

Biodiversity, ecology, and taxonomy of sediment-dwelling Dendrophylliidae (Anthozoa, Scleractinia) in the Gulf of Thailand

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Abstract

Dendrophylliidae represents one of the most speciose families of scleractinian coral, expressing a wide range of morphological and ecological traits. Recent phylogenetic analyses of the family have indicated that several conventional genera are in need of revision. In the Gulf of Thailand, dendrophylliids are predominantly found on hard-substrate reefs and pinnacles, or on soft-substrate habitats. Soft-substrate habitats in the Gulf of Thailand have been shown to host unique species assemblages and faunal ecology. Here we provided an updated phylogenetic hypothesis for the Dendrophylliidae based on newly sequenced species, and analyses integrating morphology, genetics and ecology. High-resolution Micro-CT was used to create digital versions of the studied species, allowing for non-destructive examination of internal and external features. Our findings allowed for a taxonomic assessment of the genera *Heteropsammia* and *Tubastraea*, with the species *Balanophyllia* (*Eupsammia*) *stimpsonii*, moved to the genus *Tubastraea*. They also support the polyphyly of *Dendrophyllia* and *Cladopsammia*. *In-situ* surveys provided population-density information for four dendrophylliid species from soft substrate habitats, indicating that the species *Heteropsammia moretonensis* may be the most widespread within the Gulf of Thailand. These surveys also provided novel ecological documentation associated with these corals, including proto cooperative feeding upon a sea pen by *Tubastraea stimpsonii* comb. nov., and feeding upon other cnidarians by *Heteropsammia* spp.

Keywords

free-living – *Heteropsammia* – Micro-CT – phylogenetics – synonymy – *Tubastraea*

Introduction

The taxonomy of scleractinian corals has seen major revisions and upheavals in recent years due to the application of novel analyses and techniques. The most significant of these is the utility of molecular techniques, the outputs of which have challenged traditional hypotheses derived from morphological techniques alone (Budd et al., 2010; Kitahara et al., 2016). Examples of these include the synonymizing, reorganisation or reclassification of multiple genera of common and widespread Indo-Pacific corals that belong to various families, such as Acroporidae, Coscinaraeidae, Euphylliidae, Fungiidae, Lobophylliidae, Merulinidae, Mussidae, Plerogyridae, Plesiastreidae, and Psammocoridae (Wallace et al., 2007; Benzoni

et al., 2010, 2012a, b, 2014; Gittenberger et al., 2011; Budd et al., 2012; Huang et al., 2014, 2016; Luzon et al., 2017; Juskiewicz et al., 2022; Arrigoni et al., 2023). Morphological analyses too have seen dramatic advances via tools such as high-resolution electron microscopy allowing for the study of micromorphological features, and micro-CT allowing for non-destructive visualisation and reconstruction of complex internal and external structures of coral skeletons (Budd & Stolarski 2009; Budd & Stolarski 2011; Arrigoni et al., 2019; Li et al., 2020).

A recent study of the family Dendrophylliidae Gray, 1847, integrating both molecular and advanced morphological approaches, indicated disagreement with the prior macromorphology-based phylogenetic hypothesis (Arrigoni et al., 2014).

Dendrophylliidae is the third-most speciose ($n = 183$) of the extant scleractinian coral families after Caryophylliidae ($n = 307$) and Acroporidae ($n = 271$) (Hoeksema & Cairns, 2023), and is characterised by much morphological and ecological variation. Prior to the application of molecular analyses, the first evolutionary hypothesis for the family was developed by Cairns (2001) utilizing a morphological, cladistic approach with plesiomorphic and apomorphic character states. In this work, he not only provided a comprehensive summary of the complex taxonomic history of all extant and extinct genera known at the time, but also diagnosed each based on ten characters (nine morphological, one ecological). The integration of molecular data in subsequent studies however caused a paradigm shift, with multiple later studies (Capel et al., 2020; Yiu et al., 2021; Yiu & Qiu, 2022) supporting the findings of Arrigoni et al. (2014). In particular, a large number of genera were found to be polyphyletic, with little clear indication on which characters (or combination thereof) proposed by Cairns (2001) retained broad diagnostic power among modern dendrophylliid corals. A challenge of these studies, however, remains the poor biogeographic sampling with limited molecular data available for most presently described species, or data from very few locations and depths across the geographical and bathymetrical ranges for which data is available for most species.

Historically, in Thai waters little research has been done to document corals from habitats outside of coral reefs (e.g., Nishihira & Pong-In, 1989). Indeed, the documentation of dendrophylliid corals in Thailand has largely been made via ecological or diversity studies as opposed to dedicated taxonomic investigations (Hylleberg & Aungtonya, 2013; Hoeksema & Matthews, 2015; Valderama Ballesteros et al., 2018; Yucharoen et al., 2020;

Monchanin et al., 2021). Within the Gulf of Thailand in particular, recent studies have contributed to the sparse literature on the ecology of soft-sediment-habitat-associated dendrophylliid corals (Mehrotra et al., 2016, 2019), while also highlighting the unexplored biodiversity of these habitats (Mehrotra et al., 2021). The Gulf of Thailand is a geologically young shallow basin subject to high levels of sedimentation and turbidity due to the influence of multiple rivers and streams, and anthropogenic activities (Sathiamurthy & Voris, 2006; Liu et al., 2016). Therefore, soft-substrate habitats represent a significant portion of the marine environments of the Gulf of Thailand (Printrakoon et al., 2008, Mehrotra et al., 2021).

By combining previous data from the Gulf of Thailand with dedicated surveys from hard- and soft-substrates, this study aims to expand the taxonomic and ecological understanding of dendrophylliid corals in soft-substrate habitats from the region. By utilising a combination of genetics, digital 3D-imaging, and ecology, this study adds to the growing evidence of a disagreement between the classical morphologically derived taxonomy and a modern one suggested by molecular and novel macro- and micromorphological data. We further record previously undocumented biodiversity and ecology of dendrophylliid corals in the Gulf of Thailand, and provide novel data and insights on the status of free-living corals belonging to the genera *Heteropsammia* and *Tubastraea*.

Material and methods

Sampling

A total of 15 specimens each of the species *Balanophyllia* (*Eupsammia*) *stimpsonii* (Verrill, 1865) (vouchers EKT19, EKT20 and EKTa-m), *Dendrophyllia* cf. *minima* Ogawa

& Takahashi, 2000 (vouchers HC20a-o), *Heteropsammia cochlea* (Spengler, 1781) (vouchers KT-1m, KT-2m, KT-4m, KT-?m and KTa-l) and *Heteropsammia moretonensis* Wells, 1964 (vouchers HmKT19, HmKTa-d, HmKMN21, HmKMNa-c, HmKS20, HmKSa-e) were collected by SCUBA diving from soft-substrates between 11 and 30 m depth from 11 sites across the Gulf of Thailand (fig. 1). Additionally, five specimens each of *Cladopsammia gracilis* (Milne Edwards & Haime, 1848) (vouchers RKT19, RKT20, RKTa,b, RKS20) and *Tubastraea diaphana* (Dana, 1846) (vouchers TmKT19a-e), and two specimens of *Tubastraea* cf. *chloromura* Yiu & Qiu, 2022 (vouchers YKT19c,d), were collected at 10–20 m depth from hard substrates (fringing reef and pinnacle) from the same sites via the same method. *In situ* surveys were carried out and specimens collected between 2018 and 2022. For each species, five specimens were preserved directly in 95% ethanol for use in molecular analysis, with the remaining 10 specimens being bleached in a sodium hypochlorite solution during 12–24 h for morphological analysis. One specimen of *Tubastraea diaphana* (TmKT19b) had tissue preserved for molecular analysis while the rest of the sample was later bleached for morphological analysis. All samples are deposited at the Department of Marine and Coastal Resources, Eastern Gulf of Thailand division (Prasae, Rayong) under the accession ATMEC2022a. In addition, tissues from three specimens of *Heteropsammia eupsammides* (Gray, 1849) (vouchers Ko1, Ko4 and Ko5) from Komodo Island (Indonesia) were used for molecular analysis in this study. These corals were collected at Slawi Bay, SE Lassa Island, East Komodo (08°36'08"N, 119°29'47"E) on 13 November 2002 and are presently stored at the coral collection of Naturalis Biodiversity Center (Leiden, the Netherlands) with catalogue number RMNH.COEL.39394.

Molecular analysis

For all tissues preserved for molecular analysis, DNA extraction was carried using DNeasy Blood and Tissue Kits (Qiagen Inc., Hilden, Germany). Genomic information for three regions were targeted, following Arrigoni et al. (2014). This includes two mitochondrial regions, specifically cytochrome oxidase 1 (COI) and the region between the 3'-end of COI and the 5'-end the 16S subunit (henceforth IGR) using the primers COIDENL and COIDENR, (Arrigoni et al., 2014), and ZCOI and ZCOIR (Forsmann et al., 2009) for the COI region and AGAL and DENF (Arrigoni et al., 2014) for the IGR. One nuclear region, specifically the rDNA region covering ITS1, 5.8S, ITS2 and a portion of 18S and 28S (henceforth rDNA) was also targeted using the primers A18S (Takabayashi et al., 1998) and ITS4 (White et al., 1990), or the pair 1s and 2ss (Chen et al., 1996). The nuclear histone 3 (H3) region was also amplified, using primers H3F and H3R (Colgan et al., 2000) and sequenced for all specimens, however this was not included in the present analysis. PCR was carried out using BioRads MJ Mini™ Personal Thermal Cycler (Bio-Rad Laboratories Inc., Hercules, CA, USA) with a reaction volume of 20 µl. PCR protocol for the COI region was as follows: an initial denaturing step at 94°C for 3 min; 40 cycles of denaturing at 94°C for 30 sec, annealing at 47°C for 30 sec, an extension at 72°C for 1 min, followed by a final extension at 72°C for 5 min. PCR protocol for the IGR region was: an initial denaturing step at 94°C for 3 min; 40 cycles of denaturing at 94°C for 30 sec, annealing at 51°C for 30 sec, an extension at 72°C for 1 min, followed by a final extension at 72°C for 5 min. PCR protocol for the nuclear rDNA and H3 regions was: an initial denaturing step at 94°C for 3 min; 40 cycles of denaturing at 94°C for 30 sec, annealing at 55°C for 30 sec, an extension at 72°C for 1 min, followed by a final extension at 72°C for 10 min.

In addition to sequences generated as part of this study, sequences of other specimens were acquired from Genbank based on previous studies with accession numbers available in supplementary table S1. Sequence alignment was carried out using BioEdit 7.2.5 (Hall, 1999) and then reviewed manually. Sequences were concatenated in full and analysed under both maximum likelihood, using MEGA X software v10.2 (Kumar et al., 2018), and Bayesian inference, using Mr. Bayes software v3.2 (Ronquist et al., 2012). Optimum evolutionary models for the partitioned dataset were selected using the model test feature within MEGA X with the optimum model used being GTR + G + I. Maximum likelihood analysis was conducted with 1,000 bootstrap replicates and random starting trees. Bayesian inference analysis was conducted with 50,000,000 generations and four chains with Markov chains being sampled every 1,000 generations. The first 25% generations were removed as burn-in with the rest being used to produce the 50% consensus tree. Uncorrected genetic distances for each region and each species were calculated with MEGA X to provide estimates of distance, however these were found to be uninformative at high taxonomic resolutions and were thus omitted from inferences. Attempts to find sequences pertaining to the relevant regions from a single specimen of the closely related family Poritidae were not successful, so thus sequences from multiple specimens of *Goniopora columna* Dana, 1846 were concatenated for the purposes of our analysis. Sequence information for the *Goniopora* out-group used by Arrigoni et al. (2014) could not be found for purposes of review or replication.

Morphological analysis

Bleached specimens were examined carefully utilising a simple over-the-counter magnifying lens, in conjunction with an Olympus TG6 digital camera. Morphological features were

investigated and compared to relevant literature on the Dendrophylliidae (in particular Zibrowius, 1985; Hoeksema & Best, 1991; Cairns, 2001; Cairns & Kitahara, 2012; Arrigoni et al., 2014; Filander et al., 2021; Kitahara & Cairns, 2021). Additionally, two specimens each of the four soft-substrate species and one specimen each of *Cladopsammia gracilis* and *Tubastraea diaphana* were scanned using micro computed tomography (micro-CT). Micro-CT scans were carried out using a Skyskan 1173 (Bruker, Billerica, MA, USA) using a beam energy of 120kV and a resolution of 12 μm per pixel. Additionally, 3D volumetric models of each coral were digitally reconstructed using the software 3D Slicer (Fedorov et al., 2012) to allow for detailed investigation of other key features (i.e., longitudinal septal ornamentation) and to be used as supporting material. Morphological investigations in combination with molecular analyses were integrated to provide an updated phylogenetic hypothesis of relevant dendrophylliid clades with discussions on the status of multiple groups of interest.

In situ surveys

Peak population density assessments for each sediment-dwelling dendrophylliid species were carried out at three locations across the Gulf of Thailand. Study sites were located at Mu Koh Samaesan Islands (Chonburi Province), Koh Mun Archipelago (Rayong Province) and Koh Tao (Suratthani Province) (fig. 1). At each of these locations, preliminary roving diver assessments were carried out at soft-substrate habitats up to 1 km offshore from the coast of each island. The goal of these assessments was to visually identify specific sites that hosted an approximated minimum of one individual/ m^2 of any of the four studied species. Based on this criterion, 11 study sites were chosen for a more precise assessment, with all other surveyed areas at

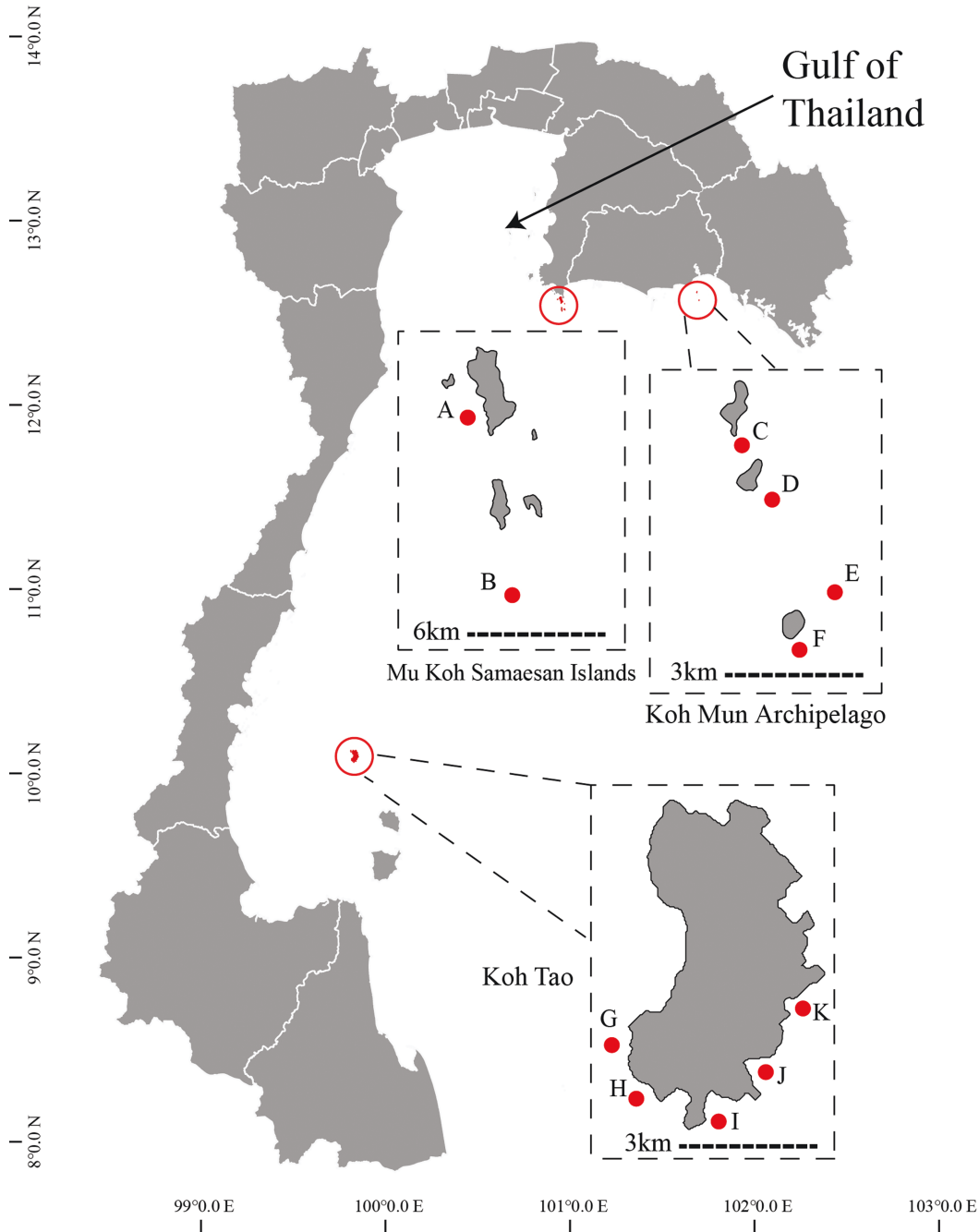


FIGURE 1 Map of survey sites in the Gulf of Thailand; A) Koh Samaesan; B) Hin Chalam; C) Koh Mun Nai; D) Koh Mun Klang; E) Site HYE21; F) Koh Mun Nok; G) Sai Nuan; H) Tao Tong; I) Taa Chaa; J) Leuk Bay; K) Tanote Bay.

each study site approximated to host fewer than one individual/m² of any of the four studied species, and thus disregarded for the present study. At each site, a 200-m transect line was laid out across the benthos perpendicular to the shoreline so as to cover a wider depth range. The depths of these transects were not standardized but were dependent on the topography of each location. At 20-m intervals along the transect line, a 1 × 1 m² quadrat was randomly placed and all dendrophylliid corals inside were counted. The mean abundance/m² (±s.e.) for each coral per site was calculated using data from the ten quadrats at each site.

Results

Digital reconstructions

All samples were successfully scanned without damage, and digital reconstructions using volumetric data were produced. In conjunction with photography of the macro-morphology of specimens, digital CT models of corals were used to investigate and map septal cycles, ornamentation and columella depth, and variation in skeletal porosity for all samples. Models generated were vital in the visualisation of internal structures and within fossae, such as in the internal chambers of *Heteropsammia* specimens or in assessing the separation (or lack of) between higher order septa and the columella in *Tubastraea* specimens. Non-destructive 'slicing' (fig. 2H, I) allowed for easy comparison and visualisation of key morphological features such as septal cycles, development of Pourtales plan, shape and structure of calicular margin, and more. All models were deposited and registered in MorphoBank (O'Leary & Kaufman, 2012, morphobank.org; project number p4369).

Molecular results

Fifty-five sequences were obtained from 21 specimens, comprising genetic information from the COI, 1GR and ITS regions. Of these, 52 sequences from 18 specimens were used for further analysis, in combination with 237 sequences from previous studies (Arrigoni et al., 2014; Capel et al., 2020; Yiu et al., 2021; Yiu & Qiu 2022) and three sequences representing the outgroup, with the resulting concatenated sequence alignment including 1977 positions representing a total of 95 specimens. The length for each marker was 601 position, 466 positions and 911 positions for COI, 1GR and ITS regions respectively. Amplification of the COI gene failed for sample HC20b, however it was included in the analysis with the remaining sequence information. Attempts were made to include a *Dendrophyllia minuscula* sequence from Terraneo et al. (2022), but mitochondrial DNA alone proved insufficient to resolve its placement within the resulting phylogeny reconstruction and was thus omitted from further analysis.

There was general agreement between the BI and ML topologies, with some differences in genus and species level clades, however ML analyses had weaker support overall (supplementary fig. 1). In contrast, the BI analysis offered higher support values across the tree, with strong support for most species-level clades (figs. 3 and 4). The main differences between the two analyses were in the specific placement of the *Duncanopsammia*/*Turbinaria* and *Heteropsammia*/*Cladopsammia* clades and fine-scale topological discrepancies in the *Tubastraea*, *Rhizopsammia*/*Cladopsammia* and *Heteropsammia* clades. The key topological differences placed *Turbinaria*/*Duncanopsammia* as forming a polytomy and the *Heteropsammia*/*Cladopsammia* clade being weakly supported in ML, whereas BI analysis showed the *Heteropsammia*/*Cladopsammia*

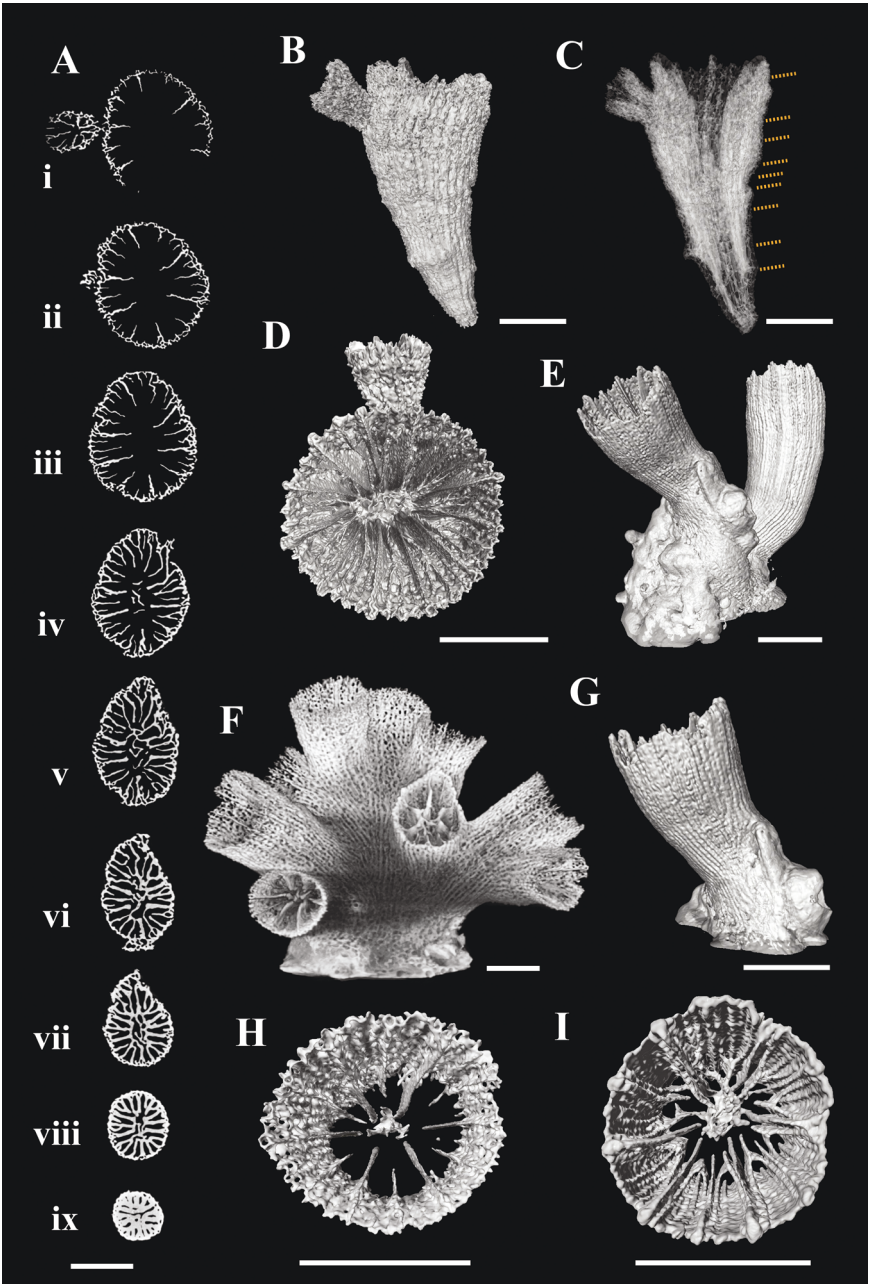


FIGURE 2 Digital images of specimens based on micro-CT scans. A–D) *Tubastraea stimpsonii* comb. nov. (EKTa) A) Series of nine transverse slices from calice margin (i) towards base (ix); B, C) lateral view with varying opacities, yellow dashed lines denote the position of slices in A; D) top down view into corallite showing calicular features. E, G, I) *Cladopsammia gracilis* (RKTa). E) lateral view of small colony specimen including holdfast; G) close-up of theca with striae visible; I) wide slice of upper portion of a single corallite showing calicular features. F, H) *Tubastraea diaphana* (TmKT19b). F) lateral view of typical colony specimen including holdfast; H) wide slice of upper portion of a single corallite showing calicular features. Scale bars: 5 mm.

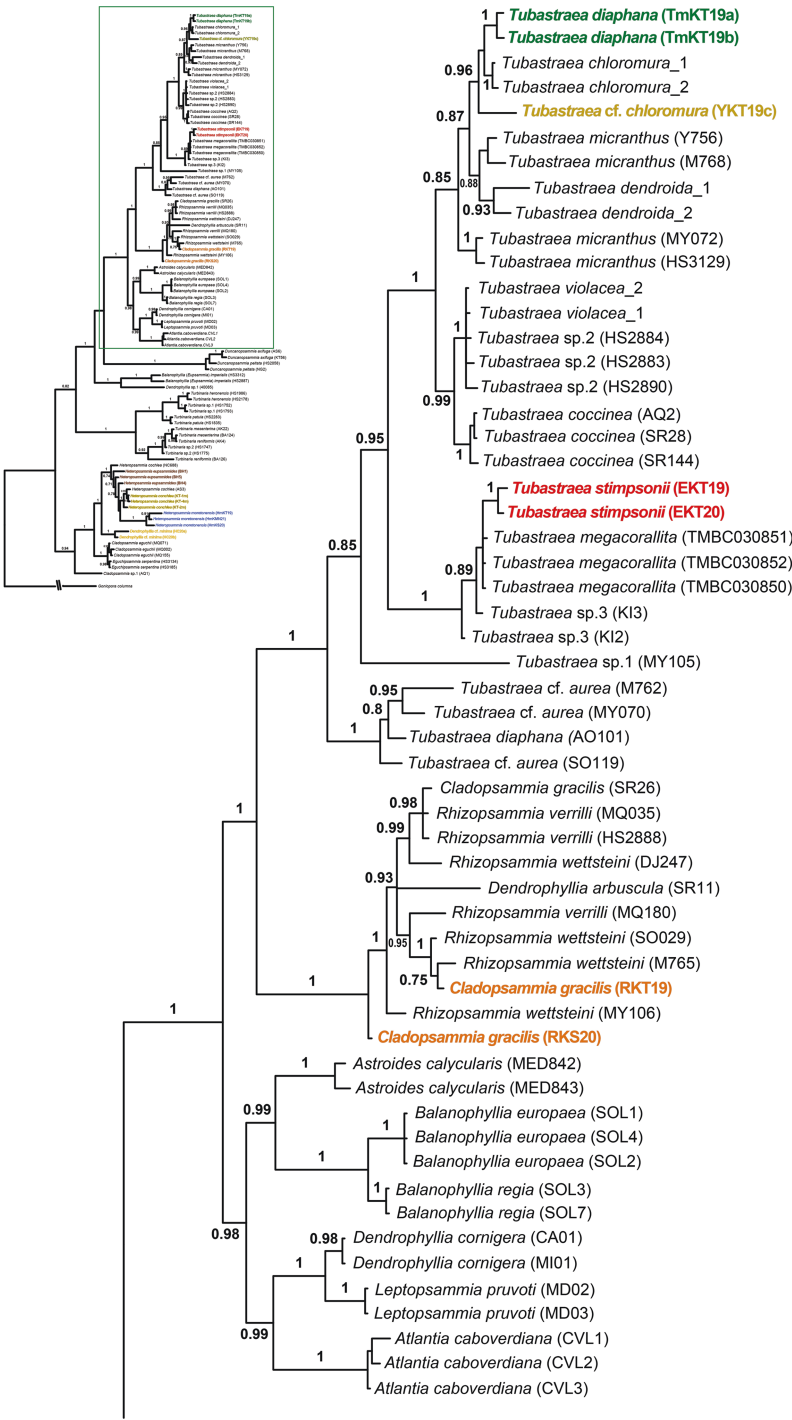
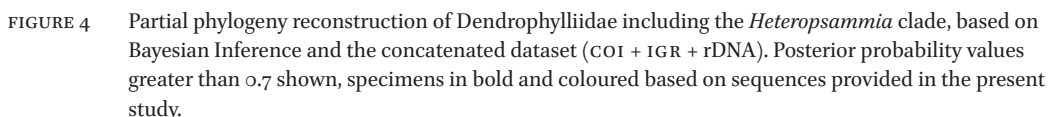


FIGURE 3 Partial phylogeny reconstruction of Dendrophyllidae including the *Tubastraea* clade, based on Bayesian Inference and the concatenated dataset (COI + 1GR + rDNA). Posterior probability values greater than 0.7 shown, specimens in bold and coloured based on sequences provided in the present study.



In both analyses however, the placement for three of the four soft-substrate species studied in this paper were consistent with strong support in BI (pp = 1) and moderate support in ML (bs < 56). Notably the relationship among *Heteropsammia cochlea* and *H. eupsammides* remains unclear, indicating a possible complex of species or highlighting the weakness of currently applied molecular techniques in resolving the species. In contrast, *Heteropsammia*

Abbreviations

CD Corallum Diameter
LCD Lowest Corallum Diameter
GCD Greatest Corallum Diameter

GCD:LCD	Ration between Greatest and Lowest Corallum Diameter
S1, S2 etc	First Septal Cycle, Second Septal Cycle etc.

Taxonomy

Tubastraea Lesson, 1830

Diagnosis. Colonial or solitary. Corallum arborescent, phaceloid, ceratoid, or massive, with plocoid corallites. Budding typically extratentacular. All extant species azooxanthellate, most attached with a single species free-living. Septa arranged hexamerously, Pourtales plan weakly developed or absent, pali absent, columella spongy. Corallum costate, lacking epitheca.

Tubastraea stimpsonii (Verrill, 1865) *comb. nov.*

Figs 2 A–D, 5 A, B, 9K

Eupsammia stimpsonii Verrill, 1865: 150.

Eupsammia stimpsoniana Verrill, 1866: 29, pl. 2: fig 3a.

? *Rhodopsammia socialis* Semper, 1872: 260–261, pl. 20: figs 1–4.

Rhodopsammia affinis Semper, 1872: 261–262, pl. 19: fig. 7a, b

? *Rhodopsammia incerta* Semper, 1872: 264, pl. 19, figs 8a, b.

Balanophyllia socialis Bourne 1905: 210, pl. 2: fig. 8A.

Balanophyllia affinis – van der Horst, 1922: 62; van der Horst, 1931: 10; Gardiner & Waugh, 1939: 240.

Leptopsammia conica van der Horst, 1922: 68, pl. 8: figs 14–15.

Balanophyllia affinis – van der Horst, 1922: 62.

Balanophyllia imperialis – van der Horst, 1926: 48 (Synonymised by Kitahara & Cairns 2021).

Balanophyllia cumingii – Gardiner & Waugh, 1939: 238, pl. 1: fig. 1.

Balanophyllia (*Balanophyllia*) *sumbayaensis* Cairns, 2001: 14, 19.

Balanophyllia stimpsonii – Zibrowius, 1985: 234–235, figs 1–14; Zibrowius & Grygier, 1985: 126–127; Cairns & Keller, 1993: 274; Cairns & Zibrowius, 1997: 176–177; Cairns et al., 1999: 24; Cairns, 2004: 313; Cairns, 2009: 23.

Balanophyllia (*Eupsammia*) *stimpsonii* – Cairns, 2001: 19; Filander et al., 2021: 5, 84–85, figs 8E, F; Kitahara & Cairns, 2021: 289–290, figs 142, 152H–J.

Material examined. Koh Tao (33 specimens): 5 from 23–25 m depth, Tao Tong (10°03'58.13"N, 99°49'4.76"E); 22 from 25–29 m depth, Tao Tong (10°03'55.05"N, 99°49'4.79"E); 5 from 25–30 m depth, Taa Chaa (10°03'39.75"N, 99°50'4.43"E).

Range. Widespread across the Indo-Pacific (Kitahara & Cairns, 2021).

Description. Corallum ceratoid with colonies becoming phaceloid, straight walled in smaller individuals, curved in larger ones, to a blunt point at the base. Colonies unattached, rarely more than 2 (up to 4) primary buds off a single axial corallite, formed by extratentacular budding at lower to upper theca. Buds may achieve sizes close to that of the axial corallite before breaking off at the base, resulting in small but conspicuous 'scars' at the thecal wall. Budding tends to occur at opposite sides of the corallite, with second buds sometimes, but rarely, occurring in close proximity to first on the same side. Secondary buds (those budding off primary buds) sometimes visible but rare, with primary buds typically detaching prior to development of secondaries). Of the 33 specimens, 14 were solitary, 11 with a single bud, 5 with two buds and 3 with four buds.

Calice very slightly elliptical (GCD:LCD = 1.0–1.2), mostly circular, regardless of corallite size with a calicular margin uneven and serrate due to exsert septa. Largest specimen 10.5 mm in CD and 24.5 mm in height, typical range of

fully grown specimens are 7–10 mm in CD and 12–20 mm in height. Synapticulotheca well developed and porous, increasing in porosity towards the calicular margin. Epitheca absent, with costae and intercostal striae distinctly visible till the bluntly pointed base. Costae conspicuously granular with short but prominent spines throughout the theca. Costae separated by relatively well-spaced striae, moderately deep, throughout the thecal wall, with the typical striated appearance of the skeleton visible in living specimens, obscured only a little by translucent tissue.

Septa hexamerously arranged, generally between 36–40 in number (maximum range 32–48) in three complete cycles with the fourth almost always incomplete and often poorly developed (a single specimen was found with a complete 4th cycle). Septa rarely truly straight, usually meandering slightly from calice to columella, with S1 and S2 often convex and thicker on one side. In some specimens septa curve a little, particularly S1 and S2, in a clockwise or anticlockwise direction towards the columella, giving a slightly twisted appearance to the corallite as a whole (Fig. 2Ai–ix). This is not reflected in the costae which are straight throughout. Septal arrangement: $S_1 > S_2 > S_3 > S_4$. Pourtalès plan present but weakly developed. S1 and S2 extending to the columella, with S2 sometimes partially obscured by fusing S3 before the columella. S3 sometimes extending to the columella, sometimes curving in towards a common S2 near the columella. S4, where visible or complete, fuse towards a common S3 higher up the corallite, therefore being quite distinct from any fusion near the columella. Fusion of pairs of S4 sometimes uneven, with one fusing to S3 higher up corallite wall than the other. Septal faces weakly granular to hispid with very small points visible on either side of axial edge, axial edges typically complete and unbroken, higher cycles lacinate to unbroken.

Columella spongy, irregular, comprised of a moderate amount of twisted laths, at the base of a deep fossa which is sometimes as deep as half the total height of the corallum.

Live specimens colour and appearance. Coralla white with pale yellowish to pink tint, as caused by the nearly transparent tissue covering the skeleton, with costae and intercostal striae prominently visible under the tissue. Tapered/pointed base of the colony often mostly white on account of thinner tissue covering the skeleton. Around the upper theca, calicular margin, and oral disk, the tissue sharply turns from translucent pink/yellow to a bright red to reddish orange, similar to that of *T. megacorallita* at Hong Kong (Yiu et al., 2021). Tentacles are distinct translucent yellow and may extend in length to greater than the GCD of any given corallum. Septa only visible in living specimens if the polyp and tentacles are made to retract somewhat.

Habitat and ecology. Specimens were found exclusively in sandy habitats, far deeper and further from the reef than shallower ranges of other scleractinians on sandy substrates, such as *Cycloseris fragilis* (Alcock, 1893), *Heterocyathus* spp., *Heteropsammia* spp. It is possible this may be due to competitive advantages of the longer ceratoid shape of the corallum in more silt-dominated habitats (with shallower soft substrates at the island hosting larger particle sizes), or perhaps due to competitive disadvantages when sharing habitats with other predatory corals (see comments on *Heteropsammia* spp. below). *Tubastraea stimpsonii* is known from soft substrates to approximately 100 m depth (Kitahara & Cairns, 2021). The species and its synonyms have been recorded ranging across the Indo-Pacific, from the Western Indian Ocean to New Caledonia, however, some ‘attached’ specimens synonymised with *B. stimpsonii* may refer to *T. megacorallita* or another as yet unidentified species.

Prey preferences of *T. stimpsonii* were not assessed in the present study, however one specimen out of the 33 found displayed a remarkable predatory strategy (Fig. 9K). A colony comprised of three polyps was found to be actively ingesting the rachis, including polyps, of a living pennatulacean. Two of the three polyps were found to be entirely wrapped around the prey colony in a seemingly cooperative strategy holding the animal in place, a strategy that has been observed in various other scleractinian corals (ter Horst & Hoeksema, 2021) including dendrophylliids (Musco et al., 2018; Gregorin et al., 2022). This is however, the only record known of a scleractinian coral predating upon a pennatulacean.

Present surveys revealed no signs of predators nor parasites upon the coral. Other species of *Tubastraea* have been found to be host to prey to the corallivorous nudibranch *Phestilla melanobranchia* Bergh, 1874 at the study site (Mehrotra et al., 2021), however these are found exclusively in coral reefs and hard-substrate areas. Despite the dietary plasticity of this nudibranch (Yiu et al., 2021), its soft substrate habitat is likely to contribute to the low likelihood of its predation by *P. melanobranchia*. It should be noted however that *T. stimpsonii* (as *B. stimpsonii*) has been recorded to host parasitic ascothoracid galls and epitoniid snails (Zibrowius, 1985). Tissue analysis revealed no signs of zooxanthellae nor other microalgal symbionts, and no corals were found to be encrusted by epibionts.

Remarks. Our specimens are very similar to those described by Verrill (1865) and by others (Filander et al., 2021; Kitahara & Cairns, 2021) that were described as *Balanophyllia (Eupsammia) stimpsonii*. The original species description is very brief: "Coral free, elongated, turbinated, blunt at base. Calicle oval, deep; columella well developed, septa broad, the principal ones with entire inner – edges, rounded. Length an inch or more; breadth of

cell.30. Interesting as a living representative of a genus hitherto known only in the fossil state. North China Sea." It is interesting to note that corresponding plates (Verrill, 1866) show a specimen with straight septa that lack any visible sign of the Pourtales plan.

To date, the most extensive description of *B. (E.) stimpsonii* is the one by Zibrowius (1985), based on an unknown number of specimens from across the Indo-Pacific. More recent descriptions include those of Filander et al. (2021) and Kitahara & Cairns (2021). The major differences between these and our specimens are that *B. (E.) stimpsonii* has been reported as having four complete cycles (Filander et al., 2021), sometimes with an incomplete fifth one (Zibrowius, 1985). Our specimens were typically found to have an incomplete fourth cycle, regardless of specimen size, with a complete fourth cycle found in a single moderately sized specimen. Nonetheless, these recent descriptions generally agree with the specimens studied presently, with the description of specimens by Kitahara & Cairns (2021) nearly identical to those presented here, with the exception of extratentacular budding documented here.

The molecular analyses presented here were able to resolve *Tubastraea megacorallita* Yiu, Chung & Qiu, 2021 from *'Balanophyllia (Eupsammia) stimpsonii* (present data) as distinct species from one another. Morphologically, the main differences between the presently described specimens and those of Yiu et al. (2021) are as follows: 1) *T. megacorallita* is attached to hard substrate as opposed to free-living on soft substrates, 2) *T. megacorallita* forms larger colonies of up to 14 corallites, 3) corallite sizes in *T. megacorallita* are significantly larger, reaching up to 25 mm in GCD, 4) *T. megacorallita* ranges from possessing three complete cycles of septa with an incomplete fourth, or complete fourth with incomplete fifth cycle, with the latter being

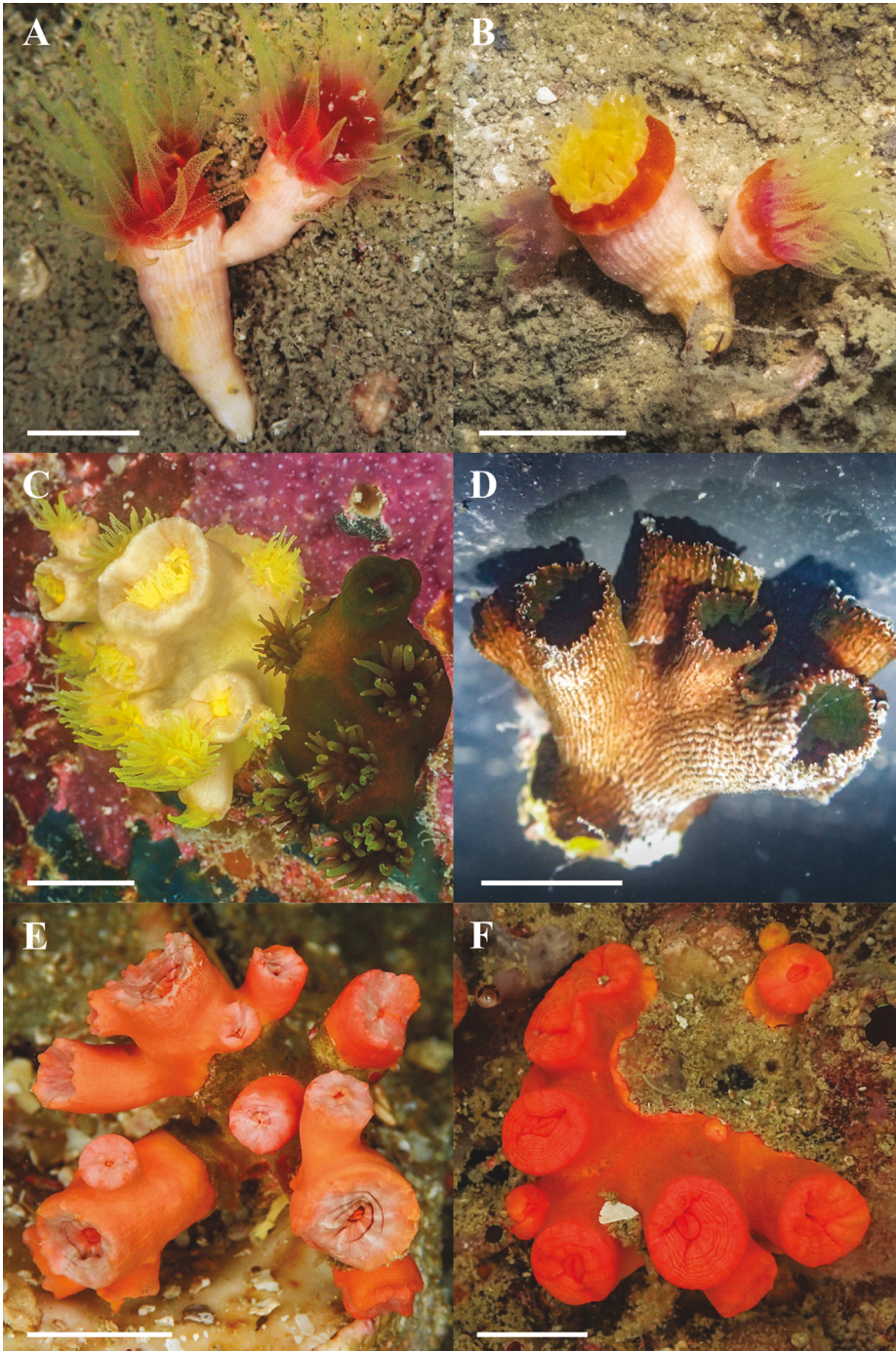


FIGURE 5 Living corals with their specimen numbers (scale bars: 10 mm). A, B) *Tubastraea simpsonii* (EKT19, EKT20); C) *Tubastraea* cf. *chloromura* (YKT19c) left and *Tubastraea diaphana* (TmKT19a) right; D) *Tubastraea diaphana* (TmKT19b); E, F) *Cladopsammia gracilis* (RKT19, RKS20).

most common. Therefore, these sister species form a clade with the following synapomorphies: 1) red oral disks, contrasting with the rest of the coral tissue; 2) small colony sizes, mostly solitary; 3) typically found in turbid, soft-substrate habitats.

Yiu et al. (2021) described *Tubastraea megacorallita* as conspecific with *Tubastraea* sp. 3 of Arrigoni et al. (2014), based on genetic evidence supporting the designation of the species within *Tubastraea*, and therefore updating the diagnosis for the genus to include specimens with a Pourtalès plan. It was further cited as being synonymised with *Tubastraea tenuilamellosa* (Milne Edwards & Haime, 1848) by Rowlett (2020), who did not mention this species, whereas it actually is considered a synonym of *T. coccinea* (Cairns, 2001).

The species most likely being referred to is '*T. titijamaensis*' (Rowlett, 2020: 508), a misspelling of *Tubastraea titijamaensis* in reference to the subspecies *T. coccinea titijamaensis* Eguchi, 1968. In the interest of brevity, we provide only brief comments of the convoluted history of *T. coccinea titijamaensis*. The original Japanese description of this subspecies, introduced as *Dendrophyllia coccinea titijamaensis* Yabe & Eguchi (in Eguchi, 1934), concerns a *nomen nudum* and is therefore invalid. This name was reintroduced, discussed and illustrated by Eguchi (1968: C71) as *Tubastraea coccinea titijamaensis*, with features bearing much similarity to that of *T. megacorallita*. When Cairns (2001: 27) referred to the misspelled '*Tubastraea coccinea titijamaensis*', he considered this taxon synonymous with *Cladopsammia gracilis* (Milne Edwards & Haime, 1848). Examination of the original specimens (and others from type localities) covered by Eguchi (1968) may enable a comparison with *T. megacorallita*.

In addition to skeletal features, Zibrowius (1985) refers to *B. stimpsonii* possessing a 'rare attached form', in reference to *Rhodopsammia*

incerta Semper, 1872, the only attached species that was synonymised with *B. stimpsonii*. This may refer to specimens described as *T. megacorallita*, which further strongly resembles *Rhodopsammia socialis* Semper, 1872 (synonymised with *B. stimpsonii*) in pigmentation. The live pigmentation (of *Rhodopsammia socialis*) according to Semper (1872) is: "exosarc pale pink, polyp with oral disc and tentacles uniformly yellowish red". Type specimens of these species as photographed by Zibrowius (1985: Plate 1, Figs. 1–14) are solitary and free-living with clearly tapered coralla typical of *B. stimpsonii*. The holotype for *R. incerta* (Zibrowius, 1986: Plate 1, Fig. 8) is conspicuously an attached solitary specimen, closely resembling a specimen identified as *Balanophyllia* sp. by Rowlett (2020: 500), which bears features of both *B. stimpsonii* and *T. megacorallita*. Future genetic and closer morphological examinations of similar specimens will be needed to clarify its taxonomic position within the family.

While it is apparent that rigorous revisions are needed in the taxonomy of Dendrophylliidae (see Discussion), in an effort to clarify we place *B. (E.) stimpsonii* within the genus *Tubastraea*. This is based on morphological, genetic and ecological evidence provided here and the recently updated morphological diagnosis of the genus *Tubastraea* to include presence with Pourtalès plan (Yiu et al., 2021). Furthermore, we consider the recently described *Tubastraea megacorallita* as a sister to *T. stimpsonii* comb. nov.. The present clade presents extensive morphological variability in coloniality, habitat and substrate attachment, agreeing with the extensive documentation of the species by Zibrowius (1985). Finally, the discovery of an epibiotic parasitic snail (family Epitoniidae) during the present study is consistent with earlier records of epitoniids hosted by *Tubastraea* corals, whereas no record of a *Balanophyllia* host is known

(Gittenberger & Hoeksema, 2013; Rodrigues-Villabos et al., 2016; Narayana & Apte, 2016).

Dendrophyllia de Blainville, 1830

Diagnosis. Colonial, colonies typically accepted as either a) phaceloid/subphaceloid bushy colonies, typically small and with minimal branching b) arborescent colonies that may reach a moderate size, with an axial corallite present, or c) true dendroid colonies with sympodial branching, which may extend to moderate to large sizes. Budding typically extratentacular. All extant species azooxanthellate and attached to the substrate Septa arranged hexamerously, Pourtalès plan present but may be weakly developed, pali may be present, columella spongy. Corallum with well-defined costae, epitheca sometimes present.

Dendrophyllia cf. *minima* Ogawa & Takahashi, 2000

Fig. 6.

? *Dendrophyllia minima* Ogawa & Takahashi, 2000: 12–13, pl.2: fig 2, pl. 4: Fig. 2.

Material examined. Twenty-nine specimens, all from 26–29 m depth, Hin Chalam (12°27'49.90"N, 100°58'4.13"E).

Range. Gulf of Thailand (present study). *Dendrophyllia minima* was described from Japan.

Description. Colonies small, bushy, formed by extratentacular budding from lower theca of larger corallites, phaceloid, lacking any sign of an axial corallite. Lower theca rapidly overgrown by calcareous algae or sponges in most specimens studied, resulting in a distinctly disconnected appearance to the colony, as is common in other colonial dendrophylliids. Budding appears to be omnidirectional, rarely more than one at a time, with buds clearly still attached to quite a large size resulting in multiple distinct 'Y-shaped' pairs throughout

the colony. In rare corallites with two buds, all budding in opposite directions, with second buds significantly smaller than first. No specimens were found with more than two budding corallites.

Corallites attached, from moderately curved to almost straight. Calice generally elliptical (GCD:LCD = 1.1–1.3), often more circular in smaller individuals, less common in larger individuals. Calicular margin distinctly uneven due to exsert septa. Largest specimen 5.5 mm in CD and 16 mm in height, typical range of fully grown specimens are 3.5–5 mm in CD and 10–15.5 mm in height. Synapticulotheca generally lacking porosity until the upper portion, increasing in porosity towards the calicular margin, with some corallites showing intermittent porosity in intercostal striae from halfway up thecal wall. Epitheca absent, though many specimens basally covered in calcareous algae and other epibionts. Costae conspicuously granular, with granules becoming smaller and more pointed down the thecal wall, giving basal theca a more hispid appearance. Costae separated by narrow striae throughout the thecal wall, with the typical striated appearance of the skeleton completely obscured in living specimens by thick tissue.

Septa hexamerously arranged, generally between 36–40 in number (maximum range 32–42) in three complete cycles with the fourth always incomplete and often poorly developed. Pourtalès plan present but weakly developed. Septal arrangement: S1 > S2 > outer S4 > inner S4 > S3 or S1 > S2 > S3 > S4, depending on the development of the fourth cycle in any given system. S1 straight, extending to the columella; S2 also straight, extending deep into the fossa but usually obscured by the fusion of higher order septa; pairs of S4 fused before a common S3, which sometimes curve towards a common S2. Fusion of S3 rare, which are typically straight and continue on

to columella when not obscured by fusing S4. S1 and S2 strongly exert but uneven, often hard to separate at calicular margin alone, S2 between $\frac{1}{2}$ to $\frac{1}{3}$ as thick as S1. Septal faces prominently granular to hispid with well-spaced points, septal edge distinctly dentate throughout before uniting at an irregularly shaped spongy columella composed of multiple twisted and pointed laths. Fossa moderately deep.

Live specimens colour and appearance. Coralla entirely yellow with limited variability in colour across different colonies. Costae and intercostal striae visible but not prominent under the tissue. Exsert S1 and S2 distinct at the calice margin with numerous translucent yellow tentacles between them. Corallite centres of the same colour as walls and tentacles.

Habitat and ecology. Colonies found growing on small rocks and rubble (coral skeletons and bivalve shells) on soft substrates at a single isolated location, between 26 m and 31 m depth. No more than 25 colonies were found. Nearby hard substrates (rocks and reefs) in shallower water showed no presence of *Dendrophyllia* cf. *minima*. No trophic nor symbiotic relationships were observed. Tissue analysis revealed no signs of zooxanthellae nor other microalgal symbionts. The bases of corallites were found to be encrusted in epibionts, specifically crustose coralline algae (Fig. 6A), often with benthic foraminifera adhered, and/or various sponges.

Remarks. The genus *Dendrophyllia* has, for over a century, been considered to consist of species that can be broadly divided into three informal groups, the features of each having changed drastically over time but which at present are generally accepted to be the following: Group 1 – arborescent colonies with large axial corallites, with budding patterns of smaller radial corallites obfuscated, Group 2 – small bushy colonies with large axial corallites and sparse branching, and Group 3

– dendroid colonies with regular sympodial branching (Cairns, 2001; Kitahara & Cairns, 2021). The single uniting feature of these is that all *Dendrophyllia* colonies emerge from a single basal stem, a character also found in various branching species of other dendrophylliid genera, such as *Duncanopsammia axifuga* (Milne Edwards & Haime, 1848), *Eguchipsammia serpentina* (Vaughan, 1907), and *Tubastraea micranthus* (Ehrenberg, 1834) (Arrigoni et al., 2014). As is the case with other dendrophylliid genera, *Dendrophyllia sensu lato* does not have a single uniting diagnostic feature, but is instead established on the combination of specific characteristics (Cairns, 2001). Recent molecular work has found the genus to be polyphyletic with species found to be close relatives of multiple distinct and often unrelated clades within the family (Arrigoni et al., 2014).

The presently described species is therefore tentatively placed within the genus *Dendrophyllia*. Our molecular analysis recovered *D.* cf. *minima* as sister to *Heteropsammia* and distant from the few other '*Dendrophyllia*' species that have been sequenced, providing further support for a polyphyletic *Dendrophyllia*. The relatively small size of corallites and colonies allows it to be easily separated from most other species of the 'bushy' species (and all arborescent and dendroid species) in *Dendrophyllia* s.l. The present species most closely resembles *Dendrophyllia minima* Ogawa & Takahashi, 2000 and bears some resemblance to *D. miniscula* (Bourne, 1905). In the latter case, while *D. miniscula* and *D.* cf. *minima* (as described here) both share considerable similarities regarding septa and calice shape, *D. miniscula* is described (and differentiated) as conspicuously arborescent with a clear basal point of attachment (Bourne, 1905).

The original description of *D. minima* by Ogawa & Takahashi (2000) was very brief

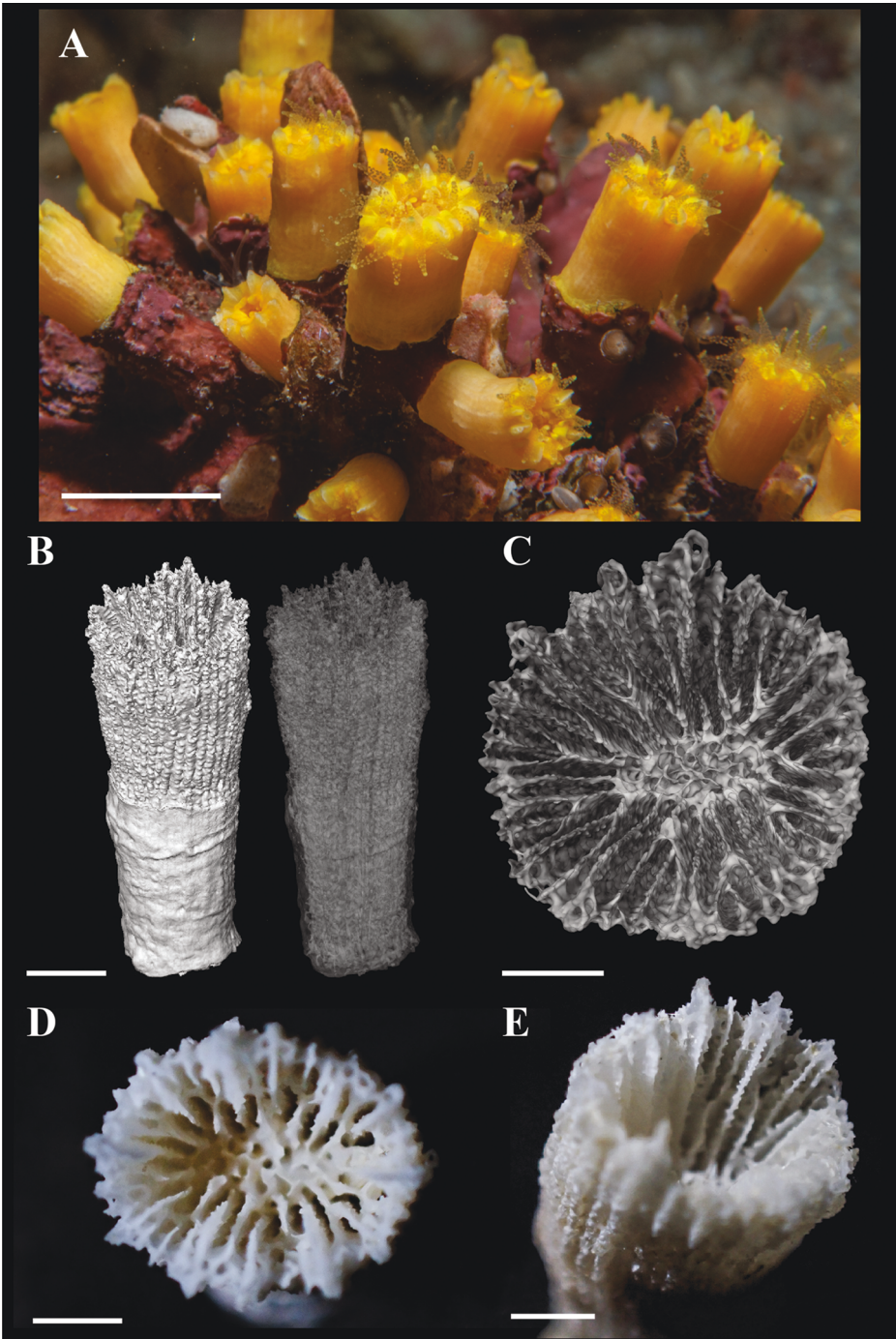


FIGURE 6 *Dendrophyllia cf. minima*. (B, C specimen HC2of, D, E specimen HC2og) A) living specimen *in situ* (scale bar: 5 mm); B) digital reconstruction of a single corallite with varying opacities highlighting external surface beneath calcified layer of coralline algae (scale bar: 2 mm); C) digital top-down view into corallite with calicular features visible (scale bar: 1 mm); D) top down view of skeleton of different specimen (scale bar: 1 mm); E) dorso-lateral skeletal view of calice (scale: bar 1 mm).

and lacked information on various diagnostic characteristics (i.e., columella, budding, and septal features such as dentition etc). Nonetheless, *D. minima* and *D. cf. minima* share numerous features such as corallite size, exsert S₁ and S₂ septa, a weakly developed Pourtalès plan, and costae with fine and pointed granulation. The main skeletal differences between the two species are the following: *D. minima* possesses four complete cycles of septa whereas *D. cf. minima* possesses only three complete cycles with a partial poorly developed fourth cycle; corallite centres in *D. minima* appear to be thin and narrow (described as 'thick' corallites) with wide septal faces reaching far from thecal wall, instead *D. cf. minima* has a relatively thinner calice with septa projecting far less from the thecal wall, particularly at the calicular margin; budding in *D. cf. minima*, rarely exceeds a single bud from multiple corallites, whereas *D. minima* is seen with corallites hosting multiple buds simultaneously (Ogawa & Takahashi, 2000: Plate II, Fig. 2; Plate IV, Fig. 2). The Pourtalès plan in *D. cf. minima* may sometimes extend to S₃, though rarely, which is not mentioned (nor visible) in the description of *D. minima*. Furthermore, *D. minima* is described as possessing an epitheca, which is not present in *D. cf. minima*, with the basal part of many mature corallites visibly connected to one another and without any calcifying epibionts obscuring the corallite bases (see supplementary fig. 2).

In situ, the colouration of living specimens between the two species is very similar, however *D. minima* was found to form larger colonies of up to 60 corallites, whereas *D. cf. minima* was found with a maximum colony size of 31 corallites, typically possessing smaller colonies of 12–24 corallites. Regarding habitat, *D. minima* was found in extremely shallow water (2 m depth) whereas *D. cf. minima* was not found shallower than 26 m,

growing exclusively on small rocks and rubble in soft-substrate habitats.

Heteropsammia Milne Edwards & Haime, 1848

Diagnosis. Corallum unattached, solitary (monostomous) or colonial (polystomous). Polystomatous state via intracalicular budding resulting in colonies of up to 40 corallites. Corallum globular to elliptical in shape, synapticulotheca porous and well developed. Thecal wall usually composed of finely serrated to granulated ridges instead of true costae, epitheca absent. Pourtalès plan present, pali may or may not be present, fossa moderately deep with a spongy columella. Base flattened or keeled with a conspicuous pore for symbiont. Juvenile coralla settling on gastropod shells. Apozooxanthellate.

Heteropsammia cochlea (Spengler, 1781)

Figs 7 D–F, I–N, 8 F–J, 9A–D, G, J.

Madrepora cochlea Spengler, 1781: 240–248, figs A–D.

Psammoseris cylicioides Tenison-Woods, 1879: 10–11; Tenison-Woods, 1880: 297–299.

Lobopsammia michelinii – Tenison-Woods, 1880: 295.

Heteropsammia michelini – Moseley, 1881: 196; Saville-Kent, 1893: 106, 177; van der Horst, 1926: 51, pl. 3: figs 14–20; Wells, 1964: 108, 120; Pichon, 1974: fig. 6; Scheer & Pillai, 1974: 65–66, pl. 32: figs 1–2.

Heteropsammia michelinii – Goreau & Yonge, 1968: 421–423, figs 1,2.

Heteropsammia cochlea – Veron & Pichon, 1980: 416–420; Fisk, 1981; Fisk, 1983: 287, 290, 291, 292, 293, 294; Zibrowius & Grygier, 1985: 129, figs 43–44; Veron, 1986: 576–577; Veron & Marsh, 1988: 123; Hoeksema & Best, 1991: 234–237, figs 24–28 (partim); Cairns, 1998: 406–408; Cairns, 1999: 132–133; Cairns et al., 1999: 27; Veron, 2000: 407; Cairns, 2001: 19–20, pl. 2: figs h–j, pl. 3: figs a–e; Cairns, 2004: 316; Pichon,

2007: 149, 153; Cairns, 2009: 25; McEnnulty et al., 2011: 64; Arrigoni et al., 2014: 8, 21, figs 1B, 2, 3H–J, 9M–O; Hoeksema & Matthews, 2015: 1227, figs 1a–c; Mehrotra et al., 2016: 323–324, fig 1; Latypov, 2017: 14, fig. 1N; Igawa et al., 2017: 1–9, figs 1d–e, h–i, l–m; Baron-Szabo & Cairns 2019: fig 11 (1a–1d); Mehrotra et al., 2019: 2–17, figs 2, 3, 7; Filander et al., 2021: 5, 104–107, figs 9O,P, 10A,B; Kitahara & Cairns, 2021: 30, 334–336, figs 176C, 178A–C.; Herrán et al., 2022: 1–10, figs 2, 3, 5, 8.

Heteropsammia michelini – Ditlev, 1980: 86, figs 113, 376.

Heterocyathus aequicostatus – Boshoff, 1981: 37.

Heteropsammia aphrodes Boshoff, 1981: 42.

Heteropsammia cochleata – Cairns, 2009: 25.

Material examined. Koh Tao (612 specimens): 300 from 11.5–19 m depth, Leuk Bay (10°04'11.65"N, 99°50'34.42"E); 189 from 13–23 m depth, Sai Nuan (10°04'45.02"N, 99°48'45.23"E); 40 from 14–18 m depth, Tao Tong (10°03'55.83"N, 99°49'9.11"E); 11 from 18.5–23.5 m depth, Tao Tong (10°03'55.05"N, 99°49'4.79"E); 46 from 18–24 m depth, Taa Chaa (10°03'39.75"N, 99°50'4.43"E); 26 from 16–30 m depth, Tanote Bay (10°5'1.47"N, 99°50'57.50"E).

Range. Widespread across the Indo-Pacific (Kitahara & Cairns, 2021).

Description. Corallum solitary, globular, with moderately rounded walls down to a wide, flattened base. Base hosting a single (very rarely more than one) efferent pore projecting downwards for an endosymbiotic sipunculan worm. Multiple smaller lateral pores visible along the lower theca (upper-mid theca in younger specimens) leading to a large internal spiral chamber hosting the sipunculid, exiting at the basal orifice. In internally examined specimens, spiral chamber typically exceeds two complete rotations, determined by coral size. Juveniles visibly encrusting

on a single gastropod shell, with any sign of encapsulated shell lost rapidly as the coral grows. Synapticulotheca well developed and porous towards the calicular margin. Lower theca very dense, shallow pores present, interspersed between the larger lateral pores for the sipunculid. Epitheca absent. Thecal wall lacking true costae, instead being covered in coarsely serrate to dentate and granular ridges which are often somewhat interconnected, with individual rows sometimes fusing and separating between calice to base. In smaller specimens, these ridges are only visible near the base, with the rest of the theca being covered coarse to fine granulations, often sharply pointed, distributed in no discernible pattern.

Calice circular to elliptical, most commonly medially constricted giving a lobed appearance. Specimens typically have a single calice however multiple calices are common. Of the specimens investigated, the majority ($n = 375$) were observed with a single calice with a single medial constriction, herein referred to as the 'normal phase' (GCD:LCD = 2.1–3.2). The medial constriction was absent or very weakly represented in many smaller specimens and some larger ones ($n = 82$) referred to as the 'elliptical' phase (GCD:LCD = 1.3–1.6). Budding intra-tentacular, during which calice and number of septa may be highly modified from the normal phase, initiated by a strengthening of the medial constriction, referred to as the 'dividing' phase. Of the specimens studied, budding was found to be incomplete with the medial constriction resulting in two mouths thinly connected in some ($n = 16$) with completed separation more common ($n = 85$). Specimens with three ($n = 17$) or four ($n = 4$) calices relatively rare. A single specimen was observed with nine distinct calices. A further 32 specimens were found with a host of amorphous contortions and growths with indistinct calicular morphology. Largest specimen

32 mm in CD and 25 mm in height, typical range of fully grown specimens observed are 14–28 mm in CD and 12–22 mm in height.

Septa hexamerously arranged, though quite variable in number and development, especially in smaller corals or dividing corallites. Typical range of full-sized specimens (>14 mm in CD) possessed 48–90 septa depending on the development of the fifth cycle, which was usually present (but often difficult to separate) but rarely fully developed. Smaller specimens (<14 mm) in the normal or elliptical phase sometimes with fifth cycle septa barely visible and incomplete. However, specimens in the dividing phase or those with multiple calices sometimes had as few as 38 septa (per calice) or over 100, though at these points ascertaining patterns of development or symmetry become extremely difficult. In all specimens Pourtales plan present and well developed.

Septal arrangement $S_1-2 > S_3 > \text{outer } S_5 > \text{inner } S_5 > S_4$ where S_1 and S_2 are equally thick and pronounced and fusing to the columella. Fusion of pairs of S_5 around common S_4 typical, continuing as single septa. These may fuse again before a common S_3 in some cases, obscuring S_3 joining columella, though in others S_3 visibly meets columella. In most corals, many of the fused pairs of S_5 will elevate and thicken considerably before joining with the columella, giving a distinct, pali-like structure to the coral as a whole. These 'pali' are irregular in their prominence and number but are clearly visible emerging from between exsert S_1 and S_2 even in living corals. Calice margin lanceted in smaller corals with lancets made up of exsert S_1 and S_2 , and their corresponding S_5 s with which they are fused, forming a regular margin with minimal difference between S_1 and S_2 . In larger corals, lancets much less pronounced and septa relatively less exsert, though with the same regularity. Columella spongy, elongate and distinctly arched, following the shape of the coral as

a whole, where ends of the columella curve downwards towards the base of the coral. Fossa usually moderately deep, though in some corals columella may begin in the upper fifth of the coral height, depending on depth of fossa and extent of arch.

Live specimens colour and appearance. Surveyed specimens are all brown in colour due to the presence of zooxanthellae. Absence of zooxanthellae leaves specimens entirely bleached (Fig. 9C), with tissue almost entirely transparent. All surveyed specimens were found to be zooxanthellate given the shallow-waters in which they were found. Mature specimens found on top of sediment, younger specimens often partially buried, but not always. Exsert S_1 and S_2 septa visible near calice margin and pali-like structures of S_5 also visible even in smaller specimens *in situ*. Oral disk ranging from plain in pattern with pigmentation ranging from white to brown as determined by symbiont concentration. Tentacles transparent, densely covered in nodules with zooxanthellae, the whole tentacle a light to dark brown appearance (clear in bleached specimens). In living specimens, thecal ridges and granulations are distinctly visible, with stronger pigment and thicker tissue in the valleys and breaks between ridges, giving the outer colouration a striated to spotted appearance.

Habitat and ecology. *Heteropsammia cochlea* is known from soft substrates across its range (Borghi et al., 2023). Specimens observed in the present study were found exclusively in soft-substrate habitats, alongside other free-living scleractinians (*Cycloseris fragilis*, *Heterocyathus* spp., *Truncatoflabellum* sp.). The majority of specimens were found at 12–20 m depth and hosting zooxanthellae, however partially or entirely bleached specimens were occasionally recorded. As an apo-zooxanthellate species, *H. cochlea* is known to inhabit shallower waters with endosymbiotic

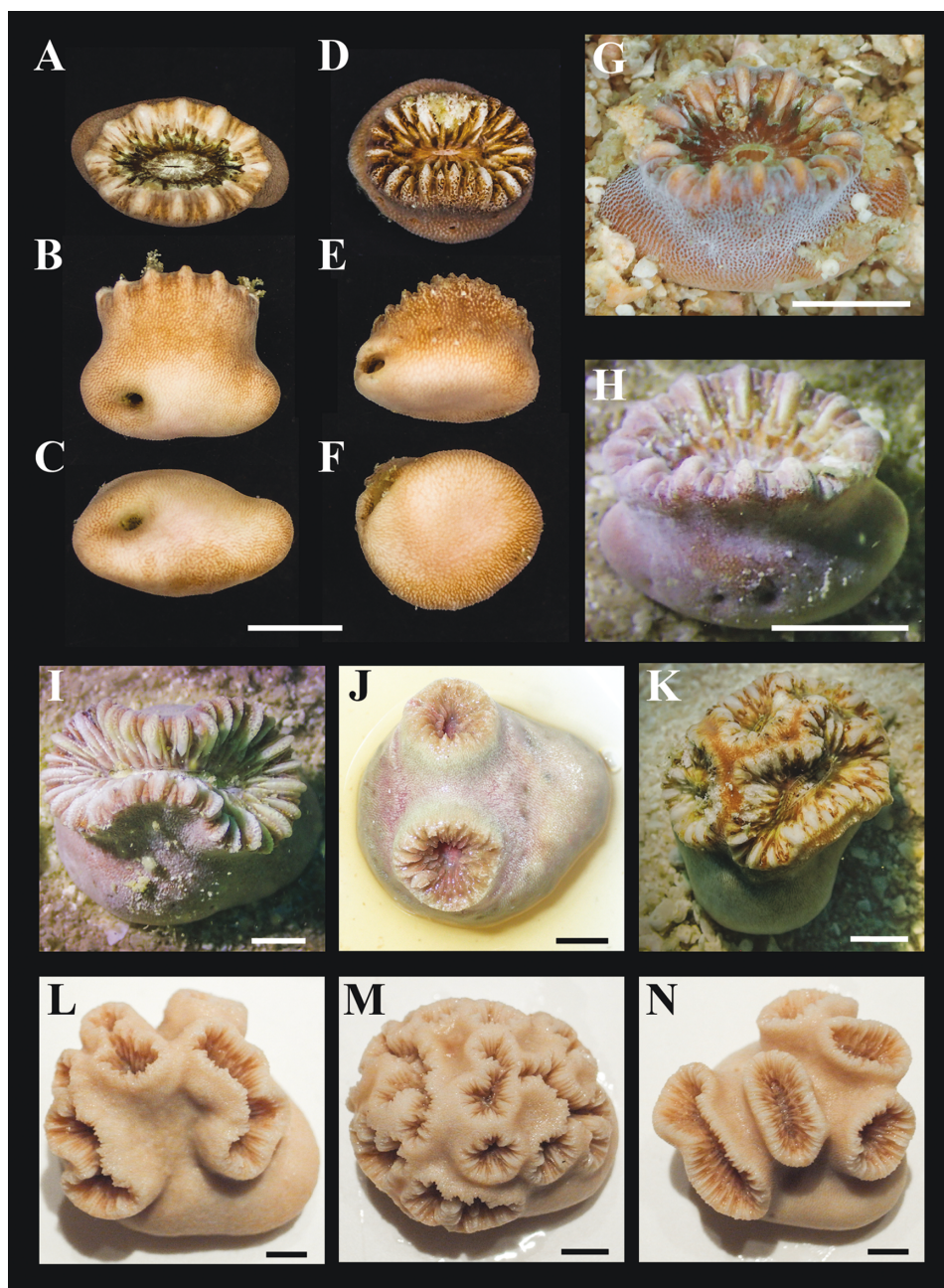


FIGURE 7 *Heteropsammia* spp. (scale bars: 5 mm). A–C) living specimen of *H. moretonensis*, showing dorsal, lateral and ventral views respectively; D–F) living specimen of small *H. cochlea*, showing dorsal, lateral and ventral views respectively; G, H) *in situ* photos of *H. moretonensis* (specimens HmKS20, HmKMN21; I–K) *H. cochlea* specimen KT-1m (one mouth, normal phase), specimen KT-2m (two mouths) and specimen KT-4m (four mouths, amorphous phase); L–N) *H. eupsammides* specimens Ko1, Ko4, and Ko5 respectively (scale bars: 5 mm). RMNH.COEL.39394. Locality: Teluk Slawi, SE Pulau Lassa, East Komodo (08°36'08"N, 119°29'47"E), 13 November 2002.

zooxanthellae but is also known from deeper waters where it relies on its heterotrophic capacity alone (Arrigoni et al., 2014; Hoeksema & Matthews, 2015).

Little is known of the predators of *H. cochlea*, however Keesing et al. (2023) recorded for the first-time widespread predation on the soft sediment dwelling *Cycloseris distorta* and *H. cf. cochlea* by the short-spined crown of thorns sea star *Acanthaster brevispinus* (Fisher, 1917). Regarding predation by *H. cochlea*, recent studies have allowed for an in-depth exploration of dietary preferences of the coral. Mehrotra et al. (2016) documented over a hundred individuals feeding and consuming salps at Koh Tao, noting how the large gape size of the coral was able to facilitate ingestion of prey larger than the coral. Following this, Mehrotra et al. (2019) observed prey capture of *Costasiella* sea slugs at the same location by *H. cochlea*, the capacity for which was attributed to its locomotive ability, allowing it to come in close proximity to the non-motile host algae *Avrainvillea*. Further investigations revealed sea slugs as prey preferences by *H. cochlea*, which were remarkably similar to those of free-living fungiid corals. The variation in palatability was suggested to be caused by differences in the chemical compounds of the different prey species, with the toxic nature of many sea slugs being well-established (Avila et al., 2018). In the present study, we further document prey capture and ingestion of the jellyfish *Pelagia* sp. (fig. 9J) as well as numerous instances of capture and ingestion of salps subsequent to the initial observations by Mehrotra et al. (2016).

In addition to endosymbiotic zooxanthellae, *H. cochlea* is known to be host to other symbionts that appear to play varying and complex roles within the coral. While not strictly endosymbionts, a sipunculan worm of the genus *Aspidosiphon* Diesing, 1851, has been found living within the coral skeleton

(Igawa et al., 2017). The precise nature of this relationship is thought to range from mutualistic to commensal, with the co-evolution and possible implications recently explored in depth by Herrán et al. (2022). These authors also studied the presence of the galeommatid bivalve *Jousseamiella* sp. within the sipunculan chamber, speculating a possible mutualistic relationship with the worm. In an earlier study, *H. cochlea* was found to contain date mussels of the species *Leiosolenus lessepsiana* (Vaillant, 1865) (Arnaud & Thomassin, 1976). Both symbiotic bivalves were not observed in the present study. Additionally, a single observation has been made of the hermit crab *Diogenes heteropsammicola* Igawa & Kato, 2017, living within the chamber of a living individual of *H. cochlea* (Fujii, 2017; Igawa & Kato, 2017). We record here evidence of a parasitic epitoniid snail (fig. 9G) utilising multiple individuals of *H. cochlea* as host. This kind of association it is not unique for the Dendrophylliidae, but it has not been reported from *Heteropsammia* before (Gittenberger & Hoeksema, 2013).

Remarks. The genus *Heteropsammia* has long been the subject of discussion and debate due to the challenges of delineating species among specimens with a notable amount of morphological variability (Hoeksema & Best, 1991; Cairns, 2001). This is despite the fact that the genus as a whole bears many striking and specialised characteristics that distinguish it readily from its congeners. The biology and taxonomic history of the genus has comprehensively been reviewed by Hoeksema & Best (1991) and Cairns (2001). Therefore, we retain our remarks to the context of the present findings. Discussions on the monostomatous vs. polystomatous nature of specimens resulted in the reinstating of the species *Heteropsammia eupsammides* (Gray, 1849) by Hoeksema & Best (1991) for large, polystomatous specimens, a distinction also

made among free-living mushroom corals (Hoeksema, 1991; Gittenberger et al., 2011).

Presently, we have studied both monostomatous and polystomatous specimens, of varying size and substrate type (sandy vs. silty), and depth. Specimens examined here were frequently found to have reached 30 mm in CD and 35 mm at the base, larger than most documented specimens of *H. eupsammides* (Hoeksema & Best 1991; Kitahara & Cairns 2021), with the average size of CD for *H. cochlea* in our study larger than those found in other regions (Hoeksema & Best 1991; Filander et al., 2021; Kitahara & Cairns 2021). Additionally, while the septal arrangement broadly agrees with the variation in previous descriptions, crucially, the ‘pali’ like structures appear to not be formed from S1 or S2 but instead emerge from the result of fused S5. In all other noteworthy and diagnostic features, our specimens concur with earlier studies.

We have attempted to evaluate the delineation between *H. cochlea* and *H. eupsammides* using morphological and molecular means. Our findings show that, at least at the present study sites, *H. cochlea* shows extensive variability in calice shape and structure, with 21% of specimens undergoing some amount of calicular division leading to polystomatous specimens. This proportion is almost similar to the 19% found in the free-living mushroom coral *Ctenactis echinata* (Pallas, 1766), which showed a significant correlation between the number of stomata and maximum corallum diameter (Hoeksema, 1991). These individuals show no other clear separation in diagnostic features, in either their internal or external skeletal morphology. Molecular analysis further fails to resolve specimens of *H. cochlea* from the Gulf of Thailand, regardless of the number of mouths, in three specimens of *H. eupsammides* from the same population as specimens used to delineate the species (Hoeksema & Best, 1991). Specimens of *H.*

eupsammides from various Indonesian localities (Ambon, Bali, Halmahera, Komodo, West Papua), which are deposited in the coral collection of Naturalis Biodiversity Center (RMNH. COEL. 18166, 18167, 33622, 39394, 41235, 42751, 41791) show calices that grow more apart from each other, even in small individuals, unlike most specimens of *H. cochlea*. Veron & Pichon (1980) and Veron (2000), who considered the two species conspecific, do not appear to have seen the specimens that they named “*Heteropsammia lobata*” and “*Heteropsammia eupsammides*”, respectively. In order to synonymize *H. cochlea* and *H. eupsammides*, specimens from additional localities need to be included in molecular analyses, preferably also from their type localities, and a more extensive morphological analysis is needed, using large numbers of specimens from localities where both coral morphs co-occur.

Heteropsammia moretonensis Wells, 1964

Figs 7 A–C, G, H, 8 A–E, 9 E, F, H, I.

Heteropsammia moretonensis Wells, 1964: 118, pl. 3: figs 1–7; Cairns et al., 1999: 27; Cairns, 2001: 20; Cairns, 2004: 316; Wallace et al., 2009: 105, 107, fig 67 A, B; Cairns, 2009: 25; Kitahara & Cairns, 2021: 338–339, figs 178 J, L.

Heteropsammia cochlea (partim) – Hoeksema & Best 1991: 235, fig. 24 f; Hoeksema & Van Ofwegen, 2004 (*in situ* photographs SW Sulawesi).

Material examined. A total of 491 specimens: 200 from 12.5–19.5 m depth, Koh Samaesan West (12°33′30.80″N, 100°56′44.71″E); 35 from 11.5–19 m depth, Leuk Bay, Koh Tao (10°04′11.65″N, 99°50′34.42″E); 55 from 15–23 m depth, Sai Nuan, Koh Tao (10°04′45.02″N, 99°48′45.23″E); 19 from 14–23 m depth, Tao Tong, Koh Tao (10°03′55.83″N, 99°49′9.11″E); 26 from 18–24 m depth, Taa Chaa, Koh Tao (10°03′39.75″N, 99°50′4.43″E); 12 from 16–30 m depth, Tanote Bay, Koh Tao (10°05′1.47″N,

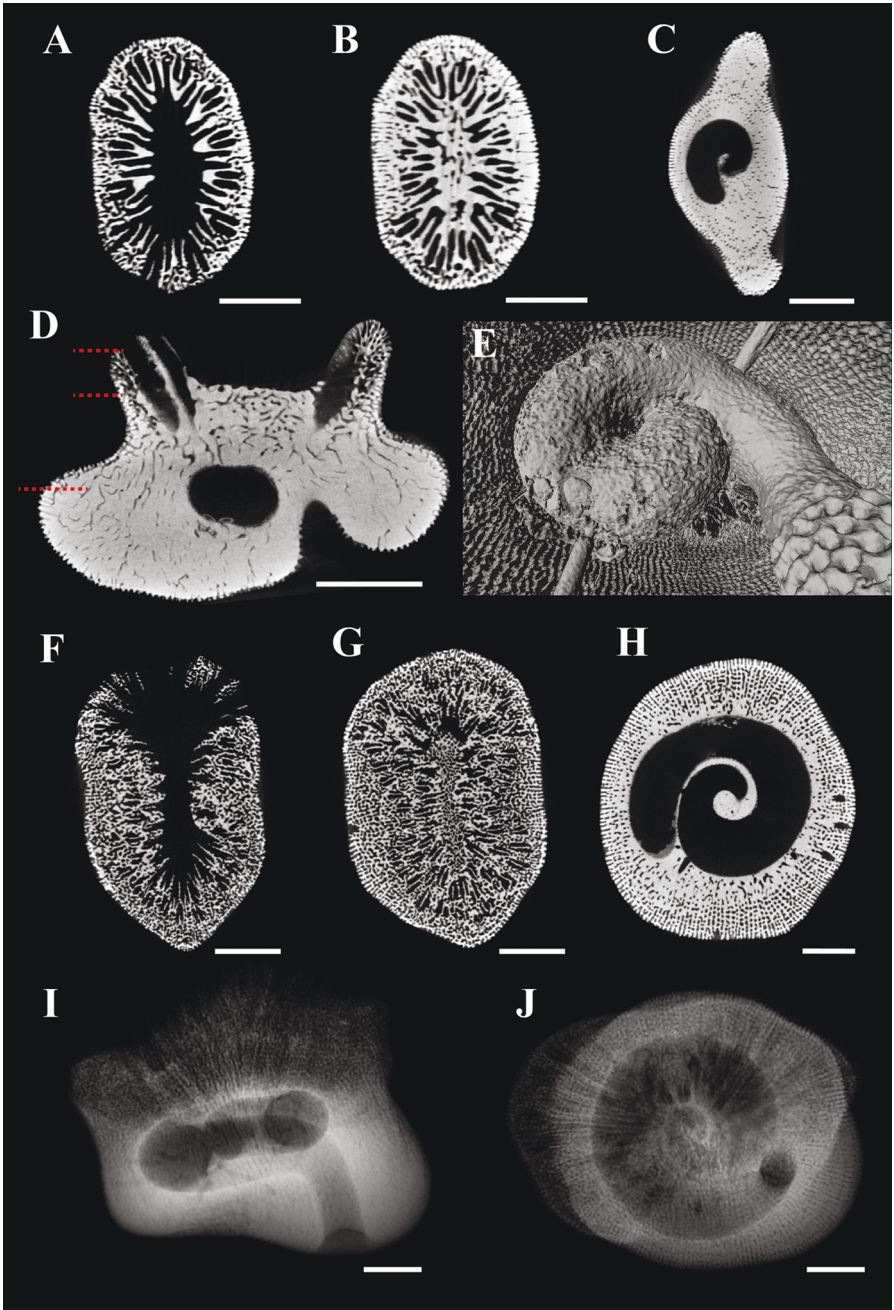


FIGURE 8 Digital reconstructions of *Heteropsammia* specimens based on Micro CT scans. A–E: *H. moretonensis* (HmKTa). A–C) a series of three transverse slices, from calice margin and base of fossa (A, B) and finally base of corallite with sipunculan chamber visible (C–D) lateral slice with yellow dashed lines denoting the position of slices in A–C, E) reconstructed view within coral, with sipunculan chamber and efferent pore channels projecting laterally. F–J: *H. cochlea* (KTa). F–H) a series of three transverse slices, from calice margin and base of fossa (F, G) and finally base of corallite with sipunculan chamber visible (C); I, J: lateral and top down (I and J, respectively) view into corallite with variable opacity and sipunculan chamber visible. Scale bars: 2.5 mm.

99°50'57.50"E); 65 from 7–11 m depth, site HYE21 (12°34'25.05"N, 101°42'24.82"E), 41 from 4.5–7.5 m depth, Koh Mun Nai East (12°36'59.85"N, 101°41'56.48"E); 28 from 7.5–9 m, Koh Mun Nai South (12°36'19.89"N, 101°41'20.97"E); 10 from Koh Mun Klang East (12°35'59.44"N, 101°41'54.77"E).

Range. Gulf of Thailand, Indonesia, Australia and New Caledonia (Kitahara & Cairns, 2021).

Description. Corallum solitary, sub-globular to elliptical, with moderately rounded walls, down to an asymmetrically keeled or 'wedge-shaped' base. Base hosting a single efferent pore projecting laterally for an endosymbiotic sipunculan worm. Base distinctly lobed with a single prominent lobe on each end of the elliptical coral, which may project out strongly almost doubling the width of the base, or may be less pronounced. Corallum typically widest at the base and calice margin, curving inwards in between resulting in a slight hour-glass shape. In some specimens, the keeled base may favour one side or another, resulting in a slightly more flattened appearance (though rarely truly flat as in *H. cochlea*). This results in the efferent pore projecting more downwards than laterally, however this is relatively uncommon. Multiple smaller lateral pores visible along the lower theca leading to an internal spiral chamber hosting the sipunculid, exiting at the basal orifice. In the few internally examined specimens, spiral chamber does not exceed one and a half complete rotations, likely limited by coral size. Juveniles visibly encrusting on a single gastropod shell, with any sign of encapsulated shell lost rapidly as the coral grows.

Calice elliptical and singular (GCD:LCD = 1.5–1.65). Multiple calices exceptionally rare, with no conclusive sign of asexual reproduction documented (see remarks). Largest specimen 12.4 mm in CD and 10.9 mm in height, typical range of fully grown specimens

are 5–11 mm in CD and 6–10 mm in height. Synapticulotheca well developed and porous throughout, porosity increasingly so towards the calicular margin. Epithecium absent. Thecal wall lacking true costae, instead being covered in granular ridges which are rarely interconnected, continuing down in broken lines from margin to base. These are visible even in smaller specimens (smallest assessed GCD 3 mm).

Septa hexamerously arranged, generally 46–48 in number (maximum range 42–48) in four typically complete cycles, with some specimens missing a few S4. Pourtalès plan present and well developed. Septal arrangement: S1–S2 > S3 > S4, resulting in a regular '1, 3, 1, 3 ...' pattern. S1 and S2, extending to the columella, either straight or slightly curved; pairs of S4 fused before a common S3, which continue towards the columella as a single septum. Calice margin lancetted. Septa exsert and well separated at the margin with S1 and S2 almost identical, followed shorter S4s (approximately $\frac{3}{4}$ to $\frac{1}{2}$ the height of S1–2), followed by even shorter S3s (approximately $\frac{3}{4}$ to $\frac{1}{2}$ the height of S4). Both S1 and S2 of almost identical thickness, followed by S3 approximately $\frac{1}{2}$ as thick as S1–2, followed by S4 approximately $\frac{1}{2}$ as thick as S3. Septal faces prominently granular to hispid with well-spaced points, septal edge however lacking dentation until quite deep into fossa, where some shallow dentation is sometimes visible. Columella spongy, elongate and flattened (lacking noticeable curve or arch). Fossa moderately deep.

Live specimens colour and appearance. Surveyed specimens all brown in colour due to zooxanthellae, occasional bleaching observed but uncommon. Exsert S1 and S2 septa visible near calice margin *in situ*, pali-like structures absent. Oral disk ranging from striated, banded, speckled to plain in pattern with pigmentation ranging from white to very dark brown, almost black, occasionally

tints of blue, purple or green. Tentacles clear with zooxanthellae concentrated on nodules, which may correspond to nematocyst batteries, giving a speckled appearance. In living specimens, thecal ridges and granulations are distinctly visible, with stronger pigment and thicker tissue in the valleys and breaks between ridges, giving the outer colouration a striated to spotted appearance.

Habitat and ecology. In the present study, *Heteropsammia moretonensis* was found exclusively in soft-substrate habitats across its range. At Koh Tao, it was found living sympatrically with *H. cochlea*, elsewhere it was found alongside other soft-substrate scleractinians (*Cycloseris fragilis*, *Heterocyathus* spp., *Truncatoflabellum* sp.). The majority of specimens were found at 15–20 m depth and hosting zooxanthellae, with partially or entirely bleached specimens rarely recorded.

The biology and ecology of *H. moretonensis* has not been investigated since its description by Wells (1964). Here we provide the first observations of prey capture and ingestion by *H. moretonensis*, recording multiple cases of salp ingestion (see supplementary fig. 2), however, the salp species ingested could not be identified. We further record two instances of anthozoan predation (fig. 9H, I), with the coral ingesting a tentacle of the sea anemone *Bolocerooides* sp., and the partial ingestion and consumption of the oral disk and labial tentacles of a ceriantharian, Arachnactidae sp. Both anthozoan prey species were regularly found in the soft-substrate habitats of surveyed sites. All studied specimens were found to be hosting sipunculan worms; besides this, little is known about its associated fauna.

Remarks. Compared to its congeners, *H. moretonensis* has received minimal attention since its description. It is rarely encountered and it may be confused with *H. cochlea*, with which it was synonymised (Hoeksema

& Best, 1991). The last author has observed *H. moretonensis* specimens in South Sulawesi (Hoeksema & Best, 1991; Hoeksema & van Ofwegen, 2004) and at Kudat off the northern tip of Borneo (Hoeksema, pers. obs.). This confusion has largely been driven by the relatively diminutive size of the species, making it resemble a juvenile form of *H. cochlea*, and some diagnostic features fitting within the variability of *H. cochlea*. Nonetheless, the genus has currently been accepted to host three species (Cairns, 2001), namely *H. cochlea*, *H. eupsammides* and *H. moretonensis*, with recent records from New Caledonia adding to those of Australia and Indonesia (Kitahara & Cairns, 2021). In an effort to clarify members of the genus *Heteropsammia*, our morphological and molecular evidence supports the distinction of *H. moretonensis* from other members of the genus *Heteropsammia*.

Heteropsammia moretonensis can be readily separated from its congeners based on several features, beyond the difference in size of the coral. The base of *H. moretonensis* is almost always keeled, with the keel facing downwards or obliquely to one side (fig. 7C). In contrast, *H. cochlea* typically possesses a flat base, even in very small specimens. The calice of *H. moretonensis* is almost exclusively ovoid (with exceptionally rare cases of division, see below) whereas the calice of *H. cochlea* is significantly more variable, ranging from ovoid, to medially constricted to twisted or meandering (fig. 9A–D). Regarding septa, *H. moretonensis* typically possesses four complete (or near complete) cycles, though an incomplete fifth was recorded by Kitahara & Cairns (2021). In addition, *H. cochlea* (in normal or elliptical phases) may reach up to six incomplete cycles, with fused S5 resulting in pali (absent in *H. moretonensis*). A crucial developmental difference between the species is in regard to budding and coloniality with a

significant fraction of *H. cochlea* specimens being observed undergoing some intra-calicular budding (see remarks for *H. cochlea*). Of the 491 specimens examined, only two were found with any sign of two calices (fig. 9E, F).

Population distribution

The Samaesan islands were found to host two species of soft-substrate associated dendrophylliids (fig. 10, supplementary table S2). Among these were the maximum population density of *Heteropsammia moretonensis* with a mean value of 18.8 individuals/m² (± 5.6 s.e.). The Samaesan islands were also found to host the only recorded population of *Dendrophyllia* cf. *minima*, at a single site with a mean peak density of 1.3 individuals/m² (± 0.8 s.e.). At the Koh Mun archipelago, only a single dendrophylliid species of soft sediment associated Dendrophylliidae was found, with mean peak densities of *H. moretonensis* ranging from 0.4 individuals/m² (± 0.2 s.e.) to 16.1 individuals/m² (± 2.5 s.e.). The island of Koh Tao was found to host the greatest diversity of soft-substrate dendrophylliids, being the only location surveyed where *H. cochlea* (from 0.3 individuals/m² \pm 0.2 s.e. to 6.2 individuals/m² \pm 2.6 s.e.) and *Tubastraea stimpsonii* (from 0 to 2 individuals/m² \pm 0.7 s.e.) occur. In contrast with the locations along the eastern part of the Gulf, Koh Tao was found to host relatively low densities of *H. moretonensis* (from 0 to 0.4 individuals/m² \pm 0.2 s.e.). The population distribution of dendrophylliids on coral reefs, pinnacles and artificial reefs, including specimens of *Cladopsammia*, *Duncanopsammia*, *Turbinaria* and attached specimens of *Tubastraea*, were not quantified in the present study. It should be noted however that specimens of *Cladopsammia eguchii* (Wells, 1982) were recorded from the waters around Koh Tao and the Koh Mun Nai archipelago (see supplementary fig. S2) and represent the first records of the species from Thai waters.

Discussion

Analyses

By utilising micro-CT techniques, we were able to investigate simultaneously both the internal features as well as some degree of micro-structural detail (i.e., denticulation on septa). In the latter case, however, this is with a trade-off in capacity, preventing ultra-high resolution analysis of features available via alternative techniques such as scanning electron microscopy (SEM). There remains therefore, features not investigated in the present study such micromorphological features of skeletons, which have been shown to have robust diagnostic value in multiple scleractinian groups, including the Dendrophylliidae (Arrigoni et al., 2014, 2019). Combined utility of SEM and high-resolution micro-CT would allow for drastic improvements in analysis of microscopic features. Our morphological assessment, in combination with molecular, biogeographic and ecological data, were nonetheless able to contribute new findings regarding the taxonomy of Dendrophylliidae.

The molecular results presented here broadly agree with those of previous analyses (Arrigoni et al., 2014; Capel et al., 2020; Yiu et al., 2021; Yiu & Qiu, 2022) supporting the general placement of the major clades. However, discrepancies arise at finer taxonomic resolutions, such as in the placement of *Turbinaria*, with our results agreeing with those of Capel et al. (2020) but which was found to be unresolved in the analysis by Arrigoni et al. (2014) and was placed as sister to the remaining Dendrophylliidae by Yiu et al. (2021). Our findings place the *Heteropsammia/Eguchipsammia* clade as sister to the rest of the family and find *Balanophyllia*, *Cladopsammia* and *Dendrophyllia* to be polyphyletic, in agreement with Arrigoni et al. (2014) and Capel et al. (2020). Distance values for all regions were generally unable to differentiate between

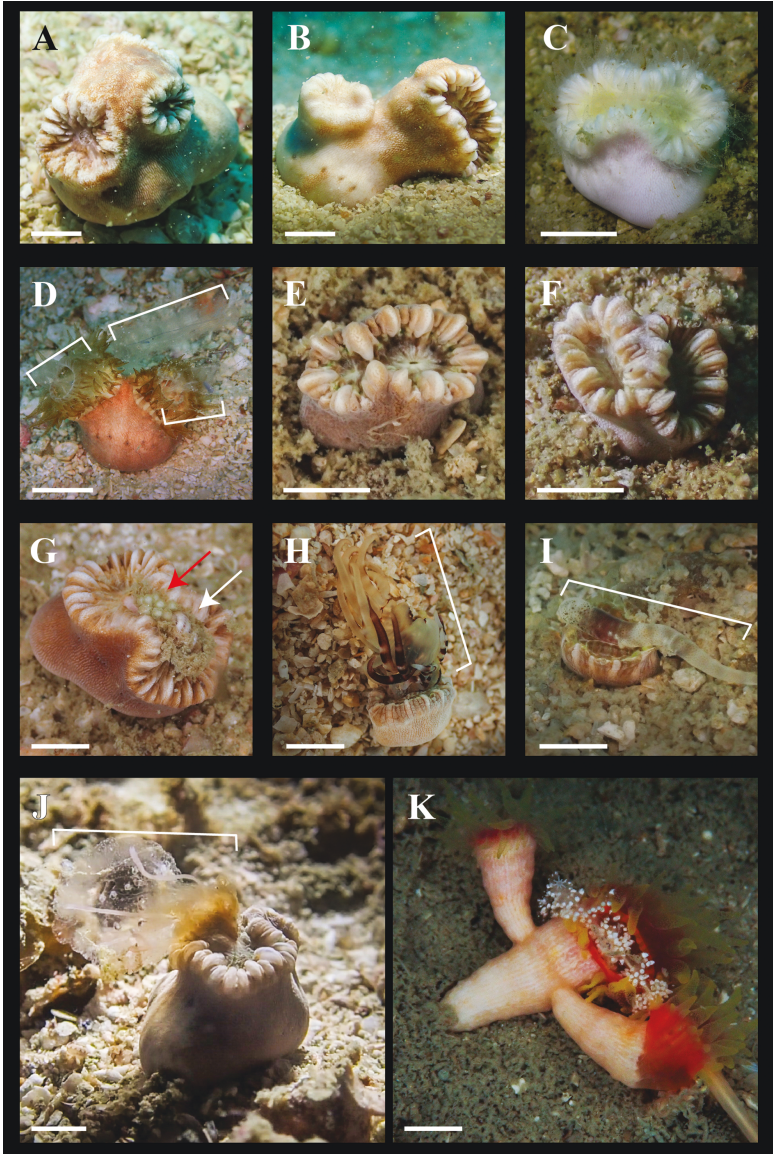


FIGURE 9 Variation in morphology and ecology of solitary soft-substrate associated Dendrophylliidae in the Gulf of Thailand. A, B) *in situ* observations of variable polystomatism in *Heteropsammia cochlea* (scale bars 5 mm); C) a bleached specimen of *H. cochlea* *in situ* (scale bar 10 mm); D) simultaneous ingestion of large salps by two mouths in a single *H. cochlea* colony, individual salps indicated by brackets (scale bar 10 mm); E,F) rare cases of division in *H. moretonensis* (scale bars 5 mm); G) ecto-parasitism on *H. cochlea* by an unidentified epitoniid snail (white arrow) with clusters of eggs (red arrow) attached to the corallite (scale bar 10 mm); H) ingestion of an oral disk of ceriantharian (white bracket) by *H. moretonensis* (scale bar 10 mm); I) ingestion of an anemone tentacle (white bracket) by *H. moretonensis* (scale bar 10 mm); J) ingestion of a medusa of *Pelagia* sp. (white bracket) by *H. cochlea* (scale bar 10 mm); K) proto-cooperative ingestion of a sea pen by two mouths in a single colony of *Tubastraea stimpsonii* (scale bar 10 mm).

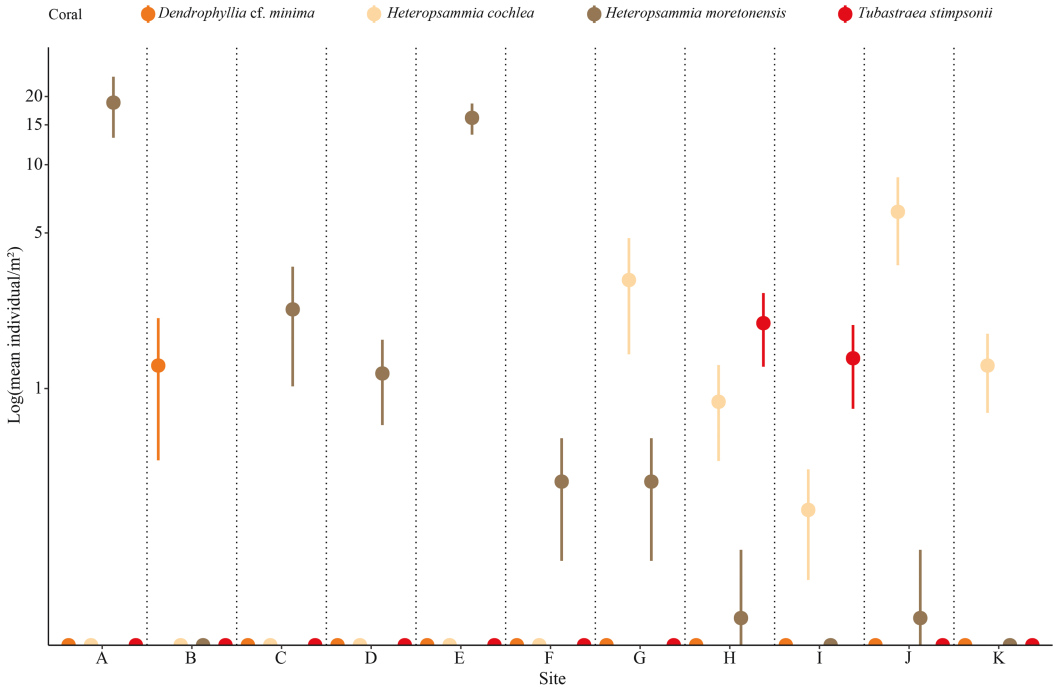


FIGURE 10 Mean population densities of dendrophylliids from soft substrate habitats at surveyed sites across the Gulf of Thailand. Vertical lines represent S.E. Location of the sites displayed in fig. 1.

closely-related species in the present analysis. The nuclear rDNA region was however somewhat able to distinguish between clades and genera, however the utility of distance values based on the presently available species and sequences remains insufficient at finer taxonomic scales. A greater sampling effort across a greater geographic, in addition to utilising phylogenomic tools (Quek & Huang, 2022), range may resolve this.

Taxonomy

Based on the presently sequenced specimens, the genus *Cladopsammia* appears to be divided between the *Heteropsammia*/*Eguchipsammia* clade, and the '*Rhizopsammia*'/*Cladopsammia* clade. Specimens identified as *Cladopsammia gracilis* follow the usage of Arrigoni et al. (2014), Cairns & Zibrowius (1997), but it is unsettled whether this common Indo-Pacific species corresponds to that described by Milne

Edwards & Haime (1848) as *Dendrophyllia gracilis*, or if another taxon is more applicable (e.g., *Cladopsammia manuelensis*, *Rhizopsammia goesi*, *R. verrilli*, *R. wettsteini*, *Balanophyllia gemmifera*). Recent observations involving many specimens of *Cladopsammia manuelensis* in the Caribbean revealed that juveniles show rhizoids instead of basal plates, which are diagnostic characters of *Rhizopsammia* and *Cladopsammia*, respectively, causing confusion about its identification (Hoeksema et al., 2019a). Examination of topotypical material and comparison with the type species, the Mediterranean *Cladopsammia rolandi*, is needed to resolve the identification and classification. Nonetheless, our molecular analyses generally agree with previous studies regarding the topological placement of this clade.

Recent studies about the genus *Tubastraea* (Yiu et al., 2021; Yiu & Qiu, 2022), in addition to the present findings and apparent

discrepancies in sample identification from previous studies, highlight the need for a close re-examination of the genus *Tubastraea*. While the genus has indeed been found to be monophyletic, multiple questions have now arisen based on these recently described species. While our findings agree with the delineation of *T. chloromura* and *T. dendroidea* as valid and separate species, they disagree with Yiu & Qiu (2022) on the relatedness of species within this group. Our findings show *T. chloromura* as sister to *T. diaphana*, with *T. dendroidea* nested among specimens identified as *T. micranthus* by Arrigoni et al. (2014). This therefore suggests the need for a closer investigation of all arborescent members of the genus, and indeed additional material for the arborescent species *Dendrophyllia ijimai* with which *T. dendroidea* bears remarkable similarity. Our findings also do not match with the specimen identification of *T. diaphana* by Arrigoni et al. (2014) with our specimen AO101 morphologically resembling (Arrigoni et al., 2014, fig. 11 J–L) and genetically clustering with *T. cf. aurea*.

The recent description of *T. megacorallita* as a newly discovered species has expanded the morphological variation within the genus to include specimens with Pourtales plan, with our findings expanding this further to include solitary and unattached specimens, raising questions about similar species. The morphology of our specimens agree strongly with the broadly accepted variation among specimens of *Balanophyllia* (*Eupsammia*) *stimpsonii*, which in turn has been found to bear distinct similarities with other specimens of the subgenus, which is characterized by free-living dendrophylliids with monocyclic development. A comprehensive review of the taxonomic history of this subgenus is provided by Cairns (2001) and is thus not repeated here. It is therefore apparent that further investigation, with sequencing efforts

in particular, be made for the remaining species of the group so as to better investigate the possible relatedness with *Tubastraea*. This would additionally help to clarify the phylogeny of *Balanophyllia*, one of the major polyphyletic genera in the family.

Another large, polyphyletic genus, *Dendrophyllia*, appears to possess morphological variability as extensive as *Tubastraea*, though genetic data suggests that specimens represent multiple distinct genera. It is possible that the three species groups suggested by Cairns (2001) and others before and after him may represent three distantly related genera, but this cannot be inferred from the insufficient number specimens for which sequences exist. Our molecular analyses consistently found *D. cf. minima* as sister to *Heteropsammia* with strong support, which was an unexpected result. Given the colonial, attached, azooxanthellate nature of *D. cf. minima*, it is not immediately clear what possible synapomorphies may be inferred between these groups, which are also widespread across other members of the family. This could perhaps be clarified by a morphological analysis of microstructural features, in addition to the molecular examination of other related species.

The genus *Heteropsammia* now represents one of the few dendrophylliid genera to have all currently accepted species sequenced, with *H. moretonensis* supported by morphological and genetic data as distinct from its congener(s). The status of *H. eupsammides* is less clear, with specimens clustered among *H. cochlea*. The predominant diagnostic separation between the two species pertains to budding, with corals being either monostomatous (*H. cochlea*) or polystomatous (*H. eupsammides*), and the related feature of the number of septa/septal cycles. This has nonetheless given rise to the challenge of separating young or immature specimens in either

species (Hoeksema & Best 1991; Filander et al., 2021; Kitahara & Cairns, 2021). Our findings of considerable calicular variation in *H. cochlea*, including the in the degree of intrastomadaeal budding, number of independent calices, and relative proportion of the different 'phases' within a single population, show considerable agreement between morphological and molecular analyses. It is therefore possible that '*H. eupsammides*' represents a colonial phase of development in *H. cochlea*, which may not always arise over time as inferred from large monostomatous specimens co-occurring with small polystomatous specimens (Hoeksema personal observation), but is instead likely mediated by mechanisms currently unknown.

The sparsity of polystomatous specimens of *H. moretonensis* (only 0.4% of specimens across three separate locations), is not surprising considering its small size, because there is not much space for more than one polyp. Instead, a smaller size may make the coral more light-weight and more mobile, which may help the coral and its worm to escape burial and to regain an upright position after overturning, as seen in other free-living corals (Hubbard, 1972; Hoeksema, 1988; Bongaerts et al., 2012; Hoeksema & Bongaerts, 2016; Sentoku et al., 2016; Hoeksema et al., 2018b). A reduction rather than an increase in coloniality with diminishing size is supported by the diversity of unrelated monostomatous or small-colony forming species, found on soft substrate habitats across the Indo-Pacific (i.e., *Heterocyathus* spp. and *Truncatoflabellum* spp.). Free-living, monostomatous species of the genus *Cycloseris* are smaller than their mushroom coral relatives and are adapted to live on sandy sea floors (Gittenberger et al., 2011; Hoeksema, 2012a, b, 2014; Hoeksema et al., 2019b). They can become even smaller by self-fragmentation (Hoeksema & Waheed, 2011), which may increase their mobility

(Hubbard, 1972; Yamashiro & Nishihira, 1995), as well as their population densities (Hoeksema et al., 2018a, 2019c). Likewise, among the dendrophylliids, such as those in the present study, also a case may be hypothesised for evolutionary size reductions. Specimens of *Tubastraea stimpsonii* represent the only members of the genus found to be living on soft substrate habitats and are conspicuous as forming the numerically smallest colonies (often solitary) in the genus. Its sister species, *T. megacoralita*, instead has retained its attached form and forms larger colonies of up to 14 corallites, as is typical for the remaining members of *Tubastraea*. Meanwhile, *D. cf. minima*, also an attached species, was found growing on rocks and rubble in soft-substrate-habitats and attained small colony sizes of typically 12–24 corallites, with no sign of adapting its morphology to a free-living form.

Ecology

Recent years have seen a rapid increase in studies focusing on biogeographic and ecological aspects of dendrophylliid corals. Many of these have focused on the competition, invasive capacity and spread of *Tubastraea* corals in the Atlantic (Creed et al., 2017; Tanasovici et al., 2020). However, the population distribution of most species remains only crudely known, as species-specific distributions have not been assessed from a large number of locations. Literature on the distribution of scleractinian corals in Thailand have been heavily focused on reef-building and zooxanthellate species, likely due to a combination of ease-of-access and growing attention to climate-driven threats. This has left a conspicuous void in the biodiversity documentation of a number of coral families such as the Caryophylliidae and the Dendrophylliidae. Our surveys aimed to provide an initial baseline understanding of the distribution of coral species dwelling on soft substrates across the

Gulf of Thailand. By carrying out numerous pilot surveys to assess locations of absence, presence and those with sparse distribution, we were able to isolate locations with population densities greater than one individual/10 m². In the Gulf of Thailand, the widespread abundance of *H. moretonensis* is in stark contrast to the highly localised populations of the other species assessed. The factors influencing prevalence and absence of coral species on soft substrates remains poorly understood. It is also relevant to see which dendrophylliids have not been recorded from soft substrates in the Gulf of Thailand. *Eguchipsammia* spp. are widespread branching corals, which are normally attached to hard substrates, but they can also be found as free-living fragmented corals on unconsolidated substrates (Cairns, 2001; Arrigoni et al., 2014; Tempera et al., 2015; Qurban et al., 2020). It is likely that this genus is also represented in the Gulf of Thailand, although such records are unknown to us. The branching dendrophylliid *Duncanopsammia axifuga* is also known to occur in high-sediment environments; although it has been implied that its range may include the southern part of the Gulf of Thailand (Veron, 2000) and may live as free-living fragments on soft substrates, it is unlikely that it can be found within the Gulf (Subhan et al., 2022).

Among the most remarkable ecological observations recorded here are the feeding strategies of three out of the four investigated coral species on soft substrates in the Gulf of Thailand. Until recently, the majority of scleractinian diets was believed to be composed of plankton (including macrozooplankton), however predation of benthic gastropods by scleractinian corals (including *H. cochlea*) have challenged these assumptions (Mehrotra et al., 2019). The *in situ* observation of a *T. stimpsonii* colony actively ingesting a pennatulacean colony not only furthers the number of known cases of proto-cooperative feeding and capture among scleractinians, but also provides

the first record of anthozoan predation upon another anthozoan. The method of proto-cooperation has been shown to be employed by colonial dendrophylliid corals to facilitate capture of prey items larger than the oral disks of the coral, such as jellyfish (Musco et al., 2018; Gregorin et al., 2022). Unlike these cases, this remarkable observation shows that proto-cooperative techniques may be utilised to capture, or at least ingest, large benthic prey too.

The presently documented observations of *H. cochlea* ingesting *Pelagia* sp., while representing a first documentation for *H. cochlea*, is among numerous recent records of salpivory and medusivory in scleractinian corals. For example, free-living fungiid corals have been shown to ingest the scyphozoan *Aurelia* and salps (Alamaru et al., 2009; Hoeksema & Waheed, 2012). Salpivory has also been reported in Caribbean reef-building corals (ter Horst & Hoeksema, 2021). However, documentation of salpivory by *H. moretonensis* represents the capacity for ingestion of large prey by dendrophylliids with moderate gape sizes, without the need of cooperative feeding as recorded in colonial taxa. This is further supported by the second and third cases of anthozoan-upon-anthozoan predation with ingestion by *H. moretonensis* of ceriantharian and actiniarian partial tissue, with both prey items being considerably larger than the oral disk of the coral. In addition, our observation of a colony of *H. cochlea* with multiple mouths independently feeding on separate salps highlights the dramatic variation in feeding behaviours available to such corals.

The findings of the present study serve to highlight the importance of surveys and biodiversity monitoring outside of coral reef habitats, and reinforce the distinction of soft substrate habitats beyond coral reefs in the Gulf of Thailand, as hosting unique diversity and species assemblages not found in other areas. These areas, often referred to as soft-sediment habitats (De Brauwier et al.,

2017; Mehrotra et al., 2021), inter-reefal habitats (Keesing et al., 2023), or ‘muck’ habitats (De Brauwer et al., 2018) continue to provide evidence of specialised biology and ecology (Mehrotra et al., 2019; Keesing et al., 2023). Offshore *Halimeda* bioherms also appear to be suitable habitats for free-living corals, such as *Heteropsammia* (Borghi et al., 2023). In the Gulf of Thailand, these areas appear to persist further offshore until the substrate is comprised of such fine particle sizes that it achieves a semi fluid-like consistency, with our surveys showing no scleractinian presence in these areas.

Previous studies have already shown that a wealth of undescribed diversity may be found in the deeper soft substrate habitats of the Gulf of Thailand (Mehrotra et al., 2017, 2020, 2021). Such surveys would not be possible without the remarkable pace of growth, and access to, SCUBA technology and tourism which allows for access to areas previously only studied via trawling and *ex situ* examination. Indeed, the shallow soft-substrate-habitats support a rapidly growing and lucrative tourism industry (De Brauwer et al., 2017; De Brauwer & Burton, 2018), the biodiversity documentation of which far outpaces the rate of scientific description and study. The challenge faced by scientists therefore is not only the documentation of biodiversity and ecology at a time of rapid biodiversity loss (Costello et al., 2010; Sigwart et al., 2018; Engel et al., 2021), but also the steadily diminishing academic emphasis on taxonomy (Halme et al., 2015; Pinto et al., 2021; Engel et al., 2021) when the growth of marine tourism has facilitated an unprecedented rate of biodiversity exploration.

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Supplementary material

Supplementary material is available online at: <https://doi.org/10.6084/m9.figshare.23126462>

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