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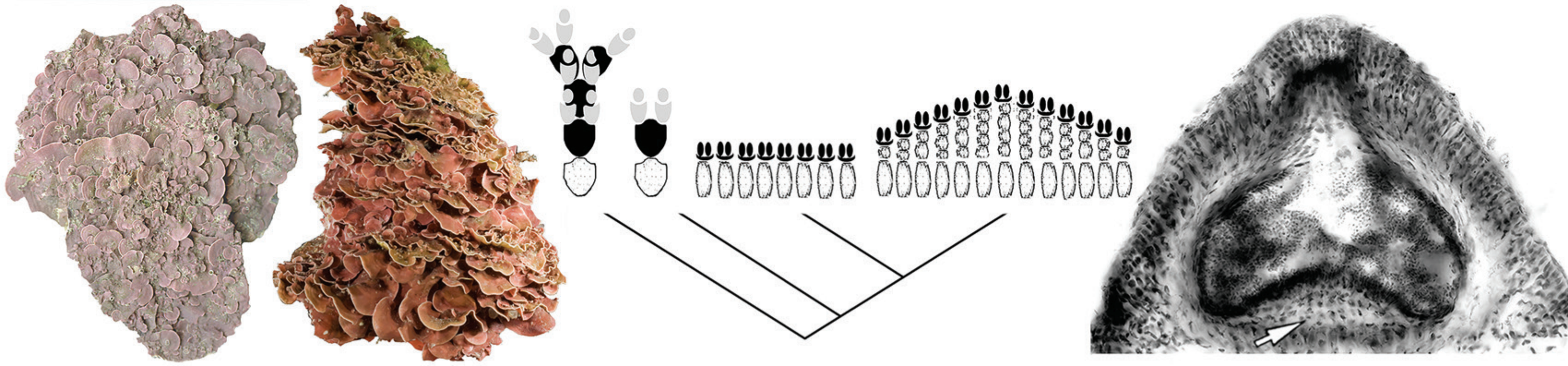

Anatomy and Classification of the Mesophyllaceae (Corallinales, Rhodophyta), Based on Phylogenetic Principles

Athanasios Athanasiadis and David L. Ballantine

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ABSTRACT

Athanasiadis, Athanasios, and David L. Ballantine. *Anatomy and Classification of the Mesophyllaceae (Corallinales, Rhodophyta), Based on Phylogenetic Principles*. Smithsonian Contributions to Botany, number 118, xii + 216 pages, 83 figures, 6 tables, 2024. — A phylogenetic analysis shows the Mesophyllaceae comprise the subfamilies Clathromorphoideae Athanas. et D. L. Ballant. subfam. nov., Protomesophylloideae Athanas. et D. L. Ballant. subfam. nov., and Mesophylloideae Athanas. et D. L. Ballant. subfam. nov., the last one including the main core of species previously assigned to *Mesophyllum* and *Leptophytum*. The Clathromorphoideae comprise the genera *Clathromorphum*, *Neopolyporolithon*, *Callilithophytum*, and the monotypic *Clathmoroa* Athanas. et D. L. Ballant. gen. nov. based on *C. tubiformis* (Y. M. Chamb., R. E. Norris, et G. W. Maneveldt) Athanas. et D. L. Ballant. comb. nov. from South Africa. Protomesophylloideae is monotypic, based on *Protomesophyllum ameleteton* Athanas. et D. L. Ballant. sp. nov. from southern Australia, New Zealand, and the Chatham Islands. The Mesophylloideae comprise the tribes Amphithallieae Athanas. et D. L. Ballant. trib. nov., Melyvonneeae Athanas. et D. L. Ballant. trib. nov., and Magnephyceae Athanas. et D. L. Ballant. trib. nov.

Amphithallieae include the genera *Amphithallia*, *Synarthrophyton*, *Carlskottsbergia*, *Capensia*, and the monotypic *Kerguelena* Athanas. et D. L. Ballant. gen. nov. (type: *K. dickiei* Athanas. et D. L. Ballant. comb. et nom. nov.) and *Masoniana* Athanas. et D. L. Ballant. gen. nov. (type: *M. kraftii* Athanas. et D. L. Ballant. comb. et nom. nov. from southern Australia).

Melyvonneeae include the genera *Phragmope*, *Mesophyllum*, *Melyvonnea*, *Perithallis*, *Thallis*, *Sunesonia*, *Printziana* (comprising the type and *P. insignis* (Foslie) Athanas. et D. L. Ballant. comb. nov. from New Zealand), and the new monotypic *Macroblastum* Athanas. et D. L. Ballant. gen. nov. based on the Mediterranean *M. dendrospermum* Athanas. et D. L. Ballant. comb. et nom. nov. (*Continued on p. vi.*)

Cover images, from left: *Magnephycus ornatus* from Clarence Cove, Bermuda Island (herb. C. Schneider 00585) and La Parguera, Puerto Rico (herb. D. L. Ballant. 7781 in MSM); spermatangial evolution in the Mesophyllaceae, from dendroid to unbranched, borne on a single layer of palisade cells (*Hyperandri*) and on a pedestal (*Magnephycus*) shown in section.

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DEDICATION

In memory of Francis Magne
(1924–2014)

ABSTRACT (*continued from p. iv*)

Magnephyceae include the genera *Kvaleya*, *Leptophytum*, *Leptothallia* Athanas. et D. L. Ballant. gen. nov. (based on *L. acervata* (Foslie) Athanas. et D. L. Ballant. comb. nov. from South Africa), *Macedonis* Athanas. et D. L. Ballant. gen. nov. (including the Aegean generitype *M. tethygenis* Athanas. et D. L. Ballant. comb. et nom. nov. and the NE Pacific *M. julieae* (Athanas. et W. H. Adey) Athanas. et D. L. Ballant. comb. nov., *M. lamellicola* (Athanas. et W. H. Adey) Athanas. et D. L. Ballant. comb. nov., and *M. kymatodis* (Athanas.) Athanas. et D. L. Ballant. comb. nov.), *Hyperandri* Athanas. et D. L. Ballant. gen. nov. (including the generitype from Pacific Mexico *H. dawsonii* Athanas. et D. L. Ballant. comb. et nom. nov., the Canarian-Caribbean *H. bisporum* (Foslie) Athanas. et D. L. Ballant. comb. nov., and the Thai *H. siamense* (Foslie) Athanas. et D. L. Ballant., comb. nov.), the monotypic *Ectocarpa* Athanas. et D. L. Ballant. gen. nov. (based on *E. capverdensis* Athanas. et D. L. Ballant., comb. et nom. nov.), *Magnephycus* Athanas. et D. L. Ballant. gen. nov. (including the Caribbean generitype *M. ornatus* (Foslie et M. Howe) Athanas. et D. L. Ballant. comb. nov., the southern Australian *M. engelhartii* (Foslie) Athanas. et D. L. Ballant. comb. nov., and the Indo-Pacific *M. simulans* (Foslie) Athanas. et D. L. Ballant. comb. nov.), *Mastophoropsis*, and *Phymatolithopsis* (the last genus being incertae sedis).

As outgroups are selected two genera of Melobesiaceae: *Melobesia* (Melobesioideae) and *Orthocarpa* Athanas. et D. L. Ballant. gen. nov. (type: *O. epicklonia* Athanas. et D. L. Ballant. sp. nov. from southern Australia, placed in Orthocarpoideae Athanas. et D. L. Ballant. subfam. nov.). They share production of a fusion cell/gonimoblast just below the carpogonia and development of both lateral and orthostichous carposporangia, whereas the Mesophyllaceae develop carposporangia mainly laterally and produce a fusion cell/gonimoblast at the level of supporting cells. A further character distinguishing the Mesophyllaceae is the development of a cell tube, a prerequisite to transfer the zygote beyond the hypogynous cell to the subtending supporting (auxiliary) cell.

Orthocarpa also accommodates several species previously placed in *Synarthrophyton*: *Orthocarpa eckloniae* (Foslie) Athanas. et D. L. Ballant. comb. nov., *O. haptericola* (Foslie) Athanas. et D. L. Ballant. comb. nov. (=*Synarthrophyton schielianum*), *O. magellanica* (Foslie) Athanas. et D. L. Ballant. comb. nov., *O. papillata* (G. W. Maneveldt, D. W. Keats, et Y. M. Chamb.) Athanas. et D. L. Ballant. comb. nov., *O. munimenta* (D. W. Keats et G. W. Maneveldt) Athanas. et D. L. Ballant. comb. nov., *O. robbenensis* (D. W. Keats et G. W. Maneveldt) Athanas. et D. L. Ballant. comb. nov., *O. pseudospora* A. S. Harv., Woelk., et A. Millar) Athanas. et D. L. Ballant. comb. nov., and *O. chejuensis* (J. Kim, H. Chung, D. Choi, et I. Lee) Athanas. et D. L. Ballant. comb. nov. The new family Lithothamnionaceae Athanas. et D. L. Ballant. nom. nov. (="Lithothamniaceae H. J. Hees 1886" nom. illeg.) and the new combination *Titanoderma chamberlainianum* (Woelk. et S. T. Cambell) Athanas. et D. L. Ballant. comb. nov. (=*Lithophyllum chamberlainianum*) are proposed. A key to Mesophyllaceae subfamilies, tribes, and genera is presented.

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Anatomy and Classification of the Mesophyllaceae (Corallinales, Rhodophyta), Based on Phylogenetic Principles

Athanasios Athanasiadis[1] *and David L. Ballantine*[2]*

INTRODUCTION

The Mesophyllaceae Athanas. have a global distribution occurring in the tropics, subtropics, and temperate seas and even grow in the Arctic and Antarctic Oceans. They are strictly marine organisms, inhabiting the littoral and sublittoral zones to at least 120 m depth (species of *Leptophytum* W. H. Adey, e.g., *L. foecundum* (Kjellm.) W. H. Adey and *L. laeve* (Foslie) W. H. Adey), growing mainly on rocks, cobbles, pebbles, shells, mangroves, or other macroalgae, including corallines. Their thalli range between a few millimeters in parasitic species (i.e., *Capensia fucorum* (Esper) Athanas. and *Kvaleya epilaeve* W. H. Adey et Sperapani) to at least 0.5 m in diameter (or thickness) in epilithic members (i.e., *Clathromorphum nereostratum* P. A. Lebednik). Like all corallines, they develop calcification in their vegetative cell walls, and therefore, anatomy studies of their reproduction require laborious and time-consuming techniques. As a result, their biology has been left behind, particularly with regard to members from the southern hemisphere. The group is usually included within the broad ecological concept of "encrusting corallines," but the phenology of particular species is unknown or poorly documented. Indeed, the term "unidentified encrusting coralline" is one of the commonest applied in marine biology textbooks and scientific publications.

There are no life history studies, except for observations of early stages in spore germination (see "Character Evolution in Mesophyllaceae"). Yet it is generally accepted that the Mesophyllaceae (like all coralline algae) exhibit a triphasic diplohaplontic life history with isomorphic gametophytes and tetrasporophytes and carposporophytes developing within carpogonial conceptacles ("keramidia" in older literature). Cytological studies confirming these observations remain to be carried out in the multiporate families (Cole 1990: 82, table 4-1), which include **Lithothamnionaceae nom. nov.**,[1] Mesophyllaceae, and Melobesiaceae J. Früh (Athanasiadis 2016b).

Historically, the recognition of the group dates back to Lemoine (1928), who erected the genus *Mesophyllum* Me. Lemoine to include *M. lichenoides* (J. Ellis) Me. Lemoine (indirectly referring to *Corallium lichenoides* J. Ellis via the given species distribution "les côtes de France et de Grande-Bretagne"), *M. incertum* (Foslie) Me. Lemoine (=*Melyvonnea* Athanas. et D. L. Ballant.), *M. erubescens* (Foslie) Me. Lemoine (=*Melyvonnea*), *M. canariense* (Foslie) Me. Lemoine (=*Melyvonnea*), *M. discrepans* (Foslie) Me. Lemoine (=*Phragmope* Athanas.), *M. simulans* (Foslie) Me. Lemoine (=*Magnephycus* gen. nov.), *M. fragilissimum* (Foslie) Me. Lemoine (incertae sedis Magnephyceae trib. nov.), *M. australe* (Foslie) Me. Lemoine (=*Lithothamnion* Heydrich), *M. laxum* Me. Lemoine (=*Melyvonnea*?), *M. pulchrum* (Weber-van Bosse et Foslie) Me. Lemoine (=*Lithothamnion*), and

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the fossil species *M. vaughanii* (M. Howe) Me. Lemoine, *M. vignyense* (Me. Lemoine) Me. Lemoine, *M. koritzae* (Me. Lemoine) Me. Lemoine, *M. concretum* (M. Howe) Me. Lemoine, *M. isthmi* (M. Howe) Me. Lemoine, and *M. paronai* (Rain.) Me. Lemoine (all with uncertain generic position within the Corallinales).

The original concept of *Mesophyllum* included only vegetative characters and, in particular, the presence of a polystromatic coaxial hypothallium supporting either a thin or a well-developed perithallium, in the latter case forming erect branches and showing cell stratification. A generitype was selected by Ishijima (1942: 174, "the genotype [*sic*] *M. lichenoides* Ellis") and was later accepted by Hamel and Lemoine (1953: 77, "Espèce-type: *lichenoides* (Ellis) Lem.").

Following the first revision of the Foslie herbarium in the Norwegian University of Science and Technology (Adey and Lebednik 1967), Adey (1970: 23, 27) recognized 50 species of *Mesophyllum* and included *Polyporolithon* L. R. Mason (1953: 316; type: *P. conchatum* (Setch. et Foslie) L. R. Mason) as a heterotypic synonym. Heydrich (1907, 1909a, 1909b, as *Sphaeranthera* Heydrich), Suneson (1937, as *Lithothamnion*), and Lebednik (1977b) studied postfertilization stages in members of the genus and demonstrated the presence of a fusion cell with a radiating gonimoblast producing lateral carposporangia from the periphery, as also described in *Clathromorphum* Foslie (Lebednik 1977b), *Neopolyporolithon* W. H. Adey et H. W. Johans. (Masaki and Tokida 1961b, as *Polyporolithon*), and *Leptophytum* (Adey 1966).

Athanasiadis and Ballantine (2014) recognized a strictly northern hemisphere distribution for 11 dioecious members of *Mesophyllum* sensu stricto, erecting *Melyvonnea* to include monoecious species with branched perithallial protuberances, spheroid carposporangial chambers (lacking a central pedestal), and elongate basal cells in pore filaments lining the canals of multiporate roofs. Adey et al. (2015) resurrected the genus *Neopolyporolithon* W. H. Adey et H. W. Johans. (1972) and also proposed *Callilithophytum* P. W. Gabrielson et al. as another segregate of *Clathromorphum*.

Therefore, the family Mesophyllaceae was erected to distinguish those multiporate corallines . . .

> possessing a central fusion cell with peripheral production of carposporangia, spermatangia of predominantly "simple" structure – "dendroid" ones sporadically observed in *Leptophytum* and certain members of *Synarthrophyton* R.A. Townsend, epithallial cells generally flattened to roundish (neither flared, nor domed), and hypothallium predominantly coaxial in *Melyvonnea* and *Mesophyllum*, to non-coaxial or with rare coaxial patches in the other members.[2] (Athanasiadis 2016b: 251)

At this stage the Mesophyllaceae included five genera in the northern hemisphere (*Clathromorphum* s.l., *Kvaleya*, *Leptophytum*, *Melyvonnea*, and *Mesophyllum*) and certain species of the southern hemisphere genus *Synarthrophyton* (the type material of which was not examined).

The new multiporate family Mesophyllaceae was differentiated from the Melobesiaceae, which develop a heterotrichous or filamentous thallus, and from the Lithothamnionaceae, which develop carposporangia across the entire fertile zone after individual fertilizations. The new family was further supported by gene phylogenies (e.g., Bailey and Chapman 1998: figs. 1, 2; Bittner et al. 2011: fig. 1; Adey et al. 2015: fig. 6).

With the exception of the NW Pacific coast, the northern hemisphere was thereby comparatively well surveyed, and attention was concentrated on the southern hemisphere. In a series of papers it was shown that the Mesophyllaceae of South Africa; South America; and Australia, New Zealand, and the Chatham Islands had been poorly studied. Several new genera (*Amphithallia* Athanas., *Capensia* Athanas., *Carlskottsbergia* Athanas., *Perithallis* Athanas., *Phragmope*, *Printziana* Athanas., *Sunesonia* Athanas., and *Thallis* Athanas.) were established by examining herbarium collections from the Natural History Museum in London, University of Gothenburg, Naturalis Biodiversity Center, Lund University, Royal Botanic Gardens Victoria, Swedish Museum of Natural History, Norwegian University of Science and Technology, and Museum of New Zealand Te Papa Tongarewa, leaving open questions as to the identity of other species found as admixtures (see, e.g., *Perithallis incisa* (Foslie) Athanas. and *Magnephycus engelhartii* (Foslie) comb. nov.).

The molecular wave of the past 30 years created further questions, as these studies uncovered our incapacity (or unwillingness) to deal with taxonomic problems applying correct laboratory techniques. A further problem appeared with the closure of museums (e.g., the Swedish Museum of Natural History, Naturalis Biodiversity Center, and Muséum National d'Histoire Naturelle) and the introduction of "icono-specimens" which practically brought us back to the time of Mikael Foslie.[3]

The present work investigates whether phylogenetic methods could clarify the relationships among the mesophylloid genera, finding patterns in the distribution of characters, or whether their structural diversity represents a case of unordered evolutionary expression.

HERBARIUM AND COLLECTOR ABBREVIATIONS

AHFH	Allan Hancock Foundation Herbarium, University of Southern California, Los Angeles, California, USA
BM	Natural History Museum, London, United Kingdom
BR	Meise Botanic Garden, Meise, Belgium
C	University of Copenhagen, Copenhagen, Denmark.
CAT	Università di Catania, Catania, Italy
CHE	Société Nationale des Sciences Naturelles et Mathématiques de Cherbourg, Cherbourg, France
DWK	D. W. Keats

FH	herbarium of W. G. Farlow
GB	University of Gothenburg, Gothenburg, Sweden
herb. Afonso-Carrillo	herbarium of Julio Afonso-Carrillo
herb. Athanas.	herbarium of Athanasios Athanasiadis
herb. Cotton	herbarium of A. D. Cotton
herb. Dickie	herbarium of G. Dickie
herb. D. L. Ballant.	herbarium of D. L. Ballantine
Herb. Lugd. Bat	Herbarium Lugduno Batavo (specimens in L)
L	Naturalis Biodiversity Center, Leiden, Netherlands
LAM	Natural History Museum of Los Angeles County, Los Angeles, California, USA
LD	Lund University, Lund, Sweden
LTB	La Trobe University, Melbourne, Australia
MEL	Royal Botanic Gardens Victoria, Melbourne, Australia
MICH	University of Michigan, Ann Arbor, Michigan, USA
MSM	University of Puerto Rico, Mayagüez, Puerto Rico
NY	New York Botanical Garden, Bronx, New York, USA
NZC	New Zealand Collection
PC	Muséum National d'Histoire Naturelle, Paris, France
S	Swedish Museum of Natural History, Stockholm, Sweden
SANT	Universidad de Santiago de Compostela, Santiago de Compostela, Spain
SNU	Seoul National University, Seoul, South Korea
TCD	Trinity College, Dublin, Ireland.
TFC	Universidad de La Laguna, San Cristóbal de La Laguna, Santa Cruz de Tenerife, Spain
TRH	Norwegian University of Science and Technology, Trondheim, Norway
UBC	University of British Columbia, Vancouver, British Columbia, Canada
UC	University of California, Berkeley, California, USA
UPS	Museum of Evolution, Uppsala, Sweden
US	Smithsonian Institution, Washington, D.C., USA
WELT	Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand
YMC	herbarium of Y. M. Chamberlain (presently in BM)

MATERIALS AND METHODS

With the lack of biosystematic studies (i.e., life history observations in culture and hybridization attempts), species circumscriptions are based on character combinations derived from morphological and anatomical observations of juvenile and fertile specimens. Specimens were examined either in the field or as liquid-preserved or dried collections. In the laboratory, specimens were examined under a Zeiss Stemi SV 6 microscope (Zeiss, Jena, Germany). For anatomical observations, transections (30–50 µm thick) were made using a Kryomat 1700 freezing microtome (Leitz, Stuttgart, Germany) on material decalcified using acetic acid (20%–45%, 5–24 h), stained and hardened in aniline blue (1%–5% solution with alcohol 96% for at least 24 h), and embedded in Hamilton's freezing solution (1 g gum arabic:30 g sucrose:1 crystal of thymol:100 mL distilled water). Microscopic preparations were mounted in ~60% Karo corn syrup (Best Food Division, CPC International, Englewood Cliffs, NJ, USA) on microscope slides. Photomicrographs were taken using a scanner (Epson Perfection V700, model J221A, Epson, Indonesia or CanoScan LiDE 200, Canon Inc., Vietnam) or a camera (Nikon D7000, Nikon Europe B.V.), the latter attached to a Zeiss Axiophot 2 microscope (Zeiss, Jena, Germany). Holotypes of the new genera *Protomesophyllum* and *Orthocarpa* have been deposited at GB. Other slides and specimens, including original material, exist in the herbarium of the senior author (herb. Athanas.), with duplicates in GB, MSM, and the herbarium of D. L. Ballantine. Herbarium abbreviations follow Holmgren et al. (1990), and nomenclature follows the Shenzhen Code (Turland et al. 2018). Descriptive terminology follows Bold and Wynne (1978) and Athanasiadis and Ballantine (2014). The following abbreviations are used in the text:

B	breadth
bp	base pair
coll.	collector
D	diameter
det.	determined
H	height
L	length
leg.	legitimated
MYA	million years ago
n	number of measurements
S.E.	Siboga Expedition
SEM	scanning electron microscope
Sith.	Sithonia (northern Greece)
SMCs	spermatangial mother cells
Stat., St., Stn.	station
W	width

Phylogenetic reconstructions were inferred using Phylogenetic Analysis Using Parsimony (PAUP, versions 3.1.1 to 4.0a), developed by David Swofford for the Macintosh computer (Swofford and Begle 1993), in combination with MacClade (versions 2.1 to 4.08a; Maddison and Maddison 1987). The heuristic algorithm was generally applied using the random-addition sequence with 100 replicates.

Character assessment was based on examination of specimens and/or literature data supported by illustrations (e.g., Adey 1966). In the phylogenetic analyses, characters were treated in a binary way (present or absent) or as multistate variables (when individual states could be unambiguously considered homologous and mutually exclusive). Characters showing variation within a genus were coded as uncertain (?) when referring to the genus as a whole (e.g., trichocyte occurrence in *Leptophytum*). All characters and character states were treated as unordered and given the same weight, except for (1) thallus organization (character 1), which was given double weight since the various states (e.g., monopodial-dorsiventral organization or heterotrichy) represent a multigene expression, and (2) pedestal formation in male conceptacles of *Hyperandri* gen. nov. and *Magnephycus* (character 19), which was considered a priori a synapomorphy (as explained below), which required a three-grade weight. Complex anatomical structures such as coaxial growth were divided into several (independent) characters, increasing the level of anatomical resolution. Autapomorphies of species were included when representing states of characters with several mutually exclusive conditions.

The data matrix includes 29 ingroup taxa (species and genera) and 40 vegetative and reproductive characters (Table 1) that could be unequivocally defined (and illustrated) at a structural level. Two genera of Melobesiaceae, *Melobesia* J. V. Lamour. and *Orthocarpa* gen. nov., were used as outgroups. DELTRAN was generally applied in the analyses. This gives preference to parallelisms over reversals, but no changes were observed using accelerated transformation (ACCTRAN). Monophyletic groups (i.e., new genera, tribes, and subfamilies) were recognized on the basis of strict consensus trees.

Two basic assumptions (axioms) underlie the above phylogenetic methods: (1) organisms are interrelated by the shortest (most parsimonious) genetic distances, and (2) life has a hierarchy

TABLE 1. Data matrix including 29 ingroup and two outgroup taxa (*Melobesia*, *Orthocarpa*) and 40 characters, some with several character states. Character coding (0,1,2,3,4,5) appears below. A question mark (?) indicates characters that are uncertain or unknown.

			1		**2**			**3**		**4**
Taxon (genera in all caps)	**1234**	**5678**	**9 0 12**	**3456**	**789 0**	**1234**	**5678**	**9 0 12**	**3456**	**789 0**
Magnephycus ornatus	0000	0011	1100	0000	1112	0000	0001	1010	1000	0011
Magnephycus engelhartii	0001	1011	1100	0000	?100	????	?001	1010	1000	0000
Magnephycus simulans	0001	1011	1100	000?	????	????	?001	1010	1000	0011
ECTOCARPA	0000	0011	1100	000?	????	????	??00	0000	0001	0001
Hyperandri bisporum	0000	0000	0100	0100	0111	????	?110	1000	0000	0000
Hyperandri siamense	0000	0000	0100	000?	????	????	?110	1?00	0000	0000
Hyperandri dawsonii	0000	0000	0100	0000	0111	????	????	????	???0	????
Macedonis tethygenis	0000	0001	1100	0101	0100	0000	0110	1000	0100	0010
Macedonis julieae	0000	0001	1100	000?	????	????	?010	1000	0100	0000
Macedonis lamellicola	0000	0000	1100	0001	1100	???0	0010	1000	0100	0000
LEPTOTHALLIA	0000	0000	0100	0100	1100	0000	0010	1000	0000	00?0
LEPTOPHYTUM	0000	01?0	?100	0?00	1100	1000	0010	1000	0000	0000
PHRAGMOPE	0002	2000	0110	0100	1100	0000	0010	0000	0000	0000
MESOPHYLLUM	0002	2000	?110	00?0	0100	2001	1010	1000	0000	0000
MELYVONNEA	0002	2000	0110	0111	0100	0002	0013	1000	0000	1100
MACROBLASTUM	0002	2000	0110	0111	2100	0002	0010	1000	0000	0000
PERITHALLIS	3002	2010	1110	0100	0100	0001	1000	1100	0010	1100
THALLIS	0001	1000	0110	0?00	0100	1001	1010	1100	0010	1100
PRINTZIANA	0002	2000	0111	0110	0100	1001	1013	1101	0010	1100
SUNESONIA	0001	1000	0110	001?	????	????	?013	1102	0010	1100
AMPHITHALLIA	1001	1010	1110	0101	2100	0200	0000	0000	0000	0000
SYNARTHROPHYTON	1001	1010	0110	0000	2100	0000	?002	1000	0000	0000
CARLSKOTTSBERGIA	1100	0010	1100	0?00	0100	1000	0001	1000	0000	0000
CAPENSIA	2100	0010	0110	0100	0100	1000	0000	1000	0000	0000
PROTOMESOPHYLLUM	0001	1000	0110	0000	0000	0000	0010	0000	0000	0000
CLATHROMORPHUM	0010	00?0	0111	1000	0000	0000	0010	0000	0000	0000
NEOPOLYPOROLITHON	0010	00?0	0011	1000	0000	1000	0010	0000	0000	0000
CALLILITHOPHYTUM	4210	00?0	0011	100?	0000	1000	0010	0000	0000	0000
CLATHMOROA	0010	00?0	0111	1000	0?00	0010	0010	0000	0000	0000
ORTHOCARPA	0000	00??	0110	0?0?	?000	0110	0010	0000	0000	0?00
MELOBESIA	5300	0000	0110	000?	0000	0110	0000	0000	0000	0000

(*continued*)

TABLE 1. (*Continued*)

Character no.	Character Description
1	Thallus organization: dorsiventral (0), bilateral (1), sympodial (2), anisobilateral (3), bilateral perithallium (4), heterotrichous (5)
2	Hypothallium: polystromatic (0), monostromatic-bilateral (1), reduced (2), monostromatic with ascending filaments (3)
3	Apical meristem gradually becoming immersed (embedded): absent (0), present (1)
4	Arching hypothallium: absent (0), patches or regions (1), predominant (2)
5	Synchronous divisions and elongations: absent (0), patches or regions (1), predominant (2)
6	Subepithallial cells short: absent (0), present (1)
7	Ascending perithallium limited: absent (0), present (1)
8	Elongate subbasal hypothallial cells: absent (0), present (1)
9	Superimposed unattached growth: absent (0), present (1)
10	Epithallial cells flattened-rectangular: absent (0), present (1)
11	Epithallial cells isodiametric: absent (0), present (1)
12	Epithallial cells elongate: absent (0), present (1)
13	Epithallial cells in series (>3): absent (0), present (1)
14	Trichocytes: absent (0), present (1)
15	Perithallial protuberances: absent (0), present (1)
16	Dioecy (0), monoecy (1)
17	Spermatangia dendroid: absent (0), rare (1), common (2)
18	SMCs lunate: absent (0), present (1)
19	SMCs on pedestal: absent (0), present (1)
20	Pedestal: absent (0), 1-celled (1), multicellular (2)
21	Fusion cell: inconspicuous or up to 3 cells (0), >4–6 supporting cells + 1–2 hypogynous cells (1), >10 supporting cells + 10 hypogynous cells (2)
22	Fusion level: supporting cell (0), hypogynous cell (1), nonprocarpy (2)
23	Orthostichous carposporangia: absent (0), present (1)
24	Carposporangial chamber: elongate (0), pedestal (1), spherical (2)
25	Gonimoblasts bend down: absent (0), present (1)
26	Multiporate conceptacles colliculate: absent (0), present (1)
27	Conceptacles embedded: absent (0), present (1)
28	Canal shape: straight (0), pyriform (1), triangular (2), wider base (3)
29	Pore cells thinner–wider: absent (0), present (1)
30	Basal pore cells branched: absent (0), present (1)
31	Basal pore cell elongate (pyriform canals): absent (0), present (1)
32	Basal pore cell elongate (in straight canals): absent (0), present (1), reduced (2)
33	Subbasal pore cell elongate (in pyriform canals): absent (0), present (1)
34	Subbasal pore cell elongate (in unbranched pore filaments): absent (0), present (1)
35	Subbasal pore cell elongate (in branched pore filaments): absent (0), present (1)
36	Basal and subbasal pore cells larger–elongate: absent (0), present (1)
37	Pore cells fewer than contiguous roof cells: absent (0), present (1)
38	Rosette cells (surface pore cells) sunken: absent (0), present (1)
39	Second roof formed by peripheral filaments: absent (0), present (1)
40	Multiporate conceptacle roof hemispherical: absent (0), present (1)

exemplified by a progressive genesis of new taxa through modification. Using characters as markers and polarizing them with the outgroup method, we are able to distinguish between advanced (recently evolved) and ancestral (primitive = basal) taxa. This is logically demonstrated in examples with few distantly related organisms, and problems appear when we attempt reconstructions of entire species complexes (that we assume to represent monophyletic groups). The reason is that the genome of related species is rather homogeneous and the expression of many characters controlled by single-copy genes that can be "switched off" in taxa of common descent and reappear in distant relatives. As a result, similar characters may indicate either a common ancestry or parallelisms (Athanasiadis 1996a).

RESULTS

DIVISIONS OF CORALLINALES

The order Corallinales was resurrected and validated by Silva and Johansen (1986) to include geniculate and nongeniculate members, as well as multiporate and uniporate ones,[4] with

Sporolithon Heydrich set apart from all other corallines because of the lack of zonately divided tetrasporangia within conceptacles (Figure 1a, features 10, 11). Earlier, Johansen (1969: 44–48) had divided the coralline algae into seven subfamilies: three nongeniculate, that is, Melobesioideae Bizzozero (multiporate including *Sporolithon*), Lithophylloideae Setch. (uniporate), and Mastophoroideae Setch. (uniporate), and three geniculate and uniporate, that is, Amphiroideae H. W. Johans., Metagoniolithoideae H. W. Johans., and Corallinoideae S. F. Gray.[5] A seventh subfamily, the Schmitzielloideae H. W. Johans. (1969), was later transferred to Gigartinales (Pueschel 1989). Johansen's (1969) classification was followed by that of Woelkerling (1988: vi, table 5.1), who treated the nongeniculate corallines in four subfamilies: Melobesioideae (multiporate), Lithophylloideae (uniporate), Mastophoroideae (uniporate), and the monotypic Choreonematoideae Woelk. (uniporate). Earlier, however, Cabioch (1971, 1972: fig. 40) had proposed a more natural classification, taking into account ontogenetic criteria and including geniculate and nongeniculate genera in the subfamilies Corallinoideae and Lithophylloideae. Cabioch (1972: 264) also accepted the separate subfamily Sporolithoideae

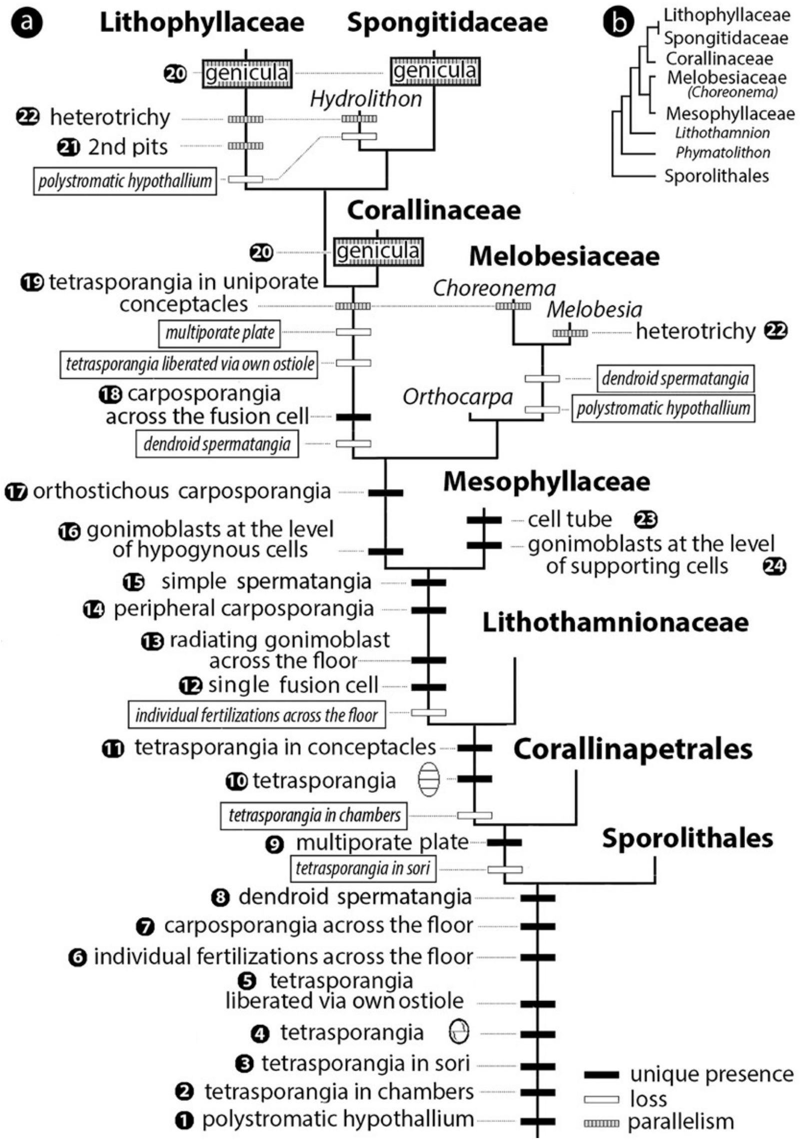


FIGURE 1. Division of Corallinales. (**a**) Morphoanatomical evolution in the Corallinales, Corallinapetrales, and Sporolithales based on parsimony. Development of genicula occurred within the uniporate families as a parallelism. For further explanation see text. (**b**) Relationships between genera and families of Corallinales and Sporolithales, as indicated by maximum likelihood analysis of 192 nSSU sequences (simplified from fig. 1 of Bittner et al. 2011).

Setch., later raised to the now widely accepted order Sporolithales L. Le Gall et G. W. Saunders.

In the first DNA phylogeny (nSSU gene), Bailey and Chapman (1996, 1998: fig. 1) reported the relationship Sporolithaceae Verheij–(Melobesioideae–Corallinoideae (Mastophoroideae (Metagoniolithoideae (Amphiroideae–Lithophylloideae)))). Bailey and Chapman (1998: 695, figs. 4, 5) also examined the distribution of seven characters but did not include significant reproductive features such as spermatangial morphology, carposporangial production, and the development of a single fusion cell. Nor was the position of the enigmatic genera *Choreonema* F. Schmitz and *Melobesia* considered. Bailey and Chapman concluded, however, that the distinction between geniculate and nongeniculate corallines was purely artificial.

Using a larger set of genera, Harvey et al. (2003a: figs. 1, 2) studied the same gene and reported the relationship Sporolithaceae–("Hapalidiaceae J. E. Gray"–Corallinaceae), with the uniporate *Choreonema* placed in the periphery of "Hapalidiaceae" as a sister taxon to two South African species of *Leptophytum* (one here recognized as *Leptothallia acervata* gen. et comb. nov.). With the single exception of *Choreonema*, Corallinaceae included all other uniporate genera, with at least one subfamily (Lithophylloideae) including both geniculate and nongeniculate members (in agreement with Cabioch and Bailey and Chapman). Harvey et al. (2003a: table 3) further divided the multiporate "Hapalidiaceae" into three subfamilies: Melobesioideae (including all known members of Lithothamnionaceae, Mesophyllaceae, and Melobesiaceae), the monotypic Choreonematoideae, and Austrolithoideae A. S. Harv. et Woelk. (including *Austrolithon* A. S. Harv. et Woelk. and *Boreolithon* A. S. Harv. et Woelk.). The anomalous position of *Choreonema* was clarified by Broadwater et al. (2002), who showed in this taxon the presence of a multiporate plate during the early development of the uniporate conceptacles. Therefore, *Choreonema* showed the direction of evolution from multiporate to uniporate tetrasporangial conceptacles, albeit as a parallelism within the multiporate Melobesioideae.

Using a different set of taxa, Broom et al. (2008: fig. 5) studied the same gene phylogeny and similarly concluded that uniporate and multiporate corallines were two distinct groups. The uniporate *Choreonema* was still resolved within the multiporate Melobesioideae.

The same gene phylogeny was studied by Kato et al. (2011: fig. 1), who focused on the relationships between members of the uniporate genera. They similarly reported uniporate and multiporate corallines as two distinct groups. *Choreonema* reappeared in the periphery of Melobesioideae, but Kato et al. did not treat any member of *Lithothamnion* or *Phymatolithon* Foslie.

Using data from an even larger group of taxa, Bittner et al. (2011: fig. 1) studied the same gene phylogeny and showed that *Lithothamnion* and *Phymatolithon* are two independent clades near Sporolithales (Figure 1b). All other multiporate genera resolved as a single group ("Hapalidiaceae"), being the sister taxon to the uniporate corallines. *Choreonema* resolved in the periphery of "Hapalidiaceae," in agreement with Harvey et al. (2003a) and Kato et al. (2011).

Using concatenated sequences from seven genes (including the nSSU gene), Peña et al. (2020: figs. 2, 3) showed *Melobesia* is located either within or in the periphery of "Hapalidiales W. A. Nelson et. al."

We have reasons to avoid the names "Hapalidiaceae" and "Hapalidiales."[6]

On the basis of the distribution of 24 widely applied features, a phylogenetic tree is constructed showing the relationships between Corallinales (and its families), Corallinapetrales Jeong et al. (2021), and Sporolithales (Figure 1a), with the topology of the terminal taxa being partly in agreement with Bittner et al. (2011: fig. 1; Figure 1b). It shows that *Lithothamnion* and *Phymatolithon* (Lithothamnionaceae) should be excluded from the other multiporate families (i.e., Mesophyllaceae and Melobesiaceae). Features supporting the exclusion of the Mesophyllaceae and Melobesiaceae from the Lithothamnionaceae are the development of simple (unbranched) spermatangia (feature 15) and a fusion cell[7] (feature 12) with a radiating gonimoblast (feature 13) producing carposporangia laterally from the periphery (feature 14). Melobesiaceae forms a clade with the uniporate families based on orthostichous[8] production of carposporangia (near the edge of the fertile zone; feature 17) and development of a fusion cell at the level of hypogynous cells (feature 16). Mesophyllaceae appears as the sister taxon, being distinguished by the development of a cell tube (feature 23) and production of radiating gonimoblasts from the supporting cells (feature 24) after the formation of a fusion cell. Finally, the uniporate families (feature 19) are distinguished by the production of carposporangia across the dorsal side of a fusion cell[9] (feature 18), whereas other differentiations such as secondary pit connections (feature 21) and heterotrichy[10] (feature 22) occur in the more recently evolved members together with the appearance of genicula as a parallelism across all uniporate families (feature 20). Sterile cells, borne beside the carpogonium, have been reported in all families of Corallinales, including Lithothamnionaceae (Suneson 1943: figs. 4F, 10D), Mesophyllaceae, and Melobesiaceae (present data), as well as in all uniporate families (Suneson 1943: fig. 42). Their development seems to be a synapomorphy for the order since their presence in Sporolithales and Corallinapetrales is so far unknown.

In Sporolithales, all studies have indicated the lack of a single fusion cell and the development of carposporangia from carpogonia across the fertile floor after individual fertilization in each carpogonium (features 6, 7; see review in Lebednik 1977b: 385, table 3; Townsend et al. 1995: 91; Bahia et al. 2015).

Similarly, in both *Phymatolithon* and *Lithothamnion*, there are only observations of fragmented or discontinuous or several small fusion cells (Suneson 1943: 12, in *Lithothamnion sonderi* Hauck; Adey 1964: pl. 5, figs. 63, 64, in *Phymatolithon rugulosum* W. H. Adey; Adey and Adey 1973: figs. 22–24, in *Lithothamnion* cf. *glaciale* Kjellm.; see review in Lebednik 1977b: table 3), as well as records of the absence (or uncertainty) of a fusion cell (Suneson 1943: 8, "no fusion-cell" in *L.* (*Phymatolithon*) *lenormandii* (F. Aresch.) Foslie, 21, "not state[d by Rosenvinge] with certainty" in *L.* (*Phymatolithon*) *purpureum* P. L. Crouan et H. M. Crouan), including the generitype of *Lithothamnion,* *L. muelleri* Rosanoff (Wilks and Woelkerling 1995: 555, "[no] large central fusion cell"). More recently, studying the postfertilization in North Atlantic species of *Phymatolithon*, Adey et al. (2018: 42–43, fig. 12) confirmed the lack of a single radiating fusion cell and the presence of "many single celled gonimoblast filaments . . . across the fertile disc, each producing a single large carposporangium." Their study consolidates all previous reports in this genus. Hence, the consensus of observations in the Lithothamnionaceae indicates the absence of a single fusion cell with a single radiating gonimoblast and the presence of independent fertilizations followed by carposporangial production across the fertile floor (as in the Sporolithales).

The presence of cruciately-decussately divided tetrasporangia in the Sporolithales (feature 4) is certainly a plesiomorphy given that this sporangium type occurs in most other rhodophytes, whereas the simultaneously divided zonate tetrasporangia (feature 10) is an apomorphy for the Corallinales (Guiry: 1978, 1990: 371). The sorial aggregation of tetrasporangia (feature 3) is also a plesiomorphic condition, occurring in several other red algal orders (e.g., Peyssonneliales) and maintained in the Sporolithales.

In terms of thallus structure, the monopodial-dorsiventral organization with a polystromatic hypothallium (feature 1) represents the ancestral (plesiomorphic) condition, being replaced by a heterotrichous organization (feature 22) in certain Melobesiaceae, in the Lithophyllaceae Athanas., and also in certain subfamilies of the Spongitidaceae Kütz. (i.e., Hydrolithoideae A. Kato et M. Baba and Mastophoroideae). Reduction of the polystromatic hypothallium to single filaments takes place in certain Melobesiaceae (i.e., in *Choreonema* and *Austrolithon*), whereas in *Callilithophytum*, *Capensia*, and *Carlskottsbergia* we see other specializations; see "Character Evolution in the Mesophyllaceae."

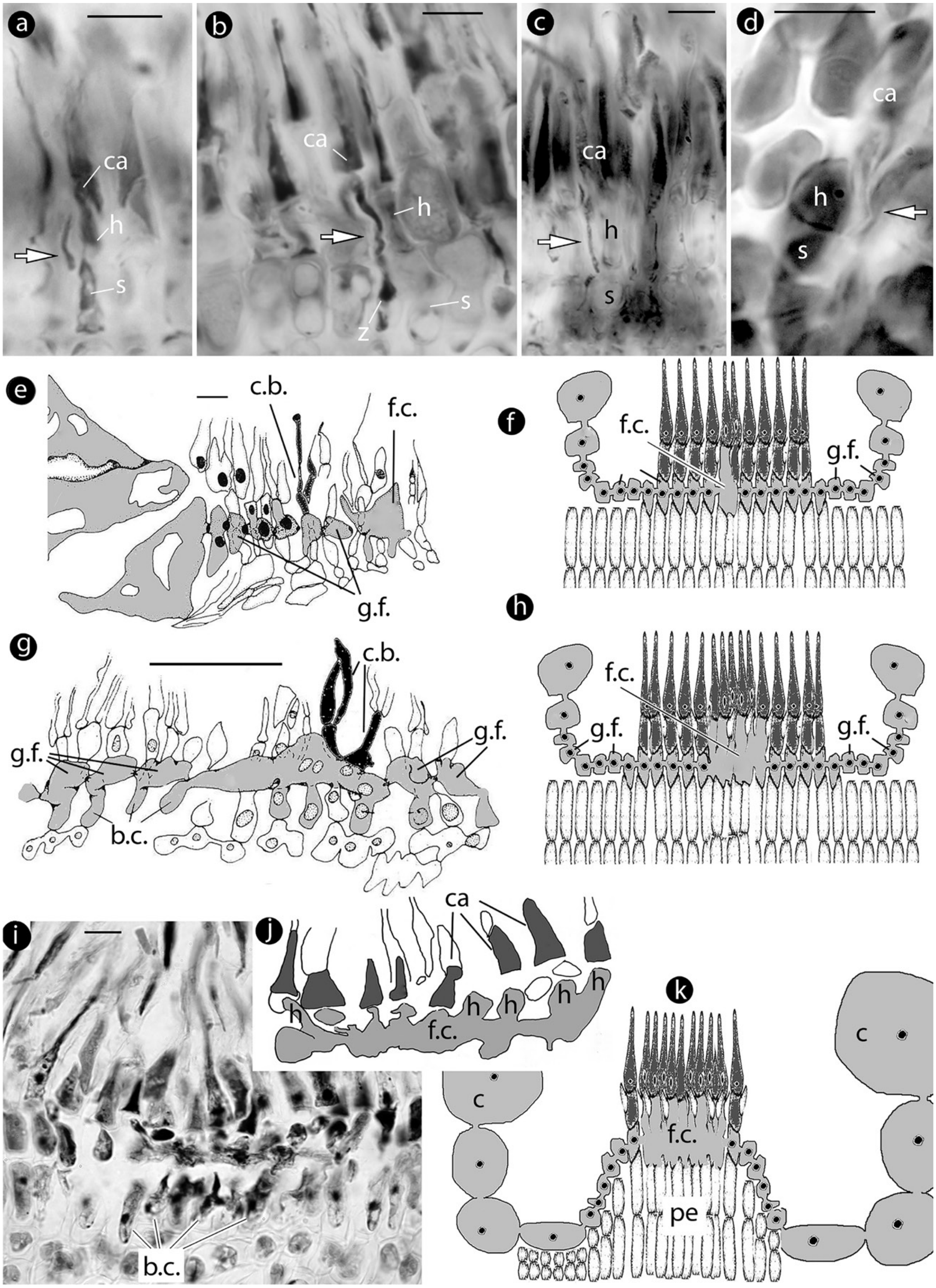
With the recognition of the new order Corallinapetrales (Jeong et al. 2021), the significance of the multiporate plate (feature 9) in the evolution of Corallinales has been downgraded. The earliest shared condition in this structure is the presence of a single canal (ostiole) for each tetrasporangium (feature 5) that was maintained until the advent of uniporate conceptacles (feature 18). The chamber formation itself (feature 2) is also a plesiomorphy, maintained in the Sporolithales and Corallinapetrales and evolved into the conceptacles (feature 11) in the Corallinales via reduction of the tissue that keeps sporangia isolated.[11] However, first, we have to assume a closer spatial distribution of sporangia, in roundish groups, resulting in the multiporate plate, first materialized above chambers (like what occurs in *Corallinapetra* T. J. Farr et al.; Nelson et al. 2015: fig. 4a). Hence, the multiporate plate originated in the ancestor of Corallinapetrales and Corallinales and was maintained as the pore plate of conceptacles in Corallinales, disappearing with the advent of uniporate tetrasporangial conceptacles.[12]

Delimitation of the Family Mesophyllaceae

The old mesophylloid assemblage included species here assigned to the new subfamilies Orthocarpoideae, Clathromorphoideae, Protomesophylloideae, and Mesophylloideae. Orthocarpoideae comprise the single genus *Orthocarpa* (type: *O. epicklonia* sp. nov.) that accommodates nearly all species previously referred to *Synarthrophyton* and here excluded from this genus because they lack a bilateral thallus organization and possess instead a monopodial-dorsiventral thallus with polystromatic hypothallium, orthostichous production of carposporangia, straight canals, and pore filaments of multiporate conceptacles composed of nondifferentiated cells (except for basal cells). The type species of *Orthocarpa* and *O. haptericola* comb. nov. share postfertilization features with *Melobesia*, and therefore, the Orthocarpoideae are placed in Melobesiaceae, expanding the circumscription of this family to accommodate even members displaying dendroid spermatangia, sterile cells, and a monopodial-dorsiventral thallus with a polystromatic noncoaxial hypothallium (which are ancestral conditions in Corallinales).

The Mesophyllaceae (including the subfamilies Clathromorphoideae, Protomesophylloideae, and Mesophylloideae) are segregated from the Melobesiaceae in developing a cell tube leading the zygote beyond the hypogynous cell to the supporting cell (Figure 2a–d) and in producing a single fusion cell at the level of supporting cells (Figure 2e–k) with subsequent development of lateral carposporangia from the periphery of the radiating gonimoblast. These characters were originally observed in members of *Mesophyllum* and *Clathromorphum* s.l. by Lebednik (1977b: 391, fig. 14). Although presently documented only in *Protomesophyllum*, *Mesophyllum*, *Printziana*, and *Thallis* (Figure 2a–d), the development of a cell tube has to be regarded as a synapomorphy

FIGURE 2. (*Opposite*) Postfertilization in Mesophyllaceae. (**a–d**) Cell tube development (arrows) from the carpogonium, bypassing the hypogynous cell and reaching the supporting cell. Note the zygote. Scale bars: 10 µm. (a) *Protomesophyllum ameleteton* (NZC0950). (b) *Mesophyllum lichenoides* (Suneson slide 131a–e in GB). (c) *Printziana insignis* (syntype in UC). (d) *Thallis capensis* (paratype in herb.Athanas.). (**e, f**) Development of an inconspicuous fusion cell in *Clathromorphum circumscriptum* with diagrammatic illustration. Modified from Lebednik (1977b: fig. 10). Scale bar: 50 µm. (**g, h**) Development of a medium-size fusion cell in *Callilithophytum parcum* with diagrammatic illustration. Modified from Lebednik (1977b: fig. 9). Scale bar: 50 µm. (**i–k**) Development of a large fusion cell in *Mesophyllum lichenoides* with diagrammatic illustrations also showing the formation of a pedestal. Modified from Athanasiadis (2018: figs. 6, 7). Scale bar: 10 µm. Abbreviations: b.c., basal cell; c, carposporangium; ca, carpogonium; c.b., carpogonial branch; f.c., fusion cell; g.f., gonimoblast filament; h, hypogynous cell; pe, pedestal; s, supporting cell.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for the Mesophyllaceae, being a prerequisite for the zygote to bypass the hypogynous cell and reach the supporting (auxiliary) cell. Fusion at the level of the supporting cell and subsequent development of a single radiating gonimoblast (Figure 2f,h) has been documented in the majority of genera of Mesophyllaceae, whereas strictly lateral production of carposporangia has been documented in all species with known postfertilization stages, with the single exception of *Clathmoroa tubiformis* comb. nov. In several members of Melyvonneeae trib. nov., gonimoblasts may even bend down to fill the gap created by pedestals (Figure 2k), whereas in *Amphithallia* the presence of a connecting filament has been documented and interpreted as nonprocarpy (probably leading the zygote to contiguous auxiliary cells; Athanasiadis 2019b).

In the Melobesiaceae the fusion cell appears at the level of hypogynous cells, and the radiating gonimoblast produces carposporangia both laterally and orthostichously (below), whereas in the uniporate families these characters merit further studies, with those available suggesting similarities with the Melobesiaceae.[13]

The Mesophyllaceae in their majority exhibit the ancestral, monopodial-dorsiventral thallus organization that occurs in all families of Corallinales (except Lithophyllaceae; Figure 1a, feature 1), lacking the more recently evolved heterotrichous organization that characterizes several members of Melobesiaceae (i.e., *Melobesia*, *Boreolithon*, *Exilicrusta* Y. M. Chamb.), and certain uniporate families (i.e., Lithophyllaceae) or subfamilies of Spongitidaceae (i.e., Hydrolithoideae and Mastophoroideae; Figure 1a, feature 22). Development of a bilateral thallus organization (Amphithallieae trib. nov.), sympodial growth (*Capensia*), and monostromatic hypothallia with bilateral ramification (*Carlskottsbergia*, *Capensia*) that occur in certain Mesophyllaceae are to be regarded as differentiations departing from the ancestral thallus organization (as supported by the present phylogenetic analysis; see “Phylogenetic Relationships in the Mesophyllaceae”).

In conclusion, the Mesophyllaceae are segregated within the Corallinales with regard to postfertilization events and, in particular, in developing a cell tube that leads the zygote beyond the hypogynous cell to the supporting cell, in producing a fusion cell with a single radiating gonimoblast at the level of supporting cells, and (with the single exception of *Clathmoroa* gen. nov.) in cutting off carposporangia only laterally from the periphery of the fertile zone (Figure 1a, features 14, 23, 24), whereas in their closest relative, the Melobesiaceae (at least in *Melobesia* and *Orthocarpa*), a cell tube is lacking, the fusion cell develops at the level of hypogynous cells (just below the carpogonia), and the radiating gonimoblast produces carposporangia both laterally and orthostichously.

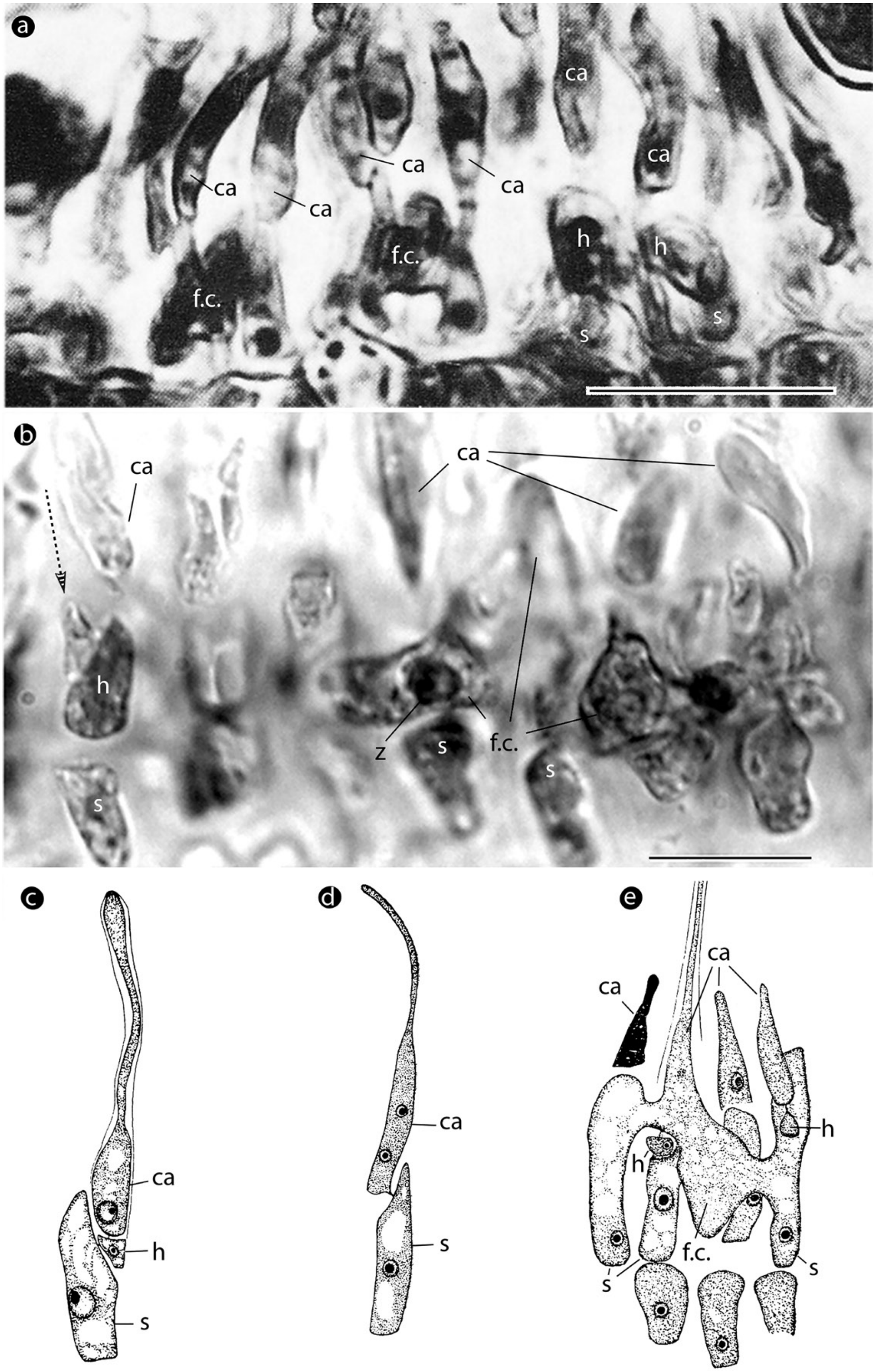
An alternative classification would be to place Orthocarpoideae in Mesophyllaceae, which would result in recognizing the lack of heterotrichy as the only character distinguishing Mesophyllaceae from Melobesiaceae. Heterotrichy, however, has evolved independently several times in the Corallinales (Figure 1a), as well as in several genera of green and brown algae (Fritch 1935), suggesting that it is a less conservative character (compared to the reproductive apparatus).

OUTGROUP TAXA *ORTHOCARPA* AND *MELOBESIA* (MELOBESIACEAE)

The genera *Orthocarpa* and *Melobesia* were examined in order to support their selection as outgroups of Mesophyllaceae, and it was concluded that they possess the largest number of similarities with the Mesophyllaceae. Indeed, *Orthocarpa* and *Melobesia* also resemble each other, sharing most of their reproductive characters, namely, monoecy, simple (unbranched) spermatangia (in the generitype *O. epicklonia*), 2- or 3-celled carpogonial branches, the lack of a cell tube (transferring the zygote), fusion at the level of hypogynous cells (just below the carpogonia; Figure 3a,b), and gonimoblast radiation at the level of hypogynous cells producing carposporangia both laterally and orthostichously from the periphery of the fertile zone. Tetrasporangial structures are also similar in these two genera, with canals of multiporate conceptacles displaying nondifferentiated pore cells (except for basal cells). *Orthocarpa* differs from *Melobesia* in sharing with the Mesophyllaceae the presence of sterile cells and the ancestral thallus organization (i.e., monopodial-dorsiventral thallus with polystromatic hypothallium). On the other hand, *Melobesia* shows a heterotrichous organization, which also occurs in certain uniporate corallines (Figure 1a).

A third member of Melobesiaceae is the parasitic genus *Choreonema*, whose thallus is composed of a conceptacle anchored to the host by a single hypothallial filament (potentially branched or reduced to a few cells). Hence, considering the thallus organization in *Orthocarpa*, *Melobesia*, and *Choreonema*, three different types occur that might be viewed as evolutionary steps from the ancestral dorsiventral condition (*Orthocarpa*)

FIGURE 3. (*Opposite*) Postfertilization stages in *Melobesia*, *Orthocarpa*, and *Choreonema* (Melobesiaceae). (**a**) *Melobesia membranacea*. Note the two separate fusions below the carpogonia at the level of hypogynous cells. Modified from Wilks and Woelkerling (1991: fig. 21). Scale bar: 10 µm. (**b**) *Orthocarpa epicklonia*. Note the fusions below the carpogonia at the level of hypogynous cells and above the supporting cells. One fusion includes the lower part of a carpogonium. A sterile cell (dashed arrow) attached to a hypogynous cell is visible (paratype). Scale bar: 10 µm. (**c–e**) *Choreonema thuretii*. Note the diminutive hypogynous cells (lost in (d)) that do not incorporate in the fusion that includes the lower part of the carpogonium with several supporting cells (Suneson 1937: fig. 34C–E). No scale. Abbreviations: ca, carpogonium; f.c., fusion cell; h, hypogynous cell; s, supporting cell.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to heterotrichy (*Melobesia*) and then to a reduced (filamentous) hypothallium (the latter also characterizing uniporate corallines such as *Amphiroa* J. V. Lamour.[14]).

In *Choreonema*, both Minder (1910: text fig. 9) and Suneson (1937: fig. 34C–E) described and illustrated a unique post-fertilization event that merits particular attention since it probably represents an intermediate condition between the Mesophyllaceae and at least *Orthocarpa* and *Melobesia* of the Melobesiaceae (including all uniporate families). In *Choreonema*, we have shrinkage (and eventually loss) of the hypogynous cell (Figure 3c,d). This condition practically makes the presence of a cell tube redundant, motivating its loss and resulting in zygote transfer, at least in *Choreonema* and *Orthocarpa*, being achieved via fusion of the lower part of the carpogonium with the subtending cells (Figure 3b,e).

Hence, the hypogynous cells of *Orthocarpa* or *Melobesia* might be regarded as a relocation of the supporting cells (following the loss of the diminutive hypogynous cell that still occurs in *Choreonema*). Indeed, Suneson also observed 2-celled carpogonia in *Choreonema*, lacking the diminutive hypogynous cell, which he interpreted as an "abnormal" condition (Suneson 1937: fig. 34D; Figure 3d).

Accounts of the three genera of Melobesiaceae, *Orthocarpa*, *Melobesia*, and *Choreonema*, are given in "Classification."

CHARACTER EVOLUTION IN THE MESOPHYLLACEAE

Thallus Organization

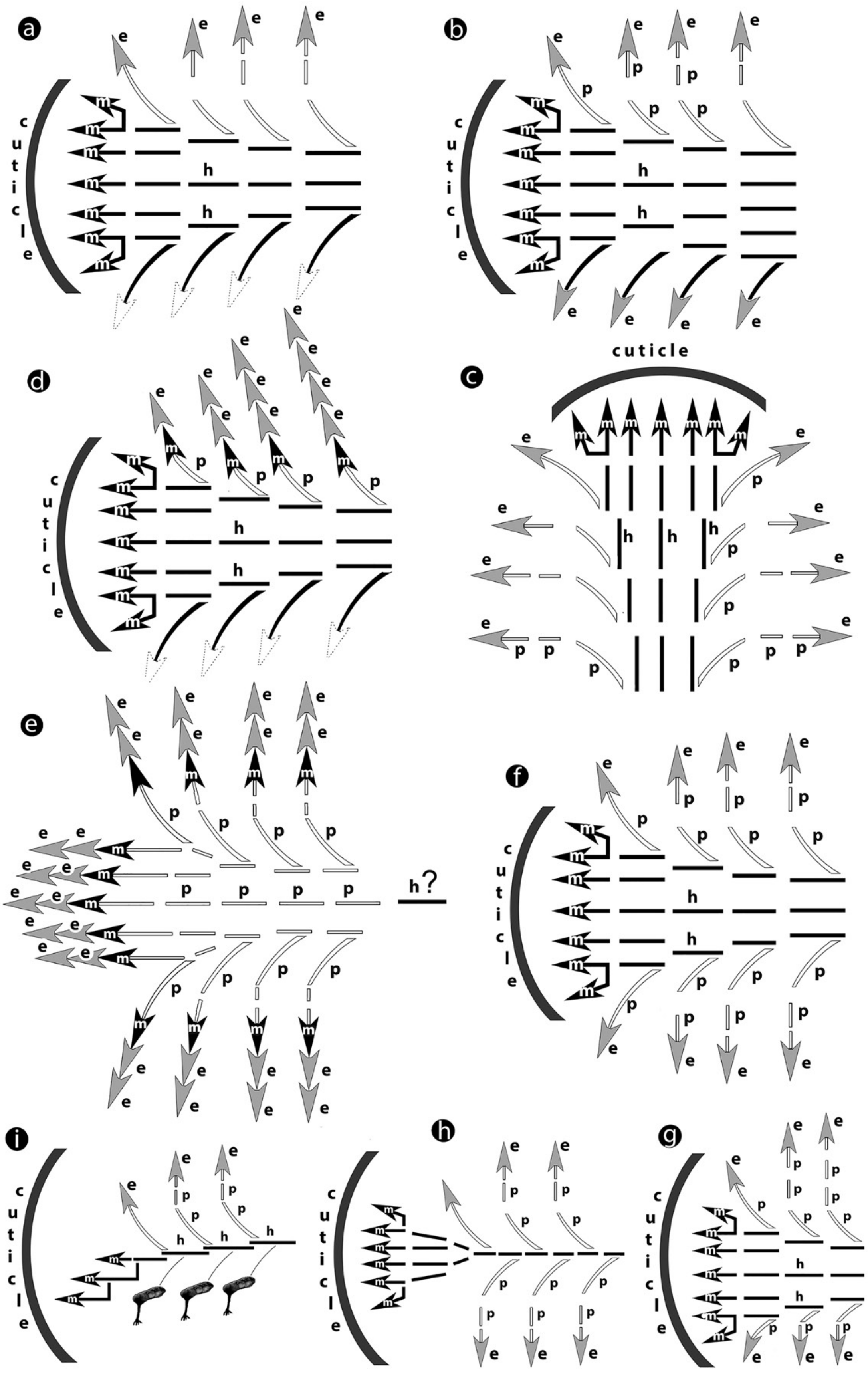
Understanding the thallus growth and organization of individual species is fundamental in perceiving the evolution of any algal group. Considering the primary (terminal) and secondary (subepithallial) meristems and the degree of growth of the tissues (hypothallium, perithallium, epithallium), at least eight types are here outlined in the Mesophyllaceae (Figure 4a-i),[15] and these types affect characters 1–3 of the phylogenetic analysis.

Monopodial-dorsiventral organization with a polystromatic hypothallium occurs predominantly in the Corallinales, Corallinapetrales, and Sporolithales and represents the ancestral (plesiomorphic) condition (see Figure 4a). It occurs in all Mesophyllaceae, as well as in *Orthocarpa* in Melobesiaceae. This growth is recognized by a group of terminal meristematic cells defining the hypothallium and operating below a protective cuticle. Via anticlinal[16] divisions, the original core of hypothallial filaments increases in length, whereas via subdichotomous divisions it increases in thickness so that peripheral filaments become displaced (dorsally and ventrally), forming an ascending perithallium[17] and descending hypothallial filaments (that face the substratum). Displaced terminal meristematic cells become epithallia, and subepithallial meristematic cells develop secondarily in the perithallium (except in Clathromorphoideae: see description below). The descending hypothallial filaments usually end in hyaline, wedge-shaped cells (facing the substratum), but in a few species with unattached growth (e.g., *Mesophyllum lichenoides*), they may bear epithallial cells (resulting from ventrally displaced terminal meristematic cells).

In *Mastophoropsis* Woelk. the above-described growth is restricted to branch tips (see Figure 4b,c), whereas in most other corallines apical growth occurs perimetrically (i.e., along the entire thallus margin, such as in *Peyssonnelia* Decne, *Cutleria* Greville, and *Zanardinia* Nardo). As a result, in *Mastophoropsis*, only vertical (or periclinal) sections along the direction of the growing tips will show the terminal meristematic cells (which produce the hypothallium with ascending, descending, or lateral perithallia ending in epithallial cells), whereas vertical sections parallel or below the growing tip will just show the internal hypothallial core supporting perithallia covered by epithallial cells (see the account for the genus; see Figure 61a-d).

In most Clathromorphoideae (i.e., in *Clathromorphum*, *Neopolyporolithon*, and most likely *Clathmoroa*), the terminal meristem progressively becomes embedded (see Figure 4d), and although the apical part maintains its function (to produce

FIGURE 4. (*Opposite*) Thallus growth in Mesophyllaceae. (**a**) The ancestral condition of monopodial-dorsiventral organization with a polystromatic hypothallium, involving terminal meristematic cells (black arrowheads) below a cuticle and defining the hypothallium (black bars). Displaced terminal filaments become ascending perithallia (white bars) with terminal epithallial cells (gray arrowheads) or descending hypothallial filaments facing the substratum. Displaced meristematic cells become epithallia. Subepithallial meristematic cells develop secondarily in the dorsal perithallium. (**b, c**) *Mastophoropsis*: as in (a), but restricted to offshoots and involving lateral production of perithallia and epithallia. (c) View from above. (**d**) *Clathromorphum*, *Neopolyporolithon*, and *Clathmoroa*: as in the ancestral type in (a), but showing gradual embedment of the dorsally displaced meristem and production of a series (>3) of epithallial cells from intercalary divisions. (**e**) *Callilithophytum*: monopodial-bilateral organization involving hypothallium reduction (black bar) and perithallial growth (white bars) producing a bilateral thallus with series (>3) of epithallial cells. (**f**) *Synarthrophyton* and *Amphithallia*: monopodial-bilateral organization with a polystromatic hypothallium, differing from the ancestral type in (a) by the development of secondary perithallia dorsally and ventrally. (**g**) *Perithallis*: differing from the ancestral type in (a) by the production of a diminutive ventral perithallium. (**h**) *Carlskottsbergia*: monopodial-bilateral organization with a monostromatic hypothallium. (**i**) *Capensia*: sympodial-dorsiventral organization with a monostromatic hypothallium. Abbreviations: e, epithallia; h, hypothallium; m, meristematic cell; p, perithallia.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hypothallial cells), the embedded part starts production of epithallial cells in series via intercalary divisions (Adey 1965: fig. 20; Adey and Johansen 1972: fig. 15; Lebednik 1977a: figs. 8e, 14a; see Figure 7a,e,g).

In *Callilithophytum* (Clathromorphoideae) the fully grown thallus shows a bilateral organization (see Figure 4e) that is the product of two events: first, the hypothallium is suppressed, and second, the perithallium takes over producing ventral and dorsal tissue, supporting series of epithallial cells and even forming conceptacles on both sides of the thallus (Adey and Johansen 1972: fig. 14; Lebednik 1977a: fig. 16d,e; Adey et al. 2015).

Monopodial-bilateral organization with a polystromatic hypothallium occurs in *Synarthrophyton* and *Amphithallia* (Athanasiadis 2019a, 2019b) and differs from the typical monopodial-dorsiventral organization by the development of secondary perithallia both dorsally and ventrally (see Figure 4f).

Anisobilateral organization (see Figure 4g) occurs in *Perithallis*, where a diminutive, 1 or 2 cells thick, ventral perithallium (that may also support trichocytes) is formed (Athanasiadis 2022). This type is intermediate between the monopodial-dorsiventral (e.g., in *Mesophyllum*) and bilateral (e.g., in *Synarthrophyton*) thallus organization.

Monopodial-bilateral organization with a monostromatic hypothallium (see Figure 4h) occurs in *Carlskottsbergia* (Athanasiadis 2019a) and is considered to be the result of the reduction of the polystromatic hypothallium.

Sympodial-dorsiventral organization with a monostromatic hypothallium (see Figure 4i) occurs in *Capensia* (Athanasiadis 2017b) and is considered to be the result of reduction of the polystromatic hypothallium with further modification in the apical growth.

A protective cuticle covering the terminal (meristematic) hypothallial cells has been recorded in all types of growth. Despite its presence, injuries of the terminal (apical) meristem have been observed in *Phragmope* that result in meristem regeneration (Athanasiadis 2020b: figs. 2a, 3a). The cuticle stops its development at the transition zone, where the dorsally (or ventrally) displaced terminal meristematic cells become epithallial cells, as in *Protomesophyllum* (see Figure 8m) or *Printziana insignis* comb. nov. (see Figure 22f) but also in *Clathromorphum* (where the apical meristem becomes embedded; see Figure 7a).

Character 1 defines six mutually exclusive states of thallus organization: monopodial-dorsiventral (0); bilateral (1); sympodial, an autapomorphy for *Capensia* (2); anisobilateral, an autapomorphy for *Perithallis* (3); bilateral perithallium with hypothallium reduction, an autapomorphy for *Callilithophytum* (4); and heterotrichous organization, an autapomorphy for *Melobesia* (5).

Character 2 defines a hypothallium that is either polystromatic (0) or monostromatic with ascending and descending filaments (*Carlskottsbergia-Capensia*; 1) or reduced in fully grown thalli (*Callilithophytum*; 2) or monostromatic with an ascending perithallium in the heterotrichous organization of *Melobesia* (3). The present phylogenetic analysis shows that the heterotrichous organization in *Melobesia* did not evolve within the Mesophyllaceae because of the reproductive characters that place *Melobesia* next to *Orthocarpa* and remote from Mesophyllaceae with monostromatic hypothallia (*Carlskottsbergia-Capensia*; see Figure 6c).

Character 3 defines the gradual embedding process of the terminal (apical) meristem that occurs in the Clathromorphoideae and has two states: absent (0) or present (1). In all other Mesophyllaceae, displaced apical meristematic cells are transformed to epithallial cells (as in *Phragmope*; Athanasiadis 2019b: fig. 2g,h).

Characters 4 and 5 define the coaxial hypothallial growth, which involves two distinct phases: the characteristic arching (character 4) and the synchronous cell divisions and elongations (character 5). Coaxial hypothallial growth (previously widely applied for members of *Mesophyllum* sensu lato) is here shown to be a synapomorphy for the tribe Melyvonneeae (see Figure 6c). This character reappears as a parallelism in the remotely related uniporate genus *Neogoniolithon* Setch. et L. R. Mason (Neogoniolithoideae, Spongitidaceae), possibly via ancient hybridization. An alternative hypothesis suggests the presence of silent genes in the Corallinales, which could be the case with the sympodial growth in *Capensia* that occurs in remotely related orders of Rhodophyta (Athanasiadis 2017b). Three states of coaxial growth are here recognized and similarly affect characters 4 and 5: apparent lack with rare patches (0), regular formation in regions or patches (1), and predominant occurrence (2). Noncoaxial hypothallial growth is apparently the plesiomorphic condition characterizing the Sporolithales, Lithothamnionaceae, Melobesiaceae, and most members of Mesophyllaceae, as well as the Spongitidaceae and the encrusting members (at least the basal thallus) of the uniporate Corallinaceae. Moreover, the present analysis indicates that the coaxial hypothallial growth has been secondarily reduced (but not entirely lost) in certain genera of Melyvonneeae (as in *Sunesonia* and *Thallis*).

Perithallial stratification is usually coupled with an arching coaxial hypothallium in the Mesophyllaceae, but it has not been documented in all species, and it is not included in the present analysis. Perithallial stratification reappears as a permanent condition in the remotely related uniporate Lithophyllaceae and in certain members of Corallinaceae (e.g., *Jania* J. V. Lamour.). Again, the underlying genetic mechanisms are speculative.

Character 6 defines the subepithallial meristem, and two states are recognized: meristematic cells that, during division, are elongate (±longer than cells below; 0) or short (±shorter than cells below; 1). Short subepithallial cells have been recorded in several genera of Magnephyceae, such as *Leptophytum*, *Kvaleya*, and *Phymatolithopsis* Jeong et al., and also in *Masoniana kraftii* comb. et nom. nov. (Amphithallieae), whereas in all other Mesophyllaceae, subepithallial meristematic cells are ±elongate, either prominently (e.g., in members of Clathromorphoideae; Lebednik 1977a: figs. 6b, 8d, 16c) or at least during cell division (as in *Leptothallia acervata*). It is possible that records of short subepithallial cells in three deepwater species of *Mesophyllum* (*M. stenopon* Athanas., *M. fluatum* W. H. Adey et al., and *M. aleuticum* P. A. Lebednik) do not reflect observations during the actual division process since elongate subepithallial meristematic cells occur in all other members of this genus.

Character 7 defines the degree of perithallial growth, and two conditions are recognized: thalli with extensive growth, in which case the perithallium embeds older conceptacles (0), or limited growth, usually not exceeding 50 μm in thickness and in which the hypothallium dominates (1). Limited perithallial growth is generally coupled with the thallus's ability to increase its thickness via production of new lamellae in superimposition (character 9), as in *Magnephycus engelhartii* (Athanasiadis 2017a: fig. 10).

Character 8 defines the development of elongate subbasal cells in the descending hypothallial filaments. This character is coded as absent (0) or present (1), but the reason for this modification is not presently understood. Such cells were first observed in *Magnephycus ornatus* comb. nov. (Foslie and Howe 1906: pl. 90, fig. 2, as *Lithothamnion mesomorphum* var. *ornatum*) and, since then, have been reported in both closely related (e.g., *Magnephycus engelhartii* [Athanasiadis 2017a; fig. 33] and species of *Macedonis* gen. nov. [see Figure 34h]) and remotely related (e.g., *Orthocarpa haptericola*; see Figure 76g) taxa.

Character 9 defines the foliose thallus, showing superimposed unattached growth, that is, composed of several partly unattached layers. This formation is coded as absent (0) or present (1) and results in a multitude of minor crevices and openings in the thallus, where various animals and algae find shelter. Such foliose thalli undoubtedly play a significant role in the ecology of their inhabitants and are most often recorded in species occurring in the tropics and subtropics, where space is limited and species often grow in close association (latitudinal diversity cline; Athanasiadis, 1996b: 238). A foliose thallus occurs in several species of Orthocarpoideae (Melobesiaceae) and Mesophylloideae (Mesophyllaceae) and also remotely related genera such as *Neogoniolithon* (Spongitidaceae) and *Lithophyllum* Philippi (Lithophyllaceae). Within *Leptophytum*, it characterizes two Arctic species (*L. jenneborgii* Athanas. and *L. arcticum* (Kjellm.) Athanas.), whose "characteristic habit sets them apart not only from Arctic congeners, but from Arctic corallines in general, and unites them with distantly related taxa from warmer waters, suggesting that they evolved before the beginning of the cooling period (mid-Tertiary) in the Arctic Ocean." (Athanasiadis 2008: 223).

Characters 10–12 define the shape of epithallial cells: flattened-rectangular, isodiametric, or elongate. These three types are apparently not mutually exclusive, as all three forms may occur in a single species (i.e., *Printziana australis* Athanas.). Hence, they are coded as independent characters, absent (0) or present (1), although the reason for this diversification is not presently understood.

Character 13 defines the capacity of the subepithallial meristem to produce long series of epithallial cells (>3) and is a diagnostic character of the subfamily Clathromorphoideae. It is coded as present (1) or absent (0). In those corallines producing a thick perithallium (see character 7), the subepithallial meristem also adds new cells to the perithallium (below the epithallium), and this bipolar meristematic activity was named "meristem split" by Adey et al. (2015: fig. 2).

Character 14 defines the development of trichocytes. Two different types have been observed: those occurring terminally among epithallial cells, terminating perithallial filaments, and those occurring on hypothallial cells and interpreted as trichocyte-like or hair cells. The latter have been reported only three times: among terminal (meristematic) hypothallial cells in *Mesophyllum aleuticum* (Athanasiadis et al. 2004: fig. 7) or as embedded cells among hypothallial filaments in *Neopolyporolithon reclinatum* (Setch. et Foslie) W. H. Adey et H. W. Johans. (Lebednik 1977: fig. 21b) and *Phragmope discrepans* (Foslie) Athanas. (2020b: fig. 3g). Terminal hair cells occur on carpogonial and tetrasporangial thalli of the filamentous Ceramioideae, most likely to increase the uptake of nutrients. They have not been recorded on male thalli, suggesting that their development may be controlled by a single-copy gene whose expression is dominant in heterozygotes (Athanasiadis 1996a). Only the former type of trichocytes has been included in the phylogenetic analysis. Trichocytes are rare or lacking in temperate to Arctic and Antarctic waters (e.g., in *Mesophyllum*, *Neopolyporolithon*, *Clathromorphum*, and *Leptophytum*, with the single exception of *L. tenue* (Kjellm.) Athanas. et W. H. Adey), whereas their presence is common in genera distributed in the tropics and subtropics (e.g., in *Melyvonnea*, *Printziana*, and *Phragmope*) and they also occur in *Orthocarpa* in the Melobesiaceae. The presence of trichocytes resolved as a synapomorphy for the subfamily Mesophylloideae, with gradual reduction (or loss) in certain genera.

Character 15 defines the development of erect perithallial protuberances, which differ from outgrowths where lamellae (thallus branches) grow back to back, as in *Phragmope* (Athanasiadis 2020b: fig. 2c). Perithallial protuberances are best developed in *Melyvonnea* (Athanasiadis and Ballantine 2014: fig. 7), gradually dominating over the basal (encrusting) part, and may become detached, forming rhodoliths. In *Mesophyllum vancouveriense* (Foslie) R. S. Steneck et R. T. Paine (Athanasiadis et al. 2004: fig. 31), perithallial protuberances may develop as a defense against grazing animals (see further comments in the species account).

Accessory Vegetative Characters Not Considered in the Analysis

In certain species, multiporate conceptacles develop a distinct rim, resulting in a sunken pore plate. This condition is recognized as an autapomorphy for species in several genera (e.g., *Mesophyllum*, *Orthocarpa*, and *Leptophytum*). In *Printziana australis* (Woelkerling and Harvey 1993: figs. 27A, 28A, as *Mesophyllum prinztianum*) and in *Macroblastum dendrospermum* comb. et nom. nov. both rimmed and convex roofs have been reported (Kaleb et al. 2011: figs. 7, 8, as *Mesophyllum macroblastum*), questioning the taxonomic value of this character.

Rhizoidal outgrowths have not been reported in the Mesophyllaceae, apart from the production of haustoria in the parasitic genera *Kvaleya* W. H. Adey et Sperapani (1971) and

Capensia (Athanasiadis 2017b). Ventral struts (excrescences), on the other hand, characterize several species within several genera (e.g., *Orthocarpa haptericola*, *Macedonis julieae* comb. nov., and *Masoniana kraftii*).

Life Histories

Field observations indicate that the Corallinales exhibit a *Polysiphonia* type of life history, with meiosis occurring in the tetrasporangia and presumed karyogamy in the carpogonia. This triphasic life cycle involves the haploid gametophyte(s), the diploid carposporophyte (that develops within the fertilized carpogonial conceptacle), and the diploid tetrasporophyte. It includes three free-living units in dioecious species (two in monoecious) with isomorphic somatic thallus, which should be represented with equal frequency in nature. However, in the absence of cytological investigations it is not possible to be certain. Tetra- or bisporangial thalli are more commonly reported, particularly at the margin of species distributions (Dixon 1973; Suneson 1982), and it is presumed that such populations are asexual, perpetuating the parental diploid phase via apomeiosis (see Athanasiadis and Rueness 1992: 11).

Character 16 defines the presence of dioecy (0) versus monoecy (1). In well-studied species showing frequent sexual reproduction (e.g., several species of *Mesophyllum*), this character is easily assessed, like it is in other red algae (e.g., members of Ceramiales; Athanasiadis 1996a). However, the occurrence of mixed phases complicates the case, and since cytological observations are lacking in the multiporate Corallinales, it is impossible to know whether reports of both monoecious and dioecious thalli reflect mixed phases or simply individuals growing close together (e.g., *Perithallis incisa*; Athanasiadis 2022: fig. 5b).

Male Reproductive Apparatus

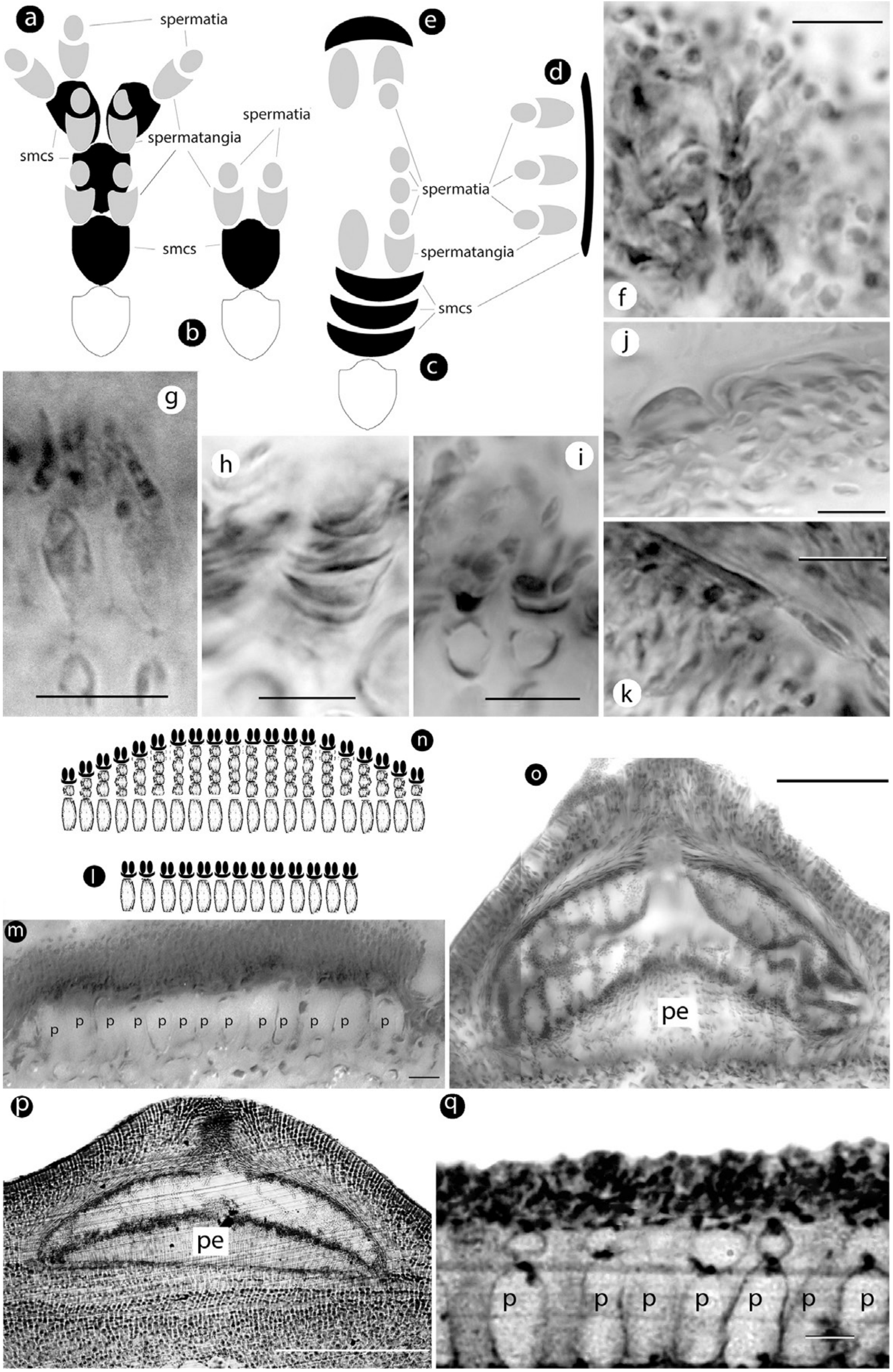
The development of dendroid (branched) spermatangia represents the ancestral (plesiomorphic) condition, which is commonly recorded in the Sporolithales and Lithothamnionaceae and sporadically reported as either a rare or common condition in certain species of Orthocarpoideae (Melobesiaceae) and Mesophylloideae (Mesophyllaceae) (see “Divisions of Corallinales”; Figure 1a).

On the other hand, the development of unbranched (simple) spermatangial structures is optimized as a synapomorphy for the Mesophyllaceae, Melobesiaceae, and all uniporate families (Figure 1a), indicating that the spermatangial apparatus has undergone simplification. Hence, the plesiomorphic, dendroid (branched) type resulted in SMCs nested on ramified vegetative filaments, usually producing two SMCs from a vegetative cell. This organization gave the dendroid structure (Figure 5a,f). The simple (unbranched) structure would thereby be the product of the reduction of the ramified filament to a single basal cell, supporting two SMCs (Figure 5b,g), which is the common condition in most genera of Mesophyllaceae and Melobesiaceae and also occurs uniformly in the uniporate families (e.g., *Tenarea* Bory; Athanasiadis 1995: fig. 30, spermatangia being incorrectly interpreted as “SMCs”). Keats and Maneveldt (1997b: fig. 54) showed a gradation in branch complexity between simple spermatangia (in *Mesophyllum*) and dendroid spermatangia in *Orthocarpa haptericola* (=*Synarthrophyton schielianum* Woelk. et M. S. Foster), which reminds us of the statement that “spermatangial branchlets [in the Ceramiales] do not always develop uniformly throughout their length” (Moe and Silva 1980: 15) but show some correlation with the degree of thallus ramification.

Character 17 defines the distribution of dendroid spermatangia and is coded as absent (0), rare (1), or common (2). Within the Mesophyllaceae, dendroid spermatangia occur generally with simple ones (as in *Macroblastum*, *Leptophytum*, and *Amphithallia*), whereas in the Melobesiaceae they can be the only type known in certain species (e.g., *Orthocarpa haptericola*).

Character 18 defines the development of simple SMCs with a lunate shape (Figure 5c,h,i) and is coded as absent (0) or present (1). Its presence is a synapomorphy for the subfamily Mesophylloideae. Lunate SMCs on the floor may develop in

FIGURE 5. (*Opposite*) Spermatangial morphology in Mesophyllaceae. (**a**) Dendroid spermatangia with SMCs producing spermatangia in pairs cutting off spermatia; (**b**) Simple (unbranched) spermatangia with spermatangia in pairs cutting off spermatia. (**c–e**) Simple spermatangia with lunate SMCs on the floor (in (c)) and the roof (in (e)) and more elongate SMCs on the walls (in (d)). (**f**) Dendroid spermatangia in *Synarthrophyton* sp. Modified from Athanasiadis (2019a: fig. 59). Scale bar: 10 µm. (**g**) Simple spermatangia lacking lunate SMCs in *Protomesophyllum ameleteton* (paratype). Scale bar: 10 µm. (**h**) Simple spermatangia with lunate SMCs in *Synarthrophyton patena*. Modified from Athanasiadis (2019a: fig. 48). Scale bar: 10 µm. (**i**) Simple spermatangia with lunate SMCs on the floor in *Leptophytum* cf. *flavescens* (Athanasiadis 2016a; TRH B3-1743). Scale bar: 10 µm. (**j**) Simple spermatangia with lunate SMCs on the roof in *Capensia fucorum* (L0056019). Scale bar: 10 µm. (**k**) Simple spermatangia on the wall in *Phragmope*. Modified from Athanasiadis (2020b: fig. 16). Scale bar: 10 µm. (**l, m**) Simple spermatangia in *Hyperandri dawsonii*, showing their development on a layer of palisade cells. Modified from Athanasiadis (2007b: fig. 36). Scale bar: 10 µm. (**n, o**) Simple spermatangia in *Magnephycus ornatus*, borne on a multilayered pedestal composed of 1 layer of palisade cells and several layers of isodiametric cells. Scale bar: 10 µm. (**p, q**) Similar pedestal formation in a Brazilian species referred to “*Mesophyllum engelhartii*.” Modified from Da Nóbrega Farias (2009: figs. 11, 13). Scales bars: 100, 10 µm, respectively. Abbreviations: p, palisade cell; pe, pedestal.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series (Figure 5c,h), and the active cells usually produce two spermatangia that release terminal series of spermatia. SMCs on the wall are elongate (Figure 5d,k), whereas those on the roof are generally less developed (Figure 5e,j).

Characters 19–20 define the presence of a pedestal on the spermatangial floor and the degree of its development in the genera *Magnephycus* and *Hyperandri*. This formation is exemplified by the production of spermatangial structures on a raised vegetative structure that is composed of a single basal layer of palisade cells in both genera (Figure 5l,m), in *Magnephycus* followed by up to 7 or 8 layers of isodiametric cells forming a pyramid (Figure 5n,o). The pedestal formation (character 19) is coded as absent (0) or present (1), whereas the degree of its development (character 20) is coded as either lacking (0) or composed of a single layer of palisade cells (1) or composed of additional layers of several isodiametric cells (2). This structure was considered a priori a synapomorphy requiring an increased weight (3 times) to achieve monophyly (see "Phylogenetic Relationships in the Mesophyllaceae"). A 2-celled pedestal composed of a layer of palisade cells and a layer of isodiametric cells has been illustrated in Brazilian thalli referred to "*Mesophyllum engelhartii*" (Da Nóbrega Farias 2009: figs. 11–13; Figure 5p,q) but probably belonging to an undescribed species (not considered in the present analysis).

Female Reproductive Apparatus

The development of carpogonial branches leading to the production of a carposporophyte involves the most sophisticated and reliable characters distinguishing orders, families, and genera in red algae. Carpogonial branches in the Corallinales are generally 2- or 3-celled (Minder 1910: fig. 9; Suneson 1937: fig. 42; Johansen 1981: figs. 19, 20; Silva and Johansen 1986: 252; Woelkerling 1988: 26; Maneveldt et al. 2007: fig. 22). Hence, the 4-celled carpogonial branches in *Amphithallia crassiuscula* (Foslie) Athanas. (2019b) must be considered an autapomorphy.

Three different modes of zygote transfer have been described in the order: (1) via a cell tube connecting the carpogonium to the supporting (auxiliary) cell of the same branch system (procarpy; Figure 2a–d), (2) via fusion of the lower part of the carpogonium with the subtending cells (Figure 3b,e), and (3) via a connecting filament that unites the carpogonium with remote cells on the fertile floor (nonprocarpy). The first type has been observed in several members of Mesophyllaceae and is an autapomorphy for this family.[18] The second type has been widely reported in the Corallinaceae (Johansen 1981: 102), in *Choreonema* (Minder 1910: pl. 1, figs. 4, 5; Suneson 1937: fig. 34E; Figure 3e), and in *Metamastophora* Setch. (Woelkerling 1980: 216), whereas the third type is recorded in *Orthocarpa haptericola* (Woelkerling and Foster 1989: fig. 31, as *Synarthrophyton schielianum*; see Figure 77a) and in *Amphithallia crassiuscula* (Athanasiadis 2019b: fig. 4e,f).

Character 21 defines the size of the fusion cell after the number and type of cells participating in the fusion and shows a gradation ranging from inconspicuous (involving up to 3 supporting cells; 0) to incorporating 4 to 6 supporting cells and possibly 1 or 2 hypogynous cells (1) to involving at least 10 supporting and 10 hypogynous cells (2). The first state (0) includes cases where the fusion cell has been recorded as "discontinuous," most likely referring to gonimoblast filaments (i.e., the section crossing them rather than the fusion cell; Athanasiadis 2018), as in *Orthocarpa epicklonia* (present data), *Melobesia membranacea* (Esper) J. V. Lamour., *Clathromorphum*, *Protomesophyllum* (present data), *Synarthrophyton*, *Amphithallia*, *Phragmope*, *Macroblastum* gen. nov. (present data), *Melyvonnea*, *Perithallis*, *Kvaleya*, and *Leptothallia* gen. nov. (present data). The second condition has been documented in *Thallis*, *Printziana* (including *Pr. insignis*; present data), *Carlskottsbergia*, *Capensia* (present data), and *Leptophytum*, whereas the third condition has been recorded in *Mesophyllum* and possibly in *Neopolyporolithon* (Masaki and Tokida 1961b: pl. 4, as *Polyporolithon*; Figure 2e–k). These three states are based on observations of sections, but in the case of *Leptophytum laeve* and *Mesophyllum philippii* (Foslie) W. H. Adey we also have illustrations of the entire fusion cell from above (Adey 1966: fig. 77; Athanasiadis 2018: fig. 10).

Character 22 defines the level of gonimoblast development and is coded as either at the level of supporting cells (0) or at the level of hypogynous cells (1) or as being nonprocarpy (2). The latter is recorded in *Amphithallia* and possibly in *Orthocarpa haptericola*, in which a connecting filament leads the zygote to remote auxiliary cells. In *Melobesia membranacea* and *Orthocarpa epicklonia*, it is the hypogynous cells that give rise to gonimoblasts, whereas in the Mesophyllaceae it is the supporting cells (together with certain hypogynous cells, sometimes involving one or two carpogonia) while the basal cells remain intact (except in *Perithallis*, in which it is the basal cells and not the hypogynous cells that participate in the gonimoblasts; Athanasiadis 2022: fig. 8e,f). The development of a single localized fusion cell with a single radiating gonimoblast and the production of carposporangia laterally from the periphery of the fertile zone are apparent synapomorphies for the Mesophyllaceae, Melobesiaceae, and all uniporate families (see "Divisions of Corallinales"; Figure 1a).

Character 23 defines the development of orthostichous carposporangia (at the edge of the periphery of the fertile zone) and is coded as absent (0) or present (1). Orthostichous carposporangia generally characterize members of Melobesiaceae and certain uniporate genera,[19] but they also occur as a parallelism in *Clathmoroa* (Clathromorphoideae, Mesophyllaceae); see also comments in the genus account.

Character 24 defines the shape of carposporangial chambers and shows three conditions, of which the ancestral one is the occurrence of elongate chambers (0). Formation of a pedestal (1) was originally described in species of *Mesophyllum* but is now also recorded as a facultative condition in several other genera of Melyvonneeae (Athanasiadis 2022: table 1). Finally, a spherical chamber (2) occurs in *Melyvonnea* and in *Macroblastum* (see Table 3).

Character 25 defines the capacity of gonimoblasts to bend down (following the chamber floor), using the empty space created by the formation of a pedestal, and is coded as absent (0) or present (1; Figure 2k).

Tetra- and Bisporangial Conceptacles

Only bisporangia or zonately divided tetrasporangia (within multiporate or uniporate conceptacles) have been recorded in the Corallinales. These characters distinguish the order from Sporolithales and Corallinapetrales, in which sporangia are ± spherical, are decussately-cruciately divided, and develop within individual chambers. Bi- or tetrasporangia are generally liberated through their own canal, a synapomorphy for the Corallinales, Corallinapetrales, and Sporolithales. Since the meiotic process normally involves a simultaneous cleavage into four spores, the presence of bisporangia is a deviation from the standard division pattern. Interestingly, both binucleate and uninucleate bisporangia have been reported in species of *Titanoderma* Nägeli (Suneson 1950, 1982, as *Lithophyllum*). Binucleate bisporangia would thereby result from failure to undergo the (simultaneous) zonate cleavages, whereas uninucleate bisporangia would result from failure to undergo the complete meiotic process (usually known as apomeiosis). Both bisporangia and zonately divided sporangia have been reported in the Mesophyllaceae, but the lack of cytological observations precludes further considerations. In the Ceramioideae, sporangium size is apparently correlated to ploidy level and can be used to distinguish polyploid taxa (Athanasiadis and Rueness 1992). That the development of enlarged sporangia probably led to the development of pedestals in carposporangial conceptacles and differentiated canals in multiporate conceptacles is discussed in Athanasiadis et al. (2004: 163) and in Athanasiadis (2022: 942).

Character 26 defines the capacity of multiporate conceptacles to develop and become embedded in a colliculate pattern (see Figures 36i, 38g, 45g), that is, closely spaced (Stearn 1986: 507). This character is coded as absent (0) or present (1).

Character 27 defines the presence of embedded conceptacles (uniporate or multiporate) in the perithallium and is coded as absent (0) or present (1).

Character 28 defines the shape of canals in multiporate conceptacles, for which the ancestral condition is the straight type (0), but it can become pyriform (1) or triangular (2) or have a wider base (3). The various types of canal shapes and pore filament differentiation in the Mesophyllaceae were recently examined (Athanasiadis 2022: fig. 1) and are here outlined in Table 2, together with those occurring in the outgroups.

Character 29 defines the development of thinner–wider pore cells in filaments lining the canals of multiporate conceptacles and is coded as absent (0) or present (1; Athanasiadis 2022: fig. 1c). This character resolved as a synapomorphy for the subfamily Mesophylloideae, with later loss in *Amphithallia*, *Phymatolithopsis*, and certain species of *Leptophytum* (i.e., *L. tenue*, *L. flavescens* (Kjellm.) Athanas.), whereas in *Phragmope*,

TABLE 2. Canal shape and pore filament differentiation in multiporate conceptacles of 29 genera of Mesophyllaceae and 2 genera of Melobesiaceae. Pore filaments in *Thallis*, *Perithallis*, *Printziana*, *Sunesonia*, and *Melyvonnea* are diagrammatically illustrated in Figure 25q-u. Abbreviations: BB, basally branched; RCS, rosette cells sunken.

Genus or species	Canal shape	Pore cells
Clathromorphum	± Straight	Nondifferentiated
Neopolyporolithon	± Straight	Nondifferentiated
Callilithophytum	± Straight	Nondifferentiated
Clathmoroa	± Straight	Nondifferentiated
Protomesophyllum	± Straight	Rhomboid
Amphithallia	± Straight	Nondifferentiated
Synarthrophyton	Triangular	Thinner–wider (along half the canal length)
Carlskottsbergia	Pyriform or ± straight	Thinner–wider, basal and subbasal cells elongate
Capensia	± Straight	Thinner–wider
Kerguelena	± Straight	Nondifferentiated
Masoniana	± Straight	Nondifferentiated
Phragmope	± Straight	Cell bars (at the level or basal cells)
Melyvonnea	± Straight-wider base	Thinner–wider, elongate basal cells, RCS
Macroblastum	± Straight	Thinner–wider
Mesophyllum	± Straight	Thinner–wider
Perithallis	± Straight	Thinner–wider, BB, subbasal elongate, RCS
Thallis	± Straight	Thinner–wider, BB, subbasal elongate, RCS
Printziana australis	± Straight-wider base	Thinner–wider, BB and elongate, subbasal elongate, ± RCS
Printziana insignis	± Straight	Thinner–wider, BB, subbasal and third cells elongate, ± RCS
Sunesonia	± Straight-wider base	Thinner–wider, BB elongate and reduced, subbasal elongate, ± RCS
Leptophytum	± Straight	Thinner–wider or nondifferentiated
Kvaleya	± Straight	Nondifferentiated?
Leptothallia	± Straight	Thinner–wider (basal and subbasal cells)
Macedonis	± Straight	Elongate subbasal cells
Hyperandri	± Straight	Thinner–wider (basal and subbasal cells)
Ectocarpa	± Straight	Larger–elongate basal and subbasal cells
Mastophoropsis	± Straight	Larger–elongate basal and subbasal cells
Magnephycus	Pyriform	Thinner–wider, basal and subbasal cells elongate
Phymatolithopsis	± Straight?	Nondifferentiated?
Orthocarpa	± Straight	Nondifferentiated (except for basal cells)
Melobesia	± Straight	Nondifferentiated (except for basal cells)

Mastophoropsis, and *Ectocarpa* gen. nov. pore cells show other modifications (Table 2). Yet, the postulation that thinner–wider pore cells evolved to overcame the "problem" of larger spores suggests that this character is a homoplasy, developing independently in individual species and possibly reflecting the event of polyploidy (Athanasiadis 2022). Indeed, thinner–wider pore cells have also been recorded in remotely related genera such as *Phymatolithon* (Athanasiadis and Adey 2006: fig. 143). In *Protomesophyllum*, *Phragmope*, *Mastophoropsis*, and *Ectocarpa*, which display other pore cell differentiations, it seems that this character never occurred, which is possibly the case for *Amphithallia*, *Phymatolithopsis*, and certain species of *Leptophytum* that lack entirely differentiated pore cells. Deletion of character 29 (as homoplasious) did not result in any changes in the taxon topology in the phylogenetic trees (see Figure 6a–c).

Character 30 defines the subdichotomous branching of basal pore cells in multiporate conceptacles and is coded as absent (0) or present (1). The branching results in two types of filaments: a filament that is similar to neighboring roof filaments and the filament lining the canal that displays further cell differentiations (Athanasiadis 2022: fig. 1f–i). Branched pore filaments resolved as a synapomorphy for *Perithallis*, *Thallis*, *Printziana*, and *Sunesonia*.

Character 31 defines the development of elongate basal cells in pyriform canals and is coded as absent (0) or present (1; Athanasiadis 2022: fig. 1l).

Character 32 defines the development of elongate branched basal cells in straight canals and is coded as absent (0), present (1), or reduced (2). The reduced condition characterizes the genus *Sunesonia* and defines its relationship to *Printziana* (Athanasiadis 2022: fig. 1g,h; see Figure 25s,t). The hypothesis that branched basal cells have been lost in the ancestor of *Melyvonnea* results in the diagnostic type exhibited by this genus as a unique apomorphy (Athanasiadis 2022: fig. 1i; see Figure 25u; Table 2).

Character 33 defines the development of elongate subbasal cells in unbranched pore filaments in pyriform canals and is coded as absent (0) or present (1; Athanasiadis 2022: fig. 1l). Characters 31 and 33 resolved as synapomorphies for the species of the new genus *Magnephycus* (*M. ornatus*, *M. engelhartii*, *M. simulans*).

Character 34 defines the development of elongate subbasal cells in unbranched pore filaments in straight canals and is coded as absent (0) or present (1; Athanasiadis 2022: fig. 1e). This character resolved as a synapomorphy for the species of the new genus *Macedonis* (*M. tethygenis*, *M. kymatodis*, *M. julieae*, and *M. lamellicola*).

Character 35 defines the development of elongate subbasal cells in branched pore filaments and is coded as absent (0) or present (1; Athanasiadis 2022: fig. 1f-h; see Figure 25q-t). This character resolved as a synapomorphy for *Perithallis*, *Thallis*, *Printziana*, and *Sunesonia*.

Character 36 defines the development of larger–elongate basal and subbasal cells in unbranched pore filaments in straight canals and is coded as absent (0) or present (1). This character is recorded in *Ectocarpa* and *Mastophoropsis* (both in the Magnephyceae; see Figures 49f, 62b,c) and is further discussed in the accounts for these two genera.

Character 37 defines a lower number of cells in pore filaments lining the canals (than in contiguous roof filaments) and is coded as absent (0) or present (1). This character reflects the specialization of pore filaments observed in *Perithallis*, *Thallis*, *Printziana*, *Sunesonia*, and also *Melyvonnea* (Athanasiadis 2022: fig. 1f–i; see Figure 25q–u).

Character 38 defines sunken rosette cells (surface pore cells) and is coded as absent (0) or present (1). This character also reflects the specialization of pore filaments observed in *Perithallis*, *Thallis*, *Printziana*, *Sunesonia*, and *Melyvonnea* (Athanasiadis 2022: fig. 1f–i).

Character 39 defines the development of an imperforate "second roof" (over the proper one) by centripetally growing peripheral filaments and is coded as absent (0) or present (1). This character was recorded in several members of Magnephyceae (see Figures 36d,e, 55c, 60l) and is not homologous to the imperforate second roof observed in *Phragmope*, which does not involve hypothallial filaments (Athanasiadis 2020b: fig. 6g,h,i).

Character 40 defines the development of a hemispherical roof in multiporate conceptacles and is coded as absent (0) or present (1). This character resolved as a synapomorphy for *Magnephycus* and *Ectocarpa* (see Figures 6c, 49d, 52a,c).

Germination Patterns

Spores of Corallinales display a 4-celled central element, the "Dumontia-type" (Chemin 1937), with subsequent differentiations into at least six types (Chihara 1974: fig. 6). Germination patterns were studied by Bressan (1980: pls. 1, 2) in *Fosliella* Kütz. in comparison to other corallines, including several species of Mesophyllaceae (Adey 1965: pl. 4, *Clathromorphum*; Cabioch 1972: 160, *Mesophyllum lichenoides*, *Leptophytum bornetii* (Foslie) W. H. Adey; Chihara 1974: fig. 3, *Melyvonnea erubescens* (Foslie) Athanas. et D. L. Ballant., *Neopolyporolithon reclinatum*, *Mesophyllum conchatum* (Setch. et Foslie) W. H. Adey, "*Lithothamnion cystocarpideum* prox."). Regarding the Mesophyllaceae, these observations should be considered preliminary pending further studies.

Species and Speciation

In the Ceramiales and particularly in the Ceramioideae, the numerous cytological and life history studies including hybridization experiments resulted in a rather firm species concept (Rueness 1978; Athanasiadis 1996a, and references therein), but in the Corallinales knowledge is largely based on morphoanatomical observations and a few culture studies of epiphytic species (e.g., Suneson 1982). These studies suggest that coralline algae follow the classic pattern of speciation via splitting of an ancestral population after gradual range expansion, followed by genetic isolation of the resultant sister populations (vicariance). Vicariance could underlie the existence of the closely related species *Mesophyllum lichenoides* and *M. expansum* (Philippi) J. Cabioch et M. L. Mendoza on the European Atlantic coast, where the former species is restricted to the British Isles, co-occurring with *M. expansum* in Galicia and southern Atlantic France, whereas *M. expansum* occurs in the Azores and extends farther south to the Canaries, penetrating into the western Mediterranean Sea (Athanasiadis and Neto 2010; Peña et al. 2015).

Species of Mesophyllaceae displaying their diagnostic reproductive and vegetative characters are clearly delineated to such an extent that the notion of sibling species seems to be redundant. Still, overlapping phenotypes are common in specimens that are sterile (or juvenile) and thereby lack their diagnostic characters, and misconceptions and misidentifications are common in the literature, often because of our failure to apply correct techniques to identify species. The case of "*Mesophyllum engelhartii*" and "*Mesophyllum erubescens*," previously considered to be two cosmopolitan taxa, is well known. Their identity has been clarified, with the former being restricted to southern Australia (Athanasiadis 2017a) and the latter occurring on the coast of Brazil and the Caribbean Sea (Athanasiadis and Ballantine 2014). Records of "*Mesophyllum engelhartii*" from South Africa have been described as *Phragmope discrepans*, whereas records of "*M. erubescens*" from Australia, New Zealand, and the Chatham Islands have been referred to *Perithallis* or *Sunesonia* (Athanasiadis 2022).

HYBRIDS

When all, or at least one, of the parent taxa can be postulated or are known, a nothotaxon is circumscribed to include all individuals derived from crossings of representatives of the stated parent taxa (International Code of Nomenclature, Articles H.3 and H.4; Turland et al., 2018). However, no specific criteria are given for the identification of nothotaxa, and hybrids in red algae have generally been regarded as not possible to recognize in the field (Rueness 1978: 250). Athanasiadis (1996a) applied five criteria to identify two hybrids in the Ceramioideae, namely, *Antithamnion* x *cruciatum* (C. Agardh) Nägeli and *Scagelothamnion* x *pusillum* (Ruprecht) Athanas., with these criteria being partly in agreement with the identification of hybrids in higher plants (Wagner 1983): (1) intermediate morphology, when entities lack autapomorphies and are distinguished by unique character combinations of the presumed parents; (2) allopolyploidy, when the number of chromosomes of an entity represents the sum of numbers existing in the presumed parents; (3) restricted distribution, when entities occur in the overlapping zone of related taxa with a wider occurrence; (4) monotypic lineages, when entities, especially genera, are poorly differentiated, in contrast to their sister taxa; and (5) rare, or total absence of, sexual reproduction, when entities fail to undergo the triphasic life history because of meiotic failure. Endopolyploidy can establish homologous chromosomes through duplication, so that synapsis and, finally, meiosis can take place, but the resulting offspring recycles the parental phase (Athanasiadis 1996a: fig. 6B). In the absence of hybridization experiments or cytological studies in the Mesophyllaceae, these criteria are only indications, but two cases of possible hybrids should be highlighted.

Lack of sexual reproduction has been recorded in several mesophylloids, for example, *Leptophytum foecundum* and *Leptophytum bornetii*, which display a similar morphology, the former widely occurring in the Arctic and the latter restricted to a few localities in the temperate northeast Atlantic. Three gene phylogenies (Adey et al. 2015: fig. 6) have pointed to an anomalous affiliation of *L. foecundum* with *Mesophyllum lichenoides*, which could be explained by a heterogeneous genome. As none of the other criteria apply, a hybridogeneous derivation of *L. foecundum* is speculative.

The Mediterranean endemic *Macroblastum dendrospermum* belongs to a monotypic genus sharing characters with both *Melyvonnea* and *Mesophyllum* but not belonging to either of them because it develops dendroid spermatangia (in addition to simple ones). Several of the above criteria apply, and hence, *M. dendrospermum* should be investigated as a putative hybrid.

PHYLOGENETIC RELATIONSHIPS IN THE MESOPHYLLACEAE

At least 24 genera (including *Phymatolithopsis* incertae sedis, Magnephyceae) and some 100 species (including 34 taxa as incertae sedis) are here recognized as members of the Mesophyllaceae. Accounts of all recognized taxa are given in "Classification." The data matrix for the phylogenetic analyses included 29 ingroup taxa (species and genera), two outgroups (*Melobesia*, *Orthocarpa*), and 40 characters (see Table 1).

Three separate analyses were performed: one including 19 genera and 10 species to show the generic affiliation of the species (Figure 6a), one to infer relationships between 23 genera within higher taxon groups and show the character distribution (Figure 6b,c), and one to examine the hypothesis that elongate basal cells in *Melyvonnea* are the result of relocation following the loss of basally branched pore cells (Figure 6d). The first analysis produced 358 equally parsimonious trees of 112 steps, and the strict consensus is shown in Figure 6a. This analysis supported three new genera: *Magnephycus* (including *M. ornatus*, *M. engelhartii*, and *M. simulans*), *Macedonis* (including *M. tethygenis*, *M. julieae*, and *M. lamellicola*), and *Hyperandri* (including *H. bisporum*, *H. dawsonii*, and *H. siamense*). The second analysis included 23 genera as terminals. The strict consensus of 48 trees of 104 steps is shown in Figure 6b, with majority consensus for certain groups, and the character distribution in 1 of the 48 equally parsimonious trees is shown in Figure 6c. The following higher taxa are recognized.

Within the Mesophyllaceae, Clathromorphoideae is segregated on the basis of the gradual embedment of the terminal (apical) meristem, which starts production of long series (>3) of epithallial cells via intercalary divisions (characters 3, 13). Clathromorphoideae comprises the genera *Clathromorphum*,

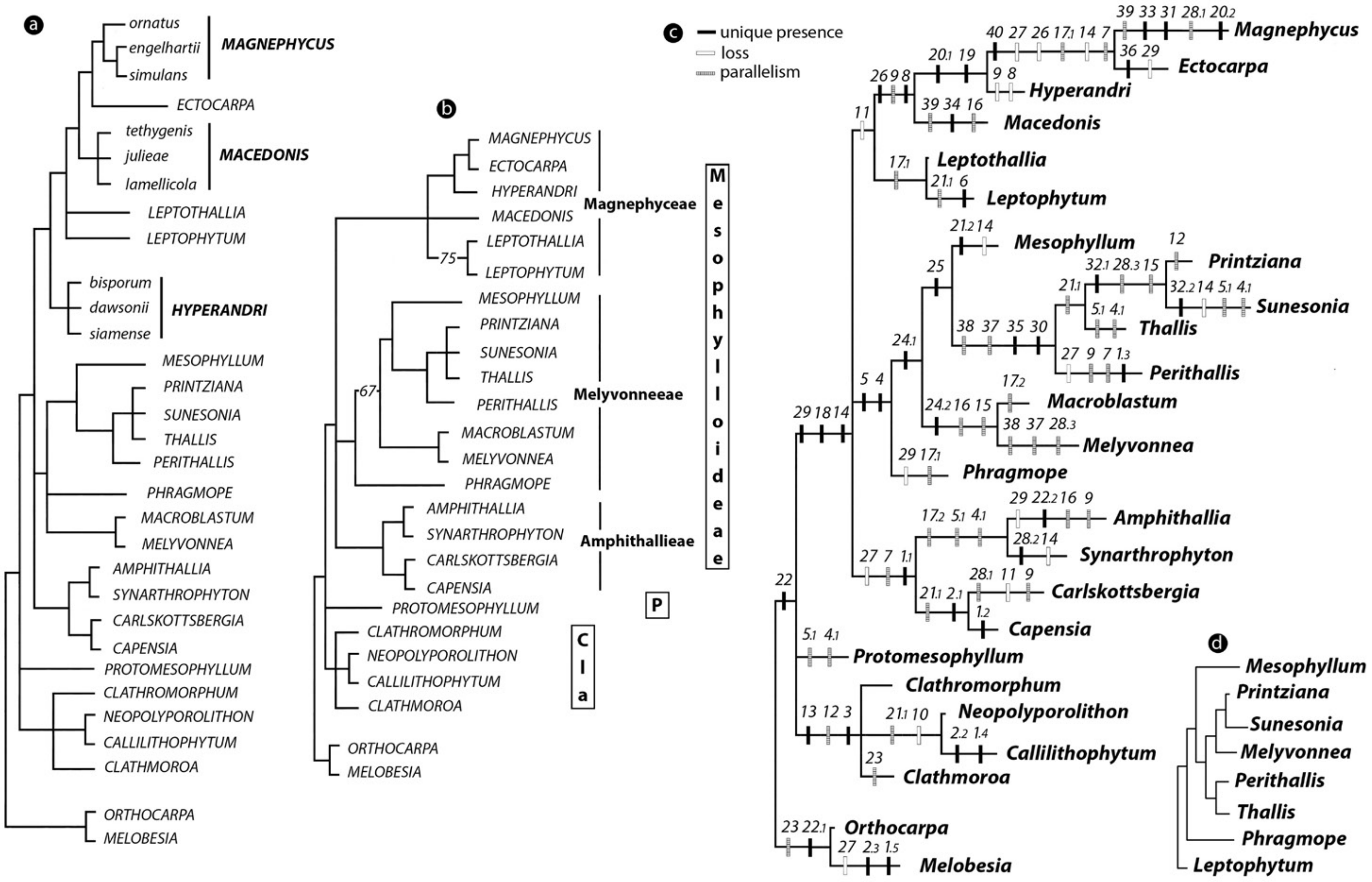


FIGURE 6. Phylogeny of Mesophyllaceae. (**a**) The strict consensus of 358 trees of 112 steps using 29 ingroup taxa and 40 characters, showing the affiliation of species within the new genera *Magnephycus*, *Macedonis*, and *Hyperandri*. (**b**) The majority consensus of 48 trees of 104 steps using 23 ingroup genera and 40 characters, showing the subfamilies Clathromorphoideae (Cla), Protomesophylloideae (P), and Mesophylloideae, the latter including the tribes Amphithallieae, Melyvonneeae, and Magnephyceae. (**c**) One of the 48 equally parsimonious trees of 104 steps, showing the distribution of 40 characters in 23 genera. (**d**) One of the four equally parsimonious trees (35 steps) based on the hypothesis that elongate basal cells in *Melyvonnea* evolved via relocation following the loss of basally divided pore filaments (Athanasiadis 2022: fig. 18e; Figure 25u). For further explanation, see text.

Neopolyporolithon, and *Callilithophytum* and the new genus *Clathmoroa* from South Africa that grows epiphytically on species of *Amphiroa* and displays orthostichous carposporangia (character 23, parallelism) in addition to lateral ones.

Protomesophylloideae includes the monotypic *Protomesophyllum* from southern and eastern Australia, New Zealand, and the Chatham Islands, a species previously subsumed under the Mediterranean *Mesophyllum macroblastum* (herein *Macroblastum dendrospermum*). *Protomesophyllum* differs by the development of rhomboid pore cells lining the canals of multiporate conceptacles, and it also lacks lunate SMCs and the thinner–wider pore cells (in filaments lining canals of multiporate conceptacles) that characterize the Mesophylloideae. In terms of thallus growth, *Protomesophyllum* shares the mode of development of Mesophylloideae (lacking the embedding process of the apical meristem that characterizes Clathromorphoideae).

Mesophylloideae includes the core of species of the former *Mesophyllum* and *Leptophytum* and is distinguished by the development of trichocytes (character 14), lunate SMCs (character 18, rectangular or elongate in all other Corallines), and thinner–wider pore cells (lining the canals of multiporate conceptacles; character 29). The latter character is, however, lacking in *Phragmope*, *Mastophoropsis*, and *Ectocarpa* (which develop other pore cell differentiations), and it is also absent in several members of Amphithallieae and in several *Leptophytum* species (which totally lack pore cell differentiations; Table 2). Therefore, the alternative scenario that thinner–wider pore cells may be a homoplasy has been discussed (see “Character Evolution in the Mesophyllaceae"). Trichocytes are secondarily reduced (becoming rare or absent) in several genera with temperate or Arctic-subarctic distribution (e.g., *Mesophyllum* and most *Leptophytum* species).

The Mesophylloideae are divided into three tribes: Melyvonneeae (including *Phragmope*, *Melyvonnea*, *Macroblastum* gen. nov., *Mesophyllum*, *Perithallis*, *Thallis*, *Printziana*, and *Sunesonia*), Amphithallieae (including *Amphithallia*, *Synarthrophyton*, *Carlskottsbergia*, *Capensia*, *Kerguelena* gen. nov., and *Masoniana* gen. nov.; the latter two genera are not included in the phylogenetic analysis), and Magnephyceae (including *Leptophytum*, *Kvaleya*, *Leptothallia* gen. nov., *Macedonis* gen. nov., *Hyperandri* gen. nov., *Ectocarpa* gen. nov., *Magnephycus* gen. nov., *Mastophoropsis*, and the incertae sedis *Phymatolithopsis*; *Kvaleya* and the latter two genera are not included in the phylogenetic analysis).

Melyvonneeae accommodates species with a predominantly arching, coaxial hypothallium (characters 4, 5), and Amphithallieae accommodates species with a bilateral thallus organization or other advanced growth types (character 1 in various states).

Magnephyceae was poorly supported, lacking unique synapomorphies. Monophyly was achieved after treating the presence of a pedestal in male conceptacles (character 19) of particular significance (and increasing its weight three times), in which case this character resolved as a synapomorphy for *Hyperandri*, *Ectocarpa*, and *Magnephycus* (Figure 6c), together with the loss of isodiametric epithallial cells (character 11) for the entire group. This treatment for character 19 is supported by the fact that this pedestal is similarly constructed, showing a single layer of palisade cells in both *Hyperandri* and *Magnephycus* (Figure 5l,m), with additional layers of isodiametric cells in *Magnephycus* (Figure 5n,o; character 20), and an intermediate condition of 1 layer of palisade cells and 1 layer of isodiametric cells in a Brazilian species that merits further study (Da Nóbrega Farias 2009: figs. 11–13, as "*Mesophyllum engelhartii*"; Figure 5p,q).

Leptophytum was clustered with *Leptothallia* (in 75% of the trees) because of the presence of rare dendroid spermatangia (character 17). The *Leptophytum-Leptothallia* clade was not supported by unique synapomorphies, which indicates that the topology is uncertain, as also indicated by the strict consensus of the first analysis of species and genera (Figure 6a).

In their majority, the Mesophyllaceae display the ancestral thallus organization, lacking heterotrichy that characterizes several members of Melobesiaceae (i.e., *Melobesia*, *Exilicrusta*, and *Boreolithon*), and certain uniporate families (i.e., Lithophyllaceae) and subfamilies (i.e., Hydrolithoideae and Mastophoroideae) of Spongitidaceae.

The present phylogenetic analysis shows that bilateral thallus organization (Amphithallieae), sympodial growth (*Capensia*), and monostromatic hypothallia with bilateral ramification (*Carlskottsbergia* and *Capensia*) are conditions departing from the ancestral monopodial-dorsiventral thallus organization that characterizes Sporolithales, Corallinapetrales, and Lithothamnionaceae.

Finally, the hypothesis that elongate basal cells in *Melyvonnea* are the result of relocation following the loss of basally divided pore filaments (Athanasiadis 2022: fig. 18e; see Figure 25u) was tested, considering (and excluding) *Macroblastum* as a hybrid and treating three characters (30, 32, 35) related to pore filament structure in *Melyvonnea* as uncertain. This analysis included seven ingroup taxa, with a member of Magnephyceae (*Leptophytum*) as an outgroup. The resulting strict consensus of four trees clustered *Melyvonnea* with *Printziana-Sunesonia-Thallis-Perithallis*. One of the four trees (with 35 steps) is shown in Figure 6d.

We need to emphasize that character coding for the other coralline families (Figure 1a) is mainly based on literature data, and studies similar to those conducted in the Mesophyllaceae and Melobesiaceae remain to be carried out and may change our present views.

Biogeography of the Mesophyllaceae

The hypothesis that in "a large group that has been in existence for a long time . . . the primitive [basal] taxa are located at the periphery of the range, in areas where the more advanced [recently evolved] members have not reached" (Goin and Goin 1973: 113) has been used to explain the Arctic and Antarctic distributions of basal ceramioid taxa, but it does not apply uniformly since the basal genus *Balliella* Itono et T. Tanaka (Delesseriopseeae) is restricted to the tropics and the subtropics (Athanasiadis 1996a and references therein).

Considering the Mesophyllaceae, we find most members of the basal subfamily Clathromorphoideae in the Arctic, subarctic, and Antarctic regions, with only one member (*Clathmoroa*) known from the subtropical South Africa.

With the exception of the Clathromorphoideae and *Leptophytum*, which also occurs in Arctic and subarctic waters,[20] the remaining Mesophyllaceae are distributed in tropical, subtropical, or temperate waters. The Amphithallieae are restricted to the southern hemisphere, whereas the Magnephyceae (i.e., *Hyperandri*, *Magnephycus*, *Macedonis*, *Ectocarpa*) occur particularly around and within the former Tethys Sea. The Melyvonneeae are distributed across both hemispheres, having their greatest diversity in South Africa, Australia, New Zealand, and the Chatham Islands (*Phragmope*, *Thallis*, *Perithallis*, *Printziana*, *Sunesonia*). *Mesophyllum* is restricted to the northern hemisphere, with *Melyvonnea* bridging the gap in the tropics and the subtropics. Still, the lack of fossil records for most genera (but *Mesophyllum* sensu lato), invalidates any thought of a putative center of origin, and two studies point to another approach of considering taxon age.

The restricted distribution of two endemic species of *Leptophytum* on the periphery of the presumed northernmost ice cover during the latest glaciation (Late Weichselian, 25,000–10,000 years ago) indicates that they are glacial survivals. Their characteristic foliose thallus (displaying unattached superimposed growth) sets them apart from not only Arctic congeners but Arctic corallines in general and unites them with distantly related taxa from warmer waters, suggesting that they might have evolved before the beginning of the cooling period (mid-Tertiary; Athanasiadis 2008).

The highly specialized pore filaments characterizing four genera from South Africa, Australia, New Zealand, and the Chatham Islands (*Perithallis-Thallis*, *Printziana-Sunesonia*) suggest a date of common origin for their ancestor deep back in geological time, when these continents and regions were closely located and biota could easily disperse around (i.e., as late as the Early Cretaceous, 135 MYA; Athanasiadis 2022: fig. 18e). Given that such complex structures originated so early, it seems highly unlikely that we will ever achieve phylogenies using molecular tools.

The here described variation in pedestal formation in male conceptacles of *Magnephycus* and *Hyperandri* (Figure 5l–q), in combination with canal and pore filament structure in these genera, could be used to elucidate further taxon relationships. Therefore, comparing the present distribution of species to the geological history of the relevant regions (Pangea, Tethys Sea) might provide evidence of the origin of ancestral taxa sharing unmistakable synapomorphies.[21] This comparison, however, would require full knowledge of the species displaying the relevant characters, which necessitates further taxonomic studies.

Molecular tools might be used to investigate more recent events, for instance, the possible advent of species into the Mediterranean from the Indo-Pacific (using the Tethyan Seaway, which was closed in the eastern Mediterranean at the latest in the Miocene, ~17 MYA; see Pielou 1979) and/or from the Pacific into the Caribbean before the Panamanian land bridge in the late Pliocene (3.1 to 5 MYA; see Bornmalm 1992).

The opening of the Bering Strait about 3 MYA (see Wilce 1990) may also have contributed to the passage of North Atlantic or North Pacific species via the Arctic Ocean. Still, long-distance dispersal in the corallines seems to be restricted to small epiphytic species (e.g., *Melobesia membranacea*),[22] whereas the present study supports the view that genera of Mesophyllaceae display restricted distributions in well-defined geographic regions. For instance, *Mesophyllum*, which is the most species rich genus of Mesophyllaceae, occurs in the temperate NE Pacific and parts of the warmer central and NE Atlantic (with a few species penetrating into the western Mediterranean and Adriatic Seas). Other genera, such as *Hyperandri*, *Magnephycus*, and *Macedonis*, show a wider Tethyan distribution that partly overlaps with the occurrence of those species of *Mesophyllum* showing warmer preference. Finally, *Leptophytum*, which is the genus of Mesophyllaceae second richest in species, shows a prevailing Arctic and subarctic distribution, but its evolutionary history might well include a warmer (Tethyan?) period, at least for its two endemic species *L. jenneborgii* and *L. arcticum*, which show spot distributions in the Arctic and are characterized by a foliose thallus (which commonly occurs in coralline algae in the tropics and subtropics).

KEY TO THE MESOPHYLLACEAE SUBFAMILIES, TRIBES, AND GENERA

1. Thalli with monopodial growth displaying meristem embedment, that is, displaced terminal meristematic cells become embedded, producing long series (>3) of epithallial cells via intercalary divisions . . . . 2 (Clathromorphoideae)
   Thalli with monopodial or sympodial growth; displaced hypothallial filaments become perithallia; displaced terminal meristematic cells become epithallia . . . . 3 (Mesophylloideae, Protomesophylloideae)
2. Thalli with bilateral growth (after hypothallial reduction) producing ascending and descending perithallia; conceptacles occurring ventrally and dorsally; thalli epiphytic on *Calliarthron* having a distinct stalk . . . . ***Callilithophytum***
   Thalli with dorsiventral growth 4
3. Spermatangial mother cells rectangular; multiporate conceptacles with rhomboid pore cells . . . . . . ***Protomesophyllum***
   Spermatangial mother cells lunate; multiporate conceptacles lacking rhomboid pore cells . . . . 9 (Mesophylloideae)
4. Thalli epiphytic, lacking a distinct stalk or foot 5
   Thalli saxicolous 6
5. Thalli epiphytic on Corallinaceae or *Ahnfeltia* . . . . ***Neopolyporolithon reclinatum***
   Thalli epiphytic on *Amphiroa* . . . . ***Clathmoroa***
6. Multiporate conceptacles spread over the thallus surface (except the margins), becoming embedded 7
   Multiporate conceptacles occurring in patches, becoming embedded or not 8
7. Thalli lacking protuberances; hypothallium composed of a few basal filaments supporting an ascending perithallium . . . . ***Clathromorphum compactum***
   Thalli occasionally producing protuberances; hypothallium prominent supporting ascending and descending filaments . . . . ***Neopolyporolithon loculosum***
8. Thalli up to 2 cm thick; hypothallium composed of a few basal filaments supporting an ascending perithallium lacking embedded conceptacles . . . . ***Clathromorphum circumscriptum***
   Thalli usually thicker; hypothallium supporting both ascending and descending filaments; embedded conceptacles present . . . . ***Clathromorphum nereostratum***
9. Thalli with monopodial bilateral (sympodial in *Capensia*) growth . . . . 10 (Amphithallieae)
   Thalli with dorsiventral growth . . . . 11 (Melyvonneeae, Magnephyceae)
10. Thalli saxicolous 12
    Thalli epiphytic 13

11. Hypothallium predominantly coaxial (patches in *Thallis* and *Sunesonia* that develop ± straight canals in multiporate conceptacles) . . . . 16 (Melyvonneeae)
Hypothallium noncoaxial (coaxial regions or patches in *Magnephycus engelhartii* and *Magnephycus simulans* that develop pyriform canals in multiporate conceptacles) . . . . 17 (Magnephyceae)
12. Thalli with elongate subepithallial meristematic cells . . . . ***Kerguelena***
Thalli with short subepithallial meristematic cells . . . . ***Masoniana***
13. Thalli epiphytic on *Gelidium* 14
Thalli epiphytic on *Ballia* 15
14. Thalli hemiparasitic, producing haustoria and a monostromatic hypothallium . . . . ***Capensia***
Thalli nonparasitic; hypothallium generally polystromatic . . . . ***Amphithallia***
15. Thalli encrusting to lamellate with monostromatic hypothallium . . . . ***Carlskottsbergia***
Thalli discoid with polystromatic hypothallium . . . . ***Synarthrophyton***
16. Multiporate conceptacles with cell bars produced from basal pore cells . . . . ***Phragmope***
Multiporate conceptacles with other differentiations in the pore filaments 18
17. Subepithallial meristematic cells short 24
Subepithallial meristematic cells elongate 25
18. Carposporangial conceptacles spherical; gametophytes monoecious 19
Carposporangial conceptacles with pedestal (or not); gametophytes dioecious 20
19. Canals of multiporate conceptacles with elongate basal cells; dendroid spermatangia absent . . . . ***Melyvonnea***
Canals of multiporate conceptacles lacking elongate basal cells; dendroid spermatangia present . . . . ***Macroblastum***
20. Multiporate conceptacles with unbranched pore filaments; pore cells ± similar in length . . . . ***Mesophyllum***
Multiporate conceptacles with branched pore filaments; pore cells with differentiations 21
21. Pore filaments 4–5-celled, composed of elongate subbasal cells 22
Pore filaments 4–5(6?)-celled, composed of elongate basal and subbasal or elongate subbasal and third cells 23
22. Thallus organization anisobilateral; hypothallium predominantly coaxial . . . . ***Perithallis***
Thallus organization dorsiventral; hypothallium with coaxial patches . . . . ***Thallis***
23. Hypothallium predominantly coaxial . . . . ***Printziana***
Hypothallium with coaxial patches; pore filaments 4-celled; basal pore cells becoming reduced and may deteriorate . . . . ***Sunesonia***
24. Thalli a few millimeters in extent, parasitic on *Leptophytum* . . . . ***Kvaleya***
Thalli larger, epilithic, epiphytic or epizoic 26
25. Thalli erect, taeniform with a midrib . . . . ***Mastophoropsis***
Thalli encrusting to foliose 27
26. Fusion cell composed of up to 6 supporting cells and 1–2 hypogynous cells . . . . ***Leptophytum***
Fusion cell inconspicuous . . . . ***Phymatolithopsis***
27. Multiporate conceptacles with pyriform canals . . . . ***Magnephycus***
Multiporate conceptacles with straight canals 28
28. Pore filaments in canals of multiporate conceptacles with elongate subbasal cells . . . . ***Macedonis***
Pore filaments in canals of multiporate conceptacles with differentiated basal and subbasal cells 29
29. Pore filaments with larger–elongate basal and subbasal cells . . . . ***Ectocarpa***
Pore filaments with thinner–wider basal and subbasal pore cells 30
30. Pedestal present in male conceptacles . . . . ***Hyperandri***
Pedestal in male conceptacles lacking . . . . ***Leptothallia***

CLASSIFICATION

CORALLINALES P. C. SILVA ET H. W. JOHANS.

MESOPHYLLACEAE ATHANAS.

Mesophyllaceae Athanas. 2016b: 251 (type: *Mesophyllum*).

Emended Diagnosis: Mesophyllaceae comprise the subfamilies Clathromorphoideae, Protomesophylloideae, and Mesophylloideae, which are segregated from their closest relative, the Melobesiaceae, with regard to postfertilization events and, in particular, in developing a cell tube that leads the zygote beyond the hypogynous cell to the supporting cell, in producing a fusion cell with a radiating gonimoblast at the level of supporting cells (or below in *Amphithallia*), and in cutting off carposporangia laterally from the periphery of the fertile zone (*Clathmoroa* shows both lateral and orthostichous development). Members of the family share with the Melobesiaceae the ancestral monopodial-dorsiventral thallus organization with polystromatic hypothallium, development of sterile cells, and dendroid spermatangia in addition to simple (unbranched) ones. Tetra- or bisporophytes exhibit multiporate conceptacles.

CLATHROMORPHOIDEAE ATHANAS. ET D. L. BALLANT. SUBFAM. NOV.

Clathromorphoideae Athanas. et D. L. Ballant. subfam. nov. (type: *Clathromorphum*).

Diagnosis: New subfamily of Mesophyllaceae comprising the genera *Clathromorphum*, *Callilithophytum*, *Neopolyporolithon*, and *Clathmoroa* gen. nov. and differing by a gradual embedding process of the dorsally displaced terminal (apical) meristem and producing series (>3) of epithallial cells via intercalary divisions.

Comments: Clathromorphoideae accommodates both epilithic and epiphytic species. *Clathromorphum* and *Neopolyporolithon loculosum* (Kjellm.) W. H. Adey et al. are saxicolous, whereas *Callilithophytum*, *Neopolyporolithon reclinatum*, and *Clathmoroa* grow as epiphytes, mainly on geniculate corallines. Apart from the diagnostic characters, which are probably unique for the coralline algae as a whole (W. H. Adey, Department of Botany, National Museum of Natural History [NMNH], Smithsonian Institution, Washington, D.C. [retired], personal communication), members of Clathromorphoideae possess dioecious gametophytes,[23] simple (unbranched) spermatangial structures,[24] carposporangial chambers with peripheral-lateral production of carposporangia from a flattened floor,[25] multiporate conceptacles with nondifferentiated pore cells lining the canals, and production of an inconspicuous or well-defined fusion cell at the level of supporting cells. The latter character was demonstrated in *Clathromorphum circumscriptum* (Strömfelt) Foslie, *Cl. nereostratum*, and *Callilithophytum parcum* (Setch. et Foslie) P. W. Gabrielson et al. by Lebednik (1977b: figs. 9, 10, 13–16). Therefore, the development of a cell tube, leading the zygote from the carpogonium to the supporting cell (bypassing the hypogynous cell) can be postulated to be a prerequisite (although not documented in members of the subfamily so far). Postfertilization stages described in members of Clathromorphoideae are similar to those of Mesophyllaceae as a whole.[26] A fusion cell develops most prominently in *Callilithophytum parcum* (Lebednik 1977b: figs. 9, 15, as *Clathromorphum*) and *Neopolyporolithon reclinatum* (Masaki and Tokida 1961a: pl. 4, as *Clathromorphum*) and less obviously in *Clathmoroa* (Chamberlain et al. 1995: fig. 22, as *Clathromorphum*) and species of *Clathromorphum* (Lebednik 1977b: figs. 10, 13, 16, *Cl. circumscriptum*, *Cl. nereostratum*). Embedded conceptacles have been reported in all northern hemisphere species (except *Cl. circumscriptum*; Lebednik 1977a: 63, 70, 71, 94, 99), as well as in the South African *Clathmoroa* (Chamberlain et al. 1995). A key to six northern hemisphere species of Clathromorphoideae was published by Lebednik (1977a: 63).

Clathromorphum Foslie

Clathromorphum Foslie 1898a: 4–5 (type: *Cl. compactum*).

Synonyms: Phymatolithon subgenus *Clathromorphum* (Foslie) Foslie 1905b: 87.

Lithothamnion subgenus *Clathromorphum* (Foslie) J. Cabioch 1972: 223.

Antarcticophyllum (Me. Lemoine) M. L. Mendoza 1976: 254; type: *A. aequabile* (Foslie) M. L. Mendoza.

Lithophyllum subgenus *Antarcticophyllum* Me. Lemoine 1913: 38.

Clathromorphum section *Endobotroideae* Foslie 1898a: 4 (type: *Cl. compactum*). Foslie (1898b: 8, 1900b: 9–10), De Toni (1905: 1726, including *Cl. compactum* and *Cl. loculosum* (Kjellm.) Foslie).

Clathromorphum section *Epibotroideae* Foslie 1898a: 5 (type: *Cl. circumscriptum*).

Etymology: After the neuter substantive κλαθρον? (lock bar) and the feminine substantive μορφη (look, outfit), with κλαθρον also being used in *Hydroclathrus* Bory (1825: 419), and justified by Montagne (1846: 37) as follows (in translation): “I take the liberty to remark that the word κλειθρον is changed to κλαθρον in the Dorian dialect (V. *Hesychius*).” Yet there is no apparent similarity between “lock bar” and *Clathromorphum*, and it is possible that the first compound is meant to be the masculine noun κλαθμος (tear), referring to the series of drop-like cells in the epithallium–perithallium, assuming that Foslie mixed up the letter m (μ) with r (ρ).

Comments: A generitype was designated by Lemoine (1911: 66). Mendoza (1976: 254) elevated *Lithophyllum* subgen. *Antarcticophyllum* to generic rank, including *A. aequabile* and *A. subantarcticum* (Foslie) M. L. Mendoza, and designating the former species as generitype. From a later examination of types, Mendoza and Cabioch (1985: 257) concluded that *A. aequabile* is a synonym of *Clathromorphum obtectulum* (Foslie) W. H. Adey and that *Antarcticophyllum* is a synonym of *Clathromorphum*. With the resurrection of *Neopolyporolithon* and the recognition of the new genera *Callilithophytum* (Adey et al. 2015) and *Clathmoroa* (herein), *Clathromorphum* presently includes three epilithic species in the Arctic, North Pacific, and North Atlantic Oceans (i.e., *Cl. circumscriptum*, *Cl. compactum*, and *Cl. nereostratum*) and two species in the Antarctic Peninsula and subantarctic islands (i.e., *Cl. obtectulum* and *Cl. lemoineanum* L. Mendoza et J. Cabioch). Four other species remain little known pending further studies (see incertae sedis Clathromorphoideae). Northern hemisphere species of *Clathromorphum* were most recently studied by Adey et al. (2013; 2015: 193). *Clathromorphum circumscriptum* and *Cl. compactum* were included in phylogenetic analyses of the nSSU, *psb*A, and *rbc*L genes, which confirmed their close relationship (Adey et al. 2015: fig. 6), as originally proposed by Foslie (1905b: 88–95), who considered them to be conspecific, differing at the level of forma.

Clathromorphum circumscriptum (Strömfelt) Foslie

Clathromorphum circumscriptum (Strömfelt) Foslie 1898a: 5.

Basionym: Lithothamnion circumscriptum Strömfelt 1886: 20–21, pl. 1, figs. 4–8.

Homotypic Synonyms: *Phymatolithon compactum* f. *circumscriptum* (Strömfelt) Foslie 1905b: 88–95.

Lithothamnion compactum f. *circumscriptum* (Strömfelt) Lund 1959: 200.

Lithothamnion circumscriptum var./f. *areolatum* Rosenvinge 1893: 774–775, nom. illeg.[27] Foslie (1895a: 161 [repr. 132], synonym, 1905b: 88, synonym), De Toni (1905: 1728, synonym), Lebednik (1977a: 64, synonym).

Heterotypic Synonyms: Lithothamnion durum Kjellm. 1889: 22, pl. 1, figs. 3–5; type locality: sublittoral, Port Clarence, Alaska, USA; syntype material[28]: in UPS, "A -000297, vii 1877" (Peña et al. 2021: 473); in TRH (C21-3516 and C21-3517), Adey and Lebednik (1967: 87, "Kjellman, USA, Alaska, Port Clarence, 7.1879, Vega Exp. [slides] 223, 224"). Foslie (1900b: 10, synonym), Lebednik (1977a: 64, synonym).

Clathromorphum durum (Kjellm.) Foslie 1898b: 8.

Lithothamnion evanescens Foslie 1895a: 165 (repr. 137), pl. 22, figs. 6–8; syntype localities: Mestervik, Malangen near Tromsø, and Marblehead, Mass.; lectotype: in TRH (C21-3518), "Collins, USA, Mass., Marblehead, 4.1889 LM41 (13)" (Adey and Lebednik 1967: 87), designated by Woelkerling (1993a: 87), Peña et al. (2021: 471, molecular synonym).

Clathromorphum evanescens (Foslie) Foslie 1898b: 8. Adey (1965: 541, synonym), Lebednik (1977a: 66, synonym).

Phymatolithon evanescens (Foslie) Foslie 1905b: 92, note 1,[29] comb. inval.

Syntype Localities: Rock pools of Hólmanäset and on balanoids deeper in Skagafjördur, Iceland.

Holotype: In S (unnumbered), material on seven slides; not reexamined (Adey et al. 2015: 196).

Habitat and Distribution: This is the most common and widely distributed species of the genus in the Arctic and subarctic, growing on rock, cobbles, pebbles, and shells in littoral pools and in the shallow sublittoral zone (typically less than 10 m depth). It requires winter temperatures of at least 2°C, and is limited by summer temperatures of ~16°C (Adey et al. 2015: 196). Thalli can be up to 15 cm in diameter and 0.5–8 cm thick (Adey 1965; Lebednik 1977a: 64; Adey et al. 2015: 196). In the North Atlantic, it is recorded from Iceland, the Faeroes (records questioned), North Norway (southern limit in Trondheimsfjord), and Greenland (see references in Athanasiadis 2016b: 251) and between Arctic Canada and New Hampshire (Adey 1965, 1971; South and Tittley 1986: 42). A record from Clew Bay (Ireland) has been considered to be inaccurate (Adey and Adey 1973: 246–247). Its North Pacific distribution ranges from the Russian coast of the Bering Sea (Kjellman 1883, 1885; Perestenko 1994; Selivanova and Zhigadlova 1997; Selivanova 2002) to Cape Erimo in Hokkaido (Masaki and Tokida 1961b, as *Cl. compactum*; Akioka and Masaki 1977; see Lebednik 1977a: 63) to southeastern Alaska (including the Aleutians; Lebednik 1977a: 68).

Comments: Both Foslie (1905b: 88–95) and Lund (1959: 200) considered this species to be a form of *Clathromorphum compactum*, and the main vegetative and reproductive characters distinguishing the two species were clarified by Adey (1965). They include the distribution of multiporate conceptacles in patches (vs. spread over the thallus in *Cl. compactum*), older conceptacles usually shedding[30] (vs. becoming embedded in the perithallium of *Cl. compactum*) and lack versus common occurrence of grooves in *Cl. compactum*. In addition, *Cl. circumscriptum* is a common species in the littoral zone, whereas *Cl. compactum* has its peak of distribution at greater depths (Adey 1965: 557–562; Lebednik 1977a: 70).

Clathromorphum compactum (Kjellm.) Foslie

Clathromorphum compactum (Kjellm.) Foslie 1898a: 4.

Basionym: Lithothamnion compactum Kjellm. 1883: 132–134 (1885: 101–102), pl. 6, figs. 8–12.

Homotypic Synonyms: Phymatolithon compactum (Kjellm.) Foslie 1905b: 88–95, including ff. "*typica*," *testaceum*, *circumscriptum*, *coalescens*.

Phymatolithon compactum f. *compactum* (Foslie) Foslie 1905b: 88, f. "*typica*."

Heterotypic Synonym: Lithothamnion circumscriptum var./f. *validum* Rosenvinge 1893: 775, fig. 3; type locality: on *Mytilus* shells, western Greenland; type: not designated. Rosenvinge (1894, "var. *validum*"), Adey (1965: 541, synonym), Lebednik (1977a: 70, synonym).

Misapplied Names: *Lithothamnion polymorphum* sensu Kjellm. 1877b: 8, Murmansk Sea. Kjellman (1883: 132, synonym) [non *Lithothamnion polymorphum* (L.) F. Aresch.].

Lithothamnion polymorphum sensu Farlow 1881: 182. De Toni (1905: 1726, synonym, "partim").

Syntype Localities: Karmakul Bay and Kostin Shar, west coast of Novaya Zemlya, Russia.

Lectotype: In TRH (C20-3470), designated by Woelkerling (1988: 161, figs. 167–170, "*Novaya Semlia, Karmakul bay*, 26/6/1875," 1993a: 54–55).

Habitat and Distribution: This is a purely Arctic species and is common in the sublittoral zone, growing on bedrock, boulders, and cobbles and, less commonly, on pebbles and shells, with a strong tendency to mesophotic depths (typically 5–20 m, depending upon turbidity). It is less abundant at localities with salinities lower than 25‰ and reaches maximum abundance at summer water temperatures of less than 6°C–8°C, requiring winter temperatures of 1°C or less (Adey et al. 2015: 194–195). Thalli can reach 12 cm in diameter and up to 20 cm in thickness, producing a hemispherical shape with age (Adey 1965: 541–542; Lebednik 1977a: 70; Adey et al. 2013: 20, 2015: 194). It is known from localities in Greenland, Iceland, Spitsbergen, Russia (Kjellman 1883, 1885), and Arctic Canada (southern limit in the Gulf of Maine; Adey et al. 2013: 3; Athanasiadis 2016b: 251). Its North Pacific distribution ranges from the Russian coast of the Bering Sea (Perestenko 1994; Selivanova and Zhigadlova 1997; Selivanova 2002) to northeastern Hokkaido (Akioka and Masaki 1977), including the Aleutians (Lebednik 1977a: 71; Adey et al. 2015: 196).

Comments: Gametophytes have not been recorded in this species (Adey 1965; Lebednik 1977a; Adey et al. 2015: 194).

Clathromorphum lemoineanum M. L. Mendoza et J. Cabioch

Clathromorphum lemoineanum M. L. Mendoza et J. Cabioch 1985: 259–260, pl. 1, figs. 1–8.

Misapplied Names: Lithophyllum subantarcticum sensu Me. Lemoine 1913: 43–44, text fig. 12. Mendoza and Cabioch (1985: 259, synonym) [non *Lithophyllum subantarcticum* (Foslie) Me. Lemoine].

Antarcticophyllum subantarcticum sensu M. L. Mendoza 1976: 258, pls. 2–3. Mendoza and Cabioch (1985: 259, synonym) [non *Antarcticophyllum subantarcticum* (Foslie) M. L. Mendoza].

Type Locality: Wandel Island, Antarctica.

Holotype: In PC (unnumbered), "I. Wandel, coll. Turquet, 1904. 1re Expédition antarctique française, 1903–1905, s/n PC" (Mendoza and Cabioch 1985).

Distribution: Apart from the type locality, the species has also been reported from Graham Land, Orcades, Terre de Feu, and the Falklands (Mendoza and Cabioch 1985; Hommersand et al. 2009). Habitat data are unknown.

Comments: In describing *Clathromorphum lemoineanum*, Mendoza and Cabioch (1985) cited the holotype in PC (annotated as above), while under *Clathromorphum obtectulum* they included *Lithophyllum aequabile* f. *wandelicum* Foslie, citing material in TRH annotated "Antarctique, île Wandel, coll. Turquet 10–27 sept. 1904, 1re Expédition antarctique française, st. n°1135, 1184, 1185, 1186, s/n°(TRH) det. Foslie: *Lithophyllum wandelica* Foslie f. *wandelica* (lectotype et autres)."

It is therefore apparent that two different Turquet elements (in PC and TRH) represent two different specimens (and species). According to the protologue and Mendoza (1976: pls. 2, 3, as *Antarcticophyllum subantarcticum*), *Cl. lemoineanum* differs from congeners in possessing a thinner thallus (to 700 µm thick), a hypothallium composed of 2–4 layers, 5–7 layers of epithallial cells and shedding multiporate conceptacles with a convex roof.

***Clathromorphum nereostratum* P. A. Lebednik**

FIGURE 7A

Clathromorphum nereostratum P. A. Lebednik 1977a: 79–88, figs. 11–15.

Type Locality: Sublittoral, 20 m depth, on ledge, south side of rocks at entrance of Constantine Harbor (51°24.36′N, 179°18.8′E), Amchitka Island (Aleutian Islands), Alaska, USA.

Holotype: In WTU (258721, (AM-C-60, 12-70-12, 17C), 12.xii.1970, 20 m depth on ledge, collected by P.A. Lebednik).

Isotype: In UBC (A54073, "AM-C-60, 12-70-12, 16B").

Habitat and Distribution: Thalli grow in littoral pools and channels and in the sublittoral attached to cobbles (less frequently on pebbles) down to at least 100 m (Lebednik 1977a: 80–88; Adey et al. 2013: 20). Lebednik recorded the species from the Aleutians, mentioning, however, that "specimens from Shimushu, Kurile Islands, identified as *C. loculosum* f. *typica* Fosl. ([Printz], 1929: pl. 41, figs. 18, 19; Nagai, 1941: 166) are almost certainly . . . *C. nereostratum*" (Lebednik 1977a: 79).

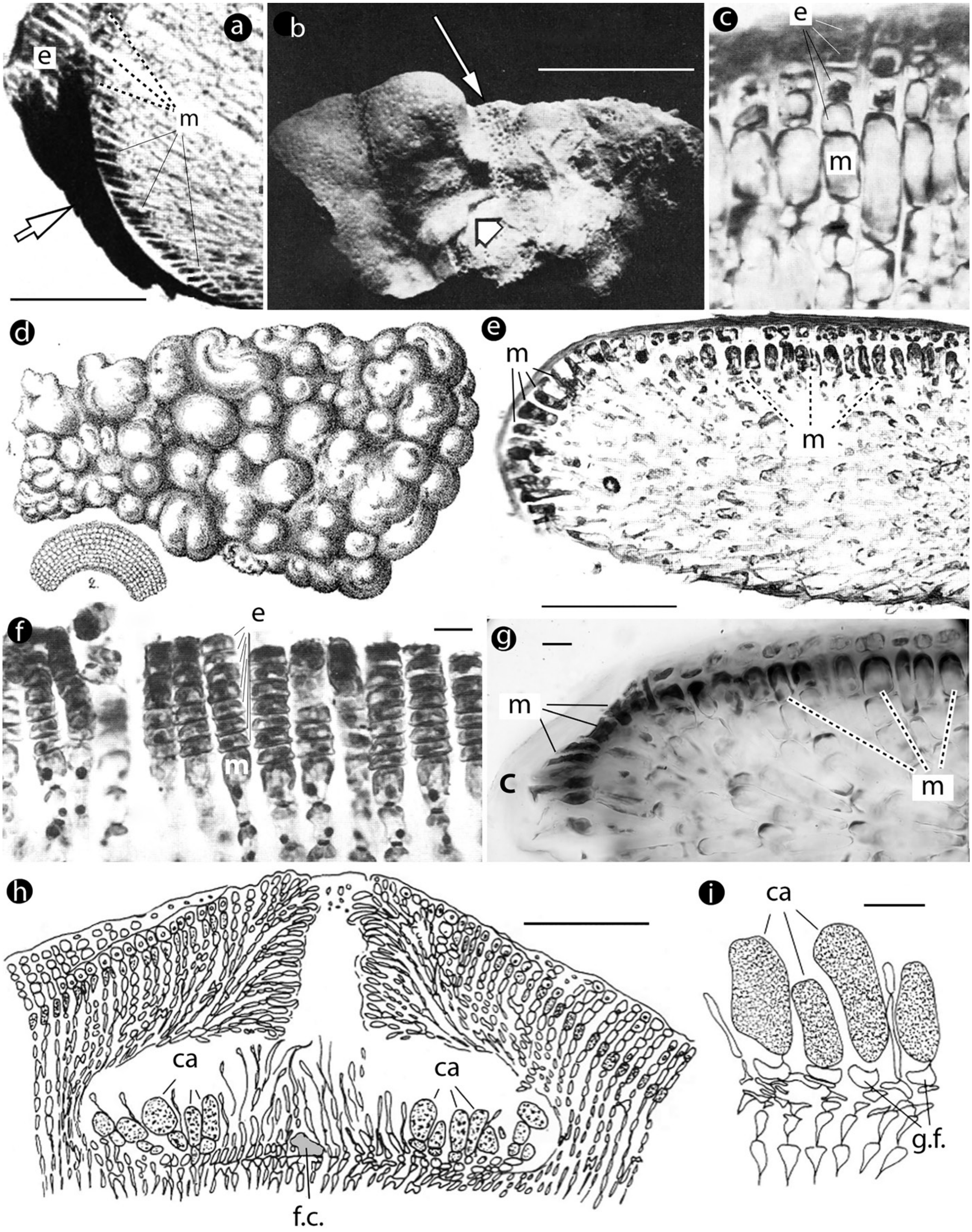
The species was later reported from the Russian coast of the Bering Sea (Karaginskii Gulf) and the Commander Islands (Perestenko 1994; Selivanova and Zhigadlova 1997; Selivanova 2002).

Comments: *Clathromorphum nereostratum* is by far the largest species in the genus (and the family Mesophyllaceae), reaching a diameter (or thickness) up to 0.5 m. It is mainly known from the protologue (Lebednik 1977a) and Lebednik's (1977b: fig. 13) postfertilization studies. Lebednik's (1977a: fig.14a) illustration of the thallus margin shows clearly the adaxially displaced terminal (apical) meristem that becomes embedded and starts production of epithallial cell layers via intercalary divisions (Figure 7a). According to Adey et al. (2015: 196), later observations "agree with those of Lebednik (1977). Crusts now known to 30 cm thick, with yearly vertical growth averaging ~360 µm . . . [and] up to ~850 years of age. Abundant asexual conceptacles produced in fall and winter; rarely gametangial conceptacles produced in summer."

***Clathromorphum obtectulum* (Foslie) W. H. Adey**

Clathromorphum obtectulum (Foslie) W. H. Adey 1970: 27.

FIGURE 7. (*Opposite*) (**a**) *Clathromorphum nereostratum*, (**b–f**) *Neopolyporolithon loculosum*, (**g**) *Neopolyporolithon reclinatum*, and (**h, i**) *Clathmoroa tubiformis*. (a) Section showing the terminal meristem protected by a cuticle (arrow), becoming gradually embedded adaxially and producing series of epithallial cells. Modified from Lebednik (1977a: fig. 14a). Scale bar: 100 µm. (b) Lectotype of *Lithothamnion loculosum*. Note the new lamella (short arrow) and the older conceptacles in pits (long arrow). Modified from Lebednik (1977a: fig. 6a, as *Clathromorphum*). Scale bar: 1 cm. (c) Section of the lectotype of *Lithothamnion loculosum*, showing the subepithallial meristem producing series of up to 4 epithallial cells. Modified from Lebednik (1977a: fig. 6b, as *Clathromorphum*). Scale bar: 10 µm. (d) The original illustrations of *Lithothamnion loculosum* (Kjellman 1889: pl. 1, figs. 1, 2, the specimen attaining 7 cm in extent). (e, f) Sections showing the terminal meristem becoming gradually embedded and producing series of up to 7 epithallial cells. Modified from Lebednik (1977a: fig. 8d,e, as *Clathromorphum*). Scale bars: 10 µm. (g) Section showing the gradual embedment of the terminal meristem below a cuticle ("Patty 23," slides in herb.Athanas.). Scale bar: 10 µm. (h, i) Postfertilization stages, showing orthostichous development of carposporangia from gonimoblast filaments and an inconspicuous fusion cell. Modified from Chamberlain et al. (2015: figs. 22, 23, as *Clathromorphum*). Scale bars: 50, 10 µm, respectively. Abbreviations: c, cuticle; ca, carposporangia; e, epithallial cells; f.c., fusion cell; g.f., gonimoblast filament; m, meristematic cell.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Basionym: Lithothamnion kerguelenum f. *obtectulum* Foslie 1899b: 10, "*obtectula*."

Homotypic Synonym: Lithothamnion obtectulum (Foslie) Foslie 1900c: 68.

Heterotypic Synonyms: Lithophyllum discoideum f. *aequabile* Foslie 1905a: 17 (repr. 3), "*aequabilis*"; type locality: South Orkney Islands; type: not designated.[31] Mendoza and Cabioch (1985: 261, synonym).

Lithophyllum aequabile (Foslie) Foslie in Me. Lemoine 1913: 39–43, text fig. 11. Foslie (1906b: 22, 1907c: 12, pl. 2, figs. 6–9), Mendoza and Cabioch (1985: 261, synonym).

Pseudolithophyllum aequabile (Foslie) W. H. Adey 1970: 12. Mendoza and Cabioch (1985: 261, synonym).

Antarcticophyllum aequabile (Foslie) M. L. Mendoza 1976: 255. Mendoza and Cabioch (1985: 261, synonym).

Lithophyllum aequabile f. *wandelicum* Foslie 1906b: 22, "*wandelica*"; type locality: Wandel Island, Antarctic Peninsula; type: not designated[32]; Printz (1929: pl. 59, figs. 15–19), Adey and Lebednik (1967: 23, as "*Lithophyllum aequabile*," "Hariot, Ile Wandel, 10-27.9.1904, Exp.Ant.Charcot, 65° 4'S, LM59 (15-19) [slides] 1129-1135, 1184-1186"), Mendoza and Cabioch (1985: 261[33]), Woelkerling (1993a: 237,[34] "lectotype").

Type Locality: Kerguelen Islands.

Lectotype: In TRH (B15-2364), Printz (1929: pl. 5, fig. 4), designated by Woelkerling (1993a: 160, "lectotype: Printz 1929, pl. 5, fig. 4"), Woelkerling et al. (2005: 316, "coll. . . . Gundersen").

Distribution: Apart from the type locality, the species has also been reported from Graham Land, Orcades, Terre de Feu, the Falklands, Terre Luis Philippe, South Georgia, Wienke Island, and Staten Island (Mendoza and Cabioch 1985; Hommersand et al. 2009). Habitat data are unknown.

Comments: Adey and Lebednik (1967: 64) listed as "type material" several specimens illustrated by Printz (1929: pl. 5, figs. 5–7), that is, "§ Gunderson, Kerguelen Is, 1898, LM5(5-7) 'D.Lith.Gauss.Exp.' [slides] 208, 1550." Adey (1970: 27) commented that the selected type material was "in very poor condition, and placement in this genus remains with some doubt." These type specimens were later reported as missing or belonging to a different collection (Woelkerling 1993a: 161; Woelkerling et al. 2005: 317), and a new lectotype was selected by Woelkerling (1993a: 160). According to Mendoza (1976: pls. 1–2, as *Antarcticophyllum aequabile*) and Mendoza and Cabioch (1985: 262, pls. 2–3), this species becomes up to 1 mm thick, and its surface is rugose with apparent protuberances. The hypothallium is composed of up to 10 layers, and the epithallium is 5- to 7-celled. Multiporate conceptacles are flush with the surface, and carposporangial conceptacles become embedded in the thallus.

***Neopolyporolithon* W. H. Adey et H. W. Johans.**

Neopolyporolithon W. H. Adey et H. W. Johans. 1972: 160 (type: *N. reclinatum*).

Comments: Lebednik (1977a) subsumed *Neopolyporolithon* in *Clathromorphum*, concluding that the characters used by Adey and Johansen (1972) were not sufficient to recognize this new genus. It appears, however, that the generitype *N. reclinatum* develops a large fusion cell (Masaki and Tokida 1961a: pls. 1–4, as *Polyporolithon*), possibly of similar size to species of *Mesophyllum*, and also differs in being a common epiphyte on diverse algae (e.g., *Bosiella* and *Corallina*). The second species of the genus, *N. loculosum*, approaches *Clathromorphum* in being saxicolous but differs in having a strongly developed hypothallium (Lebednik 1977a: 76). Gametangial and postfertilization characters in *N. loculosum* are needed (Lebednik 1977a, 1977b), and a reevaluation of the generic circumscription is pending new investigations. In addition, on the basis of DNA sequence data, Adey et al. (2015: 198) concluded that "we are aware of at least two other species passing under this name [*N. reclinatum*] in the NE Pacific, also epiphytic on geniculate corallines or on fleshy red algae, but we need additional data to be able to characterize these species."

***Neopolyporolithon loculosum* (Kjellm.) W. H. Adey, P. W. Gabrielson, G. P. Johnson, et J. J. Hernández-Kantun**

FIGURE 7B–F

Neopolyporolithon loculosum (Kjellm.) W. H. Adey, P. W. Gabrielson, G. P. Johnson, et J. J. Hernández-Kantun 2015: 198.

Basionym: Lithothamnion loculosum Kjellm. 1889: 21–22, pl. 1, figs. 1, 2.

Homotypic Synonyms: Clathromorphum loculosum (Kjellm.) Foslie 1898b: 8.

Phymatolithon loculosum (Kjellm.) Foslie 1905b: 93. Lebednik (1977a: 71, synonym).

Clathromorphum loculosum f. *loculosum* (Foslie) Foslie in Printz 1929: 29, "*typica*," pl. 41, figs. 17–19. Lebednik (1977a: 71, synonym).

Heterotypic Synonyms: Phymatolithon loculosum f. *evanidum* Foslie 1905b: 93, "*evanida*"; type locality: upper sublittoral, Etorufu, Rubetsu, Kurile Islands; lectotype: in TRH (C21-3524), Printz (1929: pl. 41, fig. 16), designated by Lebednik (1977a: 71, "Holotype," "Yendo, a few feet below low-water mark, 7.6.1903. . . . illustrated by Foslie, 1929, pl. 41 fig.16"). Woelkerling (1993a: 87,[35] "numerous intact conceptacles").

Clathromorphum loculosum f. *evanidum* (Foslie) Printz 1929: 29, pl. 41, fig. 16. Lebednik (1977a: 71, synonym).

Type Locality: Bering Island, Commander Islands, Bering Sea, Russia.

Lectotype: In TRH (C21-3520), Printz (1929: pl. 41, fig. 17), designated by Lebednik (1977a: 71, fig. 6a,b, "lectotype," "Aug. 15-19. 1879, littoral region, leg. F.R. Kjellman").

Isolectotype: In UPS (unnumbered), designated by Adey et al. (2015: 198, "Bering Island, 15-19.viii.1879, leg. F.R. Kjellman").

Habitat and Distribution: This is a common littoral alga growing in rock pools, where it forms "spheroidal protuberances.

Thalli in the sublittoral tend to be much larger, commonly over 10 cm in diameter and . . . thicker" (Lebednik 1977a: 74–76). The species is recorded from southern Alaska (Baranof Island), Cold Bay on the Alaska Peninsula, St. Lawrence Island, the western Aleutian Islands, the Commander Islands, and the Kurile Islands and north to Konyam Bay, southwest of the Bering Strait (Lebednik 1977a; Perestenko 1994; Selivanova and Zhigadlova 1997; Selivanova 2002), recorded as *Clathromorphum* by all authors.

Comments: Thalli reach 2 cm in thickness and may possess spheroid protuberances (littoral specimens; Lebednik 1977a: 71, fig. 6a,b; Figure 7b,d). The terminal hypothallial meristem becomes gradually embedded dorsally, producing up to 7 layers of epithallial cells (Lebednik 1977a: figs. 6, 8; Figure 7c,e,f). Tetrasporangial conceptacles with chambers 300–800 µm in diameter become embedded in the perithallium (Lebednik 1977a: 78, table 7). *Neopolyporolithon loculosum* has been confused with *Leptophytum arcticum* (Kjellm.) Athanas., a sublittoral species known only from the original collections in Novaya Zemlya and clearly differing by its thin, fragile, lamellate thallus with unattached superimposed growth (individual lamellae reaching 0.75–1 mm in thickness; see further comments in the account for *Leptophytum arcticum*).

Neopolyporolithon reclinatum (Setch. et Foslie) W. H. Adey et H. W. Johans.

FIGURE 7G

Neopolyporolithon reclinatum (Setch. et Foslie) W. H. Adey et H. W. Johans. 1972: 160.

Basionym: Lithothamnion conchatum f. *reclinatum* Setch. et Foslie in Foslie 1906b: 6, "*reclinata*."

Homotypic Synonyms: Lithothamnion reclinatum (Foslie) Foslie 1907b: 14.

Polyporolithon reclinatum (Foslie) L. R. Mason 1953: 319.

Clathromorphum reclinatum (Foslie) W. H. Adey 1970: 28.

Type Locality: Botany Beach, Port Renfrew, Vancouver Island, British Columbia, Canada.

Type Material: In TRH (B17-2590), Printz (1929: pl. 10, figs. 14–17), Mason (1953: 319, "type . . . Port Renfrew, Vancouver I . . . *K. Yendo* (Herb. Mus. Nidaros.)"), Adey and Lebednik (1967: 69, "type material," "§ Yendo, Canada, Vancouver Is., Port Renfrew (San Juan), 7.1901. LM10 (14-17)"), Lebednik (1977a: 94, "holotype"), Woelkerling (1993a: 187, "holotype"), Woelkerling et al. (2005: 347, "collection consists of four original round boxes").

Material Examined: Tatoosh Island: Washington State: "Patty 23," 20 November 1995, coll. R. T. Paine (slides in herb. Athanas.; Figure 7g).

Habitat and Distribution: According to Lebednik (1977a: 94, 102–103, as *Clathromorphum*), this species is a common epiphyte on *Corallina*, *Bossiella*, *Calliarthron*, and *Ahnfeltia* Fries, in rock pools and in the *Hedophyllum* Setch. zone, although sublittoral collections have been made down to ~9 m depth. The species is reported in the North Pacific from the Russian coast (Perestenko 1994, as *Clathromorphum*), including the Commander Islands (Selivanova and Zhigadlova 1997, as *Clathromorphum* on *Fucus* L.) to Hokkaido in Japan (Masaki and Tokida 1961a: pls. 1–4, as *Polyporolithon*). On the American coast, it is reported between the Gulf of Alaska and the Aleutians to California (Adey and Johansen 1972; Lebednik 1977a: 103, as *Clathromorphum*; Adey et al. 2015).

Comments: The original material in TRH consists of at least four specimens (Printz 1929, pl. 10, figs. 14–17) placed in four boxes (Woelkerling et al. 2005), and hence, a lectotype remains to be selected. Masaki and Tokida (1961a: pl. 3, fig. 6, pl. 4, as *Polyporolithon*) illustrated postfertilization stages showing lateral production of carposporangia from gonimoblasts and the presence of a large fusion cell (possibly similar to that in species of *Mesophyllum*; Athanasiadis 2018). Spermatangial structures were illustrated by Lebednik (1977a: fig. 21e), showing two to three spermatangia borne on nonlunate SMCs. Specimens provided by R. T. Paine from Tatoosh Island (Washington State) are here illustrated, showing the characteristic embedment of the dorsally displaced terminal meristem (Figure 7g). On the other hand, Adey et al. (2015: 198) noted that the taxonomy of the species requires further study since they confirmed only material on *Corallina* and *Bossiella*, although on "the basis of DNA sequence data, we are aware of at least two other species passing under this name in the NE Pacific, also epiphytic on geniculate corallines or on fleshy red algae, but we need additional data to be able to characterize these species."

Callilithophytum P. W. Gabrielson, W. H. Adey, G. P. Johnson, et J. J. Hernández-Kantun

Callilithophytum P. W. Gabrielson, W. H. Adey, G. P. Johnson, et J. J. Hernández-Kantun 2015: 199 (type: *C. parcum*).

Etymology: After the neuter substantive καλλος (beauty), referring to the host *Calliarthron*; the masculine substantive λιθος (stone); and the neuter substantive φυτον (plant), latinized with similar gender.

Comments: *Callilithophytum* is monotypic and displays a unique (for the Mesophyllaceae) thallus organization, forming an anchoring tissue ("foot") and a "hypothallium weakly developed or lacking; [and a] strongly developed . . . up- and down-turning perithallium" (Adey et al. 2015: 199; Figure 4e) with bilateral production of conceptacles (Lebednik 1977a: fig. 16d,e).

Callilithophytum parcum (Setch. et Foslie) P. W. Gabrielson, W. H. Adey, G. P. Johnson, et J. J. Hernández-Kantun

Callilithophytum parcum (Setch. et Foslie) P. W. Gabrielson, W. H. Adey, G. P. Johnson, et J. J. Hernández-Kantun 2015: 199.

Basionym: Lithothamnion parcum Setch. et Foslie in Foslie 1907a: 14–15.

Homotypic Synonyms: Polyporolithon parcum (Setch. et Foslie) L. R. Mason 1953: 318.

Clathromorphum parcum (Setch. et Foslie) W. H. Adey 1970: 27.

Type Locality: Monterey, California, USA.

Type Material: In TRH (B17-2582 and B17-2542), Mason (1953: 318, "Type . . . Herb. Mus. Nidaros."), Printz (1929: pl. 10, figs. 18–23), Adey and Lebednik (1967: 69, "type material," "§ Setchell+Gibbs. USA, Cal., Monterey, 1.10.1899, LM10 (18-23) [slides] 1576, 1577"), Woelkerling (1993a: 169, "holotype"), Woelkerling et al. (2005: 346, "B17-2542 was removed . . . from B17-2582").

Habitat and Distribution: The species is an obligate epiphyte on *Calliarthron tuberculosum* (Postels et Ruprecht) E. Y. Dawson, growing in the "continuously wetted" littoral zone and in rock pools (Lebednik 1977a: 94, as *Clathromorphum*). It is recorded between Haida Gwaii, British Columbia, and San Luis Obispo County, California, north of Point Conception (Adey et al. 2015: 199).

Comments: Mason (1953: 318) selected "type" material of *Lithothamnion parcum* in TRH that is dated "1.10.1899" (Adey and Lebednik 1967), although she examined a "Gibbs and Setchell 3057b" collection in UC dated "Jan.8.1899." However, at least six specimens were included in the TRH material (Printz 1929: pl. 10, figs. 18–23), and hence, a lectotype remains to be selected. Mason (1953: 318) further considered UC (745690) as an "isotype," but this is apparently dated "Jan.8.1899," and hence, it is not a duplicate of the original material. The species is considered to be "one of the most distinctive and easily identified non-geniculate corallines in the NE Pacific, due to its being an obligate epiphyte on *Calliarthron tuberculosum* and its thick, flat-topped and frequently somewhat concave thallus" (Adey et al. 2015: 199).

Clathmoroa Athanas. et D. L. Ballant. gen. nov.

FIGURE 7H,I

Clathmoroa Athanas. et D. L. Ballant. gen. nov. (type: *Clathmoroa tubiformis*).

Diagnosis: This new monotypic genus differs from other members of the subfamily Clathromorphoideae by the development of orthostichous carposporangia and in growing as an (obligate?) epiphyte on species of *Amphiroa*.

Etymology: The generic name is a new compound word after κλαθμος (tier) and the feminine substantive ροη (current), which is the second compound of *Amphiroa*, latinized to *roa* with similar gender.

Clathmoroa tubiformis (Y. M. Chamb., R. E. Norris, et G. W. Maneveldt) Athanas. et D. L. Ballant. comb. nov.

Clathmoroa tubiformis (Y. M. Chamb., R. E. Norris, et G. W. Maneveldt) Athanas. et D. L. Ballant. comb. nov.

Basionym: Clathromorphum tubiforme Y. M. Chamb., R. E. Norris, et G. W. Maneveldt 1995: 443.

Type Locality: Cintsa, Eastern Cape Province, South Africa.

Holotype: In L ("HLB 993.111 712"), "in intertidal pools, epiphytic on *Amphiroa ephedraea . . . R. Anderson and J. Bolton*, July 1967, YMC 89/206" (Chamberlain et al. 1995).

Habitat and Distribution: The species is reported as an epiphyte on *Amphiroa ephedraea* (Lam.) Decne, *A. anceps* (Lam.) Decne, and a third unidentified species of *Amphiroa* J. V. Lamour. It grows in littoral pools and in the sublittoral to at least 16 m depth. Fertile thalli have been collected between July and October. It is known only from Natal (Tiger Rocks) and Cape Province (Patridge Point, False Bay; Chamberlain et al. 1995: 444).

Comments: The holotype was illustrated by Chamberlain et al. (1995: figs. 2–4, 11–19, 20–23, 24–30). The number "HLB 993.111 712" was later added on the offprint referring to the holotype in L. *Clathmoroa tubiformis* was described from thalli growing on diverse species of *Amphiroa* and remains known only from the protologue that included SEM illustrations and several drawings of anatomical characters (Chamberlain et al. 1995: figs. 1–28, table 1). Chamberlain et al. (1995) distinguished the species from *Clathromorphum* s.l. by the small (no more than 73 μm in diameter) tetrasporangial chambers—indeed, the smallest known in the family Mesophyllaceae. *Clathmoroa* encircles the host and lacks superimposed unattached growth. The hypothallium is noncoaxial with terminal meristematic cells, whose subsequent embedding in the thallus was alluded to in a drawing showing the terminal meristem to be followed by several dorsal epithallial layers (Chamberlain et al. 1995: fig. 18). Subepithallial meristematic cells are elongate and support up to 5 layers of epithallial cells, while downward growing hypothallial filaments support a single layer of epithallial cells (Chamberlain et al. 1995: fig. 11). Gametophytes are dioecious, with male structures composed of simple (unbranched) SMCs (Chamberlain et al. 1995: fig. 16); their shape (lunate or not) was not clarified. Carpogonial branches are 3-celled, composed of the carpogonium, the hypogynous, and the supporting cell (Chamberlain et al. 1995: fig. 21). Following presumed fertilization, an inconspicuous fusion cell was illustrated (Chamberlain et al. 1995: fig. 22; Figure 7h), possibly including 3 cells, with gonimoblast filaments producing carposporangia both laterally and in orthostichous position (Chamberlain et al. 1995: figs. 22, 23; Figure 7h,i). No pedestal formation takes place in carposporangial conceptacles (Chamberlain et al. 1995: fig. 22; Figure 7h). Multiporate conceptacles have slightly sunken pore plates (Chamberlain et al. 1995: fig. 27), and the pore canals are straight and lined by 3 to 4 nondifferentiated pore cells (Chamberlain et al. 1995: fig. 29). Five to seven rosette cells surround pore canals of multiporate conceptacles (Chamberlain et al. 1995: fig. 30). Older conceptacles become embedded in the perithallium.

The species was further compared to *Neopolyporolithon reclinatum* and *Callilithophytum parcum* (Chamberlain et al. 1995: table 1, both taxa as *Clathromorphum*). Assuming that the terminal (apical) meristem becomes gradually displaced and embedded (Chamberlain et al. 1995: fig. 18), *Clathmoroa tubiformis* displays all features characterizing members of the subfamily Clathromorphoideae, differing by the additional development of orthostichous carposporangia and the epiphytic habit on *Amphiroa* spp.

INCERTAE SEDIS CLATHROMORPHOIDEAE

Clathromorphum annulatum (Foslie) M. L. Mendoza

Clathromorphum annulatum (Foslie) M. L. Mendoza "in J. Acosta Polo (ed.) Anales del II Congreso Latinoamericano de Ficología Marina. P. 147. 1992." Index Nominum Algarum (2023).

Basionym: Lithothamnion annulatum Foslie 1906a: 18.

Homotypic Synonym: *Mesophyllum annulatum* (Foslie) W. H. Adey (1970: 22).

Misapplied Name: ?*Lithothamnion lenormandii* sensu Lemoine 1913: 10–13, text fig. 2, "*Lithothamnium*." Mendoza et al. (1996: 36, synonym) [non *Lithothamnion lenormandii* (F. Aresch.) Foslie].

Type Locality: Betsy Cove, Kerguelen Islands.

Holotype: In TRH (B2-1679), Foslie (1908c: 206–207 [repr. 10], text fig. 1), Printz (1929: pl. 2, fig. 15), Adey and Lebednik (1967: 51, "type material," "§ Naumann, Kerguelen Is., Betsy Cove, Gazelle Exp. 1874–1875 Bot.Mus.Berlin, LM2(15) [slides] 1061–1063"), Woelkerling (1993a: 28, "holotype"), Woelkerling et al. (2005: 237, "holotype").

Comments: According to the protologue (Foslie 1906b: 18), the thallus is 100–200 µm thick and develops dense aggregations of hemispherical sporangial conceptacles (250–400 µm in external diameter) with a convex roof, later becoming sunken and developing a peripheral raised rim. Bisporangia are 110–130 × 60–70 µm (L × B). Printz's (1929: pl. 2, fig. 15) illustration shows a single crust adhering to rock.

Woelkerling (1993a: 28) noted that the "holotype is represented in TRH by three small fragments depicted in Printz (1929) . . . said by Printz . . . to have come from the Botanical Museum in Berlin," and Woelkerling et al. (2005: 237) added, "[It is annotated] *Lithoth. annulatum* (*L. polymorph*. Ask.[enasy 1888: 54] partim)," "brudst. [fragment]," "Sp. konc.foto nr. 28," and "x = ung [young] *Lithoph. consociatum*."

The species was included in the algal flora of Argentina (Mendoza et al. 1996: 36–38, pl. 8, figs. 6–9, pl. 9, fig. 11), where the combination is ascribed to Mendoza (1990: 143). However, a study of the holotype in comparison to new collections remains to be made since the position in *Clathromorphum* contradicts Adey's (1970) transfer of the species to the genus *Mesophyllum*.

Clathromorphum coalescens (Foslie) Foslie

Clathromorphum coalescens (Foslie) Foslie 1898b: 8.

Basionym: Lithothamnion coalescens Foslie 1895a: 162 (repr. 134–137), pl. 19, figs. 15–20.

Homotypic Synonyms: Clathromorphum circumscriptum f. *coalescens* (Foslie) Foslie 1900b: 10.

Phymatolithon compactum f. *coalescens* (Foslie) Foslie 1905b: 88–95.

Clathromorphum compactum f. *coalescens* (Foslie) Foslie 1908b: 12.

Syntype Localities: Inderøen, Strømmen, Munkholmen, and Röberg in Trondheimsfjord, Norway. Foslie (1894: VIII).

Type Material: In TRH (C21-3503), illustrated by Foslie (1895a) and Printz (1929: pl. 41, figs. 11, 12).

Comments: The original material has not been reexamined in a modern context, and there are no later records of this species. According to Woelkerling (1993a: 52), "[the] lectotype . . . includes slide 215 (missing) and five unnumbered slides . . . Inderøen, Strømmen, . . . coll. *M.F. Foslie*, 12 Aug. 1893. . . . The designated lectotype is the only collection labelled *Lithothamnion coalescens* found at TRH. It consists of plants attached to 41 small stones . . . housed in two boxes . . . [now] placed in a single . . . box. . . . The nature of the reported type . . . in BM (Tittley et al. 1984, p.10) . . . not determined. " Furthermore, "part of the lectotype collection, containing five of the six individuals depicted in the protologue, was listed under *Clathromorphum evanescens* in Adey and Lebednik 1967: 87" (Woelkerling et al. 2005: 493). Athanasiadis (2016b: 264, footnote 12) noted that "it remains to be shown whether the 41 small specimens represent a single gathering made at a time (Art.8.2.) and which of these specimens match those illustrated in the protologue."

Peña et al. (2021: 473) mechanically selected one (not illustrated) of the original six specimens included in Foslie's (1895a) original account that they considered to be the "narrowed" lectotype but gave no evidence that the relevant specimen is in agreement with the lengthy protologue. The partial *psb*A and *rbc*L (bp 263) sequences of the "narrowed" lectotype were identical to the similarly long ones of *C. circumscriptum*, but fully long sequences (bp 1,172–1,434) of topotypes need to be compared to support this synonymy.

Clathromorphum testaceum (Foslie) Foslie

Clathromorphum testaceum (Foslie) Foslie 1898b: 8.

Basionym: Lithothamnion testaceum Foslie 1895a: 135 (repr. 107), pl. 19, figs. 5–9.

Homotypic Synonyms: Clathromorphum compactum f. *testaceum* (Foslie) Foslie 1900b: 10, "*testacea*."

Phymatolithon compactum f. *testaceum* (Foslie) Foslie 1905b: 88–95, "*testacea*."

Type Locality: Bergsfjord, Finnmark, Norway.

Type Material: In TRH (C21-3527); illustrated by Foslie (1895a) and Printz (1929: pl. 41, fig. 14).

Comments: The species is reported only from the type locality and Helgoland (De Toni 1905: 1727, "ad insul.Helgolandiam (Kuckuck)"), and its status is pending reexamination of the original material. Woelkerling (1993a: 222–223) considered as "holotype . . . material - including . . . slide 219 and one unnumbered slide . . . [and] 20 fragments . . . some of these . . . depicted by Foslie (1895) and Printz (1929)." However, there is no indication that this material was the product of a single gathering (Turland et al., 2018: Article 8.2), and it was later considered to be a "collection" (Woelkerling et al. 2005: 497). Hence, the selection of "isotypes" by Woelkerling and Verheij (1995: 80) and Woelkerling and Lamy (1998: 363) cannot be accepted either.

"Clathromorphum fasciculatum" comb. ined.

Basionym: Millepora fasciculata Lam. 1816: 203.
Homotypic Synonyms: Melobesia fasciculata (Lam.) Harv. 1847: pl. 74.
Nullipora fasciculata (Lam.) Blainville 1834: 605.
Spongitis fasciculata (Lam.) Kütz. 1849: 699, "*Spongites*."
Lithothamnion fasciculatum (Lam.) F. Aresch. 1852: 522.
Lithophyllum fasciculatum (Lam.) Foslie 1898b: 10.
Crodelia incrustans f. *fasciculata* (Lam.) Heydrich 1911: 14.

Syntype Localities: "Différent mers."

Lectotype: In PC (unnumbered; see Basso et al. 2004: figs. 13–15).

Comments: Woelkerling and Lamy (1998: 266, figs. 113–115) showed that Lamarck's *Millepora fasciculata* included material representative of a species of *Lithothamnion*, and subsequently Basso et al. (2004) found the same material to be heterogeneous and selected as lectotype a specimen that belongs to the genus *Clathromorphum* (see Athanasiadis 2016b: 265).

PROTOMESOPHYLLOIDEAE ATHANAS. ET D. L. BALLANT. SUBFAM. NOV.

Protomesophylloideae Athanas. et D. L. Ballant. subfam. nov. (type: *Protomesophyllum*).

Diagnosis: New monotypic subfamily of Mesophyllaceae, differing by the development of rhomboid pore cells in filaments lining canals of multiporate conceptacles and sharing all other characters of Mesophylloideae except for lunate SMCs, trichocytes, and thinner–wider pore cells.

Comments: Protomesophylloideae resolved in a trichotomy with Clathromorphoideae and Mesophylloideae, differing from each by three characters (Figure 6a–c).

Protomesophyllum Athanas. et D. L. Ballant. gen. nov.

Protomesophyllum Athanas. et D. L. Ballant. gen. nov. (type: *Pr. ameleteton*).

Diagnosis: Differing from other genera of Mesophyllaceae by the character combination proposed above for the subfamily.

Etymology: After the adjective πρωτος (first) and the generic name *Mesophyllum* (after the adjectives μεσος, μεση, μεσον, and the neuter substantive φυλλον, "middle leaf"), referring to the first clade before Mesophylloideae.

Comments: *Protomesophyllum* is presently monotypic, and its generitype was previously subsumed in the Mediterranean *Mesophyllum macroblastum* (Foslie) W. H. Adey (Woelkerling and Harvey 1993; Woelkerling 1996; Harvey et al. 2005; Farr et al. 2009); the latter species is here recognized as *Macroblastum dendrospermum*. These two genera and species are clearly distinct morphoanatomically and also occupy different habitats in the field (Athanasiadis 2020b). In a comparison of sequences of the *psb*A gene (Peña et al. 2015: fig. 11), the following topology was resolved: (((((*Printziana*–*Perithallis*)-*Sunesonia*) *Melyvonnea*) (*Macroblastum*–*Mesophyllum*)) *Protomesophyllum*) *Lithothamnion*–*Phymatolithon*, which supports the peripheral position of *Protomesophyllum* with regard to Mesophylloideae and the remote taxonomic and systematic relationship between *Protomesophyllum* and *Macroblastum*. Similarly, in a study of the same gene in the "*Mesophyllum erubescens*" complex, Sissini et al. (2014: fig. 5) compared 66 mesophylloid sequences, showing that the Australian–New Zealand–Chatham "*Mesophyllum macroblastum*" forms several basal clades next to species of *Lithothamnion*. Biogeographically, *Protomesophyllum* joins the antipodal distribution exhibited by most genera of Mesophylloideae, in comparison to the northern hemisphere *Mesophyllum*, with *Melyvonnea* bridging the gap in the tropics and the subtropics.

Protomesophyllum ameleteton Athanas. et D. L. Ballant. sp. nov.

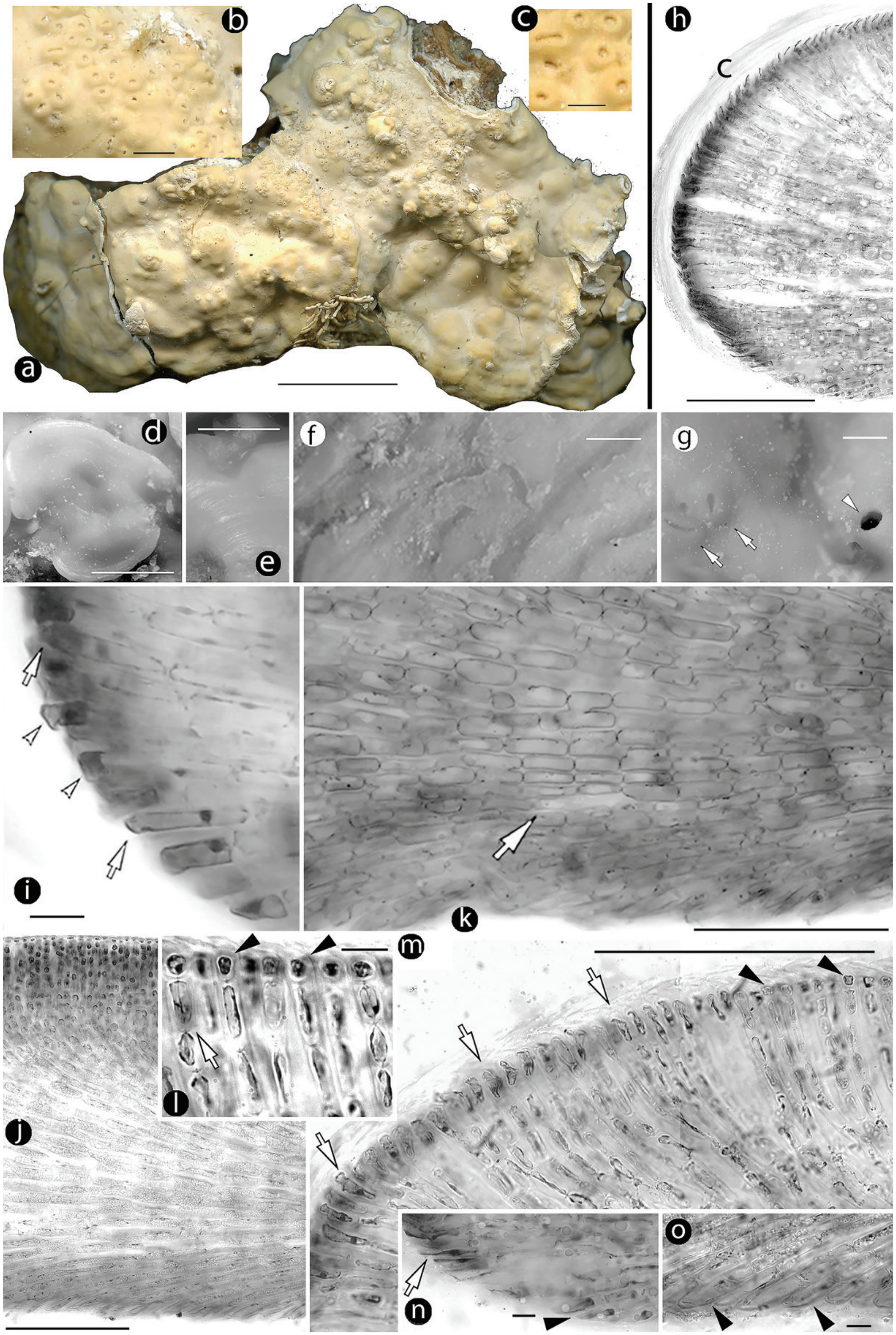
FIGURES 8–11

Protomesophyllum ameleteton Athanas. et D. L. Ballant. sp. nov.
Misapplied Name: *Mesophyllum macroblastum* sensu Woelkerling and Harvey 1993: 590, figs. 19–23 [non *M. macroblastum* (Foslie) W. H. Adey = *Macroblastum dendrospermum*].

Diagnosis: As given above for the monotypic subfamily and genus (Turland et al. 2018: Article 38.5).

Holotype: In GB (GB-0209476), a tetrasporangial specimen (Figure 8a–c).

FIGURE 8. (*Opposite*) *Protomesophyllum ameleteton*. (**a–c**) Holotype with magnification of two patches of tetrasporangial conceptacles (GB-0209476). Scale bars: 1 cm. (**d, e**) Young lamella growing in superimposition and showing striations on its surface (LTB13210). Scale bars: 1 mm. (**f**) Thallus underside showing rough texture (LTB13210). Scale bar: 500 µm. (**g**) Thallus surface with multiporate conceptacles (arrows) and an opening (arrowhead) resulting from animals (LTB13205). Scale bar: 500 µm. (**h**) Section of margin with deeply stained, terminal meristematic cells protected by a cuticle (holotype). (**i**) Section of margin showing asynchronous cell divisions (arrowheads) and cell elongations (arrows; LTB13210). Scale bar: 10 µm. (**j**) Section showing dorsiventral organization with a basal, noncoaxial hypothallium and ascending perithallial filaments (holotype). (**k**) Section showing a coaxial patch (arrow; NZ0621). Scale bar: 100 µm. (**l**) Isodiametric epithallial cells (arrowheads) supported by elongate (arrow) subepithallial cells (holotype). (**m**) Transition zone showing dorsal meristematic (arrows) cells becoming epithallial (arrowheads) cells (holotype). (**n, o**) Transition zone showing ventral meristematic (arrows) cells becoming hyaline (arrowheads) wedge-shaped cells (holotype). Abbreviation: c, cuticle.


a
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Isotypes: Slides in herb. Athanas.

Paratypes: Specimens and slides in herb. Athanas. and in GB.

Type Locality: Rye Beach, Melbourne, Victoria, southern Australia.

Etymology: The epithet *ameleteton* is a transliteration of the adjective αμελετητος, αμελετητη, αμελετητον ("the unstudied").

Material Examined: Southern Australia: Victoria: Rye Beach: males and tetrasporangial thalli, November 1989, on *Ecklonia radiata* (C. Agardh) J. Agardh holdfasts, upper sublittoral, coll. Athanas., holotype (GB), isotypes, and paratypes (herb. Athanas.).

Northeastern Tasmania: Binalong Bay: Bay of Fires (41°15′S, 148°18′E), 0–4 m deep on fixed rock, 23 February 1983, coll. S. Platt (no. 13210A, MEL2271677, LTB13210); Binalong Bay: Bay of Fires (41°15′S, 148°18′E), 0–4 m deep on *Ecklonia* Hornemann holdfast, collector S. Platt (no. 13205, MEL2269654, LTB13205), further annotated (loan 2015/10) to GB: "Portions removed and sent . . . Date removed: 8/2/2005 . . . There are 27 microscope slides associated with this collection. The dry component of this specimen comprises resin block/resin chips/SEM stubs. 10987 D Slide 10987 Sheet 1 of 2 (MEL2269654, spirit: MEL2269655)."

New Zealand: Auckland: Taiwharanui Peninsula, Jones Bay (36°22′60″S, 174°49′45″E), 24 July 2005, coll. W. A. Nelson, T. Farr, K. Neill, and S. Heesch (WELT A029290, NZC205), heterogeneous collection including tetrasporophytes and monoecious thalli of another mesophylloid with lunate SMCs and carposporophytes with distinctive pedestal; Eastern Bay of Plenty, Lottin Point, back from Tohora Point (37°33′17″S, 178°9′83″E), 18 April 2007, coll. K. Neill and S. Miller (WELT A029292, NZC2600); Northland, Matauri Bay, Patataua Bay (35°1′65″S, 173°54′85″E), 21 September 2005, coll. K. Neill and T. Farr (WELT A029295, NZC2134); Christchurch, Banks Peninsula, Taylors Mistake, south end of beach (43°35′10″S, 172°46′43″E), 28 November 2003, coll. N. Gust and M. Flanagan (WELT A028173, NZC0621), annotated "p.p. with *M. printzianum*"; West Coast, Cape Foulwind, Three Steeples (41°43′88″S, 171°28′18″E), 16 April 2003, coll. D. M. Neale (WELT A027999, NZC0525), annotated "whole collection, multiporate + uniporate fragments + 2 slides (multis)," "p.p. with *M. incisum* ?," examined by Athanasiadis and Ballantine (2014: Appendix III), "The material on the two slides shows filaments lining pore canals of multiporate roofs to exhibit elongate subbasal cells, as reported in the type of *M. incisum* (Woelkerling and Harvey 1993: fig. 14D). Other fragments in the collection apparently belong to other species."; Gisborne, Te Tapuwae O Rongokako Marine Reserve (38°35′80″S, 178°12′00″E), 9 March 2004, coll. A. Harvey, R. Harvey, D. Freeman, and W. Waitoa "TTO" (WELT A028079, NZC0950), annotated "*Mesophyllum erubescens*," "whole collection, multiporate and uniporate fragments, 3 slides (2 multiporate conceptacles, 1 male," examined by Athanasiadis and Ballantine (2014: Appendix III), "Includes a carposporangial specimen lacking coaxial hypothallium or a central pedestal in carposporangial chambers. The male thallus on the single slide (included in A028079) was not well preserved and could not be examined." Chatham Islands: Northeast tip of Hansen Bay, Okawa Point (43°46′20″S, 176°14′83″W), 22 February 2004, coll. W. A. Nelson, T. Farr, and K. Neill (WELT A027265/A, NZC0711), including one slide annotated "NZC0711 (1) volcano," tetrasporophyte fragments.

Habitat and Distribution: *Protomesophyllum ameleteton* is here described from thalli included in several collections, those of the type growing in the exposed littoral attached to haptera of *Ecklonia radiata* (Laminariales). In southern Australia, the species is also reported from littoral reef pools and in the sublittoral (to 15 m depth) on rock, glass, and the holdfasts of *Ecklonia* Hornem. and *Phyllospora comosa* (Labill.) C. Agardh (Fucaceae) (Woelkerling 1996: 201, as *Mesophyllum macroblastum*). From southeastern Australia, it is similarly recorded on haptera of these brown algae and also epizoically on mollusk shells, tube worms, abalone, barnacles, corals, and ascidians, to depths of 27 m (Harvey et al. 2003b: 670, as *M. macroblastum*). From New Zealand, there are also records from the littoral (Harvey et al. 2005: 138, as *M. macroblastum*). The species is widely distributed in southern and eastern Australia, New Zealand, and the Chatham Islands. A record of "*Mesophyllum macroblastum*" from the Cagarras Archipelago (~5 km off the coast of Rio de Janeiro; Bahia et al. 2014: figs. 6, 7, 9) is pending reexamination.

Species Description: Thalli at least 6 cm in extent and several millimeters thick (to 8.3 cm × 20 mm according to Woelkerling and Harvey 1993), encrusting and forming new lamellae in superimposition but lacking a foliose unattached superimposed habit (as in *Mesophyllum lichenoides* or *Magnephycus engelhartii*; Figure 8a). Thallus surface "polished" and striated with irregular perithallial outgrowths (to 6 mm long and 10 mm broad according to Woelkerling and Harvey 1993) and rough texture on the underside (Figure 8d–f). Animal boring in the thallus is common (Figure 8g). Thallus organization monopodial-dorsiventral with a polystromatic hypothallium, 100–200 µm thick. Terminal meristematic cells undergo anticlinal, asynchronous divisions (Figure 8h,i) producing a noncoaxial hypothallium (with coaxial patches; Figure 8j,k). Subdichotomous terminal divisions add to the thallus thickness and gradually displace hypothallial filaments dorsally (to form the perithallium) or ventrally (to form descending hypothallial filaments; Figure 8m,n). Terminal meristematic cells displaced dorsally become epithallial cells (Figure 8l,m), whereas those displaced ventrally become wedge-shaped cells facing the substratum (Figure 8n,o). Ascending hypothallial filaments support a perithallium, 50–650 µm thick (Figure 8j). Hypothallial cells are 8–42 × 5–12 µm, and perithallial cells are 5–12 × 4–9 µm (L × B; Woelkerling and Harvey 1993). Subepithallial cells are elongate (to 10 µm during cell division), each supporting a roundish to rectangular epithallial cell, 1–2 × 3–5 µm (L × B; to 6 µm long according to Woelkerling and Harvey 1993) with slightly domed outer wall (Figure 8m). Cell fusions between

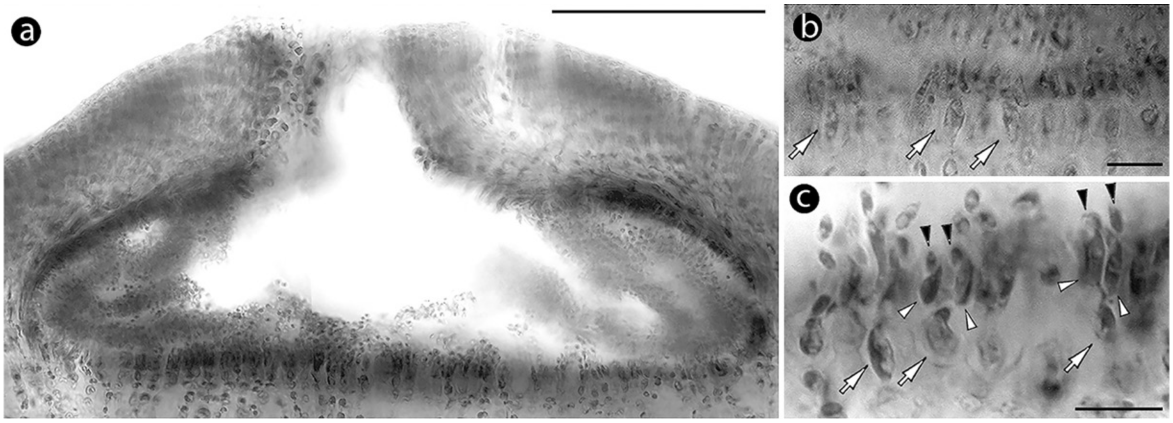


FIGURE 9. *Protomesophyllum ameleteton*: male structures (NZC0525 in (a) and (c); paratype-topotype in (b)). (**a**) Conceptacle with simple spermatangial structures all over the chamber. Scale bar: 100 µm. (**b, c**) Simple spermatangial structures on the floor. Note the elongate SMCs (arrows) cutting off terminal spermatangia in pairs (white arrowheads) that release spermatia (black arrowheads). Scale bars: 10 µm.

neighboring somatic cells common. Trichocytes and secondary pit connections not seen or reported.

Gametophytes are dioecious. Male conceptacles, 390–750 × 50–200 µm (D × H), provided with chambers 290–450 × 80–150 µm (D × H; n: 9; Figure 9a). Spermatangial structures develop on the floor, the walls, and the roof and are generally simple (unbranched) with elongate (nonlunate) SMCs (Figure 9b,c). Spermatangia develop usually in pairs from the upper wall of SMCs and release spermatia in series. Rare dendroid spermatangial structures have been reported (Woelkerling 1996: 201; Keats and Maneveldt 1997b: 465) but were not seen in the present study.

Carpogonial conceptacles, provided with chambers ~200 × 75 µm (D × H; n: 1), develop carpogonial branches across the fertile floor (Figure 10a). Carpogonial branches are 2-celled, composed of the carpogonium and a hypogynous cell (Figure 10b,c). Supporting cells do not stain similarly and are apparently part of the vegetative floor. A supporting cell bearing a 2-celled carpogonial branch and a second putative carpogonium was seen (Figure 10b; compare with *Amphithallia crassiuscula*). Following fertilization a cell tube was seen connecting the carpogonium with a supporting cell of the same branch system (procarpy; Figure 10d). No conspicuous fusion cell, in connection to zygote transfer, was detected, but fusions between adjacent supporting cells (incorporating 3 or 4 cells) have been reported (Woelkerling and Harvey 1993: fig. 23B) and were also seen in the present study (Figure 10f–i). These amalgamations are here interpreted as being part of the radiating gonimoblast filaments and do not include basal cells or neighboring hypogynous cells. Mature carposporophytes develop lateral carposporangia from the periphery of the fertile zone that may be slightly raised but definitely lack a conspicuous pedestal (Figure 10e). Carposporangial conceptacles, ~450 × 140 µm (D × H; n: 1), are provided with chambers 320–350 × 120–160 µm (D × H; 175–540 × 54–270 µm according to Woelkerling and Harvey 1993).

Multiporate conceptacles, 400–600 × 20–150 µm (D × H; n: 12), are irregularly spread on the thallus surface and may reach 800 µm in diameter when contiguous ones merge (Figure 8a–c,g). Chambers, 180–320 × 100–180 µm (D × H; n: 13; 145–270 × 90–150 µm according to Woelkerling and Harvey 1993), are provided with tetrasporangia (100–140 × 20–70 µm, L × B; n: 15; 81–135 × 29–68 µm according to Woelkerling and Harvey 1993; Figure 11a). Bisporangia were not seen or reported. Pore plates, 80–150 µm in diameter and 30–45 µm thick, are composed of 6- to 8-celled filaments and generally sunken, 20–60 µm below the roof edges (Figure 11a–d). Canals, 10–15 µm in diameter, are surrounded by 7–8 rosette cells that are common epithallial cells. Pore cells differ by their rhomboid (oblique-elongate) shape (Figure 11b–d). In views of canals from above at several levels of focus, pore cells appear to be nondifferentiated (Figure 11e–h). Conceptacles become embedded in the perithallium (Woelkerling and Harvey 1993: figs. 20D, 22C).

Comments: This species was originally described by Woelkerling and Harvey (1993: 590, figs. 19–23) using 28 collections from South Australia, Tasmania, and Victoria (and including material from the here selected type locality Rye Beach). Woelkerling and Harvey referred their material to the little-known Mediterranean *Mesophyllum macroblastum* (here recognized as *Macroblastum dendrospermum* gen. et nom. nov.), after comparison with the bisporangial type material (below), but even in the absence of gametophytes, the Australia–New Zealand–Chatham species clearly differs in lacking a predominantly coaxial hypothallium and in possessing characteristic rhomboid pore cells lining the canals of multiporate conceptacles, whereas in the Mediterranean counterpart pore cells are typically thinner–wider (see species description below). The two taxa also differ in the

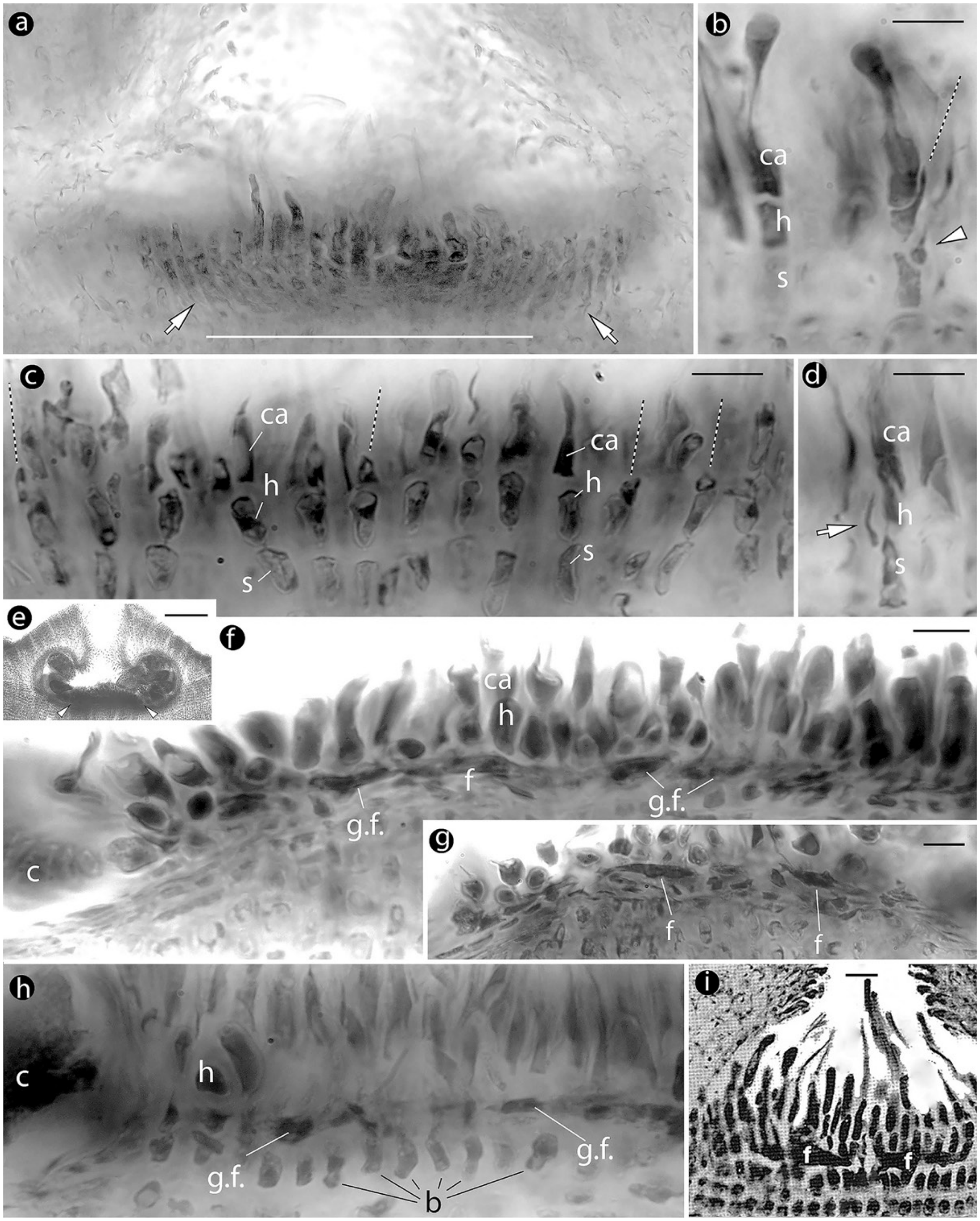


FIGURE 10. *Protomesophyllum ameleteton*: carpogonial and postfertilization stages. (**a**) Carpogonial branch development across the floor (arrows; NZC0950). Scale bar: 100 μm. (**b, c**) Two-celled carpogonial branches composed of the carpogonium and a hypogynous cell, attached to a supporting cell. A sterile cell (dashed lines) is occasionally present even on the supporting cell (arrowhead; NZC0950). Scale bars: 10 μm. (**d**) Cell tube (arrow) connecting the base of the carpogonium with the supporting cell (NZC0950). Scale bar: 10 μm. (**e**) Carposporangial conceptacle with carposporangia developed from the periphery (arrows) (NZC0950). Scale bar: 100 μm. (**f–i**) Postfertilization stages showing gonimoblast filaments undergoing fusions with neighboring cells, which do not include carpogonia, hypogynous, or basal cells (NZC0950 in (f–h); LTB13205 in (i), modified from Woelkerling and Harvey 1993: fig. 23B). Scale bars: 10 μm. Abbreviations: b, basal cell; c, carposporangium; ca, carpogonium; f, fusion; g.f., gonimoblast filament; h, hypogynous cell; s, supporting cell.

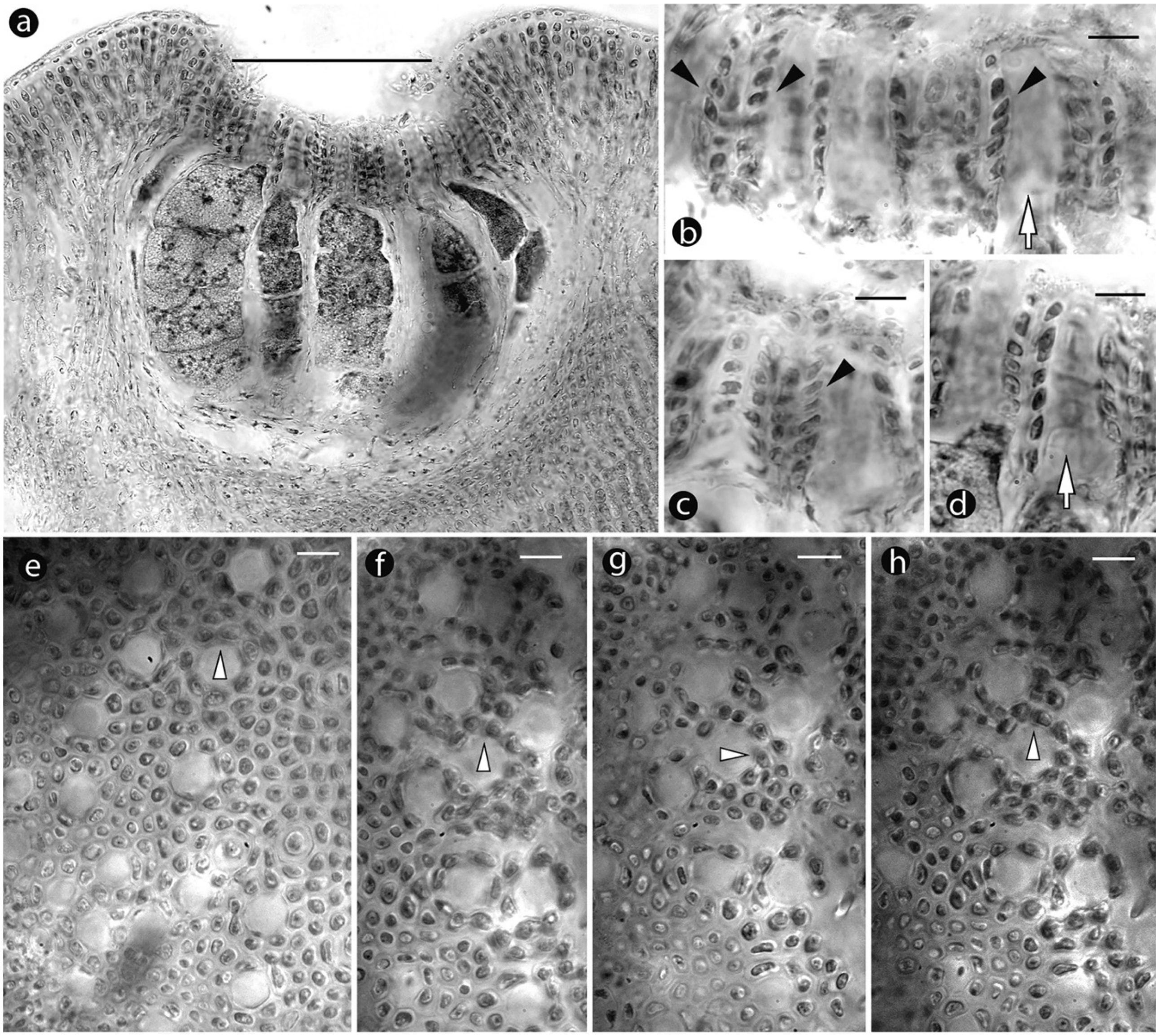


FIGURE 11. *Protomesophyllum ameleteton*: multiporate conceptacle structures (paratype-topotype in (a) and (d)–(h); holotype in (b) and (c)). (**a**) Tetrasporangial conceptacle with sunken pore plate. Scale bar: 100 µm. (**b–d**) Canals with straight shape (arrows) bordered by rhomboid (arrowheads) pore cells. Scale bars: 10 µm. (**e–h**) Pore plate in four levels of focus (from above) showing pore cells (arrowheads) of similar diameter to adjacent roof cells. Scale bars: 10 µm.

size of tetra- or bisporangial chambers (145–330 vs. 320–450 µm in the Mediterranean species), and further differences exist in their gametangial structures (see Table 3). Moreover, the two species have different ecological preferences: *Protomesophyllum ameleteton* grows in the exposed littoral and upper sublittoral, whereas the Mediterranean species is restricted to the sublittoral (to 90 m depth) and to shallow habitats with similar conditions (i.e., in caves and crevices protected from direct light and wave motion).

Woelkerling and Harvey (1993: 590) originally reported a "coaxial to non-coaxial" hypothallial growth, but this attribute was later omitted (Woelkerling 1996: 199; Harvey et al. 2003b: 670), whereas the present study shows that the hypothallium is predominantly noncoaxial (with coaxial patches; Figure 8k). Pore filaments in canals of multiporate conceptacles display pore cells that are clearly differentiated, being rhomboid in shape (possibly to help the passage of sporangia through the canal; Figure 8i,j). Regarding the size of tetrasporangial chambers, Woelkerling and Harvey (2003: 590) reported a variation of 145–270 µm in diameter (see also Woelkerling 1996: 199), whereas Harvey et al. (2003b: 670) reported chambers 230–330 µm in diameter. The present measurements (180–320 µm) are between these two sets,

TABLE 3. Comparative data for *Protomesophyllum* and genera of Melyvonneeae. Abbreviations: carpog., carpogonium; hypog., hypogynous; IDS, in different species; ND, no data; perith., perithallial; Predom., predominantly; SUG, superimposed unattached growth; supp., supporting.

Characteristic	***Protomesophyllum***[a]	***Macroblastum***[a]	***Phragmope***[b]	***Thallis capensis***[c]	***Perithallis***[c] **(2 species)**	***Printziana australis***[c]	***Sunesonia***[c] ***pseuderubescens***	***Melyvonnea*** **(4 species)**[d]	***Mesophyllum*** **(12 species)**[e]
Distribution	Southern and eastern Australia, New Zealand, Chatham	Mediterranean	South Africa	South Africa	Southern and eastern Australia, New Zealand, Chatham	Southern and eastern? Australia, New Zealand, Chatham?	Southern and eastern? Australia, New Zealand	Central and South Atlantic, South Africa, Hawaii, Japan, Indonesia, Polynesia	NE Pacific, Caribbean, Azores, Canaries, NE Atlantic to Holland and Orkney Isles, Mediterranean
Substratum	Epilithic, epiphytic	Epilithic, epizoic	Epilithic, epizoic	Epizoic, geniculate corallines	Geniculate corallines, rocks?	Rocks, *Phyllospora*	Rocks	Rocks, unattached (rhodoliths)	*Corallina, Gelidium,* corallines, rocks
Thallus habit	Encrusting	Encrusting	Encrusting	Encrusting	Orbicular, irregular lamellate, SUG	Encrusting, perith. protuberances	Encrusting, perith. protuberances	Encrusting, branched perith. protuberances	Irregular foliose to encrusting, SUG, perith. protuberances
Thallus organization	Dorsiventral	Dorsiventral	Dorsiventral	Dorsiventral	Anisobilateral	Dorsiventral	Dorsiventral	Dorsiventral	Dorsiventral
Hypothallium	Coaxial patches	Predom. coaxial	Predom. coaxial	Coaxial patches	Predom. coaxial	Predom. coaxial	Coaxial patches	Predom. coaxial	Predom. coaxial
Trichocytes	Absent	Rare	Present	Absent?	Present	Present	Absent	Present	Absent
Gametophytes	Dioecious	Monoecious	Dioecious	Dioecious	Dioecious	Dioecious	ND	Monoecious	Dioecious >10
Fusion cell	Absent	2 or 3 supp. cells	2 or 3 supp. cells + carpog. and hypog. cell	1 hypog. + >6 supp. cells	Absent	2 hypog. + >6 supp. cells	ND	Absent	hypog. + 10 supp. cells
Carposporangial chamber	Elongate	Spherical	Elongate	Elongate	Elongate	Elongate	ND	Spherical	Elongate
Pedestal in carpogonial conceptacles	Absent	Absent	Absent	Present or absent	Present or absent	Present or absent	ND	Absent	Present
Spermatangial structure	Unbranched and dendroid?	Unbranched and dendroid	Unbranched (few dendroids)	Unbranched	Unbranched	Unbranched	ND	Unbranched	Unbranched
SMCs lunate	Absent	Present	Present	Present	Present	Present	ND	Present	Present
Differentiated pore cells	Rhomboid	Thinner–wider	Cell bars	*Thallis* type	*Thallis* type	*Printziana* type	*Sunesonia* type	*Melyvonnea* type	Thinner–wider
Canal shape	±Straight	±Straight	±Straight	±Straight	±Straight	±Straight or wider base	Wider base	Wider base	±Straight
Embedded conceptacle	Present	Present	Present	Present	Absent	Present	Present	Present	Present or absent (IDS)
Bisporangia / tetrasporangia	Present / absent	Absent / present	Absent / present	Absent / present	Absent / present	Absent / present	Present / present	Present / present	Present / present

[a] Present study.
[b] Athanasiadis (2020b).
[c] Athanasiadis (2022).
[d] Keats and Chamberlain (1994) and Athanasiadis and Ballantine (2014).
[e] Suneson (1937, as *Lithothamnion*), Lebednik (1977b), Chamberlain and Irvine (1994), Athanasiadis et al. (2004), Athanasiadis and Neto (2010), Athanasiadis and Ballantine (2014), Athanasiadis (2018).

including thalli from New Zealand and Chatham, and definitely confirm the smaller chamber size of multiporate conceptacles in *Protomesophyllum* than in *Macroblastum dendrospermum* (i.e., 320–450 µm; see species description below).

The development of elongate (nonlunate) SMCs in simple (unbranched) spermatangia differs from all members of the subfamily Mesophylloideae, bridging *Protomesophyllum* with the Clathromorphoideae, the Melobesiaceae, and all uniporate corallines. Rare dendroid spermatangia were reported (but not illustrated) by Woelkerling (1996: 201) and Keats and Maneveldt (1997b: 465, "weakly branched"). Their occurrence should be understood as a plesiomorphic (relic) trait since dendroid spermatangia are common in the most basal Corallinales (Lithothamnionaceae, Sporolithales), becoming gradually replaced by simple ones in the evolution of the coralline algae. In the Mesophyllaceae, dendroid spermatangial structures occur in certain species of Amphithallieae (i.e., *Amphithallia crassiuscula*, *Synarthrophyton* sp.), in Magnephyceae (e.g., in species of *Leptophytum* and *Phymatolithopsis*), and more rarely in the Melyvonneeae (i.e., in *Phragmope discrepans* and in *Macroblastum dendrospermum*). Within the Melobesiaceae, they occur only in certain species of *Orthocarpa* (see Table 6).

Carpogonial thalli apparently produce 2-celled carpogonial branches, and mature carposporangial conceptacles lack a pedestal (Woelkerling and Harvey 1993: fig. 23 C; Woelkerling 1996: fig. 87C; Figure 10e). An "irregularly shaped fusion cell that looks discontinuous in section" (Woelkerling and Harvey 1993: 590) has been reported, and the present observations show similar fusions incorporating a few supporting cells (but no carpogonia, hypogynous, or basal cells; Figure 10f–i). These fusions apparently result during the development of gonimoblast filaments (and do not represent the fusion cell that results in association to zygote transfer). Therefore, *Protomesophyllum* belongs to those Mesophyllaceae having an inconspicuous fusion cell (often recorded as "discontinuous"), as observed in *Synarthrophyton*, *Amphithallia*, *Perithallis*, *Kvaleya*, *Phragmope*, *Macroblastum*, and *Melyvonnea*. A median condition manifested by the development of a fusion cell composed of at least 4–6 supporting and 1–2 hypogynous cells has been observed in *Thallis*, *Printziana*, *Leptophytum*, *Carlskottsbergia*, and *Capensia* (present data), whereas a maximal development is recorded in *Mesophyllum* and possibly in *Neopolyporolithon* (Masaki and Tokida 1961b: pl. 4, as *Polyporolithon*), where at least 10 supporting and 10 hypogynous cells participate in the fusion (character 21 of the phylogenetic analysis).

A sequence (nSSU) from the here studied Chatham collection (WELT A027265/A, NZC0711) resolved as the sister taxon of the South African *Phragmope* (Broom et al. 2008: table 2, fig. 5; Bittner et al. 2011: table 2, fig. 1; Peña et al. 2011: fig. 3; Athanasiadis 2020b: fig. 8c–e) and as the sister taxon to several New Zealand sequences attributed to "*Mesophyllum macroblastum*" by Sissini et al. (2014: fig. 5). One of these New Zealand sequences (FJ361449, Auckland, Matauri Bay) resolved as the most basal clade in an analysis including some 66 isolates of Mesophyllaceae (Sissini et al. 2014: fig. 5), supporting the remote taxonomic and systematic relationship of *Protomesophyllum* to other Mesophylloideae. The relationship to *Phragmope* is particularly enigmatic since "*Mesophyllum macroblastum*" has not been recorded in South Africa, which suggests that a close relationship with *Phragmope* should be nested in a remote ancestor in the very distant past (Athanasiadis 2020b: 543).

The holotype of *Protomesophyllum ameleteton* was selected from collections made during an excursion to Rye Beach arranged by William Woelkerling and accompanied by Deborah Penrose. Several specimens were found attached on the holdfasts of *Ecklonia*, one of which was here selected as the holotype, with all other specimens becoming paratypes-topotypes.

MESOPHYLLOIDEAE ATHANAS. ET D. L. BALLANT. SUBFAM. NOV.

Mesophylloideae Athanas. et D. L. Ballant. subfam. nov. (type: *Mesophyllum*).

Diagnosis: Subfamily of Mesophyllaceae, comprising the tribes Amphithallieae, Melyvonneeae, and Magnephyceae, and differing from the other subfamilies of Mesophyllaceae by the development of lunate SMCs (rectangular or elongate in all other Corallinales), trichocytes, and thinner–wider pore cells (or other types of cell differentiation) in filaments lining the canals of multiporate conceptacles.

AMPHITHALLIEAE ATHANAS. ET D. L. BALLANT. TRIB. NOV.

Amphithallieae Athanas. et D. L. Ballant. trib. nov. (type: *Amphithallia*).

Diagnosis: New tribe of Mesophylloideae, comprising the monotypic genera *Amphithallia*, *Synarthrophyton*, *Carlskottsbergia*, *Capensia*, *Kerguelena* gen. nov., and *Masoniana* gen. nov. and differing from the other tribes of the subfamily by a bilateral or sympodial thallus organization/growth.

Comments: The first four member genera are epiphytes (*Capensia* is, in addition, a hemiparasite) and have recently been recognized or emended (Athanasiadis 2017b, 2019a, 2019b). *Synarthrophyton* previously accommodated a large number of species, including *Amphithallia crassiuscula*, *Carlskottsbergia antarctica*, and several other widely distributed taxa lacking bilateral organization and here transferred to the new genus *Orthocarpa* (Orthocarpoideae, Melobesiaceae). Reinvestigation of the generitype *Synarthrophyton patena*, originally described from New Zealand, revealed that its concept should be restricted to dioecious thalli with bilateral organization and discoid, mainly unattached habit, unbranched (simple) spermatangial structures, development of gonimoblasts at the level of supporting cells, and nonorthostichous carposporangial production. Both dendroid and unbranched spermatangia have been recorded in the South African *Amphithallia crassiuscula*, which was previously included in the wide concept of *S. patena* (May and Woelkerling 1988: fig. 39). A third species and genus previously subsumed in *S. patena* (May and Woelkerling 1988:, fig. 40) is *Carlskottsbergia antarctica*, originally described from Hermite Island (Cape Horn, Chile) and occurring across the Antarctic Peninsula to subantarctic islands (Macquire Island) and New Zealand (Athanasiadis 2019a). *Carlskottsbergia* and *Synarthrophyton* share the same host (*Ballia callitricha*), whereas *Amphithallia* grows on species of *Gelidium* usually together with the hemiparasite *Capensia fucorum*. In the present phylogenetic analysis, *Capensia* clustered with *Carlskottsbergia*, sharing the development of a monostromatic hypothallium and a medium-size fusion cell. Apart from these four epiphytic (one in addition hemiparasitic) genera, the Amphithallieae also include two little-known monotypic new genera, *Kerguelena*, based on *K. dickiei* (*Melobesia kerguelena* Dickie 1876a), and *Masoniana*, the latter based on the southern Australian *M. kraftii* (*Phymatolithon masonianum* Wilks et Woelkerling 1994). Both show a saxicolous habit and are included in the tribe because of their bilateral thallus organization, straight canals of multiporate conceptacles, and lateral production of carposporangia (in *Masoniana*) or epithallium morphology (flattened-rectangular but not flared or domed). Carpogonial thalli and postfertilization stages in *Kerguelena* and *Masoniana* are unknown or poorly documented. All Amphithallieae are presently monotypic, except *Synarthrophyton*, which includes an undescribed species from southern Australia possessing dendroid spermatangia (Townsend 1979; Athanasiadis 2019a: figs. 57–59). A comparison between the six genera of Amphithallieae is given in Table 4.

Amphithallia Athanas.

Amphithallia Athanasiadis 2019b: 14 (type: *A. crassiuscula*).

Amphithallia crassiuscula (Foslie) Athanas.

Amphithallia crassiuscula (Foslie) Athanas. 2019b: 14, figs. 1–5.
Basionym: Melobesia crassiuscula Kütz. 1843: 386.
Homotypic Synonym: *Mastophora crassiuscula* (Kütz.) Kütz. 1849: 696. Kützing (1858: 47, pl. 99, fig. IIc–e).

Type Locality: On *Gelidium capense* (S. G. Gmel.) P. S. Silva, Cape of Good Hope, South Africa.

Lectotype: In L, 4081310 (barcode L0491448; in folder BE.1847238 and including three slides), selected and illustrated in Athanasiadis (2019b: fig. 1).

Comments: *Amphithallia* was previously subsumed within the broad concept of the New Zealand species *Synarthrophyton patena* (e.g., May and Woelkerling 1988: fig. 39). Reexamination of historical and recent herbarium collections (as late as 1984) revealed that the type and only species of the genus *Amphithallia*, *A. crassiuscula*, is an obligate epiphyte on *Gelidium capense*. The examined material was collected at the Cape of Good Hope, Table Bay, False Bay, and Cape Agulhas, with the host (*Gelidium capense*) being widespread in the sublittoral zone of South Africa (Stegenga et al. 1997), and South African records of "*Synarthrophyton patena*" including more localities. Sharing the same host, *Amphithallia crassiuscula* often overgrows *Capensia fucorum*, which develops haustoria upon contact with *Gelidium* spp. (Athanasiadis 2019b).

Synarthrophyton R. A. Townsend

Synarthrophyton R. A. Townsend 1979: 252 (type: *S. patena*).

Synarthrophyton patena (Hook. fil. et Harv.) R. A. Townsend

Synarthrophyton patena (Hook. fil. et Harv.) R. A. Townsend 1979: 252, figs. 1–18.
Basionym: Melobesia patena Hook. fil. et Harv. in Harvey 1849: 111, pl. 40.
Homotypic Synonyms: Mastophora patena (Hook. fil. et Harv.) Kütz. 1858: 47, pl. 99, fig. IIIa–e.
Lithophyllum patena (Hook. fil. et Harv.) Rosanoff 1866: 88, pl. 5, figs. 7–15.
Lithothamnion patena (Hook. fil. et Harv.) Heydrich (1897b: 413).
Lithothamnion lichenoides f. *patena* (Hook. fil. et Harv.) Foslie 1898b: 7.
Lithothamnion lichenoides var. *patena* (Hook. fil. et Harv.) De Toni et Forti 1923: 59.
Polyporolithon patena (Hook. fil. et Harv.) L. R. Mason 1953: 317.
Mesophyllum patena (Hook. fil. et Harv.) R. W. Ricker 1987: 173.

Type Locality: Flat Point, Castle Point, east coast of North Island, New Zealand.

Lectotype: Harvey's (1849: pl. 40) original illustration designated in Athanasiadis (2019a: 308).

Syntypes: In WELT (A009575, *pro parte*, and A009595); in BM (001043934 and 001082425); in TCD ("Colenso no 1331"; Athanasiadis 2019a).

Etymology: The generic name is a compound word, after the adverb συν (plus), the masculine noun αρθρος (joint), and the neuter substantive φυτον (plant). The epithet name is taken from "the ecclesiastic vessel, called a *Patena*" (Harvey 1849: 111)—Πατανη in Greek.

Habitat and Distribution: Thalli are exclusively attached to *Ballia callitricha* (C. Agardh) Kütz. and usually grow in association with *Carlskottsbergia antarctica*. Co-occurrence was observed at least at the type locality (WELT A009575) and in the Aucklands (LD50667, lower specimen). No evidence of (hemi) parasitism or other kinds of substrata have been reported. Being previously confused with *Carlskottsbergia antarctica*, *S. patena* is widely recorded in the earlier literature, but the confirmed records are only from New Zealand (including the type locality and the Aucklands).

Comments: *Synarthrophyton* presently accommodates its type *S. patena*, restricted to New Zealand and the Aucklands, and an undescribed species possessing dendroid spermatangial structures from southern Australia (Townsend 1979: fig. 17; Athanasiadis 2019a: figs. 57–59). Both species appear to be obligate epiphytes on *Ballia callitricha* (C. Agardh) Kütz. Further studies are needed to delineate the exact distribution of these two species in New Zealand and Australia. It could be added that a specimen

TABLE 4. Comparative data for the monotypic genera of Amphithallieae. Abbreviations: hypog., hypogynous; ND, no data; supp., supporting.

Characteristic	*Amphithallia crassiuscula*[a]	*Synarthrophyton patena*[b]	*Carlskottsbergia antarctica*[b]	*Capensia fucorum*[c]	*Kerguelena dickiei*[d]	*Masoniana kraftii*[d]
Distribution	South Africa	New Zealand, Aucklands	Southern Chile, southern Argentina, Falklands, Aucklands, New Zealand	South Africa	Kerguelen Island	Southern Australia
Host/substratum	*Gelidium*	*Ballia*	*Ballia*	Parasite on *Gelidium*	Epilithic?	Sponge, epilithic
Thallus habit	Orbicular to encrusting	Discoid	Orbicular to encrusting	Encrusting	Lamellate	Lamellate
Hypothallium	Polystromatic	Polystromatic	Monostromatic	Monostromatic	Polystromatic	Polystromatic
Subepithallial cells	Elongate	Elongate	Elongate	Elongate	Elongate	Short
Trichocytes	Present	Absent	Absent[e]	Present	Absent	Absent
Gametophytes	Monoecious	Dioecious-hermaphroditic	Dioecious	Dioecious	ND	Dioecious
Carpogonial branch	4-celled	2(3)-celled	2(3)-celled	3-celled	ND	ND
Zygote transfer	Connecting filament	ND	ND	ND	ND	ND
Fusion cell	Inconspicuous	Inconspicuous[f]	>4–5 supp. cells + 1 hypog. cell	>6 supp. cells + 1 hypog. cell?	ND	Inconspicuous
Pedestal in carpogonial conceptacles	Absent	Absent	Absent	Absent	ND	± Present
Spermatangia	Unbranched and dendroid	Unbranched[g]	Unbranched	Unbranched	ND	Unbranched and dendroid
Canal shape	Straight	Conical	Straight or pyriform	Straight	Straight	Straight
Differentiated pore cells	Absent	Along the canal base (basal, subbasal, and third cells)	Absent or present (basal and subbasal cells)	Present	Absent	Absent
Embedded conceptacles	Absent	Absent	Absent	Absent	Present	Present

[a] Athanasiadis (2019b).

[b] Athanasiadis (2019a).

[c] Athanasiadis (2017b) and present study.

[d] Wilks and Woelkerling (1994), Woelkerling (1996), and present study.

[e] Observed in two collections from southern New Zealand (Athanasiadis 2019a: 304).

[f] A "very thin" fusion cell was reported by May and Woelkerling (1988: fig. 34) in an Australian population.

[g] Branched (dendroid) spermatangia have been recorded in Australian populations (Townsend 1979: figs. 12, 17; May and Woelkerling 1988: fig. 19) that most likely belong to an undescribed new species (Athanasiadis 2019a: figs. 57–59).

possessing isobilateral thallus organization, with conceptacles on both sides of the thallus, was observed in material from the Auckland Islands (LD50667). The fact that the original account of the genus *Synarthrophyton* was based on southern Australian specimens with dendroid spermatangia (Townsend 1979: fig. 17) is not problematic since the type of a genus is the type of a species name (Turland et al., 2018: Article 10.1; i.e., *S. patena*).

Carlskottsbergia Athanas.

Carlskottsbergia Athanas. 2019a: 293 (type: *C. antarctica*).

Carlskottsbergia antarctica (Hook. fil. et Harv.) Athanas.

Carlskottsbergia antarctica (Hook. fil. et Harv.) Athanas. 2019a: 297, figs. 1–31.

Basionym: Melobesia verrucata var. *antarctica* Hook. fil. et Harv. in Harv. and Hook. 1847: 482.

Homotypic Synonyms: Melobesia antarctica (Hook. fil. et Harv.) Hook. fil. et Harv. in Harvey 1849: 111.

Lithophyllum antarcticum (Hook. fil. et Harv.) Rosanoff 1866: 82, 85.

Lithothamnion lichenoides f. *antarcticum* (Hook. fil. et Harv.) Foslie 1898b: 7, "f.? *antarctica*."

Lithothamnion antarcticum (Hook. fil. et Harv.) Foslie 1900a: 13.

Lithothamnion patena f. *antarcticum* (Hook. fil. et Harv.) Heydrich 1907: 223, footnote 5.

Lithophyllum lichenoides f. *antarcticum* (Hook. fil. et Harv.) Me. Lemoine 1911: 131.

Misapplied Name: Mesophyllum patena sensu Ricker 1987: 173, fig. 73 [non *Mesophyllum patena* (Hook. fil. et Harv.) R. W. Ricker].

Type Locality: Hermite Island, near Cape Horn, Chile.

Lectotype: In TCD (0011889, *pro parte*), designated in Athanasiadis (2019a: figs. 5–6).

Syntypes: In TCD (0011889, *pro parte*); in BM (000937135 and 000937136; see Athanasiadis 2019a).

Habitat and Distribution: Thalli grow attached to and encircling the axes of *Ballia callitricha* (C. Agardh) Kütz., usually found in association with *Synarthrophyton patena* in New Zealand and the Aucklands. No evidence of parasitism and no other kinds of substrata have been reported. The species is recorded from Chile (Sandy Point [Punta Arenas] and Hermite Island [type locality]), Argentina (Staten Island [Isla de Los Estados], Falkland Islands), New Zealand (North Island and South Island, including the type locality of *Melobesia patena*), and the Auckland and Macquarie Islands (Ricker 1987, as *Mesophyllum patena*).

Comments: *Carlskottsbergia antarctica* was previously subsumed in the wide concept of *Synarthrophyton patena* held by May and Woelkerling (1988:, fig. 40). The two species and genera share the same host, *Ballia callitricha* (C. Agardh) Kütz., but they are easily distinguished since *Synarthrophyton patena* forms discoid thalli (growing mainly unattached), whereas thalli of *Carlskottsbergia* are irregularly lamellate and usually encircle the axes of the host. No other kinds of substrata are known for these two coexisting species. Their obligate (but not parasitic) growth on *Ballia* is puzzling. *Carlskottsbergia* is also reported from the Kerguelen Islands and Tasmania (Harvey and Hooker 1847: 482), Tierra del Fuego (near the mouth of the Rio Grande; Foslie 1900b: 71), and the Falklands (Skottsberg 1941: 35, as *Lithothamnion*) and may also occur in the Antarctic Peninsula (Hommersand et al. 2009: 512, as *Synarthrophyton patena* on *Ballia*). Records of New Zealand thalli with trichocytes merit further investigation, as does the distribution of the species along the South American coast and potentially elsewhere in Australia.

***Capensia* Athanas.**

Capensia Athanas. 2017b: 556 (type: *C. fucorum*).

Comments: This hemiparasitic genus shows a unique (for the Corallinales) sympodial growth and provides the first case of a coralline infesting a noncoralline host. The generitype was previously referred to "*Millepora fucorum*" (*pro parte*), "*Melobesia patena*," or "*Melobesia capensis*" in several historical herbarium collections of Suringar, Schultes D., Wallgren "1846," Hohenacker, and Zeycher (in L and S).

***Capensia fucorum* (Esper) Athanas.**

FIGURE 12

Capensia fucorum (Esper) Athanas. 2017b: 556, figs. 1–29.

Basionym: Millepora fucorum Esper 1796: 121, pl. 23.

Heterotypic Synonyms: Lithophyllum capense Rosanoff (1866: 86–88, pl. 6, figs. 13, 15, *pro parte*).

Mesophyllum capense (Rosanoff) Y. M. Chamb. 2000: 367, figs. 1–31.

Type Locality: Cape of Good Hope, South Africa.

Lectotype: Esper's original illustrations 1 and 4, designated in Athanasiadis (2017b: fig. 1).

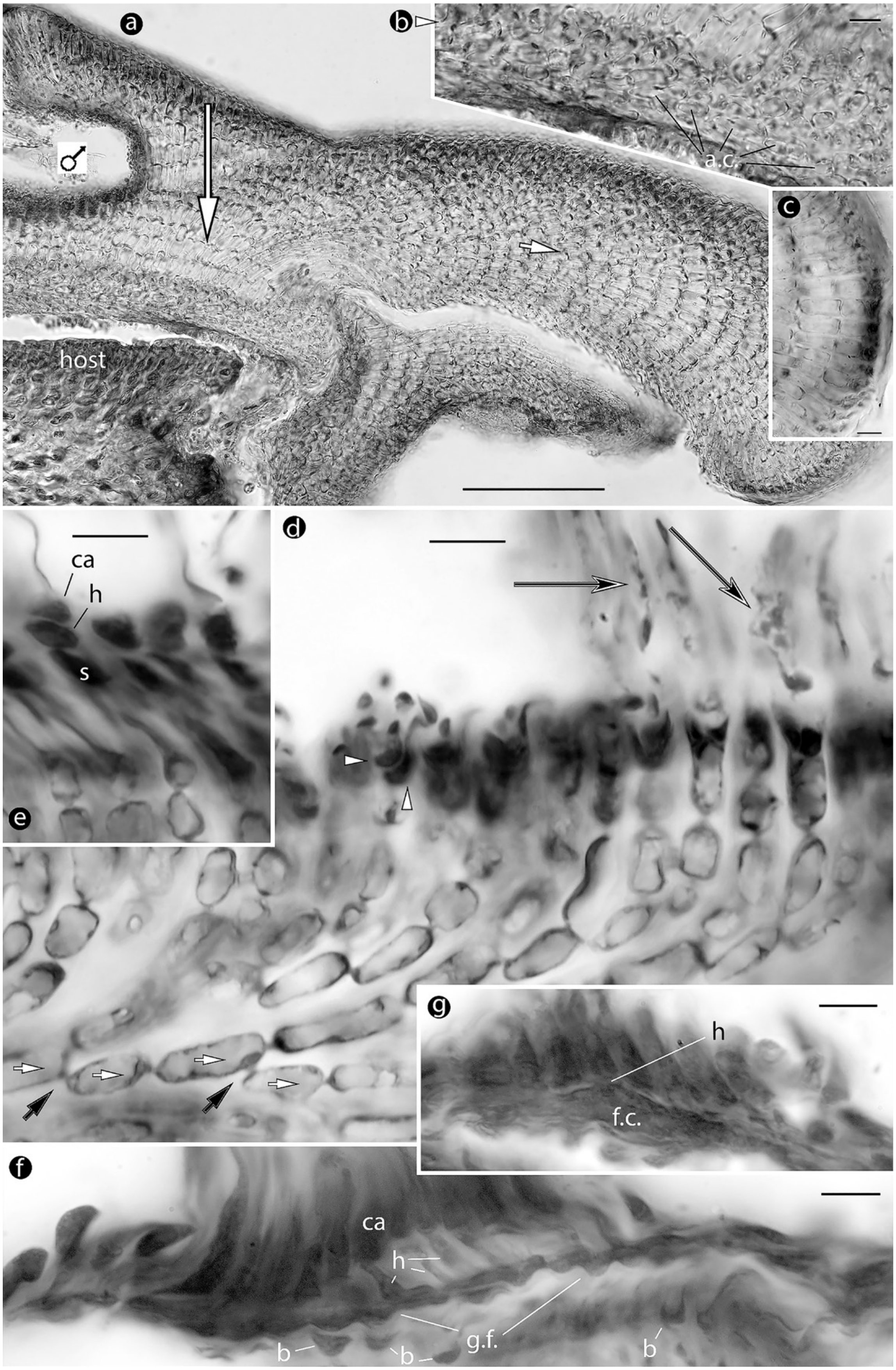
Epitype: A thallus on *Gelidium capense*, attached to the herbarium sheet A23013 (S) annotated "Tafelbay Jan. 1846. - Wallgr.," designated in Athanasiadis (2017b: figs. 2, 3).

Material Examined: Cape of Good Hope: Anonymous, "*Sphaerococcus cartilagineus infesta*," "Prom.B.Sp." (L4048989).

Habitat and Distribution: *Capensia fucorum* is a hemiparasitic species growing on *Gelidium capense* (S. G. Gmel.) P. C. Silva and *Gelidium pteridifolium* R. E. Norris in the littoral and upper sublittoral zone. It is endemic to South Africa, being recorded from Robben Island, Table Bay, Cape of Good Hope, Algoa Bay, Cape Agulhas, Rocky Bay, Palm Beach, and Western Cape (Chamberlain 2000, as *Mesophyllum capense*; Athanasiadis 2017b).

Comments: Examination of thalli from L (4048989) revealed the development of new lamellae in superimposition, lacking haustoria and displaying a monopodial-dorsiventral organization with a noncoaxial polystromatic hypothallium, showing coaxial patches, and typical terminal meristematic divisions (Figure 12a–c). It is thereby concluded that the hemiparasitic nature

FIGURE 12. (*Opposite*) *Capensia fucorum*: vegetative and reproductive structures (L4048989). (**a**) Thallus regeneration from the perithallium (long white arrow) producing a new lamella with a patch of coaxial (arrow) hypothallial cells. Scale bar: 100 µm. Note the male conceptacle and the host. (**b**) The point of thallus regeneration from the perithallium that is supported by a monostromatic hypothallium composed of series of axial cells. Scale bar: 10 µm. (**c**) Margin of the new lamella terminating in meristematic cells below a cuticle. Scale bar: 10 µm. (**d**) Young spermatangial structures protected by elongate palisade cells (long black arrows). Note the spermatangia (arrowheads) and the monostromatic hypothallium (white arrows) produced via ventral divisions (black arrows). Scale bar: 10 µm. (**e**) Three-celled carpogonial branches composed of a carpogonium, a hypogynous cell, and a supporting cell. Scale bar: 10 µm. (**f, g**) Gonimoblast filaments and a putative fusion cell. Note the basal cells and the carpogonium remain. Scale bars: 10 µm. Abbreviations: a.c., axial cell; b, basal cell; c, carposporangium; ca, carpogonium; f.c., fusion cell; g.f., gonimoblast filament; h, hypogynous cell; s, supporting cell.


a
♂
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of the species (involving a sympodial growth in a monostromatic hypothallium) is induced upon contact with its host, whereas new proliferations on the mother thallus demonstrate the ancestral thallus organization without producing haustoria. Such secondarily produced outgrowths are probably the thalli described by Chamberlain (2000: 370) as "monomerous . . . composed of a medulla [that is] plumose to occasional coaxial."

Male spermatangial structures were observed in a young state, being provided with protective palisade cells (Figure 12d), as in other Amphithallieae (cf. Harvey et al. 1994: fig. 16). A young carpogonial conceptacle was provided with 3-celled carpogonial branches, composed of the carpogonium, the hypogynous, and the supporting cells (Figure 12e). Carposporangial conceptacles were provided with gonimoblast filaments (Figure 12f) producing carposporangia laterally. A fusion cell composed of some 6 supporting cells and possibly a hypogynous cell was detected (Figure 12g), providing a further synapomorphy with *Carlskottsbergia* (character 21). According to Ott (1995: 14), plate 23 of Esper appeared in the twelfth part and "was issued with the title page for the Zweyter Theil bearing the date of 1794." Hence, the plate was published ahead of the protologue, but since the plate itself bears only the species name (without information of the host or locality) and the illustrations include unattached thalli (excluded from the species concept; Athanasiadis 2017b), it cannot stand alone as a species identification to satisfy Article 38.10 (Turland et al. 2018).

***Kerguelena* Athanas. et D. L. Ballant. gen. nov.**

Kerguelena Athanas. et D. L. Ballant. gen. nov. (type: *K. dickiei*).

Diagnosis: New genus of Amphithallieae, sharing the bilateral thallus organization with other members of this tribe and differing by a nonepiphytic and nonparasitic nature and possessing embedded conceptacles. The latter two features unite *Kerguelena* with *Masoniana,* and which differ by the possession of elongate respectively short subepithallial cells.

***Kerguelena dickiei* Athanas. et D. L. Ballant. comb. et nom. nov.**

FIGURE 13

Kerguelena dickiei Athanas. et D. L. Ballant. comb. et nom. nov.
Basionym: Melobesia kerguelena Dickie 1876a: 51.
Homotypic Synonym: *Lithothamnion kerguelenum* (Dickie) Foslie 1898b: 7. Foslie (1899b: 10, Gundersen's material), Foslie (1900c: 67–69, Dickie's and Dusén's material[36]), Foslie (1908a: 207: text fig. 2, Dickie's material).

Type Locality: Swain's Bay, Kerguelen Islands.

Lectotype: In TRH (B18-2612), Adey and Lebednik (1967: 69, "§ ex herb.Kew, Kerguelen Is., 12.1874-2.1875, LM9 (5,6) [slide] 361," where "§" = type material), Woelkerling (1993a: 133, "three holotype fragments"), Woelkerling et al. (2005: 352, "Holotype fragments . . . in a smaller round box.").

Isolectotype: In BM (unnumbered), Foslie (1908a: 207, text fig. 2), Printz (1929: pl. 9, figs. 5, 6), Tittley et al. (1984: 13), Wilks and Woelkerling (1994: 221, figs. 16A,B, 17A,B, "Swain's Bay 1875 Kerguelen island Rev.A.E. Eaton Dec.1874-Feb.1875").

Habitat and Distribution: Known only from the type material from Kerguelen Islands, presumably found attached to rocky surface at a depth of 4–6 m (Dickie 1879: 58; Lemoine 1913: 8–10).

Comments: In three accounts, Dickie provided the following information:

> *Melobesia Kerguelena*, n.sp.- Simple, slightly concave, attached by the centre of the convex surface; margin smooth, sparingly undulate; *Keramidia* [conceptacles] numerous, mostly in concentric lines; substance thick and hard. Attains a diameter of two and a half inches. The colour is mostly very pale buff variegated with pale red. (Dickie 1876a: 51)
>
> M. kerguelena, n.sp. Partim adnata, subconcava, circumscriptione orbiculari, margine parce undulata, keramidia numerosis, conspicuis, subconcentrice distributis. The description is taken from a specimen nearly entire and about two inches in diameter; there are fragments of others less regular in outline, probably owing to inequality of the surface of attachment. All are dull yellow with shades of pale red, and in texture hard and inflexible. (Dickie 1876b: 200)
>
> 3. Melobesia kerguelena, Dickie in Journ.Bot.v.15, 1876, et in Journ.Linn.Soc.xv. 200 ; simplex, 2½ poll. diam., dura, crassa, tantum in medio subtus adhaerens, subconvexa, circumscriptione orbiculari, margine laevi parce undulata, keramidiis conspicuis numerosis plerumque in seriebus concentrice dispositis. Swain's Bay in 2-3 fathoms, with the preceding [i.e. *Melobesia lichenoides* sensu Dickie = *Lithothamnion neglectum* Foslie = *Orthocarpa magellanica*?], Eaton. Mr. Eaton has an impression that this grows upon *Ballia* or *Ptilota*, but I should rather be disposed to suspect that it was attached to rocks. The description was taken from an almost complete specimen; there are fragments of others whose contour is less regular, probably through interference of external objects. All of them are in colour of a very pale buff or dull yellowish hue, varied with pale red tints. (Dickie 1879: 58)

The existence of "other fragments" was mentioned in Dickie's latter two papers (where the collector A. E. Eaton is named), but the protologue remained largely unchanged, indicating that it was based on the same material that according to Adey and Lebednik (1967) is dated between December 1874 and February 1875. This supports the view that several gatherings were included (to be considered as syntypes).

Foslie (1898b) first transferred the species to *Lithothamnion* (without comment) and later gave accounts including two other collections (Foslie 1899b, 1900c). Still, Foslie included both in Foslie (1900c) and later (Foslie 1908a: 207, text fig. 2) descriptions of the largest specimen mentioned by Dickie (1876a, 1876b, 1879), which according to Foslie (1900c: 69) is up to 7 cm in diameter and 2 mm thick. In particular, Foslie (1900c: 67–69) reported a thallus superimposition ("in part at least"), rhizoids (struts?) in the lower part of the crust, convex multiporate conceptacles (500–600 μm in diameter) becoming embedded in the thallus (chambers 500 × 250 μm), hypothallial cells 18–50 × 6–9 μm, "sending forth upwards as well as downwards perithallic rows," with cells in the upper part 11–18 × 9–11 μm and in the lower part 12–25 × 11–15 μm. No new information was provided by Foslie (1908a), other than the species was closely related to *Lithothamnion neglectum* (Foslie) Foslie (see *Orthocarpa magellanica*) and that *Lithothamnion kerguelenum* f. *fuegianum* Foslie (1905a) was to be recognized as an independent species (see *Mesophyllum fuegianum* (Foslie) W. H. Adey).

Lemoine (1913: 8–10, text fig. 1) reexamined the original material (at the BM) and reported the following (in translation):

> [This is] a crust . . . often plane and sometimes warty . . . [with] numerous conceptacles . . . forming regular concentric arches, closely placed, reaching the margin . . . 1 mm thick . . . the hypothallium . . . is . . . 150–200 (250) μm thick, composed of cells . . . 15–23 μm long and 9 μm broad. . . . At their base, hypothallial filaments bend down and sometimes form a new [ventral] perithallium. Towards the thallus surface, the hypothallium goes into a normal perithallium . . . and forms vertical filaments . . . 8–17 μm long and 7–8 μm [broad]. Perithallial thickness varies between 200 and 700 μm. The [embedded] sporangial conceptacles are arranged in concentric arches, . . . the oval cavities are 500–600 μm in diameter, while carposporangial conceptacles are triangular; . . . *L. kerguelenum* was several times collected at Kerguelen Island, and particularly in Swain's Bay together with *L. neglectum,* at a depth of 4–6 m (Foslie 1908a). It has not been found elsewhere until now.

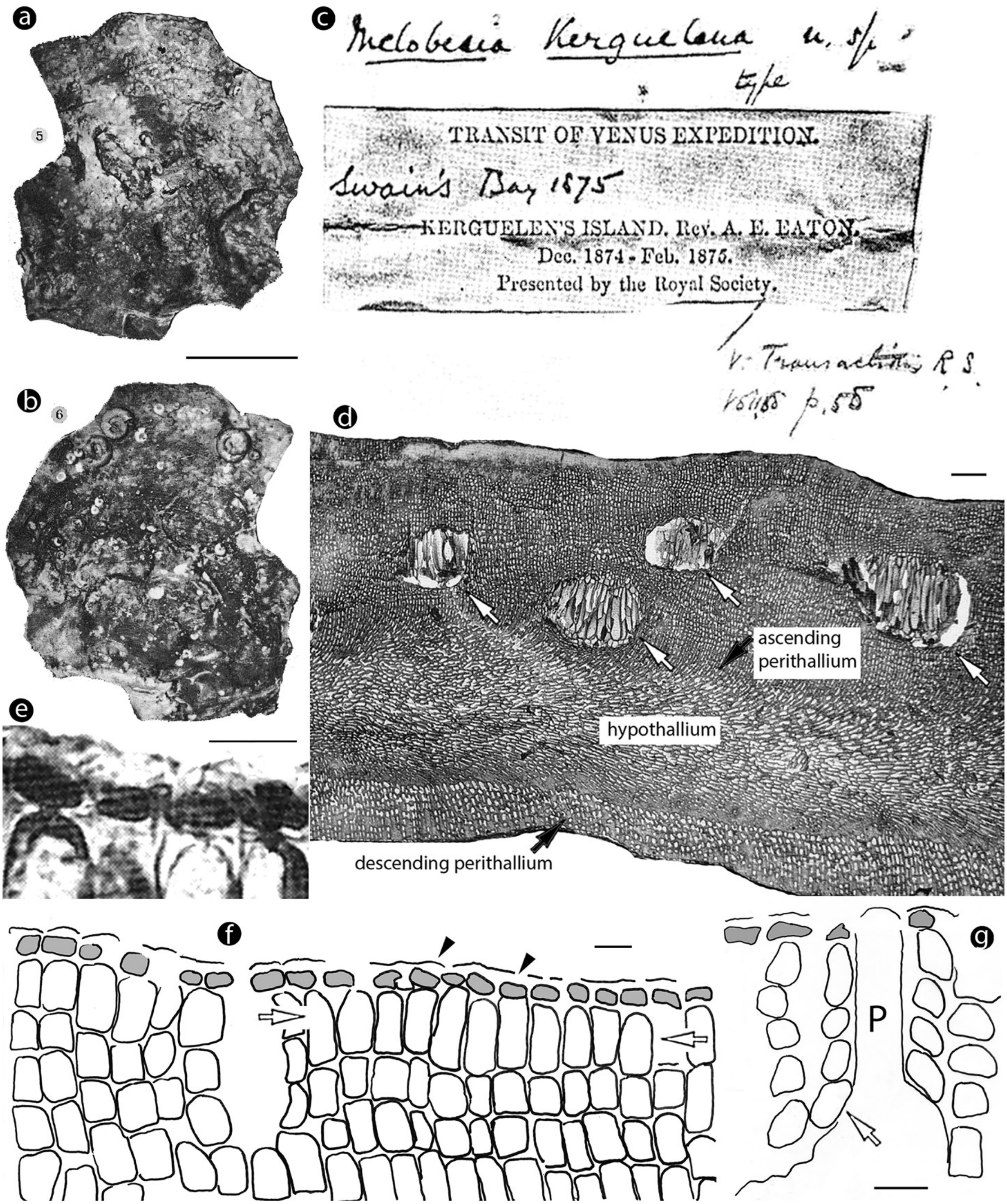
Lemoine's report of both tetrasporangial and carposporangial conceptacles indicates the presence of several thalli in the original material, which supports the view of several specimens in the original collection.

The largest specimen was described and illustrated by Foslie (1900c: 67–69, 1908a: 207, text fig. 2) and Printz (1929: pl. 9, figs. 5, 6 [in two views]; Figure 13a,b) and presently survives in TRH as "three . . . fragments, all less than 5 mm in greatest dimension" (Woelkerling 1993a: 133), with the greatest part in the BM (Wilks and Woelkerling 1994: fig. 16A). Because Adey and Lebednik (1967: 69) recognized a type status for the TRH material, this has to be considered as the lectotype, and the (larger) BM part becomes an isolectotype. In the event of more specimens in the original material at the BM (e.g., carposporangial thalli according to Lemoine 1913), they would have to be flagged as syntypes.

The isolectotype (BM) was more recently examined by Wilks and Woelkerling (1994: 197–198: figs. 16, 17, "holotype"), who illustrated the relevant label and three sections of the thallus (one showing a multiporate conceptacle; Figure 13c,d). Like Foslie (1900c: 67–69) and Lemoine (1913), Wilks and Woelkerling also described and illustrated the presence of a central core region (hypothallium) with both dorsal and ventral perithallial regions and with subepithallial cells as long or longer than those below (Figure 13d,f). Epithallial cells were illustrated as flattened to rectangular (but not flared or domed; Wilks and Woelkerling 1994: fig. 17A; Figure 13e–g). Canals of multiporate conceptacles were straight, becoming wider at the base, and lined by nondifferentiated pore cells (Figure 13g).

Wilks and Woelkerling (1994: 198) concluded that *Melobesia kerguelena* could belong to *Clathromorphum*, *Mesophyllum*, or *Synarthrophyton*, "but in the absence of male plants, the correct disposition cannot be resolved." However, the presence of both types of spermatangia in single species of Mesophylloideae, for example, in members of Magnephyceae (e.g., *Leptophytum*, *Phymatolithopsis*), Melyvonneeae (*Macroblastum*, *Phragmope*, *Printziana insignis*), and Amphithallieae (e.g., *Amphithallia crassiuscula*), indicates that this character is of no generic significance (see also "Divisions of Corallinales"; Figure 1a). On the other hand, a bilateral thallus organization in combination with the elongate subepithallial cells and the lack of a coaxial hypothallium, differentiated pore cells, or long series (>3) of epithallial cells support a position in the Amphithallieae. Indeed, because of the above character combination, *Kerguelena* is closely related to the obligate epiphyte *Amphithallia crassiuscula*, which also differs by a thinner thallus lacking embedded conceptacles.

Kerguelena dickiei differs from *Masoniana kraftii* (see species account), which develops short subepithallial cells supporting at least 1 or 2 epithallial cells. In both genera, canals of multiporate conceptacles are straight and bordered by nondifferentiated pore cells (as in *Amphithallia*). Spermatangial structures are unknown, whereas carposporangial thalli with lateral production of carposporangia have been recorded in *M. kraftii*. Both *Kerguelena dickiei* and *Masoniana kraftii* possess embedded conceptacles. These characters are sufficient to exclude these species from *Melobesia* (Melobesiaceae) and *Phymatolithon* (Lithothamnionaceae), respectively, and to recognize them as two distinct genera of Amphithallieae. Mendoza et al. (1996: 60, pl. 14, figs. 1–8) referred *Melobesia kerguelena* to *Mesophyllum fuegianum*, but their illustrations show thalli lacking a bilateral thallus organization.



Melobesia Kerguelana n. sp.
type

TRANSIT OF VENUS EXPEDITION.
Swain's Bay 1875
KERGUELEN'S ISLAND. Rev. A. E. EATON.
Dec. 1874 - Feb. 1875.
Presented by the Royal Society.

v. Transactions R.S.
Vol 168 p.58

FIGURE 13. (*Opposite*) *Kerguelena dickiei*. (**a, b**) The lectotype before its fragmentation in views from (a) above and (b) below. Reproduced from Printz (1929: pl. 9, figs 5, 6). Scale bar: 2 cm. Presently (in parts) at the BM and TRH. (**c**) The label of the isolectotype material in BM. Modified from Wilks and Woelkerling (1994: fig. 16 A). (**d**) Section of thallus showing the bilateral organization, composed of a central core of hypothallial filaments supporting ascending and descending perithallia. Note the embedded conceptacles (arrows). Modified from Wilks and Woelkerling (1994: fig. 16 B). Scale bar: 100 µm. (**e, f**) Section at the surface showing several elongate subepithallial cells (arrows) supporting single rectangular epithallial cells (arrowheads). Epithallial cells magnified in (e). Modified from Wilks and Woelkerling (1994: fig. 17A). Scale bars: 10 µm. (**g**) Section of a pore canal of a multiporate roof, showing a straight shape becoming wider toward the base (arrow). Modified from Wilks and Woelkerling (1994: fig. 17B). Scale bar: 10 µm. Abbreviation: p, pore canal.

Masoniana **Athanas. et D. L. Ballant. gen. nov.**

Masoniana Athanas. et D. L. Ballant. gen. nov. (type: *M. kraftii*).

Diagnosis: New genus of Amphithallieae, sharing the bilateral thallus organization with members of this tribe and differing by a nonepiphytic or parasitic nature and possessing embedded conceptacles and short subepithallial cells; the last character distinguishes *Masoniana* from *Kerguelena*, which differs at least by exhibiting elongate subepithallial cells.

Etymology: The new genus commemorates the American corallinologist Lucile Roush Mason, and the epithet honors our colleague Gerald T. Kraft, who found the species and greatly helped with and authored part of the monograph on the Ceramioideae (Athanasiadis 1996a).

Masoniana kraftii **Athanas. et D. L. Ballant. comb. et nom. nov.**

FIGURE 14

Masoniana kraftii Athanas. et D. L. Ballant. comb. et nom. nov.

Basionym: Phymatolithon masonianum K. M. Wilks et Woelk. 1994: 195, figs. 11–15.

Type Locality: Sublittoral, 6–12 m depth, Ninepin Point, D'Entrecasteaux Channel, Tasmania, southern Australia.

Holotype: In LTB (16679), 4 January 1993, coll. G. T. Kraft, selected and illustrated by Wilks and Woelkerling (1994: 216, fig. 11A).

Habitat and Distribution: The species grows on sponge and rock in the sublittoral zone, 4–12 m depth. It is reported from collections made in South Australia and Tasmania.

Material Examined: Australia: Tasmania: Ninepin Point, D'Entrecasteaux Channel (43°16´S, 147°10´E), 18 February 1983, coll. A. Brown, MEL2269650 (LTB16760); Ninepin Point, D'Entrecasteaux Channel (43°16´S, 147°10´E), 18 February 1983, coll. S. Platt, topotype, MEL2271683-4 (LTB12787).

Comments: The original description was based on vegetative and tetrasporangial specimens (Wilks and Woelkerling 1994: figs. 11–15), showing a lamellate, partly unattached thallus, to 15 cm in extent and 3 mm thick (Figure 14a), resembling the habit of *Kerguelena dickiei*. Struts and lamellate branches occur on the ventral side of the thallus (Wilks and Woelkerling 1994: fig. 11B). The study of the present material confirmed that the thallus organization is bilateral (Figure 14b) with short subepithallial cells borne dorsally and ventrally (Figure 14c,d). Multiporate conceptacles with a convex roof develop straight canals bordered by nondifferentiated pore cells (Figure 14g–i). In a later account, Woelkerling (1996: 185, figs. 78–79) described dioecious gametophytes. In particular, male structures were said to be either simple or branched (as in *Amphithallia crassiuscula*), and carposporophytes "lacking a central fusion cell" (possibly being inconspicuous as in *Amphithallia* and *Synarthrophyton*), producing carposporangia from the periphery of a slightly raised fertile zone (Woelkerling 1996: fig. 79C; Figure 14e). Therefore, *Masoniana* differs from other Amphithallieae by the development of short subepithallial cells that support 1 or 2 (more?) distinctively flattened or lens-shaped epithallial cells (Figure 14c,d). Within the subfamily Mesophylloideae, short subepithallial cells have also been reported in three deepwater species of *Mesophyllum* (i.e., *M. aleuticum*, *M. stenopon*, and *M. fluatum*; Melyvonneeae) and in three genera of Magnephyceae (i.e., *Leptophytum*, *Kvaleya*, and *Phymatolithopsis*); see also the accounts for these taxa. Development of ventral (perithallial) outgrowths (struts sensu Wilks and Woelkerling 1994: fig. 13C,D) also occurs in two species of *Orthocarpa* (see Table 6) and in *Macedonis julieae* (Athanasiadis and Adey 2006: fig. 64, as *Leptophytum*) and is considered to be a parallelism. The development of series of flattened perithallial cells on conceptacle roofs (Figure 14i) merits further study to locate with certainty the active meristem.

MELYVONNEEAE ATHANAS. ET D. L. BALLANT. TRIB. NOV.

Melyvonneeae Athanas. et D. L. Ballant. trib. nov. (type: *Melyvonnea*).

Diagnosis: New tribe of Mesophylloideae comprising the genera *Phragmope*, *Macroblastum* gen. nov., *Mesophyllum*, *Melyvonnea*, *Printziana*, *Sunesonia*, *Thallis*, and *Perithallis* and

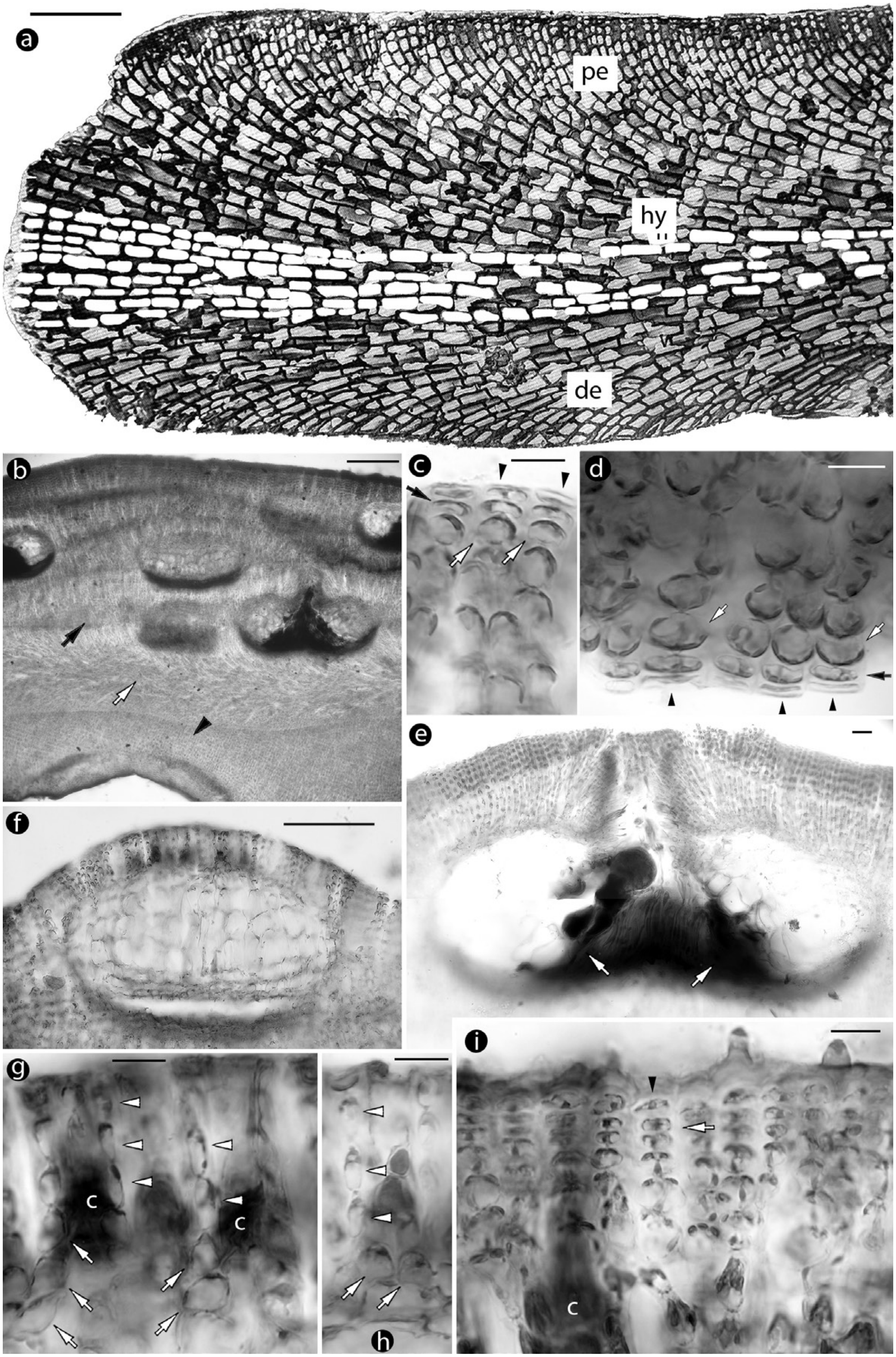

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FIGURE 14. (*Opposite*) *Masoniana kraftii*. (**a**) Section showing a central core of at least five hypothallial filaments supporting an ascending perithallium and descending hypothallial filaments (LTB12787). Modified from Wilks and Woelkerling (1994: fig. 12A). Scale bar: 100 μm. (**b**) Section of a carposporangial thallus, showing a central core of hypothallial filaments (white arrow) supporting the ascending (black arrow) and descending (arrowhead) secondary perithallia and embedded conceptacles (LTB12787). Scale bar: 100 μm. (**c**) Section at the dorsal side showing short subepithallial cells (white arrows), supporting a top epithallial cell (black arrowheads) and a second epithallial cell below (black arrow; LTB12787). Scale bar: 10 μm. (**d**) Section at the ventral side showing short subepithallial cells (white arrows), supporting a top epithallial cell (arrowhead) and a second epithallial cell below (black arrow; LTB12787). Scale bar: 10 μm. (**e**) Section of a carposporangial conceptacle, with remains of carposporangia (arrows) at the periphery of a slightly raised fertile zone (LTB12787). Scale bar: 10 μm. (**f**) Section of a multiporate conceptacle filled in with palisade cells (LTB12787). Scale bar: 100 μm. (**g, h**) Sections of pore canals of multiporate roofs, showing slightly larger basal cells. The canals are straight, and the lining cells (arrowheads) are normal roof cells (LTB12787). Scale bars: 10 μm. (**i**) Meristematic activity (arrow) taking place above a multiporate roof. One canal is visible, and a presumed epithallial cell is indicated (arrowhead), suggesting that cells below should be identified as perithallial cells (LTB12760). Scale bar: 10 μm. Abbreviations: c, pore canal; de, descending hypothallial filaments; hy, hypothallium; pe, perithallium.

differing from the other tribes of the subfamily by the development of a predominantly coaxial hypothallium (secondarily reduced to patches in *Sunesonia* and *Thallis*). Melyvonneeae share with Magnephyceae the ancestral thallus organization (monopodial-dorsiventral with polystromatic hypothallium), which has been transformed to bilateral organization in the Amphithallieae.

Comments: Melyvonneeae comprises the core of species of the former *Mesophyllum*, including genera with a predominantly coaxial hypothallium, and is further characterized by considerable differentiation in the structure of pore filaments lining canals of multiporate conceptacles, leading to the recognition of several new genera from South Africa, Australia, New Zealand, and Chatham (Athanasiadis 2020b, 2022). In particular, *Thallis-Perithallis* and *Printziana-Sunesonia* exhibit a canal structure that sets them apart from all other Mesophyllaceae (and coralline algae in general). This involves at least four specializations, namely, (1) basally branched pore filaments, (2) filaments composed of 4 or 5 (6 or more? in *Printziana*) cells, (3) the presence of elongate subbasal cells, and (4) with the exception of *Printziana* (where this character is variable), termination of pore filaments below the roof surface. Collectively, these characters represent an unmistakable synapomorphy, indicating a common ancestor at a time when South Africa, Australia, and New Zealand and Chatham were closely located and dispersal of biota was feasible, that is, between Jurassic and Early Cretaceous, 165–150 to 135 MYA (Sanmartin and Ronquist 2004: 218). *Thallis-Perithallis* and *Printziana australis–Sunesonia* form pairs, the latter one being further distinguished by the development of elongate basal cells. In *Sunesonia* the basal cells gradually become reduced and may deteriorate, so that pore filaments look like they are composed of a single elongate “basal” (formerly subbasal) cell and two top cells (Athanasiadis 2022: fig. 17p). This particular condition in *Sunesonia*, along with habitat preferences (thalli attached to rock in the sublittoral zone), development of conceptacles with a convex roof, and a thallus forming erect perithallial protuberances, explains the confusion with *Melyvonnea* (*Mesophyllum*) *erubescens*. Most significantly, however, it allows reconsideration of the evolution of pore filaments in *Melyvonnea*, relating this genus to *Thallis-Perithallis* and *Printziana-Sunesonia*. *Melyvonnea* shares with these genera at least the presence of fewer cells in pore filaments (than in adjacent roof ones) and the termination of pore filaments below the conceptacle (roof) surface. Could the “basal” elongate cells of *Melyvonnea* be a relocation, after the loss of basally branched pore cells? There is no report of basally branched pore cells in *Melyvonnea*, which suggests that if this event took place, it occurred long ago, leaving no traits in the present-day populations. The only support we presently have for this hypothesis is the deteriorating basally divided pore cells in *Sunesonia*, which could be the closest relative. Assuming that loss of basally branched pore cells did occur in the ancestor of *Melyvonnea*, causing relocation of the subbasal elongate cells to a basal position (see Figure 25u), it would lead to a natural position of this genus next to *Printziana-Sunesonia*, as supported by molecular studies (Broom et al. 2008; Peña et al. 2011; Sissini et al. 2014: fig. 5) and discussed in Athanasiadis (2022: fig. 18a–d). This evolutionary scenario is also supported by the present phylogenetic analysis under particular circumstances (Figure 6d; see also the account for *Melyvonnea*).

Development of dendroid spermatangia (a plesiomorphy characterizing the Sporolithales and Lithothamnionaceae) is lacking in nearly all members of the tribe except in *Phragmope* (where it is sporadically recorded) and in *Macroblastum* (where it occurs commonly together with simple ones).

The presence of an inconspicuous fusion cell (composed of up to 3 supporting cells) in the majority of Melyvonneeae (i.e., *Phragmope*, *Melyvonnea*, *Macroblastum*, and *Perithallis*) and in *Protomesophyllum* (Protomesophylloideae) suggests that this condition is the ancestral one, leading to a medium size in *Printziana* and *Thallis* (where 4 to 5 supporting cells and 1 or 2 hypogynous cells form the fusion cell). The fusion cell achieves maximal development in *Mesophyllum*, incorporating some 10 supporting and 10 hypogynous cells (Suneson 1937; Lebednik 1977b; Athanasiadis 2018).

Gametophytes in *Sunesonia* are unknown, suggesting that this genus could be reproducing only apomeiotically.

The name Mesophylleae Dumortier (1874: 8, 182; type: *Mesophylla* Dumortier; liverworts) precludes using the autonym genus (*Mesophyllum* Me. Lemoine) in establishing a tribal name in the Mesophyllaceae. A comparison between genera of Melyvonneeae is given in Table 3.

***Phragmope* Athanas.**

Phragmope Athanas. 2020b: 533 (type: *P. discrepans*).

***Phragmope discrepans* (Foslie) Athanas.**

Phragmope discrepans (Foslie) Athanas. 2020b: 533, figs. 1–6.

Basionym: Lithothamnion discrepans Foslie 1907b: 8.

Homotypic Synonym: Mesophyllum discrepans (Foslie) Me. Lemoine 1928: 252.

Heterotypic Synonyms: Lithothamnion synanablastum f. *speciosum* Foslie 1900a: 11, "*speciosa*"; type locality: growing on an algal ball, Grahamstown, South Africa; holotype: in TRH (B17-2591), Printz (1929: pl. 8, figs. 2, 3), Adey and Lebednik (1967: 69, "§ Becker, Afr., Cape of Good Hope, Grahamstown, 5.1899, LM8(2,3) [slides] 348, 1551"), Chamberlain and Keats (1995: figs. 4, 7, 46–51, table 1, "holotype"). Athanasiadis (2020b: 533, synonym).

Lithothamnion speciosum (Foslie) Foslie 1907b: 16.

Mesophyllum speciosum (Foslie) W. H. Adey 1970: 26.

Misapplied Name: *Mesophyllum engelhartii* sensu Chamberlain and Keats 1995 [non *M. engelhartii* (Foslie) W. H. Adey = *Magnephycus engelhartii*].

Type Locality: Grahamstown, South Africa, "presumably referring to the shores of Algoa Bay," on *Petella tabularis* Krauss (Chamberlain and Keats 1995: 141).

Lectotype: In TRH (C18-3332), Printz (1929: pl. 5, fig. 3), Adey and Lebednik (1967: 83, "type material," "§ Becker, Afr., Cape of Good Hope, 5.1899. LM5(3) Grahamstown [slides] 346, 1556"), Woelkerling (1993a: 76, "holotype"), Chamberlain and Keats (1995: 141, figs. 5, 41–45, "lectotype"), Woelkerling et al. (2005: 467, "lectotype").

Syntype: In TRH (C18-3333), on *Petella tabularis*, Grahamstown, South Africa, May 1899, H. Becker (Chamberlain and Keats 1995: figs. 6, 36–40, "isolectotype").

Habitat and Distribution: This species is one of the commonest crustose corallines on rocks and *Patella* shells in the low littoral. In the sublittoral it reaches depths down to at least 8 m depth, growing on stones, shells, *Ecklonia* holdfasts, and rock faces. Thalli are perennial and abundantly fertile in March, April, May, July, October, and November; data are not available for other months (Chamberlain and Keats 1995: 136, as *Mesophyllum engelhartii*). It is reported from Eastern Cape (Cintsa, Three Sisters, Skoenmakerskop) and Western Cape (Cape Agulhas, Brandfontein, Cape of Good Hope, Oudekraal, Bakoven, Holbaiipunt, Abdolsbaai, Doringbaai, Groenriviermond; Chamberlain and Keats 1995: 136, as *Mesophyllum engelhartii*). These data are confirmed from four collections from Doring Baal, Brandfontein, and Holbaiipunt (Athanasiadis 2020). *Phragmope discrepans* is probably endemic to South Africa.

Comments: The original material of *Lithothamnion discrepans* and *Lithothamnion synanablastum* f. *speciosum* was examined by Chamberlain and Keats (1995: figs. 5, 6, 36–45 for *L. discrepans*, figs. 4, 7, 46–51 for *L. synanablastum*, table 1) and considered to belong to the same species, named "*Mesophyllum engelhartii*.". Chamberlain and Keats (1995: 134–136) included eight other taxa as synonyms originally described from widely separated localities in the southern hemisphere, in agreement with Woelkerling and Harvey (1993: 581–582, 600). None of the cited synonyms was accepted by Athanasiadis (2020b), who resurrected *Lithothamnion discrepans* as the correct basionym for the South African species in the new monotypic genus *Phragmope*. The original material of *L. discrepans* was collected by H. Becker in May 1899 and included two separate collections, one of which (the lectotype) was illustrated by Printz (1929: pl. 5, fig. 3). Both collections included thalli attached to *Patella tabularis*. The second collection (alluded by Adey 1970: 23, "two specimens are possible") also included material attached to shells (Chamberlain and Keats 1995: fig. 6, "isolectotype").

The type of *L. synanablastum* f. *speciosum* was also collected by H. Becker in May 1899 and included two specimens, placed in the same box by Foslie (Chamberlain and Keats 1995: fig. 7) and illustrated by Printz (1929: pl. 8, figs. 2, 3). These specimens most likely represent separate gatherings.

Phragmope exhibits three diagnostic characters: (1) development of cell bars closing the canals of multiporate conceptacles, (2) frequent meristem regeneration in the hypothallium, and (3) development of a second imperforate roof (composed of perithallial cells) covering empty multiporate conceptacles. The latter structure, although not homologous, may have a function similar to the second roof produced by centripetally growing filaments that involves the hypothallium (character 39 in the phylogenetic analysis). A second roof produced by centripetally growing filaments is described in several species of Magnephyceae (e.g., members of *Magnephycus* and *Macedonis tethygenis*; see Figures 36d, 55c, 60l). On the other hand, cell bars were also seen in canals of an undescribed species from Cape Jaffa (South Australia), included as admixture in the type material of *M. engelhartii* (Athanasiadis 2020b: table 1, TRH B18-2598).

***Mesophyllum* Me. Lemoine**

Mesophyllum Me. Lemoine 1928: 251 (type: *M. lichenoides*, designated by Ishijima 1942: 174).

Heterotypic Synonyms: Polyporolithon L. R. Mason 1953: 316; type: *P. conchatum* (Setch. et Foslie) L. R. Mason. Adey (1970: 23, 27, synonym), Athanasiadis and Ballantine (2014: 418, synonym).

Stereophyllum Heydrich 1904: 198, nom. illeg.; type: *S. expansum*, designated by Lemoine (1911: 66) [non *Stereophyllum* Mitten 1859 (Musci);

non *Stereophyllum* Karsten 1889 (see Index Nominum Algarum 2023; Index Nominum Genericorum 2023)].

Comments: This is the most species rich genus of the family Mesophyllaceae. It was most recently revised by Athanasiadis and Ballantine (2014), who proposed its restriction to 11 species in the northern hemisphere. The present account follows their study, adding one more species (*M. stenopon*) from Pacific Mexico. A diagnostic feature of *Mesophyllum* is the development of a large fusion cell, involving at least 10 supporting and 10 hypogynous cells (Athanasiadis 2018: figs. 6, 7; Figure 2i–k). Pedestal formation in carposporangial conceptacles, previously considered to be an autapomorphy for *Mesophyllum*, has also been described (as a facultative condition) in the southern hemisphere genera *Perithallis*, *Thallis*, and *Printziana*, which differ in possessing highly specialized pore filaments bordering canals of multiporate conceptacles (Athanasiadis 2022: fig. 1; Table 2). Development of a cell tube, leading the zygote to the supporting (auxiliary) cell, has been observed in *M. conchatum* (Lebednik 1977a: 391) and also documented in the generitype (Athanasiadis 2018). Similar cell tubes have also been detected in *Protomesophyllum ameleteton*, *Printziana insignis*, and *Thallis capensis* (Figure 2a–d). With seven species known from the Pacific coast of North America, we may hypothesize this region is the center of origin of the genus, which also includes two endemic species in the Caribbean (*M. mesomorphum*, *M. syntrophicum*) and three other species in the Canaries and the nearby African and European coasts (*M. lichenoides*, *M. expansum*, *M. philippii*). The latter two species penetrate into the Mediterranean as far as Sicily and the Adriatic Sea. At least 72 fossil species of *Mesophyllum* sensu lato have been described (see Athanasiadis 2016b; Index Nominum Algarum 2023), but their generic affiliation is speculative, being based on the presence of a coaxial hypothallium that presently characterizes several other genera of Melyvonneeae (Table 3).

***Mesophyllum aleuticum* P. A. Lebednik**

Mesophyllum aleuticum P. A. Lebednik in Athanasiadis et al. 2004: 128, figs. 1–19.

Type Locality: Sublittoral, ~5 m depth, Constantine Harbor, Jones Creek, Amchitka Island (Aleutian Islands), Alaska, USA.

Holotype: In UBC (unnumbered, Lebednik AM-68-4, 15), 22 September 1968, coll. P. A. Lebednik.

Isotype: In GB (unnumbered).

Habitat and Distribution: This is an endemic saxicolous species growing in the littoral and sublittoral zone to at least 60 m depth. It is recorded between Shemya Island and Goloi Island (Aleutians; Lebednik 1974).

Comments: *Mesophyllum aleuticum*, *M. stenopon* from Pacific Mexico, and *M. fluatum* from Hawaii occur in the deep sublittoral zone and are the only members of the genus possessing short subepithallial meristematic cells, which suggests that these cells could be resting stages before cell division. In addition, *M. aleuticum* and *Phragmope discrepans* develop hair cells in the hypothallium (Athanasiadis et al. 2004: figs. 6, 7; Athanasiadis 2020b: fig. 3g). The function of such trichocyte-like cells remains unknown. Following fertilization, the resulting fusion cell involves at least some 8 supporting cells (Lebednik 1977b: fig. 11).

***Mesophyllum conchatum* (Setch. et Foslie) W. H. Adey**

Mesophyllum conchatum (Setch. et Foslie) W. H. Adey 1970: 23.

Basionym: Lithothamnion conchatum Setch. et Foslie in Foslie 1902b: 6–7.

Homotypic Synonyms: Lithothamnion conchatum f. *conchatum* Foslie 1906b: 6, "*typicum*."

Polyporolithon conchatum (Setch. et Foslie) L. R. Mason 1953: 317.

Type Locality: Point Joe, Monterey County, California, USA.

Lectotype: In TRH (B17-2541), designated by Mason (1953: 317, 318, as *Polyporolithon*, "Lectotype . . . Herb. Mus. Nidaros."), Adey and Lebednik (1967: 68, "§ USA, Cal., Monterey.10.1.1899, LM10 (3-6) (3 boxes) [slides] 729, 1578"), illustrated by Printz (1929: pl. 10, figs. 3–6) and Athanasiadis et al. (2004: figs. 54–64).

Syntype: In UC (737624), designated by Mason (1953: 318, "On 'Cheilosporum' [*Calliarthron*], Pyramid Point near Pacific Grove, Monterey County, California, Jan. 8, 1899, *Gibbs and Setchell 3057a*," "isotype").

Habitat and Distribution: Thalli grow exclusively on geniculate corallines (*Calliarthron*, *Bossiella*, *Corallina*) and are more often found on *Calliarthron* in the littoral zone to at least 10 m depth (Adey and Johansen 1972: 160). The species is recorded between California (type locality) and Langara Island, Queen Charlotte Islands, British Columbia (Hawkes et al. 1978: 103). The southern limit is Cambria, San Luis Obispo County, California (Mason 1953: 318, as *Polyporalithon*). Records from the NW Pacific Ocean (Tartar Strait, west of Sakhalin Island) and the Sea of Japan are unconfirmed (Lebednik 1974).

Comments: Mason (1953: 317–318), Adey and Lebednik (1967: 68), Adey (1970: 23), and Athanasiadis et al. (2004: 140) recognized at least two authentic collections: one dated "Jan.8.1899" (in UC; Mason 1953) and the material in TRH dated "10.1.1899." Although Mason examined the UC collection, she attributed the lectotype to TRH ("Herb.Mus.Nidaros."). Hence, the TRH material should be considered to be the lectotype, and the UC material should be considered to be a syntype. The study of the lectotype (TRH) showed that it is a mixture of at least four specimens and fragments (Athanasiadis et al. 2004: fig. 54), representing most likely several gatherings, and restriction to a single element may be needed. Tasmanian thalli referred to "*M. incisum*" by Woelkerling (1996: fig. 84E, F) display the type of pore filament of *M. conchatum*, and reexamination of this material is also required (Athanasiadis et al. 2004: 146).

Mesophyllum crassiusculum (Foslie) P. A. Lebednik

Mesophyllum crassiusculum (Foslie) P. A. Lebednik in Athanasiadis et al. 2004: 152.

Basionym: Lithothamnion rugosum f. *crassiusculum* Foslie 1901a: 4, "*crassiuscula*."

Homotypic Synonyms: Lithothamnion pacificum f. *crassiusculum* (Foslie) Foslie 1906b: 10, "*crassiuscula*."

Lithothamnion crassiusculum (Foslie) R. L. Mason in Setchell and Mason 1943: 93.

Heterotypic Synonym: *Lithothamnion aculeiferum* R. L. Mason in Setchell and Mason 1943: 94, "*Lithothamnium*"; type locality: Whites Point, San Pedro, Los Angeles County, California, USA; holotype: in UC 739410 (Setchell no. 1496a), 6 December 1896, coll. W. A. Setchell, including seven slides made by Lebednik (nos. 1–4, 6–8) and one slide made by Setchell annotated "TYPE," illustrated by Mason (1953: pl. 33c) and Masaki (1968: pl. 2, fig. 5); paratype: in TRH (B15-2371), January 1896, in tide pools, coll. W. A. Setchell (no. 1496a), including Foslie slide 203. Lebednik (1974, synonym), Athanasiadis et al. (2004: 155–160, synonym).

Type Locality: On pebbles in tide pools and in a small inlet in the reef, Whites Point San Pedro, Los Angeles County, California, USA.

Lectotype: In TRH (B15-2379), Printz (1929: pl. 4, fig. 13), designated by Mason (1953: 329, "Lectotype . . . Setchell 1149 . . . Herb.Mus.Nidaros."), Athanasiadis et al. (2004: 158, figs. 119–137, "Kalifornien Whites Point San Pedro Dec. 1895 Setchell, No 1149 on pebbles" includes Foslie slide 205).

Syntypes: In UC (736373, Setchell no. 1149B, collected between 23 December 1895 and 10 January 1896 by W. A. Setchell), Lebednik (1974: pl. 54, fig. I, "isotype"); in UC (736367, Setchell no. 1149, collected between 23 December 1895 and 10 January 1896 in a small inlet in the reef at Whites Points by W. A. Setchell), Mason (1953: pl. 35b, larger specimen on the left, "isotype").

Habitat and Distribution: This species forms rhodoliths, encrusting and enveloping pebbles in the littoral zone, in tide pools, and in the surf, moving freely with the wave motion. It is confirmed from California (White's Point, San Pedro, and La Jolla; Athanasiadis et al. 2004) and Baja California (Cortez Bank; Athanasiadis 2007b).

Comments: Of the two Setchell collections (nos. 1149 and 1496a) cited in the protologue (Foslie 1901a), the former was referred to *Lithothamnion crassiusculum* by Mason (in Setchell and Mason 1943: 93) and later selected as the lectotype of that species (Mason 1953: 329), with three other collections in UC (736367, 736369, 736373). The latter three collections have been considered to be syntypes (or paratypes) because their date of collection is not identical to the lectotype in TRH. Moreover, only UC736367 and UC736373 included material representative of *M. crassiusculum* (Athanasiadis et al. 2004: 158). The second (syntype) collection (Setchell no. 1496a) cited in the protologue of f. *crassiusculum* was selected by Setchell and Mason (1943: 94) as the holotype of *Lithothamnion aculeiferum* Mason, a species considered to be conspecific with *M. crassiusculum* by Lebednik (1974: pl. 52, tables 37, 38) and Athanasiadis et al. (2004: 155–160).

The Dawson material from Cortez Bank (Athanasiadis 2007b: figs. 61–63) was collected in the sublittoral (49 m depth) and was attached to rock fragments (probably detached by dredging). These specimens lack prominent perithallial protuberances, a character considered to be variable in the type (Athanasiadis et al. 2004), and exhibit specialized (thinner–wider) pore cells that occur commonly in species of *Mesophyllum* (Athanasiadis et al. 2004). It was concluded that the failure to observe specialized pore cells in the type of *M. crassiusculum* (Athanasiadis et al. 2004: 35, figs. 136, 139, 142) could be due to the fact that the material was old and badly preserved.

Mesophyllum expansum (Philippi) J. Cabioch et M. L. Mendoza

Mesophyllum expansum (Philippi) J. Cabioch et M. L. Mendoza 2003: 259.

Basionym: Lithophyllum expansum Philippi 1837: 388–389.

Type Locality: Catania, Sicily, Italy (neotype from Catania).

Neotype: In CAT (unnumbered, Catania "S. Maria La Scala, 17 July 1999"), designated by Athanasiadis (2016b: 260).

Isoneotype: Fragments of the neotype, including slides (herb. Athanas.; see Figure 17c,d).

Habitat and Distribution: This species grows just below water level and at least 90 m depth. It is a common component of the Mediterranean "coralligène," forming isolated thalli "mellangé avec" other encrusting corallines (Cabioch and Mendoza 2003: 259). It is recorded between the Azores, the Atlantic coast of Spain (Peña et al. 2015: fig. 13), the Canaries, and the western Mediterranean, including Sicily (Catania). Its occurrence in the Caribbean is doubtful (Athanasiadis and Neto 2010: 338). A previous record from the North Aegean in the eastern Mediterranean (Athanasiadis and Neto 2010: 334) is here referred to *Macroblastum dendrospermum*.

Comments: Athanasiadis and Neto (2010: 337–338) noted that

> thalli from Tenerife are not as large as those recorded from the Mediterranean, but are both tetrasporangial and gametangial, indicating that the Canaries are within the center of distribution of the species. All collections examined come from the upper sublittoral and littoral zones at "Orotava" (now Porto de la Cruz) . . . and all recently collected specimens found at TFC are from the same area where the species grows luxuriantly in the rock-pools just in front of the main harbor of the city (J. Afonso-Carrillo pers. comm.). . . . [and that]
>
> The [Azorean] four tetrasporangial records . . . from Pico, Sâo Miguel and Graciosa range from depths between 5 and 30 m . . . , these distantly located, deep records probably indicate that the species is widespread

in the Azores, but not abundant. The lack of gametophytes suggests that it may have its northernmost distribution [in the Azores].

***Mesophyllum lamellatum* (Setch. et Foslie) W. H. Adey**

Mesophyllum lamellatum (Setch. et Foslie) W. H. Adey 1970: 25.
Basionym: Lithothamnion lamellatum Setch. et Foslie in Foslie 1903: 4.

Type Locality: Cypress Point, Monterey County, California, USA.

Lectotype: In TRH (B17-2554, *pro parte*), designated by Mason (1953: 330, "Type . . . Jan.9.1899, Gibbs and Setchell 3075 (Herb.Mus.Nidaros)"), Printz (1929: pl. 8, fig. 4), Adey and Lebednik (1967: 68, "type material," "§ Setchell+Gibbs, USA, Cal., Monterey, Cypress Point, 9.1.1899, LM8(4,5) no. 3075 [slides] 825, 826"), restricted in Athanasiadis et al. (2004: 146, figs. 92, specimen indicated by arrows, 94–107).

Syntypes: In UC (266384), Mason (1953: 330, "isotype"); in UC (737622), Mason (1953: pl. 33, fig. d, pl. 36, fig. A, "isotype"), Lebednik (1974: pl. 56, figs. 1–3, "isotype"); in TRH (B17-2554, *pro parte*), illustrated by Printz (1929: pl. 8, fig. 5) and Athanasiadis et al. (2004: fig. 93).

Habitat and Distribution: According to Foslie's protologue and his annotations in TRH, this species grows in the littoral zone on geniculate corallines and also on stones or rock. Yet the lectotype is attached to a species of Gelidiaceae and a thallus of *Macedonis* (*Leptophytum*) *lamellicola*. The latter two admixtures were also observed in several other collections (Athanasiadis et al. 2004). Although *M. lamellatum* was widely recorded along the Pacific coast of North America and Pacific Mexico (Dawson 1960), later studies confirmed material only from Monterey County, California (Athanasiadis et al. 2004; Athanasiadis 2007b).

Comments: The original material was found to include admixtures, and restriction of Mason's (1953) typification was proposed (Athanasiadis et al. 2004: 146, fig. 92 specimen indicated by arrows). The selected lectotype is one of the two tetrasporophytes illustrated by Printz (1929: pl. 8, figs. 4, 5) that most likely represent different gatherings. The study of 15 collections made between Pescadero Point (Monterey County, California) and Punta Malarrimo (Baja Vizcaino, Pacific Mexico), and partly referred to *M. lamellatum* by Dawson (1960), showed that the material (presently in UC) belonged to other species (Athanasiadis 2007b).

***Mesophyllum lichenoides* (J. Ellis) Me. Lemoine**

Mesophyllum lichenoides (J. Ellis) Me. Lemoine 1928: 252.
Basionym: Corallium lichenoides J. Ellis 1768: 407, pl. 17, figs. 9–11.
Homotypic Synonyms: Millepora lichenoides (Ellis) J. Ellis et Sol. 1786: 131, pl. 23, figs. 10–12.
Millepora alga J. F. Gmelin 1791: 3789, nom. illeg. [superfluous substitute (Turland et al., 2018: Article 54.1)].
Nullipora lichenoides (J. Ellis) Templeton 1836: 470.
Melobesia lichenoides (J. Ellis) Harv. 1846: xxiii, nom. illeg. [non *Melobesia lichenoides* (Philippi) Endlicher = *Lithophyllum lichenoides* Philippi].
Mastophora lichenoides (J. Ellis) Kütz. 1849: 697.
Lithophyllum lichenoides (J. Ellis) Rosanoff ex Hauck 1883: 268, nom. illeg. [non *Lithophyllum lichenoides* Philippi 1837: 389].
Lithothamnion lichenoides (J. Ellis) Foslie 1895a: 207 (repr. 130–131).
Tenarea lichenoides (J. Ellis) Kuntze 1898: 433.
Sphaerantherea lichenoides (J. Ellis) Heydrich 1907: 222.
Mesophyllum lichenoides f. *lichenoides*.
Heterotypic Synonyms: ?Sphaeranthera lichenoides f. *densa* Heydrich 1907: 225; type locality: on *Rytiphloea pinastroides*, Jersey, Channel Islands; type: not designated.
?*Lithothamnion lichenoides* f. *depressum* Foslie 1900a: 12, "*depressa*"; type locality: Roundstone Bay, Galway, Ireland; type material: in TRH, lectotype not designated (Woelkerling 1993a: 73, "The only collection . . . lectotype"; Woelkerling et al. 2005: 357, four collections, B19-2645, B19-2646, B19-2643, B19-2647).
Mesophyllum lichenoides f. *depressum* (Foslie) Hamel et Me. Lemoine 1953: 78.
Lithothamnion lichenoides f. *epiphyticum* Foslie 1897b: 42, "*epiphytica*"; type locality: Anglesey, England; lectotype: in TRH (B19-2664), designated in Woelkerling (1993a: 84–85, "Anglesey, England . . . coll. R.W. Phillips, March 1895," synonym).
Lithothamnion lichenoides f. *pusillum* Foslie 1900a: 12, "*pusilla*," nom. illeg. [*nomen pro* f. *epiphyticum*].
?*Lithothamnion lichenoides* f. *rupincola* Foslie 1897: 4; type locality: not specified; type: not designated.

Type Locality: Cornwall, England.

Lectotype: Ellis's original illustration.

Epitype: On *Corallina*, Hannafore Point, West Looe, Cornwall, designated in Woelkerling and Irvine (1986: 382, figs. 1D, 3, 4, "neotype"), Woelkerling and Irvine (2007: 230, "epitype").

Habitat and Distribution: The species is a common epiphyte on *Corallina officinalis* L. and also grows epilithically in the lower littoral in exposed sites to 8 m depth (Chamberlain and Irvine 1994: 204). It is recorded between the Netherlands (drift material) and England (northern limit at Orkney Islands) to southern Portugal. Records from other regions, including the Mediterranean, require confirmation (Athanasiadis and Neto 2010; Peña et al. 2015: fig. 14; Athanasiadis 2016b: 261).

Comments: *Mesophyllum lichenoides* is the type of the genus and was studied in a series of papers by Heydrich (1907, 1909a, 1909b, as *Sphaeranthera*), Suneson (1937, as *Lithothamnion*), Hamel and Lemoine (1953), Cabioch (1972), Woelkerling and Irvine (1986), Chamberlain and Irvine (1994), Cabioch and Mendoza (2003), Athanasiadis and Neto (2010), and Athanasiadis (2018). A distinctive autapomorphy for the species is the development of smaller pore cells (in comparison to adjacent roof cells) lining the canals of multiporate conceptacles (Woelkerling and Irvine 1986: fig. 24; Athanasiadis and Neto 2010: figs. 26–29). *Mesophyllum lichenoides* (Suneson 1937: fig. 37; Woelkerling and Irvine 1986: fig. 16) and *M. conchatum* (Athanasiadis unpubl. data) may possess ventral epithallial cells, probably as a result of their partly unattached thallus growth, whereas in most other congeners hypothallial filaments end in wedge-shaped cells facing the substratum (Athanasiadis et al. 2004: figs. 5, 37, 69; Athanasiadis and Neto 2010: fig. 1). *Mesophyllum lichenoides*, *M. philippii*, and *M. expansum* are the only species of the genus occurring in the NE Atlantic and the western Mediterranean and Adriatic Seas. This suggests that these three species developed from a common ancestor, via isolation from the main core of congeners that occurs in the western Atlantic and NE Pacific. It further suggests that *M. lichenoides* developed in the northern Atlantic, in isolation from its closest relatives (*M. philippii*, *M. expansum*), which have their northernmost distribution in the Azores or on the Atlantic coast of northern Spain and southern France (Athanasiadis and Neto 2010; Peña et al. 2015: figs. 12, 13). Records of *M. lichenoides* from southern Australia have not been verified (Woelkerling and Harvey 1993: 596, 598).

***Mesophyllum megagastri* Athanas.**

Mesophyllum megagastri Athanas. 2007b: 224, figs. 37A–E,M, 64–81.

Type Locality: Lower littoral in sheltered "caves" beneath cliffs on SE side of La Jolla Bay, California, USA.

Holotype: In UC (unnumbered, AHFH 70355A, Dawson no. 401, *pro parte*, a carposporangial specimen ~2.5 cm in extent, attached to a pebble, 15 January 1946, coll. E. Y. Dawson), illustrated by Athanasiadis (2007b: fig. 64A).

Habitat and Distribution: This is an endemic species, known only from the type locality, where it grows attached to pebbles in the littoral zone, at sheltered sites, occasionally overgrown by *Macedonis julieae*.

Comments: The species is known only from the protologue, where it was distinguished from *M. lamellatum* in having embedded multiporate conceptacles and twice as large carposporangial conceptacles (up to 1200 µm in external diameter vs. 400–600 µm in *M. lamellatum*).

***Mesophyllum mesomorphum* (Foslie) W. H. Adey**

Mesophyllum mesomorphum (Foslie) W. H. Adey 1970: 25.

Basionym: Lithothamnion mesomorphum Foslie 1901a: 5–6.

Homotypic Synonym: *Lithothamnion mesomorphum* f. *mesomorphum* Foslie in Printz 1929: 43, "*typica*," pl. 9, figs. 7, 8.

Type Locality: Harrington Sound(?), Bermuda.

Lectotype: In TRH (B18-2615, *pro parte*, January 1879, coll. W. G. Farlow[?]), Printz (1929: pl. 9, fig. 7), designated by Athanasiadis and Ballantine (2014: 421, figs. 109B, 110).

Syntypes: In TRH (B18-2615, *pro parte*), Bermuda, January 1879, coll. W. G. Farlow(?), including remains possibly of a second specimen illustrated in Printz (1929: pl. 9, fig. 8, as *Lithothamnion mesomorphum* f. *typica*); in FH, "Bermuda," illustrated in Athanasiadis (1999: 247, fig. 19, "isotype Farlow").

Habitat and Distribution: Bermudan and Puerto Rican herbarium specimens are unattached (probably detached from hard substrata). Floridian specimens (MICH622095) are also composed of unattached fragments (collected by dredging between 12 and 32 m depth). The confirmed records are from Bermuda (Harrington Sound), Florida (Loggerhead Key, Southwest Channel), and Puerto Rico (Las Creras, Aguadilla; Athanasiadis and Ballantine 2014).

Comments: The original material is presently distributed between FH and TRH. A specimen from Foslie's herbarium in TRH was selected as the lectotype (Athanasiadis and Ballantine 2014: 421). The largest specimen studied is from Harrington Sound and reaches 13 cm in extent (MICH 622095), but the exact habitat is not known because Harrington Sound is "a quite large inland sound with a variety of habitats" (C. Schneider, Department of Biology, Trinity College, Hartford, Conn., personal communication). The name *M. mesomorphum* has been misapplied for previous Caribbean and Indo-Pacific records of specimens belonging to *Magnephycus ornatus* or *Magnephycus simulans* (Athanasiadis and Ballantine 2014: 425; present study). *Mesophyllum mesomorphum* is closely related to *M. syntrophicum* (see the species account), which is also described from Harrington Sound in the same publication by Foslie. The latter species differs by lacking a regular unattached superimposed growth and exhibiting a less developed hypothallium (up to 180 vs. 350 µm thick in *M. mesomorphum*).

***Mesophyllum philippii* (Foslie) W. H. Adey**

Mesophyllum philippii (Foslie) W. H. Adey 1970: 25.

Basionym: Lithothamnion philippii Foslie 1897: 7–8, 16–17.

Homotypic Synonyms: Lithothamnion philippii f. *philippii* Foslie 1904a: pl. 1, fig. 1, "*typica*."

Sphaeranthera philippii (Foslie) Heydrich 1907: 225.

Heterotypic Synonyms: Lithothamnion philippii f. *alternans* Foslie 1907b: 17; type locality: Tanger, Morocco; holotype: in TRH (B16-2493). Athanasiadis and Ballantine (2014: 426, synonym).

Mesophyllum alternans (Foslie) J. Cabioch et M. L. Mendoza 1998: 209.

Misapplied Names: *Lithophyllum decussatum* sensu Solms-Laubach 1881: 14, pl. 1, fig. 1, Naples. Foslie (1897: 7, synonym) [non *Lithophyllum decussatum* (J. Ellis et Sol.) Philippi].

Lithophyllum decussatum sensu Hauck (1883: 270, pl. 1, fig. 7, Adria). Foslie (1897: 7, synonym).

Sphaeranthera decussata sensu Heydrich 1900b: 315, 1901b: 587 [non *Sphaeranthera decussata* (J. Ellis et Sol.) Heydrich].

Type Locality: Sublittoral, 30–80 m depth (collected via dredging), Naples, Italy.

Lectotype: In TRH (B16-2487, *pro parte*), designated by Woelkerling (1993a: 171), Woelkerling et al. (2005: 331, "lectotype"), restricted and illustrated by Athanasiadis and Ballantine (2014: figs. 131C, 132).

Habitat and Distribution: This species is a common component of the coralligène in the western Mediterranean, growing to depths of at least 80 m. It is also recorded as a rhodolith at 100 m depth in the Tyrrhenian Sea (Basso 1995, as *M. lichenoides*). Specimens from Atlantic France (Guèthary) have been collected in the littoral zone (Cabioch and Mendoza 1998: 217). Its distribution includes the Canaries and the nearby coast of Atlantic Morocco, expanding north to the southern coast of Atlantic France (Peña et al. 2015: fig. 12). There are also records of the species from the Adriatic Sea that require confirmation (see Athanasiadis 2016b: 264–265).

Comments: Athanasiadis and Ballantine (2014: 426–427) restricted the lectotypification of Woelkerling (1993a) and reinstated the name *M. philippii* in accord with Foslie (1897, 1904a: 13–19, pl. 1, fig. 1), Printz (1929: pl. 6, fig. 3), Adey and Lebednik (1967), and Adey (1970). On the contrary, Lemoine (1911: 78), Hamel and Lemoine (1953: 83), and Cabioch and Mendoza (1998) applied the basionym *Lithothamnion philippii* (on the basis of a different type) for a species whose correct name remains unknown. *Mesophyllum philippii* is probably the most common mesophylloid in the western Mediterranean and Adriatic Seas, followed by *Macroblastum dendrospermum* (previously known as *Mesophyllum macroblastum*) and *Mesophyllum expansum*, which is apparently restricted to the western basin (including Sicily).

Mesophyllum stenopon **Athanas.**

Mesophyllum stenopon Athanas. 2007b: 229, 251, figs, 23E–H, 82–95, table 2, key.

Misapplied Name: *Lithothamnion lamellatum* sensu E. Y. Dawson 1960: 19 [non *L. lamellatum* Setch. et Foslie = *Mesophyllum lamellatum* (Setch. et Foslie) W. H. Adey].

Type Locality: Sublittoral, 36–45 m depth, at Cortez Bank (119°08′W), Pacific Mexico.

Holotype: In UC (unnumbered, AHFH 70353, Dawson no. 7967, "Box 2 of 2," *pro parte*, tetrasporangial specimen, ~4 cm in extent, 27 August 1949, coll. E. Y. Dawson), illustrated by Athanasiadis (2007b: figs. 23H, 82).

Habitat and Distribution: This is an endemic species growing in the sublittoral zone, 36–73 m depth, attached to pebbles, corals, and corallines and overgrown at least by *Macedonis* (*Leptophytum*) *julieae*. It is reported from Tanner and Cortez Banks, Guadeloupe, and Sacramento Reef, Pacific Mexico.

Comments: This is a deepwater species described from several herbarium collections of *Lithothamnion lamellatum* sensu Dawson (1960: 19) from the Pacific coast of Mexico. It was segregated on the basis of short subepithallial meristematic cells and narrow pore canals of multiporate conceptacles, the canals being 6–10 μm in diameter and ± similar in size to neighboring epithallial cells. Although gametophytes remain unknown, the presence of a predominantly coaxial hypothallium in combination with the development of thinner–wider pore cells in canals of multiporate conceptacles supports a position in the genus *Mesophyllum*. Short subepithallial meristematic cells also characterize two other deepwater species of *Mesophyllum*, namely, *M. aleuticum* and *M. fluatum* (the latter here cited as incertae sedis).

Mesophyllum syntrophicum **(Foslie) W. H. Adey**

Mesophyllum syntrophicum (Foslie) W. H. Adey 1970: 26.

Basionym: Lithothamnion syntrophicum Foslie 1901a: 6–7.

Type Locality: Harrington Sound(?), Bermuda.

Lectotype: In TRH (B16-2525, "Farlow XIII," January 1881, coll. W. G. Farlow[?]), Printz (1929: pl. 5, fig. 18), designated by Athanasiadis and Ballantine (2014: 430, fig. 134).

Syntypes: In NY (unnumbered, "Bermuda, Jan 1881," coll. W. G. Farlow, two specimens).

Habitat and Distribution: Type specimens are described as "lying loose at the bottom." Herbarium specimens are attached to polychaete tubes, stones, other hard substrata, and usually bear on their thallus the foraminiferan *Miniacina miniacea* (Pallas). A Puerto Rican specimen was collected in the upper sublittoral zone in a crevice at an exposed site, attached to a coral with other encrusting algae. The confirmed distribution includes Bermuda, Puerto Rico, and Jamaica (Athanasiadis and Ballantine 2014: 429).

Comments: The original material is presently distributed between NY and TRH, and a lectotype was selected from Foslie's herbarium in TRH (Athanasiadis and Ballantine 2014: 430). Study of the lectotype and the syntypes showed that *M. syntrophicum* differs from *M. mesomorphum* in having a predominantly encrusting and strongly adherent thallus, at least 4.3 cm in extent, with rare unattached margins, whereas *M. mesomorphum* shows a regular unattached superimposed growth and a well-developed hypothallium (up to 350 vs. 180 μm thick in *M. syntrophicum*). The thallus of *M. syntrophicum* is several millimeters thick via superimposition of lamellae (or overgrowth of other organisms such as polychaete tubes and the foraminiferan *Miniacina miniacea*). The surface is smooth and "polished" to irregular (following the underneath contour). Margins are lobate with a whitish border (cuticle). Herbarium specimens are yellow greenish. *Mesophyllum syntrophicum* and *M. mesomorphum* are rare endemic elements of the Caribbean Sea, and gametophytes of both species are unknown, probably reflecting the cold temperate preference of the genus.

Mesophyllum vancouveriense **(Foslie) R. S. Steneck et R. T. Paine**

Mesophyllum vancouveriense (Foslie) R. S. Steneck et R. T. Paine 1986: 233.

Basionym: Lithophyllum vancouveriense Foslie 1906b: 21 (repr. 5).

Heterotypic Synonym: Lithothamnion phymatodeum Foslie f. *aquilonium* Foslie 1907a: 4, "*aquilonia*"; type locality: Puget Sound, Fort Casey, Whidbey Island, Washington, USA; holotype: in TRH (C18-3350), including two slides (1447 and 1448), "Amerika Algae of Puget Sound

No 652 on holdfast of *Laminaria*, Fort Casey, Whidbey Island, Wash. 190I Setchell and Gardner Monograph pI. 4, fig. 12 Lithoph. Phymatodeum f. aquilonia prep. 1447-48," 18 June 1901, coll. N. L. Gardner; illustrated in Athanasiadis et al. (2004: figs. 29–32, synonym).

Type Locality: Port Renfrew (Port San Juan), Vancouver Island, Canada.

Lectotype: In TRH (A3-153, *pro parte*, June–July 1901, coll. K. Yendo), designated and illustrated by Athanasiadis et al. (2004: 133, fig. 20B, 26–28).

Syntype: In UC (397503), Steneck and Paine (1986: figs. 27, 29, 31, "lectotype").

Habitat and Distribution: The species grows in the littoral zone mainly on rock, but also on *Laminaria* holdfasts, coralline algae, and limpets. It is recorded from the Strait of Juan de Fuca, Tatoosh Island, Washington State, USA, to Hedley Island, British Columbia, Canada. Its southern distribution is probably more extended. The northernmost collection is at Hedley Island from Queen Charlotte Strait.

Comments: The original material in TRH, designated as the lectotype by Mason (1953: 341) and considered by her to belong to *Lithophyllum whidbeyense* Foslie, was found to be a heterogeneous collection comprising at least seven specimens belonging to at least two different taxa, and restriction was proposed (Athanasiadis et al. 2004: 133, fig. 20B). The new lectotype agreed with parts of Foslie's protologue (i.e., length of hypothallial cells and presence of a coaxial hypothallium) and later accounts of the species (e.g., Steneck and Paine 1986). This is undoubtedly the commonest saxicolous species in the region and was extensively studied by R. T. Paine, whose collections made a significant part in the study of Athanasiadis et al. (2004), with materials presently deposited in GB. *Mesophyllum vancouveriense* and *M. crassiusculum* are the only members of *Mesophyllum* that develop prominent erect perithallial protuberances, possibly as a reaction to avoid grazing by limpets and other marine animals or competitive contact with another crust (Robert T. Paine, Department of Zoology, University of Washington, Seattle, Wash. [now deceased], personal communication). Steneck and Paine (1986) reported a seasonal presence of tetrasporangial and gametangial thalli, the former occurring in winter and the latter occurring in summer.

***Macroblastum* Athanas. et D. L. Ballant. gen. nov.**

Macroblastum Athanas. et D. L. Ballant. gen. nov. (type: *M. dendrospermum*).

Diagnosis: New genus of Mesophyllaceae, belonging to the tribe Melyvonneeae of the subfamily Mesophylloideae and akin to *Mesophyllum* and *Melyvonnea*, differing from both in possessing branched (dendroid) spermatangia (in addition to simple ones) and further differing from *Mesophyllum* in being monoecious and possessing spheroid carposporangial chambers lacking a pedestal and from *Melyvonnea* in having pore cells of uniform length lining canals of multiporate conceptacles.

Etymology: The generic name is a compound word, after the neuter substantive μακρος (length) and the masculine substantive βλαστος (shoot), latinized with neuter gender.

Comments: The common presence of dendroid spermatangia in *Macroblastum* sets this genus apart from any other member of the tribe Melyvonneeae, in which only rare occurrence of this character was previously reported in *Phragmope*. Dendroid spermatangia also occur in certain members of Amphithallieae and Magnephyceae, manifesting their plesiomorphic trait, which is the standard condition in members of the basal Lithothamnionaceae and Sporolithales (Figure 1a). The putative nature of *Macroblastum* as a hybrid between species of *Melyvonnea* and *Mesophyllum* has been discussed (see "Hybrids"). A comparison between *Protomesophyllum* (Protomesophylloideae), *Macroblastum*, and other genera of Melyvonneeae is given in Table 3.

***Macroblastum dendrospermum* Athanas. et D. L. Ballant. comb. et nom. nov.**

FIGURES 15–19

Macroblastum dendrospermum Athanas. et D. L. Ballant. comb. et nom. nov.

Basionym: Lithothamnion macroblastum Foslie 1897: 16.

Homotypic Synonym: *Mesophyllum macroblastum* (Foslie) W. H. Adey 1970: 25.

Misapplied Name: *Phymatolithon* sp. sensu Athanasiadis 1987: 37 [non *Phymatolithon* Foslie].

Type Locality: Sublittoral, 30–80 m depth, Gulf of Naples, Italy.

Holotype: In TRH (B16-2435), Printz (1929: pl. 6, fig. 1), Adey and Lebednik 1967, "type material," "§ com.Zool., St., Italy, Gulf of Naples, 30-80m., LM6(1) [slide] 191"), Woelkerling (1993a: 140, "About 50% of the holotype . . . no longer present"), Woelkerling et al. (2005: 324–325, "holotype").

Etymology: The epithet is a compound word, after the neuter substantives δενδρον (tree) and σπερμα (seed), latinized with neuter gender and used in apposition, referring to the branched (dendroid) spermatangia.

Habitat and Distribution: This is a mainly epilithic species, growing between the upper sublittoral (in caves and crevices protected from direct sunlight and wave exposure) and at least 90 m depth, "mélange avec *L. stictaeforme*" or in the coralligène (Cabioch and Mendoza 2003: 259) or even epizoically (Kaleb et al. 2011: table 1). Only thalli on rocks and pebbles from the upper sublittoral (to 20 m depth) have been collected in the North Aegean Sea. *Macroblastum dendrospermum* is a Mediterranean endemic previously recorded as *Mesophyllum* (*Lithothamnion*) *macroblastum* from the Spanish, French, and Italian coasts of the western Mediterranean, Tyrrhenian, and Adriatic Seas (Hamel and Lemoine 1953; Cabioch and Mendoza 2003; Kaleb et al. 2011; Peña et al. 2015: fig. 12).

Material Examined: Tyrrhenian Sea: Gulf of Naples, holotype (TRH, B16-2435) as described above and below; La

Scarpa, Pianosa Island, October 2006, 30 m depth, coll. D. Racano (PC0116488, PC0116489).

North Adriatic Sea: Trezza San Pietro, April 2009, 15 m depth, coll. D. Poloniato (PC0116485, PC0116486); August 2008, 15 m depth, coll. D. Poloniato (PC0116487).

North Aegean Sea: Sithonia: Pigeon Cave: 1 July 1984, shaded site, 0.5 m depth, empty multiporate conceptacles, coll. Athanas. (herb. Athanas. SC.01.07.84, "*Phymatolithon* sp."); 20 June 2002, shaded site, 0.5 m depth, bisporophytes, coll. Athanas. (herb. Athanas. SC.20.06.02-Sith.18); 31 August 2003, shaded site, 1–2 m depth, gametophytes, coll. Athanas. (herb. Athanas. SC.31.08.08-Sith.44); 27 June 2012, shaded site, 1–2 m depth, males and females, coll. Athanas. (herb. Athanas. SC.27.06.12-Sith.50). Porto Cufo: 5 June 2005, 0.5 m depth, shaded site, bisporophytes, coll. Athanas. (herb. Athanas. PC.05.06.05-Sith.25; growing with *M. macedonis*); 23 June 2005, 0.5 m depth, bisporophytes, coll. Athanas. (herb. Athanas. PC.23.06.05-Sith.25); 26 June 2017, gametophytes, 2 m depth, on pebble, coll. Athanas. (herb. Athanas. PC.26.06.17-Sith.79). Kavourotrypes: 24 June 2005, 15–20 m depth, in crevices, bisporophytes, coll. Athanas. (herb. Athanas. KA.24.06.05-Sith.76).

Observations on the Protologue and the Holotype: Foslie (1897: 16–17) originally described

> [a] solitary specimen . . . from the Gulf of Naples [communicated by] Prof.Dohrn. . . . [It] forms a somewhat irregular crust 4–5 cm in diameter and about a cm thick . . . fastened to some hard object. New crusts are developed upon the primary almost in the same manner as in [*Mesophyllum*] *Philippii*, and in all being nearly related to the latter. However, it is provided with numerous, in part confluent wart-like excrescences frequently 2 mm in diameter and, therefore, it in habit rather reminds one of *L. papillosum* [*Goniolithon papillosum*] seen from above. The [roof of] conceptacles . . . [is] deeply depressed . . . nearly crater-shaped, 550–700 µ in diameter . . . [and] intersected with about 20 muciferous canals. Other conceptacles supposed to be those of antheridia are conical . . . about 400 µ in diameter.

The holotype studied here comprises three pieces, the largest being ~2.8 cm in extent (Figure 15a). The original collection also includes (1) a Foslie slide annotated "*L. macroblastum*," "191," "Neapel"; (2) a slide prepared from the "type" with the annotation "see Mendoza and Cabioch"; and (3) four paper sheets, the first annotated "*L. macr.*" with an illustration, the second annotated "*L. macroblastum*," "Prep.191, " "Neapel, " "Perith. 11x9, 11x7, 14x9, 9x9, 9x7, 14x7, 14x11, 11x11 HypothSI.," the third annotated "Sp. Konc. 500-800 µ Skorpens Tykkh . . . 300-600 µ" (thallus thickness), and the fourth annotated by Printz(?) "Pröve sendt Mme Lemoine jan.1936."

Rimed multiporate conceptacles are spread over the surface of the holotype, together with a single patch of a few uniporate (male) ones (Figure 15b). The thallus is dorsiventrally organized with a predominantly coaxial, arching hypothallium 100–250 µm thick, producing an ascending and partly stratified perithallium at least 500 µm thick (Cabioch and Mendoza 2003: fig. 6C; Figure 15c). Descending filaments end in wedge-shaped cells of varying length (Figure 15d). Hypothallial cells are 12–20 × 8–10 µm (L × B), and perithallial cells are 3–15 × 4–8 µm (L × B). Subepithallial cells are elongate (~10 µm long) and support single epithallial cells 1–2 × 6–8 µm (L × B).

Chambers of multiporate conceptacles are 370–390 × 230–260 µm (D × H; n: 2) and are either empty or provided with bisporangia, 180–220 × 25–80 µm (L × B; n: 4; Figure 15f,g). The sunken pore plate is 180–280 µm in diameter. The roof is 40–50 µm thick, composed of 7- to 8-celled filaments. Pore cells lining the canals are thinner–wider (B × W) and apparently of similar length to contiguous roof cells (Figure 15h,i). Cabioch and Mendoza (2003: fig. 6F) reported the presence of 8 or 9 rosette cells surrounding canals of multiporate roofs.

Several uniporate conceptacles occur in a patch, ~3 mm in extent (Figure 15b). A conceptacle was ~500 µm in external diameter, but the chamber was empty (Figure 15e). However, its size and shape fit male conceptacles observed in Aegean thalli of the species.

Species Description Based on Aegean Thalli: Specimens have been collected over a period of more than 35 years, originally being identified as "*Phymatolithon* sp." (Athanasiadis 1987). Thalli grow on pebbles and larger cobbles in caves and crevices in the upper sublittoral (0.5–2 m depth) and deeper (to at least 20 m).

They are protected from direct sunlight and easily distinguished by a bright red color and glancing surface. They adhere closely to the substratum, with occasional production of leafy (unattached) margins and erect (unbranched) protuberances (Figure 16a,d). A predominantly coaxial hypothallium was observed in all specimens (Figure 17a,b). Juvenile thalli with smooth surface can be confused with *Mesophyllum expansum*, which exhibits about twice as long hypothallial cells (Figure 17c,d). Ascending perithallial filaments terminate in elongate subepithallial cells (to 8 µm long), which support flattened (to rectangular) epithallial cells (Figure 17e–g). Descending hypothallial filaments end in wedge-shaped cells (Figure 17h).

Gametophytes are monoecious (Figure 18a). Male conceptacles are ~500 µm in external diameter, with chambers 215–275 × 80–100 µm (D × H; Figure 18b). Dendroid (branched) spermatangial structures occur on the roof and the floor, between simple spermatangia with lunate SMCs (Figure 18c–e).

Carposporangial conceptacles, 1,000–1,100 µm in external diameter (Figure 18a), are provided with spheroid chambers 300–440 × 150–240 µm (D × H; n: 6) and an ostiole ~220 × 100 µm (L × B; Figure 19f). Carpogonial thalli were not seen, but judging from postfertilization stages, the carpogonial branch should be 3-celled (composed of a carpogonium, the hypogynous, and the supporting cell) and attached to a basal cell (that remains connected to the vegetative floor; Figure 19a-c). Following presumed fertilization and zygote transfer (not seen), a fusion cell composed of 2 or 3 cells develops at the level of the supporting cells (Figure 19c).

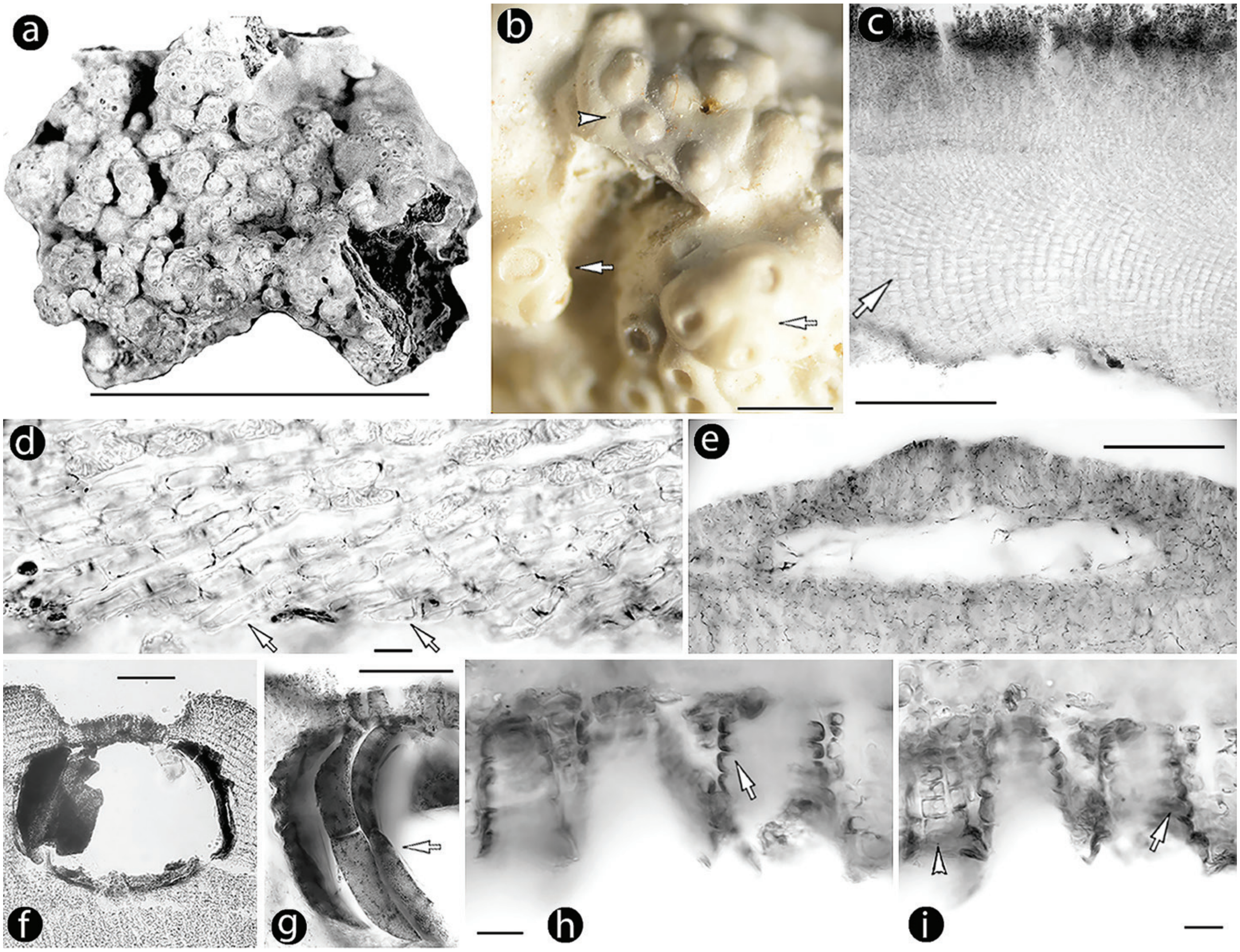

FIGURE 15. *Macroblastum dendrospermum*: holotype of *Lithothamnion macroblastum* in TRH (B16-2435). (**a**) The largest fragment in TRH. Scale bar: 2 cm. (**b**) Magnification of the surface showing several rimmed multiporate (arrows) and a few male (arrowhead) conceptacles. Scale bar: 1 mm. (**c**) Section showing a distinctively coaxial hypothallium (arrow). Scale bar: 100 µm. (**d**) Descending hypothallial filaments ending in wedge-shaped cells (arrows). Scale bar: 10 µm. (**e**) Section of a male conceptacle lacking content. Scale bar: 100 µm. (**f, g**) Sections through multiporate conceptacles with bisporangia (arrow). Scale bars: 100 µm. (**h, i**) Sections through pore canals showing thinner (arrows) and wider (arrowhead) pore cells. Scale bars: 10 µm.

Gonimoblasts radiate, receiving the cytoplasm of contiguous hypogynous cells (Figure 19a,b) and producing lateral carposporangia from the periphery of the fertile zone (Figure 19d,f). Gonimoblasts may become elevated because of a "pedestal" formed by vegetative cells below the gonimoblast filaments (Figure 19d,e). This elevation does not seem to involve decalcification of the floor (as in *Mesophyllum* spp.; see Athanasiadis et al. 2004: 139, 145, 163). Older conceptacles become embedded in the thallus, being overgrown by peripheral filaments (Figure 19g).

Multiporate conceptacles are ± immersed with chambers 320–450 × 210–350 µm (D × H). Most chambers were empty, but a few bisporangia 130–145 × 50–70 µm (L × B) were recorded. Tetrasporangia were not observed.

Comments: As late as 1953, this species was referred to the genus *Lithothamnion* because the hypothallium was not examined (Hamel and Lemoine 1953: 95, fig. 59, "Hypothalle non étudie"). Adey (1970: 25) transferred the species to *Mesophyllum* without comment, having previously examined the holotype in TRH (Printz 1929: pl. 6, fig. 1; Adey and Lebednik 1967: 66). Since then, the holotype was reexamined by Woelkerling (1993a: 140), Woelkerling and Harvey (1993: 591), and Cabioch and Mendoza (1998: 217; 2003: 265) and in the present

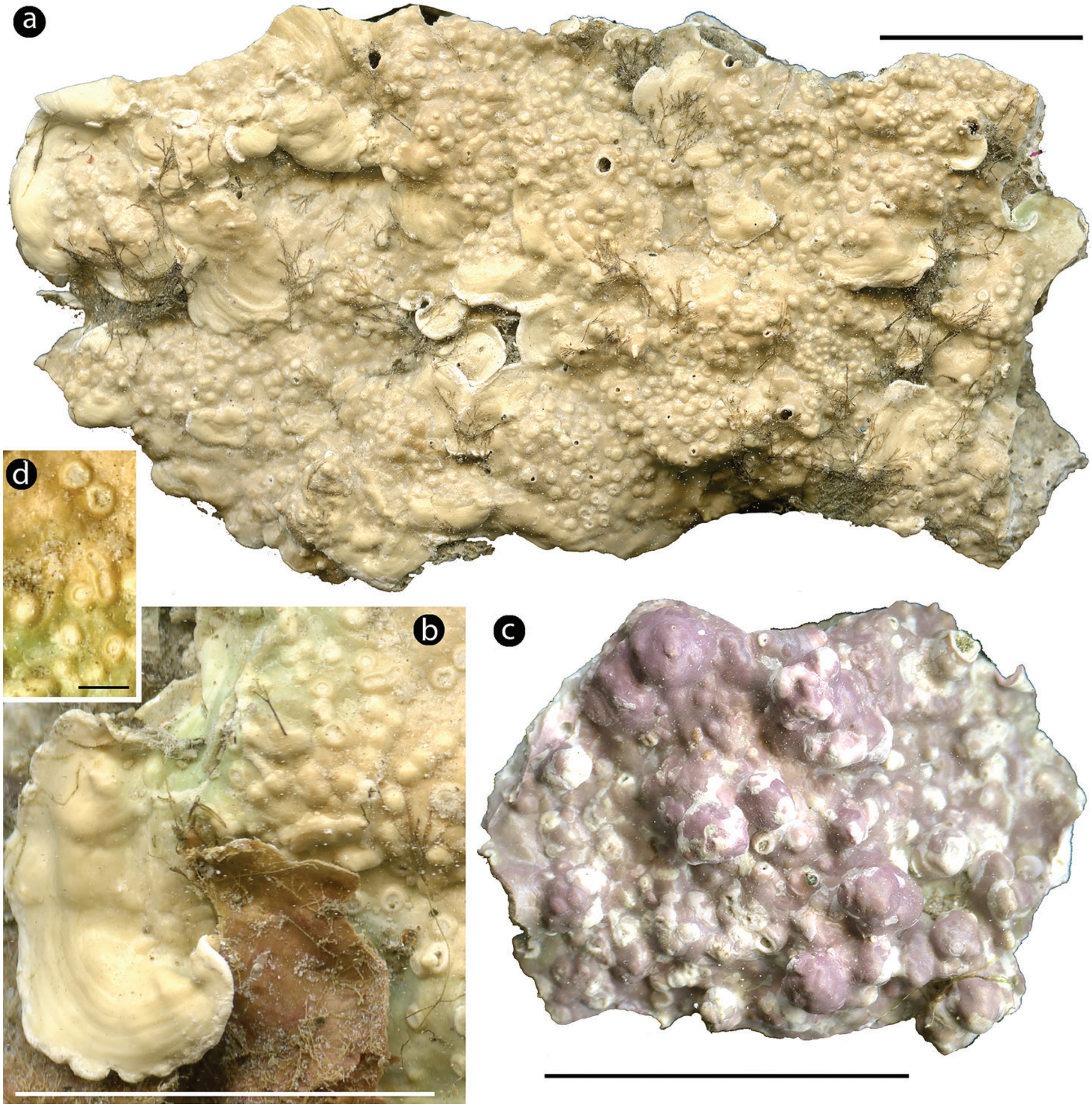

FIGURE 16. *Macroblastum dendrospermum*: Aegean thalli with lamellate outgrowths (as in (b)) or erect protuberances (as in (c)) and rimmed multiporate conceptacles (as in (d)). (**a, b, d**) Sith.25. (**c**) Sith.73. Scale bars: 1 cm in (a)–(c), 1 mm in (d).

study. Woelkerling and Lamy (1998: 352) noted the presence of isotypes (fragments of the holotype) in PC.

Woelkerling and Harvey (1993: 591) reported the species in southern Australian after concluding that "all morphological and anatomical features evident in the holotype are also evident in southern Australian plants." However, the present study shows that the holotype differs in possessing bisporangia (not known in the Australian counterpart), a predominantly coaxial hypothallium (said to be coaxial to noncoaxial in Australian thalli), thinner–wider pore cells (rhomboid in Australian thalli), and

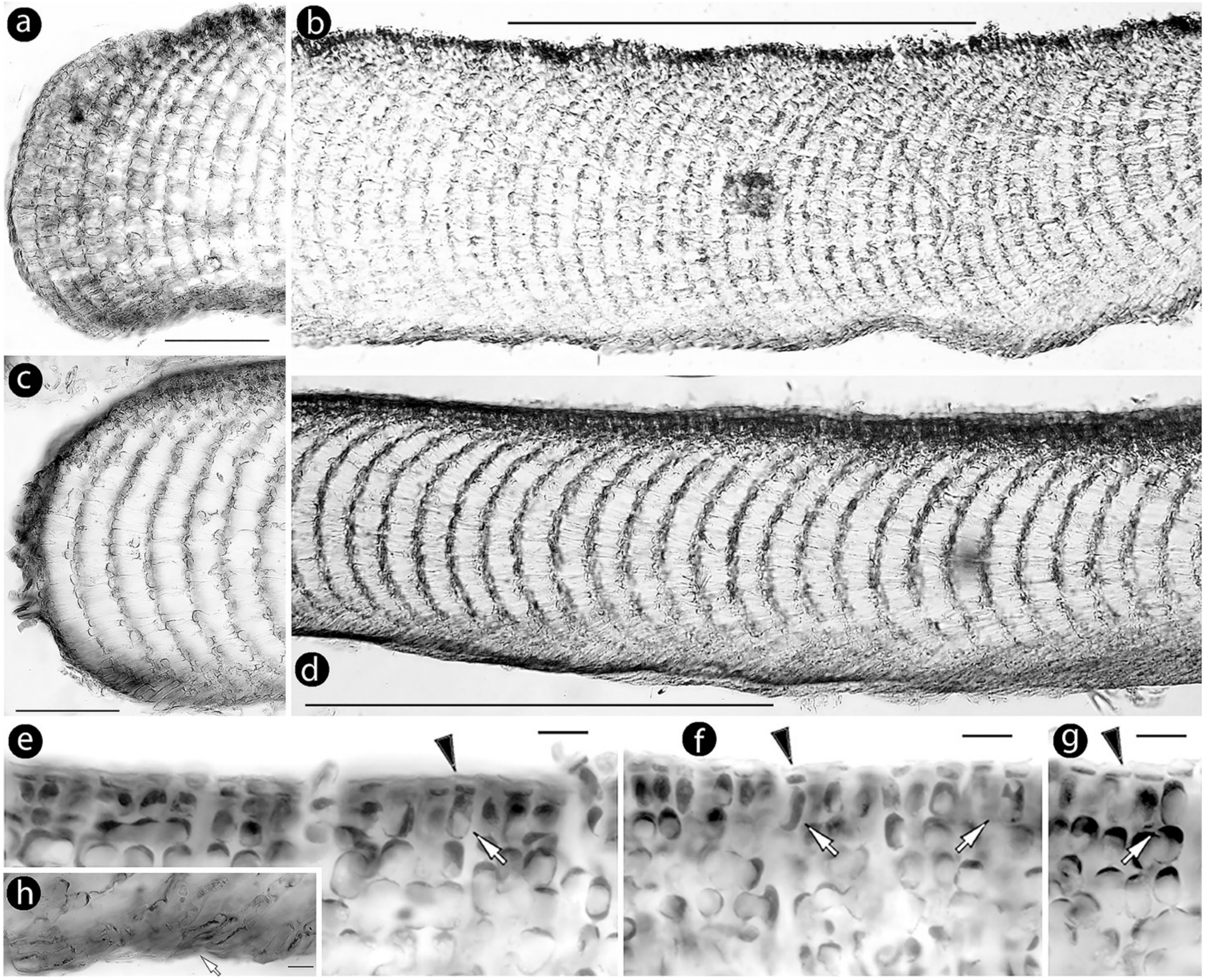

FIGURE 17. (**a, b, e–h**) *Macroblastum dendrospermum* and (**c, d**) *Mesophyllum expansum*: vegetative structures. (a–d) Sections at the margin in the two taxa, showing a coaxial hypothallium in both with about twice as long cells in *Mesophyllum expansum* (Sith.15 in (a) and (b); isoneotype in herb.Athanas. in (c) and (d)). Scale bars: 100 µm in (a) and (c), 500 µm in (b) and (d). (e–g) Sections at the surface showing flattened (arrowheads) epithallial cells and elongate subepithallial cells (arrows; Sith.50). Scale bars: 10 µm. (h) Section at the base showing descending hypothallial cells ending in wedge-shaped cells (arrow; Sith.73). Scale bar: 10 µm).

larger chambers of multiporate conceptacles (up to 390 µm in diameter vs. 270 µm in Australian thalli). More recently, Kaleb et al. (2011: fig. 14) showed the presence of rare trichocytes (absent in Australian thalli) and spheroid carposporangial chambers in Mediterranean thalli (elongate in Australian thalli). Consequently, taking into account the present information from the Aegean gametophytes, two distinct genera are established: *Macroblastum* for the Mediterranean species and *Protomesophyllum* for its southern Australian counterpart. They resolved as two remotely related taxa in the present phylogenetic analysis, requiring a position in two separate subfamilies (Mesophylloideae vs. Protomesophylloideae). Characters distinguishing *Protomesophyllum* from *Macroblastum* and other genera of Melyvonneeae are listed in Table 3.

Tetrasporangia have been reported in Tyrrhenian and Trieste specimens, collected in October or April (Kaleb et al. 2011: 225–226, table 2), and the empty chambers in the Aegean thalli suggest a similar fertility period (as all Aegean collections were

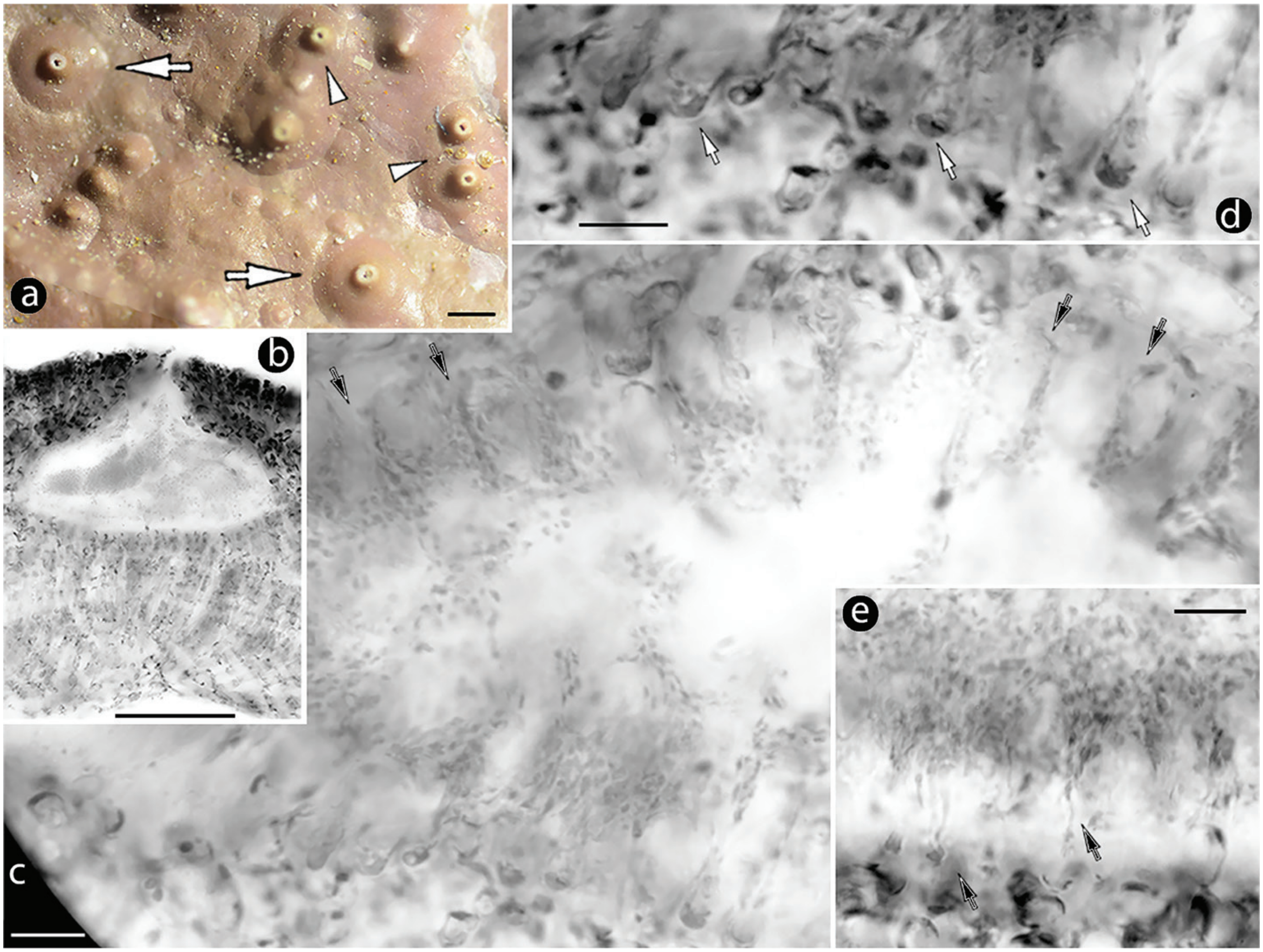

FIGURE 18. *Macroblastum dendrospermum*: gametangial conceptacles and male structures. (**a**) Surface view of male (arrowheads) and carposporangial (arrows) conceptacles (Sith.44). Scale bar: 1 mm. (**b**) Section of a male conceptacle (Sith.50). Scale bar: 100 µm. (**c–e**) Sections of embedded male chambers showing simple spermatangial structures with lunate SMCs on the floor (white arrows) and branched (dendroid) spermatangial structures on the roof and the floor (black arrows; Sith.50 in (c) and (d); Sith.79 in (e)). Scale bars: 10 µm in (c) and (d), 5 µm in (e).

made during summer). In the western Mediterranean basin, *Macroblastum dendrospermum* co-occurs with species of *Mesophyllum* (i.e., *M. philippii* and *M. expansum*) and possibly the rhodolith-forming *Mesophyllum sphaericum* (Peña et al. 2015: fig. 15) that most likely belongs to the genus *Melyvonnea* (Athanasiadis and Ballantine 2014: fig. 1). "*Mesophyllum macroblastum*" has also been reported from the Cagarras Archipelago (~5 km off the coast of Rio de Janeiro; Bahia et al. 2014: figs. 6, 7, 9), but the provided illustrations show nondifferentiated pore cells lining canals of multiporate roofs, and no reference to a coaxial hypothallium is made. In these aspects, the Brazilian thalli come closer to *Protomesophyllum* from southern Australia, New Zealand, and Chatham. It should be added that on the basis of a comparison of *psb*A sequences, Peña et al. (2015: fig. 11) showed that isolates of *Macroblastum* are distantly related to *Protomesophyllum*. See also comments under the latter genus.

Melyvonnea Athanas. et D. L. Ballant.

Melyvonnea Athanasiadis et D. L. Ballantine 2014: 391, figs. 3–108 (type: *M. canariensis*).

Comments: A diagnostic feature of this genus is the structure of the pore cells in pore filaments lining canals of multiporate conceptacles. Such filaments are composed of elongate basal cells followed by 2 to 4 smaller cells that terminate below

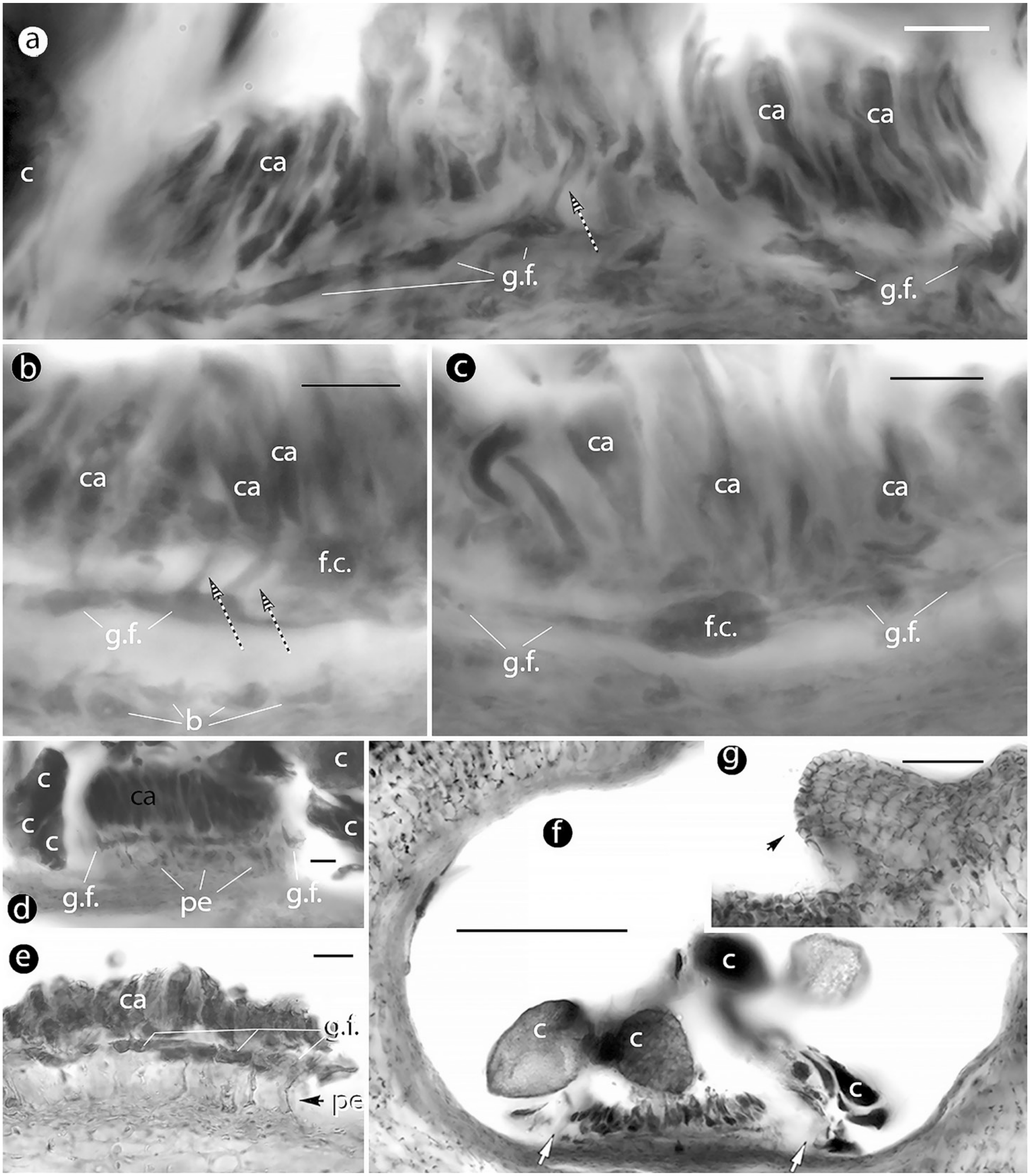
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FIGURE 19. (*Opposite*) *Macroblastum dendrospermum*: postfertilization stages. (**a–c**) Sections of carposporangial chambers. Note the fusion cell, the gonimoblast filaments, the hypogynous cell remains (dashed arrows) attached to gonimoblast filaments, the intact basal cells on the vegetative floor, and the remains of carpogonia (Sith.50). Scale bars: 10 µm. (**d, e**) Development of a vegetative pedestal from the floor to support remains of gonimoblast filaments and carpogonia, with peripheral carposporangia (Sith.50). Scale bars: 10 µm. (**f**) Section of a carposporangial chamber with peripheral production of carposporangia (arrows) on a flattened floor. Note the spheroid shape of the chamber that lacks pedestal (Sith.50). Scale bar: 100 µm. (**g**) Young thallus overgrowing an older conceptacle (arrow). Note the coaxial hypothallial growth (Sith.25). Scale bars: 100 µm. Abbreviations: b, basal cell; c, carposporangium; ca, carpogonium; f.c., fusion cell; g.f., gonimoblast filament; pe, pedestal; s, supporting cell.

the conceptacle surface (Jesionek et al. 2016: fig. 9F; Athanasiadis 2022: fig. 1i). Despite the limited structural diversity in members of the genus, the wide distribution in the tropics, subtropics, and even temperate regions (Japan and Pacific Russia; Masaki 1968; Perestenko 1994, as *Mesophyllum*) is strong evidence that *Melyvonnea* must predate both the formation of the Panamanian land bridge (3.1 to 5 MYA; see Bornmalm 1992) and the closure of the Mediterranean passage to the Indo-Pacific (about 20 MYA; see Scotese and McKerrow 1990; Scotese 1997). No attached species are presently known in the Mediterranean, but fossil records from Algeria and Libya suggest a putative occurrence in past geological times (see *Mesophyllum curtum* Me. Lemoine 1939: 92, pl. II, Tortonian, 7–10 MYA; *Mesophyllum* sp., Wray 1977: 61, fig. 52, Paleocene). Presently, *Melyvonnea* co-occurs with both *Mesophyllum* (in the Canaries and Caribbean) and *Thallis* (in South Africa). *Melyvonnea* has been associated with *Perithallis-Thallis* and *Printziana-Sunesonia* from South Africa, Australia, New Zealand, and Chatham, sharing with these genera the sunken rosette cells and pore filaments composed of fewer cells than contiguous roof filaments. The hypothesis that the elongate basal cells in *Melyvonnea* are the result of relocation, following the loss of basally branched pore cells was postulated (Athanasiadis 2022: fig. 18e; see Figure 25u). This was supported by the present phylogenetic analysis, assuming (and excluding) *Macroblastum* as a hybrid and treating three characters (30, 32, 35) of the structure of pore filaments in *Melyvonnea* as uncertain (see "Phylogenetic Relationships in the Mesophyllaceae"; Figure 6d). Carpogonial thalli in the genus remain undescribed, and postfertilization stages are poorly documented (diagrammatically) by Keats and Chamberlain (1994: figs. 24, 25), who reported a "discontinuous" fusion cell in thalli from Natal (South Africa).

The recently described *Mesophyllum sphaericum* (Peña et al. 2011: figs. 1, 2) from Benencia Island, Ria de Arousa, Galicia (Atlantic Spain) and also recorded from Mediterranean Spain (between 3 and 50 m depth; Peña et al. 2105) is a putative member of the genus *Melyvonnea*. This very species was clustered with another rhodolith from Puerto Rico, namely, *Melyvonnea aemulans* (see species account). Therefore, a "pair-species" relationship between a rhodolith and an attached form, co-occuring in the same region, can be suggested (i.e., *Mesophyllum sphaericum–Melyvonnea canariensis* and *Melyvonnea aemulans–Melyvonnea erubescens*). Still, *M. sphaericum* merits further attention, as both males and data for the hypothallium (primary or secondary) are unknown.

Melyvonnea aemulans (Foslie et M. Howe) Athanas. et D. L. Ballant.

Melyvonnea aemulans (Foslie et M. Howe) Athanas. et D. L. Ballant. 2014: 394, figs. 3–18.

Basionym: Lithothamnion fruticulosum var. *aemulans* Foslie et M. Howe 1906: 130.

Homotypic Synonyms: Lithothamnion aemulans (Foslie et M. Howe) Foslie 1908a: 17. Foslie 1908b: 9.

Mesophyllum aemulans (Foslie et M. Howe) W. H. Adey 1970: 22.

Heterotypic Synonym: ?*Mesophyllum sphaericum* Peña et al. in Peña et al. 2011: 914–917, figs. 1, 2; type locality: sublittoral, 3 m depth, Balencia Island, Ría de Arousa, Galicia, Spain; holotype: in SANT, algae 21804; isotypes: in SANT, algae 21805–21828; no specimen available on loan (27 January 2007 and February–March 2022).

Type Locality: Upper sublittoral zone, San Juan, Puerto Rico.

Holotype: In TRH (C16-3248), Printz (1929: pl. 12, fig. 21), Adey and Lebednik (1967: 80, "type material," "§ Howe, Puerto Rico, San Juan, 28.5.1903, NYBG 2237, LM12(21) [slides] 1631.2237"), Adey (1970: 22, "holotype"), Woelkerling (1993a: 19, "Holotype: NY . . . TRH"), Woelkerling et al. (2005: 453, "Holotype: divided between NY . . . and TRH"), Athanasiadis and Ballantine (2014: fig. 3B,K).

Isotype: In NY (Howe no. 2237); not available on loan (5 March 2007).

Habitat and Distribution: This is a rhodolith-forming species, lying free just below the low-tide mark. It is known only from the protologue and the later study of the holotype by Athanasiadis and Ballantine (2014).

Comments: The holotype of *M. aemulans* in TRH is a part of the original specimen illustrated by Foslie and Howe (1906: pl. 81, figs. 1, 2) before and after its fragmentation into two pieces. The species was included in the flora of the Bahamas (Howe 1920: 584), but reexamination of the relevant collection (in NY) has shown it belongs to a mastophoroid alga (Athanasiadis and Ballantine 2014: Appendix III). No further data were cited by Printz (1929: 57) or Taylor (1967: 383), who simply repeated the protologue. Adey (1970: 22) mentioned that "the sporangial plugs . . . appear to stain with phosphotungstic hematoxylin though not as darkly as in *Lithothamnium.*" No later records of the species have been reported. An attempt was made to find the species off La Parguera (Puerto Rico) during a collection of rhodoliths in April and May 2009 and also by examining collections at MSM without positive results, suggesting that the species is not commonly distributed on the coast of Puerto Rico (Athanasiadis and Ballantine 2014).

Mesophyllum sphaericum (Peña and Bárbara 2008: fig. 8A–D, as *Mesophyllum* sp.; Peña et al. 2011: figs. 1, 2) is another rhodolith, reaching 10 cm in diameter and growing down to 50 m mixed with *Phymatolithon calcareum*. It was originally described from bi- or tetrasporangial and carposporangial thalli from Benencia Island (Atlantic Spain), growing between 1 and 5 m depth. Although males and data for the hypothallium are unknown, *M. sphaericum* shares most of its other characters with *Melyvonnea aemulans*, particularly the structure of canals of multiporate roofs and the lack of trichocytes, whereas carposporangial chambers are typically spheroid as in other species of *Melyvonnea* (Peña and Bárbara 2008: fig. 8D; Peña et al. 2011: fig. 2c). *Mesophyllum sphaericum* and *Melyvonnea aemulans* clustered together in a phylogenetic analysis, but in the absence of a full comparison and the lack of information about essential data for *M. sphaericum*, its status is pending further studies (Athanasiadis and Ballantine 2014: fig. 1). More recently, *M. sphaericum* was reported from Mediterranean Spain as "unattached plants forming maerl and rhodoliths and also . . . as epilithic crusts at 20-50 m depth" (Peña et al. 2015: 28, fig. 15). A request to borrow authentic and other material of this species for examination from SANT was, however, denied.

Melyvonnea canariensis **(Foslie) Athanas. et D. L. Ballant.**

Melyvonnea canariensis (Foslie) Athanas. et D. L. Ballant. 2014: 399, figs. 19–61.

Basionym: Lithothamnion canariense Foslie 1906a: 17–18 (repr. 1–2).

Homotypic Synonym: Mesophyllum canariense (Foslie) Me. Lemoine 1928: 252.

Heterotypic Synonyms: ?*Mesophyllum canariense* var. *difforme* Me. Lemoine 1929: 33–35, "*difformis*," pl. 2, fig. 2; type locality: Puerto Orotava (Tenerife); holotype: C (unnumbered, Børgesen no. 3217, "*Mesophyllum canariense* . . . var. *difformis* nov. var.," 27 January 1921, coll. F. Børgesen).

?*Mesophyllum canariense* var. *fasciatum* Me. Lemoine 1929: 32–33, "*fasciata*," pl. 2, fig. 4; type locality: Playa de la Canteras (Gran Canaria); holotype: C (unnumbered, Børgesen no. 3777, "*Mesophyllum canariense* . . . var. *fasciata* nov. var. Gran Canaria Playa de las Canteras," 22 March 1921, coll. F. Børgesen).

Type Locality: Porto de la Cruz (Puerto Orotava), Tenerife, Canary Islands.

Lectotype: In TRH (C15-3210, *pro parte*, includes two Foslie slides, 1056 and 1057), Printz (1929: pl. 14, fig. 7), Reyes and Afonso-Carrillo (1993: fig. 1B), designated by Athanasiadis and Ballantine (2014: 399, fig. 22C).

Syntypes: In TRH (C15-3210, *pro parte*, includes Foslie slide 1012), Printz (1929: pl. 14, fig. 8), Athanasiadis and Ballantine (2014: fig. 22B); in TRH (C15-3210, *pro parte*), Reyes and Afonso-Carrillo (1993: fig. 1C), Athanasiadis and Ballantine (2014: fig. 22A); in PC (see Woelkerling and Lamy 1998: 334); in US (FT-139), Peña et al. (2011: 914, fig. 4l, "isotype").

Habitat and Distribution: Thalli grow epilithically in the littoral and sublittoral zone to at least 15 m depth (Sangil et al. 2005), protected from waves (annotations on TFC5253, TFC5631, TFC13118). According to Lemoine (1929: 31–35), the species may grow together with other corallines and *Vermetus* polychaete tubes and may be abundant in Gran Canaria (type locality of var. *fasciatum*). The species is endemic to the Canary Islands, being recorded from Tenerife, Gomera, Gran Canaria, and El Hierro.

Comments: The original material in TRH was reexamined by Adey and Lebednik (1967: 79), Reyes and Afonso-Carrillo (1993), Peña et al. (2011: 914), and Athanasiadis and Ballantine (2014). Athanasiadis and Ballantine showed that it was based on several collections made at Porto de la Cruz (previously known as Puerto Orotava), and a lectotype was selected. Moreover, in the absence of population studies, the infraspecific variation was maintained (i.e., var. *canariensis*, var. *fasciatum*, and var. *difforme*). The species was first collected at Puerto Orotava by Sauvageau in 1904 and was later reported from the nearby Island of Gomera (May 1912; the material identified by F. Heydrich), recollected by Børgesen at the type locality and Gran Canaria in 1921 (Lemoine 1929), erroneously reported from the Gulf of Guinea (Steentoft 1967: 130; see Athanasiadis and Ballantine 2014: Appendix III, TRH A4-195), reported from SE Japan (Masaki 1968: 10, pl. 4, pl. 17, figs. 1–3, as *Lithothamnion canariensis*; the material was not reexamined), and also erroneously reported from Madeira (Levring 1974: 64; see Athanasiadis and Ballantine 2014: Appendix III). Later records were made from Tenerife (Reyes and Afonso-Carrillo 1993), El Hierro, and Las Palmas (Afonso-Carrillo et al. 1984; Rojas-González and Afonso-Carrillo 2002; Sangil et al. 2005: 95, 15 m depth on rocks). The studies hitherto indicate that *Melyvonnea canariensis* is a rare endemic element. Recent attempts to find the species at Tenerife by Peña et al. (2011) and in February 2009 were fruitless (Athanasiadis and Ballantine 2014). Still, an nSSU sequence named "*Mesophyllum erubescens*" from Tenerife (undated and with unknown collector) found its way to GenBank and was used in the study of Hernández-Kantún et al. (2015: 3, table 1, figs. 1, 3). This very sequence clustered with isolates referred to *Mesophyllum erubescens* from Japan and also with the western Mediterranean–NE Atlantic *Mesophyllum sphaericum*, which, according to Athanasiadis and Ballantine (2014: 388, fig. 1), belongs to the genus *Melyvonnea*.

Melyvonnea erubescens (Foslie) Athanas. et D. L. Ballant.

Melyvonnea erubescens (Foslie) Athanas. et D. L. Ballant. (2014: 405, figs. 62–106)

Basionym: Lithothamnion erubescens Foslie (1900a: 9–10).

Homotypic Synonyms: Lithothamnion erubescens f. *americanum* Foslie 1901c: 4, "*americana*," nom. nov. illeg. [*nomen pro L. erubescens* f. *erubescens*].

Mesophyllum erubescens (Foslie) Me. Lemoine 1928: 252.

Heterotypic Synonyms: Lithothamnion erubescens f. *prostratum* Foslie 1901a: 3, "*prostrata*"; lectotype: in TRH (C15-3238, *pro parte*), 1900, coll. W. G. Farlow, XVIII, designated and illustrated by Athanasiadis and Ballantine (2014: figs. 70E, 71); type locality: Bermuda (locality unspecified).

Lithothamnion incertum Foslie 1904b: 5, stat. et nom. nov. of f. *prostratum*.

Lithothamnion incertum f. *complanatum* Foslie 1904b: 5, "*complanata*," nom. nov. illeg. [*nomen pro L. incertum* f. *incertum*].

Mesophyllum incertum (Foslie) Me. Lemoine 1928: 252.

Type Locality: Chaloup Bay, Fernando de Noronha, Brazil.

Lectotype: In TRH (C15-3212), Foslie (1904c: text fig. 15B, pl. 3, fig. 20), Printz (1929: pl. 15, fig. 16 [side view] 20 [surface view]), Adey and Lebednik (1967: 80, "type material," "§ Ridley, Lea + Ramage, Brazil, Fernando do Noronha, Chaloup Bay, SE 3(20) [slide] 340"), Adey (1970: 20, "holotype"), Woelkerling (1993a: 85, "holotype," "coll . . . Ridley, Lea Ramage, 1887"), Woelkerling et al. (2005: 454, "holotype"), Sissini et al. (2014: fig. 2, "holotype"), designated by Athanasiadis and Ballantine (2014: 405–408, fig. 62).

Syntypes: In BM? (herb. Dickie; Dickie 1874: 363, as *Lithothamnion mamillare*); in US (FT-148), Peña et al. (2011: 914, fig. 4m, "isotype").

Habitat and Distribution: Puerto Rican specimens grow just below water level to ~2 m depth, either attached to the roots of *Rhizophora mangle* L. at sheltered shady places or at exposed sunny sites attached to corals and rocks but growing in crevices protected from direct sunlight and water motion. Bermudan collections reported "just below low water mark" in sheltered places with mangrove vegetation or "in normally agitated water" (Howe 1918: 537) or attached to "the banks and on the Bermuda platform. . . . on Argus Bank at 58 m." (Frederick 1963: 65; the material was not reexamined). Data for Floridian specimens are unknown; Bird Key collections are said to be from "shallow waters" (Taylor 1928: 210; but see Athanasiadis and Ballantine 2014: Appendix III, MICH622107). A Taylor Bahamas collection (not located at MICH) was said to be from "the littoral, rocky point" (Taylor 1940: 556); Taylor (1967: 385) further specified "from rocks 3–12 dm. below low-tide line in exposed situations." Horta et al. (2011: 126) reported unattached thalli to 18 cm in diameter in a rhodolith bed (7–16 m depth) from Arvoredo Island (Santa Catarina State, Brazil).

Sissini et al. (2014: fig. 1, as *Mesophyllum*) added more sites from the Brazilian coast (to 25 m depth), as well as Veracruz (Gulf of Mexico).

The species is confirmed from Bermuda (type locality of *Mesophyllum incertum*), the Bahamas (Howe 1920), Florida, Puerto Rico, and Brazil: Fernando de Noronha (type locality), São Sebastião (Sao Paulo State; Bailey and Chapman 1998), and Arvoredo Island (Santa Catalina State; Horta et al. 2011).

Comments: It is clear from the protologue and Foslie's (1904c) later account that *Lithothamnion erubescens* was based on three specimens of *Lithothamnion mamillare* sensu Dickie (1874: 363) [non *Neogoniolithon mamillare* (Harv.) Setch. et L. R. Mason]. These specimens should be recognized as syntypes and were illustrated by Foslie (1904c: 32, text fig. 15A–C, "the type specimens," pl. 3, fig. 20 [text fig. 15 B]) and Printz (1929: pl. 15, figs. 15, 16 [20], 21). Adey and Lebednik (1967: 80) did not mention the number of specimens in TRH that they selected as "type material," and later, Adey (1970: 23) recognized the collection as "holotype," mentioning that "[a] *Neogoniolithon* species is also present in the type material." Woelkerling (1993a: 85–86) stated that "the TRH specimens collectively constitute the holotype element." Later, however, Woelkerling et al. (2005: 446) specified that the "holotype" collection in TRH (C15-3212) included "one specimen . . . depicted in a photo marked Siboga Exp. LXI text fig. 15 with two other specimens not in TRH." Hence, the remaining single specimen in TRH material was designated as the lectotype by Athanasiadis and Ballantine (2014: 406–408, fig. 62). Whether the other two (syntype) specimens exist in Dickie's herbarium in BM is unknown.

Melyvonnea erubescens accommodates the tropical and subtropical western Atlantic populations of a species previously recorded from widely disjunct regions, including South Africa (Natal), Guam, Indonesia, French Polynesia, Sakhalin, Japan, Australia, and New Zealand (see Athanasiadis and Ballantine 2014: 392; Sissini et al. 2014). Specimens from Natal (Keats and Chamberlain 1994: figs. 21–23, as *Mesophyllum*), Indonesia (Verheij 1993b: 76, figs. 87, 88, as *Mesophyllum*), and Hawaii (Adey et al. 1982: 58, as *Mesophyllum madagascariense*) differ at least in possessing SMCs mainly on the floor and were referred to *Melyvonnea madagascariensis* (Foslie) Athanas. et D. L. Ballant. (2014: 416).

Sissini et al. (2014: table 2) reported 0.0%–0.3% divergence for the *psb*A gene between Brazilian and Mexican specimens, which confirms the presence of a single species in the western Atlantic. Even specimens from Hawaii were not significantly different (differing by just 1 bp), whereas sequences from Brazilian isolates diverged from those from Japan, Vanuatu, and Fiji by 11–14 bp (2.5% to 3.2%). The molecular data so far suggest that there is introduction of *Melyvonnea erubescens* to some regions and localities of the world, but we cannot link these findings to types or names or assess the possible direction of spreading as long as sequences from type specimens have partial length (i.e., 293 bp for the *rbc*L gene in the lectotype of *M. erubescens*; Sissini et al. 2014), and several putative synonyms from the Indo-Pacific exist (some of which predate *L. erubescens*). Lemoine (1964: 238) reported *Mesophyllum erubescens* from the Cape Verde and the Canary Islands, in the latter case as a "subfossile," but without further information. Apart from a Tenerife DNA sequence in GenBank (referred to "*Mesophyllum erubescens*" and presumably belonging to *Melyvonnea canariensis*), no later records of *M. erubescens* from the Canaries or the western coast of Africa exist (Haroun et al. 2002: 165; John et al. 2004; Athanasiadis and Ballantine 2014); see also comments under *Melyvonnea canariensis*.

Melyvonnea madagascariensis (Foslie) Athanas. et D. L. Ballant.

Melyvonnea madagascariensis (Foslie) Athanas. et D. L. Ballant. 2014: 416, figs. 107–108.

Basionym: Lithothamnion erubescens f. *madagascariense* Foslie (1901d: 3, "*madagascariensis*").

Homotypic Synonyms: Lithothamnion madagascariense (Foslie) Foslie 1906a: 19 (repr. 3).

Mesophyllum madagascariense (Foslie) W. H. Adey 1970: 25.

Homotypic Synonym: ?*Lithothamnion erubescens* f. *subflabellatum* Foslie 1904c: 31, "*subflabellata*," pl. 3, figs. 23–25; type locality: Banda-anchorage, Indonesia, 18–36 m depth; lectotype: in L (0056933), 991.239-235, S.E.168, Station 240 (designated by Verheij and Woelkerling 1992: 286). Athanasiadis and Ballantine (2014: 416, synonym?).

Type Locality: Fort Dauphin (Taolagnaro), South Madagascar.

Holotype: In TRH (C15-3240), Printz (1929: pl. 14, fig. 15), Adey and Lebednik (1967: 80, "type material,: "§---- Madagascar, LM14(15), ex Mus.d'Hist.Nat.Paris [slide] 689"), Adey (1970: 25, "holotype"), Woelkerling (1993a: 142, "[coll.] Ferlus; Madagascar; [Fort Dauphin]," "holotype"), Keats and Chamberlain (1994: 179, "holotype"), Woelkerling et al. (2005: 451, "holotype fragment").

Isotypes: In PC (0118264), illustrated by Printz (1929: pl. 14, fig. 15), coll. A. Ferlus (undated), Woelkerling and Lamy (1998: 343–344); in US (Adey et al. 1982: 60).

Habitat and Distribution: Keats and Chamberlain (1994: 177) reported this species as *Mesophyllum erubescens* from Natal (South Africa) on littoral rocks and in tide pools and also in the sublittoral (on rocks and corals and in crevices) "most abundant at . . . 18–25 m" depth; thalli from Indonesia (Spermonde Archipelago and Barang Lompo, Kudigareng Lompo, Samalona, and Lombok Islands) were recorded at 0.5–35 m depth (Verheij 1993b: 61, as *Mesophyllum erubescens*), and thalli (to 15 cm in diameter) from Hawaii and Oahu were recorded at 3–12 m depth (Adey et al. 1982: 61, "10 specimens," as *Mesophyllum madagascariense*), whereas thalli from Japan were recorded on rocks below low tide (Masaki 1968: 13, as *Lithothamnion erubescens* f. *madagascariense*; Kato et al. 2011, as *Mesophyllum erubescens*). There are no later records from the type locality (Taolagnaro, Fort Dauphin, South Madagascar), and closer information about habitat and distribution awaits further study.

Comments: Although the largest portion of the original (holotype) specimen (illustrated by Printz 1929: pl. 14, fig. 15) is presently in PC (Woelkerling and Lamy 1998: 343–344), the first selection of the TRH element as type by Adey and Lebednik (1967) must be accepted, and hence, the PC fragment becomes an isotype. No trichocytes were recorded in the holotype (Keats and Chamberlain 1994: 179–180), but such cells were sporadically found in Natal thalli (Keats and Chamberlain 1994: 176).

Both Verheij (1993b: 61) and Keats and Chamberlain (1994: 176) treated *Mesophyllum madagascariense* as a junior synonym of *Mesophyllum erubescens*, whereas Adey et al. (1982: 58–61, fig. 41A–C) adopted the name *Mesophyllum madagascariense* for Hawaiian specimens, considering Caribbean thalli of *Melyvonnea* (*Mesophyllum*) *erubescens* to be a potential "species pair" (Adey 1979: table 1). Although new collections from Madagascar have not been studied so far, it appears that specimens from Natal (Keats and Chamberlain 1994: 175–177, figs. 21–23) and Indonesia (Verheij 1993b: 61–62, figs. 87, 88) differ from the western Atlantic *Melyvonnea erubescens* in having male chambers where SMCs occur mainly ("more prolific," according to Keats and Chamberlain 1994) on the floor; the latter feature was also emphasized by Adey et al. (1982: 61) in specimens from Hawaii. Putative Indo-Pacific synonyms include *Mesophyllum laxum* Me. Lemoine and *Lithothamnion erubescens* f. *haingsisianum*, both studied by Athanasiadis and Ballantine (2014: Appendix II); *Mesophyllum imbricatum* (Dickie) W. H. Adey; *Mesophyllum inconspicuum* (Foslie) W. H. Adey; and *Mesophyllum thelostegium* (Foslie) W. H. Adey. The latter three taxa remain incertae sedis and are discussed below.

Perithallis Athanas.

Perithallis Athanas. 2022: 915 (type: *P. incisa*).

Comments: Within the Mesophyllaceae, *Perithallis*, *Thallis*, *Printziana*, and *Sunesonia* develop basally branched pore filaments in canals of multiporate conceptacles. These pore filaments are 4- or 5-celled (6 or more cells in *Printziana*?) and are provided with elongate subbasal cells. Moreover, in *Perithallis*-*Thallis* pore filaments lack epithallial cells and terminate below the conceptacle surface (see Figure 25q). Despite identical canal structure, *Perithallis* differs significantly from *Thallis* in both reproductive and vegetative features, particularly in developing a ventral diminutive perithallium (anisobilateral organization) and a predominantly coaxial hypothallium and also in lacking embedded conceptacles or a conspicuous fusion cell in carposporangial conceptacles. These profound reproductive and vegetative differentiations indicate that the two genera have been isolated for a long period of time. *Perithallis* comprises the generitype *P. incisa*, which grows epiphytically, and *P. chathamensis*, which forms a much larger thallus, possibly of saxicolous nature.

A comparison between the genera of Melyvonneeae is given in Table 3.

Perithallis incisa **(Foslie) Athanas.**

Perithallis incisa (Foslie) Athanas. 2022: 916, figs. 5–9.

Basionym: Lithothamnion patena f. *incisum* Foslie 1906b: 6, "*incisa*."

Homotypic Synonyms: Lithothamnion incisum (Foslie) Foslie 1907b: 12.

Mesophyllum incisum (Foslie) W. H. Adey 1970: 24.

Polyporolithon patena var. *incisum* (Foslie) V. J. Chapman et P. G. Parkinson 1974: 202, "*incisa*."

Type Locality: Upper sublittoral, epiphyte on *Corallina* and *Amphiroa*, Island Bay, near Wellington, North Island, New Zealand.

Lectotype: In TRH (B17-2551, *pro parte*, June 1904, coll. W. A. Setchell, no. 6354, "On *Corallina* and *Amphiroa*"), designated by Athanasiadis (2022: 921, fig. 5a[G],b,e–g).

Isolectotypes: Slides in herb. Athanas.

Syntypes: In TRH (B17-2551, *pro parte*), June 1904, coll. W. A. Setchell, no. 6354; in TRH (B17-2552), June 1904, coll. W. A. Setchell, no. 6353; in TRH (B17-2553), a mixture of Setchell nos. 6353 and 6354; in TRH (B17-5150); in TRH (B17-2543).

Habitat and Distribution: This species is reported as a common epiphyte on *Haliptilon* (Decne) Lindley, *Corallina*, and *Amphiroa* and is also recorded on *Lenormandia* Sond. (Rhodomelaceae, Ceramiales). It is widely reported from southern, western, and eastern Australia, including Tasmania, and also from New Zealand (North Island) and the Auckland, Snares, and Chatham Islands (being occasionally merged within the broad concept of "*Mesophyllum erubescens*"). It is confirmed only from Victoria and the type locality (Island Bay, near Wellington). A record of "*Mesophyllum incisum*" from South Africa (Keats and Maneveldt 1997a) has been referred to *Thallis capensis* (Athanasiadis 2022).

Comments: Syntype material (in TRH) was found to be heterogeneous, including unidentified specimens with unattached growth, which necessitates the study of new collections at the type locality to describe these admixtures (Athanasiadis 2022).

Perithallis chathamensis **(Foslie) Athanas.**

Perithallis chathamensis (Foslie) Athanas. 2022: 924, figs. 10–12.

Basionym: Lithothamnion chathamense Foslie 1906b: 18 (repr. 2) "*chatamense*."

Homotypic Synonym: *Mesophyllum chathamense* (Foslie) W. H. Adey 1970: 23, "*chatamense*."

Type Locality: Chatham Islands.

Lectotype: In TRH (B18-2594, *pro parte*, includes slides 301 and 302, no date, coll. Schauinsland), Printz (1929: pl. 9, fig. 10), designated by Athanasiadis (2022: 928, fig. 10k–m).

Isolectotypes: Slides in herb. Athanas.

Syntypes: In TRH (B18-2594) "Reinbold nr. C.," including slide 546.

Habitat and Distribution: Known only from the lectotype and two recently collected specimens from the Chatham Islands. Habitat data unknown.

Comments: The original material was communicated by Reinbold to Foslie in December 1898, and the exact date of collection is unknown. The lectotype was reexamined by Keats and Chamberlain (1997, as "holotype"), and it was designated as lectotype by Athanasiadis (2022). *Perithallis chathamensis* differs from the epiphytic *P. incisa* in developing a larger thallus (at least 7.5 cm in extent) that most likely grows epilithically.

Thallis **Athanas.**

Thallis Athanas. 2022: 911 (type: *Th. capensis*).

Thallis capensis **Athanas.**

Thallis capensis Athanas. 2022: 911, figs. 2–4.

Misapplied Name: *Mesophyllum incisum* sensu Keats and Maneveldt 1997a [non *Mesophyllum incisum* (Foslie) W. H. Adey = *Perithallis incisa*].

Type Locality: Bird Island, east end of Algoa Bay, Eastern Cape, South Africa.

Holotype: In GB (GB-0219096, 22 m depth, on geniculate coralline, August 1987, coll. unknown, a tetrasporangial specimen from collection D11-YMC 90/3), illustrated by Athanasiadis (2022: fig. 2a,b).

Isotypes: Fragments (sections) of the holotype on slides (herb. Athanas.).

Paratype: D11-YMC 90/3, *pro parte*, including slides (herb. Athanas.), August 1987, 22 m depth, on geniculate coralline, collector unknown. A carposporangial specimen from collection D11-YMC 90/3.

Habitat and Distribution: Thalli grow on geniculate corallines (22 m depth) together with *Amphithallia crassiuscula* and are also reported on dead horny corals, bryozoan skeletons, stony coral skeletons, and sponges, between 9 and 14 m depth (Keats and Maneveldt 1997a: 202, as *Mesophyllum incisum*). The species is apparently endemic, known only from three localities in South Africa: Bird Island (the type locality at the east end of Algoa Bay, Eastern Cape); Cape Town; and Simonstown, Partridge Point, Western Cape Province (Keats and Maneveldt 1997a).

Printziana **Athanas.**

Printziana Athanas. 2022: 929 (type: *Pr. australis*).

Comments: *Printziana* and *Sunesonia* (see genus account) differ from other genera of Mesophyllaceae in developing elongate basal and subbasal cells (or elongate subbasal and third pore cells in *Pr. insignis*) in filaments lining canals of multiporate conceptacles (see Figure 25r–t). In *Printziana*, the pore filaments are 4- to 5(6?)-celled, whereas in *Sunesonia* they are 4-celled. The two genera also differ by the development of a predominantly coaxial hypothallium in *Printziana* (only coaxial patches recorded in *Sunesonia*). In addition, in *Sunesonia* the basal cells of pore filaments lining canals of multiporate conceptacles become reduced and may deteriorate. *Printziana* apparently accommodates several undescribed species from New Zealand, possessing bisporangia, "multirim" outgrowths on multiporate conceptacle roofs, or longer pore filaments composed of 6 (or more?) cells (Athanasiadis 2022: fig. 16j,k). A second species of *Printziana*, *Pr. insignis* from North Island (New Zealand), is formally described below differing from the generitype in lacking erect perithallial protuberances or trichocytes and possessing elongate subbasal and third pore cells (see Figure 25r).

Printziana australis Athanas.

Printziana australis Athanas. 2022: 929, figs. 13–16a–h.
Basionym: Mesophyllum printzianum Woelk. et A. S. Harv. 1993: 593.

Type Locality: Blanket Bay, Otway National Park (38°49′S, 143°34′E), Victoria, southern Australia.

Holotype: In MEL2271675 (LTB15249), 14 November 1985, coll. S. Campbell, no. 15249.

Isotypes: Slides in herb. Athanas.

Habitat and Distribution: The species grows in the upper sublittoral zone to 6 m depth, on rock, and on holdfasts of *Phyllospora comosa* (Labill.) C. Agardh (Woelkerling and Harvey 1993: 594). It is widely reported as *Mesophyllum printzianum* from southern Australia to Tasmania (Woelkerling 1996: 204), eastern Australia (Harvey et al. 2003b), New Zealand, and the Chatham Islands (Harvey et al. 2005; Farr et al. 2009) but is confirmed only from collections in Victoria, Tasmania, and New Zealand (Athanasiadis 2022).

Printziana insignis (Foslie) Athanas. et D. L. Ballant. comb. nov.

FIGURES 20–25

Printziana insignis (Foslie) Athanas. et D. L. Ballant. comb. nov.
Basionym: Lithothamnion insigne Foslie 1906b: 9.
Homotypic Synonym: *Mesophyllum insigne* (Foslie) W. H. Adey 1970: 24–25.

Type Locality: Littoral "low pools," Island Bay, near Wellington, North Island, New Zealand.

Lectotype: In TRH (B16-2431, Setchell no. 6343, *pro parte*, June 1904, coll. W. A. Setchell), illustrated by Printz (1929: pl. 5, fig. 10), designated herein (Figures 20, 21b).

Isolectotypes: Slides in herb. Athanas.

Syntypes: In TRH (B16-2431, *pro parte*; Figures 20, 21a,c,d, 22h,i, 23, slide 1165); in UC (745750, Setchell no. 6343, *pro parte*), annotated "(Lithothamnion) *Lithophyllum detrusum* low pools. Island Bay, near Wellington, New Zealand, June 1904. Was." (Figures 21g–j, 22e–g,j,k, 24, 25i–p); slides in herb. Athanas.

Habitat and Distribution: The species grows on rocks in "low pools" in the littoral zone. It is known only from the protologue and the present account.

Observations on the Protologue, Type Material, and Lectotypification: Foslie (1906b: 9) described *Lithothamnion insigne* from a Setchell collection (no. 6343) made in June 1904, at North Island, Island Bay, near Wellington (New Zealand). Foslie annotated on the lid of the box holding the original material "upper sublittoral zone" (Figure 20), whereas the syntype material in UC (745750) is annotated by Setchell "low pools."

The Norwegian protologue (Foslie 1906b: 9) reads (in translation),

> [Thalli] encrusting, incised, 0.3–0.5 mm thick, weakly proliferated, with rounded margins; [tetra]sporangial conceptacles erect, 250–500 μm in diameter, becoming usually (always ?) volcano-like, with roundish or elongate sunken roof 100–150 μm in diameter; [tetra]sporangia four-parted, 100–110 μm long and 40–50 μm broad. The alga grows on rock or overgrows other coralline algae. On smooth underlay it is strongly attached, but then shows tendency to detach. It overgrows foreign bodies and therefore its surface is uneven, or partly warty. New lamellae develop over older ones and are loosely attached. In transverse section, the hypothallium comprises a prominent part of the thallus thickness, and the medullary cells are 14–30 μm long, 5–7 μm broad. Perithallial cells are 7–11 μm long and 4–7 μm broad. I have only examined some broken pieces of this species. It is closely related to *Lithothamnion haptericolum* [*Orthocarpa haptericola*], but it follows closer the surface underneath and adheres closer to it. In addition, the cells are narrower, the conceptacles smaller and with weak and less sharp depression. The latter is formed during a later stage of the conceptacle's development and is partly, here and there, indistinct. The species shares substratum with *Lithophyllum tuberculatum*

FIGURE 20. (*Opposite*) *Printziana insignis*: the original material of *Lithothamnion insigne* in TRH (B16-2431) included in (**a**) a box and comprising (**b**) a Setchell label, (**c**) a paper pocket that held (**d**) a fragment, (**e, g, h**) three Foslie notes, (**i, j**) slides 1165 and 1166, (**f**) the specimen illustrated in Printz (1929: pl. 5, fig. 10), (**k**) a specimen annotated "x," (**l**) a specimen annotated "F," (**m**) a specimen annotated "O," and (**n, o**) the remaining specimens and fragments. The lectotype selected here is a tetrasporangial thallus attached to specimen f. Scale bar: 1 cm.

#6343
North Island, New Zealand
W. A. Setchell 6. 1904.
Island Bay near Wellington

Lithoth. insigne
og
Lithoph. tuberculatum
" detrusum
uppermost sublit. zone

Fotogr. sp.

Prep. 1165 af næstst. ved ×
– 1166 af brudst.
Lithoth. Monogr.
pl. 5, fig. 10

HERBARIUM OF THE UNIVERSITY OF CALIFORNIA

North Island, New Zealand #6343

W. A. SETCHELL, 1904

Island Bay, near Wellington.

Determined by ....

Prep. 1165 af næstst. ved ×
– 1166 af brudst.

L. insigne.
Foto. nr. 48
sp. konc.

Prep. 1165.
~~Sp.~~ M. konc.
200 – 300 μ.
Perith. | Hypoth.
11 × 5 - 14 × 7 | 14 × 7 - 32 × 7
17 × 5 9 × 5 | 11 × 7 22 × 5
7 × 4 9 × 4 | 29 × 7 25 × 5
7 × 5 | 18 × 7
11 × 7 | 29 × 5

Prep. 1166.
~~Sp.~~ M. konc. 240 – 400 μ
Perith. | Hypoth.
9 × 5
11 × 4

110 × 50
100 × 40
300 – (260) – 600 μ

Sp. konc.
240 – 400 μ
fordybninger
long. 140 – 160 μ
rund aflang

Lithoth. insigne
1166. New Zealand
Island Bay
Setchell 1904
nr. 6343 delvis

Lithoth. insigne
1165. New Zealand
Island Bay
Setchell 1904.
nr. 6343 delvis

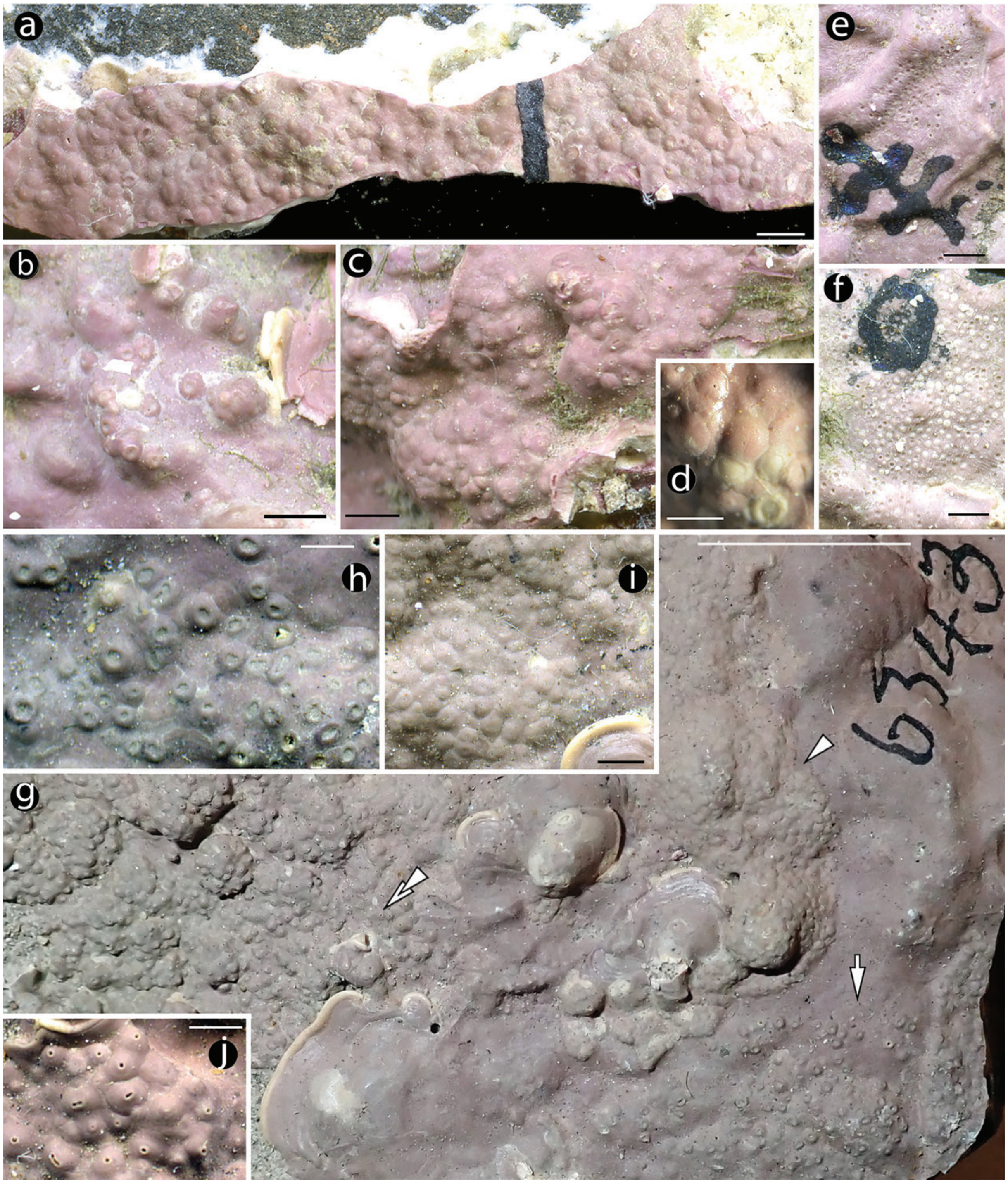

FIGURE 21. *Printziana insignis*: (**a, c-d, h–j**) syntypes and (**b**) lectotype of *Lithothamnion insigne* and syntypes of (**e**) *Lithophyllum tuberculatum* and (**f**) *Lithophyllum detrusum*. (a) Surface view of uniporate (male) conceptacles (annotated “L. insigne Foto no 48 sp.konc.” in TRH). Scale bar: 1 mm. (b) The here selected lectotype with volcano-like multiporate conceptacles (TRH) Scale bar: 1 mm. (c) The male thallus encircling the lectotype (TRH). Scale bar: 1 mm. (d) Male conceptacles (TRH). Scale bar: 500 µm. (e) *Lithophyllum tuberculatum* “F” (TRH). Scale bar: 1 mm. (f) *Lithophyllum detrusum* “O” (TRH). Scale bar: 1 mm. (g–j) Male (see (i) and arrowhead in (g)), carposporangial (see (j) and double arrowheads in (g)), and tetrasporangial (see (h) and arrow in (g)) thalli (syntypes in UC). Scale bars: 1 cm (g), 1 mm (h–j).

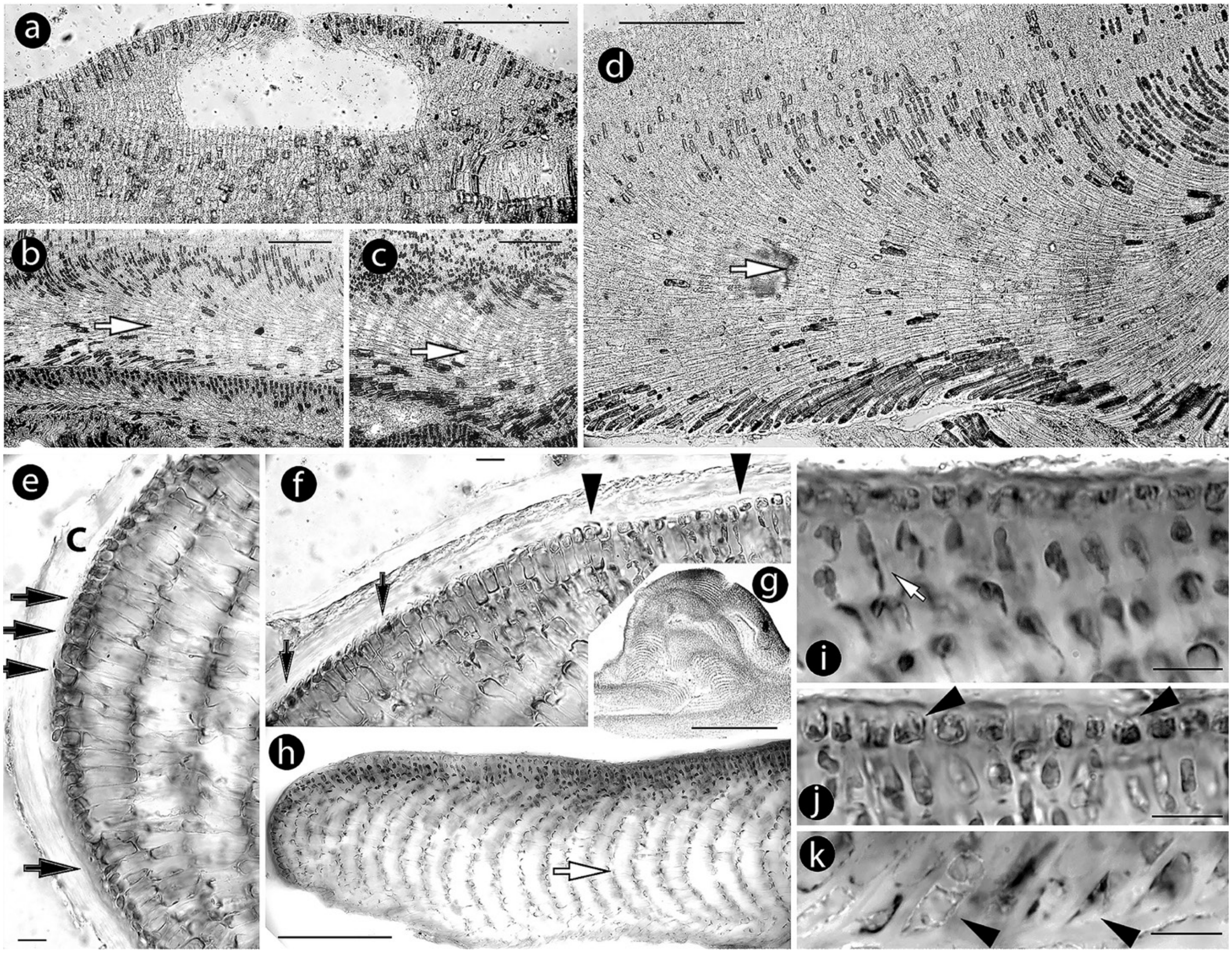

FIGURE 22. *Printziana insignis*: (**a–d**) Foslie slide (TRH, 1165) and (**e–k**) vegetative structures (syntype in UC in (e)–(g), (j), and (k); syntype in TRH in (h) and (i)). (a) Male conceptacle. Scale bar: 100 µm. (b–d) Sections showing coaxial (arrows) hypothallium. Scale bars: 100 µm. (e) Margin showing synchronous hypothallial divisions (arrows) below a cuticle. Scale bar: 10 µm. (f) Transition zone showing terminal (arrows) meristematic cells becoming epithallial cells (arrowheads). Scale bar: 10 µm. (g) Overgrowth of abutting lamellae. Scale bar: 500 µm. (h) Section showing coaxial (arrow) hypothallium. Scale bar: 100 µm. (i) Section at the surface showing elongate (arrow) subepithallial initial. Scale bar: 10 µm. (j) Squarish (arrowheads) epithallial cells. Scale bar: 10 µm. (k) Descending hypothallial cells ending in wedge-shaped cells. Scale bar: 10 µm. Abbreviation: c, cuticle.

> and *Lithophyllum detrusum* [both taxa possibly related to *Hydrolithon*]. It is only known from Island Bay near Wellington, New Zealand (Setchell, no. 6343 partly).

Lithothamnion insigne was not mentioned again in Foslie's publications. The original material in TRH comprises thalli attached to six larger rock fragments and at least five smaller ones. The collection also includes two slides (1165 and 1166), three paper sheets with Foslie's annotations, and one original label of Setchell (further annotated by Foslie; Figure 20). Foslie identified three new species in this material and described them in the same publication as *Lithothamnion insigne*, *Lithophyllum detrusum* Foslie, and *Lithophyllum tuberculatum* Foslie (Foslie 1906b: 9, 21–22). He annotated the species names on the lid of the box as follows: "*Lithoth. insigne*," "F *Lithoph. tuberculatum*," and "O [*Lithoph.*] *detrusum*" (Figure 20).

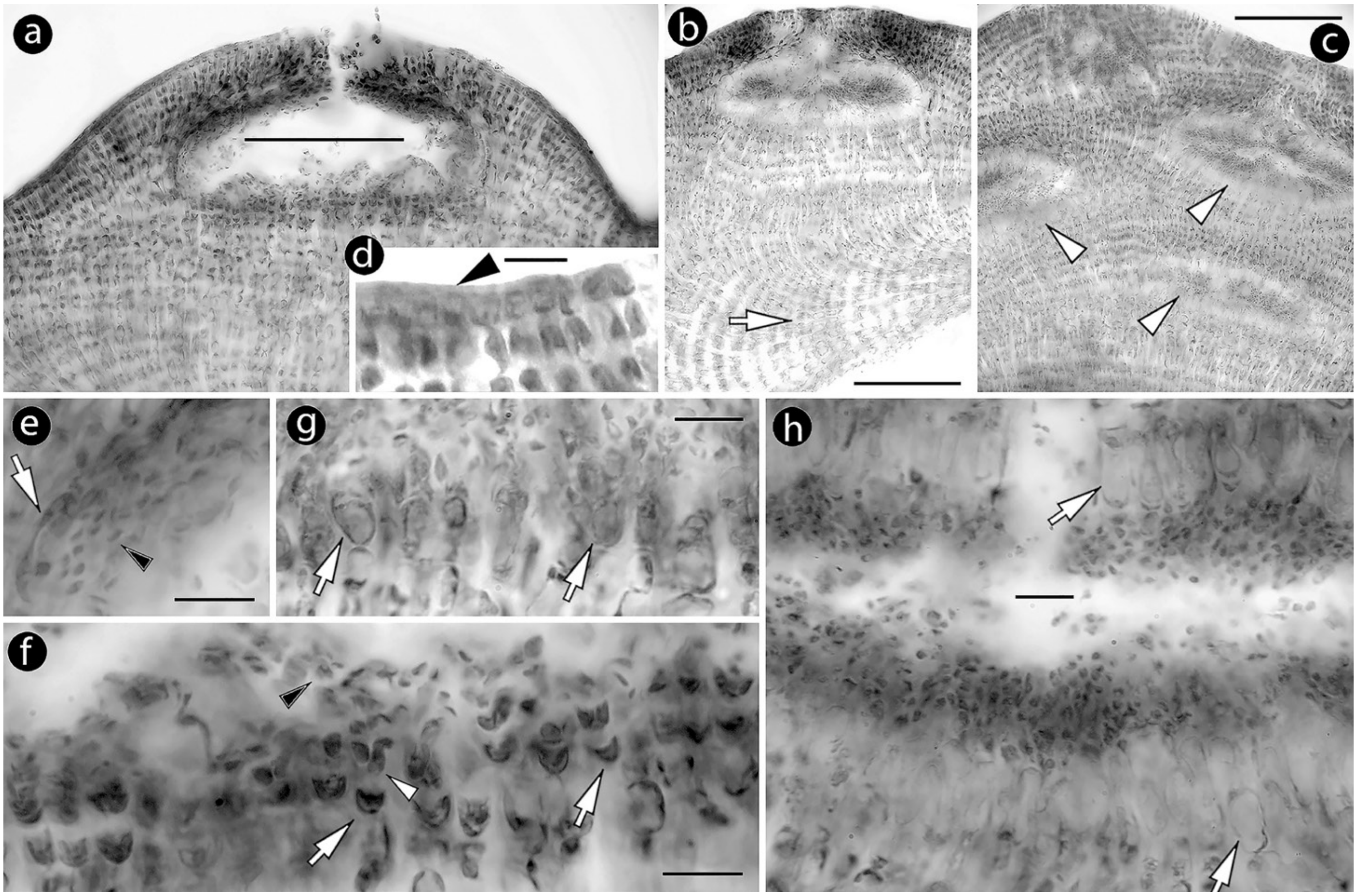

FIGURE 23. *Printziana insignis*: male structures (syntype in TRH). (**a–c**) Male conceptacles becoming embedded (arrowheads) in the perithallium that is supported by a coaxial hypothallium (arrow). Scale bars: 100 µm. (**d**) Section at the surface showing squarish (arrowheads) epithallial cells. Scale bar: 10 µm. (**e**, **f**) Spermatangial structures with SMCs (arrows) being (e) elongate on the walls and (f) lunate on the floor, cutting off spermatangia (arrowheads) that release spermatia (black arrowhead). Scale bars: 10 µm. (**g**, **h**) Older elongate SMCs (arrows). Scale bars: 10 µm.

The marks "F" and "O" appear on separate thalli on rock fragments (Figures 20, 21e,f), but no other elements referring to these two species exist in the collection. The rock fragment in the paper pocket has a straight line (indicative of *L. insigne*) and bears the species name "*L. insigne* Foto nr.48 sp.konc." (Figures 20, 21a).

However, there are no extant multiporate sporangial conceptacles on this fragment. Regarding the two slides (both annotated "Lithoth. insigne . . . New Zealand Island Bay Setchell 1904 nr.6343 delvis"), their origin was given on the Setchell label: "Præp. 1165 af neststt. ved X [slide 1165 from next biggest at x]" and "Præp. 1166 af brudst. [slide 1166 from the broadest]." Direct association with one of them can be made (Figure 20k). Slide 1165 is a radial section showing a uniporate conceptacle (most likely male), 450 × 70 µm (D × H), with an empty chamber 200 × 60 µm (D × H) and apparent coaxial hypothallial growth (Figure 22a–d). The relevant paper sheet is annotated "Prep.1165 ~~Enp.~~ [uniporate] Konc. 200–300 µ. Perith. 11x5 14x7 14x5 9x5 7x4 9x4 7x5 11x7 Hypoth. 14x7 32x7 11x7 22x5 29x7 25x5 18x7 29x5." Slide 1166 shows a nonradial, sterile section, and the annotations on the paper sheet state "Prep.1166. ~~Enp~~. [uniporate] Konc.240–400 µ" and "Perith. 9x5, 11x4 Hypoth." (no measurements given).

The two other paper sheets bear data for tetrasporangia "110 × 50" and "100 × 40" and possibly for conceptacles "300–(260)–600 µ" and "*F* . . . [illegible] Konc. 240–400 µ Fordybningen 100–140 rund –150 aflong µ [depression 100–140 round –150 elongate µm]." However, no slides with tetrasporangia or tetrasporangial conceptacles exist in B16-2431.

The tetrasporangial measurements on the notes agree with the size of tetrasporangia given in the protologue, but the size

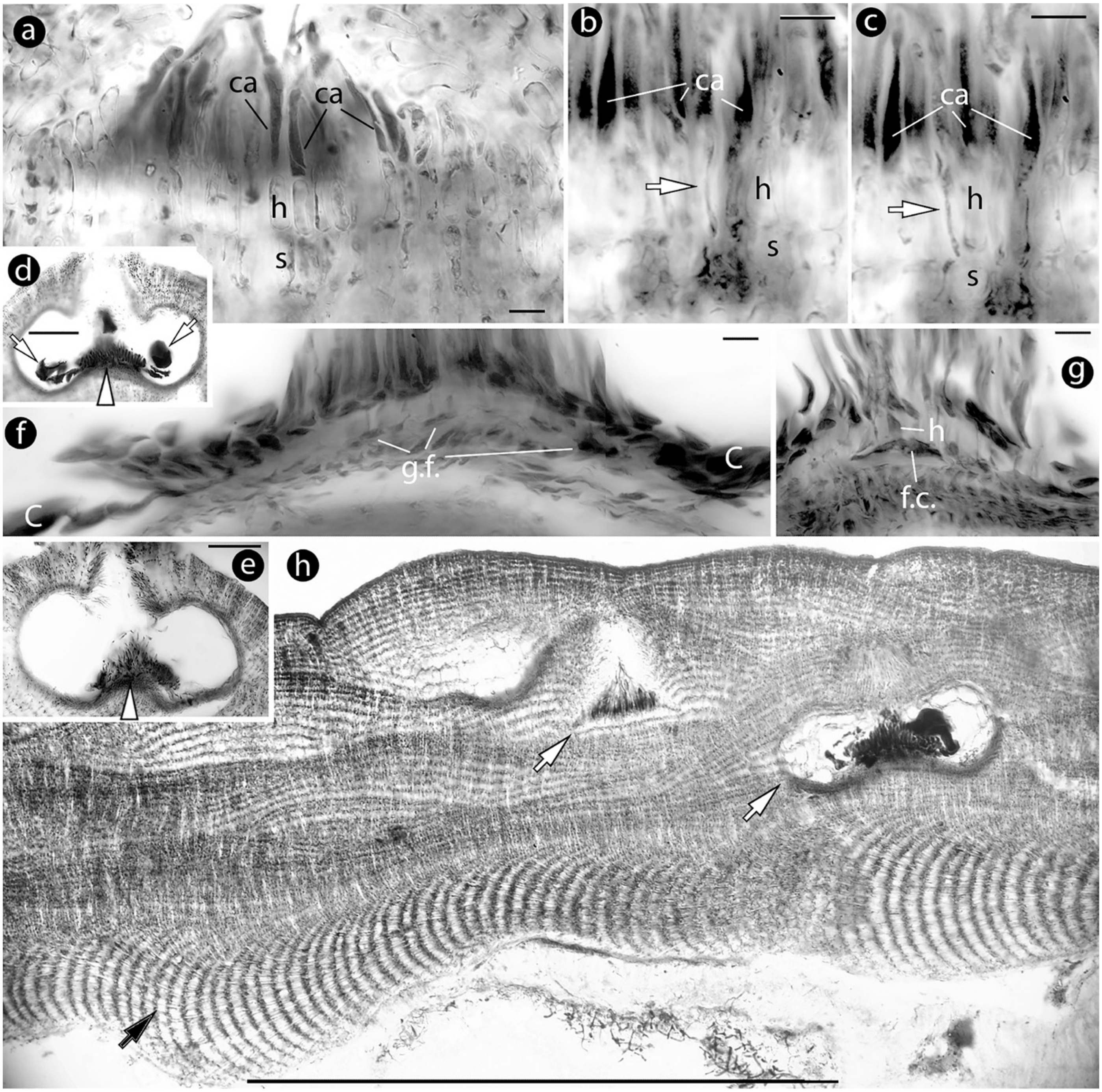

FIGURE 24. *Printziana insignis*: carpogonial branches, postfertilization stages, and carposporangial structures (syntype in UC). (**a**) Carpogonial branches showing broken carpogonia, hypogynous cells, and supporting cells. Scale bar: 10 µm. (**b, c**) Postfertilization stage with development of a cell tube (arrows) from the base of the carpogonium, bypassing the hypogynous cell and reaching the supporting cell. Scale bars: 10 µm. (**d, e**) Carposporangial conceptacles with a raised pedestal (arrowheads) and lateral production of carposporangia (arrows). Scale bars: 100 µm. (**f, g**) Gonimoblast filaments with lateral production of carposporangia and a fusion cell involving at least a hypogynous cell and 6 supporting cells. Scale bars: 10 µm. (**h**) Embedded carpogonial and carposporangial conceptacles (white arrows) in the perithallium, which is supported by a predominantly coaxial hypothallium (black arrow). Scale bar: 100 µm. Abbreviations: c, carposporangium; ca, carpogonia; f.c., fusion cell; g.f., gonimoblast filament; h, hypogynous cell; s, supporting cell.

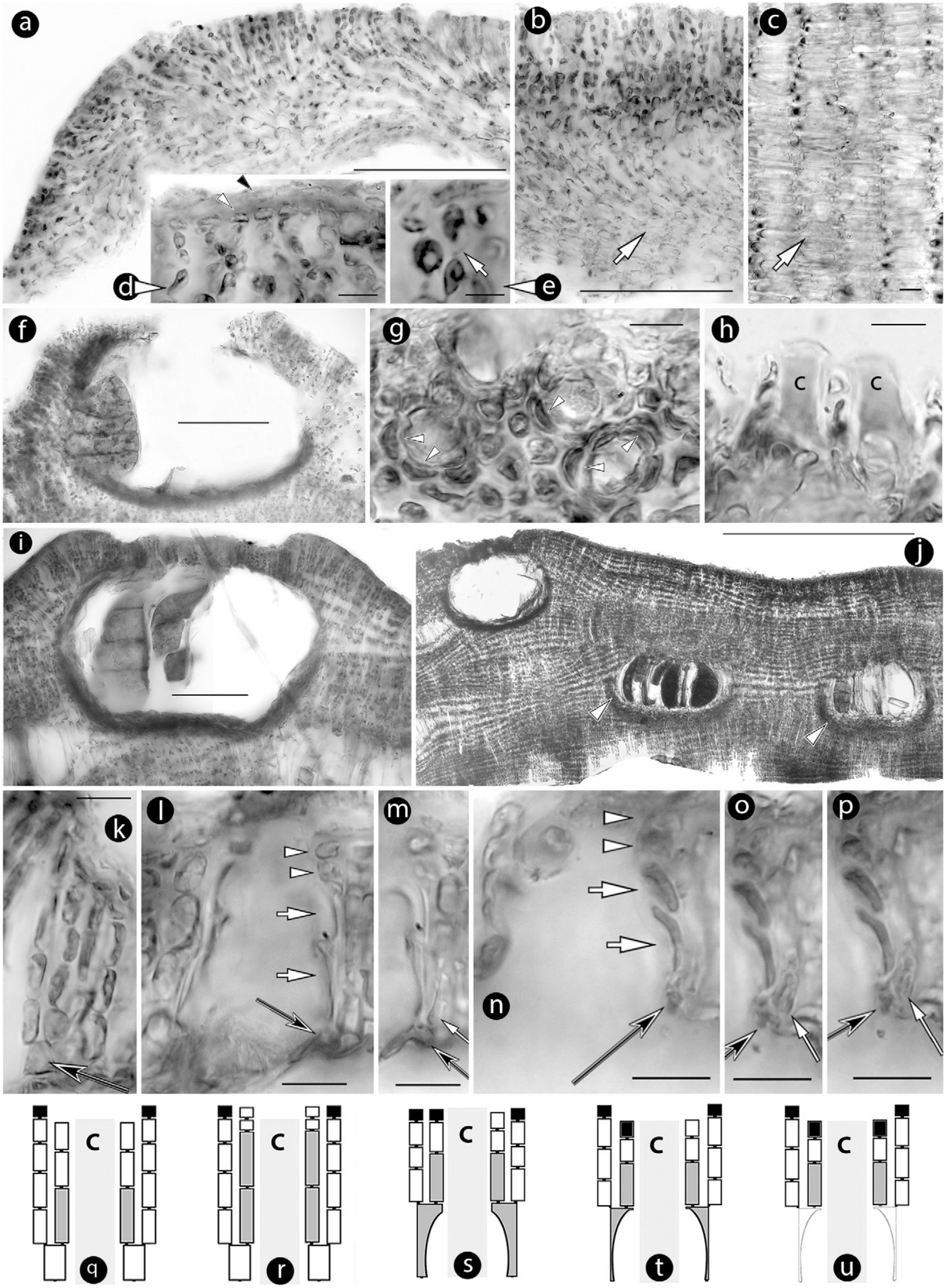
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FIGURE 25. (*Opposite*) *Printziana insignis*: (**a–p**) vegetative and multiporate conceptacle structures (lectotype in TRH in (a)–(h); syntype in UC in (i)–(p)) and (**q–u**) diagrammatic illustrations of pore filaments in the genera *Thallis*, *Perithallis*, *Printziana*, *Sunesonia*, and *Melyvonnea*. (a–c) Sections showing a noncoaxial hypothallium at the margin, becoming coaxial in the inner thallus (arrows). Scale bars: 100 µm (a,b), 10 µm (c). (d, e) Sections at the surface showing rectangular to squarish epithallial (white arrowhead) cells below a layer of older ones (black arrowhead) and elongate subepithallial (arrow) initial. Scale bars: 10 µm. (f) Tetrasporangial conceptacle. Scale bar: 100 µm. (g) View of canals from above showing thinner–wider pore cells (arrowheads). Scale bar: 10 µm. (h) Section of two canals showing top cells. Scale bar: 10 µm. (i) Tetrasporangial conceptacle with sunken pore plate. Scale bar: 100 µm. (j) Embedded tetrasporangial conceptacles (arrowheads). Scale bar: 100 µm. (k) Section of roof edge showing branched basal cell (arrow). Scale bar: 10 µm. (l–p) Sections of two canals in several levels of focus, showing 5-celled pore filaments, composed of a branched basal cell (black long arrows), supporting a normal roof filament (white long arrows), and the lining filament composed of 2 elongate (short arrows) and 2 smaller top cells (arrowheads). Note the inclination of pore cells that may partly overlap. Scale bars: 10 µm. (q) *Thallis-Perithallis*, (r) *Printziana insignis*, (s) *Printziana australis*, (t) *Sunesonia*, and (u) *Melyvonnea*, showing hypothetical loss of basal cells. Elongate pore cells are shaded, and epithallial cells are in black (no scale). Abbreviation: c, pore canal.

of the conceptacles, "300–(260)–600" (vs. 250–500 in the protologue), is in variance. Moreover, only the perithallial cell measurements on the notes (from slide 1165) agree with those in the protologue.

The only thallus marked "*L. insigne*" in the collection is the fragment in the paper pocket, which presently includes uniporate conceptacles marked with a line. Still, Foslie noted on the paper pocket "sp.konc. [sporangial conceptacles]" (Figures 20c,d, 21a). Another contradiction is that the word "Enp. [uniporate]" is eradicated in his notes, which refer to the two slides, one showing an apparent uniporate conceptacle (Figure 22a). And yet the only reproductive organs described in the protologue are the "kraterformige" (volcano-like) tetrasporangial conceptacles. These were located on one of the larger fragments (illustrated by Printz 1929: pl. 5, fig. 10), and since the protologue did not include any other reproductive characters, this fragment has been selected as the lectotype of *Lithothamnion insigne* (Figures 20f, 21b).

Adey and Lebednik (1967: 66) recognized the entire collection as "type material," and later Adey (1970: 24) recognized it as "holotype," commenting that he could not locate asexual conceptacles. Woelkerling (1993a: 127) further noted that the "holotype element contains plants on five pieces of rock one of which is depicted in Printz"; the sixth fragment in the paper pocket was mentioned in a later account (Woelkerling et al. 2005: 324).

A fragment of the lectotype and a fragment of the male thallus (encircling the lectotype) were examined (Figures 21c,d, 23a–h), along with two loose-lying sterile fragments in the box (Figure 22h,i). Part of Setchell's collection in UC (745750) was also accessed. This is more representative, including gametophytes and at least a tetrasporophyte (Figures 21g–j, 24), and the conclusion that the lectotype, the male thallus encircling it, and most of the loose-lying sterile fragments in the box, along with the UC material (described below), belong to the same species was reached.

The lectotype adheres closely to the substratum, and its margins overgrow the male thallus that encircles it. In its turn the male thallus shows unattached growth, overgrowing in part the lectotype (Figure 21c,d). The two thalli finally amalgamate in part, which is also evident in the UC material (Figure 21g–j). The thallus of the lectotype shows monopodial-dorsiventral organization with a polystromatic hypothallium, 40–100 µm thick, that may form noncoaxial patches at the margin (Figure 25a). A coaxial growth becomes evident in the main thallus, with cells 8–28 × 4–10 µm (L × B; Figure 25b,c). The perithallium becomes at least 130 µm thick, with cells 3–14 × 3–5 µm (L × B). Epithallial cells are rectangular to squarish or elongate, 3–6 × 4–5 µm (L × B), and subepithallial cells are longer (to 7 µm) than cells below during putative division (Figure 25d,e). The multiporate conceptacles reach 350–400 × 150–170 µm (D × H; n: 11) provided with chambers 230–280 × 150–160 µm (D × H; n: 2). The roof is about 50 µm thick, composed of 6- to 8-celled filaments, and has a sunken pore plate, 60–150 µm in diameter. Pore filaments lining the canals are composed of at least 4 cells that in surface view are thinner–wider toward the canal base. Canals have an apical diameter of 7–8 µm and are surrounded by 5 to 6 rosette cells. Tetrasporangia are 110–120 × 25–80 µm (n: 3; Figure 25f–h). The species description below includes data from the TRH as well as the UC specimens.

Species Description: Thalli encrusting, at least 4 cm in extent and 850 µm thick, adhering closely to the substratum (rock) and showing a tendency to form a foliose habit via unattached superimposed lamellae (Figure 21g). Erect perithallial protuberances are lacking, but abutting lamellae may form outgrowths that subsequently become overgrown by new lamellae forming projections (Figure 22g). Gametangial and tetrasporangial thalli may grow in close association and amalgamate (Figure 21g). The thallus organization is monopodial-dorsiventral, producing a polystromatic, arching, coaxial hypothallium via terminal, anticlinal synchronous divisions and elongations, protected by a cuticle (Figures 22e, 25a–c). Terminal subdichotomous divisions add to the thallus thickness and gradually displace hypothallial filaments dorsally or ventrally, the former becoming a perithallium and the latter becoming descending hypothallial filaments ending in wedge-shaped cells (Figure 22k). Terminal meristematic cells displaced dorsally become epithallial cells (Figure 22f). The hypothallium is 40–250 µm thick and supports an ascending, stratified perithallium, at least 700 µm thick (Figures 24h, 25j). Hypothallial cells are 18–25 × 4–7 µm (L × B; 14–30 × 5–7 µm, according to the protologue), and perithallial cells are 4–14 × 3–4 µm (L × B; 7–11 × 4–7 µm, according to the protologue). Subepithallial cells are distinctively elongate (to 14 µm) during division (Figures 22i, 25e), supporting a single layer of rectangular, usually squarish, to elongate epithallial cells, 2–6 × 4–5 µm (L × B; Figures 22j, 25d). Cell fusions between contiguous somatic cells are common. Trichocytes and secondary pit connections were not observed.

Gametophytes are dioecious. Male conceptacles are 200–460 × 20–120 µm (D × H) and provided with chambers 270–280 × 60–70 µm (D × H; n: 5) and a convex roof, 50–80 µm thick (Figure 23a–c). Epithallial cells are typically squarish (Figure 23d). Spermatangial structures are simple (unbranched), with lunate SMCs on the floor and elongate ones on the walls (Figure 23e,f). At the end of maturity, SMCs become elongate (Figure 23g,h).

Carpogonial conceptacles are ~420 × 120 µm (D × H; n: 1) in external diameter and provided with chambers ~170–180 × 50 µm (D × H; n: 2). Carpogonial branches extend along the entire fertile floor (Figure 24a) and are apparently composed of a carpogonium and a hypogynous cell (Figure 24a). Following fertilization, a cell tube connecting the base of the carpogonium with the supporting cell (bypassing the hypogynous cell) is formed (Figure 24b,c). Subsequent postfertilization stages (Figure 24d,e) involve the production of a fusion cell composed of at least 6 supporting cells and 1 hypogynous cell, whereas carpogonia, adjacent hypogynous cells, and basal cells remain intact and do not participate in the fusion (Figure 24f,g). Proliferations from the fusion cell form gonimoblast filaments that radiate along the fertile zone, producing carposporangia from the periphery (Figure 24d–f). A raised fertile zone (pedestal) is developed (Figure 24d,e). Carposporangial conceptacles are 230–600 × 6–70 µm (D × H) and provided with chambers 370–410 × 130–180 µm (D × H; n: 5) and a roof, 60–120 µm thick, with a central ostiole, 120 × 120–130 µm (D × H). Elongated ostioles were seen (Figure 21j), indicating conceptacle merging. Tetrasporangial conceptacles are 300–600 × 80–100 µm (D × H; n: 7) and provided with chambers 250–330 × 120–200 µm (D × H; n: 7). The roof is generally rimmed, 70–80 µm thick at the roof edges and 35–45 µm thick across the pore plate, which is 130–160 µm in diameter (Figures 21b,h, 25i–k). Roof filaments are 5- or 6-celled and can be basally branched (Figure 25k). Canals are straight, 12–14 µm in diameter, surrounded by 5 to 7 rosette cells (Figure 25g) and lined by 5-celled filaments that end at the conceptacle surface (Figure 25l–p). Basal cells of lining filaments are normal roof cells and are branched, supporting a roof filament and the rest of the lining filament, which is composed of 2 elongate and 2 shorter cells (Figure 25l–p, r). Tetrasporangia are 100–160 × 40–80 µm (L × B; n: 4; 100–110 × 40–50 µm, according to the protologue). Older gametangial and tetrasporangial conceptacles become embedded in the perithallium.

Comments: The structure of pore filaments in *Printziana insignis* differs from that of *Pr. australis* in developing a normal basal cell (similar to that in *Thallis-Perithallis*) and then 2 elongate cells (followed by 2 smaller cells; Figure 25r). Hence, the pore filament is 5-celled (4- or 5-celled in *Pr. australis*; Figure 25s), but pore filaments of at least 6 cells have also been observed in an undescribed species of the genus from New Zealand (Athanasiadis 2022: fig. 16j), and until the form variation has been studied in more collections, it is not possible to assess whether the particular type in *Pr. insignis* merits higher taxonomic (genus) status. *Printziana insignis* also differs from *Pr. australis* in lacking erect perithallial protuberances and trichocytes but shares all reproductive features, including the development of a medium-size fusion cell and a pedestal in carposporangial conceptacles. Indeed, in these characters, *Pr. insignis* is more closely related to the South African *Thallis capensis*, providing a link between these two genera

The syntype material in UC (745750) exists in a box (~21 × 12 cm) including at least five cobbles, some broken to produce duplicates. It is annotated "HERB. W.A. SETCHELL. 6343 (Lithothamnion) *Lithophyllum detrusum* low pools. Island Bay, near Wellington, New Zealand June 1904. W.A.S." The collection was surveyed illustratively, and two smaller rock pieces together with three minute fragments were borrowed for closer examination. These specimens included thalli of *Printziana insignis* and a tetrasporangial thallus of a species with short subepithallial initials (*Phymatolithopsis*?) attached to one of the rock fragments.

***Sunesonia* Athanas.**

Sunesonia Athanas. 2022: 935 (type: *S. pseuderubescens*).

Comments: *Sunesonia* is most closely related to *Printziana australis*, differing by lacking a predominantly coaxial hypothallium and trichocytes and possessing 4-celled pore filaments with reduced (or deteriorated) basal cells lining canals of multiporate roofs (Figure 25t vs. 25s). *Printziana* and *Sunesonia* differ from other genera of Mesophyllaceae in developing pore filaments (lining canals of multiporate conceptacles) with elongate basal and subbasal cells (or elongate subbasal and third pore cells in *Printziana insignis*; Figure 25r). *Sunesonia* was previously confused with the western Atlantic *Melyvonnea erubescens* since *Printziana australis*, *Melyvonnea*, and *Sunesonia* all grow in the sublittoral on rocky substratum and develop an encrusting thallus with erect perithallial protuberances. In *Melyvonnea*, the protuberances ramify and gradually dominate over the encrusting base, even becoming detached to form rhodoliths. Anatomically, *Sunesonia* lacks a predominantly coaxial hypothallial growth, which occurs in all species of *Melyvonnea* and *Printziana*. Comparing their multiporate conceptacles, those of *Printziana* are generally rimmed, occasionally with a flattened roof (Woelkerling and Harvey 1993: fig. 27A), whereas those of *Melyvonnea* and *Sunesonia* are generally convex. Pore filaments lining canals of multiporate roofs also show differences since in *Printziana* they are 4- or 5 (6?)-celled, ending at the conceptacle surface (or slightly below or above), whereas in *Sunesonia* they are generally 4-celled and terminate below the surface. In addition, basal pore cells in *Sunesonia* become reduced and may deteriorate, resembling the 3-celled pore filaments of species of *Melyvonnea* (Athanasiadis 2022: fig. 17p;

Figure 25u). *Sunesonia* apparently co-occurs with *Printziana* (but not with *Melyvonnea*) in southern Australia and New Zealand, which supports the sister taxon relationship between these genera, as proposed from both morphoanatomical and DNA sequence data (see Sissini et al. 2014; Athanasiadis 2022: fig. 18).

Sunesonia pseuderubescens Athanas.

Sunesonia pseuderubescens Athanas. 2022: 935, fig. 17a–p.

Type Locality: Ingoldsby Reef, Anglesea, Victoria, southern Australia.

Holotype: In MEL2269644 (LTB13531, collected 7 March 1983, coll. W. R. Beanland, no. 13531), illustrated by Athanasiadis (2020: fig. 17).

Isotypes: Slides in herb. Athanas.

Paratypes: In MEL, including one slide (10982 D - 10982), herbarium specimens on two sheets (both MEL2269644), and material in alcohol (MEL2269445); data of collection as for the holotype.

Habitat and Distribution: The species grows on rock in the sublittoral zone, between 3 and at least 20 m depth. It is recorded from Victoria , eastern Australia (Harvey et al. 2003b, as *M. erubescens* in part?), and western New Zealand (North and South Islands).

Comments: *Sunesonia pseuderubescens* apparently lacks sexual reproduction, in which case the present-day populations should be regarded as apomeiotic, recycling the parental (tetra- or bisporangial) phase. The species was previously confused with *Melyvonnea* (*Mesophyllum*) *erubescens* (e.g., Harvey et al. 2003b; Broom et al. 2008) because of a similar habit and possession of pore filaments with deteriorated basal pore cells (Athanasiadis 2022: fig. 17p), the latter resembling the pore filaments of species of *Melyvonnea* (Athanasiadis and Ballantine 2014: fig. 108; Figure 25u). Using sequences from the *psb*A gene, Sissini et al. (2014: table 2) demonstrated the presence of at least two species in isolates referred to "*Mesophyllum erubescens*" from New Zealand, differing by 1.6%–3.2% (7–14 bp). Two of these isolates (group New Zealand 1) were morphoanatomically identified as *Sunesonia pseuderubescens* (Athanasiadis 2022), leaving open the question of the molecular identification of the Australian holotype. See also comments under *Mesophyllum aucklandicum.*

INCERTAE SEDIS MELYVONNEEAE

Lithothamnion erubescens f. *haingsisianum* Weber-van Bosse et Foslie

Lithothamnion erubescens f. *haingsisianum* Weber-van Bosse et Foslie in Foslie 1901c: 4.

Type Locality: Haingsisi reef, Samau Island, Timor, Indonesia.

Neotype: In L (Herb. Lugd. Bat. 991.239-220, stat. 303, S.E.17), designated by Verheij and Woelkerling (1992: 279, "lectotype"), Athanasiadis and Ballantine (2014: Appendix II, figs. 168–169).

Habitat and Distribution: This entity forms rhodolith beds in the littoral zone. It is known only from the type locality and possibly Mauritius.

Comments: Foslie cited in the protologue a single type locality, namely, "Stat. 60, Siboga expedition: Haingsisi, Samau Island, Timor." Verheij and Woelkerling (1992: 279) did not find any material from "Station 60" in TRH or L and designated as "lectotype" a collection from "St. 303" deposited at L (Herb. Lugd. bot. 991.239-220). Station 303 refers to the type locality, but at a later time when Foslie (1904c: 4) revisited the place and "good-luck favored [them, as] it was spring tide . . . and [they] could observe th[e] whole reef, . . . [which] consisted chiefly of . . . f. *Haingsisiana*." Hence, all specimens from station 303 must be recognized as topotypes (but lacking the status of original material). Material from station 303 presently exists in two collections in Leiden (L0064067 [S.E.324] and L0064068 [S.E. 323]). It includes four boxes with some 30 specimens (one of the boxes also includes a specimen labeled S.E.378). Another specimen was located in UC745592 (annotated S.E. 373). All these topotypes are irregularly branched, roundish rhodoliths (up to 3.5 × 3.0 × 2.5 cm in diameter in S.E. 373 in UC) and are apparently "young specimens" (Foslie 1904c: pl. 3, figs. 1–11). Illustrations of two topotypes (Foslie 1904c: pl. 3, figs. 9, 19) are reproduced by Athanasiadis and Ballantine (2014: Appendix II, figs. 168–169), who studied several specimens from station 303 (UC 745592, "Haingsisi near Timor," S.E.373, including five slides; L, stat. 303, L0064067 [S.E.324], L0064068 [S.E. 323]). Their study confirmed Foslie's original account and, in particular, that the protuberances reach 5 mm in length and 1.1–2 mm in breadth, with secondary thallus growth showing a coaxial hypothallium and perithallial stratification. Ascending perithallial filaments support 1 or 2 flattened, occasionally flared, epithallial cells, 2–3 × 7–10 μm (L × B) and also embedded conceptacle chambers (most likely to be multiporate). The roof is ~25 μm thick, composed of 3 or 4 cells (Athanasiadis and Ballantine 2014: Appendix II, figs. 170–176). Trichocytes or secondary pit connections were not seen. Still, in the absence of observations of the pore filaments, the generic position is uncertain. Ballesteros and Afonso-Carrillo (1995: fig. 11) reported and illustrated *Mesophyllum erubescens* from Mauritius, and their single illustration shows a rhodolith with thin protuberances matching those of *L. erubescens* f. *haingsisianum*.

Mesophyllum aucklandicum (Foslie) W. H. Adey

Mesophyllum aucklandicum (Foslie) W. H. Adey 1970: 22.

Basionym: Lithothamnion fumigatum f. *aucklandicum* [Foslie 1905a: 16 (repr. 2), "*aucklandica*"].

Homotypic Synonym: *Lithothamnion aucklandicum* (Foslie) Foslie (1907b: 18).

Type Material: In TRH (C18-3330), Printz (1929: pl. 4, fig. 17), Adey and Lebednik (1967: 83, "type material,"

"§---- Auckland Is., 3.1904. Brit.Ant.Exp.Discovery, LM4(17) [slides] 932, 933"), Woelkerling (1993a: 33, "holotype"), Woelkerling et al. (2005: 466, "holotype").

Comments: The Norwegian protologue (Foslie 1905a: 16) reads (in translation),

> Crust less adherent to the substratum, the branch-like excrescences less in number and the conceptacles little larger than in the typical form. Therefore, the form may represent an independent species; but since only a few stunted specimens are known, it is referred so far to *L. fumigatum.* — Auckland Islands. The English expedition "Discovery".

In a later account, Foslie (1907b: 18) reexamined the material and reported (in translation),

> This alga was shown to differ so much from *L. fumigatum* in structure that it must be recognized as a distinct species. The crust's excrescences are small and irregularly warty and appear in small number. Hypothallial cells are 2–4(6) longer than broad, 14–29(36) µm long and 6–7(9) µm broad. Perithallial cells are partly sub square, 6–7(9) µm, partly and often vertically elongate, 9–18 µm long and 6–9 µm broad. [Tetra-bi]sporangial conceptacles are little conspicuous, apparently flattened, and weakly sunken in the middle, 250–360 µm in diameter. At maturity, the roof disintegrates completely, and the conceptacles become overgrown as usual in *L. fumigatum.* The home-obtained two specimens, appear to be weakly developed. — Auckland Islands (Brit. Ant.Exp.Discovery).

Printz (1929: pl. 4, fig. 17) illustrated a "specimen not well developed," and since Foslie (1905a, 1907b) mentioned "few stunted specimens" and "two specimens," lectotypification remains to be made. Woelkerling et al. (2005) reported that the original "collection consists of . . . one stone with attached corallines and . . . several very small fragments." On the other hand, Woelkerling (1993a) also mentioned the putative presence of duplicates at BM. Adey (1970: 22) transferred the species to *Mesophyllum*, noting that "the placement is with some question, since the hypothallium, while well-developed, is only very weakly coaxial."

Lithothamnion aucklandicum was subsumed within the broad concept of "*Mesophyllum engelhartii*" by Woelkerling and Harvey (1993: 582) and Chamberlain and Keats (1995: 134) after examination of type material, but no documentation was provided (Woelkerling and Harvey 1993: 584). The southern Australian *Lithothamnion engelhartii* (here referred to *Magnephycus engelhartii*, Magnephyceae) lacks erect protuberances and develops a foliose thallus, whereas the South African material of "*Mesophyllum engelhartii*" (Chamberlain and Keats 1995) has been referred to the encrusting species *Phragmope discrepans* (Athanasiadis 2020b). The presence of protuberances and the weakly developed coaxial hypothallium suggest that *M. aucklandicum* might be related to *Sunesonia*, whose type species *Sunesonia pseuderubescens* differs in developing larger multiporate conceptacles (270–450 µm in diameter) with a convex roof.

Mesophyllum brachycladum (Foslie) W. H. Adey

Mesophyllum brachycladum (Foslie) W. H. Adey 1970: 22.
Basionym: Lithothamnion brachycladum Foslie 1900a: 3–4.

Type Locality: Saint Helena Island, South Atlantic Ocean.

Holotype: In TRH (C16-3249), Adey and Lebednik (1967: 81, "type material," "§ Surton, St. Helena, 1899, LM12(19), Brit.Mus. 10 [slides] 336, 1360"), Woelkerling (1993a: 42–43, "holotype"), Woelkerling et al. (2005: 453, "holotype fragments").

Isotype: In BM (BM000519147 [box 30], annotated "No 10. *Lithothamnion brachycladum* Foslie (off St Helena)," "Pres . . . by Scient"), illustrated by Printz (1929: pl. 12, fig. 19).

Habitat and Distribution: Forming rhodoliths obtained by dredging. Recorded from Saint Helena Island and also reported from Angola (coll. Welwitsch).

Comments: Athanasiadis and Ballantine (2014: Appendix I, figs. 147–155) reexamined the isotype (BM) and the slides of the holotype (TRH) and observed the presence of embedded multiporate conceptacles, thinner–wider pore cells (of similar length to contiguous roof cells) along the entire length of canals of multiporate conceptacles, single flattened epithallial cells, and elongate subepithallial cells. Although no hypothallium was detected and no gametophytes have been recorded, the above character combination suggests that the species belongs to either the genus *Mesophyllum* or (in the absence of a coaxial hypothallium) Magnephyceae. The material from Angola (coll. Welwitsch), mentioned but not included in the species account, has not been located. All previous reports from the Canaries have been dismissed as misidentifications (or considered uncertain), and no other collections were located at TFC (Athanasiadis and Ballantine 2014). There are no later records of this species.

Mesophyllum cystocarpideum (Foslie) W. H. Adey

Mesophyllum cystocarpideum (Foslie) W. H. Adey 1970: 23.
Basionym: Lithothamnion cystocarpideum Foslie 1906b: 7.

Type Locality: Chatham Islands.

Lectotype: In TRH (B17-2543), Printz (1929: pl. 10, figs. 7–9, three specimens "attached to *Corallina*"), Adey and Lebednik (1967: 68, "type material," "§ leg. Maltby, com Cotton, Kew, Chatam [*sic*] Is., 11.1905, LM10 (7-9) no.39 [slides] 1191, 1192"), Adey (1970: 23, "holotype"), Woelkerling (1993a: 69, "holotype"), Woelkerling et al. (2005: 340, "holotype").

Syntypes: In BM (specimens in herb. Cotton), Tittley et al. (1984: 10).

Comments: Cotton (1907: 42–43) translated in Latin (or English) parts of the Norwegian protologue (Foslie 1906b), which reads (in translation),

> The thallus forms nearly roundish, vaguely convex or concave crusts on *Cheilosporum*, 0.4–1 cm in diameter and 0.2 to 0.5 mm thick, more or less undulate and often with irregularly incised margin. [Multiporate] Sporangial conceptacles are raised, convex or wart-like, 300–500 μm in [external] diameter, with a central circle-round or elongate and apparently deeply sunken [pore plate] 60–120 μm in diameter; tetrasporangia 160–240 × 50–80 μm; carposporangial conceptacles subconical, 300–600 μm in diameter. In a vertical section the hypothallium occupies the main part of thallus thickness and forms elongate ascending and descending arches. The cells are 12–36 × 7–11 μm. The perithallium is weakly developed with sub square or vertically elongate cells, which are double as long as broad, 9–18 × 7–11 μm. The [multiporate] sporangial conceptacles are closely standing, often merging together. The sunken part of the roof is perforated by 12–20 canals. These multiporate conceptacles closely resemble the lower carposporangial conceptacles of the same species, that without close investigation can be easily confounded with. The sunken middle part is namely often of almost similarly little diameter as the central ostiole in the last named conceptacles. This species belongs to the same series of forms as *L. patena*. In habit looks like *Lithoth. conchatum* from the Pacific North America, but it is smaller as a rule. It differs from the last named with its smaller cells and especially by its [multiporate] sporangial conceptacles that are particularly like those in *L. haptericolum* from New Zealand and *L. nitidum* from Japan. In this respect, it comes also close to *L. capense*. *Lithoth. cystocarpideum* occurred in the Chatham Islands, where it grows on *Cheilosporum wardii*. Together with one of the observed specimens, there is also a little crust of *Lithoth. patena* f. *incisa*. The species was found by H.E. Maltby and kindly sent to me by Dr. A.D. Cotton, Kew.

The type collection in TRH was more recently reexamined by Kim et al. (2004: 511, figs. 45–62), who reported thalli forming irregular foliose lamellae, up to 1 × 1.3 cm broad, attached to the geniculate coralline *Cheilosporum wardii* (Harv.) De Toni. They documented coaxial patches in an arching hypothallium and a putative (diminutive) ventral perithallium, supporting either trichocytes or epithallial cells (Kim et al. 2004: figs. 52–53, 55–56). Their observations suggest the presence of an anisobilateral organization (as in *Perithallis*). Kim et al. also recorded occasional back-to-back growth (Kim et al. 2004: fig. 51), dorsal epithallial cells with a domed or flattened outer wall (Kim et al. 2004: fig. 54), and tetrasporangial conceptacles with sunken pore plates perforated by up to 20 canals. Pore filaments terminated below the conceptacle surface and were provided with elongate cells toward the base (Kim et al. 2004: figs. 60–62). The precise structure of the canals and their pore filaments was, however, not illustrated, and it is unknown if canals are straight or pyriform or if the pore filaments are basally branched and which cells are elongated. The available data support the recognition of *Lithothamnion cystocarpideum* as a distinct species of Melyvonneeae (most likely related to *Perithallis*) whose generic position is pending the study of new collections.

Printz (1929) illustrated several specimens (most likely to be the product of several gatherings), and restriction of Adey and Lebednik's typification may be needed after comparison with the syntype material at BM. The name *Lithothamnion cystocarpideum* was apparently misapplied in Korea and Japan (Masaki 1968) for thalli redescribed as *Synarthrophyton chejuense* Kim et al. (2004: 501) and here recognized as *Orthocarpa chejuensis* (Kim et al.) comb. nov.

Mesophyllum exasperatum **(Foslie) W. H. Adey**

Mesophyllum exasperatum (Foslie) W. H. Adey 1970: 24.
Basionym: Lithothamnion exasperatum Foslie 1907a: 9.

Type Locality: Punta Arenas, Chile.

Holotype: In TRH (C15-3227), Printz (1929: pl. 14, fig. 14), Adey and Lebednik (1967: 80, "type material," "§ Thaxter, Chile, Punta Arenas (Magell. Str.), 1905a, LM14(14) herb. Farlow 1907, no 9 [slides] 1485, 1486"), Woelkerling (1993a: 88, "holotype"), Woelkerling et al. (2005: 448, "holotype").

Comments: Printz's (1929: pl. 14, fig. 14) illustration of the holotype in TRH shows a warty crust adhering to a piece of rock, ~3 cm in greatest diameter. According to the protologue, the thallus is ~500 μm thick, provided with dense protuberances 1–2 mm long and 0.5–1 mm thick. Anatomically, the hypothallium is coaxial, composed of cells 14–30 × 5–9 μm (L × B), and the perithallium is composed of cells 7–18 × 5–9 μm (L × B). In the protuberances, cells reach 22 μm in length. Tetrasporangial conceptacles are 300–500 μm in external diameter, and the roof is perforated by 50–70 pores. Tetrasporangia are 110–200 × 40–100 μm. The species is not mentioned in Foslie's later publications, and there are no other records. Adey (1970: 24) transferred the species to *Mesophyllum* without comment. Woelkerling (1993a: 88) noted that the "holotype specimen is badly fragmented," but since the material comes from the herb. Farlow (FH), it is possible that there are duplicates.

Mesophyllum fluatum **W. H. Adey, R. A. Townsend, et W. T. Boykins**

Mesophyllum fluatum W. H. Adey, R. A. Townsend, et W. T. Boykins 1982: 63–66, fig. 45A,B.

Type Locality: South central Maui, Hawaii.

Holotype: In US, 71-68-2, August 1971, coll. D. Child.

Paratypes: In US, 71-70-6, 71-68-13, 71-75, all collected in August 1971 at Maui, Molokai, and Nihoa, respectively, coll. D. Child.

Comments: This is a deepwater species described from 11 collections and distinguished by its encrusting, adherent, thin thallus (25–100 µm thick), lacking superimposed growth or erect perithallial protuberances. Anatomical characters are not illustrated but are described as including a coaxial hypothallium (20–25 µm thick), an ascending perithallium with nonelongate subepithallial cells (2–6 × 2–7 µm; L × B), and relatively small tetrasporangial (300–500 × 50–100 µm; D × H) and carposporangial (525 µm in external diameter) conceptacles, with carposporangia restricted to the periphery.

Mesophyllum fluatum is reported only from its type locality and adjacent sites of the Hawaiian Islands, from depths ranging between 60 and 90 m. "No Caribbean 'pair species' is known to exist" (Adey et al. 1982: 66). The holotype and two paratypes (D. Child 71-68-13 and 71-70-6) have been on loan to Y. M. Chamberlain as of May of 2004 (W. Adey, pers. comm.), and a later loan inquiry of material from the US did not materialize.

***Mesophyllum fumigatum* (Foslie) W. H. Adey**

Mesophyllum fumigatum (Foslie) W. H. Adey 1970: 24.
Basionym: Lithothamnion fumigatum Foslie 1901a: 7.

Type Locality: Half Moon Bay, Port Phillip, Victoria, southern Australia.

Lectotype: In TRH (B15-2360), Printz (1929: pl. 4, fig. 2), Adey and Lebednik (1967: 64, "type material," "§ Gabriel, Aust., Victoria, Port Philip 1899, LM4(2), Half-moon Bay [slide] 359"), Woelkerling (1993a: 100, "holotype"), Woelkerling et al. (2005: 315, "holotype").

Comments: The protologue (Foslie 1901a: 7) reads, in the most essential parts,

> Thallus crustlike, of indefinite shape and extent, up to about 4 mm thick, with crowded, small wartlike excrescences. Conceptacles of sporangia 250-300 µ in diameter, slightly prominent and frequently depressed in the central parts. Sporangia two-parted, 80-100 µ long by 30-50 µ. The species sticks to shells . . . The surface is uneven, provided . . . with . . . densely crowded, small, wartlike or irregular excrescences . . . 1–2 mm in diameter. . . . the feebly developed hypothallus is composed of up to 22 µm long cells . . . frequently however shorter . . . send[ing] forth perithallic . . . cells . . . which are square or rounded, 4-7 µ in diameter . . . up to 1½ times longer than broad, or up to about 12 µ long. . . . The conceptacles of sporangia are . . . always a little depressed in the central parts. The roof is traversed by about 20 . . . canals . . . The conceptacles . . . grow down into the frond in great numbers. This species . . . reminds . . . partly of *Goniolithon elatocarpum* partly *Lithothamnion Sonderi* in habit. Otherwise it seems to stand nearest to *L. funafutiense* . . . Only known from the southern coast of Australia, gathered in Half-moon Bay, Port Philip Bay, Victoria by Mr. J. Gabriel.

Woelkerling (1993a) noted that the selected "type material" by Adey and Lebednik (1967) is the only collection that comes from the type locality, and the single specimen illustrated by Printz (1929) was considered to be the holotype. However, in transferring the species to *Mesophyllum*, Adey (1970: 24) noted the presence of several specimens in TRH, "but only one was both sectioned by Foslie and appeared in the Monograph." Hence, the selected specimen has to be considered the lectotype.

Lithothamnion fumigatum was subsumed within the broad concept of "*Mesophyllum engelhartii*" by Woelkerling and Harvey (1993: 582, 597) and Chamberlain and Keats (1995: 134), but its type material has not been examined in a modern context. *Mesophyllum engelhartii* is here transferred to *Magnephycus* (Magnephyceae), a genus that lacks embedded conceptacles, whereas the South African material of "*Mesophyllum engelhartii*" (Chamberlain and Keats 1995) has been referred to *Phragmope discrepans*, which develops both embedded conceptacles and a predominantly coaxial hypothallium (Athanasiadis 2020b). Assuming that Adey (1970) did observe a predominantly coaxial hypothallium, *Mesophyllum fumigatum* is here placed in the tribe Melyvonneeae with reservation.

***Mesophyllum imbricatum* (Dickie) W. H. Adey**

Mesophyllum imbricatum (Dickie) W. H. Adey 1970: 24.
Basionym: Lithothamnion imbricatum Dickie 1877b: 486.
Homotypic Synonym: *Lithothamnion dickiei* Foslie 1900a: 7–8, nom. nov. illeg. [superfluous epithet change].

Type Locality: Sublittoral, ~11 m depth, Papeete Harbour, Tahiti, Society Islands, French Polynesia.

Lectotype: In BM (unnumbered), Papeete Harbour, Tahiti, Society Islands, no date, coll. H. Mosley, designated by Foslie (1904c: 30, text fig. 13A, "type"), Printz (1929: pl. 14, fig. 18).

Syntypes: In BM (unnumbered), illustrated by Foslie (1904c: 30, text fig. 13B–D); in TRH (C15-3229), Adey and Lebednik (1967: 80, "type material," "§ Dickie, Tahiti, Prapeetee [*sic*] Hbr, 1899, 30 Challenger Exp., LM14(18), ex Brit.Mus."), Adey (1970: 24, "Holotype"), Woelkerling (1993a: 120–121, "coll . . . H. Mosley . . . no date"), Woelkerling et al. (2005: 449, "holotype fragments"); in PC (unnumbered), Woelkerling and Lamy (1998: 348, "isotype").

Comments: Dickie's (1877b: 486) original account reads,

> Algae obtained at Papeetee [*sic*] Harbour, off Tahiti, in 20 fathoms. Lithothamnion imbricatum, n.sp. Fronde adnata, supra repetitim imbricata; lamellis crassis; ramis subhorizontalibus, compressis, lobatis, apicibus

> obtusis. Keramidiis [conceptacles] minutis, hemisphaericis, dense aggregatis. The specimens are 3 to 4 inches in diameter, much imbricated, lobed, and branched. In the dry state the colour is pale green.

Foslie (1900a) mistakenly renamed the species *Lithothamnion dickiei*, treating *L. imbricatum* as a provisional herbarium name of *L. polymorphum*, whereas Dickie clearly recognized *L. polymorphum* and *L. imbricatum* as two distinct species in two separate papers (Dickie 1877a: 450, 455, 1877b: 486).

Foslie (1900a: 7–8, 1904c: 30–31, text figs. 13A–D, 14A,B) also provided a description of the species (as *L. dickiei*), but he mixed up the original material (at the BM) with specimens at Kew Gardens referred to *L. polymorphum* by Dicke (1877a: 450, 455), and it is not clear which data pertain to the original material. It also appears from Foslie's (1904c: 30, text fig. 13A–D) illustration that the original collection included at least four specimens, with the largest (7.5 × 5.5 × 2 cm) selected by Foslie (1904c) as the type. Later, Foslie (1906b: 12) corrected his mistake, recognizing the species as *Lithothamnion imbricatum* Dickie.

The TRH material comprises only two fragments "in a small box marked '*L. imbricatum*' and 'Tahiti' and 'Brit. Mus. nr. 13' and 'Sp. konc." (Woelkerling et al. 2005: 449). Presently, it is not possible to assess whether the other specimens in TRH, PC, and BM are fragments of the single lectotype (as illustrated by Foslie 1904c and Printz 1929) or other (syntype) specimens of the original material (Foslie 1904c: text fig. 13B–D) or simply represent the material from the Kew Gardens (Foslie 1904c: text fig. 14A,B), the latter originally identified as *L. polymorphum* by Dickie (1877a: 455).

Foslie (1904c: 30) noted that the species "seems to come nearest to *Lithothamnion erubescens*," but it is possible that his opinion was based on material other than the lectotype, which is also the case for the specimen illustrated from Tearia, Tahiti (Printz 1929: pl. 14, fig. 19), whose habit resembles *Melyvonnea*. Adey (1970: 24) transferred the species to *Mesophyllum*, reporting that "sporangial plugs not seen in paraffin sections."

Mesophyllum inconspicuum (Foslie) W. H. Adey

Mesophyllum inconspicuum (Foslie) W. H. Adey 1970: 24.
Basionym: Lithothamnion inconspicuum Foslie 1907b: 19.

Type Locality: Hinga, Japan.

Lectotype: In TRH (C15-3239), Printz (1929: pl. 14, fig. 16), Adey and Lebednik (1967: 80, "type material," "§ Yendo, Japan, Hinga, 8.1900, no.785, LM14(16) [slide] 692"), Woelkerling (1993a: 124, "holotype"), Woelkerling et al. (2005: 451, "holotype").

Comments: Foslie (1901d: 3–4) originally identified

> some fragments from Hinga, collected by Mr.K. Yendo (no.785) . . . [as] very nearly related to f. *madagascariensis* [Foslie 1901d: 3]. They are however young and small, only about 1 cm in diameter, with simple or scantily divided branches. The conceptacles are of about the same size as in the latter, though not distinctly marked. With reference to structure the cells are more irregular than in any of the other forms, often smaller, and the conceptacles more frequently become overgrown by new formed tissue, while in the other forms and especially f. *americana* [Foslie 1901c = *Melyvonnea erubescens*] and f. *haingsisiana* [Weber-van Bosse et Foslie in Foslie 1901c] the whole roof often falls away and the conceptacles not so regularly become overgrown. Therefore it cannot be decided with certainty whether identical before older and well developed specimens are known.

He later described this material as a new species (Foslie 1907b). The Norwegian protologue (Foslie 1907b: 19) reads (in translation),

> *Lithothamnion inconspicuum* Fosl. mscr. Thallus branched, 1–1.5 cm in diameter, c. 0.5 cm thick, attached to the substratum via a poorly developed crust; branches closely spaced, very short, simple or sparsely divided, knobby, 1-2 mm thick; [tetra]sporangial conceptacles convex or somehow flattened, little or partly half raised, 250–400 µm in diameter; sporangia unknown. I have previously considered this alga as possibly belonging to *Lithoth. erubescens* f. *madagascariensis*, which has been raised to species, and as already said *L. conspicuum* [*sic*] stands between *L. erubescens* and *L. madagascariense*; but it differs from both in structure. The available specimens are otherwise poorly developed and apparently represent young forms of the species. It appears that little by little it becomes detached from the substratum. A single specimen resembles almost entirely a young *L. erubescens* f. *haingsisiana*, while a few others stand more closely in habit to *L. madagascariense*. The medullar hypothallial cells are 11–14(18) µm long and 6–9(11) µm broad. Perithallial cells are sub square or vertically elongate 7(6)–9 µm long and 6–7 µm broad. The roof of conceptacles is perforated by 40–50 mucous canals. – Japan: Hinga (K. Yendo, no.785).

Foslie did not mention again *L. inconspicuum* in his later publications. Printz (1929: pl. 14, fig. 16) illustrated a single specimen, ~1.5 cm in greatest diameter, and Woelkerling (1993a: 124) considered it to be the holotype, with 60% of the thallus missing. However, Foslie (1907b) made reference to several specimens, and therefore, the remaining specimen in TRH should be considered the lectotype. The branched protuberances on the encrusting thallus suggest that *M. inconspicuum* might be related to *Melyvonnea*. Foslie (1907b) himself suggested that it could be an intermediate form between *Lithothamnion erubescens* and

L. madagascariense, adding that the thallus can become detached and that a young specimen looks like (the rhodolith-forming) *L. erubescens* f. *haingsisianum*. Adey (1970: 24) transferred the species to *Mesophyllum*, commenting that he did not see sporangial plugs. The species is listed in the latest checklists from Japan (Yoshida et al. 1990, 1995, as *Lithothamnion*; Yoshida et al. 2015, as *Mesophyllum*).

Mesophyllum laxum **Me. Lemoine**

Mesophyllum laxum Me. Lemoine 1930: 60, pl. 2, fig. 3.

Type Locality: James Bay, James Island (San Salvador Island), Archipelago de Colón, Galapagos.

Holotype: In BM (000518864, box 322, includes two slides, YMC 94/9 and 5267), illustrated by Lemoine (1930: 60, pl. 2, fig. 3).

Isotype: In PC (unnumbered), Woelkerling and Lamy (1998: 382).

Habitat and Distribution: Known only from the protologue, where it is described as growing in the littoral zone in association with *Lithophyllum intermedium* Foslie.

Comments: Lemoine (1930) described and illustrated a single specimen (collector unknown) that according to modern criteria, resembles the external morphology of species of *Melyvonnea*. The holotype was reexamined during a visit to BM (October 2008; Athanasiadis and Ballantine 2014: Appendix II). Woelkerling and Lamy (1998: 382) reported the presence of minor fragments (up to 13 mm) at PC. A fragment of the holotype showed that the encrusting base lacked unattached growth and comprised at least 3 lamellae in superimposition, each 100–400 µm thick. The thallus surface produced erect perithallial protuberances at least 1.1 mm long and 1.4 mm broad. The encrusting thallus was composed of a coaxial hypothallium 70–200 µm thick, producing an ascending stratified perithallium, 110–260 µm thick, supporting 1–2 flared-like epithallial cells. Tetra- or bisporangial conceptacles were recorded, but the structure of pore canals was not observed. Conceptacles were embedded in the perithallium through centripetal growth of peripheral filaments (Athanasiadis and Ballantine 2014: Appendix II, figs. 177–182).

Mesophyllum laxum first appeared as a *nomen nudum* (Lemoine 1928: 252) and has not been recollected (Taylor 1945: 176) since the protologue (Lemoine 1930). Dr. Yvonne Chamberlain, who examined the holotype, noted “cf. *erubescens*” (in *schedula* = on the herbarium collection) and later suggested that it may be “a putative synonym of *M. erubescens*” (Yvonne M. Chamberlain, Institute of Marine Sciences, Portsmouth University, Portsmouth, UK [deceased], personal communication, 14 March 2006). The examination of the holotype has confirmed that the species exhibits several characters of *Melyvonnea*, both as regards general habit and thallus organization (i.e., coaxial hypothallial growth, perithallial protuberances with embedded conceptacles), but other significant characters such as pore canal structure are unknown to support unequivocal membership. Moreover, the occurrence of flared-like epithallial cells needs to be examined in new topotype material.

Mesophyllum nitidum **(Foslie) W. H. Adey**

Mesophyllum nitidum (Foslie) W. H. Adey 1970: 25.
Basionym: Lithothamnion nitidum Foslie 1901d: 4–5.

Type Locality: Misaki, Japan.

Holotype: In TRH (B17-2581), Printz (1929: pl. 6, fig. 10), Adey and Lebednik (1967: 69, “type material,” “§ Yendo, Japan, Misaki, 8.1900, no.784, LM6(10) [slides] 691, 1562”), Woelkerling (1993a: 158, “about 85 % of the holotype . . . depicted by Printz is no longer present”), Woelkerling et al. (2005: 345, “holotype”).

Comments: Foslie (1901d) described in the protologue a single encrusting thallus 5.5 cm in greatest diameter, 300–700 µm thick, with an irregular and somewhat knotty surface, weakly attached to the “root of other algae, here and there . . . or surrounding small parts of the substratum, with the margin more often free and bent more or less downwards.”

He added that perithallial cells are 7–12 × 4–7 µm (L × B) and tetra- or bisporangial conceptacles are “scarsely raised above the surface,” 800–1000 µm in external diameter, and the sunken pore plate (150–200 µm in diameter) is perforated by 40–50 pores. Tetrasporangia are 140–180 × 60–90 µm (L × B). Carposporangial conceptacles occurred on the same thallus together with antheridial conceptacles, the former being “subimmersed or immersed, very low conical,” and 700–900 µm in external diameter. Foslie (1901d) further considered the species to be related to *Lithothamnion muelleri*, differing by a more vigorously developed perithallium and “reproductive organs . . . [being] more superficial.” He did not mention the species again in his publications.

Printz (1929: pl. 6., fig. 10) illustrated the holotype, largely intact, and Woelkerling (1993a: 158) noted that “about 85% of the holotype . . . is no longer present.” Adey (1970: 25) transferred the species to *Mesophyllum* without comment. No other studies of *M. nitidum* have been published, but the species is listed in the checklists of macroalgae from Japan (Yoshida et al. 1990, 1995, as *Lithothamnion*, 2015, as *Mesophyllum*). The monoecious gametophytes along with the knotty encrusting base suggest that *M. nitidum* might be related to *Melyvonnea*.

Mesophyllum thelostegium **(Foslie) W. H. Adey**

Mesophyllum thelostegium (Foslie) W. H. Adey 1970: 26.
Basionym: Lithophyllum thelostegium Foslie 1907a: 4.

Type Locality: Rikitea, Tuamotu Archipelago, French Polynesia.

Lectotype: In TRH (C18-3367), Printz (1929: pl. 4, fig. 21), Adey and Lebednik (1967: 84, “type material,”

"§ Hariot, Tahiti, Rikitea, 4.1907, no 14, LM4(21) [slides] 1420, 1432, 1469"), Woelkerling (1993a: 223, "holotype"), Woelkerling et al. (2005: 474, "holotype").

Syntype: In PC (Woelkerling and Lamy 1998: 364).

Comments: The Norwegian protologue (Foslie 1907a: 4) reads (in translation),

> *Lithothamnion thelostegium* Fosl. mscr. Thallus encrusting on corals, 0.2–0.5 mm. thick, with apparent crowded protuberances 0.5–1-mm high and 0.5–0.8 mm thick, with edges concentrically zoned; [tetra]sporangial conceptacles hemispherical, 0.6–0.9 mm in diameter, the middle part finally somehow flattened; sporangia four-parted, 150–180 μm long and 40–60 μm broad; cystocarpic conceptacles conical, 600–700 μm in diameter. The hypothallium is in vertical section arranged in rays [coaxial?] in long bows upward and downward. It occupies most part of the crust thickness. Cells are 14–28 μm long and 6–9 μm broad, the measurements being somehow uncertain because of improper sectioning. Perithallial cells are sub square about 7 μm in diameter or slightly vertically elongate, 6–9, otherwise up to 11 μm long and 6–7 μm broad. Sporangial conceptacles are elevated and develop here and there between the lower protuberances, that usually look alike. The roof is perforated by 70–120 mucous canals. Cystocarpic conceptacles occur partly on the crusts, and partly on the top of the lower protuberances. They are provided with a short extending top as it is usual in *Lithothamnion*. The species reminds in habit some forms of *Lithothamnion muelleri*. Still it is more closely related to *Lithothamnion simulans* [*Magnephycus simulans*] but differs by its numerous branch like proliferations, and the longer and thinner hypothallial cells. — Tahiti: Rikitea (Mus.Paris, P.Hariot, nr.14).

Lithothamnion thelostegium was not mentioned in Foslie's later publications. Printz (1929: pl. 4, fig. 21) illustrated a single specimen, ~5 cm in greatest diameter, "almost encircling a coral axis," provided with minute erect protuberances. Adey (1970: 26) transferred the species to *Mesophyllum* without comment. Payri and N'Yeurt (1997: 891) referred it "possibly" to *Mesophyllum* (*Melyvonnea*) *erubescens*. Woelkerling and Lamy (1998: 364) found part of the original material in PC and concluded that the collector was Seurat (not Hariot), and that the collection was made in January 1904 (Woelkerling et al. 2005: 474). Following Adey and Lebednik's (1967) typification, the TRH material becomes the lectotype and the part in PC a syntype (or a putative isolectotype). The lack of a foliose habit and the presence of erect protuberances in the lectotype supports Payri and N'Yeurt (1997) tentative identification with a species of *Melyvonnea*. As noted by Woelkerling et al. (2005: 474), the protologue and the annotations on the type material (see Adey and Lebednik 1967) erroneously associate Rikitea with Tahiti (Society Islands included in French Polynesia).

Mesophyllum variabile (Foslie) W. H. Adey

Mesophyllum variabile (Foslie) W. H. Adey 1970: 26.
Basionym: Lithothamnion variabile Foslie 1906b: 10.
Homotypic Synonym: *Clathromorphum variabile* (Foslie) M. L. Mendoza et S. Molina 1994: 178.

Type Locality: Port Louis, Berkeley Sound, Falklands.

Type Material: In TRH (C18-3368), Foslie (1907c: 6–7, pl. 1, figs. 7–9), Printz (1929: pl. 5, figs. 15–17, "old specimens"), Adey and Lebednik (1967: 84, "type material," "§ Skottsberg, Falkland Is., Berkeley Sound, Port Louis, 23.7.1902, st.35, Swed.S.Pole Exp., LM5 (15-17)," "Contri.7+9" [slides] 939, 945"), Woelkerling (1993a: 233–234, "holotype"), Woelkerling et al. (2005: 474, "lectotype").

Comments: The Norwegian protologue (Foslie 1906b: 10) reads (in translation),

> Lithothamnion variabile Fosl. mscr. Thallus lamellate forming first roundish to kidney-like crusts, 0.3–1 mm thick, that grow together; later new crusts loosely laying develop on top and form a thallus 1–3 cm thick, with wart-like, sometimes short branch-like or knobby projections. Sporangial conceptacles are weakly convex or slightly prominent, 400–600 μm in external diameter.- Falkland Islands (Skottsberg).

In a later account, Foslie (1907c: 6-7) added that there

> are apparently two forms, . . . representing the same species. One . . . is composed of very small lamels, . . . subcircular or subreniform, finally somewhat confluent, with small wartlike excrescences, the other more crustily expanding with coarser, knobby or irregular projections. The lower part of the specimens is mostly dead, in the upper, living part a constant overgrowing of foreign bodies takes place, with which the alga is much encumbered. It partly grows on other algae, e.g. *Lithoph. falklandicum*. In a section the hypothallium is mostly vigorously developed, and the perithallium is stratified. The cells of the latter are rather thick-walled, mostly vertically elongated 1½ or up to twice the breadth, the length being 10–14 μ, occasionally up to 18 μ, and the breadth being 9–11 μ. The conceptacles of sporangia occur scantily and in small groups. The roof is intersected with about 90 muciferous canals. A few conceptacles examined were attacked by animals and had no sporangia. The species belongs to the same group as *Lithoth. Philippii* [*Mesophyllum philippii*] and seems to be most closely-connected with *L. synanablastum* [status unknown; see Athanasiadis 2020b] from South Africa.

Regarding the type material, Foslie (1907c) and Printz (1929) illustrated the same (three) specimens. Woelkerling

(1993a: 233) first noted that the "holotype . . . consists of six pieces . . . three . . . depicted by Foslie (1907c) and Printz (1929)" but later corrected his statement to a "Collection includ[ing] . . . seven specimens" (Woelkerling et al. 2005: 474). It is not known which of these specimens were included in Foslie's (1906b) original account, and no authentic specimens have been documented in a modern context. Hence, a lectotype remains to be selected.

Adey (1970: 26) transferred the species to *Mesophyllum*, noting that "this plant is unusual in that although the epithallium and hypothallium are distinctly *Mesophyllum*, the sporangial plugs stain strongly in phosphotungstic hematoxylin, as in *Lithothamnium*."

On the other hand, Mendoza and Molina (1994: 178) transferred the species to *Clathromorphum*, providing a short description of new material and including the following characters:

> Hypothallus composed of 3 to 8 layers . . . cells, 20–35 μm long × 7–9 μm in diameter. Perithall . . . rectangular rounded cells, 12–15–17 μm long × 6–9 μm in diameter . . . with common cell fusions. Epithallus composed of 3–4 layers of small cells. . . . multiporate conceptacle . . . chambers, 350–450 μm in diameter × 100–120 μm high.

Mendoza and Molina (1994), however, did not compare their collections to type specimens.

Mesophyllum variabile is here placed in the tribe Melyvonneeae with reservation, following Adey (1970), who noted that the hypothallium of the type material is "distinctly *Mesophyllum*," and assuming that he observed a distinctive coaxial tissue.

Mesophyllum versicolor **(Foslie) W. H. Adey**

Mesophyllum versicolor (Foslie) W. H. Adey 1970: 26.
Basionym: Lithothamnion versicolor Foslie 1907a: 3–4.

Type Locality: Port Phillip Heads, Victoria, southern Australia.

Type Material: In TRH (C16-3297), Printz (1929: pl. 12, figs. 1, 2, "fully developed specimens"), Adey and Lebednik (1967: 82, "type material, " "§ Gabriel, Austr., Vict., Port Philip Heads, 12.1906, LM12(1,2) [slides] 1323, 1324"), Woelkerling (1993a: 236, "holotype"), Woelkerling et al. (2005: 461, "holotype").

Comments: The Norwegian protologue (Foslie 1907a: 3-4) reads, in the most essential parts (in translation),

> *Lithothamnion versicolor* Fosl. mscr. Thallus 5–7 cm in diameter, 1–2 cm thick, forms irregular partly confluent growing crusts on rocks, with densely packed wart-like or short branch-like anastomosing, 2–3 mm thick, papillate excrescences; [tetra]sporangial conceptacles growing close together, convex or hemispherical, roundish or elongate, with a vaguely sunken middle part, 400–700 μm in diameter; tetrasporangia, 200–240 μm long and 50–100 μm broad. The hypothallium is mostly coaxial, irregularly, with cells 18–36 μm long and 6–9 μm broad, the perithallium develop partly a cup-like tissue (layer), cells 11–20 μm long and 6–7 μm broad. In vertical section, the conceptacles are mostly smaller than when seen from above. The sunken middle part is perforated by 40–60 large muciferous canals. The species bore mature [tetra]sporangia in December. *Lithoth. versicolor* comes close in habit to *Lithoth. Gabrielii*, but it is closest related to *L. funafutiense*, from which it differs by its numerous excrescences and small cells. — Port Philip Heads, Victoria (C. J. Gabriel).

Lithothamnion versicolor was not mentioned again in Foslie's publications. Printz (1929: pl. 12, figs. 1, 2) illustrated "two fully developed specimens" from the type locality. Woelkerling (1993a: 236) noted that "the holotype is the only collection of this species in TRH identified by Foslie," and Woelkerling et al. (2005: 461) confirmed that the type material includes two specimens. Hence, lectotypification remains to be made. Adey (1970: 26) transferred the species to *Mesophyllum* without comment. The species was considered to be conspecific with "*Mesophyllum engelhartii*" by Woelkerling and Harvey (1993: 582, 600) and Chamberlain and Keats (1995: 134), but the type of the latter species is foliose in habit, lacking protuberances (Athanasiadis 2017a), and is here referred to *Magnephycus engelhartii* (Magnephyceae), whereas the South African material of "*Mesophyllum engelhartii*" sensu Chamberlain and Keats (1995), which develops protuberances, has been referred to *Phragmope discrepans* (Athanasiadis 2020b).

The illustrated type specimens of *L. versicolor* by Printz (1929: pl. 12, figs. 1, 2) show, indeed, "short branch-like anastomosing, 2–3 mm thick, papillate excrescences," which in combination with a "mostly coaxial" hypothallium suggest that the species might be related to *Printziana australis* or *Sunesonia pseuderubescens*.

Mesophyllum vescum **(Foslie) W. H. Adey**

Mesophyllum vescum (Foslie) W. H. Adey 1970: 26–27.
Basionym: Lithothamnion vescum Foslie 1907b: 3–4.

Type Locality: Marine Laboratory at Sagami Province, Japan.

Type Material: In TRH (B2-1741), Adey and Lebednik (1967: 52, no type status, "K.Yendo, Pacific coast of middle Japan, Mar.Lab. at Sagami, 1899, no.228 [slide] 1539"), Woelkerling (1993a: 236, "Holotype . . . Yendo no.228; includes slide 1539"), Woelkerling et al. (2005: 246, "Lectotype," "Box marked . . .delvis").

Comments: The Norwegian protologue (Foslie 1907b: 3–4) reads (in translation),

> *Lithothamnion vescum* Fosl. mscr. Encrusting, c. 5 mm in diameter, 0.5–0.8 mm thick; [multiporate]sporangial

> conceptacles crowded, convex or somewhat flattened, partly emerging, 300–500 µm in diameter; sporangia two-parted, 130–160 µm long and 60–80 µm broad. The alga grows on the haptera of *Ecklonia* and on rather small stones, which lie between the haptera. A new crust develops partly over the primary one. In a vertical section, the hypothallium occupies most part of the thallus thickness; cells are 14(11)–18(22) µm long and 6–7 µm broad. The perithallium is poorly developed in the available specimens, which are apparently juvenile; cells are mostly vertically elongate, 7(6)–11 µm long and 6(5)–9 µm broad. I have previously regarded this species to be a poorly developed form of *L. engelhartii* [*Magnephycus engelhartii*]. It seems though to be more closely related to *Lithoth. bisporum* [*Hyperandri bisporum*]; but still shows closer affinity with those species being loosely attached to the substratum, among them *L. engelhartii*, and the coaxial hypothallium is more strongly developed than the perithallium.- It is only known from "The Pacific coast of middle Japan: Marine Laboratory at Sagami prov." (K. Yendo, no. 228 delvis).

The species was not mentioned in Foslie's later publications. Printz (1929) did not illustrate any material but included *L. vescum* in his key of *Lithothamnion* species as being closely related to a group of species containing tetrasporangial conceptacles (rather than bisporangial conceptacles as said in the protologue). According to Woelkerling (1993a: 236), the type material in TRH "consists . . . of a few small fragments detached from the host, *Ecklonia*." Foslie's annotation "delvis" (partly) on the box containing the type material (Woelkerling et al. 2005: 246) indicates the existence of heterogeneous specimens, and hence, lectotypification remains to be proposed. Adey (1970: 26–27) transferred the species to *Mesophyllum* without comment. No other records exist, but *Lithothamnion vescum* is listed in the checklists of macroalgae from Japan (Yoshida et al. 1990, 1995, 2015). *Mesophyllum vescum* is here placed in the tribe Melyvonneeae with reservation, following Adey's (1970) opinion. Still, the minute thallus (5 mm in diameter) in combination with the bisporangial conceptacles and the epiphytism on *Ecklonia* suggest that it may be related to *Orthocarpa eckloniae* (Orthocarpoideae, Melobesiaceae).

Mesophyllum sp.

Comments: "A single undescribed species was the dominant plant at Shishibana, near Cape Esan [eastern Hokkaido], representing 30% of coralline coverage at all depths" (Adey et al. 1976: 312).

MAGNEPHYCEAE ATHANAS. ET D. L. BALLANT. TRIB. NOV.

Magnephyceae Athanas. et D. L. Ballant. trib. nov. (type: *Magnephycus*).

Diagnosis: New tribe of Mesophylloideae comprising the genera *Leptophytum*, *Kvaleya*, *Leptothallia* gen. nov., *Macedonis* gen. nov., *Hyperandri* gen. nov., *Ectocarpa* gen. nov., *Magnephycus* gen. nov., *Mastophoropsis*, and *Phymatolithopsis* (the latter genus as incertae sedis). It differs from the other tribes of the subfamily by lacking the bilateral organization of Amphithallieae and the predominantly coaxial hypothallium of Melyvonneeae (coaxial to noncoaxial regions or patches still occur in *Magnephycus simulans* and *Magnephycus engelhartii*) and shares with Melyvonneeae the ancestral thallus organization (monopodial-dorsiventral with polystromatic hypothallium).

Comments: Magnephyceae represent the most heterogeneous assemblage of the subfamily Mesophylloideae, its genera displaying several unique differentiations, which suggests the presence of several remotely related lineages. These differentiations include the occurrence of short subepithallial meristematic cells (*Leptophytum*, *Kvaleya*, *Phymatolithopsis*), development of an erect taeniform–stipitate thallus (*Mastophoropsis*), and production of spermatangia on pedestals (*Magnephycus*, *Hyperandri*). The canal structure also shows variation, being pyriform (*Magnephycus*) or typically straight (in most other genera). Pore filaments are generally unbranched and can be nondifferentiated (in *Kvaleya*, *Phymatolithopsis*, and several species of *Leptophytum*, e.g., *L. flavescens* and *L. tenue*) or exhibit elongate subbasal cells (*Macedonis*) or elongate basal and subbasal cells (*Magnephycus*) or show larger–elongate basal and subbasal cells (*Mastophoropsis*, *Ectocarpa*). Spermatangial structures and fusion cell development varies as in other tribes, but the latter character is unknown in several genera (*Macedonis*, *Hyperandri*, *Ectocarpa*, *Mastophoropsis*, and most species of *Leptophytum*). In particular, spermatangia are either simple (unbranched) and/or dendroid (branched), whereas the fusion cell is inconspicuous in *Kvaleya*, *Leptothallia*, and *Phymatolithopsis*, having a medium size in *Leptophytum laeve*. Postfertilization stages in the genera *Macedonis*, *Hyperandri*, *Ectocarpa*, *Magnephycus*, and *Mastophoropsis* are unknown or poorly documented. No unique synapomorphies for the tribe Magnephyceae were demonstrated (Figure 6c), except the loss of isodiametric epithallial cells (character 11), which merits further study of the epithallium. Monophyly was achieved after treating the presence of a pedestal in male conceptacles (character 19) of particular systematic significance (and increasing its weight three times), in which case this character resolved as a synapomorphy for *Hyperandri*, *Ectocarpa*, and *Magnephycus* (Figure 6c). This a priori assumption is supported by the fact that this pedestal is similarly constructed in the member taxa, showing a layer of palisade cells (in *Hyperandri* and *Magnephycus*), with the addition of up to 7–8 layers of isodiametric cells in *Magnephycus* and an intermediate state shown in an undescribed Brazilian species (Figure 5p,q; see characters 19–20 in "Character Evolution in the Mesophyllaceae"). A comparison between the nine genera of Magnephyceae is given in Table 5.

Leptophytum W. H. Adey

Leptophytum W. H. Adey 1966: 324 (type: *L. laeve*).

TABLE 5. Comparative data for genera of Magnephyceae. Abbreviations: hypog., hypogynous; IDS, in different species; ND, no data; nondiff., nondifferentiated; SUG, superimposed unattached growth.

Characteristic	***Leptophytum***[a] **(8 species)**	***Kvaleya epilaeve***[b]	***Leptothallia acervata***[c]	***Macedonis***[c] **(4 species)**	***Hyperandri***[c] **(3 species)**	***Ectocarpa capverdensis***[c]	***Magnephycus***[c] **(3 species)**	***Mastophoropsis canaliculata***[d]	***Phymatolithopsis***[e] **(2 species)**
Distribution	Arctic, North Pacific, North Atlantic	Arctic	South Africa	NE America to Pacific Mexico, North Aegean Sea	Pacific Mexico, Caribbean, Canaries	Easter Island, Cape Verde, Canaries	Caribbean, Indo-Pacific, Southern Australia	Southern Australia	South Africa, southern Australia
Host/substratum	Epilithic	Parasite on *Leptophytum*	Epilithic	Epilithic, epizoic, epiphytic	Epilithic, epizoic, epiphytic	Epilithic, epizoic, epiphytic	Epilithic, epizoic, epiphytic	Epilithic	Epilithic, epizoic
Thallus habit	Encrusting, SUG (IDS)	Encrusting	Encrusting	Foliose, SUG	Encrusting	Foliose, SUG	Foliose, SUG	Taeniform-stipitate, erect thallus	Encrusting
Hypothallium	Predominantly noncoaxial	Noncoaxial	Noncoaxial	Predominantly noncoaxial	Noncoaxial	Predominantly noncoaxial	Noncoaxial with coaxial regions (IDS)	Noncoaxial	Noncoaxial
Subbasal hypothallial cell	Nonelongate	Nonelongate	Nonelongate	Elongate	Nonelongate	Elongate	Elongate	Nonelongate	Nonelongate
Subepithallial cell	Short	Short	Elongate	Elongate	Elongate	Elongate	Elongate	Elongate	Short
Trichocytes	Absent (present[f])	Absent	Present	Present or absent (IDS)	Present or absent (IDS)	Absent	Absent	Absent	Absent
Gametophytes	Dioecious or monoecious (IDS)	ND	Dioecious	Monoecious	Dioecious	ND	Dioecious	Dioecious	Dioecious
Fusion cell	>6 supp. cells + 1–2 hypog. cells	Inconspicuous	Inconspicuous	ND	ND	ND	ND	Inconspicuous	Inconspicuous
Pedestal in male conceptacles	Absent	Absent	Absent	Absent	Present	ND	Present	Absent	Absent
Spermatangia	Unbranched and dendroid	Unbranched	Unbranched (few dendroid)	Unbranched	Unbranched	ND	Unbranched (few dendroid)	ND	Unbranched and dendroid
Differentiated pore cells	Thinner–wider toward the base or nondiff. (IDS)	ND	Thinner–wider (basal and subbasal cells)	Thinner–wider, elongate subbasal cells	Thinner–wider (basal, subbasal, and third cells)	Larger–elongate basal and subbasal cells	Elongate basal and subbasal cells	Larger–elongate basal and subbasal cells	Nondiff.
Canal shape	Straight	Straight	Straight	Straight	Straight	Straight	Pyriform	Straight	Straight
Embedded conceptacles	Present or absent (IDS)	Absent	Present	Present	Present	Absent	Absent	Absent	Present or absent (IDS)

[a] Adey (1966), Athanasiadis and Adey (2006), Athanasiadis (2007a), and present study.
[b] Adey and Sperapani (1971) and Woelkerling (1988).
[c] Chamberlain and Keats (1994) and present study.
[d] Woelkerling (1978, 1988, 1996) and present study.
[e] Van der Merwe and Maneveldt (2014, "*Phymatolithon ferox*") and present study.
[f] In conceptacle roofs of *L. tenue* (Athanasiadis and Adey 2006).

Comments: With the transfer of three species from the temperate Pacific coast of North America to the new genus *Macedonis* (i.e., *Leptophytum lamellicola*, *L. julieae*, and *L. kymatodes*), *Leptophytum* becomes homogeneous, including eight Arctic, subarctic, and temperate members. In the northern hemisphere, *Leptophytum helenae* is the southernmost representative, being described from the deep sublittoral of Pacific Mexico; *L. helenae*, *L. laeve*, *L. flavescens*, *L. elatum*, and *L. tenue* are the only species of the genus in which gametophytes have been described. Six other species remain little known and are here treated as incertae sedis (i.e., *Leptophytum coulmanicum*, *L. foveatum*, and *L. granuliferum* from the southern hemisphere, *L. bornetii* and *L. elatum* from the NE Atlantic, and *L. microsporum* from the NE Pacific). Generic features that are diagnostic (in combination) include a nonparasitic nature, monopodial-dorsiventral thallus organization with a polystromatic noncoaxial hypothallium, short subepithallial meristematic cells supporting 1 or 2 (3) flattened epithallial cells (with a slightly domed outer wall), and development of a medium-size fusion cell. The latter character has so far been recorded only in the generitype *L. laeve*, in which the fusion cell incorporates at least 5–6 supporting cells and possibly 1 or 2 hypogynous cells and the radiating gonimoblast produces carposporangia laterally from the periphery of the fertile zone (Adey 1966: figs. 77, 80). Sexual reproduction is unknown in most members, but the generitype (*L. laeve*) is dioecious, and *L. tenue* is monoecious. In *L. helenae* and *L. flavescens* both male and carposporangial conceptacles are recorded, but whether they are restricted to separate thalli is unknown (Athanasiadis 2007b, 2016a: table SII). In *L. elatum* only males are recorded, suggesting dioecy (Chamberlain 1990). Spermatangial structures are predominantly simple, with dendroid spermatangia recorded in *L. tenue* and *L. elatum* and sporadically in *L. laeve*. Pore filaments display thinner–wider pore cells (toward the base) in *L. laeve*, *L. arcticum*, *L. foecundum*, and *L. jenneborgii* (Athanasiadis 2016a: table SII), whereas pore cells are nondifferentiated in *L. flavescens*, *L. tenue*, *L. elatum*, and *L. bornetii*. Trichocytes have been rarely recorded on conceptacle roofs of *L. tenue*, whereas conceptacle embedding divides the genus (as in *Mesophyllum*) into two groups: *Leptophytum flavescens*, *L. foecundum*, *L. helenae*, and *L. jenneborgii* show this character, whereas *L. adeyi*, *L. bornetii*, *L. elatum*, *L. laeve*, *L. microsporum*, and *L. tenue* lack it. In addition, the strongly adhering and strictly encrusting thallus of most species (e.g., *L. laeve* and *L. adeyi*) is apparently a stage toward thallus superimposition that occurs in *L. tenue*, with further development into a foliose habit (with unattached superimposed growth) in *L. arcticum* and *L. jenneborgii*. Whether this thallus evolution is coupled with other specializations reflecting relationships between members remains to be investigated.

Leptophytum adeyi **R. S. Steneck et R. T. Paine**

Leptophytum adeyi R. S. Steneck et R. T. Paine 1986: 235–236, figs. 32–33.

Homotypic Synonym: *Phymatolithon adeyi* (R. S. Steneck et R. T. Paine) P. W. Gabrielson in Gabrielson et al. 2000: 37.

Type Locality: North shore of Tatoosh Island, Washington State, USA.

Holotype: In US (79-TIW-2, 7 October 1979, coll. R. T. Paine), illustrated by Athanasiadis and Adey (2006: figs. 108–122).

Habitat and Distribution: The holotype specimen encrusts (and envelops) a pebble. It was collected in the littoral zone in a tide pool in a cave below a canopy of macroalgae. Both thallus grazing and diatom fouling were reported on the thallus (Steneck and Paine 1986). The species is known only from the type locality and the holotype material.

Comments: The holotype (tetrasporophyte) was reexamined by Athanasiadis and Adey (2006: 98–101, figs. 108–122, table 1), who could not match its characters to other reported fertile collections, the latter being referred by them to *Leptophytum tenue* or *Leptophytum foecundum* var. *sandrae*. Athanasiadis and Adey concluded that *L. adeyi* was most closely related to the North Atlantic *Leptophytum laeve*, which is also reported from the Pacific coast of Russia, Hokkaido, and Kukak Bay in Alaska (Athanasiadis and Adey 2006: 106).

Leptophytum arcticum **(Kjellm.) Athanas.**

FIGURES 26, 27

Leptophytum arcticum (Kjellm.) Athanas. 2007a: 477.

Basionym: Lithophyllum arcticum Kjellm. 1877a: 16, pl. 1, figs. 1–13.

Homotypic Synonyms: Lithothamnion arcticum (Kjellm.) Foslie 1898b: 7.

Mesophyllum arcticum (Kjellm.) Athanas. 1996b: 47.

Neopolyporolithon arcticum (Kjellm.) P. W. Gabrielson, S. C. Lindstrom, et Hughey 2019: 231.

Type Locality: Uddebay (74°5′N), east coast of Novaya Zemlya, western Kara Sea, Russia.

Lectotype: In UPS (unnumbered, collected in September 1875, coll. F. R. Kjellman), designated and illustrated by Athanasiadis (2001: 94, fig. 1).

Paratypes: In L (943.7-98 and 0056920, “Mare Caricum: Uddebay 30/8/1875 F.R. Kjellman”), Woelkerling and Verheij (1995: 36; Figure 26a,b); in TRH (B18-2593), Woelkerling (1993a: 30, “syntype,” “a number of fragments”), Woelkerling et al. (2005: 348–349, “paratype”).

Material Examined: Paratype in L (L0056920), as described above and below.

Habitat and Distribution: According to the protologue this species occurs abundantly at the type locality (Uddebay, western Kara Sea), growing in large numbers in the sublittoral at hard bottom, 8–18 m depth. It covers a large area, being slightly attached to *Phymatolithon purpureum* and stones, but according to Kjellman (1877a: 16, in translation), “I suspect that it finally gets free from the matrix and lies free on the bottom.” No later

FIGURE 26. *Leptophytum arcticum*: paratype of *Lithophyllum arcticum* in L (L943.7-98-L0056920), dated 30 August 1875. (**a**) The box holding the entire collection, including a label, and (**b**) several fragments showing the typical foliose habit with unattached superimposed growth. Scale bars: 2 cm.

records of the species have been reported (Athanasiadis 2001: fig. 30).

Comments: *Leptophytum arcticum* and *L. jenneborgii* differ from congeners in their foliose habit (resulting via unattached superimposed growth), which otherwise characterizes mesophylloids (and other corallines) in the tropics and subtropics, leading to the postulation that these two Arctic species evolved during warmer geological periods, presumably before the beginning of the cooling period in the mid-Tertiary (Oligocene, 23–38 MYA; Adey et al. 2001: 200–201; Athanasiadis 2008: 229). Kjellman himself was puzzled by the extraordinary finding he made, making the remark that the genus makes a jump from about 55°N to 74°N latitude (Kjellman 1877a: 18, “ett hopp från ungefär 55:te till 74:de breddgraden”) and referring in comparison to the only other European species of Mesophyllaceae known at that time from Ireland, *Mesophyllum lichenoides*.

The lectotypification of the species was made after a study of the original material in Kjellman’s herbarium in UPS (Athanasiadis 2001).

Here we provide information from the paratype in L (0056920; Figure 26a,b). It consists of five fragments that are sterile but show the typical unattached superimposed growth of the species. Thallus organization is monopodial-dorsiventral with a polystromatic hypothallium, growing by terminal divisions (Figure 27a,d). Terminal subdichotomous divisions add to the thallus thickness (Figure 27b), so that terminal meristematic cells become gradually displaced dorsally to become epithallial cells (Figure 27c), which is commonly observed in all species of Mesophyllaceae (e.g., *Phragmope*; Athanasiadis 2020b: fig. 2f–h), except members of Clathromorphoideae, which display a gradual meristem embedment. One to three flattened epithallial cells occur at a time, and new epithallial cells develop from subepithallial meristematic cells that are ± isodiametric to slightly elongate and generally shorter than cells below (Figure 27e–g). Descending hypothallial filaments end in wedge-shaped cells (Figure 27h). No evidence of an embedding process of the terminal meristematic cells like what occurs in species of *Clathromorphum* and *Neopolyporolithon* was observed (Adey and Johansen 1972: fig. 15; Lebednik 1977a: figs. 8e, 14a, 19d; Figure 7a,e,g). Hence, we can support neither the transfer of *L. arcticum* to *Neopolyporolithon* nor its synonymy with *Neopolyporolithon loculosum*, the latter species also being described by Kjellman a few years later from the Bering Island in the Bering Sea (Kjellman 1889, as *Lithothamnion loculosum*). Furthermore, the proposed synonymy was based on a comparison between a partial (263 bp) DNA sequence from type material of *L. arcticum* (UPS) and

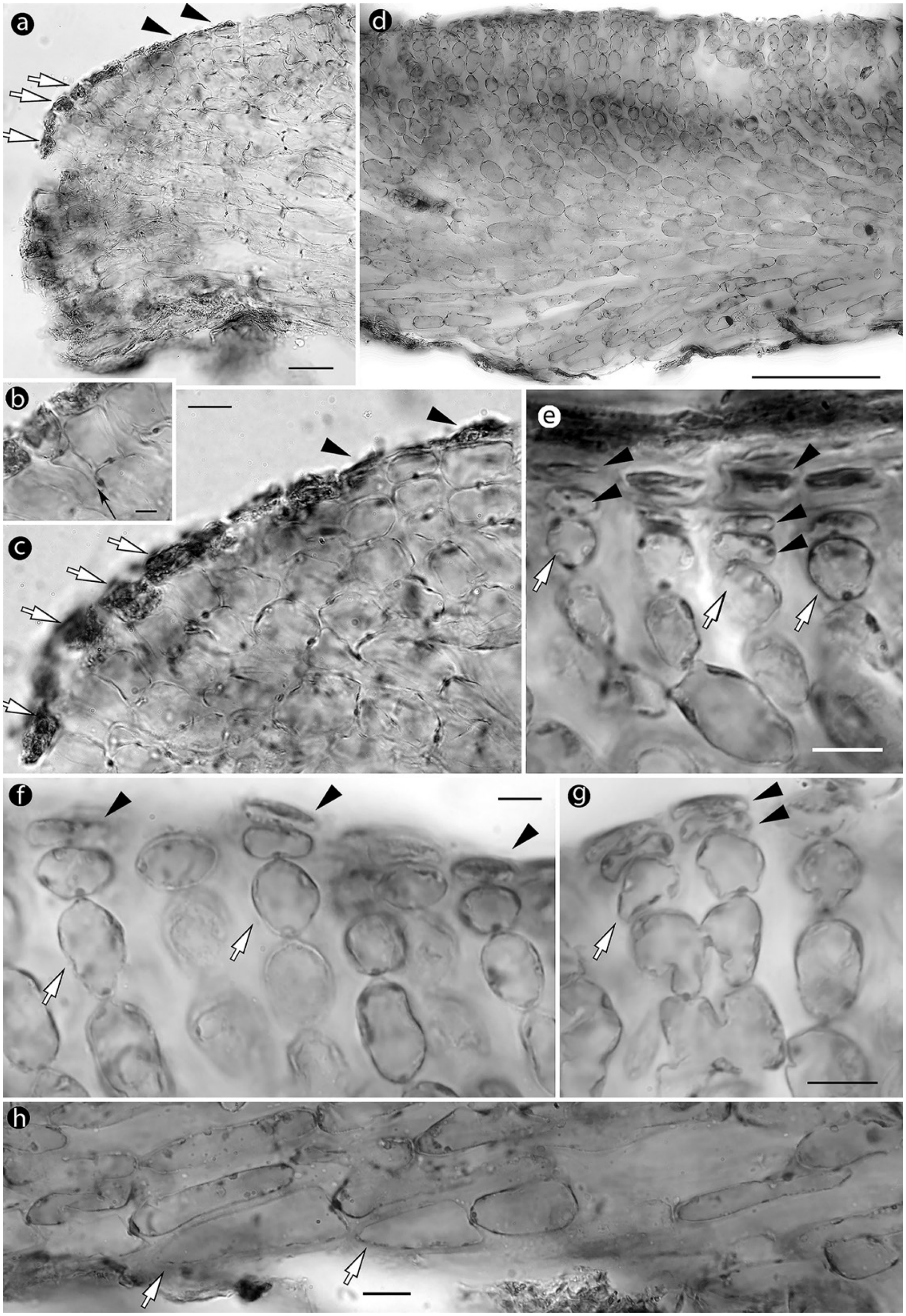


FIGURE 27. *Leptophytum arcticum*: paratype in L. (**a–c**) Sections at the margin showing terminal meristematic cells (arrows) becoming laterally displaced via subdichotomous divisions (arrow in (b)) to become epithallial cells (arrowheads in (a) and (c)). Scale bars: 10 μm. (**d**) Section showing a noncoaxial hypothallium supporting an ascending perithallium. Scale bar: 100 μm. (**e–g**) Sections at the surface showing isodiametric subepithallial cells (arrows) producing epithallial cells (arrowheads), up to 3 present at a time. Scale bars: 10 μm. (**h**) Descending hypothallial filaments ending in wedge-shaped cells. Scale bar: 10 μm.

full-length sequences of 1,384 bp of *Neopolyporolithon loculosum* (Gabrielson et al. 2019), a method that has been criticized because it assumes that no further changes take place in the unknown (longer) part of the sequence (Athanasiadis 2020a: 75).

Leptophytum flavescens **(Kjellm.) Athanas.**

Leptophytum flavescens (Kjellm.) Athanas. 2016a: 552.

Basionym: Lithothamnion flavescens Kjellm. 1883: 129–131 (1885: 98–99), pl. 6, figs. 1–7.

Type Locality: Karlsøy, Troms, North Norway.

Lectotype: In TRH (B3-1772, [10] June 1875, includes slide 184), designated and illustrated in Athanasiadis (2016a: figs. S1, S2 of the supplementary material).

Isolectotypes: In UPS (A-515201, one slide numbered 52:26, and A-003779-411659, Karlsøy, Troms, North Norway, coll. F. R. Kjellman, 10 June 1875).

Syntypes: In UPS (seven slides: A-515185 [“Bot. Mus.Upsala 52:23”], A-515186 [“Bot.Mus.Upsala 52:24”], A-515188 [“Bot.Mus.Upsala 52:25”], A-515197 [“Bot.Mus.Upsala 52:28”], A-515203 [“Bot.Mus.Upsala 52:28”], A-515221 [“Bot.Mus.Upsala 52:29”], and A-515232 [“Bot.Mus.Upsala B3:48”], most slides further annotated “Lithoth . . . flavescens,” “N.Semlja,” and/or “Karmak,” Karmakul Bay, western Novaya Zemlya, Russia, coll. F. R. Kjellman, June 1875).

Habitat and Distribution: This species is recorded from the sublittoral zone, 10–40 m depth, attached to other corallines, pebbles, and shells. It has been collected in the Troms area, North Norway (Karlsøy and Storkorsnes in Altenfjord), NW Spitsbergen (Musselbay, Liefdefjord), and western Novaya Zemlya (Karmakul Bay).

Comments: The exact date of collection of the original material is 10 June 1875, and it is stated on the isolectotype material (UPS), whereas the TRH lectotype is annotated June 1875 (“18 /6 75”). The study of the original material revealed that *L. flavescens* differs from *L. laeve* in possessing a thicker perithallium (to 900 vs. 350 μm in *L. laeve*) that embeds older conceptacles and nondifferentiated (in size or shape) pore cells in filaments lining canals of multiporate conceptacles (Athanasiadis 2016a: figs. S1–S43).

Leptophytum foecundum **(Kjellm.) W. H. Adey**

Leptophytum foecundum (Kjellm.) W. H. Adey 1966: 325.

Basionym: Lithothamnion foecundum Kjellm. 1883: 131–132 (1885: 99–100), pl. 5, figs. 11–19.

Homotypic Synonym: *Phymatolithon foecundum* (Kjellman) L. Düwel et S. Wegeberg 1996: 482.

Syntype Localities: Actinia Bay (76°8′N, 90°25′E) and Uddebay (east coast of Novaya Zemlya, at 74.5°N).

Lectotype: In UPS (unnumbered, undated), annotated “*Lithothamnion foecundum* orig. ex.” coll. F. R. Kjellman, includes five slides B3: 96, B3: 97, B3: 98, B3: 99, B3: 100, each annotated by Kjellman “*Lithothamnion foecundum* Kariska havet”), Athanasiadis and Adey (2006: 92–93, “holotype”), Düwel and Wegeberg (1996: fig. 4b, “holotype”), Alongi et al. (2002: fig. 9, “holotype”), Athanasiadis and Adey (2006: fig. 77, “holotype”), Athanasiadis (2007a: 477, “holotype”).

Syntypes: In S (unnumbered, “*Lith. foecundum* Kjellm. Alg.arct Sea . . . *Lithothamnion polymorphum* (L.) Aresch. . . . Mare Caricum: Uddebay 30 1875 F.R. Kjellma*n*”); in TRH (B2-1695), Adey and Lebednik (1967: 51), Woelkerling et al. (2005: 240, “Kjellman . . . Kariske Hav . . . Novaja Zemljas . . . ostkust vid Uddebay . . . viii. 1875,” includes slide 186).

Comments: Two (syntype) localities were cited in the protologue (Kjellman 1883), namely, Actinia Bay and Uddebay (both in the Kara Sea). Chamberlain (1990: 181) originally selected as “holotype” material in UPS from Cap Taimur, which was not included in the distribution of the species (Athanasiadis and Adey 2006: 93), and later Düwel and Wegeberg (1996) selected an undated and unlocalized specimen from the Kara Sea as “holotype” (UPS). The latter specimen was also studied by Alongi et al. (2002), Athanasiadis and Adey (2006), and Athanasiadis (2007a), who all recognized it as the “holotype.” However, it appears that at least two other (dated) (syn)type collections from Uddebay exist: one in TRH and one in S (Athanasiadis, personal observation, 2–3 December 2004), and hence, the UPS “holotype” has to be recognized as a lectotype.

Leptophytum foecundum **var.** ***foecundum***

Leptophytum foecundum var. *foecundum*.

Habitat and Distribution: The autonym variety of the species grows on pebbles, cobbles, worm tubes, shells (*Buccinum hydrophanum* Hancock), and *Laminaria* haptera, between 9 and at least 120 m depth. It is an Arctic alga widely recorded from Greenland, Spitsbergen, Iceland, northern Norway, Russia, and also Alaska (Boulder Patch, Stefansson Sound; Athanasiadis and Adey 2006: 92–93, figs. 76–87, table 1; Athanasiadis 1996b: 255–256, and references therein, 2007a: 477–485, figs. 33–55, table 1). The southernmost record in the NE Atlantic is in North Norway (Porsangerfjord and near Tromsø), where, according to Foslie (1905b: 21–23), it grows between ~9 and 37 m depth, “both on the open coast and in sheltered places where tidal waters run rather strongly . . . sporadically in small numbers of individuals together with other calcareous algae, often sharing substratum with *Lithop. laeve* . . . found . . . with sporangia in June, July, August and October.”

Comments: *Leptophytum foecundum* has also been reported from Antarctica (Zaneveld and Sanford 1980: 224–225; Alongi et al. 2002), in the latter study being erroneously treated as conspecific with the indigenous *Leptophytum coulmanicum* (here as incertae sedis Magnephyceae). Zaneveld and Sanford’s (1980) record requires confirmation in light of reported deviations regarding thallus size (said to be 1–4 mm in diameter), epithallium (said to be 1–5 cells thick), and fertility (carposporophytes are unknown in *L. foecundum*). *Leptophytum laeve* and *L. foecundum* have been included in phylogenetic analyses of the nSSU, *psb*A, and *rbc*L genes, which revealed a remote relationship (Adey et al. 2015: fig. 6). The same studies indicated a sister taxon relationship for the Arctic species *Clathromorphum compactum* and *C. circumscriptum*, as originally proposed by Foslie (1905b: 88–95), who considered them to be conspecific, differing at the level of forma. This suggests a much deeper branching for the two species of *Leptophytum*, which differ in a considerable number of characters (Athanasiadis and Adey 2006: table 1; Athanasiadis 2007a: table 1, 2016a: tables 1–2).

***Leptophytum foecundum* var. *sandrae* Athanas. et W. H. Adey**

Leptophytum foecundum var. *sandrae* Athanas. et W. H. Adey 2006: 93–98, figs. 88–107.

Type Locality: Sublittoral, 6–17 m depth, boulders with sandy patches, east side of Fleming Island, Bamfield area (48°53′N, 125°07′02″W), Canada.

Holotype: In UBC (A48009; Pace and Baillie no. 26943, 19 July 1969, coll. Pace and Baillie), designated and illustrated by Athanasiadis and Adey (2006: fig. 88).

Habitat and Distribution: Specimens have been collected in the sublittoral zone (6–17 m depth), attached to wood fragments, shells, and polychaete tubes. Variety *sandrae* is recorded from Vancouver Island (Hardy Bay; 51°N); sites off the SW coast, such as Tzartus, Wizard, Edward King, and Fleming Islands (all near Bamfield; 48°48′N); and Washington State (Channel Rocks near Seattle; 47°21′N).

***Leptophytum helenae* Athanas.**

Leptophytum helenae Athanas. 2007b: 201–207, figs. 1–22.

Type Locality: Sublittoral, 63–72 m depth, at center of Tanner Bank (approximately 32°42′07″N, 119°07′40″W), Pacific Mexico.

Holotype: In UC (unnumbered, AHFH 70351, Dawson no. 8027, *pro parte*, a tetrasporangial specimen, collected 27 August 1949 via dredging by E. Y. Dawson), illustrated by Athanasiadis (2007b: figs, 1A, 2).

Habitat and Distribution: Specimens or fragments are firmly attached to other coralline algae, corals, and polychaete tubes in the sublittoral zone, 36–72 m depth. The species is recorded only from the type locality and the nearby Cortez Bank.

Comments: This is the southernmost species of the genus in the NE Pacific. Its occurrence in the deep sublittoral indicates a preference for cold waters, which is the case with all species of *Leptophytum*. *Leptophytum helenae* is most closely related to *Leptophytum foecundum* var. *sandrae*, as the two taxa share identical multiporate conceptacle characteristics (including pore cell morphology, roof structure, embedding type, etc.). It differs from var. *sandrae* mainly in habit (lacking thallus superimposition and unattached, freely growing margins) and exhibiting sexual reproduction (only bisporophytes are known in var. *sandrae*) and shorter hypothallial cells (8–22 vs. 15–32 µm in var. *sandrae*). Further studies of new collections are needed to establish the distributional range of both taxa on the Pacific coast.

***Leptophytum jenneborgii* Athanas.**

Leptophytum jenneborgii Athanas. 2007a: 472–477, figs. 2–32.

Misapplied Name: Mesophyllum lichenoides sensu Hansen and Jenneborg 1996: 372 [non *Mesophyllum lichenoides* (J. Ellis) Me. Lemoine].

Type Locality: Sublittoral, 25–30 m depth, st. 56, Hornbækfjellet, Raudfjord, Vasahalvøya (79°50′N, 11°52′E), NW Spitsbergen.

Holotype: In GB (GB-0209477, herb. Jenneborg 79-07-31, tetrasporangial specimen 1, coll. L.-H. Jenneborg, 31 July 1979, attached to *Lithothamnion* sp.), illustrated in Athanasiadis (2007a: figs. 2–4, 10, 12, 14, 16, 19, 22, 25–27, 32).

Paratypes: In GB (GB-0209478, herb. Jenneborg 79-07-31, tetrasporangial specimen 2), illustrated by Athanasiadis (2007a: figs. 5, 13, 20, "isotype"); in GB (GB-0209479, herb. Jenneborg 79-07-31, tetrasporangial specimen 3); all paratypes were collected on the same day at the same locality and depth as the holotype but represent different gatherings.

Habitat and Distribution: Leptophytum jenneborgii grows in the sublittoral zone between 8 and 30 m depth, attached to reefs formed by a *Lithothamnion* species, cobbles, and "maerl reefs" (Hansen and Jenneborg 1996: 372). It has been collected at several sites (Sallyhavn, Fairhavn, Fugeløya, and Raudfjord) at Vasahalvøya (NW Spitsbergen).

Comments: Hansen and Jenneborg (1996: 372) reported the species (as *Mesophyllum lichenoides*) to be common "on maerl reefs dominated by *Lithothamnion glaciale* . . . at 8–15 m depth." Only tetrasporophytes and sterile specimens were found in the above collections in Jenneborg's herbarium (GB). The holotype and one of the paratypes were inhabited by a colorless minute coralline with uniporate conceptacles (220–400 µm in external diameter; Athanasiadis 2007a: fig. 32), resembling the parasite *Kvaleya epilaeve*, which was previously reported on *Leptophytum laeve* as far north as Nordkapp in Norway (Adey and Sperapani 1971: 29).

***Leptophytum laeve* (Foslie) W. H. Adey**

Leptophytum laeve (Foslie) W. H. Adey 1966: 324.

Basionym: Lithophyllum lenormandii f. *laeve* Foslie 1891: 45–46 (repr. 10–11), nom. nov. of *Lithophyllum laeve* Strömfelt 1886: 21, pl. 1, figs. 11, 12, nom. illeg. [non *Lithophyllum laeve* Kütz. 1847: 33].

Heterotypic Synonyms: ?*Lithothamnion stroemfeltii* f. *macrosporum* Foslie 1895a: 173 (repr. 145), pl. 22, fig. 12; type: not designated (Woelkerling

1993a: 141, "No specimens . . . found . . . [in TRH]"). Foslie (1905b: 17, synonym of *Lithothamnion laeve*, "I omit the two forms.").

Lithothamnion laeve f. *macrosporum* (Foslie) Foslie 1898b: 7.

Lithothamnion laeve f. *macrosporum* (Foslie) De Toni 1905: 1757, "*macrospora*."

?*Lithothamnion stroemfeltii* f. *tenuissimum* Foslie 1895a: 173 (repr. 145), "*tenuissima*"; type locality; not specified; type: not designated. Foslie (1905b: 17, synonym of *Lithothamnion laeve*, "I omit the two forms.").

Lithothamnion laeve f. *tenuissimum* (Foslie) Foslie 1898b: 7. Foslie (1900b: 15, synonym of *L. laeve* f. *tenue* (Kjellm.) Foslie [=*Leptophytum tenue* (Kjellm.) Athanas. et W. H. Adey—see species account below).

?*Lithothamnion tenue* Rosenvinge 1893: 778–771, figs. 4–7; syntype localities: several in western Greenland; lectotype: in C, Hartz no. 895, collected by N. Hartz, 20 June 1890, at Holstensborg, designated by Düwel and Wegeberg (1996: 478). Athanasiadis (2007a: 491,[37] synonym?).

Lithothamnion stroemfeltii Foslie 1895a: 145–150 (repr. 173–178), nom. illeg. [*Lithothamnion tenue* Rosenvinge 1893 was cited as a synonym].

Lithothamnion laeve (Foslie) Foslie in Rosenvinge (1898: 14), nom. illeg. [*Lithothamnion tenue* Rosenvinge 1893 was cited as a synonym].

Phymatolithon tenue (Rosenvinge) Düwel et Wegeberg 1996: 482.

Type Locality: Lower littoral, Eyrarbakki, South Iceland.

Holotype: In S (unnumbered, herb. Strömfelt, a slide annotated "*Lithophyl. laeve* n. sp. Sporangia Eyr . . . b. på sten i fjäre 4/9 83 G . . . Strömfelt"), illustrated by Düwel and Wegeberg (1996: fig. 1a–c), Adey et al. (2001: 191–198, figs. 1–18), Athanasiadis and Adey (2003: figs. 25, 26).

Epitype: In US (unnumbered, Adey WHA-66-24-J2-070–090, 23–30 m depth, Reydarfjordur [NW center; SW side of Holmanes, 65°2.5′N, 14°0.6′W], East Iceland, 29 July1966, coll. W. H. Adey), illustrated in Athanasiadis and Adey (2003: figs. 1A, 2, 8, 9 12, 13), designated by Athanasiadis (2016a).

Habitat and Distribution: Specimens encrust (and encircle) pebbles and cobbles, polychaete tubes, and shells, growing between the lower littoral (Strömfelt 1886)[38] and the sublittoral to at least 120 m depth. *Leptophytum laeve* is a strictly marine species, recorded only once from Danish Kattegat (Foslie 1905b: 131, Hesselø, 28 m depth, on *Mya* L.). It is widely reported between Massachusetts and north to eastern Arctic Canada, Greenland, Iceland, Spitsbergen, North Norway, and Russia to the British Islands (Adey 1966; Adey and Adey 1973; Lee 1980; Chamberlain 1990; Chamberlain and Irvine 1994; Adey et al. 2001; Athanasiadis 2007a; Athanasiadis 2016b, and references therein). Records from the Pacific coast of North America remain unconfirmed, but the species is also reported from the western Pacific between the Commander Islands, Ozernoi Gulf, in the Bering Sea and eastern Hokkaido (Athanasiadis and Adey 2006: 106).

Comments: In citing the type of the genus *Leptophytum*, Adey (1966: 324) proposed the combination "*Leptophytum laeve* (Strömfelt) Adey, comb. nov.," which is based on the illegitimate name *Lithophyllum laeve* Strömfelt (1886), a later homonym of *Lithophyllum laeve* Kütz. (1847: 33). In order to maintain the species epithet under the generic name *Leptophytum*, Adey et al. (2001: 194) selected the legitimate trinomial *Lithophyllum lenormandii* f. *laeve* Foslie (1891: 45–46) as *nomen novum* and new basionym (Turland et al., 2018: Article 58.1), and hence, the correct author citation for the generitype should be *Leptophytum laeve* (Foslie) W. H. Adey (1966). Previously, Paul Silva had proposed as *nomen novum* "*Lithothamnion leave* Foslie in Rosenvinge 1898" (Silva in Chamberlain 1990: 192) and later "*Leptophytum leave* W. H. Adey 1966" (Silva in Düwel and Wegeberg 1996: 472). In the former case, however, the new name is illegitimate since Foslie (in Rosenvinge 1898) had cited *Lithothamnion tenue* Rosenvinge (1893) as a synonym, whereas in the latter case the new name is invalid since Adey (1966) was obliged to select a type specimen for the new taxon that dates from 1966 (Turland et al. 2018: Articles 40.1, 40.2). Silva's proposals, together with the "epitypification" attempt of *L. laeve* with material belonging to *Phymatolithon lenormandii* (Düwel and Wegeberg 1996), although rectified with the selection of a legitimate basionym and the reestablishment of the status of the holotype of *L. laeve* after its restoration (Adey et al. 2001), caused considerable confusion surrounding the identity of the genus *Leptophytum* and its generitype (see review in Athanasiadis 2016a, 2016b). More recently, because of an increased number of congeners and the lack of gametangial information in the holotype, an epitype was selected (Athanasiadis 2016a: 555), supporting and consolidating the current concept of the species.

Leptophytum laeve is the only species of *Leptophytum* for which postfertilization stages have been documented (Adey 1966: figs. 63–80). They show the development of a medium-size fusion cell incorporating 4–6 supporting cells and possibly 1 or 2 hypogynous cells (Adey 1966: figs. 77, 80). Several Arctic records have been questioned given the uncertainty surrounding *Lithothamnion tenue* Rosenvinge (1893) (Athanasiadis 2007a) and the recognition of *Leptophytum flavescens* (Athanasiadis 2016a). It is also very likely that Kjellman's (1883, 1885) account of *Lithothamnion* (*Leptophytum*) *flavescens* included material of *L. laeve*.

Leptophytum laeve and *L. foecundum* have been included in phylogenetic analyses of the nSSU, *psb*A, and *rbc*L genes, which revealed a remote relationship (Adey et al. 2015: fig. 6). The same studies supported a sister taxon relationship for the Arctic *Clathromorphum compactum* and *C. circumscriptum*, as originally proposed by Foslie (1905b: 88–95), who considered them to be conspecific, differing at the level of forma. Hence, the much deeper branching for the two species of *Leptophytum* most likely reflects the high number of characters distinguishing them (Athanasiadis and Adey 2006: table 1; Athanasiadis 2007a: table 1, 2016a: tables 1–2; see also comments under *L. foecundum*, which has been considered to be a putative hybrid).

***Leptophytum tenue* (Kjellm.) Athanas. et W. H. Adey**

Leptophytum tenue (Kjellm.) Athanas. et W. H. Adey 2006: 74, figs. 1–27.

Basionym: Lithophyllum tenue Kjellm. 1889: 22–23, pl. 1, figs. 6–10.

Homotypic Synonyms: Lithothamnion tenue (Kjellm.) Foslie 1895a: 179, nom. illeg. [non *Lithothamnion tenue* Rosenvinge (1893: 778)].

Lithothamnion laeve f. *tenue* (Kjellm.) Foslie 1900a: 15, "*tenuis*," nom. illeg. [*Lithothamnion stroemfeltii* f. *tenuissimum* Foslie (1895a) was cited as a synonym].
Mesophyllum tenue (Kjellm.) P. A. Lebednik 1974, comb. ined.[39]

Type Locality: Sublittoral, Port Clarence, Alaska, USA.

Lectotype: In TRH (B2-1737, *pro parte*), Printz (1929: pl. 3, fig. 3), Lebednik (1974: pl. 61, figs. 1, 3), designated by Athanasiadis and Adey (2006: fig. 7).

Syntypes: In TRH (B2-1737, *pro parte*); in UPS (unnumbered; Athanasiadis and Adey 2006); in S (A2624, A2625; Athanasiadis, personal observation, 2–3 December 2004).

Habitat and Distribution: Specimens grow in the sublittoral zone on pebbles and shells of *Littorina* Férussac, *Mytilus* L., barnacles, and limpets. At the end of July, they are provided with spermatangial, carposporangial, and multiporate conceptacles (one with bisporangial remains). The species is recorded from Port Clarence (Alaska) and East Sound, Orcas Island (Puget Sound, Washington State; Athanasiadis and Adey 2006).

Comments: Among congeners, *Leptophytum tenue* comes closer to *L. flavescens* in possessing thallus superimposition and nondifferentiated pore cells in canals of multiporate conceptacles. The two species differ in multiporate conceptacle external size (350–720 µm in *L. tenue* vs. 700–1100 µm in *L. flavescens*) and embedding process (only reported in *L. flavescens*). *Leptophytum tenue* differs from the generitype *L. laeve* in being monoecious and in producing coaxial patches in the hypothallium and from all other *Leptophytum* spp. in developing (rarely) trichocytes (on conceptacle roofs; see comparison of *Leptophytum* spp. in Athanasiadis and Adey 2006: table 1). *Leptophytum tenue* is known only from the rich-in-specimens type material and a second collection from East Sound, Orcas Island (San Juan Islands, Washington State, 7.vii.1925, L. Roush no. 56, UC739472) reexamined by Athanasiadis and Adey (2006: figs. 25–27) and previously referred to *L. adeyi* (Steneck and Paine 1986: 235).

Kvaleya W. H. Adey et Sperapani

Kvaleya W. H. Adey et Sperapani 1971: 31 (type: *K. epilaeve*).

Kvaleya epilaeve W. H. Adey et Sperapani

FIGURE 28

Kvaleya epilaeve W. H. Adey et Sperapani 1971: 31–42, figs. 1–16.

Type Locality: Sublittoral, 28 m depth, on *Leptophytum laeve*, Kvaløy, off marine station, southwest corner of Tromsø, Norway.

Holotype: In US (Adey 69-2A).

Isotypes: In US (Adey slide 69-2-1,15, 14 April 1969; Adey and Sperapani 1971); in US (Adey 69-2, Adey, slide 69-2-1-14, cited in Woelkerling 1988: 167, "specimens illustrated").

Material Examined: Southern Ellesmere: on *Leptophytum laeve*, 6 September 1969, coll. R. T. Wilce (C, unnumbered).

Cape Fanshawe: Bylot Island: on *Leptophytum laeve*, 15 August 1979, leg. L.G.L., Ltd. Personnel, det. R. T. Wilce (C, unnumbered).

Habitat and Distribution: *Kvaleya epilaeve* is an obligate parasite on the thallus of *Leptophytum laeve* and possibly *L. jenneborgii*, growing in the sublittoral zone to 70 m depth. It is originally described from several collections of *L. laeve* made between the Gulf of Maine and north Labrador, West and East Iceland, and Trondheim to North Norway ("Nordkapp east to Vardø and Syltefjord on the outer coast . . . in the inner fjords . . . from Trondheimsfjord north to Kirkines"; Adey and Sperapani 1971: 69, fig. 7). Later records were made in the Arctic, including putative specimens growing on *Leptophytum jenneborgii* from the NW coast of Spitsbergen (Athanasiadis 2007a: fig. 32) and material from southern Ellesmere and Bylot Island (eastern Arctic Canada) in C (see Material Examined). A further record in *schedula* (C, unnumbered) from Boulder Patch, "Endicott, Paudae Bay, DS-11, *c.* 20' ", Alaska (coll. and det. R.T Wilce), was checked, and it was concluded that it most likely refers to male conceptacles of *Leptophytum laeve*.

Comments: Two parasitic Mesophyllaceae are known: *Kvaleya*, a putative adelphoparasite on *Leptophytum* spp. (Magnephyceae), and *Capensia* (Amphithallieae), which grows on species of the remotely related rhodophyte genus *Gelidium* (Gelidiales). Both parasites develop haustoria, but *Kvaleya* lacks plastids, as its thallus is colorless, whereas *Capensia* is colored similar to other corallines growing on the same host, which suggests a hemiparasitic nature (Athanasiadis 2017b: fig. 4). Spermatia of *Kvaleya* have been described as being "small, rounded . . . [and] develop from elongate spermatangia. . . . The long spermatangial filaments [dendroid] present in some Lithothamnieae, including the host, do not form." (Adey and Sperapani 1971: 37). Later observations confirmed that spermatangial structures are simple (unbranched; Woelkerling 1988: 169, figs. 182, 183).

Carposporophytes develop carposporangia laterally from the periphery of the fertile zone (Adey and Sperapani 1971: fig. 12; Woelkerling 1988: fig. 186), but the presence or absence of a fusion cell has been under debate. Adey and Sperapani (1971: 37, fig. 12; Figure 28a) described the presence of several "irregularly shaped fusion cells," and Lebednik (1977b: 384, table 3) interpreted the relevant information as showing a "discontinuous" fusion cell. Woelkerling (1988: fig. 186; Figure 28b) showed that there is no conspicuous fusion cell (i.e., an amalgamation of several supporting cells with neighboring hypogynous or basal cells), and hence, the previous reports of several "irregularly shaped fusion cells" or a "discontinuous" fusion cell most likely account for fusions in connection to the radiating gonimoblast filaments. Woelkerling's illustration also shows the amalgamation of remains of carpogonial branches (above the gonimoblast filaments) that could be misinterpreted as orthostichous production of carposporangia (Figure 28b).

Kvaleya is monotypic and shares most of its vegetative and reproductive characters with species of *Leptophytum*, that is,

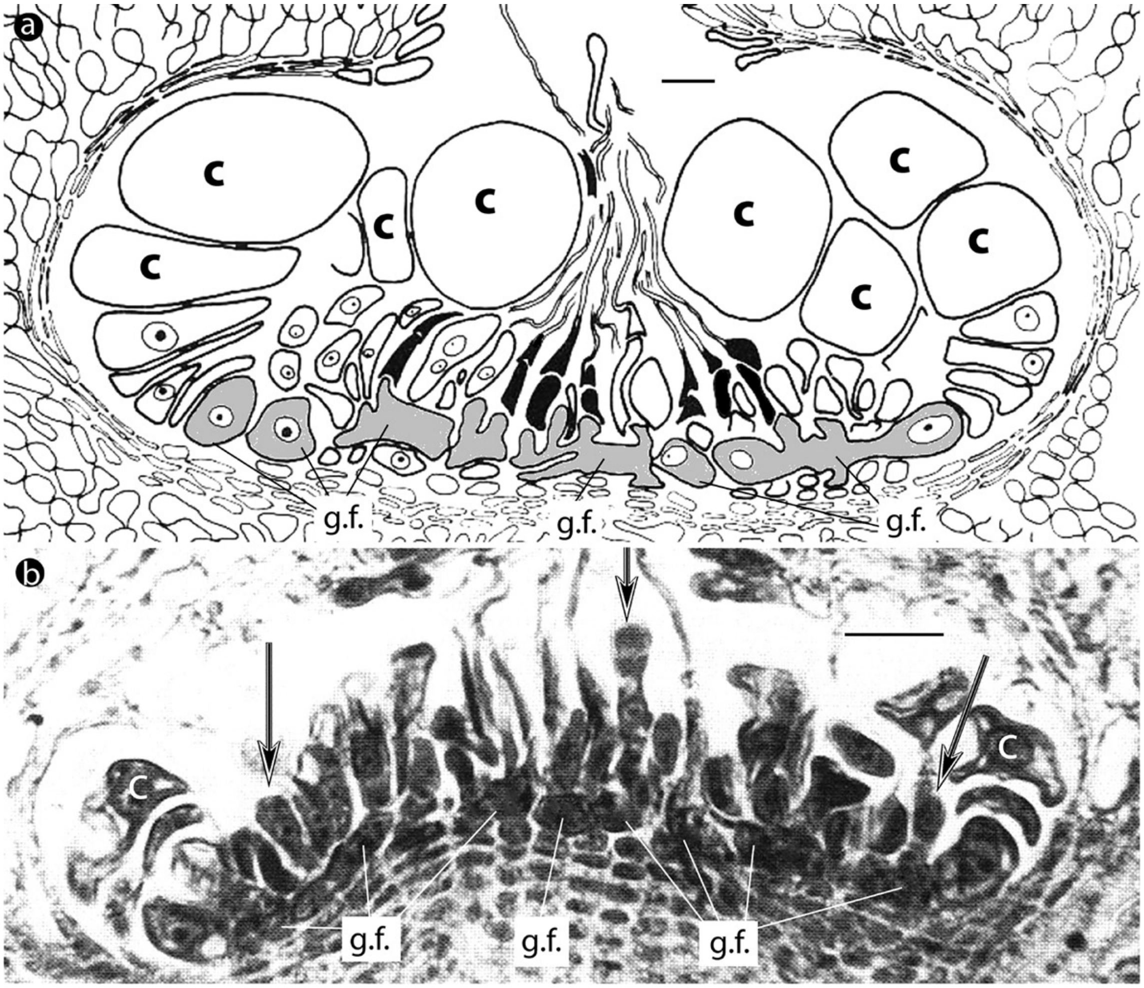


FIGURE 28. *Kvaleya epilaeve*: postfertilization stages showing gonimoblast filaments below remains of 2-celled carpogonial branches (shaded in (a)) and laterally produced carposporangia. Note the coalescing carpogonial branch remains (arrows in (b)). (**a**) Modified from Adey and Sperapani (1971, fig. 12). (**b**) Modified from Woelkerling (1988, fig. 186). Scale bars: 10 µm. Abbreviations: c, carposporangium; g.f., gonimoblast filament.

simple spermatangial structures, monopodial-dorsiventral thallus organization with a noncoaxial polystromatic hypothallium, ± isodiametric subepithallial meristematic cells (shorter than perithallial cells below), round or flattened (but not flared) epithallial cells, and lack of trichocytes (Adey and Sperapani 1971; Woelkerling 1988). This parasitic genus is here hypothesized to have developed in a common ancestor shared by *Kvaleya*'s two known hosts, *L. laeve* and *L. jenneborgii*. *Kvaleya* was not included in the present phylogenetic analysis.

Leptothallia **Athanas. et D. L. Ballant. gen. nov.**

Leptothallia Athanas. et D. L. Ballant. gen. nov. (type: *L. acervata*).

Diagnosis: New monotypic genus of the tribe Magnephyceae, differing from *Leptophytum* in possessing elongate subepithallial meristematic cells, thinner–wider pore cells restricted to the canal base of multiporate conceptacles, and an inconspicuous fusion cell (reported as "discontinuous" and most likely referring to gonimoblast filaments, as shown below).

Etymology: *Leptothallia* is a new compound word of feminine gender, after the adjectives λεπτος, λεπτη, λεπτον (thin, slender, slim) and the masculine noun θαλλος (thallus).

Comments: *Leptothallia* is based on *L. acervata*, which is here segregated from *Leptophytum* on the basis of the characters outlined above. *Leptothallia* shares with *Phymatolithopsis* the presence of an inconspicuous fusion cell and is similar to *Ph. repanda* in lacking erect perithallial protuberances but clearly differs in possessing elongate subepithallial meristematic cells (during cell division) and thinner–wider pore cells restricted to the canal base of multiporate conceptacles. Two other species from South Africa described as members of *Leptophytum* (i.e., *L. ferox* and *L. foveatum*) remain as incertae sedis (see species accounts below). The former is known only from the type collection (a single tetrasporophyte), whereas the latter develops a distinctive fusion cell (composed of at least 5–6 supporting cells) and canals provided with thinner–wider pore cells along half the canal length. Studying the phylogeny of the nSSU gene, Bailey and Chapman (1996: fig. 1, 1998: fig. 1) showed a remote relationship between isolates identified as *Leptophytum foveatum* and *Leptophytum acervatum* and later a close relationship between *L. acervatum* and *Leptophytum ferox*, which was also shown by Broom et al. (2008: fig. 1) and Bittner et al. (2011: fig. 1).

Leptothallia acervata **(Foslie) Athanas. et D. L. Ballant. comb. nov.**

FIGURES 29–33

Leptothallia acervata (Foslie) Athanas. et D. L. Ballant. comb. nov.
Basionym: Lithothamnion acervatum Foslie 1907b: 4.
Homotypic Synonym: *Phymatolithon acervatum* (Foslie) W. H. Adey 1970: 28. Van der Merwe and Maneveldt (2014: 173, figs. 1–21, 75).

Type Locality: Natal, South Africa.

Lectotype: In TRH (B1-1607, includes Foslie slide 702, Natal, coll. A. Weber-van Bosse), Printz (1929: pl. 1, fig. 15), designated by Chamberlain and Keats (1994: figs. 1, 7–10), Woelkerling et al. (2005: 226, "lectotype").

Syntype: In TRH (B1-1608, includes Foslie slide 704, Knysna, Cape Province, South Africa, coll. A. Weber-van Bosse), Printz (1929: pl. 1, fig. 14), designated by Chamberlain and Keats (1994: fig. 6), Woelkerling et al. (2005: 226, "paratype").

Material Examined: South Africa: Dalebrook: False Bay: W. Cape, on stones in the low-tide channel, 21.xi.1991, coll. YMC, 21.xi.1991, on stones in shallow pools (herb. Athanas. D2-YMC 91/212; cited as YMC and DWK 91/212 in Chamberlain and Keats 1994); Western Cape, Holbaaipunt, 26.x.1991, SE of False Bay, on stones in [shallow] pools, coll. YMC and DWK 26.xi.1991 (herb. Athanas. D5-YMC 91/252; cited as YMC and DWK 91/252 in Chamberlain and Keats 1994); on young *Patella*, Holbaaipunt, 26.xi.1991 (herb. Athanas. D6-YMC 91/251; not cited in Chamberlain and Keats 1994); Western Cape, Holbaaipunt, SE of False Bay, on stones in shallow pools (herb. Athanas. D7-YMC 91/75; cited as YMC and DWK 91/75 in Chamberlain and Keats 1994); D-22 (subsample of D2-YMC 91/212; Figure 29).

Habitat and Distribution: This species is reported to be the most abundant coralline on pebbles in tide pools in South

FIGURE 29. *Leptothallia acervata*: thallus habit of four specimens on pebbles. (**a**) D2-YMC 91/212. Scale bar: 2 cm. (**b**) D22-YMC 91/212. Scale bar: 2 cm. (**c**, **d**) D7-YMC 91/75. Scale bars: 1 cm.

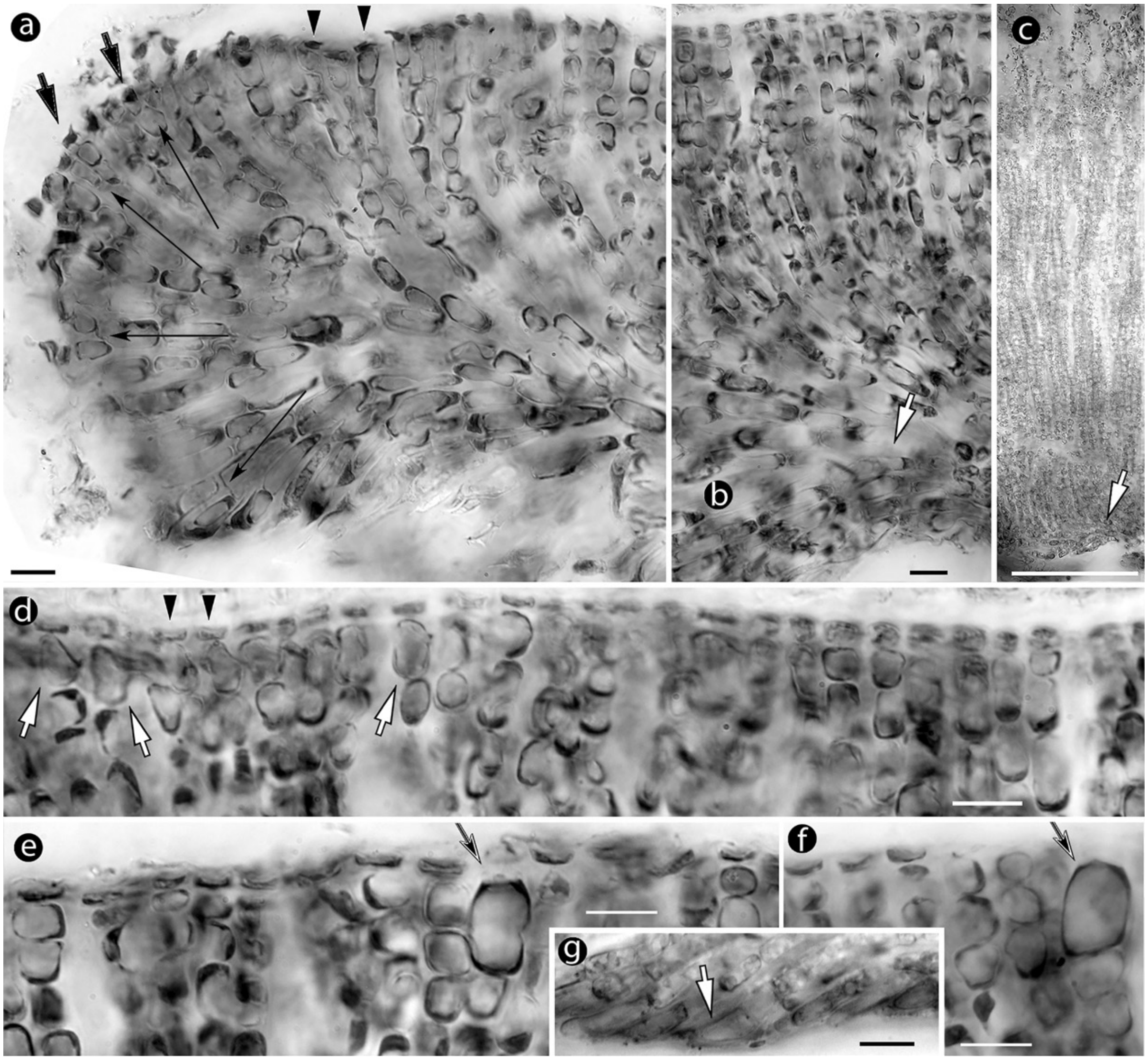


FIGURE 30. *Leptothallia acervata*: vegetative structures. (**a**) Section at the margin showing terminal meristematic cells (short black arrows), subdichotomous divisions (long black arrows), and epithallial cells (arrowheads; D6-YMC 91/251). Scale bar: 10 µm. (**b, c**) Sections showing the limited hypothallium (D6-YMC 91/251 in (b), D5-YMC 91/252 in (c)). Scale bars: 10, 100 µm, respectively. (**d–f**) Sections showing epithallial cells (arrowheads), dividing subepithallial cells (white arrows), and solitary trichocytes (black arrows; D6-YMC 91/251). Scale bars: 10 µm. (**g**) Section showing descending hypothallial filaments ending in wedge-shaped cells (D6-YMC 91/251). Scale bar: 10 µm.

Africa and also occurring in the sublittoral to at least 8 m depth. Its thallus usually envelops small stones, which are used as a cover by the sea urchin *Parechinus angulosus* (Leske). Fertile thalli have been collected in October, November, and December. It is recorded from most localities in South Africa (except the west coast or eastern Natal; Chamberlain and Keats 1994).

Species Description: Thalli are encrusting and strongly adhere to small stones, becoming confluent with crenulate margins (Figure 29). The growth is monopodial–dorsiventral with a poorly developed polystromatic hypothallium, displaying terminal meristematic cells (Figure 30a–c). Via ***subdichotomous*** divisions, meristematic cells gradually become ***displaced dorsally*** to form epithallial cells (Figure 30a). ***Subepithallial meristematic cells are slightly longer*** than cells below (during putative division), supporting single flattened epithallial cells (Figure 30d–f). Rare ***trichocytes*** may occur among epithallial cells (Figure 30e,f). Descending hypothallial filaments end in ***wedge-shaped*** cells (Figure 30g).

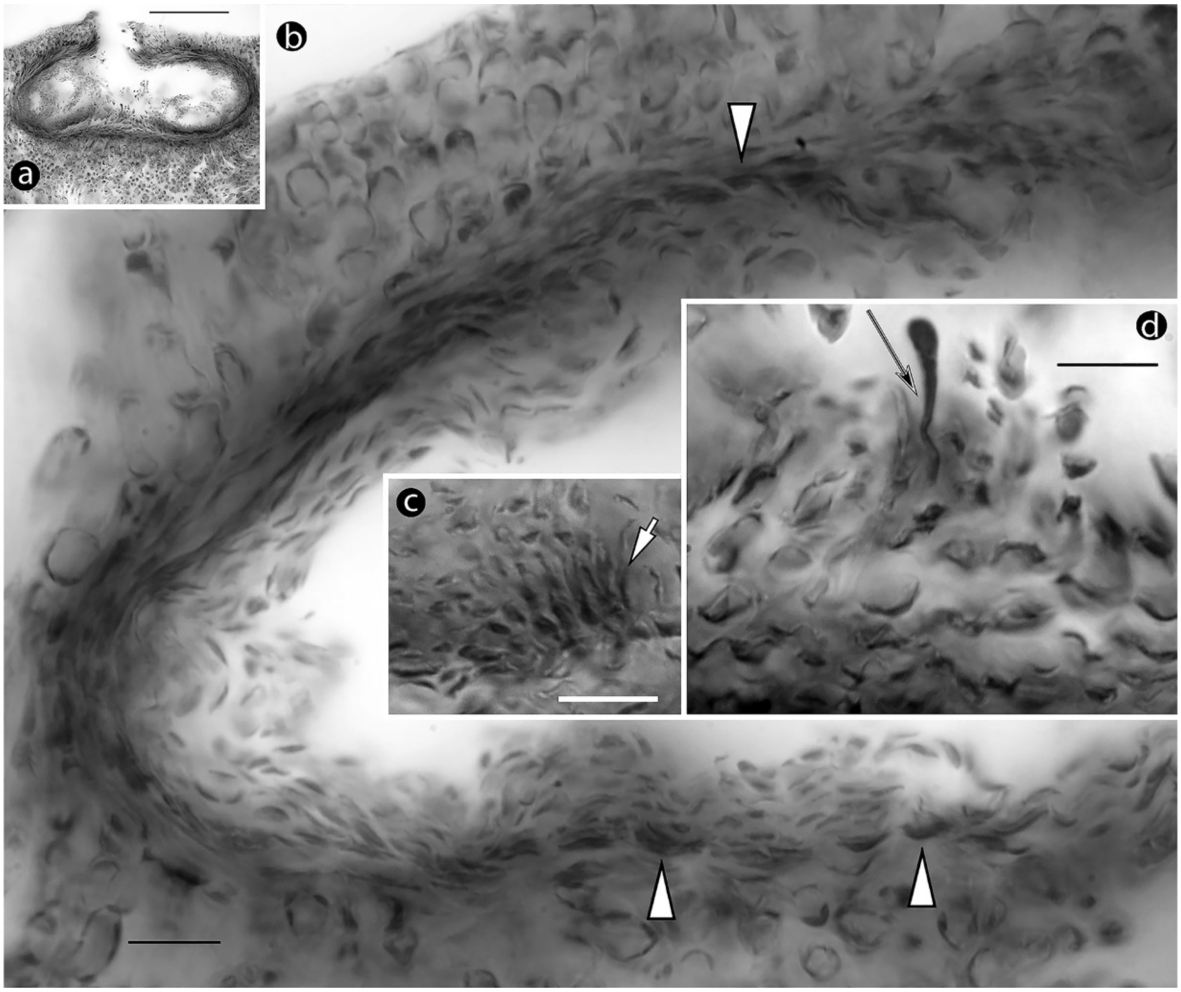


FIGURE 31. *Leptothallia acervata*: male structures (D5-YMC 91/252). (**a**) Male conceptacle. Scale bar: 100 µm. (**b**) Chamber showing the dominance of simple (unbranched) spermatangial structures with lunate SMCs (arrowheads). Scale bar: 10 µm. (**c**) A tuft of dendroid spermatangia (arrow) in the chamber center. Scale bar: 10 µm. (**d**) A putative carpogonial branch (arrow) in the chamber center. Scale bar: 10 µm.

Gametophytes are dioecious. Male conceptacles develop predominantly simple spermatangial structures with typical ***lunate*** SMCs on the roof and the chamber floor (Figure 31a,b), with a few dendroid spermatangia located in the center of the chamber (Figure 31c). The presence of putative carpogonia in the same conceptacle suggests ***hermaphroditism*** (Figure 31d).

Carpogonial thalli, early postfertilization stages, and a conspicuous fusion cell were not seen. Carposporangial conceptacles develop gonimoblast filaments that ***radiate across*** the floor (Figure 32a,b) and produce lateral carposporangia (Figure 32c,d).

Multiporate conceptacles may have sunken or convex roofs (Figure 33a,b). A canal surrounded by 7 rosette cells was seen (Figure 33c). Canals are straight except at the base, where ***basal and subbasal pore cells are thinner–wider*** and project outward (Figure 33d–g). Older conceptacles apparently lose the roof, and the chambers are filled in with perithallial tissue (Foslie 1907b) before they become embedded in the thallus (Chamberlain and Keats 1994: fig. 27).

Comments: Two collections were cited in the protologue. Adey and Lebednik (1967: 49) recognized them as “type material,” and subsequently, Chamberlain and Keats (1994: 111) selected the Natal specimen as the lectotype and the Knysta specimen as a syntype. Foslie (1907b) considered the species to be related to *Lithothamnion* (*Phymatolithon*) *tenuissimum* Foslie (1900a: 20), which is described from Sao Thomé (Gulf of Guinea) and whose status has not been examined in a modern context. The affiliation of *Leptothallia acervata* with *Phymatolithon* (Adey 1970; Van der Merwe and Maneveldt 2014) was disproven by both a comparison of gene phylogenies (Bailey and Chapman 1998: fig. 1; Broom et al. 2008: fig. 5; Bittner et al.

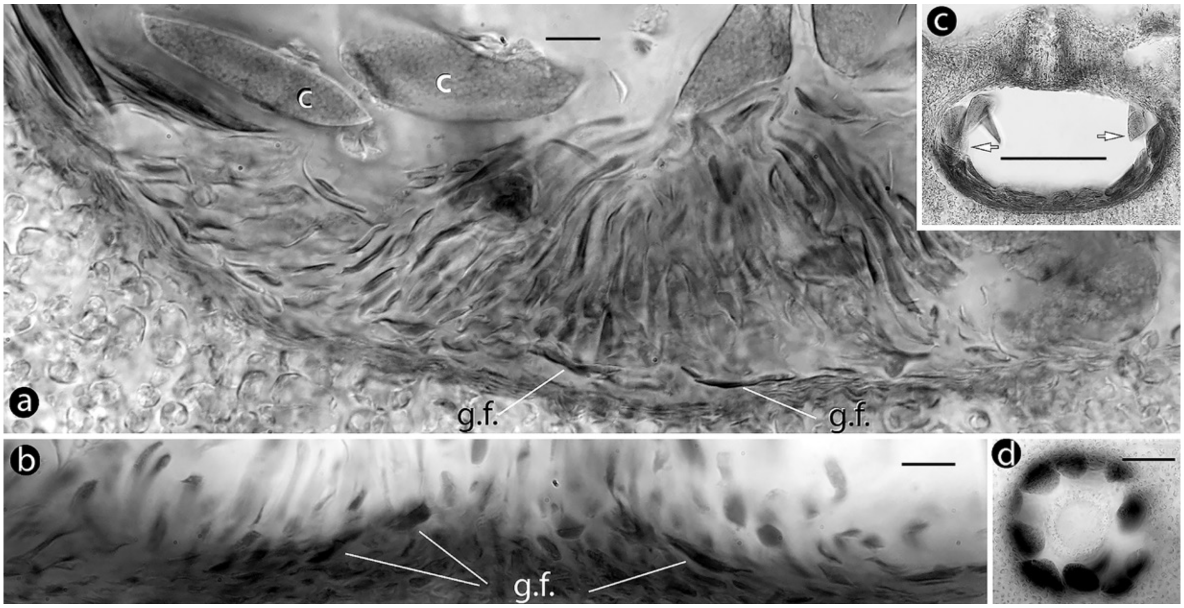


FIGURE 32. *Leptothallia acervata*: carposporangial structures and postfertilization stages. (**a, b**) Chamber showing gonimoblast filaments on the floor and peripheral carposporangia (D5-YMC 91/252). Scale bar: 10 µm. (**c**) Carposporangial conceptacle with remains of carposporangia on the walls (arrows; D5-YMC 91/252). Scale bar: 100 µm. (**d**) Peripheral carposporangia in the chamber (D22-YMC 91/212). Scale bar: 50 µm. Abbreviations: c, carposporangium; g.f., gonimoblast filament.

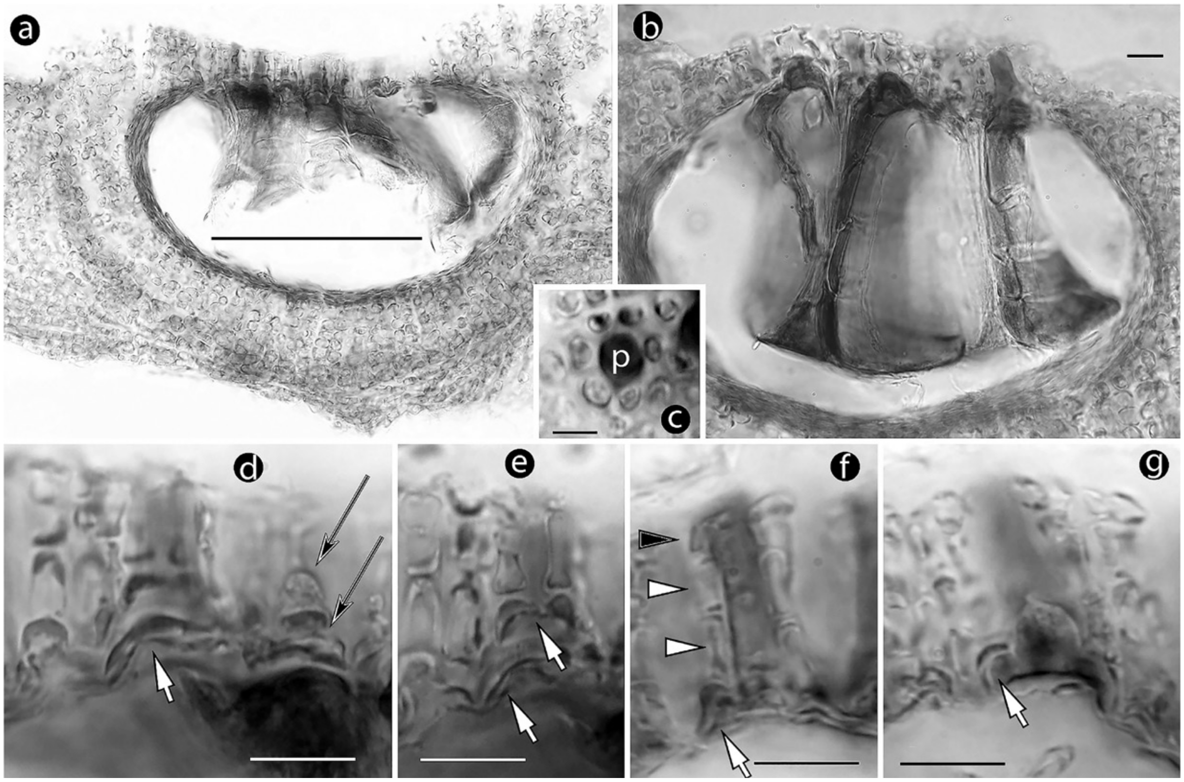


FIGURE 33. *Leptothallia acervata*: multiporate conceptacle structures (D2-YMC 91/212). (**a, b**) Sections of conceptacles with multiporate roofs. Scale bars: 100, 10 µm, respectively. (**c**) View of a canal surrounded by 7 rosette cells. (**d–g**) Sections of canals showing nondifferentiated pore cells (arrowheads) along the apical part and thinner (white arrows) and wider (black arrows) cells toward the base. Scale bars: 10 µm. Abbreviation: p, pore canal.

2011: fig. 1) and an analysis of anatomical characters, the latter showing the development of peripheral carposporangia and the common presence of both simple (unbranched) and dendroid spermatangia (Chamberlain and Keats 1994: fig. 12). The present study of four collections from the herbarium of Y. M. Chamberlain confirmed the known characters and added several new ones (***as discussed above*** in "Species Description") for this species.

Chamberlain and Keats (1994: 119) considered *Leptophytum acervatum* to be closely similar to *Leptophytum foveatum*, and a comparison between them is given under the latter taxon (below "Incertae Sedis Magnephyceae").

In the present phylogenetic analysis (Figure 6b,c), *Leptothallia acervata* was clustered with *Leptophytum*, but their sister taxon relationship is lacking unique synapomorphies and remains enigmatic since the two genera differ in significant characters, such as type of fusion cell and subepithallial cell size, and in addition display a disjunctive distribution.

Macedonis **Athanas. et D. L. Ballant. gen. nov.**

Macedonis Athanas. et D. L. Ballant. gen. nov. (type: *M. tethygenis*).

Diagnosis: New genus of Mesophyllaceae, differing from other members of the family by the production of unbranched pore filaments with elongate subbasal cells in straight canals of multiporate conceptacles.

Etymology: The generic name is the diminutive feminine noun Μακεδονις (the land of Macedonia; genitive *Macedoni-dos*).

Comments: *Macedonis* here unites four species, namely, the generitype *Macedonis tethygenis* (*Mesophyllum macedonis*) from the North Aegean Sea and *Macedonis julieae* (=*Leptophytum julieae*), *Macedonis lamellicola* (=*Leptophytum lamellicola*), and *Macedonis kymatodis* (=*Leptophytum kymatodes*) from the Pacific coast of North America. *Macedonis* displays the ancestral thallus organization (monopodial-dorsiventral with a noncoaxial polystromatic hypothallium) and is thereby clearly assigned to the tribe Magnephyceae. The genus accommodates monoecious species, lacking pedestals in gametangial conceptacles and possessing both branched and unbranched spermatangia and elongate subbasal cells in unbranched pore filaments of straight canals in multiporate conceptacles. The development of elongate subbasal hypothallial cells (character 8), a foliose thallus (character 9), and the colliculate pattern of conceptacle embedding (character 26) cluster the genus with *Hyperandri*, *Ectocarpa*, and *Magnephycus* (Figure 6c).

Macedonis tethygenis **Athanas. et D. L. Ballant. comb. et nom. nov.**

FIGURES 34–36

Macedonis tethygenis Athanas. et D. L. Ballant. comb. et nom. nov.
Basionym: Mesophyllum macedonis Athanas. 1999: 240, figs. 1–17.

Etymology: The new epithet *tethygenis* is a compound after Τεθυς (Tethys Sea) and the epithet termination -γενης (borne, originating).

Type Locality: Littoral, Pigeon Cave, 500 m south of the town of Sarti, Sithonia Peninsula, Greece.

Holotype: In GB (GB-0147029, SC010784, A. Athanasiadis no. 79, 1 July 1984, coll. Athanas.), illustrated by Athanasiadis (1999: fig. 1; Figure 34a–c).

Isotype: Fragment of the holotype (herb. Athanas.).

Habitat and Distribution: The species grows in caves and crevices in the littoral and upper sublittoral zone (0 to 2 m depth), attached to rock, and in association with other sciophilous algae, including encrusting corallines, *Peyssonnelia* spp., and the green alga *Palmophyllum crassum* (Naccari) Rabenhorst, tolerating wide temperature (12°C ± 26°C) and salinity (32‰–35‰) fluctuations, and influenced by freshwater discharges from small streams and lakes. Thalli are protected from direct sunlight and may show a preference for low-salinity waters. It is recorded from three localities on the Sithonia Peninsula (Pigeon Cave, Kalamitsi Caves, and Porto Cufo).

Material Examined: North Aegean: Sithonia: Pigeon Cave: 26 June 2002, 0–0.5 m depth, gametophytes, coll. Athanas. (herb. Athanas. SC.26.06.2002-Sith.19); 24 June 2009, 0–0.5 m depth, tetrasporophytes, coll. Athanas. (herb. Athanas. SC.24.vi.2009-Sith.78). Kriaritsi Caves: 1 August 1984, upper sublittoral, tetrasporophytes, coll. Athanas. (GB, unnumbered). Porto Cufo: 16 June 2006, 1 m depth, tetrasporophytes, before/after the cave, coll. Athanas. (herb. Athanas. PC.16.06.2006-Sith.41); 16 June 2006, 1–2 m depth, tetrasporophytes, coll. Athanas. (herb. Athanas. PC.16.06.2006-Sith.45); 3 July 2012, 1–2 m depth, tetrasporophytes, coll. Athanas. (herb. Athanas. PC.03.07.2012-Sith.63); 28 June 2014, 1–2 m depth, coll. Athanas. (herb. Athanas. PC.28.06.2014-Sith.72).

Species Description: Thalli develop foliose complexes, at least 7 cm in extent and 1.5 cm thick, moderately attached to the substratum and enveloping other organisms (Figure 34a,b). The thallus organization is monopodial-dorsiventral with a polystromatic noncoaxial hypothallium entirely lacking coaxial patches and supporting an ascending perithallium lacking perithallial protuberances. New lamellae (100–170 μm thick) develop dorsally in an unattached superimposed pattern (Figure 34c). Terminal meristematic cells operate via asynchronous divisions and elongations protected by a cuticle (Figure 34d) and producing a noncoaxial hypothallium, which via dorsal displacement of peripheral filaments produce an ascending perithallium (Figure 34e). Hypothallial cells are 16–40 × 2.5–10 μm (L × B), and perithallial cells are 5–10 × 4–12 μm (L × B). Subepithallial cells are elongate during putative division and support a single layer of epithallial cells, 3–4 × 7–8 μm (L × B; Figure 34f). Terminal trichocytes occur rarely. Descending hypothallial cells end in wedge-shaped cells (Figure 34g) and occasionally develop narrow-elongate subbasal cells (Figure 34h).

Gametophytes are monoecious. Male conceptacles are 440–500 × 140–180 μm (D × H; n: 2) and are provided with chambers 280–320 × 40–140 μm (D × H; n: 3; Figure 35a,b).

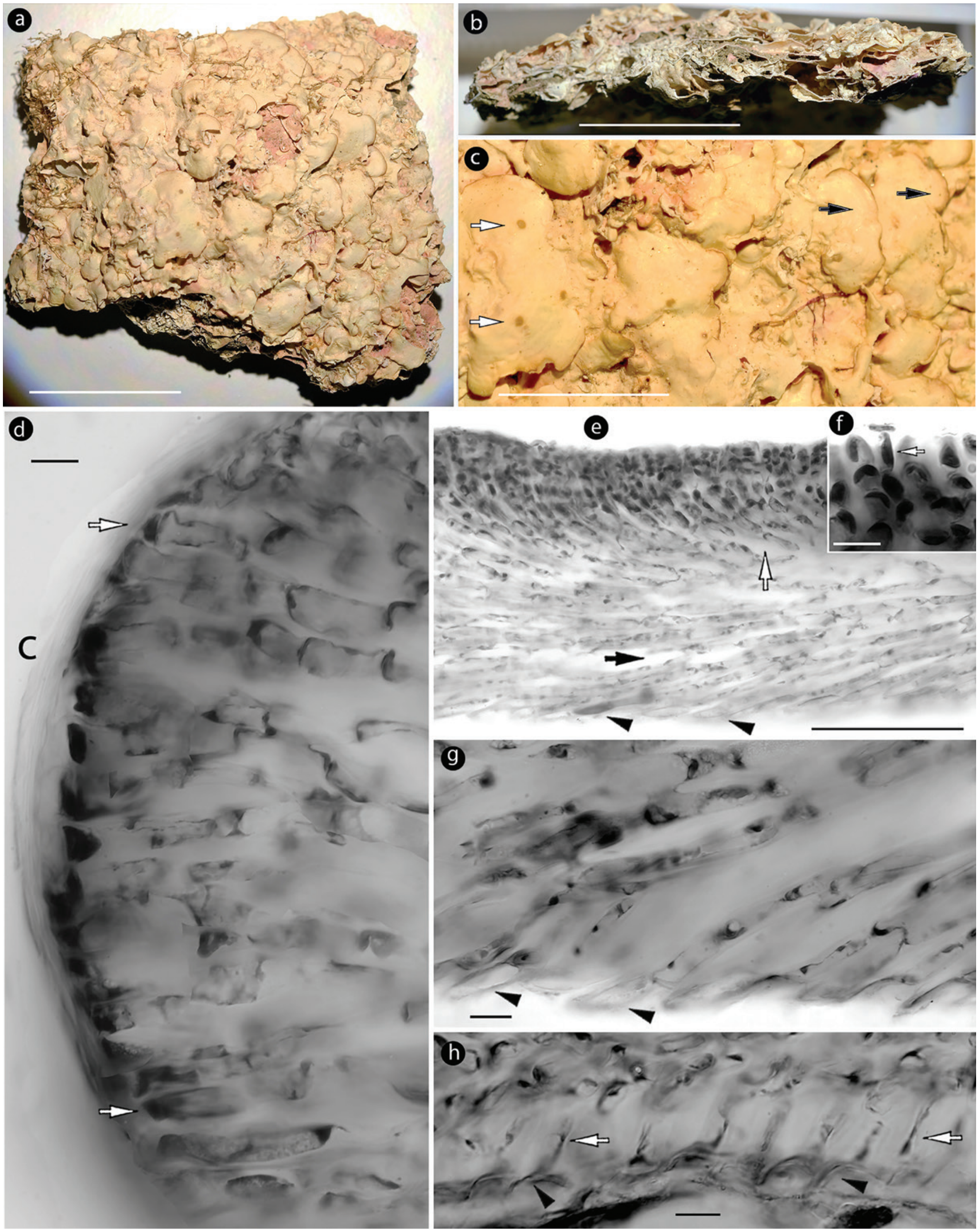


FIGURE 34. *Macedonis tethygenis*: vegetative structures. (**a–c**) The holotype in GB (GB-0147029) in surface and side views, with magnification showing tetrasporangial conceptacles (white arrows) and new lamellae (black arrows). Scale bars: 2 cm in (a) and (b), 1 cm in (c). (**d**) Margin protected by a cuticle and showing terminal meristematic cells (arrows) undergoing asynchronous divisions and elongations, producing a noncoaxial hypothallium (Sith.72). Scale bar: 10 µm. (**e**) Section demonstrating a typical dorsiventral organization with a ventral hypothallium (black arrow) and deeply pigmented dorsal perithallial filaments (white arrow). Scale bar: 100 µm. (**f**) Elongate subepithallial cell supporting a flattened epithallial cell (Sith.72). Scale bar: 10 µm. (**g**) Descending hypothallial filaments ending in wedge-shaped (arrowheads) cells (Sith.72). Scale bar: 100 µm. (**h**) Descending hypothallial filaments with narrow subbasal cells (arrows) ending in reniform cells (arrowheads; Sith.45). Scale bar: 10 µm. Abbreviation: c, cuticle.

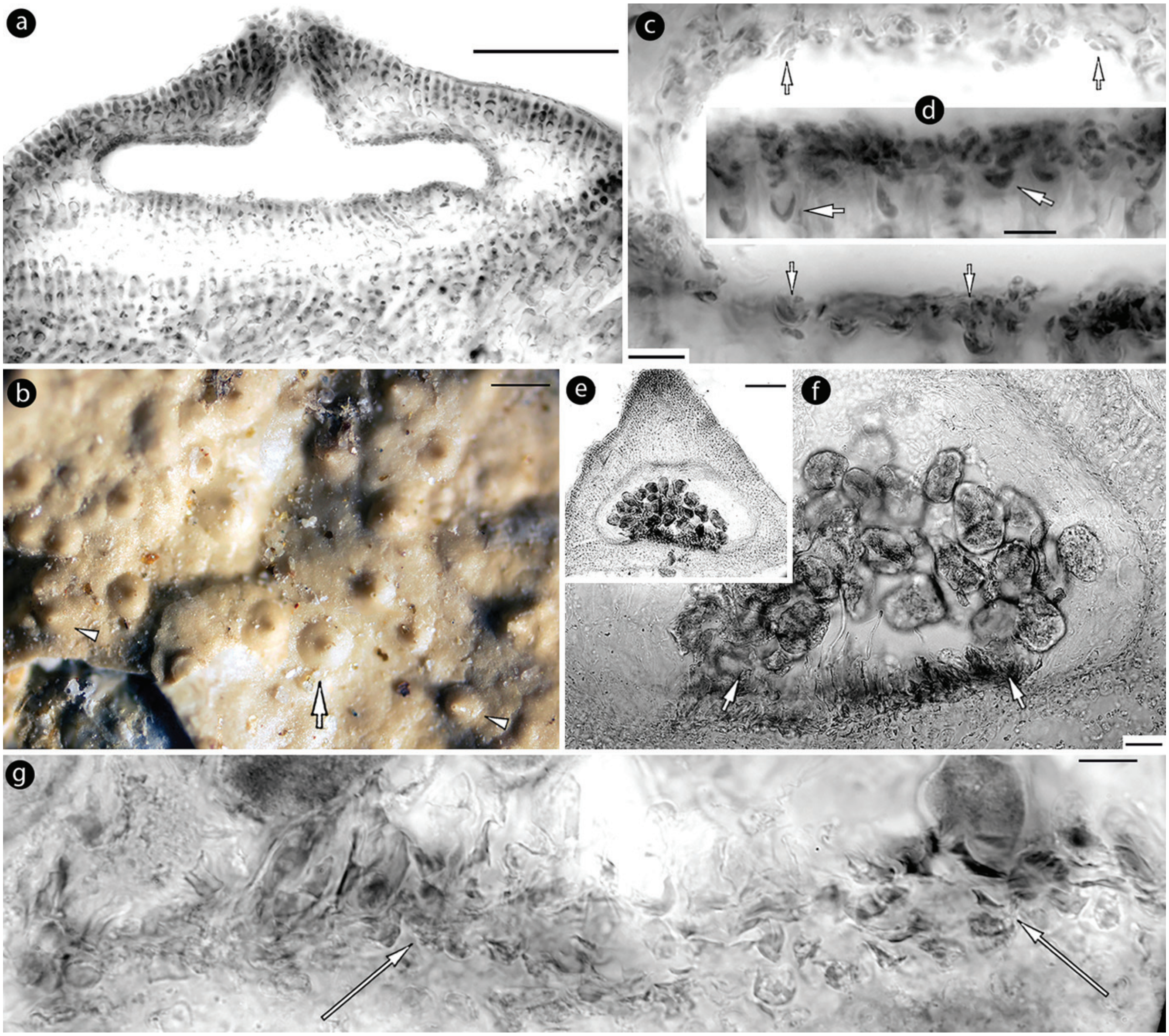


FIGURE 35. *Macedonis tethygenis*: gametangial structures (Sith.19). (**a**) Male conceptacle. Scale bar: 100 μm. (**b**) Male (arrowheads) and female (arrow) conceptacles. Scale bar: 500 μm. (**c, d**) Sections through male chambers, showing unbranched spermatangial structures on the floor and the roof (arrows). Note the lunate mature SMCs on the floor (arrows in (d)). Scale bars: 50, 10 μm, respectively. (**e**) Conical carposporangial conceptacle. Scale bar: 100 μm. (**f**) Carposporangial chamber showing peripheral production of carposporangia (arrows). Scale bar: 10 μm. (**g**) Magnification at the chamber floor showing putative gonimoblast filaments (arrows). Scale bar: 10 μm.

Spermatangial structures are simple (unbranched) and occur on the roof and the floor, which is flattened (Figure 35c,d). SMCs are lunate (Figure 35d).

Carposporangial conceptacles are conical, 560 × 400 μm (D × H; n: 1), and are provided with subspherical chambers, ~400 × 200 μm (D × H; n: 1; Figure 35b,e). Carposporangia develop from the periphery of a flattened fertile zone (Figure 36f,g). Carpogonial and postfertilization stages were not observed.

Multiporate conceptacles are 450–710 × 20–120 μm (D × H; n: 8), provided with chambers 290–500 × 100–150 μm (D × H), and are irregularly spread over the surface. The roof is convex, 30–55 μm thick, composed of 4- to 7-celled filaments and perforated by up to 108 pores (Figure 36a–c). Older conceptacles may become covered by an imperforate second roof, formed centripetally by peripheral perithallial outgrowths with basal hypothallial filaments (Figure 36d,e). Canals are typically

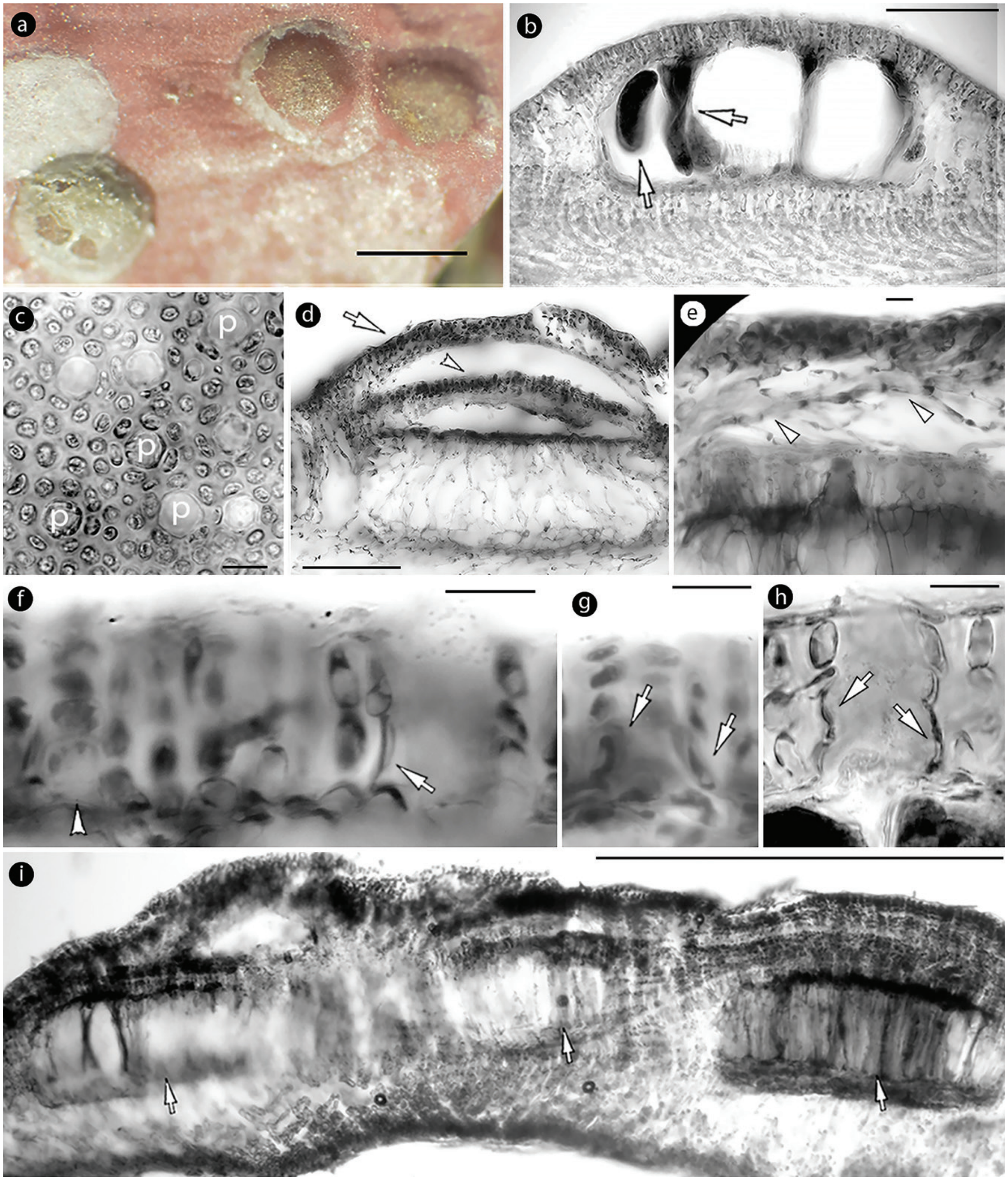


FIGURE 36. *Macedonis tethygenis*: multiporate conceptacle structures. (**a**) Multiporate conceptacles in surface view (Sith.72). Scale bar: 500 µm. (**b**) Tetrasporangial conceptacle with sporangial remains (arrows; Sith.63). Scale bar: 100 µm. (**c**) Surface view of a multiporate roof showing pore canals surrounded by 6 to 7 rosette cells (Sith.41). Scale bar: 10 µm. (**d, e**) Production of an imperforate second roof (arrow) above the older one (arrowhead; Sith.63). Scale bar: 100 µm. Note the basal hypothallial filaments (arrowheads in (e); Sith.72). Scale bar: 10 µm. (**f–h**) Sections through pore canals of multiporate roofs, showing elongate subbasal cells (arrows). Note the wider size of the subbasal cells in tangential view (arrowhead; Sith.63). Scale bars: 10 µm. (**i**) Embedded conceptacles (arrows) in a colliculate pattern (Sith.78). Scale bar: 500 µm. Abbreviation: p, pore canal.

straight, surrounded by 6 to 7 rosette cells (Figure 36c), and possess elongate subbasal cells (Figure 36f–h). Embedded conceptacles in the perithallium occur in a colliculate pattern (Figure 36i; Stearn 1986: 506, fig. 38). Both bisporangia and tetrasporangia are recorded, 60–100 × 20–40 µm (L × B).

Comments: Although it was previously concluded that the Caribbean *Magnephycus* (*Mesophyllum*) *ornatus* is the closest related taxon (Athanasiadis 1999), subsequent studies on NE Pacific Mesophyllaceae (Athanasiadis et al. 2004; Athanasiadis and Adey 2006; Athanasiadis 2007b) revealed several other related taxa, two of which are clustered with the Aegean endemic in the present phylogenetic analysis (Figure 6a). These geographically remote but closely related species include *Leptophytum julieae* and *Leptophytum lamellicola*, motivating the establishment of the new genus *Macedonis* to accommodate four taxa: the three mentioned species and *Leptophytum kymatodes*, all exhibiting the diagnostic character of the new genus (character 8). The isolated distribution of *Macedonis tethygenis* from its congeners indicates that it is, indeed, a relic (as originally suggested), most likely from the Tethyan period, when warm waters connected the tropics and subtropics around the world as a girdle. Since the original finding in 1984, *M. tethygenis* was collected at two more localities on the Sithonia Peninsula (northern Greece). Monoecious gametophytes were encountered only once at the type locality. Although a rare element of the local marine flora, *Macedonis tethygenis* may occur more commonly in the wider area of the North Aegean, which is influenced by low-salinity waters penetrating through the Dardanelles strait.

Macedonis lamellicola **(Athanas. et W. H. Adey) Athanas. et D. L. Ballant. comb. nov.**

Macedonis lamellicola (Athanas. et W. H. Adey) Athanas. et D. L. Ballant. comb. nov.

Basionym: Leptophytum lamellicola Athanas. et W. H. Adey 2006: 81–86, figs. 28–58.

Type Locality: Pyramid Point, Monterey County, California, USA.

Holotype: In UC (745618, Nichols no. 131, *pro parte*, December 1906, coll. M. B. Nichols), illustrated by Athanasiadis and Adey (2006: fig. 28).

Syntypes: In UC (745618, Nichols no. 131, *pro parte*); in GB (GB-0147025, Nichols no. 131); in herb. Athanas. (Nichols no. 131), all syntypes collected by M. B. Nichols, December 1906.

Material Examined: San Francisco County: California: Farallon Islands, Drunk Uncle Islets, West End Island, low zone, very exposed, SEFI-170, SEFI-173, SEFI-174, 27 October 2007, coll. K. A. Miller (UC, unnumbered); Mussel Flats, Southeast Farallon Island, SEFI-172, SEFI-178-179–180, 28 October 2007, coll. K. A. Miller (UC, unnumbered).

Habitat and Distribution: The species grows in the littoral and sublittoral zones to at least 9 m depth, at moderately sheltered to exposed localities, attached to rocks, barnacles, polychaetes, and other nongeniculate and geniculate coralline algae (e.g., *Corallina* L.). In California, it usually grows attached to *Mesophyllum lamellatum*. The confirmed collections are scattered from Santa Catalina Island and Monterey, San Mateo, San Francisco, and Marin Counties in California and also from Vancouver Island, British Columbia (from Whiffen Spit to Cape Scott; Athanasiadis and Adey 2006: 85).

Comments: This species was found to be a common littoral alga in the Farallon Islands (collections in UC).

Macedonis julieae **(Athanas. et W. H. Adey) Athanas. et D. L. Ballant. comb. nov.**

Macedonis julieae (Athanas. et W. H. Adey) Athanas. et D. L. Ballant. comb. nov.

Basionym: Leptophytum julieae Athanas. et W. H. Adey 2006: 87–75, figs. 59–75.

Type Locality: Sublittoral, at 6 m depth, McDougal Island, Vancouver Island (50°10.4′N, 127°40.7′W), Canada.

Holotype: In UBC (A38654, *pro parte*, 27 August 1968, coll. J. W. Markham et al.), illustrated by Athanasiadis and Adey (2006: fig. 59).

Isotypes: In UBC (A38654, *pro parte*); in GB (GB-0147028); in S (unnumbered), all isotypes collected by J. W. Markham et al. on the 27th August 1968.

Habitat and Distribution: The species grows in the littoral at sheltered to moderately sheltered sites and in the sublittoral zone to 12 m depth at sites around Vancouver Island and to 59 m depth at sites off Baja California. Specimens are ventrally attached to sponges, pebbles, shells, polychaete tubes, or geniculate and nongeniculate corallines (i.e., *Mesophyllum conchatum*, *Mesophyllum stenopon*, *Corallina* L., *Calliarthron* Manza). It is recorded from British Columbia between Grappler Inlet (48°N) and Effingham, Swiss Boy and Fleming Islands (all near Bamfield, SW Vancouver Island) and also at Numas, Kains, Solander, and McDougal Islands and Fisherman Bay (NW Vancouver Island). The northernmost record is Triple Islands (54°N). In California, it is recorded from Santa Catalina Island and Palos Verdes Point in Los Angeles (Athanasiadis and Adey 2006), and in Pacific Mexico it is recorded from Guadeloupe Island, Isla Cedros, Cortez Bank, Sacramento Reef, and Islas San Benito (Athanasiadis 2007b).

Comments: This is the most common species in Dawson's (1960) Pacific Mexico collections referred to *Lithothamnion lamellatum* (Athanasiadis 2007b). The study of the Dawson material extended considerably the southern distribution of the species, which, rather surprisingly, showed little variation in morphological, anatomical, and habitat characteristics (Athanasiadis 2007b). The most important differences in the southern populations, which still contain only bisporophytes, were their occurrence in deeper water (to 59 m) and their tendency to form patches of arching coaxial cells in the hypothallium. Other deviations observed included shorter perithallial (4–10 µm long) and hypothallial (13–45 µm long) cells and a thicker hypothallium (up to 325 µm). The presence of the species in the deep sublittoral off Baja California demonstrates its preference for colder waters.

***Macedonis kymatodis* (Athanas.) Athanas. et D. L. Ballant. comb. nov.**

Macedonis kymatodis (Athanas.) Athanas. et D. L. Ballant. comb. nov.
Basionym: Leptophytum kymatodes Athanas. 2007b: 217–222, figs. 42–60.

Type Locality: Littoral, on a "minus 1.7 feet tide" (Dawson 1960:19), 2½ miles north of South Bluff Shore station, Guadeloupe Island, Pacific Mexico.

Holotype: UC (unnumbered, AHFH 55575, Dawson no. 8605, *pro parte*, a tetrasporangial specimen, 20–21 December 1949, coll. E. Y. Dawson), illustrated by Athanasiadis (2007b: figs. 42D, 43, 44).

Habitat and Distribution: Most thalli of the type collection were found attached to a polychaete colony and a geniculate coralline and bore red algal epiphytes (e.g., *Ceramium* sp.) and hydroids on their surface. The species is known only from the type locality.

Comments: This is the largest species in Dawson's (1960: pl. 11, fig. 1) collections referred to *Lithothamnion lamellatum* (=*Mesophyllum lamellatum*), reaching at least 9 cm in extent. It is considered to be the sister taxon of *Macedonis julieae*, differing in possessing the regular development of lobate-undulate lamellae (*M. julieae* develops an irregularly foliose habit) and in reproducing by tetrasporangia (only bisporophytes are recorded in *Macedonis julieae*; Athanasiadis 2007b). The type material was commented on by Dawson (1960: 19) as follows:

> Richly developed specimens such as those from Isla Guadelupe (D. 8605, . . . show a remarkable resemblance to . . . *Lithothamnion neglectum* . . . but the very dissimilar temperature conditions under which the southern hemisphere and Pacific North American plants grow, in addition to the geographic separation, suggest that despite the morphological similarities we may be dealing with physiologically distinct species.

Lithothamnion neglectum (type locality: Kerguelen Islands) is here treated as a putative heterotypic synonym of *Orthocarpa magellanica*, differing from *Macedonis kymatodis* in possessing ventral epithallial cells and nondifferentiated pore cells in canals of multiporate conceptacles and in lacking a stratified perithallium (Keats and Chamberlain 1997: 68, figs. 68, 72–74, pl. 4).

***Hyperandri* Athanas. et D. L. Ballant. gen. nov.**

Hyperandri Athanas. et D. L. Ballant. gen. nov. (type: *H. dawsonii*).

Diagnosis: New genus of Mesophyllaceae, differing from other members of the family by the production of simple spermatangial structures on a pedestal composed of a single layer of palisade cells (Figures 51m, 40c,e); see characters 19–20 in "Character Evolution in the Mesophyllaceae."

Etymology: The generic name is a new compound word from the preposition υπερ (hyper) and the dative andri (nominative ανηρ, "male"), hereafter treated as a noun of neuter gender (analogous to protandry) and referring to the prominent elevation (i.e., a pedestal of palisade cells) on the floor of male conceptacles.

Comments: Hyperandri comprises the generitype *H. dawsonii*, *H. bisporum*, and *H. siamense*. The former two species demonstrate the diagnostic character of the genus (Figure 5l,m), whereas *H. siamense* shares most of its vegetative and other reproductive features with *H. bisporum* or *H. dawsonii*. Differences between the three species are discussed under *H. siamense*. The phylogenetic analysis clustered them together (Figure 6a), and this result is here followed pending studies of new collections. Regarding the type of canals in multiporate conceptacles, *Hyperandri* comes closer to *Leptophytum* than to any other member of the tribe (Table 5), but in the absence of information of carpogonial and postfertilization stages in the former genus further comparison is pending new studies.

***Hyperandri bisporum* (Foslie) Athanas. et D. L. Ballant. comb. nov.**

FIGURES 37–41

Hyperandri bisporum (Foslie) Athanas. et D. L. Ballant. comb. nov.
Basionym: Lithothamnion bisporum Foslie 1906a: 18 (repr. 2).
Synonyms: *Leptophytum bisporum* (Foslie) W. H. Adey 1970: 30.
Phymatolithon bisporum (Foslie) J. Afonso-Carrillo 1984: 134.

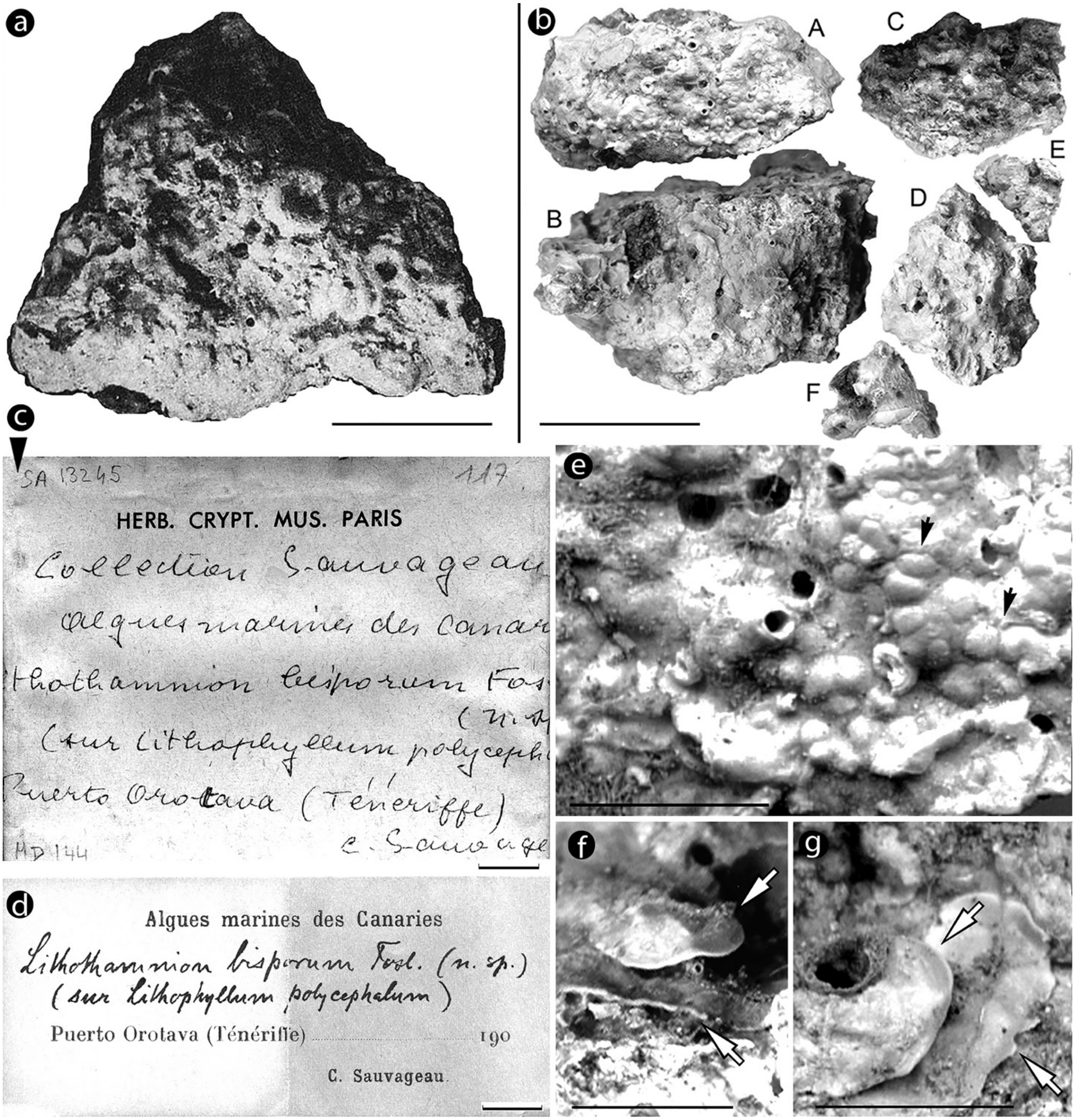
Type Locality: Puerto de la Cruz (Puerto Orotava), Tenerife, Canary Islands.

Lectotype: In TRH (B2-1680), Printz (1929: pl. 1, fig. 16), Adey and Lebednik (1967: 51, "type material," "§ Sauvageau, Canary Is. Ténériffé, Puerto Orotava –.12.1904 to –.2.1905 LM1 (19) [slides] 1058, 1059"), Adey (1970: 30, "holotype"), Woelkerling et al. (2005: 237, "holotype fragments"; Figure 37a).

Syntypes: In PC (unnumbered, December 1904 to January 1905, coll. C. Sauvageau, six fragments; Figure 37b).

Habitat and Distribution: Canarian thalli grow attached to *Titanoderma polycephalum* (Foslie) Woelk., Y. M. Chamb., et P. C. Silva; hydrozoans; shells (*Haliotis* L.); and pebbles, in the littoral and sublittoral zones to at least 15 m depth; Caribbean thalli are attached to mangrove roots, corals, *Strombus* L., and coralline algae in the littoral zone, commonly growing in association with *Magnephycus ornatus*, to at least 70 m depth. The species is recorded from the Canary Islands (Tenerife, Radazul), Bermuda (Harrington Sound), and Puerto Rico (several islets off La Parguera).

Material Examined: Canary Islands: Tenerife: Porto de la Cruz (Puerto Orotava): syntypes in PC (unnumbered, six fragments here annotated A–F, data as described above; Figures



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Collection Sauvageau

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uerto Orotava (Ténériffe)

C. Sauvage

MD 144

Algues marines des Canaries

Lithothamnion bisporum Fosl. (n. sp.)

(sur Lithophyllum polycephalum)

Puerto Orotava (Ténériffe) 190

C. Sauvageau.

FIGURE 37. *Hyperandri bisporum*: type elements of *Lithothamnion bisporum*. (**a**) The lectotype fragment as illustrated in Printz (1929: pl. 1, fig. 16, "part of the plant"). Scale bar: 1 cm. (**b**) The six syntypes in PC. Scale bar: 1 cm. (**c**) The annotation on the box in PC including the syntype material. Scale bar: 1 cm. (**d**) A second label included in the syntype material (PC). Scale bar: 1 cm. (**e**) Multiporate conceptacles (arrows) on fragment A. Scale bar: 1 cm. (**f, g**) New lamellae growing unattached (arrows) on fragment B. Scale bars: 250 µm.

37, 38); bisporophytes and males, 4 January 1921, coll. F. Børgesen (C, unnumbered, Børgesen no. 3014, the material including, according to Lemoine, "Y" *Lithothamnion ectocarpon* Fosl., "[square]" *Lithophyllum? orotavicum* Fosl., "x" *Pseudolithophyllum esperi* nov. sp.; Figure 39a,b); a male thallus on a broken *Haliotis* shell (7.4 cm in extent), 9 January 1921, coll. F. Børgesen (C, unnumbered, Børgesen no. 3106).

Radazul South: bisporophytes on pebbles, 5–15 m depth, 4 February 2009, coll. Athanas. (herb. Athanas. RAS-1A, RAS-15, RAS-17, several collections, including slides; duplicate in GB).

Bermudas: Harrington Sound: bisporophytes with few tetrasporangia and gametophytes (?) on stone fragments, just below low-water mark, 18 June 1900, coll. M. A. Howe (TRH B16-2519, Howe no. 151, "*Lith. syntrophicum*"); duplicate in NY (unnumbered, Howe no. 151).

Puerto Rico: La Parguera: Media Luna: bisporophytes, 0.5–1 m depth, 22 April 2009, coll. Athanas. (herb. Athanas. PR-131); Mario Reef: bisporophytes, 1 m depth, on dead coral, 22 April 2009, coll. Athanas. (herb. Athanas. PR-78, PR-65C); Collado Reef: bi- or tetrasporophytes on red mangrove roots, shells, and dead corals in sheltered, shady habitat, just below water level, 28 April 2009, coll. Athanas, (herb. Athanas. PR-251, PR-251B, PR-251D with *Magnephycus ornatus*; duplicates in GB and MSM); Las Pelotas: bi- or tetrasporophytes on red mangrove roots, shells, and dead corals in sheltered, shady habitat, just below water level, 28 April 2009, coll. Athanas. (herb. Athanas. PR-27B on *Strombus* L. with *Lithophyllum incrustans* R. A. Philippi, PR-33A, PR-41, PR-43B, PR-46, LP-5, LP-8; duplicates in GB and MSM); Cayo Enrique: bi- or tetrasporophytes on red mangrove roots, shells, and dead corals in sheltered, shady habitat, just below water level, 28 April 2009, coll. Athanas. (herb. Athanas. PR-14, H-2; duplicate in GB); "El Hago terrace": bisporophytes, "209 feet," 17 December 2008, coll. H. Ruiz (herb. D. L. Ballant. 7691-2 and herb. Athanas. PR-109).

Comments on the Protologue and Syntype Material: The Norwegian protologue (Foslie 1906a: 18) reads (in translation),

> *Lithothamnion bisporum* Fosl. mscr. Thallus forms up to 0.4 mm thick, irregular crusts on *Lithophyllum polycephalum*; [multiporate] sporangial conceptacles convex, 200-500, usually 300-400 in diameter; sporangia two-parted, 90-120 µm long and 30-50 µm broad. — In habit, it looks like *Lithothamnion Lenormandi*; but in dry condition the color is weakly pink-red, and the conceptacles are more irregular and less sharply defined. In structure it largely agrees with this mentioned species. It occurred very scanty in Puerto Orotava (Teneriffa), Canary Islands (Sauvageau).

Printz (1929: pl. 1, fig. 16) illustrated part of the original material growing on *Lithophyllum* (*Titanoderma*) *polycephalum* Foslie (Figure 37a), and Woelkerling and Lamy (1998: 332) reported that "most of the remaining portion of the type [is in PC] . . . broken into six fragments" (Figure 37b). There is also a letter in PC explaining that Foslie was keeping half of the fragmentary pieces of this species. Since the original material is dated between December 1904 and February 1905, we have to conclude that it was the product of several collections (made between December 1904 and February 1905). The TRH material was first designated as type by Adey and Lebednik (1967), and we have to follow this typification, recognizing the TRH element(s) as the lectotype and the six fragments in PC as syntypes (potentially isolectotypes). However, the lectotype presently comprises only tiny fragments (Woelkerling 1993a: 39) and was not examined in the present study.

We examined the PC material that exists in a box (Figure 37c) labeled "SA 13245 HERB. CRYPT. MUS. PARIS Collection Sauvageau algues marines des Canaries *Lithothamnion bisporum* Foslie (n.sp.) (sur *Lithophyllum polycephalum*) Puerto Orotava (Ténériffe) MD 144 C. Sauvageau." This contains a smaller box with six algal fragments (A–F in Figure 37b) and one label (Figure 37d) annotated "Algues marines de Canaries *Lithothamnion bisporum* Foslie (n.sp.) (sur *Lithophyllum polycephalum*) Puerto Orotava (Ténériffe) . . . 190 C. Sauvageau." The algal names are written in the hand of Foslie. The fragments are attached to a hydrozoan, but at least one of them grows on a species of *Titanoderma* (below). We could not fit the six pieces together (suggesting that different specimens might be involved). Thalli reach 2 cm in extent and are mainly encrusting, with minor lamellae growing unattached in superimposition (Figures 37e–g, 38a–c). They are bleached, but below a cover of debris and filamentous algae, the surface is violet reddish. They grow interwoven with the foraminiferan *Miniacina miniacea* (Pallas) and polychaete tubes. Fragment A is attached (at least partly) to another coralline provided with typical palisade-sinuous hypothallial cells, which most likely belongs to *Titanoderma polycephalum* (Figure 38d). Thallus organization is monopodial-dorsiventral with a polystromatic hypothallium, 70–100 µm thick, supporting an ascending perithallium to 280 µm thick (Figure 38a–d). Hypothallial cells are 12–25 × 4–10 µm (L × B), and perithallial cells are 6–15 × 4–8 µm (L × B). Subepithallial cells are longer than cells below (~8 × 3 µm; L × B), supporting single, flattened (to isodiametric-roundish) epithallial cells, 2–3 × 3–8 µm (L × B; Figure 38c,e,f). A terminal trichocyte, 28 × 8 µm (L × B), was seen (Figure 38b). Secondary pit connections were not observed.

Multiporate conceptacles are crowded, 200–480 × 40–110 µm (D × H; n: 6; Figure 37e) and provided with chambers 250–380 × 70–160 µm (D × H; n: 10). Conceptacles become embedded in the perithallium, occasionally being filled in with palisade cells. Older neighboring conceptacles become "bridged" by a third younger one borne between them and forming imbricate-colliculate complexes (Figure 38g; Stearn 1986: 506, fig. 38). Conceptacle roofs are convex, 30–40 µm thick, composed of 6- to 8-celled filaments. A pore plate, 170 × 350 µm in opposite diameters, is perforated by at least 32 canals. Pore canals are surrounded by 5–7 rosette cells that are normal epithallial cells, rarely thinner–wider (Figure 38h,i). Canals are ± straight, 8–13 µm in apical diameter, slightly wider at the base, 10–15 µm in diameter, and lined by filaments composed of thinner–wider cells toward the base (basal, subbasal, and occasionally third

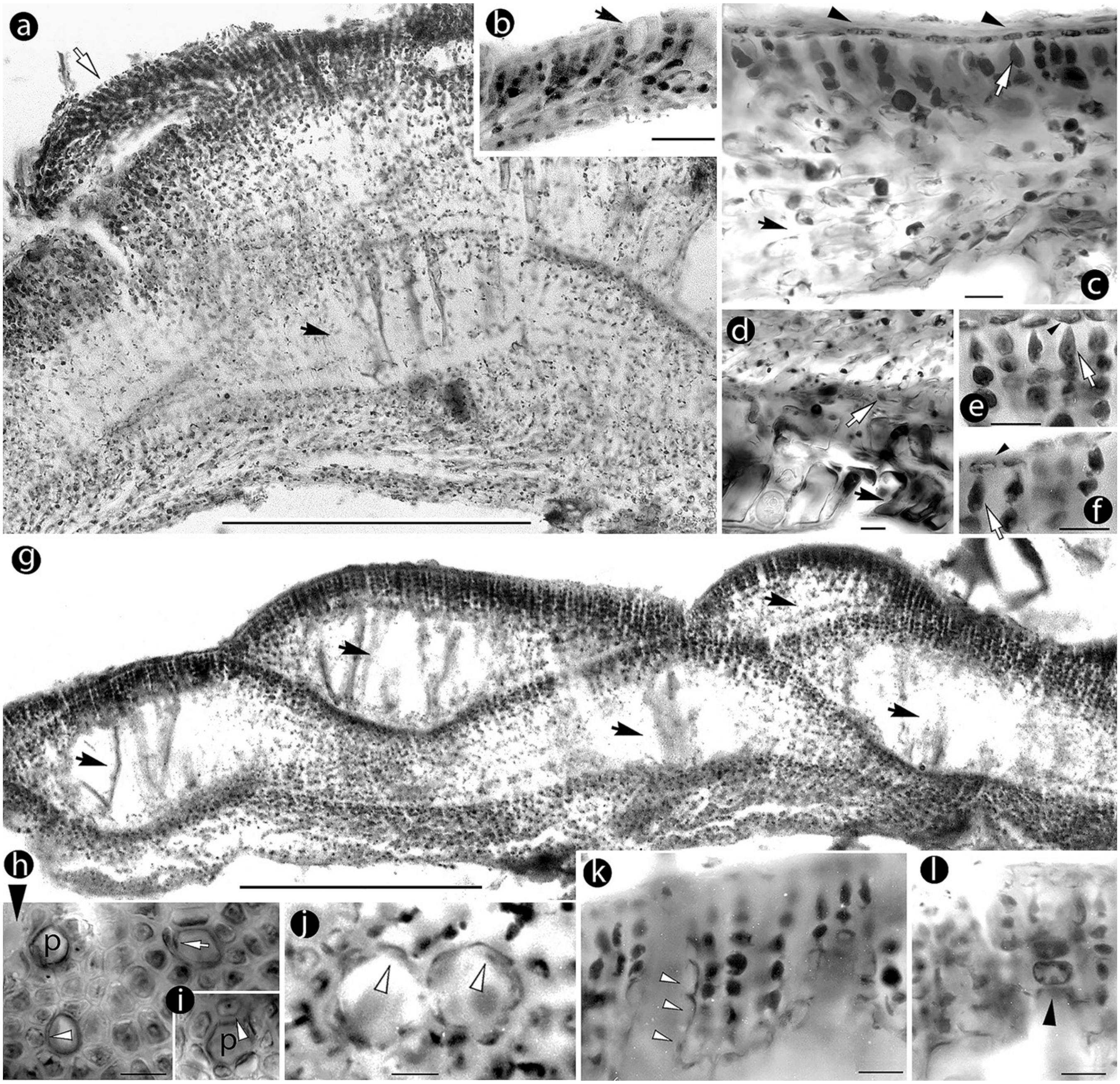


FIGURE 38. *Hyperandri bisporum*: syntypes of *Lithothamnion bisporum* in PC. (**a**) Section showing an embedded conceptacle (black arrow) and development of a new lamella in superimposition (white arrow; fragment C in PC). Scale bar: 250 µm. (**b**) Section showing a thin thallus with a terminal trichocyte (arrow; fragment C in PC). Scale bar: 25 µm. (**c**) Section showing a noncoaxial hypothallium (black arrow), flattened epithallial cells (black arrowheads), and an elongate subepithallial cell (white arrow; fragment A in PC). Scale bar: 10 µm. (**d**) Section showing the hypothallium (white arrow) growing on a second thallus with palisade-sinuous hypothallial cells (most likely belonging to *Titanoderma polycephalum*; fragment A in PC). Scale bar: 10 µm. (**e, f**) Sections showing elongate subepithallial cells (arrows) supporting single epithallial cells (arrowheads; fragment C in PC). Scale bars: 10 µm. (**g**) Section showing embedded conceptacles in typical colliculate pattern (fragment C in PC). Scale bar: 250 µm. (**h, i**) Canals surrounded by rosette cells that are typical epithallial cells (arrowheads) or thinner–wider (arrow; fragment B in PC in (h), fragment C in PC in (i)). Scale bar: 10 µm. (**j**) Canals at a lower level of focus, showing thinner–wider (arrowheads) basal or subbasal cells (fragment C in PC). Scale bar: 10 µm. (**k, l**) Sections through canals at different levels of focus, showing thinner (white arrowheads) and wider (black arrowhead) cells (fragment C in PC). Scale bars: 10 µm. Abbreviation: p, pore canal.

cells; Figure 38j–l). A sporangium remain, ~120 × 25 µm (L × B), was observed.

Species Description: Thalli are encrusting, to 4 cm in extent and at least 500 µm thick (via superimposition), adhering strongly to the substratum and lacking unattached growth or perithallial protuberances (Figures 37a,b, 38a, 39c). Young thalli produce lobate margins that may grow unattached (Figures 37f,g, 39c). Living thalli are red pink to violet in color (Figure 41a,b). Individual lamellae show monopodial-dorsiventral organization and are 25–270 µm thick, composed of a noncoaxial polystromatic hypothallium, 20–190 µm thick, supporting an ascending nonstratified perithallium 30–250 µm thick (Figures 38c, 39d). Hypothallial cells are 12–36 × 4–10 µm (L × B), and perithallial cells are 3–12 × 2–8 µm (L × B). Subepithallial cells are longer than cells below, to 12.5 × 4 µm (L × B), and support single, flattened to roundish or even flared epithallial cells, 1–4 × 3–10 µm (L × B; Figures 38c,e,f, 39e-g). Terminal trichocytes, to 18 × 10 µm (L × B), may occur sporadically on both multiporate and gametangial (male) thalli in Canarian thalli (Figures 38b, 39h). Cell fusions between contiguous vegetative cells are common. Secondary pit connections are absent.

Male thalli grow on *Haliotis* (Børgesen no. 3106) and also epilithically (on a pebble) together with bisporophytes (Børgesen no. 3014; Figures 39a, 40a,b). Uniporate conceptacles are 200–500 × 60–80 µm (D × H; n: 12). A mature chamber, ~200 × 60 µm (D × H; Figure 40c), is provided with a roof 40–55 µm thick. Spermatangial structures are simple (unbranched) with lunate SMCs and develop on the floor, the walls, and the roof (Figure 40c,d). On the floor, spermatangia occur on a centrally raised pedestal formed by a single layer of palisade cells (Figure 40c,e).

Empty carposporangial conceptacles (Bermudan thalli) are 530–950 × 295 µm (D × H; n: 2) and provided with chambers 500–570 × 295 µm high (D × H; n: 3). The floor is flattened, and the roof is 50–70 µm thick.

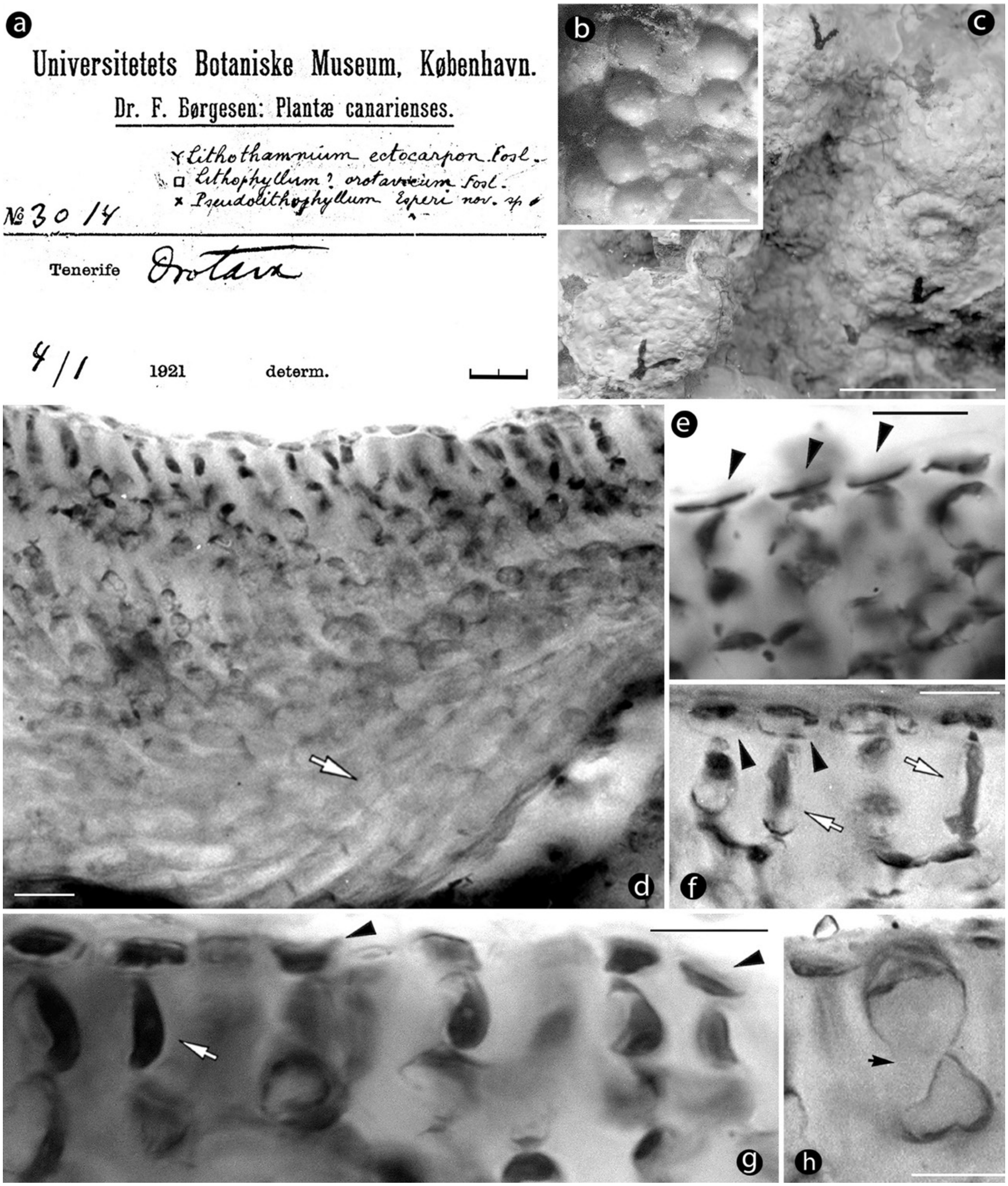
Multiporate conceptacles are 180–590 × 70–190 µm (D × H) and provided with chambers 140–400 × 100–310 µm (D × H; merged chambers reaching 470 µm in diameter; n: 56; Figures 37a, 39b, 41a–c). The roof is convex, 22–45 µm thick, composed of 5- to 8-celled filaments and perforated by 32–62 pore canals. Pore plates are 170–300 µm in diameter (n: 5). Canals are ± straight, 7–12 µm in diameter, surrounded by 5–7 rosette cells (n: 20) that occasionally are thinner–wider than contiguous epithallial cells (Figures 38h–j, 41f–h). Canals are lined by 5- or 6-celled filaments composed of thinner–wider basal and subbasal cells and occasionally even third cells (Figure 38k,l, 41i–k). Bisporangia are 55–120 × 15–70 µm (L × B; n: 58; Figure 41c), and tetrasporangia are 70–110 × 25–50 µm (L × B; n: 7; Figure 41b–e). Older conceptacles become embedded in the perithallium in a colliculate pattern, as new conceptacles develop in at least three successive layers (Figure 38g). Conceptacle embedding probably starts via centripetally growing peripheral filaments (Figure 41l).

Comments: The species was originally described from several collections made at Porto de la Cruz, Tenerife, by Sauvageau (Foslie 1906a: 18). Printz (1929: 51, pl. 1, fig. 16) illustrated "a part of the species" and added some new features in a synoptic key, including the presence of "sometimes hemispherical conceptacles" and "perithallic cells partly subquadrate, 6-7µ, partly and more frequently elongate vertically, 6-11 µ." We have not confirmed the presence of hemispherical conceptacles in the Canarian material, after studying the original and the new collections. Lemoine (in Børgesen 1929: 24, fig. 7 left) reported six collections from the type locality in Tenerife (Børgesen nos. 3058, 3104, 3109, 3141, 3167, 3189, all in C) and one from Gran Canaria (Børgesen no. 3552, "Playa de las Canteras," in C). We reexamined the six Tenerife collections and identified instead gametophytes and bi- or tetrasporophytes of *Phymatolithon lenormandii*. By contrast, we found *H. bisporum* in those collections identified by Lemoine (in Børgesen 1929: 21–22) as "*Lithothamnion ectocarpon*" (i.e., Børgesen nos. 3014 and 3106, in C). This identification is confirmed by Lemoine's account of "*L. ectocarpon*" in Børgesen (1929: 21–22), where she observed "conceptacles . . . très serrés [et] souvent ovale . . . 250 à 400 . . . jusqu'à 500 µ," whereas in the holotype of *L. ectocarpon* she correctly reported conceptacles to be "400 à 700 µ de diamètre" and the thallus to be "montre . . . [une] aspect extérieur . . . analog . . . avec *Mesophyllum lichenoides* . . . mais . . . plus délicat . . . [et] plus fragiles."

The reported larger multiporate conceptacles and the fragile thallus with unattached superimposed growth (which also occurs in *Mesophyllum lichenoides*) fit, indeed, the type of *Lithothamnion ectocarpon* from Cape Verde (here recognized as *Ectocarpa capverdensis*), whereas thalli of *H. bisporum* grow firmly attached (with rare unattached margins). On the basis of a study of the TRH lectotype, Adey (1970: 30) transferred *Lithothamnion bisporum* to *Leptophytum*. On the other hand, Afonso-Carrillo (1984: 134, figs. 15, 16, 19, 20) transferred the species to *Phymatolithon*, illustrating the presence of domed-isodiametric epithallial cells and short subepithallial cells. The latter two characters definitely support a position of the relevant material in *Phymatolithon*, but Afonso-Carrillo (1984) followed Lemoine, who based her identification on the Børgesen material (nos. 3058, 3104, 3109, 3141, 3167, 3189) that belongs, indeed, to the genus *Phymatolithon*.

The present reexamination of the PC syntype material has reestablished the identity of the species as a member of Mesophyllaceae and not *Phymatolithon*. Its generic recognition as a member of the new genus *Hyperandri* is supported by the presence of SMCs on a layer of palisade cells. The latter character was originally described in *Leptophytum hyperandri* from Pacific Mexico (Athanasiadis 2007b: figs. 35, 36; Figure 5l,m), which species has been selected as the generitype of the new genus *Hyperandri*.

We could not distinguish between Caribbean (or Bermudan) specimens and Canarian counterparts, although it appears that western Atlantic thalli lack trichocytes and rarely display thallus superimposition. As the species forms thin crusts on a variety of substrata, dispersal in historical times cannot be precluded, and the question of conspecificity remains to be answered by future



Universitetets Botaniske Museum, København.

Dr. F. Børgesen: Plantæ canarienses.

Y Lithothamnium ectocarpon Fosl.
□ Lithophyllum? orotavicum Fosl.
× Pseudolithophyllum Esperi nov. sp.

№ 3014

Tenerife Orotava

4/11 1921 determ.

FIGURE 39. *Hyperandri bisporum*: Børgesen no. 3014 (C). (**a**) The label of the collection (specimens on a single cobble), where thalli of the species are annotated "Y" and referred to "*L. ectocarpon*" by Lemoine. Scale bar: 1 cm. (**b, c**) Multiporate conceptacles ("V") annotated on thalli. Scale bars: 500 µm, 5 mm, respectively. (**d**) Section showing a noncoaxial hypothallium (arrow). Scale bar: 10 µm. (**e–g**) Sections at the surface showing elongate subepithallial cells (white arrows) supporting single epithallial cells (arrowheads) of variable shape: flattened in (e), slightly domed in (f), and trapezoid to slightly flared in (g). Scale bars: 10 µm. (**h**) Single terminal trichocyte (arrow). Scale bar: 10 µm.

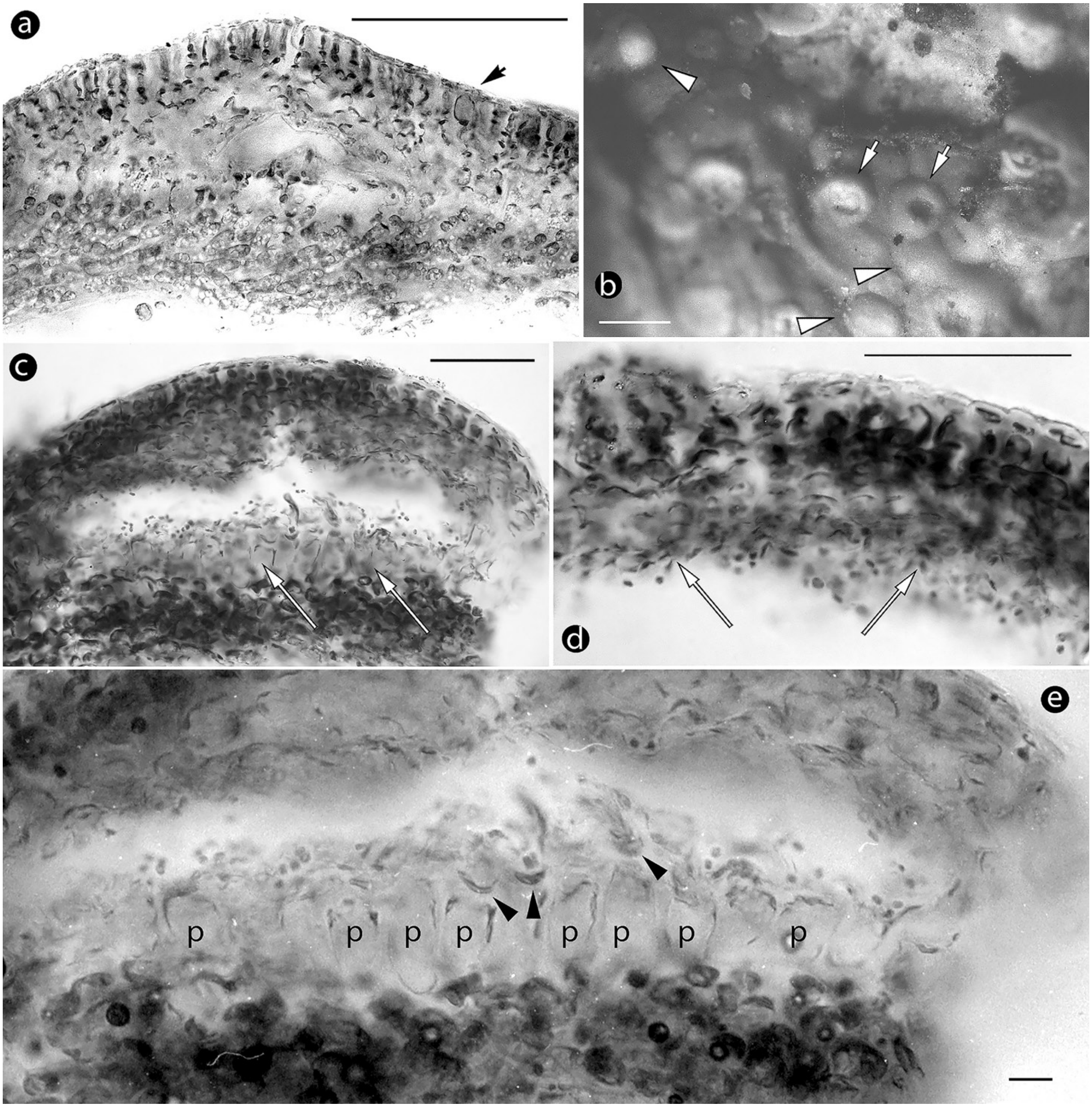


FIGURE 40. *Hyperandri bisporum*: male structures. (**a**) Young male conceptacle with trichocyte on the roof (arrow; Børgesen no. 3014). Scale bar: 125 µm. (**b**) Surface view of male conceptacles (arrowheads) on *Haliotis*, some with deteriorated roof (arrows; Børgesen no. 3106). Scale bar: 500 µm. (**c**) Male conceptacle at maturity with palisade cells on the floor (Børgesen no. 3106). Scale bar: 50 µm. (**d**) Simple spermatangial structures (arrows) on the roof (Børgesen no. 3106). Scale bar: 10 µm. (**e**) Magnification of the floor, where lunate SMCs (black arrowheads) develop on a single layer of palisade cells (Børgesen no. 3106). Scale bar: 10 µm. Abbreviation: p, palisade cell.

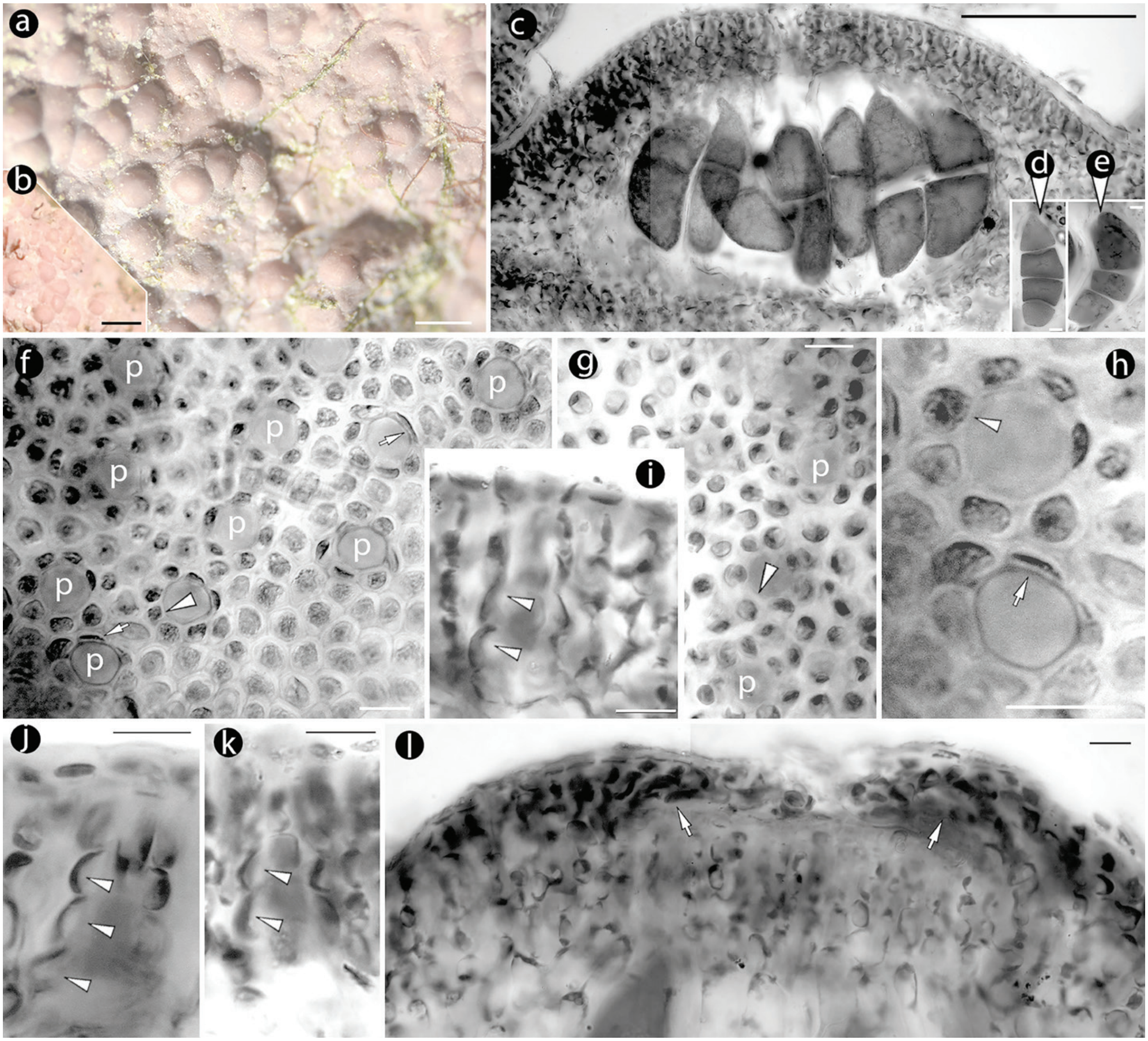


FIGURE 41. *Hyperandri bisporum*: multiporate conceptacle structures. (**a, b**) Multiporate conceptacles on thalli from Puerto Rico (PR-27B) and the Canaries (RAS-1), respectively. Scale bars: 500 μm, 1 mm, respectively. (**c**) Section of a multiporate conceptacle with bisporangia (Børgesen no. 3014). Scale bar: 100 μm. (**d, e**) Tetrasporangia (Børgesen no. 3014). Scale bars: 10 μm. (**f–h**) Pore plates with several pores, where rosette cells are either normal epithallial cells (arrowhead) or thinner–wider (arrows; RAS-1). Scale bars: 10 μm. (**i–k**) Sections through pore plates showing straight canals lined by thinner–wider cells (arrowheads) toward the basal opening (Børgesen no. 3014 in (i), RAS-1 in (j) and (k)). Scale bars: 10 μm. (**l**) Embedding process of a conceptacle via production of peripheral filaments (arrows) that grow centripetally over the roof (Børgesen no. 3014). Scale bar: 10 μm. Abbreviation: p, pore canal.

(molecular) investigations. We have also failed to find male gametophytes in the Caribbean-Bermudan material, although rare tetrasporangia and a few carposporangial conceptacles (Howe no. 151) were seen. In the western Atlantic, *Hyperandri bisporum* is at least as common as *Magnephycus ornatus* (see species account), colonizing a wider diversity of habitats in both the littoral and sublittoral zones (to ~70 m depth). *Hyperandri bisporum* might be related to *Leptophytum* sp. in Searles (1987: 106, 1988: 62, fig. 43A–D) and Schneider and Searles (1991: 236, figs. 277, 278), known from a collection at 17–21 m on Gray's Reef (August) and exhibiting smaller hypothallial cells (up to 15 µm long) and slightly smaller multiporate conceptacles (up to 430 µm in diameter, with chambers 250–325 × 90 µm). Moreover, the illustrations in Searles (1988: fig. 43C) and Schneider and Searles (1991: 236, fig. 277) show elongate subepithallial cells and a carposporangial conceptacle with flattened floor. The significance of the pedestal formation within Magnephyceae has already been discussed (see characters 19–20 in "Character Evolution in the Mesophyllaceae" and "Phylogenetic Relationships in the Mesophyllaceae").

Hyperandri dawsonii **Athanas. et D. L. Ballant. comb. et nom. nov.**

Hyperandri dawsonii Athanas. et D. L. Ballant. comb. et nom. nov.
Basionym: Leptophytum hyperandri Athanas. 2007b: 207–213, figs. 23–36.

Type Locality: Sublittoral, 36–45 m depth, at Cortez Bank ("off the international boundary at W. Long. 119° 08"), Pacific Mexico (see Dawson 1960: 19).

Holotype: In UC (unnumbered, AHFH 70353, Dawson no. 7967, *pro parte*, a male specimen attached to a limpet, 27 August 1949, coll. E. Y. Dawson), illustrated by Athanasiadis (2007b: figs. 23A, 24A).

Habitat and Distribution: Specimens are attached to limpets and dredged from the sublittoral zone (36–54 m depth) at the type locality and the nearby Sacramento Reef, Pacific Mexico.

Comments: The original material (two specimens) and a second collection from Sacramento Reef included, in total, three specimens lacking thallus superimposition and displaying a dorsiventral-monopodial organization with a polystromatic noncoaxial hypothallium (with rare coaxial patches) and an ascending and locally stratified perithallium with elongate-ovate subepithallial cells supporting 1 or 2 flattened epithallial cells. The characteristic floor elevation (pedestal) in male chambers, originally described as an autapomorphy for this species, was unexpectedly also observed in *H. bisporum*, leading to the proposal of the new genus *Hyperandri* (Figure 5, parts l,m). This elevation results from the production of a layer of palisade cells on the floor center, just below the SMCs, and because this structure was not seen in all the conceptacles, it may be induced at a later stage of their ontogeny. This structure is here interpreted as the first evolutionary step toward the production of a more elaborate pedestal, composed of additionally 7 or 8 layers of isodiametric cells, as described in *Magnephycus ornatus* (Figure 5n,o).

Multiporate or carposporangial conceptacles are not recorded in *H. dawsonii*. In *Hyperandri bisporum* and *H. siamense*, multiporate conceptacles develop straight canals and share this character with all other Magnephyceae, except *Magnephycus*, which develops pyriform canals. This indicates that despite pedestal formation in male chambers (considered to be significant and receiving a higher weight in the phylogenetic analysis), *Hyperandri* and *Magnephycus* should not be considered closely related. The phylogenetic analysis recognized instead the relationship (((*Magnephycus-Ectocarpa*) *Hyperandri*)-*Macedonis*) *Leptothallia-Leptophytum*, pointing to canal structure as being more significant and recognizing straight canals as the ancestral and pyriform canals as the advanced condition (Figure 6a–c).

Hyperandri siamense **(Foslie) Athanas. et D. L. Ballant. comb. nov.**

FIGURES 42–45

Hyperandri siamense (Foslie) Athanas. et D. L. Ballant. comb. nov.
Basionym: Lithothamnion siamense Foslie 1901b: 19–20.
Synonyms: Lithothamnion siamense f. *minutum* Foslie (1901b: 19–20, "*minuta*"). Foslie (1904c: 10, "*typica*").
Mesophyllum siamense (Foslie) W. H. Adey 1970: 26.

Lectotype Locality: Sublittoral, ~18 m depth, 27 km east of Koh Chuen Island, Chang Archipelago, Siam Gulf, Thailand.

Lectotype: In TRH (B2-1727, *pro parte*, thalli on a mussel shell, 6 February 1900, coll. J. Schmidt), illustrated by Printz (1929: pl. 1, fig. 17), designated herein (Figures 42, 45).

Syntypes: In TRH (B2-1728, *pro parte*, "11 naut. miles NW of Koh Kam on a depth of 10 fathoms (f. *minuta*)"); in TRH (B2-1729, *pro parte*, "between Koh Mesan and Koh Chuen, 15 fathoms (f. *minuta*)").

Material Examined: Thailand: lectotype and syntypes as described above and below.

Habitat and Distribution: The only material identified with certainty is the lectotype, which includes tetrasporangial thalli attached to a mussel shell, collected from 18 m depth in the Chang Archipelago, and the syntype fragment with two carposporangial conceptacles (B2-1729, *pro parte*), collected between Koh Mesan and Koh Chuen at ~27 m depth, both in the Siam Gulf.

Comments on the Protologue and Neolectotypification: *Lithothamnion siamense* was originally described by Foslie (1901b) from several collections made by J. Schmidt in the Chang Archipelago (Gulf of Siam, Thailand). In the protologue, Foslie recognized two forms, f. *minutum* and f. *simulans*, without type designation or any other indication revealing the autonym (f. *siamense*).

The protologue (Foslie 1901b: 19–20) reads, in the most essential parts,

L. siamense Fosl. mscr. Thallus forming delicate, light rosy, smooth crusts or nearly so on hard objects, 30–100 µ thick. Conceptacles of sporangia convex, rather prominent, 300–500 µ in diameter. Sporangia four-parted. Conceptacles of cystocarps conical, 350–600 µ in diameter.

f. minuta Fosl. mscr. The crust 30–60 µ thick. Conceptacles of sporangia 300–400 µ in diameter. Sporangia 60–70 µ long, 25–30 µ broad. Conceptacles of cystocarps 350–450 µ in diameter.

f. simulans Fosl. mscr. The crust 50–100 µ thick. Conceptacles of sporangia 400–500 µ in diameter. Sporangia 140–160 µ long, 60–80 µ broad. Conceptacles of cystocarps 500–600 µ in diameter. This is one of the most delicate . . . species of this genus attached . . . especially to Corals, but . . . also met with on stones, shells of Mollusks or . . . other Algae. The colour is in a dried state a light rosy, sometimes . . . with a greyish-green shade. The crust is at first almost orbicular . . . with slightly crenulate margin. In an old state it becomes . . . fully confluent . . . to 12 mm in diameter . . . [already] 3 mm in a fertile stage (f. *minuta*). But sometimes it almost covers small shells of Mollusks (f. *simulans*). It is smooth and . . . very feebly shining. The smoothness . . . depends however on . . . the substratum . . . A vertical section of the crust shows an almost coaxilate development. The hypothallic cells are . . . about 25 µ long, sending forth a rather feebly developed perithallic layer . . . [with] cells . . . partly roundish partly square, 7–10 µ in diameter . . . often with the longest diameter . . . horizontal and more frequently in vertical direction . . . exceptionally up to 14 long and 7 µ broad. The [multiporate] conceptacles . . . are scattered or somewhat crowded in any part of the crust except the peripher portion, convex, in f. *minuta* less prominent than in f. *simulans* . . . The roof is intersected with about 40 delicate muciferous canals. . . . The [carposporangial] conceptacles frequently . . . in other individuals than those of [tetra]sporangia. They are conical . . . abruptly passing into a very short and thin tip . . . [and] smaller in f. *minuta* than in f. *simulans* . . . Both forms . . . provided with the said organs in February, carpospores however more scarce than [tetra]sporangia. . . . I have seen only a solitary well developed specimen of [f. *simulans*] . . . the material also of *minuta* is scarce. . . . The present species stands nearest to *L. Lenormandi* and reminds . . . young specimens of f. *sublaevis*. . . .
[Collections]

11 naut. miles NW of Koh Kam on a depth of 10 fathoms (f. *minuta*): [B2-1728]

between Koh Mesan and Cape Liant. 9 fathoms (f. *minuta*): [not found in TRH]

15 naut. miles E. of Koh Chuen, 10 fathoms (f. *minuta* ?): [B2-1727]

between Koh Mesan and Koh Chuen, 15 fathoms (f. *minuta*): [B2-1729]

the north side of Koh Mesan in 10–15 fathoms water (f. *minuta*): [not found in TRH]

and Koh Sarlak, on *Septifer bilocularis* L. in shallow water (f. *simulans*) [B18-2626] - almost everywhere in solitary individuals.

No synonyms or illustrations were provided, and of the six cited collections, only four, B2-1727, B2-1728, B2-1729, and B18-2626, have been located in TRH (Woelkerling et al. 2005).

A few years later, Foslie (1904c: 10, 16) selected f. *minutum* as the autonym, citing it under *L. siamense* f. *typicum*, recognizing simultaneously f. *simulans* as an independent species. His choice has been accepted (Silva et al. 1987: 37; Verheij and Woelkerling 1992: 285; Silva et al. 1996: 258). Hence, of the six collections cited in the protologue (Foslie 1901b), five are to be attributed to *L. siamense*, and only one is to be attributed to *L. simulans*. Foslie illustrated two entire specimens from material collected during the Siboga Expedition (Foslie 1904c: pl. 1, figs. 1, 2, "stat.49" and "stat.64," respectively) and two sterile sections (Foslie 1904c: 11, text fig. 3A,B) made from his original material (slide 471, which belongs to the collection B2-1728).

Printz (1929: pl. 1, fig. 17) illustrated one of the original specimens "covering a shell of a mussel. Gulf of Siam: East of Koh Chuen" (presently included in B2-1727), but later authors (Adey and Lebednik 1967; Verheij and Woelkerling 1992; Woelkerling 1993a; Woelkerling et al. 2005) disregarded these elements in selecting a lectotype. Instead, Adey and Lebednik (1967: 52) selected a specimen from the Siboga Expedition, cited by Foslie (1904c: 10, "Stat. 64. Kambaragi Bay") and presently included in B2-1731 (TRH; Printz 1929: pl. 1, fig.18). Because this element was not original material, Verheij and Woelkerling (1992: 285) proposed neolectotypification with the material collected "between Mesan Island and Chuen Island, Gulf of Thailand; leg. *J. Schmidt*, 6 February 1900" (B2-1729), including Foslie slides 470 and 471 (which most likely belong to two other collections, as discussed in more detail below). As Verheij and Woelkerling misunderstood the parts belonging to separate gatherings, the new lectotype included elements potentially belonging to three different collections. The new error occurred because there is mismatch between the localities and the numbers on the four Foslie slides (470, 471, 468, 469, included in the original material); the numbers on the slides (which also appears in Foslie's notes and annotations on the box lids) do not correspond to the relevant localities written on the slides. Because Verheij and Woelkerling (1992: 285), Woelkerling et al. (2005), and W. J. Woelkerling (La Trobe University, Bundoora, Victoria, Australia; in litt. "December 2004" in TRH) accepted the locality names on the slides to be correct, further confusion occurred as slides and notes were moved from B2-1727 and B2-1728 to B2-1729 (and vice versa). However, it is logical to accept that the annotations on the box lids and the notes (which match each other and both include the number on the slides) predate the locality annotations on the slides (which were certainly made at a later stage), and hence, the correct association between slides, notes, and collections should be interpreted in the way cited by Adey and Lebednik (1967: 52) as follows:

B2-1727 includes the note "III delvis (18) Prep.470 af minute Den danske Siamexp. 1899-1900 Siambugten 15kvm Ø f. Koh Chuen 10 fv skalbund *L. siamense f. minuta*," which matches the annotation on the box lid and refers to slide 470 and the multiporate specimen in envelope "18" (the latter two elements moved to B2-1729 by Woelkerling). In terms of algal material, B2-1727 includes thalli with multiporate conceptacles overgrowing an entire mussel shell, thalli on two shell fragments, and material in envelop "18" (Figure 42).

B2-1728 includes the note "No.1 Den danske Siam exp. 1899–1900 Prep.471. *Lith. siamense* f. *minuta* Siambugten 11 Kvartmil N.V.af Koh Kam 10fv. 6/2 1900 leg. Joh. Schmidt," which matches the annotation on the box lid and refers to slide 471 with its associated note (the latter two elements moved to B2-1729 by Woelkerling). In terms of algal material, B2-1728 contains three small sterile fragments (Figure 43).

B2-1729 includes the note "IV delvis Den danske Siam exp. 1899–1900 Siambugten Mell. Koh Measn og Koh Chuen. 10–15 fv. stenbund leg Joh. Schmidt Lith.sp. Prep.468, 469 60–70 × 25–30 µ Koncept med faa sprodte kanaler Sp. med . . . [illegible] Cyst. konc. paa . . . *L. siamense* f. *minuta*," which matches the annotation on the box lid and refers to slides 468 and 469 and their respective notes with cell measurements (the latter four elements moved to B2-1728 by Woelkerling). In terms of algal material, B2-1729 includes only three fragments (one cystocarpic and the others sterile, on older broken shell fragments; Figure 44).

The elements in the three collections were left in the existing (Woelkerlingian) arrangement, but the correct association of materials is illustrated in Figures 42–44, and the error can be perceived when comparing the locality annotations on the slides with those on the notes and the box lids. Because the second typification of Verheij and Woelkerling (1992: 285) included elements (slides 470 and 471) of uncertain origin (most likely belonging to two other gatherings), it can be disregarded (Turland et al., 2018: Articles 9.3, 9.17), and a new lectotypification has to be made that takes into account the entire original material.

According to the protologue, *L. siamense* f. *minutum* forms a thin crust 30–60 µm thick, reaching a diameter of 3 mm in a fertile stage, with tetrasporangial conceptacles 300–400 µm in external diameter, tetrasporangia 60–70 × 25–30 µm (L × B), and conical carposporangial conceptacles 350–450 µm in external diameter. An almost coaxial development was also reported, but without indication of whether it occurred in one or both forms of the species. Hence, the diagnostic characters of the autonym rely upon the size of the thallus, conceptacles, and tetrasporangia; in f. *simulans* the thallus was said to reach 100 µm in thickness and to 12 mm in diameter, tetrasporangial conceptacles were said to be 400–500 µm in diameter, carposporangial conceptacles 500–600 µm in diameter, and tetrasporangia 140–160 × 60–80 µm.

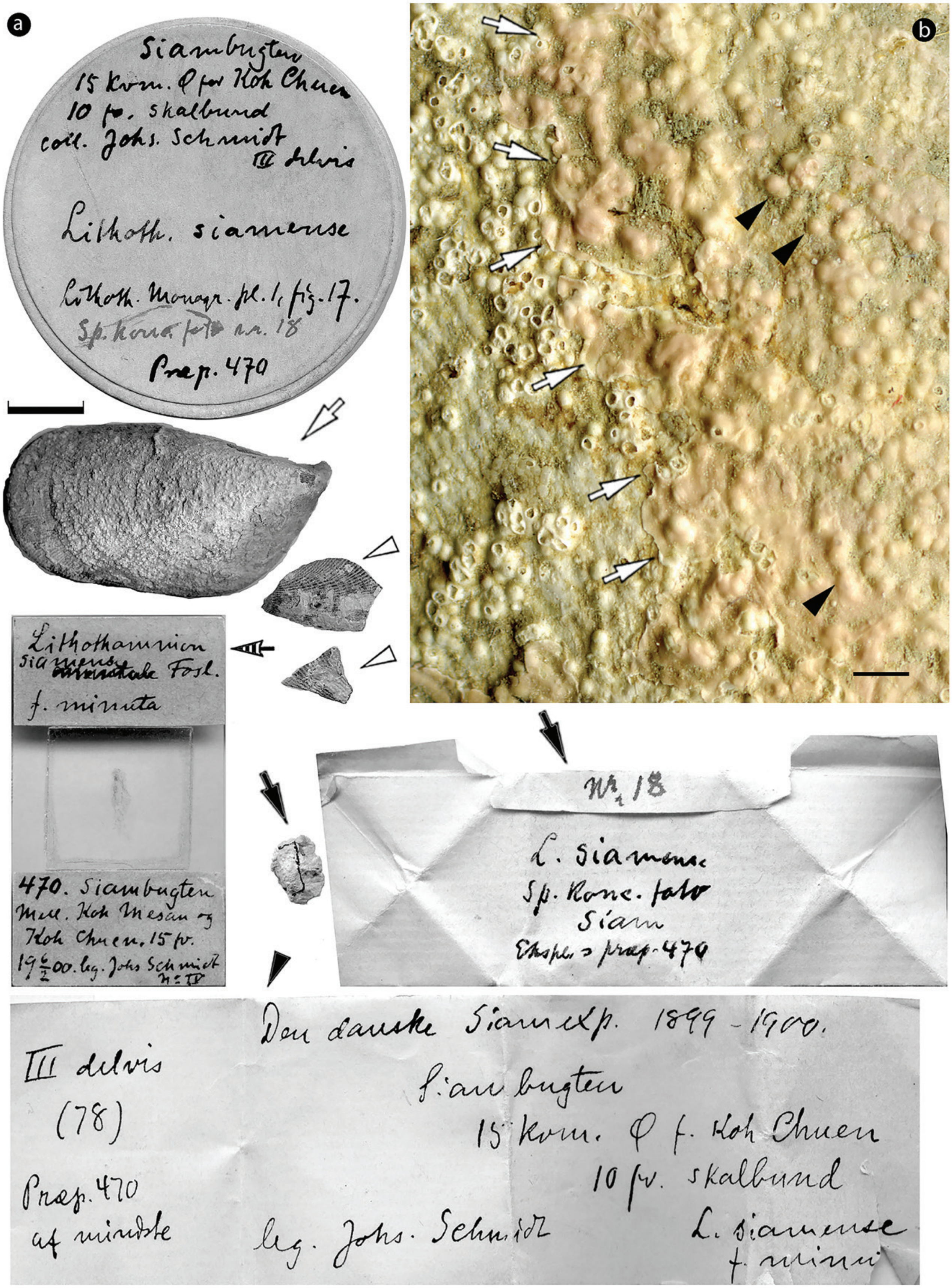
Examination of the three syntype collections (B2-1727, B2-1728, B2-1729) indicated the following:

1. None of the four slides (468, 469, 470, and 471) includes conceptacles; slide 470 (B2-1727) is badly preserved, and it is impossible to observe any structures of the material.
2. Slides 468 and 469 (B2-1729) show a thallus 25–60 µm thick, with a thin noncoaxial hypothallium ~20 µm and hypothallial cells up to ~22 µm long (data are in agreement with the protologue).
3. By contrast, the thallus in slide 471 (B2-1728) reaches 125 µm in thickness and, although in full agreement with the illustration in Foslie (1904c: 11, text fig. 3A), is in variance with the "30-60" µm said to be the thickness of f. *minutum*.
4. The noncoaxial hypothallium (in slide 471) is composed of cells 12–15 µm long (13–29 µm long and 7–13 µm broad according to Foslie's cell measurements of slide 471), and in the ascending perithallium, filaments are ~10 µm broad (cells 11–14 µm long and 9–14 µm broad according to the same Foslie note).
5. Epithallial cells in slide 471 are ~2–3 × 8 µm (L × B), but it is not possible to assess their shape (flared or not).

In conclusion, the information from the four slides is either in variance with the protologue (slide 471) or in agreement with it (slides 468 and 469) but is certainly inadequate to determine the identity of the material. Moreover, since no corrections (of the numbers or the localities) were made on the slides by Foslie or Printz, the four slides should be disregarded in selecting a lectotype.

The fragment included in the envelop annotated "18" (B2-1727) is up to 9 mm in diameter and bears at least 13 intact multiporate conceptacles (and another four with a broken roof). A small fragment was sectioned and showed that the hypothallium is noncoaxial, composed of cells 10–15 µm long and 5–8 µm broad. Epithallial cells are 2–3 × 7–9 µm (L × B). Their shape is rectangular (flattened to inflated). The few subepithallial

FIGURE 42. (*Opposite*) *Hyperandri siamense*: lectotype collection of *Lithothamnion siamense* (=*L. siamense* f. *minutum*) in TRH (B2-1727). (**a**) The here selected lectotype (white arrow) in the original box, which includes two more fragments (white arrowheads), slide 470 (hatched arrow), a note (see text; black arrowhead), and an envelope annotated "N°18" with an algal fragment (black arrows). Slide 470 is erroneously annotated "Mell. Koh Mesan og Koh Chuen, 15 fv," referring to the locality in B2-1729. Scale bar: 1 cm. (**b**) Part of the lectotype in magnification. Arrows delineate its margin, and arrowheads indicate multiporate conceptacles. Scale bar: 1 mm.



Siambugten
15 Kvm. Ø for Koh Chuen
10 fv. skalbund
coll. Johs. Schmidt
III delvis

Lithoth. siamense

Lithoth. Monogr. pl. 1, fig. 17.
Sp. Kone. foto nr. 18
Prep. 470

Lithothamnion
siamense ~~[illegible]~~ Fosl.
f. minuta

470. Siambugten
Mell. Koh Mesan og
Koh Chuen. 15 fv.
19 6/2 00. leg. Johs Schmidt
Nr. IV

Nr. 18

L. siamense
Sp. Kone. foto
Siam
Ekspl. ⊃ prep. 470

Den danske Siamexp. 1899–1900.

III delvis
(78)

Prep. 470
af mindste

Siambugten
15 Kvm. Ø f. Koh Chuen
10 fv. skalbund

leg. Johs. Schmidt

L. siamense
f. minu

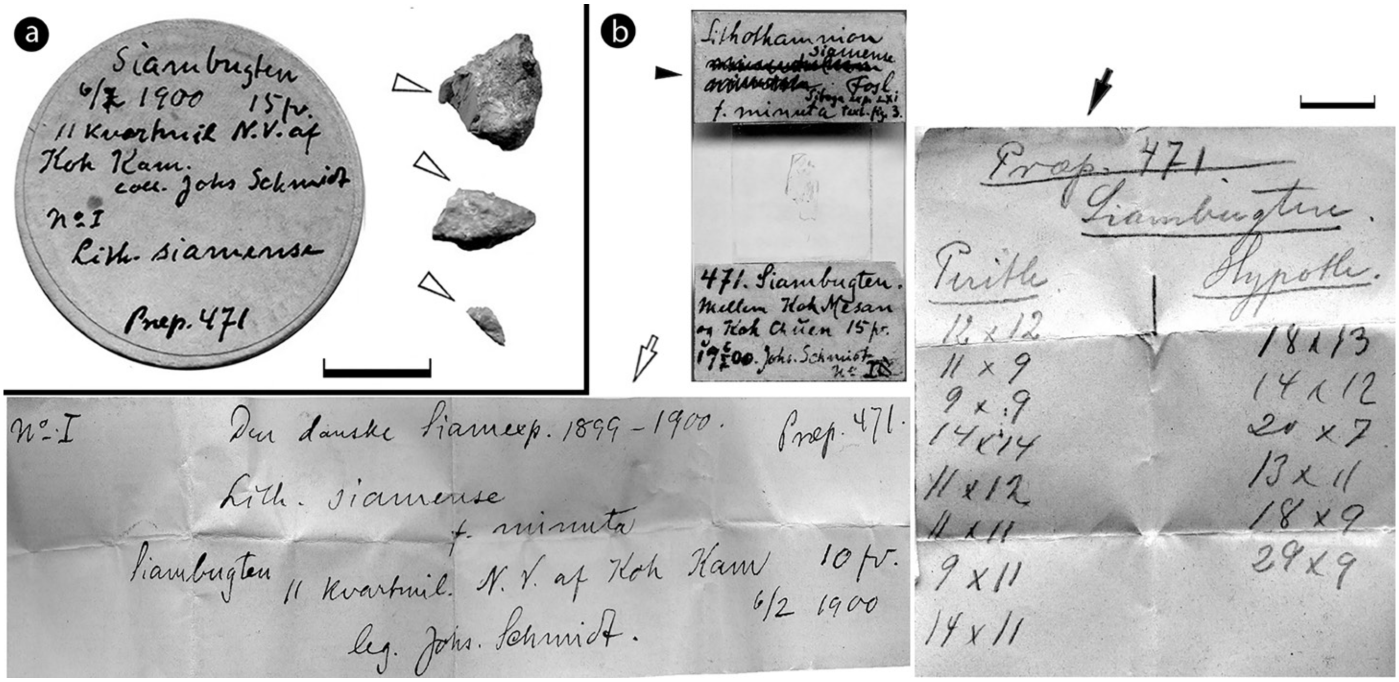


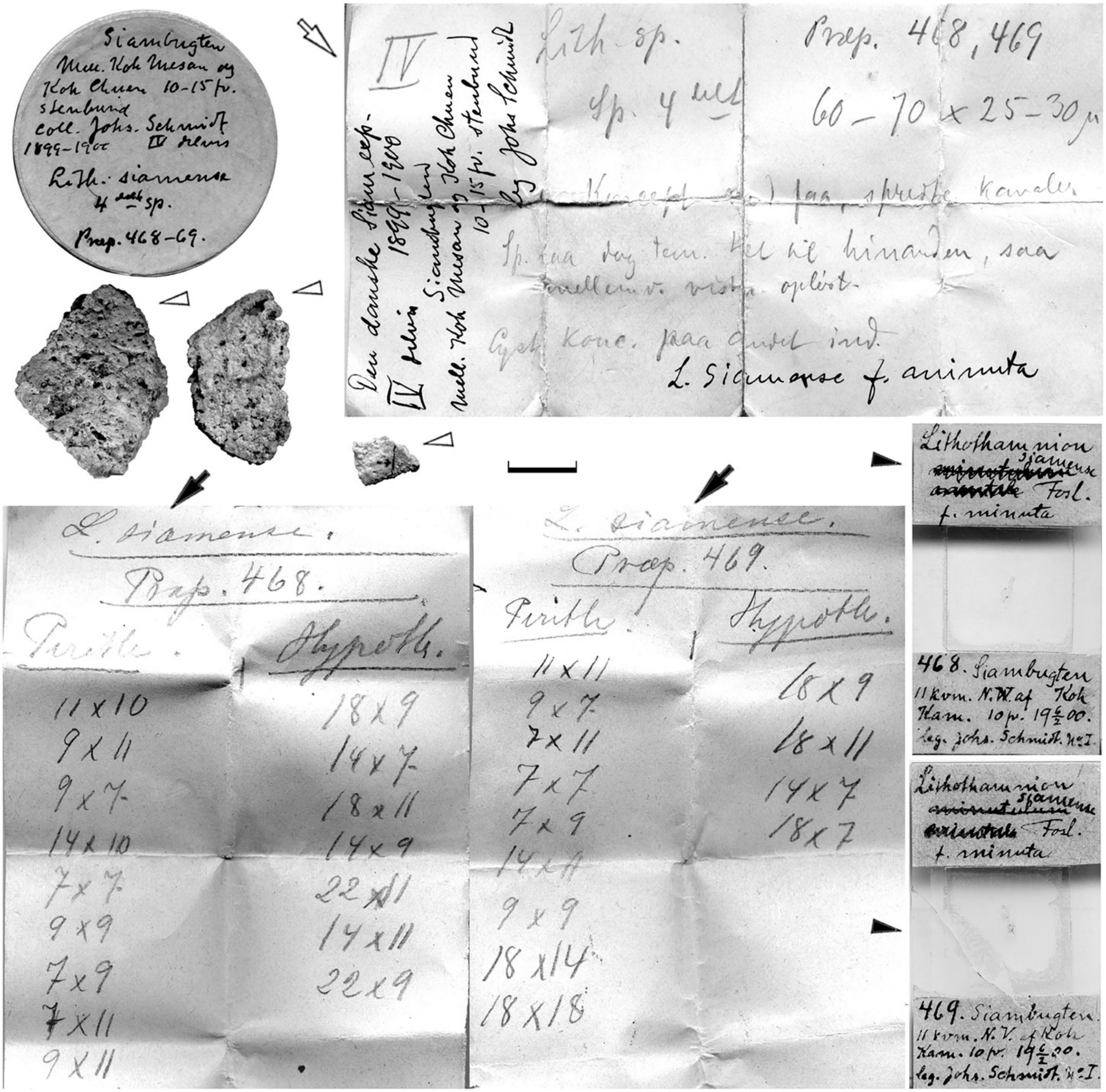
FIGURE 43. *Hyperandri siamense*: syntype collection of *Lithothamnion siamense* (=*L. siamense* f. *minutum*) in TRH (B2-1728). (**a**) The original box, which includes three algal fragments (white arrowheads). Scale bar: 1 cm. (**b**) Other materials include a note (see text; white arrow), slide 471 (black arrowhead), and a note with cell measurements pertaining to the material on the slide (black arrow). Slide 471 is erroneously annotated "Mellan Koh Mesan og Koh Chuen, 15 fv," referring to the locality in B2-1729. Scale bar: 1 cm.

cells seen are nearly isodiametric, ~7–8 µm. Conceptacles measure between 300 and 500 µm in external diameter. Chambers are 250–370 µm in diameter (n: 5), and the roof is perforated by up to 37 pores, with pore plates 220–275 µm (n: 2). Pores are 7–9 µm in diameter and surrounded by 6 rosette cells that are normal epithallial cells. No embedded conceptacles occur. The size (up to 500 µm) of the conceptacles suggests that this material belongs to f. *simulans*, but the relevant canal shape was not determined.

A small fragment with two carposporangial conceptacles was sectioned from B2-1729. The thallus is ~60 µm in thickness, and the conceptacles are 350–400 × 200 µm (D × H; n: 2), with a central ostiole up to 150 µm long and 50 µm broad and a roof 35–100 µm thick. Chambers are 200–210 × 100 µm (D × H), with a flattened fertile floor displaying peripheral development of carposporangia, 20–35 µm in diameter. Subepithallial cells (in the roof) are elongate, ~14 × 2–3 µm (L × B), supporting single, flattened epithallial cells 2–3 × 5–7 µm (L × B). The hypothallium is noncoaxial, composed of cells 15–20 × 6–8 µm (L × B). Thallus thickness (up to 60 µm) and carposporangial conceptacle size are in agreement with f. *minutum*, and therefore, this element is here considered to represent part of Foslie's concept of this taxon. However, there is no other fertile specimen in B2-1729 for comparison.

The algal fragments in B2-1728 are sterile and reach less than 1 cm in diameter.

By contrast, the material in B2-1727 includes thalli growing on an entire mussel shell (~4.1 × 2.3 cm; Figure 42a). Thalli adhere closely to the substratum, lacking unattached parts. They overgrow another encrusting coralline (with broken multiporate roofs) whose identity was not clarified (Figure 42b). In a sectioned fragment, the thallus is 42–135 µm thick (reaching 250 µm when supporting conceptacles) and composed of a noncoaxial hypothallium 18–40 µm thick, supporting an ascending perithallium 28–170 µm thick (Figure 45a–c). Hypothallial cells are 10–27 × 5–8 µm (L × B), perithallial cells are 6–18 × 3–6 µm (L × B), and subepithallial cells are up to 13 µm long, each supporting a single, flattened epithallial cell, 2–3 × 6–11 µm (L × B; Figure 45d–f). Multiporate conceptacles are spread all over the surface. They are occasionally aggregated in patches and range 260–400 µm in external diameter (n: 5), reaching a height of ~70 µm. Most of them are intact, some are senescing, and others undergo an embedding process (in the perithallium), becoming filled in with palisade cells and arranged in a colliculate pattern (Figure 45g). Chambers are 200–270 × 80–130 µm (D × H; n: 6) and provided with a few bisporangia or tetrasporangia measuring 65–70 × 25–30 µm (L × B; n: 3; Figure 45h). The roof is 30–40 µm thick, composed of 5- to 7-celled filaments (including



Siambugten
Mell. Koh Mesan og
Koh Chuen 10-15 fv.
stenbund
coll. Johs. Schmidt
1899-1900 IV delvis
Lith. siamense
4 ede sp.
Prep. 468-69.

IV

Den danske Siam exp.
1899-1900
IV delvis Siambugten
mell. Koh Mesan og Koh Chuen
10-15 fv. stenbund
by Johs Schmidt

Lith. sp.
Sp. 4 ede

Prep. 468, 469
60–70 × 25–30 μ

[illegible] Koncept. [illegible] paa sprukte kavaler
Sp. paa dag tem. [illegible] hinanden, saa
mellemv. vistn. oplöst.
Cyst. Konc. paa [illegible] ind.
L. siamense f. minuta

L. siamense.
Prap. 468.

Perith.	Hypoth.
11x10	18x9
9x11	14x7
9x7	18x11
14x10	14x9
7x7	22x11
9x9	14x11
7x9	22x9
7x11	
9x11	

L. siamense.
Prap. 469.

Perith.	Hypoth.
11x11	18x9
9x7	18x11
7x11	14x7
7x7	18x7
7x9	
14x11	
9x9	
18x14	
18x18	

Lithothamnion ~~minutulum~~ siamense
~~[illegible]~~ Fosl.
f. minuta

468. Siambugten
11 Kvm. N.W. af Koh
Ham. 10 fv. 19 6/2 00.
leg. Johs. Schmidt. No I.

Lithothamnion ~~minutulum~~ siamense
~~[illegible]~~ Fosl.
f. minuta

469. Siambugten
11 Kvm. N.V. af Koh
Ham. 10 fv. 19 6/2 00.
leg. Johs. Schmidt. No I.

FIGURE 44. *Hyperandri siamense*: syntype collection of *Lithothamnion siamense* (=*L. siamense* f. *minutum*) in TRH (B2-1729). The original box includes a note (see text; white arrow), three fragments with algal thalli (white arrowheads), slides 468 and 469 (black arrowheads), and the relevant notes with cell measurements (black arrows). Slides 468 and 469 are erroneously annotated "11 Kvm.N.V. af Koh Ham.10 fv," referring to the locality in B2-1728. Scale bar: 1 cm.

the epithallial cell). Canals are straight, ~8–10 µm in diameter, and surrounded by 6 rosette cells (n: 2; Figure 45i–k). Canals are bordered by pore filaments with thinner–wider pore cells toward the base (Figure 45k–m). Cell fusions between contiguous somatic cells are common. Trichocytes and secondary pit connections are absent.

The above description agrees with the protologue, and because this material is best preserved, it is here selected as the lectotype element. The entire shell was previously illustrated by Printz (1929: pl. 1, fig. 17, as *Lithothamnion siamense*) and represents the material originally referred to f. *minutum* by Foslie (1901b) with doubt ("?"). Because the relevant slide (470) in this collection is further annotated "Mell. Koh Mesan og Koh Chuen." and "6/2 1900" (i.e., data from the two other collections, B2-1729 and B2-1728, respectively), it has been excluded from the typification.

Species Description: Thalli to 4.1 cm long and 42–210 µm thick (reaching 250 µm when supporting conceptacles), adhering closely to the substratum and lacking unattached growth or thallus superimposition (Figure 42a). They are composed of a noncoaxial hypothallium 18–40 µm thick, supporting an ascending perithallium 28–170 µm thick (Figure 45a–c). Hypothallial cells are 10–27 × 5–8 µm (L × B), perithallial cells 6–18 × 3–6 µm (L × B) and subepithallial cells 14 × 2–3 µm (L × B), each supporting a single, flattened epithallial cell, 2–3 × 6–11 µm (L × B; Figure 45d–f). Cell fusions between contiguous somatic cells are common. Trichocytes and secondary pit connections are absent.

Carposporangial conceptacles are 350–400 × 200 µm (D × H) with a central ostiole up to 150 × 50 µm (L × B) and a roof 35–100(–150) µm thick. Chambers are 200–210 × 100 µm (D × H) with a flattened fertile floor displaying peripheral development of carposporangia, 20–35 µm in diameter.

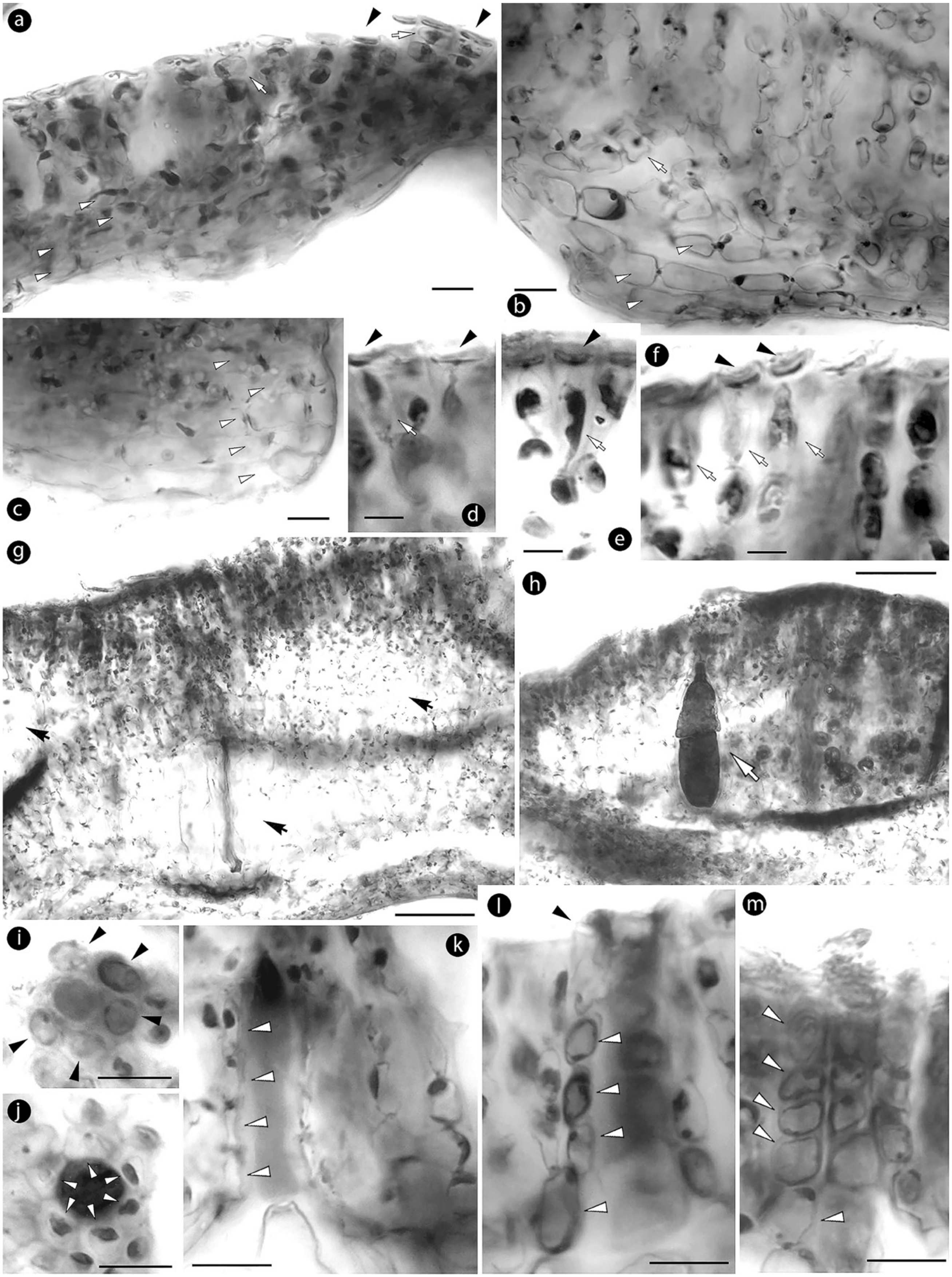
Multiporate conceptacles are 260–400 × ~70 µm in external diameter and can be aggregated in patches. Chambers are 200–270 × 80–130 µm (D × H), provided with few bisporangia or tetrasporangia 65–70 × 25–30 µm (L × B; Figure 45h). The roof is 30–40 µm thick, composed of 5- to 7-celled filaments (including the epithallial cell). Canals are straight, ~8–10 µm in diameter, and surrounded by 6 rosette cells (Figure 45i–k). Canals are bordered by pore filaments with thinner–wider pore cells toward the base (Figure 45k–m). Older conceptacles senesce or become embedded (in the perithallium), becoming filled in with palisade cells and arranged in a colliculate pattern (Figure 45g).

Comments: *Hyperandri siamense* and *H. bisporum* display similar multiporate canal structures and a colliculate pattern of conceptacle embedment. The Thai species differs, however, in lacking trichocytes and forming a thinner thallus lacking superimposition (to 210 vs. 500 µm thick in *H. bisporum* via superimposition). The latter two characters are, however, compromised in Caribbean thalli of *H. bisporum*, which lack trichocytes and develop a thinner thallus with rare superimposition. In this respect, *H. siamense* comes closer to *H. dawsonii*, which lacks both trichocytes and thallus superimposition and presently differs by a thicker thallus (to 250 µm) with development of rare coaxial patches in the hypothallium (Athanasiadis 2007b: 209). The relationship between the two Pacific species may change when more collections have been studied; knowledge of *H. siamense* presently stands on the lectotype (tetrasporophyte) and a syntype (carposporangial; B2-1729), and knowledge of *H. dawsonii* stands on the holotype (male), a paratype (male), and a third (male) specimen.

Lemoine (1966: 17) reported *Lithothamnion siamense* from Eilat (Gulf of Aqaba), indirectly implying that it was not a member of *Mesophyllum* (a genus erected by her in 1928) and probably relying upon the information from Foslie's publications. She also summarized the records of the species from the Pacific (i.e., Gulf of Siam: 17–27 m depth; Malaysian Archipelagus: 5–69 m depth; Easter Island [Lemoine 1924: 286, fig. 32a]; Tahiti [Setchell 1926: 107, with reservation]; Colombia: Island Gorgona 27 m depth [St George Exped., Lemoine, mscr. in Lemoine 1930]) and the Red Sea (Island Abulat: croisière de la Calypso, 1952; Gulf of Aden: Obock or Djibouti [Foslie 1929: pl. 1, fig. 19]). Apart from the type material, reexamination of several TRH specimens from the Red Sea (B2-1726, "*Lithoth. siamense*"), Indonesia (Tanah Djamipeah, Kambaragi Bay; B2-1731, "*L. siamense* f. *typica*"), and Sapeh Strait (B2-1732 and B2-1733, "*L. siamense*") did not provide sufficient evidence to confirm Foslie's identification.

Adey (1970: 26) transferred the species to *Mesophyllum*, noting, however, that "there is some question as to the placement of this species, since the hypothallium is highly reduced and apparently non-coaxial." *Mesophyllum siamense* was later included in catalogs and checklists of algae from the Philippines (Silva et

FIGURE 45. (***Opposite***) *Hyperandri siamense*: lectotype of *Lithothamnion siamense* (=*L. siamense* f. *minutum*) in TRH (B2-1729). Vegetative and tetra- or bisporangial structures. (**a**) Section of young thallus showing four hypothallial filaments (white arrowheads) and erect perithallial filaments with subepithallial cells of similar (or shorter) length (arrows), supporting single epithallial cells (black arrowheads). Scale bar: 10 µm. (**b, c**) Sections at the thallus base showing hypothallial filaments (white arrowheads) displaying noncoaxial growth and ascending perithallial filaments (arrow). Scale bars: 10 µm. (**d–f**) Sections at the thallus surface showing single flattened epithallial cells (black arrowheads), supported by elongate (dividing) subepithallial cells (arrows). Scale bars: 5 µm. (**g, h**) Sections of multiporate conceptacles, embedded in a colliculate pattern (black arrows) or superficial with a bisporangial remain (arrow). Scale bars: 50 µm. (**i, j**) Surface view of two pore canals surrounded by 5–6 rosette cells (arrowheads) that are similar to contiguous epithallial cells. Scale bars: 10 µm. (**k–m**) Sections of three canals showing the thinner (k) and wider (m) pore cells (arrowheads). Note that the basal cell in (l) is branched. Scale bars: 10 µm.


a
b
c
d
e
f
g
h
i
j
k
l
m

al. 1987), the Indian Ocean (Silva et al. 1996), and Polynesia (Payri and N'Yeurt 1997), but without comment.

Foslie (1904c: 10, pl. 1, figs. 3–9) described a second form, *Lithothamnion siamense* f. *pseudoramosum* (as "*pseudoramosa*"), maintained within the concept of the species by Printz, with one of the original specimens being illustrated as *Lithothamnion siamense* (Printz 1929: pl. 1, fig. 20). Verheij and Woelkerling (1992: 282–3) studied Foslie's unpublished notes in L and concluded that he had on hand seven collections in describing f. *pseudoramosum*. They designated as lectotype "Collection 673b (in L), which consists of three specimens . . . from station 258 . . . because it contains the best reproductive material." However, the selected material is not illustrated among those specimens in the protologue, and the typification by Verheij and Woelkerling (1992: 282–283) is also questioned because they selected a collection rather than a specimen (Turland et al., 2018: Article 8.2). A fragment from one of the specimens (in 673b in L) was examined and proved to be fertile, containing male conceptacles with typical simple (unbranched) spermatangia restricted to the floor. Vegetative characters of the specimen included a polystromatic, noncoaxial hypothallium, with cell fusions between neighboring cells, and an ascending perithallium terminating in single epithallial cells. Collectively, the vegetative and reproductive features (i.e., spermatangia restricted to the floor) suggest that f. *pseudoramosum* belongs to Spongitidaceae, and its status will not be further discussed.

Since the material of *L. siamense* was collected during the "Danish Siam Expedition 1899–1900," it is possible that syntype and other material may exist in the herbarium of J. Schmidt in C.

***Ectocarpa* Athanas. et D. L. Ballant. gen. nov.**

Ectocarpa Athanas. et D. L. Ballant. gen. nov. (type: *E. capverdensis*).

Diagnosis: New genus of Mesophyllaceae, sharing most of its vegetative features with *Magnephycus* and *Macedonis*, except the development of larger-longer basal and subbasal pore cells in straight canals of multiporate conceptacles. The latter character similarly occurs in the multiporate conceptacles of the erect taeniform thallus of *Mastophoropsis*, from which *Ectocarpa* differs in forming a foliose thallus with unattached superimposed growth.

Etymology: *Ectocarpa* is a new compound word of feminine gender, after the adverb εκτος (off) and the accusative case of καρπος (fruit). It was most likely used as an adjective (*ectocarpon*) by Foslie (1907b), possibly referring to the multiporate conceptacles that protrude prominently, "off" the thallus surface.

Comments: *Ectocarpa* is presently monotypic but is based on collections from widely disjunct localities, such as Easter Island, Cape Verde, and the Canaries. Although only vegetative and tetrasporangial thalli are known, *Ectocarpa* displays a rare condition in the structure of canals of multiporate conceptacles that stands as a diagnostic feature (in combination with thallus habit). This very feature unites *Ectocarpa* with the little-known and presently disjunct *Mastophoropsis* from southern Australia. Development of elongate subbasal hypothallial cells occurs across the related genera *Ectocarpa*, *Magnephycus*, and *Macedonis*. A comparison between genera of Magnephyceae is given in Table 5.

***Ectocarpa capverdensis* Athanas. et D. L. Ballant. comb. et nom. nov.**

FIGURES 46–50

Ectocarpa capverdensis Athanas. et D. L. Ballant. comb. et nom. nov.

Basionym: Lithothamnion ectocarpon Foslie 1907b: 11–12.

Homotypic Synonym: *Mesophyllum ectocarpon* (Foslie) W. H. Adey 1970: 23.

Lectotype Locality: Cape Blanco, Cape Verde, NW Africa.

Lectotype: In TRH (C18-3335), Printz (1929: pl. 8, fig. 1), Adey and Lebednik (1967: 83, "type material," "§ W.v.Bosse, Cape Blanco, Cape Verte, 29.12.1895, LM8(1) [slides] 869, 1557, 1564"), Adey (1970: 23, "lectotype"), Woelkerling (1993a: 82, "lectotype"), Woelkerling et al. (2005: 468, "lectotype"; Figure 46b)

Syntypes: In L (Herb.Lugd.Bat. 942.361.24, "*Lithothamnion ectocarpon* Fosl. (partim) Afrika Cap Blanco 29.12.1895. cfr. Die Lithoth. d. Gauss.Exp.," "Herbarium Weber-van Bosse. Rhodophyceae *Lithothamnion ectocarpon* Fosl. Exp. Chazalie leg. Versluys"), Woelkerling and Verheij (1995: 51, "isolectotype"); in TRH (A1-23, Cape Verde, Cape Blanco, 29.xii.1895, [coll.?] A. Weber-van Bosse, includes slides 1557 and 1563, filed under the lectotype *Mastophora conjuncta* Foslie), Woelkerling et al. (2005: 26, no type status); in TRH (A1-22, St. Vincent, Cape Verde, ix.1901, [coll.] Vanhöffen, filed under the name *Mastophora conjuncta* Foslie), Woelkerling et al. (2005: 26, no type status).

Habitat and Distribution: Thalli grow in association with corals, polychaetes, foraminifera, and other corallines in the littoral zone. They are recorded from several disjunct localities: Cape Blanc (Cap Verde), Canary Islands (Tenerife, La Palma), and Easter Island.

Material Examined: Cape Verde: Cape Blanco, lectotype (in TRH, as described above) and syntype (in L).

Canary Islands: Tenerife: Puerto Orotava (Porto de la Cruz): tetrasporophytes on a pebble (~7 cm in diameter), "x *Lithophyllum lobatum* nov.sp., - *Lithothamnium ectocarpon* Fosl. *Lithophyllum hirtum* nov.sp.," 9 January 1921, coll. Børgesen (slides in TFC, herb. Afonso-Carrillo, material in C presently missing [curator in C, Ruth Nielsen, University of Copenhagen, Copenhagen, Denmark (retired), personal communication], Børgesen no. 3105).

La Palma: NW coast, Cuera Bonita (P): 1–3 m depth, 13 June 1983, coll. M. C. Gill, J. Afonso-Carillo, R. Haroun, and M. Izquiulo (TFC 3001, labeled "*Mesophyllum lichenoides*").

Easter Island: Near Hanga Pilo: "in littoral region. 26.vi.1917. Carl and Inga Skottsberg, det. T. Levring 1943, The

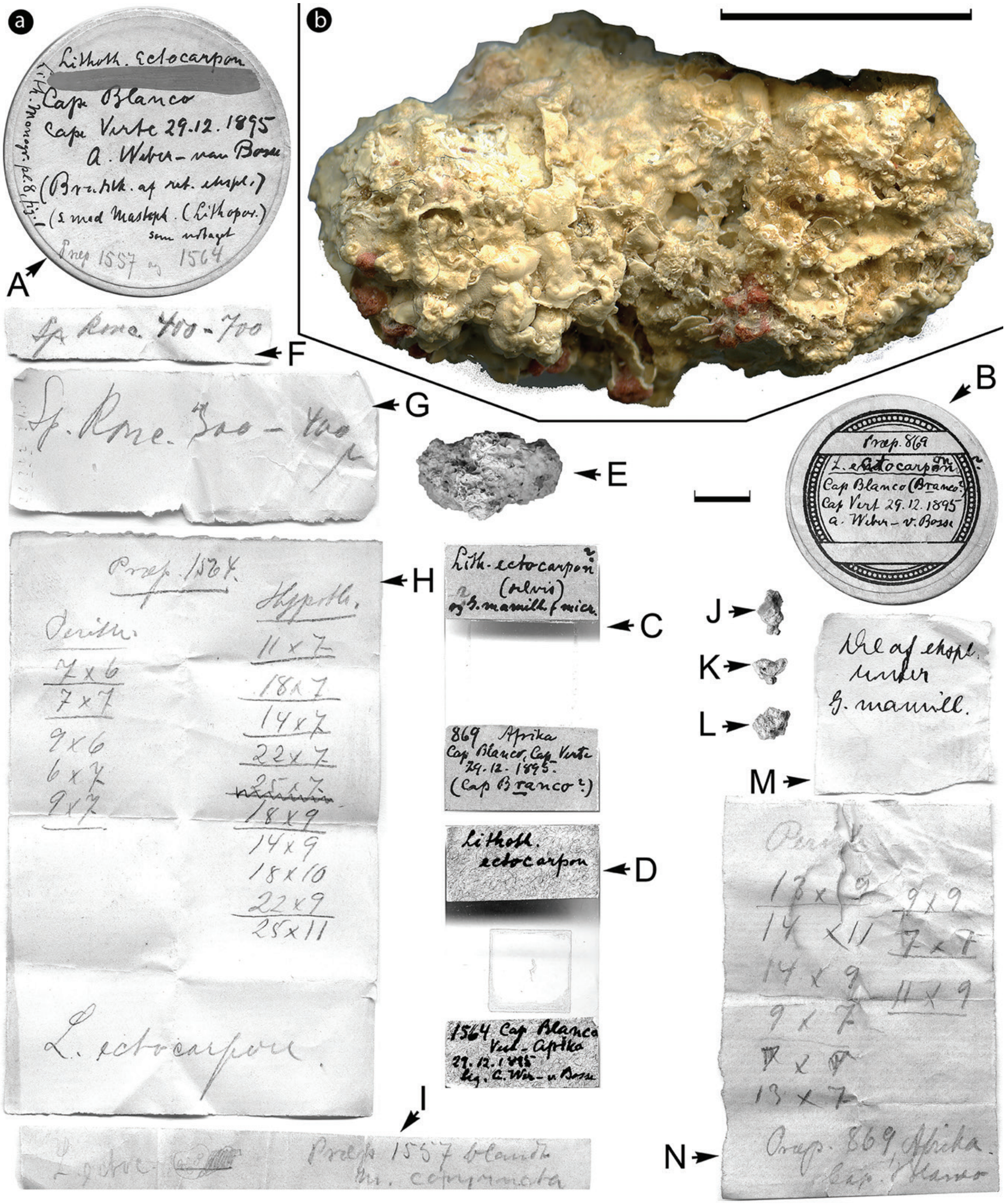


FIGURE 46. *Ectocarpa capverdensis*: lectotype of *Lithothamnion ectocarpon* in TRH (C18-3335). (**a**) Box A, which includes the lectotype specimen (E, magnified in (b)) and four labels (F–I), and box B, which comprises three minor fragments (J–L) and two paper sheets (M and N). Two slides (C and D) are placed separately. Scale bar: 1 cm. (b) The lectotype in magnification. Scale bar: 2 cm.

Swedish Pacific Expedition 1916-1917 *Lithothamnion mesomorphum* Foslie var. *ornatum* Foslie and Howe.," coll. Carl and Inga Skottsberg (GB-0195190).

Comments on the Protologue and Type Material: The Norwegian protologue (Foslie 1907b: 11–12) reads (in translation),

> *Lithothamnion ectocarpon* Fosl. mscr. Thallus lamellate, lamellae mostly very small, more or less growing together, fragile, 100–400 µm thick, often irregularly developed over each other and partly growing free, sometimes sparsely proliferated; sporangial conceptacles suppressed, hemispherical, 400–700 µm in [external] diameter; sporangia not known. In vertical section, the hypothallium occupies partly the half or the most part of the lamella thickness. [Hypothallial] cells are 14–25 µm long and 7–9(11) µm broad. Perithallial cells are partly subsquarish, 7–14(18) µm long and 7–9(11) µm broad. *Lithoth. ectocarpon* appears to be most related to *L. antarcticum* and comes close to poorly developed forms of *L. lichenoides*. Young specimens with suppressed thalli remind somewhat of *L. bisporum* or some forms of *L. lenormandi.* It partly forms layers with *Mastophora* (*Lithoporella*) *conjuncta* in alternate pattern.- West coast of Africa: Cape Blanc (A. Weber-van Bosse) and St. Vincent (Vanhöffen).

The type material in TRH (C18-3335) comprises two slides and materials placed in two round boxes (Figure 46a,b). The two slides are annotated in pencil by Foslie: "*Lithoth. ectocarpon* 1564 Cap Blanco Vest Afrika 29.12.1895 leg. a. Web-v. Bosse" and "Lith. ectocarpon ? (delvis) G. mamill. f. mica 869 Afrika Cap Blanco Cap Verte 29.12.1895 (Cap Branco ?)." The numbers "1564" and "869" on the slides link to the respective box.

The larger box is annotated "*Lithoth. Ectocarpon* Cap Blanco Cape Verte 29.12.1895 a. Weber-van Bosse (Bru . . . af ret. eksempl.) (s.[nitt] med Mastoph. (Lithopor.) som udtaget) Prep. 1557 og 1564 Lith. monogr.pl.8, fig. 1." It contains a single specimen and four labels annotated in pencil by Foslie: "Sp. Konc. 300–400," "Sp. konc. 400–700," "Prep. 1564 Perith 7x6 7x7 9x6 6x7 9x7 Hypoth. 11x7 18x7 14x7 22x7 25x7 18x9 14x9 18x10 22x9 25x11 *L. ectocarpon*," and "*L. ectoc* . . . Prep. 1557 blandt [among] *M. conjuncta*."

The smaller box is annotated "Prep. 869 *L.ectocarpon* ? Cap. Blanco (Branco ?) Cap Vert 29.12.1895 a. Weber-v.Bosse." It contains three smaller fragments, the larger up to 9 mm in extent, and two labels annotated by Foslie in pencil: "Del af eksepl. under G. mamill. [part of spec. under *Goniolithon mamillosum*]" and "Perith 13x9 14x11 14x9 9x7 7x7 13x7 9x9 7x7 11x9 Prep.869 Afrika Cap Blanco" (Figure 46a,b).

From Foslie's annotations (on the smaller box and slide 869), it appears that he was not certain if the locality name was Cap Blanco (or Cap Branco). It is also clear that Foslie moved a third slide (1557) to his collections of *Mastophora conjuncta*; slide 1557 represents part of the lectotype of the latter species that is typified with part of the same Weber-van Bosse collection (Woelkerling et al. 2005: 468).

Material from the collection from St. Vincent (coll. Vanhöffen) is presently filed under *Mastophora conjuncta* (Woelkerling et al. 2005: 26), and this transfer was apparently made by Foslie (or Printz) since Adey and Lebednik (1967: 83) found only the Cap Blanco collection filed under the name *Lithothamnion ectocarpon* (see also Adey 1970: 23). Hence, Adey and Lebednik's (1967) (lecto)typification of *Lithothamnion ectocarpon* with the specimen from the larger box (annotated "Cap Blanco Cape Verte 29.12.1895 a. Weber-van Bosse") was justified.

The lectotype reaches 2.8 cm in extent (~3 cm according to Printz 1929: pl. 8, fig. 1). It is a conglomerate of unattached superimposed lamellae, with several layers in superimposition and anastomosing (Figure 46b). Lamellae are 90–140 µm thick (100–400 µm thick according to the protologue) and fragile, encircling and consolidating polychaete tubes, individuals of the foraminiferan *Miniacina miniacea* (Pallas), and possibly other corallines (near the base). Thallus organization is monopodial-dorsiventral with a polystromatic noncoaxial hypothallium (with coaxial patches; Figure 47a,b), 40–80 µm thick, supporting an ascending nonstratified perithallium, 25–50 µm thick. Hypothallial cells are 13–28 × 5–8 µm (L × B), and perithallial cells are 6–16 × 5–6 µm (L × B). Subepithallial cells are elongate-ovate, 10–15 µm long, and support single, flattened epithallial cells, 3–5 × 9–10 µm (L × B; older ones appear concave; Figure 47c–e). Most subepithallial cells lack epithallial cells (due to damage). Cell fusions are common between contiguous vegetative cells (Figure 47g). Descending hypothallial cells become thinner before ending in basal cells (Figure 47h–j).

Multiporate conceptacles are hemispherical, 480–630 µm in external diameter (n: 5) and up to 240 µm high (n: 1), and are aggregated in groups or occur solitary (Figure 48a,b,d–f). Chambers are 320–420 × ~140 µm (D × H; n: 2). The conceptacle roofs are perforated by at least 104 pores (n: 1). Canals are 7–8 µm in diameter at the surface and 8–10 µm in diameter at the base, being encircled by 5 to 7 rosette cells that are common epithallial cells (Figure 48g–i). Canals are lined by 5-celled filaments. In views from above, at successive levels of focus, lining pore cells are nondifferentiated near the surface. In a median position, they can stain darker and be thinner–wider, ending at the base in larger cells (Figure 48j–n).

The syntype collection in L (Herb. Lugd. Bat. 942.361.24) exists in a box that includes two labels, two larger specimens, and several smaller fragments. A label in Foslie's hand reads "*Lithothamnion ectocarpon* Fosl. (partim) Afrika Cap Blanco 29.12.1895. cfr. Die Lithoth. d. Gauss.Exp." The second label has the partly printed text "Herbarium Weber-van Bosse. Rhodophyceae *Lithothamnion ectocarpon* Fosl. Exp. Chazalie leg. Versluys." The first label refers to a Gauss Expedition (apparently to the Cape Verde Islands), whereas the second label refers to a Chazalie Expedition (collector Versluys). Yet as noted by Woelkerling and Verheij (1995: 51), there is no reference to these expeditions or to "Versluys" in the protologue of *L. ectocarpon* (Foslie 1907b) or in Foslie's (1908a) later account. Hence, this

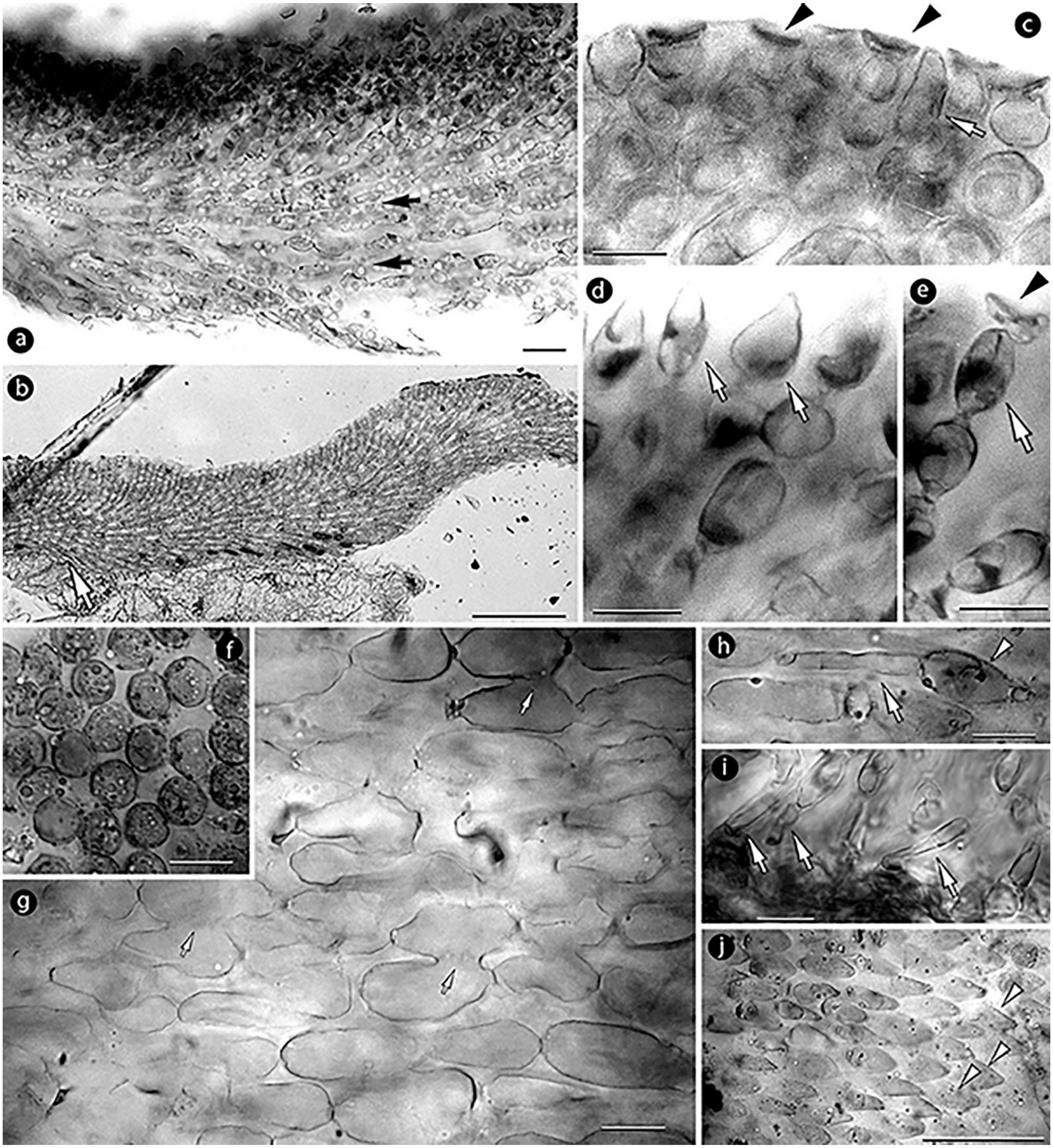


FIGURE 47. *Ectocarpa capverdensis*: lectotype of *Lithothamnion ectocarpon* in TRH (C18-3335). (**a**) Section showing a noncoaxial hypothallium (arrows). Scale bar: 25 µm. (**b**) Section showing a patch of coaxial arching cells (arrow; Foslie slide 1564). Scale bar: 100 µm. (**c–e**) Sections at the surface showing flattened (to concave) epithallial cells (arrowheads) and elongate subepithallial cells (arrows). Scale bars: 10 µm. (**f**) Surface view showing epithallial cells. Scale bar: 10 µm. (**g**) View from below showing noncoaxial arrangement of hypothallial cells with cell fusions (arrows). Scale bar: 10 µm. (**h, i**) Sections at the thallus base showing thinner subbasal hypothallial cells (arrows) and a basal cell (arrowhead). Scale bars: 10 µm. (**j**) View of the thallus from below showing basal cells arranged in a rhomboid pattern. Scale bar: 50 µm.

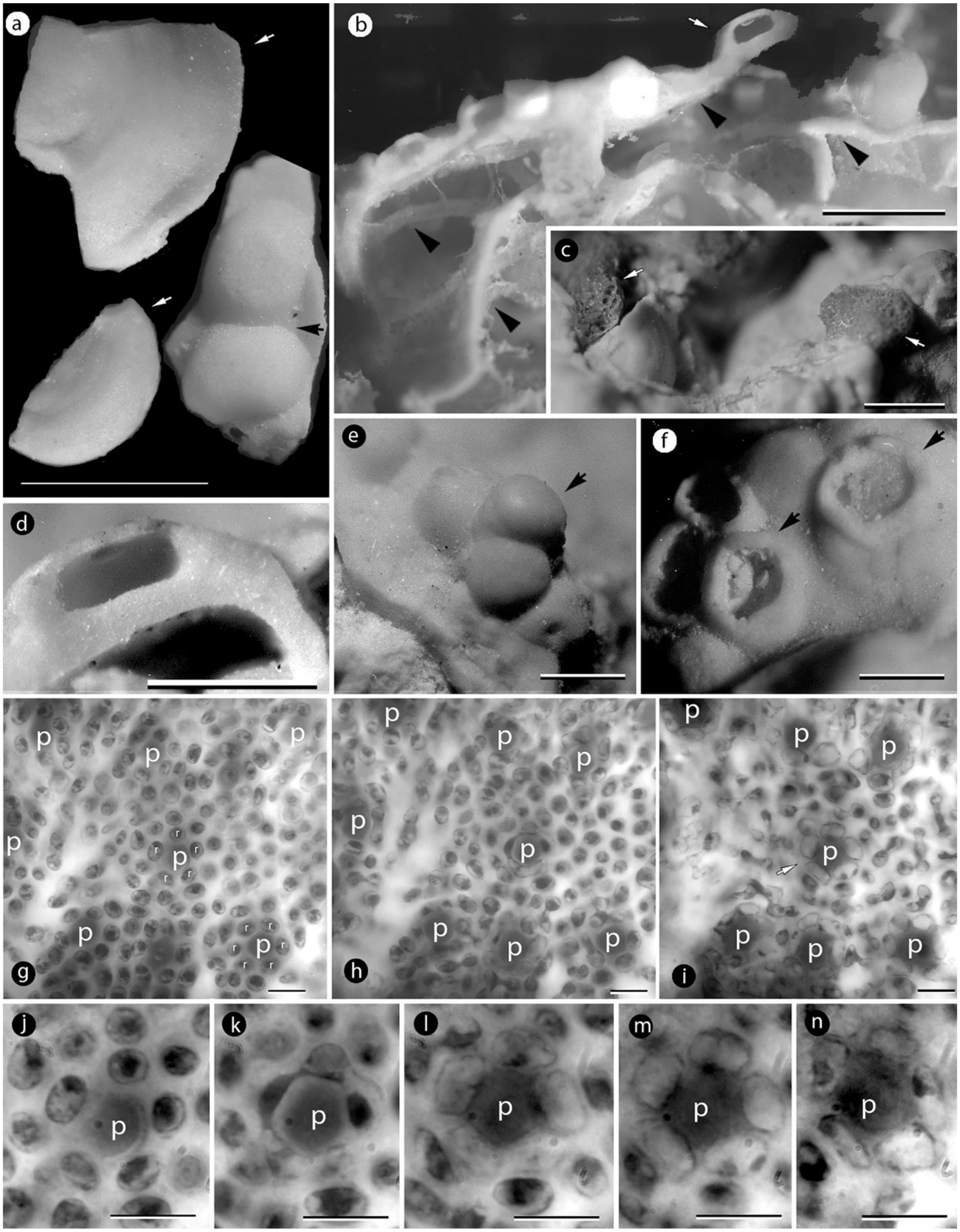


FIGURE 48. *Ectocarpa capverdensis*: lectotype of *Lithothamnion ectocarpon* in TRH (C18-3335). (**a**) Fragments with lobate margins (arrows) and two multiporate conceptacles (black arrow). Scale bar: 1 mm. (**b**) Side view of the lectotype, showing thallus superimposition (arrowheads). Scale bar: 1 mm. (**c**) View of two sponges (arrows) attached and interwoven with the thallus. Scale bar: 1 mm. (**d**) Side view of a multiporate conceptacle (indicated with an arrow in (b)). Scale bar: 500 µm. (**e**) Two intact hemispherical multiporate conceptacles. Scale bar: 500 µm. (**f**) Two conceptacles with the roofs broken off. Scale bar: 500 µm. (**g–i**) Pore plate at three levels of focus: (g) surface view where pores are surrounded by 5 or 6 rosette cells, (h) median view, and (i) basal view. (**j–n**) Magnification of a canal at five levels of focus, showing pore cells becoming larger toward the base. Scale bars: 10 µm. Abbreviations: p, pore canal; r, rosette cell.

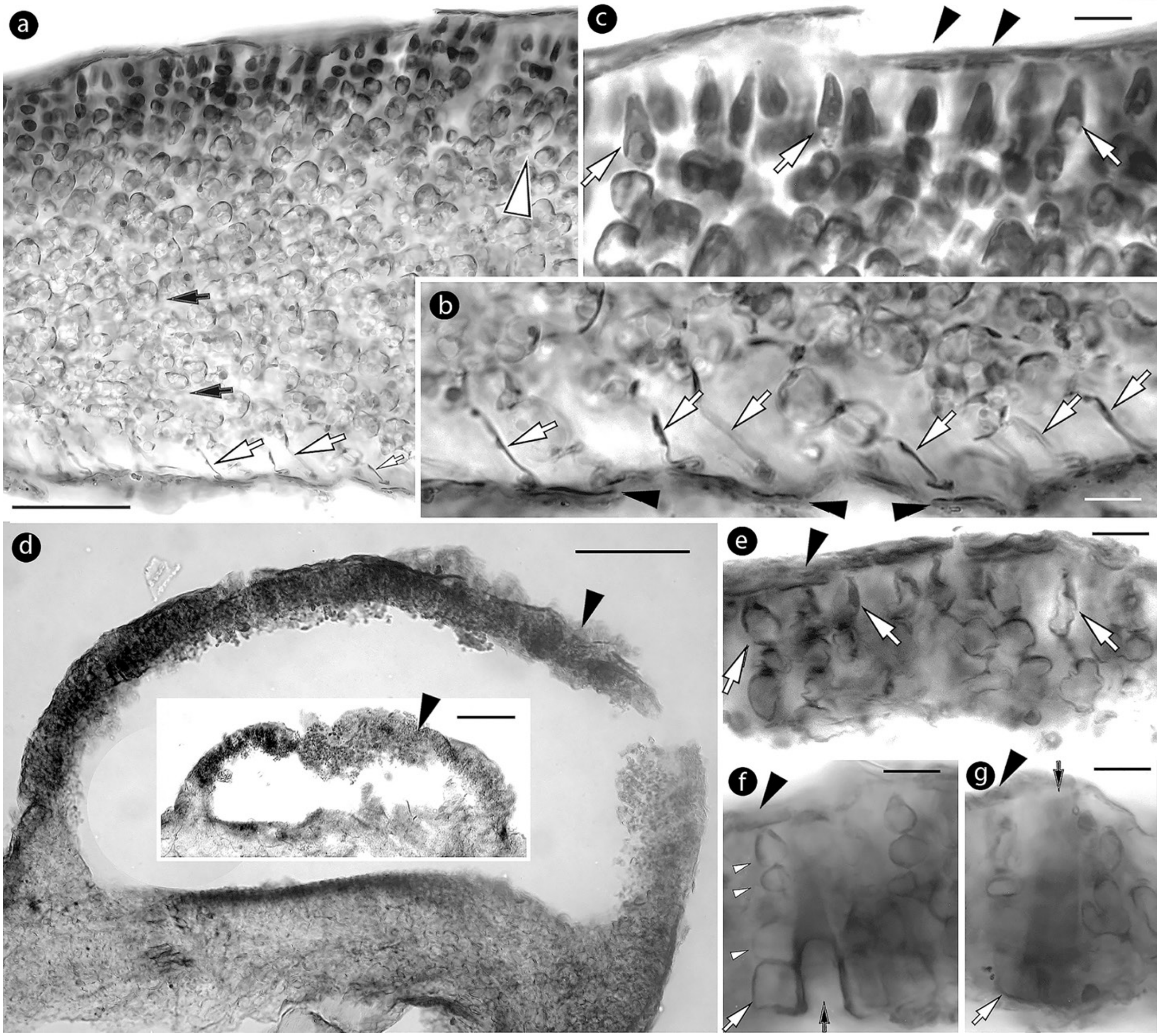


FIGURE 49. *Ectocarpa capverdensis*: vegetative and multiporate conceptacle structures (TFC 3001). (**a**) Section showing a noncoaxial hypothallium (black arrows) supporting an ascending nonstratified perithallium (arrowheads). Descending hypothallial filaments end in thinner-elongate subbasal cells (white arrows). Scale bar: 50 μm. (**b**) Magnification at the base showing elongate subbasal cells (arrows) supporting flattened (arrowheads) terminal (epithallial?) cells. Scale bar: 10 μm. (**c**) Section at the surface showing elongate-ovate subepithallial cells (arrows) supporting single flattened epithallial cells (arrowheads). Scale bar: 10 μm. (**d**) Sections of multiporate conceptacles with a typical hemispherical roof (arrowheads). Scale bars: 100 μm. (**e**) Section of conceptacle roof showing elongate subepithallial cells (arrows) supporting single epithallial cells (arrowheads). Scale bar: 10 μm. (**f, g**) Sections of two canals (black arrows) showing the lining cells (white arrowheads) becoming larger toward the base. Basal pore cells are indicated by white arrows, and epithallial cells are indicated by black arrowheads. Scale bars: 10 μm.

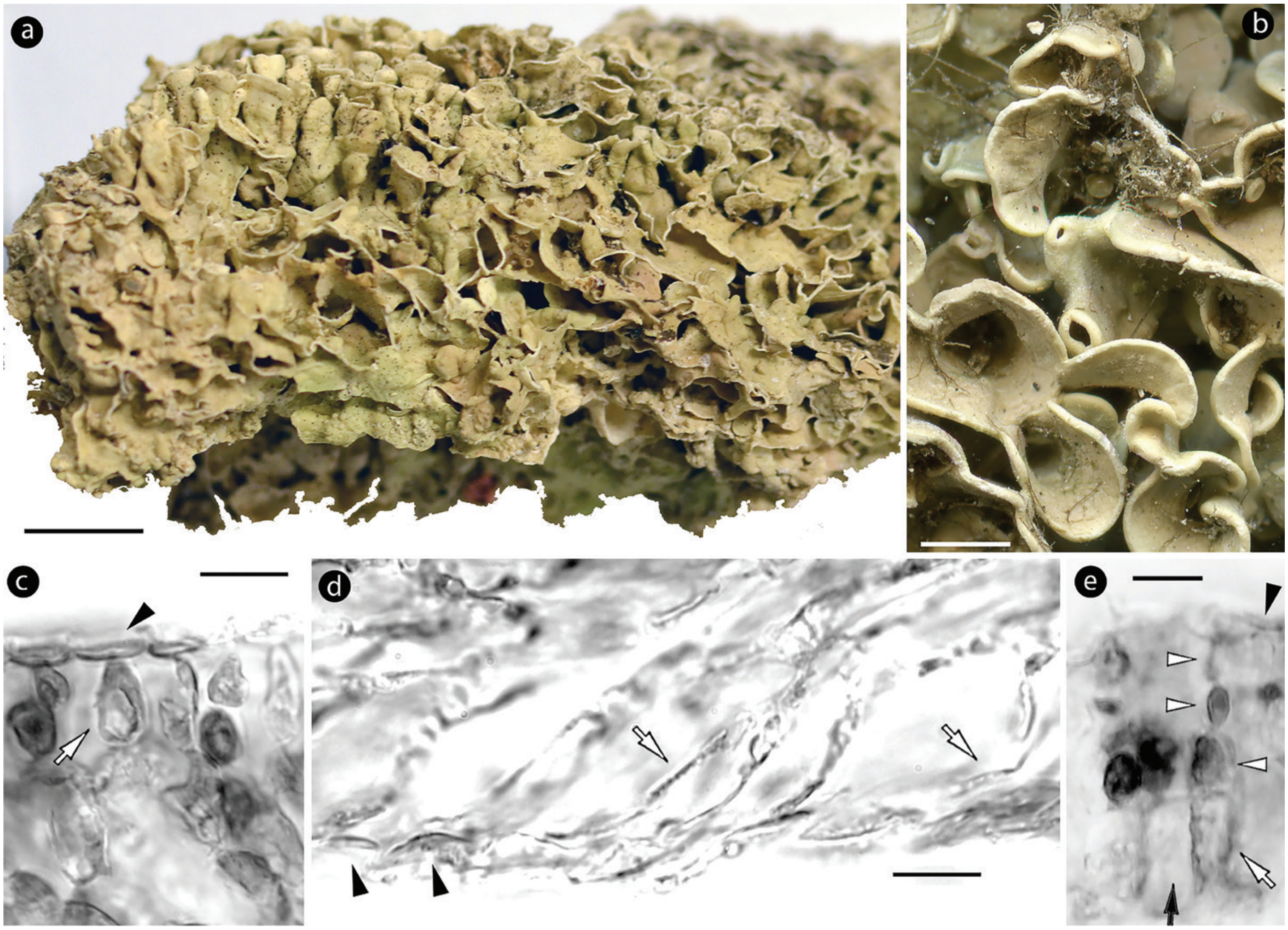


FIGURE 50. *Ectocarpa capverdensis* from Easter Island (GB-0195190). (**a**) Foliose thallus showing typical unattached superimposed growth. Scale bar: 1 cm. (**b**) Magnification of thallus surface showing funnel-like proliferations. Scale bar: 2 mm. (**c**) Section at the surface showing elongate-ovate subepithallial cells (arrow) supporting single flattened epithallial cells (arrowhead). Scale bar: 10 µm. (**d**) Magnification at the base showing elongate subbasal cells (arrows) supporting flattened (arrowheads) terminal (epithallial?) cells. Scale bar: 10 µm. (**e**) Section of canal (black arrow) showing the lining cells (white arrowheads) becoming larger toward the base. Note the basal cell (white arrow) and an epithallial cell (black arrowhead). Scale bar: 10 µm.

material in L is heterogeneous, and it is not clear which of the two specimens comes from the type locality Cape Blanco (as partly cited on one of the labels). Of the two larger specimens, one is a *Pecten* shell (~4 cm in extent) entirely covered by strongly adhering sterile thalli (not identified), and the second specimen (here tentatively referred to *E. capverdensis*) is a conglomerate body (to 4.5 cm in extent) composed of different coralline and animal species. The latter material includes thalli demonstrating unattached superimposed growth, with a noncoaxial hypothallium, composed of cells 11–26 µm long and 8–13 µm broad, giving rise to an ascending perithallium with elongate subepithallial cells (up to 15 µm long), each supporting a flattened epithallial cell (~2 × 5–9 µm; L × B). A few craterlike depressions, 350–560 µm in diameter, indicate that thalli were fertile. Uniporate conceptacles (up to 920 µm in diameter and 600 µm high) occur on the back side of the specimen (as an admixture, marked in green), probably belonging to an epiphytic species of *Mastophora* Decne, with subepithallial cells, 32–45 × 8–18 µm (L × B), and flattened epithallial cells, 2.5–4 × 17 µm (L × B).

Species Description: Thalli foliose, to 3 cm in extent (Printz 1929)—up to 10.5 cm in Easter Island specimens—and several centimeters thick (via superimposition; Figures 46b, 50a), adhering strongly to pebbles or other corallines. New lamellae grow in an unattached superimposed pattern, anastomosing, or developing funnel-like proliferations or grow back to back, finally forming a conglomerate body engulfing other organisms (hydrozoa, Bryozoa, foraminifera; Figures 46b, 48c, 50b). The thallus organization is monopodial-dorsiventral with a polystromatic noncoaxial hypothallium (with rare coaxial patches; Figures 47a,b, 49a). Individual lamellae are 90–190 µm thick, composed of a hypothallium 40–150 µm thick that supports a gradually ascending, nonstratified perithallium 25–80 µm thick. Hypothallial cells are 10–28 × 5–12 µm (L × B), and perithallial cells are 5–18 × 5–10 µm (L × B). Subepithallial cells are elongate-ovate, 10–15 µm long, supporting single, flattened epithallial cells, 2–5 × 8–10 µm (L × B; Figures 47c–f, 49c,e). Descending hypothallial filaments end in narrow subbasal cells (to 20 µm long) supporting single basal cells (Figures 47h–j, 49b). Cell fusions between contiguous vegetative cells are common (Figure 47g). Secondary pit connections and trichocytes are absent.

Gametophytes are unknown. Multiporate conceptacles are hemispherical, 480–630 µm in external diameter (to 700 according to the protologue) and 240–270 µm high (n: 6) and aggregated in groups or occur solitary (Figures 48a,b,d–f, 49d). Chambers are 320–510 × 140–240 µm (D × H; n: 4), provided with a roof 30–50 µm thick (Figure 49e), composed of 4- to 7-celled filaments, and perforated by at least 104 pores. Pore canals are ± straight, surrounded by 5 to 7 rosette cells that are common epithallial cells (Figure 48g). Canals are 7–8 µm in diameter at the surface and 7–11 µm at the base, lined by 5- or 6-celled filaments composed of cells that become larger and longer toward the base (Figures 48j–n, 49f,g, 50e). Tetrasporangial remains (130–140 × 30–50 µm; L × B) occur in Easter Island thalli (described below). Embedded conceptacles are absent.

Comments: The vegetative and reproductive characters of the lectotype of *Lithothamnion ectocarpon* are in agreement with the protologue (Foslie 1907b) and Foslie's (1908a) later account that largely repeats the protologue, apart from the statement of a "koaxillär" hypothallium (Foslie 1908a: 213). The latter may account for either a multiaxial (polystromatic) structure or coaxial patches (seen on the Foslie slide 1564; Figure 47b). However, the hypothallium of the lectotype is predominantly noncoaxial (Adey 1970: 23; Figures 47a,b,g, 49a). In discussing the affinities of *L. ectocarpon*, Foslie (1907b, 1908a) associated the species with a wide variety of corallines from both the southern and northern hemispheres, viz., *Lithothamnion antarcticum* (Hook. Fil. et Harv.) Heydrich (*Carlskottsbergia antarctica*), *Lithothamnion lemniscatum* Foslie (*Magnephycus engelhartii*?), the Canarian-Caribbean *Lithothamnion bisporum* Foslie (*Hyperandri bisporum*), and the NE Atlantic *Lithothamnion lichenoides* (J. Ellis) Hauck (*Mesophyllum lichenoides*) and *Lithothamnion lenormandii* (F. Aresch.) Foslie (*Phymatolithon lenormandii*).

Lithothamnion ectocarpon was reported from the Canary Islands by Lemoine in Børgesen (1929: 21–22, fig. 6) on the basis of material collected by Børgesen in 1921 (Børgesen nos. 3014, 3105, 3106). Reexamination of the cited collections showed that nos. 3014 and 3106 include specimens of *Hyperandri bisporum*, and the main characters distinguishing the two species are discussed below. The third collection (Børgesen no. 3105) was available only as material on a series of slides in TFC (Afonso-Carrillo 1982: 134–136, pl. 8, figs. 1–4, pl. 80, figs. 1, 6), showing the presence of hemispherical conceptacles. In transferring the species to *Mesophyllum*, Adey (1970: 23) noted that only one of the original two cited specimens was present in TRH and that the "[generic] placement . . . is with some question, since . . . the hypothallium is weak and apparently non-coaxial." There are no later Canarian records of the species (John et al. 1994: 74).

Nevertheless, a specimen with multiporate conceptacles collected in June 1983 in Cueva Bonita in La Palma was identified in TFC (no. 3001, labeled "*Mesophyllum lichenoides*"; Figure 49a–g). In this material, the conceptacles are prominently hemispherical, and pore canals display the presence of larger-longer cells lining the canal at the base (Figure 49f,g).

Present data indicate that *Ectocarpa* differs from *Hyperandri* in developing a foliose habit with larger hemispherical multiporate conceptacles that do not become embedded in the thallus and in the type of pore filaments. In addition, the hypothallium in *Ectocarpa* develops elongate subbasal cells, similar to those observed in species of *Magnephycus* and *Macedonis*. In comparison to the latter two genera, which develop a similar foliose habit, *Ectocarpa* differs by the distinct type of pore filaments in canals of multiporate conceptacles.

The collection from Easter Island (GB) included the largest thalli of the species, reaching 10.5 cm in extent, with new branches produced in superimposition as either unattached lamellae or funnel-like formations (Figure 50a,b). Individual lamellae were dorsiventrally organized, 190–200 µm thick (150–300 µm according to Levring 1943: 759), composed of a noncoaxial hypothallium producing a gradually ascending perithallium with flattened epithallial cells, 1–2 × 5–6 µm (L × B). According to Levring (1943: 759), hypothallial cells are 15–25(–30) × 7–12 µm (L × B), and perithallial cells are 5–9 × 4–6 µm (L × B; Figure 50c). Descending hypothallial filaments end in elongate-thinner subbasal cells (Figure 50d). Multiporate (tetrasporangial) conceptacles, 400–580 × 250–260 µm (D × H; n: 2), occur in groups. Chambers are 250–290 × 180–210 µm (D × H; n: 2), and pore plates are ~200 µm across. The roof is 40–50 µm thick, with canals 12–8 µm in diameter, each surrounded by 6 or 7 rosette cells. Pore filaments lining the canals are 5-celled and composed of nondifferentiated cells, except for basal cells that are larger-longer (~18 µm long; Figure 50e). Tetrasporangial remains are 130–140 × 30–50 µm (L × B). The above anatomical characters, particularly the structure of the canals, are in agreement with the lectotype, supporting a provisional position under this species name. Still, the Easter Island record expands considerably the distribution of the genus, fitting the disjunct distribution of another coralline from Easter Island that has also been recorded from the Canaries (i.e., *Fosliella paschalis* (Me. Lemoine) Setch. et N. L. Gardner; Afonso-Carrillo 1989). Finally, a collection dated 18 August 1901 from Cape Verde in herb. Lemoine (PC), referred to *Lithothamnion ectocarpon*, was found to be based on thalli possessing flared epithallial cells (Athanasiadis and Ballantine, 2014: Appendix III).

***Magnephycus* Athanas. et D. L. Ballant. gen. nov.**

Magnephycus Athanas. et D. L. Ballant. gen. nov. (type: *M. ornatus*).

Diagnosis: New genus of Mesophyllaceae, differing from other members of the tribe Magnephyceae in forming a foliose thallus with pyriform canals in multiporate conceptacles. In the generitype, spermatangia develop on a pedestal formed by up to 7 or 8 layers of isodiametric cells borne on a layer of palisade cells.

Etymology: A new compound word commemorating our colleague Francis Magne (1924–2014) and the suffix ϕυκος (phycus, seaweed), which is accepted to be of masculine gender.

Comments: *Magnephycus* comprises *M. ornatus*, *M. simulans*, and *M. engelhartii*, which all demonstrate a foliose thallus and display elongate basal and subbasal cells in pyriform canals of multiporate conceptacles (Figure 6a,c). Members of the genus differ from each other in forming a second roof over multiporate conceptacles (in *M. simulans* and *M. ornatus*), coaxial regions or patches in the hypothallium (in *M. engelhartii* and *M. simulans*), and a smaller (half the size) multiporate conceptacle (in *M. engelhartii*, in which the multiporate conceptacles are also aggregated). Male structures have been described only in the generitype, showing their characteristic formation on a pedestal (Figure 5n,o; see characters 19–20 in “Character Evolution in the Mesophyllaceae”). The development of elongate subbasal hypothallial cells (originally observed in *M. ornatus*) occurs in all members of the genus, as well as in the related genera *Ectocarpa* and *Macedonis*. A further comparison of genera of Magnephyceae is given in Table 5.

***Magnephycus engelhartii* (Foslie) Athanas. et D. L. Ballant. comb. nov.**

Magnephycus engelhartii (Foslie) Athanas. et D. L. Ballant. comb. nov.

Basionym: Lithothamnion engelhartii Foslie 1900a: 18–20.

Heterotypic Synonyms: Lithothamnion engelhartii f. *imbricatum* Foslie 1900a: 18, “*imbricata*”; type locality: not specified; holotype: in TRH (B18-2595), illustrated by Woelkerling and Harvey (1993: 583, figs. 1A–C, 2A–D). Athanasiadis (2017a: 72, synonym).

?*Lithothamnion engelhartii* f. *umbonatum* Foslie 1900a: 18, “*umbonata*”; type locality: not specified; type: not designated. Printz (1929: pl. 7, fig. 15), Woelkerling et al. (2005: 351, TRH B18-2607), Athanasiadis (2017a: 71, type not examined).

?*Lithothamnion engelhartii* f. *pseudocrispatum* Foslie 1901e: 27, “*pseudocrispata*”; type locality: Tasmania; holotype: in TRH (B18-2607), Woelkerling (1993a: 179), Woelkerling and Harvey (1993: fig. 11B), Woelkerling et al. (2005: 351). Printz (1929: pl. 7, fig. 18), Athanasiadis (2017a: 76[40]).

?*Lithothamnion lemniscatum* Foslie 1907b: 11; type locality: Cape Jaffa, South Australia; type: in TRH (B16-2432), Printz (1929: pl. 7, fig. 11), Adey and Lebednik (1967: 66, “type material,” “§ Engelhart, S.Aust., Cape Jaffa, 1899, LM7(11) [slide] 1041”), Woelkerling (1993a: 101, “holotype”), Woelkerling et al. (2005: 324, “holotype”).

Mesophyllum lemniscatum (Foslie) W. H. Adey 1970: 25.

Type Locality: Cape Jaffa, South Australia.

Lectotype: In TRH (B18-2596, *pro parte*), Printz (1929: pl. 7, fig. 13), designated by Athanasiadis (2017a: 71, fig. 1, right specimen).

Habitat and Distribution: No habitat data were given in the protologue, other than the species is “apparently scarse,” and the original material was found to be heterogeneous. A confirmed collection was defined by Woelkerling and Harvey (1993: fig. 3F) as being “detached from rock.” The species is known only from Cape Jafa (type locality) and Eyre Peninsula (Waterloo Bay, Elliston; Athanasiadis 2017a), both in South Australia.

Comments: “*Mesophyllum engelhartii*” was widely reported from western to southern Australia (Eagle Bluff, Shark Bay to Kitty Miller Bay, Phillip Island, Victoria), the eastern and southern coasts of Tasmania (Woelkerling 1996: 195), and also South Africa (Chamberlain and Keats 1995) and Brazil (Amado-Filho et al. 2010). However, the reexamination of the original material from Cape Jaffa, with comparison of new collections and literature data, showed that records from other sites in the world were misidentifications (Athanasiadis 2017a). It was also discovered that the original material comprised two different species, actualizing the need to neolectotypify this taxon and emend its circumscription. Still, the generic position of the lectotype remained uncertain, pending further studies. The present phylogenetic analysis points to *Magnephycus simulans* as its sister taxon, with an immediate relationship to *Magnephycus ornatus* (Figure 6a; see also the generic account).

The status of *Lithothamnion lemniscatum*, originally described from the same locality (Cape Jaffa, coll. A. Engelhart), remains unclarified. The Norwegian protologue (Foslie 1907b: 11) reads (in translation),

> Thallus develops small lamellae loosely attached to the substratum, partly singly or supporting each other, partly superimposed, following the substratum, 200–400 μ thick; [tetra]sporangial conceptacles weakly convex or somewhat flattened, little conspicuous, partly weakly sunken in the middle, 500 (400)–800 (900) μm in diameter; [tetra]sporangia unknown; cystocarpic conceptacles subconical, 400–600 μ in diameter. The only representative specimen of this species surrounds a bryozoan (a marine sponge). Lamellae are circle-rounded and follow the form of the substratum. When the undergrowing lamellae meet each other, they form edges or partly grow over, irregularly and in a few cases in superimposition. In vertical sections, the hypothallium comprises the main part of the crust. It is coaxial and develops arches, cells 18–36 μ long and 9–14 μ broad. The perithallium is weakly developed, cells partly subsquare 7–9(10) μ in diameter, partly and

> more often vertically elongate, 9–11(14) µ long and 7–9 µ broad. The roof of [tetra]sporangial conceptacles is perforated by c. 70 muciferous canals. *L. lemniscatum* is most closely related to *L. muelleri*, differing in its presence of small and downwardly pressed lamellae, less conspicuous conceptacles, longer and relatively narrower hypothallial cells. — South Australia, Cape Jaffa (Aug. Engelhart).

Several of the above characters fit *M. engelhartii*, in particular the arching coaxial hypothallium (which also occurs in patches in *Magnephycus simulans*), the weakly developed perithallium, and the thallus superimposition, but there are also differences such as in the size of multiporate conceptacles (up to 500 µm in *M. engelhartii* vs. 900 µm in *L. lemniscatum*). In the protologue, Foslie (1907b) mentioned a single specimen, which was illustrated by Printz (1929: pl. 7, fig. 11), but he also described multiporate and carposporangial conceptacles, which indicates the presence of separate individuals (conspecific?). Another issue is that Foslie originally referred the type material to *Lithothamnion muelleri* f. *neglectum* Foslie (1900a: 17–18) (Woelkerling 1993a: 137), a taxon lacking a coaxial hypothallium and here referred (with reservation) to *Orthocarpa magellanica*.

A second (unnamed) species form Cape Jaffa, included in the original material of *M. engelhartii* as an admixture, differs in entirely lacking patches of a coaxial hypothallium and in possessing multiporate conceptacles spread over the surface, embedded conceptacles (in a well-developed perithallium), and straight pore canals of multiporate conceptacles with cell bars developed basally (Athanasiadis 2017a: figs. 22–31, TRH B18-2598, TRH B18-2599, 2020b: table 1).

Magnephycus ornatus **(Foslie et M. Howe) Athanas. et D. L. Ballant. comb. nov.**

FIGURES 51–55

Magnephycus ornatus (Foslie et M. Howe) Athanas. et D. L. Ballant. comb. nov.

Basionym: Lithothamnion mesomorphum var. *ornatum* Foslie et M. Howe 1906: 129, pl. 80, fig. 2, pl. 90, fig. 2.

Homotypic Synonyms: Lithothamnion mesomorphum f. *ornatum* (Foslie et M. Howe) Foslie in Printz 1929: 43, pl. 9, fig. 9, "*ornata*."

Mesophyllum mesomorphum var. *ornatum* (Foslie et M. Howe) M. Wynne 1998: 110.

Mesophyllum ornatum (Foslie et M. Howe) Athanas. 1999: 246.

Misapplied Name: *Mesophyllum mesomorphum* sensu Taylor 1928: 210 [non *M. mesomorphum* (Foslie) W. H. Adey].

Type Locality: Low littoral, under rock overhang, Exuma Chain, Cave Cays, Bahamas.

Lectotype: In TRH (B18-2616, Howe no. 4021, *pro parte*, 19 February 1905, coll. M. A. Howe), illustrated by Printz (1929: pl. 9, fig. 9, as *Lithothamnion mesomorphum* f. *ornata*), designated herein (Figure 51a).

Syntypes: In TRH (B18-2616, Howe no. 4021, *pro parte*, 19 February 1905, coll. M. A. Howe); in NY (Howe no. 4021); in L (unnumbered), Woelkerling and Verheij (1995: 67); in PC (unnumbered), Woelkerling and Lamy (1998: 355–356); in UC (unnumbered, AHFH 42033 and 42063).

Habitat and Distribution: Thalli grow attached to the red mangrove *Rhizophora mangle* L., corals, and rocks or on other corallines in sheltered littoral sites, to 2 m depth, in caves, and under rocks, protected from direct sunlight, and also occur in the sublittoral zone to ~70 m depth. Littoral specimens are usually inhabited by the foraminiferan *Miniacina miniacea* (Pallas) and overgrow polychaete tubes. The species is confirmed from the Bahamas (Cave Cays, Exuma Chain), Bermudas (Clarence Cove), Puerto Rico (La Parguera), Atlantic Costa Rica (inner harbor of Portete, Limon Province), and Lesser Antilles (Barbados).

Material Examined: Bahamas: Cave Cays, Exuma Chain: lectotype and syntypes of *L. mesomorphum* f. *ornatum* in TRH (B18-2616); in BM (box 922, a single sterile specimen on a coral (?) 7 × 4 cm); and in UC (unnumbered, fragmented sterile specimens on an herbarium sheet partly attached to a geniculate coralline [AHFH 42033] and several other sterile specimens to 6 cm in a box [AHFH 42063]). All with reference to Howe no. 4021.

Bermudas: Clarence Cove (32°18′22.4″N, 64°47′00.5″W): from the waterline on rock, 18 July 2005, coll. C. W. Schneider and C. E. Lane 05-7-1 (herb. Schneider 006423); Clarence Cove (32°18.3′N, 64°48.3′W), from 0 to 1 m in grotto pool 20 July 1999, coll. C. W. Schneider and C. E. Lane 99-10-7 (herb. Schneider 005854), both specimens labeled "*Mesophyllum mesomorphum*."

Costa Rica: Inner harbor of Portete: Limon Province: in deep shade under a rock in current channel Portete, 4 August 1962, coll. E. Y. Dawson and W. Rudersdorf (UC, unnumbered, AHFH 72705, E. Y. Dawson and W. Rudersdorf 24343, identified as *Lithothamnion mesomorphum* Foslie by E. Y. Dawson).

Puerto Rico: San Juan: on corals in 0.5 m of water, tetrasporophytes, 2 June 1903, coll. M. A. Howe (TRH, B16-2522, *pro parte*, Howe no. 2295d, includes slide, identified as *Lithothamnion syntrophicum* by Foslie).

La Parguera: Collado Reef: on red mangrove roots, just below water level, gametophytes and tetrasporophytes usually growing with *Hyperandri bisporum*, 17, 22, and 28 April 2009, coll. Athanas. (herb. Athanas. PR-81, PR-86D, PR-86-E, PR-86F, C-1, PR-251A, PR-251D, PR-251G, PR-251O, PR-253, PR-ornatum 1; D. L. Ballantine no. 7781 in MSM; PR-251 in GB); Las Pelotas: on red mangrove roots, sheltered, shady habitat, just below water level, gametophytes and tetrasporophytes mixed with *H. bisporum* and *Lithothamnion* spp., 28 April 2009, coll. Athanas. (herb. Athanas. LP-1, LP-2, LP-3, LP-4, LP-6, LP-7, LP-8, LP-9, PR-22A, PR-33, PR-86B, PR-ornatum2; PR-43 in GB); Mario Reef: on red mangrove roots, just below water level, gametophytes, 22 April 2009, coll. Athanas. (herb. Athanas. PR-65C, PR-78C); Cayo Enrique: on red mangrove roots, just below water level, growing with *Lithothamnion carpoklonion*, 28 April 2009, coll. Athanas. (herb. Athanas. PR-12, PR-15, PR-15B); "Weinberg" shelf edge: on corals in crevices, sterile, 27–30 m depth, 11 May 2009, coll.

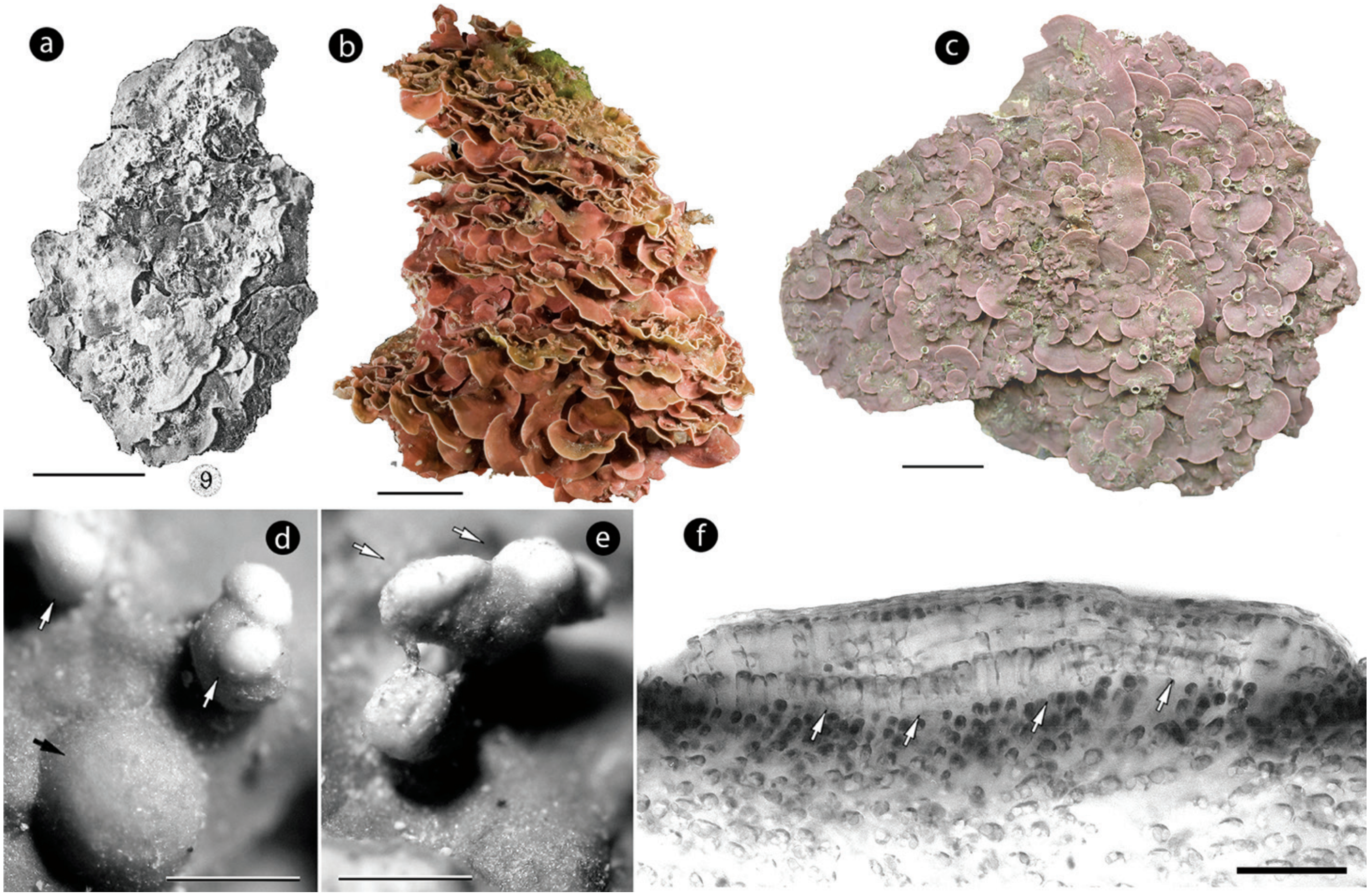


FIGURE 51. *Magnephycus ornatus.* (**a**) The here selected lectotype from the Bahamas (TRH, B18-2616, *pro parte*). Reproduced from Printz (1929: pl. 9, fig. 9). Scale bar: 1 cm. (**b**) Specimen(s) growing on red mangrove roots at La Parguera, Puerto Rico (herb. D.L. Ballant. 7781 in MSM). Scale bar: 1 cm. (**c**) Specimen(s) from Clarence Cove, Bermudas (herb. C. Schneider 006423). Scale bar: 1 cm. (**d, e**) Dorsal proliferations (white arrows) next to a multiporate conceptacle (black arrow; herb.Athanas.PR-15C). Scale bars: 500 µm. (**f**) Section of a dorsal proliferation showing development from the perithallium (arrows; herb. C. Schneider 005854). Scale bar: 50 µm.

Athanas. and H. Ruiz (herb. Athanas. PR-138, PR-139B, PR-139C); culture tank of the marine station at La Parguera, sterile, coll. D. L. Ballantine (herb. Athanas. PR-72); "hole in the wall" shelf edge, 165 feet, sterile, 5 May 2009, coll. H. Ruiz (herb. Athanas. PR-118C; "F" liquid preserved); "black wall" shelf edge: 200 feet, sterile, growing with bisporic *Hydrolithon abysophila*, 27 May 2009, coll. H. Ruiz (herb. Athanas. PR-88A).

Lesser Antilles: Barbados: St. James Parish: dredged at 60–70 m depth off the Miramar Hotel, n[orth] of Holetown, 24 February 1966, coll. W. R. Taylor (MICH 622101, Taylor no. 66-137, identified as "*Lith. mesomorphum* Foslie ?").

Virgin Islands: St. Jan: Entre Cuybay at Great St James: "Algae marinae ex insulis Danicis Indiae occidentalis. *Lithothamnium mesomorphum* Fosl. var. *ornatum* Fosl. et M. Howe determ. Legit F. Børgesen: iter tertium 1905-06. No 2143," ~27 m depth ("15 brasses"), undated (but see below), three specimens/fragments on stones and corals, multiporate conceptacles, coll. F. Børgesen (C, unnumbered; Børgesen no. 2143); Between Cruz bay and Great St James: "Algae marinae ex insulis Danicis Indiae occidentalis. Croûtes mal dévelopeés de *Lithothamnium mesomorphum* Fosl. var. *ornatum* Fosl. et M. Howe determ. Legit F. Børgesen*:* iter tertium 1905-06. No 2143 . . . Mest Vasentliget Kan koralligen og dyr," ~27 m depth, 26 March 1906, seven specimens/fragments on stones, corals, coll. F. Børgesen (C, unnumbered; Børgesen no. 2143[bis]); Cruz Bay: "Algae marinae ex insulis Danicis Indiae occidentalis. *Lithothamnium mesomorphum* Fosl. *Lithothamnium mesomorphum* Fosl. [in a different handwriting]," undated, coll. F. Børgesen (C, unnumbered; Børgesen no. 2095).

Observations on the Protologue and Lectotypification: The protologue (Foslie et M. Howe 1906: 129, pl. 80, fig. 2, pl. 90, fig. 2) reads,

> Thallus much more delicate than in the type [i.e., *Mesophyllum mesomorphum*], only 150–200 μ thick, proliferations smaller: hypothallic (medullary) cells 11–20 × 7–11 μ, those near the lower surface often very narrow, 15–25 μ × 3–6 μ with large intercellular spaces; perithallic cells (towards upper surface) mostly rounded or subquadrate-oblong in vertical section, 4–9 μ in diameter. (Plate 80, F.2; Plate 90, F.2)
>
> Bahamas: Cave Cays, Exuma Chain, low littoral on a rock-shelf under an overhang (no. 4021).
>
> The plant is yellowish-pink or salmon-colored when living. All the specimens examined are apparently sterile, yet we believe that they are to be looked upon as representing a variety of *Lithothamnion mesomorphum* Fosl. (New Melob.5.1901), originally described from Bermuda. In habit, the plants approach delicate forms of *L. lichenoides*.

Figure 2 of plate 80 shows four specimens (~10.5 × 5.5, 6.5 × 4, 5.5 × 3, and 5 × 4 cm) and figure 2 of plate 90 shows "a section (decalcified) through a proliferation and part of the main thallus, magnified 165 diameters. The ventral side shows the larger intercellular spaces."

In the introduction of their work, Foslie and Howe (1906: 128) specified that the "gross specimens and microtome-sections from which the published photographs have been taken are deposited in the museum of the New York Botanical Garden, though carefully selected duplicates, both of the gross specimens and of the microscopic preparations used, are in the possession of the senior author at Trondhjem."

The existence of several other "duplicates" in UC, PC, L, and BM, indicates that the original material ("No 4021") included a large number of specimens that was apparently the product of several gatherings. Because Foslie and Howe (1906) did not select a type element, the (four) specimens illustrated in the protologue (all in NY?), together with all materials distributed in TRH, BM (material here examined), L (Woelkerling and Verheij 1995: 67), PC (Woelkerling and Lamy 1998: 355–356), and UC (material here examined) have to be considered syntypes (Turland et al., 2018: Article 9.6), which, because of the size and number, cannot belong to a single gathering (made at the same time; Turland et al., 2018: Article 8.2). The material in TRH (B18-2616; Woelkerling et al. 2005: 352–353) comprises (1) two sterile specimens (~3.5 × 3.5 and 3.5 × 2.5 cm); (2) three slides annotated "*Lithothamnion mesomorphum ornatum* F. and H. n°4021 *Cave Cays Bhs*.," "1579," and "*Lith. mesomorphum Fosl. f. ornata Fosl. and Howe ~~994~~* 4021 New York Bot. Gard. Bahamas 19.II.1905 leg. M.A. Howe."; and (3) three labels annotated "*Squamariacea* ?," "*L. mesomorphum* f. *ornata* Prep. 1579 Perith. 9x7 11x7 9x6 7x7 Daalige perith.cell. Hypoth. Daal. hyp.cells! 18x11 22x11 14x11 14x9 11x9 22x13 22x14 14x14 18x7 18x9 Kar . . . cell . . . typen," and "NORTH AMERICAN MARINE ALGAE Distributed from the Herbarium of The New York Botanical Garden n°4021 Lithoth. mesomorphum Fosl. f. ornata Fosl. and Howe Under rock overhang, low littoral; salmon-colored Collected on the Cave Cays, Exuma Chain, Bahamas by Marchall A. Howe, February 19, 1905."

A recent examination of the two TRH specimens confirmed the data in the protologue, adding that thalli "exhibit superimposed growth with at least five lamellae . . . dorsiventrally organized . . . The hypothallium is non-coaxial . . . trichocytes occur scattered amongst epithallial cells . . . [and] no buried conceptacles [exist] . . . in the thallus" (Athanasiadis 1999: 246–247, figs. 20–22, pl. 1).

Since the TRH collection (B18-2616) includes Foslie's annotations of hypothallial and perithallial cell size, it is logical to conclude that the protologue was at least in part based on this material, and hence, the specimen illustrated by Printz (1929: pl. 9, fig. 9) is here selected as the lectotype (Figure 51a). The lectotype represents the smaller of the two specimens in TRH. Adey and Lebednik (1970: 70) listed the TRH material under *Lithothamnion mesomorphum* without varietal designation or type designation, and Woelkerling (1993a: 165) previously considered the "NY, Howe no.4021. Foslie & Howe" material as the "holotype" and the material in TRH and BM as "isotypes," without selecting a single specimen as lectotype.

Species Description: Living thalli are yellowish pink or salmon colored (according to the protologue) to red brown when growing protected from the sunlight (Figure 51b,c). Thalli are encrusting (following the contour of the substratum) to foliose, at least 8 cm in extent, growing on corals, red mangrove roots, rocks, and coralline algae, usually forming imbricate complexes, at least 1 cm thick through superimposition (at least 5 layers seen), and growing mainly unattached (Figures 51a–c, 52a,b). Dorsal proliferations start from the perithallium and develop into a new lamella (Figure 51d–f). Abutting lamellae may anastomose or grow back to back. Margins are lobate and undulate with a whitish border (cuticle; Figure 52a–c). Regular zonations occur on the underside of the thallus (arranged at a mean distance of ~115 μm between them; Figure 52b). Lamellae are dorsiventrally organized, 60–380 μm thick, composed of a noncoaxial polystromatic hypothallium 35–310 μm thick (coaxial patches of 2–3 cell rows seen sporadically), supporting an ascending perithallium 20–110 μm thick lacking stratification (Figure 52d). Hypothallial cells are 6–38 × 3–10 μm (L × B), and perithallial cells are 4–16 × 4–8 μm (L × B). Subepithallial cells are elongate-ovate, generally longer than cells below (12–16 μm in length). Epithallial cells are singly borne and flattened, ~2 × 7–10 μm (L × B; Figure 52e,f). Descending hypothallial filaments form elongate subbasal cells (to 20 μm long; Figures 52g, 55a). Cell fusions between contiguous vegetative cells are common. Secondary pit connections and trichocytes are absent.

Gametophytes are dioecious. Male conceptacles are conical, 330–750 × 180–330 μm (D × H; n: 7; Figure 53a), with chambers 200–470 × 80–180 μm (D × H; n: 8). The roof is 50–170 μm thick, provided with a central ostiole up to 170 μm long and 50–60 μm broad. Spermatangial structures develop on a pedestal, extending along the entire fertile floor and formed by up to 7 or

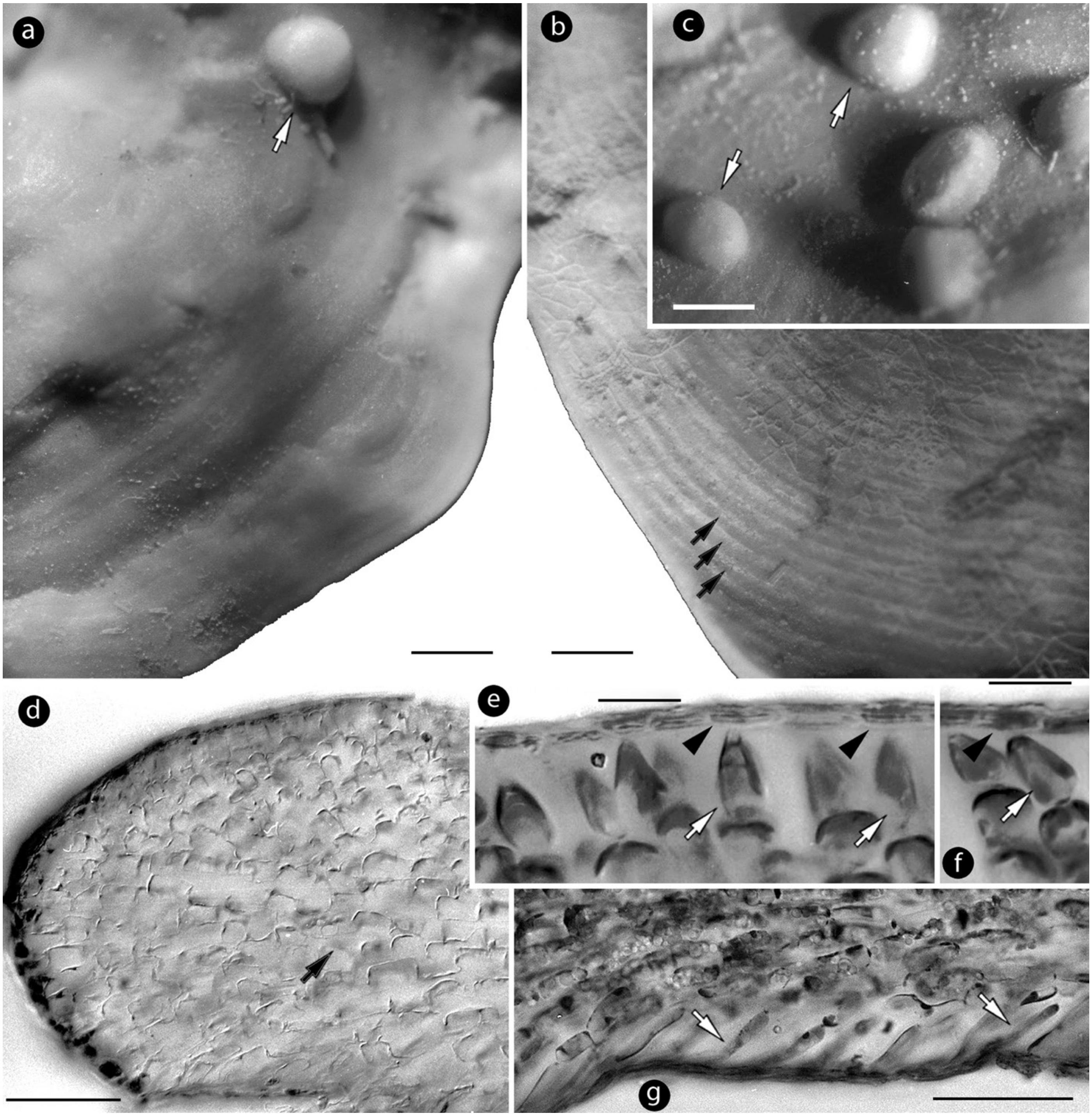


FIGURE 52. *Magnephycus ornatus*: vegetative structures. (**a–c**) Views showing typical hemispherical, multiporate conceptacles (arrows). The view of the underside in (b) shows obvious striations (black arrows; AHFH 72705 in UC). Scale bars: 500 µm. (**d**) Section at the margin showing terminal (deeply staining) meristematic cells and a noncoaxial hypothallium (arrow; AHFH 72705 in UC). Scale bar: 25 µm. (**e, f**) Sections at the surface showing flattened epithallial cells (black arrowheads) and elongate subepithallial cells (arrows; AHFH 72705 in UC). Scale bars: 10 µm. (**g**) Section showing thinner-elongate subbasal hypothallial cells (arrows; herb.Athanas.LP-2). Scale bar: 25 µm.

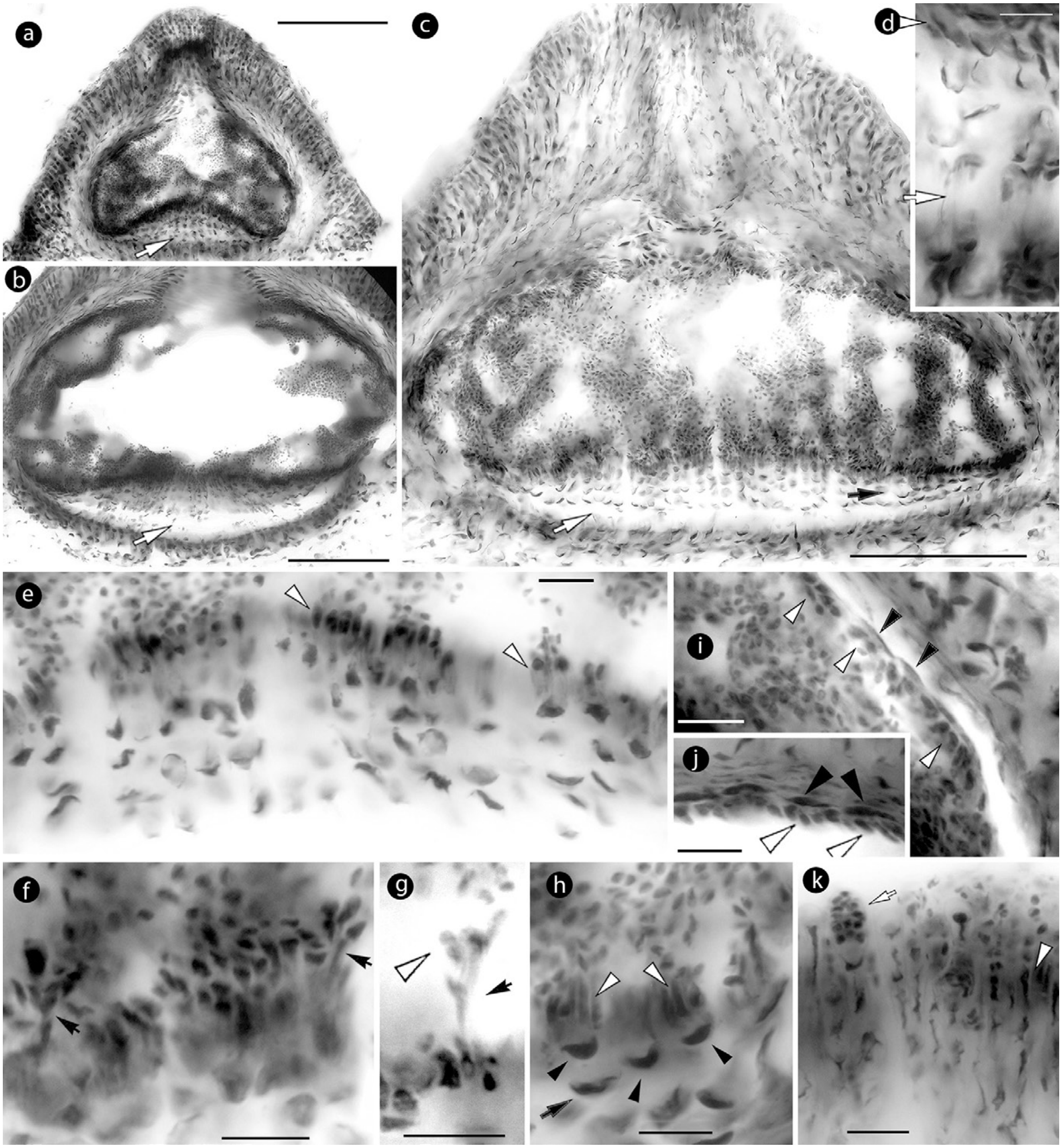
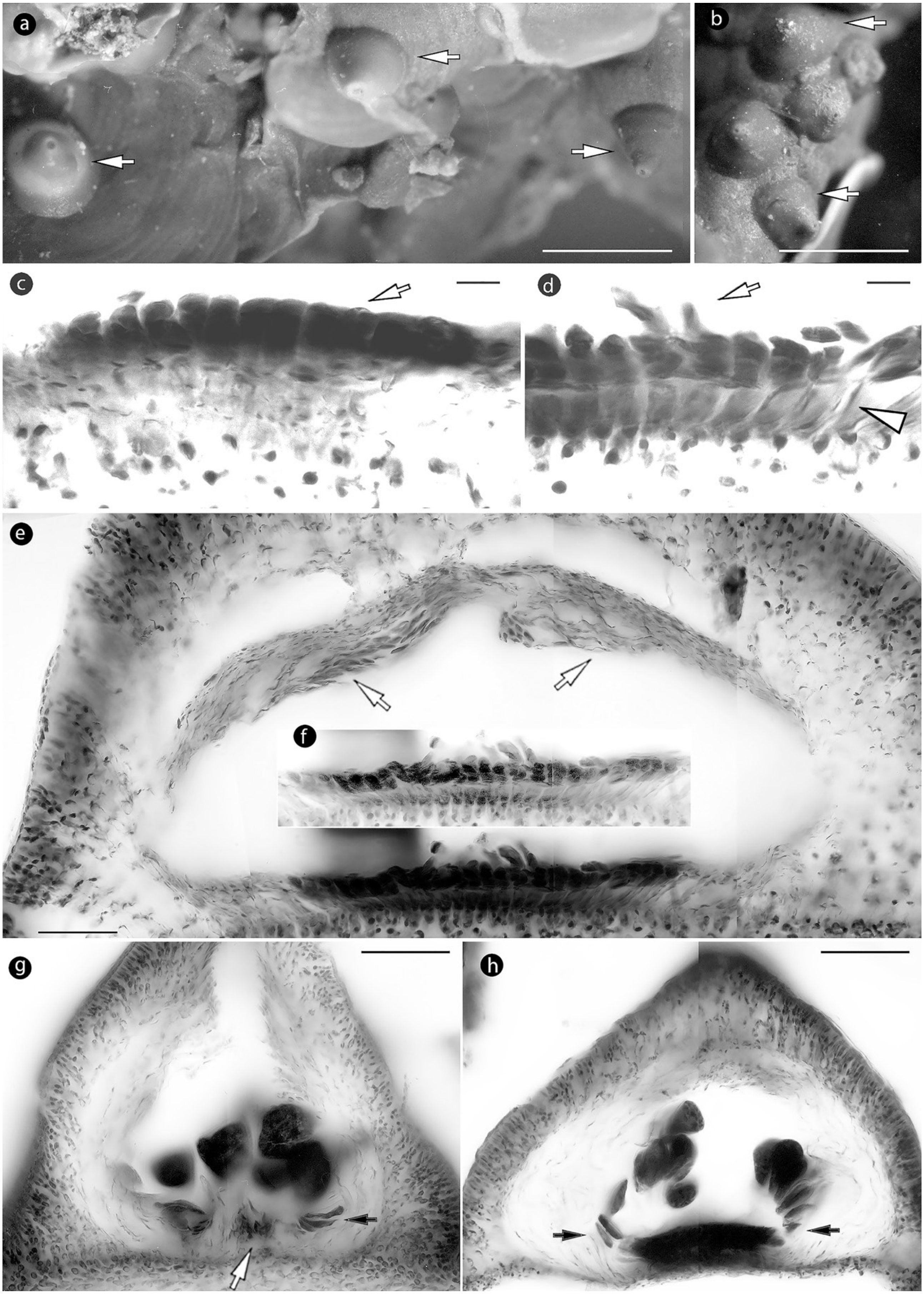


FIGURE 53. *Magnephycus ornatus*: male structures (herb.Athanas. LP-1). (**a–d**) Sections of male conceptacles showing the production of a layer of palisade cells on the floor in (d), followed by several layers of isodiametric cells. Note the inverted development in (b), resulting in the roundish chamber. Scale bars: 100 μm in (a)–(c), 10 μm in (d). (**e–j**) Simple (unbranched) spermatangial structures on the floor in (e) and (h), the roof in (j), and the walls in (i), with the rare presence of branched filaments in (f) and (g) (black arrows). Note the lunate SMCs on the floor in (h) (black arrowheads), being more elongate on the wall and the roof in (i) and (j), respectively (black arrowheads), and the uniformly roundish-elongate spermatangia (white arrowheads). (**k**) Older stage with clusters of spermatia (arrow) and deformed SMCs (arrowhead). Scale bars: 10 μm in (e)–(k).


a
b
c
d
e
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g
h

FIGURE 54. (*Opposite*) *Magnephycus ornatus*: carposporangial structures. (**a, b**) Carposporangial conceptacles (arrows; herb.Athanas. LP-1). Scale bars: 1 mm. (**c, d**) Carpogonial branch remains (arrows) across the floor. Note the subtending group of sterile cells (arrowhead) (PR-251 in GB). Scale bars: 10 µm. (**e, f**) Section through a fertile chamber showing the presence of a protective layer (arrows) below the roof (herb.Athanas. PR-251O). Scale bars: 50 µm. (**g, h**) Sections of two carposporangial conceptacles with peripheral development of carposporangia (black arrows) and carpogonial branch remains in the fertile floor (white arrow; herb.Athanas. LP-1 and PR-251A, respectively). Scale bars: 100 µm.

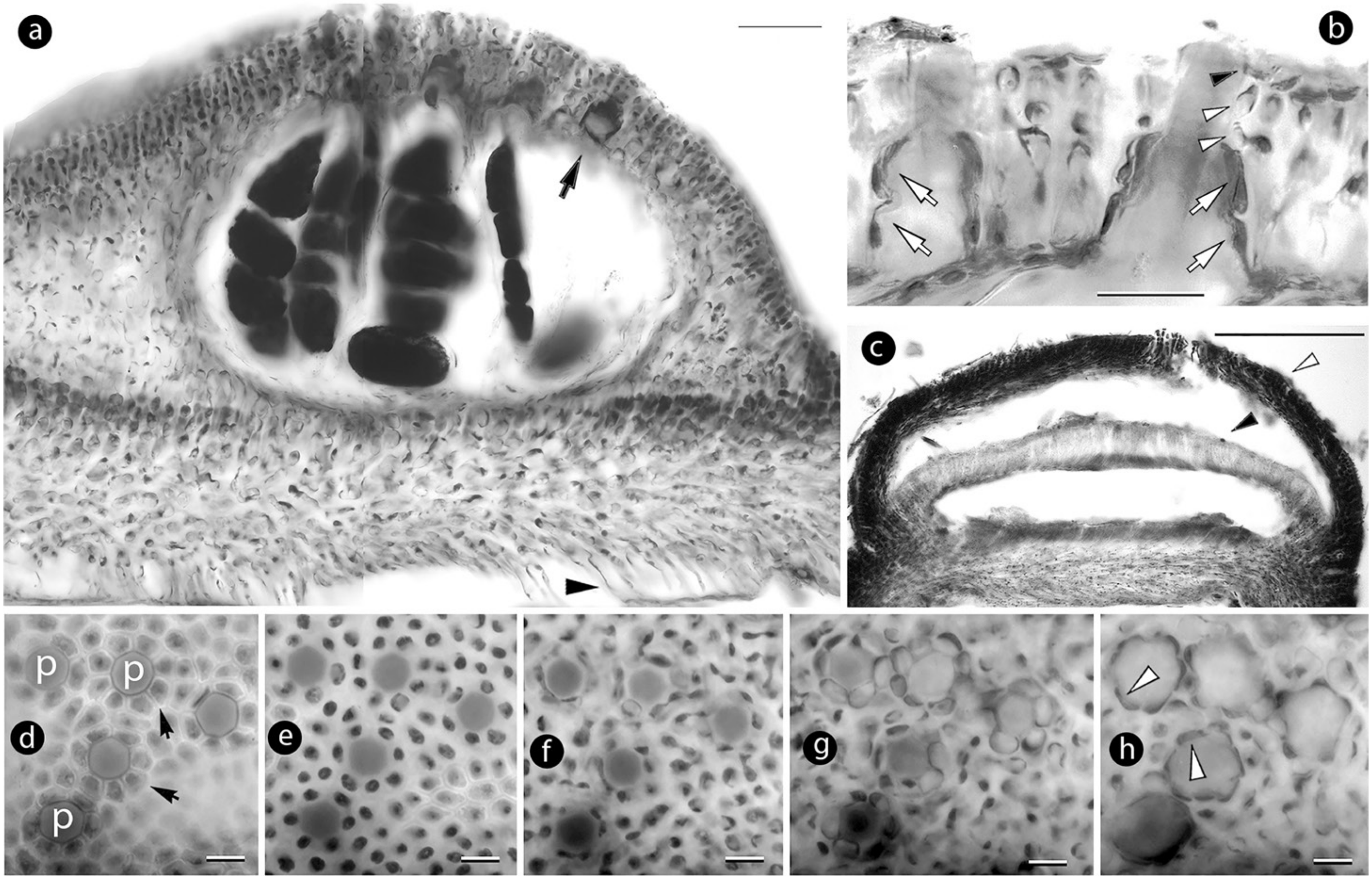


FIGURE 55. *Magnephycus ornatus*: multiporate conceptacle structures (herb.Athanas. LP-1 in (a) and (c)–(h); AHFH 72705 in UC in (b)). (**a**) Section of a tetrasporangial conceptacle with a multiporate roof with typical pyriform canals (arrow). Note the subbasal elongate hypothallial cells (arrowhead). Scale bar: 50 µm. (**b**) Section through two canals of a multiporate roof, showing the thinner–wider, elongate basal and subbasal cells (arrows) and the typical roof cells above (arrowheads). Scale bar: 20 µm. (**c**) Multiporate conceptacle (black arrowhead) overgrown by peripheral filaments (white arrowhead). Scale bar: 200 µm. (**d–h**) Pore canals in surface view at five levels of focus, starting from the surface and proceeding toward the base and showing rosette cells (arrows) that are normal roof cells but thinner–wider at the base (arrowheads) surrounding larger openings. Scale bars: 10 µm. Abbreviation: p, pore canal.

8 layers of isodiametric cells (reaching up to 100 µm high) borne on a basal layer of palisade cells (Figure 53a–e). This pedestal may occasionally fill the bottom of a roundish chamber (Figure 53b). Rare dendroid and, more commonly, simple spermatangia develop on the pedestal (Figure 53f–h), whereas only simple spermatangia occur on the walls and the roof (Figure 53i,j). Simple spermatangial structures have lunate SMCs (Figure 53h). Older stages show structures with clusters of spermatia and deformed SMCs (Figure 53k).

Carpogonial conceptacles and postfertilization stages are not recorded. Carposporangial conceptacles are conical, 500–860 × 310–525 µm (D × H; n: 14; Figure 54a,b), with elongate to hemispherical chambers 300–550 × 110–450 µm (D × H; n: 16), displaying a flattened floor with a fertile zone (200–270 µm in diameter; n: 7). Putative remains of carpogonial branches were seen resting on a series of palisade cells on the fertile floor (Figure 54c–f). Carposporangia, 30–75 × 40–52 µm (L × B), are produced laterally from the periphery of the fertile zone (Figure 54g,h). The roof is 50–220 µm thick with a central ostiole (wider at the base), 190–235 × 60–140 µm (L × B; n: 6). Development of a layer of filaments in the chamber, below the proper roof (Figure 54e), may be similar to the production of a second roof (as seen in tetrasporangial conceptacles).

Multiporate conceptacles are distinctively hemispherical (wart-like), 440–680 × 200–310 µm (D × H; n: 12; Figures 51d, 52a,c, 55a), and are provided with chambers 290–500 × 170–240 µm (D × H; n: 8). The roof is 40–50 µm thick, composed of 5- to 7-celled filaments, and perforated by 37–67 canals (n: 3). Pore plates are 200–450 µm in diameter (n: 4). Pore canals are 10–12 µm in apical diameter (n: 42), being surrounded by 6 to 8 rosette cells that are normal epithallial cells. Canals are typically pyriform (in transverse section), with the upper part lined by 3 normal roof cells and a wider basal opening, 15–22 µm in diameter, lined by basal and subbasal cells that are thinner–wider and distinctively elongate (Figure 55b,d–h). Tetrasporangia are 110–150 × 15–65 µm (L × B; n: 18). Older conceptacles senesce, leaving craterlike formations on the thallus. Peripheral filaments may overgrow conceptacles, producing a second roof (Figure 55c). Embedded conceptacles are absent.

Comments: The species was originally described as *Lithothamnion mesomorphum* var. *ornatum* from sterile, but plentiful, material collected in the Bahamas (Foslie and Howe 1906). Under this varietal name, Lemoine (1917: 155) reported specimens from St. John (U.S. Virgin Islands), and reexamination of these collections (Børgesen no. 2143 in C) confirmed the identification, with the additional observation that some thalli were provided with typical hemispherical, multiporate conceptacles. *Lithothamnion mesomorphum* var. *ornatum* was included in Howe's (1920: 584) Bahamas flora without further information. Taylor (1928: 210) reported several sublittoral (12–32 m depth) collections from Florida, but reexamination of this material (Taylor no. 1013 in MICH 622103) showed that it is representative of *Mesophyllum mesomorphum* (Athanasiadis 1999: 246; Athanasiadis and Ballantine 2014: 421). No later records appeared in Taylor's (1960: 382) algal flora from the central Atlantic. Wynne (1998: 110) recognized this entity as a variety of *Mesophyllum mesomorphum*. Athanasiadis (1999: 246) raised it to species rank, pointing out a putative sister taxon relationship with the Aegean endemic *Mesophyllum macedonis* (herein as *Macedonis tethygenis*). *Mesophyllum ornatum* was later recorded from La Parguera (Puerto Rico) as a common epiphyte on the mangrove vegetation and in deeper habitats (Ballantine et al. 2011: 295, fig. 5), and in the present review the collections range down to a depth of ~70 m. The species grows commonly in shallow, shady, sheltered habitats on hard substrata, including corals, other corallines, and, particularly, the prop roots of the red mangrove *Rhizophora mangle* L. It has even been found in the laboratory tanks of the marine station on Isla Magueyes. Both gametophytes and tetrasporophytes were recorded, but most collections were sterile, suggesting a limited fertility period. Tetrasporophytes were previously collected from Costa Rica and the U.S. Virgin Islands, whereas all the northernmost collections from the Bahamas and the Bermudas are sterile. Together with *Hyperandri bisporum* and *Melyvonnea erubescens*, these three species are the commonest Mesophyllaceae at La Parguera. Records of "*Mesophyllum mesomorphum*" from the Indo-Pacific, previously suggested to be representative of *Mesophyllum ornatum* (Ballantine et al. 2011: 296), are here referred to *Magnephycus simulans*. Records of "*Mesophyllum engelhartii*" from the Brazilian coast (Da Nóbrega Farias 2009: figs. 11–13; Figure 5p,q) show spermatangial structures on a 2-celled pedestal and are almost certainly representative of a closely related species that merits further study. The significance of the pedestal formation in the phylogeny of Magnephyceae was already discussed (characters 19–20 in "Character Evolution in the Mesophyllaceae" and "Phylogenetic Relationships in the Mesophyllaceae").

As described and illustrated in the protologue, hypothallial cells of *Magnephycus ornatus* near the lower surface are often thinner-elongate (Foslie and Howe 1906: 129, pl. 90, fig. 2; Figure 52g), which is also reported in other species of *Magnephycus* and in *Macedonis* (Figure 34h). The function of such cells remains unknown.

Trichocytes were reported in the lectotype (Athanasiadis 1999: fig. 22), but their occurrence was not confirmed in the reexamination of the TRH lectotype (or in syntype specimens), and no trichocytes were observed in the new collections. As the original report was documented only in surface view, it is likely that it was based on a misinterpretation of epithallial or subepithallial cells with part of the upper wall collapsed.

Magnephycus simulans **(Foslie) Athanas. et D. L. Ballant. comb. nov.**

FIGURES 56–60

Magnephycus simulans (Foslie) Athanas. et D. L. Ballant. comb. nov.
Basionym: Lithothamnion siamense f. *simulans* Foslie 1901b: 19–20.
Homotypic Synonyms: Lithothamnion simulans (Foslie) Foslie 1904c: 16.
Mesophyllum simulans (Foslie) Me. Lemoine 1928: 252.
Heterotypic Synonyms: Lithothamnion simulans f. *crispescens* Foslie 1904c: 16–18, pl. 1, figs. 21–23; lectotype locality: sublittoral, 27–54 m depth, sand, coral and corallines, between Nusa Besi and the NE point of Timor Island, Indonesia; lectotype: in TRH (B18-2635, collector unknown), Foslie (1904c: pl. 1, fig. 23), Printz (1929: pl. 8, fig. 18), designated by Adey and Lebednik (1967: 70, "type material," "S.E.Stat.282, no 409, Timor, Oosthoek (?), 15-17.1.1900," "§ M. crispescens," here illustrated (Figure 58a–h); isolectotype: in L (Herb. Lugd. Bat. 991.239-256, L0836984, two tetrasporangial fragments); syntypes: in L ("*Lith. simulans f. crispescens*," "S.E. 516," "Pl.I, fig. 22," "Stat. 261," three fragments, one with multiporate conceptacles), Foslie (1904c: 16, pl. 1,

fig. 22; Figure 59a–d); in L ("*L. simulans f. crispescens*," "S.E. 624," "Pl. I, fig. 21"), Foslie (1904c: 16, pl. 1, fig. 21); the two syntypes in L ("S.E. 516," "S.E. 624") are currently placed in the same box "Herb. Lugd. Bat. n°991.239260" (L0056935).

Mesophyllum crispescens (Foslie) Me. Lemoine in Børgesen 1954: 14.

Misapplied Name: ?*Mesophyllum mesomorphum* sensu Gordon et al. 1976: pl. 2, figs. 1, 2 [non *M. mesomorphum* (Foslie) W. H. Adey].

Type Locality: In shallow waters, on *Septifer bilocularis* L., Sarlak Island, Gulf of Thailand.

Holotype: In TRH (B18-2626), "§ Schmitz, Gulf of Siam, Koh Sarbak, 16.3.1900, no vii, Danish Siam.Exp. 1899-1900 [slide] 463" (Adey and Lebednik 1967: 70, "type material"), Woelkerling (1993a: 202, "holotype"), Woelkerling et al. (2005: 354, "holotype"; Figure 56a–g).

Isotype: In TRH (B18-2634), "§ Schmitz Siam" (Adey and Lebednik 1967: 70), 16 March 1900 (Figure 57a–l).

Habitat and Distribution: The type specimen is attached to *Septifer bilocularis* L., collected from shallow waters (Foslie 1901b), although according to Foslie (1904c: 17), "The species is attached to different objects, partly to shells of molluscs, partly and particularly to corals, calcareous sediment or other calcareous algae," such as "*Archaeolithothamnion erythraeum* . . . *Goniolithon Reinboldi* . . . *Lithothamnion fragilissimum* . . . *Lithophyllum moluccense* . . . *L. Bamleri* . . . *Archaeolithothamnion timorense*." It is also attached ventrally to pebbles and larger rocks, overgrowing other encrusting algae such as *Peyssonnelia*. It is reported from various sites of the Chang archipelago (Thailand), Indonesia, Hawaii Islands, and Solomon Islands (including records of its synonym *Mesophyllum crispescens*).

Material Examined: Thailand: holotype (TRH, B18-2626, sterile) and isotype (TRH, B18-2634, carposporangial and multiporate thalli) of *Lithothamnion siamense* f. *simulans* as described above and below.

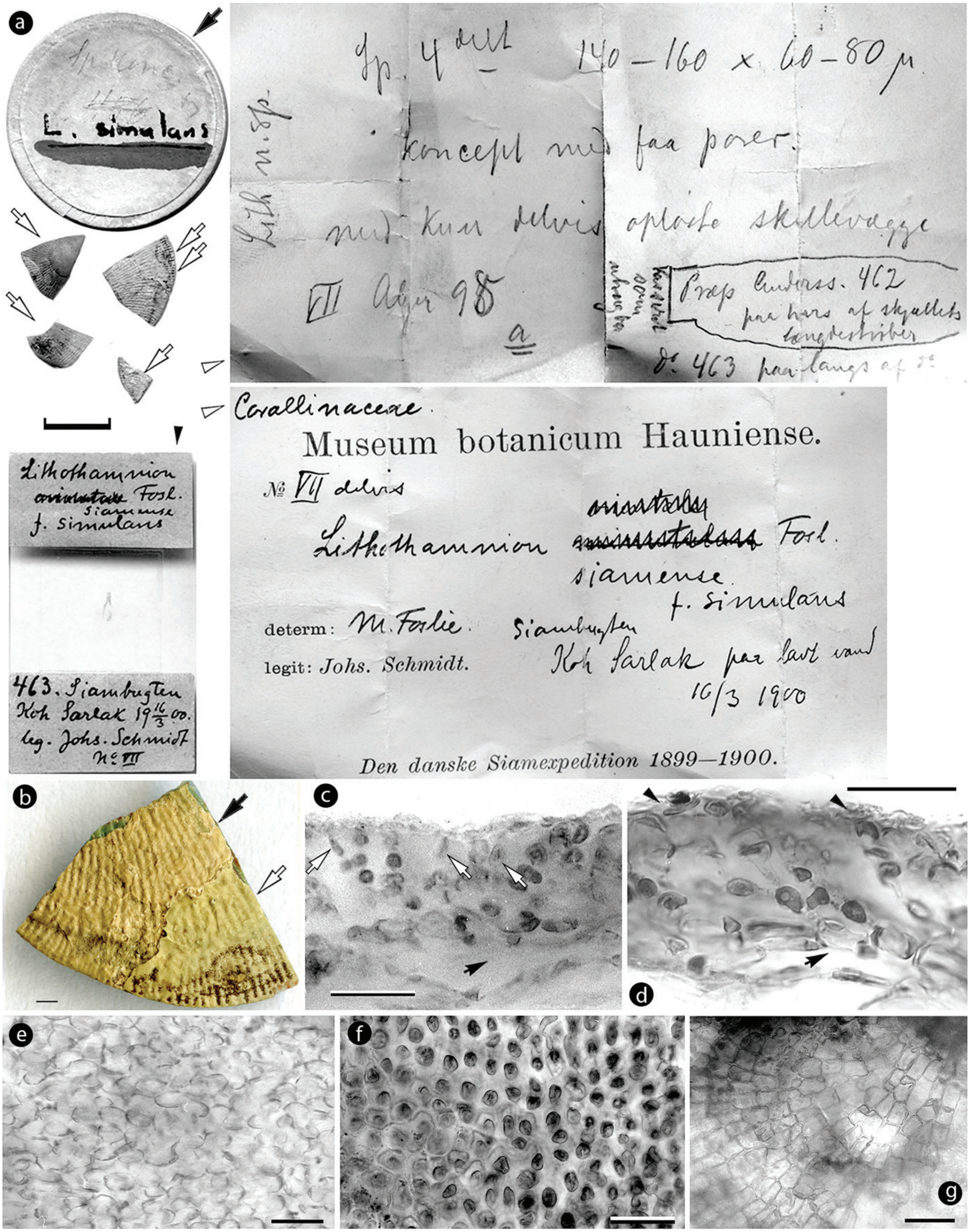
Indonesia: Oesthoek: Timor Reef: lectotype (TRH, B18-2635, sterile) and isolectotype (L0836984, multiporate) of *Lithothamnion simulans* f. *crispescens* as described above and below; Elat: west coast of Great-Kei Island Reef: syntype (L0056935, tetrasporangial or sterile) of *L. simulans* f. *crispescens* as described above and below; Buka or Cyrus Bay: south coast of Rotti Island: syntype (L0056935, sterile) of *L. simulans* f. *crispescens*, 34 m depth, as described above and below; Nusa Besi: "*L. simulans* Paa Lithoph. moluccense Siboga Exp.418 Stat.282, Nusa Besi — Timor 15-17.I.1900" (TRH, B18-2632, multiporate conceptacles); "*L. simulans* Paa Lithoph. Bamberi Siboga Exp.686b. Stat.282, Nusa Besi — Timor 15/17.I.1900 Prep." (TRH, B18-2633, multiporate conceptacles); Borneo bank: "*Lithoth. simulans*, Siboga Exp.148b.Stat.78, Lumu-Lumu-shoal, Borneo-bank. 10-11.vi.1899" (TRH, B18-2628), ". . . 34 m. Coral and coral sand" (Foslie 1904c: 16, carposporangial and multiporate conceptacles); "*Lithoth. simulans*, Siboga Exp.408c.Stat.81, Pulu Sebangkatan, Borneo-bank. 14.vi.1899" (TRH, B18-2629), "...34 m. Coral bottom and Lithothamnion" (Foslie 1904c: 16, multiporate conceptacles); Kei Island: Tual: "*L. siamense* Siboga Exp.Stat.258 S.E.1263 delvis Tual, Kei Islands 12-16.xii.1899. Lithoth. monogr.pl.1, fig. 20" (B2-1730, *pro parte*, multiporate conceptacles, includes a mastophoroid with uniporate conceptacles); Banda: "*Lithoth. simulans* Siboga Exp.185 Stat.240 Banda Vovbr.Dec.1899 Prep." (TRH, B18-2627, multiporate conceptacles and sterile); Saleyer: "*Lith. simulans,* Siboga exp.421a. Stat. 213, Saleyer, Sept.-Oktbr.1899 (Pl.I.fig.24)" (TRH, B18-2630, sterile thalli attached to *Peyssonnelia* and *Lithothamnion* sp., includes a slide annotated "text.fig. 7 A S.E.412a Stat.213, Saleyer"); "*Lith. simulans,* Siboga exp.422. Stat.213, Saleyer Sept.–Oktbr.1899 (Pl.I. fig. 25)" (TRH, B18-2631, carposporangial and multiporate conceptacles); 12 slides from the Siboga Expedition in L (L0246528, Herb. Lugd. Bat. 943.7 . . . 35, *pro parte*):

1. "*Lithoth. simulans* (Textfig. 7A) + *Goniolithon Reinboldi* S.E.421a"
2. "*Lithoth. simulans Mastoph. melobesioides Lithoth. fruticulosum*? Siboga Exped. Stat. 961"
3. "Calc. sedim.? Siboga-Exped. Stat. 1263d" (unidentified material)
4. "*Lithoth. simulans* partim S.E.190" (or S.E.140?)
5. "*Lithoth. simulans* forma + *Mastophora melobesioides* Siboga-Exped. Stat. 703" (unidentified material)
6. "*Lithoth. simulans* Siboga-Exped. Stat. 624"
7. "*Lithoth. simulans* Siboga-Exped. Stat. 422"
8. "*Lithoth. simulans* 422"
9. "Tr. *Lithoth. simulans* Siboga-Exped. S.E. 624"
10. "N.12 *Lith. simulans* Textfig. 7B. Saleyer"
11. "*Lithoth. simulans* Siboga-Exped. Syay. 516"
12. "*Lithoth. simulans* partim S.E.916" (unidentified material)

Solomon Islands: Gizo Island: New Manra: in surge channels in reef rim, 5 September 1965, coll. H. B. S. Womersley and A. Bailey (UC 1446578, Womersley and Bailey no. 542, multiporate conceptacles; Womersley and Bailey 1970: 309).

Hawaii: NW Hawaiian Islands: summer 1981, coll. Necker C. Agegian (herb. Y. M. Chamberlain; duplicate of BISH 686487, multiporate conceptacles).

Comments on the Protologue and Type Material of Lithothamnion siamense f. simulans: According to the protologue (Foslie 1901b: 19–20), *Lithothamnion siamense* f. *simulans* forms a thin crust 50–100 µm thick, with (multiporate) sporangial conceptacles 400–500 µm in external diameter. (Tetra- or bi) sporangia are 140–160 × 60–80 µm, and carposporangial conceptacles are 500–600 µm in diameter. Coaxial development was also reported in the species (without forma specification), but since this character was not observed in the type material of the autonym (see *Hyperandri siamense*), it should refer to f. *simulans*. No illustrations accompanied the protologue, and the single collection of f. *simulans* cited by Foslie (1901b) becomes the holotype (TRH B18-2626; Figure 56a). This collection exists in a box annotated "*L. simulans*" and comprises the following material:



L. simulans

Lith. n. sp.

Sp. 4 delt 140–160 × 60–80 μ

koncept med faa porer.

med kun delvis opløste skillevægge

VII Alger 98

a

Prep Undersø. 462 paa tvers af skallets længdestriber

D° 463 paa langs af D°

Corallinaceae.

Museum botanicum Hauniense.

№ VII delvis

Lithothamnion ~~orientale~~ ~~orientale~~ Fosl.
siamense
f. simulans

determ: M. Foslie. Siambugten

legit: Johs. Schmidt. Koh Sarlak paa lavt vand
16/3 1900

Den danske Siamexpedition 1899—1900.

Lithothamnion
~~orientale~~ Fosl.
siamense
f. simulans

463. Siambugten
Koh Sarlak 19 16/3 00.
leg. Johs. Schmidt
N° VII

FIGURE 56. (*Opposite*) *Magnephycus simulans*: holotype of *Lithothamnion siamense* f. *simulans* in TRH (B18-2626). (**a**) The round box (black arrow) including the four fragments of *Septifer bilocularis* L. (white arrows), the largest fragment of the holotype (two side-by-side arrows), a slide (black arrowhead), and two notes (white arrowheads). Scale bar: 1 cm. (**b**) Holotype (B18-2626, *pro parte*; white arrow) attached on the shell fragment together with another coralline alga (black arrow). Scale bar: 1 mm. (**c, d**) Sections of the holotype showing a noncoaxial hypothallium (black arrows) with ascending perithallial filaments ending in elongate subepithallial cells (white arrows) supporting flattened (arrowheads) epithallial cells. Scale bars: 25 µm. (**e**) View of the holotype from below, showing hypothallial cells displaying noncoaxial arrangement. Scale bar: 25 µm. (**f**) Surface view of the holotype showing epithallial cells. Scale bar: 25 µm. (**g**) Surface view of the admixture (black arrow in (b)), showing a monostromatic hypothallium. Scale bar: 25 µm.

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1. A slide annotated (partly stricken through by Foslie) "*Lithothamnion ~~minutula~~* Fosl. *siamense* f. *simulans*. 463. Siambugten Koh Sarlak 16/3.1900. leg. John. Schmidt n°VII"
2. A paper sheet (annotated in the hand of Foslie and translated below by T. Prestø), "Lith. n.sp.," "Sp.4delt. [sporangia 4-parted] 140–160 × 60–80 µ," "Koncept. med faa porer [concept. with few pores]," "med kun delvis opløste skillevaegge [with only partly disintegrated side walls]," "VII Alger 95 a," "Prep Anderss. 462 paa tvers af skjaellets laengdestriber Kasseret som ubrugbar [Slide Andersson 462 crosswise to the length of the mussel stripes discarded as useless]," "Ds 463 paa langs af ds [slide 463 lengthwise of this]"
3. A label annotated (partly with printed text and partly stricken through by Foslie) "*Corallinaceae*. Museum botanicum Hauniense. No VII delvis *Lithothamnion ~~minutula minutula~~ siamense* Fosl. *f. simulans* Siambugten Koh Sarlak paa lagt vand 16/3 1900 determ: M. Foslie legit: *Den danske Siam expedition 1899–1900*"
4. Four fragments of the mollusk *Septifer bilocularis* L. with sterile algal thalli attached, placed in a round box (Figure 56a).

A second collection in TRH (B18-2634) includes two boxes annotated "*L. simulans Siam*. Sp. Konc. Foto nr 75 A" and "*L. simulans Siam*. Paa *Septifer bilocularis* L. Cyst. konc." (Figure 57a). Each box includes algal material attached to a fragment of the mollusk *Septifer*. One fragment has a single uniporate conceptacle (most likely to be carposporangial), and the other has several multiporate conceptacles (Figure 57b,c). Since the material on *Septifer* was associated with the single collection of f. *simulans* in the protologue and Siam is the provenance of this taxon, it can be concluded beyond doubt that these two separately placed fragments (in B18-2634) were part of the original material (B18-2626) and hence should be considered isotypes. The annotation "*L. simulans*" on B18-2634 indicates that the separation from the original collection (B18-2626) was made after the protologue (Foslie 1901b), most likely when Foslie (1904c) reexamined his (original) material and compared it with the new collections from the Siboga Expedition.

This conclusion was reached after communication with the keeper of the Foslie herbarium in TRH (Tommy Prestø, Norwegian University of Science and Technology, Trondheim, Norway, personal communication), who pointed out in addition that

> Schmidt is regarded as legator of all specimens from Siam in the Foslie collection, except for B18-2634 which we considered legator as Anonymous. I guess the reason for doing this was the lack of physical connection to other specimens. The two small boxes making up B18-2634 are typical of the Foslie collection. Also, the labelling is made by Foslie, most likely also the name of the mussel "*Septifer bilocularis*". The two small boxes could have been split from the rest due to a) photographing and b) identification of the mussel. Later on, no one has dared to put them back again where they possibly came from. Adey and Lebednik (1967: 70) also mentioned the specimen from Siam [without data of origin], [which is an] indication that physical connection was lost before 1967. . . . There are no other specimens in the Foslie collection growing on any "*Septifer*". . . . But if locality or habitat information relating to B18-2626 says something about "*Septifer bilocularis*", then perhaps this is a link. . . . Conclusion: B18-2634 is part of the collection in B18-2626. The physical relation was somehow lost and not reestablished.

The sterile fragments of the holotype (B18-2626; Figure 56a) include two different species: one is a mastophoroid alga and is here regarded to be an admixture (Turland et al., 2018: Article 8.2), whereas the second species shows vegetative structures that are in agreement with the isotype (B18-2634) and the protologue (Figure 56b). In particular, the holotype exhibits a thallus 45–50 µm thick (50–100 µm thick after the protologue), composed of a noncoaxial hypothallium (~25 µm thick) and an ascending perithallium (~25 µm thick) with elongate subepithallial cells (at least 8.5 µm long), each supporting a single flattened epithallial cell (~1–2 × 6–12 µm; L × B). Hypothallial cells are 5–15 × 3–7.5 µm (L × B), and perithallial cells are 3–10 × 3–6 µm (L × B; Figure 56c–f).

The admixture shows a monostromatic hypothallium (Figure 56g) and most likely belongs to a member of *Pneophyllum* Kütz. or *Fosliella* M. Howe.

The thallus of the isotype (B18-2634) similarly exhibits a noncoaxial polystromatic hypothallium supporting an ascending perithallium with single flattened epithallial cells (Figure 57d–g). The multiporate conceptacles in the isotype (B18-2634) are

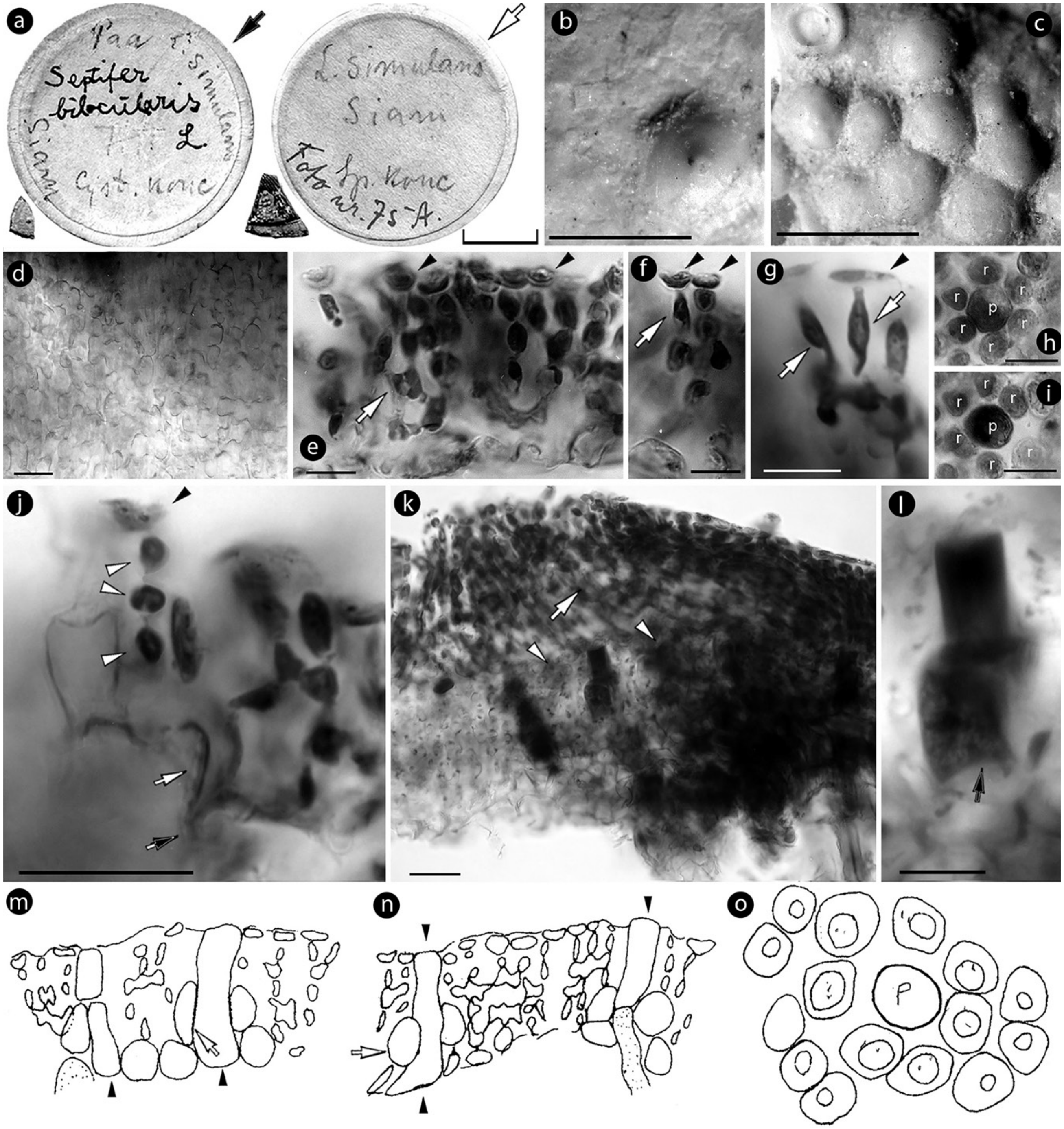

FIGURE 57. *Magnephycus simulans*: isotype of *Lithothamnion siamense* f. *simulans* in TRH (B18-2634; a–l). (**a**) The material in two boxes (arrows), each with a single fragment. Scale bar: 1 cm. (**b**) The fragment with a uniporate conceptacle in the box annotated "Cyst. konc." (black arrow in (a)). Scale bar: 1 mm. (**c**) The fragment with multiporate conceptacles in the box annotated "Sp.konc." (white arrow in (a)). Scale bar: 1 mm. (**d**) View of the hypothallium from below showing noncoaxial arrangement. Scale bar: 25 µm. (**e–g**) Sections showing ascending perithallial filaments, ending in single flattened epithallial cells (arrowheads). Note the lateral cell fusion (arrow in (e)) and the elongate subepithallial cells (arrows in (f) and (g)). Scale bars: 10 µm. (**h, i**) Surface view of two canals surrounded by 6 rosette cells. Scale bars: 10 µm. (**j**) A canal with typical shape, lined by 6 pore cells (including an epithallial cell, black arrowhead). The basal cell (black arrow) is slightly visible. Scale bar: 20 µm. (**k**) Peripheral filaments (arrow) overgrowing an old roof (arrowheads). Scale bar: 20 µm. (**l**) Canal (black arrow) with a typical pyriform shape. Scale bar: 10 µm. (**m–o**) Sections of multiporate roofs and surface view of a canal surrounded by 7 rosette cells (cells with dots). Note the canal openings (black arrowheads) and the larger subbasal cells (white arrows) lining the canals. Drawings by Y. M. Chamberlain. Putative type material of *Lithothamnion simulans*. No scale. Abbreviations: p, pore canal; r, rosette cell.

hemispherical, 345–560 µm in diameter (n: 20; 400–500 µm in diameter after the protologue; Figure 57c). Up to 6 rosette cells may surround the canal openings (Figure 57h,i). Canals display typical pyriform shape, with 6-celled filaments having elongate basal and subbasal cells (Figure 57j–l). Tetra- or bisporangia were not seen in the sectioned fragments (but sporangia 140–160 µm long and 60–80 µm broad are reported in the protologue). The single uniporate conceptacle is ~620 µm in diameter (carposporangial and 500–600 µm in diameter after the protologue). A coaxial hypothallial growth was not observed in the holotype (or isotype).

In the collections from Indonesia obtained during the Siboga Expedition, Foslie (1904c) had plenty of material of this species and was faced with its variation. He observed that the hypothallium occasionally formed a coaxial growth, which he illustrated (Foslie 1904c: 16, text fig. 7A,B, as f. *typica*)[41] and proposed a new taxonomic arrangement. He recognized *Lithothamnion siamense* f. *minutum* and *L. siamense* f. *simulans* as two distinct species, that is, *Lithothamnion siamense* and *L. simulans*, respectively (Foslie 1904c: 10, 16). He further maintained *Lithothamnion simulans* f. *simulans* (as f. "*typica*") for the entity with "a fairly closely adherent" thallus and described a new form, f. *crispescens*, "distinguished by . . . [a] more or less lamellate and crispate [thallus]." The present study of Foslie's collections (in particular, the type of f. *crispescens*) showed that patches of a coaxial hypothallium are common in *Magnephycus simulans* (see Species Description below). However, this character was not observed in the examined fragments of the holotype of *L. siamense* f. *simulans* from Siam, and the two illustrations showing the character (Foslie 1904c: text fig. 7A,B) are indeed based on Siboga Expedition collections, the character itself being described as "frequently marked" in the species (and not in one of the two forms, f. *simulans* or f. *crispescens*).

Still, coaxial development was, indeed, reported in the protologue of *L. siamense* (without forma specification), and since it was not found in the autonym (f. *minutum* = *Hyperandri siamense*), it should occur in f. *simulans*.

Later, Printz (1929: 45) united *L. siamense* f. *simulans* Foslie (1901b) with *L. simulans* f. *crispescens* Foslie (1904c: pl. 1, figs. 21, 22) but simultaneously recognized *L. simulans* f. *typicum* Foslie (1904c: pl. 1, figs. 24, 25, f. "*typica*") as a separate taxon without explaining the differences in his key (Printz 1929: 55).

A year before, Lemoine (1928) proposed the transfer of *Lithothamnion simulans* to the new genus *Mesophyllum* without comment and later reported *Mesophyllum simulans* from the Red Sea (Lemoine 1966: 16, fig. 7), describing (in translation)

> a diminutive crust on a coral slightly adherent in the center and free in the margin, nearly circular, less than 2 cm in extent and 30 µm thick at the border, becoming 110 µm thick in the thallus center and up to 300 µm high when provided with conceptacles . . . carposporangial conceptacles conical, about 850 µm in diameter and 450 µm high. . . . The hypothallium rather variable . . . with coaxial (concentric) arches not constantly; hypothallial cells measure (4–7)13–15(20) × 2.5–7 µm [L × B]. . . . The perithallium is composed of squarish cells, 6–7 µm, or rectangular, 6–15 × 6–7 µm [L × B] in stratification.

Lemoine also summarized all other records from the Red Sea, Madagascar, and the Pacific Ocean (without reexamining the relevant collections).

Adey and Lebednik (1967: 70) located the type of *L. simulans* in TRH, the only material cited in the protologue and hence the apparent holotype (Adey 1970: 26; Woelkerling 1993a: 202). Adey (1970: 26) further noted that "[a]sexual conceptacles were not located" in the holotype. No later Indo-Pacific records of *Mesophyllum simulans* have been published (Silva et al. 1987: 38, 1996: 258).

Yvonne M. Chamberlain examined "type" material of *L. simulans* from "UPS" and kindly provided three illustrations (here reproduced as Figure 57m–o; YMC 5097). Yet the presence of type material of *Lithothamnion simulans* in UPS could not be confirmed (S. Ryman, Museum of Evolution, Uppsala, Sweden, personal communication, 29 September 2009), and Chamberlain's illustrations do not show typical pyriform canals (but enlarged-elongate basal and subbasal cells).

Comments on the Protologue and Typification of Lithothamnion simulans f. crispescens: The protologue (Foslie 1904c: 16–18) reads, "*Lithothamnion simulans* Fosl.mscr. . . . f. *crispescens* Fosl.mscr.Pl.I, fig. 21-23. Thallus more or less lamellate and crispate, or plicate-leaf-like."

The specimens cited and illustrated in the protologue (Foslie 1904c: pl. 1, figs. 21–23) were collected at "Stat. n°299. Buka or Cyrus Bay, South-coast of Rotti Island. 34 m. Mud, coral and *Lithothamnion*. An intermediate form between f. *typica* and f. *crispescens*, . . attached to a coral" (Foslie 1904c: pl. 1, fig. 21; syntype in L, 0056935); "Stat. n°261. Elat, West coast of Great-Kei Island. Reef. A fertile specimen" (Foslie 1904c: pl. 1, fig. 22; syntype in L, 0056935); and "Stat. n°282. Between Nusa Besi and the N.E-point of Timor. 27-54 m. Sand, coral and *Lithothamnion*. A somewhat stunted specimen" (Foslie 1904c, pl. 1, fig. 23; B18-2635 with duplicates in L0836984).

Foslie (1904c: 17) further specified that

> if the plant is charged with extraneous objects, new crusts are formed above, which give rise to irregular or branchlike formations. Cp. Pl. I, fig. 21, representing a form intermediate between f. *typica* and f. *crispescens* . . . [The latter] form is distinguished by its thallus being more or less lamellate and crispate, or plicate-leaf-like (Pl. 1, fig. 22–23). It corresponds partly to *Lithothamnion philippii* f. *crispatum*, partly to *L. engelhartii* f. *imbricatum* . . . The species is attached . . . Occurrence: There are only a couple of specimens from each . . . station . . . This . . . seems to be indicative that the species occurs . . . sparingly over a great part of the East-Indian Archipelago . . . The Gulf of Siam.

Adey and Lebednik (1967: 70, "§ M. crispescens") cited three separate collections from station 282 and selected "S.E.st

.282, n°409, Timor, Oosthock (?), 15–17.1.1900” as type material of f. *crispescens* (TRH, B18-2635; Figure 58a). This was later justified by Adey (1970: 23) since “only one specimen of those pictured in the original description is still present in the collection” in TRH. Although “Oosthoek” was not cited in any of the collections in the protologue, the lectotype (B18-2635) is, indeed, annotated by Foslie “Pl. I, fig. 23 . . . Siboga Exp.409.Stat.282 Oosthoek. Timor Rif.” (Figure 58a), and hence, “Oosthoek. Timor Rif.” is probably the precise site “Between Nusa Besi and the N.E-point of Timor” where the collection was made.

Verheij and Woelkerling (1992: 278) reported the presence of two more specimens in L annotated “St. 282, S.E. 409” and “Oesthoek Timor 409,” including the label “S.E. 409, Pl. I, fig. 23” (L0836984, Herb. Lugd. Bat. 20.Ind.Or. 991.239 256). They concluded that this material was a part of the lectotype specimen and further specified that the fragments in L bore multiporate conceptacles. Verheij and Woelkerling also reported the presence of two syntypes in L (i.e., specimens from stations 261 and 299 cited and illustrated in the protologue).

The lectotype in TRH (B18-2635) comprises elements in a single round box annotated by Foslie on the lid, “(= Pl.I, fig. 23) *Lithoth.* ~~*Simulans*~~ *crispescens* Siboga Exp.409.Stat.282. Oosthoek Timor.Rif. 15-17.I.1900 Prep.,” and on the back side of the box, “(= Pl.I. fig. 23) *Lithoth.simulans* Siboga exp.409. Stat.282. Oosthoek Timor.Rif.15-17.I.1900 Prep.”

The box includes one specimen 2.8 × 1.4 × 0.5 cm (L × B × H), several minor thallus fragments (less than 2 mm in extent), a paper sheet annotated “Cyst. Konc. Ca 500 µ,” and one slide annotated “*Lithoth. Simulans f. crispescens* S.E.409 Stat.282 Oosthoek Timor Rif. 15-17.I.1900” (Figure 58a).

The lectotype is sterile. Adey (1970: 23) noted that “[a]sexual conceptacles were not located,” but Verheij and Woelkerling (1992: 278) reported the presence of two multiporate conceptacles (one intact and the other “on a fragment in the box”; neither was found in the present examination). The thallus is foliose because of regular superimposition of lamellae that grow mainly unattached and frequently anastomosing, inhabited on their underside by the foraminiferan *Miniacina miniacea* (Pallas).

Sections indicated a monopodial-dorsiventral thallus, 80–200 µm thick, composed of a predominantly noncoaxial hypothallium, 50–170 µm thick, frequently possessing patches of coaxial growth and supporting an ascending perithallium, 30–60 µm thick. Hypothallial cells are 14–31 × 4–8 µm (L × B). Descending hypothallial filaments end in elongate subbasal cells, 6–23 × 6–7 µm (L × B) with wedge-shaped terminal cells (arranged in a rhomboid pattern). Perithallial cells are 7–15 × 3–7 µm (L × B) and provided with elongate-ovate (to drop-like) subepithallial initials, up to 15 µm long. Epithallial cells are flattened and singly borne, 1–2 × 5–10 µm (L × B; Figure 58b–h).

The two isolectotype fragments in L (0836984) are ~2.9 and 2.7 cm in diameter. The larger one shows a thallus with coaxial hypothallial patches (Figure 59a) and bears two multiporate conceptacles, ~400–500 µm in external diameter, both protruding prominently. A third conceptacle occurred on a minor fragment in the box and was sectioned, showing a chamber ~265 µm in diameter (Figure 59b); a roof, 35–40 µm thick, composed of 6-celled filaments; and a pore plate ~300 µm in diameter. Canals are surrounded by 6 rosette cells that are normal epithallial cells. Canals are typically pyriform, lined by 6 cells, where the upper 4 cells are normal roof cells and the lower 2 cells expand abruptly at the base, showing distinctively elongate subbasal cells (Figure 59c). A zonately divided tetrasporangium, 70 × 15 µm (L × B), was seen.

Of the two syntypes in L (both numbered L0056935, Herb. Lugd. Bat. 991.239.260), thalli from Stat. 261 (S.E. 516) are provided with a few multiporate conceptacles (Figure 59d), whereas the single specimen from Stat. 299 (S.E. 624) is sterile and its more robust thallus is provided with thicker lamellae showing limited superimposition. Anatomically, the syntypes in L fully agree with the lectotype in TRH. Multiporate conceptacles are 350–500 µm in external diameter and ~120 µm high (n: 3).

Unaware of Adey and Lebednik’s (1967) lectotypification, Womersley and Bailey (1970: 309) suggested as the lectotype a fertile specimen illustrated by Foslie from Stat. 261. This specimen is one of the two syntypes in L. Similarly, Verheij and Woelkerling (1992: 278) selected as the lectotype the material in L (L991.239-256), reversing the status for the TRH duplicate to “lectotype fragment.” However, the typification by Adey and Lebednik (1967) has priority and should be followed. It should be added that Adey and Lebednik (1967: 70) selected the type of “§ *M. crispescens*,” which under Article 7.3 (Turland et al. 2018) is the same type element as for its basionym *Lithothamnion simulans* f. *crispescens*, cited by Adey and Lebednik (1967) via the data for the relevant collection in TRH.

Species Description: Thalli are foliose, at least 4.3 cm in extent and 1 cm thick, developed via regular production of new lamellae in an unattached superimposed pattern (Figure 58b). Individual lamellae are 120–220 µm thick, undulate to flattened with lobate margins (Figure 59d). The thallus underside lacks excrescences and occasionally shows zonations with basal cells arranged in a rhomboid pattern (Figure 58h). The thallus organization is monopodial-dorsiventral with a polystromatic noncoaxial hypothallium, 60–180 µm thick, producing ± regularly coaxial regions or patches (Figures 58c,d, 59a) and supporting an ascending perithallium, 20–120 µm thick. Hypothallial cells are 8–25 × 3–10 µm (L × B), and perithallial cells are 5–10 × 3–5 µm (L × B). Descending hypothallial cells end in elongate subbasal cells, 6–23 × 6–7 µm (L × B), with wedge-shaped or flattened basal cells ~2 × 10 µm (L × B; Figures 58f,g, 60a). Subepithallial cells are elongate (to 15 µm long prior to division; Figures 57f,g, 58e). Epithallial cells are flattened, 2–3 × 6–10 µm (L × B; Figures 57g, 58e). Secondary pit connections and trichocytes are absent.

Male conceptacles were not seen. Carposporangial conceptacles are ± conical, 700–1,200 × 150–250 µm (D × H; n: 19), with chambers 440–650 × 140–220 µm (D × H; n: 7) and a roof 60–130 µm thick with a central ostiole. Carposporangia are produced laterally from the periphery of a flattened fertile floor (Figure 60b,c).

Multiporate conceptacles are hemispherical (wart-like), 345–1,070 × 150–260 µm (D × H; n: 36; Figures 59b, 60d).

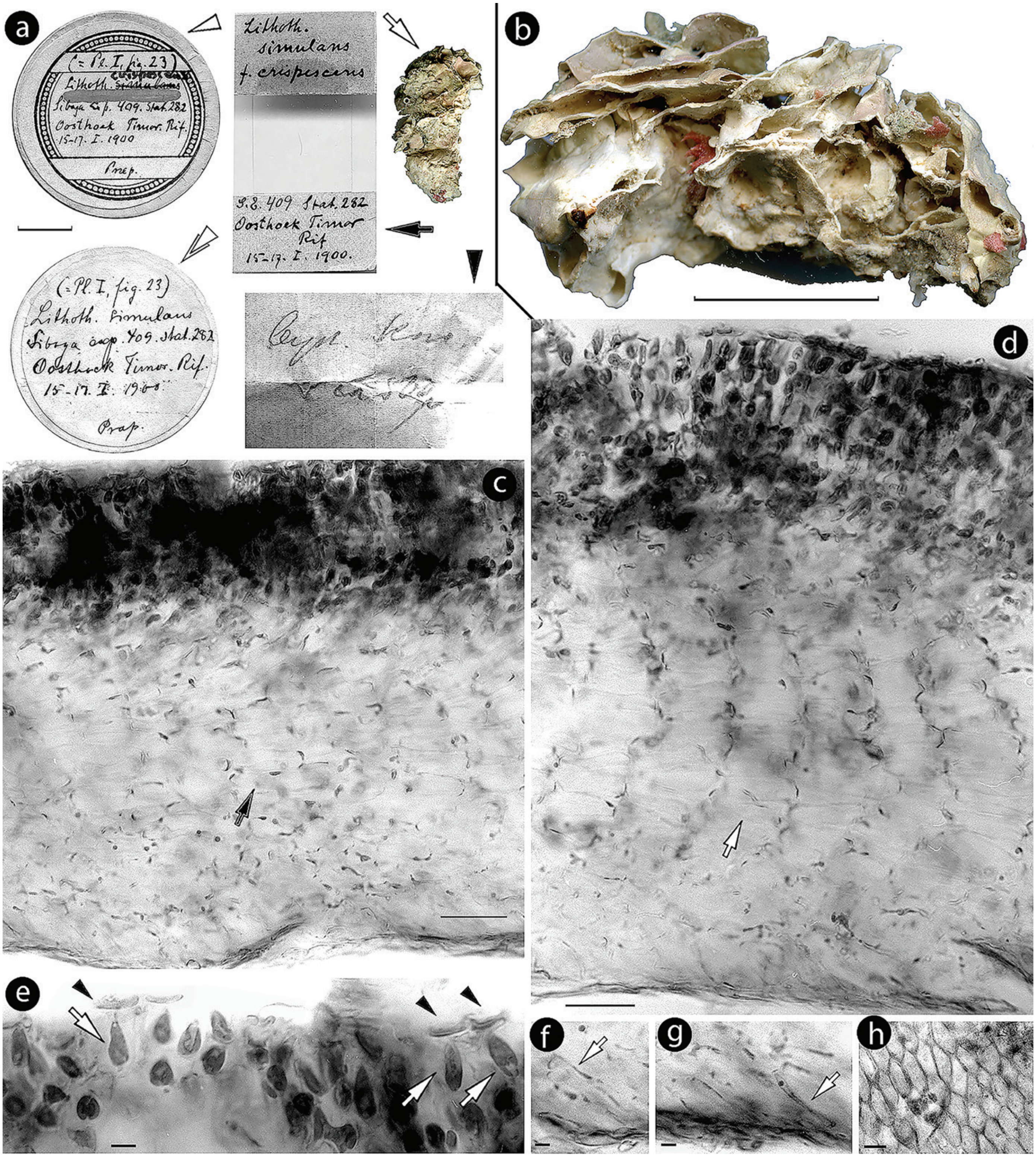

FIGURE 58. *Magnephycus simulans*: lectotype of *Lithothamnion simulans* f. *crispescens* in TRH (B18-2635). (**a**) The box, annotated both on the lid (arrowhead) and the back side (double arrowhead), including the lectotype (white arrow) and a note (black arrowhead). The slide (black arrow) is placed separately. Scale bar: 1 cm. (**b**) Side view of the lectotype specimen showing foliose habit with unattached superimposed growth. Scale bar: 1 cm. (**c, d**) Sections of the lectotype showing noncoaxial (black arrow) to coaxial growth (white arrow) in the hypothallium. Scale bars: 25 µm. (**e**) Section of the perithallium showing elongate subepithallial cells (arrows) supporting flattened epithallial cells (black arrowheads). Scale bar: 5 µm. (**f, g**) Sections at the base showing elongate subbasal cells. Scale bars: 5 µm. (**h**) View of a thallus from below showing basal hypothallial cells arranged in a rhomboid pattern. Scale bar: 5 µm.

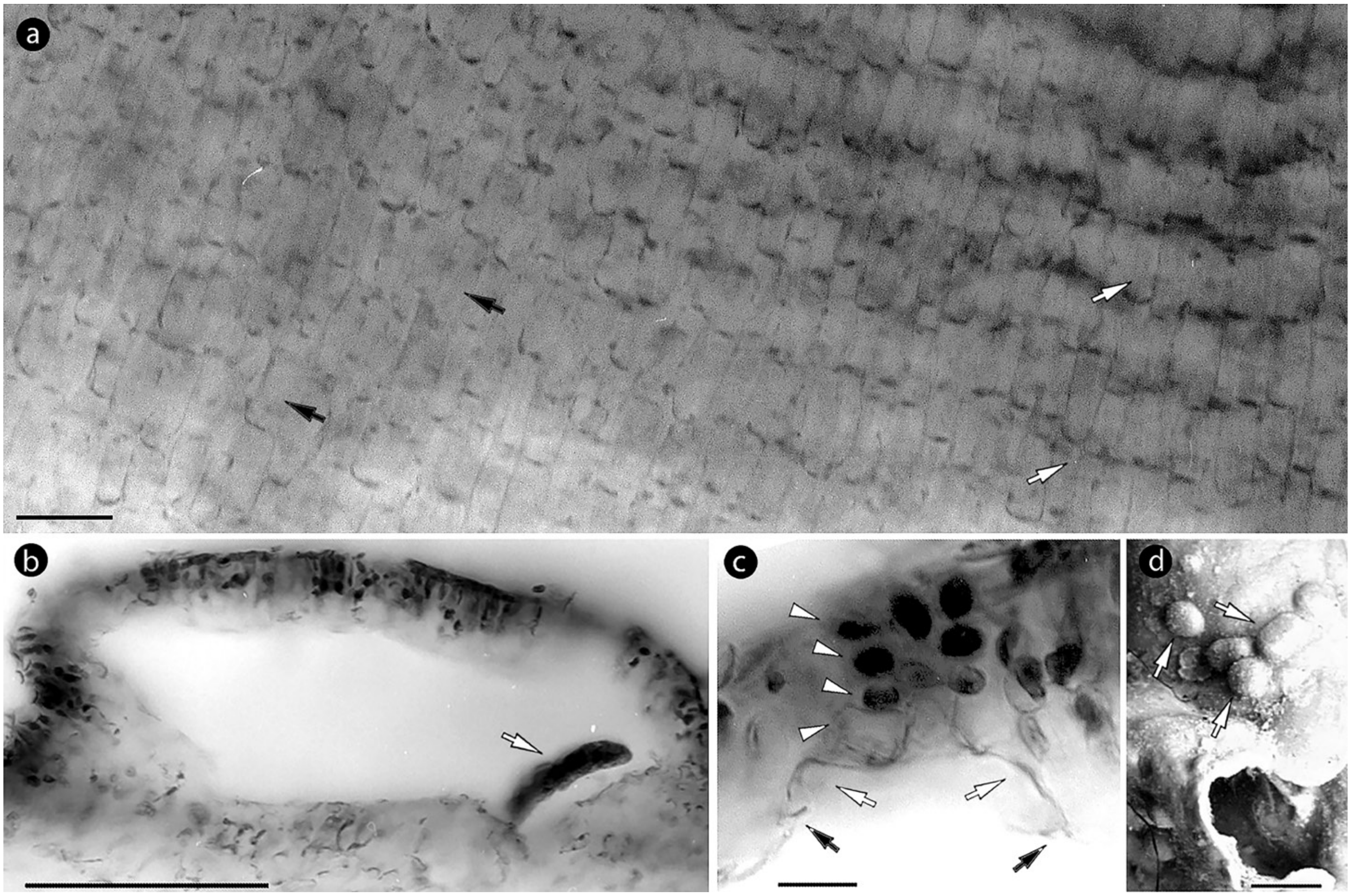

FIGURE 59. *Magnephycus simulans*: isolectotype (L0836984) and syntype (L0056935) of *Lithothamnion simulans* f. *crispescens*. (**a**) View of the hypothallium from below showing coaxial patches (white arrows) in a predominantly noncoaxial growth (black arrows; isolectotype in L, L0836984). Scale bar: 25 µm. (**b**) Section of a multiporate conceptacle showing a tetrasporangium (arrow; isolectotype in L, L0836984). Scale bar: 125 µm. (**c**) Section through a pore canal showing the widely expanded opening at the base (arrows) and 6-celled filaments lining the canal. Basal cells (black arrows) are slightly visible, whereas subbasal cells (white arrows) are distinctively elongate (isolectotype in L, L0836984). Scale bar: 10 µm. (**d**) Surface thallus view showing undulate margin and a few hemispherical multiporate conceptacles (arrows; syntype L0056935). Scale bar: 1 mm.

Chambers are 230–610 × 110–210 µm (D × H; n: 17), provided with a roof 40–62 µm thick that is composed of 6- or 7-celled filaments and perforated by up to 94 pores. Pore plates are 200–290 µm in diameter. Canals are pyriform, 7-11 µm in apical diameter and up to 25 µm in diameter at the base. Canals are surrounded by 5 to 7 rosette cells. Pore filaments lining the canals are 6- or 7-celled. Pore cells are similar to neighboring roof cells except for basal and subbasal cells, which are thinner and distinctively elongate (to 18 µm long; Figure 60e–k). Older conceptacles are covered by peripheral filaments that form a second roof (Figure 60l). Tetrasporangia are 80–130 × 30–40 µm (L × B; n: 11; Figure 60l). Embedded conceptacles are absent.

Comments: Although no male thalli were available for study, *Magnephycus simulans* displays all other characters found in species of the genus, in particular a foliose habit via unattached superimposed growth, flattened epithallial cells supported by elongate subepithallial cells, elongate subbasal hypothallial cells, thinner-elongate basal and subbasal pore cells in pyriform canals of multiporate conceptacles, hemispherical multiporate conceptacles with development of an imperforate second roof, and conical carposporangial conceptacles with a flattened floor and lateral production of carposporangia from the periphery of the fertile zone. *Magnephycus simulans* differs from the generitype *M. ornatus* in having larger multiporate and carposporangial conceptacles and ±regular patches of coaxial regions in the hypothallium. The presence of the latter character (illustrated by Foslie 1904c: text fig. 7A,B) was puzzling, until it was realized that its occurrence was variable within single specimens, including the lectotype

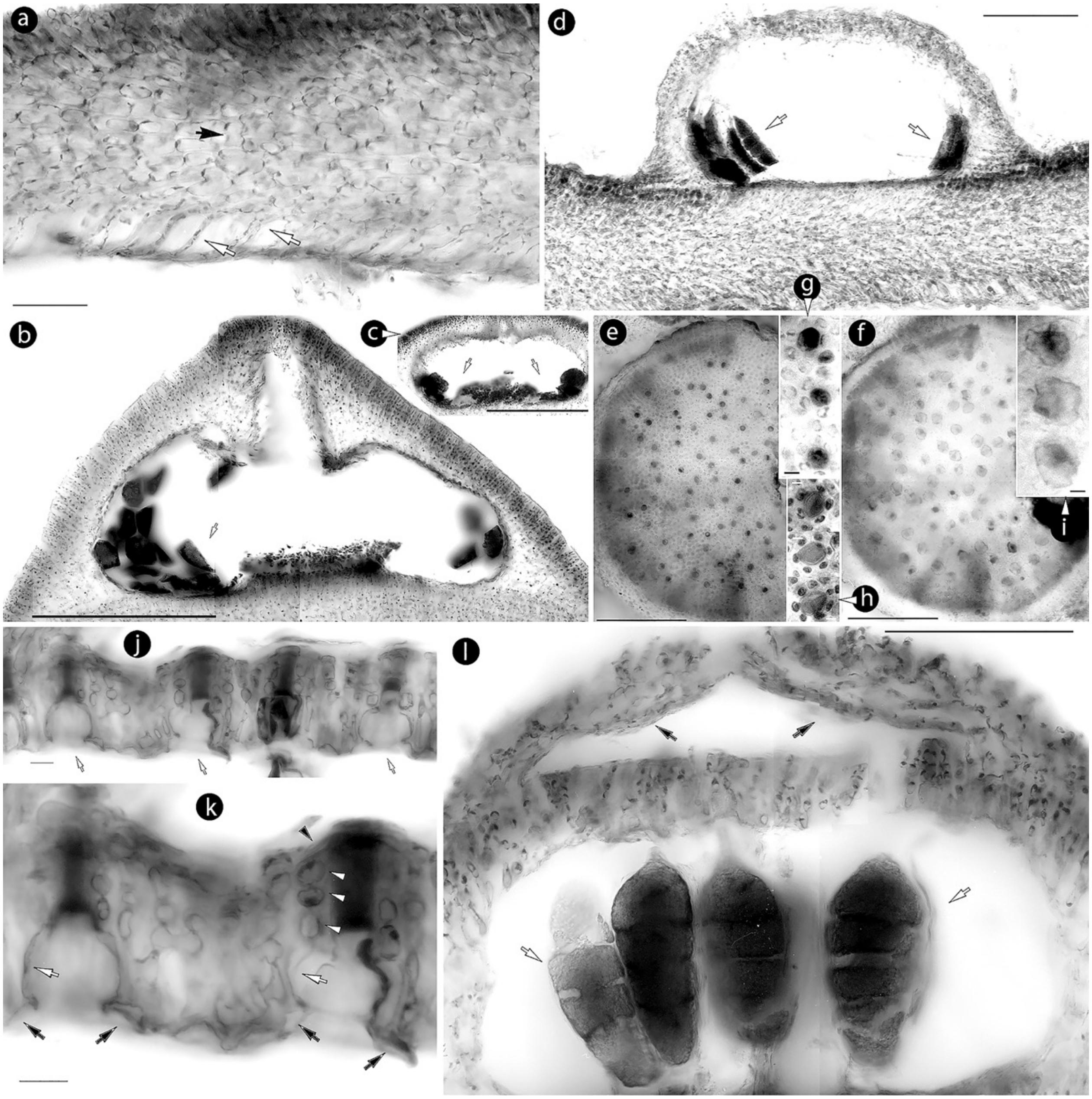

FIGURE 60. *Magnephycus simulans*: vegetative and reproductive structures. (**a**) Section showing a predominantly noncoaxial hypothallium (black arrow) with elongate subbasal hypothallial cells (white arrows; TRH, B18-2629). Scale bar: 25 µm. (**b, c**) Sections of carposporangial conceptacles showing production of carposporangia from the periphery (arrows) and a flattened floor (TRH, B18-2631 and B18-2628, respectively). Scale bars: 300 µm. (**d**) Section of a tetrasporangial conceptacle with typical hemispherical roof and tetrasporangia (arrows) in the chamber (TRH, B18-2633). Scale bar: 125 µm. (**e, f**) Views of a conceptacle roof, at two levels of focus, showing the wider canals at the base (arrowheads; TRH, B18-1730). Scale bars: 125 µm. (**g–i**) Three canals at three levels of focus (surface, middle, and base, respectively), showing 5 to 7 rosette cells and the wider openings at the base (TRH, B18-2631). Scale bars: 5 µm. (**j**) Section of a multiporate roof showing typical pyriform canals (arrows; BISHOP 686487). Scale bar: 10 µm. (**k**) Section of a multiporate roofs showing 6-celled filaments lining the pyriform canals. Note the elongate (white arrows) subbasal cells, the shorter curved basal cells (black arrows), and the terminal epithallial cell (black arrowhead; BISHOP 686487). Scale bar: 10 µm. (**l**) Section of a multiporate roof showing tetrasporangia (white arrows) and production of peripheral filaments covering and forming a second roof (black arrows; BISHOP 686487). Scale bar: 125 µm.

(Figure 58c,d) and the isolectotype (Figure 59a) of f. *crispescens* (see Lemoine 1966: 16, "*L'hypothalle est très variable . . . la disposition en rangées concentriques n'est pas constante*" [in translation, "the hypothallium is very variable . . . with coaxial (concentric) arches not constant"]). Hence, a coaxial hypothallium is not the dominant condition in the species, as also observed in the southern Australian *Magnephycus engelhartii* (Athanasiadis 2017a: figs. 3, 4, 34–37). The development of a second roof above multiporate conceptacles was also observed by Foslie (1904c: 18), who noted that "[conceptacles] are sometimes . . . overgrown by a new-formed layer of tissue extending itself over the roof before the latter gets dissolved." The latter character, in combination with larger conceptacles, presently distinguish the species from *M. engelhartii* (which lacks both).

Setchell (1926: 107, with reservation) reported *Lithothamnion simulans* from reefs in Tahiti, and Lemoine (in Børgesen 1954: 14) recorded *Mesophyllum crispescens* from Mauritius. Womersley and Bailey (1970: 309, as *Lithothamnium simulans* f. *crispescens*) reported the species from the Solomon Islands, and a study of a duplicate (UC1446578) confirmed their identification. Isaac (1971: 17) reported *Mesophyllum crispescens* from the Watamu Region and Blue Lagoon in Kenya (the record is included in Lawson 1980: 57), and Ballesteros and Afonso-Carillo (1995: 207, figs. 5–10) illustrated the species from Mauritius. However, the illustrations of the Mauritius material show a predominantly coaxial hypothallium, conspicuous trichocytes among epithallial cells, and ventral excrescences and most likely pertain to a species of *Neogoniolithon* Setch. et L. R. Mason since anatomically similar specimens with uniporate tetrasporangial conceptacles were identified in herbarium Jaasund from Tanzania (Jaasund no. 94, Masani, 18 January 1968, GB-0195189).

Gordon et al. (1976: pl. 2, figs. 1, 2) recorded *Mesophyllum mesomorphum* (Foslie) W. H. Adey from Guam (Mariana Islands), but their illustrations show a noncoaxial hypothallium and hemispherical tetrasporangial conceptacles, and therefore, the specimens most likely pertain to *Magnephycus simulans*. Other records of *M. mesomorphum* from the Indo-Pacific (see Silva et al. 1996: 258) may also pertain to *Magnephycus simulans*. Typical specimens have also been collected in the NW Hawaiian Islands (BISH686487; Figure 60j–l).

Oher collections of the species may exist in the herbarium of J. Schmidt in C since the original material of *L. simulans* was collected during the "Danish Siam Expedition 1899–1900" and the holotype is annotated "Museum botanicum Hauniense."

It should be added that the widely reported fossil *Lithothamnion crispithallus* Johnson (1957: 223; type locality: Saipan, Mariana Islands) is morphologically and anatomically similar to *Magnephycus simulans*.

Examination of TRH specimens from Seychelles (B18-2624, "*Lithoth. Simulans*") did not provide sufficient evidence to confirm Foslie's identification, and the TRH material from the Chagos Islands (B18-2623, "*L. simulans*") and Seychelles (B18-2625, "*L. simulans*") was found to possess flared epithallial cells and was provisionally referred to the genus *Lithothamnion*.

***Mastophoropsis* Woelk.**

Mastophoropsis Woelk. 1978: 210 (type: *M. canaliculata*).

***Mastophoropsis canaliculata* (Harv.) Woelk.**

FIGURES 61, 62

Mastophoropsis canaliculata (Harv.) Woelk. 1978: 210.
Basionym: Mastophora canaliculata Harv. 1860: 310.
Homotypic Synonym: *Metamastophora canaliculata* (Harv.) Setch. 1943: 132.

Type Locality: Tasmania, southern Australia.

Lectotype: In TCD (unnumbered), illustrated in Woelkerling (1978: fig. 1).

Syntypes: In TCD (unnumbered; Woelkerling 1978: 211).

Material Examined: South Australia: Mac Donnells Bay: "Algae Muellerianae, curante J.G. Agardh distributae, Mastophora hypoleuca H and W. Mac Donnells Bay. Recd Feb.1896" (BM 001216065, annotated by W. Woelkerling, *Mastophoropsis canaliculata*).

Habitat and Distribution: *Mastophoropsis canaliculata* is mainly recorded from drift specimens. Saxicolous thalli have been found in littoral cave pools and in the sublittoral, 10–18 m depth. It is reported from South Australia (Encounter Bay) to Victoria (Waterloo Bay) and Tasmania (Woelkerling 1996: 177).

Comments: The genus *Mastophoropsis* was established by Woelkerling (1978) based on the single species *Mastophora canaliculata*, previously accommodated within the genus *Metamastophora* Setch. (1943: 130, 132). Although the given generic name suggests a likeness to *Mastophora* Decne, *Mastophoropsis* exhibits an erect taeniform–stipitate habit that looks more like *Metamastophora* (both genera possessing an erect, to 15 cm high, taeniform thallus with a midrib). Despite Woelkerling's (1978: figs. 1–19; 1988: figs. 201–213; 1996: figs. 73, 74) several accounts, significant characters of *Mastophoropsis* remain unknown or poorly understood. The primary (hypothallial) growth of the thallus was not described, although sections of "branch tip[s] showing short initials" or "elongate initials" terminating a noncoaxial core of filaments were depicted (Woelkerling 1988: 182, figs. 204, 205). It was later concluded (without illustrations) that "cell elongation occur[s] mainly behind actively dividing subepithallial initials" (Woelkerling 1996: 175). The thallus organization was described as dorsiventral (Woelkerling 1978: 218; 1988: 180, figs. 208, 209; 1996: 175), with the illustrations showing a central core of (hypothallial) filaments supporting ascending and descending (perithallial) filaments ending in epithallial cells (Woelkerling 1988: figs. 204–207) and production of secondary perithallia (dorsally and ventrally) above the shown epithallia (Woelkerling 1988: figs. 208, 209). Cell fusions, both large and narrow ones, were located on vegetative cells of the internal core of filaments (Woelkerling 1988: figs. 206, 207). Trichocytes are apparently lacking.

Gametophytes are dioecious (Woelkerling 1996: 176), and conceptacles develop only dorsally. Male conceptacles were first described as comprising "simple" spermatangia developing from SMCs "situated on the floor, walls, and roof" (Woelkerling 1988: 183). This was later modified to "unbranched spermatangial filaments" (Woelkerling 1996: 176, fig. 74D, although the figure does not show any particular structure), but it was concluded (in the same paper) that "it is uncertain whether spermatangial filaments are simple or branched." Details of fertilization remain unknown, but carposporophytes develop lateral carposporangia from the periphery of gonimoblast filaments (Woelkerling 1988: figs. 210, 211, 1996: fig. 74C), as in members of the families Mesophyllaceae and Melobesiaceae (but not Lithothamnionaceae). A "small" fusion cell (Woelkerling 1988: fig. 211) was depicted, but its size was not different from cells of neighboring gonimoblast filaments. Carpogonial thalli, the mode of zygote transfer, and early postfertilization stages remain unknown.

Multiporate tetrasporangial conceptacles exhibit "pore canals lined by cells that are similar in size and shape to other roof cells" (Woelkerling 1988: fig. 213; 1996: 175, figs. 73B, 74A)—but see the character description below.

Characters related to thallus growth and organization, as well as features of tetrasporangial conceptacles, are here reviewed. In particular, primary (hypothallial) growth is restricted to the branch tips and occurs via anticlinal or subdichotomous divisions in terminal meristematic cells covered (protected) by a cuticle (Figure 61a–c). In contrast to all Mesophyllaceae (and probably Corallinales in general), apical growth is localized to branch tips and does not occur perimetrically (along the entire thallus margin). It is therefore necessary to obtain sections along the direction of the growth of the branch tips in order to observe the terminal (apical) meristem because sections below the branch tip will just reveal the terminal epithallial cells that cover most parts of the thallus. The hypothallium is noncoaxial, composed of at least 3 layers (Figure 61d), radiating near the branch tip, where at least 10 apical meristematic cells operate (Figure 61a). Hypothallial filaments become gradually displaced ventrally, dorsally, and even laterally (to the left and right), becoming perithallia, with their terminal meristematic cells becoming epithallial cells as in other Mesophyllaceae except Clathromorphoideae, in which the terminal [apical] meristem becomes gradually embedded. Transverse sections below the branch tips, perpendicular to the direction of primary (hypothallial) growth, show the presence of epithallial cells on all terminal parts of the young thallus (Figure 61c). Subepithallial initials are subsquarish but longer than cells below (Figure 61d).

Secondary, new tissues develop, first ventrally and then dorsally, above the epithallial cells and engulf the primary thallus, which remains distinct (Figure 61e,f). These dorsal and ventral secondary growths show differences in the shape and size of cells and cannot be regarded as homologous to the bilateral thallus organization of *Synarthrophyton-Amphithallia-Carlskottsbergia*. The growth mechanisms that underlie their development in *Mastophoropsis* are unknown, but Woelkerling's (1988: figs. 208, 209) illustrations (Figure 61e,f) suggest the presence of a pseudoparenchymatous tissue composed of filaments initiating from the epithallial cells. Fully grown thalli differ from all other members of Mesophyllaceae, possessing an erect habit composed of a holdfast and a stipe supporting a taeniform thallus, with ribbon-like branches dividing subdichotomously or irregularly (Woelkerling 1988: figs. 201–202).

Canals of tetrasporangial conceptacles (Figure 62a) are slightly wider at the base and lined by 5-celled unbranched pore filaments composed of normal roof cells along the apex. Basal and subbasal cells are, however, larger-longer (and hence differentiated; Figure 62b,c), showing an apparent similarity to those of *Ectocarpa capverdensis* (Figure 49f,g).

Mastophoropsis was not included in the phylogenetic analysis, pending studies of gametophytes. Its present position within Magnephyceae is supported by its thallus ontogeny, which shows the typical monopodial-dorsiventral organization with a polystromatic noncoaxial hypothallium. Terminal meristematic cells become displaced dorsally and ventrally to form epithallial cells (which occurs in Mesophyllaceae, except Clathromorphoideae). The bilateral development of secondary tissues in *Mastophoropsis* is not homologous to members of Amphithallieae (in which it occurs as a continuation of the primary growth), and a position in the Amphithallieae seems to be less likely. *Mastophoropsis* shares one more character with a member of Magnephyceae, namely, the development of larger-longer pore cells toward the canal base of multiporate conceptacles, which occurs in *Ectocarpa*. Given the conservative nature of canal differentiation in the Mesophyllaceae (Athanasiadis 2022), this is a puzzling similarity, particularly since these two genera show a disjunct distribution.

INCERTAE SEDIS MAGNEPHYCEAE

Leptophytum bornetii (Foslie) W. H. Adey

Leptophytum bornetii (Foslie) W. H. Adey 1970: 30.
Basionym: Lithothamnion bornetii Foslie 1899b: 9.

Type Locality: Cherbourg, northern France.

Holotype: In TRH (C18-3331) "§ — Fr., Cherbourg, 30.11.1853, ex herb.T-B" (Adey and Lebednik 1967: 83, "type material"), Chamberlain (1990: 181, "holotype"), Woelkerling (1993a: 41, "holotype," "includes slide 172"), Woelkerling et al. (2005: 466, "holotype . . . divided between PC and TRH"), illustrated by Chamberlain (1990: figs. 6–8).

Isotype: In PC (unnumbered), "algal fascicle 131" (Woelkerling and Lamy 1998: 332), illustrated by Chamberlain (1990: figs. 9–11).

Material Examined: British Isles: Rye Rocks: Skomer: higher rock pools, 7 November 1983, coll. Y. M. Chamberlain (BM box collection 1918, YMC 83/413); West Angle, Dyfed, north side of shore, 10 December 1984, coll. Y. M. Chamberlain (BM box collection 1980, YMC 84/417).

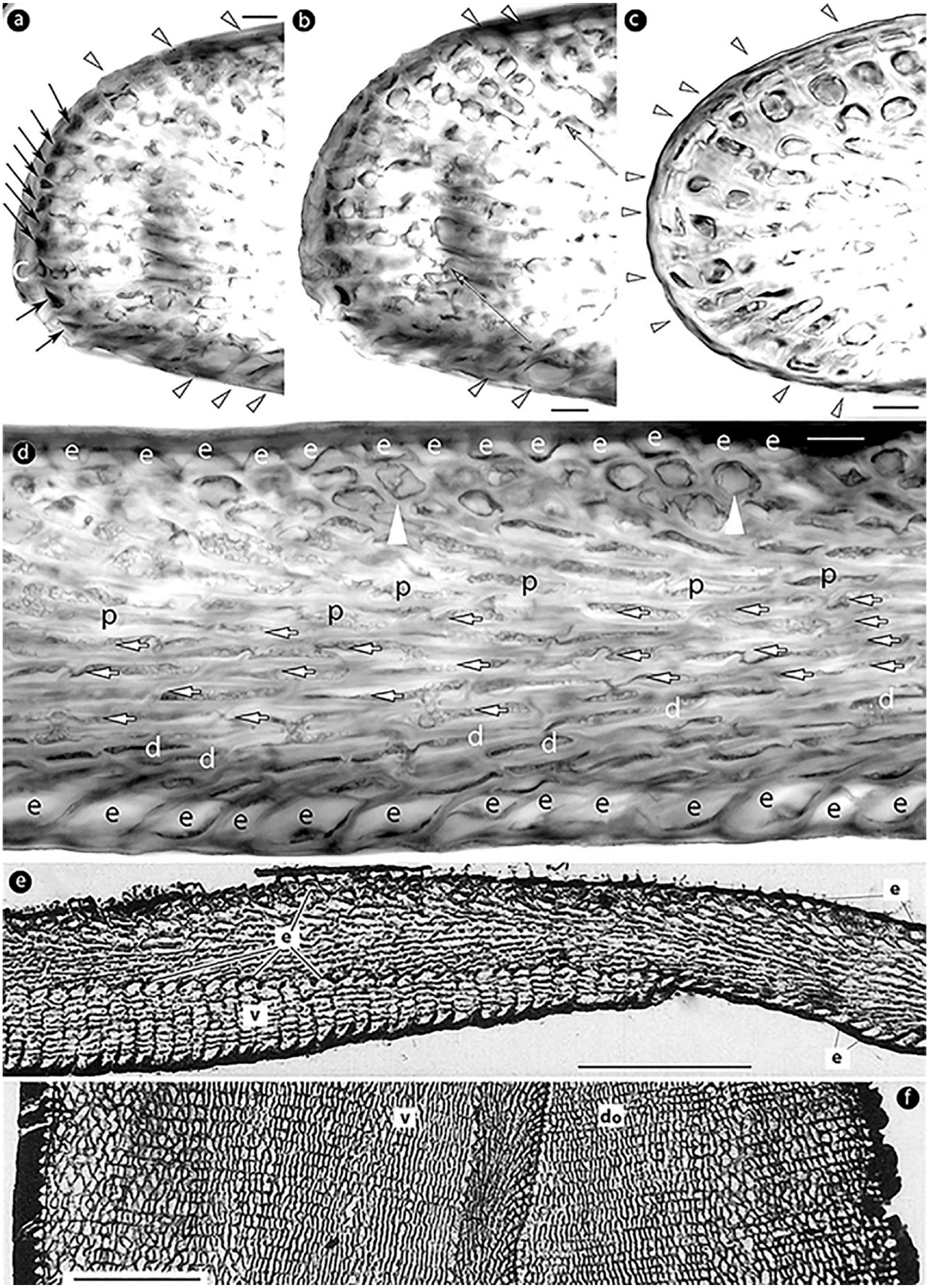
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FIGURE 61. (*Opposite*) *Mastophoropsis canaliculata*. (**a, b**) Sections along the growing margin, showing anticlinal (black arrows) and subdichotomous (white arrows) hypothallial divisions (BM 001216065). A cuticle covers the terminal meristematic cells. Scale bars: 10 µm. (**c**) Perpendicular section, showing epithallial cells (arrowheads) terminating lateral perithallial filaments, covered by a cuticle (BM 001216065). Scale bar: 10 µm. (**d**) Section along the frond, showing a core of at least three hypothallial layers supporting ascending or descending perithallial filaments terminating in epithallial cells (BM 001216065). Note the elongate subepithallial (arrowheads) cells. Scale bar: 10 µm. (**e, f**) Sections through fully grown thalli (along the growing frond) showing secondary outgrowths produced dorsally and ventrally. Note the original thallus that remains distinct as a core and that both tissues develop above the primary epithallia. Modified from Woelkerling (1988: figs. 208, 209). Scale bars: 100 µm. Abbreviations: c, cuticle; d, descending perithallial filament; do, dorsal; e, epithallial cell; p, ascending perithallial filament; v, ventral.

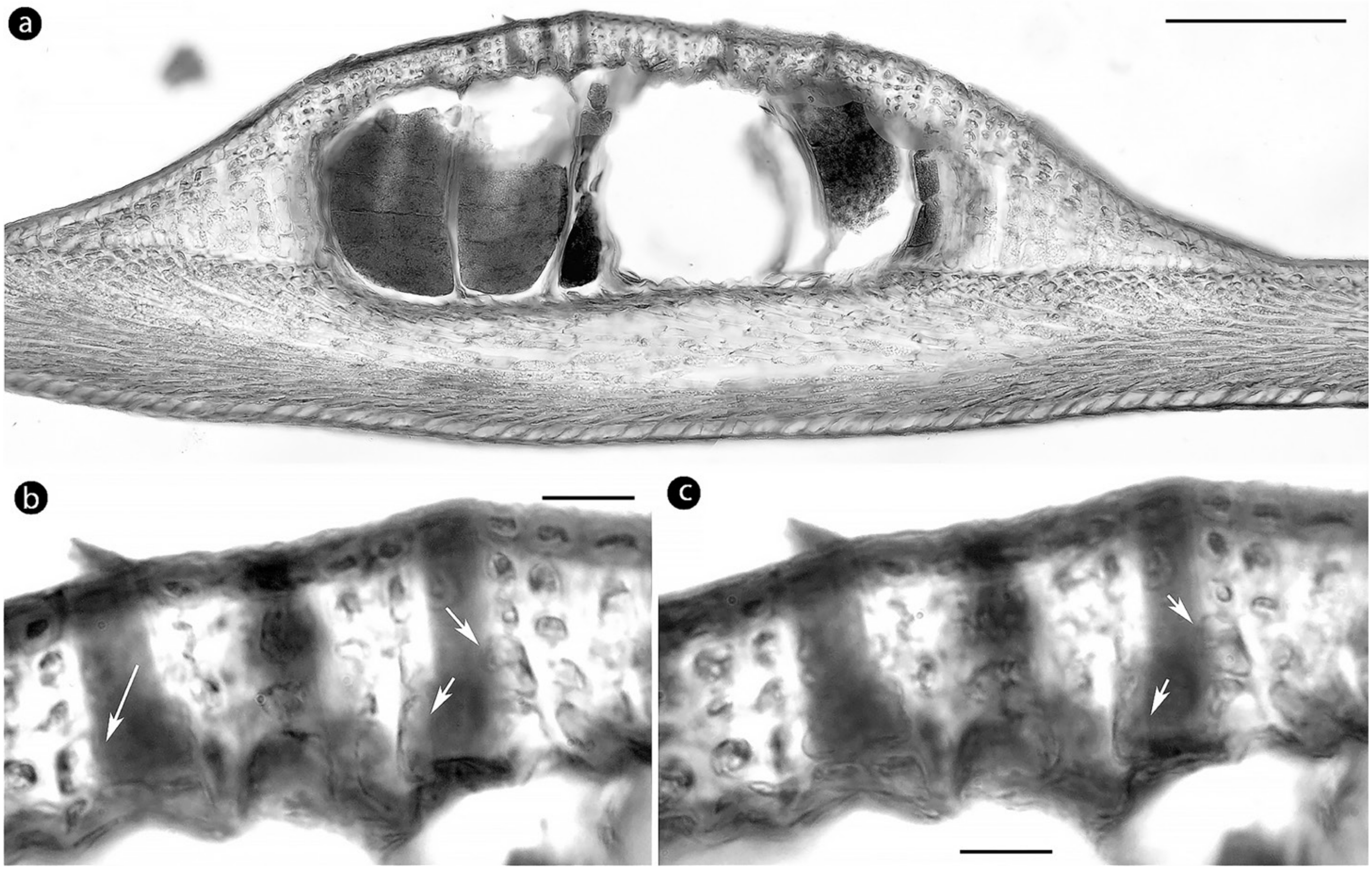

FIGURE 62. *Mastophoropsis canaliculata* (BM 001216065). (**a**) Section of tetrasporangial conceptacle. Scale bar: 100 µm. (**b, c**) Pore canals of multiporate roofs displaying larger basal and subbasal (arrows) cells lining the canals. Scale bars: 10 µm.

Habitat and Distribution: The species grows on rocks in lower littoral pools and in the upper sublittoral (1 m depth). It is confirmed by Chamberlain (1990) only from localities in southern England (i.e., south Devon, Pembroke, Ayrshire [Loch Sween], County Down) and France (Cherbourg). It is also reported from the Canaries (Lemoine in Børgesen 1929: 26) and the western Mediterranean basin (Hamel and Lemoine 1953: 92, “dragage par Feldmann, à Banyuls, par 25 m”).

Comments: The TRH holotype fragment is smaller than the isotype in PC, but it was first designated as the type by Adey and Lebednik (1967). Illustrations of both type elements were provided by Chamberlain (1990). The here studied material (YMC 83/413) confirmed that chambers of bisporangial conceptacles do not become embedded in the perithallium and are apparently shedding (Chamberlain and Irvine 1994: 168). Pore cells of multiporate conceptacles were distinctive in staining more strongly than other roof cells (as noted by Chamberlain 1990: 181) and were also thinner at the base of the canal but of similar length to contiguous roof cells. Canals could be enlarged at the base, but that was not seen constantly. No evidence of a coaxial hypothallium (or coaxial patches) was detected. The present observations confirm that *L. bornetii* differs from *L. foecundum* in lacking embedded conceptacles and in having multiporate conceptacles that are smaller (290–400 vs. 420–600 μm). Nevertheless, the lack of information from gametophytes, in combination with the presence of domed epithallial cells (Chamberlain 1990: 184–185), leaves open the possibility that this species belongs to *Phymatolithon*.

***Leptophytum coulmanicum* (Foslie) W. H. Adey**

Leptophytum coulmanicum (Foslie) W. H. Adey 1970: 30.

Basionym: Lithothamnion coulmanicum Foslie 1905a: 16 (repr. 2). Foslie (1907d: 1–2, text fig.).

Type Locality: Cape Wadsworth, Coulman Island, Ross Sea, Antarctica.

Type Material: In TRH (B2-1684), Printz (1929: pl. 2, figs. 8, 9), Adey and Lebednik (1967: 51, "type material," "§ Brit. Ant.Exp.'Discovery', Coulman Is., C.Wadsworth, 17.1.1902, LM2(8-9) [slides] 930, 931"), Woelkerling (1993a: 64, "holotype," "plants on two pieces of rock . . . do not . . . match those . . . in Printz," "collector not indicated"), Alongi et al. (2002: fig. 1, "holotype"), Woelkerling et al. (2005: 238, "holotype").

Syntypes: In BM (box 297), "two stones . . . one depicted in Printz . . . pl. 2, fig. 8" (Woelkerling and Lamy 1998: 338); in PC (unnumbered), "fragment 2 mm . . . from . . . BM" (Woelkerling and Lamy 1998: 338).

Comments: The Norwegian protologue (Foslie 1905a: 16) reads (in translation), *Lithothamnion coulmanicum* Fosl. mscr.- Thallus forming crusts with smooth surface on stone and expands with a thickness of c. 800 μm. [Bi]sporangial conceptacles are little prominent, almost discoid and 300-400 μm in diameter seen from above. Bisporangia. Coulman Island in the southern Antarctic Sea. The English expedition "Discovery."

In a later account, Foslie (1907d: 1–2, text fig.) gave a more complete description, adding that older crusts are easily detached and the thallus thickness does not exceed 800 μm, usually being less than or about 300 μm. Thalli with crenulate or irregular margins could envelop their substrata and become confluent or occasionally develop slightly elevated ridges. No excrescences occur, but the surface can be uneven following the substratum underneath. A vertical section shows the hypothallium as poorly developed, and the lower layers do not turn down markedly (see Alongi et al. 2002: fig. 5). Hypothallial cells are 12–18 × 4–7 μm. The perithallium is not stratified, and the cells are partly squarish or roundish (5–8 μm in diameter), partly and more frequently elongate, 8–12 × 6–8 μm [L x B]. Carposporangial conceptacles are hemispherical-conical, 300–400 μm in diameter (seen in a single specimen). Multiporate conceptacles are inconspicuous and occur either scattered or crowded in groups, having a convex roof. Older conceptacles become disc-shaped, 300–400 μm in diameter. The roof is perforated by 30–40 muciferous canals. Bisporangia are 20–120 × 40–50 μm. Most conceptacles are dissolved, leaving a shallow crater, later filled in by new tissue. Overgrown conceptacles in the thicker part of a crust were seen once. The entire material was 16 pebbles with thalli collected from a depth of ~32 m (18 fathoms), off Cape Wadsworth on Coulman Island near South Victoria Land, about 73°30′S, 170°W.

Woelkerling (1993) noted that the "holotype [in TRH] consists of plants on two pieces of rock [which] do not appear to match those depicted in Printz (1929)," and later, Woelkerling and Lamy (1998: 338) reported that one of the specimens illustrated by Printz (1929: pl. 2, fig. 8) was at BM. Hence, a specimen from the TRH material remains to be selected as the lectotype, and all other specimens and fragments (in TRH, BM, PC) should be syntypes (collectively, thalli attached to 16 pebbles).

Lemoine (1913: 13–14) examined one original specimen at the BM and gave the following account (translation follows original), correcting Foslie's description in several points:

> *Cette espèce, extrêmement intéressante, puisque c'est la seule qu'on ait découverte jusqu'ici dans la région de la Terre Sud-Victoria, forme un revêtement continu sur les cailloux; l'épaisseur de la croûte est extrêmement faible, 50 à 120 μ dans l'échantillon que j'ai eu entre les mains, 300 μ dans ceux que M. Foslie a étudiés. L'algue est tout à fait adhérente an substratum, et il est très difficile d'en détacher des fragments pour l'étude. Les croûtes jeunes ont une forme irrégulière; plus tard, elles entourent presque complètement le substratum; on observe quelquefois à leur surface des zones concentriques peu distinctes. La surface généralement très unie devient légèrement rugueuse et un peu irrégulière dans les spécimens âgés.* [This species, extremely interesting, since it is the only one discovered so far in this region of South Victoria Land, forms a continuous cover on pebbles; the thickness of the crust is extremely thin, 50–120 μm in the specimen I have on hand, 300 μm in those examined by Foslie. The alga adheres entirely on the substratum, and it is very difficult to remove fragments for a study. The young crusts show an irregular form, gradually almost completely engulfing the pebbles; sometimes one vaguely observes concentric zones on their surface. The surface is generally plain becoming slightly uneven and irregular in older specimens.]
>
> *Structure anatomique. — L' hypothalle est formé de files très serrées, dont les cellules sont étroites et assez longues; elles mesurent 22 à 40 μ de longueur, en général 22 à 30 μ de long et 4 à 5 μ de large. Je crois qu'il faut rectifier les dimensions que M. Foslie avait indiquées pour l'hypolhalle (12 à 18 μ.) et qui sont beaucoup trop faibles. Le perithalle, peu épais dans les échantillons très*

minces que j'ai étudiés, est formé de cellules de 8 à 12 μ. de longueur et 6 à 8 μ de largeur.

[Anatomy. — In the hypothallium the filaments are compressed, composed of thin and rather long cells, 22–30(40) × 4–5 μm [L × B]. I believe we have to rectify the measurements given by Foslie for the hypothallium (12–18 μm), which are much too small. The perithallium is slightly raised in the smaller specimens that I examined, forming cells 8–12 × 6–8 μm [L × B].]

Organes reproducteurs. — Les conceptacles à sporanges, convexes, peu proéminents, mesurent 300 à 400 μ.; leur toit est traversé par 30 à 40 canaux. Les conceptacles à cystocarps, de forme légèrement conique, mesurent 300 à 400 μ. comme les précédents. Les spores (bispores) mesurent 90 à 120 μ x 40 à 50 μ (Foslie).

[Reproduction. — [Tetra- or bi]sporangial conceptacles convex, not very prominent, 300–400 μm in diameter; their roof is perforated by 30–40 canals. Carposporangial conceptacles are slightly conical, 300–400 μm in diameter, similar to the sporangial ones. Bisporangia measure 90–120 × 40–50 μm [L × B] (according to Foslie).]

Comparaisons et differences. — La croûte stérile ressemblerait à celle du Lithoph. subantarcticum. *On voit par le' tableau (p.49 à 51) que les deux espèces sont très éloignées d'une l'autre.*

[Comparisons and differences. — Sterile crusts resemble those of *Lithophyllum subantarcticum* [*Clathromorphum lemoineanum*]. The two species, however, occupy remote positions on the key (Lemoine 1913: 49–51).]

Habitat. — L. coulmanicum a été rapporté de l'île Coulman, près la Terre Sud-Victoria, par l'expédition anglaise « The Discovery ». Elle y vivait à une profondeur de 33 mètres. J'ai étudié cette espèce sur un des échantillons types conservés au British Muséum.

[Habitat. — *L. coulmanicum* was reported from Coulman Island, near South Victoria Land, by the English Expedition "Discovery." It grows at a depth of 33 m. I studied this species from one type specimen conserved in the British Museum.]

Alongi et al. (2002: figs. 1–8) examined the TRH material and reported thalli 600–800 μm thick (but their illustration shows a thallus to 100 μm thick, in agreement with Lemoine; Alongi et al. 2002: fig. 5), adhering strongly to the substratum and exhibiting monopodial-dorsiventral organization with a smooth surface lacking protuberances. Subepithallial cells were isodiametric, supporting single, rounded to flattened (but not flared) epithallial cells. Multiporate conceptacles, apparently lacking a rim, developed chambers 240–280 × 140–180 μm (D × H), with a convex roof consisting of 5- or 6-celled filaments. Older conceptacles were embedded in the thallus. Alongi et al. (2002) concluded that *L. coulmanicum* was conspecific with the Arctic *Leptophytum foecundum*, but the Antarctic material described by Foslie (1907d), Lemoine (1913), and Alongi et al. (2002: 143, figs. 1–8) differs at least in lacking rimmed multiporate conceptacles and in having smaller conceptacle chambers (i.e., 240–280 μm in diameter vs. 245–415 μm in *L. foecundum*; Athanasiadis 2007a: table 1). Bisporangial thalli were recorded from Macquire Island (Zaneveld and Sanford 1980: 224), but the species was not included in the marine flora of this island (Ricker 1987). Hommersand et al. (2009: 512) followed Alongi et al. (2002) in listing "*Phymatolithon foecundum*" as the only species of Corallinaceae from the Ross Sea.

Leptophytum elatum Y. M. Chamb.

Leptophytum elatum Y. M. Chamb. 1990: 189, figs. 4, 25, 28, 33, 34, 36, 38, 40–44.

Type Locality: Lower littoral, on rock, West Angle, Pembroke, England.

Holotype: In BM (unnumbered, UMC 84/83, 18 February 1984, coll. Y. M. Chamberlain), illustrated by Chamberlain (1990: fig. 40).

Habitat and Distribution: This is an endemic species growing on rock or on shell debris in low intertidal pools and in the sublittoral zone. Tetrasporangial specimens were collected between December and February, and spermatangial thalli were collected in January.

Comments: Unfortunately, carposporangial thalli that would definitely settle the systematic position of this species remain unknown, and the occasional presence of "domed epithallial cells" (Chamberlain 1990: 192) in combination with the distinctive dendroid spermatangia (Chamberlain 1990: fig. 36; Chamberlain and Irvine 1994: fig. 81C) suggest an affiliation with either *Leptophytum* or *Phymatolithon.*

Leptophytum ferox (Foslie) Y. M. Chamb. et D. W. Keats

FIGURE 63

Leptophytum ferox (Foslie) Y. M. Chamb. et D. W. Keats 1994: 119, figs. 77–87.

Basionym: Lithothamnion ferox Foslie 1907b: 7.

Homotypic Synonyms: Mesophyllum ferox (Foslie) W. H. Adey 1970: 24.

Phymatolithon ferox (Foslie) G. W. Maneveldt et E. Van der Merwe in E. Van der Merwe and Maneveldt 2014: 183, figs. 22–38, 76 [excluding specimens later referred to *Phymatolithopsis prolixa* by Jeong et al. 2022].

Type Locality: Natal, South Africa.

Holotype: In TRH (B15-2357), Printz (1929: pl. 4, fig. 9), Adey and Lebednik (1967: 64, "type material," "§ W.v.Bosse, S.Africa, Natal, LM4(9) [slide] 706"), Woelkerling (1993a: 92, "holotype"), Woelkerling et al. (2005: 315, "holotype"), Chamberlain and Keats (1994: figs. 77–87, "now in two pieces," tetrasporophyte).

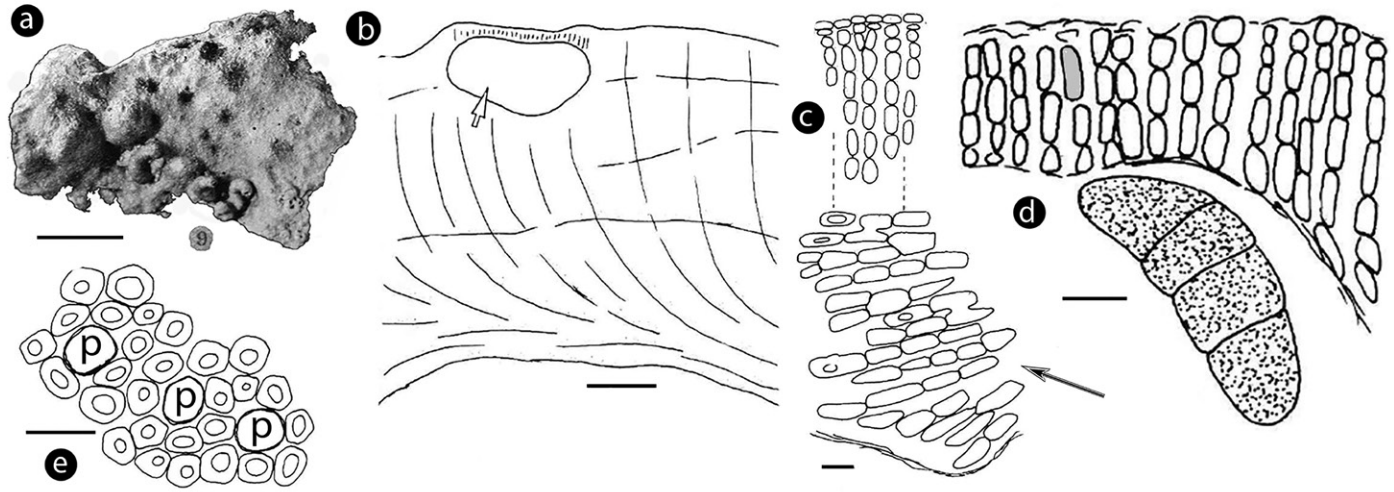

FIGURE 63. *Leptophytum ferox*. Holotype of *Lithothamnion ferox* (TRH, B15-2357). (**a**) Holotype as illustrated by Printz (1929: pl. 4, fig. 9). Scale bar: 1 cm. (**b, c**) Drawings of sections showing a dorsiventral thallus organization with noncoaxial hypothallium (black arrow in (c)) and a multiporate conceptacle (white arrow in (b)). Modified from Chamberlain and Keats (1994: figs. 84, 85). Scale bars: 100, 10 µm, respectively. (**d**) Conceptacle roof showing elongate (shaded) subepithallial cell and a tetrasporangium. Modified from Chamberlain and Keats (1994: fig. 86). Scale bar: 10 µm. (**e**) Surface view of pore canals surrounded by 6 to 8 rosette cells. Modified from Chamberlain and Keats (1994: fig. 87). Scale bar: 10 µm. Abbreviation: p, pore canal.

Comments: The Norwegian protologue (Foslie 1907b: 7) reads (in translation),

> *Lithothamnion ferox* Fosl.mscr. Encrusting, 2–7 mm thick, with few, irregular warty outgrowths, 2–5 mm in diameter; [tetra]sporangial conceptacles little or half projecting, convex or somewhat flattened, 200–300 µm in diameter; tetrasporangia 80–130 µm long and 30–40 µm broad. The alga grows on rocks, and new superimposed encrusting lamellae develop on the primary one. The unevenness of the surface is partly due to the incorporation of foreign bodies. In vertical sections the hypothallium is coaxial, but does not form arches. It is composed of cells 11–25 µm long and 7–11 µm broad. Perithallial cells are partly sub square, 6–7 µm in diameter, partly and usually vertically elongate, 7–11(13) µm long and 6–7 µm broad. In habit it resembles a large *Phymatolithon polymorphum* [*Ph. purpueum*]. Structurally, its conceptacles stand close to *Lithoth. speciosum* [*Phragmope discrepans*]; on the other hand it seems also to be related to large forms of *L. pacificum* [*Lithothamnion*] - Natal (A. Weber-van Bosse).

Printz (1929: pl. 4, fig. 9) illustrated a single specimen (the holotype) lacking apparent protuberances (Figure 63a), and Chamberlain and Keats (1994: figs. 77–87) described its habit as "flat to lumpy . . . lack[ing] protuberances." The study of the holotype by Chamberlain and Keats further shows that the thallus organization is monopodial-dorsiventral with a polystromatic noncoaxial hypothallium, lacking embedded conceptacles (Figure 63b,c). Tetrasporangial conceptacles have a flattened roof and a 4-celled thick pore plate (Figure 63d) and house tetraspores (Chamberlain and Keats 1994: figs. 82, 86). Canals are ~8 µm in diameter, surrounded by 6 to 8 rosette cells (Figure 63e). The canal structure shows pore cells that are similar in size at the top, but basal (and subbasal?) cells seem to be lacking (Chamberlain and Keats 1994: fig. 83). The illustrated tetrasporangial chambers are ~220 × 100–120 µm (D × H). Subepithallial cells are short and isodiametric, but at least those on the tetrasporangial roof appear to be partly elongate (Figure 63d). Epithallial cells are flattened (neither flared nor domed; Figure 63c).

There is no later account of this species because Van der Merwe and Maneveldt's (2014) record was later referred to *Phymatolithopsis prolixa* (Jeong et al. 2022: 165), whereas herbarium specimens identified as *Lithothamnion ferox* by Chamberlain and Keats (1994) exhibit apparent erect protuberances and are here described and cited with reservation under *Phymatolithopsis prolixa* (incertae sedis; see species account below).

Leptophytum ferox is here placed in the Magnephyceae with reservation, following Chamberlain and Keats's account of the holotype. Still, it should be mentioned that the protologue described the presence of a coaxial hypothallium lacking arches(?) and the presence of superimposed lamellae, both features not shown or commented on by Chamberlain and Keats (1994: figs. 77–87), requiring a reinvestigation of the original material in TRH.

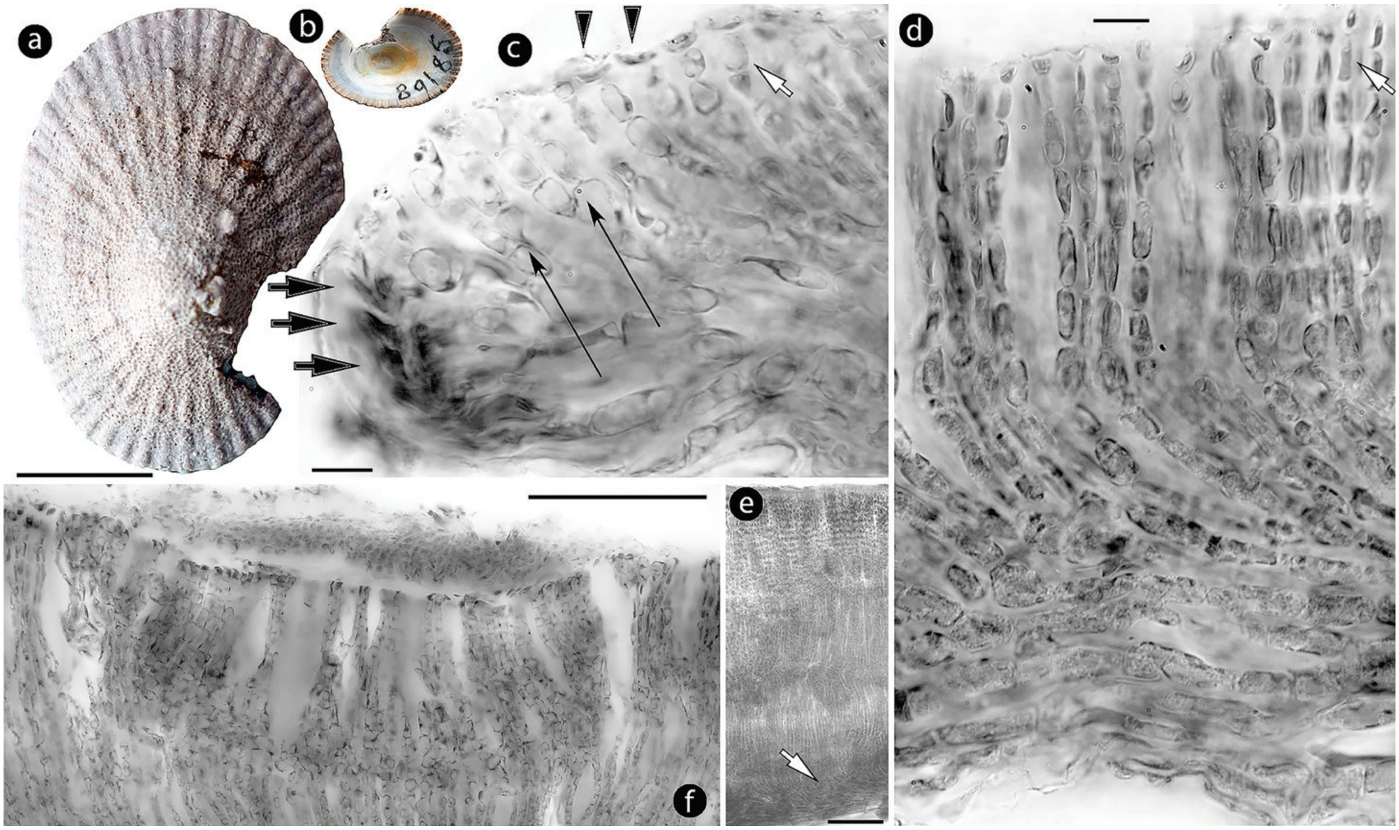

FIGURE 64. *Leptophytum foveatum*: vegetative structures (D3-YMC 89/85, except D4-YMC 91/243 in (e)). (**a, b**) Thallus on *Scutellastra*. Scale bar: 1 cm (no scale in b). (**c**) Section at the margin showing the hypothallium displaying terminal meristematic cells (short black arrows), subdichotomous divisions (long black arrows), and epithallial cells (arrowheads). Note the divided subepithallial cell (white arrow). Scale bar: 10 µm. (**d, e**) Thallus sections showing the basal hypothallium (arrow in e) supporting nearly vertical perithallial filaments. Note the elongate subepithallial cell (arrow in d). Scale bar: 10 µm. (**f**) Old conceptacle chamber refilled with perithallial filaments. Scale bar: 100 µm.

Leptophytum foveatum Y. M. Chamb. et D. W. Keats

FIGURES 64–66

Leptophytum foveatum Y. M. Chamb. et D. W. Keats 1994: 115–119, figs. 32–48.

Homotypic Synonym: *Phymatolithon foveatum* (Y. M. Chamb. et D. W. Keats) G. W. Maneveldt et E. Van der Merwe in E. Van der Merwe and Maneveldt (2014: 183).

Type Locality: Infralittoral, on rock and encircling *Dendropoma corallinaceus* (Tomlin), Yzerfontein, west coast of Western Cape Province, South Africa.

Holotype: In L (993.052 539, YMC and DWK 91/249, 24 November 1991, coll. Y. M. Chamberlain and D. W. Keats), illustrated by Chamberlain and Keats (1994: fig. 32).

Material Examined: Namibia: 8 km south of Torra Bay: intertidal on *Patella* and *Chthamalus*, 14 September 1989, coll. Rob Anderson (herb. Athanas. D3-YMC 89/85, cited in Chamberlain and Keats 1994); Yzerfontein, west coast of Western Cape Province, at low water spring tide and below, on rocks and shells, on *Scutellastra* (*Patella*) *argenvillei*, 24 November 1991, coll. YMC and DWK (herb. Athanas. D4-YMC 91/243, topotype cited in Chamberlain and Keats 1994, as YMC and DWK 91/243).

Habitat and Distribution: The species forms thin, flat, adherent thalli on rock surfaces and shells, in the lower littoral and sublittoral, often grazed by *Patella argenvillei* Krauss. Fertile thalli were collected in July, October, November, and December. It is recorded from South Africa (western Cape Province) and Namibia (Chamberlain and Keats 1994).

Comments: Two collections were examined. Both are cited in the protologue, one being a topotype. The study confirmed the data of the protologue and added several new characters (in ***bold italics*** below). In particular, thalli on small shells adhere strongly (Figure 64a,b). The growth is typical monopodial-dorsiventral with a poorly developed polystromatic hypothallium (~1/6 of the thallus) displaying terminal meristematic (hypothallial) cells (Figure 64c–e). Subdichotomous divisions add to the thallus thickness and gradually displace hypothallial filaments dorsally to form the perithallium. Displaced terminal meristematic cells become epithallial cells (Figure 64c). ***Subepithallial cells are slightly longer*** than cells below (during putative division), supporting single flattened epithallial cells (Figure 64c,d). Older conceptacle chambers can be filled in with perithallial filaments (Figure 64f).

Gametophytes are presumably dioecious (males not seen). Carpogonial and carposporangial conceptacles are ± flush with the thallus surface and develop carpogonial branches across the entire floor (Figure 65a). Carpogonial branches are ***3-celled***, composed of the carpogonium, the hypogynous, and the supporting cell (Figure 65b–d). A ***sterile*** cell may be present on the hypogynous cell (Figure 65d). ***Basal*** cells may stain similarly, but following fertilization and gonimoblast development, they remain intact, being attached to the vegetative floor (Figure 65g). Postfertilization stages involve the development of a ***fusion cell***, comprising at least 2 to 6 supporting cells and possibly 1 or 2 hypogynous cells (Figure 65g,h). Development of lateral carposporangia occurs from the periphery of the fertile zone (Figure 65e). Older carposporangial conceptacles become embedded in the thallus and are occasionally filled in with perithallial cells (Figure 65i).

Tetrasporangial conceptacles protrude very slightly (Figure 66a–d). The roof is convex, becoming sunken, as conceptacles tend to become embedded (Figure 66b–d). A thin ***second roof*** was seen in one section, covering an empty multiporate conceptacle (Figure 66c), but its ontogeny was not clarified. Canals are straight and provided with ***thinner–wider pore cells along the base*** (i.e., basal, subbasal, and occasionally third cells; Figure 66e–j).

Chamberlain and Keats (1994) considered this species to be closely related to *Leptophytum acervatum* (herein *Leptothallia acervata*), differing in (1) their covering large rock surfaces and shells (not pebbles), (2) the development of perithallial growth zones (Figure 66e), (3) their having longer hypothallial and perithallial cells (vs. ± isodiametric in *L. acervata*), and (4) their having a thicker multiporate roof, that is, 4- or 5 (6)-celled (vs. 3- or 4-celled in *L. acervata*). These differences were confirmed, but we do not consider *Leptophytum foveatum* to be closely related to *Leptothallia acervata* (or to *Phymatolithopsis repanda*) since it develops a conspicuous fusion cell and longer canals of multiporate roofs with thinner–wider pore cells along nearly half the canal length (both characters are, instead, in agreement with *Leptophytum laeve*). Furthermore, in a phylogenetic analysis of the nSSU gene, Bailey and Chapman (1996: fig. 1) reported the relationship *Leptothallia acervata* (*Clathromorphum compactum* (*Leptophytum foveatum*, "*Mesophyllum engelhartii*" from South Africa)), which suggests a remote genetic distance between *Leptothallia acervata* and *Leptophytum foveatum*. We have concluded that *Leptophytum foveatum* indeed shows the reproductive features of *Leptophytum* but differs in possessing elongate subepithallial initials.

Van der Merwe and Maneveldt (2014) reported solitary trichocytes and males in new collections, the former developing among epithallial cells (see their fig. 41) and the latter said to be both simple and dendroid in structure, both characters occurring in species of *Leptophytum*.

Leptophytum microsporum (Foslie) Athanas. et W. H. Adey

Leptophytum microsporum (Foslie) Athanas. et W. H. Adey 2006: 101, figs. 123–141.

Basionym: Lithothamnion californicum Foslie f. *microsporum* Foslie 1902b: 5–6, "*microspora*."

Homotypic Synonym: *Lithothamnion microsporum* (Foslie) Foslie in Printz 1929: 51.

Type Locality: Littoral, on pebbles and sandstone, Pacific Beach near San Diego, California, USA.

Lectotype: In TRH (B2-1716, 1901, coll. Mrs. E. Snyder, communicated by F. S. Collins, includes Foslie slide 583 and Lebednik slides 583 1 and 2), designated by Athanasiadis and Adey (2006: fig. 123).

Syntypes: In TRH (B2-1715, B2-1717, B2-1718; Athanasiadis and Adey 2006).

Habitat and Distribution: The species grows on pebbles, sandstone, and encrusting coralline algae in the littoral and sublittoral zones to at least 36 m depth. It is recorded from California and Baja California. Confirmed between Santa Catalina Island (Southern California) and Punta Entrada (Isla Magdalena, Baja California), including Pacific Beach (San Diego), La Jolla, Isla Guadalupe, and Punta Pequeña (Bahía San Juánico, Baja California; Athanasiadis and Adey 2006).

Comments: The lectotype grows on a pebble (broken into five pieces; Athanasiadis and Adey 2006: fig. 123). The largest thallus reaches ~3.3 cm in diameter. The transfer to *Leptophytum* was motivated by the presence of four characters: (1) patches of coaxial growth in a predominantly noncoaxial hypothallium, (2) flattened (and not domed or flared) epithallial cells, (3) subepithallial cells ± isodiametric and similar to or smaller in size than cells below, and (4) specialized (thinner–wider) pore cells at the base of canals of multiporate roofs (Athanasiadis and Adey 2006). However, in the absence of information from gametophytes, the generic position remains tentative, given that characters 3 and 4 have also been reported in *Phymatolithon lenormandii* (Chamberlain and Irvine 1994: fig. 74; Athanasiadis 2006: figs. 142–145). Athanasiadis and Adey (2006) examined six Dawson collections (LAM) referred to *Lithothamnion lenormandii* and identified material of *Leptophytum microsporum* in five of them. The study of another Dawson collection referred to *Lithothamnion lenormandii* (US 35725, Anacapa Island, 40 m depth) by W. Adey (unpublished data) indicated that the plant is also not representative of *Phymatolithon lenormandii*. No recent records of *L. microsporum* are known.

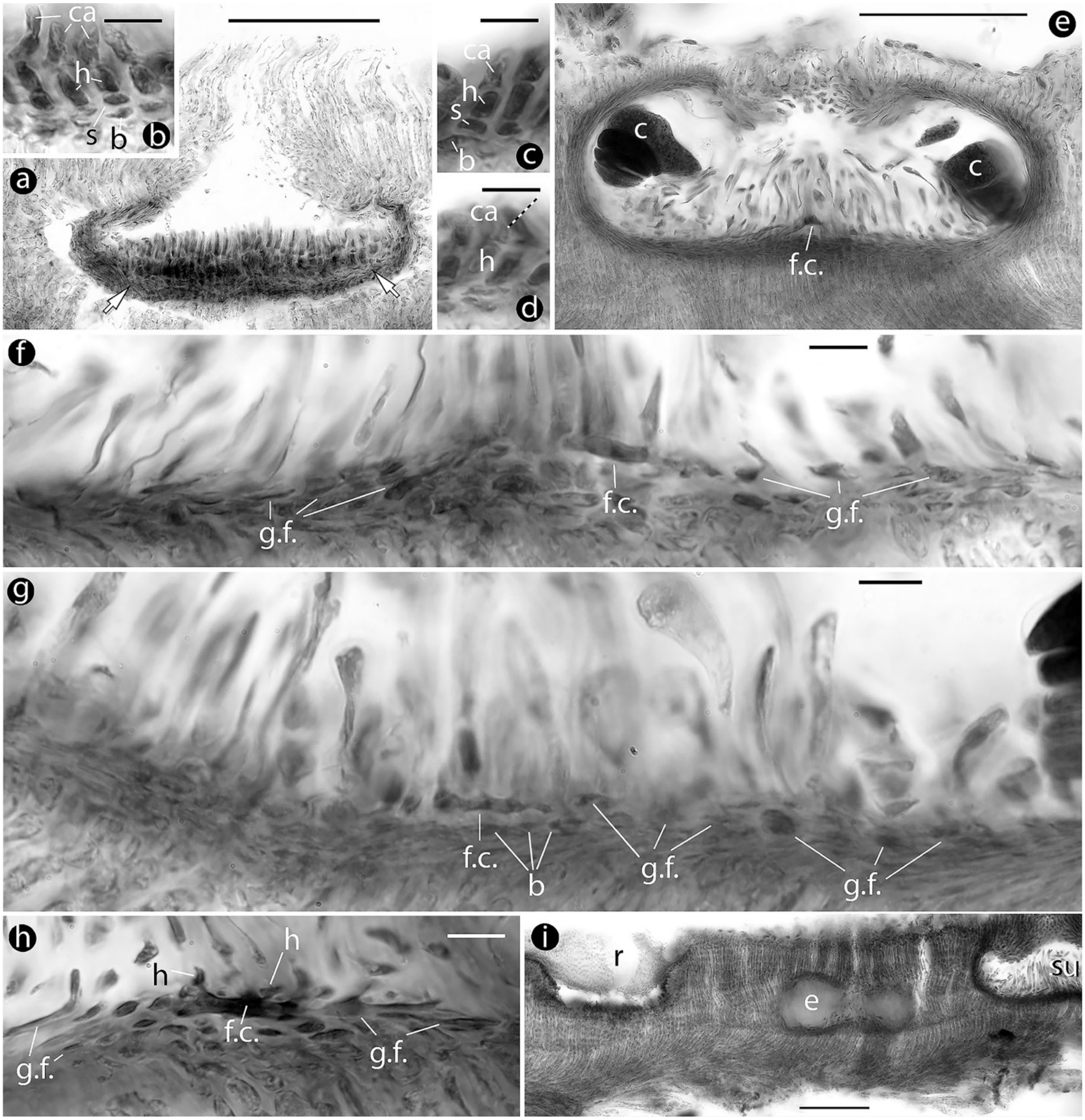

FIGURE 65. *Leptophytum foveatum*: carposporangial structures (D3-YMC 89/85). (**a**) Carpogonial conceptacle with carpogonial branches extending along the entire floor (arrows). Scale bar: 100 µm. (**b–d**) Carpogonial branches composed of 3 cells with the basal cell staining similarly: carpogonium, hypogynous, and supporting cells. Note the sterile cell (dashed line) attached to the hypogynous cell. Scale bars: 10 µm. (**e–h**) Postfertilization stages showing peripheral development of carposporangia from gonimoblast filaments that emanate from a fusion cell. Note that basal cells remain intact. Scale bars: 10 µm. (**i**) Thallus section with superficial, embedded, or deteriorated (labeled r) carposporangial conceptacles. Scale bar: 100 µm. Abbreviations: b, basal cell; c, carposporangia; ca, carpogonium; e, embedded; f.c., fusion cell; g.f., gonimoblast filament; h, hypogynous cell; r, deteriorated; s, supporting cell; su, superficial.

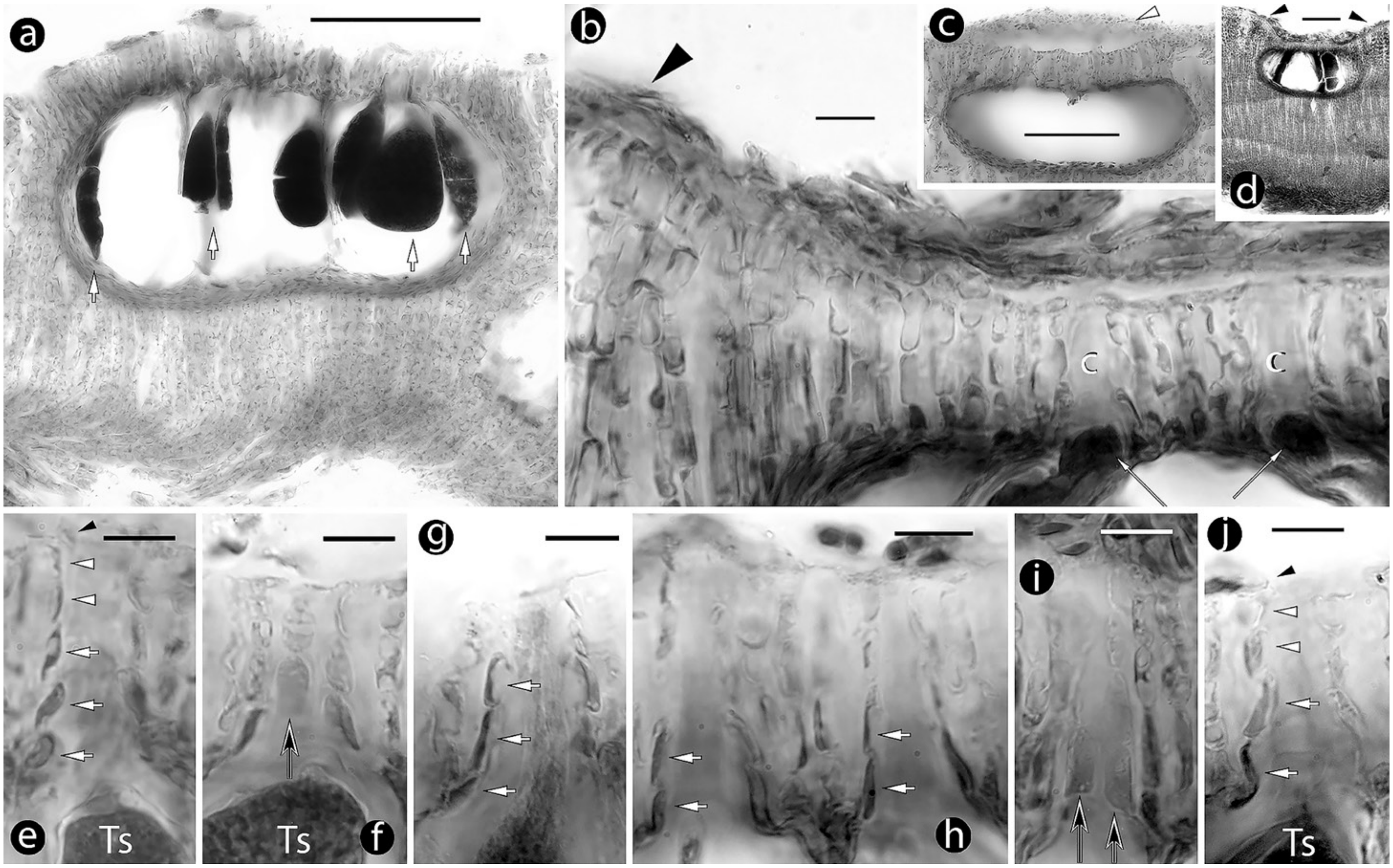

FIGURE 66. *Leptophytum foveatum*: multiporate conceptacle structures (D3-YMC 89/85 in (a) and (c); D4-YMC 91/243 in (b) and (d)–(j)). (**a**) Tetrasporangial conceptacle with tetrasporangia (arrows). Scale bar: 100 µm. (**b**) Multiporate roof with canals blocked by sporangial remains (arrows). Note the gradual embedding process (black arrowhead). Scale bar: 10 µm. (**c**) Empty multiporate conceptacle covered by an imperforate second roof (arrowhead). Scale bar: 100 µm, (**d**) Multiporate conceptacle in the process of being embedded by peripheral growth (arrowheads). Scale bar: 100 µm. (**e–j**) Pore canals in antidiametric (white arrows and arrowheads) and tangential (black arrows) sections, with tetrasporangia below. Pore filaments lining the canals are 5- or 6-celled, ending in epithallial cells (black arrowheads), with up to 3 differentiated, thinner (white arrows) and wider (black arrows) cells along the base. Scale bars: 10 µm. Abbreviations: c, canal; Ts, tetrasporangia.

***Mesophyllum fragilissimum* (Foslie) Me. Lemoine**

Mesophyllum fragilissimum (Foslie) Me. Lemoine 1928: 252.

Basionym: Lithothamnion fragilissimum Foslie 1904c: 13–17, text fig. 5, pl. 1, figs. 11–16.

Type Locality: Pulau Sebangkatan Island, Borneo Bank, Indonesia.

Lectotype: In L (0064066, Herb. Lugd. Bat. 943.7-21, station 81, S.E. 971b I, *pro parte*, 14 June 1899, coll. A. Weber-van Bosse), Foslie (1904c: pl. 1 fig. 15), Printz (1929: pl. 8, fig. 10), designated by Athanasiadis and Ballantine (2014: Appendix II, fig. 183 B).

Syntypes: In L (0064066, Herb. Lugd. Bat. 943.7-21, station 81, S.E. 971b I, *pro parte*, 14 June 1899, coll. A. Weber-van Bosse), Foslie (1904c: pl. 1, figs. 14, 16), Printz (1929: pl. 8, figs. 9, 11); in L (0056891, Herb. Lugd. Bat. 943.7-21, S.E. 971b II, 971c, 408a I, 408a II, 408b, 408c); in TRH (B18-2608, B18-2609, B18-2610), Foslie (1904c: pl. 1, figs. 11, 12, 408a-I, 13, 408b), Printz (1929: pl. 8), Woelkerling (1993a: 98), Woelkerling et al. (2005: 351), Athanasiadis and Ballantine (2014: Appendix II, fig. 183A).

Habitat and Distribution: The species grows in sublittoral reefs in association with the foraminiferan *Miniacina miniacea* (Pallas), bryozoans, other marine animals, Squamariaceae, and other corallines; known only from several localities around Borneo Bank, Indonesia.

Comments: The protologue (Foslie 1904c: 13–17, text fig. 5, pl. 1, figs. 11–16) reads,

> Thallus crustlike or more or less leaf-like, 150–500 µ. thick, horizontally extended, partly attached, scantily and irregularly prolificating. Conceptacles of sporangia convex, but very little prominent, at length somewhat flattened, crowded, 350-450 µ. in diameter. Stat. 78. Lumu-Lumu-shoal, Borneo-Bank. Stat. 81. Pulu Sebengkatan, Borneo-bank. Stat. 234. Nalahia Bay, Nusa-Laut Island. Reef.

The following thallus characteristics were emphasized by Foslie:

- An unattached superimposed growth with shining surface and rather brittle and hard consistency
- Scanty proliferations and irregular protuberances "which also are due to its covering up different objects"
- A coaxial hypothallium with hypothallial cells 18–28 × 7–14 µm and perithallial cells 12 × 5–8 µm (L × B)
- (Tetra)sporangia, ~80 × 30 µm [L x B] crowded within inconspicuous conceptacles, 350–450 µm in external diameter, with slightly convex roof, becoming somewhat flattened and perforated by 30-40 muciferous canals
- Fertility in June and November, but rather scantily

Foslie added that the "species comes nearest to *Lithothamnion Engelhartii* from the south coast of Australia . . . distinguished . . . by a thallus more spread and more freely growing. Besides it is brittler. The conceptacles are a little larger and less sharply defined . . . Young or sterile specimens are, on the other hand, hardly distinguishable from *Lithothamnion simulans.*" He further suggested a relationship to fossil corallines preserved at Leiden, mentioning that (original?) material of *Lithothamnion rosenbergii* K. Martin "includes at least two species, one of which may be identical with *L. fragilissimum,*" but after reproducing Martin's illustrations (Foslie 1904c: text fig. 6 A,B), he would "still subsume . . . [*L. rosenbergii*] under *Archaeolithothamnion* [*Sporolithon*]" since Martin's alga shows solitary cavities representing putative sporangial chambers (Foslie 1904c: text fig. 6A), whereas the section in Foslie's (1904c) text figure 6B from the north coast of New Guinea "is no doubt to be referred to . . . [a] foliaceous [species] like *Lithothamnion lichenoides*, *L. fragilissimum* and other."

The material of a second section (of a fossil specimen) was described to have a "thickness . . . 330–450 µ. The central cells of the coaxial hypothallium are 22–32 µ. long and 8–11 µ. seldom up to 14 µ. broad . . . The cells of the perithallium are commonly squarish, 6–10 µ. in diameter," and "compared with *L. fragilissimum*, the perithallic layers of both species will show almost complete conformity. The structure of the hypothallium is also much the same as in *L. fragilissimum*, but the cells are here mostly longer."

Foslie concluded that as the material of the fossil "is scarce . . . and . . . sterile . . . I don't venture to identify it at present, but at any rate I must consider it as a species closely connected with *L. fragilissimum.*"

Athanasiadis and Ballantine (2014: Appendix II) examined the six specimens illustrated in the protologue (Foslie 1904c: pl. 1, figs. 11–16; all from Station 81), stating that they are mostly fragmented, except one "almost entire and fertile . . . rather burdened with Bryozoa and other animals" (Foslie 1904c: pl. 1, fig. 11). Part of the latter specimen (~3.5 cm in extent) is in Leiden (L0056891, "S.E.408aI Pl.I, fig. 11–12 Stat.81") and is provided with inconspicuous multiporate conceptacles, ~400 µm in external diameter.

Adey and Lebednik (1967: 69) originally considered as "type material" specimens in TRH from at least two different stations ("S.E., st. 78, 81, Borneo Bank, nos. 148a, 971b, c, 10-11.6.1899"), and later, Adey (1970: 24) designated these as "co-types . . . a set of small specimens from each of two Siboga stations (one locality)." Because this lectotypification included several collections (gatherings), rather than a specimen (Turland et al., 2018: Article 8.2), it was considered to be invalid by Verheij and Woelkerling (1992: 278–279), who selected instead as a new lectotype the material in Leiden (L0064066, Herb. Lugd. Bat. 943.7-21; S.E. 971b-I) placed in a single box annotated "Pl. I, fig. 14–16" (Athanasiadis and Ballantine 2014: Appendix II, figs. 183–184). No part of this collection is present in TRH (Verheij and Woelkerling 1992). It comprises nine specimens and fragments, the largest up to 3.5 cm in extent. Because only two of them matched those illustrated in the protologue (Foslie 1904c: pl. 1, figs. 14, 15), Athanasiadis and Ballantine (2014: Appendix II, fig. 183 A,B) narrowed Verheij and Woelkerling's (1992) lectotypification to one of them bearing multiporate conceptacles.

According to the protologue, the species may reach 4.5 cm in extent, and its thallus surface may possess erect protuberances a few millimeters long (Athanasiadis and Ballantine 2014: Appendix II, figs. 186, 187). The foraminiferan *Miniacina miniacea* (Pallas) and bryozoans are attached on the underside. Protuberances occur irregularly on the surface and are the result of thallus proliferations (rather than perithallial outgrowths), as judged by the (longer) length of their internal (hypothallial) cells in relation to the perithallial cells below (Athanasiadis and Ballantine 2014: Appendix II, fig. 187). The multiporate conceptacles of the lectotype are slightly raised and aggregated in groups (Athanasiadis and Ballantine 2014: Appendix II, fig. 185). A second specimen with multiporate conceptacles is present in one of the syntype collections in Leiden ("S.E.408b Pl.I, fig. 13," included in a collection with five other boxes, all collectively labeled L0056891). Another foliose thallus with male conceptacles occurs attached to a syntype (in the box annotated "S.E. 971c"), but it lacks a coaxial hypothallium and apparently belongs to a different species.

Sections of the lectotype (and the syntype L0056891, S.E.971c) show a monopodial-dorsiventrally organized thallus, 120–330 µm thick (to 450 µm when provided with conceptacles and up to 500 µm according to the protologue), composed of a coaxial hypothallium 70–140 µm thick, producing an ascending perithallium to 190 µm thick (Athanasiadis and Ballantine 2014: Appendix II, fig. 188). Descending hypothallial cells terminate in wedge-shaped basal cells (Athanasiadis and Ballantine 2014: Appendix II, fig. 189). In views of the thallus from below, patches of hypothallial cells show noncoaxial growth (Athanasiadis and Ballantine 2014: Appendix II, fig. 190). Hypothallial cells are 12–32 × 3–10 µm (L × B), and perithallial cells are 3–25 × 3–8 µm (L × B; 18–28 × 7–14 and 12 × 5–8 µm, respectively, according to the protologue). Subepithallial cells are elongate, 3–7 × 4–8 µm (L × B), and epithallial cells are flattened, 1–2 × 8–11 µm (L × B; Athanasiadis and Ballantine 2014: Appendix II, figs. 191, 192). Cell fusions occur commonly between vegetative cells. Trichocytes and secondary pit connections are absent.

Multiporate conceptacles are 320–550 × 70–150 µm (D × H; n: 8; 350–450 µm in external diameter according to the protologue), with chambers 220–370 × 100–120 µm (D × H) either empty or with tetrasporangial remains, 80–100 × 32–40 µm (n: 4; Athanasiadis and Ballantine 2014: Appendix II, figs. 185, 193–194). The roof is convex, 35–40 µm thick, composed of 4- to 5-celled filaments and perforated by at least 40 canals (n: 1). A pore plate is 425–495 µm (in opposite diameters). Pore canals are ~8–9 µm in apical diameter, surrounded by 5 to 8 rosette cells that are common epithallial cells (Athanasiadis and Ballantine 2014: Appendix II, fig. 195). Canals are wider at the base, reaching 18–22 µm in diameter, and pore cells lining the canals are thinner–wider (Athanasiadis and Ballantine 2014: Appendix II, fig. 196). Filaments lining the canals are composed of 4 cells, and the canals appear to be straight in section (Athanasiadis and Ballantine 2014: Appendix II, figs. 196–198). No embedded conceptacles occur in the thallus, and the presence of conceptacles with broken off roofs indicates that older conceptacles are senescing. However, according to the protologue, "the conceptacles . . . in old specimen[s are] finally overgrown."

Setchell (1926: 107) listed three collections of *Lithothamnion fragilissimum* from reefs of Tahiti but gave no other information, and two years later, the species was transferred to *Mesophyllum* (Lemoine 1928: 252). There are no later records from the central Pacific (Payri and N'Yeurt 1997; N'Yeurt and Payri 2010). In describing the new fossil *Lithothamnion tanapagense* Johnson (1957: 223), Johnson briefly mentioned that "*L. fragilissimum* ha[s] a thick coaxial hypothallus." Adey and Lebednik (1967: 69), Adey (1970: 24), Verheij and Woelkerling (1992: 278–279), Woelkerling (1993a: 98), Woelkerling and Verheij (1995: 53), and Woelkerling et al. (2005: 351) provided data for the type collections in TRH and L without studying the specimens. The type material (in L) was previously examined by Yvonne M. Chamberlain, and two illustrations from her study are reproduced by Athanasiadis and Ballantine (2014: Appendix II, figs. 198, 199), both in good agreement with their account.

A tentative position of *L. fragilissimum* in *Magnephycus* is here suggested because of its foliose thallus, the partly coaxial hypothallium, and the wider canals at the base, which suggest the presence of pyriform canals (Athanasiadis and Ballantine 2014: Appendix II, figs. 190, 196).

***Mesophyllum funafutiense* (Foslie) Verheij**

Mesophyllum funafutiense (Foslie) Verheij 1993a: 238.

Basionym: Lithothamnion philippii f. *funafutiense* Foslie 1899a: 3–5, "*funafutiensis*."

Homotypic Synonym: *Lithothamnion funafutiense* (Foslie) Foslie 1901b: 17.

Heterotypic Synonym: ?*Lithothamnion funafutiense* f. *purpurascens* Foslie 1901b: 18; type locality: north side of Koh Chang, Gulf of Thailand, Thailand; lectotype: in TRH (B15-2377), Printz (1929: pl. 4, fig. 18), Adey and Lebednik (1967: 64, "type material," "§ . . . Gulf of Siam, . . . 1900, no VI., D. Dan. Siam Exp., LM4(18) [slide] 460"), Adey (1970: 26, "the one sectioned in the Monograph"), Woelkerling (1993a: 184–185), Woelkerling et al. (2005: 318, "lectotype," "Collector's name [Schmidt] listed on slide," "nordsidan af Koh Chang," "encrusting on a coral reef; 7.iii.1900; . . . [ex] Mus.bot.Haun."). Verheij (1993b: 62, synonym).

Lithothamnion purpurascens (Foslie) Foslie 1907e: 98.

Mesophyllum purpurascens (Foslie) W. H. Adey 1970: 26.

Type Locality: Tuvalu, Funafuti, off Tutanga, Polynesia.

Holotype: In TRH (C16-3254, collector unknown), Printz (1929: pl. 12 fig. 3, "type specimen"), Adey and Lebednik (1967: 81, "type material"), Adey (1970: 20, "lectotype," "three specimens are present"), Woelkerling (1993a: 100–101, "lectotype"), Woelkerling et al. (2005: 454, "lectotype," "[Anon.]; [Tuvalu]: Funafuti, off Tutanga; . . . 41 fathoms; viii.1898; slides 315–316, 1547; ex coll. Prof.Judd, Geol. Dept. Brit.Mus . . . collection B13"), Athanasiadis and Ballantine (2014: Appendix II, fig. 200).

Habitat and Distribution: The species grows on rocky substrata in the sublittoral zone, 5–35 m depth. It is recorded from the Red Sea, South Africa (Sodwana Bay and Natal; Keats and Chamberlain 1994: 183), Indonesia (Verheij 1993b: 62–63), French Polynesia (N'Yeurt and Payri 2010), and the Hawaiian Islands (Adey et al. 1982, as *M. purpurascens*), but see comments below.

Comments: In the protologue Foslie (1899a: 3–5) described a single specimen from

> 41 fathoms off Tuta[n]ga [to] . . . coincid[e] . . . with the typical form [*Mesophyllum philippii*] . . . that [is] . . . known from the Med . . . It forms a thin crust surrounding a compressed coral, about 21 cm. long and 12 cm. broad, with an irregular and rather rough surface. The crust frequently is . . . 1mm. thick, here and there somewhat thinner. It clings closely and rather firmly to the substratum, in most places sending forth a great many processes partly and most frequently short and wart-like, partly longer and branch-like, varying between 1 and 4 mm. in height and 1 and 5 mm., generally about 2 mm. in diameter, and these processes

> sometimes carry other wart-like excrescences. However, the unevenness of the crust is in the main caused either by the substratum or the growing over of extraneous objects, especially Foraminifera . . . The conceptacles of sporangia agree with those in the typical form [*Mesophyllum philippii*] with the exception of generally being a little smaller, or 600-700 µ in diameter, and the roof intersected with 70-80 muciferous canals. Besides more closely and firmly clinging to the substratum than the typical form, f. *funafutiensis* especially differs from that as regards the structure . . . but only a solitary fragment of the specimen has been examined and . . . Foraminifera grows together with the alga . . . in some parts of a section even forming almost alternate layers with the latter . . . the hypothallus . . . is often feebly developed . . . not forming regular curved cell-rows as in the typical form, but frequently [develops] more or less bent and rather short rows with irregular or elongated cells up to 24 µ long, but commonly shorter. The perithallic layer nearly agree with those in the typical form, although often less regular . . . caused by animals . . . [but] as a rule being of the same shape and size as in the said form . . . [and hence is] consider[ed] as a somewhat stunted form of *L. Philippii* [=*Mesophyllum philippii*].

No taxa were cited as synonyms, and since the entire material was a single specimen (collector unknown), it has to be the holotype. Printz (1929: pl. 12, fig. 3) provided an illustration and compared the species to other taxa (all currently referred to *Lithothamnion* and not including *L. philippii*) as follows:

> Excrescences verruciform, irregular or short branch-like and simple or subsimple, warty, approximate, 1.5–2.5 mm thick; conceptacles of sporangia 500–700 (750) µ in diameter, convex or flattish, little prominent or subprominent; perithallic cells subquadrate, 6–11 µ, or most frequently elongated vertically, 7–14 by 6–11 µ (no marked medullary layer of cells).

Woelkerling (1993a: 100–101) confirmed that the TRH specimen is the same as the one previously considered as "type material" by Adey and Lebednik (1967) and as "lectotype" by Adey (1970), who, however, stated that the entire type collection in TRH included three specimens. Another point that remains unclear is that Foslie considered the hypothallium to be "feebly developed . . . not forming regular curved cell-rows as in the typical form" (i.e., *Mesophyllum philippii*).

Keats and Chamberlain (1994: 183, figs. 43–58, 65, 66) and Adey et al. (1982, as *M. purpurascens*) recorded the species as rare, growing between 5 and 25 m at Natal and forming crusts several millimeters thick adhering to rocky substrata. Specimens have also been reported from French Polynesia, growing on dead corals in the lagoon, on the reef crest underneath *Sargassum* beds, and on the outer reef slope to 15 m deep (N'Yeurt and Payri 2010: 62). No "pair species" in the Caribbean was reported by Adey et al. (1982: 63). Verheij (1993b: 62–63, figs. 90–94), who examined the holotypes of f. *funafutiense* and f. *purpurascens*, considered them to be conspecific and reported the species between 5 and 35 m depth, citing five additional collections. In all these studies from Indonesia, Natal, and Hawaii, the hypothallium was described to be "organized in a coaxial manner" (Verheij 1993b: 63) or "coaxial" (Keats and Chamberlain 1994: 181, figs. 44, 52; Adey et al. 1982: 63).

Athanasiadis and Ballantine (2014: Appendix II, figs. 200–202) examined two collections from Indonesia. In the first one (L0246526; Verheij no. B15), they confirmed most characters attributed to this species, including the absence of trichocytes, the presence of elongate subepithallial cells, and the development of 9–12 pore cells lining canals of multiporate roofs, with the cells being similar in length to contiguous roof cells but thinner–wider near the base. They did not observe perithallial protuberances, and the hypothallium developed only coaxial patches, lacking a predominantly coaxial growth. In the second collection from Barang Lompo South (L0246532; Verheij no. 0085), cited under *Mesophyllum funafutiense* by Verheij (1993b: 62, "5 m . . . 22-i-1989"), they observed an entirely noncoaxial hypothallium and pore cells of multiporate roofs with distinctive elongate basal and subbasal cells. They concluded that the present data were insufficient to support a generic position of the species in *Mesophyllum* s.s., emphasizing the need for examining additional material in comparison to the types of both *Lithothamnion philippii* f. *funafutiense* and *Lithothamnion funafutiense* f. *purpurascens*.

Mesophyllum funafutiense is here placed in the tribe Magnephyceae with reservation, taking into account that a coaxial hypothallial growth is not regularly present in the thallus (Foslie 1899a; Athanasiadis and Ballantine 2014).

Since conspecificity with *Lithothamnion funafutiense* f. *purpurescens* remains to be demonstrated, we separately provide data for this taxon from the protologue (Foslie 1901b: 18–19) that reads, "f. purpurascens Fosl.mscr. Thallus forming up to 2 mm. thick crusts on Corals, frequently with wart-like excrescences 2–3 mm. in diameter. Conceptacles of sporangia subprominent, 550–700 µ in diameter. Conceptacles subconical, about 500 µ in diameter."

Foslie (1901b: 18–19) further stated, in the most essential parts, that the few fragmentary specimens examined were

> more or less uneven and feebly shining, generally with wart-like excrescences 2–3 mm in diameter, or sometimes thinner, scattered and branch-like processes . . . at least in part by covering up small extraneous objects or penetrating animals. A new crust occasionally is formed upon the primary. . . .the cells of the feebly developed hypothallic layer are elongated . . . up to about 20 µ long . . . The lower anticlines form a slow convergence towards matrix. The cells of the perithallic layer are much varying in shape and size, . . . 4–5 by 5–6 µ in diameter, square or rounded, or seldom with the longest

> diameter in horizontal direction or specially upwards square or more frequently vertically elongated, 7–12 µ long and 5–7 µ broad. . . . I have seen but a few conceptacles of sporangia and cystocarps. The former are slightly convex . . . The sporangia are four-parted . . . 140–170 µ long and 60–70 µ broad. . . . f. *genuina* . . . has a rosy color . . . while f. *purpurascens* is darker or lighter purplish . . .
> [Collections]
> Between Koh Mesan and Cape Liant on a depth of
> 9 fathoms (not quite certain);
> 15 naut. miles E. of Koh Chuen, 10 fathoms;
> the north side of Koh Mesan, 10–15 fathoms
> [B15-2376];
> between Koh Mesan and Cape Liant, 5–8 fathoms
> [B15-2378];
> the north point of Koh Chang on Coral-reefs
> [B15-2377];
> and Koh Kahdat in 2 fathoms water [B15-2375].

Since the material of f. *purpurascens* was collected during the "Danish Siam Expedition 1899–1900" and the lectotype is annotated "Mus[eum] bot[anicum] Hau[niense]" (Adey and Lebednik 1967: 64), it is rather possible that syntypes and other material may exist in the herbarium of J. Schmidt in C.

Phymatolithopsis **S. Y. Jeong, G. W. Maneveldt, P. W. Gabrielson, et T. O. Cho**

Phymatolithopsis S. Y. Jeong, G. W. Maneveldt, P. W. Gabrielson, et T. O. Cho in Jeong et al. 2022: 163 (type: *Ph. prolixa*?).

Comments: This recently recognized genus included *Phymatolithopsis prolixa* and *Ph. repanda* from South Africa and southern Australia, respectively, and *Ph. donghaensis* S. Y. Jeong, B. Y. Won, et T. O. Cho nom. inval.[42] from Korea. It was segregated on the basis of several characters, most of them fitting the concept of *Leptophytum*, except the presence of an inconspicuous fusion cell (said to be "discontinuous" and hence referring to gonimoblast filaments,[43] as illustrated by Van der Merwe and Maneveldt 2014: fig. 33). Although *Lithothamnion prolixum* Foslie was selected as the generitype, Jeong et al. (2022) did not examine the relevant type material, stating that the new genus was based on the "morpho-anatomical features of . . . [the species] described in detail in Van der Merwe and Maneveldt (2014, as *Phymatolithon ferox*)." Hence, unless *Phymatolithon ferox* sensu Van der Merwe and Maneveldt (2014) is, indeed, conspecific with the type of *Lithothamnion prolixum*, *Phymatolithopsis* should be typified with the material described by Van der Merwe and Maneveldt (2014: figs. 22–38, 76), which most closely corresponds to *Lithothamnion falsellum* f. *plicatum* Foslie (Turland et al. 2018: Article 10.2). Further problems exist with the type material of *Ph. repanda* (see species account). *Phymatolithopsis* has not been included in the present phylogenetic analysis, pending clarification of its type and the study of new collections. In the comparative table of genera of Magnephyceae (Table 5), the genus is represented by "*Phymatolithon ferox*" sensu Van der Merwe and Maneveldt (2014) and *Ph. repanda*.

Phymatolithopsis prolixa **(Foslie) S. Y. Jeong, G. W. Maneveldt, P. W. Gabrielson, et T. O. Cho**

FIGURE 67

Phymatolithopsis prolixa (Foslie) S. Y. Jeong, G. W. Maneveldt, P. W. Gabrielson, et T. O. Cho in Jeong et al. 2022: 164.

Basionym: Lithothamnion prolixum Foslie 1908b: 9.

Homotypic Synonym: *Mesophyllum prolixum* (Foslie) W. H. Adey 1970: 25.

Heterotypic Synonym: ?*Lithothamnion falsellum* f. *plicatum* Foslie 1900a: 10, "*plicata*"; type locality: Cape of Good Hope, South Africa; holotype: in TRH (C15-3246), Printz (1929: pl. 14, fig. 13), Woelkerling (1993a: 174, "holotype"). Chamberlain and Keats (1994: figs. 98–99), Jeong et al. (2022, synonym).

Misapplied Name: *Lithothamnion falsellum* f. *falsellum* sensu Foslie 1900a: 10, "*genuina*" [non *Lithothamnion falsellum* Heydrich 1897b: 414, pl. 3, figs. 1, 2; type locality: False Bay, South Africa].

Type Locality: Natal, South Africa.

Lectotype: In TRH (C15-3245), Printz (1929: pl. 14, fig. 10, f. "*typica*"), Adey and Lebednik (1967: 80, "type material," "§ W.v.Bosse, Afr., Natal, 1893, LM14 (9,10) [slides] 698, 699"), Adey (1970: 25, "lectotype"), Woelkerling (1993a: 177, "The lectotype . . . includes five specimens, two of which are depicted in Printz"), Woelkerling et al. (2005, "lectotype"). Chamberlain and Keats (1994: figs. 88–97, 100–105, "lectotype").

Material Examined: South Africa: west coast Cape: Cape St Martin: high shore pools, 24 March 1991, coll. G. M. Branch. (herb. Athanas. D1-YMC 91/27, cited as YMC and DWK 91/27, Western Cape in Chamberlain and Keats 1994, under "*Leptophytum ferox*").

Comments: Concerning the synonymy above, the status of *Lithothamnion falsellum* Heydrich is unknown since Heydrich's herbarium (in the Berlin Museum) is considered to be lost.

Lithothamnion falsellum f. "*genuina*" Foslie (1900a: 10) was later described as *Lithothamnion prolixum* by Foslie (1908b, 1908d). The Norwegian protologue (Foslie 1908b: 9) reads (in translation),

> Lithothmanion prolixum Fosl. Videnskabsselsk. aarsber. 1907 (1908). Lithothamnion falsellum Fosl. New or crit.calc. Alg. (1900), p. 10; non Heydr. It has been shown that this alga develops two-parted sporangia, while *L. falsellum* develops four-parted. It has to be considered therefore as a distinct species. Though I have not seen specimens of *L. falsellum* [Heydrich], it seems that they approach each other. *Lithothamnion prolixum* is attached to the substratum, either by a thin or thick crust, from where sparsely branched

> proliferations develop, partly and usually closely standing, subdichotomous, short knobby branches, with somewhat sunken tips, almost equally long, 1–2 mm thick. Form *plicata* develops small and short folded branches, closely grouped, that anastomose and finally grow together with similar height. In a section in the middle thallus part are the medulla cells 11–22(29) µm long and 6–7(9) µm broad. Perithallial cells are partly sub square, 6–7(9) µm in diameter, partly and mostly vertically elongate 7–9(11) µm long and 6–7(9) µm broad, weakly horizontally elongate. [Bi]sporangial conceptacles are convex or flattened, 200–340(400) µm in diameter. Sporangia are two-parted, 120–150 µm long and 40–70 µm broad. *Lithothamnion prolixum* stands close to *L. canariense*. It is only known from Cape of Good Hope and from Natal, although the last mentioned place can be the result of mixed etiquettes.

Regarding the original material and lectotypification of *Lithothamnion prolixum*, Adey (1970: 25) stated that "a number of possible specimens . . . are in the collection. Of those marked f. *genuina* only two are sectioned and appear in the Monograph [as f. *typica*]. The selected specimen was larger and showed better reproductive structures."

Hence, the lectotype selected by Adey is the larger specimen illustrated in Printz (1929: pl. 14, fig. 10), which also fits Chamberlain and Keats's (1994: fig. 96) illustration (Figure 67a,b). The second (smaller) specimen illustrated by Printz (1929: pl. 14, fig. 9; Figure 67c) shows an apparent similarity to *Melyvonnea*; Foslie (1908b) himself pointed out the likeness to *Lithothamnion canariense* Foslie (1906a) (*Melyvonnea canariensis*). Both specimens remain anatomically unstudied.

Lithothamnion prolixum was erroneously included in the synonymy of *Leptophytum ferox* by Chamberlain and Keats (1994: 119), who, however, stated that "*Lithothamnion ferox*, is flat to lumpy . . . and lacks protuberances [while] South African plants . . . agree closely with the lectotype . . . of the protuberant species *Lithothamnion prolixum*" (Chamberlain and Keats 1994: 124).

Moreover, Chamberlain and Keats (1994: figs. 88–97, 100–105) described and illustrated the presence of both bisporangial and carpogonial-carposporangial conceptacles in the "lectotype" of *L. prolixum*, which indicates that a confusion of specimens took place. Only the text and those illustrations in Chamberlain and Keats (1994) describing and showing vegetative and bisporangial characteristics (said to be from the lectotype of *L. prolixum*) are here reproduced (Figure 67d–g) since only bisporangial thalli were described in the protologue (Foslie 1908b). Still, two more inconsistencies merit attention: Chamberlain and Keats (1994: figs. 93, 103) illustrated canals of the "lectotype" to be either straight or lacking basal cells (Figure 67d,e), the latter based on a SEM illustration, suggesting the presence of pyriform canals (as shown in the new collections; Figure 67p–t). Moreover, the presence of elongate subepithallial cells in a sterile section (Chamberlain and Keats 1994: fig. 91, "Foslie slide 699"; Figure 67g) agrees with the new collections but not with the concept of *Phymatolithopsis* (Jeong et al. 2022: 165).

The holotype of *Lithothamnion falsellum* f. *plicatum* Foslie (1900a: 10) was illustrated by Chamberlain and Keats (1994: 124, figs. 98–99), who stated that it is "in close agreement with [thalli forming] back-to-back [lamellae] (Fig. 50) [of *L. prolixum*]." However, no anatomical characteristics were documented, and the structure of the thallus of the holotype of f. *plicatum* is unknown. No back-to-back lamellae occur in the lectotype of *Lithothamnion prolixum* (Figure 67a,b).

More recently, thalli with typical back-to-back lamellae (presumably belonging to *L. falsellum* f. *plicatum*) were described and illustrated by Van der Merwe and Maneveldt (2014: figs. 22–38, 76, as "*Phymatolithon ferox*"), and this material was later considered to be representative of the generitype of *Phymatolithopsis*, *P. prolixum*, by Jeong et al. (2022: 165).

However, until comparative studies of the types of *Lithothamnion prolixum* and *Lithothamnion falsellum* f. *plicatum* have been undertaken and the confusion about the presence of both bisporangial and carpogonial-carposporangial conceptacles in the lectotype of *L. prolixum* has been clarified, conspecificity between them and new collections remains uncertain, and this obviously affects the status of *Phymatolithopsis*.

Only a few fertile fragments with protuberances, cited under "*Leptophytum ferox*" in Chamberlain and Keats (1994: 120), were available for examination from the herbarium Chamberlain. They are roundish to irregularly proliferous (Figure 67h–k) and provided with multiporate conceptacles with a flattened roof (Figure 67l,m). Older conceptacles are not embedded in the thallus (Figure 67n). Like in *Leptothallia acervata* (Figure 30d) and in the type material of *L. prolixum* (Figure 67e,g), subepithallial cells during putative division are slightly longer than cells below (Figure 67o). Pore filaments develop differentiated (thinner–wider) basal and subbasal cells in canals of multiporate conceptacles, and the canals are distinctively pyriform (Figure 67p–t). This material (D1-YMC 91/27) agrees with the illustrations of the bisporangial lectotype of *L. prolixum* (Chamberlain and Keats 1994; Figure 67d,e), but it is clearly in contradiction to the current concept of *Phymatolithopsis* since pyriform canals and elongate subepithallial cells are not reported in the description of this genus (Jeong et al. 2022: 165).

***Phymatolithopsis repanda* (Foslie) S. Y. Jeong, G. W. Maneveldt, P. W. Gabrielson, W. A. Nelson, et T. O. Cho**

FIGURES 68–70

Phymatolithopsis repanda (Foslie) S. Y. Jeong, G. W. Maneveldt, P. W. Gabrielson, W. A. Nelson, et T. O. Cho in Jeong et al. 2022: 169.

Basionym: Lithothamnion repandum Foslie 1904b: 4, nom. et stat. nov. of *Lithothamnion lenormandii* f. *australe* Foslie 1901a: 8–9, "*australis*." Foslie (1906b: 5–6).

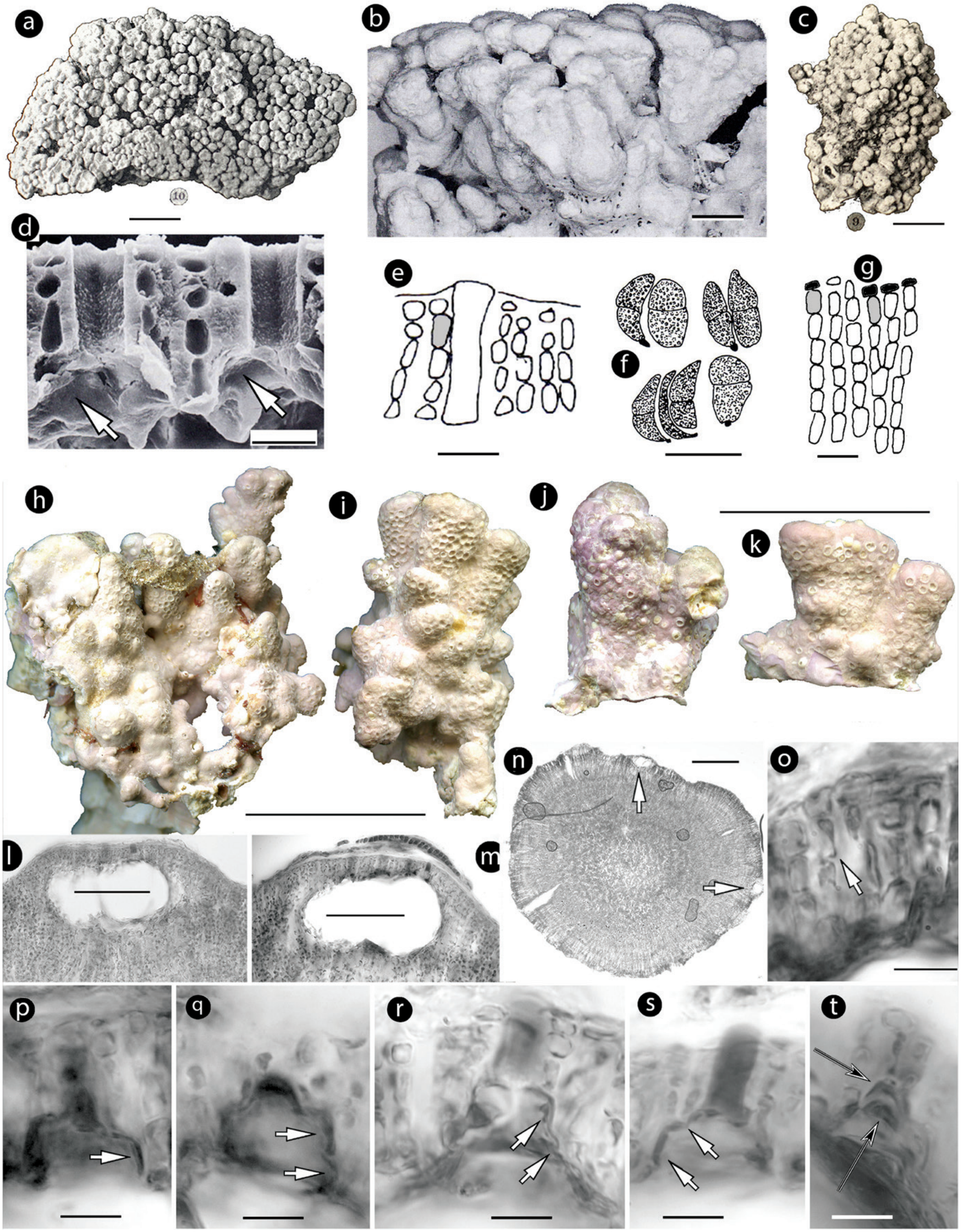
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FIGURE 67. (*Opposite*) *Phymatolithopsis prolixa*; type specimens of *Lithothamnion prolixum* (C15-3245 in (a)–(g)) and new fragments with multiporate conceptacles (D1-YMC 91/27 in (h)–(t)). (**a, b**) Lectotype of *Lithothamnion prolixum* in TRH (C15-3245, *pro parte*) as illustrated by Printz (1929: pl. 14, fig. 10 [=circled number in image]) and Chamberlain and Keats (1994, fig. 96), respectively. Scale bars: 1 cm, 5 mm, respectively. (**c**) Syntype of *Lithothamnion prolixum* in TRH (C15-3245, *pro parte*) as illustrated by Printz (1929: pl. 14 fig. 9 [=circled number in image]). Scale bar: 1 cm. (**d**) SEM of pore canals showing a 3-celled top filament lacking the basal cell(s) (arrows). Modified from Chamberlain and Keats (1994: fig. 103, "lectotype"). Scale bar: 10 µm. (**e**) A pore canal showing straight shape and an elongate subepithallial initial (shaded). Modified from Chamberlain and Keats (1994: fig. 93, "lectotype"). Scale bar: 10 µm. (**f**) Bisporangia. Modified from Chamberlain and Keats (1994: fig. 94, "lectotype"). Scale bar: 10 µm. (**g**) Thallus section showing flattened epithallial cells (in black) and elongate subepithallial initials (shaded). Modified from Chamberlain and Keats (1994: fig. 91, "Foslie slide 699"). Scale bar: 10 µm. (**h–k**) Branched protuberances with tetrasporangial conceptacles. Scale bars: 1 cm. (**l, m**) Multiporate conceptacles. Scale bars: 100 µm. (**n**) Section of a protuberance with superficial conceptacles (arrows). Scale bar: 500 µm. (**o**) Section of roof showing elongate subepithallial initial (arrow). Scale bar: 10 µm. (**p–t**) Sections of pyriform canals of multiporate conceptacles. Basal and subbasal cells are thinner (white arrows) and wider (black arrows). Scale bars: 10 µm.

Homotypic Synonyms: Leptophytum repandum (Foslie) W. H. Adey 1970: 30.

Phymatolithon repandum (Foslie) K. M. Wilks et Woelk. 1994: 190–192, figs. 54–74, 78. Van der Merwe and Maneveldt (2014: 185, figs. 54–74, 78).

Heterotypic Synonyms:? *Lithothamnion repandum* f. *asperulum* Foslie 1906b: 5, "*asperula*"; type locality: Island Bay, Wellington, New Zealand; type material: in TRH (B1-1609), Printz (1929: pl. 1, figs. 4–6), Adey and Lebednik (1967: 49, "type material," "§ Setchell, New Zealand, North Island, nos 6346-6348, 1904, LM1(4-6) [slides] 139,1141,1142,1167,1168"), Adey (1970: 29, "co-types"), Woelkerling (1993a: 31, "Lectotype . . . Setchell no.6346-6348"), Woelkerling et al. (2005: 226, "lectotype"). Wilks and Woelkerling (1994: 191, synonym).

Lithothamnion asperulum (Foslie) Foslie 1907b: 6.

Leptophytum asperulum (Foslie) W. H. Adey 1970: 29.

?*Lithothamnion absonum* Foslie 1907b: 6–7; type locality: Richard's Point in Port Phillip Bay, Victoria, Australia; type material: in TRH (B1-1606), Printz (1929: pl. 1, figs. 11, 12), Adey and Lebednik (1967: 49, "type material," "§ J. Gabriel, Aust., Richard's Point, Philip Bay, 1901. LM1(11-12) [slides] 1527-9"), Adey (1970: 29, "holotype"), Woelkerling (1993a: 14, "holotype," "includes plants on four pieces of rock, two . . . depicted in Printz"), Woelkerling et al. (2005: 226, "holotype"). Wilks and Woelkerling (1994: 191, synonym).

Leptophytum absonum (Foslie) W. H. Adey 1970: 29.

Type Locality: Halfmoon Bay, Port Phillip Bay, Victoria, southern Australia.

Lectotype: In TRH (C18-3354, *pro parte*), Adey and Lebednik (1967: 83, "type material," "§ Gabriel, Austr., Port Philip Bay, Half Moon, 14.1.1899 [slide] 358").

Material Examined: Southern Australia: Southeastern District: Reef ~2 km W of Beachport (37°28′S, 139°59′E), 26 February 1988, coll. S. Cambell (LTB15788, MEL2271639), annotated in print "*Phymatolithon repandum* (Foslie) Wilks and W. Woelkerling . . . Female . . . Portions removed and sent . . . Spirit 10988D Slide 10988 Sheet 1 of 2 (MEL: 2271639, MEL: 2271640)" and in pencil "15788 *P. repandum* possible mixture," a carposporangial thallus mixed with a species of *Lithothamnion* with typical flared epithallial cells; Post Office Rock, Beachport (37°28′S, 140°E), 6 November 1987, coll. S. Cambell (LTB15836, MEL2271641), annotated in print "*Phymatolithon repandum* (Foslie) Wilks and W. Woelkerling . . . Male . . . Portions removed and sent . . . Spirit 10989D Slide 10988 Sheet 1 of 2 (MEL: 2271641, MEL: 2271642)" and in pencil "*P. repandum* 15836"; Gippsland Plain District: Kitty Miller Bay, Phillip Island (38°31′S, 145°10′E), 12 April 1991, coll. W. J. Woelkerling (LTB16167, MEL2271643), annotated in print "*Phymatolithon repandum* (Foslie) Wilks and W. Woelkerling . . . Intertidal on rock . . . Portions removed and sent . . . Spirit 10990D Sheet 1 of 2 (MEL: 2271643, MEL: 2271644)" and in pencil "16167 *P. repandum*," patches of tetrasporangial thalli on three pebbles ~4–6 cm in extent, herein cited as LTB16167A, LTB16167B, and LTB16167C.

Habitat and Distribution: The species grows in the littoral zone, on reef surfaces and in pools, and also in the sublittoral to depths of 6 m in southern Australia (and to 50 m depth in southeastern Australia). Thalli occur most often on rocks and pebbles but are also reported on glass (epiphytic or epizoic thalli unknown). It is recorded between 10 km east of Eyre, Western Australia, to Cape Conran, Victoria, and also around Tasmania, southeastern Australia, and New Zealand (Woelkerling 1996; Harvey et al. 2003b). Records from South Africa have been excluded (Jeong et al. 2022).

Comments: As noted by Woelkerling (1993a: 36–37), *Lithothamnion repandum* Foslie (1904b) was a new status and name of the previously described *Lithothamnion lenormandii* f. *australe* Foslie (1901a). There is, however, uncertainty regarding the type element. Printz originally illustrated four specimens from different localities (Printz 1929: pl. 1, figs. 7–10). Woelkerling et al. (2005: 472) traced them to "Western Port Bay, 1903 . . . 7–9 fathoms" (C18-3357), "Port Phillip Bay, 1901" (C18-3351), "Western Port Bay, . . . very low tide, xi–xii.1903" (C18-3356), and Halfmoon Bay (C18-3354), with the latter being the original material.

Adey and Lebednik (1967: 83) listed the original material in two separate entries, "§ Gabriel, Austr., Port Phillip Bay, Half

Moon, 14.1.1899 [slide] 358" and "Gabriel, Austr., Port Phillip Bay, Half Moon, 14.1.1899, LM1(10) [slide] 516," selecting the former as "type material."

Woelkerling (1993a: 36–37) placed them together, considering that they were the product of a single gathering (i.e., the single specimen, ~4 × 4.5 cm in diameter, illustrated by Printz 1929: pl. 1, fig. 10). Later, however, Woelkerling et al. (2005: 471–472) made a thorough analysis of Foslie's annotations in TRH and observed that Foslie had placed separately in a "smaller . . . box marked with collection data and also marked *L. repandum*? delvis [in part] 'Praep. [slide] 358' . . . two fragments and a fragment packed inside a piece of paper marked '358' and a specimen . . . marked . . . *L. repandum* . . . Slide 358 marked '*Lithothamn. repandum*.'" Slide 516, which is part of the same gathering, is marked "*Lithoth. lenormandi* f. *australis* Fosl. = *repandum* (+ *L. fumigatum*?)."

This information indicates that the type material included admixtures, and hence, it is important to follow Foslie's work and trace the thalli he considered to represent *L. repandum*. Adey and Lebednik's (1967) choice to select as (lecto)type the material in the smaller box (including slide "358") seems to settle the matter, but when Wilks and Woelkerling (1994: fig. 1A) studied the type material, they illustrated five fragments as "lectotype collection," possibly showing the original specimen broken to pieces. Wilks and Woelkerling (1994: fig. 1B,C) further illustrated two sections of (tetra- or bi-)sporangial conceptacles (in the SEM), attributed to the "same plant," and most likely incorporated other data from the "lectotype collection" in their account of the species. Wilks and Woelkerling (1994: 191) further considered *Lithothamnion absonum* Foslie (1907b: 6–7) and *Lithothamnion repandum* f. *asperulum* Foslie (1906b: 5) to be synonyms of *L. repandum* without providing any documentation from the relevant types. These taxa are here kept separately as putative synonyms pending the study of their type collections.

To recapitulate, the protologue of *Lithothamnion lenormandii* f. *australe* Foslie (1901a: 8–9) reads, in the most essential parts,

> L. Lenormandi (Aresch.) Fosl . . . f. *australis* Fosl. mscr. The crust as in f. *sublaevis*, but frequently thicker, the conceptacles of sporangia less prominent, and the hypothallic cells a little larger . . . The form *australis* has been found in Half-moon Bay, Port Phillip Bay, Victoria . . . Mr. J. Gabriel.

A few years later, Foslie (1904b: 4) raised f. *australe* to species status (*L. repandum*), stating (in translation) that "it stands indeed close to [*L. lenormandii*]; but since the crust is thicker, hypothallial cells little larger and the [tetra-, bi-] sporangial conceptacles less conspicuous, it has to be considered as a distinct species.- *Lithoth. repandum* Fosl.mscr."

Then, in the most comprehensive account of the species, Foslie (1906b: 5–6) described (in translation):

> an almost flat crust, seldom more than 1 mm. Hypothallium weakly developed, cells in vertical sections 9–18 µm long and 6–9 µm broad or 1½–3 times longer than broad. Perithallium strongly developed, cells partly isodiametric, 5–7 µm in diameter, partly and more often weakly vertically elongate, seldom with a length 1½ times longer than broad, 6–9 µm long and 4–7 µm broad, here and there with the biggest length in horizontal direction. [Multiporate] conceptacles weakly developed, as a rule surrounded by a roundish depression, 200–300 (340) µm in diameter, and with 40–50 mucous canals. Carposporangial conceptacles subconical, 200–350 (400) µm in diameter; but when the upper part goes off, they become flattened. After discharge all conceptacles deteriorate and leave a depression, which little by little is re-filled with new growth layers. *Lithothamnion repandum* is closely related partly to *L. lenormandii*, but on the other side it is closely associated with *Lithothamnion tenuissimum* from West Africa's coast. It can be difficult to separate from the last mentioned species. The typical form is only known from Halfmoon Bay in Port Philip Bay, Victoria, Australia (J. Gabriel).

In the same paper, Foslie (1906b: 5) described a second form of the species, f. *asperulum* (in translation):

> f. *asperula* Fosl.mscr. The surface as a rule is more uneven than in the typical form, partly weakly knobby, and the conceptacles little smaller. In the typical form . . . The form *asperula* has usually a more uneven surface than the typical form. It is partly weakly knobby, and a new crust develops over the primary one. Perithallial cells are about of the same size as in f. *typica*, but not over 7–8 µm long. Yet, the same seems to be the case in certain specimens of the autonym. Sporangial conceptacles are as a rule a little smaller than in the autonym, 150–250 µm in diameter. Tetrasporangia are c. 80 µm long and 30-60 µm broad. Carposporangial conceptacles are 150–260 µm in diameter. Since the differences are insignificant, seems that f. *asperula* should be referred to *L. repandum*, unless I have seen too few specimens of this form . . . The form *asperula* grows almost always in company of other species, particularly *Lithoph. detrusum*. . . . f. *asperula* is found in Island Bay close to Wellington, New Zealand (Setchell, nr. 6341, 6346–6348, and 6350 partly).

Later, Foslie (1907b: 6) raised f. *asperulum* to species (*L. asperulum*), commenting that (in translation)

> In Alg.Not.II, p.5 I took up this alga as a form of *Lithoth.repandum*. In new investigations of material of the last-mentioned species, I found a single specimen

> that possesses bisporangia; previous searches in most specimens bearing numerous conceptacles were in vain. Since *L. asperulum* develops four-parted sporangia, it has to be considered a distinct species. As an addition to my previous description, I state that hypothallial cells in vertical section are 14–18 μm long and 4–7 μm broad. Perithallial cells are partly sub square, 5–6 μm in diameter, partly vertically, and not seldom horizontally elongate, 4–7 μm in the first named and 5–7 μm in the last named direction. The tetrasporangia are 80–110 μm long and 30–60 μm broad. The alga is still only known from New Zealand, where it occurs in smaller number and growing together with other algae (Setchell).

Adey and Lebednik (1967) selected three Setchell collections (nos. 6346–6348) as type material of f. *asperulum* (possibly the three specimens illustrated by Printz 1929: pl. 1, figs. 4–6), and later, Adey (1970: 29), reported nos. 6347 and 6348 as "co-types," no. 6348 as an isotype, and no. 6346 as missing. Woelkerling (1993a: 31) designated these three collections as "lectotype." These, however, represent different gatherings, and therefore, a lectotype remains to be selected from the entire material that also included Setchell no. 6341, placed in TRH under f. *asperulum*, and Setchell no. 6350, now filed under *Lithophyllum detrusum* (TRH A2-100; Woelkerling et al. 2005).

The Norwegian protologue of *Lithothamnion absonum* (Foslie 1907b: 6–7) reads (in translation),

> Encrusting, incorporating small stones or shells, 0.3–0.8 mm thick, with slightly uneven surface; sporangial conceptacles convex, 160–250 (300) μm in diameter; tetrasporangia, 90–100 μm long, 40–50 μm broad. The uneven surface is mainly the result of the form of the substratum and the inclusion of small foreign bodies. In vertical section the hypothallium is layered, with cells 9–14 (18) μm long and 5–6 (7) μm broad. Perithallial cells are partly sub square, 4–6 μm in diameter, partly weakly horizontally or weakly vertically elongate, up to 7 μm long. I have not seen with certainty carposporangial conceptacles. The alga is on the one side closely related to *Lithoth. repandum*, but displays slightly smaller cells and four-parted sporangia. On the other side, it stands very close to *Lithoth.asperulum*, from which differs mostly by the little smaller cells, little bigger and more conspicuous conceptacles, and probably represents a form of the last mentioned. It appears sporadically in the lower part of the littoral region. - Australia, Richard's Point in Port Philip Bay (J. Gabriel).

Adey and Lebednik (1967) selected as type material the two specimens illustrated by Printz (1929: pl. 1, figs. 11, 12), later considered to be the "holotype" by Adey (1970: 29), Woelkerling (1993a), and Woelkerling et al. (2005). Woelkerling (1993a: 14) noted, however, that the original collection included "plants on four pieces of rock" and that the smaller one depicted by Printz (1929) was now fragmented. These four specimens most likely represent different gatherings, and therefore, a lectotype remains to be selected from the entire material.

The three collections from LTB-MEL that we examined agreed with Foslie's (1906b) account of *L. repandum*, but not with all the characters attributed to the species by Wilks and Woelkerling (1994: figs. 1–10).

Species Description: Thalli are encrusting, 40–210 μm thick (Figure 68c,g), usually striated on their surface, which lacks erect protuberances, and have roundish margins (Figure 68a; but see Wilks and Woelkerling 1994: fig. 2D). Tetrasporangial conceptacles are spread over the thallus surface and usually show a characteristic depression on their roof (Figure 68b). Thallus growth is monopodial-dorsiventral with a polystromatic hypothallium, growing by terminal meristematic cells (Figure 68c). Hypothallial cells are 8–12 × 4–8 μm (L × B), and perithallial cells are ± isodiametric, 2–8 × 2–8 μm, diminishing in size toward the surface, and provided with characteristic, rectangular subepithallial cells, 2 × 5–6 μm (L × B; Figure 68d–f). Epithallial cells are lens shaped, 1–2 × 5–7 μm (L × B), and subepithallial meristematic cells can be wider than both young epithallial cells and perithallial cells below (Figure 68d–f). Fully grown thalli reach at least 340 μm in thickness, and the perithallium stands almost perpendicular to the hypothallium (Figure 68g).

Gametophytes are dioecious. A hermaphroditic conceptacle (chamber 100 × 65 μm; D × H) was seen (Figure 69a). Male conceptacles are 340–450 × 100–150 μm (D × H; Figure 69b), with chambers 150–290 × 60–70 μm (D × H) provided with both simple (unbranched) and dendroid spermatangial structures, the latter usually placed more centrally on the chamber floor (Figure 69c–f). SMCs on the floor are lunate (Figure 69c), whereas those of the roof are elongate (Figure 69f).

Carposporangial conceptacles are 380 × 120–150 μm (D × H), with chambers 300 × 140–200 μm (D × H), provided with peripheral carposporangia (Figure 70a). A central fusion cell was not located, but carposporangia develop laterally from the periphery of radiating gonimoblasts (Figure 70b).

Tetrasporangial conceptacles are 200–350 × 70 μm (D × H), provided with a convex roof. The roof is ~40 μm thick, composed of 7-celled filaments, becoming ~30 μm thick and composed of 4- or 5-celled filaments across the pore plate (Figure 70c). Epithallial cells of the pore plate deteriorate, leaving characteristic apical openings (Figure 70d,e). Canals (not seen) are described and illustrated to be straight, lacking differentiated pore cells (Wilks and Woelkerling 1994: fig. 6C,D). Empty embedded chambers are absent because "old conceptacles are shed as a result of successive development" (Wilks and Woelkerling 1994: 188, figs. 4A, 5C, 7A). However, the latter illustrations show older cavities filled in with new perithallial cells as they become embedded (and new conceptacles develop on top of them).

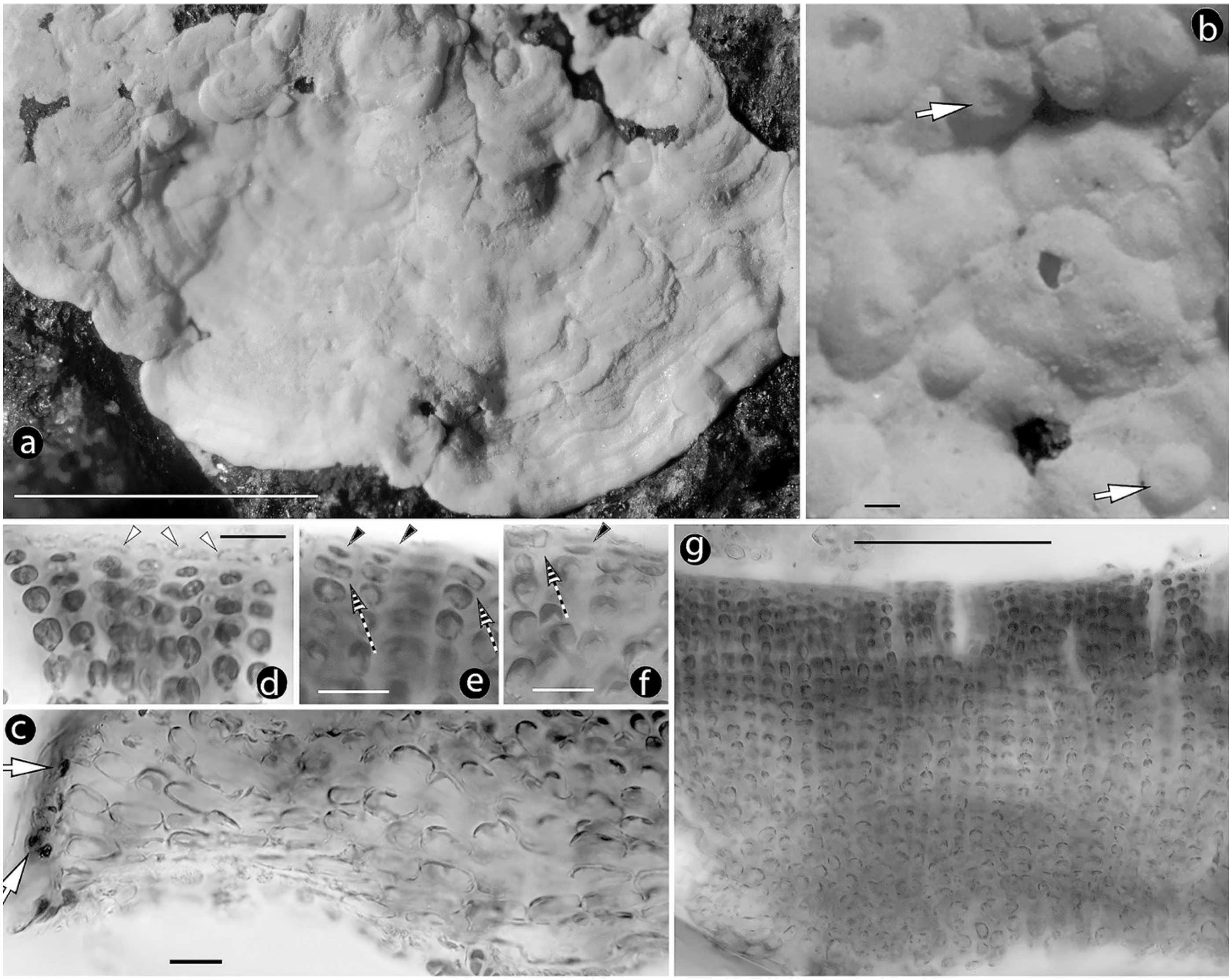


FIGURE 68. *Phymatolithopsis repanda*: vegetative structures (LTB16167C in (a) and (c), LTB16167B in (b) and (f), LTB15836 in (d), LTB15788 in (e) and (g)). (**a**) Encrusting thallus. Scale bar: 2 mm. (**b**) Tetrasporangial conceptacles with sunken pore plates (arrows). Scale bar: 100 µm. (**c**) thallus margin showing the hypothallium with terminal meristematic cells (arrows). Scale bar: 10 µm. (**d–f**) Deteriorating (white arrowheads) and new (black arrowheads) epithallial cells, with putative subepithallial cells (dashed arrows). Scale bars: 10 µm. (**g**) Thallus section showing isodiametric perithallial cells. Scale bar: 100 µm.

Comments: There have been contradicting reports about the development (or not) of a fusion cell and the place of development of carposporangia (Wilks and Woelkerling 1994: fig. 10; Harvey et al. 2003b: fig. 21C,D; Van der Merwe and Maneveldt 2014: 185, figs. 67–69). Still, these reports involve different collections and probably reflect misidentifications. In particular, Wilks and Woelkerling (1994: fig. 10A, LTB16167) showed carposporangial production across the floor (which occurs in the Sporolithales and Lithothamnionaceae), whereas their figure 10B (LTB15788) showed the peripheral type as confirmed in the present study (Figure 70a,b). Harvey et al. (2003b: fig. 21C,D) reported the distribution of carposporangia to be "across . . . the floor" but still recorded the presence of an "apparently discontinuous" fusion cell.

Finally, Van der Merwe and Maneveldt (2014: figs. 67, 69 vs. 68) showed peripheral versus across the floor development of carposporangia in two separate South African collections (UWC 93/200 vs. UWC 94/16), differing also in chamber size (~350 vs. 180 µm in diameter) and ostiole length (~170 vs. 45 µm).

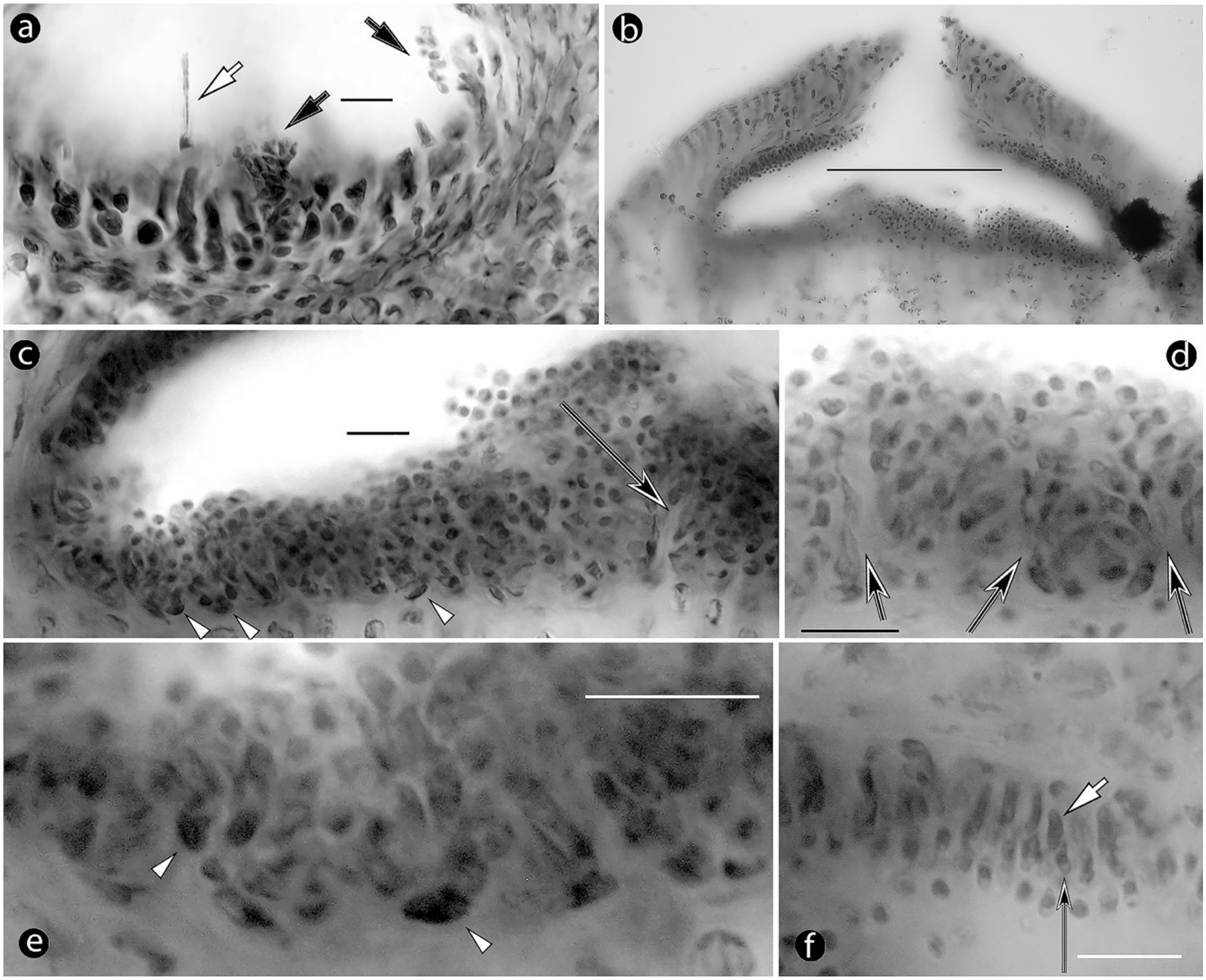


FIGURE 69. *Phymatolithopsis repanda*: male structures. (**a**) Hermaphroditic conceptacle with a carpogonial branch (white arrow) and dendroid spermatangia (black arrows) (LTB16167C). Scale bar: 10 µm. (**b**) Male conceptacle (LTB15836). Scale bar: 100 µm. (**c–e**) Spermatangial structures on the floor composed of simple (unbranched) and dendroid (black arrows) ones in the center of the chamber. Note the lunate SMCs (arrowheads) of the unbranched structures (LTB15836). Scale bars: 10 µm. (**f**) Unbranched spermatangial structures on the roof, with elongate spermatangia (white arrow) releasing spermatia (black arrow; LTB15836). Scale bar: 10 µm.

Obviously, the identification of these collections is unsatisfactory, demanding further studies that have to include a comparison with the lectotype (as selected by Adey and Lebednik 1967). More recently, the records of the species from South Africa were disproven (Jeong et al. 2022).

Several phylogenetic analyses of the nSSU gene have clustered isolates referred to *Leptothallia acervata*, *Leptophytum ferox*, *Leptophytum foveatum*, and *Phymatolithopsis repanda* within the Mesophyllaceae and remotely from *Lithothamnion-Phymatolithon* (Bailey and Chapman 1996: fig. 1, 1998: table 1, fig. 1; Broom et al. 2008: table 2, fig. 5; Bittner et al. 2011: table 2, fig. 1).

MELOBESIACEAE J. FRÜH

Melobesiaceae J. Früh 1890: 2, 4 (type: *Melobesia*).

Emended Diagnosis: Melobesiaceae comprise the subfamilies Orthocarpoideae subfam. nov. (monotypic),

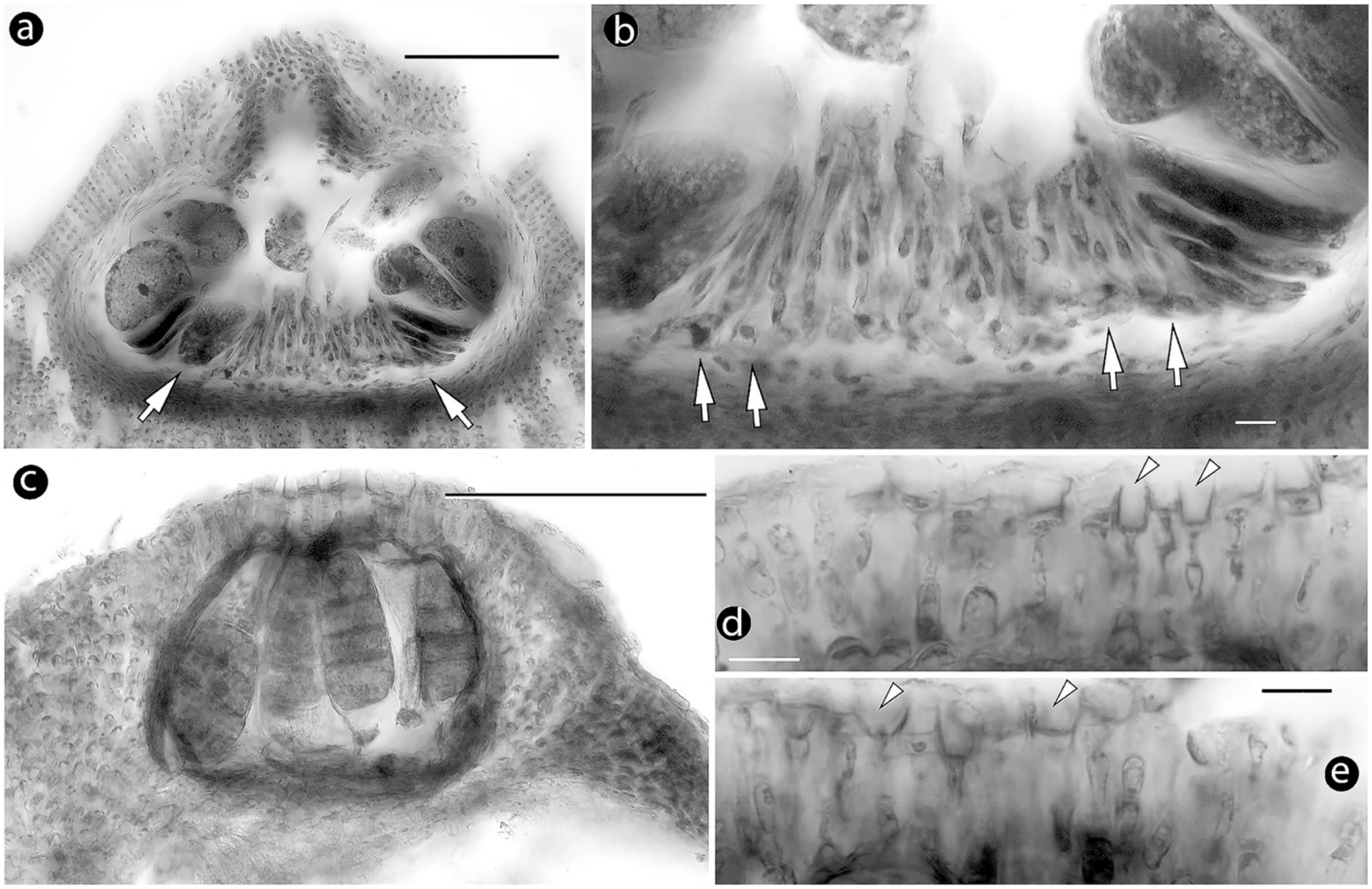


FIGURE 70. *Phymatolithopsis repanda*: carposporangial (LTB16788) and tetrasporangial (LTB16167B) structures. (**a**) Carposporangial conceptacle with peripheral development of carposporangia (arrows). Scale bar: 100 µm. (**b**) Peripheral carposporangia developed from gonimoblast filaments (arrows). Scale bar: 10 µm. (**c**) Tetrasporangial conceptacles with mature tetrasporangia. Scale bar: 100 µm. (**d, e**) Roof of tetrasporangial conceptacle with deteriorated epithallial cells (arrowheads). Scale bars: 10 µm.

Melobesioideae (*Boreolithon*, *Exilicrusta*, *Melobesia*), Choreonematoideae (monotypic), and Austrolithoideae (*Austrolithon* and *Epulo* R. A. Townsend et J. Huisman). They are segregated from their closest relative, the Mesophyllaceae, with regard to postfertilization events and, in particular, in lacking a cell tube (leading the zygote beyond the hypogynous cell to the supporting cell) and in producing instead a fusion cell between the lower part of the carpogonium and the subtending cells, from which gonimoblast filaments radiate and cut off carposporangia orthostichously and laterally. Members of the family share with the Mesophyllaceae the ancestral monopodial-dorsiventral thallus organization with a polystromatic hypothallium (Orthocarpoideae) or a heterotrichous organization (Melobesioideae) and development of sterile cells (Orthocarpoideae) and dendroid spermatangia (Orthocarpoideae) in addition to simple (unbranched) ones. Tetra- or bisporophytes exhibit multiporate conceptacles, with the exception of Choreonematoideae, which forms uniporate tetrasporangial conceptacles and exhibits a filamentous hypothallium.

Comments: Früh (1890: 1) recognized two families of fossil calcified algae, “der Siphoneae Grev. in der Trias von ostalpinem Typus und der Melobesiaceae in Eocen.,” and further considered the Melobesiaceae and the Corallinaceae to be a division of the marine Florideae (Früh 1890: 2). Under the heading “Melobesiaceae des Eocens.,” he stated, “Von den Corallineae durch den krusten-, blatt- oder korallenartigen Thallus verschieden, bilden sie mit denselben die Familie der Corallinaceae (einer Abtheilung der marinen Florideen), deren Thalluszellen durch Einlagerung” and “Die recenten Melobesiaceae der eropäischen Gewässer umfassen die Gattungen *Melobesia* Lamx, *Lithophyllum* Phil. und *Lithothamnion* Phil.,” and having also recognized the Melobesiaceae as a living family including several genera, he then described (Früh 1890: 4) the “Struktur der Lithothamnien.”: “1) *Der Lebenden Formen.* Litt. *Philippi . . .* 1837,” "*Rosanoff* . . . 1866," "*Solms Laubach* . . . 1881," "*Hauck* . . . 1885," adding that "Sämmtliche Melobesiaceae haben ursprunglich einen übereinstimmenden Thallus. Er besteht aus einer einzigen, fächerformigen, flach ausgebreiteten Zellschicht."

Previously, the name Melobesiaceae appeared in a systematic list by Cohn (1872) without references or a description. Waters (1876: 248) commented extensively on the Melobesiaceae, which he traced back to "Melobesiées" Rosanoff (1866). Waters noticed the existence of "recent Melobesiaceae . . . in the North temperate and Arctic zones." In placing "*Lithothamnium* [in] the family Melobesiaceae of the order Florideae," he observed (Waters 1876: 248) "structural difference . . . from the Corallinae . . . sufficient to separate . . . [them] into two entirely distinct classes." Still, in the title of his work, "Notes on Fossil Lithothamnia (So-Called Nulliporae)," Waters avoided the name, raising the question as to whether he finally accepted Melobesiaceae (as a family or class?) over "Nulliporae" (i.e., Nulliporaceae Johnston 1842, as *Nulliporidae*).

"The prostrate Melobesiaceae and Squamariaceae" also appeared without descriptions or references in Bennett and Murray's (1889) cryptogamic handbook.

The family is here expanded to receive the new genus *Orthocarpa*, with several congeners placed in the new subfamily Orthocarpoideae, differing from *Melobesia* mainly in possessing a dorsiventral thallus organization with polystromatic hypothallium, which is the ancestral condition in the coralline algae (see "Divisions of Corallinales"; Figure 1a). Therefore, the Melobesiaceae presently include four subfamilies: Orthocarpoideae subfam. nov. (monotypic), Melobesioideae (*Boreolithon*, *Exilicrusta*, *Melobesia*, all with heterotrichous thallus organization), Choreonematoideae (monotypic), and Austrolithoideae A. S. Harv. et Woelk. (*Austrolithon* A. S. Harv. et Woelk. and *Epulo* R. A. Townsend et J. Huisman). *Austrolithon* was placed in its own subfamily, differing from *Choreonema* in possessing a proper multiporate conceptacle roof (Harvey and Woelkerling 1995: figs. 32–39, 50), and *Epulo* (Townsend and Huisman 2004: 289) was added, differing from *Austrolithon* in "being parasitic and having conceptacles at host surface." *Boreolithon* was originally placed in the filamentous Austrolithoideae because it lacks cell fusions (Harvey and Woelkerling 1995), a character here considered to be secondarily lost (as in *Choreonema*).

The genera *Orthocarpa*, *Melobesia*, and *Choreonema* will be outlined below, the first two being considered the closest (outgroup) taxa to Mesophyllaceae. According to the present phylogenetic analyses (Figures 6a–c), the Melobesiaceae differ from the Mesophyllaceae by lacking a cell tube (transferring the zygote) and developing instead a fusion between the base of the carpogonium with the subtending cell (at least in *Orthocarpa* and *Choreonema*), the latter cells functioning as the site of the radiating gonimoblasts (Figure 3). Taking into consideration the reduced hypogynous cell in *Choreonema* (Figure 3c,d) and assuming this to be a relic condition (leading to the loss of hypogynous cells in *Melobesia* and *Orthocarpa*), cells subtending the carpogonium in other Melobesiaceae should be interpreted as a relocation of former supporting cells. This suggests that the relocation of the supporting (auxiliary) cell closer to the carpogonium resulted in making the zygote transfer via fusion possible (and the presence of a cell tube redundant). In addition, the Melobesiaceae produce orthostichous (as well as lateral) carposporangia from the periphery of the fertile zone (as in *Austrolithon intumescens* A. S. Harv. et Woelk. 1995: fig. 30).

Spermatangial structures in both *Melobesia* (Kylin 1928: fig. 20C; Wilks and Woelkerling 1991: figs. 16, 34) and *Choreonema* (Suneson 1937: pl. 3, fig. 10; Woelkerling 1987: figs. 19, 20, 1996: fig. 93D) are simple (unbranched) and lack lunate SMCs, which is also the case with the generitype of *Orthocarpa* (see genus account). However, in several other species of *Orthocarpa* we have dendroid (branched) spermatangial structures that should be interpreted as a plesiomorphic trait that is similarly maintained in certain Mesophyllaceae (e.g., *Macroblastum*, *Synarthrophyton*, *Amphithallia*, *Leptophytum*, *Leptothallia*, and *Phymatolithopsis*). In the Corallinales, dendroid spermatangia are entirely reduced with the advent of uniporate conceptacles (Figure 1a).

Gene phylogenies have indicated a peripheral position for both *Choreonema* and *Melobesia* in the Mesophyllaceae, with *Choreonema* being clustered with *Leptothallia acervata* (e.g., Harvey et al. 2003a: figs. 1, 2) and *Melobesia* being clustered with an undescribed species of *Lithothamnion*, but still on the periphery of Mesophyllaceae (Peña et al. 2020: figs. 2, 3).

ORTHOCARPOIDEAE ATHANAS. ET D. L. BALLANT. SUBFAM. NOV.

Orthocarpoideae Athanas. et D. L. Ballant. subfam. nov. (type: *Orthocarpa*).

Diagnosis: New monotypic subfamily of Melobesiaceae, differing from other members of Melobesiaceae in the development of sterile cells (beside carpogonia), dendroid (and simple) spermatangia, and a monopodial-dorsiventral thallus organization with polystromatic hypothallium.

Comments: Orthocarpoideae here accommodates the genus *Orthocarpa*, which includes species previously subsumed in the broad concept of *Synarthrophyton*, with the type of *Orthocarpa* (*O. epicklonia*) most likely being included in the broad concept of *Synarthrophyton patena* (see generic account of *Orthocarpa*). Inclusion of *Orthocarpoideae* in the Melobesiaceae results in the three diagnostic characters of the new subfamily also being included in the emended family diagnosis, as plesiomorphies.

***Orthocarpa* Athanas. et D. L. Ballant. gen. nov.**

Orthocarpa Athanas. et D. L. Ballant. gen. nov. (type: *O. epicklonia*).

Diagnosis: New genus of Melobesiaceae, differing from other members of the family in the characters of the subfamily Orthocarpoideae (as listed above) and sharing with *Melobesia* the development of gonimoblasts just below the carpogonia, orthostichous (as well as lateral) production of carposporangia, and straight canals in multiporate conceptacles lacking differentiated pore cells (except for basal cells).

Etymology: The generic name is a compound word of feminine gender, after the adjective ορθιος (standing) and the masculine substantive καρπος (fruit), referring to the erect production of carposporangia.

Comments: Apart from the generitype, *Orthocarpa* here accommodates eight more species, all previously placed in the genus *Synarthrophyton*. These species lack bilateral organization (which characterizes *Synarthrophyton*) and share a monopodial-dorsiventral thallus with polystromatic hypothallium, orthostichous production of carposporangia (except for *O. monumenta*), and straight canals of multiporate conceptacles lacking differentiated pore cells (except for basal pore cells). *Orthocarpa munimenta* further differs in possessing a slightly raised pedestal in carposporangial conceptacles, and these differentiations are here understood as autapomorphies that may support a different generic position (in the Orthocarpoideae).

Sterile cells, borne beside the carpogonium, have been reported in most species of *Orthocarpa*, and this appears to be one more character separating Orthocarpoideae from the other Melobesiaceae.

The mode of gonimoblast development remains to be investigated in most congeners, with *O. epicklonia* and *O. haptericola* apparently sharing production of gonimoblasts just below the carpogonia (as described below). Spermatangial structures range from strictly unbranched (*O. epicklonia*) to rarely branched (*O. eckloniae*) or well branched in most other members, with *O. haptericola* possessing typical dendroid (well-branched) ones. Monoecy versus dioecy divides *Orthocarpa* into two groups, with *O. magellanica* said to possess both conditions. However, it cannot be precluded that the phenomenon of mixed phases underlies such reports.

Multiporate conceptacles may have sunken pore plates or may be embedded in the thallus in different species, a variation also described for genera of Mesophyllaceae, such as *Mesophyllum* and *Leptophytum*. Several species (*O. epicklonia*, *O. eckloniae*, *O. haptericola*, *O. monumenta*, *O. pseudosora*) are recorded as epiphytes on *Ecklonia radiata* (C. Agardh) J. Agardh or *E. maxima maxima* (Osbeck) Papenfuss. Comparative data between the nine here recognized species of *Orthocarpa* are given in Table 6.

Orthocarpa epicklonia Athanas. et D. L. Ballant. sp. nov.

FIGURES 71–74

Orthocarpa epicklonia Athanas. et D. L. Ballant. sp. nov.

Diagnosis: The new species grows on *Ecklonia radiata* and differs from its putative sister taxon *Orthocarpa eckloniae* (which grows in South Africa on the stipes and holdfasts of *Ecklonia maxima*) in lacking dendroid (sparsely branched) spermatangial structures and embedded conceptacles and in developing a thinner thallus (to 210 vs. 600 μm), trichocytes, and tetrasporangial conceptacles (vs. bisporangial conceptacles) with a thinner roof (5-celled and 25–30 μm thick vs. 5–7-celled and to 78 μm thick), with canals surrounded by 5–7 (vs. 7–9) rosette cells.

Etymology: The epithet is a new compound word of feminine gender, after the adverb επι (upon) and the brown algal genus *Ecklonia*, commemorating the Danish botanist Christian Friedrich Ecklon (1795–1868). It is used as a noun in apposition and refers to the epiphytic nature of the species.

Type Locality: Exposed littoral, on holdfasts of the brown alga *Ecklonia radiata*, Rye Beach, Melbourne, Victoria, southern Australia.

Holotype: In GB (GB-0209475), a sterile specimen, November 1989, coll. Athanas. (Figure 71a).

Isotypes: Slides from the holotype in herb. Athanas. (Figure 71b–f).

Paratypes: Tetrasporangial and gametangial specimens (including slides; in herb. Athanas.; Figures 71g,h, 72–74).

Material Examined: Southern Australia: Victoria: Rye Beach: gametangial, tetrasporangial, and sterile thalli (holotype, isotypes, and paratypes, as described above and below).

Habitat and Distribution: Thalli encrust (and envelop) the holdfasts of the brown alga *Ecklonia radiata* in the exposed littoral zone. Known only from the type locality.

Species Description: Thalli are at least 2 cm in extent, 40–210 μm thick, lacking erect perithallial protuberances and exhibiting superimposed unattached growth, encrusting the holdfasts (haptera) of *Ecklonia* (Figure 71a). The thallus organization is monopodial-dorsiventral with a polystromatic noncoaxial hypothallium, 40–150 μm thick, supporting descending hypothallial and ascending perithallial filaments (Figure 71b,c). The ascending perithallium is 30–50 μm thick and nonstratified (Figure 71c). Hypothallial cells are 4–30 × 4–10 μm (L × B), and perithallial cells are 3–18 μm × 3–8 (L × B). Epithallial cells are roundish to rectangular, singly borne, 2–3 × 2–7 μm (L × B), and supported by elongate subepithallial cells 5–15 μm long (Figure 71d,e). Descending hypothallial filaments end in wedge-shaped cells (Figure 71f). Terminal trichocytes are 8–12 × 6–7 μm (L × B) with an elongate sprout to 25 μm and may rarely occur in groups among epithallial cells (Figure 71g). Thallus regeneration may occur in superimposed unattached pattern (Figure 71h). Cell fusions are present. Secondary pit connections are absent.

Gametophytes are monoecious. A male conceptacle, 150 × 50 (D × H), is provided with a chamber 140 × 50 μm (D × H) and is placed next to a carposporangial one (Figure 72a). Spermatangial structures are simple (unbranched) and occur on the floor, the walls, and the roof. SMCs are rectangular (not lunate), producing from their upper part spermatangia that release spermatia (Figure 72b,c).

Carpogonial conceptacles are 500–570 × 150–200 μm (D × H) with chambers 190–200 × 50 μm (D × H; n: 2;

TABLE 6. Comparative data for species of *Orthocarpa*. Abbreviations: cont., continuous; discont., discontinuous; epiph., epiphyte; f., figure; holdf., holdfasts; hypog., hypogynous; ND, no data; nondiff., nondifferentiated; NSW, New South Wales, SUG, superimposed unattached growth; supp., supporting.

Characteristic	*O. epicklonia*[a]	*O. eckloniae*[b]	*O. haptericola*[c]	*O. magellanica*[b]	*O. papillata*[d]	*O. munimenta*[e]	*O. robbenensis*[e]	*O. pseudospora*[f]	*O. chejuensis*[g]
Distribution	Victoria, southern Australia	Eastern Cape Province, South Africa	New Zealand, Stewart and Chatham Islands	Tierra del Fuego, Falklands, Kerguelen, Gough and Macquarie Island, southern Namibia	Northern and Western Cape Provinces, South Africa	South Africa, southern Namibia	Western Cape Province, South Africa	NSW, eastern Australia	Cheju Island, Korea
Substratum	Epiphyte on *E. radiata* holdf.	Epiph. on *E. maxima* stipes–holdf.	Epilithic, epizoic, *E. radiata* holdf.	Epilithic, epizoic	Epilithic, epizoic	Epilithic, epizoic, *E. maxima* stipes-holdf.	Epilithic	Epizoic, epiph., *E. radiata* holdf.	Epiph., epizoic, epilithic
Thallus habit and thickness	Encrusting, SUG, adhering weakly, to 210 µm	Encrusting, adhering, to 600 µm	Irregular foliose, SUG, to 400 µm	Encrusting, SUG adhering weakly–firmly, to 550 µm (2 mm)	Encrusting, warty, adhering firmly, to 700 µm	Encrusting, warty, adhering firmly, to 3,500 µm	Encrusting, warty, adhering firmly, to 1,600 µm	Encrusting, foliose, SUG, to 400 µm (f.30E)	Irregular foliose, SUG, to ~400 µm (f.17)
Ventral epithallia	Absent	Absent	Present	Absent / present	Present? (f.9)	Absent	Absent	Present (f.26C)	Locally present
Ventral perithallia	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Locally present
Hypothallium	Noncoaxial	Noncoaxial	Noncoaxial	Noncoaxial (coaxial patches)	Noncoaxial	Noncoaxial	Noncoaxial	Noncoaxial	Noncoaxial
Trichocytes	Present	Absent	Absent	Present	Present (rare)	Absent	Absent	Absent	Absent
Gametophytes	Monoecious	Monoecious	ND	Monoecious / dioecious	Dioecious	Monoecious	Dioecious	Dioecious	Monoecious / dioecious
Sterile cell	Present	Present ? (f.16)	Present	Present	Present	Present	Present	ND	Present
Fusion cell	2–3 supp. cells	2–3 supp. cells (f.17)	2–3 supp. cells (f.32)	“discont.” (f.44)	“± cont.” (f.23)	“discont.” (f.49)	“discont.” (f.19)	“discont.” (f.31D)	“discont.” (f.32)
Gonimoblast development	Hypog. cell	Hypog. cell?	Hypog. cell (f.31,32)	ND	ND	ND	ND	ND	Supp. cell? (f.32)
Pedestal in carposporangial conceptacles	Absent	Absent	Absent	Absent	Absent	Present (f.49)	Absent	Absent	Absent
Orthostichous carposporangia	Present	Present (f.17)	Present	Present (f.44)	Present (f.23)	Absent (f.49)	Present (f.19)	Present (f.31C,D)	Present (f.32)
Spermatangia	Unbranched	Dendroid (sparsely branched)	Dendroid and unbranched?	Dendroid	Dendroid	Dendroid	Dendroid	Dendroid and unbranched	Unbranched and dendroid?
Pore plate sunken	Absent	Absent	Present	Absent	Absent	Present	Present	Absent	Absent

(*continued*)

TABLE 6. (*Continued*)

Characteristic	*O. epicklonia*[a]	*O. eckloniae*[b]	*O. haptericola*[c]	*O. magellanica*[b]	*O. papillata*[d]	*O. munimenta*[e]	*O. robbenensis*[e]	*O. pseudospora*[f]	*O. chejuensis*[g]
Pore filaments	5-celled, nondiff., (except basal cells)	5–6 (7)-celled, nondiff. (f.17, 24)	5-6(7)-celled, nondiff.	4–5-celled, nondiff. (f.47, 63–64)	5–6-celled (f.29), nondiff.	5–7-celled (f.51), nondiff.	3–4-celled (f.28), nondiff.	4–6-celled (f.30B), nondiff.	5–6-celled (f.42), nondiff. (except basal and subbasal cells?)
Canal shape	Straight	Straight	Straight	Straight	Straight	Straight	Straight	Straight	Straight or pyriform? (f.42)
Rosette cells	5–7	7–9	ND	5–8	6–8	6–8 (sunken)	5–8	ND	7–8
Embedded conceptacles	Absent	Present (rarely)	Absent	Present / absent	Present	Present	Absent	Present	Absent
Bisporangia / tetrasporangia	Absent / present	Present / absent	Absent / present	Absent / present	Absent / present	Present / present	Present / present	Absent / present	Present / present

[a] Present study.
[b] Keats and Chamberlain (1997, as *Synarthrophyton*).
[c] Woelkerling and Foster (1989, as *Synarthrophyton schielianum*) and present study.
[d] Maneveldt et al. (2007, as *Synarthrophyton*).
[e] Keats and Maneveldt (1997b, as *Synarthrophyton*).
[f] Harvey et al. (2003b, as *Synarthrophyton*).
[g] Kim et al. (2004: figs. 1–44) and Masaki (1968: 11, pls. 5–6, 43–44, as *Lithothamnium cystocarpideum* “*prox.*”).

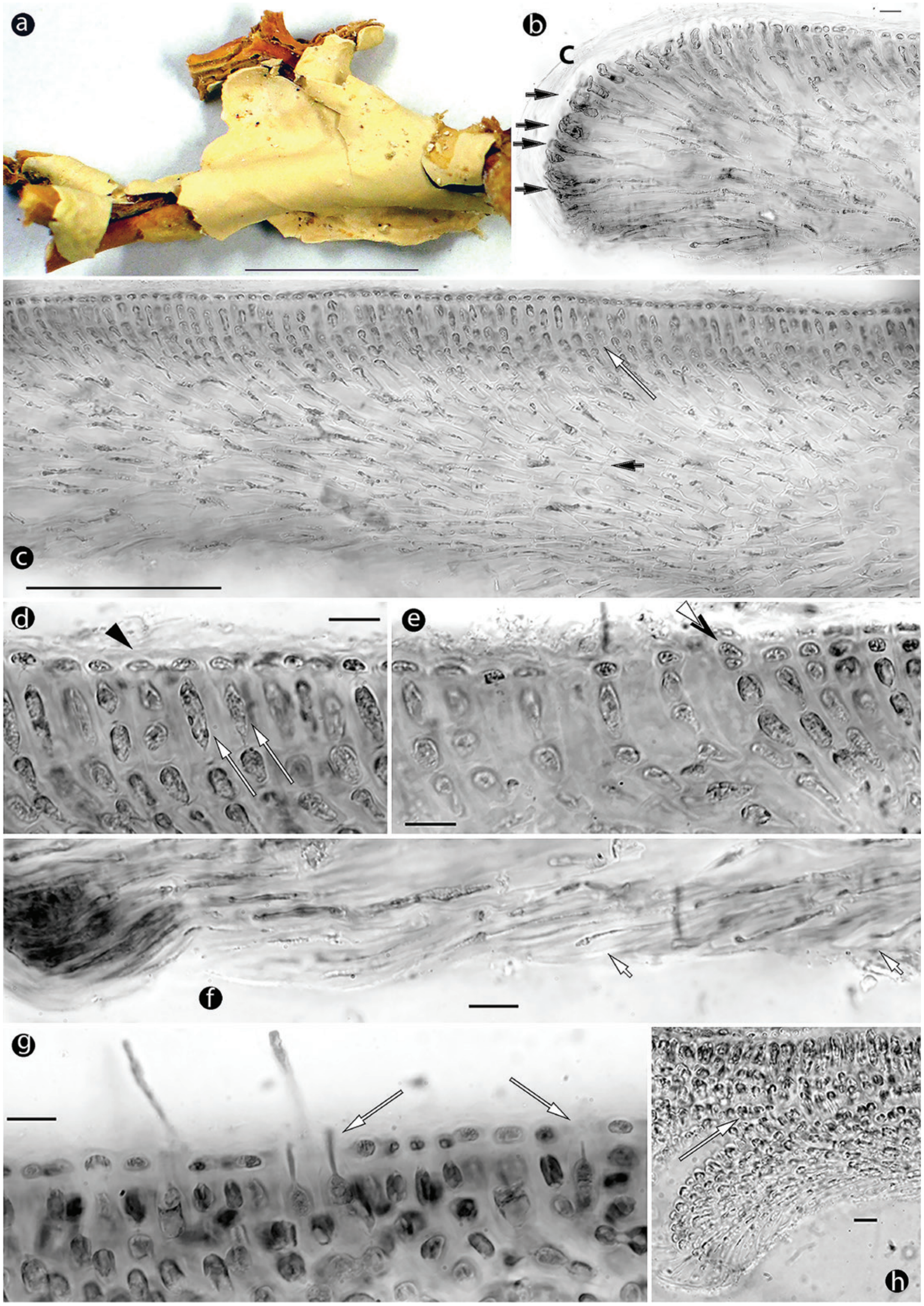


FIGURE 71. *Orthocarpa epicklonia*: vegetative structures. (**a**) Holotype in GB (GB-0209475) attached to holdfasts of *Ecklonia maxima*. Scale bar: 1 cm. (**b**) Section at the margin showing terminal meristematic cells (arrows) protected by a cuticle and undergoing asynchronous divisions and elongations, producing a noncoaxial hypothallium (isotype). Scale bar: 10 µm. (**c**) Section showing a noncoaxial hypothallium (black arrow) supporting an ascending perithallium (white arrow) lacking stratification (isotype). Scale bar: 100 µm. (**d, e**) Section at the surface showing elongate subepithallial cells (arrows) supporting 1 (arrowhead) or 2 (double arrowhead) epithallial cells (isotype). Scale bars: 10 µm. (**f**) Descending hypothallial cells ending in wedge-shaped cells (arrows; isotype). Scale bar: 10µm. (**g**) Terminal trichocytes (arrows) among epithallial cells (paratype). Scale bar. 10 µm. (**h**) Thallus regeneration (arrow) from the perithallium (paratype). Scale bar: 10 µm. Abbreviation: c, cuticle.

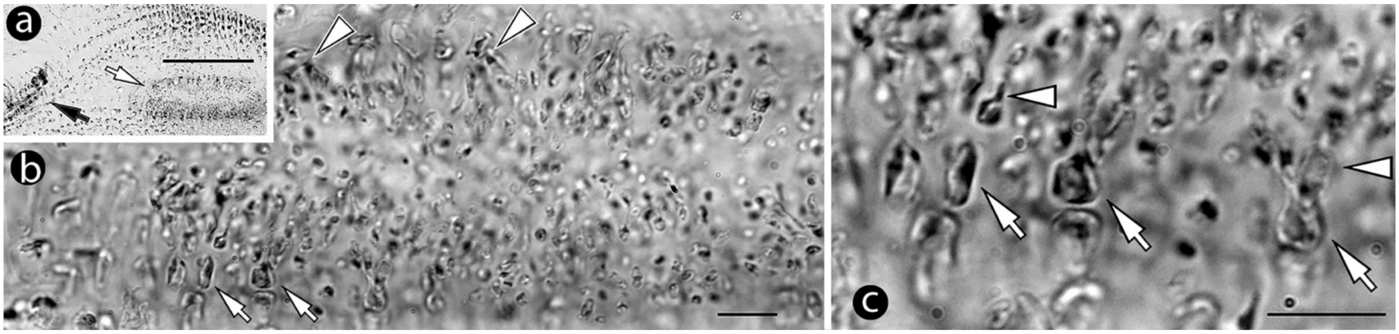


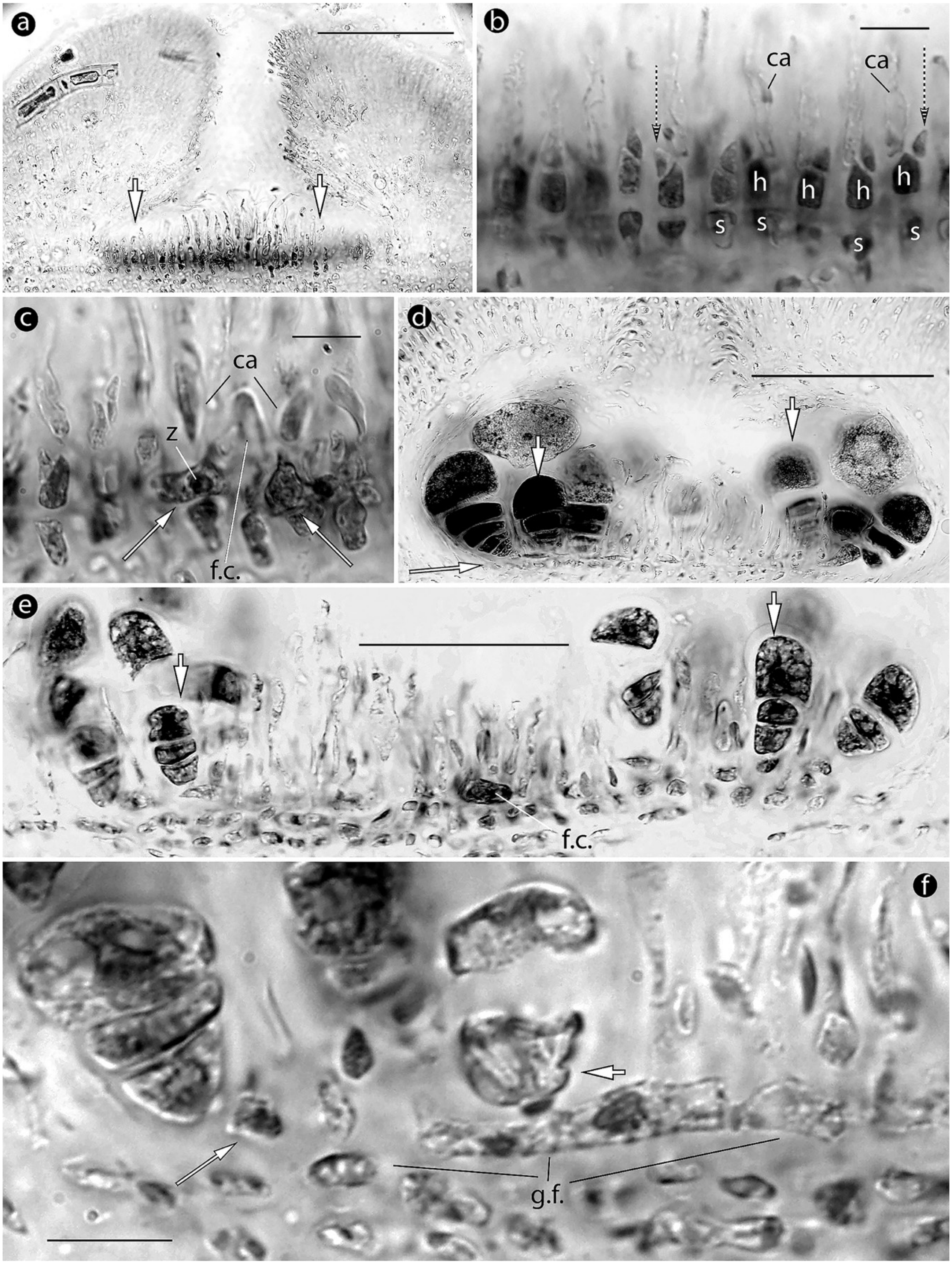
FIGURE 72. *Orthocarpa epicklonia*: male structures (paratype). (**a**) Male (white arrow) and carposporangial conceptacles (black arrow). Scale bar: 100 µm. (**b**) Chamber with simple (unbranched) spermatangial structures on the floor (arrows) and the roof (arrowheads). Scale bar: 10 µm. (**c**) Elongate SMCs (arrows) supporting spermatangia (arrowheads) that release spermatia. Scale bar: 10 µm.

Figure 73a). Carpogonial branches are 3-celled, composed of the carpogonium, the hypogynous, and the supporting cells, all staining similarly (Figure 73b). A sterile cell may exist next to the carpogonium (Figure 73b). Presumed fertilization results in fusion cell(s) between subtending cells, contiguous cells (at the same level), and the basal part of the carpogonium (Figure 73c). The occurrence of a zygote in such a fusion is documented (Figure 73c). Gonimoblast filaments develop just below the carpogonia and produce carposporangia from the periphery, both laterally and in the orthostichous position (Figure 73d–f). Carposporangial conceptacles are 450–540 × 50–250 µm (D × H), with chambers 220–290 × 90–130 µm (D × H; n:3), lacking a pedestal on the floor. The roof is 40–120 µm thick, with a central ostiole 50 × 100–120 µm (D × H).

Multiporate (tetrasporangial) conceptacles are 420–575 × 100 µm (D × H), with chambers 270–300 × 100–110 µm (D × H; n: 2; Figure 74a). The roof is convex, 25–30 µm thick, composed of 5-celled filaments, with pore plates 170–240 µm in diameter (n: 2) perforated by 54–81 canals. Canals are straight, 7–10 µm in diameter, surrounded by 5 to 7 rosette cells (Figure 74b) that are flush with the surface. Pore filaments are generally composed of nondifferentiated cells, expect for basal cells, which can be slightly thinner and project outward (Figure 74d,e). A plug, possibly a sporangial remain, was seen blocking the basal opening (Figure 74e). Tetrasporangia are 60–115 × 12–40 µm (L × B; n: 20) with initials 65 × 10 µm (L × B; Figure 74c). Bisporangia were not seen. Older conceptacles are not embedded in the thallus.

Comments: This is most likely the species illustrated by Harvey et al. (1994: fig. 2) and Woelkerling (1996: fig. 90B,E,F) growing on the holdfasts of *Ecklonia* and referred to *Synarthrophyton patena* (Hook. f. et Harv.) R. A. Townsend. However, *Orthocarpa epicklonia* differs both in habit and habitat, as well as in vegetative and reproductive features, including an encrusting thallus (vs. mainly unattached, discoidal in *S. patena*), dorsiventral organization (vs. bilateral in *S. patena*), monoecious reproduction (vs. dioecious in *S. patena*), nondifferentiated pore cells in straight canals of smaller multiporate conceptacles (vs. double-size conceptacles with differentiated pore cells toward the base of triangular canals in *S. patena*), nondifferentiated SMCs (vs. lunate in *S. patena*), and, most characteristically, the development of gonimoblast filaments just below carpogonia and orthostichous production of carposporangia (vs. at the level of supporting cells and lateral production of carposporangia in *S. patena*). The new species is closely related to *Orthocarpa eckloniae* (see species account), which grows on the stipes and holdfasts of *Ecklonia maxima* (Osbeck) Papenfuss in South Africa. The South African relative differs in lacking trichocytes and tetrasporangia and possessing dendroid (sparsely branched) spermatangial structures, a thicker thallus (to 600 µm) with

FIGURE 73. (*Opposite*) *Orthocarpa epicklonia*: carpogonial and carposporangial structures (paratype). (**a**) Carpogonial conceptacle with carpogonial branches across the entire floor (arrows). Scale bar: 100 µm. (**b**) Three-celled carpogonial branches composed of a carpogonium, a hypogynous cell, and a supporting cell. Note the sterile cells (dashed arrows). Scale bar: 10 µm. (**c**) Postfertilization stages showing the fusion (arrows) between several subtending cells just below the carpogonia and the presence of a putative zygote. Scale bar: 10 µm. (**d–f**) Orthostichous (short white arrows) and lateral (long white arrows) production of carposporangia from the periphery. Note the remains of the fusion cell and the gonimoblast filaments. Scale bars: 100, 50, and 10 µm, respectively. Abbreviations: ca, carpogonium; f.c., fusion cell; g.f., gonimoblast filament; h, hypogynous cell; s, supporting cell; z, zygote.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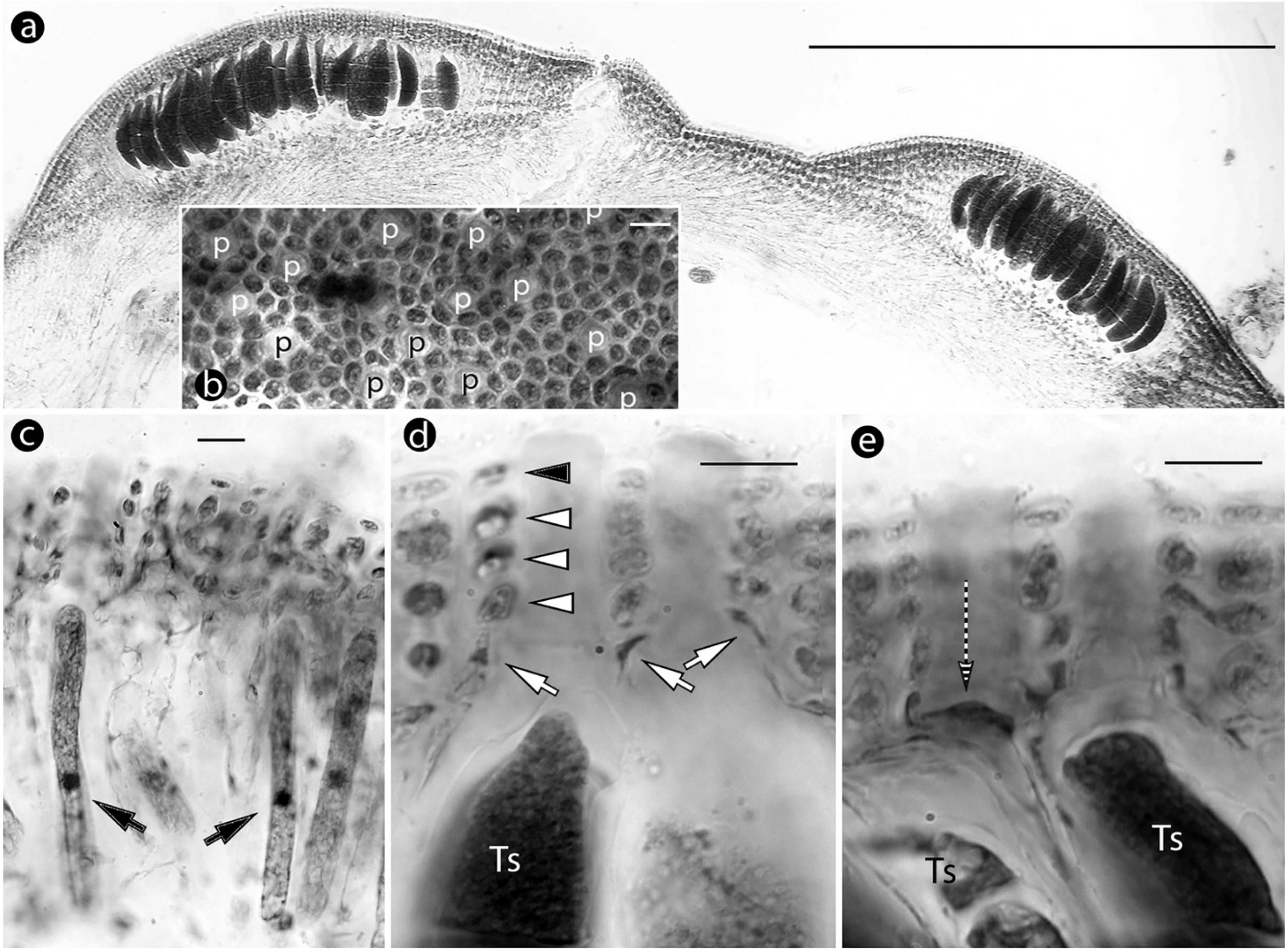


FIGURE 74. *Orthocarpa epicklonia*: multiporate conceptacle structures (paratype). (**a**) Tetrasporangial thallus with convex conceptacles. Scale bar: 500 µm. (**b**) Surface view of a pore plate with canals surrounded by 5 to 6 rosette cells. Scale bar: 10 µm. (**c**) Section of chamber showing sporangial initials (arrows). Scale bar: 10 µm. (**d, e**) Section of straight canals showing nondifferentiated pore cells (white arrowheads) ending in epithallial cells (black arrowhead) and thinner basal cells (white arrows). Note also the presence of a plug (dashed arrow). Scale bars: 10 µm. Abbreviations: p, pore canal; Ts, tetrasporangia.

embedded conceptacles, thicker bisporangial conceptacle roofs (to 78 µm thick, composed of 5- to 7-celled filaments), and pore canals surrounded by 7 to 9 rosette cells (Table 6). However, both species are known from a limited number of studies and collections, and further studies may reveal a different set of common or distinguishing characters. A further taxon that could be related is *Mesophyllum vescum* (incertae sedis Melyvonneeae).

The holotype of *Orthocarpa epicklonia* was selected from collections made during an excursion to Rye Beach arranged by William Woelkerling and accompanied by Deborah Penrose. Several specimens were found attached on the holdfasts of *Ecklonia*, one of which was herein selected as the holotype, with all other specimens becoming paratypes and topotypes.

Orthocarpa eckloniae (Foslie) Athanas. et D. L. Ballant. comb. nov.

Orthocarpa eckloniae (Foslie) Athanas. et D. L. Ballant. comb. nov.
Basionym: Lithothamnion capense f. *eckloniae* Foslie 1902a: 19.
Homotypic Synonyms: Lithothamnion eckloniae (Foslie) Foslie 1907b: 3.
Synarthrophyton eckloniae (Foslie) D. W. Keats et Y. M. Chamb. 1997: 56, figs. 1–27, tables 1–2.

Type Locality: Hout Baai, Cape of Good Hope, South Africa.

Type Material: In TRH (B2-1685), Adey and Lebednik (1967: 51, “type material,” “W.v.Bosse, Cape of Good Hope, Houtbai, 1893 [slides] 701, 731”), Woelkerling (1993a: 81, “holotype,” “slides 701, 731, 1555”), Woelkerling and Verheij (1995: 51, “isotype” in L), illustrated by Keats and Chamberlain (1997: 58, fig. 1, “holotype”), Woelkerling et al. (2005: 238–239, “holotype”).

Habitat and Distribution: The species grows in the sublittoral zone attached to the stipes and occasionally holdfasts of *Ecklonia maxima* (Osbeck) Papenfuss. Fertile thalli have been collected in February, August, and October–December (but no collections have been made in other months). It is recorded only from Western Cape Province (South Africa; Keats and Chamberlain 1997: 57).

Comments: The Norwegian protologue (Foslie 1902a: 19) reads (in translation), a form of *Lithothamnion capense* growing on *Ecklonia* differs from the autonym [*Lithothamnion capense* = *Capensia fucorum*] having smaller and significantly lower conceptacles, and hence it is taken up as a distinct form, f. *eckloniae*.

No locality or collector was given, but in a later account, Foslie (1907b: 3) elevated f. *eckloniae* to species, commenting (in translation) that it

> encircles as a crust the haptera of *Ecklonia*, 100–250 µ thick, with flat surface; [multiporate] sporangial conceptacles weakly convex, later slightly but prominently sunken in the middle, 400–600 µ in diameter; sporangia four-parted, 130–160 µ long and 40–85 µ in diameter; cystocarpic-conceptacles weakly convex, 400–600 µ in diameter. In a vertical section, the hypothallium may be weakly developed, or occupy the main part of the crust thickness; cells are 14–36 µ long and 6–9 µ broad. Perithallial cells are partly sub square, 7–9 µm, partly and mostly vertically elongated, 9(7)–11(14) µ long. The sunken roof of the sporangial conceptacles is perforated by 20–30 mucous canals. *Lithoth. Eckloniae* stands close to *L. capense* [*Capensia fucorum*]. The plant differs though by the flat thallus, that does not form projections when several crusts meet, and it never grows free or develops small proliferations as in the last named species. In addition, it is characterized by the more elongate perithallial cells. The conceptacles are lower. Amongst the real encrusting species it comes closest to *L. magellanicum*.- Cape of Good Hope: Houtbaai (A. Weber-van Bosse).

The original material in TRH was not illustrated by either Foslie (1902a, 1907b) or Printz (1929). Type material from TRH was photographed by Keats and Chamberlain (1997: figs. 1, 25–27) and was considered to represent the entire gathering (“holotype”). The latter authors also studied holotype fragments in section, illustrating carpogonial-carposporangial, bisporangial conceptacles, and the structure of the pore plate (Keats and Chamberlain 1997: fig. 27). These structures were shown to be similar to recently collected specimens (Keats and Chamberlain 1997: figs. 18, 23–24). However, in his later account Foslie (1907b) mentioned tetrasporangial conceptacles and a sunken roof and also that the thallus never grows free, characters that agree with *Capensia fucorum*, and it is possible that Foslie mixed up the two species (*O. eckloniae* vs. *C. fucorum*).

“Isotype” material was reported by Woelkerling and Verheij (1995: 51) in L, but it was neither illustrated nor described in detail, and it is not clear if this Leiden element represents a different gathering or a part of the “holotype” (TRH). *Orthocarpa eckloniae* resembles *O. epicklonia*, and their close relationship may also reflect the speciation in the genus *Ecklonia*, which is represented by two species in South Africa (*E. radiata* and *E. maxima*; Silva et al. 1996), three other species in Japan (Yoshida et al. 2015: 144), and *E. radiata* in southern Australia (Womersley 1987). *Orthocarpa eckloniae* has been reported as an epiphyte on *E. maxima* and is so far recorded from the type locality (Hout Baai), Oudekraal in the Cape Peninsula, Doringbaai on the west coast, and Betty’s Bay (SE of False Bay; Keats and Chamberlain 1997: 57). Comparative data with congeners are given in Table 6. Another taxon that could be related to *O. eckloniae* is *Mesophyllum vescum* (see incertae sedis Melyvonneeae), described as an epiphyte on *Ecklonia* from Japan and possessing a minute thallus (to 5 mm in diameter) with bisporangial conceptacles.

Orthocarpa hoptericola **(Foslie) Athanas. et D. L. Ballant. comb. nov.**

FIGURES 75–79

Orthocarpa haptericola (Foslie) Athanas. et D. L. Ballant. comb. nov.

Basionym: Lithothamnion haptericola Foslie 1906a: 8, “*haptericolum*.”

Homotypic Synonym: *Mesophyllum haptericola* (Foslie) W. H. Adey 1970: 24.

Heterotypic Synonyms: ?*Lithophyllum rhizomae* Heydrich 1897a: 51, pl. 3, fig. 4; type locality: Bay of Islands, New Zealand; type: not designated.

Synarthrophyton schielianum Woelk. et M. S. Foster 1989: 40; type locality: Chatham Islands; holotype: in WELT (A17854).

Type Locality: On holdfasts of *Ecklonia*, Island Bay, near Wellington, North Island, New Zealand.

Lectotype: In TRH (B17-2549), Printz (1929: pl. 6, fig. 11), Adey and Lebednik (1967: 68, “type material,” “§ Setchell, N.Z., N.Is., Is.Bay, 6.1904, no.6351, LM6(11) [slides] 1171, 1172”), Woelkerling (1993a: 114, “holotype”), Woelkerling et al. (2005: 342, “holotype”).

Syntype: In UC (745591, Setchell no. 6351, includes two slides, North Island, Island Bay, near Wellington, New Zealand; Figures 75, 76).

Material Examined: New Zealand: Island Bay: syntype in UC (745591, Setchell no. 6351, includes two slides and three

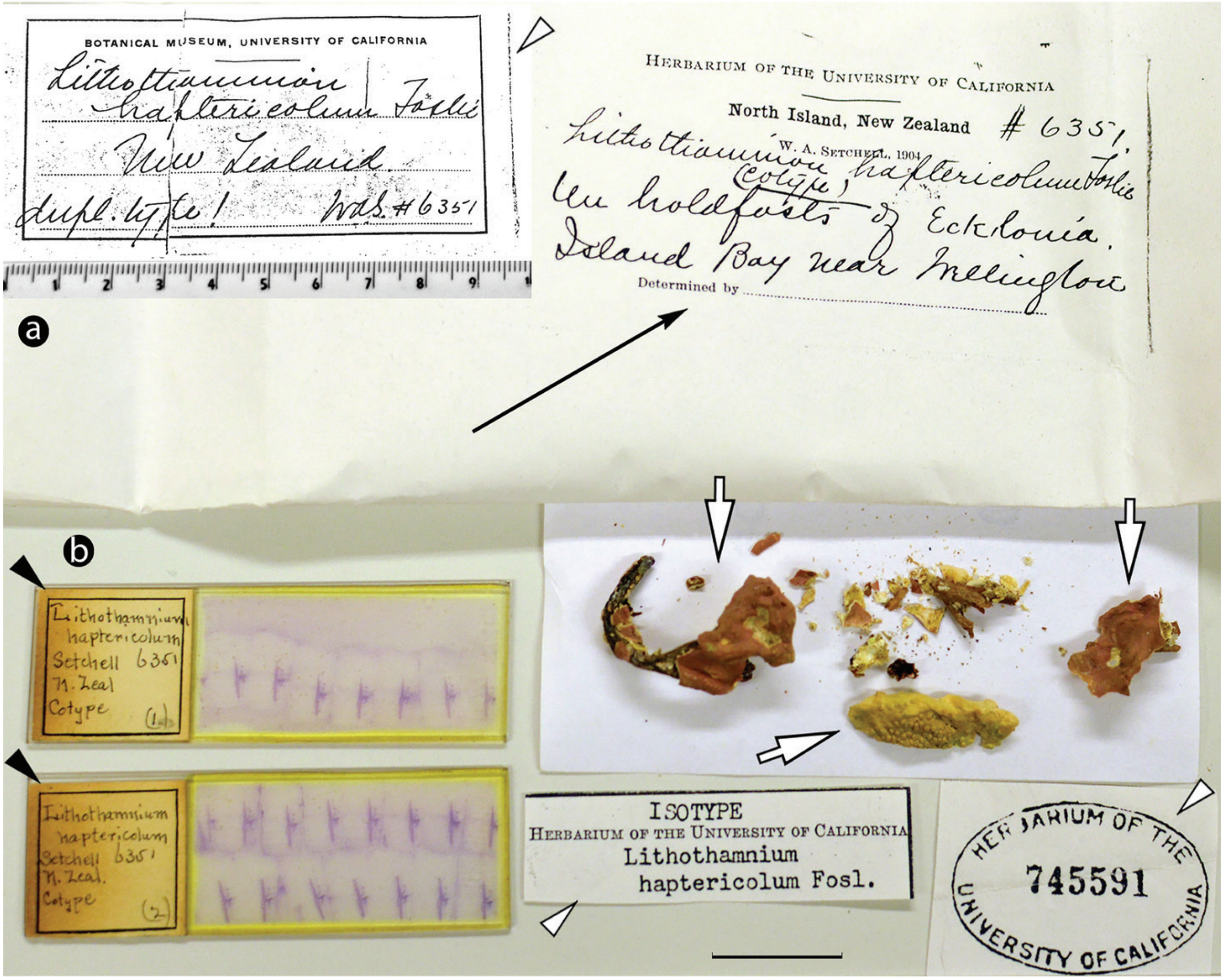
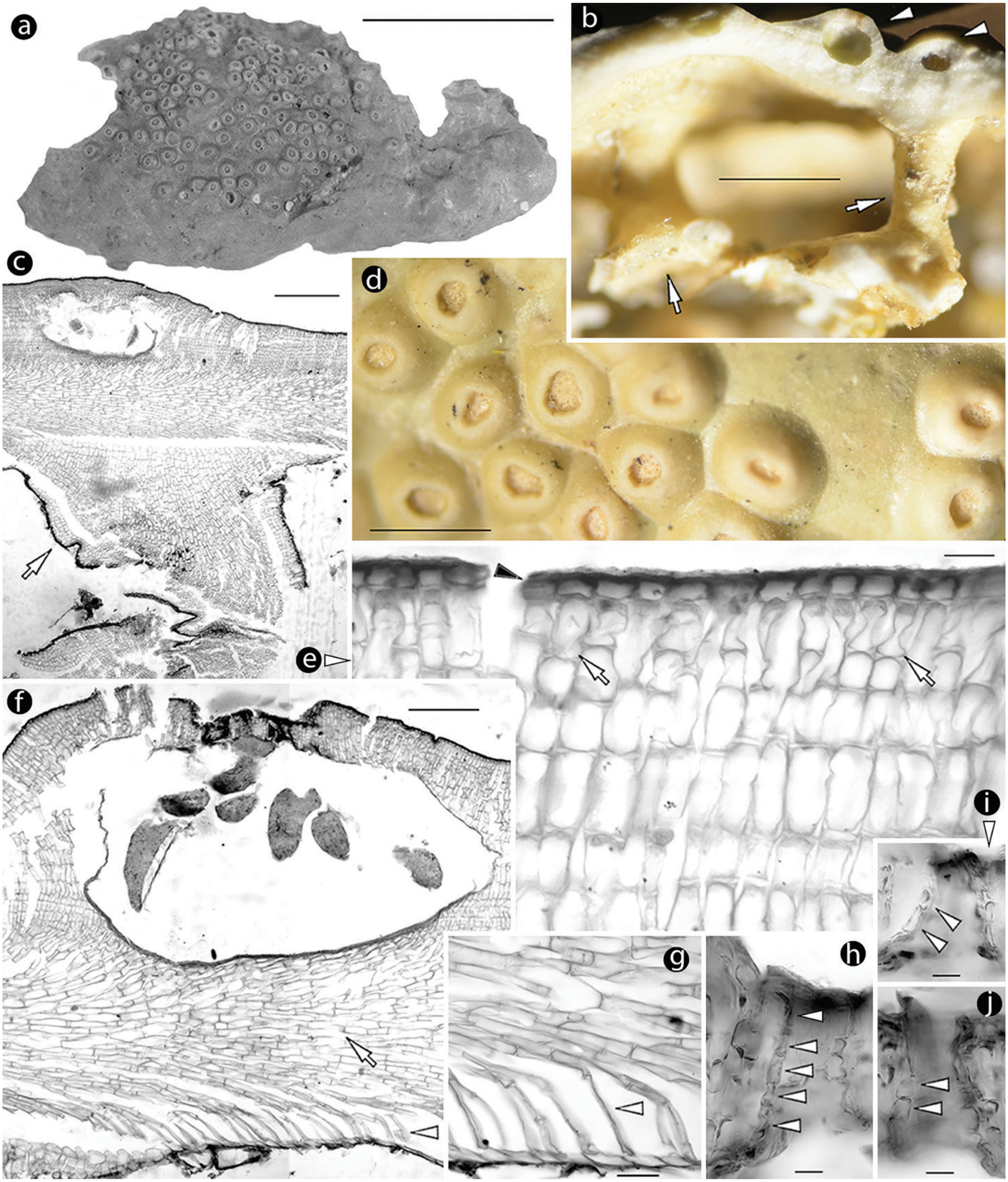


FIGURE 75. *Orthocarpa haptericola*: syntype of *Lithothamnion haptericola* in UC (745591). (**a**) The folder (black arrow) containing the material and one etiquette (arrowhead). Scale in centimeters. (**b**) Three thalli (white arrows), two slides (black arrowheads), and two more labels (white arrowheads) included in the folder. Scale bar: 2 cm.

FIGURE 76. (*Opposite*) *Orthocarpa haptericola*: vegetative and multiporate conceptacle structures (syntypes in UC; (c) and (e)–(g) from Setchell slides). (**a**) Surface view of the largest specimen in UC with volcano-like conceptacles. Scale bar: 1 cm. (**b**) Section showing two struts (arrows) with pads and two conceptacles (arrowheads). Scale bar: 1 mm. (**c**) Section of a descending strut (arrow). Scale bar: 200 µm. (**d**) Surface view of several volcano-like, multiporate conceptacles. Scale bar: 1 cm. (**e**) Section at the surface showing isodiametric-rectangular epithallial cells (arrowhead) supported by elongate (arrows) subepithallial cells. Scale bar: 10 µm. (**f**) Section of a multiporate conceptacle. Note the noncoaxial hypothallium (arrow) and the narrow subbasal hypothallial cells (arrowhead). Scale bar: 200 µm. (**g**) Section at the base showing the narrow subbasal hypothallial cells (arrowhead) that end in rhomboid cells. Scale bar: 10 µm. (**h–j**) Sections through canals of multiporate roofs, showing the lining cells (arrowheads), which are normal roof cells. Scale bars: 10 µm.


a
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specimens, ~3 × 1.5, 2.5 × 1.3, 1.4 × 0.6 cm (L × B), three labels in print or pencil: "ISOTYPE Herbarium of the University of California Lithothamnion haptericolum Fosl.," "Herbarium of the University of California North Island, New Zealand #6351. W.A. Setchell 1904 Lithothamnion haptericolum Foslie cotype on holdfast of Ecklonia Island Bay near Wellington," and "Botanical Museum, University of California *Lithothamnion haptericolum* Foslie New Zealand dupl.type ! Was # 6351," the slides annotated "*Lithothamnion haptericolum* Setchell 6351 N.Zeal. Cotype (1)" and "*Lithothamnion haptericolum* Setchell 6351 N. Zeal. Cotype (2)"; Palmer Head: Wellington: PH3 (41°20′70″S, 174°49′30″E), 11 September 2002, coll. D. Freeman and N. Alcock (WELT A27008, NZC0325), further annotated "2 slides," the slides annotated "NZC0325 multi tetra [sign] volcano"; five slides, no locality, no collector, annotated "3 multiporate + 2 uniporate. . . *Synarthrophyton schielianum*" (WELT A027006, NZC0209), the 5 slides annotated separately "NZC0209 multi volcano tetra [sign] . . . A027006," "NZC0209 multi tetra [sign] . . . A027006," "NZC0209 multi volc tetra [sign] . . . conceptacle A027006," "NZC0209 uni male [sign] . . . A027006," and "NZC0209 uni male [sign] . . . A027006"; eight slides, no locality, no collector, annotated "2 multiporate + 6 uniporate female [sign] . . . *Synarthrophyton schielianum*" (WELT A27007, NZC0210), the 8 slides annotated separately "NZC0210 multi tetra [sign] volcano . . . A027007," "NZC0210 multi tetra [sign] volcano . . . A027007," "NZC0210 uni . . . A027007," "NZC0210 uni . . . A027007," "NZC0210 uni . . . carpo A027007," "NZC0210 uni . . . carposporophyte A027007," "NZC0210 uni . . . fertile (carpo) . . . A027007," and "NZC0210 uni . . . carposporophyte A027007."

Habitat and Distribution: The species is described as a common coralline in the Chatham Islands, growing on solid rock reefs, 4–18 m depth, most abundant below 10 m on steeply sloping walls, around the margins of depressions and entrances to caves, rare on flat surfaces except in deeper (20–25 m) water. It also grows on other encrusting corallines, sponges, tunicates, and bryozoans and in association with the brown algae *Landsburgia* Harvey, *Carpophyllum* Greville, and *Macrocystis* C. Agardh (Woelkerling and Foster 1989: 57, as *Synarthrophyton schielianum*). The type material is attached to the holdfasts of *Ecklonia* (not mentioned as a substratum by Woelkerling and Foster 1989). *Orthocarpa haptericola* (as *Synarthrophyton schielianum*) has been recorded from New Zealand (Wellington, Fiordland), the Chatham Islands (Woelkerling and Foster 1989; Nelson et al. 2002), and Stewart Island (Broom et al. 2008: table 1).

Observations on the UC Syntype: The UC specimens are annotated (Figure 75a,b) similarly to the lectotype in TRH (Adey and Lebednik 1967: 68; Woelkerling et al. 2005: 342). It is not known whether they are a part of a single gathering, but it is rather likely that Setchell did several collections, resulting in several specimens, one later sent to Foslie and illustrated by Printz (1929: pl. 6, fig. 11). The latter material was selected as (lecto) type by Adey and Lebednik (1967). The UC specimens reach 3 cm in extent and are tetrasporophytes or sterile. The largest specimen is an unattached crust, to 450 µm thick (not including conceptacles), with distinctive strut-like projections on the underside and volcano-like multiporate conceptacles spread over the surface (Figure 76a,b). The thallus is dorsiventrally organized with a noncoaxial hypothallium, to 200 µm thick, producing an ascending perithallium, at least 250 µm thick. The strut-like projections reach at least 2 mm in length and develop from descending hypothallial filaments that may also develop narrow-thinner subbasal cells, 10–20 × 2–3 µm (L × B), ending in rhomboid to wedge-shaped cells (Figure 76c–g). Ascending perithallial filaments may show stratification (Figure 76i). Subepithallial cells are longer (during putative division) than cells below and support single, rectangular to isodiametric epithallial cells, ~3–4 × 5–8 µm (L × B; Figure 76e). Trichocytes and secondary pit connections were not seen.

Volcano-like multiporate conceptacles do not merge with each other and reach 600–1,000 µm in external diameter, having distinctively sunken pore plates (Figure 76d). Filaments lining the canals are 5- or 6-celled, composed of nondifferentiated pore cells (i.e., similar to contiguous roof cells; Figure 76h–j).

Comments: The material in TRH was illustrated by Printz (1929: pl. 6, fig. 11) and has to be considered the lectotype, following Adey and Lebednik's (1967) typification. Like the syntype (UC), the lectotype is a crust attached to *Ecklonia haptera*. According to the protologue (Foslie 1906: 8), the thallus is encrusting, 2–3 cm in diameter and 200–400 µm thick, following the contour of the substratum. Hypothallial filaments are composed of cells (14–)18–35(–45) × 7–11 µm (L × B). Perithallial cells are 7–15(–18) × 7–9 µm (L × B). (Tetra)sporangial conceptacles are "halvkugleformig-kraterformige" (hemispherical-craterlike), 600–1,000 µm in external diameter, and the roofs are sunken, perforated by about 50–60 pores. Carposporangial conceptacles are conical, 600–900 µm in external diameter.

Gametangial conceptacles are lacking in the UC material, which agrees in most other features with the protologue, the here examined collections from WELT (A27008, A27007, A27006), and the description of *Synarthrophyton schielianum* from the Chatham Islands (Woelkerling and Foster 1989). According to the latter authors, carpogonial branches are 3-celled, consisting of the carpogonium, the hypogynous cell, and a supporting cell, with the occasional presence of a sterile cell borne on the hypogynous cell (beside the carpogonium; Woelkerling and Foster 1989: fig. 27; Figure 77a,b). The presence of a zygote in a fertilized carpogonium was detected (Woelkerling and Foster 1989: figs. 28, 29), and three different postfertilization events were documented: (1) development of a connecting filament presumably transferring the zygote to adjacent cells at the level of supporting or basal cells (Woelkerling and Foster 1989: fig. 31; Figure 77a, dashed arrow; i.e., nonprocarpy), compare with *Amphithallia crassiuscula* in Athanasiadis (2019b, fig. 4e,f); (2) putative fusion between adjacent cells at the level of supporting cells (Woelkerling and Foster 1989: fig. 31; Figure 77a, black arrow); and (3) putative fusion between adjacent cells at the level of hypogynous cells (Woelkerling and Foster 1989: fig. 31;

FIGURE 77. *Orthocarpa haptericola*: carpogonial and postfertilization stages. (**a**) Carpogonial branches composed of a carpogonium cell and a hypogynous cell that also supports a sterile cell. Note the three different postfertilization stages: (1) production of a connecting filament (dashed arrow), (2) fusion below the hypogynous cells (black arrow), and (3) fusion at the level of hypogynous cells (white arrow). Modified from Woelkerling and Foster (1989: fig. 31). Scale bar: 10 µm. (**b**) Gonimoblast development (long arrows) at the level of hypogynous cells. Note the two fusions (arrowheads) just below the carpogonia and the sterile cells, which reveal the level of gonimoblast development. Modified from Woelkerling and Foster (1989: fig. 32). Scale bar: 10 µm. Abbreviations: c, carposporangium; ca, carpogonium; h, hypogynous cell; st, sterile cell.

Figure 77a, white arrow), with the level of fusions being revealed by the presence of sterile cells on hypogynous cells. The postulation of "multiple instances of karyogamy within a conceptacle" (Woelkerling and Foster 1989: legend of fig. 31) suggests either independent fertilizations[44] or sequential zygote transfer to several adjacent auxiliary cells.

Most significantly, however, gonimoblasts are documented at the level of hypogynous cells (Woelkerling and Foster 1989: fig. 32; Figure 77b, arrows), which indirectly supports the third type of fertilization as the functional one, indicating the position of *O. haptericola* in the Melobesiaceae. Carposporangia are produced laterally and/or orthostichously (Figure 78a,b).

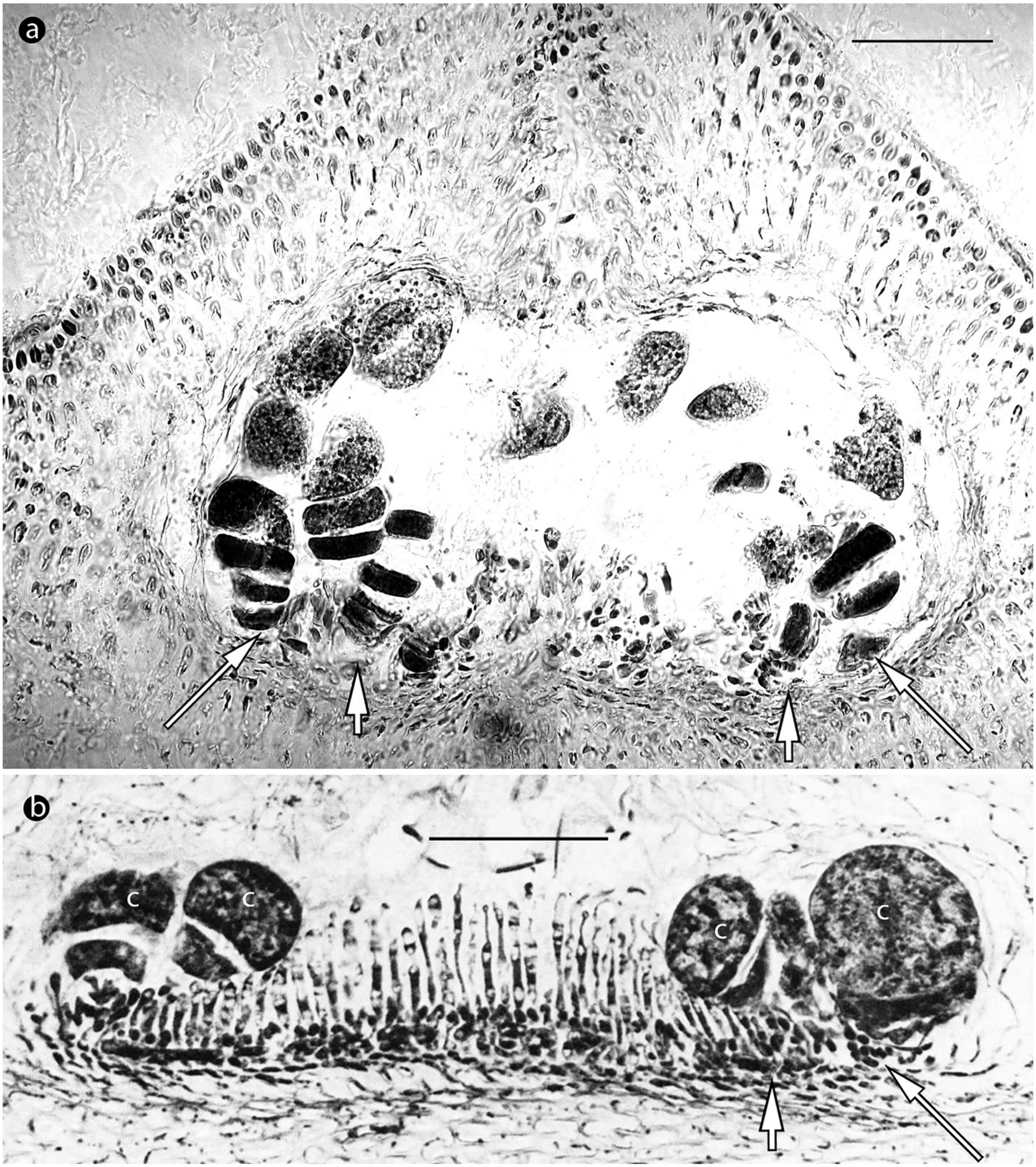


FIGURE 78. *Orthocarpa haptericola*: carposporangial structures. Production of carposporangia laterally (long arrows) and in orthostichous position (short arrows). (**a**) WELT A027007. Scale bar: 50 µm. (**b**) Modified from Woelkerling and Foster (1989: fig. 33). Scale bar: 100 µm. Abbreviation: c, carposporangium.

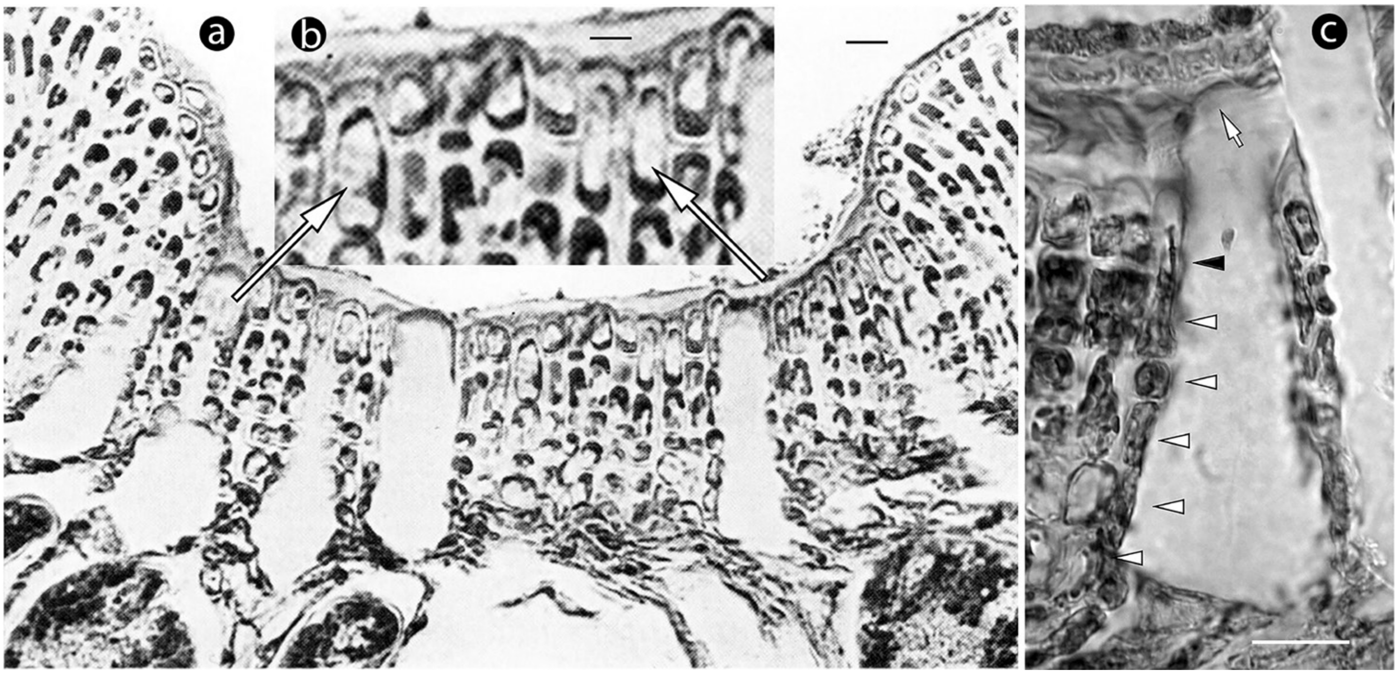


FIGURE 79. *Orthocarpa haptericola*: multiporate conceptacle structures. (**a, b**) Pore plate (magnified in (b)) showing dividing subepithallial initials (arrows) after epithallial sloughing. Modified from Woelkerling and Foster (1989: fig. 23). Scale bars: 10 µm. (**c**) Pore plate showing epithallial sloughing (arrow) and new epithallial cells below (black arrowhead). Note the canal, which is bordered by nondifferentiated pore cells (arrowheads; (WELT A027006). Scale bar: 10 µm.

In the present study, epithallial cells are documented on the pore plate of multiporate conceptacles, and therefore, their "absence" (Woelkerling and Foster 1989: fig. 23, table 2; Woelkerling and Harvey 1993: 580–1) should be considered ephemeral, following epithallial sloughing (Figure 79a–c). Tetrasporangial conceptacles with sunken pore plates are also recorded in *O. munimenta* and *O. robbenensis*, but in these species they display a lower rim.

Development of terminal inflated cells in the dendroid spermatangia (Woelkerling and Foster 1989: fig. 35) could not be confirmed in the present collections and requires closer investigation of whether these cells are distinct vegetative cells or inflated spermatangia (just before the release of spermatia). Whether gametophytes of *O. haptericola* are dioecious or monoecious also remains to be determined.

The syntype (UC) showed at least one more character not previously reported in the species, namely, the presence of narrow descending subbasal cells (Figure 76f,g). These cells were observed in the available Setchell slides (UC) but were not seen in new sections of the syntype material, indicating that their presence is facultative or rare in occurrence. Similar cells have been described in the remotely related genera *Macedonis*, *Ectocarpa*, and *Magnephycus* (Magnephyceae, Mesophyllaceae; Figures 34h, 49b, 52g).

The identity of *Lithophyllum rhizomae* Heydrich (1897a: 51–52, pl. 3, fig. 4), originally described from Bay of Islands (New Zealand), remains unclarified. This species was considered to be related to *Lithothamnion haptericola* by Foslie (1906a: 8, 1908c: 269) and De Toni (1924: 615), but authentic material has not been located so far. The protologue includes deviations from *Orthocarpa haptericola*, such as a thinner thallus (120–160 µm thick) and relatively smaller vegetative cells "Die unteren und mittleren Zellen, . . . 20 µ lang und 6 µ breit." As observed by Foslie (1906b), the only conceptacles described by Heydrich were "Cystocarpien," but these were "kraterförmige" and 600 µm in diameter, agreeing thus with the multiporate conceptacles of *O. haptericola*. The single illustration in the protologue (the apparent lectotype in the lack of specimens) does not reveal any characters other than an encrusting habit lacking erect protuberances. There are no later records of this species, and the original material is considered to be lost (Woelkerling and Nelson 2004: 86).

Simultaneously with *Lithothamnion haptericola*, Foslie (1906b: 9) described *Lithothamnion insigne* Foslie, which he considered to be (in translation) closely related to *L. haptericolum*, but its thallus . . . is more strongly attached . . . Besides the cells are thinner, the conceptacles smaller and with weak and less prominent sunk.

The present study of the type material of *Lithothamnion insigne* has shown that this species belongs to the genus *Printziana* (see *Printziana insignis*).

Orthocarpa haptericola differs from congeners most prominently by the development of ventral struts and the volcano-like tetrasporangial conceptacles, and a comparison is given in Table 6.

Orthocarpa magellanica **(Foslie) Athanas. et D. L. Ballant. comb. nov.**

Orthocarpa magellanica (Foslie) Athanas. et D. L. Ballant. comb. nov.

Basionym: Lithothamnion magellanicum Foslie 1895b: 8–9, fig. 8 of an unnumbered plate.

Homotypic Synonym: *Synarthrophyton magellanicum* (Foslie) D. W. Keats et Y. M. Chamb. 1997: 62, figs. 28–64, tables 3, 4.

Heterotypic Synonyms: ?Lithothamnion scutelloides Heydrich 1900a: 563; type locality: Saint Jean Gulf, Staten Island, Tierra del Fuego, Argentina; type material: in TRH (C18-3366), Adey and Lebednik (1967: 84, as *Lithothamnion schmitzii*, no type status, "Rocovitsa, Terra de Feu Golfe St.-Jean, 8.1.1898, no.186, LM5(11), Exp.Ant.Belgium, ex herb.Brussels [slides] 792,793"), Woelkerling (1993a: 198, "holotype fragments"), Woelkerling et al. (2005: 473–474, "holotype fragments"). Foslie (1907b: 8–10, synonym of *Lithothamnion schmitzii*), Lemoine (1913: 25, synonym of *Lithothamnion schmitzii*), Mendoza (1977: 28, synonym of *Mesophyllum schmitzii*).

?*Lithothamnion muelleri* f. *neglectum* Foslie 1900a: 17–18, "*neglecta*"; type locality: Swain's Bay, Kerguelen Islands; lectotype: in BM (unnumbered), Printz (1929: pl. 9, fig. 4, "The type specimen . . . in Royal Gardens Kew . . . Swain's Bay"); isolectotype: in TRH (B18-2619), Adey and Lebednik (1967: 70, "type material," "§ ex Herb.Kew, Kerguelen Is., LM9(4) [E]aton, ex herb.Dickie [slide] 360"), Woelkerling (1993a: 142, "lectotype," "only a few fragments"), Woelkerling et al. (2005: 353, "lectotype"). Keats and Chamberlain (1997: 62, figs. 65–70 [BM lectotype], figs. 71–74 [TRH isolectotype], synonym).

Lithothamnion neglectum (Foslie) Foslie 1902a: 19. Foslie (1908a: 207–210, text fig. 3 [lectotype], pl. 20, fig. 7).

Lithothamnion neglectum f. *neglectum* Foslie in Printz 1929: 43, pl. 9, fig. 4, f. "*typica*." Foslie (1908a: 207–210, f. "*typica*," pl. 20, fig. 7).

Mesophyllum neglectum (Foslie) W. H. Adey 1970: 25.

Synarthrophyton neglectum (Foslie) M. L. Mendoza 1990: 128. Index Nominum Algarum (2023), Mendoza et al. (1996: 52).

?*Lithothamnion neglectum* f. *fragile* Foslie 1905a: 16 (repr. 2), "*fragilis*"; syntype localities: Royal Sund (Gundersen) and Observatory Bai (Werth), Kerguelen Islands; lectotype: in TRH (B18-2621), "Gundersen . . . Royal Sund 1898," designated by Woelkerling et al. (2005: 354, "holotype"), illustrated by Foslie (1908a: 207, pl. 20, fig. 6) and Printz (1929: pl. 9, fig. 3).

?*Lithothamnion magellanicum* f. *crenulatum* Foslie 1905a: 17 (repr. 3), "*crenulata*"; type locality: Scotia Bay, South Orkney Islands; lectotype: in TRH (B1-1620), Printz (1929: pl. 2, fig. 11), Adey and Lebednik (1967: 49, "type collection," "§ Scottish Ant.Exp.1903, S.Orkney Is.,-7.1903, 9-10 fm. LM2(11) [slides] 953-955"), Woelkerling (1993a: 67, "holotype"), Woelkerling et al. (2005: 228, "holotype").

Lithothamnion crenulatum (Foslie) Foslie 1907b: 5.

Mesophyllum crenulatum (Foslie) W. H. Adey 1970: 23.

Misapplied Names: ?*Lithothamnion schmitzii* auctorum.[45] Heydrich (1901a: 541–542), Foslie (1907b: 8–11), Lemoine (1913: 25–29, text figs. 5, 6, pl. 1, fig. 3, *L. magellanicum* synonym), Mendoza (1977: 28–29, *L. magellanicum* synonym), Mendoza et al. (1996: 56, *L. magellanicum* synonym), Zaneveld and Sanford (1980: 219, *L. magellanicum* synonym) [non *Lithothamnion schmitzii* (Hariot) Heydrich = *Lithophyllum schmitzii* Hariot, Excluded Taxa].

?*Mesophyllum schmitzii* sensu R. W. Ricker (1987: 175, fig. 74a–f). Keats and Chamberlain (1997: 72, synonym) [non *Mesophyllum schmitzii* (Hariot) M. L. Mendoza].

Type Locality: Tierra del Fuego, Straits of Magellan (Chile and Argentina).

Holotype: In TRH (B2-1705), Printz (1929: pl. 2, fig. 1, "The type"), Adey and Lebednik (1967: 52, "Hariot, no.6, [New or Crit. Lith. fig. 8] . . . Ant.+subant.Cor.p.11(2), LM2(1) [slide] 2113"), Woelkerling (1993a: 142, "holotype," "includes slides 198 and 416, and one unnumbered," "About 30% of the holotype . . . is no longer present"), Woelkerling and Lamy (1998: 353, "coll . . . Hariot, 1883"), Woelkerling et al. (2005: 241, "holotype").

Isotype: In PC (unnumbered, "T.de Feu, Hariot 1883"), illustrated by Keats and Chamberlain (1997: fig. 51, arrow, "PC holotype"), Woelkerling and Lamy (1998: 353, "coll . . . Hariot, 1883").

Habitat and Distribution: The species is reported to grow on shells, chiton mollusks, encrusting corallines, and rocky substrata in the sheltered littoral to 5 m depth, including deep rock pools. Fertile specimens have been recorded in March, May, June, and December (Foslie 1907c: 4–5; Keats and Chamberlain 1997: 62). The precise type locality is unknown. The species is widely recorded from the southern hemisphere, including Tierra del Fuego (type locality), South Africa, Falklands, Straits of Magellan, South Georgia, West Antarctica (Skottsberg 1941: 79, as *Lithothamnion*), Kerguelen, Gough (Chamberlain 1965: 217, fig. 66, pl. 18, as *Lithothamnion*), and the Macquarie Islands (Ricker 1987: 175, fig. 74, as *Mesophyllum schmitzii*), but see comments below.

Comments: The protologue of *Lithothamnion magellanicum* Foslie (1895b) was based on a single specimen ("No 6") covering a shell,[46] collected by Mr. P. Hariot and said to originate from the straits of Magellan. The species was described as a thin crust, up to 300 µm thick and ~2.2 cm across, with rugged and partly smooth surface, lacking erect protuberances or unattached superimposed growth, "and the unevenness principally caused by . . . covering up small extraneous objects" (Foslie 1895b: 8).

Foslie (1895b: 8–9) acknowledged that he did not examine the structure "and therefore, I am not quite sure whether the species belongs to the subgenus *Eulithothamnion* or to *Lithophyllum*." He added that multiporate conceptacles were 300–400 µm in diameter and "never grow . . . down in the frond" and that the "roof is intersected with 70–90 muciferous canals. At maturity the whole roof falls away." "[Ma]ture [tetra]sporangia, . . . 120–130 µ long, by 40–60 µ broad. . . . This plant appears to be most nearly connected with *L. Strömfeltii* [*Leptophytum laeve*?]."

In a later contribution, Foslie (1907c: 4–5, pl. 1, figs. 1–3) added that the species is

> mostly attached to mollusc shells, sometimes to other calcareous algae or to stones . . . [and shows] smooth and faintly shining [surface] . . . conceptacles of sporangia . . . are partly convex, partly almost disc-shaped, but little prominent, sometimes feebly depressed in the central part, 300-500 µ in diameter.

He concluded that the species "occurs partly in the litoral [*sic*] region, partly and mostly in the upper part of the sublittoral [*sic*] region, and has not been met with at a greater depth than of about 14 fathoms. Fertile specimens have been taken in January, March and July."

Foslie (1905a, 1907b) considered *Lithothamnion magellanicum* to be distinct from the earlier described *Lithophyllum schmitzii* Hariot (1895), but the species was ignored by Heydrich (1901a), who recognized only *Lithothamnion schmitzii* (Hariot) Heydrich (1901a: 541). The two species were treated as synonyms by Lemoine (1913: 25), Mendoza (1977: 28–29[47]), Mendoza et al. (1996: 56), and Zaneveld and Sanford (1980: 219), with priority given to the name *Lithothamnion schmitzii*, until type material of *Lithophyllum schmitzii* (at PC) was reexamined by Keats and Chamberlain (1997) and shown to belong to a distinct species (see *Lithophyllum schmitzii* in "Excluded Taxa"). It appears, however, that Keats and Chamberlain (1997) did not find multiporate conceptacles in the type material, as described in the protologue and later confirmed in type specimens by Heydrich (1901a) and Foslie (1907b), and that the original material is heterogeneous. Therefore, only the multiporate specimens attributed to *L. schmitzii* by Heydrich, Foslie, Lemoine, Mendoza, Mendoza et al., and Zaneveld and Sanford are here cited under *Orthocarpa magellanica* with reservation.

Keats and Chamberlain (1997: 62, figs. 51–64, tables 3–4) examined the isotype of *L. magellanicum* in PC, which they considered to be conspecific with their South African material. Still, the isotype (PC) differs at least in possessing embedded conceptacles (in contrast to Foslie's observation in the holotype in TRH) and a thin and strongly adherent encrusting thallus (to 250 µm thick), characters that are lacking in all other collections referred to this species (Keats and Chamberlain 1997: tables 3, 4). We need to emphasize that the holotype of *L. magellanicum* (TRH), as illustrated by Printz (1929: pl. 2, fig. 1, "The type"), was not systematically treated by Adey (1970) and remains to be studied in a modern context.

According to Woelkerling (1993a: 198) and Woelkerling et al. (2005: 474), the holotype of *Lithothamnion scutelloides* Heydrich should be in BR ("Racovitsa no.186"), and the material in TRH (C18-3366) should be recognized as "holotype fragments." The latter was apparently examined by Foslie (1907b: 9–11), who identified it as a junior synonym of tetrasporangial material of *Lithothamnion schmitzii* (non *Lithophyllum schmitzii*; see "Excluded Taxa"). There is no later study of the type material of *L. scutelloides*.

The protologue of *Lithothamnion muelleri* f. *neglectum* Foslie (1900a: 17–18) reads, in the most essential parts,

> *Lithothamnion Muelleri* Lenorm. . . . f. *neglecta* Fosl. Calc.alg.Fuegia. *Lithothamnion lichenoides* Dickie in Journ.Linn.Soc.Vol.XV.Pag.200, and Phil.Trans.Royal Soc.London.Vol.168, Pag.58. . . . The form *neglecta* is characterized by its rather extended and more or less imbricate thallus, often with smaller or larger lamels which are more or less confluent, at length forming rather thick crust-complexes. . . . the most extreme limit of f. *neglecta* seems to be represented in the specimen mentioned by Dickie from Kerguelen land, referred by him to *L. lichenoides*. . . . taken in "Swain's Bay" . . . I have . . . examine[d] this specimen. The longest diameter is about 24 cm by a thickness of about 4 cm., growing over and between sponges. The lamels are more or less plain, 0.5–1 or up to 1.5 cm in diameter, and often rather anastomosing. It reminds one much in habit of *L. lichenoides* f. *depressa*, but shows in other respects a nearer relationship to f. *heterophylla* of the said species. However, it differs from *L. lichenoides* by a little smaller and less prominent conceptacles of sporangia. Besides the cells are on a section shown to be frequently rather short with thin walls, and in this respect pretty well agreeing with *L. Muelleri*. Among a number of specimens of the present species which I got through the kindness of Dr. Aug. Engelhart, collected at Cape Jaffa, South Australia is a specimen . . .

The Cape Jaffa material was later described by Foslie as *L. lemniscatum* (see *Magnephycus engelhartii*).

The above account by Foslie is based on the Eaton specimen (Dickie 1876b: 200), "grappled in about 2 fathoms in a tideway between two islands, incrusting two sponges" (Dickie 1879: 58, as *Melobesia lichenoides*). Later, Foslie (1902a: 19, 1908a: 207–210, text fig. 3) raised f. *neglectum* to species rank and then redescribed and illustrated the Eaton specimen, adding that the superimposed and partly free growing roundish lamellae were 0.4–0.8 mm thick and typically grouped in concentric formations. Printz (1929: pl. 9, fig. 4) selected the Kew material as (lecto)type, rendering the fragments in TRH an isolectotype. Adey (1970: 25) transferred the species to *Mesophyllum* with reservation since he did not observe a coaxial hypothallium. Keats and Chamberlain (1997: 62, tables 3, 4, figs. 65–70 [BM], figs. 71–74 [TRH]) examined both the lectotype (BM) and the isolectotype (TRH) and proposed synonymy with their South African material. Still, gametophytes are unknown in f. *neglectum*, which possesses unattached superimposed growth, lacking a coaxial hypothallium or embedded conceptacles, whereas the isotype (PC) of *L. magellanicum* was described to have embedded conceptacles; a strictly encrusting, adherent habit; and "sometimes" coaxial hypothallial patches (as also observed in South African specimens; Keats and Chamberlain 1997: 62, tables 3, 4).

The status of *Lithothamnion neglectum* f. *fragile* Foslie (1905a: 16) also remains unclarified. This entity was originally separated from the autonym (in translation) by thinner and usually less pressed, blade-like branches, based on material from Kerguelen provided by H. Gundersen and the German Antarctic expedition "Gauss".

The type material (three specimens) was illustrated by Foslie (1908a: pl. 20, fig. 6 [Gundersen], pl. 20, figs. 4, 5 [Werth]) and Printz (1929: pl. 9, figs. 1–3). Foslie (1908a: 207–210) also provided the following new characters (in translation):

> f. *fragilis* is closely similar to the typical one, differing in being smaller, thinner and more fragile, growing on mollusk shells. The surface is smooth, weakly shining, or partly with concentric lamellae. In a vertical section the hypothallium comprises about 2/3 or more of the thallus thickness. It forms arches upward and downward, with cells 18–50 (64) x 7–12 µm (L x B). The perithallium is weakly developed, with cells 12–18 (21) x 7–9 (L × B). It becomes easily detached from the substratum. The multiporate conceptacles are densely aggregated, 400–600 µm in diameter, perforated by about 50 canals. Tetrasporangia are 140–180 x 40–60 µ (L × B). The carposporangial conceptacles are conical. Apart from the typical form it comes close in habit to *L. lichenoides* f. *depressa* or *L. chathamense* . . . the South site of Royal Sound . . . f. *fragilis* (Gundersen) . . . and in the Pinguin-Gulf of Observatory-Bay, f. *fragilis* (Werth).

Adey and Lebednik (1967: 70) listed these collections separately under *Lithothamnion neglectum* as "Gundersen, Kerguelen Is., 1898, LM9(3), 'D.Lith.Guass[*sic*].Exp.6+7' [slides] 927, 928" (TRH B18-2621), "Werth, Kerguelen Is., Observatory Bay, Entenbuch (?), 13.2.1903, Guass.[*sic*]Exp. [slide] 925" (TRH B18-2622), and "Werth, Kerguelen Is., Observatory Bay, 14.2.1902" (TRH B18-2620).

Woelkerling (1993a: 97) interpreted as "holotype" the "Gundersen 1898" material, adding that "the holotype . . . consists of two shells with attached coralline material." Because in the protologue Foslie (1905a) made reference both to Gundersen and the German Antarctic expedition "Gauss," the "Gundersen 1898" material has to be recognized as the lectotype.

Woelkerling et al. (2005: 352) further divided the Gundersen "1898" material into three separate collections in TRH (B18-2613, B18-2617, and B18-2621), the first cited under *L. kerguelenum* (herein *Kerguelena dickiei* gen. et nom. nov.), the second under *L. neglectum*, and the last one under f. *fragile* ("holotype").

The Werth collection "13.2.1903" was cited under f. *fragile* (Woelkerling et al. 2005: 354, TRH B18-2622), whereas the Werth collection "14.2.1903" was cited under *L. neglectum* (Woelkerling et al. 2005: 353, TRH B18-2620).

Woelkerling et al. (2005: 352) also clarified that the two slides (927 and 928) cited by Adey and Lebednik (1967: 70) under the f. *fragile* material of Gundersen "1898" belonged to the Gundersen collection of *L. kerguelenum* (B18-2613; not listed by Adey and Lebednik 1967) but was discussed by Foslie (1899b: 10) under that species.

The original collections and specimens of f. *fragile* have not been examined in a modern context, but Foslie's (1908a) observations of an arching hypothallium, occupying 3/4 (or more) of the thallus, and a weakly developed perithallium clearly set this taxon apart from *Orthocarpa magellanica.*

The Norwegian protologue of *Lithothamnion magellanicum* f. *crenulatum* Foslie (1905a: 17) reads (in translation),

> *Lithothamnion magellanicum* Fosl. f. *crenulata* Fosl. mscr. Thallus not so strongly adherent to the substratum as in the typical form, the margin more uneven and the conceptacles partly sunken in the middle. The form stands closest to f. *Schmitzii* (Har.) Fosl.mscr. (Lithoph. Schmitzii Har.), and reminds somehow f. *taltalensis* Fosl.mscr from Taltal in Chile.

In a later account, Foslie (1907a: 5) described the hypothallium as being composed of cells 14–40 × 7–11 µm and the perithallium as being composed of cells 9–14 × 7–9 µm. The conceptacles are raised, 350–600 µm in external diameter, with clearly sunken roofs perforated by 70–80 pores. Tetrasporangia are ~120 × 40 µm (L × B).

Using data from the published literature, Lemoine (1913: 25) subsumed *L. crenulatum*, *L. scutelloides*, and *L. magellanicum* in *Lithothamnion schmitzii*. Adey (1970: 23) recognized the type of *L. crenulatum* as a distinct member of *Mesophyllum*, without comment, whereas Mendoza et al. (1996: 56) cited this species as a synonym of *Synarthrophyton schmitzii* without comparing type elements. According to Woelkerling (1993a: 67) the "holotype" of f. *crenulatum* "contains plants on two stones, one of which is depicted by Printz . . . According to Foslie's notations . . . several species are present in the collection." Adey and Lebednik (1967) selected Printz's (1929: pl. 2, fig. 11) illustrated specimen as type material, which becomes the apparent lectotype. Its identity awaits a modern examination.

Lithothamnion (*Synarthrophyton*) *magellanicum* is here transferred to *Orthocarpa* with reservation, pending the study of new topotype collections. We follow Keats and Chamberlain's (1997: figs. 44, 61, 64) documentation that shows a dorsiventral thallus organization (bilateral in *Synarthrophyton*), orthostichous carposporangia (lateral in *Synarthrophyton*), and straight canals of multiporate conceptacles lined by nondifferentiated pore cells (triangular in *Synarthrophyton* with differentiated pore cells along the canal base). It should be noted that Adey (1970) recognized at least two disparate species in the above Foslie collections, that is, *Mesophyllum crenulatum* and *Mesophyllum neglectum*, but without considering the identity of *Lithothamnion magellanicum.* We also have reservations concerning the wide form range attributed to a single species by Keats and Chamberlain (1997), particularly since embedded conceptacles were occasionally observed in the thin thallus of the isotype (PC) but not in any other collection referred to this species (Keats and Chamberlain 1997: table 4), including the holotype in TRH (Foslie 1895b). Moreover, the original material of *L. magellanicum* appears to form thin encrusting thalli, 250–300 µm thick and 2–2.5 cm across (Foslie 1895b: fig. 8; Keats and Chamberlain 1997: table 3, fig. 51), whereas the type of f. *neglectum* via superimposition forms "crust-complexes . . . about 24 cm [in diameter] by a thickness of about 4 cm" (Foslie 1900a: 18). Comparative data for the nine species of *Orthocarpa* are listed in Table 6.

***Orthocarpa munimenta* (D. W. Keats et G. W. Maneveldt) Athanas. et D. L. Ballant. comb. nov.**

Orthocarpa munimenta (D. W. Keats et G. W. Maneveldt) Athanas. et D. L. Ballant. comb. nov.

Basionym: Synarthrophyton munimentum D. W. Keats et G. W. Maneveldt 1997b: 455, figs. 29–53, table 1.

Type Locality: Upper sublittoral, on rocks, Grossebucht, Lüderitz, Namibia.

Holotype: In L (997.068 012, 14 July 1992, leg. D. W. Keats and A. Groener), illustrated by Keats and Maneveldt (1997b: fig. 29, lower specimen).

Paratypes: In UWC (92/330), illustrated by Keats and Maneveldt (1997b: fig. 29, upper two specimens, "isotypes").

Habitat and Distribution: The species is described as a common understory of kelp forests along the west coast of South Africa and southern Namibia. It encrusts bedrock, stones, shells, and holdfasts and lower stipes of *Ecklonia maxima* (Osbeck) Papenfuss. It sometimes occurs in littoral pools. It is fertile throughout the year. It has been collected from Lüderitz, Namibia, to Holbaaipunt, South Africa (collections were not made east of Holbaaipunt; Keats and Maneveldt 1997b: 456–457).

Comments: *Orthocarpa munimenta* is known from the protologue and is the only member of the genus in which orthostichous development of carposporangia has not been demonstrated. Still, the species possesses a monopodial-dorsiventral thallus organization and straight canals of multiporate conceptacles with nondifferentiated pore filaments, which exclude it from *Synarthrophyton* and support a provisional position in *Orthocarpa*. Comparative data for *O. munimenta* and its congeners are listed in Table 6.

***Orthocarpa papillata* (G. W. Maneveldt, D. W. Keats, et Y. M. Chamb.) Athanas. et D. L. Ballant. comb. nov.**

Orthocarpa papillata (G. W. Maneveldt, D. W. Keats, et Y. M. Chamb.) Athanas. et D. L. Ballant. comb. nov.

Basionym: Synarthrophyton papillatum G. W. Maneveldt, D. W. Keats, et Y. M. Chamb. 2007: 572, figs. 1–31.

Type Locality: Middle and lower littoral, on worm tubes, northern Cape province, South Africa.

Holotype: In L (0535938, "D.W. Keats and G. W. Maneveldt, 8.v.1993"), illustrated by Maneveldt et al. (2007: fig. 2, six fragments).

Isotype: In UWC (UWC 93/95), illustrated by Maneveldt et al. (2007: fig. 3, two fragments).

Habitat and Distribution: The species has been reported to be common on polychaete worm tubes and grow occasionally on rock surfaces and shells (mussels), in the middle to low shore, particularly along the sides of rock crevices and in shaded sites. It has been collected from Lüderitz, Namibia, to Cape Agulhas, South Africa (Maneveldt et al. 2007: 574).

Comments: The "fragmented" holotype was illustrated as a collection of six specimens, and the "isotype" was illustrated as a collection of two specimens (Maneveldt et al. 2007: figs. 2,3). The orthostichous development of carposporangia was illustrated by Maneveldt et al. (2007: fig. 23), but the site of gonimoblast development remains unknown. Pore filaments lining the canals of multiporate conceptacles are nondifferentiated, and the canals are straight (Maneveldt et al. 2007: fig. 29). Maneveldt et al. (2007: table 1) also provided comparative data for 10 species, 9 of which are here transferred to *Orthocarpa* since they possess dorsiventral organization, orthostichous development of carposporangia (except for *O. munimenta*), and straight canals of multiporate conceptacles with nondifferentiated pore cells. The tenth species included in their comparison is *Mesophyllum schmitzii* (see *Lithophyllum schmitzii* in "Excluded Taxa"). Comparative data for *Orthocarpa papillata* and the other eight species of the genus are listed in Table 6.

***Orthocarpa pseudospora* (A. S. Harv., Woelk., et A. Millar) Athanas. et D. L. Ballant. comb. nov.**

Orthocarpa pseudospora (A. S. Harv., Woelk., et A. Millar) Athanas. et D. L. Ballant. comb. nov.

Basionym: Synarthrophyton pseudosporus A. S. Harv., Woelk., et A. Millar 2003b: 687, figs. 26–31.

Type Locality: Sublittoral, off southwest side of Split Solitary Island, Coffs Harbour, New South Wales (NSW), eastern Australia.

Holotype: In LTB (20491, 20 June 1996, leg. A. Millar and D. Hardin), illustrated by Harvey et al. (2003b: fig. 26B).

Habitat and Distribution: The species grows on the holdfasts of *Ecklonia radiata* and on shells, sponges, and ascidians to depths of 22 m. It has been collected from Disaster Bay (NSW) northward to Tweed Heads (NSW; Harvey et al. 2003b: 693).

Comments: *Orthocarpa pseudospora* is known from the protologue and shows several characters of the genus, including a monopodial-dorsiventral thallus organization with polystromatic hypothallium, orthostichous development of carposporangia, and straight canals of multiporate conceptacles with nondifferentiated pore filaments. Regarding the subepithallial meristematic cells, Harvey et al. (2003b: 684, legend of fig. 26H) reported the initials "as short or shorter" but undergoing "cell elongation mainly within actively dividing initials," which practically differentiate *O. pseudospora* from species of *Leptophytum* and *Phymatolithopsis* (Magnephyceae), in which subepithallial dividing cells are shorter than cells below. Comparative data for the nine species of *Orthocarpa* are listed in Table 6.

Orthocarpa robbenensis **(D. W. Keats et G. W. Maneveldt) Athanas. et D. L. Ballant. comb. nov.**

Orthocarpa robbenensis (D. W. Keats et G. W. Maneveldt) Athanas. et D. L. Ballant. comb. nov.

Basionym: Synarthrophyton robbenense D. W. Keats et G. W. Maneveldt 1997b: 449, figs. 1–28, table 1.

Type Locality: Sublittoral, 10–12 m depth, on rocks in crevices, Robben Island, Western Cape Province, South Africa.

Holotype: In L (997.068 026, 14 July 1992, leg. D. W. Keats and A. Groener), illustrated by Keats and Maneveldt (1997b: fig. 1).

Isotype: In UWC (92/231), illustrated by Keats and Maneveldt (1997b: fig. 2).

Habitat and Distribution: The species has been recorded most abundantly off the west coast of South Africa at sites exposed to moderate wave action, where it forms conspicuous reddish purple (in the water) patches on bedrock and large stones at ~10–20 m depth. Reproductive material has been found from November to March. It is known only from Western Cape Province, South Africa (Keats and Maneveldt 1997b: 450–451).

Comments: *Orthocarpa robbenensis* is known from the protologue and shows several characters of this genus, including a monopodial-dorsiventral thallus organization with polystromatic hypothallium, orthostichous development of carposporangia, and straight canals of multiporate conceptacles with nondifferentiated pore filaments. Comparative data for *O. robbenensis* and its congeners are given in Table 6.

Orthocarpa chejuensis **(J. H. Kim, H. Chung, D. S. Choi, et I. K. Lee) Athanas. et D. L. Ballant. comb. nov.**

Orthocarpa chejuensis (J. H. Kim, H. Chung, D. S. Choi, et I. K. Lee) Athanas. et D. L. Ballant. comb. nov.

Basionym: Synarthrophyton chejuense J. H. Kim, H. Chung, D. S. Choi, et I. K. Lee 2004: 504, figs. 1–44, table 1, "*chejuensis*."

Misapplied Name: *Lithothamnium cystocarpideum* sensu Masaki 1968: 11 "prox.," pls. 4–5, 43–44. Kim et al. (2004: 501, 504, synonym) [non *L. cystocarpideum* Foslie].

Type Locality: Sublittoral, 10–15 m depth, on *Marginisporum crassissimum* (Yendo) Ganesan, Cheju Island, Korea.

Holotype: In SNU (98-CMP407, 18 May 1998, leg. J. H. Kim and H. Chung), illustrated by Kim et al. (2004: figs. 1, 2).

Paratype: In SNU (98-CMP408), illustrated by Kim et al. (2004: fig. 3, "isotype").

Habitat and Distribution: The species grows as an epiphyte on *Cheilosporum* (Decne) Zanardini and other geniculate corallines, species of Gelidiaceae, rocks, and shells between 5 and 15 m depth. It is recorded from Korea and Japan (Kim et al. 2004: 505).

Comments: *Orthocarpa chejuensis* is known from the protologue and a previous account by Masaki (1968: 11, as *Lithothamnium cystocarpideum* "prox."). It shows several features of *Orthocarpa*, including dorsiventral thallus organization with a polystromatic hypothallium, orthostichous development of carposporangia, and nondifferentiated pore filaments in canals of multiporate conceptacles. The development of ventral proliferations (Kim et al. 2004: figs. 14, 17, 19) is apparently localized to small patches (the whole structure projecting just 2 or 3 cells) and is probably analogous to the strut development in *Orthocarpa haptericola*. Masaki (1968: 11, pl. 44, as *Lithothamnium cystocarpideum* "prox.") illustrated the development of orthostichous carposporangia and reported the presence of a "stalk" (without illustration). Canals of multiporate conceptacles can be wider at the base because of tetrasporangial discharge (Kim et al. 2004: fig. 42), but the pore filaments apparently "do not differ from those that make up the rest of the pore plate (Figs 38, 42, 44)" (Kim et al. 2004: 511). Comparative data for *O. chejuensis* and the other species of the genus are given in Table 6.

MELOBESIOIDEAE BIZZOZERO

Melobesioideae Bizzozero 1885: 109 (type: *Melobesia*).

Comments: This subfamily comprises the genera *Melobesia*, *Boreolithon* A. S. Harv. et Woelk. (Harvey and Woelkerling 1995), and *Exilicrusta* Y. M. Chamb. (Chamberlain 1992; Athanasiadis 2016b), which possess heterotrichous thallus organization. *Boreolithon* was originally placed in the filamentous Austrolithoideae because it lacks cell fusions (Harvey and Woelkerling 1995), a character here considered to be secondarily lost, as in *Choreonema* (Choreonematoideae). The subfamily name is here attributed to Bizzozero (1885: 109), who recognized "Melobesieae Aresch." (Areschoug 1852) as a subfamily of Corallinaceae (Index Nominum Algarum 2023, old card).

Melobesia **J. V. Lamour.**

Melobesia J. V. Lamour. 1812: 186 (type: *M. membranacea*).

Comments: In its modern circumscription, *Melobesia* includes some five species (Dawson 1960; Wilks and Woelkerling 1991), but a monograph remains to be published. Members of *Melobesia* possess heterotrichous organization, with a monostromatic hypothallium supporting 3- or 4-celled erect perithallial filaments in most species and up to 26-celled filaments in *M. polystromatica* E. Y. Dawson (1960: pl. 1, fig. 4).

Melobesia membranacea **(Esper) J. V. Lamour.**

FIGURES 80, 81A,C–E

Melobesia membranacea (Esper) J. V. Lamour. 1816: 315.

Basionym: Corallina membranacea Esper 1796: pl. 12, figs. 1–4. Ott (1995: 3[48]).

Homotypic Synonyms: Epilithon membranaceum (Esper) Heydrich 1897b: 408.

Lithothamnion membranaceum (Esper) Foslie 1898b: 7.

Neotype Locality: France (presumably Atlantic coast, without specific locality).

Lectotype: Esper's original illustration, designated in Woelkerling and Chamberlain (2007: 232).

Epitype: In CN (unnumbered, herbarium Lamouroux), on *Calliblepharis ciliata*, designated and illustrated in Chamberlain (1985: 676–677, "neotype"), Woelkerling and Chamberlain (2007: 232, "epitype").

Material Examined: Suneson's (1937, as *Epilithon*) slides in GB (194a, 1–3, 192), made from material growing on *Zostera* L. and *Furcellaria* in June 1933 at Kristineberg (west coast of Sweden).

Comments: Anatomical observations of *Melobesia membranacea* were published first by Rosanoff (1866: 66: pl. 2, figs. 13–16, pl. 3, fig. 1, also as *M. corticiformis* Foslie) and later by Solms-Laubach (1881: 11, pl. 3, fig. 25, as *M. corticiformis*), Heydrich (1909a: pl. 4, figs. 5–7, as *Epilithon*), Kylin (1928: 37, figs. 19A–G, 20A–C, 21A,B, as *Epilithon*), Suneson (1937: 59, 1943: 21, as *Epilithon*), Dawson (1960: 8, pl. 25, figs. 1–3), Wilks and Woelkerling (1991: figs. 1–22), Chamberlain and Irvine (1994, fig. 94), and Woelkerling (1996: 186, figs. 69, 70).

The reexamination of Suneson's (1937) slides (in GB) showed that carpogonial branches are 2-celled, composed of a carpogonium and a hypogynous cell (Figure 80a), attached to the chamber floor. Still, broken carpogonia (composed of a trichogyne and the basal part of the carpogonium) were frequently seen and may account for reports of 3-celled carpogonial branches in the species (see further comments below). Sterile cells attached to hypogynous cells were not observed, and neither are reported in members of the genus (Lee 1970; Wilks and Woelkerling 1991). Following fertilization, the gonimoblast filaments develop below the carpogonia and radiate, producing from the periphery orthostichous carposporangia (Figure 80b,c). Contrary to Kylin's (1928) and Suneson's (1937) postulations, there is no conspicuous fusion cell, as indicated by the studies of Heydrich (1909a: pl. 4 fig. 5) and Wilks and Woelkerling (1991: figs. 20–22), and neither is documented in other species of the genus (Nichols 1908: pl. 9, figs. 1–5, *M.* (*Lithothamnion*) *mediocris* (Foslie) Setch. et L. R. Mason; Lee 1970: figs. 16D, 18, *M. mediocris*; Lebednik 1977b: fig. 18, *M. marginata* Setch. et Foslie; Wilks and Woelkerling 1991: fig. 37, *M. rosanoffii* (Foslie) Me. Lemoine). A hermaphroditic conceptacle was observed, with spermatangial structures developing simple (unbranched) structures with nonlunate SMCs (Figure 80d–f). Tetrasporangial conceptacles develop straight canals with nondifferentiated pore cells, except for basal cells that are thinner and project outward (Figure 80g–i; as in *Orthocarpa epicklonia*).

Wilks and Woelkerling (1991: 533, fig. 20; Figure 81a) described and illustrated "two or three-celled carpogonial branches" in *Melobesia membranacea*, or, more specifically, a "terminal carpogonium with a more or less elongate trichogyne and 1–2 subtending cells." Three-celled carpogonial branches were also documented for *M. mediocris* by Lee (1970: 443, fig. 16C), namely, the "carpogonial branch consisting of a carpogonium . . . and its two hypog[y]nous cells" (Figure 81b). In *Melobesia rosanoffi*, however, Wilks and Woelkerling specified the carpogonial branch as 2-celled, or, more specifically, to "consist . . . of a terminal carpogonium and one subtending cell" (Wilks and Woelkerling 1991: 526, 527). Cell tubes transferring the zygote to the subtending (hypogynous) cells have not been reported in any species of the genus, and the pattern of zygote transfer remains unknown.

Wilks and Woelkerling (1991: fig. 21; Figure 81c) further showed that in *M. membranacea*, fusions occur just below the carpogonia at the level of hypogynous cells. The occurrence of several fusion(s) between neighboring hypogynous cells is controversial since it either can be the product of independent fertilizations or can show a section not crossing a single (radiating) fusion cell.[49]

Gonimoblasts develop at the level of hypogynous cells (Wilks and Woelkerling 1991: fig. 20; Figure 81d), as also shown above in the Suneson material (Figure 80b,c). Lateral production of carposporangia was documented in *M. membranacea* by Heydrich (1909a: pl. 4, fig. 5) and Kylin (1928: fig. 19G), whereas both lateral and orthostichous production was documented in *M. marginata* by Lebednik (1977b: fig. 18; Figure 81f) and in *M. membranacea* by Woelkerling (1996: fig. 70C; Figure 81d,e). Orthostichous production was documented in *M. mediocris* by Lee (1970: fig. 16D) and is here shown in *M. membranacea* (Figure 80b,c).

Regarding the pore canals of multiporate conceptacles, the present reexamination of Suneson's slides revealed that pore cells lining the canals have differentiated basal cells that protrude outward so that canals becomes wider at the base (as described in *Orthocarpa epicklonia*; Figure 74d).

CHOREONEMATOIDEAE WOELK.

Choreonematoideae Woelk. 1987: 125 (type: *Choreonema*).

Choreonema **F. Schmitz**

Choreonema F. Schmitz 1889: 455 (repr. 214; type: *C. thuretii*).

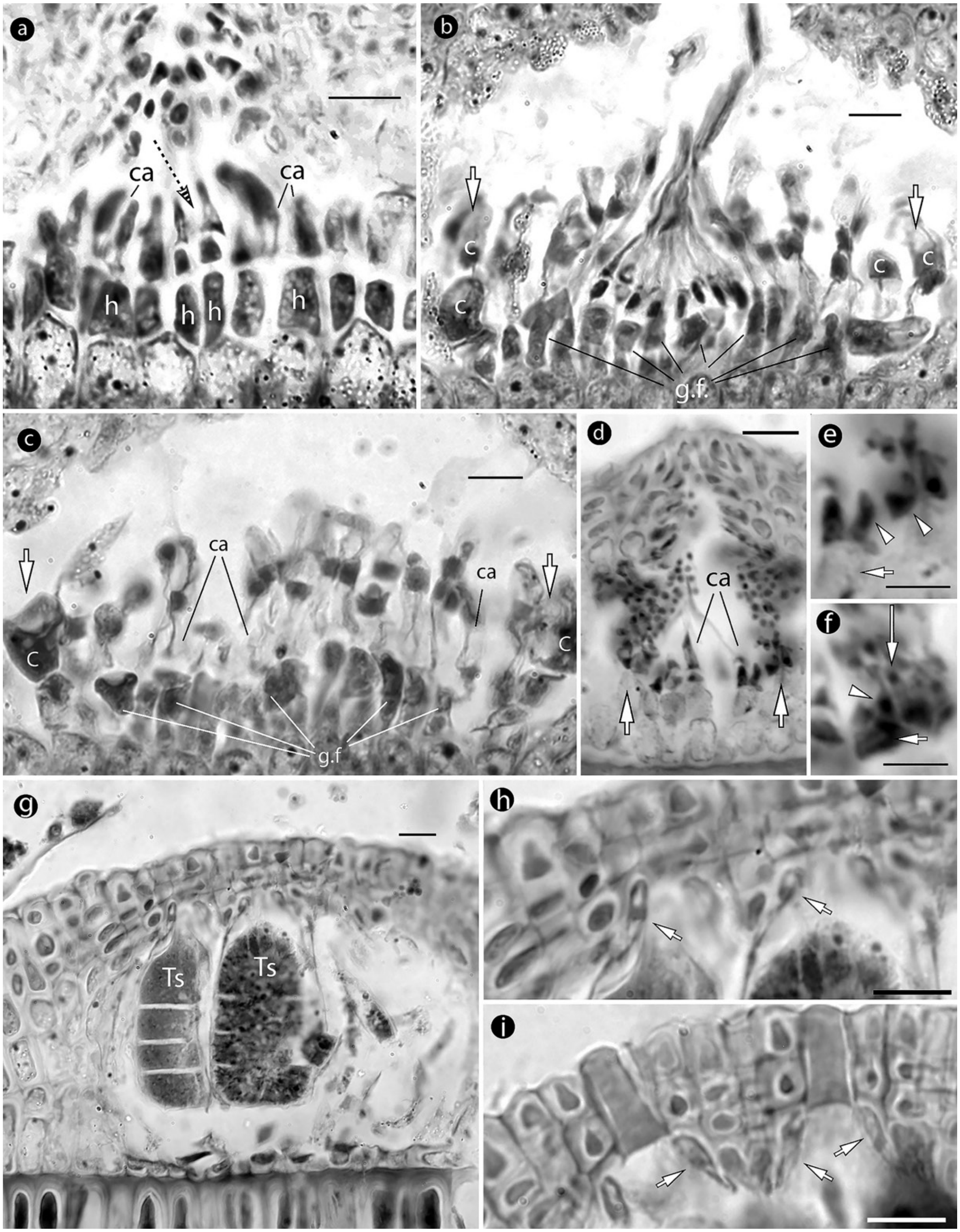


FIGURE 80. *Melobesia membranacea*: gametangial and multiporate conceptacle structures (Suneson slides in GB). (**a**) Two-celled carpogonial branches composed of a carpogonium and a hypogynous cell. Note the broken carpogonia (dashed arrow). Scale bar: 10 µm. (**b, c**) Gonimoblast filaments, just below the carpogonia, producing from the periphery orthostichous (arrows) carposporangia. Scale bars: 10 µm. (**d–f**) Hermaphroditic conceptacle with carpogonia and simple male structures with nonlunate SMCs (arrows) cutting off spermatangia (arrowheads) that produce spermatangia (long white arrow). Scale bars: 10 µm. (**g–i**) Multiporate conceptacles with tetrasporangia. Canals have thinner basal (arrows) cells. Scale bars: 10 µm. Abbreviations: c, carposporangium; ca, carpogonium; g.f., gonimoblast filament; h, hypogynous cell; Ts, tetrasporangia.

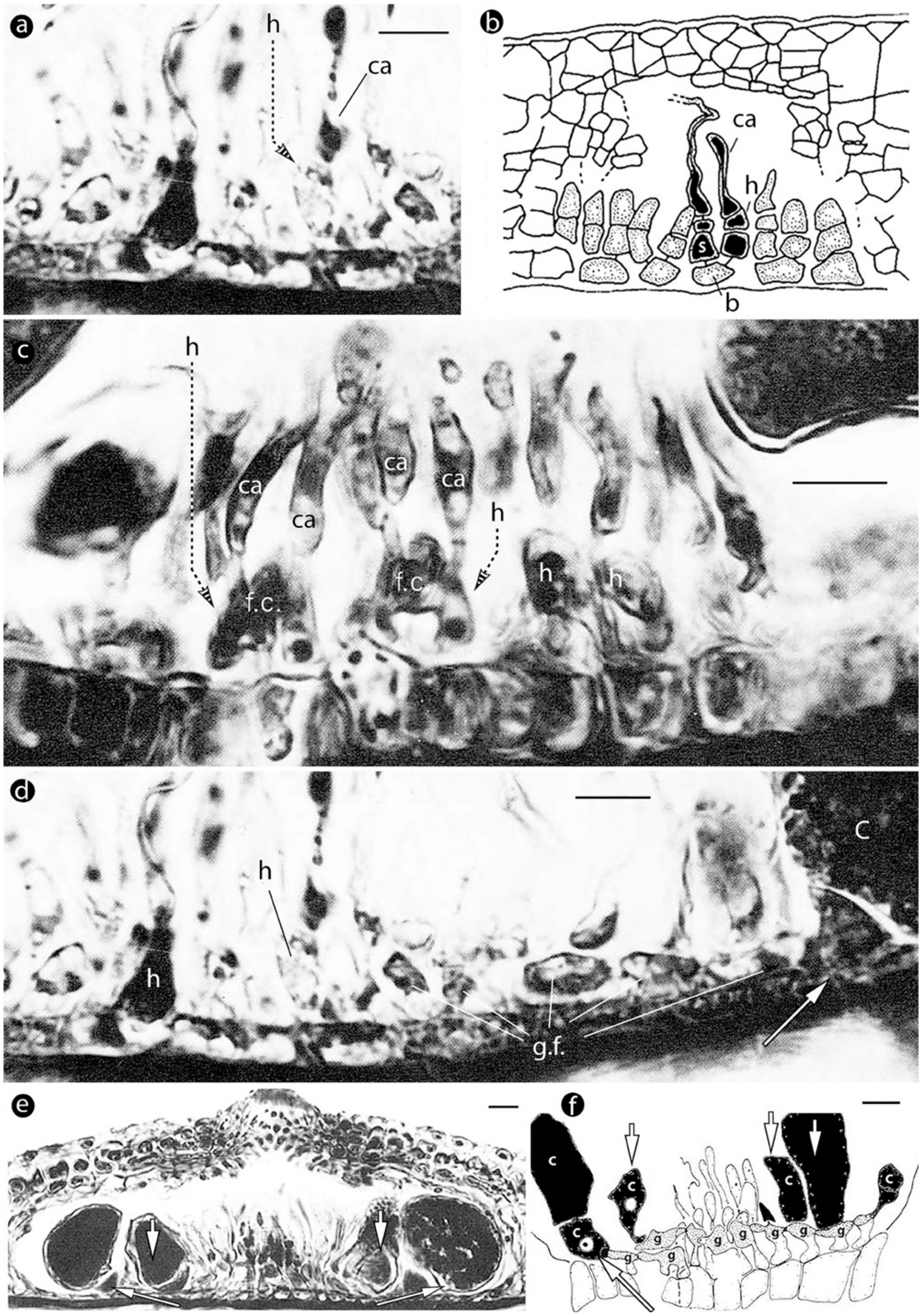


FIGURE 81. *Melobesia* species. Carpogonial branches, postfertilization stages and carposporangial structures. (**a**) Two-celled carpogonial branches in *M. membranacea*, composed of a carpogonium and a hypogynous cell. Modified from Wilks and Woelkerling (1991: fig. 20). Scale bar: 10 µm. (**b**) Three-celled carpogonial branches in *M. mediocris*, composed of a carpogonium, a hypogynous cell, and a supporting cell. Modified from Lee (1970: fig. 16C). No scale. (**c**) Two fusions between hypogynous cells, just below carpogonia in *M. membranacea*. Modified from Wilks and Woelkerling (1991: fig. 21). Scale bar: 10 µm. (**d**) Gonimoblast development at the level of hypogynous cells in *M. membranacea*. Modified from Wilks and Woelkerling (1991: fig. 20). Scale bar: 10 µm. (**e, f**) Lateral (long arrows) and orthostichous (short arrows) production of carposporangia in *M. membranacea* and *M. marginata*, respectively. Modified from Woelkerling (1996: fig. 70C) and Lebednik (1977b: fig.18), respectively. Scale bars: 10 µm. Abbreviations: b, basal cell; c, carposporangium; ca, carpogonium; f.c., fusion cell; g, gonimoblast cell g.f., gonimoblast filament; h, hypogynous cell; s, supporting cell.

Comments: Woelkerling (1987: 121) considered the generitype and only known species of *Choreonema* to be a semiendophyte in the absence of haustoria or evidence of interaction with the host (such as fusion cells) other than the basal penetrating hypothallial filament(s). However, Cabioch (1980) noted the presence of deformities in thalli inhabited by *Choreonema*. The nature of the lenticular cells on the penetrating filament(s) (Solms-Laubach 1881: pl. 3, fig. 1; Minder 1910: text fig. 4; Suneson 1937: text fig. 33A; Woelkerling 1987: fig. 14) also remains enigmatic. Carpogonial and postfertilization stages were studied by Minder (1910), Suneson (1937), and Woelkerling (1987) and were best documented by the first two authors. Woelkerling (1987: fig. 20) further reported the development of series of spermatia in chains, which is more likely to be an artifact (caused by the applied techniques), rather than a structural modification, and it was not reported by Suneson (1937: text fig. 35A,B) and not seen in the reexamination of Suneson's slides (GB).

Choreonema thuretii (Bornet) F. Schmitz

FIGURES 82, 83

Choreonema thuretii (Bornet) F. Schmitz 1889: 455.
Basionym: Melobesia thuretii Bornet in Thuret and Bornet (1878: 96, pl. 50, figs. 1–8).
Homotypic Synonym: *Endosiphonia thuretii* (Bornet) Ardissone (1883: 451).

Type Locality: Pointe de Querqueville, Manche, northern France.

Lectotype: In PC (unnumbered), selected and illustrated by Woelkerling (1987: fig. 1).

Material Examined: Suneson's (1937) slides in GB (307a, parts 2, 6, 315a, parts 4, 7, 13, 14, 28, 29, 37, 44), made from material growing on *Jania rubens* L. at Banyuls sur-mer (Mediterranean Sea).

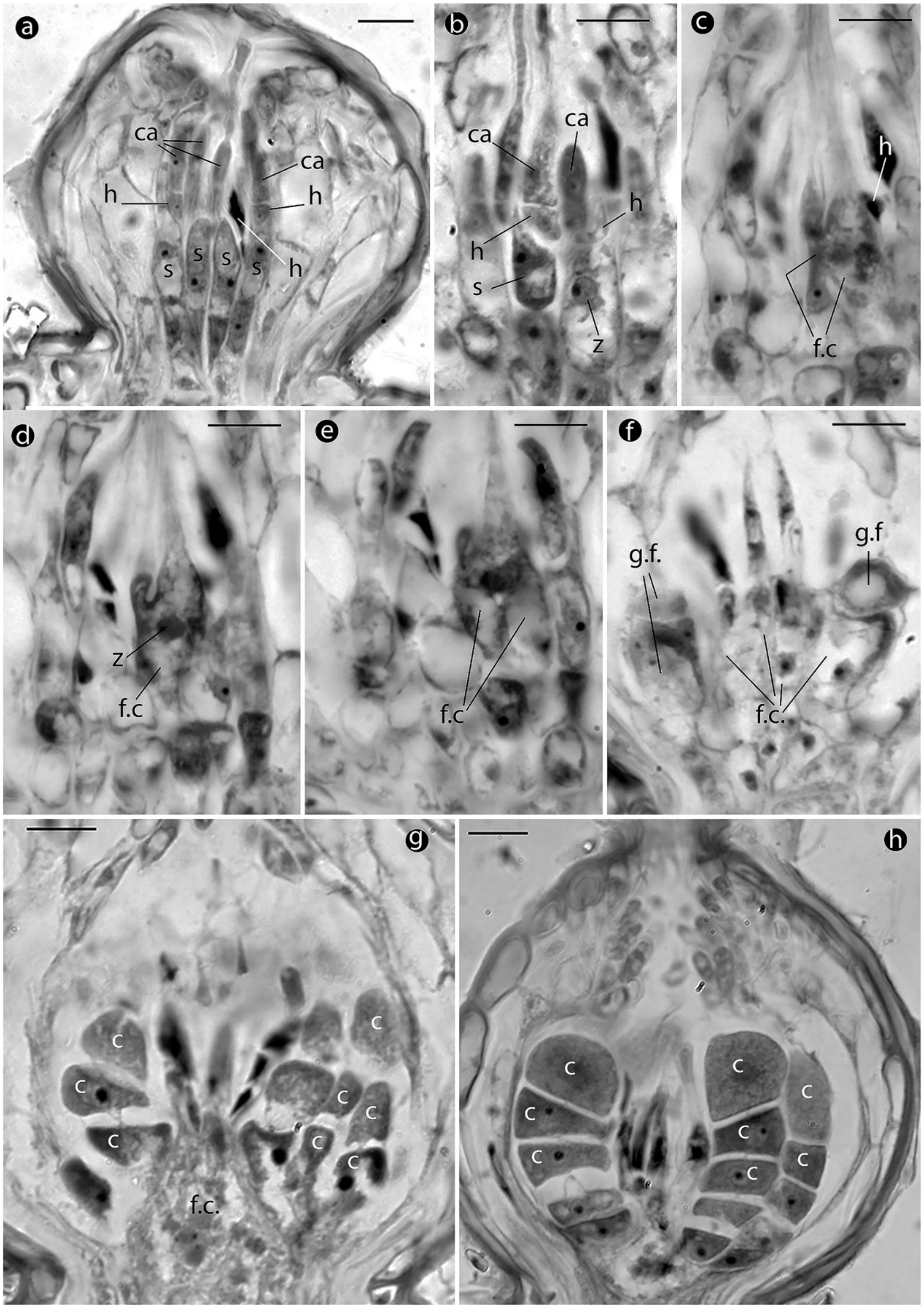
Habitat and Distribution: *Choreonema thuretii* is an obligate inhabitant of species of *Haliptilon* and *Jania* and is widely reported from the subtropics and temperate waters of the world (Woelkerling 1987: 113–114). In Europe, its northernmost records are from the west coast of Sweden (Suneson 1943).

Comments: In a series of slides, Suneson obtained all phases of the sexual reproduction of the species, in particular the simple (unbranched) spermatangial structures (Suneson 1937: fig. 35A,B), the 3-celled carpogonial branches and postfertilization stages (Suneson 1937: figs. 33, 34), and the production of tetrasporangia within uniporate conceptacles (Suneson 1937: fig. 35C,D). Regarding the carpogonial branches and postfertilization stages, Suneson (1937) described the same structures as previously documented by Minder (1910), which involve the lack of a cell tube (transferring the zygote to the supporting cell) and the presence of direct fusion of the lower part of the carpogonium with the supporting cell (Figures 3c–e, 82a–c). The position of a diminutive hypogynous cell between the carpogonium and the supporting cell (Minder 1910: text fig. 9a–c, pl. 1, figs. 1–4; Suneson 1937: fig. 34; Figure 82a,c) has been puzzling, as it could be that both Minder and Suneson misinterpreted the presence of a sterile cell, which fits the size of the reported hypogynous cell. The latter is also supported by the fact that following fertilization, this diminutive cell remains intact and does not participate in the fusion between the lower part of the carpogonium with the supporting cells (Minder 1910: pl. 1, fig. 5; Suneson 1937: fig. 34E; Figures 3e, 82c).

The reexamination of Suneson's slides (Figure 82a–h) has, however, confirmed this cell's position between the carpogonium and the supporting cell, and hence, this cell can only be interpreted as a hypogynous cell. Its diminutive size and nonparticipation (in the fusion after fertilization) suggests that it is a relic condition, manifesting the process of being entirely eliminated. Indeed, Suneson (1937: fig. 34C; Figure 3d) observed carpogonial branches lacking this diminutive hypogynous cell, which he interpreted as "Anomales Prokarp." Therefore, a plausible explanation would be to consider this diminutive hypogynous cell a relic condition, in which case *Choreonema* should be interpreted as the transition toward other Melobesiaceae (*Melobesia*, *Orthocarpa*), in which the hypogynous cell has been eliminated and its place has been taken up by the subtending supporting cell. Such an evolutionary step would explain the lack of a cell tube in the Melobesiaceae since the distance between the carpogonium and the subtending supporting cell is minimized and the need for a transfer tube becomes superfluous. If this is the case, the subtending cells in *Melobesia* and *Orthocarpa* should rather be interpreted as former supporting cells, occupying the position of the eliminated hypogynous cells.

Tetrasporangia develop within uniporate conceptacles undergoing a phase in which a putative multiporate plate was seen (Figure 83).

FIGURE 82. (*Opposite*) *Choreonema thuretii*: carpogonial and postfertilization stages (Suneson's slides in GB). Scale bars: 10 µm. (**a**) Conceptacle with several procarps, each composed of 3-celled carpogonial branches: carpogonium, hypogynous cell, and supporting cell. (**b**) Fertilization has occurred, resulting in the transfer of the zygote from the carpogonium to the supporting cell, with the hypogynous cell intact. A second 3-celled carpogonial branch (left side) is intact. (**c–e**) Fusions between neighboring supporting cells take place. Note the zygote in (d). (**f**) Early stages of peripheral gonimoblasts. (**g, h**) Gonimoblasts with orthostichous carposporangia and a visible fusion cell at an early stage. Abbreviations: c, carposporangium; ca, carpogonium; f.c., fusion cell; g.f., gonimoblast filament; h, hypogynous cell; s, supporting cell; z, zygote.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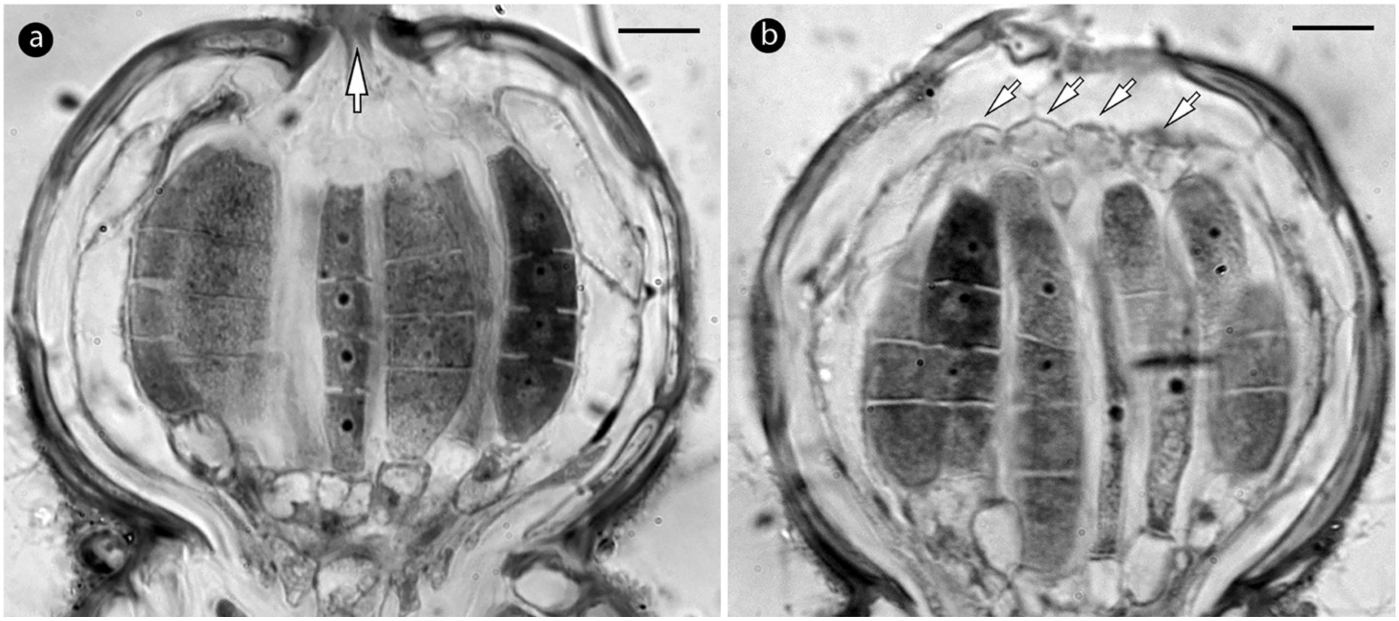

FIGURE 83. *Choreonema thuretii*: tetrasporangial conceptacle structures (Suneson's slides in GB). Scale bars: 10 µm. (**a**) Mature uniporate (arrow) conceptacle. (**b**) Younger conceptacle with putative multiporate plate (arrows).

EXCLUDED TAXA

Lithophyllum schmitzii Hariot

Lithophyllum schmitzii Hariot 1895: 98–99.

Homotypic Synonyms: Lithothamnion schmitzii (Hariot) Heydrich 1901a: 541. Foslie (1907b: 8), Lemoine (1913: 25).

Lithothamnion magellanicum f. *schmitzii* (Hariot) Foslie 1905a: 17 (repr. 3), nom. illeg.[50]

Mesophyllum schmitzii (Hariot) M. L. Mendoza 1977: 28–29, pl. 2, figs. 1–4.

Synarthrophyton schmitzii (Hariot) M. L. Mendoza, S. Molina, et P. Ventura 1996: 56, pl. 12, figs. 1, 3, pl. 13, fig. 14.

Type Locality: On shells at Cape Horn, Tierra del Fuego, Chile (Heydrich 1901a).

Type Material: In PC (unnumbered, coll. M. Michaelsen 1893), Keats and Chamberlain (1997: 68, figs. 75–79, tables 3, 4, "lectotype").

Comments: Hariot's (1895: 98–99) protologue reads (in translation),

> L.[ithophyllum] Schmitzii sp. nov. Attached to shells; the lower surface adherent, the margins not free; the thallus expanding, scarcely lobate, not imbricate, the margin thin, 300–400 µm thick, conceptacles rather numerous, with apices [roofs] entirely flattened, scarcely or not visible to the naked eye, 500 µm in diameter, with several open pores, tetrasporangia ovoid 80 × 25 µm [L × B]. The species which seems to me to be new [undescribed], was communicated to me by . . . F. W. Schmitz. . . . I cannot subsume this *Lithophyllum* to any of those that I have examined; neither can I refer it to any description so far published. The conceptacles are large, difficult to appreciate to the naked eye and they have several pores. The tetrasporangia are ovoid, rather large, since they measure 80 x 25 µm.

No illustrations, localities, or collectors were cited, but in the introduction of his work, Hariot acknowledged that the material was provided by Schmitz and it originated "en 1893, par M. Michaelsen, dans le détroit de Magellan et à la Terre de Feu." (Hariot 1895: 95). Moreover, the statement "cystocarpis" in the protologue is probably a slip (the conceptacles said to be 0.5 mm in diameter having a flat roof, with numerous pores, and are explicitly defined as tetrasporangial in his comments). Therefore, the finding of carposporangial thalli in the type material in PC (Keats and Chamberlain 1997; see also Heydrich and comments below) suggests that the original material was heterogeneous and that Hariot's (1895) term "cystocarpis" was meant to describe admixtures (not included in his final concept of the species).

Heydrich (1901a: 541–542) was the first to examine Hariot's collections in PC. He specified the type locality and the material as "Auf Muscheln vom Cap Horn (Michaelson). Nr. 50, 49e, 52c im Herb.Mus.Paris."[51] He transferred the species to *Lithothamnion* and provided the following description (here translated in the most essential parts):

> L. Schmitzii (Hariot) Heydr. mscr. . . . Thallus encrusting, 1–3 cm in diameter . . . 0.3–0.5 mm thick, very seldom 1 mm thick. Surface glancing. Sections in length show a basal layer composed of 5–6 cell series, with cells about 20 × 8 (L × B), in rather short arches arranged from the substratum to the surface . . . Tetrasporangial sori [conceptacles] spread over the thallus. The roof perforated by 40–50, 3 μm in diameter, pores . . . The conceptacles below the cuticle 250 × 150 μm (D × H). The tetraspores 120 × 32 μm (L × B), fourparted and zonately divided. Antheridia not seen, surely on different thalli. Female conceptacles 370 × 250 μm (D × H) . . . carpospores 28–30 μm in diameter.

Heydrich's description of both tetrasporangial and carposporangial conceptacles supports the view that the original material was heterogeneous, but it is not clear which of the three collections (nos. 50, 49e, 52c) included carposporangial thalli.

Foslie (1907b: 9–11) examined three Hariot and two Heydrich collections, noting (in translation) the following:

> 1. *Lithophyllum Schmitzii* n.sp. Terre de Feu 1884, scr.Har.! This is a 5 mm long fragment, that after the etiquette must be regarded as type specimen of *L. Schmitzii*. . . . It agrees fully with type specimens of *L. scutelloides* . . . *L. Schmitzii* was however recognized first and has to be accepted as the name of this species . . . [TRH C18-3365]
>
> 2. *Lithophyllum Schmitzii* Har. Terre de Feu, 1893 (Michaelsen), scr.Har.! A few small fragments resemble in habit *Lithoth. magellanicum*, similarly as to the sporangial-conceptacles. In structure it comes close to *L. Schmitzii*, but agrees best with those forms of *L. magellanicum* that are not strongly attached to the substratum. It is therefore to be regarded as a form of the last named species. [syntype material of *L. schmitzii*, TRH C18-3361]
>
> 3. *Lithophyllum hapalidioides*. Terre de Feu 1893, (Michaelsen), scr.Har.! . . . encompasses two forms. The one attached to a shell agrees with *L. magellanicum*. The other comprises small, thin crusts, that partly were attached to the substratum. This belongs apparently to *L. Schmitzii*. [putative type material of *L. schmitzii*, TRH C18-3362]
>
> 4. *Lithophyllum Schmitzii*. Cap Horn, nr. 50, scr. Heydr.! Of this I did not see all the fragments. I can therefore only repeat my earlier notes from a previous study. In habit it stands close to *L. magellanicum*, but not as regards sporangial and cystocarpic conceptacles, and in structure comes close to *L. Schmitzii*. Therefore, I have not decided if it represents a vaguely developed form of one or the other of these species. [putative type material of *L. schmitzii*, TRH C18-3364]
>
> 5. *Lithothamnion Schmitzii* (Har.) Heydr., Terre de Feu 1883, nr. 52c, scr. Heydr. This comprises partly the below described *Lithophyllum* (*Dermatolithon*) *conspectum* Fosl., partly growing together with this is a vaguely developed crust of *Lithoth. magellanicum*. [TRH A18-1184]

Foslie (1907b: 11) concluded (in translation), "All the above mentioned forms are by Heydrich referred to *L. Schmitzii*, which is thus by him interpreted in a more wide concept than did Hariot himself. As said above, I understand the type in a different sense."

Woelkerling (1993a: 185) considered Foslie's (1907b) typification to be invalid since the named "type" in TRH (C18-3365) was not collected by Michaelsen in 1893, and Woelkerling proposed instead C18-3361 as a syntype (alluding that it is a fragment of a collection in PC), later changed to "possible isolectotype" (Woelkerling et al. 2005: 473).

Lemoine's (1913: 24, 25–29, text figs. 5, 6, pl. 1, fig. 3) account of *Lithothamnion schmitzii* was based on material obtained from the Charcot expedition to Tierra del Fuego (Desolation Island), including a Hariot specimen from Tierra del Fuego, but no Michaelsen (type) collection was mentioned.

Mendoza (1977: 28–29) transferred *L. schmitzii* to *Mesophyllum*, but she did not illustrate or describe any of the "Terre de Feu" collections she discovered in PC, namely, "*Lithothamnion schmitzii* (Hariot) Heydrich, Terre de Feu, Herb.Parvor No 52C" (putative type material of *L. schmitzii*, part in TRH A18-1184), "*Lithothamnion magellanicum* Foslie!, T. de Feu, leg. Hariot 1883, det. Foslie" (isotype of *L. magellanicum* in TRH B2-1705), "*Lithophyllum* n.sp.! *schmitzii*, T. de Feu, 83 [*sic*]" (putative type material of *L. schmitzii*), "y," and "*Lithop.* (probl. *Lithothamnion magellanicum* Foslie), T. de Feu, Leg.W. Michaelson 93" (type material of *L. schmitzii*, possibly the "lectotype" alluded to by Woelkerling et al. (2005: 473) and one of the "packets" studied by Keats and Chamberlain (1997)).

Finally, Keats and Chamberlain (1997: 68–72, figs. 75–79, tables 3, 4) reexamined Hariot's collections of *L. schmitzii* in PC and reported the following:

> The PC lectotype collection (Figs 75, 78) comprises two packets . . . of small shell fragments bearing coralline crusts; the fragments are contained in a glass vial. The vial is labelled 'Lithoph. Terre du Feu, M. Michaelsen '93' in Hariot's hand and '*Mesophyllum schmitzii* (Har) Hariot - Mendoza, vu par M.L. Mendoza' in Lemoine's hand. One packet (Fig. 75) contains three pieces of shell together with the three labels . . . 'cystocarp' in Hariot's hand, '*Lithothamnion Schmitzii* (Har.) Fosl. (?) non Heydr.' in Foslie's hand and '*Lithothamnion magellanicum*' in Foslie's hand. Carposporangial conceptacles

> from crusts on the smallest piece of shell were sectioned (Fig. 71).
>
> The other packet (Fig. 78) contains four shell fragments bearing small, sterile thalli and tube worms; it is labelled 'Probabl. *Lithothamnion magellanicum*' in Foslie's hand. The thalli (Figs 75, 78) are somewhat lumpy with a smooth surface, and measure up to 700 µm thick . . . They possess a dorsiventral organization, lacking superimposed growth, and closely adhere to shells. They develop a non-coaxial hypothallium that comprises 10 % of the thallus . . . the cells are elongate and . . . terminate in rectangular cells that do not stain in anilin. The cortex (Fig. 79) is composed mainly of squarish cells . . . interspersed in part with markedly elongate ones; subepithallial cells are squarish and epithallial cells are relatively short and wide. Cell fusions (Fig. 79) occur throughout the thallus but secondary pit connections were not seen. Carposporangial conceptacles (Fig. 76) are domed, the chamber (Fig. 77) is elliptical and the roof is composed of upward-growing filaments of minute cells; the conceptacle pore is parallel-sided and relatively wide. Gonimoblast filaments (Fig. 77) are borne peripherally and are up to 5 cells long including the terminal carpospore. Old conceptacles become buried in the thallus (Fig. 77).

Under the heading "*L. schmitzii lectotype*," Keats and Chamberlain (1997: 63–64, tables 3, 4) added data for hypothallial cells (13–36 × 5–9 µm; L × B), perithallial cells (4–13 × 5–9 µm; L × B), epithallial cells (~2 × 8 µm; L × B), and subepithallial initials ("squarish," 4–5 × 6–8; L × B) and noted the lack of trichocytes and that carposporangial conceptacles produce gonimoblast filaments with peripheral production of carposporangia.

Unfortunately, Keats and Chamberlain (1997) could not match the PC material with recently collected specimens, and as they mixed up at least two separate collections (i.e., "*Lithothamnion Schmitzii* (Har.) Fosl. (?) non Heydr." and "*Lithothamnion magellanicum*" [their fig. 75, showing three specimens] and "Probabl. *Lithothamnion magellanicum*" [their fig. 78, showing four specimens]) their typification is invalid (Turland et al., 2018: Articles 8.2, 9.17).[52]

Keats and Chamberlain concluded that the examined "lectotype" specimens were not identical to *Synarthrophyton* (*Lithothamnion*) *magellanicum* (=*Orthocarpa magellanica*), but there are several critical points to this conclusion. First, no (multiporate) tetrasporangial thalli were found in the PC collections of *L. schmitzii*, which contradicts the protologue (Hariot 1895) and all later accounts (see *L. schmitzii* auctorum under *Orthocarpa magellanica*). Second, the character combination attributed to the lectotype collection does not guarantee a position within a multiporate family since dorsiventral organization with a polystromatic noncoaxial hypothallium, short subepithallial initials, and peripheral development of carposporangia also occur in genera of the uniporate Spongitidaceae (e.g., in *Spongitis*; Afonso-Carillo 1988). This indicates that the Hariot material of *Lithophyllum schmitzii* in PC, as documented by Keats and Chamberlain (1997), cannot be placed with certainty in any coralline family, and therefore, this species is here (provisionally) excluded from the Mesophyllaceae, pending a reexamination of all relevant type elements in PC and TRH (as cited by Heydrich 1901a; Foslie 1907b; Mendoza 1977; Keats and Chamberlain 1997; Woelkerling 1993; and Woelkerling et al. 2005).

***Leptophytum granuliferum* (Foslie) W. H. Adey**

Leptophytum granuliferum (Foslie) W. H. Adey 1970: 30.
Basionym: Lithothamnion granuliferum Foslie 1905a: 16 (repr. 2).

Type Locality: Observatory Island (near Staten Island), Tierra del Fuego, Argentina.

Type Material: In TRH (C18-3336), Foslie (1907c: pl. 1, figs. 10, 11, "partim"), Printz (1929: pl. 4, figs. 15, 16), Adey and Lebednik (1967: 83, "type material," "§ Skottsberg, Observatory Is., Isla de los Estados, Islei del Anonuero, Swed.S.Pole Exp., st.1, 25 m, 6.1.1902, LM4(15,16) [slides] 1189, 934"), Woelkerling (1993a: 112, "holotype"), Woelkerling et al. (2005, "holotype," "One box contains very small fragments . . . Second small box contains fragments").

Comments: The Norwegian protologue (Foslie 1905a: 16) reads (in translation),

> *Lithothamnion granuliferum* Fosl.mscr. – Thallus encrusting, thin, almost circular, later several crusts become confluent and develop finally numerous warty or branch-like excrescences that are 0.3–0.5 or nearly 1 mm in diameter. [Multiporate] conceptacles are little prominent, disc-shaped, crowded, partly confluent, c. 200 µm in diameter. Bisporangia. – Observatory Island, at Tierra del Fuego.

Later, Foslie (1907c: 7–8, pl. 1, figs. 10, 11, "partim") illustrated the habit of the species, adding that the thallus is 1–2 cm in diameter and 0.2–0.6 mm thick. The hypothallium supports both ascending perithallial filaments and shorter descending ones. Hypothallial cells are 11–30 × 6–9 µm, and perithallial cells are partly squarish or somewhat rounded (5–8 µm in diameter) to elongate (11–14 µm long). Multiporate conceptacles are 200–300 µm in external diameter, and the roof is perforated by 20–30 canals. Bisporangia are 50–60 × 20–30 µm. Carposporangial conceptacles are convex or hemispherical-conical (250–300 µm in diameter).

Foslie (1907c: 8) concluded that the species was collected at "Fuegia: The Observatory Island near the Staten Island (Skottsberg)" from 7.7 m depth ("14 fathoms"), growing together with *Lithophyllum rugosum* (Foslie) Me Lemoine, *Lithophyllum discoideum* Foslie, and *Lithophyllum decipiens* (Foslie) Foslie.

Lemoine (1913: 8) examined a specimen sent by Skottsberg and observed two tetrasporangia (65–70 × 35 μm) and some new features, namely, that (in translation) “the hypothallium is very little developed, . . . forming just one or two filaments of cells . . . [the latter] 12–15 μm long and 4 μm broad.”

Mendoza (1988: 180) reexamined the Skottsberg specimen (in PC), treating it as a “collection original de Foslie (TRH) y Lemoine (PC).” However, since the PC specimen was not included in the protologue of *L. granuliferum*, it cannot be recognized as original material, and whether it is conspecific with the type remains to be shown. Neither Lemoine (1913) nor Mendoza (1988) provided illustrations of the Skottsberg specimen in PC, and no such material is listed by Woelkerling and Lamy (1998: 398).

Printz (1929: pl. 4, figs. 15, 16) showed specimens different from those illustrated by Foslie (1907c: pl. 1, figs. 10, 11), indicating the presence of several gatherings in the original material that was not commented by Woelkerling (1993) or Woelkerling et al. (2005). Woelkerling et al. (2005: 468) noted instead that a “collection identified as *Lithothamnion magellanicum* (B2-1710) apparently was separated out by Foslie from the holotype material of *L. granuliferum*.”

Adey (1970: 30), who examined the TRH type material, transferred the species to *Leptophytum*, commenting though that the “placement . . . is with some question, since . . . asexual conceptacles were not studied.”

Hommersand et al. (2009: 512) maintained the species in *Lithothamnion*, commenting that it “is possible that . . . Antarctic specimens . . . are referable to *Phymatolithon foecundum*.”

In the absence of a modern account of the type material, *Leptophytum granuliferum* is here excluded from the Mesophyllaceae since it cannot be placed with certainty in any multiporate family.

***Mesophyllum fuegianum* (Foslie) W. H. Adey**

Mesophyllum fuegianum (Foslie) W. H. Adey 1970: 24.

Basionym: Lithothamnion kerguelenum f. *fuegianum* Foslie 1905a: 17 (repr. 3), “*fuegiana*.”

Homotypic Synonym: Lithothamnion fuegianum (Foslie) Foslie 1906b: 9. Foslie (1907c: 5–6, pl. 1 figs. 4–6), Lemoine (1913: 29–30, no fig.).

Heterotypic Synonym: ?*Mesophyllum kuehnemannii* M. L. Mendoza 1977: 25, “*kühnemanii*,” pls. 3, 4; type locality: Santa Cruz, Puerto Deseado, Sorrel, Argentina; holotype: in herb. Mendoza 3098, leg. M. L. Mendoza 18 July 1966. Mendoza et al. (1996: 60, synonym), Keats and Chamberlain (1997: 72, “appears to be similar to *S. magellanicum*”).

Type Locality: Puerto Angusto, Desolation Island, Tierra del Fuego Archipelago, Chile.

Lectotype: In TRH (B17-2544), designated and illustrated by Printz (1929: pl. 6, fig. 15, “Type . . . Fuegia, Desolation Island: Puerto Angosto”), collector P. K. H. Dusén.

Syntype: In TRH (B17-2545), Adey and Lebednik (1967: 68, “type material,” “§ Skottsberg, Falkland Is., Berkeley Sound, Port Louis, 28.t.1902, Sv.S.Pole Exp., 1901-3, LM6(12-14) ‘Ant.+sub . . . f.4’ [slide] 946”), Woelkerling (1993a: 100, “lectotype”), Woelkerling et al. (2005: 341, “lectotype”).

Comments: The Norwegian protologue of *L. kerguelenum* f. *fugianum* Foslie (1905a) reads (in translation), “*Lithothamnion kerguelenum* (Dickie) Fosl. (Calc.Alg.Fuegia) f. *fuegiana* Fosl. mscr.- Crust thinner and more uneven, and the conceptacles a little smaller than in the type form.- Maggelan Str. (cfr.l.c.) and Falklands. The Swedish Antarctic expedition.

Later, Foslie (1906b: 9) raised f. *fuegianum* to species rank, commenting (in translation)

> In Calc.Alg.Fuegia p.69 I mentioned a fragmentary coralline specimen, attached to the root of a presumably brown alga. I referred it with doubt to *Lithothamnion kerguelenum*, and in Vidensk.Selsk.Aarsber.for 1904(1905) I described it as a form of *L. kerguelenum*. After investigation of well developed specimens I must consider it as a distinct species. It is horizontally expanded, 0.2–0.6 mm thick, ± attached to the substratum and weakly branched. The species is only known from Fuegia (Dusén) and the Falklands (Skottsberg).

Thus, Foslie (1906b: 9) clarified that the protologue was based on two collections, one from Tierra del Fuego (coll. Dusén) and the other from the Falklands (coll. Skottsberg). The first collection (a single specimen) was originally referred to *Lithothamnion kerguelenum* (Dickie) Foslie (1900c: 69) with the following comment:

> a fragmentary specimen [7 cm, 1.5 mm thick] which agrees well with the above species. It is attached to . . . a decaying root, probably . . . *Macrocystis?* . . . and found washed ashore . . . In some parts two or three crusts grow over each other . . . loosely connected, and between the root-branches of the host are small crusts . . . partly nearly free. . . . The specimen is furnished with a few conceptacles of sporangia which are of the same size as the smallest in the specimen from Kerguelen land . . . As to structure it also agrees . . . with the type . . . showing a dorsiventral development even in rather old parts . . . The said specimen has been found . . . at Isla Desolacion, Puerto Angosto, P. Dusén.

Still later, Foslie (1907c: 5, pl. 1, figs. 4–6, as *L. fuegianum*) illustrated three specimens from the Falklands, adding that

> the conceptacles of [tera- or bi]sporangia are crowded, the roofs often angular, convex or flattened, subprominent, 400–700 μm in diameter, traversed by about 120 muciferous canals, . . . tetraspor[angia], 130–200 × 40–80 μm [L × B] . . . [Carposporangial] conceptacles . . . occur on other individuals . . . conical, 0.3–0.8 or up to 1 mm. in diameter. Those of antheridia, also occurring in separate individuals, are subconical,

> 200–300 µm in diameter. *L. fuegianum* belongs to the group of species of which *L. lichenoides* forms the type. . . . it is perhaps most closely connected with *L. mesomorphum*. It grows in the upper part of the sublittoral region on the coast of the Falkland Islands, [at] . . . a depth of about 1 fathom, bearing reproductive organs in July. Area: Fuegia: Desolation Island: Puerto Angosto (Dusén); the Falkland Islands: Berkeley-Sound, Port Louis (Skottsberg).

Lemoine (1913: 29–30) studied material originating from Tierra del Fuego and a Skottsberg specimen from the Falklands and largely repeated the data from Foslie's (1907c) account.

Printz (1929: pl. 6, fig. 15) illustrated and typified *Lithothamnion fuegianum* with the Dusén specimen from Isla Desolacion (Chile), stating "Fig. 15. The type-specimen attached to a decaying root. Fuegia, Desolation Island: Puerto Angosto." He also illustrated separately the Skottsberg material from the Falklands (Printz 1929: pl. 6, figs. 14–16).

Printz's typification was overlooked by later authors (Adey and Lebednik 1967: 68; Adey 1970: 24; Woelkerling 1993a: 100; Woelkerling et al. 2005: 341), who all cited the Skottsberg material as "lectotype" (without selecting a particular specimen as type), and it appears that the only account of the lectotype is Foslie's (1900c: 69) treatment of this specimen as belonging to *L. kerguelenum*, a species here referred to *Kerguelena dickiei* (Amphithallieae, Mesophyllaceae).

Mendoza et al. (1996: 60, pl. 14, figs. 1–8) treated *Mesophyllum kuehnemannii* M. L. Mendoza (1977) as a synonym of *M. fuegianum* without having studied the lectotype of *Lithothamnion kerguelenum* f. *fuegianum*. On the other hand, Keats and Chamberlain (1997: 72) commented that *M. kuehnemannii* "appears to be similar to *S*[*ynarthrophyton*] *magellanicum* [see *Orthocarpa magellanica*] but differs in having a predominantly coaxial medulla . . . [Still] Some populations of *S. magellanicum*, composed of plants with a predominantly coaxial medulla, were found during the present study."

In the absence of a modern account of the lectotype of *Lithothamnion kerguelenum* f. *fuegianum*, its identity and relationships remain unknown. The species is here provisionally excluded from the Mesophyllaceae since the available information cannot guarantee a position in this family or in the Melobesiaceae. Adey (1970) transferred the species to *Mesophyllum* but based his observations on the Skottsberg material from the Falklands.

***Mesophyllum squamuliforme* (Foslie) W. H. Adey**

Mesophyllum squamuliforme (Foslie) W. H. Adey 1970: 26.

Basionym: Lithothamnion squamuliforme Foslie 1905a: 17–18 (repr. 3–4).

Type Locality: Port Phillip Bay, Victoria, southern Australia.

Type Material: In TRH (B3-1774), Printz (1929: pl. 3, fig. 13), Adey and Lebednik (1967: 53, "type material," "§ J Gabriel, Aust., Victoria, Port Philip Bay, 1901, LM3(13) [slide] 926"), Woelkerling (1993a: 206, "holotype"), Woelkerling et al. (2005: 249, "holotype").

Comments: The Norwegian protologue (Foslie 1905a: 17–18) reads (in translation), "thallus forming pressed small crusts up to 3 mm thick. Conceptacles somehow visible, apparently varying in form and size, mostly 400 µm in diameter seen from above. The species stands close to *L. lenormandii* and *L. repandum*.- Port Philip Bay, Victoria. Comm. J. Gabriel."

The described conceptacles should be carposporangial since an original label in the type material notes the presence of carposporangial thalli (Woelkerling et al. 2005: 249, "Lithoth. n. sp. . . . konc. tyndt dække og større end rep. ogsaa cyst. [conceptacles thin covered and larger than *repandum* also cystocarpic]").

Printz (1929: pl. 3, fig. 13) illustrated a single specimen, but Woelkerling (1993a: 206) noted that the "holotype . . . includes plants on one small rock . . . depicted in Printz . . . and on a much larger rock . . . Approximately 50% of the smaller specimen is no longer present."

Hence, lectotypification remains to be made. *Lithothamnion squamuliforme* was later compared to *Lithothamnion* (now *Phymatolithon*) *lenormandii* by Foslie (1905b: 16, footnote 2), but it was not mentioned in his later publications. Adey (1970: 26) transferred the species to *Mesophyllum*, commenting that he did not see asexual conceptacles. The TRH material was also reexamined by Woelkerling and Harvey (1993: 599–600), who could not reach any taxonomic conclusion other than "no flared epithallial cells . . . were found and fractures of one conceptacle roof suggest that *Lithothamnion squamuliforme* may be conspecific with *Mesophyllum engelhartii*" (see *Magnephycus engelhartii*).

Mesophyllum squamuliforme is here provisionally excluded from the Mesophyllaceae since the available information cannot guarantee a position in any multiporate family.

***Mesophyllum syrphetodes* W. H. Adey, R. A. Townsend, et W. T. Boykins**

Mesophyllum syrphetodes W. H. Adey, R. A. Townsend, et W. T. Boykins 1982: 63, fig. 44A–C.

Type Locality: Sublittoral, 70 m depth, at southwest Molokai Island, Hawaii.

Etymology: After the adjective συρφετωδες ("unordered").

Holotype: In US, 71-72-2, coll. D. Child, illustrated by Adey et al. (1982: 64, fig. 44A).

Paratypes: In US, 71-71-1, 71-65-1, 71-73-6 (illustrated in Adey et al. 1982: fig. 44B-C), 71-82-20, 71-85-15, collected in August 1971 at Maui, Molokai, Molokai, Midway, and Oahu (coll. D. Child), respectively.

Material Examined: Indonesia: S.W. Sulawesi: Koedingareng Keke Island, 30–35 m depth, 20–21 July 1985, coll. and det. E. Verheij B.155 (L0246525); Koedingareng Keke Island, 35 m depth, 2 May 1989, coll. and det. E. Verheij 0296 "*Mesophyllum*" (L0246530).

Comments: The status of this species is uncertain since the original illustration of the holotype shows an encrusting thallus, lacking erect protuberances (Adey et al. 1982: fig. 44A), whereas a paratype specimen is clearly fruticose (Adey et al. 1982: fig. 44B, US 71-73-6). Moreover, hypothallial growth is described to be "parallel to coaxial," and the perithallium is described to possess a "faint zonate pattern," but none of these characters are illustrated. Epithallial cells are said to be "rounded," although the relevant measurements (2–4 × 4–8 µm) suggest that they are rectangular.

The here examined specimens from Indonesia are fruticose and fit well the account provided by Verheij (1993b: 63–64) for the species. The description below includes, in comparison, data from Adey et al.'s (1982) protologue in parentheses. Thalli reach 6.2 cm in extent (at least 3.8 cm according to Adey et al., fig. 44A). Individual lamellae are 70–120 µm thick (initially thin and several millimeters via superimposition), adhering to the substratum. The hypothallium is noncoaxial (parallel to coaxial), 50–60 µm thick (20–75 µm), with cells 12–20 × 3–8 µm (L × B; 10–20 × 5–9 µm). Perithallial cells are 5–8 µm long (L × B; 3–9 × 3–8 µm). Epithallial cells are roundish to slightly rectangular, 2–4 × 4–6 µm (L × B; 1–2 cells thick, 2–4 × 4–8 µm, L × B). Subepithallial cells are elongate, 3–8 × 3–5 µm (L × B; not markedly elongate). Four multiporate conceptacles measure 260–550 × 80–100 µm (D × H; 250–400 × 80–180 µm) and occasionally merge to reach 700 µm in diameter, with chambers 240–300 × 80–110 µm (D × H; 150–300 × 70–120 µm). The roof is 30–32 µm thick, composed of 4–6 cells, with a pore plate ~200 µm in diameter, perforated by at least 23 pore canals. Canals are 7–8 µm in apical diameter, each surrounded by 7 to 8 rosette cells. Pore cells lining the canals are similar to contiguous roof cells, except for basal and subbasal cells that are thinner–wider. Tetrasporangia are 58–70 × 15–20 µm (L × B; 80–90 × 25–45 µm). Trichocytes (one heterocyst seen) and secondary pit plugs are absent.

Verheij (1993b: 63–64) did not report trichocytes. He observed, however, the hypothallium to be "organized in a more or less coaxial manner." According to him, the species is collected at 20–35 m depth attached to rocks or as a rhodolith (Verheij 1993b: 63). He also cited the holotype as "re-examined" but listed data of locality depth to be "20 m." It was not possible to borrow the holotype (US) for comparison (W. Adey, NMNH [retired], pers. comm., 19 March 2010).

Another uncertainty surrounds the identity of several rhodoliths from Samalona Island (Indonesia: L0246531, Verheij no. 460), cited under *Mesophyllum erubescens* (Verheij 1993b: 61), whereas the original label of this material in L reads "*Mesophyllum syrphetodes* 0460 . . . depth 30 m transect 9 . . . 31-08-1989." Examination of this material showed that it belongs to a species of *Lithothamnion* or *Sporolithon* with distinctive flared epithallial cells.

Mesophyllum syrphetodes is here provisionally excluded from the Mesophyllaceae since the available information cannot guarantee a position in this family.

Phymatolithon muricatum Foslie

Phymatolithon (*Clathromorphum*) *muricatum* Foslie 1906a: 19 (repr. 3).
Homotypic Synonyms: Lithophyllum muricatum (Foslie) Foslie 1908b: 18.
Lithothamnion muricatum (Foslie) De Toni 1924: 622.
Pseudolithophyllum muricatum (Foslie) R. S. Steneck et R. T. Paine 1986: 224.

Type Locality: Port Renfrew, Vancouver Island, British Columbia, Canada.

Type Material: In TRH (A3-148), Printz (1929: pl. 54, figs. 24–26), Adey and Lebednik (1967: 18, "type material," "§ Yendo, Canada, Vancouver Is., Port Renfrew, 6–7, 1901, LM54 (24-26) [slides] 715–719, 721, 727").

Comments: The status of this species is pending typification since according to Woelkerling (1993a: 154), "The holotype element consists of plants on 9(–10) stones."

On the other hand, DNA sequences of material identified as *Pseudolithophyllum muricatum* resolved within the uniporate Corallineae (Corallinaceae) (Hind and Saunders 2013: 103).

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NOTES

1. The family name "Lithothamniaceae H. J. Hees 1886" adopted in Athanasiadis (2016b) to encompass the multiporate Corallinales with predominantly dendroid spermatangia and development of carposporangia across the chamber floor is not available, being a later homonym of Lithothamniaceae Schimper in Zittel (1879: 38, as "Familie. Lithothamnieae," type: *Lithothamnium* Philippi, nom. rej. [Woelkerling 1993b]). Hence, the name Lithothamnionaceae (type: *Lithothamnion* Heydrich nom. cons.) is herein proposed to replace "Lithothamniaceae H. J. Hees 1886" sensu Athanasiadis (2016b: 213) (Turland et al., 2018: Article 18.1).
2. The legitimacy of the name Mesophyllaceae against "Fam.Mesophylleae Dum." has been discussed (Athanasiadis 2020b: 546).
3. A characteristic example is the attempt to clarify the status of *Hapalidium* Kütz., asking for a loan of the type and receiving only a photographic illustration of the herbarium sheet.
4. Here applied to signify those corallines with multiporate and uniporate tetrasporangial and bisporangial conceptacles, respectively.
5. Attributed to "(Areschoug) Foslie 1908."
6. The taxonomic segregation of "Hapalidiales" from Corallinales (Nelson et al. 2015: table 3) was not supported by new findings. Nelson et al. (2015) discovered a new genus (*Corallinapetra* T. J. Farr et al.) instead related to Sporolithales, but rather than proposing a new lineage for *Corallinapetra*, they proposed the order "Hapalidiales" using a multigene phylogeny based on sequences from 19 New Zealand isolates, all of unknown or ambiguous taxonomic status: Six New Zealand isolates were named "*Mesophyllum erubescens*," but this taxon was originally described from Brazil and is presently a member of the genus *Melyvonnea*, which does not occur in New Zealand (Athanasiadis and Ballantine 2014; Sissini et al. 2014). Two New Zealand isolates were named after the Mediterranean *Mesophyllum macroblastum* (Foslie) W. H. Adey (here recognized as *Macroblastum dendrospermum* gen. et nom. nov.), in disagreement with Peña et al. (2015: fig. 11), who showed that New Zealand counterparts are not related to the Mediterranean species. The New Zealand *Synarthrophyton patena* (Hook. fil. et Harv.) R. A. Townsend was shown to include two disparate genera (Athanasiadis 2019a), and the same problem was encountered with the type material of *Mesophyllum engelhartii* (Foslie) W. H. Adey (Athanasiadis 2017a), a species originally described from South Australia. Three other terminal taxa in Nelson et al.'s (2015) study appeared as "unidentified Hapalidiaceae." For the remaining New Zealand isolates, none included type or topotype material, namely, *Phymatolithon repandum* (Foslie) K. M. Wilks et Woelk. (type locality: Port Phillip Bay, Victoria), *Lithothamnion crispatum* Hauck (type locality: Rovinj, Adriatic Sea), *Synarthrophyton schielianum* Woelk. et M. S. Foster (type locality: Chatham Islands), and *Mesophyllum printzianum* A. S. Harv. et Woelk. (type locality: Blanket Bay, Victoria).

   Hence, these 19 New Zealand isolates cannot represent the multiporate "Hapalidiales" as a whole, a group including at least 14 genera whose types were not treated by Nelson et al. (2015), that is, *Melobesia membranacea* (Esper) J. V. Lamour., *Lithothamnion muelleri* Rosanoff, *Mesophyllum lichenoides*, *Melyvonnea canariensis* (Foslie) Athanas. et D. L. Ballant., *Clathromorphum compactum* (Kjellm.) Foslie, *Callilithophytum parcum* P. W. Gabrielson et al., *Neopolyporolithon reclinatum* (Setch. et Foslie) W. H. Adey et H. W. Johans., *Leptophytum laeve*, *Kvaleya epilaeve*, *Phymatolithon calcareum* (Pallas) W. H. Adey et McKibbin, *Austrolithon intumescens* A. S. Harv. et Woelk., *Boreolithon van-heurckii* (Heydrich in Chalon) A. S. Harv. et Woelk., *Mastophoropsis canaliculata* (Harv.) Woelk., and *Choreonema thuretii* (Bornet) F. Schmitz. With three exceptions, all these species are originally described from the northern hemisphere.

   The segregation between Sporolithales and Corallinales is supported by two of the most conservative characters in red algal systematics, that is, tetrasporangium division (decussate vs. zonate) and tetrasporangium production within separate chambers versus conceptacles (Guiry 1978, 1990). On the other hand, the significance of the multiporate plate was downgraded with the erection of Corallinapetrales (Jeong et al. 2021), which shows this character to be a synapomorphy for this new order and Corallinales. Therefore, multiporate plates originated above chambers and were later relocated above conceptacles with the appearance of the Corallinales, disappearing in the uniporate corallines (Figure 1a).

   Nomenclaturally, the name Hapalidiales is based on *Hapalidium* Kütz. (1843), whose status is uncertain. The original material of the generitype *H. roseolum* Kütz. (1843) is according to the protologue sterile. However, Chamberlain (1983: 300) claimed (without documentation) that the type specimen (L941.149.413) bears tetrasporangial conceptacles with numerous pores, and therefore, she established the species as a multiporate coralline, referable to *Melobesia membranacea*. She added that "isotypes" are widely distributed, but Chamberlain (1983: 300, 306, fig. 55) considered as "isotypes" material sent by Kützing to Rosanoff (currently in CHE) dated from 1849, which cannot be original material (Athanasiadis 2016b: 270). Moreover, the type material of *H. roseolum* was growing on *Bryopsis* J. V. Lamour. (Kützing 1843), which cannot support *Melobesia membranacea*, and it was more likely a species of *Pneophyllum* Kütz. or *Fosliella* M. Howe. The latter is in agreement with Kützing's (1869: 33, pl. 92, figs. a, b) illustrations, in which the sterile crust shows concentric cell arrangement, a character attributed to species of *Pneophyllum* or *Fosliella* but not *Melobesia* (Rosanoff 1866: 67; Suneson 1943: 22). Therefore, the status of "Hapalidiaceae" and "Hapalidiales" as multiporate taxa is seriously questioned, with Chamberlain's (1983) postulations lacking documentation and Kützing's (1843, 1869) accounts and illustrations supporting a position in *Pneophyllum* or *Fosliella*, which belong to the uniporate Hydrolithoideae (Spongitidaceae).
7. There is usually a single fusion cell in each chamber, but two fusion cells have been recorded in members of Melobesiaceae (Figure 3a,b). This resembles the case of *Antithamnion cruciatum* (C. Agardh) Nägeli, in which "1 to 3 carpogonia succeed . . . fertilization along an axis (as indicated by the development of young gonimoblasts or auxiliary cells), but only one carposporophyte matur[e]s close to the apex (the other degenerating during early post-fertilization stages)" (Athanasiadis 1996a: 170).
8. Orthostichous carposporangia borne at the edge of gonimoblasts, as shown here in *Orthocarpa* (Figure 73d–f) and also earlier illustrated in members of this genus (e.g., *O. chejuense*; Masaki 1968: pl. 43, fig. 2, pl. 44, fig. 2, as *Lithothamnium cystocarpideum*), have also been observed in *Corallina* L. and *Amphiroa* J. V. Lamour. (see review in Lebednik 1977b: 385, table 4 "I").
9. Development across the entire dorsal side of a large fusion cell has been observed in several genera of Corallinaceae, such as *Arthrocardia* Decne, *Bossiella* P. C. Silva, *Calliarthron* Manza, and *Cheilosporum* (Decne) Zanardini, as well as in *Neogoniolithon* Setch. et R. L. Mason (see review in Lebednik 1977b: 385, table 4 "A") and *Amphiroa itonoi* Srimanobhas et T. Masaki

(1987: fig. 19). This pattern is, however, not homologous to the condition in the Lithothamnionaceae or Sporolithales, in which carposporangia develop individually from single carpogonia across the fertile zone (Adey and Adey 1973: figs. 22–24, in *Lithothamnion cf. glaciale* Kjellm.) and a radiating gonimoblast is lacking.

10. The heterotrichous organization was originally described by Fritsch (1935: 20) as being when "the thallus consists of two distinct parts . . . a prostrate . . . usually performing . . . the function of a holdfast and exhibiting apical growth, and giving rise to a . . . [an] erect system . . . of one or more, usually branched filaments." In this type of growth, the perithallium results from periclinal divisions on hypothallial cells, forming the ascending (perithallial) tissue, whereas hypothallial filaments remain as a monostromatic tissue (compare with *Peyssonnelia* Decne; Dixon 1973: 56, fig. 9A).
11. A tissue that keeps tetrasporangia isolated within conceptacles still occurs in certain species of *Lithothamnion* (Wilks and Woelkerling 1995: figs. 6C, 10).
12. This interpretation also invalidates the subdivision of Corallinales into two suborders, Corallinineae (uniporate) versus Mesophyllineae Athanas. (2016b, multiporate taxa) using this character alone.
13. In *Amphiroa ephedraea* (Lam.) Decne, Johansen (1968: 327, fig. 25) illustrated hypogynous cells as "supporting" cells and described the fusion to involve the "supporting" cells. In *Calliarthron*, Johansen (1969: 37, figs. 23, 24) described a fusion of the carpogonium with the hypogynous and supporting cells (Johansen 1969: 37, fig. 24), but his diagram shows intact carpogonia and a subtending fusion cell at the level of hypogynous cells. In *Bossiella* P. C. Silva, the same details were shown diagrammatically (Johansen 1973: figs. 31, 32). In ***Titanoderma chamberlainianum*** (Woelk. et S. T. Cambell) Athanas. et D. L. Ballant. comb. nov. (basionym: *Lithophyllum chamberlainianum* Woelk. et S. T. Cambell 1992: 34, figs. 16–21), a species displaying the generic features of *Titanoderma* Nägeli (Athanasiadis 2016b: 304, footnote 2), Woelkerling and Cambell (1992: fig. 21D) illustrated the development of the fusion cell at the level of hypogynous cells. However, in a second species of *Titanoderma*, Ganesan (1962: fig. 11, as *Dermatolithon*) illustrated (diagrammatically) the presence of a cell tube, connecting the carpogonium with the supporting cell in the same way as previously illustrated (diagrammatically) for a species of *Pneophyllum* by Suneson (1937: fig. 3B, as *Melobesia*). In *Metamastophora flabellata* (Sond.) Setch., Woelkerling (1980: 216, figs. 26–29) described the "fusion cell formation [to] initially involve . . . the fertilized carpogonium and its hypogynous and supporting cells," and the illustrations are similar to those in *Calliarthron* (Johansen 1969), suggesting that the fusion cell develops just below the intact carpogonia.
14. Cabioch (1988: 501, fig. 6 A,B) considered the hypothallial reduction that occurs in *Choreonema* (Melobesiaceae) homologous with that in *Amphiroa* (Lithophyllaceae), except that in *Amphiroa* the hypothallial filament first produces an erect thallus composed of perithallial filaments with terminal epithallial cells before producing conceptacles.
15. Woelkerling (1988: 11, 229) understood all types here outlined to be a single one that he named "monomerous" and that he separated from the heterotrichous organization that he called "dimerous." However, the term "monomerous" does not recognize the presence of two fundamentally different filaments that collectively form two separate tissues: the hypothallium and the perithallium (the former displaying terminal divisions and the latter displaying subepithallial divisions supporting epithallial cells and developing reproductive organs). The term "monomerous" has been widely misapplied in defining any growth displaying a polystromatic central core and a peripheral (curving) one, such as in species of *Lithophyllum* Philippi where the heterotrichous thallus secondarily produces decumbent perithallial outgrowths ("false hypothallium" sensu Cabioch 1988: 503, figs. 5G, 6D). These secondary outgrowths in *Lithophyllum* show (and have been described as) "monomerous" growth but consist entirely of perithallial filaments and are not homologous with the "monomerous" organization in *Mesophyllum* or *Lithothamnion*, in which two distinct tissues are involved (hypothallium and perithallium).
16. After αντι (opposite) and κλινη (bed, layer), that is, transverse to the layer formed by the actual divisions (vs. periclinal, i.e., parallel to that layer).
17. In the coralline algae, the origin of perithallial filaments from dorsally displaced hypothallial filaments was first observed in *Synarthrophyton patena* by May and Woelkerling (1988: 57). Nevertheless, when Woelkerling (1988: 11, 229) coined the term "monomerous," he claimed that "some derivatives contribute to a core . . . others curve outwards." This has been the standard, static view of interpreting the thallus structure of coralline algae, without considering how filaments originate in the first place. May and Woelkerling's (1988) observations are, indeed, similar to those interpreting the growth in other red algae with monopodial, multiaxial organization (e.g., *Nemalion* Duby and *Furcellaria* J. V. Lamour.; see Dixon 1973: 71, fig. 16E).
18. There are also two records: one in *Pneophyllum* (Spongitidaceae; Suneson 1937: fig. 3B, as *Melobesia*) and one in *Titanoderma* (Lithophyllaceae; Ganesan 1962: fig. 11, as *Dermatolithon*); if confirmed, they are probably best explained as parallelisms.
19. This character was originally documented in species of *Corallina* and *Amphiroa* and is marked with the letter "I" in the review of Lebednik (1977b: 385, table 4).
20. Records of *Leptophytum* from Antarctic and subantarctic waters (Zaneveld and Sanford 1980) require confirmation.
21. For example, considering the Florideophyceae by taking into account the global distribution of taxa with carpogonial branches leads to the conclusion that the origin of this class must predate the splitting of Pangea.
22. *Melyvonnea erubescens* seems to be an exception, showing limited genetic differentiation between Brazilian and certain Hawaiian isolates (Sissini et al. 2014), which could be the result of dispersal in historical times.
23. Recorded in *Clathromorphum circumscriptum* (Masaki and Tokida 1961: pl. 2, figs. 2, 5, as *Cl. compactum*; see Lebednik 1977a: 63), *Callilithophytum parcum* (Lebednik 1977a: 94, footnote 7, as *Clathromorphum*), *Neopolyporolithon reclinatum* (Lebednik 1977a: 102, as *Clathromorphum*), and *Clathmoroa* (Chamberlain et al. 1995: 445, as *Clathromorphum*).
24. Recorded in *Clathromorphum circumscriptum* (Adey 1965: pl. 5, fig. 51); *Neopolyporolithon loculosum*, *Neopolyporolithon reclinatum*, and *Callilithophytum parcum* (Lebednik 1977a: 94, figs. 10, 16f, 21e, as *Clathromorphum*); and *Clathmoroa* (Chamberlain et al. 1995: figs. 15–16, as *Clathromorphum*). Spermatangial mother cells have been illustrated as elongate to irregularly shaped but not distinctively lunate.
25. Formation of a slight pedestal has been documented in *Clathromorphum nereostratum* (Lebednik 1977a: fig. 14e; Adey et al. 2013: fig. 13B), whereas in *Clathmoroa* both lateral and orthostichous carposporangia develop (see account of the genus).
26. An exception seems to be the lack of reports of sterile cells borne beside the carpogonia (Lebednik 1977b), as observed in Protomesophylloideae (present data), in most genera of Mesophylloideae (see Athanasiadis 2020b: 540), and also in *Orthocarpa* (Orthocarpoideae, present data).
27. In the protologue, Rosenvinge (1893) considered var./f. *areolatum* to be well in agreement both with Strömfelt's species description and with material sent by Foslie and hence identical to the autonym variety of the species.
28. Lebednik (1977a: 64) cited as "holotype" the TRH material previously described by Adey and Lebednik (1967: 87). Woelkerling (1993a: 81) and Woelkerling et al. (2005: 495) considered that two separate collections (syntypes) were involved in the TRH material (one apparently annotated on the herbarium sheet (i.e. in *schedula*) as type). Peña et al. (2021) located the illustrated material in the protologue in UPS and designated it as "holotype." The date of this material was given as "vii.1877," which most likely is an error for "vii.1879"; Kjellman visited the type locality once (Kjellman 1889: 3, "Vid alla . . . ställen . . . endast kortvariga uppehåll . . . i Port Clarence 4 (22-26 juli)"). Since several collections of the original material have been located (in UPS, TRH), a lectotype needs to be selected in agreement with Article 7.11 (Turland et al., 2018).
29. "If this species is kept . . . independent . . . it is to be denominated . . . *Phymatolithon (Clathromorphum) evanescens* Fosl." Apparently proposed in anticipation and hence invalid (Turland et al., 2018: Article 36.1).
30. Embedded carpogonial conceptacles were reported by Lebednik (1977a: 64, "if not fertilized").
31. Adey and Lebednik (1967: 23) selected as "type material" "§ [Hariot] S.Orkney Is., Scotia Bay, 7.1903, Scott.Ant.Exp. 9-10 fm., LM59 (12) [slide] 948" (TRH, B15-2364), but it "consists of a single stone with plants of three species . . . [that] does not match the one shown in Printz (1929, pl. 59 fig. 12)" (Woelkerling 1993a: 20).
32. In a series of papers, Adey and Lebednik (1967: 23), Cabioch and Mendoza (1985: 261), Woelkerling (1993a: 237), and Woelkerling et al. (2005: 72) made reference to a collection in TRH (A9-439) illustrated by Printz (1929: pl. 59, figs. 15–19) comprising five specimens, recognized as the lectotype by Cabioch and Mendoza and Woelkerling. However, there is no evidence that these specimens were the product of a single gathering (Turland et al., 2018: Article 8.2), and lectotypification remains to be made.
33. "Antarctique, île Wandel, coll. Turquet 10-27 sept. 1904, 1re Expedition antarctique francaise, st. n°1135, 1184, 1185, 1186, s/n (TRH) det. Foslie:

Lithophyllum wandelica Foslie f. *wandelica* (lectotype et autres)" (Mendoza and Cabioch 1985: 261).

34. "Collected by *B Turquét*," "Foslie (1906b) cites material from three localities . . . Only one collection is . . . labelled . . . f. *wandelica*, and is thus designated here as lectotype. The lectotype . . . contains all of the specimens figured by Printz (1929) as well as fragments used in the preparation of the slides" (Woelkerling 1993a: 237).
35. Woelkerling (1993a: 87) and Woelkerling et al. (2005: 496) recognized a second Yendo collection in TRH (C21-3525) as the lectotype, but under Articles 9.10 and 9.19 (Turland et al., 2018) Lebednik's (1977a) typification has priority.
36. The Dusén material (B17-2544) was later described as *Lithothamnion kerguelenum* f. *fuegianum* Foslie (1905a:17) and selected as the type of *Lithothamnion fuegianum* by Printz (1929: pl. 6, fig. 15; see *Mesophyllum fuegianum* in "Excluded Taxa"). The Gundersen (B18-2613) and Dusén collections have not been examined in a modern context.
37. According to Athanasiadis (2007a: 491),

> Larger pore cells have also been reported in the type material of *Lithothamnion tenue* Rosenvinge (1893) from western Greenland (Düwel and Wegeberg 1996: 478), and also seen in a collection from Arctic Alaska [Stefansson Sound, Boulder Patch, 70°19.25′N 147°35.1′W 27 July 1980, bisporic, collected by R. T. Wilce, 2 hand-picked cobbles (A and B), in GB] . . . Moreover, the Alaskan thalli attained a size of 10 cm, corresponding to those reported in *Lithothamnion tenue* by Rosenvinge (1893, p. 778, '. . . diametro usque 10 ctm'), but not the maximum size recorded in *L. laeve* (see Tables 1, 2). Düwel and Wegeberg (1996) considered *L. tenue* to be conspecific with *L. laeve*, but their observations (of larger pore cells) together with the present data strongly suggest that a second distinct Arctic species is involved.

38. Strömfelt's (1886) report of the species in the lower littoral remains unconfirmed.
39. This combination appeared in Lebednik's (1974) unpublished thesis.
40. "The examined collections of f. *pseudocrispatum* in TRH [B18-2602 and B18-2603] suggest that even this taxon should be incorporated [in the species concept], but the study of the holotype in PC is crucial before such a conclusion should be reached" (Athanasiadis 2017a: 76).
41. Text fig. 7A in Foslie (1904c: 16) was produced from two slides (one in L and the other in TRH, B18-2630), with the actual specimen illustrated in Foslie (1904c: pl. 1, fig. 24). Text fig. 7B was produced from a slide in L annotated "N.12 Lith. simulans Textfig. 7B. Saleyer." Both text figures are from material collected at "Stat. 213. Saleyer and Surroundings. Reef" and represent the only material referred to "*L. simulans* f. *typica*" by Foslie (1904c).
42. The diagnostic characters of the species were neither defined nor illustrated (Turland et al., 2018: Article 44.2). Those listed in comparison to *Ph. prolixa* and *Ph. repanda* (Jeong et al. 2022: table 1) fit thalli of *Ph. repanda*.
43. In the generitype of *Leptophytum*, *L. laeve*, the fusion cell encompasses at least 5–6 supporting cells and possibly 1 or 2 hypogynous cells (Adey 1966: pl. 13, figs. 77, 80).
44. The case of *Antithamnion cruciatum* (C. Agardh) Nägeli is relevant, where "1 to 3 carpogonia succeed . . . fertilization along an axis (as indicated by the development of young gonimoblasts or auxiliary cells), but only one carposporophyte matur[e]s close to the apex (the other degenerating during early post-fertilization stages)" (Athanasiadis 1996a: 170).
45. Non *Lithothamnion schmitzii* (Hariot) Heydrich. The cited accounts include multiporate tetrasporangial thalli that were not found in a study of the type material of this species in PC (Keats and Chamberlain 1997).
46. It was later discovered that the holotype (TRH) is attached to a scale of a chiton mollusk, with the remains in PC annotated "T. de feu Hariot, 1883" (Keats and Chamberlain 1997: fig. 51; Woelkerling and Lamy 1998: 353). Hence, the PC part is technically an isotype. Keats and Chamberlain (1997: fig. 51) showed different thalli to inhabit the isotype (PC), and hence, conspecificity with the holotype (TRH) cannot be taken for granted. Moreover, Keats and Chamberlain (1997: 62) erroneously attributed the collector as "Michaelsen 1893," whereas the original label in PC states "T. de Feu Hariot, 1883" (Keats and Chamberlain 1997: fig. 51; Woelkerling and Lamy 1998: 353).
47. Mendoza (1977) cited four collections in PC as being examined (but without documentation), including (1) "*Lithothamnion schmitzii* (Hariot) Heydrich, Terre de Feu, Herb.Parvor No 52C" (part in TRH A18-1184); (2) "*Lithothamnion magellanicum* Foslie!, T. de Feu, leg. Hariot 1883, det. Foslie"; (3) "*Lithophyllum* n.sp.! *schmitzii*, T. de Feu, 83"; and (4) "*Lithop.* (probl. *Lithothamnion magellanicum* Foslie), T. de Feu, Leg.W. Michaelson 93."
48. The illustration of "*Corallina membranacea* . . . was issued in the Sechste Lieferung (1796) . . . [with] its verbal description . . . [in] 1830 . . . as *Melobesia membranacea* (Esper) Lamouroux!" (Ott 1995: 3).
49. It is relevant to cite the case of *Antithamnion cruciatum* (C. Agardh) Nägeli in which "1 to 3 carpogonia succeed . . . fertilization along an axis (as indicated by the development of young gonimoblasts or auxiliary cells), but only one carposporophyte matur[e]s close to the apex (the other degenerating during early post-fertilization stages)" (Athanasiadis 1996a: 170).
50. The name *Lithophyllum schmitzii* Hariot (1895) predates *Lithothamnion magellanicum* Foslie (1895b); see dates of publication cited in the References.
51. Collection 52c is also listed by Mendoza (1977) as present in PC, and a duplicate is in TRH (A18-1184) and is the type of *Lithophyllum conspectum* Foslie (1907b: 29). According to Woelkerling et al. (2005: 160), the collector of this collection is "Hariot . . . 1883." Part of collection 50 is also in TRH (C18-3364) and was discussed by Foslie (1907b: 9). According to Woelkerling et al. (2005: 473), the collector of this collection is "Michaelson . . . 1893." The whereabouts of collection 49e is unknown.
52. This similarly affects the "lectotypification" of Woelkerling and Lamy (1998: 325; "Lectotype . . . box collection . . . designated by Keats & Chamberlain 1997)" and Woelkerling et al. (2005: 473; "Lectotype: PC, General Herbarium (Keats & Chamberlain 1997: 68; Woelkerling 1998c: 325)").

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Index to Taxa

The following is an alphabetical list of all taxa: families, subfamilies, tribes, genera, species, and forms.