



The genus *Lithophyllum* in the north-western Indian Ocean, with description of *L. yemenense* sp. nov., *L. socotraense* sp. nov., *L. subplicatum* comb. et stat. nov., and the resumed *L. affine*, *L. kaiseri*, and *L. subreduncum* (Rhodophyta, Corallinales)

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Abstract

Based on literature, the genus *Lithophyllum* was represented in the whole Indian Ocean by 14 taxa, mostly in need of revision in a modern context. Molecular analyses integrated with morpho-anatomical comparisons between the recently revised type material of *Lithophyllum kotschyanum* Unger, and the related infraspecific taxa, lead to a resumption of *L. affine*, *L. kaiseri*, and *L. subreduncum*, and the description of *L. socotraense* sp. nov., *L. yemenense* sp. nov., and *L. subplicatum* comb. et stat. nov. Detailed accounts are provided for each species, including keys, along with information on synonymy, examined collections, distribution, habitat as well as sequence data of the 5' end of the LSU from the type specimens. The anatomical features of the tetrasporangial conceptacle that were considered collectively diagnostic for species identification are: the mean diameter of the tetrasporangial conceptacles, the length of the pore-canal in the tetrasporangial conceptacles (with the number of cells in roof filaments), the occurrence of a depression at the top of the conceptacle roof in relation to the pore opening, and the number of cells from the floor of the tetrasporangial conceptacle chamber to the thallus surface. This study provides evidence of a previously unsuspected diversity within the Red Sea and NW Indian Ocean species of *Lithophyllum*.

Key words: biodiversity, coralline algae, Foslie, Heydrich, Indo-Pacific Ocean, Red Sea, Arabian Sea, Persian Gulf, integrated taxonomy, Lithophylloideae, TRH

Introduction

The coralline flora of the Indian Ocean is insufficiently known. A survey of the literature available for the area revealed that the subfamily Lithophylloideae was represented by 19 species and infraspecific taxa, and that 8 of them were in need of a revision in a modern taxonomic context. In particular, only *Lithophyllum kotschyanum* Unger, and its infraspecific taxa *L. kotschyanum* forma *affine* and *L. kotschyanum* forma *subplicatum*, together with *L. orbiculatum* and *L. okamurae*, were listed from the NW Indian Ocean (including Red Sea, Gulf of Aden, Arabian Sea, and Persian Gulf, in the boreal emisphère, and toward the east to include the western Indian coasts; Table 1).

In the framework of a large-scale investigation on Red Sea and Indian Ocean corallines, we collected some common *Lithophyllum* plants, bearing abundant trichocytes (Basso *et al.* 2014). In order to correctly identify the species, we provided morphological and molecular data (the 5' end of the nuclear LSU) to compare the recently revised type material of *L. kotschyanum* Unger, and the related infraspecific taxa, namely *L. kotschyanum* forma *affine*, *L. kotschyanum* forma *madagascarensis*, *L. kotschyanum* forma *subplicatum* and *L. kotschyanum* forma *subreduncum*, housed at TRH (abbreviations following Holmgren continuously updated). The objective of this study is to use both morphological and molecular data to assess species delineation within this taxon. This study contributes to the discussion on coralline biodiversity in the north-western Indian Ocean and Red Sea, focusing on the genus *Lithophyllum*.

TABLE 1. *Lithophyllum* species and infraspecific taxa from the Indian Ocean, after Silva *et al.* 1996; Womersley 1996; Maneveldt *et al.* 2008; Basso *et al.* 2014. An asterisk before the binomial indicates those species that should belong to the genus *Titanoderma*, based on Bailey (1999), and Schneider & Wynne (2007). In the column of the Indian Ocean distribution, the type locality is italicized. Unchecked reports of the *Lithophyllum* species discussed here are in square brackets. Note that only *L. kotschyanum*, its infraspecific taxa *L. kotschyanum* f. *affine* and *L. kotschyanum* f. *subplicatum*, *L. orbiculatum* and *L. okamurae* were reported from the NW Indian Ocean before this study.

Indian Ocean <i>Lithophyllum</i> species	Indian Ocean distribution	modern account
<i>L. acrocamptum</i> Heydrich 1902	Kenya, <i>Madagascar</i> , Mauritius, S. Africa, Sri Lanka	Chamberlain 1996 (as <i>L. incrassatum</i>)
<i>L. bamleri</i> (Heydrich) Heydrich 1897	Comoro Islands, Sri Lanka, Indonesia (Timor)	
* <i>L. chamberlainianum</i> Woelkerling & Campbell 1992	<i>Australia</i> , Tasmania	Woelkerling & Campbell 1992
* <i>L. corallinae</i> (Crouan & Crouan) Heydrich 1897	<i>Australia</i> , Tasmania	Woelkerling & Campbell 1992
<i>L. incrustans</i> Philippi 1837	Mauritius, Reunion, S. Africa	Chamberlain 1996
* <i>L. irvineanum</i> Woelkerling & Campbell 1992	<i>Australia</i>	Woelkerling & Campbell 1992
<i>L. johansenii</i> Woelkerling & Campbell 1992	<i>Australia</i>	Woelkerling & Campbell 1992
<i>L. kotschyanum</i> Unger 1858	<i>Persian Gulf</i> [Djibouti, Laccadive Islands, Maldives, Sri Lanka, Comoro Islands, Seychelles, Madagascar, Mauritius, Reunion, Rodriguez, Diego Garcia Atoll, Cocos Islands, Kenya, Indonesia]	Basso <i>et al.</i> 2014
<i>L. kotschyanum</i> f. <i>affine</i> (Foslie) Foslie 1909	<i>Massawa</i> , <i>Red Sea</i> [Seychelles]	this paper: <i>Lithophyllum affine</i> (Foslie) Foslie
<i>L. kotschyanum</i> f. <i>subplicatum</i> (Foslie) Silva 1996	[Cocos Islands, Comoro Islands, Diego Garcia Atoll, Laccadive Islands, Maldives, Madagascar, Mauritius, Mozambique, Réunion, Seychelles]	this paper: <i>Lithophyllum subplicatum</i> (Foslie) <i>comb. et stat. nov.</i>
<i>L. okamurae</i> Foslie 1900	Cocos Islands, India, Indonesia (Timor, Semaui)	
<i>L. orbiculatum</i> (Foslie) Foslie 1900	India	Chamberlain & Irvine 1994
<i>L. pallescens</i> (Foslie) Foslie 1900	Mauritius	
<i>L. pinguinense</i> Heydrich 1901	St. Paul Island	
* <i>L. prototypum</i> (Foslie) Foslie 1905	Australia, Comoro Islands, Mauritius, Seychelles	Woelkerling & Campbell 1992
<i>L. punctatum</i> Foslie 1906	Sri Lanka	
* <i>L. pustulatum</i> (Lamouroux) Foslie 1904	<i>Australia</i> , Tasmania	Woelkerling & Campbell 1992
<i>L. pygmaeum</i> (Heydrich) Heydrich 1897	Kenya, Madagascar, Mauritius, Seychelles, Comoro Islands, Indonesia	
<i>L. stictaeforme</i> (Areschoug) Hauck 1877	<i>Australia</i>	Womersley 1996 (as <i>L. frondosum</i>)

Material and Methods

Plants were collected at several localities along the Yemeni coast of the Southern Red Sea, Gulf of Aden, Arabian Sea and Persian Gulf. Corallines were air dried prior transport to the Milan facilities and the selected type material was deposited in TRH.

The type material of *L. kotschyanum* Unger (A20-1267; A20-1272) currently housed in TRH was examined in a modern context and revised in a previous paper (Basso *et al.* 2014). Additionally, other geographically relevant specimens of type material were obtained from TRH including *Lithophyllum kotschyanum* forma *madagascarensis* (Heydrich) Foslie (A20-1283), *L. kotschyanum* forma *subplicatum* (Foslie) Silva (A20-1286), *Lithophyllum kotschyanum* forma *subreduncum* Foslie (A20-1290; A20-1291), *Lithophyllum kotschyanum* forma *affine* (Foslie)

Foslie (A20-1279), and *Lithophyllum kaiseri* (Heydrich) Heydrich (A20-1264), (further details on TRH collections are provided by Woelkerling *et al.* 2005).

Air-dried specimens for scanning electron microscopy (SEM) were fractured and mounted on aluminium stubs with silver glue. The samples were gold coated and examined in a SEM Vega Tescan TS5136XM at 20 kV at the Milano-Bicocca facilities.

For light microscopy (LM), pieces of thallus were decalcified with Tellyesniczky's solution (Bressan 1974) for 12–48 h, washed in distilled water, dehydrated through a graded ethanol series and embedded in methacrylate resin (Technovit 7100, Heraeus Kulzer, Wehrheim, Germany). Preparation of histological slides of serial sections follows Basso & Rodondi (2006). Permanent slides for LM were examined and photographed with a Leica DMRB photomicroscope.

The type material of *L. madagascarens* is a very small fragment that would have been completely destroyed for any analysis. Therefore no investigation was performed on *L. madagascarens*, following the recommendations of the TRH curator.

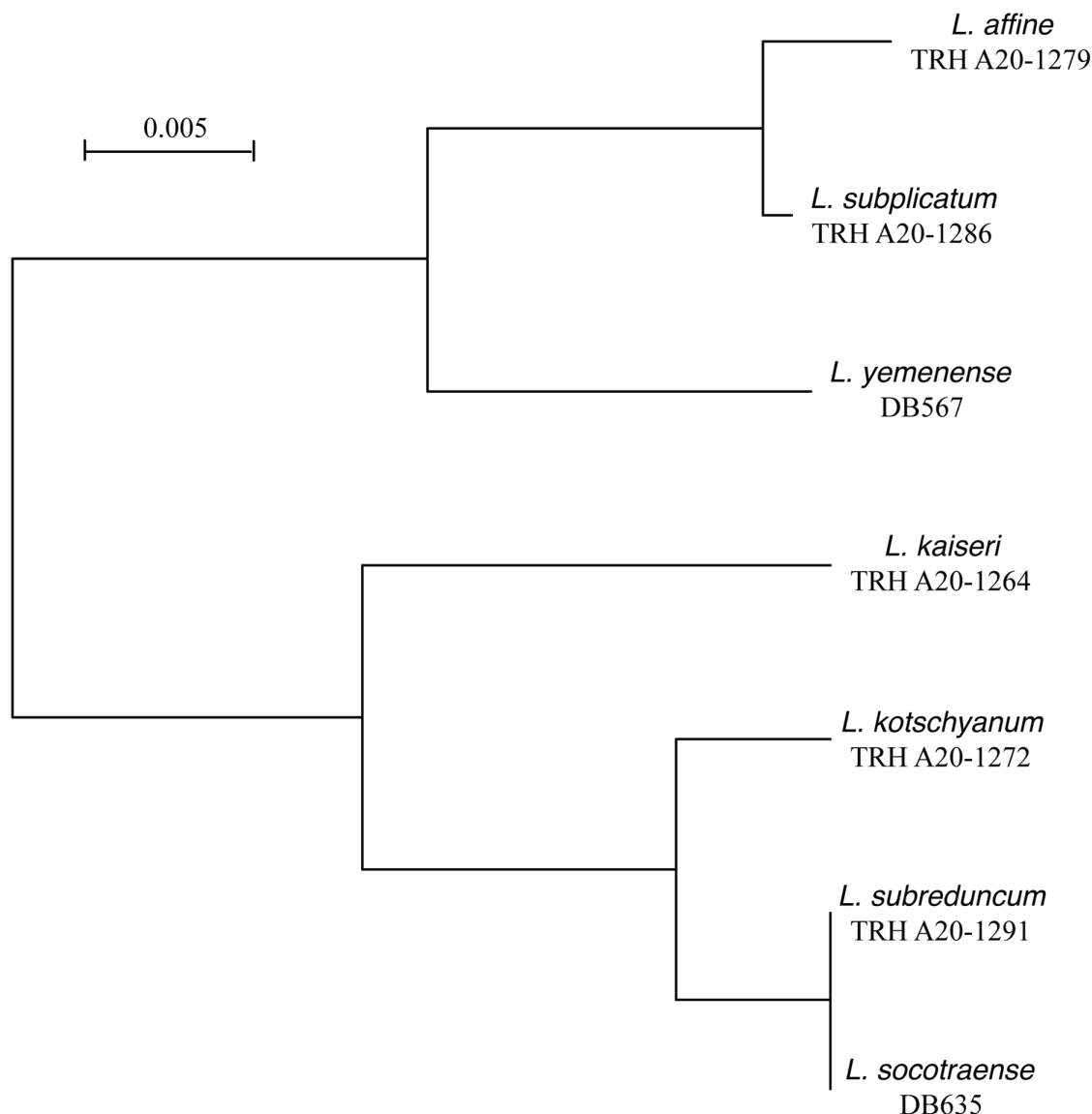


FIGURE 1. Distance analysis (Neighbor joining) performed on the 5' end of the nuclear LSU of the seven type specimens considered in this study.

Anatomical terminology follows Adey & Adey (1973) and Woelkerling (1988), and that for growth forms follows Woelkerling *et al.* (1993). Conceptacle measurements follow the system of Adey & Adey (1973) and were made directly from the SEM or under LM using a calibrated eyepiece micrometer. Cell measurements follow Basso *et al.* (2004).

For molecular analyses, specimens were sampled under the dissecting scope using a drill. Total DNA was extracted, using a DNeasy Blood & Tissue Kit (QIAGEN, Hilden, Germany), according to the manufacturer's instructions and negative controls with no tissue were included. Two reverse primers were designed to amplify with the forward primer T01N (Harper & Saunders 2001), small fragments of ca. 200 and 300bp of the 5' end of the nuclear LSU (28S): TR191 (5'CCACGGTACRCAWTTCCATG3') and TR273 (5'TCTCAAGCTACCCGACTC3') respectively. Purification and sequencing reactions were performed by Macrogen. Forward and reverse electropherograms were edited and assembled with the software Codoncode (Dedham, MA). Distance analysis was conducted on the LSU sequences from the type specimens to assess their divergence and Maximum likelihood analysis was conducted on a selection of taxa from GenBank and on the two recently collected type specimens to assess their phylogenetic relationship.

Results

Both reverse primers successfully amplified the 5 type specimens from TRH as well as 2 specimens of more recent collections. Distance analysis (Fig 1) revealed that divergences ranged from 0 between the pair A20-1291/ DB635 to 5.1 % between A20-1279 and A20-1264, A20-1272, A20-1291 and DB635.

Lithophyllum affine (Foslie) Foslie (1898: 9)

Figures 2–3; Table 2

BASIONYM: *Lithothamnion affine* Foslie (1897: 13).

NOMENCLATURAL SYNONYM: *Lithothamnion affine* f. *complanata* Foslie; *Lithothamnion affine* f. *affine* Foslie; *Lithophyllum kotschyianum* forma *affinis* (Foslie) Foslie.

LECTOTYPE: TRH, A20-1279 (Trondheim, Norway) (Fig. 2), (Woelkerling 1993: 21).

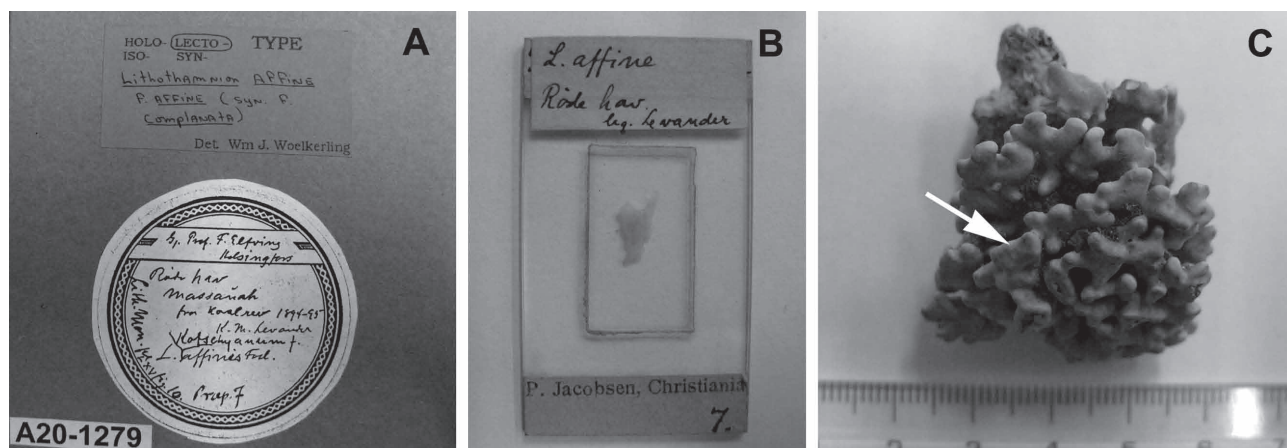


FIGURE 2. The lectotype of *Lithophyllum affine* (Foslie) Foslie in TRH. A) Box A20-1279 in TRH. B) Thin section 7, part of the lectotype A20-1279. C) The specimen A20-1279 in TRH, lectotype of *L. affine*. Note confluent and fused protuberances (arrow).

ETYMOLOGY: the specific epithet refers to the similarity (=affinity) to *L. kotschyianum*.

ILLUSTRATIONS OF TYPE MATERIAL: Printz, 1929: pl. 65, fig. 10.

TYPE LOCALITY: Massawa, Eritrea, Red Sea, collected by Levander (Woelkerling 1993; Woelkerling *et al.* 2005: 172–173).

MATERIAL EXAMINED: Red Sea: Eritrea, Massawa, from coral reef, lectotype of *L. affine* f. *affine* (leg. Levander: TRH, A20-1279).

HABITAT AND PHENOLOGY: plants attached to corals, in shallow water (depth of collection unknown).

GEOGRAPHIC DISTRIBUTION: *Lithophyllum affine* occurs in the southern Red Sea (Massawa, Eritrea). The occurrence of *L. affine* outside this area is unknown.

HABIT AND VEGETATIVE STRUCTURE: The lectotype of *Lithothamnion affine* (TRH A20-1279) is a plant originally attached to a coral, non-endophytic, with fruticose growth-form (Fig. 2C). The protuberances have a smooth surface, are mostly compressed, branched, up to about 10 mm long. The branches of adjacent protuberances are fused at their tips, forming some superposed, complanate juts (Fig. 2C). Plant structure pseudoparenchymatous. Basal or ventral

layer (= hypothallium) not observed. Peripheral region (= perithallium) composed of cell filaments curving outwards towards the thallus surface, 12–33 μm long and 10–15 μm in diameter (Fig. 3A–C). Cells of adjacent filaments joined by secondary pit connections, cell fusions not observed (Fig. 3B–C). Palisade cells not observed. Single trichocytes 37–50 μm long and about 12–14 μm in diameter occurring in the perithallium and at the thallus surface (Fig. 3B). Single epithallial cells flattened, about 10–13 μm in diameter and 2–3 μm long (Fig. 3C; Tab. 2).

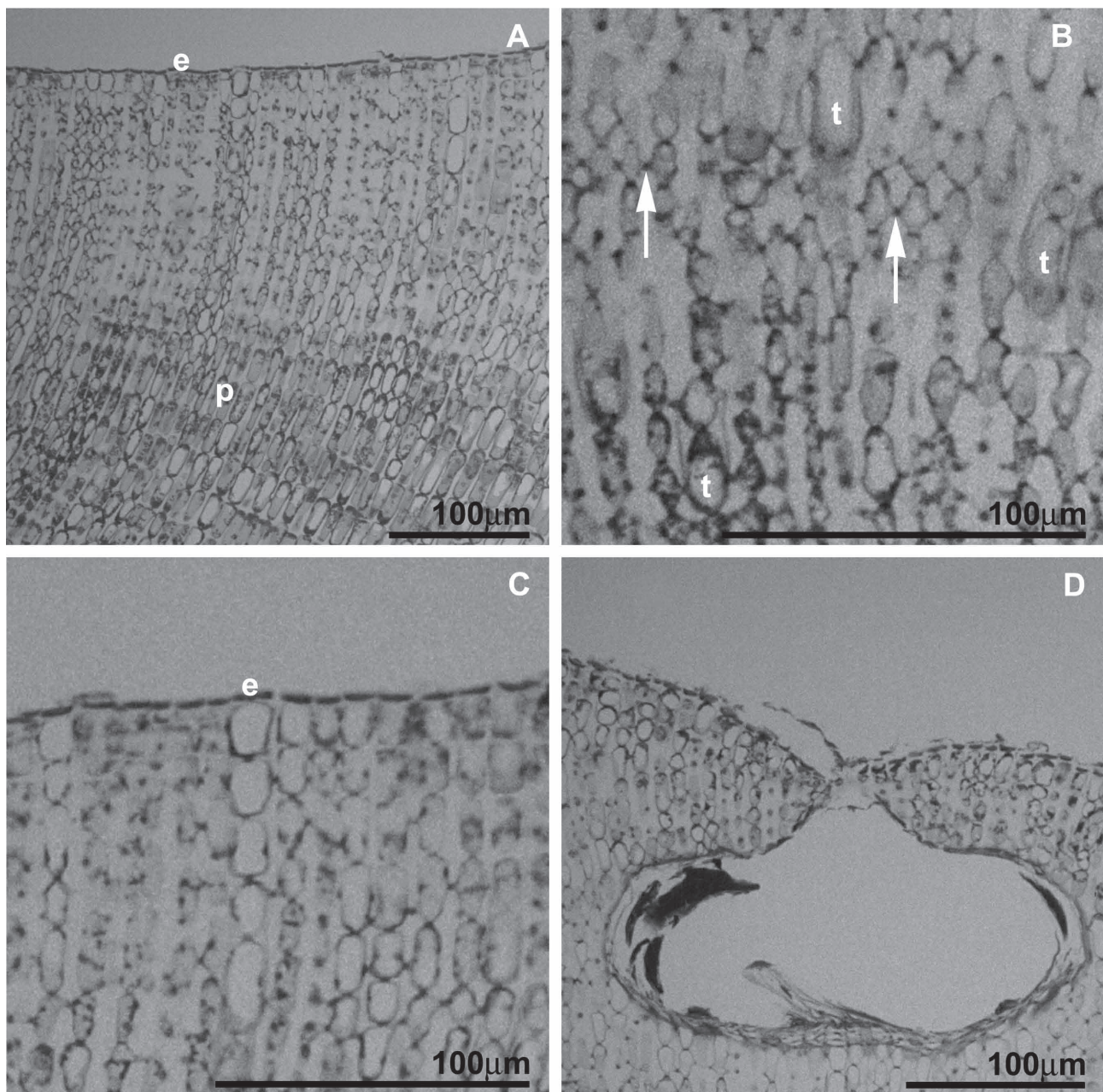


FIGURE 3. Microscopical anatomy of *L. affine*. A) Perithallial cell filaments (p) and terminal epithallial cells (e) of the lectotype of *L. affine*, slide A20-1279_12 of a decalcified fragment. B) Detail of perithallial cell filaments with secondary pit-connections (arrows) and trichocytes (t) in *L. affine*, slide A20-1279_12. C) Flattened epithallial cells (e), slide A20-1279_12. D) A tetrasporangial conceptacle in the lectotype A20-1279. Note the pore opening in a depression of the conceptacle chamber roof. Slide A20-1279_12.

REPRODUCTION: Uniporate tetrasporangial conceptacles slightly protruding or flush over the surrounding thallus surface, with aperture of the pore-canal in the centre of a depression. Chamber 250–280 μm in diameter and 110–130 μm high, with a pore-canal 60–70 μm long. Floor of the conceptacle chamber almost flat. The conceptacle chamber floor is 11 cells below the thallus surface, including the terminal epithallial cell. Roof filaments 5–6 cells long, including the terminal epithallial cell (Fig. 3D; Tab. 2). Gametangial and carposporangial conceptacles unknown.

REPRESENTATIVE SEQUENCE: KP696791 (LSU).

TABLE 2. Comparison of features and biometry of *Lithophyllum kotschyanum* Unger, *Lithophyllum affine* (Foslie) Foslie, and *Lithophyllum kaiseri* (Heydrich) Heydrich, from type material (TRH). Measurements in μm , given as mean (standard deviation). L=length; D=diameter; H=height. Asterisk on diagnostic characters.

	<i>L. kotschyanum</i> holotype	<i>L. affine</i> lectotype	<i>L. kaiseri</i> lectotype
Distribution	Persian Gulf	Massawa, S Red Sea	El Tor, N Red Sea
Life habit	non-geniculate, habit unknown	non-geniculate, growing on corals	non-geniculate, habit unknown
Growth-form	fruticose	fruticose	fruticose
Thallus organization	dimerous	not observed	dimerous
*Hypothallial cells L x D	10 (2) x 12.5 (2.9)	not observed	8.1(1.9) x 11.4 (3.5)
Perithallium zonation	yes	yes	yes
Perithallial cells L x D	19.4 (7.5) x 8.9 (1.1)	22 (9) x 12.5 (1.4)	22.5 (6.3) x 11.6 (1.9)
Epithallial cells shape	flattened	flattened	flattened
L x D	2.5 x 11 (1.4)	2.5 x 11.3 (1.8)	2.5 (0) x 11.7 (1.4)
Trichocytes	yes	yes	yes
Asexual concept. chamber	uniporate	uniporate	uniporate
*D x H	351 (21.4) x 131 (18.6)	265 (21.2) x 120 (14.1)	310 (56.6) x 105 (28.3)
*elevation	slightly protruding	slightly protruding	flush
*pore position	flush	in a depression	flush
*pore canal length	75 (10.3)	65 (7.1)	55 (n.a.)
becoming buried	yes	yes	yes
*no. of cells from floor	16–17	11	11
columella	yes	inconspicuous	no
*cells in roof filaments	7	5–6	4–5

Lithophyllum kaiseri (Heydrich) Heydrich (1897a: 412)

Figures 4–5; Table 2

BASIONYM: *Lithothamnion kaiseri* Heydrich 1897b: 64, pl. III, figs 8, 12, 13.

LECTOTYPE: TRH, A20-1264 (Fig. 4), exclusively the small specimen in the box of the syntype of Heydrich no. 60, including thin section 6, is designated here as lectotype of *Lithophyllum kaiseri* (arrow on right in Fig. 4D). The larger specimen and the thin section 1150 are here excluded from the type material of *Lithophyllum kaiseri*. Details of the nomenclatural history are reported by Woelkerling 1993: 132; Woelkerling *et al.* 2005: 170.

ETYMOLOGY: the specific epithet is dedicated to the collector, Dr. A. Kaiser (Heydrich 1897b; Woelkerling 1993: 132; Woelkerling *et al.* 2005: 170).

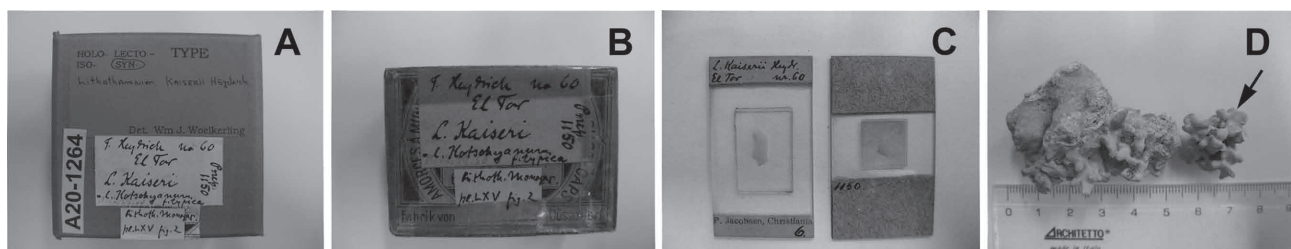


FIGURE 4. The syntype collection of *Lithophyllum kaiseri* Heydrich in TRH. A) Box A20-1264 in TRH. B) The carton box containing the syntype collection of *L. kaiseri*. C) Thin sections 6 and 1150, part of the collection A20-1264. Only slide 6 is here retained as part of the lectotype, because of the uncertain origin of slide 1150. D) The two specimens A20-1264 in TRH. The small plant (arrow) is here selected as lectotype of *L. kaiseri*. The larger specimen is excluded because of its uncertain origin.

ILLUSTRATIONS OF TYPE MATERIAL: Printz 1929: pl. 65, fig. 2.

TYPE LOCALITY: El Tor, Sinai Peninsula (Egypt), from corals.

MATERIAL EXAMINED: Red Sea: Sinai Peninsula, El Tor, syntype of *Lithophyllum kaiseri* (Heydrich) Heydrich (leg. Kaiser: TRH, A20-1264).

GEOGRAPHIC DISTRIBUTION: *L. kaiseri* is distributed in the Red Sea. The occurrence of *L. kaiseri* outside this area is unknown.

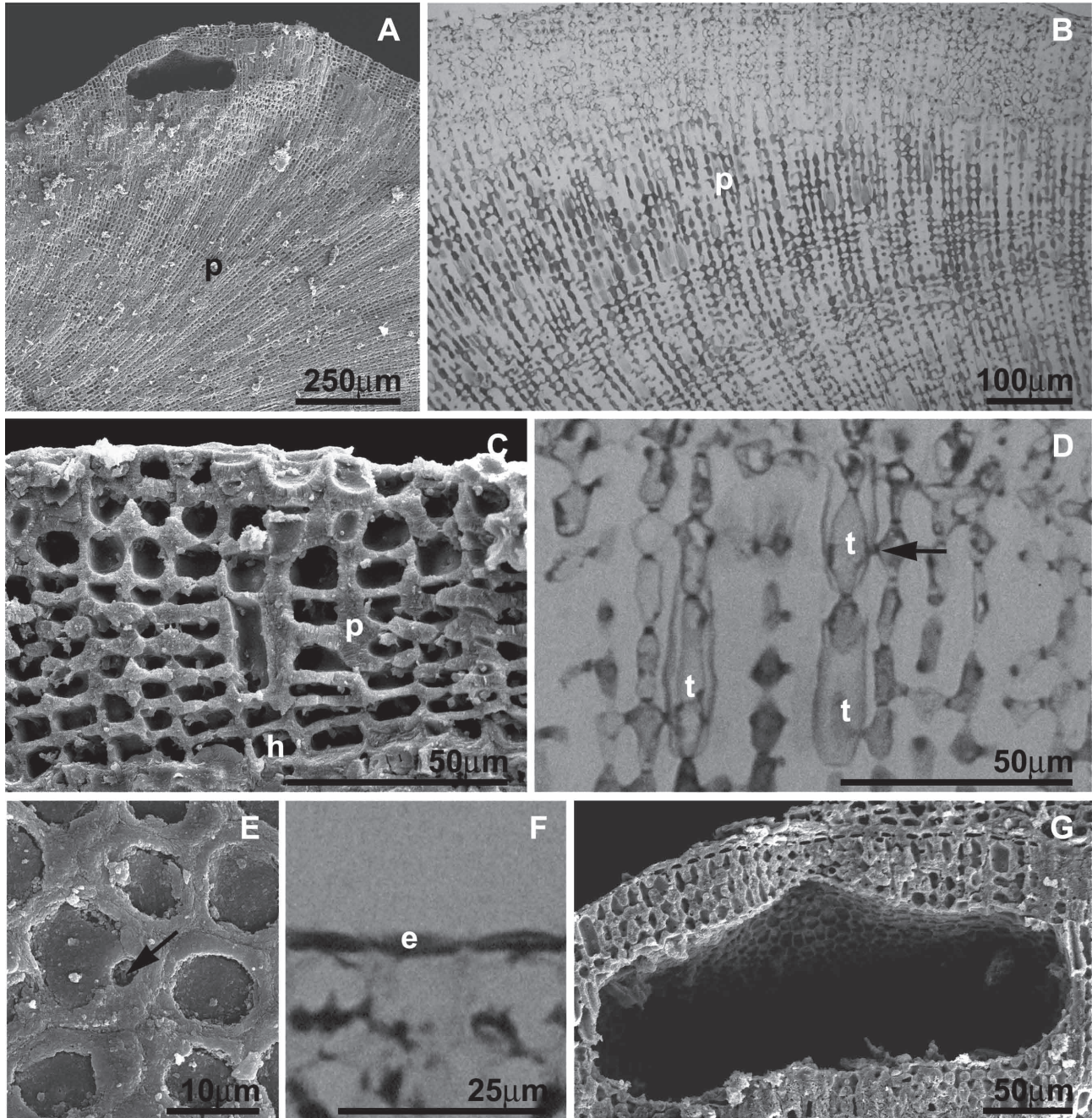


FIGURE 5. Microscopical anatomy of the small plant (Fig. 4D, arrow) lectotype A20-1264 of *L. kaiseri* in TRH. A) Perithallial cell filaments (p) and an empty uniporate conceptacle, SEM stub 08112012b12. Note trichocytes are not apparent. B) Perithallus (p) in slide A20-1264_8 with abundant trichocytes. C) Detail of a thin portion of the thallus with hypothallus (h) and perithallus (p) of cells connected by primary and secondary pit-connections. D) Same as in B; detail of secondary pit-connections (arrow) and trichocytes (t). E) Epithallial cells in surface view with trichocyte trace (arrow), SEM stub 08112012b12. F) Same as in B; flattened epithallial cells (e). G) Detail of an empty uniporate conceptacle chamber with 4–5 cells forming the roof filaments.

HABIT AND VEGETATIVE STRUCTURE: The lectotype of *L. kaiseri* (A20-1264, here designated as the small specimen only, in the box of the syntype of Heydrich; arrow in Fig. 4D) is apparently a broken fragment of a larger plant, non-endophytic, with fruticose growth-form (Fig. 4D on right). The protuberances have a smooth surface, are cylindrical

or slightly compressed, branched, up to about 8 mm long and about 2–5 mm wide. The tapering protuberances are often fused together (Fig. 4D on right). Plant structure pseudoparenchymatous (Fig. 5A–B). Basal or ventral layer (=hypothallium) dimerous, hypothallial cells 7–20 µm long and 10–15 µm in diameter. Peripheral region (=perithallium) composed of cell filaments curving outwards towards the thallus surface, L 5–30 µm long and 7–14 µm in diameter (Fig. 5B–D). Cells of adjacent filaments joined by secondary pit connections, cell fusions not observed (Fig. 5C–D). Palisade cells not observed. Single trichocytes 15–45 µm long and about 10–18 µm in diameter occurring in the perithallium and at the thallus surface (Fig. 5C–E). Single epithallial cells flattened, about 7–13 µm in diameter and 2–5 µm long (Fig. 5E–F; Tab. 2).

REPRODUCTION: Uniporate tetrasporangial conceptacles flush with the surrounding thallus surface, conceptacle chamber 270–350 µm in diameter and 85–125 µm high, with a pore-canal 55 µm long (Fig. 5G; Tab. 2). Floor of the conceptacle chamber 11 cells below the thallus surface, including the terminal epithallial cell. Roof filaments 4–5 cells long, including the terminal epithallial cell (Fig. 5G). Gametangial and carposporangial conceptacles unknown.

REPRESENTATIVE SEQUENCE: KP696793 (LSU).

***Lithophyllum subplicatum* (Foslie) comb. et stat. nov.**

Figures 6–7; Table 3

BASIONYM: *Lithophyllum okamurae* forma *subplicatum* Foslie 1901a (*K. Norske Vid. Selsk. Skr.*: 18) (Woelkerling *et al.* 2005: 173).

NOMENCLATURAL SYNONYM: *L. kaiseri*? f. *subplicata* Foslie (1903), *L. kotschyannum* f. *subplicatum* Silva in Silva *et al.* (1996, p. 248) (Woelkerling *et al.* 2005).

LECTOTYPE: TRH, A20-1286, includes slide 596 (Fig. 6) (Woelkerling 1993: 212).

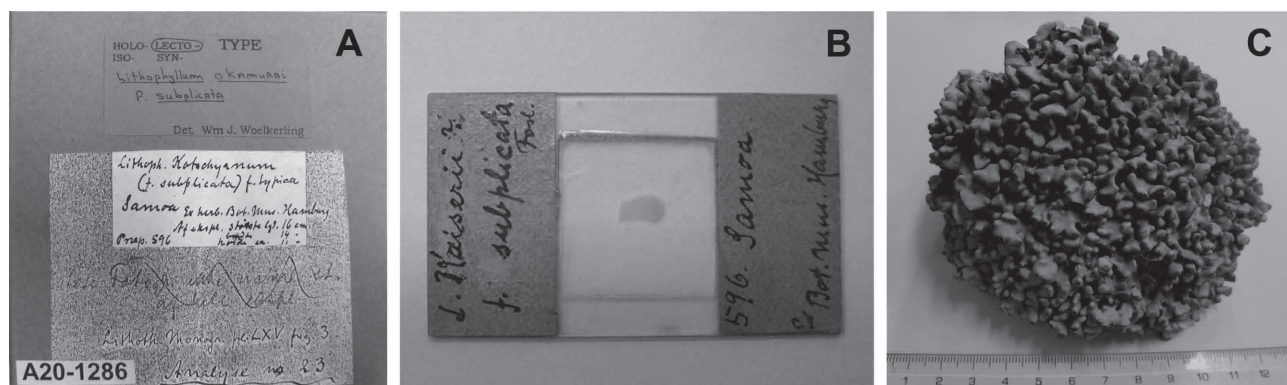


FIGURE 6. The lectotype collection of *Lithophyllum subplicatum* (Foslie) comb. et stat. nov. in TRH. A) Box A20-1286 in TRH. B) Thin section 596 part of the lectotype of *L. subplicatum*. C) The specimen A20-1286 in TRH, lectotype of *L. subplicatum*.

ETYMOLOGY: the specific epithet means “begged for”.

ILLUSTRATIONS OF TYPE MATERIAL: Printz 1929: pl. 65, fig. 3.

TYPE LOCALITY: Samoa Islands, no collector and date given; ex Botanical Museum Hamburg (Woelkerling 1993; Woelkerling *et al.* 2005).

MATERIAL EXAMINED: Pacific Ocean, Samoa Islands, the lectotype TRH A20-1286.

HABITAT AND PHENOLOGY: unknown.

GEOGRAPHIC DISTRIBUTION: *L. subplicatum* is known only from the type locality, Samoa Islands. Other entries need verification (Table 1).

HABIT AND VEGETATIVE STRUCTURE: Plants non-endophytic, with fruticose growth-form. The long protuberances are cylindrical and dichotomously branched, diverging, about 3–4 mm in diameter, flattened and anastomosing at their tips. The plant is 7 cm high and 11 cm in diameter (Fig. 6C).

Plant structure pseudoparenchymatous (Fig. 7A–B). Basal or ventral layer (= hypothallium) dimerous (Fig. 7B). Hypothallial cells 20–23 µm long and 12–20 µm in diameter (Tab. 3). Peripheral region (= perithallium) composed of filaments of cells curving outwards toward the thallus surface, 15–28 µm long and 10–18 µm in diameter (Fig. 7B). Cells of adjacent filaments joined by secondary pit connections, cell fusions not observed. Palisade cells not observed. Single trichocytes 30–53 µm long and about 12–15 µm in diameter, abundantly distributed in the perithallium and at the thallus surface (Fig. 7C). Single epithallial cells flattened, about 10–13 µm in diameter and 2–3 µm long (Tab. 3).

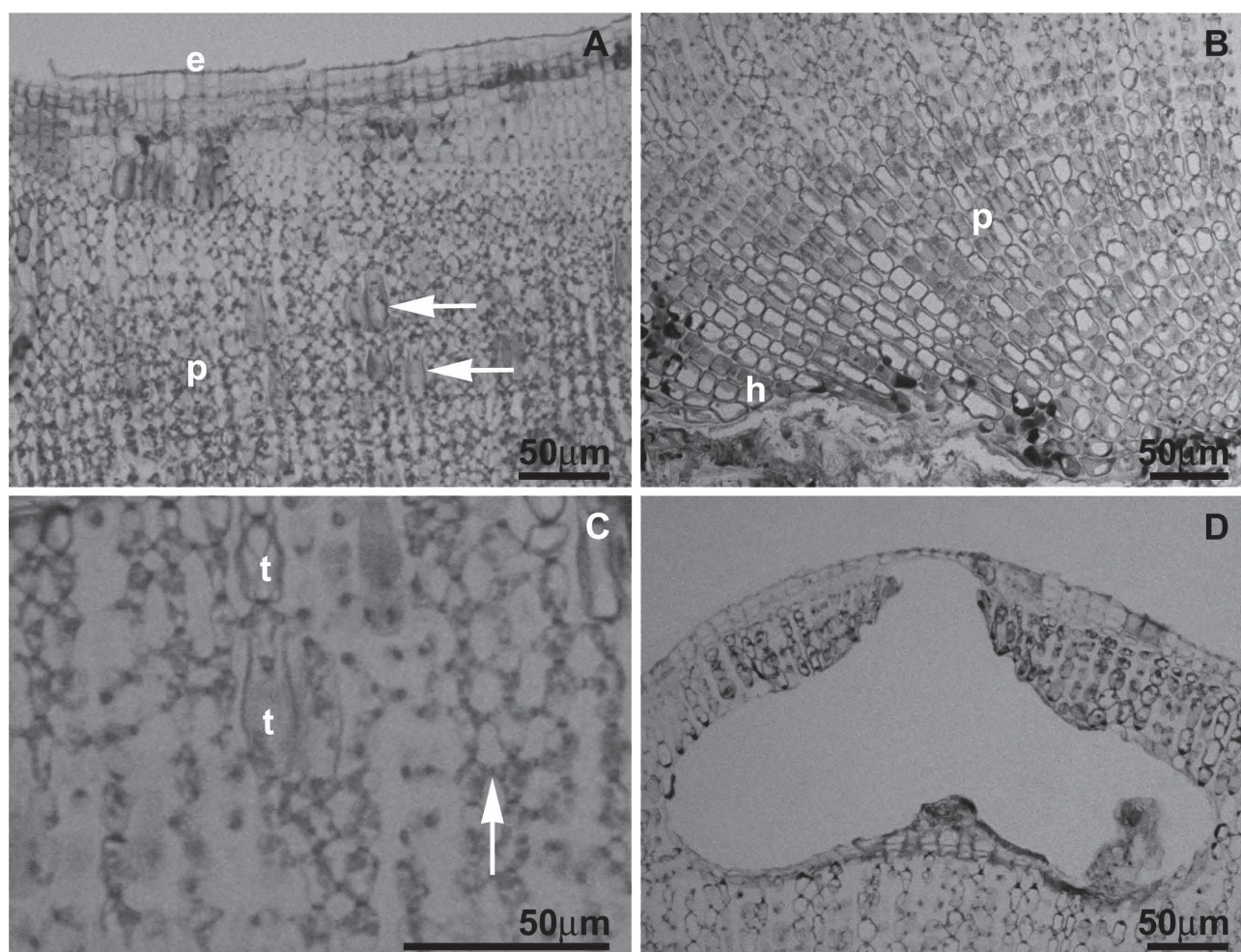


FIGURE 7. Microscopical anatomy of the lectotype of *L. subplicatum* (Foslie) *comb. et stat. nov.* TRH A20-1286 from decalcified material. A) Trichocytes (arrows) in the perithallus (p) with filaments terminating in flattened epithallial cells (e), slide A20-1286_5. B) Same as in A. Thallus dimerous, with hypothallial (ventral) cells visible on bottom left (h), each one giving rise to a filament of perithallial cells (p). C) Same as in A, with magnification of secondary pit-connections (arrow) and trichocytes (t). D) An empty uniporate conceptacle chamber with 6–8 cells in the roof filaments. Slide A20-1286_5.

REPRODUCTION: Uniporate conceptacle chambers, presumed tetra- or bisporangial, protruding over the surrounding thallus surface, becoming buried in the thallus, 330–360 µm in diameter and 100–170 µm high, with pore-canal 80–110 µm long (Fig. 7D; Tab. 3). Floor of the conceptacle chamber convex upward below a central columella. The conceptacle chamber floor is 13–15 cells below the thallus surface. Roof filaments 6–8 cells long, including the terminal epithallial cell (Fig. 7D; Tab. 3). Gametangial and carposporangial conceptacles unknown.

REPRESENTATIVE SEQUENCE: KP696792 (LSU).

***Lithophyllum subreduncum* Foslie 1901b: 10**

Figures 8–9; Table 3

NOMENCLATURAL SYNONYM: *L. kotschyanum* f. *subredunca* Foslie.

HOLOTYPE: TRH, A20-1291, includes slide 503, ex Herb. W.G. Farlow no. XXXI (Woelkerling *et al.* 2005: 174); Fig. 8.

ETYMOLOGY: the specific epithet means “more or less hooked”.

ILLUSTRATIONS OF TYPE MATERIAL: Printz 1929: pl. 65, fig. 12 (as *L. kotschyanum* f. *subredunca*).

TYPE LOCALITY: Sandwich Islands, Hawaii, collector and date unknown (Woelkerling 1993; Woelkerling *et al.* 2005).

MATERIAL EXAMINED: Pacific Ocean, Sandwich Islands, the holotype TRH A20-1291.

HABITAT AND PHENOLOGY: unknown.

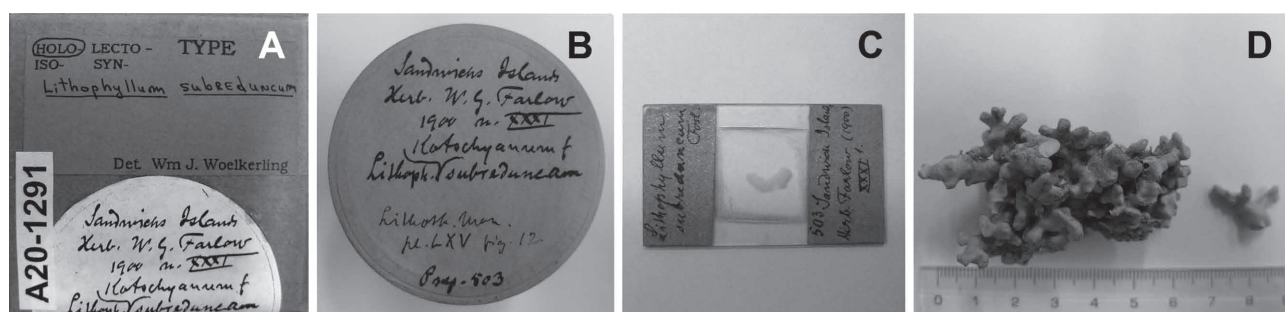


FIGURE 8. The holotype collection of *Lithophyllum subreduncum* Foslie in TRH. A) Box A20-1291 in TRH. B) The carton box containing the holotype of *L. subreduncum*. C) Thin section 503 part of the holotype of *L. subplicatum*. D) The specimen A20-1291 in TRH, holotype of *L. subreduncum*.

GEOGRAPHIC DISTRIBUTION: *L. subreduncum* is known only from the type locality, the Sandwich Islands. Other entries need verification (Table 1).

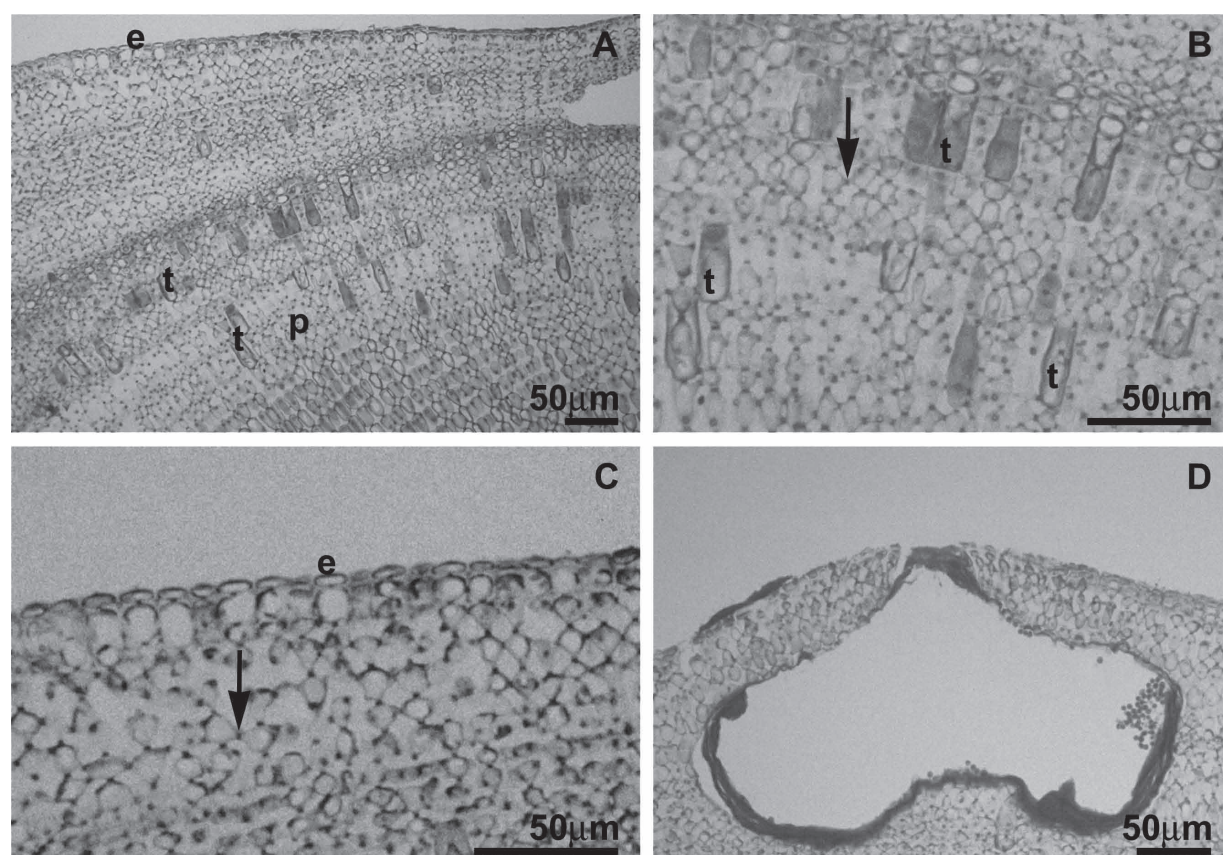


FIGURE 9. Microscopical anatomy of the holotype of *L. subreduncum* Foslie, slide A20-1291_2. A) Vegetative thallus with abundant trichocytes (t) in the perithallus (p), and epithallial flattened cells (e). B) Details of the secondary pit-connections (arrow) in the perithallus and the abundant trichocytes (t). C) Magnification of secondary pit-connections (arrow) and epithallial cells (e). D) A tetrasporangial conceptacle with remain of a central columella.

HABIT AND VEGETATIVE STRUCTURE: Plants non-endophytic, with fruticose growth-form. The protuberances are cylindrical and branched, about 4 mm in diameter, up to 14 mm long, irregularly flattened and anastomosing at their tips (Fig. 8D). Plant structure pseudoparenchymatous (Fig. 9A). Basal or ventral layer (= hypothallium) dimerous. Hypothallial cells 20–23 μm long and 12–15 μm in diameter (Tab. 3). Peripheral region (= perithallium) composed of filaments of cells curving outwards toward the thallus surface, 20–24 μm long and 12–15 μm in diameter (Fig. 9A–C). Cells of adjacent filaments joined by secondary pit connections, cell fusions not observed. Palisade cells not observed. Single trichocytes 27–33 μm long and about 12–15 μm in diameter, abundantly distributed in the perithallium and at the thallus surface (Fig. 9A–B). Single epithallial cells flattened, about 10–13 μm in diameter and 2–4 μm long (Fig. 9C).

REPRODUCTION: Uniporate conceptacle chambers, presumed tetrasporangial, weakly protruding over the surrounding thallus surface, becoming buried in the thallus, 330 µm in diameter and 130 µm high, with pore-canal 80 µm long (Fig. 9D; Tab. 3). Floor of the conceptacle chamber convex upward below a central columella. The conceptacle chamber floor is 15–16 cells below the thallus surface. Roof filaments 5 cells long, including the terminal epithallial cell (Fig. 9D; Tab. 3). Gametangial and carposporangial conceptacles unknown.

REPRESENTATIVE SEQUENCE: KP696788 (LSU).

***Lithophyllum socotraense* sp. nov.**

Figure 10; Table 3

HOLOTYPE: sample DB635 (leg. Caragnano: Socotra, 15.iii.2010) including stub 09062010b6 and histological slide DB635-SO20b, conserved in TRH (TRH-A3881).

TABLE 3. Comparison of features and biometry of *Lithophyllum subplicatum* (Foslie) *comb. et stat. nov.*, *Lithophyllum subreduncum* (Foslie) Foslie, from type material (TRH), and of *Lithophyllum socotraense* sp. nov., *Lithophyllum yemenense* sp. nov. Measurements in µm, given as mean (standard deviation). L=length; D=diameter; H=height. Asterisk on diagnostic characters.

	<i>L. subplicatum</i> lectotype	<i>L. subreduncum</i> holotype	<i>L. socotraense</i>	<i>L. yemenense</i>
Distribution	Samoa Islands, Pacific Ocean	Hawaii, Pacific Ocean	Socotra Is., Arabian Sea	Red Sea, Aden Gulf, Arabian Sea
Life habit	non-geniculate, unknown	non-geniculate, unknown	non-geniculate, as rhodoliths	non-geniculate, attached or as rhodolith
Growth-form	fruticose	fruticose	warty to lumpy	lumpy to fruticose
Thallus organization	dimerous	dimerous	dimerous	dimerous
*Hypothallial cells L x D	21.7 (1.4) x 16.7 (3.8)	20.8 (1.2) x 14.2 (1.2)	15.8 (0.5) x 14.6 (1.6)	11.9 (3.5) x 12.5 (1.8)
Perithallium zonation	yes	yes	yes	yes
Perithallial cells L x D	24.2 (4.9) x 12.5 (3.2)	21.8 (1.3) x 13.8 (1.3)	16.9 (3.5) x 10.3 (0.1)	15.6 (5.7) x 10.2 (1.6)
Epithallial cells shape	flattened	flattened	flattened	flattened
L x D	2.5 (0) x 10.8 (1.4)	2.9 (0.4) x 11 (1.2)	3.9 (1.2) x 10.7 (2.5)	2.8 (0.8) x 10.1 (1.8)
Trichocytes	yes	yes	yes	yes
Asexual concept. chamber	uniporate	uniporate	uniporate	uniporate
*D x H	343.3 (15.3) x 150 (35.1)	330 (n.a.) x 130 (n.a.)	213.4 (24.3) x 82.1 (11)	273.3 (19.5) x 103 (12.5)
*elevation	protruding	slightly protruding	slightly protruding	flush or weakly protruding
*pore position	flush	flush	flush	flush
*pore canal length	95 (15.3)	80 (n.a.)	50.8 (4.5)	52.1 (4.3)
becoming buried	yes	yes	yes	yes
*no. of cells from floor	13–15	15–16	9–11	11–14
columella	yes	yes	yes	yes
*cells in roof filaments	6–8	5	4–5	4–6
Male conceptacles	unknown	unknown	unknown	
D x H (excl. canal)				272.5 (26.3) x 41 (3.5)
pore canal length				46 (6.5)
Female concept. D	unknown	unknown	unknown	170
Carposporangial concept.	unknown	unknown	unknown	
D x H				325 x 125
pore canal				75

ETYMOLOGY: the specific epithet refers to the type locality, the island of Socotra, Yemen.

TYPE LOCALITY: Yemen, Indian Ocean, Ras Adho on the NE coast of Socotra Island, 22 m depth.

MATERIAL EXAMINED: Indian Ocean, NE Socotra Island: Rosh, 16 m, samples DB615-616 (leg. Caragnano: 12.iii.2010); Ras Adho, 22 m (the holotype) and 13 m (sample DB636) (leg. Caragnano: 16.iii.2010).

HABITAT AND PHENOLOGY: plants unattached as rhodoliths, enveloping coral fragments at nucleus, at depth > 12 m.

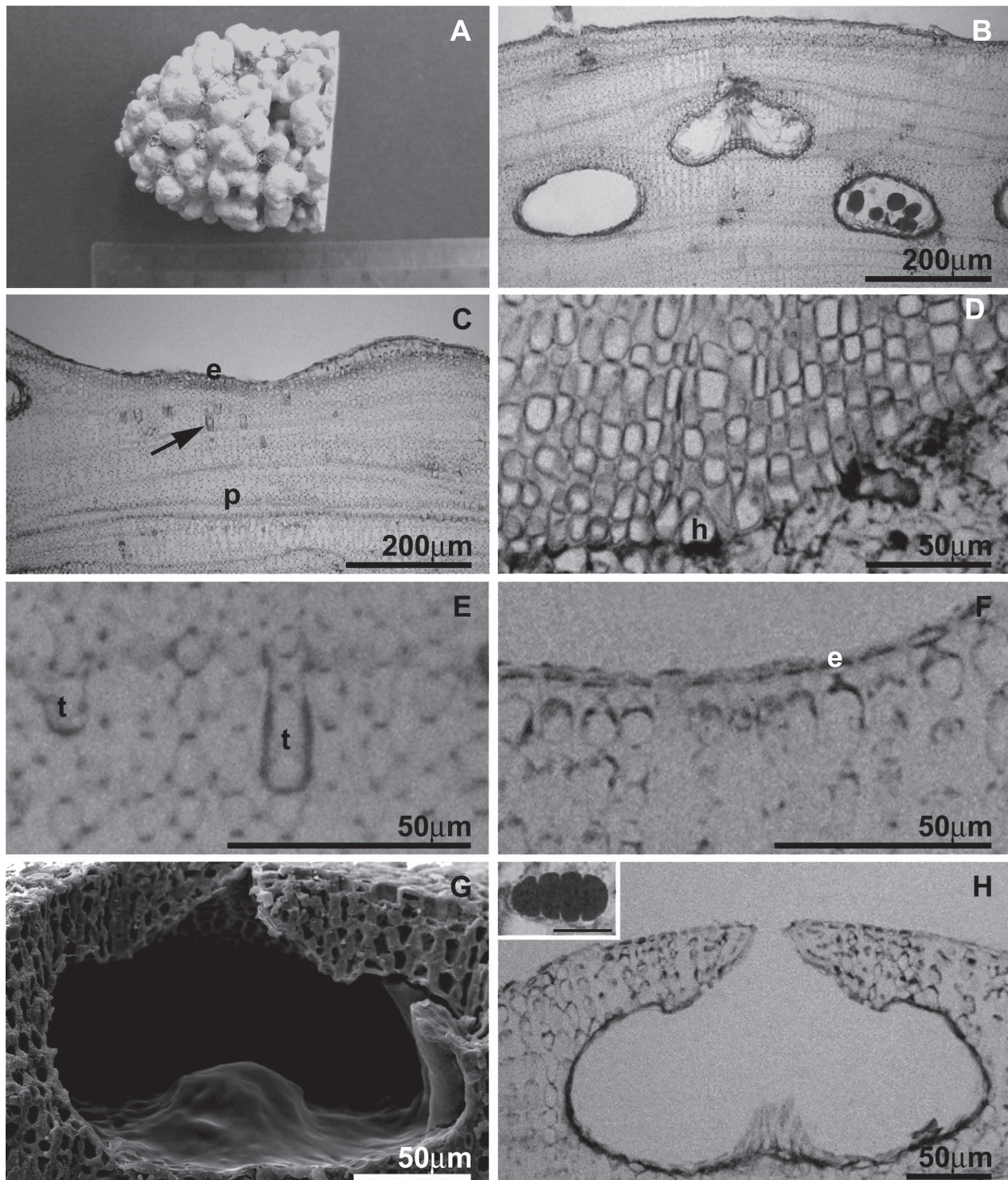


FIGURE 10. *Lithophyllum socotraense* sp. nov. A) The holotype, sample DB635, a rhodolith, conserved in TRH. Note the lumpy growth-form. The sample has been cut for histological analyses. B) Microscopic anatomy of a fertile thallus, slide DB635-SO20b_9. C) Sparse trichocytes (arrow) in the perithallus (p) of sample DB636, slide DB636-SO25b_7; e = epithallial cells. D) Same as in C, detail of ventral hypothallial cells (h) and the dimerous organization of the thallus. E) Same as in C, magnification of trichocytes (t). F) Flattened epithallial cells (e) in slide DB635-SO20b_10. G) Tetrasporangial conceptacle with central columella in the holotype, SEM stub 09062010b6. H) Holotype sample DB635. Tetrasporangial conceptacle in slide DB635-SO20b_10; inset: a tetraspore, slide DB635-SO20b_7.

GEOGRAPHIC DISTRIBUTION: *L. socotraense* nov. sp. is known only from the NW Indian Ocean, Socotra Island.

HABIT AND VEGETATIVE STRUCTURE: Plants non-endophytic, with warty to lumpy growth form. The protuberances have a smooth surface, up to about 5 mm long and about 3–6 mm wide (Fig. 10A).

Plant structure pseudoparenchymatous (Fig. 10B–C). Basal or ventral layer (= hypothallium) dimerous (Fig. 10D). Hypothallial cells 15–18 μm long and 11–18 μm in diameter (Tab. 3). Peripheral region (= perithallium) composed of filaments of cells curving outwards toward the thallus surface, 12–23 μm long and 10–13 μm in diameter (Fig. 10C–D). Cells of adjacent filaments joined by secondary pit-connections, cell fusions not observed (Fig. 10D–F). Palisade cells not observed. Single trichocytes 22–58 μm long and about 12–13 μm in diameter, abundantly distributed in the perithallium and at the thallus surface (Fig. 10C, E). Single epithallial cells flattened, about 7–15 μm in diameter and 2–5 μm long (Fig. 10F).

REPRODUCTION: Uniporate tetrasporangial conceptacle chambers protruding over the surrounding thallus surface, becoming buried in the thallus, 180–250 μm in diameter and 60–90 μm high, with pore-canal 45–60 μm long (Fig. 10G–H; Tab. 3). Floor of the conceptacle chamber convex upward below a central columella. The conceptacle chamber floor is 9–11 cells below the thallus surface. Roof filaments 4–5 cells long, including the terminal epithallial cell (Fig. 10H; Tab. 3). Gametangial and carposporangial conceptacles not found.

REPRESENTATIVE SEQUENCES: KP696790 (LSU), KP976402 (CO1) & KP976409 (*psbA*).

Lithophyllum yemenense sp. nov.

Figures 11–12; Table 3

HOLOTYPE: sample DB567 (tetrasporangial plant, Fig. 11; legit Caragnano: Balhaf, Yemen, iii.2008), including histological slides DB567-13y2, DB567-13y4, conserved in TRH (TRH-A3882).

ETYMOLOGY: the specific epithet is dedicated to the Arabian country where samples were collected.

TYPE LOCALITY: Balhaf, Yemen, on biogenic calcareous rock, 2 m depth.

MATERIAL EXAMINED: Red Sea: Yemen, Kamaran, 1.5 m (legit Caragnano: DB575-576, 28.ix.2009); Indian Ocean: Gulf of Aden, Yemen, Balhaf, 2–3 m (leg. Benzoni: DB559, ix 2006; DB563, xi.2006; leg. Caragnano: DB568-570, iii.2008; DB657, DB659, DB660, DB692, xi.2008); Yemen, Socotra Is., 9 m (leg. Caragnano: DB612, iii.2010).

GEOGRAPHIC DISTRIBUTION: *L. yemenense* is distributed in the Red Sea, Gulf of Aden and Arabian Sea. The occurrence of *L. yemenense* outside this area is unknown.

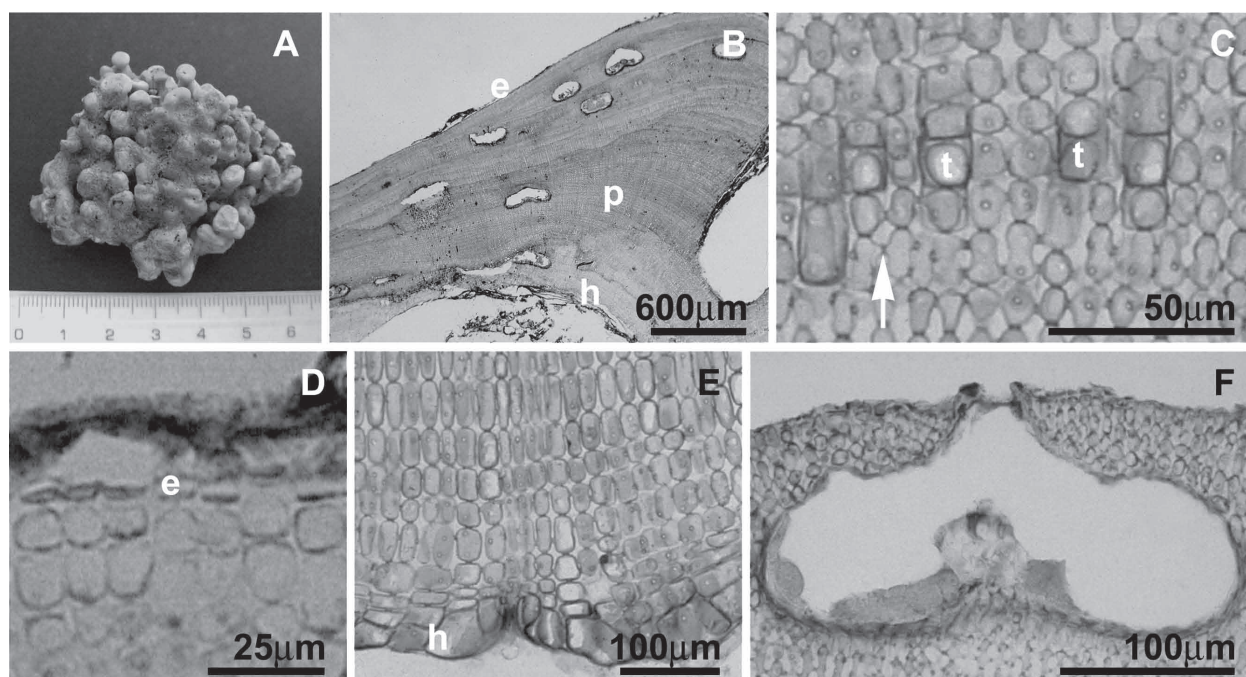


FIGURE 11. *Lithophyllum yemenense* sp. nov. A) The holotype, sample DB567 conserved in TRH. B) Appearance of a fertile portion of the holotype; h=hypothallus; p=perithallus; e=epithallial cells, slide DB567-13y4. C) Same as in B, detail of secondary pit-connections (arrow) and trichocytes (t). D) Magnification of the flattened epithallial cells (e), slide DB567-13y2. E) Detail of B to show the dimerous organization with a ventral one-cell layer of hypothallial cells (h) each one giving rise to the perithallial filaments, slide DB567-13y5. F) Uniporate tetrasporangial conceptacle chamber with floor showing a central columella, slide DB567-13y2.

HABIT AND VEGETATIVE STRUCTURE: The coralline may be attached on corals or other biogenic substrate or form unattached nodules (rhodoliths). Thallus non-endophytic, encrusting, lumpy to fruticose. The protuberances, up to about 10 mm long and about 2–5 mm wide, have a smooth surface, are cylindrical or compressed, branched, sometimes fused and apically enlarged and flattened (Fig. 11A).

Plant structure pseudoparenchymatous (Fig. 11B–E). Basal or ventral layer (= hypothallium) dimerous, hypothallial cells 7–20 µm long and 10–15 µm in diameter (Fig. 11E). Peripheral region (= perithallium) composed of cell filaments curving outwards towards the thallus surface, 5–30 µm long and 7–14 µm in diameter (Fig. 11B–E). Cells of adjacent filaments joined by secondary pit connections, cell fusions not observed (Fig. 11C). Palisade cells not observed. Single trichocytes 15–45 µm long and about 10–18 µm in diameter occurring in the perithallium and at the thallus surface (Fig. 11C). Single epithallial cells flattened, about 7–13 µm in diameter and 2–5 µm long (Fig. 11D; Tab. 3).

REPRODUCTION: Uniporate tetrasporangial conceptacles flush or weakly protruding above the surrounding thallus surface, conceptacle chamber 250–300 µm in diameter and 80–120 µm high, with a pore-canal 50–61 µm long (Fig. 11B, F; Tab. 3). Floor of the conceptacle chamber with a central columella, 11–14 cells below the thallus surface. Roof filaments 4–6 cells long, including the terminal epithallial cell (Fig. 11F).

Gametangial thalli dioecious; carpogonia and spermatangia produced in separate uniporate conceptacles (Fig. 12). Spermatangial filaments unbranched, arising from the male conceptacle chamber floor (Fig. 12A). Mature male conceptacle roof weakly raised above the surrounding thallus surface or flush, composed of 5–7 layers of cells above the chamber. Male conceptacle chambers 250–315 µm in diameter and 40–45 µm high, plus a pore canal 38–55 µm long (Fig. 12A, Tab. 3).

Female conceptacles chamber about 170 µm in diameter. Carposporangial conceptacle chamber 325 µm in diameter, 125 µm high, with a pore-canal about 75 µm long (Fig. 12B, Tab. 3). Carposporophyte composed of a central fusion cell and short peripheral gonimoblast filaments bearing terminal carposporangia (Fig. 12B).

REPRESENTATIVE SEQUENCES: KP696789 (LSU), KP976401 (CO1) & KP976408 (*psbA*).

A ML phylogenetic analysis inferred from *psbA* (Fig. 13) revealed that the two last species (*L. socotraense* and *L. yemenense*) were only distantly related to the specimens so far sequenced for this gene and available in GenBank.

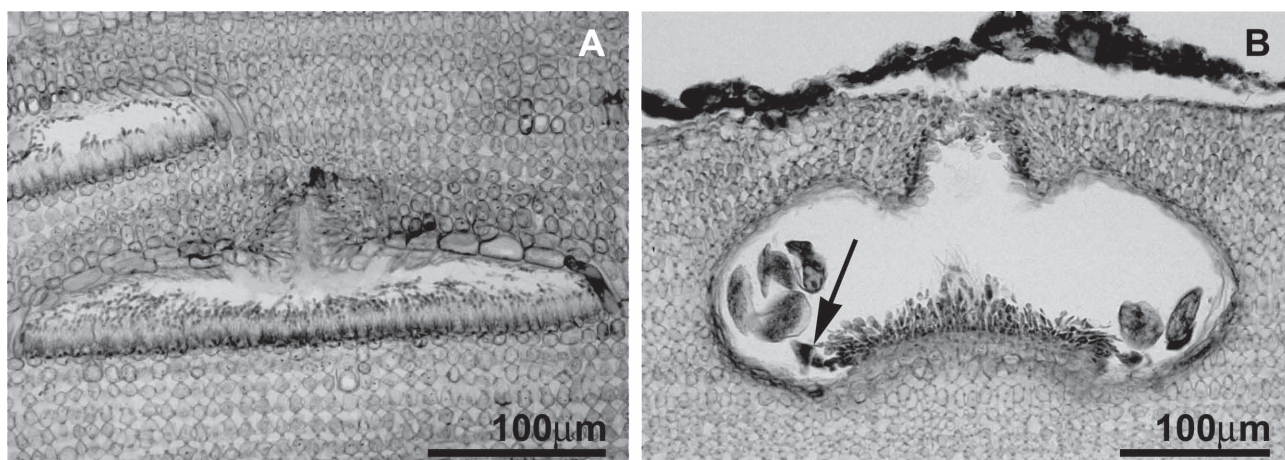


FIGURE 12. *L. yemenense* sp. nov., male and carposporangial plants. A) Male conceptacle with unbranched spermatangial filaments, slide DB563-4ya4. B) Carposporangial conceptacle with short peripheral gonimoblast filaments (arrow) bearing terminal carposporangia. Sample DB569, slide DB569-10y5.

Discussion

Trichocytes occur in all the *Lithophyllum* species dealt with in this paper (Basso *et al.* 2014).

After some nomenclatural changes (details in Woelkerling *et al.* 2005), *Lithophyllum kaiseri* Heydrich (Heydrich) was treated by Foslie (1909) as heterotypic synonym of *L. kotschyianum* (Woelkerling *et al.* 2005). The syntype of *Lithothamnion kaiseri* Heydrich (TRH, A20-1264) includes two specimens and two slides. Foslie annotated that the largest specimen was not confidently identified, probably exchanged with another box (Woelkerling *et al.* 2005). For this reason we selected the smallest fragment as the lectotype of *Lithophyllum kaiseri*. Lemoine (1965) already questioned the validity of the synonymy of *L. kaiseri* with *L. kotschyianum*, and the results of our morphological analyses support the separation of the two species. In particular, the morphological characters that can be comparatively used to identify

L. kaiseri are: the smaller conceptacles almost flush with the surrounding thallus surface, the conceptacle floor placed 11 cells from thallus surface (16–17 in *L. kotschyanum*), and only 4–5 cells in roof filaments (7 in *L. kotschyanum*, Tab. 2).

In his protologue of *Lithothamnion affine*, Foslie (1897) described the new species with details concerning its habit: plant attached and growing on corals, surrounding the coral branches, or rhodoliths “fastened to smaller stones ...forms roundish or somewhat lobed balls on the bottom, 3–5 cm in diameter...”. Later (1898) Foslie transferred *Lithothamnion affine* into *Lithophyllum*, without change in rank, and finally (Foslie 1909; Prinz 1929) reduced it to the rank of form as *Lithophyllum kotschyanum* f. *affine* (Woelkerling 1993; Woelkerling *et al.* 2005). He also described the two forms *complanata* and *tuberosa* on the basis of their growth form and shape of protuberances. The form *complanata* corresponds to the lectotype (= *Lithophyllum affine* f. *affine*, Woelkerling *et al.* 2005).

Our results, however, point to a separation of the two species, since *L. affine* Foslie (Foslie) is morphologically separated from the holotype of *L. kotschyanum* on the basis of its smaller tetrasporangial conceptacles with a pore opening on an apical depression of the conceptacle roof, the conceptacle floor placed 11 cells from thallus surface (16–17 in *L. kotschyanum*), and only 5–6 cells in roof filaments (7 in *L. kotschyanum*, Tab. 2; Fig. 1).

L. kotschyanum Unger, *L. kaiseri* (Heydrich) Heydrich and *L. affine* (Foslie) Foslie have similar and variable growth-form, although the integration of morphological and molecular results support their separation (Fig. 1; Tab. 2). Morphologically, the mean diameter of the tetrasporangial conceptacles, the length of the pore-canal in the tetrasporangial conceptacles (with the number of cells in roof filaments), the occurrence of a depression at the top of the conceptacle roof and the number of cells from the floor of the tetrasporangial conceptacle chamber to the thallus surface are the characters that appear collectively diagnostic for their segregation (Tab. 2 and dichotomous key). In this respect, it is worth mentioning that counting the cells at the periphery of the tetrasporangial conceptacle chamber is a very delicate operation, whose precision is easily compromised by the imperfect orientation of the thallus. Therefore we recommend to use this character with caution and, when possible, in combination with other diagnostic characters.

The lectotype of *L. okamurai* Foslie forma *subplicata* Foslie 1901a (TRH, A20-1286) has growth-form and microscopical anatomy similar to the holotype of *L. kotschyanum* Unger, including trichocyte occurrence and morphology (Fig. 7, Tab. 2). *L. okamurai* Foslie forma *subplicata* Foslie was transferred into *L. kaiseri* f. *subplicata* by Foslie (1903), and then into *L. kotschyanum* f. *subplicatum* by Silva in Silva *et al.* (1996) (Woelkerling *et al.* 2005).

The holotype of *Lithophyllum subreduncum* Foslie 1901b (TRH, A20-1291) has growth form and microscopical anatomy very similar to that of the holotype of *L. kotschyanum* Unger, including the trichocyte occurrence and morphology (Fig. 9, Tab. 2). This observation explains Foslie’s conclusions, who reduced it to the rank of form after eight years from the description of *Lithophyllum subreduncum* as a new species, under the combination *Lithophyllum kotschyanum* Unger forma *subreduncum* Foslie (Foslie 1909; Woelkerling *et al.* 2005). Our analyses demonstrate that the two species differ from *L. kotschyanum* Unger on the basis of LSU divergence and microscopic anatomy (Fig. 1; Tabs 1–2). The comparison of the infraspecific variability of fresh collections from the type localities is a task beyond the aim of the present study. Pending further studies, we decide to follow a conservative approach by keeping the original combination for *L. subreduncum* Foslie 1901b, and considering *L. kotschyanum* f. *subplicatum* as a separate entity, under the new status and combination *L. subplicatum* (Foslie).

Lithophyllum kotschyanum Unger, *L. kaiseri* (Heydrich) Heydrich, *L. subreduncum* Foslie, *L. subplicatum* and *L. affine* (Foslie) Foslie and the new species, *L. socotraense*, and *L. yemenense* have similar and variable growth-form, although the integration of results from molecular analysis and microscopical anatomy separate them as distinct species (Figs 1, 13).

The reverse primers designed in this study successfully amplified the 5’end of the LSU in herbarium specimens older than one century. The strategy to amplify short fragments to overcome the issue of degraded DNA in old specimens was appropriate and opens new perspectives to rationalize taxonomic studies of coralline algae. Amplified fragments displayed divergence up to 5.1% between *L. affine* and *L. kaiseri*, *L. kotschyanum*, *L. subreduncum* and *L. socotraense*. It is noteworthy to stress that *L. subreduncum* and *L. socotraense* have identical sequences, nonetheless, the nuclear LSU has been shown to sometimes lack of variation among closely related species (e.g. Le Gall & Saunders 2010). Therefore, different nuclear LSU strongly supports species separation, and on the contrary, the apparent conspecificity based on this poorly variable LSU fragment appears questionable. In this case, morphology supports species separation: *L. subreduncum* differs from *L. socotraense* in having much larger and higher tetra-bisporangial conceptacle chamber, a longer pore canal and 15–16 cells from conceptacle floor instead of 9–11 (Tab. 2), and, moreover, the two specimens have been collected in different geographic regions. We have no data about the natural variability of *L. subreduncum* at its type locality (Hawaii), and the state of conservation of the type material does not allow to achieve further molecular

results, nevertheless the decision to consider *L. subreduncum* and *L. socotraense* as separate species is presently the most conservative.

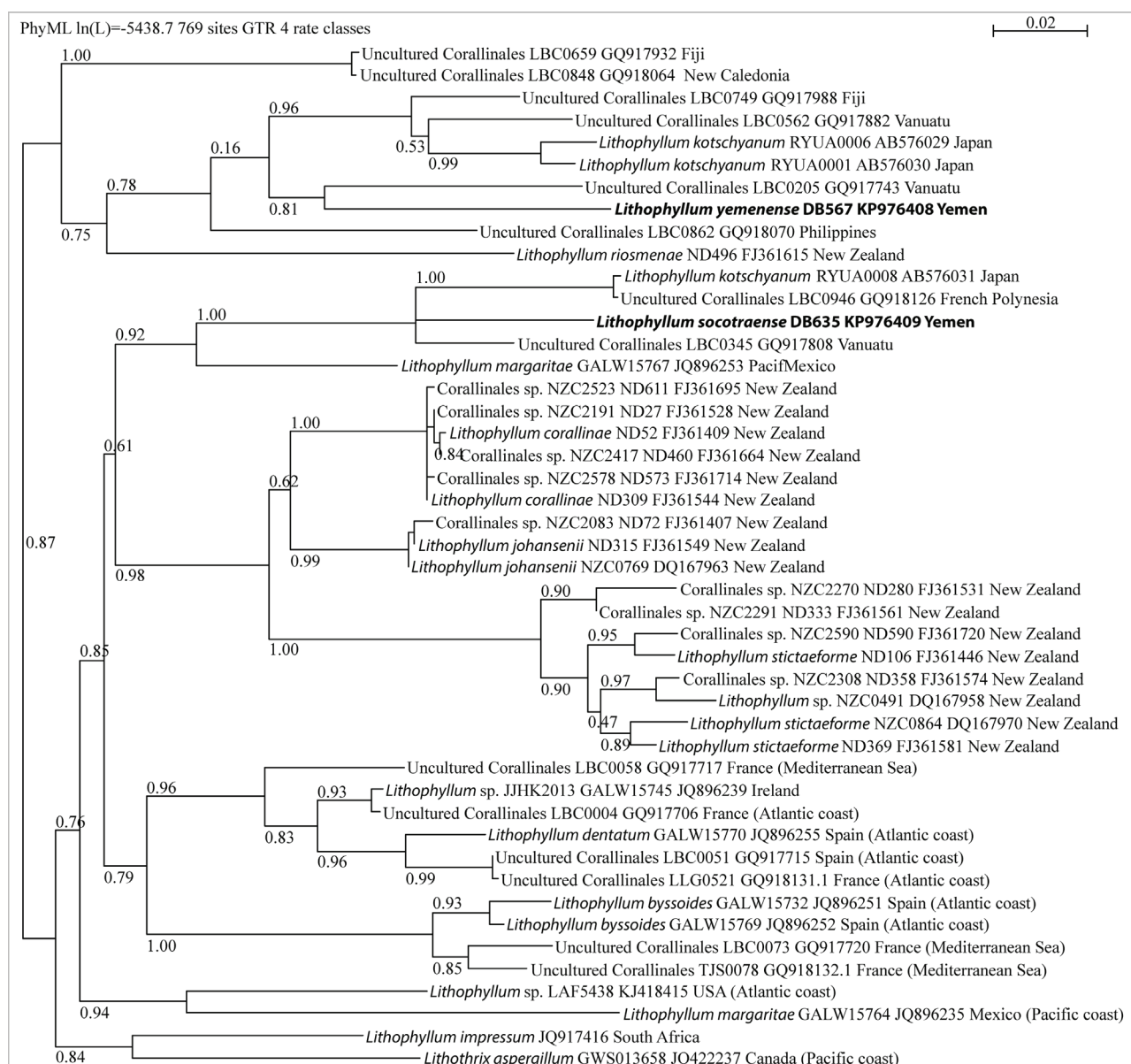


FIGURE 13. Phylogenetic analysis inferred from *psbA* including sequences from GenBank (with either incomplete or doubtful identification) and the type specimens of *L. socotraense* and *L. yemenense*. Supports at nodes are bootstrap values (1000 replicates).

The anatomical features of the tetrasporangial conceptacle that are here considered collectively diagnostic for species identification in *Lithophyllum* are: the mean diameter of the tetrasporangial conceptacles, the length of the pore-canal in the tetrasporangial conceptacles (with the number of cells in roof filaments), the occurrence of a depression at the top of the conceptacle roof and the number of cells from the floor of the tetrasporangial conceptacle chamber to the thallus surface (dichotomous key).

We demonstrate here a previously unsuspected diversity within the Red Sea and NW Indian Ocean species of *Lithophyllum*, that increase in number from 3 (*L. kotschyianum*, *L. orbiculatum* and *L. okamurae*) to 7 (with the addition of *L. affine*, *L. kaiserii*, *L. socotraense* and *L. yemenense*). The occurrence of *L. subplicatum* and *L. subreduncum* outside their type localities in the Pacific Ocean requires further confirmation. On the basis of literature data (Silva *et al.* 1996; Guiry & Guiry 2015), more than one hundred species of *Lithophyllum* are presently considered taxonomically accepted, although many of them, including *L. orbiculatum* and *L. okamurae*, lack a modern account or need confirmation of their geographic distribution. The complete revision of this material is beyond the aim of this work, and constitutes a challenge for future studies.

Key to species of *Lithophyllum* from north-western Indian Ocean[§]

1. Plant known with warty-lumpy growth form (Fig. 10A)2
Plant known with fruticose growth form (Fig. 6C)3
2. Mature tetra-bisporangial conceptacle slightly protruding above the thallus surface, chamber 180–250 (mean 213) µm in diameter, and 60–90 (mean 82) µm in height, chamber floor 9–11 cell layers below the surrounding thallus surface.....*L. socotraense*
Mature tetra-bisporangial conceptacle flush or weakly protruding above the thallus surface, chamber 250–300 (mean 273) µm in diameter, and 80–120 (mean 103) µm in height, floor 11–14 cell layers below the surrounding thallus surface *L. yemenense*
3. Pore canal aperture in the centre of a depression (Fig. 3D), conceptacle chamber 250–280 µm in diameter and 110–130 µm in height, floor 11 cells below the thallus surface, and 5–6 cells in roof filaments, inconspicuous columella.....*L. affine*
Pore canal aperture of the tetrasporangial conceptacle chamber flush with the surface of the chamber roof (Fig. 7D, 10H), other characters collectively not as above4
4. Mature tetra-bisporangial conceptacle with floor > 15 cell layers below the surrounding thallus surface.....5
Mature tetra-bisporangial conceptacle with floor ≤ 15 cell layers below the surrounding thallus surface (Fig. 10H)6
5. Mature tetra-bisporangial conceptacle with chamber 310–380 (mean 351) µm in diameter, floor 16–17 cell layers below the thallus surface, and 7 cells in roof filaments..... *L. kotschyianum*
Mature tetra-bisporangial conceptacle with chamber 330 µm in diameter, floor 15–16 cells below the thallus surface, and 5 cells in roof filaments *L. subreduncum*
6. Mature tetra-bisporangial conceptacle with no evident columella on the chamber floor (Fig. 5G), chamber 270–350 (mean 310) µm in diameter, floor 11 cell layers below the surrounding thallus surface, 4–5 cells in roof filaments..... *L. kaiseri*
Mature tetra-bisporangial conceptacle with central columella on the chamber floor (Fig. 10G–H), other characters collectively not as above7
7. pore canal length 50–61 µm long..... *L. yemenense*
pore canal length >61 µm long.....8
8. Mature tetra-bisporangial conceptacle with 6–8 cells in roof filaments *L. subplicatum*
Mature tetra-bisporangial conceptacle with 5 cells in roof filaments *L. subreduncum*

[§]The occurrence of *L. subplicatum* and *L. subreduncum* in the NW Indian Ocean requires further confirmation.

Acknowledgments

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