

Systematics of the order Corallimorpharia (Cnidaria: Anthozoa)

by

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Abstract

Systematic position and status of Corallimorpharia in Hexacorallia have been controversial because members of Corallimorpharia have intermediate morphology between Actiniaria and Scleractinia. Inferences concerning monophyly and sister relationships of corallimorpharians using morphological and molecular characters have been inconsistent. The inconsistency may be caused by poor taxon sampling of Corallimorpharia. Doubts about the phylogeny of Corallimorpharia persist.

I conducted phylogenetic analyses using morphological and molecular data to provide a comprehensive investigation of phylogeny of Corallimorpharia. Morphological and molecular data were congruent, and all data sets support monophyly of Corallimorpharia, and sister relationship with Scleractinia. Within Corallimorpharia, two evolutionary lineages, cylindrical body corallimorpharians and discoidal body corallimorpharians, were recovered.

Due to the lack of unique morphological characters defining Corallimorpharia, the scleractinian skeleton, which is the only character to separate Corallimorpharia from Scleractinia, is essential to determine the hierarchical rank of Corallimorpharia in Hexacorallia. One hypothesis is that the scleractinian skeleton is not homologous in all scleractinians, and therefore is not phylogenetically meaningful in defining

Scleractinia. The hypothesis is supported by evidence from the fossil record, molecular phylogeny of Scleractinia, and environmental effects on calcification.

Therefore, I propose Corallimorpharia and Scleractinia are suborders of the order Madreporaria, as Schmidt (1974) suggested. In Corallimorpharia, there has been no consensus on the number of valid family and genera. I therefore provide a taxonomic revision at the genus-level based on re-examination of type material. I used five morphological character categories that are phylogenetically meaningful. The type species of each genus is redescribed for those known in less detail and diagnostic keys to genera and families are provided. I conclude that there are three valid families and 11 valid genera in suborder Corallimorpharia.

The revision at the genus level is the first step to revise classification at the species level. There is no consensus in the number of valid species in most corallimorpharians genera. There are 41 nominal species in Corallimorpharia.

Taxonomic revision at the species level will provide information about diversity and biogeography of corallimorpharians.

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Table of contents

Acknowledgments	5
Table of contents	7
List of figures	9
List of tables	11
Chapter I. Introduction	12
Chapter II. Morphology of Corallimorpharians	25
2-1. General morphology	25
2-2. Tentacles	28
2-3. Cnidae	32
Chapter III. Generic revision of the Corallimorpharia	36
3-1. Introduction	40
3-2. Material	44
3-3. Methods	48
3-4. Results and Discussion	50
Family Corallimorphidae	52
Family Ricordeidae	75
Family Discosomatidae	83
Chapter IV. Phylogeny of the Corallimorpharia	124
4-1. Taxon sampling and character selection	124
4-2. DNA extraction and PCR amplification	130
4-3. Sequencing	132

4-4. Alignment	132
4-5. Phylogenetic analyses	132
4-6. Results	136
4-7. Discussion	146
Chapter V. Conclusion	156
References	159
Appendix 1. Data matrix of morphological characters	180
Appendix 2-5. Sequence alignments	183

List of figures

Figure	1-1.	Schematic cross-section of hexacorallian orders	13
Figure	1-2.	Body forms of corallimorpharians	14
Figure	1-3.	Hypothesis on phylogeny of the Corallimorpharia	17
Figure	1-4.	Phylogenetic hypothesis of systematics of the Corallimorpharia ...	20
Figure	2-1.	Oral view of corallimorpharians	26
Figure	2-2.	Types of tentacle-free zones on oral disc	27
Figure	2-3.	Tentacle shapes	30
Figure	2-4.	Longitudinal section of oral disc of <i>Discosoma neglecta</i>	31
Figure	2-5.	Types of cnidae in Corallimorpharia	35
Figure	3-1.	Distribution of corallimorpharians	51
Figure	3-2.	<i>Corynactis viridis</i> Allman, 1846	59
Figure	3-3.	<i>Corallimorphus profundus</i> Moseley, 1877	63
Figure	3-4.	<i>Pseudocorynactis caribbeorum</i> den Hartog, 1980	68
Figure	3-5.	<i>Sideractis glacialis</i> Danielssen, 1890	71
Figure	3-6.	<i>Nectactis singularis</i> Gravier, 1918	74
Figure	3-7.	<i>Ricordea florida</i> Duchassaing and Michelotti, 1860	82
Figure	3-8.	<i>Discosoma nummiforme</i> Rüppel and Leuckart, 1828	90
Figure	3-9.	<i>Discosoma fowleri</i> (Fowler, 1889)	95
Figure	3-10.	<i>Discosoma neglecta</i> (Duchassing and Michelotti, 1860)	99
Figure	3-11.	<i>Orinia torpida</i> Duchassaing and Michelotti, 1860	107
Figure	3-12.	<i>Actinotryx sanctithomae</i> Duchassaing and Michelotti, 1860	108

Figure 3-13.	<i>Amplexidiscus fenestrafer</i> Dunn and Hamner, 1980	113
Figure 3-14.	<i>Rhodactis rhodostoma</i> (Ehrenberg, 1834)	119
Figure 3-15.	<i>Metarhodactis boninensis</i> Carlgren, 1943	123
Figure 4-1.	Strict consensus tree of 12 most parsimonious trees based on morphological characters	140
Figure 4-2.	Maximum likelihood tree generated based on 18S rDNA data	141
Figure 4-3.	Maximum likelihood tree generated based on 28S rDNA data	142
Figure 4-4.	Maximum likelihood tree generated based on 16S mtDNA data	143
Figure 4-5.	Strict consensus tree of 2 most parsimonious trees based on combined molecular data	144
Figure 4-6.	Maximum likelihood tree generated based on combined molecular data	145

List of tables

Table 3-1.	Comparisons of classification schemes	37
Table 3-2.	Comparisons of type species of nominal genera	41
Table 3-3.	Type specimen of the type species for each nominal genus	46
Table 4-1.	Taxa included in morphological analysis	127
Table 4-2.	Taxa included in molecular analyses	128
Table 4-3.	Primer sequences used	131
Table 4-4.	Thermoprofiles for PCR reactions	131

CHAPTER I. INTRODUCTION

Corallimorpharia is an order of anthozoan subclass Hexacorallia. Other members of Hexacorallia are Actiniaria (sea anemones), Ceriantharia (tube anemones), Zoanthidea (zoanthids), Antipatharia (black corals), and Scleractinia (stony corals). Members of Actiniaria, Corallimorpharia, and Scleractinia have paired monomorphic mesenteries that are added in couples around the circumference of the animal during ontogeny, while paired mesenteries in Zoanthidea are not monomorphic, and those in other hexacorallians are not paired and coupled (Figure 1-1).

Members of Corallimorpharia, often called coral-like sea anemones, are solitary or clonal polyps without a skeleton. The body is cylindrical (Figure 1-2, A and B) or discoidal (Figure 1-2C), and the size ranges from 5 to 10 mm oral disc width up to 450 mm. The column is smooth and soft or firm. The tentacles are retractile or non-retractile, and have or lack acrospheres (globular ends that contain dense nematocysts). In the coelenteric space, the mesenteries are numerous and often irregularly arranged. The musculature is very weakly developed. The nematocyst composition is spirocysts, holotrichs, and microbasic *b*- and *p*-mastigophores. Corallimorpharians are widely distributed from tropical to polar areas, and from shallow to deep water. The deepest record of a corallimorpharian species is *Nectactis singularis*, a specimen of which was collected at 5005 m (Gravier, 1922).

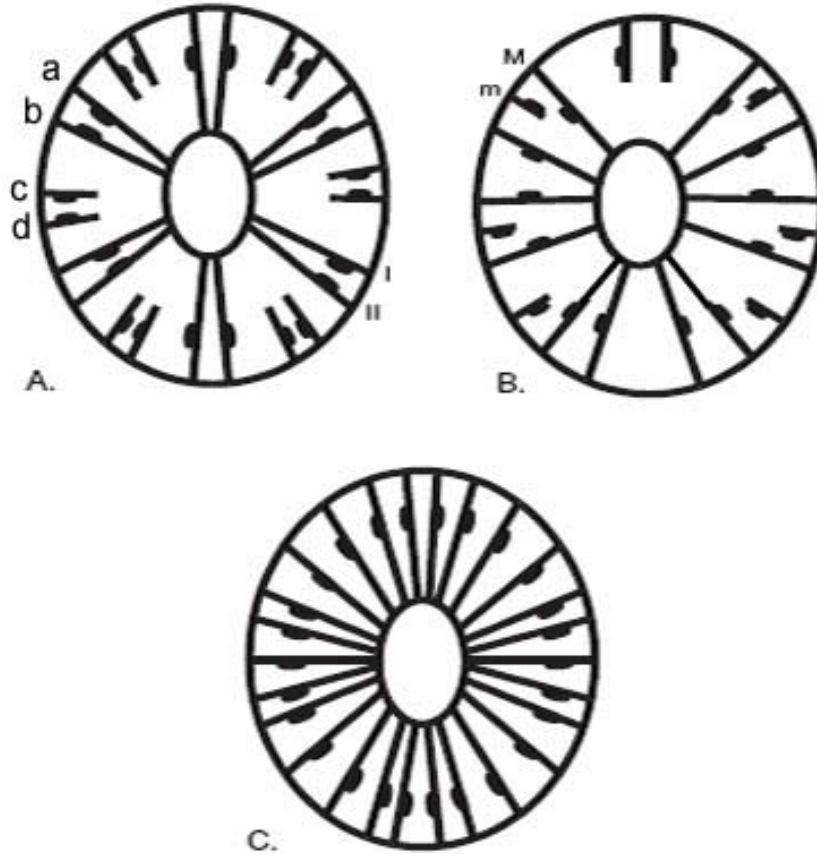


Figure 1-1. Schematic cross-section of hexacorallian orders (modified from Daly et al. 2003, p. 421, Figure 1). The radial lines represent mesenteries, the central oval represents the actinopharynx, and the filled oval on each mesentery represents the retractor muscle. A: hexamerously arranged paired, and coupled mesenteries in Actiniaria, Corallimorpharia, and Scleractinia. Mesenteries labeled a, b, I, and II are complete; c and d are incomplete; a and b, c and d, and I and II are paired; I and II are coupled with a and b; B: hexamerously arranged paired, and coupled mesenteries in Zoanthidea. Mesenteries labeled M and m are a dimorphic pair; C: unpaired coupled arrangement of Ceriantharia.

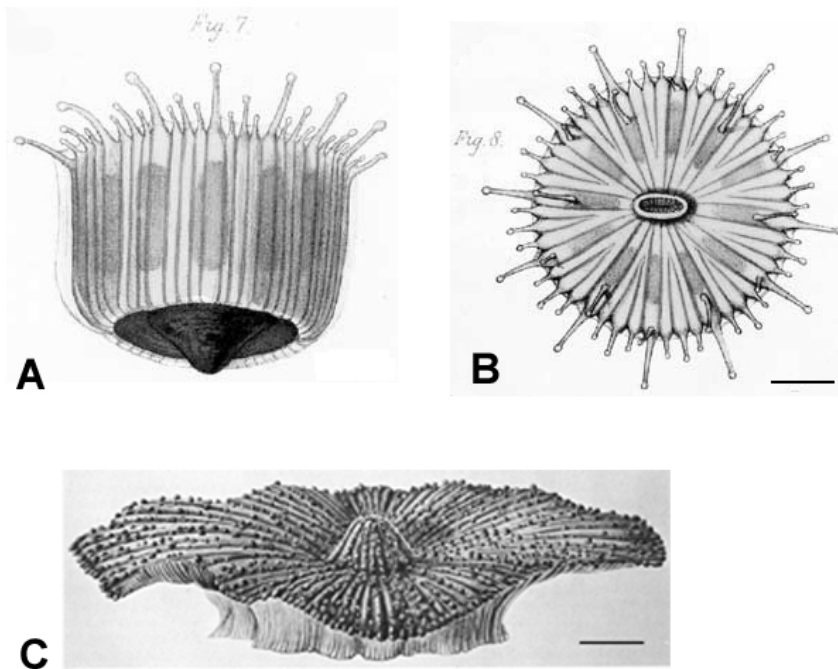


Figure 1-2. Body forms of corallimorpharians. A: side view of *Corallimorphus profundus* Moseley, 1877; B: oral disc of *Corallimorphus profundus* Moseley, 1877 (Moseley, 1877, Plate XLV, fig. 7, fig. 8); C: *Actinodiscus neglecta* (Duchassaing and Michelotti, 1860) (Cutress, 1979, p. 97, Fig. 3). Scale bar = 10 mm.

Corallimorpharians may dominate benthic communities in both temperate regions (Chadwick, 1991) and tropical regions (den Hartog, 1980). In particular, on coral reefs, corallimorpharians often and are abundant in shallow water, where they form aggregations (den Hartog, 1980; Chadwick-Furman and Spiegel, 2000; Muhando et al., 2002). Some corallimorpharians reproduce asexually so can increase their population relatively quickly. They can endure physical stresses such as exposure to

air during low tides better than stony corals (Chadwick, 1991; Muhando et al., 2002). Some corallimorpharians are aggressive. Mesenterial filaments may be extruded through the tips of the discal tentacles and the mouth when the animal is disturbed (Elliot and Cook, 1989; Fautin and Mariscal, 1991; personal observation). Extruded mesenterial filaments may digest either a prey or a potential competitor for space -- often another anthozoan (Lang, 1973; Logan, 1984; Chadwick, 1987) -- outside of the body. The aggressiveness, asexual reproduction, and high tolerance to environmental stress may be competitive advantages of corallimorpharians in shallow waters: corallimorpharians can rapidly occupy recently opened space caused by natural and/or anthropogenic disturbances on coral reefs (den Hartog, 1997; Langmead and Chadwick, 1999; Kuguru et al., 2004).

OBJECTIVES

The purpose of this study was to evaluate the systematic position and status of the Corallimorpharia within Hexacorallia. To clarify its membership, I revised the classification of the order. The revision includes identifying new characters for genus-level diagnosis and redescriptions of genera based on type species. The data gathered from the revision were used for phylogenetic analyses.

PHYLOGENY OF THE CORALLIMORPHARIA

The systematic position and taxonomic status of the Corallimorpharia have been debated. Corallimorpharians have morphology intermediate between the members of the orders Actiniaria and Scleractinia (Dunn, 1982). A corallimorpharian resembles a sea anemone in lacking a calcareous skeleton, and the tentacle arrangement of most corallimorpharians is similar to that of an actinarian of the family Stichodactylidae, in that multiple tentacles arise from the space between members of a mesenterial pair and one tentacle arise from the space between mesenteries of two adjacent pairs (Duerden, 1898; den Hartog, 1980). However, the internal anatomy of a corallimorpharian is less similar to that of a sea anemone than to that of a stony coral. Most actinarians have well-developed basilar muscles and ciliated filaments on the mesenteries (Dunn, 1981). By contrast, a corallimorpharian and a stony coral lack well-developed basilar muscles and ciliated filaments (den Hartog, 1980).

Additionally, the composition and distribution of nematocysts of corallimorpharians are more like those of scleractinians than those of actinarians; both scleractinians and corallimorpharians bear many large holotrichs in their mesenterial filaments (Duerden, 1898; den Hartog, 1980).

Four possible hypotheses of the systematic position of corallimorpharians have been considered: Corallimorpharia is monophyletic and forms an order (Figure 1-3C); Corallimorpharia forms a monophyletic group but belongs entirely within Actiniaria (Figure 1-3A) or Scleractinia (Figure 1-3B); Corallimorpharia is not monophyletic and belongs partly to Actiniaria and partly to Scleractinia (Figure 1-3D).

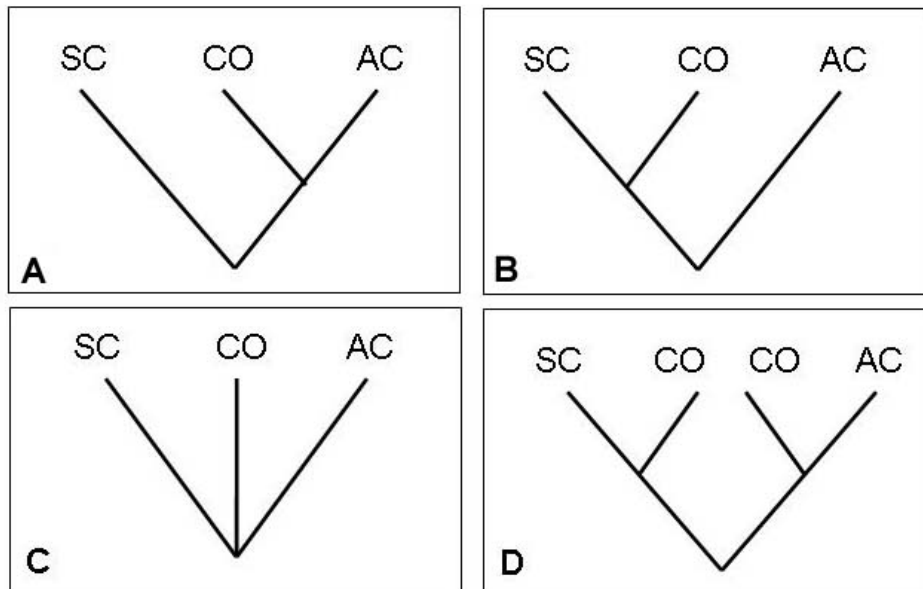


Figure 1-3. Hypothesis on phylogeny of the Corallimorpharia. AC indicates Actiniaria; CO indicates Corallimorpharia; SC indicates Scleractinia.

Corallimorpharia has been considered a subgroup within Actiniaria by some (Figure 1-3A). Andres (1883) united all the forms that have radially arranged tentacles, including some corallimorpharians, in family Stichodactylinae [sic] of order Actiniaria. Duerden (1898, 1900) considered corallimorpharians closely related to stichodactyline anemones based on similarities of tentacle arrangement between corallimorpharian genus *Ricordea* Watzl, 1922 and actinarian genus *Stichodactyla* Brandt, 1835. The stichodactylines have been assigned to various higher systematic ranks by later authors: Haddon and Shackleton (1893) and Haddon (1898) called them an order, Carlgren (1900) a tribe, and Duerden (1900) a sub-order.

However, recognizing similarities of internal anatomy and nematocysts between Scleractinia and species currently included in the Corallimorpharia, scientists such as Krempf (1904), Stephenson (1921, 1922), Weill (1934), and Hand (1966) considered Corallimorpharia as a subgroup in Scleractinia (Figure 1-3A). Krempf (1904) concluded that corallimorpharians represent scleractinian corals without a skeleton, and he proposed the names Sclerocorallia for Scleractinia and Asclerocorallia for Corallimorpharia. Stephenson (1922) suggested classifying the Corallimorpharia among the Madreporaria (= Scleractinia). Schmidt (1972, 1974) concluded that Corallimorpharia and Scleractinia should be included in a higher group, Madreporaria, based on the composition of nematocysts. den Hartog (1980) concluded that Corallimorpharia should be included in the Scleractinia as a sub-order. Romano and Cairns (2000) and Won et al. (2001) inferred Corallimorpharia may belong to

monophyletic Scleractinia based on a mitochondrial gene (16S mtDNA) (Romano and Cairns, 2000) and a nuclear ribosomal gene (18S rDNA) (Won et al., 2001, Figure 1-4C). Medina et al. (2006) supported the monophyly of Corallimorpharia, but within Scleractinia (Figure 1-4E). Although Duerden (1898) had noticed the similarity of Corallimorpharia and Scleractinia, he maintained the corallimorpharians in the Stichodactylinae.

Corallimorpharia also has been considered a separate group, equal in rank to Actiniaria and Scleractinia (Figure 1-3C). Carlgren (1940, 1943, 1949) listed four differences between the two groups: the calcareous skeleton, the tentacular arrangement, the cnidom, and the structure of the mesoglea. Wells and Hills (1956) accepted Carlgren's perspective. Daly et al. (2003) (Figure 1-4D) concluded that Corallimorpharia is an order as currently accepted based on phylogeny using combined data sets of morphological and molecular data, they but stated the need for more extensive taxon sampling.

Corallimorpharia has been considered as a non-monophyletic group (Figure 1-3D) by some. Fautin and Lowenstein (1994) supported the non-monophyly of corallimorpharians and paraphyletic assemblage of corallimorpharians and scleractinians based on radioimmunological data (Figure 1-4A); Chen et al. (1995) suggested a polyphyletic assemblage of corallimorpharians and actinarians based on sequences of nuclear large subunit ribosomal gene (28S rDNA) (Figure 1-4B).

Inferences concerning monophyly and sister relationships of corallimorpharians using morphological and molecular characters have been inconsistent. The inconsistency may be caused by poor taxon sampling of Corallimorpharia. Doubts about the phylogeny of Corallimorpharia persist.

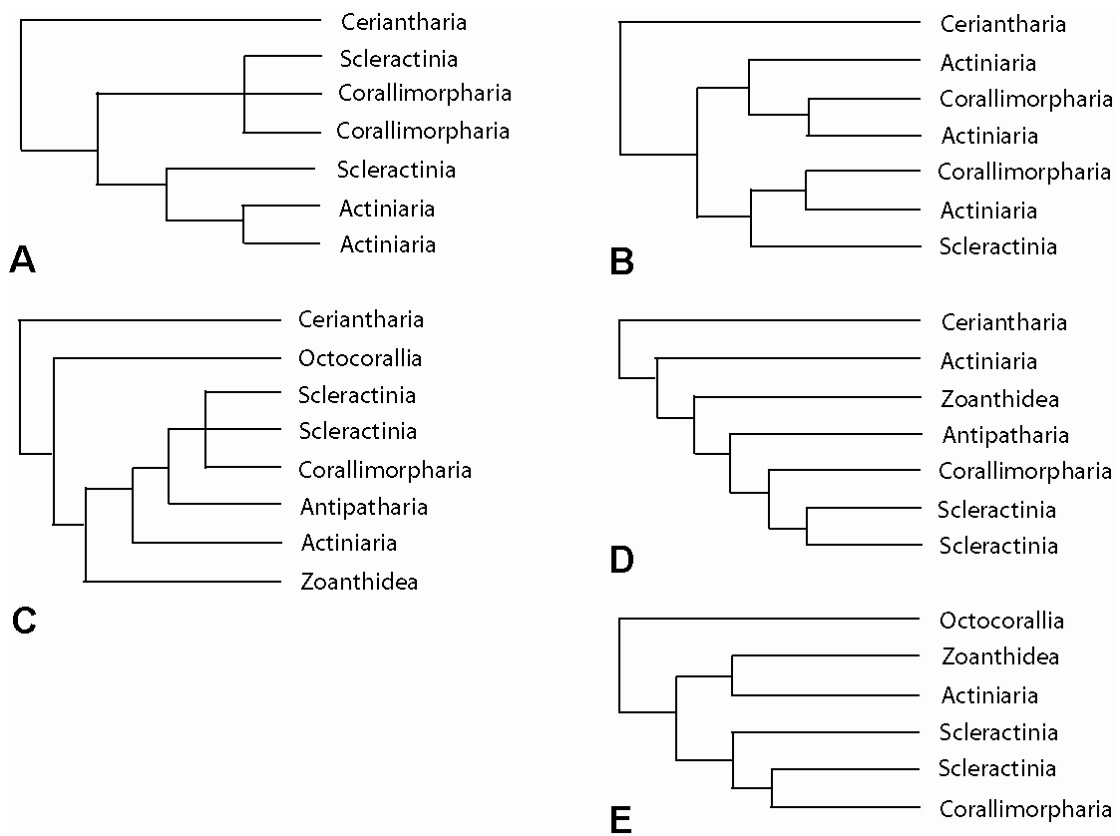


Figure 1-4. Phylogenetic hypothesis of systematics of the Corallimorpharia. A: Fautin and Lowenstein, 1994; B: Chen et al., 1995; C: Won et al., 2001; D: Daly et al., 2003; E: Medina et al., 2006.

My study aimed to include representatives of every valid genus in Corallimorpharia to resolve phylogenetic questions of monophyly and sister relationships of the order. The study was conducted using morphological and molecular characters (see Chapter IV). I compiled a data matrix of molecular (18S rDNA, 28S rDNA, and 16S mtDNA), and 33 morphological characters of corallimorpharians, actiniarians, and scleractinians. Morphological characters include internal anatomy of scleractinian polyps, which is the only character that is available to compare among the three orders. Scleractinian polyp anatomy has not been studied extensively and information about it is almost absent in the literature except for some studies in the late nineteenth century (eg., Duerden, 1898) because characters traditionally used for taxonomy and phylogeny of Scleractinia are features of the calcareous skeleton. The data were analyzed under maximum parsimony and maximum likelihood criteria, parsimony analysis for morphology, and parsimony and likelihood analyses for molecular data sets.

I inferred that Corallimorpharia is a monophyletic taxon, and according to cladistic inference based on combined data set, Scleractinia is the sister group of Corallimorpharia. The calcareous exoskeleton is traditionally considered as an essential attribute of membership in Scleractinia (Duerden, 1898; Stephenson, 1921); therefore all extent hexacorallian polyps with a calcareous skeleton belong to Scleractinia. However, the traditional view has been challenged based on the

morphological similarities between a corallimorpharian polyp and a scleractinian polyp, and molecular phylogeny of Scleractinia. Studies on molecular phylogeny of Scleractinia support the idea that the skeleton may have arisen multiple times, and may not be homologous between major clades of corals (Fautin and Lowenstein, 1994; Romano and Palumbi, 1996; Romano and Cairns, 2000; Stanley and Fautin, 2001). In fact, the phylogenetic value of the calcareous skeleton has been re-evaluated in the cnidarian class Hydrozoa: the ability to form a calcareous skeleton is no longer considered a major taxonomic feature. All hydrozoans with a calcareous skeleton were initially grouped in Hydrocorallina, but each of two subgroups, Milleporina and Stylasterina, is now considered more closely related to a skeletonless taxon than to the other. Thus calcareous skeletons have been lost or have evolved independently (Petersen, 1979; Lindner, 2003). Similarly, Foraminifera, previously thought to include only shelled amoebae, includes naked species (Pawlowski et al., 1999).

TAXONOMIC REVISION OF THE CORALLIMORPHARIA

There are literature inventories of corallimorpharians (Stephenson, 1922; Carlgren, 1949; den Hartog, 1980; den Hartog et al., 1993; Fautin, 2006). However, the species composition and the number of valid families and genera have been unclear due to the inconsistency in usage of names. The descriptions of some genera were too short and simple to distinguish genera, so it has been difficult to place species in the proper genus.

I examined the type specimens of type species of all 16 nominal genera. Examination of type specimens allowed me to identify new characters to distinguish each genus, to emend descriptions of genera of uncertain validity, and to gather morphological characters for phylogenetic analyses. Information on type specimens is available from “Hexacorallians of the World” (Fautin, 2006). In case no type specimens were designated or type material is damaged, I examined non-type specimens of type species borrowed and collected. I collected specimens of *Actinotryx sanctithomae* Duchassing and Michelotti, 1860, *Ricordea florida* Duchassing and Michelotti, 1860, and *Rhodactis rhodostoma* (Hemprich and Ehrenberg in Ehrenberg, 1834), the type species of three genera. Collecting specimens from the field provided much information such as color, habitat, and symbiotic associations.

Based on comparative morphology of the type species, I agree with authors such as Stephenson (1922), Carlgren (1949), den Hartog (1980), and den Hartog et al. (1993) on the status of nine genera. Seven genera, *Corynactis*, *Corallimorphus*, *Pseudocorynactis*, *Nectactis*, *Sideractis*, *Ricordea*, and *Amplexidiscus*, are valid; two genera, *Sphincteractis* and *Isocorallion*, are invalid. The validity of the seven remaining genera is questionable. All those genera are in family Discosomatidae. Most genera in the family have been confused with and are in partial synonymy each other because the brief original descriptions provide only limited criteria for distinguishing genera.

The validity of the seven genera is evaluated based on five phylogenetically meaningful morphological character categories. The explanations of the characters, diagnostic features, and detailed discussion of each of the seven genera are in chapter III. The type species of each genus is redescribed for those known in less detail, its cnidae are diagnosed, and taxonomic/nomenclature issues are discussed.

I recognize five genera in family Corallimorphidae, *Corynactis*, *Pseudocorynactis*, *Corallimorphus*, *Nectactis*, and *Sideractis*; five genera in family Discosomatidae, *Discosoma*, *Actinotryx*, *Rhodactis*, *Metarhodactis*, and *Amplexidiscus*; and one genus, *Ricordea*, in family Ricordeidae.

CHAPTER II. MORPHOLOGY OF CORALLIMORPHARIANS

2-1. General morphology

Cnidarian polyps are characterized as being at the “tissue grade of construction” (Hyman, 1940), which means their specialized cells are grouped into tissues, but the tissues do not compose organs or organ systems. In spite of the simple structure, the anatomy of corallimorpharian polyps can be quite complex.

Between the outer layer, ectoderm, containing many cnidae, and the inner layer, endoderm, is a supporting layer of gelatinous substance termed mesoglea (Shick, 1991). The mesoglea, secreted by the cells of the epithelia, may be very thin, or thick. The polyp has the oral disc at the distal end (Figure 2-1) and the pedal disc at the proximal end. A mouth is located at the center of the oral disc and is connected to a tubular short actinopharynx, while tentacles encircle or cover the oral disc. Tentacles can be differentiated into discal and marginal tentacles depending on the position: discal tentacles are situated on the oral disc and marginal tentacles are situated at the margin of the oral disc. Tentacles may cover most of the area of the oral disc, or there may be a tentacle-free zone on the oral disc. A tentacle-free zone is either among the discal tentacles or between discal and marginal tentacles (Figure 2-2). The internal cavity, or coelenteron, is divided by mesenteries, longitudinal sheets of tissue that extend from the column wall. The mesenteries extending from column wall to the

actinopharynx are complete, and incomplete mesenteries do not extend all the way to the actinopharynx (Carlgren, 1949). The free edge of the mesentery has unilobed mesenterial filaments that bear gland cells and cnidae. The musculature of corallimorpharians is very weakly developed or absent. The retractor muscle which runs longitudinally along the mesentery, is slightly convex on a transverse section, and consists of endodermal epitheliomuscular cells embedded in the mesoglea (Fautin and Mariscal, 1991). The marginal sphincter muscle, a circular muscle, is endodermal in corallimorpharians. The retractor and sphincter retractor muscles work together for contraction of a polyp: “the retractor effects rapid symmetrical depression of the oral disc” and “contraction of the sphincter acts as a drawstring and covers the retracted oral disc and tentacles” (Shick, 1991, p. 11).

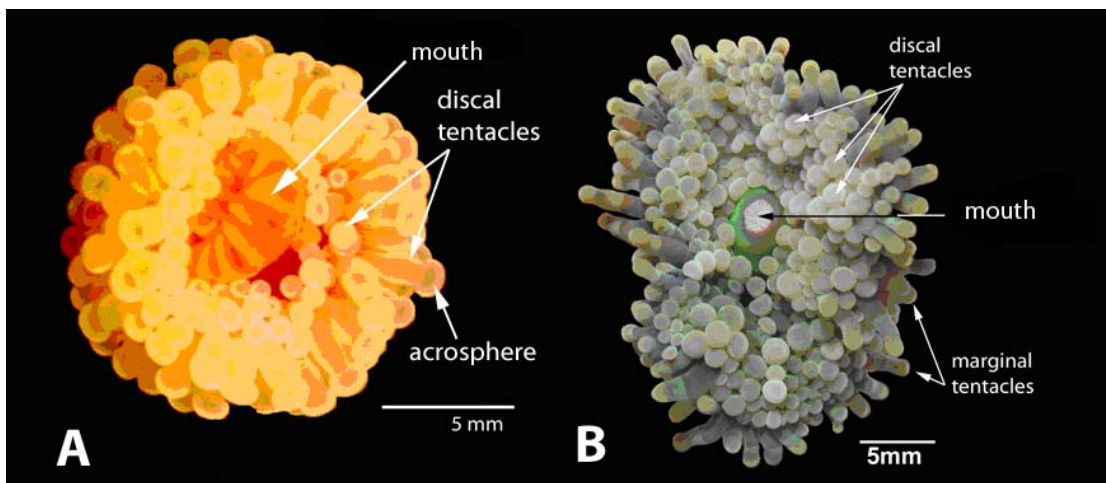


Figure 2-1. Oral view of corallimorpharians. A: *Corynactis californica* Carlgren, 1936; B: *Ricordea florida* Duchassing and Michelotti, 1860

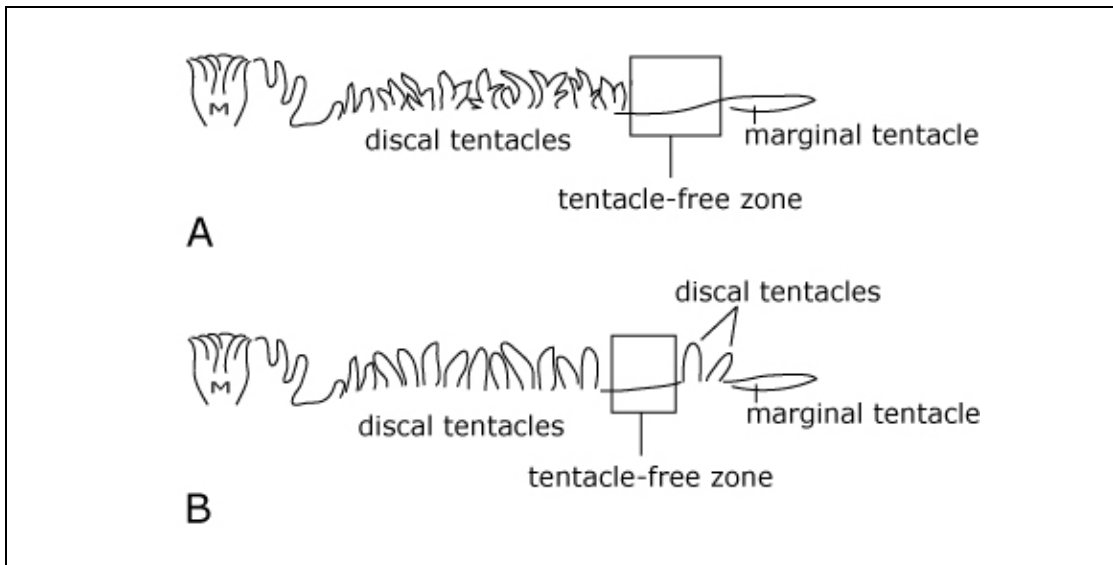


Figure 2-2. Types of tentacle-free zones on oral disc. A: between discal and marginal tentacles; B: among discal tentacles.

Cnidae are the defining characteristic of phylum Cnidaria, and are especially important characters in anthozoan taxonomy (Doumenc and Van Praët, 1987; Fautin, 1988; Fautin and Mariscal, 1991). The morphology, size, and distribution of cnidae are used to define groups within Corallimorpharia, and they are required for a description (Carlgren, 1900; Cutress, 1955; Mariscal, 1974; Fautin, 1988). Types of cnidae observed in corallimorpharians are described in section 2-3.

2-2. Tentacles

Tentacles are considered to be evaginations of all three layers of the oral disc (Fautin and Mariscal, 1974), or “any projection of the oral disc that occurs between one pair of mesenteries or between mesenteries of two adjacent pairs” (Ardelean, 2003, p. 36). In Anthozoa, at least five functions of tentacles are known: prey capture, defense, swimming, agonistic interactions, and harboring zooxanthellae (Fautin and Mariscal, 1974).

Tentacle shape is an important family- and genus-level character in corallimorpharian taxonomy. Comparison across corallimorpharian genera is complicated by non-standardized terminology concerning tentacles. In this study, I found four tentacle morphologies and standardized the terminology of each type.

Corallimorpharian tentacles can be either capitate or non-capitate. A capitate tentacle is well defined: a simple tentacle that possesses a globular end, called an acrosphere (Figure 2-3A). An acrosphere contains numerous nematocysts. A capitate tentacle is longer than other types of tentacles in corallimorpharians. Capitate tentacles are not associated with zooxanthellae. Capitate tentacles occur in family Corallimorphidae: they are retractile in *Corynactis* and *Pseudocorynactis*. In *Corallimorphus*, *Sideractis*, and *Nectactis* only non-retractile capitate tentacles have been reported from preserved specimens; retractability needs to be evaluated with live specimens.

Discoidal corallimorpharians have non-capitate tentacles. Non-capitate tentacles vary in morphology. Those tentacles have been described as small, bumpy, wart-like, or urn-like (e.g., Stephenson, 1922; Carlgren, 1900, 1949; den Hartog, 1980). Therefore, I elaborate on the terms for non-capitate tentacle shape.

The three types of non-capitate tentacles in Corallimorpharia are branched, digitiform, and papilliform. All three types of tentacles are non-retractile and harbor zooxanthellae. Branched tentacles (Figure 2-3B) vary morphologically among species in the number of branches and branching pattern, but they are short (length does not exceed 10 mm). Branched tentacles are common in family Discosomatidae.

Digitiform tentacles (Figure 2-3C) are finger-shaped: each is simple and slender with a blunt tip. Digitiform tentacles are common in family Discosomatidae. Digitiform tentacles and branched tentacles exist together in some corallimorpharians. For example, in the genus *Rhodactis*, marginal tentacles are digitiform and discal tentacles are branched. Papilliform tentacles (Figure 2-3D) are very short with blunt tips; their length is too small to measure, but they project from the surface of the oral disc. They are common in families Discosomatidae and Ricordeidae.

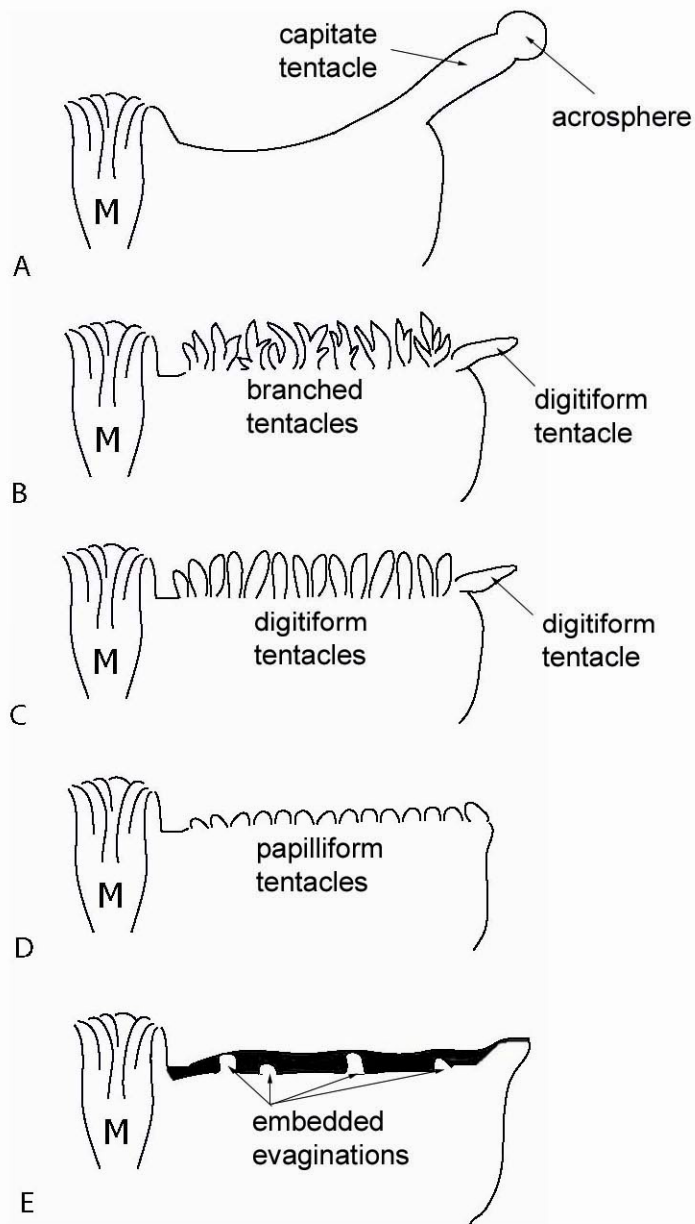


Figure 2-3. Tentacle shapes. A: a capitate tentacle; B: branched tentacles; C: digitiform tentacles; D: papilliform tentacles; E: embedded evaginations of endoderm of the oral disc (black layer indicates mesoglea). The thickness of mesoglea is not shown in A-D because it varies among species and among specimens.

I found evaginations of the endodermal layer of the oral disc that do not project from the surface of the oral disc: some of them can reach the surface of the oral disc, but they are embedded in thick mesoglea (represented as a black layer in figure 2-3E). These occurred in two small specimens of *Discosoma neglecta* (Carlgren, 1900). Based on histological sections of these specimens (Figure 2-4), it is clear that embedded evaginations 1) are hollow, 2) communicate with the coelenteric space like other types of tentacles, and 3) harbor zooxanthellae. I conclude that an embedded evagination is a developmental stage of a papilliform tentacle. In other similar-sized or larger specimens of the species, I observed papilliform discal tentacles covering the oral disc (Figure 4-10).

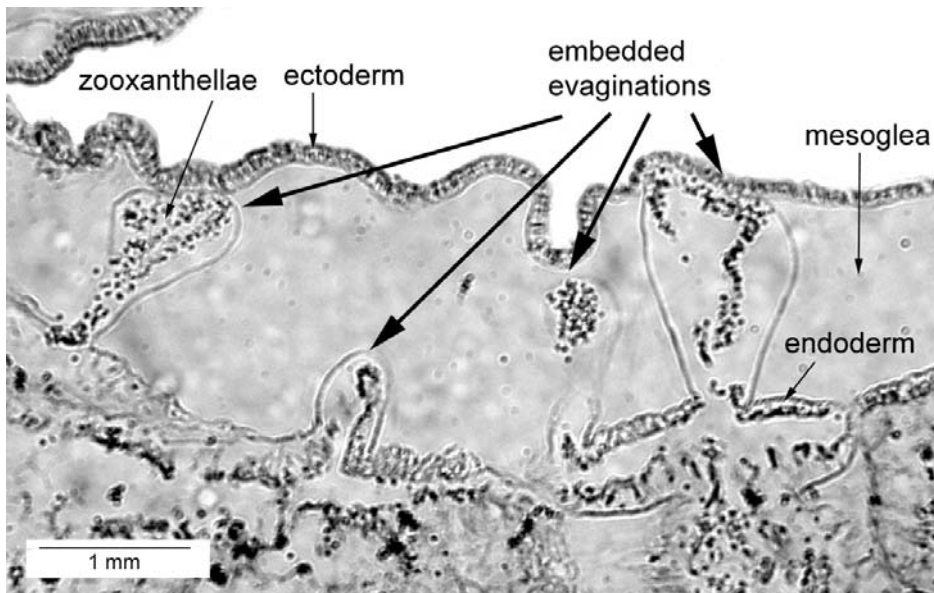


Figure 2-4. Longitudinal section of oral disc of *Discosoma neglecta* (Carlgren, 1900).

2-3. Cnidae

Cnidae are membrane-enclosed cellular secretions of the Golgi apparatus, consisting of a capsule and an eversible tubule (Slautterback and Fawcett, 1959; Slautterback, 1961; Skaer, 1973). Cnidarian systematists have considered types of types cnidae an important systematic character and have defined the cnidom as the census of cnidae present in a species (Weill, 1934). Cnidom and information on the size and distribution of cnidae are now considered as a requirement for the description of virtually any soft-bodied anthozoan (Carlgren, 1900; Cutress, 1955; Mariscal 1974; Fautin 1988). The presence or absence of any major type of cnidae is of particular importance in ordinal, familial, and generic definitions (Carlgren, 1949; Cutress, 1955; Fautin, 1988). The cnidom and distribution of cnidae of corallimorpharians are major features that show a similarity with the Scleractinia.

Cnidae are classified in three major categories, spirocysts, nematocysts, and ptychocysts. Spirocysts and ptychocysts each comprise a single type of cnida. Spirocysts are present only in Anthozoa and ptychocysts are found only in one order of Anthozoa, Ceriantharia. Nematocysts are diverse: Weill (1934) divided them into 16 categories based on observations made through the light microscope primarily of the discharged tubule. Additional nematocyst types were subsequently identified (Carlgren, 1940; Cutress, 1955; Schmidt, 1972; Mariscal, 1974, den Hartog, 1980). Various systems of nomenclature have been devised to cope with this diversity,

including Stephenson's (1929), which was also used by den Hartog (1980) and Schmidt (1969, 1972), although, generally nematocyst classification is based on that of Weill (1934) with modifications made by Carlgren (1940), Cuttress (1955), and Mariscal (1974).

Following the classification and the terminology of Mariscal (1974), I identified the cnidae of corallimorpharians. According to Carlgren (1949), corallimorpharians contain spirocysts, atrichs, holotrichs, and microbasic *b*- and *p*- mastigophores. However, the higher resolution achieved by modern light microscopes and the scanning electron microscope have revealed that atrichs are spined; thus atrichs and holotrichs are actually the same (Cuttress, 1955; Westfall, 1965; Calder, 1974; Schmidt, 1974; Bigger, 1976; Marsical et al. 1977; Heeger et al., 1992; Östman et al. 1995; Östman, 2000). Therefore I identified four major types of cnidae in corallimorpharians: spirocysts, microbasic *b*- and *p*- mastigophores, and holotrichs. Within holotrichs, three types were distinguished that differed in capsule size and coiling patterns of the tubule.

Definition of types of cnidae of corallimorpharians:

Holotrich: type of cnida defined by a tubule with spines along the entire length.

Type I (Holotrichs I, Figure 2-5A): tubule coiled into three or four figure eights. Length of capsule up to 250 μm .

Type II (Holotrichs II, Figure 2-5B): tubule coiled into three to ten loops. Length of capsule around 100 μm .

Type III (Holotrichs III, Figure 2-5C): tubule densely coiled into numerous loops in capsule. Length of capsule around 100 μm .

Microbasic *b*-mastigophore (Figure 2-5E): type of cnida defined by a tubule with a barbed, basal shaft less than 3 times capsule length. No V-shaped notch at base of shaft in undischarged state; shaft tapers into tubule in discharged state.

Microbasic *p*-mastigophore (Figure 2-5F and 2-5G): type of cnida defined by a tubule with a barbed, basal shaft less than 3 times capsule length. Smooth tubule. V-shaped notch at base of shaft in undischarged state; shaft abruptly narrows into tubule in discharged state.

Hoplotelic microbasic *p*-mastigophore (Figure 2-5D): type of cnida defined by a tubule with a barbed, basal shaft less than 3 times capsule length. Tubule spined. V-shaped notch at base of shaft in undischarged state; shaft abruptly narrows into tubule in discharged state.

Spirocyst (Figure 2-5H): type of cnida defined by a thin, single walled capsule containing a long, spirally coiled, unarmed tubule of uniform diameter.

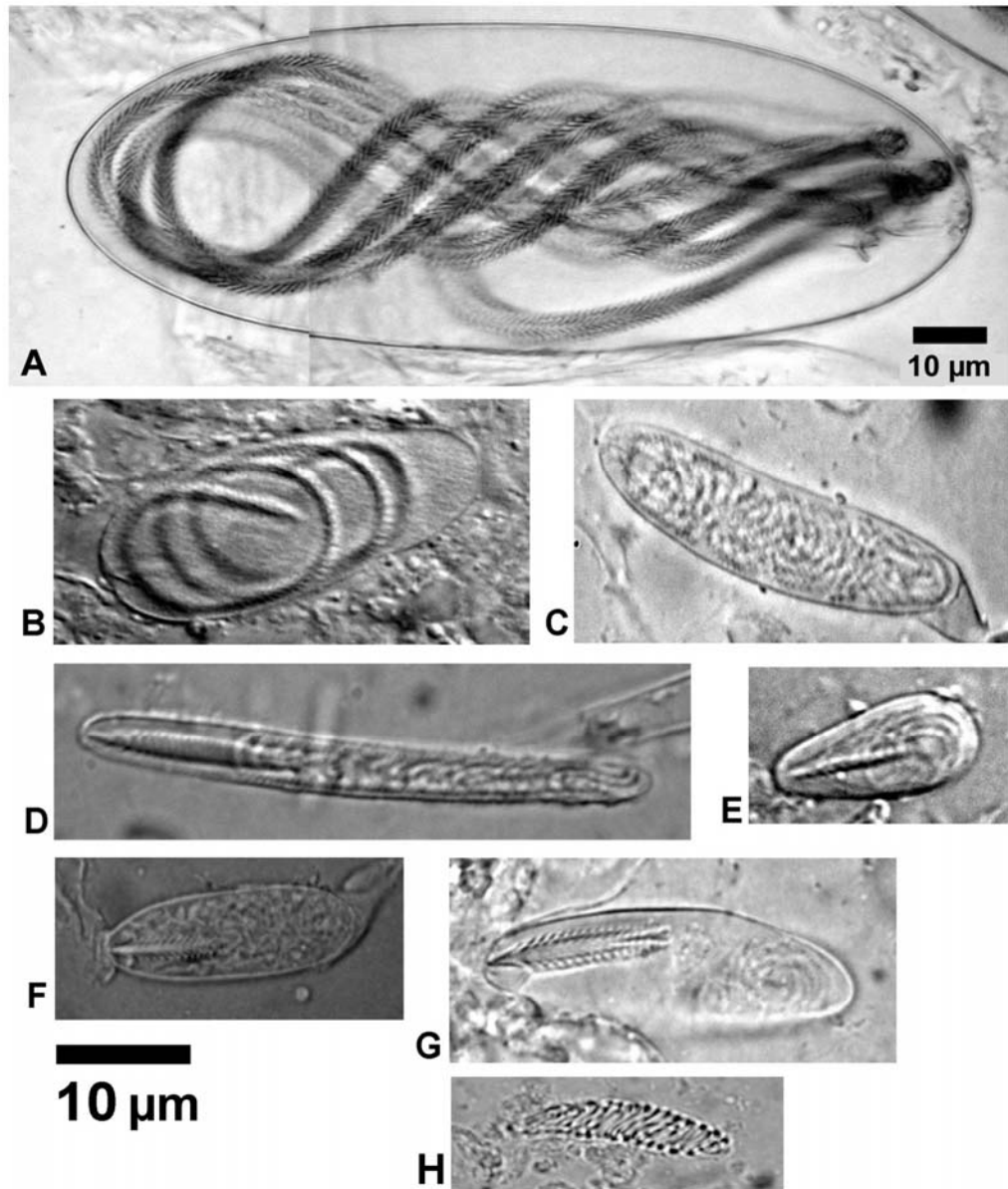


Figure 2-5. Types of cnidae in Corallimorpharia. A: Holotrich I; B: Holotrich II; C: Holotrich III; D: Hoplotelic microbasic *p*- mastigophore; E: Microbasic *b*-mastigophore; F-G: Microbasic *p*- mastigophore; H: spirocyst

CHAPTER III. GENERIC REVISION OF THE CORALLIMORPHARIA

3-1. Introduction

Although there are inventories of corallimorpharians (Andres, 1883; Stephenson, 1922; Carlgren, 1949; den Hartog, 1980; Fautin, 2006), there is no consensus about the number of valid genera and families. I investigated the validity of the 16 nominal genera based on five categories of morphological characters, body form, tentacle shape and arrangement, sphincter muscle development, nature of mesenteries, and cnidae composition, that have been used by other authors. Based on those characters, Stephenson (1922) recognized 10 genera in two families: three in Corallimorphidae, six in Discosomatidae, and *Nectactis*. He was uncertain about the proper family for *Nectactis* because the lack of discal tentacles prevented the genus being included in family Corallimorphidae. Carlgren (1949) recognized 10 genera in three families: two in Sideractidae, three in Corallimorphidae, and five in Actinodiscidae. den Hartog (1980) considered tentacle shape and arrangement to vary among members in a genus, and recognized seven genera in four families: one in family Discosomatidae, one in family Ricordeidae, three in family Corallimorphidae, and two in family Sideractidae (Table 3-1).

Table 3-1. Comparisons of classification schemes.

Genus	Author	Stephenson (1922)	Carlgren (1949)	den Hartog (1980, 1993)	Cha (this study)
<i>Sideractis</i> Danielssen, 1890		n.a.	valid ³	valid ⁶	valid ⁶
<i>Nectactis</i> Gravier, 1918		valid ¹	valid ³	valid ⁶	valid ⁶
<i>Corallimorphus</i> Moseley, 1877		valid	valid	valid	valid
<i>Isocorallion</i> Carlgren, 1900		n.a.	invalid	invalid	invalid
<i>Corynactis</i> Allman, 1882		valid	valid	valid	valid
<i>Sphincteractis</i> Zamponi, 1976		n.a.	n.a.	invalid	invalid
<i>Pseudocorynactis</i> den Hartog, 1980		n.a.	n.a.	valid	valid
<i>Actinotryx</i> Duchassing and Michelotti, 1860		valid	invalid	invalid	valid
<i>Discosoma</i> Rüppell and Leuckart, 1828		valid	valid ⁴	valid	valid
<i>Orinia</i> Duchassing and Michelotti, 1860		valid	valid	invalid	invalid
<i>Phialactis</i> Fowler, 1888		n.a.	invalid	invalid	invalid
<i>Paradiscosoma</i> Carlgren, 1900		valid	valid	invalid	invalid
<i>Rhodactis</i> Milne Edwards and Haime, 1851		valid	valid	invalid	valid
<i>Metarhodacis</i> Carlgren, 1943		n.a.	valid	invalid	valid
<i>Amplexidiscus</i> Dunn and Hamner, 1980		n.a.	n.a.	invalid	valid
<i>Ricordea</i> Duchassing and Michelotti, 1860		valid ²	valid ⁵	valid ⁷	valid

1: Stephenson (1922) did not assign *Nectactis* to a family

2: classified in family Discosomatidae

3: classified in family Sideractidae

4: Carlgren (1949) used the name *Actinodiscus*

5: classified in family Corallimorphidae

6: classified in family Corallimorphidae

7: classified in family Ricordeidae

n.a.: the genus was not included for the study or not described at the time

The five morphological categories are recovered as phylogenetically informative (see chapter IV). Polyp shape, tentacle shape and arrangement, sphincter muscle development, and cnidae composition separated two clades in Corallimorpharia. Cnidae composition and nature of mesenteries supported the Corallimorpharia and Scleractinia clade, and were informative within the two clades in Corallimorpharia. For example, the genus *Pseudocorynactis* is separated from the other cylindrical body corallimorpharians by having directive mesenteries and lacking incomplete mesenteries. The major morphological characters of each nominal genus are summarized in Table 4-2.

Body form has been the primary character used to assign corallimorpharians to a family. Cylindrical body corallimorpharians are represented by *Corynactis*, *Corallimorphus*, *Pseudocorynactis*, *Sideractis*, and *Nectactis*. They do not have zooxanthellae, and have a wide vertical range of distribution from shallow to deep water. Discoidal body corallimorpharians are represented by *Actinotryx*, *Discosoma*, *Metarhodactis*, *Orinia*, *Paradiscosoma*, *Phialactis*, *Rhodactis*, and *Amplexidiscus*. They have zooxanthellae, and therefore their vertical distribution range is limited to shallow water. The sphincter muscle is treated as a genus-level character: *Corallimorphus* does not have a marginal sphincter muscle, *Corynactis* and *Pseudocorynactis* have a strongly developed marginal sphincter muscle. Nature of mesenteries is treated as a genus-level character: *Pseudocorynactis* was described by den Hartog (1980) as differing from *Corynactis* because members of

Pseudocorynactis have only complete mesenteries. Cnidae composition has been used as a character used as a family- and genus-level character. *Ricordea* was assigned to the family Corallimorphidae by Carlgren (1949) mainly because of spirocysts in the tentacles.

The shape and arrangement of tentacles are the most distinctive characters in live animals. The morphology of tentacles changes with preservation, but type of tentacles in a genus is constant; den Hartog (1980) considered tentacle shape and arrangement to vary at the species-level. All cylindrical-bodied corallimorpharians have capitate tentacles, and all discoidal-bodied corallimorpharians have non-capitate tentacles. Various types of non-capitate tentacles are a genus-level character. Two genera of cylindrical body corallimorpharians, *Sideractis* and *Nectactis*, are distinguished from *Corynactis*, *Corallimorphus*, and *Pseudocorynactis* based having one tentacle per inter-mesenterial space.

Based on morphological characters, seven of the 16 genera (*Corynactis*, *Corallimorphus*, *Pseudocorynactis*, *Sideractis*, *Nectactis*, *Ricordea* and *Amplexidiscus*) have been considered valid by many authors (e.g., Stephenson, 1922; Carlgren, 1949; den Hartog, 1980, 1993, 1997; Fautin, 2006) and two (*Sphincteractis* and *Isocorallion*) are considered junior synonyms of *Corynactis* and *Corallimorphus* respectively (Carlgren, 1949; den Hartog, 1980; Dunn, 1984).

The validity of the remaining seven genera (*Actinotryx*, *Discosoma*, *Metarhodactis*, *Orinia*, *Paradiscosoma*, *Phialactis*, and *Rhodactis*) was investigated based on the five categories of morphological character. Members of those genera are discoidal body corallimorpharians. Based on tentacle shape, *Actinotryx*, *Orinia*, and *Rhodactis* are distinguished from *Discosoma*, *Paradiscosoma*, *Phialactis*, and *Metarhodactis*. *Actinotryx* and *Orinia* differ from *Rhodactis* in having a tentacle-free zone on the oral disc and marginal sphincter muscle. Based on examination of the type species, I did not find differences between *Actinotryx sanctithomae*, the type species of *Actinotryx*, and *Orinia torpida*, the type species of *Orinia* by monotypy; therefore I synonymized *Orinia* with *Actinotryx*. The type species of three genera, *Discosoma*, *Paradiscosoma*, and *Phialactis*, are very similar in five major morphological characters; therefore I synonymized *Paradiscosoma* and *Phialactis* with *Discosoma*. *Metarhodactis* resembles species of *Discosoma* in overall morphology, but *Metarhodactis* differs from *Discosoma* in having numerous hoplotelic microbasic *p*-mastigophores in mesenterial filaments. Based on my examination, I synonymized three of the seven genera, and recognized four genera, *Actinotryx*, *Discosoma*, *Metarhodactis*, and *Rhodactis*.

Conclusively, I recognize five genera in family Corallimorphidae, *Corynactis*, *Pseudocorynactis*, *Corallimorphus*, *Nectactis*, and *Sideractis*; five genera in family Discosomatidae, *Discosoma*, *Actinotryx*, *Rhodactis*, *Metarhodactis*, and *Amplexidiscus*; and one genus, *Ricordea*, in family Ricordeidae.

Table 3-2. Comparisons of type species of nominal genera.

Type species	<i>Corynactis viridis</i>	<i>Corallimorphus profundus</i>	<i>Pseudocorynactis caribbeorum</i>	<i>Sideractis glacialis</i>	<i>Nectactis sigularis</i>	<i>Ricordea florida</i>
Characters						
Shape of marginal tentacles	capitate	capitate	capitate	capitate	capitate	capitate or digitiform
Shape of discal tentacles	capitate	capitate	capitate	n/a (no discal tentacles)	n/a (no discal tentacles)	papilliform
Tentacle/coelenteron relationship	one tentacle per exocoel, multiple per endocoel	one tentacle per exocoel, multiple per endocoel	one tentacle per exocoel, multiple per endocoel	one tentacle per exocoel and per endocoel	one tentacle per exocoel and per endocoel	one tentacle per exocoel, multiple per endocoel
Tentacle-free zone on oral disc	No	No	No	Yes	Yes	No
Nematocyst composition	<ul style="list-style-type: none"> • Holotrichs up to 80 µm • Spirocysts numerous • Microbasic <i>p</i>-mastigophore • Microbasic <i>b</i>-mastigophore 	<ul style="list-style-type: none"> • Holotrichs up to 250 µm • Spirocysts numerous • Microbasic <i>p</i>-mastigophore • Microbasic <i>b</i>-mastigophore • Hoplotelic microbasic <i>p</i>-mastigophore 	<ul style="list-style-type: none"> • Holotrichs up to 200 µm • Spirocysts numerous • Microbasic <i>p</i>-mastigophore • Microbasic <i>b</i>-mastigophore • Hoplotelic microbasic <i>p</i>-mastigophore 	<ul style="list-style-type: none"> • Holotrichs up to 200 µm • Spirocysts numerous • Microbasic <i>p</i>-mastigophore • Microbasic <i>b</i>-mastigophore 	<ul style="list-style-type: none"> • Holotrichs up to 100 µm • Spirocysts numerous • Microbasic <i>p</i>-mastigophore • Microbasic <i>b</i>-mastigophore • Hoplotelic microbasic <i>p</i>-mastigophore 	<ul style="list-style-type: none"> • Holotrichs up to 100 µm • Spirocysts numerous • Microbasic <i>p</i>-mastigophore • Microbasic <i>b</i>-mastigophore • Hoplotelic microbasic <i>p</i>-mastigophore
Nature of mesentery	complete and incomplete	complete and incomplete	complete only	complete and incomplete	complete only	complete and incomplete
Sphincter muscle development	Distinctive – diffuse	Absent	Distinctive - diffuse	Absent	Absent	Absent
Endosymbionts	No	No	No	No	No	Yes

Table 3-2. Comparisons of type species of nominal genera.





Type species	<i>Actinotryx sanctithomae</i>	<i>Orinia torpida</i>	<i>Rhodactis rhodostoma</i>	<i>Metarhodactis boninensis</i>
Characters				
Shape of marginal tentacle	digitiform (length: 3-4 mm in preservative)	digitiform (length: 2-3 mm in preservative)	digitiform (length: 4-5 mm in preservative)	absent
Shape of discal tentacles	papilliform or branched 	papilliform 	branched 	reduced papilliform or branched 
Tentacle/coelenter on relationship	one tentacle per exocoel, multiple per endocoel	one tentacle per exocoel, multiple per endocoel	one tentacle per exocoel, multiple per endocoel	one tentacle per endocoel multiple per exocoel
Tentacle-free zone on oral disc	Yes: Between marginal and discal tentacles	Yes: Between marginal and discal tentacles	No	No
Nematocyst composition	<ul style="list-style-type: none"> • Holotrichs up to 250 µm • Microbasic <i>p</i>-mastigophore • Microbasic <i>b</i>-mastigophore 	Type specimen has been damaged: impossible to measure nematocysts.	<ul style="list-style-type: none"> • Holotrichs up to 160 µm • Microbasic <i>p</i>-mastigophore • Microbasic <i>b</i>-mastigophore 	<ul style="list-style-type: none"> • Holotrichs up to 180 µm • Microbasic <i>p</i>-mastigophore • Hoplotelic microbasic <i>p</i>-mastigophore • Microbasic <i>b</i>-mastigophore
Nature of mesentery	complete and incomplete	unknown	complete and incomplete	complete and incomplete
Sphincter muscle development	Weak – diffuse	Unknown	Absent	Absent
Endosymbionts	Yes	Unknown	Yes	Yes

Table 3-2. Comparisons of type species of nominal genera.

Type species	<i>Discosoma nummiforme</i>	<i>Paradiscosoma neglecta</i>	<i>Phialactis neglecta</i>	<i>Amplexidiscus fenestrafer</i>
Characters				
Shape of marginal tentacle	reduced digitiform (length: very short)	absent or reduced digitiform (length: very short)	reduced digitiform (length: very short)	digitiform
Shape of discal tentacles	reduced papilliform or branched	reduced papilliform or branched	reduced papilliform or branched	digitiform
Tentacle/coelenteron relationship	one tentacle per exocoel, multiple per endocoel	one tentacle per exocoel, multiple per endocoel	one tentacle per exocoel, multiple per endocoel	one tentacle per endocoel multiple per exocoel
Tentacle-free zone on oral disc	No	No	No	Yes: Within a field of discal tentacles
Nematocyst composition	<ul style="list-style-type: none"> • Holotrichs up to 160 µm • Microbasic <i>p</i>-mastigophore • Microbasic <i>b</i>-mastigophore 	<ul style="list-style-type: none"> • Holotrichs up to 160 µm • Microbasic <i>p</i>-mastigophore • Microbasic <i>b</i>-mastigophore 	<ul style="list-style-type: none"> • Holotrichs up to 160 µm • Microbasic <i>p</i>-mastigophore • Hoptotelic microbasic <i>p</i>-mastigophore • Microbasic <i>b</i>-mastigophore 	<ul style="list-style-type: none"> • Holotrichs up to 220 µm • Microbasic <i>p</i>-mastigophore • Hoptotelic microbasic <i>p</i>-mastigophore • Microbasic <i>b</i>-mastigophore
Nature of mesentery	complete only	complete and incomplete	complete and incomplete	complete and incomplete
Sphincter muscle development	Absent	Weak - diffuse	Weak - diffuse	Absent
Endosymbionts	Yes	Yes	Yes	Yes

3-2. Material

Material examined is listed in the description of each species.

Museum abbreviations:

MLP - Museo de La Plata (Argentina)

MOM - Musée Océanographique, Monaco (Monaco)

UBMZ - Museum of Zoology, University of Bergen (Norway)

RMNH - Nationaal Natuurhistorisch Museum, Leiden (The Netherlands)

SMNH - Naturhistoriska Riksmuseet, Stockholm (Sweden)

UUZM - Evolutionsmuseet, Uppsala Universitet (Sweden)

BMNH - British Museum Natural History, London (United Kingdom)

CAS – California Academy of Sciences, San Francisco, California (USA)

KUNHM – Kansas University Natural History Museum, Lawrence, Kansas (USA)

NMNH – National Museum of Natural History (Smithsonian Institution), Washington, D. C. (USA)

I examined the type specimens of the type species of each nominal genus. Examination of type specimens allowed me to identify new characters to distinguish each genus, to amend diagnosis of genera of uncertain validity, and to gather morphological characters for phylogenetic analyses. Information on type specimens is available from the “Hexacorallians of the World” (Fautin, 2006) (Table 3-3). In case no type specimens were designated or the type material is damaged, I examined non-type specimens of type species that I borrowed and collected. I collected specimens of *Actinotryx sanctithomae*

Duchassing and Michelotti, 1860, *Ricordea florida* Duchassing and Michelotti, 1860, and *Rhodactis rhodostoma* (Ehrenberg, 1834), all type species. Collecting specimens from the field provided much information such as color, habitat, and symbiotic associations.

Table 3-3. Type species for each nominal genus. Data from the database “Hexacorallians of the World” (Fautin, 2006).

Type species	Type specimens	Museum and Catalog number	Type locality
<i>Discosoma nummiformis</i>	Syntype	Naturhistoriska Riksmuseet, Stockholm; Cat. 1156	Tor, Red Sea
<i>Actinotryx sanctithomae</i>	?	Not known	St. Thomas, Jamaica
<i>Orinia torpida</i>	Syntype	Naturhistoriska Riksmuseet, Stockholm; Cat. 71	St. Thomas, Jamaica
<i>Phialactis neglecta</i>	Syntype	British Museum Natural History; Cat. 1894.2.7.1.	Papeete, Tahiti, French Polynesia
<i>Paradisosoma neglecta</i>	?	Not known	St. Thomas, Jamaica
<i>Rhodactis rhodostoma</i>	?	Not known	Tor, Red Sea
<i>Metarhodactis boninensis</i>	Syntype	Evolutionismuseet, Uppsala Universitet; Cat. 632	Port Lloyd, Bonin Islands (Ogasawara), Japan
<i>Amplexidiscus fenestrafer</i>	Holotype	California Academy of Sciences; Cat. 015553	Lizard Island, Great Barrier Reef, Australia

Table 3-3. Type species for each nominal genus. Data from the database “Hexacorallians of the World” (Fautin, 2006).

Type species	Type specimens	Museum and Catalog number	Type locality
<i>Sideractis glacialis</i>	Holotype	Museum of Zoology, University of Bergen; Cat. 9796	Norwegian North Atlantic Expedition 1876-1878 station 237 (70.68°N, 10.17°W)
<i>Nectactis singularis</i>	Syntype	Musée Océanographique, Monaco; Cat. 130023	Prince Albert I of Monaco 1895: Princesse-Alice et l'Hirondelle station 749 (38.91°N, 21.21°W)
<i>Sphinctractis sanmatiensis</i>	Holotype	Museo de La Plata; Cat. 8.504	San Matias Gulf, Rio Negro, Argentina
<i>Corallimorphus profundus</i>	Syntype	The Natural History Museum, London; Cat. 1889.11.25.4	Challenger Expedition, station 300 (32.30°S, 77.70°W)
<i>Corynactis viridis</i>	?	Not known	Cook Haven and coast of Cornwall, United Kingdom
<i>Pseudocorynactis caribbeorum</i>	Holotype	Nationaal Natuurhistorisch Museum, Leiden; Cat. 11481	Between Piscadera Bay and Blauw Bay, Curaçao
<i>Ricordea florida</i>	?	Not known	Port of St. Thomas, Jamaica

3-3. Methods

1) Collecting

Specimens of Corallimorpharia were collected by hand (California in May 2002), and by snorkeling and scuba diving (Oman in May 2004, Panama in August 2004, and St. Thomas, US Virgin Islands in August 2004). Most tropical shallow-water corallimorpharians attach to dead coral skeletons or rocks. To avoid damage to specimens, the substratum to which the specimen was attached was taken.

2) Geographic coordinates

Geographic coordinates of collected specimens were obtained with an Eagle 12-channel GPS receiver at the point of specimen collection. For specimens preserved in museum collections, and the geographic coordinates, if not given, were inferred from the place of collection.

3) Preservation

For morphological study, specimens were preserved in 10% formalin and some of them were transferred to 70% ethanol. For molecular study, specimens or part of a specimen were preserved in absolute or 95% ethanol. The specimens were cataloged and deposited in the Division of Invertebrate Zoology, Natural History Museum and Biodiversity Research Center, University of Kansas (KUNHM).

4) Histology

Specimens were prepared for embedding with an American Optical T/P 8000 tissue processor. Tissue was embedded in Paraplast®, and sectioned at 8-10 µm.

Hematoxylin and eosin were used for staining (Humanson, 1979), and stained slides were mounted using Canada balsam.

5) Cnidae

Undischarged cnidae from preserved specimens were examined at 400x and 1000x in squash preparations using a light microscope equipped with differential interference optics. Squash preparations were made from the tip of discal and marginal tentacles, the column, and the mesenterial filaments of each specimen. Sigma Scan Pro version 4.01.003 measurement software was used to measure the length and the width of undischarged capsules projected onto a Summa Sketch digitizing tablet (Summagraphics).

The number of capsules measured is indicated as “n” in the results for cnidae of each species; the ratio between the number of specimens in which that type of cnida was found to the number of specimens examined for that tissue is indicated as “N.”

6) Photography

Photographs of whole specimens, cnidae, and histological slides were made using Nikon Coolpix 950 digital camera. Photos were manipulated in Adobe Photoshop (version 5.5 and 7.0) to enhance contrast.

3-4. Results

Suborder CORALLIMORPHARIA Carlgren, 1940

Diagnosis (modified from Carlgren, 1949)

Solitary or clonal polyps without calcareous skeleton. Shallow water corallimorpharians solitary, or often clonal; deep water ones mainly solitary. Body cylindrical or discoidal. Width of oral disc from 10 mm to 450 mm. Mouth oval. Tentacles retractile or non-retractile. Tentacle shape: capitate, digitiform, papilliform, or branched. One or more tentacles communicate with each endocoel and exocoel. Column smooth with weak longitudinal muscles. Actinopharynx short. No siphonoglyphs. Mesenteries numerous and often irregularly arranged. Mesenterial filaments unilobed and often containing numerous holotrichs. Sphincter muscle present or absent. Retractor muscles weak. Basilar muscles absent or weak. Cnidom: holotrichs, microbasic *p*- and *b*- mastigophores, spirocysts.

Distribution

Corallimorpharians are distributed widely from shallow to deep water and from tropical to polar areas. The localities of corallimorpharians species published are shown in Figure 3-1.

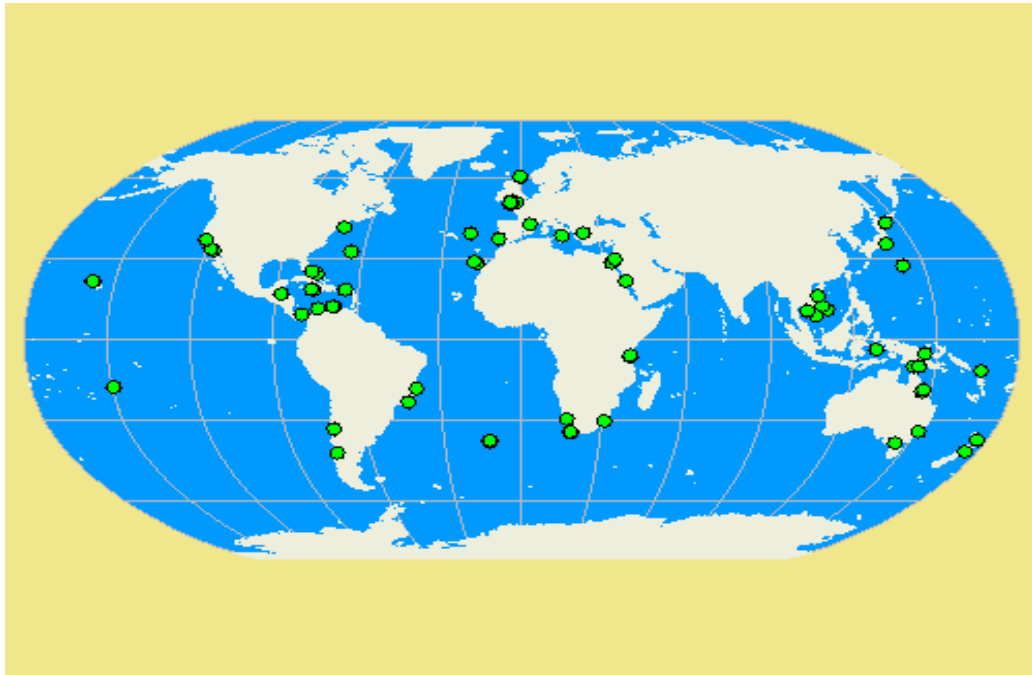


Figure 3-1. Distribution of corallimorpharians (Fautin, 2006). Green dots indicate known distribution of corallimorpharians.

Key to families of suborder Corallimorpharia

- | | | |
|----|---|------------------|
| 1. | Every tentacle capitate ----- | Corallimorphidae |
| | Not every tentacle capitate ----- | 2 |
| 2. | Spirocysts very rare or absent in tentacles ----- | Discosomatidae |
| | Spirocysts common in tentacles ----- | Ricordeidae |

Family CORALLIMORPHIDAE Hertwig, 1882

Synonymy

Sideractiidae Danielssen, 1890

Diagnosis

Cylindrical: oral disc as wide as or slightly wider than pedal disc. All tentacles capitate, retractile or not. Tentacle-free zone absent or present. One or more tentacles communicate with each endocoel and exocoel. Column smooth, mesoglea thin or thick. Mesenteries numerous and often irregularly arranged. Marginal sphincter muscle endodermal or absent. Retractor muscles weak. Basilar muscles absent. Spirocysts numerous in tentacles. Solitary or clonal. Not associated with zooxanthellae.

Nomenclatural/ Taxonomic notes

I consider the family Sideractidae Danielssen, 1890, a junior synonym of Corallimorphidae Hertwig, 1882. Monotypic genera *Sideractis* Danielssen, 1890, and *Nectactis* Gravier, 1918, were assigned by Carlgren (1949), den Hartog (1980), and Dunn (1982) to family Sideractidae Danielssen, 1890, because they lack discal tentacles. Riemann-Zürneck (1979) and den Hartog (1993) discussed the resemblances between *Nectactis singularis* Gravier, 1918, type species of *Nectactis*, and *Corallimorphus*: all members of both genera share the absence of discal tentacles communicating with the exocoels. *Sideractis glacialis*, the type species of *Sideractis*, is similar to species of Corallimorphidae: in polyp size, capitate tentacles, and

cylindrical body. It is similar to *Corynactis* and *Pseudocorynactis*; and the absence of discal tentacles is shared with *Nectactis singularis*. I therefore reject placing *Sideractis* and *Nectactis* in a family of their own. I agree with den Hartog (1993) in synonymizing Sideractidae Danielssen, 1890, with Corallimorphidae Hertwig, 1882. Phylogenetic analysis using morphological characters supports the inclusion of *Sideractis* and *Nectactis* in the Corallimorphidae (see Chapter III, Figure 3-1).

Key to genera of family Corallimorphidae

- | | | |
|----|--|-------------------------|
| 1. | No more than one tentacle per endocoel and exocoel ----- | 2 |
| | More than one tentacle arise from an endocoel ----- | 3 |
| 2. | All mesenteries complete ----- | <i>Nectactis</i> |
| | Not all mesenteries complete ----- | <i>Sideractis</i> |
| 3. | Polyps solitary ----- | 4 |
| | Polyps clonal ----- | <i>Corynactis</i> |
| 4. | All mesenteries complete ----- | <i>Pseudocorynactis</i> |
| | Not all mesenteries complete ----- | <i>Corallimorphus</i> |

Genus *Corynactis* Allman, 1846

Synonymy

Draytonia Duchassaing and Michelotti, 1860

Sphincteractis Zamponi, 1976

Diagnosis (modified from den Hartog et al., 1993)

Column long when fully expanded, subglobular when retracted. Tentacles retractile (Figure 3-1, B and C). 2-6 endocoelic tentacles arranged in radial rows; one tentacle per exocoel. Exocoelic tentacles longer than endocoelic tentacles. Mesenteries complete and incomplete. No directive mesenteries. Sphincter muscle endodermal, diffuse. Asexual reproduction by longitudinal fission usual. Often gregarious. Cnidom: spirocysts, holotrichs, microbasic *b*- and *p*- mastigophores.

Nomenclatural/ Taxonomic notes

Corynactis Allman, 1846, is one of the most distinctive genera in Corallimorpharia. *Draytonia* was erected for the species *D. myrcia* by Duchassaing and Michellotti, 1864, based on the difference in presence of "glandulae chromatophae virides" along the margin of the oral disc. Andres (1883) and den Hartog (1980) considered this difference as a variation and synonymized *D. myrcia* with *Corynactis parvula*. Duchassaing and Michellotti (1864) did not designate any type material and type specimens are no longer extant. I agree that *D. myrcia* is a species in *Corynactis* based on the original description.

Sphincteractis was erected for *S. sanmatiensis* by Zamponi, 1976, based on its distinct endodermal marginal sphincter muscle. Zamponi (1976) considered

Corynactis to lack a sphincter muscle, but *Corynactis* is characterized by a distinct endodermal sphincter muscle. The synonymization of *Sphincteractis* with *Corynactis* was discussed in den Hartog (1993) and Genzano et al. (1996). The type species of *Sphincteractis*, *S. sanmatiensis*, was synonymized with *Corynactis carnea* by Genzano et al. (1996). Both species were described from San Matias Gulf, Argentina. Zamponi (1976) stated that the type material, Museo de La Plata, Argentina; catalog number 8.504, contained a holotype, but the type lot contains four specimens. Therefore, they are syntypes. The specimens are damaged. However, based on similarities in polyp size, capitate tentacles, clonal polyps, and endodermal sphincter muscle, I agree with den Hartog (1993) and Genzano et al. (1996) in synonymizing *Sphincteractis* with *Corynactis*.

Type species: *Corynactis viridis* Allman, 1846

Other species examined: *Corynactis californica* Carlgren, 1936

***Corynactis viridis* Allman, 1846**

Synonymy

Corynactis viridis Allman, 1846: Gosse, 1860; Andres, 1883; Weill, 1934; Manuel, 1981; Ates, 1987; Manuel, 1988; den Hartog, 1993

Corynactis Allmani Thompson, 1847

Corynactis allmani (Thompson, 1847): Cocks, 1851

Body shape, size and color

Column diameter 5-9 mm, oral disc diameter 7-9 mm, pedal disc diameter 8-15 mm; column length 8-15 mm; tentacle length 4-8 mm. Color: brown in alcohol to pale yellow in formalin. According to Allman (1846), in life color of species various: column whitish, yellowish, green, orange, purple, brownish, pinkish; margin of oral disc often with bright green line; usually tentacle stalks same with column coloration; acrosphere white, creamy, pink, red, purple.

Oral disc and tentacles

Oral disc circular or oval-shape (Figure 3-2A). Tentacles capitate (Figure 3-2, A and C); 24-28 endocoelic radial rows of 2-5 tentacles in each radial row; 1 tentacle in each exocoelic space; total number of tentacles 112-128.

Internal anatomy

24-30 pairs of mesenteries in two or three cycles: first cycle of complete and fertile or sterile mesenteries with well-developed filaments, second cycle of incomplete and sterile mesenteries with filaments, third cycle of very short and sterile mesenteries without filaments (Figure 3-2E); often mesoglea of mesenteries thickened parietally. Sphincter muscle distinct, endodermal, diffuse (Figure 3-2D). Retractor muscles weak, diffuse (Figure 3-2E).

Cnidae: measured from three specimens, each of KUNHM 001882, RMNH 17743, and RMNH17776.

Acrospheres:

Spirocysts	22.33-73.02 x 2.34-5.30 μm	n= 35, N=3/3
Holotrichs III	53.45-84.52 x 27.70-25.34 μm	n= 21, N=3/3

Microbasic <i>b</i> -mastigophores	31.26-53.04 x 3.32-6.25 μm	n= 31, N=3/3
Microbasic <i>p</i> -mastigophores	24.37-35.10 x 5.02-6.32 μm	n= 29, N=3/3
Microbasic <i>p</i> -mastigophores	43.82-72.33 x 5.60-6.88 μm	n= 24, N=3/3
Tentacle stalks:		
Spirocysts	24.84-36.77 x 2.35-5.20 μm	n= 47, N=3/3
Mesenterial filaments:		
Holotrichs II	40.57-55.45 x 14.73-17.55 μm	n= 25, N=3/3
Holotrichs III	65.32-80.45 x 30.21-43.08 μm	n= 25, N=3/3
Microbasic <i>b</i> -mastigophores	8.35-11.26 x 2.87-3.46 μm	n= 12, N=2/3
Microbasic <i>p</i> -mastigophores	20.37-50.05 x 5.41-6.35 μm	n= 24, N=3/3
Column		
Spirocysts	20.13-36.44 x 2.52-4.64 μm	n= 30, N=3/3
Holotrichs III	32.5-57.82 x 8.26-16.49 μm	n= 23, N=3/3
Microbasic <i>b</i> -mastigophores	16.12-25.54 x 3.68-6.47 μm	n= 34, N=3/3
Microbasic <i>p</i> -mastigophores	15.23-28.46 x 5.11-8.03 μm	n= 35, N=3/3
Microbasic <i>p</i> -mastigophores	32.66-53.56 x 6.20-11.09 μm	n= 21, N=3/3

Type specimens and locality

No type specimen designated.

Type locality: British Isles

Other material examined

England

KUNHM 001882: Plymouth; Oct-5-2003; 3 specimens

RMNH 17743: Plymouth, breakwater; 50°20'N, 4°10'W; Aug-1969; 2 specimens

Ireland

RMNH 17776: Southwest coast, County Cork, near Skibberdeen; 51°30'N, 9°20'W;

Aug-10-1978; 2 specimens

France

RMNH 11426: Brittany, Roscoff, north of Ile de Batz; 48°40'N, 4°W; depth 80 m;

Jul-28-1976; 2 specimens

Nomenclatural/ Taxonomic Notes

Because type material is not available, I examined the specimens used in den Hartog (1993) to redescribe *Corynactis viridis* Allman, 1846. I selected three specimens to measure cnidae; a specimen of KUNHM 001843 and two specimens of RMNH 17743 and 17776 were collected from near the type locality. The cnidae measurements provided in this study correspond well to the data in den Hartog (1993).

Geographical distribution

Corynactis viridis is known from around Ireland, on the south and west coast of Britain, to extreme northern Scotland (Manuel, 1981). The known distribution in continental coast of Europe is from northern France southward along the coast of Spain (Ramil and Pulpeiro, 1990). den Hartog et al. (1993) reported the species in the Mediterranean and in the Macronesian Islands: Madeira Archipelago, Azores, Canary Islands, and Selvagens Islands. It is reported from shallow water to 80 m deep.

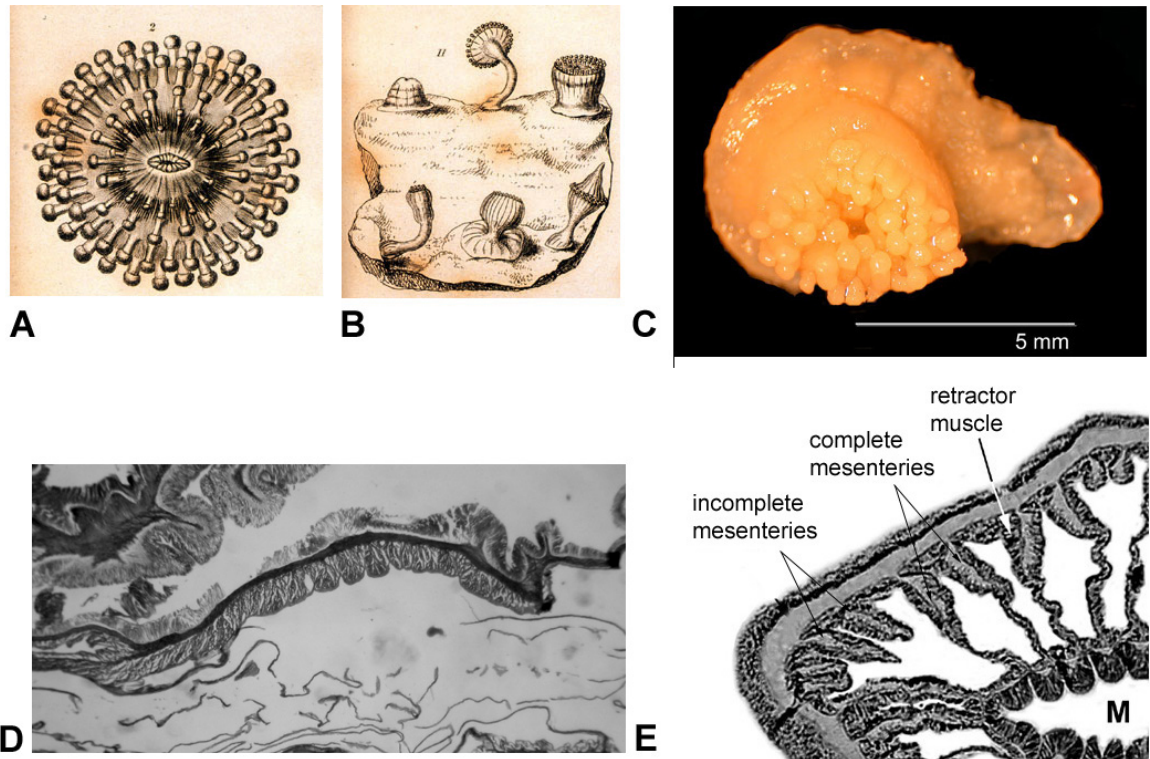


Figure 3-2. *Corynactis viridis* Allman, 1846. A : oral disc (Allman, 1846, Plate XI , fig. 2); B: various body forms (Allman, 1846, Plate XI , fig. 1); C: whole specimen (RMNH 11734); D: longitudinal section of endodermal sphincter muscle (KUNHM 001843); E: mesenteries and retractor muscle (KUNHM 001843).

Genus *Corallimorphus* Moseley, 1877

Synonymy

Isocorallion Carlgren, 1900

Diagnosis (modified from Carlgren, 1949)

Tentacles non-retractile. 2 endocoelic tentacles arranged in radial rows; one exocoelic tentacle. Tentacle-free zone between mouth and discal tentacles. Column with thick mesoglea. Mesenteries complete and incomplete. Sphincter muscle absent.

Gonochoric. Cnidom: spirocysts, holotrichs, microbasic *b*-mastigophores, Hoplotelic microbasic *p*-mastigophores.

Nomenclatural/ Taxonomic notes

Corallimorphus Moseley, 1877, was established based on descriptions of *C. profundus* and *C. rigidus*. Carlgren (1949) recognized *C. profundus* as the type species because of page priority. *Isocorallion hertwigi* Carlgren, 1900, the type species of *Isocorallion*, was synonymized with *Corallimorphus rigidus* by Carlgren (1943), who is the author of *Isocorallion hertwigi*. Carlgren (1900) erected the new genus *Isocorallion* for a Hertwig's specimen, but in 1943, when he had the chance to examine additional material, he concluded that *I. hertwigi* belongs in *Corallimorphus*. Therefore, *Isocorallion* is a junior synonym of *Corallimorphus*.

Type species: *Corallimorphus profundus* Moseley, 1877

***Corallimorphus profundus* Moseley, 1877**

Synonymy

Corallimorphus profundus: Hertwig, 1882; Andres, 1883; Stephenson, 1920, 1922; Carlgren, 1928; Carlgren and Stephenson, 1929; Carlgren, 1949; Dunn, 1984

Body shape, size and color

Column diameter 25-48 mm, oral disc diameter 28-50 mm, pedal disc diameter 24-45 mm; column length 15-25 mm; tentacle length up to 8 mm. Color yellow in preservation.

Oral disc and tentacles

Oral disc circular. Discal tentacles in cycles; marginal tentacles alternately long and short; endocoelic tentacles longer than exocoelic tentacles. Total number of tentacles 66 in BMNH 1889.11.25.4.

Internal anatomy

I was not allowed to make histological sections of the type specimens. Therefore, the description of internal anatomy is based on the original description and Dunn (1984). 24-30 pairs of mesenteries in two or three cycles: first cycle of complete and fertile or sterile mesenteries with well-developed filaments, second cycle of incomplete and sterile mesenteries with filaments, third cycle of very short and sterile mesenteries without filaments; often mesoglea of mesenteries thickened parietally. Sphincter muscle absent.

Cnidae: measured from two syntypes, BMNH 1889.11.25.4., and 1889.11.25.5.

Acrospheres:

Spirocysts	32.18-67.35 x 3.45-5.25 μm	n= 18, N=2/2
Holotrichs I	193.3-252.3 x 15.3-18.7 μm	n= 11, N=2/2
Microbasic <i>b</i> -mastigophores	42.36-67.69 x 3.59-4.90 μm	n= 19, N=2/2
Hoplotelic microbasic <i>p</i> -mastigophores	113.2-203.98 x 3.78-4.83 μm	n= 20, N=2/2
Tentacle stalks:		
Spirocysts	30.84-49.16 x 3.94-7.50 μm	n= 24, N=2/2
Mesenterial filaments:		
Holotrichs III	80.46-103.35 x 16.86-22.57 μm	n= 20, N=2/2
Microbasic <i>b</i> -mastigophores	16.70-19.73 x 4.52-5.60 μm	n= 11, N=1/2
Hoplotelic microbasic <i>p</i> -mastigophores	53.46-70.90 x 8.34-11.05 μm	n= 20, N=2/2
Column		
Hoplotelic microbasic <i>p</i> -mastigophores	100.55-118.50 x 18.06-21.46 μm	n= 6, N=1/2

Type specimens and locality

Syntypes:

BMNH 1889.11.25.4: Challenger Expedition, station 300; 32.30°S, 77.70°W; depth 2514 m; 1 specimen

BMNH 1889.11.25.5: Challenger Expedition, station 293; 38.93°S, 104.92°W; depth 3702 m; 1 specimen

Nomenclatural/ Taxonomic notes

The cnidae data are compared with those of Dunn (1984), which is the first redescription of *Corallimorphus profundus*. Hoplotelic microbasic *p*-mastigophores are very rare in column tissue, but Dunn (1984) also found the type of nematocysts in the column.

Geographical distribution

Corallimorphus profundus is known from the Antarctic. The vertical distribution ranges from 132 to 3660 meters (Dunn, 1984).

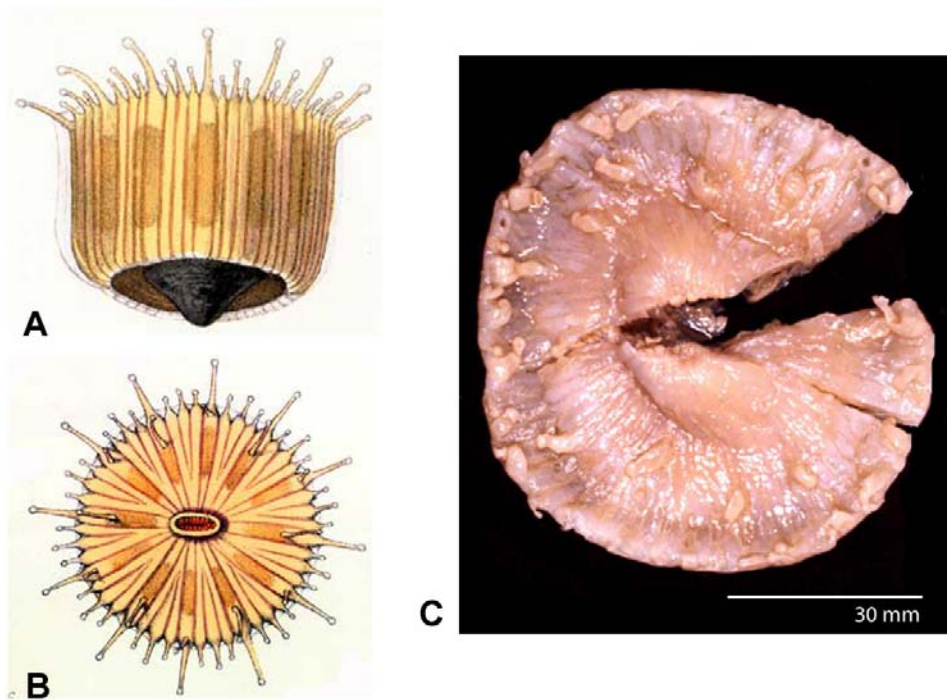


Figure 3-3. *Corallimorphus profundus* Moseley, 1877. A: side view (Mosley, 1877, Plate XLV, fig. 7); B: oral disc (Mosley, 1877, Plate XLV, fig. 7, fig. 8); C: oral disc of syntype (BMNH 1889.11.25.4.)

***Genus Pseudocorynactis* den Hartog, 1980**

Diagnosis (modified from den Hartog, 1980)

Column long when fully expanded, subglobular form when retracted. Tentacles retractile (Figure 3-4, B and C). 3-5 endocoelic tentacles arranged in radial rows; one tentacle per exocoel. Exocoelic tentacles longer than endocoelic tentacles. Tentacle-free zone between mouth and discal tentacles. Mesenteries complete. Two directive mesenteries. Sphincter muscle endodermal, diffuse. Solitary. Cnidom: spirocysts, holotrichs, microbasic *b*- and *p*- mastigophores, hoplotelic microbasic *p*-mastigophores.

Nomenclature/Taxonomic Notes

There are two known species in *Pseudocorynactis*: *P. caribbeorum* and *P. caboverdensis*. Both species differ from *Corynactis* by large size, solitary habit, and the absence of asexual reproduction. Long spirocysts (Figure 3-4C) and slender holotrichs II (Figure 3-4D) are distinctive. Another character likely to be of generic importance is the mesenteries: in *P. caribbeorum* all mesenteries are complete and able to gametogenesis, whereas in species of *Corynactis*, at least some mesenteries are incomplete.

Type species: *Pseudocorynactis caribbeorum* den Hartog, 1980

***Pseudocorynactis caribbeorum* den Hartog, 1980**

Body shape, size and color

Occasionally oral disc exceeds diameter of pedal disc; polyps connected by basal expansion; contracted specimens mammiform. Column diameter 26-32 mm, oral disc diameter 32-35 mm, pedal disc diameter 26-30 mm; column length 25-35 mm; tentacle length 10-16 mm in preserved expanded specimens. Pale yellow in formalin. According to den Hartog (1980) in life color of species various: upper column pale to vivid orange, lilac, orange-brown, yellowish brown, purplish brown, with or without opaque, whitish, greenish, or blackish streaks or specks; lower column often less intensely colored than upper column, 6 dark longitudinal bands; oral disc semi-transparent; mouth opaque white; tentacles colorless with vivid orange-red acrospheres.

Oral disc and tentacles

Oral disc circular; 25-30 endocoelic radial rows of 3-5 tentacles in each radial row; 1 tentacle in each exocoel; total number of tentacles 125-180.

Column

Mesenterial insertions clearly visible through column in some specimens preserved in formalin (Figure 3-4, A and B).

Internal anatomy

I was not allowed to make histological sections of the type specimens. Therefore, the description of internal anatomy is based on the original description, den Hartog

(1980). 23, 25 pairs of complete, fertile mesenteries: 2 pairs of directives (Figure 3-3E). Sphincter muscle distinct, endodermal, diffuse (Figure 3-4F).

Cnidae: measured from holotype (RMNH 11481) and paratype (RMNH 11479)

Acrospheres:

Spirocysts	53.23-183.21 x 3.75-7.45 μm	n= 35, N=2/2
Holotrichs II	92.33-106.4 x 5.42-6.88 μm	n= 11, N=2/2
Holotrichs III	146.2-193.34 x 14.56-17.44 μm	n= 20, N=2/2
Microbasic <i>b</i> -mastigophores	35.26-50.24 x 4.71-6.34 μm	n= 30, N=2/2
Hoplotelic microbasic <i>p</i> -mastigophores	111.3-136.3 x 5.32-6.84 μm	n= 31, N=2/2

Tentacle stalks:

Spirocysts	21.33-40.01 x 2.33-4.50 μm	n= 18, N=2/2
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Mesenterial filaments:

Holotrichs III	62.40-82.35 x 24.31-31.84 μm	n= 22, N=2/2
Microbasic <i>b</i> -mastigophores	12.50-13.43 x 3.22-4.26 μm	n= 7, N=1/2
Microbasic <i>p</i> -mastigophores	18.62-24.59 x 6.01-7.35 μm	n= 20, N=2/2

Column

Holotrichs III	33.39-41.06 x 10.35-12.30 μm	n= 20, N=2/2
Microbasic <i>b</i> -mastigophores	10.32-22.30 x 3.88-6.59 μm	n= 18, N=2/2
Microbasic <i>p</i> -mastigophores	17.41-29.08 x 6.43-8.31 μm	n= 19, N=3/3

Type specimens and locality

Holotype:

RMNH 11481; Curaçao, southcoast, between the entrance of Piscadera Bay and
Blauw Bay; depth 6-15 m; Oct-30-1972

Paratype:

RMNH 11479; Curaçao, southcoast, between the entrance of Piscadera Bay and
Blauw Bay; depth 6-15 m; Apr-1971

Distribution

Pseudocorynactis caribbeorum occurs in the southern and eastern Caribbean. The
vertical distribution is 6-50 m deep (den Hartog, 1980).

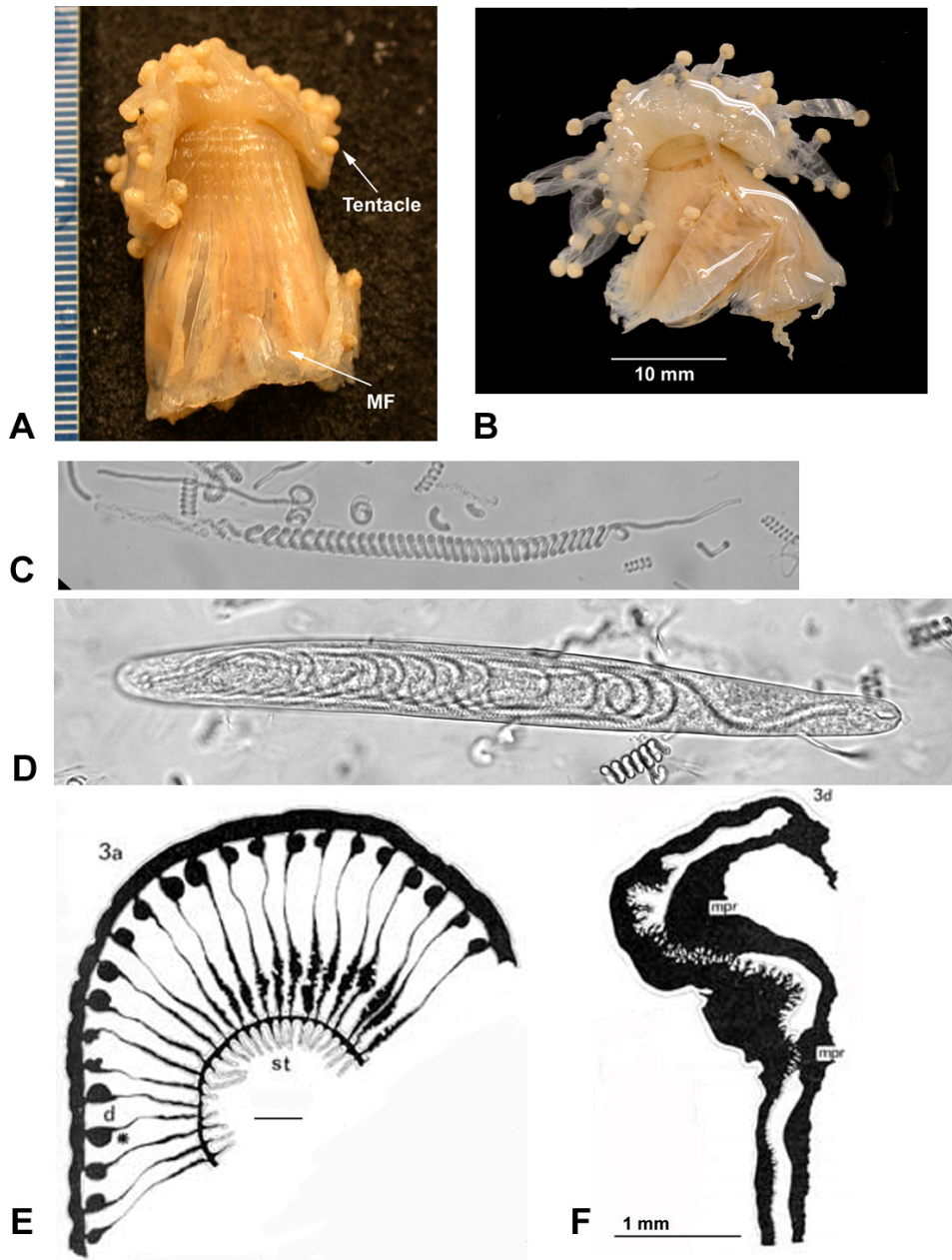


Figure 3-4. *Pseudocorynactis caribbeorum* den Hartog, 1980. A-B: whole body of holotype, note visible mesenterial insertion and acrospheres; C: long spirocysts in an acrosphere (RMNH 11481); D: slender holotrichs II in an acrosphere (RMNH 11481); E: a pair of directive (den Hartog, 1980, p. 21, Fig. 3); F: weak endodermal sphincter muscle (den Hartog, 1980, p. 21, Fig. 3). MF: mesenterial filaments.

Genus *Sideractis* Danielssen, 1890

Diagnosis (modified from Danielssen, 1890)

Tentacles non-retractile. Tentacles arranged in radial rows; one endocoelic, one exocoelic tentacle. Tentacle-free zone on oral disc. Mesenteries complete and incomplete. Sphincter muscle absent. Solitary. Cnidom: spirocysts, holotrachs, microbasic *b*- and *p*- mastigophores.

Nomenclature/ Taxonomic notes

Sideractis was established by Danielssen in 1890 based on monotypy, *S. singularis* Danielssen, 1890. Danielssen's original description is too simple and the illustration does not represent diagnostic features to identify the species. The type specimen of the species is damaged, so it was limited to examine anatomy of the species in detail. Therefore the description of the anatomy of the species is based on published descriptions (Carlgren 1921, 1940; den Hartog et al., 1993) and my own observation. Cnidae data collected from a syntype specimen.

Type species: *Sideractis glacialis* Danielssen, 1890

***Sideractis glacialis* Danielssen, 1890**

Body shape, size and color

Oral disc width not exceeds 15 mm, pedal disc width not exceeds 12 mm, column length not exceeds 12 mm, tentacle length up to 8 mm. According to Danielssen (1890), in life pedal disc width not exceeds 20 mm.

Oral disc and tentacles

Oral disc circular; tentacle-free zone on oral disc. The number of tentacles 26 in type specimen, UBMZ 9796.

Internal anatomy

I was not allowed to make histological sections of the type specimens. Therefore, the description of internal anatomy is based on the original description, Danielssen (1890). 6 pairs of complete, fertile mesenteries; various number of incomplete, sterile mesenteries.

Cnidae: measured from holotype (UBMZ 9796)

Acrospheres:

Spirocysts	26.30-76.47 x 2.85-5.25 μm	n= 12, N=1/1
Holotrichs I	106.7-194.3 x 17.8-24.3 μm	n= 8, N=1/1
Microbasic <i>b</i> -mastigophores	14.37-22.34 x 4.56-5.43 μm	n= 4, N=1/1
Microbasic <i>p</i> -mastigophores	76.4-94.45 x 6.57-7.34 μm	n= 10, N=1/1

Tentacle stalks:

Spirocysts	34.45-48.58 x 3.84-5.60 μm	n= 18, N=1/1
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Mesenterial filaments:

Holotrichs II	68.44-85.27 x 24.34-26.85 μm	n= 20, N=1/1
Microbasic <i>b</i> -mastigophores	14.56-16.21 x 4.56-4.70 μm	n= 2, N=1/1
Microbasic <i>p</i> -mastigophores	27.46-32.46 x 5.64-6.95 μm	n= 10, N=1/1

Column

Microbasic <i>b</i> -mastigophores	13.67-15.81 x 4.21-4.86 μm	n= 7, N=1/1
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Microbasic *p*-mastigophores 34.56-38.48 x 6.52-8.43 μm n= 5, N=1/1

Type specimens and locality

Syntype:

UBMZ 9796: Norwegian North Atlantic Expedition 1876-1878 station 237, 70.68°N, 10.17°W

Geographical distribution

The species was known from Jan Mayen and the Trondheim, Vest, and Hardanger fiords in Norway. The type specimen from Jan Mayen was found on a stone (Danielssen, 1890). The depth the species reported from 220-500 m.

Nomenclature/ Taxonomic notes

The illustration in the original description is not accurate and confusing compare to actual type specimen (Figure 3-5).

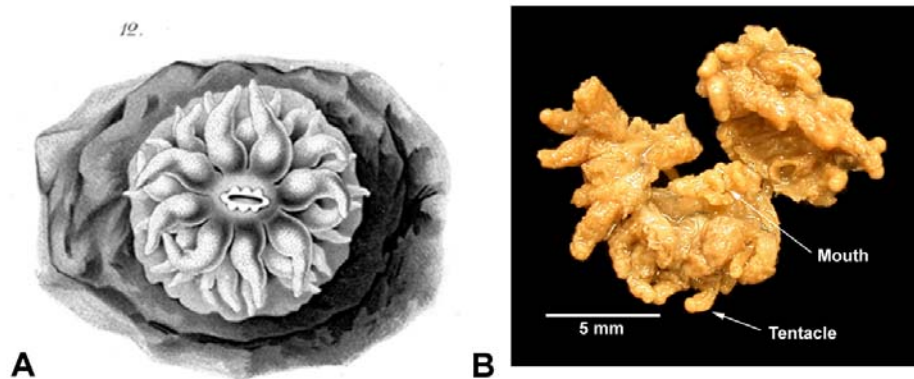


Figure 3-5. *Sideractis glacialis* Danielssen, 1890. A: illustration in the original description (Danielssen, 1890, pl. 1, fig. 1); B: whole specimen of holotype (UBMZ 9796).

Genus *Nectactis* Gravier, 1918

Diagnosis (modified from Gravier, 1918)

Tentacles non-retractile. Tentacles arranged near the margin in 2 cycles, one endocoelic, one exocoelic tentacle. Tentacle-free zone on oral disc. Mesenteries complete. No directive mesenteries. Sphincter muscle absent. Retractor muscles weak. Solitary. Cnidom: spirocysts, holotrichs, microbasic *b*- and *p*- mastigophores.

Type species: *Nectactis singularis* Gravier, 1918

***Nectactis singularis* Gravier, 1918**

Body shape, size and color

Oral disc width not exceeds 25 mm, pedal disc width not exceeds 20 mm, column length not exceeds 10 mm.

Oral disc and tentacles

Oral disc circular or oval-shape. Tentacles length up to 5 mm (most tentacles macerated). Tentacles arranged in two cycles; one endocoelic cycle with up to 30 tentacles, one exocoelic cycle with up to 30 tentacles. Endocoelic tentacles longer than exocoelic tentacles. The number of tentacles up to 60.

Internal anatomy

I was not allowed to make histological sections of the type material. Therefore, the description of internal anatomy is based on the original description. 30 pairs of mesenteries all complete, fertile or sterile.

Cnidae: measured from two specimens, each of MOM 130023 and MNHM 1224

Acrospheres:

Spirocysts	28.20-34.57 x 4.23-5.56 μm	n= 10, N=2/2
Holotrichs II	78.8-95.5 x 22.4-24.4 μm	n= 10, N=2/2
Microbasic <i>b</i> -mastigophores	16.47-21.59 x 4.35-5.21 μm	n= 6, N=2/2
Microbasic <i>p</i> -mastigophores	81.49-89.06 x 6.32-7.54 μm	n= 11, N=2/2

Mesenterial filaments:

Holotrichs II	72.48-80.40 x 22.43-28.45 μm	n= 9, N=2/2
Microbasic <i>b</i> -mastigophores	13.08-14.31 x 4.20-4.35 μm	n= 3, N=2/2
Microbasic <i>p</i> -mastigophores	26.37-30.23 x 6.12-6.39 μm	n= 4, N=2/2

Column

Microbasic <i>b</i> -mastigophores	11.24-14.81 x 3.78-4.46 μm	n= 6, N=2/2
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Type specimens and locality

Syntypes:

MOM 130023: S. A. Le Prince de Monaco, station 753, 39°50-54'N 17°57'-18°06'W;
depth 4360 m, Sep-18-1896; 11 specimens

MOM 130135: S. A. Le Prince de Monaco, station 749, 38°54-55'N 21°06'45"-
18°45'W; depth 5005 m; Sep-16,17-1896; 5 specimens

Other materials examined

MNHM 1215: Golfe de Gascogne N/O "Jean Charcot" BIOGAS 6, station no. CP20,
44°23'N 04°51'W; depth 4459 m; Oct-29-1974; 5 specimens

MNHM 1224: Golfe de Gascogne N/O “Cryos” BIOGAS 5, station no. CP05,
46°29’N 10°20’W; depth 3850 m; Jun-19-1974; 4 specimens

Geographical distribution

The species is known from Iberian deep sea basin east of Azores and Bay of Biscay.

The known vertical distribution ranges from 3850-5005 m.

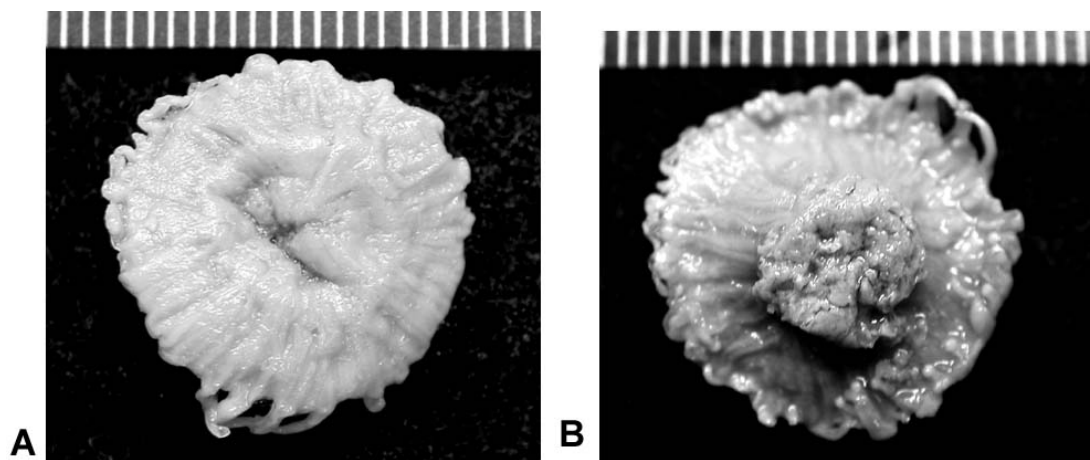


Figure 3-6. *Nectactis singularis* Gravier, 1918. A: oral disc of syntype (MOM 130023); B: pedal disc of syntype (MOM 130023).

Family RICORDEIDAE Watzl, 1922

Diagnosis (modified from Watzl, 1922)

Discoidal body: Oral disc wider than pedal disc; in some specimens pedal disc irregular. One, or often, more mouths. Two types of tentacles: capitate or digitiform discal tentacles, some branched; digitiform or capitate marginal tentacles. Tentacles arranged in radial rows over the endocoels; non-retractile. No tentacle-free zone. Mesenteries complete and incomplete, often irregularly arranged. Sphincter muscle absent. Basilar muscle absent. Spirocysts in tentacles. Solitary, often gregarious. Associated with zooxanthellae.

Nomenclatural/ Taxonomic notes

Ricordea is the single genus in Ricordeidae, and has intermediate morphology between Corallimorphidae and Discosomatidae (den Hartog, 1980). *Ricordea* resembles Corallimorphidae in cnidae composition based on the presence of spirocysts, and in tentacle shape that some marginal tentacles are capitate as in Corallimorphidae. However, tentacle arrangement is similar to that of Discosomatidae, and marginal tentacles are very short and non-retractile despite some of them are capitate. Species of *Ricordea* have discoidal body and are unable to withdraw oral disc and tentacles. Because member of *Ricordea* have both attributes of Discosomatidae and Corallimorphidae, Stephenson (1922) placed the genus in Discosomatidae and Carlgren (1949) assigned *Ricordea* to the Corallimorphidae. In this study, I concluded to accommodate the genus in a family its own, Ricordeidae

Watzl, 1922, as proposed by Watzl (1922) and den Hartog (1980) based on the distinctive morphological characters of *Ricordea* from members of Discosomatidae. According to phylogeny of Corallimorpharia, *Ricordea* is more closely related to genera of Discosomatidae than those of Corallimorphidae (see chapter IV). To reflect the phylogeny to the classification, *Ricordea* needs to be placed in family Discosomatidae. However, as discussed in chapter III, the relationships among genera are not conclusive at this moment due to the lack of comprehensive taxon sampling in Corallimorphidae and the limitation of genetic markers used in molecular analyses. Indeed the systematic position of *Ricordea* in Corallimorpharia is not consistent in molecular analyses: 28S rDNA data support *Ricordea* in Corallimorphidae, while 16S rDNA data support *Ricordea* in Discosomatidae. The question about the systematic position of *Ricordea* needs to be addressed in further studies.

Genus *Ricordea* Duchassaing and Michelotti, 1860

Diagnosis: Same as in the family.

Type species: *Ricordea florida* Duchassaing and Michelotti, 1860

***Ricordea florida* Duchassaing and Michelotti, 1860**

Synonymy

Heteranthus floridus (Duchassaing and Michelotti, 1860): McMurrich, 1889

Corynactis bahamensis Watzl, 1922

Body shape, size and color

Oral disc diameter 10-36 mm, pedal disc diameter 8-25 mm, column length up to 5 mm. Color: beige to pale yellow in formalin, in life mouth red or bright green, tip of tentacles bright green, stalk of tentacles brown, column brown or green to dull green (Figure 3-7, B-D).

Oral disc and tentacles

Oral disc circular; four mouths observed from one specimen (KUNHM 002373).

Tentacles numerous; at least ten tentacles on each endocoel and more than one tentacles on each exocoel. Tentacles arranged radially (Figure 3-7B); often difficult to recognize arrangement in clonal specimens due to irregularities from asexual reproduction. The number of endocoelic rows 46 to 92.

Internal anatomy

The number of mesenteries numerous, often arranged irregularly. Sphincter muscle absent.

Cnidae: measured from four specimens; each from KUNHM 002373, KUNHM 002392, USNM 56603, and USNM 19043

Marginal tentacles:

Holotrichs III	67.11-76.61 x 11.94-14.45 μm	n=25, N=4/4
Hoploteleic <i>p</i> -mastigophores	93.87-121.59 x 7.17-8.83 μm	n=34, N=4/4
Spirocysts	42.17-75.65 x 2.14-3.67 μm	n=36, N=4/4
Microbasic <i>b</i> -mastigophores	50.25-75.74 x 4.98-7.30 μm	n=38, N=4/4
Microbasic <i>b</i> -mastigophores	21.40-38.58 x 3.20-9.18 μm	n=24, N=4/4

Discal tentacles:

Holotrichs III	59.77-75.97 x 11.91-15.12 μm	n=65, N=4/4
Hoplotelic <i>p</i> -mastigophores	76.50-83.21 x 6.84-8.90 μm	n=46, N=4/4
Spirocysts	34.52-55.21 x 2.63-3.79 μm	n=36, N=4/4
Microbasic <i>b</i> -mastigophores	18.93-26.47 x 3.15-4.52 μm	n=27, N=4/4

Mesenterial filaments

Holotrichs II	41.74-49.68 x 12.82-15.19 μm	n= 25, N=4/4
Holotrichs III	50.81-61.79 x 22.56-26.38 μm	n= 37, N=4/4
Microbasic <i>p</i> -mastigophores	35.31-55.99 x 7.39-13.95 μm	n= 57, N=4/4

Column

Holotrichs II	41.74-49.68 x 12.82-15.19 μm	n= 25, N=4/4
Holotrichs III	50.81-61.79 x 22.56-26.38 μm	n= 37, N=4/4
Microbasic <i>p</i> -mastigophores	35.31-55.99 x 7.39-13.95 μm	n= 57, N=4/4

Type specimens and locality

No type specimens designated.

Type locality: St. Thomas, US Virgin Islands

Other material examined

Belize, British Honduras

USNM 56576: Carrie Bow Cay; May-5-1974; 1 specimen

USNM 56582: Carrie Bow Cay; May-5-1974; 5 specimens

USNM 56602: Carrie Bow Cay; May-23-1974; 1 specimen

USNM 56903: Carrie Bow Cay, Outer Fore Reef Slope; depth 18 m; Mar-23-1978; 4 specimens

St. Thomas, US Virgin Islands

KUNHM 002373: Water Is. Sprat point, 18°81'N 64°54'W; depth 10 m; Aug-19-2004; 5 specimens

KUNHM 002375: Hull Bay, 18°29'N 64°55'W; depth 0.3-0.5 m; Aug-20-2004; 4 specimens

KUNHM 002376: Coki Bay, 18°35'N 64°86'W; depth 5 m; Aug-21-2004; 5 specimens

KUNHM 002377: N. Saba Is., 18°21'N 64°58'W; depth 5 m; Aug-18-2004; 5 specimens

St. John, US Virgin Islands

USNM 52014: Reef Bay; depth 19 m; Jan-5-1961; 5 specimens

Bocas del Toro, Panama

KUNHM 002392: Isla Colon, Boca del Drago, 09°15'N 82°19'W ; depth 2 m; Aug-10-2004; 2 specimens

KUNHM 002393: Crawl Cay, 09°15'N 92°07'W; depth 2 m; Aug-6-2004; 4 specimens

Bonaire

RMNH 11499: South-west coast, 2 miles north of Kralendijk; 3-5 m deep; Apr-9-1922; 2 specimens

Curaçao

RMNH 11495: South-coast, between Piscadera Bay and Blauw Bay; depth 36 m; Jul-9-1973; 1 specimen

RMNH 11496: South-coast, between Piscadera Bay and Blauw Bay; depth 45 m; Apr-21-1973; 1 specimen

Jamaica

USNM 19043: Port Royal Cays; 1 specimen

USNM 51540: Kingston, South East Cay; depth 1 m; Sep-5-1959; 7 specimens

Puerto Rico

USNM 51082: La Parguera, Majimo Reef; Jan-1959; 30 specimens

USNM 94777: La Parguera, Media Luna Reef; Oct-1-1984; 1 specimen

Geographical distribution

Ricordea florida is a common Caribbean species, not reported from the Gulf of Mexico and so far also not from Brazilian reefs. The known vertical distribution ranges 1 to 45 meters.

Nomenclatural/ Taxonomic notes

McMurrich (1889) considered *Ricordea florida* is a species of the actinarian genus *Heteranthus* Klunzinger, 1877, and made a new combination, *Heteranthus floridus* (Duchassaing and Michelotti, 1860). However, he realized that *Heteranthus* was a junior synonym of *Ricordea*, and he corrected this misinterpretation himself in McMurrich (1896). *Corynactis bahamensis* Watzl, 1922, was described from a single, preserved specimen. Watzl stated that the specimen is 1 cm in diameter with 200 to 300 tentacles associated with zooxanthellae. However, *Corynactis* is a non-

zooxanthellae genus and the illustration in the original description of *C. bahamensis* (Figure 3-7E) does not resemble a *Corynactis* species at all. Based on Watzl's observation, in my view, *C. bahamensis* is a small specimen of *Ricordea florida*. Cnidae data gathered in this study is relatively well corresponding to the data in den Hartog (1980), but the length of hoplotelic microbasic *p*-mastigophores in marginal tentacles measured in this study is longer than the one in den Hartog (1980).

Biological notes

The symbiotic association between *Ricordea florida* and a shrimp, *Periclimenes rathbunae*, is reported from Belize (Ritson-Williams and Paul, 2007).

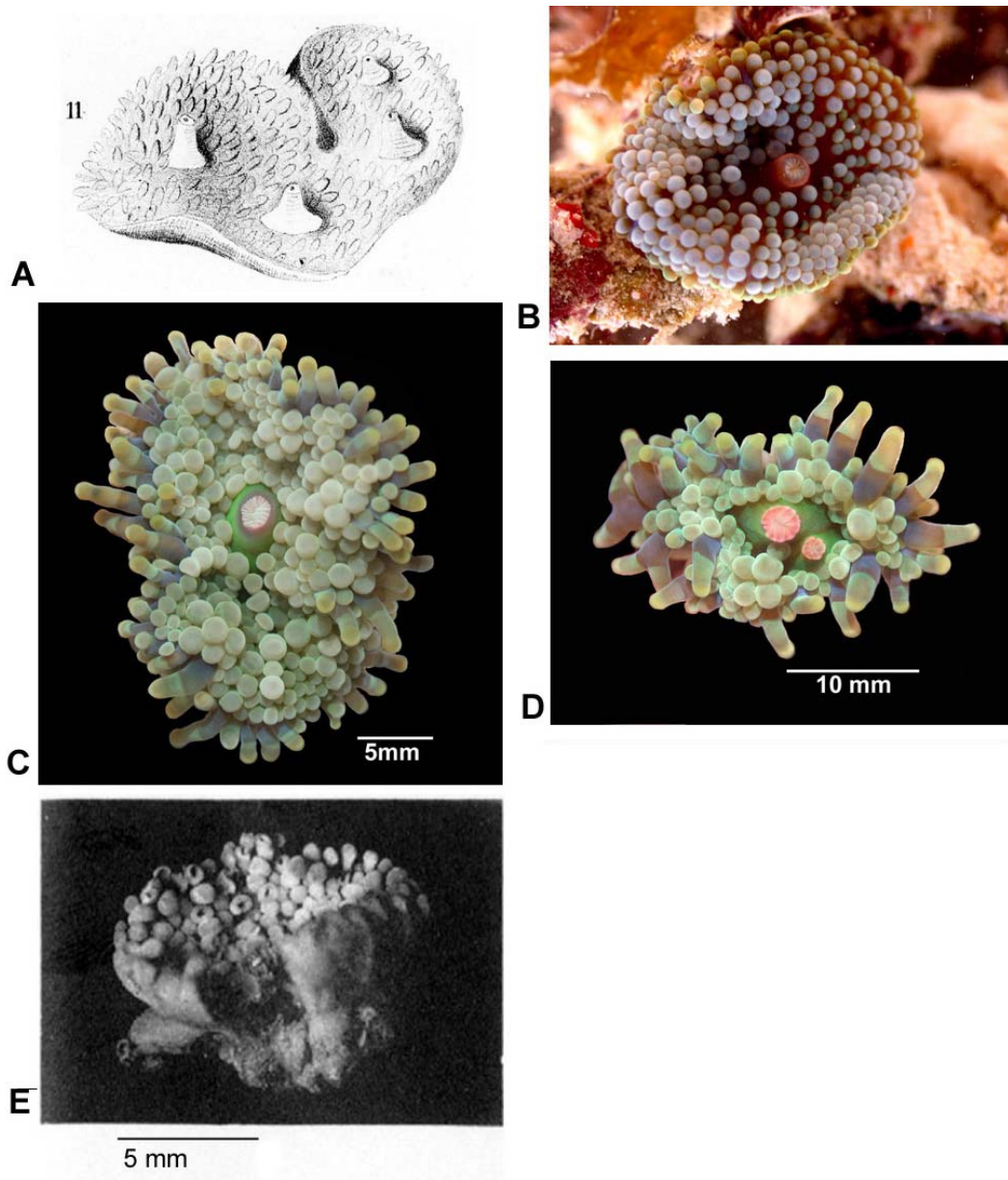


Figure 3-7. *Ricordea florida* Duchassaing and Michelotti, 1860. A: illustration in the original description (Duchassaing and Michelotti, 1860, Plate VI, fig. 11); B: radial tentacle arrangement (KUNHM 002377); C: oral disc with irregular tentacle arrangement (KUNHM 002375); D: two mouths on oral disc (KUNHM 002373); E: illustration of the original description of *Corynactis bahamensis* Watzl, 1922.

Family DISCOMATIDAE Duchassaing and Michelotti, 1864

Synonymy

Discosomae Duchassaing and Michelotti, 1864

Discostominae Verrill, 1869

Rhodactidae Andres, 1883

Phialactidae Fowler, 1888

Actinodiscidae Carlgren, 1949

Diagnosis (modified from Carlgren, 1949)

Discoidal body: oral disc wider than pedal disc. Two types of tentacles: branched or papilliform discal tentacles, reduced digitiform marginal tentacles, sometimes marginal tentacles absent. Tentacles non-retractile; arranged in radial rows, often discal tentacles densely arranged in central field, sparsely arranged in area near margin and mouth. Tentacle-free zone absent or present. Mesenteries complete and incomplete, numerous and often irregularly arranged. Sphincter muscle very weak or absent. Retractor muscles weak. Basilar muscle weak or absent. Spirocysts very rare or usually absent. Often gregarious. Associated with zooxanthellae.

Nomenclatural/ Taxonomic notes

The family Discosomatidae is established based on *Discosoma* Rüppell and Leuckart, 1828. Duchassaing and Michelotti (1864) introduced the family name Discosomae. Verrill (1869) accepted Ehrenberg's incorrect change of the genus name *Discosoma* into *Discostoma* (Ehrenberg, 1834), and proposed a sub-family Discostominae of the family Thalassianthidae in Actiniaria. However, these taxa are objective synonyms

because they are based on genus *Discosoma* Rüppell and Leuckart, 1828. Therefore, Discosomae Duchassaing and Michelottis, 1864 has priority over Discostominae Verrill, 1869. Because the proper suffix of a family name is -idae, the correct family name is Discosomatidae Duchassaing and Michelotti, 1864. Unfortunately Carlgren (1949) did not use valid names, *Discosoma* and Discosomatidae, because he followed de Blainville (1830, 1834) in replacing the name *Discosoma* by the junior name *Actinodiscus*. Accordingly he used the family name Actinodiscidae for Discosomatidae, adding another junior synonym. Phialactidae Fowler, 1888 is subjective junior synonym because of the subjective synonymy of *Phialactis* and *Discosoma*. Andres (1883) introduced family name Rhodactidae for genus *Rhodactis*. However, based on morphology, *Rhodactis* differs in tentacle shape and length. In my view it is not realistic to assign a family for *Rhodactis* itself, therefore Rhodactidae Andres, 1883 is a subjective junior synonym of Discosomatidae.

Key to genera of family Discosomatidae

1. Digitiform marginal tentacles ----- 2
Reduced marginal tentacles or none at all ----- 3
2. No tentacle-free zone on oral disc, branched discal tentacles -- *Rhodactis*
Tentacle-free zone on oral disc ----- 4
3. Hoplotelic *p*-mastigophores absent in mesenterial filaments --- *Discosoma*
Hoplotelic *p*-mastigophores present in mesenterial filaments -- *Metarhodactis*
4. Branched discal tentacles ----- *Actinotryx*
Digitiform discal tentacles ----- *Amplexidiscus*

Genus *Discosoma* Rüppell and Leuckart, 1828

Synonymy

Actinodiscus de Blainville, 1830

Discostoma Ehrenberg, 1834

Phialactis Flower, 1888

Paradiscosoma Carlgren, 1900

Diagnosis (modified from den Hartog, 1980)

Tentacles extremely short, shorter than 1 mm. Two types of tentacles: none or reduced digitiform marginal tentacles, papilliform discal tentacles. No tentacle-free zone. Mesenteries complete and/or incomplete. Sphincter muscle absent or very weak. Basilar muscle absent. Cnidom: holotrichs, microbasic *b*- and *p*- mastigophores.

Nomenclatural/ Taxonomic notes

The nomenclatural issues of the name *Discosoma* are discussed in den Hartog (1980).

De Blainville (1830) replaced the name *Discosoma* by *Actinodiscus*, clearly stating the genus name is based on *Discosoma nummiforme* Rüppel and Leuckart, 1828.

Ehrenberg (1834) stated *Discosoma* is a junior homonym of a genus of lizards, *Discosomus* Oken, 1816, and proposed to change the name into *Discostoma*.

However, according to International Commission on Zoological Nomenclature (ICZN) Art. 58d, *Discosomus* Oken is not a homonym. In fact, *Discosomus* Oken was published as the name rejected for nomenclatural purposes (ICZN, 1956), and listed in the Official Index of Rejected and Invalid names in Zoology (ICZN, 1963) (den Hartog, 1980). Based on my examination, the type species of *Phialactis*, *Ph. neglecta* Fowler, 1888, and the type species of *Paradiscosoma*, *Pa. neglecta* Carlgren, 1900, are well accommodated in *Discosoma* based on diagnostic characters of the two species described below.

Type species: *Discosoma nummiforme* Rüppell and Leuckart, 1828

Other species examined: *Discosoma neglecta* (Duchassing and Michelotti, 1860)

Discosoma fowleri (Fowler, 1889)

Discosoma carlgreni (Watzl, 1922)

***Discosoma nummiforme* Rüppell and Leuckart, 1828**

Synonymy

Actinodiscus nummiforme (Rüppell and Leuckart, 1828): Carlgren, 1949

Body shape, size and color

Oral disc diameter 18 mm, pedal disc diameter 12 mm; column length 5 mm. In life oral disc diameter 16-32 mm, pedal disc diameter 14-22 mm; column length up to 7 mm. Color: pale yellow in formalin. In life color of species various: column brown; tentacles same with column coloration (Figure 3-8C).

Oral disc and tentacles

Discal tentacles papilliform, marginal tentacles reduced digitiform; arranged in radial rows, arrangement of each row varies: tentacles too numerous to count the number of endocoelic and exocoelic tentacles.

Internal anatomy

All mesenteries complete (Figure 3-8E); number of mesenteries varies: approximately 32 pairs in a small specimen, 48 pairs in a large specimen. Sphincter muscle absent.

Cnidae: measured from the syntype specimen, SMNH 1156, and three non-type specimens, each of KUNHM 002080, 002081, and 002094

Marginal tentacles:

Holotrichs I	68.42-93.48 x 23.03-38.42 μm	n= 18, N=3/4
Holotrichs II	28.33-31.02 x 6.33-11.43 μm	n= 26, N=4/4
Microbasic <i>b</i> -mastigophores	17.32-24.32 x 3.44-5.21 μm	n= 24, N=3/4
Microbasic <i>p</i> -mastigophores	17.83-29.35 x 4.33-7.58 μm	n= 21, N=3/4

Discal tentacles:

Holotrichs I	68.33-102.35 x 28.37-43.44 μm	n= 18, N=2/4
Holotrichs II	31.93-46.75 x 9.36-12.05 μm	n= 28, N=3/4
Microbasic <i>p</i> -mastigophores	16.93-26.46 x 4.96-10.34 μm	n= 35, N=4/4

Mesenterial filaments:

Holotrichs I	86.29-154.85 x 53.26-73.44 μm	n= 29, N=4/4
Holotrichs II	30.48-63.42 x 16.42-22.63 μm	n= 32, N=3/4
Holotrichs III	36.45-58.03 x 10.88-18.34 μm	n= 24, N=3/4
Microbasic <i>p</i> -mastigophores	33.40-42.38 x 6.33-8.42 μm	n= 32, N=4/4
Microbasic <i>p</i> -mastigophores	17.68-26.08 x 4.53-6.49 μm	n= 21, N=2/4

Column

Microbasic <i>b</i> -mastigophores	18.92-24.33 x 4.68-9.32 μm	n= 20, N=2/4
Microbasic <i>p</i> -mastigophores	25.37-36.49 x 5.93-11.23 μm	n= 21, N=3/4

Type specimens and locality

Syntype: SMNH 1156: Red Sea, Tor; 28.23°N, 33.61°W; 1 specimen

Other material examined

Oman

KUNHM 002079: Bandar Khayran near aquaculture weirs, 23°30'27"N, 58°45'37"W;
depth 5 m; May-17-2004; 1 specimen

KUNHM 002080: Bander Jissah, 23°33'26"N, 58°39'04"W; depth 6 m; May-18-2004;
1 specimen

KUNHM 002081: Bander Jissah, 23°33'26"N, 58°39'04"W; depth 6 m; May-18-2004;

1 specimen

KUNHM 002089: Between Bander Kharyan and Bander Jissah, 23°32'01"N,

58°41'57"W; depth 9 m; May-20-2004; 1 specimen

KUNHM 002090: Bander Jissah, 23°33'26"N, 58°39'04"W; depth 7.6 m; May-20-

2004; 2 specimens

KUNHM 002092: Fahal Island, 23°32'01"N, 58°41'57"W; depth 6 m; May-21-2004;

2 specimens

KUNHM 002094: Cemetery Bay (Bandar Sidab), 23°36'41"N, 58°36'02"W; depth 12

m; May-21-2004; 1 specimen

Geographical distribution

D. nummiforme is known from Red Sea, East Africa, and the Gulf of Oman. This species lives in shallow water: the depth does not exceed 12 m.

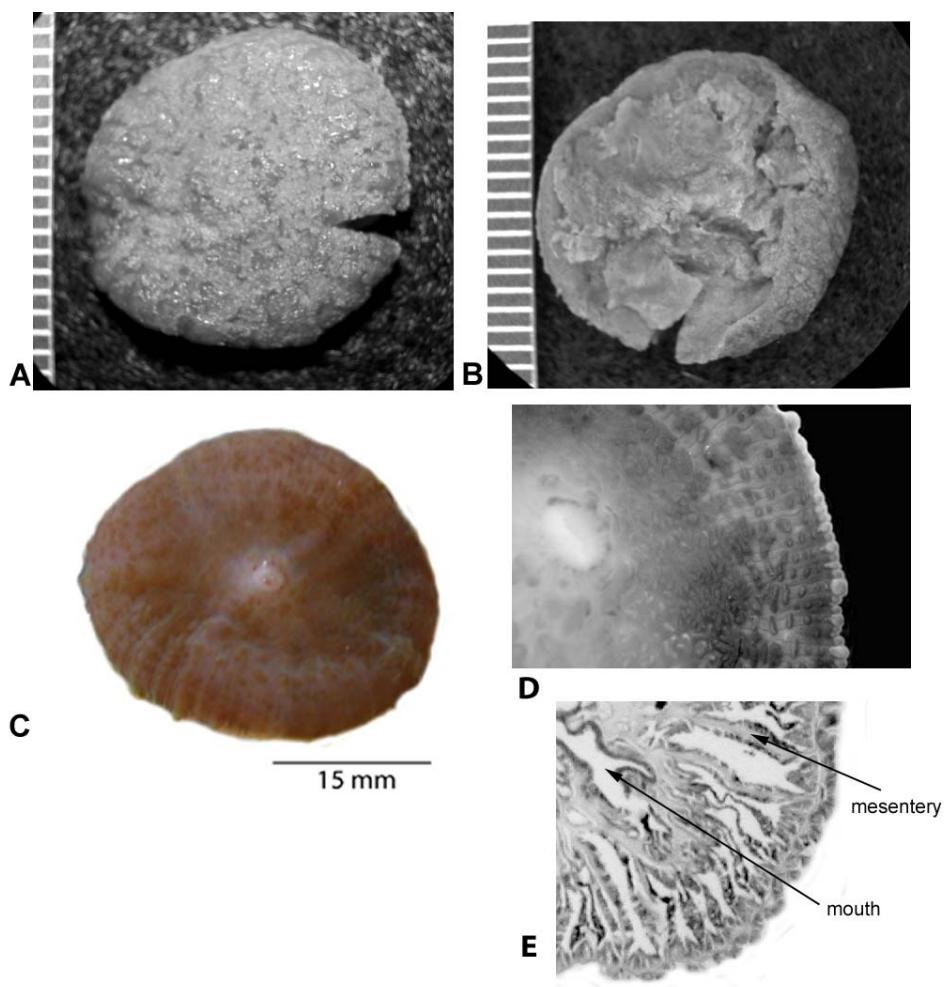


Figure 3-8. *Discosoma nummiforme* Rüppell and Leuckart, 1828. A: oral disc of syntype specimen (SMNH 1156); B: pedal disc of syntype specimen (SMNH 1156); C: oral disc of live material (KUNHM 002092); D: reduced marginal tentacles (KUNHM 002092); E: transverse section (KUNHM 002090), note complete mesenteries.

***Discosoma fowleri* (Fowler, 1889)**

Synonymy

Phialactis neglecta Fowler, 1889

Ricordea neglecta (Fowler, 1889): Haddon, 1898

Rhodactis neglecta (Fowler, 1889): Carlgren, 1900; Carlgren, 1949

Actinodiscus neglecta (Fowler, 1889): Cutress, 1979

Discosoma fowleri (Fowler, 1889): den Hartog, 1980

Body shape, size and color

Oral disc diameter 21-40 mm, pedal disc diameter 15-20 mm; column length up to 20 mm. Color: yellow in 70% alcohol.

Oral disc and tentacles

Oral disc circular; margin crenulated in large specimens. Discal tentacles papilliform, marginal tentacle reduced digitiform arranged in radial rows: 3-14 in an endocoelic row, no tentacles in an exocoelic row (Figure 3-9, B and C).

Internal anatomy

Mesenteries complete or incomplete; at least three cycles (Figure 3 -9D), number of mesenteries varies: approximately 72 pairs (12 complete, 60 incomplete) in a small specimen, 86 pairs (18 complete, 68 incomplete) in a large specimen. Sphincter muscle weak, diffuse.

Cnidae: measured from the holotype (BMNH 194.2.7.1) and two specimens, each of USNM 50485 and 52492

Marginal tentacles:

Holotrichs II	32.45-41.33 x 6.45-7.41 μm	n= 13, N=3/3
Holotrichs III	35.57-37.46 x 10.59-12.32 μm	n= 13, N=3/3
Microbasic <i>b</i> -mastigophores	13.45-16.46 x 4.57-5.80 μm	n= 16, N=3/3
Microbasic <i>p</i> -mastigophores	12.33-16.66 x 4.32-6.08 μm	n= 21, N=3/3
Discal tentacles:		
Holotrichs III	37.30-43.06 x 9.84-15.55 μm	n= 14, N=3/3
Microbasic <i>b</i> -mastigophores	13.22-15.32 x 4.55-5.70 μm	n= 9, N=2/3
Microbasic <i>p</i> -mastigophores	16.97-29.35 x 3.08-6.74 μm	n= 21, N=3/3
Mesenterial filaments:		
Holotrichs I	162.47-220.65 x 64.32-82.16 μm	n= 28, N=3/3
Holotrichs II	34.93-58.34 x 16.13-22.58 μm	n= 33, N=3/3
Microbasic <i>p</i> -mastigophores	36.49-43.72 x 7.02-10.83 μm	n= 41, N=3/3
Microbasic <i>p</i> -mastigophores	13.44-20.75 x 3.96-5.84 μm	n= 22, N=3/3
Column		
Holotrichs III	15.89-17.44 x 4.90-6.72 μm	n= 8, N=2/3
Microbasic <i>b</i> -mastigophores	12.97-18.43 x 5.40-6.32 μm	n= 12, N=2/3
Microbasic <i>p</i> -mastigophores	13.05-18.29 x 4.08-7.29 μm	n= 30, N=3/3

Type specimens and locality

Syntype:

BMNH1894.2.7.1: French Polynesia, Tahiti, Papeete, 17.52°S 149.58°E; depth 0-10 m; 1 specimen (cut in two pieces)

Other material examined

French Polynesia

USNM 50485: Society Islands, Tahiti, Papeete, Motu Uta Reef, Quarantine Island; depth 2 m; Mar-17-1956; 1 specimen

USNM 52492: Society Islands, Tahiti, Papeete, Motu Uta Reef, Quarantine Island; depth 1 m; Apr-10-1957; 87 specimens

USNM 52494: Society Islands, Bora Bora, Tereia Point, Fanui Bay; depth 1 m; Apr-25-1957; 30 specimens

Nomenclatural/Taxonomic notes

Discosoma neglecta (Fowler, 1888) is a junior homonym of *Discosoma neglecta* (Duchassaing and Michelotti, 1860). Therefore, *Discosoma fowleri* was proposed as a substitute name for *Phialactis neglecta* Fowler by den Hartog (1980).

The type specimen of *Discosoma fowleri* (Fowler, 1888) was small (the width of oral disc is approximately 12 mm), but the specimen was cut in pieces, thus the size may not be an accurate measurement. The anatomy and cnidae of *D. fowleri* have been documented in Fowler (1888) and Cutress (1979), and there are a few points need to be discussed. Fowler (1888) stated that the tentacles do not have nematocysts, but I found several types of nematocysts from both discal and marginal tentacles. The number of nematocysts found is relatively small to the ones of other tissues such as mesenterial filaments, and it is not surprising that Fowler did not find nematocysts with considerations in technical limitations, and in the number of specimens examined: Fowler (1888) examined only one specimen. The “large cnidocil” (Figure

3-9E) found by Fowler (1888) is holotrichs I. The size of the capsule and coiling pattern of tubule fit well in the definition of holotrichs I (Figure 3-9E, see chapter II). Cutress (1979) documented that the species has spirocysts, but he found only one spirocyst from marginal tentacle. From my examinations, I did not find any spirocysts from three specimens, thus I assume that Cutress's tissue squash was contaminated.

Geographical distribution

The species is known from Tahiti.

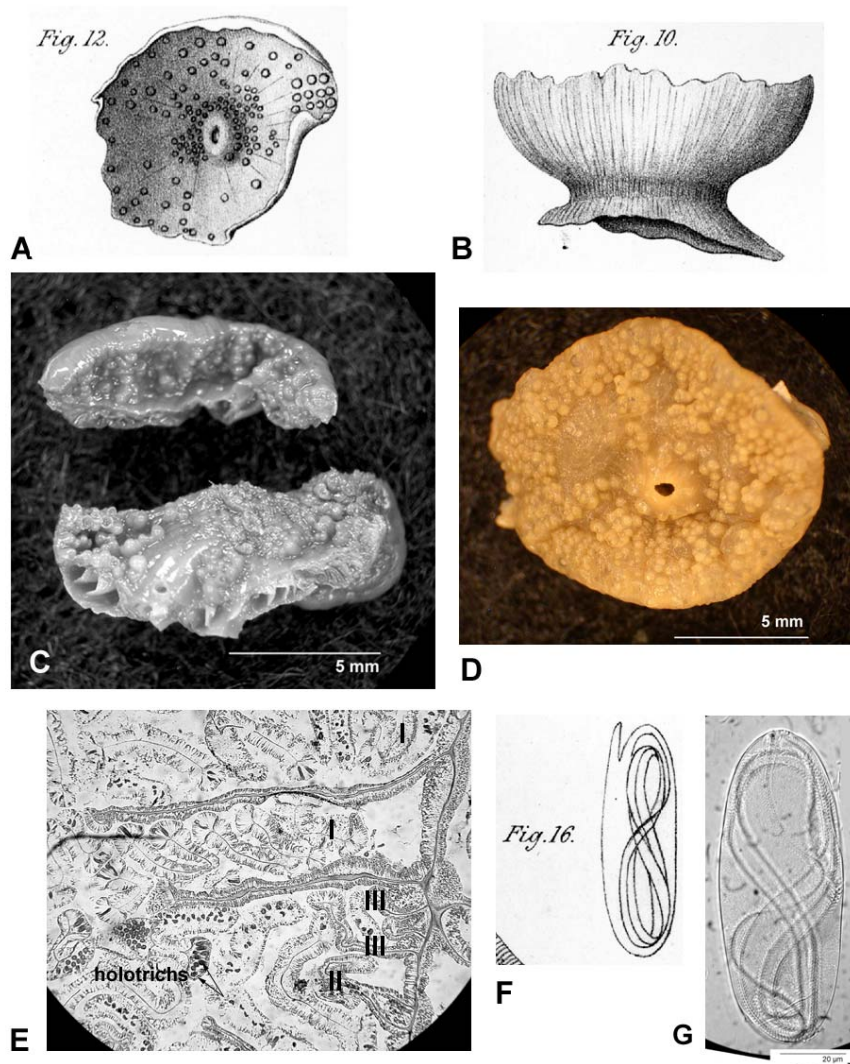


Figure 3-9. *Discosoma fowleri* (Fowler, 1889). A: oral disc view from the original description (Fowler, 1888, Plate XV, fig. 12); B: side view from the original description (Fowler, 1888, Plate XV, fig. 10); C: syntype specimen (BMNH 1894.2.7.1); D: whole specimen (USNM 52494); E: transverse section (USNM 52494), note three cycles of mesenteries (I, II, and III) and holotrichs in mesenterial filaments; F: “large cnidocil” (Fowler, 1888, Plate XV, fig. 16); G: holotrichs I from mesenterial filaments.

***Discosoma neglecta* (Duchassaing and Michelotti, 1860)**

Synonymy

Isaura neglecta Duchassaing and Michelotti, 1860

Paradiscosoma neglecta (Duchassaing and Michelotti, 1860): Carlgren, 1900;

Carlgren, 1943: Carlgren, 1949

Discosoma neglecta (Duchassaing and Michelotti, 1860): den Hartog, 1980

Body shape, size and color

Oral disc diameter 15-60 mm, pedal disc diameter 12-35 mm; column length up to 30 mm. Color: yellow in formalin.

Oral disc and tentacles

Oral disc circular; margin drawn out into a variable number of distinct outgrowths, large marginal outgrowths often alternate with smaller ones, tips of outgrowths often trifid (Figure 3-10, A and B). Discal tentacles arranged in radial rows papilliform, immature discal tentacles embedded in mesoglea (Figure 3-10), irregular arrangement in an endocoelic row. Marginal tentacles absent.

Internal anatomy

Mesenteries complete and incomplete; number of mesenteries varies. Sphincter muscle very weak, diffuse (Figure 3-10E).

Cnidae: measured from three specimens, two of USNM 51674 and one of USNM 51674

Discal tentacles:

Holotrichs III	32.45-53.86 x 8.29-12.89 μ m	n= 20, N=2/3
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Microbasic <i>b</i> -mastigophores	12.06-18.33 x 4.67-5.32 μm	n= 12, N=2/3
Microbasic <i>p</i> -mastigophores	17.20-36.35 x 4.90-6.59 μm	n= 28, N=3/3
Mesenterial filaments:		
Holotrichs I	134.85-161.39 x 52.90-77.26 μm	n= 18, N=2/3
Holotrichs II	32.98-61.50 x 14.33-20.48 μm	n= 32, N=3/3
Microbasic <i>p</i> -mastigophores	30.80-44.02 x 5.90-11.23 μm	n= 21, N=2/3
Microbasic <i>p</i> -mastigophores	16.84-27.80 x 4.10-6.25 μm	n= 24, N=3/3
Column		
Holotrichs III	22.90-25.49 x 5.33-5.90 μm	n= 6, N=2/3
Microbasic <i>b</i> -mastigophores	14.50-21.30 x 4.32-5.97 μm	n= 18, N=2/3
Microbasic <i>p</i> -mastigophores	12.89-30.97 x 4.68-6.30 μm	n= 32, N=3/3

Type specimens and locality

No type specimens designated.

Type locality: Caribbean Sea, Antilles; 16.26°N 62.52°W

Other material examined

Curaçao

RMNH 12006: south coast; depth 15 m; Jul-18-1973; 5 specimens

RMNH 12007: south coast; depth 5-10 m; Aug-25-1972; 6 specimens

RMNH 12008: south coast; Nov-1971; 1 specimen

Jamaica

USNM 52505: Port Royal, Biddlecomb shoal; depth 20 m; Dec-3-1961; 2 specimens

St. John, US Virgin Islands

USNM 51674: Cabritt Horn Point; depth 22.5 m, Mar-24-1960; 1 specimen

Nomenclatural/ Taxonomic notes

Isaura neglecta was originally described as by Duchassing and Michelotti, 1860. The genus *Isaura* belongs to the order Zoanthidea and authors unfortunately did not provide clear reasons for their placement of the species in *Isaura*. Carlgren (1900) reexamined the species and he established a new genus *Paradiscosoma*. Therefore, *Paradiscosoma neglecta* (Duchassaing and Michelotti, 1860) is the new combination for *I. neglecta* Duchassing and Michelotti, 1860. Carlgren (1900) reasoned that the genus *Paradiscosoma* is distinctive in having marginal lobes instead of marginal tentacles in other species in *Discosoma*. Stephenson (1922) accepted Carlgren's perspective and stated that "*Paradiscosoma* differs from *Discosoma* with margin of disc thrown into small lobes. Otherwise like *Discosoma*." I recognized that the marginal lobes of *P. neglecta* are histologically identical to the rest of the margin (Figure 3-10C), thus the presence of marginal lobes of *P. neglecta* is unique character of the species. However, except the marginal lobes, the species is well accommodated in *Discosoma* based on major diagnostic characters (see Table 3-2). Therefore, I treated the presence of marginal lobes of *P. neglecta* as a species-level character, and synonymized *Paradiscosoma* with *Discosoma* in this study. The size of holotrichs I in mesenterial filaments measured in this study is slightly smaller than the one in den Hartog (1980). Holotrichs III in column is very rare.

Geographical distribution

The species is known from Caribbean Sea: Bahamas, St. Thomas, Jamaica, and Haiti.

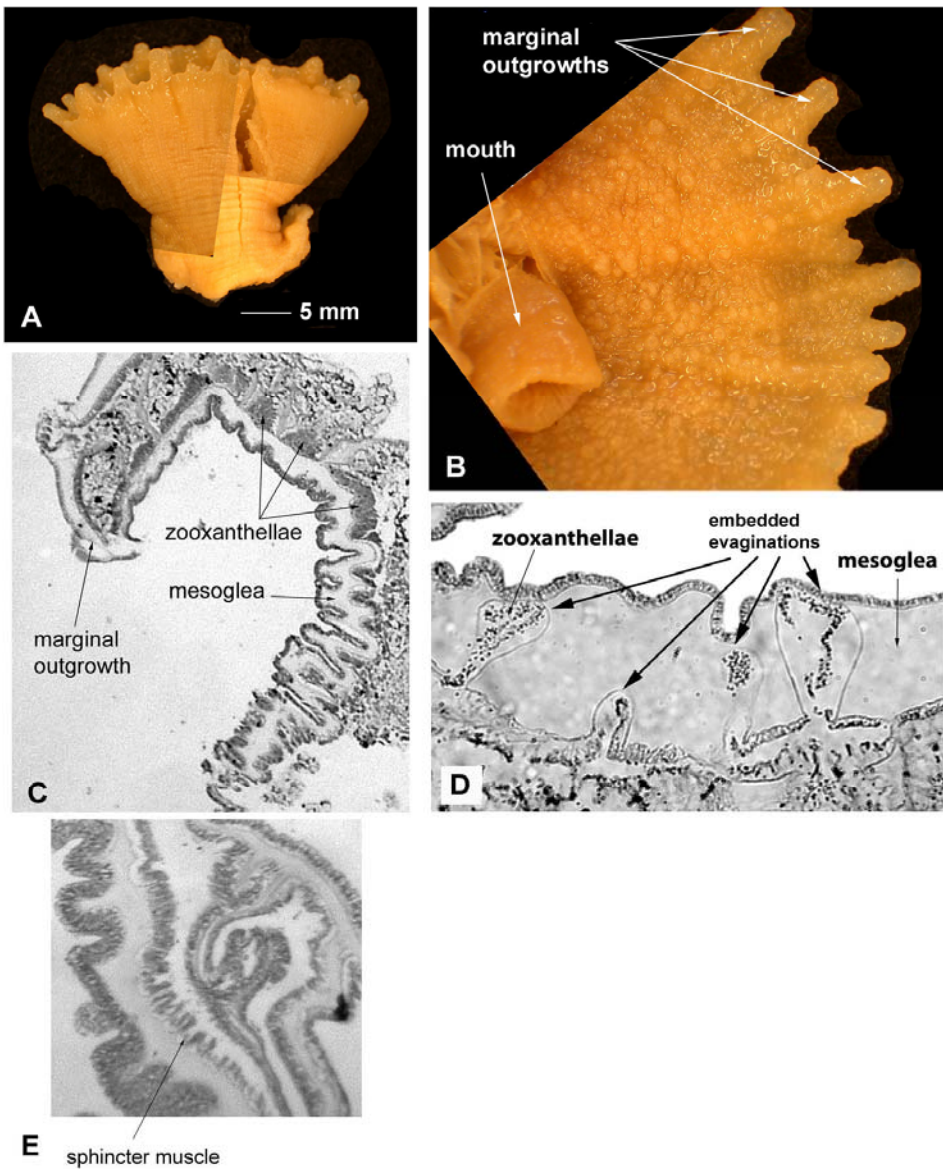


Figure 3-10. *Discosoma neglecta* (Duchassaing and Michelotti, 1860). A: whole body (USNM 52505); B: oral disc and marginal outgrowths (USNM 52505); C: longitudinal section of a small specimen (RMNH 12007); D: embedded oral disc evaginations of a small specimen (RMNH 12007); E: longitudinal section (USNM 52505), note weak marginal sphincter muscle.

Genus *Actinotryx* Duchassaing and Michelotti, 1860

Synonymy

Orinia Duchassaing and Michelotti, 1864

Diagnosis

Two types of tentacles: papilliform, often branched discal tentacles, digitiform marginal tentacles. Tentacle-free zone between discal tentacles and marginal tentacles.

Mesenteries complete and incomplete. Sphincter muscle endodermal, weak, diffuse.

Asexual reproduction by longitudinal fission usual. Often gregarious. Cnidom:

holotrichs, microbasic *b*- and *p*- mastigophores.

Nomenclatural/ Taxonomic notes

The synonymy of *Actinotryx* is discussed at nomenclatural/ taxonomic notes of the type species.

Type species: *Actinotryx sanctithomae* Duchassaing and Michelotti, 1860

***Actinotryx sanctithomae* Duchassaing and Michelotti, 1860**

Synonymy

Actinotryx Sancti Thomae Duchassaing and Michelotti, 1860

Orinia torpida Duchassaing and Michelotti, 1860

Rhodactis Sancti Thomae (Duchassing and Michelotti, 1860): McMurrich, 1889

Actinotryx Sancti-Thomæ Duchassing and Michelotti, 1860: Haddon, 1898

Actinotryx macropapillata Weill, 1929

Rhodactis sancti thomae (Duchassing and Michelotti, 1860): Carlgren, 1949

Discosoma sanctithomae (Duchassing and Michelotti, 1860): den Hartog, 1980

Body shape, size and color

Oral disc diameter 15-35 mm, pedal disc diameter 7-24 mm (pedal disc expansion excluded); column length to 5 mm. Color: brown in alcohol to pale yellow in formalin. In life color of species various: column brown, purple, green; tentacles same with column coloration, often brighter than column color (Figure 3-12B).

Oral disc and tentacles

Oral disc circular; small tentacles around mouth (Figure 3-12B). Discal tentacles papilliform, often branched in larger specimens, arranged in radial rows: 3 to 8 discal tentacles in endocoelic row in small specimens, arrangement irregular in larger specimens (Figure 3-12, C and D). Marginal tentacles digitiform.

Internal anatomy

The number of mesenteries varies: approximately 80 pairs (24 complete, 56 incomplete) in a small specimen, 168 pairs (44 complete, 124 incomplete) in a large specimen. Sphincter muscle endodermal, very weak, diffuse (Figure 3-12E).

Cnidae: measured from four specimens, each of USNM 56548, KUNHM 002369, 002391, and 002395

Marginal tentacles:

Holotrichs I	72.42-121.53 x 35.07-51.19 μm	n= 33, N=4/4
Holotrichs II	33.05-42.93 x 7.46-13.77 μm	n= 18, N=4/4
Holotrichs III	31.76-48.52 x 6.03-9.96 μm	n= 32, N=4/4

Microbasic <i>b</i> -mastigophores	18.44-29.08 x 4.21-5.63 μm	n= 22, N=4/4
Microbasic <i>p</i> -mastigophores	16.97-30.37 x 4.51-8.60 μm	n= 25, N=4/4
Discal tentacles:		
Holotrichs I	73.90-120.08 x 37.40-50.78 μm	n= 33, N=4/4
Holotrichs II	35.32-49.65 x 13.08-18.44 μm	n= 46, N=4/4
Microbasic <i>p</i> -mastigophores	18.44-23.96 x 5.11-9.24 μm	n= 26, N=4/4
Mesenterial filaments:		
Holotrichs I	162.47-250.65 x 64.32-82.16 μm	n= 28, N=4/4
Holotrichs II	34.93-58.34 x 16.13-22.58 μm	n= 33, N=4/4
Microbasic <i>p</i> -mastigophores	36.49-43.72 x 7.02-10.83 μm	n= 41, N=4/4
Microbasic <i>p</i> -mastigophores	13.44-20.75 x 3.96-5.84 μm	n= 22, N=4/4
Column		
Microbasic <i>b</i> -mastigophores	16.30-20.18 x 5.36-8.72 μm	n= 36, N=4/4
Microbasic <i>p</i> -mastigophores	21.48-35.50 x 6.94-10.31 μm	n= 30, N=4/4

Type specimens and locality

No type specimens designated.

Type locality: St. Thomas, Virgin Islands

Other material examined

British Honduras

USNM 56548: Carrie Bow Cay, sand through on outer fore reef; depth 15-18 m; Mar-25-1978; 1 specimen

St. Thomas, US Virgin Islands

KUNHM 002369: Brewers Bay; 18°20.0'N, 64°58.8'W; depth 0.7 m; Aug-15-2004; 6 specimens

KUNHM 002371: N. Saba Is.; depth 3-6 m; Aug-18-2004; 10 specimens

KUNHM 002372: Water Is., Sprat Point; 18°18'09.1"N, 64°54'19.4"W; depth 6-7.5 m; 10 specimens

Bocas del Toro, Panama

KUNHM 002391: Cayo Adriana; 09°14'45.6"N, 82° 10'41.3"W; depth 12 m; Aug-9-2004; 1 specimen

KUNHM 002395: Crawl Cay; 09°15'261"N, 82° 7'787"W; depth 2-4 m; Aug-6-2004; 2 specimens

KUNHM 002396: Crawl Cay; 09°15'261"N, 82° 7'787"W; depth 2-4 m; Aug-6-2004; 2 specimens

Jamaica

USNM 19042: Port Royal Cay; 3 specimens

USNM 51641: Port Royal Cay, on reef flat; Dec-1-1959; 10 specimens

Puerto Rico

USNM 53260: Parquera, Cayo Enrique, on dead coral; depth 1 m; Aug-18-1964; 22 specimens

Geographical distribution

Actinotryx santithomae is known from all around the Caribbean Sea.

Nomenclatural/ Taxonomic notes

The brief original description provides only limited criteria for delimitating the species. Fortunately, the original description contains an illustration including several critical morphological features for recognition of *Actinotryx sanctithomae* (Figure 3-12A): branched discal tentacles, digitiform marginal tentacles, and tentacle-free zone on the oral disc. The synonymy of *A. sanctithomae* and *Orinia torpida* has been discussed in McMurrich (1905), Stephenson (1922), Carlgren (1934), and den Hartog (1980). Both species are described from St. Thomas, US Virgin Islands by Duchassaing and Michelotti (1864). In the original description, authors stated that *Orinia torpida* is characterized by tubular openings (“orifices tubuleux”) (Figure 3-12A). Later Carlgren (1900, 1934), McMurrich (1905), and Stephenson (1922) re-examined the single specimen deposited in the Duchassaing and Michelotti collection in the Zoological Museum of Turin. McMurrich (1905) stated not every tentacle has a terminal opening, and Stephenson (1922) concluded that the tubular opening is actually the collapsed vesicular tentacles. Although Carlgren (1900) recognized the similarities of the two species in two types of tentacles and tentacle-free zone on the oral disc, in his later paper (Carlgren, 1934), he concluded *O. torpida* differs from *A. sanctithomae* based on the shape and the arrangement of these tentacles. den Hartog (1980) examined the type specimen of *O. torpida* and he concluded that *O. torpida* is an abnormal specimen of *A. sanctithomae*. I agree on the synonymy of den Hartog (1980) based on my own examination of syntype specimen of *O. torpida* (SMNH Cat. 71). Even though the syntype specimen of *O. torpida* has been damaged and only a

wedge left (Figure 3-11B), a few critical morphological characters of the specimen have left: shape of discal tentacles is palmate and presence of tentacle-free zone on oral disc. The comparisons between two type species are shown in Table 3-2. In my view, tubular openings of discal tentacles may be caused by the common behavior of many species in Discosomatidae: they extrude mesenterial filaments through tentacle tips and mouth when they disturbed.

The *Actinotryx* has been confused with genera *Discosoma* and *Rhodactis*. The name of genus *Discosoma*, represented by the type species *D. nummiforme*, was introduced by Rüppel and Leuckart in 1828. *Rhodactis rhodostoma* (Hemprich and Ehrenberg in Ehrenberg, 1834) known from Red Sea is the type species of *Rhodactis*. McMurrich (1889) and Carlgren (1949) considered *Actinotryx* is a synonym of *Rhodactis* based on branched discal tentacles and absence of sphincter muscle. However, I found weak sphincter muscle (Figure 3-12D) from the specimen collected from St. Thomas, US Virgin Islands, which separate *Actinotryx* from *Rhodactis*. I also found papilliform discal tentacles (Figure 3-12C) as well as branched ones (Figure 3-12D) from the specimens of *Actinotryx sanctithomae*. den Hartog (1980) synonymized *Actinotryx* with *Discosoma* because he considered traditional genus-level diagnostic characters – tentacle-free zone and shape of discal tentacles -- with very little diagnostic value. However, *Actinotryx sanctithomae*, the type species of genus *Actinotryx*, differs from *Discosoma nummiforme* in external morphology and the measurement of nematocysts (Table 3-2). The distinctions between two type species strongly support the separation

of genus *Actinotryx* from genus *Discosoma*, and resuscitation of *Actinotryx*.

Discosoma has been applied to species that has features like extremely reduced papilliform discal tentacles, no naked zone on oral disc, and absence or presence of reduced marginal tentacles. While based on observations and original description and illustration of the type species, *Actinotryx* has features such as branched discal tentacles, digitiform marginal tentacles, and presence of naked zone on oral disc between marginal and discal tentacles. *A. sanctithomae* is easily distinguished from *Discosoma* and *Rhodactis* in field based on diagnostic keys provided in this study.

Weill (1929) incorrectly identified *Actinotryx sanctithomae* and proposed a new name *Actinotryx macropapillata* for *A. sanctithomae*. In 1934, he corrected his misidentification himself based on the original description (Duchassing and Michelotti, 1864) and subsequent description (Duerden, 1900). Therefore, *Actinotryx macropapillata* is a junior synonym.

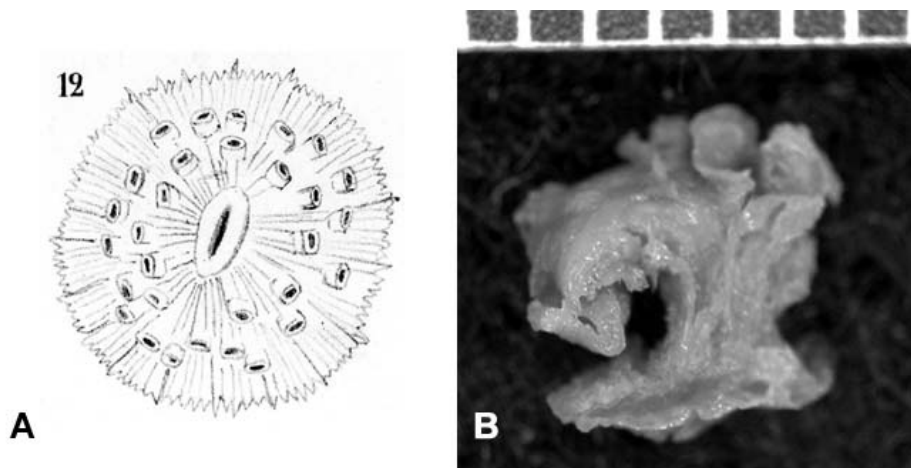


Figure 3-11. *Orinia torpida* Duchassaing and Michellotti, 1860. A: illustration from the original description (Duchassaing and Michelotti, 1860, Plate VII, fig. 12); B: Syntype specimen (SMNH 71).

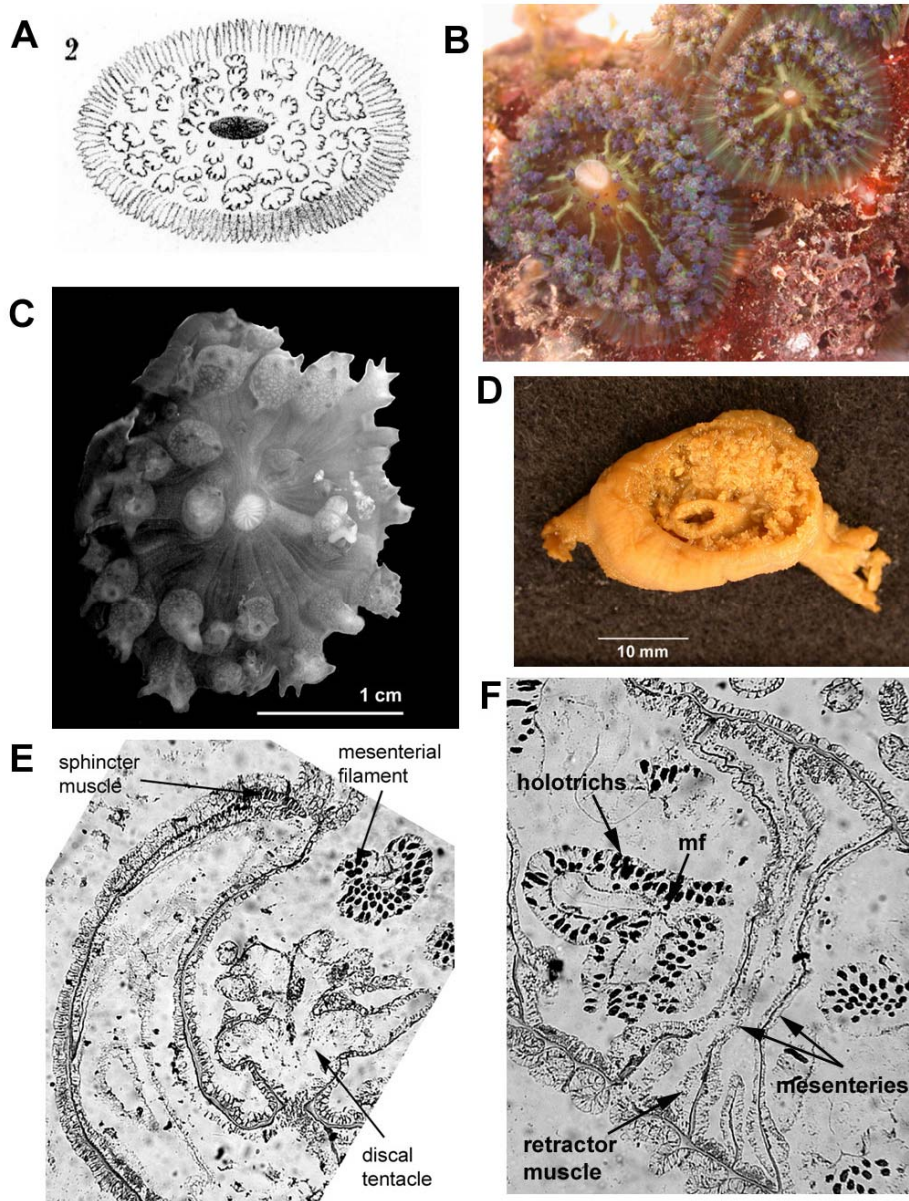


Figure 3-12. *Actinotryx sanctithomae* Duchassaing and Michelotti, 1860. A: illustration in the original description (Duchassaing and Michelotti, 1860, Plate VII, fig. 2); B: species in life; C: oral disc (KUNHM 002371); D: whole body (UNSM 19042); E: longitudinal section of oral disc (KUNHM 002371); F: transverse section (KUNHM 002371).

Biological notes

The aggressive behavior of *Actinotryx sanctithomae* is reported. Miles (1991) observed that the tropical corallimorpharian *A. sanctithomae* uses both marginal tentacles and mesenterial filaments to damage adjacent scleractinian corals. He found that in 75% of cases where *A. sanctithomae* was adjacent to a scleractinian there were areas of dead coral associated with the area of contact.

A symbiotic association with shrimp species, *Periclimenes yucatanicus*, is reported from St. Croix, US Virgin Islands and from Martinique (Williams and Williams, 1982; Spotte et al., 1991; Ritson-Williams and Paul, 2007).

Genus *Amplexidiscus* Dunn and Hamner, 1980

Diagnosis (modified from Dunn and Hamner, 1980):

Tentacles digitiform. Tentacle-free zone between outermost and inner discal tentacles. Mesenteries complete. Sphincter muscle absent. Basilar muscles weak. Solitary or gregarious. Cnidom: holotrichs, microbasic *b*- and *p*- mastigophores, spirocysts (rare).

Type species: *Amplexidiscus fenestrafer* Dunn and Hamner, 1980

***Amplexidiscus fenestrafer* Dunn and Hamner, 1980**

Synonymy

Discosoma fenestrafer (Dunn and Hamner, 1980): den Hartog, 1997; Uchida and Soyama, 2001

Body shape, size and color

Oral disc diameter up to 450 mm, pedal disc diameter up to 180 mm; column length up to 50 mm. Color: pale yellow in formalin. According to Dunn and Hamner (1980) in life oral disc dull grey-greenish brown, lighting toward margin; column similar to that of oral disc distally, fading basally to color of pedal disc.

Oral disc and tentacles

Tentacles digitiform, endocoelic, discal tentacles longer than marginal tentacles. Marginal tentacles sparse, little shorter when oral disc expanded, digitiform when oral disc enfolded. Area immediately around mouth may lack tentacles. Several tentacles may occur in tentacle-free zone occasionally.

Internal anatomy

I was not allowed to make histological sections of the type specimens. Therefore, the description of internal anatomy is based on the original description, Dunn and Hamner (1980). Mesenteries very narrow, most or all complete, approximately 500 pairs in average-sized animal. Sphincter muscle absent.

Cnidae: measured from the holotype (CASIZ 15553) and the paratype (CASIZ 15554)

Marginal tentacles:

Holotrichs I	86.32-139.43 x 30.45-52.48 μm	n= 20, N=2/2
Holotrichs II	43.42-53.80 x 13.36-21.45 μm	n= 12, N=2/2
Holotrichs III	34.66-68.20 x 5.63-10.46 μm	n= 20, N=2/2
Microbasic <i>p</i> -mastigophores	16.97-30.25 x 3.46-7.49 μm	n= 18, N=2/2
Sprirocysts	19.35-22.35 x 3.06-3.93 μm	n= 2, N=1/2

Discal tentacles:

Holotrichs I	105.33-120.46 x 49.48-46.05 μm	n= 6, N=2/2
Holotrichs II	42.33-53.47 x 14.38-19.36 μm	n= 31, N=2/2
Microbasic <i>p</i> -mastigophores	17.44-21.84 x 3.98-8.12 μm	n= 13, N=2/2
Sprirocysts	18.64-26.52 x 4.38-5.86 μm	n= 3, N=1/2

Mesenterial filaments:

Holotrichs I	154.65-218.40 x 51.68-62.36 μm	n= 18, N=2/2
Holotrichs II	43.57-62.71 x 13.42-20.46 μm	n= 28, N=2/2

Hoplotelic microbasic <i>p</i> -mastigophores	24.57-48.46 x 6.42-10.33 μm	n= 30, N=2/2
Column		
Holotrichs II	48.33-60.35 x 13.06-21.38 μm	n= 16, N=2/2
Microbasic <i>p</i> -mastigophores	17.32-24.60 x 6.06-9.46 μm	n= 24, N=2/2
Microbasic <i>b</i> -mastigophores	16.42-26.33 x 5.59-8.37 μm	n= 18, N=2/2

Type specimens and locality

Holotype:

CASIZ 15553: Lizard Island, Great Barrier Reef, Queensland, Australia; 14°40'S, 145°30'E; depth 10 m; Jan-8-1977; 1 specimen

Paratype:

CASIZ 15554: Lizard Island, Great Barrier Reef, Queensland, Australia; 14°40'S, 145°30'E; depth 10 m; Jan-8-1977; 1 specimen

Geographical distribution

Amplexidiscus fenestrafer is known from Great Barrier Reef, Australia and Madang Province, Papua New Guinea.

Nomenclatural/ Taxonomic notes

Spirocysts in discal and marginal tentacles are very rare as discussed in Dunn and Hamner (1980).

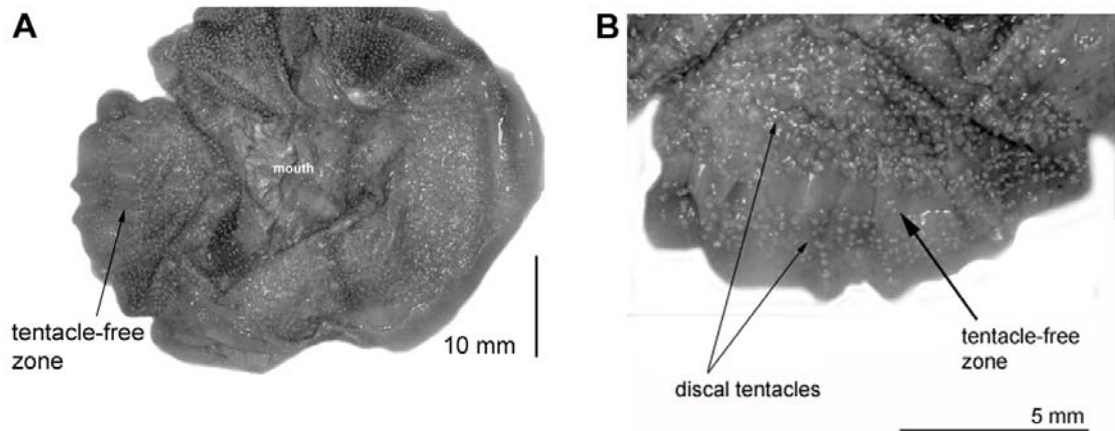


Figure 3-13. *Amplexidiscus fenestrafer* Dunn and Hamner, 1980. A: whole specimen of the holotype (CASIZ 15553); B: tentacle-free zone on the oral disc.

Genus *Rhodactis* Milne Edwards and Haime, 1851

Diagnosis

Two types of tentacles: branched discal tentacles and digitiform marginal tentacles, non-retractile. No tentacle-free zone. Mesenteries complete and incomplete. One directive mesentery. Sphincter muscle absent. Asexual reproduction by longitudinal fission usual. Often gregarious. Cnidom: holotrichs, microbasic *b*- and *p*-mastigophores.

Nomenclatural/ Taxonomic notes

The synonymy of *Rhodactis* is discussed at nomenclatural/ taxonomic notes of the type species.

Type species: *Rhodactis rhodostoma* (Hemprich and Ehrenberg in Ehrenberg, 1834)

***Rhodactis rhodostoma* (Hemprich and Ehrenberg in Ehrenberg, 1834)**

Synonymy

Metridium rhodostoma Hemprich and Ehrenberg in Ehrenberg, 1834

Rhodactis rhodostoma (Ehrenberg, 1834): Milne Edwards and Haime, 1851

Discosoma rhodostoma (Ehrenberg, 1834): den Hartog, 1980

Body shape, size and color

Oral disc diameter 25-38 mm, pedal disc diameter 22-30 mm; column length up to 12 mm. In life oral disc diameter up to 45 mm, column length up to 15 mm.

Color: pale yellow in formalin. In life color of species various: column brown to purple; tentacles similar to column coloration; mouth bright purple or white (Figure 3-14A).

Oral disc and tentacles

Two types of tentacles: branched discal tentacles (Figure 3-14, B and C) and digitiform marginal tentacles. Tentacles arranged in radial rows: discal tentacles more branched, densely arranged distally; tentacles immediate near of mouth shorter; 5-12 distal tentacles in an endocoelic row.

Internal anatomy

The number of mesenteries varies: approximately 72 pairs (24 complete, 48 incomplete) in a small specimen, 124 pairs (36 complete, 68 incomplete) in a large specimen. One directive (Figure 3-14D). Sphincter muscle absent.

Cnidae: measured from three specimens, each of KUNHM 002093, USNM 52016, and USNM 52478

Marginal tentacles:

Holotrichs I	97.61-97.60 x 44.52-49.96 μm	n= 11, N=2/3
Holotrichs II	39.13-49.66 x 12.48-20.19 μm	n= 24, N=3/3
Holotrichs III	31.17-49.67 x 4.74-9.23 μm	n= 31, N=3/3
Microbasic <i>b</i> -mastigophores	18.34-20.85 x 5.63-7.65 μm	n= 22, N=2/3
Microbasic <i>p</i> -mastigophores	23.16-26.68 x 8.11-10.52 μm	n= 24, N=3/3

Discal tentacles:

Holotrichs I	145.33-155.03 x 78.05-80.04 μm	n= 14, N=3/3
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Holotrichs II	39.32-48.63 x 14.77-18.45 μm	n= 21, N=3/3
Microbasic <i>p</i> -mastigophores	21.86-26.29 x 6.45-10.82 μm	n= 24, N=3/3
Microbasic <i>b</i> -mastigophores	18.50-23.53 x 5.85-6.49 μm	n= 18, N=3/3
Mesenterial filaments:		
Holotrichs I	150.89-178.96 x 72.22-91.22 μm	n= 12, N=2/3
Microbasic <i>p</i> -mastigophores	35.23-41.91 x 9.86-12.98 μm	n= 32, N=3/3
Column		
Holotrichs III	25.42-42.33 x 8.56-16.55 μm	n= 20, N=3/3
Microbasic <i>p</i> -mastigophores	18.33-32.89 x 4.57-10.24 μm	n= 30, N=3/3
Microbasic <i>b</i> -mastigophores	14.86-19.35 x 4.35-6.47 μm	n= 16, N=2/3

Type specimens and locality

No type specimens designated.

Type locality: Red Sea, Tor

Other material examined

Oman

KUNHM 002093: Fahal Island, 23°32'01"N 58°41'57"W; depth 6 m; May-21-2004; 3 specimens

KUNHM 002099: Bander Khayran, 23°31'39"N 58°44'23"W; depth 7.5 m; May-27-2004; 4 specimens

KUNHM 002100: Bander Khayran, 23°31'39"N 58°44'23"W; depth 6 m; May-27-2004; 3 specimens

Madagascar

USNM 52016: Nosy Be, Nosy Komba, Point Ambarionaomby; depth 2 m; Aug-18-1960; 4 specimens

Red Sea, Gulf of Aqaba

USNM 52478: Israel, Eilat; depth 1 m; Apr-29-1962; 1 specimen

Nomenclatural/ Taxonomic notes

Rhodactis rhodostoma (Hemprich and Ehrenberg in Ehrenberg, 1834) was originally described as *Metridium rhodostoma*. The author neither designated type specimens nor provided reasons for placing the species in an actiniarian genus *Metridium* because there were only two genera of sea anemones at that time. Later Milne Edwards and Haime (1851) realized that the species is different from any members of *Metridium* in tentacle shape and arrangement, and established the genus *Rhodactis* based on *Metridium rhodostoma* Hemprich and Ehrenberg in Ehrenberg, 1834. den Hartog (1980) synonymized *Rhodactis* with *Discosoma*. den Hartog (1980) considered the supposed generic characters, the presence or absence of marginal tentacles, the presence or absence of a tentacle-free zone, and the shape of discal tentacles, as variations at species-level. He studied only three Caribbean species, *Discosoma sanctithomae* (*Actinotryx sanctithomae* in this study), *Rhodactis carlgreni* (*Discosoma carlgreni* in this study), and *Paradiscosoma neglecta* (*Discosoma neglecta* in this study), but he did not examine the type species of *Rhodactis* and *Discosoma*. Based on my examination of the type species of *Rhodactis* and *Discosoma*, there are distinctive characters that differentiate the genera (Table 4-3).

Rhodactis rhodostoma differs from *Discosoma nummiforme* in shape and length of discal tentacles, and length of marginal tentacles; therefore, I conclude that *Rhodactis* is a valid genus in Discosomatidae.

Biological notes

Langmead and Chadwick-Furman (1999) observed polyps of the corallimorpharian *Rhodactis rhodostoma* overgrowing encrusting macroalgae, sponges, scleractinian corals, and zoanthids at Eilat, in the northern Red Sea. Furthermore they were able to describe a competitive hierarchy within the stony corals with regard to the outcome of agonistic interactions between *R. rhodostoma* with members of the families Faviidae and Mussidae being observed in standoff interactions, whilst Acroporidae, Pocilloporidae and Poritidae were either damaged or overgrown. The terminal ends of the oral disk marginal tentacles of *R. rhodostoma* were bulbous or swollen during contact with other cnidarians, including having significantly thicker ectoderm and a higher proportion of holotrichous nematocysts than did 'normal' filiform marginal tentacles of this species. Also polyps of *R. rhodostoma* were observed to overgrow zoanthids, hydrozoan corals, sponges and encrusting macroalgae on a fringing reef at Eilat in the northern Red Sea (Muhandro et al., 2002).

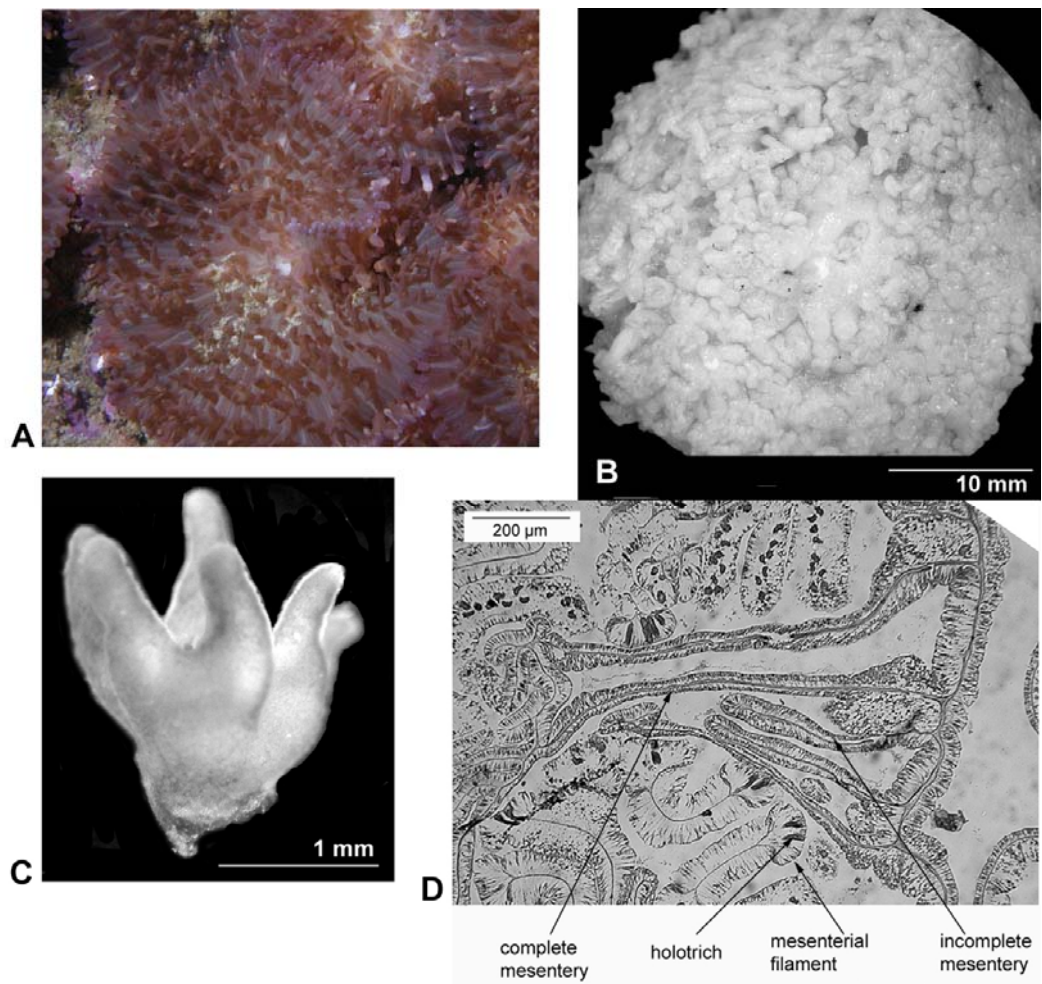


Figure 3-14. *Rhodactis rhodostoma* (Ehrenberg, 1834). A: species in life (KUNHM 002093); B: whole specimen (USNM 52016); C: branched discal tentacle; D: mesenterial arrangement (KUNHM 002100).

Genus *Metarhodactis* Carlgren, 1943

Diagnosis

Discal tentacles papilliform or branched, no marginal tentacles. No tentacle-free zone. Mesenteries complete and incomplete. Sphincter muscle absent. Cnidom: holotrachs, microbasic *b*- and *p*- mastigophores, hoplotelic microbasic *p*-mastigophores numerous in mesenterial filaments.

Nomenclatural/ Taxonomic notes

Metarhodactis Carlgren, 1943 was established based on the type species, *M. boninensis* Carlgren, 1943. den Hartog (1980) questionably synonymized *Metarhodactis* with *Discosoma* and stated the need of examining nematocysts composition of type species to verify his synonymization. Although external morphology is similar to members of *Discosoma*, *Metarhodactis* can be distinguished from most genera in Discosomatidae by possessing numerous hoplotelic microbasic *p*-mastigophores in mesenterial filaments (Figure 3-15C). Hoplotelic microbasic *p*-mastigophores are present in the family Corallimorphidae. Despite hoplotelic microbasic *p*-mastigophores are found in genus *Amplexidiscus*, they are much less numerous. Because the composition of nematocysts is generic character in hexacorallian taxonomy, in this study, I conclude that *Metarhodactis* is a valid genus in the family Discosomatidae.

Type species: *Metarhodactis boninensis* Carlgren, 1943

***Metarhodactis boninensis* Carlgren, 1943**

Synonymy

Metarhodactis boniensis Carlgren, 1943: Carlgren, 1949

? *Discosoma boninensis* (Carlgren, 1943): den Hartog, 1980

Body shape, size and color

Oral disc diameter up to 25 mm, pedal disc diameter up to 15 mm; column length 4-12 mm. Color: pale yellow in formalin.

Oral disc and tentacles

Oral disc circular or oval-shape; often slightly crenulated. No marginal tentacles.

Discal tentacles papilliform or branched; simpler toward margin of oral disc. Tentacles arranged in radial row (Figure 3-15A); branched discal tentacles arrange in endocoelic rows, papilliform tentacles arrange in exocoelic rows. The number of tentacles vary according to the size of specimens; more tentacles in larger specimens.

Internal anatomy

Mesenteries arranged irregularly: 24 complete mesenteries, numerous incomplete mesenteries sterile without well-developed filaments. Sphincter muscle absent.

Cnidae: measured from the syntype (Uuzm 632) and two specimens of USNM 50099

Discal tentacles:

Holotrachs II	33.20-50.02 x 10.82-16.52 μm	n= 45, N=3/3
Microbasic <i>p</i> -mastigophores	13.88-18.55 x 4.33-7.57 μm	n= 21, N=3/3
Microbasic <i>b</i> -mastigophores	12.55-14.81 x 1.78-2.31 μm	n= 22, N=3/3

Mesenterial filaments:

Holotrichs I	134.1-184.13 x 63.75-73.69 μm	n= 24, N=3/3
Holotrichs II	38.28-47.30 x 12.30-14.25 μm	n= 20, N=3/3
Hoplotelic microbasic <i>p</i> -mastigophores	42.23-79.12 x 3.09-5.41 μm	n= 19, N=3/3

Column

Holotrichs II	37.25-43.31 x 13.15-17.97 μm	n= 20, N=3/3
Microbasic <i>b</i> -mastigophores	14.50-17.60 x 4.79-6.46 μm	n= 22, N=3/3
Microbasic <i>p</i> -mastigophores	16.33-21.49 x 6.12-8.42 μm	n= 36, N=3/3

Type specimens and locality

Syntype:

UUZM 632: Port Lloyd, Bonin Islands, Japan; 27.14°N 142.20°W; depth 0-9 m; 2 specimens

Other material examined

Northern Mariana Islands

USNM 50099: Saipan Islands; May-3-1949; 5 specimens

Nomenclatural/ Taxonomic notes

Specimens of USNM 50099 were identified by O. Carlgren, who described the genus and the species. One specimen of USNM 50099 has a small polyp attached to the column of larger specimen (Figure 3-15B). This specimen provides evidence of asexual reproduction of the species.

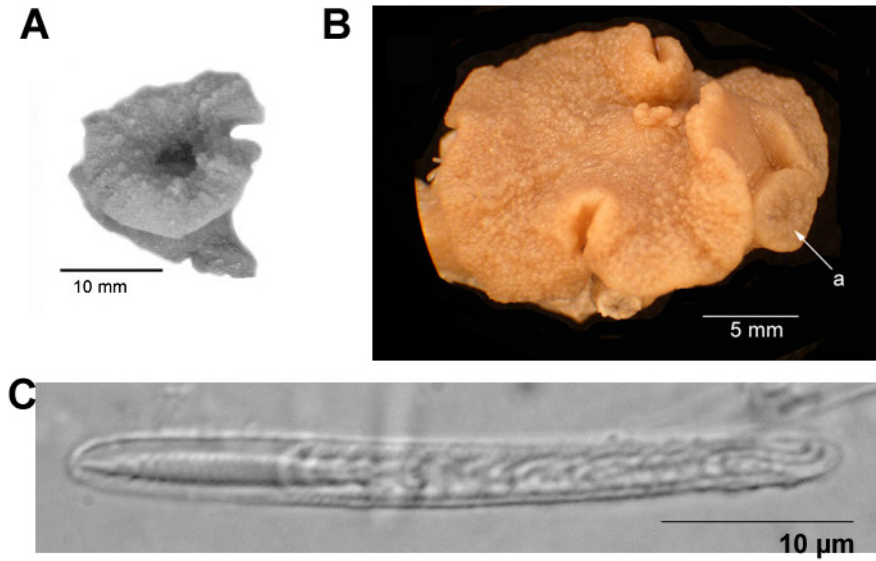


Figure 3-15. *Metarhodactis boninensis* Carlgren, 1943. A: whole specimen of the syntype; B: whole specimen (USNM 50099), note a polyp reproduced by asexual reproduction (a); C: hoplotelic microbasic *p*-mastigophore in mesenterial filaments (USNM 50099).

CHAPTER IV. PHYLOGENY

4-1. Taxon sampling and character selection

The primary goal was to include at least one species representing each of the 11 valid corallimorpharian genera in my analyses. The diagnostic features for the genera included are described in chapter IV. Corallimorpharian species included in the analyses are restricted to those treated in detail in the taxonomic section of this study. To investigate sister group relationships of Corallimorpharia, I included representatives of the both evolutionary lineages of Scleractinia, complex and robust (Romano and Cairns, 2000), and taxa representing three of the four tribes of Actiniaria, Acontiarina, Endomyaria, and Athenaria (Carlgren, 1949; Dunn, 1982). The genus *Cerianthus* of order Ceriantharia was used as an outgroup for analyses. Cerianthids are widely recognized as the sister group to the remaining orders Actiniaria, Corallimorpharia, and Scleractinia (Schmidt, 1974; Fautin and Lowenstein, 1992; Bernsten et al., 1999). Chen et al. (1995) found *Cerianthus* to be the deepest node within Anthozoa in a phylogeny derived from 28S rDNA data. Ceriantharia was the deepest node in the hexacorallian branch according to phylogenetic inference based on 16S rDNA by France et al. (1996).

Morphological analyses:

Characters were collected from specimens of type species rather than from the literature. If only one or two specimens were available, the original description or the

redescriptions of the taxon were also used as a source of data. Seven species of Actiniaria, each from a different genus, were included. Two genera (*Anthopleura* and *Stichodactyla*) belong to tribe Endomyaria, three genera (*Aiptasia*, *Bathypheilia*, and *Metridium*) belong to tribe Acontaria, and two genera (*Edwardsia* and *Nematostella*) belong to tribe Athenaria. Seven species of Scleractinia, each from a different genus, were included. Three genera (*Caryophyllia*, *Oculina*, and *Montastrea*) belong to the robust lineage, and four genera (*Balanophyllia*, *Goniopora*, *Porites*, and *Pavona*) belong to the complex lineage. The characters of polyp anatomy were taken from Doumenc et al. (1987) or from histological sections I made of the genera *Oculina*, *Montastrea*, *Porites*, and *Pavona*. A total of 33 characters was assembled (Appendix 1), one of calcareous exoskeleton, 10 of external morphology, nine of internal morphology, seven of cnidae, and six of polyp organization, reproduction, symbioses, and habitat. The methods for gathering morphological data are documented in chapter III. Of 33 characters, 29 were binary. Multiple states were generated for the remaining 4 characters and they were treated as unordered. Unknown characters, coded as “?”, were used in case the character could not be obtained due to poor preservation condition, or other technical limitations. The list of taxa is shown in Table 4-1.

Molecular analyses:

Ten species of eight genera in Corallimorpharia, 11 species of seven genera in Actiniaria, and 18 species of 14 genera in Scleractinia were included. Sequences of

12 species are newly generated for this study, 10 of corallimorpharians, one of an actiniarian (*Bathyphellia australis*), and one of a scleractinian (*Fungiacyathus marenzelleri*). Three genera of corallimorpharians, *Pseudocorynactis*, *Sideractis*, and *Nectactis*, were not included in molecular analyses because of the lack of tissue samples (members of those genera are rare). Data sets were assembled with sequences from GenBank and the sequences I obtained. For the combined data set, in case all sequences were not available for a species, I integrated sequences for different genes from two or three species of a genus into a single row of data. Missing and inapplicable molecular data were coded as “?”. The list of taxa is shown in Table 3-2.

I used three widely-used mitochondrial and ribosomal markers, 16S mtDNA, 18S rDNA, and 28S rDNA. The three markers were chosen because they are effective for resolving relationships at family- or order-level in Cnidaria (e. g. Chen et al., 1995; Romano and Palumbi, 1996; Chen et al., 1996; Bernston et al., 1999; Romano and Cairns, 2000; Shearer et al., 2002; Won et al., 2000; Daly et al., 2003; Medina et al., 2006; Bugler and France, 2007).

Table 4-1. Taxa included in morphological analysis.

Higher taxon	Tribe or Suborder	Family	Genus
Corallimorpharia	-	Discosomatidae	<i>Actinotryx</i>
	-	Discosomatidae	<i>Amplexidiscus</i>
	-	Corallimorphidae	<i>Corallimorphus</i>
	-	Corallimorphidae	<i>Corynactis</i>
	-	Discosomatidae	<i>Discosoma</i>
	-	Discosomatidae	<i>Metarhodactis</i>
	-	Corallimorphidae or Sideractidae	<i>Nectactis</i>
	-	Corallimorphidae	<i>Pseudocorynactis</i>
	-	Discosomatidae	<i>Rhodactis</i>
	-	Corallimorphidae or Ricordeidae	<i>Ricordea</i>
	-	Corallimorphidae or Sideractidae	<i>Sideractis</i>
Actiniaria	Acontiaria	Aiptasiidae	<i>Aiptasia</i>
	Endomyaria	Actiniidae	<i>Anthopleura</i>
	Acontiaria	Bathypheilliidae	<i>Bathypheilia</i>
	Athenaria	Edwardsiidae	<i>Edwardsia</i>
	Acontiaria	Metridiidae	<i>Metridium</i>
	Athenaria	Edwardsiidae	<i>Nematostella</i>
	Endomyaria	Stichodactylidae	<i>Stichodactyla</i>
Scleractinia	Dendrophylliinae	Dendrophylliidae	<i>Balanophyllia</i> ¹
	Caryophylliina	Caryophylliidae	<i>Caryophyllia</i> ²
	Fungiina	Poritidae	<i>Goniopora</i> ¹
	Faviina	Faviidae	<i>Montastrea</i> ²
	Faviina	Oculinidae	<i>Oculina</i> ²
	Fungiina	Agaraciidae	<i>Pavona</i> ¹
	Fungiina	Poritidae	<i>Porites</i> ¹
Ceriantharia		Cerianthidae	<i>Cerianthus</i>

1: complex scleractinian lineage; 2: robust scleractinian lineage.

Table 4-2. Taxa included in molecular analyses, with GenBank accession numbers for sequence used. Bolded GenBank accession numbers indicate the sequences I obtained in this study. CO: Corallimorpharia; AC: Actinaria; SC: Scleractinia; CE: Cerianthata.

Higher taxon	Tribe or suborder	Species	18S	28S	16S
CO	-	<i>Actinotryx sanctithomae</i>	EF589070	EF589075	EF589056
	-	<i>Amplexidiscus fenestrafer</i>	EF589071	EF589076	EF589053
	-	<i>Corallimorphus pilatus</i>	EF589066	EF589084	EF589060
	-	<i>Corynactis californica</i>	EF589065	EF589083	EF589059
	-	<i>Corynactis viridis</i>	EF589064	EF589082	EF589058
	-	<i>Discosoma nummiforme</i>	EF589068	EF589078	EF589051
	-	<i>Discosoma neglecta</i>	EF589069	EF589077	EF589052
	-	<i>Metarhodactis</i> sp.	EF589073	EF589079	EF589055
	-	<i>Rhodactis rhodostoma</i>	EF589072	EF589080	EF589054
	-	<i>Ricordea florida</i>	EF589067	EF589081	EF589057
AC	Acontiaria	<i>Aiptasia pulchella</i>	AY297437	U69684	AY345875
	Endomyaria	<i>Anthopleura kurogane</i>	Z21671	-	-
	Endomyaria	<i>Anthopleura dixoniana</i>	-	U69686	-
	Endomyaria	<i>Anthopleura elegantissima</i>	-	-	U40292
	Acontiaria	<i>Bathypheilia australis</i>	EF589063	EF589086	EF589062
	Athenaria	<i>Edwardsia elegans</i>	AF254376	AY345870	-
	Acontiaria	<i>Metridium senile</i>	U19550	-	AF000023
	Athenaria	<i>Nematostella vectensis</i>	AF254382	AY345871	AY169370
	Endomyaria	<i>Stichodactyla helianthus</i>	U52977	-	-
	Endomyaria	<i>Stichodactyla tapetum</i>	-	U69687	-
	Endomyaria	<i>Stichodactyla</i> sp.	-	-	AY345874

SC	Dendrophylliinae	<i>Balanophyllia elegans</i> ¹	U52973	-	-
	Dendrophylliinae	<i>Balanophyllia regia</i> ¹	-	AF265626	AF265587
	Caryophylliina	<i>Caryophyllia inornata</i> ²	-	AF265642	AF265587
	Caryophylliina	<i>Catalaphyllia jardinei</i> ²	AY372255	AF265637	L76000
	Dendrophylliinae	<i>Dendrophyllia gracilis</i> ¹	-	AF265627	AF265588
	Dendrophylliinae	<i>Enallopsammia rostrata</i> ¹	AF052885	AF265631	U40294
	Caryophylliina	<i>Flabellum impensum</i> ¹	-	AS265649	AF265582
	Fungiina	<i>Fungia scutaria</i> ²	AF052884	AF265631	L76005
	Fungiina	<i>Fungiacyathus marenzelleri</i> ¹	EF589074	EF589085	EF589061
	Faviina	<i>Lobophyllia hataii</i> ²	AY372252	-	-
	Faviina	<i>Lobophyllia hemprichii</i> ²	-	AF265624	L76013
	Faviina	<i>Montastrea annularis</i> ²	AF238267	AB126790	
	Faviina	<i>Montastrea cavernosa</i>	-	-	AY580333
	Faviina	<i>Oculina patagonica</i> ²	-	AF265636	AF265601
	Fungiina	<i>Pavona varians</i> ¹	AF052883	AF263350	L76016
	Fungiina	<i>Porites compressa</i> ¹	-	AF265630	L76020
	Fungiina	<i>Porites lutea</i> ¹	AY722788	-	-
	Dendrophylliinae	<i>Tubastrea coccinea</i> ¹	Z92906	AF265625	L76022
CE	-	<i>Cerianthus borealis</i>	AF052897	-	U40288
		<i>Cerianthus</i> sp.	-	U69678	-

1: complex scleractinian lineage; 2: robust scleractinian lineage.

4-2. DNA extraction and PCR amplification

Molecular sequence data were collected from material preserved in 95% or absolute ethanol. DNA was extracted using the DNeasyTM Tissue Kit from Qiagen (catalog no. 69504), following the procedure included with the DNeasyTM Tissue kit.

The small subunit ribosomal RNA gene (18S rDNA) was amplified from whole genome preparations using a set of nested primers (Table 4-3) that generated three sequence fragments (Apakupakul et al., 1999; Daly et al., 2003) totaling 1800 base pairs. Partial fragments of 28S ribosomal DNA gene (300 base pairs) and 16S mitochondrial DNA (1200 base pairs) were amplified (Cunningham and Buss, 1993; Chen et al., 1995; Romano and Palumbi, 2000).

Each 25 μ l polymerase chain reaction (PCR) mixture contained 9.5 μ l RNase-free pure water, 12.5 μ l *Taq* master mix (Qiagen catalog no. 201443), 1 μ l forward primer (10 μ M), 1 μ l reverse primer (10 μ M), and 1 μ l DNA template. The PCR reaction was run on a Bio-Rad Thermo Cycler. For gel purification, 100 μ l PCR reactions were run; each contained four times the amount of each reagent listed above. The PCR thermal profile for each gene is listed in Table 4-4. PCR products were purified using QIAquick PCR Purification kit (Qiagen catalog no. 28104) or QIAquick Gel Extraction Kit (Qiagen catalog no. 28704). The 100 μ l PCR products were run out on a 1.0% or 1.5% agarose gel, removed from the gel, and purified.

Table 4-3. Primer sequences used

Locus	Primers	Primer sequence	Source
18S	18A	5'-AACCTGGTTGATCCTGCCAGT-3'	Apakupakul et al., 1999; Daly et al., 2003
	18L	5'-CCAACTACGAGCTTTTAACTG-3'	Apakupakul et al., 1999; Daly et al., 2003
	18C	5'-CGGTAATTCCAGCTCCAATAG-3'	Apakupakul et al., 1999; Daly et al., 2003
	18Y	5'-CAGACAAATCGCTCCACCAAC-3'	Apakupakul et al., 1999; Daly et al., 2003
	18B	5'-TGATCCTTCCGCAGGTTACCT-3'	Apakupakul et al., 1999; Daly et al., 2003
	18O	5'-AAGGGCACCACCAGGAGTGGAG-3'	Apakupakul et al., 1999; Daly et al., 2003
16S	16Sg-5'	5'-TCGACTGTTTACCAAAAACATAGC-3'	Cunningham and Buss, 1993
	16SI-3'	5'-TTTAAAGGTCGAACAGACC-3'	Cunningham and Buss, 1993
28S	28F	5'-GGCGACCCGCTGAATTCAAGCATAT-3'	Chen et al., 1995
	28R	5'-AACTTTCCTCACGGTACTTGT-3'	Romano and Palumbi, 2000

Table 4-4. Thermoprofiles for PCR reactions.

Locus	Primers	Thermoprofiles
18S	18A, 18L, 18C,	1 cycle at 94°C (2 min), 50°C (1 min), and 72°C (2 min);
	18Y, 18B, 18O	29 cycles at 94°C (30 sec), 52°C (1 min), and 72°C (1 min)
28S	28F, 28R	1 cycle at 94°C (2 min), 50°C (1 min), and 72°C (2 min);
		25 cycles at 92°C (30 sec), 52°C (1 min), and 72°C (1 min)
		10 cycles at 94°C (30 sec), 45°C (30 sec), and 72°C (45
16S	16Sg-5', 16SI-3'	sec); 30 cycles at 94°C (30 sec), 50°C (30 sec), and 72°C (1 min)

4-3. Sequencing

Sequencing was done at the KUNHM DNA sequencing facility using ABI prism BigDye dye-terminator chemistry (Perkin-Elmer Applied Biosystems) and following ABI protocols.

4-4. Alignment

A Basic Local Alignment Search Tool (BLAST, <http://www.ncbi.nlm.nih.gov/BLAST/>) search was used to find regions of local similarity between sequences. BLAST compares nucleotide sequences to sequence databases, and calculates the statistical significance of matches. Sequence data were aligned using MUSCLE (<http://www.drive5.com/muscle/>), a multiple sequence alignment program. MUSCLE was used because the program provides faster and more accurate alignment than other alignment programs (Edgar, 2004). Alignments were refined using BioEdit (<http://www.mbio.ncsu.edu/BioEdit/bioedit.html>).

4-5. Phylogenetic analysis and molecular clock dating

Phylogenetic analyses were performed using PAUP 4.05 (<http://paup.csit.fsu.edu/>) in conjunction with MacClade (<http://macclade.org/macclade.html>). To reconstruct phylogeny, two commonly used methods, maximum parsimony (MP) and maximum likelihood (ML), were applied. MP infers a phylogenetic tree by minimizing the total number of evolutionary steps required to explain a given set of data (Felsenstein,

2004). MP is based on shared and derived characters; therefore, it tries to provide information on the ancestral states. But evolution may not have occurred following a minimum number of changes, because the same change may have happened independently along different branches, and some changes may have involved intermediate steps. ML evaluates a hypothesis about evolutionary history in the data set. The topology with the highest maximum probability is chosen (Felsenstein, 2004). Advantages of ML over MP are: 1) ML may have lower variance, so is less affected by sampling error, and 2) ML is statistically well founded, so it can statistically evaluate various tree topologies. The disadvantage of ML is that the result depends on the model of evolution.

The most parsimonious trees were searched using a heuristic search with 100 random additions of sequences. Bootstrap indices were calculated for 1000 replicate searches. The bootstrap is widely applied in the phylogenetic literature to indicate confidence level of the results (Felsenstein, 1985, 2004). For ML analysis, the best-fit model of DNA substitution and parameter estimates used for tree construction were chosen by performing hierarchical likelihood ratio tests (Huelsenbeck and Crandall, 1998; Harris and Crandall, 2000) using PAUP 4.05 (Swofford, 2001) and ModelTest 3.0 (Posada and Crandall, 1998). Heuristic ML searches were performed using fast stepwise-addition and 500 bootstrap replicates. To evaluate the degree of incongruence of data sets, the partition homogeneity test was performed. In case data sets were not incongruent, combined analyses were performed.

All characters were given equal weight, and were unordered; the character state optimization setting ACCTRAN was in effect. ACCTRAN optimization will interpret ambiguity as a synapomorphy, which may be appropriate for missing (but not inapplicable) data. For each analysis that produced more than one tree, I obtained a strict consensus tree with the method “Compute consensus” in PAUP. The morphological data matrix is shown in Appendix 1, and the molecular data matrix is shown in appendix 2.

For the molecular clock dating, I first performed the log likelihood ratio test (LRT; Felsenstein, 1981) between the clock enforced ML tree and the clock non-enforced ML tree that compared the likelihood scores with and without the clock assumption on the trees of combined molecular data. When the data rejected the clock with significant p value, I used cross-validated penalized likelihood method in r8s (Sanderson, 2004; <http://ginger.ucdavis.edu/r8s/>). The program r8s allows incorporating multiple calibration points rather than a single, fixed calibration point, and then calculates the most likely ages of nodes given the remaining constraints and substitutions in the data set (Sanderson, 2004). Penalized likelihood is a semi-parametric approach that allows different substitution rates between ancestral and descendent branches. This method reduces the number of arbitrary alternatives by assigning a penalty that increases with the abruptness of rate change between adjacent branches. The penalty (or “smoothing” parameter) is calculated by removing part of

the data, reestimating the remaining model parameters, and using the fitted model parameters to predict the data that were removed. The cross validation option is useful to find the optimal level of smoothing (Sanderson, 2004).

Fossil data for three genera in Scleractinia, *Fungia*, *Pavona*, and *Oculina*, allowed calibration points: *Fungia* arose in the Miocene, 24 Mya, *Pavona* arose in the Early Oligocene, 34 Mya, and *Oculina* arose in the Middle Cretaceous, 100 Mya (Wells, 1956; Foster, 1986; Budd, 1991; Veron, 1995). I chose the three points because the clades of *Pavona-Fungiacyathus* and *Fungia-Cataphyllia*, and the node of *Oculina* are relatively well supported in my ML analysis. The origin of Scleractinia at 240 Mya in Mid-Triassic (Deng and Kong, 1984; Qi, 1984; Morycowa, 1988), was used as the calibration point of a basal node.

4-6. Results

1. Morphological data (Figure 4-1):

Parsimony analysis of the morphological data produced 12 trees of length = 96 with a consistency index (CI) of 0.55 and a retention index (RI) of 0.68. The strict consensus tree had two polytomies, neither basal. Morphological characters unambiguously supporting each node are indicated in Figure 4-1.

2. Molecular data

Likelihood-ratio tests determined that the General Time Reversible (GTR) model of evolution was the most appropriate for each gene individually, and for the combined data sets of all genes. The GTR model allows the four nucleotides to be present in different frequencies. The model assumes each pair of nucleotide substitutions has a different rate, and a symmetric substitution matrix. In other words, A changes into T at the same rate that T changes into A (Hillis et al., 1996; Li, 1997; Felsenstein, 2004). In all data sets, the MP and ML trees were not incongruent based on the partition homogeneity tests.

2-1. 18S rDNA data (Figure 4-2):

A total of 1871 characters was collected: 1258 characters were constant, 330 variable characters were parsimony-uninformative, and 283 characters were parsimony-informative. Parsimony analysis produced 18 trees of length = 1104

with a CI of 0.73 and a RI of 0.72. Maximum likelihood analysis produced a topology with $-\ln$ likelihood 8769.0938.

2-2. 28S rDNA data (Figure 4-3):

A total of 339 characters was collected: 191 characters were constant, 39 variable characters were parsimony-uninformative, and 109 characters were parsimony-informative. Parsimony analysis produced 2 trees of length = 371 with a CI of 0.55 and a RI of 0.72. Maximum likelihood analysis produced a topology with $-\ln$ likelihood 2462.7699.

2-3. 16S mtDNA data (Figure 4-4):

A total of 984 characters was collected: 466 characters were constant, 173 variable characters were parsimony-uninformative, and 345 characters were parsimony-informative. Parsimony analysis produced 11 trees of length = 1060 with a CI of 0.70 and a RI of 0.84. Maximum likelihood analysis produced a topology with $-\ln$ likelihood 6263.1777.

2-4. Combined molecular data (Figure 4-5):

For MP analysis, a total of 737 characters was collected: 283 18S rDNA parsimony-informative characters, 109 28S rDNA parsimony-informative characters, and 345 16S mtDNA parsimony-informative characters. According to the partition homogeneity test, data sets are not incongruent ($p=0.996$). The

parsimony analysis of the combined molecular data set produced two equally the most parsimonious trees of length = 2062 with a CI of 0.57 and a RI of 0.76. For ML analysis, a total of 3194 characters were combined: 1871 of 18S rDNA, 339 of 28S rDNA, and 984 of 16S mtDNA. The combined data set produced a topology with $-\ln$ likelihood 17498.8625.

3. Phylogenetic relationships:

All data sets support the monophyly of each of the three orders, Actiniaria, Corallimorpharia, and Scleractinia; Corallimorpharia and Scleractinia are sister taxa. Actiniaria is sister taxon to Corallimorpharia-Scleractinia.

Monophyly of Actiniaria is supported by trilobed mesenterial filaments and the presence of siphonoglyphs, 5 substitutions in 18S rDNA, 7 substitutions in 28S rDNA, and 25 substitutions in 16S mtDNA. Within Actiniaria, three clades are recognized, each clade corresponding to the tribe of Carlgren (1949). Athenaria is the basal group and sister group to Endomyaria - Acontaria clade. 16S mtDNA did not resolve the relationships among tribes.

The monophyly of Scleractinia is supported by calcareous exoskeleton, 5 substitutions in 18S rDNA, 6 substitutions in 28S rDNA, and 14 substitutions in 16S mtDNA. Within Scleractinia, two lineages, complex and robust, are supported by all molecular data sets.

The monophyly of Corallimorpharia is supported by 3 substitutions in 18S rDNA, 7 substitutions in 28S rDNA, and 13 substitutions in 16S mtDNA. Although the monophyly is well supported by molecular data, two anatomical characters that define corallimorpharians are shared with scleractinians: unilobed mesenterial filaments and large holotrichs. Within Corallimorpharia, two clades, cylindrical body group (C1) and discoidal body group (C2), are recognized based on morphological data, 16S mtDNA, and the combined molecular data. 18S rDNA data did not support the two clades. Based on 28S rDNA data, *Ricordea*, a discoidal corallimorpharian genus, clusters with genera in C1.

4. Molecular clock dating

Molecular clock dating estimates the divergence time of Corallimorpharia from the ancestral lineage of the Corallimorpharia-Scleractinia clade at 262 Mya (Late Permian).

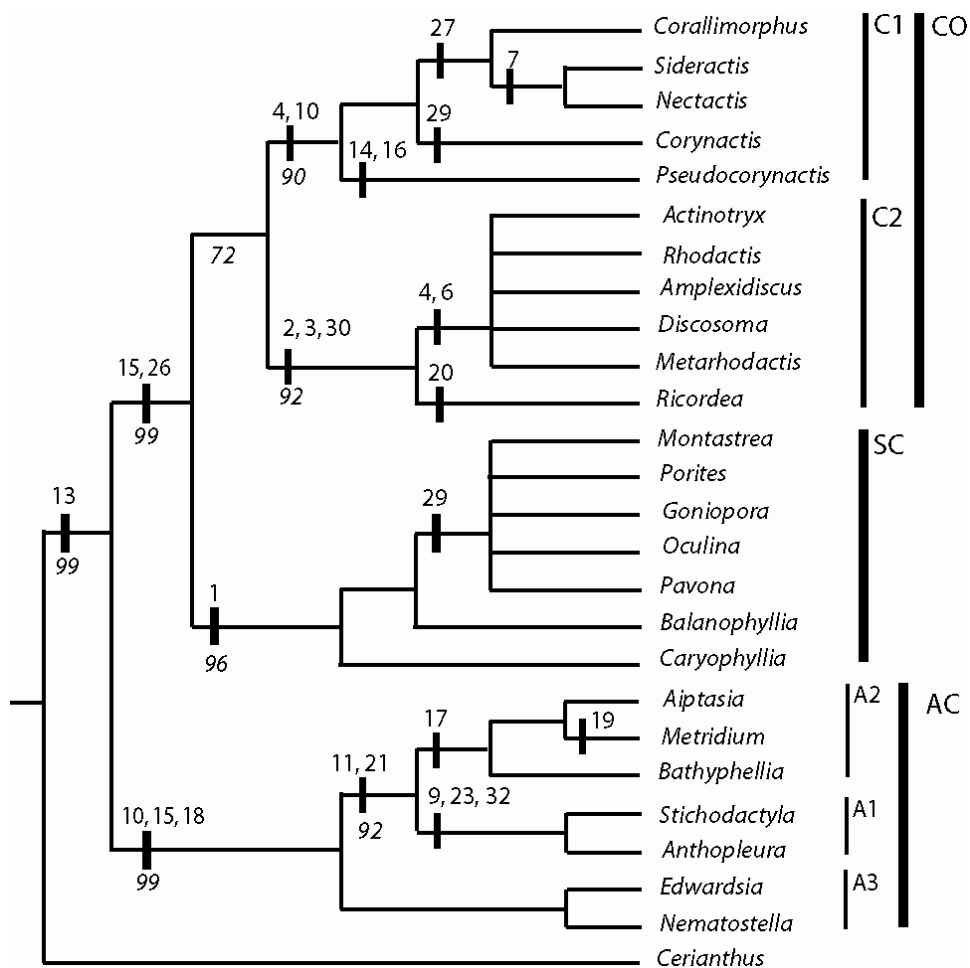


Figure 4-1. Strict consensus tree of 12 most parsimonious trees based on morphological characters (CI= 0.55; RI= 0.68) inferred using the heuristic method in PAUP. Numbers above the branches represent the characters unambiguously supporting the node. Numbers below the branches represent the percentage of 1000 non-parametric bootstrap replications. Branches without number are supported by bootstrap value of less than 70%. AC: Actiniaria; CO: Corallimorpharia; SC: Scleractinia; C1: clade 1 in Corallimorpharia; C2: clade 2 in corallimorpharia; A1: Endomyaria in Actiniaria; A2: Acontiaria in Actiniaria; A3: Athenaria in Actiniaria.

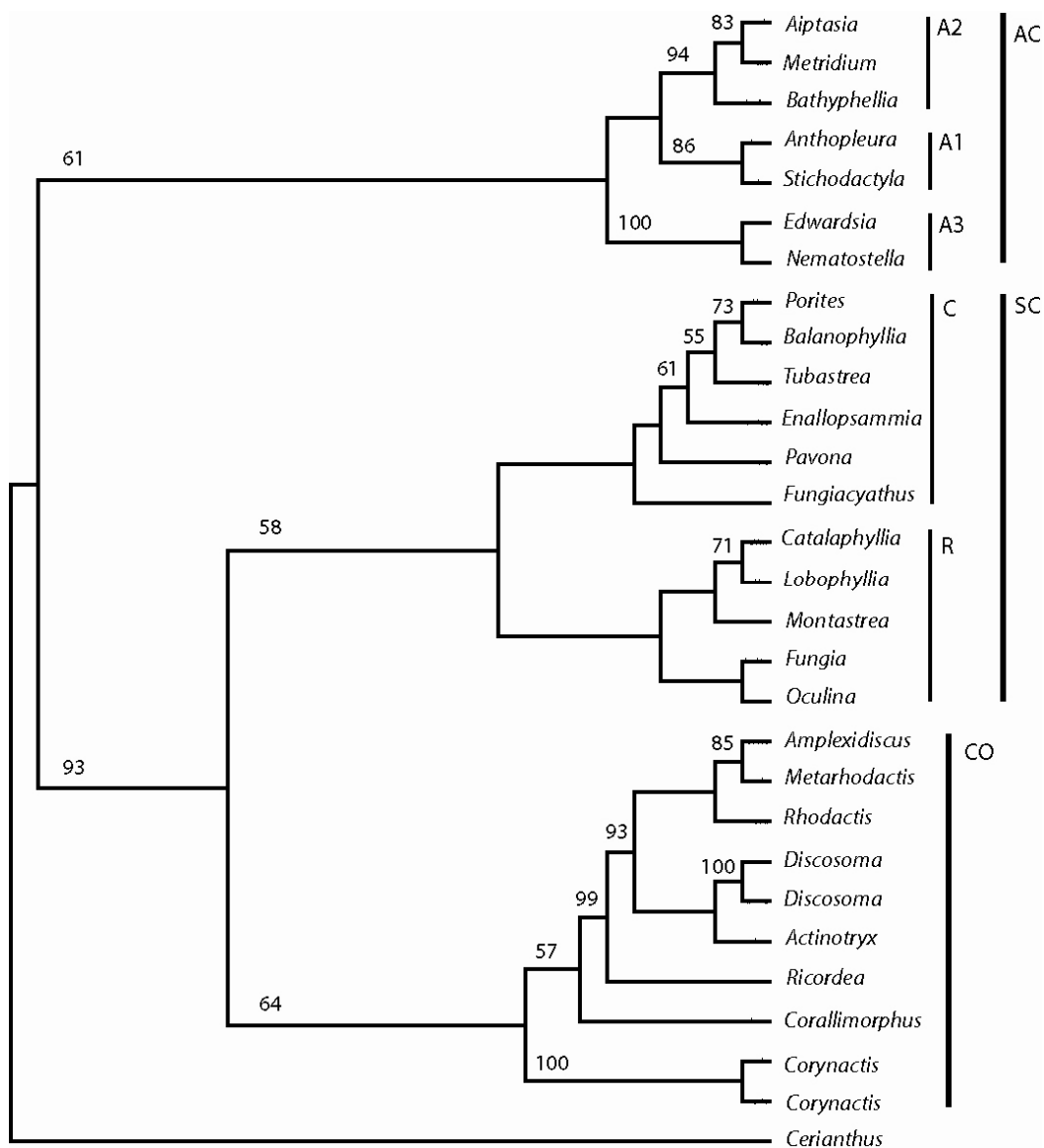


Figure 4-2. Maximum likelihood tree generated based on 18S rDNA data using GTR model, heuristic search, random stepwise addition with 500 repetitions. Numbers above the branches represent the percentage of 1000 non-parametric bootstrap replications. Branches without number are supported by bootstrap value of less than 50%. AC: Actiniaria; CO: Corallimorpharia; SC: Scleractinia; R: robust scleractinian coral; C: complex scleractinian corals; A1: Endomyaria in Actiniaria; A2: Acontiarina in Actiniaria; A3: Athenaria in Actiniaria.

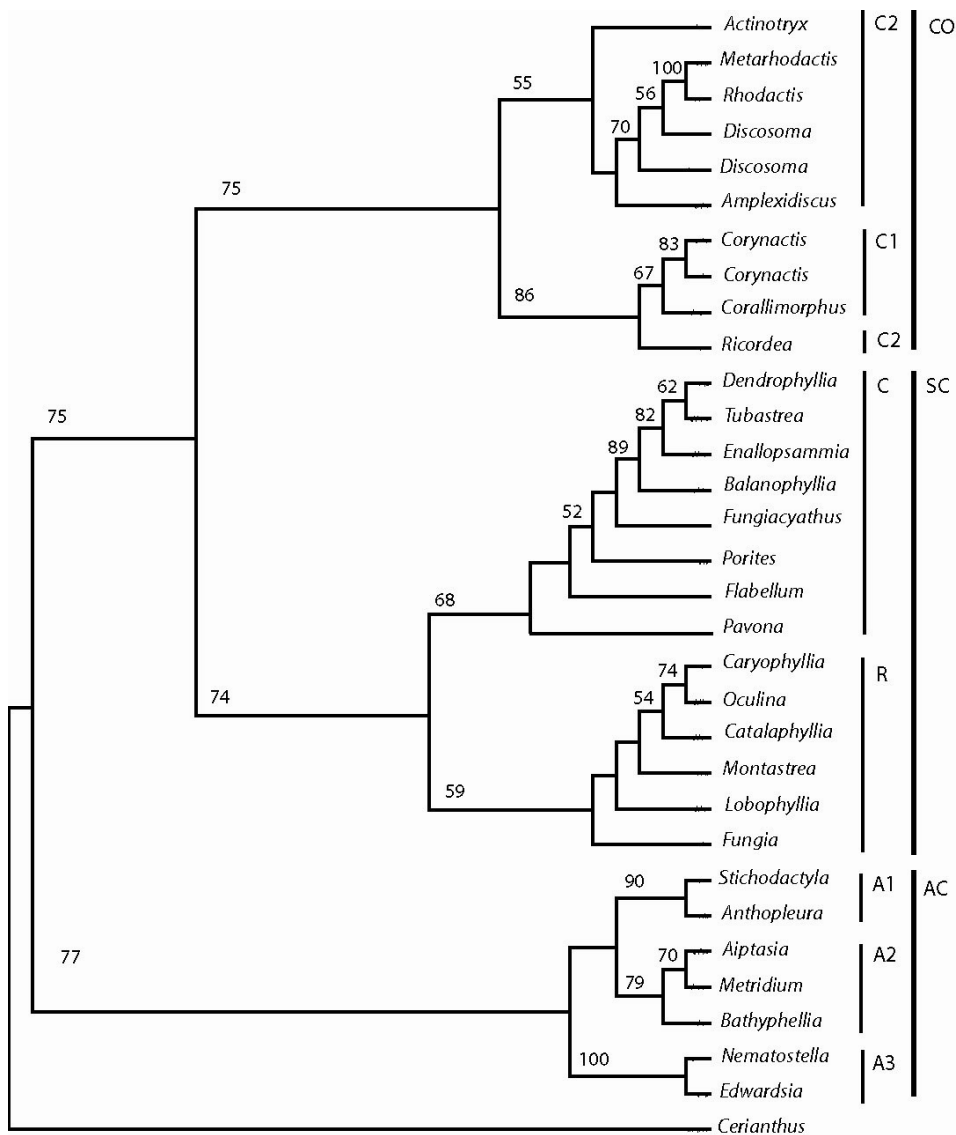


Figure 4-3. Maximum likelihood tree generated based on 28S rDNA data using GTR model, heuristic search, random stepwise addition with 500 repetitions. Numbers above the branches represent the percentage of 1000 non-parametric bootstrap replications. Branches without number are supported by bootstrap value of less than 50%. AC: Actiniaria; CO: Corallimorpharia; SC: Scleractinia; R: robust scleractinian coral; C: complex scleractinian corals; C1: clade 1 in Corallimorpharia; C2: clade 2 in corallimorpharia; A1: Endomyaria in Actiniaria; A2: Acontaria in Actiniaria; A3: Athenaria in Actiniaria.

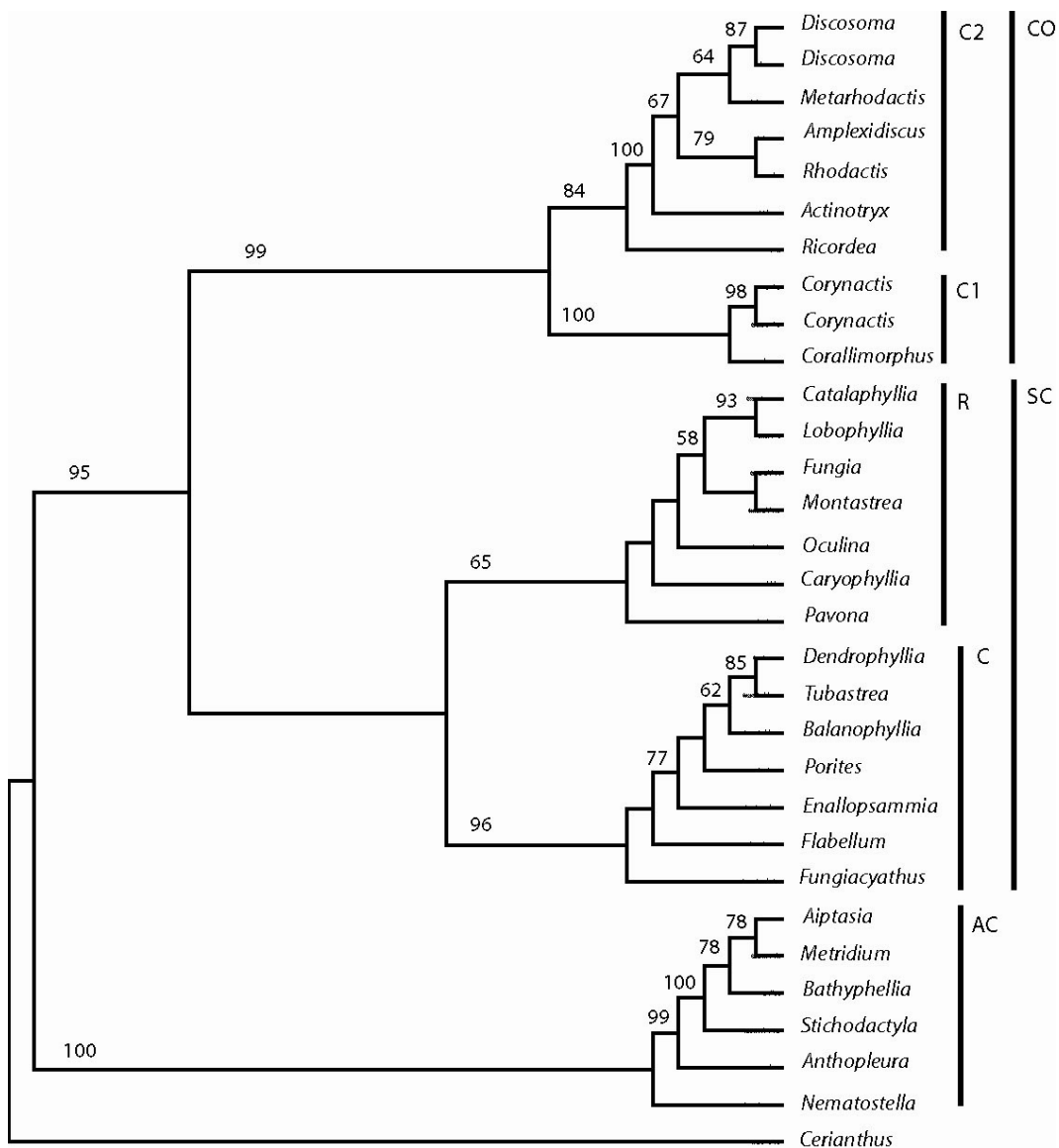


Figure 4-4. Maximum likelihood tree generated based on 16S mtDNA data using GTR model, heuristic search, random stepwise addition with 500 repetitions. Numbers above the branches represent the percentage of 1000 non-parametric bootstrap replications. Branches without number are supported by bootstrap value of less than 50%. AC: Actiniaria; CO: Corallimorpharia; SC: Scleractinia; R: robust scleractinian coral; C: complex scleractinian corals; C1: clade 1 in Corallimorpharia; C2: clade 2 in corallimorpharia.

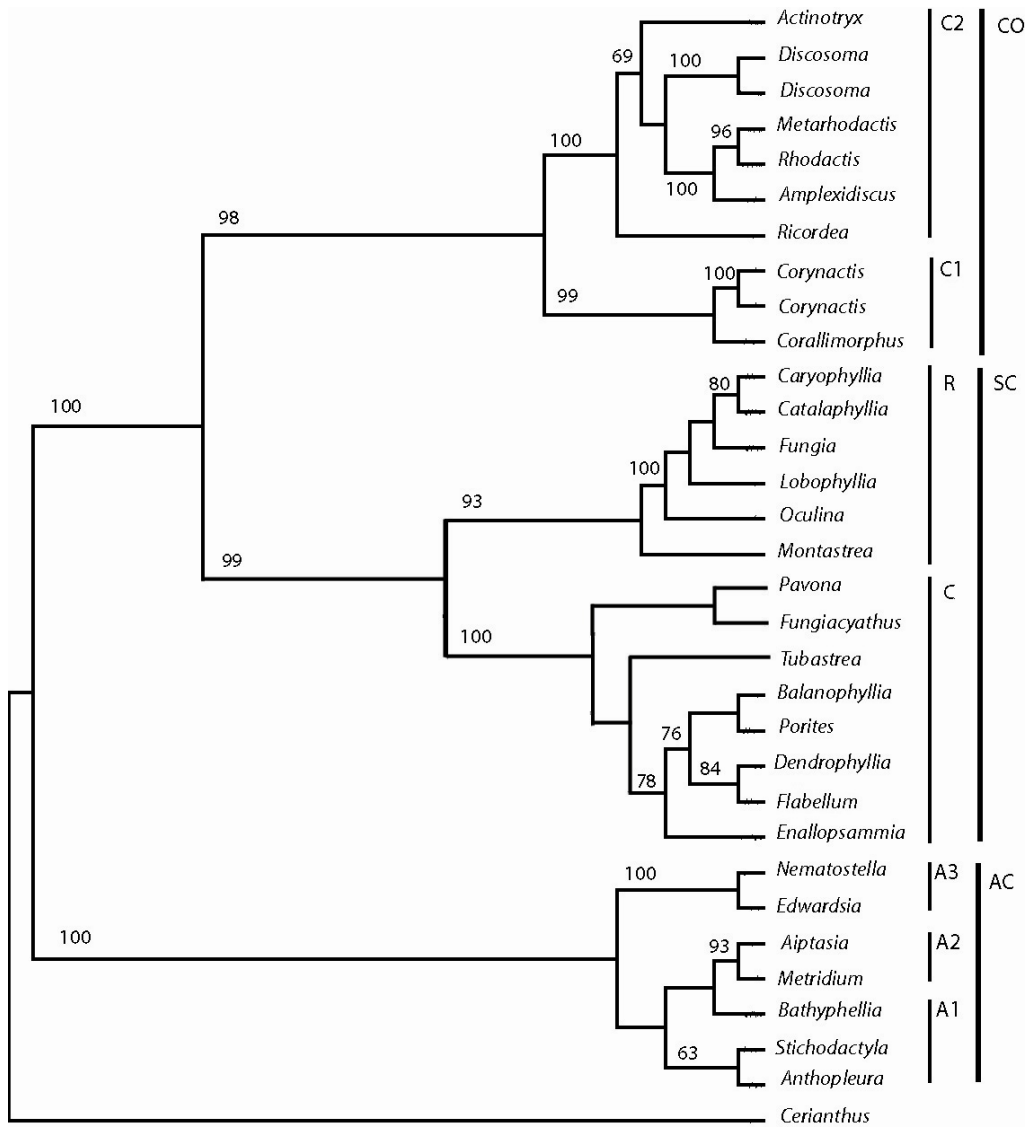


Figure 4-5. Strict consensus tree of two most parsimonious trees based on combined molecular data. Numbers above the branches represent the percentage of 1000 non-parametric bootstrap replications. Branches without number are supported by bootstrap value of less than 70%. AC: Actiniaria; CO: Corallimorpharia; SC: Scleractinia; R: robust scleractinian coral; C: complex scleractinian corals; C1: clade 1 in Corallimorpharia; C2: clade 2 in corallimorpharia.

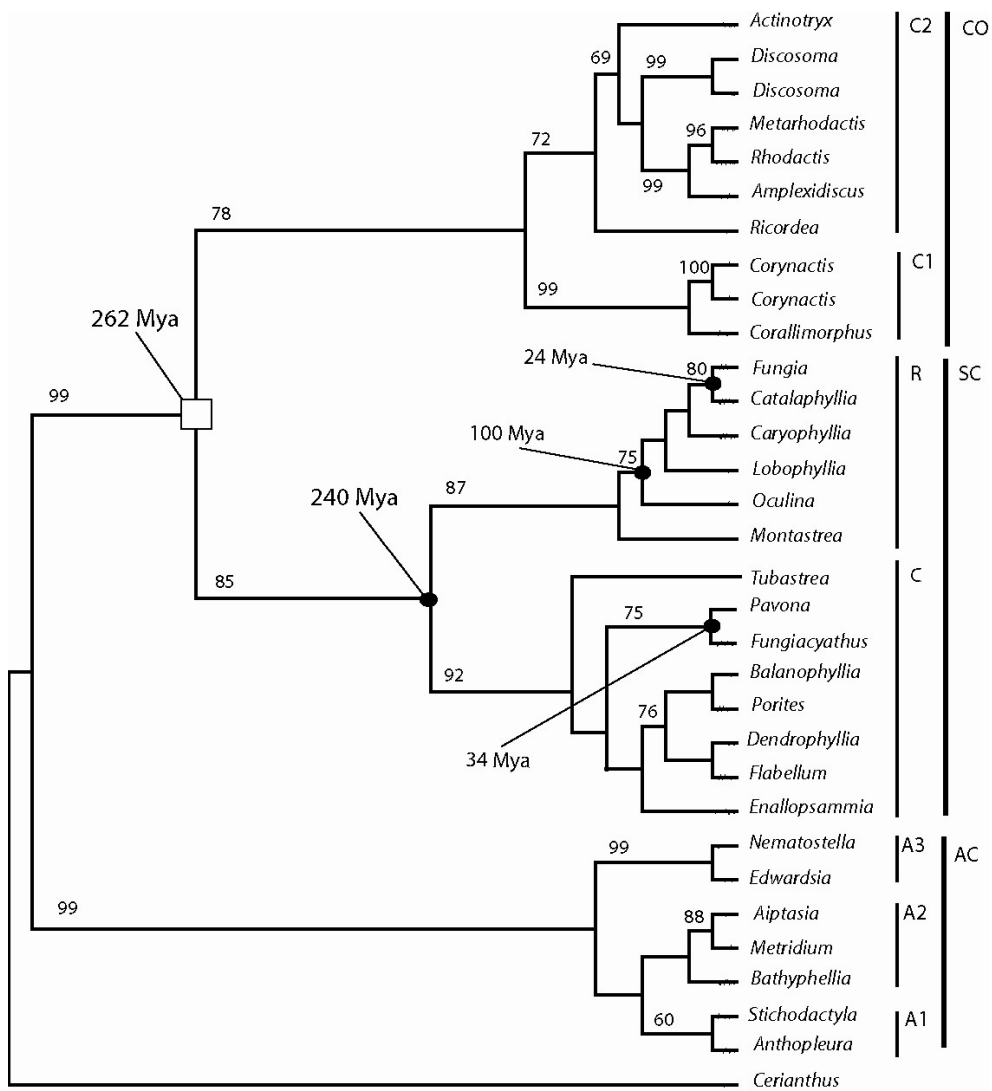


Figure 4-6. Maximum likelihood tree generated based on combined molecular data using GTR model, heuristic search, random stepwise addition with 500 repetitions. Numbers above the branches represent the percentage of 1000 non-parametric bootstrap replications (Felsenstein, 1985). Branches without number are supported by bootstrap value of less than 50%. AC: Actiniaria; CO: Corallimorpharia; SC: Scleractinia; R: robust scleractinian coral; C: complex scleractinian corals; A1: Endomyaria in Actiniaria; A2: Acontiarina in Actiniaria; A3: Athenaria in Actiniaria. Filled circles are the calibrations points for molecular clock dating, and empty squares are estimated divergence time.

4-7. Discussion

Monophyly and interordinal relationships of Corallimorpharia

Both morphological and molecular data sets suggest that Corallimorpharia is a monophyletic group. The monophyly of Corallimorpharia contradicts the inferences in Fautin and Lowenstein (1992) and Chen et al. (1995), and but concur with those of Daly et al. (2003) and Medina et al. (2006).

Monophyly is more robustly supported by molecular than morphological data. Relative to molecular data, morphological data support monophyly with a lower bootstrap value (0.72). Although the corallimorpharians cluster together on the tree, the two anatomical characters that define corallimorpharians are shared with scleractinians: unilobed mesenterial filaments and large holotrichs. The lack of any unique character defining the order indicates that the ordinal rank assigned to corallimorpharians is not appropriate. The lack of morphological characters supporting monophyly of corallimorpharians may be evidence of close kinship between Corallimorpharia and Scleractinia, or may be caused by the small number of characters collected for the analyses. According to Daly et al. (2003), characters of ultrastructure may provide more robust evidence to support the monophyly of corallimorpharians. But I conclude that Corallimorpharia and Scleractinia are subgroups of a higher taxon.

Within Corallimorpharia, I recognize the two clades that had been recognized by den Hartog (1980, 1993) based on morphological characters. Clade C1 (Figure 4-1) includes members of Corallimorphidae, which represent cylindrical-bodied corallimorpharians characterized by long, unbranched, capitate tentacles, no zooxanthellae, pedal disc nearly as wide as oral disc, and firm body. Within the C1 clade, the shallow-water genera, *Corynactis* and *Pseudocorynactis*, are basal to the deep-water genera, *Corallimorphus*, *Nectactis* and *Sideractis*, based on morphological data. Clade C2 includes members of Discosomatidae and *Ricordea* (Figure 4-1), which represent discoidal-bodied corallimorpharians characterized by an oral disc much wider than the pedal disc, many short, often branched tentacles containing zooxanthellae, and soft body. Three of the data sets consistently support sister relationships between the two clades in Corallimorpharia; 18S rDNA does not. Medina et al. (2006) concluded that the discoidal-bodied clade is derived from the cylindrical-bodied clade, but they included only one taxon of the cylindrical-bodied clade (*Corynactis*) in their analyses, so their taxon sampling may not be sufficient to resolve the relationships between the two clades.

Phylogenetic resolution beyond the family level using either morphological data or molecular data is limited. Although the results based on morphology and 16S DNA resolve relationships between the two clades in Corallimorpharia, the relationships among genera of Corallimorpharia were not resolved. Morphological data generated a

polytomy among genera of Discosomatidae and the position of the genera in molecular analyses varies. The lack of resolution is probably due to the conserved nature of nuclear genes and the slow evolution of the mitochondrial genome in Cnidaria (Shearer et al., 2002). The usefulness of genetic markers used in this study, 16S mtDNA, 18S rDNA, and 28S rDNA, has been debated for more than 10 years (Chen et al., 1995, 1996; France et al., 1996; Bernsten et al., 1999; Romano and Cairns, 2000; Won et al., 2001; Daly et al., 2002). Other faster evolving nuclear-loci, including complete DNA sequences of 28S rDNA and protein-coding genes, are currently under investigation by the NSF funded Assembling the Cnidarian Tree of Life project (<http://cnidarian.info>) to get better resolution of phylogenetic relationships at genus and species level.

I included most of valid genera in Corallimorpharia to resolve phylogenetic relationships within Corallimorpharia and among the three orders, Actiniaria, Corallimorpharia, and Scleractinia. However, three genera in family Corallimorphidae, *Sideractis*, *Nectactis*, and *Pseudocorynactis*, are missing in molecular analyses due to the lack of tissue samples. The inclusion of three taxa in further phylogenetic study will possibly provide better resolution on evolutionary relationships between the two clades in Corallimorpharia, and relationships in family Corallimorphidae.

Actiniaria, Corallimorpharia, and Scleractinia: interordinal relationships

The monophyly of Actiniaria is well supported by both morphological and molecular data. Within Actiniaria, Endomyaria and Acontiaria form a clade based on sphincter muscle, basilar muscle, and basitrichs. Athenaria is basal to the Endomyaria-Acontiaria cluster. The phylogenetic inferences on interorder relationships in Actiniaria concur with Daly et al. (2003). However, the taxon sample size is too small to resolve the relationships within Actiniaria.

The monophyly of Scleractinia is supported by both morphological and molecular data. Two evolutionary lineages, complex and robust clades (Romano and Cairns, 2000), are confirmed by my molecular data. Morphological data support the monophyly of Scleractinia, but do not provide evidence supporting the two clades. The lack of resolution is probably due to the limited information on scleractinian polyp anatomy. The polyp anatomy of scleractinians has received little emphasis because taxonomy of Scleractinia is based on skeletal structure (Romano and Cairns, 2000). However, the information on scleractinian polyp anatomy is important because as an independent data set from molecular data polyp anatomy may further support or refute the inferred clades.

Actiniaria is basal to the Corallimorpharia-Scleractinia cluster as Daly et al. (2003) and Brugler and France (2007) inferred. Corallimorpharia and Scleractinia are sister

taxa as proposed by Duerden (1898), Schmidt (1974), den Hartog (1980), Romano and Cairns (2000), Won et al. (2001), Daly et al. (2002, 2003), and Brugler and France (2007). The Scleractinia-Corallimorpharia clade is strongly supported by morphological and molecular data. In this study, many of the traditional diagnostic features are recovered as phylogenetically informative characters. Based on data collected in this study, the similarity in tentacle arrangement between corallimorpharians and stichodactyline actinarians is an example of parallel evolution.

The relationships among Actiniaria, Corallimorpharia, and Scleractinia provide an insight on evolution of the scleractinian skeleton in Hexacorallia. The most parsimonious interpretation of the interordinal relationships is that a skeleton arose only once in the ancestor of Scleractinia, a skeletonless polyp. The idea that scleractinians were derived from skeletonless polyps is widely accepted (Scrutton and Clarkson, 1989; Stanley and Fautin, 2001; Stanley, 2003). My findings on divergence times of corallimorpharians and the date scleractinians arose support the hypothesis that corallimorpharians diverged from the ancestor of the Corallimorpharia-Scleractinia lineage at 262 Mya and the two clades of scleractinians diverged at 240 Mya. The most parsimonious interpretation of the relationships between Scleractinia and the most-closely related skeletonless hexacorallians is reflected in the classification of Carlgren (1949), which assumes the homology of the scleractinian skeleton within Scleractinia: Corallimorpharia is primarily separated from

Scleractinia due to the lack of calcareous exoskeleton. All extant hexacorallian polyps with calcareous exoskeleton belong to Scleractinia.

However, the most parsimonious interpretation does not concur with Hand (1966), and Fautin and Lowenstein (1994) supporting the hypothesis that the ancestor to the Actiniaria-Corallimorpharia-Scleractinia clade in Hexacorallia had a calcareous exoskeleton, which was lost multiple times. Hand (1966) reasoned that paired mesenteries, which arose in the common ancestor of the three taxa, evolved in polyps having a calcareous septum between a pair of mesenteries; they persist in non-skeletalized hexacorallians, which are descendants of skeletalized polyps, with no obvious function. In Fautin and Lowenstein (1994), they inferred that a skeletalized polyp is ancestral form of non-skeletalized hexacorallians based on calibrating the tree using radioimmunoassay of proteins from animals at the known divergence point for two scleractinian lineages, 240 Mya.

Although my results support the hypothesis that scleractinians were derived from non-skeletonized polyps, it is difficult to conclude directionality in the relationship between skeletalized and non-skeletalized taxa because of the lack of a fossil record of skeletonless hexacorallians.

Ordinal placement of Corallimorpharia

Due to the lack of unique morphological characters defining Corallimorpharia, the scleractinian skeleton, which is the only character to separate Corallimorpharia from Scleractinia, is essential to determine the ordinal placement of the Corallimorpharia in Hexacorallia. The phylogenetic value of the scleractinian skeleton has been challenged by the hypothesis that the scleractinian skeleton could have disappeared and appeared multiple times (Fautin and Lowenstein, 1994; Romano and Palumbi, 1996; Romano and Cairns, 2003). If the the scleractinian skeleton is not an essential attribute of Scleractinia, Corallimorpharia and Scleractinia may need to be combined into one order due to the similarities in their polyps. The hypothesis of multiple origins of the scleractinian skeleton is supported by the phylogenetic relationship between Scleractinia and Corallimorpharia (Romano and Palumbi, 1996; Romano and Cairns, 2000; Medina et al., 2006), and the ephemerality of the scleractinian skeleton is supported by the fossil record (Wells, 1956; Veron, 1995; Oliver, 1996), and ecological and experimental evidence (Buddemeier and Fautin, 1996; Fine and Tchenov, 2007).

Based on the fossil record, there is an approximately 10 Mya gap between the Permian extinction (251 Mya) and the appearance of scleractinian fossils (240 Mya). The first Mid-Triassic scleractinian fossils are represented by numerous higher taxa, up to nine suborders of Scleractinia appeared in the mid-Triassic with no known common ancestor (Vaughan and Wells, 1943; Wells, 1956; Veron, 1995; Stanley, 2003). The modern scleractinians are not descendants of Paleozoic rugosan corals as

has been proposed (Vaughan and Wells, 1943; Veron, 1995): they differ in septa symmetry and the crystal form of their calcium carbonate skeleton (Oliver, 1980; Scrutton and Clarkson, 1991; Romano and Palumbi, 1996; Stanley and Fautin, 2001).

The explosive appearance of scleractinian fossils after the gap may be explained by the “naked coral” hypothesis (Stanley, 2003), which supports the idea that multiple lineages of skeletonless anthozoans gave rise to various calcified scleractinian-like corals through aragonitic biomineralization; thus the scleractinian skeleton represents “a grade of organization” (Stanley, 2003, p. 224). Several molecular studies support the multiple origins of the scleractinian skeleton. Romano and Palumbi (1996) proposed the evolutionary divergence of scleractinians at 300 Mya. They stated the 60 Mya gap between the dates from fossil (240 Mya) and molecules may be explained as a period in which scleractinians did not have skeletons, and the great morphological diversity of scleractinians may represent polyphyletic origins of the scleractinian skeleton. Romano and Cairns (2000) concluded that scleractinian skeletons may have evolved as many as four times in Scleractinia.

The environmental and experimental data provide more empirical evidence of ephemerality of the scleractinian skeleton. Recent data support that physicochemical conditions of seawater have an effect on the calcification of scleractinians (Buddemeier and Fautin, 1996; Gattuso et al., 1999; Kleypas et al., 1999; Langdon, 2000; Ezaki, 2000; Stanley and Fautin, 2001; Feely et al., 2004). Calcification rates of

some modern reef organisms decline with decreasing calcium carbonate saturation of sea water; saturation state is reduced by high atmospheric CO₂ values (Smith and Buddemeier, 1992; Buddemeier and Fautin, 1996; Kleypas et al., 1999). The 10 Mya gap between Permian extinction and the appearance of scleractinian fossils was the time when carbonate deposition was suppressed globally (Stanley, 1988). My finding on divergence time of Corallimorpharia (262 Mya, Late Permian) from the ancestral lineage when there was a dramatic increase of atmospheric CO₂, which would be unfavorable for calcification, and divergence time of the two clades of Scleractinia (240 Mya) is consistent with the scenario of high calcium carbonate saturation in the Middle Triassic, which would be favorable for calcification (Sandberg, 1983).

The impact of saturation state of seawater on the calcification of scleractinians was illustrated experimentally by Fine and Tchernov (2007). When they kept scleractinians of two species, *Oculina patagonica* and *Madracis pharensis*, in low pH sea water, which would occur with high atmospheric CO₂ thus low calcium carbonate saturation, the calcareous exoskeleton disappeared; when the animals were returned to high pH sea water (high calcium carbonate saturation, under current atmospheric conditions), the calcareous exoskeleton reappeared. The influence of environmental factors on calcification rates is reflected in contemporary biogeography: in the tropics, waters are supersaturated with aragonite and anthozoan communities are dominated by zooxanthellate scleractinians, while in undersaturated high latitude waters, skeletonless anthozoans, both zooxanthellate and azooxanthellate, are abundant

whereas scleractinians are azooxanthellate and relatively uncommon (Buddemeier and Fautin, 1994, 1996).

Based on my results supporting the hypothesis that the ancestral form of scleractinians was a skeletonless polyp and the evidence on ephemerality of the scleractinian skeleton, I agree with the idea of Fautin and Lowenstein (1994) that it is difficult to separate corallimorpharians from scleractinians: Scleractinia needs to be redefined, and Corallimorpharia cannot hold the rank equivalent to that of Scleractinia as currently accepted.

I, therefore, propose that the Corallimorpharia and Scleractinia are suborders of order Madreporaria because no morphological characters uniquely distinguish Corallimorpharia from Scleractinia, as was suggested by Schmidt (1974). The etymology of Madreporaria is madre, mother (from Latin mater, mtr-) + -pora (from Latin porus, calcareous stone, stalactite).

The emended classification of Hexacorallia is

Class Anthozoa

 Subclass Hexacorallia

 Order Actiniaria

 Order Madreporaria

 Suborder Scleractinia

 Suborder Corallimorpharia

CHAPTER V. CONCLUSION

This study provides phylogenetic analyses for the Corallimorpharia. Systematic position and status of Corallimorpharia in Hexacorallia have been controversial because members of Corallimorpharia have intermediate morphology between Actiniaria and Scleractinia. Some authors (Andres, 1883; Duerden, 1898, 1900) inferred corallimorpharians are a part of Actiniaria, and others (Stephenson, 1922; den Hartog, 1980) inferred that corallimorpharians are a part of Scleractinia. Carlgren (1949) and Wells and Hills (1956) inferred that Corallimorpharia is equivalent to both Actiniaria and Scleractinia.

Previous studies on molecular phylogeny of Hexacorallia did not provide a consensus on systematic relationships of the Corallimorpharia possibly due to insufficient taxon sampling of Corallimorpharia. Some (Fautin and Lowenstein, 1994; Chen et al. 1995; Romano and Cairns, 2000; Won et al. 2001) suggested Corallimorpharia forms a paraphyletic or polyphyletic assemblage with actinarians and/or scleractinians, and others (Daly et al. 2003; Medina et al. 2006; Brugler and France, 2007) inferred that Corallimorpharia is a monophyletic group. The interpretation of the relationship between monophyletic Corallimorpharia and Scleractinia differ among authors: Corallimorpharia is inferred to be a part of Scleractinia (Medina et al., 2006) or as a sister taxon (Daly et al., 2003; Brugler and France, 2007).

I conducted phylogenetic analyses using morphological and molecular data to provide a comprehensive investigation of phylogeny of Corallimorpharia. Morphological and molecular data were congruent, and were used to reject the hypothesis that corallimorpharians form a paraphyletic or polyphyletic assemblage with Actiniaria and Scleractinia. All data sets support monophyly of Corallimorpharia, and sister relationship with Scleractinia. Within Corallimorpharia, two evolutionary lineages, cylindrical body corallimorpharians and discoidal body corallimorpharians, were recovered. Based on estimated divergence time of Corallimorpharia and Scleractinia using molecular data, the ancestral form of Corallimorpharia-Scleractinia clade is likely to have been a skeletonless polyp.

Due to the lack of unique morphological characters defining Corallimorpharia, the scleractinian skeleton, which is the only character to separate Corallimorpharia from Scleractinia, is essential to determine the hierarchical rank of Corallimorpharia in Hexacorallia. One hypothesis is that the scleractinian skeleton is not homologous in all scleractinians, and therefore is not phylogenetically meaningful in defining Scleractinia. The hypothesis is supported by evidence from the fossil record, molecular phylogeny of Scleractinia, and environmental effects on calcification. Therefore, I propose Corallimorpharia and Scleractinia are suborders of the order Madreporaria, as Schmidt (1974) suggested.

In Corallimorpharia, there has been no consensus on the number of valid family and genera. I therefore provide a taxonomic revision at the genus-level based on re-examination of type material. The revision is focused on the seven of the 16 nominal genera, for which validity is questionable. I used five morphological character categories that are phylogenetically meaningful. The type species of each genus is redescribed for those known in less detail and diagnostic keys to genera and families are provided. I conclude five of the seven genera are valid. Thus, I conclude that there are three valid families and 11 valid genera in suborder Corallimorpharia.

The revision at the genus level is the first step to revise classification at the species level. There is no consensus in the number of valid species in most corallimorpharians genera. There are 41 nominal species in Corallimorpharia.

Taxonomic revision at the species level will provide information about diversity and biogeography of corallimorpharians.

REFERENCES

- Allman, G. J. 1846. Biological contributions. Description of a new genus of helianthoid zoophytes. *Annals and Magazine of Natural History* 17: 417-419.
- Andres, A. 1883. *Le Attinie (Monografia)*. Coi Tipi der Salviucci, Roma. Pp. 460.
- Apakupakul, K., M. E. Siddall, and E. Burrelson. 1999. Higher-level relationships of leeches based on morphology and gene sequences. *Molecular Phylogenetics and Evolution* 12:350–359.
- Ardelean, A. 2003. Reinterpretation of some tentacular structures in actinodendronid and thalassianthid sea anemones (Cnidaria: Actiniaria). *Zoologische Verhandelingen, Leiden*. 345: 31-40.
- Ates, R. M. L. 1987. *Corynactis viridis*, die Juwelanemone. *Die Aquarien-und Terrarien-Zeitschrift* 40(7): 314-316.
- Bernston, E. A., S. C. France, and L. S. Mullineaux. 1999. Phylogenetic relationships within the class Anthozoa (Phylum Cnidaria) based on nuclear 18S rDNA sequences. *Molecular Phylogenetics and Evolution* 13 : 417-433.
- Bigger, C. H. 1976. The acrohagial response in *Anthopleura krebsi*: intraspecific and interspecific recognition. In: G. O. Mackie (ed.), *Colenterate Ecology and Behavior*. Plenum Press, New York.
- Brugler, M.R. and S.C. France. 2007. The complete mitochondrial genome of the black coral *Chrysopathes formosa* (Cnidaria: Anthozoa: Antipatharia) supports classification of antipatharians within the subclass Hexacorallia. *Molecular Phylogenetics and Evolution* 42: 776-788.

- Budd, A. F. 1991. Neogene paleontology in the northern Dominican Republic. 11. Family Faviidae (Anthozoa: Scleractinia). Part I. *Bulletins of American Paleontology* 101(338): 5-83.
- Buddemeier R. W. and D. G. Fautin. 1996. Global CO₂ and evolution among the Scleractinia. *Bulletin de l'Institut Océanographique, Monaco, Spécial* 14: 33-38.
- Calder, D. R. 1974. Nematocysts of the coronate scyphomedusa, *Linuche unguiculata*, with a brief re-examination of scyphozoan nematocyst classification. *Chesapeake Sci.* 15: 170-173.
- Carlgren, O. 1900. Ostafrikanische Actinien. Gesammelt von Herrn Dr. F. Stuhlmann 1888 und 1889. *Mittheilungen aus dem Naturhistorischen Museum* 17: 21-144.
- Carlgren, O. 1921. Actiniaria I. Danish Ingolf Expedition 5 (9): 1-241.
- Carlgren, O. 1940. A contribution to the knowledge of the structure and distribution of the cnidae in the Anthozoa. *Kungliga Fysiografiska Sällskapets Handlingar* 51: 1-62.
- Carlgren, O. 1943. East-Asiatic Corallimorpharia and Actiniaria. *Kungliga Svenska Vetenskaps-Akademiens Handlingar* 20(6): 1-43.
- Carlgren, O. 1945. Further contributions to the knowledge of the cnidom in the Anthozoa especially in the Actiniaria. *Kungliga Fysiografiska Sällskapets Handlingar* 56: 3-24.
- Carlgren, O. 1949. A survey of Ptychodactaria, Corallimorpharia and Actiniaria. *Kungliga Svenska Vetenskaps-Akademiens Handlingar* 1(1): 1-121.

Carlgren, O. and T. A. Stephenson. 1929. Actiniaria. In: E. A. Briggs ed. *Australasian Antarctic Expedition 1911-14 Under the Leadership of Sir Douglas Mawson, O.B.E., D.Sc., B.E., F.R.S. Scientific Reports. Series C.-Zoology and Botany.* Alfred James Kent, Government Printer, Sydney.

Carlos, A. A., B. K. Baillie, M. Kawachi, and T. Maruyama. 1999. Phylogenetic position of *Symbiodinium* (Dinophyceae) isolates from tridacnids (Bivalvia), cardiids (Bivalvia), a sponge (Porifera), a soft coral (Anthozoa), and a free-living strain. *Journal of Phycology* 35: 1054-1062.

Chadwick, N. E. 1987. Interspecific aggressive behavior of the corallimorpharian *Corynactis californica* (Cnidaria: Anthozoa): effects on sympatric corals and sea anemones. *Biological Bulletin* 173: 110-125.

Chadwick, N. E. 1991. Effects of the anemone *Corynactis californica* on subtidal predation by the sea stars in the southern California bight. *Bulletin of Marine Sciences* 48(3): 623-634.

Chadwick, N. E. and C. Adams. 1991. Locomotion, asexual reproduction, and killing of corals by the corallimorpharian *Corynactis californica*. *Hydrobiologia* 216/217: 263-269.

Chadwick-Furman N. E. and M. Spiegel. 2000. Abundance and clonal replication in the tropical corallimorpharian *Rhodactis rhodostoma*. *Invertebrate Biology* 119: 351-360.

Chadwick-Furman N. E., M. Spigel, and I. Nir. 2000. Sexual reproduction in the tropical corallimorpharian *Rhodactis rhodostoma*. *Invertebrate Biology* 119: 361-369

- Chen, C. A., D. M. Odorico, M. T. Lohuis, J. E. N. Veron, and D. J. Miller. 1995. Systematic relationship within the Anthozoa using the 5' end of the 28S rDNA. *Molecular Phylogenetics and Evolution* 4: 175-183.
- Chen, C-L. A. and I-M. Chen. 1995. Spatial variability of size and sex in the tropical corallimorpharian *Rhodactis* (= *Discosoma*) *indonensis* (Cnidaria: Corallimorpharia) in Taiwan. *Zoological Studies* 34(2): 82-87.
- Chen, C. A., B. L. Willis, and D. J. Miller. 1996. Systematic relationships between tropical corallimorpharians (Cnidaria: Anthozoa: Corallimorpharia): utility of the 5.8S and internal transcribed spacer (ITS) regions of the rRNA transcription unit. *Bulletin of Marine Science* 59: 196–208.
- Cocks, W. P. 1851. Actiniæ (or sea-anemones), procured in Falmouth and its neighbourhood, by W. P. Cocks, Esq., from 1843-1849. *Annual Report of the Royal Cornwall Polytechnic Society* 19: 3-11.
- Cunningham, C. W. and L. W. Buss. 1993. Molecular evidence for multiple episodes of paedomorphosis in the Family Hydractiniidae. *Biochemical Systematics and Ecology* 21:57-69.
- Cutress, C. E. 1955. An interpretation of the structure and distribution of cnidae in Anthozoa. *Systematic Zoology* 4: 120-137.
- Cutress, C. E. 1979. *Bunodeopsis medusoides* Fowler and *Actinodiscus neglectus* Fowler, two Tahitian sea anemones: redescription and biological notes. *Bulletin of Marine Science* 29(1): 96-109.

de Blainville, H. M. D. 1830. Dictionnaire des Sciences Naturalles. F.G. Levrault, Strasbourg, Paris. 631 pp.

de Blainville, H. M. D. 1834. Manuel d'Actinologie ou de Zoophytologie. F.G. Levrault, Paris, Strasbourg. 644 pp.

Daly M., D. L. Lipscomb, and M. W. Allard. 2002. A simple test : evaluating explanations for the relative simplicity of the Edwardsiidae (Cnidaria : Anthozoa). *Evolution* 56: 502-510.

Daly, M., D. G. Fautin, and V. A. Cappola. 2003. Systematics of the Hexacorallia (Cnidaria: Anthozoa). *Zoological Journal of the Linnaean Society* 139: 419-437.

Danielssen, D. C. 1890. *Actinida*. In: Den Norske Nordhavs-Expedition 1876-1878. Zoologi. Grøndahl and Søn, Christiania. 184 pp.

Deng, Z. and L. Kong. 1984. Middle Triassic corals and sponges from Southern Guizhou and Eastern Yunnan. *Acta Palaeontologica Sinica* 23: 489-504.

Doumenc, D. A. and M. Van Praët. 1987. Ordre des Actiniaires, ordre des Ptychodactiaires, ordre des Corallimorphaires. In : Doumenc D., ed. *Traité de Zoologie, Tome III, Fascicle 3*. Paris : Masson, 257-401.

Duchassaing de Fombressin, P. and G. Michelotti. 1860. *Mémoire sur les Coralliaires des Antilles*. Imprimerie Royale, Turin. Pp. 89.

Duchassaing de Fombressin, P. and G. Michelotti. 1864. *Supplément au mémoire sur les Coralliaires des Antilles*. Imprimerie Royale, Turin. Pp. 112.

- Duchassaing de Fombressin, P. 1870. *Revue des Zoophytes et des Spongiaires des Antilles*. Chez Victor Masson et Fils, Paris. Pp. 52.
- Duerden, J. E. 1897. The Actinaria around Jamaica. *Journal of the Institute of Jamaica* 2: 449-465.
- Duerden, J. E. 1898. On the relations of certain Stichodactylinae to the Madreporaria. *Journal of the Linnean Society of London (Zoology)* 26 : 635-653.
- Duerden, J. E. 1900. Jamaican Actinaria II. *Scientific Transactions of the Royal Dublin Society* 7: 133-208.
- Dunn, D. F. 1981. The clownfish sea anemones : Stichodactylidae (Coelenterata : Actinaria) and other sea anemones symbiotic with pomacentrid fishes. *Transactions of the American Philosophical Society* 71: 3-115.
- Dunn, D. F. 1982. Cnidaria. In: Parker S. P., ed. *Synopsis and Classification of Living Things*. Vol. I. New York : McGraw-Hill, 669-706.
- Dunn, D. F. 1984. More Antarctic and Subantarctic sea anemones (Coelenterata: Corallimorpharia and Actinaria). *Antarctic Research Series* 41: 1-42.
- Dunn, D. F. and W. Hamner. 1980. *Amplexidiscus fenestrafer* n. gen., n. sp. (Coelenterata: Anthozoa), a tropical Indo-Pacific corallimorpharian. *Micronesica* 16(1): 29-36.
- Edgar, R.C. 2004. MUSCLE: a multiple sequence alignment method with reduced time and space complexity. *BMC Bioinformatics* 5(1): 113.

Ehrenberg, C. G. 1834. Beiträge zur physiologischen Kenntniss der Corallenthiere im allgemeinen, und besonders des rothen Meeres, nebst einem Versuche zur physiologischen Systematik derselben. *Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin* 1: 225-380.

Elliot, J. and Cook, C. B. 1989. Diel variation in prey capture behavior by the corallimorpharian *Discosoma sanctithomae*: mechanical and chemical activation of feeding. *Biological Bulletin* 176: 218-228.

Ellis, J. 1768. An account of the Actinia sociata, or clustered animal-flower, lately found on the sea-coasts of the new-ceded islands. *Philosophical Transactions of the Royal Society of London* 57: 428-437.

England, K. W. 1992. Actiniaria (Cnidaria: Anthozoa) from Hong Kong with additional data on similar species from Aden, Bahrain and Singapore. *The Marine Flora and Fauna of Hong Kong and Southern China* Part III, pp. 49-95.

Ezaki, Y. 2000. Palaeoecological and phylogentic implications of a new scleractinian genus from Permian sponge reefs, South China. *Palaeontology* 43:199–217.

Fautin, D. G. 1988. Anthozoan dominated benthic environments. *Proceedings of 6th International Coral Reef Symposium* 3: 231-236.

Fautin, D. G. 1988. The importance of nematocysts to actiniarian taxonomy. In: Hessinger D. A., Lenhoff, H. M., eds. *The Biology of Nematocysts*. New York: Academic Press, 487-500.

Fautin, D. G. 2006. Hexacorallians of the world: sea anemones, corals, and their allies. <http://hercules.kgs.ku.edu/hexacoral/anemone2/index.cfm>.

- Fautin, D. G. and J. M. Lowenstein. 1994. Phylogenetic relationships among scleractinians, actinarians, and corallimorpharians (Coelenterata: Anthozoa). *Proceedings of the 7th International Coral Reef Symposium 2*: 665-670.
- Fautin, D. G. and R. M. Mariscal. 1991. Cnidaria: Anthozoa. In: Harrison F. W. and Westfall, J. A., eds. *Microscopic Anatomy of Invertebrates*, Vol. 2. New York: Wiley-Liss, 267-358.
- Fautin, D. G. and M. Daly. In press. Actiniaria, Corallimorpharia, and Zoanthidea (Cnidaria: Anthozoa) of the Gulf of Mexico. *The Gulf of Mexico: Its Origin, Waters, and Marine Life*, volume 3, David Camp, Editor. Harte Institute, Corpus Christi, Texas.
- Felsenstein, J. 1981. Evolutionary tree from DNA sequences: a maximum likelihood approach. *Journal of Molecular Evolution* 17: 368-376.
- Felsenstein, J. 2004. *Inferring phylogenies*. Sinauer Associates, Inc. Massachusetts. pp. 664.
- Fine, M. and D. Tchernov. 2007. Scleractinian coral species survive and recover from decalcification. *Science* 315 (5820): 1811.
- Fowler, G. H. 1888. Two new types of Actiniaria. *Quarterly Journal of Microscopical Science* 29: 143-152.
- Foster, A. B. 1986. Neogene Paleontology in the Northern Dominican Republic. 3. Family Poritidae (Anthozoa: Scleractinia). *Bulletins of American Paleontology* 90(325): 45-123.

France, S. C., P. E. Rosel, J. E. Agenbroad, L. S. Mullineaux, and T. D. Kocher. 1996. DNA sequence variation of mitochondrial large-subunit rRNA provides support for a two-subclass organization of the Anthozoa (Cnidaria). *Molecular Marine Biology and Biotechnology* 5: 15-28.

Genzano, G. N., F. H. Acuña, A. C. Excoffon, and C. D. Pérez. 1996. Cnidarios bentónicos de la Provincia de Buenos Aires. Lista sistemática, distribución y estrategias de Colonización. *Jornadas Pampeanas de Ciencias Naturales* 6: 113-121.

Gosse, P. H. 1860. *A History of the British Sea-Anemones and Corals*. Van Voorst, Paternoster Row, London. 362 pp.

Gravier, C. 1918. Note préliminaire sur les hexactiniaires recueillis au cours des croisières de la Princesse-Alice et de l'Hirondelle de 1888 à 1913 inclusivement. *Bulletin de l'Institut Océanographique* (Monaco) 346: 1-24.

Gravier, C. 1922. Résultats des campagnes scientifiques accomplies sur son yacht par Albert Ier Prince Souverain de Monaco publiés sous sa direction avec le concours de M. Jules Richard. Imprimerie de Monaco. Monaco. 104 pp.

den Hartog, J. C. 1980. Caribbean shallow water Corallimorpharia. *Zoologische Verhandelingen* 176: 1-83.

den Hartog, J. C. 1997. The sea anemone fauna of Indonesian coral reefs. In: Tomascik, T., A. J. Mah, A. Nontji, and M. K. Moosa, eds. *The Ecology of the Indonesian Seas*. Periplus Editions, Republic of Singapore, pp. 351-370.

den Hartog, J. C., O. Ocaña, and A. Brito 1993. Corallimorpharia collected during the CANCAP expeditions (1976-1986) in the south-eastern part of the North Atlantic. *Zoologische Verhandelingen* 282: 3-76.

Haddon, A. C. 1898. The Actinaria of Torres Straits. *Scientific Transactions of the Royal Dublin Society* 6(2): 393-520.

Haddon, A. C. and A. M. Shackleton. 1893. Description of some new species of Actinaria from Torres Straits. *Scientific Transactions of the Royal Dublin Society* 8 (1): 116-131.

Hand, C. 1966. On the evolution of the Actinaria. In: Rees W. J., ed. *The cnidarians and their evolution*: Academic Press, 135–146.

Hargitt, C. W. 1911. *Cradactis variabilis*: an apparently new Tortugan actinian. *Papers from the Tortugas Laboratory of the Carnegie Institution of Washington* 3 : 51-53.

Harris, D. J. and K. A. Crandall. 2000. Intragenomic Variation Within ITS1 and ITS2 of Freshwater Crayfishes (Decapoda: Cambaridae): Implications for Phylogenetic and Microsatellite Studies. *Molecular Biology and Evolution* 17: 284-191.

Hedgpeth, J. W. 1854. Anthozoa: the anemones. *Fisheries Bulletin of the Fish and Wildlife Service* 55: 285-290.

Heeger, T., H. Müller, and U. Mrowietz. 1992. Protection of human skin against jellyfish (*Cyanea capillata*) stings. *Marine Biology* 113: 669-678.

Hertwig, R. 1882. Report on the Actiniaria dredged by H.M.S. Challenger during the years 1873-1876. *Report on the Scientific Results of the Voyage of the H.M.S. Challenger during the years 1873-76 (Zoology)* 6(1): 1-136.

Hertwig, R. 1888. Report on the Actiniaria dredged by H.M.S. Challenger during the years 1873-1876. *Report on the Scientific Results of the Voyage of the H.M.S. Challenger during the years 1873-76 (Zoology)* 26(3): 1-56.

Hillis, D. M., C. Moritz, and B. K. Mable. 1996. *Molecular Systematics*. Sinauer Associates, Inc. USA.

Humann, P. and N. DeLoach. 2002. *Reef creature identification: Florida, Caribbean, Bahamas*. New World Publication, Jacksonville. 448 pp.

Humason, G. L. 1979. *Animal Tissue Techniques*, 4th edition. San Francisco: Freeman and Company. 661 pp.

International Commission on Zoological Nomenclature (ICZN). 1956. Opinion 417. Rejection for nomenclatorial purposes of volume 3 (Zoologie) of the work by Lorenz Oken entitled "Okens Lehrbuch der Naturgeschichte" published in 1815-1816. *Opin. Decl. Int. Comm. Zool. Nomen.*, 14(1): 1-42.

International Commission on Zoological Nomenclature (ICZN). 1964. International Code of Zoological Nomenclature adopted by the XV International Congress of Zoology: i-xix, 1-767. *International Trust for Zoological Nomenclature*, London.

Knowlton, N. and B. D. Keller. 1985. Two more sibling species of alpheid shrimps associated with the Caribbean sea anemones *Bartholomea annulata* and *Heteractis lucida*. *Bulletin of Marine Science* 37: 893-904.

Krempf, A. 1904. Liste des Hexanthides rapportés de l'Océan Indien (Golfe de Tadjourah) par M. Ch. Gravier. *Bulletin du Muséum National d'Histoire Naturelle (Paris)* 11: 191-196.

Kuguru, B. L., Y. D. Mgaya, M. C. Öhman, and G. M. Wagner. 2004. The reef environment and competitive success in the Corallimorpharia. *Marine Biology* 145: 875-884.

Johnston, G. 1847. *A History of the British Zoophytes*. John Van Voorst, London. 488 pp.

Le Sueur, C. A. 1817. Observations on several species of the genus *Actinia*. *Journal of the Academy of Sciences of Philadelphia* 1: 149-154.

Lang, J. C. 1973. Interspecific aggregation by scleractinian reef corals. 2. Why the race is not the only to the swift. *Bulletin of Marine Sciences* 23: 260-279.

Lang, J. C. 1984. Whatever works: the variable importance of skeletal and of non-skeletal characters in scleractinian taxonomy. *Palaentologica Americana* 54: 18-44.

Langmead, N. and N. Chadwick. 1999. Marginal tentacles of the corallimorpharian *Rhodactis rhodostoma*. 1. Role in competition for space. *Marine Biology* 134: 479-489.

Li, W. H. 1997. *Molecular Evolution*. Sinauer Associates, Sunderland, Massachusetts.

- Linder, A. 2003. A preliminary DNA-based phylogeny of stylasterid hydrocorals (Cnidaria; Hydrozoa; Stylasteridae). In: 7th International Conference on Coelenterate Biology, 2003.
- Logan, A. 1984. Interspecific aggregation in hermatypic corals from Bermuda. *Coral Reefs* 3: 131-138.
- Longhurst, A. 1998. *Ecological geography of the sea*. Academic Press, San Diego. 398 pp.
- McMurrich, J. P. 1887. Notes on the fauna of Beaufort, North Carolina. *Studies at the Biological Laboratory of the Johns Hopkins University (Baltimore)* 4(2): 55-63.
- McMurrich, J. P. 1889. A contribution to the actinology of the Bermudas. *Proceedings of the Academy of Natural Sciences of Philadelphia* 41: 102-126.
- McMurrich, J. P. 1896. Notes on some actinians from the Bahama Islands, collected by the late Dr. J. I. Northrop. *Annals of the New York Academy of Sciences* 9: 181-194.
- McMurrich, J. P. 1898. Report on the Actiniaria collected by the Bahama Expedition of the State University of Iowa, 1893. *Bulletin from the Laboratories of Natural History, State University of Iowa* 4(3): 225-249.
- McMurrich, J. P. 1905. A revision of the Duchassaing and Michelotti actinian types in the Museum of Natural History, Turin. *Bollettino del Musei di Zoologia ed Anatomia Comparata* 20(494): 1-23.

- Manuel, R. L. 1981. British Anthozoa keys and notes for the identification of the species, No. 18 in Synopses of the British Fauna. Academic Press, London, New York, Toronto, Sydney, San Fransisco. 241 pp.
- Mariscal, R. N. 1974. Nematocysts. In: L. Muscatine and H. M. Lenhoff (eds.), *Coelenterate Biology*. Academic Press, New York.
- Mariscal, R. N., E. J. Conklin, and C. H. Bigger. 1977. The ptychocyst, a major new category of cnidae used in the tube construction by cerianthid anemone. *Biological Bulletin* 152 : 392-405.
- Medina, M., A. G. Collins, T. L. Takaoka, J. V. Kuehl, and J. L. Boore. 2006. Naked corals: skeleton loss in Scleractinia. *Proceedings of the National Academy of Sciences* 103(24): 9096-9100.
- Milne Edwards, H. 1857. *Histoire Naturelle des Coralliaires ou Polypes Proprement Dits*, vol. 1. Librairie Encyclopédique de Roret, Paris. 326 pp.
- Milne-Edwards, H. and J. Haime. 1851. *Archives du Muséum d'Histoire Naturelle Volume: 5: Monographie des polypiers fossiles des terrains palfozoiques, pricidie d'un tableau ginerale de la classification des polypes*. Gide et J. Baudry, Paris. 502 pp.
- Miles, J.S. 1991. Inducible agonistic structures in the tropical corallimorpharian, *Discosoma sanctithomae*. *Biological Bulletin* 180: 406 415.
- Morycowa, E. 1988. Middle Triassic Scleractinia from the Cracow-Silesia region, Poland. *Acta Paleontologica Polonica* 33(2): 91-121.

Moseley, H. N. 1877. On new forms of Actiniaria dredged in the deep sea; with a description of certain pelagic surface-swimming species. *Transactions of the Linnean Society (London)* 1: 295-305.

Muhando, C. A., B. L. Kuguru, N. E. Wagner, N. E. Mbijje, and M. E. Öhman. 2002. Environmental effects on the distribution of corallimorpharians in Tanzania. *Ambio* 31: 558-561.

Oliver, W. A. 1980. The relationship of the scleractinian corals to the rugose corals. *Paleobiology* 6(2): 146-160.

Oliver, W. A. 1996. Origins and relationships of Paleozoic coral groups and the origin of the Scleractinia. *Paleontological Society Papers* 1: 107–134.

Östman, C., A. Aquirre, M. Myrdal, P. Nyvall, J. Lindstrom and M. Björklund. 1995. Nematocysts in *Tubularia larynx* (Cnidaria, Hydrozoa) from Scandinavia and the northern coast of Spain. *Scientia Marina* 59(2): 165-179.

Östman, C. 2000. A guideline to nematocyst nomenclature and classification, and some notes on the systematic value of nematocysts. *Scientia Marina* 64(1): 31-46.

Pax, F. 1910. Studien an westindischen Actinien. *Zoologische Jahrbücher Suppl.* 11(2): 157-330.

Pawlowski, J., I. Bolivar, J. Fahrni, C. de Vargas, and S. S. Bowser. 1999. Naked foraminiferans revealed. *Nature* 399: 27.

- Petersen, K. W. 1979. *Development of coloniality in Hydrozoa*. In: Larwood G, Rosen BR, eds. *Biology and Systematics of Colonial Organisms*, Academic Press, p. 105–139.
- Posada, D. and K. A. Crandall. 1998. Modeltest: testing the model of DNA substitution. *Bioinformatics* 14 (9): 817-818.
- Qi, W. 1984. An Anisian Coral fauna in Guizhou, South China. *Paleontographica Americana* 54: 187-190.
- Ramil, F. and E. F. Pulpeiro. 1990. Inventario de los Antozoos de Galicia, A checklist of the Anthozoa of Galicia. *Boletín de la Real Sociedad Española de Historia Natural. Sección Biológica* 86: 17-30.
- Ritson-Williams, R. and V. J. Paul. 2007. *Periclímenes yucatanicus* and *Periclímenes rathbunae* on unusual corallimorph hosts. *Coral Reefs* 26: 147.
- Romano, S. L. and S. D. Cairns. 2000. Molecular phylogenetic hypotheses for the evolution of scleractinian corals. *Bulletin of Marine Science* 67: 1043–1068.
- Romano, S. L. and S. R. Palumbi. 1996. Evolution of scleractinian corals inferred from molecular systematics. *Science* 271: 640–642.
- Rüppell, E. and F. S. Leuckart. 1828. *Atlas zu der Reise im Nördlichen Afrika von Eduard Rüppell, Neue Wirbellose Thiere des Rothen Meers*. Heinr. Ludw. Brvnnner, Frankfurt am Main. 47 pp.
- Sandberg, P. A. 1983. An oscillating trend in Phanerozoic nonskeletal carbonate mineralogy. *Nature*. 305:19–22.

- Sanderson, M. J. 2004. *r8s, version 1.70: User's manual*. Section of evolution and ecology. Davis, CA: University of California.
- Schmidt, H. 1969. Die Nesselkapseln der Aktinien und ihre differentialdiagnostische Bedeutung. *Helgoländer Wissenschaftliche Meeresuntersuchungen* 19: 284-317.
- Schmidt, H. 1972. Die Nesselkapseln der Anthozoen und ihre Bedeutung für die phylogenetische Systematik. *Helgoländer Wissenschaftliche Meeresuntersuchungen* 23: 422–458.
- Schmidt, H. 1974. On evolution in the Anthozoa. *Proceedings of the 2nd International Coral Reef Symposium* 1: 533–560.
- Scrutton, C. T. and E. N. K. Clarkson. 1991. A new scleractinian-like coral from the Ordovician of the Southern Uplands, Scotland. *Paleontology* 34: 179–194.
- Sebens, K. P. 1976. The ecology of Caribbean sea anemones in Panama: utilization of space on a coral reef. In *Coelenterate Ecology and Behavior*, G. O. Mackie ed., Plenum Press, New York, pp. 67-78.
- Shearer, T. L., M. J. Van Oppen, S. L. Romano, and G. Worheide. 2002. Slow mitochondrial DNA sequence evolution in the Anthozoa (Cnidaria). *Molecular Ecology* 11: 2475-2487.
- Shick, J. M. 1991. *A Functional Biology of Sea Anemones*. Chapman & Hall, London and other cities. 395 pp.

- Skaer, R. J. 1973. The secretion and development of nematocysts in siphonophores. *Journal of Cell Science* 13: 371-393.
- Slautterback, D. B. 1961. *Nematocyst development*. In: The Biology of *Hydra* and of some other Coelenterates. Lenhoff, H. M. and Loomis, W. F. eds., pp. 77-129. University of Miami Press, Coral Gables.
- Slautterback, D. B. and D. W. Fawcett. 1959. The development of the cnidoblasts of *Hydra*: an electron microscope study of cell differentiation. *Journal of Biophysical and Biochemical Cytology* 5: 441-451.
- Smith, S. V. and R. W. Buddemeier. 1992. Global change and coral reef ecosystems. *Annual Review of Ecology and Systematics* 23: 89-118.
- Spotte, S., R.W. Heard, P.M. Bubucis, R.R. Manstan, and J.A. McLelland. 1991. Pattern and coloration of *Periclimenes rathbunae* from the Turks and Caicos islands, with comments on host association in other anemone shrimps of the West Indies and Bermuda. *Gulf Research Reports* 8: 301-311.
- Stanley, G. D. Jr. and D. G. Fautin. 2001. The origins of modern corals. *Science* 291: 1913-1914.
- Stanley, G. D. Jr. 2003. The evolution of modern corals and their early history. *Earth-Science Review* 60: 195-225.
- Stephenson, T. A. 1920. On the classification of Actiniaria. Part I. *Quarterly Journal of Microscopical Science (New Series)* 64: 425-574.

Stephenson, T. A. 1921. On the classification of Actiniaria. Part II. -- Consideration of the whole group and its relationships, with special reference to forms not treated in Part I. *Quarterly Journal of Microscopical Science (New Series)* 65: 493-576.

Stephenson, T. A. 1922. On the classification of Actiniaria. Part III. *Quarterly Journal of Microscopical Science (New Series)* 66: 247-319.

Swofford, D. L. 2001. *PAUP**. *Phylogenetic Analysis Using Parsimony (*and Other Methods)*. Version 4. Sinauer Associates, Sunderland, Massachusetts.

Trench, R. K. and R. J. Blank. 1987. *Symbiodinium microadriaticum* Freudenthal, *S. goreauii* sp. nov., *S. kawagutii* sp. nov. and *S. pilosum* sp. nov.: gymnodinioid dinoflagellate symbionts of marine invertebrates. *Journal of Phycology* 23: 469-481.

Uchida, H. and I. Soyama. 2001. *Sea Anemones in Japanese Waters*. TBS, Japan. 157 pp.

Varela, C., I. Santana, M. Ortiz, R. Lalana, H. Caballero, and P. Chevalier. 2001. Adiciones a la actinofauna (Anthozoa: Actiniaria y Corallimorpharia), de Cuba. *Revista de Investigaciones Marinas* 22(3): 187-190.

Vaughan, T. W., and J. W. Wells. 1943. Revision of the suborders, families, and genera of the Scleractinia. *Special Papers of the Geological Society of America* 44: 1-363.

Veron, J. E. N. 1995. *Corals in Space and Time: Biogeography and Evolution of the Scleractinia*. Cornell University Press, Ithaca, N.Y., 321 pp.

- Verrill, A. E. 1864. Revision of the polypi of the eastern coast of the United States. *Memoirs of the Boston Society of Natural History* 1: 1-45.
- Verrill, A. E. 1868. Synopsis of the polyps and corals of the North Pacific Exploring Expedition, under Commodore C. Ringgold and Capt. John Rodgers, U.S.N., from 1853 to 1856. Collected by Dr. Wm. Stimpson, Naturalist to the Expedition. Part IV. Actiniaria. *Communications of the Essex Institute* 5(3): 315-330.
- Verrill, A. E. 1869. Synopsis of the polyps and corals of the North Pacific Exploring Expedition, under Commodore C. Ringgold and Capt. John Rodgers, U.S.N., from 1853 to 1856. Collected by Dr. Wm. Stimpson, naturalist to the Expedition. Part IV. Actiniaria. *Proceedings of the Essex Institute* 6: 51-104.
- Verrill, A. E. 1898. Descriptions of new American actinians, with critical notes on other species, I. *American Journal of Science and Arts* 6: 493-498.
- Verrill, A. E. 1899. Descriptions of imperfectly known and new actinians, with critical notes on other species, II. *American Journal of Science and Arts* 7(4): 41-50.
- Verrill, A. E. 1900. Additions to the Anthozoa and Hydrozoa of the Bermudas. Anthozoa. *Transactions of the Connecticut Academy of Arts and Sciences* 10(2): 551-572.
- Verrill, A. E. 1905. The Bermuda Islands. Part IV. Geology and paleontology, and Part V. An account of the coral reefs. *Transactions of the Connecticut Academy of Arts and Sciences* 12: 45-348.
- Watzl, O. 1922. Die Actiniarien der Bahamainseln. *Arkiv für Zoologi* 14(24): 1-89.

- Weill, R. 1934. Contribution à l'étude des cnidaires et de leurs nématocytes I. *Travaux de la Station Zoologique de Wimeraux* 10: 1–347.
- Weinland, D. F. 1860. Über Inselbildung durch Korallen und Mangrovebüsche im mexikanischen Golf. *Württembergische Naturwissenschaftliche Jahreshefte* 16: 31-44.
- Wells, J. W. and D. Hill. 1956. Anthozoa. In: Moore RC, ed. *Treatise on Invertebrate paleontology, Part F, Coelenterata.* : Geological Society of America/University of Kansas Press, F161–F477.
- Westfall, J. A. 1966. The differentiation of nematocysts and associated structures in the Cnidaria. *Zeitschrift fuer Zellforschung und Mikroskopische Anatomie* 75: 381-403.
- Williams E. H. J. and L. B. Williams. 1982. First report of *Periclimenes yucatanicus* (Ives) (Decapoda, Palaemonidae) in association with a corallimorpharian anemone. *Crustaceana* 42: 318-319.
- Won, J. H., B. J. Rho and J. I. Song. 2001. A phylogenetic study of the Anthozoa (phylum Cnidaria) based on morphological and molecular characters. *Coral Reefs* 20: 39–50.
- Zamponi, M. O. 1976. Enmienda a la familia Sideractiidae Danielssen 1890 (Anthozoa: Corallimorpharia) con la creacion de *Sphincteractis sanmatiensis* gen. et sp. nov. *Physis (Buenos Aires)* 35A(91): 127-133.

Appendix 1. List of morphological characters used in cladistic analysis:

- 1 Calcareous exoskeleton: absent (0); present (1)
- 2 Polyp body shape: cylindrical (column elongated) (0); plate-like (column short and oral disc wider than pedal disc) (1)
- 3 Oral disc is fully covered with tentacles: no(0); yes(1)
- 4 Marginal tentacle: none or very reduced (0); capitate (1); digitate (2); branched (3); papilliform (4)
- 5 Discal tentacle: none (0); capitate (1); digitate (2); branched (3); papilliform (4)
- 6 Tentacle-free zone on oral disc: absent (0); present (1)
- 7 Tentacle/coelenteron relationship: one tentacle per endocoel and per exocoel (0); one tentacle per exocoel, multiple per endocoel (1)
- 8 Tentacle retractile: no (0); yes (1)
- 9 Column: smooth (0); tuberculated (1)
- 10 Sphincter muscle: absence (0); present (1)
- 11 Basilar muscle: absent (0); present (1)
- 12 Coupled mesenteries: absent (0); present (1)
- 13 Paired mesenteries: absent (0); present (1)
- 14 Type of mesenteries: only perfect (0); perfect and imperfect (1)
- 15 Nature of mesenterial filaments: unilobed (0); trilobed (1)
- 16 Directive mesenteries: no (0); yes (1)
- 17 Acontia: absent (0); present (1)
- 18 Siphonoglyph: absent (0); present (1)
- 19 Catch tentacles: absent (0); present (1)
- 20 Spirocyst: absent (0); present (1)
- 21 Basitrichs: absent (0); present (1)
- 22 Microbasic p-mastigophors: absent (0); present (1)
- 23 Microbasic b-mastigophors: absent (0); present (1)
- 24 Holotrichs: absent (0); present (1)

- 25 Hoplotelic p-mastigophors: absent (0); present (1)
- 26 Large holotrichs (larger than 100 um): absent (0); present (1)
- 27 Occurrence depth: shallow (0); deep (1)
- 28 Occurrence area: polar (0); temperate only (1); tropical only (2); temperate and tropical (3); temperate and polar (4)
- 29 Polyp organization: solitary (0); colonial (1); clonal (2)
- 30 Zooxanthellae: absent (0); present (1)
- 31 Mesogleal cell inclusion: absent/rare (0); present (1)
- 32 Asexual reproduction: absent (0); present (1)
- 33 Sexuality: hermaphroditic (0); gonochoric (1); hermaphroditic and gonochoric (2)

Appendix 2. Alignment of 16S mtDNA sequences

```

[           10           20           30           40           50]

Discosoma_num      -----GGAATGTCATATGAAAGAGAA-GT
Discosoma_neg      -----GGAGGG-CA-ATG-ATGTAGA-GT
Amplexidiscus      -----GGCGAG-CAAATG--AGTAGA-GT
Rhodactis          -----GGA-AG-CATTGA--AGTAGA-GT
Metarhodactis      -----GCCCAG-CATTTG-ATGTAGAAGT
Actinotryx        -----GACAAGCTAAATGCATGTAGACGT
Ricordea          -----AAG-TAA-TG-ATGTAGACGT
Corynactis_v      -----T-AA-T--CCGAAAGTTAATT
Corynactis_c      -----TGTGAA-T-TCTGAAAGTTAATT
Corallimorphus    -----TGTGAA-TATGTGGAAGTTA-TT
Balanophyllia     -----
Dendrophyllia     -----
Tubastrea         -----
Enallopsammia    -----TGAAGGTAGAAGT
Porites           -----
Flabellum         -----
Fungiacyathus     -----
Pavona            -----
Caryophyllia     -----
Catalaphyllia     -----
Oculina           -----
Lobophyllia       -----
Fungia            -----
Montastrea        -----
Anthopleura       TCGACTGTTTACCAAAAACATAGCTCTCTGCTAAAGCTAAATGCTGAAGT
Aiptasia          TCGACTGTTTACCAAAAACATAGCTCTCTGCTAAAGCTAAATGCTGAAGT
Bathypbellia      -----CTGCCAAAGCTAAATGCTGAA--
Metridium         -----
Stichodactyla     TCGACTGTTTACCAAAAACATAGCTCTCTGCTAAAGCTAAATGCTGAAGT
Nematostella      -----
Cerianthus        -----AAAGGAGCCCTAAAGT

[           60           70           80           90          100]

Discosoma_num      ATGAAGGGTGAGACCTGCCCTATGGTTGTATCTAAAGGGGTCGG-TAGG
Discosoma_neg      ATGAAGGGTGAGACCTGCCCTATGGTTGTATCTAAAGGGGTCGG-TAGG
Amplexidiscus      ATGAAGGGTGAGACCTGCCCA-ATGGTTGTATCTAAAGGGGTCGG-TAGG
Rhodactis          ATG-AGGGTGAGACCTGCCCA-ATGGTTGTATCTAAAGGGGTCGG-TAGG
Metarhodactis      ATG-AGGGTGAGACCTGCCCT-ATGGTTGTATCTAAAGGGGTCGG-TAGG
Actinotryx         ATGAGGGGTGAGACCTGCCCA-ATGGTTGTATCTAAAGGGGTCGG-TAGG
Ricordea           ATGGGGGTGAGTC-TGCCCA-ATGGTTGTATCTGAAGGGGTCGG-TAGG
Corynactis_v       ATGGGGGTGAGACCTGCCCA-ATGGTTGTATCTAAAAGGGTCGG-TTGG
Corynactis_c       ATGGGGGTGAGACCTGCCCA-ATGGTTGTATCTAAAAGGGTCGG-TTGG
Corallimorphus    ATGGGGGTGAGACATGCCCA-GTGGTTGTATCTAAAAGGGTCGG-TTGG
Balanophyllia     -----GTCTCTAAAAGGGTTGG-TAGA
Dendrophyllia     -----GTATCTAAAAGGGTTGG-TAGA
Tubastrea          -----GTATCTAAAAGGGTTGG-TAGA
Enallopsammia     ATGAAAGGTGAGAMCTGCCCA-ATGGTTGTATCTAAAAGGGTTGG-TAGA
Porites            -----GTATCTAAAAGGGTTGG-TAAA
Flabellum         -----GTATCTAAAAGGGTTGG-TAGA
Fungiacyathus     -----
Pavona            -----GTATCTTAGAAGGTTGG-TAAG
Caryophyllia      -----GTATCTAAAAAGTTTG-TTTT
Catalaphyllia     -----GTATCTAAAAAGTTTG-TTTT
Oculina           -----GTATCTAAAAAGTTTG-TTTT
Lobophyllia       -----GGATCTAAAAAGTTTG-TTTT
Fungia            -----GTATCTAAAAAATTTG-TTTT
Montastrea        -----CCT-----TGATACCTGTTAGTCCTG----
Anthopleura       ATGGAGGGTGAAGCCTGCCCG-ATGGTTGTATCTGAAAAGGTTGGCTAAG
Aiptasia          ATGGAGGGTGAAGCCTGCCCA-ATGGTTGTATCTAAAAGAGTTGGCTAAG
Bathypbellia      -----
Metridium         -----
Stichodactyla     ATGGAGGGTGAAGCCTGCCCA-ATGGTTGTATCTAAAAGAGTTGGCTAAG
Nematostella      ---GAGGTGACGCCTGCCCA-ATGGTTGTATCTAAAAGAGTCGATAAGA
Cerianthus        ATAGGAGGTGAAGCCTGCCCT-ATGGTTGTACCTGAAATAATAAC-AAAG

```

[110 120 130 140 150]

Discosoma_num GCCGAAATTATAAGACAATTGAATGGCTGCGGTAACCGTGACCGTGAAA
Discosoma_neg GCCGAAATTATAAGACAATTGAATGGCTGCGGTAACCGTGACCGTGAAA
Amplexidiscus GCCGAAATTATAAGACAATTGAATGGCCGCGGTAACCGTGACCGTGAAA
Rhodactis GCCGAAATTATAAGACAATTGAATGGCCGCGGTAACCGTGACCGTGAAA
Metarhodactis GCCGAAATTATAAGACAATTGAATGGCTGCGGTAACCGTGACCGTGAAA
Actinotryx GCCGAAATTATAAGACAATTGAATGGCTGCGGTAACCGTGACCGTGAAA
Ricordea GTCGATTCTATAAGACAATTGAATGGCTGCGGTAACAGTGACCGTGAAA
Corynactis_v GCCGACTTTATAAGACAATTGAATGGCTGCGGTAACACTGACCGTGAAA
Corynactis_c GCCGACTTTATAAGACAATTGAATGGCTGCGGTAACACTGACCGTGAAA
Corallimorphus GCCGACTTTATAAGACAATTGAATGGCTGCGGTAACACTGACCGTGAAA
Balanophyllia GCCAGCTTTATAAGACAATTAAATGGCCGCGGTAACACTGACCGTGATA
Dendrophyllia GCCAGCTTTATAAGACAATTAAATGGCCGCGGTAACACTGACCGTGATA
Tubastrea GCCAGC-TTATAAGACAATTAAATGGCCGCGGTAACACTGACCGTGATA
Enallopsammia GCCAGCTTTATAAGACAATTAAATGGCCGCGGTAACACTGACCGTGATA
Porites GCCAACTTTATAAGACAATTAAATGGCCGCGGTAACACTGACCGTGATA
Flabellum GCCAGCTTTATAAGACAATTAAATGGCCGCGGTAACACTGACCGTGATA
Fungiacyathus -----AATTTAATGGCCGCGGTAACCTTTGACCGTGATA
Pavona GCGAATTTATAAGACAATTAAATGGCTGCGGTAACACTGACCGTGAAA
Caryophyllia GCTCAC-TAATAATGACAATTAAATGGCCGCGGTAACACTGACTGTGAAA
Catalaphyllia GCTTAT-TAATAAGACAGCTAAATGGCCGCGGTAACACTAAGTGAAA
Oculina GCTTAC-TAATAAGACAATTAAATGGCCGCGGTAACACTAAGTGAAA
Lobophyllia GCTTAT-TAATAAGACAATTAAATGGCTGCGGTAACACTAAGTGAAA
Fungia GCTTAT-TAATAAGACAATTAAATGGCCGCGGTAACACTAAGTGAAA
Montastrea GCCGTA--AACGATGAANACTAGATGTCGCGCGGTAACAATAACC-----A
Anthopleura GTCAACTTCATAAGGGCAATTGAATGGCCGCGGTAACACTGACCGTGATA
Aiptasia GTCAACTTCATAAGGGCAATTGAATGGCCGCGGTAACACTGACCGTGATA
Bathypbellia -----
Metridium -----TCACTGACCGTGATA
Stichodactyla GTCAACTTTATAAGGGCAATTGAATGGCCGCGGTAACACTGACCGTGATA
Nematostella GTCAACTTTATAAGGACAATTGAATGGCCGCGGTAACACTGACCGTGATA
Cerianthus CAGTTATTTATAAGACAATTAAATGGCCGCGTTATACCTGACTGTGAAA

[160 170 180 190 200]

Discosoma_num ATGTAGCGTAATCAATAGTCAATTAATTGTTGGCCGGTATGAATGGTGTC
Discosoma_neg ATGTAGCGTAATCAATAGTCAATTAATTGTTGGCCGGTATGAATGGTGTC
Amplexidiscus ATGTAGCGTAATCAATAGTCAATTAATTGTTGGCCGGTATGAATGGTGTC
Rhodactis ATGTAGCGTAATCAATAGTCAATTAATTGTTGGCCGGTATGAATGGTGTC
Metarhodactis ATGTAGCGTAATCAATAGTCAATTAATTGTTGGCCGGTATGAATGGTGTC
Actinotryx ATGTAGCGTAATCAATAGTCAATTAATTGTTGGCCGGTATGAATGGTGTC
Ricordea ATGTAGCGTAATCAATTGTCAATTAATTGTTGGCCGGTATGAATGGTGTC
Corynactis_v ATGTAGCGTAATCAATAGTCAATTAATTGTTGGCCGGTATGAATGGTGCC
Corynactis_c ATGTAGCGTAATCAATAGTCAATTAATTGTTGGCCGGTATGAATGGTGCC
Corallimorphus ATGTAGCGTAATCAATAGTCAATTAATTGTTGGCCGGTATGAATGGTGCC
Balanophyllia ATGTAGCGTAATCAATAGTCAATTAATTGTTGGCCGGTATGAATGGTGTC
Dendrophyllia ATGTAGCGTAATCAATAGTCAATTAATTGTTGGCCGGTATGAATGGTGTC
Tubastrea ATGTAGCGTAATCAATAGTCAATTAATTGTTGGCCGGTATGAATGGTGTC
Enallopsammia ATGTAGCGTAATCAATAGTCAATTAATTGTTGGCCGGTATGAATGGTGTC
Porites ATGTAGCGTAATCAATAGTCAATTAATTGTTGGCCGGTATGAATGGTGTC
Flabellum ATGTAGCGTAATCAATAGTCAATTAATTGTTGGCCGGTATGAATGGTGTC
Fungiacyathus ATGTAGCGTAATCAATAGTCAATTAATTGTTGGCCGGTATGAATGGTGTC
Pavona ATGTAGCGAATAAATAGTCAATTAATTGTTGACCGGTATGAATGGTGTC
Caryophyllia ATGTAGCGCAATCAATTGTCAATTAATTGTTGACCGGTATGAATGGTGTC
Catalaphyllia ATGTAGCGTAATCAATTGTTAATTAATTGTTGACCGGTATGAATGGTGTC
Oculina ATGTAGCGTAATCAATTGTCAATTAATTGTTGACCGGTATGAATGGTGTC
Lobophyllia ATGTAGCGTAATCAATTGTTAATTAATTGTTGACCGGTATGAATGGTGTC
Fungia ATGTAGCATAATAGATTGTCAATTAATTGTTGACTGGTATGAATGGTATC
Montastrea ATGTAGCGT-ATCTAACGTCAATTAATTGTTGACTGGGATGAATGGTAGC
Anthopleura ATGTAGCGTAATCAATAGCCAATTAATTGTTGGCCGGTATGAATGGCATC
Aiptasia ATGTAGCGTAATCAATAGCCAATTAATTGTTGGCCGGTATGAATGGCGTC
Bathypbellia -----GGCCGGTATGAATGGCGTC
Metridium ATGTAGCGTAATCAATAGCCAATTAATTGTTGGCCGGTATGAATGGCGTC
Stichodactyla ATGTAGCGTAATCAATAGCCAATTAATTGTTGGCCGGTATGAATGGCGTC
Nematostella ATGTAGCGTAATCAATAGCCAATTAATTGTTGGCCGGTATGAATGGCGTC
Cerianthus ATGTAGCGCAATCAATCGTCAATTAATTGTTGACAAGTATGAATGGCGTC

[210 220 230 240 250]

Discosoma_num ACGAAGGTCTCACTGTCTTAAGAAAATCCCTTGTGAAATTGAATTTGTAG
Discosoma_neg ACGAAGGCCTCACTGTCTTAAGAAAATCCCTTGTGAAATTGAATTTGTAG
Amplexidiscus ACGAAGGTCTCACTGTCTTAAGAAAATCCCTTGTGAAATTGAATTTGTAG
Rhodactis ACGAAGGTCTCACTGTCTTAAGAAAATCCCTTGTGAAATTGAATTTGTAG
Metarhodactis ACGAAGGCCTCACTGTCTTAAGAAAATCCCTTGTGAAATTGAATTTGTAG
Actinotryx ACGAAGGTCTCACTGTCTTAAGAAAATCCCTTGTGAAATTGAATTTGTAG
Ricordea ACGAAGGCCTCACTGTCTTAAGAAAATCTCCTTGTGAAATTGAATTTGTAG
Corynactis_v ACGAGGGTCTCACTGTCTTAAGAAAATCCCCAGTAAAATTGAATTTGTAG
Corynactis_c ACGAGGGTCTCACTGTCTTAAGAAAATCCCCAGTAAAATTGAATTTGTAG
Corallimorphus ACGAGGGTCTCACTGTCTTAAGAAAATCCCCAGTAAAATTGAATTTGTAG
Balanophyllia ACGAGGGTCTCACTGTCTTAAGAAAATTTCCAGTAAAATTGATT--TGG
Dendrophyllia ACGAGGGTCTCACTGTCTTAAGAAAATTTCCAGTAAAATTGAATTTGTAG
Tubastrea ACGAGGGTCTCACTGTCTTAAGAAAATTTCCAGTAAAATTGAATTTGTAG
Enallopsammia ACGAGGGTCTCACTGTCTTAAGAAAATTTCCAGTAAAATTGAATTTGTAG
Porites ACGAGGGTCTCACTGTCTTAAGAAAATGTCCAGTAAAATTGAATTTGTAG
Flabellum ACGAGGGTCTCACTGTCTTAAGAAAATTTCCAGTAAAATTGAATTTGTAG
Fungiacyathus ACGAGGGTCTCACTGTCTTAAGAAAATTTCCAGTAAAATTGAATTTGTAG
Pavona ACGAGGGTCTCGCTGTCTTAAGAGAGTTTCCAGTAAAATTGAACCTGTAG
Caryophyllia ACGAAAAGTTCTTCTGTTTTAAAAAACACTCAAGGAAAATTGAATTTGTAG
Catalaphyllia ACGAAAAGTTCTTCTGTCTTAAAAAAATACTTAATGAAAATTGAATTTGTAG
Oculina ACGAAAAGTTCTTCTGTCTTAAAAAAATACTTAATGAAAATTGAATTTGTAG
Lobophyllia ACGAAAAGTTTCTGTCTTAAAAAAATACTTAATGAAAATTGAATTTGTAG
Fungia ACGAAAAGTTTCTGTCTTAAAAAAATACTTAATGAAAATTGAATTTGTAG
Montastrea ACGAAAAGTTTCTGTATTGAGAAAACCGTAATGAAAATTGAATATGTAG
Anthopleura ACGAAGGCCCCACTGTCTTAAGAGGACTCTCCATGAAAATTGAAATCGTAG
Aiptasia ACGAAGGCCCCACTGTCTTAAGAGGACTCTCCATGAAAATTGAAATCGTAG
Bathypbellia ACGAAGGCCCCACTGTCTTAAGAGGACTCTCCATGAAAATTGAAATCGTAG
Metridium ACGAAGGCCCCACTGTCTTAAGAGGACTCTCCATGAAAATTGAAATCGTAG
Stichodactyla ACGAAGGCCCCACTGTCTTAAGAGGACTTTCCATGAAAATTGAAATCGTAG
Nematostella ACGAAGGCCCCACTGTCTCAAGAAGACCCCCGTGAAAATTGAAATCGTAG
Cerianthus ACGAGTGCTTCACTGTCTTAAGAAAATCCAGTAAAATTGAATTCGTAG

[260 270 280 290 300]

Discosoma_num TGAAGATGCTACATTCAAATTTGTTAGACGAAAAGTCCCCATGGAACCTTTA
Discosoma_neg TGAAGATGCTACATTCAAATTTGTTAGACGAAAAGTCCCCATGGAACCTTTA
Amplexidiscus TGAAGATGCTACATTCAAATTTGTTAGACGAAAAGTCCCCATGGAACCTTTA
Rhodactis TGAAGATGCTACATTCAAATTTGTTAGACGAAAAGTCCCCATGGAACCTTTA
Metarhodactis TGAAGATGCTACATTCAAATTTGTTAGACGAAAAGTCCCCATGGAACCTTTA
Actinotryx TGAAGATGCTACATTCAAATTTGTTAGACGAAAAGTCCCCATGGAACCTTTA
Ricordea TATTGATGCTACATCAAATTTGTTAGACGAGAAGTCCCCATGGAACCTTTA
Corynactis_v TGATGATGCTACATAAAAAATTTGTTGGACGAGAAGTCCCCATGAAACTTTA
Corynactis_c TGATGATGCTACATAAAAAATTTGTTGGACGAGAAGTCCCCATGAAACTTTA
Corallimorphus TGATGATGCTACATAAAAAATTTGTTGGACGAGAAGTCCCCATGAAACTTTA
Balanophyllia TGAAGATGCTACATCCAAATTTGTTAGACAAGAAGTCCCCATGGAACCTTTA
Dendrophyllia TGAAGATGCTACATCCAAATTTGTTAGACAAGAAGTCCCCATGGAACCTTTA
Tubastrea TGAAGATGCTACATCCAAATTTGTTAGACAAGAAGTCCCCATGGAACCTTTA
Enallopsammia TGAAGATGCTACATCCAAATTTGTTAGACAAGAAGTCCCCATGGAACCTTTA
Porites TGAAGATGCTACATCCAAATTTGTTAGACAAGAAGTCCCCATGGAACCTTTA
Flabellum TGAAGATGCTACATCCAAATTTGTTAGACAAGAAGTCCCCATGGAACCTTTA
Fungiacyathus TGAAGATGCTACATCCA-ATTGTTAGACAAGAAGTCCCCATGGAACCTTTA
Pavona TGAAGATGCTACATCAAATTTGTTAGACAAGAAGTCCCCATGGAACCTTTA
Caryophyllia TGAAGATGCTACATTAATAATGTTAGACGAGAAGTCCCCATGGAGCTTTA
Catalaphyllia TGAAGATGCTACATTAATAATGTTAGACGAGAAGTCCCCATGGAGCTTTA
Oculina TGAAGATGCTACATTAATAATGTTAGACGAGAAGTCCCCATGGAGCTTTA
Lobophyllia TGAAGATGCTACATTAATAATGTTAGACGAGAAGTCCCCATGGAGCTTTA
Fungia TGAAGATGCTACATTAATAATGTTAGACGAGAAGTCCCCATGGAGCTTTA
Montastrea TTAAGATGCAACG-CGAAAAAGTAAGCCGAGAAGTCCCATGTAGCTTTA
Anthopleura TGAAGATGCTACGTCCATATTGTTAGACGAAAAGACCCCATTTGAGCTTTA
Aiptasia TGAAGATGCTACGTCCATATTGTTAGACGAAAAGACCCCATTTGAGCTTTA
Bathypbellia TGAAGATGCTACGTCCATATTGTTAGACGAAAAGACCCCATTTGAGCTTTA
Metridium TGAAGATGCTACGTCCATATTGTTAGACGAAAAGACCCCATTTGAGCTTTA
Stichodactyla TGAAGATGCTACGTCCATATTGTTAGACGAAAAGACCCCATTTGAGCTTTA
Nematostella TGAAGATGCTACGTCCAAATTTGTTAGACGAAAAGACCCCATTTGAGCTTTA
Cerianthus TTAAGATGCTACG-TAATTTTGTAGACGAAAAGACCCATTAAGCTTTA

```

[          310          320          330          340          350]

Discosoma_num      CTGGAGACTTATGTGG-----TCTATCTG-
Discosoma_neg      CTGGAGACTTATGTGG-----TCTATCTG-
Amplexidiscus     CTGGAGACTTATGTGG-----TCTATCTG-
Rhodactis         CTGGAGACTTATGTGG-----TCTATCTG-
Metarhodactis     CTGGAGACTTATGTGG-----TCTATCTG-
Actinotryx       CTGGAGACTTATGTGG-----TCTATCTG-
Ricordea          CTGGAGATTTATATGG-----CCTATCTG-
Corynactis_v      CTGGAGACTTATGTGGCTTGTGCTGACTGATCGAACTAGGCTCAATCAGT
Corynactis_c      CTGGAGACTTATGTGGCTTGTGCTGACTGATCGAACTAGGCTCAATCAGT
Corallimorphus    CTGGAGACTTATAAGGCTTGTGCTGACTGATCGAACTAGGCTCAATCAGT
Balanophyllia     CTGGAAACTTATGTGGCTT---AAATTAATT-----TATTTCTT-
Dendrophyllia     CTGGAAACTTATGTGGCTT---AAATTAATT-----TATTTCTT-
Tubastrea         CTGGAAACTTATGTGGCTT---AAATTAATT-----TATTTCTT-
Enallopsammia     CTGGAAACTTATGTGGCTT---AAATTAATT-----TATTTCTT-
Porites           CTGGAAACTTATGTGGCTT---AAATTAATT-----TATTTCTT-
Flabellum         CTGGAGACTTATGTGGCTT---AAATTAATT-----TATTTCTT-
Fungiacyathus     CTGGAGACTTATGAGGCTT---AAATTAATT-----TATTTCTT-
Pavona            CTGGAGACTTATGTG-CT----CCCTTAATTG-----GCTGACTT-
Caryophyllia      CTGAAAGCCTAAAAGACT----CCCTTAATTG-----AATTTTTT-
Catalaphyllia     CTGAGGGCTTAGAAGACT----CCCTTAATTG-----ATTTTATA-
Oculina           CTGAAAGCTTAAGAGACT----CCCTTAATTG-----ATTTTCTA-
Lobophyllia       CTGAGGGCTTAGGGGCT----CCGTTAATTG-----TTTCTA-
Fungia            CTGAAACTTAAGAGGCT----CCGTTAATTG-----ATTTTCTA-
Montastrea        CTAGAAATTTGAGAGACT----CCGTTAATTG-----GTTTCTA-
Anthopleura       CTAAGACTTGTATGGC-----CGA-----AATAACTT-
Aiptasia          CTAAGACTTGCATGGC-----TCAAATA-----
Bathypheilia      CTAAGACTTGCATGGC-----TCAAATA-----
Metridium         CTAAGACTTGCATGGC-----TCAAATA-----
Stichodactyla     CTAAGACTTGCATGGC-----TCAAATA-----
Nematostella      CTAGAAACTTGCATGGCTT---AA-----ATTAACTT-
Cerianthus        CTGGATGCTTATGTTGTCT---TAATAAATAGATATAATGAATGGTTAA

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[          360          370          380          390          400]

Discosoma_num      -----ACGAATAGATAGTTTAGATTATGTGGTGTAACTGTT--
Discosoma_neg      -----ACGAATAGATAGTTTAGATTAGGTGGTGTAACTGTT--
Amplexidiscus     -----ACGAATAGATAGTTTAGATTATGTGGTGTAACTGTT--
Rhodactis         -----ACGAATAGATAGTTTAGATTATGTGGTGTAACTGTT--
Metarhodactis     -----ACGAATAGATAGTTTAGATTAGGTGGTGTAACTGTT--
Actinotryx       -----ACGAATAGATAGTTTAGATTATGTGGTGTAACTGTT--
Ricordea          -----ACAGATAAATGTTTAGATTATGTGGTGTAACTGTTTT
Corynactis_v      GAAAGCATCTAACAAATAAATAGCTTAGACTATGTGGTGTAAACCGTTTT
Corynactis_c      GAAAGCATCTAACAAATAAATAGCTTAGACTATGTGGTGTAAACCGTTTT
Corallimorphus    GAAAGCATCTAACAAATAAATAGCTTAGACTATGTGGTGTAAACCGTTTT
Balanophyllia     -----ACAAATAAATAG-TTTTTAAATGTGGTGTAACTCT--
Dendrophyllia     -----ACAAATAAATAG-TTTTTAAATGTGGTGTAACTCT--
Tubastrea         -----ACAAATAAATAG-TTTTTAAATGTGGTGTAACTCT--
Enallopsammia     -----ACAAATAAATAGTTTTTAAATGTGGTGTAAACCCCT--
Porites           -----ACAAATAAGTAG-TTTTTAAATGTGGTGTAACTCT--
Flabellum         -----ACAAATAAATAG-TTTTTAAATGTGGTGTAAACCCCT--
Fungiacyathus     -----ACAAATAAATAG-TTTTTAAATGTGGTGTAACTCT--
Pavona            -----AAATAG-TTTTTAAATGTGGTGTACTCAAC--
Caryophyllia      -----TATTTATT--
Catalaphyllia     -----
Oculina           -----
Lobophyllia       -----
Fungia            -----
Montastrea        -----TGCCTCAGCT--
Anthopleura       -----AAATAAAAAGTTTAGATAATGTGG---GATCCGTT--
Aiptasia          ----ATTTGATTTAAATAAAAAGTTTAGATAATGTGG---GACCCGTT--
Bathypheilia      ----ATTTGATTTAAATAAAGAGTTTAGATAATGTGG---GATCCGTT--
Metridium         ----ATTTGATTTAAATAAAAAGTTTAGATAATGTGG---GACCCGTT--
Stichodactyla     ----ATTTGATTTAAATAAAGAGTTTAGATAATGTGG---GATCCGTT--
Nematostella      -----AAATAAAAAGTTTAGATAA---GGTGGATCCGTT--
Cerianthus        TGCATATTAATAAGATAATTAATATAGTTAATAAAGAAGAAATAGTA--

```

[410 420 430 440 450]

```

Discosoma_num -----
Discosoma_neg -----
Amplexidiscus -----
Rhodactis -----
Metarhodactis -----
Actinotryx -----
Ricordea AAGTGAAAAATATATAGGTGTTCTTAGAGTAGTCTTCAGACTAAAGTAA
Corynactis_v ATTTAAAACTTTAGGGAGTAGTGTTTAGAGTAGTCTTCAGACTAAAGTAA
Corynactis_c ATTTAAAACTTTAGGGAGTAGTGTTTAGAGTAGTCTTCAGACTAAAGTAA
Corallimorphus ATTTAAAACTTTAGGGAGTAGTGTTTAGAGTAGTCTTCAGACTAAAGTAA
Balanophyllia -----TGGATTAAC-----
Dendrophyllia -----TGGATTAAC-----
Tubastrea -----TGGATTAAC-----
Enallopsammia -----TGGATTAAC-----
Porites -----TGGATTAAT-----
Flabellum -----CGGATTAAC-----
Fungiacyathus -----CGGATTACC-----
Pavona -----CGGGTAG-----
Caryophyllia -----CGGGTAG-----
Catalaphyllia -----CGGGTAG-----
Oculina -----CGGGTAG-----
Lobophyllia -----CGGGTAG-----
Fungia -----CGGGTAG-----
Montastrea -----CGTGTAGTG-----
Anthopleura -----
Aiptasia -----
Bathypbellia -----
Metridium -----
Stichodactyla -----
Nematostella -----
Cerianthus -----ATATTCTTA-----

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[460 470 480 490 500]

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Discosoma_num -----GTT
Discosoma_neg -----GTT
Amplexidiscus -----GTT
Rhodactis -----GTT
Metarhodactis -----GTT
Actinotryx -----GTT
Ricordea AAAACACATGTAT-----GAAAATTTAGTT
Corynactis_v AAAACACATATGTTTTTTTTTACA---CCCGCCTCTTCAAATTTAGGTT
Corynactis_c AAAACACATATGTTTTTTTTTACAGACCCGGCCTCTTCAAATTTAGGTT
Corallimorphus AAAACACATGTATATTTTTTAGAGACCCGGCCTCTTCAAATTTAGGTT
Balanophyllia -----GAGGGTT
Dendrophyllia -----GAGGGTT
Tubastrea -----GAGGGTT
Enallopsammia -----GAGGGTT
Porites -----TGGGGTT
Flabellum -----TAGGGTT
Fungiacyathus -----TAGGGTT
Pavona -----TAGGGTT
Caryophyllia -----
Catalaphyllia -----
Oculina -----
Lobophyllia -----
Fungia -----
Montastrea -----GTT
Anthopleura -----TTGGTT
Aiptasia -----TCCGGTT
Bathypbellia -----TCCGGTT
Metridium -----TCCGGTT
Stichodactyla -----TCCGGTT
Nematostella -----AAGGCT
Cerianthus -----TTCAGTA

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[510	520	530	540	550]
Discosoma_num	AGTAAATTC	CA-CTCTTT	TATTTTAAGAG	---GGCTAACT	CTTCTTTTGA
Discosoma_neg	AGTAAATTC	CA-CTCTTT	TATTTTAAGAG	---GGCTAACT	CTTCTTTTGA
Amplexidiscus	AGTAAATTC	CA-CTCTTT	TATTTTAAGAG	---GGCTGACT	CTTCTTTTGA
Rhodactis	AGTAAATTC	CA-CTCTTT	TATTTTAAGAG	---GGCTGACT	CTTCTTTTGA
Metarhodactis	AGTAAATTC	CA-CTCTTT	TATTTTAAGAG	---GGCTAACT	CTTCTTTTGA
Actinotryx	AGTAAATTC	CA-CTCTTT	TATTTTAAGAG	---GACTAACT	CTTCTTTTGA
Ricordea	AGTAAACTC	CA-CTTTTT	TATTTTAGAG	---GGTAACT	CTTCTTTTGA
Corynactis_v	AGTCAAAC	TCA--TCTTTT	TATTTAAGAA	---AGCTAACT	CTTCTTTTGA
Corynactis_c	AGTCAAAC	TCA-CTCTTT	TATTTAAGAA	---AGCTAACT	CTTCTTTTGA
Corallimorphus	AGTCAAAC	TCA-CTCTTT	TATTTAAGAA	---AGCTAACT	CTTCTTTTGA
Balanophyllia	AGAAAAGCT	CA-CTCTTT	TATTTAAGAA	---AGCCAAC	TCAAATTTTA
Dendrophyllia	AGAAAAGCT	CA-CTCTTT	TATTTAAGAA	---AGCCAAC	TCAAATTTTA
Tubastrea	AGAAAAGCT	CA-CTCTTT	TATTTAAGAA	---AGCCAAC	TCAAATTTTA
Enallopsammia	AGAAAAGCT	CA-CTCTTT	TATTTAAGAA	---AGCCAAC	TCAAATTTTA
Porites	AGAAAAGCT	CA-CTCTTT	TATTTAAGAA	---AGCCAAC	TCAAACCTTA
Flabellum	ATAAAGGCC	CA-CTCTTT	TATTTAAGAA	---AGCCAAC	TCAAACCTTA
Fungiacyathus	AGAAAAGCT	CA-CTCTTT	TATTTAAGAA	---AGCCAAC	TCAAAGAATTA
Pavona	AGAAAAGCT	CA-CT	TTTTATTTAAGAA	---AGCCAAC	TAAAAATATA
Caryophyllia	-----	-----	-----	GGCAACGCA	ACCCACGT
Catalaphyllia	-----	-----	-----	GGCAACGCA	ACCCACGT
Oculina	-----	-----	-----	GGCAACGCA	ACCCACGT
Lobophyllia	-----	-----	-----	GGCAACGCA	ACCCACGT
Fungia	-----	-----	-----	GGCAACGCA	ACCCACGT
Montastrea	AGAAAAGCT	CA-TGC	-----	AGGGAACGCA	ACCCACGT
Anthopleura	AATGAAAC	ACCACCTCTTT	TATTTAAGAG	---AGCTAAC	CTTGT-----
Aiptasia	AATGAAAC	ACCACCTCTTT	TATTTAAGAG	---AGCTAAC	ATTAC-----
Bathypheilia	AATGAAAC	ACCACCTCTTT	TATTTAAGAG	---AGCTAAC	ATTAC-----
Metridium	AATGAAAC	ACCACCTCTTT	TATTTAAGAG	---AGCTAAC	ATTAC-----
Stichodactyla	AATGAAAC	ACCACCTCTTT	TATTTAAAAG	---AGCTAAC	ATTGC-----
Nematostella	AATGAAAC	ACCACCTCTTT	TATTTAAGAG	---AGCTAAC	CTTT-----
Cerianthus	TATTTAAT	CCT-TTATAT	CAATATAAAT	GAAAGACT	ATTTCTCCAC----
[560	570	580	590	600]
Discosoma_num	GTAAAGTTA	-ATT-GTGGG	--TACC--ACCAC	-TT--G-AGT	-GT-AA
Discosoma_neg	GTAAAGTTA	-ATT-GTGG	---TACC--ACCAC	-TT--G-AGT	-GT-AA
Amplexidiscus	ATAAAGTTA	--TT-CTGG	---TACC--ACCAC	-TT--G--GT	-GT-AA
Rhodactis	ATAAAGTTA	--TT-CTG	---TACC--ACCAC	-TT--G--GT	-GT-AA
Metarhodactis	ATAAAGTTAG	ATT-CTGG	---TACCC-ACCAC	-TTTTAG-AGT	-GT-AA
Actinotryx	GTAAAGTTAG	ATTGCTG	---TACCC-ACCAC	-TT--AG-A--GT	-AA
Ricordea	ATTAAGTT	CGATTGGTGGGGGT	ACC--ACC-C-TTTT	-GGAG--GTGAA	
Corynactis_v	ATTAAGTT	CGATTGGTGGGGGT	TACCCACCACATTTT	TAGGAGTGGTGAA	
Corynactis_c	ATTAAGTT	CGATTGGTGGGGGT	TACCCACCACATTTT	TAGGAGTGGTGAA	
Corallimorphus	ATTAAGTT	CGATTGGTGGGGGT	TACCCACCACATTTT	TAGGAGTGGTGAA	
Balanophyllia	T-----	-----	-----	-----	-----
Dendrophyllia	T-----	-----	-----	-----	-----
Tubastrea	T-----	-----	-----	-----	-----
Enallopsammia	T-----	-----	-----	-----	-----
Porites	T-----	-----	-----	-----	-----
Flabellum	T-----	-----	-----	-----	-----
Fungiacyathus	T-----	-----	-----	-----	-----
Pavona	T-----	-----	-----	-----	-----
Caryophyllia	TT-----	-----	-----	-----	-----
Catalaphyllia	-----	-----	-----	-----	-----
Oculina	T-----	-----	-----	-----	-----
Lobophyllia	-----	-----	-----	-----	-----
Fungia	-----	-----	-----	-----	-----
Montastrea	T-----	-----	-----	-----	-----
Anthopleura	-----	-----	-----	-----	-----
Aiptasia	-----	-----	-----	-----	-----
Bathypheilia	-----	-----	-----	-----	-----
Metridium	-----	-----	-----	-----	-----
Stichodactyla	-----	-----	-----	-----	-----
Nematostella	-----	-----	-----	-----	-----
Cerianthus	-----	-----	-----	-----	-----

[610	620	630	640	650]
Discosoma_num	TT---	GGATTAGAGAAATGAGGTAAGTTAGACAGTTTGGTTGGGGCGATC			
Discosoma_neg	TT---	GGATTAGAGAAATGAGGTAAGTTAGACAGTTTGGTTGGGGCGATC			
Amplexidiscus	TT---	GGGTTAGAGAAATGAGGTAAGTTAGACAGTTTGGTTGGGGCGATC			
Rhodactis	TT---	GGGTTAGAGAAATGAGGTAAGTTAGACAGTTTGGTTGGGGCGATC			
Metarhodactis	TTTCTGGGTTAGAGAAATGAGGTAAGTTAGACAGTTTGGTTGGGGCGATC				
Actinotryx	TT-C-	GGATTAGAGAAATGAGGTAAGTTAGACAGTTTGGTTGGGGCGATC			
Ricordea	--	TCTGGGTTAGAGAAATGAGGTAAGTTAGAAAATTTGGTAGGGGCGATC			
Corynactis_v	TTTCTGGGTTAGAGAAATGGGGTAAGTTAGACAGTTTGGTAGGGGCGATC				
Corynactis_c	TTTCTGGGTTAGAGAAATGGGGTAAGTTAGACAGTTTGGTAGGGGCGATC				
Corallimorphus	TTTCTGGGTTAGAGAAATGGGGTAAGTTAGACAGTTTGGTAGGGGCGATC				
Balanophyllia	-----	GTCTTTGGGATTTGATAAGTGGGACAGTTTGGTTGGGGCGACC			
Dendrophyllia	-----	GTCTTTGGGATTTAGATAAGTGGGACAGTTTGGTTGGGGCGACC			
Tubastrea	-----	GTCTTTGGGATTTAGATAAGTGGGACAGTTTGGTTGGGGCGACC			
Enallopsammia	-----	GTCTTTGGGATTTGATAAGTGGGACAGTTTGGTTGGGGCGACC			
Porites	-----	GTCTTTGGGATTTGATAAGTGGGACAGTTTGGTTGGGGCGACC			
Flabellum	-----	GTCTTTGGGATTTGATAAGTGGGACAGTTTGGTTGGGGCGACC			
Fungiacyathus	-----	GTCTTTGGGATTTGATAAGTGGGACAGTTTGGTTGGGGCGACC			
Pavona	-----	GTTTTTGGGATTTGATAAGTGGGACAGTTTGGTTGGGGCGACC			
Caryophyllia	-----	TTGCAAGCAATAGGCTAGACAGTTTGGTTGGGGTGATA			
Catalaphyllia	-----	TTGCCAGCTTTAAGCGGGACAGTTTGGTTGGGGCGACA			
Oculina	-----	TAGTTGCAAGCTTTAAGCGGGACAGTTTGGTTGGGGCGACA			
Lobophyllia	-----	CCGTTGCCAGCATTAAAGCGGGACAGTTTGGTTGGGGCGACA			
Fungia	-----	TTGCAAGCTTTAAGTAGGACAGTTTGGTTGGGGCGACA			
Montastrea	-----	TTTAGTTGCCAGCATTAGTTGGACAGTTTGGTTGGGGCGACA			
Anthopleura	-----	AGGGAGAATGCAAGTTGGATAGTTTGGTTGGGGCGACC			
Aiptasia	-----	AGGGATAGTGTAAGTTGGATAGTTTGGTTGGGGCGACC			
Bathypheilia	-----	AGGGATAGTGTAAGTTGGATAGTTTGGTTGGGGCGACC			
Metridium	-----	AGGGATAGTGTAAGTTGGATAGTTTGGTTGGGGCGACC			
Stichodactyla	-----	ATGGATAATGTAAGTTGGATAGTTTGGTTGGGGCGACC			
Nematostella	-----	AGGGACAATGCGAGTTTGGATAGTTTGGTTGGGGCGACC			
Cerianthus	-----	TTAAGAAATGGATTAGTATGTTAGACAGTTTGGTTGGGGCGACC			
[660	670	680	690	700]
Discosoma_num	GCCTTTTAAAAAGTAACGAAGGTGGGCTTAAAGATACATATTTAATAGTT-				
Discosoma_neg	GCCTTTTAAAAAGTAACGAAGGTGGGCTTAAAGATACATATTTAATAGTT-				
Amplexidiscus	GCCTTTTAAAAAGTAACGAAGGTGGGCTTAAAGATACATATTTAATAGTT-				
Rhodactis	GCCTTTTAAAAAGTAACGAAGGTGGGCTTAAAGATACATATTTAATAGTT-				
Metarhodactis	GCCTTTTAAAAAGTAACGAAGGTGGGCTTAAAGATACATATTTAATAGTT-				
Actinotryx	GCCTTTTAAAAAGTAACGAAGGTGGGCTTAAAGATACATATTTAATAGTT-				
Ricordea	GCCTTTTAAAAAGTAACGAAGGTGGGCTTAAAGATACATATTTAATAGTT-				
Corynactis_v	GCCTTTTAAAAAGTAACGAAGGTGGGCTTAAAGATACATATTTAATAGTT-				
Corynactis_c	GCCTTTTAAAAAGTAACGAAGGTGGGCTTAAAGATACATATTTAATAGTT-				
Corallimorphus	GCCTTTTAAAAAGTAACGAAGGTGGGCTTAAAGATACATATTTAATAGTT-				
Balanophyllia	GCCTTTTAAAAAGTAACGAAGGTGGGCTTAAAGATACATATTTAATAGTT-				
Dendrophyllia	GCCTTTTAAAAAGTAACGAAGGTGGGCTTAAAGATACATATTTAATAGTT-				
Tubastrea	GCCTTTTAAAAAGTAACGAAGGTGGGCTTAAAGATACATATTTAATAGTT-				
Enallopsammia	GCCTTTTAAAAAGTAACGAAGGTGGGCTTAAAGATACATATTTAATAGTT-				
Porites	GCCTTTTAAAAAGTAACGAAGGTGGGCTTAAAGATACATATTTAATAGTT-				
Flabellum	GCCTTTTAAAAAGTAACGAAGGTGGGCTTAAAGATACATATTTAATAGTT-				
Fungiacyathus	GCCTTTTAAAAAGTAACGAAGGTGGGCTTAAAGATACATATTTAATAGTT-				
Pavona	GCCTTTTAAAAAGTAACGAAGGTGGGCTTAAAGATACATATTTAATAGTT-				
Caryophyllia	GTTTTTTAAAAAGTAACGAAAACGAACTATGAA----TCATTAGT-----				
Catalaphyllia	GTTTTTTAAAAAGTAACGAAAACGAACTATGAA----TCATTAGT-----				
Oculina	GTTTTTTAAAAAGTAACGAAAACGAACTATGAA----TCATTAGT-----				
Lobophyllia	GTTTTTTAAAAAGTAACGAAAACGAACTATGAA----TCATTAGT-----				
Fungia	GTTTTTTAAAAAGTAACGAAAACGAACTATGAA----TCATTAGT-----				
Montastrea	GCCTTTTAAAAA---ACCGGAGGTAGGCTTTGACGACGTCAATAGT-----				
Anthopleura	ACCTTTTAAAAAGGTAACGAAGGTGAGCTTAAAGGTCCTAGTTAATAGCTA				
Aiptasia	ACCTTTTAAAAAGGTAACGAAGGTGAGCTTAAAGGTCCTAGTTAATAGCTA				
Bathypheilia	ACCTTTTAAAAAGGTAACGAAGGTGAGCTTAAAGGTCCTAGTTAATAGCTA				
Metridium	ACCTTTTAAAAAGGTAACGAAGGTGAGCTTAAAGGTCCTAGTTAATAGCTA				
Stichodactyla	ACCTTTTAAAAAGGTAACGAAGGTGAGCTTAAAGGTCCTAGTTAATAGCTA				
Nematostella	ACCTTTTAAAAAGGTAACGAAGGTGAGCTTAAAGGTCCTAGTTAATAGCTA				
Cerianthus	CCCTTAAAAAGGATAAAGTGGGGCACTAAGGTAATAAAGAAAGA-----				

[710	720	730	740	750]
Discosoma_num	GTCGCTGACTGTGAAGGGGGAGCCCTGAGCAGACACTAGAAAAAGCC-T				
Discosoma_neg	GTCGCTGACTGTGAAGGGGGAGCCCTGAGCAGACACTAGAAAAAGCC-T				
Amplexidiscus	GTCGCTGACTGTGAAGGGGGAGCCCTGAGCAGACACTAAAAAGAGCC-T				
Rhodactis	GTCGCTGACTGTGAAGGGGGAGCCCTGAGCAGACACTAAAAAGAGCC-T				
Metarhodactis	GTCGCTGACTGTGAAGGGGGAGCCCTGAGCAGACACTAAAAAGAGCC-T				
Actinotryx	GTCGCTGACTGTGAAGGGGGAGCCCTGAGCAGACACTAAAAAGAGCC-T				
Ricordea	GTCGCTGACTGTGAAGGGGGGCGCCCTGAGCAGACACTAAAAACAGCC-T				
Corynactis_v	GTCGCTGACTGTGAAGGGGGGCGCCCTGAGCAGACACTAAAAACCGCC-T				
Corynactis_c	GTCGCTGACTGTGAAGGGGGGCGCCCTGAGCAGACACTAAAAACCGCC-T				
Corallimorphus	GTCGCTGACTGTGAAGGGGGGCGCCCTGAGCAGACACTAAAAACCGCC-T				
Balanophyllia	TATGTCATACTGCCAAGGGGGAATCCTGAGCAGGCACCTT-----ACTT				
Dendrophyllia	TATGTCATACTGCCAAGGGGGAATCCTGAGCAGGCACCTT-----ACTT				
Tubastrea	TATGTCATACTGCCAAGGGGGAATCCTGAGCAGGCACCTT-----ACTT				
Enallopsammia	TATGTCATACTGCCAAGGGGGATCCTGAGCAGACACTT-----ACTT				
Porites	TATGTCATACTGCCAAGGGGGAATCCTGAGCAGGCACCTT-----ATT				
Flabellum	GATGTCATACTGCCAAGGGGAGATCCTGAGCAGACACTT-----ACTT				
Fungiacyathus	GATGTCATACTGCCAAGGGGAGATCCTGAGCAGACACTT-----CTTT				
Pavona	TATGTCATACTGCTAAGGGGAGACCCAGAGCAGACACTT-----GTCCTT				
Caryophyllia	--TGTCATAGTGCGCATGTTTCACTCTGA---AAACTGAAGAGACATT				
Catalaphyllia	--TGTCATACTAGC----TTCACCCTGAAAA-ATTTTTTAAGGGACA-T				
Oculina	--TGTCAT-CGGAGC----TTCACCCTGAAAA-ATTTTTTAAGGGACA-T				
Lobophyllia	--TGTCAT-CGTAGC----TTCACCCTGAAAA-ACTTTTTAAGGGACA-T				
Fungia	--TGTCATAAGGC-----TTCACCTCTGA-AAGATTTTTAAGAGACATT				
Montastrea	---GTCATCATGCCCC--TTACGCCCTTGAGCT-ACTTTCTAAGGGACATT				
Anthopleura	GTGGCCTGACTGCAACGGGGACATCCCAGCAGACACTGGTAATCTCT--				
Aiptasia	GTGGCCTGACTGCAAGGGGGACGTCTCGAGCAGACACGT-----CCTT				
Bathypheilia	GTGGCCTGACTGCAAGGGGGACGTCTCGAGCAGACACGT-----CCTT				
Metridium	GTGGCCTGACTGCAAGGGGGACGTCTCGAGCAGACACGT-----CCTT				
Stichodactyla	GTGGCCTGACTGCAAGGGGGACGTCTCGAGCAGACACGT-----CCTT				
Nematostella	GTGGCCTGACTGAGA-GGGGACACCCCGAACAGACACTG-----A				
Cerianthus	---GCTTGACTGTAAG--AGGGCCCTCAACAGACACGA-----				
[760	770	780	790	800]
Discosoma_num	TGTGCGGGTAATGGTGGGTTGCAGTGACCCGTTA-ATTTAAGGTGAAAGA				
Discosoma_neg	TGTGCGGGTAATGGTGGGTTGCAGTGACCCGTTA-ATTTAAGGTGAAAGA				
Amplexidiscus	TGTGCGGGTAATGGTGGGTTGCAGTGACCCGTTA-ATTTAAGGTGAAATA				
Rhodactis	TGTGCGGGTAATGGTGGGTTGCAGTGACCCGTTA-ATTTAAGGTGAAATA				
Metarhodactis	TGTGCGGGTAATGGTGGGTTGCAGTGACCCGTTA-ATTTAAGGTGAAAGA				
Actinotryx	TGTGCGGGTAATGGTGGGTTGCAGTGACCCGTTA-ATTTAAGGTGAAATA				
Ricordea	TGTGCGGGTAATAGTG-GTTGCAGTGACCCGTTT--TTTTAAGGTGAAATA				
Corynactis_v	TGTGCGGGGAATAGTGGGTTGCAGTGACCCGTTG-ATTTAAGGTGAAATA				
Corynactis_c	TGTGCGGGGAATAGTGGGTTGCAGTGACCCGTTG-ATTTAAGGTGAAATA				
Corallimorphus	TGTGCGGGGAATAGTGGGTTGCAGTGACCCGTTG-ATTTAAGGTGAAATA				
Balanophyllia	TTT-----AGGTGGGTTAAGTGACCCGTTA-ATTTAGGGTGAATA				
Dendrophyllia	TTT-----AGGTGGGTTAAGTGACCCGTTA-ATTTAGGGTGAATA				
Tubastrea	TTT-----AGGTGGGTTAAGTGACCCGTTA-ATTTAGGGTGAATA				
Enallopsammia	TTT-----AGGTGGGTTAAGTGACCCGTTA-ATTTAGGGTGAATA				
Porites	TTT-----AGGTGGGTTAAGTGACCCGTTA-ATTTAGGGTGAATA				
Flabellum	TTT-----AGGTGGGTTAAGTGACCCGTTG-ATTTAGGGTGAATA				
Fungiacyathus	TTG-----AGGTGGGTTAAGTGACCCGTTA-ATTTAGGGTGAATA				
Pavona	TGG-----TGGTGGGTTAAGTGACCCGTTA-GCTCAGAGTGAAGG				
Caryophyllia	TGG-----GGTGTGTTTTA-TGATCTATTG--TTTTGAATGCAAAA				
Catalaphyllia	TTT-----TGGTGTGTTTTA-TGATCCGTTG--TTTGAATGAAAAA				
Oculina	CTT-----TGGTGTGTTTTA-CGATCCGTTG--TTTGAATGAAAAA				
Lobophyllia	TTT-----TGGTGTGTTTTA-TGAACCGTTG--TTTGAATGAAAAA				
Fungia	TTT-----TAGTGTGTTTTA-TGATCCGTTG--TTTGAATGAAAAA				
Montastrea	TTTT-----GTGTGCTACAATGCTACGGAGATTGTGTAGTGAATA				
Anthopleura	-----CAGTGGGTTATAGTGACCCGTTA-TCTTAGAGTGAATA				
Aiptasia	AGGG-----ATGTGGACTATAGTGACCCGTTA-TCTTAGTGTGAATA				
Bathypheilia	AGGG-----ATGTGGACTATAGTGACCCGTTA-----				
Metridium	AGGG-----ATGTGGACTATAGTGACCCGTTA-TCTTAGTGTGAATA				
Stichodactyla	AGGG-----ATGTGGGCTATAGTGACCCGTTA-TCTTAGTGTGAATA				
Nematostella	TGTTT-----AGTGGGTCATAATGACCCGTTCTGTTTATAGTGTGAATA				
Cerianthus	-----AAGTGGGTAAT-TGACCCGTTA--ATAAAGTGGGATT				

[810 820 830 840 850]

Discosoma_num GTTAACGATAAACAAATAAAAAGTTACTCTGGGGATAACAGCGCAATAACG
Discosoma_neg GTTAACGATAAACAAATAAAAAGTTACTCTGGGGATAACAGCGCAATAACG
Amplexidiscus GTTAACGATAAACAAATAAAAAGTTACCCTGGGGATAACAGCGCAATAGCG
Rhodactis GTTAACGATAAACAAATAAAAAGTTACCCTGGGGATAACAGCGCAATAGCG
Metarhodactis GTTAACGATAAACAAATAAAAAGTTACCCTGGGGATAACAGCGCAATAACG
Actinotryx GTTAACGATAAACAAATAAAAAGTTACCCTGGGGATAACAGCGCAATAACG
Ricordea GTTAACGATAAACAAATAAAAAGTTACCCTGGGGATAACAGCGCAAT-GCG
Corynactis_v GTTAACGATAAACAAATAAAAAGTTACTCTGGGGATAACAGCGCAATAACG
Corynactis_c GTTAACGATAAACAAATAAAAAGTTACTCTGGGGATAACAGCGCAATAACG
Corallimorphus GTTAACGATAAACAAATAAAAAGTTACTCTGGGGATAACAGCGCAATAACG
Balanophyllia GTTAACGATAAAGCAATAAAG-----
Dendrophyllia GTTAACGATAAAGCAATAAAG-GTTACCCTGGGGAT-----
Tubastrea GTTAACGATAAAGCAATAAAGTTACCCTGGGGAT-----
Enallopsammia GTTAACGATAA-CAAATAAAAAGTTACCCTGGGGATAA-----ATAACG
Porites GTTAACGATAAACAAATAAAAAGTTACCCTGGGGAT-----
Flabellum GTTAACGATAAAC- AATTAAGTTACCCTGGGGAT-----
Fungiacyathus GTTAACGATAACAGATCAAAGTTACCCTG-----
Pavona GTTAACGATAAACAAATAAAAAGTTACCCTGGGGAT-----
Caryophyllia GATAATG-AAAGCAGATCCCAGTTACCCTGGGGAT-----
Catalaphyllia AACACG-AAAACAATAAAAAGTTACCCTGGGGAT-----
Oculina AATAACG-AAAACAATAAAAAGTTACCCTGGGGAT-----
Lobophyllia AATAACG-AAAACAATAAAAAGTTACCCTGGGGAT-----
Fungia AATAACG-AAAACAATAAAAAGTTACCCTGGGGAT-----
Montastrea AATAACG-AAAGCTAATATCGGTTACCCTG-----CGT-----
Anthopleura GTTGCGATCAACGAATAAAAAGCTACCATGGGGATAACAGCGTTATATCG
Aiptasia GTTGACGATCAACGAATAAAAAGCTACCATGGGGATAACAGCGTTATATCG
Bathypheilia -----TC-----
Metridium GTTGACGATCAACGAATAAAAAGCTACCATGGGGAT-----
Stichodactyla GTTGACGATCAACGAATAAAAAGCTACCATGGGGATAACAGCGTTATATCG
Nematostella GGCGACGATCAACGATAAAAAGCTACCATGGGGATAACAGCGTTATATCG
Cerianthus GTTAACGATAAACAAATAAAAAGTTACTATAGGGATAACAGCGTAATATTG

[860 870 880 890 900]

Discosoma_num TTTGAGGGGTTTTCTTGATGACGATGTTTGCACCTCGATGTTGAATTGC
Discosoma_neg TTTGAGGGGTTTTCTTGATGACGATGTTTGCACCTCGATGTTGAATTGC
Amplexidiscus TTTGAGGGGTTTTCTTGATGACGATGTTTGCACCTCGATGTTGAATTGC
Rhodactis TTTGAGGGGTTTTCTTGATGACGATGTTTGCACCTCGATGTTGAATTGC
Metarhodactis TTTGAGGGGTTTTCTTGATGACGATGTTTGCACCTCGATGTTGAATTGC
Actinotryx TTTGAGGGGTTTTCTTGATGACGATGTTTGCACCTCGATGTTGAATTGC
Ricordea T-AGAGGTTT--C-----
Corynactis_v TTAGAGGGTTTTCTTGATGACGATGTTTGCACCTCGATGTTGAATTGC
Corynactis_c TTAGAGGGTTTTCTTGATGACGATGTTTGCACCTCGATGTTGAATTGC
Corallimorphus TTAGAGGGTTTTCTTGATGACGATGTTTGCACCTCGATGTTGAATTGC
Balanophyllia -----
Dendrophyllia -----
Tubastrea -----
Enallopsammia TTTGAGAG-----GCGATG-----TCGATGTTGA----C
Porites -----
Flabellum -----
Fungiacyathus -----
Pavona -----
Caryophyllia -----
Catalaphyllia -----
Oculina -----
Lobophyllia -----
Fungia -----
Montastrea -----CGTAGGCTGCAACT-----C
Anthopleura TTAGAGAG-CTTTATCGACGACGATGTTTGCACCTCGATGTTGAATTGC
Aiptasia TTAGAGAGTTTTCATCGACGACGATGTTTGCACCTCGATGTTGAATTGC
Bathypheilia -----
Metridium -----
Stichodactyla TTAGAGAG-TTTCATCGACGACGATGTTTGCACCTCGATGTTGAATTGC
Nematostella TTAGAGAG-TTAAATCGACAACGATGTTTGCAG-----
Cerianthus TTAGAGAGTTCACATTAACAACAATGTTTGCACCTCGATGTTGAATTGC

[910 920 930 940 950]

Discosoma_num GGCATCCTG-GGGTGCAGTCGCTCCCAAGGGTGGGTCTGTTCGTCCATTA
 Discosoma_neg GGCATCCTG-GGGTGCAGTCGCTCCCAAGGGTGGGTCTGTTCGTCCATTA
 Amplexidiscus GGCATCCTG-GGGTGCAGTCGCTCCCAAGGGTGGGTCTGTTCGTCCATTA
 Rhodactis GGCATCCTG-GGGTGCAGTCGCTCCCAAGGGTGGGTCTGTTCGTCCATTA
 Metarhodactis GGCATCCTG-GGGTGCAGTCGCTCCCAAGGGTGGGTCTGTTCGTCCATTA
 Actinotryx GGCATCCTG-GGGTGCAGTCGCTCCCAAGGGTGGGTCTGTTCGTCCATTA
 Ricordea -----
 Corynactis_v GGCATCCTG-GGGTGCAGTCGCCCCAAGGGTGGGTCTGTTCGTCCCTTA
 Corynactis_c GGCATCCTG-GGGTGCAGTCGCCCCAAGGGTGGGTCTGTTCGTCCCTTA
 Corallimorphus GGCATCCTG-GGGTGCAGTCGCCCCAAGGGTGGGTCTGTTCGTCCCTTA
 Balanophyllia -----
 Dendrophyllia -----
 Tubastrea -----
 Enallopsammia GGCATCCTG-GGGTGC-----
 Porites -----
 Flabellum -----
 Fungiacyathus -----
 Pavona -----
 Caryophyllia -----
 Catalaphyllia -----
 Oculina -----
 Lobophyllia -----
 Fungia -----
 Montastrea GCCTACGTGAAGGAG-----GATCGT-----
 Anthopleura GGCACCCTG-GGGTGCAGCCGCCCCAAGGGTGGGTCTGTTCGACCTTTA
 Aiptasia GGCACCCTG-GGGTGCAGCCGCCCCAAGGGTGGGTCTGTTCGACCTTTA
 Bathypheilia -----
 Metridium -----
 Stichodactyla GGCACCCTG-GGGTGCAGCCGCCCCAAGGGTGGGTCTGTTCGACCTTTA
 Nematostella -----
 Cerianthus GGCATCCTGAGGGTGCAGAAGCTCTTAAAGGTTAGTCTGTTCGACTATGA

[960 970 980]

Discosoma_num AAGCCTTACATGATTTGATTT-----
 Discosoma_neg AAGCCTTACATGATTTGATTTTCATT---CGGT
 Amplexidiscus AAGCCTTACATGATTTGTTTTATCTTCCGCGGT
 Rhodactis AAGCCTTACATGATTTGTTTTCCCTTTCC-CGAG
 Metarhodactis AAGCCTTACATGATTTGG-TTTCCTTT---CGGT
 Actinotryx AAGCCTTACATGA-TTGATTTCAATTTTC-GGTA
 Ricordea -----
 Corynactis_v AAGCCTTACATGATTTGGGTTTCATTC-----
 Corynactis_c AAGCCTTACATGATTTGGGTTTCATTC---CGAT
 Corallimorphus AAGCCTTACATGATTTGGGTTTCATTC---CGAT
 Balanophyllia -----
 Dendrophyllia -----
 Tubastrea -----
 Enallopsammia -----
 Porites -----
 Flabellum -----
 Fungiacyathus -----
 Pavona -----
 Caryophyllia -----
 Catalaphyllia -----
 Oculina -----
 Lobophyllia -----
 Fungia -----
 Montastrea -----
 Anthopleura A-----
 Aiptasia AA-----
 Bathypheilia -----
 Metridium -----
 Stichodactyla AA-----
 Nematostella -----
 Cerianthus AA-----

Appendix 3. Alignment of 28S rDNA sequences

```

[
      10      20      30      40      50]
Actinotryx      -----TATC-GGGA-G-AAGA--ACTAACCAAGGATTACCTCAGTAACGGC
Amplexidiscus  -----AGCGGGAG----CAAGAACTAACACGGATTACCTCAGTAACGGC
Discosoma_neg   -----AAGCCGGAA-GAAGAAGAACTAAAAAGGATTACCTCAGTAACGGC
Discosoma_num   -----AAGCCGGAA-GAAGAAG-CTAAAAAGGATTACCTCAGTAACGGC
Metarhodactis  -----AAGC-AGAG--ACGG--ACTAACAGGATTACCTCAGTAACGGC
Rhodactis      -----AAGCCGGAG-GGAATG--ACTAACAGGATTACCTCAGTAACGGC
Ricordea       -----AGC-GGCA-GGACGA--ACTAAC-AGGATTACCCAGTAATGGC
Corynactis_v   -----AC-GGTA-GCAGA---ACTAAC-AGGATTACCTAGTAATGGC
Corynactis_c   -----AC-GGTA-GCAGC---CTAACCAAGGATTACCTAGTAATGGC
Corallimorphus -----CAACCGTAACGCAGAGAATAAC-AGGATTACCTAGTAATGGC
Catalaphyllia  -TAATAAGC-GGAG-GAAAAGAACTAACCAAGGATTACCTCAGTAACGGC
Caryophyllia   -TAATAAGC-GGAG-GAAAAGAACTAACCAAGGATTACCTAGTAACGGC
Oculina        -----CTAACCAAGGATTACCCAGTAACGGC
Fungia         -TAATAAGC-GGAG-GAAAAGAACTAACCAAGGATTACCCAGTAACGGC
Lobophyllia    -TAATAAGC-GGAG-GAAAAGAACTAACCAAGGATTACCTCAGTAACGGC
Montastrea     -----CTAACCAAGGATTACCTCAGTAACGGC
Dendrophyllia -TAATAAGC-GGAG-GAAAAGAACTAACCAAGGATTACCCAGTAACGGC
Tubastrea      -TAATAAGC-GGAG-GAAAAGAACTAACCAAGGATTACCCAGTAACGGC
Enallopsammia -TAATAAGC-GGAG-GAAAAGAACTAACCAAGGATTACCCAGTAACGGC
Balanophyllia -TAATAAGC-GGAG-GAAAAGAACTAACCAAGGATTACCCAGTAACGGC
Flabellum      -TAATAAGC-GGAG-GAAAAGAACTAACCAAGGATTACCCAGTAACGGC
Fungicyathus   -----TC-GGGG-GGAAGA--ACTAACCAAGGATTACCTAGTAACGGC
Porites        -TAATAAGC-GGAG-GAAAAGAACTAACCAAGGATTACCTCAGTAACGGC
Pavona         -----CTAACCAAGGATTACCCAGTAACGGC
Edwardsia     -TAATAAGC-GGAG-GAAAAGAACTAACCAAGGATTACCCAGTAACGGC
Nematostella  -TAATAAGC-GGAG-GAAAAGAACTAACCAAGGATTACCCAGTAACGGC
Anthopleura   -TAATAAGC-GGAG-GAAAAGAACTAACCAAGGATTACCCAGTAATGGC
Stichodactyla -TAATAAGC-GGAG-GAAAAGAACTAACCAAGGATTACCCAGTAATGGC
Bathypbellia  -TAGTAAGC-GGAG----AAAGAATAAC-AGGATTACCCAGTAATGGC
Aiptasia      TAAGTAAGC-GGAG-GAAAAGAACTAACCAAGGATTACCCAGTAATGGC
Metridium     TAAGTAAGC-GGAG-GAAAAGAACTAACCAAGGATTACCCAGTAATGGC
Cerianthus_28S -TAATAAGC-GGAG-GAAAAGAACTAACCAAGGATTACCCAGTAACGGC

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[
      60      70      80      90     100]
Actinotryx      GAGTGAAGCGGGAACGGCTCAAATTGGAAATCTCCGTTGC-TTGCAGC-A
Amplexidiscus  GAGTGAAGCGGGAACGGCTCA-ATTGAAATCTCCGTTGCTTTGCAGC-A
Discosoma_neg   GAGTGAAGCGGGAACGGCTCAAATTGGAAAACCTCCGTTGC-TTGCAGCA
Discosoma_num   GAGTGAAGCGGGAACGGCTCAAATTGGAAA--CTGTTGCTTTGGAGCCA
Metarhodactis  GAGCGAAGCGGGAACGGCTCAAATTGGAAA--CTGTTGCTCTGGAGC-C
Rhodactis      GAGCGAAGCGGGAACGGCTCAAATTGGAAA--CTGTTGCTCTGGAGC-C
Rhodactis      GAGCGAAGCGGGAACGGCTCAAATTGGAAAACCTCCGTTGCTCTGCAGC-C
Ricordea       GAGCGAAGCGGGAAGAGCTCAAATTGGAAATCTCCGTTGCTTTGCAGCAA
Corynactis_v   GAGCGAAGCGGGAAGAGCTCAAATTGGAAATCTCCGTTGCTTTGCAGCAA
Corynactis_c   GAGCGAAGCGGGAAGAGCTCAAATTGGAAATCTCCGTTGCTCTGCAGCAC
Corallimorphus GAGCGAAGCGGGAAGAGCTCAAATTGGAAATCTCTGTCTGCTCCGCGGCAA
Catalaphyllia  GAGTGAAGCGGGAAGAGCTCAAATTGGAAATCTCTGATGC-CTGCAGC-T
Caryophyllia   GAGTGAAGCGGGACCAGCTCAAATTGGAAATCTCTGATGC-CTGCAGC-T
Oculina        GAGTGAAGCGGGAACAGCTCAAATTGGAAATCTCTGGTGC-TTGCAGC-C
Fungia         GAGTGAAGCGGGATGAGCTCAAATTGGAAATCTCTGGTGC-TTGCAGC-C
Lobophyllia    GAGTGAAGCGGGAGAGCTCAAATTGGAAATCTCCGATGC-TTGCAGC-T
Montastrea     GAGTGAAGCGGGAAGAGCTCAAATTGGAAATCTCCAATGC-CTGCAGC-T
Dendrophyllia GAGTGAAGCGGGAATAGCTCAAATTGGAAATCTCCAACGC-TTGCAGC-T
Tubastrea      GAGTGAAGCGGGAATAGCTCAAATTGGAAATCTCCAACGC-TTGCAGC-T
Enallopsammia GAGTGAAGCGGGAATAGCTCAAATTGGAAATCTCCAACGC-TTGCAGC-T
Balanophyllia GAGTGAAGCGGGAATAGCTCAAATTGGAAATCTCCAACGC-TTGCAGC-T
Flabellum      GAGTGAAGCGGGAAGAGCTCAAATTGGAAATCTCCAACGC-TTGCAGC-T
Fungicyathus   GAGCGAAGCGGGAATAGCTCAAATTGGAAATCTCCAACGC-TTGCAGC-T
Porites        GAGTGAAGCGGGAATAGCTCAAATTGGAAATCTCCAACGC-TTGCAGC-T
Pavona         GAGTGAAGCGGGAAGAGCTCAAATTGGAAATCTCCAAGGC-CTGAAGC-T
Edwardsia     GAATGAAAC-GGAAGAGCTCAAATTGGAAATCGCCGTTGCCTTGACC--A
Nematostella  GAATGAAAC-GGAAGAGCTCAAATTGGAAATCGCCGTTGCCTTGACC--A
Anthopleura   GAATGAAGCGGGAACAGCTCAAATTGGAAATCTCCGTTGC-CGGC----
Stichodactyla GAATGAAGCGGGAACAGCTCAAATTGGAAATCTCCGTTGC-TTGA----
Bathypbellia  GAATGAAGCGGGAAGAGCTCAAATTGGAAATCTCCGTTGC-GTGC---A
Aiptasia      GAATGAAGCGGGAACAGCTCAAATTGGAAATCTCCGTTGC-TTGCAC--A

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Metridium	GAATGAAGCGGGAACAGCTCAAATTTAAAATCTCCGTTGC-TTGAC--A
Cerianthus_28S	GAGTGAAGC-GGAACAGCTCAAACCTTGAATCTCCATTGCTTTGCG---A
[110 120 130 140 150]
Actinotryx	CGGCGAATTGTAATT-TCGAGAAGCGCTTTCTCGGCGGA-CCGGGCGCGC
Amplexidiscus	CGGCGAATTGTAATT-TCGAGAAGCGCTTTCTCGGCGGA-CCGGGCGCGC
Discosoma_neg	CGGCGAATTGTAATT-TCGAGAAGCGCTTTCTCGGCGGA-CCGGGCGCGC
Discosoma_num	CG-CGAATTGTAATTTTCGAGAAGCGCTTTCTCGGCGGA-CCGGGCGCGC
Metarhodactis	C--CGAATTGTAATTTTCGAAAAGCGCTTTCTCGGCGGA-----GCGCGC
Rhodactis	C--CGAATTGTAATTTTCGAAAAGCGCTTTCTCGGCGGA-----GCGCGC
Ricordea	CGGCGAATTGTAATTTTCGAGAAGCGCTTTCTCGGCGGA-TCGGACCCGC
Corynactis_v	CGGCGAATTGTAATT-TCGAGAAGCACTTTCTCGGCGGA-TCGGACTTGC
Corynactis_c	CGGCGAATTGTAATT-TCGAGAAGCACTTTCTCGGCGGA-TCGGACTTGC
Corallimorphus	CGGCGAATTGTAATT-TCGAGAAGCACTTTCTCGGCGGA-TCGGACCGC
Catalaphyllia	CGGCGAATTGTAATT-TCGAGAAGCACTTTCTAGGTGGA-TCGGCAGTGC
Caryophyllia	CGGCGAATTGTAATT-TCGAGAAGCACTTTCTAGGTGGA-TCGGTCTGTC
Oculina	CGGCGAATTGTAATT-TCGAGAAGCACTTTCTAGGTGGA-TCGGTCTGTC
Fungia	CGGCGAATTGTAATT-TCGAGAAGCACTTTCTAGGTGGA-TCGGTCTGTC
Lobophyllia	CGGCGAATTGTAATT-TCGAGAAGCACTTTCTAGGTGGA-TCGGTCTGTC
Montastrea	CGGCGAATTGTAATT-TCGAGAAGCACTTTCTAGGTGGA-TCGGTCTGTC
Dendrophyllia	CGGCGAATTGTAATT-TCGAGAAGCACTTTCTAGGTGGA-TCGGTCTGTC
Tubastrea	CGGCGAATTGTAATT-TCGAGAAGCACTTTCTAGGTGGA-TCGGTCTGTC
Enallopsammia	CGGCGAATTGTAATT-TCGAGAAGCACTTTCTAGGTGGA-TCGGTCTGTC
Balanophyllia	CGGCGAATTGTAATT-TCGAGAAGCACTTTCTAGGTGGA-TCGGTCTGTC
Flabellum	CGGCGAATTGTAATT-TCGAGAAGCACTTTCTAGGTGGA-TCGGTCTGTC
Fungicyathus	CGGCGAATTGTAATT-TCGAGAAGCACTTTCTAGGTGGA-TCGGTCTGTC
Porites	CGGCGAATTGTAATT-TCGAGAAGCACTTTCTAGGTGGA-TCGGTCTGTC
Pavona	CGGCGAATTGTAATT-TCGAGAAGCACTTTCTAGGTGGA-TCGGTCTGTC
Edwardsia	CGGCGAATTGTAATT-TCGAGAAGCACTTTCTAGGTGGA-TCGGTCTGTC
Nematostella	CGGCGAATTGTAATT-TCGAGAAGCACTTTCTAGGTGGA-TCGGTCTGTC
Anthopleura	--CAGAATTGTAATTTTCGAGAAGCACTTTCTAGGGGCTACCCGTGCCGT
Stichodactyla	--CCGAATTGTAATTTTCGAGAAGCACTTTCTAGGGGCTCCGGGCGCGT
Bathypheilia	CGCCGAATTGTAATTTTCGAGAAGCACTTTCTAGGGGCTCCGGGCGCGT
Aiptasia	CGGCGAATTGTAATTTTCGAGAAGCACTTTCTAGGGGCTCCGGTCTGTC
Metridium	CGGCGAATTGTAATTTTCGAGAAGCACTTTCTAGGGGCTCCGGTCTGTC
Cerianthus_28S	TGGCGAATTGTAATTTTCGAGAAGCACTTTCTAGGGGCTCCGGTCTGTC
[160 170 180 190 200]
Actinotryx	CTAAGTTGCTTGGAACAGCAGCTCGCAGAGGGTGACAACCCCGTCTGTGG
Amplexidiscus	CTAAGTTGCTTGGAACAGCAGCTCGCAGAGGGTGACAACCCCGTCTGTGG
Discosoma_neg	CTAAGTTGCTTGGAACAGCAGCTCGCAGAGGGTGACAACCCCGTCTGTGG
Discosoma_num	CTAAGTTGCTTGGAACAGCAGCTCGCAGAGGGTGACAACCCCGTCTGTGG
Metarhodactis	CTAAGTTGCTTGGAACAGCAGCTCGCAGAGGGTGACAACCCCGTCTGTGG
Rhodactis	CTAAGTTGCTTGGAACAGCAGCTCGCAGAGGGTGACAACCCCGTCTGTGG
Ricordea	CTAAGTTGCTTGGAACAGCAGCTCGCAGAGGGTGACAACCCCGTCTGTGG
Corynactis_v	CTAAGTTGCTTGGAACAGCAGCTCGCAGAGGGTGACAACCCCGTCTGTGG
Corynactis_c	CTAAGTTGCTTGGAACAGCAGCTCGCAGAGGGTGACAACCCCGTCTGTGG
Corallimorphus	CTAAGTTGCTTGGAACAGCAGCTCGCAGAGGGTGACAACCCCGTCTGTGG
Catalaphyllia	CTAAGTTGCTTGGAACAGCAGCTCGCAGAGGGTGACAACCCCGTCTGTGG
Caryophyllia	CTAAGTTGCTTGGAACAGCAGCTCGCAGAGGGTGACAACCCCGTCTGTGG
Oculina	CTAAGTTGCTTGGAACAGCAGCTCGCAGAGGGTGACAACCCCGTCTGTGG
Fungia	CTAAGTTGCTTGGAACAGCAGCTCGCAGAGGGTGACAACCCCGTCTGTGG
Lobophyllia	CTAAGTTGCTTGGAACAGCAGCTCGCAGAGGGTGACAACCCCGTCTGTGG
Montastrea	CTAAGTTGCTTGGAACAGCAGCTCGCAGAGGGTGACAACCCCGTCTGTGG
Dendrophyllia	CTAAGTTGCTTGGAACAGCAGCTCGCAGAGGGTGACAACCCCGTCTGTGG
Tubastrea	CTAAGTTGCTTGGAACAGCAGCTCGCAGAGGGTGACAACCCCGTCTGTGG
Enallopsammia	CTAAGTTGCTTGGAACAGCAGCTCGCAGAGGGTGACAACCCCGTCTGTGG
Balanophyllia	CTAAGTTGCTTGGAACAGCAGCTCGCAGAGGGTGACAACCCCGTCTGTGG
Flabellum	CTAAGTTGCTTGGAACAGCAGCTCGCAGAGGGTGACAACCCCGTCTGTGG
Fungicyathus	CCAAGTTGCTTGGAACAGCAGCTCGCAGAGGGTGACAACCCCGTCTGTGG
Porites	CTAAGTTGCTTGGAACAGCAGCTCGCAGAGGGTGACAACCCCGTCTGTGG
Pavona	CTAAGTTGCTTGGAACAGCAGCTCGCAGAGGGTGACAACCCCGTCTGTGG
Edwardsia	CCAAGTTGCTTGGAACAGCAGCTCGCAGAGGGTGAAAACCCCGTCCACGG
Nematostella	CCAAGTTGCTTGGAACAGCAGCTCGCAGAGGGTGAAAACCCCGTCCACGG
Anthopleura	CCAATTTGCTTAGGAACAGCAGCTCGCAGAGGGTGAAAACCCCGTCCACGG

Stichodactyla CCAAGTTGCTTGGAACAGCACGTACATAGAGGGTGACAA-CCCCTGTGTG
 Bathypheilia CCAAGTTGCTTGGAACAGCACGTACATAGAGGGTGACAAACCCCGTGTGTG
 Aiptasia CCAAGTTGCTTGGAACAGCACGTACATAGAGGGTGAAAACCCCGTGTGCGG
 Metridium CCAAGTTGCTTGGAACAGCACGTACATAGAGGGTGAAAACCCCGTGTGCGG
 Cerianthus_28S CTAAGTTGTTTGGAACTGCACATCGTAGAGGGTGACAAATCCCGTGGCTG

210 220 230 240 250]
 Actinotryx C--GAGTCC--GGCCGCTCACGATGTGCTTTTCGAAGAGTCGGGTTGTTTGG
 Amplexidiscus C--GAGTCC--GGCCGCTCACGATGTGCTTTTCGAAGAGTCGGGTTGTTTGG
 Discosoma_neg CT-GAGTCC--CGCCGCTCACGATGTGCTTTTCGAAGAGTCGGGTTGTTTGG
 Discosoma_num CT-GAGTCC--CGCCGCTCACGATGTGCTTTTCGAAGAGTCGGGTTGTTTGG
 Metarhodactis CTTGAAGTC--CGCCGCTCACGATGTGCTTTTCGAGAGTCGCGTTGCTTGG
 Rhodactis CTTGAAGTC--TGCCGCTCACGATGTGCTTTTCGAGAGTCGCGTTGCTTGG
 Ricordea CA-GGGCCCCGGCCGCTCACGATGTGCTTTTCGAAGAGTCGCGTTGTTTGG
 Corynactis_v CA-GAGTCC--GGCCGCTCACGATGTGCTTTTCGAAGAGTCGCGTTGTTTGG
 Corynactis_c CA-GAGTCC--GGCCGCTCACGATGTGCTTTTCGAAGAGTCGCGTTGTTTGG
 Corallimorphus TA-GCGCCC--GGCCGCTCACGATGTGCTTTTCGAGAGTCGCGTTGTTTGG
 Catalaphyllia CAGGCTGCCGGCCGCTGACGATGTGCTTTTCGAGAGTCGGGTTGTTTGG
 Caryophyllia CAGGCGGCC--GGCCGCTCACGATGTGCTTTTCGAGAGTCGGGTTGTTTGG
 Oculina CAGGCGACC--GGCCGCTCACGATGTGCTTTTCGAGAGTCGGGTTGTTTGG
 Fungia CAGGCGGCC--GGCCGCTCACGATGTGCTTTTCGAAGAGTCGGGTTGTTTGG
 Lobophyllia CAGGCGACC--GGCCGCTCACGATGTGCTTTTCGAAGAGTCGGGTTGTTTGG
 Montastrea C--GGCCGCC--GGCCGCTCACGATGTGCTTTTCGAAGAGTCGGGTTGTTTGG
 Dendrophyllia CT-ACGGCC--GACCGCTCACGATGTGCTTTTCGAAGAGTCGGGTTGTTCCGG
 Tubastrea CT-ACGGCC--GACCGCTCACGATGTGCTTTTCGAAGAGTCGGGTTGTTCCGG
 Enallopsammia CA-ACGGCC--GACCGCTCACGATGTGCTTTTCGAAGAGTCGGGTTGTTCCGG
 Balanophyllia CA-ACGGCC--GGCCGCTCACGATGTGCTTTTCGAAGAGTCGGGTTGTTCCGG
 Flabellum CACGCGTCC--GGCCGCTCACGATGCGCTTTTCGAAGAGTCGGGTTGTTTGG
 Fungicyathus CACGTCGCC--GGCCGCTCACGATGTGCTTTTCGAAGAGTCGGGTTGTTTGG
 Porites CCCTCGGCC--GGCCGCTCACGATGTGCTTTTCGAAGAGTCGGGTTGTTTGG
 Pavona CCCCGGAC--GGCCGCTCACGATGTGCTTTTCGAAAAGTCGGGTTGTTTGG
 Edwardsia CCCCGGTTT--GGCCGCCAACGATGCGCTTTCCACAAGTCGGGTTGCTTGA
 Nematostella CCCCGGTTT--GGCCGCCAACGATGCGC--TTCGACAAGTCGGGTTGCTTGA
 Anthopleura CCC--GGAC--GCCGC--GACGATGGCCTTTTCGACAAGTCGGGTTGCTTGA
 Stichodactyla CCCGGAACC--GGCCGCTCACGATGCGCTTTTCGACAAGTCGGGTTGCTTGA
 Bathypheilia CCCGGAACC--GGTCGCGACGATGCGCTTTTCGACAAGTCGGGTTGCTTGA
 Aiptasia CCCGATTCC--GGCCGTTTACGATGTGCTTTTCAACAAGTCGGGTTGCTTGA
 Metridium CC-GACCTC--GGTCGTTTACGATGTGCTTTTCGACAAGTCGGGTTGTTTGG
 Cerianthus_28S CACACAGCG--CACTGTTGACGATGCGCTTTTCACGGGCTTGGCCACCTTGG

[260 270 280 290 300]
 Actinotryx GAATGCAGCCCCAAAATGGGTGGTAAACTCCATCTAAAGCTAAATACGGGC
 Amplexidiscus GAATGCAGCCCCAAAATGGGTGGTAAACTCCATCTAAAGCTAAATACGGGC
 Discosoma_neg GAATGCAGCCCCAAAATGGGTGGTAAACTCCATCTAAAGCTAAATACGGGC
 Discosoma_num GAATGCAGCCCCAAAATGGGTGGTAAACTCCATCTAAAGCTAAATACGGGC
 Metarhodactis GAATGCAGCCCCAAAATGGGTGGTAGATTTTCATCTAAAGCTAAATACGGAC
 Rhodactis GAATGCAGCCCCAAAATGGGTGGTAGATTTTCATCTAAAGCTAAATACGGAC
 Ricordea GATTGCAGCCCCAAAACGGGTGGTAAACTCCATCTAAAGCTAAATATCGGC
 Corynactis_v GATTGCAGCCCCAAAACGGGTGGTAAACTCCACCTAAAGCTAAATATTGGC
 Corynactis_c GATTGCAGCCCCAAAACGGGTGGTAAACTCCACCTAAAGCTAAATATTGGC
 Corallimorphus GATTGCAGCCCCAAAACGGGTGGTAGACTTTCACCTAAAGCTAAATATCGGC
 Catalaphyllia GATTGCAGCCCCAAAAGTGGTGGTAGACTTTCATCTAAAGCTAAATACGGGC
 Caryophyllia GAATGCAGCCCCAAAATGGTGGTAAACTCCATCTAAAGCTAAATACTGGC
 Oculina GAATGCAGCCCCAAAATGGTGGTAAACTCCATCTAAAGCTAAATACTGGC
 Fungia GAATGCAGCCCCAAAATGGTGGTAAACTCCATCTAAAGCTAAATACTGGC
 Lobophyllia GATTGCAGCCCCAAAATGGTGGTAAACTCCATCTAAAGCTAAATACTGGC
 Montastrea GATTGCAGCCCCAAAATGGTGGTAAACTCCATCTAAAGCTAAATACTGGC
 Dendrophyllia GAATGCATCCCCAAAATGGTGGTAAACTCCATCTAAAGCTAAATATTGAC
 Tubastrea GAATGCATCCCCAAAATGGTGGTAAACTCCATCTAAAGCTAAATATTGAC
 Enallopsammia GAATGCATCCCCAAAATGGTGGTAAACTCCATCTAAAGCTAAATATTGAC
 Balanophyllia GAATGCATCCCCAAAATGGTGGTAAACTCCATCTAAAGCTAAATATTGAC
 Flabellum GAATGCAGCCCCAAAATGGTGGTAAACTCCATCTAAAGCTAAATACTGAC
 Fungicyathus GAATGCAGCCCCAAAATGGTGGTAAACTCCATCTAAAGCTAAATATTGAC
 Porites GAATGCAGCCCCAAAATGGTGGTAAACTCCATCTAAAGCTAAATACTGAC
 Pavona GAATGCAGCCCCAAAATGGTGGTAAACTCCATCTAAAGCTAAATACTGAC

Edwardsia	GAATGCA-CC-A----G-----
Nematostella	GAATGCAGCCCA----G-----
Anthopleura	GAATGCA-CC-A---CG-----
Stichodactyla	GAATGCA-CC-----CG-----
Bathypbellia	GAATGCAGCCCAAAAACGGGTGGTAAACTCCATCTAAAGCTAAATACTGGC
Aiptasia	GAATGCAGCCCAAAAATGGGTGGTAAACTCCATCTAAAGCTAAATATTGGC
Metridium	GAATGCAGCCCAAAAATGGGTGGTAAACTCCATCTAAAGCTAAATATTGGC
Cerianthus_28S	-A-TCCAGTATTAA-TG-----

[310	320	330]
Actinotryx	GCGAGACCGATAGCGA-----			
Amplexidiscus	GCGAGACCGATAGCGA-----			
Discosoma_neg	GCGAGACCGATAGCGA-----			
Discosoma_num	GCGAGACCGATAGCGA-----			
Metarhodactis	GCGAGACCGATAGCGA-----			
Rhodactis	GCGAGACCGATAGTGA-----			
Ricordea	GCGAGACCGATAGTGA-----			
Corynactis_v	GCGAGACCGATAGTGA-----			
Corynactis_c	GCGAGACCGATAGTGA-----			
Corallimorphus	GCGAGACCGATAGTGAACAAGTACCGTGAGGGAAAGT--			
Catalaphyllia	GTGAGACCGATAGTGA-----			
Caryophyllia	GTGAGACCGATAGTGA-----			
Oculina	GTGAGACCGATAGTGA-----			
Fungia	GTGAGACCGATAGCGA-----			
Lobophyllia	GTGAGACCGATAGCGA-----			
Montastrea	GTGAGACCGATAGCGA-----			
Dendrophyllia	GTGAGACCGATAGCGA-----			
Tubastrea	GTGAGACCGATAGCGA-----			
Enallopsammia	GTGAGACCGATAGCGA-----			
Balanophyllia	GTGAGACCGATAGCGA-----			
Flabellum	GTGAGACCGATAGCGA-----			
Fungicyathus	GTGAGACCGATAGCGAACAAGTACCGTGAGGGAAAGTT--			
Porites	GTGAGACCGATAGCGA-----			
Pavona	GTGAGACCGATAGCGA-----			
Edwardsia	-----			
Nematostella	-----			
Anthopleura	-----			
Stichodactyla	-----			
Bathypbellia	ACGAGACCGATAGCGAACAAGTACCGTGAGGGAAAGTAA			
Aiptasia	ACGAGACCGATAGCGA-----			
Metridium	ACG-----			
Cerianthus_28S	-----			

Appendix 5. Alignment of combined molecular data

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[
      10      20      30      40      50]
Actinotryx      GACAAGTAATGTTAGCGAGGAAAGGGGCGTAGGCCGAAATAATGTACGG
Amplexidiscus  GGCGAGCAATGATAG-GAAGGAAAAGGGCGTAGGCCGAAATAATGCACGG
Anthopleura    TCTGCTAGCTATCTGAGGAGAGGGAAGGTGTAACCTCAACTCGGTGCAACG
Aiptasia       TCTGCTAGCTATCTGAGGAGGAAAGAGTGAAGTCAACTCGGTGCAACG
Balanophyllia  -----AAGGGTGTAGACCAGCTTAATACAACG
Bathypbellia   -CTGCCAGCTATCTGA-----
Caryophyllia   -----AAAAGTTTTTCTCAC-ATATACAACG
Catalaphyllia  -----AAAAGTTTTTCTTAT-AAACACAACA
Cerianthus     -----AAGGCCTAAGGGAAGTGATAAAAAAGAGTTATTAATCTCCG
Corallimorphus TGTGAATTGTGATTT-TGGGAAAAGGGCGTTGGCCGACTTAATGTAACG
Corynactis_c   TGTGAATTCTGATTTATGGGAAAAGGGCGTTGGCCGACTTAATGTAACG
Corynactis_v   --T-AAT-CCGATTTATGGGAAAAGGGCGTTGGCCGACTTAATGTAACG
Dendrophyllia -----AAGGGTGTAGACCAGCTTAATACAACG
Discosoma_neg  GGAGGGC-ATGTTAG-GAAGGACAGGGGCGTAGGCCGAAATAATGTACGG
Discosoma_num  GGAATGCTATGAAGA-GAAGGACAGGGGCGTAGGCCGAAATAATGTACGG
Edwardsia      -----GACGAAAAGAGCGAAGATCACTTTGATGCAACG
Enallopsammia -----TGGTAGAGAAAAGAAAAGGGTGTAGACCAGCTTAATACAACG
Flabellum      -----AAGGGTGTAGACCAGCTTAATACAACG
Fungia         -----AAAAATTTTTCTTAT-AAATACAACA
Fungiacyathus -----TTCATTG
Lobophyllia    -----AAAAGTTTTTCTTAT-AAATATAACA
Metarhodactis  GCCCAGCTTTGTTAGAG-AGGACAGGGGCGTAGGCCGAAATAATGTATGG
Metridium      -----TACC
Montastrea     -----TTTAGTCT---CCGTA-ATACAGTGAC
Nematostella   -----GACGAAAAGAGCGAAGATCACTTTGATGCAACG
Oculina        -----AAAAGTTTTTCTTAC-AAATACAACA
Pavona         -----TAAGGTGTAAGCGAATTAATTAACG
Porites        -----AAGGGTGTAAACCACTTAATACAACG
Rhodactis      GGA-AGCTTGAATAG-G-AGGAAAAGGGGCGTAGGCCGAAATAATGCACGG
Ricordea       ---AAGTA-TGTTAGCGGGGTAGGGGCGTAGGTCGATTTAATGTAAGG
Tubastrea      -----AAGGGTGTAGACCAGC-TAATACAACG
Stichodactyla  TCTGCTAGCTATCTGAGGAGGAAAGAGTGAAGTCAACTTGGTGCAACG

[
      60      70      80      90      100]
Actinotryx      CATCATCGCTGTAGTCTCAGAAATCCCCTGTAGAAATCAATAGATGGAGG
Amplexidiscus  CATCATCGCTGTAGTCTCAGAAATCCCCTGTAGAAATCAATAGATGGAGG
Anthopleura    CTTACCCGCATAGCCCCAGAGGCTCTCCACAGAAGCCTAAAGAATGGAA
Aiptasia       CTTACCCGCCGTAGCCCCAGAGGCTCTCCACAGAAGCCTAAAGAATGGAA
Balanophyllia  CTTTCATCGCTGTGGTCTCAGGAATTTCCAG-GGAAACCAATAAGTGGAGG
Bathypbellia   -----GCCGTAGCCCCAGAGGCTCTCCACAGAAGCCTAAAGAATGGAA
Caryophyllia   TACCTTCACTGTAATTTCTAAAACACTCAATAGAAATAAATAGTGGGGA
Catalaphyllia  TATCTTTACTGTAATTTCTAAAATACTTAATAGAAATAAAAAGGTGGGGA
Cerianthus     TACCTCAACGTGTCTTGAGAAAAACCCAGCATAGTATTAAGAATAGGG
Corallimorphus CATCATCGCTGCGGTCTCAGAAATCCCAGTAGATAAAAAATGGGTGAAGG
Corynactis_c   CATCATCGCTGCGGTCTCAGAAATCCCAGTAGATAAAAAATGGGTGAAGG
Corynactis_v   CATCATCGCTGCGGTCTCAGAAATCCCAGTAGATAAAAAATGGGTGAAGG
Dendrophyllia CTTTCATCGCTGTGGTCTCAGGAATTTCCAGTAGAAACCAATAAGTGGAGG
Discosoma_neg  CATCATCGCTGTAGCCTCAGAAATCCCCTGTAGAAATCAATAGATGGAGG
Discosoma_num  CATCATCGCTGTAGTCTCAGAAATCCCCTGTAGAAATCAATAGATGGAGG
Edwardsia      CTTACCCGCCGTAGCCCCAGAGCCCCCGCAGAAGCCAAAAGAATGGAG
Enallopsammia CTTTCATCGCTGTGGTCTCAGGAATTTCCAGTAGAAACCAATAAGTGGAGG
Flabellum      CTTTCATCGCTGTGGTCTCAGGAATTTCCAGTAGAAACCAATAAGTGGAGG
Fungia         TATAATCATATAATTTTTAAAATACTTAATAGAAATAAAAAGGTGGGGA
Fungiacyathus CTTTCATCGCTGTGGTCTCAGAAATTTCCAGTAGAAACC-ATAAGTGGAGG
Lobophyllia   TATCTTTACTGTAATTTCTAAAATACTTAATAGAAATAAAAAGGTGGAGA
Metarhodactis  CATCATCGCTGTAGCCTCAGAAATCCCCTGTAGAAATCAATAGATGGAGG
Metridium     CTTACCCGCATAGCCCCAGAGGCTCTCCACAGAAGCCTAAAGAATGGAA
Montastrea    C-TCCCGCTACGGTAAACTGGGGCCGCACATGTTAGCGAATAGAGTAAG
Nematostella  CTTACCCGCCGTAGCCCCAGAGCCCCCGCAGAAGCCAAAAGAATGGAG
Oculina       TATCTTCACTGTAATTTCTAAAATACTTAATAGAAATAAAAAGGTGGGGA
Pavona        CAAAATCACTGTGGTCTCGGGAATTTCCAGTAGAAACTAATAAGTGGAGG
Porites       CTTTCATCGCTGTGGTCTCAGAAATGTCCAGTAGAAACCAATAAGTGGAGG
Rhodactis     CATCATCGCTGTAGTCTCAGAAATCCCCTGTAGAAATCAATAGATGGAGG
Ricordea     CATCTTCGCTGTAGCCTCAGAAATCCTGTAATTACAATTAGGTGGAGG

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Tubastrea	CTTCATCGCTGTGGTCTCAGGAATTTCCAGTAGAAACCAATAAGTGGAGG
Stichodactyla	CTTCACCGCCGTAGCCCCAGAGGCTTTCCACAGAAGCCTAAAGAATGGAA
[
	110 120 130 140 150]
Actinotryx	AGACATGTG-----TCTATCTG-----ACGAGTTAGATTTTACTGT
Amplexidiscus	AGACATGTG-----TCTATCTG-----ACGAGTTAGATTTTACTGT
Anthopleura	AGACGTATG--CGA--AATAACTT-----AAAATAGATAT-GTCCGT
Aiptasia	AGACGCATG-----TCAAATAATTGATTTAAATAGATAT-GCCCGT
Balanophyllia	AAACATGTGAAATTATTATTCTT-----ACAAAT-TTTAATTTACCTC
Bathypbellia	AGACGCATG-----TCAAATAATTGATTTAAAGTAGATAT-GTCCGT
Caryophyllia	AAGCAAAAACCCCTTATAATTTT-----TTTTAT
Catalaphyllia	GGGCAGAAAACCCCTTATAATTTTATA-----
Cerianthus	ATGCATGTGTAATAAAAAATGGTTATATAAATAAGATTAGTTATGAATAGT
Corallimorphus	AGACATAAGTGACTGCTCAATCAGGCACCTAACAAATCAGACTTTTACCGT
Corynactis_c	AGACATGTGTGACTGCTCAATCAGGCACCTAACAAATCAGACTTTTACCGT
Corynactis_v	AGACATGTGTGACTGCTCAATCAGGCACCTAACAAATCAGACTTTTACCGT
Dendrophyllia	AAACATGTGAAATTATTATTCTT-----ACAAAT-TTTAATTTACCTC
Discosoma_neg	AGACATGTG-----TCTATCTG-----ACGAGTTAGATTTTACTGT
Discosoma_num	AGACATGTG-----TCTATCTG-----ACGAGTTAGATTTTACTGT
Edwardsia	AAACGCATGAA-----ATTAACTT-----AAAATAGATA-GGTCCGT
Enallopsammia	AAACATGTGAAATTATTATTCTT-----ACAAATTTTAAATTTACCC
Flabellum	AGACATGTGAAATTATTATTCTT-----ACAAAT-TTAAATTTACCC
Fungia	AAACAAGAGCCGTTATATTTTCTA-----
Fungiacyathus	AGACATGAGAAATTATTATTCTT-----ACAAAT-TTAAATTTACCTC
Lobophyllia	GGGCAGGGGCGCTTAT-TTTTCTA-----
Metarhodactis	AGACATGTG-----TCTATCTG-----ACGAGTTAGATTTTACTGT
Metridium	AGACGCATG-----TCAAATAATTGATTTAAATAGATAT-GCCCGT
Montastrea	AAATGAGAACCCTTATGCCCTCCG---GAACCGGC-GGTGCTTCTCAGC
Nematostella	AAACGCATGAA-----ATTAACTT-----AAAATAGATA-GGTCCGT
Oculina	AAGCAAGAACCCTTATATTTTCTA-----
Pavona	AGACATGT-CCCTTATGCTGACTT-----AT-TTAAATTTGCTCAA
Porites	AAACATGTGAAATTATTATTCTT-----ACAAAT-TTAAATTTACCTC
Rhodactis	AGACATGTG-----TCTATCTG-----ACGAGTTAGATTTTACTGT
Ricordea	AGATATATG-----CCTATCTG-----ACAGATTAGATTTTACTGT
Tubastrea	AAACATGTGAAATTATTATTCTT-----ACAAAT-TTTAATTTACCTC
Stichodactyla	AGACGCATG-----TCAAATAATTGATTTAAAGTAGATAT-GTCCGT
[
	160 170 180 190 200]
Actinotryx	-----GTAATTTATGGGACTATCTTCTTTTGAGAACATAGA
Amplexidiscus	-----GTAATTTATGGGGCTGTCTTCTTTTGAAAACGTAGA
Anthopleura	-----TTGATGAACACTGGAGCTACTTGT-----A
Aiptasia	-----TCCGATGAACACTGGAGCTAATTAC-----A
Balanophyllia	TGATTAAC--GAGGGAAAGCTATGAAGCCATCAAATTTTAT---GCTTT
Bathypbellia	-----TTCGATGAACACTGGAGCTAATTAC-----A
Caryophyllia	CGGTAG-----GGCAGCAACCCACGTT-----T
Catalaphyllia	CGGTAG-----GGCAGCAACCCACGTT-----T
Cerianthus	AATTCCTA--TTCAATTTATCTTAGGACTATCTCCAC-----TAAGA
Corallimorphus	ATGCTTAGGATTTGGTCAACTATGAAGCTATCTTCTTTTGAATCGGTAGA
Corynactis_c	ATGTTTAGAGTTAGGTCAACTATGAAGCTATCTTCTTTTGAATCGGTAGA
Corynactis_v	ATGTTTAGAGTTAGGTCAACTATGAAGCTATCTTCTTTTGAATCGGTAGA
Dendrophyllia	TGATTAAC--GAGGGAAAGCTATGAAGCCATCAAATTTTAT---GCTTT
Discosoma_neg	-----GTAATTTATGGGGCTATCTTCTTTTGAGAAGATAGA
Discosoma_num	-----GTAATTTATGGGGCTATCTTCTTTTGAGAAGATAGA
Edwardsia	-----AAGATGAACACTGGAGCTA-CTTT-----A
Enallopsammia	TGATTAAC--GAGGGAAAGCTATGAAGCCATCAAATTTTAT---GCTTT
Flabellum	CGATTAAC--TAGGTAAAGCCAAGAAGCCATCAAACCTTTAT---GCTTT
Fungia	CGGTAG-----GGCAGCAACCCACGTT-----T
Fungiacyathus	CGATTACC--TAGGGAAAGCTAAGAAGCCATCAAAGAATTAT---GCTTT
Lobophyllia	CGGTAG-----GGCAGCAACCCACGTT-----CCGT
Metarhodactis	-----GTAATTTATGGGGCTATCTTCTTTTGAAAACGTAGA
Metridium	-----TCCGATGAACACTGGAGCTAATTAC-----A
Montastrea	CTGTAGTG--AGATGGTTAGTC---AACGAGCAACCCACGTT---TTAGT
Nematostella	-----AAGATGAACACTGGAGCTA-CTTT-----A
Oculina	CGGTAG-----GGCAGCAACCCACGTT---TAGT
Pavona	CGGTAG---TAGGGAAAGCTATGAAGCCATTAATAATATAT---GTTTT
Porites	TGATTAAT--TGGGGAAAGCTATGAAGCCATCAAACCTTAT---GCTTT
Rhodactis	-----GTAATTTATGGGGCTGTCTTCTTTTGAAAACGTAGA

Ricordea TTTCTTAGGATTAGTAAACTATGGGGTTATCTTCTTTTGAATCGGTAGA
 Tubastrea TGATTAAC--GAGGGAAAGCTATGAAGCCATCAAATTTTAT---GCTTT
 Stichodactyla -----TCCGATGAACACTAGAGCTAATTGC-----A

[210 220 230 240 250]
 Actinotryx GAAATGAGGTTTACGTTTCGCCTAGAGGTGGTTAAGATACAATTATT-GTC
 Amplexidiscus GAAATGAGGTTTACGTTTCGCCTAGAGGTGGTTAAGATACAATTATT-GTC
 Anthopleura GGGAGAATGCTTGTGTCCACCTGGAGGTAGTTAAGTCCGAGTACTAGTG
 Aiptasia GGGATAGTGTTTGTGTCCACCTGGAGGTAGTTAAGTCCGAGTACCAGGTG
 Balanophyllia GGGATTTGATTTGGCGTCCGCCAAGAGGCGGTTAAGATATACTTG---TAT
 Bathyphellia GGGATAGTGTTTGTGTCCACCTGGAGGTAGTTAAGTCCGAGTACCAGGTG
 Caryophyllia TGCAAGCAATCTACTTTAGTTTAGAAAACAATATGAA----CATG-----T
 Catalaphyllia TGCCAGCTTTTCGGCTTCAGTTTAAAAACAATATGGA----CATG-----T
 Cerianthus ATGGATTAGTTTACGTCCCCAGTGGGGCATAAGGTAATAAGAG-----
 Corallimorphus GAAATGGGGTTTACGATCGCCTAGAGGTAGGTAAGATACAATTACT-GTC
 Corynactis_c GAAATGGGGTTTACGATCGCCTAGAGGTAGGTAAGATACAATTACT-GTC
 Corynactis_v GAAATGGGGTTTACGATCGCCTAGAGGTAGGTAAGATACAATTACT-GTC
 Dendrophyllia GGGATTAGATTGGCGTCCGCCAAGAGGCGGTTAAGATATACATG---TAT
 Discosoma_neg GAAATGAGGTTTACGTTTCGCCTAGAGGTGGTTAAGATACAATTATT-GTC
 Discosoma_num GAAATGAGGTTTACGTTTCGCCTAGAGGTGGTTAAGATACAATTATT-GTC
 Edwardsia GGGACAATGCTTTTGTCCACCTGGAGGCAGTTAAGTCCGAGTACAAGTG
 Enallopsammia GGGATTTGATTTGGCGTCCGCCAAGAGGCGGTTAAGATAACCTTG---TAT
 Flabellum GGGATTTGATTTGGCGTCCGCCAAGAGGCGGTTAAGATACAATG---GAT
 Fungia TGCAAGCTTTTAGCTTCAGTTTAGAAAATAATATGGTAA--CATG-----T
 Fungiacyathus GGGATTTGATTTGGCGTCCGCCAAGAGGCGGTTAAGATACAATTG---GAT
 Lobophyllia TGCCAGCATTCGGCTTCAGTTTAAAAACAATATGG-----CATG-----T
 Metarhodactis GAAATGAGGTTTACGTTTCGCCTAGAGGTGGTTAAGATACAATTATT-GTC
 Metridium GGGATAGTGTTTGTGTCCACCTGGAGGTAGTTAAGTCCGAGTACCAGGTG
 Montastrea TGCCAGCATTTTGTCT-CAGCCG-GGGGAGGTTGGACGACGCAAG-----
 Nematostella GGGACAATGCTTTTGTCCACCTGGAGGCAGTTAAGTCCGAGTACAAGTG
 Oculina TGCAAGCTTTTCGGCTTCAGTTTAGAAAACAATATG---CATG-----T
 Pavona GGGATTGGATTGACGTCGCCAAGAGGCGGTTAAGATGTAGATG---TAT
 Porites GGGATTGGATTGGCGTCCGCCAAGAGGCGGTTAAGATATACTTG---TAT
 Rhodactis GAAATGAGGTTTACGTTTCGCCTAGAGGTGGTTAAGATACAATTATT-GTC
 Ricordea GAAATGAGGTTTAAAGATCGCCTAGAGGTG-GTAAGATACAATTACT-GTC
 Tubastrea GGGATTAGATTGGCGTCCGCCAAGAGGCGGTTAAGATATACATG---TAT
 Stichodactyla TGGATAATGTTTGTGTCCACCTGGAGGTAGTTAAGTCCGAGTACCAGGTG

[260 270 280 290 300]
 Actinotryx TTGCTGTGAAGGGAGCCCTGCACACTAAAGAGCCTGTGTTGGGTGCGCTA
 Amplexidiscus TTGCTGTGAAGGGAGCCCTGCACACTAAAGAGCCTGTGTTGGGTGCGCTA
 Anthopleura CTGCTGCAACGGACATCCCACACTGGATCTCT-----CAGGTATGCCA
 Aiptasia CTGCTGCAAGGGACGTTCTGCACACGT-----CCAGGG-ATGACATGCCA
 Balanophyllia TATCTGCCAAGGGAATCCTGCGCACTT-----ACTTT--AGGGTTAGCTA
 Bathyphellia CTGCTGCAAGGGACGTTCTGCACACGT-----CCAGGG-ATGACATGCCA
 Caryophyllia TATGTGCGCATTTCACTCT--AACTTGGAGACATGG---GTGTTT-TTG
 Catalaphyllia TATCTTAGC--TTCACCCTAAATTTTTTGGGACATTT--TGTGTTT-TTG
 Cerianthus CTGCTGTAAGAGGGCCCTCACACACGA-----AAGGTAA-CTA
 Corallimorphus TTGCTGTGAAGGGGCCCCCTGCACACTAAACCGCCTGTGGTAGGTGCGCTG
 Corynactis_c TTGCTGTGAAGGGGCCCCCTGCACACTAAACCGCCTGTGGTAGGTGCGCTG
 Corynactis_v TTGCTGTGAAGGGGCCCCCTGCACACTAAACCGCCTGTGGTAGGTGCGCTG
 Dendrophyllia TATCTGCCAAGGGAATCCTGCGCACTT-----ACTTT--AGGGTTAGCTA
 Discosoma_neg TTGCTGTGAAGGGAGCCCTGCACACTAGAAAAGCCTGTGTTGGGTGCGCTA
 Discosoma_num TTGCTGTGAAGGGAGCCCTGCACACTAGAAAAGCCTGTGTTGGGTGCGCTA
 Edwardsia CTGCTGAGA-GGACACCCACACACTG-----TGTT--AGGTATACCT
 Enallopsammia TATCTGCCAAGGGATCCTGCACACTT-----ACTTT--AGGGTTAGCTA
 Flabellum TATCTGCCAAGGAGATCCTGCACACTT-----ACTTT--AGGGTTAGCTG
 Fungia TATAGGC---TTCACTCT-AATTTTTTGGACATTT--TATGTTT-TTG
 Fungiacyathus TATCTGCCAAGGAGATCCTGCACACTT-----CTTTG--AGGGTTAGCTA
 Lobophyllia TATCTTAGC--TTCACCCTAAACTTTTTTGGGACATTT--TGTGTTT-ATG
 Metarhodactis TTGCTGTGAAGGGAGCCCTGCACACTAAAGAGCCTGTGTTGGGTGCGCTA
 Metridium CTGCTGCAAGGGACGTTCTGCACACGT-----CCAGGG-ATGACATGCCA
 Montastrea TATATGCCCTTACGCCTTGCACACTGGGACATTTT--TGCACATAC
 Nematostella CTGCTGAGA-GGACACCCACACACTG-----TGTT--AGGTATACCT
 Oculina TATCGGAGC--TTCACCCTAAATTTTTTGGGACACTT--TGTGTTT-TTG
 Pavona TATCTGCTAAGGAGACCCAGCACACTT-----GTCTGGA-TGGGTTAGCTA

Porites TATCTGCGAAGGGAATCCTGCGCACTT-----ATTT--AGGGTTAGCTA
Rhodactis TTGCTGTGAAGGGAGCCCTGCACACTAAAAAGCCTGTGTTGGGTGCGCTA
Ricordea TTGCTGTGAAGGGGCCCTGCACACTAAACAGCCTGTGTTA-GTGGCCTT
Tubastrea TATCTGCCAAGGGAATCCTGCGCACTT-----ACTTT--AGGGTTAGCTA
Stichodactyla CTGCTGCAAGGGACGTCTCGCACACGT-----CCAGGG-ATGGCATGCCA

[310 320 330 340 350]
Actinotryx ATTAAGGATAGTTACTAAAAAATCCCAATGGTCTTGTGTTGTAATCAATT-
Amplexidiscus ATTAAGGATAGTTACTAAAAAATCCAGTGGTCTTGTGTTGTAATTTATTG-
Anthopleura TCTAGAGGTAGTTGCTCAGAAAACCATTTAA-TACCGCCCTAT-----T
Aiptasia TCTAGTGGTAGTTGCTCAGAAAACCATTTAATCACCGCCCTAT-----T
Balanophyllia ATTAGGGATAGTTACTAGAAAAG-----
Bathypheilia -----
Caryophyllia -TTTGAACAAGATATAAGAGCCTCC-----
Catalaphyllia -TTGAAAAAACACAAAAAATCC-----
Cerianthus -AAAAAGGTTGTTACTAAAAAATATATAATCATCATATATA-----T
Corallimorphus ATTAAGGATAGTTACTAAAAAATCCAAAGTCTTGTTCGTGCGTCACAG
Corynactis_c ATTAAGGATAGTTACTAAAAAATCCAAAGTCTTGTTCGTGCGTCACAT
Corynactis_v ATTAAGGATAGTTACTAAAAAATCCAAAGTCTTGTTCGTGCGTCAC-T
Dendrophyllia ATTAGGGATAGTTACTAGCAAAATCC-----
Discosoma_neg ATTAAGGAGAGTTACTAAAAAATCCCAATGGTCTTGTGTTGTAATTTCTG-
Discosoma_num ATTAAGGAGAGTTACTAAAAAATCCCAATGGTCTTGTGTTGTAAT-----
Edwardsia TTTAGAGTTAGGCGCTCAGGAACCATTTAA-AACCA-----G
Enallopsammia ATTAGGGATAGTTACTA-AAAATCC--ATA-----T-----T
Flabellum ATTAGGGATAGTTACTAA-ATATCC-----
Fungia -TTGAAAAAAAATACAAAAAATCC-----T
Fungiacyathus ATTAGGGATAGTTAAATAAGCATCC-----T
Lobophyllia -TTGAAAAAAAATACAAAAAATCC-----
Metarhodactis ATTAAGGAGAGTTACTAAAAAATCCCAATGGTCTTGTGTTGTTAG-TCTG-
Metridium TCTAGTGGTAGTTGCTCAGAAAACCA-----T
Montastrea AAAGTAGATTGCGAATTGTACCACGCAC-----A---T-----T
Nematostella TTTAGAGTTAGGCGCTCAGGAACCATTTAA-AACCA-----G
Oculina -TTGAAAAAAAATACAAAAAATCC-----
Pavona GCCAGAGAGGTTACTAAAAAATCC-----T
Porites ATTAGGGATAGTTACTAAAAAATCC-----
Rhodactis ATTAAGGATAGTTACTAAAAAATCCAGTGGTCTTGTGTTGTAATCCTTA-
Ricordea -TTAAGGATAGTTACTAAAAAATCCAGAGT-C-----
Tubastrea ATTAGGGATAGTTACTAGAAAATCC-----T
Stichodactyla TCTAGTGGTAGTTGCTCAGAAAACCATTTAA-CACCGCCCTAT-----G

[360 370 380 390 400]
Actinotryx ----ACTTACTAAGAT-GCAGCACAAACAAAGC-TGGAGATGGTACGGATG
Amplexidiscus --ACCGTACCTCAGATGGCAGCACAAACAAAGC-TGGAGATGGTACGGATG
Anthopleura TGCTTGTCTCAAAGATAGCACTATTACGTGAC-TGTCTCCGTGTTGGTTG
Aiptasia TGCTTGTCTCAAAGATAGCACTATTACCTGAC-TGTCTCTGTTAGTTCT
Balanophyllia -----
Bathypheilia --CTCGTGTTAGA---TGCACTATTACCTGAC-TGTCT-TTCTTTATTTCT
Caryophyllia -----
Catalaphyllia -----
Cerianthus TGCTTGTCTCAAAGATAGCACCGTCCGCCAACGTGTAGTGGATGTTTCT
Corallimorphus TGTGTGGCGCTAAGAGTAGACTATAACCAAAC-TGTATCCTGTTGTGTCAC
Corynactis_c TGCTTGTCTCAAAGATAGCACTATAACCAAACCTGTATCTGTTTGTGTCAC
Corynactis_v TGCTTGTCTCAAAGATAGCACTATAACCAAACCTGTATCTGTTTGTGTCAC
Dendrophyllia -----
Discosoma_neg CTCTTTTCTTAAGATAGCAGCACAAACAAAGG-TAGAGATGCTGCGGATG
Discosoma_num CTCTTTTCTTAAGATAGCAGCACAAACAAAGG-TAGAGATGCTGCGGATG
Edwardsia TGCTTGTCTCAAAGATAGCACTATT-ACCGAC-TGTCTCTC{AG}TTTGG
Enallopsammia TGCTTGTCTCAAAGATAGCACTATAACCAAAC-AGTATATCTTTGGATC
Flabellum -----
Fungia TGCTTGTCTCAAAGATAGCACTATAACCTAAC-TGTAT-TTCTTTGGATC
Fungiacyathus TGCTTGTCTCAAAGATAGCACTATTACCAAAC-TGTAT-TCATTTGGATC
Lobophyllia -----
Metarhodactis GCAGTCTCGATTAAGATCGCTGACAACGAAAG-TGGAGATGGTACGGATG
Metridium TGCTTGTCTCAAAGATAGCACTATTACCTGAC-TGTCTCTCTTTAGTTCT
Montastrea TGCTTGTCTCAAAGATAGCACTATTACCAAAC-TGTAT-TTCTTTGGATC
Nematostella TGCTTGTCTCAAAGATAGCACTATT-ACCGAC-TGTCTCTC{AG}TTTGG
Oculina -----ACACTATAACCAAAC-TGTAT-TTATTTGGATC

Pavona	TGCTTGTCTCAAAGATAGCACTATTACCAAAC-TGTAT-TCATTGGATC
Porites	CTACCGATTGAATGGTAGTATTATC----AACGAATATATTCTTTGTATC
Rhodactis	--ACCGTACCTCAGATGGCAGCACAAACAAAGC-TGGAGATGGTGCGGATG
Ricordea	-----ACTTACTAAGTGCAGCACAAACAAAGC-TGGAGACTGTATGTAAG
Tubastrea	TGCTTGTCTCAAAGATAGCACTGTTACCAAAC-AGTATATTCTTTGGATC
Stichodactyla	TGCCTCTTTCAAAGATAGCCCT-TTACGTGAC-TGTCTCCGTGTTGGTTG
[410 420 430 440 450]
Actinotryx	TAT-GAGAACTCCTACGTTTCGGTATCCGTGATCTCCCTG---CT-GCT
Amplexidiscus	TAT-CAGAACTCCTACATATAGGTATGCGTGATCTCCCTG---CT-GCT
Anthopleura	TCTGTAGGAACTCCTCTATATAGGAATGCGCGGTGCCCTGC-GTCTGGC
Aiptasia	TCT-TAGAACTCCTCTATATAGGAATGCGTGACGCCCCCGC-GTTTAGT
Balanophyllia	-----
Bathypbellia	TCT-TAGGAACTCCTCTATATAGG-ATGCGTGACCGCTCCGC-GTTAAT
Caryophyllia	--T-GGAAACTCCTCCATATAGG-AT-CGTGATCTCCTTACAATC-GGT
Catalaphyllia	--T-GGAAACTCCTCCATATAGG-AT-CGTGATCTCCTTACAATC-GGT
Cerianthus	CCC-GAGAACTCCTATTTCATGGG-AT-CGTGTAATATCCG---TGAGGT
Corallimorphus	TCTGGAGAACTCCTACATACAGCTATCCGTGATCTCCCT-GGTCTGGCT
Corynactis_c	CCTGGAGAACTCCTACATACAGCTAG-CGTGATCCCCTGGG-TTTGAT
Corynactis_v	CCTGGAGAACTCCTACATACAGCTAGCCGTGATCCCCTGGG-TTTGAT
Dendrophyllia	-----
Discosoma_neg	TAT-CAGAACTCCTACGTTTCGGTATGCTTGATCTCCCTG---CT-GCT
Discosoma_num	TAT-CAGAACTCCTACGTTTCGGTATGCTTGATCTCCCTG---CT-GCT
Edwardsia	CCC-TAGAACTCCTCTATATAGGAA{AT}GG--GACCATCCTGC-GTCT
Enallopsammia	TCT-GGGAAATCCCCCATATAGGGATCCGTATCCTCTTA---TC-GAT
Flabellum	-----
Fungia	TCT-GGGAAACCCCTCCATATAGGGAT-CGTGATCCTCTTA---TT-GAT
Fungiacyathus	TCT-GGGATACTCCTCCATATAACGGT-CGTGATTTCTTA---TT-GAT
Lobophyllia	----GGAAACTCCTCCAGATAGGGAG-CTTGATCCTCTTCATTT-GCT
Metarhodactis	TAT-GAGAACTCCTACATACAGGTATGCGTGATCTCCCTGG--CT-GCT
Metridium	TCT-TAGAACTCCTCTATATAGGAATGCGTGACGCCCCCGC-GTTTAGT
Montastrea	TAT-GGGAACTCCTCCATATAGG-AT-CGTGATCTCCTTA---TTGGCT
Nematostella	CCC-TAGAACTCCTCTATATAGGAA{AT}GG--GACCATCCTGC-GTCT
Oculina	TCT-GGGAACTCCTCCATATAGG-AT-CGTGATCCCCTTA---TC-GAT
Pavona	TCT-GGGATACTCCTCCATATAACGGT-CGTGATTTCTTAG--TT-GAT
Porites	TTTTCGGAAATGTCCCTACATAGCGATCCTTCACTCTTTAGGCTTGGAT
Rhodactis	TAT-CAGAACTCCTACATATAGGTATGCGTGATCTCCCTG---CT-GCT
Ricordea	TATGGAGAACTCCTATATTCAGCAATCCGTGATCTCCCTGGCTCT-GCT
Tubastrea	TCTCGGAAATCTCTCCATATAGGGAT-CGTGATCCCCTTA--CTGGAT
Stichodactyla	TCTGTAGGAACTCCTCTATATAGGATTGCGCGGTGCCCTGC-GTCTGGC
[460 470 480 490 500]
Actinotryx	TCCCATTGCCAACTCA-TCCGG-AAGAAGATGGTGTG--CAGGGGTGGA
Amplexidiscus	TCCCATTGTCAACGCA-TCCGG-AAGAAGATAGTGTG--CAGGGGTGGA
Anthopleura	CCCCATCGTCGACGCATCTCGGCAAGAGGATAAGGTGTGGCAAGGGTGA
Aiptasia	TCTCATCATCAATGTA-GTTGGCATGAGGATAATGTTG-GCAAAGGTGGA
Balanophyllia	-----G-----TATTG-GTAAGAGTGGG
Bathypbellia	TCTCATCATCAATGTA-CTCGGCAAGAGGATAAT-TTG-GCAAAGGTGGA
Caryophyllia	TTCCGGTGTAAAGGCAGTCCCT-AAGAAGAAAAT-TTG-GCCGGAGTGGG
Catalaphyllia	TTCCGGTGTAAAGGCAGTCCCT-AAGAAGAAAAT-TTG-GCCGGAGTGGG
Cerianthus	GCCGGGTGTCCGCAGG-TCTCT-A{AT}GAGGGTAACTCCG--GGATGGC
Corallimorphus	TCTCATTGTCAATTCACCTCCGT-AAGCAGATAAATTTG-ATAAGGGTTCA
Corynactis_c	TCTCACTGTCAACTCGCTCCGT-AAGCAGATAAATTTG-ACAAGGGTTGA
Corynactis_v	TCTCACTGTCAACTCGCTCCGTGAAGCAGATAAT-TTG-ACAAGGGTTGA
Dendrophyllia	-----
Discosoma_neg	TCCCATTGCCAACTCA-TCCGG-AAGAAGATGGTGTG-GCAGGGGTGGA
Discosoma_num	TCCCATTGCCAACTCA-TCCGG-AAGAAGATGGTGTG-GCAGGGGTGGA
Edwardsia	TCCCATCGTCAGCGCA-CTCGGCATGAGGATAATGTTG-GCAAAGGTGGA
Enallopsammia	TCCCATTCTCAACTCAGTCCGT-AAGAAGATAAATTTG-GCCAGAGTGGG
Flabellum	-----
Fungia	TCCCATTGTCAACTCA-TCCGT-AAGAAGATAAATTTG-CAAGAGTGGG
Fungiacyathus	TCCCATGGTCAACTCA-TCCGT-AAGAAGATGATATTG--CAAGAAATGGA
Lobophyllia	TTCCATTGTTAACATA-TTCGT-GAGAAGGAAATATTG--TAAGAGTGGG
Metarhodactis	TCCCATTGTCAACTCA-TCCGG-AAGAAGATAGT-TTGTGCAGGGGTGGA
Metridium	TCTCATCATCAATGTA-CTTGGCATGAGGATAATGTTG-GCAAAGGTGGA
Montastrea	TCCCATTGTCAACTCA-TCCGT-AACAAAATAAATATTG-GTAAGAGTGGG

Nematostella TCCCATCGTCAGCGCA-CTCGGCATGAGGATAATGTTG-GCAAGGGTGG
 Oculina TCCCATGGTCAACTCAGTCCGT-AACAAGATAATATTG--CAAGAGTGG
 Pavona TCCCATGGTCAACTCA-TCCGT-AAGAAGATGAT-TTG--CAAGAATGGA
 Porites TTTCATTGCCAACTCAGTCCGTGAAGAAAATAATACGGTGC-AAAAGTGG
 Rhodactis TCCCATTGTCAACGCA-TCCGG-AAGAAGATAGTGTG--CAGGGTGG
 Ricordea TCTCATTGCCAACTCACTCCGTGAAGCAGATGATATTGGACAGGGGTTCA
 Tubastrea TCCCATTGTCAACTCA-TCCGT-AAGAAGATAATATTG-GCAGGAGTGG
 Stichodactyla CCCCATCGTCGACGCATCTCGGCAAGAGGATAAGGTGTGGCAAGGGTGG

[510 520 530 540 550]
 Actinotryx C--CTAGCATA--AAAGCTTCGAGAATGCGTCACTGCTTAGTTCCGTAAA
 Amphelidiscus C--CTAACATA--AAGGCCACGAGAATGCGTCACTGCTTAGTTTCGTAAA
 Anthopleura C-GCTAACATAGCCAGATT-ATAGAAGA-ATCGTGGCCTAAGTTTGTAA
 Aiptasia C-GCTAACATAGCAAGATTATTAGAAGA-ATGACTCCCTAAGTTTCGTA
 Balanophyllia T--CGGACATA---AAGCTATTAGAATG-ATGACTCTTAAAATCCGTAG
 Bathyphellia C-GCTAACATAGCAAGATTATTATAAGAAACGATTCCCTGAGTTTCGTA
 Caryophyllia T--ATAACATA--AG-----
 Catalaphyllia T--ATAACATA--AG-----
 Cerianthus C--CTAACATA--CAGATTGTTATAGGAATGAGTCGGCGAGGCGTGTGG
 Corallimorphus CC-CTAACATA--AAAGCTATGAGAATGAAGGACTCCTTAAGCTTGCAGA
 Corynactis_c CC-CTAACATA--AAAGCTATTAGAATGAAGGACTCCTTCAGTTTGCAAA
 Corynactis_v CC-CTAACATA--AAAGCTATTAGAATGAAGGACTCCTTCAGTTTGCAAA
 Dendrophyllia -----
 Discosoma_neg C-TCTAGTCAT--AAAGCTTCGTGAATGCGTCACTGCTTAGTTCCCTAAA
 Discosoma_num C-TCTAGTCAT--AAAGCTTCGTGAATGCGTCACTGCTTAGTTCCCTAAA
 Edwardsia C-GCTAACATAGCAAGATTATTAGAAGA-ATTATTGCCTAAGTTTCGTGAC
 Enallopsammia CT-CTAACATA--AAAGCTATTAGAATG-ATGACTCTTAAAATCCGTAG
 Flabellum -----
 Fungia CT-CTAACATA--AAAGCTATTAGAATA-ATGACTCCTTAAATCCGTAG
 Fungiacyathus C--CTAGCATATAAAAGCTATTAGGATG-ATGACTCCTTAAATGCGTAAA
 Lobophyllia T--ATAACATA--AG-----
 Metarhodactis CTTCTAACATA--AAGGCCACGAGAATGCGTCACTGCTTAGTTTCGTAAA
 Metridium C-GCTAACATAGCAAGATTATTAGAAGA-ATGATTCCCTAAGTTTCGTA
 Montastrea C--CTAACATA--AAAGCTATTAGAATA-ATCACTGCTTAAATCCGTAG
 Nematostella C-GCTAACATAGCAAGATTATTAGAAGA-ATTATTGCCTAAGTTTCGTGAC
 Oculina C--CTAACATA--AAAGCTATTAGAATG-ATGGCCCTGAAATCCGTAAA
 Pavona C--CTAGCATA--AAAGCTATTAGGATG-ATGACTCCTTAAATGCGTAAA
 Porites CTTCCGGAC-TATAAA-----
 Rhodactis C--CTAACATA--AAGGCCACGAGAATGCGTCACTGCTTAGTTTCGTAAA
 Ricordea CCTCTAGCATATAAAAGCTTCGAGAATGAGTCACTCCTTCAGCCCGCAA
 Tubastrea CT-CTAACATA--AAAGCTATTAGAATG-ATGACTCCTAAAATCCGTAG
 Stichodactyla CCGCTAACATAGCCAGATTATTAGAGGA-ATGATTGCCTAAGTTTGTAA

[560 570 580 590 600]
 Actinotryx GTCCAAGTGTGCGCCCTTAGCTCTGCGCCCGCGCTCTGG-GACAGAGGGT
 Amphelidiscus GTCCGAGTGTGCTCCCTTAACTCTTCGCCGACCCGCTTGCAGCCGAGGG
 Anthopleura CTCGGAATCATTTCCTTAGATCTGTGCC-CGC-CCCGAACGGAGCAG
 Aiptasia CTCGGAACGCTCTCCCTTAGATCTGTGCCCGCG-CCCGAACGGAGCAG
 Balanophyllia ACTCAAGT-GGTTCCCTTAGCTTTGCGCCCATGC-TCTGGAACAGAGCGT
 Bathyphellia CTCCGATCGGTCTCCCTT-G-TCTGTGCCCGCG-CCCG-CACG-AGCAG
 Caryophyllia -----
 Catalaphyllia -----
 Cerianthus CGGTGGACACTCTCCCTCAGCTCCGTGCCCTC---CTTAAAGGAAAGC
 Corallimorphus GTCCAAGTGACTTTTGGTTGGGCATCCACGGCGTGCATGCGGAAGTGGT
 Corynactis_c GTCCAAGTGGTTTCCCTTAGCTCTGTACCCATAT-TCTGGAACAGAGCGT
 Corynactis_v GTCCAAGTGGTTTCCCTTAGCTCTGTACCCATAT-TCTGGAACAGAGCGT
 Dendrophyllia -----
 Discosoma_neg GTCCAAGTGTGCGCTTTGCACTCTGTACTCGCACTCTGCAGCGCTT----
 Discosoma_num GTCCAAGTGTGCGCTTTGCACTCTGTACTCGCACTCTGCAGCGCTT----
 Edwardsia CTTCCGACCGTATCCCTTAGCTTTGTGCCCGGC-CCCGAACGGAGCCA
 Enallopsammia GTCCAAGTGTGTTCCCTTAGCTTTGCGCCCATAC-TCTGGAACAGAGCGC
 Flabellum -----
 Fungia GTCCAAGTGGTATCCCTTAGCTTTGCGCCCATGC-TCTGGAACAGAGCGC
 Fungiacyathus ATCCAAGTGTGATCCCTTAGCTCTGCGCCCATAC-TCTGGAACAGAGCGC
 Lobophyllia -----
 Metarhodactis GTCCGAGTGTGCTCCCTTAGAGCCTTAAATGCGCGAACGCTC-----

Metridium	CTCCGAACGTTCTCCCTTAGATCTGTGCCCCCGC-CCCAGAACGGAGCAG
Montastrea	GTCCAAGTGGCTTCCCTTAGCTCTGCGCCCATAC-TCTGGAACAGAGCGC
Nematostella	CTTCGGACGGTATCCCTTAGCTTTGTGCCCGGC-CCCAGAACGGAGCCA
Oculina	GCACAAGTGGGTTCCCTTAGCTTTGCGCCACAC-TCTGGGACAGAGAGT
Pavona	ATCCAAGTGTATCCCTTAGCTCTGCGCCCATAC-TCTGGAACAGAGCGC
Porites	-----
Rhodactis	GTCCGAGTGTGTCCTTAACTCTTGCCTGACCCGCTTGGACCCGGAGGG
Ricordea	GTCCAAGTGTGCGCCCTTAGCTCTGCGCCCGCGC-TCTGGGACAGAGGGT
Tubastrea	ATCCAAGTGTTTTCCCTTAGCTTTGCTCCCTAC--CTGGAACAGAGCGG
Stichodactyla	CTCGAATCGGTTCCCTTAGATCTGTGCC-----

[610	620	630	640	650]
Actinotryx	TGA-TGCCGGGTCATCGCCAGGAAGAAAAA--TGA-AGA-CAATCCGTG				
Amplexidiscus	GAA-TGCCGTGGTATCATTGAA-----GAG-CAAGCAATCCGTG				
Anthopleura	CGAATGCCAATTCATCGCACCTCGAGGCTTTAGAGAAAGACACCTTATG				
Aiptasia	CGACTGCCAATTCATCGCACCTCGAGGTC--AGGAGAAAGACACCTTATG				
Balanophyllia	CGC-CGCCGGTTCATCGCACCTCGAGG----TAGAGAAAGACAACCCGTG				
Bathypbellia	-GACTGCCAAGTCATCAT-----TGGAG-AAAGC-CCTTATG				
Caryophyllia	-----TAGAGAAAGACAACCTCGTG				
Catalaphyllia	-----TAGAGAAAGACAATCCGTG				
Cerianthus	GACCTCCAAGTCATCGCACCTCAAGGTC--TAGAGAAAGACACCTCGTG				
Corallimorphus	ACT-GATCTAAAGGGT-----AAACGAAGC-ACTTGCG				
Corynactis_c	CGA-TGTTGGGTCATCGCACC--TCGAGGTC--ATACGC--CAACTTGCG				
Corynactis_v	CGA-TGTTGGGTCATCGCACC--TCGAGGTC--ATACGA--C-CACTTGCG				
Dendrophyllia	-----TAGAGAAAGACAACCCGTG				
Discosoma_neg	-----GAAAGAAAGAAATCCGTG				
Discosoma_num	-----GAAAGAAAGAAATCCGTG				
Edwardsia	CGATTGTCAAGTCATCG-----TAGAGAAAGACACCCATA				
Enallopsammia	CGA-TGCCGGGTCATCGCACC--TCGAGGTCATAGAGAAAGACAACCCGTG				
Flabellum	-----TAGAGAAAGACAACCCGTG				
Fungia	CGA-TGCCGAGTCATCGCACC--TCGAGGTCATAGAGAAAGACAACCCGTG				
Fungiacyathus	CGA-TGCCGAGTCATCGCACCCATCGAGGTC--TGGGAGA-CAACTCGCG				
Lobophyllia	-----TAGAGAAAGACAATCCGTG				
Metarhodactis	-----GAG-CGG-ACATCCGCG				
Metridium	CGACTGCCAATTCATCGCACCTCAAGGTC-----				
Montastrea	CGA-TGCCGAGTCATCGCACC--TCGAGGTC-----CAATCCGTG				
Nematostella	CGATTGTCAAGTCATCG-----TAGAGAAAGACACCCATA				
Oculina	CGA-TGCCGAGTCATC-----CAACCCGTG				
Pavona	CGA-TGCCGAGTCATCGCACC--TCGAGGTC-----CAACCCGTG				
Porites	-----TAGAGAAAGACAATCCGTG				
Rhodactis	GAA-TGCCGTGGTATCATTGAA-----GAGGATG-ACATCCGCG				
Ricordea	TGA-TGCCGGGTCATCGCCAGGAAGAAAAA--GCAGCGA-C-ACCTGCG				
Tubastrea	CGA-TTTCGGGGGGTGCCTGGGAGGTCCTTAGAGAAAGACAACCCGTG				
Stichodactyla	-----TAGAGAAAGACACCTTATG				

[660	670	680	690	700]
Actinotryx	CGGGTTCGTT-TCAG-AGAAATGGTCCGA-CGGCGCCTTACACGCACCCT				
Amplexidiscus	CGGGTTCGTTTTCAG-AGAAATGGGCCGA-CGGCGCCTTACACGCACCCT				
Anthopleura	CATGTTTCGTT-CC---CAAGTGATAGCTACGTGCCTCTACACA-ACCCT				
Aiptasia	CATGTTTCGTT-TCAC-AGAAGTGATCCGATCGTGTCTCTACACATAACCT				
Balanophyllia	TAGGTTCAAC-TCGG-TGAGGGGATCCGA-TGGCGTCTTATACGCACCCT				
Bathypbellia	GATATTTCGTT-GCG--ACAAGTGGTACAGTCGGGCTCTACACATACCCT				
Caryophyllia	CAGGTTTGAT-CCAG-TGAGGGGA-ATGA-TGTCGTCTTACACGCACCCT				
Catalaphyllia	GAGGTTTGAT-CCAG-TGAGGGGATATGA-TGCAGTCTTACACGCACCCT				
Cerianthus	CATGTTTCATTTTCG--AGAAGTG-TACGATG-CTGTCTTACAGTACCCG				
Corallimorphus	GAGGTTTGTCTCCGGAAGAAGTGATCTGA-TGACGCCTTACACGCACCCC				
Corynactis_c	GAGGTTTCGTTTCCAGACGGAGTGATCCGA-TGACTTCTTACACGCACCCT				
Corynactis_v	GAGGTTTCGTTTTCAGAAGGAGTGATCCGA-TGACTTCTTACACGCACCCT				
Dendrophyllia	TATGTTCAAC-TCGG-TGAGGGGATCCGA-TGGCGTCTTATACGCACCCT				
Discosoma_neg	CGGGATCGTT-TCAGCAGAAATGGGCCGA-CGGCGCCTTACACGCACCCT				
Discosoma_num	CGGGA-TGTTTTGAGCA-AAATGGGCCGA-CGGCGCCTTACACGCACCCT				
Edwardsia	GATGTCCGTTCTAC-AGACGTGGTCTTGCTGACGCTCCGTGCAAGACC				
Enallopsammia	TAGGTTCAAC-TCGG-TGAGGGGATCCGA-TGGCGTCTTATACGCACCCT				
Flabellum	GAGGTTCAAC-TCGG-TGAGGGGATCCGA-TGACGCCTTATACGCACCCT				
Fungia	GAGGTTTGGT-TCAG-CGAGGGGATCCGA-TGCGGCCTTACATGCACCCT				
Fungiacyathus	TAGGTTCAAC-TCGG-TGAGGGGATCCGA-TGTGGCCTTATACGCACCCC				

Lobophyllia	GAGGTTTCGAT-TCAG-TGAGAGGATACGA-TGTGGTCTTACACGCACCCT
Metarhodactis	CGGG--TGTTTCGAG-C-AAATAGGCCGA---GCGCCTTACACGCACTGT
Metridium	-----
Montastrea	GAGGTTCAAT-CCAG-TGAGGGGATATGA-TGCGGTCTTACAGGCACCCT
Nematostella	GATGTGCGTTCAC-AGACGTGGTCTTGCTGACGCTCCGTGCAAGACCC
Oculina	CAGGTTTGGT-TCAG-CGAGGGGATATGA-TGTCGTCTTACATGCACCCT
Pavona	GAGGTTCAAG-CAAG-TGAGGGGATCCGA-CACCGTCTTACACGCACCCT
Porites	TATGTTCAAC-TCGG-TGAAGGGATACGA-TGTCGTCTTATACATACCCT
Rhodactis	CGGG--TGTTTCGAG-C-AAATAGTCCGA---GCGCCTTACACGCACCTGT
Ricordea	GGGGATCGTTTCCAG-CGGAATGGGCCGA-TGACCCCTTACACACACCCT
Tubastrea	TAGGTTCAAC-TCGG-TGAGGGGATCCGA-TGGCGTCTTATACGCACCTT
Stichodactyla	CATGTTTCGTT-TGA---CAAGTGATACGGTCGGGCCTCTACACATACCCT

[710 720 730 740]

Actinotryx	GTG--GAGTCGGCCTCTGGAAGCTTGAGTGACCTCGGGCC
Ampplexidiscus	GTG--GAGTCGGCCTCTGGAAGCTTGAGTGACCTCGGGCC
Anthopleura	GTGCC--GGA-GCC-GGCGACAGCTAA-CG-----
Aiptasia	GCGCCGATTTCGGCTTCTGAACAGCTAAGTGACCTTTGACC
Balanophyllia	GTGA-ACGGCGGCCTCTGGAAGGTCGATCTACCTTTAGTC
Bathypheilia	GTGCCGGAACGGTCCGCGGACAGCTAAGCGACCTCTGACC
Caryophyllia	GTGAGGCGGGCGCCCGTGGCAGGTTGAGTTACCTCTGGTT
Catalaphyllia	GTGAGGCTGCGGCCTGTGGCAGGTTGTGGTGCCTCCGGTT
Cerianthus	GCTACACAGCCACTTGGCACGGGCTG-GTG-----
Corallimorphus	GTGA-GCGCCGGCCTTTGGCAGCTTGTGCGGCTCTCGGCT
Corynactis_c	GTGA-GAGTCGGCCTCTGGAAGCTTGTGCGACCTTGGCT
Corynactis_v	GTGA-GAGTCGGCCTCTGGAAGCTTGTGCGACCTTGGCT
Dendrophyllia	GTGT-ACGGCGACCTCTGGAAGGTCGATCTACCTTTAGTC
Discosoma_neg	GTGT-GAGTCCGCCTCTGGAAGGTTGAGTGACCTCGGGCC
Discosoma_num	GTGT-GAGTCCGCCTCTGGAAGGTCGAGTGACCTCGGGCC
Edwardsia	ACGCCGCTTGGCCACGGACAGCTAAG-G-----
Enallopsammia	GTGT-ACGGCGACCTCTGGAAGGTCGATCTACCTTTAGTC
Flabellum	GTGACGCGTTCGGCCTCCGGAAGTTGAGCTACCTTAGTC
Fungia	GTGAGGCGGGCGCCCTCTGGAAGGTTGAGTTACCTCTGGTC
Fungiacyathus	GTGACGTCGCGGCCTCTGGAAGGTTGAGCTACCTTTAGTC
Lobophyllia	GTGAGGCGACGGCCTGTGGAAGGTTGTGTTACCTCTGGTC
Metarhodactis	GTCTTGAAGTCGCCTCTGGCAGCCTGAGTGGTTTCGAGCC
Metridium	-----
Montastrea	GTG-GGCCGCGGCCTGTGGAAGGTTGTGTTACCTCTGGTC
Nematostella	ACGCCGCTTGGCCACGGACAGCTAAG-G-----
Oculina	GTGAGGCGACGGCCTGTGGCAGGTTGAGTTACCTCTGGTT
Pavona	GTGCCGCGGAGGCCTCTGGAAGGTTGAGCTACCTCTGGTC
Porites	GTGCCTCGCGGCCTCTGGAAGGTTGAGATACCTTAGTC
Rhodactis	GTCTTGAAGTTGCCTCTGGCAGCCTGAGTGGTTTCGAGCT
Ricordea	GTGA-GGGCCGGCCTCTGGAAGGTTGTGCGACCTTCGGCT
Tubastrea	GTGT-ACGGCGACCTCTGGAAGGTCGATCTACCTTTAGTC
Stichodactyla	GTGCCGGAACGGCCTGCGGACAGCTAA-CG-----