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New distribution records of three species of soft corals (Octocorallia: Malacalcyonacea) from the central Indian Ocean islands

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Original Article

Abstract

Lakshadweep forms the northernmost extension of the Central Indian Ocean Islands Ecoregion. Although 37 species of soft corals have been reported previously, their taxonomic identity and genetic diversity remain poorly resolved. In this study, we applied an integrated taxonomic approach combining external morphology, sclerite characteristics, and partial mitochondrial *mtMutS* gene sequences to identify soft corals from Lakshadweep. Three species, *Lobophytum catalai*, *Sclerophytum polydactylum*, and *Dendronephthya hemprichi*, were confirmed from the Lakshadweep Archipelago. These findings provide updated records for the region and contribute to a better understanding of the soft coral diversity in the Lakshadweep Archipelago. The results form a useful baseline for future research and conservation of octocorals in Indian coral reef ecosystems.

Keywords: *Integrated taxonomy, mitochondrial DNA, mtMutS, Lakshadweep Archipelago*

Introduction

The soft corals of the Order Malacalcyonacea (Class Octocorallia), commonly known as octocorals, are sedentary, colonial marine animals distributed mostly in the Indo-Pacific region (Bayer, 1973; Fabricius and Alderslade, 2001). They are an important component of the coral reef ecosystem as they contribute significantly to biomass and provide microhabitats for associated organisms (Bayer, 1961; Buhl-Mortensen and Mortensen, 2005; Haverkort-Yeh *et al.*, 2013; Shahbazi *et al.*, 2021). Compared to their reef-building Scleractinian coral counterparts, there is a knowledge gap about the relationships

between octocorals and their associated fauna (Stella *et al.*, 2011; Calcinaï *et al.*, 2013; Gaikwad *et al.*, 2021).

The Lakshadweep archipelago is a group of oceanic coral islands that lie between latitudes 8°-14°N and longitudes 71°-74°E, situated on the northern part of the Laccadive-Chagos ridge in the central Indian Ocean (Mallik, 2017). Generally, information on octocorals from the central Indian Ocean islands, such as the Maldives and Lakshadweep, is very limited. The first comprehensive survey of this region was conducted by Gardiner (1903), who documented the fauna and geography of the Maldives and Laccadive Archipelago during the 1899–1900 expedition. Apart from the 'Investigator Expedition' collections (T and Henderson, 1906 and Thomson and Simpson, 1909), the taxonomic reports on Maldives and Lakshadweep soft corals are found in the publications of Pratt (1903, 1905), Hickson (1903, 1905), van Ofwegen and Vennam (1991), Alderslade and Shirwaiker (1991), Vennam and van Ofwegen (1996), Mary and Sluka (2014), and Narayanankutty *et al.* (2025).

Soft corals have received comparatively less research attention than reef-building scleractinian corals. The first record of the Lakshadweep soft corals goes back to van Ofwegen and Vennam (1991), who reported 19 species from the islands of Kavaratti, Agatti, and Bangaram. Then, Aderslade and Shirwaiker (1991) reported 17 species from the Kavaratti atoll. Vennam and van Ofwegen (1996) reported 11 species from different islands. These works come from the expeditions conducted in 1985, 1987-1989, and 1992 by the National Institute of Oceanography, India. The purpose of this collection was to study the bioactive compounds of soft corals. Then, 44

species of soft corals were identified from the Minicoy islands by Mary and Sluka (2014), and they were not confirmed at the species level. A recent study by Narayanankutty *et al.* (2025) identified 15 soft coral species: 12 at the genus level and 3 at the species level.

For octocoral molecular analysis, the mtMutS gene evolves more rapidly than COI, making it a more suitable barcoding marker for octocoral identification (McFadden *et al.*, 2011; McFadden *et al.*, 2014; Benayahu *et al.*, 2018). Molecular analysis can resolve the identity of cryptic species, is a useful tool for characterising morphological variants of species, and rapidly assesses and compares the biodiversity of octocorals (McFadden *et al.*, 2017; Benayahu *et al.*, 2018; Quattrini *et al.*, 2019; Shahbazi *et al.*, 2021).

In this study, we employ an integrative taxonomic approach combining morphology and mtMutS sequence data to assess soft coral diversity in Lakshadweep. We report three new distributional records and provide updated molecular confirmation of regional octocoral diversity. This study establishes a baseline framework for future biodiversity assessment and phylogenetic research in the central Indian Ocean.

Material and methods

Sample collection and morphological analysis

The collection was made from 2021 to 2022 from the different islands of Lakshadweep. The specimens were collected using SCUBA diving at depths of 5 to 30 m. Materials were preserved in 75% EtOH, and small tissue pieces were stored in 100% molecular-grade EtOH for DNA extraction. The specimens were deposited in the Biodiversity Lab, Kerala University of Fisheries and Ocean Studies, Kochi, India. The specimens were identified to the genus level following Fabricius and Alderslade (2001), and the sclerites were extracted from the tissue using 10% Sodium hypochlorite.

During the study period, samples were opportunistically collected from certain reef areas in the Lakshadweep Islands. Due to logistical and weather-related factors, the sampling effort was limited to easily accessible locations. Consequently, a subset of the regional soft coral diversity is represented by the geographic coverage and number of specimens.

DNA extraction and amplification

DNA was extracted from ethanol-preserved samples using the Puregene DNA isolation kit (Invitrogen Thermo Fisher

Scientific, USA). The mitochondrial mutS homolog (*mtMutS*) region was amplified by PCR, yielding fragments of 700–800 bp. Each reaction (25 μ L) contained 12.5 μ L master mix, 1 μ L each primer, 1 μ L MgCl₂, 8.5 μ L nuclease-free water, and 1 μ L template DNA. Amplification used primers ND42625F (5'-TACGTGGYACAATTGCTG-3') (Lepard, 2003) and Mut-3458R (5'-TSGAGCAAAGCCACTCC-3') (Sánchez *et al.*, 2003b). PCR conditions were: 94 °C for 3 min, followed by 35 cycles of 94 °C for 30 s, 58 °C for 90 s, 72 °C for 1 min, and a final extension at 72 °C for 5 min. PCR products were purified using the Nucleopore Sure Extract Kit (Genetix, India). The PCR product was sequenced using the Sanger method at AgriGenome Pvt. Ltd (Kochi, India). Four sequences were generated as part of the study.

Sequencing was performed using BigDye Terminator v3.1 (Applied Biosystems) following the manufacturer's protocol, and chromatograms were analysed with Sequencing Analysis Software v5.2. The sequences were compared in NCBI-BLAST for identification. *Sinularia* mtMutS sequences and outgroup taxa from Sarcophytonidae were retrieved from GenBank. Alignment was performed using BioEdit v7.1.3.0 (Hall, 1999).

Phylogenetic analyses

Four new *mtMutS* sequences were generated and added to a dataset, including two as outgroups, and were aligned using BioEdit 7.1.3.0 (Hall, 1999) and trimmed to 735 bp. The pairwise genetic distance was calculated using MEGA X (Kumar *et al.*, 2018) using the K2P (Kimura 2-parameter) model (Table 1). The maximum likelihood (ML) analysis was performed in IQ-TREE 2.2.0 (Ly-Trong *et al.*, 2022) with the best partition scheme and ultrafast bootstrap support for 1000 iterations. The resultant tree was visualised in iTOL (<https://itol.embl.de>) (Letunic and Bork, 2021). The generated sequences were deposited in GenBank under accession numbers PV695213-PV695216 (Table 2).

The current analysis did not include nuclear 28S rDNA markers and mitochondrial cytochrome oxidase I (COI). COI is less useful for differentiating closely related taxa in octocorals due to its comparatively modest substitution rates and low species-level resolving power (France and Hoover, 2002; McFadden *et al.*, 2010). Additionally, the limited availability of

Table 1. The interspecific distance between the clades represents families

	Clade 1	Clade 2	Clade 3
Clade 1			
Clade 2	7.7		
Clade 3	9.2	9.9	
Clade 4	10.7	11.2	8.3

Table 2. Voucher information and GenBank accession numbers of mtMutS sequences generated in the present study from Lakshadweep

Species	Voucher No.	Locality	Gene	GenBank Accession No.
<i>Dendronephthya hemprichi</i>	BDLKUFOS-03-002	Kavaratti	mtMutS	PV695213
<i>Lobophytum catalai</i>	BDLKUFOS-04-001	Kavaratti	mtMutS	PV695214
<i>Sclerophytum polydactylum</i>	BDLKUFOS-04-002A	Agatti	mtMutS	PV695215
	BDLKUFOS-04-002B	Kavaratti	mtMutS	PV695216

28S rDNA sequences for nephtheid taxa in public databases restricts their comparative utility. Because of its somewhat better phylogenetic resolution in octocorals, *mtMutS* was chosen as the main molecular marker (McFadden *et al.*, 2006, 2010).

Results

A consolidated checklist of soft corals from Lakshadweep is provided (Table 3), including 37 previously reported species and the three new records documented in this study. This research increases the known soft coral diversity of the archipelago to 40 species.

Morphological identification

Lobophytum catalai Tixier-Durivault, 1957 (Figs. 1a-b):

Systematics

Phylum – Cnidaria Verrill, 1865

Subphylum – Anthozoa Ehrenberg, 1834

Class – Octocorallia Haeckel, 1866

Order – Malacalcyonacea McFadden, van Ofwegen & Quattrini, 2022

Family – Sarcophytidae Gray, 1869

Genus – *Lobophytum* Marenzeller, 1886

Type Locality: Fiji Islands

Original name: *Lobophytum catalai* Tixier-Durivault, 1957

Synonyms: *Lobophytum nodosum* Tixier-Durivault, 1969

Taxonomic Reference: Tixier-Durivault, A. (1957). The Alcyonaires of the Museum: I. Family Alcyoniidae. IV. Genus *Lobophytum* (Fin). Bulletin of the National Museum of Natural History, Paris, Ser. 2. 29 (1): 106-111.

Material examined: BDLKUFOS-04-001 (Fig. 1a, b), a piece of a colony collected from the Lagoon area, Kavaratti, Lakshadweep Islands, India. 5 m. Nayana Narayanankutty. 27 February 2022.



Fig. 1. *Lobophytum catalai*. a. Excitu photo. b. Sclerites from the areas A; Lobes, B. Basilaires

Table 3. Checklist of soft coral species reported from the Lakshadweep archipelago based on previous literature (n = 37) and the present study (n = 3 new records)

No.	Species	Locality	Reference
	Phylum- Cnidaria		
	Subphylum- Anthozoa		
	Class-Octocorallia		
	Order-Malacalcyonacea		
	Family- Cladiellidae McFadden, van Ofwegen and Quattrini, 2022		
	Genus-Cladiella Gray, 1869		
1	<i>Cladiella krempfi</i> (Hickson, 1919)	Agatti, Kavaratti, Androth	van Ofwegen and Vennam 1991; Alderslade and Shirwaike 1991; Narayanankutty <i>et al.</i> , 2025
2	<i>Cladiella pachyclados</i> (Klunzinger, 1877)	Agatti, Androth, Bangaram, Kalpeni, Kavaratti	Vennam and van Ofwegen, 1996
	Genus- Klyxum Alderslade, 2000		
3	<i>Klyxum flaccidum</i> (Tixier-Durivault, 1966)	Kavaratti	van Ofwegen and Vennam, 1991

No.	Species	Locality	Reference
	Family-Nepentheidae Gray, 1862		
	Genus-Dendronephthya Kükenthal, 1905		
4	<i>Dendronephthya hemprichi</i> (Klunzinger, 1877)	Kavaratti	Present study
	Family- Sarcophytidae Gray, 1869		
	Genus- Lobophytum Marenzeller, 1886		
5	<i>Lobophytum altum</i> Tixier-Durivault, 1956	Bangaram	van Ofwegen and Vennam, 1991
6	<i>Lobophytum batarum</i> Moser, 1919	Kavaratti	Alderslade and Shirwaika, 1991
7	<i>Lobophytum catalai</i> Tixier-Durivault, 1957	Kavaratti	Present study
8	<i>Lobophytum crassum</i> von Marenzeller, 1886	Kavaratti	van Ofwegen and Vennam, 1991; Vennam and van Ofwegen, 1996
9	<i>Lobophytum durum</i> Tixier-Durivault, 1956	Kavaratti	Alderslade and Shirwaika, 1991
10	<i>Lobophytum pauciflorum</i> (Ehrenberg, 1834)	Agatti, Androth, Bangara, Kavaratti	van Ofwegen and Vennam, 1991; Vennam and van Ofwegen, 1996; Narayanankutty <i>et al.</i> , 2025
11	<i>Lobophytum schoedei</i> Moser, 1919	Bangaram	van Ofwegen and Vennam, 1991
12	<i>Lobophytum strictum</i> Tixier-Durivault, 1957	Kavaratti	Alderslade and Shirwaika, 1991
13	<i>Lobophytum tecticum</i> Alderslade and Shirwaika, 1991	Kavaratti	Alderslade and Shirwaika, 1991
	Genus- Sarcophyton Lesson, 1834		
14	<i>Sarcophyton crassocaule</i> Moser, 1919	Agatti	van Ofwegen and Vennam, 1991
15	<i>Sarcophyton glaucum</i> (Quoy and Gaimard, 1833)	Kavaratti	Alderslade and Shirwaika, 1991
16	<i>Sarcophyton serenei</i> Tixier-Durivault, 1958	Kavaratti	Alderslade and Shirwaika, 1991
17	<i>Sarcophyton spinospiculatum</i> Alderslade and Shirwaika, 1991	Kavaratti	Alderslade and Shirwaika, 1991; Vennam and van Ofwegen, 1996
18	<i>Sarcophyton trocheliophorum</i> von Marenzeller, 1886	Agatti, Bangaram, Kavaratti	Alderslade and Shirwaika, 1991; Vennam and van Ofwegen, 1996
	Genus- Sclerophytum Pratt, 1903		
19	<i>Sclerophytum abhishiktae</i> (van Ofwegen and Vennam, 1991)	Agatti	van Ofwegen and Vennam, 1991
20	<i>Sclerophytum abruptum</i> (Tixier-Durivault, 1970)	Agatti, Androth, Kavaratti	Alderslade and Shirwaika, 1991; Vennam and van Ofwegen, 1996
21	<i>Sclerophytum densum</i> (Whitelegge, 1897)	Kavaratti	van Ofwegen and Vennam, 1991
22	<i>Sclerophytum dissectum</i> (Tixier-Durivault, 1945)	Kavaratti	Vennam and van Ofwegen, 1996
23	<i>Sclerophytum elongatum</i> (Tixier-Durivault, 1970)	Kavaratti	van Ofwegen and Vennam, 1991
24	<i>Sclerophytum facile</i> (Tixier-Durivault, 1970)	Agatti	van Ofwegen and Vennam, 1991
25	<i>Sclerophytum gaveshaniae</i> (Alderslade and Shirwaika, 1991)	Kavaratti	Alderslade and Shirwaika, 1991
26	<i>Sclerophytum gaweli</i> (Verseveldt, 1978)	Bangaram	van Ofwegen and Vennam, 1991
27	<i>Sclerophytum gravis</i> (Tixier-Durivault, 1970)	Kavaratti	Vennam and van Ofwegen, 1996
28	<i>Sclerophytum gyrosum</i> (Klunzinger, 1877)	Kavaratti	Alderslade and Shirwaika, 1991
29	<i>Sclerophytum hirtum</i> Pratt, 1903	Agatti, Kavaratti	Alderslade and Shirwaika, 1991; van Ofwegen and Vennam, 1991; Vennam and van Ofwegen, 1996
30	<i>Sclerophytum inegans</i> (Tixier-Durivault, 1970)	Agatti	van Ofwegen and Vennam, 1991
31	<i>Sclerophytum jasmineae</i> (Alderslade and Shirwaika, 1991)	Kavaratti	Alderslade and Shirwaika, 1991
32	<i>Sclerophytum kavartiense</i> (Alderslade and Shirwaika, 1991)	Kavaratti	Alderslade and Shirwaika, 1991
33	<i>Sclerophytum leptoclados</i> (Ehrenberg, 1834)	Kavaratti	Vennam and van Ofwegen, 1996
34	<i>Sclerophytum lochmodes</i> (Kolonko, 1926)	Bangaram	van Ofwegen and Vennam, 1991
35	<i>Sclerophytum murale</i> (May, 1899)	Agatti, Kavaratti	Alderslade and Shirwaika, 1991; van Ofwegen and Vennam, 1991; Vennam and van Ofwegen, 1996
36	<i>Sclerophytum numerosum</i> (Tixier-Durivault, 1970)	Bangaram	van Ofwegen and Vennam, 1991
37	<i>Sclerophytum parulekari</i> (Alderslade and Shirwaika, 1991)	Kavaratti	Alderslade and Shirwaika, 1991
38	<i>Sclerophytum polydactylum</i> (Ehrenberg, 1834)	Kavaratti, Agatti	Present study
39	<i>Sclerophytum querciforme</i> Pratt, 1903	Kavaratti	Alderslade and Shirwaika, 1991; Narayanankutty <i>et al.</i> , 2025
40	<i>Sclerophytum variabile</i> (Tixier-Durivault, 1945)	Agatti	van Ofwegen and Vennam, 1991

Diagnosis: Colony encrusting to low mound-like with distinct digitate lobes; lobes rounded distally and laterally compressed. Surface polyps dimorphic: autozooids elevated, arranged irregularly on lobe surfaces; siphonozooids minute, scattered between autozooids (5–8 siphonozooids between adjacent autozooids). Sclerites are predominantly barrel-shaped and spindles; lobes contain elongated spindles with simple or slightly branched tubercles; the surface layer of the stalk bears small rods and clubs. Distinguished from *L. pauciflorum* by the denser arrangement of siphonozooids and the presence of smaller surface clubs.

Description

Colony form: The colony forms a thick, encrusting base with an expanded, disc-like capitulum bearing short, finger-like lobes. Lobes are broad, rounded at the apices, and slightly flattened laterally. The surface is even to slightly wrinkled when preserved.

Polyps: Polyps dimorphic. Autozooids are conspicuous and retractile, each with eight tentacles arranged irregularly on the lobe surface. Siphonozooids are minute, numerous, and scattered between the autozooids, numbering approximately 5–8 between two autozooids.

Sclerites: Sclerites are abundant throughout all tissues. Surface layer of lobes: densely packed spindles, 0.10–0.20 mm in length, with simple to complex tubercles. Interior of lobes: longer spindles, up to 0.30 mm, slightly curved, with prominent tubercles. Surface layer of stalk: small rods and clubs, 0.05–0.10 mm in length, mostly with warted heads. Interior of stalk: irregular spindles, some branched, up to 0.25 mm long. Barrel-shaped sclerites are common throughout the colony and form a diagnostic character.

Colour: In life, colonies are reported as beige to light brown; preserved material appears greyish beige.

Habitat: Occurs in shallow lagoonal habitats and reef flats, attached to hard substrates or coral rubble at depths of 3–10 m.

Remarks: *L. catalai* is morphologically similar to *L. pauciflorum* but differs in hosting a greater number of siphonozooids between autozooids and having smaller surface clubs. Essentially, the main difference lies in the arrangement and density of polyps and the variation in lobe spindles. The Lakshadweep specimen closely matches the diagnostic features described for *L. catalai*.

Distribution: Widespread in the Indo-Pacific: Guam, American Samoa, Micronesia, Vanuatu, New Caledonia, Marshall Islands,

French Polynesia, Cook Islands, and Fiji. Reported in India from the Andaman and Nicobar Islands (Jayasree *et al.*, 1996; Rao and Devi, 2003). The present record extends the distribution to the Lakshadweep Archipelago, Arabian Sea, India.

Sclerophyllum polydactylum (Ehrenberg, 1834) (Figs. 2a–b)

Systematics

Phylum – Cnidaria Verrill, 1865

Subphylum – Anthozoa Ehrenberg, 1834

Class – Octocorallia Haeckel, 1866

Order – Malacalcyonacea McFadden, van Ofwegen & Quattrini, 2022

Family – Sarcophytidae Gray, 1869

Genus – *Sclerophyllum* Pratt, 1903

Type locality: Red Sea

Original name: *Lobularia polydactyla* Ehrenberg, 1834

Synonyms: *Alcyonium polydactylum* (Ehrenberg, 1834); *Amocella polydactyla* (Ehrenberg, 1834); *Lobularia polydactyla* Ehrenberg, 1834; *Sinularia polydactyla* (Ehrenberg, 1834); *Sinularia compressa* Tixier-Durivault, 1945; *Sinularia candidula* Verseveldt and Benayahu, 1983.

Taxonomic reference: Ehrenberg, C. G. (1834). *Beiträge zur physiologischen Kenntniss der Corallenthiere im Allgemeinen, und besonders des Rothen Meeres, nebst einem Versuch zur physiologischen Systematik derselben*. Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin, 225–380.

Material examined: BDLKUFOS-04-002A. Inner reef slope, Agatti Island, Lakshadweep, India (10°52'N, 72°11'E), at 10 m depth. Collected by Abdul Riyas, 25 March 2021. BDLKUFOS-04-002B (Figs. 2a–b): Lagoon area, Kavaratti Island, Lakshadweep, India (10°33'N, 72°38'E), at 5 m depth. Collected by Nayana Narayanankutty, 27 February 2022.

Diagnosis: Colony with distinct, firm stalk and numerous digitate lobes of varying sizes, crowded at the capitulum. Polyps monomorphic; siphonozooids absent. Autozooids are small, with openings visible as minute pits on the lobe surface. Sclerites are predominantly clubs and spindles, showing considerable variation in form and size. Surface layer of lobes contains small to long clubs with wide, ornamented heads; surface layer of stalk with broader clubs and irregularly shaped rods. Interior tissues contain thick, elongated spindles and irregular sclerites.

Distinctive features setting *S. polydactylum* apart from related taxa include the combination of crowded lobes, absence of siphonozooids, and the presence of clubs with wide heads and irregular stalked sclerites.



Fig. 2. *Sclerophyllum polydactylum*. a. *Excitu* photo. b. Sclerites from the areas – A. Clubs and Spindles of the surface layer, top of colony. B. Clubs and Spindles of the surface layer base of the colony. C. Spindles of the interior of the top and base of the colony

Description

Colony form: Colony erect, lobate, with a well-defined stalk supporting a capitulum bearing crowded, digitiform lobes. Lobes vary in size and may be fused at the base. The surface is smooth, with visible polyp apertures as small pits.

Polyps: Polyps are monomorphic; autozooids are small and evenly spread across lobe surfaces. Siphonozooids are absent, a key diagnostic feature of the species.

Sclerites: Surface layer of lobes: small to long clubs (0.05–0.20 mm), with broad heads covered by tubercles; stalk clubs generally broader. Interior of lobes: elongated spindles (up to 0.30 mm), often slightly curved, with prominent tubercles. Surface of stalk: wide clubs and irregular rods (0.10–0.25 mm). Interior of stalk: thick, irregular spindles (up to 0.35 mm). Sclerites show moderate variability in form, with both symmetrical and irregular types.

Colour: Yellowish-green in life; greyish-yellow when preserved.

Habitat: Occurs in shallow lagoonal and reef slope environments, attached to hard substrates or coral rubble, at depths of 3–15 m.

Remarks: Historically classified as *Sinularia*, *Sclerophyllum polydactylum* has been reclassified following recent phylogenomic evidence supporting Sclerophyllum as a distinct monophyletic lineage within Sarcophytidae (McFadden *et al.*, 2022). The Lakshadweep specimens match the diagnostic features of *S. polydactylum*, notably the absence of siphonozooids, crowded lobes, and broad-headed clubs in the surface layer of the stalk.

Distribution: Widely distributed in the tropical Indo-Pacific, including the Red Sea, Persian Gulf, Maldives, Sri Lanka, India (Gulf of Kutch, Andaman and Nicobar), Oman, Iran, Saudi Arabia, Mozambique, Tanzania, Mauritius, Indonesia, Papua New Guinea, Australia, Guam, Chinese Taipei, New Caledonia, and the western Pacific.

Dendronephthya hemprichi (Klunzinger, 1877) (Figs. 3 a-b)

Systematics

Phylum – Cnidaria Verrill, 1865

Subphylum – Anthozoa Ehrenberg, 1834

Class – Octocorallia Haeckel, 1866

Order – Malacalcyonacea McFadden, van Ofwegen & Quattrini, 2022

Family – Nephtheidae Gray, 1862

Genus – *Dendronephthya* Kükenthal, 1905

Type locality: Red Sea

Original name: *Spongodes hemprichi* Klunzinger, 1877

Synonym: *Spongodes hemprichi* Klunzinger, 1877

Taxonomic Reference: Klunzinger, C. B. (1877). The coral animals of the Red Sea. 1: The Alcyonarians and Malacoderms. Gutmannsche Buchhandlung, Berlin. pp. 98.

Material examined: BDLKUFOS-03-002 (Figs. 3a–b), a colony fragment collected from the reef slope area, Kavaratti Island, Lakshadweep, India (10°33'N, 72°38'E), at a depth of 15 m, collected by Nayana Narayanankutty and Minu Thomas on 13 February 2022.

Diagnosis: Colony glomerate with a flat encrusting base and erect, tree-like branches. The stem and branches are thick, covered with dense, hemispherical polyps arranged in compact clusters. Polyps monomorphic, not retractile. Polyp stalks present, with rounded heads bearing supporting bundles of sclerites. Supporting bundle broad, rigid, and projects slightly beyond the polyp head. Sclerites are mostly

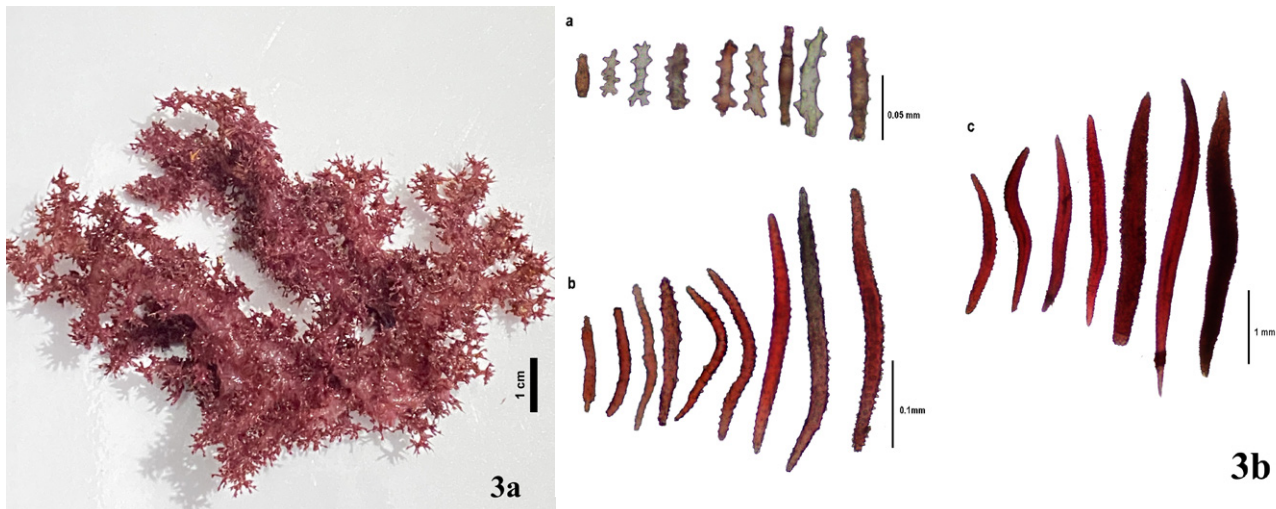


Fig. 3. *Dendronephthya hemprichi* a. Excitu photo. b. Sclerites of the A. Irregular shape from stalks, B. Spindles of polyp, C. Spindles of supporting bundle

spindles, bright red in colour, with long, prominent warts; tentacles contain small, flattened, irregularly shaped sclerites forming a mesh-like pattern.

Distinctive features: compact, bushy colony; red-coloured sclerites; polyps in dense, hemispherical clusters; well-developed supporting bundle projecting beyond polyp head.

Description

Colony form: The colony forms a compact, tree-like mass (glomerate) with a broad, flattened base firmly attached to rock or a hard substrate. Branches are short and thick, arising from the main stalk, and densely covered with hemispherical clusters of polyps.

Polyps: Polyps are monomorphic, non-retractile, with a short stalk and a rounded, inflated head. Each polyp bears a prominent supporting bundle of large, warted spindles that extend slightly beyond the head's surface. Tentacles are armed with minute, irregular, flattened sclerites arranged in transverse rows.

Sclerites: Supporting bundle: large spindles, 0.40–0.60 mm long, red in colour, with prominent warted tubercles. Polyp body: small spindles, 0.15–0.30 mm, slender with warted surfaces. Tentacles: minute, flattened and irregularly shaped sclerites forming a reticulate pattern. Stalk: larger, irregular spindles with coarser warts.

Colour: Colony bright wine red in life; sclerites deep red; in preservation, fades to pale reddish-brown.

Habitat: Attached to hard substrates on reef slopes and

overhangs at depths of 10–20 m; prefers moderate current conditions typical of lagoonal reef slopes.

Remarks: *Dendronephthya hemprichi* is characterised by compact, bushy colonies with dense, hemispherical polyps and red, spindle-shaped sclerites. The species is one of the more recognisable *Dendronephthya* taxa in the Red Sea region, often distinguished by its bright red pigmentation and well-developed supporting bundles. This report is among the first documented occurrences of *D. hemprichi* from the Lakshadweep Archipelago, extending its known distribution westward within the Indian Ocean.

Distribution: Reported from the Red Sea, Saudi Arabia, Egypt, and the Gulf of Aqaba; also recorded from the western Indian Ocean, including the coasts of Sudan and Eritrea, and now from the Lakshadweep Islands, India.

Molecular identification: For the phylogenetic analysis, we included more species to compare intra- and interspecific variation. Phylogenies were constructed using a total of 25 sequences of the *mtMutS* gene, including the NCBI-retrieved sequences (21) and generated sequences (4). The best substitution model for the gene was HKY+G. In general, nodes that were well supported with bootstrap values (>70) (Fig. 4). The *mtMutS* sequences obtained for the species name have been deposited in GenBank under accession numbers PV695213–PV695216.

Based on the phylogenetic tree, two distinct clades of soft corals were recovered in the analysis. The two clades are divided into four subclades at the genus level. The first clade comprises the genus *Dendronephthya* under the family Nephtheidae, and the second clade comprises the family

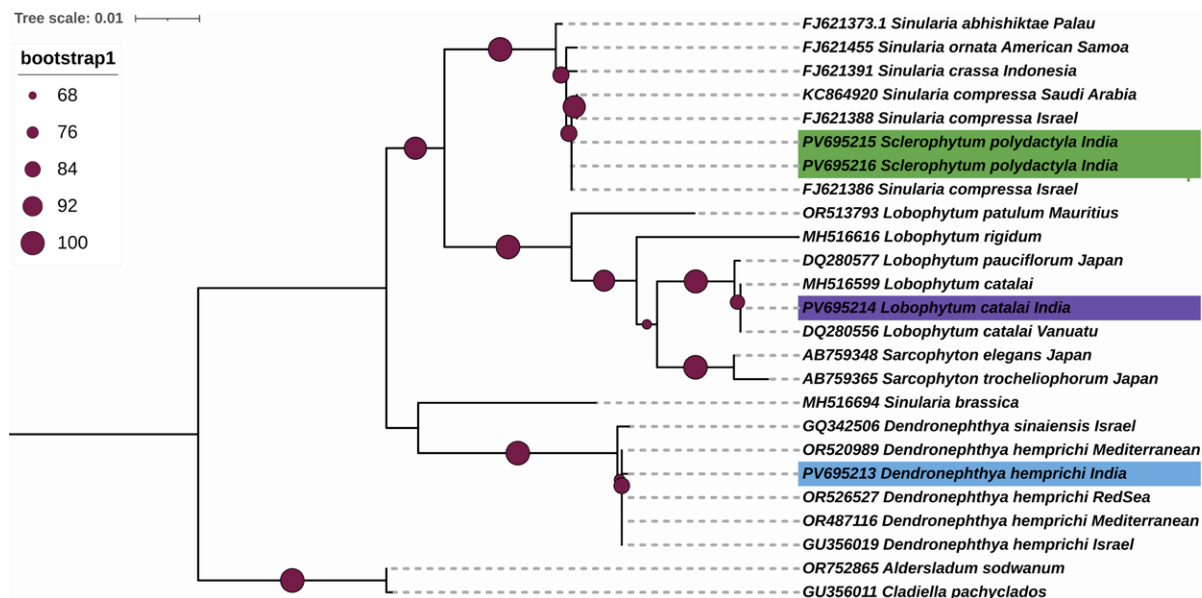


Fig. 4. Maximum likelihood phylogenetic tree of families Sarcophytidae, Sinulariidae, and Nephthidae based on 734 bp of *mtMutS* sequence. Values along the nodes are percentage bootstrap based on 1000 iterations

Sarcophytidae. The Sarcophytidae clade was divided into two subclades; one clade represents the genus *Sclerophyllum*, and the other one represents the genera *Lobophyllum* and *Sarcophyton*. The clade that formed a monophyletic group of the genus *Sclerophyllum* includes the genera *Lobophyllum* and *Sarcophyton*.

In the *Dendronephthya* clade, one species of *Dendronephthya hemprichi* was identified from the Lakshadweep, and *D. hemprichi* from the Mediterranean Sea, the Red Sea, and Israel were placed in a single clade. Still, there was a genetic difference of 0 – 0.2% between them. For the species from the Red Sea and Lakshadweep, the genetic difference was zero. Then, the *Sclerophyllum* clade, with two sequences from the Lakshadweep clade, including *Sclerophyllum polydactylum* from Saudi Arabia and Israel, showed genetic differences of 0–0.1%. The *Lobophyllum* species from Lakshadweep is a clade with *Lobophyllum catalai* from the South China Sea and Vanuatu, with zero genetic differences. The morphological and genetic analysis of our species confirmed it as *Dendronephthya hemprichi*, *Sclerophyllum polydactylum*, and *Lobophyllum catalai*.

The interspecific distance between the four clades mentioned in Table 1: clade 1 was the family Sinulariidae. The genetic distance clearly shows the difference from other clades of the genus, ranging from 7.7 to 10.7%. Clade 2 represents the genus *Dendronephthya* under the family Nephthidae. This clade also shows a high bootstrap value, and the genetic difference between the genera was 0.1-0.5%. The interspecific

genetic distance between the other clades ranged between 7.7 to 11.2%. Clades 3 and 4 represent the family Sarcophytidae, which supports higher bootstrap values. Clade 3 represents the genus *Sclerophyllum* with a genetic distance in the genus of 0.1 to 0.7%. The interspecific genetic distance between the clades was 8.3 to 9.9%. Clade 4 comprises the genera *Lobophyllum* and *Sarcophyton*, with a mean genetic distance between the genera of 0.3-4.1%. The interspecific distance between the clades was 8.3 to 11.2%.

Discussion

Until now, no study has used molecular techniques to identify the soft corals from the Lakshadweep islands. Previous studies in the Lakshadweep archipelago reported 37 species belonging to three families: Cladiellidae, Sarcophytidae, and Nephthidae (van Ofwegen and Vennam, 1991; Alderslade and Shirwaiker, 1991; Vennam and van Ofwegen, 1996; Mary and Sluka, 2014; Narayanankutty *et al.*, 2025). We emphasise that most previous records of soft corals in the Lakshadweep were based on morphological rather than molecular data. Identification of soft corals was difficult due to their complex structure, cryptic species, and incomplete knowledge of their diversity and distribution (McFadden *et al.*, 2014; Fabricius and Alderslade, 2001). Using the octocoral molecular marker *mtMutS* and the morphological characters, we identified a new record of three species, *Dendronephthya hemprichi*, *Lobophyllum catalai* and *Sclerophyllum polydactylum*, from the Lakshadweep Islands. We have not used the other common genetic markers, COI and 28S, because they are unavailable across all species.

A small number of specimens collected from specific reef locations in the Lakshadweep Islands formed the basis for the present investigation. A more comprehensive understanding of species distribution and intraspecific variability could be achieved with increased geographic sampling across more islands and reef ecosystems, even if morphological and genetic data consistently confirm the identification of the taxa under study. The biogeographic and taxonomic interpretations presented here may be enhanced by future research involving larger sample sizes and broader spatial coverage.

The morphological distinctions between the members of the genera *Lobophytum* and *Sarcophyton* in the family Sarcophytidae are less obvious, and their relationship may be paraphyletic. The genus *Sclerophytum* is easily distinguished from the Genus *Lobophytum* and *Sarcophyton* by the presence of siphonozooids (McFadden *et al.*, 2006). These three genera are widespread and conspicuous in shallow waters of the Indo-Pacific region. The *Sclerophytum* was the sister group to *Lobophytum* and *Sarcophyton* (McFadden *et al.*, 2006). The species of *Sclerophytum*, the clade formed by monophyletic intra- and interspecific divergence, are not clearly distinguished (Benayahu *et al.*, 2018; Quattrini *et al.*, 2019). Among various species in the genus *Sclerophytum*, there has been a chance of hybridisation; this difference can be due to divergence in isolation (Quattrini *et al.*, 2019). From the different regions of India, 23 species of *Lobophytum* and 44 species of *Sclerophytum* were reported. In the Lakshadweep, a total of nine *Lobophytum* species and 20 *Sclerophytum* species were identified.

The genus *Dendronephthya* is characterised by a wide range of bright colours and is found in the tropical waters of the Indo-Pacific Ocean. They are azooxanthellate (Fabricius *et al.*, 1995) and occur across a wide range of depths (Fabricius and Alderslade, 2001; Grossowicz and Benayahu, 2012). The species classification of the family Nephtheidae is based on morphology (Cordeiro *et al.*, 2022) compared with other soft corals under the family Sarcophytidae. Nowadays, more insights are obtained from phylogenetic analyses of complete mitochondrial genomes (Williamson *et al.*, 2022). The taxonomy of the genus *Dendronephthya* is quite problematic, and there are no reliable tools for adequately determining species, nor is there any known phylogenetic molecular signal (McFadden *et al.*, 2010). In the Nephtheidae species, variation in morphology complicates identification; it may be due to polymorphism within the species (Haverkort-Yeh *et al.*, 2013).

Mary and Sluka (2014) identified seven types of *Dendronephthya* colonies at the genus level from Minicoy Island, Lakshadweep. A total of 58 species of the Genus *Dendronephthya* were identified across different coral reefs in the Indian region, with most of the records from the Andaman and Nicobar Islands.

The fauna of Lakshadweep overlaps with that of the Red Sea and the Western Indian Ocean. Both regions group with the respective species of *Dendronephthya hemprichi* and *Sclerophytum polydactylum*, and the genetic differences range from 0% to 0.1%.

An important contribution to the understanding of the diversity of soft corals and the functioning of reefs in the central Indian Ocean is the documentation of *Lobophytum catalai*, *Sclerophytum polydactylum*, and *Dendronephthya hemprichi* from Lakshadweep. *Lobophytum* and *Sclerophytum* species are recognised as significant space-occupying octocorals that impact the competitive dynamics and benthic community structure on tropical reefs. They frequently interact with scleractinian corals through allelopathic interactions (Coll *et al.*, 1982; Fabricius and Alderslade, 2001). The soft coral *Dendronephthya* adds to the complexity of the ecosystem and provides structural microhabitats for small invertebrates and reef-associated fauna (Fabricius and Alderslade, 2001). Soft corals influence substratum competition and coral-algal interactions, and certain species are known to generate secondary metabolites that mediate anti-predatory and competitive interactions. Both azooxanthellate and zooxanthellate soft corals engage in plankton capture and nutrient cycling through either photosynthesis (in symbiotic species) or suspension feeding, which enhances reef production. (Coll *et al.*, 1982; Dinesen, 1983; Fabricius and Alderslade, 2001). In terms of biogeography, the presence of these taxa in Lakshadweep broadens their known range in the Indian Ocean and strengthens faunal linkages among the Maldives, the Arabian Sea, and the larger Indo-Pacific reef systems. Their existence highlights the ecological significance of Lakshadweep reefs as part of regional biodiversity and indicates favourable hydrodynamic conditions.

For long-term reef monitoring, baseline biodiversity records are vital, especially in areas susceptible to anthropogenic disturbances, coral bleaching, and climate change. Precise taxonomic documentation enhances the scientific foundation for conservation planning and management strategies across the archipelago and improves species inventories. Soft corals may become increasingly significant in the ecological roles of reefs experiencing shifts in community composition and can greatly contribute to reef structural complexity. Consequently, identifying these species expands Lakshadweep's known biodiversity and offers essential information for future ecological assessments, monitoring efforts, and marine conservation initiatives in the central Indian Ocean.

Conclusions

This study provides the first integrative taxonomic assessment of soft corals from the Lakshadweep Islands using combined morphological and molecular approaches. The documentation

of three new distributional records increases the known diversity of the archipelago and establishes a baseline for future biodiversity monitoring and conservation initiatives. Expanded geographic sampling and multilocus molecular analyses are recommended to further resolve octocoral diversity in the central Indian Ocean.

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Author contributions

Conceptualisation: NN, SS; Methodology: NN, CAR; Data Collection: NN, MT, KKI, CAR; Data Analysis: NN, MT; Writing–Original Draft: NN; Writing–Review and Editing: NN, KKI, SS; Supervision – KKI, SS.

Data availability

The data are available and can be requested from the corresponding author.

Conflicts of interest

The authors declare that they have no conflict of financial or non-financial interests that could have influenced the outcome or interpretation of the results.

Ethical statement

This study was conducted in accordance with the ethical standards and guidelines established by the Committee for Control and Supervision of Experiments on Animals (CPCSEA), Government of India. All procedures involving animals/humans/the environment, etc., were approved by the appropriate institutional review boards or ethics committees of the Department of Science and Technology, Union Territory of Lakshadweep, Kavaratti, Lakshadweep (LD-0400/1/2/2017- S&TUTLKS), as the case may be.

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Reference

Alderslade, P. and P. Shirwaiker. 1991. New species of soft corals (Coelenterata: Octocorallia) from the Laccadive Archipelago. *The Beagle: Records of the Northern Territory Museum of Arts and Science*, 8 (1): 189-233.

Bayer, F. M. 1961. The shallow-water Octocorallia of the West Indian region. *Studies on the Fauna of Curaçao and other Caribbean Islands*, 12 (1): 1-373.

Bayer, F. M. 1973. Colonial organisation in octocorals. In: Boardman RS, Cheetham AH, Oliver WA (eds). *Animal Colonies*. Dowden, Hutchinson and Ross, Stroudsburg, p. 69-94.

Benayahu, Y., L. P. van Ofwegen and C. S. McFadden. 2018. Evaluating the genus *Cespitularia* Milne Edwards & Haime, 1850 with descriptions of new genera of the family Xenidiidae

(Octocorallia, Alcyonacea). *ZooKeys*, 754: 63-101.

Buhl-Mortensen, L. and P. B. Mortensen. 2005. Distribution and diversity of species associated with deep-sea gorgonian corals off Atlantic Canada. *Cold-water corals and ecosystems*, p. 849-879.

Calcinai, B., G. Bavestrello, M. Bertolino, D. Pica, D. Wagner and C. Cerrano. 2013. Sponges associated with octocorals in the Indo-Pacific, with the description of four new species. *Zootaxa*, 3617 (1): 1-61.

Coll, J. C., S. La Barre, P. W. Sammarco, W. T. Williams and G. J. Bakus. 1982. Chemical defences in soft corals (Coelenterata: Octocorallia) of the Great Barrier Reef: a study of comparative toxicities. *Mar. Ecol. Progr. Ser.*, 8: 271-278.

Cordeiro, R. T. S.; A. N. Carpinelli, R. B. Francini-Filho, B. de Moura Neves, C. D. Pérez, U. de Oliveira, P. Sumida, H. Maranhão, L. H. U. Monteiro, P. Carneiro and M. V. Kitahara. 2022. Neospongodes Atlantica, a Potential Case of an Early Biological Introduction in the Southwestern Atlantic. *Peer J*. 10: e14347.

Dinesen, Z. D. 1983. Patterns in the distribution of soft corals across the central Great Barrier Reef. *Coral Reefs*, 1: 229-236.

Fabricius, K. E. and P. Alderslade. 2001. *Soft corals and sea fans: a comprehensive guide to the tropical shallow water genera of the central-west Pacific, the Indian Ocean and the Red Sea*. Townsville, Queensland: Australian Institute of Marine Science, viii + 264 pp

Fabricius, K. E., A. Genin and Y. Benayahu. 1995. Flow-dependent herbivory and growth in zooxanthellae-free soft corals. *Limnology and Oceanography*, 40 (7): 1290-1301.

France, S. C. and L. L. Hoover. 2002. DNA sequences of the mitochondrial COI gene have low levels of divergence among deep-sea octocorals (Cnidaria: Anthozoa). *Hydrobiologia*, 471: 149-155.

Gaikwad, S., K. De, M. Nanajkar and S. Sautya. 2021. Octocoral colonies as spawning ground for the cuttlefish *Sepiella inermis* (Cephalopoda: Sepiidae). *Symbiosis*, 85 (1): 115-121.

Gardiner, J. S. (Ed.). 1903. *The Fauna and Geography of the Maldive and Laccadive Archipelagoes: Being the Account of the Work Carried on and of the Collections Made by an Expedition During the Years 1899 and 1900 (Vol. 1)*. University Press.

Grossowicz, M. and Y. Benayahu. 2012. Differential morphological features of two Dendronephthya soft coral species suggest differences in feeding niches. *Mar. Biodivers.*, 42: 65-72.

Hall, T. A. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. In *Nucleic acids symposium series*, 41: 95-98.

Haverkort-Yeh, R. D., C. S. McFadden, Y. Benayahu, M. Berumen, A. Halász and R. J. Toonen. 2013. A taxonomic survey of Saudi Arabian Red Sea octocorals (Cnidaria: Alcyonacea). *Mar. Biodivers.*, 43: 279-291.

Hickson, S. J. 1903. The Alcyonaria of the Maldives Part I. The genera *Xenia*, *Telesto*, *Spongodes*, *Nephtya*, *Paraspongodes*, *Chirone-phthya*, *Siphonogorgia*, *Solenocaulon*, and *Melitodes*. *The Fauna and Geography of the Maldive and Laccadive Archipelagoes*, 2, pls2-34.ies of the Gulf of Mannar, 3 (19): 247-268.

Hickson, S. J. 1905. The Alcyonaria of the Maldives. Part III. The Families Muricidae, Gorgonellidae, Melitodidae and the Genera Pennatula and Eunephtya. In: Gardiner, J.S. (ed.). *The Fauna and Geography of the Maldive and Laccadive Archipelagoes*. Being the Account of the Work carried on and of the Collections made by an Expedition during the years 1899 and 1900. Cambridge University Press, London, p. 807-826

Jayasree, V., K. L. Bhat and A. H. Parulekar. 1996. Occurrence and distribution of soft corals (Octocorallia: Alcyonacea) from the Andaman and Nicobar Islands. *J. Bombay Nat. Hist. Soc.*, 93: 202-209.

Kükenthal, W. 1905. Versuch einer Revision der Alcyonarien. II. Die Familie der Nephthyiden. 2. Teil. Die Gattungen Dendronephthya n.g. und Stereonephthya n.g. *Zool. Jahrb.*, 21: 511-522.

Kumar, S., G. Stecher, M. Li, C. Knyaz and K. Tamura. 2018. MEGA X: molecular evolutionary genetics analysis across computing platforms. *Mol. Biol. Evol.*, 35 (6): 1547-1549.

Lepard, A. B. 2003. *Analysis of variation in the mitochondrial encoded msh1 in the genus Leptogorgia (Cnidaria: Octocorallia) and implications for population and systematics studies* (Doctoral dissertation, University of Charleston, South Carolina). USA, ~150 pp.

Letunic, I. and P. Bork. 2021. Interactive Tree Of Life (iTOL) v5: an online tool for phylogenetic tree display and annotation. *Nucleic Acids Res.*, 49 (W1): W293-W296.

Ly-Trong, N., S. Naser-Khdour, R. Lanfear and B. Q. Minh. 2022. AliSim: a fast and versatile phylogenetic sequence simulator for the genomic era. *Mol. Biol. Evol.*, 39 (5): msac092.

Mallik, T. K. 2017. Coral atolls of Lakshadweep. Arabian Sea, Indian Ocean, MOJ Ecology Environmental Sciences, 2 (2): 68-83.

Mary, A. G. and R. D. Sluka. 2014. Biodiversity and distribution of octocorals of Minicoy Atoll, Lakshadweep. *Atoll Research Bulletin*, 602: 1-17.

McFadden, C. S., L. P. van Ofwegen and A. M. Quattrini. 2022. Revisionary systematics of Octocorallia (Cnidaria: Anthozoa) guided by phylogenomics. *Bull. Soc. Syst. Biol.*, 1 (3): 1-79.

McFadden, C. S., Y. Benayahu, E. Pante, J. N. Thoma, P. A. Nevarez and C. S. France. 2011. Limitations of mitochondrial gene barcoding in Octocorallia. *Mol. Ecol. Resour.*, 11 (1): 19-31.

McFadden, C. S., S. C. France, J. A. Sánchez and P. Alderslade. 2006. A molecular phylogenetic analysis of the Octocorallia (Cnidaria: Anthozoa) based on mitochondrial protein-coding sequences. *Mol. Phylogenet. Evol.*, 41 (3): 513-527.

McFadden, C. S., R. Haverkort-Yeh, A. M. Reynolds, A. Halász, A. M. Quattrini, Z. H. Forsman, Y. Benayahu and R. J. Toonen. 2017. Species boundaries in the absence of morphological, ecological or geographical differentiation in the Red Sea octocoral genus *Ovabunda* (Alcyonacea: Xenidiidae). *Mol. Phylogenet. Evol.*, 112: 174-184.

McFadden, C. S., A. M. Reynolds and M. P. Janes. 2014. DNA barcoding of xeniid soft corals

- (Octocorallia: Alcyonacea: Xenidiidae) from Indonesia: species richness and phylogenetic relationships. *Syst. Biodivers.*, 12 (2): 247-257.
- McFadden, C. S., J. A. Sánchez and S. C. France. 2010. Molecular phylogenetic insights into the evolution of Octocorallia: a review. *Integr. Comp. Biol.*, 50 (3): 389-410.
- Nayana Narayanankutty, Minu Thomas, K. K. Idrees Babu and S. Sureshkumar. 2025. An Assessment of soft coral (Anthozoa: Octocorallia; Malacalcyonacea) species diversity and distribution from the Kavaratti atoll, Lakshadweep archipelago, Central Indian Ocean. *J. Mar. Atmos. Res.*, 4 (2): 1-8.
- Pratt, E. M. 1903. The Alcyonaria of the Maldives. Part II. The genera Sarcophytum, Lobophytum, Sclerophytum and Alcyonium. *Fauna Geogr. Maldive Laccadive Arch.*, 2: 503-509.
- Pratt, E. M. 1905. Report on some Alcyoniidae collected by Prof. Herdman at Ceylon in 1902. Herdman, WA and Honell, J., Report to the Government of Ceylon on the pearl and Oyster fisheries of the Gulf of Mannar, 3 (19): 247-268
- Quattrini, A. M., T. Wu, K. Soong, M. S. Jeng, Y. Benayahu and C. S. McFadden. 2019. A next-generation approach to species delimitation reveals the role of hybridisation in a cryptic species complex of corals. *BMC Evol. Biol.*, 19: 1-19.
- Rao, D. V. and D. Kamla. 2003. Studies on the soft corals (Octocorallia: Alcyonacea) of Andaman Islands, Bay of Bengal. *Rec. Zool. Surv. India*, 206: 1-99.
- Sánchez, J. A., C. S. McFadden, C. S. France and H. R. Lasker. 2003. Molecular phylogenetic analyses of shallow-water Caribbean octocorals. *Mar. Biol.*, 142: 975-987.
- Shahbazi, S., N. Sakhaei, H. Zolgharnein and C. S. McFadden. S. 2021. A molecular systematic survey of the Iranian Persian Gulf octocorals (Cnidaria: Alcyonacea). *Mar. Biodivers.*, 51: 1-18.
- Stella, J. S., M. S. Pratchett, P. A. Hutchings and G. P. Jones. 2011. Diversity, importance and vulnerability of coral-associated invertebrates. *Oceanogr. Mar. Biol.*, 49: 43-116.
- Thomson, J. A. and J. J. Simpson. 1909. An account of the alcyonarians collected by the Royal Indian Marine Survey Ship 'Investigator' in the Indian Ocean. II. The alcyonarians of the littoral area. Trustees of the Indian Museum, Calcutta. 2: 1-319.
- Thomson, J. A. and W. D. Henderson. 1906. An account of the alcyonarians collected by the Royal Indian Marine survey ship 'Investigator' in the Indian Ocean. I. The alcyonarians of the deep sea. Trustees of the Indian Museum, University of Aberdeen. p. 1-128.
- Tixier-Durivault, A. 1958. Revision de la famille des Alcyoniidae: les genres Sarcophytum et Lobophytum. *Zool. Verh.*, 36 (1): 1-179.
- van Ofwegen, L. and J. E. Vennam. 1991. Notes on Octocorallia from the Laccadives (SW India). *Zool. Meded.*, 65 (9): 143-154.
- Vennam, J. and L. van Ofwegen. 1996. Soft corals (Coelenterata: Octocorallia: Alcyonacea) from the Laccadives (SW India), with a re-examination of *Sinularia gravis* Tixier-Durivault, 1970. *Zool. Meded.*, 70 (29): 437-454.
- Williamson, J. E., M. R. Gillings, R. J. Nevatte, D. Harasti, V. Raoult, T. M. Ghaly and T. F. Gaston. 2022. Genetic differentiation in the threatened soft coral *Dendronephthya australis* in temperate eastern Australia. *Austral Ecol.*, 47 (4): 804- 817.