CHARACTER EVOLUTION IN LIGHT OF PHYLOGENETIC ANALYSIS AND TAXONOMIC REVISION OF THE ZOOXANTHELLATE SEA ANEMONE FAMILIES THALASSIANTHIDAE AND ALICIIDAE

BY

ANDREA L. CROWTHER

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Chairperson Daphne G. Fautin

Paulyn Cartwright

Marymegan Daly

Kirsten Jensen

William Dentler

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The Dissertation Committee for ANDREA L. CROWTHER

certifies that this is the approved version of the following dissertation:

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Chairperson Daphne G. Fautin

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ABSTRACT

Aliciidae and Thalassianthidae look similar because they possess both morphological features of branched outgrowths and spherical defensive structures, and their identification can be confused because of their similarity. These sea anemones are involved in a symbiosis with zooxanthellae (intracellular photosynthetic algae), which is implicated in the evolution of these morphological structures to increase surface area available for zooxanthellae and to provide protection against predation. Both families have been classified in Endomyaria; the phylogenetic relationships within this group are poorly known. I analyzed mitochondrial and nuclear sequences to hypothesize phylogenetic relationships between and within Aliciidae and Thalassianthidae. I recovered Thalassianthidae as monophyletic and nested in a well-supported clade containing some members of Stichodactylidae, within the larger Endomyaria clade. Monophyly of Aliciidae was not recovered, but all members were affiliated with the larger Metrididoidea clade, and closely related with Boloceroididae. Sea anemones in a symbiotic relationship with crabs of the genus *Lybia* have been identified as *Triactis producta*, which I confirmed with molecular data. The similarity between Aliciidae and Thalassianthidae is a case of convergence, supported by both molecular and morphological data. The branched outgrowths and spherical defensive structures in Thalassianthidae are of the oral disc, while in Aliciidae they are projections of the column. To understand the diversity of species possessing branched outgrowths and spherical structures, I did a morphological revision of both Aliciidae and Thalassianthidae. From the seven nominal genera and 16 nominal species of Aliciidae, I found four genera and nine species to be valid. From the five nominal genera and 11 nominal species of Thalassianthidae, I found two genera and seven species to be valid. Each family, genus, and species has been redescribed.

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There is a pleasure in the pathless woods,
There is a rapture on the lonely shore,
There is society, where none intrudes,
By the deep sea, and music in its roar:
I love not man the less, but Nature more,
From these our interviews, in which I steal
From all I may be, or have been before,
To mingle with the Universe, and feel
What I can ne'er express, yet cannot all conceal.

Roll on, thou deep and dark blue Ocean – roll!
Ten thousand fleets sweep over thee in vain;
Man marks the earth with ruin – his control
Stops with the shore; -- upon the watery plain
The wrecks are all thy deed, not does remain
A shadow of man's ravage, save his own,
When for a moment, like a drop of rain,
He sinks into thy depths with bubbling groan,
Without a grave, unknell'd, uncoffin'd, and unknown

From Childe Harold's Pilgrimage by Lord Byron

Nature is amazing. The ocean fills me with awe every time I see it, and I appreciate every opportunity to explore the marine world. Working with intriguing sea anemones provided a perfect opportunity for me to continue my explorations in the marine realm.

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MAIN BODY

CHAPTER 1: General Introduction

Convergent morphologies are a persistent problem with members of the soft-bodied Order Actiniaria (sea anemones), because of the relatively simplistic, diploblastic body plans these anemones possess. Unrelated anemones have evolved similar morphologies in response to similar environmental or symbiotic conditions; for example, sea anemones symbiotic with hermit crabs have evolved multiple times. The morphology of these sea anemones is convergent, because the species that form symbioses with crabs belong to four families that are not each other's closest relatives (Daly *et al.* 2004, Gusmão & Daly 2010, Crowther *et al.* 2011). Members of the actiniarian families Aliciidae and Thalassianthidae possess similar morphological features – branched outgrowths and defensive spheres. Most of these species are found in predominantly shallow tropical waters, and the sea anemones have presumably evolved similar morphological features convergently due to their symbiotic relationship with zooxanthellae. However, the hypotheses that (1) these two families are each monophyletic, and (2) that they are not each other's closest relatives, have never been tested using rigorous molecular phylogenetic or morphological analyses.

Aliciidae and Thalassianthidae: two families containing species with branched outgrowths and spherical defensive structures

Sea anemones can form intimate relationships with zooxanthellae (intracellular algae); the zooxanthellae use sunlight to produce carbohydrates that are assimilated by the sea anemones (Muscatine & Hand 1958, Trench 1971, Gladfelter 1975). This symbiosis is presumably implicated in the evolution of morphological structures for increasing habitable space available to accommodate the zooxanthellae. Some sea anemones symbiotic with zooxanthellae, such as members of Stichodactylidae, possess a large, undulating oral disc covered with many tentacles, whereas some Acintiidae sea anemones (*e.g. Oulactis, Phyllactis*) possess an elaborate marginal ruff. Some sea anemone possess branched outgrowths that serve to increase surface area; sea anemones with outgrowths are inferred thereby to accommodate more zooxanthellae and intercept more light than is possible in sea anemones lacking such structures (Gladfelter 1975).

The possession of branched outgrowths housing zooxanthellae coupled with spherical structures is a character combination characteristic of two families, Aliciidae and Thalassianthidae. In Thalassianthidae, the branched outgrowths are the many tentacles of the oral disc (Fig 1.1a,c), whereas in Aliciidae, the branched outgrowths are the pseudotentacles of the column (Fig 1.1b,d). Associated with the branched outgrowths in these two families are spherical structures dense with nematocysts (intracellular stinging capsules unique to Cnidaria), presumed to prevent predation. In Thalassianthidae, these are the nematospheres, which are specialized tentacles situated near the margin of the oral disc (Fig 1.1c). In Aliciidae, these are the vesicles, which are bubble-like outgrowths on the column or pseudotentacles (Fig 1.1d).

The branched outgrowths and spherical defensive structures of Aliciidae and Thalassianthidae look and function similarly, hence why members of these groups have been confused in the literature. Even though the branched outgrowths and spherical defensive structures are on the column in aliciids, the placement of the morphological characters is not always clearly visible. In the presence of light, it is the branched outgrowths of the column that are expanded, while the unbranched tentacles of the oral disc are retracted and hidden from view (Gladfelter 1975), illustrated by the aliciid species *Triactis producta* in figure 1.1b. In this posture, the branched pseudotentacles and spherical vesicles of *Triactis producta* look like the branched tentacles and spherical nematospheres of *Thalassianthus aster* (Fig 1.1a). Correct identification is important because representatives of both Aliciidae and Thalassianthidae have been reported to cause pain to humans if stung (Williamson *et al.* 1996, Erhardt & Knop 2005) and have been used in toxicological studies (Mizuno *et al.* 2000, 2007, 2012, Oshiro *et al.* 2001, Nagai *et al*. 2002a,b, Uechi *et al.* 2005a,b, Satoh *et al*. 2007).

Rodríguez *et al.* (in Daly *et al.* 2007) stated that many families defined in Carlgren's (1949) catalog are likely not to be monophyletic, and the monophyly of Aliciidae and Thalassianthidae has not been tested in recent studies. Neither family has been studied taxonomically as a unit for many years; thus, revising the definitions of genera and species is long over-due. By simultaneously analyzing specimens from both families, I will investigate the similarities and differences of the branched outgrowths and spherical defensive spheres. Details of these structures could reveal apomorphies to support the monophyly of each family and/or identify genera and species. In addition, a close morphological analysis could give insight into the homology of branched outgrowths and spherical defensive structures found in Aliciidae and Thalassianthidae.

A combined molecular and morphological approach to understanding morphological convergence of Aliciidae and Thalassianthidae

There is a need for a hypothesis of evolutionary relationships for the families Aliciidae and Thalassianthidae because recent phylogenies have not included adequate sampling (Daly *et al.* 2008, Rodríguez *et al.* 2008, Gusmão & Daly 2010, Rodríguez & Daly 2010, Rodríguez *et al.* 2012). In addition, a robust hypothesis of evolutionary relationships could establish or refute monophyly of groups of interest, and allow for an evolutionary interpretation of morphological features. In this dissertation, I use molecular data to reconstruction a phylogenetic tree for Actiniaria in order to address the questions 1) *are Aliciidae and Thalassianthidae each monophyletic* and 2) *are Aliciidae and Thalassianthidae each other's closest relatives?* I do this by sampling more aliicids and thalassianthids than any other study to date, and analyzing molecular data from these species to reconstruct a hypothesis of evolutionary relationships. I then investigate the evolution of branched outgrowths and defensive spheres throughout the tree. This allows me to elucidate whether this combination of morphological features has evolved once or multiple times in Actiniaria, and provides insight into the evolutionary relationships within and between the actiniarian families Aliciidae and Thalassianthidae.

In addition to a robust hypothesis of evolutionary relationships, understanding the evolution of anemones possessing branched outgrowths and spherical defensive structures requires an accurate account of diversity and anatomy of each species. Species delimitation in a group should be based on multiple lines of evidence when available (de Queiroz 2007, Weins 2007, Ross *et al.* 2010). Futher, while a phylogenetic perspective may illuminate the relationships between taxa and enable inferences about character evolution, a taxonomic revision based on a careful examination of morphology may provide insight into characters and identify problematic or invalid species. Here, I perform a taxonomic revision of the actiniarian families Thalassianthidae and Aliciidae to address the questions 1) *how many valid species are present in each family* and 2) *are branched outgrowths and defensive spheres possessed by species in each families homologous?*

Both molecular and morphological approaches are valid approaches for understanding the relationships of examined species. However, while each can inform the other, analyzing results simultaneously can help to fully understanding the evolution of the group. Here, I integrate morphological and molecular data to examine the families Thalassianthidae and Aliciidae, and I present a phylogenetic revision of Thalassianthidae and Aliciidae.

This dissertation entails interrelated tasks, which are set out as separate chapters. The contents of these chapters are summarized below.

Chapter 2: Phylogenetic relationships and character evolution of sea anemones possessing branched outgrowths and defensive spheres

In Chapter 2 I investigate the monophyly and placement of Thalassianthidae and Aliciidae using phylogenetic analyses of molecular data. The molecular phylogenies presented by Daly *et al.* (2008), Rodríguez *et al.* (2008), and Rodríguez *et al.* (2012) did not shed light on the monophyly of either family because they analyzed just one aliciid sample and no thalassianthid samples. My study is the first phylogenetic analysis to incorporate multiple aliciid and thalassianthid sequences. With a well-corroborated phylogenetic hypothesis, I analyze the evolution of branched outgrowths and spherical defensive structures.

Chapters 3 and 4: Morphological revision of Thalassianthidae and Aliciidae, respectively

The species and generic delineations in Thalassianthidae and Aliciidae are unclear. Stephenson (in Carlgren 1949, p. 4) suspected that Carlgren (1949), in his survey of Actiniaria, had recognized too many genera of anemones as valid, stating "I cannot resist the suspicion, also, that Carlgren has now recognized rather too many genera, that some of them might well be fused, and that the distinctions between them are sometimes very slight." This is especially true for genera in Thalassianthidae for which there are very few characters that differentiate the genera. As with many families in Actiniaria, some of the nominal genera and species of

Thalassianthidae and Aliciidae were described from few specimens, so the boundaries are based on limited knowledge regarding morphological variation and geographic distribution. By analyzing the type specimens and conducting my own fieldwork, I study many specimens in an attempt to characterize the variability found within Thalassianthidae and Aliciidae. Generic and species boundaries are made after analysis of data from all available specimens.

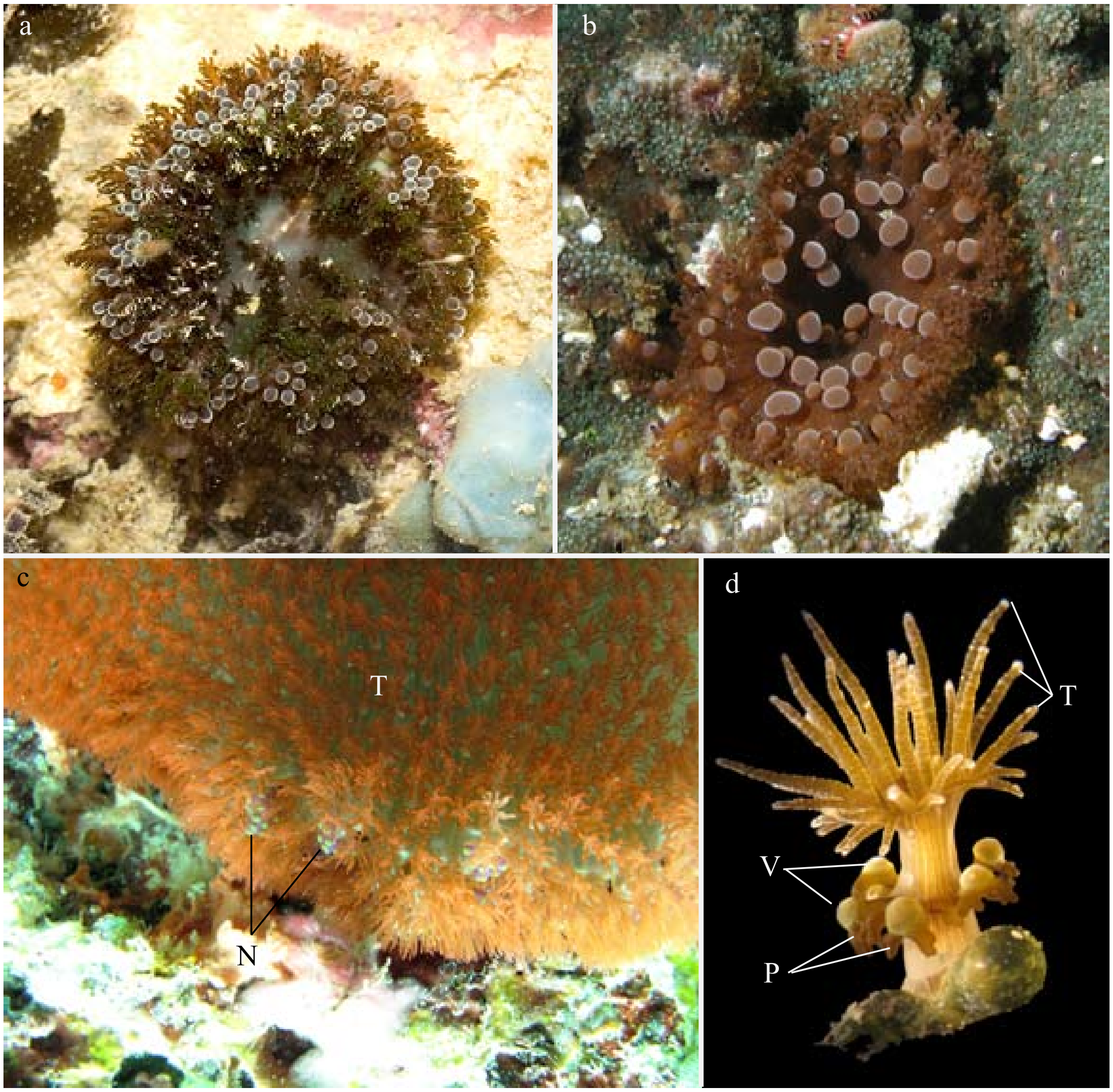

Figure 1.1. a,b) shared morphological features of branched outgrowths and defensive spheres a) *Thalassianthus aster* from Singapore b) *Triactis producta* from Oman c) *Thalassianthus hemprichii* from Palau, close-up of oral disc with dense covering of branched tentacles, and nematospheres near margin d) *Triactis producta* from Mo'orea, photograph of whole individual from side, tentacles on oral disc, pseudotentacles and vesucles from column. Figure legend: N = nematospheres, T = tentacles, P = pseudotentacles, V = vesicles.

CHAPTER 2: Phylogenetic relationships of sea anemones possessing branched outgrowths and defensive spheres

Although we can no doubt decide a few points connected with Actinian evolution with some degree of confidence, there is a great deal which must remain entirely uncertain

(Stephenson, in Carlgren 1949, pg 4)

Introduction

Stephenson (in Carlgren 1949) stated that some of the evolutionary relationships within Actiniaria are uncertain, but our knowledge has improved greatly due to recent phylogenetic studies (Daly 2002, Daly *et al.* 2008, Rodríguez *et al.* 2008, Gusmão & Daly 2010, Rodríguez & Daly 2010, Rodríguez *et al.* 2012). These studies either provide a broad overview of Actiniaria or focus on non-endomyarian sea anemones. Thalassianthidae are lacking and Aliciidae represented by one species, so the phylogenetic placement and monophyly of these families has remained elusive. Furthermore, none of the numerous phylogenies published have sampled heavily within Endomyaria, which is the clade of sea anemone in which both Aliciidae and Thalassianthidae have been most recently classified (Carlgren 1949, Fautin 2011). Thus, relationships within Endomyaria remain tenuous.

In this chapter, I sample DNA from a number of specimens of Aliciidae and Thalassianthidae, and apply phylogenetic methods to these molecular data to reconstruct a hypothesis of evolutionary relationships. This phylogeny includes numerous representatives of Aliciidae, Thalassianthidae, and other Endomyaria. The resulting phylogeny allows me to investigate the monophyly and placement of Aliciidae and Thalassianthidae to address the following questions: *1) Are Aliciidae and Thalassianthidae monophyletic? 2) Do sea anemones with branched outgrowths and defensive spheres form a single, monophyletic clade (are Aliciidae and Thalassianthidae each other's closest relatives)?* I furthermore address whether vesicles possessed by members of different genera of Aliciidae are homologous and document the types of vesicles present in each genus.

Monophyly and phylogenetic placement of Thalassianthidae

Members of Thalassianthidae are found in shallow localities of the Indo-West Pacific Ocean. Stephenson (1920) and Carlgren (1949) placed Thalassianthidae in Endomyaria, primarily due to the presence of an endodermal marginal sphincter muscle and lack of acontia. The monophyly of Thalassianthidae has not been questioned, although genera placed in this family have changed through various iterations of the classification system proposed (see Chapter 3 for details). Several classifications (Carlgren 1900, 1949, Stephenson 1921) have proposed a close relationship to Stichodactylidae, Capneidae, or Phymanthidae, based on tentacle arrangement; all families have members that possess multiple tentacles per endocoel. Thalassianthids have not been represented in any of the molecular phylogenies to date, so the monophyly or placement has not been tested using phylogenetic analyses.

Monophyly and phylogenetic placement of Aliciidae

Two main hypotheses have been proposed for the phylogenetic placement of Aliciidae. In the classification of Carlgren (1949), which is used by most sea anemone systematists, Aliciidae is considered an endomyarian. In contrast, Schmidt (1974) and Den Hartog (1994, 1997) proposed that Aliciidae was part of the subordinal group (mistakenly ranked as 'tribe')

Boloceroidaria; members of Boloceroidaria lack marginal sphincter and basilar muscles and possess longitudinal muscles of the column. One aliciid, *Triactis producta*, and one boloceroidid, *Boloceroides mcmurrichi*, were included in the multi-gene phylogenies of Daly *et al.* (2008), Rodríguez & Daly (2010), and Rodríguez *et al.* (2012). The placement of *T. producta* and *B. mcmurrichi* was not stable among the three phylogenies, so their relationships are unknown. In the same three phylogenies (Daly *et al.* 2008, Rodríguez & Daly 2010, Rodríguez *et al.* 2012), *T. producta* was never recovered as being closely related to any endomyarians. Instead, it was recovered with strong support to be a member of the Metridioidea clade that contains species predominantly from the traditionally recognized Acontiaria, Mesomyaria, and Boloceroidaria clades (Rodríguez *et al.* 2012). In only one phylogeny (Daly *et al.* 2008) were *T. producta* and *B. mcmurrichi* recovered as sister taxa. In addition, *T. producta* has been identified as one of the anemone species that is able to form symbiotic relationships with *Lybia* crabs (see below). However, *Lybia* crab symbionts have never been sampled for inclusion in phylogenetic analyses.

Lybia *crab symbiont identity*

Crabs of the genus *Lybia* possess a pair of modified first chelae (Fig 2.1b,d,e) that are delicate (Borradaile 1902) and thus ineffective for defense, feeding, or grasping heavy objects (Borradaile 1902, Duerden 1905, Guinot 1976). Each chela holds a small sea anemone (Fig 2.1), with which it forms a symbiotic relationship (Richters 1880, Borradaile 1902, Duerden 1905, Guinot *et al.* 1995, Verrill 1928, Cutress 1977, Karplus *et al.* 1998). The identification of anemones in symbiosis with *Lybia* crabs is difficult due to their small size and the possibility that important morphological features may be lacking (Fig 2.1 b,d). Sea anemones symbiotic with

Lybia crabs have been ascribed to a number of genera, including *Actinia* (by Richters 1880), *Bunodeopsis* (by Duerden 1905), *Sagartia* (by Duerden 1905, Verrill 1928), and *Triactis* (by Schmitt 1965, Cutress 1977, Karplus *et al*. 1998). *Triactis* belongs to the genus Aliciidae; thus, sampling *Lybia* crab symbionts for morphological and molecular analyses was important for resolving their identity and determining their possible placement within Aliciidae. To this end, I obtained four *Lybia* crabs with anemone symbionts from Hawai'i and the Indian Ocean to include in this analysis.

Evolution of morphological features

The branched outgrowths and spherical defensive structures of Aliciidae and Thalassianthidae look and function similarly, but are not homologous features. In Thalassianthidae, the outgrowths are of the oral disc, whilst in Aliciidae they are of the column. McMurrich (1889a, p. 40), when discussing pseudotentacles, the branched outgrowths of aliciids, stated, "…perhaps the pseudotentacles are to be compared to the peculiar evaginations of the disk which characterize Thalassianthinae, though their origin from the column wall precludes anything more than a general comparison." The molecular phylogeny provides an independently derived framework of relationships with which to explore the evolution of morphological characters such as branched outgrowths and defensive spheres.

In Thalassianthidae, the morphology with increased surface area and volume to incorporate and display a large number of zooxanthella are the tentacles of the oral disc. Members of Thalassianthidae possess a wide oral disc covered with many small, branched tentacles radially arranged in endocoels. In the family, the branched endocoelic tentacles are in two general shapes; palmate with branches in one plane, or pine tree-shaped with branches in multiple planes.

In Aliciidae, the morphology with dense zooxanthellae are the pseudotentacles of the column. Pseudotentacles, unique to Aliciidae, were first described and illustrated by Duchassaing de Fonbressin & Michelotti (1860) in their description of *Lebrunia*. Pseudotentacles are referred to as 'external tentacles' and 'exterior thick tentacles stalked' by Duchassaing de Fonbressin & Michelotti (1860) and Klunzinger (1877), respectively; this terminology indicates the authors thought the branched outgrowths were specialized tentacles of the oral disc. Hertwig (1882) uses the term pseudotentacle to refer more accurately to the outgrowths of the column. The name pseudotentacle alludes to how similar in form these outgrowths are to tentacles – both are essentially hollow outgrowths of endoderm and ectoderm. McMurrich (1889b) considered pseudotentacles to be characteristic of a group, and established Subtribe Dendromelinae, based on this character. Three of the four genera of Aliciidae possess pseudotentacles; *Alicia*, the type genus, lacks pseudotentacles. In the remaining three genera, differences in pseudotentacle number, position, and morphology will be investigated.

The spherical defensive structures of Aliciidae and Thalassianthidae are similar because of their shape and have ectoderm dense with nematocysts. In Thalassianthidae, the spherical defensive structures are specialized endocoelic tentacles called nematospheres. Stephenson (1921, p. 575) described them as, "A tentacle which has become converted into a short structure rounded at the end, or into a practically sessile sphere, and the ectoderm of at least part of which is crowded with nematocysts." The nematocysts of nematospheres are basitrichs (Carlgren 1949). Within the family, nematospheres either are closely packed to form a continuous band or in grape-like clusters on lobes of oral disc.

In Aliciidae, the spherical defensive structures are bubble-like outgrowths of the column or the pseudotentacles called vesicles. The term vesicle is also used to describe bubble-like column outgrowths of certain genera of Actiniidae (*Phlyctenactis* and *Phlyctenanthus*) and *Bunodeopsis* of family Boloceroididae. The vesicles of *Phlyctenactis* and *Phlyctenanthus* are not defensive: they do not have dense concentration of nematocysts, as seen in Aliciidae and *Bunodeopsis*. Vesicles of Aliciidae and *Bunodeopsis* are dense with microbasic amastigophores, but aliciids also have macrobasic amastigophores. A more precise term for the vesicles of Aliciidae and *Bunodeopsis* is mastigophoral vesicles to distinguish them from Actiniidae vesicles. In this dissertation, I use the term vesicle to refer to mastigophoral vesicles.

There are various forms of vesicles in family Aliciidae. Some vesicles are single spheres, referred to as simple vesicles. Alternatively, vesicles are composed of a cluster of spheres, referred to as compound vesicles. Vesicles may be attached directly to column or pseudotentacles, referred to as sessile vesicles. Alternatively, vesicles may attach to column or pseudotentacles with a stalk, referred to as stalked vesicles. An understanding of the homology of such complex characters may be informed by the reconstruction of a phylogeny, which can then serve as an independent framework for investigating character evolution. Here, I code terminal taxa for characters relating to branched outgrowths and spherical defensive structures, as well as other characters of interest. I visualize the distribution of these characters to better understand their evolution.

Materials and Methods

Taxon sampling and gene choice

Most specimens targeted for this study were collected by hand while snorkeling or SCUBA diving, and some were purchased online from aquarium supply stores. Other sequences were downloaded from GenBank (Benson *et al.* 2005). The complete dataset (Table 2.1) includes 101 sea anemone specimens and one zoanthid specimen. In all analyses, the zoanthid species, *Savalia savaglia,* was used as an outgroup. Zoanthidea was chosen as an outgroup because it is a monophyletic order within Hexacorallia, and had the same genes available on GenBank as what I include in my study. I include just one zoanthid outgroup so my results are comparable with recent large-scale Actiniaria phylogenies (Rodríguez & Daly 2010, Rodríguez *et al.* 2012). I include 20 specimens of species in Aliciidae, all but one new, including representatives of all four genera. I include seven specimens of species in Thalassianthidae, all new. I also include four specimens of *Lybia* crab symbionts. Because the phylogenetic placement of Aliciidae and Thalassianthidae was unknown, I include representatives from most sea anemone families, with multiple specimens from species-rich families (*e.g.* Actiniidae, Hormathiidae) and from families hypothesized to be closely related to Aliciidae (*e.g.* Boloceroididae) and Thalassianthidae (*e.g.* Stichodactylidae and Actinodendridae). The genes were selected from both mitochondrial (12S, 16S, CO3) and nuclear (18S, 28S) regions to span a range of evolutionary rates. These genes have also been used previously for anemone phylogenies (Daly *et al.* 2008, Rodríguez & Daly 2010, Rodríguez *et al.* 2012); my new sequences will complement the published sequences, but also allow me to use published anemone sequences from GenBank to supplement my data matrix.

Molecular data collection and analysis

DNA was extracted from most specimens using commercial Qiagen DNeasy Blood and Tissue Kit, following methods of Daly (2002). If an extraction had low quality or quantity DNA, the specimen was re-extracted using a standard phenol-chloroform protocol. Because aliciids produce copious amounts of mucus, and the polysaccharides of mucus can inhibit extraction of DNA, aliciids were extracted using either Omega Biotek E.Z.N.A. Mollusc DNA Isolation Kit (Omega Biotek, USA) or a protocol from McFadden *et al.* (2006). The McFadden *et al.* (2006, p. 291) protocol incorporates Nucleon Phytopure (GE Healthcare), which is "a resin designed to remove excess polysaccharides."

A NanoDrop 2000 Spectrophotometer (Thermo Scientific) was used to measure the DNA concentration and purity. When additional DNA was needed and no additional tissue available, I used the Genomiphi DNA Amplification Kit (GE Healthcare) to increase the volume of the original DNA extraction. Mitochondrial DNA (12S, 16S, and CO3) and nuclear DNA (18S and 28S) were amplified. Primer sequences for PCR and sequencing reactions from the following sources: 12S (Chen *et al.* 2002), CO3 and 16S (Geller & Walton 2001), 18S (Medlin *et al.* 1998, Apakupakul *et al.* 1999), and 28S (Medina *et al*. 2001, Voigt *et al.* 2004, Cartwright *et al*. 2008, Evans *et al*. 2008) (see Appendix A for primer sequences).

Targeted gene regions were amplified using PCR on a Peltier Thermal Cycler (BioRad), following the protocol of Daly *et al.* (2008). PCR reactions were 25 μL reactions for all gene primer sets except for the complete 28S gene; the complete 28S gene reactions were 50 μL because of the greater number of sequencing reactions needed (Appendix B). PCR products were size selected on a 1% agarose gel via electrophoresis; only PCR products that had a band of the appropriate size were sent for sequencing. For PCR products that showed two bands, indicating that DNA was amplified from two sources (most likely the sea anemone and the zooxanthellae), the band of the appropriate size was cut from the gel, purified using the Qiagen MinElute Gel Extraction Kit (Qiagen, MD), then cloned using the Invitrogen TOPO TA Cloning Kit (Invitrogen, CA). Colonies were purified for DNA using Qiagen QIAprep Miniprep Kit (Qiagen, MD), then sent for sequencing.

Purification and direct sequencing of PCR products were by Cogenics (Houston, TX) and High Throughput Genomics Center (Seattle, WA). Raw sequences were blasted against the NCBI database. Editing of sequences was done using Sequencher 4.7 (GeneCodes 2005) and Geneious (Biomatters). Alignment of each marker was done using MAFFT (Katoh *et al.* 2002) or MUSCLE (Edgar 2004a, b). Alignments were viewed using Seaview (Galtier *et al.* 1996, Guoy *et al.* 2010) and adjusted by hand and trimmed if necessary. Alignments were run through the program Gblocks (Castresana 2000, Talavera & Castresana 2007) to remove ambiguously aligned regions. Model testing was conducted using jmodeltest (Posada 2008) for the following partitions: 12S, 16S, CO3, 18S, 28S, mitochondrial, nuclear. Model selection was based on Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC). Separate gene alignments were concatenated with assistance from a Python script.

Maximum likelihood analyses were run using RAxML-vi-HPC 2.2.3 (Stamatakis 2006) for separate genes, combined mitochondrial, combined nuclear, all genes except 28S, and combined five-gene dataset. The combined five-gene dataset was analyzed twice – once without and once with the specimens from the *Lybia* crab symbionts. The 28S dataset was problematic for alignment; sequences downloaded from GenBank were an approximately 1,100 base pairs fragment at the 5' end of the molecule, referred to as 5' fragment in Table 2.2. Most of the new sequences were an approximately 2,600 base pairs fragment at the 3' end of the molecule, referred to as 3' fragment in Table 2.2. Any fragment over 2,000 base pairs had overlap with the published molecule. Concatenated datasets were partitioned into separate genes so each gene could be assigned a separate model of evolution. Support was assessed with 1,000 bootstrap replicates. Bayesian analyses were conducted on the mitochondrial, nuclear, all genes except 28S, and five-gene (with and without *Lybia* crab symbionts) datasets, using MrBayes (Huelsenbeck & Ronquist 2001, Ronquist & Huelsenbeck 2003). Four runs of 20 million generations with eight chains were cued in MrBayes. FigTree v1.3.1 (Rambaut 2009) and Mesquite (Maddison & Maddison 2007) were used to view and edit the topologies resulting from analyses.

Lybia *crab symbiont identity*

Four specimens of sea anemones symbiotic with *Lybia* crabs were added to the combined five-gene matrix. This matrix was analyzed using a maximum likelihood phylogenetic framework to determine the specimens' closest relatives.

Evolution of morphological features

Using the five-gene (without *Lybia* symbionts) matrix, terminal leaves are coded for morphological features. Details of morphological features and coding are listed in Table 2.2. Ancestral character state reconstructions were not performed on the five-gene phylogenies because deeper nodes were poorly resolved.

Results

Datasets with ambiguously aligned regions removed by Gblocks were analyzed but did not alter topology compared to datasets still containing ambiguously aligned regions, and therefore are not included in the results. A summary of each dataset, including the number of taxa, unaligned length, and aligned length is provided in Table 2.3. The appropriate models of evolution for separate datasets under AIC and BIC are shown in Table 2.4. In most of the analyses, two major clades, Endomyaria and Metridioidea, are recovered. Figures 2.2–2.11 show the phylogenies resulting from the Maximum Likelihood analyses. Nodes with bootstrap values of 70 or above are interpreted as well supported. Table 2.5 provides a summary of the major clades relevant to Aliciidae and Thalassianthidae that are recovered in datasets. The combined datasets result in trees with most resolved nodes compared to the separate genes. The 28S analysis failed to recover monophyletic Metridioidea or Endomyaria clades. Instead, all of the incomplete GenBank sequences clustered together in a derived position in the tree.

Monophyly and phylogenetic placement of Thalassianthidae

Thalassianthidae is recovered as a well-supported monophyletic clade in all datasets except CO3 and mitochondrial matrices. Consistently, members of the genera *Thalassianthus* and *Cryptodendrum* are reciprocally monophyletic, though their relationship is not always highly supported. In all analyses, Thalassianthidae form a clade in Endomyaria that is nested within a group containing some members of Stichodactylidae. The larger Stichodactylidae+Thalassianthidae clade is supported in all analyses (Fig 2.2–2.11). The members of Stichodactylidae that are not included in the Stichodactylidae+Thalassianthidae clade are the species *Heteractis aurora* and *H. crispa;* instead they are placed in a well-supported derived clade containing *Phymanthus* and *Macrodactyla* representatives (Fig 2.10, 2.11).

Monophyly and phylogenetic placement of Aliciidae

In the ML analysis of the combined five-gene dataset, Aliciidae is not monophyletic (Table 2.5, Fig 2.10, 2.11). In the combined five-gene analyses, most of the aliciid genera are monophyletic with good support – the exception is *Triactis* in the dataset without *Lybia* symbionts (Fig 2.10). In this situation, one *Triactis* specimen is not most closely related to all other *Triactis* specimen and instead is sister to a *Phyllodiscus+Triactis* clade (Fig 2.10). Three genera from Aliciidae (*Lebrunia*, *Triactis*, and *Phyllodiscus*) form a well-supported clade in the combined five-gene datasets with and without *Lybia* crab symbionts (Fig 2.10, 2.11). Boloceroididae is monophyletic, with good support, in most analyses (Fig 2.2–2.3, 2.5–2.11).

In none of the combined five-gene analyses are members of Aliciidae recovered within the Endomyaria clade; instead they form a clade with Boloceroididae that is nested as a derived clade of Metridioidea (Fig 2.11). When *Lybia* symbionts are excluded, the representatives of *Alicia* are most closely related to Aiptasiidae (Fig 2.10), which is nested within the larger Metridioidea clade, sister to the rest of Aliciidae+Boloceroididae clade.

Lybia *crab symbiont identity*

Sequences from all four sea anemones symbiotic with *Lybia* crabs are nested with members of *Triactis producta*, a relationship that has high support (Fig 2.11). The inclusion of the *Lybia* symbiont specimens altered the relationships in comparison with the analysis without these specimens (Fig 2.10). *Triactis producta* formed a well-supported monophyletic clade with the *Lybia* symbiont specimens (Fig 2.11, Table 2.5) compared to *Triactis producta* forming a paraphyletic clade in the analysis without *Lybia* symbiont specimens (Fig 2.10). In the analysis with *Lybia* symbionts, the genus *Alicia* is sister to the rest of Aliciidae+Boloceroididae (although with a bootstrap support of 47) (Fig 2.11), whereas in the analysis lacking the *Lybia* symbionts, *Alicia* was sister to Aiptasiidae (bootstrap support of 62), which was then sister to the rest of Aliciidae+Boloceroididae (Fig 2.10).

Evolution of morphological features

Morphological features are mapped onto the maximum likelihood phylogeny from the combined five-gene (without *Lybia* symbionts) matrix (Fig 2.12–2.14). Branched outgrowths, defensive spheres, and radially arranged tentacles have evolved multiple times in multiple families (Fig 2.12, 2.13). The branched outgrowths and defensive spheres are separated into outgrowths of the oral disc (Fig 2.13) and column (Fig 2.14). The families Actinodendridae and Thalassianthidae both possess branched tentacles and defensive spheres. One family, Aliciidae, possesses branched outgrowths and defensive spheres of the column (Fig. 2.14). Defensive spheres evolved three times (Fig 2.14). The combination of pseudotentacles and vesicles are features of a clade containing three of the four Aliciidae genera (Fig 2.14).

Discussion

Monophyly and phylogenetic placement of Thalassianthidae

Thalassianthidae is consistently recovered as monophyletic, which is not surprising as morphological traits also support the monophyly of this group. Thalassianthids are the only sea anemones to possess multiple branched tentacles per endocoel in addition to nematospheres. The included specimens of *Thalassianthus*, which possess lobes of the oral disc, form a clade that is sister to *Cryptodendrum,* whose members lack lobes.

The placement of Thalassianthidae in Endomyaria is supported morphologically by the conspicuous endodermal marginal sphincter muscle (Carlgren 1949). The thalassianthids are nested within a well-supported clade that includes most of the Stichodactylidae, including the type genus *Stichodactyla*. Members of this clade all possess multiple tentacles per endocoel, although this feature is not unique to this clade (Fig 2.13). Other families whose members possess multiple tentacles per endocoel, such as Homostichanthidae and Capneidae, were not included in this analysis.

The Stichodactylidae members not included in the Stichodactylidae+Thalassianthidae clade are the species *Heteractis aurora* and *H. crispa*. These two species are found closely related to *Phymanthus* (Phymanthidae), *Phyllactis* (Actiniidae), and *Macrodactyla* (Actiniidae). The close relationship of *Heteractis aurora* and *H. crispa* is supported by Dunn's (1981) observation that these two species closely resemble each other. The separation of *H. magnifica* from congeners *H. aurora* and *H. crispa* in the phylogenies is also supported by findings by Dunn (1981), who reported that *H. magnifica* differed from all other species of *Heteractis* by the refractive endoderm of the upper column. This character is shared with some species of *Stichodactlya*, along with multiple tentacles per endocoel.

The separation of *Heteractis*, in particular the type species *H. aurora*, from other Stichodactylidae has been proposed by England (1988), who found macrobasic amastigophore nematocysts present in *H. aurora* but not in *Stichodactyla* specimens. England (1988) separated the genus *Heteractis* from Stichodactylidae and reinstated the family Heteractidae. In light of previous hypotheses and phylogenies presented here, it is clear that the family Stichodactylidae (including *Stichodactyla* and *Heteractis*) should be revised, particularly because Thalassianthidae was recovered nested within a Stichodactylidae clade.

Monophyly and phylogenetic placement of Aliciidae

Aliciidae is not recovered to be monophyletic in any of the phylogenetic analyses (Fig 2.2–2.11). Despite the non-monophyly of Aliciidae indicated by the phylogenies, I will treat the family as a whole unit in the morphological revision chapter (Chapter 4). Three of the four aliciid genera (*Lebrunia*, *Triactis*, *Phyllodiscus*) consistently form a well-supported clade, but the placement of the other genus, *Alicia,* is not consistent across datasets. The placement of *Alicia*, the type genus of Aliciidae, is important to determine for systematic and nomenclatural reasons.

My results support Schmidt's (1974) hypothesis of relationships with Aliciidae members more closely related to Boloceroididae than to Endomyaria. However, in contrast to Schmidt's (1974) hypothesis of an early diverging clade of Aliciidae and Boloceroididae, my results suggest that aliciids and boloceroidids are more derived (Fig 2.10, 2.11). Daly *et al.* (2008) recovered a well-supported sister relationship between *Triactis* and *Boloceroides*; Aliciidae and Boloceroididae share features such as possession of microbasic amastigophores and ectodermal longitudinal muscles of the column (Carlgren 1949, Schmidt 1974).

Another family whose members possess ectodermal longitudinal muscles of the column is Aiptasiidae (Carlgren 1949, Schmidt 1974). In the combined five-gene dataset excluding *Lybia* crab symbionts, members of *Alicia* are sister to Aiptasiidae (Fig 2.10). This close relationship of *Alicia* and Aiptasiidae has also been found in preliminary analyses of a larger Actiniaria dataset (pers. comm. E. Rodríguez), and Rodríguez & Daly (2010) recovered *Triactis* as sister to Aiptasiidae. The close relationship of aliciids, boloceroidids, and aiptasiids in some of the phylogenies presented here (Fig 2.2, 2.10, 2.11) are congruent with some morphological features, in particular the well-developed longitudinal musculature in the uppermost part of the column (Schmidt 1974), which Carlgren (1947) stated could be an important character for classification of anemones. The relationships recovered in both of the combined five-gene datasets support this notion, with a derived clade comprised of Aliciidae, Boloceroididae, and Aiptasiidae recovered with good support. Future studies should include members of Gonactiniidae, which also possess well-developed longitudinal muscles of the column (Carlgren 1947, 1949).

Aiptasiids possess nematocyst-laden threads called acontia, a feature shared by many members of Metridioidea, but lacking in Aliciidae and Boloceroididae. The consistent recovery of aliciid members within the Metridioidea clade suggests that acontia were gained in early evolution of Metridioidea (Fig 2.12), but subsequently lost for members of Aliciidae and Boloceroididae. Alternatively, acontia could have been lost in the Aiptasiidae+Boloceroididae+Aliciidae clade, and regained in the Aiptasiidae lineage. The phylogenies of Daly *et al*. (2008), Rodríguez & Daly (2010), and Rodríguez *et al*. (2012) also suggest that acontia have been lost in various taxa, including Aliciidae, Boloceroididae, and *Paranthus*. I, too, recover these three groups of acontia-less species to be nested in the Metridioidea clade, supporting the hypothesis that acontia were lost evolutionarily in these taxa, and therefore multiple times in Metridioidea. Acontia used to define the group Acontiaria, of which all members have acontia, however, the Acontiaria group has not been recovered in recent phylogenies. Instead a clade consisting predominantly of acontia-bearing taxa, but also including some taxa that lack acontia, has been recovered; this group is referred to as Metridioidea (see Rodríguez *et al*. 2012).

Lybia *crab symbiont identity*

In all analyses, including separate gene analyses not shown, the *Lybia* crab symbionts are most closely related to specimens of *Triactis producta* and never found closely related to *Bunodeopsis* (Family Boloceroididae) or *Sagartia* (Family Sagartiidae). The *Lybia* crab symbionts also possessed macrobasic amastigophore nematocysts on the column, which is further evidence these sea anemones are in the family Aliciidae. Both the molecular and cnidae results support that the *Lybia* crab symbionts are members of the species *Triactis producta*.

Triactis producta usually possess pseudotentacles projecting from the column, and vesicles attached to the pseudotentacles or column. The *Lybia* crab symbionts lacked any projections of the column (Fig 2.1 b,d). The symbiosis between the sea anemone and the crab is such that the crab holds onto the anemones mid-column (Fig 2.1 b,d), with chelae that have sharp, fine hooks (Fig 2.1 e) (Guinot 1976). Sea anemones with outgrowths of the column would make this difficult. Whether the crab chooses anemones that lack column outgrowths, and if the development of column features on the sea anemone is impeded by the symbiosis, is unknown and untested in this study. Observations have shown that once the anemone is out of the relationship, vesicles start to form on the column (pers. comm. Y. Schnytzer). I have observed that for column morphology of *T. producta*, vesicles are the first projection to form, followed by pseudotentacles (see results in Chapter 4).

The specimens I obtained of anemones symbiotic with *Lybia* crabs included three representatives from the Indian Ocean, and one from Hawai'i in the Pacific Ocean, as well as from two species of *Lybia, L. tesselata* from the Indo-Pacific and *L. edmondsoni* from Hawai'i. It is still unknown how many species of sea anemones are associated with *Lybia* crabs, *Triactis producta* may not be the only species of sea anemone involved in this symbiosis, despite all four specimens I analyzed nesting with *T.producta*. In fact, Duerden (1905) showed that *Lybia* crabs could change their symbionts, and even hold two different species of anemones in each chela. Adding more specimens of sea anemone symbionts may show more species involved in this symbiosis.

Verrill (1928) described a new species of sea anemone, *Sagartia pugnax*, and cited it as a symbiont of both *Lybia tesselata* and *Polydectus cupulifer*. Figure j of Verrill (1928) shows an illustration of the symbiotic sea anemone with acontia extended through the column wall – a feature that characteristic of *Sagartia*. What is not clear from the Verrill's (1928) account is whether the sea anemone specimen in Figure j was symbiotic with *Polydectus* or *Lybia*, or whether all sea anemone specimens he encountered possessed acontia. It is possible that small specimens of *Triactis producta* and *Sagartia* can look very similar when in association with crabs, as symbiotic *T. producta* lack the distinctive column morphology of non-symbiotic *T. producta*. Cutress (1977) considered that some of the specimens described by Verrill (1928) were *T. producta* and not *Sagartia pugnax*; however, it is not known which subset of the specimens he considered which, and whether *T.producta* were associated with *Lybia* or *Polydectus*. Cutress (1977) stated that Duerden (1905) had mis-identified *Bunodeopsis* as specimens belonging to *T.producta,* and also synonymized *Actinia prehensa*, the first sea anemone described in association with *Lybia* crabs, with *T.producta.*

It is possible that multiple species of anemones are symbiotic with *Lybia* crabs. Duerden (1905) observed that one *Lybia* crab individual could change species of symbionts, from

Bunodeopsis to *Sagartia*, and could even hold different species in each chela. The acontia observed in the symbiont anemone by Duerden (1905) and Verrill (1928) rule out that these anemones were *Triactis producta*, as this species lacks acontia; so at least two species of anemones have been recorded in this symbiosis. For the crab, it is possible that any small-sized anemone is suitable for the symbiosis, as all anemones possess cnidae; it is unknown whether the selection of the anemone is based on anything except size.

Evolution of morphological features

The pattern of relationships recovered suggests that sea anemone possessing both branched outgrowths and defensive spheres have evolved three times (Fig 2.12). The combination of these characters are exhibited in three families, Actinodendridae, Thalassianthidae, and Aliciidae, that are not recovered as each others' closest relatives. Some members of other families possess either branched outgrowths (*e.g. Phymanthus* of Phymanthidae) or defensive spheres (*e.g. Phyllactis* of Actiniidae), but not both. The non-monophyly of a clade containing branched outgrowths and defensive spheres is reasonable because of the morphological differences among the families. Re-coding characters gives a clearer indication that these characters are not homologous, and convergence has lead to sea anemones evolving superficially similar morphological features. Finding Actinodendridae to be monophyletic and nested within Endomyaria supports Ardelean's (2003a) results. Ardelean (2003b) showed the branched tentacles of Actinodendridae and Thalassianthidae to be superficially similar.

The re-coding of branched outgrowths and defensive spheres as projections of either the oral disc or column shows the very distant relationship of species that possess projections of the oral disc and the column, and different morphological evolutionary histories for each genus (Fig 2.13, 2.14). Branched outgrowths and defensive spheres of the oral disc evolved twice in the Endomyaria clade, once in Actinodendridae and once in Thalassianthidae. The defensive spheres of the column have evolved three times; most instances of defensive spheres of the column are found in representatives of Aliciidae. An alternative explanation of evolution of vesicles is that they evolved once in a clade containing Aliciidae, Boloceroididae, and Aiptasiidae, then were subsequently lost in *Boloceroides* and Aiptasiidae. Because of the similarities of vesicles of *Alicia* and all other Aliciidae genera, especially in relation to possession of macrobasic amastigophores, it is likely that the vesicles of all Aliciidae genera are homologous. The vesicles of *Bunodeopsis* are similar in morphology, but do not have macrobasic amastigophores. The branched outgrowths of the column, the pseudotentacles, are recovered as being evolved only once, in a clade consisting of three of the four genera of Aliciidae. The pseudotentacles of the three genera share features such as position, cnidae, and musculature, so a clade consisting of these three genera is not unexpected.

The defensive spheres of Thalassianthidae and Aliciidae are neither homologous, nor contain the same type of nematocysts, yet species that possess defensive spheres have been reported to be toxic. This suggests that toxicity within Actiniaria has evolved multiple times, including many families, not just Thalassianthidae and Aliciidae. Actinodendridae have the common name of Hell's Fire Anemone because of the nasty sting to humans (Hansen & Halstead 1971). *Phyllodiscus semoni* should be considered very dangerous following a report that a man died after being stung by this species (Erhardt & Knop 2005). Species of Thalassianthidae, *Triactis*, and *Lebrunia* have all been reported to cause irritation to the skin (Fishelson 1970, Levy *et al.* 1970, Herrnkind *et al.* 1976, Williamson *et al.* 1996). Species in other families such as

Hormathiidae, Aiptasiidae, and Actiniidae have also been reported to sting humans, so it is clear toxicity is widespread in Actiniaria.

Conclusion

In this study, I investigated whether Aliciidae and Thalassianthidae were each monophyletic, and if they were closely related. To do so, phylogenetic analyses of molecular data from a broad sample of Actiniaria provided a framework of evolutionary relationships. Resulting phylogenies provided evidence supporting the monophyly of Thalassianthidae and the thalassianthid genera, *Thalassianthus* and *Cryptodendrum*. Support was also gained for the placement of Thalassianthidae in Endomyaria. Aliciidae was not recovered as monophyletic, but missing data may have influenced this result. The three pseudotentacle-bearing genera consistently formed a well-supported clade. Aliciidae members were found closely related to Boloceroididae and Aiptasiidae members, placed in the larger group Metridioidea, and never found closely related to endomyarians.

Branched outgrowths and defensive spheres of Thalassianthidae and Aliciidae are convergent characters, but clearer definitions reveal more precise evolutionary histories for each genus of Aliciidae and Thalassianthidae. For specimens lacking diagnostic morphology, such as sea anemones symbiotic with *Lybia* crabs, molecular data provides an alternative form of information. By analyzing *Lybia* symbionts along with other species of sea anemones, I found the *Lybia* symbionts belong to aliciid *Triactis producta*.

In future studies, additional genes may be added to the matrix to resolve more nodes. Other mitochondrial genes, such as CO1, may help to resolve deeper nodes. The terminal nodes may be resolved with the addition of the nuclear loci ITS, which has been used successfully by other sea anemone studies (Stoletzki & Schierwater 2005, Acuña *et al.* 2007, Worthington-Wilmer & Mitchell 2008, Gusmão 2010). Increased taxon and gene sampling may lead to the recovery of a monophyletic Aliciidae, and provide further insight into the evolution or vesicles in this diverse family.

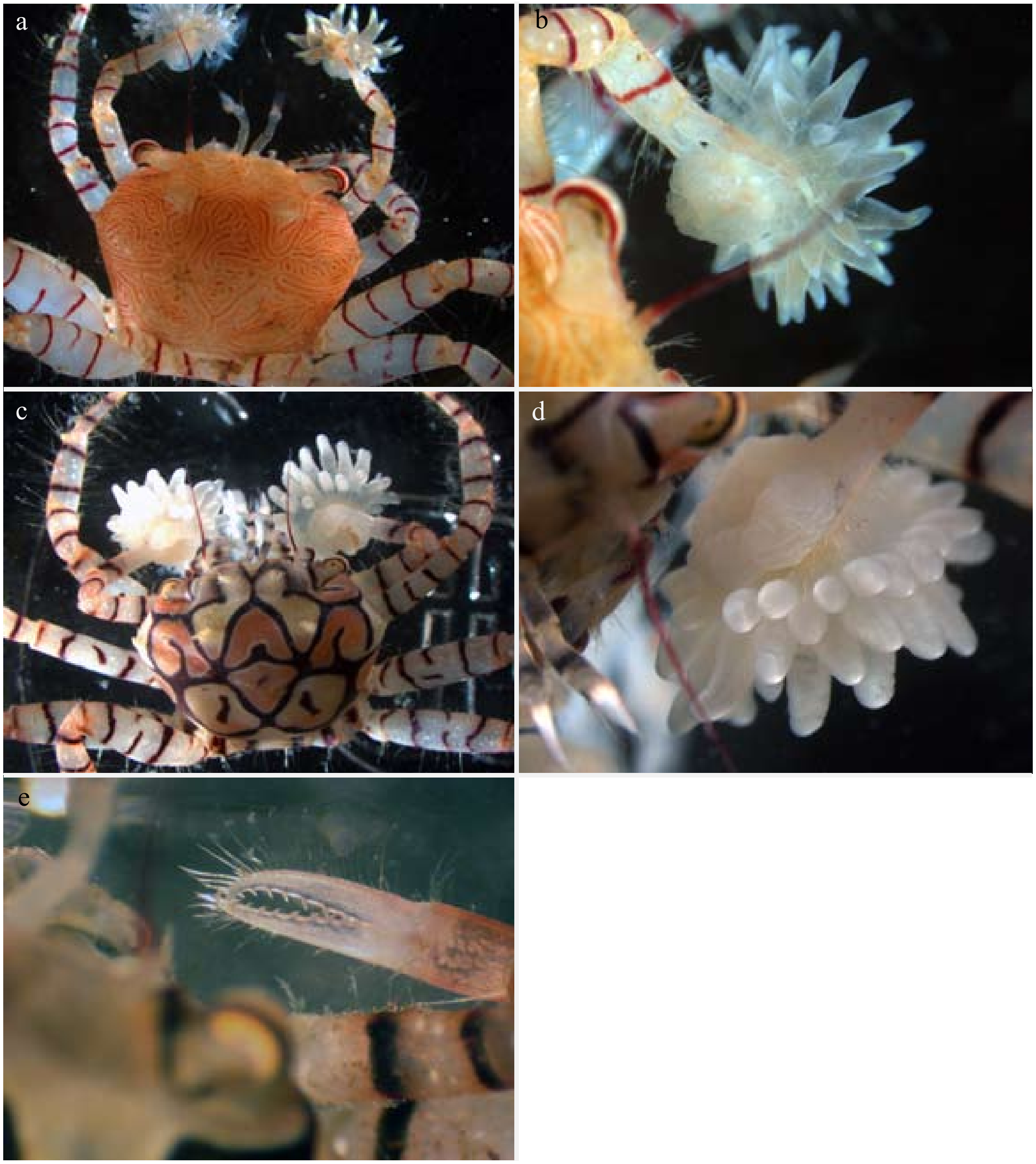

Fig 2.1. *Lybia* crabs and symbionts. a,b) *Lybia edmondsoni* and sea anemone from Indian Ocean c,d) *Lybia tesselata* and sea anemone from Hawai'i e) modified chela from *Lybia tesselata* without sea anemone.

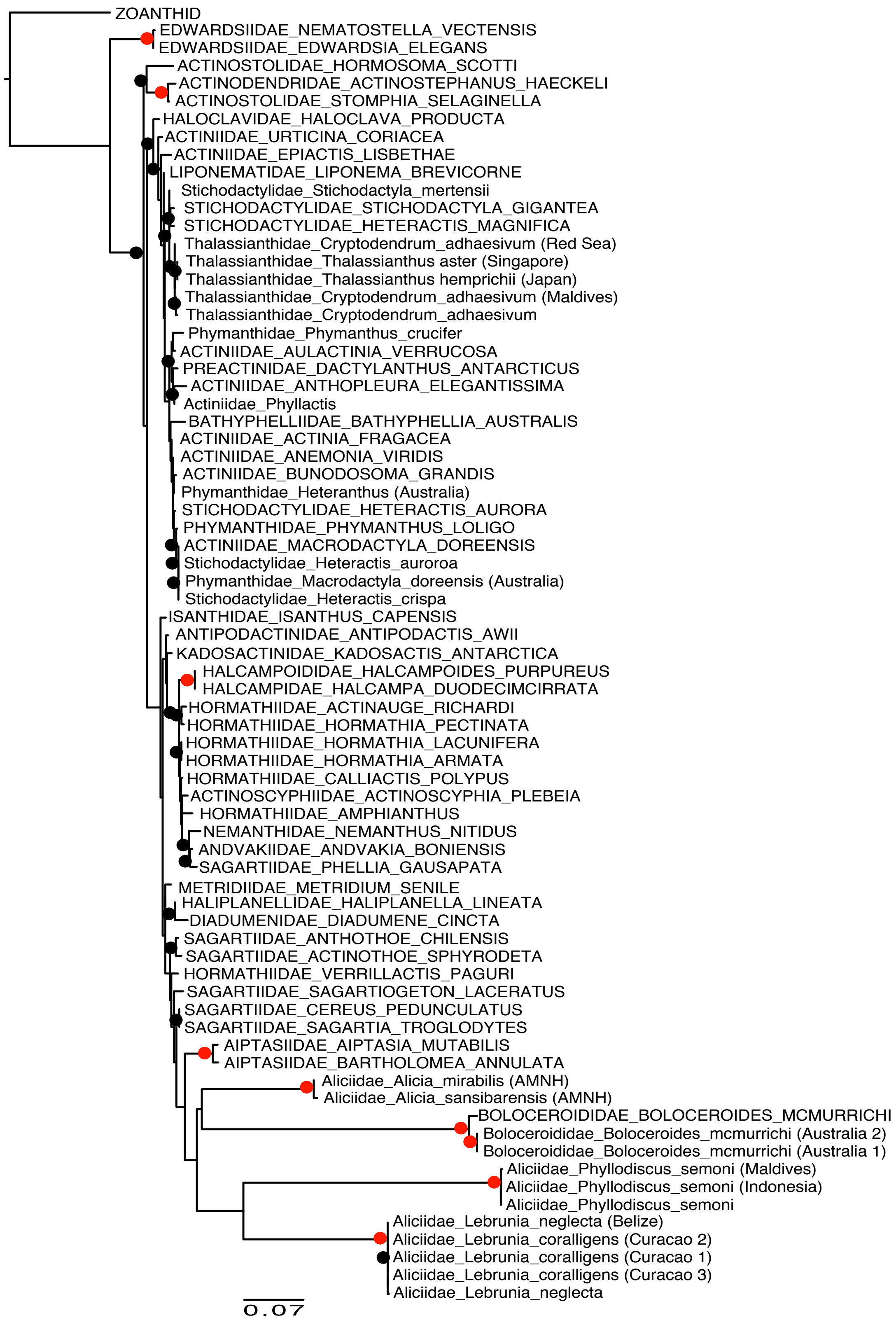

Fig 2.2. Phylogeny from Maximum Likelihood analyses of 12S dataset. Samples in all caps from GenBank, lowercase from this study. Support assessed from 1000 bootstrap replicates; red for 100, black for >50.

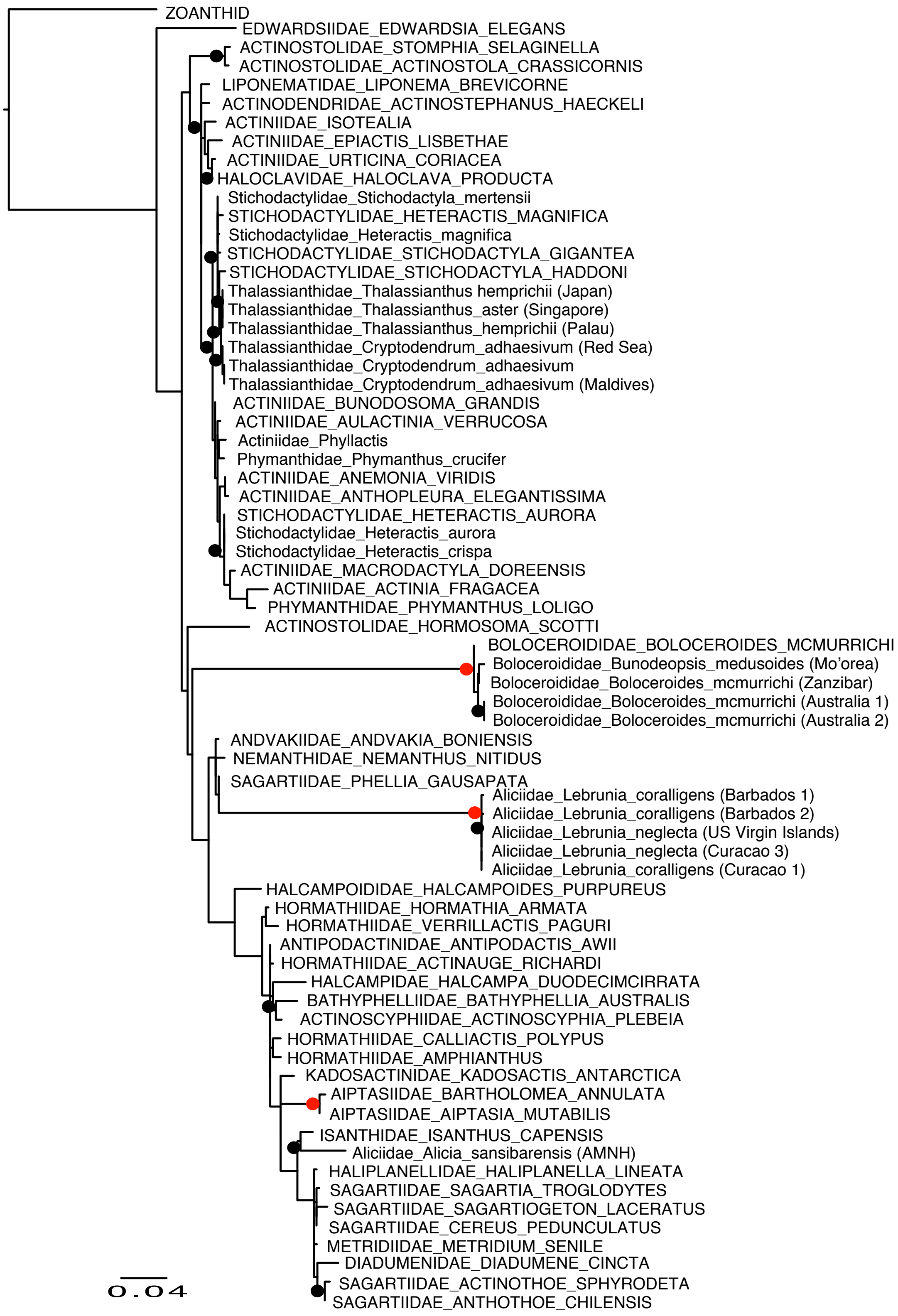

Fig 2.3. Phylogeny from Maximum Likelihood analyses of 16S dataset. Samples in all caps from GenBank, lowercase from this study. Support assessed from 1000 bootstrap replicates; red for 100, black for >70.

Fig 2.4. Phylogeny from Maximum Likelihood analyses of CO3 dataset. Samples in all caps from GenBank, lowercase from this study. Support assessed from 1000 bootstrap replicates; red for 100, black for >70.

Fig 2.5. Phylogeny from Maximum Likelihood analyses of mitochondrial dataset. Samples in all caps from GenBank, lowercase from this study. Support assessed from 1000 bootstrap replicates; red for 100, black for >70.

Fig 2.6. Phylogeny from Maximum Likelihood analyses of 18S dataset. Samples in all caps from GenBank, lowercase from this study. Support assessed from 1000 bootstrap replicates; red for 100, black for >70.

Fig 2.7. Phylogeny from Maximum Likelihood analyses of 28S dataset. Samples in all caps from GenBank, lowercase from this study. Support assessed from 1000 bootstrap replicates; red for 100, black for >70.

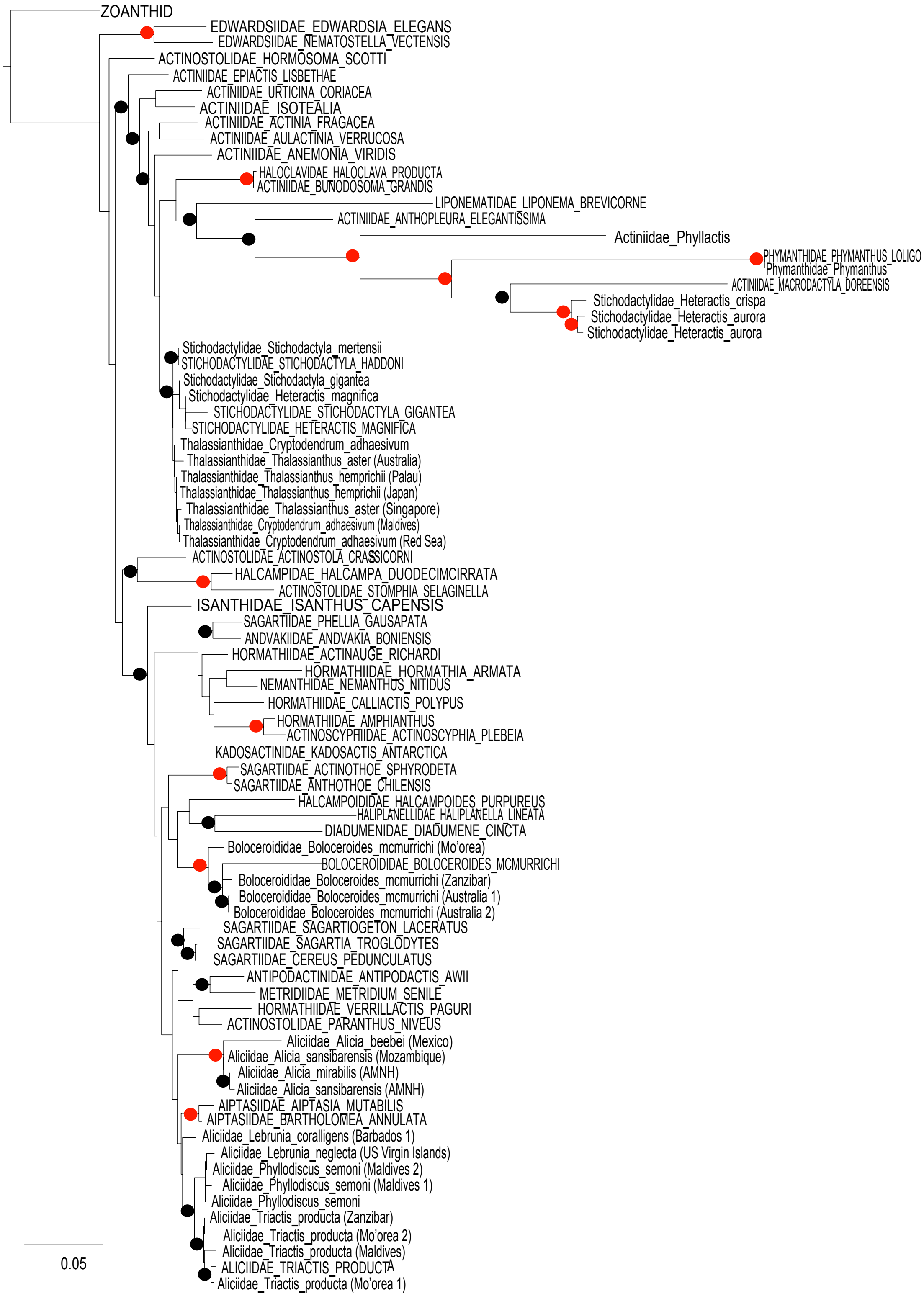

Fig 2.8. Phylogeny from Maximum Likelihood analyses of nuclear dataset. Samples in all caps from GenBank, lowercase from this study. Support assessed from 1000 bootstrap replicates; red for 100, black for >70.

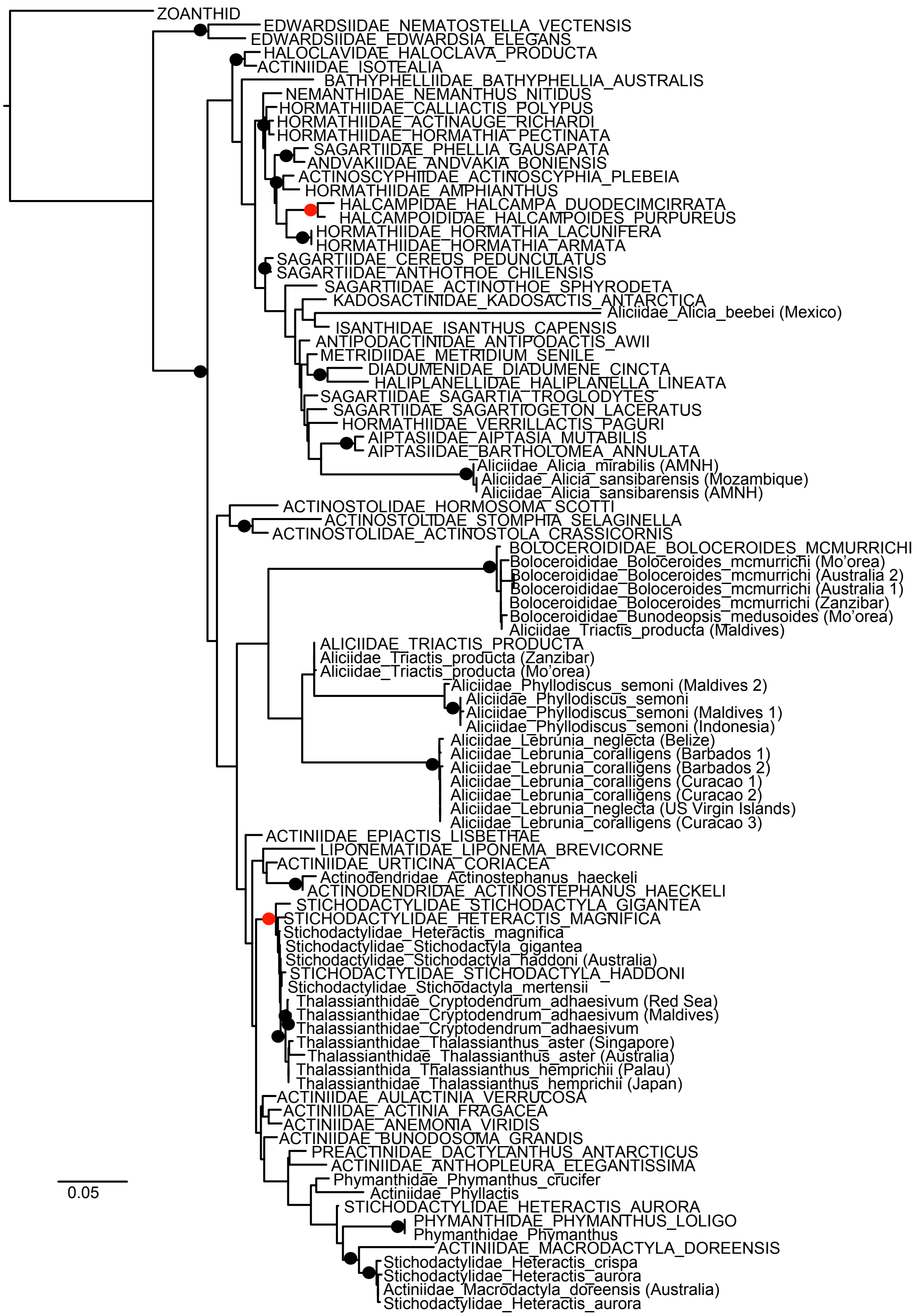

Fig 2.9. Phylogeny from Maximum Likelihood analyses of all genes except 28S dataset. Samples in all caps from GenBank, lowercase from this study. Support assessed from 1000 bootstrap replicates; red for 100, black for >70.

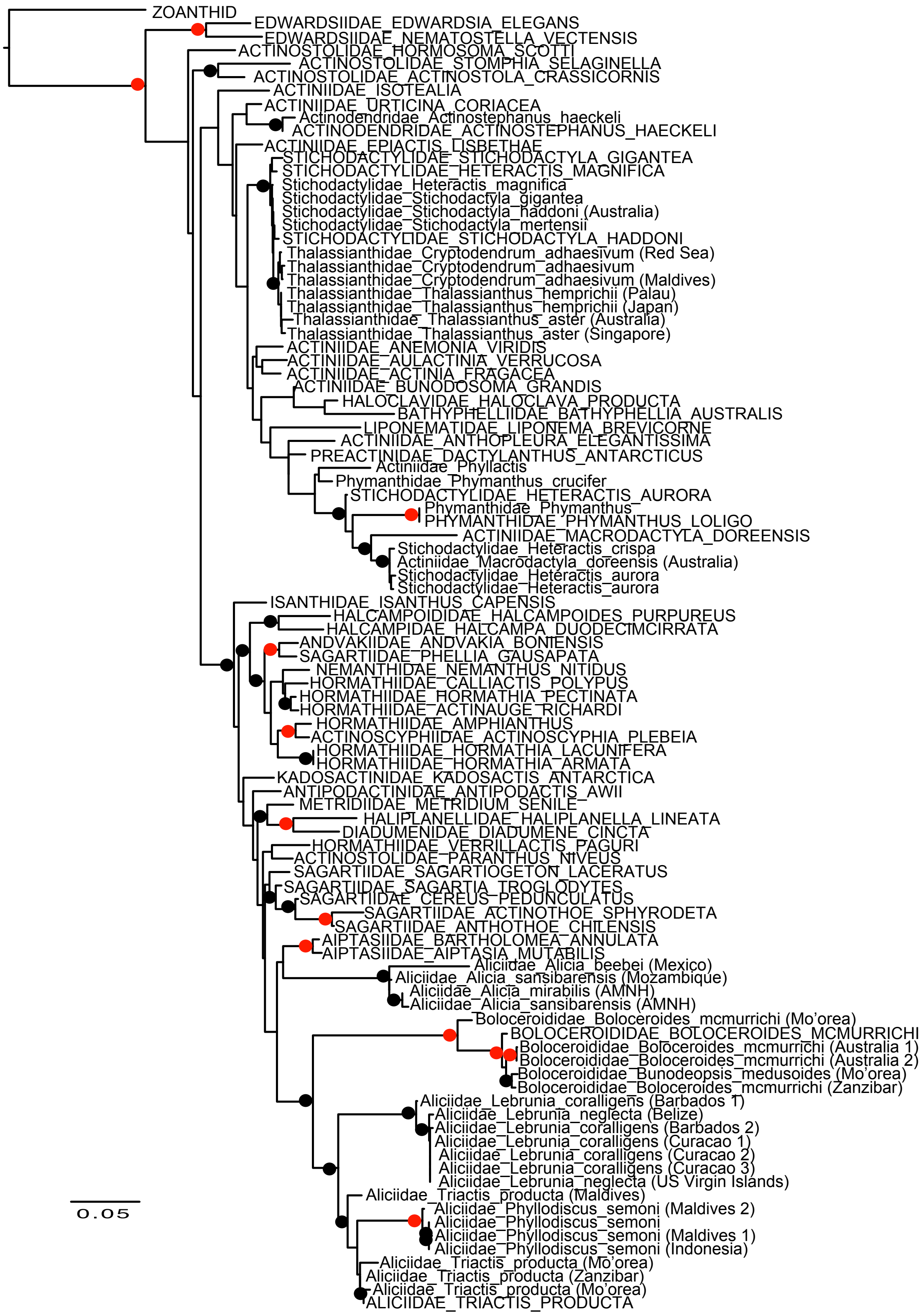

Fig 2.10. Phylogeny from Maximum Likelihood analyses of complete dataset. Samples in all caps from GenBank, lowercase from this study. Support assessed from 1000 bootstrap replicates; red for 100, black for >70.

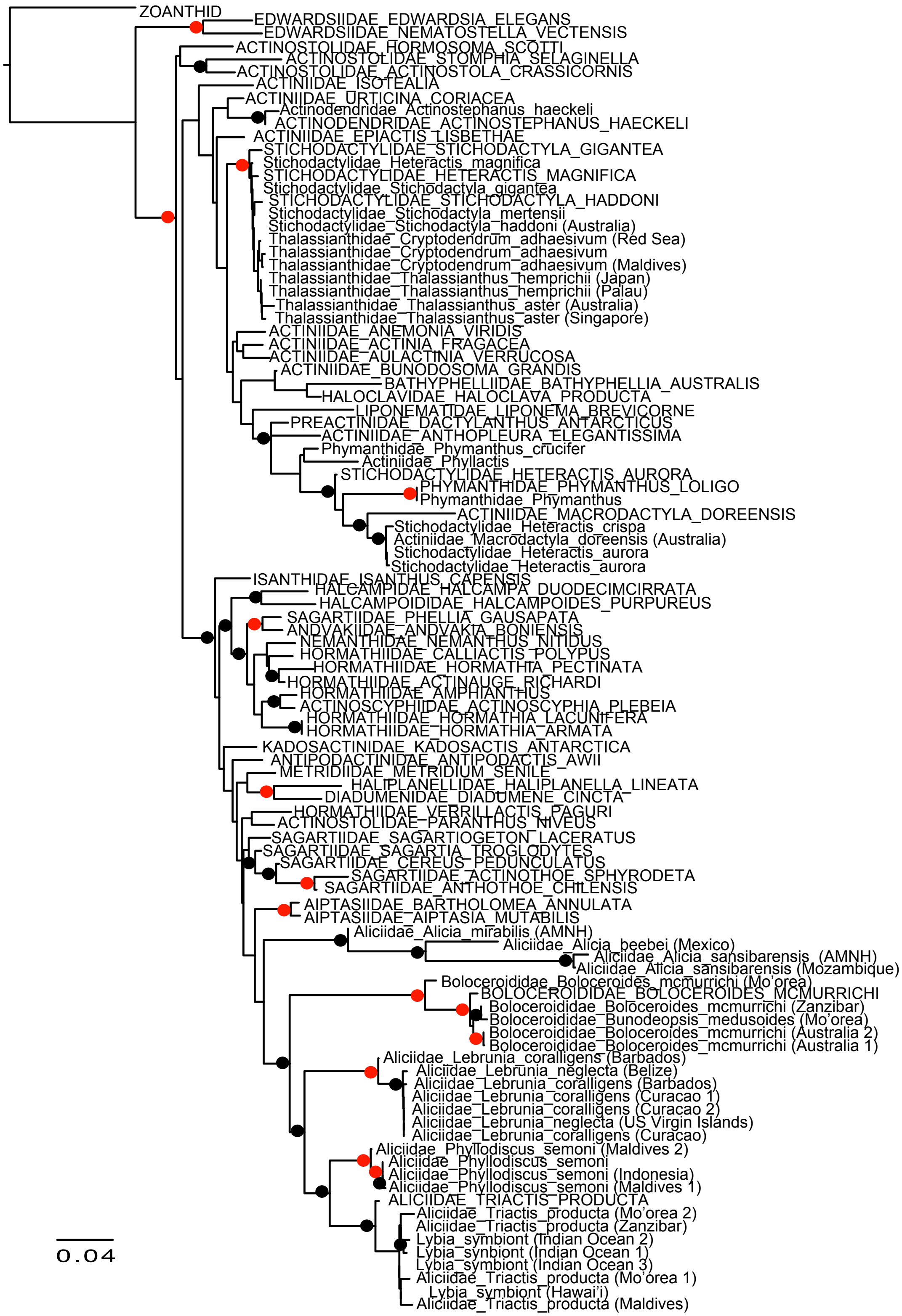

Fig 2.11. Phylogeny from Maximum Likelihood analyses of complete dataset, including *Lybia* crab symbionts. Samples in all caps from GenBank, lowercase from this study. Support assessed from 1000 bootstrap replicates; red for 100, black for >70.

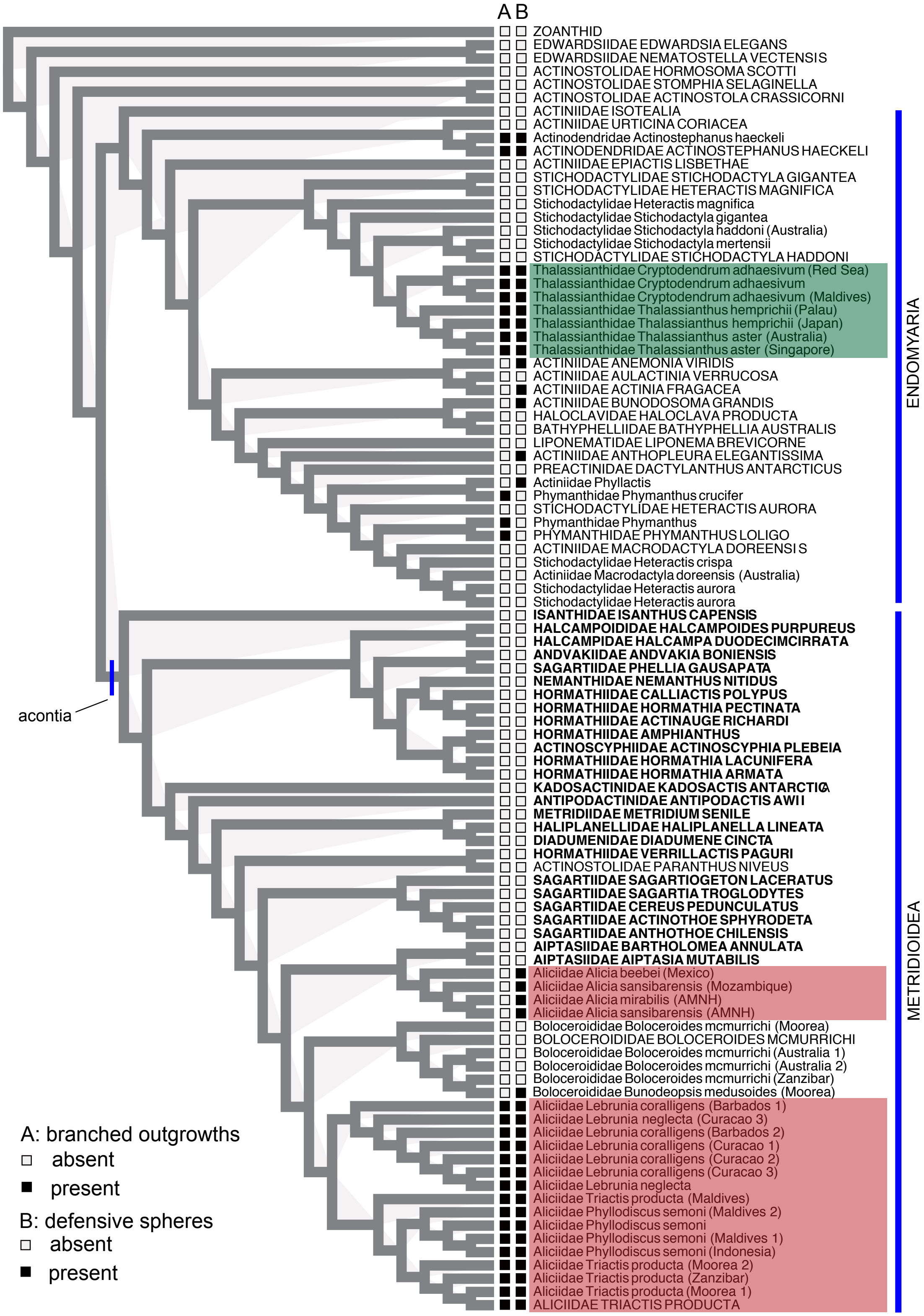

Fig 2.12. Morphological character states coded on combined five-gene without *Lybia* symbiont phylogeny. Thalassianthidae members highlighted in green, Aliciidae members highlighted in red. Bold taxa possess acontia. For further explanation of character coding, see Table 2.2.

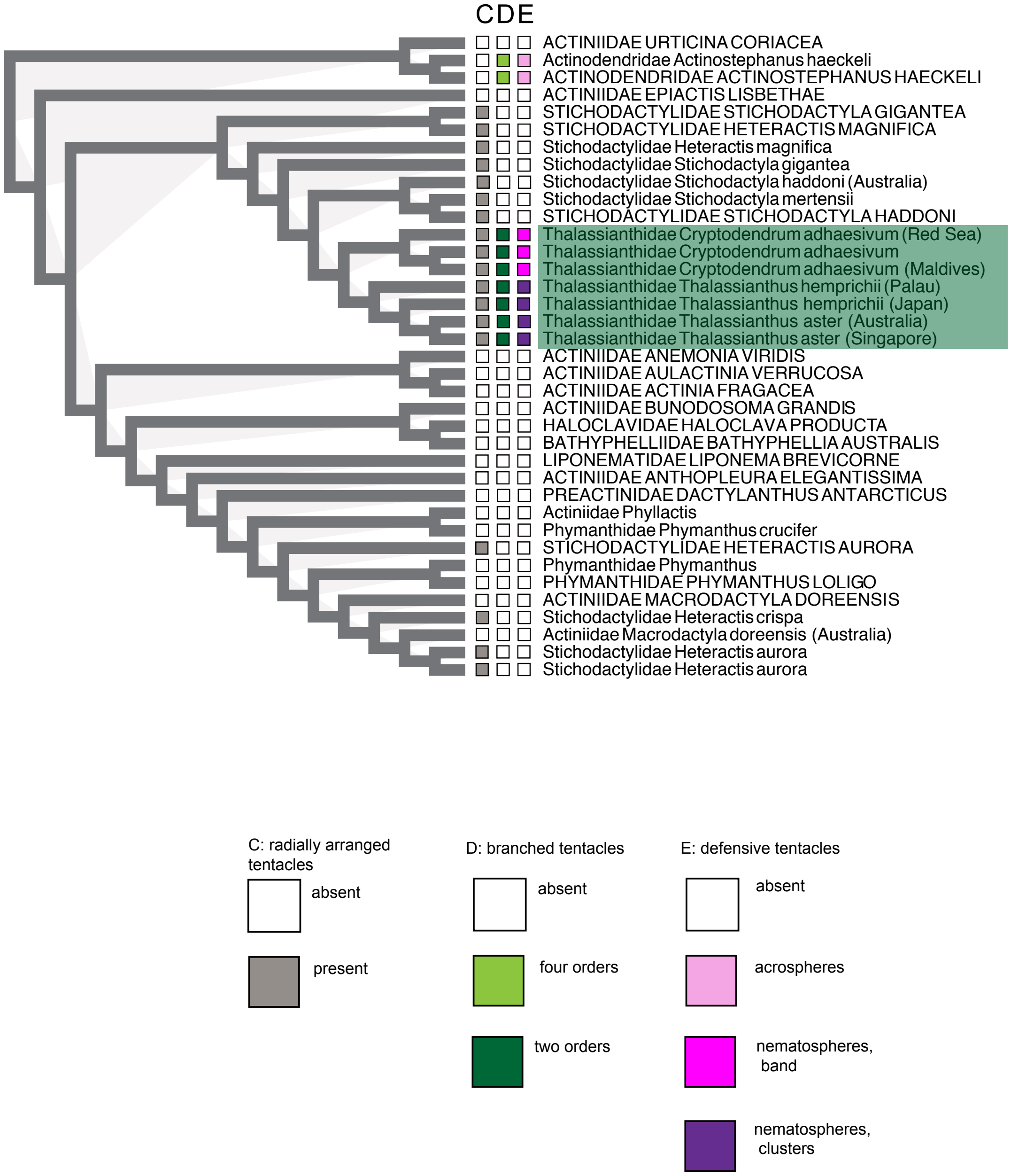

Fig 2.13. Morphological character states coded on inset of combined five-gene without *Lybia* symbiont phylogeny. Thalassianthidae members highlighted in green. For further explanation of character coding, see Table 2.2.

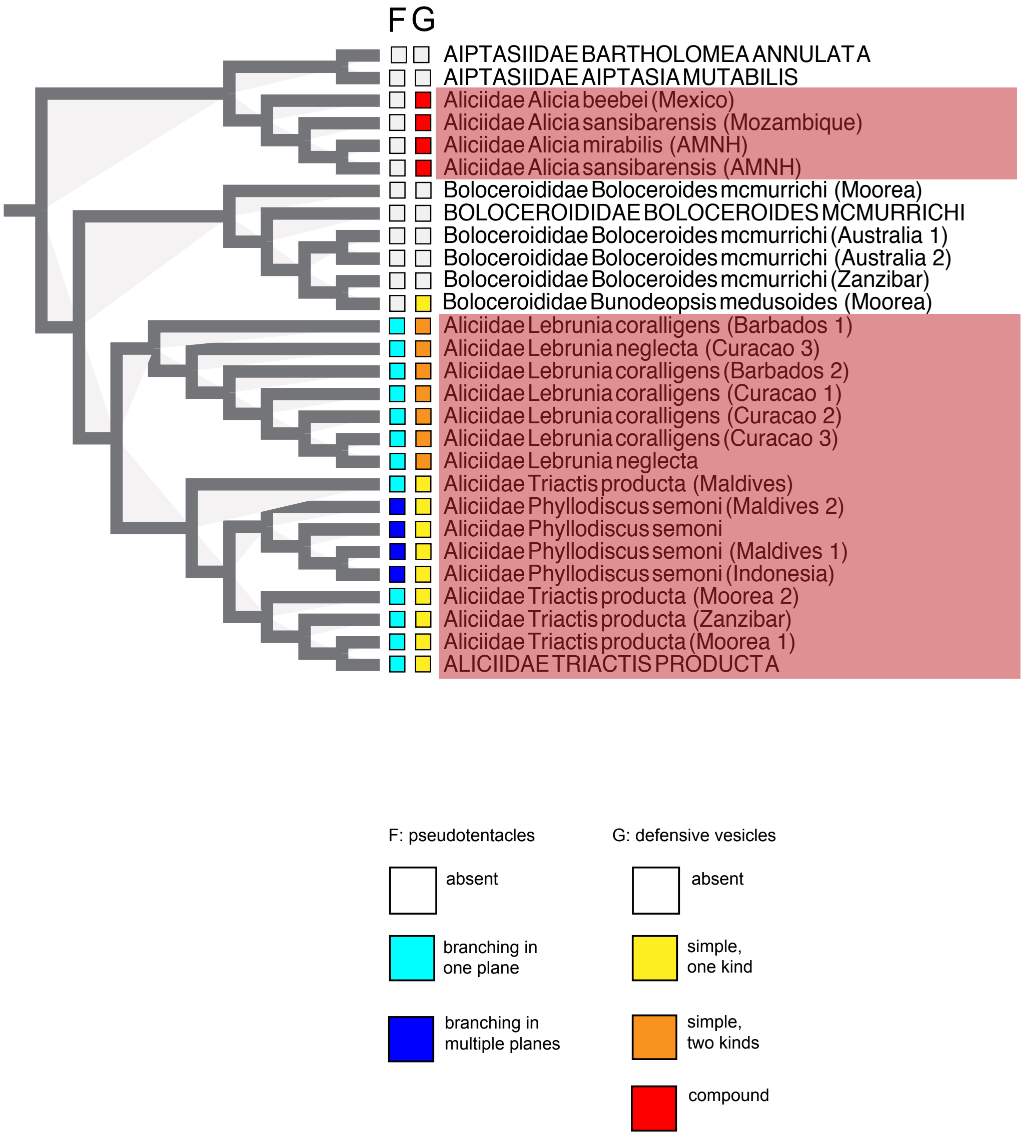

Fig 2.14. Morphological character states coded on inset of combined five-gene without *Lybia* symbiont phylogeny. Aliciidae members highlighted in red. For further explanation of character coding, see Table 2.2.

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Table 2.1. List of sequences used in this study. Bold indicate sequences new for this study, Accession numbers for sequences from GenBank.

	12S	16S	CO3	18S	28S 5' fragment	28S 3' fragment
Zoanthid	AY995905.1	AY995925.1	NC008827.1	HM044299.1	HM044298.1	HM044298.1
Actiniidae - *Actinia fragacea*	EU190714.1	EU190756.1	GU473334.1	EU190845.1	EU190802.1	–
Actiniidae - *Anemonia viridis*	EU190718.1	EU190760.1	GU473335.1	EU190849.1	EU190806.1	–
Actiniidae - *Anthopleura elegantissima*	EU190713.1	EU190755.1	GU473333.1	EU190844.1	EU190801.1	–
Actiniidae - *Aulactinia verrucosa*	EU190723.1	EU190766.1	FJ489484.1	EU190854.1	EU190812.1	–
Actiniidae - *Bunodosoma grandis*	EU190722.1	EU190765.1	GU473336.1	EU190853.1	EU190811.1	–
Actiniidae - *Epiactis lisbethae*	EU190727.1	EU190771.1	GU473360.1	EU190858.1	EU190816.1	–
Actiniidae - *Isotealia*	–	GU473290.1	GU473354.1	GU473306.1	GU473322.1	–
Actiniidae - *Macrodactyla doreensis*	EU190739.1	EU190785.1	GU473342.1	EU190867.1	EU190828.1	–
Actiniidae - *Macrodactyla doreensis* (Australia)	**KC812137**	–	–	–	–	–
Actiniidae - *Phyllactis* sp.	**KC812124**	**KC812148**	**KC812221**	**KC812170**	–	–
Actiniidae - *Urticina coriacea*	GU473282.1	EU190797.1	GU473351.1	EU190877.1	EU190840.1	–
Actinodendridae - *Actinostephanus haeckeli*	–	–	**KC812222**	–	–	–
Actinodendridae - *Actinostephanus haeckeli*	EU190720.1	EU190762.1	GU473353.1	–	–	–
Actinoscyphiidae - *Actinoscyphia plebeia*	EU190712.1	EU190754.1	FJ489476.1	FJ489437.1	EU190800.1	–
Actinostolidae - *Actinostola crassicornis*	–	EU190753.1	GU473332.1	EU190843.1	EU272904.1	–
Actinostolidae - *Hormosoma scotti*	EU190733.1	EU190778.1	GU473366.1	EU190863.1	EU190822.1	–
Actinostolidae - *Paranthus niveus*	GU473277.1	GU473295.1	GU473344.1	GU473311.1	GU473327.1	–
Actinostolidae - *Stomphia selaginella*	GU473280.1	GU473298.1	GU473349.1	GU473314.1	GU473331.1	–
Aiptasiidae - *Aiptasia mutabilis*	FJ489408.1	FJ489418.1	FJ489505.1	FJ489438.1	FJ489469.1	–
Aiptasiidae - *Bartholomea annulata*	EU190721.1	EU190763.1	FJ489483.1	EU190851.1	EU190809.1	–
Aliciidae - *Alicia beebei* (Mexico)	–	–	–	**KC812172**	–	**KC812198**
Aliciidae - *Alicia mirabilis* (unpublished from AMNH)	**KC812126**	–	–	–	**KC812199**	**KC812199**
Aliciidae - *Alicia sansibarensis* (Mozambique)	–	–	–	**KC812173**	–	**KC812200**
Aliciidae - *Alicia sansibarensis* (unpublished from AMNH)	**KC812125**	**KC812149**	**KC812223**	**KC812171**	–	**KC812197**
Aliciidae - *Lebrunia coralligens* (Barbados 1)	–	**KC812150**	–	**KC812174**	–	**KC812201**
Aliciidae - *Lebrunia coralligens* (Barbados 2)	–	**KC812151**	–	–	–	–
Aliciidae - *Lebrunia coralligens* (Curacao 1)	**KC812127**	**KC812152**	–	–	–	–
Aliciidae - *Lebrunia coralligens* (Curacao 2)	**KC812128**	–	–	–	–	–
Aliciidae - *Lebrunia coralligens* (Curacao 3)	**KC812129**	–	–	–	–	–
Aliciidae - *Lebrunia coralligens* (Belize 1)	**KC812130**	**KC812153**	–	–	–	–
Aliciidae - *Lebrunia danae* (US Virgin Islands)	**KC812131**	**KC812154**	**KC812224**	–	–	**KC812202**
Aliciidae - *Phyllodiscus semoni* (Malidives 1)	**KC812132**	–	–	**KC812175**	–	**KC812203**
Aliciidae - *Phyllodiscus semoni* (Malidives 2)	–	–	–	**KC812176**	–	**KC812204**
Aliciidae - *Phyllodiscus semoni* (Indonesia)	**KC812133**	–	–	–	–	–
Aliciidae - *Phyllodiscus semoni*	**KC812134**	–	–	**KC812177**	–	**KC812205**

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Table 2.1 continued.

	12S	16S	CO3	18S	28S 5' fragment	28S 3' fragment
Aliciidae - *Triactis producta*	EU490525.1	–	GU473350.1	EU190876.1	EU190839.1	–
Aliciidae - *Triactis producta* (Maldives)	–	–	**KC812225**	–	–	**KC812206**
Aliciidae - *Triactis producta* (Mo'orea 1)	–	–	–	**KC812178**	–	**KC812207**
Aliciidae - *Triactis producta* (Mo'orea 2)	–	–	–	–	–	**KC812208**
Aliciidae - *Triactis producta* (Zanzibar)	–	–	–	**KC812179**	–	**KC812209**
Andvakiidae - *Andvakia boniensis*	EU190717.1	EU190759.1	FJ489479.1	EU190848.1	EU190805.1	–
Antipodactinidae - *Antipodactis awii*	GU473271.1	GU473286.1	GU473337.1	GU473303.1	GU473319.1	–
Bathyphelliidae - *Bathyphellia australis*	FJ489402.1	FJ489422.1	FJ489482.1	–	–	–
Boloceroididae - *Boloceroides mcmurrichi*	GU473270.1	EU190764.1	–	EU190852.1	EU190810.1	–
Boloceroididae - *Boloceroides mcmurrichi* (Mo'orea)	–	–	–	**KC812182**	–	**KC812213**
Boloceroididae - *Boloceroides mcmurrichi* (Australia 1)	**KC812135**	**KC812155**	**KC812226**	**KC812180**	–	**KC812211**
Boloceroididae - *Boloceroides mcmurrichi* (Australia 2)	**KC812136**	**KC812156**	–	**KC812181**	–	**KC812212**
Boloceroididae - *Boloceroides mcmurrichi* (Zanzibar)	–	**KC812157**	–	–	–	**KC812210**
Boloceroididae - *Bunodeopsis medusoides* (Mo'orea)	–	**KC812158**	**KC812227**	–	–	–
Diadumenidae - *Diadumene cincta*	EU190725.1	EU190769.1	FJ489490.1	EU190856.1	EU190814.1	–
Edwardsiidae - *Edwardsia elegans*	EU190726.1	EU190770.1	GU473338.1	AF254376.2	AY345870.1	–
Edwardsiidae - *Nematostella vectensis*	EU190750.1	–	FJ489501.1	AF254382.1	AY345871.1	–
Halcampidae - *Halcampa duodecimcirrata*	JF832966.1	EU190776.1	–	AF254375.1	EU190820.1	–
Halcampoididae - *Halcampoides purpureus*	EU190735.1	EU190780.1	–	AF254380.1	EU190824.1	–
Haliplanellidae - *Haliplanella lineata*	EU190730.1	EU190774.1	FJ489506.1	EU190860.1	EU190819.1	–
Haloclavidae - *Haloclava producta*	EU190734.1	EU190779.1	GU473340.1	AF254379.1	EU190823.1	–
Hormathiidae - *Actinauge richardi*	EU190719.1	EU190761.1	FJ489480.1	EU190850.1	EU190807.1	–
Hormathiidae - *Amphianthus*	FJ489413.1	FJ489432.1	FJ489502.1	FJ489450.1	FJ489467.1	–
Hormathiidae - *Calliactis polypus*	FJ489404.1	FJ489424.1	FJ489485.1	FJ489442.1	FJ489457.1	–
Hormathiidae - *Hormathia armata*	EU190731.1	EU190775.1	FJ489491.1	EU190861.1	FJ489460.1	–
Hormathiidae - *Hormathia lacunifera*	FJ489409.1	FJ489428.1	FJ489492.1	FJ489446.1	FJ489461.1	–
Hormathiidae - *Hormathia pectinata*	FJ489415.1	FJ489430.1	FJ489497.1	FJ489448.1	FJ489465.1	–
Hormathiidae - *Verrillactis paguri*	FJ489414.1	FJ489433.1	FJ489503.1	FJ489451.1	FJ489468.1	–
Isanthidae - *Isanthus capensis*	JF832967.1	GU473291.1	GU473362.1	GU473307.1	GU473323.1	–
Kadosactinidae - *Kadosactis antarctica*	FJ489410.1	EU190782.1	FJ489504.1	EU190865.1	EU190825.1	–
Liponematidae - *Liponema brevicorne*	EU190738.1	EU190784.1	GU473341.1	EU190866.1	EU190827.1	–
Lybia crab symbiont (Hawai'i)	**KC841870**	–	–	**KC841873**	–	**KC841875**
Lybia crab symbiont (Indian Ocean 1)	**KC841868**	–	–	**KC841872**	–	**KC841876**
Lybia crab symbiont (Indian Ocean 2)	**KC841867**	–	–	**KC841871**	–	**KC841877**
Lybia crab symbiont (Indian Ocean 3)	**KC841869**	–	–	**KC841874**	–	**KC841878**
Metridiidae - *Metridium senile*	EU190740.1	AY345876.1	FJ489494.1	JF832981.1	EU190829.1	–

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Table 2.1 continued.

	12S	16S	CO3	18S	28S 5' fragment	28S 3' fragment
Nemanthidae - *Nemanthus nitidus*	EU190741.1	EU190787.1	FJ489495.1	EU190868.1	EU190830.1	–
Phymanthidae - *Phymanthus crucifer*	**KC812138**	**KC812159**	**KC812228**	–	–	–
Phymanthidae - *Phymanthus loligo*	EU190745.1	EU190791.1	GU473345.1	EU190871.1	–	–
Phymanthidae - *Phymanthus*	–	–	–	**KC812183**	–	–
Preactiniidae - *Dactylanthus antarcticus*	GU473272.1	–	GU473358.1	–	–	–
Sagartiidae - *Actinothoe sphyrodeta*	FJ489401.1	FJ489421.1	FJ489481.1	FJ489440.1	FJ489455.1	–
Sagartiidae - *Anthothoe chilensis*	FJ489397.1	FJ489416.1	FJ489470.1	FJ489434.1	FJ489453.1	–
Sagartiidae - *Cereus pedunculatus*	EU190724.1	EU190767.1	FJ489471.1	EU190855.1	EU190813.1	–
Sagartiidae - *Phellia gausapata*	EU190744.1	EU190790.1	FJ489473.1	EU190870.1	EU190833.1	–
Sagartiidae - *Sagartia troglodytes*	EU190746.1	EU190792.1	FJ489499.1	EU190872.1	EU190834.1	–
Sagartiidae - *Sagartiogeton laceratus*	EU190748.1	EU190794.1	FJ489500.1	EU190874.1	EU190836.1	–
Stichodactylidae - *Heteractis aurora*	EU190729.1	EU190773.1	–	–	–	–
Stichodactylidae - *Heteractis aurora*	**KC812139**	**KC812160**	**KC812229**	**KC812184**	–	–
Stichodactylidae - *Heteractis aurora*	–	–	–	**KC812185**	–	–
Stichodactylidae - *Heteractis crispa*	**KC812140**	**KC812161**	**KC812230**	**KC812186**	–	–
Stichodactylidae - *Heteractis magnifica*	EU190732.1	EU190777.1	GU473361.1	EU190862.1	EU190821.1	–
Stichodactylidae - *Heteractis magnifica*	–	**KC812162**	**KC812231**	**KC812187**	–	–
Stichodactylidae - *Stichodactyla gigantea*	EU190747.1	EU190793.1	GU473347.1	EU190873.1	EU190835.1	–
Stichodactylidae - *Stichodactyla gigantea*	–	–	**KC812232**	**KC812188**	–	–
Stichodactylidae - *Stichodactyla haddoni*	–	FJ417090.1	–	FJ417089.1	–	–
Stichodactylidae - *Stichodactyla haddoni* (Australia)	–	–	**KC812233**	–	–	–
Stichodactylidae - *Stichodactyla mertensii*	**KC812141**	**KC812163**	**KC812234**	**KC812189**	–	–
Thalassianthidae - *Cryptodendrum adhaesivum*	**KC812142**	**KC812164**	**KC812235**	**KC812190**	–	**KC812214**
Thalassianthidae - *Cryptodendrum adhaesivum* (Maldives)	**KC812143**	**KC812165**	**KC812236**	**KC812191**	–	**KC812215**
Thalassianthidae - *Cryptodendrum adhaesivum* (Red Sea)	**KC812144**	**KC812166**	**KC812237**	**KC812192**	–	**KC812216**
Thalassianthidae - *Thalassianthus aster* (Australia)	–	–	**KC812240**	**KC812195**	–	**KC812219**
Thalassianthidae - *Thalassianthus aster* (Singapore)	**KC812146**	**KC812167**	**KC812241**	**KC812196**	–	**KC812220**
Thalassianthidae - *Thalassianthus hemprichii* (Palau)	–	**KC812168**	**KC812238**	**KC812193**	–	**KC812217**
Thalassianthidae - *Thalassianthus hemprichii* (Japan)	**KC812145**	**KC812169**	**KC812239**	**KC812194**	–	**KC812218**

Table 2.2. Coding of morphological features.

	Morphological character	Coding	Details
A	branched outgrowths	absent	branched outgrowths absent
		present	branched outgrowths present
B	defensive spheres	absent	defensive spheres absent
		present	defensive spheres present
C	radially arranged tentacles	absent	one tentacle per endocoel or exocoel
		present	multiple tentacles per endocoel or exocoel
D	branched tentacles	absent	simple tentacles
		four orders	tentacles with up to four orders of branches
		two orders	tentacles with up to two orders of branches
E	defensive tentacles	absent	no specialised feature of tentacle for defense
		acrospheres	swellings of tentacles dense with nematocysts
		nematospheres, band	specialised tentacles, situated in a band
		nematospheres, clusters	specialised tentacles, situated in clusters
F	pseudotentacles	absent	pseudotentacles absent
		branching in one plane	pseudotentacles branch in one plane perpendicular to body axis
		branching in multiple planes	pseudotentacles branch in multiple planes
G	defensive vesicles	absent	defensive vesicles absent
		simple, one kind	simple defensive spheres of one kind
		simple, two kinds	simple defensive spheres of two kinds
		compound	compound defensive spheres

Table 2.3 Summary of datasets analyzed.

	number of taxa	unaligned length	aligned length
12S	73	619-860	960
16S	70	270-716	781
CO3	68	243-794	780
mitochondrial	87	n/a	2,647
18S	73	626-1,825	2,017
28S	69	449-3,777	3,788
nuclear	80	n/a	5,885
all except 28S	95	n/a	4,744
all genes (no *Lybia* symbionts)	97	n/a	8,532
all genes (with *Lybia* symbionts)	101	n/a	8,638

Table 2.4 Models of evolution estimated for each dataset under Akaike and Bayesian Information Criterion.

	AIC	BIC
12S	GTR+G	GTR+G
16S	HKY+G	HKY+G
CO3	HKY+G	HKY+G
18S	GTR+G	SYM+G
28S	GTR+G	GTR+G
all genes	GTR+G	GTR+G

Table 2.5 Summary of relationships from separate analyses. Bold indicate bootstrap support at node 70 or above.

	12S	16S	CO3	mt	18S	28S	nu	all except 28S	all (no *Lybia* symbionts)	all (with *Lybia* symbionts)
Thalassianthidae monophyletic	**Y**	Y	N	N	**Y**	**Y**	Y	**Y**	**Y**	Y
Thalassianthus monophyletic	N	**Y**	N	N	N	N	N	Y	Y	Y
Cryptodendrum monophyletic	N	**Y**	N	Y	N	N	N	**Y**	Y	Y
Thalassianthidae nested with Stichodactylidae	**Y**	**Y**	**Y**	Y	Y	N	**Y**	**Y**	**Y**	**Y**
Thalassianthidae in Endomyaria	**Y**	**Y**	**Y**	Y	**Y**	N	**Y**	Y	Y	Y
Aliciidae monophyletic	N	N	N	N	N	N	N	N	N	N
Alicia monophyletic	**Y**	n/a	**Y**	**Y**	N	**Y**	**Y**	N	**Y**	**Y**
Lebrunia monophyletic	**Y**	**Y**	n/a	**Y**	n/a	N	N	**Y**	**Y**	**Y**
Phyllodiscus monophyletic	**Y**	n/a	n/a	**Y**	**Y**	N	N	Y	**Y**	**Y**
Triactis monophyletic	n/a	n/a	n/a	n/a	**Y**	**Y**	**Y**	N	N	**Y**
Aliciidae in Metridoidea	Y	Y	*Alicia* **Y**, *Triactis* and *Lebrunia* N	*Alicia* **Y**, *Triactis* and *Lebrunia* N	Y	N	**Y**	*Alicia* Y, *Triactis* and *Lebrunia* N	**Y**	**Y**
Aliciidae closely related to Boloceroididae	Y	N	*Alicia* **N**, *Triactis* and *Lebrunia* **Y**	*Alicia* **N**, *Triactis, Phyllodiscus* and *Lebrunia* Y	N	N	N	*Alicia* N, *Triactis, Phyllodiscus* and *Lebrunia* Y	**Y**	**Y**
Triactis+Phyllodiscus	n/a	n/a	n/a	N	**Y**	Y	**Y**	Y	**Y**	**Y**
(Lebrunia(Triactis+Phyllodiscus))	n/a	n/a	n/a	N	Y	N	Y	Y	**Y**	**Y**

Chapter 3: Morphological revision of Thalassianthidae

"Es ist völlig den Actinien ähnlich, allein durch die verästelten und gefiederten Tentakeln unterscheidet es sich hinlänglich davon"

(Rüppell & Leuckart, 1828, p. 5)

"It is completely similar to other anemones, except for the branching and feathery tentacles, which distinguish it sufficiently" – translated by Crowther.

Introduction

From the first description of *Thalassianthus aster* Rüppell & Leuckart, 1828*,* the type species of *Thalassianthus* Rüppell & Leuckart, 1828, the branched nature of the tentacles has been an important character to distinguish the genus from other genera (see quote above from the genus description). Through most of the 1800s, specific, generic, subfamilial, and familial diagnoses relied on the presence of branched outgrowths to adjudicate membership in this group (Rüppell & Leuckart 1828, de Blainville 1830, 1834, Quoy & Gaimard 1833, Milne Edwards & Haime 1851, Milne Edwards 1857, Klunzinger 1877, Kwietniewski 1896, 1897, Haddon 1898). For example, descriptions by Milne Edwards (Milne Edwards & Haime 1851, Milne Edwards 1857) of genera in Thalassianthinae, including *Thalassianthus, **Actinodendron*** **de Blainville, 1830***,* *Actineria* de Blainville, 1830*, **Megalactis*** **Hemprich & Ehrenberg in Ehrenberg, 1834***,* ***Phymanthus*** **Milne Edwards & Haime, 1851***,* ***Sarcophinanthus*** **Lesson, 1830***,* and

Heterodactyla Hemprich & Ehrenberg in Ehrenberg, 1834, were placed together because of the branched tentacles. However, tentacles of anemones now considered not being thalassianthids (bolded in list above) differ in branching geometry from those of Thalassianthidae (Ardelean 2003a).

Thalassianthidae comprises five nominal genera and 11 nominal species, all recorded from the Red Sea and the tropical Indo-West Pacific Ocean at depths less than 30 m. Carlgren (1949) and Rodríguez *et al*. (in Daly *et al.* 2007) considered four genera and eight species valid. However, based on my assessment of specimens and their attributes, I consider that the characters used are ineffective in separating the four genera; their definitions include terms or statements that do not allow easy comparison (Table 3.1). For example, the pedal disc is described as well developed for *Thalassianthus* and *Heterodactyla*, wide for *Actineria*, and broad for *Cryptodendrum*; it is not clear if these terms mean different things (in particular wide vs broad) or are mutually exclusive (for example, could a well developed pedal disc also be wide or broad?). Moreover, body size was used to separate the genera *Thalassianthus* and *Heterodactyla*, but was not included in the generic descriptions of *Actineria* and *Cryptodendrum.* In relation to the sphincter muscle descriptions seem similar for each genus despite different wording; sphincter muscles are listed as either weak or very weak and restricted to circumscribed. *Thalassianthus* differs from the remaining genera by apparently lacking directive mesenteries and not having a greater number of mesenteries distally than proximally. I study more specimens than any other researcher to gain a better understanding of variability of morphological characters, and therefore make informed inferences regarding generic and specific boundaries. In investigate *1) How many genera and species are valid in Thalassianthidae? 2)*

What is the morphological variation of nematospheres and branched tentacles in Thalassianthidae?

A combination of characters unites members of Thalassianthidae. Nematospheres are specialized tentacles found only in members of Thalassianthidae; the tentacles have a blunt rounded to spherical distal end, which is dense in basitrichs (Carlgren 1949). Thalassianthids also possess multiple tentacles per endocoel, a character used by Andres (1883a) to define his family Stichodactylinae, in which he included the thalassianthid genera *Cryptodendrum* and *Heterodactyla*. McMurrich (1889c) employed the feature to diagnose the Stichodactylina sub-tribe, a rank he used to group families. Families Stichodactylidae Andres, 1883a, Capneidae Gosse, 1860, Homostichanthidae Carlgren, 1900, Phymanthidae Andres, 1883a, and Thalassianthidae are all currently characterized as possessing more than one tentacle per endocoel. Stephenson (1921, p. 533) believed the possession of more than one tentacle per endocoel is a useful character to join families of subtribe Stichodactylina and "represent relationships very naturally".

Thalassianthus Rüppell & Leuckart, 1828, *Epicladia* Ehrenberg, 1834, *Heterodactyla* Ehrenberg, 1834, and *Actineria* de Blainville, 1830, all of which have branched tentacles, have been considered close relatives since the inception of Thalassianthidae, with the exception of Andres (1883a), who moved *Heterodactyla* to family Stichodactylinae, subfamily Criptodendridae with *Cryptodendrum*. Ehrenberg (1834) recognized the similarities between the monotypic Red Sea genera *Thalassianthus* and *Epicladia* and Klunzinger (1877) synonymized them. The genus *Actineria* is the thalassianthid genus least discussed in the literature; its two species were described from Tonga and NE Australia (Quoy & Gaimard 1833, Haddon & Shackleton 1893).

Heterodactyla, which was also described from the Red Sea, is similar to *Thalassianthus* in structure of the nematospheres, as was recognized by Ehrenberg (1834), Klunzinger (1877), Haddon (1898), and Stephenson (1922). Carlgren (1900) stated that *Heterodactyla* differed from *Thalassianthus* in that it had well-developed directives mesenteries connected to siphonoglyphs. *Thalassianthus* and *Heterodactyla* were separated by Carlgren (1949) based primarily on number of siphonoglyphs and directives: specimens originally classified as *Thalassianthus* possess no or many siphonoglyphs, irregularly arranged mesenteries, and no directives, whereas specimens originally classified as *Heterodactyla* possess two siphonoglyphs with directives attached and fairly regularly arranged mesenteries. *Thalassianthus* specimens are generally small and found in clusters, whereas *Heterodactyla* specimens are generally larger and found individually.

Similarities between *Thalassianthus* and *Heterodactyla* were recognized by Haddon (1898, p. 486) in his monograph describing the Actiniaria of the Torres Strait; he ended the discussion of *Heterodactyla hemprichii* Ehrenberg, 1834 with the statement "but it is possible that this will prove to be a member of the genus *Thalassianthus.*" Haddon (1898) did not explain his reasoning but this statement clearly shows that the distinction between the two genera is vague. Stephenson (1922, p. 296) had a similar view, and stated, "the presence of several siphonoglyphs in some species, and no directives, of two siphonoglyphs and two pairs of directives in others, seems no valid ground for separation". Therefore, he synonymized *Heterodactyla* with *Thalassianthus*, and stated, "I have joined *Thalassianthus* and *Heterodactyla* because I cannot find any really important differences between them." However, in his catalog, Carlgren (1949) considered both genera valid.

Cryptodendrum Klunzinger, 1877, the genus of Thalassianthidae to be described most recently, is the most distinctive and widespread genus of the family. Klunzinger (1877) first placed it in the subfamily Phyllactinae of the family Thalassianthidae. The other then-valid thalassianthid genera were classed in a different subfamily, Thalassianthinae. Subsequent placement of *Cryptodendrum* has been inconsistent; Carlgren (1900, 1949) grouped *Cryptodendrum* with *Thalassianthus*, *Heterodactyla*, and *Actineria*, while Haddon & Shackleton (1893) erected a new family for *Cryptodendrum*, family Criptodendridae. However, Haddon (1898) placed *Cryptodendrum* back into Thalassianthidae along with *Thalassianthus, Heterodactyla, Actineria, Sarcophianthus,* and *Amphiactis*.

Because the genera and species do not have clear delineation among them, I observed and compared multiple specimens to assess variability of multiple morphological characters. From my observations of thalassianthids of a range of sizes and from a range of localities, including type material, I conclude that Thalassianthidae comprises two genera and six species. I found that two characters, lobes of the oral disc and arrangement of nematospheres, are important to differentiate the genera (Table 3.2), and I found that the other characters previously used (Table 3.1) were variable or not well defined enough to delineate genera. In the following account I provide redescriptions of the genera and species I find to be valid.

Methods and materials

Collection techniques

Specimens were observed and photographed *in situ,* then collected by hand in the intertidal zone, or snorkeling or SCUBA diving for subtidal specimens. During collection, care was taken not to damage the sea anemone specimen. For the specimens that were strongly attached to the substrate, I chiseled or broke off the substrate part to which the specimen was attached. Having the specimen unharmed and attached to the original specimen meant higher rate of survival for the anemone once collected. After collection, each specimen (or lot of specimens if multiple at one site) were placed in a plastic zip lock bag with seawater then sealed and transported back to land.

Once back at facilities on land, the sea anemones were transferred to plastic dishes with fresh seawater. Further observations and photographs of live specimens, including behavior, could be done – in some instances with the aid of a dissecting microscope. If a compound microscope was available, squashes of cnidae from live material were done to view fired capsules – this allows more accurate identification of particular nematocyst types (e.g. the presence or absence of a thread to signify a *p*-mastigophore or amastigophore).

Photographing equipment

Photographs for field and lab work were taking using a Canon G10 digital camera, with a Canon underwater housing for underwater photographs. Because most species of Thalassianthidae and Aliciidae are found to depths where sunlight can penetrate, I did not need to use a strobe or flash to photograph.

Preservation

After observations and photographs of the live specimens were completed, a sub-sample of the specimen was preserved in 95–100% ethanol or RNALater (Ambion) for future DNA extraction. The pedal disc was usually the tissue sub-sampled, as this part of thalassianthid and aliciid anemones has the lowest density of zooxanthellae residing in the endoderm. The remainder of the specimen was fixed in 10% seawater formalin solution; specimens were not transferred to any other preservative. For soft-bodied anemones the property of formalin that cross-links proteins to stabilize the tissues and musculature is beneficial (and necessary for histology). Transferring sea anemone specimens to ethanol is avoided, as the ethanol dehydrates the tissues causing them to become more brittle and less acceptable for histological purposes. Formalin fixation is known to denature DNA and therefore making DNA extraction and amplification difficult, yet not impossible.

Museum (abbreviation list)

In addition to specimens that I collected from the field, specimens already part of museum collections were examined. See Appendix C for a list of the museums, and their abbreviations used in this work.

Specimen examination

External anatomy of whole specimens was examined, sometimes with the aid of a dissection microscope. External morphology examined included tentacle (types, length, number, arrangement), oral disc (diameter, shape), column (length, width, region specialization, outgrowth), pedal disc (diameter, nature), and if present, vesicles (number, position, types), and pseudotentacles (number, length, position, branching pattern). Internal morphology relating to mesenteries including number, arrangement, fertility arrangement, filament distribution, and stomata. Microanatomical details on musculature (marginal sphincter, retractor, basilar, parietobasilar) were examined from histological slides.

Histology

To observe microscopic details of muscles and mesentery details, some specimens were sectioned for histology. Longitudinal and cross sections of 5–10 µm to observe marginal sphincter muscle and mesenterial arrangement and details, respectively, were made from specimens. Before being embedded, sections were dehydrated in a series of ethanol steps, cleared with toluene, and infiltrated with paraffin. Sections were placed on slides and then stained with Gomori trichrome (Menzies 1959) or hematoxylin and eosin (Presnell & Schreibman 1997), then coverslipped with Canada Balsam.

Cnidae

Cnida preparations were made from the tentacles, mesenterial filaments, actinopharynx, nematospheres, vesicles, pseudotentacles, and column by smashing tissue with water under a coverslip. Preparations were examined using differential interference contrast (Nomarski) optics at 1,000X. For each tissue type, the length and width of at least 15 undischarged capsules were measured for each type of cnida for each specimen. Results of the cnidae survey for a species is reported as the length and width (in µm) measurement range, how many capsules were measured, and the ratio of how many specimens this capsule was found in out of all investigated. Representative cnidae were photographed using SPOT Idea digital camera (Diagnostic Instruments) attached to the compound microscope and lined to a Dell laptop computer. Nomenclature for nematocyst types follows Weill (1934) modified by Carlgren (1940a) and Mariscal (1974).

Taxonomic accounts

Thalassianthidae Milne Edwards, 1857

Diagnosis (based on Carlgren 1949; bold indicates additions, italics indicate replacements)

Thenaria (Endomyaria) with well developed *pedal disc*. Column with more or less distinct verrucae distally. **Endodermal marginal** sphincter weak, restricted or circumscribed**. Tentacles short, of three kinds: dendritic endocoelic, nematospheric endocoelic, and dendritic exocoelic**. **Oral disc diameter equal to or greater than pedal disc diameter. Fosse present**. Oral disc sometimes thrown into numerous short, cyclically arranged, permanent lobes; or sometimes not. The lobes, when present, bear on the oral side dendritic **endocoelic** tentacles which are continued on the disc and radially arranged, on the aboral side a group of nematospheres. At the margin, a cycle of dendritic exocoelic tentacles, **no more than one per exocoel**. Longitudinal muscles of tentacles absent or very weak. **Mouth small, central.** Pairs of mesenteries numerous, many *complete*, directives present or absent. Retractors well developed, diffuse, band-like. Parietobasilar muscles weak, basilar muscles well developed. Distribution of gametic tissue varying, the mesenteries of the first cycle, apart from the directives, may be fertile. Cnidom: spirocysts, basitrichs, microbasic *p*-mastigophores.

Valid genera

Thalassianthus Rüppell & Leuckart, 1828 (Type genus)

Cryptodendrum Klunzinger, 1877

KEY:

1 a) Oral disc without permanent lobes, nematospheres form a continuous band on oral disc inside exocoelic dendritic tentacles

……………………………*Cryptodendrum*

b) Oral disc with permanent lobes, nematospheres clustered on aboral side of lobes

………………………………*Thalassianthus*

Discussion

Based on molecular and morphological data, I find Thalassianthidae to be a monophyletic family in Endomyaria. All its members possess a single dendritic tentacle per exocoel, multiple nematospheric tentacles per endocoel, and multiple dendritic endocoelic tentacles. All phylogenies (Figs 2.2, 2.3, 2.6-2.11) except the CO3 (Fig 2.4) and mitochondrial (Fig 2.5) recovered a well-supported monophyletic Thalassianthidae. This indicates that nematospheres and radially arranged branched tentacles have a single origin at the most recent common ancestor of Thalassianthidae (Fig 2.13). The placement of Thalassianthidae nested in a larger clade incorporating some Stichodactylidae representatives was a consistent and well-supported result from my analyses (See Chapter 2 for further discussion).

There had been debate over the number of valid genera of Thalassianthidae for many years, Stephenson (1922) being one of the most persistent in his view that there should be fewer valid than nominal genera. I consider two of the five nominal genera valid, *Thalassianthus* and *Cryptodendrum* (Table 3.2). Some characters that had been used previously to separate the genera (Table 3.1), such as size, relate to age and/or condition of the specimen. The two genera I find valid based on morphological features are sometimes recovered as reciprocally monophyletic, such as 16S (Fig 2.3), all except 28S (Fig 2.9), combined five-gene (Fig 2.10) and combined five-gene with *Lybia* symbionts (Fig 2.11) phylogenies, but the nodes are not necessarily well-supported.

Specimens originally identified in *Thalassianthus* and *Heterodactyla* share many features; most notably, both have lobes of the oral disc. I conclude that the main purported differences between *Thalassianthus* and *Heterodactyla,* number of siphonoglyphs and directive mesenteries, are not generically important. Characters such as these don't distinguish any other genera in Actiniaria. Additionally, I found these traits to be variable among specimens studied; I therefore synonymize *Heterodactyla* with *Thalassianthus.* Similarly*, Actineria* shares characters that overlap with both *Heterodactyla* and *Thalassianthus*; according to Carlgren (1949), both *Actineria* and *Heterodactyla* supposedly possess directives, and the oral discs of *Thalassianthus* and *Actineria* are deeply folded and relatively free from tentacles compared to that of *Heterodactyla*. Because no characters set *Actineria* apart from *Thalassianthus*, I synonymize *Actineria* with *Thalassianthus*.

Cryptodendrum, the most widespread and the most distinctive genus in Thalassianthidae, is the only thalassianthid to lack permanent lobes of the oral disc, and possesses a band of nematospheres. The branching pattern of the dendritic endocoelic tentacles differs between *Cryptodendrum* and *Thalassianthus*: in *Thalassianthus*, the endocoelic dendritic tentacles have secondary projections from a main shaft, whereas in *Cryptodendrum*, the base of the tentacle is divided into multiple finger-like projections.

Thalassianthus Rüppell and Leuckart, 1828

Synonymy

Actineria de Blainville, 1830

Epicladia Ehrenberg, 1834

Heterodactlya Ehrenberg, 1834

Gender

Masculine

Diagnosis (based on Carlgren 1949, bold indicates additions, italics indicates replacements)

Small to large sized thalassianthid. Dendritic endocoelic tentacles *hand-shaped or pinnate*. Dendritic exocoelic tentacles orally-aborally flattened, and their accessory *projections* irregularly arranged. Longitudinal muscles of tentacles and radial muscles of oral disc ectodermal, the former very weak. Oral disc margin undulated **or not**, from little to two-thirds of the oral disc without tentacles. Mouth circular. Siphonoglyph number variable: **all specimens have at least two**. Directives *sometimes present*. No more mesenteries distally than proximally. **Large oral stomata, sometimes small marginal stomata present.** Parietobasilar muscles weak but forming a fold. Some *complete* and stronger imperfect mesenteries fertile.

Distribution

Red Sea and tropical Indo-West Pacific Ocean.

Valid species

Thalassianthus aster Rüppell & Leuckart, 1828 (Type species)

Thalassianthus villosa (Quoy & Gaimard, 1833)

Thalassianthus hemprichii (Ehrenberg, 1834)

Thalassianthus hypnoides (Saville-Kent, 1893)

Thalassianthus dendrophora (Haddon & Shackleton, 1893)

KEY:

1 a) Oral disc with undulating oral disc margin and folded oral disc.

……………………………....2

b) Oral disc without undulating oral disc margin and folded oral disc.

……………………………. *T. aster*

2 a) Oral disc mostly free of tentacles, lobes clavate.

……………………………………....3

b) Oral disc mostly covered with tentacles, lobes finger-like.

……………………………………....4

3 a) Approximately 200 lobes.

……………………………………….*T. villosa*

b) Approximately 300–400 lobes.

…………………………….*T. dendrophora*

4 a) Lobes small (length 8 mm or less), oral disc shallowly folded.

………………………………….*T. hemprichii*

b) Lobes large (length 10 mm or greater), oral disc deeply folded.

………………………………….*T. hypnoides*

Discussion

Thalassianthus, Heterodactyla, and *Actineria* were previously separated based on presence of directives and size of individual (Carlgren 1949). Individuals of *Thalassianthus aster* (type species of *Thalassianthus*) are small with irregular mesenterial arrangement lacking directives, and found in groups in shallow areas of the reef (Fishelson 1970). In contrast, individuals of *Thalassianthus hemprichii* (type species of *Heterodactyla*) and *Thalassianthus villosa* (type species of *Actineria*) are large and solitary with regular mesenterial arrangement with directives.

The mesentery irregularity and lack of directives are likely connected (McMurrich 1897), and loss of regularity may be due to asexual reproduction or regeneration (Stephenson 1928). Fishelson (1970) reported that *Thalassianthus aster* individuals reproduce asexually, and are found in groups in shallow, high-energy regions of the reef. Within a genus, asexual reproduction can be gained or lost multiple times, as seen by Geller & Walton (2001) in *Anthopleura*. I think this is a similar situation to the genus *Thalassianthus*; instead of large solitary individuals being classified as different genera (e.g. *Heterodactyla* or *Actineria*), I think they are just species of *Thalassianthus* that produce predominantly via sexual reproduction.

Thalassianthus is now the only genus in Thalassianthidae to possess permanent lobes of the oral disc. Based on observations of many specimens, I found that features such as size and color do not distinguish species, but features such as shape of lobes, number of lobes in similar-sized individuals, size of lobe in similar-sized individuals, and extent of folding of the oral disc do serve to distinguish six valid species.

The molecular results support the synonymy of *Heterodactyla* with *Thalassianthus*, as the specimens available of nominal species *Heterodactyla hemprichii* and *Thalassianthus aster* were found to be closely related in most phylogenies, with very short branches indicating little genetic difference between the nominal genera. The sequences available for *Thalassianthus* are from two species: *Thalassianthus aster* and *T. hemprichii*. The reciprocal monophyly of these two species was not recovered in any of the phylogenies. However, relationships within the genus were not always resolved or well-supported.

Thalassianthus aster Rüppell & Leuckart, 1828

Figs 3.1–3.4

Tables 3.3–3.4

Synonymy

Thalassianthus aster Rüppell & Leuckart, 1828, p. 5–6

Epicladia quadrangula Hemprich & Ehrenberg in Ehrenberg, 1834, p. 266

Thalassianthus senckenbergianus Kwietniewski, 1896, p. 390–391

Thalassianthus kraepelini Carlgren, 1900, p. 91–93

Type localities and specimens

Thalassianthus aster type locality and syntypes: Egypt, Red Sea, Tor; SMF 35 (6 specimens), SMNH 5632 (1 specimen).

Epicladia quadrangula type locality and syntypes: Egypt, Red Sea, Tor; ZMB 199 (2 specimens), ZMB 201 (2 specimens), ZMB 202 (4 specimens).

Thalassianthus senckenbergianus type locality and syntypes: Indonesia, Moluccas, Ternate Island; PMJ 64 (4 specimens), SMNH 4862 (1 specimen), SMF 102 (11 specimens), ZMB 3581 (5 specimens).

Thalassianthus kraepelini type locality and holotype: East Africa, Tanzania, Zanzibar, Tumbatu; ZMF C2591 (1 specimen).

Material examined

Table 3.3.

Description

Pedal disc

Circular to oval (Fig 3.1a), adherent. Diameter to 40 mm. Thick ectoderm, opaque, mesenterial insertions visible in some specimens. Beige.

Column

Cylindrical, diameter smaller than pedal disc (Fig 3.1b). Length to 60 mm. Firm, opaque, uniform in color. Longitudinal rows of non-adhesive verrucae in endocoels (Fig 3.1c). Beige. Live coloration: light purple to whitish-gray (reported for *Thalassianthus aster* by Rüppell & Leuckart [1828] and Carlgren [1900]), white, sometimes yellow (reported for *Thalassianthus aster* by Klunzinger [1877]).

Oral disc

Not folded, flat in most specimens. Diameter to 60 mm. From half to two-thirds surrounding mouth free from tentacles (Fig 3.1d). Mouth central (Fig 3.1d). Two or more siphonoglyphs. Lobes finger-shaped (Fig 3.1e): length to 7 mm, width to 4 mm. Fosse 0.5–1 mm deep. Beige in preservation. Live coloration: violet (reported for *Epicladia quadrangula* by Ehrenberg [1834]), white to white-gray with blackish or blue-gray radiations (reported for *Thalassianthus aster* by Klunzinger [1877]), mottled brown (reported for *Thalassianthus aster* by Carlgren [1900]), olive with darker radial stripes (reported for *Thalassianthus kraepelini* by Carlgren [1900]).

Tentacles

Dendritic exocoelic tentacles of variable shape (Fig 3.1f-h), but usually same morphology within an individual (pinnate with blunt filaments) (Fig 3.1f-h). Length to 3.5 mm. Nematospheres (Fig 3.1e) in clusters of up to 15, rarely with tip of bulb split. Dendritic endocoelic tentacles of variable shape (Fig 3.1i-k), even within an individual; morphology from palmate, to spindle-shaped with four neat rows of short filaments (Fig 3.1i), to thin central shaft with filaments not in rows (Fig 3.1j), to club-shaped with filaments concentrated near tip (Fig 3.1k). Multiple rows (to 5) of dendritic endocoelic tentacles communicate with a single endocoel. Beige in preservation. Live coloration of dendritic endocoelic tentacles: purple-green (reported for *Thalassianthus aster* by Rüppell & Leuckart [1828]), violet (reported for by Ehrenberg [1834]), gray to gray-blue (reported for *Thalassianthus aster* by Klunzinger [1877]), light grayish-brown (reported for *Thalassianthus aster* by Carlgren [1900]), green (reported for *Thalassianthus kraepelini* by Carlgren [1900]). Live coloration of nematospheres: grey to reddish (reported for *Thalassianthus aster* by Klunzinger [1877] and Carlgren [1900]), olive-brown or purple with green tip (reported for *Thalassianthus kraepelini* by Carlgren [1900]).

Mesenteries and internal anatomy

To five or six orders of mesenteries; lower ones complete. Directives attached to siphonoglyphs in individuals with two siphonoglyphs; individuals with more than two siphonoglyphs lack directives (Fig 3.2a). Retractor muscles diffuse (Fig 3.2a). Marginal sphincter muscle circumscribed, situated toward base of fosse on column side (Fig 3.2b).

Cnidae

Fig 3.3 and Table 3.4.

Habitat and ecology

Most recorded from shallow water, aggregated, attached to live or dead branched scleractinians (Rüppell & Leuckart 1828, Ehrenberg 1834, Fishelson 1970) or at edge of crevices (Klunzinger 1877). Fishelson (1970) reported *T. aster* multiplying by longitudinal fission in the Red Sea, which would explain the inconsistency in number of siphonoglyphs among individuals, and the occurrence of aggregations. A footnote in Carlgren (1900) stated that specimens are found at very low tide and exposed to the air.

Symbionts

Zooxanthellae in endoderm, particularly in tentacles.

Distribution

Tropical Indo-West Pacific, from Red Sea to Indonesia. Fig 3.4.

Discussion

From my observations, I conclude that many characters are variable within specimens, including tentacle morphology and nematosphere arrangement. I could not find clear distinctions among type material of the four nominal species. Characters that had been used to delineate species, such as size, color, tentacle morphology, and number of nematospheres per cluster, are variable among the individuals I observed, and I therefore synonymize

Thalassianthus kraepelini and *T. senckenbergianus* with *T. aster*. I concur with Klunzinger (1877) in his synonymy of *Epicladia quadrangula* with *T. aster*. I provide cnidae data from multiple individuals (Table 3.4), which was similar to what Carlgren (1945) reported. There was a difference in size of basitrichs of the endocoelic dendritic tentacles, and Carlgren (1945) reported microbasic *p*-mastigophores from the actinopharynx that I did not find.

Carlgren (1900) distinguished *Thalassianthus kraepelini* from other species of *Thalassianthus* based on column length, number of complete mesenteries, and color of nematospheres, stating that it was taller than *T. aster* in relation to the diameter of the body, but I observed syntypes of *T. aster* that had similar body proportions to *T. kraepelini*. I counted a similar number of mesenteries (5 orders) in the holotype of *T. kraepelini* and in syntypes of *T. aster* (5–6 orders), and observed that mesenteries of the lower 1–3 orders were complete in all specimens of both nominal species. Carlgren (1900) also recorded that *T. kraepelini* had nematospheres of the same color as the dendritic endocoelic tentacles, different to what had been recorded in *T. aster*, which had contrasting colors of nematospheres and dendritic endocoelic tentacles. However, because color is not considered important for species distinctions in sea anemones (Stephenson 1918), and individuals of *Cryptodendrum adhaesivum* vary in color, this is not a good character for species delineation.

Thalassianthus senckenbergianus was separated from the other *Thalassianthus* species by Kwietniewski (1896) based on the palmate dendritic endocoelic tentacles. In contrast, *T. aster* and *E. quadrangula* possess tentacles that have a central shaft with lateral projections (Kwietniewski 1896, 1897). Carlgren (1900) noted that the tentacles of *T. kraepelini* reminded him of those of *T. senckenbergianus*. I did observe some *T. senckenbergianus* individuals with palmate tentacles, but some of the syntypes also have pinnate dendritic endocoelic tentacles, similar to what was described for *T. aster* and *E. quadrangula*. Palmate and pinnate tentacles of were observed in a single individual.

Epicladia quadrangula was described as possessing dendritic endocoelic tentacles that are spindle-shaped, with four near rows of short projections arranged regularly so that the cross-section of a tentacle is square. Single individuals (including a syntype) possess both spindle-shaped and feather-shaped dendritic endocoelic tentacles. *Thalassianthus senckenbergianus* was separated from the other *Thalassianthus* species based on fewer nematospheres (Kwietniewski 1896, 1897). This character is also highly variable, the number of nematospheres observed in the syntypes of *T. kraepelini, T. aster, T. senckenbergianus,* and *E. quadrangula* overlapping.

Thalassianthus hemprichii (Ehrenberg, 1834)

Figs 3.5–3.8

Tables 3.5–3.6

Synonymy

Heterodactyla hemprichii Ehrenberg, 1834, p. 266

Type localities and specimens

Heterodactyla hemprichii type locality: Egypt, Red Sea, Sinai Peninsula, near Sharm al-Sheikh; no type specimens.

Material examined

Table 3.5.

Description

Pedal disc

Irregular shape, adherent. Thick ectoderm, opaque, mesenterial insertions not visible. Live: white, with bright purple spots on limbus (Fig 3.5a), diameter to 120 mm. Preserved: beige, diameter to 70 mm.

Column

Cylindrical, flares slightly from distal to proximal end. Length to 80 mm. Firm, opaque, mesenterial insertions not visible. Longitudinal rows of non-adhesive verrucae in endocoels of flared region (Fig 3.5b). Live: pale red, pink with carmine spots, yellow, white distally to gray proximally. Preserved: beige.

Oral disc

Circular, mostly flat (Fig 3.5c), but can be deeply folded; much wider than pedal disc. In living individuals, diameter to 300 mm; in preserved individuals, diameter to 140 mm. Most of oral disc covered with tentacles; small area around mouth free of tentacles. Most individuals with two siphonoglyphs (Fig 3.5d) (one individual observed with three), directives attached to siphonoglyphs. Finger-shaped lobes near margin of oral disc (Fig 3.5e); fosse approximately 1 mm deep. Live: gray-blue, white, brown, green. Preserved: beige.

Tentacles

Dendritic exocoelic tentacles robust, variable morphology (Fig 3.5f-g), most with wide central shaft with short, blunt projections on lateral sides; some with opposite branching. Length to 20 mm. Some nematospheres with split bulbs, some with multiple spheres per stalk, most simple bulb on stalk, to 37 per lobe, diameter to 1 mm (Fig 3.5h). Dendritic endocoelic tentacles numerous, arranged in neat radial rows on lobes and oral disc; in most individuals long, narrow shaft bearing scattered fine projections along length (Fig 3.5i-k), but some individuals with bushy, club-shaped, or bifurcate/trifurcate dendritic endocoelic tentacles. Live: Dendritic endocoelic tentacles gray, purple, gray-red with white tips, brown, rusty red (Fig 3.5b-e,h), lemon-yellow with brown core, with some endocoels with lighter tents. Nematospheres bright amethyst with green apex (Fig 3.5e,h). Dendritic exocoelic tentacles: pink, gray-red. Preserved: all tentacles beige.

Mesenteries and internal anatomy

Mesenteries to 7 orders; those of lower orders complete. Sexes separate. Retractor muscles diffuse (Fig 3.6a,b). Directives attached to siphonoglyphs (Fig 3.6a). Marginal sphincter muscle small, circumscribed, positioned near base of fosse on column side (Fig 3.6c-h).

Cnidae

Fig 3.7 and Table 3.6.

Habitat and ecology

Most individuals with pedal disc attached deep within crevice, column extended so oral disc lies over exposed surface. If disturbed, can retract column and pull oral disc into crevice. Occur in shallow reefs to 10 m, most in 0–3 m.

Symbionts

Zooxanthellae in endoderm, particularly in tentacles.

Distribution

Tropical Indo-West Pacific, from Red Sea to Kiribati. Fig 3.8.

Discussion

My observations correspond closely to the original description and other more recent accounts of *Heterodactyla hemprichii*, including information regarding size, mesentery arrangement, marginal sphincter muscle, and coloration. I provide information regarding the cnidom for this species that was lacking from published literature. Compared to other species of Thalassianthus, the oral disc of *T. hemprichii* is relatively flat, with only gentle waves of the margin compared to the deep undulations of *T. hypnoides*, for example. The tentacles of *T. hemprichii* are arranged neatly in endocoelic rows on the oral disc, so that it is possible to trace an endocoel from the margin to the mouth in either a live or preserved individual. Tentacles cover more of the oral disc than I observed in any other species of *Thalassianthus*.

Thalassianthus hypnoides (Saville-Kent, 1893)

Figs 3.9–3.11

Tables 3.7–3.8

Synonymy

Heterodactyla hypnoides Saville-Kent, 1893, p. 148–149

Type localities and specimens

Heterodactyla hypnoides type locality: Australia, Queensland, Great Barrier Reef, opposite Cape Flattery; no type specimens.

Material examined

Table 3.7.

Description

No live material was available; live observations from Saville-Kent (1893).

Pedal disc

Nearly circular or oval (Fig 3.9a), diameter to 65 mm. Thick ectoderm, opaque, mesenterial insertions not visible. Preserved: beige.

Column

Cylindrical (Fig 3.9b). Length to 55 mm. Firm, thick, opaque. Non-adhesive verrucae in longitudinal endocoelic rows. Live: stone gray to pale green. Preserved: beige.

Oral disc

Folded, margin undulate (Fig 3.9c). Diameter to 140 mm. Lobes large, length to 20 mm, width to 6 mm (Fig 3.9c). Tentacles cover approximately ¾ of oral disc, area around central mouth free of tentacles. Two or three siphonoglyphs. Live: stone gray to pale green. Preserved: beige.

Tentacles

Dendritic exocoelic tentacles robust, with thick central shaft bearing blunt lateral projections (Fig 3.9e), width to 5 mm, length to 20 mm. Small individuals with 3–7 nematospheres per lobe, large individuals with 6–27 per lobe (Fig 3.9d). Dendritic endocoelic tentacles with narrow central shaft and fine projections scattered on distal half of shaft (Fig 3.9f), some bifurcate or trifurcate, width to 2 mm, length to 20 mm. Live: nematospheres amethyst (no green tip), dendritic endocoelic bright green. Preserved: all tentacles beige.

Mesenteries and internal anatomy

To six or seven orders or mesenteries. Directives attached to siphonoglyphs (Fig 3.9g). Sexes separate. Large oral and small marginal stomata. Marginal sphincter muscle small, near base of fosse on column side (Fig 3.9h).

Cnidae

Fig 3.10 and Table 3.8.

Habitat and ecology

From intertidal to 20 m depths in reefal areas.

Symbionts

Zooxanthellae in endoderm, particularly in tentacles.

Distribution

Tropical Pacific Ocean from Great Barrier Reef to Indonesia. Fig 3.11.

Discussion

Saville-Kent (1893) separated this species from *Heterodactyla hemprichii* based on the number of nematospheres per lobe: *Thalassianthus hypnoides* with 20–30, *T. hemprichii* with 10 or fewer. I found that the number of nematospheres per lobe is highly variable within and between individuals, some specimens of *T. hemprichii* having as many as 37. The difference between these two species is the deep and convoluted oral disc folding in *T. hypnoides*, the regular, neatly arranged tentacles in *T. hemprichii*, and the smaller lobes relative to oral disc diameter in *T. hemprichii*. I provide cnidae measurements for *T. hypnoides* for the first time. Although the cnidoms of *T. hypnoides* and *T. hemprichii* are similar, *T. hemprichii* possess a small size basitrich in the nematosphere and endocoelic dendritic tentacles that is not present in *T. hypnoides*.

Thalassianthus villosa (Quoy & Gaimard, 1833)

Figs 3.12–3.14

Tables 3.9

Synonymy

Actineria villosa Quoy & Gaimard in de Blainville, 1830, p. 288

Type specimens and localities

Actineria villosa type locality and holotype: Tonga; MNHN 2387 (1 specimen).

Material examined

Only holotype available, see section above.

Description

Pedal disc

Circular to oval; adherent. Thick, opaque, mesenterial insertions not visible. Preserved diameter to 65 mm, cream/beige (Fig 3.12a).

Column

Cylindrical, transversely furrowed (Fig 3.12e), flared at both ends (Fig 3.12b). Non-adhesive verrucae in longitudinal endocoelic rows. Live: purplish-grey (Quoy & Gaimard 1833). Preserved: cream/beige, length to 60 mm.

Oral disc

Flat (Fig 3.12c), margin sometimes folded. Diameter to 80 mm. Approximately 200 lobes, to 10 mm long, project from endocoels near margin (Fig 3.12d), alternately larger and smaller. Most of oral disc free from tentacles (Fig 3.12c). Live diameter to 120 mm, greyish around mouth (Quoy & Gaimard 1833). Preserved: cream.

Tentacles

Exocoelic dendritic tentacles 1 mm length, 2 mm width. Nematospheres 12–40 per lobe; either project directly from lobe, or part of grape-like cluster attached to lobe; as many as 6 per grape-like cluster (Fig 3.12d). Endocoelic dendritic tentacles on oral side of lobe (Fig 3.12d,f), small pine-cone shape, length 1 mm. Multiple dendritic tentacles per endocoel, radially arranged, to 10 tentacles across coelenteric space. All tentacles cream in preservation. Live tentacles white, nematospheres yellow (Quoy & Gaimard 1833).

Mesenteries and internal anatomy

200 pairs of mesenteries; same number distally as proximally.

Cnidae

Fig 3.13 and Table 3.10.

Symbionts

Zooxanthellae in endoderm, particularly in tentacles.

Distribution

Tonga (Fig 3.14). Records from Japan in Uchida & Soyama (2001) are doubtful; they likely refer to the aliciid *Phyllodiscus semoni*; see discussion of that species.

Discussion

The only specimen available for observation was the holotype, which matched closely to published details of morphological features of the species. The tentacle morphology and internal anatomy were hard to determine because the specimen had not been preserved well.

Thalassianthus dendrophora (Haddon & Shackleton, 1893)

Figs 3.15–3.16

Synonymy

Actineria dendrophora Haddon & Shackleton, 1893, p. 123

Type localities and specimens

Actineria dendrophora type locality and inferred syntype: Australia, Queensland, Torres Strait, Murray Islands, Mer Island; one histological slide at Museum of Zoology, Lund University, Sweden (no catalog number).

Material examined

Only one slide available, see section above.

Description

The description is based on published accounts from Haddon & Shackleton (1893) and Haddon (1898).

Pedal disc

Slightly expanded (Fig 3.15a) compared to width of column, cream.

Column

Thick layer of mesoglea. Verrucae in longitudinal rows corresponding to exocoels. Pinkish, length to 70 mm.

Oral disc

Smooth, wide, 125 mm diameter. Mouth on cone, pale. Most of oral disc free from tentacles. Two siphonoglyphs. Margin with non-permanent folds, and 300–400 endocoelic lobes (Fig 3.15a,c), lobe length 10 mm. Translucent pinkish-brown with green sheen.

Tentacles

Dendritic exocoelic tentacles length 1 mm, width 2 mm. Nematospheres 12–40 per lobe (Fig 3.15b); either project directly or part of grape-like cluster from lobe; as many as 6 per grape-like cluster. Dendritic endocoelic dendritic tentacles small pine-cone shape, length 1 mm. All tentacles cream in preservation. Live tentacles white or same color as oral disc, nematospheres yellow or pink with cream tip.

Mesenteries and internal anatomy

Marginal sphincter muscle circumscribed to restricted, palmate (Fig 3.15c,d).

Cnidae

Not available.

Habitat and ecology

Surface of reef.

Symbionts

Zooxanthellae in endoderm, particularly in tentacles.

Distribution

Torres Straits, Australia (Fig 3.16).

Discussion

Thalassianthus dendrophora remains valid. However, it is possible it is synonymous with *T. villosa*. Haddon & Shackleton stated, “This species is quite distinct from the only hithero described species of the genus *A. villosa* (Quoy et Gaim.)” (1893, p. 123), although they did not specify how it differed. The main difference I can deduce between the species is the number of lobes. Kwietniewski (1897) commented that the number of lobes in *Thalassianthus senckenbergianus* increases with size of the individual. I infer that this is also true for *T. villosa* and *T. dendrophora*. The pedal disc diameter of *T. dendrophora* was not given. However, both the oral disc diameter and column length of *T. dendrophora* (125 mm, 70 mm, respectively) are larger than they are in *T. villosa* (80 mm, 60 mm, respectively). It is possible that the larger number of lobes recorded for *T. dendrophora* is because it is a larger individual, not because it is a different species to *T. villosa*.

This species was reported by Haddon (1898, p. 487) to undergo longitudinal fission, similar to what has been reported for *Thalassianthus*: “I could not observe in the living animal the symmetry and multiples of radii, partly because of the incipient fission, but more particularly, as is usual with these species with dendritic tentacles, on account of their apparent irregularity”. The specimen in Haddon’s (1898) drawing (Fig 3.15a) had two mouths.

Cryptodendrum Klunzinger, 1877

Synonymy

Cryptodendrum Klunzinger, 1877

Stoichactis Doumenc, 1973

Gender

Neuter

Diagnosis (modified from Dunn 1981, additions in bold)

Thalassianthid with medium to large body. Oral disc not lobed, densely covered with many short tentacles. **Inside single row of dendritic exocoelic tentacles, a continuous, broad band of nematospheres. Short dendritic endocoelic tentacles, hand-shaped, radially arranged occupy the inner greater part of the oral disc**. **One to three well developed siphonoglyphs.** Mesenteries numerous, more at margin than base.

Distribution

Indo-West Pacific.

Valid species

Cryptodendrum adhaesivum Klunzinger, 1877 (Type species)

Discussion

Cryptodendrum is clearly separated from *Thalassianthus*, based on a combination of characters. In *Cryptodendrum*, the nematospheres form a distinct, uninterrupted band close to the margin of the oral disc; in *Thalassianthus*, the nematospheres occur in clusters on the aboral sides of the permanent lobes of the oral disc. The separation of the genera based on molecular sequences was not as clear, with reciprocal monophyly of *Thalassianthus* and *Cryptodendrum* rarely recovered or well supported. The *C. adhaesivum* sequences were recovered as each others' closest relatives in 16S (Fig 2.3), mitochondrial (Fig 2.5), all except 28S (Fig 2.9), and combined five-gene phylogenies (Figs 2.10, 2.11), but the monophyly was not always well supported.

Cryptodendrum adhaesivum Klunzinger, 1877

Figs 3.17–3.25

Tables 3.12–3.14

Synonymy

Cryptodendrum adhäsivum Klunzinger, 1877, p. 86

Stoichactis digitata Doumenc, 1973, p. 175, 194–198, Fig 4, Pl V Fig A–B

Type localities and specimens

Cryptodendrum adhaesivum type locality and syntypes: Egypt, Red Sea, Koseir; ZMB 1877 (2 specimens), SMNH 1159 (1 piece).

Stoichactis digitata type locality and syntypes: French Polynesia, Tuamotu Archipelago, Gambier Islands; MNHN 2038 (1 specimen); French Polynesia, Marquesas Islands, MNHN 2540 (1 specimen).

Material examined

See Table 3.12.

Description

Pedal disc

Irregularly shaped (Fig 3.17a), conforms to substrate, adherent. Thick, opaque, mesenterial insertions not visible. Live: diameter 40–90 mm, highly variable in color. Of specimens examined, cream with bright orange flecks (KUDIZ 3027), light beige (ZRC Cni 0332). Preserved: diameter to 40 mm, beige, furrowed.

Column

Column flares distally and proximally (Fig 3.17b). Length to 70 mm. Firm, opaque, mesenterial insertions not visible. Longitudinal rows of non-adhesive verrucae (Fig 3.17c), verruca width 1–2 mm. Color variable. Live: pinkish cream with bright orange flecks and bright orange verrucae (KUDIZ 3027, Fig 3.18b), beige, darker at distal end, gradually lightens toward proximal end to honey-beige (ZRC Cni 0332), yellowish lower column with maroon dots, fuchsia upper column with yellow verrucae (Dunn 1981), white with orange flecks below and orange verrucae above (Dunn 1981), whiteish with red, brown, or yellow-brown spots or flecks (Klunzinger 1877), yellowish white with irregular blotches of pale olive green or dull orange (Haddon 1898). Preserved: beige to dark green, transversely ridged from contraction.

Oral disc

Circular, flat when expanded. When disturbed, can be cup-shaped and folded (Fig 3.19). Margin crenulated. Most of oral disc covered with tentacles, only small area immediately surrounding circular, central mouth free from tentacles (Fig 3.18a,c). Nearly all individuals with two diametrically opposed siphonoglyphs (Fig 3.18c) (one specimen examined with only one siphonoglyph and Doumenc [1973] reported an individual with three siphonoglyphs). Fosse approximately 1 mm deep. Live: diameter up to 600 mm, white, mouth white tinged with bright yellow (KUDIZ 3027, Fig 3.18a,c). Preserved: diameter approximately 90 mm, dark beige.

Tentacles

Dendritic exocoelic tentacles with wide main shaft (diameter 1–2 mm) and finer projections distally, length to 10 mm. Multiple spherical endocoelic nematospheres per endocoel; up to 10 nematospheres across endocoel. Nematospheres packed together to form an uninterrupted band up to 15 mm wide just inside ring of exocoelic tentacles (Fig 3.17e,f). Individual nematospheres of 1 mm attach directly to oral disc. Dendritic endocoelic tentacles densely packed in rows in endocoels, cover most of oral disc. Dendritic endocoelic tentacles of endocoels smaller than those of exocoels; average length of dendritic endocoelic tentacles 3 mm. Dendritic endocoelic tentacles all palmate, but variable within individual. Some fields of dendritic endocoelic tentacles reach closer to the mouth than others (Fig 3.17d). All tentacles very adhesive in life. Live: dendritic exocoelic tentacles brown, nematospheres green to brown, dendritic endocoelic tentacles dark green (KUDIZ 3027, Fig 3.18). Dendritic exocoelic tentacles and nematospheres brown with yellow/cream tips, dendritic endocoelic tentacles dark green with bright green tips (ZRC Cni 0332). Preserved: all beige (Fig 3.17e,f) or dark green or brown (Fig 3.17b,d).

Color can be in wide range. In general, endocoelic branched tentacles in contrast to color of nematospheres (Fig 3.19), although may be same color (Fig 3.20e). Coloration of live specimens observed in Egypt and the Maldives and depicted in field guides are in Table 3.13.

Mesenteries and internal anatomy

To five or six orders, all with filaments. Lower orders complete. Directives attached to siphonoglyphs. All may be fertile, except directives. Sexes separate. Retractor muscles diffuse

(Fig 3.21). Marginal sphincter muscle endodermal, circumscribed, situated near base on column side of fosse (Fig 3.22).

Cnidae

See Fig 3.23 and Table 3.14.

Habitat and ecology

Attached to hard substrate, from intertidal to 25 m. Most individuals with pedal disc attached in deep crevice, in cryptic location such as under coral overhangs or bommies. Oral disc spreads out over surface (Fig 3.19e). Once disturbed, can contract column to pull oral disc down into crevice (Fig 3.18, 3.19a-d,f). Common inhabitant of shallow reefs in Red Sea, Egypt.

Symbionts

Cryptodendrum adhaesivum is the only thalassianthid to form symbiotic associations with anemonefish (Fig 3.20e,f), in this case *Amphiprion clarkii*; this species of anemonefish forms associations with other sea anemones of the families Actiniidae and Stichodactylidae (Fautin & Allen 1992). The shrimp *Thor discosomatis* and *Periclimenes affinis* have been reported as symbionts of *C. adhaesivum* (see Fricke 1967, Fishelson 1970, Fransen 1997). Humes (1982) reported the copepod species *Doridicola magnificus* and *Lambanetes gemmulatus* living symbiotically with *C. adhaesivum*. Zooxanthellae dense in the endoderm of tentacles.

Distribution

Indo-West Pacific, from Red Sea to French Polynesia. Fig 3.24.

Discussion

Individuals of *Cryptodendrum adhaesivum* are distinctive because they lack lobes, but possess both branched tentacles and nematospheres, the latter forming a distinct band close to the margin of the oral disc. This band of nematospheres is usually a contrasting color to the other tentacles. This species has been given the common name of pizza anemone (Sprung & Delbeek 1997, Fenner 1998, Fosså & Nilsen 1998, Sprung 2001, Baine & Harasti 2007). The sticky tentacles lead to the species epithet *adhaesivum*, which has been rendered to the common name, the adhesive sea anemone (Fautin & Allen 1992, Allen & Steene 2002, Gosliner *et al*. 1996, Weinberg 1996, Fenner 1998). Klunzinger (1877) commented on the resemblance of this species to *Discosoma giganteum* (a synonym for *Stichodactyla haddoni* and *S. gigantea*). Both *S. haddoni* and *S. gigantea* have a large oral disc (which may be undulated) and covered in tentacles. However, species of *Stichodactyla* have only one type of simple (not branched) tentacle.

In his publication on sea anemones from the Torres Strait in Australia, Haddon (1898) discussed how the marginal sphincter muscle from specimens observed by Kwietniewski (1896) differed from those he observed, and suggested that this may be a character to separate species. Carlgren (1950) disagreed with Haddon (1898) that the differences in sphincter muscle in *Cryptodendrum adhaesivum* were distinctive enough to separate species. The variation in marginal sphincter muscles from the literature (Fig 3.25) and specimens I observed (Fig 3.22) is shown. The variation among these relates to the extent of the mesoglea through the sphincter muscle. In the published literature, the sphincter muscle figured in Kwietniewski (1896, Fig 3.25a), Carlgren (1950, Fig 3.25c), and Dunn (1981, Fig 3.25d) have a longer shaft of mesoglea infiltrating into the endodermal sphincter muscle, compared to the muscle figured in Haddon

(1898, Fig 3.25b). I observed similar amounts of variation in marginal sphincter morphology among specimens I investigated (Fig 3.22b,d,f). The placement of the marginal sphincter muscle was consistent through the literature and my observations (Fig 3.22a,c,e): at base of fosse, slightly toward the column side of the fosse.

Cryptodendrum adhaesivum has the widest known distribution of all thalassianthids, although, across the range, there is very little morphological variation of the species except for color (Fig 3.19, Fig 3.20, Table 3.13). Within a single reef in Dahab, Egypt, I observed five individuals all differently colored (Fig 3.19), so there appears to be no geographical pattern of coloration.

Conclusions

In this study, I performed a family-level revision to address the question of how many valid species comprise Thalassianthidae, and to provide an in-depth morphological description of their branched outgrowths and defensive spheres. To do so, I compared more thalassianthid specimens than any other study, and find two genera and six species to be valid. I find the possession of lobes and nematosphere morphology and placement to be important characters to aid in identification of genera and species in Thalassianthidae. Thalassianthids occur over a large geographic distribution, and I was unable to cover the whole range with my fieldwork. Despite this, I sampled more specimens and species of this family than any study to date. Out of all of the thalassianthids, *Cryptodendrum adhaesivum* has the widest distribution, while *Thalassianthus dendrophora* and *T. villosa* have been found from just one locality each. Further fieldwork in areas such as NE Australia, the only recorded locality of both *T. dendrophora* and *T. villosa*, will likely provide more evidence regarding the validity of these species.

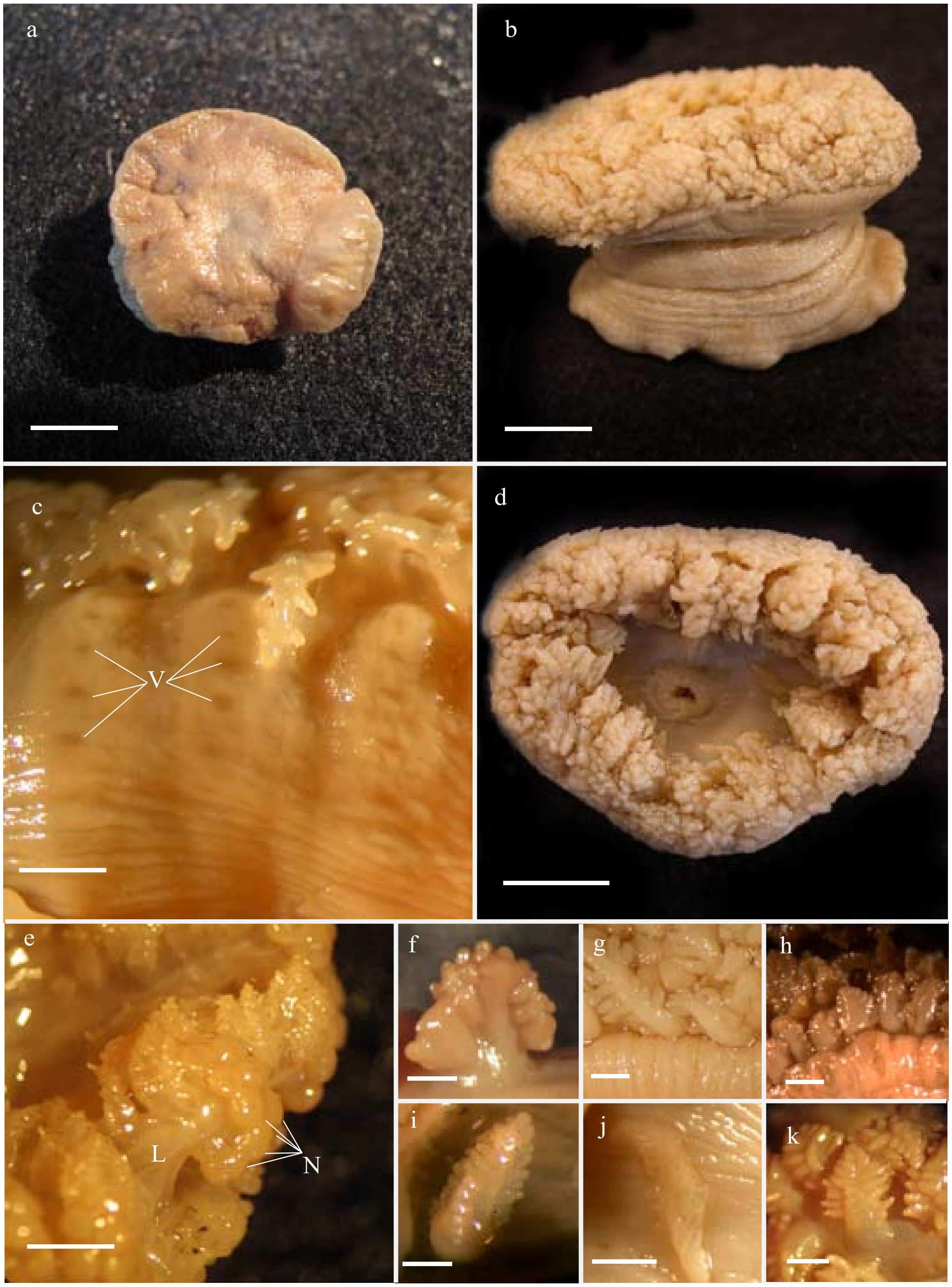

Fig 3.1. *Thalassianthus aster.* a) pedal disc, SMNH 111221, scale bar = 10 mm b) side-on view of syntype SMNH 5632, scale bar = 10 mm c) longitudinal rows of verrucae, SMNH 111220, scale bar = 2 mm d) oral disc of syntype SMNH 5632, scale bar = 10 mm e) lobe, SMNH 111220, scale bar = 3 mm f-h) exocoelic dendritic tentacles, scale bar = 1 mm f) SMNH 111220 g) SMNH 5632 h) LO 891/3021 i-k) endocoelic dendritic tentacles, scale bar = 1 mm i) ZMB 202 j) SMNH 5632 k) SMNH 111221. Figure legend: L = lobe, N = nematosphere, V = verrucae.

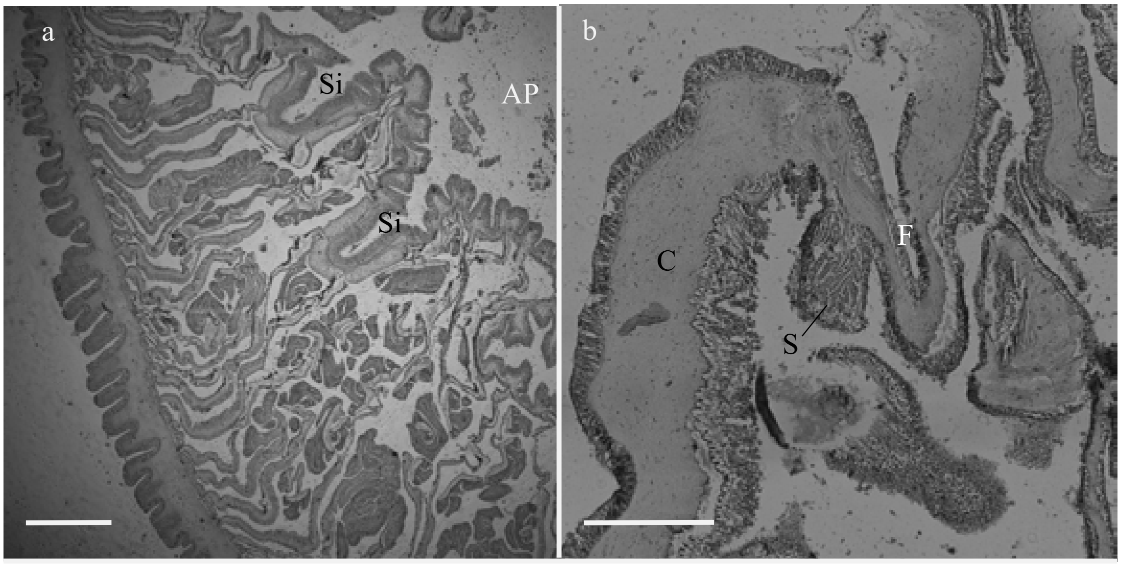

Fig 3.2. *Thalassianthus aster*. Histological slides of a) diffuse longitudinal retractor and b) marginal sphincter muscles from RMNH Coel 39759. a) Note multiple siphonoglyphs. Scale bar = 10 mm. Figure legend: AP = actinopharynx, C = column, F = fosse, S = sphincter muscle, Si = siphonoglyph.

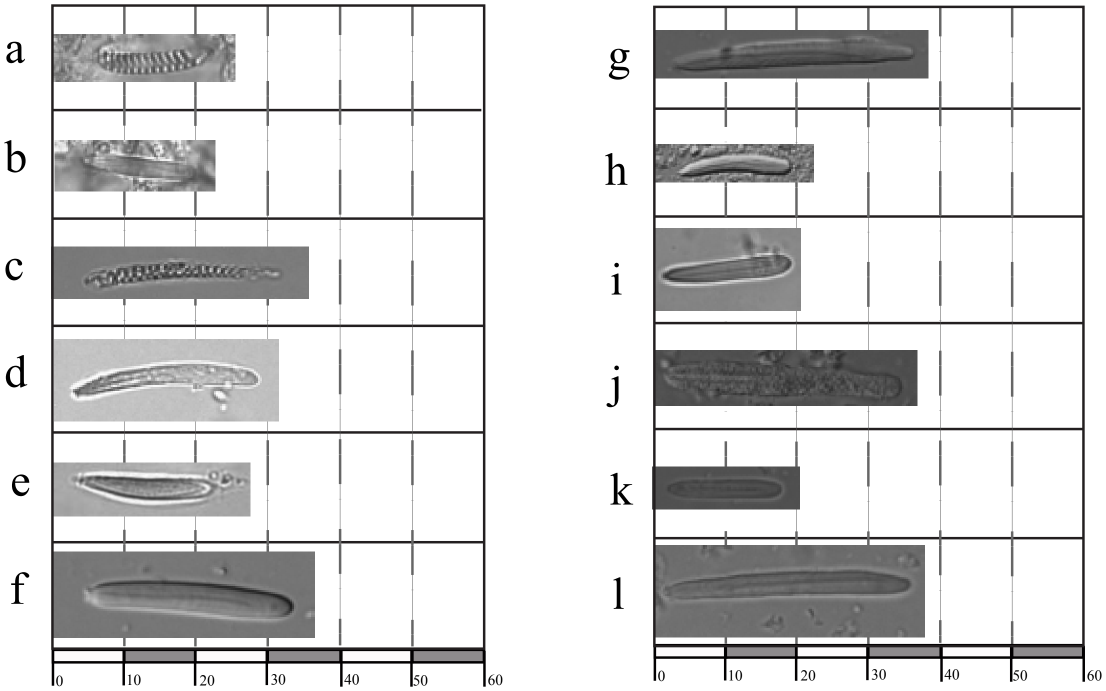

Fig 3.3. Cnidae from various tissues of *Thalassianthus aster*. Lowercase letters correspond to measurements in Table 3.4. Tissue source: a,b) exocoelic tentacles c,d) nematospheres e) endocoelic branched tentacles f) actinopharnx g) oral disc i-k) mesenterial filaments. Scale bar in micrometers.

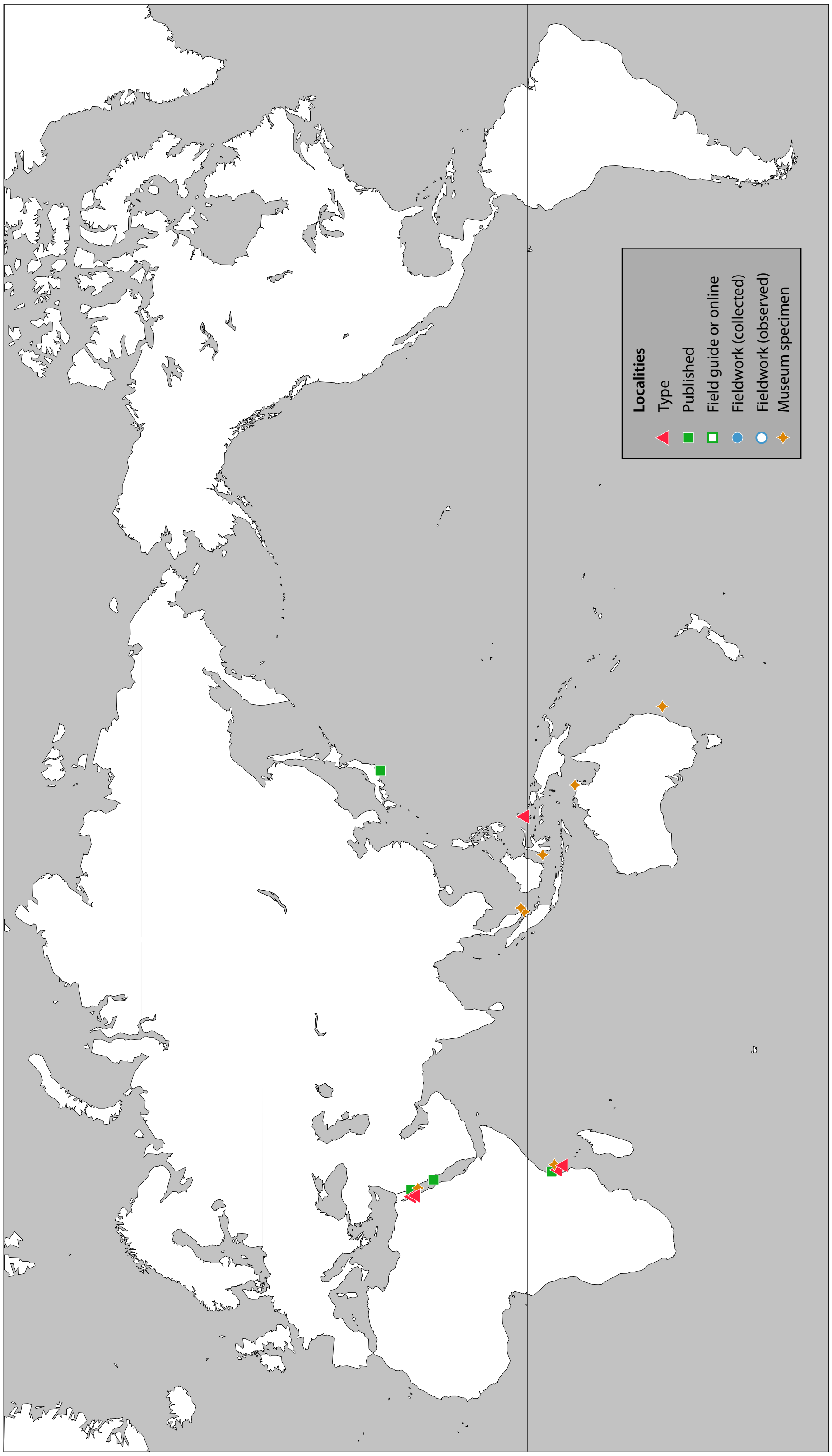

Fig 3.4. Localities of *Thalassianthus aster*.

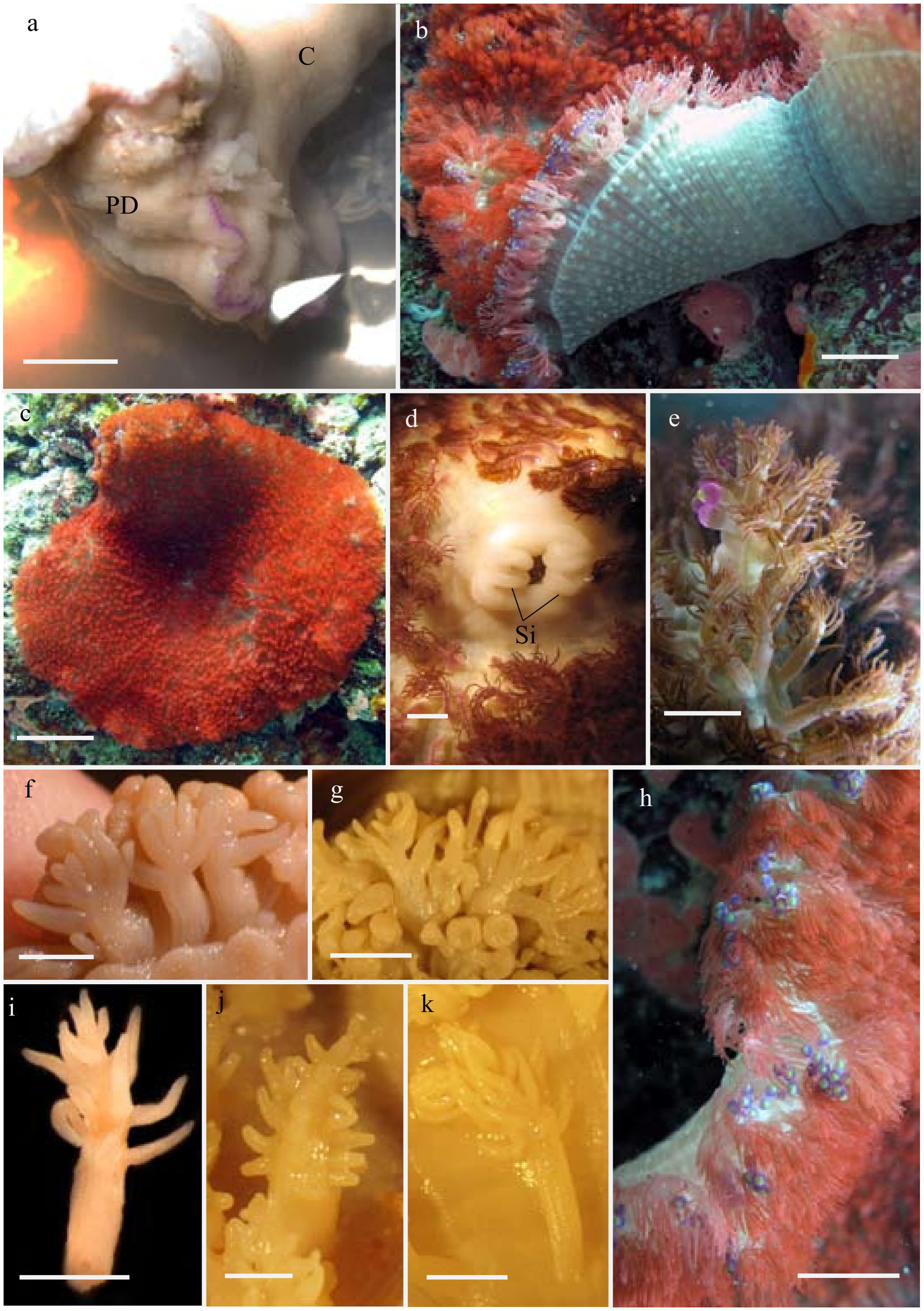

Fig 3.5. *Thalassianthus hemprichii*. a-e,h,k) KUDIZ 3165 f,i) USNM 53281 g,j) RMNH Coel 39745. a) limbus and pedal disc , scale bar = 10 mm b) non-adhesive verrucae on column, scale bar = 10 mm c) flat oral disc covered with tentacles, scale bar = 30 mm d) mouth with two siphonoglyphs, scale bar = 10 mm e) lobe of oral disc, scale bar = 2 mm f-g) exocoelic dendritic tentacles, scale bar = 1 mm h) margin of oral disc with nematospheres clustered on lobes, scale bar = 10 mm i-k) endocoelic dendritic tentacles, scale bars = 1 mm. Figure legend: C = column, PD = pedal disc, Si = siphonoglyph.

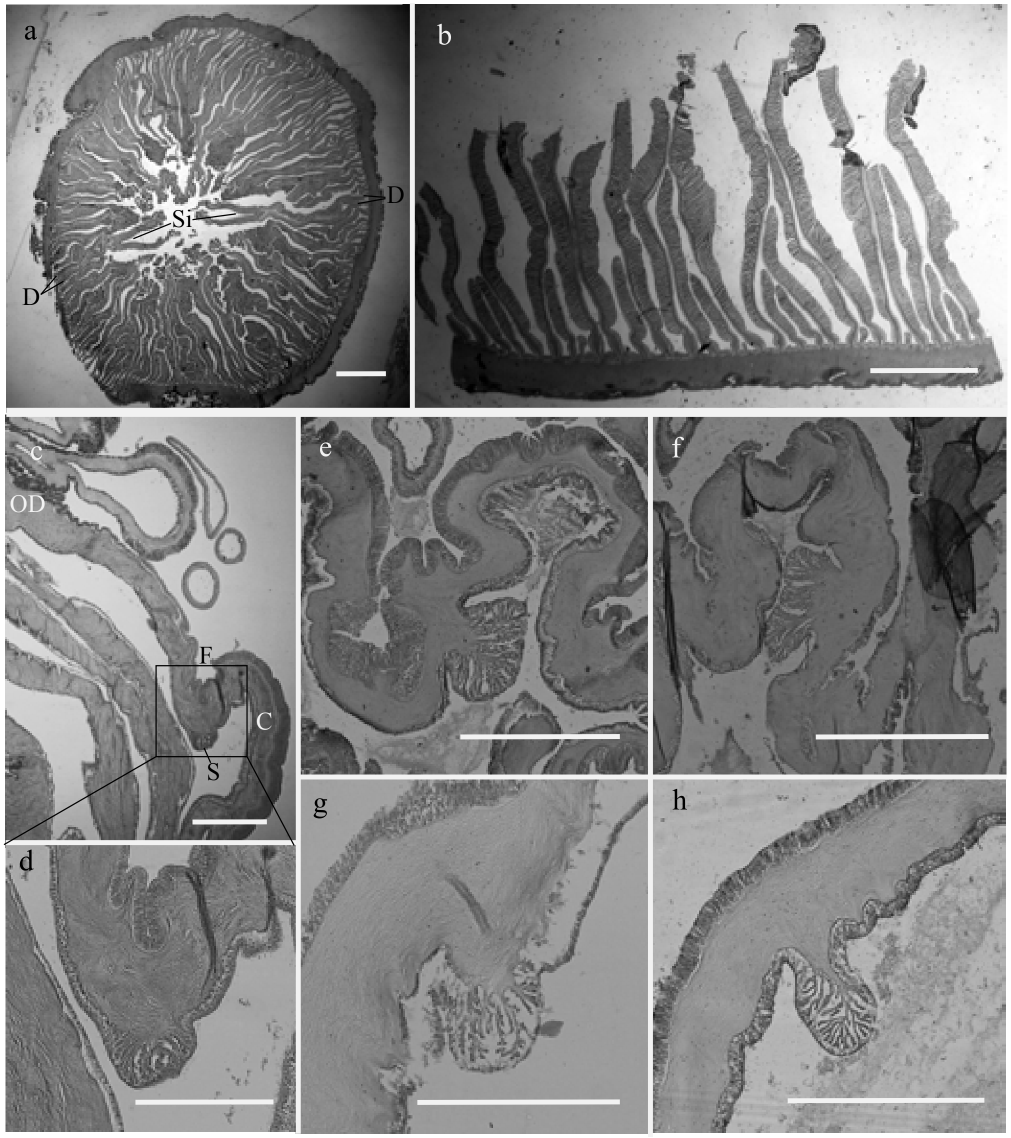

Fig 3.6. *Thalassianthus hemprichii.* a-b) Cross-section showing diffuse longitudinal retractor muscles of a) RMNH Coel 39765 and b) CAS 050115. Longitudinal section showing various marginal sphincter muscles from c,d) CAS 050115 e) RMNH Coel 39776 f) KUDIZ 3165 g) KUDIZ 1155 h) RMNH Coel 39765. Scale bars = 10 mm. Figure legend: C = column, D = directive mesentery, F = fosse, OD = oral disc, S = marginal sphincter muscle, Si = siphonoglyph.

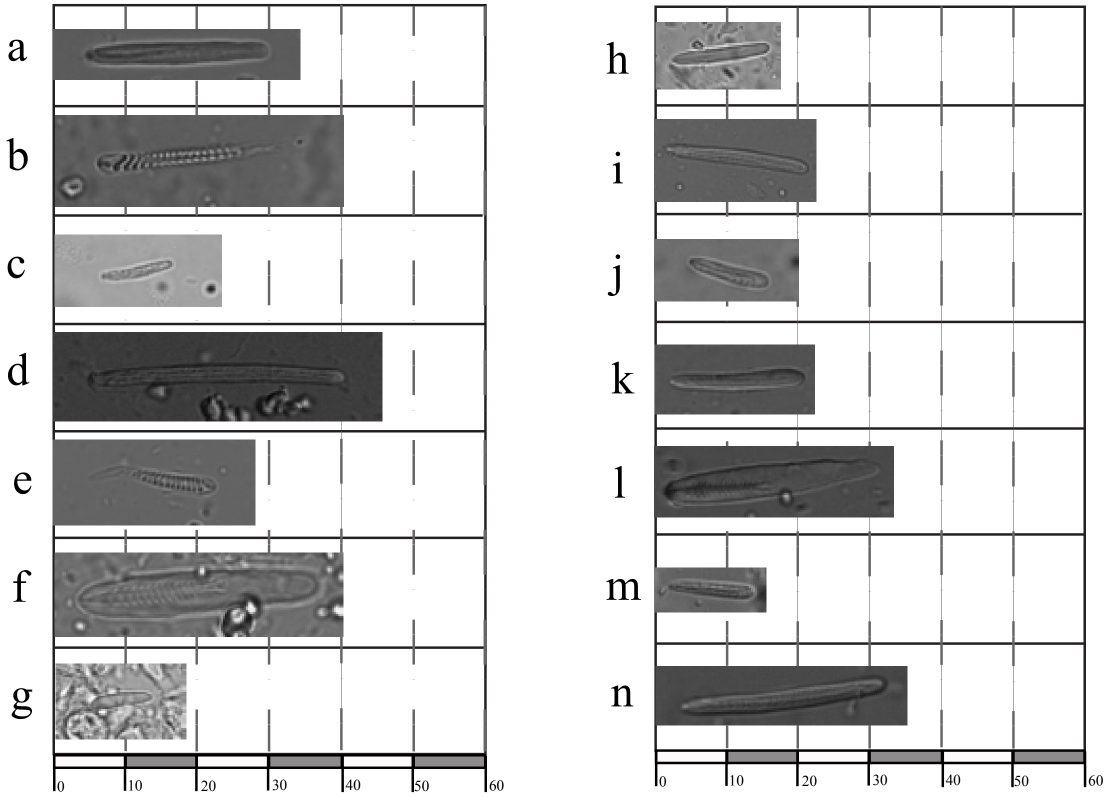

Fig 3.7. Cnidae from various tissues of *Thalassianthus hemprichii*. Lowercase letters correspond to measurements in Table 3.6. Tissue source: a) exocoelic tentacles b-d) nematospheres e-h) endocoelic branched tentacles i) actinopharnx j) oral disc k) column l-n) mesenterial filaments. Scale bar in micrometers.

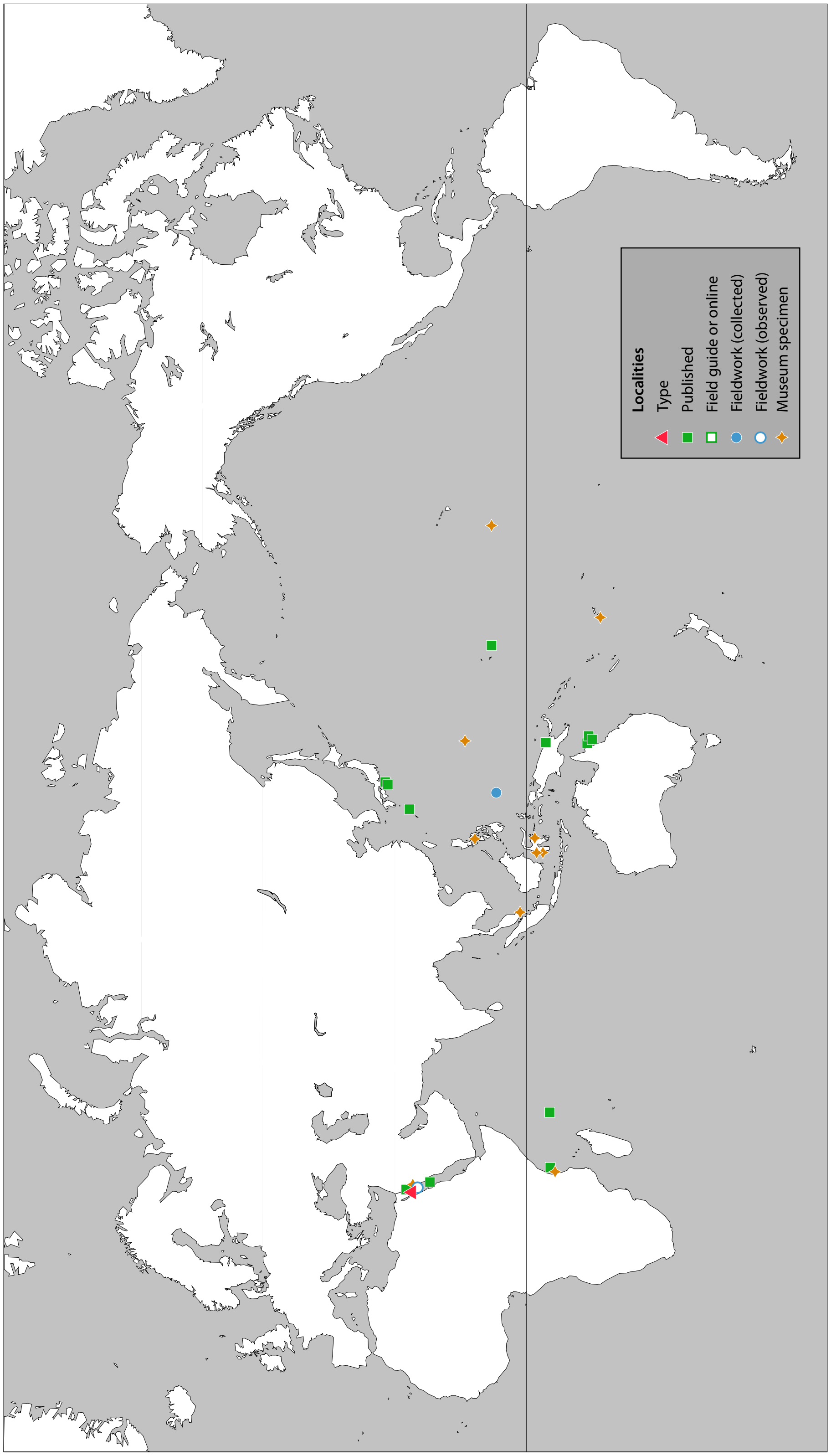

Fig 3.8. Localities of *Thalassianthus hemprichii*.

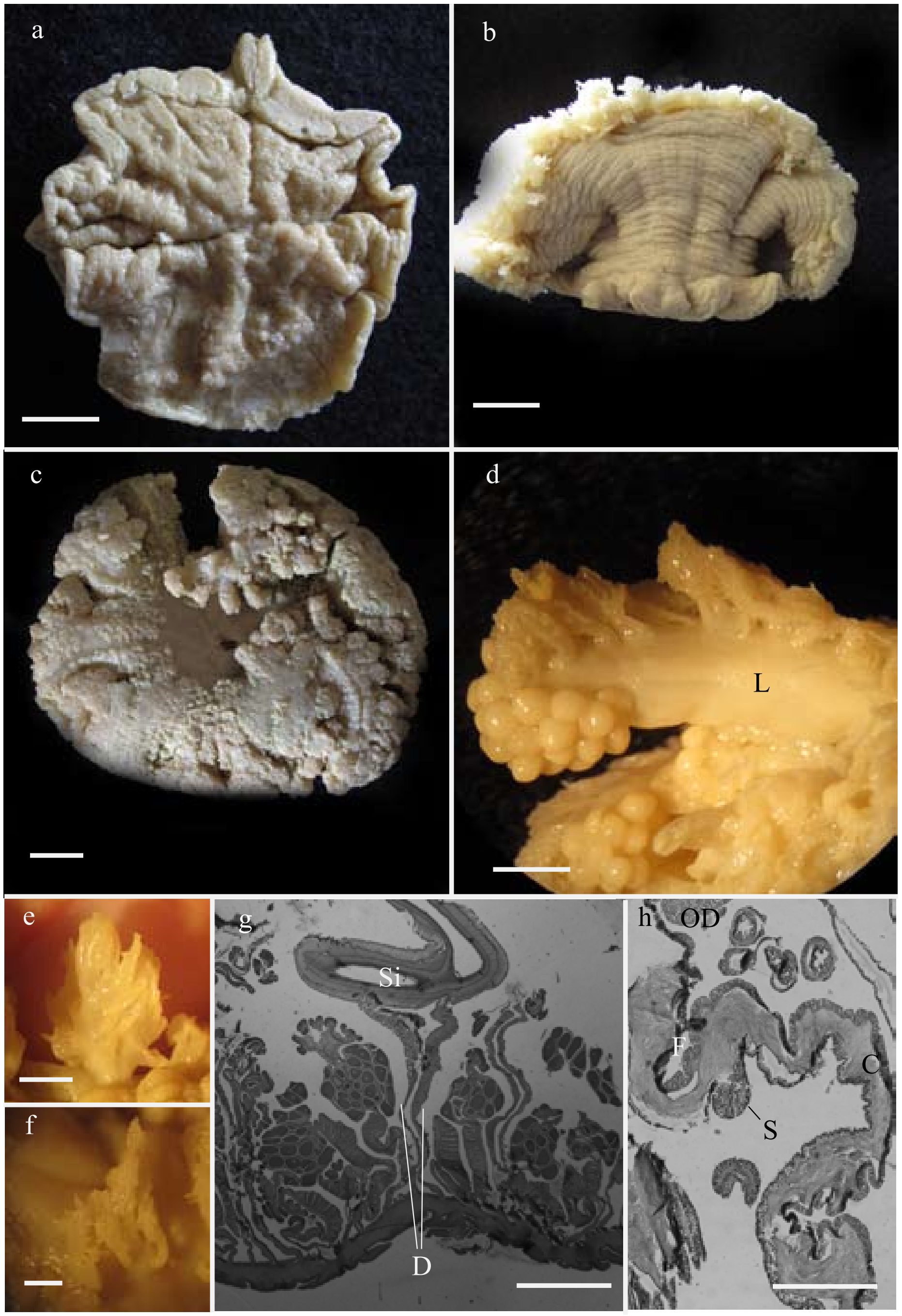

Fig 3.9. *Thalassianthus hypnoides*. a) pedal disc, RMNH Coel 39743, scale bar = 10 mm b) column, RMNH Coel 39743, scale bar = 20 mm c) oral disc, CAS 060342, scale bar = 20 mm d) lobe, with endocoelic dendritic tentacles on oral side and nematospheres on aboral side, RMNH Coel 39743, scale bar = 20 mm e) exocoelic dendritic tentacle, RMNH Coel 39743, scale bar = 1 mm f) endocoelic dendritic tentacles, RMNH Coel 39743, scale bar = 1 mm g) cross-section through mesenteries at level of actinopharynx, RMNH Coel 39743, scale bar = 10 mm h) longitudinal section at margin, CAS 060342, scale bar = 10 mm. Figure legend: C = column, D = directive mesentery, F = fosse, L = lobe, OD = oral disc, S = marginal sphincter muscle, Si = siphonoglyph.

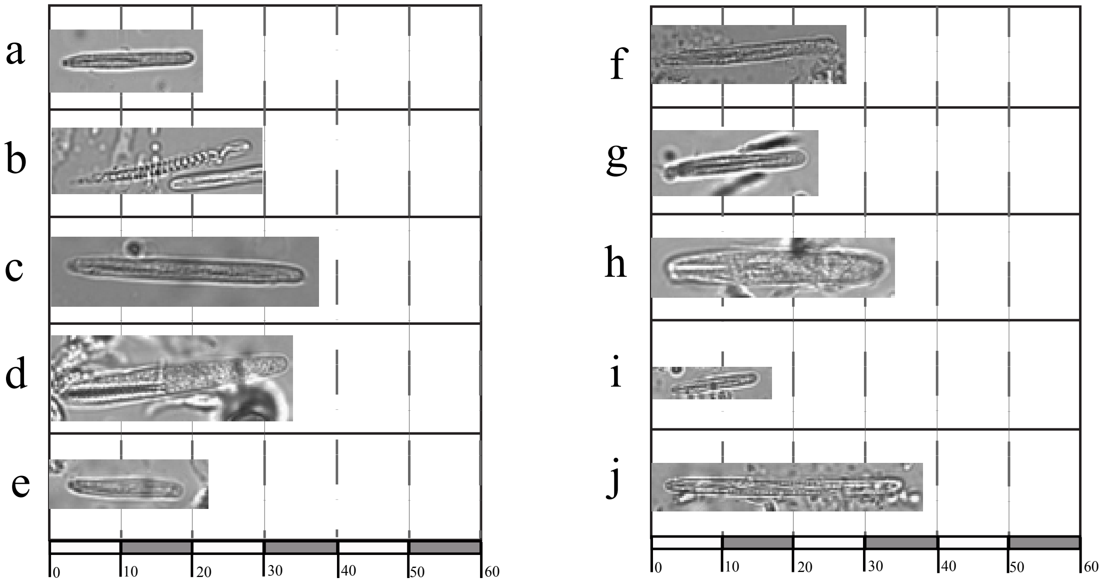

Fig 3.10. Cnidae from various tissues of *Thalassianthus hypnoides*. Lowercase letters correspond to measurements in Table 3.8. Tissue source: a) exocoelic tentacles b-c) nematospheres d,e) endocoelic branched tentacles f) actinopharnx g) column h-j) mesenterial filaments. Scale bar in micrometers.

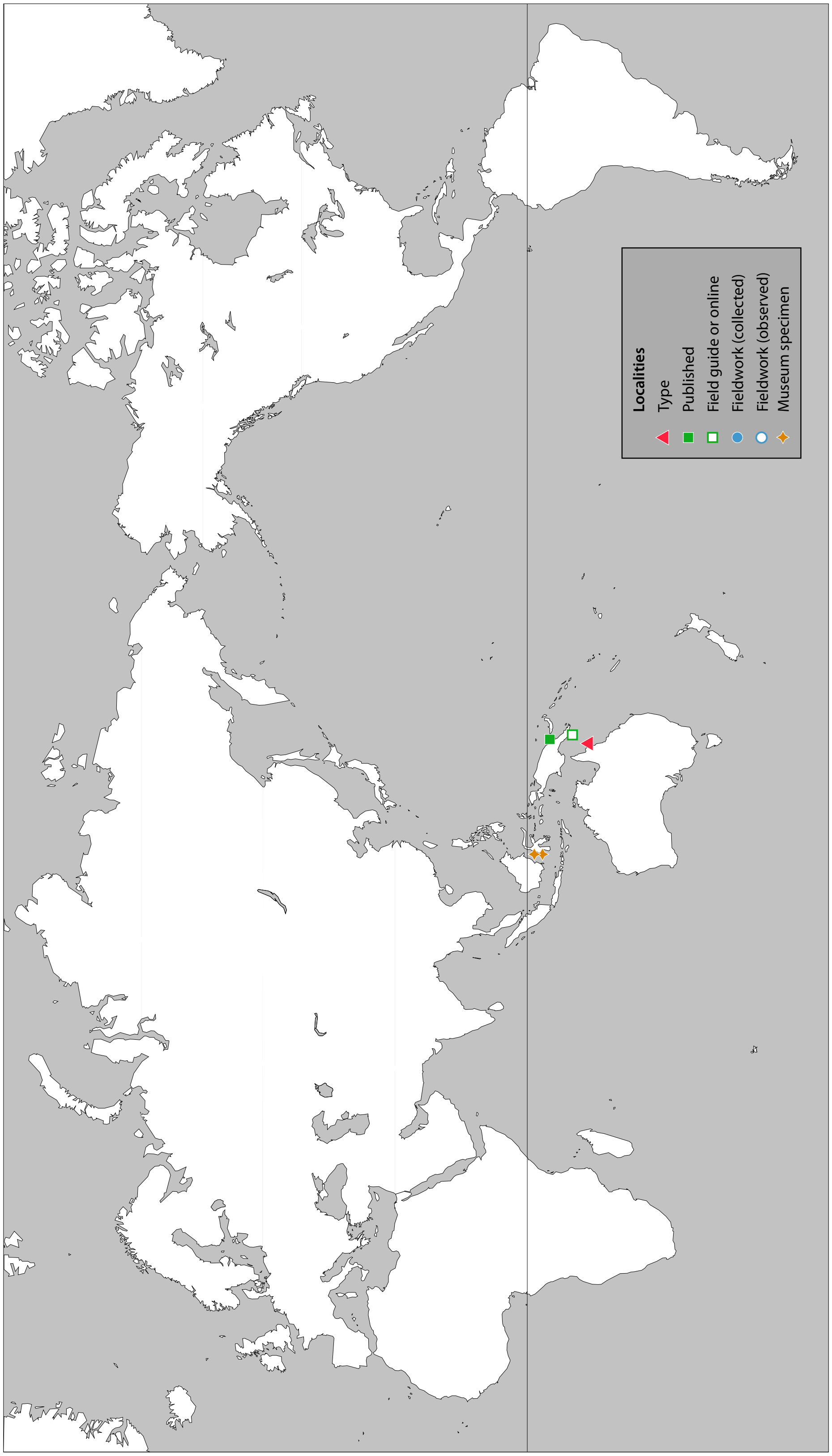

Fig 3.11. Localities of *Thalassianthus hypnoides*.

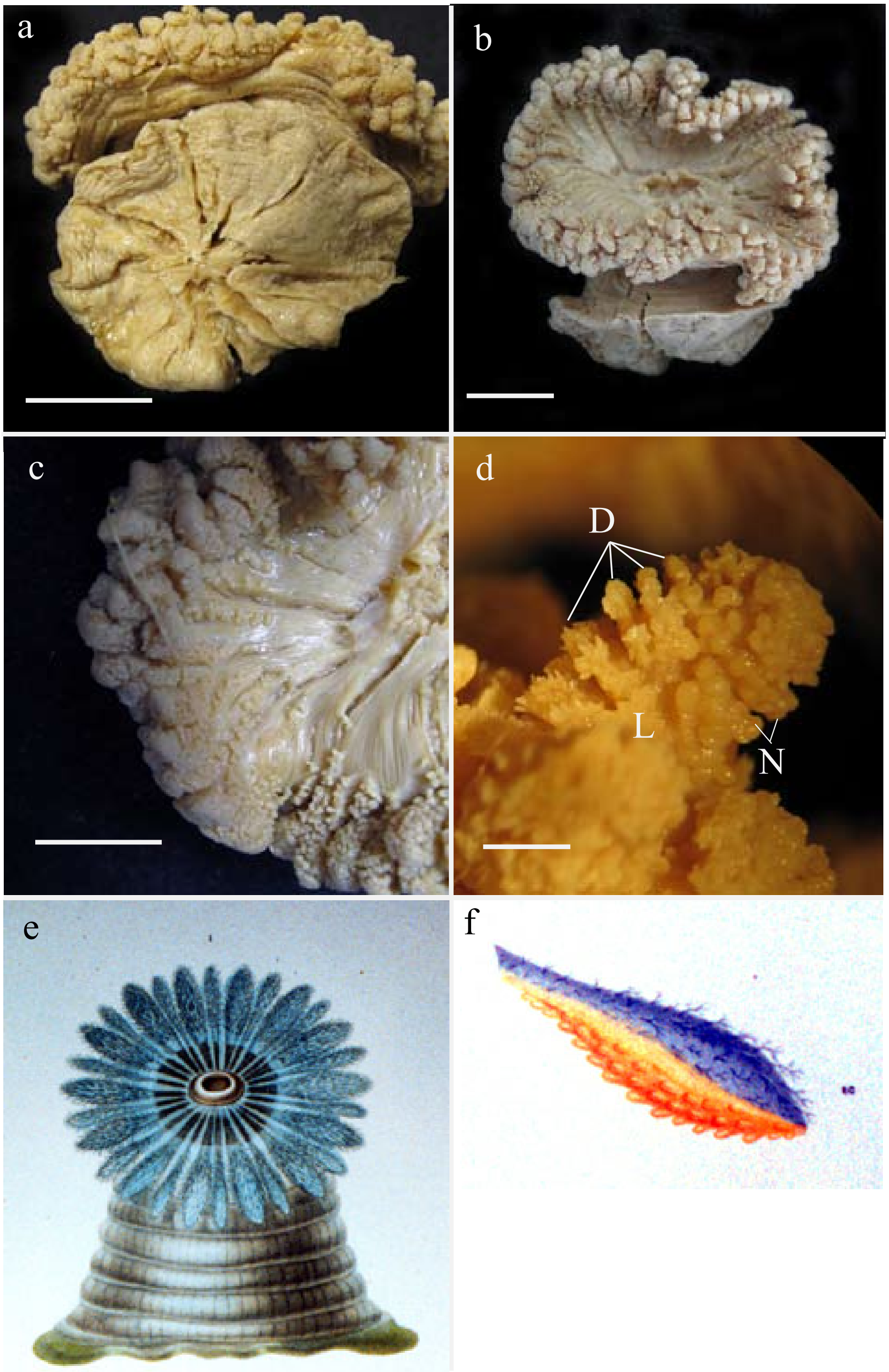

Fig 3.12 *Thalassianthus villosa*. a-d) syntype (MHNH 2387) a) pedal disc, scale bar = 20 mm b) whole individual, scale bar = 20 mm c) oral disc with lobes and radially arranged endocoelic dendritic tentacles, scale bar = 20 mm d) Lobe, with endocoelic dendritic tentacles and nematospheres, scale bar = 5 mm. e,f) Plate XI, Fig 1 and 2 from Quoy & Gaimard (1833). e) whole specimen, f) lobe with endocoelic dendritic tentacles and nematospheres attached. Figure legend: D = endocoelic dendritic tentacle, L = lobe, N = nematosphere.

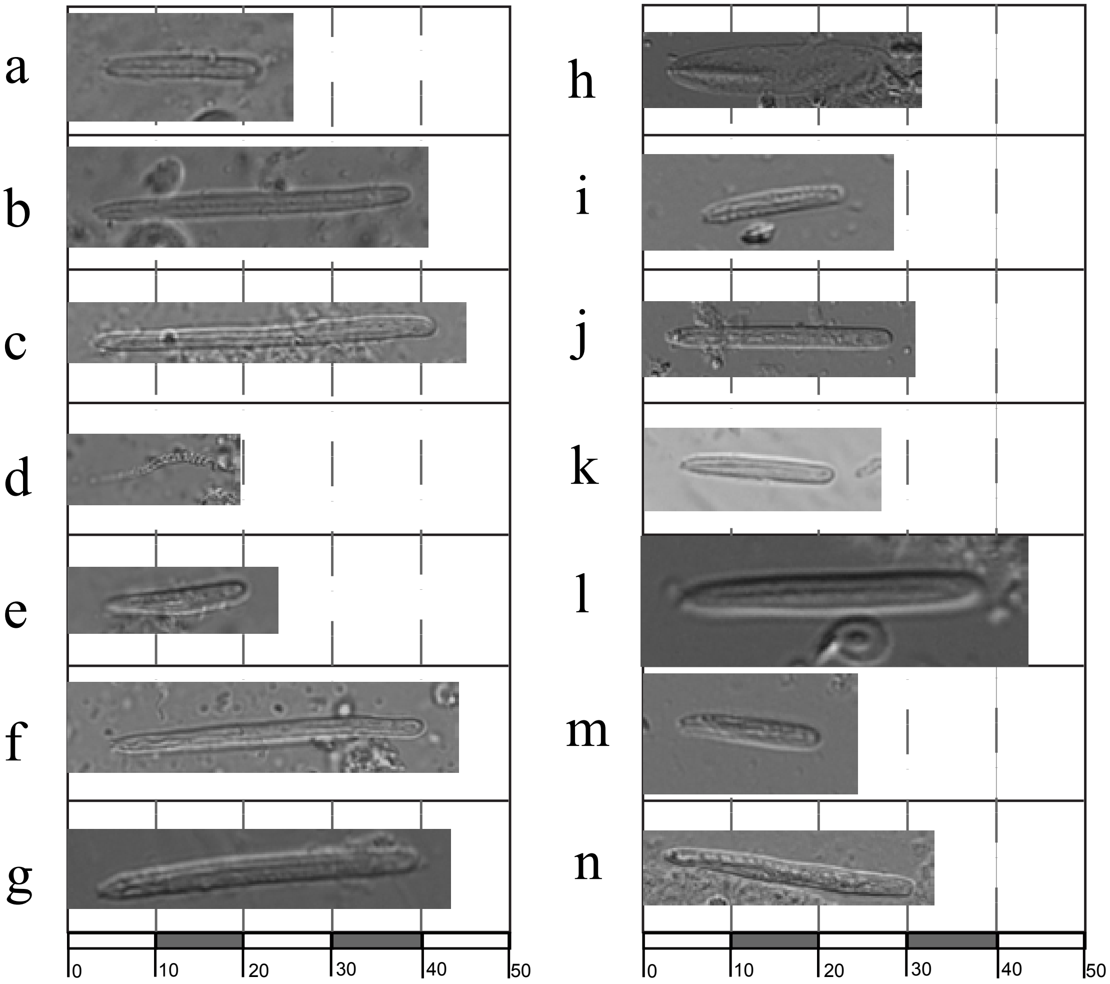

Figure 3.13. Cnidae from various tissues of *Thalassianthus villosa*. Lowercase letters correspond to measurements in Table 3.9. Tissue source: a,b) exocoelic tentacles c) nematospheres d-f) endocoelic branched tentacles g) actinopharnx h-j) oral disc k,l) column m,n) mesenterial filaments. Scale bar in micrometers.

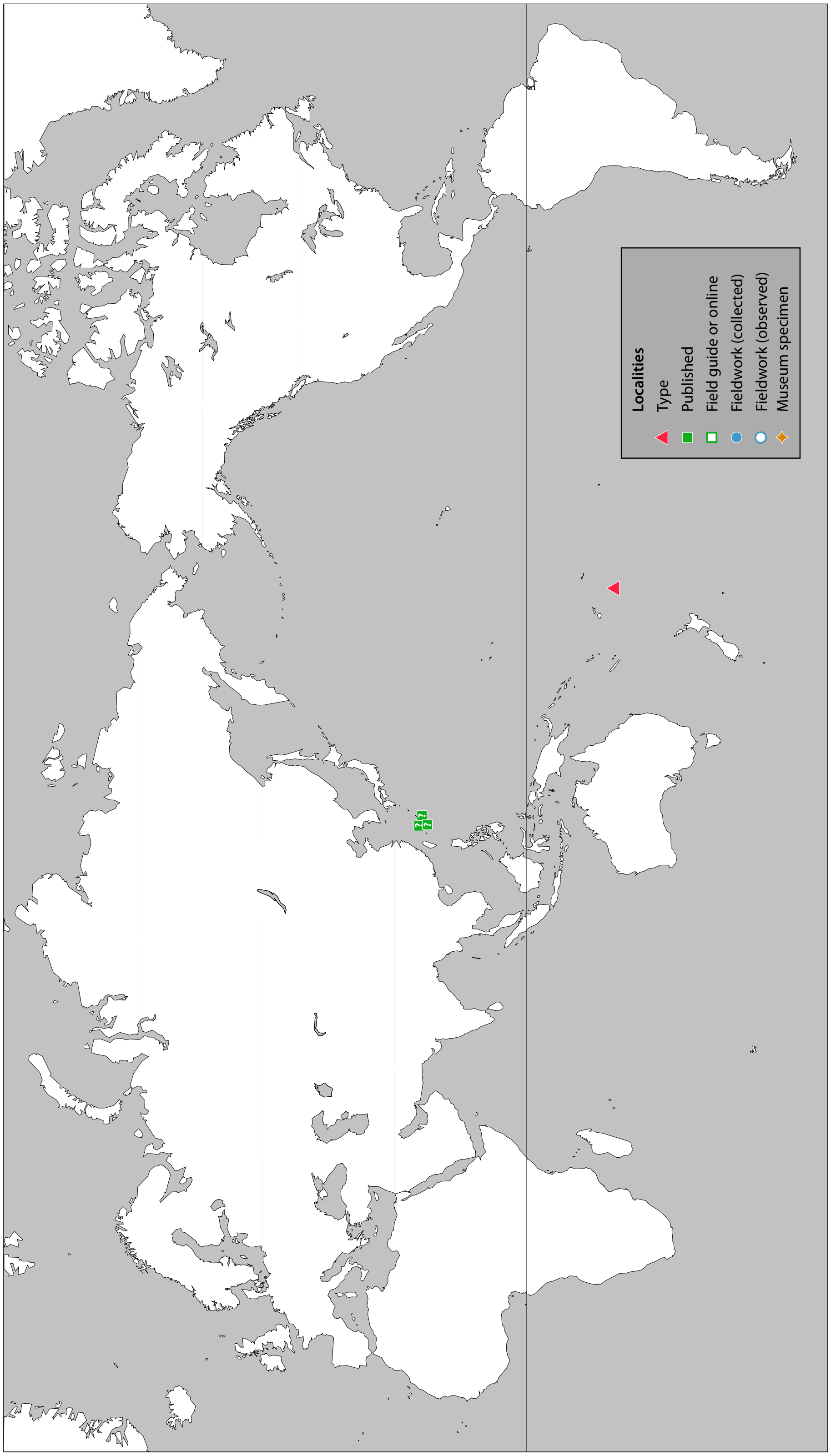

Figure 3.14. Localities of *Thalassianthus villosa*.

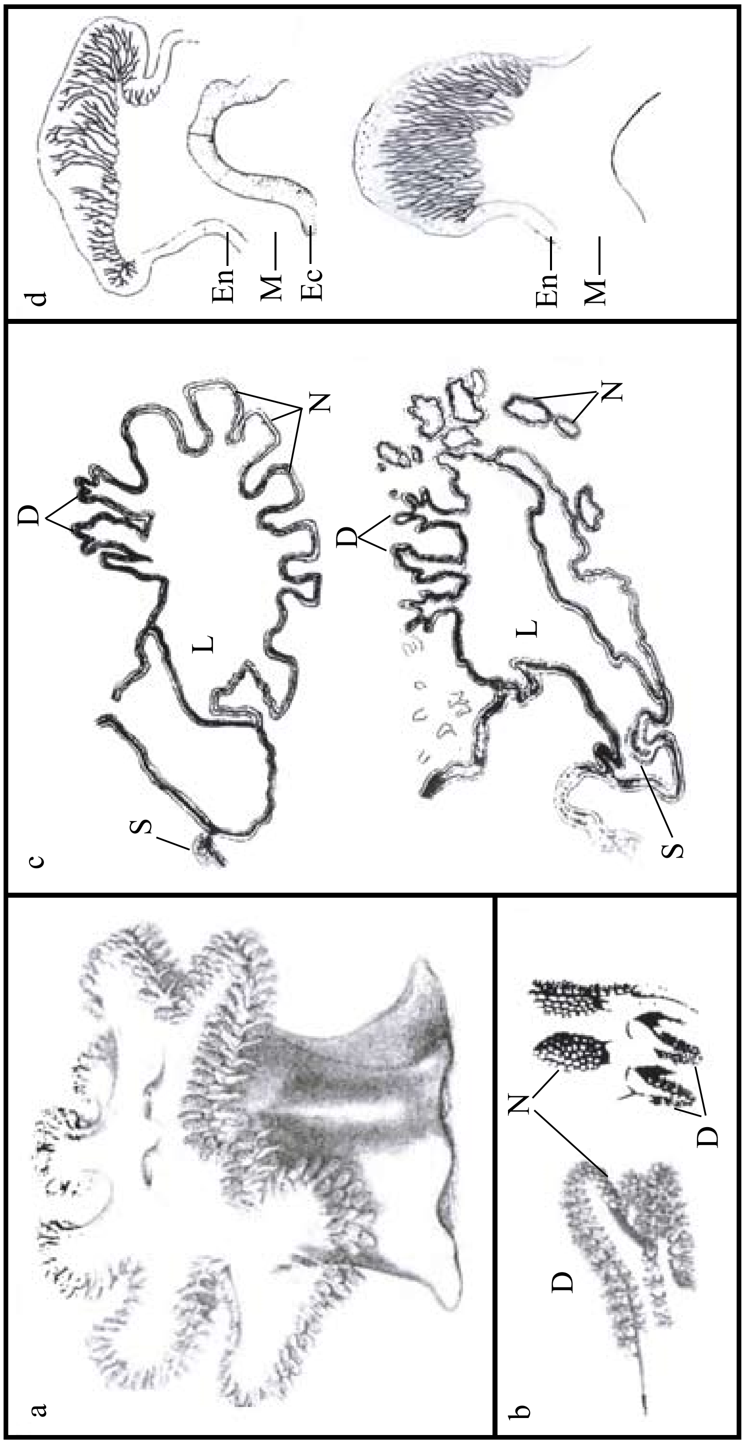

Figure 3.15. *Thalassianthus dendrophora*, from Haddon (1898). a) whole individual, note two mouths depicted, and oral disc mostly free from tentacles b) lobes of oral disc, showing position of endocoelic dendritic tentacles and nematospheres. View from side (left) and from aboral (right) aspects. c) Longitudinal sections through two lobes and oral disc margin. d) Longitudinal section through two marginal endodermal sphincter muscles. Figure legend: D = endocoelic dendritic tentacle, En = endoderm, Ec = ectoderm, L = lobe, M = mesoglea, N = nematosphere, S = marginal sphincter muscle.

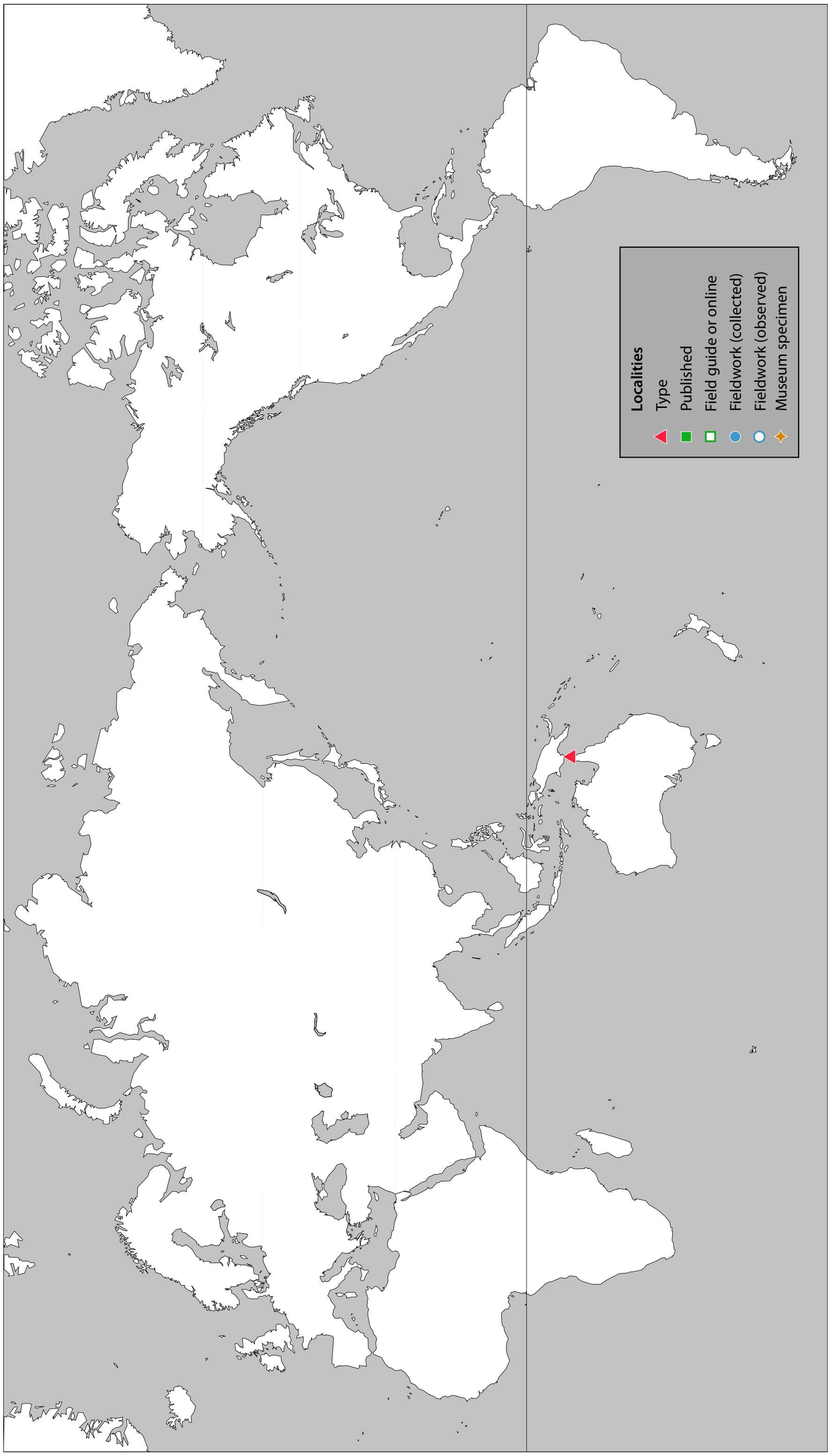

Figure 3.16. Localities of *Thalassianthus dendrophora*.

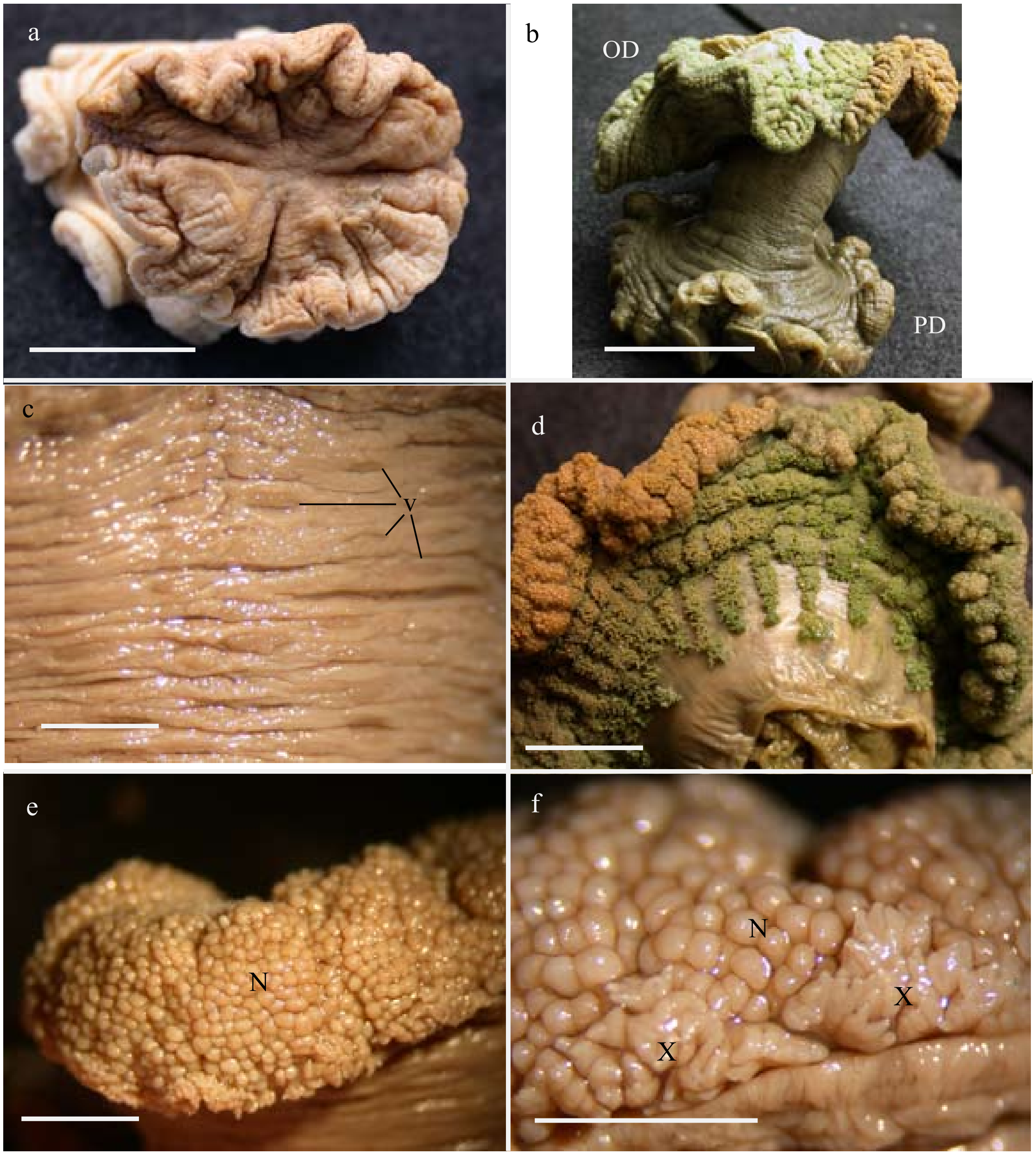

Fig 3.17. *Cryptodendrum adhaesivum*. a) pedal disc of PMJ Coel 77, scale bar = 20 mm b) mid-column region of PMJ 843 with smallest diameter, flares in diameter at oral and pedal discs, scale bar = 20 mm c) non-adhesive verrucae on column of SMNH 1159, scale bar = 2 mm d) oral disc and tentacle fields of PMJ 843, scale bar = 20 mm e) nematosphere band of SMNH 1159, scale bar = 5 mm f) nematospheres and exocoelic tentacles of SMNH 1159, scale bar = 5 mm. Figure legend: v = verrucae, OD = oral disc, X = exocoelic tentacles, F = fosse, S = marginal sphincter muscle, C = column, N = nematospheres.

Fig 3.18. *Cryptodendrum adhaesivum.* Photographs of recently collected specimen (KUDIZ 3027). a) whole individual, looking down on oral disc, scale bar = 20 mm b) flared distal part of column with orange verrucae, scale bar = 1 mm c) central white mouth with bright yellow tinge, and two white siphonoglyphs, scale bar = 10 mm d) all three tentacle types, scale bar = 10 mm. Figure legend: D = endocoelic dendritic tentacles, M = mouth, N = nematospheres, Si = siphonoglyphs, V = verrucae, X = exocoelic tentacles.

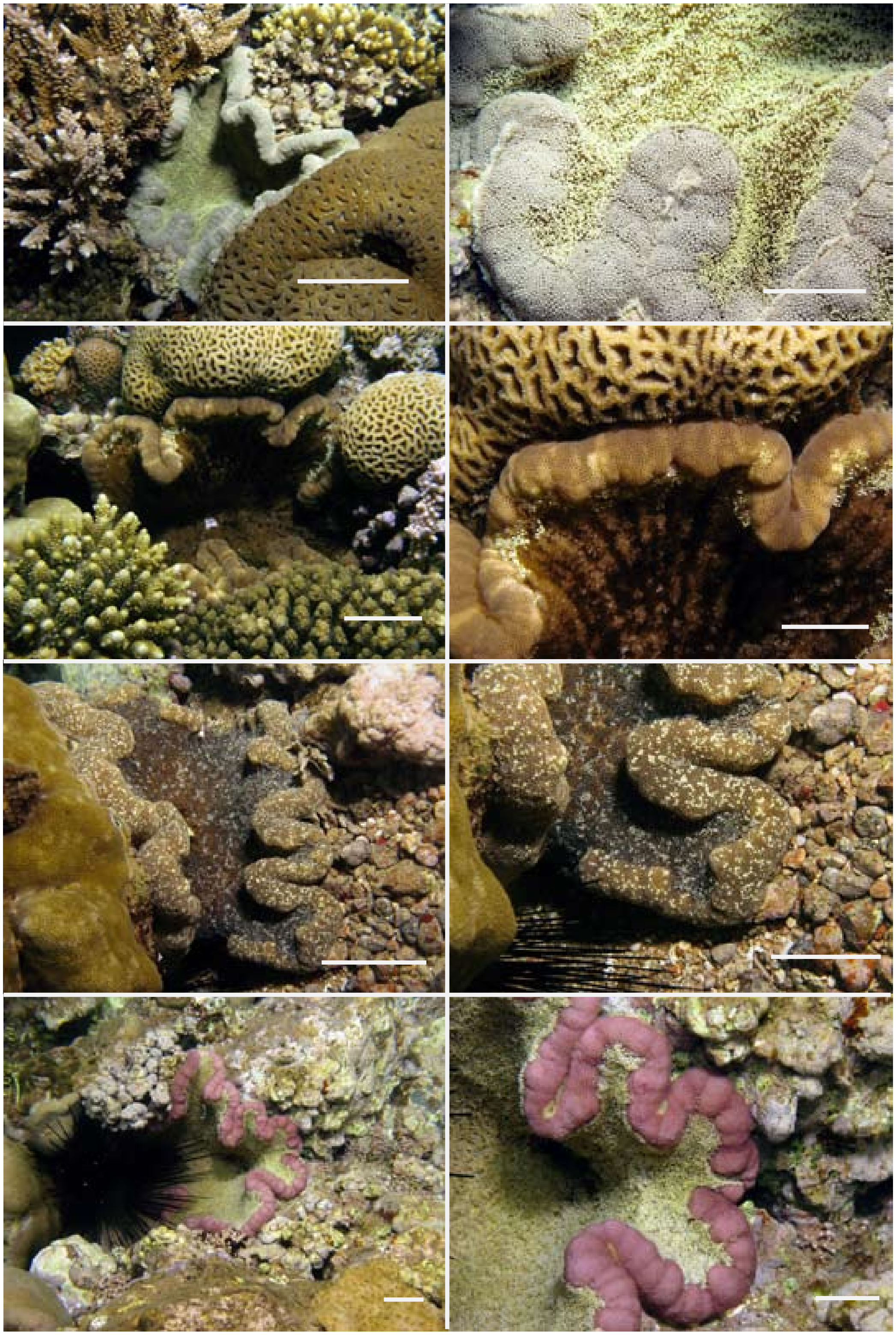

Fig 3.19. *Cryptodendrum adhaesivum.* Some of the individuals observed at Dahab, Egypt during fieldwork, note wide color variation found at one locality. Photographs on left (scale bar = 50 mm) of whole individual, photos on right (scale bar = 20 mm) showing closer view of tentacles. Photographs taken by Christian Alter.

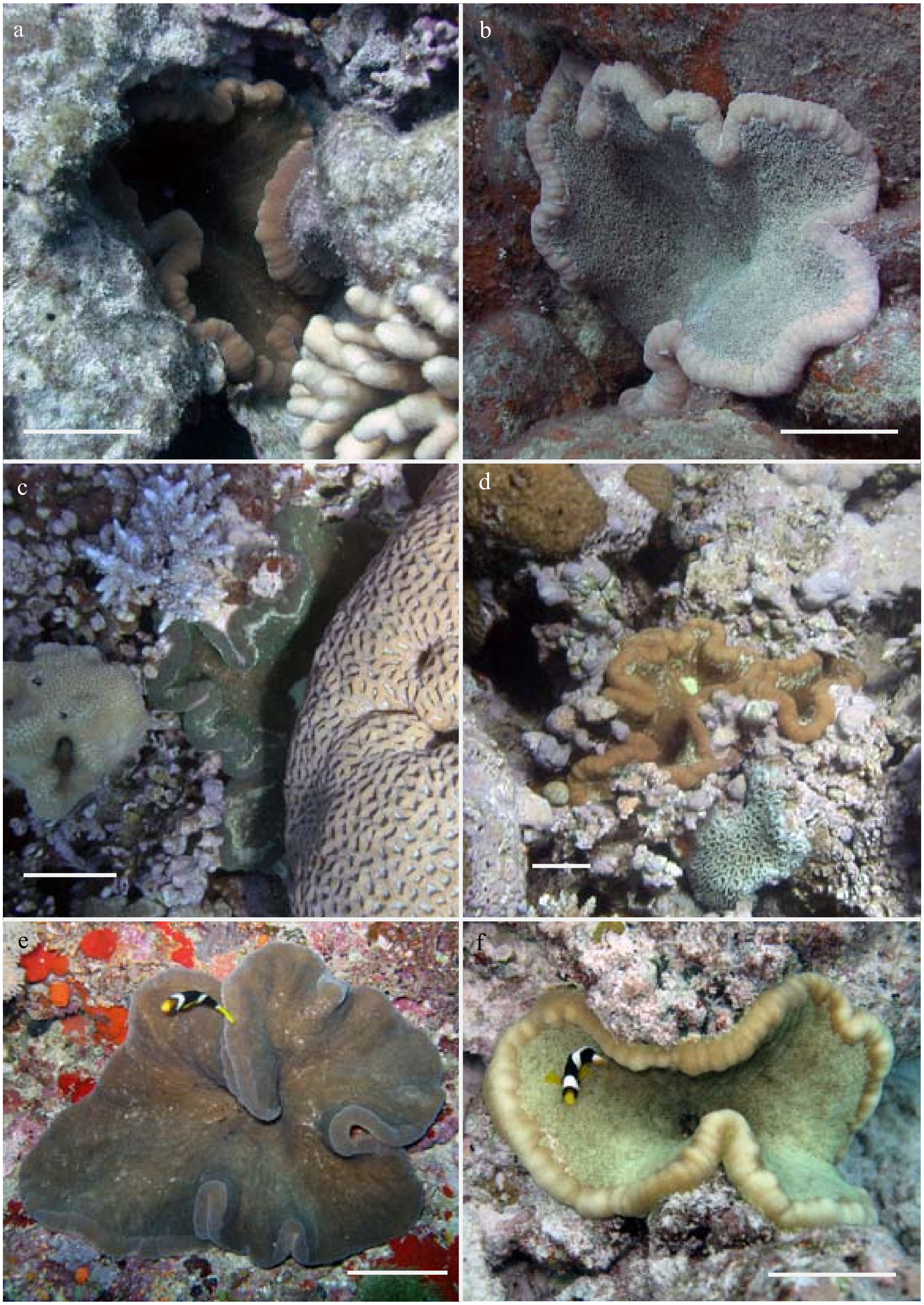

Fig 3.20. *Cryptodendrum adhaesivum. In situ* photographs of individuals from Egypt and the Maldives showing variation in coloration. a-d) from Dahab, Egypt e-f) from the Maldives, with symbiont *Amphiprion clarkii*. Scale bars = 50 mm.

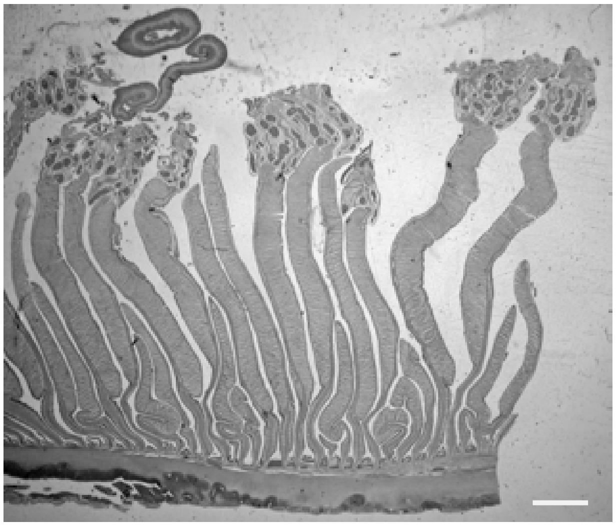

Fig 3.21. *Cryptodendrum adhaesivum*. Cross section (KUDIZ 3027) showing diffuse, well-developed retractor muscles of mesenteries, scale bar = 200 µm.

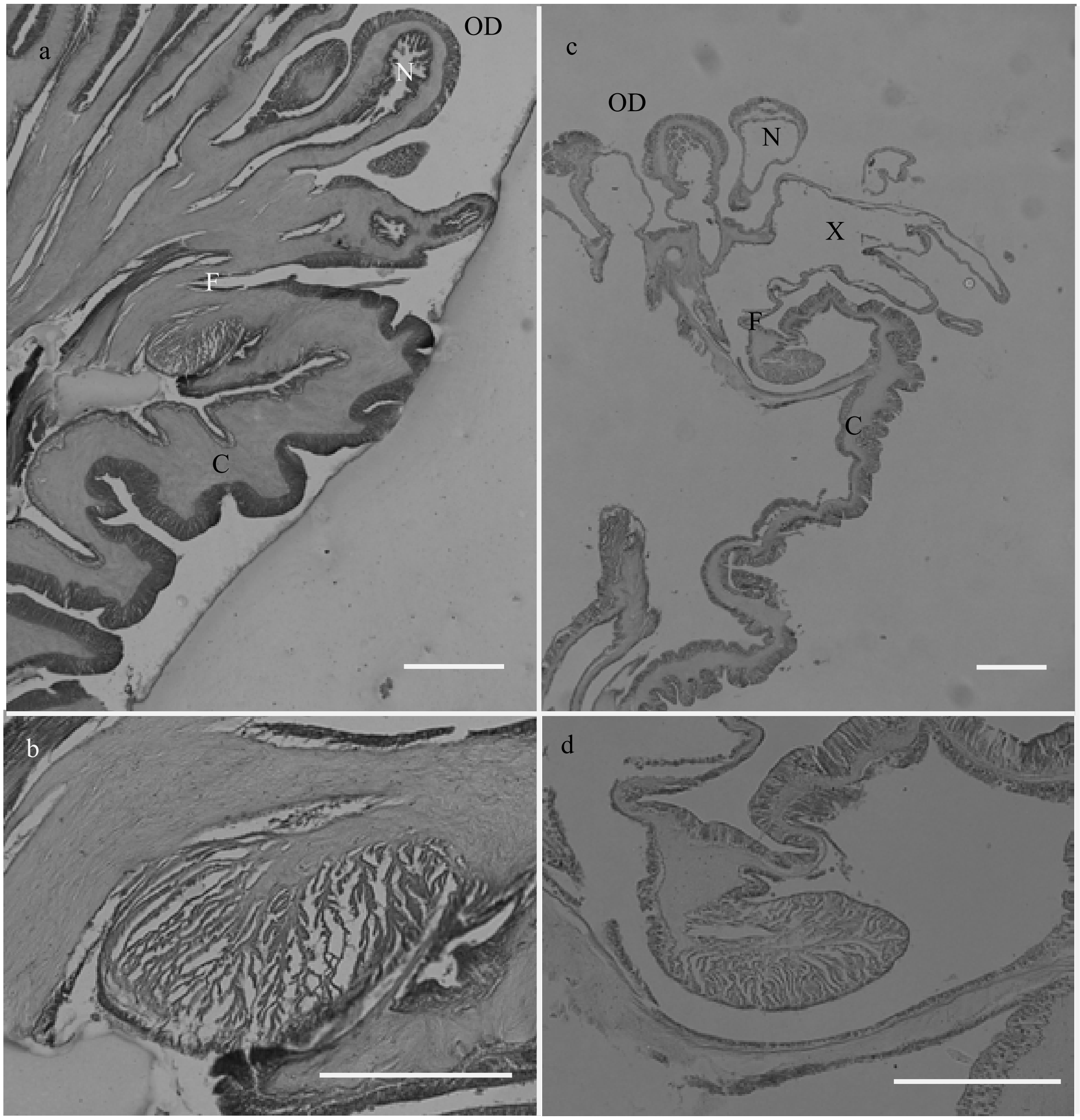

Fig 3.22. *Cryptodendrum adhaesivum*. Longitudinal sections showing position and detail of marginal sphincter muscles. a,b) KUDIZ 3027 c,d) KUDIZ 1660. a) scale bar = 100 µm b) scale bar = 100 µm c) scale bar = 200 µm d) scale bar = 100 µm. Top panel shows position of marginal sphincter muscle toward bottom of fosse, on aboral side. Lower panel shows closer detail of marginal sphincter muscle. Figure legend: OD = oral disc, N = nematospheres, X = exocoelic tentacle, F = fosse, C = column.

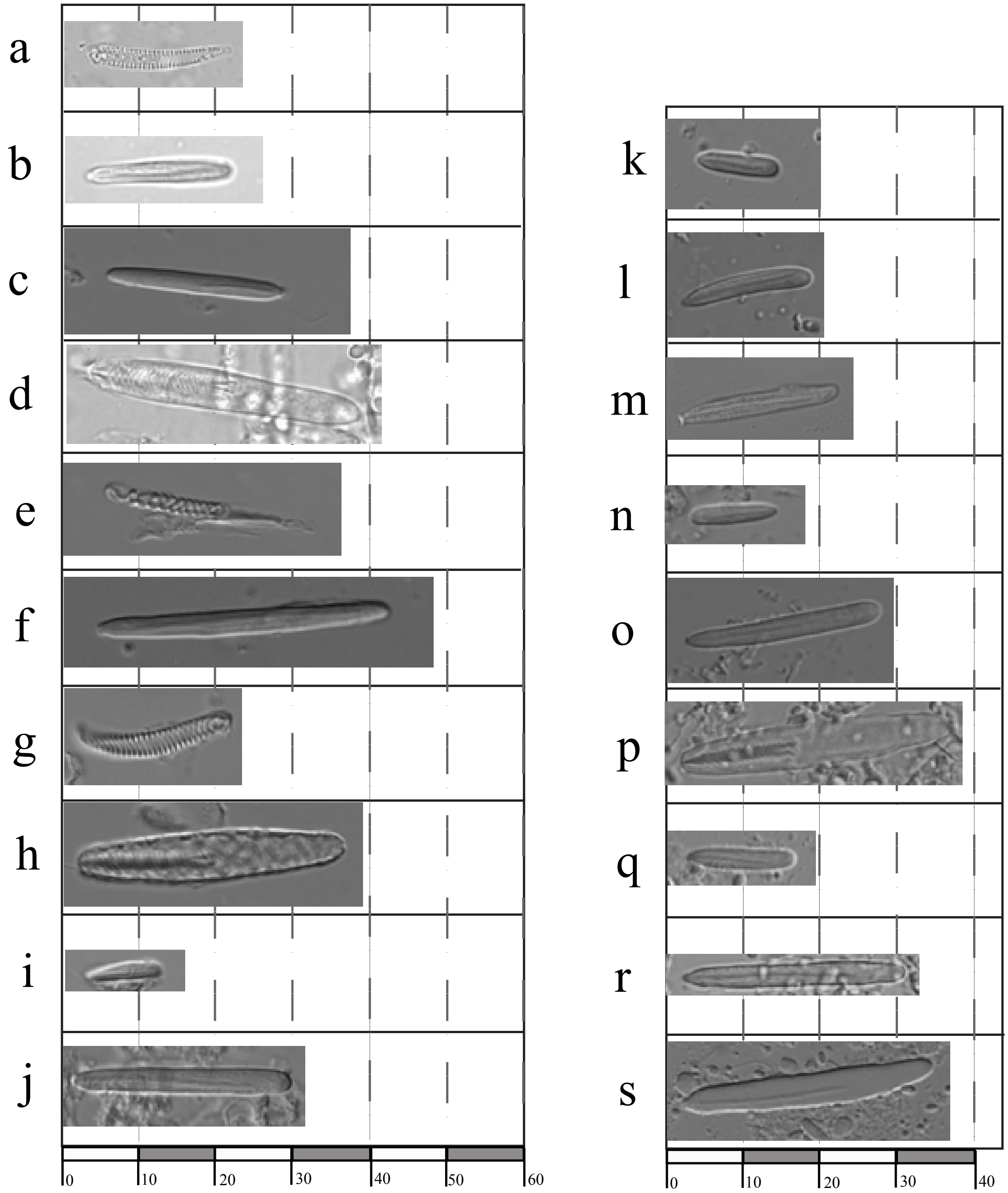

Fig 3.23. Cnidae from various tissues of *Cryptodendrum adhaesivum*. Lowercase letters correspond to measurements in Table 3.12. Tissue source: a-d) exocoelic tentacles e,f) nematospheres g-j) endocoelic branched tentacles k,l) actinopharnx m) oral disc n,o) column p-s) mesenterial filaments. Scale bar in micrometers.

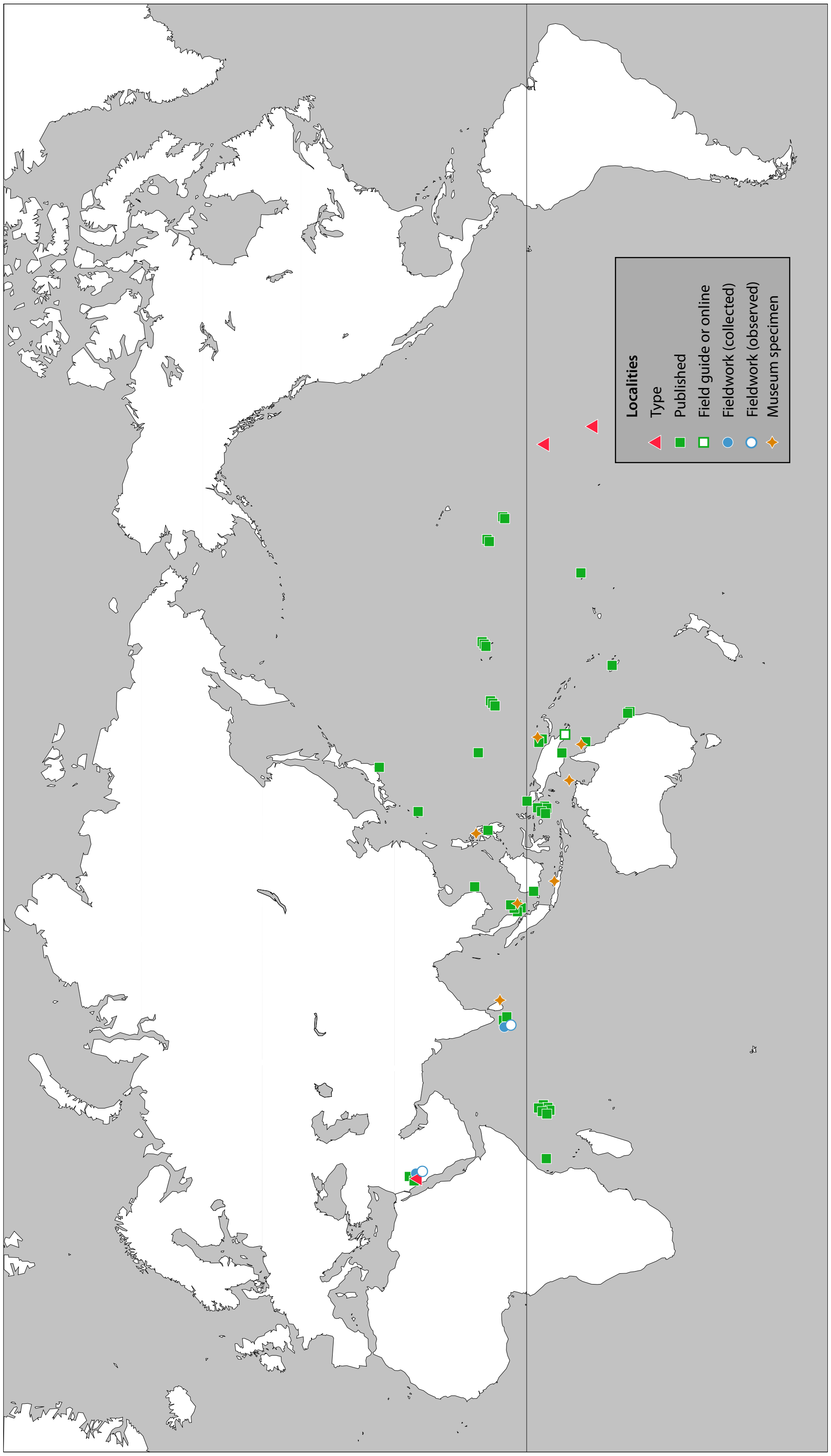

Figure 3.24. Localities of *Cryptodendrum adhaesivum*.

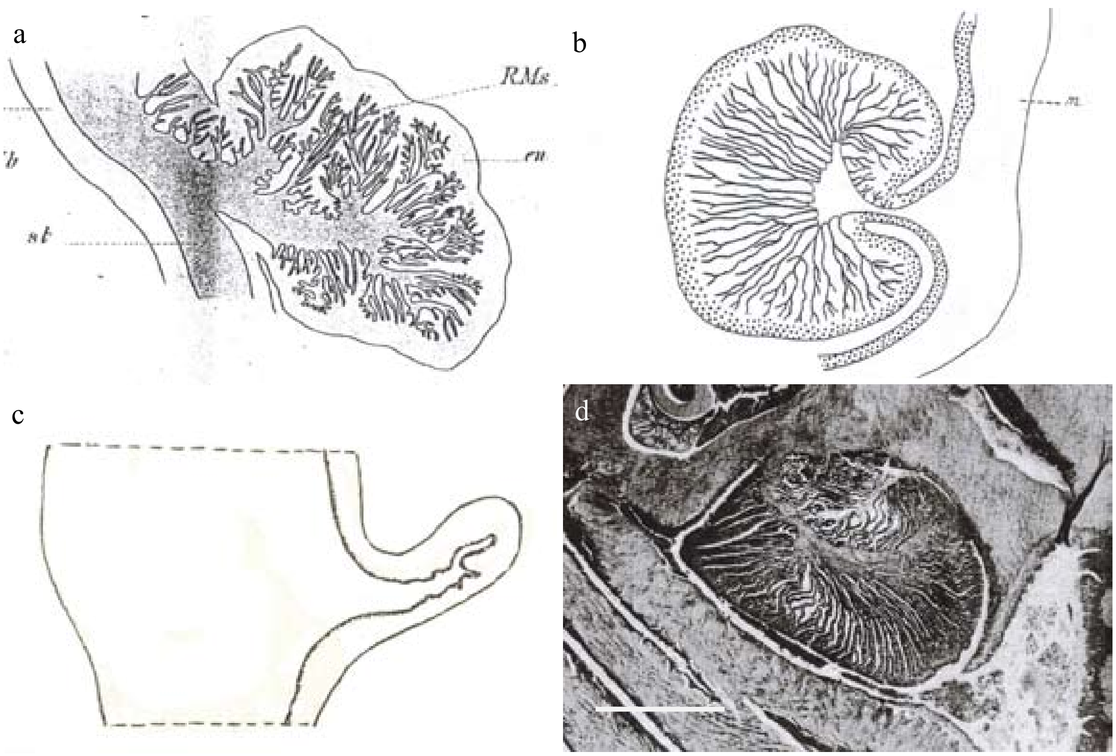

Fig 3.25. *Cryptodendrum adhaesivum*. Variation of marginal sphincter muscles depicted in figures from the literature. a) from Kwietniewski (1896) b) from Haddon (1898) c) from Carlgren (1951) d) from Dunn (1981), scale bar = 125 µm.

Table 3.1. Generic characteristics for genera of Thalassianthidae, according to Carlgren (1949).

	Thalassianthus	***Heterodactyla***	***Actineria***	***Cryptodendrum***
pedal disc	well developed	well developed	wide	broad
body size	small to medium	medium to very large	[not given]	[not given]
verrucae placement	upper column	upper part of column	vertical rows in upper column	small, in upper column
sphincter muscle	weak, restricted to circumscribed	very weak, restricted to circumscribed	weak, restricted	weak to very weak, circumscribed
directive mesenteries	absent	present	present	present
number of mesenteries	no more distally than proximally; numerous mesenteries	more distally than proximally; numerous pairs of mesenteries,	[not given]	more mesenteries at the margin than at the base
mesentery arrangement and fertility	several perfect	at least 3 cycles perfect	many perfect; all stronger mesenteries except directives fertile	all stronger mesenteries except directives fertile

Table 3.2. Characters used in this study to diagnose valid thalassianthid genera.

	Thalassianthus	***Cryptodendrum***
permanent lobes on oral disc	absent	present
nematospheres	in clusters on aboral sides of lobes	in uninterrupted band on oral disc

Table 3.3. Specimens examined, *Thalassianthus aster*. Bold entries indicate newly-collected specimens.

Catalog Number	Status	Original ID	Number of Specimens	Locality	Depth (m)
KUDIZ 3354		**Thalassianthidae**	**1**	**Singapore**	
KUDIZ 3355		**Thalassianthidae**	**1**	**Singapore**	
LO 891/3012		*Thalassianthus aster*	2	Red Sea	
MTQ G61255		***Thalassianthus***	**1**	**Australia, Lord Howe Island**	
PMJ Coel 64	syntype	*Thalassianthus senckenbergianus*	4	Indonesia	
PMJ Coel 758		*Thalassianthus aster*	1		
RMNH Coel 39759		*Thalassianthus*	11	Indonesia	3-4
RMNH Coel 39762		*Thalassianthus*	66	Indonesia	0.5
RMNH Coel 39763		*Thalassianthus*	22	Indonesia	2.5
RMNH Coel 39764		*Thalassianthus*	16	Indonesia	0.1-0.3
SMF 35/6	syntype	*Thalassianthus aster*	6	Red Sea	
SMF 102/11		*Thalassianthus senckenbergianus*	11	Indonesia	
SMNH 4862	syntype	*Thalassianthus senckenbergianus*	1	Indonesia	
SMNH 5632	syntype	*Thalassianthus aster*	1	Red Sea	
SMNH 111220		*Thalassianthus aster* var *fuscus*	1	Tanzania, Zanzibar	
SMNH 111221		*Thalassianthus aster*	3	Tanzania, Zanzibar	
ZMB 199	syntype	*Epicladia quadrangular*	2	Red Sea	
ZMB 201	syntype	*Epicladia quadrangular*	2	Red Sea	
ZMB 202	syntype	*Epicladia quadrangular*	4	Red Sea	
ZMB 3581	syntype	*Thalassianthus senckenbergianus*	5	Indonesia	
ZMB 4744		*Thalassianthus aster*	1	Tanzania, Zanzibar	
ZMH C2579		*Thalassianthus aster*	1	Tanzania, Zanzibar	
ZMH C2582		*Thalassianthus aster*	1	Tanzania, Zanzibar	
ZMH C2591	holotype	*Thalassianthus kraepelini*	1	Tanzania, Zanzibar	
ZMH C2601		*Thalassianthus aster* var *fusca*	2	Tanzania, Zanzibar	
ZMH C2618		*Thalassianthus aster*	6	Tanzania, Zanzibar	
ZMH C2628	syntype	*Thalassianthus aster* var *grisea*	3	Tanzania, Zanzibar	
ZRC CNI 0050		**Thalassianthidae**	**2**	**Singapore**	
ZRC CNI 0051		**Thalassianthidae**	**1**	**Singapore**	

Table 3.4. Distribution and size of cnidae of *Thalassianthus aster*. Measurements given as range in length x width of undischarged capsules in µm (outlier measurements in parentheses), {number of capsules measured}, [ratio of number of individuals in which that type of cnidae was found to the number of individuals examined]. Subjective frequency of cnida type indicated as very common, common, or rare. Letters in parentheses correspond to images in Fig 3.3.

	Thalassianthus aster this study	*Thalassianthus aster* Carlgren 1945
EXOCOELIC TENTACLES		
spirocyst (a)	13-22 x 2-3 {10} [1/5] common	
basitrich (b)	10-26 x 2-3 {76} [5/5] common	
NEMATOSPHERES		
spirocyst (c)	20-34 x 2-4 {52} [5/5] v. common	
basitrich (d)	29-41 x 2.5-4 {61} [5/5] v. common	
ENDOCOELIC BRANCHED TENTACLES		
basitrich (e)	14-25 x 2-3 {67} [5/6] common	
basitrich		33.8-39.5 x 2.5-3
ACTINOPHARYNX		
microbasic p-mastigophore		28.2-31.7 x 4.2-4.9
basitrich (f)	19-33 (39) x 2-4 {32} [5/6] common	24-31 (38) x 2.8-3.5
ORAL DISC		
basitrich (g)	13-16 x 2.5-3.5 {14} [1/6] common	
COLUMN		
basitrich (h)	14-25 x 2-3.5 {56} [6/6] common	16.9-21 x 2-2.5
MESENTERIAL FILAMENTS		
microbasic p-mastigophore (i)	22-35 x 4-7 {51} [6/6] common	34-32.4 (35.2) x 4.2-4.9
basitrich (j)	12-18 x 1.5-2.5 {33} [4/6] common	12.7-14 (16.9) x 1.5-2
basitrich (k)	26-38 x 2.5-3.5 {30} [4/6]	26.8-31 x 2.8-3.5

Table 3.5. Specimens examined, *Thalassianthus hemprichii*. Bold entries indicate newly-collected specimens.

Catalog Number	Status	Original ID	Number of Specimens	Locality	Depth (m)
BMNH 1954.6.28.17		*Heterodactyla hemprichii*	1	Australia, Great Barrier Reef	
BMNH 1995.1543		*Heterodactyla hemprichii*	1		
BMNH 1995.1759-1760		*Heterodactyla hemprichii*	2	Indonesia	2
BMNH 1996.435		*Heterodactyla hemprichii*	1	Singapore	
CAS 050115		*Heterodactyla*	1	Guam	3
CAS 060380		*Heterodactyla hemprichii*	1	Papua New Guinea	7
KUDIZ 1155		*Heterodactyla*	1	Fiji	
KUDIZ 1659		*Heterodactyla*	1	Papua New Guinea	2-3
KUDIZ 3165		***Heterodactyla hemprichii***	**1**	**Palau**	**7**
LO histology slides		*Heterodactyla hemprichii*	13 slides	Red Sea	
RMNH Coel 39745			1	Indonesia	3
RMNH Coel 39750		*Heterodactyla*	1	Indonesia	1-10
RMNH Coel 39756		*Heterodactyla*	1	Indonesia	0.5
RMNH Coel 39765		*Thalassianthus*	1	Indonesia	0-10
RMNH Coel 39771		*Thalassianthus*	3	Indonesia	
RMNH Coel 39774		*Thalassianthus*	1	Indonesia	
RMNH Coel 39776		*Heterodactyla*	1	Indonesia	
RMNH Coel 39857		*Phyllodiscus semoni*	1	Philippines	3
SMNH 111222		*Heterodactyla hemprichii*	piece	Egypt, Red Sea	
USNM 53281		*Heterodactyla hemprichii*	1	Kiribati	
ZMB 150		*Heterodactyla hemprichii*	1		
ZMB H612		*Heterodactyla hemprichii*	1	Red Sea	
ZMB 1876		*Heterodactyla hemprichii*	1	Red Sea	
ZMH C2590		*Heterodactyla hemprichii*	1	Zanzibar	

Table 3.6. Distribution and size of cnidae of *Thalassianthus hemprichii*. Measurements given as range in length x width of undischarged capsules in µm (outlier measurements in parentheses), {number of capsules measured}, [ratio of number of individuals in which that type of cnidae was found to the number of individuals examined]. Subjective frequency of cnida type indicated as very common, common, or rare. Letters in parentheses correspond to images in Fig 3.7.

	Thalassianthus hemprichii this study
EXOCOELIC TENTACLES	
basitrich (a)	16-25 x 2.5-3 {27} [2/2] common
NEMATOSPHERES	
spirocyst (b)	20-35 x 2-3 {21} [2/3] common
basitrich (c)	11-15 x 2 {16} [2/3] common
basitrich (d)	36-43 x 2.5-3 {40} [3/3] v. common
ENDOCOELIC BRANCHED TENTACLES	
spirocyst (e)	16-17 x 2 {3} [1/2] rare
microbasic p-mastigophore (f)	28-35 x 5-6 {6} [1/2] rare
basitrich (g)	9.5-12 x 2-2.5 {10} [1/2] common
basitrich (h)	16-17 x 2.5-3 {3} [2/2] rare
ACTINOPHARYNX	
basitrich (i)	18-30 x 2.5-3 {27} [2/2] v. common
ORAL DISC	
basitrich (j)	10-13 x 2-3 {15} [1/2] common
COLUMN	
basitrich (k)	18-21 x 2.5-3 {25} [2/2] common
MESENTERIAL FILAMENTS	
microbasic p-mastigophore (l)	24-31 x 5-6 {25} [2/2] common
basitrich (m)	11-15 x 2-2.5 {25} [2/2] v. common
basitrich (n)	29-35 x 3 {25} [2/2] v. common

Table 3.7. Specimens examined, *Thalassianthus hypnoides*.

Catalog Number	Status	Original ID	Number of Specimens	Locality	Depth (m)
CAS 060342		*Heterodactyla hypnoides*	1	Papua New Guinea	1
RMNH Coel 39743		*Thalassianthus*	2	Indonesia	
RMNH Coel 39769			1	Indonesia	20

Table 3.8. Distribution and size of cnidae of *Thalassianthus hypnoides*. Measurements given as range in length x width of undischarged capsules in µm (outlier measurements in parentheses), {number of capsules measured}, [ratio of number of individuals in which that type of cnidae was found to the number of individuals examined]. Subjective frequency of cnida type indicated as very common, common, or rare. Letters in parentheses correspond to images in Fig 3.10.

	Thalassianthus hypnoides this study
EXOCOELIC TENTACLES	
basitrich (a)	17-23 x 2-2.5 {11} [1/1] v. common
NEMATOSPHERES	
spirocyst (b)	20-33 x 2-3 {10} [1/1] common
basitrich (c)	34-38 x 2.5-3 {12} [1/1] common
ENDOCOELIC BRANCHED TENTACLES	
microbasic p-mastigophore (d)	29-36 x 5 {11} [1/1] common
basitrich (e)	15-18 x 2 {4} [1/1] rare
ACTINOPHARYNX	
basitrich	15-20 x 2.5-3 {2} [1/1] v. rare
basitrich (f)	25-30 x 2.5-3 {10} [1/1] common
COLUMN	
basitrich (g)	18-22 x 2-3 {13} [1/1] v. common
MESENTERIAL FILAMENTS	
microbasic p-mastigophore (h)	28-35 x 5-5.5 {12} [1/1] v. common
basitrich (i)	13-15 x 2 {12} [1/1] v. common
basitrich (j)	32-38 x 2.5-3 {10} [1/1] v. common

Table 3.9. Distribution and size of cnidae of *Thalassianthus villosa*. Measurements given as range in length x width of undischarged capsules in µm (outlier measurements in parentheses), {number of capsules measured}, [ratio of number of individuals in which that type of cnidae was found to the number of individuals examined]. Subjective frequency of cnida type indicated as very common, common, or rare. Letters in parentheses correspond to images in Fig 3.13.

	Thalassianthus villosa this study
EXOCOELIC TENTACLES	
basitrich (a)	16-20 x 2.5-3 {13} [1/1] common
basitrich (b)	36-40 x 2.5-3 {15} [1/1] v. common
NEMATOSPHERES	
basitrich (c)	37-42 x 3 {15} [1/1] v. common
ENDOCOELIC BRANCHED TENTACLES	
spirocyst (d)	11-20 x 2 {5} [1/1] rare
basitrich	12 x 2 {1} [1/1] v. rare
basitrich (e)	16-19 x 2-3 {9} [1/1] common
basitrich (f)	36-44 x 2.5-3 {15} [1/1] v. common
ACTINOPHARYNX	
basitrich	13-14 x 2.5 {2} [1/1] v. rare
basitrich (g)	27-39 x 2.5-3 {15} [1/1] v. common
ORAL DISC	
microbasic p-mastigophore (h)	27-30 x 6-7 {6} [1/1] rare
basitrich (i)	12-14 x 2.5-3 {15} [1/1] common
basitrich (j)	26-34 x 3 {15} [1/1] common
COLUMN	
basitrich (k)	16-19 x 2.5 {15} [1/1] common
basitrich (l)	33-41 x 2.5-3 {5} [1/1] rare
MESENTERIAL FILAMENTS	
basitrich (m)	12-16 x 2-3 {15} [1/1] common
basitrich (n)	28-31 x 3 {15} [1/1] v. common

Table 3.10. Specimens examined, *Cryptodendrum adhaesivum*. Bold entries indicate newly-collected specimens..

Catalog Number	Status	Original ID	Number of Specimens	Locality	Depth (m)
BMNH 1995.1559		*Cryptodendrum adhaesivum*	1	Singapore	
BMNH 1995.1560		*Cryptodendrum adhaesivum*	1	Singapore	
BMNH 1995.1561		*Cryptodendrum adhaesivum*	1	Australia, Great Barrier Reef	
KUDIZ 1660		*Cryptodendrum adhaesivum*	1	Papua New Guinea	3.5
KUDIZ 3027		***Cryptodendrum adhaesivum***	**1**	**Egypt, Red Sea**	**2**
MTQ G59159		*Cryptodendrum adhaesivum*	1	Australia, Northern Territory	2-3
PMJ Coel 77		*Cryptodendrum adhaesivum*	2		
RMNH Coel 12893		*Cryptodendrum adhaesivum*	1	New Caledonia	
RMNH Coel 18690		*Cryptodendrum adhaesivum*	1	Seychelles	15
RMNH Coel 18691		*Cryptodendrum adhaesivum*	1	Seychelles	
RMNH Coel 18702		*Cryptodendrum adhaesivum*	2	Seychelles	
RMNH Coel 18705		*Cryptodendrum adhaesivum*	1	Seychelles	4
SMNH 1159	syntype	*Cryptodendrum adhaesivum*	piece	Egypt, Red Sea	
USNM 50108		*Cryptodendrum adhaesivum*	1	Marshall Islands	0
USNM 51071		*Cryptodendrum adhaesivum*	1	Micronesia, Yap Islands	
USNM 51072		*Cryptodendrum adhaesivum*	1	Micronesia, Yap Islands	
USNM 52455		*Cryptodendrum adhaesivum*	1	United States Minor Outlying Islands, Line Islands	
USNM 52506		*Cryptodendrum adhaesivum*	1	Kiribati, Line Islands	
USNM 53321		*Cryptodendrum adhaesivum*	1	Marshall Islands	
USNM 53323		*Cryptodendrum adhaesivum*	1	Kiribati, Line Islands	
USNM 53338		*Cryptodendrum adhaesivum*	1	Marshall Islands	
USNM 1112472		*Cryptodendrum* sp.	1	French Polynesia	
USNM 1120874		*Cryptodendrum adhaesivum*	1	Philippines	
USNM 1120875		*Cryptodendrum adhaesivum*	1	Marshall Islands	
ZMB 1877	syntype	*Cryptodendrum adhaesivum*	2	Egypt, Red Sea	
ZMB 2058		*Cryptodendrum adhaesivum*	1		
ZMB 5115		unidentified	1	Papua New Guinea	

Table 3.11. Color combinations of endocoelic branched tentacles and nematospheres of *Cryptodendrum adhaesivum* observed during fieldwork.

Endocoelic branched tentacles	Nematospheres	Source
gray	white	Sprung & Delbeek (1997)
gray	purple	Sprung & Delbeek (1997), Sprung (2001)
speckled blue	beige	Observed
dark blue	bright blue	Observed
blue	white	Erhardt & Knop (2005)
light green	gray	Observed
light green	light purple	Observed, Baine & Harasti (2007)
light green	golden brown	Observed
dark green	gray	Sprung (2001)
dark green	purple	Fautin & Allen (1992), Colin & Arneson (1995), Weinberg (1996), Fosså & Nilsen (1998), Erhardt & Knop (2005)
dark green	light brown	Observed
dark green	light green	Gosliner *et al.* (1996), Allen & Steene (2002), Erhardt & Knop (2005)
dark green	dark green	Observed
light brown	beige	Observed
light brown	caramel brown	Observed
speckled dark brown	golden brown	Fautin & Allen (1992)
speckled dark brown	speckled light brown	Observed
dark brown	light brown	Observed, Sprung & Delbeek (1997)
dark brown	dark brown	Observed, Erhardt & Knop (2005)

Table 3.12. Distribution and size of cnidae of *Cryptodendrum adhaesivum*. Measurements given as range in length x width of undischarged capsules in µm (outlier measurements in parentheses), {number of capsules measured}, [ratio of number of individuals in which that type of cnidae was found to the number of individuals examined]. Subjective frequency of cnida type indicated as very common, common, or rare. Letters in parentheses correspond to images in Fig 3.23.

	Cryptodendrum adhaesivum this study	*Cryptodendrum adhaesivum* Carlgren (1940)	*Cryptodendrum adhaesivum* Carlgren (1950)	*Stoichactic digitata* Doumenc (1973)	*Cryptodendrum adhaesivum* Dunn (1981)
EXOCOELIC TENTACLES					
spirocyst (a)	19-34.5 x 2.5-4 {41} [4/4] common				15-20.5 x 2.5-3.5 (4.1) {17} [3]
basitrich (b)	18-35 x 2.5-4.5 {59} [4/4] v. common		16.2-26.8 x 2-2.5		(16.4) 17.2-26.2 x 2.5-3.3 {22} [3]
basitrich (c)	20-24 x 3 {3} [1/4] v. rare				
microbasic p-mastigophores (d)	37-45 x 5-7 {16} [2/4] rare		38-42 x 5.6		
NEMATOSPHERES					
spirocyst (e)	19-40 x 2.5-3.5 {42} [3/3] common			20-25 x 2.5	(13.1) 15-31.2 (34.4) x 2-3.1 {22} [4]
basitrich (f)	32-41 x 2-4 {40} [3/3] v. common		29.6-36.7 x 2-2.5 (2.8) numerous	35-39 x 3-3.5	34.4-40.2 x 2.5-3.3 {32} [4]
microbasic amastigophores				42-47 x 8	
ENDOCOELIC BRANCHED TENTACLES					
spirocyst (g)	14-35 x 2.5-4 {36} [3/3] common			25 x 2.5	17.5-33.6 (36.9) x 2.5-3.8 (4.9) {25} [4]
microbasic p-mastigophore (h)	33-46 x 5.5-8 {35} [3/3] v. common	37-38 (41) x 5.5-6	32.4-43.7 x 4.2-5.6		
microbasic p-mastigophore		37-38 x 5.5-7			
microbasic amastigophore				40-47 x 8-9	
basitrich (i)	9-12 x 2 {13} [2/3] rare	17-19 x 2-2.5	15.5-29.6 x 2.2-2.5		9.8-11.5 (17.2) x 1.8-2.5 {7} [4]
basitrich (j)	20-36 x 3.5-4.25 {20} [3/3] common	17-24 x 2			
basitrich	36.5-41 x 2.5-3 {11} [1/2] common	32.5-37.5 x 2		35-39 x 3-3.5	34.4-40.2 x 2.5-3.3 {12} [2]
ACTINOPHARYNX					
spirocyst					20.5-27.9 x 3.1-3.3 {6} [2]
microbasic p-mastigophore		47 x 7			
basitrich (k)	8-12 x 2-2.5 {25} [2/2] common	26-32.5 x 2	18.3-19.7 x 2.8 few		11.5-20.5 x 2.1-3.1 {10} [2]
basitrich (l)	17-21 x 3 {17} [2/2] v. common				
basitrich	24-32 x 2.5-4 {20} [1/1] v. common		25.4-32.4 x 2.8		26.2-33.6 (35.3) x 2.7-3.9 {20} [3]
ORAL DISC					
basitrich (m)	19-25 x 3 {15} [1/1] common				
COLUMN					
basitrich (n)	9-12 x 2 {15} [1/2] common	20.5-24 x 2.5	19.7-22.6 x 2.8 numerous		20.0-26.3 x 2.5-3.8 {48} [4]
basitrich (o)	18.5-30 (35) x 2-4 {30} [2/2] common			30-39 x 3-4	38.5-41.8 x 2.5-3.3 {4} [2]
MESENTERIAL FILAMENTS					
microbasic p-mastigophore (p)	30-39 x 5-8 {34} [3/3] common	32.5-38 x 5.5-7	31-35.2 x 5.6		(33.6) 37.7-42.6 x 5.7-6.6 {15} [4]
basitrich (q)	10.5-17 x 2-2.5 {42} [3/3] common	11.5-14 x 1.5	17-19.7 x 2.5 few		11.5-13.9 x 1.8-2.5 {11} [3]
basitrich (r)	20-30 x 2-3 {25} [2/3] common	25.5-32 (40) x 2.5-3	25.4-29 x (2.5) 3		(22.1) 25.4-38.5 x 2.5-4.4 {24} [4]
basitrich (s)	28-40 x 2-4 {31} [2/3] common				

Chapter 4: Morphological revision of Aliciidae

Introduction

Aliciidae has not been the subject of a morphological revision since the erection of the family, even though the number of valid genera and species has been debated (Stephenson 1922, Carlgren 1949, Doumenc 1973). Carlgren (1924) discussed generic membership within the family, but did not investigate the number of valid species. I use many specimens, including type material if available, to *1) determine generic and species boundaries in Aliciidae* and *2) investigate variation in morphological features*. I also investigate hypotheses regarding proposed generic and species synonymies by using more specimens and new methods compared to previous taxonomists. There are seven nominal genera and 16 nominal species of Aliciidae (Table 4.1), with only four of these species having known type specimens.

Family background

Alicia Johnson, 1861, the type genus of Aliciidae, was originally placed in the family Bunodidae Gosse, 1858; the genera in Bunodidae were grouped together based on their possession of tubercles on the column. A strong circumscribed endodermal marginal sphincter muscle characterizes most of the other genera of Bunodidae, such as *Bunodes* Gosse, 1855, but this feature does not characterize *Alicia*. Duerden (1895) realized *Alicia* was different from the other genera in this respect, and moved *Alicia* to a new family, Aliciidae. In Aliciidae, Duerden (1895) included *Cystiactis* Milne Edwards, 1857, and *Bunodeopsis* Andres, 1881, both of which are characterized by a diffuse marginal sphincter muscles and hollow processes and vesicles over the greater part of the column, also reported for *Alicia*.

McMurrich (1889a) first erected “subtribe” (a category he used for a group of families) Dendromelinae to house the current aliciid genus *Lebrunia* Duchassaing de Fonbressin & Michelotti, 1860, but later (McMurrich 1896) reduced it to a family rank, Dendromelidae. Pax (1910, 1924), Duerden (1897), Verrill (1899, 1901), and McMurrich (1905) continued using Dendromelidae as the family name; Poche (1914) chose to rename this family Lebruniidae. The family and genus diagnosis were essentially the same, with the main distinguishing feature being the cycle of bifurcating outgrowths (term used for pseudotentacles) immediately proximal to the tentacles. McMurrich (1896) added the genera *Ophiodiscus* Hertwig, 1882 and *Hoplophoria* Wilson, 1890 to Dendromelidae, based on their possession of pseudotentacles. Duerden (1898) stated Aliciidae and Dendromelidae are very similar, and should therefore be united, even though Aliciidae was then composed only of genera with vesicles/tubercles, none with column outgrowths. In 1921, Stephenson moved *Lebrunia* to Phyllactiidae Milne Edwards, 1857, joining it with other genera such as *Phyllactis* Milne Edwards and Haime, 1851, *Cradactis* McMurrich, 1893, *Phymactis* Milne Edwards, 1857, and *Bunodeopsis*, although these genera did not share many characters. Carlgren (1924) recognized *Lebrunia* as being closely related to the other valid aliciids. *Lebrunia* shares with *Phyllodiscus* Kwietniewski, 1897, and *Triactis* Klunzinger, 1877, the possession of pseudotentacles, but is separated from them by the fertile primary mesenteries (except directives).

McMurrich (1889a, 1893) and Haddon (1898) placed *Phyllodiscus* and *Triactis* in the family Phyllactidae alongside *Lebrunia*. Phyllactidae was characterized by “prolongations from the margin of the column” (Haddon 1898, p. 435); this interpretation of the outgrowths meant that genera such as *Oulactis* and *Phyllactis* were included with *Phyllodiscus* and *Triactis* in this family. Their well-developed marginal ruff characterizes both *Oulactis* Milne Edwards and

Haime, 1851 and *Phyllactis*, which is different to the morphology of *Phyllodiscus* or *Triactis*, whose projections are from the mid-column, not the margin, and possess different cnidae. Haddon (1898) considered the inclusion of *Phyllodiscus* and *Triactis* in this family to be dubious, and thought *Phyllodiscus* was better placed in Aliciidae. Stephenson (1921) moved *Phyllodiscus* (also encompassing *Triactis*) into Aliciidae, removing all but *Alicia* and *Phyllodiscus* (also encompassing *Triactis*) from Aliciidae. Duerden (1898) suggested that *Lebrunia* should be moved into Aliciidae, but instead, Stephenson (1921) moved the genus into Phyllactidae.

After his doubt on whether Aliciidae was a homogenous group (Carlgren 1900), Carlgren (1924) investigated genera possessing vesicles and pseudotentacles further. His conclusions agreed with Stephenson's (1921) actions, with members of Aliciidae being reduced in number to include *Alicia*, *Phyllodiscus* (also encompassing *Triactis*), and *Lebrunia*. Other genera possessing tubercles on the column were grouped in the family Phyllactidae. Carlgren (1949) designated *Alicia*, *Lebrunia*, *Triactis*, and *Phyllodiscus* as the members of Aliciidae, all characterized by simple or compound vesicles or outgrowths, and vesicles with macrobasic amastigophore nematocysts.

Previously proposed hypotheses to test

Four of the seven nominal genera and 10 of the 16 nominal species of Aliciidae are currently considered valid (Fautin 2011), respectively. Stephenson (1922), Carlgren (1949), and Doumenc (1973) have suggested that the number of genera and species should be reduced further. Most of these species were described from one or a few specimens, so their variability and geographic distribution are unknown.

Ontogenetic stages of a single species may have been described as separate species. All species of *Lebrunia* possess between four and eight pseudotentacles; larger specimens with more branched pseudotentacles are identified as *Lebrunia neglecta* Duchassaing de Fonbressin & Michelotti, 1860, while the name *L. coralligens* (Wilson, 1890) is applied to smaller specimens with less branched pseudotentacles (Corrêa 1964). Other than size, there is little difference in the diagnoses of the two species, both having similar distributions (Fig 4.1). Duerden (1898, p. 457) commented, "the two are found to agree extremely closely in habit, and in all their anatomical and histological characters." Duerden (1898) and Carlgren (1949) hypothesized that the smaller specimens may be juvenile specimens of *L. neglecta*.

Similarly, Stephenson (1922) and Doumenc (1973) both speculated that *Triactis producta* (as *T. cincta*) are small specimens of *Phyllodiscus semoni* Kwietniewski, 1897. The difference between the species appears to be the size and extent of the pseudotentacle branching. Because each genus is monotypic, synonymizing one species into the other is effectively synonymizing the genera too. Stephenson (1922, pg. 281) wrote "It seems not unlikely that *Phyllodiscus* is identical with *Triactis*, but it would be well to wait for the anatomy of *T. producta* before assuming that and changing the name".

Phyllodiscus currently contains only *P. semoni* Kwietniewski, 1897. The thorough species description was based on one specimen from one locality. Since then, specimens with *Phyllodiscus* attributes have been photographed from various localities, showing a large array of morphological variation. This variation has led to speculation (Den Hartog 1997) that there are multiple species of *Phyllodiscus;* I investigate how many species there are of *Phyllodiscus* using morphometric analyses.

The genus *Alicia* currently has six valid species, three known from only one locality each. Species boundaries within this genus are difficult to determine, because there is a large variation in coloration within a locality (*e.g.* the Red Sea, based on field photos), and the distribution of each species is unknown. The type species, *Alicia mirabilis* Johnson, 1861, has been recorded from the Mediterranean, as well as the North and South Atlantic Ocean, extending to the southern coast of Brazil. *Alicia uruguayensis* Carlgren, 1927, is known from just one locality, also in the southern coast of Brazil. Schmidt (1972) proposed the most recent taxonomic changes in *Alicia;* he synonymized *Alicia costae* Panceri, 1868, described from the Gulf of Naples, with *Alicia mirabilis*, described from the Canary Islands in the Atlantic Ocean.

Material and methods

For materials and methods relating to specimen collection, cnidae analysis, and histology, refer to material and methods section of Chapter 3.

Species delineation in Lebrunia

I measured the pedal disc diameter of 159 individuals of *Lebrunia*, regardless of species identification. For each individual, I recorded the number of pseudotentacles and branch orders of a pseudotentacle. A branch order was defined as the region between points where the pseudotentacle branched dichotomously (Fig 4.2). The maximum number of branch orders for an individual represents the greatest growth achieved. Results were plotted on a scatterplot. I recorded the number of mesenteries proximally and the number of tentacles from a subset of 45 individuals of a range of sizes; these results were plotted on a scatterplot and color-coded for the number of mesenteries. The statistical program Minitab 14 (Minitab, Inc. 2005) was used for analyses and graph production.

Generic delineation between Triactis *and* Phyllodiscus

I observed pseudotentacle and vesicle details of specimens of *Triactis* and *Phyllodiscus*. The attributes examined are total number of pseudotentacles and vesicles, number of pseudotentacles and vesicles per intermesenterial space, number of branching directions of pseudotentacles, placement of vesicles on pseudotentacles, and size of pseudotentacles and vesicles. I also recorded pedal disc diameter, number of mesenteries proximally, and number of tentacles.

Species delineation in Phyllodiscus

I recorded measurements and counts relating to the pseudotentacles and vesicles, the only morphological features to exhibit variation between preserved individuals of *Phyllodiscus*. Pedal disc diameter was also measured as an indication of size. Individuals were grouped in three morphotype categories: cake, branched, pom-pom (Fig 4.3a-c). Morphometric analysis of pseudotentacle and vesicle features addressed the following traits (measurements in millimeters unless specified): diameter of peduncle (where pseudotentacle connects to scapus), density of peduncles on column (number per 3cm^2 of column), total length of pseudotentacle, number of orders of branching of pseudotentacle, number of directions of branching of pseudotentacle, density of vesicles on pseudotentacle (number per 1cm^2 area of pseudotentacle), range of vesicle diameter, maximum vesicle diameter, minimum vesicle diameter.

I ran Principal Components Analysis, a Cluster Analysis, and a Multivariate Scatterplot on raw and ln-transformed data using the statistical program JMP 9 (SAS Institute Inc. 2007).

Results

I find Aliciidae to be monophyletic, because all, and only, members of this family possess macrobasic amastigophoral vesicles. I did not find evidence of endodermal marginal sphincter muscles, nor marginal ruffs – which are morphological features of some genera (e.g. *Bunodes, Phyllactis*) that have previously been linked to some aliciids. Of the four genera I find to be valid (*Alicia, Lebrunia, Triactis,* and *Phyllodiscus*), all but *Alicia* possess pseudotentacles. Redescriptions of valid genera and species are in the "Taxonomic accounts" section.

Species delineation in Lebrunia

The number of branch orders in pseudotentacles of individuals differed by as much as two. The number of branch order ranges from zero to 12; the frequency of the branch orders has a bimodal distribution (Fig 4.4a); the two modes are two and seven. Only one individual had five branch orders. The scatterplot of branch order and pedal disc diameter (Fig 4.4b) is continuous. Individuals with 48 or fewer mesenteries proximally (black points) all have three or fewer branch orders, whereas individuals that have more than 48 mesenteries proximally (red points) have four or more branch orders (Fig 4.4c).

Generic delineation between Triactis *and* Phyllodiscus

The pseudotentacle morphology differs considerably between *Triactis* and *Phyllodiscus*, with *Phyllodiscus* possessing pseudotentacles that branch in multiple directions, multiple pseudotentacles per intermesenterial space, vesicles attached to any side of the pseudotentacles, greater number of pseudotentacles and vesicles (Table 4.2). Individuals belonging to *Phyllodiscus* also possessed greater numbers of tentacles and mesenteries proximally, even in small (8 mm pedal disc diameter) individuals, therefore these morphological characters were not correlated with size of individual.

Species delineation in Phyllodiscus

Neither the Cluster Analysis (Fig 4.5a) nor the Principle Components Analysis (Fig 4.5b) discriminated among the examined specimens. The Multivariate Scatterplot showed no correlation between any of the variables.

Discussion

Testing species delineation in Lebrunia

Although there was a continuous distribution of number of branch orders among the individuals of *Lebrunia* I observed, incorporating the number of mesenteries proximally onto the scatterplot shows two distinct groups. The first of these, with 48 or fewer proximal mesenteries, small pedal disc, and few branch orders, corresponds to *L. coralligens*. The other group corresponds to *L. neglecta;* even at the same pedal disc diameter, these animals have an extra order of mesenteries compared to *L. coralligens* individuals. The number of mesenteries provides a good character separating these species. From my results, *L. coralligens* pseudotentacles have zero to three branch orders, and *L. neglecta* at least four.

Generic delineation between Triactis *and* Phyllodiscus

Stephenson (1921, 1922) believed that *Phyllodiscus semoni* represented a fully mature anemone, whereas two other nominal species represented immature forms: *P. cincta*, the most immature, and *P. indicus*, slightly more developed. Stephenson (1921, 1922) had at his disposal the original description of *P. semoni* and *P. cincta*, and only a few specimens of *P. indicus*. These anemones share an Indo-West Pacific distribution and pseudotentacles on which are vesicles.

When Stephenson (1921, 1922) moved *Hoplophoria cincta* into *Phyllodiscus*, and named another species (*P. indicus*) in the genus, he noted that a description of the anatomy of *Triactis producta* was needed before *Phyllodiscus* could be synonymized with *Triactis*. Doumenc (1973), commenting on the same issue of the lack of difference between *Triactis* and *Phyllodiscus*, stated that the only difference between the two is the number of tentacles and the diameter of the crown of pseudotentacles. Deeming that insufficient, Doumenc (1973) synonymized *Phyllodiscus* with *Triactis*.

From my observations of hundreds of individuals of *Triactis* and *Phyllodiscus*, I have established the morphological boundaries for each genus, showing clear differences that had not been highlighted before (Table 4.2). The number and morphology of the pseudotentacles are the most distinctive attributes: compared to *Triactis*, the pseudotentacles of *Phyllodiscus* are more numerous, and multiple pseudotenacles can correspond to a single intermesenterial space. As well, the pseudotentacles of *Phyllodiscus* branch in multiple directions and the vesicles occur on any side of the pseudotentacles.

Most importantly, these features do not correlate with size of the individual. Although most of the individuals of *Phyllodiscus* examined were much larger than the individuals of *Triactis*, I observed some individuals of *Phyllodiscus* that were the same size or smaller than individuals of *Triactis*. Compared to *Triactis*, specimens of *Phyllodiscus* that have a small pedal disc diameter still possess pseudotentacles that branch in multiple directions, and still possess a greater number of mesenteries proximally (Fig 4.3d). Another difference between the two is that in *Triactis*, the pseudotentacles show more regular and even development and arrangement around the scapus compared to *Phyllodiscus*. In *Triactis* and *Lebrunia* there is a discrete ring on the scapus where pseudotentacles develop, in *Phyllodiscus* there is a larger and less defined area on the scapus where pseudotenacles develop.

I establish a clearer understanding of the variation of morphology within each genus. Within *Triactis*, the pseudotentacle and vesicle morphology is consistent, and variation in pseudotentacle morphology within the genus reflects growth and developmental stage. *Phyllodiscus*, on the other hand, has immense variation in morphology, especially of the pseudotentacles (Hoeksema & Crowther 2011). Based on my observations, I consider *Phyllodiscus* and *Triactis* to be separate monotypic genera.

Species delineation in Phyllodiscus

Hoeksema & Crowther (2011) documented multiple morphotypes of *Phyllodiscus semoni* from reefs of the Makassar Strait in Indonesia. Morphometric analyses of the pseudotentacles did not show any groupings of morphotypes. I infer that different morphotypes, largely due to the pseudotentacle morphology, do not necessarily correspond to distinct species. This inference is strengthened by additional observations that some individuals possess characteristics of multiple morphotypes, and therefore within the survey there was a gradation of morphology rather than specific morphotypes. Ongoing research will investigate whether genetic data can shed more light on the issue of whether *Phyllodiscus* is a monotypic genus.

Taxonomic accounts

Aliciidae Duerden, 1895

Diagnosis (based on Carlgren 1949, changes indicated in bold)

Thenaria (Endomyaria) with a broad pedal disc. Column **divided into scapus and capitulum, the latter may have weak longitudinal muscles and opaque spots containing dense cnidae. Scapus** with simple or compound vesicles or with **pseudotentacles** which **may be** branched in their ends. **Simple** vesicles occur on the **pseudotentacles;** with microbasic and macrobasic amastigophores. The **capitulum** may have weak longitudinal muscles, and spots containing spirocysts and few nematocysts. No distinct **marginal** sphincter. Margin tentaculate, no fossa. Tentacles long with spots as in upper part of column. Longitudinal muscles of tentacles and radial muscles of oral disc ectodermal. Two siphonoglyphs. Pairs of **complete** mesenteries six, sterile or fertile. Two pairs of directives. Retractors diffuse, weak or rather strong. Basilar muscles weak or well developed. Cnidom: spirocysts, basitrichs, microbasic *p*-mastigophores, microbasic and macrobasic amastigophores.

Valid genera

Alicia Johnson, 1861 (Type genus)

Lebrunia Duchassaing de Fonbressin & Michelotti, 1860

Triactis Klunzinger, 1877

Phyllodiscus Kwietniewski, 1897

KEY:

1 a) Pseudotentacles absent. Vesicles simple or compound, attached directly to scapus or stalked. Tentacles numerous, very long and sinuous, commonly curled at distal ends.

……………………………………………….*Alicia*

b) Pseudotentacles on scapus. All vesicles simple, attached to pseudotentacles or rarely to scapus.

……………………………………………2

2 a) Pseudotentacles in multiple whorls, branch in multiple directions. Vesicles of one kind, but multiple sizes, occur on all sides of pseudotentacles, rarely on scapus.

……………………………………..…*Phyllodiscus*

b) Pseudotentacles in single whorl of scapus. Vesicles of one or two kinds. If branched, branch in one direction, perpendicular to oral-aboral axis.

……………………………………………3

3 a) Multiple pseudotentacles in whorl. At most developed stage, one pseudotentacle in every intermesenterial space, and base of pseudotentacles fused to form a continuous region at junction of scapus and capitulum. Most developed and largest pseudotentacles extend past edge of fused region to form branched region of pseudotentacle. Vesicles simple, attached directly to pseudotentacles, rarely to scapus, some individuals with

stalked vesicles. To three or four vesicles on largest pseudotentacle.

……………………………………………*Triactis*

b) Between two and nine pseudotentacles in whorl per individual, most commonly six. Pseudotentacles form only in intermesenterial endocoels of lower order mesenteries. Pseudotentacles always distinct from one another, do not fuse. Vesicles simple, either raised hemispheres or flat opaque patches of ectoderm. Vesicles at distal end or oral side of pseudotentacles, rarely on scapus.

…………………………………………….*Lebrunia*

Discussion

None of the molecular datasets produced a phylogenetic hypothesis that supported the monophyly of Aliciidae to include *Alicia*, *Lebrunia*, *Triactis*, and *Phyllodiscus* (Figs 2.2–2.11). A clade consisting of the three pseudotentacle-bearing genera (*Lebrunia, Triactis, Phyllodiscus*) was recovered with high support from the combined five-gene analyses (Fig 2.10, 2.11, 2.14). Since only members in this clade possess pseudotentacles, this indicates that the pseudotentacles of *Lebrunia, Triactis*, and *Phyllosdiscus* are homologous.

The monophyly of Aliciidae is supported by morphology; this is the only family with members that possess vesicles with macrobasic amasitigopore nematocysts. The macrobasic amastigophores of aliciids are different to macrobasic amastigophores that have been reported from Diadumenidae and Antipodactinidae (pers. comm. A. Reft and E. Rodriguez). The nematocysts reported as macrobasic amastigophores of Diadumenidae and Antipodactinidae are most likely microbasic amastigophores with a slightly longer shaft, and also lack features of aliciid macrobasic amastigophores seen using Scanning Electron Microscopy (pers. comm. A. Reft).

Alicia Johnson, 1861

Synonymy

Cladactis Panceri, 1868

non *Cladactis* Verrill, 1869

Gender

Feminine

Diagnosis (based on Carlgren 1949, changes indicated in bold)

Aliciidae with well developed **pedal** disc. Column delicate, divisible into scapus and capitulum. Scapus with vesicles, simple or stalked and compound, containing microbasic and macrobasic amastigophores. **Compound and stalked vesicles in ring at distal end of scapus.** Tentacles **numerous**, long and slender, **may be curled at end**, with spots as in the capitulum. Two weak siphonoglyphs. Six pairs of **complete** and sterile mesenteries. Retractors weak. Parietobasilar and basilar muscles very weak.

Distribution

Tropical and temperate, shallow to 80 m. Caribbean Sea, Atlantic Ocean, Pacific Ocean, Mediterranean Sea.

Valid species

Alicia mirabilis (Johnson, 1861) (Type species)

Alicia pretiosa (Dana, 1846)

Alicia sansibarensis Carlgren, 1900

Alicia beebei Carlgren, 1940b

Alicia uruguayensis Carlgren, 1927

Discussion

Members of *Alicia* are distinctive and easy to identify to genus because they are the only sea anemones bearing dense simple or compound vesicles on a very delicate column wall. These striking sea anemones are frequently photographed by divers (Fig 4.9d,e), particularly in the Mediterranean. The monophyly of *Alicia* was recovered in most molecular phylogenies (Fig 2.2, 2.4, 2.5, 2.7, 2.8, 2.10, 2.11), although, sequences were only available for three of the five species.

Of the seven nominal species, type specimens are known for only two: *Alicia sansibarensis* and *A. uruguayensis*. Five of the seven species were described from single specimens; the other two were described using two and three specimens. *Alicia sansibarensis, A. beebei, A. rhadina,* and *A. uruguayensis* have not been recorded from anywhere other than the type locality. For a large proportion of the genus, therefore, the extent of the distribution of species is not known and variability is poorly documented.

Even though there are clear morphological characters to diagnose the genus *Alicia*, the characters to separate the species are not as clear. Characters such as mesenterial arrangement lack variation among species. Most species possess four orders, with first order complete and orders two to four incomplete, and if information available, first order sterile while the rest fertile. The exception is *Alicia pretiosa*, where specimens, even at the same size as specimens of other species, have three instead of four orders of mesenteries. This species is also distinguished from the others by the possession of a red spot on the oral side of the proximal part of the tentacles (Haddon & Shackleton 1893).

There is little variation in external or internal morphology among *Alicia* specimens; the most variation in the genus is seen in coloration. In fact, the variation in color within and among species of *Alicia* is large; in the species description of *Alicia sansibarensis*, Carlgren (1900) stated the vesicles of an individual were predominantly violet, but could also be yellow, white, brown-red, or pink. Similar colors were also recorded for *A. mirabilis, A. costae, A. pretiosa,* and *A. rhadina.* Schmidt (1972) proposed that the color of an individual is related to the brightness of the locality, noting that in clear waters, *A. mirabilis* tends to be green-brown to dark green, whereas in turbid water individuals a more orange-yellow. No similar observations are available for other species of *Alicia*, so it is unknown whether this information will hold true.

Apart from color, the most variable morphological feature among members of the genus is the vesicle. Vesicle density may vary among individuals of a species, as proposed by Schmidt (1972) for *Alicia mirabilis*. He suggested that differences could be due partly to size and age of an individual, as younger or smaller individuals may have smaller and fewer vesicles, but he suggested this could also be a consequence of environmental influences such as water flow. The number of vesicles on the distal stalks was originally used to separate species *A. mirabilis* and *A. costae*, but has since been considered too variable among individuals to be a specific character (Schmidt 1972). In his discussion of the synonymy of *A. costae* with *A. mirabilis*, Schmidt (1972) posited that individuals found in the Atlantic have denser vesicles than individuals in the Mediterranean, due to the higher water motion in the Atlantic.

Seaton (1981) considered that the difference originally separating *Alicia mirabilis* and *A. costae*, the number of vesicles on distal stalks, was greater than the difference separating most other species in *Alicia*, yet Schmidt (1972) synonymized the two species. Seaton (1981) speculated that if *A. costae* had been synonymized with *A. mirabilis*, then even fewer species should be considered valid; he thought *A. costae*, *A. uruguayensis*, *A. beebei*, and *A. sansibarensis* should be junior synonyms of *A. mirabilis*, and *A. rhadina* a junior synonym of *A. pretiosa*. Despite not having clear morphological characters to delineate the rest of the species, I use cnidae to provide some resolution. *Alicia beebei* has the most distinctive cnidom, with unique types and size classes compared to the other species, and *A. uruguayensis* could be distinguished from *A. mirabilis* due to size of cnidae. *Alicia pretiosa* also possesses unique size classes of cnidae compared to other species in the genus.

Alicia mirabilis (Johnson, 1861)

Fig 4.6–4.9

Tables 4.3–4.4

Synonymy

Actinia mirabilis Johnson, 1861, p. 303–305

Cladactis costae Panceri, 1868, p. 30–32

Type specimens and localities

Alicia mirabilis type locality and syntypes: Madeira Archipelago, Madeira, Bay of Funchal, no type material.

Cladactis costa type locality and syntypes: Italy, Gulf of Naples, northern Capri Island, no type material.

Material examined

Table 4.3.

Description

Pedal disc

Circular to oval, some irregular (Fig 4.6a). Diameter of preserved specimens 15–130 mm. Adherent. Pale brown or yellow-green in life, translucent. Cream in preservation, opaque. No pattern. Limbus with ~ 96 radial furrows from mesenterial insertions; concentric furrows from contraction.

Column

Cylindrical when expanded (Fig 4.6b), conical when oral disc completely retracted. Length of preserved specimens 30–70 mm, expanded specimens to 200 mm. Delicate tissue, mesenterial insertions visible as bright white lines. Scapus with vesicles. Pale brown, beige, or yellow-green in life, translucent, greenish-gray preserved. Capitulum translucent, free from outgrowths, about ¼ length of scapus.

Vesicles

Most compound, stalked, cover most of scapus. When contracted, vesicles form unbroken coat; when expanded, scapus visible between vesicles (Fig 4.6c). Colors range from purple, green, brown, white, black, orange, or brick red; can be multicolored within individual. Some stalks opaque white and some orange in one individual. Distal most compound stalks up to 60 vesicles. Usually six distal-most compound stalks on scapus.

Oral disc

Circular, flat (Fig 4.6d). Diameter of preserved specimens 7–30 mm. Tissue thin. Pale brown or yellow-green, translucent. Mesenterial insertions visible as white lines. Central mouth oval, lips inflated in some specimens, 10–12 mm greatest length. Actinopharynx rich brown in life, opaque, strongly furrowed with 12 longitudinal creases. Two siphonoglyphs, not distinct.

Tentacles

Simple, taper to blunt point, elongated, rather slender. Preserved length to 40 mm, width to 4 mm. Yellow-green, rust, or pale brown with black band proximally in life, cream in preservation. Nematocyst batteries visible as opaque spots, tips opaque. Numerous, to 96, compactly set in 3 rows near margin. In life, longer than column.

Mesenteries and internal anatomy

Very thin, delicate. 48–96 mesenteries in 3–4 hexamerously arranged orders. First order complete, sterile. Orders two to four incomplete, fertile. Yolk-poor eggs (~100 um) round, smooth. Sperm pointed apically. Filaments on all mesenteries. Retractors diffuse. No marginal stomata. Marginal sphincter muscle endodermal, diffuse, elongate, extends length of capitulum, according to Duerden (1895, 1897), absent according to Schmidt (1972); I did not observe a marginal sphincter muscle.

Cnidae

Fig 4.7 and Table 4.4.

Habitat and ecology

Attached lightly to hard substrate such as sea grass or sea fan. Detach readily and float with inflated base up (Johnson 1861, Fig 4.6e). Habitually found in elevated locations so long tentacles free to float in water stream, particularly at night. Schmidt (1972) reports that sea anemone *Cribrinopsis crassa* eats *A. mirabilis*.

Distribution

Mediterranean and Caribbean Seas, and the Atlantic Ocean from Madeira Archipelago and Canary Islands in the north, to southern coast of Brazil (Fig 4.8).

Discussion

Of all the *Alicia* species, *Alicia mirabilis* has been published on the most (Fig 4.9a,b), photographed by divers (Fig 4.9c,d), and found from the greatest number of localities (Fig 4.8). It has also been used on a stamp from Portugal (Fig 4.9e). Johnson's (1861) description, based on a single specimen collected at the Bay of Funchal, Madeira, was a thorough account of the external morphology, with a figure, but lacked information on internal anatomy. *Cladactis costa* Panceri, 1868 was described from a single specimen collected in the Gulf of Naples. The original description was thorough for elements of the external morphology, and included detailed figures. Duerden (1895, 1897) provided further information regarding internal morphology for *Alicia* species *A. costae* and *A. mirabilis*, respectively. Specimens I observed were within the variation of morphological characters that had been recorded for *A. mirabilis* and *A. costae*.

Andres (1884) separated *Cladactis mirabilis* and *Cladactis costa* (the only other species in the genus at the time) based on the number of vesicles in the distal-most stalks; *C. mirabilis* has approximately 60, whereas *C. costa* has only 10–30. Schmidt (1972) published the most detailed description of *A. mirabilis*, including details of external and internal morphology, cnidae, ecology, distribution, and reproduction, observing that individuals of *A. costae* can possess more than 60 vesicles on the distalmost stalks – refuting the significance of the feature Andres (1884) used to separate the species. Schmidt (1972) therefore synonymized *A. costae* with *A. mirabilis*. Based on this decision, Seaton (1981) discussed a valid point about what this means for the genus and number of valid species, which will be considered further in the *Alicia* genus discussion section.

Cnidae I measured were within the range of cnidae measurements provided by Carlgren (1940a), Schmidt (1972), and Seaton (1981) (Table 4.4). There are a few differences, where certain size classes were found by Seaton (1981) and not by others, but these were mostly classified as sparse.

Alicia pretiosa (Dana, 1846)

Fig 4.10–4.12

Tables 4.5–4.6

Synonymy

Actinia pretiosa Dana, 1846, p. 137, Fig. 20

Alicia rhadina Haddon & Shackleton, 1893, p. 117, 127–128

Type specimens and localities

Alicia pretiosa type locality and syntypes: Fiji, Vanua-levu, Sandalwood Bay, no type specimens.

Alicia rhadina type locality and syntypes: Australia, Queensland, Cape York, Albany Pass, no type specimens.

Material examined

Table 4.5.

Description

Pedal disc

Circular to oval (Fig 4.10a). Diameter of live specimen (KUDIZ 3168) 4–8 mm, of preserved specimens 4–50 mm. Opaque, cream in preservation, no pattern, tissue thicker than proximal column. Mesenterial insertions not easily visible, except at limbus, where mesenterial insertions visible as light lines. In life, attached to hard substrate (rock, scleractinian coral), but able to detach easily and inflate to float in water.

Column

Cylindrical when expanded (Fig 4.10b), conical when retracted. Length 5 mm in live specimen (KUDIZ 3168, Fig 4.10b), 5–30 mm in preserved specimens. Scapus translucent in live specimens (Fig 4.10b,c), pinkish or cream translucent in most preserved specimens, sometimes cream to off-white opaque. Capitulum translucent in live specimens, white to cream in preserved specimens, with white spots formed by dense patches of cnidae.

Vesicles

Vesicles red in live specimen (KUDIZ 3168, Fig 4.10c). Compound stalked vesicles (Fig 4.10d) from endocoels of primary mesenteries, to 20 vesicles. At mid-column, simple or compound vesicles present, sessile or stalked. At proximal end of column, simple sessile vesicle between each mesentery pair. Stalks transparent, cnidae-dense pad opaque. In life brown, red, or greenish grey. KUDIZ 3168 vesicles with outer ring of yellow, middle ring of red, and yellow center in life (Fig 4.10b,c). Dana (1846, p. 137) described vesicles of *Actinia pretiosa* as "rich carmine, with a white border." In some specimens, vertical rows of vesicles alternate among different colors, for example one row of brown vesicles bounded by row of white vesicles on either side.

Oral disc

Flat, circular. Diameter of live specimen 5 mm, of preserved specimen 8–11 mm. Tissue thin, mesenterial insertions visible as white lines. White, translucent. No pattern, but with opaque spots from dense cnidae patches. Central mouth oval, lips inflated in some specimens; white in preservation; KUDIZ 3168 had red mouth and actinopharynx in life (Fig 4.10b,c). In preserved specimen, actinopharynx white to cream, opaque, strongly furrowed. Siphonoglyphs sometimes difficult to discern.

Tentacles

All of similar appearance: slender, taper to blunt tips, some with pore at tip. Inner longer than outer; longest to 50 mm, width at base to 2 mm in preserved specimens. In live specimens translucent, or golden brown with red spot on oral side of proximal part of tentacle (Haddon & Shackleton 1893), spotted with dense cnidae patches, sometimes with band of color around proximal end (Fig 4.10b,c). In preserved specimens beige, cream, or white, translucent with opaque spots, opaque tip, and opaque ring where attached to oral disc. 24–70 arranged in 2 cycles.

Mesenteries and internal anatomy

Very thin, transparent. To 48 pairs of mesenteries hexamerously arranged in four orders. Members of first order complete; members of second and third order incomplete, all with filaments. Same number distally and proximally. Specimens examined did not possess gametes, and no information is available from published literature.

Cnidae

Fig 4.11 and Table 4.6.

Habitat and ecology

Shallow localities of the West Pacific Ocean. KUDIZ 3168 was collected from a cave in Palau with very silty substrate, and was the smallest specimen examined.

Distribution

West Pacific Ocean, from Australia to Japan. Fig 4.12.

Discussion

I consider *Alicia rhadina* Haddon & Shackleton, 1893, to be a junior synonym of *Alicia pretiosa* (Dana, 1864), because I find no defining characteristics in the original descriptions to set the two apart. Haddon (1898, p. 434) stated he found *A. rhadina* to be "close to *Alicia* (or *Actinia*?) *pretiosa*, but I think it is a new species" without giving reasons. The original descriptions each were based on a single specimen, and stated only external morphological characters. The two species match in number of mesenteries and tentacles, and in patterning of tentacles. Both species possess a dark spot on the proximal, oral side of their outer tentacles (Fig 4.10f), a feature that has not been recorded in any other *Alicia* species. Although there is no type material for either species, the original descriptions provide enough information that matched with observations of live and preserved material, that I synonymize the two species.

Alicia rhadina was described from Cape York, North Queensland, Australia, and has not been recorded since. *Alicia pretiosa* was described from Fiji; the only other record of *A. pretiosa* is Japan (Uchida & Soyama 2001). Although I was unable to confirm this identification, it is highly likely that a species found in the tropical central and South Pacific will also be found in Japan. Other examples in Aliciidae with a similar distribution include *Triactis producta* and *Phyllodiscus semoni*. A specimen from Japan I did examine (CAS 161241) fit the description of *Alicia pretiosa*.

The cnidome of *Alicia pretiosa* had two unique size classes to set it apart from available information from other species of *Alicia*. In the mesenterial filaments, *A. pretiosa* had a small sized microbasic p-mastigophore, and in the tentacles, a wider second type of microbasic amastigophore. These cnidae differences, coupled with the mesentery number and tentacle patterning make this species unique. It was difficult to ascertain whether other specimens I observed were *A. pretiosa*. CAS 161241 possesses more mesenteries proximally than published for *A. pretiosa* or *A. rhadina*: 96 compared to 48. However, it possesses the same number of tentacles (48) as described by Dana (1846) and Haddon & Shackleton (1893). The distribution of *A. pretiosa* may be wider than presented in this species treatment, potentially Indo-West Pacific; please refer to the *Alicia* genus discussion for further information.

Alicia sansibarensis Carlgren, 1900

Fig 4.13–4.16

Tables 4.7–4.8

Synonymy

Alicia sansibarensis Carlgren, 1900, p. 28–30

Type specimens and localities

Alicia sansibarensis type locality and syntypes: Zanzibar, Tumbatu, SMNH 1169 (1 specimen), ZMH C2592 (1 specimen), ZMH C2597 (1 specimen).

Material examined

Table 4.7

Description

Pedal disc

Circular, slightly concave, pulled in at mesenterial insertions. Diameter of live syntypes 50–70 mm (Carlgren 1900), of preserved specimens 10–50 mm. Slightly wider than proximal column, and wider than oral disc. Tissue thicker than proximal column, opaque. Cream to beige, no pattern. Mesenterial insertions visible as radiating depressions, concentric furrows due to contraction (Fig 4.13a). At limbus, mesenterial insertions visible as light lines, and correspond to notches of pedal disc edge. In life, attached to hard substrate (rock, scleractinian coral) in sandy areas.

Column

Preserved specimens conical when oral disc retracted (Fig 4.13b). Length of live syntype 60–80 mm, of preserved specimens 13–70 mm. Capitulum translucent, cream, smooth with opaque spots formed by dense patches of cnidae; 3–4 mm long in preserved specimens. Scapus yellowish beige color, with pink vertical stripes in life (Fig 4.13c, Carlgren 1900), cream or beige opaque in preserved specimens. Majority of scapus covered with vesicles.

Vesicles

Most vesicles compound and stalked (Fig 4.13b), rarely simple and sessile. At distal end of scapus, compound stalked vesicles (Fig 4.13d) from endocoels of primary mesenteries. Endocoels of lower order mesenteries with more compound and stalked vesicles; most developed compound vesicles with up to 40 vesicles per stalk. At proximal end of column, stalks shorter, and vesicles densely packed in horizontal rows. Stalks transparent, cnidae-dense pad opaque. In life, vesicles predominantly violet, but can be yellow, white, brown-red, or pink. Specimen Copenhagen #1 possesses two distal-most compound stalked vesicles much longer than other; stalks measure 10 mm long and 3.5 mm wide, and have vesicles along length, densest at distal end (Fig 4.13e).

Oral disc

Flat, circular. Diameter 8–40 mm. Tissue thin. Cream, opaque, no pattern. Central mouth oval, lips inflated in some specimens; cream in preservation. Actinopharynx brownish-red, strongly furrowed longitudinally (due to mesenterial insertions) and vertically (due to contraction). Siphonoglyphs cream.

Tentacles

All of similar appearance. Inner longer than outer; longest to 70 mm, width at base to 2 mm. In preserved specimens beige, cream, or white, translucent with opaque spots, opaque tips, and opaque ring where attached to oral disc. In live specimens, glossy pink, with darker pigmentation at proximal end (Carlgren 1900). Opaque spots with dense cnidae patches. At least 48 and as many as 60, arranged in two cycles at margin.

Mesenteries and internal anatomy

Thin, white or cream, opaque mesenteries. Oral stomata, no marginal stomata. Forty-eight pairs of mesenteries hexamerously arranged in four orders (please see note regarding original description in discussion). Mesenteries of first order complete, sterile; of second to fourth orders incomplete, fertile. All mesenteries with filaments. Sexes presumably separate. Same number distally and proximally.

Cnidae

Fig 4.14 and Table 4.8.

Habitat and ecology

Shallow localities of the Indian Ocean.

Distribution

Western Indian Ocean (Fig 4.15).

Discussion

Carlgren (1900) provided a detailed description of *A. sansibarensis*, including external morphology, internal anatomy, and cnidae. Syntypes are in fairly good condition, which is rare for this genus. *Alicia sansibarensis* is the only species of the genus known from the Indian Ocean, being described from Zanzibar and collected recently in Mozambique. It is possible that specimens of *Alicia* photographed in the Red Sea (Fig 4.16) are also *A. sansibarensis*, based on external morphology and distribution. The specimen collected from Mozambique (housed at AMNH) is slightly smaller than the syntypes from Zanzibar, but agrees in number of mesenteries, tentacles, and vesicles at distalmost scapus. Despite fieldwork in Zanzibar and the Red Sea, I was unable to collect any specimens of *A. sansibarensis*.

Parulekar (1990) recorded *A. sansibarensis* in India, but I doubt the sea anemone is an *Alicia*. Parulekar (1990) lists *A. sansibarensis* as burrowing; specimens of *Alicia* are usually attached, even though lightly, to a hard or firm substrate. They are not known to burrow, thereby making the identification of this species dubious.

Alicia sansibarensis is the only species of *Alicia* to have sequences from two specimens. The two specimens were receovered as sister in the 18S (Fig 2.6) and all except 28S (Fig 2.9) phylogenies, but not in the 28S (Fig 2.7), nuclear (Fig 2.8), or combined five-gene (Fig 2.10, 2.11) phylogenies.

Alicia beebei Carlgren, 1940b

Fig 4.17–4.19

Tables 4.9–4.10

Synonymy

Alicia beebei Carlgren, 1940b p. 211–212

Type specimens and localities

Alicia beebei type locality and syntypes: Mexico, Gulf of California, Arena Bank, no type material.

Material examined

Table 4.9.

Description

Pedal disc

Circular to oval, wide, slightly concave (Fig 4.17a). Diameter 20–80 mm. Slightly wider than proximal column, and wider than oral disc. Tissue thicker than proximal column, opaque, buff brown or dark beige, no pattern. Mesenterial insertions visible as dark lines. At limbus, mesenterial insertions visible as restrictions of the circular pedal disc.

Column

Cylindrical to conical when retracted (Fig 4.17b). Length 25–85 mm. Scapus dark beige translucent, covered with vesicles. Capitulum translucent, beige.

Vesicles

Most vesicles compound and stalked, very rarely simple and sessile. At distal end of scapus, stalks protrude from endocoels of primary mesenteries, up to 20 vesicles (Fig 4.17c). Proximal scapus provided with sessile vesicles, crowded toward base, more scattered distally. In life, vesicles can be brown, red, dark pink, white, gold, and green (Fig 4.17c).

Oral disc

Flat, circular (Fig 4.17d). Diameter 15–30 mm. Tissue thin, beige. Large central mouth oval, lips inflated in some specimens. Actinopharynx cream to beige, opaque, strongly furrowed (Fig 4.17d,e). Siphonoglyphs difficult to discern. In USNM 49397, mouth oval, longest diameter 15 mm, mouth diameter half that of oral disc (diameter 30 mm) (Fig 4.17e).

Tentacles

All of similar appearance, taper to blunt tips. Inner longer than outer; longest to 120 mm, width at base to 4 mm. USNM 49397 distal curled ends have become entwined (Fig 4.17b). In preserved specimens translucent, beige or cream, scaly pattern from dense cnidae patches, proximal part of tentacles opaque, yellowish-brown. 92–100 arranged in 2 cycles.

Mesenteries and internal anatomy

Very thin, transparent. Hexamerously arranged in four orders. Members of second to fourth order incomplete, all with filaments. Same number distally and proximally. All specimens observed sterile.

Cnidae

Fig 4.18 and Table 4.10.

Habitat and ecology

Attached to hard surfaces such as rocks or black coral, from shallow to depths of 64 m. Found in areas with loose rock or sandy substrate. USNM 49397 found in tide pool.

Distribution

Gulf of Mexico and southern California coast. Fig 4.19.

Discussion

Alicia beebei was described by Carlgren (1940b), who provided details of the external morphology and nematocyst measurements from a single specimen collected from the Gulf of California, Mexico. In 1951, Carlgren supplemented this description with details of a larger specimen of *A. beebei*, also from the Gulf of California. External morphology measurements from specimens in the present study were within the bounds of the original material (Carlgren 1940b, 1951). Although there is no type material, I was able to observe the voucher specimen from Carlgren (1951). In addition, I studied a specimen from the Gulf of California collected by Carlos Sanchez.

I provide information on the oral disc cnidae, which Carlgren (1940b, 1951) did not include. I observed an additional size class of microbasic *p*-mastigophore in the tentacles and actinopharynx, and microbasic amastigophore in the vesicles (Table 4.10). The unique microbasic *p*-mastigophores of *Alicia beebei* were found only in small numbers, and designated as rare in the table. The largest difference between what Carlgren (1940b, 1951) recorded for the cnidae of *A. beebei* and what I observed, are the sizes of microbasic amastigophores of the actinopharynx; I observed larger microbasic amastigophores than what Carlgren (1940b, 1951) observed. Carlgren (1940b) recorded an extra type of nematocyst in the mesenterial filaments, but could not determine whether this was a microbasic amastigophore or *p*-mastigophore. Carlgren (1951, p. 481) commented that the specimen studied was larger than the holotype and "The nematocysts also larger throughout." This could be a cause of differences in cnidae measurements between individuals, as seen in Table 4.10, where there are different sets of measurements for cnidae of the vesicles obtained from different sized individuals.

The effect of individual size on external morphology is unknown. The holotype, with a pedal disc diameter of 20 mm, is recorded as having 2–7 vesicles per stalk (Carlgren 1940b). The voucher specimen from Carlgren's (1951) paper, USNM 49397, possesses a pedal disc with diameter of ~75–80 mm, and up to 20 vesicles in the distal-most stalks. The uncataloged specimen from Loreto, Mexico, also possesses 20 vesicles per stalk, but had a pedal disc diameter of 35 mm. The latter two specimens have 96 mesenteries and approximately 96 tentacles; this information is unknown from the holotype.

Carlgren, even after having described two other *Alicia* species (*A. sansibarensis* in 1900 and *A. uruguayensis* in 1927), did not provide additional information or distinguishing features in his accounts of *A. beebei*. Distribution and cnidae size differences distinguish this species from others of the genus. The other species found in the Pacific Ocean is *A. pretiosa*, which has fewer mesenteries and tentacles than *A. beebei*.

Alicia uruguayensis Carlgren, 1927

Fig 4.20–4.21

Tables 4.11

Synonymy

Alicia uruguayensis Carlgren, 1927, p. 18–19

Type specimen and locality

Alicia uruguayensis type locality and syntypes: Southern Brazil (Carlgren [1927, 1949] stated off Uruguay), SMNH 86 (2 specimens).

Material examined

Table 4.11.

Description

Pedal disc

Circular. Diameter 13–20 mm, slightly wider than proximal column, and wider than oral disc. Opaque, cream/beige in preservation, no pattern. Slightly concave. Concentric rings from contraction, radial indentations from mesenterial insertions.

Column

Conical when retracted (Fig 4.20a). Length 17–20 mm. Scapus beige or cream in preserved specimens. Capitulum beige.

Vesicles

Compound with 2–6 spheres per stalk, very few simple. Average diameter of sphere 0.75 mm. All distal-most vesicles missing.

Oral disc

Circular. Diameter 9–10 mm. Tissue thin, mesenterial insertions visible as ridges. Cream, opaque. No pattern. Central mouth oval, cream in preservation. Actinopharynx cream, opaque, strongly furrowed. Mouth and actinopharynx inflated, protruding from oral disc. Siphonglyphs not clearly distinguished.

Tentacles

Most tentacles missing from specimen. 48 in two cycles, judging from apertures where tentacles were attached (Fig 4.20b).

Mesenteries and internal anatomy

Same number of mesenteries proximally and distally. Specimens not well preserved internally, no other information available.

Cnidae

No information.

Habitat and ecology

80 m, blackish clay.

Distribution

Off the coast of southern Brazil (Fig 4.21).

Discussion

Carlgren's (1927) description of *A. uruguayensis* does not provide many details of external morphology, and no information of internal morphology. He does provide nematocyst data for the species. The poor description is because the specimens were "very badly preserved and partly damaged" (Carlgren 1927, p. 19), which also made it difficult for me to gain any additional useful information from the syntypes. Even the number of tentacles is inferred from the number of holes around the oral disc, as they were all lost. I was unable to observe the number of mesenteries, due both to poor preservation and one specimen being heavily damaged. The distalmost stalks with vesicles are also missing, the holes on the column where they were attached clearly visible. The cnidom reported by Carlgren (1927) indicated that the actinopharynx cnidae or *A. uruguayensis* are larger than those of *A. mirabilis*.

When Carlgren (1927) described *Alicia uruguayensis*, *A. mirabilis* was known only from Maderia in the North Atlantic, and *A. costae* from the Mediterranean. It was not until Corrêa (1973) identified specimens of *A. mirabilis* from Brazil did the known distribution of *A. mirabilis* widen to the western Atlantic. Following this, Zamponi *et al.* (1998) identified and recorded *A. mirabilis* from more regions of Brazil, so now the southern-most locality recorded for *A. mirabilis* is less than 1,000 km from the *A. uruguayensis* locality. Currently, *A. mirabilis* are known to occur to depths of 50 m, while *A. uruguayensis* occur at 80 m.

The individuals of *A. uruguayensis* are some of the smallest *Alicia* encountered in this study. This may, or may not, be correlated with lower percent coverage of the scapus by vesicles, and that most vesicles were compound with only two or four divisions. This species is known from only one locality, in the Atlantic Ocean off the coast of southern Brazil. It is sympatric with *A. mirabilis* (Fig 4.22), according to published localities of *A. mirabilis* in Brazil (Zamponi *et al.* 1998).

From the data available, *Alicia uruguayensis* is sympatric with *A. mirabilis*, with cnidae size differences and depth separating the two species. The disjunct distribution of *A. mirabilis* from the North to West Atlantic needs further investigation. Specimens from the Western Atlantic identified as *A. mirabilis* need to be confirmed as such, but observing *Alicia* specimens in that region. If cnidae of specimens from the Western Atlantic overlap in size with cnidae reported from *A. uruguayensis*, there could be one species in the Western Atlantic. Whether that species is *A. mirabilis* or *A. uruguayensis* would require comparison with specimens from the North Atlantic, as Madeira Islands is the type locality of *A. mirabilis*. If there is no overlap in cnidae with *A. uruguayensis*, then these two species remain sympatric.

Lebrunia Duchassaing de Fonbressin and Michelotti, 1860

Synonyms

Taractea Andres, 1883a

Stauractis Andres, 1883a

Oulactis pro parte Duchassaing de Fonbressin and Michelotti, 1860

Rhodactis pro parte Duchassaing de Fombressin and Michelotti, 1866

Hoplophoria Wilson, 1890

Cradactis pro parte Hargitt, 1911

Gender

Feminine

Diagnosis (based on Carlgren 1949, changes indicated in bold)

Aliciidae with smooth column. **One ring of pseudotentacles just proximal to tentacles. Pseudotentacles 2–9 per individual, dense with zooxanthellae (dark brown color, some also with lighter pigmentation); ends may be branched in one plane perpendicular to oral-aboral axis. Vesicles attached at distal end or on oral surface of pseudotentacles: all simple, but can be hemispheric and raised, or opaque patch on ectoderm;** contain micro- and macrobasic amastigophores. **Capitulum** with weak longitudinal muscles and spots of spirocysts and nematocysts. Tentacles, inner longer than outer, with **opaque** spots as on **capitulum**. Longitudinal muscles of tentacles and radial muscles of oral disc ectodermal. Two distinct siphonoglyphs. Six perfect pairs of mesenteries and several **pairs** incomplete. Complete mesenteries, except directives, fertile. Retractors diffuse, moderately developed. Parietobasilar muscles weak, basilar muscles well developed.

Distribution

Tropical Caribbean Sea and western Atlantic Ocean to approximately 30 m.

Valid species

Lebrunia neglecta Duchassaing de Fonbressin & Michelotti, 1860 (Type species)
Lebrunia coralligens (Wilson, 1890)

Discussion

Members of the genus *Lebrunia* all possess pseudotentacles in one whorl, and can have two forms of vesicles. Genetic data support monophyly of *Lebrunia*, as members of the genus are always most closely related to one another and distantly related to other genera (Fig 2.2, 2.3, 2.5, 2.9, 2.10, 2.11). With the combined five-gene analyses, *Lebrunia* was recovered as monophyletic with high support, with bootstrap value of 100 when *Lybia* symbiont specimens were included and 99 when they were not.

There are two valid species of *Lebrunia, L. neglecta* and *L. coralligens*. The initial suggestion that *L. coralligens* was a juvenile form of *L. neglecta* by Duerden (1898) has pervaded the literature through to recent times (Carlgren 1949, Corrêa 1964, Stanton 1977, Dube 1981). The genus *Lebrunia* was most recently reviewed by Corrêa (1964), who found specimens of *L. coralligens* were smaller than specimens of *L. neglecta* and possess pseudotentacles that branched twice at most, a point that Dube (1981) reiterated, while pseudotentacles of *L. neglecta* branch more than twice. Corrêa (1964) also proposed that specimens of *L. coralligens* could be a neotenous form of *L. neglecta.* Corrêa (1964) was unable to conclusively test the hypothesis that the name *L. coralligens* had been applied to juveniles of *L. neglecta* because she lacked individuals of intermediate sizes. The lack of intermediate sizes available to study was also an issue for Duerden (1898), so both Duerden (1898) and Corrêa (1964) kept the species separate.

Previous workers lacked individuals of intermediate sizes (Duerden 1898, Corrêa 1964), so could not provide resolution on this issue. By observing specimens from museum collections and collecting specimens from the field, I was able to observe individuals of a wide size range and can confirm that *L. coralligens* is a separate and valid species, not a juvenile form of *L. neglecta*. Compared to similar sized individuals of *L. neglecta, L. coralligens* possess fewer mesenteries (no more than 48), and pseudotentacles with fewer branch orders (three at most), with no overlap with small specimens of *L. neglecta*. The combination of these two characters can be used to distinguish these two species.

The molecular results did not support two reciprocally monophyletic species within *Lebrunia*. Instead, representatives of *Lebrunia neglecta* and *L. coralligens* were nested together (Fig 2.2, 2.3, 2.5, 2.10, 2.11) or related to other species (Fig 2.7, 2.8). However, missing data could have influenced this result. As shown in Table 2.1, the gene sequences available for *Lebrunia* species is patchy, and most information on relationships from molecular data comes from mitochondrial genes 12S and 16S. Mitochondrial genes, in this instance, may not have appropriate rates of evolution to determine species-level relationships (Hellberg 2006), and nuclear genes may provide better resolution at species level (Hellberg 2007). Despite the genetic sequences not providing evidence for separate species, the morphometric analyses of psuedotentacle morphology, in conjunction with mesentery number provides evidence for two species, hence I consider *L. neglecta* and *L. coralligens* to be the two valid species of the genus.

Lebrunia, described by Duchassaing de Fonbressin & Michelotti in 1860, was the first genus diagnosed by branched outgrowths of the column, later called pseudotentacles. As the only genus of sea anemone in the Caribbean Sea and Atlantic Ocean to possess pseudotentacles, members of *Lebrunia* are easily recognized. The appearance of the pseudotentacles has been compared to brown algae (Duerden 1897, McClendon 1911), Herrnkind *et al.* (1976) suggesting that mimicking a brown algae could increase prey capture as unsuspecting prey blunders into toxic pseudotentacles. *Lebrunia* are toxic to humans (Wilson 1890, Herrnkind *et al.* 1976, Stanton 1977, Sanchez-Rodriguez & Cruz-Vazquez 2006, pers. obs.), like other aliciids.

Verrill (1899) and McMurrich (1905) found that *Actinodactylus neglectus* Duchassaing, 1850, is a juvenile of *Lebrunia neglecta,* and postulated that perhaps *Actinodactylus* Duchassaing, 1850, could be synonymous with *Lebrunia*. However, the type species of *Actinodactlyus, A. boscii*, was poorly described, has not reported since it was described, and lacks type material; thus, the status of *Actinodactylus* remains uncertain. If *Actinodactylus* and *Lebrunia* are synonyms, then *Actinodactylus* would have priority over *Lebrunia*. McMurrich (1905, p. 8) commented that "uncertainty renders it advisable to hesitate" before making any changes, and therefore I continue to provisionally recognize *Actinodactylus* until such time as its status can be properly evaluated.

Lebrunia neglecta Duchassaing de Fonbressin & Michelotti, 1860

Figs 4.23–4.25

Tables 4.12–4.13

Synonyms

Oulactis danae Duchassaing de Fonbressin & Michelotti, 1860, p. 47, Plate VII fig 10

Lebrunia neglecta Duchassaing de Fonbressin & Michelotti, 1860, p. 48, Plate VII, fig 8

Actinodactylus neglectus Duchassaing de Fonbressin & Michelotti, 1860, p. 44–45

?Rhodactis musciformis Duchassaing de Fombressin & Michelotti, 1864, p. 38

Type specimens and localities

Lebrunia neglecta type locality and syntypes: US Virgin Islands, St. Thomas, no type material.

Oulactis danae type locality and syntypes: US Virgin Islands, St. Thomas, no type material.

Material examined

Table 4.12.

Description

Pedal disc

Circular, oval, to irregular (Fig 4.23a). Same color and texture as proximal column – generally cream, beige, brown, or green in life, beige in preservation. Diameter of live specimens 10–30 mm, of preserved specimens 3–60 mm. Tissue thin, mesenterial insertions visible as light lines. Concentric furrows in contracted specimen. In life, pedal disc attached firmly to hard substrate (rock, scleractinian coral), most common in cryptic locality such as on underside of rock or coral colony (Fig 4.23c–e).

Column

Cylindrical. Length of preserved specimens 10–35 mm. Proximal column cream, beige, brown, or green in life, cream to light brown in preservation. Smooth, except in narrow ring just below tentacles where pseudotentacles are situated.

Pseudotentacles

4–9 per individual, most commonly 5 or 6. Develop in endocoels of lower order mesenteries, only one pseudotentacle per endocoel. Morphology variable, but most branched dichotomously between 4 and 12 times in one direction, perpendicular to oral-aboral body axis. Highly extensible; length to 300 mm. Pseudotentacles of one individual may not be identical. Peduncle 3–8 mm diameter arises from column. Distal ends of pseudotentacles may be narrow and pointed (Fig 4.23b–d), or wider and blunt (Fig 4.23e). All pseudotentacles golden to dark brown, (Fig 4.23d,e) some individuals with white or gray pigment in longitudinal stripes on oral side (Fig 4.23b–c).

Vesicles

Raised hemisphere (Fig 4.23b, Fig 4.24a) of variable density, size, and morphology. Within an individual, may be of different sizes but same morphology. On oral side of pseudotentacles, commonly at vertices of branches. Color variable, opaque; most commonly silver gray, can be pinkish brown.

Oral disc

Flat, circular (Fig 4.23f). Diameter 10–25 mm. Tissue thin, transparent, mesenterial insertions visible as white lines. White, cream, beige, pink, same color as capitulum; no pattern. Central oval mouth.

Tentacles

Slender, taper to blunt tip (Fig 4.23f). Inner longer than outer; length to 35 mm, width at base to 1.5 mm. All tentacles of similar appearance. White, cream, beige, light brown; translucent with opaque spots and tips. Commonly 96–120, up to 200, in 2–3 whorls at margin of oral disc.

Mesenteries and internal anatomy

Very thin, transparent. Between 90 and 192, hexamerously arrayed in four or five orders. First order fertile. All other orders incomplete, fertile. Separate sexes. Retractors well developed (Fig 4.24b). More numerous distally than proximally.

Cnidae

Fig 4.25 and Table 4.13.

Habitat and ecology

Individuals attach to hard substrate in cryptic locations, such as underside or crevice of rock or coral colony (Fig 4.23b–e), to 30 m. Occurs as individual, not in aggregations; if multiple individuals in close proximity, never in same crevice.

Symbionts

Herrnkind *et al.* (1976) and Stanton (1977) recorded commensals of *Lebrunia neglecta,* including shrimps *Periclimenes pedersoni, P.* c.f. *rathbunae, P.* c.f. *anthophilus, P. yucatanicus,* and *Thor amboinensis,* crabs *Mithrax commensalis* and *Stenorhynchus seticornis,* ophioroid *Ophioderma rubicundum*, and a clinid fish. Each species of commensal resides in a slightly different microhabitat of a specimen (Stanton 1977).

Distribution

Tropical localities of Caribbean Sea and West Atlantic Ocean (Fig 4.26).

Discussion

Duchassaing de Fonbressin & Michelotti (1860: Plate VII, Fig. 10) described *Oulactis danae* as possessing dichotomous tentacles with round tubercles. They also described *Lebrunia neglecta,* in a new genus that possesses five sprawling highly dichotomous pseudotentacles proximal to the simple tentacles (Duchassaing de Fonbressin & Michelotti 1860: Plate VII Fig. 8). McMurrich (1889a) was the first to refer to the external appendages of *L. neglecta* as pseudotentacles, a term that had been proposed by Hertwig (1882) for the deep sea genus

Ophiodiscus. Verrill (1899, 1901) recognized that the dichotomous outgrowths with tubercles of *O. danae* were pseudotentacles with vesicles, and moved the species to *Lebrunia*.

McMurrich (1889a, 1889b, 1896, 1905) and Duerden (1897) provided more information on the variation within *Lebrunia neglecta*, particularly regarding size and coloration of individuals, numbers of tentacles and mesenteries, number and size of pseudotentacles, and appearance of vesicles. Verrill (1899) used vesicle appearance to separate *L. danae* and *L. neglecta*: prominent in *L. danae*, not in *L. neglecta*. However, Duerden (1898) described specimens of *L. neglecta* possessing prominent vesicles. McMurrich (1905) and Verrill (1901) both questioned the species distinction based on vesicle appearance recognizing that vesicle form is variable. McMurrich (1905, p. 9) concluded, "it seems to me that the development of the vesicles is more or less variable, and indeed, that they may vary greatly even in a single individual according as they are expanded or retracted." I have observed variation in vesicle form within individuals, and the nominal species do not differ in other aspects of their morphology.

In his synonymy, McMurrich (1905, p. 9) stated, "that *L. Danae* [sic] and *L. neglecta* are identical, the latter term having the priority." Carlgren (1924, 1949) and Corrêa (1964, 1973) recorded *L. danae* as the valid name and type species of *Lebrunia* over *L. neglecta*, without any justification. However, according to ICZN (Article 67.2), the type species of a genus must be one that was originally described in the genus, so I agree with Fautin *et al*. (2007) that *L. neglecta* is the type species of this genus, by monotypy. Additionally, McMurrich (1905), acting as First Reviser of the genus *Lebrunia*, designated *L. neglecta* as the valid name over *L. danae*, so in accordance with ICZN (Article 24.2 and 24.2.2) the precedence of names is fixed by the First Reviser, and *L. neglecta* is the valid name instead of *L. danae*.

Lebrunia coralligens (Wilson, 1890)

Fig 4.27–4.30

Tables 4.14–4.15

Synonyms

Hoplophoria coralligens Wilson, 1890, p. 379–386

Cradactis variabilis Hargitt, 1911, p. 52–53

Type specimens and localities

Hoplophoria coralligens type locality and syntypes: Bahamas, Abaco, no type material.

Cradactis variabilis type locality and syntypes: USA, Florida, Gulf of Mexico, Dry Tortugas, no type material.

Material examined

Table 4.14.

Description

Pedal disc

Flat, circular. Diameter of live and preserved specimens 1–13 mm, approximately same diameter as proximal column. Same color and texture as proximal column; white, cream, beige, pinkish brown. Tissue thin, mesenterial insertions visible as opaque lines (Fig 4.27 a).

Column

Cylindrical. Length of live and preserved specimens 1–7 mm. Thin-walled. Proximal column white, cream, beige, pinkish to golden brown in live specimens, beige in preserved.

Pseudotentacles

Unbranched or dichotomously branched (Fig 4.27b–f) at most 2–3 times. Extensible in life, length to 20 mm in life and preservation. Brown (Fig 4.27a,d,e,f) or brown with white stripes (Fig 4.27b,c); stripes may be on oral or aboral side of pseudotentacles; one color pattern within an individual. 3–6 pseudotentacles per individual, one per endocoel of second order mesenteries (Fig 4.28a). Within an aggregation, generally all individuals with pseudotentacles of one type; however, some individuals with both branched and unbranched pseudotentacles.

Vesicles

Number and position on pseudotentacle variable between individuals: single terminal (Fig 4.27e), single on oral side (Fig 4.27b–d), or one or two on oral side (Fig 4.27f, Fig 4.28b). Terminal vesicles round, silver-gray (Fig 4.27e). Pseudotentacle with single terminal vesicles never branched. Vesicles on oral side of pseudotentacle oval, silver gray or white (Fig 4.27b–d,f). Up to two vesicles per pseudotentacle (Fig 4.28b). Pseudotentacle with oral side vesicles may be branched or not.

Oral disc

Flat, circular (Fig 4.27f), diameter 2–10 mm in life and preservation. Tissue thin, mesenterial insertions visible as light lines. Golden brown, no pattern, mouth tinged with white. Central mouth.

Tentacles

Slender, taper to blunt tip. Length to 20 mm in life and preservation. All tentacles of similar appearance. White, cream, beige, or golden brown, translucent with opaque spots and tips. 20–48 per individual in 2–3 whorls at margin.

Mesenteries and internal anatomy

Very thin, transparent. 24–48 mesenteries, hexamerously arrayed in 2–3 orders. First order fertile, second and third order fertile. Approximately same number of mesenteries distally and proximally. Simultaneous hermaphrodite, male and female gametes on same mesentery (Fig 4.28c).

Cnidae

Fig 4.29 and Table 4.15.

Habitat and ecology

Individuals occur in aggregations (Fig 4.27b–e), to 20 m, in crevices of rock or dead coral; pseudotentacles extend so exposed to light.

Reproduction and development

Of all the aliciid species, *Lebrunia coralligens* has the most information regarding reproduction and development. It is reported to be reproductive in spring and early summer (Hargitt 1911, Lewis 1984). Internal brooding of propagules occurs (Hargitt 1911, McClendon 1911, Duerden 1899, pers. obs.) (Fig 4.28d), with up to 50 larvae released from a single adult (Lewis 1984). Duerden (1899) reported that all larvae released at same time were of similar size and therefore age. Planula are approximately 1 mm in length and 0.5 mm diameter at apical end (Lewis 1984), possess zooxanthellae (Duerden 1899, Lewis 1984), and starting to form eight mesenteries. Lewis (1984) reported planula were negative phototropic, most frequently settled around pedal disc of adults, and showed aggregated settlement behavior in his laboratory-based experiments. This behavior would explain the aggregations of individuals found in nature. Planulae settle within 24 hours of release from adult, and pigment moves into radial pattern (McClendon 1911, Lewis 1984). Once settled, mouth and tentacles start forming at distal end. Pseudotentacles do not form until later, after about 20 tentacles have been formed (McClendon 1911) or six weeks after settlement (Lewis 1984).

Distribution

Tropical localities of the Caribbean Sea and West Atlantic Ocean (Fig 4.30).

Discussion

From a single specimen collected in the Bahamas, Wilson (1890) described *Hoplophoria coralligens,* the species epithet chosen because the animal lived in coral. One of the distinguishing characters that Wilson (1890, p. 382) described are the "four large and conspicuous organs" proximal to the circle of tentacles. The genus *Lebrunia* was considered for this new species by Wilson (1890), but he put it in *Hoplophoria* rather than *Lebrunia* because its pseudotentacles were not branched. He did note, "whether there is any relationship between *Hoplophoria* on the one hand and *Ophiodiscus* of Hertwig and the peculiar *Lebrunea neglecta* on the other, cannot yet be discussed" (Wilson 1890, p. 386).

Duerden (1897) recognized that even though the pseudotentacles branched fewer times in specimens of *Hoplophoria coralligens* than what had been recorded in *Lebrunia*, the presense of pseudotentacles meant this species belonged in *Lebrunia*. He identified newly collected specimens of *L. coralligens* that had six pseudotentacles that branch between 2–3 times, hence increasing our knowledge of the variation in morphology within the species (Duerden 1897). Duerden (1897, p. 457) also disputed McMurrich's (1896) suggestion that *H. coralligens* is synonymous with *Viatrix globulifera*, stating, "there is no doubt, however, that it [*H. coralligens*] belongs to the genus *Lebrunea*". Verrill (1899) did doubt it, suggesting the species could be synonymous with *Diplactis Bermudiensis*. Duerden (1899) defended his decision that placement in *Lebrunia*, asserting that Verrill's (1899) opinions were not based on any specimens, because Verrill had not seen either species of *Lebrunia*.

In 1911, Hargitt described a new species, *Cradactis variabilis,* and McClendon (1911) described details of the natural history for it, including a detailed account of the reproduction and development. Hargitt (1911) considered *Lebrunia, Oulactis,* and *Cradactis* as possible genera for it, and although none was a perfect fit and he showed that the new species was similar to *Lebrunia* species in habitat and possessing 6–8 dichotomous fronds, he decided to place the species in *Cradactis* provisionally. From Hargitt's (1911) description and figures and observations of many specimens, it is clear that the species *Lebrunia coralligens* is variable in morphology, in particular the branching of pseudotentacles. What was described for *C. variabilis* corresponds to the original description of *L. coralligens,* rather than *L. neglecta*, with respect to the size of individuals and branch order number of pseudotentacles. I therefore synonymize *C. variabilis* with *L. coralligens,* and do not agree that *C. variabilis* is a synonym of *L. neglecta* as proposed by Hedgpeth (1954).

Häussermann (2003) moved *Cradactis digitata* McMurrich, 1893, to *Actinostella*, and listed *Cradactis* as a junior synonym of *Actinostella*. However, *Cradactis* as used by Hargitt (1911) is different from the *Cradactis* as used by McMurrich (1893). Hargitt's (1911) *C. variabilis* is a junior synonym of *L. coralligens*, and not similar to species of the actiniid genus *Actinostella*. Therefore, *Cradactis* pro parte McMurrich, 1893, is a junior synonym of *Actinostella*, and *Cradactis* pro parte Hargitt, 1911, is a junior synonym of *Lebrunia*.

Triactis Klunzinger, 1877

Synonyms

non *Thelactis* Klunzinger, 1877

Viatrix pro parte Haddon & Shackleton, 1893

Hoplophoria pro parte Haddon, 1898

Phyllodiscus pro parte Stephenson, 1921, 1922; Carlgren, 1945

Gender

Feminine

Diagnosis (based on England 1987, changes indicated in bold)

Aliciidae with well developed pedal disc. Scapus may have small vesicles **proximal to** margin, capitulum may have opaque spots. Margin with **one distal ring** of stalked **pseudotentacles;** in young specimens these occur sparingly and are little branched, closer together and dichotomously branched in larger specimens. **Distal end of pseudotentacles may or may not branch; if branched, branch perpendicular to oral-aboral axis. Hemispheric vesicles** on **oral side of pseudotentacles**. Stalks of pseudotentacles few, with longitudinal weak bands of endodermal muscle. Six pairs of **complete** mesenteries and several **incomplete** pairs. Retractor and parietobasilar muscles weak.

Distribution

Shallow tropical Indo-West Pacific.

Valid species

Triactis producta Klunzinger, 1877 (Type species)

Discussion

Individuals of the genus *Triactis* are distinguished from other aliciids by one kind of simple vesicle, attached only to the oral side of a pseudotentacle, never on the aboral side or tip, multiple vesicles per pseudotentacle, only one pseudotentacle per intermesenterial space, pseudotentacles in a distinct whorl at distal end of scapus, and pseudotentacles that branch in one direction. Considering the distinctive features, and the lack of morphological variation throughout the distribution of this genus, non-monophyly of *Triactis* was recovered by combined except 28S (Fig 2.9) and combined five-gene (Fig 2.10) phylogenies. However, seeing as most of the genetic information analyzed for *Triactis* representatives was from nuclear 28S (Table 2.1), the phylogeny from combined except 28S dataset may be unreliable to place *Triactis*.

Viatrix cincta was described from an individual possessing pseudotentacles that were not branched many times (see Plate XXIII, Fig 11–15 of Haddon 1898). Stephenson (1921, 1922) described an individual possessing pseudotentacles with more branch orders as a new species *Phyllodiscus indicus*. By comparing the figures from Haddon (1898, Plate XXIII, Fig 11–15) and Stephenson (1921, Fig 18), it can be seen that the pseudotentacles of *Viatrix cincta* and *Phyllodiscus indicus* are similar to pseudotentacles of *Triactis producta*, in having branching perpendicular to the body axis. During my fieldwork, I encountered individuals of both of these developmental stages of the pseudotentacles, and more stages, from one aggregation of *Triactis producta* at one locality. The distinctive column morphology of *Triactis producta* is lacking from the *Lybia* symbiont specimens (Fig 2.1b,d). However, the *Lybia* symbionts look similar to individuals of *Triactis producta* I observed in the field that lacked column outgrowths (Fig 4.40a, 4.42b black arrows).

Triactis was erected by Klunzinger (1877) for specimens collected from the Red Sea, which he described as *T. producta* in the same paper (Fig 4.31a,b). In the genus description, Klunzinger (1877) recorded three types of tentacles: thick branching, short spherical, and filamentous. Because of the branched tentacles, Andres (1883a) proposed that *Triactis* was closely related to *Phymanthus*. However, Andres (1883a) noted that the mouth protruded on a retractable cone, and admitted that this feature differs from the flat oral disc of *Phymanthus*. The thick branched and short spherical tentacles of *Triactis* described by Klunzinger (1877) are pseudotentacles and vesicles, respectively, and are not tentacles with lateral projections as seen in *Phymanthus* specimens.

Haddon & Shackleton (1893) described *Viatrix cincta* from Australia as possessing six club-like enlargements of the column. This is more accurate than how Klunzinger (1877) described them, as tentacles. Haddon (1898) moved *Viatrix cincta* into *Hoplophoria* because species in this genus also possessed pseudotentacles, then Carlgren (1945, 1949) moved the species to the genus *Triactis*, because *Hoplophoria* individuals were recorded only from the Caribbean, whilst *Triactis* were recorded from the Indo-Pacific.

Carlgren (1949, 1950) described the pseudotentacles as occurring at mid-column, whereas England (1987) stated that they are situated at the margin. Cruicial to arbitrating these interpretations is the position and definiton of the margin. The margin should be considered the border where the column joins the oral disc, just below the base of the tentacles (Carlgren 1949), and not necessarily where the marginal sphincter is, because some species lack marginal sphincter muscles. Carglren's (1949, 1950) specification that the capitulum is distal to the pseudotentacles verifies that he considered the pseudotentacles mid-column and not at the margin. In *Triactis producta*, the capitulum is present (Fig 4.32a), and compared to the scapus is thin-walled, lighter color, and has different cnidae (Stephenson 1928).

England (1987) appears to have interpreted the placement of the margin in *Triactis producta* individuals differently. His figure (England 1987, p. 234) depicts a longitudinal section of *T. producta*, which has labeled distally to proximally: tentacle, capitulum, sphincter, vesicles, fosse, and margin. The scapus is proximal to the margin, but is not labled in the figure. In this interpretation, England (1987) considers the junction between the scapus and capitulum to be the margin, hence why he considered the pseudotentacles to occur at the margin.

Despite the slightly different wording and interpretation of features, Carlgren (1949, 1950) and England (1987) are describing the same placement of the pseudotentacles of *Triactis producta*. From the literature and my observations, I interpret that the pseudotentacles occur mid-column. I agree with Haddon's (1898) interpretation that pseudotentacles occur near the junction of the scapus and capitulum, and not at the margin, which I consider to occur at junction of the capitulum and oral disc.

The position of, or even presence of, marginal sphincter muscle is not well established. Most authors did not state nature of marginal sphincter muscle (*e.g.* Klunzinger 1877, Andres 1883a,b, Haddon & Shackleton 1893, Stephenson 1921, 1922, Carlgren 1950), or the marginal sphincter muscle is absent (*e.g.* Haddon 1898, Carlgren 1949, Doumenc 1973, England 1987). I did not observe a marginal sphincter muscle.

The only person to record marginal sphincter muscle in *Triactis producta* was England (1987); though, he noted that it was apparent in only one of the specimens he was studying, and absent in another. England (1987, p. 233) stated that the weak sphincter muscle recalled "that depicted by Haddon (1898: 439, text fig) in *Hoplophoria cincta*". However, on the description of the sphincter muscle, Haddon (1898, p. 438) states, "I cannot be certain that there is any sphincter at all." Also, the text figure of Haddon (1898, p. 439) depicts as cross-section through a mesentery, not a longitudinal section through the margin. England (1987, p. 233) does admit that the sphincter muscle he observed "may have been due to the influence of other muscles on the degree of folding of the circular muscles of the column." I interpret that the only record of a marginal sphincter muscle of *Triactis producta* specimens is dubious, and the marginal sphincter muscle is absent. I have emended the generic diagnosis of *Triactis* to state that the pseudotentacles occur in a ring at the distal end of the scapus.

Triactis producta Klunzinger, 1877

Figs 4.31–4.42

Tables 4.16–4.17

Synonyms

non *Thelactis simplex* Klunzinger, 1877, p. 79

Triactis producta Klunzinger, 1877, p. 85–86

Viatrix cincta Haddon & Shackleton, 1893, p. 117, 127

Phyllodiscus indicus Stephenson, 1921, p. 561

Sagartia pugnax Verrill, 1928, p. 18–19

Type localities and specimens

Triactis producta type locality and syntypes: Red Sea, no type specimens.

Viatrix cincta type locality and syntypes: Australia, Torres Strait, no type specimens.

Phyllodiscus indicus type locality and syntypes: Maldives, no type specimens.

Sagartia pugnax type locality and syntypes: USA, Hawaii, Oahu, AMNH 1585 (1/2 specimen), BPBM D113 (2 specimens).

Material examined

Table 4.16.

Description

Pedal disc

Circular. Diameter of live and preserved specimens 1–15 mm, same as proximal scapus (Fig 4.33a). Same color and texture as proximal column – cream or beige, sometimes brown, in live specimens. Tissue thin, some mesenterial insertions visible as light beige or pink lines. In life, attached to firm substrate, usually scleractinian coral or rock.

Column

Cylindrical. Expanded length 1–30 mm and diameter 1–15 mm in live and preserved specimens (Fig 4.33b). Scapus same color and texture as pedal disc. Capitulum very delicate and thin-walled, white or cream, translucent; diameter slightly less than that of scapus.

Pseudotentacles

Each starts as simple projection, branching only at distal end: branching irregular (Fig 4.33c). Pseudotentacles of lower order endocoels branched, (Fig 4.32b,c); pseudotentacles of higher order endocoels unbranched (Fig 4.32b,c). Dark brown from dense zooxanthellae, some with iridescent green or pink tinge on tips, no pattern. Pseudotentacles form in wide region of scapus.

Vesicles

Vary in size within and between individuals. Diameter 0.5–2 mm. Attach directly to pseudotentacle (Fig 4.33c), or borne on short stalk (Fig 4.33d,e). Largest vesicles in distal region of largest pseudotentacle. Some individuals with multiple vesicles per pseudotentacle (Fig

4.33f), but only on largest pseudotentacles. Occur only in zooxanthellate region of a pseudotentacle. Opaque, with bright silver ring around outer edge (Fig 4.34): grey in most specimens, but may be pale pink, green, bright orange, bright pink seen (Fig 4.35). Usually, color within individual homogenous, between individuals variable.

Oral disc

Flat, circular. Diameter 1–10 mm, usually slightly less than pedal disc. In live and preserved specimens thin, mesenterial insertions visible as white or beige lines (Fig 4.36). Cream, beige, or white, translucent, some with opaque spots from dense cnidae patches, no pattern. Central mouth.

Tentacles

Slender, taper slightly to blunt tips; all of similar appearance. Inner longer than outer; length to 20 mm, width to 0.5 mm. White, cream, or golden brown tinge, translucent with opaque spots all over surface, including at tip (Fig 4.36), in life and preservation. Usually 48, but as many as 60, hexamerously arrayed in 2–3 cycles.

Mesenteries and internal anatomy

Mesenteries very thin, transparent, some with zooxanthellae in endoderm. Mesenteries hexamerously arranged in three orders: those of first order sterile, those of second and third orders incomplete, some fertile (Fig 4.37a). Separate sexes. Retractors diffuse (Fig 4.37b). Directives attached to siphonoglyphs (Fig 4.37c).

Cnidae

Figure 4.38 and Table 4.17.

Habitat and ecology

Attached by flat pedal disc to firm substrate such as dead or live scleractinian coral (particularly *Porites* and *Acropora*) and rocks. Common to depths between 1 and 15 m where light penetration is strongest, but may occur as deep as 30 m. Most common in aggregations, either in crevices of rocks or at vertices of branched scleractinian colony.

Distribution

Triactis producta is widespread in the Indo-West Pacific (Fig 4.39).

Symbionts

Cutress (1977) and Fishelson (1970) reported *Triactis producta* as one of the species symbiotic with crabs of the genus *Lybia*. The crab holds the sea anemone in modified chela, using the anemone for protection against predators. Zooxanthellae dense in endoderm of pseudotentacles.

Discussion

The original description of *Triactis producta* is thorough, and with the figure, diagnostic (Fig 4.31). *Triactis producta* is the only species of the genus; I found little difference in tentacle and mesentery number or mesentery arrangement among individuals covering a large size and geographic range. I found more size-classes of cnidae in each tissue type compared to what had been recorded by Carlgren (1945) and Doumenc (1973). In the tentacles and column, I found a smaller basitrich size class, while Carlgren (1945) reported an additional size of microbasic amastigophore. I found an extra size class of microbasic amastigophore in mesenterial filaments. The cnidom reported by Doumenc (1973) has the fewest types and sizes, but those presented concur with my findings.

Pseudotentacle number and branching varied most: the larger the individual, the more pseudotentacles and the more their branching. Pseudotentacle morphology was influenced by the size of the individual and varied between putative clonemates at one locality (see below). In one aggregation in Mo'orea, some individuals had a smooth column lacking vesicles and pseudotentacles (Fig 4.40a) and zooxanthellae concentrated in the oral end and tentacles. Other individuals (Fig 4.40b) possessed a single well-developed vesicle and two developing pseudotentacles and more tentacles and mesenteries than depicted in Fig 4.40a, while some possessed multiple vesicles and pseudotentacles at various stages of development in one discrete ring (Fig 4.40c), and some had more fully developed pseudotentacles and vesicles (Fig 4.40d).

This range of character states encompasses what is known of the nominal species *Viatrix cincta* (reported in Haddon & Shackleton 1893, Haddon 1898, Carlgren 1950, Doumenc 1973) and *Phyllodiscus indicus* (Fig 4.31c, reported in Stephenson 1921, 1922). I therefore agree with England (1987) that *Viatrix cincta* and *Phyllodiscus indicus* are synonyms of *Triactis producta*, which is the sole valid species of *Triactis*.

Carlgren (1947, p. 14) asserted that *Thelactis simplex* Klunzinger, 1877 was "probably nothing but a very young *Triactis producta*," stating the conical warts around the column were early development stages of the pseudotentacles. Although this is possible, I think it more likely that Klunzinger (1877) was referring to a species of *Bunodeopsis.* It was a lone specimen attached to algae in shallow lagoonal areas, which is a habitat more similar to that of *Bunodeopsis* than of *Triactis,* the latter of which is generally found in aggregations and attached to a firm substrate. Members of *Bunodeopsis* possess vesicles on the column and in a ring mid-column.

In the field, individuals of *Triactis producta* occur in cryptic locations and in aggregations composed of closely packed individuals, with pseudotentacles of one individual overlapping those of another, and pedal discs of neighboring individuals in contact. Most frequently, these animals are attached to live or dead scleractinian coral. In branched corals such as *Acropora* and *Porites*, the anemones are hidden, situated at the vertices of skeleton branches (Fig 4.41a). Another common habitat is crevices of corals or boulders (Fig 4.41b). More rarely, specimens are on the sides of shallow rocks that are slightly buried in the sandy substrate (Fig 4.41c), and the individuals of one aggregation I observed were attached to a demosponge (Fig 4.41d).

I observed multiple smaller, less developed individuals surrounding a larger, more developed individual (Fig 4.42). It is possible these smaller individuals were produced via asexual reproduction, which has been reported for this species (Den Hartog 1997). The larger individual in Fig 4.42 has dense concentrations of zooxanthellae in a discrete ring at the limbus (see white arrow in Fig 4.42); this could be the region where clonal individuals pinch off via constriction, and therefore could obtain zooxanthellae from the parent.

Phyllodiscus Kwietniewski, 1897

Gender

Masculine

Diagnosis (based on Carlgren 1949, changes indicated in bold)

Aliciidae with broad pedal disc. **Proximal part of scapus smooth, distally a broad zone of pseudotentacles in multiple whorls, radially arranged, branched in multiple planes. Pseudotentacles with few branched bands of longitudinal endodermal muscle. Attached to pseudotentacles, and rarely on column, simple hemispheric vesicles of variable size.** A few branched bands of longitudinal endodermal muscles in the **pseudotentacles**. Capitulum short with ectodermal longitudinal muscles. Sphincter indistinct, diffuse. **Tentacles to about 200, hexamerously arranged.** Longitudinal muscles of tentacles and radial muscles of oral disc ectodermal. **Gametes on all but first order mesenteries.** Retractors weak. Basilar muscles rather well developed.

Distribution

Shallow tropical Indo-West Pacific.

Valid species

Phyllodiscus semoni Kwietniewski, 1897 (Type species)

Discussion

Kwietniewski (1897) placed *Phyllodiscus* in Phyllactiidae, along with other genera having branched outgrowths. Haddon (1898) suggested Aliciidae would be a more appropriate placement, although Aliciidae contained genera with tubercles or vesicles of the column. Stephenson (1921) placed *Phyllodiscus* in Aliciidae to join *Alicia*.

Individuals of *Phyllodiscus* are easily distinguished from other aliciids by their multiple whorls of pseudotentacles, multiple planes of branching of pseudotentacles, and vesicles on all sides of pseudotentacles. Molecular data support the monophyly of *Phyllodiscus* (Fig 2.2, 2.5, 2.6, 2.9-2.11). I do not agree with suggestions of Stephenson (1922) and Doumenc (1973) that *Triactis* individuals are juveniles of *Phyllodiscus*. I find *Triactis* individuals to be small individuals (at most 35 mm column length), with pseudotentacles in one distinct whorl that branch in one plane, and vesicles only on oral side of pseudotentacles.

Two genera of sea anemones most confused with *Phyllodiscus* are *Actinodendron* and *Actineria*, because all three have branched outgrowths. *Actinodendron* (and others in the family Actinodendridae) are burrowing anemones, and therefore have long cylindrical bodies; neither *Phyllodiscus* nor *Actineria* individuals have long cylindrical bodies, but both attach to hard substrates. Correct identification of sea anemones, particularly toxic species, is important for public safety and for understanding the evolution of toxicity in sea anemones.

Phyllodiscus semoni Kwietniewski, 1897

Figs 4.43–4.37

Tables 4.18–4.19

Synonyms

Phyllodiscus Semoni Kwietniewski, 1897, p. 11–17

Type specimens and localities

Phyllodiscus semoni type locality and syntypes: Indonesia, Ambon, PMJ 707 (1 specimen), SMNH 4080 (piece), SMNH 4081 (piece).

Material examined

Table 4.18.

Description

Pedal disc

Limbus circular to irregular (Fig 4.43a). Diameter of live and preserved specimens 1.2–90 mm, most individuals 25–60 mm. Slightly wider than proximal column, and always much wider than oral disc. Color and texture as proximal column – generally translucent cream/beige in life and opaque in preservation, no pattern. Tissue thin, mesenterial insertions clearly visible as opaque lines; concentric furrows in contracted specimen. In life, attached firmly to hard substrate (rock, scleractinian coral).

Column

Column length of preserved specimens 2–90 mm, most 35–60 mm. Proximal scapus translucent to opaque, cream, smooth (Fig 4.43b). Distal scapus with pseudotentacles and vesicles. Capitulum translucent, white to cream, smooth.

Pseudotentacles

Length variable, 4–65 mm; single individual can embody entire range. Pedunculate: peduncle diameter variable, 3–14 mm. Morphology and coloration variable (Fig 4.44). In life, observed colors across individuals include white, gray, cream, beige, rusty red, and green, to mottled (Fig 4.44). No pattern, but may follow coloration of organisms in surrounding environment (*e.g.* golden green except at tips which are white, presumably mimicking scleractinian coral *Seriatopora hystrix* (Fig 4A,B of Hoeksema & Crowther 2011). Multiple per intermesenterial space, radially arranged. Usually different sizes of pseudotentacles in one intermesenterial space, similar size arranged in whorls; largest communicate with lower mesenterial orders. Pseudotentacles branch up to 5 orders. Some possess subunit complexes of vesicles and small, short branches (Fig 4.43c, Fig 4.45a).

Vesicles

Raised, no stalk (Fig 4.43c). May be of multiple sizes on one individual; diameter 0.25–2 mm. Most vesicles on pseudotentacles, predominantly at vertices of branches, occur on all sides of pseudotentacles; some on scapus. Density variable. Opaque, cream to gray.

Oral disc

Flat, most circular, some with slightly wavy margin (Fig 4.43d). Most specimens between 15–30 mm diameter; smallest 2 mm, largest 50 mm in preserved specimens. Tissue thin, mesenterial insertions visible as white lines. Cream, beige, or greenish, translucent. No pattern, some opaque spots from dense patches of cnidae. Central mouth oval, agape in most preserved specimens; lips inflated in some specimens. Actinopharynx cream, opaque, strongly furrowed.

Tentacles

All of similar appearance: slender, taper to blunt tips, some with pores at tip, very few bifurcate. Longest to 45 mm, width at base to 1.5 mm. Beige, cream, or greenish tinge especially at base (Fig 4.43d), translucent with opaque spots, opaque tips. To 200, hexamerously arranged in 2–3 whorls.

Mesenteries and internal anatomy

Very thin, most individuals with dense zooxanthellae in endoderm, transparent. Oral stomata present. Between 87 and 130, hexamerously arranged in four (rarely three or five) orders. Those of second and third order incomplete, fertile. Those of fourth and rare fifth order incomplete, some fertile with filaments, but usually very small, lacking gametes. Very rarely mesenteries of same pair unequal in size, or one missing. Some individuals with more and some with fewer mesenteries distally than proximally, and some with approximately same number distally and proximally. Some individuals simultaneously hermaphroditic (Fig 4.45b).

Cnidae

Fig 4.46 and Table 4.19.

Habitat and ecology

In the Spermonde Archipelago of Sulawesi, *Phyllodiscus semoni* occurs predominantly in the mid-shelf zone (Hoeksema & Crowther 2011). Individuals attach flat pedal disc to firm substrate, such as dead or live scleractinian coral (particularly *Porites* and *Acropora*) and rocks. Usually in depths between 1 and 15 m where light penetration is strongest, but may occur as deep as 20–25 m. Can occur as isolated individuals or in aggregations, one or more aggregations of separate morphotypes may occur at one locality (Figs 7, 10 of Hoeksema & Crowther 2011).

Distribution

Tropical Indo-West Pacific (Fig 4.47).

Symbionts

Zooxanthellae in endoderm, particularly dense in pseudotentacles. Pontoniid shrimp, including *Periclimenes brevicarpalis, Anocylomenes sarasvati,* and *A. venustus* live on and around *Phyllodiscus semoni* individuals (Fransen 1997, Humann & DeLoach 2010, Hoeksema & Crowther 2011) (Fig 4.43e). Wentletrap snails *Epitonium* parasitize individuals (Kokshoorn *et al*. 2007) (Fig 4.43f).

Toxicology and misidentification

The nematocysts of *Phyllodiscus semoni* contain toxins that can cause damage to human skin, from mild rash and irritation to blistering welts, ulcers and skin necrosis (Williamson *et al.* 1996). Therefore, swimming beaches and inlets in Okinawa, Japan, have been closed when *Phyllodiscus* numbers increases (JD Reimer, pers. comm.). Erhardt & Knop (2005) reported that a fisherman in the Philippines died after being stung by a *Phyllodiscus*. Toxicological analyses of sea anemones identified as *Phyllodiscus* show that the toxins, of the actinoporin family (Nagai *et al.* 2002a), were fatal to shrimp (Nagai *et al.* 2002a), can cause severe renal failure in rats (Mizuno *et al.* 2007), and can cause hemolysis of fish and mammalian red blood cells (Nagai *et al.* 2002b).

Uechi *et al*. (2005a,b) reported on the toxicology of a sea anemone in Okinawa, the species referred to as *Actineria villosa* by Oshiro *et al*. (2001). However, the sea anemone identified as *A. villosa* in Figure 2 of Oshiro *et al.* (2001) clearly shows *Phyllodiscus semoni* of a branched morphotype (Hoeksema & Crowther 2011). This same misidentification is shown in Uchida & Soyama (2001, p. 26). Uechi *et al.* (2005a) stated, "*A. villosa* is morphologically quite similar to coral…" (p. 379), which is more like a *Phyllodiscus* specimen (see figures in Hoeksema & Crowther 2011), rather than a specimen of *Actineria.* Uechi *et al.* (2005a,b, 2010) refer multiple times to the similarity between the toxin from their study organism (Avt-1) to the toxin extracted from *Phyllodiscus semoni* (Pstx20). The N-terminal sequences match completely (Uechi *et al.* 2005b), and there is a 99% amino acid similarity (Uechi *et al.* 2005a), corresponding to one base pair difference in 179 bases (Alegre-Cebollada *et al.* 2007). I am confident that the records of *A. villosa* from Japan by Oshiro *et al.* (2001), Uchida & Soyama (2001), and Uechi *et al.* (2005a,b, 2010), all refer to a branched morphotype of *Phyllodiscus semoni*.

I believe that in a report of a stinging sea anemone in Vietnam, Hansen & Halstead

(1971) refer to two species of sea anemones under the name *Actinodendron plumosum*. *Actinodendron plumosum* has a powerful sting, and long branched tentacles – two features similar to those of *Phyllodiscus semoni* (if the pseudotentacles are confused with tentacles). The specimens referred to by Hansen & Halstead (1971) were "found on the shady side of rocks," reminiscent of a *P. semoni* individual that attaches to hard substrate, not of an *A. plumosum* individual that burrows in soft sediments, and the authors refer to "flowery" and "top hat" forms (Hansen & Halstead 1971, p. 125). The "flowery" form (Fig 2b Hansen & Halstead 1971) is most certainly a close-up of *P. semoni*, with tentacles shown surrounded by pseudotentacles. The "top hat" form (Fig 3, Hansen & Halstead 1971) is very similar to the morphotype termed a "cake" shape by Kwietniewski (1896, 1897). Figure 4b (Hansen & Halstead 1971) shows a macrobasic amastigophore, a type of nematocyst known from Aliciidae, the family to which *Phyllodiscus* belongs.

Discussion

This is currently the only species of *Phyllodiscus* and it is one of the most polymorphic sea anemones; even if this variability represents several species, few other sea anemone genera possess this much morphological variation. The function (if any) of the morphological variation is unknown; it may be camouflage. Hoeksema & Crowther (2011) documented how *Phyllodiscus* can appear like other organisms or blend into the background of their environment (Figs 3–6 and 7–8, respectively, of Hoeksema & Crowther 2011). I infer the lack of variation in pseudotentacle morphology among individuals in close proximity as evidence for asexual reproduction. I assume that individuals cannot alter their morphotype within their life; the pseudotentacle branching is too extensive and sea anemone morphology is not known to be plastic.

Multiple specimens of *Phyllodiscus semoni* were included in molecular analyses, and were all found as closest relatives in all of the phylogenies (see Fig 2.2, 2.5, 2.6, 2.9, 2.10, 2.11) except 28S (Fig 2.7) and nuclear (Fig 2.8). The branches between *P. semoni* individuals are very short, indicating the high similarity of the sequences. The clade of *P. semoni* supports a single evolution of pseudotentacle branching in multiple planes – this is the only species of sea anemone with this feature (Fig 2.13).

Conclusions

In this study, I completed a family-level revision to address how many valid genera and species Aliciidae comprised of, and to provide a detailed morphological description of branched outgrowths and defensive spheres for each genus and species. To do so, I compared more aliciid specimens than any other study, and find four genera and nine species to be valid. I find the possession of pseudotentacle and vesicle morphology and placement to be important characters to aid in identification of genera and species in Aliciidae. The genus *Alicia* has five valid species, but there are very few characters to separate these species. *Lebrunia neglecta* is the type species of *Lebrunia*, and the other valid species is *L. coralligens. Lebrunia coralligens* anemones are smaller individuals with pseudotentacles with fewer branches and mesenteries compared to individuals of *L. neglecta*. *Triactis* and *Phyllodicus* are both widespread monotypic genera, valid species of *T. producta* and *P. semoni*, respectively.

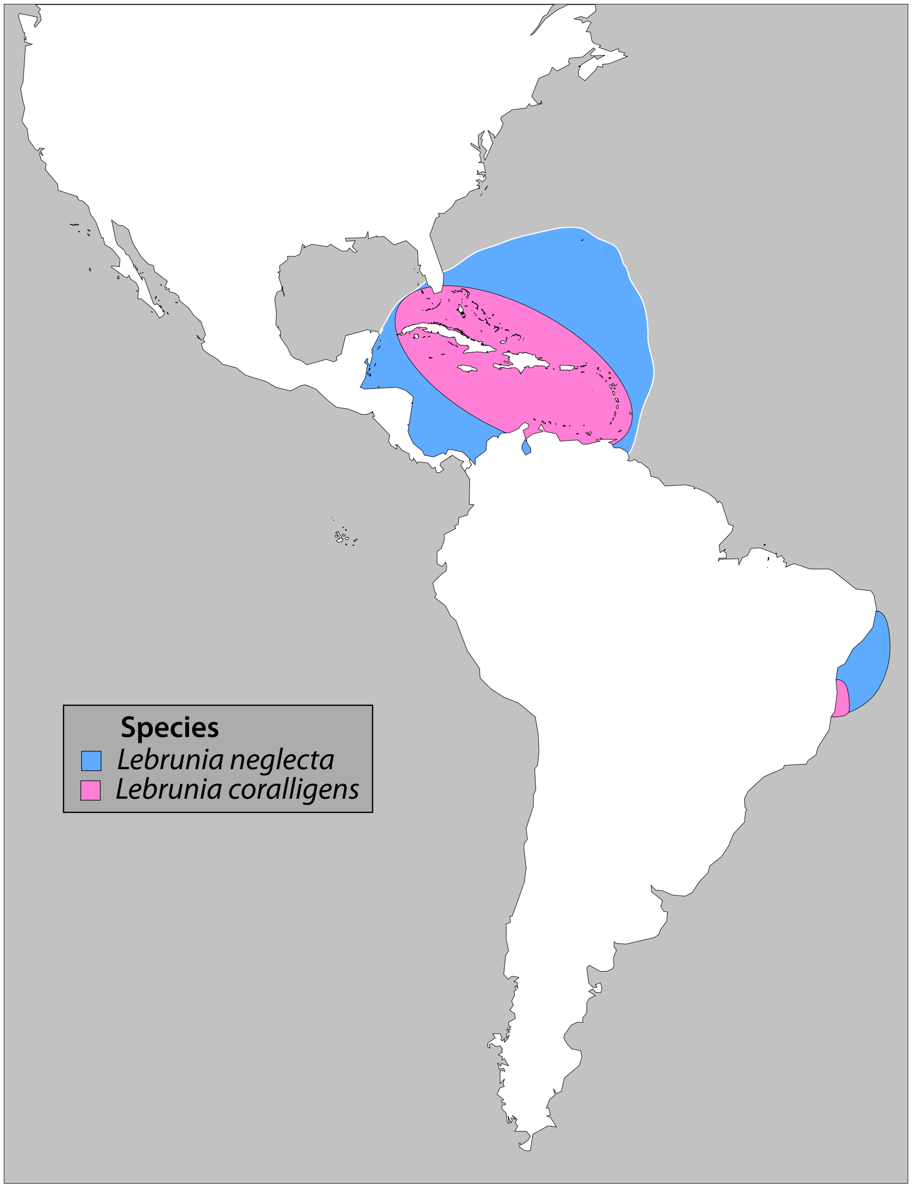

Fig 4.1. Recorded distribution of *Lebrunia neglecta* and *L. coralligens*. Note the overlapping distribution of species.

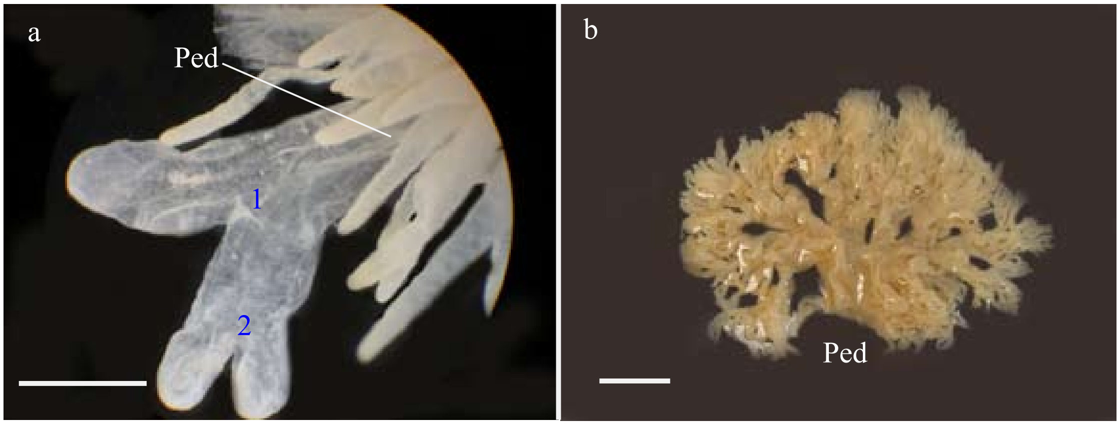

Fig 4.2. a) *Lebrunia coralligens* pseudotentacle with two branch orders, USNM 42625, scale bar = 2 mm. Note uneven branching. b) *Lebrunia neglecta* pseudotentacle with 13 branch orders, USNM 56912, scale bar = 10 mm. Figure legend: Ped = peduncle of pseudotentacle that is attached to scapus.

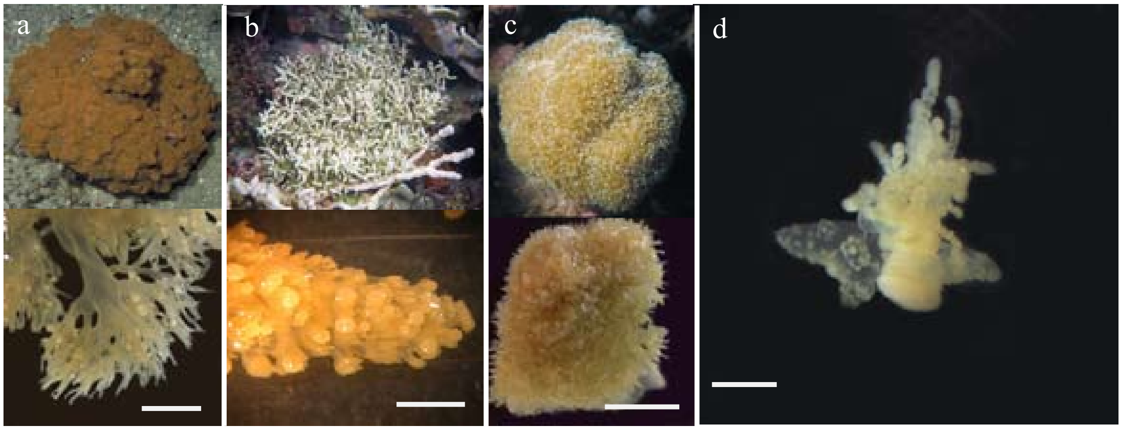

Fig 4.3. *Phyllodiscus semoni*. a) cake morphotype, whole and pseudotentacle detail, scale bar = 10 mm b) branched morphotype, whole and pseudotentacle detail, scale bar = 10 mm c) pom-pom morphotype, whole and pseudotentacle detail, scale bar = 10 mm d) small individual with two well developed pseudotentacles, RMNH Coel 39709, scale bar = 2 mm.

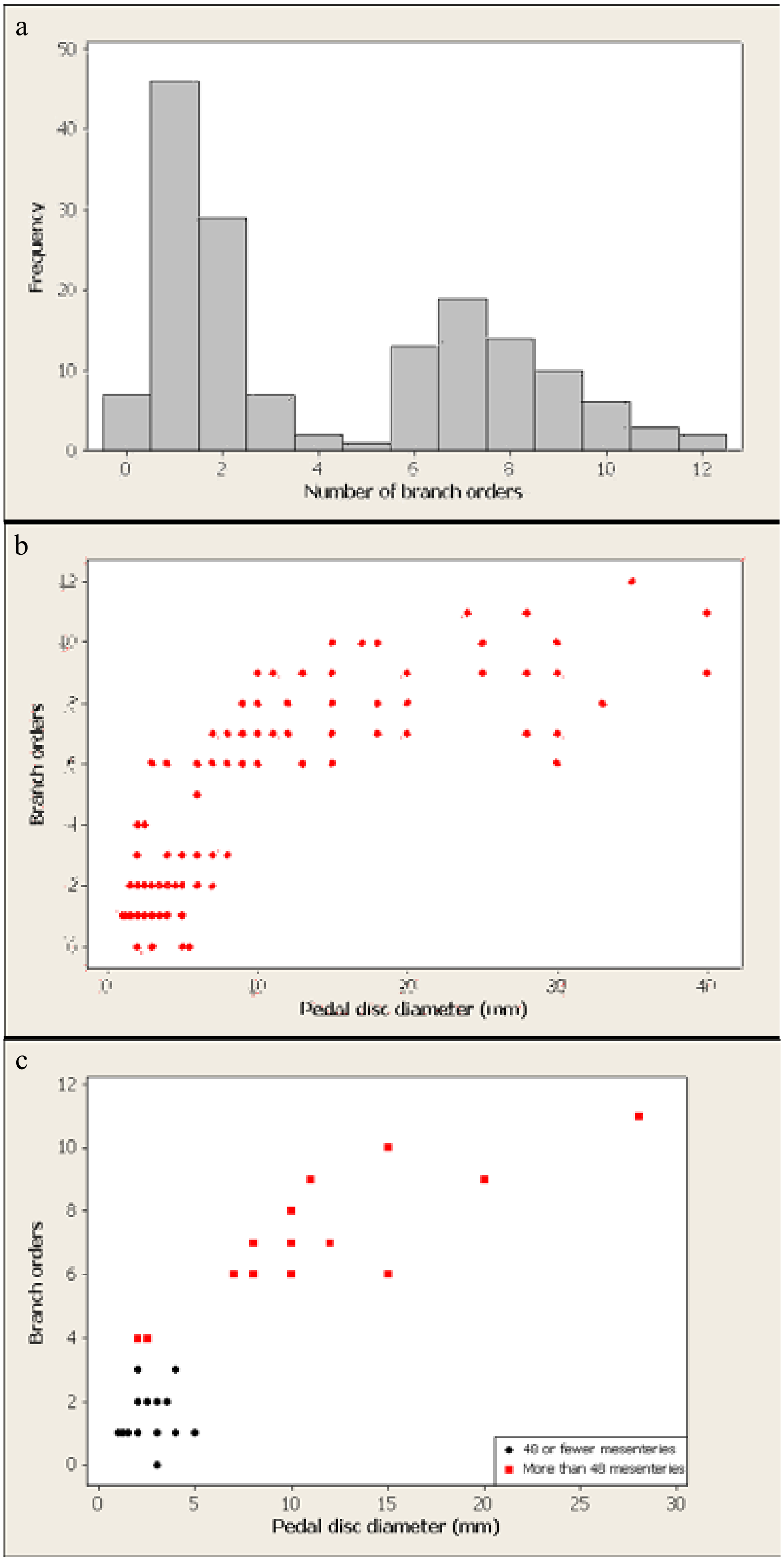

Fig 4.4. a) Histogram of individuals, based on number of branch orders. b) Scatterplot of number of branch orders and pedal disc diameter (mm). c) Scatterplot from (b), with individuals coded for mesentery number.

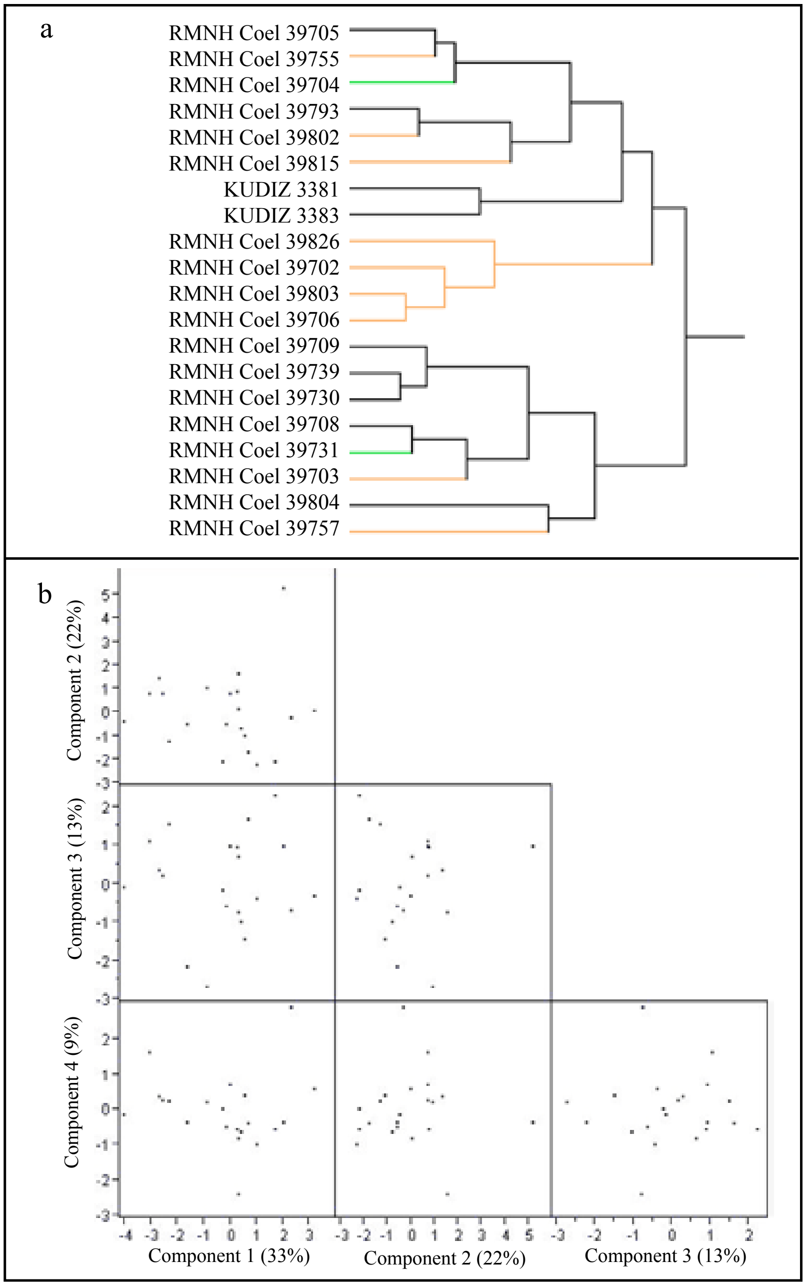

Fig 4.5. a) Cluster analysis of morphometric measurements b) Principal Component Analysis scatterplots for first four components. Note, for either graph, the non-clustering of individuals of same morphotype. Color coding for morphotype: black = cake, orange = branched, green = pom-pom.

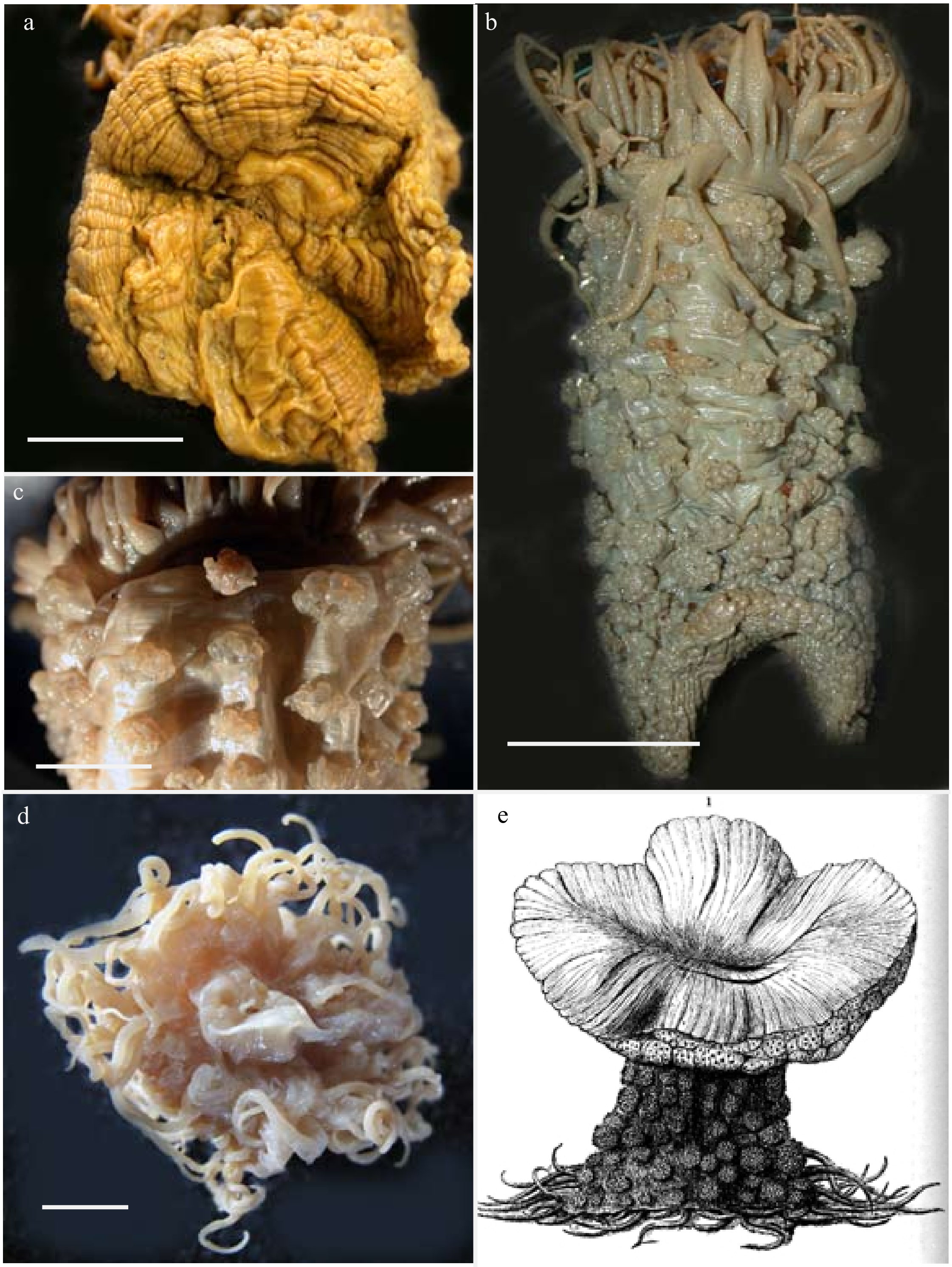

Fig 4.6. *Alicia mirabilis.* a) pedal disc of preserved specimen with mesenterial insertions visible as dark lines, SMF 1911, scale bar = 30 mm b) whole individual, with vesicles on scapus, SMNH 644, scale bar = 30 mm c) compound stalked vesicles, SMNH 644, scale bar = 10 mm d) oral disc and mouth, KUDIZ 3130, scale bar = 10 mm e) figure 1 from Johnson (1861), detached individual with inflated pedal disc, pedal disc at top of figure.

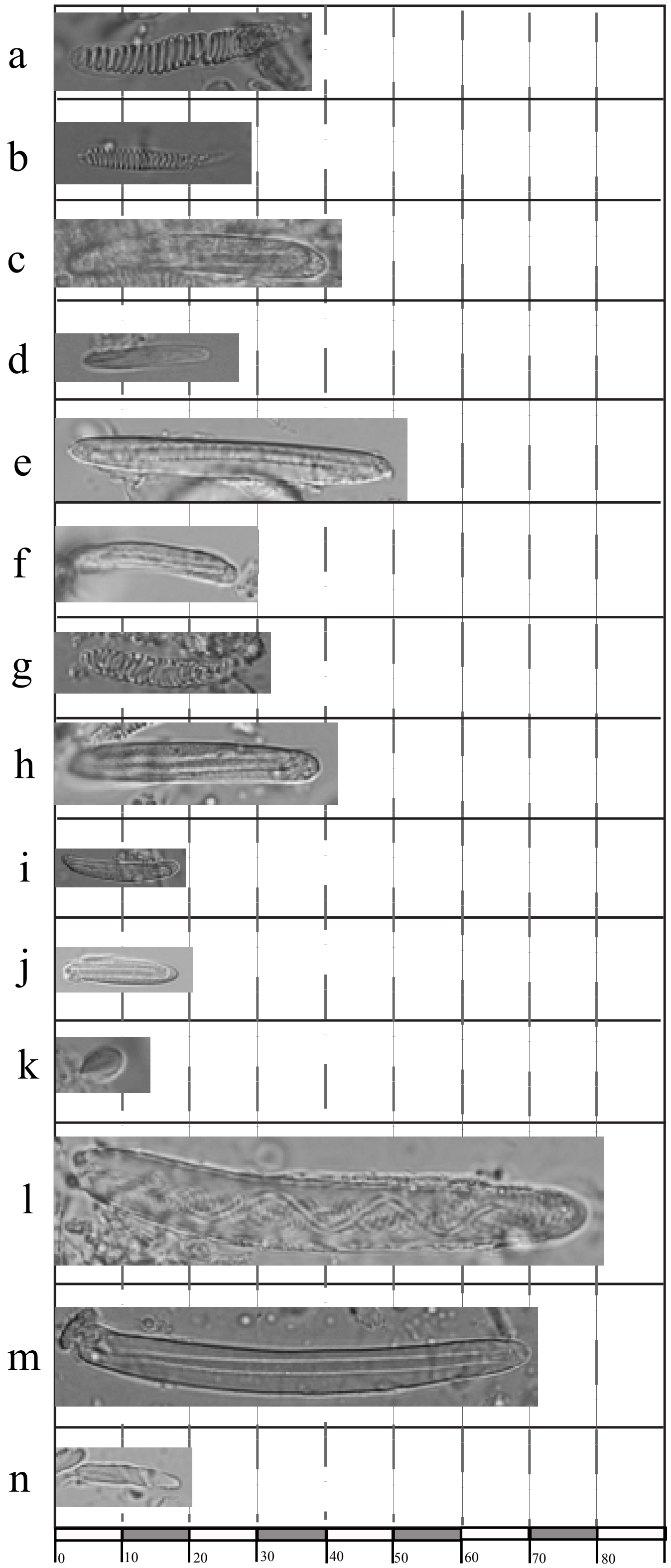

Fig 4.7. Representative cnidae from various tissues of *Alicia mirabilis*. Lowercase letters correspond to measurements in Table 4.4. Tissue source: a-d) tentacles e,f) actinopharnx g-i) oral disc j,k) mesenterial filaments l-n) vesicles. Scale bar in micrometers.

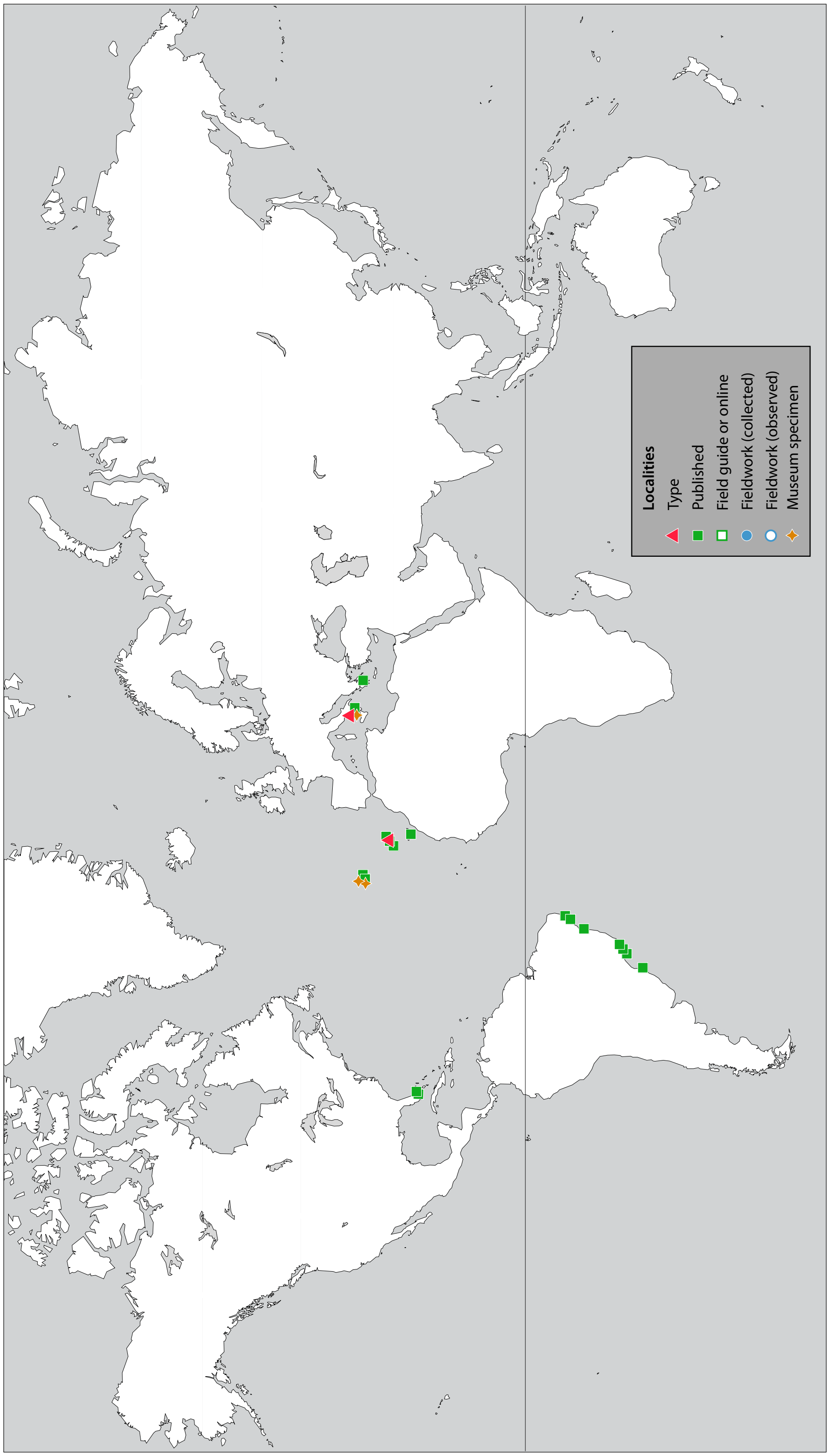

Fig 4.8. Recorded localities of *Alicia mirabilis*.

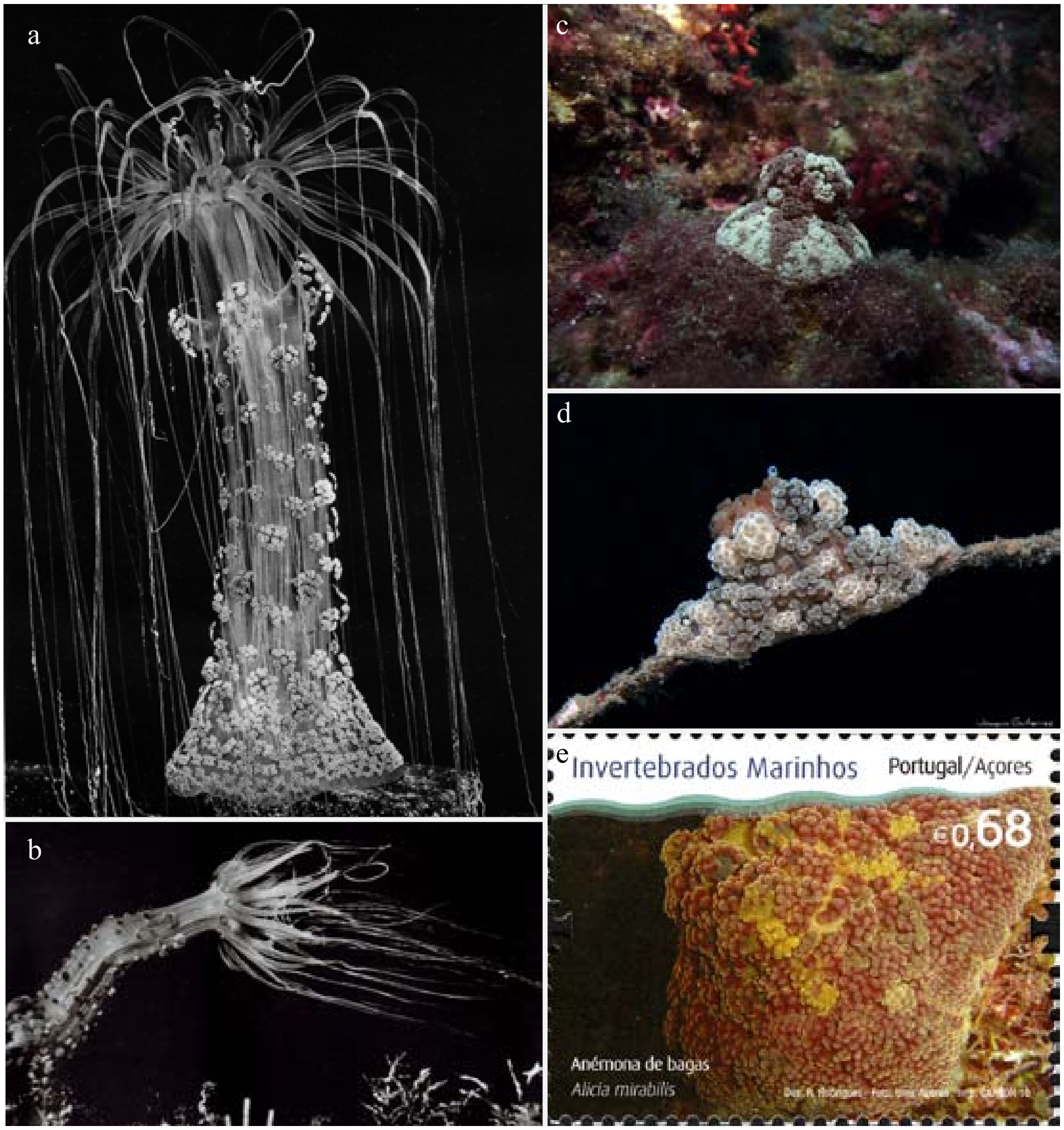

Fig 4.9. *Alicia mirabilis*. a,b) extended specimen with long, fine tentacles (from Schmidt 1972) c,d) retracted specimen c) from Western Mediterranean (http://gps-tsc.upc.es/comm/jriba/personal_data.html) d) from Canary Islands (http://www.flickr.com/photos/fotografiasubmarina/7006094154/in/set-72157627420923025) e) pictured on stamp from Azores, Portugal.

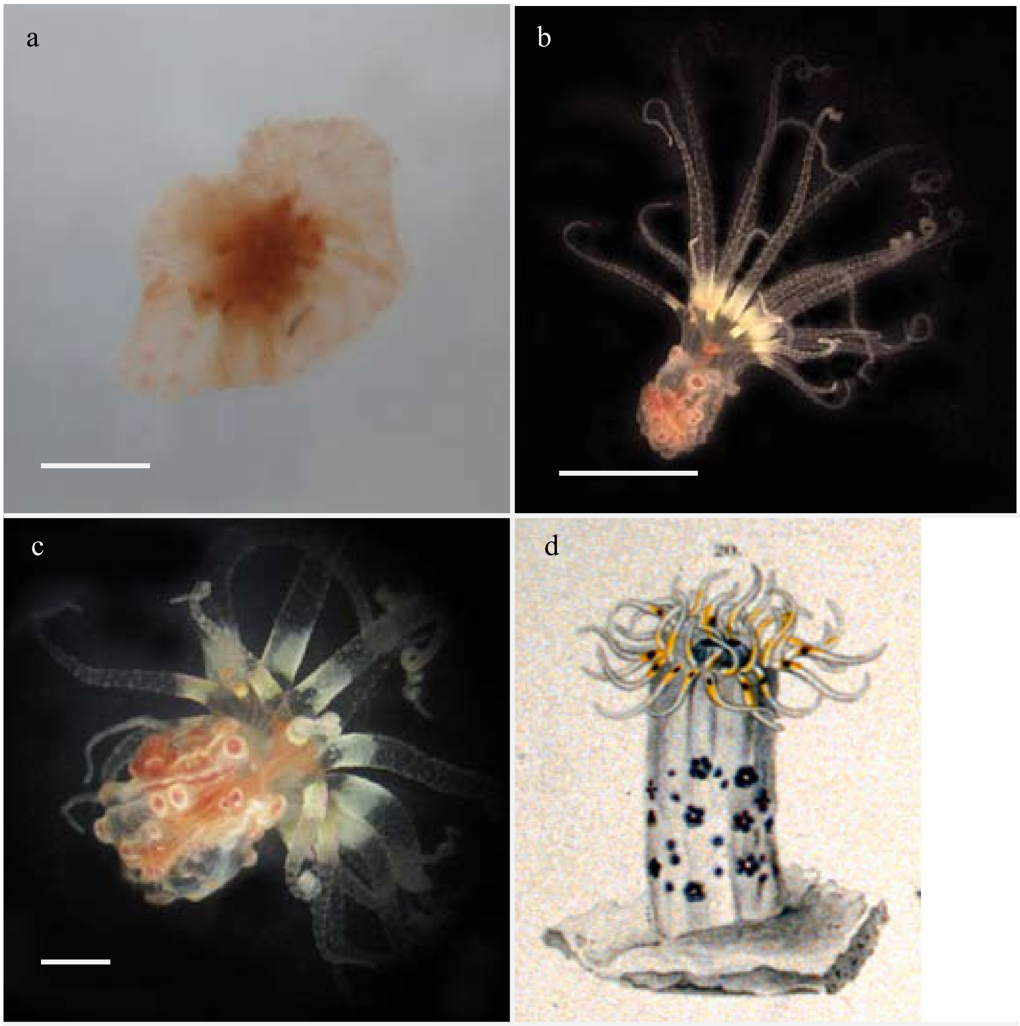

Fig 4.10. *Alicia pretiosa.* a) pedal disc, circular to oval shape, live KUDIZ 3168, scale bar = 2 mm b) whole specimen from side, showing delicate and translucent scapus with colored vesicles, live KUDIZ 3168, scale bar = 5 mm c) closer view of vesicles, live KUDIZ 3168, scale bar = 2 mm d) Figure 20 from Dana (1846), note dark spot on distal oral part of tentacles.

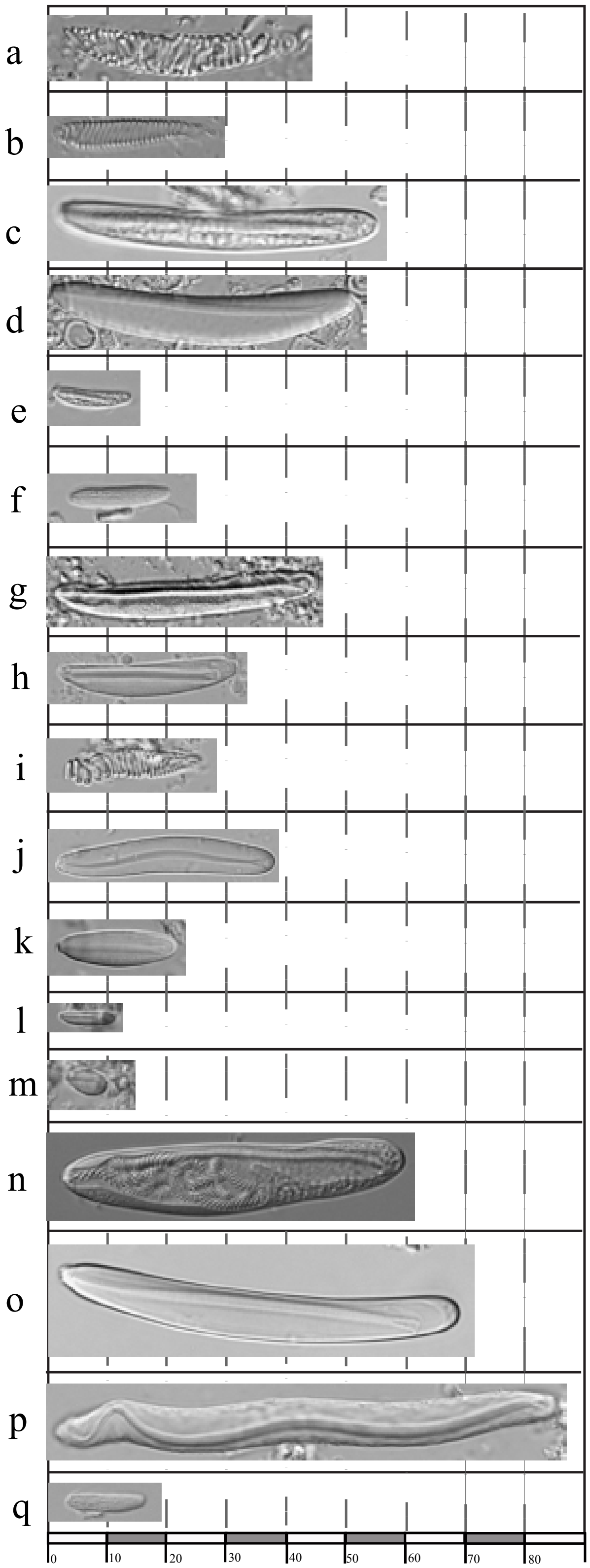

Fig 4.11. Representative cnidae from various tissues of *Alicia pretiosa*. Lowercase letters correspond to measurements in Table 4.6. Tissue source: a-f) tentacles g,h) actinopharnx i,j) oral disc k-m) mesenterial filaments n-q) vesicles. Scale bar in micrometers.

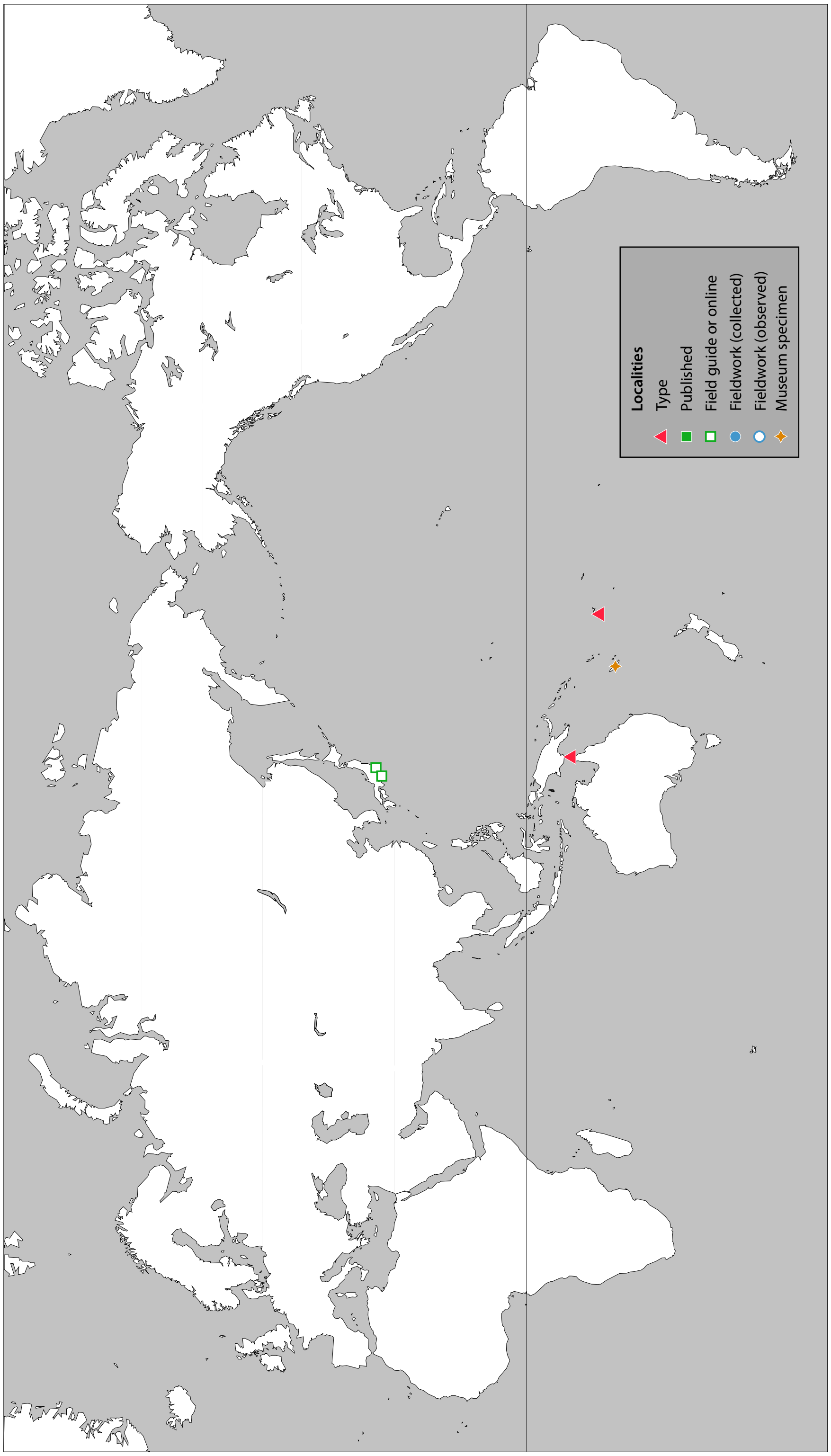

Fig 4.12. Recorded localities of *Alicia pretiosa*.

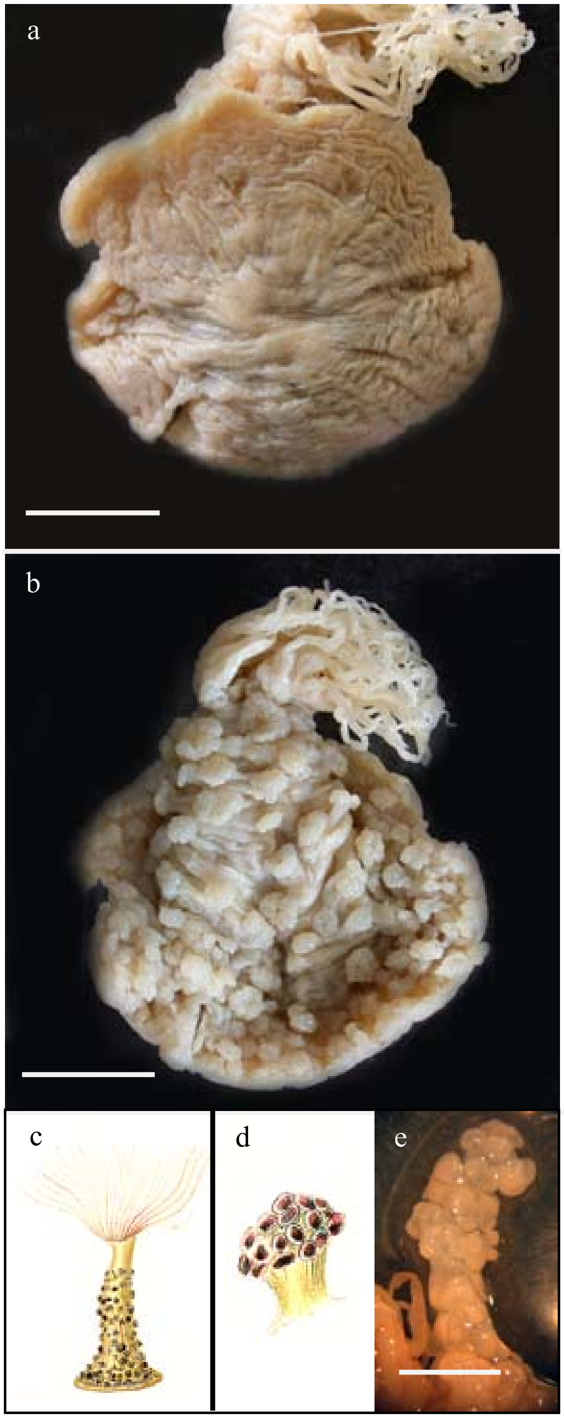

Fig 4.13. *Alicia sansibarensis.* a,b) syntype ZMH C2592 a) pedal disc, scale bar = 10 mm b) whole individual, scapus with vesicles, scale bar = 10 mm c,d) figures from Carlgren (1900) c) whole individual d) peduncle with group of vesicles, attached to distal column e) specimen in Zoologisk Museum, Copenhagen, compound stalked vesicle, scale bar = 5 mm.

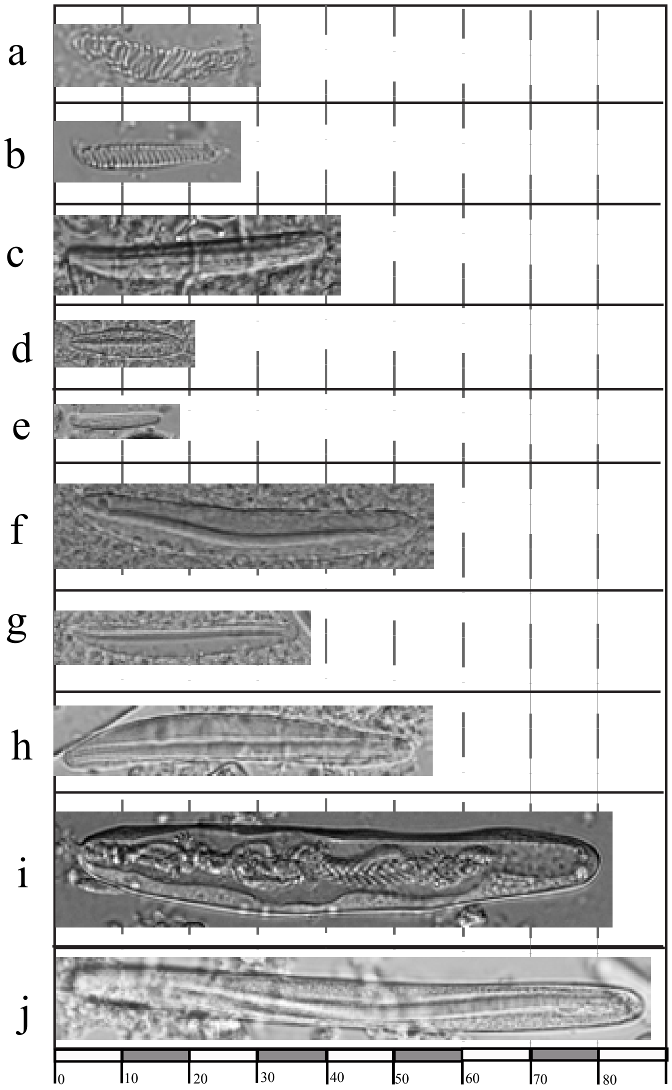

Fig 4.14. Representative cnidae from various tissues of *Alicia sansibarensis*. Lowercase letters correspond to measurements in Table 4.8. Tissue source: a-e) tentacles f,g) actinopharnx h) oral disc i,j) vesicles. Scale bar in micrometers.

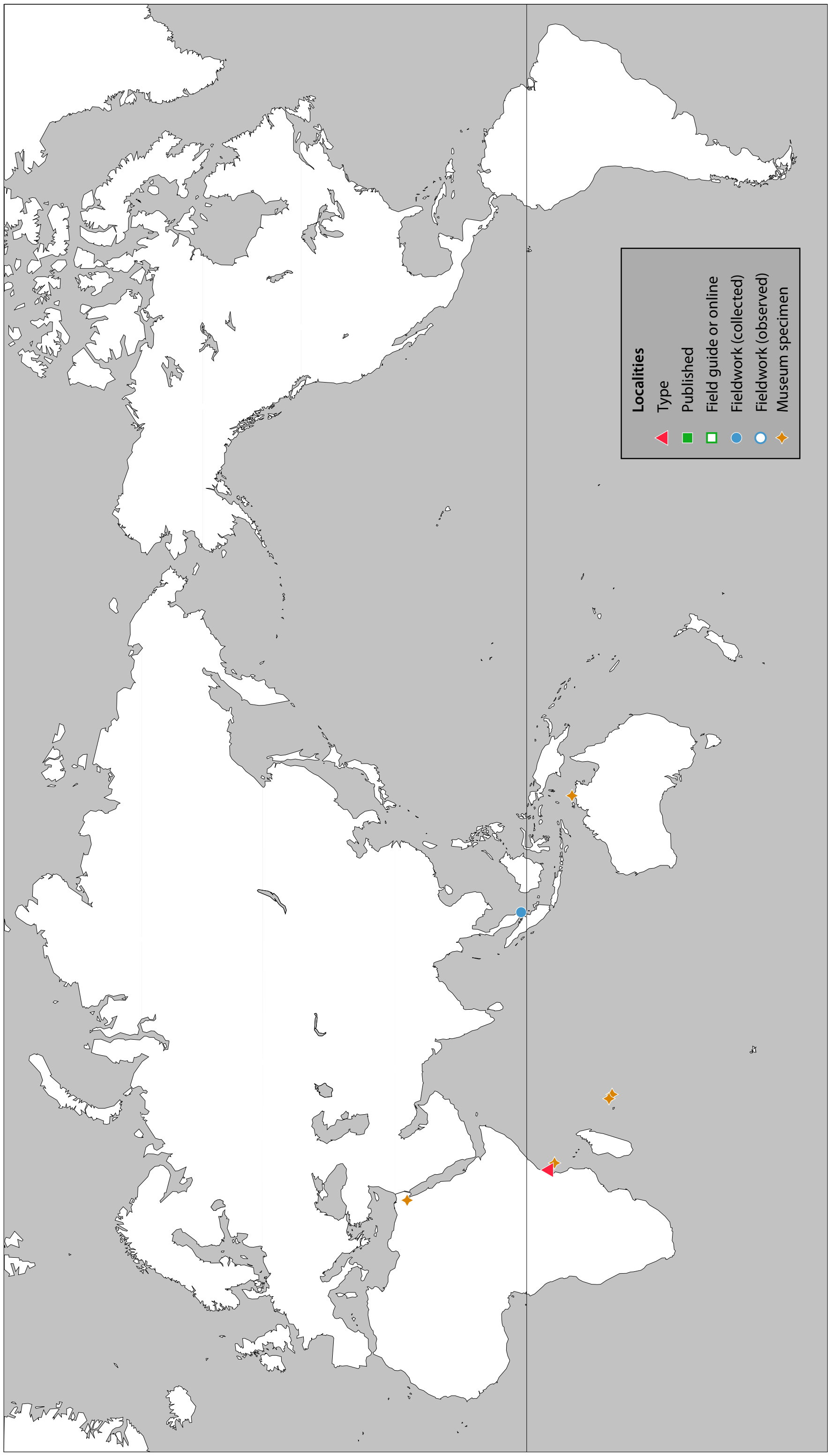

Fig 4.15. Recorded localities of *Alicia sansibarensis*.

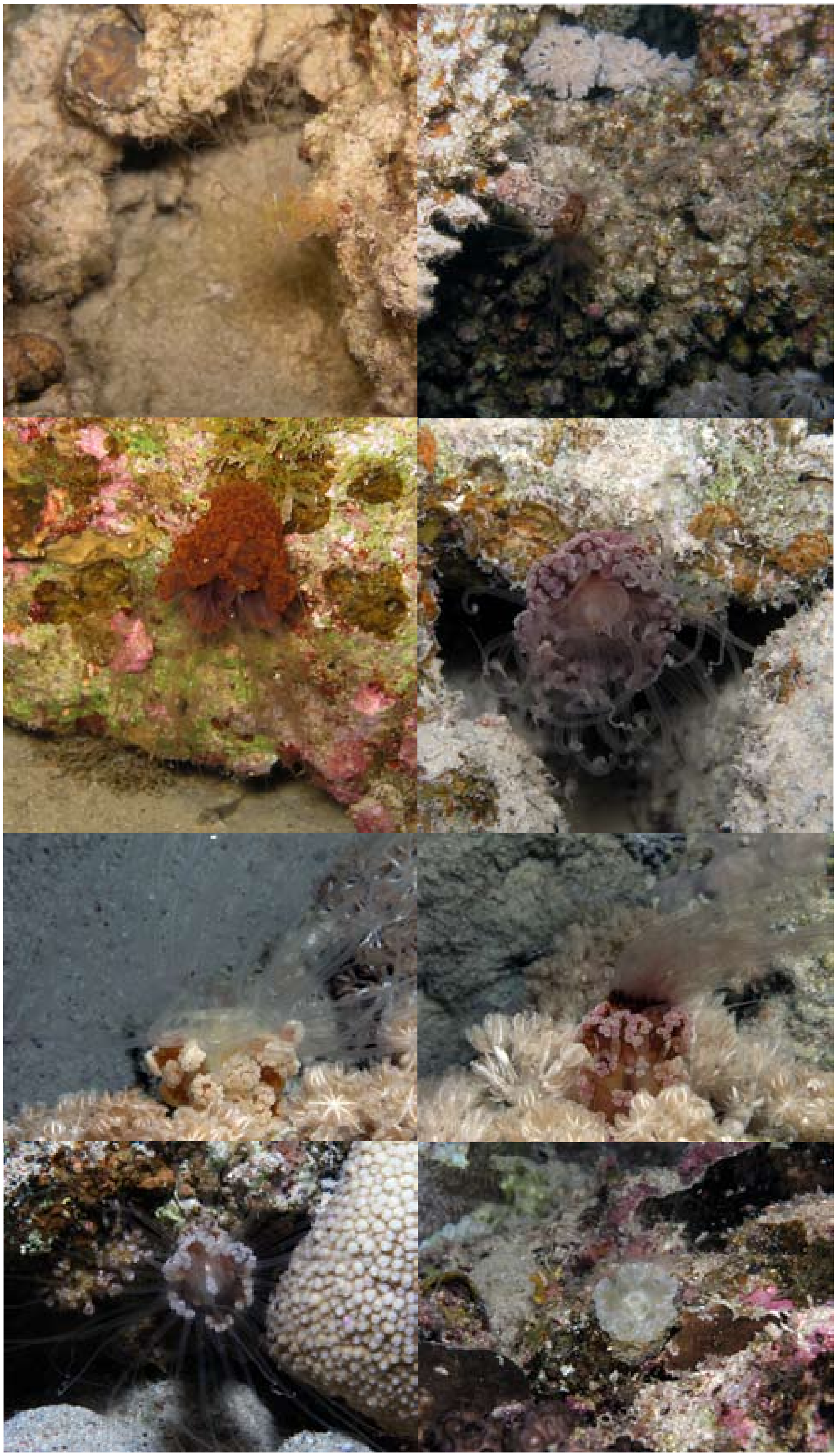

Fig 4.16. *Alicia* specimens photographed from the Red Sea. Note range of coloration among specimens. Photographs by Christian Alter.

Fig 4.17. *Alicia beebei.* a) pedal disc of preserved individual with mesenterial insertions visible as dark lines, USNM 49397, scale bar = 20 mm b) whole individual, vesicles covering scapus, long tentacles, USNM 49397, scale bar = 20 mm c) whole individual *in situ* from Loreto, Mexico, Gulf of California, photograph by Carlos Sanchez, arrow indicating distal peduncle with large number of vesicles d) oral disc and mouth, uncataloged specimen collected from Gulf of Mexico, scale bar = 10 mm e) oral disc and mouth, USNM 49397, scale bar = 10 mm.

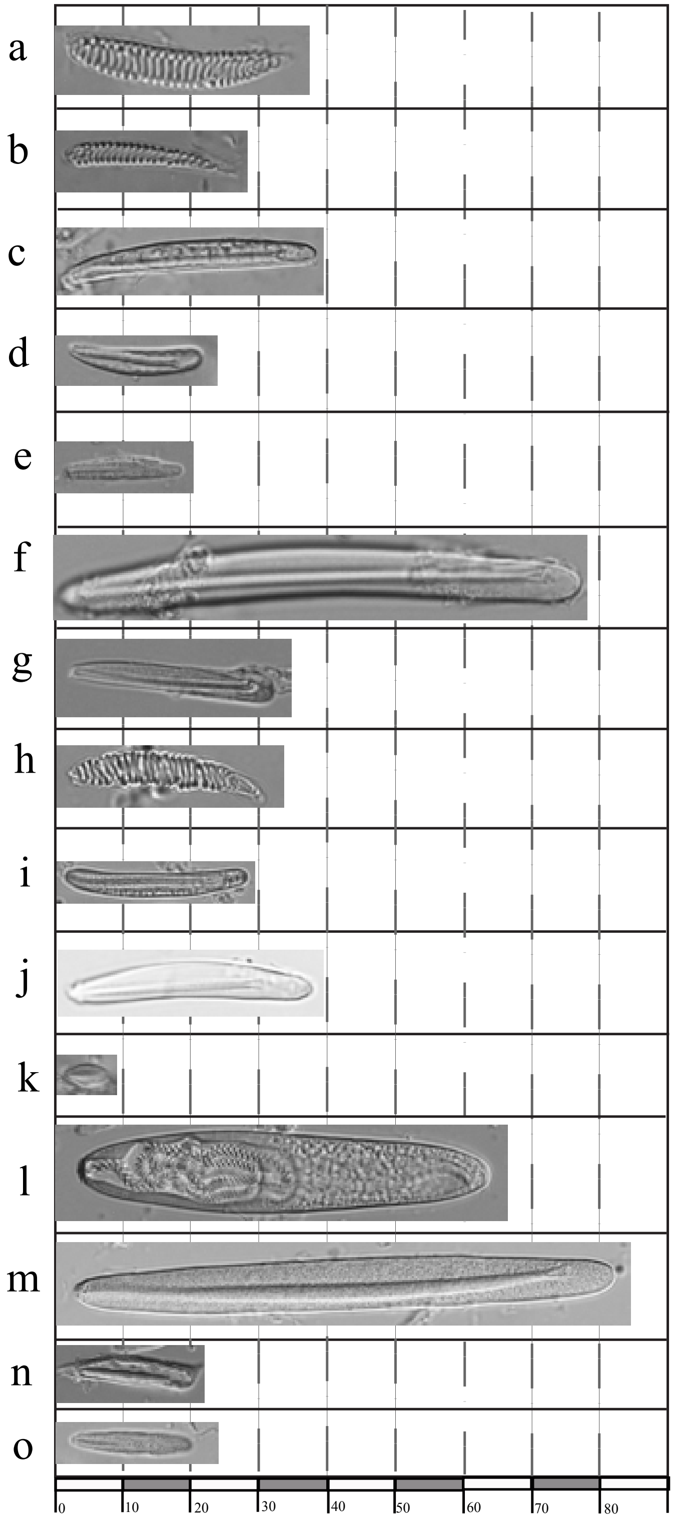

Fig 4.18. Representative cnidae from various tissues of *Alicia beebei*. Lowercase letters correspond to measurements in Table 4.10. Tissue source: a-e) tentacles f,g) actinopharnx h,i) oral disc j,k) mesenterial filaments l-o) vesicles. Scale bar in micrometers.

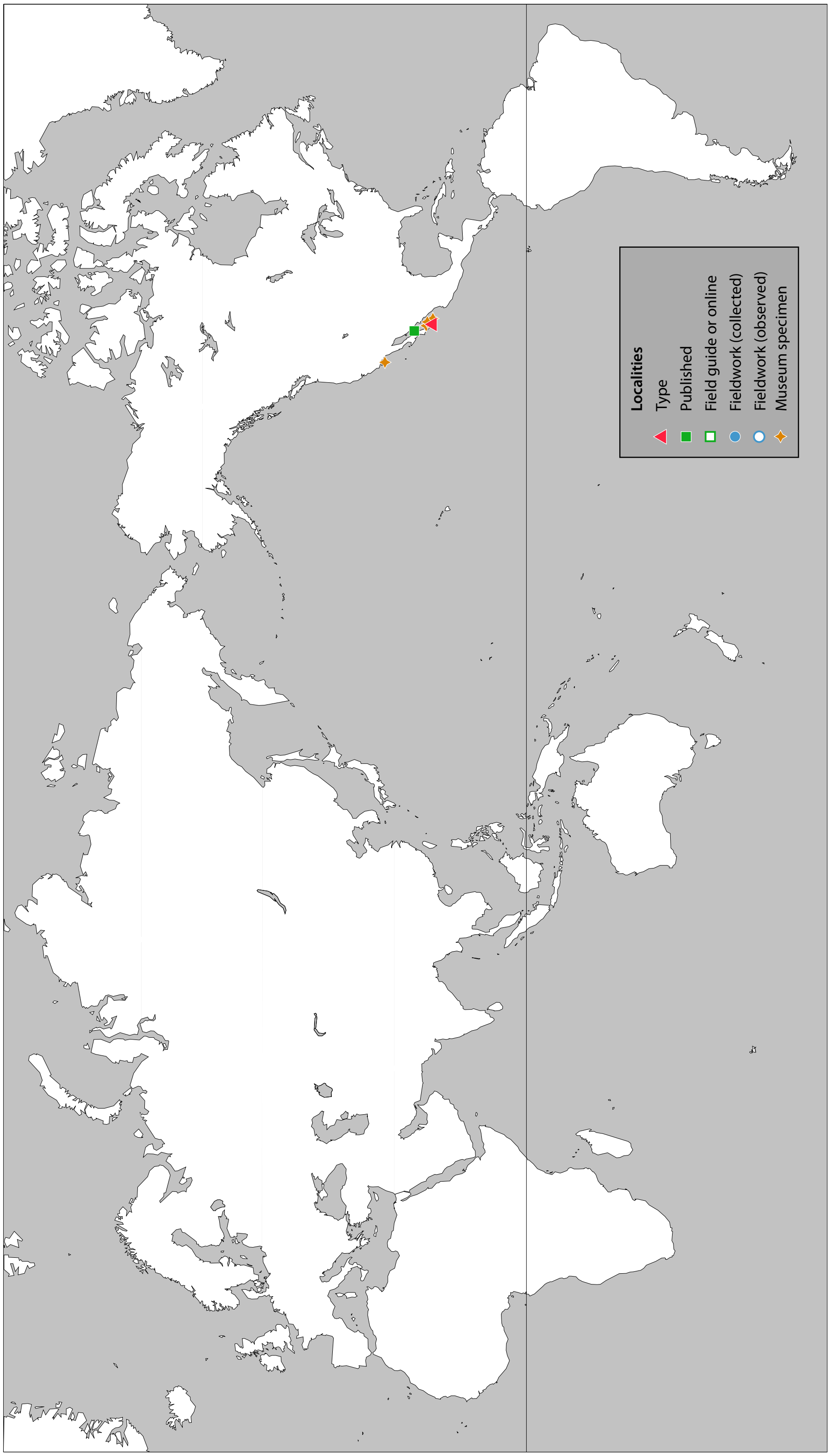

Fig 4.19. Recorded localities of *Alicia beebei.*

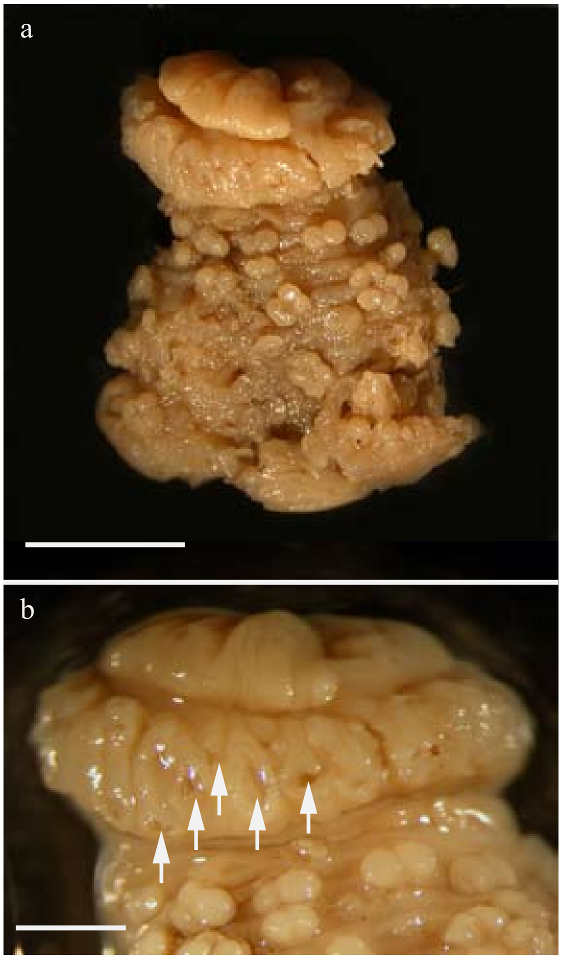

Fig 4.20. *Alicia uruguayensis.* a) whole individual, SMNH 86, scale bar = 10 mm b) side view of oral disc and distal part of column, SMNH 86, scale bar = 5 mm, arrows indicating some of the holes where tentacles were attached.

Fig 4.21. Recorded localities of *Alicia uruguayensis*.

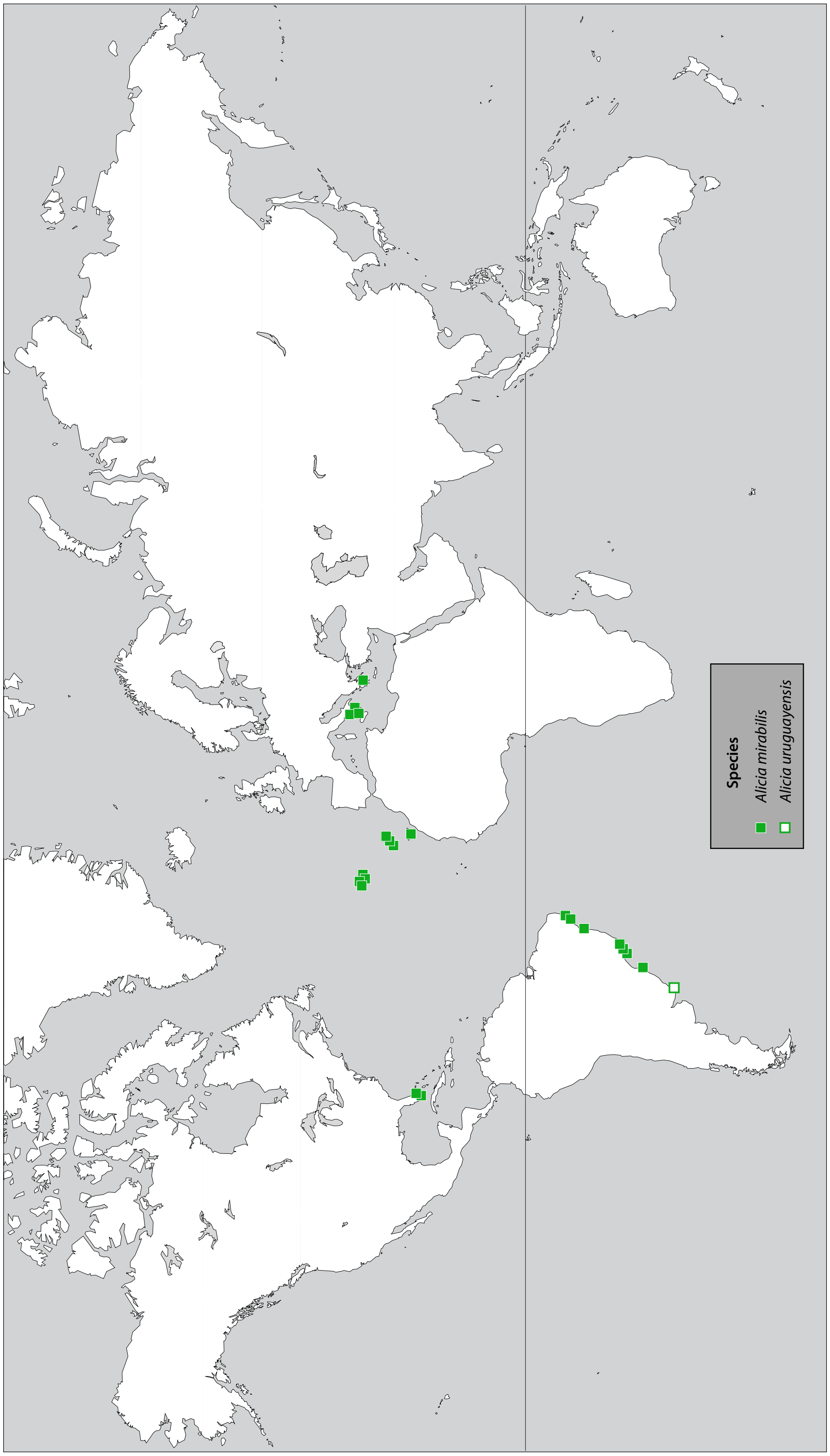

Fig 4.22. Recorded localities of *Alicia mirabilis* and *A. uruguayensis.*

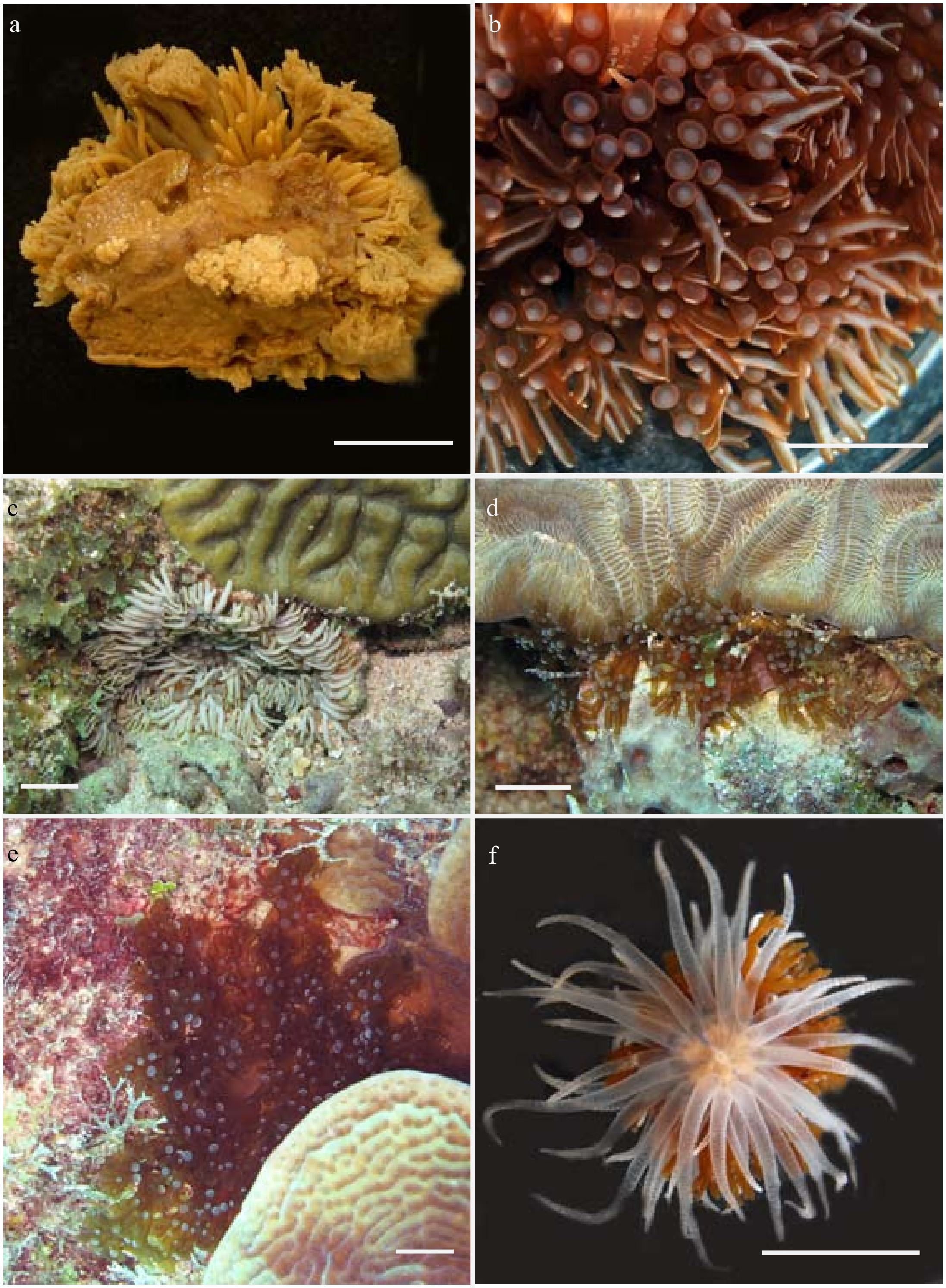

Fig 4.23. *Lebrunia neglecta.* a) pedal disc of preserved specimen, KUDIZ 2365 b) close-up of brown pseudotentacles with gray markings, KUDIZ 3247, Belize, Carrie Bow Cay c) individual *in situ* with light gray pseudotentacles, KUDIZ 3177, Curaçao, near Water Plant d) individual *in situ* with brown pseudotentacles, KUDIZ 3183, Curaçao, Snake's Bay e) individual *in situ* with brown pseudotentacles, KUDIZ 3176, Curaçao, near Water Plant e) tentacles, oral disc, and mouth, KUDIZ 3249. Scale bars = 20 mm.

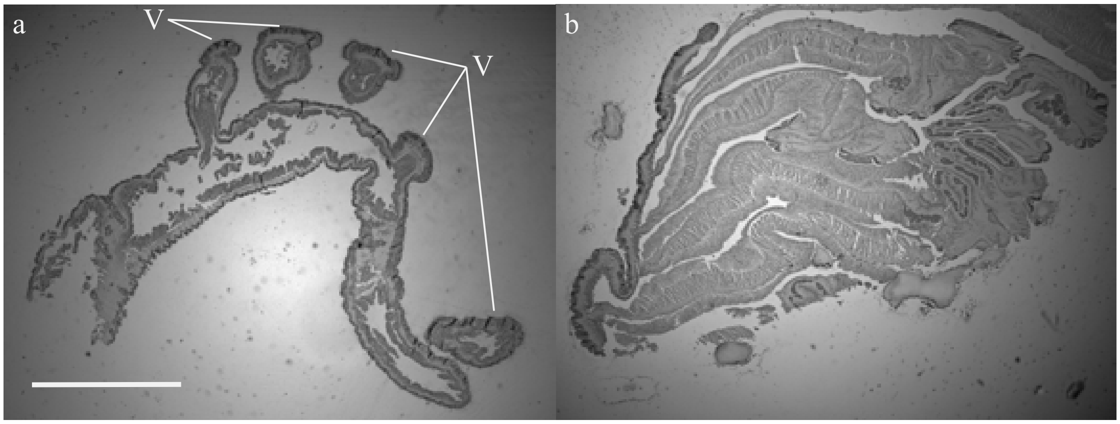

Fig 4.24. *Lebrunia neglecta*. a) longitudinal section through single pseudotentacle with multiple raised vesicles, KUDIZ 3247, scale bar = 10 mm b) cross section through mesenteries, showing well developed retractor muscles, KUDIZ 3247. Figure legend: V = vesicle.

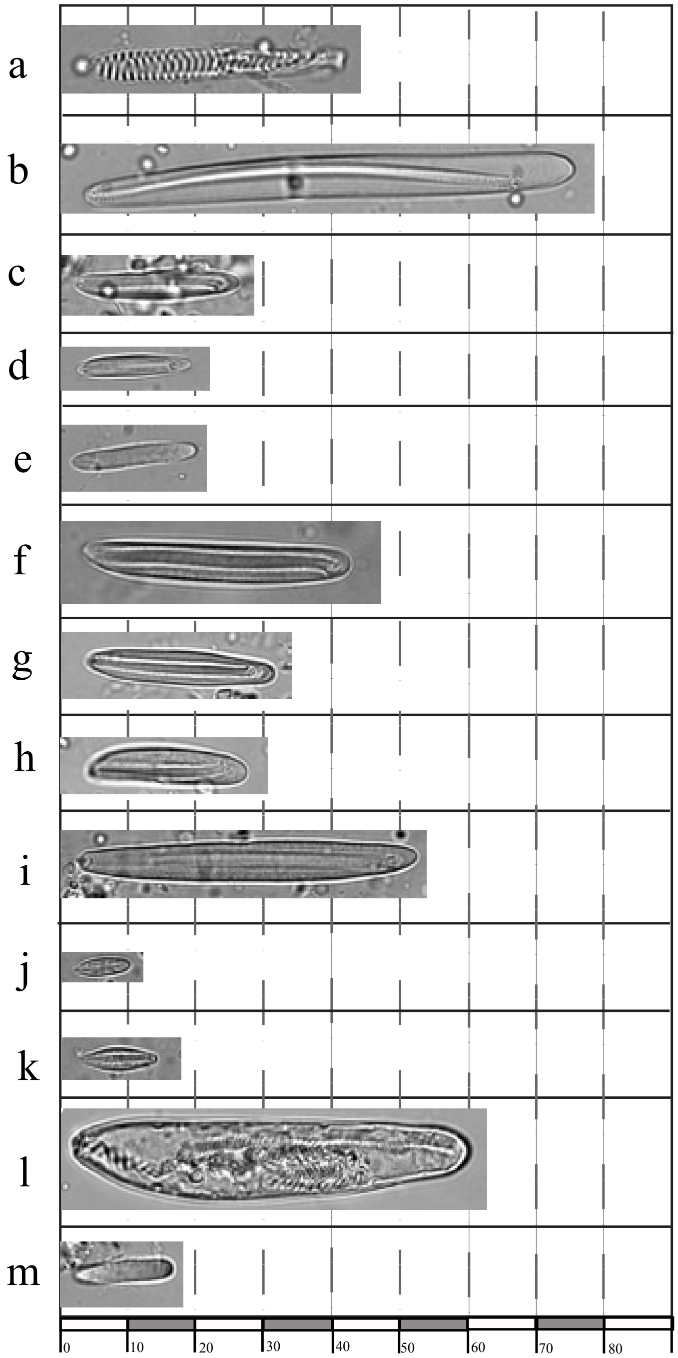

Fig 4.25. Representative cnidae from various tissues of *Lebrunia neglecta*. Lowercase letters correspond to measurements in Table 4.13. Tissue source: a-e) tentacles f) actinopharnx g,h) oral disc i-k) mesenterial filaments l,m) vesicles. Scale bar in micrometers.

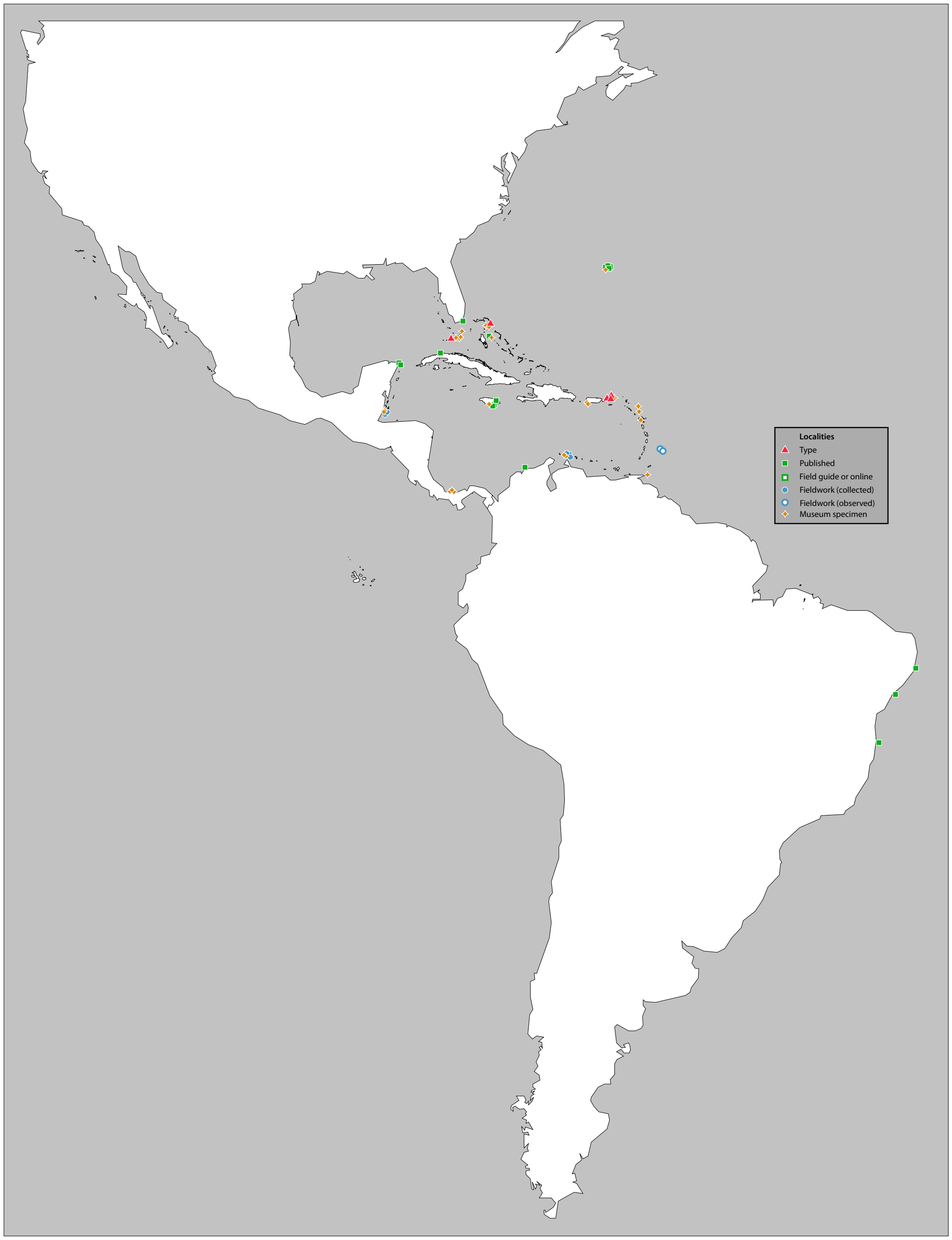

Fig 4.26. Recorded localities of *Lebrunia neglecta.*

Fig 4.27. *Lebrunia coralligens.* a) pedal disc with mesenterial insertions visible as lighter lines, KUDIZ 3182 b) multiple individuals *in situ*, KUDIZ 3172, Barbados, Church Point c) multiple individuals *in situ*, KUDIZ 3186, Curaçao, Piscadera Bay d) multiple individuals *in situ*, KUDIZ 3170, Barbados, Tropicana Reef e) multiple individuals *in situ*, KUDIZ 3182, Curaçao, Snake's Bay f) tentacles, oral disc, and mouth, KUDIZ 3170. Scale bars = 2 mm.

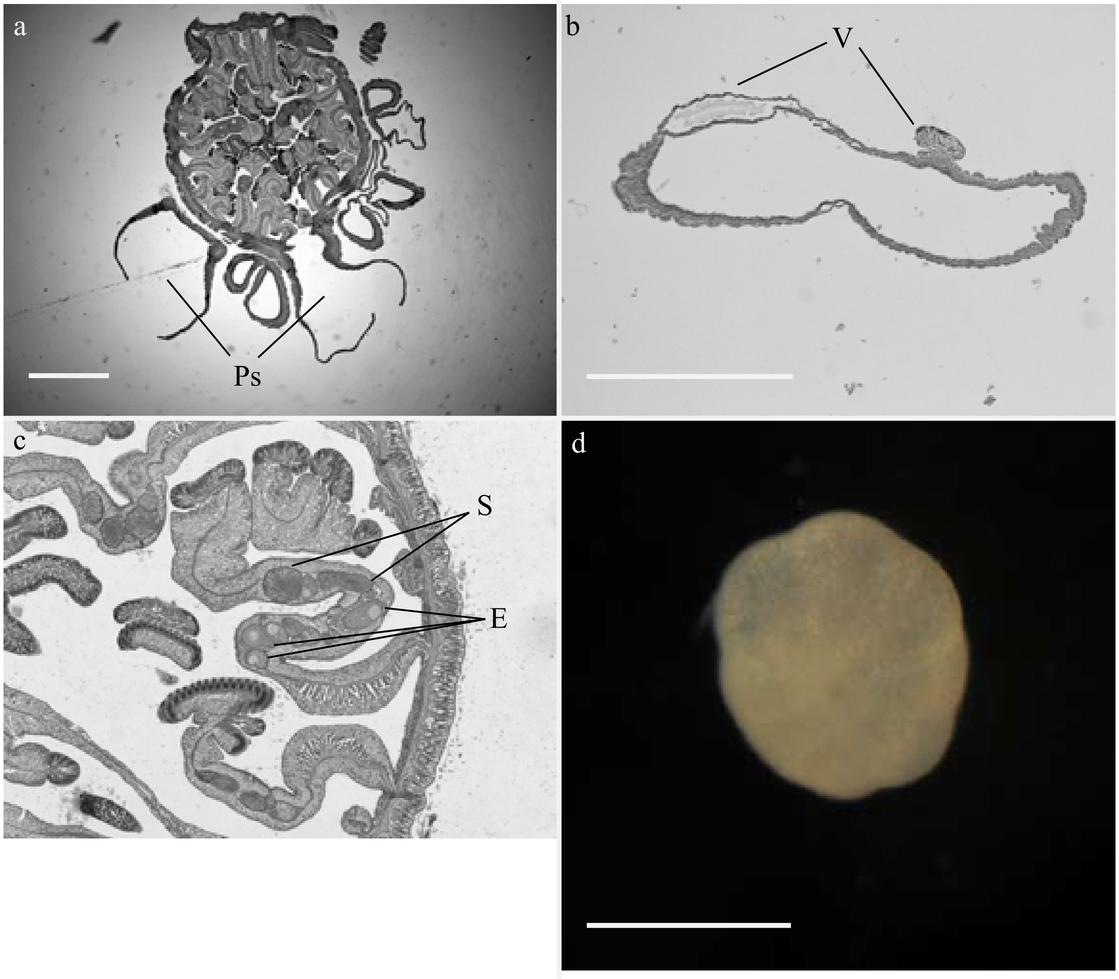

Fig 4.28. *Lebrunia coralligens.* a) cross section, KUDIZ 3181, with pseudotentacles, note pseudotentacle communicating with endocoel of higher order mesentery pair, scale bar = 5 mm b) longitudinal section through pseudotentacle with vesicles; dense patch of cnidae on left, raised vesicle on right, KUDIZ 2361, scale bar = 10 mm c) cross section of second order mesenteries, egg and sperm packets on same mesentery, KUDIZ 2361 d) brooded individual from adult, KUDIZ 3170, scale bar = 1 mm. Figure legend: E = egg, Ps =

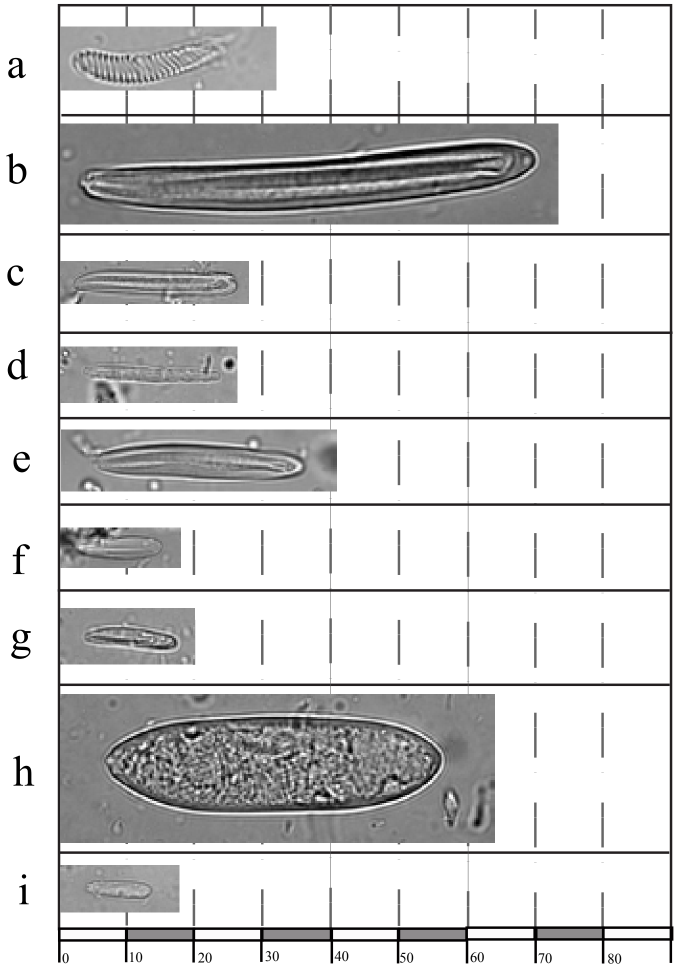

Fig 4.29. Representative cnidae from various tissues of *Lebrunia coralligens*. Lowercase letters correspond to measurements in Table 4.15. Tissue source: a-d) tentacles e-g) mesenterial filaments h,i) vesicles. Scale bar in micrometers.

Fig 4.30. Recorded localities of *Lebrunia coralligens*.

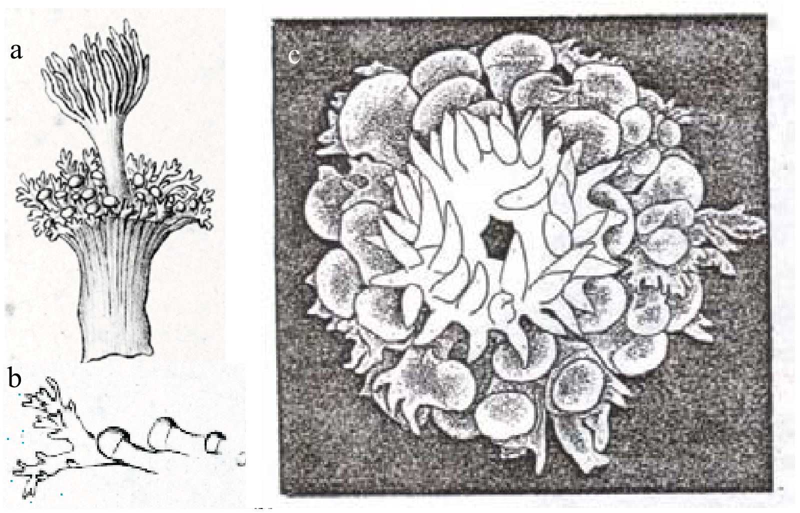

Fig 4.31. *Triactis producta*. Figures from original descriptions. a) *Triactis producta*, whole, side view. Plate VI, figure 8 from Klunzinger (1877). b) *Triactis producta*, pseudotentacle with vesicles. Plate VI, figure 8 from Klunzinger (1877). c) *Phyllodiscus indicus*, whole, view looking down onto oral disc and tentacles (white) and pseudotentacles and vesicles (shaded). Figure 18 from Stephenson (1921).

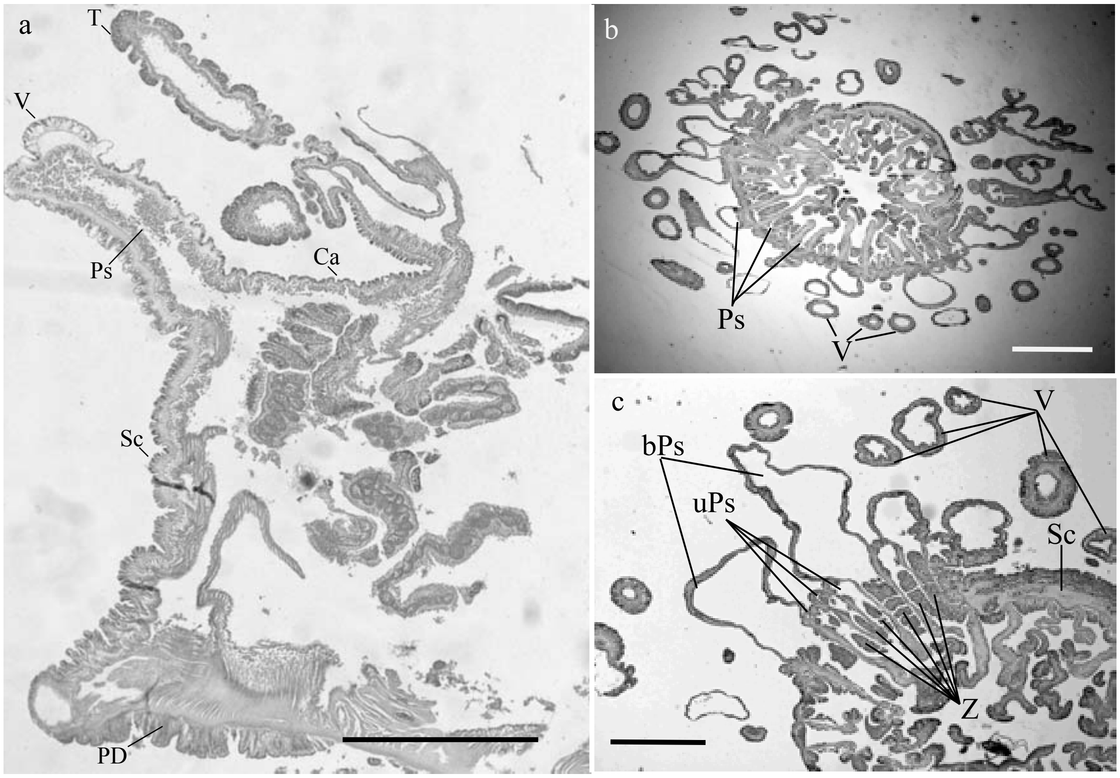

Fig 4.32. *Triactis producta*. a) longitudinal section of whole individual, note separation of scapus and capitulum, KUDIZ 3374 b,c) cross section showing pseudotentacle placement in relation to mesenteries b) cross section of whole individual, KUDIZ 3210 c) cross section through scapus wall and multiple pseudotentacles, KUDIZ 3210. Scale bars = 5 mm. Figure legend: bPs = branched pseudotentacle, Ca = capitulum, PD = pedal disc, Ps = pseudotentacle, Sc = scapus, T = tentacle, uPs = unbranched pseudotentacle, V = vesicle, Z = zooxanthellae.

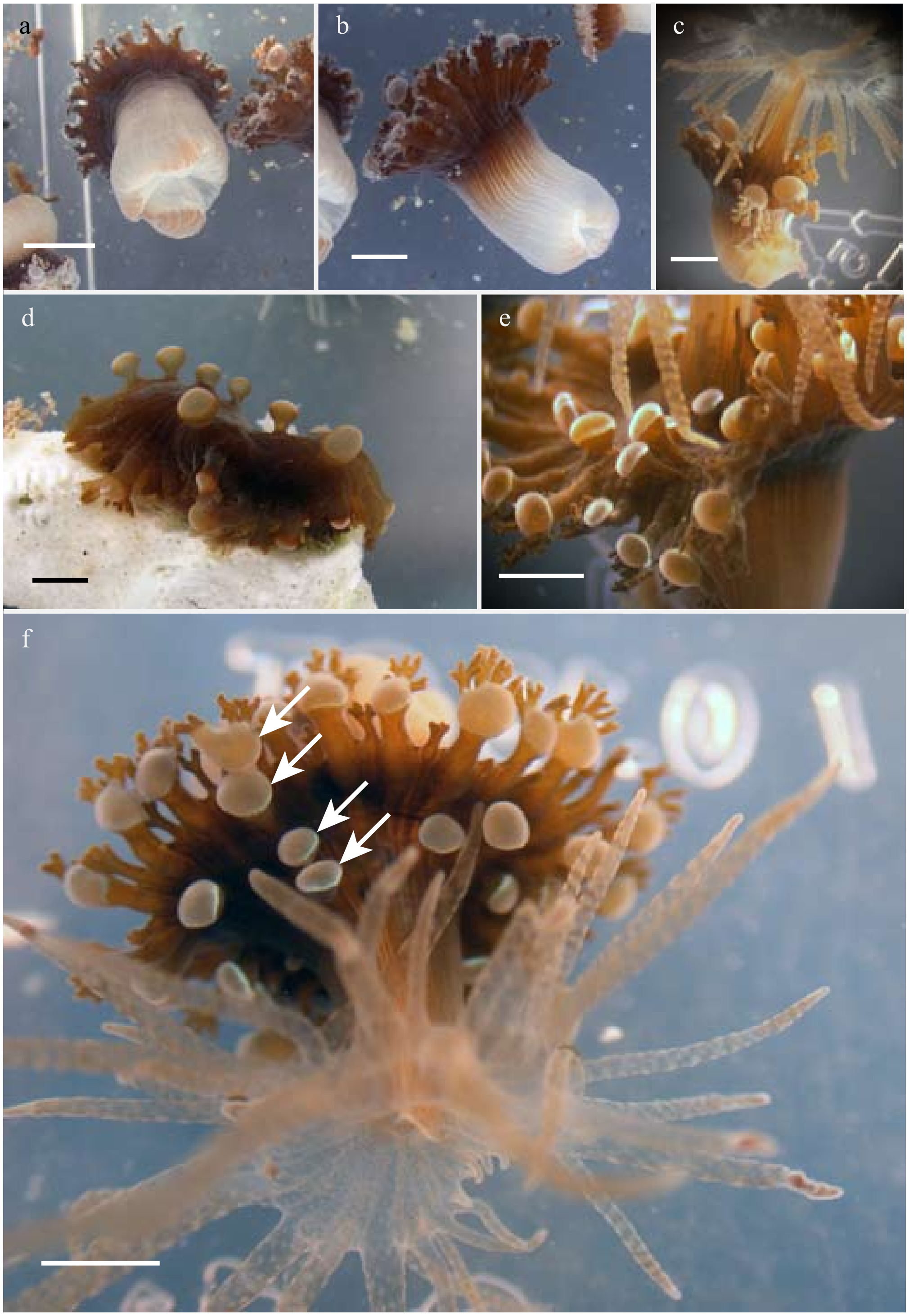

Fig 4.33. *Triactis producta*. a) pedal disc b) scapus, with mesenterial insertions as light lines, no vesicles on aboral side of pseudotentacles c) pseudotentacles with sessile vesicles, note branching occurs perpendicular to oral-aboral axis and at distal ends of pseudotentacles d,e) stalked vesicles, individual in (d) has retracted oral disc and tentacles. f) Individual with four vesicles in one endocoel, indicated with arrows. All scale bars = 2 mm.

Fig 4.34. *Triactis producta*. Sessile vesicles on pseudotentacle, with silver ring at base of vesicle. Scale bar = 2 mm.

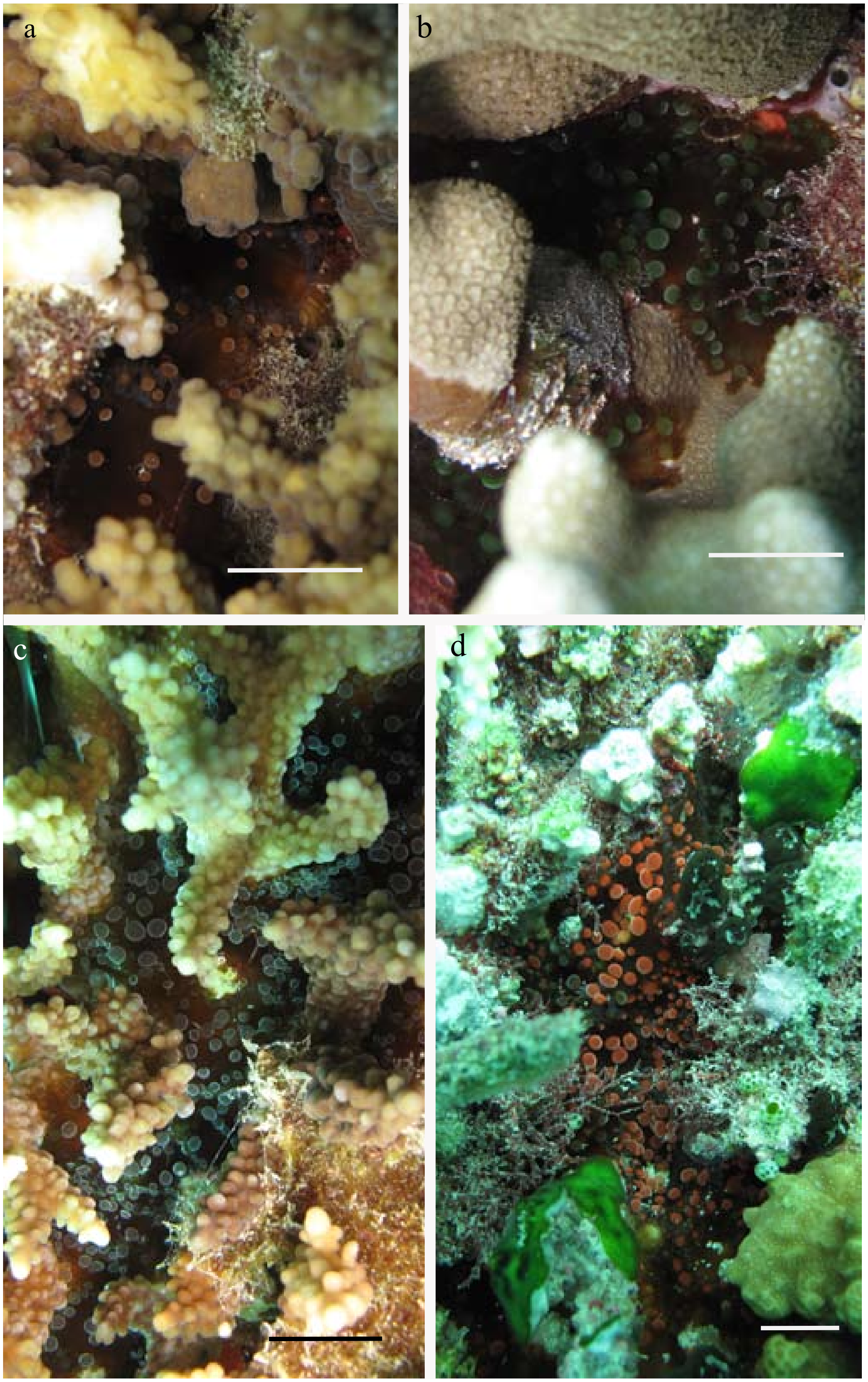

Fig 4.35. *Triactis producta*. Various colors of vesicles a) orange, b) green, c) grey, d) pink. Scale bars = 20 mm. Note only pseudotentacles and vesicles visible, oral disc and tentacles retracted during the day.

Fig 4.36. *Triactis producta*. Individual with expanded oral disc and tentacles. Note translucent oral disc and tentacles lacking zooxanthellae. Tentacles with opaque spots and tip. Scale bar = 5 mm.

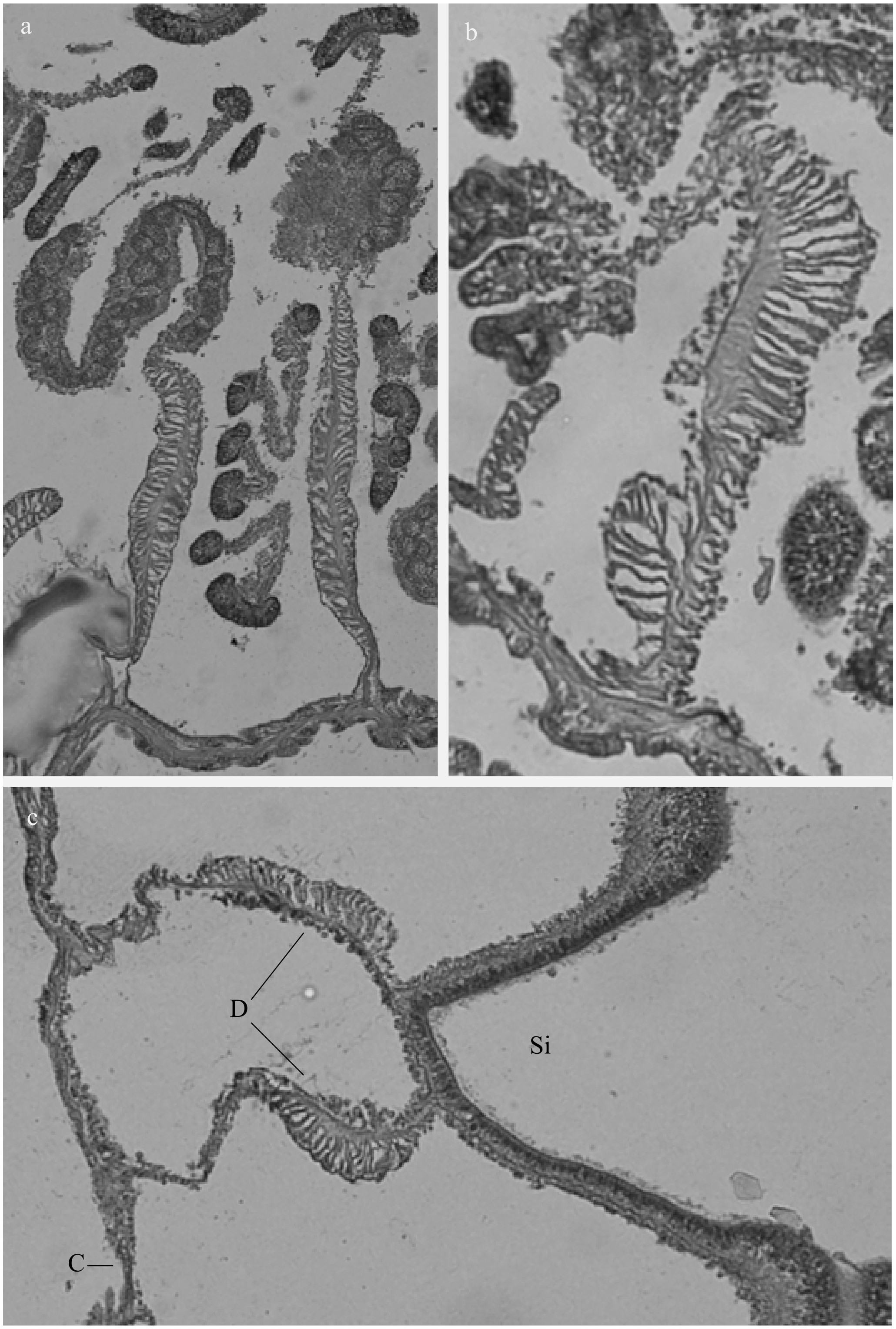

Fig 4.37. *Triactis producta*. a) fertile second order mesentery pair b) diffuse retractor muscle and parietobasilar muscle of second order mesentery c) directive mesenteries attached to column and siphonoglyph. Figure legend: C = column, D = directive, Si = siphonoglyph.

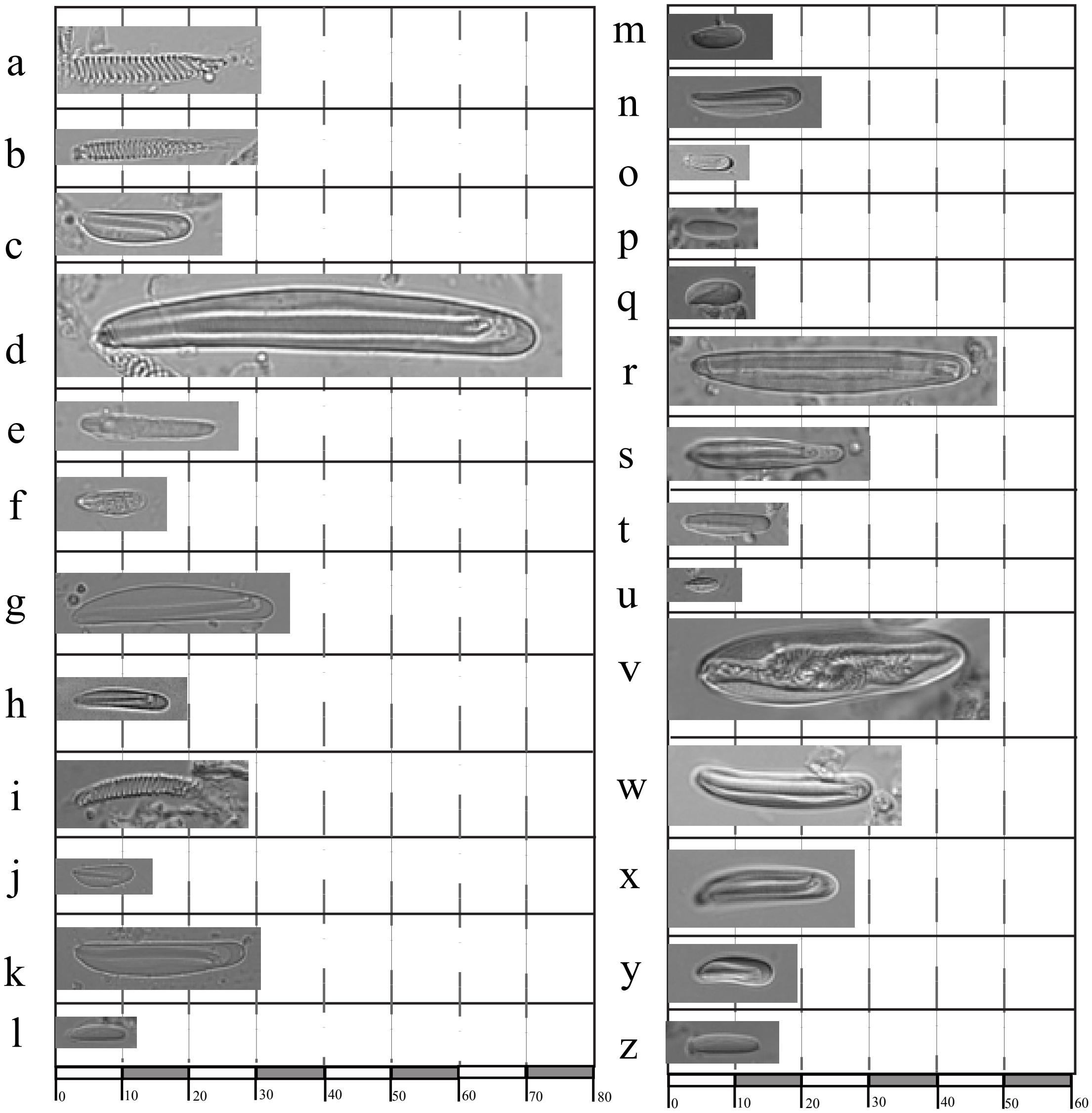

Fig 4.38. Representative cnidae from various tissues of *Triactis producta*. Lowercase letters correspond to measurements in Table 4.17. Tissue source: a-f) tentacles g,h) actinopharnx i-m) oral disc n-q) column r-u) mesenterial filaments v-z) vesicles. Scale bar in micrometers.

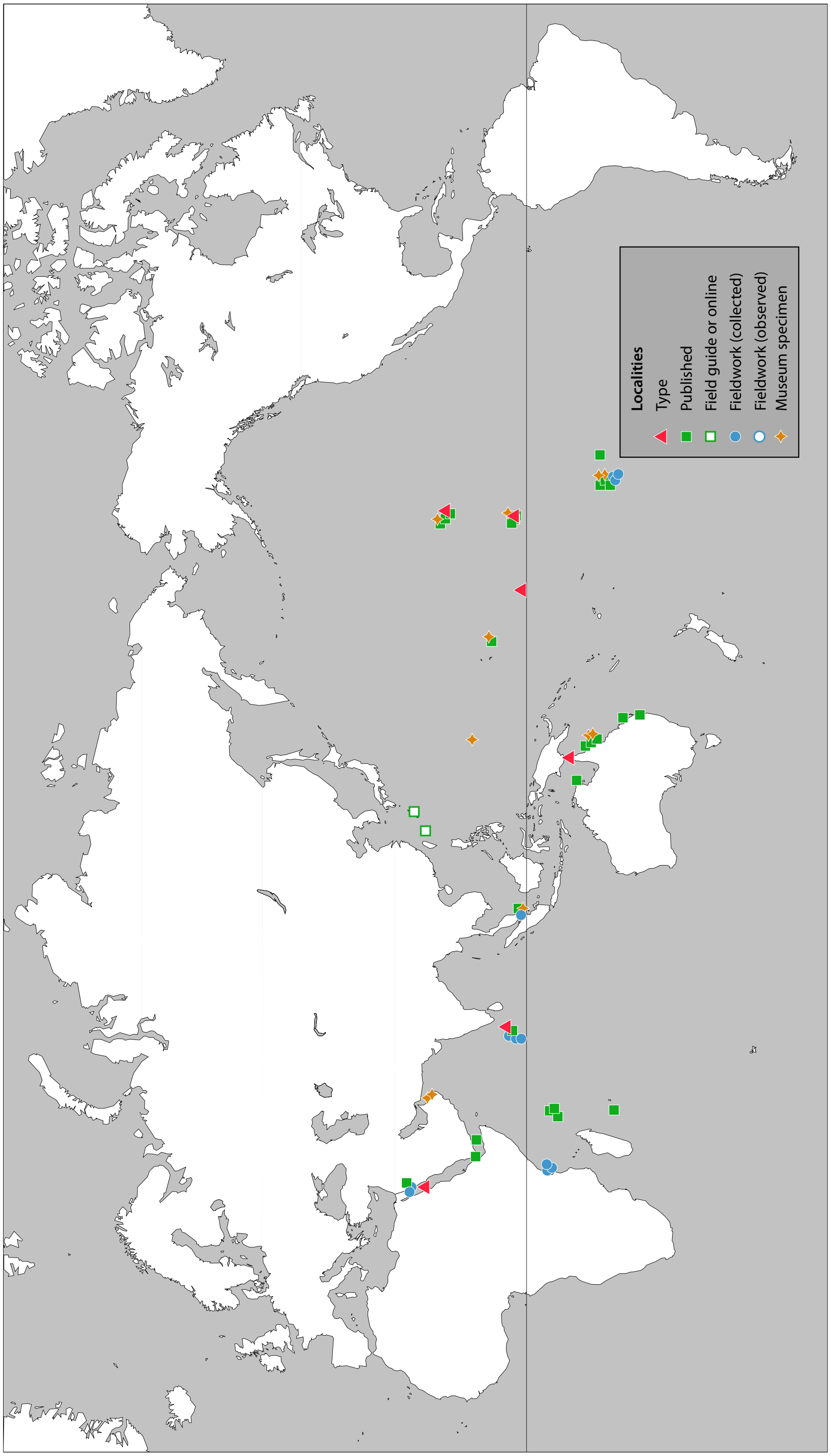

Fig 4.39. Recorded localities of *Triactis producta*.

Fig 4.40. *Triactis producta*. Stages of pseudotentacle and vesicle development.
a) smooth column, no pseudotentacles or vesicles b) one well-developed vesicle, developing pseudotentacles c) multiple pseudotentacles and vesicles in various stages of development d) full whorl of branched pseudotentacles with sessile vesicles. Scale bar = 3 mm.

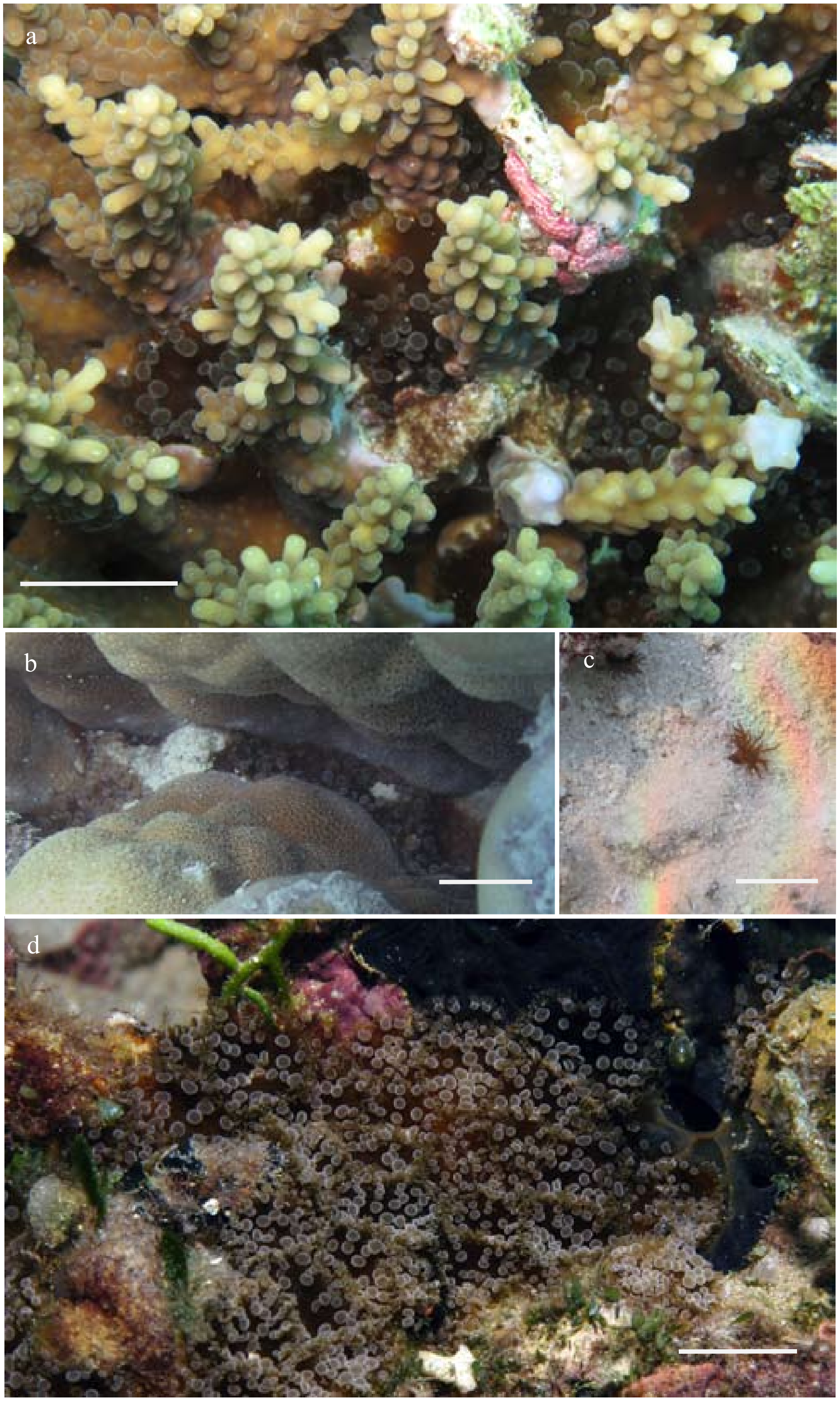

Fig 4.41. Cryptic habitats of *Triactis producta*. a) at vertices of scleractinian coral colonies b) in crevices of rocks or scleractinian corals c) attached to rock that was buried in sand d) attached to demosponge. Scale bars = 20 mm.

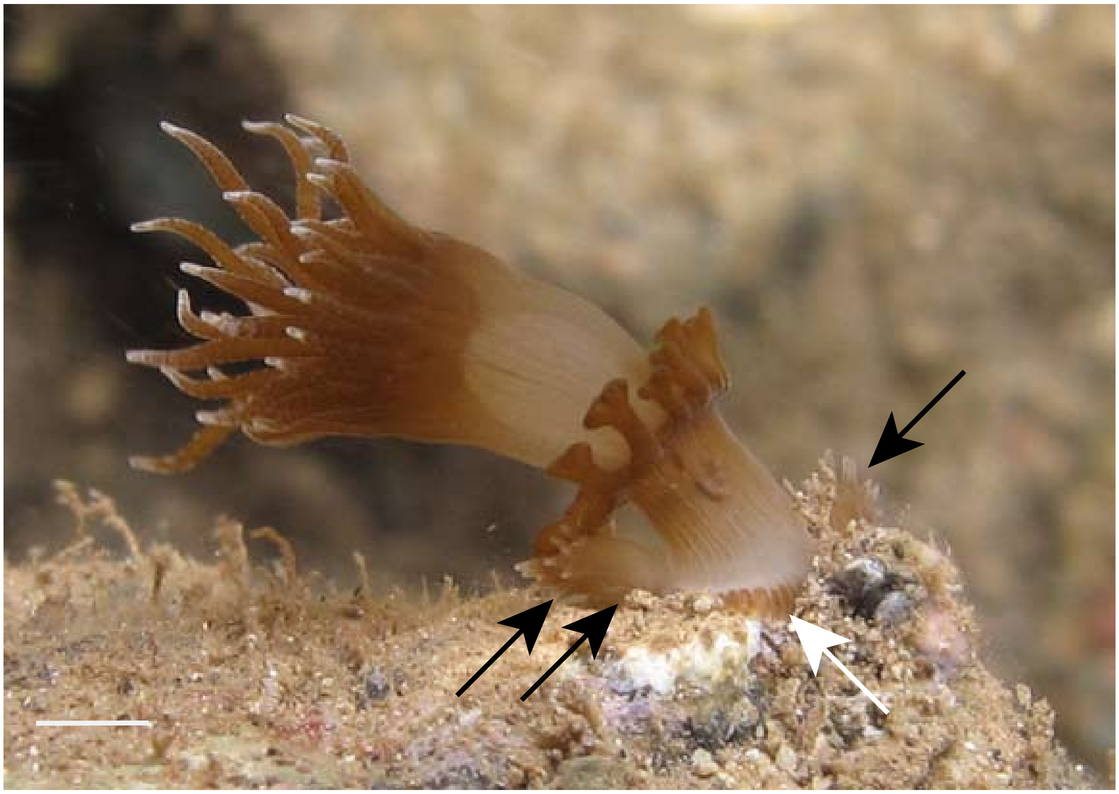

Fig 4.42. *Triactis producta*. Large individual surrounded by three smaller individuals (black arrows). Note dense zooxanthellae at limbus of larger individual (white arrows). Scale bar = 10 mm.

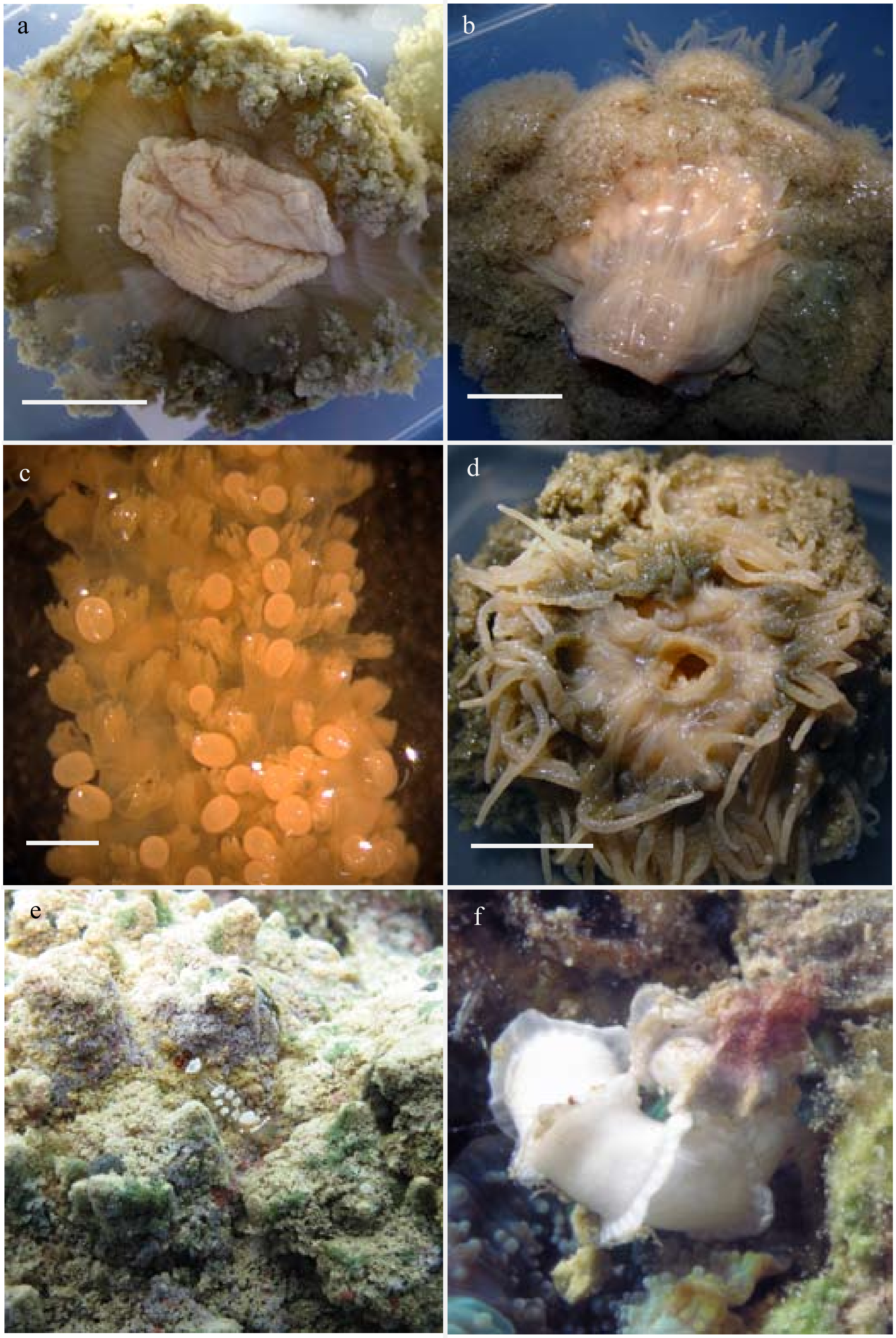

Fig 4.43. *Phyllodiscus semoni*. Morphology and symbionts. a) pedal disc, RMNH Coel 39739, scale bar = 20 mm b) proximal scapus with mesenterial insertions visible as lighter lines, RMNH Coel 39704, scale bar = 20 mm c) vesicles and pseudotentacle subunits, RMNH Coel 39702, scale bar = 2 mm d) oral disc with central mouth, RMNH Coel 39730, scale bar = 10 mm e) shrimp symbiont, *Periclimenes brevicarpalis* f) snail parasite, *Epitonium* sp., photo by Bert Hoeksema.

Fig 4.44. *Phyllodiscus semoni*, individuals *in situ* of variable morphotypes. a) Maldives, Velavaru, photo Andrea Crowther, KUDIZ 3381 b) Indonesia, Hoga, photo Harry Erdhart c) Philippines, Siquijor, photo Harry Erdhart d-o) Indonesia, photos by Bert Hoeksema d) Indonesia, Ternate, RMNH Coel 30712 g) Indonesia, Ternate, RMNH Coel 30711.

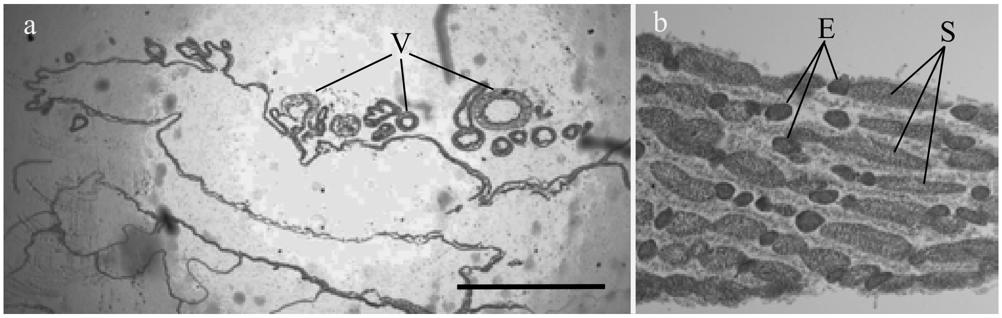

Fig 4.45. *Phyllodiscus semoni.* a) longitudinal section through part of pseudotentacle, vesicles of multiple sizes attached to pseudotentacle, CAS 65156, scale bar = 2 mm b) cross section showing eggs and sperm packets on same second order mesentery, RMNH Coel 39730. Figure legend: E = egg, S = sperm packet, V = vesicle.

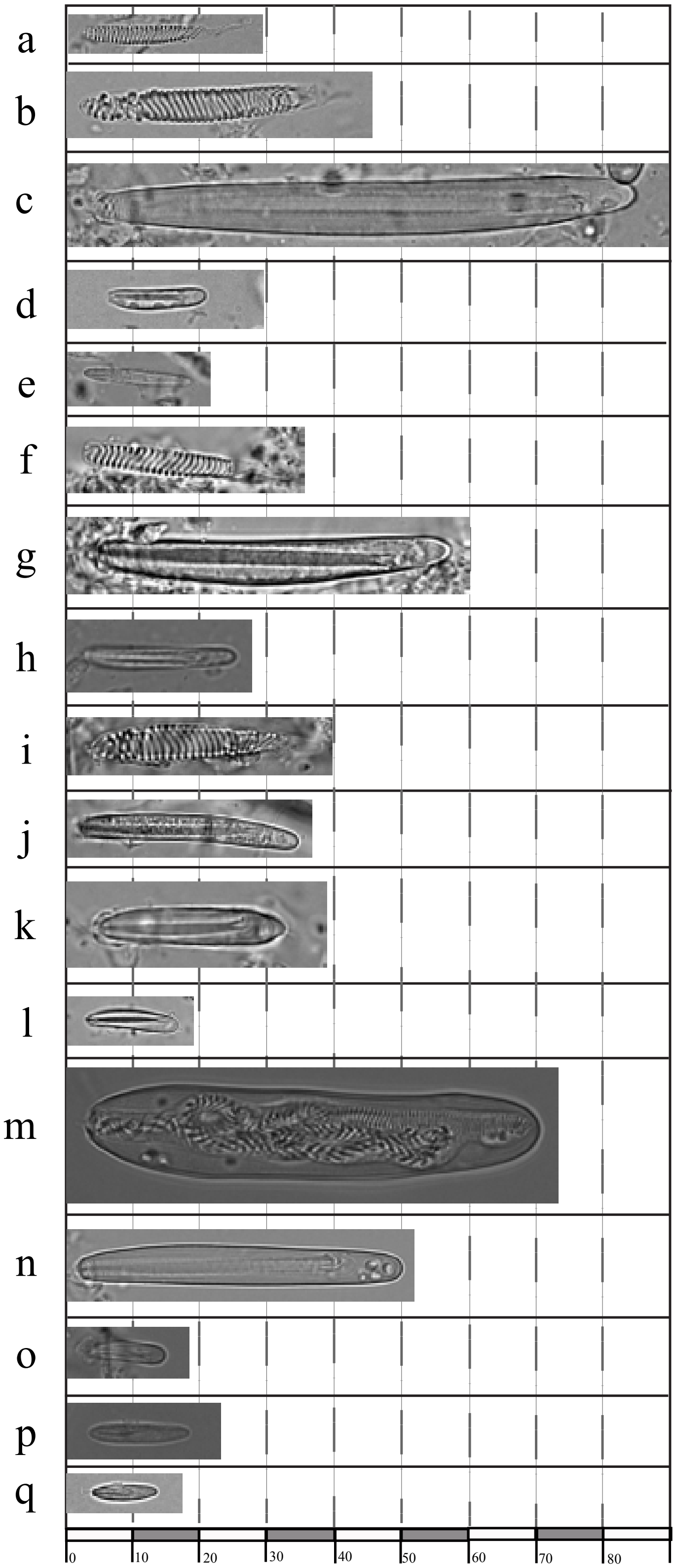

Fig 4.46. Representative cnidae from various tissues of *Phyllodiscus semoni*. Lowercase letters correspond to measurements in Table 4.19. Tissue source: a-e) tentacles f-h) actinopharnx i,j) oral disc k) column l) mesenterial filaments m-q) vesicles. Scale bar in micrometers.

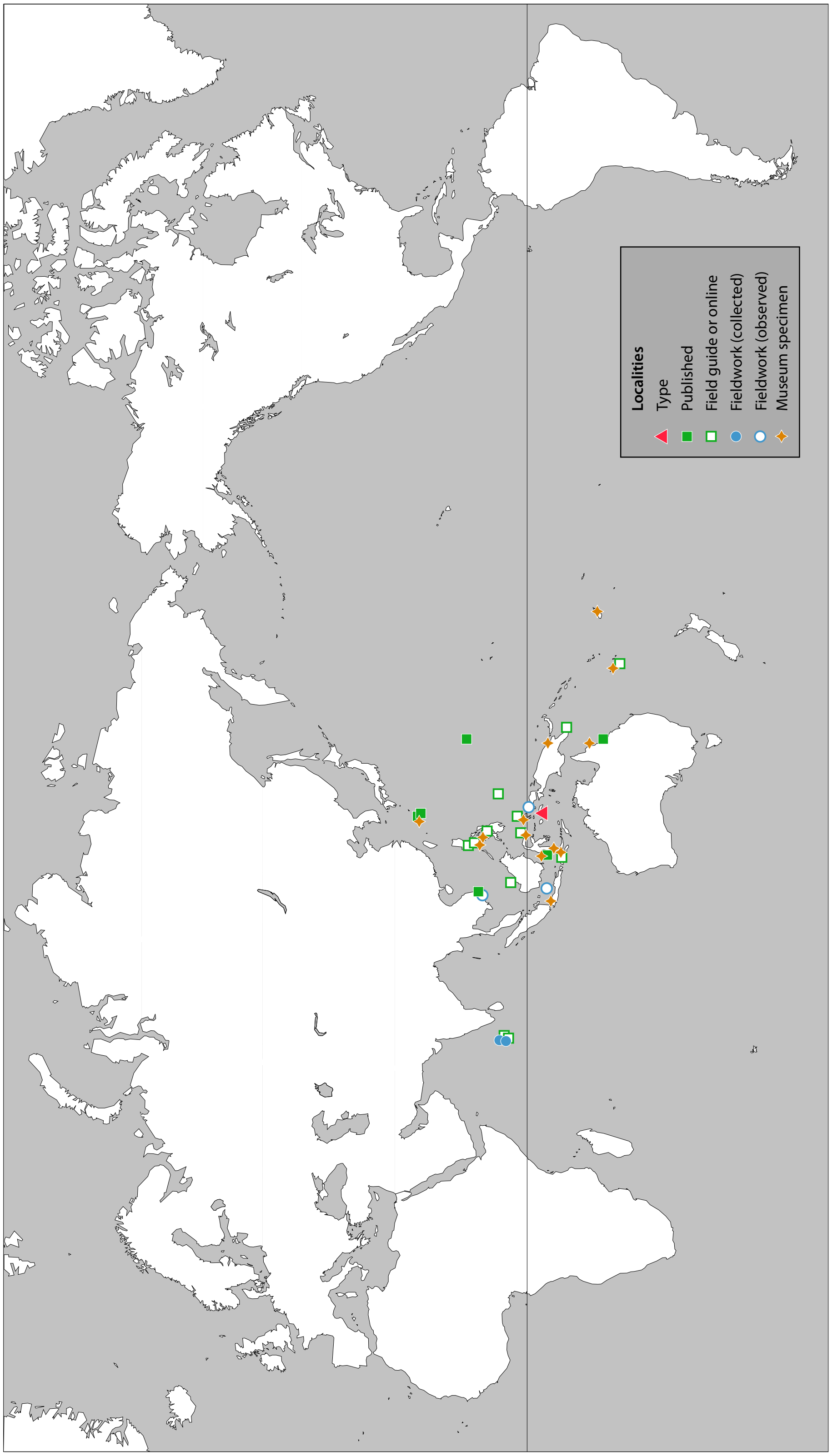

Fig 4.47. Recorded localities of *Phyllodiscus semoni*.

Table 4.1. Nominal genera and species and type specimen availability of Aliciidae.

Nominal genera	Nominal species	Type specimens
Alicia		
	Actinia mirabilis	N
	Actinia pretiosa	N
	Alicia rhadina	N
	Alicia sansibarensis	Y
	Alicia uruguayensis	Y
	Alicia beebei	N
Cladactis		
	Cladactis Costae	N
Lebrunia		
	Oulactis danae	Y
	Lebrunia neglecta	N
Hoplophoria		
	Hoplophoria coralligens	N
Cradactis		
	Cradactis variabilis	N
Triactis		
	Triactis producta	N
	Triactis cincta	N
Phyllodiscus		
	Phyllodiscus Semoni	Y
	Phyllodiscus indicus	N

Table 4.2. Characters separating *Triactis* and *Phyllodiscus*.

Feature	*Triactis*	*Phyllodiscus*
Number of pseudotentacles per intermesenterial space	1	many
Number of vesicles per intermesenterial space	up to 3	many
Vesicle placement on pseudotentacles	only on oral side	on all sides
Number of branching directions	1	many

Table 4.3. Specimens of *Alicia mirabilis* examined.

Catalog Number	Status	Original ID	Number of Specimens	Locality	Depth (m)
BMNH 1987.10.27.1		*Alicia mirabilis*	1	Azores	
BMNH 1987.10.27.2		*Alicia mirabilis*	1	Azores	
BMNH 72.8.1.6		*Alicia, Cladactis*		Mediterranean	
KUDIZ 3129		*Alicia mirabilis*		USA, Florida, Boca Rotan Inlet	1-2
KUDIZ 3130		*Alicia mirabilis*		USA, Florida, Boca Rotan Inlet	1-2
SMF 1911	voucher	*Alicia mirabilis*	1	Italy, Naples	
SMNH 349		*Cladactis costae*	1	Italy, Naples	
SMNH 350		*Alicia costae*	1	Italy, Naples	
SMNH 644		*Alicia costae*	1	Italy, Naples	
USNM 1112413		*Alicia mirabilis*	1	Azores, Bahia Mos., Terceira Island	

Table 4.4. Distribution and size of cnidae of *Alicia mirabilis* from this study and literature. Measurements given as range in length x width of undischarged capsules in µm (outlier measurements in parentheses), {number of capsules measured}, [ratio of number of individuals in which that type of cnidae was found to the number of individuals examined]. Frequency of cnida type indicated as either very common, common, or rare. Letters in parentheses correspond to images in Fig 4.7.

	Alicia mirabilis this study	*Alicia mirabilis* Schmidt 1972	*Alicia mirabilis* Seaton 1981	*Alicia costae* Carlgren (1940)
TENTACLES				
spirocyst - robust (a)	31-45 x 6-7 {15} [1/1] common	30-53.3 x 3.6-9.1	17.6-44 x 2.4-7.6 {18}	22.5-46 x 6
spirocyst - gracile (b)	(15) 20-29 x 3 {15} [1/1] common			
microbasic amastigophore (c)	43 x 6 {1} [1/1] v. rare	52-102.2 x 5-10.9	29.6-54.4 x 6-8.4 (20)	43-62 x 6.5-7
microbasic amastigophore		46-93 x 6.5-15.5	9.8-14 x 2.8-4 (16)	63-70 x 8.5-10
microbasic p-mastigophore			73.6-92.8 x 7.2-8.8 (5)	
basitrich (d)	12-17 x 2 {10} [1/1] rare	16.9-26 x 2.3-3.6	13.6-20 x 2.3-3.1 (15)	15-18 x --
basitrich			23.2-30.4 x 2.4-3.6 (7)	
macrobasic amastigophore			48.8-62.4 x 9.2-11.2 (14)	
ACTINOPHARYNX				
microbasic amastigophore (e)	43-55 x 5-6.5 {12} [1/1] common	46-74.4 x 6-9.3	41.6-60 x 5.5-6.4 (10)	48-84 x 5-7
microbasic p-mastigophore (f)	24-37 x 4 {12} [1/1] common			
ORAL DISC				
spirocyst - robust (g)	20-30 x 4-6 {10} [1/1] v. common			
microbasic amastigophore (h)	38-46 x 5-6 {12} [1/1] v. common			
microbasic amastigophore (i)	18 x 4 {1} [1/1] rare			
MESENTERIAL FILAMENTS				
microbasic amastigophore (j)	16-23 (29) x 3.5-5 {12} [1/1] common	24.7-38 x 3.9-7.2	14.4-23.2 x 4-5.2 (14)	27-46.5 x 5-6
microbasic amastigophore/p-mastigophore		6.5-14 x 2.6-5	9.6-12.8 x 2.4-3.2 (20)	10-11.5 x 2-2.5
microbasic p-mastigophore (k)	6-7 x 3-4 {10} [1/1] common		5.6-8.4 x 2.6-3.8 (13)	5.5-8.5 x 2.8
basitrich				18 x --
VESICLE				
macrobasic amastigophore (l)	70-90 x 11-15 {15} [1/1] v. common	58.9-108.6 x 9.5-17.1	74.4-97.6 x 10.8-14.4 (13)	94-96 x 12-14
macrobasic amastigophore				84-110 x 12-14
microbasic amastigophore (m)	68-88 x 7-8.5 {15} [1/1] common	77.5-117.9 x 6.2-12.4	68.8-94.4 x 8-9.6 (13)	47-55 x 6.5-7
microbasic amastigophore				76-120 x 7-10
basitrich (n)	14-21 x 2-3 {15} [1/1] common	19.5-26 x 2.3-4.5	12-20 x 2.3-3.2 (12)	14-19 x 2
basitrich			24-28.8 x 2.4-3.2 (5)	17-25 x 2.8
spirocyst - robust			27.2-46.4 x 2.4-6.4 (10)	48 x 6-7 (contaminant?)
spirocyst - gracile				26 x 2.5 (contaminant?)

Table 4.5. Specimens of *Alicia pretiosa* examined. Bold entries indicate specimens collected for this study.

Catalog Number	Status	Original ID	Number of Specimens	Locality	Depth (m)
CAS 161241		Aliciidae	1	Japan, Ryukyu Islands, Okinawa	
KUDIZ 3168		***Alicia pretiosa***	**1**	**Palau, Koror, Soft Coral Arch**	**6**
L XX/6530		*Alicia pretiosa*		New Caledonia	

Table 4.6. Distribution and size of cnidae of *Alicia pretiosa* from this study and literature. Measurements given as range in length x width of undischarged capsules in µm (outlier measurements in parentheses), {number of capsules measured}, [ratio of number of individuals in which that type of cnidae was found to the number of individuals examined]. Frequency of cnida type indicated as either very common, common, or rare. Letters in parentheses correspond to images in Fig 4.11.

	Alicia pretiosa this study
TENTACLES	
spirocyst - robust (a)	28-45 x 6-9.5 {14} [1/1] common
spirocyst - gracile (b)	20-28 x 2-4 {15} [1/1] common
microbasic amastigophore (c)	42-59 x 5-6 {12} [1/1] common
microbasic amastigophore (d)	49-60 x 7-9 {8} [1/1] common
microbasic p-mastigophore (e)	12-15 x 3-4 {3} [1/1] rare
basitrich (f)	10-17 x 2 {15} [1/1] v. common
ACTINOPHARYNX	
microbasic amastigophore (g)	40-50 x 5-6.5 {15} [1/1] v. common
microbasic p-mastigophore (h)	25-33 x 4-5 {8} [1/1] common
ORAL DISC	
spirocyst - robust (i)	20-30 x 5-8 {11} [1/1] common
microbasic amastigophore (j)	34-41 x 5-6.5 {11} [1/1] common
MESENTERIAL FILAMENTS	
microbasic amastigophore (k)	18-23 x 5-5.5 {15} [1/1] v. common
microbasic p-mastigophore (l)	9-12 x 2-3.5 {11} [1/1] v. common
microbasic p-mastigophore (m)	5-7 x 3-4.5 {12} [1/1] common
COMPOUND VESICLE	
macrobasic amastigophore (n)	(54) 65-70 x 9.5-13 {6} [1/1] common
microbasic amastigophore (o)	50-79 x 6.5-8.5 {14} [1/1] v. common
microbasic amastigophore (p)	85-94 x 8-10 {3} [1/1] rare
basitrich (q)	11-16 x 2 {11} [1/1] common
LIMBUS VESICLE	
macrobasic amastigophore	44-63 x 9-12 {9} [1/1] common
microbasic amastigophore	52-70 x 6-8 {14} [1/1] v. common
microbasic p-mastigophore	10-13 x 2.5-3 {6} [1/1] rare
basitrich	9-15 x 2.25 {15} [1/1] v. common

Table 4.7. Specimens of *Alicia sansibarensis* examined. Bold entries indicate specimens collected for this study.

Catalog Number	Status	Original ID	Number of Specimens	Locality	Depth (m)
AMNH		*Alicia cf sansibarensis*	1	Mozambique	24-38
KUDIZ 2986		***Alicia***	**1**	**Singapore, Cyrene**	
L 02/3067		*Alicia sansibarensis*	1	Gulf of Suez	
MAGNT C5749			1	Australia, Northern Territory	
SMNH 1169	syntype	*Alicia sansibarensis*	quarter	Tanzania, Zanzibar, Tumbatu	
ZMH C2592	syntype	*Alicia sansibarensis*	1	Tanzania, Zanzibar, Tumbatu	
ZMH C2597	syntype	*Alicia sansibarensis*	1	Tanzania, Zanzibar, Tumbatu	
ZMB 4746		*Alicia sansibarensis*	1	Tanzania, Zanzibar, Kokotoni	
ZRC Cni 0635		***Alicia***	**1**	**Singapore, Cyrene**	

Table 4.8. Distribution and size of cnidae of *Alicia sansibarensis* from this study and literature. Measurements given as range in length x width of undischarged capsules in µm (outlier measurements in parentheses), {number of capsules measured}, [ratio of number of individuals in which that type of cnidae was found to the number of individuals examined]. Frequency of cnida type indicated as either very common, common, or rare. Letters in parentheses correspond to images in Fig 4.14.

	Alicia sansibarensis this study	*Alicia sansibarensis* Carlgren (1900)
TENTACLES		
spirocyst - robust (a)	23-30 x 4-6 {15} [1/1] v. common	48 x --
spirocyst - gracile (b)	18-25 x 3-4 {14} [1/1] common	
microbasic amastigophore (c)	35-45 x 5-6 {12} [1/1] common	52 x --
microbasic p-mastigophore (d)	18-21 x 5 {2} [1/1] rare	
basitrich (e)	14-17 x 2-3 {15} [1/1] v. common	
ACTINOPHARYNX		
microbasic amastigophore (f)	44-56 x 6-7 {15} [1/1] v. common	44-60 x --
microbasic p-mastigophore (g)	34-39 x 5 {3} [1/1] rare	
ORAL DISC		
spirocyst - robust		48 x --
microbasic amastigophore (h)	47-55 x 6-7 {15} [1/1] v. common	44 x --
MESENTERIAL FILAMENTS	not available	
VESICLE		
macrobasic amastigophore (i)	79-93 x 11-14 {15} [1/1] v. common	80 *
microbasic amastigophore (j)	(80) 89-110 x 8-9 {13} [1/1] common	

Table 4.9. Specimens of *Alicia beebei* examined. Bold entries indicate specimens collected for this study.

Catalog Number	Status	Original ID	Number of Specimens	Locality	Depth (m)
BMNH 1986.9.16.7-8		*Alicia cf. beebei*	2	USA, W coast of California	
CAS 29077		*Alicia beebei*	1	Mexico, Gulf of California, NE end of Isla San Jose	5
CAS 29078		*Alicia beebei*	1	Mexico, Gulf of California, Las Animas Islet	45
CAS 95902		*Alicia beebei*	1	Mexico, Gulf of California, W side of Isla San Francisco	20
CAS 95911		*Alicia beebei*	1	Mexico, Gulf of California, outside of Puerto Escondido	10
CAS 95953		*Alicia beebei*	1	Mexico, Gulf of California, SE side of Isla del Espiritu Santo	60
CAS 110535		*Alicia beebei*	1	Mexico, Gulf of California, Bahia Los Frailes	57
AMNH		***Alicia beebei***	**6**	**Mexico, Gluf of California, Loretto**	
USNM 49397	voucher	*Alicia beebei*	1	Mexico, Gulf of California, Puerto Escondido	

Table 4.10. Distribution and size of cnidae of *Alicia beebei* from this study and literature. Measurements given as range in length x width of undischarged capsules in µm (outlier measurements in parentheses), {number of capsules measured}, [ratio of number of individuals in which that type of cnidae was found to the number of individuals examined]. Frequency of cnida type indicated as either very common, common, or rare. Letters in parentheses correspond to images in Fig 4.18.

	Alicia beebei this study	*Alicia beebei* Carlgren (1940, 1951)
TENTACLES		
spirocyst - robust (a)	30-45 x 5.5-7 {15} [1/1] v. common	17-41 x 2.5-6
spirocyst - gracile (b)	20-32 x 3-4 {15} [1/1] v. common	
microbasic amastigophore (c)	48-58 x 5-6.5 {15} [1/1] common	43-59.2 x 5-8.5
microbasic p-mastigophore (d)	18-23 x 2-3 {10} [1/1] rare	
basitrich (e)	15-21 x 2-3 {15} [1/1] rare	13-21 x 2-2.8
ACTINOPHARYNX		
microbasic amastigophore (f)	67-76 x 7-8 {15} [1/1] v. common	(26) 36-41 (46) x 4.5-5
microbasic p-mastigophore (g)	31-52 x 4-6 {7} [1/1] rare	
ORAL DISC		
spirocyst - robust (h)	21-35 x 5-6 {14} [1/1] common	
microbasic amastigophore (i)	19-29 x 3.5-5 {15} [1/1] v. common	
microbasic amastigophore	45-50 x 5.5-7 {6} [1/1] rare	
MESENTERIAL FILAMENTS		
microbasic amastigophore (j)	30-38 x 5-6 {15} [1/1] v. common	35.2-45 x 7
microbasic amastigophore/p-mastigophore		24-29 x 4
microbasic p-mastigophore [tear-shaped] (k)	7 x 4 {5} [1/1] rare	7-12.7 x 2.5-4
VESICLE		
macrobasic amastigophore (l)	64-80 x 9.5-12 {15} [1/1] v. common	59-72 x 12 [from 1940]
microbasic amastigophore (m)	(55) 73-103 (120) x 6-9 {15} [1/1] common	60-77 x 6-8.5 [from 1940]
microbasic amastigophore (n)	19-25 x 4 {12} [1/1] common	
microbasic amastigophore		67.7-84.6 x 10-11.3 [from 1951]
microbasic amastigophore		80.4-86.8 x 8.5-9.2 [from 1951]
basitrich (o)	14-20 x 2-3 {15} [1/1] rare	12-21 x 2-3.5

Table 4.11. Specimens of *Alicia uruguayensis* examined.

Catalog Number	Status	Original ID	Number of Specimens	Locality	Depth (m)
SMNH 86	syntypes	*Alicia uruguayensis*	2	Brazil, southern coast	80
LO (no catalog number)		*Alicia uruguayensis*	3 slides	Brazil, southern coast	80

Table 4.12. Specimens of *Lebrunia neglecta* examined. Bold entries indicate specimens collected for this study.

Catalog Number	Status	Original ID	Number of Specimens	Locality	Depth (m)
BMNH 1901.3.8.29-30		*Lebrunea neglecta*	2	Jamaica, Port Royal Cays	
BMNH 1951.4.7.97-99		*Lebrunia coralligens*	3	Cayman Islands, Reef north of Water Cay	
KUDIZ 1891		*Lebrunia danae*	1	USA, Florida, Vaca Key, Gulf side at Old Clark House	1
KUDIZ 2365		*Lebrunia danae*	4	US Virgin Islands, St. Thomas, Hull Bay	0.3-0.5
KUDIZ 2424		*Lebrunia danae*	1	Panama, Bocas del Toro, Bocas Torito Bay	0.3-1
KUDIZ 2425		*Lebrunia danae*	1	Panama, Bocas del Toro, Cayo Adriana	
KUDIZ 2426		*Lebrunia danae*	1	Panama, Bocas del Toro, Cayo Adriana	
KUDIZ 2427		*Lebrunia danae*	1	Panama, Bocas del Toro, Crawl Cay	3-4
KUDIZ 2428		*Lebrunia danae*	1	Panama, Bocas del Toro, Red point	3
KUDIZ 2430		*Lebrunia danae*	1	Panama, Bocas del Toro, Red point	3
KUDIZ 2431		*Lebrunia danae*	1	Panama, Bocas del Toro, Crawl Cay	3-4
KUDIZ 3176		***Lebrunia danae***	**1**	**Curaçao, Reef just offshore from Water Plant**	**10**
KUDIZ 3177		***Lebrunia danae***	**1**	**Curaçao, Reef just offshore from Water Plant**	**6**
KUDIZ 3178		***Lebrunia danae***	**1**	**Curaçao, Reef just offshore from Water Plant**	**3**
KUDIZ 3180		***Lebrunia danae***	**1**	**Curaçao, Reef just offshore from Water Plant**	**3**
KUDIZ 3249		***Lebrunia danae***	**1**	**Belize, Carrie Bow Cay, Reef east of Cay**	**13.3**
KUDIZ 3247		***Lebrunia danae***	**1**	**Belize, Carrie Bow Cay, shallow patch reef just north of Cay**	**2**
KUDIZ 3249		***Lebrunia danae***	**1**	**Belize, Carrie Bow Cay, Reef east of Cay**	**13.3**
KUDIZ 3361		*Lebrunia danae*		USA, Florida, American Shoal	9-10
KUDIZ 3362		*Lebrunia danae*		USA, Florida, Monroe County, Patch reef	6-7
KUDIZ 3363		*Lebrunia danae*		USA, Florida, American Shoal	9-10
KUDIZ 3364		*Lebrunia danae*	1	USA, Florida, Carysfort Reef Light, Biscayne National Monument	3
L 08/3157		*Lebrunia neglecta*	2	Bahamas, Andros	
L 09/3067		*Lebrunia neglecta*	2	Bahamas, Andros	
L 09/3068		*Lebrunia neglecta*	4	Bahamas, Andros	
L 09/3078		*Lebrunia neglecta*	2	Bahamas, Andros	
RMNH Coel 11009		*Lebrunia danae*	4	Curaçao, Awa di Osstpunt.	
RMNH Coel 11010		*Lebrunia danae*	2	Curaçao, between Piscadera Bay and Blau Bay	
RMNH Coel 11007		*Lebrunia danae*	2	Puerto Rico, near La Paquera	
RMNH Coel 23899		*Lebrunia danae*	1	Panama Canal Zone, Caleta Id	5
RMNH Coel 11008		*Lebrunia danae*	5	Curaçao, Slangeribaai.	
RMNH Coel 11013		*Lebrunia danae*	1	Curaçao, Piscadera Bay	
SMNH 361		*Lebrunea neglecta*	1	Jamaica	
SMNH 362		*Lebrunea neglecta*	1	USA, Florida	
SMNH 363		*Lebrunea neglecta*	1	Curaçao, Schotlegat	1
USNM 51042		*Lebrunia danae*	1	Puerto Rico, La Parguera, La Gata Island	
USNM 52007		*Lebrunia danae*	1	Virgin Islands of the United States, St. John Island, Reef Bay	20
USNM 53261		*Lebrunia danae*	2	Puerto Rico, Cayo Enrique, S Of La Parguera	1
USNM 54170		*Lebrunia danae*	1	Guadeloupe, Grande Terre, Pointe A Pitre, East Of Cochons Island	
USNM 54211		*Lebrunia danae*	1	British Virgin Islands, Tortola Island, Sopers Hole, West End Flats	1
USNM 54212		*Lebrunia danae*	1		
USNM 54213		*Lebrunia danae*	1		
USNM 54217		*Lebrunia danae*	1		
USNM 56911		*Lebrunia danae*	1	Belize, Carrie Bow Cay, Transect On Fore Reef Slope	27.5
USNM 56912		*Lebrunia danae*	1	Belize, Carrie Bow Cay, Reef Flat	
USNM 56913		*Lebrunia danae*	1	Belize, Curlew Cay	4.6
USNM 56914		*Lebrunia danae*	2	Belize, Curlew Cay	4.6
USNM 1004414		*Lebrunia danae*	1	Bahamas, Lyford Cay	4
USNM 1004415		*Lebrunia danae*	1	Bahamas, Abaco Island, Hopetown Reef	
USNM 1004419		*Lebrunia danae*	1	British Virgin Islands, Tortola Island, Sopers Hole, West End Flats	1
USNM 1004464		*Lebrunia danae*	1	Bermuda	
USNM 1004963		*Lebrunia danae*	1	Barbuda Island, Spanish Point	
ZMB 5172		*Lebrunia danae*	1	Tortugas, Bird Key Reef	

Table 4.13. Distribution and size of cnidae of *Lebrunia neglecta* from this study and literature. Measurements given as range in length x width of undischarged capsules in µm (outlier measurements in parentheses), {number of capsules measured}, [ratio of number of individuals in which that type of cnidae was found to the number of individuals examined]. Frequency of cnida type indicated as either very common, common, or rare. Letters in parentheses correspond to images in Fig 4.25.

	Lebrunia neglecta this study	*Lebrunia danae* Carlgren 1945
TENTACLES		
spirocyst (a)	20-50 x 3-7 {79} [7/7] v. common	
spirocyst	15-22 x 2-3.5 {26} [3/7] common	
microbasic amastigophore (b)	60-92 (105) x 5-9 {90} [7/7] v. common	67.7-73.3 x 6.3-7
microbasic amastigophore		50-64.9 x 5.6-6.3
microbasic amastigophore		31-50.8 x 5-5.6
microbasic amastigophore (c)	19-34 x 4-5 {30} [4/7] common	29.6-45 x 4.2-5.5
microbasic amastigophore (d)	11-21 x 2.5-4.5 {62} [6/7] common	16.9-21 x 3.5
microbasic amastigophore		19.7 x 3.5
basitrich (e)	14-26 x 3-4 {42} [4/7] common	
ACTINOPHARYNX		
microbasic amastigophore (f)	29-55 (66) x 4-8 {49} [3/4] common	36.7-45 x 5.6-6.3
microbasic p-mastigophore	10-12 x 3-4 {9} [2/4] rare	
unspecified nematocyst		10.6-18.3 x 3.4
COLUMN		
macrobasic amastigophore	23-37 x 6-15 {26} [3/6] rare	
microbasic p-mastigophore (g)	17-33 x 3.5-7 {64} [5/6] v. common	
microbasic amastigophore (h)	16-27.5 x 4-6 {43} [3/6] common	15.5-19.7 x 3.5-4
basitrich	9.5-16 x 2.5-4 {15} [2/6] rare	
MESENTERIAL FILAMENTS		
microbasic amastigophore (i)	35-60 x 4-8.5 {67} [6/6] v. common	36.7-45 x 5.6-6.3
microbasic p-mastigophore (j)	9-20 x 2-4.5 {49} [5/6] common	
microbasic p-mastigophore - squarish (k)	10-15 x 3-6 {41} [4/6] common	
basitrich	9-14 x 2.5-4 {28} [2/6] rare	10-14 x 2.5
basitrich		14 x 2.5
unspecified nematocysts		9.2-12 x 2.8-3.5
unspecified nematocysts		10.7-14.1 x 2.8-3.5
VESICLE		
macrobasic amastigophore	90-110 x 15-25 {10} [2/7] rare	
macrobasic amastigophore (l)	45-89 x 12-20 {98} [7/7] v. common	
microbasic amastigophore	13-40 x 3-7 {81} [4/7] common	
basitrich (m)	6-19.5 x 4 {12} [2/7] rare	
PSEUDOTENTACLE		
spirocyst	22-46 x 4-5.5 {12} [1/1] rare	
basitrich	8-11 x 2-4 {20} [2/2] common	
basitrich	14-17 x 4-6 {14} [1/1] rare	
basitrich		15.5-35.2 x 4.2-5.6
basitrich		19.7-35.2 x 4.2-5.6
basitrich		28.2-31 x 5.6
macrobasic amastigophore		35.2-73 x 12-15
macrobasic amastigophore		45-70 x 10-16
macrobasic amastigophore		49.3-63.4 x 11.3-15.5
PEDUNCLE		
microbasic amastigophore		12.7-15.5 x 3.5-4
microbasic amastigophore		19.7-14.1 x 3.5-4.2
BRANCHES		
basitrich		11.3-19 x 3-4
basitrich		11.3-15.5 x 3-4
microbasic amastigophore		12.7-19.7 x 4
microbasic amastigophore		14.1-31.7 x 3.5-5.5

Table 4.14. Specimens of *Lebrunia coralligens* examined. Bold entries indicate specimens collected for this study.

Catalog Number	Status	Original ID	Number of Specimens	Locality	Depth (m)
BMNH 1901.3.8.31-33		*Lebrunia coralligens*	5	Jamica, Port Royal Cays	
KUDIZ 2361		*Lebrunia coralligens*	7	US Virgin Islands, St. Thomas, near Marine Station dock	
KUDIZ 2364		*Lebrunia coralligens*	3	US Virgin Islands, St. Thomas, Water Is., Sprat Point	6-8
KUDIZ 2368		*Lebrunia coralligens*	2	US Virgin Islands, St. Thomas, Coki Bay	3
KUDIZ 3170		***Lebrunia coralligens***		**Barbados, Tropicana Reef**	**22.8**
KUDIZ 3171		***Lebrunia coralligens***		**Barbados, Church Point**	
KUDIZ 3172		***Lebrunia coralligens***		**Barbados, Church Point**	
KUDIZ 3173		***Lebrunia coralligens***		**Barbados, Greatledge**	
KUDIZ 3174		***Lebrunia coralligens***		**Barbados, Greatledge**	
KUDIZ 3175		***Lebrunia coralligens***		**Barbados, Patch reef near Pamir Wreck**	
KUDIZ 3181		***Lebrunia coralligens***	**11**	**Curaçao, Snake's Bay**	**20**
KUDIZ 3182		***Lebrunia coralligens***	**1**	**Curaçao, Snake's Bay**	**6-7**
KUDIZ 3183		***Lebrunia coralligens***	**2**	**Curaçao, Snake's Bay**	**20**
KUDIZ 3184		***Lebrunia coralligens***	**4**	**Curaçao, Piscadera Bay**	
KUDIZ 3185		***Lebrunia coralligens***	**1**	**Curaçao, Piscadera Bay**	
KUDIZ 3186		***Lebrunia coralligens***	**2**	**Curaçao, Piscadera Bay**	
KUDIZ 3187		***Lebrunia coralligens***	**4**	**Curaçao, Piscadera Bay**	
KUDIZ 3188		***Lebrunia coralligens***	**3**	**Curaçao, Piscadera Bay**	
RMNH Coel 11004		***Lebrunia coralligens***	**3**	**Curaçao, Slangenbaai**	
RMNH Coel 11005		*Lebrunia coralligens*	12	Bonaire, SW coast	
RMNH Coel 11006		*Lebrunia coralligens*	9	Curaçao, Piscadera Bay	
SMNH 364		*Lebrunia coralligens*	1	Jamaica	

Table 4.15 Distribution and size of cnidae of *Lebrunia coralligens* from this study and literature. Measurements given as range in length x width of undischarged capsules in µm (outlier measurements in parentheses), {number of capsules measured}, [ratio of number of individuals in which that type of cnidae was found to the number of individuals examined]. Frequency of cnida type indicated as either very common, common, or rare. Letters in parentheses correspond to images in Fig 4.29.

	Lebrunia coralligens this study	*Lebrunia coralligens* Carlgren 1945
TENTACLES		
spirocyst (a)	13-24 x 2-5 {115} [7/8] v. common	27 x 4
microbasic amastigophore (b)	30-90 x 4.5-9 {167} [8/8] v. common	52.2-63.5 x 5-5.5
microbasic amastigophore (c)	13-20 x 3-3.5 {17} [3/8] rare	19.7 x 3.5
basitrich (d)	14-32 x 2-3 {70} [6/8] common	19.7-25 x 2.2-2.5
basitrich	10-22 x 2-4 {43} [5/8] rare	
ACTINOPHARYNX		
microbasic amastigophore		22.6-32.4 x 3.5
microbasic p-mastigophore		11.3-12.7 x 2.8-3
COLUMN		
microbasic amastigophore	10-17 x 3-4 {47} [5/7] common	11.3-16.9 x 3-3.5
basitrich	7-16 x 2-4.5 {45} [5/7] common	8.5-10 x 2
MESENTERIAL FILAMENTS		
microbasic amastigophore (e)	31-39 x 5-5.5 {15} [3/3] v. common	32.4-41 x 4.2-5.5
microbasic amastigophore		18.3 x 4.2
microbasic p-mastigophore (f)	10-14 x 3-5 {26} [3/3] v. common	11.3-14.3 x 2.8-3.5
microbasic p-mastigophore (g)	9-15 x 2-3 {30} [3/3] v. common	
VESICLE		
macrobasic amastigophore (h)	45-73 (94) x 11-20 {108} [7/7] v. common	59.2-79 (89) x 12.7-15.5 (17)
microbasic amastigophore	16-26 x 3-5 {30} [5/7] rare	11.3-31 x 2.8-5.5
microbasic amastigophore	76-96 x 12-20 {10} [1/7] rare	56.4-63.5 x 4.2-5.5
basitrich (i)	9-27.5 x 2-5 {63} [5/7] common	18.3-24 x 2.2

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Table 4.16. Specimens of *Triactis producta* examined. Bold entries indicate specimens collected for this study.

Catalog Number	Status	Original ID	Number of Specimens	Locality	Depth (m)
BMNH 1954.6.28.15		*Triactis cincta*	30	Australia, Queensland, Great Barrier Reef	
BMNH 1954.6.28.16		*Phyllodiscus cincta*		Australia, Queensland, Great Barrier Reef	
BMNH 1983.4.8.14-24		*Triactis producta*	42	Singapore, Pulau Semakau	
BMNH 1983.4.8.25-26		*Triactis producta*	2	Singapore, Pulau Biola	
BMNH 1983.4.8.27-30		*Triactis producta*	14	Gulf of Aden	2
BMNH 1995.774		*Triactis producta*	1	Singapore	
KUDIZ 2001		*Triactis producta*		Oman, Bandar Khayran near aquaculture weirs	
KUDIZ 2027		*Triactis producta*		Oman, Bandar Khayran near aquaculture weirs	3
KUDIZ 2063		*Triactis producta*		Oman, Bandar Khayran	1.5
KUDIZ 2066		*Triactis producta*		Oman, Bandar Khayran	1.5
KUDIZ 3024		***Triactis producta***	**10**	**Egypt, Red Sea, Sinai Peninsula, Dahab**	**30**
KUDIZ 3025		***Triactis producta***	**20**	**Egypt, Red Sea, Sinai Peninsula, Dahab**	**30**
KUDIZ 3026		***Triactis producta***	**12**	**Egypt, Red Sea, Sinai Peninsula, Dahab**	**30**
KUDIZ 3200		***Triactis producta***	**31**	**Mo'orea, Papetoai**	**0.5**
KUDIZ 3202		***Triactis producta***	**41**	**Mo'orea, north of old hotel on east shore of Cook's Bay**	**0.5**
KUDIZ 3204		***Triactis producta***	**13**	**Mo'orea, mangroves near Haapiti**	**0.5**
KUDIZ 3205		***Triactis producta***	**20**	**Mo'orea, Old jetty, Pihaena**	**0.5-2**
KUDIZ 3206		***Triactis producta***	**2**	**Mo'orea, Lighthouse, North of Temae**	**1.5**
KUDIZ 3207		***Triactis producta***	**27**	**Mo'orea, Atiha Bay**	**0.5-1.5**
KUDIZ 3209		***Triactis producta***	**2**	**Mo'orea, Papetoai**	**0.5-2**
KUDIZ 3210		***Triactis producta***	**34**	**Mo'orea, Papetoai**	**0.5-2**
KUDIZ 3233		***Triactis producta***		**Tanzania, Zanzibar, Chumbe Island**	**3-6**
KUDIZ 3234		***Triactis producta***		**Tanzania, Zanzibar, Chumbe Island**	**3-6**
KUDIZ 3235		***Triactis producta***	**1**	**Tanzania, Zanzibar, Kokotoni**	**4**
KUDIZ 3236		***Triactis producta***	**2**	**Tanzania, Zanzibar, reef off Bawe Island**	**4**
KUDIZ 3356		***Triactis producta***	**10+**	**Singapore, St. John's Island, water table**	
KUDIZ 3357		***Triactis producta***	**10+**	**Singapore, St. John's Island, water table**	
KUDIZ 3358		***Triactis producta***		**Singapore, St. John's Island, water table**	
KUDIZ 3365		***Triactis producta***	**28**	**Maldives, Kaafu (North Male) Atoll, Ihuru Island, House Reef**	**6**
KUDIZ 3366		***Triactis producta***	**7**	**Maldives, Kaafu (North Male) Atoll, Ihuru Island, House Reef**	**5**
KUDIZ 3367		***Triactis producta***	**15**	**Maldives, Kaafu (North Male) Atoll, Dhon Bibi Haa**	**10**
KUDIZ 3368		***Triactis producta***	**8**	**Maldives, Kaafu (North Male) Atoll, Dhon Bibi Haa**	**6**
KUDIZ 3371		***Triactis producta***	**10**	**Maldives, Kaafu (North Male) Atoll, Japanese Gardens**	**6**
KUDIZ 3374		***Triactis producta***	**20**	**Maldives, Kaafu (North Male) Atoll, Vabbinfaru Island, House Reef**	**6**

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Table 4.16 continued.

Catalog Number	Status	Original ID	Number of Specimens	Locality	Depth (m)
KUDIZ 3377		***Triactis producta***	**17**	**Maldives, South Nilandhe Atoll, Meedhoo Island, Meedhoo Corner**	**6.5**
KUDIZ 3378		***Triactis producta***	**9**	**Maldives, South Nilandhe Atoll, Meedhoo Island, Meedhoo Corner**	**4.1**
KUDIZ 3379		***Triactis producta***	**20**	**Maldives, South Nilandhe Atoll, Lhohi Caves**	**8.6**
QM G5300		*Triactis producta*		Australia, Queensland, Great Barrier Reef, Heron Island	
QM G58758		*Triactis producta*		Australia, Queensland, Moreton Bay, Shark Gutter	
QM G59162		*Triactis producta*		Australia, Northern Territory, Nhulunbuy (Gove), Arafura Sea	
USNM 51611		*Triactis producta*	2	Kiribati, Line Islands, Christmas Island, 2 Mile From London Village	0.2
USNM 51652		*Triactis producta*	20	Marshall Islands, Ralik Chain, Enewetak Atoll, Lagoon	1
USNM 51653		*Triactis producta*	10	French Polynesia, Society Islands, Bora Bora, Farepiti Point, Lagoon	1
USNM 51654		*Triactis producta*	16	French Polynesia, Society Islands, Huahine, Baie Fare, Lagoon	1
USNM 51655		*Triactis producta*	27	French Polynesia, Tuamotu Archipelago, Maiai, Tikahau, Lagoon	1
USNM 51656		*Triactis producta*	14	USA, Hawaii, Oahu Island, Hanauma Bay	
USNM 51657		*Triactis producta*	4	USA, Hawaii, Oahu Island, Hanauma Bay	
USNM 51658		*Triactis producta*	1	French Polynesia, Society Islands, Moorea, N Coast Just W Of Papetoai Bay	1
USNM 52374		*Triactis producta*	2	Northern Mariana Islands, Saipan Island	
USNM 52375		*Triactis producta*	2	Marshall Islands, Ralik Chain, Bikini Atoll, Outer Reef	
USNM 52376		*Triactis producta*	2	Marshall Islands, Ralik Chain, Rongerik Atoll, Latoback Island, Lagoon Reef	
USNM 52509		*Triactis producta*	1	USA, Hawaii	
USNM 55618		*Triactis producta*	1	Marshall Islands, Ratak Chain, Majuro Atoll	

Table 4.17. Distribution and size of cnidae of *Triactis producta* from this study and literature. Measurements given as range in length x width of undischarged capsules in µm (outlier measurements in parentheses), {number of capsules measured}, [ratio of number of individuals in which that type of cnidae was found to the number of individuals examined]. Frequency of cnida type indicated as either very common, common, or rare. Letters in parentheses correspond to images in Fig 4.38.

	Triactis producta this study	*Triactis producta* Carlgren 1945	*Triactis cincta* Doumenc 1973
TENTACLES			
spirocyst - robust (a)	26-35 x 4-6 {80} [5/7] common		25-28 x 4-5
spirocyst - gracile (b)	15-29 x 2-4.5 {105} [7/7] common		
microbasic amastigophore (c)	10.5-21 x 3-5 {64} [7/7] common	12.7-16.9 x 3.5-4.2	
microbasic amastigophore		32.4-46.5 x 3.5-5.6	
microbasic amastigophore (d)	46-86 x 5.5-9 {95} [7/7] v. common	55-65.5 x 6.3-7	52-62 x 6-10
basitrich (e)	16-25 x 2-3 {50} [6/7] v. common	15.5-22.6 x 2.2-3	
basitrich (f)	10-12 x 4-5 {62} [5/7] common		
ACTINOPHARYNX			
microbasic amastigophore (g)	30-39 x 4-6 {103} [7/7] common	42.3-52.2 x 5.6-6.3	
microbasic amastigophore (h)	12-20 x 3-5 {90} [7/7] common	11.3-21 x 3.5	
ORAL DISC			
spirocyst - robust (i)	18-29 x 4-6 {75} [7/7] v. common		
microbasic amastigophore (j)	8-13 x 3-4 {100} [7/7] common		
microbasic amastigophore (k)	23-32 x 4.5-5.5 {75} [5/7] common		
basitrich (l)	9-11 x 2-3 {59} [6/7] common		
basitrich (m)	8-12 x 4-4.5 {50} [5/7] common		
COLUMN			
microbasic amastigophore (n)	12-24 x 3.5-5.5 {87} [7/7] v. common	19.7-29.6 x 4.2-5.5	
microbasic amastigophore		10-15.5 x 2.8-4.2	
microbasic p-mastigophore (o)	8-10 x 2-3 {54} [7/7] common	7-12 x 4.2	
basitrich (p)	8-11 x 2-3 {65} [7/7] common	8.5-10.6 x 2	
basitrich (q)	8.5-12 x 4-6 {55} [5/7] common		
MESENTERIAL FILAMENTS			
microbasic amastigophore (r)	40-50 x 6-7 {77} [7/7] commoon	49.3-56.4 x 8.5-11.3	55-60 x 8-9
microbasic amastigophore (s)	18-35 x 3.5-6 {56} [7/7] common	14.1-21 x 3.5-4.2	
microbasic amastigophore (t)	11.5-15 x 2.5-5 {60} [6/7] common		
microbasic p-mastigophore (u)	7-9 x 3.5-5 {80} [7/7] common	6.3-10 x 3.5-4.2	8-9 x 3-4
VESICLE			
macrobasic amastigophore (v)	28-54 x 9-15 {85} [7/7] v. common		44-45 x 10-13
microbasic amastigophore (w)	35-56 (80) x 5.5-8 {70} [7/7] common		50-53 x 8.5
microbasic amastigophore (x)	17-30 x 4-5 {50} [5/7] common		13-14 x 3.5
microbasic amastigophore (y)	8-20 x 3-4 {50} [5/7] common		
basitrich (z)	9-13 x 2-3 {81} [7/7] common		
basitrich	10-12 x 3.5-4.5 {40} [7/7] rare		
PEDUNCLE			
microbasic amastigophore		8.5-15.5 x 3-3.5	
PSEUDOTENTACLE			
macrobasic amastigophore		39.5-57.8 x 10.6-15.5	
microbasic amastigophore		38-57.8 x 6-7	
BRANCHES			
microbasic amastigophore		32.4-36.6 x 4.2	
microbasic amastigophore		21-38 x 4.2-5.6	
microbasic amastigophore		8.5-18.3 x 3-4.2	
basitrich		10-14 x 2	

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Table 4.18. Specimens of *Phyllodiscus semoni* examined. Bold entries indicate specimens collected for this study.

Catalog Number	Status	Original ID	Number of Specimens	Locality	Depth (m)
CAS 65156	voucher	*Phyllodiscus semoni*	1	Australia, Queensland, near Townsville	
CAS 65157	voucher	*Phyllodiscus semoni*	1	Australia, Queensland, near Townsville	
CAS 67949	voucher	*Phyllodiscus semoni*	3	Australia, Queensland, near Townsville	
CAS 67950	voucher	*Phyllodiscus semoni*	2	Australia, Queensland, near Townsville	
CAS 67951	voucher	*Phyllodiscus semoni*	3	Australia, Queensland, near Townsville	
CAS 75678		*Phyllodiscus semoni*	1	Philippines, E side of Palawan Island,	5
CAS 108443		*Phyllodiscus*	1	Japan, Ryukyu Islands, Okinawa, Seragaki Tombs	33
CAS 118847		*Phyllodiscus semoni*	1	Philippines, Luzon Island, Batangas Province	
KUDIZ 3381		***Phyllodiscus semoni***	**1**	**Republich of the Maldives, South Nilandhe Atoll, Velavaru Island**	**2**
KUDIZ 3383		***Phyllodiscus semoni***	**1**	**Republich of the Maldives, Kaafu (North Male) Atoll, Ihuru Island**	**2**
PMJ 707	syntype	*Phyllodiscus Semoni*	1	Indonesia, Moluccas Islands, Ambon	0-3
RMNH Coel 39702		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, Samalona Reef	3-4
RMNH Coel 39703		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, SW of Barang Lompo	8
RMNH Coel 39704		*Phyllodiscus semoni*	2	Indonesia, Ambon, Ambon Bay, N coast near Tawiri	2
RMNH Coel 39705		*Phyllodiscus semoni*	5	Indonesia, SW Sulawesi, Spermonde Archipelago, W of Kudingareng Keke	6
RMNH Coel 39706		*Phyllodiscus semoni*	1	Indonesia, Ambon, Ambon Bay, N coast near Laha	1-2
RMNH Coel 39707		*Phyllodiscus semoni*	1	Philippines, Cebu Strait, W of Bohol, SE side of Cabilao Island	3
RMNH Coel 39708		*Phyllodiscus semoni*	1	Indonesia, Ambon, Ambon Bay, N coast near Laha	4
RMNH Coel 39709		*Phyllodiscus semoni*	7	Indonesia, SW Sulawesi, Spermonde Archipelago, Kudingareng Keke Reef	7-8
RMNH Coel 39710		*Phyllodiscus semoni*	1	Indonesia, Halmahera mainland, Tanjung Sidangolo	12
RMNH Coel 39711		*Phyllodiscus semoni*	1	Indonesia, Halmahera mainland, Tanjung Ratemu	6
RMNH Coel 39712		*Phyllodiscus semoni*	1	Indonesia, Halmahera, Tidore, Tanjung Ebamadu	7
RMNH Coel 39713		*Phyllodiscus semoni*	1	Indonesia, Halmahera, Ternate, Ternate Harbour	10
RMNH Coel 39714		*Phyllodiscus semoni*	1	Indonesia, N Sulawesi, Selat Lembeh, Pulau Lembeh, N of Pulau Burung	3
RMNH Coel 39715		*Phyllodiscus semoni*	1	Indonesia, N Sulawesi, Selat Lembeh, bay S of Pulau Putus	6
RMNH Coel 39716		*Phyllodiscus semoni*	3	Indonesia, N Sulawesi, Selat Lembeh, between Tanjungnanas and Teluk Kungkungan	1.5-2.5
RMNH Coel 39717		*Phyllodiscus semoni*	1	Indonesia, N Sulawesi, Selat Lembeh, bay S of Pulau Putus	2.5
RMNH Coel 39718		*Phyllodiscus semoni*	1	Indonesia, N Sulawesi, Selat Lembeh, S of Tanjung Batuangus,	1
RMNH Coel 39719		*Phyllodiscus semoni*	1	Indonesia, Moluccas, Ambon, Hitu, Ambon Bay	
RMNH Coel 39720		*Phyllodiscus semoni*	1	Indonesia, Moluccas, Ambon, Hitu, N coast, Kaitetu (near Hila)	2
RMNH Coel 39721		*Phyllodiscus semoni*	3	Indonesia, Moluccas, Ambon, W-side of Pombo Island	1-2
RMNH Coel 39722		*Phyllodiscus semoni*	5	Indonesia, Moluccas, Ambon, Hitu, Ambon Bay	2
RMNH Coel 39723		*Phyllodiscus semoni*	13	Indonesia, Moluccas, Ambon, W-side of Pombo Island	1-2
RMNH Coel 39724		*Phyllodiscus semoni*	1	Indonesia, Java Sea, Kepulauan Seribu	33
RMNH Coel 39725		*Phyllodiscus semoni*	1	Indonesia, Ambon, Ambon Bay, near Tawiri	3-4

Table 4.18 continued.

Catalog Number	Status	Original ID	Number of Specimens	Locality	Depth (m)
RMNH Coel 39726		*Phyllodiscus semoni*	1	Indonesia, N Sulawesi, Selat Lembeh, bay S of Pulau Putus	2
RMNH Coel 39727		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, Pulau Badi	23
RMNH Coel 39728		*Phyllodiscus semoni*	1	Indonesia, Komodo Island, NE cape	
RMNH Coel 39729		*Phyllodiscus semoni*	1	Indonesia, N Sulawesi, Selat Lembeh	
RMNH Coel 39730		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, Kudingkareng Keke	4
RMNH Coel 39731		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, Kudingkareng Keke	10
RMNH Coel 39732		*Phyllodiscus semoni*	2	Indonesia, Celebes, Samalona	1.5
RMNH Coel 39733		*Phyllodiscus semoni*	1	Indonesia, NE Taka Bone Rate	10-11
RMNH Coel 39734		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, Kudingkareng Keke	18
RMNH Coel 39735		*Phyllodiscus semoni*	1	Indonesia, Ambon, Ambon Bay, N coast near Tawiri	1-5
RMNH Coel 39736		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, SW side of Pulau Badi	20
RMNH Coel 39737		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, SW side of Pulau Badi	20
RMNH Coel 39738		*Phyllodiscus semoni*	1	Indonesia, Ambon, Ambon Bay, N coast near Tawiri	2
RMNH Coel 39739		*Phyllodiscus semoni*	6	Indonesia, SW Sulawesi, Spermonde Archipelago, NW of Kudingareng Keke	3
RMNH Coel 39740		*Phyllodiscus semoni*	1	Indonesia, NW Java (Java Sea), Kepulaun Seribu, Pulau Putri	2
RMNH Coel 39779		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, W side of Samalona Island	15
RMNH Coel 39780		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, W side of Bone Lola	13
RMNH Coel 39781		*Phyllodiscus semoni*	2	Indonesia, SW Sulawesi, Spermonde Archipelago, NW side of Kudingareng Keke	9
RMNH Coel 39782		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, N side of Pulau Papandangang	2
RMNH Coel 39783		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, E of Barang Lompo	11
RMNH Coel 39784		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, NW of Barang Lompo	16
RMNH Coel 39785		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, SW of Barang Lompo	6
RMNH Coel 39786		*Phyllodiscus semoni*	2	Indonesia, SW Sulawesi, Spermonde Archipelago, SW of Barang Lompo	6
RMNH Coel 39787		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, W of Kudingareng Keke	13
RMNH Coel 39788		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, NW side of Barang Lompo	2
RMNH Coel 39789		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, W side of Kudingareng Keke	4
RMNH Coel 39790		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, NW side of Bone Baku	4
RMNH Coel 39791		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, W side of Kudingareng Keke	9
RMNH Coel 39792		*Phyllodiscus semoni*	18	Indonesia, SW Sulawesi, Spermonde Archipelago, N of Kudingareng Keke	4.6
RMNH Coel 39793		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, W side of Bone Lola	6
RMNH Coel 39794		*Phyllodiscus semoni*	3	Indonesia, Ambon, N coast, Manuala beach, W of Hila	2
RMNH Coel 39795		*Phyllodiscus semoni*	1	Indonesia, Ambon, Ambon Bay, N coast near Tawiri	2

Table 4.18 continued.

Catalog Number	Status	Original ID	Number of Specimens	Locality	Depth (m)
RMNH Coel 39796		*Phyllodiscus semoni*	1	Indonesia, Ambon, Ambon Bay, N coast near Tawiri	2
RMNH Coel 39797		*Phyllodiscus semoni*	1	Indonesia, Ambon, Ambon Bay, N coast near Tawiri	2
RMNH Coel 39798		*Phyllodiscus semoni*	3	Indonesia, SW Sulawesi, Spermonde Archipelago, Gusong Panyoa	3
RMNH Coel 39799		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, SW side of Kudingareng Keke	14
RMNH Coel 39800		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, SW side of Kudingareng Keke	12
RMNH Coel 39801		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, W side of Samalona Island	15
RMNH Coel 39802		*Phyllodiscus semoni*	2	Indonesia, SW Sulawesi, Spermonde Archipelago, N of Kudingareng Keke	4
RMNH Coel 39803		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, NW side of Bone Lola	7
RMNH Coel 39804		*Phyllodiscus semoni*	3	Indonesia, SW Sulawesi, Spermonde Archipelago, Bone Lola	10
RMNH Coel 39805		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, W side of Samalona Island	4
RMNH Coel 39806		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, W side of Samalona Island	6
RMNH Coel 39807		*Phyllodiscus semoni*	2	Indonesia, SW Sulawesi, Spermonde Archipelago, W side of Bone Baku	9
RMNH Coel 39808		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, W side of Bone Baku	11
RMNH Coel 39809		*Phyllodiscus semoni*	2	Indonesia, SW Sulawesi, Spermonde Archipelago, W side of Bone Lola	11
RMNH Coel 39810		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, W side of Bone Lola	9
RMNH Coel 39811		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, W side of Bone Lola	4
RMNH Coel 39812		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, W of Bone Tambung	16
RMNH Coel 39813		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, W side of Bone Batung	3
RMNH Coel 39814		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, W side of Badi Island	7
RMNH Coel 39815		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, NW side of Samalona Island	6
RMNH Coel 39816		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, E of Samalona Island	9
RMNH Coel 39817		*Phyllodiscus semoni*	2	Indonesia, SW Sulawesi, Spermonde Archipelago, E of Samalona Island	2
RMNH Coel 39818		*Phyllodiscus semoni*	4	Indonesia, SW Sulawesi, Spermonde Archipelago, W of Samalona Island	5
RMNH Coel 39819		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, W of Samalona Island	7
RMNH Coel 39820		*Phyllodiscus semoni*	2	Indonesia, Ambon, N coast near Morela	0-35
RMNH Coel 39821		*Phyllodiscus semoni*	1	Indonesia, Ambon, N coast near Morela	0-35
RMNH Coel 39822		*Phyllodiscus semoni*	1	Indonesia, NW Seram, Kotania Bay, NE of Pulau Marsego	0-30
RMNH Coel 39823		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, SW of Barang Lompo	12
RMNH Coel 39824		*Phyllodiscus semoni*	2	Indonesia, SW Sulawesi, Spermonde Archipelago, SW of Barang Lompo	5
RMNH Coel 39825		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, SW of Barang Lompo	9
RMNH Coel 39826		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, SW of Barang Lompo	12
RMNH Coel 39827		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, NW of Barang Lompo	7

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Table 4.18 continued.

Catalog Number	Status	Original ID	Number of Specimens	Locality	Depth (m)
RMNH Coel 39828		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, NW of Barang Lompo	3
RMNH Coel 39829		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, N of Kudingareng Keke	6
RMNH Coel 39830		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, N of Kudingareng Keke	4
RMNH Coel 39831		*Phyllodiscus semoni*	1	Indonesia, Ambon, Ambon Bay, N coast near Laha	1-2
RMNH Coel 39832		*Phyllodiscus semoni*	1	Indonesia, Ambon, Ambon Bay, N coast near Laha	1-2
RMNH Coel 39833		*Phyllodiscus semoni*	1	Indonesia, Ambon, Ambon Bay, N coast near Laha	1-2
RMNH Coel 39834		*Phyllodiscus semoni*	1	Indonesia, Ambon, Ambon Bay, N coast near Laha	1-2
RMNH Coel 39835		*Phyllodiscus semoni*	1	Indonesia, Ambon, Ambon Bay, N coast near Laha	1-2
RMNH Coel 39836		*Phyllodiscus semoni*	1	Indonesia, Ambon, Ambon Bay, N coast near Laha	1-2
RMNH Coel 39837		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, W side of Kudingareng Keke	11
RMNH Coel 39838		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, W side of Kudingareng Keke	8
RMNH Coel 39839		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, W side of Kudingareng Keke	10
RMNH Coel 39840		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, W side of Kudingareng Keke	12
RMNH Coel 39841		*Phyllodiscus semoni*	3	Indonesia, SW Sulawesi, Spermonde Archipelago, W side of Kudingareng Keke	14
RMNH Coel 39842		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, W side of Kudingareng Keke	5
RMNH Coel 39843		*Phyllodiscus semoni*		Indonesia, SW Sulawesi, Spermonde Archipelago, W side of Kudingareng Keke	9
RMNH Coel 39844		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, W side of Kudingareng Keke	3
RMNH Coel 39845		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, W side of Kudingareng Keke	14
RMNH Coel 39846		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, W side of Kudingareng Keke	13
RMNH Coel 39847		*Phyllodiscus semoni*	6	Indonesia, SW Sulawesi, Spermonde Archipelago, NW side of Kudingareng Keke	5
RMNH Coel 39848		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, NW side of Kudingareng Keke	19
RMNH Coel 39849		*Phyllodiscus semoni*	3	Indonesia, SW Sulawesi, Spermonde Archipelago, NW side of Kudingareng Keke	20
RMNH Coel 39850		*Phyllodiscus semoni*	9	Indonesia, SW Sulawesi, Spermonde Archipelago, NW side of Kudingareng Keke	5
RMNH Coel 39851		*Phyllodiscus semoni*	11	Indonesia, SW Sulawesi, Spermonde Archipelago, NW side of Kudingareng Keke	5
RMNH Coel 39852		*Phyllodiscus semoni*	11	Indonesia, SW Sulawesi, Spermonde Archipelago, NW side of Kudingareng Keke	7
RMNH Coel 39853		*Phyllodiscus semoni*	5	Indonesia, SW Sulawesi, Spermonde Archipelago, NW side of Kudingareng Keke	5
RMNH Coel 39854		*Phyllodiscus semoni*	1	Indonesia, SW Sulawesi, Spermonde Archipelago, NW side of Kudingareng Keke	9
RMNH Coel 39855		*Phyllodiscus semoni*	2	Indonesia, SW Sulawesi, Spermonde Archipelago, NW side of Kudingareng Keke	5
RMNH Coel 39856		*Phyllodiscus semoni*	4	Indonesia, SW Sulawesi, Spermonde Archipelago, NW side of Kudingareng Keke	5
RMNH Coel 39857		*Phyllodiscus semoni*	1	Philippines, Cebu Strait, W of Bohol, N side of Cabilao Island	3
RMNH Coel 39858		*Phyllodiscus semoni*	3	Indonesia, N Sulawesi, Selat Lembeh, between Tanjungnanas and Teluk Kungkungan	1.5-2.5
RMNH Coel 39859		*Phyllodiscus semoni*	1	Philippines, Cebu Strait, W of Bohol, NW side of Cabilao Island	2
SMNH 4080	syntype	*Phyllodiscus semoni*	pieces	Indonesia, Moluccas Islands, Ambon	0-3
SMNH 4081	syntype	*Phyllodiscus semoni*	pieces	Indonesia, Moluccas Islands, Ambon	0-3

Table 4.19. Distribution and size of cnidae of *Phyllodiscus semoni* from this study and literature. Measurements given as range in length x width of undischarged capsules in µm (outlier measurements in parentheses), {number of capsules measured}, [ratio of number of individuals in which that type of cnidae was found to the number of individuals examined]. Frequency of cnida type indicated as either very common, common, or rare. Letters in parentheses correspond to images in Fig 4.46.

	Phyllodiscus semoni this study	*Phyllodiscus semoni* Carlgren 1945
TENTACLES		
spirocyst - gracile (a)	19-30 x 3-4.5 {39} [2/2] v. common	(51) 55-62 x 7-8.5
spirocyst - robust (b)	34-48 x 5-8 {27}[2/2] v. common	
microbasic amastigophore (c)	90-104 x 9-10 {30} [2/2] v. common	86-94.5 x 7-10 (15)
microbasic amastigophore		
microbasic amastigophore		
microbasic p-mastigophore (d)	13-16 x 2.5-3 {5} [1/2] rare	
basitrich (e)	17-20 x 3 {15} [1/1] common	
ACTINOPHARYNX		
spirocyst (f)	23-40 x 4-5.5 {15} [1/1] common	
microbasic amastigophore (g)	48-65 x 6-8 {15} [1/1] v. common	45.8-52 x 6.3-7
microbasic p-mastigophore (h)	20-30 x 3-3.5 {6} [1/1] rare	
ORAL DISC		
spirocyst - robust (i)	(26) 30-37 x 5-6 {15} [1/1] common	
microbasic amastigophore (j)	51-60 x 6-8 {15} [1/1] common	
microbasic amastigophore		
COLUMN		
spirocyst		63.7-73.3 x 12-15.5 (17)
microbasic amastigophore (k)	21-37 x 4-6 {19} [2/2] common	(25.4) 31-57.8 x 5-6.3
microbasic amastigophore		8.5-15.5 x 2.8-3.5
microbasic p-mastigophore		
basitrich	22-27 x 4.5-6 {12} [2/2] rare	24-29.6 x 2.8-4
MESENTERIAL FILAMENTS		
microbasic amastigophore		42.3-48.6 (52.2) x 7-7.5
microbasic amastigophore		
microbasic p-mastigophore (l)	12-16 x 3.5-4 {15} [1/1] common	8.5-14 (18) x 2.5-3.5
basitrich		16.9-24 x 2.2-2.8
PEDAL DISC		
microbasic amastigophore	21-28 x 5-6 {12} [1/1] common	24-28.2 x 4.2-5
basitrich	11-15 x 2-3.5 {13} [1/1] common	
VESICLE		
macrobasic amastigophore (m)	67-76 x 12-15 {27} [2/2] v. common	
macrobasic amastigophore		
microbasic amastigophore (n)	49-58 x 6-8 {15} [1/2] v. common	
microbasic p-mastigophore (o)	12-17 x 2-3 {11} [1/2] rare	
basitrich (p)	12-15 x 2-4 {25} [2/2] common	
basitrich (q)	8-13 x 2.5-4 {11} [2/2] common	

CONCLUSIONS

In this study, I investigate whether sea anemones that possess branched outgrowths and defensive spheres, but belong to different families, have features due to convergent evolution. By analyzing molecular and morphological data from both families simultaneously, I was able to confirm that members of Aliciidae and Thalassianthidae are not closely related, despite looking similar. Instead, Thalassianthidae members are most similar molecularly and morphologically to some members of Stichodactylidae. Aliciidae members are most similar molecularly and morphologically to members of Boloceroididae and Aiptasiidae. The non-relatedness of Aliciidae and Thalassianthidae supports the hypothesis of convergent evolution of the branched outgrowths and defensive spheres.

Symbiotic relationships can be an influential force on evolution in a group, and in this case, potentially in the evolution of morphological features. Members in the unrelated families, Aliciidae and Thalassianthidae, have evolved morphological features that look and function similarly. The symbiotic relationship with zooxanthellae is likely implicated with the formation of these structures, as defensive spheres defend the branched outgrowths that house large numbers of zooxanthellae. Various morphological features that perform similar functions have also evolved, possible due to symbiosis with zooxanthellae, such as branched lateral projections of tentacles in *Phymanthus*, or specialized parts of tentacles dense with nematocysts called acrospheres in Actinodendridae. Throughout Actiniaria, it is clear that different morphological features perform similar functions – a consequence of the relative simplicity of their diploblastic body plans.

Phylogenetic analyses of molecular data recovered Thalassianthidae members most closely related to members of Endomyaria, while Aliciidae members was most closely related to members of Metridioidea. Mapping of the morphological features of branched outgrowths and defensives spheres on the phylogeny show this combination of character has evolved multiple times. Further recoding of characters recovered a single origin for nematospheres and pseudotentacles, but multiple origins for branched tentacles and vesicles. Molecular data also provided an alternative way to identify specimens that lack distinctive morphology – in this case, sea anemones that are symbiotic with crabs of the genus *Lybia*. Without distinctive branched outgrowths and defensives spheres, it would be difficult to identify these specimens as *Triactis producta*, but using molecules, I found samples of *Lybia* symbionts were most closely related with *Triactis producta* samples.

I determine that Thalassianthidae is a monophyletic family with two valid genera and seven valid species (Chapter 3). I find that presence/absence of lobes of oral disc and positioning of nematospheres to be characters to diagnose genera in Thalassianthidae. I agree with a previous hypothesis (Stephenson 1922) that *Heterodactyla* is a synonym of *Thalassianthus*, and I synonymize *Heterodactyla* and *Actineria* with *Thalassianthus*. I find number, shape and size of lobes, coverage of oral disc by tentacles, and depth of oral disc folds provides to be characters to diagnose species.

I determine that Aliciidae has four valid genera and 11 valid species (Chapter 4). I find the number, position, and branching anatomy of pseudotentacles as well as type and position of vesicles to be characters to diagnose genera in Aliciidae. I do not agree with previous hypotheses (Stephenson 1922, Doumenc 1973) that *Triactis* specimens are juvenile *Phyllodiscus* specimens. I find both *Triactis* and *Phyllodiscus* to be valid genera, separated based on number and branching anatomy of pseudotentacles. I also find that *Lebrunia coralligens* specimens are not juvenile specimens of *L. neglecta*, as had been previously hypothesized (Duerden 1898, Carlgren 1949). My analyses show that a combination of number of branch orders and number of mesenteries can separate the two species of *Lebrunia*.

My research shows that careful analyses of morphology, in conjunction with analyses of molecular data, provide information to support generic and species boundaries in Aliciidae and Thalassianthidae. This approach was particularly helpful when dealing with convergent characters, which allow species to look similar, despite not being closely related.

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APPENDIX A: Primer sequences for PCR and sequencing reactions.

Gene	Primer name	Primer Sequence	Reference
12s	12S-F	AGCCACACTTTCACTGAAACAAGG	Chen *et al.* 2002
	12S-R	GTTCCCYYWCYCTYACYATGTTACGAC	Chen *et al.* 2002
16s	ANEM16SA	CACTGACCGTGATAATGTAGCGT	Geller & Walton 2001
	ANEM16SB	CCCCATGGTAGCTTTTATTCG	Geller & Walton 2001
CO3	AnthCOIIIF	ACTTTTCAAGGTCTTCACACCRTGGTT	Geller & Walton 2001
	COIIIR	CAAACCACATCTACAAAATGCCAATATC	Geller & Walton 2001
18s	A	AACCTGGTTGATCCTGCCAGT	Medlin *et al.* 1988
	L	CCAACTACGAGCTTTTTAACTG	Apakupakul *et al.* 1999
	C	CGGTAATTCCAGCTCCAATAG	Apakupakul *et al.* 1999
	Y	CAGACAAATCGCTCCACCAAC	Apakupakul *et al.* 1999
	O	AAGGGCACCACCAGGAGTGGAG	Apakupakul *et al.* 1999
	B	TGATCCTTCCGCAGGTTCACCT	Medlin *et al.* 1988
28s	F63 mod	ACCCGCTGAAYTTAAGCATATHANTMAG	Medina *et al*., 2001
	F63sq	AATAAGCGGAGGAAAAGAAAC	Medina *et al*., 2001
	F97	CCYYAGTAACGGCGAGT	Cartwright *et al.* 2008, Evans *et al.* 2008
	F635sq	CCGTCTTGAAACACGGACC	Medina *et al*., 2001
	F1379sq	GACAGCAGGACGGTGGYCATGG	Medina *et al*., 2001
	F1383	GGACGGTGGCCATGGAAGT	Cartwright *et al.* 2008, Evans *et al.* 2008
	F1586	GTGCAGATCTTGGTDGNAGTAGCAAATATTC	Medina *et al*., 2001
	F1689	CTAAGMSRYAGGGAAAYTC	Cartwright *et al.* 2008, Evans *et al.* 2008
	F2076sq	TAACYTCGGGAWAAGGATTGGCTC	Medina *et al*., 2001
	F2766sq	AGTTTGGCTGGGGCGGYACA	Medina *et al*., 2001
	F2800	GCAGGTGTCCTAAGGYRAGCTC	Voigt *et al.,* 2004
	R635sq	GGTCCGTGTTTCAAGACGG	Medina *et al*., 2001
	R1411sq	GTTGTTACACACTCCTTAGCGG	Medina *et al*., 2001
	R1630	CCYTTCYCCWCTCRGYCTTC	Medina *et al*., 2001
	R2077sq	GAGCCAATCCTTWTCCCGARGTT	Medina *et al*., 2001
	R2084	AGAGCCAATCCTTTTCC	Cartwright *et al.* 2008, Evans *et al.* 2008
	R2766sq	CAGRTGTRCCGCCCCAGCCAAACT	Medina *et al*., 2001
	R2800	GAGCTYRCCTTAGGACACCTGC	Voigt *et al.,* 2004
	R3238	SWACAGATGGTAGCTTCG	Cartwright *et al.* 2008, Evans *et al.* 2008
	R3256	GAGGCGTTCAGTCATAATC	Cartwright *et al.* 2008, Evans *et al.* 2008
	R3264	TTCYGACTTAGAGGCGTTCAG	Medina *et al*., 2001

APPENDIX B: PCR reactions.

25 µL reactions

(for 12s, 16s, COIII, and 18s primer sets)

12.5 µL Qiagen *Taq* PCR master mix

5.0 µL forward primer (5 µM)

5.0 µL reverse primer (5 µM)

1.5 µL BSA

1.0 µL DNA template

50 µL reactions

(for complete 28s primer sets)

25.0 µL Qiagen *Taq* PCR master mix

10.0 µL forward primer (5 µM)

10.0 µL reverse primer (5 µM)

3.0 µL BSA

2.0 µL DNA template

APPENDIX C: Abbreviations used in text and specimen tables with corresponding institution names and information.

Abbreviation	Institution name
AMNH	American Museum of Natural History, New York, NY, USA
BMNH	The Natural History Museum, London, England
CAS	California Academy of Sciences, San Francisco, CA, USA
KUDIZ	Division of Invertebrate Zoology, the University of Kansas Biodiversity Institute, Lawrence, KS, USA
LO	Museum of Zoology, Lund University, Lund, Sweden
MNHN	Museum National d'Histoire Naturelle, Paris, France
MTQ	Museum of Tropical Queensland, Townsville, Australia
PMJ	Phyletisches Museum, Jena, Germany
QM	Queensland Museum, Brisbane, Australia
RMNH	NCB Naturalis, Leiden, the Netherlands
SMF	Senckenberg Museum, Frankfurt, Germany
SMNH	Naturhistoriska Riksmuseet, Swedish Museum of Natural History, Stockholm, Sweden
USNM	United States National Museum of Natural History, Smithsonian Institution, Washington, DC, USA
ZMB	Museum für Naturkunde der Humboldt Universität, Berlin, Germany
ZMH	Zoologisches Museum, Hamburg, Germany
ZRC	Raffles Museum of Biodiversity Research, National University of Singapore, Republic of Singapore