

Abstract

Coral reef ecosystems depend on the balanced interplay of constructive and destructive processes and are increasingly threatened by environmental change. In this context bioeroding sponges play a significant role in carbonate cycling and sediment production. They occasionally aggravate erosional processes on disturbed reefs. Like other coral ecosystems, Indian reefs have suffered from local and global effects. However, the systematic affiliation and diversity of many Indian bioeroding sponges and their infestation rates are largely confused or unknown. The present study describes a new bioeroding sponge species, *Cliona thomasi* sp. nov. from the central west coast of India. It belongs to the *Cliona viridis* species complex, displaying the key characters of tylostyles and spirasters, as well as harbouring photosymbiotic dinoflagellates. Specific morphological characteristics and molecular data from nrITS1 DNA and 28S rDNA distinguished *C. thomasi* sp. nov. from other known *C. viridis* complex and a number of *Sphaciospongia* species. The historic sample of “*Suberites coronarius*” from Mergui Archipelago (*sensu* Carter, 1887), but not from the Caribbean (*sensu* Carter, 1882), is conspecific with *C. thomasi* sp. nov. *C. thomasi* sp. nov. is locally very abundant, appears to be a key bioeroder, and thus regular monitoring of its abundance, distribution and infestation patterns is recommended.

Keywords: Coral reef sponges, Grande Island, Malvan Marine Sanctuary, molecular-morphological taxonomy, phylogeny, description.

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Introduction

Tropical coral reefs are marine habitats well recognized for their rich biodiversity and ecosystem services (e.g. Moberg & Folke, 1999). The health, resilience, and persistence of these ecosystems rely on an intricate interplay of physical, chemical and biological components that govern constructional and erosional processes (e.g. Hoegh-Guldberg et al., 2007; Worm et al., 2006). Bioerosion is one of these processes and plays a large role in carbonate-dominated habitats such as coral and mollusk reefs (Perry & Harborne, 2016; Schönberg et al., 2017a). Bioerosion is the degradation of hard materials by living organisms (Neumann, 1966), contributing the negative part of the biogenic cycling of calcium carbonate (CaCO₃) on tropical coral reefs (Schönberg et al., 2017a). Globally, bioeroding sponges are the dominant macroborers (Schönberg et al., 2017b), i.e. macrobiotic endoliths that live in and erode CaCO₃ substrates.

The taxonomy of bioeroding sponges is challenging. This is due to a high degree of morphological, and phenotypic variability (Calcinai et al., 1999; Hill, 1999; Hill & Hill, 2002; Schönberg, 2008), to the occasional lack of specific, unambiguous spiculation for some species groups, and in some cases to lost or inaccessible type material (Schönberg & Beuck, 2007; Schönberg, 2013). In consequence, some species groups of bioeroding sponges are taxonomically insufficiently resolved, and especially in the Indian Ocean. This includes the *Cliona celata* Grant, 1826 species complex, and the genera *Cliothosa*, *Pione* and *Spheciospongia* (Schönberg et al., 2017b). Indian *Cliona* aff. *viridis*, *Cliona* aff. *celata*, *Pione* and *Cliothosa* species were historically simply identified as species that were already described from the Atlantic, assuming a wide distribution or cosmopolitanism. However, more recent results suggest that cosmopolitanism is not a common trait in bioeroding sponges, and that “species” with distributions across different oceans are often complexes of cryptic species with similar morphology (Boury-Esnault et al., 1999; de Paula et al., 2012; Xavier et al., 2010). A number of *Spheciospongia* species were described specifically from India (often as *Spirastrella* species; e.g. Dendy, 1905, 1916), but this genus is also badly resolved, because the genus is quite diverse in the Indian Ocean, and its morphological characters can be highly variable (Schönberg et al., 2017b). Tylostyle dimensions in *Spheciospongia* species have a wide range of lengths due to dermal tylostyles often being only about half as long as choanosomal tylostyles (e.g. Dendy, 1905). Relying predominantly on spicule traits may thus be insufficient to characterise the local community of bioeroding sponges, and histological or molecular analyses are necessary (Bickford et al., 2006).

One species complex stands out as a particularly important and difficult group: species closely related to *Cliona viridis* (Schmidt, 1862). These species have been discussed as (1) very competitive

reef organisms that are long-lived and can infest, overwhelm and kill live corals (e.g. González-Rivero et al., 2011; López-Victoria & Zea 2005; Schönberg, unpubl. data; Schönberg & Wilkinson 2001), (2) sponges with comparatively high rates of growth and bioerosion (Calcinai et al., 2007; Holmes et al., 2009; López-Victoria & Zea, 2005; Schönberg, 2002a, 2003; Schönberg, 2006; Schönberg et al., unpubl. data), (3) sponges with a high resilience against environmental change (Schönberg et al., 2017b; Schönberg & Suwa, 2007), (4) but also sponges with a particularly difficult taxonomy (e.g. Schönberg, 2002b; Schönberg et al., 2017b). These four points give this species complex a special status and suggest a significant research need. Information on the taxonomy and ecology of Indian sponges of the *C. viridis* complex is presently insufficient and unreliable. Annandale (1915), Carter (1887), Dendy (1916), Kumar (1925) and Thomas (1972, 1979, 1986, 1989) reported and described different species of this complex from India. However, these authors often used names that are presently only accepted for Atlanto-Caribbean species, most descriptions remained short and insufficient, and their accounts need to be revisited (Schönberg et al., 2017b). The occurrence of bioeroding sponge species in the Indian region is hence not well understood and requires a systematic analysis. In such cases, molecular taxonomy in addition to morphology may assist in identifying difficult or separating cryptic species (Bickford et al., 2006; Escobar et al., 2012; Leal et al., 2016; Xavier et al., 2010).

This publication aims to distangle some erroneous accounts of *C. viridis* complex species from western Indian coral reefs near Goa. The present systematic study includes both morphological as well as molecular analyses, and describes the new species *C. thomasi* sp. nov. that is closely related to *Cliona orientalis*.

Materials and methods

Study sites

Specimens of bioeroding sponges were collected during 2015-2017 from the coral reefs of the Malvan Marine Sanctuary (site I; 15°58'N 73°30'E) and the Grande Islands (site II; 15°21'N and 73°45'E, Fig. 1) in the central eastern Arabian Sea. The sites represent two nearshore coral reefs at the central west coast of India, at a distance of approximately 54 nautical miles from each other. The sites also represent little-studied coral reef ecosystems in India.

The Malvan Marine Sanctuary is one of the seven marine sanctuaries in India and comprises a nearshore discontinuous reef, surrounding the north-eastern side of the Island and running parallel to the shore located 50 m to 200 m away from the shore (De et al., 2015) Numerous submerged, exposed rocks and the Sindhudurg Island provide suitable substratum and protected habitat for coral

settlement and growth (Untawale & Dhargalkar, 2002). The site Grande Islands consists of two elongated islands, Ilha de São Jorge and Grande Island, which are located 2 km away from the coast (Mote, pers. obs.). Generic diversity of corals at Grande Island is relatively low in comparison to the other reefs of India (Manikandan et al., 2016).

Sponge collection and morphological studies

Bioeroding sponges were collected while SCUBA diving between 4 and 10 m water depth from three different stations from each of the two study sites (Figs. 1-2; Supplement 1). Sponge fragments were removed using hammer and chisel, placed separately into pre-labeled and sealable plastic bags and then immediately preserved in 96% ethanol at the field site. During collection, careful observations were made about the phenotypic characters of the sponge samples, such as macromorphology, color and substrate. The preserved samples were brought to the laboratory on ice and studied at the CSIR-National Institute of Oceanography, Goa. In the laboratory, sponge-infested substrata were broken open and studied under a stereomicroscope (SZX10, Olympus, Gurgaon, India). The detailed morphological analyses inclusive of the skeleton arrangement, spicule types and dimensions were made following Rützler (1974) and Schönberg (1999). Briefly, spicule preparations for both light and scanning electron microscopy (SEM) were obtained after 12h digestion of sponge tissue with 70% nitric acid heated to 80°C. Spicules were rinsed with distilled water and dehydrated in 96% ethanol, concentrating the spicules partly by sedimentation, partly by centrifugation before carefully removing the supernatant. The final spicule-ethanol suspension was carefully mixed, spread, dried and mounted on microscope slides (in DPX mountant, Loba Chemie, Mumbai, India; or Eukitt, Sigma Aldrich, Sydney, Australia). Spicules were similarly spread and dried on SEM stubs, but without adhesive, and gold-sputtered for 15-20 minutes in a compact vacuum coating system (12157EQ, SPI-Module Sputter Coater, Global Nanotech, Mumbai, India, or DSR1 desk sputter coater PM View, NewSpec, Myrtle Bank, Australia). Stubs were viewed with a JMS-5800LV scanning electron microscope (Jeol, Peabody, USA), and SEM photographs were taken using a TM3030 Plus Tabletop Microscope (Hitachi, Singapore). Viewing with light microscopy and micrometer eyepiece generated spicule dimensions (Olympus bright field microscope, Gurgaon, India; DMLED microscope, Leica, Macquarie Park, Australia). In four specimens 100 tylostyles were measured for biometric analyses (for our specimens MGB 21, MGB 23, MGB 33 and MGB 35, the latter two being part of the type series; Supplements S2-S3). Depending on specimen and comparisons needed, dimensions for taxonomic comparisons were then obtained as tylostyle maximum length and shaft width, as well as tyle width and length, and spiraster total length including spines, width without spines, and a count of bends. These were measured for 20 spicules of

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each spicule type per sponge specimen, if enough spicules could be found on the slide. We aimed to include only fully formed megascleres and to ignore slim and unfinished tylostyles (following methods in Schönberg & Beuck, 2007). For our target species from West India this meant to exclude most spicules of <12 µm shaft width. In comparatively short tylostyles the shaft width was proportionally slimmer than in long tylostyles, and overall we accepted tylostyles with a length : width ratio of <30 as fully formed spicules, even if they were occasionally slimmer than 12 µm. In this way we measured the first 20 tylostyles that were not obscured or broken. Relying on fully formed tylostyles generated quite stable and uniform means among different specimens of the same species and reduced the overlap of spicule dimensions between different species (Supplements S4-5 provide raw data and descriptive statistics in summary).

We compared spicule characters of the Indian material with representative collection vouchers (Supplement S6). This comparative material included subsamples of dried or wet specimens and slide preparations of sections, tissue plucks and spicules. Vouchers were from the second author's reference collection (CS), the British Museum of Natural History (BMNH), the Liverpool World Museum (LIVCM), and the Paris Natural History Museum (MNHN). After our analyses were completed, representative vouchers were selected from the Indian sponges and kept as reference material. A type series was deposited and registered at the National Institute of Oceanography Taxonomic Reference Centre, Goa, India (NIO). Further material was housed in the reference specimen collection of the Biological Oceanography Division of the NIO, and is also accessible for loan requests.

DNA extraction, amplification, and sequencing

DNA was extracted from representative subsamples of the Indian sponge with a DNeasy kit according to the manufacturer's protocol (Qiagen, Hilden, Germany). DNA was amplified using the following primers: nrITS1 DNA 5'AAAAGTCGTAACAAGGTTTCCG3' and 5'TTGCGTTCAAAGACTCGATG3' for a forward and reverse copy, respectively (after Escobar et al., 2012); the D2 region of 28S rDNA with 5'AAGGTGAAAAGTACTTTGAAAAGA3' and 5'TCCGTGTTTCAAGACGGGTC3' for a forward and reverse copy, respectively (after Barucca et al., 2007). The amplifications were carried out in an Mastercycler (Applied Biosystems, Foster City, USA) under the following conditions (30 cycles): an initial denaturing cycle for 2 min at 94°C, 30 s at 52°C, and 60 s at 72°C. This was followed by (35 cycles): 50 s at 94°C, 45 s at 48°C, and 60 s at 72°C. The amplified DNA was purified with a PCR Clean-Up Kit according to the manufacturer's protocol (Sigma Aldrich, Bangalore, India). The final DNA product was sequenced (ABI 3130xl sequencer, Applied Biosystems, Foster City, USA), and the obtained chromatogram was edited using

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the ABI sequence scanner software 1.0v. All the sequences were deposited in GenBank (NCBI; Benson et al., 2013) under the accession numbers MG367332-MG367341 (note that our specimen field references start with “MGB” and have different numbers in comparison to the NCBI numbers that coincidentally start with “MG”; the numbers are matched in Table 1).

Alignment and phylogenetic analysis

All sequences were aligned with Clustal W with the default parameters (gap open = 15; gap extension = 6.66; gap distance = 4 (Thompson et al., 1994). The alignment of the sequences was checked for the potential occurrence of nuclear pseudogenes using the genetic code for invertebrate mitochondria and for no frame-shift mutations, which would indicate that these sequences originated from a non-functional gene region. Obtained sequences were compared to published data of clionaid sponges (Table 1), and we jointly analyzed our sequences with the NCBI sequences from other *Cliona* species in MEGA v6.06 (Tamura et al., 2013). The most suitable models of the molecular evolution for each gene and the concatenated data were determined using the best fit substitution model Tamura-Nei modelT as indicated by model test 2 based on the Akaike Information Criterion (AIC; Dariba et al., 2012). To assess whether some of the Indian samples formed a distinct monophyletic clade relative to congeneric samples from other locations, we reconstructed a phylogenetic tree in MEGA v6.06 using Maximum Likelihood (ML) with complete deletion of character positions containing gaps and missing data (Tamura et al., 2013). Evolutionary distances were computed employing the Kimura 2-parameter method (K2P; Kimura, 1980), and support for individual nodes was based on 1000 non-parametric bootstrap estimates (Felsenstein, 1985). The K2P distances were also used to compare levels of genetic differentiation between the sequences generated in this study and the published *Cliona* sequences.

Results

General Observations

Within the material sampled for the larger project, ten specimens displayed morphology similar to *C. viridis* complex species. All of them appeared to belong to the same species and were studied in more detail (Supplement S4). Other species dissimilar to *C. viridis* were observed, and a few specimens were presently included into the phylogenetic analyses (Figs. 3-4), but these species will be treated and published elsewhere. Within this extra material, sample MGB 20 was also close to the *C. viridis* complex, but did not cluster together with our core material, MGB 12 associated with *Cliona rhodensis* and had tylostyles consistent with *Cliona celata* complex species, while MGB 24 separated out distantly from all other *Cliona* species and obviously did not belong to the Clionaida,

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despite some morphological similarity (Figs. 3-4). All analysed species yielded sequences for both 28S rDNA and nrITS1 DNA with lengths of 450 and 350 nucleotides, respectively. Phylogenetic analyses showed similar tree topologies for both nrITS DNA and 28S rDNA regions and clearly placed our material into the *C. viridis* complex. The phylogram from nrITS DNA generated three major clusters representing a clade with Indo-Pacific *C. aff. viridis* species, a group with Atlanto-Caribbean *C. aff. viridis* species and one for the *C. celata* species complex (Fig. 3). Similar clustering occurred in the phylogram from the 28S rDNA region, but with additional species groups distributed through it and recognizing four different species from our sample sites (Fig. 4). Among all samples four specimens clustered within the Indo-Pacific *viridis* group and are below described as *C. thomasi* sp. nov. (samples MGB 21, MGB 23, MGB 33, MGB 35). Further, the clustering of *C. thomasi* sp. nov. as a distinct clade within the *viridis*-like species in both the phylograms with strong bootstrap values of 97% and 89% supported our morphological findings that suggested we had a new species.

Abbreviations

α -morphology, habit with mostly endolithic tissue and surface papillae; **AC**, Atlanto-Caribbean; **β -morphology**, habit with mostly endolithic tissue and coherent superficial tissue crust; **BMNH**, British Museum of Natural History, London; **δ -morphology**, massive or larger endolithic habit with erect fistular extensions, living mostly buried within sediments; **FLsk**, Florida Keys sample series; **γ -morphology**, massive, free-living habit, different shapes; **IP**, Indo-Pacific; **nrITS**, Nuclear ribosomal internal transcribed spacer, a DNA region; **MED**, Mediterranean; **MGB**, Maharashtra Gene Bank; **MNHN**, Paris National Museum of Natural History; **NCBI**, National Center for Biotechnology Information; **NIO**, National Institute of Oceanography, Goa, India; **NIO/BOD**, Laboratory collection of the Biological Oceanography Division, NIO, Goa; **PCR**, polymerase chain reaction; **VC**, *viridis* complex.

Systematics

Order Clionaida Morrow & Cardenas, 2015

Family Clionadae D'Orbigny, 1851

Genus Cliona Grant, 1826

***Cliona thomasi* sp. nov**

Figs. 2 and 5-7)

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Taxonomic background

Synonymy: BMNH 1887.6.1.4 = *Suberites coronarius sensu* Carter (1887) = *Anthosigmella varians sensu* Schönberg (2001; referring to Carter's 1887 specimen). *Cliona coronaria* from the Gulf of Kachchh (Dendy, 1916). However, NOT *Suberites coronarius sensu* Carter (1882), being a junior synonym of *Cliona varians*. Name “*coronarius*” thus not available for present material. *Cliona orientalis sensu* Thomas (1972, 1979, 1986). *Cliona varians sensu* Devi et al. (2011). Likely also *Cliona varians sensu* Kiruba-Sankar et al. (2016) and Raghunathan (2015a, 2015b) from the Andaman and Nicobar Islands.

Type locality: Grande Island near Goa, and Malvan Marine Sanctuary, West India.

Species diagnosis: Brown endolithic *Cliona* species in α (papillate) and β morphology with γ tendencies (thinly to very thickly encrusting). Mature tylostyles robust, quite straight with round, well demarcated, terminal tyles. Tylostyles superficially arranged in palisade, at right angle to surface and piercing it, in choanosome as weakly defined fibres. No dermal spiraster crust. Choanosomal, delicate spirasters, mostly C- or bow-shaped, with short, densely arranged compound spines on convex side of shaft. In photosymbiosis with *Symbiodinium* sp., and member of the *Cliona viridis* species complex. Erosion evenly distributed (in *Porites*, *Favites*, oyster shell), with small, rounded erosion chambers. Inhabiting live and dead corals and bivalves.

Etymology: The species was named in honour of Dr. P. A. Thomas who contributed extensively to our understanding of sponges from India and the Western Indian Ocean, including many accounts on bioeroding sponges.

Material examined

West Indian material of *C. thomasi* sp. nov., nrITS1 and 28SrRNA sequences available for the Grande Island type series and two specimens from the Malvan Marine Sanctuary (Genbank accession numbers listed in [Table 1](#)):

Holotype:

Cliona thomasi sp. nov. NIO 1002, field reference MGB 35; β -morphology sponge in dead coral rubble (*Porites* sp.), Grande Island, West India, 15°21'14.2"N 73°45'57.8"E, 8 m, collected by S. Mote, 20/Nov/2016.

Paratypes 1-3:

1 – *Cliona thomasi* sp. nov. NIO 1005, field reference MGB 33; β-morphology sponge in live massive *Porites* sp., Grande Island, West India, 15°21'14.2"N 73°45'57.8"E, 5 m, collected by S. Mote, 18/Apr/2016.

2 – *Cliona thomasi* sp. nov. NIO 1003, field reference MGB 6; β-morphology sponge in *Porites* sp., Malvan Marine Sanctuary, West India, 16° 03'52.80"N 73°27'17.1"E 8 m, collected by S. Mote, 20/Nov/2015.

3 – *Cliona thomasi* sp. nov. NIO 1004, field reference MGB 8; β-morphology sponge on live oyster shell, Malvan Marine Sanctuary, West India, 16°02'31.6"N 73°27'43.0" E, 8 m, collected by S. Mote, 20/Nov/2015.

Other material viewed and here accepted as conspecific with *C. thomasi* sp. nov.:

Cliona thomasi sp. nov. NIO/BOD/P1, field reference MGB 1; β-morphology sponge in live massive *Favites* sp., Malvan Marine Sanctuary, 16°03'84.0"N 73°27'43.7"E, 8 m, collected by S. Mote, 20/Nov/2016.

Cliona thomasi sp. nov. NIO/BOD/P2, field reference MGB 21; β-morphology sponge in live coral (massive *Porites* sp.), Malvan Marine Sanctuary, West India, 16°02'31.6"N 73°27'43.1"E, 8 m, collected by S. Mote, 22/Nov/2016. *Cliona thomasi* sp. nov. NIO/BOD/P3, field reference MGB 7; β-morphology sponge in dead *Porites* sp., Malvan Marine Sanctuary, West India, 16°02'20.2"N 73°28'13.54"E, 6 m, collected by S. Mote, 20/Nov/2015.

Cliona thomasi sp. nov. NIO/BOD/P4, field reference MGB 23; β-morphology sponge in live coral (massive *Porites* sp.), Malvan Marine Sanctuary, West India, 16°03'84.0"N 73°27'43.3"E, 8 m, collected by S. Mote, 22/Nov/2016. *Cliona thomasi* sp. nov. NIO/BOD/P5, field reference MGB 9; β-morphology sponge in live massive *Favites* sp., Malvan Marine Sanctuary, 16°03'84.0"N 73°27'43.7"E, 8 m, collected by S. Mote, 20/Nov/2015.

Cliona thomasi sp. nov. NIO/BOD/P6, field reference MGB 10; β-morphology sponge in live massive *Favites* sp., Malvan Marine Sanctuary, 16°03'84.5"N 73°27'45.7"E, 8 m, collected by S. Mote, 20/Nov/2015.

Cliona thomasi sp. nov. NIO 776. Erroneously identified by P. A. Thomas in 2005 as *Cliona varians*, β morphology sponge in unidentified coral substrate, Gulf of Mannar, Palk Straits, Southeast India, 9°16'N 79°12'E, 4 m, collected by P. Devi, 15/Apr/2004 (see Devi et al., 2011),

Cliona thomasi sp. nov. BMNH 1887.6.1.4; β-morphology sponge in coral substrate. Erroneously

identified by Carter (1887) as *Suberites coronarius* (a synonym of *Cliona varians*), his field reference 73; erroneously accepted by Schönberg (2002b) as *Anthosigmella varians*; β -morphology sponge in coral, Mergui Archipelago, Myanmar, Andaman Sea, collected 01/Jun/1887.

Comparative, disparate material

Cliona caribbaea, LIVCM.ZI.77 (designated holotype), Carter's reference 346 from the "Argo" Expedition 1876; α -morphology sponge. St. Vincent Island, SW Caribbean, collected by H. H. Higgins during the "Argo" Expedition 1876-1877.

Cliona orientalis, Schönberg field reference CS-MAG-B-14: β -morphology sponge in massive dead cf. *Porites* sp. Magnetic Island, Great Barrier Reef, Australia, 19°11'52S 146°48'49E, 5 m, collected by C. Schönberg, 1997.

Cliona varians, BMNH 1954.3.9.396; γ -morphology sponge. Bahamas, Western Atlantic. Bowerbank collection reference 35, Carter (1882) identification as *Suberites coronarius*.

Cliona varians, BMNH 1954.3.9.398; γ -morphology sponge. Honduras, Caribbean, Western Atlantic. Bowerbank collection reference 35, Carter (1882) identification as *Suberites coronarius* (Carter's designated holotype for the name *S. coronarius*, a junior synonym of *C. varians*).

Cliona varians, BMNH 1954.3.9.399; γ -morphology sponge. Jamaica, Caribbean, Western Atlantic. Bowerbank collection, notes on slide "Ord. VI., F. 2, G. 10", Carter (1882) identification as *S. coronarius*.

Cliona varians, Schönberg field reference CS-FLsk-08; γ -morphology sponge. Looe Key, Florida Keys, USA, 24°32'N 81°24'W, 13 m, collected by C. Schönberg, 06/Jul/2008.

Cliona viridis, Schönberg field reference CS-MED-6, α -morphology sponge in coralline algae. Blanes Harbour, Spain, Mediterranean, 41°40'18N 2°47'56E, 5 m, collected by C. Schönberg, 2002.

Spheciospongia inconstans, BMNH 1934.11.24.402; bud-like sponge fragment. Identified by Dendy (1922) as *Spirastrella globularis*. Andaman Islands, collected 23/Nov/1923.

Spheciospongia poterionides, MNHN DJV 23 (designated holotype); γ -morphology sponge in vase shape. Originally described as *Spirastrella poterionides* by Vacelet & Vasseur (1971). Madagascar, ca. 23°22'S 43°39'E, collected 25/May/1964.

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Sphaciospongia solida, BMNH 26.87.5.2.103.a (designated holotype); δ -morphology sponge. Described by Ridley & Dendy (1886) as *Spirastrella solida*. Challenger collection, 33 m, Philippines,.

Sphaciospongia tentorioides, BMNH 1907.2.1.24.a (designated holotype), Herdman collection reference 239, field reference 239; δ -morphology sponge on calcareous debris. Described by Dendy (1905) as *Spirastrella tentorioides*. Sri Lanka.

Sphaciospongia vagabunda previously published as *Suberites trincomaliensis sensu* Carter (1887), BMNH 1954.3.9.446, Bowerbank reference 11/31; δ -morphology sponge. Eastern Sri Lanka, ca. 8°27'60"N 81°12'59"E, collected by D. Johnston, Nov/1881.

Sphaciospongia indet., recorded as *Spirastrella cuspidifera*, BMNH 1936.3.4.166; γ - or δ -morphology sponge. Oman, 18°03'30"N 57°02'30"E, 40 m, Murray Expedition, 29/Oct/1933.

Taxonomic description of *Cliona thomasi* sp.nov.

External morphology: Both, in α - and β -morphology in the field, with tendency to γ -morphology in thick specimens, but without fistular processes typical for δ specimens. Papillate α sponges in *Turbinaria* and *Favites* spp., individuals up to 20–40 cm in total diameter. Papillae circular or oval, very small, 0.3–0.8 mm in diameter (Fig. 2; Supplement S1). Encrusting β to γ sponges forming patches of 60–100 cm in diameter, with epilithic tissue 0.5–3 cm thick (Fig. 2.1–2.2). Surface smooth. Texture hard and incompressible due to underlying coral skeleton. Live colour beige–brown to dark brown, in alcohol initially pale brown with green surface, later fading. Oscules in live β sponges lighter in colour than remaining surface, being pale yellow, occasionally with blue hues (Supplement S1). Choanosome pale yellow in all observed specimens.

Excavation pattern: Boring 2–3 cm into substrate, initially exploiting existing porosity of coral, but also forming small, rounded chambers pitted with erosion scars (Fig. 5.1–5.2). Macroscopic appearance of bioerosion traces in β specimens dense and eroded to similar porosity apart from marginal extensions. In α specimens in more patchy distribution. Chambers of 1–1.5 mm in diameter, with minute connecting tubes and filled with tissue (Fig. 5.3–5.4).

Spicules: Megascleres unusually robust tylostyles (mean length : width ratio of shaft 24.3), widest mid-shaft or slightly above, commonly strongly tapering. Predominantly straight, occasionally with very slight bend in upper 5th of shaft, with sharp point, last sixth of shaft near tip occasionally slightly angling away from main axis. Tyles as a rule perfectly round and well-formed, well demarkated, always terminal, but occasionally with second tylar ring at about 50 μ m below main tyle

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or incomplete tyle anywhere on shaft. Tyles usually marginally shorter than wide, in fully formed tylostyles of similar width as shaft, with weakly to strongly pronounced neck crease, only rarely with single or few vesicles (Fig. 6; Supplements S4-5).

No discernible overall size difference between tylostyles from palisade and choanosomal fibres, but preparations irrespective of spicule origin with 2-22% noticeably shorter and wider tylostyles, on average 77% of length of main, longer tylostyles (Supplements S4-5). Shorter type of tylostyle apparently choanosomal, but no specific role or location identified.

Overall average tylostyle dimensions as shaft length x shaft width x tyle width x tyle height: main longer type 353 x 14.7 x 16.5 x 16.3 µm; perceived shorter type 271 x 12.6 x 14.9 x 14.6 µm (details in Supplements S2-5). Microscleres spirasters, most predominantly C-shaped, also frequently bow- or S-shaped (can be unequal), very few short-helical or with straight shaft (Fig. 6). Two specimens from the Malvan Marine Sanctuary (MGB 21, MGB 23) with presumably aberrant spirasters, mostly of shallow omega shape, with thicker axes, reduced spination and often with wider parts or nodes, partly as tylar swellings, partly as merged spines (Fig. 6.2-6.3); same specimens also with above average frequency of malformed tylostyles (strongly truncated or reduced to globule or oxea, secondary tylar swellings, small side-branches). However, low frequency of mildly “aberrant” spirasters and tylostyles also occasionally present in other specimens. Spines in typical spirasters along convex side of shaft, as tiny bouquets on short stalks, distributed in very regular distance to each other. Spination terminally stronger and more pronounced, occasionally forming dense, cauliflower-like caps. Spirasters of comparatively uniform size, very slim and usually near 1 µm wide, commonly 15-19 µm in total length (details in Supplements S4-5). Single, rare occurrences of unusual microscleres here viewed as contamination: spirasters with conical spines (e.g. Fig. 6.4), spherasters, oxyasters.

Skeleton: Ectosomal skeleton tylostyles in palisade not covered by spiraster crust (Figs. 5.5, 7.1-7.2). Choanosome with low spicule content, skeleton consisting of ill-defined fibres of tylostyles within erosion chambers and in parallel with chamber walls, often aligned pointing into same direction (Fig. 5.4). Choanosomal spirasters mostly associated with membranous parts (Figs. 5.6, 7.3).

Distribution: Western Indo-Pacific realm (Spalding et al., 2007): eastern rims of the Northern Indian Ocean (Fig. 1). Okha, Gulf of Katchchh, Northwest India (Dendy, 1916; as *Cliona coronaria*), Malvan and Grande Island, central West India (our material), South India, Palk Straits (Devi et al., 2011; as *Cliona varians*; Thomas, 1972, 1979, 1986; as *Cliona orientalis*), Mergui Archipelago,

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Myanmar (Carter, 1887; as *Suberites coronarius*). Assumed also Andaman and Nicobar Islands (Kiruna-Sankar et al., 2016; Raghunathan, 2015a, 2015b; as *Cliona varians*).

Ecology: The sponges were sampled from 4–10 m water depth. Distribution to deeper water was not confirmed or rejected, but we assume a prevalence in shallow waters due to the photosymbiosis with *Symbiodinium* sp. In the Malvan Marine Sanctuary *Cliona thomasi* sp. nov. occurs predominantly in live coral (*Turbinaria mesenterina* (de Lamarck, 1816), *Porites compressa* (Dana, 1846), *Favites melicerum* (Ehrenberg, 1834), and *Pseudosiderastrea tayamai* (Yabe & Sugiyama, 1935); the latter two being more commonly infested; one of our specimens inhabited a live oyster), but also in dead coral, e.g. as rubble. Where in β -morphology, the sponges usually completely cover the surfaces of entire corals.

Remarks

The tylostyle shape of *Cliona thomasi* sp. nov. and the lack of a clear size difference between dermal and choanosomal tylostyles suggested that our West Indian sponges in encrusting to massive growth form belonged to the genus *Cliona*, rather than to *Sphaciospongia* (Fig. 6; Supplements S4-5). We were thus able to immediately reject all *Sphaciospongia* species reported from the Indian Ocean or West Pacific that we had included for comparison (Supplements S5-6). Consistently, these had longer choanosomal tylostyles than commonly occurring in *Cliona* species and a second, dermal tylostyle type that was about 60% of the length of the former. *C. thomasi* sp. nov. also appeared to have a shorter tylostyle type, but this differed not as strongly from the main tylostyle as in *Sphaciospongia* spp. (ca. 80% of the length of the main tylostyles; Supplements S2-3) and was apparently restricted to the choanosome and not associated with the dermal palisade. *Sphaciospongia* megascleres were mostly variable subtylostyles with subtle, elongated tyles very unlike the pronounced, round tyles observed in *C. thomasi* sp. nov.

Further, our samples clearly belong to the *C. viridis* (Schmidt, 1862) species complex. This is indicated by our molecular results, but also by a series of morphological and ecological characters such as bioeroding activity, the brown colour, the presence of tylostyles and slender spirasters with multi-split spines, and the occurrence of dinoflagellate photosymbionts (Rosell & Uriz, 2002; Schönberg, 2002b; Schönberg & Loh, 2005; Schönberg et al., 2005). After coming to this decision, our specimens were then difficult to further identify to species level. On one hand similarities to other Indo-Pacific *C. viridis* species prevented conclusive decisions, on the other hand decisions presented in earlier publications added to the confusion or provided misleading information that required careful consideration. We quickly excluded the Indo-Pacific *C. viridis*-like species *Cliona*

caesia Schönberg, 2000 and *Cliona minuscula* Schönberg et al., 2006, because they are known only in α -morphology and have no spirasters (Schönberg, 2000; Schönberg et al., 2006; Supplement S6). Moreover, *C. caesia* has light blue oscular collars, and *C. minuscula* has much smaller tylostyles than *C. thomasi* sp. nov. *Cliona subulata* Sollas, 1878 is another α -morphology sponge. The original sample site of *C. subulata* is unknown, but the species is assumed to be from the Indo-Pacific (Schönberg et al., 2017b). However, spirasters in *C. subulata* are helical and have characteristic, long and discrete spines unlike those on the spirasters of *C. thomasi* sp. nov. (Sollas, 1878; Supplement S6). *Cliona albimarginata* Calcinai et al., 2005 has a very similar habit compared to *C. thomasi* sp. nov., but its fully grown tylostyles are significantly slimmer, and the tyles are oval and elongated in *C. albimarginata*, but predominantly spherical in *C. thomasi* sp. nov. (Calcinai et al., 2005; Supplement S6). *C. albimarginata* spirasters display more irregular shapes and are less frequently C-shaped than in *C. thomasi* sp. nov. *C. orientalis* Thiele, 1900 also has a very similar habit in β -morphology, as well as very similar spicule dimensions and spicule shapes compared to *C. thomasi* sp. nov. (Thiele, 1900; Supplement S6). *C. orientalis* microscleres are predominantly helical spirasters, however, and only occasionally C-shaped. Considering that spicule dimensions can vary to some degree with environmental conditions (Bavestrello et al., 1993a, 1993b; Cárdenas & Rapp 2013; Mercurio et al., 2000; Valisano et al., 2012), initially we could not safely exclude *C. orientalis*. We had similar problems with the comparison to *Cliona varians* (Duchassaing & Michelotti, 1864). Even though *C. varians* occurs in the Caribbean, it shares morphologic characters with *C. thomasi* sp. nov., especially when considering the microscleres. *C. varians* is known for its C-shaped spirasters or “anthosigmas”, which as in *C. thomasi* sp. nov. is by far the most predominant form of the microscleres (Supplement S6; Figs. 6, 7.4-7.6). However, the tylostyles in *C. varians* are longer and slimmer than in *C. thomasi* sp. nov., with oval, elongated tyles that are often subterminal (Fig. 7.4, 7.7; Supplements S5-6). These characters appeared to provide reasonable grounds to distinguish the two species despite the similarities of the microscleres, but as previous publications from India had reported *C. varians*, we carefully searched the historical literature for further information.

We became aware of a possible conspecificity with Carter’s (1882, 1887) *Suberites coronarius* (Carter, 1882), which Dendy (1916) transferred to *Cliona* after he correctly recognised that the species was actively bioeroding (Supplement S6). The problem was that Carter’s material did not refer to one, but to two species (see Annandale, 1915; Dendy, 1916; Thiele, 1900). His 1882 Caribbean material was synonymised with *C. varians*, a species name which had seniority (van Soest, 2010). This rendered the name “*coronarius*” unavailable, even though Carter’s (1887) specimen from Mergui Archipelago was clearly different from *C. varians* and still needed a name.

Earlier workers had recognised the similarities with *C. orientalis* and declared Carter's Mergui specimen and a very similar Dendy (1916) specimen from northwestern India as conspecific with this species (Annandale, 1915; Dendy, 1916; Thiele, 1900). This decision was followed by Thomas (1972, 1979, 1986), who worked again on similar sponges from the Palk Strait (Supplement S6). To further complicate things, Topsent (1918) created the new genus *Anthosigmella* based on a Caribbean specimen of *S. coronarius* = *C. varians* and its peculiar C-shaped spirasters that were not helical and tended to have spicule accumulations at the ends to the shaft. Topsent (1918) observed a massive specimen and declared that this was not a bioeroding sponge. To make matters yet worse, Schönberg (2002) received Carter's (1887) Mergui specimen labeled "type" when requesting material for *C. varians* and did not notice the differences in spicule characters, then accepting this specimen as *Anthosigmella varians*. The confusion between the Caribbean and the Indian Ocean material was so entangled that we felt the need to look into some common Caribbean *C. viridis* species in addition to Indo-Pacific species to understand the ramifications of identifications and distributions of *C. viridis* species.

Spicular comparisons helped us to confirm that the Caribbean *C. varians* was different from our Indian material and that respective earlier reports for *C. varians* from the Indian Ocean should be considered as wrong (e.g. Calcinaï et al., 2000; Immanuel et al., 2015; Namboothri & Fernando, 2012; Supplement S6). The tylostyles in *C. varians* are overall slimmer than in *C. thomasi* sp. nov. (Fig. 7.4, 7.7), and the characteristic anthosigmas in the former species are more regular and uniform in overall shape, unlike in our samples, where the spirasters can commonly be J- or hook-shaped (Fig. 6, 7.5-7.6). However, Carter's (1887) "*Suberites coronarius*" from Mergui was a very good match. An additional sample was located in the National Institute of Oceanography, Goa (Devi et al., 2011), and we also regard a report by Dendy (1916) from the Gulf of Katchchh as conspecific with *C. thomasi* sp. nov. Other reports for *C. viridis* complex species could not as easily be aligned with our material (Supplements S5-6), and molecular analyses became unavoidable in order to confirm or reject conspecificity with existing *C. viridis* complex species (Table 1).

We successfully extracted DNA from the specimens listed in Table 1. Regrettably, the historical museum material did not presently yield useful molecular data that would have allowed direct comparison with our material. Moreover, the nrITS1 phylogram led to ambiguous results. *Pione* clustered together with *C. viridis* species, and *C. delitrix* Pang, 1973 and "*C. laticavicola*" (Pang, 1973) did not form a tight clade (Fig. 3), even though recent results showed that the latter two are conspecific (Chaves-Fonnegra et al., 2017). Results such as these can possibly be explained with sample contamination by the DNA of other species that were sampled during the same program.

Bioeroding sponge tissue is difficult to extract, and some species can mingle or occur in close vicinity of each other (Schönberg, pers. obs.). When plucking tissue out of the substrate it is difficult to know whether a disparate species neighbours the target material or whether the plucked material contains exclusively tissue from a single species. In addition, specific sequences in the ITS region often evolve faster than those of other biomarkers, so that resulting intragenomic variability can result in alignment problems (Vollmer & Palumbi, 2004; Yang et al., 2017), and this marker may not be the best to elucidate taxonomic and systematic relationships within the Clionaida. The more conservative 28S region previously generated good results for clionaid sponges in this context (Barucca et al., 2007; Leal et al., 2015; Xavier et al., 2010), and we will more strongly rely on the respective phylogram (Fig. 4).

The molecular analyses based on 28S again confirmed that our West Indian sponges belonged to the *C. viridis* species complex, but in the same time their sequences differed from all comparative material available on GenBank and clustered separately (Figs. 3-4). This excluded not only the morphologically very similar, Indo-Pacific species *C. orientalis*, but also common Caribbean sponges such as *C. caribbaea* Carter, 1882, *C. tenuis* Zea and Weil, 2003 and *C. varians*, as well as the Atlanto-Mediterranean species *C. viridis*.

Taking molecular and morphological results into account together, we concluded that mainly due to the spicule dimensions and shapes, our material was most likely a new species that we here described. The most distinctive characters of *C. thomasi* sp. nov. include its very robust and straight tylostyles with round tyles and the predominantly C-shaped, very slim spirasters. Based on spicule observations we also regard Thomas' (1972, 1979, 1986) "*orientalis*" specimens from Palk Strait as conspecific. Dendy's (1916) "*Cliona coronaria*" from Okha in Gujarat, NW India appears to be conspecific as well, which was not further assessed, however. Reports of "*Cliona varians*" in India were also tentatively included as synonyms for *C. thomasi* sp. nov., assuming that respective identifications were likely based on the high frequency of C-shaped spirasters (Kiruna-Sankar et al., 2016; Raghunathan, 2015a, 2015b; but these were mere reports and did not provide descriptions). According to these findings, we can presently report a distribution of *C. thomasi* sp. nov. for Northwest to South India and the Mergui Archipelago, with possible additional occurrence around the Andaman and Nicobar Islands. Because of the convoluted circumstances of this taxonomic-systematic investigation, we summarised respective information in [Supplement S6](#).

Discussion

It is now widely accepted that the guild of bioeroding sponges contains a number of insufficiently resolved species complexes with similar morphological characters (Schönberg et al., 2017b). As a consequence a number of species have traditionally, but erroneously been grouped under one name and were regarded as cosmopolitan or as having a wide distribution across different oceans (e.g. Xavier et al., 2010). With molecular taxonomy being increasingly used in addition to morphological studies, new species have been recognised and described, as well as morphological features identified that characterise and distinguish them within these difficult groups (e.g. Boury-Esnault et al., 1999).

The *Cliona viridis* species complex is one of the most difficult species complexes within the Clionaida, causing confusion through history as well as in recent studies (see examples in Supplement S6). As has been done for other groups, brown endolithic sponges have commonly been lumped under the same name per bioregion, but this group is particularly speciose. The Caribbean/Floridian *C. caribbaea* and *C. varians* were eventually resolved into the partially sympatric *C. acephala*, *C. caribbaea*, *C. aprica*, *C. paucispina*, *C. tenuis*, *C. tumula* and *C. varians*; the Mediterranean *C. viridis/nigricans* were accepted as *C. labiata*, *C. viridis* and *C. parenzani*, but some workers still recognise older synonyms as possibly valid (Longo et al., 2017); and respective Indo-Pacific species are presently recognised as *C. albimarginata*, *C. caesia*, *C. minuscula*, *C. orientalis*, and likely *C. subulata* and *C. vallartense*. All these species harbour symbiotic dinoflagellates that are thought to provide essential nutrients to their hosts (Fang et al., 2014; Weisz et al., 2010). This may in part explain the diversity of this group, the large average specimen size and fast growth rates, their competitive strength and their success in general (Schönberg et al., 2017b). *C. viridis* complex species are as a rule among the most dominant and destructive macroborers on coral reefs (Schönberg, 2001; Schönberg et al., 2017b), and *C. thomasi* sp. nov. is abundant and aggressive as well.

We therefore think that like some other *C. viridis* complex species, *C. thomasi* sp. nov. can aggravate coral bioerosion where it is common. Should abundances of *C. thomasi* sp. nov. increase, this could cause a gradual phase shift from constructional to erosional conditions on local reefs. Increasing abundances of *C. viridis* species have repeatedly been linked to disturbance in reef environments (e.g. Rützler, 2002; Schönberg & Ortiz, 2009). Bioeroding sponges of the *C. viridis* complex are believed to be relatively tolerant to environmental deterioration and able to benefit from increased substrate availability after coral mortality (reviewed in Schönberg et al., 2017a, 2017b). At our West Indian sample sites reports on reduced reef health largely related to sedimentation (De et

al., 2015, 2017; Hussain et al., 2016; Manikandan et al., 2016). At Carter's (1887) and Dendy's (1916) historical sample sites of *C. thomasi* sp. nov. pollution and thermal bleaching may be more relevant (De et al., 2017). Thomas' (1972, 1979, 1986) sample sites in Palk Strait have undergone degradation due to coral mining, pollution and bleaching events (Manikandan et al., 2014). The Andaman and Nicobar Islands have been regarded as comparatively unperturbed reef environments, but river sediment discharge into the Bay of Bengal, tsunami damage and global change have taken their toll (e.g. Brown, 2007). We therefore think that monitoring the abundance, distribution and boerosion capacity of dominant *C. viridis* complex species such as *C. thomasi* sp. nov. is essential in order to recognise changes in the benthic community over time and to develop suitable strategies for protecting and managing the coral reef ecosystem in the region (Schönberg, 2015).

Acknowledgments

We thank the Director of the CSIR-National Institute of Oceanography, Goa for providing access to all the facilities. K. De, V. Patil, A. Pujari and R. Nagesh, A. Hussain assisted during sample collection, A. Sardar with the SEM analysis, M. Nanajkar and R. Singh provided support for laboratory analysis. C. E. Sherlock and J. Perera from the London Natural History Museum assembled and sent extensive specimen loans and provided information about historical collection material. We sincerely thank S. Mills from the Canberra Department of Agriculture, Water and Resources for assisting us with the import of the London collection material into Australia. CS thanks J. Fromont, O. Gomez and S. Arklie for providing access to microscopy equipment through the Western Australian Museum and the Australian Institute of Marine Science. This study forms part of the PhD thesis of SM. We acknowledge financial support through RGSTC, Government of Maharashtra for GenBank project GAP2871. This is NIO contribution number.....

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Fig. 1. Known and putative sample sites for *Cliona thomasi* sp. nov. along the western coast of India and Myanmar, as well as around the Andaman and Nicobar Islands. (1.1) Overview with all locations shown. (1.2) Our sample site I at Grande Island, Goa. (1.3) Our sample site II at Malvan Marine Sanctuary, Maharashtra. (4-8) Locations for earlier records for *C. thomasi* sp. nov. (under other names): (4) Reported by Carter (1887) at the Mergui Archipelago, Myanmar, as *Suberites coronarius*. (5) Reported by Dendy (1916) at Okha, in the Gulf of Katchchh, as *Cliona coronaria*. (6) Reported by Thomas (1972, 1979) and Devi et al. (2011) in the Palk Straits, as *Cliona orientalis*. (7) Unconfirmed reports as *Cliona varians* from South Andaman and neighbouring sites (Raghunatan, 2015b; Kiruba-Shankar et al., 2016). (8) Unconfirmed report as *Cliona varians* from Great Nicobar Island (Raghunatan, 2015a). Background map of the Indian Ocean adapted from a map by S. Hindia, from Wikipedia (2017).

Fig. 2: The encrusting-endolithic sponge *Cliona thomasi* sp. nov. in different coral substrates. (2.1) In live *Favites* sp. (2.2) In live, but partially bleached *Porites* sp. (2.3) In live *Turbinaria mesenterina*. (2.4) Spreading from dead substrate into live *T. mesenterina*.

Fig. 3. Phylogenetic tree reconstructed from nrITS1 sequences from *Cliona thomasi* sp. nov. and comparative material. The tree topology is based on Maximum Likelihood. The number above the branches are support values, only values over 50% are shown. Samples from western India are printed in bold. All other sequences were obtained from GenBank. Sample names retrieved from GenBank were presently retained, although Chaves-Fonnegra et al. (2017) found that *Cliona laticavicola* is conspecific with *Cliona delitrix*.

Fig. 4. Phylogenetic tree reconstructed from 28S rDNA sequences from *Cliona thomasi* sp. nov. and comparative material. The tree topology is based on Maximum Likelihood. The number above the branches are support values, only values over 50% are shown. Samples from western India are printed in bold. All other sequences were obtained from GenBank.

Fig. 5: Morphological characters of *Cliona thomasi* sp. nov. viewed by scanning electron microscopy. (5.1) *C. thomasi* sp. nov. (holotype NIO 1002; MGB 35) in coral substrate. Two pores in coral skeleton unaltered, two enlarged by sponge erosion and filled with sponge tissue (arrows). (5.2) Erosion scars formed by *C. thomasi* sp. nov. have no microsculpturing and are smooth (NIO/BOD/P4; MGB 23). (5.3) Bioerosion chambers are connected with minute apertures (NIO/BOD/P4; MGB 23). (5.4) Dense choanosome tissue entirely fills the chambers (NIO/BOD/P4; MGB 23). Tylostyles are often loosely distributed, but aligned in the same direction. (5.5) Dermal tylostyles form a palisade and are not obscured by a dermal crust of spirasters (NIO/BOD/P4; MGB 23). (5.6) Spirasters are concentrated on membranous parts of the choanosome (NIO/BOD/P4; MGB 23, enlargement from 5.4). For the online version we highlighted (only) endolithic tissue in 5.1 and 5.4 orange, tylostyles in 5.4-5.5 blue and spirasters in 5.6 yellow.

Fig. 6. Scanning electron microscopy images of spicules of *Cliona thomasi* sp. nov. (7.1) Tylostyles and spirasters of the holotype (NIO 1002; MGB 35). The upper 4 tylostyles represent the larger type, the lower 4 the smaller type of tylostyles, of which the upper 3 each would have been considered as mature and fully formed (7.2-7.3) Slightly aberrant (?) “type 2” spirasters of NIO/BOD/P2 (MGB 21) and NIO/BOD/P4 (MGB 23), respectively, which were predominantly bow-shaped, generally thicker and had shorter, often reduced spines that could merge, or had tylar swellings. (7.4) NIO 776 had more delicate spirasters with more pronounced spine bouquets. From this sponge we also display an example of a branching spiraster (arrow, 2x the enlargement) and of a putatively foreign spiraster with conical spines.

Fig. 7. *Cliona thomasi* sp. nov. morphological characters, in comparison with Carter’s (1882) Caribbean “*Suberites coronarius*” = *Cliona varians*, from historic tissue pluck preparations as viewed under the light microscope. (7.1) *C. thomasi* dermal palisade with slightly denatured symbiotic dinoflagellates (paratype 1 – NIO 1005; MGB 33). (7.2) Inhalant

pore from NIO 776, lacking any evidence for dermal spirasters. (7.3) Choanosomal membrane with symbiotic dinoflagellates and spirasters (Paratype 1 – NIO 1005; MGB 35). (7.4) Spicules in a fragment of choanosomal tissue in *Cliona varians* BMNH 1954.3.9.398 from Honduras (holotype for Carter's "*Suberites coronarius*"). (7.5) C-shaped spirasters in *C. thomasi* sp. nov. (holotype – NIO 1002; MGB 35). (7.6) C-shaped spirasters in *C. varians* (BMNH 1954.3.9.398). (7.7) A comparison between characteristically shaped tylostyles in *C. thomasi* sp. nov. (top) and *C. varians* (bottom). Tylostyles are slimmer in *Cliona varians* and have an oval tyle.

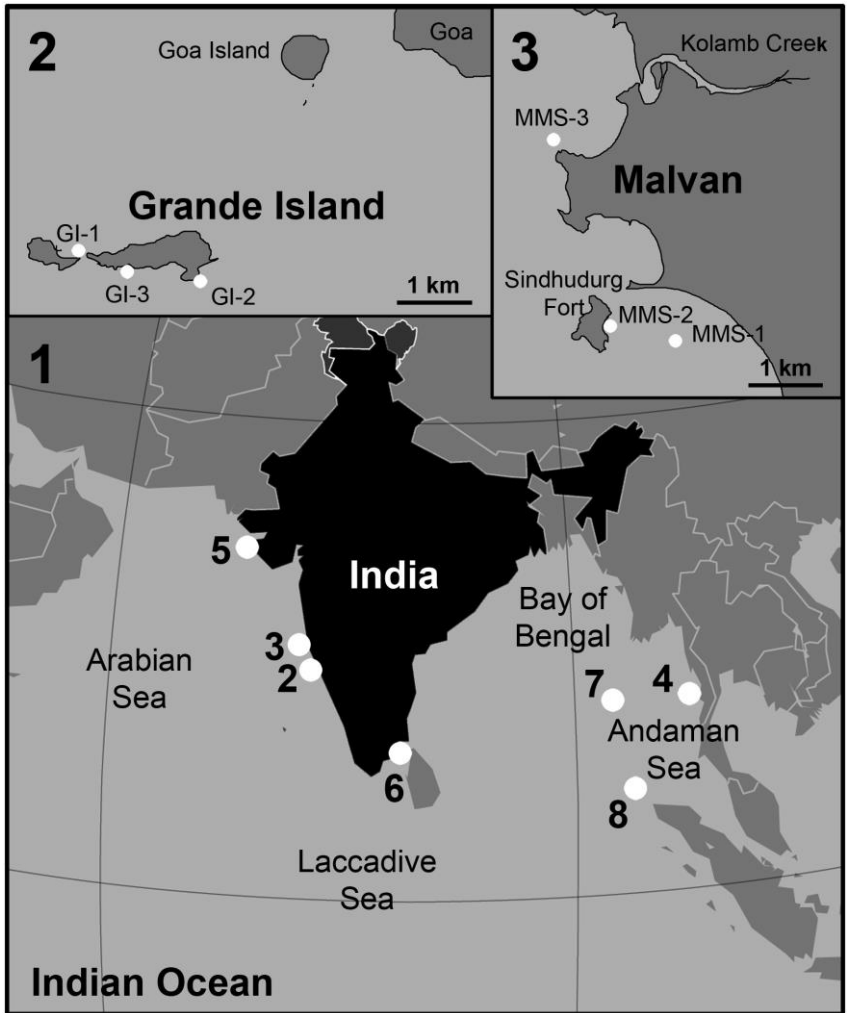


Fig. 1

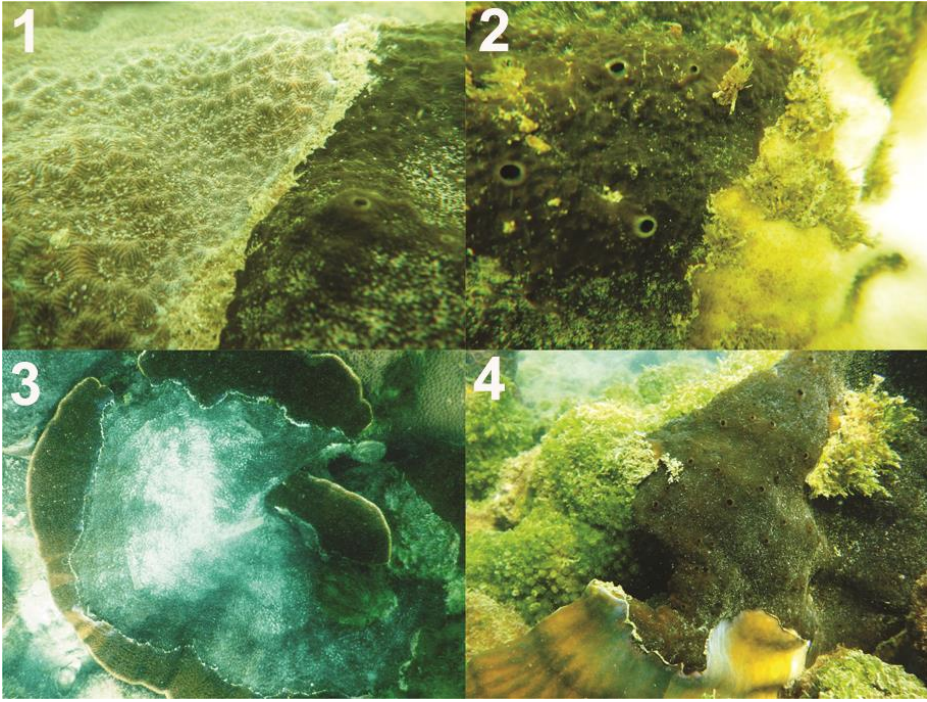


Fig. 2

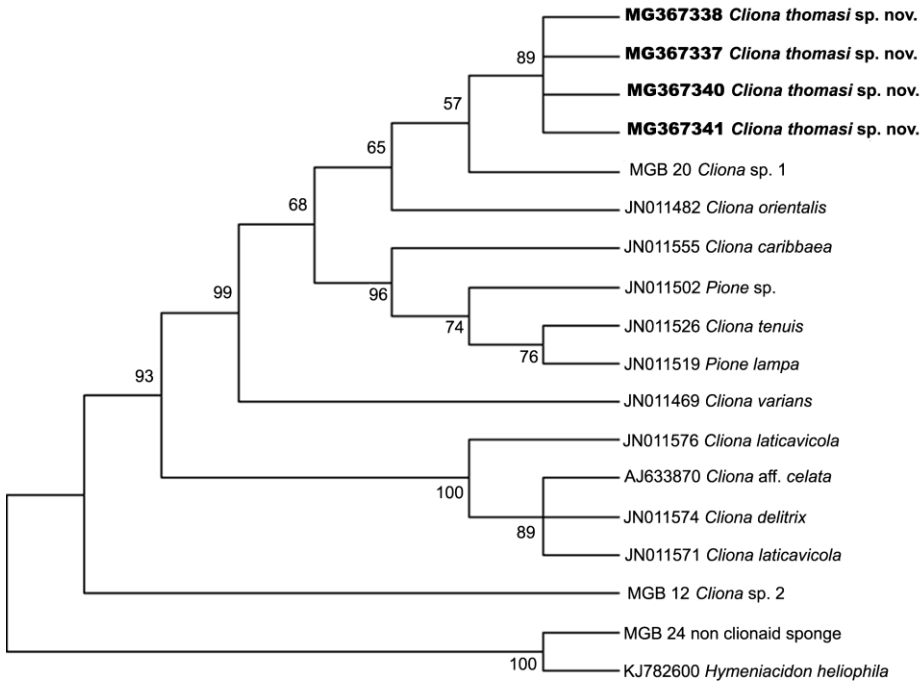


Fig.3

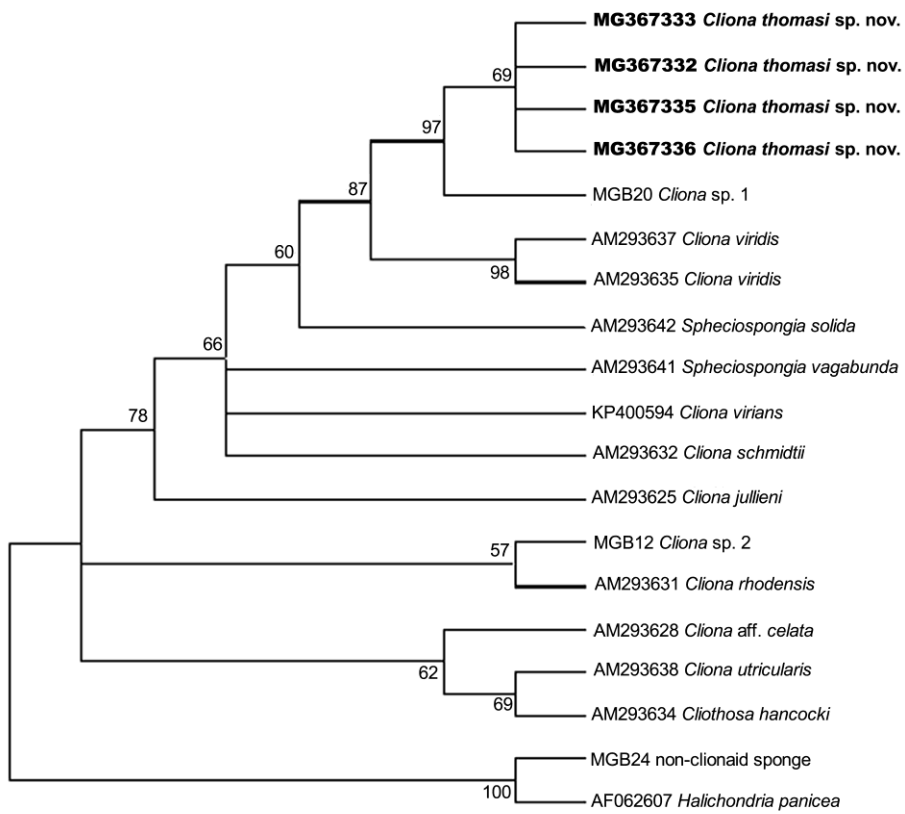


Fig.4

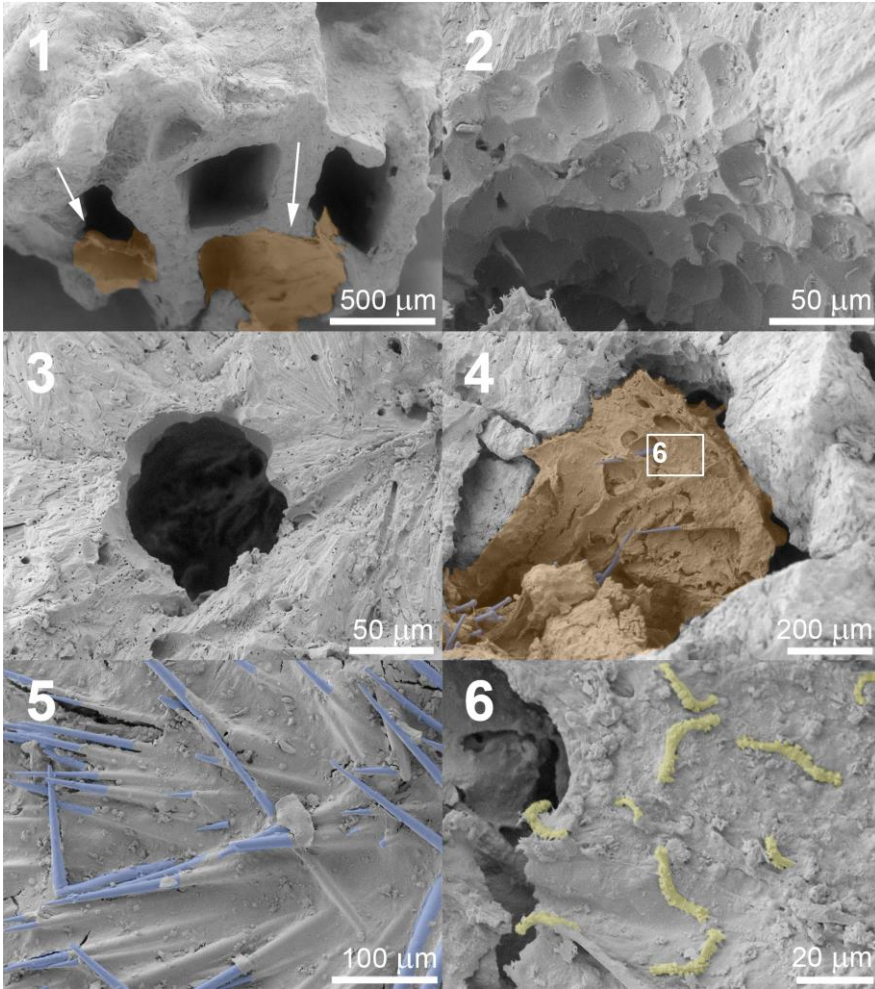


Fig.5

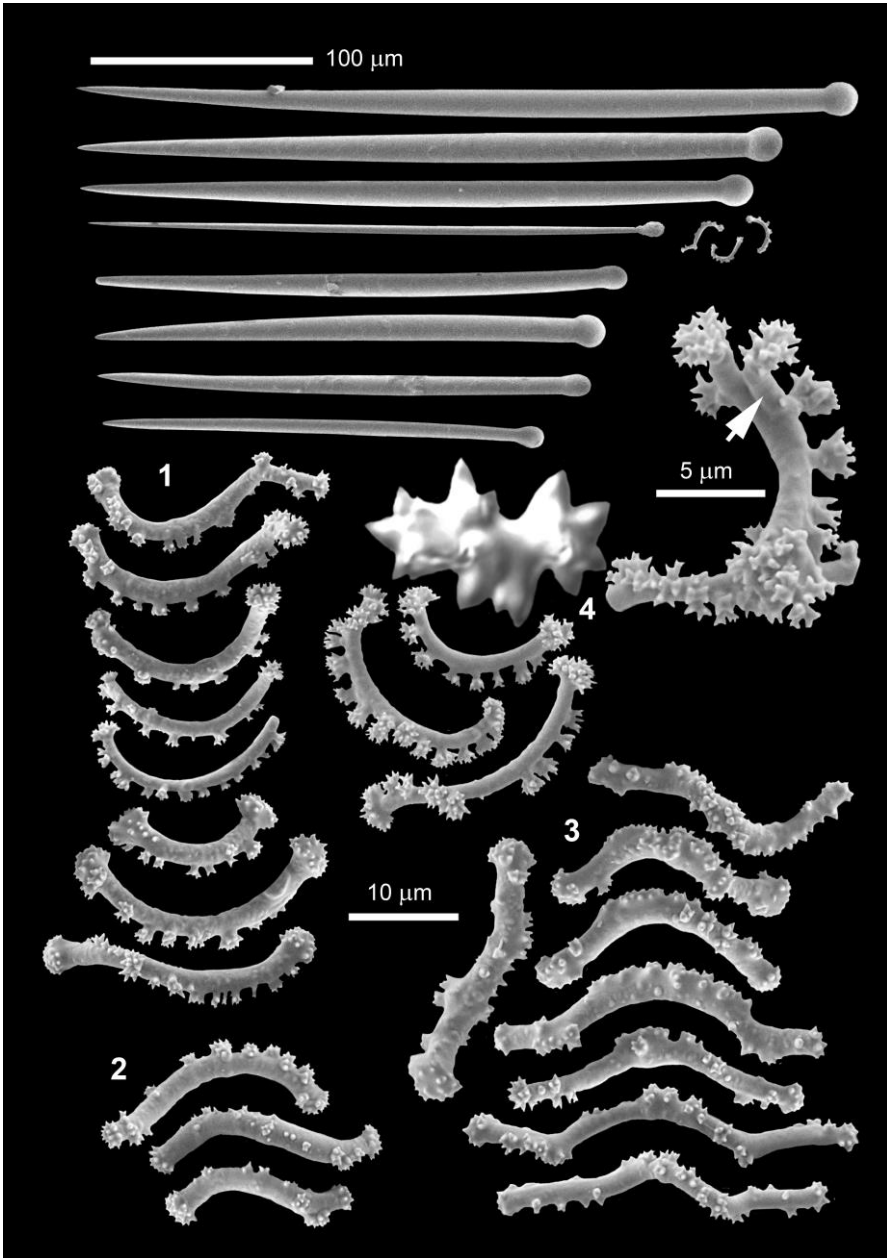


Fig.6

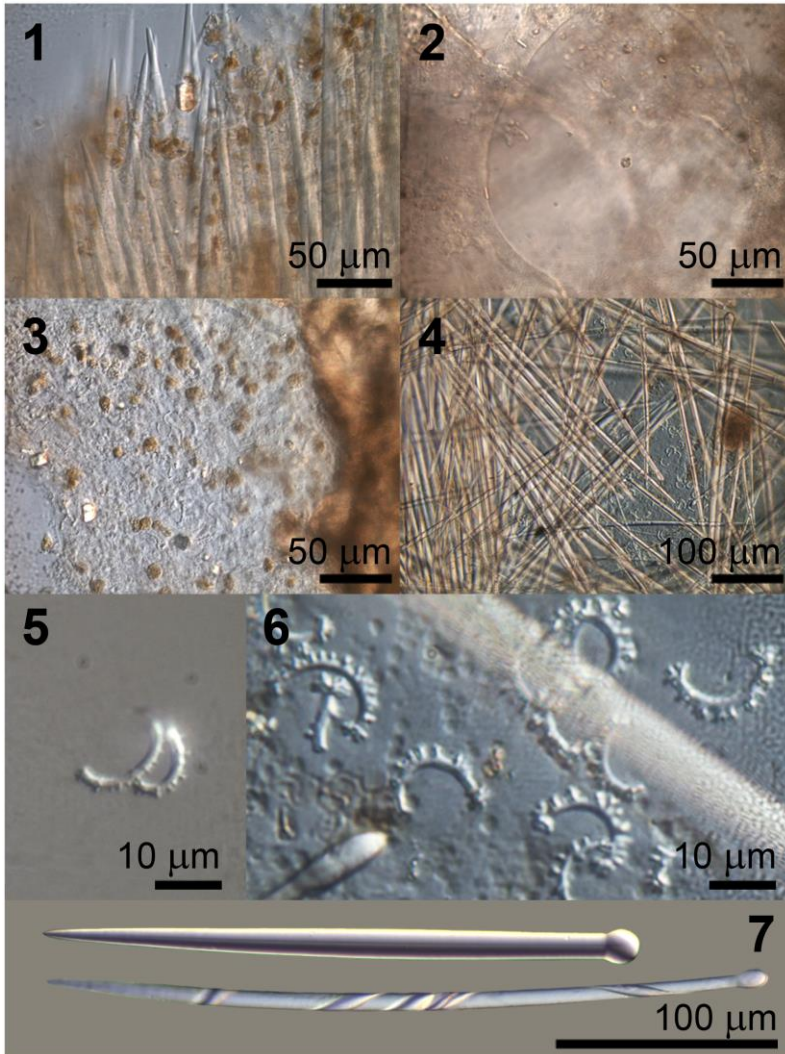


Fig.7

Table 1. Molecular data sets used for the phylogenetic analyses in reference to *Cliona thomasi* sp. nov. NA – no data available, indet. – species not further identified, NIO – National Institute of Oceanography (Goa), unreg. – unregistered, coll. – collection, INV-POR – Porifera collection of the Instituto de Investigaciones Marinas y Costeras, Museo Nacional de Historia Marina de Colombia (Santa Marta), MNRJ – Museu Nacional, Universidade Federal do Rio de Janeiro. Species names here listed are largely reproduced as previously published, but note that clustering in the phylogenetic trees partly suggests different species affiliations.

Species	Field reference	Collection reference	GenBank reference for nrITS1	GenBank reference for 28SrRNA	Published reference, type material
<i>Cliona thomasi</i> sp. nov.	MGB 21	NIO 1003	MG367337	MG367332	Present study
<i>Cliona thomasi</i> sp. nov.	MGB 23	NIO 1004	MG367338	MG367333	Present study
<i>Cliona thomasi</i> sp. nov.	MGB 33	NIO 1005	MG367340	MG367335	Present study, paratype 1
<i>Cliona thomasi</i> sp. nov.	MGB 35	NIO 1002	MG367341	MG367336	Present study, holotype
<i>Cliona</i> sp. 1, indet. aff. <i>Cliona viridis</i>	MGB 20	NIO, unreg.	NA	NA	Present study
<i>Cliona</i> sp. 2, indet. aff. <i>Cliona rhodensis</i>	MGB 12	NIO, unreg.	NA	NA	Present study
Porifera indet. (not a clionaid)	MGB 24	NIO, unreg.	NA	NA	Present study

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<i>Cliona varians</i>	NA	INV-POR; MNRJ	JN011469	KP400594.1	Escobar et al. (2012); Leal et al. (2016)
<i>Cliona cf. celata</i>	NA	Coll. B. Calcinai	AJ633870	AM293628	Barucca et al. (2007); Wörheide et al. (2004)
<i>Cliona viridis</i>	NA	Coll. B. Calcinai	NA	AM293637	Barucca et al. (2007)
<i>Cliona viridis</i>	NA	Coll. B. Calcinai	NA	AM293635	Barucca et al. (2007)
<i>Sphaciospongia solida</i>	NA	Coll. B. Calcinai	NA	AM293642	Barucca et al. (2007)
<i>Sphaciospongia vagabunda</i>	NA	Coll. B. Calcinai	NA	AM293641	Barucca et al. (2007)
<i>Cliona schmidti</i>	NA	Coll. B. Calcinai	NA	AM293632	Barucca et al. (2007)
<i>Cliona rhodensis</i>	NA	Coll. B. Calcinai	NA	AM293631	Barucca et al. (2007)
<i>Cliona utricularis</i>	NA	Coll. B. Calcinai	NA	AM293638	Barucca et al. (2007)
<i>Clithosa hancocki</i>	NA	Coll. B. Calcinai	NA	AM293634	Barucca et al. (2007)
<i>Cliona orientalis</i>	NA	INV-POR	JN011482	NA	Escobar et al. (2012)
<i>Cliona caribbaea</i>	NA	INV-POR	JN011555	NA	Escobar et al. (2012)
<i>Pione</i> sp.	NA	INV-POR	JN011502	NA	Escobar et al. (2012)
<i>Pione lampa</i>	NA	INV-POR	JN011519	NA	Escobar et al. (2012)
<i>Cliona tenuis</i>	NA	INV-POR	JN011526	NA	Escobar et al. (2012)
<i>Cliona delitrix</i>	NA	INV-POR	JN011574	NA	Escobar et al. (2012)
<i>Cliona delitrix</i> (?), as <i>Cliona laticavicola</i>	NA	INV-POR	JN011576, JN011571	NA	Escobar et al. (2012)
<i>Hymeniacion heliophila</i>	NA	NA	KJ782600	NA	Yang et al. (2013)

Halichondria panicea

NA

NA

NA

AF062607

Chombard et al. (1997)
