Certain Actiniaria (Cnidaria, Anthozoa) from the Red Sea and tropical Indo-Pacific Ocean

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Contents

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Synopsis

Thirteen species of sea-anemone from the tropical Red Sea and the Indo-Pacific Ocean are described in detail and notes are given on a further three. Certain taxonomic characters are discussed, marginal spherules are re-defined and the concept 'nematocyst signature' is introduced. The genus *Edwardsia* de Quatrefages, 1841, is revised. Details of two nematocyst types found in the nemathybomes are given, newly designated pterotrich and microbasic t-mastigophore. The genus *Edwardsioides* Danielssen, 1890, is re-established and the related genus *Edwardsianthus* nov. introduced. Descriptions are given of *Edwardsia hantuensis* sp. nov., *Edwardsianthus pudica* (Klunzinger, 1877) comb. nov., and *Scolanthus armatus* (Carlgren, 1931) comb. nov.

Triactis producta Klunzinger, 1877 (Aliciidae) is redescribed. Descriptions are given of the actiniid species *Anthopleura dixoniana* (Haddon & Shackleton, 1893), *A. handi* Dunn, 1977, *A. nigrescens* (Verrill, 1928), and *A. waridi* (Carlgren, 1900). The genus *Gyractis* Boveri, 1893, is re-established to accommodate the species *G. excavata* Boveri, 1893, and its relation to *Aulactinia* Verrill, 1864, is discussed. Three new genera are proposed in the Actiniidae: *Mesactinia* gen. nov., *Neocondylactis* gen. nov. and *Telactinia* gen. nov.; and the included species *Telactinia citrina* (Haddon & Shackleton, 1893) comb. nov., *Mesactinia ganensis* sp. nov. and *Neocondylactis singaporensis* sp. nov. are described. The scope of the family Stichodactylidae is widened to include the genus *Entacmaea* Ehrenberg, 1834; and the genus *Antheopsis* Carlgren, 1900, is reinstated. New information is given on the species *Entacmaea quadricolor* Rueppell & Leuckart, 1828, and *Antheopsis malayensis* sp. nov. is described. The date of Carlgren's definition of the family Hormathiidae is discussed. A note is given on the inclusion of the conspecific *Actinia decorata* (Dana, 1846) with *Calliactis polypus* (Forsskål, 1775).

The three species *Carcinactis dolosa* Riemann-Zürneck, 1975, *Carcinactis ichikawai* Uchida, 1960, and *Verrillactis paguri* (Verrill, 1969*a*) are compared.

Type designations

Type material is designated of the nominal species *Antheopsis malayensis* sp. nov. (p. 274), *Edwardsia hantuensis* sp. nov. (p. 221), *Mesactinia ganensis* gen. nov., sp. nov. (p. 263) and *Neocondylactis singaporensis* gen. nov., sp., nov. (p. 265).

Priapus polypus Forsskål, 1775, is designated type species of the genus *Calliactis* Verrill, 1969*b* (p. 279), family Hormathiidae.

Type species are designated of the genera *Edwardsianthus* gen. nov. (p. 224) and *Edwardsioides* Danielssen, 1890 (p. 224), family Edwardsiidae; *Mesactinia* gen. nov. (p. 261), *Neocondylactis* gen. nov. (p. 265) and *Telactinia* gen. nov. (p. 268), family Actiniidae.

Introduction

Little taxonomic work on tropical sea-anemones has been published since Carlgren's (1950*a*,*b*) papers on the Actiniaria and Corallimorpharia of the Great Barrier Reef, South Queensland and New South Wales. The only substantial publication since 1950 has been that of Dunn (1981) on the clownfish sea-anemones. The opportunity was taken, during military service, to collect Actiniaria and Corallimorpharia from a variety of tropical and sub-tropical sites; in Aden and Bahrain in 1966; in Gan, Addu Atoll, Maldives, in 1970 and 1971; and in Singapore and Malaysia (Penang and Pulau Tioman) from 1969 to 1972. The collection comprised some 50 species of which 13 are described here and notes on a further 3 included. In addition numerous locality records of anemones not treated taxonomically are included. The study was augmented by material from the British Museum (Natural History) and specimens kindly made available by others from Sri Lanka, Hawaii, the Tuamoto Isles, Hong Kong, Madagascar and Egypt. The new material has been deposited in the British Museum (Natural History).

Methods

The collecting sites are described according to habitat. A species list from each habitat is given. Not all the species found are described in this paper, but lists of them are included to show the wide variety that occurred in these areas and to provide faunal records. In the areas investigated four distinct habitats were studied as follows.

(a) Mangrove swamp. Here Actiniaria and Corallimorpharia were absent, although Stephenson, Stephenson & Tandy (1931: 38) recorded some specimens from a pool near the mangroves of Low Isles in the Great Barrier Reef. Mangrove areas were examined in Singapore and around Pulau Tioman, Malaysia.

(b) Intertidal mud with occasional rocks, but not associated with mangroves. In Aden, near the Causeway below Jebel Hadid, one such area was rich in actiniarians. They included *Edwardsianthus pudica* (Klunzinger, 1877), comb. nov., *Antheopsis koseirensis* (Klunzinger, 1877), *Stichodactyla gigantea* (Forsskål, 1775), *Heteranthus verraculatis* Klunzinger, 1877, found in the mud, and *Aiptasia* sp., *Anthopleura stellula* (Ehrenberg, 1834) and *Haliplanella luciae* (Verrill, 1898) found on small stones, pieces of rope and an old oil drum. Large numbers of hermit crabs (species not determined) were found in this area, possibly attracted by fishermen's offal, but the crabs never had associated symbiotic anemones. Other Cnidaria observed included *Cassiopeia* sp. (Scyphozoa), *Cladonema* sp. (Hydrozoa: hydroid stage), and a large cerianthid.

At Singapore several similar areas occurred on the northern coast, including Pungol Point and Pasir Ris which were examined. Numerous specimens of *Actinothoe* sp. were found on several different species of *Nassarius* spp. (Gastropoda), and *Neocondylactis singaporensis* gen. nov. sp. nov., *Scolanthus armatus* (Carlgren, 1931) and a large cerianthid were observed in the mud. *Anthopleura dixoniana* (Haddon & Shackleton, 1893) comb. nov. was found in small holes in an outcrop of yellow sandstone at Pungol Point and on stones of a broken wall at Pasir Ris, both locations being at Mean High Tide Level. Another muddy habitat at Singapore was an area which has now been reclaimed at Bedok. From here were collected specimens of *Paracondylactis* sp., *Sagartianthus* sp. associated with the crab *Diogenes diogenes*, and *Stichodactyla gigantea* (Forsskål, 1775). On the south coast of Pasir Panjang and Buona Vista was a diverse area of mud, sand and gravel with patches of the green alga *Halophila ovalis*. Here was again found *Actinothoe* sp. on *Nassarius* spp., and also *Edwardsia hantuensis* sp. nov., *Stichodactyla gigantea* (one large and several small specimens with symbiotic shrimp), and a cerianthid.

(c) Fringing coral reefs. Three zones were recognized:

1. The reef flat, usually comprising coarse sand with occasional rocks and coral heads.
2. The reef edge, an area extending back from the outer edge for some ten metres. This area comprised coral debris and sand with large coral heads and occasional hard rock, especially where wave action was high. Shelter from wave action was associated with growth of many living corals and algae.
3. The reef slope, fairly steep and comprised entirely of coral debris, which continued down to depths of more than thirty metres around the islands off Singapore and to greater depths in parts of the reefs at Gan and elsewhere. In other localities it consisted of rocks covered with many species of corals and occasional actinians.

On the reef flats surrounding the Singapore islands, particularly Pulau Hantu, the following species were noted in the sand: *Actinodendron* sp., *Edwardsianthus pudica* comb. nov., *Metapeachia tropica* (Panikkar, 1939), *Scolanthus armatus* comb. nov., *Stichodactyla gigantea*, *S. kenti* (Haddon

& Shackleton, 1893), and several species of Discosomatidae. On the Cyrene Reef, however, the reef flat was covered with *S. kenti*. On Gan, from similar habitats on the reefs inside the lagoon, *E. pudica*, *S. kenti* and *Rhodactis* sp. were recorded. At the reef edge the number of species was correlated with the amount of wave action. If the edge was composed only of rock and was subject to heavy wave action few actinians or corallimorpharians were present. In Gan the only species found was *Gyractis excavata* Boveri, 1893, inhabiting cracks and crevices in extremely hard rock, but in Aden it was associated in such places with *Phymanthus loligo* (Ehrenberg, 1834). *Gyractis excavata* has been recorded from similar locations in Hawaii (as *Actiniogeton sesere* by Dunn, 1974*b*: 181–188) and Fiji (J.S. Ryland, personal communication). Where wave action was low, as at Singapore and inside the lagoon of Gan, the reef edge was composed of living coral and sand. Many actinians occurred here, attached to coral stems above or below the sand. *Edwardsianthus pudica* comb. nov., *Radianthus malu* (Haddon & Shackleton, 1893), *Phymanthus muscosus* Haddon & Shackleton, 1893, and a cerianthid occurred in the sand. Among the corals and attached to their stems were *Cryptodendron adhaesivium* Klunzinger, 1877, *Entacmaea quadricolor* (Rueppell & Leuckart, 1828), *Telactinia citrina* comb. nov.; and the corallimorpharians *Rhodactis bryoides* (Haddon & Shackleton, 1893), *R. rhodostoma* (Ehrenberg, 1834), *Metarhodactis boninensis* Carlgren, 1943, and *Ricordea yuma* (Carlgren, 1900).

Reef slopes composed of rock were usually covered with corals, and few actinians were seen. This was so at Gan where no actinians were found during several dives made in the area. The only anemone seen was on the wreck of the oil tanker *British Loyalty*. If the reef slope consisted of coral debris the surface was mobile preventing animals retaining a hold, and few animals of any species were found. At the foot of such reef slopes, at 30–40 m depth, specimens of *Radianthus malu* and *R. macrodactyla* (Haddon & Shackleton, 1893) were occasionally found, but their small number suggests that they may have been displaced from the reef edge. In some areas of Pulau Hantu and Pulau Tioman, outcrops of rock occurred on the reef slope with the tops just below Mean Low Water Springs (MLWS). These locations seemed favoured by *Radianthus magnifica* (Quoy & Gaimard, 1833).

In coral areas that had been devastated by storms, human activity, or the starfish *Acanthaster planci* (Linnaeus, 1758), it was observed that the area was first reoccupied by *Rhodactis* sp. This corallimorpharian appeared to colonize rapidly and large areas covering many square metres were soon carpeted. This was noted at Pulau Tioman and again in Gan where the reef corals alongside the jetty had been destroyed by abrasion by ships at low water.

(d) Rocky areas, not associated with reefs. In the intertidal zone these were the habitat for *Aiptasia* sp., *Anthopleura dixoniana*, *A. stellula* and *A. waridi* (Carlgren, 1900) comb. nov.; and also for *Corynactis* sp. In deeper waters actinians were found also on antipatharians: for example, several specimens of *Nemanthus* sp. were found on the main stems of black corals in Pulau Tioman.

Around Singapore Islands there were many specimens of gorgonians and whip corals at depths between 4 and 40 metres. Despite prolonged searching no actinians were found on them.

Collection. Specimens were removed with the substrate to which they were attached or were prised carefully from it. Attempts to loosen specimens from the substrate by chemical means rarely worked, the anemones closing up tightly and remaining strongly attached. Soda water and weak solutions of formaldehyde and bleach were tried unsuccessfully.

With burrowing anemones such as *Edwardsianthus* spp. and cerianthids it was found most effective to dig gently downwards to a depth of 40–50 cm but 30–40 cm away from the animal and then to tunnel underneath it before attempting capture. It was not uncommon to lose a specimen, since when disturbed most burrowing species contract rapidly and move downwards.

Preservation. Specimens were narcotized in 3·5–4·0% $MgSO_4.7H_2O$ in sea water. In the field this was not always possible so $MgSO_4$ crystals were added to a vessel of sea water containing the specimen. With small specimens 30 minutes was adequate for narcotization, but larger specimens were left overnight and some were still not completely narcotized by morning. For large specimens, menthol or a combination of menthol and $MgSO_4$ was also used overnight. When an anemone had lost tactile sensitivity 40% formaldehyde solution was injected from a pipette or hypodermic syringe into the enteron via the mouth, care being taken to avoid inflating it. 10% formaldehyde solution was then sprayed from a pipette over the outside of the specimen. Finally it was transferred to a fresh container containing 10% formaldehyde-sea water solution and labelled. Specimens were transferred to 70% C_2H_5OH later on. Storage in formaldehyde-sea water solution for prolonged periods sometimes hinders subsequent staining and the tissues may start to macerate.

Other methods of killing and preserving specimens have been used (Lee, 1921: 521), but not always successfully. The use of hot Bouin's fluid on specimens of *Anthopleura waridi* resulted in the ectoderm becoming detached, with consequent loss of the nematocysts from the spherules at the margin and in the fosse, and this led to an incorrect determination (England, 1969: 5).

Corallimorpharians, such as *Rhodactis rhodostoma*, were the most difficult to preserve, since they exuded mucus when chemicals were added to the water to narcotize them. The mucus not only prevented narcotization but seemed to hinder fixation of the tissue by formaldehyde, especially internally. Fixing in 70% C_2H_5OH overcame the difficulty but the specimens tended to be badly contracted. Glutaraldehyde was used with good results.

Examination of material. Specimens were examined with a dissecting microscope under alcohol. At this stage it was useful to stain some of the smaller species in bulk with borax carmine to facilitate the observation of certain features, such as sphincter muscles, micro-mesenteries and suckers on the column if present. Alcoholic picro-indigo-carmine was found a better stain than borax carmine for showing micro-mesenteries that hardly break the surface of the endoderm, and which would normally be detected only be means of serial sections. If it was desired to remove this stain differentiation in 70% C_2H_5OH was used. Continued changes of 70% C_2H_5OH removed the stain completely from most specimens, but occasionally picro-indigo-carmine became permanent, depending perhaps on the method of fixation. Alternatively, if acid alcohol (0·5% HCl, 70% C_2H_5OH) was used the stain was both differentiated and fixed. This method of bulk staining greatly reduced the need for cutting sections.

If sections were required selected pieces of the specimen were removed and stained with borax carmine (unless already stained). Histological sections were cleared in cedarwood oil or terpineol and embedded in paraffin wax (m. pt. 55–57°C) or Fibrowax (m. pt. 57°C). Double embedding in celloidin and Fibrowax was also employed. 10 μm sections were cut using a Cambridge rocking microtome. Most of the sections were counter-stained with picro-indigo-carmine (Stephenson, 1928: 55–56), but other staining methods used included Ehrlich's haematoxylin and eosin, and Mallory's triple stain (Peacock, 1966: 421 & 441). Drawings prepared from the stained sections were made without the aid of a camera lucida. Where part of an illustration was left blank it was because the specimen was inadequate at that point (Figs 3d, 10b). Where an illustration is intended to be diagrammatic this is stated.

Nematocysts. Squash preparations were made of small portions of preserved tissue, approximately 1 mm^2, from tentacles, column, actinopharynx and filaments, and also from acontia, spherules, nemathybomes and vesicles, when present, to identify the types of nematocyst and to measure them. The samples taken from tentacles, column and actinophrynx were obtained by scraping off ectoderm: this avoided contamination with nematocysts from the endodermal epithelium or filaments, or from acontia which, when present, frequently extended from the enteron into the tentacles. The selected tissue was treated with 2% aqueous $KMnO_4$ on a slide for 2 minutes, the solution removed with filter paper and a drop of glycerine placed on the tissue. It was then teased and afterwards gently squashed under a coverslip by finger pressure using a little sideways movement. It was necessary to exert only gentle pressure at this stage, before examining the preparations to identify the types of nematocyst present. Large holotrichs and spirocysts were easily damaged or completely destroyed if too much pressure had been applied or too much sideways motion given to the coverslip. It was at this stage still possible to see the nematocysts *in situ* in the tissue and to confirm their presence in that position. When only a few nematocysts occurred in certain positions it was sometimes difficult to be certain that they belonged there and were not contaminants from elsewhere. When doubt existed serial sections were examined to confirm their true location. After the types of nematocyst had been determined and any large, easily damaged nematocysts measured, the preparation was subjected to further squashing to break up the tissue surrounding the nematocysts. The majority of nematocysts were thereby clearly displayed, mostly lying flat. Three separate slides of the tissue from each location were examined. Sometimes replicate preparations were stained with 1% methylene blue or 1% acid fuchsin. Methylene blue stains atrichs, basitrichs and heterotrichs intensely so that they stand out from the surrounding tissue, but the capsular contents cannot be seen. If basitrichs and atrichs of a similar size range occurred in the same piece of tissue it would not be possible to separate them under these conditions. For general work and identification of the capsular contents of undischarged nematocysts staining with $KMnO_4$ was best. The $KMnO_4$ partially macerated the tissue but did not damage the nematocysts or alter their size. When the nematocyst contents remained indistinct after staining, identification was achieved using a 100x phase contrast objective.

Each preparation was scanned under oil immersion and the largest and smallest capsules of each undischarged nematocyst type were observed and measured ($\pm 0{\cdot}5$ µm) with an eyepiece micrometer. It was usual to measure 20–30 capsules of each type from three slides, and the size ranges reported here summarize these measurements. If fewer than 10 nematocysts were found altogether, the number seen was recorded as well as their size range (see Tables).

Terminology. The nematocyst nomenclature of Weill (1934) as modified by Carlgren (1940*a*: 3–4) has been used. Each nematocyst type is illustrated under each species. In addition two types of nematocyst originally noted by Carlgren (1940*a*: 23), the pterotrich and microbasic t-mastigophore, are redescribed and named (p. 219–221).

To describe the anatomy and structure of sea-anemones the terminology of Stephenson (1928, 1935) has been used throughout, though modified in places (see below).

Reappraisal of certain taxonomic characters

Marginal spherules. All blister-shaped protuberances occurring on the margin or in the fosse are termed spherules in this work (Fig. 1).

Since they include all three layers of the body wall they are similar in structure to verrucae but the ectoderm in this case is non-adhesive. Some spherules bear verrucae or adhesive spots on their outer faces. Spherules may have a battery of densely packed specific nematocysts, or they may have only a few nematocysts of the same types and size ranges as elsewhere in the column. A nematocyst battery, when present, is an addition to the spherule and often stands out from it, either as a cap completely covering it or as a small projection easily seen in both live and preserved material (Fig. 1a, c-e). Spherules showing this extent of variation, together with spherules devoid of nematocyst batteries, can occur with a single specimen, for example in *Anthopleura handi* (p. 245).

Many protuberances are armed with a large battery of atrichs and in the literature have been termed either acrorhagi or spherules, but if the battery of nematocysts is absent they have been called pseudo-acrorhagi or pseudo-spherules. The term acrorhagi was proposed by Andres, 1883: 283. Kwietniewski used the term 'Randblaschen' (1897*b*: 33), and others the term 'Randsackchen' (alternatively spelt 'Randsacken') (Lager, 1911: 219). Haddon, Kwietniewski and Lager appear each to have used these terms for both acrorhagi and pseudo-acrorhagi, so that it is not clear to which genus many of the species they described are best referred. It is now considered that acrorhagi are found, for example, in *Actinia*, *Anemonia*, *Anthopleura* and *Oulactis*, while pseudo-acrorhagi are found in *Paracondylactis*, *Gyractis* and in some other genera.

Some sea-anemones have marginal spherules which instead of atrichs possess large numbers of nematocysts of other types. *Telactinia citrina* comb. nov., and to a lesser extent *Mesactinia* gen. nov., for example, have large batteries of basitrichs (see p. 263, 270). Again, *Triactis* has spherules both in the fosse and on marginal peduncles armed with micro- and macrobasic amastigophores. The term acrorhagus is no longer useful because it includes at least three varieties of spherule for which precise terms are needed and it is not used in this account. Also, the term pseudo-acrorhagus

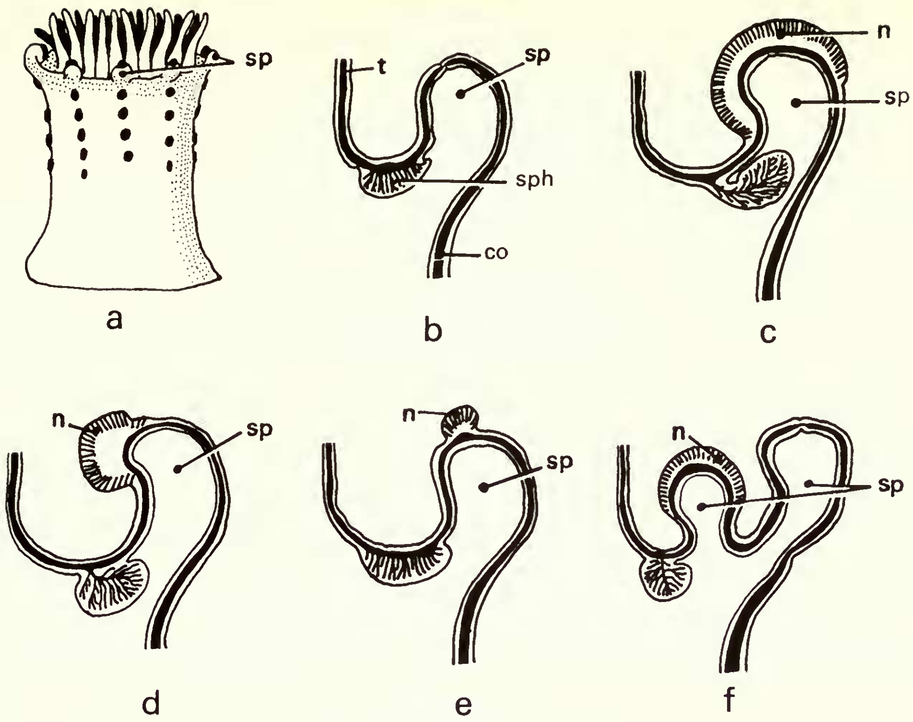

Fig. 1 Variation in marginal spherules (diagrammatic). (a) Typical appearance of *Anthopleura* sp. with large atrichal marginal spherules. (b) A marginal spherule lacking a nematocyst battery. (c) An atrichal marginal spherule completely capped by a nematocyst battery. (d) An atrichal marginal spherule with a small nematocyst battery, bent into the fosse. (e) Same, but upright. (f) Marginal spherule (to right) without a nematocyst battery but with an atrichal spherule in the fosse (as in *Anthopleura waridi*). (co column, n nematocyst battery, sp spherule, sph sphincter, t tentacle.)

(pseudo-spherule) is a misnomer in that a spherule is always present, whether it has a battery of nematocysts or not.

It is proposed that the term acrorhagus be dropped in favour of spherule. When spherules are specialized by the presence of specific nematocysts in a definite battery they can be classified as follows:

a.	spherules armed with atrichs	Atrichal spherules
b.	spherules armed with basitrichs	Basitrichal spherules
c.	spherules armed with micro- and macrobasic mastigophores	Mastigophoral spherules

The position of a spherule can be on the margin, in the fosse or on the column. A full designation of a spherule of an *Anthopleura* specimen might be 'atrichal marginal spherule', or of one of *Actinia* 'atrichal spherule in the fosse'. Spherules are often armed with more than one type of nematocyst so the name applied is that of the more important or most numerous nematocyst present.

The term 'nematosphere', used to described the bunches of spherules on stalks between the tentacles of *Heterodactyla hemprichi* Ehrenberg, 1834, is retained.

Sphincter muscle. The type of sphincter has been used as a taxonomic character in the tribe Thenaria at various levels, for example:

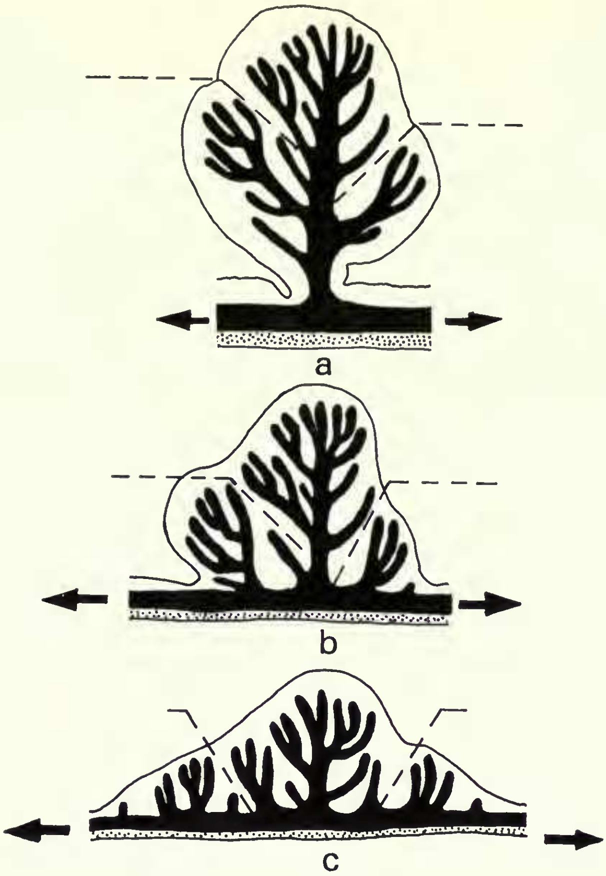

Fig. 2 Variation within a single sphincter due to state of expansion of the crown (diagrammatic). (a) A typical 'circumscribed-pinnate' sphincter. (b) A 'circumscribed-diffuse' sphincter (c) A 'diffuse' sphincter. Arrows indicate directions of expansion, dashed lines divide the sphincter into its elements. (Stippled, endoderm; black, mesogloea; white, endoderm.)

Subtribe level	Genera with endodermal sphincter	Endomyaria
	Genera with mesogloeal sphincter	Mesomyaria
Genus level	To separate genera that might otherwise form one large genus, for example in the Actiniidae:	
	Sphincter circumscribed	*Epiactis*
	Sphincter diffuse	*Entacmaea*
	Sphincter absent	*Phialoba*
Species level	The presence of a strong or a weak sphincter may be used to distinguish species	

In some species the sphincter is consistently of the same type, and unless the specimen is extremely distorted it is of uniform appearance in transverse section. In other species variation is observed as shown below in *Anthopleura dixoniana* (Fig. 18) and *Gyractis excavata* (Fig. 27). The sphincter of *A. dixoniana* varies from circumscribed to diffuse even within a single specimen.

The size and appearance of a sphincter can also differ within a species between one group or colony of individuals and another. Haddon was unaware of this when he proposed two species separated on this character, *Actinioides dixoniana* and *A. papuensis*, of which only one proved valid.

The appearance of a sphincter in transverse section depends on its degree of contraction and on the state of expanison of the crown (Fig. 2). As the crown expands its circumference increases and some mesogloeal folds of the sphincter are drawn outwards into the mesogloea of the margin. When a circumscribed sphincter is involved its main stem (see Fig. 2a) becomes assimilated and the branched folds spread out and become smaller until in the extreme case they are assimilated into the body wall. A striking example of this was seen in an Australian species *Epiactis australiensis* Carlgren, 1950*c* (Fig. 3). The first sections examined, cut parallel with the directive axis, appeared to have several separate sphincters (Fig. 3a), one large and four small. A transverse section taken at an angle of 45° to the first showed some of the smaller sphincters coalescing with the main muscle (Fig. 3b). A section cut at 90° to the directive axis showed all the smaller sphincters absorbed into the main muscle (Fig. 3c). A further change was seen at the next 45° position where the muscle passed through the mesentery (Fig. 3d). The muscle folds have not been drawn since they were completely anastomosed with those of the mesentery, but there were three separate sphincters.

Variation in the appearance of a single sphincter muscle around the margin due to local differences in its degree of contraction suggests that apparently different types of sphincter may prove to be the same. Figure 2 shows how a circumscribed sphincter transforms into a diffuse one. If the circumscribed sphincter is divided into its elements or mesogloeal folds, as indicated by the dashed lines in Figure 2a, the individual parts can be identified in the so-called diffuse sphincter (Fig. 2c). When this model is applied to the sphincters of *Anthopleura dixoniana* (Fig. 18) and *Gyractis excavata* (Fig. 27), each species is shown to have a sphincter which assumes several facies in transverse sections. Similar variation in the sphincter musculature is found in many other species, as for example in *Anthopleura nigrescens* (Fig. 22) and *Mesactinia ganensis* gen. nov., sp. nov. (Fig. 29). If the model in Figure 2 is applied, however, the sphincter muscles can be used at least at species level as a taxonomic character.

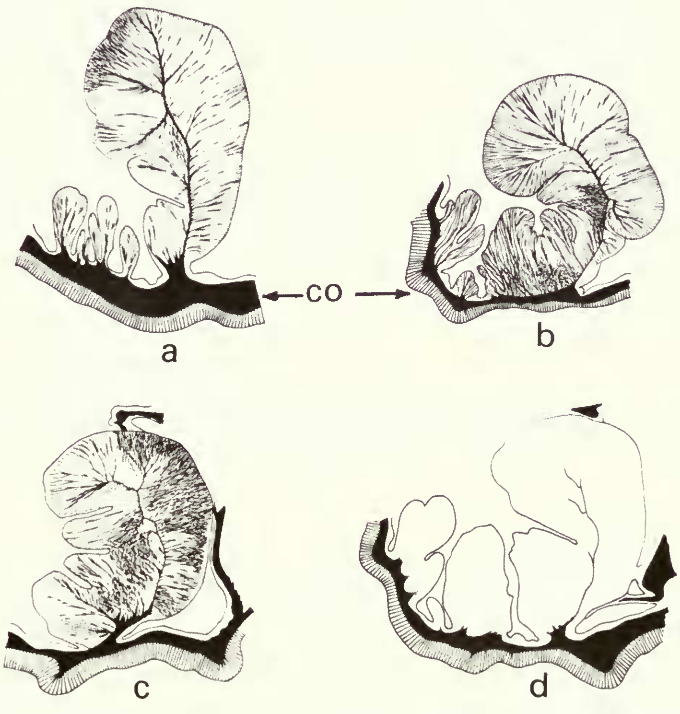

Fig. 3 *Epiactis australiensis*. Vertical sections showing variation of the sphincter in one specimen due to expansion of the crown. (a) At the directive axis, (b) at 45 degrees to the directive axis, (c) at 90 degrees to the directive axis and (d) at 45 degrees to the directive axis where the sphincter passes through the mesentery. (Hatched, ectoderm; black, mesogloea; white, endoderm; co column.)

Mesenterial arrangement. The relation of the number of tentacles, and hence of the number of mesenteries at the disk, to the number of mesenteries at the base is considered to be of generic importance. Three categories are recognized:

a. more mesenteries proximally than distally
b. same number of mesenteries distally as proximally
c. more mesenteries distally than proximally

These categories appear to be clear cut but in practice they intergrade. The mesenteries may develop from the base upwards, as for example in some species of *Anthopleura*, so that there are a few more at the base than at the margin. The reverse is also true, when tentacles and the corresponding mesenteries appear at the margin and grow downwards, as in *Mesactinia ganensis* gen. nov., sp. nov. It is also possible for mesenteries to appear at margin and base simultaneously and grow towards the centre of the column. An equal number of mesenteries may occur distally and proximally in juveniles but later on the number of mesenteries at the base might increase more rapidly than the number of tentacles, resulting finally in a difference of a complete cycle. Some species of sea-anemone have very small mesenteries at the margin and/or at the base, where they are little more than gussets of tissue as for example the microcnemes of *Edwardsia*. Among acontiate anemones *Calliactis polypus* (see England 1971: 25) may have minute mesenteries at both margin and limbus, but there are always more tentacles than basal mesenteries. *Verrillactis paguri* (Verrill, 1869*a*) has more small mesenteries at the limbus than at the margin. It is possible for the mesenteries to appear normally at the margin and grow downwards, but further down the column to develop only into small elevations of tissue, seen in transverse section, to comprise mesogloea covered with endoderm (as in *Mesactinia ganensis* gen. nov., sp. nov., p. 263). Only careful observation, for example by bulk staining of the specimens, will detect their presence (p. 209).

The presence of just a few more mesenteries at margin or base is not considered to be of generic importance and such specimens can be classified under (b). Only when there are at least half a cycle more mesenteries present at margin or limbus should a specimen be referred to categories (a) or (c).

Nematocysts. The types and size-ranges of nematocysts have been used as taxonomic characters from species to family level. Carlgren (1949: 86) used the presence or absence of certain nematocyst types in the acontia to define families, and in many other papers he used their size-range to identify species. Hand (1955, 1956) was the first to illustrate all the cnidome of an individual species. He grouped them according to that part of the specimen from which the different types of nematocysts came (tentacles, column, actinopharynx, filaments and, when appropriate, nemathybomes, spherules and acontia). This method has been adopted here for the following reasons:

a. The diagrams show the shape and structure of the nematocysts found, and obviate confusion over the terms used to name them. Several names now exist for each nematocyst type. For example, a single type has been termed basitrich (Weill, 1934), microbasic b-mastigophore (Cutress, 1955: 128), b-rhabdoid (Schmidt, 1969: 298), and spirula (den Hartog, 1980: 7, after Stephenson, 1928: 62–63).

b. It provides a 'nematocyst signature' of each species which can be used for rapid comparison with the 'signatures' of others. When species belonging to different families and to some extent to different genera are compared, a clear distinction between 'signatures' is usually apparent. Figures 40–42 illustrate generic differences between three acontiate species. But when congeneric species are compared only small differences in the size ratios of the two or three nematocyst types in one part may separate species. Figures 19, 21, 23 and 25 illustrate the closeness of the 'signatures' in four congeneric species. In fact these 'signatures' are so similar that, in the absence of morphological information, they might have been interpreted as coming from a single species.

Taxonomic section

Suborder **NYNANTHEAE** Carlgren, 1898
Subtribe **ATHENARIA (ABASILARIA)** Carlgren, 1898
Family **EDWARDSIIDAE** Andres, 1881
Genus ***EDWARDSIA*** de Quatrefages, 1841

Edwardsia de Quatrefages, 1841: 427.
Scolanthus Gosse, 1853: 153.
Halcampa: Panceri, 1869: 1 (part).

NOMENCLATURE. An application to the International Commission on Zoological Nomenclature to conserve the generic name *Edwardsia* de Quatrefages, 1841, and the family name EDWARDSIIDAE Andres, 1881, was submitted by Williams (1979) and was favourably resolved in Opinion 1294 (*Bulletin of Zoological Nomenclature* 42: 31–33).

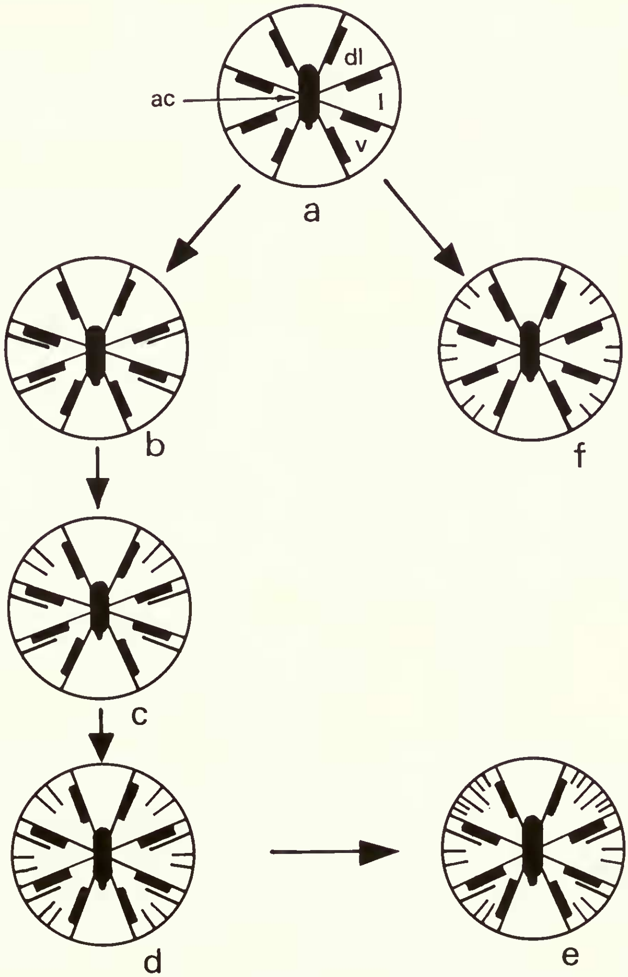

Fig. 4 *Edwardsia*. Development of mesenteries and their relation to the number of tentacles. (a) '*Edwardsia*' stage. (b) 12 tentacle stage. (c) 16 tentacle stage. (d) 24 tentacle stage. (e) 32 tentacle stage. (f) '*pudica*' arrangement, 20 tentacles. (ac actinopharynx, dl dorso-lateral exocoel, l lateral exocoel, v ventral exocoel. Retractor muscles represented as black rectangles; lumen of pharynx not shown.)

TYPE SPECIES. *Edwardsia beautempsi* de Quatrefages, 1842, by designation by Carlgren (1949: 23).

DEFINITION. Edwardsiidae (sensu Carlgren, 1949: 22) with column divided into physa, scapus, scapulus and capitulum; physa short, ampullaceous, without nemathybomes or cuticle. Scapus long with nemathybomes sunk in the mesogloea. *Nemathybomes always containing two types of nematocyst.* Siphonoglyph weak, ventral. Mesenteries comprising eight macrocnemes (perfect) and at least four microcnemes (imperfect) which are very weak and in capitulum only; *first four microcnemes always paired with macrocnemes.* Gonads, filaments, and parietal and retractor muscles on macrocnemes only. Parietal muscles well developed, retractors strong-diffuse to restricted-reniform. Cnidome: spirocysts, basitrichs, pterotrichs, microbasic amastigophores and t-mastigophores.

REMARKS. Fifty-five nominal species were referred to *Edwardsia* by Carlgren (1949) but only about four more have been described since, and some of the original fifty-five have been shown by Manuel (1977) and Williams (1981) to be invalid. Williams recognized 40 valid species, but much literature searching is still necessary before a single species can be confidently identified. The task can be reduced if certain species are eliminated on conspicuous taxonomic characters and placed in other genera. The two characters in question are the presence of one or two types of nematocyst in the nemathybomes, and the pattern of development of the microcnemes.

Carlgren (1921: 28) noticed that one type of nematocyst was present in the nemathybomes of some species of *Edwardsia* and two types in others. He used this character to differentiate between species, although he did not use it in his later survey of the whole order (Carlgren, 1949). Other authors have noted this character without using it taxonomically, though Williams (1981) listed the nominal species of *Edwardsia* under these and other headings.

In this work species with only one type of nematocyst (basitrichs) in the nemathybomes were separated from those with two types (pterotrichs and microbasic t-mastigophores, p. 219). The presence or absence of a type of nematocyst is usually considered to be of generic or higher significance.

The arrangement of the microcnemes is also regarded here as a generic character. Microcnemes develop after the eight macrocnemes in two ways. Normally four arise (Fig. 4a) in the lateral and ventral exocoels and are paired with the ventro-lateral and dorso-lateral couples, and four more arise as two pairs in each dorsal exocoel (Fig. 4b-c)). They correspond to the 16 tentacles. In some species the two pairs of microcnemes do not develop and there are only 12 tentacles instead of 16.

The plan of development may continue with four more pairs of microcnemes arising in the lateral and ventral exocoels, corresponding to 24 tentacles (Fig. 4d). In some species development continues with pairs of secondary microcnemes arising in the dorsal exocoels as well, one pair on each side of the first pair (Fig. 4e). Species with this arrangement have up to 32 tentacles.

Examples of species with each of these arrangements are:

12 tentacles	*E. duodecemtentaculata* Carlgren, 1931
16 tentacles	*E. longicornis* Carlgren, 1921
24 tentacles	*E. carneola* (Verrill, 1928)
32 tentacles	*E. timida* de Quatrefages, 1842

A maximum of 28 tentacles in *E. timida* was recorded by Manuel (1977: 492, Fig. 4), but his illustration shows that microcnemes were absent from the dorsal exocoels, only two pairs of microcnemes occurring there instead of the usual three pairs.

Up to 36 tentacles have been recorded in some species, for example *E. timida* (= *E. callianthus* Rawlinson, 1935) and *E. sipunculoides* (Stimpson, 1853; Carlgren, 1931). In such instances additional pairs of microcnemes occur in the lateral exocoels or, as shown by Stephenson (1935), in the ventral exocoels. Other anomalies are known. One microcneme of a pair may develop before the other resulting in an odd number of tentacles. This has been observed in *E. vivipara* Carlgren, 1950*c*. Dixon (1886) also noted anomalies, in *E. timida*.

The second pattern of development of microcnemes results in a quite different arrangement. After the eight macrocnemes have formed the four single microcnemes do not develop in the lateral and ventral exocoels but six pairs of microcnemes arise, one pair in each exocoel (Fig. 4f). This results in 20 tentacles. It is not yet known whether all microcnemes appear at the same time, as seems probable, or whether they develop in certain exocoels first. This type of arrangement was first noted by Faurot (1895) in *E. adenensis* Faurot, 1895. Bourne (1916) drew attention to it when describing *E. rakaiyae* Bourne, 1916, and discussed a possible interpretation of the sequence of development of the tentacles and micromesenteries. Stephenson (1935: fig. 108A) found that same arrangement in an edwardsiid from Low Island on the Great Barrier Reef. The species was subsequently named *E. stephensoni* by Carlgren (1950*b*), but is here referred to *Edwardsianthus pudica* (Klunzinger, 1877) comb. nov. All recorded specimens of *E. pudica* have six pairs of microcnemes. Similarly, I have examined 57 specimens of *E. gilbertensis* (Carlgren, 1931) and all had six pairs. This arrangement of microcnemes separates the two species *E. pudica* and *E. gilbertensis* from those that develop mesenteries in the normal way.

Table 1 The species of *Edwardsia* de Quatrefrages, 1841.

Species	Number of Tentacles	Nemathybomes arrangement	Dimensions of nematocysts from nemathybomes (µm)	Source of data
E. annamensis Carlgren, 1943	16	rows	41·0–60·6 × 4·2–5·6 42·3–60·6 × 2·0–2·8	Carlgren, 1943: 19
[1]*E. beautempsi* de Quatrefages, 1842	16	rows	39·0–65·0 × 4·5–6·0 45·0–64·0 × 2·5–3·0	Manuel, 1977: 487
E. californica McMurrich, 1913	16	rows	115–153 × 6·3–7·0 72·0–77·0 × 2·5	Carlgren, 1936: 18
E. capensis Carlgren, 1938	18	rows	68.0–86.0 × 5.5–6·0 67·0–72·0 × 2·5	Carlgren, 1938: 19
E. claparedi (Panceri, 1869)	16	rows	97·0–154 × 5·0–7·0 69·0–95·0 × 2·5–3·0	Manuel, 1981: 198; 1977: 487
E. elegans Verrill, 1869*c*	16	rows	67·0–101 × 6·5–7·0 67·0–84·0 × 2·5–3.0	Carlgren, 1931: 16–18
E. hantuensis sp. nov.	16	rows	62·7–105·6 × 4·6–6·6 54·8–68·2 × 2·6	p. 222
[2]*E. ivelli* Manuel, 1975	16	rows	24·0–33·0 × 2·5–3·0 20·0–30·0 × 2·0–3·0	Manuel, 1975: 705–711
E. longicornis Carlgren, 1921	16	rows	36·0–84·0 × 3·5–5·0 36·0–65·0 × 2·0–2·5	Manuel, 1977: 487
E. maroccana Carlgren, 1931	16	rows	131–156 × 6·0 74·0–84·0 × 2·0–2·5	Carlgren, 1931: 15–16
E. octoradiata Carlgren, 1931	16	rows	55·0–79·0 × 3·5–4·0 35·0–43·0 × 2·5	Carlgren, 1931: 13–15
E. sanctaehelenae Carlgren, 1941	12	rows	56·4–81·8 × 5·0–5·6 42·3–49·3 × 2·0–2·5	Carlgren, 1941: 1
E. sulcata (Verrill, 1864)	14–16	rows	84·6–104·3 × 7·0 52·2–67·7 × 4·2	Carlgren, 1950*d*: 22
E. tintrix Annandale, 1915	16	rows	65·0–89·0 × 4.5 46·0–53·0 × 2·0–2·5	Carlgren, 1925: 19
E. tuberculata Düben & Koren, 1847	16	rows	(72)110–190 × 4·0–7·0 60·0–96·0 × 2·5	Carlgren, 1921: 29
E. carlgreni (Carlgren, 1921)	16	scattered	62·0–74·0 × 5·0 36·0–53·0 × 2·5	Carlgren, 1921: 3; see Williams, 1981: 351
E. danica Carlgren, 1921	14–20	scattered	46·0–72·0 × 4·5 24·0–43·0 × 2·0–3·5	Carlgren, 1921: 37
E. novazelanica Farquhar, 1898	16–24	scattered	41·0–56·0 × 3·5–4·5 34·0–41·0 × 2·0	Carlgren, 1924: 184–187 (*E. tricolor* Stuckey, 1908)
E. sipunculoides (Stimpson, 1853)	18–30	scattered	65·0–74·0 × 6·0 41·0–50·0 × 3·5	Carlgren, 1931: 22–23

[1]Type species of genus. [2]possibly *Edwardsioides*.

Using these two characters species whose nemathybomes have only basitrichs, that is, just one type of nematocyst, can be removed from the genus *Edwardsia* and subdivided into two new generic groupings based on the mesenterial arrangements. The species in which relevant data could be found in the literature are listed in Tables 1–3. The generic groupings are given in Figure 5.

Danielssen (1890) introduced the genus *Edwardsioides* to accommodate *E. vitrea* Danielssen, 1890. This is the earliest generic name available for the group comprising those species with only one nematocyst type in the nemathybomes and four microcnemes, paired with four macrocnemes.

The final group (Table 3) comprises those species with one type of nematocyst in the nemathybomes but no microcnemes in the first cycle of mesenteries. The generic name *Edwardsianthus* gen. nov. is proposed here with *Edwardsia pudica* Klunzinger, 1877, as the type species.

Further subdivision of the genera *Edwardsia, Edwardsioides* and *Edwardsianthus* is possible according to whether the nemathybomes are arranged in rows or scattered on the column. Subdivision is unnecessary in *Edwardsianthus* which has only two species and in *Edwardsioides* in which only one out of fourteen species has the nemathybomes arranged in rows. However, the 19 species referred to the genus *Edwardsia* can be divided with some advantage. They fall into two groups, 4

Table 2 The species of *Edwardsioides* Danielssen, 1890.

Species	Number of Tentacles	Nemathybome arrangement	Dimensions of nematocysts from nemathybomes (μm)	Source of data
E. andresi Danielssen, 1890	12	scattered	48·0–67·0 × 3·5–4·0	Carlgren, 1921: 49
E. arctica Carlgren, 1921	16	rows/ scattered	38·0–60·0 × 4·0–5·0	Nemathybomes scattered in proximal part. Carlgren, 1921: 39
E. duodecemtentaculata Carlgren, 1931	12	scattered	33·0–48·0 × 2·5–3·0	Carlgren, 1931: 4
E. finmarchica Carlgren, 1921	26	scattered	36·0–48·0 × 3·0–4·0	Carlgren, 1921: 55
E. fusca Danielssen, 1890	12	scattered	31·0–36·0 × 2·0–2·5	Carlgren, 1921: 28
E. islandica Carlgren, 1921	16	scattered	36·0–48·0 × 2·0–2·5	Carlgren, 1921: 47
E. japonica Carlgren, 1931	16	scattered	74·0–101 × 2·5–3·5	Carlgren, 1931: 12
E. kameruniensis Carlgren, 1927	20	scattered	45·0–63·0 × 3·5–4·5	Carlgren, 1927: 478
E. meridionalis Williams, 1981	16(18)	scattered	29·0–50·7 × 2·6–4·7	Williams, 1981: 325
E. norvegica Carlgren, 1942	16	scattered	47·0–58·0 × 3.0	Carlgren, 1942: 60
E. timida de Quatrefages, 1842	32	scattered	32·0–75·0 × 3·5–7·0	Manuel, 1977: 491
E. vegae Carlgren, 1921	16	scattered	84·0–100 × 3·0	Carlgren, 1921: 53
[1] *E. vitrea* Danielssen, 1890	16	scattered	36·0–42·0 × 3·0–3·5	Carlgren, 1921: 49
E. vivipara Carlgren, 1950*c*	16	scattered	26·8–38·1 × 3·5–4·5	Carlgren, 1950*c*: 1
E. jonesi Seshaiya & Cutress, 1969	12	rows	48·0–72·0 × 4·5–5·5	Seshaiya & Cutress, 1969: 73

[1]Type species of genus.

Table 3 The species of *Edwardsianthus* gen. nov.

Species	Number of Tentacles	Nemathybome arrangement	Dimensions of nematocysts from nemathybomes (μm)	Source of data
[1] *E. pudica* Klunzinger, 1877	20	scattered	37·0–44·0 × 2·5	Carlgren, 1931: 18–21 (see p. 227)
E. gilbertensis Carlgren, 1931	16–20	rows	31·0–41·0 × 2·0–3·0	Carlgren, 1931: 10–11

[1]Type species of genus.

species having the nemathybomes scattered on the column and 15 species having them in rows. This division has not been formalized here because it may be advantageous to subdivide the genus at a later date on a different character, namely the types of nematocyst in the nemathybomes (see p. 219).

Species of *Edwardsia* listed by Carlgren (1949: 23–24) and other authors but not included here have been omitted either because they have been shown to be conspecific with the species listed or because insufficient data is available to make it possible to place them in one of the three genera proposed. Williams (1981) listed all species referred to the genus *Edwardsia* with comments on their validity and synonyms.

EDWARDSIIDAE

With nemathybomes sunk in the mesogloea of scapus, physa present

- One type of nematocyst in nemathybomes
  - Four microcnemes of first cycle paired with macrocnemes — *Edwardsioides* Danielssen, 1890
  - Microcnemes of first cycle absent — *Edwardsianthus* gen. nov.
- Two types of nematocyst in nemathybomes
  - Four microcnemes of first cycle paired with macrocnemes — *Edwardsia* Quatrefages, 1841

Fig. 5 Edwardsiidae. Distinctions between the genera *Edwardsia, Edwardsioides* and *Edwardsianthus* gen. nov.

Nematocyst types in the nemathybomes of Edwardsia. Manuel (1977: 488, Fig. 2) illustrated two types of nematocyst that he termed microbasic b-mastigophores from *E. beautempsi*, and two other types from *E. timida*. The types illustrated under *E. beautempsi* were not identical, but were similar to those described by Carlgren (1940*a*: 23, Fig. V, figs 7–8, 12–13) from *E. longicornis*. One type of nematocyst (Manuel 1977, Fig. 2E) differs from the normal b-mastigophore (or basitrich) in that the armature of the thread can be divided into four distinct regions. A similar nematocyst has been studied, both discharged and undischarged, from specimens referred to *E. tuberculata* Düben & Koren, 1847: 267, from off Rame Head, South Devon (Fig. 6a-c). The basal part of the thread is folded and bears a few short pointed spines arranged spirally, corresponding to Schmidt's 'faltstuck' (Schmidt 1969: 294, Fig. 5). Then follows a length of thread with a feature so far unique in nematocyst morphology (Fig. 6b). It is a heavily armed portion having many thick close-set spines that are not arranged spirally around the thread but lie in three rows along it. They recall in appearance the flight feathers of an arrow (Fig. 6b), rather than conforming to Carlgren's impression of a membrane. Above this extraordinary region there are a few large spines arranged spirally, reducing sharply in size to those of the longest and distalmost part of the thread which is armed with minute spines arranged spirally throughout its length. The basal part of the thread is no more than $1\frac{1}{2}$ times wider in diameter than the remainder. This nematocyst type, therefore, incorporates features of both haplonemes and mastigophores. Shaft and thread are of nearly the same diameter, resembling the basitrich in morphology, but a 'faltstuck' is present and the spines are set close together as in the mastigophore. The undischarged capsule resembles in appearance that of a basitrich, apart from the folded part of the thread near the tip of the capsule. The straight part of the thread, in the undischarged capsule, does not show evidence of the spines except at the bottom, but has a thin line running along its length in the centre. The bottom of the capsule contains most of the coiled part of the thread, only a small section of the thread extending into the upper part, as a loose loop (Fig. 6a). The armature of the coiled thread is clearly visible.

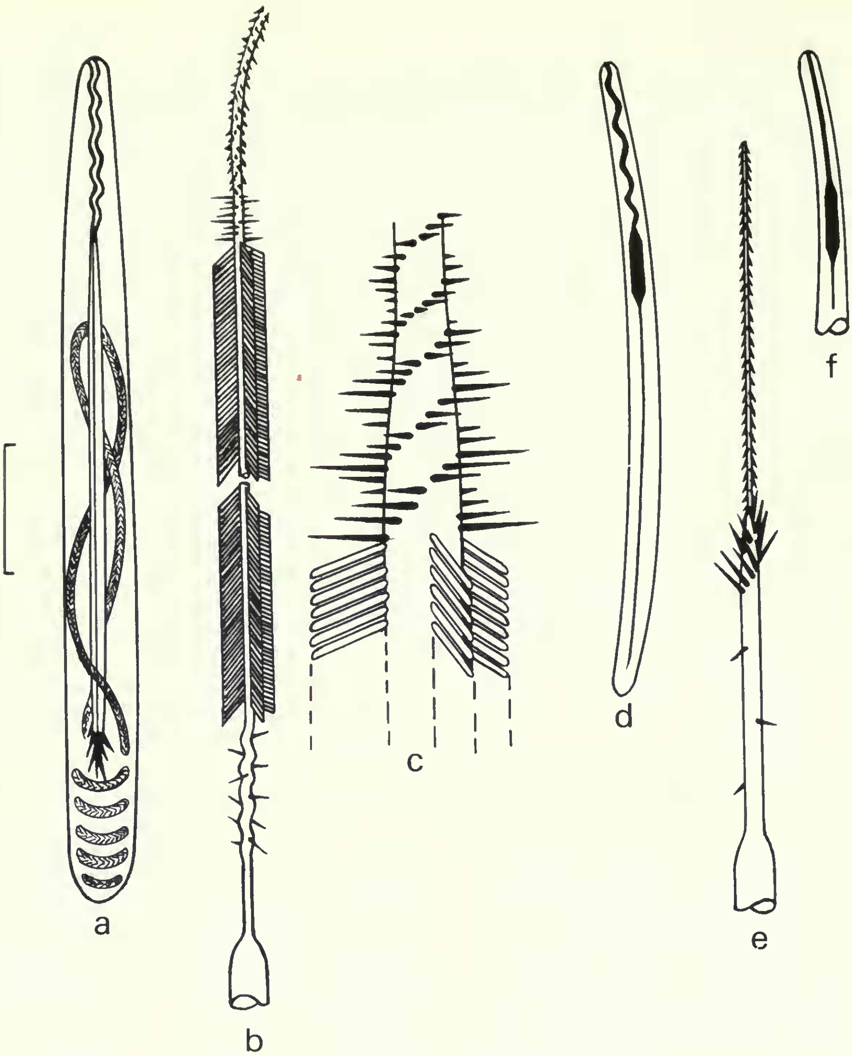

Fig. 6 Nematocysts of the nemathybomes of *Edwardsia tuberculata* (diagrammatic). (a) Undischarged pterotrich. (b) Discharged thread of same, showing types of spines and their arrangements on the thread. (c) Part of same enlarged. (d) Undischarged microbasic telotrichous mastigophore (t-mastigophore), with folded shaft. (e) Part of same, discharged, showing position of large spines at the head of the shaft. (f) Part of same showing alternative, unfolded shaft, undischarged. Scale: (a,d) = 20 μm, remainder not to scale.

Since the lower part of the thread is only slightly wider than the remainder, and because the undischarged capsule resembles a basitrich more than a mastigophore, I propose to classify this nematocyst type among the haplonemes. The name 'pterotrich' is suggested. The undischarged capsule can be recognised from the 'faltstuck' and the few large protruding spines at the end of the straight portion of the thread.

The other type of nematocyst (Carlgren 1940*a* Fig. V, figs 7–8; Manuel 1977, fig. 2F) is a mastigophore in that when discharged it shows a definite shaft with parallel sides and a distinct thread (Fig. 6d-f). The diameter of the shaft is some four times that of the thread, not with shaft and thread of the same diameter as illustrated by Carlgren. It cannot, however, be classified as a b-mastigophore since the shaft has spines only at the forward end (Fig. 6e). Although the discharged capsule resembles Weill's (1934) microbasic euryteles there is no swelling at the end of the shaft and before discharge the capsule resembles rather a basitrich with a thickened portion in the centre of the straight part of the thread. Weill might possibly have termed this nematocyst a microbasic telotrichous mastigophore, for which the shortened form microbasic t-mastigophore is proposed.

Manuel (1977, figs 2G-H) illustrated two nematocysts of one type from the species *E. timida* which appear to be basitrichs, but from his illustrations it is not possible to be certain. If the two nematocysts are the same and two clearly defined size ranges are present then the nematocysts of this species differ from those of other *Edwardsia* species and a new genus would be appropriate to accommodate *E. timida*. Alternatively, if all nematocysts from the nemathybomes fall into a single range then the species might be transferred to the genus *Edwardsioides*. The figures quoted by Manuel (1977: 491) suggest that the species should be so referred. Other species currently included in *Edwardsia* (Table 2) may also present the same problem, the size-ranges of nematocysts overlapping in both length and diameter, for example *E. ivelli* Manuel, 1975: 705–711.

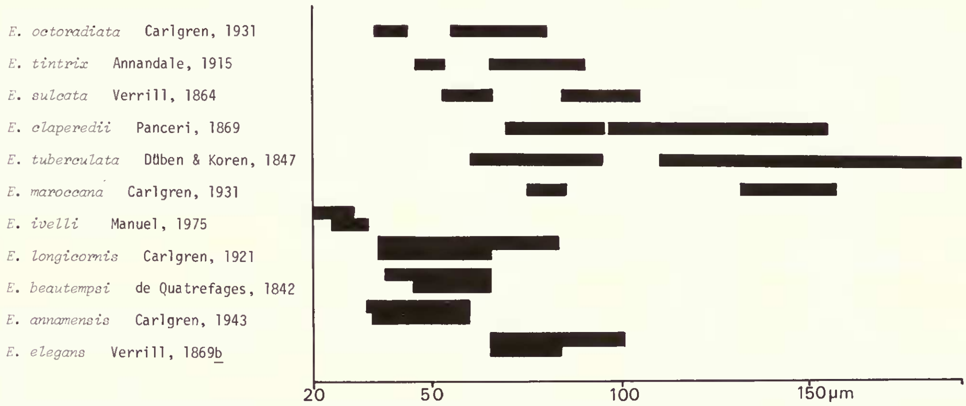

Fig. 7 Comparison of nematocyst size ranges in nemathybomes of certain edwardsiids. (Sources of data as in Table 1.)

A bar chart (Fig. 7) of the size ranges of nematocysts in the nemathybomes of species of *Edwardsia* shows an interesting variation. In certain species the two size ranges are distinct (*E. claparedi*, *E. tuberculata*), whereas in others the two ranges overlap (*E. beautempsi*, *E. longicornis*). These species are cited since the types of nematocyst in their nemathybomes are well known. It is too early to say if there is any significance in this variation, but it will at least assist in identifying species of *Edwardsia*.

Edwardsia hantuensis sp. nov.
Figs 8–9

MATERIAL EXAMINED. Singapore: Pulau Hantu, 1 specimen, 19 Sep 1970, BMNH 1983.4.8.1. Size in spirit 30 mm high, 5 mm wide.

DESCRIPTION. *External appearance.* Column divided into physa, scapus, scapulus and capitulum. Scapus with eight rows of large prominent nemathybomes and an easily removed cuticle. Near scapulus nemathybomes close together but towards physa further apart. Tentacles up to 16, long, smooth, tapered. *Anatomy.* Eight macrocnemes and up to eight microcnemes in typical *Edwardsia* manner. Retractors strong, diffuse, with 25–28 muscle processes, some branched, arising from mesogloeal sheet (Fig. 8a). Parietal muscles large, well developed, on both sides of mesogloea,

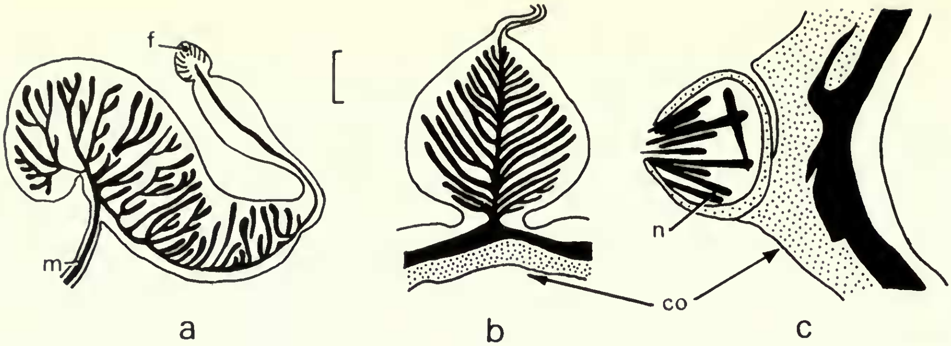

Fig. 8 *Edwardsia hantuensis* sp. nov. BMNH 1983.4.8.1. Transverse sections of (a) retractor muscle, (b) parietal muscle, (c) nemathybome. Scale: (a-c) = 50 µm. (co column, f filament, m mesentery, n nematocysts. Stippled, ectoderm; black, mesogloea; white, endoderm.)

cross-sectional area nearly half that of main retractor in same area of column (Fig. 8b). Microcnemes small. Nemathybomes (Fig. 8c) large, with both pterotrichs and microbasic t-mastigophores (p. 223, Fig. 9). Physa without a central pore but many cinclides present near tip of each exocoel. *Cnidome*. See Table 4 and Figure 9. The size ranges of the nematocysts of the nemathybomes are the overall ranges. The pterotrichs in the nemathybomes nearest the scapulus are smaller than those of the nemathybomes near the physa. For example, 62·7–75·8 × 4·0–5·3 µm near scapulus, 92·4–105·6 × 5·3–6·6 µm near physa. *Colour*. Column light sienna, nemathybomes white.

RECORDED DISTRIBUTION. Recorded only from Singapore (present material).

Table 4 Size ranges of cnidae of *Edwardsia hantuensis* sp. nov. compared with those reported from *E. sulcata* (Verrill) and *E. elegans* Verrill (in µm).

Location/ type of cnida	*E. hantuensis* sp. nov. Singapore (BMNH 1983.4.8.1)	*E. sulcata* (Verrill) Massachusetts from Carlgren, 1950*d*: 23	*E. elegans* Verrill Maine from Carlgren, 1931: 16
Tentacle			
Spirocyst	11·8–18·9 × 1·8–3·5	...	...
Basitrich	10·6–23·6 × 1·5	21·0–26·3 × 2·8–3·5	17(19)–29(31) × 2·5–3·0
Capitulum			
Basitrich	10·6–11·8 × 1·8	...	...
Nemathybome			
Pterotrich	62·7–105·6 × 4·6–6·6	84·6–104·3 × 7·0	67·0–101 × 6·5–7·0
Microbasic t-mastigophore	54·8–69·2 × 2·6	52·2–67·7 × 4·2	67·0–84·0 × 2·5–3·0
Actinopharynx			
Basitrich	11·8–26·0 × 2·0–3·5	...	12·0–16·0 × 1·5 29·0–36·0 × 2·5(3)
Microbasic amastigophore	26·0–30·7 × 5·8–7·0	...	29·0–31·0 × 5·0
Filament			
Basitrich	12·0–17·7 × 2·4	...	...
Basitrich	17·7–22·4 × 3·5	19·0–22·6 × 2·5–2·8(3·5)	...
Microbasic amastigophore	18·9–23·6 × 4·1–5·8	24·0–28·2 × 4·5–7·0	...
Microbasic p-mastigophore	21·2–28·3 × 3·5–4·1		

HABITAT. On reef flats in sand, Mean Low Tide Level (MLTL).

REMARKS. The presence of nemathybomes with both pterotrichs and microbasic t-mastigophores places this species in the genus *Edwardsia*.

The characters of this species are similar to those of *Edwardsia sulcata* (Verrill, 1864) sensu Carlgren, 1950*d*: 22, and *E. elegans* Verrill, 1869*c*. However, there are some differences in the

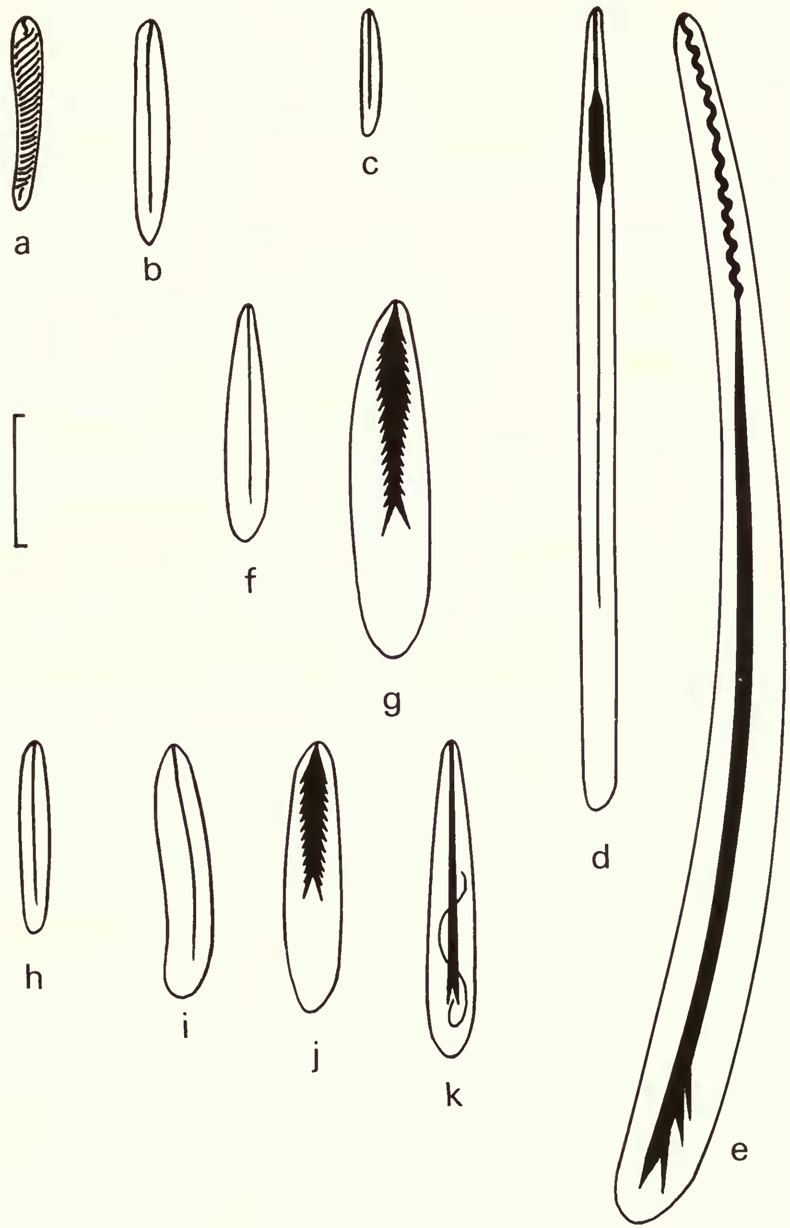

Fig. 9 *Edwardsia hantuensis* sp. nov., nematocyst signature (see Table 4). *Tentacle* (a) spirocyst, (b) basitrich. *Capitulum* (c) basitrich. *Nemathybome* (see Fig. 6) (d) microbasic t-mastigophore, (e) pterotrich. *Actinopharynx* (f) basitrich, (g) microbasic amastigophore. *Filament* (h-i) basitrichs, (j) microbasic amastigophore, (k) microbasic p-mastigophore. Scale: (a-k) = 10 µm.

nematocyst size ranges between these two species and the present material (see Table 4 for comparison). The large difference between the size ranges of the pterotrichs at top and bottom of the column may also be significant. Such differences have not been described before, as far as can be ascertained, and investigations into possible differences within specimens of other species are required.

The present material is, therefore, provisionally referred to a new species, *Edwardsia hantuensis* sp. nov.

Genus *EDWARDSIOIDES* Danielssen, 1890

Edwardsioides Danielssen, 1890: 100, pl. 5, fig. 3; pl. 16, figs 4–10.
Edwardsia: Carlgren, 1921: 28, 39, 43, 47, 53, 55; Carlgren, 1927: 478; Carlgren, 1931: 4–7, 12–13; Carlgren, 1942: 60; Carlgren, 1950*c*: 1; Seshaiya & Cutress, 1969: 73; Manuel, 1977: 491; Williams, 1981: 325.

DEFINITION. Body divisible into physa, scapus, scapulus and capitulum; physa short, without nemathybomes or cuticle. Scapus long with nemathybomes sunk in mesogloea and *containing only one type of nematocyst, basitrichs.* Siphonoglyph weak, ventral. Mesenteries: eight perfect (macrocnemes) and at least four imperfect (microcnemes) which are minute and usually confined to region of capitulum. *First four microcnemes always paired with macrocnemes.* Gonads, filaments, and parietal and retractor muscles on macrocnemes only. Parietal muscles well developed: retractors strong-diffuse to restricted-reniform. Cnidome: spirocysts, basitrichs, and microbasic amastigophores.

TYPE SPECIES. *Edwardsioides vitrea* Danielssen, 1890: 100, by present designation.

REMARKS. No specimen of this genus was found in the collection, but material of *E. vivipara* Carlgren (1950*c*: 1–2, fig. 1) from South Australia has been examined and the type of nematocyst in the nemathybomes in that species confirmed as a basitrich.

Genus *EDWARDSIANTHUS* nov.

Edwardsia: Klunzinger, 1877: 80; Faurot, 1895: 121; Carlgren, 1900: 46; Bourne, 1916: 517–518; Carlgren, 1931: 7; Carlgren, 1950*b*: 428, (part).
Edwardsiella Andres, 1883: 305 (part).

DEFINITION. Body divisible into physa, scapus, scapulus and capitulum; physa short, without nemathybomes or cuticle. Scapus long with nemathybomes sunk in mesogloea; cuticle present. Nemathybomes having only one type of nematocyst, basitrichs. Tentacles usually 20. Siphonoglyph weak, ventral. Eight perfect mesenteries (macrocnemes) and six pairs of imperfect mesenteries (microcnemes), minute and restricted to distal part of column. Imperfect mesenteries never paired with perfect mesenteries. Gonads, filaments, and parietal and retractor muscles on macrocnemes only. Parietals well developed; retractors strong-diffuse to restricted-reniform. Cnidome: spirocysts, basitrichs, microbasic amastigophores.

TYPE SPECIES. *Edwardsia pudica* Klunzinger, 1877, by original designation.

Edwardsianthus pudica (Klunzinger, 1877) comb. nov.
Figs 10–12

Edwardsia pudica Klunzinger, 1877: 80, pl. 6, fig. 3; Carlgren, 1931: 18–20, figs 16–17.
Edwardsiella pudica Andres, 1883: 309; Carlgren, 1900: 46, pl. 1, fig. 5.
Edwardsia adenensis Faurot, 1895: 121, pl. 6, fig. 5, pl. 7, fig. 6, text-figs 8–9.
?*Edwardsia vermiformis* Bourne, 1916: 517, pl. 51, fig. 3.
Edwardsia rakaiyae Bourne, 1916: 518, pl. 51, fig. 4, text-fig. 1.
Edwardsia bocki Carlgren, 1931: 7–9, figs 5–6.
Edwardsia stephensoni Carlgren, 1950*b*: 428–429, figs 1–2.

MATERIAL EXAMINED. Singapore: Pulau Jong, 1 specimen, 17 May 1970, BMNH 1983.4.8.2; Pulau Hantu, 2 specimens, 19 Sep 1970, BMNH 1983.4.8.3–4; Pasir Panjang, 1 specimen, 23 Feb 1971, BMNH 1983.4.8.5. Aden: below Jebel Hadid, 5 specimens, Aug 1966, BMNH 1983.4.8.6–9.

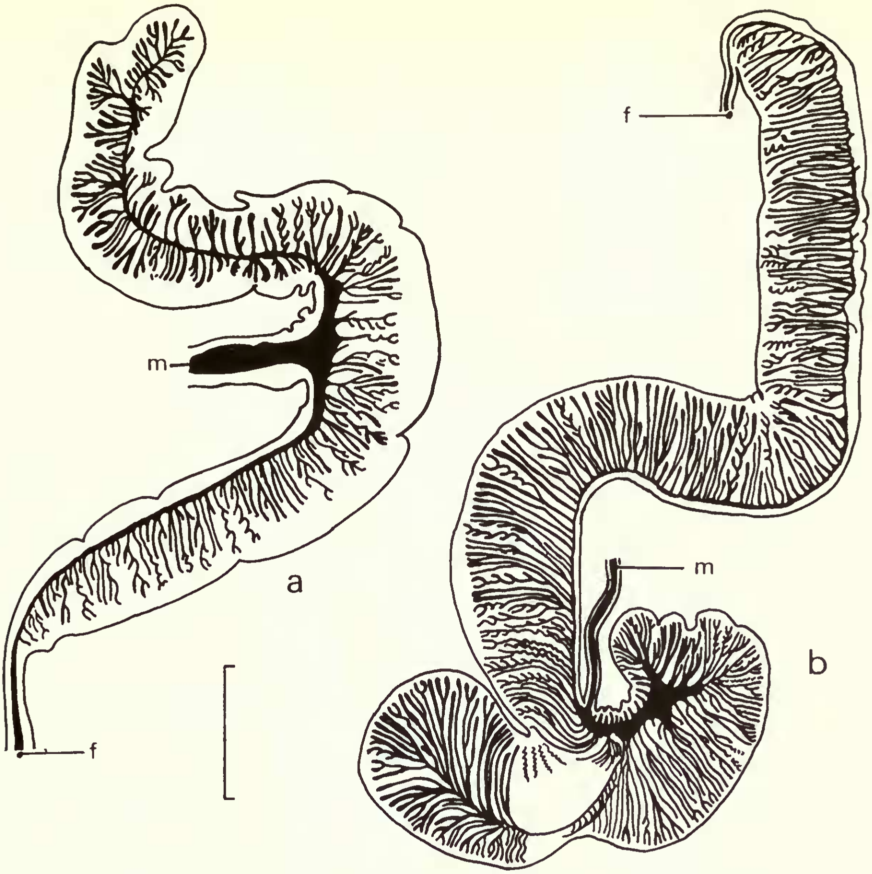

Fig. 10 *Edwardsianthus pudica* comb. nov. Variation in size and development of retractor muscles seen in transverse sections of two specimens: (a) Aden, BMNH 1983.4.8.6; (b) Singapore, BMNH 1983.4.8.3. Scale: (a-b) = 500 µm. (f filament, m mesentery, black, mesogloea; white, endoderm.)

Madagascar, 3 part specimens, Thomassin coll., Museum National d'Histoire Naturelle, Paris. Great Barrier Reef: *Edwardsia stephensoni* (syntypes), 3 specimens, BMNH 1954.6.28.3–4,6. In addition a specimen was seen alive on Gan Island, Addu Atoll, Maldives, March 1970, but not collected.

Description. Height up to 200 mm, diameter up to 15 mm. Divisions of column distinct. Capitulum thin walled, translucent, mesenteries within clearly visible in life; scapulus thin walled, lacking nemathybomes and cuticle, scapus thick walled, cuticle easily removed, with numerous small nemathybomes scattered irregularly over its length becoming most numerous towards physa, physa thin walled, lacking nemathybomes or terminal pore but having cinclides which are mostly endodermal evaginations; ectodermal suckers or tenaculi occasionally present (Fig. 11c). Tentacles up to 20, in two cycles 8, 12; long, slender, tapered. Mouth raised on cone. *Anatomy*. Eight macrocnemes arranged according to *Edwardsia* plan, one pair of microcnemes in each of the six exocoels. Microcnemes extremely small; having appearance of a pair of lips. In sections musculature comprising a single vertical layer of fibres over the complete surface. Microcnemes not extending below capitulum. Macrocnemes with both retractor muscles and parietal muscles well developed (Figs 10a-b, 11a-b); in sections retractors (Figs 10a-b) diffuse, with numerous closely packed high muscle folds, branched and unbranched, sometimes arranged in a pattern of several unbranched folds together, followed by one or sometimes 2-3 branched folds with a series

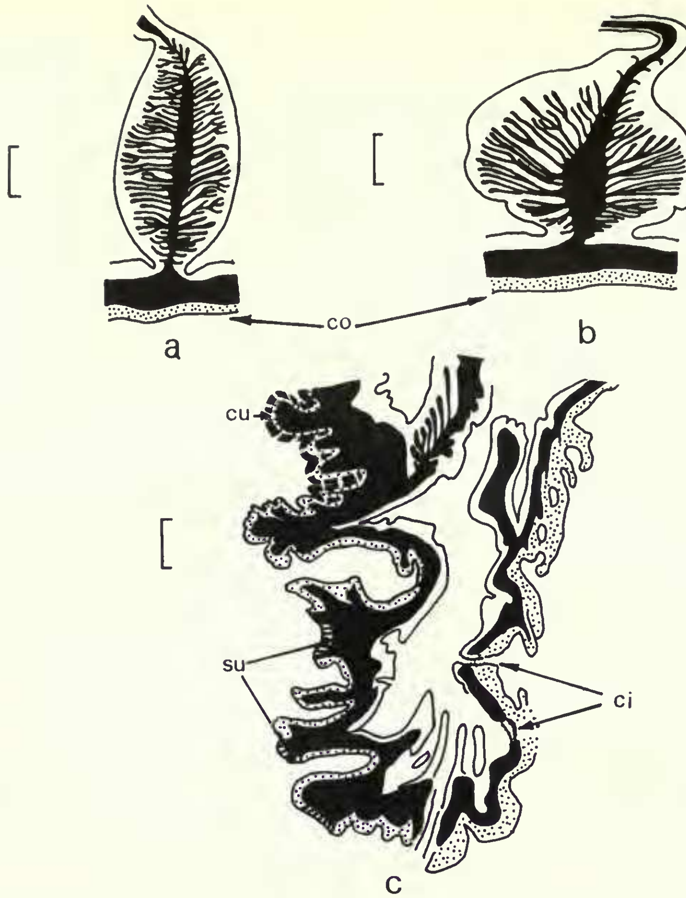

Fig. 11 *Edwardsianthus pudica* comb. nov. (a) Transverse section of parietal muscle, Aden, BMNH 1983.4.8.6; (b) Transverse section of parietal muscle, Singapore, BMNH 1983.4.8.3; (c) Vertical section through physa, Aden, BMNH 1983.4.8.6. Scale: (a-b) = 100 μm, (c) = 250 μm. (ci cinclides, co column, cu cuticle, su suckers. Barred, cuticle; stippled, ectoderm (modified at suckers); black, mesogloea; white, endoderm.)

of small curved off-shoots. Near column wall retractor is circumscribed, that is developing on both sides of extended mesogloeal sheet (Figs 10a,b). This part of mesogloeal sheet continuous with that of mesentery and sometimes itself branched (Fig. 10b). Parietal muscles well developed equally on each side of mesentery (Fig. 11a-b). Macrocnemes fertile, species apparently dioecious. Longitudinal muscles of tentacles ectodermal with short unbranched folds. Zooxanthellae present in endoderm of disk, tentacles, capitulum and actinopharynx. *Cnidome*. See Table 5 and Figure 12. *Colour*. Column light sienna, nemathybomes white. Capitulum delicate translucent purple to white. Tentacles of two colour varieties (a) delicate magenta-pink with thin purple line running from white tip to disk, (b) light-green with thin orange line. Disk white to cream.

DISTRIBUTION. Recorded from the Red Sea (Klunzinger, 1877), Aden (Faurot, 1895, as *E. adenensis*, and present material), Zanzibar (Carlgren, 1931), the Maldives, Singapore (present material), Papua New Guinea (Bourne, 1916 as *E. rakaiyae* and possibly as *E. vermiformis*), Fidschi Island (Carlgren, 1931 as *E. bocki*) and the Great Barrier Reef (Carlgren, 1950*b*, as *E. stephensoni*).

HABITAT. MLTL on reef flats or shores, in coarse or muddy sand.

Table 5 Size-ranges of cnidae of *Edwardsianthus pudica* comb. nov. (in µm).

Location/ Type of cnida	Localities of specimens				
	Singapore (BMNH 1983.4.8.3)	Singapore (BMNH 1983.4.8.4)	Aden (BMNH 1983.4.8.7)	Aden (BMNH 1983.4.8.9)	*E. stephensoni* Low Isle (BMNH 1954.6.28.3)
Tentacle					
Spirocyst	9·4–18·9 × 1·7–3·0	10·6–17·1 × 1·7–3·5	11·8–20·0 × 1·7–3·6	11·8–21·2 × 1·7–3·0	13·3–23·8 × 2·6–3·0
Basitrich	14·2–29·5 × 2·5–3·0	8·2–27·1 × 1·7–2·4	14·2–23·6 × 1·7–2·4	11·8–27·1 × 2·4	14·0–29·6 × 2·2–3·5
Capitulum					
Basitrichs	...	10·6–11·8 × 1·7	...	10·6–13·0 × 2·4	12·0–17·9 × 2·6
Nemathybome					
Basitrich	41·3–52·0 × 3·0	35·4–41·3 × 3·0–3·5	42·5–49.6 × 2·4–3·0	44·8–55·4 × 2·5–3·0	36·0–46·5 × 2·8–3·0
Actinopharynx					
Basitrich	17·7–43·7 × 2·5–3·5	11·8–30·7 × 1·7–3·0	17·7–28·3 × 1·7–3·5	14·2–33·0 × 4·1–5·3	11·3–33·0 × 2·6–3·3
Microbasic amastigophore	31·9–37·8 × 5·8–7·0	20·1–30·7 × 4·7	29·5–30·7 × 5·8–8·2	28·3–33·7 × 4·1–5·3	23·2–29·8 × 4·0–4·6
Filament					
Basitrich	13·0–33·0 × 1·7–3·0	11·8–33·0 × 2·5–3·0	11·8–27·1 × 1·7–3·5	16·5–31·8 × 1·7–3·0	12·7–31·7 × 2·8–3·3
Basitrich	31·0–40·1 × 4·7–5·8	27·1–35·4 × 2·5–3·0	21·2–30·7 × 3·0–4·1	27·1–33·0 × 3·0–3·5	30·4–39·0 × 3·5–4·5
Microbasic amastigophore	26·0–31·9 × 5·8–7·0	22·4–27·1 × 5·2–5·8	18·9–24·8 × 4·7–5·8	22·4–28·3 × 4·1–4·7	22·6–32·4 × 4·2–6·0

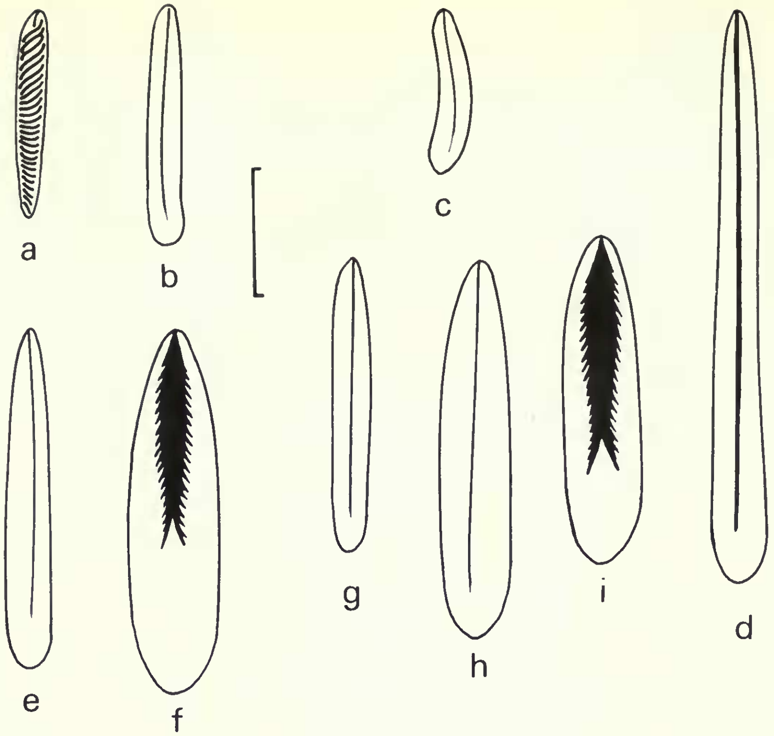

Fig. 12 *Edwardsianthus pudica* comb. nov., nematocyst signature (see Table 5). *Tentacle* (a) spirocyst, (b) basitrich. *Capitulum* (c) basitrich. *Nemathybome* (d) basitrich. *Actinopharynx* (e) basitrich, (f) microbasic amastigophore. *Filament* (g-h) basitrichs, (i) microbasic amastigophore. Scale: (a-i) = 10 μm.

REMARKS. Five specimens from Aden resembled *Edwardsia pudica* Klunzinger, 1877, and *sensu* Carlgren (1900, 1931). That is, they had scattered small nemathybomes over the whole scapus containing only one type of nematocyst, and also 20 tentacles, corresponding to eight macrocnemes and six pairs of microcnemes, an arrangement unique in this genus. The three Singapore specimens were smaller and more delicate than those from Aden, but they had better developed retractor muscles in that the free edge of the retractor had a branched fold: however, this is a difference in degree (Fig. 10b). No other differences were found and since the other characters were similar, the specimens were referred to the present species.

The mesenterial arrangement is unusual in that it does not follow the usual development to the simple *Edwardsia* stage (p. 215). Other nominal species having this arrangement are *E. gilbertensis* Carlgren, 1931, *E. stephensoni* Carlgren, 1950*b* and *E. bocki* Carlgren, 1931. *E. gilbertensis* would seem valid since its nemathybomes are arranged in eight rows and the retractors poorly developed in contrast to the arrangements in *E. pudica*. The descriptions of both *E. stephensoni* and *E. bocki* closely resemble that of *E. pudica* suggesting that the three are conspecific. In the first two of these nominal species the retractors of the macrocnemes as illustrated by Carlgren are strong and well developed and the individual muscle folds follow the same plan as in *E. pudica*. That is, there are several unbranched folds followed by one or more branched folds, the pattern repeating itself along the muscle. The nemathybomes in both species are small, and scattered over the scapus. Also, the nematocysts are of the same type and have the same size range as in *E. pudica*. Carlgren did not record the presence of microbasic amastigophores in the actinopharynx, though they were scarce. The only description of *E. bocki* was made before nematocysts had been classified. *E. stephensoni* is conspecific with *E. pudica* and so apparently is *E. bocki*.

Two of the five nominal species described by Bourne (1916) from Papua New Guinea appear similar to *E. pudica*. These are *E. vermiformis* and *E. rakaiyae*. Bourne stated: '*E. vermiformis* . . . the muscle banners which were evidently large, with complicated, much branched folds . . . characteristic edwardsian structures (nemathybomes) are scattered over the areas between the longitudinal grooves of the scapus'. '*E. rakaiyae* . . . micromesenteries . . . 12 in number, two each sulco-lateral, lateral, or sulculo-lateral inter-mesenterial spaces'. Although Bourne's illustrations are inadequate for identification, his descriptions clearly include characters of *E. pudica*. Bourne himself suggested that *E. vermiformis* was similar to Klunzinger's figure, but without looking at the tentacles, disk and actinopharynx of the specimen it would be difficult to be certain. The well developed retractor muscle of *E. pudica* is the largest known of any *Edwardsia* species. Therefore, the presence of much branded mesogloeal folds of the retractors and the nemathybomes scattered over the column indicate that *E. vermiformis* might be referred to *E. pudica*.

From the details given by Bourne of *E. rakaiyae* there is little doubt that the species is identical with *E. pudica*. The presence of pairs of microcnemes between the main mesenteries, the 20 tentacles arranged 8 + 12, the enormously developed retractors, and the nemathybomes scattered over the column, are all diagnostic. Hence *E. rakaiyae* is referred to *E. pudica*.

A search for Bourne's material was made by R.L. Manuel at Oxford University but only one of his original slides, of *E. mamillata*, was found. *E. mamillata* seems not closely related to *E. pudica* since the retractor muscle is very weak. If the material were found it might still be possible to identify the species from the nematocysts in the nemathybomes and the arrangement of mesenteries.

Genus ***SCOLANTHUS*** Gosse, 1853.

Scolanthus Gosse, 1853: 157; Manuel, 1981: 266.
Edwardsia: Gosse, 1860: 254; Fischer, 1888: 22; Carlgren, 1931: 2.
Isoedwardsia Carlgren, 1921: 56; Carlgren, 1949: 24.
Alfredus Schmidt, 1979: 212.

Definition. Edwardsiidae with column divided into capitulum, scapulus and scapus. Proximal part of body rounded and like rest of scapus with nemathybomes scattered or in rows. Scapus with more or less well developed cuticle. Tentacles 16—20. Siphonoglyph ventral, feebly developed. Mesenteries, retractors and parietal muscles as in *Edwardsia*. Ciliated tracts of filament sometimes discontinuous. Cnidome: spirocysts and basitrichs; possibly also microbasic amastigophores in one species.

Type Species. *Scolanthus callimorphus* Gosse, 1853: 159, by monotypy.

Remarks. Manuel (1981) suggested that species having microbasic amastigophores and once referred to the genus *Isoedwardsia*, itself referred to *Scolanthus*, should be placed in a separate genus. The presence or absence of a type of nematocyst is usually considered to be a character of generic or higher importance. Certainly *S. armatus* (see below) does not have microbasic amastigophores and, from published data on the six species of *Isoedwardsia* originally included, only *I. nidarosiensis* Carlgren, 1942: 61, has this type of nematocyst. The descriptions of the other species were published between 1920 and 1931 at a time when Carlgren and other workers did not differentiate between types of nematocysts. *I. nidarosiensis* is provisionally referred to *Scolanthus* until the type specimen can be re-examined.

Scolanthus armatus (Carlgren, 1931) comb. nov.
Figs 13–14

Edwardsia armata Carlgren, 1931: 2–4, figs 1–2; Carlgren, 1949: 24.

Material Examined. Singapore: Pulau Hantu, 2 specimens, 19 Sept 1970; Pasir Panjang and Pungol Point, 1 specimen each location, 11 Feb 1971, BMNH 1983.4.8.10–13. Great Barrier Reef: Three Isles, 1 specimen, University of Queensland Expedition, 1973.

Description. Column divided into capitulum, scapulus and scapus. Proximal end of scapus

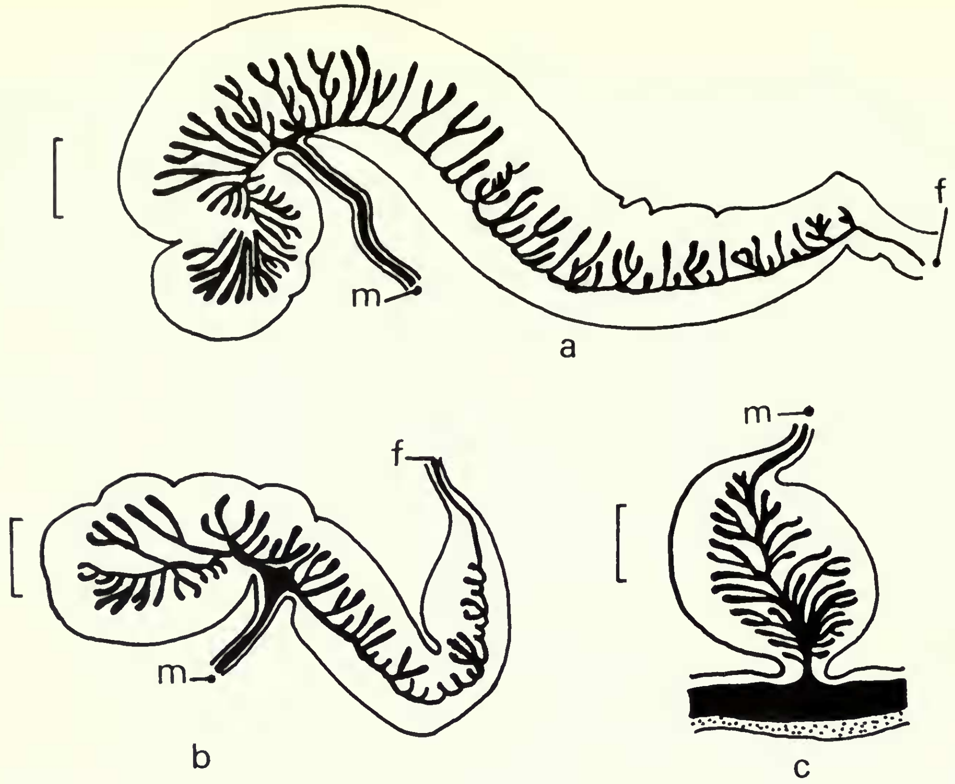

Fig. 13 *Scolanthus armatus* comb. nov. (a-b) Transverse section of retractor muscles, BMNH 1983.4.8.10–11. (c) Same specimen as (a), transverse section of parietal muscle. Scale: (a) = 100 µm, (b) = 20 µm, (c) = 40 µm. (m mesentery, f filament, Stippled, ectoderm; black, mesogloea; white, endoderm.)

Table 6 Size ranges of cnidae of *Scolanthus armatus* comb. nov. (in µm).

	Localities of specimens			
Location/ Type of cnida	Singapore (BMNH 1983.4.8.10)	Singapore (BMNH 1983.4.8.11)	Singapore (BMNH 1983.4.8.13)	Fiji *Edwardsia armata* (after Carlgren 1931: 2)
Tentacle				
Spirocyst	18·8–27·1 × 1·2–1·8	13·0–23·6 × 1·8	13·0–24·8 × 1·8–2·4	19·0–26·0 × 2·0–2·5
Basitrich	47·2–87·3 × 3·0–4·1	42·5–81·4 × 3·0–4·1	47·2–70·8 × 4·1–4·7	52·0–72·0 × 3·0–3·5
Capitulum				
Basitrich	11·8–15·3 × 2·4	...	...	...
Nemathybome				
Basitrich	43·7–76·6 × 4·1–5·8	47·2–70·8 × 4·1–5·8	63·7–69·6 × 4·1	40·0–70·0 × 3·5–4·5
Actinopharynx				
Basitrich	24·8–31·9 × 2·4	21·2–28·3 × 2·4–3·0	28·3–30·7 × 2·4	17·0–24·0 × 2·0–2·5
Basitrich	43·7–64·9 × 2·4–4·7	43·7–51·9 × 4·1–4·7	38·9–47·2 × 4·7–5·8	34·0–41·0 × 4·5–5·0
Filament				
Basitrich	23·6–33·0 × 2·4–3·0	22·4–29·5 × 3·0	27·0–36·5 × 2·4–3·0	...
Basitrich	39·0–48·3 × 3·5–4·7	25·0–47·2 × 3·5–4·7	33·0–49·6 × 4·7–5·8	...

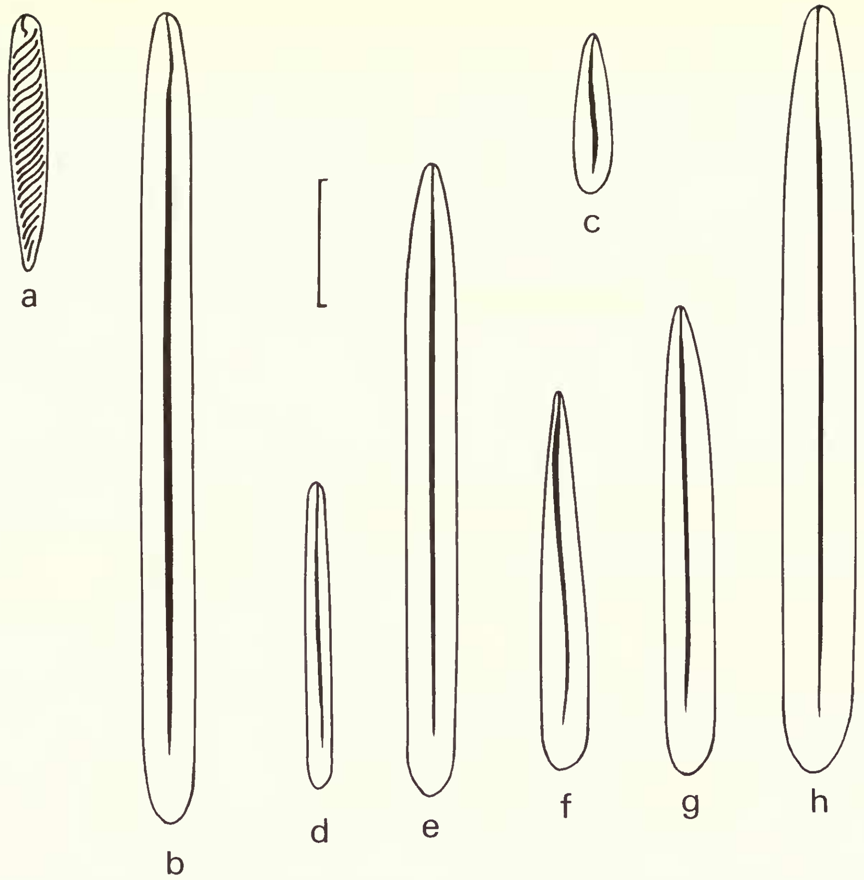

Fig. 14 *Scolanthus armatus* comb. nov., nematocyst signature (see Table 6). *Tentacle* (a) spirocyst, (b) basitrich. *Capitulum* (c) basitrich. *Actinopharynx* (e-f) basitrichs. *Filament* (g-h) basitrichs. Scale: (a-h) = 10 μm.

normally rounded but may be flattened by attachment to stones. Scapus with small, prominent, but irregularly scattered nemathybomes extending to proximal tip of column. Scapulus indistinct, without nemathybomes. Capitulum distinct, mesenterial insertions into endoderm visible through transparent wall. Tentacles up to 16, long, slender, capitate. Mouth at top of cone. Column in preserved specimens 45 mm high, 5 mm wide. *Anatomy*. Eight macrocnemes and up to eight microcnemes, developing in normal *Edwardsia* pattern. Microcnemes of dorsal exocoels developing last, normally in pairs but both of a pair not always arising together. Retractors of macrocnemes strong, diffuse (Fig. 13a-b), outer part developing as extension of mesentery whence muscle folds arise on both sides of mesogloeal sheet. Microcnemes small, confined to region of capitulum. Parietal muscles well developed. *Cnidome*. See Table 6 and Figure 14. *Colour*. Capitulum translucent with red markings, scapus light orange-brown with white nemathybomes. Tentacles translucent with white capitate tips.

Distribution. Fidschi Island, Viti Levu, Fiji (Carlgren, 1931). Singapore: Pulau Hantu, Pasir Panjang and Pungol Point; Great Barrier Reef: Three Isles (present material).

Habitat. In coarse to muddy sand, MLTL. Often with other edwardsiid species, for example *Edwardsia hantuensis* sp. nov., *Edwardsianthus pudica* comb. nov. and *Edwardsianthus gilbertensis* comb. nov.

REMARKS. The present material resembles *Edwardsia armata* Carlgren, 1931, in having irregularly scattered nemathybomes, 16 tentacles with prominent capitate tips bearing large nematocysts, and an identical mesenterial arrangement. The size range and types of cnidae given by Carlgren also correspond although in the actinopharynx the nematocysts of the present material were larger than in that studied by him. However, the size range of cnidae can vary a little within any species (Table 6) and the range may be usual in this species. Carlgren assumed that the rounded lower end of the column of this species was a physa, an assumption easily made when the cuticle is missing. However, sections of the present material revealed no physa. The nemathybomes and cuticle, reduced in thickness, were present almost to the base of the proximal end. Such specimens cannot be referred to the genus *Edwardsia* and should be placed in the genus *Scolanthus* (= *Isoedwardsia*) (see Manuel 1981).

There seems to be no other species referred to the genera *Isoedwardsia* and *Scolanthus* which these specimens resemble. None has capitate tips, and the cnidae are different in size (Table 7). The present specimens are, therefore, referred to *S. armatus*.

I am grateful to Mrs U. Canfield for drawing my attention to the absence of a physa in this species.

Table 7 The species of *Scolanthus*.

Species	Number of Tentacles	Nemathybome arrangement	Dimensions of nematocysts from nemathybomes (μm)	Source of data
S. armatus (Carlgren, 1931)	16	scattered	43·7–76·6 × 4·1–5·8	p. 230
[1]*S. callimorphus* Gosse, 1853	16	scattered	60·0–90·0 × 3·0–5·0	Manuel, 1981: 265
S. curacaoensis Pax, 1924	16	scattered	38(43)–53 × 2·5(3)	Carlgren, 1931: 26
S. ignotus (Carlgren, 1920)	17–20	scattered	34·0–48·0 × 3·0–3·5	Carlgren, 1920: 149
S. ingolfi (Carlgren, 1921)	16	scattered	50·0–60·0 × 4·0–5·0	Carlgren, 1921: 56
? *S. nidarosiensis* (Carlgren, 1942)	16	scattered	62·0–67·0 × 2·5–3·0	Carlgren, 1942: 61

[1]Type species of genus.

Tribe **THENARIA** Carlgren, 1898
Family **ALICIIDAE** (Duerden, 1895; Duerden, 1897)
Genus ***TRIACTIS*** Klunzinger, 1877

Triactis Klunzinger, 1877: 85; Carlgren, 1949: 44; Carlgren, 1950*b*: 433.
Viatrix: Haddon & Shackleton, 1893: 127 (part).
Hoplophoria Haddon, 1898: 438 (part).
Phyllodiscus: Stephenson, 1922: 280 (part); Carlgren, 1940*a*: 31.

DEFINITION. (*sensu* Carlgren, 1949: 44). Aliciidae with well developed pedal disk. Column divided into capitulum and scapus, sometimes scapus with small vesicles below margin. *Margin with stalked outgrowths (peduncles)* which in young specimens occur sparingly and are little branched, in older ones close together and dichotomously branched. Hemispherical mastigophoral spherules on stalks near branches of peduncles *and in fosse*. Stalks few, with longitudinal weak bands of endodermal muscle. Sphincter weak or absent. Tentacles hexamerously arranged, distally with spots as on column. Longitudinal muscles of tentacles and muscles of oral disk ectodermal. Two siphonoglyphs. Six pairs of perfect mesenteries and several imperfect pairs. Two pairs of directives. Retractor and parietobasilar muscles weak. Cnidome: spirocysts, basitrichs, microbasic and macrobasic amastigophores, possibly also microbasic b-mastigophores.

TYPE SPECIES. *Triactis producta* Klunzinger, 1877, by monotypy.

REMARKS. Carlgren (1949: 44) stated that the outgrowths of the column occurred in the middle, but later he stated that 'the upper part of the column (the capitulum) above the outgrowths is more thin walled than the lower part, and somewhat narrower just above them, and has ectodermal muscles and groups of spirocysts' (Carlgren, 1950*b*: 433). Two comments on Carlgren's views can be made. Firstly, the peduncles are outgrowths of the margin and not of the middle of the column, so that Carlgren's later statement is correct. The difference in thickness between the column wall and the capitulum is shown in Figure 15. Secondly, the presence of spirocysts in the capitulum was not confirmed. Examination of serial sections from two specimens did not reveal any spirocysts in this region and they occurred only in the tentacle tips. The nematocysts of the capitulum are microbasic amastigophores and basitrichs (microbasic b-mastigophores?). However, the presence of weak ectodermal muscle in the capitulum is confirmed.

The generic definition of *Triactis* is modified from that given by Carlgren (1949) to reflect the position of the peduncles and the presence of a capitulum. His reference to vesicles on the pedicels and peduncles is amended to spherules (see p. 210). Carlgren (1949) specified no sphincter but in one of the present specimens a weak sphincter was apparent, recalling that depicted by Haddon (1898: 439, text fig.) in *Hoplophoria cincta*. However, this may have been due to the influence of other muscles on the degree of folding of the circular muscles of the column. In a second specimen no sphincter was found.

Triactis producta Klunzinger, 1877
Figs 15–16

Triactis producta Klunzinger, 1877: 85, p. 6, fig. 8.
Viatrix cincta Haddon & Shackleton, 1893: 127.
Hoplophoria cincta Haddon, 1898: 438–439, pl. 23, figs 11–15.
Phyllodiscus indicus Stephenson, 1921: 561, fig. 18; Stephenson, 1922: 280; Stephenson, 1928: 18, fig. 11.
Phyllodiscus cinctus Stephenson, 1922: 280; Stephenson, Stephenson & Tandy, 1931: 38; Carlgren, 1940*a*: 31, fig. 8.2.
Triactis cincta: Carlgren, 1945: 7; Carlgren, 1947: 14; Carlgren, 1950*b*: 433.

MATERIAL EXAMINED. Aden: 14 specimens, 17 Jul 1966, BMNH 1983.4.8.27–30. Singapore: Pulau Semakau, 42 specimens, 22 Feb 1970, BMNH 1983.4.8.14–24; Pulau Biola, 2 specimens, 13 Sept 1970, BMNH 1983.4.8.25–26.

DESCRIPTION. Column with scapus and capitulum, definite margin, and deep fosse. Margin with peduncles each branched into several pedicels, the latter each terminating in or capped by a small mastigophoral spherule. Large mastigophoral spherules on upper surfaces of peduncles close to branches. A second mastigophoral spherule may occur at foot of each peduncle, in fosse, especially near directive axis (Fig. 15.) Major outgrowths up to twelve, corresponding to primary and secondary mesenterial cycles. Between major outgrowths smaller ones may be present. Column mostly smooth but small vesicles may occur over 1st- and 2nd-cycle endocoels though their appearance may be due to contraction. Capitulum either withdrawn so that tentacles lie over or among the outgrowths, or fully extended to nearly same height as rest of column. Tentacles up to 48, long, slender, tips blunt, surface granular due to small groups of nematocysts, their size increasing thickness of ectoderm. Disk small, central mouth on top of cone. Height of column to 7 mm, diameter across peduncles 8 mm. *Anatomy*. Mesenteries hexamerously arranged in three cycles, two pairs of directives supporting siphonoglyphs. 1st cycle perfect, fertile. Retractors weak, diffuse, mesogloeal branches thick, with few muscle folds. Parietobasilar muscles weak absent. Basilar muscles present. Weak sphincter found in one specimen but indistinct or absent in all others. Longitudinal muscles of tentacles and radial muscles of disk ectodermal; in sections folds short, mostly unbranched. Ectodermal longitudinal muscle processes on capitulum. Zooxanthellae present in endoderm of column, disk, peduncles and spherules. *Cnidome*. See Table 8 and Figure 16. The size ranges of certain types of nematocysts were found to differ considerably between groups of specimens collected from a single locality, but the cnidome was constant. Nematocysts in tentacles, column and actinopharynx labelled 'b-mastigophores' may be a form of basitrich. *Colour*. Column translucent pale brown with a much darker overlay of small

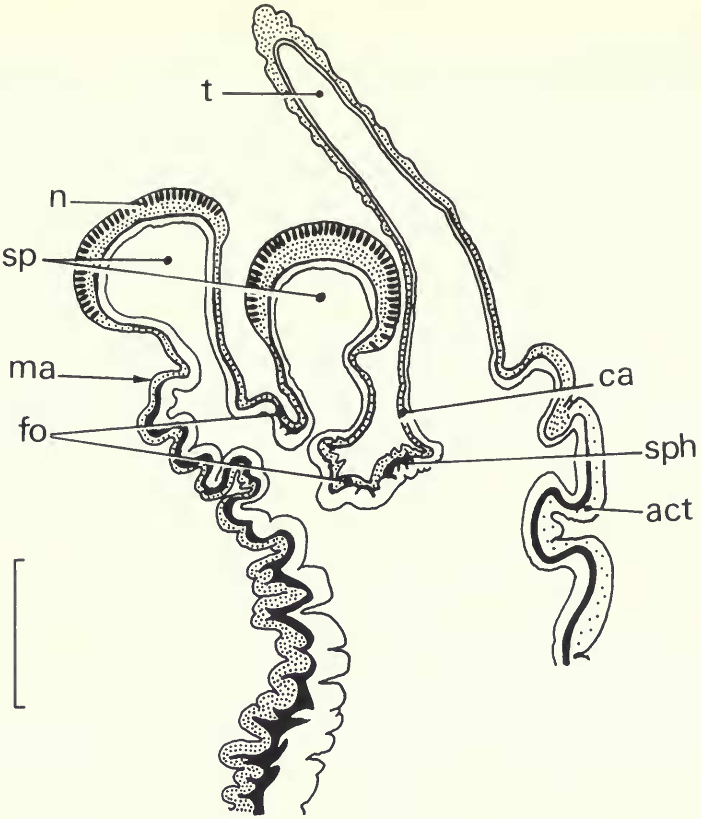

Fig. 15 *Triactis producta*, BMNH 1983.4.8.27. Vertical section through part of column and crown showing two mastigophoral spherules, one on a pedicel from the margin (to left) and one in the fosse (to right), a tentacle, the disk and adjacent actinopharynx. Scale: = 500 μm. (act actinopharynx, ca capitulum, fo base of fosse, ma margin, n nematocysts, sph sphincter, sp spherules, t tentacle. Stippled, ectoderm; black, mesogloea; white, endoderm.)

spots on its lower part grading to continuous beneath peduncles. Capitulum dark brown with pale translucent vertical lines. Tentacles translucent mottled with white, disk pale brown, mouth orange-brown. Upper surfaces of peduncles and fosse with iridescent blue-green sheen over brown ground colour. Spherules white on outer surface, but golden orange within from zooxanthellae.

Distribution. Known from several widely spaced localities: Red Sea (Klunzinger, 1877), Maldives (Stephenson, 1921, 1922, as *Phyllodiscus indicus*), Torres Straits (Haddon & Shackleton, 1893 as *Viatrix cincta*), Great Barrier Reef (Carlgren, 1950*b* as *Triactis cincta*), Aden and Singapore (present material).

Habitat. Usually reported on scleractinian coral, both living and dead. The specimens from Singapore were on *Pavona frondifera* Lamarck (det. Dr S. H. Chuang, University of Singapore). Those from Aden were on similar coral fronds, at depth 2 m, there being several specimens on each.

Remarks. The presence of branched outgrowths with large mastigophoral spherules on the peduncles (p. 211), and of similar spherules in the fosse, suggests that these specimens should be referred to a species of *Triactis*. The specimens from Aden and Singapore differed slightly, especially in nematocyst size, but the differences are considered too small to justify recognition of two taxa.

Klunzinger (1877) proposed the genus *Triactis* to accommodate *T. producta*, a species from the

Red Sea. His description and illustrations of the species were clear and the specimens from Aden can be referred to it with confidence.

Haddon & Shackleton (1893) collected similar specimens from the Torres Strait and provisionally referred them to the genus *Viatrix* Duchassaing & Michelotti, 1866, under the specific name *V. cincta* Haddon & Shackleton, 1893. Later, following statements by McMurrich (1893, 1896), Haddon (1898) referred the species to the genus *Hoplophoria* Wilson, 1890. According to

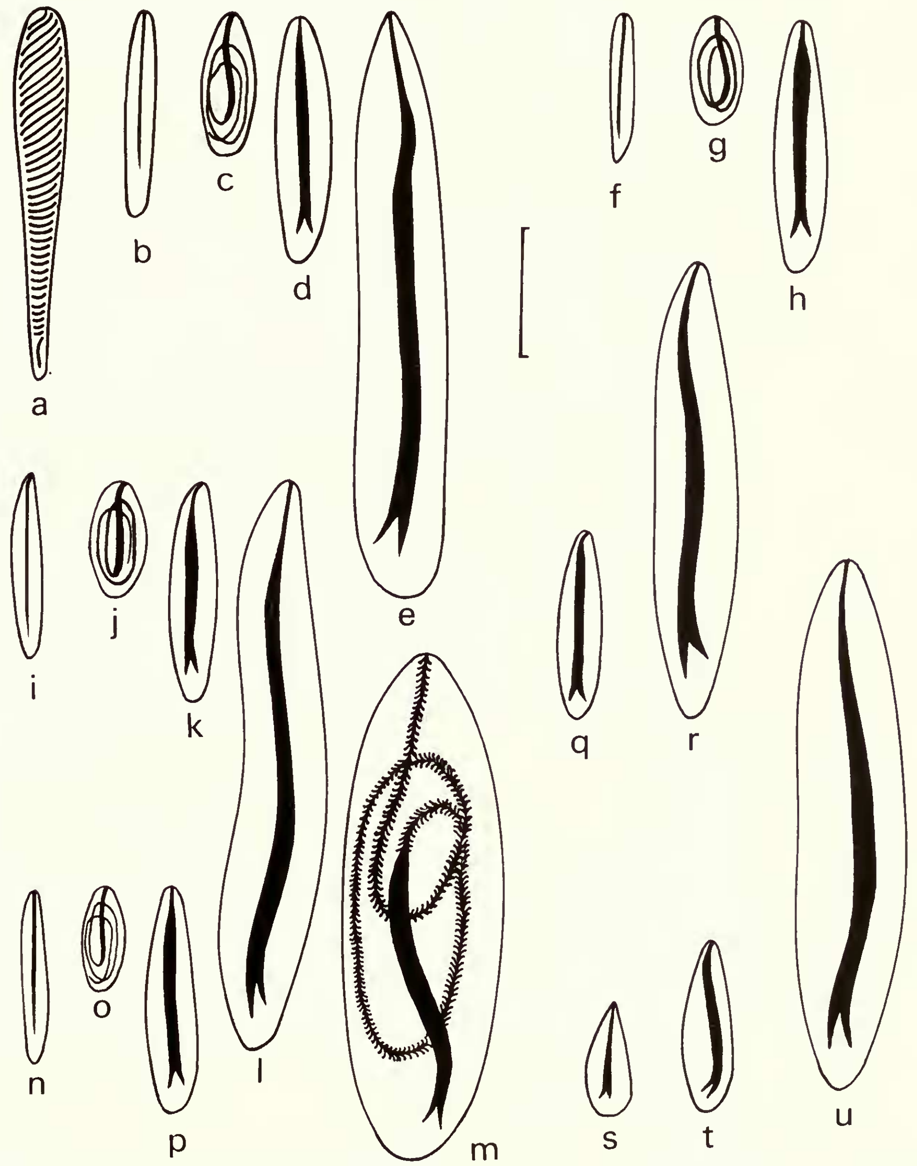

Fig. 16 *Triactis producta*, nematocyst signature (see Table 8). *Tentacle* (a) spirocyst, (b) basitrich, (c) microbasic b-mastigophore, (d-e) microbasic amastigophore. *Column* (f) basitrich, (g) microbasic b-mastigophore, (h) microbasic amastigophore. *Spherules, major* (i) basitrich, (j) microbasic b-mastigophore, (k-l) microbasic amastigophores, (m) macrobasic amastigophore. *Spherules, minor* (n) basitrich, (o) microbasic b-mastigophore, (p) microbasic amastigophore. *Actinopharynx* (q-r) microbasic amastigophores. *Filament* (s-u) microbasic amastigophores. Scale: (a-u) = 10 μm.

Table 8 Size ranges of cnidae of *Triactis producta* (in μm).

Location/ Type of cnida	Localities of specimens: Aden (BMNH 1983.4.8.19)	Aden (BMNH 1983.4.8.20)	Singapore (BMNH 1983.4.8.27)	Singapore (BMNH 1983.4.8.25)
Tentacles				
Spirocysts	16·6–37·6 × 2·6–4·0	14·4–37·2 × 2·0–4·8	11·9–46·2 × 2·0–6·7	23·2–33·0 × 2·6–4·6
Basitrichs	13·2–19·9 × 1·5	16·8–19·2 × 2·0	19·9–23·1 × 1·5	9·3–16·6 × 2·0
Microbasic b-mastigophores	9·3–12·0 × 3·3–4·0	9·6–12·0 × 3·6	9·9–16·6 × 3·3–6·0	10·0–11·3 × 3·3
Microbasic amastigophores	10·6–16·6 × 3·3–4·0	14·4–20·4 × 3·6	9·9–28·5 × 3·3–5·3	20·5–31·1 × 4·0
Microbasic amastigophores	29·8–56·7(66·0) × 6·0–6·7	42·0–56·4(72·0) × 6·0–7·2	36·4–64·4(67·3) × 4·6–8·0(9·9)	31·3–56·1(72·8) × 4·6–6·6
Column				
Basitrichs	9·2–11·2 × 1·5	10·6 × 1·5 (3 only)	7·9–9·9 × 1·3	7·2–10·8 × 2·0
Microbasic b-mastigophores	5·3–8·6 × 4·0	8·0–10·0 × 4·6–5·3	6·7–11·2 × 2·6–3·3	7·2–10·8 × 2·6–3·0
Microbasic amastigophores	7·9–19·9 × 2·6–4·0	7·3–25·8 × 3·3–4·0	11·9–19·9 × 2·6–4·0	12·0–34·8 × 3·0–4·8
Spherules-major				
Basitrichs	10·6–19·9 × 2·0	11·3–19·2 × 2·0–2·6	12·0–18·0 × 2·0	8·6–19·2 × 2·0–2·6
Microbasic b-mastigophores	6·6–13·3 × 2·6–4·0	8·6–10·0 × 3·3–4·0	. . .	5·3–12·0 × 2·0–3·3
Microbasic amastigophores	16·6–25·1 × 4·0–4·6	6·6–26·5 × 3·3–4·0	6·7–28·5 × 2·6–4·6	6·7–27·1 × 2·6–4·6
Microbasic amastigophores	36·4–51·5 × 6·0–6·7	33·0–65·0(78·0) × 5·3–8·0	30·0–63·6(85·0) × 5·4–8·4(10·5)	33·0–59·4 × 4·6–6·6
Macrobasic amastigophores	26·4–39·7 × 8·0–11·9	28·5–39·6 × 9·3–10·6	(33·6)41·6–63·4(71·3) × 11·9–16·6	33·0–59·4 × 9·3–13·3

Spherules-minor				
Basitrichs	9·3–14·6 × 2·0	10·0–15·2 × 2·0	8·0–14·6 × 2·0	10·0–16·6 × 2·0–2·6
Microbasic b-mastigophores	8·0–9·3 × 3·3–4·0	7·3–8·0 × 4·0	8·0–10·6 × 4·0	6·6 × 3·3 (1 only)
Microbasic amastigophores	6·6–22·5 × 2·6–4·0	10·0–27·8 × 3·3–5·3	7·3–26·5 × 2·6–4·0	6·6–25·2(34·3) × 3·3–4·6(6·0)
Actinopharynx				
Microbasic amastigophores	13·3–19·2 × 2·6	10·0–20·0 × 3·3–4·0	11·9–19·9 × 2·6–3·3	12·0–16·8 × 2·4–3·0
Microbasic amastigophores	29·8–39·7 × 4·6–6·0	29·1–41·6 × 5·3–7·3	30·5–49·5 × 4·6–8·0	24·0–42·0 × 3·6–4·8
Filaments				
Microbasic amastigophores	6·7–11·2 × 3·3–4·4	8·0–10·0 × 3·3	7·9–10·6 × 3·3–4·0	6·0–10·8 × 3·0–3·6
Microbasic amastigophores	9·2–18·5 × 3·3–4·0	11·0–21·2 × 3·3–4·0	10·5–16·5 × 2·6–4·0	9·6–15·6 × 2·0
Microbasic amastigophores	23·8–53·5 × 4·0–8·6	36·3–54·0 × 6·0–8·0	50·0–62·0 × 7·3–9·2	39·6–60·0 × 6·0–7·8

Haddon the name *Hoplophoria* was introduced, but not defined, by Wilson (1890) to accommodate an actinian collected in the Bahamas. McMurrich, however, wrote: 'It seems fairly certain that this species is identical with *Viatrix globulifera* originally described by Duchassaing & Michelotti (1860)'. If McMurrich's statement were correct then the genus *Viatrix* Duchassaing & Michelotti, 1866, would take precedence over *Hoplophoria* Wilson, 1890, so why Haddon (1898) employed the later name for the genus is not clear. Still, Haddon's description was adequate to refer his material to the genus *Triactis* (*sensu* Carlgren, 1947) and to identify the specimens from Singapore, shown here to be conspecific with *T. producta* (see below).

Carlgren (1950*b*), after studying material from Low Island, suggested that *Triactis cinctus* and *T. producta* were conspecific. This suggestion is confirmed from the present study of specimens from Aden and Singapore. The species name *T. producta* Klunzinger, 1877, has priority over *T. cincta* (Haddon & Shackleton, 1893) and is employed here.

Phyllodiscus indicus Stephenson, 1921, is here considered conspecific with *Triactis producta*. When first described the species was referred to *Phyllodiscus* Kwietniewski, 1897, but only provisionally since the anatomy of *Triactis* was incompletely known. Stephenson included in the same genus *P. semoni* Kwietniewski, 1897: 407, and *Hoplophoria cincta* (Haddon & Shackleton, 1893: 127). Stephenson's description of *P. indicus* and his illustration (Stephenson, 1921, Fig. 18) show that his concept of *Phyllodiscus* is identical with *Triactis* sensu Klunzinger. However, *Phyllodiscus* Kwietniewski, 1897, is regarded as valid and *P. semoni* is not referred to *Triactis* (following Carlgren, 1924: 11).

Family **ACTINIIDAE** (Rafinesque, 1815)

Nomenclature. Williams, Cornelius & Clark (1982), in proposing validation of the family name Actiniidae, considered that the earliest use of this family name was by Goldfuss (1820). However, L. B. Holthuis of Leiden has since informed the International Commission on Zoological Nomenclature of an earlier use, by Rafinesque (1815: 155) (Holthuis, Opinion 1295, *Bulletin of Zoological Nomenclature* 42: 34–36). The family name has been validated by the Commission. Dating of the Rafinesque work follows Iredale (1911).

Genus ***ANTHOPLEURA*** Duchassaing & Michelotti, 1860

Actinia (Isacmaea) Ehrenberg, 1834: 34 (part).
Tarastephanus Brandt, 1835: 1 (part).
Monostephanus Brandt, 1835: 10 (part).
Cereus: Milne Edwards, 1857: 266.
Bunodes: Gosse, 1855: 274; Gosse, 1860: 195, 198; Johnson, 1861: 302; Klunzinger, 1877: 77; Andres, 1881: 318; Andres, 1883: 423; Pennington, 1885: 167; Dixon, 1889: 310; Duerden, 1898: 454; Carlgren, 1898: 19; Carlgren, 1900: 66; Stuckey, 1908: 368; Fischer, 1889: 301 (part).
Isacmaea: Milne Edwards, 1857: 288.
Anthopleura Duchassaing & Michelotti, 1860: 49; Duchassaing & Michelotti, 1866: 126; Andres, 1883: 440.
Aegeon Gosse, 1865: 41.
Evactis Verrill, 1969*b*: 470; Andres, 1883: 446.
Actinioides Haddon & Shackleton, 1893: 126; Haddon, 1898: 424; Kwietniewski, 1897: 33 (389); Duerden, 1898: 453; Carlgren, 1900: 63; Carlgren, 1938: 32; Pax, 1907: 79; Pax, 1908: 490.
Isactinia Carlgren, 1900: 53.
Cribrina: McMurrich, 1901: 18; McMurrich, 1904: 287; Pax, 1908: 474.
Bunodactis: Pax, 1920: 31; Pax, 1926: 23; Stephenson, 1921: 529; Stephenson, 1922: 271.
Tealiopsis: Verrill, 1922: 110; Verill, 1928: 26.
Anthostella Carlgren, 1938: 38.

Nomenclature. The generic name *Anthopleura* Duchassaing & Michelotti, 1860, is used here following the practice of Carlgren (1949), Stephenson (1935) and Manuel (1981).

Definition. Actiniidae with well developed pedal disk. Column with adhesive verrucae arranged in more or less distinct vertical rows especially in the upper part. *Heterotrichs present in* *column ectoderm.* Atrichal marginal spherules present *or atrichal spherules in fosse.* Atrichs suppressed here in some specimens. Sphincter weak to strong, endodermal, diffuse to circumscribed. Tentacles simple, hexamerously or irregularly arranged, longitudinal muscles ectodermal or meso-ectodermal. Numerous perfect mesenteries, all stronger ones fertile. About the same number of mesenteries distally and proximally but, since mesenteries grow from base upwards in some species, a few more may be found proximally. Retractors of stronger mesenteries diffuse, sometimes restricted. Cnidome: spirocysts, atrichs, heterotrichs, basitrichs and microbasic amastigophores.

TYPE SPECIES. *A. krebsi* Duchassaing & Michelotti, 1860, by monotypy.

REMARKS. The characteristic nematocysts of the marginal spherules are a distinctive feature of the genus *Anthopleura.* They are usually referred to as atrichs but are possibly of two types, atrichs and heterotrichs. *Anthopleura* spp. lacking atrichs and heterotrichs in the spherules are provisionally assigned to the genus. Examples are *Anthopleura dixoniana* (Haddon & Shackleton, 1893) and *A. handi* Dunn, 1977, redescribed here. Species lacking atrichs in the spherules but having other characters of *Anthopleura* were often mistakenly assigned to the genus *Bunodactis* (now referred to the genus *Aulactinia,* see Dunn, Fu-Shiang Chia & Levine, 1980: 2078, also p. 255). The best character by which *Anthopleura* can be distinguished from *Bunodactis* is the presence of heterotrichs in the ectoderm of the column. They are not found in species referred to *Bunodactis, Aulactinia* or *Gyractis.* Their reported occurrence is listed in Table 9. It is interesting that Schmidt (1972: 91–92) did not find them in *A. balli* (Cocks, 1851) from the Mediterranean, nor Carlgren when first describing *A. sanctaehelenae* Carlgren, 1941: 4, and the generic affinity of these species needs re-appraisal. The distinctive heterotrichs of the column (see Figs 19h, 21h, 23h, and 25h) should not be confused with the atrichs that sometimes occur only at the limbus in certain

Table 9 *Anthopleura* spp. having heterotrichs in column ectoderm.

Species	Nematocyst referred to as:	Source of data
A. annae Carlgren, 1940*b*	Atrichs	Carlgren, 1940*b*: 4
A. artemisia (Pickering in) Dana, 1846: 38	Atrichs	Hand, 1955: 65, Fig. 15
A. asiatica Uchida & Muramatsu, 1958	Holotrichs	Uchida & Muramatsu, 1958: 118, Fig. 5
A. aureoradiata (Stuckey, 1909)	Atrichs	Carlgren, 1950*c*: 4
A. dixoniana (Haddon & Shackleton, 1893)	Heterotrichs	England (see p. 242)
A. elegantissima (Brandt, 1835)	Atrichs	Hand, 1955: 59, Fig. 13
A. handi Dunn, 1977	Atrichs	Dunn, 1977: 8
A. hermaphroditica Carlgren, 1898	Atrichs	Carlgren, 1959: 22
A. insignis Carlgren, 1940*b*	Atrichs (limbus only?)	Carlgren, 1940*b*: 4
A. krebsi Duchassaing & Michelotti, 1860	Atrichs	Carlgren & Hedgepeth, 1952: 154
A. kurogané Uchida & Muramatsu, 1958	Holotrichs	Uchida & Muramatsu, 1958: 114, Fig. 2
A. michaelseni (Pax, 1920)	Atrichs	Carlgren, 1938: 45
A. midori Uchida & Muramatsu, 1958	Holotrichs	Uchida & Muramatsu, 1958: 112, Fig. 1
A. mortenseni Carlgren, 1941	Atrichs	Carlgren, 1941: 3
A. nigrescens (Verrill, 1928)	Heterotrichs	England (see p. 249)
A. orientalis Averincev, 1967	Atrichs	Averincev, 1967: 70
A. pacifica Uchida 1938	Basitrichs/heterotrichs	Uchida & Maramatsu, 1958: 116, Fig. 3
A. pannikkarri Parulekar, 1968	Holotrichs	Parulekar, 1968: 590–595
A. rubripunctata (Grube, 1840)	Haplonemes	Schmidt, 1972: 89
A. stellula (Ehrenberg, 1834)	Haplonemes	Schmidt, 1970: 24
A. varioarmata Watzl, 1922	Atrichs	Carlgren, 1952: 374
A. waridi (Carlgren, 1900)	Heterotrichs	England (see p. 252)
A. xanthogrammica (Brandt, 1835)	Atrichs	Hand, 1955: 52, Fig. 11

*Uchida & Maramatsu list basitrichs but illustrate heterotrichs.

anemones, but usually in large numbers, as for example in *Epiactis prolifera* Verrill, 1869*b* (personal observation), *Bunodactis maculosa* Carlgren, 1954, and *Isanemonia australis* Carlgren, 1950*c*.

Anthopleura dixoniana (Haddon & Shackleton, 1893)
Figs 17–19

Actinioides dixoniana Haddon & Shackleton, 1893: 126; Haddon, 1898: 424–426, pl. 22, fig. 6, pl. 27, figs 1–2.
Actinioides papuensis Haddon, 1898: 426–428, pl. 22, fig. 7, pl. 27, figs 3–7.
Actiniogeton papuensis: Carlgren, 1949: 62.
Anthopleura dixoniana: Carlgren, 1938: 32; Carlgren, 1949: 54.

MATERIAL EXAMINED. Singapore: Changi Creek, 50 specimens, 16 Feb 1970 BMNH 1983.8.4.1–50; Pungol Point, 26 specimens, 19 May 1970, BMNH 1983.8.4.51–77; Pasir Panjang, 9 specimens, 24 Jun 1970, BMNH 1983.8.4.76–85. Torres Strait: Mabuaing, 2 specimens, coll. A. C. Haddon, Cambridge University Zoological Museum, Co177 (in jar labelled *Actinioides sesere*). Specimens also examined from Hong Kong and Gan, Addu Atoll, Maldives.

DESCRIPTION. Column tall, height about twice diameter when extended, upper part with vertical rows of small prominent verrucae, each row topped at margin by a large spherule that may or may not be atrichal; but some specimens lacking atrichal marginal spherules. Spherules simple or compound with nematocyst batteries, when present, located on top and inner faces. Verrucae extending onto outer surfaces of spherules. Tentacles varied in number, up to 60, slender, tapered, in two circlets, inner longer than outer. Disk flat; base present. *Anatomy*. 3–8 siphonoglyphs seen, each supported by directives. Number of mesenteries varied but most are perfect; number of tentacles same as number of mesenteries at base of column (Table 10). Typical arrangements of mesenteries in apparent cycles are shown in Figure 17. Mesenteries apparently in three cycles but not hexamerously arranged, all or most of the 1st cycle being directives. Retractor muscles weak-diffuse; parietobasilar muscles weak with free inner edge. Sphincter weak-diffuse to circumscribed and varied between specimens (Fig. 18). Marginal spherules endocoelic; mostly atrichal, some lacking atrichs interspersed irregularly with atrichal spherules. Zooxanthellae present. Largest specimen, height 10 mm, diameter 10 mm. *Cnidome*. See Table 11 and Figure 19. *Colour*. Column either pale green to yellowish green near limbus, becoming grey towards margin, covered with small yellow spots; or deep brown near the limbus becoming pale greenish white above with white vertical lines. Marginal spherules green or brown with orange-brown or golden-yellow spots or patches (atrichal regions). Verrucae grey. Tentacles with brownish tint on upper surface broken by 2–4 translucent white elliptical patches. Disk brown, tinged with green and yellow around the mouth and with cream or white patches over the endocoels.

Table 10 *Anthopleura dixoniana*. Relation between numbers of tentacles, mesenteries, directivies, siphonoglyphs and spherules. Each line of the table represents one specimen.

Tentacles	Mesenteries at base	Directive mesenteries	Siphonoglyphs	Spherules
18	9 pairs	3 pairs	3	8
21	10 pairs	4 pairs	4	11
34	17 pairs	5 pairs	5	...
38	19 pairs	5 pairs	5	20
39	19 pairs + 1	6 pairs	6	20
42	22 pairs	5 pairs	5	19
62	...	5 pairs	5	20

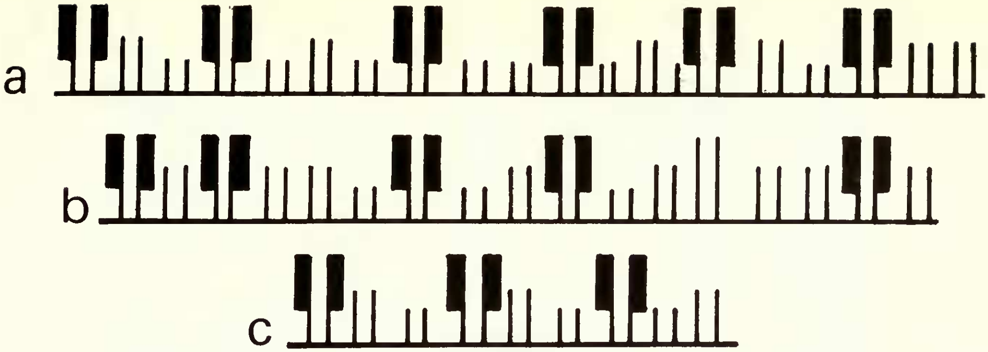

Fig. 17 *Anthopleura dixoniana* Complete mesenterial arrangements of 3 specimens. (a) BMNH 1983.8.4.1; (b) BMNH 1983.8.4.2; (c) BMNH 1983.8.4.4. (black rectangles = directive mesenteries.)

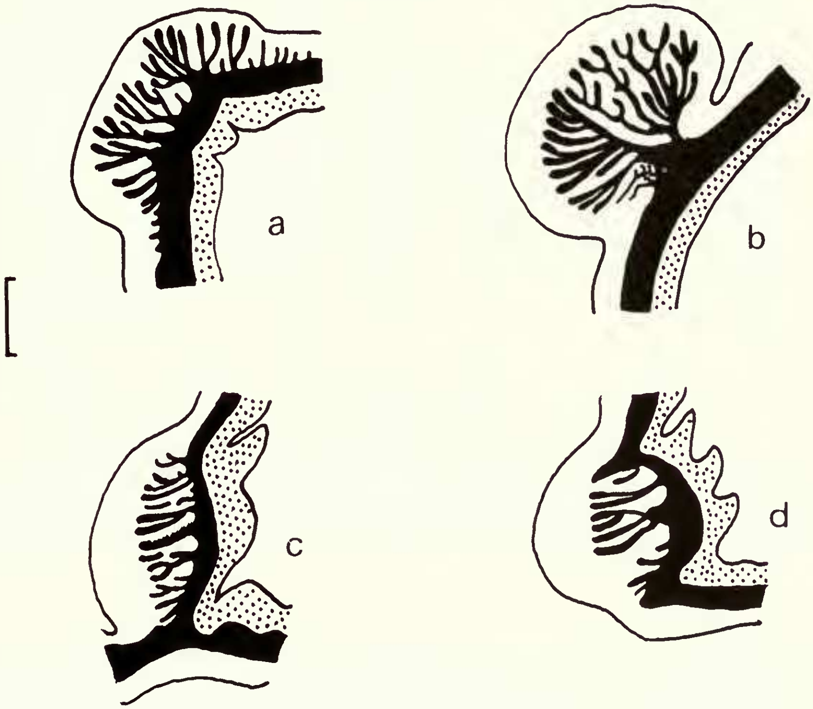

Fig. 18 *Anthopleura dixoniana* Vertical sections of two specimens to show variation of sphincter muscle. (a-b) Singapore, BMNH 1983.8.4.51; (c-d) Singapore, BMNH 1983.8.4.1. Scale: (a-b) = 65 µm, (c-d) = 30 µm. (Stippled, ectoderm of fosse; black, mesogloea; white, endoderm.)

DISTRIBUTION. Recorded from Torres Strait (Haddon & Shackleton, 1893, as *Actinioides dixoniana* and *A. papuensis*), the Maldives, Singapore, and Hong Kong (present material).

HABITAT. In holes in rocks and stones; many specimens aggregating in a small area, but not close to each other; upper shore.

REMARKS. The presence of atrichal marginal spherules, verrucae on the column, and a uniform number of mesenteries at margin and base, place this species in the genus *Anthopleura*. The varied

Table 11 Size ranges of cnidae of *Anthopleura dixoniana* (in µm).

Location/ Type of cnida	Identity of specimens from Singapore				
	(BMNH 1983.8.4.51)	(BMNH 1983.8.4.52)	(BMNH 1983.8.4.76)	(BMNH 1983.8.4.77)	(BMNH 1983.8.4.78)
Tentacle					
Spirocyst	9·8–20·8 × 2·0–2·3	10·8–20·4 × 2·0–3·6	10·0–22·5 × 1·8–2·4	16·8–24·0 × 2·4–3·0	12·0–21·6 × 2·4–3·0
Basitrich	13·0–16·3 × 2·0	12·0–18·0 × 2·0–2·4	16·2–20·0 × 2·4	14·4–19·2 × 2·4–3·0	13·2–18·0 × 1·8–2·4
Column					
Basitrich	11·1–13·7 × 2·0	12·0–14·4 × 2·4	12·5–16·2 × 1·8	11·0–16·8 × 2·4–3·0	10·8–13·2 × 1·8–2·4
Heterotrich	11·1–14·3 × 3·3–4·6	11·4–15·6 × 3·6–4·2	12·5–16·2 × 3·7	13·2–18·0 × 3·6–4·2	12·0–15·6 × 3·0–3·6
Marginal Spherule					
Spirocyst	16·3–26·0 × 2·0–2·6	19·5–28·0 × 2·0–2·6	21·2–25·0 × 1·8	18·0–32·4 × 2·0–2·4	. . .
Basitrich	9·1–10·4 × 1·3	9·6–11·1 × 1·3	11·2–13·7 × 1·2–1·8	10·8–14·4 × 1·2–1·8	8·4–13·0 × 1·8
Heterotrich	24·7–33·8 × 2·6–3·3	25·4–37·0 × 2·0–4·0	31·2–42·5 × 3·7–4·8	27·6–44·4 × 3·0–4·2	. . .
Atrich	26·0–35·8 × 3·3–4·6	26·0–35·8 × 3·3–4·6	32·5–42·5 × 3·7–4·8	28·8–48·0 × 3·7–6·0	. . .
Actinopharynx					
Basitrich	11·1–13·7 × 2·0–2·6	12·0–20·4 × 2·4–3·0	9·6–14·4 × 1·8–2·4	9·6–12·0 × 1·8	9·6–18·0 × 1·8–2·4
Basitrich	14·3–21·5 × 2·6–3·3	. . .	15·6–26·4 × 2·4–3·0	19·2–27·6 × 2·4–3·0	12·0–21·6 × 2·4–3·0
Microbasic amastigophore	16·6–19·5 × 4·0	18·0–20·4 × 3·6–4·8	16·2–21·6 × 3·6–4·8	15·6–20·4 × 3·6–4·8	15·6–19·2 × 3·6–4·8
Filament					
Basitrich	9·8–13·0 × 1·3	9·8–13·2 × 1·2–1·8	9·6–16·8 × 1·8	10·8–18·0 × 1·8	9·6–15·6 × 1·8
Basitrich	20·2–26·7 × 4·0–4·6	21·6–27·6 × 3·6–5·4	21·6–32·4 × 3·6–4·8	21·6–28·8 × 2·4–3·0	19·2–26·4 × 4·2–5·4
Microbasic p-mastigophore	10·4–13·0 × 3·3	10·8–13·2 × 3·0–3·6	12·0–14·4 × 2·4–3·0	12·0–15·6 × 2·4–3·0	10·8–14·4 × 2·4–3·6
Microbasic amastigophore	16·3–21·5 × 3·3–4·6	16·8–21·6 × 3·0–4·2	16·8–22·8 × 3·6–4·8	16·8–21·6 × 3·0–4·8	12·0–20·4 × 3·0–6·0

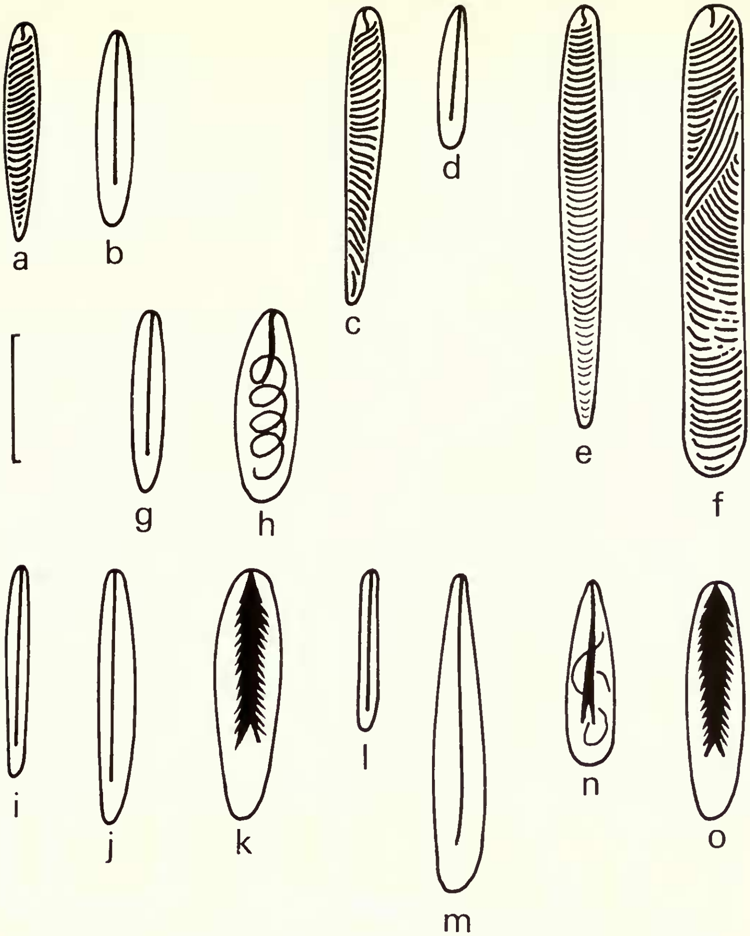

Fig. 19 *Anthopleura dixoniana*, nematocyst signature (see Table 11). *Tentacle* (a) spirocyst, (b) basitrich. *Marginal spherule* (c) spirocyst, (d) basitrich, (e) heterotrich, (f) atrich. *Column* (g) basitrich, (h) heterotrich. *Actinopharynx* (i-j) basitrichs, (k) microbasic amastigophore. *Filament* (l-m) basitrichs, (n) microbasic p-mastigophore, (o) microbasic amastigophore. Scale: (a-o) = 10 μm.

number of siphonoglyphs supported by directives recalls the genus *Actinioides* Haddon & Shackleton, 1893, proposed to accommodate the then newly described *A. dixoniana, A. papuensis* and *A. sesere*. The first two were distinguished purely on sphincter character and colour. Both species were stated by Haddon (1898) to have several siphonoglyphs, all supported by directives. *A. sesere* was separated from the others again on the character of the sphincter, but it is not clear from the description if the *A. sesere* material had many siphonoglyphs. The Pasir Panjang specimens had a sphincter similar to that illustrated by Haddon (1898, pl. 27, fig. 1; see Fig. 18b) in *A. dixoniana*, and had several siphonoglyphs supported by directives. No other species of *Anthopleura* has been reported with these characters, but see *A. waridi* (p. 250) which differs from the present material in having the atrichal spherules in the fosse and not on the margin. It is thus apparent that the specimens are referable to *A. dixoniana*. The Changi Creek specimens, although smaller than the others, had a sphincter similar to that in *A. papuensis* and can be referred to this species. The specimens from Pasir Panjang and Pungol Point had sphincters similar to those of *A. dixoniana*. Examination of the nematocysts of these two species, however, showed no difference in either type

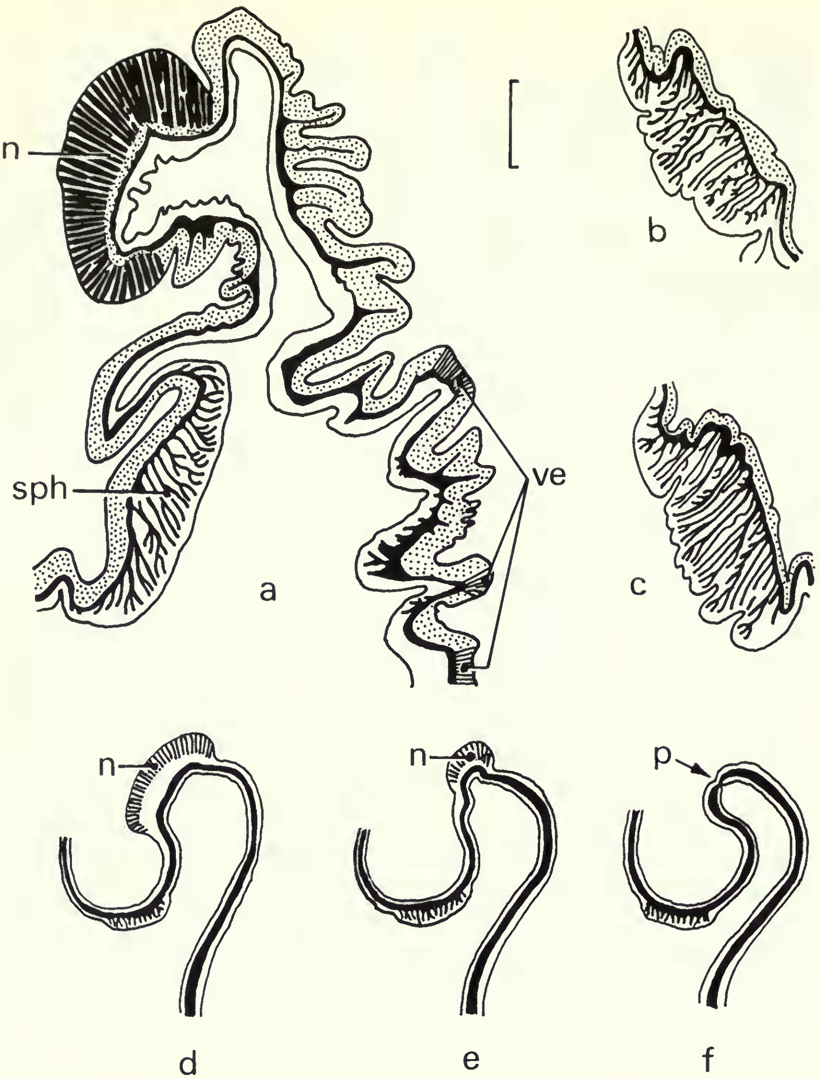

Fig. 20 *Anthopleura handi.* (a) Vertical section through margin showing spherule and sphincter, BMNH 1983.8.24.51. (b-c) Difference between sphincter muscles in vertical section of two other specimens. (d-e) Extremes of size of nematocyst batteries on atrichal marginal spherules. Scale: (a-c) = 10 μm, (d-f) arbitrary. (n nematocysts, p pore, sph sphincter, ve verrucae. Stippled, ectoderm; black, mesogloea; white, endoderm.)

or size range (Table 11). The sphincter, in section, could differ between specimens. A range from weak-diffuse to fairly strong restricted sphincter muscles was found in both *A. dixoniana* and *A. papuensis*. Hence *A. papuensis* can be confidently referred to *A. dixoniana*.

Haddon's original specimens labelled *A. sesere*, preserved in Cambridge University Zoological Museum, comprised two species in one jar. Most were certainly '*A. sesere*' (now referred to *Gyractis excavata*, p. 255), but two specimens were identified as *A. dixoniana*. One of these had eight pairs of directives supporting eight siphonoglyphs among twenty-six pairs of mesentries.

Carlgren (1938: 32), when placing the similar species *Actiniogeton sultana*, suggested that *Actinioides dixoniana* should be referred to *Anthopleura*, especially since Haddon had depicted large acrorhagi. Carlgren stated that if the marginal spherules of *A. dixoniana* were true acrorhagi, and if more mesenteries were present at the base than at the margin, the species should be referred to *Anthopleura* and the genus *Actinioides* would lapse. *A. dixoniana* clearly possesses atrichal marginal spherules (true acrorhagi), but the number of mesenteries is about the same distally and proximally. However, since this is true of nearly all species of *Anthopleura* a difference of only a few more mesenteries at margin or base is of no consequence (p. 214). Hence *Actinioides* should be referred to *Anthopleura*. The present specimens are, therefore, referred to *Anthopleura dixoniana* with which *A. papuensis* is conspecific.

Anthopleura handi Dunn, 1977
Figs 20–21

?*Anthopleura hermaphroditica* Carlgren, 1898: 23, fig. 18; Carlgren, 1921: 148; Carlgren, 1927: 32; Carlgren, 1949: 54, pl. 2, fig. 2; Carlgren, 1959: 22.
Anthopleura handi Dunn, 1977: 54–64, figs 1–8.

Material Examined. Singapore: Pasir Ris, 15 specimens, 24 Mar 1970 BMNH 1983.8.24.51–60.

Description. Column tall when extended, mostly smooth but with small inconspicuous verrucae near margin continuing onto marginal spherules. Marginal spherules haphazardly arranged, large to small (Figs 20a, d, e). Some spherules with atrichs but usually without. Tentacles tapered, smooth, in two circlets, inner slightly longer than outer. Disk flat; mouth large; two distinct siphonoglyphs. Base slightly smaller in diameter than disk. *Anatomy*. Sphincter diffuse (Fig. 20a-c). Mesenteries hexamerously arranged in up to four cycles; first three cycles perfect and fertile, including directives; 4th cycle incomplete, usually without filaments. Retractor muscles weak, diffuse, restricted in contraction; mesogloeal folds much branched. Parietobasilar muscles prominent, inner edge detached from mesentery. Basilar muscles present. Two well developed siphonoglyphs supported by directives. Usually same number of mesenteries distally and proximally but sometimes with additional mesenteries at either base or disk. Four specimens examined had arrangements shown in Table 12. Although verrucae often indistinct in life, in histological section structure can be seen. Imperforate cinclides located at centre of column in primary endocoels, up to 6 cinclides in a vertical row; arising as endodermal invaginations. Dioecious; broods, two embryos found in enteron of one specimen. Zooxanthellae not found. *Cnidome*. See Table 13 and Figure 21. *Colour*. Specimens from Pasir Ris were white. See Dunn (1977: 54–55) for other colour varieties.

Table 12 *Anthopleura handi*. Relation between numbers of tentacles, mesenteries at disk and base and spherules in four specimens (BMNH 1983.8.24.51–60).

	Mesenteries		
Tentacles	Disk	Base	Spherules
50	50	...	25
50	50	58	24
54	54	58	24
69	70	64	30

Distribution. Malaysia (Dunn, 1977) and Singapore (present material).

Habitat. Attached to mussels in sand, MLTL.

Table 13 Size ranges of cnidae of *Anthopleura handi* and *A. hermaphroditica* (in μm).

Location/ Type of cnida	Localities of specimens: Singapore (BMNH 1983.8.24.51)	Singapore (BMNH 1983.8.24.52)	Singapore (BMNH 1983.8.24.53)	Hawaii (Dunn 1977: 57–59)	Chile *A. hermaphroditica* (after Carlgren, 1959: 22)
Tentacle					
Spirocyst	11·8–22·4 × 1·8–3·5	13·0–21·2 × 2·4–3·6	11·3–19·9 × 1·4–2·6	9·9–24·3 × 2·1–3·7	. . .
Basitrich	14·1–23·6 × 1·8–2·4	17·7–22·4 × 2·4	15·9–21·8 × 2·4	15·3–24·7 × 1·8–3·6	21·0–24·0 × 2·8–3·0 (15·5–18·3)
Column					
Basitrich	9·4–16·5 × 1·8	10·6–15·3 × 1·8	13·3–16·5 × 1·8	11·7–20·7 × 1·8–3·1	17·0–24·0 × 2·8–3·5 (14·0–15·5)
Heterotrich	15·3–22·4 × 3·6–4·2	16·5–18·9 × 3·0–4·2	14·2–23·3 × 3·0–4·2	18·0–28·8(34·2) × 2·7–4·1(4·5)	19·7–31·0 × 4·2–6·3 (14·0–15·5)
Marginal Spherule					
Spirocyst	. . .	17·7–29·5 × 1·8–2·4	19·9–23·2 × 2·0–3·3	12·4–24·3 × 1·8–4·1	. . .
Basitrich	8·2–15·3 × 1·8	11·8–14·2 × 1·8	16·6 × 2·0 (1 only)	10·8–20·6(25·2) × 1·6–3·6	. . .
Heterotrich	Absent	29·5–43·6 × 3·0	31·8–48·2 × 2·6–4·0	27·0–43·3(50·4) × 3·2–4·5(6·3)	39·5–51·0 × 5·0–5·6 (28·2–35·2)
Atrich	Absent	38·9–49·5 × 3·6–4·8	39·6–46·2 × 4·0–4·6		
Actinopharynx					
Basitrich	11·8–17·7 × 1·8	11·8–14·2 × 1·8	13·2–14·6 × 1·8	(16·5)19·6–30·6(33·0) × 2·1–3·7	22·6–28·2 × 4·0–5·0 (. . .)
Basitrich	20·0–24·8 × 2·4–3·0	15·3–26·0 × 2·4–3·0	15·3–23·8 × 2·0		
Microbasic amastigophone	17·7–21·2 × 3·6–5·8	15·3–20·0 × 4·2–4·7	13·2–19·9 × 3·3–4·0	16·5–22·7(24·7) × 4·1–6·2	21·0–24·0 × 4·2–4·5 (. . .)
Filament					
Basitrich	10·6–11·8 × 1·2	8·2–10·6 × 1·2	. . .	8·2–20·0 × 1·8–3·2	. . .
Basitrich	26·0–33·0 × 3·6–4·7	23·6–29·5 × 3·6–4·8	21·2–29·8 × 3·0–3·6	24·3–37·1(39·1) × 3·2–5·4	24·0–35·2 × 4·2–5·6 (24·0–29·6)
Microbasic p-mastigophore	11·8–15·3 × 3·0	11·8–17·7 × 2·4–3·0	10·6–14·2 × 2·4	(14·4)16·5–24·7 × (2·5)3·6–7·2)	19·7–25·4 × 4·2–7·0 (18·3–21·0)
Microbasic amastigophore	18·9–21·2 × 4·0	15·3–20·0 × 3·0–5·8	14·0–18·9 × 3·6–4·7)		

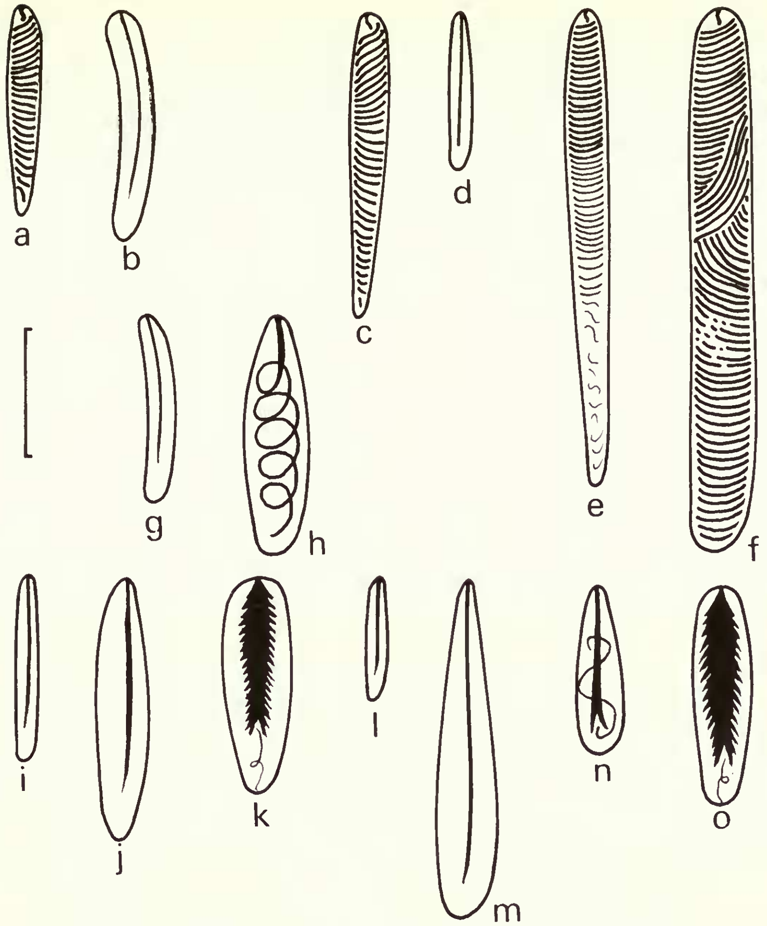

Fig. 21 *Anthopleura handi*, nematocyst signature (see Table 13). *Tentacle* (a) spirocyst, (b) basitrich. *Marginal spherule* (c) spirocyst, (d) basitrich, (e) heterotrich, (f) atrich. *Column* (g) basitrich, (h) heterotrich. *Actinopharynx* (i-j) basitrichs, (k) microbasic amastigophore. *Filament* (l-m) basitrichs, (n) microbasic p-mastigophore, (o) microbasic amastigophore. Scale: (a-o) = 10 μm.

REMARKS. The verrucated column and the atrichal marginal spherules suggest that this species is best referred to *Anthopleura*. Of the many included species only three or four have been found to brood, *A. hermaphroditica* Carlgren, 1898), *A. aureoradiata* (Stuckey, 1909; see Carlgren, 1950*c*: 4), *Anthopleura* sp. Atoda, 1945: 274, and *A. handi* Dunn, 1977: 54).

In the present material the mesenterial arrangement, sphincter characteristics and nematocyst data were as reported by Dunn in *A. handi*. There were in addition cinclides in the centre of the column and both atrichs and heterotrichs in the marginal spherules (Table 13 and Figure 21). The size ranges of the cnidae differed only slightly from those in Dunn's account and need not be considered further.

Dunn suggested that *A. handi* differed from *A. hermaphorditica* in having the sphincter diffuse, not well developed and circumscribed. Carlgren stated that the sphincter was circumscript with a tendency to become mesogloeal near its base, but his illustration (1949, pl. 2, fig. 2) appears to show a circumscript sphincter. The section was probably taken from the region where the sphincter passed through the mesentery, where the muscle folds of the sphincter and mesenteric retractor or transverse muscles might have interwoven. This might account for Carlgren's conclusion that the sphincter tended to become mesogloeal. The plane of section might account for a lamella of mesogloea between the sphincter and the column mesogloea, the sphincter in reality being diffuse. The sphincter of *A. hermaphroditica* is similar to that of *A. handi* (Figs 20a, b, c) but appears much larger. Carlgren's specimens of *A. hermaphroditica* should be re-examined.

Carlgren (1959: 22) gave the nematocyst size ranges in two specimens of *A. hermaphroditica*. In one specimen they were close to those found by Dunn and myself, but the ranges of his second specimen were so different, particularly in tentacles and column, as to suggest a distinct species. Comparison of the size ranges of this specimen with those of *Bunodactis hermaphroditica* (*sensu* Carlgren, 1959: 23) suggests that it belongs to that species. The presence of atrichs, however, precludes *Bunodactis*. The question arises as to whether *B. hermaphroditica* is best referred to *Bunodactis* or should be considered within the scope of *Anthopleura* but with the atrichs of the marginal spherules absent or suppressed (p. 239).

Carlgren stated that *A. hermaphroditica* is hermaphrodite but male gonads were not seen in the present specimen. Two specimens had young in the enteron as well as eggs on the gonads.

The only differences recorded here between *A. handi* and *A. hermaphorditica* are the presence of cinclides in *A. handi* and its considerably fewer tentacles. Carlgren reported a maximum of 90 tentacles in *A. hermaphroditica* whereas Dunn found a maximum of 61 in 200 specimens of *A. handi* and a maximum of 69 was found in the present material.

It seems best to recognize provisionally both *A. handi* and *A. hermaphroditica* until Carlgren's material can be re-examined and the identity of the latter established.

Anthopleura nigrescens (Verrill, 1928)
Figs 22–23

Tealiopsis nigrescens Verrill, 1928: 26, pl. 5A-B.
Bunodactis nigrescens: Carlgren, 1949: 65.
Anthopleura nigrescens: England, 1969: 5; Dunn, 1974*a*: 377–382, figs 1–4.

MATERIAL EXAMINED. Holotype: United States National Museum of Natural History,

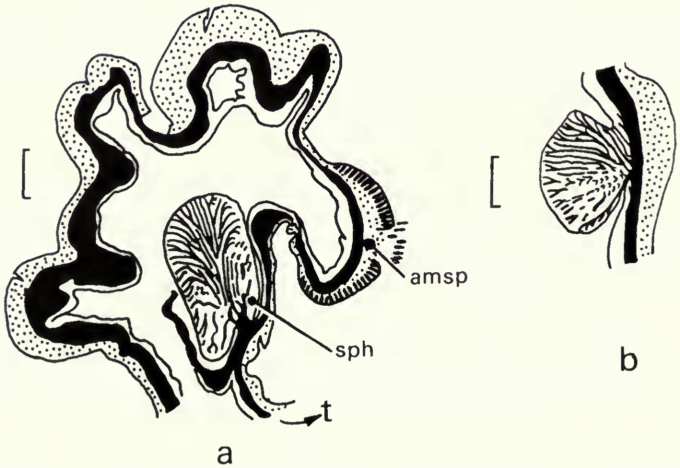

Fig. 22 *Anthopleura nigrescens* (United States National Museum 209154). (a) Vertical section through margin showing position of an atrichal marginal spherule and strong circumscribed sphincter. (b) Vertical section of restricted diffuse sphincter of a smaller specimen. Scale: (a) = 200 µm, (b) = 100 µm. (amsp atrichal marginal spherule, sph sphincter. Stippled, ectoderm; black, mesogloea; white, endoderm.)

Washington D.C., 1925–1485. Paratype: American Museum of Natural History 1480. Hawaii: 2 specimens, coll. C. E. Cutress, 1955, USNM 209154; 3 specimens, coll. D. F. Dunn (pers. coll.). Hong Kong: 2 specimens, coll. B. Morton, 20 Mar 1981. India: Cochin, coll. Kuruvilla Matthew, 1968, BMNH 1983.8.4.86. Australia: North Queensland, 2 specimens, coll. R. Muffley, James Cook University, Townsville, Queensland.

DESCRIPTION. See Dunn (1974*a*: 377–382, figs 1–4).

DISTRIBUTION. Hawaii (Verrill, 1928 as *Tealiopsis nigrescens*, Cutress, 1955 and Dunn, 1974*a*); Hong Kong, Queensland, and India (present material).

REMARKS. The species is readily identified by the heavily verrucated column, the prominent atrichal marginal spherules and the irregularly arranged mesenteries with several siphonoglyphs never supported by directive mesenteries. The spherules are normally large with verrucae on the outer face. The large nematocyst batteries are located on the crown of the spherule, often turned into the fosse, and are easily distinguished even in preserved material. Usually all spherules are atrichal. The sphincter varied from restricted-diffuse (Fig. 22b) to strong-circumscribed (Fig. 22a), and was frequently larger than indicated by Dunn (1974*a*). The sphincter of the holotype is strong-circumscribed, similar to Figure 22a. Dunn recorded 80 tentacles in samples from a Hawaiian population but a specimen from the present material has as many as 167. *Cnidome*. See Table 14 and Figure 23. The size ranges are slightly larger than those quoted by Dunn, but the differences would seem so small as to indicate that only one taxon is involved.

Table 14 Size ranges of cnidae of *Anthopleura nigrescens* (in μm).

Location/ Type of cnida	Localities of specimens: Hawaii 'Holotype' (USNM 1925–1485)	Hawaii 'Paratype' (AMNH 1485)	Hawaii (present material)	
Tentacle				
Spirocyst	24·0–3·0	14·1–26·4 × 1·8–3·0	14·4–28·8 × 1·8–2·4	14·4–27·4 × 1·8–3·0
Basitrich	...	...	12·0–14·4 × 1·2	12·0–13·2 × 1·8
Basitrich	18·0–21·6 × 1·2–1·8	15·6–20·4 × 1·8–2·4	18·0–24·0 × 1·2–1·8	18·0–24·0 × 1·8
Column				
Basitrich	9·6–20·4 × 2·4–3·0	...	9·6–24·0 × 1·8–3·0	13·2–24·0 × 2·4–3·0
Heterotrich	...	...	16·8–24·0 × 3·0–4·0	19·2–21·6 × 3·6
Marginal spherule				
Spirocyst	26·4 × 2·4	...	...	...
Basitrich	9·6–13·2 × 1·8	12·0–20·4 × 1·8	9·6–13·2 × 1·2	8·4–19·2 × 1·8
Atrich	33·6–54·0 × 3·6–5·4	absent	33·6–54·0 × 3·6–5·4	43·2–54·0 × 3·6–4·8
Heterotrich	30·0–42·0 × 3·0–3·6	absent	31·2–42·0 × 3·0–3·6	30·0–42·0 × 3·0–3·6
Actinopharynx				
Basitrich	10·8–16·2 × 1·8	9·6–12·0 × 1·8	10·8–16·8 × 1·8	10·8–13·2 × 1·8
Basitrich	18·0–25·2 × 2·4–3·0	21·6–26·4 × 2·5–3·0	18·0–25·2 × 2·4–3·0	21·6–28·8 × 2·4–3·0
Microbasic amastigophore	19·0–20·0 × 3·6	19·2–24·0 × 3·0–3·6	19·2–20·4 × 3·6 (3 only)	19·2 × 3·6 (1 only)
Filament				
Basitrich	13·2–16·9 × 2·4	10·8–18·0 × 1·8	13·2–18·0 × 2·4	14·4–18·0 × 1·8
Basitrich	22·8–31·2 × 3·6–4·8	27·6–31·2 × 3·6–4·2	22·8–31·2 × 3·6–4·8	24·0–31·2 × 3·6–4·2
Microbasic p-mastigophore	...	...	14·4 × 2·4 (1 only)	9·6–15·6 × 2·4–3·0
Microbasic amastigophore	18·2–23·4 × 3·0–4·0	18·0–21·6 × 3·6	15·6–19·2 × 3·0–3·6	16·8–20·4 × 3·0–3·6

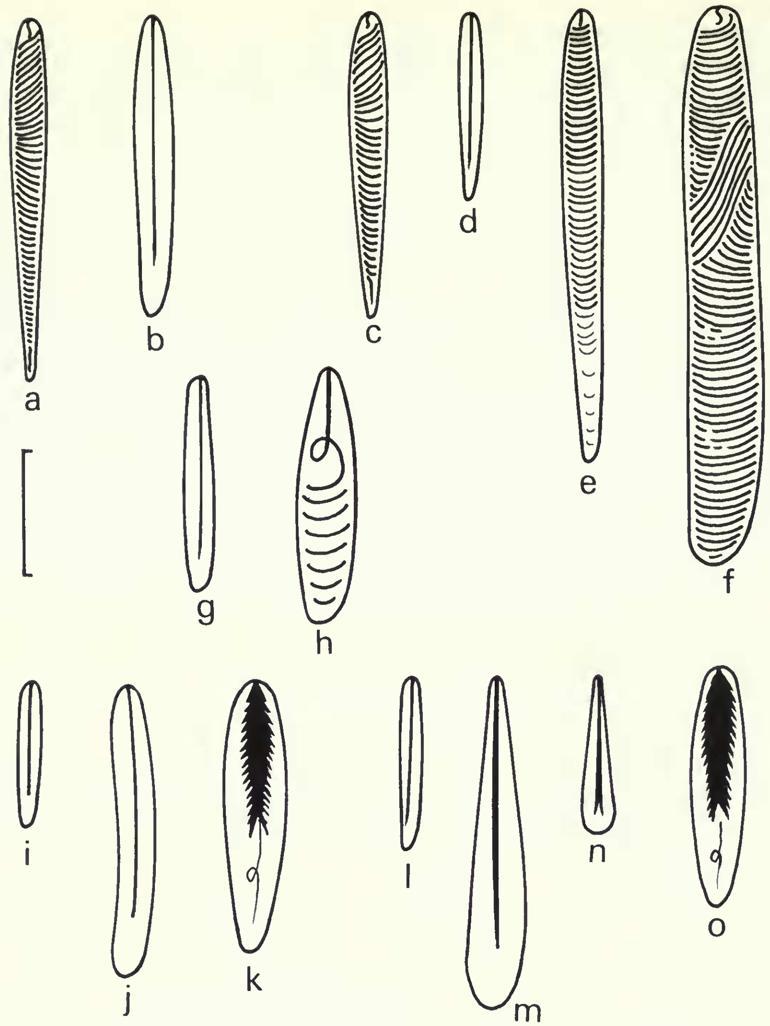

Fig. 23 *Anthopleura nigrescens*, nematocyst signature (see Table 14). *Tentacle* (a) spirocyst, (b) basitrich. *Marginal spherule* (c) spirocyst, (d) basitrich, (e) heterotrich, (f) atrich. *Column* (g) basitrich, (h) heterotrich. *Actinopharynx* (i-j) basitrichs, (k) microbasic amastigophore. *Filament* (l-m) basitrichs, (n) microbasic p-mastigophore, (o) microbasic amastigophore. Scale: (a-o) = 10 μm.

Anthopleura waridi (Carlgren, 1900), comb. nov.
Figs 24–26

Bunodes waridi Carlgren, 1900: 66–67, pl. 1 fig. 17.
Bunodactis waridi: Carlgren, 1949: 65; England 1969: 5.

Material Examined. Aden: Sapper Bay, 38 specimens, Sep 1966, BMNH 1983.8.4.87–106, 109–113. S. India: Mandapam Camp, 2 specimens, coll. C. E. Cutress, 15 Feb 1963, BMNH 1983.8.4.107–108.

Description. Column tall with vertical rows of adhesive verrucae, large in upper part of column becoming progressively smaller towards the limbus and extending to it. Each row of verrucae terminating at margin in a large spherule on the parapet. Inside fosse a separate atrichal spherule on each primary endocoel and usually on 2nd and 3rd cycle endocoels, but sometimes irregularly arranged. Atrichal spherules small to large, tentaculoid, sometimes located close to but always separated from the marginal spherules (Figs 24a, d, e). Tentacles slender, tapered, arranged in three or more cycles. Disk flat. Base present. *Anatomy*. Sphincter strong, circumscribed (Fig. 24b).

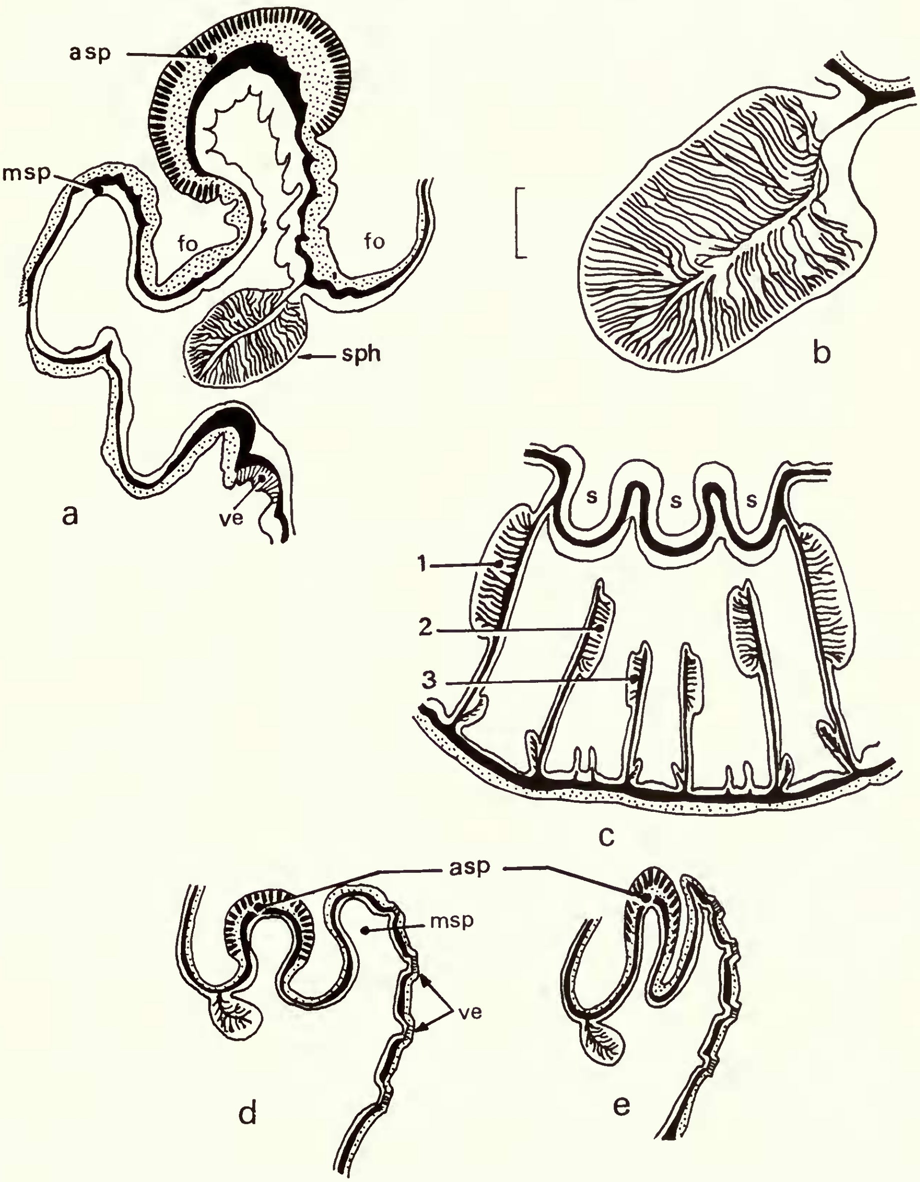

Fig. 24 *Anthopleura waridi*. (a) Vertical section of margin and sphincter with an atrichal spherule in the fosse, BMNH 1983.8.4.89. (b) Sphincter of (a) enlarged. (c) Development of triple pairs of directive mesenteries, in transverse section of column of same specimen. (d-e) Variation in shape of atrichal and marginal spherules in vertical sections of margin. Scale: (a) = 135 µm, (b) = 45 µm, (c-e) not to scale. (asp atrichal spherule, fo fosse, msp marginal spherule, s siphonoglyphs, sph sphincter, ve verruca, 1,2,3 are mesenteries of 1st, 2nd and 3rd pairs respectively. Stippled, ectoderm; black, mesogloea; white, endoderm.)

Mesenteries regularly or irregularly arranged, in up to four cycles; 1st and 2nd cycles perfect, 3rd cycle imperfect, 4th cycle only rudimentary, in some specimens not reaching disk. Siphonoglyphs 1–5, always supported by directives; sometimes in groups of three, with or without additional siphonoglyphs in other areas of actinopharynx. Mesentery development starting basally and proceeding upwards, resulting in a few more mesenteries at base than at top of column in some specimens; but in others number is same (Table 15). Retractor muscles strong, diffuse, on first cycle mesenteries, sometimes restricted. Parietobasilar muscles well developed, basilar muscles weak. Gonads on all older mesenteries including directives. Filaments absent from some younger cycles. Largest specimen, in contraction, height 13 mm, disk diameter 10 mm. *Cnidome*. See Table 16 and Figure 25. *Colour*. Column dull olive-green with bright or crimson verrucae; tentacles and disk translucent crimson.

Table 15 *Anthopleura waridi*. Relation between numbers of tentacles, mesenteries at disk and base, siphonoglyphs and spherules in four specimens (see BMNH 1983.87–106, 109–113).

	Mesenteries			
Tentacles	Disk	Base	Siphonoglyphs	Spherules
40	40	40	3	20
60	60	72	2	27
75	70	104	3	26
96	96	104	3	24

Table 16 Size ranges of cnidae of *Anthopleura waridi* (in µm).

Location/ Type of cnida	Specimens from Aden (BMNH 1983.8.4.84)	(BMNH 1983.8.4.85)	(BMNH 1983.8.4.86)
Tentacle			
Spirocyst	14·4–24·0 × 1·8–3·0	14·4–26·5 × 2·0–3·0	15·2–29·1 × 2·0–4·0
Basitrich	12·0–18·0 × 1·8–2·4	15·2–20·5 × 2·0–2·6	15·9–21·8 × 2·0–2·6
Column			
Basitrich	12·0–16·8 × 1·8–2·4	13·3–23·2 × 2·0–3·3	13·3–22·5 × 2·0–3·3
Heterotrich	18·0–21·6 × 3·0–3·6	15·2–29·5 × 4·6–6·0	20·0–26·5 × 5·3–6·0
Marginal spherule			
Spirocyst	13·3–36·3 × 2·0–4·0	17·2–33·0 × 2·0–3·3	23·2–37·0 × 3·3–4·0
Basitrich	12·0–16·8 × 2·0–2·4	11·3–15·2 × 2·0	12·0–20·4 × 2·0–2·4
Atrich	35·0–44·2 × 5·3–6·6	35·7–47·5 × 5·3–6·6	32·4–48·0 × 4·2–6·0
Heterotrich	32·4–41·0 × 4·6–5·3	29·8–44·2 × 4·0–5·3	32·4–44·4 × 3·6–4·8
Actinopharynx			
Basitrich	12·0–13·0 × 1·8	10·0–12·6 × 2·0–2·4	10·8–12·0 × 1·8
Basitrich	21·6–24·0 × 2·4	21·2–23·2 × 2·4–4·0	20·4–24·0 × 2·4
Microbasic amastigophore	18·0–20·4 × 4·2–4·8	18·5–21·2 × 4·0–4·6	18·0–24·0 × 4·8–5·4
Filament			
Basitrich	12·0 × 1·8	...	...
Basitrich	20·4–27·6 × 3·6–4·8	23·2–33·0 × 4·6–5·3	23·0–33·0 × 4·6–8·0
Microbasic p-mastigophore	12.0–14·4 × 2·4	16·6 × 3·3 (1 only)	...
Microbasic amastigophore	16·8–18·0 × 3·6–4·2	15·9–20·0 × 3·3–4·0	16·6–25·2 × 4·0–5·3

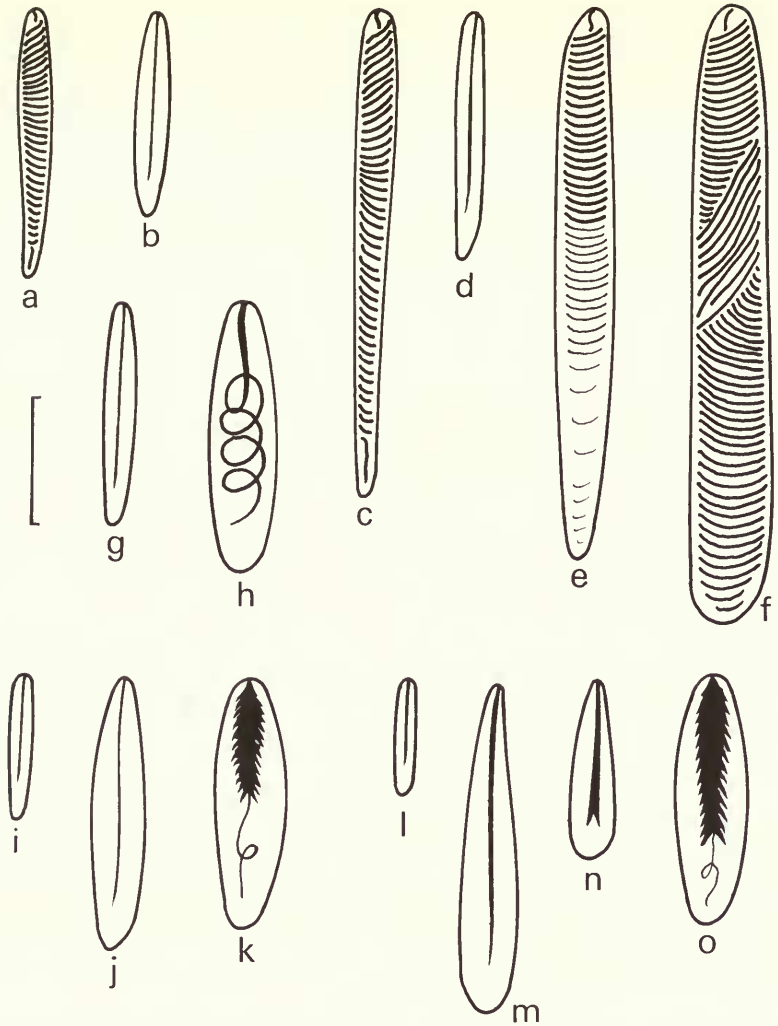

Fig. 25 *Anthopleura waridi*, nematocyst signature (see Table 16). *Tentacle* (a) spirocyst, (b) basitrich. *Spherule in the fosse* (c) spirocyst, (d) basitrich, (e) heterotrich, (f) atrich. *Column* (g) basitrich, (h) heterotrich. *Actinopharynx* (i-j) basitrichs, (k) microbasic amastigophore. *Filament* (l-m) basitrichs, (n) microbasic p-mastigophore, (o) microbasic amastigophore. Scale: (a-o) = 10 µm.

DISTRIBUTION. Zanzibar (Carlgren, 1900, as *Bunodes waridi*), Aden and S. India (present material).

HABITAT. Aden specimens found in old shells of rock oyster (*Crassostrea* sp.) and barnacles. Indian specimens on pieces of stone.

REMARKS. The verrucated column and atrichal spherules suggest that the material should be referred to *Anthopleura*. The presence of atrichal spherules in the fosse instead of on the parapet, and additional spherules on the parapet, indicate a different genus; but other characters of the species, especially the types of nematocyst, resemble those found in other species of *Anthopleura*. Also in some species of *Anthopleura* the nematocyst battery of a marginal spherule often forms a separate protuberance on the top or on the inner face (p. 210).

The colour in life recalls Carlgren's illustration of 1900 (pl. 1, fig. 17). Whilst colour of a species

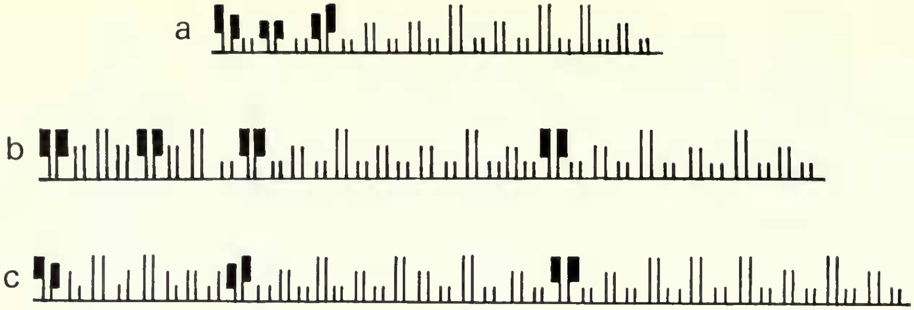

Fig. 26 *Anthopleura waridi.* Variation in arrangement of mesenteries in three specimens. (a) BMNH 1983.8.4.87, (b) BMNH 1983.8.4.88, (c) BMNH 1983.8.4.89. Directive mesenteries indicated by black rectangles.

is often of limited value in identification, in *A. waridi* it is distinctive and diagnostic. Carlgren stated that the species had forty-eight tentacles, twenty-four rows of verrucae and possessed 'pseudorandsackchen'. His illustration shows verrucae extending to the limbus. Carlgren (1949: 65) subsequently referred *A. waridi* to the genus *Bunodactis*. Examination of some poorly preserved specimens led me to identify them as *Bunodactis* (England, 1969: 5) (p. 209). Carlgren's description gives little additional information to assist in the identification since he did not describe the anatomy.

The only published description of a species of *Anthopleura* matching the particular mode of increasing the number of directive mesenteries and siphonoglyphs found in *A. waridi* is that of *A. dixoniana*. It appears that when a siphonoglyph is formed the area between the directives may develop further mesenteries. The two nearest the directives have their retractors facing outwards to complete two new pairs of directives: the next pair forms between the mesenteries of the second pair, possibly also to become directives (Fig. 24c). Additional pairs (non-directives) form between pairs of directives in the usual manner. Single siphonoglyphs meanwhile divide into two or three separate siphonoglyphs (Figs 24c and 26).

A. dixoniana differs from *A. waridi* in having atrichal spherules only on the margin and not also in the fosse; and in most of the 1st-cycle mesenteries being directives, which appear to arise in a different sequence. The sphincter of *A. dixoniana* is weak and varies in appearance while that of *A. waridi* is consistently strong-circumscribed. *A. nigrescens* (Verrill, 1928) also has several siphonoglyphs but they are never supported by directives as in *A. waridi*.

The remaining species of *Anthopleura* are not known to have atrichal spherules in the fosse or irregularly arranged mesenteries, and need not be considered further. The present material is, therefore, referred to *A. waridi* comb. nov.

Genus *GYRACTIS* Boveri, 1893

Gyractis Boveri, 1893: 241–253.
Actinioides Haddon & Shackleton, 1893: 126 (part); Haddon & Duerden, 1896: 1 (part); Haddon, 1898: 428 (part); Carlgren, 1900: 63; Carlgren, 1920: 151–153; Carlgren, 1938: 32.
Actiniogeton Carlgren, 1938: 32; Carlgren, 1949: 62; Carlgren, 1954: 579–580; Dunn, 1974*b*: 181–188.

DEFINITION. Actiniidae with well developed pedal disk. Column with longitudinal rows of adhesive verrucae. Marginal spherules large, often digitate, lacking atrichs. Sphincter weak, diffuse to circumscribed. Tentacles and mesenteries regularly or irregularly arranged. Siphonoglyphs two or more, which may or may not be connected to directive mesenteries. About same number of mesenteries distally as proximally. Retractor and parietobasilar muscles weak, diffuse; basilar muscles present. Asexual reproduction by fission probably frequent. Cnidome: spirocysts, basitrichs and microbasic amastigophores.

TYPE SPECIES. *G. excavata* Boveri, 1893; by original designation.

REMARKS. Dunn, Fu-Shiang Chia & Levine (1980: 2078) have suggested that since *Aulactinia* (= *Bunodactis*) has been defined as being with or without marginal spherules (pseudospherules) some confusion might arise with the genus *Actiniogeton*, here regarded congeneric with *Gyractis*.

Aulactinia capitata Verrill, 1864, the type species of *Aulactinia*, lacks marginal spherules, as does *A. incubans* Dunn *et al.*, 1980. Other species originally referred to this genus [*B. reynaudi* (Milne Edwards, 1857), *B. mortenseni* (Carlgren, 1924), *B. maculosa* Carlgren, 1954, and *B.* (= *Epiactis*) *novazealandica* (Stephenson, 1918)] also lack marginal spherules (personal observation). Marginal cinclides are usually present, with consequent slight swelling of the margin between the mesenterial insertions, but spherules are absent (p. 210). Hence these species should not be placed in the same genus as one having prominent, often large, marginal spherules, as exist in *Gyractis excavata*. To resolve this problem it is suggested that *Aulactinia* be re-defined to include only species lacking marginal spherules. Species currently referred to *Aulactinia* (or *Bunodactis*) that have prominent marginal spherules should be transferred to *Gyractis*, the definition of which now accommodates both regularly and irregularly arranged species. The difference between regularly and irregularly arranged mesenteries is considered here to be a specific rather than a generic character.

Carlgren's (1938, 1949) definitions of *Actinioides* (= *Actiniogeton*), however, included only those species having irregularly arranged mesenteries. If this were the only difference between *Actiniogeton* and *Aulactinia*, then *Actiniogeton* could be considered congeneric with *Aulactinia*.

Dunn *et al.* (1980: 2077) discussed the presence of atrichs in the ectoderm of the outer tentacles of *Aulactinia incubans*. As they pointed out, those occur only sporadically and are about the same size as the basitrichs. It may be that such atrichs are partially discharged basitrichs in which the straight part of the thread has been discharged and then broken off. I have seen a similar artefact in species referred to other genera. It is possible that partial discharge occurs during killing and preservation, followed by the loss of the discharged portion by either chemical action or normal handling.

Gyractis excavata Boveri, 1893
Figs 27–28

Gyractis excavata Boveri, 1893: 250, pl. 10, figs 3–4, 6.
Gyractis pallida Boveri, 1893: 251, pl. 20, figs 1–2, 5.
Actinioides sesere Haddon & Shackleton, 1893: 126; Haddon, 1898: 428, pl. 22, figs 8–9, pl. 28, figs 1–2.
Actinioides sultana Carlgren, 1900: 63, pl. 1, figs 12–13; Carlgren, 1938: 33–35, figs 13–15.
Actinioides rapanuensis Carlgren, 1920: 151–153, figs 8–10.
Actiniogeton sesere: Carlgren, 1949: 62; Carlgren, 1954: 579–580, figs 9–11; Dunn, 1974*b*: 181–188, figs 1–6.
Actiniogeton rapanuensis: Carlgren, 1949: 62.
Actiniogeton sultana: Carlgren, 1949: 62.

MATERIAL EXAMINED Aden: 43 specimens, Oct 1966, BMNH 1983.8.24.1–10, 41–50; Maldives: Gan, Addu Atoll, 10 specimens, 8 Mar 1970, BMNH 1983.8.24. 11–20. Singapore: Pulau Biola, 29 specimens, 13 Sep 1970, BMNH 1983.8.24.21–40. Hawaii: 2 specimens, coll. D. F. Dunn, 1973. Torres Straits: Mabuaing, 4 specimens, coll. A. C. Haddon, Cambridge University Zoological Museum Co 177, type material of *Actinioides sesere* Haddon & Shackleton, 1893.

DESCRIPTION. Column short, verrucae in vertical rows, with debris and stones attached. Verrucae continuing onto large digitate marginal spherules, sometimes distorting them into frondose appearance. Verrucae small in clearly defined rows, or large irregularly arranged due to growth and distortion. Margin distinct. Fosse shallow, sometimes almost disappearing in full expansion. Disk wider than column, mouth sometimes raised on cone. Tentacles short, stout, tapered, in four or five circlets, occupying about one third of disk. Inner circlets in some specimens spaced away from third and succeeding ones. Pedal disk present. *Anatomy*. Siphonoglyphs 2–11. Directives absent. Mesenteries continuous from base to disk, arranged irregularly with at least 1st and 2nd

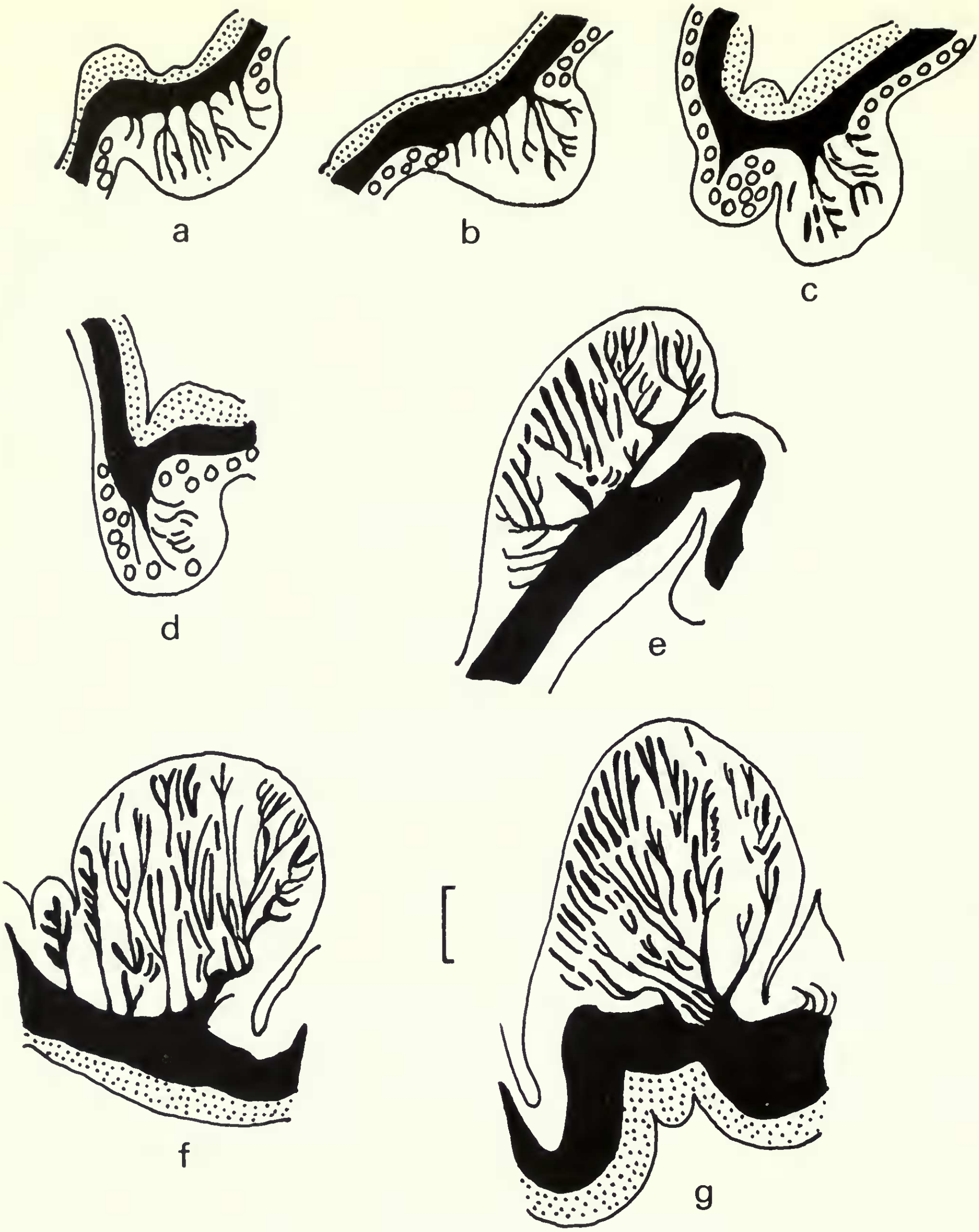

Fig. 27 *Gyractis excavata* Variation of sphincter muscle within and between specimens from different localities illustrated by vertical sections. (a-d) Aden, BMNH 1983.8.24.1–10. (e-g) Gan, BMNH 1983.8.24.11–20. (c-g) illustrate discontinuities noted in text (p. 258). Scale (a-d) = 25 μm, (e-g) = 50 μm. (Stippled, ectoderm; black, mesogloea; white, endoderm; circles, zooxanthellae.)

cycles perfect and usually a few of 3rd cycle; first three cycles fertile, 4th usually without filaments or gonads. Although gonads present, species habitually reproducing by fission, from base upwards. Retractor muscles diffuse to restricted-diffuse; parietobasilar muscles prominent, without free edge. Basilar muscles well developed (Dunn, 1974*c*). Sphincter muscle varied even within a single specimen, from weak-diffuse to weak-circumscribed (Fig. 27). Zooxanthellae present in

Table 17 Size ranges of cnidae of *Gyractis excavata* (in µm).

Location/ Type of cnida	Localities of specimens				
	Aden (BMNH 1983.8.24.1)	Aden (BMNH 1983.8.24.2)	Aden (BMNH 1983.8.24.3)	Gan (BMNH 1983.8.24.11)	Gan (BMNH 1983.8.24.12)
Tentacle					
Spirocyst	14·4–24·0 × 2·0–3·6	14·4–24·0 × 2·4–3·0	13·0–21·5 × 2·4–3·0	14·4–26·4 × 2·4–3·0	15·6–25·2 × 2·4–3·6
Basitrich	12·0–18·0 × 2·4–3·0	12·0–19·2 × 2·4–3·0	12·0–20·2 × 2·0–3·0	14·1–19·5 × 2·4–3·0	12·0–21·6 × 2·4–3·0
Column					
Basitrich	15·6–18·0 × 2·0–2·4	13·2–18·0 × 2·0	8·5–17·6 × 2·4	8·5–18·0 × 2·0–2·4	12·0–19·2 × 2·0–2·4
Actinopharynx					
Basitrich	. . .	. . .	9·8–13·0 × 2·0	. . .	. . .
Basitrich	16·8–22·8 × 2·4–3·0	19·2–24·0 × 3·6	18·2–24·7 × 2·6	18·2–24·1 × 2·4–3·6	18·0–28·8 × 2·4–3·6
Microbasic amastigophore	21·6–26·4 × 4·2	22·8–26·4 × 3·6–4·2	20·8–22·8 × 4·0–4·6	20·8–24·7 × 4·6–5·2	16·9–22·8 × 4·0–4·6
Filament					
Basitrich	10·8–16·8 × 2·4	10·8–16·8 × 2·0–2·4	9·8–18·0 × 2·0	9·8–14·3 × 2·0	10·4–14·4 × 2·0
Basitrich	21·4–32·4 × 2·4–4·2	22·8–32·4 × 3·0–3·6	20·8–32·4 × 2·6–3·3	26·0–32·4 × 3·3–4·0	28·8–34·8 × 3·6–4·8
Microbasic p-mastigophore	12·0–14·4 × 2·4	13·2–14·4 × 2·4–3·0	13·0–15·0 × 2·4	18·3 × 2·4 (2 only)	13·2–15·6 × 3·6–4·2
Microbasic amastigophore	18·0–25·2 × 3·6–4·8	19·2–22·8 × 3·6–4·2	19·5–22·8 × 4·0–4·6	18·2–26·0 × 4·0–4·6	20·8–26·4 × 3·6–4·2

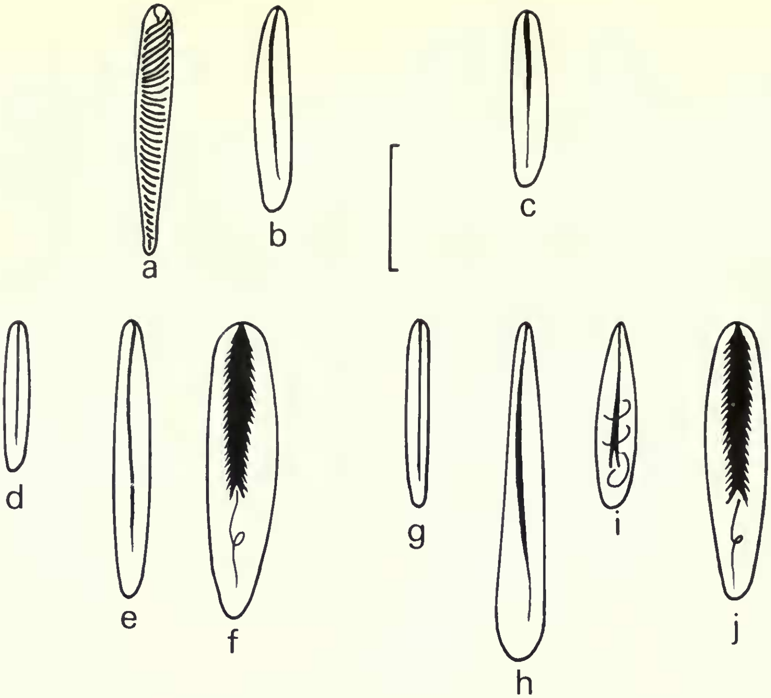

Fig. 28 *Gyractis excavata*, nemotocyst signature (see Table 17). *Tentacle* (a) spirocyst, (b) basitrich. *Column* (c) basitrich. *Actinopharynx* (d-e) basitrichs, (f) microbasic amastigophore. *Filament* (g-h) basitrichs, (i) microbasic p-mastigophore, (j) microbasic amastigophore. Scale: (a-j) = 10 µm.

endoderm of tentacles, disk, upper column and filaments. *Cnidome*. See Table 17 and Figure 28. Basitrichs of spherules of same size range as those of column. Microbasic amastigophores of actinopharynx scarce. *Colour*. Column flesh at base grading upwards through green to grey near margin. Verrucae bright green or pink. Disk and tentacles of three colour morphs: (a) disk grey, tentacles brown with white subterminal band; (b) disk green, tentacles brownish, lacking subterminal band; (c) disk and tentacles patterned green with irregular pink markings.

DISTRIBUTION. Reported from Torres Strait (Haddon & Shackleton, 1893, as *Actinioides sesere*), Sri Lanka (Boveri, 1893), Zanzibar and Durban (Carlgren, 1900, 1938, as *Actinioides sultana*), W Australia (Carlgren, 1954, as *Actiniogeton sesere*), Hawaii (Dunn, 1974*b* as *Actiniogeton sesere*), Aden, Gan and Singapore (present material) and Fiji (J. S. Ryland, pers. comm., det. D. Fautin).

HABITAT. Numerous in rock crevices on exposed outer edges of reefs, and many carpet large areas. At the Aden and Gan localities many specimens packed tightly together into cracks in a red granite or basalt. In Singapore on dead coral.

REMARKS. The specimens from Aden and Gan seemed to be of two species. Those from Aden, while having the same coloration and general form as those from Gan and occupying a similar habitat, were more delicate. The verrucae of the Aden population were smaller and arranged in vertical rows. The spherules too were smaller and not distorted by verrucae; and the sphincters were much weaker (Fig. 27). On the other hand the sphincter was of the same pattern throughout and the apparent interpopulation differences could be found in a single specimen. The muscle folds of the sphincters from both localities were often discontinuous (Fig. 27c-g), but this was not considered an artefact. All specimens of the samples examined had several siphonoglyphs without directive

Table 18 Comparison of cnidae size ranges of certain conspecific species of *Gyractis* (in µm).

Location/ Type of cnida	*Actinioides sesere* (Cambridge Univ. Zool. Mus. Coll. A.C. Haddon)	*Actiniogeton sultana* (Carlgren 1938)	*Actiniogeton sesere* (Carlgren 1954)	*Actiniogeton sesere* Hawaii. Coll. D. F. Dunn	*Actiniogeton rapanuensis* (Carlgren 1920)
Tentacle					
Spirocyst	14·4–19·2 × 1·8–2·4	11·0–22·0 × 1·5–2·5	...	10·4–19·5 × 2·0	12·0–26·0 × 1·0–2·5
Basitrich	12·0–24·0 × 1·8–3·0	14·0–18·0 × 2·0–2·5	12·7–17·0 × 2·5–2·8	13·0–26·0 × 2·6–4·0	16·0–19·0 × 2·0
Column					
Basitrich	8·4–16·8 × 1·2–2·4	14·0–17·0 × 2·0–2·5	14·0–17·0 × 2·8	9·8–19·5 × 2·0	13·0–17·0 × 2·8
Actinopharynx					
Basitrich	19·2–24·0 × 2·4	21·0–24·0 × 3·0–3·5	17·0–24·0 × 3·5	18·2–29·3 × 2·6–3·3	17·0–24·0 × 2·5
Microbasic amastigophore	22·8–4·6 (1 only)	21·0–24·0 × 5·0	19·7–21·0 × 5·0–6·0	20·8–28·4 × 4·6–5·9	...
Filament					
Basitrich	10·8–15·6 × 2·0	...	14·8–18·3 × 2·0	9·5–13·0 × 2·0	...
Basitrich	24·0–31·2 × 2·4–3·6	28·0–31·0 × 3·0–3·5	25·0–28·0 × 4·2	26·0–33·6 × 2·6–4·0	...
Microbasic p-mastigophore	12·0–14·4 × 2·4–3·6	...	...	14·3–16·3 × 2·6	...
Microbasic amastigophores	15·6–25·2 × 3·0–4·8	19·0–24·0 × 4·5–5·0	25·0–28·0 × 4·2	19·5–26·0 × 4·0–5·2	...

Note: The data from Haddon's and Dunn's material were obtained by myself. Haddon did not give data on nematocysts; and my findings in respect of Dunn's material differ slightly from those previously published (Dunn, 1974*b*; see p. 186).

mesenteries, and the size ranges and types of cnidae present were identical. The specimens from Singapore had the same variations as those from Aden and Gan.

Boveri (1893: 250–252) described two species of sea-anemone which differed only in the type of sphincter, and because they were not bilaterally symmetrical he proposed a new family, the Holoactiniidae, to include them. He proposed the genus *Gyractis* to accommodate the two species and named them *G. excavata* and *G. pallida*. His definition of *Gyractis* included a verrucated column and digitate marginal spherules, and the tentacles were said to occupy approximately half of the area of the disk with a clear gap between the 2nd and 3rd cycles. According to Boveri's description these two species lacked directive mesenteries, as the pairs of retractor muscles always faced each other: hence the absence of bilateral symmetry. He stated that there were no siphonoglyphs but if each were little differentiated from the rest of the actinopharynx there might nevertheless have been many. Boveri's illustrations of both species (1893, pl. 10, figs 1–6) show the whole animal, the arrangement of the tentacles and of the sphincter muscles, which together with the absence of directive mesenteries conform to the description given here. The colour varieties described by Boveri encompass those recorded above. The present material is thus referred solely to *Gyractis excavata* Boveri, 1893, the first of his two species. The second species, *G. pallida*, is here considered conspecific with *G. excavata*, since it has been shown that the sphincter can vary within a single specimen (Fig. 27). Under the first reviser principle the name *excavata* is given priority over *pallida*.

Though the description of *Actinioides sesere* (Haddon, 1898: 428) was incomplete the verrucated column, the capitulum provided with well defined conical acrorhagi, and the absence of gonadial grooves, show that the species is similar to *G. excavata*. Examination of four of Haddon's specimens held at Cambridge University Zoological Museum (by kind permission of the curator Dr C. B. Goodhart) confirmed that the species was identical with that of Boveri. There were no directive mesenteries but there were many siphonoglyphs, 7, 8, 9 and 9 being recorded. The types and size ranges of the cnidae taken from one of the specimens were close to those found in the present material (Table 18). *Actinioides sesere* is thus considered conspecific.

Actinioides sultana Carlgren, 1900: 63, was based on material from Zanzibar, and later redescribed (Carlgren, 1938: 33) from material collected from Durban. Carlgren's illustrations (1938, fig. 13) and description, including the size ranges of cnidae (Table 18), conform to the range of *G. excavata* given here. The coloration described by Carlgren resembles closely that which I have seen. Also, the sites at Aden and Gan were identical to that described by Carlgren (1938: 34) as 'low water, numerous specimens, congregated closely together and forming carpets on flat rocks'. Thus *A. sultana* is also considered conspecific with *G. excavata*.

Carlgren (1938: 23) also commented on the genus *Actinioides* Haddon & Shackleton, 1893, which Stephenson (1922: 271) had supposed was congeneric with *Bunodactis*. Carlgren pointed out that if *Actinioides dixoniana*, the type species of the genus *Actinioides*, were shown to have acrorhagi proper (that is, with atrichs), and if there were more mesenteries at the base than at the margin, then the genus *Actinioides* would indeed lapse. Since the species *A. sultana* (Carlgren, 1938: 33) certainly belonged neither to *Bunodactis* nor to *Anthopleura*, Carlgren said a new genus was required and he proposed *Actiniogeton* (Carlgren, 1938: 32). It has been shown that *Actinioides dixoniana* is best referred to *Anthopleura* (p. 240–245), and *Actiniogeton* might thus become a valid genus. However, for the reasons stated (p. 255) *Actiniogeton* is here considered to be congeneric with *Gyractis*.

Actinioides rapanuensis Carlgren, 1920: 151, was said to lack siphonoglyphs and directives. Its sphincter varies as in *G. excavata* and the size ranges of the cnidae reported resemble those of the present material (Table 18). It is thus considered that siphonoglyphs are probably present, although the species was first thought to lack them as were *A. sesere* and *A. sultana*. Thus *A. rapanuensis* is regarded conspecific with *G. excavata*.

Actiniogeton sesere (Dunn, 1974*b*: 181–188), based on material from Hawaii, has all the characters but one of *G. excavata*. The exception, recorded by Dunn, was a single atypical structure having the appearance of siphonoglyph. But in two specimens she kindly lent me 3 and 5 siphonoglyphs were found. In her description the presence of microbasic p-mastigophores in the column ectoderm is mentioned. The present specimens from Gan seemed to lack them, but in some specimens from Aden occasional microbasic amastigophores were seen. The ratio of microbasic amastigophores to basitrichs was 1 : 466 (4 amastigophores, 1860 basitrichs and 2 spirocysts). In one of Dunn's specimens 1035 basitrichs were counted but no amastigophores and it seems possible that in Dunn's paper the types and size ranges of the cnidae in the column and in the actinopharynx were inadvertently transposed.

Revised data on type and size range of cnidae from one of Dunn's specimens are given in Table 18. *A. sesere* sensu Dunn, 1974*b*, is also considered conspecific with *G. excavata*.

Carlgren (1947: 14–15) examined some specimens which he believed to have been studied by Boveri. In a personal communication to Carlgren, Boveri stated that he had placed specimens of both *G. excavata* and *G. pallida* in a jar without a label. Carlgren found artrichal marginal spherules in the specimens and he thought they were *Gyractis*. He concluded that *Gyractis* was congeneric with *Anthopleura*. Carlgren also stated that several other specimens in small jars from a Dr Ondaajte's collection, the source of Boveri's material, similarly had atrichal marginal spherules; and some of these specimens were accompanied by figures showing a rich variety of colour. Several species of *Anthopleura* which occur in the Indian Ocean have bright colours but the only one likely to be confused anatomically with *Gyractis* is *A. nigrescens*. It too has several siphonoglyphs and no directive mesenteries (p. 248–250) but it can be distinguished from *Gyractis* by its prominent atrichal spherules with conspicuous nematocyst batteries, and in contrast its colour is usually dull brown to black. From Carlgren's remarks there seems no evidence to connect the specimens he examined with Boveri's *Gyractis* material, and in view of Boveri's excellent description it is doubtful that Carlgren's specimens were *Gyractis*.

Of the four remaining species originally referred to *Actiniogeton* Carlgren, 1949, *A. papuensis* Haddon, 1898: 426, is conspecific with *Anthopleura dixoniana* (p. 240–245). From the original description *Actinioides spenceri* Haddon & Duerden, 1896: 159, is unlikely to be referrable to *Gyractis*, since it is reported as having more mesenteries at the base than at the margin and possibly atrichal marginal spherules. However, when Carlgren (1938: 33) examined Haddon & Duerden's slides of *A. spenceri* he could not detect the presence of atrichs though he reported spherules to be present.

Actinioides ambonensis Kwietniewski, 1897: 389, needs to be re-examined before a decision can be made: it was described as having regularly arranged mesenteries, two siphonoglyphs and 24 conical spherules but Carlgren (1938: 33) was doubtful of these details.

Genus *MESACTINIA* nov.

DEFINITION. Actiniidae with wide pedal disk. Column smooth, short, with scapus and capitulum. Margin with prominent perforate spherules, with one or more small suckers on the outer surface. Siphonoglyphs varied in number. Mesenteries regularly or irregularly arranged, with or without directives; growing from disk downwards, but same number distally as proximally. Some mesenteries of last cycle weak near base.

Many perfect mesenteries; at least 1st and 2nd cycle fertile. Sphincter diffuse-weak. Asexual reproduction common. Retractor muscles diffuse, parietobasilar and basilar muscles well defined. Cnidome: spirocysts, basitrichs, microbasic amastigophores and microbasic p-mastigophores.

TYPE SPECIES. *Mesactinia ganensis* gen. nov., sp. nov., by monotypy.

REMARKS. A new genus is proposed to include a species of actiniid having the above characters. Carlgren (1949) listed only two genera having spherules (pseudospherules) and having the same number of mesenteries distally and proximally: *Tealianthus* Carlgren, 1927: 38, had the 1st cycle sterile, and *Isotealia* Carlgren, 1898: 25, had the first two cycles sterile. The species which *Mesactinia* is proposed to accommodate has the 1st and 2nd cycles fertile and thus differs from species usually referred to either of the other genera. Although the type species of *Mesactinia* usually shows an irregular arrangement due to asexual reproduction, the definition allows for the presence of species with regular arrangements of mesenteries and tentacles.

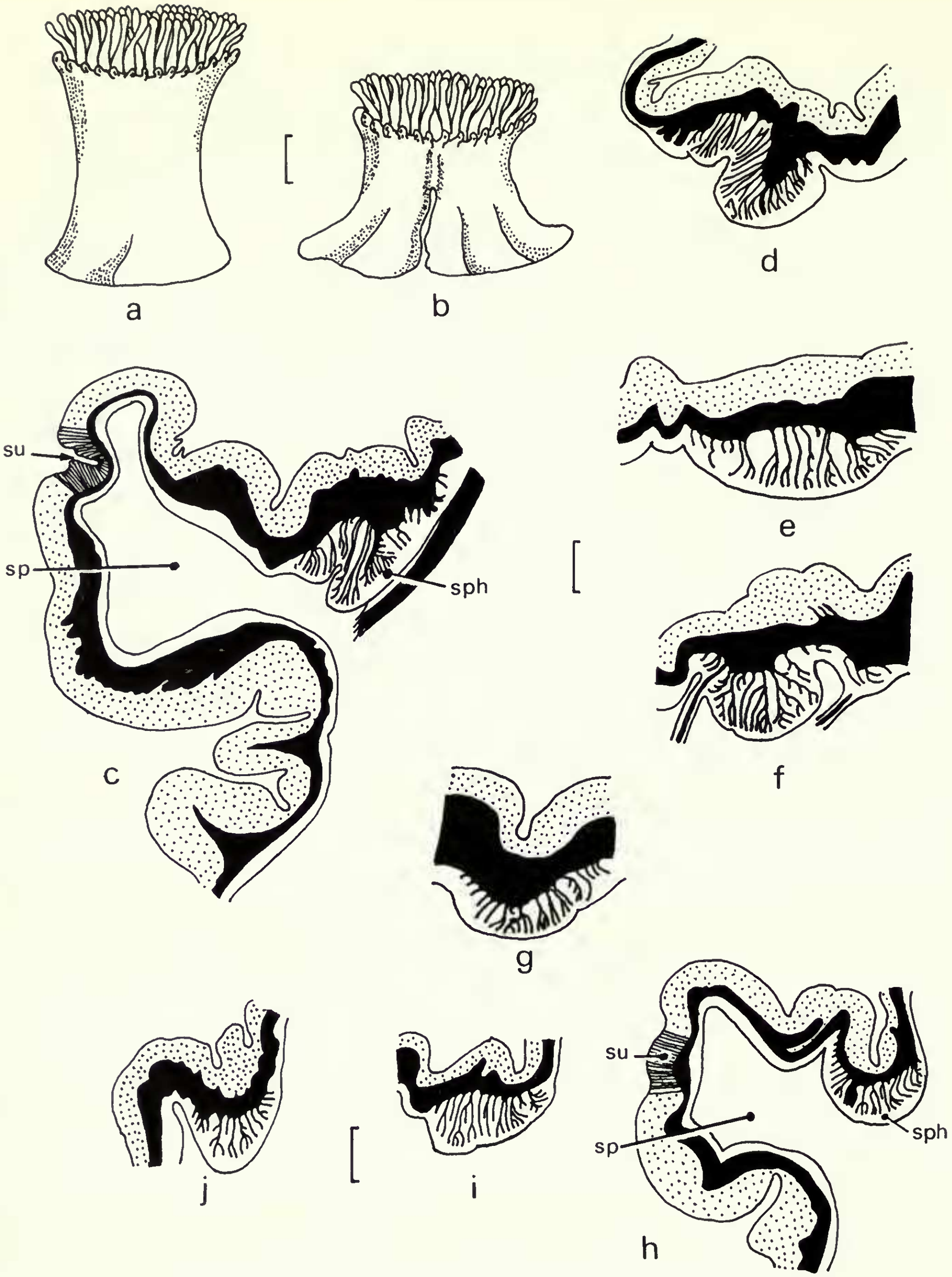

Fig. 29 *Mesactinia ganensis* gen. nov., sp. nov. (a) General appearance. (b) A specimen dividing into two from the base. (c) Vertical section of margin, BMNH 1984.2.9.90. (d-g) Variation in sphincter muscle in vertical sections of BMNH 1984.2.9.111–119. (h) Vertical section of margin of specimen from Singapore, BMNH 1984.2.9.83. (i-j) Vertical section showing variation in sphincter between two specimens from Singapore. Scale: (a-b) = 4 mm, (d-j) = 90 μm. (sp marginal spherule, sph sphincter, su sucker. Stippled, ectoderm; black, mesogloea; white, endoderm.)

Mesactinia ganensis gen. nov., sp. nov.
Figs 29–30

Type Locality and Material. Holotype: Gan Island, Addu Atoll, Maldives, 10 Feb 1970, BMNH 1984.2.9.90. Paratypes: Gan Island, 10 specimens, 10 Feb 1970, BMNH 1984.2.9.2–8; c. 50 specimens, 7 Mar 1970, BMNH 1984.2.9.10–69. Singapore: Pulau Biola, 20 specimens, 13 Sep 1970, BMNH 1984.2.9.88–110; Pungol Point, 10 specimens, 11 Feb 1971, BMNH 1984.2.9.111–119. Malaysia: Pulau Tioman, 25 specimens, BMNH 1984.2.9.120–145.

Description. Column slightly taller than wide or about equal in height and diameter, smooth with regularly or irregularly arranged large perforate marginal spherules on clearly defined parapet (Fig. 29a, b). Spherules with one or two small suckers on outer surface (Fig. 29c, h). Fosse shallow, capitulum distinct. Tentacles up to two hundred, long, slender, with rounded tips which are often dilated in life, but not capitate since special types or concentrations of nematocysts absent; in several cycles, inner about half way between mouth and margin, a clear gap between this cycle and next outer one. Oral disk wider than column, sometimes lobed; when contracted forming long funnel into body. Frequently reproducing by longitudinal fission, commencing at pedal disk (Fig. 29b). *Anatomy*. Mesenteries irregularly arranged, in four to five cycles, without directives. Sometimes one mesentery of a pair smaller than the other. Siphonoglyphs up to five, small to almost inconspicuous, or prominent. About same number of mesenteries distally as proximally, occasionally a few more distally since they grow from margin to base (p. 214). Near base mesenteries of last cycle extremely small and only visible as line on column wall, but apparent in sections. At least older mesenteries perfect and fertile, later cycles lacking filaments. Retractor muscles present. Oral and marginal stomata present. Sphincter varied, weak-diffuse (Figs 29d-i).

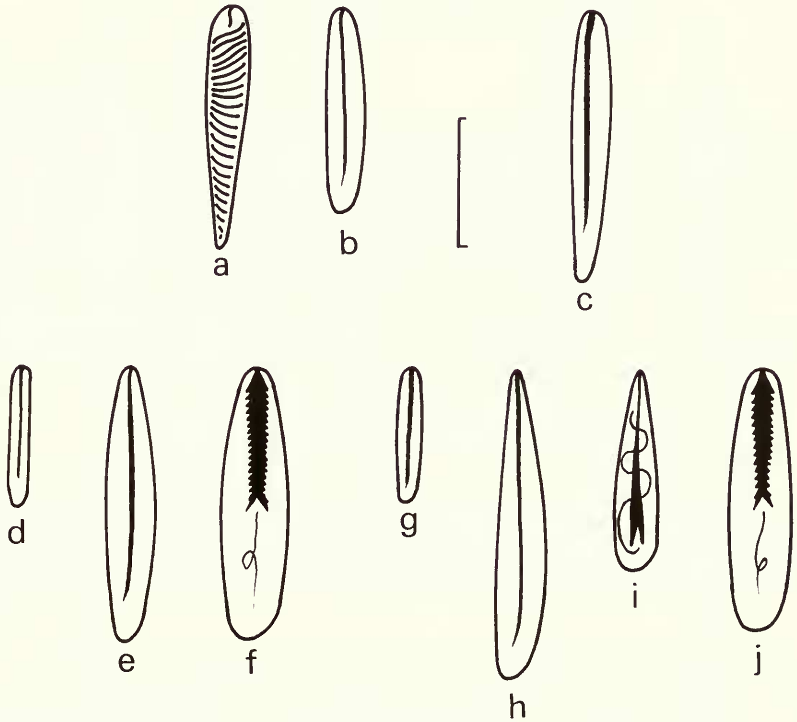

Fig. 30 *Mesactinia ganensis* gen. nov., sp. nov., nematocyst signature (see Table 19). *Tentacle* (a) spirocyst, (b) basitrich. *Column* (c) basitrich. *Actinopharynx* (d-e) basitrichs, (f) microbasic amastigophore. *Filament* (g-h) basitrichs, (i) microbasic p-mastigophore, (j) microbasic amastigophore. Scale: (a-j) = 10 μm.

Table 19 Size ranges of cnidae of *Mesactinia ganensis* gen. nov., sp. nov. (in µm).

Location/ Type of cnida	Localities of specimens				
	Gan-Addu Atoll 'Holotype'	Pulau Biola (BMNH 1984.2.9.88)	Pungol Point (BMNH 1984.2.9.111)	Pungol Point (BMNH 1984.2.9.112)	Pungol Point (BMNH 1984.2.9.113)
Tentacle					
Spirocyst	13·3–22·5 × 2·6–4·0	14·0–21·2 × 2·6–4·0	15·9–25·2 × 2·6–4·0	13·3–23·8 × 2·0–3·3	16·5–23·6 × 2·0–2·4
Basitrich	15·2–20·0 × 2·0–2·6	13·3–18·5 × 2·6–3·3	15·9–20·0 × 2·6	14·0–21·2 × 2·6–3·3	15·3–20·0 × 2·4–3·3
Column					
Basitrich	20·0–28·5 × 2·6	17·9–23·2 × 2·6	18·5–26·5 × 2·6	20·5–25·8 × 2·6	14·2–23·6 × 2·4–3·0
Actinopharynx					
Basitrich	9·3–10·0 × 2·0	...	10·6 × 2·0	...	8·2–10·6 × 2·0
Basitrich	19·2–24·5 × 3·3–4·0	18·5–22·5 × 3·3	17·9–24·5 × 3·3–4·0	19·2–24·5 × 2·6–4·0	14·2–23·6 × 2·4–2·0
Microbasic amastigophone	20·5–24·5 × 3·3–4·0	20·5–23·2 × 4·6–5·3	23·2–25·2 × 5·3	23·2–25·2 × 4·6–5·3	20·0–23·6 × 3·3–4·6
Filament					
Basitrich	10·0–10·6 × 2·0	10·0–11·3 × 2·0	10·0–10·6 × 2·0	10·6–11·0 × 2·0	8·2–9·4 × 2·0
Basitrich	25·2–29·8 × 3·3–4·0	24·5–31·7 × 3·3–4·0	25·2–28·5 × 4·0	24·5–29·8 × 3·3–4·6	17·7–29·5 × 2·6–3·3
Microbasic p-mastigophore	16·6–21·8 × 2·6–3·3	15·9–23·8 × 3·3–4·0	13·3–21·8 × 3·3–4·0	14·0–20·0 × 3·3–4·0	13·0–20·0 × 3·0–3·5
Microbasic amastigophore	19·2–24·5 × 3·3–4·6	18·5–23·2 × 3·3–4·6	21·2–24·5 × 3·3–4·6	17·9–24·5 × 3·3–4·6	18·9–22·4 × 3·5

Circular muscle folds of column low, comprising mostly unbranched single folds. Marginal spherules on most endocoels, and in adult specimens on some exocoels. Zooxanthellae present in endoderm of tentacles, disk and upper column. *Cnidome*. See Table 19 and Figure 30. Marginal spherules with basitrichs of same size range and type as column. *Colour*. Column rosy pink grading to green towards margin. Tentacles brown with faint blue sheen, sometimes with white bar near base. Disk brown, mouth flesh tone. Spherules brown with white tips. Occasional specimens had column yellowish grading to green near margin, with disk brown tinged green, and spherules brown with bright green tips.

Distribution. Recorded from the Maldives, Singapore, and Pulau Tioman on the east coast of Malaysia (type series).

Habitat. Specimens from Gan on dead stags-horn coral (*Acropora* sp.), many specimens on each branch, about 1 m below MLTL, near reef edge. Similar habitat in Singapore but also on stones in mud above MLTL. Associated with the population at Pulau Tioman was *Antheopsis malayensis* sp. nov. (p. 274).

Remarks. Some of the characters of the present species are similar to those of *Telactinia citrina* comb. nov. (p. 269), especially the large marginal spherules and the nematocyst signature. *T. citrina*, however, is separated as having more mesenteries at the margin that at the base, the youngest cycles ending abruptly near the margin; whereas the present species has about the same number of mesenteries throughout the column. Further, the number of siphonoglyphs in *Mesactinia ganensis* gen. nov., sp. nov. varies up to a maximum of five and they are never supported by directives. Hence *M. ganensis* cannot be accommodated in *Telactinia* as defined here. The species is, therefore, referred to a new genus *Mesactinia* nov.

Genus ***NEOCONDYLACTIS*** nov.

? *Paracondylactis* Carlgren, 1934: 28 (part).

Definition. Actiniidae with elongate column having verrucae in upper part, lower column being smooth. Margin distinct with marginal spherules. Sphincter diffuse to restricted-diffuse, weak. Tentacles simple, hexamerously arranged. Two siphonoglyphs supported by directives. Same number of mesenteries distally and proximally, all or almost all perfect; all fertile including directives. Retractors diffuse. Cnidome: spirocysts, basitrichs and microbasic amastigophores.

Type Species. *Neocondylactis singaporensis* gen. nov., sp. nov., by monotypy.

Remarks. A new genus is required to cover species having the characters defined above. Figure 31 shows the characters of *Neocondylactis* gen. nov. and related genera.

Neocondylactis singaporensis gen. nov., sp. nov.
Figs 32–33

? *Paracondylactis hertwigi*: Carlgren, 1934: 28.

Type Locality and Material. Holotype: Singapore: Pungol Point, 19 May 1970, BMNH 1983.11.81.1. Paratypes: Pungol Point, 9 specimens, 19 May 1970, BMNH 1983.11.18.7–15; 3 specimens, Feb 1971, BMNH 1983.11.18.16–19; Pasir Ris, 6 specimens, 24 Mar 1970, BMNH 1983.11.18.2–6.

Description. Column elongate, trumpet shaped, disk much wider than base; hour-glass shaped in contraction. Upper part of column with twenty-four vertical rows of endocoelic verrucae, up to six per row. Margin with large spherules, some of which may be compound (Fig. 32a). Often small additional exocoelic spherules in older specimens. Sometimes verrucae on outer face of spherules. Lower part of column smooth. Tentacles long, slender, tapering to rounded tip, up to 48. Disk flat, mouth with two siphonoglyphs. Base adherent. Height 25 mm contracted, extending up to 75 mm; diameter contracted 15 mm widening to 20 mm. *Anatomy*. Mesenteries arranged hexamerously, in

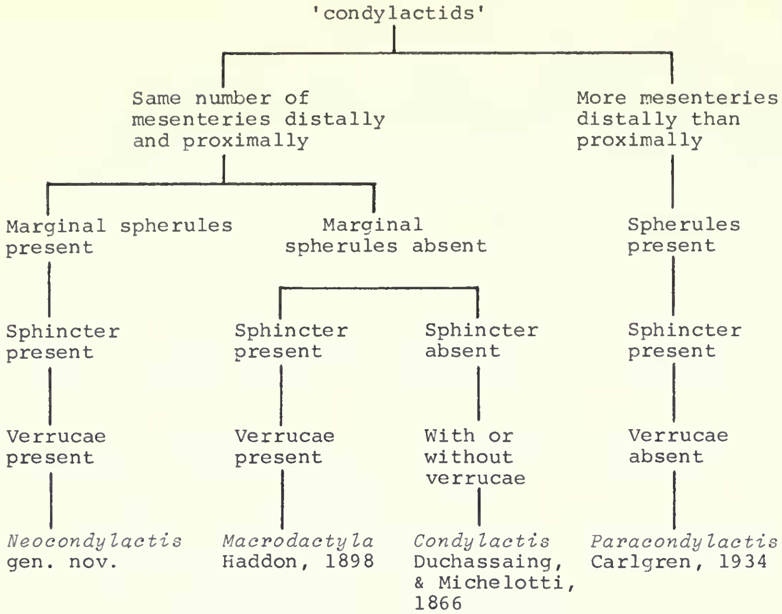

Fig. 31 Key to genera *Neocondylactis* gen. nov., *Macrodactyla, Condylactis* and *Paracondylactis.*

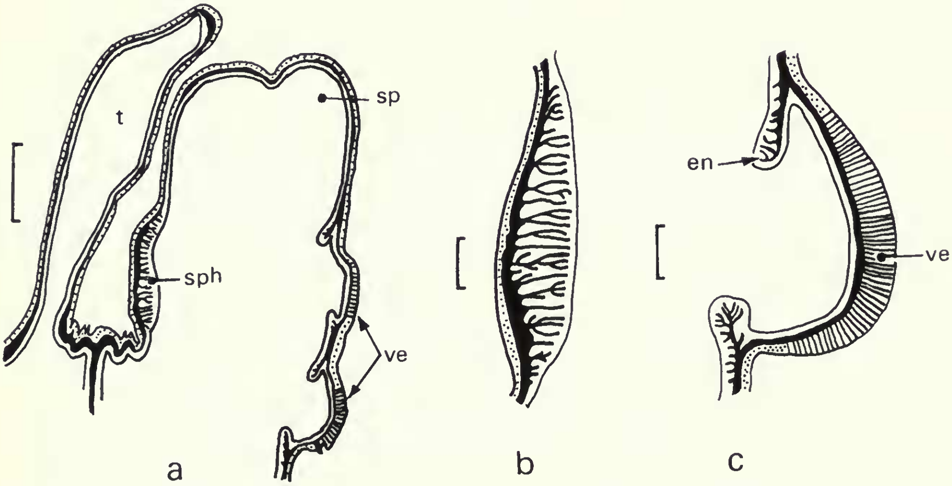

Fig. 32 *Neocondylactis singaporensis* gen. nov., sp. nov. (a) Vertical section through margin. (b) Vertical section through sphincter muscle. (c) Vertical section through a verruca, illustrating apparent sphincters consisting of thickened circular muscle. Scale: (a) = 200 μm, (b-c) = 50 μm. (en endodermal circular muscle, sp spherule, sph sphincter, t tentacle, ve verruca. Stippled, ectoderm; black, mesogloea; white, endoderm.)

three cycles, 6—6—12 pairs; all or almost all perfect, 1st cycle attached along whole length of actinopharynx, 2nd cycle along upper half and 3rd cycle attached along distal quarter only. Same number of mesenteries at margin as at base. Filaments not extending to base, occupying only two thirds of length of mesentery. Gonads located in upper part of mesentery only. All mesenteries fertile, including directives. Siphonoglyphs prolonged aborally with extension of actinopharynx on

Table 20 Size ranges of cnidae of *Neocondylactis singaporensis* gen. nov., sp. nov. (in μm).

Location/ Type of cnida	Localities of specimens Pungol Point 'Holotype'	Pasir Ris (BMNH 1983.11.18.2)	Pungol Point (BMNH 1983.11.18.7)
Tentacle			
Spirocyst	11·7–22·8 × 2·0–2·6	9·9–23·2 × 1·3–2·6	15·9–23·2 × 2·6–3·3
Basitrich	16·3–21·5 × 2·0–2·6	15·9–19·9 × 2·0–2·6	13·3–16·6 × 2·0
Column			
Basitrich	9·1–16·3 × 2·0	7·9–16·6 × 1·3–2·0	9·3–16·6 × 2·0–2·6
Actinopharynx			
Basitrich	18·9–29·3 × 2·6–3·3	16·6–22·5 × 2·0–2·6	23·2–26·5 × 2·6–4·0
Microbasic amastigophore	15·6–20·8 × 4·0–4·6	15·9–18·5 × 3·3–4·6	17·2–21·1 × 4·0
Filament			
Basitrich	10·4–11·7 × 1·3	9·9–17·2 × 1·3	9·8–11·1 × 1·3–2·0
Basitrich	26·0–33·2 × 4·0–4·6	23·2–28·7 × 3·3–4·2	28·0–35·8 × 4·0–4·6
Microbasic p-mastigophore	13·0–16·9 × 2·6	10·6–14·5 × 2·4–3·3	13·0–19·5 × 2·6–3·3
Microbasic amastigophore	16·3·20·8 × 3·3–4·6	14·5–19·9 × 3·3–4·6	16·3–21·5 × 4·0

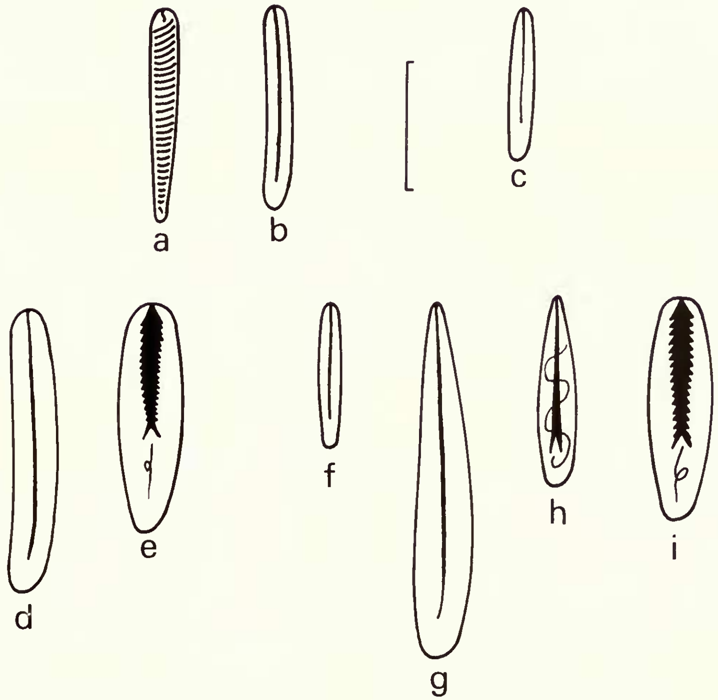

Fig. 33 *Neocondylactis singaporensis* gen. nov., sp. nov., nematocyst signature (see Table 20). *Tentacle* (a) spirocyst, (b) basitrich. *Column* (c) basitrich. *Actinopharynx* (d) basitrich, (e) microbasic amastigophore. *Filament* (f-g) basitrichs, (h) microbasic p-mastigophore, (i) microbasic amastigophore. Scale: (a-i) = 10 μm.

each side; supported by directives. Retractor muscles diffuse, strong; parietobasilar and basilar muscles present. Marginal stoma large, oral stoma small. Sphincter weak to strong, diffuse (Fig. 32b). Circular muscle folds of column low, thicker near verrucae and in sections of well extended specimens apparently forming small sphincters at bases of verrucae (Fig. 32c) which are concentrations of circular muscle round verrucal depressions. In contracted specimens verrucae appearing normal in section. *Cnidome*. See Table 20 and Figure 33. *Colour*. Column flesh colour to translucent white near base grading to greenish-white near margin. Prominent brown or green vertical lines along the mesenterial insertions. Verrucae white to off-white. Tentacles with two longitudinal brown or green lines on either side, with white or translucent spots between.

DISTRIBUTION. Recorded only from Singapore (present material).

HABITAT. Above MLTL in sand and mud, with base attached to small stones and disk lying on surface of substrate with outspread tentacles.

REMARKS. *Neocondylactis singaporensis* gen. nov., sp. nov., superficially resembles species of *Condylactis* Duchassaing & Michelotti, 1866: 125, which have elongate columns and verrucae on their upper parts. The species referred to *Condylactis*, however, have neither marginal spherules nor a sphincter, both of which are present in *N. singaporensis*. Other genera with partly similar characters are *Macrodactyla* Haddon, 1898: 431, and *Paracondylactis* Carlgren, 1934: 28; but *Macrodactyla* lacks a fosse and marginal spherules, and *Paracondylactis* has more mesenteries distally than proximally. Since no other described genus has the characters of the present species a new genus is proposed.

Genus ***TELACTINIA*** nov.

Anemonia: Haddon & Shackleton, 1893: 125 (part).
Actinia: Haddon, 1898: 416–418 (part).
Isactinia: Carlgren, 1947: 11; Carlgren, 1949: 55.
non *Isactinia* Carlgren, 1900: 53.

NOMENCLATURE. The genus name *Telactinia* is derived from the arabic 'telata' meaning three, the third variation on *Actinia*.

SCOPE. One species, *Anemonia citrina* Haddon & Shackleton, 1893.

DEFINITION. Actiniidae with pedal disk well developed. Body short. Column smooth, but sometimes an occasional verruca in upper part. At margin a ring of well developed, perforate, basitrichal spherules. Fosse shallow. Sphincter endodermal, diffuse-weak to minute. Oral disk in older specimens lobed. Tentacles short, tapering or of equal diameter throughout, numerous, their longitudinal muscles ectodermal. Siphonoglyphs one or two, pairs of directives nil to two. Many more mesenteries at margin than at base, several pairs perfect; most, including directives, fertile. Retractors diffuse. Parietobasilar muscles weak. Basilar muscles present. Cnidome: spirocysts, basitrichs and microbasic amastigophores.

TYPE SPECIES. *Anemonia citrina* Haddon & Shackleton, 1893: 125.

REMARKS. The genus *Isactinia* was introduced by Carlgren (1900: 53) to accommodate *I. badia* Carlgren, 1900: 53–55, but later (Carlgren, 1947) he referred this species to the genus *Anthostella* Carlgren, 1938: 38. *Anthostella* had the same number of mesenteries distally as proximally, and had atrichal marginal spherules between which were spherules without atrichs. Carlgren's (1900) definition of *Isactinia* mentioned that the mesenteries were numerous. He noted fifty pairs of mesenteries (i.e. 100 mesenteries) to 107 tentacles, indicating that the numbers of mesenteries at base and margin were about the same. *I. citrina* has 48 pairs of mesenteries at the base to 400 or more tentacles, indicating a difference of almost two cycles between base and margin (Carlgren, 1947). The two species differ sufficiently for it to seem appropriate now to establish a new genus to accommodate one of them.

The genus *Anthostella* now seems referable to *Isactinia* as defined in Carlgren, 1900, and *Anthostella* and *Isactinia* are probably referable to *Anthopleura* (p. 238). The species originally included in *Isactinia* have the same number of mesenteries at margin and base, a smooth column with more or less distinct longitudinal rows of spots, and atrichal marginal spherules. As just mentioned the species which Carlgren (1947) later referred to *Isactinia*, however, have more mesenteries at margin that at base. *Isactinia* Carlgren, 1900, was defined differently and it seems consistent to propose a new genus to include some of the species referred to *Isactinia* today. The genus *Telactinia* nov. is proposed to embrace the single known species having more mesenteries distally than proximally.

Telactinia gen. nov. ***citrina*** (Haddon & Shackleton, 1893)
Figs 34–35

Anemonia citrina Haddon & Shackleton, 1893: 125; Stephenson, Stephenson & Tandy, 1931: 57.
Actinia citrina: Haddon, 1898: 416–418, pl. 22, figs 1–2, pl. 26, figs 1–5.
Isactinia ignota Carlgren, 1947: 11; Carlgren, 1950*b*: 434–436, text-figs 7–10.
Isactinia citrina: Carlgren, 1949: 55.
Isactinia lobata Carlgren, 1950*b*: 436–437, text-fig. 11.

MATERIAL EXAMINED. Singapore: Horse Shoe Reef, 1 specimen, 22 Feb 1970, BMNH 1983.11.18.24; Pulau Hantu, 3 specimens, 5 May & 17 Sep 1970, BMNH 1983.11.18.22–23, 25; Cyrene Reef, 1 specimen, 12 Oct 1969, BMNH 1983.11.18.20.

DESCRIPTION. Column mostly smooth but occasional verrucae present near margin, in one specimen a single row of verrucae. At margin a circle of large, prominent, basitrichal spherules, often irregularly arranged, on parapet. Shallow fosse present. Tentacles about 400, in several circles near outer edge of disk; short, tapered, or of equal diameter throughout, tips blunt-rounded or expanded into small spheres, but not capitate. Margin and outer part of disk often deeply folded. Centre of disk flat with small mouth. Pedal disk wider than column. *Anatomy*. Although tentacles may appear capitate, no terminal concentration of nematocysts on tentacle; nematocysts at tip same type and size range as elsewhere in tentacle. Thus tentacles desribed as not capitate, terminal expansions due to contraction or weaker mesogloea. Tentacles arranged hexamerously, in at least seven cycles, or irregularly. Mesenteries arranged hexamerously, or irregularly with more mesenteries on one side than other. One specimen with 44 pairs of mesenteries at centre of

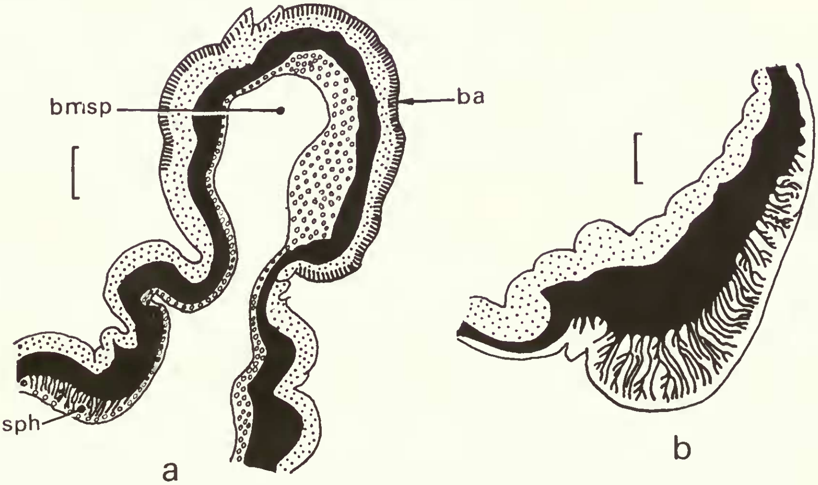

Fig. 34 *Telactinia* gen. nov. *citrina*. Vertical sections to show (a) basitrichal marginal spherule, (b) sphincter muscle, BMNH 1983.11.18.24. Scale: (a) = 150 µm, (b) = 50 µm. (ba basitrichs, bmsp endocoel of bastrichal marginal spherule, sph sphincter. Stippled, ectoderm; black, mesogloea; white, endoderm; circles, zooxanthellae in endoderm.)

column, 18 pairs on one side and 26 on the other. Two siphonoglyphs supported by directives in all specimens. At centre of column four cycles of mesenteries present, sometimes with one or two additional pairs of a 5th cycle; at margin six cycles. Most 5th cycle mesenteries extending for short vertical distance before becoming reduced to no more than a line that may reach base; 6th cycle mesenteries ceasing abruptly and little more than gussets but representing a complete cycle more at margin than at base. First four cycles fertile, including directives; up to 24 pairs perfect. Retractor muscles strong-diffuse, parietobasilar muscles weak, basilar muscles well developed. Oral and marginal stomata present. Endocoelic perforate basitrichal marginal spherules occurring over all major endocoels, with some on endocoels of younger mesenterial pairs. One specimen with 110 spherules, including 14 over 5th cycle endocoels. Basitrichs here extraordinarily numerous and densely packed, recalling arrangement of atrichs in atrichal spherules (Fig. 34a). Sphincter usually uniform between specimens, weak-diffuse (Fig. 34b). Zooxanthellae in endoderm of tentacles and disk. *Cnidome*. See Table 21 and Figure 35. *Colour*. Column off-white with some irregular green patches; marginal spherules white; disk brown to greenish-brown with white radial markings; tentacles brown with translucent white band near tip, which is often bright green.

Table 21 Size ranges of cnidae of *Telactinia* gen. nov. *citrina* (in μm).

	Localities of specimens			
Location/ Type of cnida	Cyrene reef (BMNH 1983.11.18.20)	Horseshoe reef (BMNH 1983.11.18.24)	Pulau Hantu (SW) (BMNH 1983.11.18.22)	Pulau Hantu (SW) (BMNH 1983.11.18.25)
Tentacle				
Spirocyst	13·2–26·5 × 2·0–5·3	20·0–26·5 × 3·3–4·6	13·3–26·5 × 2·6–4·6	12·0–29·8 × 2·6–5·3
Basitrich	15·2–20·0 × 2·6–3·3	15·2–18·5 × 2·6–3·3	15·2–18·5 × 2·6–3·3	8·0–24·5 × 2·6–3·3
Column				
Basitrich	20·0–23·2 × 2·6	20·5–25·8 × 2·0–2·6	18·5–23·8 × 2·6	18·5–27·8 × 2·6–3·3
Actinopharynx				
Basitrich	16·6–22·5 × 2·6–4·0	16·6–22·5 × 3·3–4·0	16·6–23·2 × 4·0	17·2–23·2 × 2·6–3·3
Microbasic amastigophore	23·2–24·5 × 4·0–6·0	20·0–23·8 × 4·0–5·3	. . .	23·8–27·8 × 4·0–4·6
Filament				
Basitrich	11·3–13·3 × 2·0	9·3–11·3 × 2·0	8·0–11·3 × 2·0	10·0–11·3 × 2·0
Basitrich	27·8–35·6 × 4·0–4·6	26·5–30·4 × 3·3–4·0	26·5–29·8 × 4·0–4·6	24·5–33·0 × 3·3–4·0
Microbasic p-mastigophore	11·3–18·5 × 2·6–3·3	13·3–16·6 × 2·6–3·3	13·3–16·6 × 3·3–4·0	12·0–19·2 × 2·6–3·3
Microbasic amastigophore	20·0–23·2 × 4·0–4·6	16·6–23·2 × 3·3–4·6	20·0–23·2 × 4·0–4·6	21·2–26·5 × 3·3–4·6

DISTRIBUTION. Reported from Torres Strait (Haddon & Shackleton, 1893, as *Anemonia citrina*), Great Barrier Reef (Carlgren, 1950*b* as *Isactinia citrina*, *I. lobata*, and *I. ignota*), and Singapore (present material).

HABITAT. Isolated specimens on coral stems.

REMARKS. From the descriptions of this species by Haddon & Shackleton (1893) and Haddon (1898) it is clear that the present material is identical with theirs. Haddon's (1898) specimens had a smooth column, many well defined marginal spherules, a folded margin in older specimens, a diffuse sphincter, and more mesenteries distally than proximally. There were 200 tentacles but 60–70 pairs of mesenteries. The number of mesenteries noted would depend on the position of the transverse sections, but a slightly larger difference might be expected. Haddon found one pair of directives but did not record the presence of siphonoglyphs. All the present specimens had two

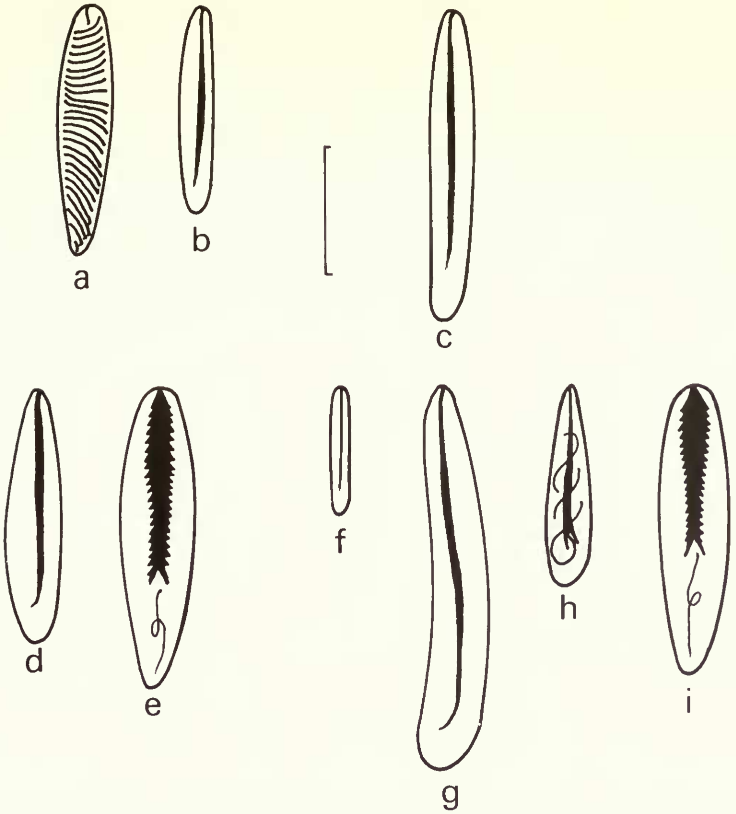

Fig. 35 *Telactinia* gen. nov. *citrina*, nematocyst signature (see Table 21). *Tentacle* (a) spirocyst, (b) basitrich. *Column* (c) basitrich. *Actinopharynx* (d) basitrich, (e) microbasic amastigophore. *Filament* (f-g) basitrichs, (h) microbasic p-amastigophore, (i) microbasic amastigophore. Scale: (a-i) = 10 µm.

Table 22 Comparison between cnida type and size in *Telactinia citrina* gen. nov. and *Isactinia* species (in µm).

Location/ Type of cnida	*Telactinia citrina* (present material)	*Isactinia ignota* (Carlgren 1950*b*)	*Isactinia lobata* (Carlgren 1950*b*)	*Isactinia olivacae* (Parry 1951)*
Tentacle				
Spirocyst	12·0–26·5 × 2·6–5·3	...	...	...
Basitrich	15·2–20·0 × 2·6–3·3	14·1–19·7 × 2·8–3·5	15·5–18·3 × 2·5–3·0	15·5–25·4 × 3·0
Column & spherule				
Basitrich	18·5–27·8 × 2·6–3·3	18·3–26·0 × 2·5–3·0	19·7–26·8 × 2·4–2·8	14·0–17·0 × 2·5
Actinopharynx				
Basitrich	16·6–23·2 × 2·6–4·0	16·8–22·6 × 2·8–3·5	18·3–22·6 × 3·0–3·5	19·7–24·0 × 3·5
Microbasic amastigophore	20·0–27·8 × 4·0–6·0	16·9–21·8 × 4·2–5·6	...	17·0 × 3·5 (1 only)
Filament				
Basitrich	8·0–13·3 × 2·0	14·0–19·0 × 2·8	10·0 × 1·5	11·3–12·7 × 4·0
Basitrich	24·5–35·6 × 3·3–4·6	27·0–32·4 × 2·5–4·2	21·0–24·0 × 2·8	19·7–22·6 × 4·5
Microbasic p-mastigophore	11·3–19·2 × 2·6–4·0	...	...	...
Microbasic amastigophore	16·6–26·5 × 3·3–4·6	14·0–22·4 × 4·2–5·6	18·3–21·1 × 4·2	17·0–22·6 × 3·5–4·5

*Carlgren's measurements from Parry's material (Carlgren, 1954: 593).

siphonoglyphs. The generic definition is here constructed to include specimens with an irregular number of directives and siphonoglyphs. Haddon & Shackleton (1893) referred the species to the genus *Anemonia*, but that is inappropriate if *Anemonia* is defined as comprising species with atrichal marginal spherules and more mesenteries proximally than distally. Since *T. citrina* has more mesenteries distally, *T. citrina* should then not be referred to *Actinia* as it was by Haddon (1898), since that genus comprises species having atrichal spherules in the fosse and the same number of mesenteries distally and proximally. The present specimens from Singapore are, therefore, referred to a new genus *Telactinia* gen. nov. (see above).

Carlgren (1950*b*) separated *Isactinia ignota* from *T. citrina* on the form of the sphincter. In Carlgren's sections the sphincter superficially differed from the structure illustrated by Haddon (1898, pl. 26, fig 2), but in detail it was similar.

The different sphincters of four specimens differing in size are shown in Carlgren's text-figures 7–10. Each illustration nevertheless depicts the same type: the example in text-figure 7 is least developed and the one in text-figure 8 the most developed and similar to a well developed sphincter of *T. citrina*. Carlgren (in Stephenson, *et al.*, 1931: 57) initially suggested that *I. ignota* was conspecific with *T. citrina* but when describing it (Carlgren, 1947) he proposed a separate species. It is considered here to be conspecific with *T. citrina*.

Isactinia lobata Carlgren, 1950*b*: 436–437, was proposed on the grounds that Stephenson had informed Carlgren that the tentacles tended to be capitate compared with filiform in *I. citrina* and *I. ignota*. The sphincter was weak. He gave details of the nematocyst types and size ranges which are similar to those of *T. citrina* (see Table 22). In view of these similarities *I. lobata* is here referred to *T. citrina*.

Material of *Isactinia olivacea* Parry, 1951: 108, was examined by Carlgren (1954: 593–594) who found that while one specimen could be referred to *Isactinia* the other was *Cnidopus verater* (Drayton, 1846). He listed the types and size ranges of the nematocysts (Table 22). The basitrichs in the filaments were smaller in size than those of *I. citrina*. *I. olivacea* should perhaps be referred to *Telactinia*, possibly as a second species, but further examination is first required to confirm the ratio of the number of tentacles to the number of mesenteries at the base.

Carlgren (1945: 10) described the nematocysts of *I. mesembryanthemum* (Ehrenberg, 1834: 36) and it appears that it should not be referred to *Isactinia* since it had atrichs in the spherules. All other species at one time referred to *Isactinia* have subsequently been shown to be referrable to different genera.

Family **STICHODACTYLIDAE** Andres, 1883

DEFINITION. Endomyaria with well developed pedal disk. Column smooth or with suckers or verrucae. *Ectoderm of column always containing microbasic amastigophores (p-mastigophores).* Tentacles long or reduced, wart-shaped, or short, one per exocoel, located marginally; some older endocoels having one tentacle or a number of tentacles arranged in radial rows. Sphincter endodermal, diffuse to circumscribed, weak to absent. Longitudinal muscles of tentacles and radial muscles of oral disk ectodermal. Pairs of perfect mesenteries numerous, stronger ones with or without directives, fertile. Retractor muscles diffuse, weak to strong. Cnidome: spirocysts, atrichs, basitrichs, microbasic amastigophores and microbasic p-mastigophores.

REMARKS. Dunn (1981: 37) re-employed the name Stichodactylidae Andres, 1883, in place of Stoichactiidae Carlgren, 1900: 72, on the grounds of priority. She included the genera *Heteractis* Milne Edwards & Haime, 1851 (including the congeneric *Radianthus* Kwietniewski, 1896) and *Stichodactyla* Brandt, 1835 (including the congeneric *Stoichactis* Haddon, 1898) within its scope.

However, *Heteractis aurora* Quoy & Gaimard, 1833: 141, the type species of the genus *Heteractis* Milne Edwards, 1857: 10, differs from other species referred to the genus *Radianthus* Kwietniewski, 1896: 389, in having macrobasic amastigophores in the ectoderm of the tentacles and column, and in the actinopharynx and filaments (England, in press). *Radianthus* is, therefore, considered a valid genus with *Radianthus kukenthali* Kwietniewski, 1896: 389, the type species.

The Stichodactylidae is separated from the Actiniidae mainly on the presence of more than one tentacle communicating with some or all of the older endocoels in the former compared with the latter, in which there is only one tentacle in each endocoel. Stephenson (1922: 298) included the genus *Antheopsis* (Simon, 1892) Carlgren, 1900, in the Stoichactiidae, so as to include species that had one or only a few tentacles communicating with the older endocoels as opposed to those having them in definite radial rows. My efforts to trace the Simon, 1892, work have been unsuccessful. It was cited by Carlgren, 1900, as an Inaugural Dissertation from the University of Munich. The work was printed, but is not listed in the British Museum Catalogue of Printed Books and seems to have remained unpublished. Hence the genus *Antheopsis* is taken to date from Carlgren, 1900, which included a definition, pending clarification of the availability of the name as employed by Simon. *Proof note: A photocopy of Simon's work has now been obtained by the British Museum (Natural History).*

Carlgren (1949: 73) did not support this view and referred *Antheopsis* Simon, 1892, to the genus *Radianthus* Kwietniewski, 1896. However, elsewhere Carlgren (1950*a*: 139) recognized the genus *Antheopsis* in order to accommodate a then newly described species, *A. australiensis* Carlgren, 1950*a*. Examination of specimens referred by Carlgren to *A. australiensis* failed to find microbasic amastigophores in the column or tentacle ectoderm. The species is probably referrable to *Aulactinia*. Carlgren, (1900: 104) repeated his earlier comments about *A. koseirensis* (Klunzinger, 1877) that only one tentacle communicates with even the strongest endocoels. It is possible that more than one tentacle occurs occasionally on the older endocoels in *A. koseirensis* but specimens from Egypt and Aden examined during the present work did not have secondary tentacles (unpublished data). Carlgren (1900: 104; 1950*a*: 141) stated that he considered *Antheopsis* to be a stichodactylid genus differing from actiniids in having numerous bifid tentacles.

A previously unrecognized character may be used to distinguish the Stichodactylidae from the Actiniidae. In the Stichodactylidae, ectodermal microbasic amastigophores are present in either the column or the tentacles or in both. The definition of the Stichodactylidae is modified to include this character. Species in which they are absent from these regions are referred to the Actiniidae.

This type of nematocyst is known to occur in only one genus in the Actiniidae, *Entacmaea* Ehrenberg, 1834. The presence of microbasic amastigophores in the Stichodactylidae may have been overlooked because they are often scarce. However, they are usually larger than those in the actinopharynx or filaments and so are conspicuous in squashes and in sections. Although they usually occur in the ectoderm of both tentacles and column there are at least two species which lack them in the tentacles. *Antheopsis concinnata* Lager, 1911, and *Stichodactyla helianthus* (Ellis, 1768) (unpublished observations).

Although Dunn (1981: 80) did not report microbasic amastigophores or p-mastigophores from the column of *Stichodactyla helianthus*, I have found them in a specimen from Andros in

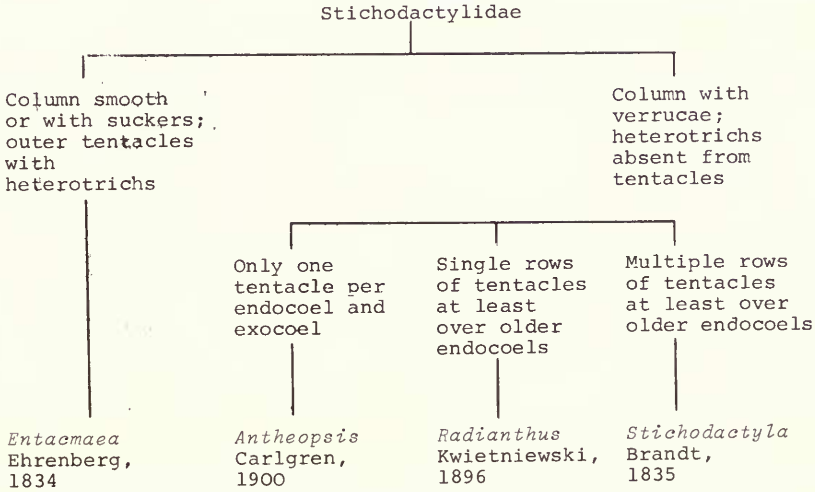

Fig. 36 Key to the genera of the Stichodactylidae.

the Caribbean provided by Dr G. F. Warner, University of Reading. The size range was 27·6.–34·8 × 5·3–6·0 μm.

Dunn (1981: 21) recorded the presence of microbasic amastigophores on the column of *Entacmaea quadricolor* (Rueppell & Leuckart, 1828). I have found them in the tentacles as well and also observed heterotrichs in the outer tentacles (see below). Dunn discovered small secondary tentacles occurring occasionally over some of the older endocoels. These were found also on a specimen from Singapore (BMNH 1984.2.15.1, see below). Assessment of these characters suggests that *Entacmaea* has more affinity with the Stichodactylidae than with the Actiniidae and it is here transferred to the Stichodactylidae.

Since Carlgren (1950*a*: 141) reinstated the genus *Antheopsis* a second species has been reported that is referred to that genus, and it is redefined here.

A key to the genera of the Stichodactylidae is given in Figure 36.

Genus *ANTHEOPSIS* Carlgren, 1900

Antheopsis (Simon, 1892: 30); Carlgren, 1900: 104; Carlgren, 1950*a*: 140; Stephenson, 1911: 300.
Bunodes: Klunzinger, 1877: 77; Andres, 1883: 451.
Radianthus: Carlgren, 1949: 73 (part).
Heteractis: Dunn, 1981: 38 (part).

NOMENCLATURE. Availability of this genus is discussed on page 273.

DEFINITION. Stichodactylidae with wide pedal disk. Oral disk sometimes lobed. Column with verrucae in upper parts and sometimes suckers below, extending to limbus. Only one tentacle communicating with older endocoels: occasionally one or two secondary tentacles, but never forming radial rows. Sphincter circumscribed through diffuse to absent. Mesenteries hexamerously or irregularly arranged; same number proximally and distally; all stronger ones fertile. Siphonoglyphs varied in number, with or without supporting directives. Retractor muscles diffuse, parietobasilar and basilar muscles present. Cnidome: spirocysts, basitrichs, microbasic amastigophores and p-mastigophores.

TYPE SPECIES. *Bunodes koseirensis* Klunzinger, 1877, by original designation.

Antheopsis malayensis sp. nov.
Figs 37–38

MATERIAL EXAMINED. Holotype: Malaysia, Pulau Tioman, BMNH 1984.2.9.1. Paratypes: 7 specimens, same locality, 27 March 1970, BMNH 1984.2.9.2–8.

DESCRIPTION. Column cylindrical to trumpet shaped, disk wider than centre of column (Fig. 37a). Margin crenulate, no true spherules. Verrucae present on margin and upper column in vertical rows of about 10, over both endo- and exocoels; lower down column reduced to suckers, recalling *Sagartia*. Near limbus suckers scattered over column. Fosse shallow. Tentacles mostly tapered, with blunt tips, sometimes inflated subdistally giving capitate appearance. Up to 65 tentacles, one communicating with each endo- and exocoel. Base narrower than disk. Column short. Average extended height 15–25 mm, disk diameter 25 mm. *Anatomy*. Siphonoglyphs 2–10, not supported by directives. Mesenteries irregularly arranged with about twelve pairs perfect; all youngest fertile, most bearing filaments with ciliated tracts; same number distally and proximally, but in centre of column youngest cycles small. No directives. Large oral and small marginal stomata present. Retractor muscles diffuse-weak, parietobasilar and basilar weak. No sphincter (Fig. 37b). Zooxanthellae present in endoderm of tentacles, disk and column. *Cnidome*. See Table 23 and Figure 38. *Colour*. Light green throughout.

DISTRIBUTION. Known from type locality only.

HABITAT. Densely packed on stems of dead stags-horn coral (*Acropora* sp.) 1 m below MLTL. Also associated with *Mesactinia ganensis* gen. nov., sp. nov. (p. 263) on same coral. Whether the two

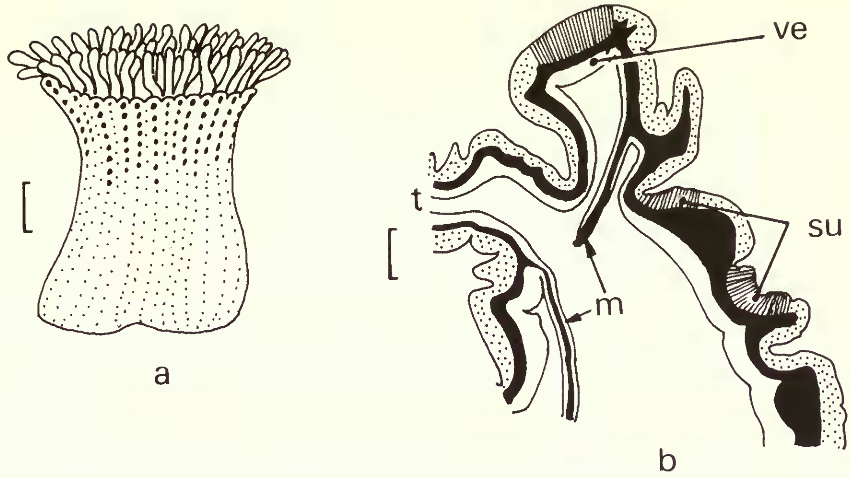

Fig. 37 *Antheopsis malayensis* sp. nov. BMNH 1984.2.9.1–8. (a) General appearance, side view. (b) Vertical section through margin showing verrucae and suckers; note absence of sphincter muscle. Scale: (a) = 4 mm, (b) = 100 µm. (m mesentery, su suckers, t tentacle, ve verruca. Stippled, ectoderm; black, mesogloea; white, endoderm; hatched, adhesive areas.)

Table 23 Size ranges of cnidae of *Antheopsis malayensis* sp.nov. (in µm).

	Locality of specimens		
Location/ Type of cnida	Pulau Tioman 'Holotype'	Pulau Tioman (BMNH 1984.2.9.2)	Pulau Tioman (BMNH 1984.2.9.3)
Tentacle			
Spirocyst	12·0–24·0 × 2·4–3·6	14·6–26·5 × 2·0–2·6	14·6–29·8 × 2·0–4·0
Basitrich	15·6–28·8 × 2·4–3·0	16·6–17·1 × 2·0–2·6	20·0–26·5 × 2·6–3·3
Microbasic amastigophore	24·0–30·0 × 4·0–6·0	21·2–25·2 × 4·6–5·3	21·2–28·5 × 4·6–5·3
Column			
Spirocyst	24·0–25·2 × 3·0	23·2–28·5 × 2·6	21·8–27·8 × 3·3
Basitrich	18·0–22·8 × 2·4	16·6–23·2 × 2·0–2·6	21·2–25·2 × 2·6
Microbasic amastigophore	24·0–26·4 × 4·8–6·0	...	22·8–28·5 × 4·6–5·3
Actinopharynx			
Basitrich	9·6–16·8 × 2·0	...	15·2–16·6 × 2·0
Basitrich	20·4–28·8 × 3·0	23·8–29·8 × 2·6	26·5–29·8 × 3·3
Microbasic amastigophore	19·2–24·0 × 4·2	23·2–25·2 × 4·6	22·5–27·6 × 4·6–5·3
Filament			
Basitrich	14·6–17·2 × 2·0	13·3–18·5 × 2·0	14·6–16·6 × 2·0
Basitrich	15·2–23·2 × 3·3	17·9–20·0 × 2·6–3·3	13·3–20·0 × 3·3–4·0
Basitrich	25·8–32·3 × 5·3–6·6	23·2–33·0 × 4·0–5·3	29·8–36·3 × 4·6–6·0
Microbasic amastigophore	21·8–27·1 × 4·6–5·3	21·2–26·5 × 4·0–4·6	21·2–26·5 × 4·0–4·6

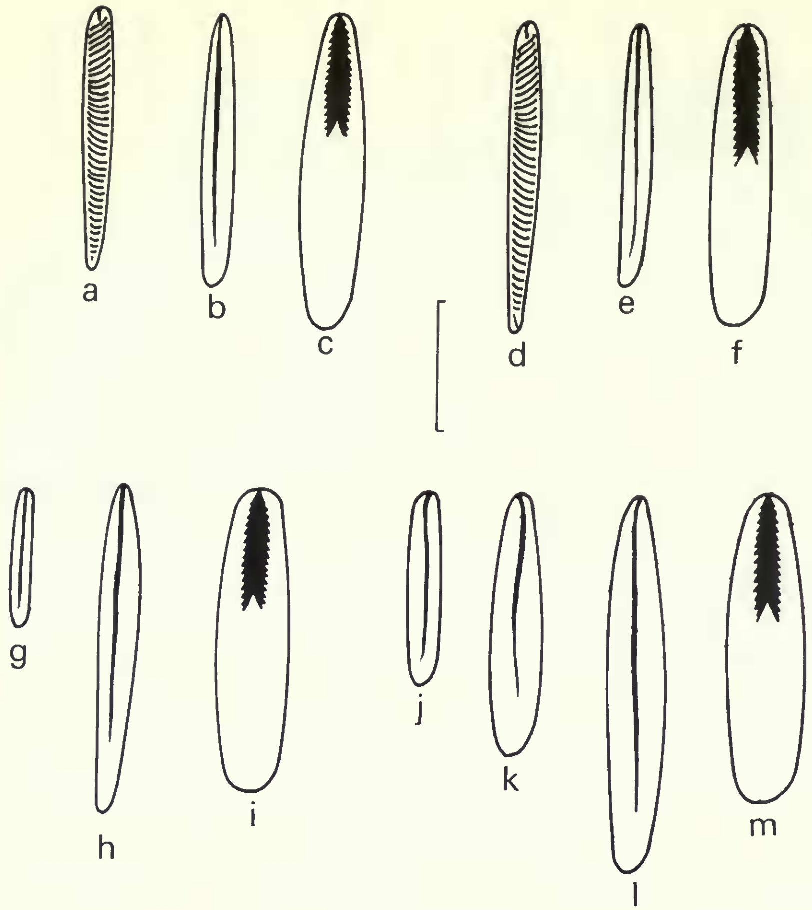

Fig. 38 *Antheopsis malayensis* sp. nov., nematocyst signature (see Table 23). *Tentacle* (a) spirocyst, (b) basitrich, (c) microbasic amastigophore. *Column* (d) spirocyst, (e) basitrich, (f) microbasic amastigophore. *Actinopharynx* (g-h) basitrichs, (i) microbasic amastigophore. *Filament* (j-l) basitrichs, (m) microbasic amastigophore. Scale: (a-m) = 10 μm.

species keep in separate groups or are mingled is not known. The species was not discovered until noticed among preserved specimens of *M. ganensis*.

REMARKS. The presence of microbasic amastigophores in the tentacles and on the column indicates affinity with species of Stichodactylidae. The single tentacle per endo- and exocoel and the verrucated column suggest that the present material should be referred to the genus *Antheopsis*. Stephenson (1922: 300) listed 10 species of *Antheopsis* but several have the tentacles in radial rows and are referred to *Radianthus*, and another, *A. carlgreni* Lager, 1911, is referred to *Entacmaea*. The three species *A. koseirensis* (Klunzinger, 1877), *A. glandulosa* Lager, 1911, and *A. kwietniewski* Lager, 1911, differ from the present material in having regularly arranged mesenteries and a sphincter. It is, therefore, proposed to refer the present material to a new species, *Antheopsis malayensis* sp. nov.

Genus *ENTACMAEA* Ehrenberg, 1834

For synonymy see Dunn, 1981: 13–14.

DEFINITION. Stichodactylidae with well developed pedal disk. Column smooth or with small suckers in upper part. Margin distinct, without spherules; fosse deep. One tentacle per endocoel and per exocoel, but in large specimens a small subsidiary tentacle may occasionally be found close to or on the tentacles of older cycles. Subsidiary tentacles never forming radial rows. Ectoderm of outer tentacles with heterotrichs. Longitudinal muscles of tentacles and radial muscles of oral disk ectodermal. Siphonoglyphs varied in number, normally supported by directives. Perfect mesenteries numerous; all stronger ones, including directives, fertile. More mesenteries at margin than at base. Sphincter weak to strong, diffuse; rarely absent. Cnidome: spirocysts, heterotrichs, basitrichs, microbasic amastigophores and p-mastigophores.

TYPE SPECIES. *E. quadricolor* Ehrenberg, 1834, by monotypy.

Entacmaea quadricolor Ehrenberg, 1834

For synonyms see Dunn, 1981: Fig. 39.

MATERIAL EXAMINED. Red Sea: Egypt, 2 specimens, coll. Dr F. A. Shoukr. Singapore: Pulau Hantu, 1 specimen, 18 Jan 1970, BMNH 1984.2.15.1; Pulau Biola, 1 specimen, 13 Sep 1970, BMNH 1985.2.13.7.

REMARKS. There is little to add to the comprehensive description given by Dunn (1981: 15–28, figs 5–10). In the present material there are small suckers scattered over the upper part of the column, and additional types of nematocysts in certain areas. The suckers are not visible in whole preserved specimens but are easily seen in histological sections and resemble those depicted by Stephenson (1928: 13–14, fig. 8c) in *Sagartia elegans* Dalyell, 1848.

There is a dense concentration of nematocysts inside the fosse and over the margin. Most are basitrichs, a few are microbasic amastigophores, and spirocysts are absent. The nematocysts are

Table 24 Size ranges of cnidae of *Entacmaea quadricolor* (in μm).

	Locality of specimens			
Location/ Type of cnida	Egypt (Red Sea) Coll. F. A. M. Shoukr	Egypt (Red Sea) Coll. F. A. M. Shoukr	Pulau Hantu (BMNH 1984.2.15.1)	Pulau Biola (BMNH 1985.2.13.7)
Tentacles				
Spirocyst	18·5–39·6 × 2·6–5·3	18·5–35·0 × 2·0–6·0	16·6–33·7 × 2·0–4·6	18·0–35·0 × 2·6–4·0
Basitrich	10·6–12·6 × 2·6–3·0	11·3–14·6 × 3·3	8·6–10·0 × 2·0	...
Basitrich	18·5–26·5 × 3·3–6·0	18·5–25·8 × 3·3–5·3	16·6–25·2 × 4·6–5·3	17·2–27·8 × 4·0–5·3
Heterotrich	24·5–30·4 × 4·0–4·6	25·2 × 4·6 (1 only)	23·8–27·8 × 4·0–4·6	20·5–29·8 × 3·3
Microbasic amastigophore	28·5–37·6 × 5·3–6·6	29·1–36·3 × 5·3–6·6	33·0–44·9 × 6·0–6·6	28·5–35·0 × 5·3–6·0
Column				
Basitrich	11·3–12·0 × 2·0–2·6	10·6–13·3 × 2·0–2·6	10·0–11·3 × 2·0	9·3–12·0 × 2·0
Basitrich	21·8–26·5 × 2·6–3·3	17·9–26·5 × 2·6–4·0	17·9–27·7 × 3·3	18·5–24·5 × 2·6–3·3
Microbasic amastigophore	33·0–41·6 × 5·3–6·6	31·7–41·0 × 6·6–7·2	39·6–50·2 × 6·0–7·2	30·1–42·9 × 5·3–6·6
Actinopharynx				
Basitrich	18·5–26·5 × 4·0–4·6	18·5–25·8 × 4·0–4·6	18·5–26·5 × 3·3–4·0	20·0–25·2 × 3·3–4·0
Microbasic amastigophore	26·5–29·8 × 5·3–6·0	22·5–29·8 × 6·0–6·6	30·1–38·3 × 4·6–6·6	24·5–31·1 × 4·6–5·3
Filament				
Basitrich	13·3–15·2 × 3·3–4·0	12·0–14·0 × 2·6–3·3	11·3–13·3 × 2·6	12·0–13·3 × 2·0
Basitrich	21·2–25·8 × 4·0–5·3	20·0–24·5 × 3·3	16·6–26·5 × 3·3	17·9–20·0 × 3·3
Microbasic p-mastigophore	19·2–21·8 × 5·3–6·0	20·0–22·5 × 4·6–6·0	23·2–26·5 × 4·0	20·0–23·2 × 4·0–4·6
Microbasic amastigophore	24·5–29·8 × 6·0–6·6	21·2–29·8 × 5·3–6·6	31·7–36·3 × 5·3–6·0	28·5–33·0 × 4·6–5·3

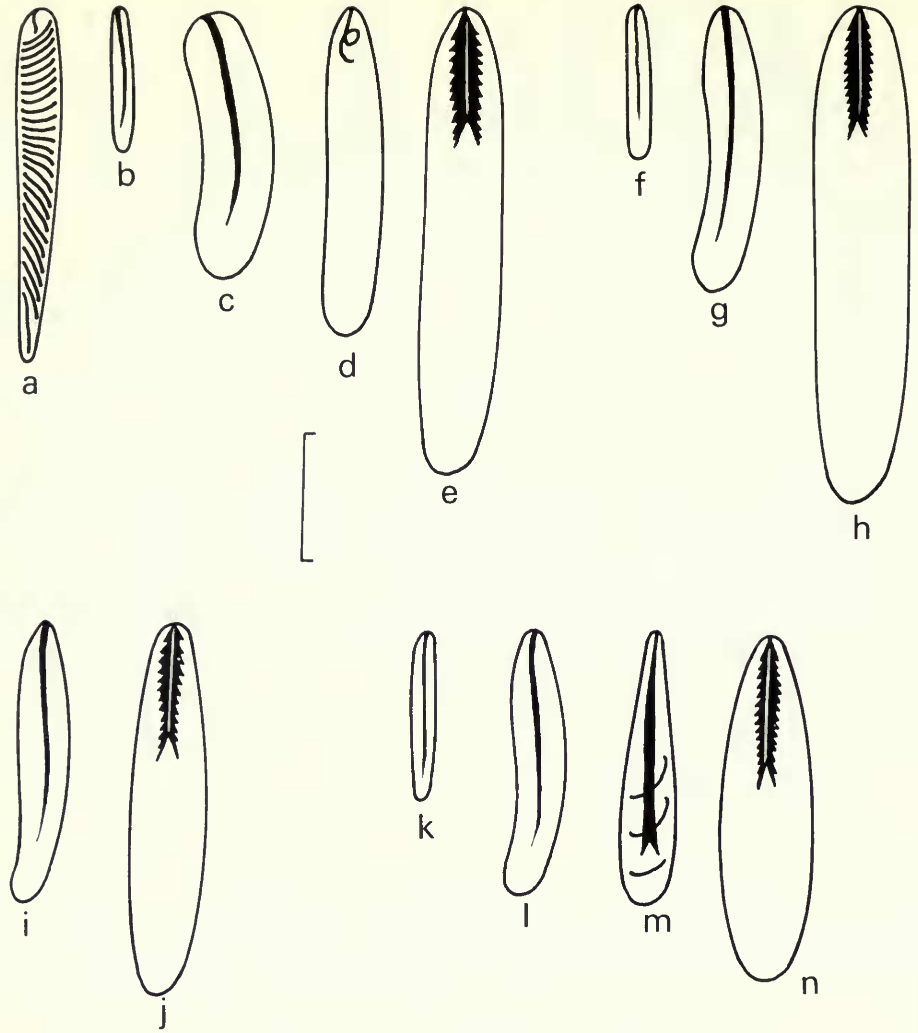

Fig. 39 *Entacmaea quadricolor*, nematocyst signature (see Table 24). *Tentacle* (a) spirocyst, (b-c) basitrichs, (d) heterotrich, (e) microbasic amastigophore. *Column* (f-g) basitrichs, (h) microbasic amastigophore. *Actinopharynx* (i) basitrich, (j) microbasic amastigophore. *Filament* (k-l) basitrichs, (m) microbasic p-mastigophore, (n) microbasic amastigophore. Scale: (a-n) = 10 μm.

closely packed as in a spherule and this feature continues around the margin. Microbasic amastigophores have been found in the ectoderm of the tentacles and the column by examination of squash preparations and serial sections. Heterotrichs have been found on some tentacles, confined mostly to the outer cycles.

Dunn (1981: 24) considered that specimens with regularly arranged mesenteries belong to the same species as those with irregularly arranged mesenteries, but it is customary to use this character to differentiate species. All specimens discussed here have a regularly arranged internal anatomy.

Cnidome. See Table 24 and Figure 39. The basitrichs of the tentacles and of the column ectoderm differ in shape from those found in the Actiniidae and Stichodactylidae. They are much broader and have a thread that is easily seen under the light microscope.

Sub-tribe **ACONTIARIA** Carlgren, in Stephenson, 1935
Family **HORMATHIIDAE** Carlgren, 1932

NOMENCLATURE. Carlgren (1949: 91) gave the authority for the Hormathiidae as Carlgren, 1925*c*, but did not indicate the publication. None of the three references given by Carlgren dated 1925 mentioned Hormathiidae. His earliest suggestion that certain genera should be separated from the Sagartiidae was Carlgren, 1928, when he placed the name Hormathiiden in brackets after Sagartiidae in the generic definitions of *Paracalliactis* Carlgren, 1928, *Calliactis* Verrill, 1869*b*, *Phelliactis* Simon, 1982, and *Chondrophellia* Carlgren, 1928. It was not until 1932 that he gave his reason. Carlgren (1932: 262) then stated that the family Chondractiniidae Stephenson, 1920: 478, which was based on the sub-family Chondractiniinae Haddon, 1889: 305, must be referred to the Hormathiidae since the genus *Chondractinia* Lutken, 1860: 190, was congeneric with *Hormathia* Gosse, 1859: 47. In fact *Chondractinia* is a *nomen nudum* since, according to Haddon, no definition was given. The correct authority for the family Hormathiidae is, therefore, Carlgren, 1932.

Genus *Calliactis* Verrill, 1869*b*

Priapus Forsskål, 1775: 102.
Actinia: de Blainville, 1830: 293 (part); Dana, 1846: 139 (part).
Cribrina Ehrenberg, 1834: 40.
Cribrina (Tristemma) Brandt, 1835: 293.
Calliactis Verrill, 1869*b*: 481.
Adamsia: Haddon & Shackleton, 1893: 130.

DEFINITION. Hormathiidae with well developed pedal disk. Column smooth, slightly differentiated into scapus (which has a weak cuticle) and scapulus, or undifferentiated, often thick; sometimes with numerous ectodermal invaginations which do not pierce the wall. Cinclides always present in lower part of column. Sphincter strong, mesogloeal. Tentacles rather short, tapered, more numerous than mesenteries at base, their longitudinal muscles ectodermal. Radial muscles or oral disk more or less embedded in mesogloea. Siphonoglyphs two, broad. Six pairs of perfect, sterile mesenteries. Retractor muscles diffuse, weak, parietobasilar muscles weak or well developed. Often commensal with hermit crabs. Cnidome: spirocysts, basitrichs, microbasic amastigophores.

TYPE SPECIES. *Priapus polypus* Forsskål, 1775, by present designation (p. 280).

Calliactis polypus (Forsskål, 1775)

Priapus polypus Forsskål, 1775: 102.
Actinia polypus: de Blainville, 1830: 292; de Blainville, 1834: 327.
Cribrina polypus: Ehrenberg, 1834: 40.
Actinia decorata Dana, 1846: 139; Dana, 1849, pl. 3 fig. 24; Dana, 1859: 8.
Adamsia decorata: Milne Edwards, 1857: 281.
Calliactis polypus Klunzinger, 1877: 76, pl. 5, fig. 1; Hertwig, 1882: 74–76; Carlgren, 1900: 75, pl. 1, figs 3–4; Carlgren, 1938: 76–77; Carlgren, 1949: 97; England, 1971: 23–29, pl. 1, figs A-C, pl. 2, fig. 1.
Adamsia miriam Haddon & Shackleton, 1893: 130.
Calliactis miriam Haddon, 1898: 457, pl. 23, fig 25; Stephenson *et al.*, 1931: 72; Carlgren, 1950*a*: 141–142; Carlgren, 1950*b*: 444 (part).
Calliactis armillatus Verrill, 1928: 20 (part).

MATERIAL EXAMINED. The Maldives: Gan Island, Addu Atoll, 6 specimens on 2 gastropods, 8 Mar 1970, BNMH 1985.2.13.2–6; associated with 2 specimens of *Verrillactis paguri* (Verrill, 1869*a*), BMNH 1985.2.13.1.

DESCRIPTION. For detailed description see England (1971: 23–29). The specimens from Gan were smaller than those described in that paper and had only 48 pairs of mesenteries at the centre of the column, but the main characters of the species were present.

REMARKS. A nominal species additional to those listed earlier (England, 1971) can be referred to *C. polypus*: *Actinia decorata* Dana, 1849 (= *Adamsia decorata* Milne Edwards, 1857), originally

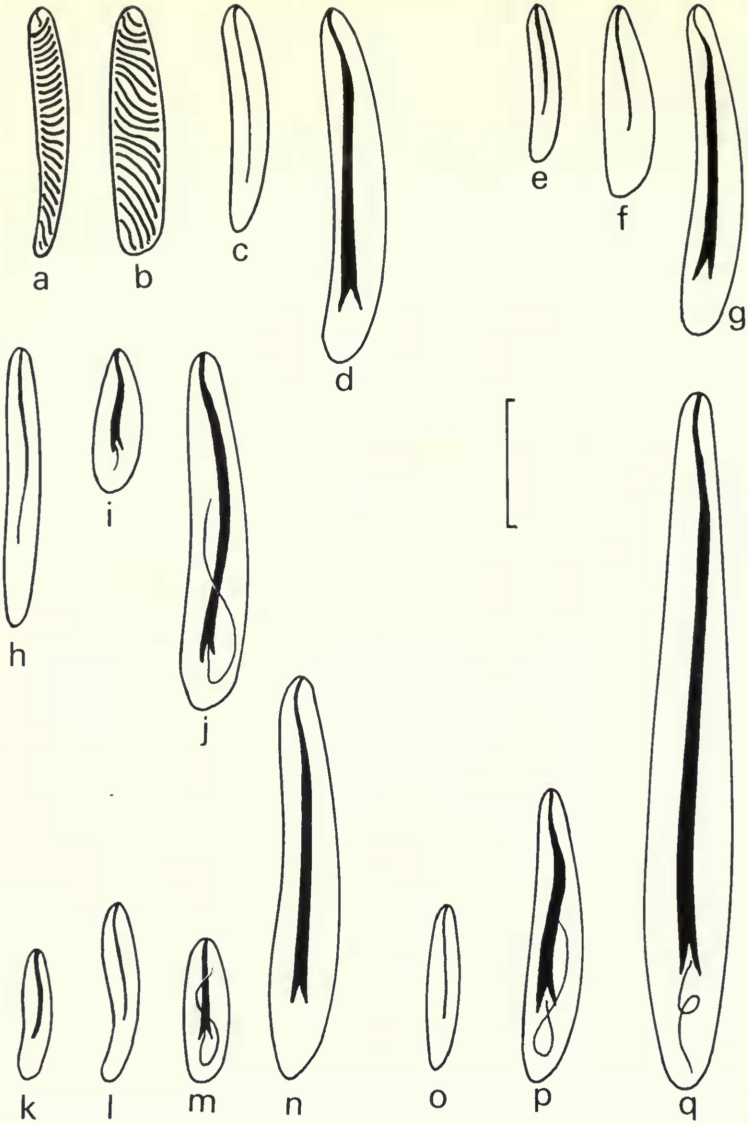

Fig. 40 *Carcinactis ichikawai*, nematocyst signature (after Uchida, 1960). *Tentacle* (a-b) spirocysts, (c) basitrich, (d) microbasic amastigophore. *Column* (e-f) basitrichs, (g) microbasic amastigophore. *Actinopharynx* (h) basitrich, (i-j) microbasic amastigophores. *Filament* (k-l) basitrichs, (m-n) microbasic amastigophores. *Acontia* (o) basitrich, (p-q) microbasic amastigophores. Scale: (a-q) = 10 μm.

found at 'Honden Island'. This species was not considered in the earlier paper because it was not then possible to determine the whereabouts of Honden Island. With the assistance of the Department of the Hydrographer of the Royal Navy, Honden Island was found to be that better known as Puka Puka in the Tuamoto group. Among the material previously examined some was collected from the same area as Dana's material and it seems more probable than before that *Actinia decorata* is conspecific with *C. polypus*. *Priapus polypus* Forsskål, 1775, is, therefore, designated type species of the genus *Calliactis* Verrill, 1869*b*.

DISTRIBUTION. Red Sea (Klunzinger, 1877), Aden (England, 1971), Mombassa (A. K. Totton coll., BMNH 1955.6.9.96–97), Chagos Archipelago (J. S. Gardiner coll., BMNH 1939.7.3.45–46), Maldives (J. S. Gardiner coll., BMNH 1939.7.3.35–38); K. W. England coll., present material, BMNH 1985.2.13.2–6), Malay Straits (Challenger coll., BMNH 1889.11.25.67), Christmas Island (BMNH 1935.3.5.1), Hawaii (Verrill, 1928), Great Barrier Reef: Low Isles (Carlgren, 1950*a*, 1950*b*), Tuamoto Archipelago (Dana, 1948, as *Actinia decorata*, and England, 1971).

Family **SAGARTIIDAE** Gosse, 1858, s.str.
Genus ***VERRILLACTIS*** England, 1971

Calliactis Verrill, 1928: 20 (part).
Verrillactis England 1971: 29.

DEFINITION. Sagartiidae with broad pedal disk. Column smooth or with ectodermal invaginations that do not pierce the column wall, divisible into scapus and scapulus. Mesenteries arranged hexamerously or irregularly, with number at base about twice that at margin; 6–12 pairs, perfect and sterile. 1–2 siphonoglyphs which may not be supported by directives. Sphincter mesogloeal,

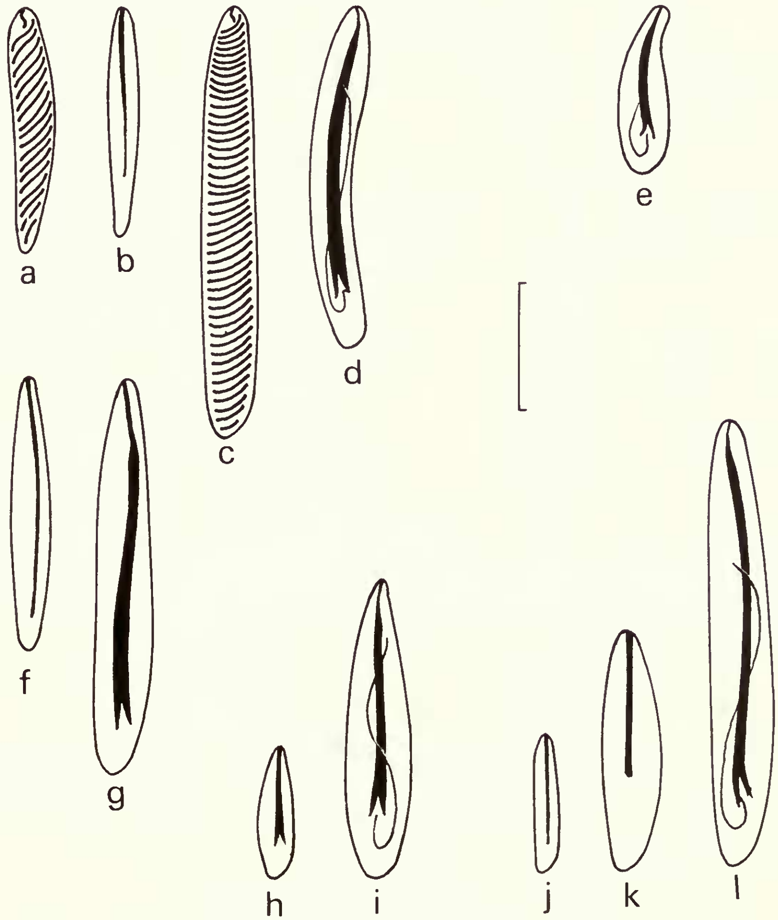

Fig. 41 *Verrillactis paguri*, nematocyst signature (after England, 1971). *Tentacle* (a) spirocyst, (b) basitrich, (c) atrich, (d) microbasic amastigophore. *Column* (e) microbasic amastigophore. *Actinopharynx* (f) bastrich, (g) microbasic amastigophore. *Filament* (h-i) microbasic amastigophores. *Acontia* (j-k) basitrichs, (l) microbasic amastigophore. Scale: (a-l) = 10 μm.

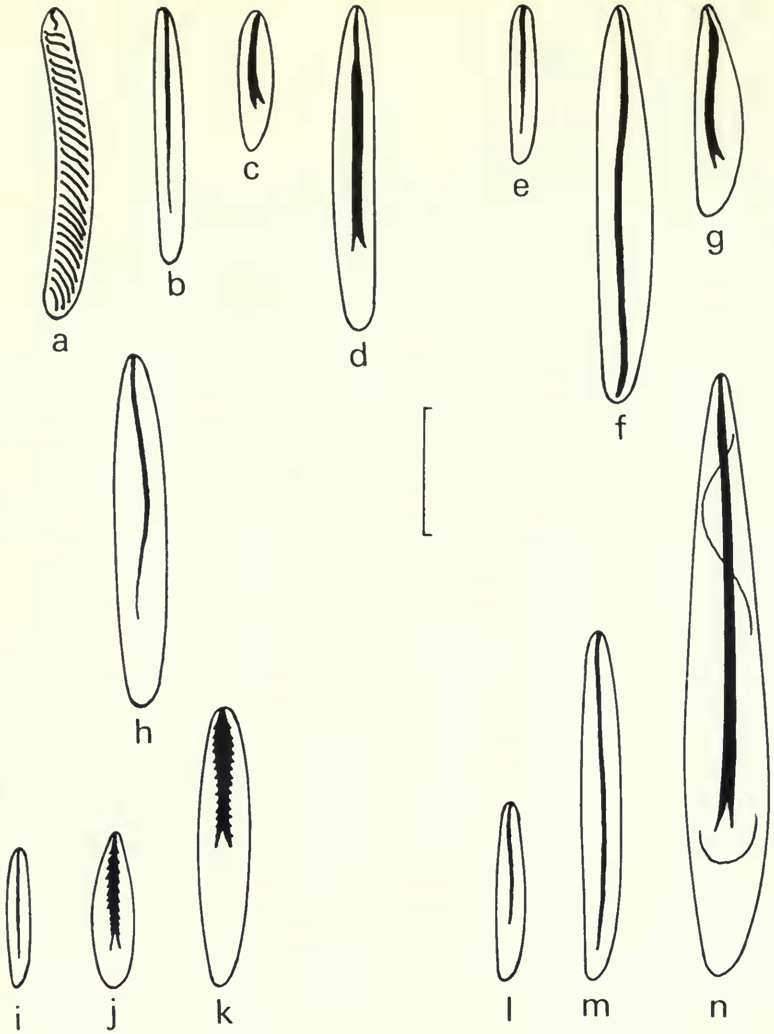

Fig. 42 *Carcinactis dolosa*, nematocyst signature (after Riemann-Zürneck, 1975). *Tentacle* (a) spirocyst, (b) basitrich, (c-d) microbasic amastigophores. *Column* (e-f) basitrichs, (g) microbasic amastigophore. *Actinopharynx* (h) basitrich. *Filament* (i) basitrich, (j-k) microbasic amastigophores. *Acontia* (l-m) basitrichs, (n) microbasic amastigophore. Scale: (a-n) = 10 μm.

strong. Cinclides absent. Tentacles: inner longer than outer, some forming catch tentacles bearing large atrichs. Acontia with three distinct types of nematocyst; *two types of basitrichs and one type of microbasic amastigophore*. Commensal with hermit crabs, often with *Calliactis polypus*. (p. 279).

TYPE SPECIES. *Sagartia paguri* Verrill, 1869*a*, by monotypy.

Verrillactis paguri (Verrill, 1869*a*)

DESCRIPTION. For detailed description and synonyms see England (1971).

MATERIAL EXAMINED. 2 specimens, Maldives, Gan Island, Addu Atoll, 8 Mar 1970, BMNH 1985.2.13.1.

REMARKS. At the time of the original description the presence of cinclides was in doubt. On examination of the material from Gan the absence of cinclides was confirmed.

England (1971: 33) suggested that *V. paguri* Verrill, 1869*a*, was a new combination for *Sagartia paguri* Verrill, 1869*a*. (A difficulty is that Verrill's descriptions are brief, so that they cannot easily be compared.) However, Ross and Wada (1975: 1738) found an anemone on a left chela of *Diogenes edwardsi* (Dehaan) which lacked acontia and which was probably *S. paguri* Verrill. Since Verrill (1869*a*) stated that *S. paguri* occurred on this crab it seems likely that *Verrillactis paguri* is distinct. Examinations of specimens from the crab *D. edwardsi* is desirable before a decision is made.

Riemann-Zürneck (1975: 85) suggested that the nominal genus *Verrillactis* England, 1971, should be referred to *Carcinactis* Uchida, 1960: 595. The latter stated that species referred to *Carcinactis* have the mesenteries divided into macrocnemes and microcnemes. If so, the genus would be better referred to the Isophelliidae than to Sagartiidae. Uchida's figures 4–5 indicate a clear demarcation between cycles 1–3 and 4, giving 24 pairs of macrocnemes and 24 pairs of

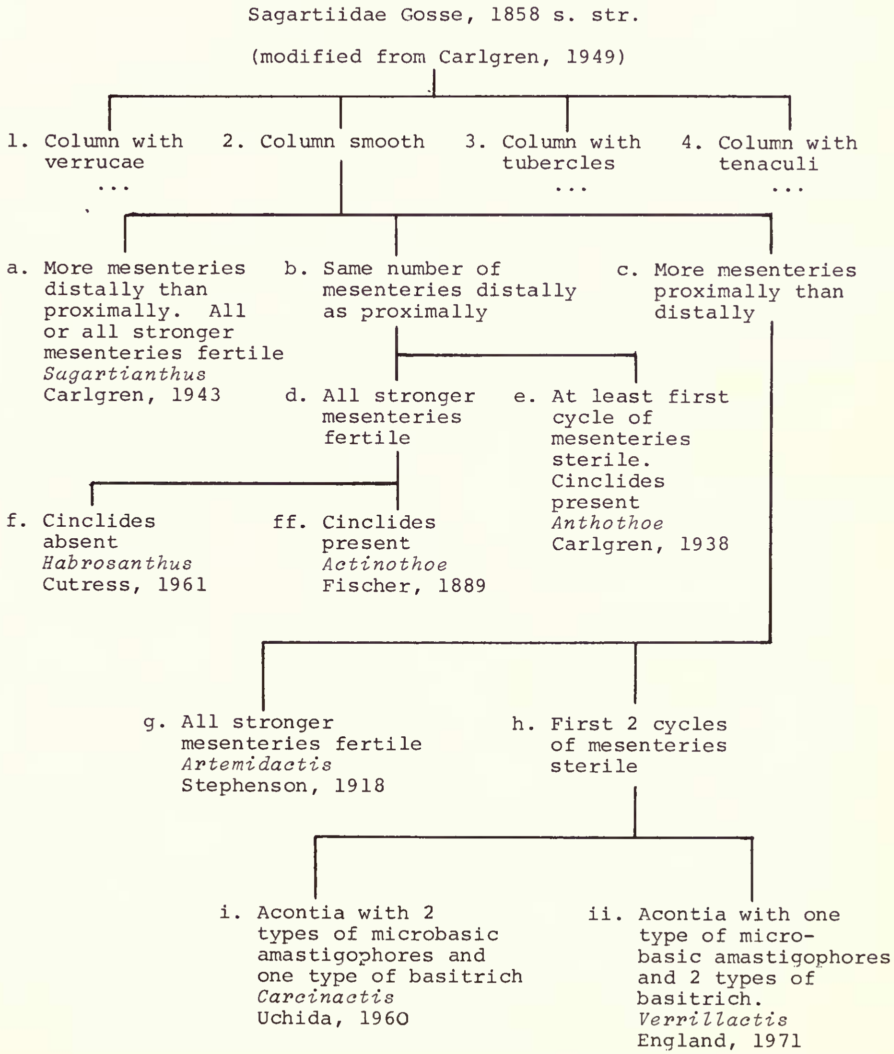

Fig. 43 Key to certain genera of the Sagartiidae.

microcnemes near the margin. These figures also illustrate a pair of directives not connected with a siphonoglyph; although Uchida specified 'siphonoglyphs two, associated with directive mesenteries'. His figure 6 did depict a siphonoglyph supported by directives, and his figure 7 showed that the 3rd, 4th and 5th cycles were successively smaller in size. Possibly the sections shown in Uchida's figures 4 & 5 had been cut through the column up into the disk, but outside the mouth, so that they would have omitted the actinopharynx and siphonoglyphs. Although the mesenteries decreased regularly in size from 1st to last cycle, this also led to their having the appearance of macrocnemes and microcnemes. *Carcinactis* is thus better referred to the Sagartiidae, as defined by Uchida, and reference to macrocnemes and microcnemes perhaps deleted from the definition.

The nematocysts of the acontia of *Carcinactis ichikawai* were illustrated by Uchida (1960: 598; fig. 1) as one type of basitrich and two types of microbasic amastigophores, suggesting that the two genera should be held distinct.

Carcinactis dolosa Riemann-Zürneck, 1975, also has two types of basitrich and one type of microbasic amastigophore in the acontia, but the larger type of basitrich differs from that in the species referred to *Verrillactis*. There is also difference in the types that occur in other parts of the two species. Nematocyst signatures of *Carcinactis ichikawai* Uchida, 1975: 598, *Verrillactis paguri, sensu* England, 1971: 32, and *C. dolosa* Riemann-Zürneck, 1975: 77, deduced from published data, are shown in Figures 40–42. The nematocyst differences indicate that the three species should be referred to three different genera and, therefore, that *C. dolosa* should be removed from *Carcinactis*. Riemann-Zürneck showed that *C. dolosa* has the same number of mesenteries at the margin as at the base (382 tentacles actually counted in 6 cycles of regularly arranged mesenteries ($6+6+12+24+48+96=192$ pairs, $=384$ tentacles), whereas both *Carcinactis* and *Verrillactis* have more mesenteries at the limbus than at the margin. *Carcinactis dolosa* has characters resembling those of species referred to *Actinothoe* Fischer, 1889, and *Sagartiogeton* Carlgren, 1924, though these genera are regarded as having only one type each of basitrich and of microbasic amastigophore in the acontia. These genera need to be examined further before a positive generic referal can be made. A provisional key to the genera of Sagartiidae to which these species might be referred is given in Figure 43.

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Index

Valid names are in Roman type, new names in **bold** type and invalid names in *italics*. New combinations are indicated by an asterisk (*). Main page references are in **bold** type.