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Sea anemones (Cnidaria: Actiniaria) of Singapore: shallow-water species known also from the Indian subcontinent

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Abstract. We document for the first time five species of intertidal and shallow subtidal sea anemones (members of cnidarian order Actiniaria) from the Republic of Singapore. *Bunodosoma goanense* den Hartog & Vennam, 1993, *Pelocoetes exul* (Annandale, 1907), and *Stephensonactis ornata* Panikkar, 1936, were previously known only from India; they occur primarily on the north (Johor Straits) side of Singapore. *Actinoporus elongatus* Carlgren, 1900, and *Paracondylactis sinensis* Carlgren, 1934, which occur primarily on the south (Singapore Straits) side of Singapore, have been reported from India and elsewhere. In addition, we discuss *Cancrisocia expansa* Stimpson, 1856, a subtidal species that occurs in the Johor Straits, and that has been known mainly from East Asia and in the crustacean literature because it is symbiotic with the crab *Dorippoides facchino*. We confirm that *C. expansa* belongs to family Actiniidae, not to family Sagartiidae, and distinguish it from *Paraiptasia radiata*, a sea anemone un-named in a report from India; this species, the most widespread we have recorded in Singapore, has been known only in east Asia as far west as Singapore. *Metapeachia tropica* (Panikkar, 1938), which also occurs in both Singapore and the Indian subcontinent, is the subject of a separate publication.

Key words. Actiniidae, Anthozoa, Capneidae, Haliactiidae

INTRODUCTION

We provide data on appearance and distribution as well as notes on anatomy for six species of intertidal and shallow subtidal sea anemones (members of cnidarian order Actiniaria) from the Republic of Singapore, five of them new records for the country. Sixteen species of Singaporean sea anemones that were scientifically well known and for which there were no taxonomic or nomenclatural problems were

another study (Yap et al., 2014). Prior to our research, 16 species of sea anemones had been recorded from Singapore in the scientific literature: six were included in our previous publications, one is included in Yap et al. (2014), and one is included in this report. We have collected in the shallow waters of Singapore, specimens of perhaps two dozen species of anemones in addition to those reported here and in our previous publications. For relevant nomenclatural matters, we act as First Revisers; the Principle of the First Reviser is explained in Article 24.2.1 of the International Code of Zoological Nomenclature (the "Code") (International Commission on Zoological Nomenclature, 1999).

the subject of a previous publication (Fautin et al., 2009), and two that had been less well known are the subject of

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© National University of Singapore ISSN 2345-7600 (electronic) | ISSN 0217-2445 (print) from India and have been recorded from nowhere else: *Bunodosoma goanense* den Hartog & Vennam, 1993, *Pelocoetes exul* (Annandale, 1907), and *Stephensonactis ornata* Panikkar, 1936. *Actinoporus elongatus* Carlgren, 1900, reported from India under the name *A. elegans*, a Caribbean congener, was described from East Africa and has been reported from northeastern Australia; we document it also in Hawai'i. *Paracondylactis sinensis* Carlgren, 1934, has been reported from China as well as India. Another species with a similar distribution is *Metapeachia tropica* (Panikkar, 1938), which was described from India and was mentioned by England (1987) as occurring in Singapore; it is the subject of the study by Yap et al. (2014), who also described a new species from Singapore that is similar to *M. tropica* and that might occur in India as well.

Three of the six species we discuss were initially described

Reciprocally, we identify the anemone symbiotic with a snail reported in a note from southern India by Dave & Mankodi (2009) as *Paraiptasia radiata*, a species we documented from Singapore (Fautin et al., 2009); theirs is the first record of the species in India, to our knowledge. We differentiate *P. radiata* from *Cancrisocia expansa* Stimpson, 1856, a subtidal species that occurs in the Johor Straits, that is symbiotic with the crab *Dorippoides facchino*, and that has been reported from Singapore but is known mostly from the crustacean literature. We confirm that *C. expansa* is a member of family Actiniidae, not of family Sagartiidae; many anemones symbiotic with crustaceans belong to Sagartiidae.

MATERIAL AND METHODS

Animals were observed in situ; some specimens were collected for detailed study. They were observed before being preserved in either formalin or ethanol; some were photographed in the field and some in the laboratory. We report our observations of animals from Singapore; we remark on differences with published observations. Details of musculature and mesentery arrangement were visualised in histological sections 8 µm thick stained with hematoxylin and eosin (Humason, 1967).

Voucher specimens are in the Zoological Reference Collection, Raffles Museum of Biodiversity Research, Department of Biological Sciences, National University of Singapore (ZRC) and the Division of Invertebrate Zoology, University of Kansas Natural History Museum, Lawrence, Kansas, USA (KUNHM). We examined specimens in the Museum of Tropical Queensland, Townsville, Queensland, Australia (MTQ), the Bernice P. Bishop Museum, Honolulu, Hawai'i, USA (BPBM), and the U.S. National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA (USNM), and refer to the Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA (YPM) and to the Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania, USA (ANSP).

Conventions for data on cnidae are those of White et al. (1999); terminology follows that of Mariscal (1974). Cnidae were viewed at 1000×; measurements are given as ranges of length by width; single capsules that fell outside the typical range are in parentheses. The number of capsules measured is indicated by n, and for species in which more than one individual was examined, the ratio of the number of animals in which that type of cnida was found to the number in which it was sought, is indicated by N.

Photographs were taken by Ria Tan, except as noted.

The synonym list for each species contains reference to the first citation of the species by a particular name. For some species, some of the names are misapplications or misidentifications; nonetheless, we list them because they are names that have been used to refer to that species. For a complete list of references concerning taxonomy and biogeography of a species, see Fautin (2013). Comparisons

with other species focus on distinguishing that species from others that occur in Singapore; these comparisons should not be used elsewhere, because species not found in Singapore may not be well differentiated.

TAXONOMY

Actiniidae Rafinesque, 1815

Bunodosoma goanense den Hartog & Vennam, 1993 (Figs. 1, 2)

- =? Bunodosoma granulifera (Leseur [sic], 1817): Parulekar, 1968: 142
- =? Bunodosoma granulifera (Leseur [sic]): Haque, 1977: 36, 39 Bunodosoma goanensis den Hartog and Vennam, 1993: 610–617 (original description)

Material examined. Singapore: Punggol Jetty Beach (ZRC. CNI.0614 ×1; ZRC.CNI.0615 ×3; ZRC.CNI.0652 ×1; ZRC. CNI.0653 ×3); Buoy CAAS 2 in Johor Straits (photographed but not collected); Singapore: Pulau Ubin, Tanjung Tajam (photographed but not collected).

Live appearance/external anatomy. Column, tentacles, and oral disc appear solid deep red, maroon, or mauve, some individuals with greenish cast. Column covered from margin to limbus with non-adhesive small, spherical papillae in clear longitudinal rows (Fig. 1); when column very extended, papillae appear to be arranged in rings. Papillae pink near column, becoming darker red at distal end. Pink to light red simple marginal projections situated at margin; one communicates with each endocoel (so alternate with exocoelic tentacles). Fosse pronounced but not deep. Oral and pedal discs and column about same diameter, but column may be narrower than discs, or oral disc may be slightly narrower than pedal disc. Column typically about as long as its diameter.

Oral disc of most individuals red-maroon, of some bluishgrey or greenish, in which case red mesenterial insertions are visible. Raised lips red or greenish; actinopharynx reddish. Many short, tapered, pointed tentacles (Fig. 1) occupy entire oral disc except immediately around mouth: those nearest mouth held perpendicular to oral disc (direction commonly termed "upward," which can be ambiguous for animal not on horizontal surface), those nearer margin held successively at an angle toward the margin (held "outward"), those at margin droop over margin (held "downward"). A blue-grey line occurs along the entire length of oral face of some tentacles.

Oral disc unmarked except six short blunt light (yellowish or orangish) lines may run between mouth and tentacles communicating with primary endocoels; more rarely, a white spot marks top of each siphonoglyph.

Pedal disc light red (even pink) with dark radial lines marking mesenterial insertions (Fig. 1). Limbus slightly scalloped due to bulge at each inter-mesenterial space.



Fig. 1. Bunodosoma goanense: living animal, from Punggol. Photograph by Ria Tan.

Size. Oral and pedal discs typically 30 mm; tentacles 10–20 mm long (about equal to oral disc radius). Animal can extend column to 100 mm length.

Preserved appearance. Oral disk brownish-grey, without markings; raised lips and siphonoglyph white or whitish. Tentacles shorter than in life; dark green or grey-green. Column brown to tan (Fig. 2); a dark green dot may mark each spherical papilla. Pedal disc whitish-grey; mesenterial insertions not visible through it.

Internal anatomy. See den Hartog & Vennam (1993). Kidney-shaped endodermal marginal sphincter muscle arises on marginal side of fosse. Marginal stomata present.

Cnidae. Cnidom spirocysts, basitrichs, holotrichs, microbasic *p*-mastigophores. We found sizes and distribution of cnidae nearly precisely as reported by den Hartog & Vennam (1993) for specimens from western India.

Natural history. Animals sensitive to light: tentacles contract in area where light shines on them. Tentacles very sticky in life, exuding copious mucus.

Habitat. Attached to rocks (e.g., near Punggol Jetty; also a single specimen at Tanjung Tajam on Pulau Ubin, a photograph of which is at http://wondercreation.blogspot. sg/2012/12/highlights-of-trips-with-northern.html) or other firm substrata (a buoy).

Distribution. First record for Singapore; otherwise known only from India and possibly Bangladesh (see below).

Comparison with other species. Individuals of this species cannot be confused with those of any other sea anemone in Singapore: the solid, dark colour, and the entirely papillose column are unmistakable. In contrast with many other sea anemones of Singapore, individuals of this species attach to solid objects, including rocks and artificial substrata such as buoys.



Fig. 2. Bunodosoma goanense: preserved (ex lot ZRC.CNI.0653), from Punggol. Photograph by Nicolas Yap Wei Liang.

Remarks. The original rendering of the name was incorrect: according to Code Article 31.2, the species name, being an adjective in the genitive case, must agree in gender with the genus. The gender of *Bunodosoma* is neuter; the species name must therefore be rendered *goanense*.

This account supplements the original description, which was based on specimens that were "not very well preserved" (den Hartog & Vennam, 1993: 610). Those specimens were from Gujarat, Maharashtra, and Goa. Although den Hartog & Vennam (1993: 616) stated this species is "presumably more widely distributed" than that, they asserted that the records of Bunodosoma granuliferum by Parulekar (1968) from Bombay and by Haque (1977) from Bangladesh, while clearly not of the named species, a Caribbean native, are "unlikely to be identical" with B. goanense, either, based on colour, for which the authors appear to have depended on photographic slides. Given the variability in colour and markings we have seen in Singapore, that colour of an animal's tentacles lightens with expansion, and that this animal is so distinctive otherwise, we are of the opinion that the records of Bunodosoma by Parulekar (1968) and Haque (1977) are likely to refer to B. goanense.

Cancrisocia expansa Stimpson, 1856 (Figs. 3–5)

Cancrisocia expansa Stimpson, 1856: 376 (original description) Sagartia expansa: Andres, 1883: 394 Carcinophila expansa: Verrill, 1928: 16 (lapsus)

Material examined. Singapore: Johor Straits (ZRC.CNI.0746 ×1; ZRC.CNI.0747 ×1; ZRC.CNI.0748 ×1; ZRC.CNI.0749 ×1; ZRC.CNI.0752 ×1; ZRC.CNI.0760 ×1; ZRC.CNI.0764 ×1; ZRC.CNI.0768 ×1; ZRC.CNI.0815 ×2; ZRC.CNI.0816 ×1; ZRC.CNI.0822 ×1; ZRC.CNI.0839 ×2; ZRC.CNI.0843 ×1); Changi Beach (ZRC.2008.523 ×1). Elsewhere: Thailand: Gulf of Thailand, Chonburi (ZRC.2000.0921 ×1).

Live appearance/external anatomy. Base attached to a plate-like structure (Figs. 3, 4) that we refer to as a platform (described below), carried by crab *Dorippoides facchino* (Fig. 5; plate 1.B in Guinot et al., 1995). Platform and base of anemone nearly ovoid to distinctly kidney-shaped (Fig. 91(2) in Pei, 1998). Pedal disc transparent (Fig. 4); mesenterial insertions visible as light lines through it; mesenteries on concave side of platform narrower than those on other. Limbus may be slightly scalloped due to bulge at each intermesenterial space (Fig. 4).

Column rises eccentrically from base: central relative to long axis but nearer concave side of platform on short axis. Column light greenish-grey to greenish-brown or even orangish, with longitudinal white stripes that do not quite reach limbus (Figs. 4, 5; contrary to drawing that is fig. 91(1) in Pei, 1998): prominent stripes extending from margin (or just proximal to it) alternate with narrower stripes confined to basal region (Figs. 4, 5; plate 1.B in Guinot et al., 1995). Translucency of column especially evident when base detached from platform. Fosse very shallow.

Oral disc typically ovoid (Figs. 3, 4); colour of column; may have 24 radial white stripes (along insertions of primary and secondary mesenteries), those along directive mesenteries broader than others; space between members of a directive pair of mesenteries may be pigmented white, at least near mouth (Fig. 4). Directive axis – indicated by two symmetrical siphonoglyphs – aligned with long axis of base (Fig. 4). Tentacles confined to marginal half of oral disc; to ~200. Each tentacle tapered to a point; colourless, transparent (Figs. 4, 5), some with faint transverse stripes.

Size. Base $12-17 \times 20-30$ mm: shorter axis about half to three-quarters length of longer; same size as or slightly larger than platform to which attached. Oral disc about half the size of base. Expanded column diameter ~ 10 mm, length slightly greater than shorter basal radius; retracted column length equal to or slightly less than shorter basal radius. All tentacles about length of oral disc radius (to $\sim 5-6$ mm long) or marginal ones may be somewhat to much shorter than others, and those above concave side of platform may be shorter than those on convex side. Original bivalve shell typically about one third length and width of platform, offset to concave side.

Preserved appearance. Colour absent, lines faint to absent (Fig. 3). Flaccid. Tentacles may be slightly shorter than in life; those of contracted individual may be bulbous. Base may contract/shrink so slightly smaller than platform (Fig. 3).

Internal anatomy. Six pairs of mesenteries complete. All mesenteries have filaments. More mesenteries proximally than distally: members of highest cycle (generally the sixth) present only near base. Retractor muscles diffuse, poorly developed. Animals gonochoric, with at least mesenteries of third and fourth orders fertile—thus mesenteries of highest and lowest order sterile. No marginal sphincter muscle.



Fig. 3. *Cancrisocia expansa* adherent to platform: preserved neotype (ZRC.CNI.0822) from Johor Straits. Photograph by Nicholas Yap Wei Liang.



Fig. 4. Cancrisocia expansa: alive, attached to platform, from Johor Straits. Photograph by Arthur Anker.



Fig. 5. Cancrisocia expansa: alive, carried by individual of crab Dorippoides facchino; from Johor Straits. Photograph by Arthur Anker.

Cnidae. Spirocysts, basitrichs, microbasic *p*-mastigophores and/or *p*-mastigophores (Table 1).

Natural history. The base of an individual of *Cancisocia expansa* is attached to (and about the size of) a flat, ovoid to kidney-shaped platform that the crab *Dorippoides facchino* carries over its carapace by its hindmost two pairs of legs. Most platforms consist of an eccentrically positioned bivalve shell around which the anemone secreted chitinous material

Table 1. Cnidae of Cancrisocia expansa. Data from Pei (1998), the only measurements previously published for the species, included for comparison (based on unspecified number of capsules from unspecified number of specimens).

Tissue	Cnida Type	Source	Range Length × Range Width	n	N
Tentacles	Spirocysts	Fautin et al. Pei	13.0–24.2 × 2.0–4.0 μm 15.0–24.0 × 1.5–3.0 μm	32	3/3
	Basitrichs	Fautin et al. Pei	13.0–16.0 × 2.0–2.2 μm 15.0–27.0 × 1.5–3.0 μm	11	1/3
	Microbasic <i>p</i> -mastigophores	Fautin et al. Pei (as microbasic mastigophores)	$21.7–28.3 (30.2) \times 3.0–4.5 \mu m$ $24.0–27.0 \times 4.5–5.4 \mu m$	30	3/3
Actinopharynx	Basitrichs	Fautin et al. Pei	(13.6) 15.2–22.2 × 2.0–5.1μm 16.5–30.0 × 1.5–3.0 μm	26	2/3
	Microbasic <i>p</i> -mastigophores	Fautin et al. Pei (as microbasic mastigophores)	(24.0) 26.3–31.3 (35.4) × 3.0–5.0 μ m 24.0–31.5 × 3.0–4.5 μ m	26	3/3
Mesenterial filaments	Microbasic <i>p</i> -mastigophores	Fautin et al. Pei (as microbasic mastigophores)	21.7–33.3 × 3.0–5.1μm 9.0–36.0 × 1.5–4.5 μm	40	2/2
	Microbasic <i>p</i> -mastigophores	Fautin et al.	$(5.1) \ 7.1-10.1 \times 3.0-5.1 \ \mu m$	20	2/2
	Microbasic <i>p</i> -mastigophores	Fautin et al.	18.2–22.2 × 7.1–10.1 μm	10	1/2
Pei also recorded	spirocysts 15.0–21.0 × 1.5–3.0 µ	um and basitrichs 9.0-26	.0 × 1.5–4.5 μm		
Column	Microbasic <i>p</i> -mastigophores	Fautin et al. Pei (as microbasic mastigophores)	$12.1-21.2 \times 4.0-6.1 \mu m$ $15.0-21.0 \times 4.5-6 \mu m$	20	2/2

μm

as it grew; in some instances, the shell extends to the edge of the platform on one side. Rings concentric with the original shell (remarked on first by Verrill, 1869; fig. 91(2) of Pei, 1998) provide evidence of growth. We infer the platform is secreted much like the carcinoecium made by sea anemones of the genus Stylobates (see Dunn & Liberman, 1983); thus the remark by Verrill (1869: 59) that Cancrisocia "is the only genus of Actinidæ, except Adamsia (A. palliata), in which a solid secretion is formed by the basal disk" was clearly premature. Holthuis & Manning (1990) and Guinot et al. (1995) summarised history of knowledge of this symbiosis; in both cases, much of the literature cited is based on a few repeated reports.

The anemone can retract but does so only reluctantly, then expands again readily.

Habitat. Muddy bottoms.

Distribution. Most accounts of the anemone are in the crustacean literature, associated with discussions of the host crab. Henderson (1893) reported the crab from several places in southern India, and Alcock (1897: 279) noted that the Indian Museum contained "very numerous specimens from the East coast [of India] ... and a few from the Andamans." Both remarked on its association with a sea anemone.

Lanchester reported a specimen of what he termed *Dorippe* facchino from Singapore, "which carries on its dorsum a small anemone, with a bivalve shell interposed" (1900a: 769), and one from Patani carrying "a small anemone on its back with a bivalve shell and ?Gastropod operculum interposed" (1900b: 553). Plate 1.B in Guinot et al. (1995) showed an anemone carried by a specimen of D. facchino collected off the east coast of Singapore.

Cancrisocia expansa is among anemones from China included in a book by Pei (1998). She recorded it from 12 sites, all just south of Hong Kong, presumably in the vicinity of the type locality, at depths of 5.5 to 62 m.

Comparison with other species. In Singapore, specimens of Cancrisocia expansa may be confused with those of Paraiptasia radiata. Individuals of both associate with animals of other species and are longitudinally striped with white; they are of similar size. However, individuals of the two differ in shape, their symbionts are of different taxa, and we have found specimens of C. expansa only subtidally, whereas those of P. radiata occur mainly intertidally. Most important for taxonomy, although perhaps not for identification, an individual of C. expansa lacks acontia whereas one of P. radiata has them. In our experience, P. radiata is the most widespread species of sea anemone in

Singapore, living on pieces of broken shell and on gastropod shells inhabited by hermit crabs, as well as on the several species of living gastropod we documented. It is one of several species of sea anemones living on gastropod shells in Singapore – therefore, small size and symbiosis with a gastropod are not sufficient to identify it.

Specimens of *C. expansa* we collected in Singapore conform to the description by Stimpson (1856: 376): "Found on the common *Dorippe* of the China seas, attached by the posterior legs of the animal"; the words "base suboblong, slightly arcuated, with rounded, subtruncate extremities" describe many individuals we examined. Members of the acontiate species Carcinactis ichikawai, described from Oshoru Bay, near Otaru, Japan, associate with a crab identified by Uchida (1960) as Dorippe granulata (now Paradorippe granulata). Syntypes of this anemone in the USNM (catalog number 51426) are more cylindrical and robust than those of C. expansa, and two of the three specimens appear to have been attached to concave objects (see photographs in Fautin, 2013). Further, Plate I, figure 1 of the description (Uchida, 1960) shows three longitudinally striped anemones on an object carried by a crab, but we have never seen more than one individual of *C. expansa* carried by a crab.

Remarks. We failed to find acontia in any individuals of *C. expansa*. Their absence accords with the taxonomy of Pei (1998), who placed the species in family Actiniidae. Neither the description of the species (Stimpson, 1856) nor the re-description (Verrill, 1869) mentioned acontia but Verrill placed *C. expansa* in subfamily Sagartinæ, and Andres (1883) moved it to genus *Sagartia*. The presumption of acontia may have derived from their being characteristic of many—but not all—species of sea anemones symbiotic with crustaceans. Another exception is the actiniid genus *Stylobates*, members of which form carcinoecia (e.g., Dunn et al., 1981). The catalog to anemones of the world by Carlgren (1949) did not contain an entry for either this genus or this species.

The sizes of both the platform and the specimens of *C. expansa* we found in Singapore varied little, but size of the crab carrying them varied considerably. The brief original description of the anemone by Stimpson (1856) did not mention size, but the redescription by Verrill (1869: 60) stated "Longest diameter of base two inches," which agrees well with all animals we examined from Singapore. The host crab in Plate 1.B of Guinot et al. (1995) is much larger than the anemone; by contrast, Figure 5 illustrates a crab narrower than the anemone and its platform, and resembles Plate II, figure 1 in Verrill (1869), which accords with his statement (page 58) "covers the carpax of *Dorippe*."

In discussing *Dorippe dorsipes* and *D. facchino* from Madras, Hornell (1923: 935) stated the crab carries a thin bivalve shell, and, in many cases, "on the surface of shell [is] a little pale-coloured anemone"; the statement was illustrated by a drawing labeled "*Dorippe dorsipes* carrying an anemone seated upon a shell." The radially striped anemone is on a bivalve shell much larger than its pedal disc diameter; neither

the words nor the illustration accord with our experience of *Cancrisocia expansa* in Singapore, from which we infer that Hornell may have been referring to an anemone of another species, and that the two species of crab may associate with anemones of different species.

Because type specimens of *Cancrisocia expansa* are unknown (see below) and more than one species of anemone are carried by dorippid crabs, we believe there is "an exceptional need" (Code Article 75) for a neotype to serve as an objective bearer of the name *Cancrisocia expansa*.

We select as neotype specimen ZRC.CNI.0822, one of those we collected in the Johor Straits. It was collected on 5 October 2012, during the Comprehensive Marine Biodiversity Survey of Singapore, by a beam trawl that started at 1°23.581"N, 103°59.593"E, ended at 1°23.529"N, 103°59.990"E, and ranged in depth from 5.6 to 14.7 m. Preserved, the neotype has a pedal disc diameter of 24 mm along its long axis, slightly smaller than the platform to which it is still attached (Fig. 3).

Code Article 75 deals with neotypes, Article 75.3 stipulating the conditions under which a neotype may be designated; fulfillment of each condition follows:

Article 75.3.1. We designate the neotype "with the express purpose of clarifying the taxonomic status ... of" *Cancrisocia expansa*;

Article 75.3.2. This publication contains "a statement of the characters that [we] regard as differentiating [Cancrisocia expansa] from other taxa";

Article 75.3.3. Above are "data and description sufficient to ensure recognition of the specimen designated";

Article 75.3.4. Our "reasons for believing the ... holotype ... to be lost or destroyed, and the steps ... taken to trace it" follow. Fautin did not find type specimens of any of the 11 species described by Stimpson (1856) at YPM, which does have type specimens of some anemones first documented in collections of the North Pacific Exploring Expedition (Fautin, 2013), including *Phellia arctica* Verrill, 1868, and *Amphiactis orientalis* Verrill, 1869. Nor did Fautin find type specimens in the USNM or the ANSP, in the Proceedings of which Stimpson published his description of *Cancrisocia expansa*; a message dated 6 January 2013, from Gary Rosenberg, curator at the ANSP, confirms that the museum seems not to possess type material of *C. expansa*.

Article 75.3.5. In this publication, we have presented "evidence that the neotype is consistent with what is known of the former name-bearing type from the original description";

Article 75.3.6. "The neotype came as nearly as practicable from the original type locality." Stimpson (1856: 376) documented an unspecified number of specimens from the "China seas"; Verrill (1869: 60) stated that specimens were from "Near Hong Kong ... in six fathoms, mud." The neotype specimen is from a similar depth, in mud, in an area

considered part of the South China Sea (which Wikipedia defines as "encompassing an area from the Singapore and Malacca Straits to the Strait of Taiwan: http://en.wikipedia.org/wiki/South China Sea, consulted 6 January 2014).

Article 75.3.7. "The neotype is ...the property of" the ZRC, "a recognised scientific or educational institution ... that maintains a research collection, with proper facilities for preserving name-bearing types, and that makes them accessible for study."

Paracondylactis sinensis Carlgren, 1934 (Figs. 6, 7)

Gyrostoma sp.: Menon, 1927: 36-37

Paracondylactis sinensis Carlgren, 1934: 26-28 (original description)

Paracondylactis dawydoffi Carlgren, 1943: 27–28 (original description)

Paracondylactis davydoffi [sic]: Carlgren, 1949: 55

Paracondylacts indicus Parulekar, 1966: 38, 40 (nomen nudum) Paracondylacts indicus Dave in Parulekar, 1968: 143, 145 (original description)

Paracondylactis sp. Misra, 1975: 46

Paraconodylactis [sic] indicus: Haque, 1977: 36, 39

Paracondylactis sagarensis Bhattacharya, 1979, cited by Parulekar, 1990: 219, 221, 223, 226 (nomen nudum)

Material examined. Singapore: Changi Point beaches (ZRC. CNI.0057 ×1; ZRC.CNI.0336 ×1; ZRC.CNI.0337 ×1; ZRC. CNI.0338 ×1; ZRC.CNI.0339 ×1; ZRC.CNI.0344 ×2; ZRC. CNI.0346 ×1; ZRC.CNI.0347 ×1; ZRC.CNI.0348 ×1); Tanah Merah (not collected); Marina East (ZRC.CNI.0351 ×1; KUNHM 003220 ×1); Big Sister's Island (ZRC.CNI.0056 ×1); Lazarus Island (ZRC.CNI.0669 ×1; ZRC.CNI.0670 ×1; ZRC.CNI.0671 ×1); Seringkat-Kias (ZRC.CNI.0947 ×1); St. John's Island (not collected); Pulau Ubin (not collected). Elsewhere: India: Mandapam Camp (USNM 1222025 ×1; USNM 1222046 ×1; USNM 1222136 ×1).

Live appearance/external anatomy. Animal burrows in soft sediment: only oral disc and tentacles seen at sediment surface, most held parallel to or drooping onto surface (Fig. 6). Mesenterial insertions may be visible as dark radial lines through greenish-grey or colourless, flat oral disc. Tentacles (typically 96) translucent, tapered, and pointed (Figs. 6, 7); occur on marginal half of oral disc, outermost arising directly from margin. Most tentacles colourless (Figs. 6, 7), although some have small scattered circular spots on oral face and sides and in one animal some had rusty colouration at junction with oral disc; terminal opening of each may appear to be dark spot. Ovoid to circular mouth that is colourless in most individuals, rarely encircled by dark or rust-coloured ring (Fig. 6); two symmetrical siphonoglyphs visible at ends.

Smooth column flared at distal end; equal diameter most of length but base may be flared. Mesenterial insertions visible as light lines through column that is unmarked, typically rusty red (Fig. 7) (one was colourless); distalmost column lighter in colour or dull brown; in contraction may seem to have small non-adherent bumps. Fosse lacking. About 48 projections (perforated pseudospherules) at margin same



Fig. 6. Paracondylactis sinensis: alive in situ at Tanah Merah. Photograph by James Koh.



Fig. 7. *Paracondylactis sinensis*: alive (reflected in container). Photograph by Tan Swee Hee.

colour as distalmost column but with light tip, endocoelic (i.e., alternate in position with outermost tentacles). Mesenterial insertions visible as light lines through base.

Size. Oral disc to 65 mm diameter; tentacles 50 mm long or so—thus about as long as oral disc diameter, inner ones slightly longer than outer. Column diameter typically about 50 mm, length somewhat to 3-4 times longer than oral disc diameter; one measured 110 mm long after having been dug from sediment, but one anchored 500 mm deep.

Preserved appearance. Commonly flaccid, colourless, although tentacle tips dark in some. Tentacles contract to about one-third oral disc diameter.

Internal anatomy. Anatomy regular. Mesenteries flaccid, grow from margin; those of highest order do not reach base; one member of each pair of highest order may be better developed than other. All mesenteries except those of highest order or two complete. Retractor muscles diffuse, not well-developed (Fig. 18 in Carlgren, 1943); marginal and oral stomata small. Weak, diffuse endodermal sphincter muscle (Fig. 17 in Carlgren, 1943).

Cnidae. Cnidom spirocysts, basitrichs, microbasic amastigophores. We found sizes and distribution of cnidae similar to those reported by Parulekar (1966) for specimens from Maharashtra and nearly precisely as reported by den Hartog & Vennam (1993) for specimens from western India.

Natural history. Burrows deeply in soft sediment. One intertidal specimen was seen at low tide eating a fish.

Habitat. Intertidal to shallow subtidal on muddy sand shores; found near but not in seagrass beds.

Distribution. First record for Singapore: these animals occur on coasts of both the Johor and Singapore Straits. Known across the tropical Indian Ocean from Mozambique, and the western North Pacific to Japan (den Hartog & Vennam, 1993).

Comparison with other species. The absence of distinctive features, including its smooth column, makes this species unique among those that burrow into soft sediment in Singapore.

Remarks. We consider the name *Paracondylactis indicus* as used by Parulekar (1966) to be a *nomen nudum* as defined in the Glossary of the Code: although the "measurements of cnidae" den Hartog and Vennam (1993: 629) cited as evidence that Parulekar (1966) made the name available, those measurements do not purport "to differentiate the taxon," as required by Article 13.1. It is a minor matter because, as documented also by den Hartog & Vennam (1993), Parulekar (1968) definitely made the name available.

The section of the publication by den Hartog & Vennam (1993) dealing with this species is entitled "*Paracondylactis* cf. *sinensis*" but den Hartog & Vennam (1993: 629) also asserted "we regard *P. indicus* Parulekar, 1966, as a subjective junior synonym of *P. sinensis* Carlgren, 1934." We agree that the names they list refer to the same species that we collected in Singapore.

Family Capneidae Gosse, 1860

Actinoporus elongatus Carlgren, 1900 (Figs. 8–10)

Actinoporus elongatus Carlgren, 1900: 283-287 (original description)

Actinoporus elegans: Menon, 1927: 39 (misidentification)

Material examined. Singapore: Marina East (ZRC.CNI.0335 ×1; ZRC.CNI.0345 ×1); Big Sister's Island (ZRC.CNI.0569 ×1); Cyrene Island (photographed but not collected). Elsewhere: India: Kusadai Island (USNM 1121795 ×1); Australia: Queensland, Pallarenda (MTQ G59163 ×1; MTQ G59164 ×1); USA, Hawai'i, Maui (BPBM-D 2250 ×1).

Live appearance/external anatomy. Column creamy white (Figs. 8, 9), slightly tapered toward base; when expanded, mesenterial insertions visible through column as light longitudinal lines. Distalmost column with many longitudinal



Fig. 8. Actinoporus elongatus: alive after collection on Big Sister's Island. Photograh by James Koh.



Fig. 9. Actinoporus elongatus: alive in situ on Cyrene Island. Photograph by Ria Tan.



Fig. 10. Actinoporus elongatus. Longitudinal section at margin of specimen from Hawai'i showing strong endodermal sphincter muscle (sphincter length about 1 mm, fosse about 3 mm deep). Photograph by Daphne G. Fautin.

rows of verrucae all ~1 mm diameter, each with dark center (Fig. 8); to 4 verrucae per endocoelic row, 1–2 per exocoelic row. Column circumferentially folded in contraction; can narrow at any point along its length (as in Fig. 8): some individuals widest halfway along column, other individuals narrowest there.

Flat or domed brown oral disc scalloped, not retractile; covered with very short tentacles, from margin nearly to mouth; arrayed in radial rows along each endocoel and exocoel (Fig. 9); each row 2+ mm wide. Each tentacle a greyish stalk bearing numerous spheroidal bulbed protrusions each ~0.5 mm diameter; multiple spheroidal protrusions may be connected to each stalk, so these tentacles may be considered branched. Marginal edge of each intermesenterial space protruded (Fig. 9; Fig. 2 in Carlgren, 1900), thin-walled, with 3–4 dark spots on oral face; endocoelic protrusions with 4–5 lobes, typically tip of each lobe conspicuously tipped with bright white in life (white disappears on preservation). Mouth with low lips; single siphonglyph creamy in colour (Figs. 8, 9). Fosse deep (Fig. 10).

Base flared, attached to firm object buried as much as 500 mm deep.

Size. Column to 500 mm long in vivo, greatest width about 50 mm; oral disc to nearly 100 mm diameter. Tentacles no more than several mm long. In preservation, column may contract and retract to 100–130 mm long.

Preserved appearance. May be dark brown but ectoderm easily rubbed off so may appear mottled.

Internal anatomy. Symmetry regular. Mesenteries thin; retractor muscles large, diffuse, shape can be nearly reniform, with detached portion. Very strong, circumscript sphincter muscle on marginal side of deep fosse near distal end (Fig. 10). Longitudinal muscles ectodermal, circular endodermal. Margin smooth, ectoderm thin.

Cnidae. Cnidom spirocysts, basitrichs, microbasic *b*-mastigophores, microbasic *p*-mastigophores (Table 2). Tentacles with dense spirocysts, which appear to occur in patches where basitrichs rare to absent. Despite specimen from Hawai'i being smaller than the others, cnidae were of identical size: thus cnida size appears not to vary with animal size.

Natural history. Burrows into soft sediment; attached to firm object at depth. Strong retractor muscles make animal difficult to remove from substratum.

Habitat. Specimens of this species occur in Singapore only where there is extensive sand.

Distribution. First record for Singapore, where we have found *Actinoporus elongatus* on the Singapore Straits side of the island and the southern offshore islands. This species ranges across the tropical Indo-Pacific from the east coast of Africa to Hawai'i.

Table 2. Cnidae of *Actinoporus elongatus* including specimens in USNM, MTQ, and BPBM. Data from original description (Carlgren, 1900) included for comparison (based on unspecified number of capsules from one or two specimens).

Tissue	Cnida Type	Source	Range Length × Range Width	n	N
Tentacles	Spirocysts	Fautin et al. Carlgren (termed "dünnwandigen Nesselzellen")	24.0–42.0 × 2.0–3.0 μm 20–24 μm long	45	5/5
	Basitrichs	Fautin et al.	24.0–42.0 × 2.0–3.0 μm	37	4/5
Column	Basitrichs	Fautin et al. Carlgren (termed "dünnwandigen Nesselzellen")	13.3–19.8 × 2.0–3.2 μm 12–16 μm long	41	4/5
Actinopharynx	Basitrichs	Fautin et al.	$17.0-20.0 \times 2.0-3.5 \ \mu m$	41	4/4
	Microbasic <i>b</i> -mastigophores	Fautin et al.	(23.0) 25.0–38.0 × 2.8–4.5 μm	49	4/4
	· .	Carlgren (termed "nicht so dickwandig wie die gewohnlichen Nesselzellen und breiter in dem proximalen Ende als in dem distalen")	26–28 μm long		
	Microbasic <i>p</i> -mastigophores	Fautin et al.	30.0–41.0 × 6.0–9.0 μm	39	4/4
	7 01	Carlgren (termed "dünnwandigen Nesselzellen")	28–32 × 10–12 μm		
Mesenterial filaments	Basitrichs	Fautin et al.	(9.2) $14.0-24.0 \times 2.0-3.2 \ \mu m$	49	4/4
	Microbasic <i>p</i> -mastigophores	Fautin et al.	24.0–31.0 (32.7) × 4.8–7.0 μm	42	4/4

Comparison with other species. In having many short tentacles covering the oral disc, an individual of Actinoporus elongatus superficially may resemble one of the genus Stichodactyla. The tentacles of Stichodactyla are digitiformthat is, they are unbranched; by contrast, those of A. elongatus are branched, with multiple bumps emanating from a single stalk that arises from the oral disc. The oral disc of A. elongatus is commonly domed, whereas in most specimens of Stichodactyla the oral disc undulates. The column of Stichodactyla is much narrower than the oral disc, by contrast with A. elongatus, in which oral disc and distal column are similar in diameter (Figs. 8, 9). Further, the column of A. elongatus is much longer than that of Stichodactyla, extending far into the soft substratum (which means that the animal can retract further). In short, a specimen of A. elongatus is unmistakable, with its combination of a long, relatively broad column and many short branched tentacles covering the flat or domed oral disc. A photograph in Colin & Arneson (1995) on page 131 (image 587) identified as Stichodactyla ?tapeum from Manado, Indonesia, is clearly of A. elongatus; it is shown with a shrimp of the genus Periclimenes that is about as long as the oral disc radius.

Remarks. The genus *Actinoporus* contains two species, the type species *A. elegans* Duchassaing, 1850, which occurs in the Caribbean, and *A. elongatus*, which Carlgren (1900) clearly differentiated in describing the species from East Africa. Menon (1927) questioningly applied the name *A. elegans* to a specimen he found in southern India, but the caption of the illustration of it refers to it only as *Actinoporus* sp.; particularly in light of our findings, we infer this record refers to *A. elongatus*.

Aside from that by Menon (1927), the only scientific publication on the species is a study of reproduction and feeding in north Queensland, Australia, by Clayton & Collins (1992), who provided no information on how the specimens were identified. Data from the two specimens we collected from Pallarenda, near Townsville, Queensland, Australia, the specimen we examined from Maui, Hawai'i, the specimen we examined from India, and those from Singapore are consistent with those described by Carlgren (1900).

Family Haliactiidae Carlgren, 1949

Pelocoetes exul (Annandale, 1907) (Figs. 11–13)

Metridium schillerianum var. exul Annandale, 1907: 48–73 (original description)

Pelocoetes exul: Annandale, 1915: 69, 76; 86-88

Material examined. Singapore: Sungei Buloh (ZRC. CNI.0052 ×1; ZRC.CNI.0399 ×1). Elsewhere: India, Maharashtra, Thane Creek and Ulhas River estuary (KUNHM 001578 ×1); India, Bombay, Cuffe Parade (USNM 1122215 ×1).

Live appearance/external anatomy. Column divided into narrow capitulum and broader scapus, with collar between;



Fig. 11. *Pelocoetes exul*: alive in situ at Kranji. Note branching of compound, pedicellate tentacles. Photograph by Ria Tan.



Fig. 12. *Pelocoetes exul*: alive after collection at Sungei Buloh. Note longitudinal rows of cinclides and emergent acontia. Photograph by Ria Tan.

oral disc flares abruptly at distal end of capitulum; proximal end may be bulbous. Scapus grayish, with 48 yellowish longitudinal stripes (Figs. 11, 12). Every fourth stripe, except at the distalmost end, is actually a longitudinal row of raised white, slit-like cinclides (Fig. 12) that span endocoelic space: thus 12 rows of cinclides, six longer rows (communicating with primary endocoels) alternating with six shorter rows (communicating with secondary endocoels); in a longer row, distalmost 15 or so cinclides largest, diminishing in size proximally (Fig. 12). Acontia may be emitted through cinclides. Mesenterial insertions visible as light longitudinal lines on capitulum, dark lines on scapus (Fig. 12).

Oral disc grey, unpatterned, rudimentary, with 12 unmarked tentacles, each of which may have white at base: 6 single tentacles arise beside mouth, alternate with 6 compound, pedicellate ones at margin (Figs. 11, 13) (one individual had 7 pedicellate tentacles, two beside one another). Each compound tentacle a single pedicel bearing (typically) 6



Fig. 13. Oral disc of *Pelocoetes exul*: alive after collection at Sungei Buloh. 12 inner simple tentacles alternate with 12 compound, pedicallate tentacles having (typically) four branches, two simple and two bifurcate. Photograph by Ria Tan.

branches, two central ones arrayed radially (one nearer mouth, one nearer margin), with two on each side arrayed along margin. Pedicel is half the length of inner tentacle; tentacle beyond branch point about same size as inner, unbranched tentacle. All tentacles translucent, same grey as oral disc, darkening toward tip; pointed (Figs. 11, 13). Central mouth dark; actinopharynx grey, everted slightly at distal end; two symmetrical deep siphonoglyphs (Fig. 13). No fosse: outer tentacles arise at margin.

Size. Expanded column 35–50 mm long (of which capitulum 5–7 mm long), scapus 7–10 mm diameter (more or less equal throughout). Oral disc to 20 mm diameter. Contracted column length 10–20 mm; oral disc and column diameter 5–7 mm; longest tentacles ~3 mm.

Preserved appearance. Animal colourless; tentacles tips darker than rest. Flaccid.

Internal anatomy. Six pairs of macrocnemes (primary cycle) only complete mesenteries, of which two are symmetrically positioned directives; two orders of microcnemes. More than one intermesenterial space communicates with each compound tentacle. Retractor muscles diffuse (text-fig. 3 in Panikkar, 1938). No sphincter muscle.

Cnidae. Cnidom spirocysts, basitrichs, microbasic amastigophores and/or *p*-mastigophores (not having examined cnidae from live specimens, we are uncertain if the microbasic mastigophores are amastigophores or *p*-mastigophores or both). Data on cnidae provided by Carlgren (1925), Panikkar (1938), and Parulekar (1966) do not agree entirely. Carlgren (1925), who measured them from one specimen, did not specify types but gave only dimensions; Panikkar (1938: 684) specified types only for acontia and

only as "penicilli and spirulae," capsules of the former being about five times longer and twice as wide as those of the latter; Parulekar (1966) listed acontia as containing basitrichs that were 2–3 times as long and twice as wide as the microbasic *p*-mastigophores; the acontia nematocysts we measured were, for both types, larger than those reported by Carlgren (1925), but similar in size to those reported by Parulekar (1966) although the basitrichs were smaller than the mastigophores.

Natural history. These animals can be difficult to maintain in captivity. Because they live in vertical burrows into which they can withdraw, we found they expand in captivity best when put into tubes (of slightly greater diameter than the column) that are propped upright; this is how Fig. 13 was obtained. It is similar to the strategy described by Annandale (1915: 86), who poked vertical holes in mud in which to "plant the anemone."

Specimens of *Pelocoetes exul*, like those of *Stephensonactis ornata*, expand mainly at night, an observation also made by Annandale (1915).

Although an animal has relatively few tentacles, because they branch, the oral disc seems relatively densely covered.

Habitat. Mud. Found in Singapore in mangrove habitats at mid-intertidal level. Seems confined to Johor Straits side of Singapore (but not found on Pulau Ubin): not found in mangroves of Semakau.

Distribution. First record for Singapore. Previously known only from east and west coasts of India (Annandale 1907, 1915; Panikkar, 1938; Parulekar, 1966, 1968, 1990).

Comparison with other species. Pelocoetes exul and Stephensonactis ornata occur together in muddy areas of Singapore, particularly where mangrove trees grow; the latter is 10–100 times more common than the former. Judging by specimens from elsewhere we have found in museums and been sent, this seems a typical proportion of the two species; Panikkar (1938) remarked on the relative rarity of P. exul. Being of similar size, in the field, covered in mud, P. exul and S. ornata are difficult to differentiate, but they are clearly separable: the everted distal end of the actinopharynx of P. exul lacks the complexity and rugosity of that of S. ornata; the pattern of striping of the column and the width of the stripes differs between P. exul and S. ornata; all tentacles of S. ornata are simple, but some of those of P. exul are compound.

Remarks. Initially, Annandale (1907) considered this a subspecies of *Metridium schillerianum*, but in 1915, he described the genus *Pelocoetes* for it, with its only species the one originally described as *M. s. exul*. Also in 1915, he described the genus *Phytocoetes* with two species that are very similar, one of which (*Ph.gangeticus*) he had initially interpreted as the young of *M. s. exul*.

Annandale (1915), Carlgren (1925), and Panikkar (1938) provided extensive detail on the anatomy and histology of anemones of this species; both Carlgren and Panikkar corrected some misstatements of Annandale.

Stephensonactis ornata Panikkar, 1936 (Figs. 14–17)

Stephensonactis ornata Panikkar, 1936: 232, 235, 239–242, 247 (original description)

Material examined. Singapore: Sungei Buloh (ZRC. CNI.0053 ×1; ZRC.CNI.0054 ×4; ZRC.CNI.0378 ×5; ZRC. CNI.0392 ×5; ZRC.CNI.0393 ×5; ZRC.CNI.0394 ×40; ZRC.CNI.0395 ×5; ZRC.CNI.0396 ×9; ZRC.CNI.0397 ×4; ZRC.CNI.0398 ×10; ZRC.CNI.0852 ×6; KUNHM 002919 ×3; KUNHM 003223 ×5; KUNHM 003225 ×5); Pasir Ris (ZRC.CNI.0256 ×1); Kranji Reservoir Park (ZRC. CNI.0405 ×10; ZRC.CNI.513 ×5; at least three more lots). India: Maharashtra, Thane Creek and Ulhas River estuary (KUNHM 001583 ×1; KUNHM 001585 ×1; KUNHM 001586 ×1; KUNHM 001585 ×1; KUNHM 001586 ×1; KUNHM 001585 ×1; India, Tamil Nadu, Porto Novo (USNM 1121853 ×14).

Live appearance/external anatomy. Column divided into narrower grayish capitulum that can telescope into broader orange scapus; extreme proximal end may be deep orange, may bulge or spread like a pedal disc. Longitudinal white stripes entire length prominent in most specimens (Figs. 14–16), typically fainter at ends; narrow in proximal part of scapus, and in some individuals entire length of scapus. Stripes arrayed in six groups of four in distal scapus: in each

group, central two stripes wider, filling entire intermesenterial space, with flanking two narrower, running only along mesenterial insertion (Fig. 14); this pattern less prominent proximally (Fig. 15, contracted specimen). Mesenterial insertions visible as light lines. Cinclides dark, transverse, unelevated slits arrayed along alternate intermesenterial spaces of distal scapus (not capitulum); to 50 in a row. Acontia may be emitted through cinclides.

Oral disc flares abruptly at distal end of capitulum; no fosse so outermost tentacles arise at margin. Pointed tentacles hardly tapered; 96, regularly arrayed; marginal ones no more than half as long as inner ones, narrower as well (Fig. 16). Tentacles translucent, most unmarked (rare ones with dark spot on oral face), dark in contraction; in expansion typically oral side of tentacle pale orange colour of column, rare ones with light white "frosting" at base (Fig. 14, right) or tip (Fig. 14, left), aboral side dark. Very narrow oral disc orange, some individuals with one or a few radial grey stripes (Fig. 14, right). Mouth small, slit-like; distal end of actinopharynx everted as 12 raised elongated radial protrusions (Fig. 17): each protrusion 2–3 mm long, <1 mm across, narrowest where emerges from mouth, broadening marginally, divided at marginal edge into several lumps.

Colour of extreme distal capitulum, which constitutes underside of oral disc, may be all light, all dark, but commonly light with dark wedges, each wedge encompassing up to six tentacles. Grey of capitulum extends along mesenterial insertions onto base of tentacles on aboral side greatest distance along central two tentacles, shorter distance along flanking ones, and shortest distance outermost two.



Fig. 14. Stephensonactis ornata: alive in situ at at Sungei Buloh (left) and Kranji (right). Photographs by Ria Tan.



Fig. 15. Stephensonactis ornata: alive in situ at Sungei Buloh (left) and Kranji (right). Photographs by Ria Tan.

Size. Expanded column diameter to 20 mm, length to 100 mm (but some were buried 150–200 mm deep, so highly extensible); in contraction, capitulum to 5 mm long \times ~10 mm diameter; scapus to 15 mm long \times 12 mm diameter. Expanded oral disc to 35 mm diameter. Inner tentacles to 30+ mm long. Preserved animal typically 15–40 mm long, diameter 5–12 mm, longest tentacles to 10–15 mm (small individuals 10–15 mm long, column 1–2 mm diameter, oral disc 3 mm diameter).

Preserved appearance. Colour and pattern may be absent; column of some pinkish brown or pale orange; mesenterial insertions visible as light lines length of column. Cinclides not individually discernible, but where they occur on distal scapus appear as dark stripes (absent on narrower capitulum); most acontia straight (some loosely coiled), most emerge near proximal end of scapus. Actinopharynx greyish-green, siphonoglyphs lighter colour. Column may kink. Proximal column extremely narrow in many specimens. Tentacles may be shallowly longitudinally corrugated.

Internal anatomy. Six pairs each of macrocnemes (primary cycle) and microcnemes (secondary cycle) extend entire length of column; third cycle of mesenteries and higher, all constituting microcnemes, confined to distal end. All macrocnemes, including both pairs of directives, fertile; sexes separate. One pair of directives may be more strongly developed than other. Retractor muscles strong, diffuse (Text-figs. 5, 7 in Panikkar, 1936). No sphincter muscle.

Cnidae. Cnidom spirocysts, basitrichs, microbasic amastigophores and/or *p*-mastigophores (not having examined cnidae from live specimens, we are uncertain if the microbasic mastigophores are amastigophores or *p*-mastigophores or both).

Natural history. Anemones expand mainly at night. The column commonly is constricted at the point acontia are emitted. Mud may adhere to the column, trapped in mucus



Fig. 16. *Stephensonactis ornata*: alive in situ at Pasir Ris, showing expanded and contracted individuals. Photograph by Ria Tan.



Fig. 17. *Stephensonactis ornata*: alive in lab. Oral disc. Photograph by James Koh.

(which Panikkar, 1936, noted is copiously secreted). Panikkar (1935: 178; 1936: 239) stated "the throat-ridges ... [take] an active part in feeding."

Habitat. Mud. Found in Singapore in mangrove habitats at mid-intertidal level. Appears to be confined to Johor Straits side of Singapore (but not found on Pulau Ubin): not found in mangroves of Semakau.

Distribution. First record for Singapore. Previously known only from east and west coasts of India (Pannikar, 1936; Parulekar, 1990).

Comparison with other species. Ridges on the oral disc, which constitute the distal end of the actinopharynx, are diagnostic among species in Singapore (and are distinctive in general: Text-fig. 2B in Panikkar, 1936). This species is distinguished from *Pelocoetes exul*, which is also vermiform and burrows into mud in mangroves of Singapore, by 1) simple tentacles, and 2) dark markings on the distal capitulum along the mesenterial insertions or forming broad wedges, running onto the oral disc.

The acontia appear to contain the same types of nematocysts as do those of *P. exul*: the basitrichs are of similar dimensions, but the microbasic mastigophores of *S. ornata* are smaller.

Remarks. Panikkar (1936: 241) described *Stephensonactis ornata* as "greenish-brown, with orange stripes on the column"; the colour of Singapore specimens appeared different than that to us, but the stripes were conspicuous. Stephenson (1928: 69) stated that, as taxonomic features of sea anemones, "colour alone is erratic in its distribution among individuals, species and genera, and that for identification little reliance can be placed upon it. But the essential structure of a pattern ... is much more stable within a species..."

Six species of vermiform anemones (Pelocoetes exul, Pelocoetes minimus, Phytocoetes gangeticus, Phytocoetes sinensis, Phytocoeteopsis ramunnii, and Stephensonactis ornata) in four genera have been described from brackish muds, all except the fourth from eastern India (Fautin, 2013) (the second-listed species was described as *Pelocoetes minima* but because the genus is masculine, the species, an adjective, must be rendered with a terminal -us). Ideas put forth by Annandale (1907, 1915) and Panikkar (1936, 1937) concerning evolutionary relationships among the genera and species known at the time, as a way of justifying this taxonomic diversity, are outdated—and, frankly, quaint. Carlgren (1925) reassessed the taxonomy of the anemones known at the time from a major brackish-water habitat of India (Chilka Lake). Subsequently, however, Panikkar (1937: 415) remarked that "These four genera show a remarkable uniformity of general structure," and Panikkar (1938: 673) referred to the genera as "close allies." Thus it seems that these animals bear detailed re-examination.

DISCUSSION

Three of the six species of sea anemones that are the subject of this paper are known only from Singapore and India: Bunodosoma goanense, Pelocoetes exul, and Stephensonactis ornata. This is also true of Metapeachia tropica, which is dealt with by Yap et al. (2014), and possibly the new species they describe. Individuals of these species occur in appropriate habitats along the coast of the Bay of Bengal and on islands in the Bay of Bengal; Singapore may represent the easternmost extent of these species. Of the 16 species of anemones discussed by Fautin et al. (2009), Singapore is the westernmost extent of three, Actinodendron arboreum, Anthopleura buddemeieri, and Macrodactyla doreensis. The first two are more widespread than the last, individuals of which occur only along the western Pacific rim (An. handi has a distribution pattern similar to the first two, although it was described from the Malacca Straits, not far north of Singapore, so Singapore is not quite its westernmost record).

Singapore had been thought to be the westernmost extent also of *Paraiptasia radiata*, but it is clearly the species in the photograph illustrating a note by Dave & Mankodi (2009) concerning the anemone in India. Specimens of Pa. radiata in the USNM further document the species in India. When we first examined its contents, USNM 122045 consisted of 18 anemones attached to 12 of the 17 snail shells, 10 anemones free in the container, and five snails lacking attached anemones. These animals were collected on 15 March 1963, on Cuffe Parade, Bombay, presumably by Charles E. Cutress (he was in India then, working for the USNM collecting sea anemones; other lots are recorded as having been collected by him at that time). Although the title of the note by Dave & Mankodi (2009) is "Species specific association of sea anemones," as stated above, its associations in Singapore are non-specific.

Eleven other species recorded in Singapore by Fautin et al. (2009) are known from India as well, or are likely to occur there. Heteractis magnifica and Stichodactyla haddoni occur throughout the tropical Indian Ocean, including India, and into the central tropical Pacific; Cryptodendrum adhesivum, Entacmaea quadricolor, Heteractis crispa, Stichodactyla gigantea, and S. tapetum have a similar extent, although they have not been recorded in India. Similarly, Boloceroides mcmurrichi has not been recorded in India but B. hermaphroditica has been (under the synonym B. gopalai), and B. hermaphroditica, which extends to the western Indian Ocean, may be synonymous with B. mcmurrichi (see Fautin, 2013). The other three species reported by Fautin et al. (2009) from Singapore that are known in or likely to occur in India are: Anthopleura nigrescens is known from India but no further west, although it extends into the eastern Pacific; An. dixoniana is unrecorded from India but is known in the Maldives and east to the Pacific Rim; and Diadumene lineata, which is cosmopolitan, has been reported from India as well. Of the other two species included in this paper, Actinoporus elongatus spans the tropical Indo-West Pacific, from the coast of Africa to Hawai'i, and Paracondylactis sinensis occurs from India to China. Thus, of the 24 species

we have reported from Singapore thus far, 18 are known from India as well, or are likely to occur there.

With this biogeographical context, we consider it unlikely that any of the 18 species that occur in both Singapore and India is invasive in Singapore, although the opportunity for invasions is high, Singapore lying at a maritime crossroads. That was the reason that Singapore was founded as an entrepôt for human commerce—nearly a millennium before its current incarnation begun by Sir Stamford Raffles in 1817 (e.g., Moore & Moore, 1969); the location is also an ideal biogeographical meeting ground. In particular, Diadumene lineata, one of the species we have recorded from Singapore, is documented as invasive in many parts of the world, but eastern Asia is considered its original home (Zabin et al., 2004). We find animals of diverse morphology in Singapore, and the distribution we have recorded for other species of anemones accords with that of D. lineata. The only species we report here that has biology conforming in some respects to that of an invader is B. goanense: it is known only from the north side of Singapore, near port areas, and is extremely hardy (at this writing, three specimens have been kept in an office aquarium for three years). However, it does not propagate asexually to our knowledge: it has not done so in our aquarium, and individuals are widely spaced, in the field as well as the aquarium. Animals do not engage in intraspecific aggression, despite possessing acrorhagi, structures used in aggression by some species (e.g., Bigger, 1980); although that could be interpreted as evidence that they are genetically identical (Francis, 1973), the individuals we have examined vary slightly in markings, evidence that they are not clonemates. Further, an individual grows much larger than invasive sea anemones with which we are familiar.

Two of the species reported here from Singapore for the first time (*Pelocoetes exul* and *Stephensonactis ornata*) live only in the mangal. Some individuals of three reported previously (*Anthopleura handi*, *Diadumene lineata*, and *Paraiptasia radiata*) live in the mangal, although some do not, which is also true of another species not yet identified (and possibly new). Thus the statement by England (1987: 207), in reference to "mangrove swamp[s]" of Singapore that "Here Actiniaria and Corallimorpharia were absent" is clearly erroneous.

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