecular Phylogenetic Analyses of Shallow-water Caribbean Octocorals. Marine Biology 142: 975–987. https://doi. org/10.1007/s00227-003-1018-7
- Sánchez JA, Aguilar C, Dorado D, Manrique N (2007) Phenotypic plasticity and morphological integration in a marine modular invertebrate. BMC Evolutionary Biology 7: 122. https://doi.org/10.1186/1471-2148-7-122
- Sars M (1856) Nouveau polypes In: Sars M, Koren J, Danielssen DC (Eds) Fauna Littoralis Norvegiae 2: 63–79. [pl 10, figs 18–27; pl 11, figs 1–9] [English translation in Annals and Magazine of Natural History 20: 238–239, 1857] https://doi. org/10.1080/00222935709487910
- Satterlie RA, Case JF (1978) Neurobiology of the gorgonian coelenterates, Muricea californica and Lophogorgia chilensis. II. Morphology. Cell & Tissue Research 187: 379–396. https:// doi.org/10.1007/BF00229604
- Satterlie RA, Case JF (1979) Neurobiology of the gorgonian coelenterates, *Muricea californica* and *Lophogorgia chilensis*. I. Behavioural physiology. Journal of Experimental Biology 79: 191–204. http://www.jeb.biologists.org/content/79/1/191
- Schimbke GO (1915) Studien zur Anatomie der Gorgonaceen. Archive Naturgeschichte (A) 80(11): 1–81. [pls 1–4] https://www.zobodat.at/pdf/Archiv-Naturgeschichte\_80A\_11\_0001-0081.pdf
- Sebens KP, Miles JS (1988) Sweeper Tentacles in a Gorgonian Octocoral: Morphological Modifications for Interference Competition. Biological Bulletin 175(3): 378–387. https://doi. org/10.2307/1541729
- Sherwood OA, Heikoop JM, Sinclair DJ, Scott DB, Risk MJ, Shearer C, Azetsu-Scott K (2005) Skeletal Mg/Ca in *Primnoa resedaeformis*: relationship to temperature? In: Freiwald A, Roberts JM (Eds) Cold-water Corals and Ecosystems. Springer-Verlag, Berlin-Heidelberg, 1061–1079. https://doi.org/10.1007/3-540-27673-4\_53
- Stephens J (1909) Alcyonarian and madreporarian corals of the Irish coasts, with description of a new species of *Stachyodes* by Professor S.J. Hickson, F.R.S. Department of Agriculture and Technical Instruction for Ireland, Fisheries Branch. Scientific Investigations, Dublin 1907(5): 1–28. [pl 1]
- Stiasny G (1937) Die Gorgonacea der Siboga-Expedition. Supplement II, Revision der Scleraxonia mit ausschluss der Melitodidae und Coralliidae. Siboga-Expedition Monograph 13b8: 1–138. [pls 1–8]
- Stiasny G (1943) Die Gorgonarien-Familie Acanthogorgiidae Kükenthal & Gorzawsky mit besonderer Berucksichtigung des Materials der Siboga-Expedition. Vorlaufige Mitteilung. Zoologischer Anzeiger 141(5/6): 127–133.
- Stiasny G (1947) De Gorgonarien-Familie Acanthogorgiidae Kükenthal & Gorzwasky (met bijzondere Inachtneming van het Materiaal der Siboga-Expeditie). Verhandelingen Koninklijke Nederlandsche Akademie van Wetenschapp, Afdeeling Natuurkunde, Tweede Sectie 43(2): 1–93. [pls 1–3]
- Studer T (1879) Ubersicht der Anthozoa Alcyonaria, welche wahrend der Reise SMS 'Gazelle' um die Erde gesammelt wurden. Monatsbericht der Könilich Preussischen Akademie der Wissenschaften zu Berlin, Sept.-Okt. 1878: 632–688. [pls 1–5]
- Studer T (1887) Versuch eines Systemes der Alcyonaria. Archiv für Naturgeschichte 53(1): 1–74. [pl 1]

- Studer T (1894) Reports on the dredging operations off the west coast of Central America to the Galápagos, to the west coast of Mexico, and in the Gulf of California, in charge of Alexander Agassiz, carried on by the U.S. Fish Commission steamer 'Albatross', during 1891, Lieutenant ZL Tanner, USN., commanding. Bulletin of the Museum of Comparative Zoology 25(5): 53–69.
- Studer T (1901) Alcyonaires provenant des campagnes de l'Hirondelle (1886–1888). Résultats des Campagnes Scientifiques, Monaco 20: 1–64. [pls 1–11] https://doi.org/10.5962/bhl. title.58246
- Thomson JA, Dean LMI (1931) The Alcyonacea of the Siboga Expedition with an addendum to the Gorgonacea. Siboga-Expedition Monograph 13d: 1–227. [pls 1–28]
- Thomson JA, Henderson WD (1905a) Report on the Alcyonaria collected by Professor Herdman, at Ceylon, in 1902. In: Report to the Government of Ceylon on the Pearl Oyster Fisheries of the Gulf of Manaar, Part 3, supplementary report 20: 269–328. https://biodiversitylibrary.org/page/1865785
- Thomson JA, Henderson WD (1905b) On the Alcyonaria. Supplementary. Collected by Professor WA Herdman. In: Report to the government of Ceylon on the Pearl Oyster Fisheries of the Gulf of Manaar, Part 4. Supplementary Report 28: 167–186. https://biodiversitylibrary.org/page/1936026
- Thomson JA, Henderson WD (1906) The Alcyonarians of the deep sea. An account of the alcyonarians collected by the Royal Indian Marine Survey Ship Investigator in the Indian Ocean. Part 1. The Alcyonarians of the deep sea. The Indian Museum, Calcutta, 1–132. [pls 1–10] https://biodiversitylibrary.org/page/21071101
- Thomson JA, Russell ES (1910) Alcyonarians collected on the Percy Sladen Trust Expedition by Mr. J. Stanley Gardiner. Part I, the Axifera. Transactions of the Linnean Society of London, series 2: Zoology 13(2): 139–164. https://doi.org/10.1111/j.1096-3642.1910.tb00515.x
- Thomson JA, Simpson JJ (1909) An account of the alcyonarians collected by the Royal Indian Marine Survey Ship Investigator in the Indian Ocean. II. The alcyonarians of the littoral area. Trustees of the Indian Museum, Calcutta, 319 pp. https://doi.org/10.5962/bhl.title.8279
- Tsounis G, Rossi S, Grigg R, Santangelo G, Bramanti L, Gili JM (2010) The exploitation and conservation of precious corals. In: Gibson RN, Atkinson RJA, Gordon JDM (Eds) Oceanography and Marine Biology: An Annual Review 48: 161–212. https://doi.org/10.1201/ EBK1439821169-c3
- Tsounis G, Rossi S, Bramanti L, Santangelo G (2013) Management hurdles for sustainable harvesting of Corallium rubrum. Marine Policy 39: 361–364. https://doi.org/10.1016/j. marpol.2012.12.010
- Tu T-H, Altuna A, Jeng M-S (2015a) Coralliidae (Anthozoa: Octocorallia) from the INDE-MARES 2010 expedition to north and northwest Spain (northeast Atlantic), with delimitation of a new species using both morphological and molecular approaches. Zootaxa 3926: 301–328. https://doi.org/10.11646/zootaxa.3926.3.1
- Tu T-H, Dai C-F, Jeng M-S (2015b) Phylogeny and systematics of deep-sea precious corals (Anthozoa: Octocorallia: Coralliidae). Molecular Phylogenetics and Evolution 84(2015): 173–184. https://doi.org/10.1016/j.ympev.2014.09.031

- Tu T-H, Dai C-F, Jeng M-S (2016) Taxonomic revision of Corallidae with descriptions of new species from New Caledonia and the Hawaiian Archipelago. Marine Biology Research 12(10): 1003–1038. https://doi.org/10.1080/17451000.2016.1241411
- Valenciennes A (1855) Extrait d'une monographie de la famille des Gorgonidees de la classe des polypes. Comptes Rendus Académie des Sciences, Paris, 41: 7–15. [Abridged English translation in Annals and Magazine of Natural History (2)16: 177–183. This describes the first use of sclerites in classification; no illustrations.] https://doi.org/10.5962/bhl. part.28683
- Verrill AE (1864) List of the polyps and corals sent by the Museum of Comparative Zoology to other institutions in exchange, with annotations. Bulletin of the Museum of Comparative Zoology at Harvard College 1(3): 29–60. https://biodiversitylibrary.org/ page/6587563
- Verrill AE (1865) Synopsis of the polyps and corals of the North Pacific Exploring Expedition, under Commodore C. Ringgold and Captain John Rogers, U.S.N., from 1853 to 1856. Collected by Dr Wm Stimpson, naturalist of the Expedition. With description of some additional species from the west coast of North America. Proceedings of the Essex Institute, Salem 4: 181–196.
- Verrill AE (1866) Classification of Polyps. (Extracts from a Synopsis of the Polypi of the North Pacific Exploring Expedition) Part I. Communications, Essex Institute, Salem 4: 145–152. https://biodiversitylibrary.org/page/34752272
- Verrill AE (1868a) [1868–1870] Notes on Radiata in the Museum of Yale College. 6. Review of the corals and polyps of the west coast of America. Transactions of the Connecticut Academy of Arts and Sciences (1<sup>st</sup> edn) 1: 377–422 [1868], 423–502 [1869], 503–558 [1870]. [pls. 5–10] [The regular edition up to page 502 was destroyed by fire after distribution of the author's edition of 150 copies; the reprinted edition issued in 1869 contains nomenclatural changes marked "Reprint" and thus constitutes a separate publication.] https://biodiversitylibrary.org/page/13465394
- Verrill AE (1868b) Notes on Radiata in the Museum of Yale College. No. 6. Review of the corals and polyps of the West Coast of America. Transactions of the Connecticut Academy of Arts and Sciences (2<sup>nd</sup> edn) 1(2): 377–422.
- Verrill AE (1868c) Critical remarks on halcyonoid polyps in the museum of Yale College, with descriptions of new genera. American Journal of Science and Arts 45: 411–415.
- Verrill AE (1869) Notes on Radiata in the Museum of Yale College. No. 6. Review of the corals and polyps of the West Coast of America. Transactions of the Connecticut Academy of Arts and Sciences (2<sup>nd</sup> edn) 1(2): 423–502.
- Verrill AE (1878) Description of a new species of *Paragorgia* from Jervis Inlet, BC Canadian Naturalist and Quarterly Journal of Science: with proceedings of the Natural History Society of Montreal 8(8): 476. www.biodiversitylibrary.org/bibliography/7534#summary
- Verrill AE (1879a) Notice of recent additions to the marine Invertebrata of the northeastern coast of America, with descriptions of new genera and species and critical remarks on others. Part I – Annelida, Gephyraea, Nemertina, Nematoda, Polyzoa, Tunicata, Mollusca, Anthozoa, Echinodermata, Porifera. Proceedings of the United States National Museum 2: 165–226. https://doi.org/10.5479/si.00963801.76.165

- Verrill AE (1879b) Preliminary check-list of the marine invertebrates of the Atlantic coast, from Cape Cod to the Gulf of Saint Lawrence. Prepared for the United States Commission of Fish and Fisheries, 1–32.
- Verrill AE (1883) Report on the Anthozoa, and on some additional species dredged by the 'Blake' in 1877–1879, and by the US Fish Commission steamer 'Fish Hawk' in 1880–82. Bulletin of the Museum of Comparative Zoology, Harvard 11: 1–72. [pls 1–8] https:// biodiversitylibrary.org/page/4621758
- Verrill AE (1922) The Alcyonaria of the Canadian Arctic Expedition, 1913–1918, with a revision of some other Canadian genera and species. Report of the Canadian Arctic Expeditions 8(G): 1–164.
- Verseveldt J (1940) Studies on Octocorallia of the famillies Briareidae, Paragorgiidae and Anthothelidae. Temminckia, A Journal of Systematic Zoology 5: 1–142. [figs 1–52]
- Wainwright SA, Dillon JR (1969) On the orientation of sea fans (Genus Gorgonia). Biological Bulletin 136: 130–139. https://doi.org/10.2307/1539674
- Watling L, France SC, Pante E, Simpson A (2011) Biology of Deep-water octocorals. In: Lesser M (Ed.) Advances in Marine Biology, Volume 60, Elsevier, 41–122. https://doi. org/10.1016/B978-0-12-385529-9.00002-0
- West JM, Harvell CD, Walls AM (1993) Morphological plasticity in a gorgonian coral (*Briare-um asbestinum*) over a depth cline. Marine Ecology Progressive Series 94: 61–69. https://doi.org/10.3354/meps094061
- Whitelegge T (1897) The Alcyonaria of Funafuti. Part II. Memoirs of the Australian Museum 3(5): 307–320. [pls 16–17] https://doi.org/10.3853/j.0067-1967.3.1897.498
- Williams GC (1990) A new genus of dimorphic soft coral from the south-western fringe of the Indo-Pacific (Octocorallia; Alcyoniidae). Journal of Zoology, London 221: 21–35. https:// doi.org/10.1111/j.1469-7998.1990.tb03772.x
- Williams GC (2000) A new genus and species of stoloniferous octocoral. Zoologische Mededelingen, Leiden 73: 333–343. https://www.repository.naturalis.nl/record/216181
- Williams GC (2013) New taxa and revisionary systematics of alcyonacean octocorals from the Pacific Coast of North America (Cnidaria, Anthozoa). ZooKeys 283: 15–42. https://doi. org/10.3897/zookeys.283.4803
- Williams GC, Cairns SD (2001–2017) Systematic list of valid octocoral genera. http://researcharchive.calacademy.org/research/izg/OCTOCLASS.htm
- Wood HI, Spicer JI, Widdicombe S (2008) Ocean acidification may increase calcification rates, but at a cost. Proceedings Biological Sciences 275: 1767–1773. https://doi.org/10.1098/ rspb.2008.0343
- Wright EP, Studer T (1889) Report of the Alcyonaria collected by HMS 'Challenger' during the years 1873–1876. Challenger Reports: Zoology 31(64): 1–314. [pls 1–43] https:// biodiversitylibrary.org/page/12701689
- Yilmaz A, De Lange G, Dupont S (2008) Impact of Acidification on Biological, Chemical and Physical Systems in the Mediterranean and Black Sea Mediterranean. Mediterranean Science Committee (CIESM), Monograph Series 36: 124.
- Ziveri P (2012) Research turns to acidification and warming in the Mediterranean Sea, IM-BER (Integrated Marine Biogeochemistry and Ecosystem Research). Newsletter, Issue 20, May 2012.

# Appendix I

## List of material examined - Part I

(Material examined = whole colony study plus multiple sclerite preparations; all with light microscopy, plus selected colonies under SEM, shown in figures associated with text)

# Anthothela argentea Studer, 1894

Material examined. No specimens in SBMNH collection.

**Other material, not examined.** – ±1 colony; USA, off California coast, west of Channel Islands, Fieberling Guyot, 32°27'36"N, 127°47'36"W, 490 m; coll. R/V 'Alvin', 10 October 1990; USNM 94428 [wet].

# Anthothela pacifica (Kükenthal, 1913)

**Material examined.** 1 lot **USA, California** – 1 colony; San Diego County, edge of ridge running through Rodriquez Seamount, slightly northwest of West Cortes Basin, due west of southern tip, San Clemente Island, on sponge, 32°37'43"N, 120°05'04"W, 950–1150 m; coll. skipper of vessel 'Calafia' (California Department of Fish and Game – Long Beach, California), 9 August 1978; SBMNH 265939 [wet].

**Other material examined.** – ±1 colony; USA, California, San Diego County, San Diego, Point Loma, ~32°40'38"N, 117°15'08"W, 201–262 m; coll. R/V 'Albatross', 4 March 1904; USNM 49519 [wet]. (Additional label in jar indicated "*Anthothela argentea*.")

# Paragorgia arborea var. pacifica (Verrill, 1922)

**Material examined.** ~2 lots **USA, California** – 1 branch fragment; Orange County, San Clemente Island, between Pete Bay, 3–10 miles E X (N+S) of island, ~32°55'48"N, 118°24'19"W, 1000 m; coll. unknown, 19 July 1978; SBMNH 422977 [wet]. –2 branch fragments; California, Monterey County, Monterey Bay, 5.8 miles, 314° T from Point Pinos Light to Mid Point, 36°43'00"N, 122°01'45"W, 436–809 m; coll. R/V 'Velero IV', stations 7462-61 or 7463-61, 10 October 1961; SBMNH 422976 [wet].

**Other material examined.** – 1 colony/fragment; USA, California, Ventura County, off San Nicolas Island, (from fishermen's net); coll. unknown, March 1985; donated by R Williams, of "The Sea;" CBA #85.14.2 [dry]. -- USA, California, Monterey County, Davidson Seamount, 1,313 m; coll. unknown, 2003; USNM 1014919 [wet].

## Paragorgia regalis Nutting, 1912

Material examined. No apparent material in SBMNH collection.

**Other material examined.** – 1 colony fragment; USA, California, Santa Barbara County, west of San Miguel Passage on Rodriquez Seamount, 33°57'12"N, 121°08'41"W, 1,840 m; coll. unknown, 14 October 2003; USNM 1027063 [wet].

### Paragorgia stephencairnsi Sánchez, 2005

Material examined. No material in SBMNH collection.

**Other material examined.** – 1 colony; USA, California, west of California Channel Islands, Fieberling Guyot, 36°26'00"N, 127°47'36"W, 490 m; coll. DS/V 'Alvin', 16 October 1990; USNM 94437 (**Paratype**) [wet].

#### Paragorgia yutlinux Sánchez, 2005

Material examined. No material in SBMNH collection.

**Other material examined.** – 1 colony; USA, California, west of the California Channel Islands, Fieberling Guyot, from summit of seamount, 32°26'00"N, 127°47'42"W, 487 m; coll. DS/V 'Alvin', 21 October 1990; USNM 90345 [wet].

#### Sibogagorgia californica sp. nov.

Material examined. -6 lots USA, California - 1 branch fragment; Los Angeles County, Santa Catalina Island, 7 miles WSW of Church Rock, substrate loose rock, 33°14'40"N, 118°11'10"W, 276-282 m; coll. R/V 'Velero III', station 1323-41, 18 May 1941; SBMNH 422971 [wet]. -1 branch fragment; Los Angeles County, 5.5 SE of Santa Catalina Island, on boulders and gravel, 33°15'30"N, 118°12'50"W, 264–273 m; coll. R/V 'Velero III', station 1172-40, 20 August 1940; SBMNH 422972 [wet]. -1 branch fragment; Los Angeles County, Santa Catalina Island, 6.25 miles NE or E.NE X E of Long Point, with rocks, sponges, cyclostomes, 33°25'20"N, 118°14'40"W, 415– 486 m; coll. R/V 'Velero III', station 1400-41, 8 September 1941; SBMNH 422973 [wet]. -1-2 branch fragments; Los Angeles County, Santa Catalina Island, 5.7 miles, 123° T to West End, 33°30'55"N, 118°43'15"W, 300 m; coll. R/V 'Velero IV', station 24471-76, 8 March 1976; SBMNH 422974 [wet]. -multiple branch fragments; Los Angeles County, Santa Barbara Island, 6.7 miles, 330° T from N Light, dredge, tangles (2 large boulders with much small rock, rock bottom), 33°33'27"N, 119°04'00"W, 255 m; coll. R/V 'Velero IV', station 2062-51, 18 October 1951; SBMNH 422975 [wet]. USA, Oregon – multiple branches; Lincoln County, 55.98 miles W of coast, 44°33'30"N, 125°12'42"W, 1600 m; coll. "Oregon State University-R/V 'Yaquina', Cruise Y6810C," 15 October 1968; SBMNH 422978 [wet]. -1 large colony; off coast, 46°06'22"N, 124°55'03"W, 1123 m; coll. Astoria RB-01-05, G Hendler, RV 'Ronald H. Brown' (NOAA) and S/V 'Ropos', Dive R602-Bio-0008, 3 July 2001; LACoMNH Marine Biodiversity Center #374 [wet].

### Hemicorallium ducale (Bayer, 1955)

**Material examined.** One lot (possibly this species). **USA, California** – 2 colonies + fragments; USA, California, Los Angeles County, Catalina Basin, N of San Clemente Island, 33°04'49"N, 118°29'52"W, 1,091 m; coll. P Gregory, California Fish and Game, Long Beach, 15 November 1977; SBMNH 471940 [wet].

**Other material examined.** – 1 colony; USA, California, West of Channel Islands, Fieberling Guyot, "Sea Pen Rim," 32°27'36"N, 127°49'30"W, 640 m; coll. DS/V 'Alvin', 14 October 1990; USNM 94459 [wet].

# Hemicorallium imperiale (Bayer, 1955)

Material examined. No material in SBMNH collection.

**Other material examined.** – multiple fragments; USA, California, Fieberling Guyot Seamount, 32°23'00"N, 127°47'00"W, ~600 m; coll. unknown, August 1989; USNM 85082 [wet].

# Hemicorallium regale (Bayer, 1956)

## Material examined. No material in SBMNH collection.

**Other material examined.** –1 colony; USA, California, Davidson Seamount; 1,482 m; coll. unknown, 2003; USNM 1014918 [wet]. –fragment; USA, California, west of Channel Islands, Fieberling Guyot, 32°27'36"N, 127°49'30"W, 640 m; coll. DS/V 'Alvin', 7 December 1990; USNM 94460 [wet].

# Acanthogorgia gracillima var. typica Kükenthal, 1909 (? A. gracillima var. lata Kükenthal, 1909)

**Material examined.** 1 lot **USA, California** – 1 colony; California, Ventura County, Channel Islands, 33°57'35"N, 119°28'34"W, 160 m; coll. M Love from submersible 'Delta', 8 October, 2005; with his number: A6662; SBMNH 423074 [wet].

**Other material examined.** – 1 fragment (multiple colonies); USA, northern Pacific Ocean, Hawaii, Cross Seamount, 18°43'55"N, 158°15'41"W, 388.56 m; coll. Smith, 10 October 2004; USNM 1071429 [dry]. –1 colony; USA, northern Pacific Ocean, Hawaii, Cross Seamount, 18°41'17"N, 158°17'58"W, 477 m; coll. RB Moffitt and EH Chave, 6 February 2003; USNM 1014741 [dry]. –multiple colonies; USA, northern Pacific Ocean, Hawaii, Necker Island, Seamount east of island, 23°13'55"N, 163°31'07"W, 1720 m; coll. A Baco-Taylor, 1 November 2003; USNM 1072361 [wet]. –(?) multiple colonies; USA, northern Pacific Ocean, Hawaii, Pioneer Bank, 25°34'27"N, 173°30'22"W, 1,743.7 m; coll. A Baco-Taylor, 9 October 2003; USNM 1072344 [wet].

## Acanthogorgia species A (= ? Acalycigorgia)

**Material examined.** 1 lot **USA, California** – 2 colonies; Monterey County, Monterey Bay, from Point Piños Light to Mid Point, ~36°41'36"N, 122°01'51"W, 439–814 m; coll. R/V 'Velero IV', stations 7462-61 or 7463-61, 10 October 1961; SBMNH 423075 [wet].

Other material examined. – 1 colony; USA, California, off San Francisco, Mulberry Seamount, ~37°26'48"N, 123°23'22"W, 1,255–1,455 m.; coll. N/B 'Scofield',

location 38, 13 February 1950; CAS-IZ 96671 [wet]. --1 colony; USA, Alaska, Aleutian Islands, Adak Canyon, ~51°23'29"N, 177°07'38"W, 1,728 m; coll. R Stone using ROV 'Jason II', project ID # J2098-4-4, 29 July 2004; [dry].

## Muricella complanata Wright & Studer, 1889

Material examined. No confirmed identification of material in SBMNH collection.

**Other material examined** (Identification not confirmed). – 1 colony; USA, California, Santa Barbara County, Santa Barbara Channel, ~12 south of Santa Barbara, midway between Santa Barbara city and Santa Cruz island, oil platform (settling plates), ~34°13'39"N, 119°41'12"W, ~182 m; coll. MMS III Voucher, Survey, settling plates (incidental), station: exploratory wellsite Lease Number 0522, 6 February 1994; #0001942 [wet]. --2 colonies (2 lots); USA, California, Monterey County, Monterey Bay, Point Piños Light House, bearing S 3 degrees: distant 9.3 miles, ~36°46'14"N, 121°55'23"W, 518–649 m; coll. R/V 'Albatross', California Coastal Cruise 1904, Station #4461, 12 May 1904; CAS-IZ #s 5310 and 96669 [wet].


# A review of gorgonian coral species (Cnidaria, Octocorallia, Alcyonacea) held in the Santa Barbara Museum of Natural History research collection: focus on species from Scleraxonia, Holaxonia, Calcaxonia – Part II: Species of Holaxonia, families Gorgoniidae and Plexauridae

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#### Abstract

Gorgonian coral specimens from the Holaxonia, families Gorgoniidae and Plexauridae held in the collection of the Santa Barbara Museum of Natural History (SBMNH) were reviewed and evaluated for species identification. The specimens were collected from within, and adjacent areas of, the California Bight. The SBMNH collection has encompassed within it a large percentage of specimens collected by the Allan Hancock Foundation (AHF) 'Velero' Expeditions of 1931–1941 and 1948–1985. This historic collection displays an emphasis on species belonging to the Holaxonia, particularly the gorgoniids and plexaurids; thus, this second part presents a thorough discussion of well-known genera from within the California Bight, with more extensive discussions of several genera that have historically, and currently, led to confusion (and thus, misidentification). A brief discussion of a California Bight grouping, referred to within as the "red whips," is presented; this grouping encompasses several species with very similar colony appearance across a number of genera. Two species, the gorgoniid *Leptogorgia chilensis* (Verrill, 1868) and the plexaurid *Chromoplexaura marki* (Kükenthal, 1913) each required the designation of a neotype from within the collection. A new species in the genus *Eugorgia* Verrill, 1868, a whip or thread-like form be-

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longing to the family Gorgoniidae, is described. One additional plexaurid genus (*Placogorgia*) is discussed, a genus not commonly reported for the California Bight region. This is the first comprehensive work, in three parts, focusing on all species of gorgonian coral known to inhabit the California Bight. This paper, Part II of the full work, continues the systematic review of all species represented in the Santa Barbara Museum of Natural History research collection begun in Part I.

#### **Keywords**

Allan Hancock Foundation (AHF) – 'Velero' Expeditions, cryptic species, local endemics, museum collection, new *Eugorgia* species, *Placogorgia*, "red whips", soft corals, "thread-like" forms

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# Introduction

As defined in Part I of this work, the term gorgonian used in this paper refers to those alcyonacean octocorals belonging to the groups Scleraxonia, Holaxonia and Calcaxonia. These organisms are modular colonies, usually extensively branched, displaying a stiff central, internal axis (composed of calcite and gorgonin), in both main stem and all branches, composed of either fused sclerites, or sclerites composed of scleroproteinous gorgonin. The entire axial skeleton is covered with soft tissue coenenchyme filled with numerous calcareous sclerites, either embedded in it or lying on its surface. The supporting axial skeleton allows for colonies to achieve large size (some species) and allows for the display of both highly branched colonies, known as sea fans, as well as long, slender forms known as sea whips.

The gorgonian Holaxonia are the most numerous of the gorgonian corals found in the Santa Barbara Museum of Natural History's (SBMNH) research collection. While a fair number of specimens, representing the families Gorgoniidae and Plexauridae were already present, with the acquisition of gorgonian materials from the Allan Hancock Foundation 'Velero' Expeditions, the holdings within the collection were greatly enhanced. Many of the specimens not only needed rebottling, but extensive work had to be done to identify (or to correct identification of), not only the specimens that were already in the collection, but the many specimens collected during the 'Velero' years of operation. As many of the genera in these two families have been thoroughly reviewed elsewhere (Breedy and Guzmán 2007, 2016, 2018, Breedy et al. 2009), I am providing only brief descriptions for most. More problematic genera, or genera and species that have not been well studied, are given more extensive coverage and discussion. Not all of the Holaxonia holdings in the SBMNH collection are covered here. Part III of this review will cover two of the genera that were most in need of work and required more thorough discussion.

# Materials and methods

Nearly all of the specimens examined in this work (housed currently as part of the Santa Barbara Museum of Natural History's permanent research collection, Invertebrate Laboratory), were collected over a period of years dating from the 1930s to the present, in either dry or wet condition. A large percentage of these specimens came to the SBMNH through a diverse 10,000-lot cnidarian collection, a portion of the Allan Hancock Foundation (AHF) collection built upon the historic 'Velero' expeditions of 1931–1941 and 1948–1985. Not only are gorgonian specimens housed in the cnidar-ian section of the entire invertebrate collection, but there are gorgonians housed elsewhere within the collection; for instance, gorgonian coral fragments are housed in the museum's mollusk collection (the mollusks in question were found on, and collected with, a species of gorgonian), or in other sections of the museum's cnidarian collection (such as zoanthid anemones collected on gorgonian corals). Scattered throughout other portions of the museum's invertebrate collection are bryozoans, barnacles, or brittle stars that were collected from within or on gorgonian coral colonies and were preserved with the gorgonian they were living with. To assist with the identification of the SBM-NH specimens, examinations of specimens of known species from or collected in the Bight were performed on material found in the collections of the National Museum of Natural History, Smithsonian (**USNM** = NMNH), the California Academy of Sciences, San Francisco (**CAS**), the Los Angeles County Museum of Natural History (**LA-CoMNH**), Scripps Institute of Oceanography (**SIO**), the Monterey Bay Aquarium Research Institute (**MBARI**), Moss Landing Marine Laboratories (**MLML**) and the small museum which is a part of the Cabrillo Marine Aquarium in San Pedro, California (**CMA**) (see Appendix 1: List of material examined). These were compared to SBMNH specimens, informing the identification of species represented in the SBMNH collection. Additionally, several National Oceanographic and Atmospheric Administration (NOAA) offices throughout the country provided further material for study.

All specimens were examined for gross colony morphology; more importantly, examination of the calcareous sclerites, present in different parts of the colony, was conducted for nearly all specimens. The standard method for sclerite extraction (tissue sample in common household bleach) was performed, and light microscopy via a compound Olympus (CH) microscope, was used initially to determine the genus to which a specimen belonged. Scanning Electron Microscopy (SEM) of the sclerites was then undertaken. All samples were coated with gold, using a Cressington Sputter Coater Unit, 108auto. Samples were examined and digital images taken, using a Zeiss Scanning Electron Microscope EVO 40, at 10 kV. This second part covers some fourteen species, classified as holaxonians belonging to the families Gorgoniidae and Plexauridae. A summative overview of species housed in the SBMNH research collection, from these specific groups, is included below.

This information regarding species and lots of specimens examined for Part II for colony morphology and sclerites (either through light microscopy or SEM) is a sum-

Part II: Collective specimen and species data.

# of specimens analyzed with sclerite preparations	~260
# of specimens examined without sclerite preparation	0
Breakdown of specimens examined:	
# of specimens analyzed from SBMNH collection	~184
# of specimens analyzed from USNM-Smithsonian	19
# of specimens analyzed from CAS	13
# of specimens analyzed from other institutions	54
Total # of species that received sclerite observations	14
# of new species described	1
Breakdown of species examined:	
# of species from the SBMNH collection	14
# of species from USNM-Smithsonian	7
# of species from CAS	3
# of species from other sources	10
# of species shown in Figures (colony)	13
# of species shown in Figures (either light microscopy and/or SEM of sclerites)	14

	SBMNH	Other institutions	Colony figure	Sclerite figure
Adelogorgia phyllosclera	Yes	Yes	Yes	Yes
Eugorgia daniana	Yes	Yes	Yes	Yes
Eugorgia rubens	Yes	Yes	Yes	Yes
Eugorgia ljubenkovia sp. nov.	Yes	Yes	Yes	Yes
Leptogorgia chilensis	Yes	Yes	Yes	Yes
Leptogorgia diffusa	Yes	Yes	Yes	Yes
Leptogorgia filicrispa	Yes	Yes	Yes	Yes
Leptogorgia flexilis	Yes	Yes	Yes	Yes
<i>Leptogorgia</i> sp. A	Yes	Yes	Yes	Yes
Chromoplexaura marki	Yes	Yes	Yes	Yes
Muricea californica	Yes	Yes	Yes	Yes
Muricea plantaginea	No	Yes	No	Yes
Muricea fruticosa	Yes	Yes	Yes	Yes
<i>Placogorgia</i> sp. A	No	?	Yes	Yes

Species covered in this part.

mation of the more detailed information to be found in the Appendix 1: List of material examined – Part II. It is evident from this summative overview that the SBMNH research collection illustrates diversity and abundance of species from the holoaxonian group found within or near the California Bight.

# Systematic accounts

(Classification used throughout this paper conforms to that of Bayer 1981c)

## Diagnosis of the Order

Alcyonacea Lamouroux, 1816

(Gorgonian corals, as defined previously)

Octocorals with uniformly short gastrovascular cavities; colonies typically arborescent, rarely lobate or incrusting, producing more or less specialized three-dimensional axial skeletal structures: either a distinct central axis of horny (gorgonin) or calcareous material (or both), or a central medullar zone of calcareous sclerites which are loosely or inseparably bound together by horny or calcareous matter.

## Holaxonia Studer, 1887

With distinct central axis composed of horny material alone or of horny material more or less heavily permeated with calcareous substance, continuous or with alternating horny and calcareous joints. In center of axis is a relatively narrow, largely hollow, tubular space partitioned into series of small chambers, referred to as the cross-chambered central chord. Calcareous material of the peripheral zone of axis is in nonscleritic form (single exception in Keroeididae).

#### Key to Families represented in SBMNH collection (Holaxonia)

1	Axis horny, with a chambered, hollow, soft central chord2
_	Axis not horny, but is a solid axis, with no soft, central, hollow core
	See Calcaxonia, Part III
2	Axis purely horny, composed of scleroprotein, without any calcareous
	deposits
_	Axis horny, but some calcareous material may be present in some forms; hol-
	low, horny, soft-chambered central chord is wide; there is a peripheral zone
	of hollow, horny spaces containing calcareous material; cortex is thick, with
	an inner and outer layer, formed by systematic longitudinal canals; polyps
	retractile into prominent calyces
3	Axis perforated by a wide, cross-chambered central chord; cortex thin; polyps
	not retractile; sclerites spikey and conspicuous
_	Distinct hollow, horny, soft-chambered central chord that perforates axis is
	narrow; axial cortex surrounding the core is very dense; polyps fully retractile,
	into low calyces

## List of species

Class Anthozoa Subclass Octocorallia Haeckel, 1866 Order Alcyonacea Lamouroux, 1816 Holaxonia Studer, 1887 Family Gorgoniidae Lamouroux, 1812 Adelogorgia phyllosclera Bayer, 1958 Eugorgia daniana Verrill, 1868 Eugorgia rubens Verrill, 1868 Eugorgia ljubenkovia sp. nov. Leptogorgia chilensis (Verrill, 1868) Leptogorgia diffusa (Verrill, 1868) Leptogorgia filicrispa Horvath, 2011 Leptogorgia flexilis (Verrill, 1868) Leptogorgia species A [? = Leptogorgia tricorata Breedy & Cortés, 2011] Family Plexauridae Gray, 1859 [= Muricidae] Chromoplexaura marki (Kükenthal, 1913) Discussion concerning diversity of "red whip" forms Muricea californica Aurivillius, 1931

Muricea plantaginea (Valenciennes, 1846) = M. appressa Verrill, 1864
Muricea fruticosa Verrill, 1868
(following genus formerly part of: [Stenogorgiinae = old Paramuriceidae]
Placogorgia species A

## **Descriptions of species**

## Family Gorgoniidae Lamouroux, 1812

**Diagnosis.** Axis purely horny, composed of carbonate hydroxylapatite with narrow but distinct chambered central chord; cortex little loculated, if at all. Polyps fully retractile, some forming low calyces (polyp-mounds), scattered or biserially disposed. Axis/polyp coenenchyme moderately thick, packed with spindles and capstans with regular belts of tubercles; in certain genera modified into disc spindles, scaphoids, or unilaterally spinous forms. Anthocodial armature weak, in form of crown composed of flat rodlets with scalloped edges, or lacking entirely. Colonies of diverse form, from unbranched to pinnate, closely reticulate or foliate.

## Genus Adelogorgia Bayer, 1958

Adelogorgia Bayer, 1958: 46; 1979: 1026–1027. Breedy and Guzmán 2018: 329.

## Type species. Adelogorgia phyllosclera Bayer, 1958.

**Diagnosis.** Genus originally included in family Plexauridae (Bayer 1958). Presence of moderately thick coenenchyme; polyps communicate directly with system of longitudinal canals. Exterior coenenchyme contains derivatives of short, stout capstans called double wheels/discs; large, leaf-like expansions (on one side) up to 0.15 mm long; spindles with tubercles in transverse rows, to 0.2 mm, some developed as leaf clubs. Interior layers of coenenchyme contain only spindles. Anthocodiae weakly to moderately armed with flat rods, 0.15–0.3 mm long.

**Etymology.** *Adelo-* is Greek for unknown. When Bayer described this genus in 1958 it was a new, unknown gorgonian genus; however, Bayer did not discuss the derivation.

# Adelogorgia phyllosclera Bayer, 1958

Figures 1, 2A, B, 3A-C

*Adelogorgia phyllosclera* Bayer, 1958: 46–47; figs 3a–f, 4a, b, 9b, c. Breedy and Guzmán 2018: 330–333.

**Type locality.** USA, California, La Jolla, South of Scripps Institution, La Jolla Canyon, 30–33 m.

**Type specimens. Holotype** USNM 50186; [dry]. **Paratypes** listed under "other material" in "Appendix 1: List of material examined" for this species.

**Material examined.** ~26 lots (see Appendix 1: List of material examined). All specimens at USNM were examined for comparison purposes.

Description. Colony (Figure 1) heavy; bushy to fan-shaped, branching strictly in single plane, particularly in young colonies ( $\leq 20$  cm height), but with branches occasionally growing irregularly as colony gets older (up to 0.6 m in height, usually less than 0.3 m); branching dichotomous, irregular and lateral, not pinnate (Figure 2A), with knobby to smooth branches. Color of live colony red or orange-red, polyps yellow to yellow-orange; axis slender, orange. Dry specimens brilliant red, rusty red, maroon-rust to black. Branches 2.0–4.5 mm in diameter, ascending into a meandering, sinuous form; terminal branches short (3.0–4.0 cm), slightly swollen at distal ends (Figure 2B). Trunk diameter measures up to ~6.0 mm. Axis in dead/dry specimens, within all branches of older part of colony, black, smooth, without conspicuous striations; in branches of younger portions of colony, maroon. Outer layer of axis abundantly loculate, texture of axis weak, flexible in terminal portion of branches, rather brittle in base area. Polyps with weak operculum, composed of two to four curved spindles in every segment, arranged en chevron; sclerites in polyps not arranged transversely, not forming collaret. Polyps able to retract down to surface or upper marginal edge of low to moderate calyces, these moderately elevated as low bumps off branch surface (0.5–0.8 mm tall, 1.2 mm across), situated some 2.0–2.5 mm distance apart, distributed over entire surface of all branches; margin of calyces not dentate. Sclerites (Figure 3) of polyps straight or curved rods, sculptured with simple conical warts, arranged en chevron, two to four sclerites at base of each tentacle. Coenenchyme spiculation in two layers; layers determined by shape of sclerites seen in each. Exterior layers of coenenchyme with stout capstans (0.1 mm), and spindles (0.2 mm); (latter more common), some less commonly present as having leaves or scales over one surface; few appear as leaf clubs. Numerous sclerites with sculpturing on one side modified into leafy projections (double-discs) as seen in Figure 3B (appear occasionally as sclerites analogous to disc-spindles of Eugorgia); in many cases, sclerites (0.1-0.15 mm) strongly characteristic of this form; proportion of leafy sclerites to ordinary ones in outer layer of coenenchyme varies only slightly. Ordinary ones are most abundant, while leafy ones, though sometimes rare, are always present. Axial sheath (interior layer of coenenchyme) contains symmetrical spindles (0.16 mm) only; no capstans, clubs or leafy scales. Sclerites of outer layer red; of inner layer nearly colorless.

**Etymology.** The root *phyllo-* (Greek) = leaf; *sclero-* (Greek) = hard scale. Species is unusual in the leafy appearance of one sclerite type, a key characteristic in identifying the species. However, Bayer gave no explanation for either genus or species names.

**Common name.** Chuck's gorgonian; Orange gorgonian; Shady-leafed gorgonian; Hard-leaved gorgonian; Hidden gorgon (these names appear in a variety of field/diving guides for the area such as Gotshall 2005, Kerstitch and Bertsch 2007).

**Distribution.** Based on collection location data, from Upper Baja, California to southern California. Generally known from La Jolla area of southern California. One specimen from Catalina Island, Bird Rock, SBMNH 51252 (one of several from Santa Catalina Island), indicates this species does range a bit north of La Jolla, California.



Figure 1. Adelogorgia phyllosclera, SBMNH 51252. Colony measures 16.5 cm × 15.0 cm.

**Biology.** Commonly encountered in southern California in kelp beds; depth range of 20–300 m (Gotshall 2005). An anecdotal note (J Ljubenkov, penciled notation on a species list) stated: "*Adelogorgia phyllosclera* is a deep water form; it is a major deep water gorgonian and replaces *Muricea* on sewage pipes" (verified by staff of LACSD and OCSD). Two specimens, USNM 50186 and SBMNH 422894 (Point Loma),

support numerous epizootic anemones (perhaps *Epizoanthus* Gray, 1867). On others, a flat, grayish incrustation (perhaps bryozoan) can be seen. Some balanoid barnacles are present over the surface of some specimens examined, in the form of prominent cysts ("galls") on the branches, which protrude out from the axis through a coenenchymal covering. One specimen (SBMNH 422893) harbors a small brittle star, wrapped around a portion of the main trunk. No zooxanthellae present in the tissues, particularly true of USNM 50186; specimen examined for their presence by Bayer.

**Remarks.** Among the eight to ten specimens that Bayer examined in 1958, there appeared to be three main areas that showed variation: thickness of branches, development (size) of the calyces (if present), and proportions of different sclerite forms (those with leafy sculpturing as compared to common spindles/capstans) (Bayer unpublished ms 7, Cairns 2009). Specimens at SBMNH do illustrate variation in branch diameter. Terminal branches range in diameter from 2.0–4.5 mm. Branches with smallest diameter have very distinct, prominent calyces, arising conically from their base, but thicker branches have less conspicuously prominent calyces, actually coenenchymal mounds appearing as low bumps; polyps fold into simple openings that appear as pores. One specimen at NMNH, USNM 50187, is of an extreme form; some of the branches are quite slim, bearing very pronounced calyces. It became clear that similar variations were not of taxonomic significance. Other more slender specimens exhibit a wide range of variation in branch diameter.

Most field/diving guides imply that this species is fairly contained within, and to, the region of La Jolla, California. Several of the SBMNH specimens argue against this; it appears that this particular species ranges a bit further south (upper/lower Baja) than had been previously reported. Three lots examined and confirmed correct as to their genus identification (at least) implied either: 1) a range that extends further south and/or 2) the presence of several other species, including Adelogorgia telones Bayer, 1979, and one or more of the species recently described by Breedy and Guzmán (2018), in the collection. As to potential range of distribution, Bayer (1979) made the following comment in his description of A. telones: "Although it (A. phyllosclera) seem(ed) to be rather common in the vicinity of La Jolla, collections made farther to the south, in Baja California, by the same team of divers, (did) not include it (A. phyllosclera). Neither does it occur in other collections from Baja California and the Gulf of California taken by diving or dredging, nor in collections obtained by the US Fish Commission steamer 'Albatross' by dredging and trawling at many localities along the coast of Central America and South America". There are, however, several specimens in the SBMNH collection taken from northern Baja California that clearly appeared to be this species (see Appendix 1: List of material examined). Further sightings/collections would help to confirm this species' total range (where it may either transition to A. telones, or other recently discovered species, or has a definite southern limit, with A. telones and other species then appearing some distance further south). In the examination of specimens from California locations, and those from the Galápagos Islands, in the SBMNH collection, the distinctive differences that would separate species were not clear; all specimens, with one exception (completely bleached, SBMNH 422891 from Santa Cruz Island, Galápagos Islands), are the distinctive red color of this species. A. telones, by contrast, is typically either yellow or white (Bayer 1979, Breedy and Guzmán 2018). Bayer (1979) stated that, in a comparison



**Figure 2.** *Adelogorgia phyllosclera*. **A** SBMNH 422403 [dry], slightly magnified image of branches **B** SBMNH 51252 [wet], rounded, slightly club-shaped branch tips.

of the two species, *A. phyllosclera* has: 1) branching that is more crooked and open, 2) polyps that form distinctly hemispherical or blunt-conical calyces (as opposed to calyces being inconspicuous or not really present at all), and 3) sclerites somewhat larger, with double wheels/discs somewhat different in shape along with being more elaborately sculptured. Based on the coloring of specimens (with one exception) in the SBMNH



**Figure 3.** *Adelogorgia phyllosclera*, SBMNH 51252, SEM image. Sclerites red-orange in color. **A** Short warted spindles (middle and right, potentially anthocodial sclerites) **B** Characteristic "leaf scale" sclerites **C** Warted coenenchymal spindles. Compare leaf scales shown here to those seen in Bayer 1979 (figs 5c, 6c).

collection, along with Bayer's (1958) discussion of variation in characters within this species, there are unanswered questions regarding distribution of this species and the potential for several other species, as represented in the SBMNH collection. Both *A. phyllosclera* and *A. telones* are accepted species in the WoRMS Data Base (Cordeiro et al. 2018a), along with three others.

#### Genus Eugorgia Verrill, 1868

Lophogorgia (pars) Horn, 1860: 233.
Gorgonia (pars) Verrill, 1864: 33; 1866: 327.
Leptogorgia Verrill, 1864: 32.
Eugorgia (pars) Verrill, 1868c: 414.
Eugorgia Verrill, 1868b: 406–407. Studer 1887: 64–65. Bielschowsky 1918: 39. Kükenthal 1924: 343. Bielschowsky 1929: 170. Stiasny 1951: 63. Bayer 1951: 99; 1981: 921. Breedy et al. 2009: 8.

Type species. *Leptogorgia ampla* Verrill, 1864; by subsequent designation Verrill 1868b: 386.

**Diagnosis.** Breedy et al. (2009) did a thorough review of this genus (well represented in the SBMNH collection). Sclerites chiefly disc spindles, capstans or double discs (wheels); double discs up to 0.05 mm long, spindles 0.12–0.18 mm, not developed as clubs; ordinary spindles present in small numbers in some species. Anthocodiae unarmed; sclerites, if present, flat rods and platelets with lobed margins. Polyps fully retractile into coenenchyme, slightly raised to prominent mounds, forming polyp-mounds, in longitudinal rows; often evenly distributed on all sides of branches. Branching is lateral, dichotomous (partial) or pinnate-like, in one plane; if bushy, branches in multiple planes; no anastomoses. Axis contains network of frequently mineralized organic filaments. Colony colors quite variable, depending on species.

#### Eugorgia daniana Verrill, 1868

Figures 4, 5, 6, 7

*Eugorgia daniana* Verrill, 1868a; 1868b [1869]: 409–410; pl V, fig. 14; pl VI, fig. 7. Bielschowsky 1918: 45. Kükenthal 1924: 346. Bielschowsky 1929: 181. Stiasny 1951: 65. Prahl et al. 1986: 17. Breedy et al. 2009: 17–20.

Type locality. Central America: Pearl Islands; Costa Rica, Gulf of Nicoya.

Type specimens. Syntype series (Breedy et al. 2009): MCZ 723 [dry]; MCZ 7080 [dry]; YPM 1551a-d and 1629a, b [dry]; YPM 5146 [dry].

**Material examined.** ~10 lots (see Appendix 1: List of material examined). Was unable to examine the type specimens, but utilized descriptions and images noted in Breedy et al. (2009).

**Description.** Collection lot examined, shown in Figures 4 (whole colony), 5 (branch magnified to show prominent polyps), 6 and 7 (sclerites, light microscopy and SEM, respectively), generally matches description given in Breedy et al. (2009: 17–20, 35). Color of branches tended generally to dark orangey-red, with coenenchyme base of polyp-mounds red, upper portion of polyp-mounds gold-orange; overall impression is that colony is basically red. Sclerites (Figure 6) either bright to deep red or yellow-



**Figure 4.** *Eugorgia danianae*, SBMNH 422897. Shows complex branching that creates wide, flat fan. Colony is 24 cm high × 25.5 cm broad at widest point.

green in color, mixed together. In some instances an individual sclerite can be bicolored (red at one end, other end yellow-green); sclerites as double discs, relatively large; inner wheels thin, with sharp edges, outer ones terminal, not half as large, also sharp-edged (Figure 7A) (see remarks below).

Common name. Red gorgonian (Gotshall 1998).

**Distribution.** As recorded by Verrill (1868a and 1868b [1869]) found in Panama and the Pearl Islands, 11–15 m (this according to FH Bradley); also seen in the Gulf of Nicoya, Costa Rica (JA McNiel). Other notations indicated that it could extend down to Peru (see Breedy et al. 2009: table 4 for full, known distributional range). Based on one specimen, USNM, 57302, taken in Escondido Bay, near San Diego County, San Diego, California, the overall range would extend from San Diego, California (at least), through Central America, possibly down to South America. Assuming *E. daniana* is a distinct species, it is then present in Central and Lower Gulf of California, living in the same area with *Eugorgia aurantiaca* Horn, 1860. Thus, southern-most end of the California Bight may be the northern-most limit (and as a separate species, *E. daniana* extends just a bit further north and further south than *E. aurantiaca*).



Figure 5. Eugorgia danianae, SBMNH 422897. Close-up of pinnate branching pattern.

**Biology.** Generally found on offshore reefs and islands; prefers clean, planktonrich waters and generally found at depths to ~30 m (Gotshall 1998).

**Remarks.** While description generally matches that given in Breedy et al. (2009), I would make the following caveats: first, the colony color as described by Verrill was as a bright yellow, streaked and blotched with dark red on both branches and polyps. The color seen in specimens here lies somewhat intermediate to that described in Olvera et al. (2018) for *E. aurantiaca* and *E. daniana*; overall, dark orange-red. Divers have anecdotally described the living colony as having slender red branches, with white (colorless) polyps.

For Verrill (1868b [1869]: 411), "In the mode of branching, the size and structure of the branchlets, and color (*E. aurantiaca*) closely resembles (*E. daniana*)," which he separated primarily on the basis of the very different size and form of the sclerites, especially of the double discs; for Verrill, these were the defining feature in designating this species as distinct from *E. aurantiaca*. In my examinations, the larger, "sharp" double discs were always present (distinctive of *E. daniana*). However, in a few specimens used for comparison, labeled as *E. aurantiaca*, the presence of sharper double discs was noted (misidentified specimens?); this condition was contrary to the generally slightly smaller size of the double discs that are commonly seen in *E. aurantiaca*, where discs are described as being generally rounded, inner and outer discs very close together. In subsequent comparisons, the polyps were not always so densely packed in *E. daniana* as was seen in *E. aurantiaca* (no overlapping of polyps). With regards to branching pattern, specimens of *E. aurantiaca* often had a far more distinctive (and decidedly sym-



**Figure 6.** *Eugorgia danianae*, SBMNH 422897, light microscopy array, 10× magnification. Note jagged, sharp-edged, double discs and color variety. Sclerites will appear orangey-yellow collectively but individuals can be deep, bright red, yellow-green, or bicolored, with a maximum length up to ~100 µm.

metrical) pattern of pinnate branching, with majority of secondary branches (branchlets) of similar length, all generally lying in one plane as compared to that seen in *E. daniana*. SBMNH specimens of *E. daniana* nearly always had their terminal-most, thin, slender branchlets curving out of one plane. Without molecular investigation, there is no clear, definitive confirmation that *Eugorgia aurantiaca* and *Eugorgia daniana* are indeed separate species. There are many overlapping features, in terms of potential branch pattern, form, and size of sclerites, and general color. The differences could be accounted for as variation within one species. However, examination of numerous examples of both those identified as *E. aurantiaca* and *E. daniana* allowed for observation of the differences in the double discs that Verrill used to distinguish these two species (differences can be obvious). For now, it seems appropriate to recognize two separate species until further studies prove otherwise.

Of note is that WoRMS Data Base (Cordeiro et al. 2018b) does list *E. aurantiaca* and *E. daniana* as separate species, but that *E. daniana* has been accepted as *Leptogorgia daniana*. Very few species of *Leptogorgia* (*L. ramulus* Milne Edwards & Haime, 1857, is one of few) display the shorter branch lengths seen consistently in species of *Eugorgia* nor the irregular and pinnate branching of the *Eugorgia*, which are morphological characters; it is understood that this acceptance is based on the molecular work that



**Figure 7.** *Eugorgia danianae*, SBMNH 422897, SEM image. Representative sclerite of each form. **A** Double-disc **B** Coenenchymal sclerite **C** Anthocodial sclerite. Images here compare well with those shown in Breedy et al. 2009 (fig. 8).

was done by Soler-Hurtado et al. (2017). Of note is the rationale for this genus change, with Soler-Hurtado et al. (2017) noting the 1999 ICZN Principle of Priority (Article 23). In the work of Olvera et al. (2018), this species is listed as a species of *Eugorgia* and is not included in the list of *Leptogorgia* species that are discussed.

# Eugorgia rubens Verrill, 1868

Figures 8, 9, 10A–D

*Eugorgia rubens* Verrill, 1868b [1869]: 411 [not figured]. Studer 1894: 69. Bielschowsky 1918: 45.

Kükenthal 1924: 346. Bielschowsky 1929: 183. Breedy et al. 2009: 29-31.

**Type locality.** SE Pacific Ocean, South America, Peru, Piura Dept., Paita. The type locality is often incorrectly spelled as Payta.

Type specimens. Type-YPM 1779 [dry]; MCZ 36047 (slide of holotype).



**Figure 8.** *Eugorgia rubens*, SBMNH 422900. Colony 45 cm tall, 18 cm across (through broadest, middle section). Scale bar: 2 cm.



Figure 9. Eugorgia rubens, SBMNH 45562. Magnified, showing branching and extended polyps.

**Material examined.** ~ 50 lots (see Appendix 1: List of material examined). Was unable to examine the type specimen, but examined many others at NMNH, CAS, etc.; this is easily recognizable and comparison to type was not necessary.

**Description.** In general, all SBMNH material (along with supplemental lots) examined falls in line with the description and images provided for this species by Breedy et al. (2009: 5–7, 29, 31, 42). Whole colony (Figure 8), branch pattern (Figure 9), and basic sclerite forms (Figure 10) demonstrate the identifiable characteristics for the species.

**Etymology.** *Rube-* is the Latin for red, or reddish, presumably in reference to this species' color. However, there is no explanation for species name given by Verrill.

**Common name.** Purple gorgonian (Gotshall 1994); Purple sea fan; Reddish true gorgon. Common name not specified in Cairns et al. (1991; 2003).

**Distribution.** From southeastern Pacific Ocean (type locality: Peru [Paita]), to southern and central California (Santa Barbara mainland and Channel Islands). Depth range from shallow subtidal to deeper than 100 meters. An extensive number of specimens were examined; collection location data shows geographic and depth ranges.

**Biology.** Found at depths usually greater than 10–30 m. Work by Lissner and Dorsey (1986) showed a range of depth for this species along Tanner and Cortes Banks and the Santa Rosa-Cortes Ridge off of southern California as follows: At depths < 49 meters, the species was sparse, at depths ranging from 49–79 meters, the species was very abundant to abundant, from 79–91 meters the species was commonly seen, and at depths below 91 meters was again sparse. In e-mail correspondence with C Bauder (and subsequently T Laidig at NOAA, December 2010), this species may actually



**Figure 10.** *Eugorgia rubens*, SBMNH 45562, SEM image. Color of sclerites purple. Representative sclerite of each form. **A** Anthocodial sclerites **B** Anthocodial sclerite or small sclerite of coenenchyme **C** Coenenchymal spindles **D** Double disc spindles. Images here compare well with those shown in Breedy, et al. 2009 (fig. 15).

occur at depths greater than originally thought, extending much further north than previously reported (the specimen that called attention to this greater depth was photographed by C Bauder at Point Lobos, Carmel Bay, at 66.5 m). A thorough examination of specimens taken from these greater depths at this, and other more northerly locations, should be done. From a list found in Museum records, depth ranges for this species from selected California sites (south to north) are as follows: **Mainland:** Tijuana River: 36 m; Point Loma: 21–42 m; La Jolla: 20–64 m; San Pedro: 17–33 m; Carpinteria: 36 m; **Islands and Seamounts:** Coronados Islands: 39 m; San Clemente Island: 9–20 m; also common around the San Benito Islands off Baja, California.

Several dry specimens examined showed the presence of distinct galls produced by a species of acorn barnacle, projecting out through the coenenchyme. One of the wet specimens examined had a pronounced mass of red algae, with sponge, hydroids, worm tubes, etc. On another wet specimen, white scaly-looking patches were present, one patch so dense it looked like a cushion. On both of these wet specimens, the masses of growth were generally only present on areas of the colony where the axis was fully exposed. There is also evidence of the presence of ovulid snails from the Genus *Simnia* (*Neosimnia*) Risso, 1826 (species *S. barbarensis* Dall, 1892 and *S. loebbekiana* Weinkauff, 1881) as well as *Simnialena rufa* (Sowerby III, 1832) in the branches of both California (Santa Barbara, East Beach, Slate Reefs, 24–27 m; 1 April 1967 and off Newport Beach, 6 m; 18 Dec. 1964) and Mexican-collected specimens (from Sonora, Guaymas, Miramar Cove, 0.9–2 m; October, 1965; however, latter of questionable species identification).

**Remarks.** Type specimen donated to YPM by FH Bradley who originally received it from Mrs George Petrie. Not recorded in early monographs on the alcyonarian fauna of California (Nutting 1909; Kükenthal 1913). While I was unable to examine the type specimen, all specimens in the SBMNH research collection are readily identifiable as this species. In truth, many of the specimens in the SBMNH collection are excellent examples of this species; examination of the type was not necessary.

NMNH has several catalogued lots in their collection with location records from the Santa Barbara Channel and the California Channel Islands (many of these identified to genus only); also several lots identified to species, collected in the area of La Jolla: Scripps Canyon, La Jolla Canyon, as well as the southern part of California and Del Mar. In addition, NMNH has several lots collected by C Limbaugh. Several of these are from the La Jolla area, but as well, from a couple of locations not previously recorded, including the Richfield Oil Island, Redondo Beach, and Rocky Point, in close proximity to Point Vicente, at the south end of Santa Monica Bay. In addition, the Cabrillo Marine Aquarium, in San Pedro, California has a few dry specimens of this species in its museum, and as well, displayed live specimens in tanks on exhibit to the public; generally, all were collected from the local area. This is a very common species in Southern California waters and is an accepted species in the WoRMS Data Base (Cordeiro et al. 2018b).

#### Eugorgia ljubenkovia sp. nov.

http://zoobank.org/48F9BA66-D012-44A5-8C8F-1EEAE2279548 Figures 11A, B, 12A, B, 13A–C

**Type locality.** Isla Cedros, Baja, Mexico.

**Type specimens. Holotype** Santa Barbara Museum of Natural History, SBM-NH 422333.

Material examined. ~5 lots (see Appendix 1: List of material examined).



**Figure 11.** *Eugorgia ljubenkovia* sp. nov., SBMNH 472232. **A** View of long, coiled specimen strands; when fully extended, longest strand length ~37 cm. Strand diameter (excluding polyp mound) ~1.0 mm **B** Magnification of branch strand, showing small, rounded polyp mounds.

**Diagnosis.** Colony an obvious whip-like form, no apparent holdfast, with minimal to no branching (not common to genus), branches fairly slender, with both branch ends pointed; sclerites double-disc spindles, with disc edges quite angular and sharp, characteristic of genus.

**Description.** Colonies (Figure 11A) incomplete, with exception of one (total strand length of complete one, 58.5 cm; length of largest colony fragment, -37 cm); diameter 1.0 mm (largest diameter up to 3.0 mm, when polyps included); few with tiny holdfast; long, thin, stiff, wiry strands, none or very few primary or secondary branches (unusual for species in this genus); what branches are present come off at right angles to main stem, then curve some five cm distant or more from branching point; branch pattern (one colony) more dichotomous or lateral. Tips of branches



**Figure 12.** *Eugorgia ljubenkovia* sp. nov., SBMNH 472232, light microscopy sclerite array. **A** 10×, showing rounded spindles and double discs. Note apparent quadriradiate, upper right **B** Sclerite array at 10×, illustrating stout, sharp-toothed double discs (seen in some species of *Eugorgia*). Sclerite color is white, but may give colony a very, very pale pink cast when in the tissue. Largest sclerites up to 100  $\mu$ m, those shorter, rounder up to 70–75  $\mu$ m.

(both ends) terminate in small arrowhead configuration. Coenenchyme very thin; axis visible through it in some areas; color of colonies generally pure white, light creamy beige to very, very pale pink, both coenenchyme and polyps; axis red-gold, with greenish cast. Small polyp mounds (no more than 1.0 mm tall, 1.0–1.5 mm broad at base) moderately prominent, rounded, conically broad bumps arranged in nearly opposite (occasionally alternate) pattern, lateral, giving strands flattened appearance from front to back (closer examination revealed polyps on all sides); very thin ridge line (longitudinal ridge) runs down middle of both "front" and "back" of branch; appears as bare "thread," slightly raised; overall, polyps give branches a distinct zig-zag edge on lateral sides. Polyps (Figure 11B) sit very close together, bases touching; greatest distance between polyps ~1.0 mm. Polyp aperture oval-shaped to thin slit, aligned with long axis of branch. Sclerites (Figures 12, 13) small; predominant type are double disc spindles (Figure 13B), with disc edges quite angular and sharp (common in species of *Eugorgia*); also, slightly longer, symmetrical spindles (more typical of species in genus *Leptogorgia*, Figure 13C) and occasionally, crosses (quadriradiates); all are colorless.

**Etymology.** Proposing *Eugorgia ljubenkovia*, to honor John Ljubenkov, a southern California cnidarian biologist, colleague and friend of many Southern California Association of Marine Invertebrate Taxonomists (SCAMIT) members.

Common name. John's wire gorgonian.

**Distribution.** Known from collection events undertaken by staff of Orange County Sanitation District and one lot taken in South Bay, Isla Cedros ('Velero IV') in 1949; thus, at this time, known from southern California and northernmost Baja, Mexico.



**Figure 13.** *Eugorgia ljubenkovia* sp. nov., SBMNH 472232, SEM image. Sclerite color is white, but may give colony a very, very pale pink cast when in tissue. **A** Anthocodial sclerites **B** Double-discs (teeth evident in most) **C** Coenenchymal spindles.

**Biology.** Moderate occurrence, indicated by OCSD collection events; not occurring at great depth (~30–35 m). Hydroids (fuzzy mass) attached to bare axis on one colony (SBMNH 472233); elsewhere on same colony, barnacle galls, barnacles completely covered with gorgonian's coenenchyme.

**Remarks.** All colonies have shape of a thin, whip-like *Leptogorgia* species, and may exhibit the same presumed lifestyle as that of Leptogorgia filicrispa Horvath, 2011 or that of species in the genus Thesea Duchassaing & Michelotti, 1860. However, sclerites most distinctive in being largely double discs, characteristic of species in the genus Eugorgia. Originally, was tentatively identified as a possible Heterogorgia Verrill, 1868c by J Ljubenkov; these specimens did not show the characteristic collaret, point and thorn sclerites of that genus (and that genus does not display distinct double discs, as seen here). Originally, SBMNH 422333 was shelved with specimens of the genus Thesea; despite the long, thinner branch strands and possible lifestyle similarity, no large spheroidal bodies, characteristic of Thesea were found. Also, this species (in five lots), is not additional material of the species L. filicrispa (Horvath, 2011), as jagged double discs are not seen in that species, and sclerites in that species can be variably colored. This species is a unique mix of colony form seen in some *Leptogorgia* with the sclerites of a Eugorgia. The long, thin wiry condition of the stems may be the result of environmental circumstances, involving both substrate (sandy or soft bottom sediment) and water flow. From examination of all specimens, it seems possible that some strands have no attachment base, but instead have terminal tips at both ends of strand. Further in situ work would need to be undertaken to document the environmental conditions under which this species lives.

## Genus Leptogorgia Milne Edwards & Haime, 1857

Gorgonia (pars) Pallas, 1766: 160. Milne Edwards and Haime 1857 (pars): 157.
Leptogorgia Milne Edwards & Haime, 1857: 163. Verrill 1864 (pars): 31, 33; 1868b: 387; 1869b: 420. Studer 1887 (in Wright): 64. Bielschowsky 1918: 18. Kükenthal 1919: 851; 1924: 324–325. Bielschowsky 1929: 81. Stiasny 1943a: 87. Bayer 1951: 98–99; 1956a: F212; 1961: 214. Grasshoff 1988: 97; 1992: 54. Williams 1992: 231. Williams and Lindo 1997: 500. Bayer 2000: 609. Breedy and Guzmán 2005: 2; 2007: 6. Horvath 2011: 46. Breedy and Cortés 2011: 63.

Lophogorgia Milne Edwards & Haime, 1857: 167. Nutting 1910c: 3, 4. Kükenthal 1924:
 322. Bielschowsky 1929: 73. Stiasny 1943: 87. Bayer 1951: 99; 1956a: F212; 1961:
 194. (Type species by monotypy: *Gorgonia palma* Pallas, 1766 [South Africa]).

Type species. Gorgonia viminalis Pallas, 1766; subsequent designation by Verrill 1868a.

**Diagnosis.** Sclerites primarily symmetrical spindles, most without unilateral fusion of warts to form discs; shorter ones may have warts on one side fused like those of disc spindles; long ones symmetrical or with warts on one side simple, conical, elsewhere complex tubercles in various arrangements (several whorls). Coenenchyme generally contains only spindles and radiate capstans with symmetrically developed tuberculation; warts/tubercles mostly in two whorls on capstans. Anthocodial armature flattened rods; sometimes, ovoid platelets. Colonies little-branched, long, slender, whip-like, or short with branching variable: pinnate, lateral or dichotomous, in one plane or bushy; color of colonies highly variable. Colonies either attached to substrate with holdfast or lying free on substrate. Axis consistent for family, containing network of organic filaments, frequently mineralized. Polyps fully retractile into coenenchyme; slightly raised, mound-like, around apertures.

**Remarks.** Bayer (1951) stated that *Leptogorgia* contains many species in temperate and tropical waters; although represented practically around the world, the center of distribution seems to be the west coast of Central America (Breedy and Guzmán 2007, Breedy and Cortés 2011, Breedy and Guzmán 2012).

#### Leptogorgia chilensis (Verrill, 1868)

Figures 14A, B, 15A–D

Plexaura rosea Philippi, 1866: 118 (junior homonym, Breedy and Guzmán 2007).

Leptogorgia rosea Phillipi, 1892: 7 (as: Verrill 1868b: 406 (nec Leptogorgia rosea Milne Edwards & Haime, 1857: 134).

(?) Litigorgia (?) rosea: Verrill 1868a; 1868b: 406. Philippi 1892: 7.

Nec Litigorgia flexilis Verrill, 1868a.

Leptogorgia (?) chilensis Verrill, 1868b: 406.

*Leptogorgia chilensis* Kükenthal, 1919: 772; 1924: 355. Bielschowsky 1929: 132. Breedy and Guzmán 2007: 22–25.

**Type locality.** Apparently, originally collected from Chile, south of Valparaiso, and off Algarrobo. For **neotype** (designated here), northeastern Pacific Ocean, North America, USA, California, Santa Barbara County, Goleta, Sands Beach, ~6 m; coll. R/V 'Vantuna' Cruise #469, November 2001.

**Type specimens.** Location of original type specimen not known. **Neotype** (here designated) SBMNH 422953 [wet].

Material examined. ~25 lots (see Appendix 1: List of material examined).

**Description.** *Colony* (Figure 14A) not reticulate; bushy, often lanky; branches spread out, in loosely subpinnate or dichotomous, irregular branching (Figure 14B) pattern; color of living colony orange-red to orangey salmon-pink. Limbaugh (unpublished key) described color as a rich salmon pink; polyps white; dry specimens pale orange to light salmon pink. Branches and branchlets very cylindrical, long, often greater than 30 mm in length, slender (2.0 mm), usually smooth and whip-like, with unbranched, pointed ends. Branches/branchlets lie roughly in one plane (not always); some branching in all directions. Colony height to 3 ft (~92 cm); usually 2 ft (~61 cm) or less. Polyps generally flush in complete retraction, forming oblong apertures, extending in all directions around the branches. Generally, several longitudinal grooves (in bare area between polyps) present. Tentacles on polyps taper at tips and bear two rows of lateral pinnules, slightly displaced to the oral side. Sclerites (Figure 15A–D) commonly spindles having acute or subacute warted ends extending beyond second



**Figure 14.** *Leptogorgia chilensis*, SBMNH 422953. **A** Colony measures 25 cm, maximum length, 13.5 cm, broadest width **B** Detail of branching pattern (branch diameter  $\leq 2.0$  mm), and gall formation created by species of barnacle, a common occurrence on this and other gorgonian species.

ring of warts on either side of median girdle; also capstans (two whorls with end tufts), modified as disk-spindles. Anthocodial sclerites small rods, thin, sparsely ornamented; sclerites generally orange in color. What is shown here (Figure 15) comparable to that shown in Breedy and Guzmán (2007: Figure 14, page 24).

**Etymology.** *Lepto-* is Greek for fine or slender; the root *chilensis-*, likely indicative of the original type locality. No discussion of the derivation of the species name was found.

**Common names.** Pink sea whip; Pink gorgonian; Red gorgonian; Common red sea whip; Chilean crested gorgon; Carmine sea spray; Violet sea spray (from a variety of field/diving guides, conversations with local divers, etc.).

**Distribution.** Several general guidebooks, including that by Gotshall and Laurent (1979), state distribution as Monterey Bay to San Benitos Islands in Baja, California. Cairns et al. (1991, 2003) did not list this species. Specimens were collected locally (Santa Barbara area, 9–22 m) for studies done by Satterlie and Case (1978, 1979) on the neurobiology of gorgonian coelenterates. NMNH has numerous lots collected from La Jolla Canyon (USNM 50179), Scripps Canyon (USNM 50191), and southern California (USNM 52442). However, examination and comparison of sclerites taken from many "red whip" forms indicated that likely range of *Leptogorgia chilensis* is



**Figure 15.** *Leptogorgia chilensis*, SBMNH 422953, SEM image. Color of sclerites is orange-red. **A** Anthocodial sclerites **B–D** Spindles of coenenchyme. Images closely match those shown in Breedy and Guzmán 2007 (fig. 14).

from Anacapa Island off the California coast (thus, from the middle of the California Bight), south, perhaps to the coast of Chile. Further discussion regarding distribution of this species can be found in the "Remarks" section of this description. That discussion may further clarify some of the confusion regarding this species of "red whip" amongst several others. Other "red whips" that extend from the middle of the California Bight northward, and overlap with *L. chilensis* in the extreme southern end of their range, may well be one or more different species (see "Discussion concerning diversity of "red whip" gorgonian forms," following description of *Chromoplexaura marki*.)

**Biology.** Gotshall and Laurent (1979) mentioned that this species likes offshore pinnacles, depths of 50 to ~200 feet (15–61 m). Another guidebook (Snyderman 1987) stated that: "Reds are very common on the Channel Islands and on offshore pinnacles as far north as Monterey." "Reds" would certainly include this species, but the term "reds" is not exclusively a reference to this species. Found at depths greater than 60 ft (18 m); at Catalina, 40 ft (12 m). Range given elsewhere as 15–60 m deep. Lissner and Dorsey (1986) recorded a maximum depth of 77 m for this species on Tanner and Cortes Banks, off southern California. From a list for California sites, both mainland and islands, with depth ranges indicated, we see: **Mainland**: Tijuana River: 36 m; Point Loma: 18–42 m; La Jolla: 17–64 m; San Pedro: 12–33 m; Redondo Beach: 12 m; Santa Barbara: 9 m; **Islands**: Rock Pile (Seamount 8 miles S. Coronados Islands): 30 m; Coronados Islands: 15–39 m; Santa Clemente Island: 5–21 m; Santa Catalina Island: 8–26 m; Anacapa Island: 6–9 m; Santa Cruz Island: 2–6 m; Santa Rosa Island: 5–8 m.

This species has been studied both electrophysiologically and morphologically by Satterlie and Case (1978, 1979), and has been the subject of several studies regarding its (and other gorgonian species) relationships with other organisms, such as the obligate commensal barnacle Conopea galeata (Linnaeus, 1771), formerly Balanus galeatus Linnaeus, 1771(Gomez 1973, Lewis 1978, Standing et al. 1984, Crisp 1990, Langstroth and Langstroth 2000). I have seen in multiple instances that these barnacles cluster as galls, attached to the axial skeleton of this species and are overgrown by the gorgonian's soft outer tissue. Balanus nubilis Darwin, 1854 is recorded as having been seen on the axial skeleton of dead "Lophogorgia" (Leptogorgia chilensis) in Monterey Bay (Langstroth and Langstroth 2000) (questionable gorgonian species identification); this may be opportunistic as it populates widely different sites in addition to this species. As well, several mollusk species have been recorded in association with this species, such as Tritonia festiva Stearns, 1873, as reported by Gomez (1973) and several snails of the genus Neosimnia (now Simnia), such as Neosimnia barbarensis Dall, 1892 (Theodor 1967, as referenced in Langstroth and Langstroth 2000). An unidentified field guide indicated that the ovulid snail Delonovolva Sowerby III, 1881 lives and feeds on the branches of this gorgonian. Still other organisms may be seen associated with this species, such as other species of cnidarian; "red" gorgonian is often colonized by the zoanthid anemone, Parazoanthus lucificum, now Savalia lucifica (Cutress & Pequenat, 1960), and likely other species, ultimately resulting in the death of all or most of the red gorgonian polyps (Patton 1972, as referenced in Langstroth and Langstroth 2000). In the SBMNH collection, data for several wet specimens on the Zoanthinaria shelves indicated this gorgonian as the substrate. A specimen, SBMNH 45570, collected from Avalon area of Santa Catalina Island, has Epizoanthus induratum Cutress & Pequenat, 1960 attached, while SBMNH 45549M, collected from the NE end of Anacapa Island, has Epizoanthus leptoderma Cutress & Pequenat, 1960 attached to it and SBMNH 45550, collected from the Pinnacle off the quarry, near Avalon on Catalina Island, has Savalia lucifica (Cutress & Pequenat, 1960)

attached to it. As well, a specimen of *L. chilensis* (SBMNH 265962), recently collected by Scott Clark in 2010, on Platform A as part of a survey for Milton Love, has approximately one third of its branches festooned with a creamy yellow zoanthid. There is some specific substratum choice indicated here, and is apparently common among colonial zo-anthids. On SBMNH 422944 (see Appendix 1: List of material examined–Part II), there are large clumps of hydroid, but only on bare axis portions of the branches in the colony.

According to Langstroth and Langstroth (2000), other organisms may be found associated with this species (although there is a question as to species identification of the gorgonian they discussed, as the examples are all from Carmel and Monterey Bays, in northern California; I suspect they may actually be looking at organisms on *Chromoplexaura marki*). They mention the bryozoan *Celleporina robertsonae*, now recognized as *Costazia robertsonae* (Canu & Bassler, 1923), the Broken-back shrimp *Heptacarpus flexus* (Rathbun, 1902), which may scavenge on sclerites, mucus and even toxic tissues from the surface of the gorgonian, a caprellid amphipod, specifically a skeleton shrimp, *Metacaprella anomala* (Mayer, 1903), whose color may derive from their acquiring the pigment ingested while scavenging the gorgonian's sloughed off debris, and the very small hermit crab *Parapagurodes hartae* McLaughlin & Jensen, 1996 (now recognized as *Pagurus hartae* (McLaughlin & Jensen, 1966), as noted in McLaughlin and Asakura 2004), recorded as being found only at depths of several hundred meters (presumably on this species; identification of host gorgonian may be incorrect), in southern California.

As described by Fenical et al. (1981), work was undertaken to extract what has been described as a neuromuscular toxin, lophotoxin, from several species of *Lophogorgia* (*Leptogorgia*); *L. chilensis* has subsequently been found to produce this chemical, as well (Fenical et al. 1981). "Therefore, the distribution of toxin-producing gorgonians extends from Panama Bay northward to Point Conception, California" (Fenical et al. 1981). Also, it appears that gorgonians are able to distinguish (chemically?) between self colonies and not-self colonies (Langstroth and Langstroth 2000, citing Theodor 1970).

**Remarks.** Harden (1979?) stated this as being one of the most common sea whips from southern California; my examinations confirm this. However, the fact that this is such a common species in southern California has led many to assume that all "red whip" forms (or those red and moderately branched forms), are this species, to the exclusion of others. The reality is that there are other red whip species which can easily be mistaken for *L. chilensis*; a cursory look by eye alone can (and has led) to misidentification.

Characteristics ordinarily used for separating *Lophogorgia* from *Leptogorgia*, the flattened branches and arrangement of zooids all around the branches and branchlets, are so variable as to be useless for generic distinctions (Bayer 1951). Round as well as flattened branches may occur in the same colony, and biserial zooid distribution can be found with little difficulty. Furthermore, specimens of *Leptogorgia* (typical in all other respects) may have zooids distributed all around the branchlets. Bayer first placed the genus *Lophogorgia* in synonymy with *Leptogorgia* in 1951; based on the work done by Grasshoff (1988), Bayer (2000) was then able to support that synonymy. Bayer used a specimen from Santa Catalina Island, collected at approximately 15 m to conclude that: "*Leptogorgia chilensis* (= *Lophogorgia*, as labeled)."

As this is one of the most common sea whips from southern California, it is not surprising that it has often appeared in live aquarium displays. The Cabrillo Marine Aquarium, in San Pedro, California, had a number of live colonies of this species on display in the public area; all were collected in the local area. As well, the Aquarium of the Pacific, in Long Beach, had a live display of this species in one of its tanks; these also were collected in local southern California areas. However, it is not likely the only species of "whip" that appears in southern California. In any event, it is likely not a common form in northern California. The transitional areas around Point Conception (and waters northward beyond the Bight) offer some intriguing distributional scenarios that will require further exploration. While of similar appearance in general colony form and color, material collected by staff of Olympic Coast National Marine Sanctuary that I examined in Washington State the summer of 2006 (tentatively identified as Swiftia spauldingi) indicated the possibility of several other species of "red whip" along the western United States' coast. Based on examinations of several other "red whip" forms, it appeared that the upper geographic limit for this species would be Point Conception, California. "Red whips" further north were determined to be one or more different species. This is covered further in the "red whip" discussion included in the remarks made regarding the quintessential "red whip" of the northwestern California coast, Chromoplexaura marki.

Looking at location records for specimens collected and identified as L. chilensis (with confirmed identification), I noted that if type locality is correct, L. chilensis should range from the colder waters off the coast of Chile up through the warmer waters of Central America and Mexico before again encountering the cooler waters of the southern California Bight. How is this possible? What would the depth parameters, substrate features, distance from shore and specific distributional pattern (continuous or fragmented) look like for this species? The missing type material confounds the issue. The material used for Philippi's (1866) description of L. rosea could not be located and no recently collected material from Chile resembling this species is apparently available. Breedy and Guzmán (2007) used California specimens for their description of this species. They "do not exclude the possibility (that) the material from California actually represents another species, but (to date) it most resembles Philippi's description." What is needed is a new specimen collected from the Valparaiso area of Chile, so that a definitive neotype could be established, and then used for comparisons. Until that occurs, I have designated a neotype from among the specimens in the SBMNH collection. Perhaps what we now call L. chilensis in southern California waters is actually a southern California endemic in need of its own species name, with a far more restricted range than has been implied previously. This is a prime example of a situation where the presumption that any "red whip" found in the southeastern or northeastern Pacific Ocean is likely L. chilensis (considered to be quite common), is faulty. The only way to resolve questions surrounding this species is to intentionally examine all "red whip" specimens (in any collection) that may have been collected from California and to intentionally undertake the collecting of material from Chile to southern California, at discrete intervals noting not only latitude/longitude but depth.

In the multiple examinations made of "red whip" forms, a specimen of what had been identified as *Leptogorgia caryi* Verrill, 1868 was examined. This was a dry specimen

from NMNH (USNM 5988), collected at Catalina Island, California. In examining it, along with several specimens of L. chilensis, there appeared no marked differences between these specimens, either in overall colony form or in the appearance of sclerites. My initial impression was that *L. caryi* Verrill, 1868 might not stand as a valid species. Interestingly, Breedy and Guzmán (2007) examined the same specimen from NMNH. Independently, they came to the same conclusion regarding L. carvi that I did; the specimen was *L. chilensis*, with *L. caryi* a dubious species designation. Cordeiro et al. (2018c) shows L. chilensis as an accepted species, while L. caryi is designated as nomen dubium. Additionally, L. caryi was linked to another "red whip," Euplexaura (now the genus Chromoplexaura, Williams 2013a) marki, with the species E. (Chromoplexaura) marki being a junior synonym of L. caryi (Cairns et al. 2003). The sclerites in this NMNH specimen definitively put it in the genus Leptogorgia; sclerites of any specimen identified as E. (Chromoplexaura) marki certainly did not fit the sclerite description of any in the genus Leptogorgia. Thus, E. (Chromoplexaura) marki is not a junior synonym of L. caryi. This was subsequently verified (ITIS Report, accessed online June 2011). Further, a specimen identified by Nutting (1909) as L. caryi was collected near San Francisco (and well above what I believe is the upper geographic limit for *L. chilensis*). This specimen was supposedly deposited in the Museum of Comparative Zoology at Harvard University, but Breedy and Guzmán could not locate it for examination. Based on its collection locality, it would seem that the original identification of this missing specimen is in error. I have concluded that the range of distribution that was stated in the discussions above, and confirmed generally by Breedy and Guzmán, seems to accurately pinpoint where this particular species is found. That it may overlap several other red whip forms in the northern end of its range only emphasizes the need for thorough sclerite examination of specimens collected, particularly in the transitional area from southern to northern California. Future molecular work on "red whips" in the transitional area of southern to northern California may answer the question more definitively.

#### Leptogorgia diffusa (Verrill, 1868)

Figures 16A, B, 17, 18A–D

Litigorgia diffusa Verrill, 1868a; 1868b: 397–398.

Gorgonia (Litigorgia) diffusa Verrill, 1868c: 415.

- *Leptogorgia diffusa* Verrill, 1868a; 1868b: 397–398; pl V, fig. 6; pl VI, fig. 3; 1869b: 421. Nutting 1910d: 5. Bielschowsky 1918: 30; 1929: 112. Kükenthal 1919: 771; 1924: 329–330. Hickson 1928: 413–414. Stiasny 1935: 29. Breedy and Guzmán 2007: 32–37.
- Nec *Leptogorgia diffusa*: Stiasny 1951: 71 [Guyane Française, Ile Royale] = (*Leptogorgia punicea* (Milne Edwards & Haime, 1857) [see Bayer 1961]).
- *Leptogorgia rubra* Bielschowsky, 1918: 29 [nomen nudum]; 1929: 92–94. Kükenthal 1919: 911–912; 1924: 325.

Lophogorgia diffusa: Prahl et al. 1986: 21.



**Figure 16.** *Leptogorgia diffusa*, SBMNH 423090. **A** Colony measures 19–20 cm tall, 13.5 cm wide, at widest point **B** Close up, branch tips and placement of polyps on branch surface.

**Type locality.** (Lectotype) Gulf of Panama, Panama, Pearl Islands; additionally (Paralectotypes) Gulf of Nicoya, Costa Rica.

**Type specimens. Holotype**, as *Litigorgia diffusa* Verrill, 1868); YPM 1659a [dry]. **Lectotype** Breedy and Guzmán 2007: YPM 1659 [dry]. **Paralectotypes** Breedy and



**Figure 17.** *Leptogorgia diffusa*, SBMNH 423090, light microscopy, 10×, showing sclerites typical of genus and this species. Note pale yellow anthocodial sclerite, upper middle portion of field, amongst deep red to mauve-pink spindles. Longest sclerites may be part of the anthocodial armature.

Guzmán 2007: MCZ 7081 [dry]; YPM 5151 [wet]. Breedy and Guzmán (2007) believe it unlikely that YPM 1659a or 1659b are this species.

**Material examined.** 4 lots (see Appendix 1: List of material examined). I was unable to examine the designated type specimens, but again, distinctive characters of the species made this unnecessary for ID of SBMNH specimens.

**Description.** *Colony* form (Figure 16A), appearance of branch and polyp placement (with overall effect of polyp placement that of serrated or zig-zag appearance; Figure 16B) and sclerites (Figures 17, 18A–D) correspond with that given in description of the species in Breedy and Guzmán (2007: 32–36), although in the SBMNH material examined, the anthocodial sclerites (Figure 18A) seem exceptionally long.

**Etymology.** Latin *diffuses-* means spreading, perhaps in reference to open shrub-like appearance that the branches create. No discussion of the species name is given by Verrill.

Distribution. From Panama and Costa Rica to southern California, at least.

**Remarks.** The lax, flattened branches, large polyps that produce zig-zag appearance, large (and in this case, long) anthocodial rods and the dull brick-red coloring are clear diagnostic features for this species. The species is listed as an accepted form in Cordeiro et al. (2018c).



**Figure 18.** *Leptogorgia diffusa*, SBMNH 423090, SEM image. **A** Anthocodial sclerites; some were surprisingly and unexpectedly long **B–D** Coenenchymal spindles. Images, for the most part, match those shown in Breedy and Guzmán 2007 (figs 23, 24).

# *Leptogorgia filicrispa* Horvath, 2011 Figures 19, 20, 21, 22B–N

Leptogorgia filicrispa Horvath, 2011: 45-52.

**Type locality.** Mexico, Baja, California, off Boca Flor de Malva, SE of Punta Tosca, -24°11'07.04"N, 111°21'03.08"W, 69–87 m.



**Figure 19.** *Leptogorgia filicrispa*, USNM 1106683-Paratype. Full view of an amazingly large collection of branch strands, showing the multi-colored strands; entire mass measuring  $20 \text{ cm} \times 12-13 \text{ cm}$ .

**Type specimens. Holotype** SBMNH 423057; [dry]; **Paratypes** SBMNH 423079 [dry]; USNM 1106683 [dry]; USNM 1106684 [dry]; USNM 1106685 [dry].

Material examined. ~9 lots (see Appendix 1: List of material examined).

Description. Colony primarily unbranched; if branched, loosely and little branched in one plane, lateral or pinnate to subpinnate, occasionally dichotomous, not usually bushy; many long (~20-30 cm), slender (0.5-1.0 mm, excluding polyps), whip-like branches (many collected and, presumably, found together as shown in Figure 19), somewhat flattened but never greatly expanded to form lamellar ridges, with free ends more than 50 mm long. Branches very slender, somewhat sinuous from end to end, seeming to curve loosely back on themselves, like fine wire, yet stiff and brittle (Figure 20); tapering towards tips, also very slender. Branches likely grow from these tips; some strands with growth tip at both ends. With specimens available, base seen on several colonies (each colony usually a single strand with none, one or two branches) quite small, and usually affixed to a small rock or pebble; majority of colonies without a base. Not definitively known whether lack of a base (no attachment) is an artifact of collection, or common condition; those with attachment are a more rare situation (no attachment far more commonly seen in collected specimens). Axis very slender; ranging in color from black/dark brown to a translucent brown or reddish brown. Color of living colony, in situ, unknown. In all specimens examined, several uniform color


**Figure 20.** *Leptogorgia filicrispa*, SBMNH 423057-Holotype. Two single strands, each showing a different pink color variant. Image originally published as figure 1B in Horvath (2011, Proceedings of the Biological Society of WA 124: 1, 47).

phases were seen. Dry specimen strands exhibited color range from mauve to salmon pink to a much lighter cotton-candy pink to cream to pure white. Polyp-mounds small, conical projections (roughly 1.0 mm in height) on each side of branch (Figure 21); polyps not crowded (1.0–3.0 mm apart), arranged alternately in one or two lateral rows along sides of the branchlets. On some branches, a thin, medial line can be seen running down middle of the flattened branch, between alternate-situated polyps. Sclerites (Figure 22) are spindles, as described by Bayer (1956) for genus, typically with an absence of other specialized forms of sclerite. In this species, spindles thick, tapered; with warts low, rounded; with acute or subacute warted ends, extending beyond a second ring of warts on either side of median girdle. Long spindles generally symmetrical; some with warts on one side simple and conical, elsewhere more complicated. Very few shorter ones with warts of one side fused like those of disc spindles. Flat, tentacular sclerites large; on average sclerites can measure 0.1 mm long by 0.05 mm wide. Generally, sclerites without much color; if colored, typically light pink.

**Etymology.** The species designation is derived from the Latin root *fili*- for thread, and the Latin root *crispa*- for curled or twisted; designation reflects overall strand ap-



**Figure 21.** *Leptogorgia filicrispa*, SBMNH 423057-Holotype. Close-up of branch, showing spacing of polyps; Scale bar: 1.0 mm. Image originally published as figure 1C in Horvath (2011, Proceedings of the Biological Society of WA, 124: 1, 47).

pearance, which is thread-like, stiff and wiry; strands of this species reminiscent of the stiff, wiry, curled body of an adult horsehair worm.

Common name. Multi-colored wire gorgonian.

**Distribution.** Based on collection locations for specimens in SBMNH collection, LACoMNH collection and those examined in collection at NMNH, from at least Ventura, California south to coast of Baja, into Gulf of California. Perhaps southern end of the California Bight is the northern limit for this species.

**Biology.** A comment was made (Grigg 1972) about gorgonian colonies having "a loosely branched and whip-like shape when located in circular basins where water flow is turbulent." Apparently this condition can be seen on shallow reefs to depths of 25 m (Grigg 1972). In this instance, it is suspected that regardless of water motion, the species consistently displays this distinctly thread-like form. Noteworthy point: an Atlantic form, *Leptogorgia stheno* Bayer, 1952, is normally unattached to any substrate; generally, many of the strands in the SBMNH material appear to exhibit that condition, as well. Having never seen this species in situ, and with no confirmed reports from other observers, thus far, nothing more can be stated about this species' biology.

**Remarks.** The species as described (Horvath 2011), shown as an accepted species in Cordeiro et al. (2018c), had strong similarities to *Leptogorgia setacea* Pallas, 1766 and shared many with *L. stheno* Bayer, 1952, both of which are species found in the western Atlantic. Differences were apparent in geographic location, coloring of sclerites, and subtly, in branch diameter; may be a twin species of an Atlantic form. Based on numerous strands in the NMNH material as well as material from Boca Flor De Malva at SBMNH and LACoMNH (and two other examples, both dry that were



**Figure 22.** *Leptogorgia filicrispa*, SBMNH 423057-Holotype. SEM image, originally published as figure 2B–N in Horvath (2011, Proceedings of the Biological Society of WA, 124: 1, page 48). Image prepared by D Geiger, SBMNH. Color of sclerites variable, from white, cream, to pale, bright or deep pink, generally measuring in the range of 55–80  $\mu$ m; coenenchymal spindles, scale bar 20  $\mu$ m (**B–F, H–J**), coenencymal sclerite, scale bar 100  $\mu$ m (**G**); anthocodial sclerites, scale bar 20  $\mu$ m (**K–N**).

examined [see Appendix 1: List of material examined, Other material examined], one specimen from SW Punta San Juanico, outer coast, Baja, California and the other from deep water off Redondo Beach, California, US), it is possible that this species is actually very common. While perhaps not very obvious, looking nothing like the standard of a sea fan (or even a sea whip), it is suspected that this species is routinely overlooked or regarded as nothing more than a batch of dead coralline algae. Further collection is necessary, and when found, depending on environmental conditions, the question of colonies attached or not should be addressed.

## Leptogorgia flexilis (Verrill, 1868)

Figures 23A, B, 24A–C

Gorgonia (Eugorgia) flexilis Verrill, 1868c: 415.

Litigorgia flexilis Verrill, 1868a; 1868b: 400-401.

Leptogorgia flexilis Verrill, 1868b: 400–401; pl V; fig. 11; 1869b: 421. Nutting 1910d:
5. Bielschowsky 1918: 29. Kükenthal 1919: 771; 1924: 326. Hickson 1928: 414–416. Bielschowsky 1929: 96. Stiasny 1943: 82. Breedy and Guzmán 2007: 40–44.

Type locality. Archipelago Las Perlas, Panama, 11-15 m.

**Type specimens. Syntypes** Breedy and Guzmán 2007: YPM 1553a, b [dry]; MCZ 4123 (722) [dry].

Material examined. 5 lots (see Appendix 1: List of material examined). Designated types not examined.

**Description.** An examination of SBMNH material revealed that colony form (Figure 23A), branch and polyp appearance (Figure 23B) and sclerites (shown here, Figure 24), are comparable with images shown in Breedy and Guzmán (2007: 40–44).

**Etymology.** The root *flexi-* is Latin for pliant, bendable, referring to the apparently flexible, droopy, slender branchlets of the live colony. However, Verrill does not give any rationale for the species name.

**Distribution.** Panama, north into lower third of California Bight (off Santa Catalina Island and adjacent California mainland sites).

**Remarks.** Initially, the drooping branches were considered to be more an artifact of preservation and the containers initially used when collected (branches bent downward so specimen would fit in the jar). However, descriptions by others (Breedy and Guzmán 2007), indicated that this is a normal branch configuration. Initial preservation in harsh chemicals caused drooping, pliant branchlets to become anything but; now quite brittle and easily broken. SBMNH 422942 is a nice, large colony but badly fragmented due to those early preservation efforts. As well, much of its color has leached out, with any particular branch colored from almost white to tan to pinkish red.

*Leptogorgia flexilis* is an accepted species in the WoRMS Data Base (Cordeiro et al. 2018c).

*Leptogorgia* species A Figures 25A, B, 26A–C, 27A–D

[? = *Leptogorgia tricorata* Breedy and Cortés 2011]

**Type locality and type specimens.** There is a need for further confirmation of species identification regarding SBMNH specimens, through examination of other definitively identified specimens, as well as the type specimens for *L. tricorata* (**Holotype UCR**)



**Figure 23.** *Leptogorgia flexilis*, SBMNH 422941. **A** shows colony color, and interesting disposition of branches, with tendency to droop. Colony, gently extended, ~30–40 cm tall **B** Close up of several branches. Note marked point of branch tip on end of lowest branch.

**1833; Paratypes UCR 1834, 1835, 1836** and **1837**). The holotype was collected in Cocos Island National Park, Isla Manuelita NW, taken on 8 September 2006 at a depth of 14 m. The paratypes were collected from Cocos Island National Park as well, either at Isla Manuelita or Roca Sucia.

Material examined. ~11 lots (see Appendix 1: List of material examined).

**Description.** *Colonies* (Figure 25A) non-reticulate; main stem ~14 cm long, arising from thin, flat attachment structure; latter gives off generally dichotomous (or irregular), mostly lateral, few to moderate, elongated, sometimes slightly crooked branches; these may divide again, often not; upright growth pattern in most, overall giving colony the appearance of a candelabra. Stem and branches rounded, nearly uniform, 1.0–2.0 mm diameter, not including polyps. Branches bend outwards in



**Figure 24.** *Leptogorgia flexilis*, SBMNH 422941, SEM image. Sclerite color deep orange. **A** Anthocodial sclerite **B** Sclerites of coenenchyme (last of which may actually be an anthodocial sclerite) **C** Quadriradiate from coenenchyme. Images match those shown in Breedy and Guzmán 2007 (fig. 30).

broad curve at axils; terminal branches from 2.5–7.5 cm long, without division, blunt at end. Few branchlets, rounded and slightly crooked. (One lot, SBMNH 422334, a simple, single whip-like, unbranched to minimally branched fragment, where diameter tends to smallest measurements of range, length ~37 cm, but not complete; other fragments much shorter, as above). Stem, branches and branchlets covered on all sides



**Figure 25.** *Leptogorgia* species A, SBMNH 423080. Two specimens from same lot. **A** shows branching, the tortuous condition seen in some branches, and bright yellow color, with prominent calyces/polyps. Larger colony measures 6.0 cm × 3.0 cm **B** Close up of branches, showing bright yellow coenenchyme and prominent, conical mounds with white polyps.

with prominent conical polyps, when extended (Figure 25B); when contracted, nearly flush with branch surface; apertures circular. Polyps measure 0.2 mm tall (extended), 1.7 mm wide; spacing between them 2.0–2.5 mm apart. Arrangement of polyps does not delineate median groove. Color of all colonies, regardless of colony shape, bright lemon yellow or gold; most sclerites bright lemon-yellow or gold; the few straight, less warted sclerites, pale or colorless. Sclerite shapes (Figures 26A–C, 27A–D) not diverse; mostly spindles, heavily warted; warts form regular belts; belts either evenly spaced (six to seven belted rings) or belts much closer together, largest at middle of spindle and outwards toward spindle tips progressively smaller, creating in silhouette sclerites that appear in elongated diamond shape (Figures 26C, 27C); some few (Figure 27D) of these with dense triangular collection of warts at each end with very narrow, median waist; very few straight, not as heavily warted, spindles. In a compari-



**Figure 26.** *Leptogorgia* sp. A, SBMNH 423080, Light microscopy image. All sclerites in SBMNH material are deep yellow in color. **A–C** Increasing magnifications of coenenchymal sclerites. In some specimens examined, the longest sclerites measured ~280–360  $\mu$ m, and the smaller, more slender sclerites measured somewhere between 180–260  $\mu$ m.

son with images from Breedy and Cortés (2011, Figure 2), similarities between the sclerites shown in their image and the one included here in Figures 26C and 27 are strong, with exception of tentacular sclerites (rods); SBMNH specimens may be *L. tricorata* Breedy & Cortés, 2011.

**Distribution.** From specimens examined within the California Bight, limited range from Cortes Bank up to California Channel Islands, but see also Breedy and Cortés (2011) and "Remarks" below.

**Biology.** Barnacle galls present on a number of specimens (SBMNH 423084 and SBMNH 422903).

**Remarks.** This assemblage of specimens still not identified with certainty; despite the apparent similarity with *Leptogorgia tricorata* Breedy & Cortés, 2011, it seemed unlikely that a species from the shallow waters of Cocos Island would be seen in the California Bight. Yet, its species name, using an adjective derived from the Latin root *tricoratus*-, meaning to make tricks, is applicable, as no one I spoke to who regularly collects within the Bight (LACSD, OCSD) recalled ever seeing this species. Nearly all specimens in the SBMNH collection were collected in southern California in 1940 and 1941. A few specimens more recently collected (recent being late 1970s) are also included in the collection. Since then, however, no specimens that might be this species have been encountered or reported in any collecting events to the present. All specimens examined have slightly thicker branch diameter than that seen in *Thesea* Duchassaing & Michelotti, 1860 (which they can resemble on a superficial level; this especially true of fragments of SBMNH 422334; one other specimen in collection, SBMNH 13304, from a station off Point Loma, is



**Figure 27.** *Leptogorgia* sp. A, SBMNH 423080, SEM image. **A** Anthocodial sclerites **B** Coenencyhmal sclerites of odd shape **C–D** Coenenchymal spindles. Compare this SEM with SEM images shown in Breedy and Cortés (2011).

identical), and color that is generally bright lemon yellow-gold, with very markedly colored sclerites, which display a very angular, elongated diamond-shape (refer to Figures 26C, 27C here and Figure 2 in Breedy and Cortés 2011). None of the large, spheroidal bodies common to *Thesea* were seen in these specimens; *Thesea* was eliminated as a possibility. What prevents a positive identification (as *L. tricorata*) was a difference in aperture shape (circular vs. oblong) when polyps are contracted and complete absence of the tentacular rods, characteristic of *L. tricorata*. Multiple sclerite arrays were prepared, none of which displayed even a hint of the tentacular rods. While the material is older, it is in very good shape, having always been kept as wet specimens, with no evidence of formalin contact. Until further specimens can be found and collected from waters in southern California, within the Bight, and thoroughly examined, it seemed best to place these in the genus *Leptogorgia* without species designation (*L. tricorata* does seem a strong possibility; however, lack of tentacular scleritic rods is problematic).

An additional piece of information regarding *L. tricorata* can be found in the work of Soler-Hurtado et al. (2017). Based on molecular analysis, they have proposed that *L. tricorata* should now be considered a derived form in the genus *Pacifigorgia* Bayer, 1951 (see page 226, Soler-Hurtado et al. 2017). Cordeiro et al. (2018d) does not show this proposed emendation of the genus *Pacifigorgia* in the WoRMS Data Base; *L. tricorata*, however, is shown as an accepted species in the genus *Leptogorgia*. I would add that the branching morphology in the SBMNH specimens is not reflective of branching patterns usually seen species of *Pacifigorgia*.

### Family Plexauridae Gray, 1859

**Diagnosis.** Colonies of very diverse form, generally with thick branches arising laterally, dichotomously (in some, pinnately). Polyps completely retractile or forming distinct calyces into which anthocodiae can be withdrawn. Axis with wide, chambered central chord; peripheral zone of loculated horny material, usually containing nonscleritic calcareous matter (common tendency toward heavy calcification of base in old colonies). Coenenchyme thick, perforated by system of longitudinal canals surrounding axis, delimiting outer coenenchymal layer from inner one (axial sheath), which differ in spiculation. Sclerites usually include some form of club; some with spindles only, oval bodies, rods or large quadriradiates.

**Remarks.** Due to the highly variable nature of genera and species placed in this family, this is a complex, often confusing group of organisms. Ultimately, the best means to understanding this family was to study, in total, each of the several genera placed in it that are seen in California waters. In this part (Part II), emphasis has been placed on *Chromoplexaura* (formerly *Euplexaura*) *marki* Williams, 2013a (part of a collective group referred to as the "red whip" species) and genera *Muricea* Lamouroux, 1821 and *Placogorgia* Studer, 1887 (Wright and Studer 1889). While the genera *Swiftia* Duchassaing & Michelotti, 1864 and *Thesea* Duchassaing & Michelotti, 1860 are also included in this family, it was necessary to cover those with a more extensive study, discussed in Part III. The genus *Thesea*, as represented in California waters, additionally requires still further examination; ongoing study of that genus is in progress, and will require a separate discussion, to be presented at a later date.

# Plexaurinae Family Plexauridae [= Muricidae]

### Genus Chromoplexaura Williams, 2013

Chromoplexaura Williams, 2013a (part): 31, 34–35.

### Type species. Euplexaura marki Kükenthal, 1913.

**Diagnosis.** Tall, erect, generally planar colonies, bright red; if branched, lateral (not extensively branched, if present, at all), from single, basal stem. Upper branches slender, elongate, most slightly curved, distally less dense; denser proximally and lower in colony. Polyps fully retractile; on all sides of branches and stem, as numerous slightly rounded, low to flat protuberances. Sclerites also red; robust spindles, and radiates, some ellipsoidal to sub-spherical in shape; prominent sclerite a long spindle with prominent, cone-shaped caps at each end and obvious median "waist" (herein referenced with new terminology: the double-dunce cap or double-dunce). Contains a single species from the temperate eastern Pacific (generally, California to Washington; slight possibility of presence in Canadian (even Alaskan) waters).

**Etymology.** Derived from the Greek *chroma*- referring to color, and the gorgonian generic name *plexaura*- in reference to the bright color of the colonies.

**Remarks.** Diagnosis for the genus *Euplexaura* (Kükenthal, 1913a) was examined for comparison with that of the recently proposed genus *Chromoplexaura* Williams, 2013a. The species placed in this new genus is well represented in the SBMNH collection, fitting the description given by Williams (2013a, 32–39). The original placement of the temperate Eastern Pacific species in the genus *Euplexaura* was adhered to for an entire century, based on the original description of Kükenthal (1913a). That original description was little referenced, and specimens of the species in this genus collected along the California coast post-1913 were often misidentified. Both the genus (as represented in CA) and the locally collected species received virtually no further attention until my work began on the SBMNH collection in 2002; a subsequent inquiry of Dr Williams (e-mail conversation, March 2011) was made, regarding what his perspective on the species was. Williams' (2013a) establishment of a new genus for this temperate gorgonian is justified.

#### Chromoplexaura marki (Kükenthal, 1913)

Figures 28, 29A, B, 30A, B, 31A–C, 32A, B, 33A, B, 34A–C, 35A–E, 36, 37A1–4, B1–3, 38A–E

*Euplexaura marki* Kükenthal, 1913: 266–269; text figs G, H, J, K, pl 8 fig. 11; 1924: 93–94. *Chromoplexaura marki* (Kükenthal, 1913): Williams 2013a: 36–39; figs 12–17.

**Type locality.** For the original specimen, USA, Southern California, 64–616 m. (Identification cannot be confirmed.) For proposed **Neotype**, collected in Northeastern



**Figure 28.** In situ image of what appears to be *Chromoplexaura marki*, DSCN5297. Colony seen off Oregon coast. Without initial examination of sclerites, originally thought to be *Swiftia simplex*; examination of sclerites aligned it with *C. marki*. There can be remarkable similarity in external gross appearance between the two species. Image courtesy of Peter Etnoyer, NOAA, 2010.



**Figure 29.** *Chromoplexaura marki*, SBMNH 423060 (Neotype). **A** This specimen, measuring 24–26 cm at greatest length, bears two different types of barnacle, a species that appears to be that of an acorn barnacle (forming the galls on this specimen), and clusters of a barnacle species that appears to be a "Lepas-type." The sclerites from this colony aligned with known specimens of *C. marki* **B** Branch tips at greater magnification.



**Figure 30.** *Chromoplexaura marki*, SBMNH 423062. **A** Specimen (whole colony). Sclerites did not always consistently match sclerites seen in the species, illustrating variable nature of sclerite forms. Colony measures ~16 cm × 10 cm **B** Close up, branches and branch tips, clearly showing bright red-orange color and distinctly white polyps of the species *C. marki*.

Pacific, USA, California, Monterey County, Monterey, BLM Reference Station 360 (Burch #40128), ~22 m; coll. T Burch, 18 August 1940.

**Type specimens.** Repository for the original type specimen unknown. Proposed **Neotype** (designated here), SBMNH 423060 [dry].

Material examined. ~60 lots (see Appendix 1: List of material examined).

**Description.** *Colony* (Figures 28, 29Å, 30Å, 31Å, 32Å, 33Å) shape can be a wide, broad, moderate to sparsely branched fan, typically in one plane or simple, unbranched; initial branching lateral, progressing to branches that tend to project more up than out; sometimes projecting/winding more in a "front" or "back" direction; with broader membranous base; main branches can divide repeatedly, all secondary branches off larger ones having same diameter; round in cross-section; distal ends often slightly swollen; see Figures 29B, 30B, 31B, C (See Remarks below for further discussion of overall colony shape). Axis proteinaceous, generally well calcified, not very flexible, with hollow core. Color of axis variable between white, yellowish, and light brown. Color of living colony base, stem and branches bright coral red (orange-red), bright red, or dark red; red color enhanced by color of the sclerites, which are a bright, pale, transparent red. Polyps are (pale) yellow-colored when living; (Johnson and Snook (1927) stated the color of *E. marki* to be coral-red, with the living polyps yellowish



**Figure 31.** *Chromoplexaura marki*, SBMNH 423072. **A** Colony with coenenchyme of a bright orangered color with conspicuous white polyps. Sclerites did not always consistently match sclerites seen in the species, illustrating variable nature of sclerite forms. Specimen measures ~15.5 cm ×  $\leq 2$  cm **B** Branch close-up, showing conspicuous white polyps **C** Close up of branch tip.

white). When polyps visible in preserved specimens, they appeared white/cream. Coenenchyme moderately thick, rising in wall of polyp as eight very short folds. Polyps sit ~2.0 mm distant; polyps ~2.0 mm high, 1.0 mm broad, when extended; polyps fully retractile into coenenchyme surface, forming very low, rounded bumps ("polypmound"); aperture suggestive of a goblet/chalice shape; fortification of polyps weak. Kükenthal (1913a) stated that there are no calyces in this species, or at least are so negligible as to be virtually nonexistent (in describing *Euplexaura marki*, he indicated that there should be two transverse rings of large sclerites, one over folds in the polyp head and a second just below insertion of the tentacles). Sclerites of polyp body red, while sclerites of tentacles smaller, colorless, transparent, but of similar form. Occasionally, tentacle sclerites can be a bent spindle (Figures 34A–C, 35A–E, 36, 37A1–4, B1–3, 38A–E). Found initially in a specimen identified as this species (USNM 51500) was



**Figure 32.** *Chromoplexaura marki*, SBMNH 265948. **A** Very small colony, 4.0 cm in length, excluding mass at base, which appears to be a sponge. Sclerites did not always consistently match sclerites seen in the species, illustrating variable nature of sclerite forms **B** Close up of extended polyps on single branch, each measuring  $\leq 1.0$  mm in height.

a sclerite form that was not clearly featured in sclerite descriptions for the genus, or other known species (Figures 34A–C, 35C, 36, 37A1, B1, 38B): in outer surface of branch coenenchyme lie sclerites whose basic form is a thick spindle, but on these sit two or more belts of very big, jagged warts. Through the development of these large warts, the spindle can have a contour that is nearly oval (these might be the tuberculate spheroids mentioned in original description; apparently a key sclerite form, for the genus *Euplexaura*, at least) to a distinct diamond shape. Occasionally, one can find



**Figure 33.** *Chromoplexaura marki*, SBMNH 265935. **A** Two colonies, larger of the two (only 7.0 cm tall) with conspicuous brittle star attached. Sclerites did not always consistently match sclerites seen in the species, illustrating variable nature of sclerite forms **B** Close up of branch tip, showing placement of calyces, color of polyp body and tentacles.

on both ends of these spindles, dense triangular caps (Figure 34A–C, 35C, 36, 37A1, B1, 38B) separated by a smooth, usually thin, median waist, so that in this case, the term double spindle (double-head) could apply; these are characteristic and conspicuous of multiple specimens examined, and henceforth referred to as the double-dunce cap. Size of these outer spindles fluctuated considerably, with smallest only 0.05 mm in length, but often bigger (~0.2 mm). Those deeper into coenenchyme of branches had similar form, but warts were more rounded (Figures 35B, 37A3, B3, 38C). All of the more superficial sclerites are red, making the strong bright red color of the colony fairly pronounced.



**Figure 34.** *Chromoplexaura marki*, SBMNH 423060, light microscopy arrays. **A** 4× magnification. Note in particular the "triangular-capped" spindle designated with arrow. This sclerite form is never seen in specimens from the genus *Swiftia* (some species in genus *Swiftia* can look superficially like this species in overall colony form) **B** Additional image at 4× magnification of sclerites, illustrating further examples of "triangular-capped" spindles appearing commonly in *Chromoplexaura marki* **C** 10× magnification of sclerites, showing variety, with particularly clear example of the "triangular-capped" spindle, indicated with arrow.



**Figure 35.** *Chromoplexaura marki*, SBMNH 423060, SEM image. **A** Anthocodial sclerites **B** Small coenenchymal forms **C** Larger, distinctive "double dunce-cap" spindles **D** Odd spindle **E** Still smaller coenenchymal sclerites. Images match variety shown in Williams 2013a (figs 14–17).

Etymology. Species named in honor of EL Mark of Harvard University.

**Common names.** MBARI (seen in a hall display, Summer 2008) referred to this species (and to any species from northern California appearing as a "red whip") as "Red licorice gorgonian".

**Distribution.** Southern California; littoral and coast-abyssal (Kükenthal, 1924, as *Euplexaura marki*). Johnson and Snook (1927) noted the species living in deep water,



**Figure 36.** *Chromoplexaura marki*, SBMNH 423062, light microscopy array of sclerites,  $10 \times$  magnification. Two sclerites, marked with arrows, are those that define the species (compare with those shown in Figure 34). The large central sclerite, just to left of image center, is > 100 µm in length, while non-capped spindles measure 100–130 µm.

taken with a dredge; specimens were collected off the Oregon coast, and are either in the Oceanography Department of Oregon State University, or in the personal collection of FP Belcik. Nutting (1909) reported numerous collection points, at stations near San Nicolas Island, and for stations near Point Piños Lighthouse, Monterey Bay. Likely, range extends from southern California to waters off Washington coast. There is the possibility that the species extends further north, to Alaska; further examinations of specimens from that area are in progress.

**Biology.** An unidentified, anecdotal comment indicated that this form is seen in the assemblage of organisms found at the head of Carmel Submarine Canyon, located offshore at San Jose Creek Beach, near Carmel, California; considered part of a deepwater assemblage that begins to appear at depths between 21–30 m, where turbulence is minimal and fine sediments accumulate on surface irregularities of rock walls. Between 30–61 m, the fauna appears to change very little, suggesting that many of these deep-water forms extend to greater depths.

The neotype designated here (SBMNH 423060, Figure 29) bears on several branches, enlargements that are in actuality gall-like growths, containing epizoic barnacles of the genus *Conopea* (likely *Conopea galeata*). This is a consistent, common obligate commensal barnacle of gorgonians (Langstroth and Langstroth 2000). On SBMNH 423069 (previously SBMNH 40612), a large cluster of commensal acorn barnacles was seen, on bare-axis portions of the branches. Another specimen, SBMNH 423078, had attached to its bare axis something having, in general appearance, the wooly, cotton-like spittle-bug mass that insects are known to produce on plant stems.



Figure 37. *Chromoplexaura marki*, SEM images. A SBMNH 423061 A1 Double dunce-cap forms A2 Slightly smaller double dunce-cap forms A3 Coenenchymal sclerites A4 Anthocodial form B SBMNH 423072 B1 Double dunce-cap sclerites B2 Elongated spindles from coenenchyme B3 Coenenchymal sclerites. Images match variety shown in Williams 2013a (figs 14–17).

Conspicuous brittle stars are intertwined on branches on the specimen from off Newport, Oregon, SBMNH 423073.

**Remarks.** Cordeiro et al. (2018f) lists *Chromoplexaura marki* as the only species in the genus *Chromoplexaura* in the WoRMS Database.



**Figure 38.** *Chromoplexaura marki*, SEM images, representative forms. SBMNH 265937. **A** Anthocodial form **B** Typical double-dunce-cap **C** Smaller (developing?) double dunce-cap **D–E** Coenenchymal sclerites. Images match variety shown in Williams 2013a (figs 14–17).

Kükenthal (1913a) had initially suggested that this species may equal *Psammogorgia* arbuscula (Nutting, 1909) but later stated that characteristics of this species were completely different. The separation of these two species is reflected in Kükenthal (1924), with separate descriptions for *E. marki* and *P. arbuscula* (syn. *Echinogorgia arbuscula*).

Bayer (1956a), in his description of the two genera in question, *Euplexaura* Verrill, 1869 (colony in one plane) and *Psammogorgia* Verrill, 1868 (colony bushy), indicated some slight overlap.

Kükenthal (1913a; 1924) noted that prior to the discovery of this species, other species in the genus (*Euplexaura*) had only been found in the area of East Asia, from Japan to Singapore and West Australia. It appeared that this was the first red-colored member seen in *Euplexaura* and was the first of the genus from the west coast of North America.

In overall colony shape, some branching occurs; however, more often colony is a single, or rarely branched, stem; any branching from base results in a single or very scarcely branched "whip." This would have been unique to this eastern Pacific species, along with its obvious, predominantly red sclerites, if it were truly in the genus *Euplexaura* (in most species of the genus, the sclerites are colorless); hence the need for the establishment of the new genus by Williams (2013a). In general colony color and shape, it would be quite easy to simply assume that this organism is *Leptogorgia chilensis*, but an examination of sclerites reveals the distinct differences.

Cairns et al. (2003) had this species listed as a junior synonym of Leptogorgia caryi Verrill, 1868; as noted previously, this is not the case. According to unpublished notes by Bayer, C. (E.) marki might have been synonymous with Psammogorgia spauldingi (now referred to as Swiftia spauldingi). A possible synonymy was considered, with both Swiftia spauldingi (Nutting, 1909), and/or Swiftia simplex (Nutting, 1909). After examinations of multiple samples of what has been labeled as this species and those labeled as S. spauldingi or S. simplex, if any synonymy were to exist, it would be that between C. (E.) marki and S. spauldingi. With the very obvious large, broad spindles, the double-dunce sclerite, I consider this a separate species, but it does exhibit a strong superficial similarity to S. spauldingi and there are some shared sclerite forms. An initial conclusion arrived at some years ago (regarding synonymy with S. spaulding), seemed to have support with the discovery of a comment made by Bayer (1979). While the statement was an unexpected one to find in this particular article, finding it was noteworthy. It read "The colonies of A(delogorgia) telones are similar in general aspect to those of Euplexaura marki Kükenkthal (= Psammogorgia abuscula sensu Nutting, not Verrill) and the closely related (if not identical) Psammogorgia spauldingi Nutting, both of which have longer and less sinuous branches." However, no anthocodial rods in the form of a fingerbiscuit, a key characteristic sclerite of species in the genus Swiftia Duchassaing & Michelotti, 1864, have been found in C. (E.) marki specimens, and the initial conclusion was dismissed. A further discussion of California "red whip" diversity follows below and correlations are discussed in Part III of this collection review, on Swiftia cf. spauldingi, but also in the description for Swiftia simplex.

An examination of several specimens (collected by P Etnoyer on a West Coast Survey for NOAA, in the Fall of 2010) was done at Etnoyer's request. Made available were actual specimens, along with several in situ shots. In digital images, the littlebranched colonies were a dirty brick-red or pink (Figure 28); coloring was seen in both extended polyps and throughout branch coenenchyme. An initial diagnosis of the specimens via still images was *Swiftia simplex*. However, upon physical examination, the polyps themselves were actually white (indicating that only the tentacles were the pinkish color of the coenenchyme) and an examination of the sclerites revealed the large, broad double-dunce spindles so characteristic of C. (*E.*) *marki*. If one were to see a colony with little branching, having an overall dirty brick-red to pink color, and did not dissect out a polyp to reveal their white color, or examine the sclerites, an errone-ous identification could be made. These specimens presented something of a quandary. Superficially, they looked very much like confirmed *Swiftia simplex*, yet the sclerites revealed something different. There is a possibility that *C*. (*E.*) *marki* has color variants, with one looking very much like *Swiftia simplex*. Thus, specimens previously identified in various museum collections as *C*. (*E.*) *marki* may not belong to the genus *Chromoplexaura* at all if double-dunce sclerites are not found, but finger-biscuit rods are.

MBARI has encountered many single or few-branched whips in their investigations. Many of these specimens have been recorded in video and in still photography; a few have actually been collected. A number of principal investigators identify many of these distinct whips as being this species (in genus *Euplexaura*, now *Chromoplexaura*). However, some of those identified as this species may actually be *Swiftia simplex*; in overall shape very comparable, but in *S. simplex*, the color leans to a dull brick red rather than the usual bright red hue, and polyps of *S. simplex* are always the same color as the coenenchyme, not the ". . . .white, cream or yellow" polyps described for this species by Kükenthal (1913a, 1924), Johnson and Snook (1927) or Williams (2013). Collection of an array of these "whips" when encountered, along with examination of their sclerites and molecular testing of tissue could help to clear up any confusion surrounding these red whip species; in collaboration with E Berntson, M Everett and their colleagues at Northwest Fisheries Science Center (Port Orchard and Seattle, Washington), those needed examinations are currently being conducted.

# Discussion concerning diversity of "red whip" forms

From a morphological perspective, with numerous sclerite preparations having been conducted by myself and my research students, it is reasonable to discuss the "red whip" *Chromoplaxaura marki*, and its high degree of variability that could mistakenly lead investigators to name it something else (especially true if colony samples are not taken and/or no sclerite examinations are done). "Red whip" gorgonian species within the California Bight (and in geographic areas immediately adjacent, north- and southwards) present challenges. In the SBMNH collection were found a number of "red whip" specimens, identified by earlier investigators, as the widely common *Leptogorgia chilensis*, but whose sclerites and/or colony form were not that of *L. chilensis. L. chilensis* appears as a predominantly thin-branched, but none-the-less, highly branched species, usually seen as a broad fan. Based on location records found for specimens at the NMNH, CAS, etc., it appears that *L. chilensis* is the major "red" species from approximately Central California southward, primarily inhabiting the subtidal zone, often

sharing space with *Eugorgia rubens* and both *Muricea californica* Aurivillius, 1931 and *Muricea fruticosa* Verrill, 1868a. (See distribution map for "red whips," Appendix 2: Map A1 and Appendix 3: Table of characteristics, Table A1. For comparison, distribution of another species of *Leptogorgia*, *L. flexilis*, which could be mistaken for *L. chilensis*, is shown along with distribution range for several of the whip-like species from the genus *Swiftia*.) The other specimens of "red whip" in the SBMNH collection, usually (but not always) appeared as less branched or completely unbranched, slender, but not thin, colonies with very different arrays of sclerites. Locality data indicated their appearance as being far more common in waters of the northern Central California coast, extending northwards, slightly overlapping the range of *L. chilensis*, but usually from waters of greater depth. Potential species would thus be: *Chromoplexaura (Euplexaura) marki, Swiftia simplex*, or *Swiftia spauldingi*.

Within this group of predominantly California-collected "red whip" specimens, further subgroupings could be made (based on the appearance of the sclerites): Subgroup 1, "red whip" forms that closely resembled examples of colony variation in *Chromoplexaura* (*E.*) *marki*, but which might be specimens of *Swiftia spauldingi* and a few indeterminate specimens, looking far more like *S. spauldingi* than anything else. These few specimens are colonies with shorter, chunkier, more heavily warted spindles, along the lines of those from the specimen at NMNH (USNM 78385), labeled as *Swiftia spauldingi*, collected in Monterey Bay. Further collection efforts are required, particularly in the transitional area of California's Point Conception, so as to document extent of occurrence in and near the California Bight. The notion of cryptic species or transitional endemics may apply here, not an unusual occurrence in a region like the California Bight; an equally likely possibility may be that of hybridization between certain species.

Other remaining small, odd whip-like colonies (in five separate lots), SBMNH 265946, 265947, 265948, and 265949, comprising Subgroup 2, bore a stronger superficial resemblance to a specimen collected by J Ljubenkov (which he misidentified as Muricella complanata Wright & Studer, 1889, and as yet, are still not confirmed as to their identification). These are the most difficult to link with a known genus or species. Most of these very small fragments are a bright, vivid red (or reddish pink), and have noticeably white polyps. At this point, they most closely fit very small specimen examples of the morphological variety seen in C. marki. But, the sclerites generally did not closely match those seen in known "red whip" species. There are few to none of the double dunce-caps of C. marki, the simple spindles of L. chilensis, or the spindles and rods that can typically be seen in any species from the genus Swiftia (however, Swiftia kofoidi (Nutting, 1909) does not always display the definitive rod-shaped sclerite). Unfortunately, compounding the problem is the overall condition of the specimens; they are very small, without much coenenchymal tissue. There is now so little material to work with that without collecting more material, continued work with these specimens would destroy what is left; none of these are identified to my satisfaction. Without more material, collected in the same areas as these lots, I cannot proceed further with a conclusive identification (see Appendix 1: List of material examined.)

Two additional lots (SBMNH 423066 and 423067) presented with sclerites somewhat intermediate between that seen in those labeled as L. chilensis and the above mentioned subgroups. Location data indicated the possibility of them being examples of *L*. chilensis, but sclerites did not fit as cleanly as would have been expected. I considered the possibility of these specimens being part of an array of cryptic species (within one or more of these genera and species) or that these gorgonians are either transitional endemic or hybridized forms. Currently, these are listed as material examined labeled L. chilensis, but further examinations may alter that placement. Based on location records, each of these several specimens may demonstrate a need for establishing different colony types as different subspecies (cryptic species?), but could equally show degree of overlap (and possible morphological transitions) of various known species. An attempt has been made to show key characteristics of each (refer to Appendix 3: Table A1). Overlap of these gorgonians confirmed my understanding of the California Bight as being an area of tremendous diversity (and as a result, an area where confusion regarding very similar-looking forms can occur), an area understood ecologically as an environmental disjunction. This overlap supports the admonition to anyone working in this geographical area, encountering these gorgonians, to collect and examine multiple specimens and to do extensive sclerite preparations in those comparisons. Further collection efforts will be helpful in documenting the extent of occurrence of each of these species, not only in the California Bight, but in areas adjacent to it, both north and south, with final determination likely coming from molecular comparison studies, which could confirm such concepts as cryptic species or regional (Point Conception) transitional endemics. Somewhat fortuitously, an interesting and pertinent statement was discovered in the introduction to the first volume of "New Zealand Inventory of Biodiversity: Volume I: Kingdom Animalia," edited by Dennis P Gordon (2009). To quote: "Often, what we think is a single species turns out to be a complex of closely related cryptic (hidden) species that resemble each other so closely their existence had been overlooked." This may well be the situation for "odd red whips" and several species of Swiftia (along with other genera) in the eastern Pacific. Appendix 2: Map A1 shows the distributional ranges and geographical overlap of known species and possible endemic intermediates.

Pertinent specimens at CAS were examined. For a substantial gorgonian collection of eastern North Pacific Ocean species, CAS has taken the correct stance on "red whips" from California and parts north; twenty four out of twenty five lots (identified as *Euplexaura marki*, now *Chromoplexaura marki*) are from Morro Bay and areas north, with most from Monterey Bay and Oregon. According to the database, they do not have specimens of either *Swiftia simplex* or *Swiftia spauldingi*; three specimens are listed as *Euplexaura simplex* (genus name usage not seen elsewhere, erroneously proposed by Harden). Material from several other sources (NOAA, NMFS, MBARI, etc.) were examined to broaden the scope of my understanding of eastern Pacific "red whips". There was little doubt that "red whips" seen by MBARI would likely not be *L. chilensis*. That would be the case for two reasons: depth at which colonies are seen, and location where MBARI researchers are doing their work (well north of the California Bight). A dry specimen of *Chromoplexaura (Euplexaura) marki* collected in Monterey, California, housed in the Smithsonian collection (USNM 51500), was of interest. It displayed sclerites very different from what would be seen in *L. chilensis*, but also did not clearly display the key sclerite form for the genus *Chromoplexaura*, the large double dunce-cap sclerite. Of further interest was the fact that NMNH listed only three specimens of *Leptogorgia chilensis*, all from La Jolla, San Diego or southern California, but had two lots of *Lophogorgia chilensis*, taken off the Washington coast! These were collected in 2006 at depths of 84 and 232 meters, on that year's NOAA "Deep Sea Coral and Sponge Habitat Expedition." These latter two are more likely either *Swiftia spauldingi* or one of the other species mentioned above.

### Genus Muricea Lamouroux, 1821

- Muricea (pars) Lamouroux, 1821: 36. (pars) Blainville 1834: 509. (pars) Ehrenberg 1834: 134. Dana 1846: 673. (pars) Milne Edwards 1857: 142. Duchassaing and Michelotti 1864: 14. (pars) Kölliker 1865: 135. (pars) Verrill 1868b: 418–419; 1868c: 411; 1869a: 449–450. Kent 1870: 84, pl 41, figs 13–17, (?) 36–37. (pars) Studer 1878–1879: 649. Studer 1887: 58. Wright and Studer 1889: 93, 133 + pl. Gorzawsky 1908: 8. Nutting 1910a: 9. Kükenthal 1919: 752, 835; 1924: 141. (pars) Riess 1929: 383–384. Aurivillius 1931: 102–103. Deichmann 1936: 99. Bayer 1956a: F210; 1959a: 12; 1961: 179–180. Tixier-Durivault 1969; 1970a, b, c: 154. Bayer 1981c: 930 [in key only]; 1994: 23–24. Marques and Castro 1995: 162. Hardee and Wicksten 1996: 127–128. Castro et al. 2010: 779. Breedy and Guzmán 2015: 6–7; 2016b: 7–8.
- *Emuricea* (pars) Verrill, 1869a: 449. Studer 1887: 58. Wright and Studer 1889: pl LVI. Nutting 1909: 718. Thomson and Simpson 1909: 258. Kükenthal 1919: 836. Reiss 1919: 397–398. Kükenthal 1924: 149–150. Thomson 1927: 48–49. Reiss 1929: 397. Aurivillius 1931: 50 (emended). Deichmann 1936: 104.

Eumuricea (Muricea) Bayer, 1981: 930 (key). Breedy and Guzman 2015: abstract, 28.

**Type species.** *Muricea spicifera* Lamouroux, 1821, by subsequent designation Milne Edwards and Haime 1850: lxxx. Kükenthal (1924) listed *Muricea muricata* (Pallas, 1766) as the type. [*M. specifera* was later synonymized with *Muricea muricata* Pallas, 1766 *apud* Bayer, 1961: 179–180]

**Diagnosis.** Arborescent colonies richly branched (dichotomously or laterally), often in one plane. Branch diameter moderate to very thick, tendency to curve upwards, most nearly parallel to one another, tips tending to slightly swollen. Calyces shelflike, on all sides, close-set, prickly, tubular or distinctly projecting (at right angle or upwards); stiffened by large, fusiform sclerites; aperture wide and eight-rayed; polyps fully retractile. Axis purely horny; weakly loculated (if at all). Sclerites usually fusiform, long, often massive, spindles (up to 3.0 mm in length), obviously sculptured, with strong outer or terminal spines, or both, arranged in calycular wall longitudinally; rarely some irregular forms. Anthocodial sclerites numerous, small spindles, forming at most weak, slightly differentiated transverse crown or collaret below tentacles, converging on bases of tentacles. Sclerites in genus stated as generally, markedly stockier, denser and thicker; a bit larger overall, than those seen in many other genera.

**Remarks.** The genus *Muricea* may contain at least a dozen species specifically found in the eastern Pacific; however, species descriptions, and their potential synonymies, needed review. The work of Breedy and Guzmán (2015, 2016a, 2016b) has been of help. But, the California Bight is a complex area in the eastern Pacific, and may hold some surprises with regards to this genus. To date two, perhaps three, species are commonly recorded from the California Bight; others, however, occasionally may appear. A more extensive and thorough discussion of this genus as it appears specifically in the California Bight may be required. A further investigation is also necessitated by the fact that the number of species of Mexican *Muricea*, in both the SBMNH collection and other collections, is far greater than the number of species currently known to occur within the California Bight. While the review of the genus *Muricea* and its species by Breedy and Guzmán (2015, 2016a, 2106b) is helpful, further investigation of *Muricea* found in the eastern Pacific waters of California and upper Baja, Mexico is still required; specimens from the SBMNH and LACoMNH will be helpful in such investigations.

# Muricea californica Aurivillius, 1931

Figures 39A, B, 40A–D, 41A–C

- ? Gorgonia plantaginea Valenciennes, 1846: pl 15 (non Lamarck).
- ? *Muricea appressa* Verrill, 1864: 37; 1866b: 329; 1869a: 44. Grigg 1970: xiv, 20, 25, 207; 1977: 280.)

? Muricea appressa flavescens Verrill, 1868a; 1869a: 446 (? nec Verrill, 1864: 37).

*Muricea californica* Aurivillius, 1931: 111–114, fig, p 113. Hardee and Wicksten 1996: 130–132. Breedy and Guzmán 2016b: 32–34.

**Type locality.** North Pacific Ocean, California Channel Islands, Santa Catalina Island, Gulf of Santa Catalina, 2–27 m.

**Type specimens. Syntype** USNM 44188 [wet]; **Lectotype** USA: Swedish Museum of Natural History 1122 [wet]. Syntype specimen was examined; a common form in California waters, often easily identified.

Material examined. ~32 lots (see Appendix 1: List of material examined).

**Description.** *Colony* (Figure 39A) non-reticulate; up to 100 cm wide, 120 cm high, usually 60 cm or less. Loose, dichotomous, irregular branching primarily in one plane, forming heavy fan-shaped colony; some primary and secondary branches extend out of plane. Branches thick, averaging 2.0–5.0 mm in width; curve to lie parallel with main branch. Branching lateral, terminals of even thickness or tapering slightly. Outer coenenchyme mostly occluded by calyces (Figure 39B). Calyces distally open cups, erect,



**Figure 39.** *Muricea californica*, SBMNH 422921. **A** Whole colony, 25.5 cm × 15 cm **B** View of branch tip magnified to show prominent, somewhat rounded calyces.

very elongated, prominent, conical in shape, 0.8–1.1 mm tall, 1.0–1.5 mm across, 1.0– 2.0 mm apart (close together, but not overlapping), protruding 45 to 90 degrees away from branch when polyp extended (extendable to 3.0 mm). When polyp not extended, calyx lying close to and curving into stem, broad and smooth (like bracts in a partially closed pine cone). Upper lip varies, from those without sclerites to having definite lip. Calyces extend in all directions around branches. Tentacles taper at tip; bear two rows of lateral pinnules that are slightly displaced to the oral side. Color of living colony generally rusty brown; ranges from golden-brown to dark reddish orange to reddish brown to brown to dark brown. Axis reddish brown at base; becomes light yellow-brown at tips. Polyps most commonly yellow; golden orange, bright yellow, pale yellow, creamy yellow, even white; all polyps of a branch the same color. Possibility that more than one color of polyp per colony occurs (demonstrated in digital images sent to me by Mary Wicksten, and examination of specimens). Dry colonies dark rusty brown. Sclerites (Figure 40A-D) rust red to golden-brown. Sclerites predominantly club-shaped with large, rounded spines or pointed tubercles projecting from broader, club-shaped end; other end tapering, covered with tubercles (Figure 41C). Outer coenenchyme consisting of small sclerites, to 0.5 mm long, torch-like, with processes often continuing ir-



**Figure 40.** *Muricea californica.* **A–C** SBMNH 422911, SBMNH 422914, and SBMNH 422361, respectively; light microscopy arrays, 4× magnification, showing diverse mix of sclerites seen in the species **D** Light microscopy array, the "torch-like," multi-toothed sclerites so typical of *M. californica*, shown at 10× magnification. In **D** the middle, upside-down torch measures some 580 µm, the middle upright torch measures ~400 µm, while the torch lower down measures 480 µm.

regularly down one side, other end tapering, covered with tubercles. Some spindles fusiform, bent very slightly in middle, or having large processes in middle projecting outward. Inner coenenchyme spindles small, fusiform, set with distinct tubercles.

Sclerites examined compared to those shown by Hardee and Wicksten (1996); there can be dense coverings of warts, but condition not seen on all sclerites; some sclerites have dense covering of warts at one end, but not at other end. On largest sclerites, warts are large, very few a bit bigger than those shown by Hardee and Wicksten (1996) for *M. fruticosa*. Many more of largest sclerites have flame-like teeth at one end, not down entire length of one side. In drawings and photographs examined of those believed to be, or labeled, this species, much larger tubercle bumps are seen. Regarding flame-like teeth, on some sclerites there are scattered, randomly-placed spines running down the side, but many more have flame-like teeth only coming off one end (reminiscent of a flaming torch; Figure 41C). Surface bumps can be dense, but not always, not over whole surface (true of some). For this species, stocky, dense clubs and torches very evident; overall, sclerites give impression of being a bit larger and more densely warted



**Figure 41.** *Muricea californica*, SBMNH 265938, SEM image. **A**, **B** Axial sheath sclerites **A** Very jagged spindles **B** Moderately "toothed" spindles **C** Calycular/coenenchymal torch-type spindles. Compare/ contrast with those shown in Breedy and Guzmán 2016 (fig. 21).

than those that may be from *Muricea appressa*. Refer to Figure 42, shown as *Muricea plantaginea* (Valenciennes, 1846); largest sclerites, however, not nearly as large as those seen in *M. fruticosa*.

**Etymology.** Surmise that the name *californica* refers to the species type locality; no explanation for the species derivation was found.

**Common name.** California golden gorgonian; California's purple one; California rust gorgonian; Brown sea fan (so called in a variety of field/diving guides).

**Distribution.** Stated as ranging from Point Conception, through Baja (Santa Maria) to the Gulf of California; range extending further south is possible. Grigg (1977) remarked that if *M. californica* is identical to *M. appressa* (See Harden 1969; Grigg 1970 for rationale), southern limit for this species is then Zorritos, Peru. From the following list of California sites, running from south to north, note depth ranges indicated. On the **Mainland**: Point Loma: 5–18 m; La Jolla: 3–27 m (USNM 50190, was collected at 11 m, in La Jolla, at the Torrey Pines kelp bed, 5 miles north of Scripps Institution); USNM 77286 was collected at Corona Del Mar, Newport Bay; Newport Beach: 2–12 m; San Pedro: 3–18 m; yet another at NMNH (USNM 52485) was collected along the southern coast. **Islands**: Coronados Islands: 5–24 m; Santa Catalina Island: 5–30 m.

**Biology.** Common in kelp beds (Ricketts, 4<sup>th</sup> Ed. 1968); found at depths greater than 3 m, perhaps being one of the most common gorgonians from southern California (Hardee and Wicksten 1996). Grigg (1977) noted it as a species seen in the rocky sublittoral zone off California at depths between one and 30 meters.

As colonies grow, they form annual growth rings in the skeleton (Grigg 1974; Bertsch 1984). Colonies grow separately sexed, requiring 5–10 years to reach sexual maturity with a maximum longevity of ca. 50 years (Grigg 1975). Grigg (1977) indicated that mortality could be caused by abrasion from suspended particulate matter when there are high waves, smothering by sand and by encrustation due to presence of zoanthid cnidarians *Savalia lucifica* (Cutress & Pequenat, 1960) and *Epizoanthus induratum* Cutress & Pequenat, 1960. On specimens of *Muricea* (potentially this species) located on Shale Reef, between Corona del Mar and Laguna Beach, *Savalia lucifica* was found (a wet SBMNH specimen, as yet uncataloged). As well, SBMNH 422359 has a heavy growth of some form of epizoanthid. Presence of the colonial anemone *Corynactis californica* (Carlgren, 1936) may also be an important source of mortality.

Satterlie and Case (1978) used this species extensively in studies on the neurobiology of gorgonian coelenterates, which they obtained locally (Santa Barbara area, at depths of 4–11 m). In a study done by Lissner and Dorsey (1986), it was noted that while this species was common around the Channel Islands and rocky areas of the mainland, it was conspicuously absent on the Tanner and Cortes Banks, and on the Santa Rosa-Cortes Ridge. In an anecdotal notation made by R Grigg, the reason could be that populations of *Muricea* species may be limited by cold water and/or poor dispersal abilities of the larvae. Grigg (1977) stated that *Muricea* species rarely cover more than 1% of the sea bed, where space is fully occupied.

Considering associations this species has with other organisms, Humes and Lewbel (1977) reported two species of *Acanthomolgus* Humes & Stock, 1972 (cyclopoid copepods) for the first time from the eastern Pacific in association with this gorgonian, from an area near La Jolla, California (Quast Reef). They indicated that these copepods are consistent members of the epifaunal community on the gorgonian, found with the gorgonian throughout the year. In association with SIO/BIC #CO 1600, there appeared

to be the exoskeletal remains of either skeleton shrimp, or some other small, (and now pale) crustacean. Notes from H Bertsch (1984) indicated that sometimes the ovulid snail *Simnia (Neosimnia) vidleri* (GB Sowerby III, 1881) could be found eating this gorgonian; Grigg (1974) reported that the only fish known to feed on *Muricea* species is the Garibaldi *Hypsypops rubicunda* Girard, 1854 (from Clarke 1970). A specimen, from Baja, South Bay, Isla Cedros (SBMNH 422363), had very well developed acorn barnacle galls, completely overgrown and covered by healthy-looking coenenchyme; only the barnacles' uppermost valves were visible. They appeared to have been well protected and secured to their gorgonian host. One additional specimen (SBMNH 422362) displays a bare axis at the tip of several branches; obvious barnacles are attached to these bare-tip sites. Overall, extensive organismal growth is uncommon on *Muricea* specimens, both wet and dry, housed in the SBMNH collection.

Remarks. Conflicting comments about this species (comparing it with Muricea fruticosa Verrill, 1868a) have been made, particularly with regards to polyp color (Ricketts 3rd Ed, 1962; Ricketts et al. 5th Ed, 1985; Harden MS thesis 1969; unpublished pencil notation, Harden; Harden PhD dissertation 1979). In reading these it was clear to me that some identified the species by presence of yellow polyps, while others did so by white ones. There is no doubt that discrepancies regarding polyp color have carried into current identification of the species. It would be well to remember that color is hard to determine in underwater situations, in ambient light conditions, or with artificial light sources. In some of the oldest descriptions, polyp color was not always clearly stated, most likely due to collection procedures and gaps of time that ensued between collection and actual examination. There is evidence, based on my own examinations, that M. californica can have yellow or white polyps (even different colored polyps in different locations within the same colony). Confirmation came via e-mail correspondence with M Wicksten, and is stated in Hardee and Wicksten (1996: 129, 138). Divers comment that often colonies closely situated side-by-side, with basically the same colony form (thickly branched, usually in one plane), with the distinctively common brown coenenchyme, can display markedly yellow polyps in one colony and in the other (closely adjacent) one, obvious white ones. Because the colony form is so similar (perhaps due solely to current flow in the immediate area, thus an environmental condition), but polyp color so different, the two are considered (and identified) as being different species, that with yellow polyps, M. californica and those with white polyps, M. fruticosa. Yet, there is the question as to whether polyp color can be an accurate means of identification in situ, especially under low light conditions, or if color variation is genetically inherent. Questions that still require further study: 1) are colonies (yellow polyps vs. white polyps) two distinct species? 2) If so, are the two species so similar that they can hybridize? Or, 3) do two color morphs of this species exist (in southern California, at least, each with the characteristic large, planar, generally dichotomously branched colony shape)? Only an examination of sclerites, with notation made of polyp color at the time of collection, could clearly answer these questions. Channel Islands National Park, in annual fish surveys, identifies M. fruticosa as that with white polyps, while *M. californica* has yellow polyps. The Aquarium of the Pacific in Long Beach (via phone communication with P Clarkson, March 2003) identifies them in the same way. Unfortunately, most specimens originally identified as this species in the SBMNH collection had either sat in formalin since initial collection, had been in alcohol quite a long time, or are extremely dry; there is no color to be seen in the polyps (even if at one time they had color) and data labels usually do not indicate polyp color at time of collection. Fresh material has been requested from local sources, as they incidentally collect, to help clarify identification of this, and very similar looking species.

Allen (1976) stated that *M. californica* had been common at Corona del Mar in the past, and D Kushner from Channel Islands National Park (phone comm., March 2003) stated that there has been an enhanced abundance of *M. californica* observed in recent years at San Onofre, almost to the point of taking over, becoming quite abundant in the area. This is an area where I would expect to find this species, as it appears to be common in southern California, extending into Baja, but this growth spurt seemed a somewhat unusual event. The small collection of dry specimens (and of living specimens on public display) at the San Pedro Cabrillo Marine Aquarium holds many colonies identified as this species, collected in the surrounding local area and off the southern California Channel Islands.

Coloring of actual sclerites was often of little help, but observation of sclerite size and shape was crucial. Some of the specimens identified originally as M. californica (and for that matter, some identified as *M. appressa*) were actually the typical variant of M. fruticosa, but because of condition of colony, method of preservation and transitional sclerite forms, it was initially difficult to clearly separate the species; calyx appearance was used as well, but again, groupings into distinct clusters was not always easy/clear. There was inclination to think that some specimens, listed as M. californica (likely because of overall colony shape), but from far more southern (Mexican or even Central American) collection locations, might actually be M. appressa or M. fruticosa. Without fresh material (having specific data location, observation of polyp color recorded, along with more extensive and careful extraction and preparation of the large and jagged sclerites, so as not to break them or break off the teeth), can these Muricea specimens be confidently assigned a species name. As Muricea californica seems the most common form, those listed in the Appendix 1 (List of material examined) are listed as M. californica, unless it was very clear, based on calyx appearance and sclerite form/size, that they were another species. Examination of recent, locally collected colonies (SBMNH Sea Center, Aquarium of the Pacific, Long Beach and OCSD), while not numerous in quantity or large in size, was invaluable. Sclerite size and shape were noted, along with calyx shape and confirmed polyp color. It would appear that M. californica has a wide range of polyp coloring (rarely white to commonly yellow or rich gold), while its sclerites are distinct in not having the large, densely warted, rounded spindles common to M. fruticosa (which only displays white polyps). In situ identification, therefore, can be challenging if the colony in question has white polyps; both *M. californica* (occasionally) and *M. fruticosa* (typically) have white polyps, while M. appressa (as M. plantaginea, included briefly below, for comparison) seems to always

display yellow polyps, (which is normal for *M. californica*). Despite the challenges regarding in situ identification, *M. californica* (as well as *M. fruticosa* and *M. appressa* (= *M. plantaginea*) are all recognized as separate species in the WoRMS Database (Cordeiro et al. 2018g).

## Muricea plantaginea (Valenciennes, 1846)

Figure 42A–K

Gorgonia plantaginea Valenciennes, 1846: pl 15.

nec Gorgonia plantaginea Lamarck, 1815: 163.

- nec *Eunicea plantaginea* Valenciennes, 1855: 13; Milne Edwards and Haime 1857: 146, 151.
- *Eunicea tabogenesis* Duchassaing & Michelotti, 1860: 17; 1864 [1866]: 111. Kükenthal 1924: 145.

Eunicea ransoni Stiasny, 1937: 331, 334-336, figs 5, 6, 7.

- Muricea appressa Verrill, 1864: 37 [January]; 1866: 329; 1868a: 412; 1869a: 444–446; pl VIII, fig. 13. Kükenthal 1919: 752; 1924: 145. Reiss 1929: 390–391. Hardee and Wicksten 1996: 132–136 (syn. n).
- Muricea appressa var. flavescens Verrill, 1869a: 446. Kükenthal 1919: 752; Kükenthal 1924: 145 (syn. nov.). Hickson 1928: 371–372. Reiss 1929: 389–390. Stiasny 1943: 72–74.

Muricea plantaginea Lamarck, 1836: 333. Breedy and Guzmán 2016b: 25-32.

- *Muricea californica* Aurivillius, 1931: 111–114 [according to Grigg, 1977: 280, after Grigg, 1970: xiv, 20, 25, 207].
- *Muricea tenella* Verrill, 1869a: 446–448. Kükenthal 1919: 752; 1924: 145. Hickson 1928: 371–372. Reiss 1929: 389–390. Stiasny 1943: 72–74.

**Type locality. Holotype** Mazatlán, Mexico, Voyage sur la Frégate La Vénus, MA Du Petit Thouars, 1836–1839. Also, Peru, Tumbes Department, Zorritos, 3–5 fm [6–9 m]. Specimen from NMNH (USNM 33585, and many others) collected in the North Pacific, Panama.

**Type specimens. Syntype** YPM 1616A of *Muricea appressa* var. *flavescens*. As well, housed at NMNH, USNM 33585, listed as a **Syntype**, with SEM image #2517; [dry]. Syntype specimen at NMNH was examined.

**Material examined.** A number of lots housed in SBMNH collection (see Appendix 1: List of material examined).

**Remarks.** Included here is a brief commentary on this species, and an SEM plate (Figure 42A–K) is provided as a means of comparison, because as Grigg (1977) stated "this could be synonymous with *M. californica.*" However, the work of Hardee and Wicksten (1996) led them to conclude that *M appressa* (= *M. plantaginea*) is not synonymous with *M. californica.* Based on my own observations and research, *M. appressa* is more likely to be found south of the California Bight (Baja, CA Sur, Ecuador,



Figure 42. Muricea plantaginea (= Muricea appressa), SBMNH 422909 (Ecuador) and SBMNH 422417 (Baja CA Sur). Image included for comparison between sclerites found in *M. californica* and those seen in *M. plataginea* [= *M. appressa* Breedy & Guzmán, 2016]. SEM image. A–F SBMNH 422909 (A–C);
E–F Calycular/coenenchymal sclerites A Elongated, jagged spindles B Small torch-type C Rounded, stout torches D Shorter, jagged spindles (axial sheath) E Unilateral spinous spindle F A second unilateral spinous form tending to torch shape G–K SBMNH 422417 Calycular and coenenchymal sclerites G Fan-shaped sclerite H Large, truncated unilateral spinous spindles I Stout prickly spindle J Rounded, unilateral spinous type K Torch-types typical of *M. californica*. Compare sclerites A–F with those shown in Breedy and Guzmán 2016 (fig. 15, for *M. plantaginea*) and sclerites G–K with those shown in Breedy and Guzmán 2016 (fig. 21, for *M. californica*).

Galápagos, etc.). Johnson and Snook (1927) made mention of storm-washed living specimens of *Eunicea* Lamouroux, 1816 (but no reference to a species) with the living polyps yellowish white (the black and white photograph of a specimen shown in that volume looked most like a somewhat worn specimen of either *M. californica*, or perhaps *M. fruticosa* typical). While those identified as *M. appressa* in the SBMNH collection generally seemed more prickly in overall appearance (as compared to *M. californica*), along with slightly smaller-diameter branches, any cursory visual inspection of gorgonian specimens from this genus could misidentify species. A more intentional study of calyx shape along with further comparisons of sclerites from freshly collected specimens over the total range of the Bight to clarify the possible synonymy of this species with *Muricea californica* is underway. I am inclined to keep *Muricea appressa* (= *M. plantaginea*) a separate species while this further study is being conducted.

Several additional locations were noted for this species in Verrill's (1864; 1869a) description: Panamá and the Pearl Islands, in pools at extreme low water; ex. FH Bradley; also, JH Sternbergh and FH Bradley. Also, records from Nicaragua, Corinto; ex. JA McNiel and from Mexico, La Paz; ex. J Pedersen. Note that all of these locations lie well south of the California Bight's southern boundary.

Compounding the confusion surrounding *Muricea* species, particularly in the southern portion of California's geographical range, is that in the following description of *Muricea fruticosa*, two very distinct colony forms must be mentioned: that which looks very much like the typical *Muricea californica* (the typical colony shape, albeit with white polyps, according to most encountering it in the field) and that with a far smaller, stiffer, shorter-branched cespitose or fruticose bushy shape, a distinctly different variant of *M. fruticosa* according to Verrill (1868a; 1869a). As this latter variant is not encountered in the southern California Bight it is not discussed here.

### Muricea fruticosa Verrill, 1868

Figures 43A, B, 44A, B, 45A–D, 46, 47A, B, 48A–E

*Muricea fruticosa* Verrill, 1868a; 1869a: 428–430; pl 7, fig. 2. Kükenthal 1919: 752; 1924: 142–143. Hardee and Wicksten 1996: 129–130. Breedy and Guzmán 2016b: 9–14.

Muricea fruticosa var. typica Verrill, 1868a; 1869a: 428–430. Kükenthal 1924: 142. Muricea fruticosa var. miser Verrill, 1869a: 430. Kükenthal 1919: 752; 1924: 143. Thesea crosslandi Hickson, 1928: 354–356 (syn. nov.).

Pseudothesea crosslandi (Hickson, 1928). Stiasny 1943: 64-66 (syn. nov.)

Type locality. (Lectotype) Panama, Pearl Islands, 11–14 m.

**Type specimens. Lectotype** YPM 1574C [dry]; additionally, YPM 1660 [wet], YPM 1792 (fragment from Lectotype) [dry], and YPM 3067C [dry], are all listed as **Syntypes**. There are several specimens listed as **Syntypes** at NMNH: for instance, USNM 52292 [dry], with SEM images from stub #239. Syntype material at NMNH was examined.


**Figure 43.** *Muricea fruticosa*, SBMNH 422430 (as seen in California waters). Colony shows pale base area tending to darker, colored branch tips. **A** Whole colony, 15 cm tall × 11.0–11.5 cm broad **B** Closer view of branch tip showing conical calyces forming shelf-like projections off branch surface.

Material examined. -14 lots (see Appendix 1: List of material examined).

Description. Colony (Figures 43A, 46) fairly large; dense, abundant branching; not reticulate. Branching irregularly dichotomous (also seen as cespitose/fruticose, tightly bush-shaped variant, with rather small, somewhat clavate branchlets outside California Bight; variant description not discussed here). Prominent, spreading, spinose calyces create rough texture to branches of colony. Colony (of Figure 46) very bushy; not in one plane. Colony stands up to three feet (90 cm) tall (Figure 43A), but usually shorter (30 cm). Main stem stout, short, arising from large, irregular base, usually dividing at once into several large, thick, unequal main branches, rapidly dividing and subdividing in irregular manner; branching extensive, such that main branches soon lost among crowded, crooked secondary branches. Branches and branchlets usually not more than 7.0-12 mm apart; branching can be in one plane, but not always. Small branches near ends often divide in irregular dichotomous manner, sometimes coalesce; very numerous, nearly equal in size, usually distinctly curved and crooked, spreading out at origin with a broad curve. Terminal branchlets short, 7.0-40 mm long, 2.0-3.0 mm thick, often curved, not tapering, either ending evenly or clavately, with obtusely rounded ends. In overall appearance, can look much like the colony shape of *M. californica* (perhaps reflective of similar environmental conditions). Color of living colony generally brown (darker) with white polyps; mostly deep reddish orange, rusty-brown; branchlet tips and calyces deep reddish brown, color generally fading to yellowish brown in



**Figure 44.** *Muricea fruticosa*, SBMNH 265940, light microscopy arrays. **A, B**  $4\times$  magnification, with diverse sclerites shown for the species. Of particular interest are prominent sclerites, indicated by arrows, in **B** (the tardigrade-like form mentioned in text description). In **B** the lower, middle sclerite measures some 1300 µm in length, the one up and to the right of that measures 1133 µm; thinner spindles measure between 200–300 µm in length.

proximal portion of branchlets, fading into light yellow, tinged with brown in main branches and trunk. Dry specimens orange-rusty brown, while polyps are pure white, situated on upper side of calyces; near distal end, aperture filled with yellow polyp sclerites, arising from bases of tentacles. Horn-like axis yellowish wood-brown at base



**Figure 45.** *Muricea fruticosa*, SBMNH 265940, SEM image. **A**, **D** Calycular and coenenchymal unilateral spinous spindles **B**, **C** Axial sheath **A** Large nudibranch-type sclerites **B** Typical spindle **C** Smaller spindles **D** tardigrade-type spindles.

and in larger branches (Hardee and Wicksten 1996 stated axis dark brown at base); darker reddish brown, translucent in smaller branches; light amber-yellow, translucent, slender up into branchlet tips. Calyces close together, but not overlapping, spreading outward and upward, 45 degrees from branch when closed, nearly 90 degrees with polyp extended; prominent, with conspicuous shelves opening distally, conical to columnar, larger and closer (1.0 mm) toward tips (Figure 43B), approximately as high (1.0–2.0 mm) as they are broad (1.0–1.5 mm); on larger branches low, rounded, without prolonged lower lip, better developed than at base where they are flatter, small and spread apart (2.0 mm). Those better developed have an obvious lower lip, sharp and long with very large, long, stout sclerites as spindles (some of which approximately as long as the calvces) which lie parallel to each other, projecting past upper margin of lower lip, giving colony a prickly feel when touched; upper lip small or barely noticeable. As calyces do not overlap, outer, thin coenenchyme easily seen lying between calyces, characterized by extremely large, stout, sclerites, visible to naked eye, and curving around them, often larger than calyces; these sclerites may be missing near base of colony or in poorly preserved specimens. Sclerites (Figure 44A, B) vary in color from brownish yellow and yellowish white to deep reddish brown. Largest sclerites (of outer coenenchyme), reddish orange-brown in color, up to 3.0 mm long; several shapes visible (Figures 44A, B, 45, 47A, B, 48A–E). One shape, very distinct, mostly stout, blunt and truncate, almost rectangular; longer, large, massive ones rather thick in middle, tapering somewhat abruptly at ends, densely, evenly covered by small tubercles (Verrill 1868 stated longer ones covered by small, sharp spinules on one side; other parts covered with crowded rough warts; these I refer to as tardigrade-like sclerites; Figures 44A, B, 45D, 47B, 48E). Second largest form irregularly fusiform, covered with tubercles; third form (Figure 48D) hook-shaped either on one end, both ends curving inward, or one end forked, the other tapering to a point; the latter often covered on ends with small, sparse, occasionally spiny tubercles, becoming more densely covered with tubercles toward the center, usually found around base of calyces. Medium-sized sclerites (~1.0 mm) more regular, fat (stout) in middle usually tapering to acute points; one side or one end covered with quite large, very sharp, simple projections, other side with densely crowded, rough microtuberculate warts. Sclerites of inner coenenchyme distinctly smaller, color ranging from yellow to white, fusiform, slender, often tapering to sharp point, covered with distinctly raised tubercles or warts (Figure 48B). Calyx sclerites long, up to 1.6 mm, very irregular and oddly shaped, mostly fusiform, one end often forking slightly or very noticeably, evenly covered with distinct tubercles, with some unilaterally spinose projections.

Generally, sclerites shown in Hardee and Wicksten (1996) appear to have extremely dense coverings of warts and bumps, the latter smallish in size. As well, they seem to cover a greater portion of the surface area of the sclerite as compared to those seen in drawings for sclerites of *M. californica*. Examinations of sclerites, for specimens identified as this species, reveal that sclerites can have flame-like teeth, these running almost the full length of the sclerite, on a side (what are termed nudibranch sclerites (Figure 45A), as those of Matamoros-Rosales (1984), rather than at an end such as seen in a torch. Very largest sclerites (tardigrade-like) rounded, densely warted, with projections coming off one of the longer sides, creating the appearance of legs and claws (like those of a tardigrade; Figures 44, 45D, some in Fig. 48E). Generally, sclerites have very dense tubercle coverings. The largest sclerites in this species are decidedly larger than those of *M. californica*; this will be the case despite what might have been concluded



**Figure 46.** *Muricea fruticosa*, SBMNH 265945. Colony measures ~7.5 cm × 4.0 cm. Visible in image is the pale cream/yellow base/lower trunk; trunk intensifies and darkens to brownish orange towards branch tips. Notice swollen appearance of branch tips.

from having only looked at polyp color. This agrees with data provided in both Harden (1969) and Grigg (1970).

The colony shown in Figure 46 displays a few odd features, warranting further mention. Branching primarily pinnate to dichotomous. Colony measures ~7.5 cm tall, 4.0 cm wide. Slightly central main stem runs entire height of colony, with some slight curving laterally in random sections of stem; multiple branches all begin directly above or from base, many coming off of main stem. Branches often angle out a very

short distance then curve upwards. Primary branches average 3.0-4.0 mm long, diameter ~1.0-2.0 mm (excluding calyces); diameter appears consistent from axillary branch points to branch tips. Calyces very columnar (1.0-2.0 mm wide, ~3.0 mm tall), heavily covered with longitudinally-oriented sclerites; polyps, many partially to fully extended from calyces, cream or light yellow; appear smooth. Calyces on all sides of branches, in some areas of colony very dense, in other areas calyces with some little distance between themselves, where sclerites can be seen on coenenchyme surface, lying sometimes longitudinally with the branches, sometimes not; latter more transverse (or oriented slightly in a triangular pattern) at base of calyces; calyces cover entire colony, right down onto coenenchymal surface of colony's base. Calyces generally appear distinct reddish brown due to large, conspicuous sclerites. Color of colony generally darker distally, reddish brown, grading from free branch tips of colony to much lighter yellow or cream proximally, in stem and base (due to light-colored sclerites, usually small in size); polyps appear very light yellow, cream to white. Majority of calyx-bearing polyps appear such that they give colony an overall swollen appearance (as though branches of colony are covered with small, round grapes). This is the most unique feature of this colony; this may reflect an active reproductive state at the time of collection; specimen's reproductive condition is still a question. Some calvces, scattered on all branches, tend to curve upwards slightly. The sclerites shown in both light microscopy (Figure 47A, B) and SEM (Figure 48A-E) in some ways match those for the colony of Figures 43–45, and yet in other ways do not clearly point to it being the same species. Based on this single specimen in the SBMNH collection (SBMNH 265945), from Long Beach, California, it requires further study. The biology of this colony, and its swollen appearance, has not been further explored or explained to date, other than to indicate that specimen was collected from very far into the back channels of Long Beach Harbor, quite a distance from open water (D Cadien, LACSD, pers. comm.).

**Etymology.** Latin, *fruticosu-* meaning shrubby (bush-like); Verrill gave no specifics as to the derivation of the species name.

**Common name.** Brown gorgonian; Fruitful purple one; Bushy rust gorgonian; Robust gorgonian (as indicated in various field/diving guides).

**Distribution.** Potentially from Panama, up along California coast, perhaps as far north as Los Angeles County, California, with maximum, though infrequent, northern limit Point Conception, California. In a list of California sites, showing depth ranges, the following are indicated: **Mainland**: Point Loma: 5–14 m; La Jolla: 3–12 m; (USNM 50192 was collected at 11 m at La Jolla, in the Torrey Pines kelp bed, 5 miles north of Scripps Institution); Newport Beach: 0–12 m; San Pedro: 0–15 m; Santa Barbara: 5–8 m; Naples Reef: 5–11 m; **Islands**: Coronados Islands: 2–12 m; San Clemente Island: 21 m; Santa Catalina Island: 5–18 m.

**Biology.** Seen more commonly in southern areas of California kelp beds (Ricketts, 4<sup>th</sup> Ed. 1968); also, offshore pilings. Seen as well in lowest intertidal zone, outer Los Angeles Harbor; one of the most common species in southern California, in 15–30 m depths, Point Conception to Baja California (Grigg 1977; Gotshall 1994, 2005). Both this and *M. californica* seem to prefer subtidally occurring solid substrata at depths



**Figure 47.** *Muricea fruticosa*, SBMNH 265945, light microscopy arrays. **A**  $4\times$  magnification, showing large spindles with pronounced conical spinules; central, vertically aligned one, measures 650 µm **B**  $10\times$  magnification of similar large spindles. Sclerite denoted by arrow is 0.875 mm in length, with a maximum length for this spindle form ~1.0 mm.

between 1.0-30 m (Grigg 1977). Lissner and Dorsey (1986) reported that while this species is common around the California Channel Islands and rocky areas of the mainland, it is conspicuously absent on the Tanner and Cortes Banks and the Santa Rosa -Cortes Ridge. Grigg (anecdotal communication) reported that populations of Muricea may be limited by cold water and/or poor dispersal abilities of the larvae. Grigg (1974) stated that this species is ca. one-tenth as abundant as M. californica off La Jolla. Based on work done by Grigg, it was estimated that a colony 30 cm high is ~20 years old. As very few colonies are seen larger than that, few colonies likely exceed this age. Mortality attributed mostly to abrasion, occurring when particulate matter is suspended in the water during periods of high waves and by smothering coming from accumulations of sand. One untitled and unpublished identification guide stated that colonies are able to survive in some of the most polluted near shore waters, as well as uncontaminated offshore waters. It appears this species is immune to encrustations known to cause mortality in M. californica. (SBMNH 422390, collected by MacGinitie in Newport Bay, if indeed this species-original identification indicated it was, based on white polyps, but sclerites do not support the identification-does have several galls produced by an acorn-type barnacle, on bare axis as well as on an area covered by coenenchyme.) Apparently fed upon by only one species of fish, the Garibaldi Hypsypops rubicunda. Grigg (1974) calculated that between 10% and 15% of annual growth of this species and *M. californica* is cropped by Garibaldi predation.

**Remarks.** Gift of FH Bradley; collected below low, low-water mark. Panama and (?) Pearl Islands, 6–8 fm (11–15 m) (Verrill 1869a). Identified as *Muricea fruticosa* var. *typica* (?).

There are two specimens at NMNH identified as this species, with SEM images: USNM 57171, SEM 237-238 (label reads 'Albatross' 28-29) and also, "*Muricea fruticosa* 



**Figure 48.** *Muricea fruticosa*, SBMNH 265945, SEM image. **A** Possible anthocodial sclerites **B** Spindles from the axial sheath **C** An unusual quadriradiate spindle from coenenchyme **D** Calycular/coenenchymal unilateral spinous spindles **E** Prominent calycular/coenenchymal tardigrade-type spindles.

Verrill," collected by Limbaugh, from St. (Cape) Lucas Canyon, SEM image 999. NMNH has an additional lot (USNM 52486), collected at Point Vicente, California, along with material in the "Limbaugh" Collection, which could well be this species, having been collected from the following locations (multiple lots): from California, at Huntington Beach Gas & Electric Steam Plant discharge pipe; from Baja, at Turtle Bay. For all colonies of *Muricea* found in the California Bight, there is the possibility of other species in the genus not previously reported as appearing in the Bight, which may have very similar shape, etc. to the commonly recognized species described here. Perhaps there are new, undescribed species. It may well be that previously described species other than the standards make appearances in the Bight, and do so more often than previously thought. This possibility is supported by the fact that climatic factors can greatly expand ranges, even if only temporarily. A number of Mexican species may occasionally (or more often) make an appearance in the California Bight during certain substantial climatic/atmospheric events, such as an El Niño.

This conclusion has some support; Hardee and Wicksten (1996) in their closing paragraphs state "(a)lthough our material could be identified as (simply) *M. fruticosa* and *M. californica*, it is possible that other species of *Muricea* occur in southern California." They recommended that a comparison of a series of specimens be made. This would help to clarify which previously described species are valid and which are "merely growth forms." I agree with that recommendation. Fresh *Muricea* colonies, collected in a very intentional manner, from south to north, both within the Bight and to the south outside the Bight, must be done; that collection process is underway, with the help of the Santa Barbara Museum of Natural History's Sea Center staff, staff of the Aquarium of the Pacific in Long Beach, California and staff of both the Los Angeles (LACSD) and Orange County (OCSD) Sanitation Districts. With the dramatic weather events we have recently experienced here in California, it will be interesting to see whether other species of the genus are making an appearance, for any length of time.

#### Genus Placogorgia Studer, 1887

Placogorgia Studer, 1887: 56 [without species]. Wright and Studer 1889: 113. Nutting 1912: 83. Kükenthal 1919: 841; 1924: 209–210. Deichmann 1936: 141–142. Bayer 1956a: F206; 1959b: 54–55. Grasshoff 1977 (pars): 26. Muzik 1979: 80–81.
? nec *Placogorgia* Nutting (part), 1910a: 76 [= *Discogorgia* Kükenthal]. Clematissa Studer, 1887: 106–107. Pseudothesea Kükenthal, 1919: 843. Discomuricea Gordon, 1926: 521.

**Type species.** *Placogorgia atlantica* Wright & Studer, 1889; SM Wright and Studer 1889 (= *Pseudothesea* Kükenthal, 1919).

**Diagnosis.** Colonies usually branched laterally in one plane; main stem generally long; primary branches with tendency to curve upwards; primary branches tend to run parallel with main stem, tips button-shaped, prominent swellings. Polyp height moderately low, on all sides of branches; especially dense at branch tips. Calyces truncated, cone shaped, armed with spindles (thorn scales). With crown (collaret) and points arrangement (= operculum of Paramuricidae): each of eight points composed of two-three pointed, convergent spindles in triangular arrangement above collaret of spinous

rods, latter forming spiny transverse ring; fairly large triangular space free from sclerites between each point, situated in tentacle base. Thorn scales of calyx typically large, coarse, thick; wider than tall, each with broad, abundantly branched basal root (broad, flat), and a (usually) short, stout, more or less laciniated but usually strong, blunt spine; these sclerites overlap like roof tiles. Coenenchymal sclerites diverse spindles, simple, branched, often flattened, occasionally with one or more projections. Outer coenenchyme with long, often bent, sclerites (spindles), blunt points on both ends; at calyx base these form enclosing annular ring.

Placogorgia species A

Figures 49, 50A, B, 51A-C, 52A-G

**Type locality and type specimens.** Until there is species confirmation, no information can be provided.

**Material examined.** ~5 lots (see Appendix 1: List of material examined). While labeled *Placogorgia* material was examined at NMNH, nothing resembled in any way the specimens in the SBMNH collection.

Description. Colony (Figures 49, 50A) generally branched in one plane; rarely, few reticulate; colony height (base to tip of upper-most branch) approximately 20-21 cm.; long, generally dichotomous branches and branchlets, moderately thick, cylindrical; branch diameter thickness averages 5.0 mm (including calyces); meandering sinuously, branches bent upward, parallel with main stem (not always obvious); tips of branches and branchlets swollen, to rounded 8.0-mm diameter (Figure 50B). Main stem bifurcates (sometimes), some distance  $(\pm 10 \text{ cm})$  from base; branches then again bifurcate at ~1.0->5.0 cm from first division. Further branching asymmetrical. Not all branches subdivide; of those that do, distance from previous subdivision varies. Polyps distributed over entire surface, sparsely placed at base, becoming progressively most crowded at branch tips. Color of freshly collected specimens, via video and still image (Figure 49), pale pinkish tan with conspicuous, fluffy, cotton candy-pink polyps; in preserved (dry) specimens, color dull tan-brown (Figure 50A, B); axis color slightly darker brown. Calyces moderately low, ~1.0 mm tall, 2.0 mm across, 2.5 mm apart; blunt/rounded, conical, armed with sclerites of various shape. Coenenchyme (relatively thin) contains long, blunt-ending spindles, often bent; largest bent spindles 0.3-0.6 mm L, 0.05-0.1 mm H (average 0.5 mm L  $\times$  0.08 mm H), often with strong external spines (Figure 52D). Distinctive sclerites often like thorn-scales or thorn-stars; small, spinulate or laciniate ones predominantly calycular (Figures 52E–G). Anthocodial sclerites difficult to extract; sclerites of collaret also blunt-ended, bent spindles, at base of polyp, tending to circular arrangement. A few as large, heavy, tapered spindles, sometimes with several heavy, rough spines projecting from one side; some few (the calycular sclerites) as branched torches (Figure 52B); also, crutch-types (Figures 51A, 52C); some few as crosses and irregular ones, most as unilateral spiny shapes (Figure 51B, C). Color of sclerites cream to very light tan, at least in specimens that are long dry.



**Figure 49.** *Placogorgia* species A. In situ image, as seen in the Santa Barbara Channel. Image 6435B\_Snook\_018, taken by L. Snook. Image courtesy of Milton Love, UCSB.

**Distribution.** For genus (based on material found/examined at NMNH and other institutions, such as CAS) from Point Conception (California Bight) to Gulf of California (eastern North Pacific Ocean); western Pacific from Hawaii south to Philippines and Indonesia. NMNH also has specimens in this genus collected from off the coast of Chile in the southeastern Pacific Ocean; these look very different from the one described here.

**Biology.** May be considered a subtidal to deep-sea genus; this based on collection data for known species.

**Remarks.** Bayer's review of the genus (1959b), and description of a new species from Florida, was invaluable for understanding the SBMNH specimens; a thorough discussion of both the calycular thorn scales and the cortical sclerites was provided. For specimens described here, the calycular thorn scales were difficult to extract; most of the material studied was quite dry, but an examination of wet specimens (SBMNH 422968 and 422970) revealed that the form labeled "E" in Bayer (1959) is the closest



**Figure 50.** *Placogorgia* species A, SBMNH 422970. **A** Colony measures 28 cm tall (excludes missing base) × 9.0 cm broad **B** Magnification of branch tips; one tip malformed due to presence of barnacle gall.

fit to what is seen in these specimens. Cortical sclerites in these specimens best fit those labeled "K," "L," and "M" (latter, in part; Bayer 1959). As well, sclerites seen in these specimens also corresponded as follows to Diechmann's (1936) illustrations for several species in the genus *Placogorgia* from the Atlantic Ocean: pl 15, figs 19–20 best match those identified as cortical thorn scales, pl 15, figs 23–24 best match those likely caly-cular (branched torch) thorn scales, while pl 15, figs 26 and 32 match the blunt-ended spindles seen here. Nearly all sclerite shapes in this unidentified species are far broader in their root than they are tall; based on interpretation of the key in Bayer's review I have made a tentative placement of this species in the genus *Placogorgia*.

There are multiple species of *Placogorgia* from the Atlantic, as well as a number of species from the South Pacific and Indian Oceans (Kükenthal 1924). Only a few records were found from the southeastern Pacific: unidentified species found west of southern Chile (USNM 80162 [wet] and 98863 [wet]), and a number of unidentified specimens from the western North Pacific (Hawaii), such as USNM 75077; none were from the eastern North Pacific. There was one reference by Harden (1979) indicating that the species, using one of the same specimens currently discussed here (SBMNH 422969), is *Placogorgia ramosa* (Wright and Studer 1889), stating that it is synony-



**Figure 51.** *Placogorgia* species A. SBMNH 422970, Light microscopy arrays,  $10 \times$  magnification. **A** Some of the more unusually shaped sclerites **B–C** Several highly ornamented and distinctive sclerites. Crutch form -80 µm tall, thin spindles measure in the range of 150–191 µm in length, larger, thicker spindles are -250 µm long, with unusual forms, such as **B**, the tall, spikey sclerite measuring some 300–350 µm tall and that appearing as a very large quadriradiate (**C**) measuring 280 µm across.

mous with *Paramuricea ramosa* (Wright & Studer, 1889). Cordeiro et al. (2018i) does not list a species *P. ramosa* in the list of recognized *Placogorgia* species in the WoRMS Database; Harden's designation does not inform the identification of the SBMNH specimen in any way. As well, I could not find any other indication that *Paramuricea ramosa* is synonymous with *Placogorgia ramosa*.



**Figure 52.** *Placogorgia* species A. SBMNH 422970, SEM image. **A** Small capstan form **B** Chunky torch-type spindle **C** Crutch-type spindles **D** Long spindles **E** Thorn scales typical of the genus **F** Small, developing thorn scale, dorsal view **G** More developed thorn scales, dorsal view.

Muzik (1979) stated that coenenchyme in species of *Placogorgia* is filled with diverse spindles that are simple, branched and often flattened, occasionally with one or more projections; this is descriptive of what was seen here. Muzik (1979) also stated that the calycular thorn scales are wider than tall, the projection usually short, with the base broad and flat. The Hawaiian species described by Muzik (1979) with their distinctive features

were of interest: the presence of 1) broad calycal thorn scales and 2) very branched, flattened sclerites of the coenenchyme. It seemed best to place the examined specimens in the SBMNH collection within the genus *Placogorgia* based on the appearance of the sclerites, but other genera are under consideration. However, any link between an eastern Pacific locality and described members of this genus, or any other possible genera, cannot be made (Ekman 1935: 66, 1953: 40; Bayer and Deichmann 1960).

Should specimens in the SBMNH collection represent a new species, this would be the first description of a species from this genus in the northeastern Pacific Ocean; if not a new species, then this is the first record of a known species of *Placogorgia* (seen elsewhere) from the northeastern Pacific Ocean; further study of specimens is currently underway.

# Conclusions

The SBMNH research collection, including substantial material from the Allan Hancock Foundation's 'Velero' Expeditions, provides a good representation of the families Gorgoniidae and Plexauridae (and many species included therein) from the area known as the California Bight. The collection effectively displays the variation (and differences) of species found in the California Bight as compared with other locations which may also harbor the same species. While many species from the collection match well with species collected in other locations, there are some intriguing differences seen in many specimens taken from within the Bight that reflect, perhaps, the dynamic environmental system that is the California Bight.

As the family Plexauridae is so well represented in the SBMNH collection, two of the remaining genera in the family, *Swiftia* and *Thesea*, will be discussed more thoroughly in Part III of this work, completing the full and comprehensive review of all species recorded to date as appearing in the California Bight, based on the SBMNH research collection, and specifically on the many specimens that came to SBMNH through the Allan Hancock Foundation's historic 'Velero' Expeditions collection events.

#### References

- Allen RK (1976) Common Intertidal Invertebrates of Southern California Revised Edition. Peek Publications, Palo Alto, California, 316 pp.
- Aurivillius M (1931) The gorgonians from Dr. Sixten Bock's expedition to Japan and the Bonin Islands, 1914. Kungliga Svenska Vetenskapsakademiens Handlingar (ser. 3) 9(4): 1–337.
- Bayer FM (1951) A revision of the nomenclature of the Gorgoniidae (Coelenterata: Octocorallia), with an illustrated key to the genera. Journal of the Washington Academy of Sciences 41(3): 91–102. https://repository.si.edu/handle/10088/866
- Bayer FM (1952) New western Atlantic records of octocorals (Coelenterata: Anthozoa), with descriptions of three new species. Journal of the Washington Academy of Sciences 42(6): 183–189. https://repository.si.edu/handle/10088/868

- Bayer FM (1956) Octocorallia, Part F. Coelenterata. In: Moore RC (Ed.) Treatise on Invertebrate Paleontology. Geological Society of America and University of Kansas Press, Lawrence-Kansas, F166–F231.
- Bayer FM (1958) Les Octocoralliaires plexaurides des cótes occidentals d'Amérique. Mémoires du Muséum National d'Histoire Naturelle (nouvelle série; série A, Zoologie) 16(2): 41–56. https://repository.si.edu/handle/10088/891
- Bayer FM (1959a) Octocorals from Surinam and the adjacent coasts of South America. Studies on the Fauna of Suriname and other Guianas 6: 1–43, figs 1–21. https://repository.si.edu/ handle/10088/881
- Bayer FM (1959b) A review of the gorgonacean genus *Placogorgia* Studer, with a description of *Placogorgia tribuloides*, a new species from the Straits of Florida. Journal of the Washington Academy of Sciences 49(2): 54–61. https://repository.si.edu/handle/10088/883
- Bayer FM (1961) The shallow-water Octocorallia of the West Indian Region: (A manual for marine biologists). In: Hummelinck W (Ed.) Studies on the Fauna of Curacao and other Caribbean Islands 12(55): 1–373. Martinus Nijhoff, The Hague.
- Bayer FM (1979) Adelogorgia telones, a New Species of Gorgonacean Coral (Coelenterata: Octocorallia) from the Galápagos Islands. Proceedings of the Biological Society of Washington 91(4): 1026–1036. https://repository.si.edu/handle/10088/890
- Bayer FM (1981) Key to the genera of Octocorallia exclusive of Pennatulacea (Coelenterata: Anthozoa) with diagnoses of new taxa. Proceedings of the Biological Society of Washington 94(3): 902–947. https://repository.si.edu/handle/10088/978
- Bayer FM (1994) A new species of the gorgonacean genus *Muricea* (Coelenterata: Octocorallia) from the Caribbean Sea. Precious Corals & Octocoral Research 3: 23–27. [pls 3–7] https://repository.si.edu.handle/10088/993
- Bayer FM (2000) A new species of *Leptogorgia* from the eastern Pacific (Coelenterata: Octocorallia: Holaxonia). Proceedings of the Biological Society of Washington 113(3): 609–616. www.biodiversitylibrary.org/part/49186#/summary
- Bayer FM, Deichmann E (1960) The Ellisellidae (Octocorallia) and their bearing on the zoogeography of the eastern Pacific. Proceedings of the Biological Society of Washington 73: 175–182. https://repository.si.edu/handle/10088/6195
- Bertsch H (1984) Notes from Hans Bertsch: Gorgonians-The Ocean's Fanciful Menorahs and Christmas Trees. Shells and Sea Life 16(12): 246–248.
- Bielschowsky E (1918) Eine Revision der Familie Gorgoniidae. Inaugural-Dissertation zur Erlangung der Doktorwürde der Hohen Philisophischen Facultät der Schlesischen Friedrich-Wilhelms-Universität zu Breslau, Buchdruckerei H Fleischmann, Breslau, 66 pp.
- Bielschowsky E (1929) Die Gorgonarien Westindien. 6. Die Familie Gorgoniidae, zugleich eine Revision. Zoologische Jahrbücher, Supplement 16: 63–234.
- Blainville HMD de (1834) Manuel d'Actinologie ou de Zoophytologie. FG Levrault, Paris, 1–644. [102 pls] https://doi.org/10.5962/bhl.title.8768
- Brancato MS, Bowlby CE, Hyland J, Intelmann SS, Brenkman K (2007) Observations of Deep Coral and Sponge Assemblages in Olympic Coast National Marine Sanctuary, Washington. Cruise Report: NOAA Ship 'McArthur II' Cruise AR06-06/07. Marine Sanctuaries Conservation Series NMSP-07-03. Joint publication of U.S. Department of Commerce, National Oceanographic and Atmospheric Administration, and National Marine Sanctu-

ary Program, Silver Spring, Maryland, 48 pp. http://aquaticcommons.org/2278/1/bowlby3.pdf

- Breedy O, Cortés J (2011) Morphology and taxonomy of a new species of *Leptogorgia* (Cnidaria: Octocorallia: Gorgoniidae) in Cocos Island National Park, Pacific Costa Rica. Proceedings of the Biological Society of Washington 124(2): 62–69. https://doi.org/10.2988/10-18.1
- Breedy O, Guzmán HM (2005) A new species of *Leptogorgia* (Coelenterata: Octocorallia: Gorgoniidae) from the shallow waters of the eastern Pacific. Zootaxa 899: 1–11. https://doi. org/10.11646/zootaxa.899.1.1
- Breedy O, Guzmán HM (2007) A revision of the genus *Leptogorgia* Milne Edwards & Haime, 1857 (Coelenterata: Octocorallia: Gorgoniidae) in the eastern Pacific. Zootaxa 1419: 1–90. https://doi.org/10.11646/zootaxa.1419.1.1
- Breedy O, Guzmán HM (2012) A new species of *Leptogorgia* (Cnidaria: Anthozoa: Octocorallia) from Golfo Dulce, Pacific, Costa Rica. Zootaxa 3182: 65–68. https://doi.org/10.11646/ zootaxa.3182.1.7
- Breedy O, Guzmán HM (2015) A revision of the genus *Muricea* Lamouroux, 1821 (Anthozoa, Octocorallia) in the eastern Pacific. Part I: Eumuricea Verrill, 1869 revisited. ZooKeys 537: 1–32. https://doi.org/10.3897/zookeys.537.6025
- Breedy O, Guzmán HM (2016a) Corrigenda: Breedy O, Guzman HM (2015) A revision of the genus *Muricea* Lamouroux, 1821 (Anthozoa, Octocorallia) in the eastern Pacific. Part I: *Eumuricea* Verrill, 1869 revisited. ZooKeys 553: 149–153. https://doi.org/10.3897/zookeys.553.7471
- Breedy O, Guzmán HM (2016b) A revision of the genus *Muricea* Lamouroux, 1821 (Anthozoa, Octocorallia) in the eastern Pacific. Part II. ZooKeys 581: 1–69. https://doi.org/10.3897/ zookeys.581.7910
- Breedy O, Guzmán HM (2018) Revision of the genus Adelogorgia Bayer, 1958 (Cnidaria: Anthozoa: Octocorallia) with the description of three new species. Zootaxa 4369(3): 327– 348. https://doi.org/10.11646/zootaxa.4369.3.2
- Breedy O, Guzmán HM, Vargas S (2009) A revision of the genus *Eugorgia* Verrill, 1868 (Coelenterata: Octocorallia: Gorgoniidae). Zootaxa 2151: 1–46. https://repository.si.edu/handle/10088/11792
- Cairns S (2009) Influence of Frederick (Ted) M. Bayer on deep-water octocoral research. Marine Ecology progressive Series, Suppl. 1 397: 7–10. https://doi.org/10.3354/ meps08066
- Canu F, Bassler RS (1923) North American Later Tertiary and Quaternary Bryozoa. Bulletin of the United States National Museum 125: 1–302. [pls 1–47] https://doi.org/10.5479/si.03629236.125.i
- Carlgren O (1936) Some West American sea anemones. Journal of the Washington Academy of Sciences 26: 16–23.
- Castro CB, Medeiros MS, Loiola LL (2010) Octocorallia (Cnidaria: Anthozoa) from Brazilian reefs. Journal of Natural History 44: 763–827. https://doi. org/10.1080/00222930903441160
- Clarke TA (1970) Territorial Behavior and Population Dynamics of a Pomacentrid Fish, the Garibaldi, *Hypsypops rubicunda* (Girard). Ecological Society of America 40(2): 189–212. https://doi.org/10.2307/1942295

- Committee on Common Names of Cnidaria and Ctenophora (American Fisheries Society). In: Cairns S (Ed.) (1991) Common and Scientific Names of Aquatic Invertebrates from the United States and Canada: Cnidaria and Ctenophora. American Fisheries Society, Bethesda, Maryland, 75 pp.
- Committee on Common Names of Cnidaria and Ctenophora (American Fisheries Society),. In: Cairns S (Ed.) (2003) Common and Scientific Names of Aquatic Invertebrates from the United States and Canada: Cnidaria and Ctenophora, Revised 2<sup>nd</sup> edn. American Fisheries Society, Bethesda, Maryland, 126 pp.
- Cordeiro R, van Ofwegen L, Williams G (2018a) World List of Octocorallia. *Adelogorgia* Bayer, 1958. http://www.marinespecies.org/aphia.php?p=taxdetails&id=267204
- Cordeiro R, van Ofwegen L, Williams G (2018b) World List of Octocorallia. *Eugorgia* Verrill, 1868. http://www.marinespecies.org/aphia.php?p=taxdetails&id=267424
- Cordeiro R, van Ofwegen L, Williams G (2018c) World List of Octocorallia. *Lept-gorgia* Milne Edwards and Haime, 1857. http://www.marinespecies.org/aphia. php?p=taxdetails&id=125302
- Cordeiro R, van Ofwegen L, Williams G (2018d) World List of Octocorallia. *Pacifigorgia* Bayer, 1951. http://www.marinespecies.org/aphia.php?p=taxdetails&id=267665
- Cordeiro R, van Ofwegen L, Williams G (2018e) World List of Octocorallia. *Euplexaura* Verrill, 1869. http://www.marinespecies.org/aphia.php?p=taxdetails&id=220195
- Cordeiro R, van Ofwegen L, Williams G (2018f) World List of Octocorallia. *Chromoplexaura* Williams, 2013. http://www.marinespecies.org/aphia.php?p=taxdetails&id=724230
- Cordeiro R, van Ofwegen L, Williams G (2018g) World List of Octocorallia. *Muricea* Lamouroux, 1821. http://www.marinespecies.org/aphia.php?p=taxdetails&id=177745
- Cordeiro R, van Ofwegen L, Williams G (2018h) World List of Octocorallia. *Eunicea* Lamouroux, 1816. http://www.marinespecies.org/aphia.php?p=taxdetails&id=2913225
- Cordeiro R, van Ofwegen L, Williams G (2018i) World List of Octocorallia. *Placogorgia* Wright and Studer, 1889. http://www.marinespecies.org/aphia.php?p=taxdetails&id=125312
- Crampon JE (Ed.) (2005) Station logs of the R/V 'Velero IV', 1948–1985, in two parts. Part I, June 1948 to December 1971; Part II, January 1972 to June 1985. University of Southern California, 1–793 [Part I], 795–1537 [Part II]. [+ Errata]
- Crisp DJ (1990) Gregariousness and systematic affinity in some North Carolinian (USA) barnacles. Bulletin of Marine Science 47(2): 516–525.
- Cutress CE, Pequenat WE (1960) Three new Zoantharia from California. Pacific Science 14: 89–100.
- Dall WH (in Williamson MB, 1892) An annotated list of the shells of San Pedro Bay and vicinity, with descriptions of two new species by WH Dall. Proceedings of the United States National Museum 15(898): 179–220. [pls 19–23] https://doi.org/10.5479/si.00963801.15-898.179
- Dana JD (1846) Zoophytes. United States Exploring Expedition during the years 1838, 1839, 1840, 1841, 1842, under the command of Charles Wilkes, USN Vol. 7. Lea and Blanchard, Philadelphia, 740 pp. [45 text figs Atlas, Zoophytes. 61 pls, 1849; See nos. 21, 22, 25, and 26 in Haskell DC: The United States Exploring Expedition, 1838–1842 and its publications 1844–1874. Greenwood Press, New York, 1968.]

- Darwin C (1854) A monograph on the subclass Cirripedia 2. Balanidae, Verrucidae. Ray Society of London, 684 pp. [11 text figs, 30 pls]
- Deichmann E (1936) XLIX. The Alcyonaria of the western part of the Atlantic Ocean. Memoirs of the Museum of Comparative Zoology at Harvard College, Vol. LIII. Cambridge, Massachsetts, 1–317. [37 pls] https://biodiversitylibrary.org/page/4363631
- Duchassaing P, Michelotti G (1860) Mémoire sur les Coralliaires des Antilles. Mémorie della Reale Accademia delle Scienze di Torino (ser. 2) 19: 279–365. [Reprint paged 1–88] https://doi.org/10.5962/bhl.title.11388
- Duchassaing P, Michelotti G (1864) Supplement au Mémoire sur les Coralliaires des Antilles. Mémorie della Reale Accademia delle Scienze di Torino (ser. 2) 23: 97–206. [Reprint paged 1–112]
- Duchassaing P, Michelotti G (1866) Supplement au Mémoire sur les Coralliaires des Antilles. Memoria della Reale Accademia delle Scienze di Torino (ser. 2) Tome 23: 1–112. [11 pls]
- Ehrenberg CG (1834) Beitrage zur physiologischen Kenntniss der Corallenthiere im allgemeinen, und besonders des rothen Meeres, nebst einem Versuche zur physiologischen Systematik derselben. Abhandlungen der Königlichen preussischen Akademie der Wissenschaften zu Berlin. Aus dem Jahre 1832. Erster Theil, 380 pp.
- Ekman S (1935) Tiergeographie des Meeres. Akademische Verlagsgesellschaft Leipzig, 542 pp. [244 figs]
- Ekman S (1953) Zoogeography of the Sea. Sidgwick and Jackson, London, 417 pp. [121 figs] https://doi.org/10.2307/1439946
- Fenical W, Okuda RK, Bandurraga MM, Culver P, Jacobs RS (1981) Lophotoxin: a novel neuromuscular toxin from Pacific sea whips of the genus *Lophogorgia*. Science 212: 1512– 1514. https://doi.org/10.1126/science.6112796
- Girard C (1854) Observations upon a collection of fishes made on the Pacific coast of the United States by Lieutenant W.P. Trowbridge, USA for the Museum of the Smithsonian Institution. Proceedings of the Academy of Natural Sciences of Philadelphia 7: 142–156.
- Gomez ED (1973) Observations on feeding and prey specificity of *Tritonia festiva* (Stearns) with comments on other tritoniids (Mollusca: Opisthobranchia). The Veliger 16: 163–165.
- Gordon DP (2009) New Zealand Inventory of Biodiversity. Volume I. Kingdom Animalia. Canterbury University Press: Christchurch, New Zealand, 568 pp.
- Gordon I (1926) Notes on a number of muriceid genera (Alcyonaria, Gorgonaceae), with special reference to spiculation. Proceedings of the Zoological Society of London 1926: 509–531. [pl 1] https://doi.org/10.1111/j.1469-7998.1926.tb08111.x
- Gorzawsky H (1908) Die Gorgonaceenfamilien der Primnoiden und Muriceiden. Inaugural-Dissertation zur Erlangung der philosophischen Doktorwurde der-hohen philosophischen Fakultat der Kongelige Universität Breslau, Buchdruckerei H Fleischmann, Breslau, 49 pp.
- Gotshall DW (1994) Guide to Marine Invertebrates: Alaska to Baja California. Sea Challengers, Monterey, 105 pp.
- Gotshall DW (1998) Sea of Cortez Marine Animals. Sea Challengers, Monterey, 110 pp.
- Gotshall DW (2005) Guide to Marine Invertebrates: Alaska to Baja California (2<sup>nd</sup> edn). Sea Challengers-Shoreline Press, Santa Barbara, 117 pp.
- Gotshall DW, Laurent LL (1979) Pacific Coast Subtidal Marine Invertebrates: A Fishwatcher's Guide. Sea Challengers, Los Osos, CA, 107 pp.

- Grasshoff M (1977) Die Gorgonarien des ostlichen Nordatlantik und des Mittelmeeres. III. Die Familie Paramuriceidae (Cnidaria, Anthozoa). 'Meteor' Forschungs-Ergebnisse D27: 5–76. [figs 1–73]
- Grasshoff M (1988) The genus *Leptogorgia* (Octocorallia: Gorgoniidae) in West Africa. Atlantide Report 14: 91–147. [14 pls]
- Grasshoff M (1992) Die Flachwasser-Gorgonarien von Europa und Westafrika (Cnidaria, Anthozoa). Courier Forschungsinstitut Senckenberg 149: 1–135. [figs 1–155, tabs 1–4, pls 1–7]
- Gray JE (1859) On the arrangement of zoophytes with pinnated tentacles. Annals and Magazine of Natural History (3)4: 439–444. https://doi.org/10.1080/00222935908697159
- Gray JE (1867) Additional note on *Corallium johnsoni*. Proceedings of the Zoological Society of London 1867: 125–127.
- Grigg RW (1970) Ecology and Population Dynamics of the Gorgonians, *Muricea californica* and *Muricea fruticosa* (Coelenterate: Anthozoa). PhD Dissertation, San Diego-California: University of California, San Diego. [Abstracts International, 31B: 2153]
- Grigg RW (1972) Orientation and growth form of sea fans. Limnology and Oceanography 17(2): 185–192. https://doi.org/10.4319/lo.1972.17.2.0185
- Grigg RW (1974) Growth rings: annual periodicity in two gorgonian corals. Ecology 55: 876–881. https://doi.org/10.2307/1934424
- Grigg RW (1975) Age structure of a longevous coral: a relative index of habitat suitability and stability. American Naturalist 109: 647–657. https://doi.org/10.1086/283035
- Grigg RW (1977) Population dynamics of two gorgonian corals. Ecology 58: 278–290. https:// doi.org/10.2307/1935603
- Hardee M, Wicksten MK (1996) Redescription and taxonomic comparison of three eastern Pacific species of *Muricea* (Cnidaria: Anthozoa). Bulletin of the Southern California Academy of Sciences 95(3): 127–140. http://biodiversitylibrary.org/page/39810558
- Harden DG (1969) A histochemical and statistical study of spicule morphology and variation in the genus *Muricea*. Master's Thesis, California State University, San Diego.
- Harden DG (1979) Intuitive and Numerical Classification of East Pacific Gorgonacea (Octocorallia). PhD Dissertation, Illinois: Illinois State University, 214 pp.
- Hickson SJ (1928) Papers from Dr Theodor Mortensen's Pacific Expedition 1914–16. XLVII. The Gorgonacea of Panama Bay together with a description of one species from the Galápagos Islands and one from Trinidad. Videnskabelige Meddelelser Fra Dansk Naturhistorisk Forening 85: 325–422. [pls 4–6]
- Horn GH (1860) Descriptions of three new species of Gorgonidae, in the collection of the Academy. Proceedings of the Academy of Natural Sciences Philadelphia, 12: 233. https://biodiversitylibrary.org/page/1801690
- Horvath EA (2011) An unusual new "sea fan" from the northeastern Pacific Ocean (Cnidaria: Octocorallia: Gorgoniidae). Proceedings of the Biological Society of Washington 124(1): 45–52. https://doi.org/10.2988/10–27.1
- Humes AG, Lewbel GS (1977) Cyclopoid copepods of the genus *Acanthomolgus* (Lichomolgidae) associated with a gorgonian in California. Transactions of the American Microscopical Society 96(1): 1–12. https://doi.org/10.2307/3225957

- Humes AG, Stock JH (1972) Preliminary notes on a revision of the Lichomoligdae, cyclopoid copepods mainly associated with marine invertebrates. Bulletin Zoölogisch Museum, Universiteit van Amsterdam 2(12): 121–133.
- Integrated Taxonomic Information System ITIS (2011). On-line Database. http://www.itis.gov/index.html
- Johnson ME, Snook HJ (1927) Seashore Animals of the Pacific Coast. MacMillan and Company, New York, 659 pp.
- Kent WS (1870) On the calcareous spicula of the Gorgonaceae: their modification of form, and the importance of their characters as a basis for generic and specific diagnosis. Monthly Microscopical Journal 3: 76–94. [pls 41–42] https://doi.org/10.1111/j.1365-2818.1870.tb06326.x
- Kerstitch A, Bertsch H (2007) Sea of Cortez Marine Invertebrates (2<sup>nd</sup> edn). Sea Challengers, Monterey, 124 pp.
- Kölliker RA von (1865) Icones histiologicae oder Atlas der vergleichenden Gewebelehre. Zweite Abtheilung. Der feinere Bau der hoheren Thiere. Erstes Heft. Die Bindesubstanz der Coelenteraten. Verlag von Wilhelm Engelmann, Leipzig, 87–181. [pls 10–19, 13 text figs] https://doi.org/10.5962/bhl.title.11946
- Kükenthal W (1913) Über die Alcyonarienfauna Californiens und ihre tiergeo-graphischen Beziehungen. Zoologische Jahrbucher Abteilung fur Systematik 35(2): 219–270. https:// doi.org/10.5962/bhl.part.16718
- Kükenthal W (1919) Gorgonaria. Wissenschaftliche Ergebnisse der deutsche Tiefsee-Expeditionen 'Valdivia' 1898–99 13(2): 1–946. [pls 30–89]
- Kükenthal W (1924) Gorgonaria. Das Tierreich, Vol. 47. Walter de Gruyter & Company, Berlin, 478 pp.
- Lamarck JB de (1815) Sur les polypiers corticiferes. Mémoires du Muséum Histoire Naturelle, Paris, Vol. 1: 401–416, 467–476. Vol. 2: 76–84, 157–164, 227–240.
- Lamarck JB de (1836) Histoire naturelle des animaux sans vertèbres, ou tableau général des classes, des ordres, et des genres de ces animaux. Deuxième ed. Revue et augmentée...par mm Deshayes GP, Dujardin F, Milne Edwards H, von Nordmann A. Tome deuxième. Histoire des polypes. JB Bailliere, Paris, 684 pp. https://doi.org/10.5962/bhl.title.11562
- Lamouroux JVF (1812) Extrait d'un mémoire sur la classification des polypiers coralligènes non entièrement pierreux. Nouveau Bulletin Sciences par la Société Philomathique, Paris 3(No. 63): 181–188. https://archive.org/details/cbarchive\_42584\_extraitdunmemoiresurlaclassifi9999/page/n2
- Lamouroux JVF (1816) Histoire des polypiers coralligènes flexibles, vulgairement nommés Zoophytes. A Caen, De l'Imprimerie du F Poisson, 560 pp. [pls 1–19] https://doi. org/10.5962/bhl.title.11172
- Lamouroux JVF (1821) Exposition méthodique des genres de l'ordre des polypiers, avec leur description et celles des principales espèces, figurées dans 84 planches; les 63 premières appartenant à l'Histoire Naturelle des Zoophytes d'Ellis et Solander. chez Mme Veuve Agasse, Paris, 115 pp. [pls 1–84] https://doi.org/10.5962/bhl.title.11328
- Langstroth L, Langstroth L (2000) A Living Bay: The Underwater World of Monterey Bay. Series in Marine Conservation, 2. University of California and Monterey Bay Aquarium, Berkeley, 287 pp.

- Lewis CA (1978) A review of substratum selection in free-living and symbiotic cirripeds. In: Chia FS, Rice ME (Eds) Settlement and metamorphosis of marine invertebrate larvae. Elsevier, New York, 207–218.
- Linnaeus C (1771) Mantissa plantarum altera; generum editionis VI (and) specierum editionis II. Laurentii Salvii, Stockholm, Sweden 6: 143–587.
- Lissner AL, Dorsey JH (1986) Deep-water biological assemblages of a hard-bottom bank-ridge complex of the Southern California Continental Borderland. Bulletin of the Southern California Academy of Sciences 85(2): 87–101.
- Marques ACSJ, Castro CB (1995) Muricea (Cnidaria, Octocorallia) from Brazil, with description of a new species. Bulletin of Marine Science 56(1): 161–172. https://www.ingentaconnect.com/content/umrsmas/bullmar/1995/00000056/00000001/art00010
- Matamoros-Rosales R (1984) Sistemática y Distribución de los Corales Blandos (Coelenterata, Octocorallia: Orden Gorgonacea) de la Bahía de Mazatlán Sinaloa, México. Tesis de Biologo, Facultad de Ciencias, Universidad Nacional Autonoma de México, México.
- Mayer P (1903) Die Caprellidae der Siboga-Expedition. Siboga Expedition 34: 1–160. https:// doi.org/10.5962/bhl.title.53742
- McLaughlin PA, Asakura A (2004) Reevaluation of the hermit crab genus *Parapagurodes* McLaughlin and Haig, 1973 (Decapoda: Anomura: Paguroidea: Paguridae) and a new genus for *Parapagurodes doederleini* (Dofiein, 1902). Proceedings of the Biological Society of Washington 117: 42–56.
- McLaughlin PA, Jensen GC (1996) A new species of hermit crab of the genus Parapagurodes (Decapoda: Anomura: Paguridae) from the eastern Pacific, with a description of its first zoeal stage. Journal of Natural History London 30: 841–854. https://doi. org/10.1080/00222939600770471
- Milne Edwards H, Haime J (1850) A monograph of the British fossil corals. Part 1: Introduction; corals from the Tertiary and Cretaceous formations. Palaeontographical Society London, 1–71. [pls 1–11] https://archive.org/details/monographofbriti00miln
- Milne Edwards H, Haime J (1857) Histoire naturelle des coralliaires ou polypes proprement dits, Vol. I. Libraire Encyclopédique de Roret, Paris, 1–326. [8 pls, numbered A1–6, B1, B2] https://doi.org/10.5962/bhl.title.11911
- Muzik KM (1979) A systematic revision of the Hawaiian Paramuriciidae and Plexauridae (Coelenterata: Octocorallia). PhD Dissertation, University of Miami, Coral Gables, Florida, USA.
- Nutting CC (1909) Alcyonaria of the California coast. Proceedings of the United States National Museum 35: 681–727. https://doi.org/10.5479/si.00963801.35-1658.681
- Nutting CC (1910a) The Gorgonacea of the Siboga Expedition. III. The Muriceidae. Siboga Expedition Monograph 13b: 108. [22 pls] https://biodiversitylibrary.org/page/12044392
- Nutting CC (1910b) The Gorgonacea of the Siboga Expedition. IV. The Plexauridae. Siboga Expedition Monograph 13b1: 1–20. [4 pls] https://biodiversitylibrary.org/page/12044392
- Nutting CC (1910c) The Gorgonacea of the Siboga Expedition. VII. The Gorgoniidae. Siboga Expedition Monograph 13b4: 1–10. [pls 1–3] https://biodiversitylibrary.org/ page/12044392
- Nutting CC (1912) Descriptions of the Alcyonaria collected by the US Fisheries Steamer 'Albatross' primarily in Japanese waters during 1906. Proceedings of the United States National Museum, 43(1923): 1–104. [21 pls] https://doi.org/10.5479/si.00963801.43-1923.1

- Olvera U, Hernández O, Sánchez C, Gómez-Gutiérrez J (2018) Two new endemic species of Gorgoniidae (Cnidaria, Anthozoa, Octocorallia) from Revillagigedo Archipelago, Mexico. Zootaxa 4442(4): 523–538. https://doi.org/10.11646/zootaxa.4442.4.2
- Pallas PS (1766) Elenchus zoophytorum systems generum adumbrations generaliores et specierum cognitarum succinactas descriptions cum selectis auctorum synonymis. Hagae Comitum, 451 pp. https://doi.org/10.5962/bhl.title.6595
- Patton WK (1972) Studies on the animal symbionts of the gorgonian coral, *Leptogorgia virgulata*. Bulletin Marine Science 22(2): 419–431. https://www.ingentaconnect.com/content/umrsmas/bullmar/1972/00000022/00000002/art00009?crawler=true
- Philippi RA (1866) Kurze Beschreibung einiger chilenischen Zoophyten. Archiv Für Naturgeschichte 32: 118–120.
- Philippi RA (1892) Los zoofitos Chilenos del Museo Nacional. Anales Museo Nacional Chile, primera seccion (Zoologia) 5: 1–11. [pls 1–2]
- Prahl H von, Escobar D, Molina G (1986) Octocorales (Octocorallia: Gorgoniidae y Plexauridae) de aguas someras del Pacifico colombiano. Revista de Biología Tropical 34(1): 13–33.
  [ill] https://revistas.ucr.ac.cr/index.php/rbt/article/view/24352/0
- Reimer J, Sinniger F (2018) World List of Zoantharia. World Register of Marine species. http://www.marinespecies.org/aphia.php?p=taxdetails&id=488983
- Ricketts EF, Calvin J (1962) Between Pacific Tides (3<sup>rd</sup> edn, Revised by J Hedgpeth). Stanford University Press, Palo Alto, 516 pp.
- Ricketts EF, Calvin J (1968) Between Pacific Tides (4<sup>th</sup> edn, Revised by J Hedgpeth). Stanford University Press, Palo Alto, 614 pp.
- Ricketts EF, Calvin J, Hedgpeth JW, Phillips. DW (1985) Between Pacific Tides (5<sup>th</sup> edn). Stanford University Press, Stanford, 652 pp.
- Riess M (1919) in: (Kükenthal 1919) Gorgonaria. Wissenschaftliche Ergebnisse der deutsche Tiefsee-Expeditionen 'Valdivia' 1898–99 13(2): 1–946. [pls 30–89]
- Riess M (1929) Die Gorgonarien Westindiens. Kapitel 8. Die Familie Muriceidae. Zoologische Jahrbucher Supplement 16(2): 377–420. [pl 8]
- Risso JA (1826) Histoire naturelle des principales productions de l'Europe méridionale et particulièrement de celles des environs de Nice et des Alpes maritimes 4: 1–439. [12 pls (FG Levrault Paris and Strasbourg)] https://doi.org/10.5962/bhl.title.58984
- Rathbun MJ (1902) Descriptions of new decapod crustaceans from the west coast of North America. Proceedings of the United States National Museum 24: 885–905. https://doi. org/10.5479/si.00963801.1272.885
- Satterlie RA, Case JF (1978) Neurobiology of the gorgonian coelenterates, *Muricea californica* and *Lophogorgia chilensis*. II. Morphology. Cell & Tissue Research 187: 379–396. https://doi.org/10.1007/BF00229604
- Satterlie RA, Case JF (1979) Neurobiology of the gorgonian coelenterates, *Muricea californica* and *Lophogorgia chilensis*. I. Behavioural physiology. Journal of Experimental Biology 79: 191–204 www.jeb.biologists.org/content/79/1/191.full.pdf
- Snyderman M (1987) California Marine Life: A Field Guide. Marcor Publishing, Port Hueneme-California, 255 pp.
- Snyderman M (1998) California Marine Life. Roberts Rinehart Publishers, Niwot-Colorado, 192 pp.

- Soler-Hurtado MM, López-González PJ, Machordom A (2017) Molecular phylogenetic relationships reveal contrasting evolutionary patterns in Gorgoniidae (Octocorallia) in the Eastern Pacific. Molecular Phylogenetics and Evolution, 111(2017): 219–230. https://doi. org/10.1016/j.ympev.2017.03.019
- Sowerby I GB (1832) Characters and descriptions of new species of Mollusca and Conchifera collected by Mr Cuming in 1827–1830. Proceedings of the Committee of Science and Correspondence of the Zoological Society of London 1832(2): 25–33, 50–61, 113–120, 173–179, 194–202.
- Sowerby III GB (1881) Thesaurus conchyliorum, Volumes 1–5, or Monographs of genera of shells. London, 1847–1887. https://doi.org/10.5962/bhl.title.10596
- Standing JD, Hooper IR, Costlow JD (1984) Inhibition and induction of barnacle settlement by natural products present in octocorals. Journal of Chemical Ecology 10(6): 823–834. [illustrations] https://doi.org/10.1007/BF00987966
- Stearns REC (1873) Descriptions of a new genus and two new species of nudibranchiate mollusks from the coast of California. Proceedings of the California Academy of Science Series 5: 77–78.
- Stiasny G (1935) Die Gorgonacea der Siboga-Expedition. Supplement I, Revision der Plexauridae. Siboga-Expedition Monograph 13b7: 1–106. [pls 1–7]
- Stiasny G (1937) Deux nouvelles espèces de Plexaurides des Indes Occidentalis. Bulletin du Muséum National Histoire Naturelle, Paris (2) 9(5): 330–336. [7 figs] https://www.biodiversitylibrary.org/part/217795#/summary
- Stiasny G (1943) Gorgonaria von Panama. Aus der Sammlung Dr Theodor Mortensen, Zoologisk Museum, Kopenhagen. Videnskavelige Meddelelser fra den Dansk Naturhistoriske Forening 107: 59–103.
- Stiasny G (1951) Alcyonides et gorgonides des collections du Muséum National d'Histoire Naturelle (II). Memoires du Muséum National d'Histoire Naturelle, Paris (n.s.) A, 3(1): 1–80. [pls 1–22]
- Studer T (1879) Ubersicht der Anthozoa Alcyonaria, welche wahrend der Reise S.M.S. 'Gazelle' um die Erde gesammelt wurden. Monatsbericht der Könilich Preussischen Akademie der Wissenschaften zu Berlin, September-Oktober 1878: 632–688. [pls 1–5]
- Studer T (1887) Versuch eines Systemes der Alcyonaria. Archiv für Naturgeschichte 53(1): 1–74. [pl 1]
- Studer T (1894) Reports on the dredging operations off the west coast of Central America to the Galápagos, to the west coast of Mexico, and in the Gulf of California, in charge of Alexander Agassiz, carried on by the US Fish Commission steamer 'Albatross', during 1891, Lieutenant ZL Tanner, USN, commanding. Bulletin of the Museum of Comparative Zoology 25(5): 53–69.
- Theodor JL (1967) Contribution à l'étude des gorgons. VI. La dénudation des branches de gorgons par des mollusques prédateurs. Vie et milieu 18(1–A): 73–78.
- Theodor JL (1970) Distinction between "self" and "not-self" in lower invertebrates. Nature 227: 690–692. https://doi.org/10.1038/227690a0
- Thomson JA (1927) Alcyonaires provenant des campagnes scientifiques du Prince Albert Ier de Monaco. Résultats des Campagnes Scientifiques Monaco 73: 1–77. [pls 1–6]

- Thomson JA, Simpson JJ (1909) An account of the alcyonarians collected by the Royal Indian Marine Survey Ship Investigator in the Indian Ocean. II. The alcyonarians of the littoral area. Trustees of the Indian Museum, Calcutta, 319 pp. https://doi.org/10.5962/bhl.title.8279
- Tixier-Durivault A (1969) Les Alcyoniidae des Tuamotu (Murur-oa) et des Gambier. Cahiers du Pacifique 13: 133–156. [May]
- Tixier-Durivault A (1970a) Octocoralliaires. Campagne de la 'Calypso' au large des côtes atlantiques de l'Amérique du Sud (1961–1962). Annales de l'Institut Océanographique Monaco 47: 145–169.
- Tixier-Durivault A (1970b) Les octocoralliaires de Nouvelle-Calédonie. L'Expédition française sur les récifs coralliens de la Nouvelle-Calédonie 4: 171–350. [figs 1–173]
- Tixier-Durivault A (1970c) Les octocoralliaires de Nha-Trang (Viet-Nam). Cahiers du Pacifique 14: 115–236. [figs 1(map)-74. (September 1970.) Map, fig. 1, is a fold-out not within the pagination]
- Valenciennes A (1846) Zoophytes. In: Du Petit-Thouars A (Ed.) Voyage autour du monde sur la frégate la 'Venus', pendant les années 1836–1839. Atlas de Zoologie (No text.) pls 1–15.
- Valenciennes A (1855) Extrait d'une monographie de la famille des Gorgonidees de la classe des polypes. Comptes Rendus Académie des Sciences, Paris 41: 7–15. [Abridged English translation in Annals and Magazine of Natural History (2)16: 177–183. This describes the first use of sclerites in classification; no illustrations.] https://doi.org/10.5962/bhl.part.28683
- Verrill AE (1864) List of the polyps and corals sent by the Museum of Comparative Zoology to other institutions in exchange, with annotations. Bulletin of the Museum of Comparative Zoology at Harvard College 1(3): 29–60. https://archive.org/details/cbarchive\_33759\_ listofthepolyps and corals sent by 1863/page/n2
- Verrill AE (1866) On the polyps and corals from Panama with descriptions of new species. Proceedings of the Boston Society of Natural History 10: 323–357.
- Verrill AE (1868a) [1868–1870] Notes on Radiata in the Museum of Yale College. 6. Review of the corals and polyps of the west coast of America. Transactions of the Connecticut Academy of Arts and Sciences, (First Edition) 1: (377–422, 1868; 423–502, 1869; 503–558, 1870. [pls 5–10] [The regular edition up to page 502 was destroyed by fire after distribution of the author's edition of 150 copies; the reprinted edition issued in 1869 contains nomenclatural changes marked "Reprint" and thus constitutes a separate publication.] https://biodiversitylibrary.org/page/13465394
- Verrill AE (1868b) Notes on Radiata in the Museum of Yale College. No. 6. Review of the corals and polyps of the West Coast of America. Transactions of the Connecticut Academy of Arts and Sciences (2<sup>nd</sup> edn) 1(2): 377–422.
- Verrill AE (1868c) Critical remarks on halcyonoid polyps in the museum of Yale College, with descriptions of new genera. American Journal of Science and Arts 45: 411–415.
- Verrill AE (1869a) Notes on Radiata in the Museum of Yale College. No. 6. Review of the corals and polyps of the West Coast of America. Transactions of the Connecticut Academy of Arts and Sciences (2<sup>nd</sup> edn) 1(2): 423–502.
- Verrill AE (1869b) Critical remarks on the halcyonoid polyps with descriptions of new species in the Museum of Yale College, no. 4. American Journal of Science and Arts, series 2 48: 419–429. https://doi.org/10.2475/ajs.s2-48.143.244

- Weinkauff HC (1881) Die Gattungen *Cypraea* und *Ovula*. In: Martini and Chemnitz, Systematisches Conchylien Cabinet (2<sup>nd</sup> edn) 5(3): 167–215. https://doi.org/10.5962/bhl.title.53460
- Williams GC (1992) The Alcyonacea of southern Africa. Gorgonian octocorals (Coelenterata, Anthozoa). Annals of the South African Museum 101(8): 181–296. www.biodiversitylibrary.org/part/74548#/summary
- Williams GC (2013a) New taxa and revisionary systematics of alcyonacean octocorals from the Pacific Coast of North America (Cnidaria, Anthozoa). ZooKeys 283: 15–42.https://doi. org/10.3897/zookeys.283.4803
- Williams GC (2013b) The Deepest Known Corals. California Academy of Sciences, San Francisco, California. http://researcharchive.calacademy.org/research/izg/orc\_home.html
- Williams GC, Lindo KG (1997) A Review of the Octocorallian Genus *Leptogorgia* (Anthozoa: Gorgoniidae) in the Indian Ocean and Subantarctic, with Description of a New Species and Comparisons with Related Taxa. Proceedings of the California Academy of Sciences 49(15): 499–521. [12 figs, 2 tabs] https://www.biodiversitylibrary.org/part/52978#/summary
- Wright EP, Studer T (1889) Report of the Alcyonaria collected by HMS 'Challenger' during the years 1873–1876. Challenger Reports: Zoology 31(64): 1–314. [pls 1–43] https://www. archive.org/details/reportonscientif04grea/page/87/mode/1up

# Appendix I

## List of material examined – Part II

(Material examined = whole colony study plus multiple sclerite preparations; all with light microscopy, plus selected colonies under SEM, shown in figures associated with text)

#### Adelogorgia phyllosclera Bayer, 1958

**Material examined.** -25 lots. **USA, California** – fragments, plus full colony; San Diego County, San Diego, Point Loma, 32°41'28"N, 117°16'53"W, station PL-13, no depth recorded; coll. SCCWRP, Sea Quest, 10 September 1975; LACoMNH Marine Biodiversity Center and SBMNH 422894 [wet]. – 1 fragment; Los Angeles County, off the southern California Channel Islands, seaward of Newport Beach, 33°34'02"N, 118°02'20"W, 96 m; coll. M Love via submersible 'Delta', 6 October 2005; (his number: A6651), SBMNH 422893 [wet]. –1 colony; Los Angeles County, Catalina Island, Bird Rock, 33°27'00"N, 118°29'14"W, 50 m; coll. R Given, July 1977; SBMNH 51252 [wet]. –1 colony; Los Angeles County, Santa Catalina Island, .33 miles, 180° T from Ship Rock Light, 33°27'19"N, 118°29'34"W, 58 m; coll. R/V 'Velero IV', station 2132-52, 22 July 1952; SBMNH 422308 [wet]. –1 colony; Los Angeles County, Santa Catalina Island, 4 miles, 140° T from Ship Rock Light, at Isthmus Cove, by dredge, 33°27'36"N, 118°28'58"W, 76 m; coll. R/V 'Velero IV', station 12400-68, 17 October 1968; SBMNH 423087 [dry]. –1 colony; Los Angeles County, off Santa Monica, South Banks, 33°53'00"N, 118°31'00"W, by trawl, 82–100 m; coll. unknown,

10 October 1978; SBMNH 422892 [wet]. MEXICO, Baja California Sur (Pacific Coast) - multiple fragments; southwest of Punta San Eugenio, 8.5 miles S of Canal de Dewey, 27°42'15"N, 115°05'02"W, 89 m; coll. R/V 'Velero III', station 1259-41, 27 February 1941; SBMNH 422309; [wet]. -3 colonies; Isla Natividad, 7.5 miles SSW of island, 27°44'17"N, 115°14'40"W, 115–120 m; coll. R/V 'Velero III', station 1258-41, bottom of loose rocks, coral, 27 February 1941; SBMNH 422403 [dry]. MEXICO, Baja California Norte (Pacific Coast) - multiple colonies; 8 miles W of Isla Cedros, 28°05'45"N, 115°31'35"W, 117-118 m; coll. R/V 'Velero III', station 1253-41, 26 February 1941; SBMNH 422310 [wet]. -multiple colonies/fragments; 1.5 miles off north end of Isla Cedros, 28°23'20"N, 115°11'52"W, 100-109 m; coll. R/V 'Velero III', station 1264-41, 28 February 1941; SBMNH 422311 [wet]. CENTRAL AMER-ICA - 1 colony, (no base); Panamá, Veraguas, off Bahía Honda, rock, sand and mud, 07°45'35"N, 81°35'35"W, 55-91 m; coll. R/V 'Velero III', station 863-38, 01 March 1938; SBMNH 423058 [dry]. SOUTH AMERICA - multiple fragments; northern Pacific Ocean, Ecuador, Galápagos Islands, Off Bindloe (=Marchena Island), 00°18'20"N, 90°31'00"W, 27 m; coll. R/V 'Velero III', Station 310-35, 3 December 1934; SBMNH 422312 [wet]. -1 colony (bleached); southern Pacific Ocean, Galápagos Islands, Santa Cruz Island, off Gordon Rocks, 00°33'30"S, 90°09'45"W, 46–55 m; coll. R/V 'Velero III', station 317-35, 8 December 1934; SBMNH 422891 ('Velero' label written in error, 317-37) [wet]. Note: Specimens listed from Central/South America possibly one or more of several new species recently described by Breedy and Guzmán 2018.

**Other material examined. USA, California** – 1 fragment; San Diego County, taken off shore, BI 53-4, SIO 61-517, 32°38'33"N, 117°15'34"W, 30 m, with dredge; coll. unknown, 19 November 1953 (0900); SIO-CO 457 [wet]. –2 fragments; San Diego County, SI 50, from Canyon Rim, 80 m; coll. unknown, 2 October 1965; SIO-CO 1683 (two specimens in the one lot) [wet]. –San Diego County, Canyon Rim, SL 49-b. 80 m; coll. R Grigg, 2 October 1965 (1200); SIO-CO 1605 [wet]. –San Diego County, off La Jolla, Station 8, La Jolla Canyon, 114-40 m, rock dredge–rock, sand, clay; coll. unknown, 7 January 1954; SIO-CO 1588 [wet]. –multiple colonies; San Diego County, La Jolla, La Jolla Canyon, South Wall, 64 m; coll. C Limbaugh and party, 11 September 1957; [NMNH collection, no catalog number, dry]. –Los Angeles County, Santa Monica, 33°52'08"N, 118°34'05"W, 73 m; coll. unknown, 29 March 1974; SIO-CO 1579 [wet].

**Other material, not examined. USA, California** – San Diego County, San Diego, 32°45'06"N, 117°30'00"W, 9–24 m; coll. C Limbaugh, Station 1166, 3 July 1906; USNM 57456 [wet]. –2 colonies; USA, California, San Diego County, La Jolla, 400 miles west of Point La Jolla, 18–21 m; coll. C Limbaugh, 14 December 1953; Para-type–USNM 50187 [dry]. –6 colonies; USA, California, San Diego County, La Jolla, La Jolla Canyon, 46–52 m; coll. C Limbaugh, 8 October 1955; Paratype–USNM 50188 [dry]. –1 colony; USA, California, San Diego County, La Jolla Canyon, 40–43 m; coll. R Ghilardi and party, 19 January 1956; Paratype–USNM 50635 [dry]. –USA, California, San Diego County, La Jolla Canyon, 40–43 m; coll. R/V 'Albatross', Station 4328, 8 March 1904; USNM 51320 [dry].

#### Eugorgia daniana Verrill, 1868

Material examined. ~10 lots MEXICO, Baja California Sur (Pacific Coast) – 1 colony; 2 miles, 220° T from Punta San Eugenio, 27°49'30"N, 115°05'10"W, 38 m; coll. R/V 'Velero IV', station 11514-67, 15 June 1967; SBMNH 422895 [wet]. MEXICO, Baja California Norte (Pacific Coast) – 1 colony; Isla Cedros, coast side, 28°13'00"N, 115°10'00"W; coll. Pacific BioMarine, received from Carmelita Freeman, 26 April 1974; SBMNH 422897 [DH 423 = SBMNH-10]; [dry]. –1 colony; Isla Cedros, 10 miles S of Punta Norte on east side of island, 28°13'00"N, 115°10'00"W, 9 m; coll. R McPeak, 22 February 1983; SBMNH 422404 (B1545) [dry]. MEXICO, Baja California Norte (Gulf of California) – 1 colony; Bahía de Los Angeles, Isla Mitlan, 29°04'00"N, 113°31'00"W, 6 m; coll. R McPeak, 12 September 1980; SBMNH 422405 [dry]. MEXICO (Gulf of California) – 1 colony; Sonora, Bahía de Cholla (= Choya), 31°20'46"N, 113°38'14"W; coll. J Wilkins, 23 February 1959; SBMNH 422896 [DH 433 = SBMNH-20] [dry].

**Other material examined** – fragment; northern Pacific Ocean, Mexico, Baja California Sur, offshore island of Isla Socorro, outside Punta Tosca, ~18/19°00'00"N, 112°00'00"W, 21 m; coll. unknown, 4 February 1964; SIO CO 1686 [wet]. –1 colony; northern Pacific Ocean, Mexico, Baja California Sur, Puerto (Bahía) San Bartolomé (Tortugas or Turtle Bay); coll. unknown, 14 March 1961; USNM 52484 [dry]. –fragment; USA, California, San Diego County, Loma Sea Valley, due west of Point Loma, by otter trawl 1, ST-908, 326–351 m; coll. Fager party, 21 January 1965; SIO CO 1684 (Acc. No. BI 65-33) [wet]. –1 colony; California, San Diego County, San Diego, Escondida Bay; coll. unknown, 14 November 1868; USNM 57302 [dry].

#### Eugorgia rubens Verrill, 1868

Material examined. ~ 50 lots. USA, California - 1 colony; California Channel Islands, on a specimen shell of Haliotis sorenseni (SBMNH 349096); coll. Leon Bray, 1964 [dry]. -1 fragment; Orange County, 1 mile S of Newport Harbor, 33°36'30"N, 117°54'30"W, vertical south face of shale reef, 17 m; coll. R Given, by hand, SCU-BA, 05 October 1957; SBMNH 422313 [wet]. -1 colony (stripped); Santa Catalina Island, 1.5 miles, 130° T from Long Point Light, urchins, crinoids, dead brachiopod, diversified, very rich, 33°23'48"N, 118°21'16"W to 33°22'57"N, 118°19'54"W, 84 m; coll. R/V 'Velero IV', Station 2226-53, 28 February 1953; SBMNH 422314 [wet]. -1-2 colonies; Los Angeles County, Santa Catalina Island, between Avalon and Long Point, 33°23'30"N, 118°21'50"W, 55-80 m; coll. R/V 'Velero III', station 1167-40, 08 August 1940; SBMNH 422407; SBMNH-14 [dry]. -colony fragments; Los Angeles County, .33 miles, 180° T from Santa Catalina Island, Ship Rock Light, dredge-brachiopods, rocky sand bottom, 33°27'19"N, 118°29'34"W, 58 m; coll. R/V 'Velero IV', station 2132-52, 22 July 1952; SBMNH 422315[wet]. -multiple fragments; Los Angeles County, 7.35 miles, 89° T to Manhattan Beach Pier, 33°53'18"N, 118°32'45"W, 58 m; coll. R/V 'Velero IV', station 24493-76, 10 March 1976; (with label- AHF 24493, BLM Ref. station 360; Leg. Mo. 08); SBMNH 422099 [wet]. fragment; Los Angeles County, off Rocky Point, close to Point Vicente, S end of Santa Monica Bay, -33°44'33"N, 118°25'28"W; coll. by C Limbaugh; 5 October 1941; SBMNH 422898 [wet]. -multiple fragments; Los Angeles County, 10.75 miles W. of Point Dume, on loose rock, sponge, 34°00'00"N, 119°01'20"W, 87 m; coll. R/V 'Velero III', station 1276-41, 23 March 1941; SBMNH 422324 [wet]. -1 colony; Ventura County, Rincon, 34°22'27"N, 119°28'27"W, 98 m; coll. P Brophy, commercial otter trawl, 01 May 1968; SBMNH 422901 [DH 421 = SBMNH-08; dry]. -1 colony; Ventura County, Anacapa Island, 34°01'00"N, 119°21'43"W, 11 m; coll. B Scronce and M Conboy, by hand, SCUBA, 29 January 1964; SBMNH 422900 [DH 432 = SBMNH-19; dry]. -1 colony; Ventura County, Anacapa Island, 34°01'00"N, 119°21'43"W, reef and cove, northeast end of island, 11 m; coll. B Scronce and party, by hand, SCUBA, 29 January 1964; SBMNH 45561 [ex MacGinitie collection; wet]. -1 colony; Ventura County, Anacapa Island, 34°01'00"N, 119°21'43"W, reef and cove, northeast end of island, 17-18 m; coll. B Scronce and party, 29 January 1964; SBMNH 45562 [ex MacGinitie collection; wet]. -1 fragment; Ventura County, Anacapa Island, windward side, 34°00'36"N, 119°24'02"W, 15-24 m; coll. M Hamann and S Bobzin, 21 February 1998; SBMNH 345323 [wet]. -1 colony; Santa Barbara County, Santa Cruz Island, 34°01'14"N, 119°41'05"W, seaward side; 15–18 m; coll. W Hary, February 1967; SBMNH 422411 [dry]. -1 colony fragment; Santa Barbara County, basin off Santa Cruz Island (Santa Barbara Basin/Channel), 15.5 mi., 139°T, from Santa Barbara Light, Santa Barbara, CA, 34°20'15"N, 119°37'45"W, 51 m; coll. T Phillips, R/V 'Velero IV', station 13617-69, 13 November 1969; SBMNH 422409 [DH 428 = SBMNH-15; dry]. -small colony and fragments; Monterey County, Point Sur, 36°16'07"N, 121°55'13"W, 65 m; coll. T Laidig, NMFS-FED, Santa Cruz, 13 October 2007; SBMNH 235537 [dry]. MEXICO, Baja California Sur (Pacific Coast) - several fragments; 28 miles, 199° T from Abreojos Light, S of Punta Abreojos, dredge-brachiopods, #12 coarse sand and rock, 26°17'15"N, 113°41'45"W (end), 100 m; coll. 'Velero IV', station 1709-49, 7 March 1949; SBMNH 422327 [wet]. -1 colony; 6.5 miles, 167° T from Punta Abreojos, dredge-coarse mud and sand, mud bottom, 26°35'27"N, 113°31'45"W (end), 51 m; coll. R/V 'Velero IV', station 1954-50, 29 April 1950; SBMNH 422316 [wet]. -2 colonies; SE of Isla Asunción, pinnacles near the "6 fathom spot,27°06'28"N, 114°17'30"W, 23-27 m; coll. RH McPeak, station B, 11-14 Nov. 1981; SBMNH 422412 [dry]. -2 colonies; 8.5 miles south of Canal de Dewey, sand, broken shell, gravel, 27°42'15"N, 115°05'02"W (end), 89 m; coll. R/V 'Velero III', station 1259-41, 27 Feb. 1941; SBMNH 422323 [wet]. MEXICO, Baja California Norte (Pacific Coast) - 1 colony; Islas San Benitos, 28°18'10"N, 115°33'20"W, in *Phyllospadix*, 5 m; coll. Santa Catalina Island Lab, 15 August 1977; SBMNH 422413 [dry]. -1 colony; 8 mi. SW of Isla Cedros, green, fine sand, coral, 28°00'00"N, 115°29'00"W (end), 115–118 m; coll. R/V 'Velero III', station 1254-41, 26 Feb. 1941; SBMNH 422318 [wet]. -several colonies; 8 miles W of Isla Cedros, gravel, loose rock, 28°05'45"N, 115°31'35"W (end), 116-118 M; coll. R/V 'Velero III', station 1253-41, 26 Feb. 1941; SBMNH 422317 [wet]. -1 colony; 1.5 miles off N end of Isla Cedros, fine sand, broken shell, 28°22'18"N, 115°11'00"W (end), 82– 100 m; coll. R/V 'Velero III', station 1263-41, by small dredge, 28 Feb. 1941; SBM-NH 422329 [wet]. –1 fragment; 1.5 miles off N end of Isla Cedros, shale, pebbles, 28°23'20"N, 115°11'52"W (end), 100–109 m; coll. R/V 'Velero III', station 1264-41, by small dredge, 28 Feb. 1941; SBMNH 422328 [wet]. –multiple fragments; 6.5 miles SW of Punta San Carlos, dredge, rocky bottom, 29°33'30"N, 115°35'28"W (end), 36 m; coll. R/V 'Velero IV', station 1944-50, 25 April 1950; SBMNH 422325 [wet]. –1 colony; 4 mi. N of Isla Todos Santos, on rock, 31°52'10"N, 116°49'25"W (end), 73 m; coll. R/V 'Velero III', station 1244-41, 24 Feb. 1941; SBMNH 422319 [wet]. **MEXICO, Baja California Sur (Gulf of California)** – 1 fragment; E of Isla San Francisco (Francisquito), sandy mud, 24°47'25"N, 110°31'20"W, 109 m; coll. R/V 'Velero III', station 651-37, 9 March 1937; SBMNH 422330 [wet].

Other Material Examined. USA, California – San Diego County, San Diego, off Point Loma, 32°35'05"N, 117°20'02"W, 91-101 m, by otter trawl; coll. R/V 'E.B. Scripps' (student cruise), A Fleminger, 15 November 1980; SIO-CO 912 [wet]. -1 colony; San Diego County, Canyon Rim, 80 m; coll. R Grigg, Cruise SI 49a, 2 October 1965; (was SIO/BIC CO 1593(b), now SIO-CO 2087(a)); [wet]. -1 fragment; San Diego County, Canvon Rim, 77–80 m; coll. unknown, Cruise SI 50, 02 October 1965; (was SIO/BIC CO 1683(a), now SIO-CO 2088, 2089 or 2090) [wet]. -San Diego County (?), Sea Lab SL 49-d, 80 m; coll. R Grigg, 2 October 1965; SIO-CO 1578 [wet]. -San Diego County, La Jolla, La Jolla Canyon, 47 m; coll. R Ghilardi and party, 4 March 1959; SIO-CO 1685; [wet]. -1 colony; San Diego County; Station 2104, 86 m; det. M Lilly and D Pasko, City of San Diego, MBL, 26 July 1996; [dry]. –1 colony; Los Angeles County, San Clemente Island, NE side, at Forbidden Reef, 33°00'51"N, 118°20'37"W; coll. J Cooper, 11 June 1982; MLML CO 109 [wet]. -Los Angeles County, Santa Monica, 33°52'08"N, 118°34'05"W (end), 73 m; 29 March 1974; SIO-CO 1629 [wet]. –Ventura County, Anacapa Island, south side, 34°00'00"N, 119°26'00"W, 15–26 m; coll. FG Hochberg, 20 November 1964. LA-CoMNH No. 64-28 [wet].

#### Eugorgia ljubenkovia sp. nov.

**Material examined.** 5 lots; two specimens of species in SBMNH collection from Mexico; another 3 lots, collected by staff of OCSD in California waters, now housed at SBM-NH. – fragment; USA, California, Orange County, off Huntington Beach, by Van Veen grab, ~33°36'34"N, 118°02'32"W, 30 m; coll. OCSD, Survey 94–100, station 34, Rep. 1, 1994; material from J Ljubenkov; SBMNH 472234 [wet]. –numerous fragments; USA, California, Orange County, off Huntington Beach, otter trawl, ~33°35'41"N, 117°59'34"W, 35 m; coll. OCSD, Survey 8718, station T-2, Rep. 1, Haul 1, 13 January 1987; Bottle 0011, SBMNH 472232 [wet]. –1 colony + fragment; USA, California, Orange County, off Huntington Beach, otter trawl, at night, ~33°35'57"N, 118°02'47"W, 36 m; coll. OCSD, Survey 8836, station T-6, Rep. 1, 1988; Bottle 0080, SBMNH 472233 [wet]. **MEXICO, Baja California Norte y Sur** – 1 strand; 28 miles south of Punta Abreojos, bearing 199° T from Abreojos Light, 26°17'30"N, 113°41'45"W, 98 m; coll. R/V 'Velero IV', station 1709-49, 7 March 1949; SBMNH 472245 [wet]. –colony fragments; Isla Cedros, S Bay, dredge—sand and mud, *Lovena* (heart urchin), sponges, 28°04'21"N, 115°17'50"W (end), 29 m; coll. R/V 'Velero IV', station 1703-49, 5 March 1949; SBMNH 422333–**Holotype** [wet].

# Leptogorgia chilensis (Verrill, 1868)

Material examined. ~25 lots. USA, California - 1 colony (partial); Los Angeles County, Farnsworth Bank, dredge—bryozoan, 33°20'39"N, 118°30'55"W (end), 15 m; coll. R/V 'Velero IV', 1904-49, 7 September 1949; SBMNH 422940 [wet]. -1+ colony; Los Angeles County, 5 miles, 152° from San Pedro Breakwater, 33°38'20"N, 118°12'00"W, 31-35 m; coll. R/V 'Velero III', station 1232-41, 15 February 1941; SBMNH 423066 [wet]. -1+ colony + fragments; Los Angeles County, 2.25 miles south of San Pedro Breakwater, 33°40'30"N, 118°14'20"W, 27 m; coll. R/V 'Velero III', station 1207-40, 24 November 1940; SBMNH 423067 [wet]. -two fragments; Los Angeles County, Palos Verdes Estates, 33°47'18"N, 118°24'47"W; coll. T Burch, station 40129, 22 August 1940; SBMNH 422954 [wet]. -multiple fragments; Los Angeles County, 7.35 miles, 89° T to Manhattan Beach Pier, 33°53'18"N, 118°32'45"W (end), 58 m; coll. R/V 'Velero IV', station 24493-76, 10 March 1976; SBMNH 422943 [wet]. -2 colonies; Ventura County, Anacapa Island, 34°00'14"N, 119°23'41"W, 6 m; coll. unknown, 24 January 1963; with hydroid colony on one branch; SBMNH 422944 [wet]. -1 colony; Ventura County, Anacapa Island, 100 yards out from Cat Rock, 34°00'13"N, 119°25'16"W, 17-18 m; coll. B Scronce and party, 30 October 1962; SBMNH 422945 [wet]. -1 colony; Santa Barbara County, -6 miles south and west of Summerland coast, on northwest corner of Platform "A", ~34°20'49"N, 119°38'25"W, ~39 m; coll. S Clark, 3 December 2010; SBMNH 265962 [wet]. -1 colony; Santa Barbara County, Goleta, Sands Beach, 34°24'00"N, 119°53'00"W, ~6 m; coll. R/V 'Vantuna' Cruise, 469-Mar. Bio, November 2001; SBMNH 422953-Neotype [wet]. MEXICO, Baja California Sur (Pacific Coast) - 1 colony + branch fragments; 6.5 miles, 167° T from Punta Abreojos, dredgecoarse mud and sand, mud bottom, 26°35'27"N, 113°31'45"W (end), 51 m; coll. R/V 'Velero IV', station 1954-50, 29 April 1950; SBMNH 422947 [wet]. -2 colonies; Canal de Dewey, opposite Punta San Eugenia, coralline, rock, 27°49'40"N, 115°06'20"W (end), 38-47 m; coll. R/V 'Velero III', station 1260-41, 27 February 1941; SBMNH 422949 [wet]. -1 colony; 2 miles, 220° T from Punta San Eugenia, 27°49'30"N, 115°05'10"W (end), 38 m; coll. R/V 'Velero IV', station 11514-67, 15 June 1967; SBMNH 422950 [wet]. MEXICO, Baja California Norte (Pacific Coast) - 1 fragment; South Bay, Isla Cedros, rock, along margin of kelp bed, 28°04'45"N, 115°21'05"W, 18-27 m; coll. R/V 'Velero III', 287-34, 10 March 1934; SBMNH 422951 [wet]. -1 colony, incomplete; 6.5 miles SW of Punta San Carlos, dredge-rocky bottom, 29°33'30"N, 115°35'28"W (end), 36 m; coll. R/V 'Velero IV', station 1944-50, 25 April 1950; SBMNH 422952 [wet].

Other material examined. USA, California – 3 fragments; San Diego County, Canyon Rim, 73 m; coll. R Grigg, Cruise SI 49a, 4 October 1965; SIO/BIC 1593(a) [wet]. -1 strand; San Diego County, Canyon Rim, 70-73; coll. unknown, Cruise SI 50, 2 October 1965; SIO/BIC CO 1683(c) [wet]. -2 lots; colony/fragments; San Diego County, Scripps Submarine Canyon, off Scripps Institute, 15-21 m & 23-30 m; coll. C Limbaugh, December 1953; [Limbaugh Collection, NMNH, dry]. -1+colony/ fragments; San Diego County, La Jolla Canyon, one quarter mile off Scripps Institute, 46 m; coll. C Limbaugh, 23 July 1954; [Limbaugh Collection, NMNH, dry]. -colony/ fragments; San Diego County, one quarter mile off Point La Jolla, edge of kelp bed, 18-21 m; coll. C Limbaugh, 14 December 1953; [Limbaugh Collection, NMNH, dry]. -colony/fragments; San Diego County, 1 mile north of La Jolla, 29 m; coll. C Limbaugh, 11 February 1952; [Limbaugh Collection, NMNH, dry]. -1 colony; Los Angeles County, San Clemente Island, NE side of island, Forbidden Reef, 33°01'26"N, 118°20'17"W; coll. J Cooper, by SCUBA, 11 June 1982; MLML C0108 [wet]. -colony/fragments; Los Angeles County, Redondo Beach, Santa Monica Bay, Streetcar Reef, ~33°51'00"N, 118°25'04"W, 15 m; coll. unknown, 18 July 1961; [Limbaugh Collection, NMNH, dry]. -colony/fragments; Los Angeles County, Redondo Beach, Santa Monica Bay, Streetcar Reef, 18 m; coll. unknown, 14 September 1961; [Limbaugh Collection, NMNH, dry]. –colony/fragments; Ventura County, ~10 miles south of Santa Barbara, California, Richfield Oil Island, 5–9 m; coll. unknown, 16 May 1961; [Limbaugh Collection, NMNH, dry]. -1 colony (possibly this species); Santa Barbara County, S side of Santa Cruz Island, Smuggler's Cove, 34°01'13"N, 119°32'25"W, washed up on cobbles; coll. N Moore, det. EA Horvath, photographed only, 10 March 2008 [dry]. MEXICO, Baja (Pacific Coast) - colony/fragments; MEXICO, Baja California Sur, Bahia Tortugas area, ~15–18 m; coll. J Stewart, November 1959; [Limbaugh Collection, NMNH, dry]. -colony/fragments; MEXICO, Baja California Norte, Isla Guadalupe, 42 m; coll. J Stewart and party, February 1960 [Limbaugh Collection, NMNH, dry].

**Other material, not examined** – 1 specimen: USA, California, Santa Barbara County, Santa Cruz Island, Smuggler's Cove, 21 m.; coll. B Scronce and party, by diving, 24 January 1963; [DH 426 = SBMNH-13 [dry], missing from SBMNH collection.

# Leptogorgia diffusa (Verrill, 1868)

**Material examined.** 4 lots. **MEXICO (Gulf of California)** – 1 colony; Sonora, Cabo Tepoca, 30°15'45"N, 112°53'20"W, on shore–rock and reef; coll. R/V 'Velero III', station 1077-40, 4 February 1940; SBMNH 423089 [dry]. –multiple colonies; Sonora, off Rocky Point, mud, sand and shell, 31°19'50"N, 113°39'10"W (end), 18–20 m; coll. R.V 'Velero III', station 1072-40, 2 February 1940; SBMNH 423088 [dry]. –1 colony; Sonora, Bahia de Choya (Cholla), ~31°21'19"N, 113°37'26"W; coll./legit. JW with # 038-1, 25 February 1959; SBMNH 423090 [dry].

**Other material examined** –1 colony; USA, California, San Diego County, San Diego, off shore; coll. J Stewart, 1965; CAS IZ 97890 [dry].

# Leptogorgia filicrispa Horvath, 2011

**Material examined.** ~9 lots. **USA, California** – 2 fragments (1 lot); Ventura County, off Ventura Harbor, collected with ovulid snails, 34°14'00"N, 119°19'00"W, 20–50 m; coll. P Brophy, trawled by dragnets, August 1968; SBMNH 423079 [housed in vial, in ovulid snail collection, *Neosimnia* nec *Simnia loebbeckeana*, SBMNH 423103, dry]. **MEXICO, Baja California Sur (Pacific Coast)** – multiple colonies (1 lot); off Boca Flor de Malva, SE of Punta Tosca, 24°11'07"N, 111°21'03"W, 69–87 m; coll. J McLean on R/V 'Searcher', Station 31–32, No. 71–16, 1 February 1971; SBMNH 423057–**Holotype** [DH 415 = SBMNH-06, dry].

**Other material examined. MEXICO (Gulf of California)** – several fragments: Gulf of California, Sonora, Mexico, Guaymas, 28°15'00"N, 111°48'00"W (end), 64-75 m; coll. unknown, 21 March 1960; USNM 75099 [wet]. -numerous fragments/colonies; Sonora, Cabo Tepoca, 30°20'30"N, 113°08'00"W, 56-67 m; coll. R Parker, 31 March 1960; (with a station number: P-212-60); USNM 1106683 [dry]. MEXICO, Baja California Sur (Pacific Coast) - multiple fragments/colonies; Cabo San Lucas Canyon, ~22°54'09"N, 109°22'45"W, on sand bottom, 30 m; coll. W North and C Limbaugh, March 1959; USNM 1106685 [dry]. -multiple fragments; off Boca Flor de Malva, SE of Punta Tosca, 24°11'07"N, 111°21'03"W, 69-87 m; coll. J McLean on R/V 'Searcher', Station 31-32, No. 71-16, 1 February1971; LA-CoMNH—Holoparalectotype [DH 218, SBMNH06, dry]. -multiple fragments; off Boca Flor de Malva, SE of Punta Tosca, 24°11'07"N, 111°21'03"W, 69-87 m; coll. J McLean on R/V 'Searcher', Station 31-32, No. 71-16, 1 February1971; LA-CoMNH—Holoparalectotype [DH 415, SBMNH06, dry]. -multiple fragments; Cabo San Lazaro, 24°48'00"N, 112°19'12"W, by shrimp trawler, 65-73 m; coll. C Limbaugh, sometime in the 1950s; USNM 1106684 [dry]. -several fragments; Magdalena Bay, ~24°38'11"N, 111°58'15"W, 86 m; coll. unknown on R/V 'Albatross', 8 April 1889; USNM 57144 [wet]. -multiple fragments; SW Punta San Juanico, outer coast, ~26°12'33"N, 112°30'49"W, (no depth recorded); coll. unknown, 29 January 1971; LACoMNH [DH240, dry].

# Leptogorgia flexilis (Verrill, 1868)

**Material examined.** 5 lots. **USA, California** – 1 colony fragment (base missing); Los Angeles County, San Pedro, 6.9 miles, 139° T from Point Fermin, dredge–sand, 33°37'04"N, 118°11'50"W (end), 45 m; coll. R/V 'Velero IV', 2042-51, 20 July 1951; SBMNH 422941 [wet]. –2 lots; colony, fragmented; Los Angeles County, between White's Point and Portuguese Bend, 33°42'54"N, 118°20'07"W (end), by beam trawl, 22 m; coll. R/V 'Velero IV', station 1644-48, 19 November 1948; SBMNH 422942 [dry & wet]. **MEXICO, Baja California Sur (Pacific Coast)** – fragments; 28 miles, 199° T from Abreojos Light, S of Punta Abreojos, dredge–brachiopods, beam trawl–# 12 coarse sand and rock, 26°17'15"N, 113°41'45"W (end), 100 m; coll. R/V 'Velero IV', station 1709-49, 7 March 1949; SBMNH 422946 [wet]. –1 colony + multiple fragments; 2 miles, 142° T from Thurloe Head, 27°35'45"N, 114°49'15"W, no depth recorded; coll. R/V 'Velero IV', station 11842-67, 7 December 1967; SBMNH 422948 [wet].

## Leptogorgia sp. A (? = Leptogorgia tricorata Breedy and Cortés 2011)

Material examined. ~10-11 lots. USA, California – 2 colonies, 1 fragment; 9.5 miles NW of buoy, Cortes Bank, white sand, rock, 32°33'15"N, 119°15'15"W, 91 m; coll. R/V 'Velero III', station 1342-41, 10 June 1941; SBMNH 423080 [wet]. -4 colonies; Los Angeles County, Santa Catalina Island, 1 mile SW of Ben Weston Point, mud, sand, gravel, 33°20'55"N, 118°30'45(35)" W (end), 82-89 m; coll. R/V 'Velero III', station 1316-41, 17 May 1941; SBMNH 422334 [wet]. -1 colony; Los Angeles County, Santa Catalina Island, Bird Rock, ~33°27'05"N, 118°29'10"W, 46 m; coll. R Given, July 1977; SBMNH 423083 [wet]. -1 fragment; Los Angeles County, Santa Catalina Island, off Bird Rock, rock, coarse shell, kelp; sm. dredge boat, 33°27'20"N, 118°29'00"W (end), 56-73 m; coll. R/V 'Velero III', station 1187-40, 29 September 1940; SBMNH 423081 [wet]. -1 fragment; Ventura County, Santa Barbara Island, N of island, 33°30'58"N, 119°00'50"W, on gray sand, 67-73 m; coll. R/V 'Velero III,' station 1177-40, 9 September 1940; SBMNH 422903 [wet]. -2 colony fragments; Los Angeles County, off Rocky Point, close in proximity to Point Vicente (S end of Santa Monica Bay), ~33°44'33"N, 118°25'28"W; coll. C Limbaugh, 5 October 1941; SBMNH 423082 [wet]. -numerous colonies/fragments; 10.75 miles W of Point Dume, on loose rock and sponge, 34°00'15"N, 119°01'30"W (end), 86-87 m; coll. R/V 'Velero III', station 1276-41, 23 March 1941; SBMNH 422340 [wet]. -fragment; Santa Barbara County, Channel Island area, ~34°06'56"N, 119°42'49"W, by trawl; coll. P Brophy; SBMNH 423084 [wet].

**Other material examined** – fragment; Mexico, Baja California Norte (Gulf of California), NE of Isla San Jose, Isla Las Animas, 28°42'14"N, 112°55'43"W, epizooic on "black coral, 36–42 m; coll. Adcock and Markham, Station D-24B, 11 August 1965 (identified in error by Harden as *Heterogorgia tortuosa*); CAS-IZ 96757 [wet]. –1 colony; USA, California, San Diego County, near coast of San Diego, no depth recorded; coll. J Stewart (UCSD diver), 1965 (identified in error by Harden as *H. tortuosa*); CAS-IZ 98140 [dry]. –1 strand; USA, California, San Diego County, Canyon Wall (1200), 82 m; coll. R Grigg, Cruise SL 49c, 2 October 1965; SIO-CO 1594 [wet]. –colony fragment; USA, California, Ventura County, Channel Islands, 10 miles E of San Nicolas Island, ~33°12'19"N, 119°43'29"W, 91 m; coll. (possible 'Albatross' collection, according to Harden; identified in error as *Heterogorgia papillosa*), 29 March 1917; CAS-IZ 34636 [wet].

**Other material, not examined** – Japan, Shizuoka, Honshu Island, Suruga Bay, Omae Zaki, 34°35'00"N, 138°15'00"E; coll. R/V 'Albatross', station nos. 3727-3735, US Fish Commission, 16 May 1900, 62–89 m; USNM 50248 [wet].

## Chromoplexaura marki (Kükenthal, 1913)

Material examined. ~60 lots. USA, California - (?)1 colony; Ventura/Los Angeles County, 20-22 miles south of San Nicolas Island, rocky, 32°51'00"N, 119°23'45"W, 118-136 m; coll. R/V 'Velero III', 1344-41, 11 June 1941; SBMNH 423071 [wet]. -4 fragments (2 lots); Los Angeles County, Santa Catalina Island, 5 miles SE of Church Rock, 33°16'00"N, 118°13'45"W (end), 215 m on sand, loose washed rock; coll. R/V 'Velero III', Station 1350-41, 12 June 1941; SBMNH 265946 [wet]. -multiple fragments/colonies (two lots); Los Angeles/Ventura County, off San Nicolas Island, with sponge, rock, 33°16'10"N, 119°24'30"W (end), sponge and rock, 51-56 m; coll. R/V 'Velero III', 1123-40, 12 April 1940; SBMNH 423061 [wet]. -3 colonies, 1 fragment; Los Angeles County, 2.5 miles SE of Seal Rocks, Santa Catalina Island, 33°17'20"N, 118°15'35"W (end), rock, lumpy gray sand, sponge, urchin, gorgonians, hermits, 158-173 m; coll. R/V 'Velero III', station 1429-41, 25 October 1941; SBMNH 265948 [wet]. -1 colony; Los Angeles County, 5 miles, 152° T from San Pedro Breakwater, 33°38'20"N, 118°12'10"W (end), coarse sand, dead shell, clay, 31-35 m; coll. R/V 'Velero III', 1232-41, 15 February 1941; SBMNH 423066 [wet]. -1 colony; Los Angeles County, 2.25 miles south of San Pedro Breakwater, 33°40'30"N, 118°14'20"W (end), sand, pebble, broken shell, 27 m; coll. R/V 'Velero III', 1207-40, 24 November 1940; SBMNH 423067 [wet]. -multiple fragments (bearing numerous brittle stars); Santa Barbara County, Santa Cruz Island, 13 miles, 5° T to Gull Island Light, 33°44'00"N, 119°51'00"W, 155 m; coll. R/V 'Velero IV', station 24329-76, 21 January 1976; SBMNH 265935 (with label reading: 24329 BFI) [wet]. –fragment; Santa Barbara County, 16.5 miles SE X S of South Point, Santa Rosa Island, 33°38'35"N, 119°58'05" (end) W, rocks, crinoids, brittle stars, 131-140 m; coll. R/V 'Velero III', station 1397-41, 27 August 1941; SBMNH 265936 [wet]. -1 colony; Santa Barbara County, Santa Rosa Island, 6.27 miles, 341° T to Ford Point, 33°48'45"N, 119°59'20"W (end), 104 m; coll. R/V 'Velero IV', station 23065-75, 18 October 1975; SBMNH 265937 (with label reading: 23065 6C) [wet]. -1 colony; Santa Barbara, County, San Miguel Island, 3.7 miles, 21° T to Crook Point, 33°56'48"N, 120°21'42"W (end), 118 m; coll. R/V 'Velero IV', station 24882-76, 28 April 1976; SBMNH 265949 (with label reading: 24882 CH) [wet]. -1 colony; Santa Barbara County, south side of Santa Cruz Island, gray sand, shell, 33°57'45"N, 119°38'20"W (end), 67-73 m; coll. R/V 'Velero III', 1191-40, 30 September 1940; SBMNH 423068 [wet]. -1 colony; 2.6 miles, 140° T to Cavern Point, Santa Cruz Island, 34°04'30"N, 119°34'18"W (end), 76 m; coll. R/V 'Velero IV', station 24863-76, 27 April 1976; SBMNH 423064 [wet]. -1 colony (fragments); Ventura County, 1 mile, 231.5° T from Ventura Pier Light, 34°10'00"N, 118°26'57"W, no depth; coll. R/V 'Velero IV', station 5828-58, 21 August 1958; SBMNH 265947 [wet]. -(?)1 colony; Monterey County, off San Jose Creek Beach (N end), Carmel Submarine Canyon, 36°32'00"N, 121°56'00"W, 12-38 m; coll. J H McLean; 1960-1964; SBMNH 423070 [wet] (formerly part of Los Angeles County Museum collection). -1 small colony; Monterey County, Point Sur, 36°17'02"N, 121°57'09"W, 56 m, on large rock; coll. D Starr, NMFS-FED, Santa Cruz, 13 October 2007; SBMNH 235536 [dry]. -1 fragment; Monterey County, southwest of Point Pinos, 36°37'25"N, 121°58'25"W, rock and sponges, 47 m; coll. R/V 'Velero III', 891-38, 8 August 1938; SBMNH 423062 [wet]. -1 colony; Monterey County, Monterey Bay, 1.15 miles, 347° T from Point Pinos Light, on rock, 36°38'54"N, 121°56'15"W; coll. R/V 'Velero IV', station 6437-59, 30 September 1959; SBMNH 423065 [wet]. -fragments; Monterey County, Monterey Bay, off Point Pinos, rock, crinoids, brittle stars, 36°39'50"N, 121°58'00"W, 89-98 m; coll. R/V 'Velero III', station 890-38, 8 August 1938; SBMNH 423063 [wet]. -1 colony; Monterey County, Monterey, 36°47'00"N, 122°02'00"W, ~22 m; coll. T Burch, BLM Ref. Sta. 360, 18 August 1940, with label (Burch # 40128); SBM-NH 423060-Neotype [dry]. -1 colony + fragments; Monterey, Monterey, 36°47'00"N, 122°02'00"W, ~22 m; coll. T Burch, possible BLM Ref. Sta. 360, 18 August 1940, with label (Burch # 40128); SBMNH 423072 [wet]. -1 colony; Monterey County, Monterey, 36°47'00"N, 122°02'00"W, ~30-45 m; coll. T Burch (Acc. No. 3665), BLM Ref. Sta. 360, 18 August 1940; SBMNH 422954 [wet]. -1 colony; Santa Cruz County, Santa Cruz, 36°57'07"N, 122°00'36"W, 30 m; coll. Kinnetics Lab; Station 1, 7 July 1978; with barnacles growing on the colony, where some branches come off of main "stem;" SBMNH 423069 (previous no. 40612, not in Data Base; specimen originally labeled *Psammogorgia torreyi*). [wet]. USA, Oregon – 1 colony plus fragments; Lincoln County, 15 nautical miles off coast of Newport, Oregon, Station NH-15, 44°39'28"N, 124°24'29"W, 85 m; coll. R/V 'Yaquina', Cruise Y6906C, 27 June 1969; SBMNH 423073 [wet].

Other material examined. USA, California - multiple fragments; San Luis Obispo County, 27° off Avila Beach, starting just N of bell buoy, around Souza Rock, ~35°10'35"N, 120°44'16"W, 36 m; coll. R/V 'NB Scofield', Field No. 53-B-25, 9 June 1953; CAS-IZ-96742 [wet]. -1 colony; San Luis Obispo County, ~10 miles S of Morro Bay, near Point, ~35°22'01"N, 121°02'55"W, 9 m; coll. abalone diver via scuba ("Ed"), 1964; CAS-IZ 97951 [dry]. -1 colony; Monterey County, between Point Lobos and Sabrina Point, ~36°31'28"N, 121°57'03"W, 364 m; coll. Capt. Alioti, on Shrimper 'Jackie Boy' (lot 2), 4 March 1972; CAS-IZ 96735 [wet]. -1 colony; Monterey County, Carmel Bay, off San Jose Creek Beach (Monastery Beach), ~36°31'34"N, 121°55'50"W, 38 m; coll. D Sullivan, 20 May 1962; CAS-IZ 96746 [wet]. -1 colony + 1 fragment; Monterey County, Monterey Bay, bearing S 25° E, 5.4 miles off Point Piños lighthouse, ~36°35'49"N, 122°00'13"W 170 m; coll. USBCF 'Albatross', station 4543, Haul # 816, 1904 SIO/BIC CO 361 [wet]. -1 colony/fragments; Monterey County, Monterey Bay, bearing N 87° W, 1.74 miles off Point Piños lighthouse, ~36°38'30"N, 121°57'45"W, 64 m; coll. USBCF 'Albatross', station 4441, 1904SIO/BIC CO 1810 [wet]. (Both SIO/BIC CO 361 and CO 1810, are labeled *P. arbuscula*; this is in error, based on location data.) -1 colony; Monterey County, Monterey Bay, Monterey Bay Canyon Wall, ~36°52'37"N, 121°56'50"W, 500–600 m; coll. C Mah, R/V 'Point Sur', 28 February 1997; CAS-IZ 108905 [wet]. -2 colonies; Monterey County, Monterey
Bay, Continental Shelf, ~36°52'37"N, 121°56'50"W, 150-160 m; coll. C Mah, R/V 'Point Sur', 14 April 1998; CAS-IZ 113071 [wet & dry]. -colonies; Monterey County, Monterey Bay, Monterey Canyon, canyon wall, ~36°52'37"N, 121°56'50"W, 600-700 m; coll. C Mah, R/V 'Point Sur', 14 April 1998; CAS-IZ 113072 [wet]. -1 colony; San Francisco County, ? Farallon Islands, ~37°44'22"N, 123°03'13"W, no depth recorded; coll. unknown, with exception of "Trawl no. PC1-1: sample no. 1," 23 September 1991; CAS-IZ 96747 [wet]. -1 colony; Humboldt County, Blunt's Reef, off Cape Mendocino, California, ~40°25'56"N, 124°27'28"W; coll. Turkington, May 1910; det. by Bayer; USNM 51500 [dry]. USA, Oregon and Washington - 1 colony; no specific location data, 600 m; coll. A Carey Jr., R/V 'Acona', Station OTB-36 16 June 1964; CAS-IZ 143903 [wet]. -1 colony and 1 fragment; Coos County, off coast, Coquille Bank, ~42°54'23"N, 124°51'16"W, 257 m; coll. P Etnoyer, NOAA "West Coast Survey, Fall 2010, 3 November 2010; BS004 (CB 50001-002) and BS005 (CB 50001-003) [wet]. -fragment; off Oregon coast, Heceta Bank, 43°55'58"N, 124°55'55"W, 140 m; coll. Heceta RB-00-05, G Hendler; RV 'Ronald H. Brown' (NOAA) and S/V 'Ropos', Dive R534-Rk-009, 24 June 2000; LACoMNH Marine Biodiversity Center processing number 233 [wet]. -fragment; off Oregon coast, Heceta Bank, 43°56'52"N, 124°56'36"W, 189 m; coll. Heceta RB-00-05, G Hendler; RV 'Ronald H. Brown' (NOAA) and S/V 'Ropos', Dive R535-Bio-2, 3, 4, or 13, 24 June 2000; LACoMNH, Marine Biodiversity Center processing number 379 [wet]. -1 colony; off Oregon coast, Heceta Bank, 43°58'07"N, 124°51'10"W, hard bottom covered with invertebrates, 117.9 m; coll. A Valdés by ROV; RV 'Ronald H. Brown' (NOAA) and S/V 'Ropos', Dive 615, 10 July 2001; LACoMNH, Marine Biodiversity Center processing number 100 [wet]. -1 colony; off Oregon coast, Heceta Bank, 43°59'16"N, 124°52'59"W, rocky area, collected with a large rock, 81.1 m; coll. A. Valdés by ROV; RV 'Ronald H. Brown' (NOAA) and S/V 'Ropos', Dive 613, 9 July 2001; LACoMNH Marine Biodiversity processing center number 85 [wet]. -1 colony; off Oregon coast, Heceta Bank, 44°09'11"N, 124°49'29"W, 81 m; coll. Heceta RB-00-05, G Hendler; RV 'Ronald H. Brown' (NOAA) and S/V 'Ropos', Dive R530-Bio-0012, 21 June 2000; LACoMNH, Marine Biodiversity Center processing number 205 [wet]. -1 colony; off Oregon coast, Heceta Bank, 44°11'08"N, 124°48'24"W, rocky bottom, collected with rock, 74.3 m; coll. R Embley by ROV; RV 'Ronald H. Brown' (NOAA) and S/V 'Ropos'; Dive 608, 7 July 2001; LACoMNH, Marine Biodiversity Center processing number 56 [wet]. -2 colonies; off Oregon coast, Heceta Bank, 44°11'14"N, 124°50'03"W, rocky bottom, collected with rock with gorgonian attached, 81.8 m; coll. N Puniwai by ROV; RV 'Ronald H. Brown' (NOAA) and S/V 'Ropos', Dive 608, 7 July 2001; LACoMNH, Marine Biodiversity Center processing number 55 [wet]. -1 colony; off Oregon coast, Heceta Bank, 44°13'20"N, 124°52'26"W, 98 m; coll. Heceta RB-00-05, G Hendler; RV 'Ronald H. Brown' (NOAA) and S/V 'Ropos', Dive R538-Rk-0003, 26 June 2000; LACoMNH Marine Biodiversity Center processing number 263 [wet]. -2 colonies; Lincoln County, off Newport, -44°40'10"N, 124°27'12"W, 110 m; coll. Dr JE Mc-Cauley, R/V 'Acona', no collection date given; CAS-IZ 24639 [wet]. -2 colonies + fragments; Lincoln County, 112.01 miles SW of Yaquina Head Light, 44°40'00"N,

126°21'12"W, 2,856 m; coll. A Carey, OSU, Station OTB-30, 20 May 1964; SBM-NH 423078 [wet]. –1 colony; Eastern N Pacific, Tillamook County, off Oregon coast, due W of Nehalem Bay State Park, 45°38'55"N, 124°06'03"W, ~80 m; coll. NFSC, 2006 expedition; CB 34213-093, FRAM 100105460 [wet]. –1 colony, North Pacific, off Oregon/Washington border, Clatsop County, due W of Tillamook Head, and mouth of Columbia River, ~46°13'30"N, 124°22'31"W, ~113 m; coll. NFSC, 2006 expedition; CB 34210-023, FRAM 100105455 [wet]. –3 colonies; North Pacific, Grays Harbor County, off Washington State, due W of Quinault Beach Resort, ~47°01'33"N, 124°39'10"W, ~98 m; coll. NFSC, 2006 expedition; CB 34210-025, FRAM 00105453 [wet]. –1 colony, North Pacific, off Washington coast, Grays Harbor County, ~47°06'07"N, 124°32'17"W, 73 m; coll. NFSC, WCGS 2006; CB 34210-020, FRAM 100105450 [wet].

**Other material, location not known.** WCGS 2006, Oregon – CB 34213-047, FRAM 100105469 (provided by E Berntson, NOAA Fisheries Office, Port Orchard, WA).

**Other material, not examined** – several colonies; USA, N Pacific Ocean, California, Monterey County, Carmel, 26 m; [YPM 8877A and YPM 8877B; notation of "questionable form," wet].

#### Muricea californica Aurivillius, 1931

Material examined. ~33 lots. USA, California - (?)1 colony; Orange County, Newport Bay, 33°35'37"N, 117°52'51"W, on rocks of outer jetty, below extended low tide; coll. G MacGinitie, October 1946; SBMNH 422390 [wet]. -multiple colonies/fragments; Orange County, Newport Beach, "The Pipeline," ~33°36'23"N, 117°55'50"W, depth not recorded; coll. Aquarium of the Pacific, Long Beach (for SBMNH Sea Center), early summer, 2010; SBMNH 265938 [wet]. –1 colony; Orange County, Newport Bay, 33°37'11"N, 117°53'41"W, depth not recorded; coll. G Sphon, 08 January 1953; SBMNH 422920 [DH 451 = SBMNH-35; dry]. -2+ colonies; Orange County, off Huntington Beach, with a beam trawl, 33°38'30"N, 118°00'20"W, 7-36 m; coll. R/V 'Velero III', 1127-40, 20 April 1940; SBMNH 422360 [1 dry, others wet]. -1 colony; Los Angeles County, San Pedro, Point Fermin, 33°41'00"N, 118°16'00"W; coll. R/V 'Velero IV', station 1578-46, 20 December 1946; data from label, not Station Log (NOTE: from August 1942-July 1948, no Station Log notes; ship not running consistently during WWII?); SBMNH 422361[wet]. -fragment; Los Angeles County, San Pedro, inside of Point Fermin, on shore-rock wall and loose rock, 33°42'45"N, 118°16'45"W; coll. R/V 'Velero III', station 1217-40, 30 November 1940; SBMNH 422357 [wet]. -multiple colonies; Los Angeles County, San Pedro, Point Fermin, 33°42'18"N, 118°17'35"W, 13 m; with data station number: 50 3 T147, 17 June 1916; SBMNH 422375[wet]. -several colonies in 3 lots; Los Angeles County, San Pedro Breakwater, on shore, 33°42'08"N, 118°16'05"W; coll. R/V 'Velero III', station 1230-41, 26 January 1941; SBMNH 422358 [wet]. -1 colony; Los Angeles County, between White's Point and Portuguese Bend, beam trawl-bryozoa, corals, sea mouse,

gorgonacea, 33°42'54"N, 118°20'07"W (end), 22 m; coll. R/V 'Velero IV', station 1644-48, 19 November 1948; SBMNH 422359 [wet]. -1 colony; Los Angeles County, between White's Point and Portuguese Bend, 33°42'54"N, 118°20'07"W, 22 m; coll. R/V 'Velero IV', station 1644-48, 19 November 1948; SBMNH 422919 [drv]. -1 colony (stripped); Ventura County, Rincon Beach, 30°20'10"N, 119°24'35"W, on beach; coll. N Moore, 2 March 2008; SBMNH 422918 [dry]. -1 colony; Santa Barbara County, Anacapa Island, 34°00'13"N, 119°25'16"W, 100 yards out from Cat Rock, 17–18 m; coll. B Scronce, and party, 30 October 1962; SMBNH 45564; [wet]. -1 colony; Santa Barbara County, Anacapa Island, 34°00'13"N, 119°25'16"W, 100 yards out from Cat Rock, 17-18 m; coll. B Scronce, and party, 30 October 1962; SBMNH 45563; [wet]. -1 colony; Ventura County, Port Hueneme, off the north jetty, 34°09'26"N, 119°13'42"W, 11 m; coll. M Conboy and D Sprong, 16 January 1963; SBMNH 422911 [DH 448 =SBMNH-32; dry]. -3 colonies; Ventura County, Port Hueneme, 34°09'26"N, 119°13'42"W, 11 m; coll. M Conboy and D Sprong, 16 January 1963; SBMNH 422913 [DH 449 =SBMNH-33, dry]. -2 colonies; Santa Barbara County, Carpinteria, several miles east of Carpinteria State Beach, 34°23'36"N, 119°31'31"W, between splash and high inter-tidal, up on rocks and exposed beach; coll. EA Horvath, between 27-30, January 2006; SBMNH 422372 & 422373 [wet]. -2 colonies; Santa Barbara County, Carpinteria, off Carpinteria State Beach, 34°23'36"N, 119°31'31"W; coll. C Watters and J Henry, det. EA Horvath; 18 February 2008; SBMNH 422914 [dry]. -1 fragment; Santa Barbara County, Santa Barbara, Naples Reef, 34°26'24"N, 119°56'60"W, 15 m; coll. S Anderson and party, 11 November 1998; SBMNH 345324; [wet]. MEXICO, Baja California Sur (Pacific Coast) - 2 colonies + fragments; Cabo San Lucas, 22°52'49"N, 109°54'32"W; coll. unknown, 22 March 1936; SBMNH 422921 [dry]. -1 colony; off Thurloe Head, on rock with gorgonids, 27°36'50"N, 114°50'50"W, 15-18 m; coll. R/V 'Velero III', station 283-34, 9 March 1934; SBMNH 422369 [wet]. MEXICO, Baja California Norte (Pacific Coast) - 1 fragment; Isla Cedros, South Bay, on rock along margin of kelp bed, 28°04'45"N, 115°21'05"W, 18–27 m; coll. R/V 'Velero III', station 287-34, 10 March 1934; SBMNH 422363 [wet]. -2 colonies; Baja, 6.5 miles SW of Punta San Carlos, dredge-rocky bottom, 29°33'30"N, 115°35'28"W (end), 36 m; coll. R/V 'Velero IV', station 1944-50, 25 April 1950; SBMNH 422362 [wet]. MEXICO, Baja California Norte (Gulf of California) - 2 colonies; Roca Consag, 31°12'17"N, 114°33'39"W; coll. L Findley, 9 July 1973; Nos. 207/208, University of Arizona; SBMNH 422376 [wet]. MEXICO (Gulf of California) – 1 colony; Sonora, South of Isla Tiburon, sand, shell, 28°43'45"N, 112°17'50"W, 36 m; coll. R/V 'Velero III', 566-36, 11 March 1936; SBMNH 422384 [wet]. SOUTH AMERICA - 1 fragment; Ecuador, off Cape San Francisco, 00°37'10"N, 80°00'30"W, 27 m; coll. R/V 'Velero III', station 850-38, 23 February 1938; SBMNH 422427 [dry].

**Other material examined. USA, California** – San Diego County, La Jolla, Quast Rock, 21 m; coll. R Kiwala, by scuba, 7 April 1969; SIO/BIC CO 1600 [wet]. –San Diego County, La Jolla, Quast Rock, 20 m; coll. R Grigg, December 1967; SIO/BIC CO 1632. –San Diego County, La Jolla, Quast, 20 m; coll. unknown, October 1966; SIO/BIC CO 1641. –1 lot; San Diego County, Quast Rock, 65 feet; coll. unknown, 29 October 1965; SIO/BIC CO 1945 [wet]. –2 colonies/fragments; Orange County, just south and east of Huntington Beach, ~33°36'50"N, 117°59'13"W, 18 m; coll. OCSD, station T0, Haul 1, 29 February 2012 [wet]. –Los Angeles County, off San Clemente Island, 32°35'29"N, 118°19'02"W, near Station # 2, in restricted area, by SCUBA; coll. J Cooper, 11 June 1982; MLML C0110 [wet]. –colonies/fragments; Los Angeles County, Santa Catalina Island, just outside Blue Cavern Marine Protected Area, near "The Quarry," ~33°25'53"N, 118°26'49"W, depth unknown; coll. Aquarium of the Pacific, Long Beach, early summer, 2010 [wet]. –Los Angeles County, Coast Station, Palos Verdes, off Marineland of the Pacific, 33°43'58"N, 118°25'12"W, 10–15 m; large boulders with sand between; coll. R Grigg, 7 January 1967; SIO/BIC CO 1596. **MEXICO** – Baja California Norte, Punta Banda, station 2 (no other data); 20 July 1968; SIOBIC CO 1943 "a1-a4", and probably "b" as well.

All lots SIO/BIC CO 1860 – CO 1939; most of these lots probably this species, a few mixed in likely *M. fruticosa*, but no specific collection location data is readily available. In the "Limbaugh" Collection housed at NMNH, other collection locations could include: (USA) the Richfield Oil Island (Ventura County, ~10 miles south of Santa Barbara, California), Newport Bay (California), in the Huntington Beach Gas and Electric Steam Plant discharge pipe (California), and from Baja: Gulf of Punta Final, Turtle Bay and off Cape San Lucas. There are SIO/BIC CO 1943 and CO 1945, but these are not included in any official listing, and there appeared to be no data to go with the numbers.

**Other material, not examined** (but photographed) or examined/photographed (not collected) – 1 colony; N Pacific Ocean, USA, California, Los Angeles County, San Clemente, ~33°25'21"N, 117°37'22"W, on the beach; photographer A Nelson, det. EA Horvath; 1 March 2008. –1 colony; N Pacific Ocean, USA, California, Ventura California, Santa Barbara Channel Islands, Anacapa Island, ~34°00'19"N, 119°24'55"W, big tidal pool; photographer N Downend, det. EA Horvath; 14 April 2008.

# Muricea plantaginea (Valenciennes, 1846) [= M. appressa Verrill, 1864]

Material examined. ~4 lots. MEXICO, Baja California Sur (Pacific Coast) – 1 colony; Bahia de Santa Maria, 24°42'20"N, 112°14'10"W, 58 m; coll. R/V 'Velero III', station 760-38, 5 January 1938; SBMNH 422418; [dry]. –1 colony; Punta Asunción, 27°07'28"N, 114°17'48"W, 7 m; coll. RH McPeak, 15 October 1980; SBMNH 422417 [dry]. MEXICO, Baja California Norte (Gulf of California) –1 colony; Isla Partida, off White Rock, 28°55'30"N, 113°05'35"W, 82 m; coll. R/V 'Velero III', station 557-36, 8 March 1936; SBMNH 422416 [dry]. MEXICO (Gulf of California)

-1 colony; Sonora, Guaymas, Ensenada Carrizal, 27°52'12"N, 110°51'00"W; coll. P LaFollette; August 1960; SBMNH 422912 [DH 450 =SBMNH-34; Also: # 0413, and A339, dry].

**Other material, not examined.** USNM 52301 and USNM 52303 were both collected in the N Pacific, USA, California, Los Angeles County, off San Pedro; no

other data given. A third, USNM 94678, may also be this form, as it is from the same collection location. Additionally, from the Limbaugh collection of specimens housed at NMNH, locations for possible examples of this species include: Baja California Sur (Cabo San Lucas; Cape San Lucas Canyon; Bahia de Los Angeles); Baja California Norte (an area near South Cedros Island; perhaps Punta Final and Turtle Bay) and USA, California, San Diego County, La Jolla (Scripps submarine canyon). Further sclerite examinations need to be made.

# Muricea fruticosa Verrill, 1868

Material examined. - 14 lots. USA, California - 1 colony (fragmented); Orange County, Newport Channel, Balboa, shore collected on a -1.6 tide, 33°36'02"N, 117°52'50"W; coll. R/V 'Velero III', station 1224-41, 25 January 1941; SBMNH 422383 [wet]. -1 fragment (albino form or bleached-FG Hochberg); Los Angeles County, Santa Catalina Island, Salta Verde Point, 15 m, 33°19'00"N, 118°25'20-27"W; coll. R Given, 1 May 1967; SBMNH 422389 [wet]. -several colonies; Los Angeles County, Santa Catalina Island, Big Fisherman's Cove, 33°20'40"N, 118°29'07"W, 3 m; coll. R Setzer, 22 August 1968; SBMNH 422374 [wet]. -1 colony; Los Angeles County, Palos Verdes, east of Portuguese Bend, 33°43'00"N, 118°19'57"W, 15 m; coll. unknown, 6 November 1949; SBMNH 422428 [dry]. -1 colony; Los Angeles County, Long Beach, Long Beach Harbor, Back Channel, just east of Terminal Island, 33°45'41"N, 118°13'07"W, 7.6 m; coll. DB Cadien, rocky subtidal station I/S7, 31 March 1980; SBMNH 265945 [wet]. -1 fragment; Los Angeles County, Santa Monica Bay, ~33°56'07"N, 118°27'59"W; coll. Aquarium of the Pacific, Long Beach (for SBMNH Sea Center), early summer, 2010; SBMNH 265940 [wet]. -2 colonies (1 incomplete); Santa Barbara County, Santa Cruz Island, Smugglers Cove, 34°01'19"N, 119°32'31"W, 6 m; coll. B Scronce and party, 24 January 1963; SBMNH 422430 [DH 477 = SBMNH-31, dry]. -1 fragment; Santa Barbara County, Mohawk Reef, 34°23'40"N, 119°43'48"W, 4 m; coll. S Anderson, by hand, SCUBA, 01 November 1998; SBMNH 345325 [wet]. MEXICO, Baja California Sur (Pacific Coast) -1 colony; Escondido Bay area, Isla Danzante to Punta Candeleros, 25°47'15"N, 111°15'30"W; coll. R McPeak, 30 March 1981; SBMNH 422429; [dry]. -1 colony; 2 miles, 142° T from Thurloe Head, 27°35'45"N, 114°49'15"W, no depth reported; coll. R/V 'Velero IV', station 11842-67, 7 December 1967; SBMNH 422910; [wet]. -fragment; Scammons Lagoon, Isla Piedras, high littoral under flat sandstone, 27°46'00"N, 114°15'20"W; coll. W Williams on Kenyon-Williams Expeditions, station M12, 30 April 1946; SBMNH 422387 [wet]. MEXICO, Baja California Norte (Pacific Coast) - 1 colony; Baja, 6.5 miles SW of Punta San Carlos, dredge-rocky bottom, 29°33'30"N, 115°35'28"W (end), 36 m; coll. R/V 'Velero IV', 1944-50; 25 April 1950; SBMNH 422386 [wet]. MEXICO (Gulf of California) - 1 colony; Sonora, Guaymas, "Bahia de Conos" (El Carrisito), 27°52'00"N, 110°54'15"W, subtidal, less than 9 m, attached to rocks; coll. P LaFollette, 8-12 August 1960; SBMNH 422916 [DH 452 =SBMNH-36; ? 0336; ? A332, dry]. -1 colony/2 fragments; Sonora, Guaymas, "Bahia de Conos" (El Carrisito) 27°52'00"N,

110°54'15"W, less than 9 m, attached to rocks; coll. P LaFollette, 5–12 August 1960; SBMNH 422917 [DH 455 =SBMNH-39; ? A20; ? A332; ?0336, dry]. –4 colonies, 2 other fragments; Sonora, Guaymas, Ensenada Carrizal, 27°52'12"N, 110°51'00"W; coll. P LaFollette, 5–13 August 1960; SBMNH 422915 [DH 453 =SBMNH-37; ? PIL-A19; ? A332; ? 0335, dry].

**Other material examined. USA, California** – colony; Dana Point, N of, 33°32'41"N, 117°48'36"W, 48–53 m; coll. T Matsui, with otter trawl on R/V 'Agassiz', 29 March 1974; CO/SIO 1628 (M-15, OT-8) [wet/dry?]. –CO/SIO 1939 also identified as this species, but no other data could be found.

# Placogorgia sp. A

**Material examined.** ~5 lots. **USA, California** – 1 colony, in fragments; Orange County, Oceanside, 33°10'29"N, 117°23'09"W, Station IP-B1046, caught in shark net, 138 m; coll. B Brophy, 1971; SBMNH 422969 [DH 844 = SBMNH-51; dry]. –multiple fragments; Los Angeles County, off Santa Monica, South Banks, 34°00'21"N, 118°29'57"W, 82–100 m; coll. Pacific BioMarine, commercial trawl, 10 October 1978; SBMNH 422970 [wet]. –1 colony fragment; Ventura County, California Channel Islands, NW edge of Hueneme Canyon, 34°02'20"N, 119°18'07"W, 145 m; coll. NMFS Dive 32, 23 September 2011; SBMNH 235579 [dry]. –fragment; Ventura County, California Channel Islands, slightly NE of East Anacapa, 34°02'20"N, 119°18'13"W, 140 m; coll. M Love from submersible 'Delta', 14 October 2005; with his number: A6689; SBMNH 422968 [wet]. **MEXICO, Baja California Norte (Pacific Coast)** – multiple fragments; 5.5 miles S of Islas San Benito, fine green sand, coarse grey sand, 28°13'18(55)" N, 115°33(35)'15(05)" W (end), 120–147 m; coll. R/V 'Velero III', station 1251-41, 26 February 1941; SBMNH 422966 [wet].

**Other material examined** – 1 piece; USA, California, Orange County, northern edge of San Gabriel Canyon, off Huntington Beach, trawl, ~33°33'49"N, 118°08'40"W, 113 m; coll. DB Cadien, EMAP Voucher, Survey SCBPP, southern California Bight, Station 1476 (ID by J Ljubenkov, not collected by MEC), 29 July 1994 [wet].



**Map A1.** Distribution of gorgonian "red whip" forms. Includes species that are predominantly seen as a whip rather than a branched colony as well as several species that, while usually branched, do frequently display a slender, whip-like body type. Ranges determined from all material examined, with emphasis on specimens housed in SBMNH collection.

# Appendix 3

**Table A1.** Contrasts and comparisons of key "red whip" species and/or species of the genus *Swiftia*, as represented in SBMNH collection.

Red Whip species	Location, S to N	Location Depth	Colony Branching	Colony Color	Polyp Spacing	Polyp Height	Sclerite Color	Sclerite Form	Sclerite Size
Leptogorgia flexilis	Magdalena Bay, Baja to San Diego, CA	11 meters to ?	Thin, drooping branches; highly branched colony	Red/pink to tan/beige Polyps white to very pale orange	No more than 1 mm	No more than 1 mm	Bright Salmon	Spindles & Capstans	.03–.09 mm
Leptogorgia chilensis	N of Magdalena Bay to Santa Cruz Is., CA	Approx. 15–80 m	Thin branches; moderately branched	Orange- red Polyps white	1 mm	Generally, almost flush	Bright Salmon	Spindles & Capstans	.0305 mm
Red Whip (?"Transitional/ Regional Endemic")	San Diego, CA to off Oregon coast	?20–2,000 meters	Moderate thickness to branches; slightly branched to not branched	Orange- red Polyps white	Varies from 1 to 2 mm	Generally, from flush to nearly 1 mm; rarely taller	Salmon	Spindles & Dbl. Spinds.	Approx. 0.1 mm
Red Whip (?"Transitional/ Regional Endemic")	San Diego, CA to off Oregon coast; possible extension to WA coast	Approx. 12–150 m	Moderately thin branches, whip-like; slightly branched	Orange- red Polyps white (?pale pink)	Varies from 1 to 2 mm	Generally, consistently flush, rarely taller; on some, prominent	Salmon	Spindles & Dbl. Spinds.	Approx. 0.1 mm
"? <i>Swiftia</i> Transitional/ Regional species"	N Los Angeles County to Point Conception	Approx. 104–173 m	Single branches; also slightly branched (if so, dichotomous)	Bright red to salmon- pink Polyps white	Less than 1 mm	Approx. 1 mm	Salmon	Spindles; very few Capstans, Dbl. Spinds. or Rods	From 0.04 mm to nearly +.16 mm
Swiftia simplex	N Los Angeles County to Alaska	200–900 m	Single branches; sometimes slightly branched	Pinkish-red (Brick-red) Polyps pinkish-red	No more than 2 mm	Approx. 1 mm	Pinkish-red (Brick color) Rods orange	Spindles, Capstans, Rods and Dbl. Spinds.	.1–.3 mm
Chromoplexaura marki	Point Conception to Cape Mendocino, CA (?further north to WA state, on to Alaska)	20–60 m; possibly deeper (to 600 m)	Single branches; sometimes slightly to moderately branched	Bright red, orange, even pinkish Polyps white or colored	2 mm	Nearly flush to 2 mm	Salmon to reddish	Spindles, Capstans, Ovals and Dbl. Spinds; NO Rods	0.05 mm to ~ 0.2 mm
Swifita spauldingi	Monterey Bay, CA to off Washington coast (?further north to Alaska)	40 to at least 300 m	Moderate branch thickness; branched to some degree	Orange- red Polyps white or very pale pink	about 1 mm	Nearly flush to often very conspicuous, rounded	Salmon to pinkish- orange; some yellow; Rods orange	Spindles, Capstans, Rods and Dbl. Spinds.	About 0.1 mm

Polyp Height: includes both calyx and actual polyp.



# A review of gorgonian coral species (Cnidaria, Octocorallia, Alcyonacea) held in the Santa Barbara Museum of Natural History research collection: focus on species from Scleraxonia, Holaxonia, Calcaxonia – Part III: Suborder Holaxonia continued, and suborder Calcaxonia

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#### Abstract

Alcyonacean (Gorgonian) coral species from Holaxonia (not previously reviewed in this three-part work), family Plexauridae, as well as species in Calcaxonia were reviewed. Specimens examined were collected from the California Bight and adjacent areas, many now held in the research collection of the Santa Barbara Museum of Natural History (SBMNH). The collection has incorporated numerous specimens collected by the Allan Hancock Foundation (AHF) 'Velero' Expeditions of 1931–1941 and 1948–1985. This historic collection displays an emphasis on species belonging to the Holaxonia, particularly gorgoniids and plexaurids. This third part of the larger work presented a thorough, in-depth discussion of at least one genus (*Swiftia* Duchassaing & Michelotti, 1864) in the Plexauridae found within the California Bight that has generated some taxonomic confusion; in that discussion are comments on other genera (such as *Psammogorgia* Verrill, 1868a, to which several species had been previously ascribed). The discussion of *Swiftia* includes description of a morphological trend (encompassing colony form, color and sclerite form), likely influenced by geography and ecology, not noted or discussed previously. Additionally, a preliminary discussion of the genus (*Thesea* Duchassaing & Michelotti, 1860) was presented; this genus, both historically

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and currently, has not been fully examined in California waters. Finally, a short review was given for the few species of Calcaxonia represented in the SBMNH research collection. This paper, Part III of the full review, continued and concludes the systematic examination of species represented in the SBMNH research collection begun in Part I, continued in Part II, focusing on all species of gorgonian coral held in the SBMNH research collection, known to currently inhabit the California Bight and adjacent areas.

#### **Keywords**

Allan Hancock Foundation (AHF) – 'Velero' Expeditions, colony form, deep-water gorgonians, geographical/ecological variation, museum collection, sclerite morphology, soft corals, *Swiftia*, *Thesea*, "thread-like" forms

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# Introduction

Species in the family Plexauridae (Holaxonia) are well represented in the Santa Barbara Museum of Natural History's (SBMNH) research collection. While a sufficient number of specimens, representing the genera Swiftia Duchassaing & Michelotti, 1864 and Thesea Duchassaing & Michelotti, 1860, were already present, with the acquisition of gorgonian materials from the Allan Hancock Foundation (AHF) 'Velero' Expeditions, the collection was enhanced. Studies were undertaken to identify (or to correct identification of) not only specimens already in the collection, but the many specimens collected during the 'Velero' years of operation that were being added to the collection. Additionally, the staff of a number of National Oceanographic and Atmospheric Administration (NOAA) facilities throughout the country generously provided additional material, representing the genus Swiftia, for study. In that multiple-year study, the key morphological features were clarified, and an interesting south to north morphological trend, likely predicated on geographic and ecological parameters was defined. Additionally, the SBMNH has an extensive holding of specimens in the genus Thesea collected off California; this genus requires further work. A preliminary discussion of the situation as seen in California waters is presented. Holdings in the genus Thesea have been significantly enhanced by collection and survey work done by both the Los Angeles County and Orange County Sanitation Districts (LACSD, OCSD, respectively). Finally, while representation of the Calcaxonia and its members is not extensive, the SBMNH research collection does include specimens from both the families Primnoidae and Isididae; these are briefly described and discussed, concluding this review of the SBMNH alcyonacean gorgonian research collection, begun with Parts I and II.

# Materials and methods

A large majority of the specimens examined in this work (housed currently as part of the Santa Barbara Museum of Natural History's permanent research collection, invertebrate laboratory), were collected over a period of years dating from the 1930s to the present, in either dry or wet condition. A large percentage of these specimens came to the SBMNH through a diverse 10,000-lot cnidarian collection, a portion of the Allan Hancock Foundation (AHF) collection built upon the historic 'Velero' expeditions of 1931-1941 and 1948-1985. To assist with the identification of the SBMNH specimens, examinations of specimens of known species from or collected in the Bight were performed on material found in the collections of the National Museum of Natural History, Smithsonian (USNM = NMNH), the California Academy of Sciences, San Francisco (CAS), the Los Angeles County Museum of Natural History (LACoMNH), Scripps Institute of Oceanography (SIO), the Monterey Bay Aquarium Research Institute (MBARI), Moss Landing Marine Laboratories (MLML) and the small museum which is a part of the Cabrillo Marine Aquarium in San Pedro, California (CMA) (see Appendix 3: List of material examined). These were compared to SBMNH specimens, informing the identification of species represented in the SBMNH collection. Additionally, several National Oceanographic and Atmospheric Administration (NOAA) offices throughout the country provided further material for study; the genus Swiftia is predominantly represented in that material.

All specimens were examined for gross colony morphology; more importantly, examination of the calcareous sclerites, present in different parts of the colony, was conducted for nearly all specimens. The standard method for sclerite extraction (tissue sample in common household bleach) was performed, and light microscopy via a compound Olympus (CH) microscope, was used initially to determine the genus to which a specimen belonged. Scanning Electron Microscopy (SEM) of the sclerites was then undertaken. All samples were coated with gold, using a Cressington Sputter Coater Unit, 108auto. Samples were examined, and digital images taken using a Zeiss Scanning Electron Microscope EVO 40, at 10 kV. This third part covers some eighteen

# of specimens analyzed with sclerite preparations	~275
# of specimens examined without sclerite preparation	5-10
Breakdown of specimens examined:	
# of specimens analyzed from SBMNH collection	~125
# of specimens analyzed from USNM-Smithsonian	50
# of specimens analyzed from CAS	3–5
# of specimens analyzed from other institutions (primarily NOAA)	~97–100
Breakdown of species examined:	
Total # of species that underwent sclerite observations	~18
# of new species described	0
# of species examined from the SBMNH collection	-9
# of species examined from USNM-Smithsonian	13
# of species examined from CAS	3
# of species examined from other sources (primarily NOAA and Scripps)	10
# of species shown in Figures (colony)	9
# of species shown in Figures (either light microscopy and/or SEM of sclerites)	9

Part III: Collective specimen and species data

	SBMNH	Other institutions	Colony figure	Sclerite figure
Swiftia kofoidi	Yes	Yes	Yes	Yes
Swiftia pacifica	Yes	Yes	Yes	Yes
Swiftia simplex	Yes	Yes	Yes	Yes
Swiftia spauldingi	No	Yes	Yes	Yes
Swiftia torreyi	No	Yes	No	No
Swiftia pusilla	No	Yes	No	No
Thesea spp.	Yes	Yes	Yes	Yes
Thesea variabilis	No	Yes	No	No
Callogorgia kinoshitai	Yes	Yes	Yes	Yes
Parastenella pacifica	Yes	Yes	Yes	Yes
Parastenella ramosa	No	Yes	No	No
Pulmarella longispina	Yes	Yes	Yes	Yes
Primnoa pacifica	No	Yes	No	No
Narella sp.	No	Yes	No	No
Acanella sp.	No	Yes	No	No
<i>Isidella</i> sp.	Yes	Yes	No	No
Keratoisis sp.	Yes	Yes	Yes	Yes
<i>Lepidisis</i> sp.	No	Yes	No	No

Species covered in this part:

species, spread over roughly eleven genera. A summative overview of species housed in the SBMNH research collection is included below.

This information for Part III (examination of colony morphology and sclerites) is a summation of more detailed information found in the Appendix 3: List of material examined – Part III. It is evident from this summative overview that the SBMNH research collection houses species from the holaxonian family Plexauridae, specifically the genera *Swiftia* and *Thesea*, but lacks a comprehensive collection of calcaxonian species present in the California Bight.

#### Systematic accounts

(Classification used throughout this paper conforms to that of Bayer 1981c)

#### Diagnosis of Holaxonia Studer, 1887

With distinct central axis composed of horny material alone or of horny material more or less heavily permeated with calcareous substance, continuous or with alternating horny and calcareous joints. In center of axis is a relatively narrow, largely hollow, tubular space partitioned into series of small chambers, referred to as the cross-chambered central chord. Calcareous material of the peripheral zone of axis is in nonscleritic form (single exception in Keroeididae).

# Key to the genus *Swiftia* and the California "red whips" (many mistaken for *Swiftia* or other "red whip" genera and species)

1 Coenenchyme of moderate thickness, containing spindles and warted clubs; clubs are coarse, irregular thorn-clubs, usually pink or red (no purple or lavender sclerites), uncommonly yellow or white; color of colony a bright red to orange-red ..... Genus Psammogorgia (only briefly discussed for comparison purposes; there are no species of this genus represented in the CA Bight) Coenenchyme of moderate thickness, containing spindles and/or capstans, but no warted clubs; color red, orange, pinkish-red, reddish-purple (genera including those of Leptogorgia, Chromoplexaura, Swiftia; first two genera list-Colonies primarily single, whip-like; or few, slender branches, loose, long; if 2 multiple branches, only loosely flabellate, perhaps irregularly dichotomous. Colonies can be sparsely to rather densely branched, opposite/alternate or pinnate; possibly reticulated. Polyp mounds prominent, conical, creating branch profile such that zig-zag pattern seen. Colors orange-red, salmon, brick-red to deep red or a deep reddish-purple......6 Acute or subacute spindles with warts forming rings/disks; small, thin, mini-3 mally warted anthocodial rods (pale orange); see Part II.... Leptogorgia chilensis Sclerites as spindles, capstans; may have conspicuous fingerbiscuit rods ......4 4 Polyp mounds flush, or very slightly raised as low mounds, or more obvious rounded protuberances. If colonies branched, mostly dichotomous ......5 Polyp-mounds (? calyces) broad conical to cylindrical; with (?) collaret; anthocodia exsert; polyp color generally pale pink to nearly white ..... appearance between L. chilensis and C. marki, see Part II; regional endemic?) 5 Color of colony orange, orange-red or red, with heavy branches, mostly lateral; may appear dichotomous. Anthocodia white; spindles as large doubledunce caps; fingerbiscuit rods absent; shallow to moderately deep water (see Part II).....Chromoplexaura marki Color of colony red/orange, salmon to coral, with moderately heavy branches, irregularly dichotomous. Anthocodia white; polyp mounds rounded protuberances, closely spaced; small, short spindles and double-spindles; fingerbiscuit rods present, heavily warted ...... Swiftia cf. spauldingi Color of colony pinkish red (brick red), few branches round, of moderate uniform diameter. Anthocodia red; polyp mounds not prominently raised, generally flush; large spindles long, thin; pronounced fingerbiscuit rods or6 Color of colony bright orange, polyps white; moderately branched in pinnate pattern. Polyps widely spaced, as large, prominent, conical mounds, usually in irregular biserial rows; anthocodia well-developed, often exsert. Spindles short, thorny; those longer, slender; few to no anthocodial bars (fingerbiscuit rods) ......Swiftia kofoidi Color of anthocodia (well-developed, often exsert) and polyps deep red to deep gray/greenish-red, coenenchyme deep red. Moderately branched; in general, an opposite/alternate pattern. Polyp mounds lateral, prominent, rounded, moderately to closely spaced. Sclerites symmetrical capstans and spindles; anthocodial bars (fingerbiscuit rods) clearly seen, large, warted...... Color of colony deep reddish-purple; branches usually opposite from main stem, commonly anastomosing. Polyp mounds truncated, tubular cones, scattered on all sides of branches, closely spaced. Spindles of moderate length, sometimes slightly curved, deep reddish-purple; anthocodial fingerbiscuit rods orange, very conspicuous...... Swiftia torrevi

# List of species of Holaxonia Studer, 1887

Class Anthozoa Subclass Octocorallia Haeckel, 1866 Order Alcyonacea Lamouroux, 1816 Holaxonia Studer, 1887 Family Plexauridae Gray, 1859 *Swiftia* cf. *kofoidi* (Nutting, 1909) *Swiftia pacifica* (Nutting, 1912) *Swiftia simplex* (Nutting, 1909) *Swiftia cf. spauldingi* (Nutting, 1909) *Swiftia torreyi* (Nutting, 1909) *Swiftia pusilla* (Nutting, 1909) *Thesea* spp.

# Descriptions of species of Holaxonia Studer, 1887

# Genus Swiftia Duchassaing & Michelotti, 1864

Gorgonia (part) Valenciennes, 1855: 12.

Swiftia Duchassaing & Michelotti, 1864: 13. Kükenthal 1924: 236. Deichmann 1936: 185–186. Bayer 1956: F206. Grasshoff 1977: 161. Muzik 1979: 167. Bayer 1981: 945. Breedy et al. 2015: 329.

Stenogorgia Verrill, 1883: 29 [= Swiftia, des. by Deichmann 1936: 186]. Grieg 1887:
5, 18. Studer (and Wright) 1887: 64. Studer 1901: 51. Nutting 1909: 723;
1910c: 6. Jungersen 1917: 1186. Bielschowsky 1918: 45. Kükenthal 1924: 347 (Stenogorgia synonymy).

*Platycaulos* Wright & Studer, 1889: 61, 146–147. Nutting 1912: 94. Bayer 1981: 945. *Callistephanus* Wright & Studer, 1889: 62, 148. Nutting 1912: 96. Bayer 1981: 945. *Allogorgia*, Verrill, 1928: 8.

Thesea (pars) Verrill, 1869: 428.

Filigorgia Stiasny, 1937: 307.

**Type species.** *Gorgonia exserta* Ellis & Solander, 1786: 87 (non *Thesea exserta* Duchassaing & Michelotti, 1860); [= *Stenogorgia* Verrill, 1883].

**Diagnosis.** Colonies chiefly in one plane, with lax branching (dichotomous or pinnate-like); branches/branchlets tend to curve upwards; in some species, anastomoses possible (fan-like); in others, minimal branching or none. Polyps widely scattered, or crowded; often lateral or biserial, forming prominent conical or cylindrical mounds; on tips of branchlets, two polyps always opposed; conical anthostele seldom retracted; generally, polyps retractile. Anthocodiae commonly tall, exsert. Coenenchyme thin to moderate, somewhat rough/granular, outer layer filled not only with spinous rods or spindles, but with capstans having warts more or less conspicuously modified as double disks; some capstans quite foliate; inner layer mostly restricted to areas between longitudinal canals, containing only small capstans. Mound margins, base of tentacles, with numerous rows of conspicuous, stout spindles as bar-like rods, characteristic for species in the genus (fingerbiscuit shaped; see Bayer et al. 1983, pp 72–73, pl 19, figs 184–185). Axis is horny, flexible, somewhat flattened. Colony colors generally red, red-orange, pink or white.

**Etymology.** Deichmann (1936) stated that the definition of the genus *Swiftia* corresponded exactly with *Stenogorgia* Verrill, 1883; the problem discussed there stemmed from a misinterpretation of *G. exserta* Ellis & Solander, 1786 by Verrill (also by Kükenthal 1924). See remarks, following.

**Remarks.** The stout, anthocodial rods (seen at mound margins and bases of tentacles), are definitive for this genus. Examinations of multiple specimens (several different species) within this genus usually revealed the appearance of these rods; when present, looking much like the fingerbiscuit sclerite form shown in Bayer et al. (1983) for the genera *Clavularia* Blainville, 1830 and *Ptilosarcus* Verrill, 1865 (neither of these gorgonian genera), where sclerites are described as minute, flattened rods (rods here have a bit of depth). Further examinations (multiple species) revealed that some individual colonies of species in the genus did not have these conspicuous rod forms (having only spindles and capstans). Other colonies displayed spinous spindles and/ or capstans and anthocodial rods; some few species had only the fingerbiscuit rods, numerous throughout all tissue structures. The rod form is not always easy to obtain in a sclerite array; some specimens without rods may actually have them, but they may be quite small, not very numerous and very widely scattered. A trend observed is that colonies further north in the Pacific (Alaska) have very obvious rods, while specimens of some of the same species collected in California (specifically central and southern California) may have rods, but infrequently. By way of comparison, in several species from the genus examined from waters in/near New Zealand, some had only rods, and no other form of sclerite. It appeared that colder, temperate to subpolar species had the rods (to the exclusion of all others) but species from warmer, albeit temperate water, tended to display a minimal number or complete absence of rods. Examination of many more specimens, collected in both hemispheres from poles to equator, could reveal further insight into the appearance of this key sclerite form. To further clarify questions surrounding location ranges for each of the *Swiftia* species discussed, Appendix 2: Map A1 shows the distributional range of each and Appendix 1: Table A1 shows key features used to distinguish one species from another.

Regarding use of the generic name *Swiftia*, Muzik (1979) stated: "(t)o preserve the generic name <u>Swiftia</u> a petition to" the International Commission on Zoological Nomenclature "(ICZN) must be made;" uncertain as to whether this was ever done. "For a full explanation, see Challenger Reports 31: 146 and Deichmann 1936: 185" (Muzik 1979). The complete explanation can be found in Deichmann (1936) and Muzik (1979: 168); they serve to confirm the confusion that had developed, through the work of previous investigators, regarding generic status for the species discussed below. In Madsen (1970: 5), "A total of about a dozen gorgonarian species referred or referable to *Swiftia* (syn. *Stenogorgia*) from widely scattered localities in all three oceans have been recorded, but only a few of them are sufficiently described." In the WoRMS Database (Cordeiro et al. 2018), status of this genus has been accepted, but Breedy et al. (2015: 329) stated that a "thorough review is needed in order to clarify taxonomic problems related to *Swiftia*." This paper attempts to clarify some of the issues related only to those species that are found in, near, or extending geographically slightly south or north of the California Bight.

#### Swiftia kofoidi (Nutting, 1909)

Figures 1A, B, 2A-G, 15A-E, 16A, B, 17A-C

Stenogorgia kofoidi Nutting, 1909: 724, pl 89 (figs 5, 6), pl 90 (fig. 6).

**Type locality.** USA, California, Monterey Bay, bearing S 67°E, 3.7 mi off Point Piños light-house, ~36°38'00"N, 121°55'00"W, 119–135 m.

Type specimens. Holotype USNM 25432 [wet]; specimen was examined.

Material examined. ~20-25 lots (see Appendix 3: List of material examined).

**Description.** *Colony* (Figure 1A) flabellate, loosely branched, sparsely reticulate; often large areas of open space between branches; on rare occasions, branches anastomose; irregular, pinnate branching chiefly in one plane. Appears moderately delicate; some distance from base, main stem generally divides into several main branches, center one ascending nearly unbranched, lateral ones at first widely divaricating, then



**Figure 1.** *Swiftia kofoidi*, SBMNH 422965 (delicate orange "morph"). **A** Colony 7.5 cm at tallest point, 7.5 cm broad at widest point **B** Closer view of several branch tips showing distinctive placement of the calyces, creating zig-zag profile of each branch. Scale bars: 2 cm (**A**); 1 cm (**B**).

ascending, giving forth pinnate branches which tend to be opposite, often irregular. Branchlets ~6.0 mm apart (where regular), somewhat flattened (0.5–1.0 mm); terminal branchlets usually end with two oppositely disposed polyps (Figure 1B). Polyps form prominent, conical, volcano-shaped mounds, with broad base (not boxy), with distinct exsert anthocodiae; polyps scattered or biserial (Figure 1B), in two irregular, lateral rows, creating a very narrow front and back; laterally, opposite or (often) alternate on branchlets; colony and branch profile appearing in form of zig-zag pattern. Polyps more numerous on front than behind; mound summits 2.0-4.0 mm apart on one lateral side, 0.6–1.0 mm high, surmounted by 0.4–1.0 mm tall anthocodiae, ~1.5 mm across. Margins with eight-lobed edge; outer sides of tentacles crowded with sclerites, tentacles retractile, bent inward at rest. Coenenchyme thin; outer layer filled with spinous rods, spindles, and capstans. Color of living colony typically true salmon, also bright orange to deep coral red; polyps may be same color (paler), cream or white; axis dark greenish-brown, lightening distally. Sclerites (Figure 2A-G) can be always exclusively small to somewhat long, warty (thorny), slender spindles, larger ones often curved. On shorter, thorny ones, some have very prominent, jagged teeth, projecting off one side (reminiscent of sclerites seen in some *Muricea*); also few small, elongated ones with median waists ("some as granules, some as foliate capstans," Nutting 1909). In current examinations, those that almost appeared as radiate nuggets could be the granular-appearing or foliate capstans mentioned by Nutting (1909). As well, some can resemble torches, and can be quite evident; these may be the shorter, thorny ones mentioned above. Mound surface sclerites lie transversely. Sclerites in tentacles described as stout, blunt rods; in all specimens examined (identified as this species), rods were sometimes rarely seen in very small numbers, but never obvious.

**Etymology.** Named in honor of Professor CA Kofoid from the University of California.

**Common name.** None specifically indicated. Could appropriately be called the Orange 'rick-rack' gorgonian.

**Distribution.** Found off California and Oregon coasts (refer to Appendix 3: List of material examined). Off California in locations between 175 and 218 m, off Oregon in 101–106 m, at 126 m and at 138 m. Speculative range from Upper Baja, California, to NE of Tanner Bank in the south (USNM 59817), along southern California coast through Monterey Bay (**Holotype**, USNM 25432), to south of the Farallon Islands, California (USNM 57235). May continue range northward, off the coast (NW) of Portland, Oregon (USNM 53972), at least (as well, possibly USNM 49538 and USNM 56989, both from Heceta Bank, Oregon). Extreme range makes identification of some specimens questionable; possible range overlap with similar-looking species, *S. pacifica* (Nutting, 1912). If following a slightly deeper, moderately cooler, water gradient in southerly locations, then a possibility. Appendix 2: Map A1 shows apparent range of this species in relation to those such as *S. pacifica* and *S. torreyi* (Nutting, 1909) that it might be confused with when viewed in situ.

**Biology.** Appears to be a moderate depth to deep-water species, generally deeper off California coast, slightly shallower in more northerly locales. Several lots of this species in SBMNH collection displayed associated organisms: on several, the attached organism looked like a clump of small bubbles, reminiscent of that which "spittle bugs" produce on branches of some land plants; at least some of these clumps were small anemones. Some specimens had species of hydroid attached; few colonies harbored tiny Ophiuroidea.

**Remarks.** Multiple labels associated with some specimens examined (some with as many as three different labels, each with a different genus/species name, as determined by three separate investigators), complicated identification. This called into question whether all of them were indeed *S. kofoidi*, a different species in the genus *Swiftia* or some other gorgonian (belonging to an entirely different genus); some specimens had been identified previously as belonging to the genus *Psammogorgia* (sclerites did not support this).

Bayer made personal notations in his copy of Nutting (1909), indicating that this species was "stouter than *torreyi*, calyces closer, bars in anthocodiae large and stout. Similar to *Callistephanus pacificus* Nutting, 1912: Pg. 96." This species is stouter than *S. torreyi* (in the form of the polyps, and in total colony height), but polyps rarely as close together as those in *S. torreyi*, nor were the large, stout bars that Bayer mentioned obvious; additionally, the color is completely different for these two. In other respects, specimens strongly match images for this species given by Nutting (1909). Bayer's notation regarding similarity between it and *Callistephanus pacificus* Nutting, 1912 is generally affirmed. Overall, most similar to *Swiftia pacifica*, but *S. kofoidi* is often more open and delicate; many colonies of *S. pacifica* can be thicker-branched and bulky in overall appearance (Figures 15, 21). The bright orange color (salmon), overall delicate appearance, widely-spaced polyp mounds and very distinct, jagged/sharp zig-zag profile (due to predominantly alternate and lateral placement of prominent polyps) of this



**Figure 2.** *Swiftia kofoidi*, SBMNH 422965, SEM image. **A** Potential anthocodial sclerites **B** Very elongated spindles, prevalent in species in CA and Mexican waters **C** Irregular spindles **D** Truncated, diskspindle/capstan forms **E** Unusual quadri-radiate **F** Jagged torch-like form **G** Shorter, jagged spindles

species set it apart from the other two species (*S. pacifica* or *S. torreyi*) that it is often compared with. As indicated in the WoRMS Database (Cordeiro et al. 2019), this species has accepted status.

The California Academy of Sciences (CAS) has some thirty cataloged records (only some identified to species) from this genus in its collection. Eleven of them are from

Alaska and are likely Swiftia pacifica. Of the remaining, sixteen or so were identified as this species. Most of these however, were collected from northern California (Monterey Bay, Humboldt County, Sonoma County, Marin County; many likely the more northerly-dwelling S. pacifica). The Monterey Bay Aquarium Research Institute (MBARI) collection records indicated specimens of this species, collected and/ or surveyed/photographed throughout their study areas (of those identified as this species, many may actually be S. pacifica). One colony examined via video/photo, was T1101-A21; based on colony shape and color, it appeared to be this species. Sclerite examination of the actual specimen could have confirmed it as such but specimen was not collected. Two other data collection events should be considered. However, neither of the specimens in question were located; they apparently are not housed at the National Museum of Natural History, Smithsonian (NMNH). Both from: North Pacific Ocean, USA, California, Monterey County: [Monterey Bay], bearing S 46°E, 8.4 miles off Point Piños light-house and S 76°E, 3 miles off Point Piños light-house, at 1,544 m and 109 m, respectively. Both collected by USBCF 'Albatross', at stations 4546 and 4554, respectively.

# Swiftia pacifica (Nutting, 1912)

Figures 3A, B, 4A–D, 5A, B, 6A–F, 21A, B, 22A–D, 23A, B

Swiftia pacifica (Nutting, 1912): 96, 97, pl 14 (figs 2, 2a) and pl 21 (fig. 6) [= Stenogorgia pacificus Nutting, 1912]: Muzik 1979: 168–173, fig. 26, pl XXVI.
Callistephanus pacificus Nutting, 1912: 96, 97.
Allogorgia exserta Verrill, 1928: 8.
Swiftia rosea pacificus (Nutting, 1912): stat. nov. Madsen 1970: 8.

**Type locality.** For holotype, unknown (erroneously labeled); for type, 'Albatross' Station 4781, 52°14'30"N, 174°13'00"W, south and east of the Bering Sea. (See Remarks below.)

**Type specimens. Holotype** USNM 49513 (colony portion only); **Type** USNM 30024; both specimens were examined.

Material examined. ~23 lots (see Appendix 3: List of material examined).

**Description.** *Colony* moderately sized (up to 18–19 cm tall), planar, flabellate, flexible, rubbery in appearance (Figure 3A); branches nearly forming net-like reticulations, but usually not anastomosing; generally, moderate open appearance to branches. Main stem extends upwards some few cm (above base), 1.0–2.0 mm wide; branches from main stem opposite or alternate, coming off at 45° to 90° angles, then tending upwards; distance between branches 0.5–2.0 cm; terminal branches to 2.0 cm long, 1.0 mm in diameter. Polyps lateral (mostly alternate, sometimes opposite), very few on front, with back generally free of polyps, thus flat; polyps conical (sometimes tubular), three, four or five per cm, arising from small mounds (Figure 3B); anthostele 0.5–2.0 mm H, 1.0–2.0 mm W (seeming rather broad and boxy), anthocodiae preserved exert up to 2.0 mm long, but often appearing as dense tuft with 1.0 mm or less



**Figure 3.** *Swiftia kofoidi* [? *Swiftia pacifica*] (thicker dark red "morph"), SBMNH 232036. **A** Colony measures 6.0 cm tall, 5.5 cm broad at widest point, demonstrating zig-zag appearance of branches due to calycular placement **B** Branch close-up, showing placement of prominent conical calyces on branches; calyces measure ~1.0 mm tall.

showing above polyp mound. At distal end of terminal branches, two (or two pair) oppositely disposed polyps. Color of colony bright to deep crimson or muddy red (brick-red) in life, but both darker and lighter red (dull pink) colonies occur; polyps sometimes dark greenish-grey; sclerites bright red or orange (rods) to pale pinkish-red (most common color, usually true of spindles and capstans). Sclerites (Figures 4A–D,



**Figure 4.** *Swiftia kofoidi* [? *Swiftia pacifica*], SBMNH 232036, SEM image. **A** Truncated, jagged disk-spindle/capstan-like forms **B** Elongated spindles **C** Might be a typical "fingerbiscuit-rod" form typical of the genus; seen very rarely, if at all in this species **D** An irregular spindle.

5A, B, 6A–F) symmetrical; unilaterally developed superficial capstans and spindles, 0.08 to 0.17 mm long in coenenchyme; flatter warty spindles to 0.35 mm in layer below; also eight radiates. Axial sheath sclerites short (to 0.12 mm), narrow-waisted, blunt-ended. Anthocodial bases can have numerous prominent blunt bars (fingerbiscuit rods, in shape comparable to a bacterial rod), curved or straight (Figures 5B, 6D);

arranged transversely at bases, more longitudinal at distal end. Examination of multiple specimens did not always reveal presence of rods, but when present, very obvious. Pinnular scales 0.06–0.1 mm long.

**Etymology.** Species name likely refers to locality where type specimen was collected, outer Aleutian Islands, Alaska in the North Pacific.

**Distribution.** North Pacific Ocean, Aleutian Islands, Alaska down to California (not a common occurrence), and from Alaska down through western Pacific to Hawaii. Range determined from collection location information provided with specimens examined (see Appendix 3: List of material examined).

**Biology.** Usually bathyal, but depth range extends from ~18 to  $\ge 2,000$  m, based on depth information provided with specimens examined.

**Remarks.** Bayer made personal notations in his copy of Nutting (1909); species is quite similar to *Swiftia kofoidi*. In overall shape, this species ranges from a rather open-spaced and delicately appearing colony (rarely) to one that seems bulkier. The zig-zag profile is evident but is much more rounded (less jagged-looking) than that of *S. kofoidi*. Polyp mounds in *S. pacifica* are somewhat lower, more rounded than those seen in *S. kofoidi*. In Nutting's 1912 description, he noted this species' "very close resemblance to *Calllistephanus koreni* Wright and Studer" but also added that "(g)eographical considerations render it unlikely that the two are identical." Madsen (1970) noted that the species described here so closely agreed "with the Scandinavian *rosea* (it too, has radiate capstans among the spicules) that it is reasonable to consider it its amphiboreal representative, and to regard it as a subspecies of *rosea*, stat. nov. [*Swiftia rosea* (Grieg 1887)];" an example of a discontinuous circumboreal octoocral.

Examination of specimens collected in the Gulf of Mexico, 2009 (provided by P Etnover, NOAA's National Ocean Service Office, South Carolina), indicated Madsen may have been correct. Three specimens were sent (without collection data). Sclerite preparations were performed, and specimens were tentatively identified as S. pacifica; when informed (pers. comm. from A Quattrini, then a doctoral candidate, Temple University) that these three were actually collected from the Gulf of Mexico, further investigation was warranted. Specimens of S. pallida Madsen, 1970 had been examined and sequenced (via barcoding of those specimens), and a close match was found between S. pallida specimens and other lots of the same specimens examined. Referring back to Madsen's (1970) discussion, S. pallida was considered by Madsen to be, at most, a subspecies of Swiftia rosea (Swiftia rosea pallida Madsen, 1970), of the north Atlantic, based on the color of its colony form (pale gray) and sclerites (colorless). S. pacifica from the Pacific Ocean, examined here (considering Madsen) looked very similar to the species S. rosea (which could certainly be the correct species identification for the three specimens from the Gulf of Mexico sent by Etnoyer) in its colony color, branch detail, arrangement of polyps and shape of its sclerites. It appeared that S. pacifica (eastern North Pacific), S. rosea of the Atlantic and its subspecies, S. pallida (a northern Atlantic bathyal form) were strongly related. S. rosea is the nominate form, found not only in the bathyal North Atlantic, but also in the Scandinavian sublittoral (Madsen 1970). It would appear that the species described here could be the Pacific Ocean extension (of



**Figure 5.** *Swiftia pacifica*, specimen 41-39-1 (Alaska Fisheries Service, Gulf of Alaska); looking in same form of that seen in Figure 3, light microscopy arrays. **A** (4×) showing variety of sclerites, particularly the characteristic "fingerbiscuit-rod" seen in the genus *Swiftia*. Sclerites from specimen examined for Bob Stone, Alaska Fisheries Service **B** Higher magnification, 10×, showing all sclerite forms, including obvious anthocodial fingerbiscuit-rods. The larger spindles measure ~300 µm long, smaller spindles of ~200 µm, and the rods range from 308–370 µm in length.

the Atlantic species *S. rosea*) in its distribution, having moved into the Pacific Ocean via waters circumscribing the North Pole. It can be inferred that as *S. pacifica* appeared in the Pacific, it dispersed down the western coast of the North American continent



**Figure 6.** *Swiftia pacifica*, specimen 41-100A-2 (Alaska Fisheries Service, Gulf of Alaska, via Bob Stone), SEM image. **A** Long spindles **B** Jagged disk-spindle/capstan-like sclerites **C** Thick, elongated rod-like spindles **D** Anthocodial "fingerbiscuit-rod" forms characteristic of the genus **E** Irregular spindles **F** Odd irregular spindles.

(at least as far as, generally, central California), just as *S. rosea* has apparently spread across the north Atlantic and down the eastern side of the North American continent (and presumably, into the Gulf of Mexico, perhaps as a new subspecies). The WoRMS Database (Cordeiro et al. 2019) shows the accepted status of this species.

Muzik (1979) noted discrepancies regarding locality for the holotype. The specimen is housed in the Bishop Museum, Hawaii (as *Allogorgia exserta*, #101), with a portion of it housed at NMNH (USNM 49513). This specimen "agrees in details of color, sclerites, and polyp size and shape with the type from Alaska of <u>Swiftia pacifica</u> (USNM 30024) collected from the Aleutians in 1906 and described by Nutting in 1912. One can conclude that there was an error in the locality of the so-called Hawaiian specimen. It is entered in the Bishop Museum catalog as 'Albatross' 2742 without locality. Entry 2741 is from Station 3353 off Panama. Prior to that station, the 'Albatross' had been collecting in the Pacific Northwest, so it is conceivable that this <u>S. pacifica</u> was collected there and later confused." It appeared that normal range for *Swiftia pacifica* is from central/northern California northward, but occasionally may appear south of that range. CAS has thirty cataloged records from this genus; of these, eleven lots are from Alaska, and are likely *Swiftia pacifica*.

There appeared to be a distinct morphological trend, from southern to northern waters, along the California coast up through the coastal areas of Oregon, Washington and Alaska that required discussion; a proposed explanation for the range distribution of this species follows the descriptions of all species (with red color) found in or near the Bight covered in this paper. Briefly, an extensive examination of colonies collected from Baja California to the remote northern aspect of the Bering Sea (see Appendix 3: List of material examined) revealed a very distinctive trend in the appearance of colonies and sclerites from south to north. The sequential trends seen within the two species, *S. kofoidi* and *S. pacifica* (or morphs of one) are discussed in the Further Remarks section (along with variation in sclerite morphology of other eastern Pacific *Swiftia* species). The observation of this phenomenon has never been discerned or noted previously.

#### Swiftia simplex (Nutting, 1909)

Figures 7, 8A, B, 9A, B, 10A-H, 24A-D, 25A, B, 26A-C, 27A, B

Psammogorgia simplex Nutting, 1909: 720, pl 88 (figs 4, 5), pl 90 (fig. 4).

**Type locality.** [USA], California, Santa Cruz Island, bearing N 35°E, 7 miles off Point San Pedro, ~34°02'02.76"N, 119°31'11.77"W, 447–510 fm [813–927 m].

**Type specimens. Syntype** USNM 25431 and USNM 43130 [both wet]; both specimens were examined.

Material examined. ~24 lots (see Appendix 3: List of material examined).

**Description.** Colony (Figures 7, 8A) straggling, whip-like, not always erect; branched slightly, mostly unbranched; largest specimens ~13+ cm tall. Stem round, slender, of uniform diameter throughout. On stem/branches, polyps uniformly distributed on all sides, not crowded (Figure 8B), up to 2.0 mm apart; tubular, small, ~1.0 mm high, usually higher than broad; when polyps contracted, nearly flush with branch surface. Coenenchyme moderately thick; color of living colony, including pol-



**Figure 7.** In situ shot, identified as *Swiftia simplex*. This is what one would expect to see of live colony. Notice strong similarity to that seen in Figure 28, Part II. As specimen was not collected, identification cannot be confirmed. Image (02\_57\_27\_20) courtesy of Lonny Lundsten and Kim Fulton-Bennet, "(c) 1992 MBARI."



**Figure 8.** *Swiftia simplex*, SBMNH 422979. **A** Entire colony, ~21 cm long, diameter ≤3 cm, including calyx **B** Branch close-up showing calyx placement on branch. Scale bar: 3 cm (**A**).

yps, salmon, brick reddish-pink (commonly) to coral-red throughout; sclerites reddish-pink; rods reddish-orange; sometimes long, warty spindles colored and colorless. Sclerites (Figures 9A, B, 10A–H) of three main kinds: 1) small double-spindles, rosettes, stars and/or small clubs, found mostly in superficial layer of coenenchyme (all



**Figure 9.** *Swiftia simplex*, specimen #81-99B-1 (Alaska Fisheries Service), light microscopy arrays. **A**  $4 \times$  magnification, showing long, slender spindles and anthocodial fingerbiscuit-rods **B**  $10 \times$  magnification of sclerites, emphasizing fingerbiscuit-rods of anthocodium. These rods measure between 340–350 µm, while long, thin spindles measure between 430–500 µm. Specimen provided by Bob Stone, Alaska Fisheries Service.

much less numerous than second kind; clubs much less numerous than other kinds); 2) larger spindles, slender, pointed, some slightly curved, covered with regularly distributed small warts (Figure 10A–C); 3) not always numerous, but when present, very conspicuous, colored anthocodial rods (fingerbiscuit rods; Figures 9A, B, 10H);

moderately to heavily warted, much shorter than long spindles, longer than first type. Polyps, generally, with spindle-shaped sclerites in walls and near/on tentacular bases, arranged more or less in chevrons. Otherwise, longitudinally arranged.

**Etymology.** Earlier genus designation (Nutting, 1909), *psammo-* = sand); *simplex-* = simple, perhaps referencing the very simple, usually unbranched colony, found generally on soft-bottomed sites. However, no derivation for species name given in Nutting's (1909) description.

Common name. Whip coral (suggested: Brick-red whip coral).

**Distribution.** Kükenthal (1919), in Chun: California, coast to abyssal. Total distributional range (surmised from collection location data reported by various institutions) extends from southern California Channel Islands (and further west--San Juan and Rodriquez Seamounts), up the coast of California (Monterey Bay, Carmel Canyon), sparsely along Oregon coast (Tillamook Head, Columbia River), to Washington coast (Grays Harbor, Quinault Canyon, Queets; general site locations off Oregon and Washington gleaned from NMNH material), up to Gulf of Alaska, found on seamounts and elsewhere (NMNH material, Alaska Fisheries Service). Fairly recent collection event (2008, Olympic Coast National Marine Sanctuary) produced at least one sample that may be this species, collected at ~48°07'53"N, 125°05'20"W at 335 m.

**Biology.** Appears to prefer at least subtidal depths, generally deeper, according to collection location data; frequently encountered on Seamounts (~190–900 m). MBARI T630-A13 had attached to it what appeared to be a cluster of white eggs (cluster identity not determined); these flexible branch strands, projecting up into localized water currents, would make good attachment sites for eggs needing oxygenation and/ or flow to keep them clean, being suspended above muddy bottoms found at depth.

Remarks. CAS has three specimens (likely this species), all from northern California (Cordell Bank, W of Point Reyes, CAS-IZ-96739; off Pigeon Point in San Mateo County, CAS-IZ-96744 and Eel River Canyon in Humboldt County, CAS-IZ-96758), labeled as Euplexaura simplex. This is a hitherto unknown application of a genus name, done by D Harden in the early 1970s (likely, an attempt to be comparable with the then named Euplexaura marki). This genus designation is incorrect; the specimen is the species Swiftia simplex. While Nutting (1909) placed it in the genus Psammogorgia Verrill, 1868a, geographic location of specimen(s) he described, geographic locations of specimens examined here, appearance of sclerites, along with molecular work conducted by M Everett et al. (2016), do not warrant that species designation either. While the WoRMS Database (Cordeiro et al. 2019) did indicate an accepted status for this species designation under the genus Swiftia, it also showed accepted status for the species as Psammogorgia simplex (Cordeiro et al. 2018). Based on the genus description for Psammogorgia by Verrill (1868a), Bayer (1958) on the morphological characters mentioned above and discussion provided by Bayer and Deichmann (1960), which also discussed the probability of appearance in the Panamanian province, material examined in this work warrants placement in the genus Swiftia, not in the genus Psammogorgia.

Sclerite examinations revealed a few individual colonies (several species) in the genus *Swiftia* (such as that shown in Figure 8), with minimal/no fingerbiscuit rods.



**Figure 10.** *Swiftia simplex*, specimen #81-99B-1, SEM image. **A** Elongated spindles **B** Moderate-length spindles **C** Shorter spindles **D** Thick, elongated rod-like spindles **E** Less jagged double-disk/capstan-like forms **F** Tiny, odd spindle **G** Irregular spindles **H** Anthocodial "fingerbiscuit-rod" forms typical of genus. Alaska Fisheries Service.

Nothing examined and identified as *Chromoplexaura marki* (Kükenthal, 1913) (species closest in superficial colony appearance) ever displayed these rods, as expected for this genus. It was easy to understand how identification done in the field, on in situ colonies (with water depth distorting color), could label colonies from the two species

(this and *C. marki*) as the same organism. Current examinations discussed here shed some light on the confusion. The explanation provided regarding *S. pacifica* in Further Remarks section, is an attempt to clarify (and explain) why some colonies of *Swiftia* have scleritic anthocodial rods and others do not.

California specimens identified from the genus *Euplexaura* (now the genus *Chro-moplexaura* Williams, 2013) on several MBARI video clips that were viewed could actually be this species. *C. marki* (which this species can so closely resemble), is usually bright deep red, with white or pale yellow anthocodiae/polyps (Kükenthal 1913, 1924; also Johnson and Snook 1927) but not always (see discussion, Part II, this work) while this species is a dull pinkish to brick red color, with colony coenenchyme and anthocodiae/polyps the same color; sclerites are very different for the two genera. It is likely that MBARI is seeing both this species and *C. marki*, but not able to clearly distinguish between the two due to color distortion at depth under field conditions, if not collecting.

A specimen (R1159\_EPI\_164\_0015) collected by Olympic Coast National Marine Sanctuary in 2008 superficially appeared to be this species; polyps were mostly contracted into very round, prominent mounds, although these had larger dimension than that given in the above description (tentacles were more or less the same salmon color as the coenenchyme, but polyp bodies, closely proximal to branch, were white when dissected out). Based on further examinations, specimen was tentatively identified as *Swiftia spauldingi* (Nutting, 1909); however, lack of fingerbiscuit rods points in the direction of *Chromoplexaura marki*. Recent DNA sequencing (communications with M Everett, NOAA affiliate, 2013–2014) indicated that some *Swiftia* species might need subdividing (three different species or variants a possibility).

#### Swiftia cf. spauldingi (Nutting, 1909)

Figures 11, 12A, B, 13A, B

Psammogorgia spauldingi Nutting, 1909: 721, 722, pl 89 (figs 3, 4), 90 (fig. 7). *Euplexaura marki* Kükenthal, 1913: 266; noted by Bayer 1979: 1034. *Chromoplexaura marki* (Kükenthal, 1913): Williams 2013.

Type locality. [USA], North Pacific, California, Monterey Bay, Pacific Grove.

**Type specimens. Holotype**; transferred from Hopkins Marine Laboratory Collection; [USNM 91854, wet]; specimen was examined.

**Material examined.** ~9 lots (see Appendix 3: List of material examined). [See also discussion regarding "red whip" forms, in Remarks section for species *Chromoplexaura marki* discussed in Part II of this work.]

**Description.** *Colony* (Figure 11) low, moderately bushy (tending to one plane); flabellate. Sparsely branched; irregularly dichotomous, subdividing some distance above base; branches round in cross section. Terminal branches somewhat stout, 5.0–10.0 cm long, as large as main stem, nearly as round (2.0–3.0 mm thick); slender, whip-like.



**Figure 11.** *Swiftia spauldingi*, CB#34806-455. Full colony height approximately 12 cm. Image taken by Carla Stehr, courtesy of Ewann Berntson, National Fisheries Science Center, Port Orchard, WA.

Polyps scattered closely, uniformly, over surface on all sides, as very low, fairly large, somewhat rounded warts; in some specimens, scarcely raised above general surface of colony, almost entirely included, hardly evident (flush), seeming to be nearly absent, yet in others readily visible; less than 1.0 mm across, 1.0 mm apart. Color of living colony bright coral or salmon-orange; sclerites range from yellowish to very pale red (most commonly, moderate to pale salmon pink), with orange rods; polyps, in preserved specimens, appear to be pure white, while in some colonies (preserved) can appear light salmon-pink. Sclerites (Figures 12A, B, 13A, B) of several kinds, but generally small, short, exceedingly warty spindles and double-spindles. Sclerites in body wall of polyps somewhat longer, more slender spindles (double-spindles), with more delicate warts and points, tapered with wide, median space, but stout, scarcely acute (but never as long as those seen in other eastern Pacific species of *Swiftia*). Bayer (1956) noted



**Figure 12.** *Swiftia spauldingi*, CB#34806-455, light microscopy arrays. **A**  $4\times$  magnification **B** $10\times$  magnification; anthocodial fingerbiscuit-rods very obvious, measuring from 128–171 µm. The dense "ovals" measure between 100–115 µm; smallest sclerites are ~86 µm.

these longer sclerites as symmetrical or with warts on one side simple and conical, elsewhere compound. With appearance of two or three whorls of large, compound, rough warts on each end, those nearest middle usually the largest. These longer sclerites tend to longitudinal arrangement in body wall in eight rows; rows sometime extending part way up outer sides of tentacles. Stouter sclerites (double-spindles) also tapered with wide median space, but shorter, blunt, each end with two or three crowded, usually somewhat confused whorls of large rough warts, forming large terminal cluster. (Bayer, 1956 noted these sclerites as having warts of one side fused like those of disc spindles). In some colonies identified as this species, presence of sclerite form approaching that of double heads (Figure 13A, top row), with narrow median space and large cluster of closely crowded warts on each end, resembling dark, dense triangular tip; these sclerites are of particular interest in comparison with Chromoplexaura marki and the double dunce-cap sclerite. Other heads shorter, lacking median space, entirely covered with crowded warts. Crosses, with four short, roughly-warted branches said to occur frequently; not evident in examinations undertaken. Fingerbiscuit rods (Figure 13B) more heavily warted than those seen in other species from genus (but may not be abundantly present).

Etymology. Named in honor of Mr MH Spaulding from Stanford University.

**Distribution.** Rarely, southern California (Los Angeles County); may extend from central California, northern California Channel Islands, north to coast of Washington State (Strait of Juan de Fuca). Distribution based on specimens examined with collection location data, from several sources (NMNH, NOAA offices, MBARI). The specimen collected by Olympic Coast National Marine Sanctuary in 2008, collected at 335 m, ~48°07'53"N, 125°05'20"W, confirmed WA coastal waters as a location for this species.

**Biology.** Conspicuous Ophiuroidea found intertwined on branches, as those seen on specimen from "Oregon State, R/V 'Yaquina' NH15" (SBMNH 423073) and that collected by Olympic Coast National Marine Sanctuary in 2008.

**Remarks.** Multiple labels (NMNH) were associated with some specimens examined, along with differences in literature usage of the genus name *Swiftia* and at least one specimen at NMNH had been given the name *Psammogorgia spauldingi* (while elsewhere, Bayer's SEM files, the folder of SEM images for this same specimen, was labeled "*Leptogorgia caryi = Swiftia spauldingi*," with the numbers "57157, SEM 2787 & 2790" [note use of the genus name *Swiftia*]; however, this synonymy designation is in error).

The discussion of *Chromoplexaura marki* in Part II (along with remarks given for *S. simplex*) is pertinent. At least one specimen of *C. marki* examined had sclerites very similar to those seen in *S. spauldingi*, but there were no anthocodial fingerbiscuit rods. Could *S. spauldingi* sometimes be seen as a less-branched colony, resembling *C. marki* (or be very unbranched, and look more like *S. simplex*)? *S. simplex, S. spauldingi* and *C. marki* can have similar colony appearance; but the first two will have the fingerbiscuit rods, and only the latter two will have sclerites showing other similarities of form (but not entirely). A key difference (and justification for keeping the two, *C. marki* and *S. spauldingi*, as separate species) is the consistent lack of fingerbiscuit rods in



**Figure 13.** *Swiftia spauldingi*, CB#34806-455, SEM image. **A** An array of coenenchymal sclerites (spindles) **B** An array of, primarily, "fingerbiscuit-rods," the characteristic sclerites for the genus. Images prepared by Carla Stehr, courtesy of Ewann Berntson, National Fisheries Science Center, Port Orchard, WA.
*C. marki*, but which does have the unusual double dunce-cap spindles that are only uncommonly seen in *S. spauldingi* (and in this latter species, usually smaller-sized; refer to Figure 13A). Bayer (1979: 1034) offered support for a synonymy between the two, but this synonymy seems questionable. More specimens will need to be collected and examined. Despite confusion regarding the status of this species, Cordeiro et al. (2019), shows *S. spauldingi* as the accepted name, with *Psammogorgia spauldingi* the only synonymized name.

## Swiftia torreyi (Nutting, 1909)

Swiftia torreyi Nutting, 1909: 721 pl 89 (figs 1, 2), pl 90 (fig. 5) [= Psammogorgia torreyi Nutting, 1909].

**Type locality.** [USA], California, Monterey Bay, 36°38'00"N, 121°55'00"W (bearing S 78°E, 6.8 miles) off Point Piños light-house, 755–958 fm [1373–1742 m].

Type specimens. Holotype USNM 25433, [wet]; specimen was examined.

**Material examined.** None of the material examined (~16 lots) came from the SBMNH collection (see Appendix 3: List of material examined).

Description. Colonies strictly flabellate (usually), ~15-30 cm tall, ~16-17 cm in breadth. Branches commonly anastomosed; branches dense, closely spaced. Main stem bears branches on opposite sides separated by distance of 4.5 mm to +7.0 mm; branches generally thin (no more than 1.0 mm wide) in appearance. The whole forms a loose reticulation, somewhat comparable to that seen in a few species of the genus Pacifigorgia, such as P. gracilis (Kükenthal, 1924). Polyp mounds slightly truncated to (commonly) tubular cones, 1.0 mm high or less, can be as wide as high; extended polyp can add ~1.0 mm to height; distributed primarily on sides of branches, ~2.0 mm or less apart on one lateral side. In front view, there appeared to be two opposite rows, but can be alternate; body and tentacles of polyps tend to bend (curl) toward front of colony somewhat, giving appearance of numerous polyps on the colony's front, when just a very few, scattered, are present; often back of colony without polyps or very few. Curling of polyp body and polyp tentacles gives colony a somewhat lacy look. Color of living colony dark, purplish-red (maroon), deep brick red to nearly black throughout; when placed in alcohol, tends to nearly black. Sclerites warty spindles, generally; those on stem, branches smaller than those on polyps. Largest appear to be those in polyp walls and basal parts of tentacles; large, warty, fusiform, sometimes curved, arranged longitudinally, extending downward in meridional bands to near base of polyps. Smaller spindle-types almost with appearance of a radiate (capstan) shape; some few almost appear as disk spindles. Some few club-shaped sclerites, nearly all of which are the warty, fusiform type. Rods (fingerbiscuit shape) very conspicuous, when present, though not always numerous; generally not heavily warted; most sclerites rich reddish-purple; conspicuous rods vibrant pumpkin orange. The color combination of purple-red and orange is unmistakable.

**Etymology.** Named in honor of Dr Harry B Torrey from the University of California. **Common name.** Dwarf red gorgonian.

Distribution. From MBARI, CAS and Moss Landing Marine Lab (MLML) collection data, found in Monterey Bay ('Albatross' stations 4514, 4537, 4546). Range may extend from northern-most end of California Bight to areas off mid-Washington coast (Quinault Canyon, 47°28'59"N, 125°11'45"W; some specimens listed as this species may be S. pacifica; further examination required). If specimens, identified as this species off Oregon and Washington coasts, are actually S. pacifica, then range for this species from at least Rodriguez Seamount, ~33°59'16"N, 120°59'52"W (west of San Miguel Passage) to Pioneer Seamount (~37°17'44"N, 123°29'58"W) off California; there are ample records at MBARI for sightings of this species in the region between these two seamounts. NMNH records extend the range up through Oregon and Washington, as far north as the mouth of the Strait of Juan de Fuca (48°32'42"N, 124°52'44"W). A recent collection by Olympic Coast National Marine Sanctuary (2008), with specimen collected at ~47°55'16"N, 125°30'00"W, 429 m, was examined, confirming species does extend up into waters of Washington State. As well, one specimen (apparently this species, not examined) was collected from San Diego, Point Loma, at 201–262 m [USNM 49522]. This would put the species in the Bight, but identification may be incorrect. Species most commonly found in the region of Monterey Bay.

**Biology.** MBARI records would indicate a moderately deep-water form (1,029–2,200 m). It also seems to prefer steep walls of seamounts based on collection details.

**Remarks.** A brief description is included here as this species is often confused with others in the genus by field investigators, when simply viewing colony morphology in situ (it has been found just north of the California Bight's upper geographic limit), and completes, to date, descriptions for all colored species within the genus *Swiftia* currently known to exist in the waters along the western North American continent.

In minor ways, previously published descriptions roughly matched that published for Muricella complanata Wright & Studer, 1889; Harden (1979) listed M. complanata as synonymous with this species, and an unpublished Bayer annotation noted: "Muricella complanata = a Swiftia?" Overall, however, descriptions did not match. A brief study of CAS specimens identified by Harden was undertaken, but did not sufficiently clear up his proposed synonymy. For two specimens identified by Harden as this species, one had no locality data; the other was from Monterey Bay. Identifications made by Harden often proved problematic. While definitive specimens with correct identification were needed, was not able to locate specimens with confirmed identification as Muricella complanata in any of the research collections examined so as to compare known specimens of Swiftia torreyi against it; study of new material, which needs to be collected, is required. As well, Harden (1979: 171, unpublished PhD dissertation) did designate Psammogorgia torreyi Nutting, 1909 (= Swiftia torreyi Nutting, 1909). Cordeiro et al. (2018) does show P. torreyi with accepted status, but that as well, Swiftia torreyi is also given accepted status (Cordeiro et al. 2019). Based on a number of descriptions given for members of the genus Psammogorgia and

Bayer and Deichmann's (1960) statement regarding the marine province where Psammogorgia is likely to be found, specimens examined and studied, identified as Swiftia torreyi, cannot be synonymously identified with any Psammogorgia species. At the time that Bayer and Deichmann were working (1960), they suggested that Psammogorgia would not/does not occur anywhere outside of the Panamanian province, which then encompassed the area from Cape Blanco, Peru to Lower Baja California, including the Gulf of California (Verrill 1868a, b, c, 1870). As discussed in current literature (Briggs and Bowen 2011), there now exists a California Transition Zone (CTZ), within the Oregon province, extending from Monterey, California to Los Angeles; the California province then extends from Los Angeles to Magdalena Bay, Mexico. Running south of Magdalena Bay around the tip of the Baja California Peninsula, and including all of the Gulf of California, is the Cortez province, with the Panamanian province now extending from the mouth of the Gulf of California to the Gulf of Guayaquil on the border between Ecuador and Peru. Specimens of Swiftia described in this work barely make an appearance in upper portions of the California province, but appear no further south, based on a review of all the collection location data for all specimens examined. What is of interest is their appearance in the upper California province, the CTZ and the northeastern Pacific province. In any event, that still definitively puts all specimen/species of the genus Psammogorgia outside of the California Bight, either in the Cortez or Panamanian provinces.

Bayer (unpublished annotations) contemplated differences between this species, *S. kofoidi* and *S. pacifica*; his comments do not entirely fit with what has been determined for the species here, and in Nutting's 1909 description. However, he stated that the species is a "slender form, . . ." whereas *S. kofoidi* is "stouter than *torreyi*. . ." (this can be confirmed). "Similar to *Callistephanus pacificus* Nutting, 1912, pg. 96." "*P. pacificus* is *Swiftia pacifica*, a brighter red species, with more robust branches, found commonly in waters of Washington and Alaska (bathyal North Pacific). *S. pacifica* is, generally, comparatively more sparsely-branched, with distinctive bar-like sclerites on the anthocodiae and eight-radiates," than is this species.

Several portions of statements in the discussion section of Breedy et al. (2015: 332) were of interest. Those sections read much the same as several statements this author made regarding the above five species of *Swiftia* in an earlier, pre-revision draft of this volume submitted for review in the spring of 2014. It was interesting to see those comments used as contrast for the new Chilean species that was described.

In the MLML collection, one specimen (C0072) of this species was found; the orange rod sclerite form, generally seen below the tentacles, and anastomosing branches were present (a note furnished with the specimen made a point of the distinctive rods). Two others were labeled as such, but either color was markedly off or, more significantly, branching pattern did not match (no branch anastomoses). Of the MBARI specimens examined, at least six appeared to be this species. Some were originally identified as *S. kofoidi*, but it is fairly certain they are this species; the deep purple-red color is a consistent characteristic, along with many anastomosed branches. As well, presence (or absence) of the vibrant orange rods was a telling feature; if other colonies seen in videos were collected, they should be examined for their sclerites. Overall, colony C0072 has a very distinct deep red-wine color, numerous, dense, thin, anastomosing branches, with polyps having a tendency to curl. In most colonies, a definite front and back is present; the sclerite form that is most evident and obvious in this species is the vibrant orange bacillus-shaped, fingerbiscuit rod, easily seen in a light microscopy array.

# Further remarks: Consideration of morphological trends, based on geography and possible ecology, of eastern Pacific *Swiftia* species, focusing on those species with colored colonies.

As alluded to in remarks for the description of Swiftia pacifica, there appears to be a subtle, yet distinct gradual variation in colony morphology and sclerite form, seen in multiple species of the genus Swiftia from the eastern North Pacific, displayed along a geographical and ecological continuum. Historically, the genus Swiftia has been assigned variably to the Gorgoniidae, Paramuriceidae and Plexauridae at different times over an historical time frame (Bielschowsky 1918; Deichmann 1936; Bayer 1956; 1961). It is also a genus (particularly so within the context of the eastern Pacific Ocean), that has received limited (and very sporadic) attention (Duchassaing and Michelotti 1864; Verrill 1883 [as Stenogorgia]; Wright and Studer 1889 [as Cal*listephanus*]; Kükenthal 1924 (Stenogorgia synonymy); Deichmann 1936 [Stenogorgia = Swiftia]; Madsen 1970; Muzik 1979), often resulting in mixed and, at times, confusing species identification. Confusion over identification of species within the genus in the northeastern Pacific stems, in part, from a lack of material, and material collected during widely separated collection events with little or no attempt to look at all pertinent species comprehensively over a wide geographical area. In truth, the presence of the genus Swiftia in the eastern North Pacific is an interesting, but, likely multifaceted evolutionary story. Early work that pointed to an explanation for the presence of pertinent species of Swiftia in the eastern Pacific began with the work of Madsen (1970). Madsen considered Nutting's (1912) species, particularly in reference to S. pacifica, collected south of the Bering Sea, as a subspecies of the Atlantic species S. rosea and concluded that Nutting's species was an "amphiboreal representative" of S. rosea, thus making S. rosea an example "of a discontinuous circumboreal octocoral" (Madsen 1970). Thus, the presence of Swiftia in the eastern North Pacific could represent a progressive migration of a particular species found in the Atlantic, that has worked its way through waters of the North Pole and ultimately down into eastern Pacific waters. His work also discussed what he considered a subspecies of S. rosea, that being S. rosea pallida (that one or more species, either from the Atlantic or the Pacific, may be related to); Grasshoff (1977) listed the two (S. rosea rosea and S. rosea pallida) as two distinct species.

While molecular work (Wirshing et al. 2005; Thoma 2013; Quattrini, pers. comm., Quattrini et al. 2014) has revealed new insights into relationships between *Swiftia* and other genera as well as molecular connection between several species within the genus, both from the Atlantic and the Pacific, in some aspects, supporting Mad-

sen's (1970) hypothesis, many questions still remain. Molecular work on species in this genus has been undertaken or is currently in progress (M Everett, NOAA affiliate, numerous pers. comm. and Everett et al. 2016); this will certainly shed more light on the origins and dispersal of the genus. The discussion here, however, does not focus on how *Swiftia* member species came to be in the eastern North Pacific, or how they relate to other species in other parts of the world; the focus here is what has occurred morphologically within several member species since the migration and establishment of the genus in the eastern North Pacific. The variations in morphology (both in colony form and color as well as sclerite appearance) are likely to have occurred in response to ecological factors linked to geography.

While working to clarify what species within the genus Swiftia were present in the eastern Pacific, it became clear that there was a set of trends in colony appearance, color and sclerite form for Swiftia kofoidi (Nutting, 1909), Swiftia pacifica (Nutting, 1912) and Swiftia simplex (Nutting, 1909) throughout their distributional ranges in the eastern Pacific, from the Bering Sea, Alaska, USA to upper Baja, Mexico (Isla Cedros). The geomorphological changes that can be seen in S. koifoidi and S. pacifica (both species forming markedly fan-like colonies) point to one or more of several different hypotheses. These hypotheses are: 1) either these two species are in actuality the same species, with considerable transitional geographic variability seen from south to north within their distributional range (ecological morphs), 2) these two species are distinct species but show high degrees of intermediary form in areas where they overlap (perhaps similar enough to hybridize), 3) these two species are distinct species but display, in the center portion of their range, interesting examples of regional endemism or 4) that both are distinct species, highly subject to varying environmental/ecological parameters, sharing some responses to ecological factors in areas where they live together (factors such as colder water, and depth). In the case of Swiftia simplex (a species that displays a whip-like colony form), it has been determined to be a single species (Everett et al. 2016) but shows geographic and thus perhaps, ecological trends in its sclerite morphology over a vast distance.

After examining well over 100 specimens (multiple times over a span of several years (see Appendix 3: List of material examined), transitional variations in colony shape, colony color, branch diameter, polyp distance on branches and in sclerite form became apparent. The geographic range of the specimens examined, and those species discussed here, are shown in Figure 14. Those in the extreme northern end of the range (Bering Sea, Aleutian Islands, Alaska) best show the definitive features of the genus while those furthest south consistently lack some of the key details. The northern-most end of the geographic continuum would be the area into which colonies of the genus first moved in their migration from the northern Atlantic, establishing the origin point for colonies that are now seen further south in this northeastern Pacific Ocean continuum.

The current study of *Swiftia* began with specimens collected at the southern end of this continuum. In the species *Swiftia kofoidi* (the species which appears most commonly in the California Bight based on collection data of specimens examined),



**Figure 14.** Geographic range of specimens utilized in this study; numbers shown reference Figures 15–27 mentioned in the text, with approximate location delineated by position of the number on the map. Red: *S. kofoidi*, Blue: *S. pacifica*, Fuschia: *S. kofoidi/pacifica* (a specimen decidedly intermediate between the two species), Orange: *S. simplex* and Turquoise: Canadian waters for which specimens are needed.

colony color is often a vibrant pale salmon-orange (Figures 1, 15), with polyps/ tentacles fairly large, often white or a very pale yellow, very widely spaced, giving branches of the colony a distinct "rick rack" profile and overall, a rather delicate appearance, its thin branches rather lacy and open. In colonies collected in either the waters of Baja, Mexico or southern California, very rarely would fingerbiscuit rods be found; sclerite arrays consistently showed a distinct lack of the key sclerite form (referred to as an anthocodial fingerbiscuit rod), but instead the long spindles seen in Figures 2B, 4B would be common, always exceptionally long and thin. As well, numerous shorter, thorny capstan-types, along with a variety of other odd sclerite shapes (such as a torch) in far smaller numbers (Figures 16, 17) were often seen. Of interest is the colony shown in Figure 3, having the general appearance of *S. pacifica*, but collected in southern California, displaying very long, thin spindles and very few fingerbiscuit rods (Figure 4C).



**Figure 15.** Colonies collected/examined from the southern end of the geographic continuum, identified as *Swiftia kofoidi*. **A** SBMNH 422965; scale bar 1 cm **B** SBMNH 422957; 7 cm H × 10.5 cm W **C** SBMNH 422959; 10 cm H × 10 cm W **D** SBMNH 232036, looking more like *S. pacifica*; 6.5 cm H × 5 cm W **E** SBMNH 422963; 7 cm H × 7.5 cm W.



**Figure 16.** Common sclerite forms seen in colonies collected from the southern end of the geographic continuum, using standard light microscopy. **A** Sclerites taken from SBMNH 422965 **B** Sclerites from SBMNH 232036.

As specimens collected in the vicinity of the CA Bight's northern edge were examined (including specimens collected above Point Conception), the slender spindles and shorter, thorny capstans were still displayed, but on occasion there would be a few sclerites that nearly matched the key sclerite form of the genus (the fingerbiscuit rod), but were usually longer than expected (best described as a "Cheetos" cheese puff), as seen in Figures 19, 20. These latter, however, were by no means common; many colonies identified as *S. kofoidi* did not display them.

As specimens collected even further north were examined (along the coasts of Oregon, Washington and on up to Alaska), colony appearance was more and more as that



**Figure 17.** Common sclerite forms seen in colonies collected from the southern end of the geographic continuum, using SEM. **A, B** Sclerites from SBMNH 422965 **C** Sclerites from SBMNH 232036.

seen in Figure 3, but the long spindles became shorter and shorter in specimens collected further and further north, while the fingerbiscuit rods became more and more common, obvious and larger (Figures 5A, 6A, C, D). Off the central coast of Oregon to the central portion of Washington State, the colonies looked more and more like *S. pacifica* (occasional colonies looking like *S. kofoidi* were found, however; Figure 18), but there was a marked transition (tendency to being shorter) in the appearance of long



**Figure 18.** Colonies collected/examined from the central portion of the geographic continuum, ranging from roughly Monterey County, CA to southern Washington State. **A** LACoMNH (NOAA #CB 34019) **B** NOAA FRAM #100220840; scale bar 1 cm **C** MLML #C0072; size not determined **D** NOAA FRAM #100112080 (CB 34406-040); 11.5 cm H × 6.4 cm W **E** NOAA #CB 50003-008; 16.5 cm H × 12.6 cm W **F** LACoMNH (NOAA #CB 34010); 15 cm H × 19 cm W.

spindles while fingerbiscuit rods became more and more obvious. Again, it appeared as though *S. kofoidi* and *S. pacifica* might be: 1) two colony morphs of the same species, with "transitional" sclerite appearance (long or short spindles in some combination with presence or near absence of fingerbiscuit rods) or 2) interbreeding (two morphs of



**Figure 19.** Variation in common sclerite forms seen in colonies from the central portion of the continuum, in SEM. **A** Coenenchymal sclerites from NOAA FRAM #100112080 (CB 34406-040) **B** Polyp and tentacular sclerites from the same specimen. SEM images taken by Carla Stehr (NOAA), provided by Ewann Berntson (NOAA).



**Figure 20.** Common sclerite forms seen in colonies collected from the central portion of the geographic continuum, using standard light microscopy. **A, B** NOAA FRAM #100112070 **C** NOAA FRAM #100220840 **D** NOAA #CB 50001-004 **E** OCNMS #EPI 202 **F** OCNMS #EPI/SUC 216.

the same species) but equally 3) could be displaying degrees of hybridization between two very similar, but different species.

For specimens identified as *Swiftia pacifica*, the species appeared to be far more common the further north in location specimens were collected from. Only on rarest occasions did a colony reveal itself as a specimen of this species in the CA Bight (Figure 15D); it was far more common north of the CA Bight, on up through waters off Oregon, Washington and Alaska (Figures 18, 21). While unable to examine specimens collected off of Canada and its associated islands, it is hard to imagine that it would not be found in the waters of that region.



**Figure 21.** Colonies collected/examined from the northern end of the geographic continuum, confirmed identification as *Swiftia pacifica*. **A** OCNMS #OC06\_0531, EPI 127 **B** NOAA 41-39-1 (AB17-0010). Image of specimen shown in A provided by Mary Brancato (OCNMS); specimen shown in B provided by Robert Stone (NOAA).

In terms of *S. pacifica*'s overall appearance in the eastern Pacific, the colony was often (but not always) more robust, being thicker-branched and bulky in overall appearance (Figures 3, 15D, 18A, B, C, 21A), the color more commonly a deeper crimson red to brick-red (often with a grey or green tinge); polyps were a bit smaller (typically more boxy), and often (not always) much more closely situated next to each other, but not as closely situated as polyps seen in the species *S. torreyi* (Nutting, 1909); polyp/ tentacle color usually a slightly darker version of the colony coenenchyme. However, throughout its range (Oregon, Washington, even in the far northern parts of its range, such as Alaska, the Bering Sea, Aleutian Islands), there were specimens that looked in overall appearance much more like the delicate colony form of *S. kofoidi* (yet color more in keeping with the darker red shades; for example Figures 18D, F, 21B). In some few of these latter specimens, in sclerite arrays, a lack of the fingerbiscuit rod could be found, though this was a fairly rare event (Figure 22C, D). However, the farther north a specimen was collected, the fingerbiscuit rods would be visible, obvious, with a vibrant orange to pumpkin color (Figures 20B, F, 22A, B, 23A, B). This sclerite form is characteristic in specimens identified as this species (Nutting, 1912). Additionally, long spindles became less and less numerous; those present were slender but displayed far shorter length than those seen in *S. kofoidi*. With specimens collected in waters off northern Washington to the Bering Sea, Alaska, the colonies very much looked like that of *S. pacifica*, a very deep gray-red, with much shorter long, thin spindles and very evident fingerbiscuit rods, as shown in Figures 5, 6.

In summary, at the extreme ends of the range (Baja and southern California vs. Bering Sea, Alaska), there is, in the south, the appearance of a delicate and bright orange colony and in the north the appearance of a thicker, denser colony of a deep red to gray-red. This could lead to the conclusion that there are two separate species, even as specimens found in the middle of the range showed an interesting mix of colony morphology, colony color and presence or absence of certain sclerite forms.

Morphologically at least, it would seem that *S. kofoidi* and *S. pacifica* are separate species. However, it was difficult to clearly see, as specimens from areas intermediary in the range were examined and considered, that they were separate species. It is these intermediate mixes of features in the areas of both Washington and Oregon, to the shores of the northern CA Bight boundary that are of most interest. Specimens from Oregon or northern California could look more like *S. kofoidi* in colony shape, but color was off, or there were hints of something that resembled a fingerbiscuit rod. Specimens from Washington or Oregon could look far more like *S. pacifica* in color and colony form, but sclerite arrays revealed what had been seen in arrays of sclerites from specimens clearly identified as *S. kofoidi*. Yet, overall, the sclerites labeled as "Cheeto-type" or those called the fingerbiscuit rods, became more and more common in specimens, the further north the specimens were collected.

*Swiftia simplex* revealed itself, morphologically, to be a single species, but within the species, as specimens were examined (following collection along the south-to-north continuum), while colony morphology (usually a single or rarely, minimally-branched stem) and color (a pinkish, dirty, brick-red), remained consistent (Figures 7, 8, 24), specimens in areas further north always displayed the fingerbiscuit rod (Figures 25B, 26, 27) while those in more southerly locations lacked the fingerbiscuit rod sclerite (the change in the appearance of this sclerite form, present to absent, appeared roughly in the vicinity of the northern edge of the CA Bight), but lack of fingerbiscuit rods could be confirmed as far north as Monterey Bay in some specimens; an example is SBMNH 422979 (See Figure 25A).

Are *S. kofoidi* and *S. pacifica* two separate species? Based on colony form, coenenchyme color, polyp color, size and placement, it would seem so. If so, are they similar enough in genetic makeup to be able to readily hybridize? Based on what has been related here in terms of morphological aspects, this might be a viable possibility, especially in the waters off Washington and Oregon down to the area of the northern



**Figure 22.** Common sclerite forms seen in colonies of *S. pacifica* collected from the northern portion of the geographic continuum, using standard light microscopy. **A** NOAA #41-39-1 (AB17-0010) **B** NOAA #CB 50003-021 **C, D** NOAA #CB 50003-032.

CA Bight. Preliminary molecular work (M Everett, NOAA affiliate, personal communications) might lead to such a conclusion. However, the sclerite arrays demonstrated by both species turned out to be less clear. Generally, more southern-collected species lacked any hint of the fingerbiscuit rod. The further north a specimen was collected, the more likely the fingerbiscuit rods were to be seen. But, there were many exceptions to this generality. The general trend could mean an ecological response: thicker, shorter fingerbiscuit rods in the colder waters of the northern part of the total range (where food may be more abundant and energy to generate thicker and more forms of sclerite is available), and thinner, more slender spindles, but not the formation of rods, in the warmer to moderate temperate waters in the southern part of the total range (where food supplies may be more variable and/or less abundant, thus less energy available for extensive sclerite formation). In support of this hypothesis, two specimens (of an, as yet, undescribed species) of *Swiftia* in New Zealand's National Institute of Water and Atmospheric Research, Ltd. (NIWA) Research Collection (not yet cataloged, but with the following identification numbers: the first, NZ01, Stn Z11059, Stn KAH0204/32, collected 17 April 2002, 780–810 m [wet] and the second, U582 [wet]) were examined, from waters offshore, northeast side of North Island, New Zealand, in which, throughout the entire colony, the only sclerite form to appear in multiple sclerite preparations undertaken were the fingerbiscuit rods. Is this sclerite form then a response to depth and/or variable temperatures? For *S. kofoidi* and *S. pacifica*, the intermediate, and variable, mix of sclerites in the intermediate region of the south-to-north continuum along the continental western US coast could represent responses to variable environmental conditions, prevalent in the vicinity of the western US coast, where major currents running through this area wax and wane throughout the seasons and years, subject to storm vagaries, etc.

Are the two species actually subspecies or ecological morphs of one species? (In this case, a case could be made that the one species retain the name Swiftia pacifica.) Molecular studies done by M Everett (NOAA affiliate, Port Orchard, WA) seemed to indicate a close affinity of the current two species. Based on the morphological studies reported here, especially with regards to those found in a wide central, intermediate area of the range (from northern California to the central-northern Washington coast), where there was wide variation and a mix of features in the specimens, especially with regards to the mix of sclerites seen in those specimens, the idea of the two really representing a wide array of ecological response in one species, perhaps to some shared ecological feature, is not outside the realm of possibility. There is however, an alternative hypothesis: presence of many regional endemic species, each with its own set of parameters, chosen from the array of features discussed here; this may require the need for further species designations for each endemic form, if indeed, they exist. More specimens need to be collected in the near future, with intentional effort made to hone in on specific areas within the north-to-south continuum, most notably in Canadian waters and in the "transitional, intermediate zone" of the continuum (Point Arguello to Point Conception, CA), to explore this conjecture. Molecular work being undertaken by M Everett and her lab now, and in future (especially should new collection events occur), will further clarify some of this.

As for *S. simplex*, it is a less complicated situation. In the southern portion of its range, where there is a tendency not to produce fingerbiscuit rods, the condition could be an ecological response to some environmental factor (be it temperature or food supplies, as examples) while the appearance of the fingerbiscuit rods, consistent with collection locations further north, in much deeper/colder water, equally could be an ecological response to those colder water conditions. Based on the work of Everett et al. (2016), there is a high level of gene flow within this single species throughout its range along the west coast of the United States.

In conclusion, differences in colony size, shape, branch diameter, polyp placement on branches, and color as well as presence or absence of key sclerite forms was obvious. These differences have generated degrees of confusion as to species identification along



**Figure 23.** Sclerites from a specimen collected in the northern portion of the geographic continuum, in SEM. **A, B** From NOAA #41-100A-2 (AB17-0009).



**Figure 24.** Colonies collected/examined from throughout the geographic continuum (shown **A–D** from south to north), identified as *Swiftia simplex*. **A** SBMNH 422979 **B** NOAA #CB 34013 **C** NOAA #CB 34212-039 **D** NOAA CRW\_3636 8; 35 cm H × 17–20 cm W. Image **C** Courtesy of Ewann Berntson (NOAA, WA); image **D** Courtesy of Robert Stone (NOAA, AK).

that geographical gradient. As those differences are considered, the conclusion could be drawn that the differences reflect ecological conditions and colony responses to them. They could, however, also lead to the assignment of distinctly different colony forms as different, but yet remarkably similar, species. Conversely, all colonies along the geo-



Figure 25. Sclerite arrays of *S. simplex* seen using light microscopy. **A** SBMNH 422979 **B** NOAA 81-99B-1 (AB12-0127).

graphic range could actually be representatives, in a single species, of a high degree of variability in response to varying ecological situations. More work needs to be done to categorically determine whether *S. pacifica* (in its transition down the western coast of North America into southern California) is a single species or whether it has developed into a different species, represented as *S. kofoidi*, below the California Bight's northern boundary. Further morphological study, intimately tied to molecular examinations, could help to further clarify the mechanisms (ecological or otherwise) behind the visible morphological/structural transitions seen throughout the geographic continuum discussed here, and aide in the confirmation of either separate species (*S. kofoidi* and *S. pacifica*) or a single, highly flexible and variable species that represents the eastern Pacific Ocean extension of the nominant Atlantic species, *Swiftia rosea*. For the present, reference is made to *S. kofoidi* and *S. pacifica* as separate, but closely related, species.

## Swiftia pusilla (Nutting, 1909)

*Eumuricea pusilla* (Nutting, 1909): 718, 719; pl 88 (figs 3, 4). Kükenthal 1924: 152. *Swiftia pusilla* (Nutting, 1909): comb. nov. Breedy and Guzmán 2015: 22, 23.

**Material examined.** No material in the SBMNH collection (see Appendix 3: List of material examined).

**Diagnosis.** Colonies likely small; branching presumed irregular; with material available, not possible to confirm plane configuration; may present only a few branches or is unbranched. A main stem could give rise to roughly alternate branches, at irregular intervals. Main stem and branches may tend to curve upwards, almost running parallel to one another; stem and branches with nearly same diameter; branches can be slightly swollen. Polyps on all sides of branches, fairly dense, roughly arising off branch surface at right angles; occasionally slanting, bending upwards; may give appearance of biserial rows, but often not distinct, usually sitting on opposite sides of branch. Pol-



**Figure 26.** Sclerites of *S. simplex* in SEM. **A** NOAA #CB 34011;  $\mathbf{A}_1$ -sclerites from coenenchyme,  $\mathbf{A}_2$ -sclerites from polyp tentacles **B** NOAA #CB 34212-039, primarily coenenchymal sclerites **C** Also from #CB 34212-039, primarily sclerites from the polyp. All SEM images in this figure prepared by Carla Stehr (NOAA), provided by Ewann Berntson (NOAA).

yps vertically placed, conical and prominent, perhaps slightly raised; distal-most end somewhat widened, showing eight-rayed figure in retraction. Anthocodiae appear to retract vertically into truncated tips, with polyps completely able to retract tentacles. Very few sclerites that could be extracted were generally sharp, acute needles (spindles).



**Figure 27.** Further sclerite arrays in SEM, for a specimen from the far northern end of the continuum. **A, B** From NOAA #81-99B-1 (AB12-0127).

Present in coenenchyme (relatively thin) of polyps, coarse spindles; many unsymmetrical spindles bearing crenulated warts, jagged edges and processes. Marginal sclerites tending to converge as eight calycular processes, tips projecting more or less distinctly. In polyp body walls, spindles may be partially overlapping, transverse in orientation; not arranged in convergent double-rows. No presence of any fingerbiscuit rods could be detected. Colonies (when live?) colored in shades of brown; faded to gray or white with time (preservatives).

**Type locality. Holotype** USA, California, San Diego County, San Diego, Point Loma, 176 meters.

**Type specimen. Holotype** NMNH 25430 [wet/dry]; all material was examined (as well as could be done), several times.

**Remarks.** Examination of preserved material at NMNH, both wet and dry, was not at all enlightening. Specimens very small; wet material in very bad shape, due to protracted storage in formalin (while now water washed and placed in 70% ETOH, the damage had already been done, long ago). The dry fragment was very small, thin and whitish, with zig-zag appearance. This correlated with photographs shown in Nutting's (1909) work. No other institution, where collections were examined, had any material with this species designation. Nutting's (1909) description of the colony, being more or less flabellate and in one plane, does not negate the possibility of his specimen being in the genus *Swiftia* (appearance of polyps on branches is similar), but there is doubt as to whether this is a separate species; specimens in question may be badly preserved or bleached examples of something else. In general, appearance of fragments most closely resembled a species of *Thesea* (fragments bleached?) and any species in the genus *Thesea* should have the distinctly large, spheroidal sclerite form (not seen in this specimen, but minimal material available to work with, highly degraded). Or it may be a species

belonging to genera that can display long, thread-like colonies, such as *Leptogorgia*, *Eugorgia* (new species described in this work, Part II) or even an aberrant, bleached *Swiftia*. The notion that this colony form, described by Nutting, is not an accurately named species, or even a member of the genus *Eumuricea*, has support in final comments made by Kükenthal (1924), translated here: "(i)n no case does this form belong to *Eumuricea*, arguing against it in comparison is the overall construction (shape), the arrangement of the polyps in two lateral rows, their wide distance from one another, as well as the form of the coenenchymal sclerites." This means that Nutting's material at NMNH does not belong in the genus *Eumuricea*; unfortunately, with the material in such poor condition, it may never be possible to clearly confirm what genus and species the specimens do belong to. As Breedy and Guzmán (2015) have elected to place it in the genus *Swiftia*, Kükenthal's comments are supported. Notably, no mention of this species is made in the WoRMS Database listing of accepted species in the genus *Swiftia*.

SBMNH has several lots (provided by both OCSD and LACSD) in its possession that closely resemble the fragments held by NMNH. They are without color (white) or very, very pale yellow, and show the polyp pattern seen in Breedy and Guzmán (2015: fig 11). However, they also very closely resemble, in branch form (diameter, polyp placement), some sclerites (in the predominance of longish spindles, and the unsymmetrical sclerites with jagged edges), and the dull coloring, the specimens that many field investigators in southern California are calling a paler, less common species of Thesea. The fragments shown in Nutting (1909: figs 3, 4), and those shown in Breedy and Guzmán (2015: fig. 11A), closely resemble what is seen with local, somewhat less abundant, specimens of a species of Thesea. In sclerite examinations of these paler, less common, "Thesea-like" specimens, they do not clearly match the sclerite forms that are seen in species of Swiftia, and while they come closer in matching the sclerites seen in the commonly encountered Thesea species, they do not exactly match those sclerites either. Based on that seen in numerous examinations of both locally collected specimens of both Swiftia and Thesea, encompassing a number of species, the suggestion would be that Nutting's Eumuricea pusilla might be a species of Thesea rather than a Swiftia. Nothing can be certain until more specimens that fit his original description can be located, collected and studied. With Eumuricea rigida having been recently assigned to the genus Thesea (Ofwegen, 2014), there is a likely possibility that S. (E.) pusilla might need to likewise be assigned to the genus Thesea.

#### Genus Thesea Duchassaing & Michelotti, 1860

- *Thesea* = *Acis* (non *Acis*, Billberg, 1820, Lesson 1830) Duchassaing & Michelotti, 1860: 18, 19; 1864: 12–14. Kölliker 1865: 136. [*Thesea.* = *Acis* (pars) Wright and Studer 1889: 56.
- Acis Kükenthal, 1919: 836.
- *Thesea* Duchassaing & Michelotti, 1860: 18, 19. Nutting 1912: 80. Kükenthal 1924: 153, 154. Deichmann 1936: 110–112. Bayer 1956: F206-F207; 1958: 50; 1981: 945.

non *Thesea* Nutting, 1910a: 50 {= *Placogorgia*}. Riess 1929: 401 [= *Scleracis*: see Deichmann, 1936: 111].

non Elasma (non E. Jaennicke, 1866); Studer (and Wright) 1887: 58.

non *Elasmogorgia* Wright & Studer, 1889: 132. Hickson 1905: 814. Nutting 1909: 717 (California = *Thesea*). Thomson and Simpson 1909: 238. Nutting 1910a: 45. Thomson and Russell 1910: 159. Nutting 1912: 85. Kükenthal 1919: 752, 836; 1924 (pars): 148]. Thomson and Dean 1931: 199. Matsumoto and Ofwegen 2016: 4.

Evacis (nomen nudum) Verrill, 1912: 373, 377 [Des. Deichmann, 1936].

Euacis Aurivillius, 1931: 126.

*Filigella* Gray, 1868: 443. Kinoshita (pars) 1909: 1. Verrill 1912: 389. Kükenthal 1919: 762, 844. Aurivillius 1931: 126–129. Deichmann 1936: 147. Bayer 1956: F206. Muzik 1979: 142, 143; Matsumoto and Ofwegen 2016: 2, 16, 19.

non *Filigella = Elasmogorgia* Kinoshita, 1909: 1, 4, 5. Kükenthal 1924: 148.

Heterogorgia (pars) Verrill, 1868c: 413. Nutting 1910a: 87.

**Type species.** *Thesea exserta* Duchassaing & Michelotti, 1860 (non *Gorgonia exserta* Ellis & Solander, 1786) = *Thesea guadalupensis* Duchassaing & Michelotti, 1864.

**Diagnosis.** Colonies moderately threadlike, some (rare) sparsely branched in one plane; slightly flexible branches slender, long, each ascending to slightly expanded, stout, possibly truncated, distal branch tip; terminates with flattened arrow-head-like tip; proximal end, when free, also drawn into arrow-head (looking as distal end), or with small attachment disk; axis horny; coenenchyme thin. Calyces distinct, roughly placed alternately; low-domed with eight marginal teeth formed by simple converging spindles. Sclerites of coenenchyme in two layers: outer one containing large, spheroidal/oval or plate-like bodies, outer faces of which are commonly undulated, generating a wash-board appearance (key sclerite form for genus); inner layer including warted spindles of smaller diameter.

Remarks. Kinoshita (1909) and Aurivillius (1931) considered the genus Filigella synonymous with Elasmogorgia. This synonymy was called into question by Matsumoto and Ofwegen (2016) in statements made regarding two distinct species. They stated that Filigella mitsukurii is actually Euplexaura mitsukurii and that there is only one species in the genus Elasmogorgia, that being Elasmogorgia filiformis Wright & Studer, 1889 (closely resembling a species in the genus Astrogorgia Verrill, 1868); in actuality, there now are three accepted species in this genus, listed accordingly by Cordeiro et al. (2019) in the WoRMS Database. Considering the characteristics of the two genera (Euplexaura Verrill, 1869 and Elasmogorgia), neither E. mitsukurii or E. filiformis belong in the genus Thesea; thus Elasmogorgia is not synonymous with Thesea. However, Matsumoto and Ofwegen (2016) did state that the genus Filigella is a synonym of *Thesea*. The basis for this might be the fact that the genus descriptions given by Bayer (1956a) for Thesea and Filigella overlap, in part; this would explain the suggestion of synonymy between the two genera made by Bayer in 1958. Bayer (1958) synonymized the two genera Filigella Gray and Elasmogorgia Wright and Studer with the West Atlantic genus Thesea Duchassaing & Michellotti, and transferred the genus

to the family Plexauridae from the family Paramuriceidae (latter no longer a currently recognized taxon). Bayer (1981) then stated that Filigella was a synonym of Thesea; based on the recent work of Matsumoto and Ofwegen (2016), Elasmogorgia must be removed from Bayer's 1958 synonymy, while Filigella's synonymy might be retained. According to Utinomi (1961) however, the coenenchyme of *Filigella* is thinner and less distinctly displays the two layers seen in most plexaurids; as well, anthocodial armature is more powerful so as to form an operculum, typical of the group formerly known as the paramuriceids. Based on this, he considered it better to retain the genus name Filigella than to unite it with the plexaurid genus Thesea. Muzik (1979) also did not synonymize Thesea with Filigella; her rationale was that Filigella had a distinct collaret (having something more like a true operculum), along with numerous scales forming the tentacle backs. While Filigella was considered to be similar to Thesea, Thesea was stated to have "bulky boots" (Muzik, 1979: 143) forming its (collaret's) points. She went on to surmise that, "depending on the importance of anthocodial armature, these three genera (Thesea, Filigella, along with Muricella) may remain distinct or one day be merged into one genus." The NMNH did not use/recognize Filigella during times when author visited and worked in the collection; Thesea was the genus designation used. From examinations of specimens at NMNH, etc., noting specimen identification while also considering the synonymy discussion given here, Thesea and Filigella may or may not be synonymous; the genus Thesea is used here for colonies from California (and Mexican) waters. Elasmogorgia (and its species, including E. filiformis) is not considered, based on the recent work of Matsumoto and Ofwegen (2016). Cordeiro et al. (2019), in the WoRMS Database, indicated the genus Thesea as having accepted status, and they list some twenty-eight species within the genus; however, neither Thesea [non Elasmogorgia] filiformis (Nutting, 1909) or Thesea variabilis (Studer, 1894) are included in that listing.

## Thesea spp. (one or more unidentified species)

Figures 28A, B, 29A, B, 30A-C, 31A-E, 32A-C

- ? Thesea filiformis (Nutting, 1909 [non Elasmogorgia]), comb. nov. and/or. . .
- ? Thesea variabilis (Studer, 1894) = Psammogorgia variabilis Studer, 1894: 67; [in Bayer 1958a: 51, 52, fig. 7].

**Type locality and type specimens.** As a determination of species encompassed within this assortment of specimens from the eastern Pacific has not yet been established/confirmed, information regarding type locality and identification of any type specimens must await further study.

Material examined. ~65 lots (see Appendix 3: List of material examined).

**Description.** *Colony* (Figure 28A) simple; long, thin, single, whip-like (wiry), unbranched stems or sparingly branched (branch can arise near small attachment disk/ base, if present, or anywhere along length of long strand, at sharp angle or nearly per-



**Figure 28.** *Thesea*, spp., SBMNH 422414. **A** Colony 23 cm from base attachment point on rock to tip (attachment was very tenuous; rock now separated from colony) **B** Closer view of branches, branch tip and pattern of calyces on branch surface.

pendicular to primary strand; not usually longer than main strand); many specimens show neither end of branch/stem as having a base, each terminating with a bluntlypointed arrowhead (usually three small polyps arranged in one plane) as do all branches coming off of main stem; all strands slender and flexible. Branchlets somewhat flattened, 1.0–3.0 mm wide, 1.0 mm thick; stem/branch length generally no more than 0.3 m ( $\leq$ 1 foot). Calyces (Figure 28B) low (~  $\leq$  0.5–0.7 mm high), conical, broad domes



**Figure 29.** *Thesea* spp., SBMNH 422414. **A** Light microscopy sclerite array, 4× magnification, showing different sclerite forms seen in specimens of *Thesea*; large, dense sclerites characteristic for members of the genus **B** 10× magnification, illustrating not only dense sclerite form, but also common spindle form. Very densely warted sclerites range from 317–450 µm, slightly shorter, dense spindles ~220 µm, and those sclerites that are thinner, less warted measure 190–200 µm in length.

with basal diameter ~1.8 mm (hard to determine; calyx walls slope very gradually into general surface of thin, transparent [can be, but not usually] coenenchyme); each rising slightly above general surface, nearly right angled, on all sides of stem and branches (in some colonies, appear to stand taller). Placement slightly alternate; although some calyces tend to be lateral, and alternate, actually present on all sides of stem and any branches, somewhat distant, irregularly separated by a space ~0.0-3.0 mm. Calyces ovate (sometimes round) in cross-section; longer diameter parallel with stem. Polyps usually completely retracted, almost entirely concealed by indrawn margins. Sometimes, polyps fully retracted, with large, visible opening above tentacles; margin edge easily seen, usually displaying eight triangular teeth-like projections; individual sclerites on tentacles not easily seen. Collaret not easily seen on most specimens; may not be present at all. Color of living colonies range from yellowish-beige or tannish-beige, dirty white to bright white (also perhaps bright golden yellow?); with white or cream polyps; axis pale yellow to yellowish brown to dark brown or black. Sclerites (Figures 29A, B, 30A-C, 31A-E, 32A-C) generally medium-sized spindles (average ~0.2 mm L X 0.07 mm W); largest-sized heavy, conspicuous, densely warted (dense, elongate footballs), often one-sided, covered with very jagged projections. Also many smaller sclerites: some slender spindles with surfaces covered. Largest sclerites found on stem between calyces; although often invading walls of the latter, usually of a slightly more slender type, appearing as small, short spindles arranged transversely on lower parts; a few (almost as blunt-ended scales) with several closely layered (two or three deep), vertically placed around margin, their ends forming moderately conspicuous circlet of points, annulations or oval markings around margins when viewed from above. Collaret consists of two or more circular rows of spindles; difficult to see in many colonies (see Remarks section, below). Coenenchyme filled with compact layer of short stout spindles lying



**Figure 30.** *Thesea* spp., SBMNH 265941, light microscopy array. **A** 4× magnification, showing dense sclerites as typical "football (arrow)," a key characteristic of the genus **B** Same specimen, SBMNH 265941, 10× magnification **C** One additional array, 10× magnification; shows distinctly dense warting of "typical" sclerite. Sclerites in **C** extracted from specimen T0-61, provided by research/survey staff, Los Angeles County Sanitation District.

lengthwise of stem; in gross examination of coenenchyme surface, stout spindles and/or spheroidal bodies very evident, dense in number. However, largest spheroidal or platelike bodies common to genus not always abundant in sclerite arrays, but always present, exceedingly evident, very densely warted with jagged, bumpy edges.



**Figure 31.** *Thesea* spp., SBMNH 422352, SEM image. **A** Possible, small developing inner coenenchymal sclerites **B**, **E** Characteristic, large, spheroidal sclerites of outer coenenchyme **C** Tentacular sclerites **D** Inner coenenchymal sclerites

**Etymology.** The Latin *fili-* = "thread;" and *form-*, the Latin for "form or shape;" could refer to the slender thread- or wire-like nature of the branches; this branch pattern was seen consistently in all specimens examined (regardless of what species might be represented). Thus, specimens from at least one species group could potentially be named *Thesea filiformis*, but could not be synonymous with *Elasmogorgia filiformis* 



**Figure 32.** *Thesea* spp., SBMNH 422344, SEM image. **A** Possible tentacular sclerites **B** Inner coenenchymal sclerites **C** Large spheroidal sclerites of outer coenenchyme, characteristic of genus.

Wright & Studer, 1889. For *T. variabilis*, variability is implied, but whether that is in regards to such characters as colony form, branch thickness or sclerite appearance, the description given by Bayer (1958) is not clear; he does, however, indicate that the colonies he examined displayed variety of color.

**Distribution.** For this assemblage of specimens, from the northern Channel Islands, California, south to Baja, California, based on location data (see Appendix 3:

List of material examined). NMNH has *T. filiformis* in their collection; those specimens were examined and they indeed belong in the genus *Thesea* (for example, USNM 30295, from San Diego, Point Loma, resembles those in SBMNH collection). It has been determined that many specimens collected by both LASD and OCSD are similar to those in SBMNH collection. NMNH has several other specimens (USNM 57172, Baja, CA; 57173 Baja, CA and 57525, from California, Point Loma) that also resembled those in SBMNH collection, or those collected by both LASD and OCSD. As to *T. variabilis*, the two specimens examined at NMNH (USNM 50633 and 50634) were both collected from La Jolla Canyon, San Diego County, CA.

**Biology.** Found on sand/soft mud bottoms to depths of at least 30 m, based on collection data for many specimens in SBMNH collection. Branches of these colonies can be found with any number of other organisms growing on, or associated with, them. On specimens examined, both wet and dry, were found: 1) round, gall-like growths formed by a species of acorn barnacle (protruding out through the coenenchyme, 2) presence of a *Lepas*-like barnacle (found primarily on bare, exposed axis, rather than on strands with coenenchyme intact; one specimen with a note: "*Scalpellum*," where barnacle was conspicuously affixed to strand), 3) presence of ovulid snails (genus *Neosimnia*), 4) intertwined with arms of Ophiuroidea, 5) sometimes with other kinds of cnidarian attached at base of colony; often mixed in with species of sea pen, having the same body form (thin strand-like colonies) and 6) some with what appeared to be a kind of worm (? ribbon worm) curled around the branch strands.

Muzik (1979) made the comment that "colony shape is largely environmentally, not genetically determined" in the *Thesea-Filigella-Muricella* genera cluster. Colonies will be "large, planar, even branched . . . when on a large firm substrate, but filiform on rubble." The species group discussed here consistently grew on something other than large, firm substrates (based on consistent slender, filiform appearance of branch strands), confirmed through images provided by staff of LACSD and OCSD. Their growth and presence on a softer or rubble bottom would dictate aspects of their biology, such as materials fed upon, means of anchorage (or lack thereof), etc.

**Remarks.** Of interest are specimens belonging to the genus *Thesea* that are consistently, and regularly collected by Los Angeles and Orange County Sanitation District (LACSD and OCSD) staff; these look very comparable to many lots of specimens housed in SBMNH collection. Both LACSD and OCSD regularly label the majority of their collected samples as "*Thesea* species B;" it appeared that this is the species described here, so plentiful in the SBMNH collection. These will have a tan, light beige to dull cream coloring. Based on the number of lots housed in SBMNH collection (see Appendix 3: List of material examined), and the consistent collection records that both LACSD and OCSD report, *Thesea* is very common in California waters. Also of interest are specimens (determined as belonging to this genus), present in both SBMNH collection (in fewer numbers) and collected by LACSD and OCSD, that have a noticeably yellower color than the typical *Thesea* described above. It was the range of color displayed in the SBMNH collection lots (and of those collected regularly by LACSD and OCSD) that was of more than passing interest. Nutting (1909) stated color for

Elasmogorgia filiformis from California (incorrect genus) as clear, light gray, with axis dark brown, and Nutting (1912) stated color (for same species, again incorrect genus) as rather dark brown; axis almost black (was unable to determine if these two statements by Nutting, regarding color, were for dry specimens, but likely). Multiple wet specimens examined revealed variable color in both coenenchyme and axis, without consistent color pairing, despite no real differences in appearance of sclerites (aside from color). With no apparent, clear-cut differentiation in variation of the sclerites (aside from color) in most of the arrays examined from colonies colored beige, white, or yellow, initial consideration was that all were several color morphs of the same species. At present, colonies are being treated as such; more extensive examinations currently being conducted may reveal differences that would warrant colonies of varying color being given separate taxonomic designations. Additionally, a small number of lots within the collection have far smaller, stouter (almost equal in width and length) dense sclerites; these are very similar in length to the less heavily warted spindles that are seen. The possibility that these specimens need to be separated out has not been excluded, but different environmental circumstances may account for these variations.

Determination as to whether or not an actual operculum was present on calyces was (and is as yet) not clarified. Kinoshita (1909), Kükenthal (1924) and Deichmann (1936) all specifically made mention, and described arrangements of, sclerites that form the operculum in this genus. In one known species the operculum was described as being strong, each flap consisting of three spindles forming an acute-angled triangle, reinforced by others lying parallel to these, or disposed longitudinally on distal parts of tentacles. In another species, the operculum was described as being composed of three to six pairs of spindles in converging double rows. Neither pattern was clearly seen in specimens examined. Considering the accepted definition of an operculum, and those families where one is quite evident, it did not seem that in this genus there is such a structure in the correct sense of that term; it might be more accurate to speak of a collaret, or a crown and points arrangement. Neither Kinoshita (1909), Kükenthal (1924) or Deichmann (1936) provided any clear illustrations of the situations they discussed regarding an operculum. Fabricius and Alderslade (2001) speak of the family as having crown and points, with no mention of an operculum. Despite an issue of semantics, or incorrect use of the term operculum, the simple fact was that very few colonies examined provided even one or a few calyces where a clear view could be had of what was covering over the tentacles. The eight tooth-like projections of the calyx margin were evident (on many), but any pattern of sclerites that might have been overlying the indrawn tentacles was another matter. The dry, often brittle nature of many of the specimens compounded the problem. With fresh material, more malleable to work with, this question could definitively be answered.

Regarding the species *T.* [non *Elasmogorgia*] *filiformis* (Nutting, 1909), Nutting reported a specimen taken from off San Pedro, California coast, in the University of California collection, as well as one described in Nutting (1909), from 'Albatross' station 4349, Point Loma light-house, NE 6.5 miles, 136–244 m (unable to locate them, thus these specimens could not be examined). He also reported specimens taken in the Dutch East Indies at 112 meters, and the specimen described in Nutting (1912) was

taken from 'Albatross' station 4837, Tateisha Zaki Light, S 53 E 8 miles, 104 m. These latter two may not be the same species as the other two mentioned.

Regarding Thesea variabilis, there are no apparent specimens of the species in the SBMNH collection (see Appendix 3: List of material examined). Based on collection data for the specimens at NMNH (USNM 50633 & USNM 50634, from La Jolla Canyon, San Diego), this species required inclusion here but was unable to determine if these specimens are this species or actually a morph of T. [non Elasmogorgia] filiformis. Commonly called the White gorgonian, "Thesea variabilis resembles very narrowly by its exterior aspect some of the Thesea's of the 'American Indies' " (Bayer 1958). Drawings of sclerites from Thesea guadalupensis that Bayer (1958) provided for comparison with T. variabilis showed that the resemblance is more than superficial. The only real difference seen was that the sclerites of *T. variabilis* were smaller than those of T. guadalupensis (and of roughly the same size as those seen in T. [non E.] filiformis). "The sclerites are in limited accord, as are the external characters. Thus, there is no doubt that the eastern Pacific species belongs to the genus Thesea, a genus that was formerly thought to be restricted to the 'American Indies.' " While noted on a list found in SBMNH files, indicating California sites and depth ranges (40-46 m, in the La Jolla area, only), there is no certainty that other coastal areas of California (even just southern California), would be an actual locality for this species. In Bayer's personal SEM files, images were found for Thesea variabilis Studer = Psammogorgia variabilis. These did not fully resolve identification issues but does lead to further consideration of this species belonging to the genus Psammogorgia rather than the genus Thesea. Found at depths greater than 100 ft [-33 m], on the two specimens Bayer examined (1958), barnacles that were present formed prominent cysts on the branches.

Overall branching pattern described puts *T. variabilis* at odds with the colony form commonly seen and named as *Thesea* spp. in southern California, where branches simply appear as long thin strands, often with no apparent base, both ends of each strand/branch frequently terminating in a flattened, arrowhead shape. From images sent by LACSD and OCSD, many have an attachment to the substrate simply by being partially buried in the soft bottom sand or mud. USNM 50633 and USNM 50634 appeared more as a flattened bush, with indication of an actual base structure, and had branches of a thicker diameter, with a slightly more yellow coloration. They did not appear as the many colonies in the SBMNH collection, but their sclerites were very comparable. Thus, there might be the possibility that *T. variabilis* and *T.* [non *E.*] *filiformis* are the same, with variable colony form (attached forms, with actual base structure, more extensively branched, even almost as a fan, while those with no attachment base more thread-like); perhaps this is a case of different living conditions dictated by the surrounding environment resulting in different colony morphologies.

Generally, this multiple-lot assemblage is composed of specimens that are best described as a conglomerate of what could be called *Thesea filiformis* (with few possible morphs) or is composed of a few different species. Based on location data for all, *T. filiformis* for all may be the better choice; further studies will need to be done, but there is no doubt that the genus *Thesea* is commonly encountered in southern California waters.

## Diagnosis of the Suborder Calcaxonia Grasshoff, 1999

Group of families lacking chambered axial core. In axis, large amounts of non-scleritic calcareous material present, either in the form of calcite or aragonite, deposited between horny fibers, or present as central core, or with solid internodal sections alternating with nodes of pure gorgonin in segmented axis.

Remarks. With the exception of one species (Plumarella longispina Kinoshita, 1908a), Calcaxonia is not well represented in the SBMNH collection, although there is every indication that calcaxonian species are represented in the California Bight through multiple genera and species (see Appendix 3: List of material examined). Several species (Callogorgia kinoshitai (Kükenthal, 1913) and Parastenella pacifica Cairns, 2007) are each represented in the collection by no more than three to six separate colonies (plus numerous colony fragments); species that fall within the genera Isidella Gray, 1858 and Keratoisis Wright, 1869 are present in the collection, but are represented by only one or two colonies each. As all are deep-water taxa, this is not surprising. Unfortunately, specimens provided little material to work with, such that comparing/ contrasting one specimen with another was not always possible. Furthermore, a number of the specimens in the collection are not in good shape; some are represented by a single branch, or portion thereof, rather than an intact, complete colony. In some, if all colony branches are present, the coenenchyme is largely or completely lacking. Even having material from another institution did not always help; often these are only identified to genus (due to very recent collection events), and when they are identified to species (often as new species), the material in the SBMNH collection often lacked some key structure that could have made comparison with a well-known, or newly described species, possible. Thus, the descriptions given here for species in this suborder from the collection are not always complete. More material is required, and further extensive comparisons with other specimens from other institutions are needed, to clarify not only what is present in the SBMNH collection, but to also clearly indicate which species have regular occurrence in the California Bight.

## Key to Families represented in SBMNH collection (Suborder Calcaxonia)

## List of species of Calcaxonia Grasshoff, 1999

Class Anthozoa Subclass Octocorallia Haeckel, 1866 Order Alcvonacea Lamouroux, 1816 Suborder Calcaxonia Grasshoff, 1999 Family Primnoidae Milne Edwards, 1857 Callogorgia kinoshitai (Kükenthal, 1913) Parastenella pacifica Cairns, 2007 Parastenella ramosa (Studer, 1894) Plumarella longispina Kinoshita, 1908 Primnoa pacifica Kinoshita, 1907 Narella Gray, 1870 Family Isididae Lamouroux, 1812 Acanella Gray in Wright, 1869 Isidella Gray, 1857 Keratoisis Wright, 1869 Lepidisis Verrill, 1883

#### Descriptions of species of Calcaxonia Grasshoff, 1999

## Family Primnoidae Milne Edwards, 1857

**Diagnosis.** Axis of strongly calcified material embedded in gorgonin, unjointed, arranged in undulated concentric layers; core not a soft, chambered central chord. Attachment base a calcareous disc; rarely, a branched, rhizoidal structure. Colonies usually profusely branched, rarely flagelliform. Polyps single, in pairs, or in regular whorls, heavily armored with calcareous scales (sclerites primarily scales in all species), permanently exsert; in contraction, tentacles in-folded. Polyps protected by eight triangular scales making up distinct operculum, below which scales of polyp body aligned in eight rows, some of which may be reduced or missing on adaxial side; rarely (single species) scales not regularly arranged, operculum undifferentiated. In coenenchyme, a layer of plates or scales, commonly elongate, some with inner layer of stellate sclerites. Scales always distinguished by cruciform extinction pattern seen in polarized light.

**Remarks.** A rationale for the distinction between the use of the words calyx and polyp required in reference to the family. S Cairns (pers. comm.), in a conversation with P Alderslade some years ago, determined that the term calyx should be reserved for those polyps that can contract to a small mound (such as those seen in the plexaurids), and that the primnoid morphology is a polyp. Thus, there is no calyx to be seen in this family; projections and living animals are called polyps; that usage has been incorporated here.

## Genus Callogorgia Gray, 1858

Gorgonia Pallas, 1766: 160 (pars). Linnaeus 1767: 1289 (pars). Ellis and Solander 1786: 67 (pars).

Muricea Dana, 1846: 675 (pars).

Prymnoa Ehrenberg, 1834: 357 (pars).

Primnoa Milne Edwards & Haime, 1857: 139 (pars). von Koch 1878: 457; 1887: 85.

*Callogorgia* Gray, 1857 [1858]: 286. Bayer 1956: F220; 1961 [1962]: 296. Carpine and Grasshoff 1975: 102. Bayer 1981: 938; 1982: 119, 120. Bayer and Stefani 1989: 455. Bayer 1998: 162, 163. Cairns and Bayer 2002: 841–845; 2009: 29, 40. Cairns 2010: 425 (Hawaiian species); 2016: 58 (New Zealand species); 2018a: 6 (key to Indo-Pacific species); 2018b: 3. Cairns and Wirshing 2018: 8, 18, fig. 40.

Calligorgia Gray, 1870: 35 (unjustified emendation). Studer 1878 [1879]: 645; 1887: 51.

*Fanellia* Gray, 1870: 45. Bayer 1982: 134, 135. Bayer and Stefani 1989: 470, 471. Cairns and Bayer 2009: 40, 41. Cairns and Wirshing 2018: 8, 18.

*Xiphocella* Gray, 1870: 56 (type species, *Gorgonia verticillata*: sensu Esper, 1797: 156, by monotypy).

? Callicella Gray, 1870: 37 (type species, Callicella elegans Gray, 1870, by monotypy).

- *Caligorgia* Wright & Studer, 1889: 75–77 (pars; unjustified emendation). Versluys 1906: 55 (pars). Kükenthal and Gorzawsky 1908: 19. Kinoshita 1908a: 34.
- Nutting, 1908: 574. Kükenthal 1912: 320(?); 1915b: 146; 1919: 362 (pars); 1924: 267. Deichmann 1936: 158.

Type species. Gorgonia verticillata Pallas, 1766 (by monotypy).

**Diagnosis.** Colonies usually branched pinnately, some rarely dichotomously, mostly in one plane; axis longitudinally striated, commonly iridescent. Polyps in regular whorls, strongly bent inward toward axis. Adaxial rows of body scales reduced; opercular scales distinctly differentiated from body scales, not overreached by marginals (which do not bend inward over them); sclerites usually elaborately sculptured externally, with ridges, crests or small granules; cortical sclerites thick, pebble-like or more elongate.

**Remarks.** WoRMS Database (Cordeiro et al. 2019) gives this genus accepted status, with this spelling.

## Callogorgia kinoshitai (Kükenthal, 1913)

Figures 33A, B, 34A, B, 35A–E

Callogorgia kinoshitae Kükenthal, 1913: 264–266; text figs E, F, pl 8, fig. 10 (= Caligorgia kinoshitae Kükenthal, 1913: 264–266 [spelling difference]); 1919: 370; 1924: 270.

Callogorgia kinoshitae: Bayer 1982: 122. Cairns 2007b: 512 (listed). Cairns and Bayer 2009: 29 (listed).

(?) Caligorgia sertosa Wright & Studer, 1889: 75–77. Nutting 1909: 715.

**Type locality.** USA, California, 218–2472 m. Possible collection location for type La Jolla, San Diego, based on work of Kükenthal (1913; 1924).



**Figure 33.** *Callogorgia kinoshitai*, SBMNH 422990. **A** Colony; height (base missing) ~30 cm **B** SBM-NH 422982, branch close-up, illustrating arrangement of polyps in whorls, each polyp curving strongly upward and inward toward branch.

**Type specimens.** Repository of type(s) unknown.

Material examined. 6 lots (see Appendix 3: List of material examined).

Description. Colony (Figure 33A) flabellate, usually branched in regularly alternate, pinnate pattern; some colonies (often main branches) rarely dichotomous; most branches in one plane. Maximum colony height over 30 cm (base excluded); average height of colonies in SBMNH collection ±15 cm. Central stem slightly bent in geniculate (jointed, zig-zag) pattern, giving off branches at angles or joints; few branches give off branchlets in similar manner. Distance between branches/branchlets on same side of central stem roughly one cm (slightly larger than one cm closer to base and less than one cm toward tips of branchlets). All branchlets unbranched, parallel to each other. Distal ends of branchlets extremely thin, more flexible, with branchlets often recurved back on themselves. Axis stiff, longitudinally striated; creamy yellow to tan, covered with fairly thin coenenchyme. Color of living colony (?)white to creamywhite; perhaps very light pinkish-beige; color in alcohol creamy whitish-beige to light tan. Five or six polyps (rarely four) regularly arranged in each whorl (most common number being five); whorl diameter 2.1-2.2 mm; generally, four to five whorls per centimeter of branch length. Minimal distance between whorls no more than 1.0 mm (often less), but evident. Polyps 2.0 mm tall; slightly clavate, covered in four to eight rows of nearly spindle-shaped (rods) sclerites; polyps strongly curved from base outward, upward and inward toward axis (Figure 33B), thus apertures directed toward


**Figure 34.** *Callogorgia kinoshitai*, SBMNH 422982. **A** Light microscopy array, 4× magnification, showing variety of large scales (body wall, coenenchymal, opercular, etc.) as well as very small coenenchymal rod-like sclerites **B** Array of representative scales,  $10\times$  magnification, SBMNH 422982; **a** abaxial body wall scale, indicated by arrow **b** possible inner lateral or abaxial from polyp base **c** outer lateral scale **d** opercular scale. Opercular scales average 239 µm in length, body wall scales range in breadth from 117–217 µm and very small spindles ~28 µm in length.

stem or branch. Sclerites (Figures 34A, B, 35A–E) predominantly scales, flattened (sometimes oblong, fusiform; some appearing as flattened caveman clubs) on stem and branches, with long tooth-like spines, and radiating ribs. Outer sclerite surface may also have many small to medium-sized warts, bumps and granules. Scales im-



Figure 35. *Callogorgia kinoshitai*, SBMNH 422982, SEM image. A Small, developing coenenchymal rods **B** Very flattened, "odd" coenenchymal rods **C** Coenenchymal rods **D** Opercular scales **E** Highly ridged abaxials (polyp tip). Sclerite forms shown here correspond to figures shown in Cairn and Bayer 2002 for species in the genus.

bricating (like roof tiles), fan-shaped on polyp walls. Aperture edge of polyp with ctenate marginal scales, inside of which are bases of eight opercular scales; these form tall, pyramidal opercula, with height ~0.5 mm. Opercular scales (Figures 34Bd, 35D) distinctly differentiated from body scales, not overreached by marginals, not bending

inward over them. Individual opercular scales elongate triangles, especially on abaxial side, forming a conspicuous, elongated spine when polyp is fully retracted; these scales bear thickened, longitudinal ridges on their inner surface, ending with truncated points. Opercular scales up to ~0.65 mm long by 0.2 mm wide at broader end; adaxial opercular scales much smaller. Upper layer (ring) of marginal scales (Figure 35E) large, with radiating ribs, furrowed at their edge; others (proceeding proximally) show these markings feebly, if at all. Longitudinal rows of scales on polyp body commonly numbering seven (rarely eight), best seen on abaxial and lateral sides (inner lateral scales number four on each side of polyp); only abaxial rows of body scales complete. Adaxial rows reduced or absent; if present, generally two scales placed distally, two proximally, revealing large area of naked adaxial wall; thus, total number of scales within a row varies, but typically eight (with six to nine possible) scales in row; most numerous on exposed, abaxial side. Largest body wall scales, abaxial (Figures 34Ba, b, 35E); abaxial scales near tip of polyp smaller, those of adaxial side up to ~0.1 mm across by 0.1 mm tall. Lateral scales slightly smaller (Figure 34Bc). Coenenchymal sclerites (Figure 35A–C) dense, as elongated, nearly spindle-shaped rods often covered with numerous thorns or prickles.

Etymology. Named in honor of Kumao Kinoshita of Japan (Cairns 2018).

**Distribution.** *Callogorgia kinoshitai* appears to extend from Monterey Bay to as far south as Chile, based on collection location data found recorded at several institutions (see Appendix 3: List of material examined). Based on specimens housed in SBMNH collection, it would appear that the species does extend further north, into waters off Oregon and Washington (USA).

**Biology.** Generally found in deep water (averaging 800–1,000 meters). Intertwined amongst branches may be found moderate to large Ophiuroidea, along with either what appear to be anemones (quite large, very fleshy and wrinkled) and/or possibly a type of acorn barnacle, attached to stems and branches.

Remarks. Kükenthal (1919, 1924) speculated that the species C. kinoshitae(i) might be a junior synonym of Caligorgia sertosa Wright & Studer, 1889 (note error in spelling of genus name), as described by Nutting (1909). Nutting (1909) indicated five localities for what he called C. sertosa, all in the vicinity of USA, California, San Diego, Point Loma light-house. Nutting also established the type for C. sertosa, that being collected at Station 192, off Kei Island, South Pacific, 255 m, by R/V 'Challenger'. Perhaps Nutting's specimens from the San Diego area should be ascribed to this species rather than to C. sertosa. In any event, the two are indeed separate species. Researchers with greater exposure to, and expertise on, this species (SD Cairns) should be consulted regarding legitimacy of C. sertosa as senior synonym. Cordeiro et al. (2019) does not show this synonymy in the WoRMS Database. Earlier descriptions for both C. kinoshitae(i) and C. sertosa found in Kükenthal (1919) clearly indicated the distinct differences used to distinguish between these two species. Based on locations of collection events, with C. sertosa having its type collected from Kei Island in the South Pacific, the two appear to be separate, distinct species.

#### Genus Parastenella Versluys, 1906

non Stenella Gray, 1866: 213 [a cetacean].

Stenella Gray, 1870: 48. Studer 1878 [1879]: 643; 1887: 50. Wright and Studer 1889: 56 [pars; *S. doederleini*, *S. spinosa*]. Kinoshita 1908a: 27, 28. Kükenthal 1915b: 151, 152 [pars]; 1919: 443–445 [pars; key to species]; 1924: 303 [pars; key to species]. Molander 1929: [pars]. Aurivillius, 1931: 289, 290 [pars].

Stenella (Parastenella) Versluys, 1906: 39, 45.

Candidella (Parastenella) Bayer, 1956: F222.

Parastenella Bayer, 1961: 295 [ill. key to genus]; 1981: 936 [key to genus]. Bayer and Stefani 1988: 454 [key to genus]. Cairns 2007a: 245–247; 2007b: 518. Table 2 [generic revision, tabular key to species]. Cairns and Bayer 2009: 31, 45, 46. Cairns 2010: 434 [key to species]; 2011: 23; 2016: 94–96

Type species. Stenella doederleini Wright & Studer, 1889; subsequent designation Bayer 1956a.

**Diagnosis.** Colonies primarily branched, planar dichotomous; occasionally slightly bushy. Polyps arranged in either whorls of up to four, in pairs, or isolated, generally standing perpendicular to branch. Operculum well developed, opercular scales decidedly keeled on inner surface. Marginal scales eight, in alternate position with respect to opercular scales. All polyps, generally, completely covered with five to eight longitudinal rows of body wall scales; outer surfaces covered with small granules. Coenenchymal scales arranged in one layer. Tentacular rods sometimes present.

**Remarks.** Genus holds accepted status, shown in WoRMS Database (Cordeiro et al. 2019).

#### Parastenella pacifica Cairns, 2007

Figures 36A, B, 37A–C, 38A–E

Parastenella pacifica Cairns, 2007b: 526, 527; figs 1C; 8, 9.

**Type locality.** USA, Oregon, west of Cape Meares, 45°25'18"N, 125°11'01"W, 1498–1527 m.

Type specimen. Holotype USNM 1071799 [dry]; type was not examined.

Material examined. 1 lot (see Appendix 3: List of material examined).

**Description.** *Colony* (Figure 36A) with dichotomous branching, somewhat irregular, generally in one plane; some SBMNH specimens slightly bushy, flabellate, up to +30 cm in height (next largest, 14 cm tall). In largest colonies branchlet tips tend to droop down, curling slightly back on themselves (Figure 36A); branching intervals vary from ~3.5 cm distance at lower end of main stem (near base) to less than 1.0 cm near branch/branchlet tips. Polyps (Figure 36B) with opercula well differentiated; usually spaced 0.5–1.5 mm apart in/as singles, pairs or whorls of up to three, erect



**Figure 36.** *Parastenella pacifica*, SBMNH 422983. **A** Colony (attachment base missing), ~15 cm × 13 cm, at widest point **B** Branch tip close-up.

(perpendicular to axis), or slightly bent downward toward stem. Polyp height 2.0–3.5 cm, flared distally with slender, delicate stalk, heavily armored with calcareous scales. Polyps found on numerous branches, tending to favor one side of colony. Axis as described for family; visible through single layer of white, translucent coenenchymal scales; dark to light brown in color. Color of living colony (?)cream or white; in alcohol, cream to light tan. Sclerites are scales (Figures 37A–C, 38A–E); marginal scales (standard number eight) alternating in position from opercular scales (latter forming



**Figure 37.** *Parastenella pacifica*, SBMNH 422983. Light microscopy arrays, scleritic scales. **A** An assortment **a** possible marginal scale **b** abaxial body wall scale **c** opercular scale **B** 10×-magnified image; marginal scale **C** 10×-magnified image; opercular scale.

distinct operculum, creating obvious projection out from polyp). Marginal scales (Figures 37Aa, 37B, 38C) all of similar shape and size, most showing broad, shallow apical flute; these generate symmetrical rosette when viewed from above. Submarginal body wall scales (Figures 37Ab, 38A) roughly arranged in eight longitudinal rows, each row with three to four scales that appear to overlap those in adjacent rows; distal end obviously rounded, no fluting apparent; flutes absent on submarginal abaxial body wall



**Figure 38.** *Parastenella pacifica*, SBMNH 422983, SEM image. **A** Abaxial body wall scales **B** Coenenchymal scale **C** Marginal scales **D** Opercular scales **E** Pinnular sclerites. Compare to those shown in Cairns 2007 (Figure 9).

scales. Otherwise, polyp completely covered with body wall scales, including adaxial region. Opercular scales (Figures 37Ac, 37C, 38D) alternate with marginal scales (as opposed to overlapping them) around polyp; triangular shape, prominently keeled on inner surface; most all of similar size (0.5 mm in length, on average). Coenenchymal scales (Figure 38B, possibly) generally elliptical, very evident on branches (resembling

sea pansy rachis or water lily pad), in one thin layer; few with irregular shape. Pinnular sclerites (Figure 38E) small rods, with granular surface.

**Etymology.** The species name *pacifica-* in reference to its general location; stated to be closely similar to *Parastenella atlantica* (Cairns (2007b). Cairns suggested that these could form a geminate (twin species) pair, differing largely in having ranges in different oceans. The species designation is listed as accepted in WoRMS Database (Cordeiro et al. 2019)

**Distribution.** Deep-water species (~1,500–2,086 m, currently known to live on the continental slope off Oregon up to British Columbia (Queen Charlotte Islands); see Appendix 3: List of material examined. Material in the SBMNH collection came from an area north of the California Bight's northern limit; whether it will be found further south (into the California Bight) remains to be seen.

**Biology.** Of the many fragments/partial colonies present in the one lot from the SBMNH collection, one of the fragments has bits of a distinguishable, pale orange ophiuroid (brittle/basket star) intertwined/tangled within it. This could either be an artifact of collection or a true living condition. The specimen from Moss Landing Marine Labs (see Appendix 3: List of material examined) also showed presence of Ophiuroidea; based on the nature of their location, etc. within the colony, likely a living situation, not an artifact.

**Remarks.** Sclerites in specimens from SBMNH were consistently a bit smaller than those from holotype shown in Cairns (2007b). Furthermore, the SBMNH material not generally in good condition; was often difficult to get good microscopic arrays showing enough of the different forms of body wall scales (abaxials, laterals and adaxials) so as to see clear differences. The coenenchymal sclerites on branches were very evident, however, and examination of sclerites showed clearly the broad, shallow fluting. While tentacular rods are considered common in this species, sometimes very few would be found in the fragments examined; the condition of many of the polyps may partly explain their absence. Further examination of undamaged colonies, collected from the same area, may better reveal their presence.

#### Parastenella ramosa (Studer, 1894)

Stenella ramosa Studer, 1894: 64, 65.

- Stenella (Parastenella) ramosa (Wright & Studer, 1889): 56. Versluys 1906: 47, 48. Kükenthal & Gorzawsky, 1908: 34, 35. Kükenthal 1919: 445; 1924: 303.
- *Parastenella ramosa* Cairns, 2007b: 518–523, figs 1E, 4, 5. Cairns and Bayer 2009: 31 (listed). Cairns 2011: 24, 25.
- ? Stenella doederleini Studer, 1894: 64; see Remarks, below.

**Material examined.** No specimens in SBMNH collection (see Appendix 3: List of material examined).

**Remarks.** Species included here as collection records examined (see Appendix 3: List of material examined) show a distributional range that includes the California Bight. Based

on those collection records, this is a deep-water species that has been collected off the west coast of Central America, and from areas of the California coast, to just north of the Santa Barbara Channel Islands (Rodriquez Seamount). It has also been collected from Monterey Bay (Davidson Seamount), north to Oregon, Washington, Vancouver Island to Gulf of Alaska; 665–1750 m. Cairns (2011) stated that the known distributional range of this species now extends west to Adak Canyon in the Aleutian Islands and the Commander Islands, Russia. This represents a substantial range, encompassing the California Bight region.

Cairns (2007b) stated that given the similarity of Parastenella doederleini (Wright & Studer, 1889) and Parastenella ramosa, "it is likely that Studer's (1894) identification of S. doederleini from off Panama at 1,429 m (specimen missing from MCZ), taken quite close to the type locality of *P. ramosa*, is probably also *P. ramosa*." This species is generally most similar to the type for the genus, P. doederleini (Wright & Studer, 1889). That specimen was collected from off Sagami Bay, Japan at 3,427 m. Cairns (2007b) differentiated between the two; P. doederleini has more elongated and slender marginal flutes, more delicate polyps and coenenchymal scales with one or more small rounded knobs either at their center and/or on their perimeter. Specimens of P. ramosa examined (indicated in the Appendix 3: List of material examined), exhibited polyps more distinctly directed downwards and the marginal flutes were slightly broader than those seen in *P. doederleini*. A check of the WoRMS Database (Cordeiro et al. 2019) show both P. ramosa and P. doederleini as separate, accepted species. As well, P. ramosa can easily be distinguished from *P. pacifica* by the latter having obviously broad, shallow marginal flutes, eight rows of submarginal body wall scales and the absence of flutes on submarginal abaxial body wall scales; P. ramosa exhibits narrow, tubular marginal flutes, five rows of submarginal body wall scales and abaxial body wall scales with flutes. Additionally, Cairns (2011) stated that the confirmed presence of nematocyst pads on the inner surface of the marginal scales in this species might be the case for all species in the genus, as suggested in Cairns, 2010.

## Genus Plumarella Gray, 1870

Cricogorgia Milne Edwards, 1857: 6, pl B2, fig. 6 [nomen nudum]. Gray 1870: 36, 37.
Plumarella Gray, 1870: 36. Studer 1887: 51. Wright and Studer 1889: xlix, 73, 74, 281.
Versluys 1906: 13, 14. Kinoshita 1908a: 6–8. Kükenthal 1915b: 144, 145 [key to genus and species]; 1919: 340–343 [key to genus and species]; 1924: 255 [key to genus and species]. Diechmann 1936: 155, 156 [key to genus]. Bayer 1956: F220; 1961: 293 [ill. key to genus]; 1981: 936 [key to genus]. Bayer and Stefani 1988: 454 [key to genus]. Fabricius and Alderslade 2001: 244, 245. Cairns and Bayer 2004b: 448, 449 [key to western Atlantic species]; Cairns and Bayer 2009: 29, 39, 40. Cairns 2011: 7–9; 2016: 51, 52; 2018b: 39. Cairns and Wirshing 2018: 1, 11.

**Type species.** Gorgonia penna Lamarck, 1815; subsequent designation by Wright & Studer, 1889: 73.

**Diagnosis.** Branching in one plane, pinnate, with branches close together in many colonies. Polyps biserial, alternate (rarely, opposite) or irregularly scattered; never in whorls or pairs. All eight rows of body scales present; adaxial surface usually has fewer scales; inner face of opercular scales with inconspicuous apical keel, or none; opercular scales aligned with marginals. Sclerites of coenenchyme (some species) as scales or warty radiates in lower parts of colony and inner cortex.

Remarks. Genus bears accepted status in WoRMS Database (Cordeiro et al. 2019).

## Plumarella longispina Kinoshita, 1908

Figures 39A, B, 40A–H

**Type locality.** N. Pacific Ocean, Japan, Honshu Island, Sagami Bay, Okinose Bank, 600 m.

**Type specimens. Holotype** USNM 50117 [dry]; branch (from holotype), donated by Tokyo Imperial Museum; this material was examined. Main colony presumably still housed in collection at Tokyo Imperial Museum (all scientific and "natural materials" collections housed separately at what is now called the National Museum of Nature and Science); was unable to verify or confirm catalog number.

Material examined. ~33 lots (wet/dry) (see Appendix 3: List of material examined).

Description. Colony (Figure 39A) exhibits dense, alternate, pinnate branching in one plane, leading to flabellate form. Main stem somewhat flattened, giving rise to alternate main branches at irregular distances; both main stem and branches may subdivide. Each main branch gives forth regularly alternate, slightly smaller branches that do not subdivide. Branchlets flattened, 1.5 mm thick (Figure 39B). Polyps small, short, cylindrical projections, 0.5 mm tall (to summit of operculum), 0.5 mm across, 1.5 mm apart; arranged laterally in two opposite rows on flattened stems, branches and branchlets; some polyps placed such that they project toward a front side of colony, with back of colony smooth; strictly alternate to strictly opposite in different parts of colony, with upper edge of one polyp ordinarily reaching to base of next one above. Polyp aperture pointed upward, slightly outward. Walls of polyps armed with sclerites; these conspicuous, flattened scales, vary greatly in size and form in different polyps. Color of colony (? alive) generally white; dry or in alcohol, dull creamy-white; some preserved colonies light grayish-brown, with surfaces of stem and branches being more distinctly gray. Sclerites (Figure 40A-H) quite varied in form, generally more or less flattened into scales; thin, cycloid. Key characteristic sclerite a flattened basal portion bearing on its distal edge long thorn-like processes (spines) projecting above margin of polyp (Figure 40E). Many scales ornamented with convex, ctenate margin. Surfaces of scales ornamented with evenly, closely distributed granules, irregularly placed nodular warts and occasional spines. Typical arrangement of scales on polyp wall is eight lon-

*Plumarella longispina* Kinoshita, 1908a: 14, 15. Nutting 1909: 716. Kükenthal 1924: 260, 261.



**Figure 39.** *Plumarella longispina*, SBMNH 422394. **A** Colony, 14 cm tall × 15 cm wide **B** Branch tips. Scale bar: 2 cm (**A**).

gitudinal rows, each row having roughly four scales in a ring; two proximal rings composed of broad curved scales with their distal convex edges ctenate, distal-most marginal ring composed of scales (with no keel), bearing prominent thorn-like, unwarted spines extending beyond end of operculum. Marginal spines usually number from two to six, two of which (abaxial) are often distinctly longer than the others. Operculum composed of eight irregularly shaped scales, not keeled, points of which often joined into spine-like processes (Figure 40F–H). Adcauline opercular scales reduced to narrow band, the antero-lateral processes from proximal rings of sclerites being the only ones that meet to complete the ring on abcauline side.

**Etymology.** From the Latin, *longi-* = long and *spina-* = spine; long-spined, referencing the spinose marginal sclerites that extend beyond end of operculum on polyps.

**Distribution.** Found off California coast between ~55–735 m. Of specimens examined, could not confirm that this species is found off the Oregon coast (thus far, all specimens examined were collected either from Baja California [Mexico] and California [USA] or Washington [USA]; it seems odd that it would skip an entire area between CA and WA). Based on material collected by staff of Olympic Coast National Marine Sanctuary (May, 2006 and July, 2008) that was examined, seen off northwest Washington coast at depths of at least ~208–309 m. Specimens from the genus have been taken in Alaskan waters (Bering Sea, etc.) in depths from 85–2514 m; collection data for these specimens can be found by doing a search of the online data base for the NMNH, Smithsonian, Invertebrate Collection. Listings of this particular species (by Wing and Barnard 2004; Heifetz et. al. 2005; and Stone and Shotwell 2007) mentioned in Cairns, 2011, could not be confirmed.

**Biology.** Work by Lissner and Dorsey (1986) along Tanner and Cortes Banks and the Santa Rosa-Cortes Ridge area off southern California showed a depth range as follows: at depths <67 m the species is sparse, at depths ranging from 67–122 m the species is common to abundant, and at depths below 122 m, again becoming sparse. Deepwater video images taken by MBARI indicated the possibility of the genus (perhaps this species) being more common at greater depth (at least in some areas) than once thought.

In all specimens examined, only one had any other organism associated with it; on this specimen there appeared two anemones, both on branches near the tip. One, the larger of the two, is on the exposed axis. On this same specimen, on the area of branches just above the base, there appeared to be the anchor tendrils from the egg case of a shark. These tendrils are quite thin, but with the stiff curl they usually display. Egg cases were noticeable on specimens collected by OCNMS in May 2006. Colonies of this species are quite rigid, so it is likely that they provide good anchorage.

**Remarks.** A key data point in the distribution of this species was Nutting's specimen locality (1909): 'Albatross' station 4359, Point Loma light-house, 32°42'00"N, 117°14'00"W (N 85, E 9 miles), 191 fathoms (347 m). This specimen currently housed at NMNH (USNM 25429); specimen was examined.

In a comparison with a different species (from the Aleutian Islands, *Plumarella spicata* Nutting, 1912), it presented marginal scales that were similar in shape to those seen in this species, but the spinous process of the marginal scales in *P. longispina* are much less ornamented. As well, all of the operculars in the species described here display areas of surface that appear very smooth and undecorated; in *P. spicata*, surface ornamentation is more prevalent, although perhaps not continuous along entire surface. Colony form of *P. spicata* (delicate and flimsy, more or less dichotomously branched), does not match what is seen for this species.

Unless there are very subtle differences, e.g., characteristics that might specify several subspecies, this species seemed to be one of the most abundant deep-water prim-



**Figure 40.** *Plumarella longispina*, SBMNH 422394, SEM image. **A, B** Body wall scales **C** Flatter coenenchymal scales **D** Marginal scales **E** Marginal spinous sclerites **F–H** Opercular scales (worn). Compare/ contrast these images with those shown in Cairns 2011 (Figure 5, *P. spicata*).

noids occurring in the California Bight (and elsewhere). Its overall colony form is quite distinctive, and easily recognizable. While appearing to be quite delicate, closer examination and handling indicated that it is actually fairly hardy. In the near future, an examination of all specimens in the SBMNH collection will have to be undertaken, with special attention paid to any feature(s) that could be assessed as a key characteristic that might show some degree of variability. The question arose as to whether there are transitional variations over the entire range of this species, and if so, whether those variations might subdivide the specimens, such that they point in the direction of distinct subspecies (or for that matter, species). Molecular studies on any of those groupings could add further clarity. However, it may be that this is simply an enormously successful species, thus very common, with adequate and successful dispersal abilities. Cordeiro et al. (2019) shows *P. longispina* with accepted species status.

#### Genus Primnoa Lamouroux, 1812

Primnoa Lamouroux, 1812: 188; 1816: 442. Johnston 1847: 171. Gray 1870: 44. Studer 1878 [1879]: 642; 1887: 49. Wright and Studer 1889: xlviii. Versluys 1906: 84–85. Kinoshita 1908a: 42. Kükenthal 1915b: 143 [key to genus]; 1919: 357–360 [key to genus]; 1924: 265–266 [key to genus and species]. Bayer 1956: 220, fig. 157, 1; 1961: 294 [illustrated key to genus]; 1981: 937 [key to genus]. Bayer and Stefani 1988: 454 [key to genus]. Cairns and Bayer 2005: 226–228 [revision and key to species]. Cairns and Bayer 2009: 30, 41, 42. Cairns 2011: 19. Lithoprimnoa Grube, 1861: 174–175.

Lithoprimnoa: Lithoprimnoa arctica Grube, 1861, by monotypy.

**Type species.** *Gorgonia lepadifera* Linnaeus, 1767 (= *Gorgonia resedaeformis* Gunnerus, 1763), by monotypy.

**Diagnosis.** Dichotomously branched, arborescent form with polyps not arranged in whorls but closely crowded on all sides of branches and branchlets; polyps distinctly curved downward toward axis. Marginal scales eight, operculum strongly developed. Tentacles bear small, thorny rods.

**Remarks.** This genus, in the form of *P. resedaeformis* (Gunnerus, 1763), has been known since the earliest days of science (1605), and *P. resedaeformis* (Atlantic species to which the species discussed here is most closely related) is one of the most often reported deep-water octocorals. It is likely that the Atlantic *Primnoa* were some of the very first deep-water octocorals to be seen and acknowledged (Cairns and Bayer 2005).

Genus, with accepted status in WoRMS Database (Cordeiro et al. 2019), mentioned here due to evidence provided by collection records examined (see Appendix 3: List of material examined), which showed a distributional range that includes the California Bight. Based on those collection records (NMNH), this is a deep-water form that has been collected off the California coast, from a southern location of La Jolla, San Diego to a northern location of Monterey Bay. As well, NMNH, OC-NMS and MBARI, through collection and video records, also indicated sightings or collections off Oregon, Washington, British Columbia to the Gulf of Alaska, at 64-≥1000 m. This represents a substantial range but does include the entire California Bight region. Additionally, Cairns and Bayer (2005, 2009), along with Heikoop et al. (2002) and Risk et al. (2002), reported species of *Primnoa* from the subantarctic Pacific sector. Sánchez (in Gordon 2009), reported species of *Primnoa* off New Zealand coasts.

## Primnoa pacifica Kinoshita, 1907

- *Primnoa pacifica* Kinoshita, 1907: 232; 1908a: 42–45, text figs 8–9, pl 3, figs 19–20, pl 6, fig. 49; 1908b: pl 18, fig. 3; 1909: 2, 3, text fig. Wing and Bernard 2004: 24, fig. 15. Cairns and Bayer 2005: 233–239. Stone and Shotwell 2007: 72, 93, 107, in situ fig. 2.23. Whitmire and Clarke 2007: 152 (listed). Cairns and Bayer 2009: 30 (listed). Cairns 2011: 19.
- *Primnoa resedaeformis* var. *pacifica* Kukenthal, 1915b: 146; 1919: 361–362. Aurivillius 1931: 295–296.

Primnoa japonica Verrill, 1922: 15 (nomen nudum).

Primnoa resedaeformis pacifica Kukenthal, 1924: 267, fig. 152. Heifetz et al. 2005: 132. Primnoa resedaeformis forma pacifica Broch, 1935: 29–33, figs 17a-e, 18a; 1940: 20,

21. Naumov 1955: 66, pl 11, fig. 5.

**Material examined.** No specimens in SBMNH collection (see Appendix 3: List of material examined).

**Remarks.** Members of this genus display, in texture and color (when preserved in alcohol) that reminiscent of large-curd cottage cheese, arranged into branches. *P. resedaeformis* from the Atlantic is known to Canadian fishermen commonly as Seacorn or Popcorn coral. (On a first examination of preserved specimens, which were creamy yellow-white in alcohol, the appearance of popcorn immediately came to mind.) Information given here primarily focuses on *Primnoa pacifica* typical; known distribution ranges from Honshu, Japan; California, north to at least the Aleutian Islands and Gulf of Alaska (Cairns and Bayer 2005). *P. pacifica* is known by some (anecdotal, via fishermen working in the Pacific) as Red tree coral (when living, the colony's pink color is quite beautiful), as well as Seacorn or Popcorn coral.

This species has now been synonymized with *P. willeyi* Hickson, 1915, following work done by Cairns and Bayer (2005, 2009); this is shown in the WoRMS Database (Cordeiro et al. 2019), where it is considered in the Database as *Primnoa pacifica* var. *willeyi* (Hickson, 1915).

Research staff at OCNMS originally believed that *Primnoa* occurred only on hard substrates (such as large boulders, and exposed bedrock) in areas of low turbidity, at a minimum yearly temperature of 3.7 °C, at depths of at least 9–800 m (Brancato et al. 2007). However, the OCNMS expedition in May of 2006 noted its location at several sites having muddy or sandy bottoms.

Verrill noted, in his original unpublished notes for the 'Blake' Expedition manuscript (transcribed by Bayer in personal notes but not published with the plates in Bayer and Cairns 2004) that in the deep sea, because of the "absolute stillness of the water," many deep-dwelling forms exhibited extreme delicacy and fragility. He noted that numerous examples of the more delicate features occurred in the family Primnoidae. At depth, this species has been found with crinoids intertwined amongst its branches; it may further provide shelter within its branches for species of deep-water rockfish (Brancato et al. 2007). While Verrill noted (unpublished personal note transcriptions made by Bayer) that many of the deep-sea Alcyonaria are "phosphorescent" (bioluminescent), no recent information was found that could confirm/deny that characteristic for this species, or any other in the family.

The specimen mentioned in the Appendix 3: Other material, may be the southernmost report in eastern Pacific (USA) waters for a specimen of this genus and species. Occurring as far south as La Jolla, California, it may also be found further north into the California Bight, perhaps off the Channel Islands, in deep water. Of the thirteen genus records noted at CAS, the majority of specimens are from Alaska; their only record of this species is from the Sea of Japan. MBARI has records (provided by L Lundsten) for colonies known to belong in the Family Primnoidae, but most are not identified to genus or species. It would not be surprising if some of those specimens represent species within this genus, if not this species. As this manuscript was in preparation, a colony fragment (this genus and likely this species) was located (by myself and my research student, C Schaefer, in 2015) in material sampled from LACoMNH; fragment was found in fishing nets in 1981, set in SW Alaskan waters.

#### Genus Narella Gray, 1870

- Narella Gray, 1870: 49. Deichmann 1936: 168. Bayer 1951: 41–43; 1956: F222; 1961: 295 (key); 1981: 937 (key); 1995: 147, 148; 1997: 511. Cairns and Bayer 2003: 618, 619; 2004a: 7–10. Cairns and Baco 2007: 392, 393 [a more complete synonymy and discussion]. Cairns and Bayer 2008: 84–86; 2009: 2, 30, 31, 43. Cairns 2012: 14. Taylor and Rogers 2017: 4. Cairns 2018a: 20, 21; 2018b: 19. Cairns and Taylor 2019: 1–15.
- Stachyodes Wright and Studer in Studer, 1887: 49; 1901: 40. Wright and Studer 1889: xlvii, 53. Versluys 1906: 86–88. Thomson and Henderson 1906a: 35. Kinoshita 1907: 233; 1908a: 45–47. Thomson and Russell 1910: 142. Kükenthal 1912: 59; 1915b: 152; 1919: 452–456; 1924: 308, 309.

*Calypterinus* Wright and Studer in Studer, 1887: 49. Wright and Studer 1889: xlviii, 54. (?) *Calyptrophora* (pars) Verrill (in Bayer and Cairns 2004).

Type species. Primnoa regularis Duchassaing & Michelotti, 1860.

**Type locality.** North Atlantic Ocean, Caribbean Sea, St. Lucia, south of 13°36'27"N, 61°03'36"W, 514 m.

**Type specimen. Neotype** of type housed at NMNH (USNM 49385, wet); not examined.

Material examined. None housed at SBMNH.

**Diagnosis.** Colonies of moderate size (to 50 cm height), branched dichotomously or pinnately (some few trichotomously) in single plane, or unbranched. Polyps conspicuous, facing downward, in discrete whorls or pairs, non-retractile. Axis continuous; strongly calcified, especially in lower branches; generally grey to black, sometimes with metallic sheen; down center of axis (longitudinally grooved) is solid core of calcareous material. Base a discoidal holdfast, for attachment to solid substrates. Sclerites are scales, on polyps, usually numbering sixteen to eighteen on each polyp (not counting tentacular sclerites), arranged in three or four pairs of large unfused abaxial body wall scales that partially encircle polyp, but rarely meet adaxially; arranged so as to have definite pattern and number. With adaxial buccal scales commonly present, one well developed buccal in each row. Operculum consists of eight (four pairs) generally triangular scales, each with distinct longitudinal medial keel on inner surface, with corresponding trough on outer surface. Tentacles can contain few to numerous, minute, flat rodlets; coenenchymal sclerites elongate or elliptical scales, often with tall longitudinal keels.

**Distribution.** Exclusively deep water (55–4,594 m), found worldwide (Cairns and Bayer 2008; 2009). The genus is noted (Cairns and Baco 2007) as having the second deepest location record of all primnoid genera (4,594 m in the Gulf of Alaska). In addition to species from the Atlantic, there are some 23 species recorded (Cairns and Baco 2007) from regions in the Pacific (Alaska, Japan, Hawaiian Islands, Indonesia and eastern Pacific). Also, a few species are recorded from either the SW Indian Ocean, the Galápagos Islands or off Antarctica (Cairns and Baco 2007). Cairns stated (2007b) that species of *Narella* have been found along the southern California coast, from both San Marcos Seamount (2,193 m), and Rodriquez Seamount (664 m). These specimens were very fragmented and could not be definitively identified, but each one may represent an undescribed species. Some 54 named species are considered valid within this genus currently, as seen in the WoRMS Database, listed by Cordeiro et al. (2019).

**Biology.** In Studer's 1894 description of *N. ambigua*, he discussed the presence of an annelid worm from family Eunicidae Berthold, 1827 that had established itself on the coenenchyme. It apparently sought shelter under the wing-shaped extensions, in a space (a tunnel of sorts) produced by the greatly enlarged basal scales of each of the neighboring polyps. In personal note transcriptions (unpublished) made by Bayer, Verrill had outlined thoughts he had concerning the deeper water gorgonians. Regarding the annelid worm found in Studer's specimen, Verrill (unpublished personal note transcriptions made by Bayer) discussed a comparable situation and referred to Studer's 1894 examination.

**Remarks.** The genus is presented here; based on collection records examined (NMNH), there is indication of a distributional range that includes the California Bight. Based on those collection records (NMNH), this is a deep-water genus that has been collected (if only as fragments) several times off the southern California coast (Cairns 2007b).

According to Cairns and Baco (2007) and Cairns (2007b), there were some 38 recognized species (that number has increased, according to Cordeiro et al. 2019), making this a species-rich genus; in fact, it is said to be the most prolific of the primnoid genera (Cairns 2007b). Of those, there may be at least a few species that could potentially be found in or near the California Bight; *Narella ambigua* Studer, 1894 is one species that might yet be found in the Bight. CAS has seven records of this genus (none identified to species), coming from Hawaii and Alaska. MBARI has posted on-line images of those in this genus found on Davidson Seamount, photographed at depths of 2,669 and 3,079 m. Only one specimen identified to this genus has been recorded as having been collected by MBARI staff, but there are a few additional video observations. This one collected specimen was taken in the general area slightly north and west of San Miguel Island, California Channel Islands. Of interest is a specimen housed at NMNH; from California, Rodriquez Seamount, W of San Miguel Passage, 34°02'17"N, 121°02'49"W, 662 m; coll. unknown, date unknown; USNM 1027059 [wet]. The MBARI specimen and the one at NMNH appeared to be from the same collection event. It is the shape and sculpturing of the abaxial body wall scales that are the best means to identifying a species in the genus; however, finer details regarding sculpturing of scales can only be seen with SEM. Further work with unidentified species housed at CAS and NMNH should be undertaken.

#### Family Isididae Lamouroux, 1812

**Diagnosis.** Axis distinctly segmented, composed of alternating purely horny (gorgonin) nodes and nonscleritic calcareous, mostly solid, internodes (in some, hollow); internodes may be colored, quite smooth or with small projections or ridges. Base may be either a root-like calcareous structure for anchoring colony in soft substrate or a basal disc for attachment to hard object. Colonies whip-like, profusely branched, bushy or fan-like, with polyps retractile (or not). Majority of species in family found in deeper waters; all members of family commonly called Bamboo coral.

#### Genus Acanella Gray in Wright, 1869

*Acanella* Gray in Wright, 1869: 23–26. Gray 1870: 16. Wright in Studer 1887: 44. Nutting 1910b: 14. Kükenthal 1915a: 117, 119; 1919: 573; 1924: 414. Deichmann 1936: 243. Bayer 1956: F222; 1981: 941 (key). Bayer and Stefani 1987a: 51 (key); 1987b: 941 (key).

Isidella Muzik, 1978: 737.

**Type species.** *Mopsea arbusculum* Johnson, 1862.

**Type locality.** Atlantic Ocean, Canada, Nova Scotia, Sable Island, ~43°56'10"N, 59°56'10"W, 503 m.

**Type specimen. Type** (status not researched); YPM 4744 [dry]; as *Acanella normani* Verrill, 1878a, now considered synonymous with *Acanella (Mopsea) arbuscula* (Johnson, 1862).

Material examined. No specimens of this genus in collection at SBMNH.

**Diagnosis.** Colonies densely or openly bushy, moderate-sized (no more than 20 cm); usually anchored in soft substrates (ooze or fine sand) by lobate, root-like hold-fast, in deep water. Colonies generally larger and compressed (to one meter in height) when attached to hard substrates. Internodes white; nodes generally some shade of brown. Branched in whorls (three to six, at least in upper parts) from horny nodes; internodes solid, shorter (up to 2.0 cm). Polyps generally non-retractile, often prominent, columnar; coenenchyme thin. Sclerites of polyps mostly spindles; some flattened blunt rods, with fine prickles or low warts. Larger spindles and/or rods in body wall; sometimes rods conspicuously projecting between bases of tentacles. Small, slightly flattened, sometimes thorny, rods and/or double stars in pharyngeal walls.

**Etymology.** While members of this genus are commonly referred to as a type of Bamboo coral, no discussion of genus name derivation was found. Genus is listed with accepted status by Cordeiro et al. (2019).

**Distribution.** Deep water, throughout all oceans, based on an examination of collection records for specimens housed at various institutions (MBARI, NMNH, CAS).

**Biology.** Verrill (unpublished personal note transcriptions made by Bayer) stated that most of the deep water Alcyonaria are bioluminescent; "among the 'phosphorescent' gorgonians, the abundant deep-sea species, *Acanella normani* Verrill, 1878 was very 'phosphorescent.' It is also very well protected by sclerites and has a highly developed root-like branching base for anchorage in the deep-sea ooze. This has allowed it to become one of the commonest and most widely diffused of all deep-sea genera."

From examinations of recent deep-water video and digital stills (MBARI), species in this genus are usually seen on a muddy/sandy soft bottom. *Acanella dispar* Bayer, 1990 (a species that was described from material taken in Hawaii, and thus, found in the Pacific Ocean) is the only species noted (thus far) that inhabits a hard bottom and has a stout trunk.

**Remarks.** Discussion of this genus included as there are reports of unidentified species (noted by MBARI in collection/video records undertaken by them) found north of the California Bight. It is not certain what, if any, species from this genus occur within the Bight, geographically lying some distance south of MBARI's usual study locations. However, the California Bight has not been fully explored specifically for deeper water gorgonian forms; there is the possibility of species from this genus being found within it.

Andrews et al. (2005) discussed a specimen of this genus collected off San Francisco, California that was used in an age determination study of a gorgonian colony, and MBARI (posting on-line) displayed an image of a specimen, identified to this genus, sighted on Davidson Seamount, at a depth of 1,682 m (photograph taken 28 January 2006). From the MBARI data lists, roughly four specimens collected have been identified to this genus. Several other observations, without collection, have also been recorded in the area extending from southwest of Morro Bay to off the coast of Oregon (lat./long range of 35/36–45°N, 122–130°W). As for the total number of species within this genus, most are from the Atlantic; Cordeiro et al. (2019) in the WoRMS Database list 13 species. CAS has five specimens recorded, three from Japan and two from USA, Massachusetts, off Martha's Vineyard, while the NMNH has quite a few specimens (~305), from either Hawaii, Japan, the Philippines, or Indonesia; however, the vast majority are from the North Atlantic. Pacific Ocean species include the previously mentioned *A. dispar* Bayer, 1990 as well as *A. sibogae* Nutting, 1910b and *A. weberi* Nutting, 1910b. Further expeditions, with collection and study, need to be done to determine if species from this genus occur within the California Bight.

#### Genus Isidella Gray, 1857

- Isidella Gray, 1857 [1858]: 283; 1870: 14. Verrill 1883: 13. Studer [and Wright] 1887: 44. Kükenthal 1915a: 118; 1919: 564, 783; 1924: 414. Deichmann 1936: 239. Madsen 1944: 8. Bayer 1956: F222; 1981: 941 (key). Carpine and Grasshoff 1975: 107. Bayer and Stefani 1987a: 51 (key); 1987b: 941 (key). Bayer 1990: 207. Etnoyer 2008: 543. Brugler and France 2008: 126–127. Watling et al. 2011: 76, fig. 2.11. Dueñas et al. 2014: 20. Cairns 2018a: 37.
- Isis. G. von Koch, 1887: 90 [description of Isis neapolitana Koch (= Isidella elongata [Esper, 1788])].

#### Type species. Isis elongata Esper, 1788.

Type locality. Generally, eastern North Atlantic; likely, Mediterranean Sea.

Type specimen. Location of type specimen unknown.

Material examined. 2 lots (see Appendix 3: List of material examined.)

Diagnosis. Colonies sparsely branched from horny nodes, dichotomously (at ~30–35° angle; also trichotomously or lateral), generally in one plane, thus colony usually open, flat and spreading; a candelabrum shape possible. Internodes long, with axis in preserved colonies white; axis of nodes orangey-gold/brown; coenenchyme colorless. Branching not in whorls; branches moderately slender; distance from one branch to next (thus from node to node, establishing internode length) long, 3.5-4.0 cm; calcareous internodes hollow (distal tips; solid at proximal ends), longitudinally grooved, straight (or nearly so); horny nodes three-pronged, 3.0-5.0 mm tall at joints of older branches, but a simple cylinder (~1.0 mm tall) at joints of younger branches. Base of main stem a calcareous root, lobate, for anchoring in soft substrate or discoid, calcareous holdfast for anchorage on hard substrate. Polyps non-retractile and cylindrical. Sclerites of polyps mostly long rodlets that do not project between bases of tentacles; or stout, slightly prickly needles. Verrill (unpublished personal note transcriptions made by Bayer) made reference to "girdled ellipses," which are elongated scales with rounded ends having a notable median constriction or emargination on each edge; these sclerites are normal in all Isididae.

**Etymology.** All members of this genus are commonly called Bamboo coral, but no discussion of exact derivation could be found; genus has accepted status in the WoRMS Database (Cordeiro et al. 2019).

**Distribution.** Deep water, likely worldwide; at depths averaging ~1,000 m (determined from collection records of various institutions, such as MBARI and NMNH).

**Biology.** Can grow to very large size, perhaps able to attain great age (Andrews et al. 2005). Despite the calcareous nature of the internodes, as is true of many deepsea gorgonians, species in this genus can be somewhat delicate and fragile. Quieter waters of the deep sea likely allow for the larger size.

**Remarks.** Inclusion of the genus reflects locality data for the few collection and video records made by MBARI and NMNH off southern California. Of particular interest is USNM 1082174; specimen collection by D Clague (MBARI) on 'Tiburon' dive #630, 16 October 2003 (see Further remarks, below). No sclerite preparations could be done for specimens in SBMNH collection, as no coenenchyme tissue is present.

There are some six species recognized in this genus, according to Cordeiro et al. (2019); at least two are from the Atlantic. The species described by Bayer (1990), *Isidella trichotoma*, Etnoyer (2008), *Isidella tentaculum*, and Cairns (2018a), *Isidella tenuis*, are confirmed from the Pacific. As access to deeper areas becomes more common, it is certainly possible that new species will be found.

Of specimens examined at CAS, none were identified to species. One specimen came from California, Humboldt County, two were from Oregon and two were from Alaska. None (as able to determine) are recorded in web-posted MBARI images, but some two dozen-plus specimens have been sampled (with even more video observations made) by MBARI in a region encompassing an area just west of San Miguel Island in the northern California Channel Island group extending northward to an area SW of San Francisco (lat./long range = 34–37°N, 121–123°W). From the collection at NMNH, the one specimen (identified as *Isidella tentaculum* Etnoyer, 2008) is of interest; taken off California at Rodriquez Seamount, 34°01'26"N, 121°05'59"W, 846.9 m; USNM 1082174. The holotype for this species, is USNM 1076658, collected by P Etnoyer in the Gulf of Alaska, on Dickins Seamount, 7 August 2004 (see Etnoyer 2008). A paratype of this species is found in the SBMNH collection, SBMNH 369349 (Gulf of Alaska, Welker Seamount). Only further study with collection can determine how much further south members of this genus can range, and whether or not they are present in the California Bight.

## Genus Keratoisis Wright, 1869

Figures 41A, B, 42A–C, 43A–E

- *Ceratoisis* Wright, 1868: II, p. 427 (name only). Verrill 1883: 10. Wright and Studer 1889: 26. Hickson 1907: 5. Nutting 1908: 570.
- *Keratoisis* Wright, 1869: III, p. 23, 24. Gray 1870: 18. Studer 1878: 662. Wright [and Studer], 1889: xlii-xliii, 25, 26. Thomson and Henderson 1906b: 429. Nutting 1910b: 9. Kükenthal 1915a: 117, 120, 121. Molander 1929: 78. Grant 1976: 30.
  (= *Bathygorgia* Wright & Studer, 1889: 691; Cairns and Bayer 2005, listing only).

**Type species.** *Keratoisis grayi* (Wright, 1869). Some few years ago, UNESCO-IOC Register of Marine Organisms proposed the possibility of *Keratoisis ornata* Verrill, 1878 being a synonym of the type. Information provided on World Register of Marine Species (WoRMS) indicated that that synonymy is now accepted (Cordeiro et al. 2019).



**Figure 41.** Genus *Keratoisis*, SBMNH 422980. **A** Branch fragment; coenenchyme thin, translucent yellow, easily coming off underlying axis; the fragment measures ~15 cm long **B** Close up of polyps and very thin coenenchyme on branch fragment.

**Type locality.** Specific locality of type unknown; generally, bathyal, from NE to NW Atlantic Ocean; also Mediterranean Sea.

Type specimen(s). Location of the type species could not be determined.

Material examined. ~3 lots (see Appendix 3: List of material examined.)

**Diagnosis.** Colonies (Figure 41A) branched (few and distant, ~5.0 cm from one branch to next), with branches arising at nearly 90° angle, on same side, or opposite(?); near a node or from middle to end of long (4.0–5.0 cm), calcareous internode, then



**Figure 42.** Genus *Keratoisis*, SBMNH 422980, light microscopy arrays. **A**  $4\times$  magnification, showing sclerites, most notably very long needle form **B** Array of shorter needles,  $10\times$  magnification **C** Image specifically highlights very long needles characteristic of species in genus *Keratoisis*. Long needle-like sclerites range from 620–775 µm in length, while very small spindles average ~80 µm.

slightly curving; no secondary branching; some unbranched; generally uniplanar. Base can be either root-like calcareous structure for anchoring into soft substrate or a basal disc for attachment to a hard substrate. Axis as seen in the family; internodes calcareous, white, not composed of fused sclerites, hollow (often) or solid; and purely proteinaceous, horny, shorter (2.0 mm tall), reddish-brown to dark brown nodes, alternating with internodes. Overall color of colony (preserved) creamy yellowish; coenenchyme translucent yellow. Polyps (Figure 41B) cylindrical, height between 4.0-8.0 mm; not retractile. Polyps irregularly arranged, but with tendency toward biserial arrangement; in general, somewhat curved, distal part of polyp body with eight longitudinal rows of spindles and needles, some projecting beyond tentacles. Tentacles of polyp form a rounded top, like a mushroom, with individual tentacles usually visible. Distance between polyps no more than 1.0 cm but usually less. Coenenchyme very thin, transparent; straw-yellow in specimens examined. Sclerites (Figure 42A-C, 43A-E) generally long, fusiform spindles; some (Figure 43B) very long (needles) and others (Figure 43A, C-E) more numerous, of moderate length, in coenenchyme and polyp bodies; those in coenenchyme not always obvious; polyps armed with eight-plus, needle-like sclerites (largest), often (not always) projecting beyond tentacles as sharp marginal spines between bases of tentacles, coming from eight longitudinal rows of spindles and needles. Sclerite surfaces seemingly smooth, or (if present) with dense low warts, in parallel. Stellate forms seen in pharynx. Sclerites colorless to light tan, depending on species.

**Etymology.** No clear derivation for this genus name was found. All members of this genus are referred to as species of Bamboo coral. Genus *Keratoisis* is accepted;



Figure 43. Genus *Keratoisis*, SBMNH 422980, SEM image. **A, C–E** Moderate-length spindles **B** Very long, fusiform spindles (needles) characteristic of genus.

WoRMS Database (Cordeiro et al. 2019) shows the spelling variation, *Ceratoisis* Verrill, 1883, as synonymized with *Keratosis* Wright, 1869.

**Biology.** It had been noted (Verrill, 1922) that this genus included some of the largest known species of the family; specimens of *K. ornata* (now *K. grayi*), from considerable depth, on the banks off Newfoundland and Nova Scotia, can be ~ four feet high. As well, this genus is composed of species that may live to considerable

age. Andrews et al. (2005) stated that age for some of these coral colonies may exceed 200 years.

**Remarks.** Discussion of the genus included here, as several fragmented specimens in the collection of SIO and NMNH were collected off California (see Appendix 3: List of material examined and discussion in this section). The speculation is that this genus may be seen throughout much of the Pacific Ocean, at depth, based on collection location data found via on-line databases, etc. Several species that might be of interest with regards to the California Bight could include *K. paucispinosa* (Wright & Studer, 1889) ranging from Alaska to Hawaii, *K. philippinensis* (Wright & Studer, 1889), which is generally a western Pacific form, ranging from Russia to Indonesia and *K. flabellum* (Nutting, 1908), which apparently has only been recorded from Hawaii. *K. profunda* (Wright, 1885), recorded from Alaska and Japan (as noted by B Wing and G Williams in Andrews et al. 2005), was at first thought to be the only species in this genus actually listed for the northeastern Pacific Ocean. However, *K. profunda* is no longer recognized as belonging to this genus, having been accepted as *Bathygorgia profunda* Wright, 1885 (Cordeiro et al. 2019).

Of the approximately fourteen specimens identified as belonging to this genus, housed in the collection at CAS, roughly half are from California; the other half from either Alaska or Hawaii. Of these fourteen, most are not identified to species, but of those that are, three of the four species mentioned above are listed, with the two records from California that have species identification listed as K. flabellum and K. philippinensis; no opportunity to verify those identifications. The southernmost California records seen previously were from Monterey Bay and from the now extensively studied Davidson Seamount; one other specimen from this genus collected/photographed by MBARI (shown on a public website) at Davidson Seamount noted it as being collected at 1,455 m. Searching Excel data sheets from MBARI (provided by L Lundsten in 2008), three dozen or so specimens have been collected over the last few years, but there are many more video observations (many of those will be multiple observations of the same organism) that have been identified as belonging to this genus. NMNH has records of specimens belonging to this genus from both Oregon and Alaska, and of note are several other specimens: those from Fieberling Guyot, 32°26'00"N, 127°47'36"W, 490 m, 16 October 1990; USNM 94443, and those from Rodriguez Seamount, 33°57'12"N, 121°08'41"W, 1840 m, 14 October 2003; USNM 1027077, both of these areas off the California coast.

## Genus Lepidisis Verrill, 1883

Lepidisis Verrill, 1883: 18 [pars]. Studer 1894: 62. Kükenthal 1915a: 117, 119; 1919: 569 [pars]; 1924: 417 [pars]. Deichmann 1936: 240–242 [pars]. Bayer 1956: F222 [pars]. Muzik 1978: 737. Grasshoff 1986: 30. Bayer 1989: 198, 201. Bayer 1990: 204, 205.

non Lepidisis Grant, 1976: 30 (= Keratoisis).

Acanella Verrill, 1883: 13 [pars]. Wright and Studer 1889: 29 [pars].

*Bathygorgia* Wright, 1885: 691 (type species, *Bathygorgia profunda* Wright, 1885 by monotypy). Wright and Studer 1889: 32.

*Ceratoisis* Wright & Studer, 1889: 26 [pars]. Hickson 1907: 5 [pars]. Kükenthal 1915a: 120 [pars]; 1919: 585 [pars]; 1924: 423 [pars]. Deichmann 1936: 246 [pars].

*Keratoisis* Bayer, 1956: F222 [pars]. Tixier-Durivault 1966: 434 [pars]. Grant 1976: 15 [pars].

**Type species.** *Lepidisis caryophyllia* Verrill, 1883; subsequent designation Kukenthal, 1915a (*L. caryophyllia* accepted species; proposed synonymy for *Lepidisis vitrea* Verrill, 1883 has been accepted as shown in WoRMS Database, Cordeiro et al. 2019).

Type locality. Generally, northern and western Atlantic Ocean; bathyal.

Type specimen(s). Location of type unknown.

Material examined. No specimens of this genus in collection of SBMNH.

**Diagnosis.** Colonies simple, unbranched, or (rarely) sparsely branched from horny nodes; internodes hollow. In overall shape, whip-like, often exhibiting spiral growth form. Base root-like, for anchorage in deep-water bottoms of soft ooze or fine sand. Polyps non-retractile. Sclerites of polyps projecting needles and elongate scales.

**Etymology.** No explanation was found for the rationale behind the naming of this genus; they are however, commonly called Sea whips.

Distribution. A deep-water genus, likely found worldwide.

**Biology.** The apparent fragile and delicate nature of many deep-sea species of gorgonian in this suborder, including this genus, may demonstrate the relaxation of certain selection pressures in the deep sea, as proposed by Childress (1995) for deep-water forms. As well, many deep-water forms of Alcyonaria can be bioluminescent. This was certainly true for species described by Muzik (1978) seen in Hawaiian waters; further studies should reveal whether that feature is true of other members in this genus.

Remarks. To date, there are approximately a dozen species recognized and accepted within the genus (Cordeiro et al. 2019); brief discussion is included based on location data for specimens collected (or at least noted) by both MBARI and NMNH. Both institutions have specimens that were either collected or note locations that put them in close proximity of, if not actually in, the California Bight, but only a very few described species have potential for being located within the region (although new species are certainly possible as deep-water sites are further explored). There are two specimens of interest housed at NMNH: one from California Channel Islands, San Nicolas Island, ~40 miles SW of the island, 32°31'08"N, 119°42'10"W, 950 m; coll. J Ljubenkov, no date given; USNM 59821 [wet], the other from California, Fieberling Guyot, W of Channel Islands, 32°27'36"N, 127°49'30"W, 640 m; coll. un-known, via submersible 'Alvin', 14 October 1990; USNM 94447 [wet]. A posted MBARI image showed a pink specimen from Davidson Seamount, at 2,683 m. MBARI data records indicated that approximately a dozen different samples have been taken, classified as belonging to this genus, with many more video-recorded sightings, in the vicinity of 32–35–37°N, 121– 122-123°W. CAS has only three specimens, none of them from California waters; none

of these specimens have been identified to species. This is a genus that requires further study; only with collection events south of Monterey Bay, in and near central California or some distance west of the northern California Channel Islands, will we know the extent to which members of this genus are present within the California Bight.

The description given by Studer, 1894 for *Lepidisis inermis* originally did not seem to fit with general characteristics ascribed to members of the genus. He did, however, in his description, mention similarities with *Ceratoisis (Keratoisis) nuda* Wright & Studer, 1889; this was later recognized as synonymous with *Lepidisis nuda* (Wright & Studer, 1889); the species *L. inermis* has branching from the internodes. It would appear that in some instances, sparse branching does occur in some species within the genus *Lepidisis*.

## Discussion (summation of Parts I, II, and III)

Originally, SBMNH inhouse listings indicated that no more than a few dozen (at most) gorgonian coral species existed in the California Bight. This comprehensive study of the holdings in the SBMNH Invertebrate Research Collection, bolstered by a significant incorporation of specimens collected by the Allan Hancock Foundation (AHF) 'Velero' Expeditions of 1931–1941 and 1948–1985, donated to the SBMNH, revealed that central and southern California temperate water species are far more numerous and diverse than previously thought, with most not easily identifiable to species by cursory examination. This diversity is not surprising, in light of the fact that the California Bight is an area rich in species, the result of three major bodies of water all convening off the southern and central California coast, along with the presence of many different microhabitats (coastal shallow, subtidal, deep water, long coastlines with scattered bays, as well as several channel basins with islands, ridges, canyons and basin-like depressions). The array of gorgonian coral specimens housed at SBMNH, while not large in total number, well represents this broad diversity, with some species revealing wide ranges of distribution within this geographic region.

Specimens in the SBMNH collection displayed one or the other of the two basic body configurations seen in gorgonians (branched and fan-shaped or slender and whip-like), revealed over a wide range of species. Uniplanar configuration is a possibility for fan-shaped colonies, but many species with extensive branching displayed a more three-dimensional aspect to their colony shape. This is an accurate reflection of the environmental conditions under which many live. In examinations of a number of colonies (of various species) their plasticity was very evident. This aspect of gorgonian biology implied that a more flexible body form was possible than was indicated in older literature where descriptions were given of colony form for a species. A species, while described as being "always in one plane," was often rarely so. All specimens examined were identified to species whenever possible, and species likely to occur in the CA Bight have all been considered. Taxonomic listings of higher order taxa were provided where applicable and simple taxonomic keys to families were included for each of the suborder designations; keys to genera, and most species, were not. The goal of this three-part work was to provide a comprehensive review that would enable most field researchers to identify most gorgonians encountered in California waters. Consideration had be given to the fact that the SBMNH collection is composed of more than just the typical, commonly encountered species. Accompanying the discussion of a few problematic genera (genera that presented taxonomic questions where there are multiple species present in the SBMNH collection, most notably the genus *Swiftia*, Part III), a key to species is provided. In some instances, no previous description existed for the conditions and characteristics seen in a specimen. This was particularly true of several thread- or whip-like forms. One of these thread-like gorgonians was described earlier (Horvath 2011), and a second thread-like form had to be introduced in Part II as a new species (*Eugorgia ljubenkovia* sp. nov.).

Understanding the significance and variability of sclerites continues to be essential to the identification of alcyonacean gorgonian corals. While it takes time to become familiar with these structures, they are foundational to species identification. The best source for identifying both common and more unusual forms of sclerite continues to be the work by Bayer et al. (1983), but as more, and unusual, species are discovered and described, new sclerite forms will need to be added to the listing of sclerite shapes (such as the "double-dunce cap" proposed for *Chromoplexaura marki* or the "tardi-grade-like" spindle seen in *Muricea fruticosa* in Part II).

The "red whips" (most from family Plexauridae) were of particular interest. While at times difficult to link each of several different groups (red and "whip-like") to species previously named, it ultimately required that California "red whips" be divided between at least two families and three or four different genera and species. These "red whips" continue to be a focus of study. Likewise, the entire genus *Thesea*, as found in the California Bight, presented the same whip-like body form, but this genus presented several additional challenges with regards to taxonomy, largely due to the fact that the genus had been studied far more extensively in the Atlantic (Deichmann 1936), but little studied in the eastern Pacific. In this case (and in some other instances) the thread- or whip-like body form could be attributable to simple genetics but may also (and equally) be a response to specific environmental or microhabitat conditions, demonstrating again the plasticity of these organismal multi-unit colonies.

Two distinct audiences might find helpful the work related in this review; those researchers whose primary interests are the gorgonian coral species of the California Bight or the eastern Pacific Ocean (and indeed, forms of gorgonian, in general) and those field biologists, ecologists and taxonomists who encounter gorgonian corals in the context of survey and study of other marine phyla. The work presented in this three part-work does not completely resolve all outstanding taxonomic questions regarding eastern Pacific species. There are several taxon groups that still need extensive work from a taxonomic perspective. As well, new species are likely to become more common or evident in collections. It may be that many new species are already housed in those collections, but have not been looked at, or, because of insufficient material to make comparisons with, have been looked at, then placed back into a drawer as no satisfying conclusions could be drawn.

## Conclusions

While the gorgonian material at SBMNH encompasses a good working collection, reflecting to a significant degree the diversity of these animals as seen within the California Bight, it is apparent that further material is needed to enhance and complete the research collection. As access to deep-water sites, not only in the California Bight, but throughout the United States' coastal eastern Pacific region improves and becomes a more common occurrence (hopefully), the discovery of new forms of gorgonian are certainly a possibility. However, the SBMNH research collection, and this study review, has already revealed several key things: 1) a higher diversity of both genera (those previously reported and several not previously reported) and species (encompassing those previously reported, those already known but newly reported for the CA Bight, as well as entirely new species) occurs in the region than was initially thought, 2) that a greater degree of understanding is necessary to adequately know the genus Swiftia and those morphologically similar "Red whip" forms, 3) that some interesting and significant geographical/ecological trends (transitional endemics, etc.) exist within certain genera along the California coast, and 4) that morphological plasticity is clearly displayed, likely reflecting both genetic makeup and response to several dynamic environmental conditions.

The collection highlights several taxonomic groups still in need of further study ("Red whips," the genera *Thesea* and *Muricea*) and those groups/genera where further collected material would be invaluable (*Paragorgia, Sibogagorgia, Placogorgia, Acan-thogorgia, Swiftia*, Primnoidae, to name but a few). And most significantly, were it not for some of those early expedition pioneers working in the eastern Pacific, notably the Allan Hancock Foundation's 'Velero' Expeditions of 1931–1941 and 1948–1985, we would not have nearly as much material to work with as we do. The SBMNH collection will, with effort, continue to evolve, becoming an ever more valuable research tool as the work continues. As the SBMNH is the sole repository for the bulk of the AHF cnidarian collection, and one of the few museum collections in California (indeed, throughout all the western coastal United States) that has been fully curated and extensively reviewed and studied, focusing on gorgonians of the California Bight region, the SBMNH research collection is a significant resource for those studying this cnidarian group.

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# References

- Andrews AH, Cailliet GM, Kerr LA, Coale KH, Lundstrom C, DeVogelaere AP (2005) Investigations of age and growth for three deep-sea corals from the Davidson Seamount off central California. In: Freiwald A, Roberts, JM (Eds) Cold-water Corals and Ecosystems. Springer-Verlag, Berlin-Heidelberg, 1021–1038. https://doi.org/10.1007/3-540-27673-4\_51
- Aurivillius M (1931) The gorgonians from Dr. Sixten Bock's expedition to Japan and the Bonin Islands, 1914. Kungliga Svenska Vetenskapsakademiens Handlingar (ser. 3), 9(4): 1–337.
- Bayer FM (1951) A revision of the nomenclature of the Gorgoniidae (Coelenterata: Octocorallia), with an illustrated key to the genera. Journal of the Washington Academy of Science 41(3): 91–102. https://repository.si.edu/handle/10088/866
- Bayer FM (1956) Octocorallia, Part F. Coelenterata. In: Moore RC (Ed.) Treatise on Invertebrate Paleontology. Geological Society of America and University of Kansas Press, Lawrence-Kansas, F166–F231.
- Bayer FM (1958) Les Octocoralliaires plexaurides des cótes occidentals d'Amérique. Mémoires du Muséum National d'Histoire Naturelle (nouvelle série; série A, Zoologie) 16(2): 41–56. https://repository.si.edu/handle/10088/891
- Bayer FM (1961) The shallow-water Octocorallia of the West Indian Region: (A manual for marine biologists). In: Hummelinck W (Ed.) Studies on the Fauna of Curacao and other Caribbean Islands, 12(55): 1–373. Martinus Nijhoff, The Hague.
- Bayer FM (1979) Adelogorgia telones, a New Species of Gorgonacean Coral (Coelenterata: Octocorallia) from the Galápagos Islands. Proceedings of the Biological Society of Washington 91(4): 1026–1036. https://repository.si.edu/handle/10088/890
- Bayer FM (1981) Key to the genera of Octocorallia exclusive of Pennatulacea (Coelenterata: Anthozoa) with diagnoses of new taxa. Proceedings of the Biological Society of Washington 94(3): 902–947. https://repository.si.edu/handle/10088/978
- Bayer FM (1982) Some New and Old species of the Primnoid Genus *Callogorgia* Gray, with a revalidation of the Related Genus *Fanellia* Gray (Coelenterata: Anthozoa). Proceedings of the Biological Society of Washington 95(1): 116–160. https://repository.si.edu/handle/10088/972
- Bayer FM (1989) A new isidid octocoral (Coelenterata: Gorgonacea) from the Galápagos Rift. Boletim de Zoologia, University Sao Paulo, Brazil 10: 197–208. [fig. 1, 1–3 pls] https:// doi.org/10.11606/issn.2526-3358.bolzoo.1986.122351
- Bayer FM (1990) A new Isidid Octocoral (Anthozoa: Gorgonacea) from New Caledonia, with Descriptions of Other New Species from elsewhere in the Pacific Ocean. Proceedings of the Biological Society of Washington 103(1): 205–228. https://repository.si.edu/handle/10088/987
- Bayer FM (1995) A new species of the gorgonacean Genus Narella (Anthozoa: Octocorallia) from Hawaiian waters. Proceedings of the Biological Society of Washington 108(1): 147–152. [figs 1–3] https://repository.si.edu/handle/10088/995
- Bayer FM (1997) Narella nuttingi, a new gorgonacean octocoral of the Family Primnoidae (Anthozoa) from the eastern Pacific. Proceedings of the Biological Society of Washington 110(4): 511–519. [5 figs] https://repository.si.edu/handle/10088/1002

- Bayer FM (1998) A Review of the Circumaustral Genus *Fannyella* Gray, 1870 with Descriptions of five new species. Senckenbergiana Biologica 77(2): 161–204. https://repository.si.edu/handle/10088/1003
- Bayer FM, Cairns SD (Eds) (2004) The Alcyonaria of the 'Blake' Expeditions: The Unpublished Plates. Courtesy of The Ernst Mayr Library, Museum of Comparative Zoology, Harvard University. Department of Zoology, National Museum of Natural History, Washington, DC. 1–9. [1–156 pls, Index and References]
- Bayer FM, Deichmann E (1960) The Ellisellidae (Octocorallia) and their bearing on the zoogeography of the eastern Pacific. Proceedings of the Biological Society of Washington 73: 175–182. https://repository.si.edu/handle/10088/6195
- Bayer FM, Grasshoff M, Verseveldt J (Eds) (1983) Illustrated Trilingual Glossary of Morphological and Anatomical Terms Applied to Octocorallia. EJ Brill/Dr W Backhuys, Leiden, the Netherlands, 75 pp. https://repository.si.edu/handle/10088/6237
- Bayer FM, Stefani J (1987a) Isididae (Gorgonacea) de Nouvelle-Calédonie. Nouvelle cle des genres de la famille. Bulletin de Muséum National d'Histoire Naturelle, Paris (4)9(A)1: 47–106, incl. 1–30 pls https://repository.si.edu/handle/10088/1007
- Bayer FM, Stefani J (1987b) New and previously known taxa of isidid octocorals (Coelenterata: Gorgonacea), partly from Antarctic waters, with descriptions of new taxa. Proceedings of the Biological Society of Washington 100(4): 937–991. [figs 1–31] https://repository. si.edu/handle.net/10088/1006
- Bayer FM, Stefani J (1989) Primnoidae (Gorgonacea) de Nouvelle-Calédonie. Bulletin de Muséum national d'Histoire Naturelle, Paris (4) 10(3): 449–518. [1–42 pls] https://repository.si.edu/ handle/10088/2392
- Berthold AA (1827) Latreille's Natürliche Familien des Thierreichs. Aus dem Franzosischen, mit Anmerkungen und Zusätzen. Weimar, Verlage Landes-Industrie-Comptoirs, 227– 228. https://doi.org/10.5962/bhl.title.11652
- Bielschowsky E (1918) Eine Revision der Familie Gorgoniidae. Inaugural-Dissertation zur Erlangung der Doktorwürde der Hohen Philisophischen Facultät der Schlesischen Friedrich-Wilhelms-Universität zu Breslau, Buchdruckerei H Fleischmann, Breslau.
- Blainville HMD de (1828–1830) Malacozoaires ou Animaux Mollusques in Faune Francaise. Levrault, Paris, livr. 28 (1830): 241–320. https://biodiversitylibrary.org/page/24432019
- Brancato MS, Bowlby CE, Hyland J, Intelmann SS, Brenkman K (2007) Observations of Deep Coral and Sponge Assemblages in Olympic Coast National Marine Sanctuary, Washington. Cruise Report: NOAA Ship 'McArthur II' Cruise AR06-06/07. Marine Sanctuaries Conservation Series NMSP-07-04. Joint publication of U.S. Department of Commerce, National Oceanographic and Atmospheric Administration, and National Marine Sanctuary Program, Silver Spring, Maryland, 48 pp. http://www.aquaticcommons.org/2278/1/ bowlby3.pdf
- Breedy O, Guzmán HM (2015) A revision of the genus *Muricea* Lamouroux, 1821 (Anthozoa, Octocorallia) in the eastern Pacific. Part I: Eumuricea Verrill, 1869 revisited. ZooKeys 537: 1–32. https://doi.org/10.3897/zookeys.537.6025
- Breedy O, Cairns SD, Häussermann V (2015) A new alcyonacean octocoral (Cnidaria, Anthozoa, Octocorallia) from Chilean fjords. Zootaxa 3919(2): 327–334. https://doi. org/10.11646/zootaxa.3919.2.5

- Briggs JC, Bowen BW (2011) A realignment of marine biogeographic provinces with particular reference to fish distributions. Journal of Biogeography 39(1): 12–30. https://doi. org/10.1111/j.1365-2699.2011.02613x
- Broch Hj (1935) Oktokorallen des Nördlichsten Pazifischen Ozeans und ihre Beziehungen zur Atlantischen Fauna. Avhandlinger utgitt av det Norske Videnskaps-Akademi I Oslo. I. Matematisk-naturvidenskapelig Klasse, 1935 1: 1–53.
- Broch Hj (1940) Anthozoa, mainly from Pacific waters, collected by USSR expeditions 1903– 1932. Explorations des Mers de l'USSR 23: 5–22. [figs 1B]
- Brugler MR, France SC (2008) The mitochondrial genome of a deep-sea bamboo coral (Cnidaria, Anthozoa, Octocorallia, Isididae): Genome structure and putative origins of replication are not conserved among octocorals. Journal of Molecular Evolution 67(2): 125–136. https://doi.org/10.1007/s00239-008-9116-2
- Cairns SD (2007a) Studies on western Atlantic Octocorallia (Gorgonacea: Primnoidae). Part 8: New records of Primnoidae from the New England and Corner Rise Seamounts. Proceedings of the Biological Society of Washington 120(3): 243–263. https://doi. org/10.2988/0006-324X(2007)120[243:SOWAOG]2.0.CO;2
- Cairns SD (2007b) Calcaxonian Octocorals (Cnidaria; Anthozoa) from Eastern Pacific Seamounts. Proceedings of the California Academy of Sciences 58(25): 511–541. https:// repository.si.edu/handle/10088/7491
- Cairns SD (2010) Review of Octocorallia (Cnidaria: Anthozoa) from Hawai'i and Adjacent Seamounts. Part 3: Genera *Thouarella*, *Plumarella*, *Callogorgia*, *Fanellia*, and *Parastenella*. Pacific Science 64(3): 413–440. https://doi.org/10.2984/64.3.413
- Cairns SD (2011) A Revision of the Primnoidae (Octocorallia: Alcyonacea) from the Aleutian Islands and Bering Sea. Smithsonian Contributions to Zoology Number 634: v, 1–55. https://doi.org/10.5479/si.00810282.634
- Cairns SD (2012) New Zealand Primnoidae (Anthozoa: Alcyonacea) Part I. Genera *Narella, Narelloides, Metanarella, Calyptrophora,* and *Helicoprimnoa.* NIWA Biodiversity Memoirs 126: 1–71.
- Cairns SD (2016) The Marine Fauna of New Zealand: Primnoid octocorals (Anthozoa, Alcyonacea)-Part 2. *Primnoella, Callozostron, Metafannyella, Callogorgia, Fanellia* and other genera. NIWA Biodiversity Memoirs 129: 1–131.
- Cairns SD (2018a) Deep-water octocorals (Cnidaria, Anthozoa) from the Galápagos and Cocos Islands. Part 1. Suborder Calcaxonia. ZooKeys 729: 1–46. https://doi.org/10.3897/ zookeys.729.21779
- Cairns SD (2018b) Primnoidae (Cnidaria: Octocorallia: Calcaxonia) of the 'Okeanos Explorer' expeditions (CAPSTONE) to the central Pacific. Zootaxa 4532(1): 1–43. https://doi. org/10.11646/zootaxa.4532.1.1
- Cairns SD, Baco A (2007) Review and five new Alaskan species of the deep-water octocoral *Narella* (Octocorallia: Primnoidae). Systematics and Biodiversity 5(4): 391–407. https://doi.org/10.1017/S1477200007002472
- Cairns SD, Bayer FM (2002) Studies on Western Atlantic Octocorallia (Coelenterata: Anthozoa). Part 2: The genus *Callogorgia* Gray, 1858. Proceedings of the Biological Society of Washington 115(4): 840–867. https://repository.si.edu/handle/10088/7542

- Cairns SD, Bayer FM (2003) Studies on western Atlantic Octocorallia (Coelenterata: Anthozoa). Part 3: The genus *Narella* Gray, 1870. Proceedings of the Biological Society of Washington 116(3): 617–648. https://repository.si.edu/handle/10088/1243
- Cairns SD, Bayer FM (2004a) Narella Gray, 1870 (Coelenterata, Octocorallia): proposed conservation of usage by designation of a neotype for its type species Primnoa regularis Duchassaing & Michelotti, 1860. Bulletin of Zoological Nomenclature 61(1): 7–10. https:// repository.si.edu/handle/10088/6203
- Cairns SD, Bayer FM (2004b) Studies on western Atlantic Octocorallia (Coelenterata: Anthozoa). Part 5: The genera *Plumarella* Gray, 1870; *Acanthoprimnoa*, n. gen.; and *Candidella* Bayer, 1954. Proceedings of the Biological Society of Washington 117(4): 447–487. https://repository.si.edu/handle/10088/7495
- Cairns SD, Bayer FM (2005) A review of the Genus *Primnoa* (Octocorallia: Gorgonacea: Primnoidae), with the description of two new species. Bulletin of Marine Science 77(2): 225–256. https://repository.si.edu/handle/10088/124
- Cairns SD, Bayer FM (2008) A Review of the Octocorallia (Cnidaria: Anthozoa) from Hawai'i and Adjacent Seamounts: The Genus *Narella* Gray, 1870. Pacific Science 62(1): 83–115. https://doi.org/10.2984/1534-6188(2008)62[83:AROTOC]2.0.CO;2
- Cairns SD, Bayer FM (2009) A generic revision and phylogenetic analysis of the Primnoidae (Cnidaria: Octocorallia). Smithsonian Contributions to Zoology 629: 1–79. https://doi.org/10.5479/si.00810282.629
- Cairns SD, Taylor ML (2019) An illustrated key to the species of the genus *Narella* (Cnidaria, Octocorallia, Primnoidae). ZooKeys 822: 1–15. https://doi.org/10.3897/zookeys.822.29922
- Cairns SD, Wirshing HH (2018) A phylogenetic analysis of the Primnoidae (Anthozoa: Octocorallia: Calcaxonia) with analyses of character evolution and a key to the genera and subgenera. BMC Evolutionary Biology 18(66): 1–20. https://doi.org/10.1186/s12862-018-1182-5
- Carpine C, Grasshoff M (1975) Les gorgonaires de la Méditerranée occidentale. Bulletin de l'Institute Océanographique Monaco 71(1430): 1–140. [figs 1–62, 1 pl.]
- Childress JJ (1995) Are there physiological and biochemical adaptations of metabolism in deep-sea animals? Trends in Evolution and Ecology 10: 30–36. https://doi.org/10.1016/S0169-5347(00)88957-0
- Chun C (1903) Aus den Tiefen des Weltmeeres. Schilderungen von der Deutschen Tiefsee-Expedition (2<sup>nd</sup> Edition). Verlag von Gustav Fischer, Jena, i-x + 592 pp. [46 pls, 3 charts, 482 text figs]
- Cordeiro R, van Ofwegen L, Williams G (2018a) World List of Octocorallia. *Clavularia* Blaineville, 1830. Accessed through : World Register of Marine species. http://www.marinespecies.org/aphia.php?p=taxdetails&id=125286
- Cordeiro R, van Ofwegen L, Williams G (2018b) World List of Octocorallia. *Swiftia* Duchassaing and Michelotti, 1864. World Register of Marine species. http://www.marinespecies. org/aphia.php?p=taxdetails&id=125314
- Cordeiro R, van Ofwegen L, Williams G (2018c) World List of Octocorallia. *Psammogorgia* Verrill, 1868. World Register of Marine species. http://www.marinespecies.org/aphia. php?p=taxdetails&id=267768

- Cordeiro R, van Ofwegen L, Williams G (2018d) World List of Octocorallia. *Psammogorgia simplex* Nutting, 1909. World Register of Marine species. http://www.marinespecies.org/ aphia.php?p=taxdetails&id=290863
- Cordeiro R, van Ofwegen L, Williams G (2018e) World List of Octocorallia. *Psammogorgia torreyi* Nutting, 1909. World Register of Marine species. http://www.marinespecies.org/ aphia.php?p=taxdetails&id=290865
- Cordeiro R, van Ofwegen L, Williams G (2018f) World List of Octocorallia. *Thesea* Duchassaing and Michelotti, 1860. World Register of Marine species. http://www.marinespecies. org/aphia.php?p=taxdetails&id=125315
- Cordeiro R, van Ofwegen L, Williams G (2019a) World List of Octocorallia. *Swiftia kofoidi* (Nutting, 1909). World Register of Marine species. http://www.marinespecies.org/aphia. php?p=taxdetails&id=286417
- Cordeiro R, van Ofwegen L, Williams G (2019b) World List of Octocorallia. *Swiftia pacifica* (Nutting, 1912). World Register of Marine species. http://www.marinespecies.org/aphia. php?p=taxdetails&id=1036537
- Cordeiro R, van Ofwegen L, Williams G (2019c) World List of Octocorallia. *Swiftia simplex* (Nutting, 1909). World Register of Marine species. http://www.marinespecies.org/aphia. php?p=taxdetails&id=1036547
- Cordeiro R, van Ofwegen L, Williams G (2019d) World List of Octocorallia. *Swiftia spauldingi* (Nutting, 1909). World Register of Marine species. http://www.marinespecies.org/aphia. php?p=taxdetails&id=286420
- Cordeiro R, van Ofwegen L, Williams G (2019e) World List of Octocorallia. *Swiftia torreyi* (Nutting, 1909). World Register of Marine species. http://www.marinespecies.org/aphia. php?p=taxdetails&id=1036552
- Cordeiro R, van Ofwegen L, Williams G (2019f) World List of Octocorallia. *Elasmogorgia* Wright and Studer, 1889. World Register of Marine species. http://www.marinespecies. org/aphia.php?p=taxdetails&id=267406
- Cordeiro R, van Ofwegen L, Williams G (2019g) World List of Octocorallia. Primnoidae Milne Edwards, 1857. World Register of Marine species. http://www.marinespecies.org/ aphia.php?p=taxdetails&id=125278
- Cordeiro R, van Ofwegen L, Williams G (2019h) World List of Octocorallia. Callogorgia Gray, 1858. World Register of Marine species. http://www.marinespecies.org/aphia. php?p=taxdetails&id=125317
- Cordeiro R, van Ofwegen L, Williams G (2019i) World List of Octocorallia. *Callogorgia ki-noshitae* Kükenthal, 1913. World Register of Marine species. http://www.marinespecies. org/aphia.php?p=taxdetails&id=286493
- Cordeiro R, van Ofwegen L, Williams G (2019j) World List of Octocorallia. *Callogorgia ki-noshitai* (Kükenthal, 1913). World Register of Marine species. http://www.marinespecies. org/aphia.php?p=taxdetails&id=1055877
- Cordeiro R, van Ofwegen L, Williams G (2019k) World List of Octocorallia. *Parastenella* Versluys, 1906. World Register of Marine species. http://www.marinespecies.org/aphia. php?p=taxdetails&id=267700

- Cordeiro R, van Ofwegen L, Williams G (2019l) World List of Octocorallia. Parastenella pacifica Cairns, 2007. World Register of Marine species. http://www.marinespecies.org/aphia. php?p=taxdetails&id=409581
- Cordeiro R, van Ofwegen L, Williams G (2019m) World List of Octocorallia. *Parastenella ramosa* (Studer, 1894). World Register of Marine species. http://www.marinespecies.org/aphia.php?p=taxdetails&id=290684
- Cordeiro R, van Ofwegen L, Williams G (2019n) World List of Octocorallia. *Plumarella* Gray, 1870. World Register of Marine species. http://www.marinespecies.org/aphia. php?p=taxdetails&id=177839
- Cordeiro R, van Ofwegen L, Williams G (2019o) World List of Octocorallia. *Plumarella long-ispina* Kinoshita, 1908. World Register of Marine species. http://www.marinespecies.org/aphia.php?p=taxdetails&id=287671
- Cordeiro R, van Ofwegen L, Williams G (2019p) World List of Octocorallia. *Primnoa* Lamouroux, 1812. World Register of Marine species. http://www.marinespecies.org/aphia. php?p=taxdetails&id=125321
- Cordeiro R, van Ofwegen L, Williams G (2019q) World List of Octocorallia. *Primnoa pacifica* Kinoshita, 1907. World Register of Marine species. http://www.marinespecies.org/aphia. php?p=taxdetails&id=286539
- Cordeiro R, van Ofwegen L, Williams G (2019r) World List of Octocorallia. *Narella* Gray, 1870. World Register of Marine species. http://www.marinespecies.org/aphia. php?p=taxdetails&id=125319
- Cordeiro R, van Ofwegen L, Williams G (2019s) World List of Octocorallia. Isididae Lamouroux, 1812. World Register of Marine species. http://www.marinespecies.org/aphia. php?p=taxdetails&id=125276
- Cordeiro R, van Ofwegen L, Williams G (2019t) World List of Octocorallia. *Acanella* Gray, 1870. World Register of Marine species. http://www.marinespecies.org/aphia. php?p=taxdetails&id=125303
- Cordeiro R, van Ofwegen L, Williams G (2019u) World List of Octocorallia. *Isidella* Gray, 1857. World Register of Marine species. http://www.marinespecies.org/aphia. php?p=taxdetails&id=125305
- Cordeiro R, van Ofwegen L, Williams G (2019v) World List of Octocorallia. *Keratoisis* Wright, 1869. World Register of Marine species. http://www.marinespecies.org/aphia. php?p=taxdetails&id=125306
- Cordeiro R, van Ofwegen L, Williams G (2019w) World List of Octocorallia. *Lepidisis* Verrill, 1883. World Register of Marine species. http://www.marinespecies.org/aphia. php?p=taxdetails&id=125307
- Dana JD (1846) Zoophytes. United States Exploring Expedition during the years 1838, 1839, 1840, 1841, 1842, under the command of Charles Wilkes, USN Vol. 7. Lea and Blanchard, Philadelphia, 1–6 + 1–740. [45 text figs (Atlas, Zoophytes). 61 pls, 1849] [See nos. 21, 22, 25, and 26 in Haskell DC: The United States Exploring Expedition, 1838–1842 and its publications 1844–1874. Greenwood Press, New York, 1968.]. sil.si.edu/digitalcollections/usexex/follow-01.htm
- Deichmann E (1936) XLIX. The Alcyonaria of the western part of the Atlantic Ocean. Memoirs of the Museum of Comparative Zoology at Harvard College, Vol. LIII. Cambridge, Massachusetts, 317 pp. [+ 37 pls] https://doi.org/10.5962/bhl.title.49348
- Duchassaing P, Michelotti G (1860) Mémoire sur les Coralliaires des Antilles. Memorie della Reale Accademia delle Scienze di Torino (ser. 2) 19: 279–365. [Reprint paged 1–88] https://doi.org/10.5962/bhl.title.11388
- Duchassaing P, Michelotti G (1864) Supplement au mémoire sur les Coralliaires des Antilles. Memorie della Reale Accademia delle Scienze di Torino (ser. 2) 23: 97–206. [Reprint paged 1–112] https://doi.org/10.5962/bhl.title.105196
- Dueñas LF, Alderslade P, Sánchez JA (2014) Molecular systematics of the deep-sea bamboo corals (Octocorallia: Isididae: Keratoisidinae) from New Zealand with descriptions of two new species of *Keratoisis*. Molecular Phylogenetics and Evolution 74: 15–28. https://doi. org/10.1016/j.ympev.2014.01.031
- Ehrenberg CG (1834) Beitrage zur physiologischen Kenntniss der Corallenthiere im allgemeinen, und besonders des rothen Meeres, nebst einem Versuche zur physiologischen Systematik derselben. Abhandlungen der Königlichen preussischen Akademie der Wissenschaften zu Berlin. Aus dem Jahre 1832. Erster Theil, 1–380.
- Ellis J, Solander D (1786) The natural history of many curious and uncommon zoophytes, collected from various parts of the globe by the late John Ellis, systematically arranged and described by the late Daniel Solander. London, printed for Benjamin White and Son, at Horace's Head, Fleet-Street and Peter Elmsly, in the Strand, 1–7 + 1–208. [1–63 pls] https://doi.org/10.5962/bhl.title.2145
- Esper EJC (1788–1830) Die Pflanzenthiere in Abbildungen nach der Natur mit Farben erleuchtet nest Beschreibungen. Theil 1, 1–96, 1788; Theil 2, 97–180, 1792. Fortset-zungen der Pflanzenthiere. Theil 1, 1–64, 1794; 65–116, 1795; 117–168, 1796; 169–230, 1797. Raspischen Buchhandlung, Nurnberg, 1–7 + 1–320; 1–304; 1–285 + 1–230; 1–48, 428 pls
- Etnoyer PJ (2008) A new species of *Isidella* bamboo coral (Octocorallia: Alcyonacea: Isididae) from Northeast Pacific seamounts. Proceedings of the Biological Society of Washington 121(4): 541–553. https://doi.org/10.2988/08-16.1
- Everett MV, Park LK, Berntson EA, Elz AE, Whitmire CE, Keller AA, Clarke ME (2016) Large-Scale Genotyping-by-Sequencing Indicates High Levels of Gene Flow in the Deep-Sea Octocoral *Swiftia simplex* (Nutting, 1909) on the West Coast of the United States. PLOS One 11(10): eo165279. https://doi.org/10.1371/journal.pone.0165279
- Fabricius KE, Alderslade P (2001) Soft Corals and Sea Fans: A Comprehensive Guide to the tropical shallow-water genera of the Central-West Pacific, the Indian Ocean and the Red Sea. Australian Institute of Marine Science, Queensland, Australia, 264 pp.
- Gordon DP (Ed) (2009) New Zealand Inventory of Biodiversity. Volume I. Kingdom Animalia. Canterbury University Press: Christchurch, New Zealand, 568 pp.
- Grant R (1976) The marine fauna of New Zealand: Isididae (Octocorallia: Gorgonacea) from New Zealand and the Antarctic. New Zealand Oceanographic Institute, Memoir 66: 1–56. [figs 1–51] http://trove.nla.gov.au/version/13604396

- Grasshoff M (1977) Die Gorgonarien des ostlichen Nordatlantik und des Mittelmeeres. III. Die Familie Paramuriceidae (Cnidaria, Anthozoa). 'Meteor' Forschungs-Ergebnisse D27: 5–76. [figs 1–73]
- Grasshoff M (1986) Die Gorgonaria der Expeditionen von 'Travailleur' 1880–1882 und 'Talisman' 1883 (Cnidaria: Anthozoa). Bulletin de Muséum National d'Histoire Naturelle, Paris (4)8(A)1: 9–38. [figs 1–9]
- Grasshoff M (1999) The shallow water gorgonians of New Caledonia and adjacent islands (Coelenterata: Octocorallia). Senckenbergiana Biolologica 78(1/2): 1–245.
- Gray JE (1858) Synopsis of the families and genera of axiferous zoophytes or barked corals. Proceedings of the Zoological Society of London 1857: 278–294. [pp 278–288 published 28 Jan 1858; pp 289–294, 23 Feb 1859] https://doi.org/10.1111/j.1096-3642.1857. tb01242.x
- Gray JE (1866) Notes on the Skulls of Dolphins, or Bottlenose Whales in the British Museum. Proceedings of the Zoological Society of London 1866: 211–216. https://biodiversitylibrary.org/page/28627683
- Gray JE (1868) Descriptions of some new genera and species of Alcyonid corals in the British Museum. Annals and Magazine of Natural History (4)2: 441–445. https://doi. org/10.1080/00222936808695849
- Gray JE (1870) Catalogue of the lithophytes or stony corals in the collection of the British Museum. British Museum, London, [1–6] + 1–51. https://doi.org/10.5962/bhl.title.32670
- Grieg JA (1887) Bidrag til de norske Alcyonarier. Bergens Museum Aarsberetning for 1886: 1–26. [9 pls]
- Grube E (1861) Beschreibung Einer Neuen Coralle (*Lithoprimnoa arctica*) und Bemerkungen über ihre Systematische Stellung. Breslau Schlesischen Gesellschaft für vaterländische Culture 1(2): 167–176. [3 pl.]
- Gunnerus JE (1763) Om en Soevext, allevegne ligesom besat med Fro/ehuuse, *Gorgonia resedaeformis*. Trondhjemske Selskabs Skrifter 2: 321–329. [9 pl.]
- Harden DG (1979) Intuitive and Numerical Classification of East Pacific Gorgonacea (Octocorallia). PhD Thesis, Illinois State University, Illinois, 214 pp.
- Heifetz J (2002) Coral in Alaska: Distribution, abundance, and species associations. Hydrobiologia 471: 19–28. https://doi.org/10.1023/A:1016528631593
- Heifetz J, Wing BL, Stone RP, Malacha PW, Courtney DL (2005) Corals of the Aleutian Islands. Fisheries Oceanography 14(Suppl. 1): 131–138. https://doi.org/10.1111/j.1365-2419.2005.00371.x
- Heikoop JM, Hickmott DD, Risk MJ, Shearer CK, Atudorei V (2002) Potential Climate Signals from the Deep-Sea Gorgonian Coral *Primnoa resedaeformis*. Hydrobiologia 471: 117–124. https://doi.org/10.1023/A:1016505421115
- Hickson SJ (1905) The Alcyonaria of the Maldives. Part III. The families Muriceidae, Gorgonellidae, Melitodidae, and the genera Pennatula, Eunephthya. In: Gardiner, JS (Ed.) The Fauna and Geography of the Maldive and Laccadive Archipelagoes, 2(4): 807–826. [pl 67.]
- Hickson SJ (1907) Coelenterata I: Alcyonaria. National Antarctic (Discovery) Expedition. British Museum. Natural History 3: 1–15. [1 pl.]

- Hickson SJ (1915) Some Alcyonaria and a *Stylaster* from the west coast of North America. Proceedings of the Zoological Society London 37: 541–557. https://doi.org/10.1111/j.1469-7998.1915.00541.x
- Johnson JY (1862) Descriptions of two corals from Madeira, belonging to the genera *Primnoa* and *Mopsea*. Proceedings of the Zoological Society of London 1862: 45–246. [pl. 31. (Also in Annals and Magazine of Natural History (3)11: 299–300, April 1863] https://biodiversitylibrary.org/page/31577289
- Johnson ME, Snook HJ (1927) Seashore Animals of the Pacific Coast. MacMillan and Company, New York, 659 pp.
- Johnson ME, Snook HJ (1955) Seashore Animals of the Pacific Coast. MacMillan and Company, New York, 1–14 + 1–659. [1–11 pls]
- Johnston G (1847) A history of the British zoophytes. Second edition. John Van Voorst, London, Vol. 1, 1–16 + 1–488. [Vol. 2, 1–74 pls]
- Jungersen HFE (1917) The Alcyonaria of East Greenland. Meddelelser om Gronland, udgivne af Commissionen for Ledelsen af de geologiske og geographiske undersogelser i Gronland, Kjobenhavn 23: 1186.
- Kinoshita K (1907) Vorläufige Mitteilung uber einige neue japanische Primnoidkorallen. Annotationes Zoologicae Japonenses 6(3): 229–237.
- Kinoshita K (1908a) Primnoidae von Japan. Journal of the College of Science, Imperial University, Tokyo 23(12): 1–74. [pls 1–6]
- Kinoshita K (1908b) On the Primnoidae, a family of the Gorgonacea. I. Dobutsugaku zasshi 20(240): 409–419; (241): 453–459; (242): 517–528; (243): 1–10.
- Kinoshita K (1909) On some muriceid corals belonging to the genera *Filigella* and *Acis*. Journal of the College of Science, Imperial University, Tokyo 27(7): 1–16 [1–2 pls]
- Koch G von (1878) Das Skelet der Alcyonarien. Morphologisches Jahrbucher 4: 447–449.
- Koch G von (1887) Die Gorgoniden des Golfes von Neapel und der angrenzenden Meeresabschnitte. Fauna und Flora des Golfes von Neapel 15: 1–10 + 1–99. [1–10 pls]
- Kölliker RA von (1865) Icones histiologicae oder Atlas der vergleichenden Gewebelehre. Zweite Abtheilung. Der feinere Bau der hoheren Thiere. Erstes Heft. Die Bindesubstanz der Coelenteraten. Verlag von Wilhelm Engelmann, Leipzig, [1–6] + 87–181. [10–19 pls, 13 text figs] https://doi.org/10.5962/bhl.title.11946
- Kükenthal W (1912) Die Alcyonaria der deutschen Sudpolar-Expedition 1901–1903. In: Drygalski E von (Ed.) Deutsche Sudpolar-Expedition 1901–1903, Band 13. Zoologie (3): 289–349. [20–23 pls]
- Kükenthal W (1913) Über die Alcyonarienfauna Californiens und ihre tiergeo-graphischen Beziehungen. Zoologische Jahrbucher Abteilung fur Systematik 35(2): 219–270. https:// doi.org/10.5962/bhl.part.16718
- Kükenthal W (1915a) System und Stammesgeschichte der Isididae. Zoologischer Anzeiger 46: 116–126. https://biodiversitylibrary.org/page/29985624
- Kükenthal W (1915b) System und Stammesgeschichte der Primnoidae. Zoologischer Anzeiger, 46(5): 142–158. https://biodiversitylibrary.org/page/29985650
- Kükenthal W (1919) Gorgonaria. Wissenschaftliche Ergebnisse der deutsche Tiefsee-Expeditionen 'Valdivia' 1898–99, 13(2): 1–946. [30–89 pls]

- Kükenthal W (1924) Gorgonaria. Das Tierreich, Vol. 47. Walter de Gruyter & Company, Berlin, 1–28 + 478 pp.
- Kükenthal W, Gorzawsky H (1908) Japanische Gorgoniden. I. Teil: Die Familien der Primnoiden, Muriceiden und Acanthogorgiiden. In: Beitrage zur Naturgeschichte Ostasiens. Abhandlungen der mathematische-physics. Klasse der K. Bayer. Akademie der Wissenschaften. Supplement-Band 1(3): 1–71. [+ 1–4 pls]
- Lamarck JB de (1815) Sur les polypiers corticifères. Mémoires du Muséum Histoire Naturelle. Paris Vol. 1: 401–416, 467–476. Vol. 2: 76–84, 157–164, 227–240.
- Lamouroux JVF (1812) Extrait d'un mémoire sur la classification des polypiers coralligènes non entièrement pierreux. Nouveau Bulletin Sciences par la Société Philomatique, Paris 3(63): 181–188. https://archive.org/details/cbarchive\_42584\_extraitdumemoiresurlaclassifi9999/page/n2
- Lamouroux JVF (1816) Histoire des polypiers coralligènes flexibles, vulgairement nommés Zoophytes. A Caen, De l'Imprimerie du F. Poisson, 1–84 + 1–560. [1–19 pls] https://doi. org/10.5962/bhl.title.11172
- Linnaeus C (1767) Systema naturae. Editio duodecima, reformata. Holmiae. 1(2): 533–1327. [+ 18 lvs.] https://biodiversitylibrary.org/page/461997
- Lissner AL, Dorsey JH (1986) Deep-water biological assemblages of a hard-bottom bank-ridge complex of the Southern California Continental Borderland. Bulletin of the Southern California Academy of Sciences 85(2): 87–101.
- Madsen FJ (1944) Octocorallia. Danish Ingolf-Expedition 5(13): 65 pp. [53 figs, 1 pl.]
- Madsen FJ (1970) Remarks on Swiftia rosea (Grieg) and related species. Steenstrupia 1(1): 1-10.
- Matsumoto AK, Ofwegen LP van (2016) Species of *Elasmogorgia* and *Euplexaura* (Cnidaria, Octocorallia) from Japan with a discussion about the genus *Filigella*. ZooKeys 589: 1–21. https://doi.org/10.3897/zookeys.589.8361
- Milne Edwards H, Haime J (1857) Histoire naturelle des coralliaires ou polypes proprement dits, Vol. I. Libraire Encyclopédique de Roret, Paris, 1–34 + 1–326. [8 pls, numbered A1–6, B1–2] https://doi.org/10.5962/bhl.title.11574
- Molander AR, Bock S, Odhner T, Nordenskjöid O (1929) Die Octactiniarien. Further Zoological Results of the Swedish Antarctic Expedition, 1901–1903. 2(2): 1–4 + 1–86.
- Muzik KM (1978) A bioluminescent gorgonian, Lepidisis olapa, new species (Coelenterata: Octocorallia) from Hawaii. Bulletin of Marine Science 28(4): 735–741. [figs 1–4] https:// www.researchgate.net/publication/233508596\_A\_Bioluminescent\_Gorgonian\_Lepidisis\_Olapa\_New\_Species\_Coelenterata\_Octocorallia\_from\_Hawaii
- Muzik KM (1979) A systematic revision of the Hawaiian Paramuriciidae and Plexauridae (Coelenterata: Octocorallia). PhD Thesis, Coral Gables, University of Miami, Florida.
- Naumov DV (1955) Species of coelenterates. In: Pavlovskii EN (Ed.) Atlas of the invertebrates of fareastern seas of USSR Academy of Sciences (Akademiya Nauk), Moscow (in Russian) 51–68. [7–11 pls]
- Nutting CC (1908) Descriptions of the Alcyonaria collected by the US Bureau of Fisheries steamer 'Albatross' in the vicinity of the Hawaiian Islands in 1902. Proceedings of the United States National Museum 34: 543–601. [41–51 pls] https://doi.org/10.5962/bhl. title.49592

- Nutting CC (1909) Alcyonaria of the California coast. Proceedings of the United States National Museum 35: 681–727. https://doi.org/10.5479/si.00963801.35-1658.681
- Nutting CC (1910a) The Gorgonacea of the Siboga Expedition. III. The Muriceidae Siboga Expedition Monograph 13b: 108 pp. [+ 22 pls] https://doi.org/10.5962/bhl.title.11324
- Nutting CC (1910b) The Gorgonacea of the Siboga Expedition. V. The Isidae. Siboga Expedition Monograph 13b2: 1–24. [1–6 pls] https://doi.org/10.5962/bhl.title.11324
- Nutting C.C (1910c) The Gorgonacea of the Siboga Expedition. VII. The Gorgoniidae. Siboga Expedition Monograph 13b4: 1–10. [1–3 pls] https://doi.org/10.5962/bhl.title.11324
- Nutting CC (1912) Descriptions of the Alcyonaria collected by the US Fisheries Steamer 'Albatross' primarily in Japanese waters during 1906. Proceedings of the United States National Museum 43(1923): 1–104. [21 pls] https://doi.org/10.5479/si.00963801.43-1923.1
- Ofwegen LP van (2014) *Thesea rigida* (Thomson, 1927). World Register of Marine Species. http://www.marinespecies.org/aphia.php?p=taxdetails&id=286444
- Pallas PS (1766) Elenchus zoophytorum systems generum adumbrations generaliores et specierum cognitarum succinactas descriptions cum selectis auctorum synonymis, Hagae Comitum, 451 pp. https://doi.org/10.5962/bhl.title.6595
- Quattrini A, Etnoyer PJ, Doughty C, English L, Falco R, Remon N, Rittinghouse M, Cordes EE (2014) A phylogenetic approach to octocoral community structure in the deep Gulf of Mexico. Deep Sea Research Part II: Topical Studies in Oceanography 99: 92–102. https:// doi.org/10.1016/j.dsr2.2013.05.027
- Read G, Fauchald K (2019) World Polychaeta database. Eunicidae Berthold, 1827. World Register of Marine species. http://www.marinespecies.org/aphia.php?p=taxdetails&id=966
- Riess M (1929) Die Gorgonarien Westindiens. Kapitel 8. Die Familie Muriceidae. Zoologische Jahrbucher Supplement 16(2): 377–420. [8 pl.]
- Risk MJ, Heikoop JM, Snow MG, Beukens R (2002) Lifespans and Growth Patterns of Two Deep-Sea Corals: *Primnoa resedaeformis* and *Desmophyllum cristagalli*. Hydrobiologia 471: 125–131. https://www.researchgate.net/publication/225386976\_Lifespans\_and\_ growth\_patterns\_of\_two\_deep-sea\_corals\_Primnoa\_resedaeformis\_and\_Desmophyllum\_cristagalli
- Stiasny G (1937) Catalogue raisonné des alcyonides, gorgonides, zoanthids, et pennatulides des la Collection H. Michelin. Bulletin du Muséum national d'Histoire naturelle Paris (2)9: 391–397.
- Stone RP, Cairns SD (2017) Deep-Sea Coral Taxa in the Alaska Region: Depth and Geographical Distribution. NOAA Deep Sea Coral Data Portal. https://repository.si.edu/handle/ 10088/34994
- Stone RP, Shotwell SK (2007) State of Deep Coral Ecosystems in the Alaska Region: Gulf of Alaska, Bering Sea and the Aleutian Islands. In: Lumsden SE, Hourigan TF, Bruckner AW, Dorr G (Eds) The State of Deep Coral Ecosystems of the United States: 2007. NOAA Technical Memorandum, CRCP-3, Silver Spring-Maryland, 65–108.
- Studer T (1879) Ubersicht der Anthozoa Alcyonaria, welche wahrend der Reise S.M.S. 'Gazelle' um die Erde gesammelt wurden. Monatsbericht der Könilich Preussischen Akademie der Wissenschaften zu Berlin, Sept.-Okt, 1878: 632–688. [1–5 pls]
- Studer T (1887) Versuch eines Systemes der Alcyonaria. Archiv für Naturgeschichte 53(1): 1–74. [1 pl.]

- Studer T (1894) Reports on the dredging operations off the west coast of Central America to the Galápagos, to the west coast of Mexico, and in the Gulf of California, in charge of Alexander Agassiz, carried on by the US Fish Commission steamer 'Albatross', during 1891, Lieutenant ZL Tanner, USN, commanding. Bulletin of the Museum of Comparative Zoology 25(5): 53–69.
- Studer T (1901) Alcyonaires provenant des campagnes de l'Hirondelle (1886–1888). Résultats des Campagnes Scientifiques, Monaco 20: 1–64. [1–11 pls] https://doi.org/10.5962/bhl. title.58246
- Taylor ML, Rogers AD (2017) Primnoidae (Cnidaria: Octocorallia) of the SW Indian Ocean: new species, genus revisions and systematics. Zoological Journal of the Linnean Society, 181: 70–97. https://doi.org/10.1093/zoolinnean/zlx003
- Taylor ML, Cairns SD, Agnew D, Rogers AD (2013) A revision of the genus *Thouarella* Gray, 1870 (Octocorallia: Primnoidae), including an illustrated dichotomous key, a new species description, and comments on *Plumarella* Gray, 1870 and *Dasystenella* Versluys, 1906. Zootaxa 3602(1): 1–105. https://doi.org/10.11646/zootaxa.3602.1.1
- Thoma JN (2013) Molecular and Morphological Diversity of Sea Fans with Emphasis on Deepsea Octocorals of the Order Alcyonacea Lamouroux, 1812. PhD Dissertation, Louisiana: University of Louisiana at Lafayette. (1–12): 171 pp.
- Thomson JA, Dean LMI (1931) The Alcyonacea of the Siboga Expedition with an addendum to the Gorgonacea. Siboga-Expedition Monograph 13d: 1–227. [1–28 pls]
- Thomson JA, Henderson WD (1906a) The Alcyonarians of the deep sea. An account of the alcyonarians collected by the Royal Indian Marine Survey Ship 'Investigator' in the Indian Ocean. Part 1. The Alcyonarians of the deep sea. The Indian Museum, Calcutta, 1–16 + 1–132. [1–10 pls] https://biodiversitylibrary.org/page/12037640
- Thomson JA, Henderson WD (1906b) Second preliminary report on the deep-sea Alcyonaria collected in the Indian Ocean. Annals and Magazine of Natural History (7)18: 427–433. https://doi.org/10.1080/00222930608562641
- Thomson JA, Russell ES (1910) Alcyonarians collected on the Percy Sladen Trust Expedition by Mr J Stanley Gardiner. Part I, the Axifera. Transactions of the Linnean Society of London, series 2: Zoology 13(2): 139–164. https://doi.org/10.1111/j.1096-3642.1910.tb00515.x
- Thomson JA, Simpson JJ (1909) An account of the alcyonarians collected by the Royal Indian Marine Survey Ship 'Investigator' in the Indian Ocean. II. The alcyonarians of the littoral area. Trustees of the Indian Museum, Calcutta, 319 pp. https://doi.org/10.5962/bhl.title.8279
- Tixier-Durivault A (1966) Octocoralliaires. Faune de Madagascar 21:1–456. [figs 1–399]
- Utinomi H (1961) Noteworthy octocorals collected off the southwest coast of Kii Peninsula, Middle Japan. Part 2. Telestacea, Gorgonacea and Pennatulacea. Publications of the Seto Marine Biological Laboratory 9(1): 197–228. [7–10 pls] https://doi.org/10.5134/174656
- Valenciennes A (1855) Extrait d'une monographie de la famille des Gorgonidees de la classe des polypes. Comptes Rendus Académie des Sciences, Paris 41: 7–15. [Abridged English translation in Annals and Magazine of Natural History (2)16: 177–183. This describes the first use of sclerites in classification; no illustrations.] https://doi.org/10.5962/bhl.part.28683
- Verrill AE (1865) Synopsis of the polyps and corals of the North Pacific Exploring Expedition, under Commodore C Ringgold and Captain John Rogers, USN, from 1853 to 1856.

Collected by Dr Wm. Stimpson, naturalist of the Expedition. With description of some additional species from the west coast of North America. Proceedings of the Essex Institute, Salem 3, 5(3): 17–50. https://biodiversitylibrary.org/page/33204514

- Verrill AE (1868a) [1868–1870] Notes on Radiata in the Museum of Yale College. 6. Review of the corals and polyps of the west coast of America. Transactions of the Connecticut Academy of Arts and Sciences (First Edition), 1: 377–422, 1868; 423–502, 1869; 503–558, 1870. [pls 5–10] [The regular edition up to page 502 was destroyed by fire after distribution of the author's edition of 150 copies; the reprinted edition issued in 1869 contains nomenclatural changes marked "Reprint" and thus constitutes a separate publication.] https://biodiversitylibrary.org/page/13465394
- Verrill AE (1868b) Notes on Radiata in the Museum of Yale College. No. 6. Review of the corals and polyps of the West Coast of America. Transactions of the Connecticut Academy of Arts and Sciences (Second Edition) 1(2): 377–422.
- Verrill AE (1868c) Critical remarks on halcyonoid polyps in the museum of Yale College, with descriptions of new genera. American Journal of Science and Arts 45: 411–415. https://babel.hathitrust.org/cgi/pt?id=hvd.32044072277114;view=1up;seq=5
- Verrill AE (1869) Critical remarks on the halcyonoid polyps with descriptions of new species in the Museum of Yale College, no. 4. American Journal of Science and Arts series 2, 48: 419–429. https://doi.org/10.2475/ajs.s2-48.143.244
- Verrill AE (1878) Notice of recent additions to the marine fauna of the eastern coast of North America, No. 2. American Journal of Science and Arts (3)16: 371–378. https://doi. org/10.2475/ajs.s3-16.95.371
- Verrill AE (1883) Report on the Anthozoa, and on some additional species dredged by the 'Blake' in 1877–1879, and by the U.S. Fish Commission steamer 'Fish Hawk' in 1880–82. Bulletin of the Museum of Comparative Zoology, Harvard 11: 1–72. [1–8 pls] https:// www.researchgate.net/publication/291870146\_Report\_on\_the\_Anthozoa\_and\_on\_ some\_additional\_species\_dredged\_by\_the\_Blake\_in\_1877-1879\_and\_by\_the\_US\_Fish\_ Commission\_steamer Fish\_Hawk\_in\_1880-82
- Verrill AE (1912) The Gorgonians of the Brazilian coast. Journal of the Academy of Natural Sciences, Philadelphia (2)15: 373–404. [1 fig., 29–35 pls]
- Verrill AE (1922) The Alcyonaria of the Canadian Arctic Expedition, 1913–1918, with a revision of some other Canadian genera and species. Report of the Canadian Arctic Expeditions 8(G): 1–164. https://doi.org/10.5962/bhl.title.64187
- Verrill AE (1928) Hawaiian shallow water Anthozoa. Bernice P Bishop Museum Bulletin 49: 1–30. [pls 1–5] https://doi.org/10.5962/bhl.title.58574
- Versluys J (1906) Die Gorgoniden der Siboga Expedition II. Die Primnoidae. Siboga-Expedition Monograph, Brill EJ, 13a: 1–187. [figs 1–178, 1–10 pls, chart]
- Watling L, France SC, Pante E, Simpson A (2011) Chapter 2: Biology of Deep-Water Octocorals. Advances in Marine Biology 60: 41–122. https://doi.org/10.1016/B978-0-12-385529-9.00002-0
- Whitmire CE, Clarke ME (2007) State of Deep Coral Ecosystems of the U.S. Pacific Coast: California to Washington. In: Lumsden SE, Hourigan TF, Bruckner AW, Dorr G (Eds) The State of Deep Coral Ecosystems of the United States, 2007. NOAA Technical Memo-

randum, CRCP-3, Silver Spring-Maryland, 109–154. https://www.coris.noaa.gov/activities/deepcoral\_rpt/Chapter3\_PacificCoast.pdf

- Williams GC (2013) New taxa and revisionary systematics of alcyonacean octocorals from the Pacific Coast of North America (Cnidaria, Anthozoa). ZooKeys, 283: 15–42. https://doi. org/10.3897/zookeys.283.4803
- Williams GC, Breedy O (2016) A New Species of Whip-like Gorgonian Coral in the Genus Swiftia from the Gulf of the Farallones in Central California with a Key to Eastern Pacific species in California (Cnidaria, Octocorallia, Plexauridae). Proceedings of the California Academy of Sciences Series 4, 63(1): 1–13. https://doi.org/10.3897/zookeys.629.10828
- Wing BL, Barnard DR (2004) A field Guide to Alaskan Corals. NOAA Technical Memoires, NMFS-AFSC-146, 67 pp. www.afsc.noaa.gov/publications/afsc-tm/noaa-tm-afsc-146.pdf
- Wirshing HH, Messing CG, Douady CJ, Reed J, Stanhope MJ, Shivji MS (2005) Molecular evidence for multiple lineages in the gorgonian family Plexauridae (Anthozoa: Octocorallia). Marine Biology 147: 497–508. https://doi.org/10.1007/s00227-005-1592-y
- Wright EP (1868) Notes of deep-sea dredging. Annals and Magazine of Natural History (4)2: 423–427. https://doi.org/10.1080/00222936808695845
- Wright EP (1869) On a new genus of Gorgonidae from Portugal. Annals and Magazine of Natural History (4)3: 23–26. [3 text figs] https://doi.org/10.1080/00222936908695873
- Wright EP (1885) The Alcyonaria. In: Tizard JH, Moseley HN, Buchanan JY, Murray J (Eds) Report of Scientific Research, Challenger. Narrative of the Cruise of H.M.S. 'Challenger' with a general account of the scientific results of the expedition, 1(2): 689–693. [figs 234–236]
- Wright EP, Studer T (1889) Report of the Alcyonaria collected by H.M.S. "Challenger" during the years 1873–1876. Challenger Reports: Zoology, 31(64): 1–72 + 1–314. [1–43 pls] www.archive.org/details/reportonscientif04grea/page/87/mode/1up

# Appendix I

Red Whip species	Location, S to N	Location Depth	Colony Branching	Colony Color	Polyp Spacing	Polyp Height	Sclerite Color	Sclerite Form	Sclerite Size
Leptogorgia flexilis	Magdalena Bay, Baja to San Diego, CA	11 meters to?	Thin, drooping branches; highly branched colony	Red/pink to tan/beige Polyps white to very pale orange	No more than 1 mm	No more than 1 mm	Bright Salmon	Spindles & Capstans	0.03– 0.09 mm
Leptogorgia chilensis	N of Magdalena Bay to Santa Cruz Is., CA	Approx. 15–80 m	Thin branches; moderately branched	Orange- red Polyps white	1 mm	Generally, almost flush	Bright Salmon	Spindles & Capstans	0.03– 0.05 mm
Red Whip (?"Transitional/ Regional Endemic")	San Diego, CA to off Oregon coast	?20-2,000 meters	Moderate thickness to branches; slightly branched to not branched	Orange- red Polyps white	Varies from 1 to 2 mm	Generally, from flush to nearly 1 mm; rarely taller	Salmon	Spindles & Dbl. Spinds.	Approx. 0.1 mm
Red Whip (?"Transitional/ Regional Endemic")	San Diego, CA to off Oregon coast; possible extension to WA coast	Approx. 12–150 m	Moderately thin branches, whip-like; slightly branched	Orange-red Polyps white (?pale pink)	Varies from 1 to 2 mm	Generally, consistently flush, rarely taller; on some, prominent	Salmon	Spindles & Dbl. Spinds.	Approx. 0.1 mm
"?Swiftia Transitional/ Regional species"	N Los Angeles County to Point Conception	Approx. 104– 173 m	Single branches; also slightly branched (if so, dichotomous)	Bright red to salmon- pink Polyps white	Less than 1 mm	Approx. 1 mm	Salmon	Spindles; very few Capstans, Dbl. Spinds. or Rods	From 0.04 mm to nearly +.16 mm
Swiftia simplex	N Los Angeles County to Alaska	200– 900 m	Single branches; sometimes slightly branched	Pinkish-red (Brick-red) Polyps pinkish-red	No more than 2 mm	Approx. 1 mm	Pinkish-red (Brick color) Rods orange	Spindles, Capstans, Rods and Dbl. Spinds.	0.1– 0.3 mm
Chromoplexaura marki	Point Conception to Cape Mendocino, CA (?further north to WA state, on to Alaska)	20–60 m; possibly deeper (to 600 m)	Single branches; sometimes slightly to moderately branched	Bright red, orange, even pinkish Polyps white or colored	2 mm	Nearly flush to 2 mm	Salmon to reddish	Spindles, Capstans, Ovals and Dbl. Spinds; NO Rods	$\begin{array}{l} 0.05 \text{ mm} \\ \text{to} \cong \\ 0.2 \text{ mm} \end{array}$
Swifita spauldingi	Monterey Bay, CA to off Washington coast (?further north to Alaska)	40 to at least 300 m	Moderate branch thickness; branched to some degree	Orange-red Polyps white or very pale pink	about 1 mm	Nearly flush to often very conspicuous, rounded	Salmon to pinkish- orange; some yellow; Rods orange	Spindles, Capstans, Rods and Dbl. Spinds.	About 0.1 mm

**Table A1.** Contrasts and comparisons of key "red whip" species and/or species of the genus *Swiftia*, as represented in SBMNH collection.

Polyp Height: includes both calyx and actual polyp.



**Map A1.** Distribution of species in genus *Swiftia* seen in, or immediately adjacent to, the California Bight. Range extensions are not definitive, but illustrative of the geographic distribution of specimens housed in SBMNH collection.

# Appendix 2

# Appendix 3

# List of material examined - Part III

(Material examined = Whole colony study plus multiple sclerite preparations; all with light microscopy, plus selected colonies under SEM, shown in figures associated with text)

# Swiftia cf. kofoidi (Nutting, 1909)

Material examined. -20–25 lots. USA, California – 2 colonies; Los Angeles County, 5.5 or 6 miles off SE end, or SE of, Santa Catalina Island, 33°15'00"N, 118°11'35"W (end), gravel, rock, 264-282m; coll. R/V 'Velero III', station 1188-40, 29 September 1941; SBMNH 422955 [wet]. -1 colony; Los Angeles County, 6.25 miles NE or ENE X E of Long Point, Santa Catalina Island, 33°25'20"N, 118°14'40"W (end), rocks, sponges, cyclostomes, 415-486 m; coll. R/V 'Velero III', station 1400-41, 8 September 1941; SBMNH 422956 [wet]. -several fragments; Los Angeles County, San Pedro Channel, 70 Fathom Bank, on rock and pebbles, 33°24'15"N, 118°00'35"W (end), 238 m; coll. R/V 'Velero III', station 1213-40, 30 Nov. 1940; SBMNH 422957 [wet]. -fragment; Los Angeles County, off Redondo Beach, 33°49'55"N, 118°25'45"W (end), on gray mud and shell, 175-218 m; coll. R/V 'Velero III', station 1137-40, 5 May 1940; SBMNH 422958 [wet]. -1 colony; 6.7 miles, 330° T from N Light, Santa Barbara Island, dredge, tangles-2 large boulders and much small rock, rock bottom, 33°33'27"N, 119°04'00"W (end), 255 m; coll. R/V 'Velero IV', station 2062-51, 18 October 1951; SBMNH 422959 [wet]. -fragment; Santa Barbara County, Santa Rosa Island, 16.5 miles SSE of East Point, 33°40'55"N, 119°52'30"W (end), rocks, crinoids, sponges, 136–138 m; coll. R/V 'Velero III', station 1385-41, 25 August 1941; SBMNH 422960 [wet]. -1 fragment; Santa Barbara County, 10 miles SE X 1/2E of South Point, Santa Rosa Island, 33°46'30"N, 119°58'30"W (end), mud, rock and gravel, 195-227 m; coll. R/V 'Velero III', station 1393-41, 26 August 1941; SBMNH 422961 [wet]. -multiple fragments (one lot); Santa Barbara County, Santa Rosa Island, 7.37 miles, 350° T to East Point, 33°48'40"N, 119°56'20"W (end), 116 m; coll. R/V 'Velero IV', station 23291-75, 13 November 1975; SBMNH 422964 (with label reading: 23291 CH) [wet]. -2 colonies, fragmented (no base); Santa Barbara County, Santa Rosa Island, 2.59 miles, 291.5° T to Ford Point, 33°54'00"N, 120°00'00"W, 40 m; coll. R/V 'Velero IV', station 23290-75, 13 November 1975; SBMNH 422962 (with label reading: 23290 CH) [wet]. -2 colonies, on deep-water bivalve; Santa Barbara Channel, 34°15'00"N, 120°00'00"W, ~136 m; coll. Peterson, BLM, by dredge, June 1964; SBMNH 422967 [wet]. -2 colonies, fragmented (no base); Santa Barbara County, Santa Rosa Island, 6.1 miles, 50° T to Sandy Point, 33°56'00"N, 120°20'00"W (end), 127 m; coll. R/V 'Velero IV', station 24879-76, 28 April 1976; SBMNH 422963 (with label reading: 24879 CH) [wet]. MEXICO, Baja California Norte (Pacific Coast) - 1 colony; west coast side of Isla Cedros, 28°13'02"N, 115°15'01"W; coll. Pacific BioMarine, 26 April, 1974; SBMNH 422965 [DH ? = SBMNH-41, dry].

**Other material examined.** –1/few fragments; USA, California, Santa Barbara County, off Point Conception, 34°26'23"N, 120°28'31"W, SWFC station 5, 727 m; coll. R Snodgrass, 6 March 1986; SIO/BIC CO2024 [wet]. –1 colony; USA, California, Monterey County, Monterey Bay, 36°26'39"N, 122°01'47"W, ~684 m; coll. G McDonald, 14 August 1974; MLML C0072 [wet]. –1 colony; USA, California, Monterey County, Monterey Bay, ~36°46'15"N, 121°53'27"W, 504 m; coll. G McDonald, 29 September 1973; MLML C0060 [wet]. –1 colony; USA, California, Monterey County, Ascension Canyon, 36°55'05"N, 122°27'30"W, attached to sea anemones, ~1,245 m; coll. unknown, 4 June 1984 MLML C0140 [wet]. –colony; USA, California, Monterey County(?); coll. MBARI, T138-A1, NOAA CB 33994 [wet].

No locality could be ascribed to an additional colony as the station number did not correspond with the year; coll. unknown; 'Albatross', station (4- or) 5054, 1904; SIO/BIC CO360 [wet].

### Swiftia pacifica (Nutting, 1912)

**Material examined**: ~23 lots. **USA, California** – 1 colony + 1 fragment (2 lots); Ventura County, ~6 miles due south of Anacapa Island, Pilgrim Banks (Piggy Bank), at intersection of Santa Cruz Canyon and Pilgrim Banks, between Anacapa and Santa Cruz Islands, Channel Islands National Marine Sanctuary, 33°55'15"N, 119°28'18"W, 280–320 m; coll. NOAA vessel, 'McArthur II', Leg 3, 27 June-02 July 2010; NOAA ID Nos.: K2\_01\_062710\_03 and K2\_01\_062710\_10; SBMNH 232035/232036 [wet].

Other material examined. USA, California - 1 colony; Humboldt County, off Cape Mendocino, on the edge of Gorda Escarpment, 40°18'42"N, 124°59'06"W, 1,063 m; coll. NOAA, WCGS, 2007; CB 34406-040, FRAM/Cutting Barcode 112080 [wet]. USA, Oregon - 1 colony; Coos County, off Oregon coast, S and W of Bandon, ~43°01'37"N, 124°48'36"W, ~218 m; coll. NOAA, 2006; CB 34213-063, FRAM/Cutting Barcode 100105485 [wet]. -1 colony; Lane County, off Oregon coast, on Heceta Bank, near southern edge of Heceta Escarpment, due W of Florence, ~43°56'42"N, 124°55'06"W, ~397 m; coll. NOAA, 2006; CB 34213-054, FRAM/Cutting Barcode 100105476 [wet]. -1 colony; off Oregon coast, Heceta Bank, 43°57'10"N, 124°50'38"W, hard bottom, 134.8 m; coll. A Valdés by ROV; RV 'Ronald H. Brown' (NOAA), and S/V 'Ropos', Dive 615, 10 July 2001; LACoM-NH Marine Biodiversity processing center number 99 [wet]. -2 colonies; off Oregon coast, Heceta Bank, 44°04'04"N, 124°55'11"W, muddy bottom, collected with small rock, sponge, 159.7 m; coll. A Valdés by ROV; RV 'Ronald H. Brown' (NOAA) and S/V 'Ropos', Dive 606, 6 July 2001; LACoMNH Marine Biodiversity processing center number 36 [wet]. -1 colony; Lincoln County, off coast, north of Hydrate Ridge, 44°46'01"N, 125°03'27"W, 1,159 m; coll. NOAA, RACE, CB 50003-008, 1996 [wet]. -1 colony; off Oregon coast, 46°06'22"N, 124°55'03"W, 1123.5 m; coll. Astoria RB-01-05, G Hendler; RV 'Ronald H. Brown' (NOAA) and S/V 'Ropos', Dive R602-Bio-0007, 3 July 2001; LACoMNH Marine Biodiversity Center process-

ing number 373 [wet]. USA, Washington –multiple colonies; Grays Harbor County, Ouinault Canvon, 47°32'05"N, 125°11'05"W, 558 m; coll. R/V 'John N. Cobb', 16 March 1962, USNM 53971 (labeled as S. torreyi) [wet]. -multiple colonies/3 lots; Jefferson County, W of Queets, 47°35'13"N, 125°09'17"W, 549 m; coll. R/V 'John N. Cobb', 16 March 1962; USNM 57219, 57220 and 57221 [wet]. -1 colony; Juan de Fuca Canyon, 47°55'06"N, 125°29'02"W, 429 m; coll. OCNMS Survey Expedition, 2008; EPI 202 [wet]. - fragments; Clallam County(?), no specific location or collection data provided; coll. OCNMS Survey Expedition, 2008; Jar 807, EPI 230 [wet]. -fragments; Clallam County, E edge of Swiftsure Bank, ~21 miles W of Ozette, 48°08'31"N, 125°11'10"W, 267 m; coll. OCNMS Survey Expedition, 2008, 12 July 2008; Jar 795, EPI/SUC 216 [wet]. -several colony fragments; Clallam County, off coast, just south of Cape Flattery, 48°10'05"N, 125°07'01"W, 230 m; coll. P Etnoyer, NOAA West Coast Survey, Fall 2010, 5 November 2010; BS007 [wet]. -1 colony; Clallam County, approx. 9–12 miles SW of Cape Flattery, Olympic Coast National Marine Sanctuary, 48°18'11"N, 124°56'10"W, 265.7 m; coll. OCNMS Survey Expedition, 2006, 1 June 2006; Jar 713, OC06-003, EPI 127 [wet]. -1 colony; Clallam County, approx. 9-12 miles SW of Cape Flattery, Olympic Coast National Marine Sanctuary, 48°18'13"N, 124°56'10"W, 250.4 m; coll. OCNMS Survey Expedition, 2006, 1 June 2006; Jar 714 [wet]. -colonies in 3 lots; Clallam County, approx. 9-12 miles SW of Cape Flattery, Olympic Coast National Marine Sanctuary, 48°18'17"N, 124°56'08"W, 251.5 m; coll. OCNMS Survey Expedition, 2006, 1 June 2006; Jars 381-A, B and C [wet]. -1 fragment; Clallam County, E edge of Swiftsure Bank, just W of entrance to Strait of Juan de Fuca, -10 miles from Cape Flattery, Olympic Coast National Marine Sanctuary, 48°24'33"N, 124°57'45"W, 273 m; coll. OCNMS Survey Expedition, 2008, 9-13 July 2008; Jar 733, EPI 153 [wet]. USA, Alaska -1 colony; Gulf of Alaska, no lat/long, no depth, no date; Alaska Fisheries Science Center, NOAA Fisheries, 41-39-1 [dry]. -1 colony; Bering Sea, Aleutian Islands, near islands, SE of Agattu Island, 52°13'55"N, 174°13'24"W, 881 m; coll. R/V 'Albatross', station 4781, 7 June 1906; USNM 30024 (labeled as Callistephanus pacificus) [wet]. -colonies; Gulf of Alaska, Denson Seamount, 53°56'58"N, 137°23'51"W, 2,432 m; coll. Amy Baco-Taylor using 'Alvin' DSR/V, 3 August 2004; USNM 1075771 [dry]. -1 colony; 26 miles south of Chowiet Island, 55°36'12"N, 157°05'39"W, 86 m; coll. NOAA, RACE, 2000; CB 50003-021 [wet]. -1 colony; Gulf of Alaska, ~57°37'29"N, 136°37'09"W, 803 m; coll. unknown, 19 July 2004; Alaska Fisheries Science Center, NOAA Fisheries, 41-100A-2 [dry]. -colonies; Gulf of Alaska, Kayak Island, 59°29'06"N, 144°50'42"W, 601-800 m; coll. unknown, 31 July 2002; USNM 1011170 [dry].

**Other material, not examined.** – colony (?); Hawaii (likely an error in location); coll. R/V 'Albatross', 1902; part of a specimen from Bishop Museum collection, #101– as **Holotype**; USNM 49513 (labeled as *Allogorgia exserta*) [wet].

Additional specimens collected from the Bering Sea, Pribilof Islands and British Columbia (Queen Charlotte Islands) found in NMNH collection.

#### Swiftia simplex (Nutting, 1909)

**Material examined.** ~24 lots. **USA, California** – 1 colony; North Pacific, Monterey County, Monterey Bay, 5.4 miles (5.8 miles), 313°T (314°T) from Point Piños Light to Mid Point, 36°42'05"N, 122°01'45"W (end), 436–809 m; coll. R/V 'Velero IV', station 7462-61 or 7463-61, 10 October 1961; SBMNH 422979 [wet].

Other material examined. USA, California - Eastern N Pacific, San Juan Seamount, 33°05'46"N, 120°56'57"W, 746.2 m; coll. MBARI staff, PI, D Clague, 2 May 2004; MBARI T665-A5, 2004-123 [wet]. -1 colony; Los Angeles County, Channel Islands, Santa Barbara Island, bearing N 49°, W 4.7 miles, 815 m; coll. USBCF 'Albatross', station 4416, SW, Rock, 1904; potential Paratype (?); SIO/BIC CO990 [wet]. -Eastern N Pacific, Santa Barbara County, Channel Islands, Santa Cruz Island, Point San Pedro, ~34°02'03"N, 119°31'12"W, 817-933 m; coll. R/V 'Albatross', 14 April 1904; Syntype, USNM 25431, (Nutting) [dry]. –Eastern N Pacific, Santa Barbara County, Channel Islands, Santa Cruz Island, Point San Pedro, ~34°02'03"N, 119°31'12"W, 817-933 m; coll. R/V 'Albatross', 14 April 1904; Syntype, USNM 43130, (Nutting) [dry]. -Eastern N Pacific, West of San Miguel Passage, Rodriguez Seamount, 34°01'12"N, 121°04'48"W, 895.3 m; coll. MBARI staff, PI, D Clague, 15 October 2003; MBARI T630-A13 [wet]. -Eastern N Pacific, West of San Miguel Passage, Rodriguez Seamount, 34°03'00"N, 121°03'00"W, 637.6 m, on an Arkosic sandstone erratic; coll. MBARI staff, PI, D Clague, 13 October 2003; MBARI T628-R22-1 [wet]. -Eastern N Pacific, West of San Miguel Passage, Rodriquez Seamount, 34°03'00"N, 121°03'00"W, 689 m; coll. MBARI staff, PI, D Clague, 13 October 2003; MBARI T628-A6 [wet]. - Eastern N Pacific, NE of Davidson Seamount, just S of Monterey Bay, ~36°44'24"N, 122°02'24"W, 870-911 m; coll. MBARI staff, PI, D Clague, 24 June 2007; MBARI T1104-A6 [wet]. -Monterey County, Monterey Bay, in channel, 732-914 m; coll. unknown, 25 June 1925; USNM 77287 [dry]. -Monterey County, Monterey Bay, ~36°27'41"N, 122°06'37"W, 504 m; coll. G McDonald, 29 September 1973; MLML C0051 [wet]. -San Mateo County, off Pigeon Point, ~37°10'55"N, 122°23'40"W, 273 m; coll. M/V 'Joseph Alioto', no collection date; CAS-IZ 96744 [wet] (as Euplexaura simplex). -Eastern N Pacific, Carmel Canyon, 198 m; coll. M Morris, 12 April 1976; MLML C0038 [wet]. -Eastern N Pacific, Pioneer Seamount, ~37°24'03"N, 123°32'24"W, 847.5 m; coll. MBARI staff, PI, D Clague, 19 June 2007; MBARI T1101-A20 [wet]. -Marin County, W of Point Reyes, Cordell Bank National Marine Sanctuary, southwest of Cordell Bank, ~37°56'34"N, 123°28'19"W, 182-396 m; coll. N.B. 'Scofield', 25 August 1949; CAS-IZ 96739 [wet] (as Euplexaura simplex). -1 colony; Mendocino County, off the coast, 39°12'28"N, 124°10'30"W, 991 m; coll. NOAA, WCGS, 2006; CB 34212-014 [wet]. –Humboldt County, Eel River Canyon, ~40°38'01"N, 124°21'26"W, 364 m; coll. RR Talmadge on R/V 'Flicker', December 1966; CAS-IZ 96758 [wet] (as Euplexaura simplex). USA, Oregon – 2 colonies; off Oregon coast, Heceta Bank, 43°56'35"N, 124°57'11"W, 340 m; coll. Heceta RB-00-05, G Hendler; RV 'Ronald H. Brown' (NOAA) and S/V 'Ropos', Dive R534-bio-0001, 23 June 2000; LACoMNH Marine Biodiversity Center processing number 227 [wet]. -1 colony; off Oregon coast,

Heceta Bank, 44°11'33"N, 124°58'15"W, cold seep, 275 m; coll. N Puniwai by ROV; RV 'Ronald H. Brown' (NOAA) and S/V 'Ropos', Dive 609, 8 July 2001; LACoMNH, Marine Biodiversity Center processing number 68 [wet]. –1 colony; Lincoln County, off the coast, north of Hydrate Ridge, 44°46'01"N, 125°03'27"W, 1,159 m; coll. NOAA, RACE, 1996; CB 50003-009 [wet]. **USA, Washington** –2 colonies; Grays Harbor County, 11 miles south of Quinault Canyon, 47°13'49"N, 125°07'35"W, 838 m; coll. NOAA, WCGS, 2007; CB 34405-028, FRAM/Cutting Barcode 105535 and FRAM/Cutting Barcode 127018. –1 colony; Jefferson County, between Juan de Fuca Canyon and Quinault Canyon, 47°38'09"N, 125°33'45"W, 1,184 m; coll. NOAA, WCGS, 2006; CB 34212-039, FRAM/Cutting Barcode 100081368 [wet]. **USA, Alaska** –North Pacific, Gulf of Alaska, 56°06'54"N, 144°15'45"W, 546–664 m; coll. unknown, 2 July 2000; USNM 1006328 [dry]. –1 colony; Gulf of Alaska, ~57°54'15"N, 137°33'20"W, 601 m; coll. unknown, 21 July 2008; Alaska Fisheries Science Center, NOAA Fisheries, 81-99B-1 [dry].

Unknown location: WCGS 2006–2006H30 (No FRAM or CB number), provided by E Berntson, NOAA Fisheries Office, Port Orchard, WA.

# Swiftia cf. spauldingi (Nutting, 1909)

# Material examined. ~9 lots

**Other material examined.** – Eastern North Pacific, USA, California, Monterey County, Monterey Bay, in channel, 128 m; 13 April 1928; USNM 78385 [dry]. – Eastern North Pacific, USA, California, Monterey County, Monterey Bay; **Holotype**, USNM 91854 [wet]. –Eastern North Pacific, USA, California, Monterey County, Monterey Bay, 146 m; 22 January 1930; USNM 77289 [dry]. –Eastern North Pacific, USA, California, Monterey Bay, 91 m; 8 February 1930; USNM 77288 [dry]. –1 colony; Eastern North Pacific, Oregon, Curry County, 21 miles slightly north and west of Gold Beach, 42°27'26"N, 124°50'24"W, 452 m; coll. NOAA/NFSC, WCGS, 2008; CB 34806-455, FRAM/Cutting Barcode 100116455 [wet]. –Eastern North Pacific, Washington State, W of Juan de Fuca Strait, 48°30'00"N, 124°57'00"W, 49 m.; 24 September 1888; USNM 75052 [dry].

Several other lots [wet], indicating collection locations off the coast of USA, Oregon, Lane County, at Heceta Bank [USNM 57165, wet], and in the Strait of Juan de Fuca, USA, Washington [USNM 57158, wet].

# Swiftia torreyi (Nutting, 1909)

# Material examined. ~16 lots.

**Other material examined. USA, California** – San Diego County, San Diego, Point Loma, 31°59'53"N, 116°59'59"W, 201–262 m; coll. R/V 'Albatross', station 4311, 4 March 1904; USNM 49522 [wet]. –Eastern N Pacific, Rodriquez Seamount, west of San Miguel Passage, 34°02'57"N, 121°06'03"W, 1,029 m; coll. MBARI staff, PI, D Clague, 15 October 2003; MBARI T630-A7 [wet]. –Eastern N Pacific, Rodriquez Seamount,

west of San Miguel Passage, 34°02'57"N, 121°06'03"W, 1,029 m; coll. MBARI staff, PI, D Clague, sample T630-A7, 15 October 2003; USNM 1027078 [wet]. -Eastern N Pacific, Davidson Seamount, ~35°41'51"N, 122°41'58"W; coll. MBARI staff, PI, A DeVogeleare, 22 May 2002; MBARI T429-A20C [wet]. - Monterey County, Monterey Bay, 36°38'00"N, 121°55'00"W (bearing S 78°E, 6.8 miles) off Point Piños light-house, 1,373–1,742 m; coll. USBCF 'Albatross', station 4530, 27 May 1904; Holotype-USNM 25433 [wet]. -Monterey County, Monterey Bay, 36°38'00"N, 121°55'00"W (bearing S 78°E, 6.8 miles) off Point Piños light-house, 1,373–1,742 m]; coll. USBCF 'Albatross', station 4530, 27 May 1904; Holotype-USNM 43147 [wet]. -Monterey County, Monterey Bay, 36°38'00"N, 121°55'00"W (bearing S 74°E, 7.4 miles) off Point Piños light-house, 1,574.77-1,942.4 m; coll. R/V 'Albatross', station 4537, 31 May 1904, det. Nutting; Paratype-USNM 58985 [dry]; previous lat./long., 1,566-1,931 m; CAS-IZ 96786 [wet]. -Monterey County, Monterey Bay, 146 m; coll. unknown, 20 February 1930; USNM 87968 [dry]. -Monterey County, Monterey Bay, Point Piños, 36°38'00"N, 121°55'00"W, 1,381–1,752 m; coll. R/V 'Albatross', station 4530, 27 May 1904; USNM 91878 [wet]. -Monterey County, Monterey Bay, 36°38'00"N, 121°55'00"W (bearing S 46°E, 8.4 miles) off point Piños light-house, 1,552.82 m; coll. R/V 'Albatross', station 4546, 3 June 1904, det. Nutting; Paratype–USNM 91896 [drv]. -Monterey County, Monterey Canyon, Point Sur, by beam trawl; coll. MLML staff on class cruise, PI, K Coale, 7 April 2008; no station or collection number [wet]. -Eastern N Pacific, Pioneer Seamount, ~37°23'49"N, 123°23'58"W, depth unknown; coll. MBARI staff, PI, D Clague, 18 June 2007; MBARI T1100-A7, 61807 [wet]. - Eastern N Pacific, Pioneer Seamount, ~37°23'49"N, 123°23'58"W, 847.5 m; coll. MBARI staff, PI, D Clague, 19 June 2007; MBARI T1101-A21, 61907 [wet]. USA, Washington -Grays Harbor County, Quinault Canyon, 47°28'59"N, 125°11'45"W, 558 m; coll. R/V 'John N Cobb', 16 March 1962; USNM 53971 [wet] (? on ID). -1 colony; Clallam County, edge of Swiftsure Bank, W of Olympic Peninsula, -47°55'54"N, 125°29'11"W, 429 m; coll. OCNMS Survey Expedition 2008, 12 July 2008; Jar 787, EPI 202 [wet]. -Olympic Peninsula, Clallam County, 48°07'22"N, 125°50'39"W, depth not indicated; coll. R/V 'Miller Freeman', 2000 west coast slope fisheries survey, 12 October 2000; USNM 100840 [wet]. -Strait of Juan de Fuca, ~2,200 m; coll. MBARI staff, PI, D Stakes, 4 September 2004; MBARI T738-A1, 2004-248 [wet].

**Other material examined.** – USA, California, Monterey County, Monterey Bay, 36°38'00"N, 121°55'00"W (bearing S 39°E, 10.7 miles) off Point Piños light-house, 716–953 m; coll. USBCF 'Albatross', station 4514; repository unknown. –1 colony; no location data or date; CAS-IZ 96794 [wet].

#### Swiftia pusilla (Nutting, 1909)

Material examined. No specimens in SBMNH collection.

**Other material examined.** – fragment; USA, California, San Diego County, San Diego, Point Loma, ~32°39'10"N, 117°17'47"W, 166–177 m; coll. R/V 'Albatross', station 4361, 15 March 1904; USNM 25430, **Holotype** [wet & dry]. (Identification still uncertain.)

### Thesea sp. (various possible species, such as T. filiformis, T. mitsukurii?)

Material examined. ~65 lots. USA, California - 1 fragment; San Diego County, off Point Loma, mud, ~32°38'30"N, 117°13'20"W, 64-69 m; coll. 'EW Scripps', 9 October 1946; (in ovulid snail collection, with shells of Neosimnia loebbeckeana), SBMNH 13304 [dry]. -multiple fragments; San Diego County, off Point Loma, 32°39'00"N, 117°14'00"W, with an ID H46-102; SBMNH 422908 [wet]. -2 fragments; San Diego County, San Diego, from a station off Point Loma, ~32°41'03"N, 117°16'35"W; coll. MBL, no other data; SBMNH 265944 [wet]. -fragments; San Diego County, San Diego, from a station off point Loma, station SD-1 ~32°41'03"N, 117°16'35"W, 61 m; coll. MBL, 12 January 1998; SBMNH 265943 [wet]. -fragments; San Diego County, 2.1 miles, 268° T from Scripps Institute Pier, Hayward grab-compact green mud, 32°52'00"N, 117°18'00"W, coll. R/V 'Velero IV', station 4757-56, 8 December 1956; SBMNH 422346 [wet]. - fragments; Los Angeles County, San Clemente Island, 1 mile NE of Castle Rock, gray sand, 33°03'00"N, 118°36'20"W (end), 84-91 m; coll. R/V 'Velero III', station 1326-41, 8 June 1941; SBMNH 422339 [wet]. -strands; Los Angeles County, Santa Catalina Island, 1 mile SW of Ben Weston Point, mud, sand, gravel, 33°20'55"N, 118°30'35"W (end), 82–89 m; coll. R/V 'Velero III', station 1316-41, 17 May 1941; SBMNH 265942 [wet]. -fragments; Los Angeles County, off Corona del Mar, 33°35'48"N, 117°52'48"W, 46 m; coll. MacGinitie, 21 February 1954; SBMNH 422355 [wet]. -multiple fragments; Los Angeles County, Catalina Island, Ship Rock, 33°27'00"N, 118°29'00"W, 82-101 m; coll. J Morin, 7 July 1977; SBMNH 422353 [wet]. -strands; Los Angeles County, Catalina Island, 2 mi. W of Church Rock, mud, sand, 33°17'25"N, 118°21'50"W (end), 82-96 m; coll. R/V 'Velero III', station 1321-41, 18 May 1941; SBMNH 422338 [wet]. -multiple strands; Los Angeles County, Santa Catalina Island, White Cove, mud and sand, 33°23'05"N, 118°21'00"W, 66-75 m; coll. R/V 'Velero III', station 998-39, 12 August 1939; SBMNH 422335 [wet]. -a few strands; Los Angeles County, Santa Catalina Island, off Bird Rock, rock, coarse shell, kelp, 33°27'20"N, 118°29'00"W (end), 56-73 m; coll. R/V 'Velero III', station 1187-40, by small dredge boat, 29 Sept. 1940; SBMNH 422347 [wet]. -fragments; Los Angeles County, N of Santa Catalina Island, off Eagle Bank, gray sand, 33°27'40"N, 118°30'00"W (end), 73-78 m; coll. R/V 'Velero III', station 1178-40, 10 September 1940; SBMNH 422345 [wet]. -multiple fragments; Los Angeles County, 3.6 miles, 250° T from Newport Beach Pier, Hayward grab-dark green, sandy silt, 33°35'12"N, 117°59'52"W; coll. R/V 'Velero IV', station 5087-57, 22 May 1957; SBMNH 422337 [wet]. -multiple colony fragments; Los Angeles County, 8.6 miles, 142° T, from Point Fermin, dredge-sand, 33°35'34"N, 118°11'03"W (end), 49 m; coll. R/V 'Velero IV', station 2043-51, 20 July 1951; SBMNH 422332 [wet]. -multiple strands/colonies; Los Angeles County, Palos Verdes Estates, Bluff Cove, 33°47'18"N, 118°24'47"W; coll. T Burch, station 40129, 22 August 1940; SBMNH 423086 [wet]. -multiple strands; Los Angeles County, off Redondo Beach, 33°50'48"N, 118°24'51"W, 27-91 m; coll. T Burch, station 3929, 3 August 1939; SBMNH 265941 [wet]. -multiple fragments; Santa Monica, Santa Monica Bay, 33°51'35"N, 118°26'49"W, by VanVeen grab, 60 m; coll. City of Los Angeles, Environmental Monitoring Division, 21 July 2003; LACoMNH

Marine Biodiversity Center process number 10231 [wet]. -3 samples (combined), multiple strands; Los Angeles County, near Hyperion Stack, between Castle Rock and the Manhattan Beach Pier, lot 4068–.85 miles, 285° T from Hyperion Stack, 33°55'58"N, 118°26'52"W, lot 4069.9 miles, 294°T from Hyperion Stack, 33°56'07"N, 118°26'51"W, lot 4071–1.4 miles, 235° T from Hyperion Stack, 33°54'57"N, 118°27'15"W; coll. R/V 'Velero IV', stations 4068, 4069 & 4071, 16 April 1956; SBMNH 422907, [wet]. multiple colonies/fragments; Los Angeles County, Santa Monica Bay, dredge-rocky bottom, 33°52'16"N, 118°31'44"W (end), 67 m; coll. R/V 'Velero IV', station 3539-55, 12 October 1955; SBMNH 422344 [wet]. -numerous fragments (colonies); Los Angeles County, Santa Monica, 34°00'02"N, 118°30'41"W, 61 m; coll. SCCWRP, station S-20, 16 April 1974; SBMNH 422354 [wet]. - fragments/colonies; Santa Barbara County, 3 miles south of Santa Barbara, 34°22'23"N, 119°40'21"W, 76 m; coll. P Scott, 29 September 1986; SBMNH 422352 [wet]. –numerous fragments/colonies (mixed species?); Santa Barbara County, 3 miles south of Santa Barbara, 34°22'23"N, 119°40'21"W, 76 m; coll. P Scott, 29 Sept. 1986; with barnacles, possibly from the genus Lepas attached; SBMNH 422356 [wet]. -several fragments (long); Santa Barbara County, Santa Barbara, 2 miles off Lighthouse, 34°22'01"N, 119°43'12"W, 55 m; coll. J Vucci and J Butterfield, 29 April 1974, with an otter trawl on a sand and rock bottom; SBMNH 422905 [DH 416 =SBMNH-01; dry]. -fragment/colony; Santa Barbara County, N of Santa Barbara, 5 Mile Reef, 34°45'00"N, 123°02'00"W, 204 m; coll. P Brophy, 4 June 1967; SBMNH 45694 [wet]. -1 fragment; Santa Barbara County, N of Santa Barbara, 5 Mile Reef, 34°45'00"N, 123°02'00"W, 204 m; coll. P Brophy, 4 June 1967; [DH, SBMNH-05; SBMNH 422906; dry]. -several colonies; California Channel Islands, by trawl, 55 m; coll. P Brophy, April 1974; SBMNH 45596 [wet]. -1 colony, with base (?); California Channel Island area, by trawl; coll. P Brophy; SBMNH 45606 [wet]. -fragment/colony; Santa Barbara County, Santa Cruz Basin, in a beam trawl, 10.5 miles, 242° S from Anacapa Lighthouse, 33°55'00"N, 119°35'45"W, 909 m; coll. T Phillips, 'Velero IV', station 13621-69, 14 November 1969; SBMNH 45598 [wet]. -1 colony fragment; Santa Barbara County, 3.7 miles, 21° T to Crook Point, San Miguel Island, 33°56'48"N, 120°21'42"W (end), 118 m; coll. R/V 'Velero IV', station 24882-76, 28 April 1976; SBMNH 422904 [wet]. MEXICO, Baja California Sur (Pacific Coast) - multiple fragments; 7 miles, 260° T from Punta Abreojos, sigsbee trawl, sand and mud bottom, 26°39'48"N, 113°40'43"W (end), 44 m; coll. R/V 'Velero IV', station 1953-50, 20 April 1950; SBMNH 422342 [wet]. -1 colony; 8.5 miles S of Canal de Dewey, sand, broken shell, gravel, 27°42'15"N, 115°05'02"W (end), 89 m; coll. R/V 'Velero III', station 1259-41, 27 February 1941; SBMNH 422343 [wet]. MEXICO, Baja California Norte (Pacific Coast) - multiple colonies; 8 miles SW of Isla Cedros, green, fine sand, coral, 28°00'00"N, 115°29'00"W (end), 115-118 m; coll. R/V 'Velero III', station 1254-41, 26 February 1941; SBMNH 422350 [wet]. -1 colony (with base, on flat, black rock); Isla Cedros, Cabo de San Augustin, SW of island, 8 miles, 243° T, dredge-fine sand, mud bottom, 28°01'02"N, 115°29'30"W (end), 109 m; coll. R/V 'Velero IV', station 1948-50, 27 April 1950; SBMNH 422341 [wet]. –fragment; off Islas San Benitos, S of islands, fine green sand, 28°12'45"N, 115°35'15"W (end), 129-173

m; coll. R/V 'Velero III', station 1010-39, 20 August 1939; SBMNH 422348 [wet]. –1 fragment; 5.5 miles S of Islas San Benitos, fine green sand, coarse grey sand, 28°13'55"N, 115°35'05"W (end), 120–147 m; coll. R/V 'Velero III', station 1251-41, 26 February 1941; SBMNH 422351 [wet]. –1 colony; outer coast, SE of Cabo San Quintin, 30°17'40"N, 115°54'40"W, 40–55 m, bottom composed of shale; coll. J McLean and P LaFollette, at 'Searcher' station 226-227 71-150, 17 October 1971; SBMNH 422414 [dry]. –multiple colony fragments; 8.21 miles, 324° T from Isla San Martin, dredge–sea stars, sand, 30°35'05"N, 116°11'49"W (end), 67 m; coll. R/V 'Velero IV', station 1692-49, 3 March 1949; SBMNH 422336 [wet]. –multiple fragments; 4 miles N of Todos Santos Island, shell, mud, gray sand, 31°53'20"N, 116°48'15"W, 75 m; coll. R/V 'Velero III', station 1245-41, 24 February 1941; SBMNH 422349 [wet].

Other material examined. USA, California - strands; San Diego County, La Jolla Canyon, N wall, Wheeler's Bank, 46 m; coll. J Stewart, 19 December 1959; (in Limbaugh Collection, NMNH) [dry]. -strands; San Diego County, San Diego, Point Loma, 137-245 m; coll. R/V 'Albatross', 12 March 1904 (Nutting, 1912); USNM 030295 [wet]. -strands; San Diego County, San Diego, straight off Point La Jolla, 101-183 m; coll. Fager, with otter trawl 1, station-908, 28 January 1965; SIO/BIC CO 996. --strands; San Diego County, San Diego, from a station off point Loma, station SD-13; coll. MBL; no other data given [wet]. -strands; San Diego County, off La Jolla, 32°52'12"N, 117°17'24"W, 73.2-Van Veen grab (0.18m<sup>2</sup>), fine silty mud; coll. R/V 'Oconostota', F Rokop and S Luke, November 1969; SIO/BIC CO992. --strands; San Diego County, N La Jolla, 32°52'36"N, 117°17'48"W, 73 m, sand and shells; coll. unknown, Haul 1092, 19 June 1906; SIO/BIC CO997. -strands; San Diego County, off San Onofre, 91 m, M-15, OT-4, to 33°13'06"N, 117°29'36"W (end), with 25' otter trawl; coll. Matsui and Burnett, R/V 'Agassiz', 29 March 1974; SIO-CO993, BI 74-4 [wet]. -strands; San Diego County, off San Onofre, 33°16'30"N, 117° 30'30"W, M-15, OT-5, 25' otter trawl, 27 m; coll. T Matsui, R/V 'Agassiz', 29 March 1974; SIO/ BIC CO994. -strands; San Diego County, off San Onofre, 33°16'00"N, 117°31'00"W, M-15, OT-6, 25' otter trawl, 54 m; coll. T Matsui, R/V 'Agassiz', 29 March 1974; SIO/ BIC CO995. -strands; San Diego County, off shore from Canyon de Las Encinas, 24 m; coll. C Turner, California Fish and Game, Terminal Island; 1 June 1967; (SIO-CO998) [wet]. -strands; Orange County, northern edge of San Gabriel Canyon/Newport Canyon, south of, and between, Huntington Beach and Newport Beach, trawl, ~33°34'20"N, 117°59'51"W, 60 m; coll. OCSD, station T-22, Haul 1, 28 February 2012 [wet]. -strands; Orange County, northern edge of San Gabriel Canyon/Newport Canyon, slightly eastward towards Newport Beach, Van Veen grab, ~33°34'22"N, 117°59'31"W, 59 m; coll. OCSD, station T-9, replicate 1, 15 July 2002 [wet]. strands; Orange County, western edge of Newport Canyon, south of Newport Beach, trawl, ~33°34'51"N, 117°57'21"W, 55-60 m; coll. OCSD, station T-3, 22 February 2012 [wet]. -strands; Orange County, off Huntington Beach, trawl, ~33°35'57"N, 118°02'47"W, 36 m; coll. OCSD Survey 8612, station T-6, replicate 1, 1986 (vial with label "OCSD 0010") [wet]. -strands; Orange County, off Huntington Beach, trawl, ~33°35'57"N, 118°02'47"W, 35 m; coll. OCSD, station T-6, Haul 1, 22 February

2012 [wet]. –strands; Los Angeles County, San Pedro, south of Point Fermin, northern edge of San Pedro escarpment, PV Trawl, T5 transect, ~33°41'07"N, 118°19'36"W, 137 m; coll. LACSD, station T5-137, 14 February 2012 [wet]. –fragment; Los Angeles County, (?)just south and west of San Pedro, PV Benthic, ~33°41'32"N, 118°20'14"W, 152 m; coll. LACSD, station E8 rock (8B?), JMB; Marine Biology Lab, City of Los Angeles), 16 July 1992 [wet]. –strands; Los Angeles County, off Torrance, Redondo Canyon, PV Trawl, T0 transect, ~33°48'34"N, 118°25'51"W, 61 m; coll. LACSD, station T0-61, 16 February 2012 [wet]. –strands; Los Angeles County, off Torrance, Redondo Canyon, PV Trawl, T0 transect, ~33°48'50"N, 118°26'22"W, 137 m; coll. LACSD, station T0-137, 16 February 2012 [wet]. –strands; Los Angeles County, Santa Monica, 33°52'30"N, 118°34'00"W, 25' otter trawl, 73 m; coll. R/V 'Agassiz', T Matsui, M-15, OT-10, 29 March 1974; SIO/BIC CO1246 [wet].

Two specimens examined, SIO/BIC CO1856; SIO/BIC CO1859, had no collection data that could be found.

#### Thesea variabilis Studer, 1894

Material examined. No apparent specimens of this species in SBMNH collection.

**Other material examined.** – 1 colony; USA, California, San Diego County, 400 m off shore of Scripps Institution, 50 m; coll. C Limbaugh, 23 July 1954; USNM 50633 [dry]. –single colonies in 3 lots; USA, California, San Diego County, La Jolla Canyon, South Wall, 43 m; coll. R Ghilardi and J Stewart, 02 January 1957; USNM 50634 [1 wet lot, 2 dry lots].

### Callogorgia kinoshitai (Kükenthal, 1913)

Material examined. 6 lots. USA, Oregon – Lane County, off the Oregon coast, 61.59 miles NW of light house and Sealion Cave, 44°02'11"N, 125°05'09"W, 1,400–1,600 m; coll. R/V 'Yaquina', Cruise 6710, 30 October 1967; SBMNH 422982 [wet]. USA, Washington – Clallam County, approximately 105 mi W of Cape Flattery, 48°36'30"N, 127°00'48"W, 2,189 m; coll. R Ruff, OSU, R/V 'Yaquina', Cruise DWD/BMT 9 = OSU BMT 558, 11 September 1971; SBMNH 422990 [wet]. –Clallam County, approximately 105 mi W of Cape Flattery, 48°36'30"N, 127°00'48"W, 1,998 m; coll. R Ruff, OSU, R/V 'Yaquina', Cruise DWD/BMT 10 = OSU BMT 559, 11 September 1971; SBMNH 422991 [wet].

**Other material examined.** – 1–2 fragments; USA, California, San Diego County, San Diego, Point Loma light-house, ~32°42'00"N, 117°14'00"W, (N. 82°30' E. 5.9 miles), 220–240 m; coll. R/V 'Albatross', station 4356, 1904; SIO/BIC CO991 [wet]. –3 fragments; USA, California, San Diego County, San Diego, Point Loma light house, ~32°42'00"N, 117°14'00"W, no depth recorded; coll. 'Albatross', station 4359, 1904; SIO/BIC CO1808 [wet]. –several fragments; USA, California, San Diego County, off San Diego, off Point Loma light-house, 33°02'15"N, 120°36'30"W, 2,468 m; coll. 'Albatross', station 4391, 1904; SIO/BIC CO1809 [wet]. **Other material, not examined.** – Eastern S Pacific, South America, Zapallar, Chile, 350 m; 27 September 1977; USNM 75125 [wet]. –USA, California, San Diego County, San Diego, Point Loma, 245–283 m; 15 March 1904; USNM 30084 [wet]. –USA, California, San Diego County, San Diego Trough, ? station R-37, 32°26'02"N, 117°25'54"W, 1,194–1,097 m, by otter trawl, in mud; coll. F Rokop, R/V 'Agassiz', 21 April 1971; SIO/BIC CO1523. –USA, California, Monterey County, Pacific Grove, Monterey Bay, Point Piños, 36°38'16"N, 121°55'46"W, 1,381–1,752 m; 27 May 1904; USNM 49611 [wet]. –USA, California, Monterey County, Pacific Grove, Monterey Bay, Point Piños, 36°38'16"N, 121°55'46"W, 1,575–1,942 m; 31 May 1904; USNM 30030 [wet]. –USA, California, Monterey County, Pacific Grove, Monterey Bay, Point Piños, 36°38'16"N, 121°55'46"W, 1,575–1,942 m; 31 May 1904; USNM 43126 [wet]. –USA, California, Monterey County, Pacific Grove, Monterey Bay, Point Piños, 36°38'16"N, 121°55'46"W, 1,575–1,942 m; 31 May 1904; USNM 43126 [wet]. –USA, California, Monterey County, Pacific Grove, Monterey Bay, Point Piños, 36°38'16"N, 121°55'46"W, 1,575–1,942 m; 31 May 1904; USNM 43126 [wet]. –USA, California, Monterey County, Pacific Grove, Monterey Bay, Point Piños, 36°38'16"N, 121°55'46"W, 1,575–1,942 m; 31 May 1904; USNM 58986 [dry]. –USA, California, San Francisco Bay, 37°48'36"N, 122°14'15"W (label error: Monterey Bay), 1,609–1,476 m; 20 March 1975; USNM 75231 [wet].

-SIO/BIC CO946 is also identified as this species, but no locality data could be found.

# Parastenella pacifica Cairns, 2007

**Material examined.** 1 lot. **USA, Oregon** – numerous colonies/fragments; Oregon, Lane County, off Oregon coast, 58.14 mi NW of Sealion Cave, 44°21'53"N, 125°14'01"W, 2,086 m; coll. R/V 'Acona', OSU, Cruise 6408, haul OTB 41; SBM-NH 422983 [wet].

# Parastenella ramosa (Studer, 1894)

Material examined. No apparent specimens of this species in SBMNH collection.

**Other material examined.** – 1 colony; N Pacific Ocean, USA, off Central California coast, Rodriquez Seamount, 34°02'26"N, 121°02'24"W, 735 m; 16 October 2003; USNM 1102453 [wet]. –2 colonies; N Pacific Ocean, USA, off Central California coast, Rodriquez Seamount, west of San Miguel Passage, 34°03'06"N, 121°03'00"W, 663 m; 13 October 2003; USNM 1027058 [wet]. –fragment; N Pacific Ocean, USA, off Central California, Rodriquez Seamount, ~34°03'11"N, 121°03'04"W, 664.6 m; coll. MBARI staff, PI, D Clague, 14 October 2003; MBARI T628-A12 [wet]. –1+ colony; USA, California, Monterey County, Monterey Bay, 36°27'09"N, 122°01'28"W, 950 m; coll. W Nybakken, 27 October 1988; MLML C0177 [wet].

# Plumarella longispina Kinoshita, 1908

**Material examined.** -33 lots. **USA, California** – fragment; San Diego County, W end of Cortes Bank, dredge–rocks, 32°33'24"N, 119°15'13"W (end), 82 m; coll. R/V 'Velero IV', station 1882-49, 26 August 1949; SBMNH 422399 [wet]. –fragments; San

Diego County, W end of Cortes Bank, Snapper–Foraminifera sand, algae, 32°35'05"N, 119°18'52"W, no depth recorded; coll. R/V 'Velero IV', station 1876-49, 26 August 1949; SBMNH 422398 [wet]. -many fragments; San Diego County, 9.5 miles SW of Tanner Bank, 32°36'30"N, 119°20'00"W, loose rock, coralline, 131 m; coll. R/V 'Velero III', station 1346-41, 11 June 1941; SBMNH 422397 [wet]. -fragments; San Diego County, 9.5 miles NW of buoy, Cortes Bank, 32°33'15"N, 119°15'15"W, white sand, rock, 91 m; coll. R/V 'Velero III', station 1342-41, 10 June 1941; SBMNH 422395 [wet]. -1 colony, no base; Orange County, 33°32'47"N, 118°07'31"W, 216 m; coll. M Love, and party, with submersible 'Delta', 6 October 2005; with M Love's number: A6649; SBMNH 422402 [wet, with small tip in 95% alcohol for sequencing]. - fragment; Los Angeles County, Santa Catalina Island, 7.25 miles SE of Seal Rocks, 33°14'25"N, 118°10'45"W, 276–364 m; coll. R/V 'Velero III', station 1430-41, 25 September 1941; SBMNH 422396 [wet]. -10 fragments (3 lots); Los Angeles County, Santa Catalina Island, 2.5 to 7.5 miles SE of Seal Rocks, 33°17'30"N, 118°15'55"W, approx. 164 m; coll. R/V 'Velero III', station 1429-41, subset station (?) D1, D2 or D3, 25 October 1941; SBMNH 422394 [dry; 1 wet]. ]. –2 colonies in 2 lots; Los Angeles County, Santa Catalina Island, off Avalon, 33°20'40"N, 118°19'31"W, 155-182 m; coll. R Fay, by trawl, 31 January 1974; SBMNH 45553 [wet]. -1 fragment; Los Angeles County, Santa Catalina Island, Avalon, 33°20'40"N, 118°19'31"W, taken alive with beam trawl off PBM boat; coll. unknown; legit. P Brophy, 31 January 1971; SBMNH 45555 [wet, with second label, data below (\*)]. -multiple fragments; Los Angeles County, 15.42 miles, 248° T to Jewfish Point, Santa Catalina Island, 33°24'58"N, 118°01'00"W, 318 m; coll. R/V 'Velero IV', station 22790-75, 18 September 1975; SBMNH 422923 [wet]. -1 fragment; Los Angeles County, San Pedro Channel, 70 fathom Bank, 33°24'15"N, 118°01'15"W (end), rock, sponge, 156–235 m; coll. R/V 'Velero III', station 1212-40, 30 November 1940; SBMNH 422400 [wet]. -1 fragment; Los Angeles County, Santa Catalina Island, off Emerald Bay, in mud, 33°28'55"N, 118°30'05"W, 118–164 m; coll. R/V 'Velero III', Station 909-39, 29 January 1939; SBMNH 422393 [wet]. -1 colony; Los Angeles County, 4.5 miles, 113° T to Santa Barbara Island, N. Light, 33°30'55"N, 119°05'26"W (end), 255 m; coll. R/V 'Velero IV', station 24455-76, 7 March 1976; SBMNH 422922 [wet]. -1 colony; Los Angeles County, 6.7 miles, 330° T from N Light, Santa Barbara Island, dredge, tangles-2 large boulders and much small rock, rock bottom, 33°33'27"N, 119°04'00"W (end), 255 m; coll. R/V 'Velero IV', station 2062-51, 18 October 1951; SBMNH 422391 [wet]. –2 fragments; Los Angeles County, 10.4 miles, 351.5° T from N Light, Santa Barbara Island, dredge and tangles-mollusks, annelids, shrimps, Lovenia, brittle stars, mud bottom, 33°39'09"N, 119°03'00"W (end), 300 m; coll. R/V 'Velero IV', station 2061-51, 18 October 1951; SBMNH 422433 [dry]. - (\*)1 fragment; Santa Barbara County, Santa Barbara, 34°23'28"N, 119°41'39"W, 109–164 m; coll. P Brophy, 26 April 1974; SBMNH 422925 [DH 420 = SBMNH-07, dry]. -multiple colony fragments; Santa Barbara County, 6.25 miles SE of South Point, Santa Rosa Island, rocky bottom with alcyonarians, 33°51'00"N, 120°00'20"W, 84 m; coll. R/V 'Velero III', 1291-41, 11 April 1941; SBMNH 422432 [dry]. -1 colony; Santa Barbara County, 1.3 miles, 154° T from San Pedro Point, Santa Cruz Island, dredge-Ophiothrix, few mollusks and sponges, bottom sand, 34°00'57"N, 119°30'10"W (end),

55 m; coll. R/V 'Velero IV', station 3021-55, 2 April 1955; SBMNH 422392 [wet]. –1 colony, Santa Barbara County, no base; Santa Barbara Channel, soft coral–snail and growth in separate container, 34°02'40"N, 119°18'57"W, 150 m; coll. M Love, 28 September 2004 (photo taken); SBMNH 422401[wet]. **MEXICO, Baja California Sur (Pacific Coast)** – 1 fragment; 9.5 miles W of Punta Malarrimo (just S of Isla Cedros), dredge–rocks, sand bottom, 27°49'00"N, 114°42'09"W (end), 16 m; coll. R/V 'Velero IV', station 2024-51, 18 April 1951; SBMNH 422431 [dry]. **MEXICO, Baja California Norte (Pacific Coast)** – multiple fragments; 25.4 miles, 181° T from Punta Banda Light, 31°19'00"N, 116°44'00"W (end), 264 m; coll. R/V 'Velero IV', station 10986-66, 19 February 1966; SBMNH 422924 [wet].

Other material examined. - 7+ fragments; N Pacific Ocean, Mexico, Baja California Norte, Cabo Colnett, 30°58'00"N, 116°22'00"W, 100-101 m; coll. D Brown and party, by midwater trawl 20, 24 November 1964; SIO/BIC CO1690 [wet]. -several fragments; Mexico, Baja California Norte, 40-mile Bank, 32°00'08"N, 117°56'16"W., 183 m; coll. by dredge; 'EW Scripps', 10 June 1938; Shepard No. 69, Access. No. BI 38-1, SIO/BIC CO403[wet]. - N Pacific Ocean, USA, California, San Diego County, San Diego, Point Loma, 32°41'57"N, 117°14'51"W, 179-402 m; 15 March 1904; USNM 25429 [wet]. – N Pacific Ocean, California, Channel Islands area, 33°45'51"N, 119°12'16"W, 250 m; 30 October 2002; USNM 1026795 [wet]. -N Pacific Ocean, California, Los Angeles County, Channel Islands, Santa Catalina Island, Gulf of Catalina, Dakins Cove (Avalon), ~33°20'47"N, 118°19'30"W, 146 m; 8 April 1897; USNM 49591 [dry]. -N Pacific Ocean, California, Los Angeles County, Channel Islands, Santa Catalina Island, Gulf of Catalina, Avalon, 155–183 m; 31 January 1974; USNM 73755 [wet]. - N Pacific Ocean, California, Monterey County, Monterey Bay, in Channel, 732 m; 9 July 1925; USNM 77285 [dry]. -N Pacific Ocean, California, Mendocino County, Point Arena, 38°57'45"N, 124°03'05"W, 437 m; 25 September 1890; USNM 49585 [wet]. -multiple colonies; North Eastern Pacific, off Oregon coast, Heceta Bank, hard bottom, 43°57'10"N, 124°50'35"W, 135 m; coll. A Valdés by ROV, RV 'Ronald H. Brown' (NOAA) and S/V 'Ropos,' Dive 615, 10 July 2001; LACoMNH Marine Biodiversity processing center number 99 [wet].

Specific location data for ~six lots collected by OCNMS during May 2006 collecting expedition was not accessible; report was published in July 2007 (Marine Sanctuary Conservation Series, NMSP-07-04). This species was found in the Survey Sites numbered 1, 11, 30 and 31, all located within the Olympic 2 Essential Fish Habitat (EFH) Conservation Area. As well, a specimen was collected by OCNMS in July 2008; data not available for publication at this time but is likely from the same area as the 2006 material. The 2008 material likely sent to NMNH, Smithsonian, for housing in the collection there.

# Primnoa pacifica Kinoshita, 1907

Material examined. No apparent specimens of this species in SBMNH collection.

**Other material examined.** –1 colony; USA, southern coast of California, San Diego County, off La Jolla, near Soledad Hill, ~32°51'21"N, 117°18'24"W, 205–234

m; coll. R/V 'Albatross', 8 March 1904; USNM 57557 [wet]. –1 colony; USA, California, Monterey County, Monterey Bay, 36°21'46"N, 122°07'51"W, 1,609 m; coll. McDonald, Anderson, Antrim, 20 March 1975; MLML C0118 [wet]; specimen sent from same event to the Smithsonian, NMNH, in 1979.

### Narella Gray, 1870

Material examined. No apparent specimens from this genus in SBMNH collection.

### Acanella Gray in Wright, 1869

Material examined. No specimens of this genus in collection at SBMNH.

### Isidella Gray, 1858

**Material examined.** 2 lots. **USA (Oregon, Alaska)** – 3 fragments; USA, Oregon, Curry County, 29.79 miles W of Gold Beach, 44°24'17"N, 125°00'38"W, 1,244 m; coll. R/V 'Yaquina', Cruise Y7002 B, OSU, 19 February 1970; SBMNH 422981 [wet]. –1 complete (broken) colony; USA, Alaska, Gulf of Alaska, Welker Seamount, 55°01'05"N, 140°19'11"W, 1,049 m; coll. A Baco-Taylor, using submersible 'Alvin', dive 4035, sample 24, 11 August 2004; SBMNH 369349; [dry]. (This latter det. by P Etnoyer as *Isidella tentaculum*, new species, labeled as the **Paratype**).

# Keratoisis Wright, 1869

**Material examined:** ~3 lots. **USA, California** – multiple fragments; USA, California, Monterey County, Monterey Bay, 5.4–5.8 miles, 314° T from Point Piños Light to Mid Point, 36°43'00"N, 122°01'45"W, 436–809 m; coll. R/V 'Velero IV', stations 7462-61 or 7463-61, 10 October 1961; SBMNH 422980 [wet].

**Other material examined.** – 1 fragment; Eastern N Pacific, USA, California, Jasper Seamount, 30°21'54"N, 122°44'02"W, 1,375–1,910 m; coll. H Staudigel, by dredge, SEATOMADO Expedition, 2 November 1980; SIO CO2246 [wet]; this specimen could very likely be *Keratoisis (Bathygorgia) profunda* Wright. –fragments; Eastern N Pacific, USA, California, Fieberling Guyot, west of California Channel Islands, 32°23'25"N, 127°44'30"W, depth unknown; coll. unknown, 20 May 1991; USNM 93937 [wet].

# Lepidisis Verrill, 1883

Material examined. No specimens of this genus in collection of SBMNH.

**Other material examined.** – fragments; N Pacific Ocean, USA, California, Ventura/ Los Angeles Counties, Channel Islands, ~40 miles SW of San Nicholas Island, 32°31'08"N, 119°42'10"W, 950 m; coll. J Ljubenkov, date collected not reported; USNM 59821 [wet].

#### AUTHOR GUIDELINES

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- Electronic Journal Articles: Mallet J, Willmott K (2002) Taxonomy: renaissance or Tower of Babel? Trends in Ecology and Evolution 18 (2): 57-59. doi: 10.1016/ S0169-5347(02)00061-7.
- Paper within conference proceedings: Orr AG (2006) Odonata in Bornean tropical rain forest formations: Diversity, endemicity and applications for conservation management. In Cordero Rivera A (Ed) Forest and Dragonflies. Fourth WDA International Symposium of Odonatology, Pontevedra (Spain), July 2005. Pensoft Publishers, Sofia-Moscow, 51-78.
- **Book chapters:** Mayr E (2000) The biological species concept. In: Wheeler QD, Meier R (Eds) Species Concepts and Phylogenetic Theory: A Debate. Columbia University Press, New York, 17-29.
- **Books:** Goix N, Klimaszewski J (2007) Catalogue of Aleocharine Rove Beetles of Canada and Alaska. Pensoft Publishers, Sofia-Moscow, 166 pp.
- Book with institutional author: International Commission on Zoological Nomenclature (1999) International code of zoological nomenclature. Fourth Edition. London: The International Trust for Zoological Nomenclature.
- **PhD thesis:** Dalebout ML (2002) Species identity, genetic diversity and molecular systematic relationships among the Ziphiidae (beaked whales). PhD thesis, Auckland, New Zealand: University of Auckland.
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