

The genus *Leptophytum* (Melobesioideae, Corallinales, Rhodophyta) on the Pacific coast of North America

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We provide a first account of the genus *Leptophytum* on the Pacific coast of North America, after re-examining the types and representative collections of species previously associated with *Leptophytum*, *Mesophyllum* and *Lithothamnion* of the Melobesioideae. Six species are recognized, distributed between Alaska (Port Clarence) and Baja California (Isla Magdalena), viz.: *Leptophytum tenue* (Kjellman) *comb. nov.* from Port Clarence and Orcas Island in Puget Sound (Washington State), *L. adeyi* from Tatoosh Island (Washington State), *L. lamellicola* sp. nov. from California (Monterey and San Mateo Counties) and southern Vancouver Island, *L. julieae* sp. nov. from SW and SE Vancouver Island and the Queen Charlotte Islands, *L. foecundum* var. *sandrae* var. nov. from southern Vancouver Island and Seattle (the typical variety *foecundum* being restricted to the Arctic and North Atlantic Oceans), and *L. microsporum* (Foslie) *comb. nov.* from southern California (Santa Catalina I.) to Baja California (Isla Magdalena). All species display the following characters, which unite them with North Atlantic congeners: noncoaxial (or predominantly noncoaxial) hypothallium, flattened epithallial cells, shedding conceptacles, and no perithallial protuberances. Sexual species (*L. lamellicola* and *L. tenue* in the North Pacific, and *L. laeve* and *L. elatum* in the North Atlantic) develop predominantly simple spermatangial mother cells with few branched ones occurring centrally or in other places on the chamber floor. Chambers of carposporangial conceptacles display a flattened floor with peripheral development of carposporangia. The NE Pacific species differ from each other in: (1) thallus adhesion (*L. lamellicola* and *L. julieae* grow partly unattached), (2) hypothallial growth (patches of coaxial cells occur regularly in *L. lamellicola* and less frequently in *L. foecundum*, *L. tenue* and *L. microsporum*), (3) perithallial stratification (present in *L. lamellicola*, *L. julieae* and *L. foecundum*), (4) size of subepithallial meristematic cells (distinctively elongate-ovate in *L. julieae*), (5) embedded multiporate conceptacles (present in *L. lamellicola*, *L. julieae* and *L. microsporum*), and (6) pore cell morphology of multiporate conceptacles. Each taxon is formally described, and its features are illustrated, tabulated and discussed. A dichotomous key to the six NE Pacific species is also provided together with an emended generic description that encompasses nine Northern and three Southern Hemisphere species.

KEY WORDS: *adeyi*, Corallinales, *foecundum*, *julieae*, *lamellicola*, *Leptophytum*, Melobesioideae, *microsporum*, Rhodophyta, *sandrae*, taxonomy, *tenue*

INTRODUCTION

The first record of the genus *Leptophytum* Adey (1966) on the Pacific coast of North America was made by Steneck & Paine (1986), who described the new species *L. adeyi* Steneck & R.T. Paine from material collected in intertidal rock pools at Tatoosh Island, Washington State. *Leptophytum* was previously widely reported from cold to warm temperate regions of both hemispheres (Adey 1970, fig. 13), including species descriptions from Antarctica (Zaneveld & Sanford 1980), Arctic Russia, Scandinavia, Iceland, the British Isles, and the North Atlantic coast of the United States (Adey 1966, 1968, 1970; Adey & Adey 1973). More recently the genus has been studied in the British Isles and Atlantic France (Chamberlain 1990; Chamberlain & Irvine 1994), South Africa (Chamberlain & Keats 1994) and also recorded from Japan (Adey *et al.* 1976) and Pacific Russia (Selivanova & Zhigadlova 1997; Selivanova 2002). Other putative records of *Leptophytum* are based on species records or descriptions under other generic names from Atlantic France and Spain (Adey & Adey 1973,

p. 347), the western Mediterranean (Babbini & Bressan 1997) and the Kara Sea (Athanasiadis 2001).

Despite its apparent similarity to the genus *Mesophyllum* Lemoine (Lebednik 1977a, table 4, fig. 19; Lebednik 1978, figs 8–12), *Leptophytum* was considered to be a heterotypic synonym of *Phymatolithon* Foslie by Düwel & Wegeberg (1996), who proposed epitypification of the generitype *Leptophytum laeve* (Foslie) Adey with material belonging to *Phymatolithon lenormandii* (Areschoug) Adey.

The re-examination of the holotype of *Leptophytum laeve* by Adey *et al.* (2001) showed that this element is in agreement with Strömfelt's (1886) protologue and all later descriptions of *L. laeve* but not the selected epitype. To restore the conception of the species after the misinformed epitypification and salvage the name *Leptophytum*, which is widely used and deeply anchored in our understanding of the taxonomy, phylogeny and evolution of the Melobesioideae (see Adey 1966, 1968; Adey & Sperapani 1971; Adey & Adey 1973; Lebednik 1977a, 1978; Johansen 1981; Chamberlain & Irvine 1994; Chamberlain & Keats 1994; Bailey & Chapman 1996, 1998; Adey *et al.* 2001; Athanasiadis 2001; Bailey *et al.* 2004), we have proposed conservation of *L. laeve* in its original sense (Athanasiadis & Adey 2003).

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In this article, we examine the species of *Leptophytum* occurring in the NE Pacific. We recognize six species: *L. adeyi*, two species new to the genus [*L. tenue* (Kjellman) *comb. nov.* and *L. microsporum* (Foslie) *comb. nov.*], two species new to science (*L. lamellicola* sp. nov. and *L. julieae* sp. nov.), and a new variety for Pacific representatives of *L. foecundum* (Kjellman) Adey (*L. foecundum* var. *sandrae* var. nov.). We describe the vegetative and reproductive characters of each taxon, discuss the taxonomic value of characters and provide an emended description of *Leptophytum*.

MATERIAL AND METHODS

Herbarium collections including slides were made available through generous loans from GB, LAM, TRH, UBC, UC, UPS and US (herbarium abbreviations follow Holmgren *et al.* 1990). In addition, specimens were received from the private herbaria of R. Wilce and R. Paine. Fragments of material were studied by light microscopy (methods and equipment as described in Athanasiadis *et al.* 2004) and by scanning electron microscopy (SEM), using a Zeiss DSM 940 (Zeiss, Jena, Germany), after the material was coated with gold/palladium using a Polaron E-5000 (Polaron Equipment Limited, Watford, Hunts, England) at about 1.2 KV for c. 2 min. Photographs were taken through a Zeiss Axiophot 2 (Zeiss, Jena, Germany), and drawings were made using a camera-lucida attached to a Leitz Dialux 20 EB (Leitz, Toronto, Canada). Morphological observations of entire specimens were made using a Zeiss Stemi SV 6 (Zeiss, Jena, Germany).

Terminology follows Athanasiadis *et al.* (2004). In particular, cell length is the distance between primary pit-connections, and cell breadth (or diameter) is the thickness of the cell lumen (i.e. excluding the cell wall) in most cells where cell breadth more or less equals thickness. In several species we observed specialized, 'thinner-wider' pore cells, as previously described in other species of *Mesophyllum* and *Leptophytum* (see Athanasiadis & Adey 2003; Athanasiadis *et al.* 2004). These pore cells exhibit different thickness and breadth. In perpendicular section (in relation to the length of the pore cell), cell thickness refers to the thinner dimension of the cell lumen, and cell breadth to the wider dimension (which is slightly curved; Fig. 100, arrows). In longitudinal section, depending on the level of sectioning (or focus), different pore cells may demonstrate either cell length \times cell thickness (hence individual pore cells appear to be thinner; Figs 103, 104, white arrowheads) or cell length \times cell breadth (hence they appear to be wider; Figs 103, 104, black arrowheads). Pore plate diameter defines the length between the most remote pores of multiporate conceptacle roofs. The abbreviations TS (transverse section, plural TSs) and SMC (spermatangial mother cell, plural SMCs) are used.

Data for Suneson's (1943) material of *Phymatolithon lenormandii* (see Comments under *L. microsporum*) are as follows:

Strömmarna, Kristineberg, Swedish west coast, 5–6 m depth, 7 July 1938, *Suneson* slides No 551: 1 & 3, GB (unnumbered, herb. Suneson); Strömmarna, Kristineberg, Swedish west coast, 10 August 1938, *Suneson* slides 583a: 1, 3, 4, 6–10, GB (unnumbered, herb. Suneson); Öresund norr om Ven, 19 June 1939, 15 m, *Suneson* slide 624b: 7, GB (unnum-

bered, herb. Suneson); Stora Kornö, Kristineberg, 29 August 1939, *Suneson* slides 670: 2 & 3, GB (unnumbered, herb. Suneson). The methods of preparation of this material are described in Suneson (1937, pp. 5–6).

OBSERVATIONS

Leptophytum Adey (1966, p. 323)

TYPE SPECIES: *L. laeve* (Foslie) Adey (1966, p. 324) (= *Lithophyllum laeve* Strömfelt 1886, p. 21, *nom. illeg.* see Adey *et al.* 2001, p. 194); designated by Adey (1966, p. 324).

NOMENCLATURE: As late as 1960, the type of *L. laeve* Strömfelt was '[a] collection by Strömfelt, 1883, in the Riksmuseum, Stockholm' (Dawson 1960, p. 18), and the species description included 'the characteristically very large tetrasporangial conceptacles . . .' (Dawson loc. cit.), a feature clearly distinguishing this taxon from any other coralline alga in the North Atlantic north of Scotland (Adey & Adey 1973) and in the Arctic Ocean (Kjellman 1883). More recently, two new elements have been associated with the type of this species; viz., a Strömfelt slide with fragments of the original material (in S) and an 'epitype' designated by Düwel & Wegeberg (1996), the latter element clearly belonging to a different species and genus (Adey *et al.* 2001; Athanasiadis & Adey 2003). Our proposal to conserve *L. laeve* Strömfelt in its original sense (Athanasiadis & Adey 2003) was not recommended by the Committee for Algae (Compère 2004, p. 1066), who nevertheless observed that '[t]he effectiveness of the epitypification may be questioned since the epitype . . . was a . . . collection comprising several specimens.' Because Art. 9.14 of the ICBN (Greuter *et al.* 2000, p. 15) allows correction of such a mistake for neotypes and lectotypes only 'found to refer to a single gathering but more than one specimen' (by narrowing the typification later to a single specimen), we argue that the epitypification is indeed noneffective and therefore that the only type for *L. laeve* is the material in S, which is in full agreement with the original concept of this species (Adey *et al.* 2001; Athanasiadis & Adey 2003).

GENERIC DESCRIPTION: Algae nongeniculate, encrusting, more or less adhering to the substrate (except in *L. lamellicola* and *L. julieae*, which grow partly unattached); thallus organization dorsiventral, composed of a polystromatic hypothallium giving rise to an ascending perithallium and descending hypothallial filaments ending in wedge-shaped cells; hypothallium noncoaxial or predominantly noncoaxial (certain Northern Hemisphere species developing regular or rare patches of coaxial cells arranged in series of 2–15 arching rows); perithallium locally stratified or not, lacking protuberances (except in *L. ferox* (Foslie) Y.M. Chamberlain & Keats); subepithallial meristematic cells short, more or less similar or smaller in size than cells below (except in *L. julieae* and *L. lamellicola*; in these species being longer during cell division); epithallium when present composed of 1 or 2 (rarely 3) cells, generally flattened (a few species have domed surface cell walls); thallus surface in the SEM demonstrating cells with thin wall ridges (*Leptophytum*-type) in several species; cell fusions between somatic cells common; secondary pit-connections absent; trichocytes generally absent (present in *L. tenue*); gametophytes monoecious or dioecious; all conceptacle types developing 1–4 cells below the epithallium, raised at maturity (except in *L. foecundum*, *L. adeyi* and *L. microsporum*, where multiporate conceptacles can be flush with the surface); zonately divided bi- and/or tetra-sporangia produced collectively within chambers and having thick cap walls (apical plugs), resulting in a multiporate roof (each sporangium

with its own pore opening); pore canals of multiporate conceptacles bordered by specialized (thinner-wider) cells at the canal base (not reported in *L. tenue*, *L. bornetii* (Foslie) Adey, *L. elatum* Y.M. Chamberlain or Southern Hemisphere species); roof of gametangial conceptacles developed by peripheral filaments that have terminal meristem and grow centripetally; SMCs predominantly simple, borne on the floor, the walls and the roof of the chamber; SMCs originally covered by a protective layer of columnar cells and at maturity becoming lunate in shape (in TS), after producing from their upper part up to three spermatangia at a time; simple SMCs occurring together with few branched (dendroid) SMCs, the latter borne centrally or in other places on the chamber floor; carposporangial conceptacles with peripheral production of carpospores and a more or less flattened floor.

COMMENTS: The original description of *Leptophytum* (Adey 1966, pp. 323–324) was based on *L. laeve* and *L. foecundum*, both widely distributed in the North Atlantic and Arctic Oceans, and included the following generic characters: (1) thalli encrusting and thin, (2) hypothallium polystromatic, producing a gradually ascending perithallium and descending filaments, (3) epithallium absent or composed of a few thin-walled cells, (4) subepithallial meristematic cells short, (5) perithallial cells gradually increasing in length and becoming buried in the thallus, (6) conceptacle primordia 'shallow' (i.e. formed adventitiously from the upper 1–3 perithallial cells), (7) asexual sporangia with thick cap walls resulting in a multiporate roof, (8) filaments bordering the pores of multiporate conceptacles composed of specialized cells, (9) roof of gametangial conceptacles formed by peripheral filaments, (10) gonimoblasts formed at the periphery of an irregular fusion cell, and (11) SMCs formed on the floor, the walls and the roof of the chamber (Adey 1966, pp. 323–324). Adey (1970, p. 29) later transferred eight more species to the genus, viz. *L. absonum* (Foslie) Adey (type locality: Port Phillip Bay, Victoria), *L. asperulum* (Foslie) Adey (type locality: Bay of Islands, New Zealand), *L. bisporum* (Foslie) Adey (type locality: Puerto Orotava, Tenerife, Canary Islands), *L. bornetii* (type locality: Cherbourg, Atlantic France), *L. coulmanicum* (Foslie) Adey (type locality: Cape Wadsworth, Coulman Island, Antarctica), *L. granuliferum* (Foslie) Adey (type locality: Observatory Island, Antarctica), *L. repandum* (Foslie) Adey (type locality: Halfmoon Bay, Port Phillip Bay, Victoria) and *L. taltalense* (Foslie) Adey (type locality: Taltal, Chile). He also provided an emended generic description that included four new characters: (12) hypothallium noncoaxial, (13) perithallium not layered, (14) cell fusions abundant, and (15) epithallium (when present) generally composed of a single layer of cells.

Lebednik (1977a, 1978) compared the postfertilization stages and development of spermatangial conceptacles in several coralline genera and pointed out two more characters, viz. (16) presence of a protective cell layer above the SMCs (as shown in Adey 1966, figs 82 and 88), and (17) development of predominantly simple SMCs, except those borne centrally on the floor of the chamber (as shown in Adey 1966, fig. 83; Lebednik 1978, fig. 10).

Steneck & Paine (1986) described the new species *L. adeyi* from the coast of Washington State. Chamberlain (1990) studied the genus in the British Isles, providing new information

about *L. laeve*, *L. bornetii* and *L. foecundum* and describing the new species *L. elatum* from Dorset (England) and Pembroke (Wales). Chamberlain (1990, p. 198) added four new generic characters, viz. (18) thalli adhering to the substrate, flat to lumpy but lacking protuberances and branches, (19) flattened or domed epithallial cells demonstrating a *Leptophytum*-type surface in the SEM, (20) conceptacles of all types raised, and (21) gametophytes dioecious.

Wilks & Woelkerling (1994) transferred *L. repandum* to *Phymatolithon*, including *L. absonum* and *L. asperulum* in the list of synonyms (but without providing any data on the types). Critical taxonomic studies that include the study of types and/or topotype material are also lacking for *L. bisporum*, *L. coulmanicum*, *L. granuliferum* and *L. taltalense*.

In the same year, Chamberlain & Keats (1994) described three new species of *Leptophytum* from South Africa, viz. *L. acervatum* (Foslie) Y.M. Chamberlain & Keats, *L. foveatum* Y.M. Chamberlain & Keats and *L. ferox*. They also compared the genera of the Melobesioideae using 7 of the above 21 characters (i.e. characters 2, 4, 10, 11, 12, 17 and 19) and two autapomorphies (distinguishing the monotypic *Kvaleya* Adey & Sperapani and *Mastophoropsis* Woelkerling). This comparison indicated that *Leptophytum* could be separated from other Melobesioideae by possessing a unique character combination and having character (17) as an autapomorphy (Chamberlain & Keats 1994, table 2). The same conclusions were reached by Adey *et al.* (2001) and Athanasiadis (2001, table 2), who further emphasized that *Leptophytum* was more closely related to *Synarthrophyton* Townsend and *Mesophyllum* than to any other nonmonotypic genus of the Melobesioideae.

We emend (underlined below) the above generic characters based on observations of the NE Pacific species: (4) subepithallial meristematic cells short (except in *L. julieae* and *L. lamellicola*), (6) conceptacle primordia 'shallow' (formed adventitiously from the upper 1–4 perithallial cells), (8) filaments bordering the base of pore canals of multiporate conceptacles composed of specialized (thinner-wider) cells at the canal base (not recorded in *L. tenue*, *L. bornetii*, *L. elatum* or species of the S. Hemisphere), (12) hypothallium noncoaxial or predominantly noncoaxial (certain N. Hemisphere species develop coaxial patches more or less regularly) (13) perithallium locally stratified or not, (15) epithallium composed of 1 or 2 (rarely 3) cells, (17) SMCs predominantly simple with few branched SMCs formed centrally or in other places on the chamber floor, (18) thalli more or less adhering to the substrate (except in *L. lamellicola* and *L. julieae*, which grow with parts of their thalli unattached), flat to lumpy but lacking perithallial protuberances and branches (except in *L. ferox*), (20) conceptacles of all types raised (except in *L. foecundum*, *L. adeyi* and *L. microsporum*, where multiporate conceptacles may be flush with the surface), and (21) gametophytes dioecious or monoecious. In addition, we recognize two new characters: (22) SMCs lunate in shape during early stages of fertility, and (23) chambers of carposporangial conceptacles with more or less flattened floor.

The results of this study also confirm that Northern Hemisphere species of the *Leptophytum*-*Mesophyllum* complex form two discrete groups: (1) species possessing simple SMCs only, carposporangial chambers with centrally raised floor (resulting in distinctive dumbbell-shaped chambers), and a predominantly coaxial hypothallium, and (2) species having pre-

dominantly simple and few branched SMCs (the latter restricted to the floor), carposporangial chambers with more or less flattened floor, and a noncoaxial (or predominantly noncoaxial) hypothallium. The former species have been placed in *Mesophyllum* (Athanasiadis *et al.* 2004), and the latter species are here referred to *Leptophytum*.

Leptophytum tenue (Kjellman) *comb. nov.*

Figs 1–27

BASEONYM: *Lithophyllum tenue* Kjellman (1889, pp. 22–23, pl. 1, figs 6–10).

HOMOTYPIC SYNONYMS: *Lithothamnion tenue* (Kjellman) Foslie (1895, p. 179), *nom. illeg.* [non *Lithothamnion tenue* Rosenvinge (1893, p. 778)]; *Lithothamnion laeve* (Foslie) Foslie f. *tenue* (Kjellman) Foslie (1900, p. 15, ‘*tenuis*’); *Mesophyllum tenue* (Kjellman) Lebednik (1974), *comb. ined.*

LECTOTYPE: In TRH (unnumbered), on a broken *Mytilus* L. shell; collected by F. R. Kjellman 22–26 July 1879; previously illustrated by Printz (1929, pl. 3, fig. 3, as *Lithothamnion*) and Lebednik (1974, pl. 61, figs 1, 3, as *Mesophyllum*) (Figs 7–10); designated herein [Mikael Foslie’s label reads: ‘Lith. Monogr. pl. 3, fig. 3. *L. tenue* (Kjellm.) Vega-Exp: sp. konc. foto n° 24 A Arkt. amerika: Port Clarence 1879. leg. F. R. Kjellman’].

ISOLECTOTYPES: (1) In TRH (unnumbered), on three stone fragments in the larger box that also contains the lectotype, collected by F. R. Kjellman 22–26 July 1879 (Fig. 11). (2) In TRH (unnumbered), on a single stone fragment in the smaller box, including a Foslie slide # 311, collected by F. R. Kjellman 22–26 July 1879, illustrated by Printz (1929, pl. 3, fig. 2, as *Lithothamnion*) and Lebednik (1974, pl. 61, fig. 2, as *Mesophyllum*) [Foslie’s label reads ‘Lith. Monogr. pl. 3, fig. 2. *L. tenue* 188. Port Clarence prep. 311’].

SYNTYPES: (1) In UPS (unnumbered, herein collection 1), on *Mytilus*, *Littorina*, limpets, barnacles and pebbles; collected by F. R. Kjellman, 22–26 July 1879 (Figs 1–6, 12–16, 17, 19, 20, 24) [Kjellman’s label reads ‘Herb. Musei Botanici Upsaliensis Herb. Kjellman. *Lithophyllum tenue* Kjellm. Stilla Oc. Port Clarence, 22–26/7/1879, F. R. Kjellman’]. (2) In UPS (unnumbered, herein collection 2), on three pebbles, collected by F. R. Kjellman, 22–26 July 1879 [Kjellman’s label reads ‘Herb. Musei Botanici Upsaliensis Herb. Kjellman. *Lithophyllum tenue* Kjellm. Stilla Oc. Port Clarence, 22–26/7/1879, F. R. Kjellman’]. (3) In UPS (unnumbered, herein collection 3), on a single pebble, collected by F. R. Kjellman, 22 July 1879 (Figs 18, 21–23) [Kjellman’s two labels read ‘Vega-Expedition 1878–80, Arktiska Amerika: Port Clarence 1879/22/7. F. R. Kjellman’ and ‘*Lithothamnion tenue* Kjellm., *Lithophyllum durum* Kjellm.’]. (4) In UPS (unnumbered, herein collection 4), on two pebbles, collected by F. R. Kjellman, 22 July 1879 [*pro parte*: includes material of *Clathromorphum*; Kjellman’s two labels read ‘Vega-Expedition 1878–80, Arktiska Amerika: Port Clarence 1879/22/7. F. R. Kjellman.’ and ‘*Lithothamnion durum* Kjellm., *Lithophyllum tenue* Kjellm.’]; this material is also annotated by M. Foslie ‘*Clathromorphum circumscriptum* (Strömf.) Fosl. f. *tenuis* (Kjellm.)’.

TYPE LOCALITY: Port Clarence (Alaska), Bering Sea, in the upper sublittoral region.

HABITAT: Specimens grow in the sublittoral zone on pebbles and

shells of *Littorina*, *Mytilus*, barnacles and limpets. At the end of July, they are provided with spermatangial, carposporangial and multiporate conceptacles (one with bisporangial remains).

DISTRIBUTION: Port Clarence (Alaska) and East Sound, Orcas I. (Puget Sound, Washington State).

MATERIAL EXAMINED: **United States:** Alaska. Lectotype, isolectotypes and syntypes as cited above. Washington State. East Sound, Orcas Island, San Juan Islands, 7 July 1925, L. Roush 56, UC # 739472 (Figs 25–27).

OBSERVATIONS ON TYPE MATERIAL AND NEOLECTOTYPIFICATION: Kjellman’s (1889, p. 23) Swedish description of *Lithophyllum tenue*, given after the Latin diagnosis reads in translation: ‘Port Clarence, abundant; grew within the sublittoral region, attached to stones and *Mytilus* shells; spore production completed.

‘Species description. External form. The thallus is encrusting, 2–3 cm in diameter, almost paper-thin, pale pink with blue-gray streaks, non-glossy, smooth, but with more or less clearly prominent concentric striations toward the periphery, solid but brittle, with a clearly enlarged, pale margin, sometimes smooth-edged, sometimes irregularly notched, or quite deeply lobed with rounded lobes.

‘Thallus structure. The basal part of the coaxial [i.e. multiaxial] system is less developed than the upper part. The cell rows diverge quite strongly from the central plane at first, but then develop parallel to it. They consist of cells 25 µm long and 10 µm broad. The ascending filaments diverge quite strongly, [their cells?] are prismatic with 5 or 6 planes, and even when calcified are sharply delimited and easily separated from each other. Their lower cells are generally longer than broad, whereas those above are almost as long as broad, and the diameter of the cell lumen is just twice the thickness of the cell wall.

‘Reproductive organs. The same specimens have both carposporangial and sporangial conceptacles, but although both types are present they occur in different numbers. Both develop above the surface of the crust and look alike, but carposporangial conceptacles are always higher and hemispherical to conical, while the sporangial conceptacles are compressed hemispherical. Their diameter at the base is 300 to 400 µm. On older specimens the conceptacles appear in great masses and intermingle on the crust in longer or shorter concentric chains.’

Kjellman did not compare his material to other species. His observation of (tetra- or bi-?) sporangial and carposporangial conceptacles on the same thallus is apparently based on observations of gametophytes growing side-by-side with thalli bearing multiporate conceptacles (see below; Fig. 9). We observed only one bisporangium in a conceptacle of the material in TRH (all other conceptacles being empty), and Kjellman concluded that ‘spore production [was] completed.’ Kjell-

Figs. 1–6. *Leptophytum tenue* (syntype collection 1 in UPS).

Fig. 1. Thalli attached to *Mytilus* (A), *Littorina* (B), pebbles (C), barnacles (D), and limpets (E), with the original label.

Fig. 2. SEM surface view of vegetative thallus (on *Littorina*) showing vague rims around epithallial cells, probably covered by detritus.

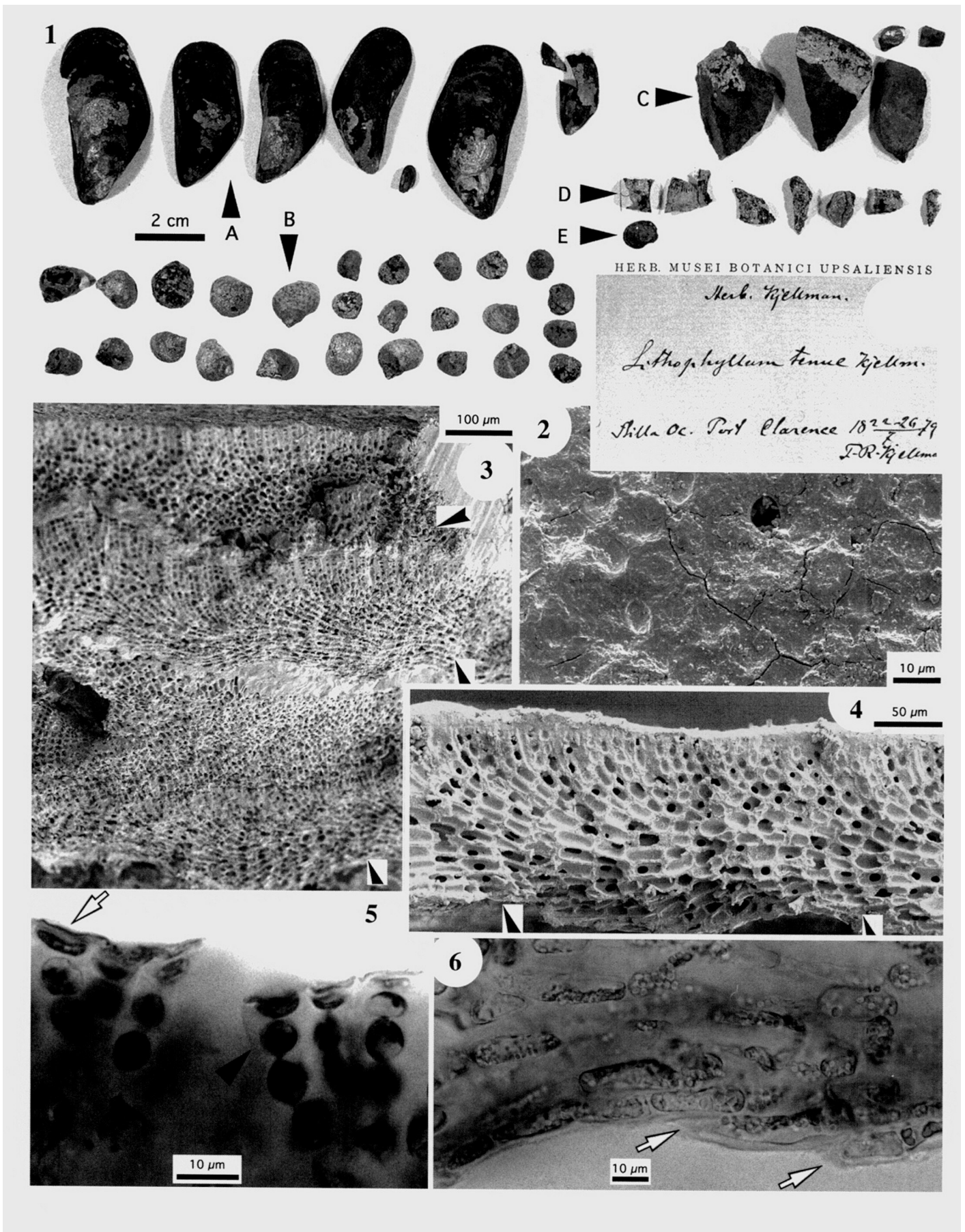
Fig. 3. SEM view in TS of three lamellae (arrowheads) in superimposition (thalli on *Littorina*).

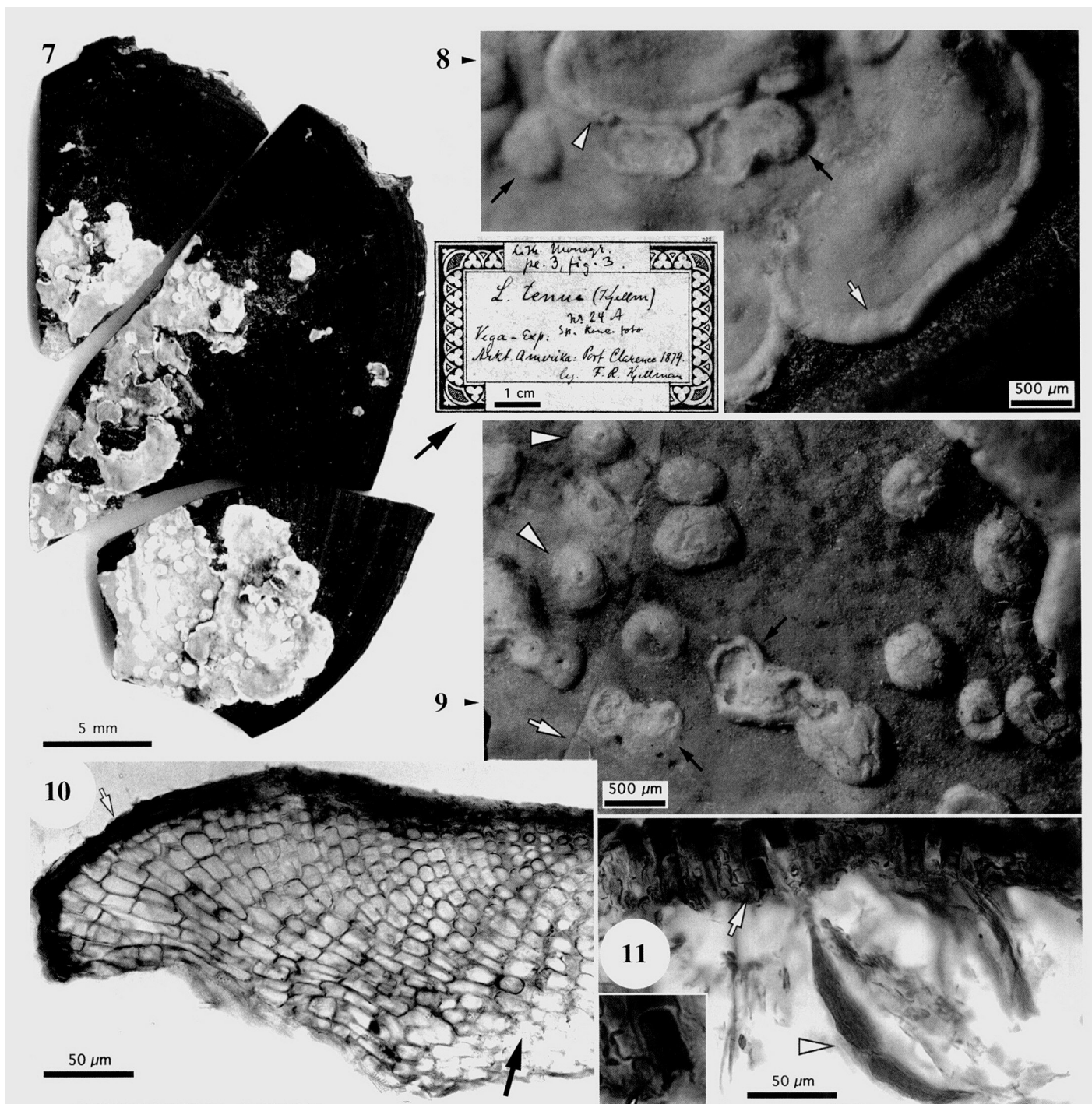
Fig. 4. SEM view in TS of a lamella showing coaxial patches in the hypothallium (arrowheads) and numerous cell fusions (shown as dark holes on shared cell walls) (thallus on *Littorina*).

Fig. 5. Thallus in TS showing flattened epithallial cells (arrow) and short, isodiametric subepithallial initials (arrowhead) (thallus on *Mytilus*).

Fig. 6. Thallus base in TS showing terminal, wedge-shaped hypothallial cells (arrows) (thallus on *Mytilus*).

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Figs. 7–11. *Leptophytum tenue* (lectotype and isotype in TRH).

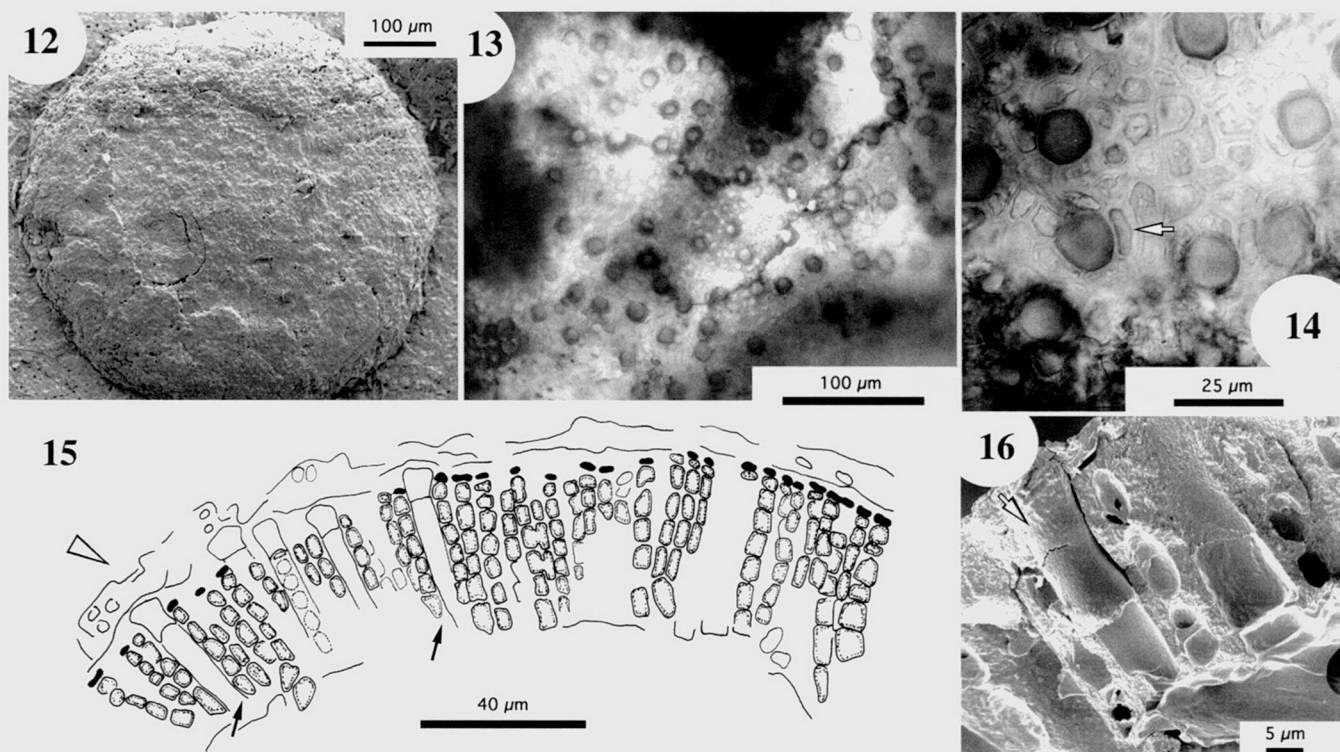
Fig. 7. The lectotype, comprising several thalli growing on *Mytilus* and placed in Foslie's original box (arrow; in lower magnification).

Fig. 8. Surface view of thallus near margin covered by a cuticle (white arrow). Note thallus superimposition (arrowhead) and the few, intact or degenerate multiporate conceptacles (black arrows; lectotype).

Fig. 9. Surface view of two individuals growing side by side (their border indicated by white arrow). Thallus on left with uniporate conceptacles (arrowheads). Note the degenerate (multiporate) conceptacles on thallus on right (black arrows; lectotype).

Fig. 10. Thallus margin in TS covered by a cuticle (white arrow) and showing patches of coaxial cells (black arrow) in a mainly noncoaxial hypothallium (lectotype; Lebednik slide # 2).

Fig. 11. Conceptacle roof in TS with bisporangium (arrowhead). Pores of the roof plugged and bordered by normal roof cells (arrow; magnified in the box) (isotype on rock fragment).



Figs. 12–16. *Leptophytum tenue* (syntype collection 1 in UPS; thalli on *Littorina*).

Fig. 12. SEM surface view of a multiporate conceptacle covered by detritus. Note the sharp distinction of the conceptacle roof from the thallus surface (suggesting peripheral constriction; cf. Fig. 23).

Fig. 13. Surface view of a multiporate conceptacle roof showing pore openings.

Fig. 14. Surface view of pores surrounded by rosette cells that are normal epithallial cells or occasionally thinner-wider cells (arrow).

Fig. 15. Drawing of a multiporate conceptacle roof in TS. Note the nondifferentiated roof cells (arrows) bordering pore canals and the detritus covering the roof (arrowhead).

Fig. 16. SEM view of a multiporate roof in TS showing two pores (one is plugged; arrow).

man's term 'koaxila system' [also adopted in his account of *Lithothamnion* (now *Clathromorphum*) *loculosum* Kjellman (1889, p. 21) and *Lithothamnion foecundum* (Kjellman 1883, p. 131 [English reprint, p. 99])] almost certainly refers to a multiaxial (polystromatic) hypothallium rather than to a co-axial hypothallium.

We refer to the four unnumbered folders of *Lithophyllum tenue* in Kjellman's herbarium (UPS) as collections 1, 2, 3 and 4 (as noted above).

Collection 1 is the richest; it includes at least 46 specimens (the largest c. 1.3 cm in diameter). All specimens are firmly attached to small pebbles and stone fragments and shells of *Littorina*, barnacles, *Mytilus*, and limpets (Fig. 1).

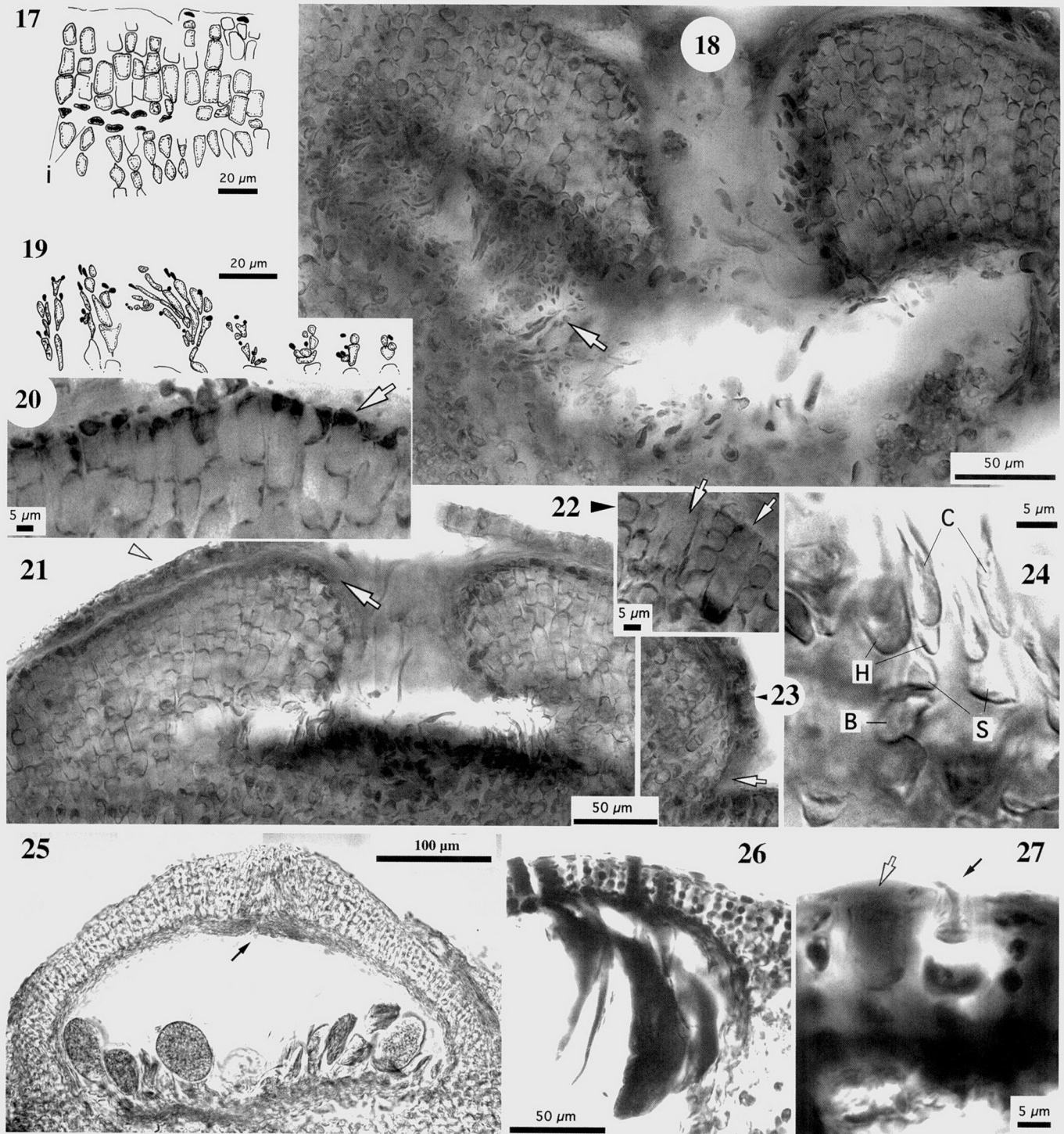
Collection 2 includes specimens with multiporate and uniporate conceptacles attached to three pebbles (the largest one c. 11.5 cm in length and 3.5 cm broad). The largest specimen in collection 2 reaches 3 cm in extent.

Collection 3 includes gametangial specimens attached to a pebble c. 9 cm in length and 4 cm broad.

Collection 4 comprises specimens attached to two pebbles. One of these specimens belongs to the genus *Clathromorphum* Foslie, having a noticeably thicker thallus and a surface covered with crater-like depressions (i.e. remains of conceptacle cavities), 200–240 µm in diameter. Foslie, who apparently examined this material, identified it as *C. circumscriptum*. The other specimens in this collection are sterile and have a glossy thallus with striations on the surface. Foslie identified the lat-

ter specimens as *Lithothamnion laeve* f. *tenue* (Kjellman) Foslie.

The material of *Lithophyllum tenue* in Foslie's herbarium (TRH) comprises specimens placed in two boxes. The first (and larger) box includes specimens attached to 3 small stone fragments and 3 *Mytilus* fragments (Fig. 7). The *Mytilus* shell (intact) has previously been illustrated by Printz (1929, pl. 3 fig. 3). This box is annotated 'Lith. Monogr. pl. 3, fig. 3. *L. tenue* (Kjellm.) Vega-Exp: sp. konc. foto n? 24 A Arkt. amerika: Port Clarence 1879. leg. F. R. Kjellman' (Fig. 7, arrow) and also contains a paper sheet with a manuscript (written by Foslie) '*L. tenue* = *L. flaves foecum*? . . . [the last two epithets stricken through] *laeve* f. *tenue*? Konzept. . . en 180 µlang ca. 75 µm høje [high] Taget [Roof] ca. 35 µm tykt . . . Skorpe [Crust] . . . af alger . . . dyn [detritus]. . . over koncept. – ny skorpe oev . . . r . . . De hoi konc. Skr. . in. . . sig far dyn som havet taget? . . . Cyst. konc. Lar. . . The second (smaller) box includes the stone fragment illustrated × Printz (1929, pl. 3, fig. 2) and is annotated 'Lith. Monogr. pl. 3, fig. 2 *L. tenue* . . . Port Clarence prep. 311'. This box also contains a manuscript (written × Foslie) that reads: '*Lithoph. tenue* (Beringshavet) Prep. 311. Perith. 18 × 7, 14 × 7, 18 × 6, 20 × 7, 14 × 6, 18 × 10, 14 × 10, 11 × 9, 9 × 7, 7 × 7, 14 × 9, 9 × 9, 11 × 7, 9 × 7, 6 × 6, 7 × 6 Hypoth. 20 × 9, 18 × 11, 18 × 9, 18 × 7, 14 × 9, 14 × 11, 22 × 9, 20 × 11, 11 × 7, 14 × 7, 22 × 11, 25 × 7, 22 × 7'. The entire TRH material is placed in a larger box containing a fragment embedded in



Figs. 17–27. *Leptophyllum tenue*.

Fig. 17. Drawing of a gametangial conceptacle primordium in TS situated 3 or 4 cells below the epithallium (syntype collection 1 in UPS; thallus on *Littorina*).

Fig. 18. Male conceptacle in TS in which a branched (dendroid) SMC (arrow) is visible (syntype collection 3 in UPS; thallus on pebble).

Fig. 19. Drawings of male SMCs on the floor of a conceptacle. Both branched (on left) and simple (on right) structures are present (spermatia in black; spermatangia and SMCs shadowed; syntype collection 1 in UPS; thallus on *Littorina*).

Fig. 20. Apical part of gametangial roof (in TS; similar in position to that indicated by arrow in Fig. 21). Roof filaments have terminal meristematic cells and elongate subterminal cells (syntype collection 1 in UPS; thallus on *Mytilus*).

Figs. 21–23. Carpogonial conceptacle (in TSs) showing remains of carpogonial branches on more or less flattened central floor. Note detrital material (arrowhead) covering roof, two trichocyte-like cell remains (Fig. 22, arrows), constriction at point where side wall meets thallus surface (Fig. 23, arrow), and terminal meristematic cells on roof (Fig. 21, arrow) (syntype collection 3 in UPS; thallus on pebble).

Fig. 24. Carpogonial conceptacle in TS showing remains of 2-celled carpogonial branches, each comprising a carpogonium (C) and hypogynous cell (H), supported by a single cell (S) attached to a basal (B) cell (syntype collection 1 in UPS; thallus on *Littorina*).

paraffin (annotated '*Lithophyllum tenue* Kjellm. Port Clarence, Alaska Nr. 24 A Herb. Mus. Nid.') and three slides. Two of the slides, made by P. Lebednik, are annotated '*Lithop. tenue* Kjellm. Port Clarence Alaska Nr. 24 A Herb. Mus. Nid. Lectotype Lebednik slide #1' and '... slide #2'. The third slide is an original Foslie slide annotated '*Lithophyllum tenue* Kjellm. = *Lithophyllum laeve* (Strömf.)... f. *tenue* [the last name being stricken through] 311 arct. amer. (Beringsh.) Port Clarence Vega exp. 1879. ... leg. Kjellman'.

The TRH material has previously been examined by Lebednik (1974, pls 61, 62, tables 45, 46), who designated as lectotype 'the specimens in the Foslie herbarium' because 'Adey (personal communication) was unable to find any of Kjellman's original material in Sweden'. Lebednik's lectotypification is also confirmed by separate labels attached to the entire collection in TRH as 'Lectotypus *Lithophyllum tenue* Kjellman, ... Foslie prep. 311, Lithoth. Monogr. pl. 3, fig. 2. Determinavit: Phillip A. Lebednik, February 1976. ...' and on the slide covers (containing the three slides) as 'Lectotypus *Lithophyllum tenue* Kjellman'.

The *Mytilus* fragments in TRH contain several individuals of *L. tenue* growing side by side, and reaching 1 cm in extent (Fig. 7). The thalli adhere firmly to the substrate, even along their margins, which have a whitish border (cuticle) (Fig. 8, white arrow). Several uniporate conceptacles can appear next to multiporate ones (Fig. 9, arrowheads), because different individuals can grow side by side (Fig. 9, white arrow), rather than develop mixed phases (as suggested by Kjellman). Multiporate conceptacles are roundish in surface view and 440–580 µm in external diameter, and contiguous ones may merge, attaining 440 µm × 680 µm in opposite diameters (Fig. 9, black arrows). Uniporate conceptacles are 300–500 µm in external diameter. TSs of the vegetative thallus near the margin show a dorsiventral organization. Individual lamellae are c. 170 µm thick and develop a cuticle at the margin. The hypothallium is predominantly noncoaxial, displaying occasionally coaxial patches composed of up to 3 or 4 cell arches in a series (Fig. 10, black arrow). Hypothallial cells are 15–40 µm long and 5–10 µm broad. Ascending hypothallial filaments produce a nonstratified perithallium composed of isodiametric cells, 7–10 µm in diameter. The material on the stone fragments (in the same box) is less representative, comprising remains of both sterile and fertile individuals, the latter up to 1.2 cm in diameter and provided with multiporate conceptacles up to 500 µm in external diameter. In one sectioned conceptacle, remains of a bisporangium were found (Fig. 11, arrowhead). The conceptacle roof is pierced by canals that are bordered by normal roof filaments (Fig. 11, arrow).

The single stone fragment in the second (smaller) box in TRH includes several individuals with uniporate or multiporate conceptacles, the former 200–260 µm and the latter 440–660 µm in external diameter. The number 311 on this box suggests that the similarly numbered slide comes from these specimens. Yet, the material on the slide indicates that the

substrate is organic and is several mm thick (probably a *Mytilus* shell).

A comparison of the TRH material with the UPS specimens indicated that they are both representative of *L. tenue*, with the exception of UPS collection 4, which contains heterogeneous material. Because collections 1 and 2 are dated 22–26 July, collections 3 and 4, 22 July, and those in TRH only with the year (1879), it is clear that they represent various gatherings of specimens made by Kjellman between 22 and 26 July 1879 in Port Clarence and can all be considered part of the type collection. Despite the fact that the largest and most representative collection of *L. tenue* exists in Kjellman's herbarium in UPS, Lebednik's (1974, 1976 annotations in herb.) lectotypification of *L. tenue* with the material in TRH, apparently sent to Foslie by Kjellman, must be followed (Art. 9.17; Greuter *et al.* 2000, p. 15) as the TRH specimens are clearly a part of the original material. Hence, the four UPS collections are here recognized as syntypes. Because the TRH material is a subsample of the collections in UPS, containing several specimens, we are motivated to select a single lectotype specimen (see Art. 9.14; Greuter *et al.* 2000, p. 15), and therefore we designate the thalli on the *Mytilus* shell as lectotype (Figs 7–10). It should be added that, because we do not know if the TRH subsample represents a single gathering (as required by Art. 9.14, to consider Lebednik's lectotypification effective under Art. 8.1 and 8.2), our typification should be regarded as an independent (neo)lectotypification.

The description below is based on fragments of specimens growing on barnacles, *Mytilus* and *Littorina* shells (the TRH lectotype and UPS collection 1) and on pebbles or stone fragments (a TRH isoelectotype with multiporate conceptacles, in the same box containing the lectotype, and UPS collections 2 and 3). The specimen illustrated in the protologue (Kjellman 1889, pl. 1, fig. 6, specimens on a left *Mytilus* shell valve) was not found in either the UPS or TRH collections.

MORPHOLOGY: Thallus encrusting, 1–3 cm in diameter, firmly attached to the substrate (shells, barnacles, pebbles and stone fragments) (Figs 1, 7). Margin adherent, lobed, with a distinct whitish border (cuticle) (Fig. 8). Surface smooth, mostly covered by detritus and cell wall remains, which mask the contour of the epithallial cells (Fig. 2).

ANATOMY: Thallus dorsiventral, individual lamellae 85–200 µm thick (Figs 3, 4, 10). Up to 3 lamellae superimposed so that thalli reach 660 µm in height (Fig. 3, arrowheads). Hypothallium polystromatic and noncoaxial (Figs 3, 4, 10), 70–130 µm thick, growing by terminal meristematic cells protected by a cuticle (Fig. 10). Patches of coaxial cells, composed of up to 4 cell rows, occurring sporadically in parts of the hypothallium (Figs 4, arrowheads, 10, black arrow). Hypothallial cells in the main core 12–40 µm long and 5–10 µm broad (14.5–39 by 5–12 µm, Lebednik 1974). Hypothallial cells near thallus base reaching 46 µm in length and terminating in wedge-shaped cells (Fig. 6, arrows). Perithallium

←
Fig. 25. Carposporangial conceptacle in TS across the periphery of the ostiole (arrow) and consequently at the periphery of the fertile zone, showing carposporangia on flattened floor. (UC 739472).

Fig. 26. Tetrasporangium within a multiporate conceptacle (UC 739472).

Fig. 27. Intact trichocyte (black arrow) next to damaged one (white arrow) on multiporate roof (UC 739472).

50–120 μm thick, composed of cells 4–23 μm long and 3–10 μm broad (6–13 by 5–11 μm , Lebednik 1974) (Figs 5, 10). Epithallial cells borne singly, flattened and mostly wider than perithallial cells below, 2–5 μm long and 6–10 μm broad (Fig. 5, arrow). Subepithallial initials similar or smaller in size than perithallial cells below (Fig. 5, arrowhead). Cell fusions common between contiguous somatic cells (Fig. 4). Secondary pit-connections not seen. Elongate terminal cells, similar to trichocyte remains, present on the roof of conceptacles (Fig. 22, arrows).

REPRODUCTIVE STRUCTURES: Monoecious. All conceptacles raised and generally provided with a constriction at the point where the side wall meets the surface (Fig. 23, arrow). Multiporate conceptacles hemispherical, 350–720 μm in external diameter (402–720 μm , Lebednik 1974, table 46) and 140–270 μm high (Fig. 12). Chambers elliptical, 250–500 μm long and 90–150 μm high ($n = 5$). Conceptacle roofs convex or slightly flattened, lacking a rim, and covered by detrital material (Figs 12, 15, arrowhead). The detritus totally hiding pore openings (Fig. 12), or broken off and uncovering a roof perforated by 73–83 pores ($n = 4$) (Fig. 13) or more in merged conceptacles. Pore plates 250–480 μm in diameter (up to 550 μm in two merged conceptacles). In TSs of roof, pore canals appearing straight and relatively narrow, 7–13 μm in diameter (Fig. 15), surrounded by a group of 6–8 rosette cells similar in shape and size to contiguous epithallial cells or occasionally thinner-wider (Fig. 14, arrow). Pore canals bordered by filaments composed of 5–7 normal roof cells (Figs 11, 15, arrows), plugged (Figs 11, 16, arrow) or unplugged. Roof 40–60 μm thick, composed of 6- to 8-cell filaments, including the epithallial cell (Fig. 15). Only one bisporangium, c. 140 μm in length by 25 μm in breadth, detected in sectioned conceptacles (Fig. 11, arrowhead).

Primordia of gametangial conceptacles occurring 3 or 4 cells below the epithallium (Fig. 17). Male conceptacles 200–500 μm in external diameter (212–254 μm , Lebednik 1974, table 46) and 80–140 μm high ($n = 4$). Chambers 120–260 μm in diameter and 40–90 μm high ($n = 3$) (Fig. 18). Roof thickness ranging from 50 to 100 μm , characteristically thicker in the centre where the ostiole, 30–60 μm in diameter, is situated. SMCs developing on the floor, walls and roof of the chamber, predominantly simple, but a few branched SMCs observed near the centre of the floor (Figs 18, 19). Branched SMCs usually forming dendroid-like structures composed of up to 4 elongate cells (Figs 18 arrow, 19). Whether simple SMCs are lunate in shape was not established.

Female conceptacles 300–500 μm in external diameter (reaching 980 μm when two merge) and 100–220 μm high ($n = 6$) (424–551 μm in external diameter of carposporangial (?) conceptacles, Lebednik 1974, pl. 46), with remains of carpogonial branches. Roof 70–130 μm thick, with a central ostiole 30–130 μm in diameter, formed by peripheral, centripetally growing filaments originating in the perithallium but having distinctive terminal meristematic cells (Figs 20, 21, arrows). Roof filaments developing terminal trichocyte-like cells (Fig. 22, arrows). Roof characteristically constricted along its periphery where the side walls meet the thallus surface (Fig. 23, arrow). Chambers 270–450 μm in diameter and 40–150 μm high ($n = 5$) (Fig. 21). Central fertile area remaining more or less flattened, where remains of supporting

cells bear one or two, 2-celled carpogonial branches (Fig. 24). Carposporangia seen in a few chambers, but their site of development not established. Gametangial conceptacles covered by detritus (Fig. 21, arrowhead), like multiporate conceptacles. Embedded conceptacles not seen, suggesting older conceptacles of all types gradually degenerate (Fig. 9, black arrows).

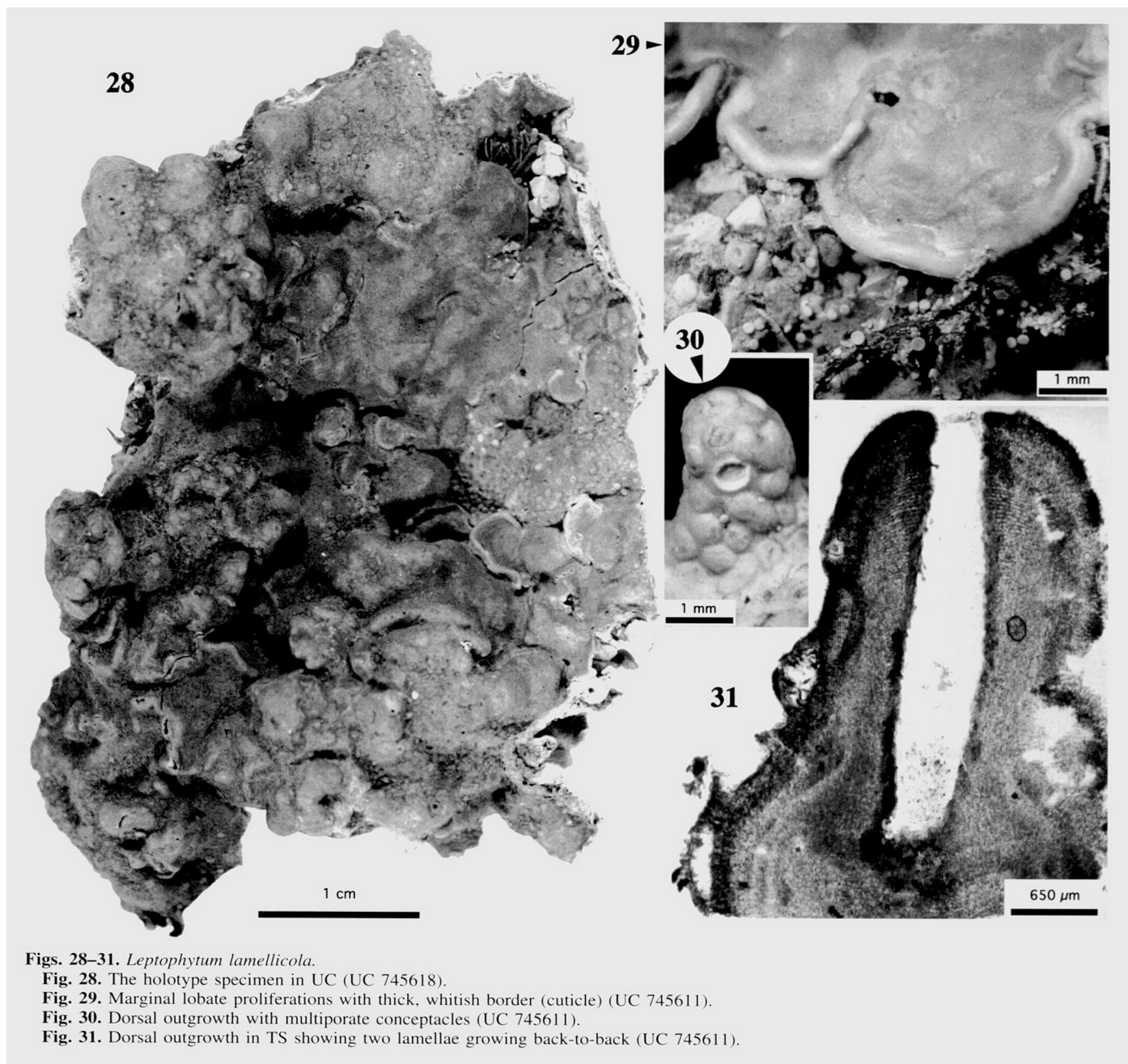
COMMENTS: The transfer of *Lithophyllum* (*Lithothamnion*) *tenu* to *Leptophyllum* here is motivated by a combination of characters that includes: (1) 'shallow' conceptacle primordia, (2) predominantly simple SMCs together with few branched SMCs near the centre of the chamber floor, (3) carposporangial conceptacles having a flattened fertile floor, (4) a predominantly noncoaxial hypothallium with patches of coaxial cells, (5) flattened (not flared or domed) epithallial cells, and (6) short subepithallial initials. Characters 2, 3 and 4 preclude a position in the genus *Mesophyllum* whereas characters 2 and 6 preclude an affiliation with *Synarthrophyton* (species of which have dendroid SMCs as the dominant type and elongate subepithallial initials; see Adey *et al.* 2001; Athanasiadis 2001, table 2; Athanasiadis *et al.* 2004). Moreover, characters 1, 2, 5 collectively preclude a position in *Phymatolithon*, and characters 2, 5 and 6 preclude a position in *Lithothamnion* (see Chamberlain & Irvine 1994; Adey *et al.* 2001; Athanasiadis 2001, table 2).

Patches of coaxial hypothallial cells are here reported for the first time in *Leptophyllum*, and they are also found in other Pacific species of the genus (see below) and in two Arctic species associated with *Leptophyllum* (Athanasiadis 2001).

At the species level, *Leptophyllum tenu* shows two autapomorphies, viz. constriction in the periphery of the side walls of conceptacles and terminal trichocytes on the conceptacle roofs. The species appears to be most closely related to the genotype *Leptophyllum laeve*, differing in having thinner lamellae (up to 200 μm vs 650 μm in *L. laeve*), thallus superimposition (not reported in *L. laeve*), smaller multiporate conceptacles with fewer pores (up to 720 μm in external diameter vs 1000 μm in *L. laeve*) and nondifferentiated basal pore cells (generally differentiated in *L. laeve*).

According to Lebednik (1974), *L. tenu* was probably collected by Kjellman on the eastern and northern shores of Port Clarence, at the north end of the Bering Sea, where rocky substrate is found. Lebednik found no specimens that could be attributed to *L. tenu* on the south shore of the Alaska Peninsula, south of the Bering Sea. Three other collections in TRH, cited by Adey & Lebednik (1967, p. 52, as *Lithothamnion tenu*), represent material collected by Saunders (Kukak Bay, Harriman Alaska Expedition no 425, 4 July 1899) and N. Hartz (Greenland, Holstensborg 1889) and identified as *Lithothamnion laeve sensu stricto* by Foslie (Lebednik 1974). *Leptophyllum tenu*, therefore, is known only from its type locality and a collection from East Sound, Orcas Island, Washington, previously identified as *L. adeyi* by Steneck & Paine (1986, p. 235).

In the Orcas Island collection (UC 739472), individual lamellae are 160–210 μm thick, composed of hypothallial cells 18–40 μm long by 5–12 μm broad, perithallial cells 5–12 μm long by 5–8 μm broad, and flattened epithallial cells c. 2 μm long by 8 μm broad. Carposporangial conceptacles develop peripheral carposporangia (Fig. 25, arrow indicates ostiole



Figs. 28–31. *Leptophytum lamellicola*.

Fig. 28. The holotype specimen in UC (UC 745618).

Fig. 29. Marginal lobate proliferations with thick, whitish border (cuticle) (UC 745611).

Fig. 30. Dorsal outgrowth with multiporate conceptacles (UC 745611).

Fig. 31. Dorsal outgrowth in TS showing two lamellae growing back-to-back (UC 745611).

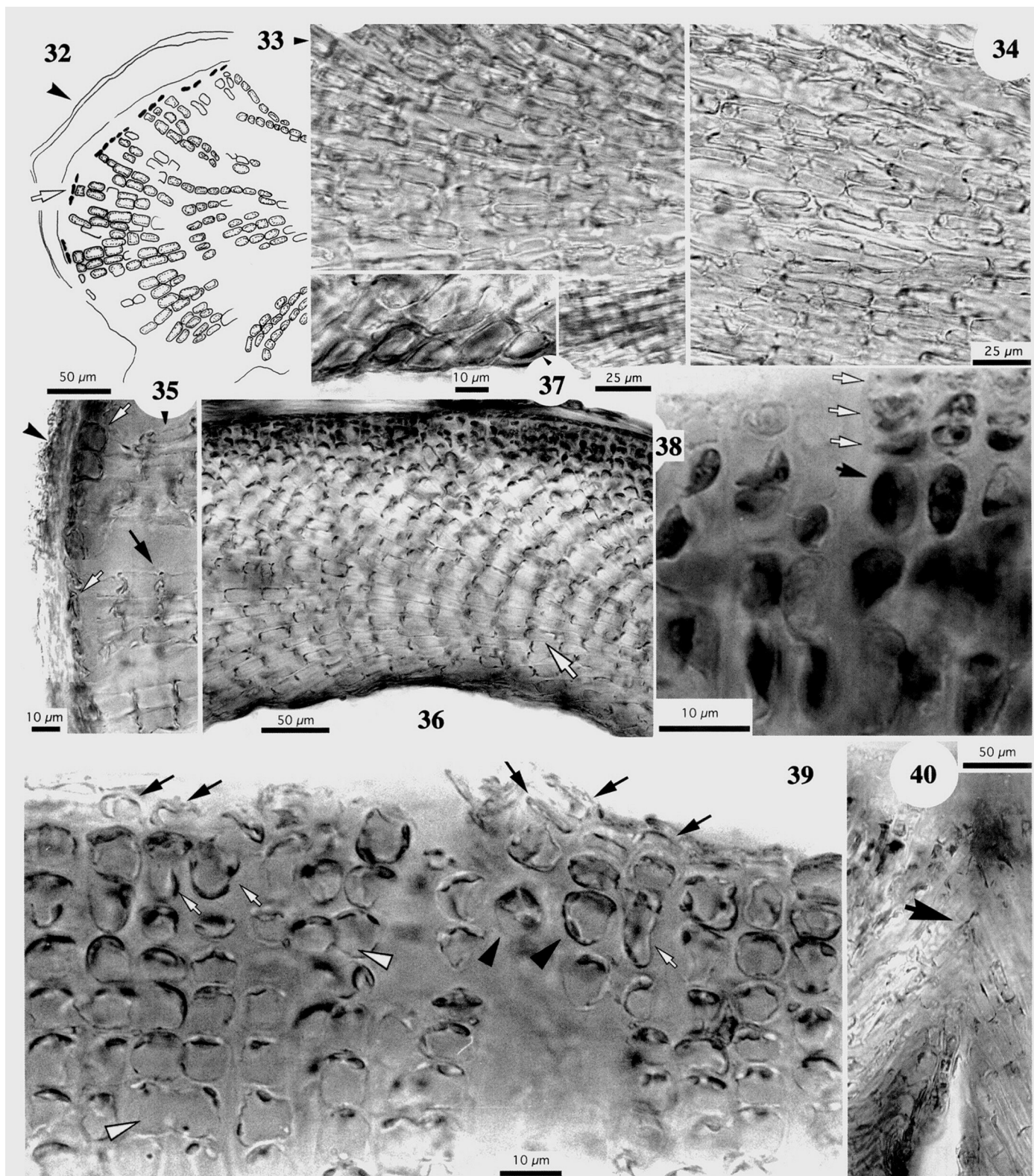
wall), whereas multiporate conceptacles develop zonately divided tetrasporangia (100–130 μm long and 30–35 μm broad) (Fig. 26). Roofs of both carposporangial and tetrasporangial conceptacles are characteristically constricted at their periphery and bear terminal trichocytes (*c.* 15 μm long and 10 μm broad) (Fig. 27, arrows). Multiporate conceptacles are hemispherical, 300–560 μm in external diameter and 100–140 μm in height. Their chambers are 310–320 μm in diameter and 100–150 μm high, having convex to flattened roofs, 50–80 μm thick, composed of 5- or 6-celled filaments and perforated by up to 85 pores (at least 112 in two merged conceptacles that reach 625 μm in external diameter). Pore canals are straight and bordered by normal roof cells. Pore openings are surrounded by 5–8 rosette cells. In all these characters, these thalli largely agree with the type material of *L. tenue*. They differ from *L. adeyi* mainly in having much larger hypothallial

cells (up to 40 μm vs 28 μm in *L. adeyi*) and larger multiporate conceptacles (up to 560 μm vs 400 μm in *L. adeyi*) provided with trichocytes, peripheral constrictions and non-differentiated pore cells (the latter three characters not recorded in *L. adeyi*).

Leptophytum lamellicola sp. nov.

Figs 28–58

Algae crustaceae vel foliosae, usque ad 6 cm diametro, in saxis et algis aliis coralloidibus geniculatis vel nongeniculatis prostratae; thallus in substrato adhaerens, partim libere crescens, lamellis superimpositis, 100–2500 μm crassis; color thalli roseus vel rubropurpureus, albidus in marginibus integris lobatisque; hypothallus polystromaticus, praecipue noncoaxialis (cum partibus coaxialibus), ex cellulis 10–43 μm longis compositus; perithallus ex cellulis minoribus, gradatim ascendentibus compositus; cellulae extimae mer-



Figs. 32–40. *Leptophytum lamellicola*.

Fig. 32. Drawing of thallus margin in TS showing terminal darkly staining meristematic cells (arrow) protected by cuticle (arrowhead; holotype).

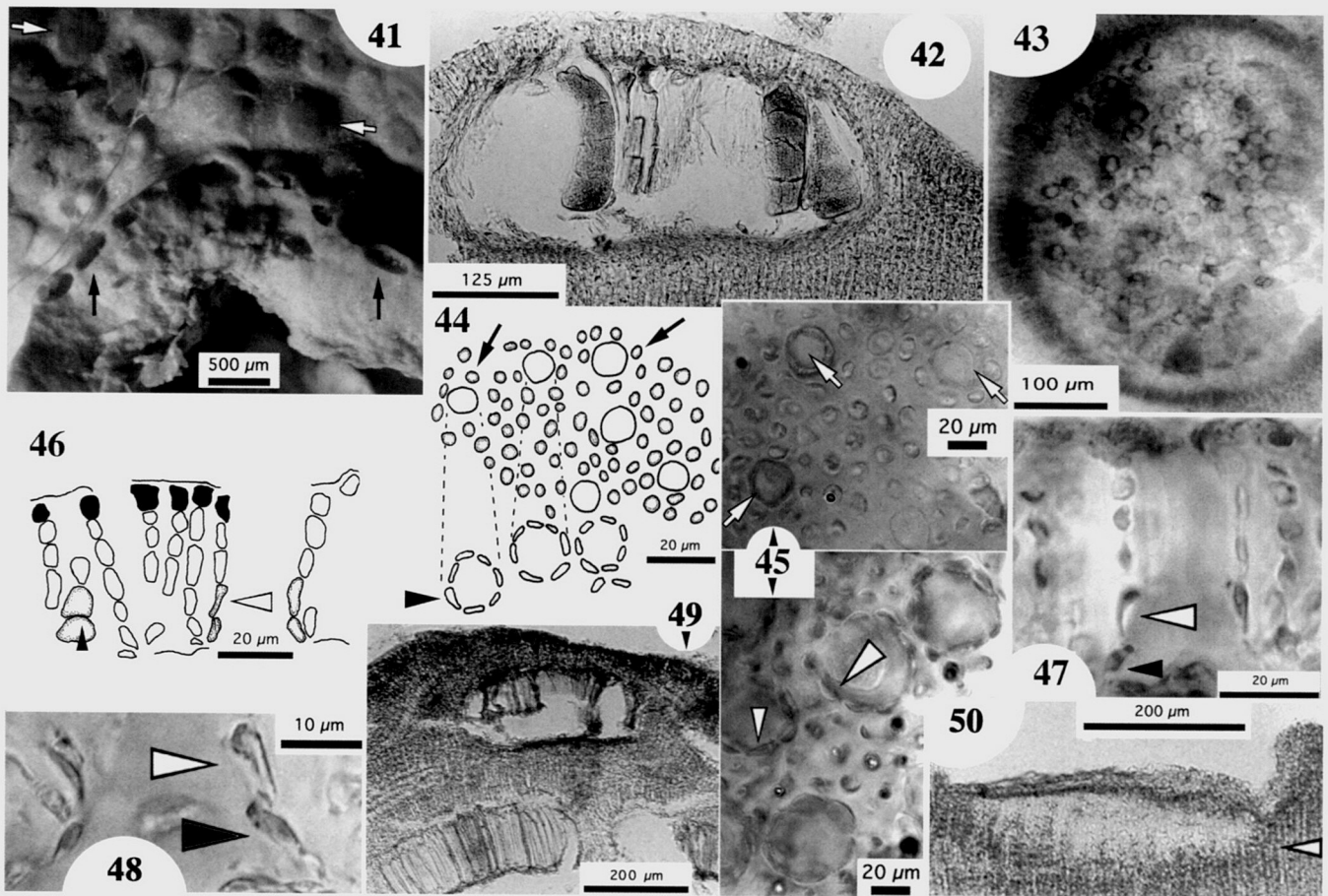
Fig. 33. Thallus in TS showing ascending and descending, vaguely coaxial, arching hypothallium (holotype).

Fig. 34. Thallus in TS showing noncoaxial hypothallium (isotype).

Fig. 35. Thallus margin in TS showing terminal meristematic cells (white arrow), covered by cuticle (arrowhead), and patches of coaxial hypothallial cells (black arrow) (UBC A48025).

Fig. 36. Thallus in TS showing series of coaxial arches of hypothallial cells (UC 739466).

Fig. 37. Thallus base in TS showing wedge-shaped terminal hypothallial cells (holotype).



Figs. 41–50. *Leptophyllum lamellicola*.

Fig. 41. Numerous multiporate conceptacles in surface view (white arrows) and in TS (black arrows) on thallus surface (holotype).

Fig. 42. Tetrasporangial conceptacle in TS (holotype).

Fig. 43. Surface view of multiporate roof (holotype).

Fig. 44. Drawing of pores in surface view at two levels of focus, showing apical openings surrounded by normal epithallial cells (arrows) and thinner-wider pore cells (arrowhead) encircling the base of the canal (isotype).

Fig. 45. Views of pores at two levels of focus, showing apical openings (arrows) surrounded by normal epithallial cells and thinner-wider pore cells (arrowheads) near basally enlarged canals (isotype).

Fig. 46. Drawing of two pore canals in TS, showing the bordering filaments composed of specialized cells near base: basal and subbasal pore cells thinner (white arrowhead) -wider (black arrowhead) (the section tangential to the canal) (holotype).

Figs. 47, 48. Sections across two pore canals of multiporate conceptacles, showing specialized darkly staining basal (black arrowheads) and subbasal (white arrowheads) cells that are thinner than contiguous roof cells (Fig. 47). Note basal cells projecting outwards and subbasal cells more elongate (holotype).

Fig. 49. Thallus in TS showing embedded chambers of multiporate conceptacles filled with palisade cells (LAM AHFH 70290).

Fig. 50. Remains of conceptacle in TS with chamber (arrowhead) filled with new perithallial cells (holotype).

istematicae perithalli tantum tempore divisionis elongatae, 1–3 cellulis epithallibus complanatis obductae; conjunctiones cellularum contingentium vulgares; trichocellulae absentes; conceptacula tetrasporangifera multiporosa, 320–680 μm diametro externo, 60–200 μm alta; tectum conceptaculi maturi convexum vel complanatum, 30–65 μm crassum, 47–102 poris instructum; fila poros conceptaculorum cingentia ex 5 vel 6 cellulis composita, cellulis versus basem tenuioribus-latiores; cellulae subbasales porum cingentes elongatae et cellulae basales extrinsecus percurrentes; cavitates 250–530

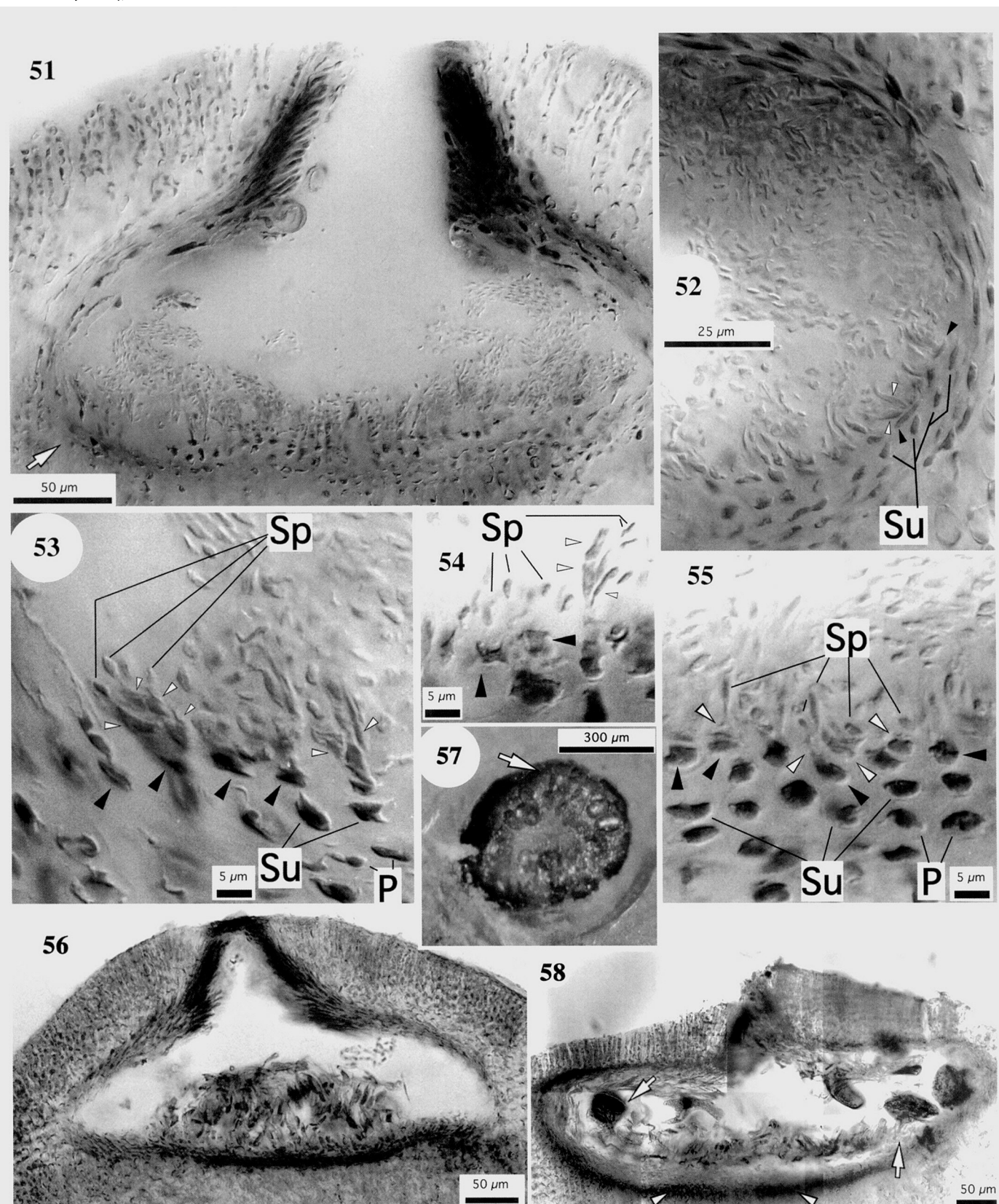
μm in diametro et 100–240 μm altae; tetrasporangia 100–170 μm longa et 20–75 μm lata; gametophyta monoica; cavitates conceptaculorum marium maturorum 170–460 μm in diametro et 70–200 μm altae; cavitates conceptaculorum carposporangialium maturorum 250–560 μm in diametro et 80–250 μm altae; spermatangia et carposporophyta ut vulgo in genere.

Algae crustose to foliose, up to 6 cm in diameter, prostrate on rocks and other nongeniculate and geniculate coralline algae; thallus attached to the substratum and partly growing free, with superim-

Fig. 38. Thallus in TS showing three epithallial cells (white arrows) and subepithallial initials (black arrow) similar in size to perithallial cells below (holotype).

Fig. 39. Thallus in TS showing 1 or 2 flattened epithallial cells (black arrows) on each perithallial filament and dividing subepithallial initials (white arrows) slightly longer than cells below. Note locally stratified perithallium (white arrowhead) and deep epithallial sloughing that removes the upper cell of recently divided subepithallial cells leaving the daughter-cell intact (black arrowheads) (UBC A48025).

Fig. 40. Abutting lamellae establishing cell fusions (holotype).



Figs. 51–58. *Leptophytum lamellicola* (isotype).

Fig. 51. Male conceptacle in TS provided with simple and branched (arrow; magnified in Fig. 53) spermatangial structures on chamber floor.

Fig. 52. Male conceptacle in TS showing simple SMCs (black arrowheads) on chamber floor, wall and roof. Note elongate SMCs on wall bearing several spermatangia (white arrowheads). SMCs are borne singly on supporting cells (Su).

Fig. 53. Male conceptacle in TS showing several branched spermatangial structures. SMCs (black arrowheads) on chamber floor, supporting branched spermatangia (white arrowheads) that have just released spermatia (Sp). SMCs are borne singly on supporting cells (Su) connected to perithallial cells (P).

posed lamellae 100–2500 μm thick; colour rose to red-purple with whitish margins that are entire and lobate; hypothallium polystromatic, mainly noncoaxial (with coaxial parts), composed of cells 10–43 μm in length; perithallium composed of smaller and gradually ascending cells; ultimate meristematic perithallial cells elongate only during division, covered by 1–3 epithallial cells; cell fusions between contiguous cells common, trichocytes absent; tetrasporangial conceptacles multiporate 320–680 μm in external diameter, and 60–200 μm high; roofs of mature conceptacles convex to flattened, 30–65 μm thick, with 47–102 pores; filaments bordering the pores composed of 5 or 6 cells, composed of thinner-wider cells at the base; subbasal pore cells elongate and basal pore cells projecting outwards; chambers 250–530 μm in diameter and 100–240 μm high; tetrasporangia 100–170 μm long and 20–75 μm broad; gametophytes monoecious; chambers of male conceptacles 170–460 μm in diameter and 70–200 μm high; chambers of carposporangial conceptacles 250–560 μm in diameter and 80–250 μm high; spermatangia and carposporophytes as for the genus.

TYPIFICATION: We have studied a subsample of UC 745618 containing at least 24 tetrasporangial and gametangial specimens/fragments of *Leptophytum lamellicola* growing together with a few specimens/fragments of *Mesophyllum lamellatum* (Setchell & Foslie) Adey. After separating the two species, we have selected one of the largest specimens of *L. lamellicola* as the holotype (Fig. 28), making the other specimens/fragments isotypes. The holotype is a tetrasporophyte.

HOLOTYPE: In UC (745618), collected by M. B. Nichols (Nichols 131), December 1906 (Fig. 28).

ISOTYPES: (1) In UC (745618). (2) In GB (unnumbered; Nichols 131). (3) In herb. Athanas. (Nichols 131). All isotypes collected by M. B. Nichols, December 1906.

ETYMOLOGY: The epithet *lamellicola* is a compound noun in apposition of the words *lamellis* (dative of plural of *lamella*) and the suffix *cola*, defining the association of the species with *Mesophyllum lamellatum*.

TYPE LOCALITY: Pyramid Point, Monterey County, California.

HABITAT: Littoral and sublittoral zones, to at least 9 m depth, at moderately sheltered localities, attached to rocks, barnacles, polychaetes and other nongeniculate and geniculate coralline algae (*Corallina* L.); in California usually growing attached to *Mesophyllum lamellatum*.

DISTRIBUTION: United States and Canada. Scattered collections from Santa Catalina Island and Monterey, San Mateo and Marin Counties in California and from Vancouver Island, British Columbia (from Whiffen Spit to Cape Scott).

MATERIAL EXAMINED: **United States:** California. Holotype and isotypes (as described above); Cypress Pt., Monterey Co., attached to *Corallina* and *M. lamellatum*, 14 December 1906, Nichols 162, UC 745676; Cypress Pt., Monterey Co., 9 January 1899, W. A. Setchell & R. E. Gibbs 3075, TRH [mixed with the lectotype of *M. lamellatum* (see Athanasiadis *et al.* 2004, fig. 92), the Foslie label reads: "... # 3075 *Lith. lamellatum* Setch. et Fosl. Kalifornien Cypress Point Monterey 9.1.1899 leg. W.A. Setchell et R. E. Gibbs ..."]; Cypress Pt., Monterey Co., 13 October 1928, Roush 111, UC 739466 [mixed with *M. lamellatum*]; Duxbury Reef, Marin Co., 17 November 1906, Nichols 29, UC 745606; Pyramid Pt., Pacific Grove, Monterey Co., tetrasporic, 14 December 1906, Nichols 119,

UC 745610 & Nichols 176, UC 745600; Pt. Lobos, Monterey Co., tetrasporic & gametangial thalli, 13 October 1928, Roush 104, UC 739469 [mixed with *M. lamellatum*]; Pigeon Pt., San Mateo Co., tetrasporic, 19 October 1930, Roush 146, UC 745611 [mixed with *Pseudolithophyllum muricatum* sensu Steneck & Paine (1986)]; Long Point, Santa Catalina Island, intertidal, rocky shore, tetrasporic on polychaete tubes and barnacles, 30 November 1948, Dawson 5656, LAM (AHFH 70290) [mixed with a mastophoroid coralline].

Canada: British Columbia, Vancouver Island, West side of Edward King Island, 9 m, rocky, moderately sheltered, 48°49'42"N, 125°13'05"W, 19 August 1969, Baillie & Pace 27706, UBC A48025; Amphitrite Point, midintertidal, 48°54'N, 125°33'W, multiporate conceptacles, 1 June 1969, O'Brien 25115, UBC A40267; east side of Cape Scott, 50°47.1'N, 128°25.5'W, 11 August 1968, Markham & *al.* 20811, UBC A36639; Whiffen Spit, 48°21'N, 123°43'W, 25 October 1966, M.C., D.P., B.B. 19814, UBC A34583 [mixed with *Mesophyllum vancouveriense* (Foslie) Steneck & R. T. Paine].

MORPHOLOGY: Thalli encrusting to foliose, up to at least 6 cm across, attached to geniculate (*Corallina* sp.) and nongeniculate coralline algae, rocks, barnacles and polychaetes, with proliferations developing ventrally, dorsally and from the margin. Marginal proliferations partly overgrowing the parent crust so that the thallus reaches several mm in thickness. Thallus conforming to irregularities in the substrate, which are projected on its surface in the form of outgrowths. Margins lobate and free (unattached), with a whitish border (cuticle, Fig. 29), sometimes bending down to protect the terminal meristem, or even growing back-to-back (Fig. 31). Dorsal proliferations sometimes growing back-to-back and forming branches (resembling perithallial protuberances), up to 3 mm long and 2 mm broad (Figs 30, 31). Thalli on geniculate coralline algae, partly unattached, developing ventral excrescences, which grow around the branches of the host. Thalli more firmly attached to other substrates, but margins usually free. Colour varying from brownish to purple-red to light pink. The underside of the holotype and isotypes commonly inhabited by a species of the diatom *Coscinodiscus* Ehrenberg.

ANATOMY: Thallus dorsiventrally organized. Individual lamellae 100–2500 μm thick, composed of a hypothallium 150–800 μm thick (Figs 32–37) produced by terminal cell divisions (Figs 32, 35, white arrows). Patches of vaguely (Fig. 33) to strongly (Fig. 36, arrow) coaxial hypothallial cells present in all specimens examined, but hypothallium is predominantly noncoaxial (Fig. 34). Coaxial regions composed of up to 15 arching cell rows, developing through synchronous divisions and elongations of the terminal meristem (Fig. 35). Ascending hypothallial filaments producing a perithallium, 150–1200 μm thick (Fig. 36), and descending hypothallial filaments ending in wedge-shaped cells (Fig. 37). Perithallial stratification sometimes occurring locally (Fig. 39, white arrowheads). Hypothallial cells 10–43 μm long and 5–11 μm broad. Perithal-

Fig. 54. TS of male conceptacle at chamber floor level showing two simple (black arrowheads) and one branched spermatangial structure. The latter composed of branched spermatangia (white arrowheads). Both simple and branched spermatangial structures have released spermatia (Sp).

Fig. 55. Male conceptacle in TS showing simple SMCs (black arrowheads) on chamber floor supporting spermatangia (white arrowheads) that liberate spermatia (Sp). Note lunate SMCs (black arrowheads) and lunate to compressed supporting (Su) and perithallial (P) cells.

Fig. 56. Female conceptacle in TS with remains of carpogonial branches in centre of flattened chamber floor.

Fig. 57. Surface view of carposporangial conceptacle where roof has been lifted off. Note peripheral position of carposporangia (arrow).

Fig. 58. Carposporangial conceptacle in TS showing peripheral development of carposporangia (arrows) and flattened central zone (arrowheads).

lial cells 3–20 μm long and 3–10 μm broad. One or 2 (rarely 3; Fig. 38, white arrows) epithallial cells developing on individual perithallial filaments; these cells more or less flattened (in TS), 2–5 μm long and 4–9 μm broad (Figs 38, 39). Epithallial sloughing common, removing at least 3 cell layers (i.e. 2 epithallial cells and the upper cell of the just divided subepithallial cell; Fig. 39, black arrowheads). Subepithallial meristematic cells similar in size to cells below (Fig. 38, black arrow; Fig. 39, black arrowheads), except during division when they are longer, reaching 12 μm in length (Fig. 39, white arrows). Cell fusions occurring between contiguous somatic cells, sometimes developing between abutting lamellae (Fig. 40). Secondary pit-connections and trichocytes not seen.

REPRODUCTIVE STRUCTURES: Monoecious. All conceptacles raised. Multiporate conceptacles crowded, occurring in patches on branches (Fig. 30) and the main thallus (Fig. 41), 320–680 μm in external diameter ($n = 23$), reaching 900 μm when two conceptacles merge (usually maintaining a border distinguishing them), 60–200 μm high ($n = 8$) and having a convex (rarely flattened) roof lacking a peripheral rim (Fig. 42). Chambers elliptical, 250–530 μm in diameter (up to 580 μm when two merge) and 100–240 μm high ($n = 12$). Roof 30–65 μm thick, composed of 5- to 7-celled filaments and perforated by 47–102 pores ($n = 6$) (Fig. 43). Pore plates 240–370 μm in diameter. Pores surrounded by 6–8 rosette cells, which are normal epithallial cells (Figs 44, 45, arrows). Pore canals bordered by 5- or 6-celled filaments composed of non-differentiated roof cells, except near the base, where the basal cells can project outwards (Figs 47, 48, black arrowheads) and subbasal cells can be elongate (Figs 46, 47, white arrowheads); these specialized cells are also thinner (Figs 45, 46, white arrowheads) -wider (Figs 44, 46 black arrowheads, Fig. 45), tending to encircle the canal (Figs 44, 45, arrowheads), and stain more darkly (Fig. 48, arrowheads). Pore canals c. 10–11 μm in diameter at the apex and c. 13–14 μm in diameter at the base. Tetrasporangia 100–170 μm long and 20–75 μm broad ($n = 15$). Mature conceptacles similar in colour to the rest of the thallus whereas older conceptacles with yellow-whitish roofs. Embedded tetrasporangial chambers filled with colourless palisade cells in one collection (Fig. 49) although the mode of embedding not observed. In all other collections, conceptacles gradually degenerating, first losing their roof and leaving crater-like depressions, which subsequently fill with perithallial cells (Fig. 50).

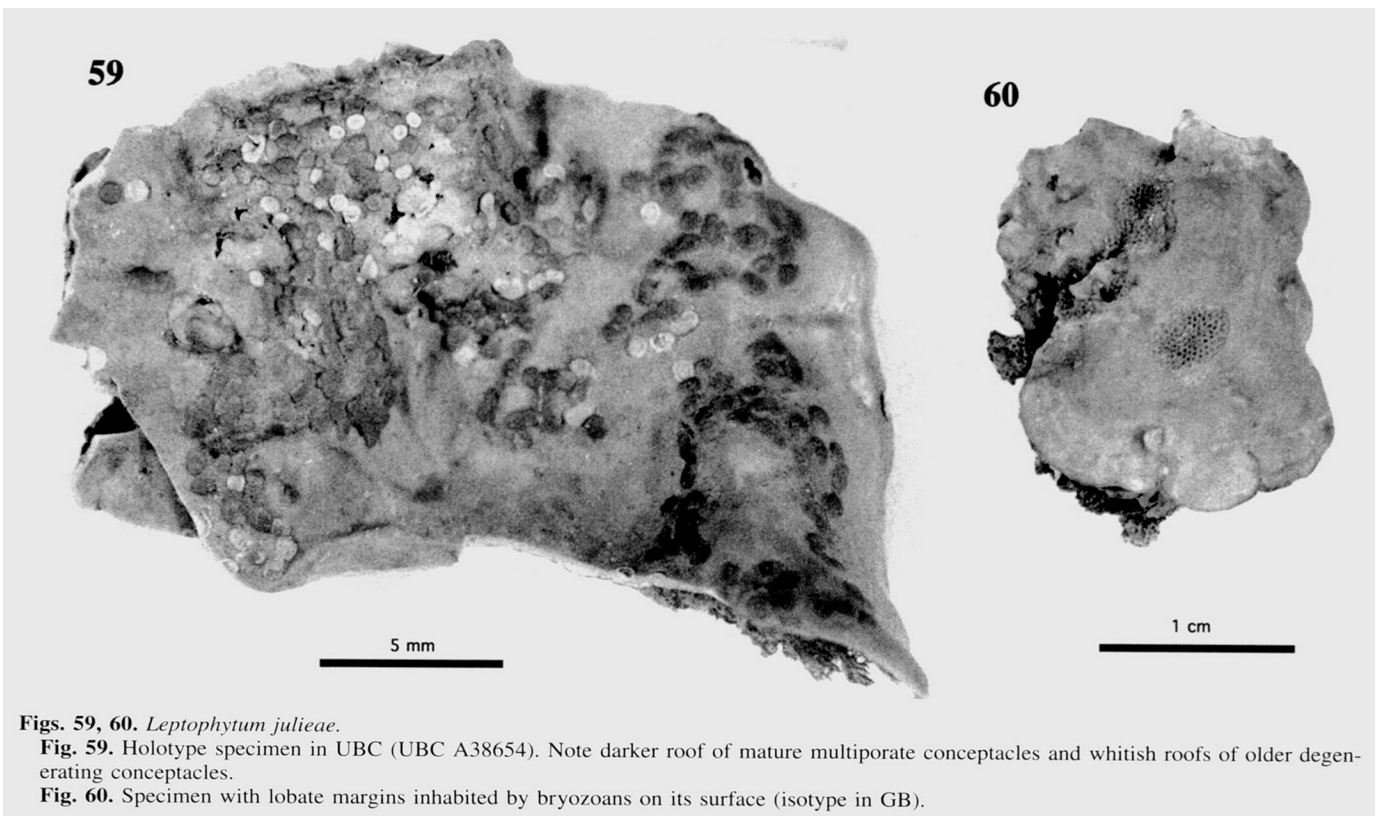
Gametangial conceptacles of each sex may occur side by side, and male conceptacles generally smaller than female ones. Male conceptacles 270–560 μm in external diameter and 40–170 μm high. Chambers elliptical, 170–460 μm in diameter and 70–200 μm high ($n = 20$), reaching 620 μm in diameter when 3 conceptacles merge. Roof 40–180 μm thick, thicker in the centre where the conical ostiole has a basal opening 80–100 μm in diameter and an apical opening c. 20 μm in diameter (Fig. 51). Spermatangial structures developing all over the chamber. SMCs predominantly simple (unbranched) and developing singly on supporting cells (Figs 52, 54, 55); a few SMCs at the periphery of the floor branched, supporting both spermatangia and new SMCs (Figs 53, 54). Released spermatia occur all over the chamber (Figs 51, 52; just liberated spermatia shown in Figs 53–55). Lunate SMCs present (Fig. 55, black arrowheads), but most SMCs rectan-

gular to irregularly shaped (Figs 53, 54) on the floor and more elongate on the walls and the roof (Fig. 52). Supporting and perithallial cells of the floor compressed (Fig. 55).

Carposporangial conceptacles 430–700 μm in external diameter and 130–240 μm high. Chambers elliptical to hemispherical, 250–560 μm in diameter and 80–250 μm high ($n = 34$). Roof 30–120 μm thick, thicker in the centre where the conical ostiole has an opening 60–100 μm in diameter near the base and 35–45 μm in diameter at the top (Fig. 56). Carpogonial branch systems extending 140–320 μm across the central part of the floor, which remains more or less flattened (Figs 56, 58, arrowheads). Carposporangia 40–60 μm in diameter, developing along the periphery (Figs 57, 58, arrows). Embedded gametangial conceptacles not seen.

COMMENTS: *Leptophytum lamellicola* has previously been confused with *Mesophyllum lamellatum*, as the two species often grow side by side. Indeed, the type material of *M. lamellatum* in TRH contains both taxa (Athanasiadis *et al.* 2004, fig. 92). This is also the case with the original collection of *L. lamellicola* (UC 745618), which contains more than 100 specimens/fragments of these two species (R. Moe, personal communication), a subsample of which was examined. Collections UC 739466 (Roush 111) and UC 739469 (Roush 104) also contain specimens of *L. lamellicola* growing together with *M. lamellatum*. Yet, the two species are easily distinguished under a stereoscope, because *L. lamellicola* lacks a predominantly coaxial hypothallium that is so distinctively present in *M. lamellatum* (seen on the inside of broken lamellae or in the zonation on the thallus surface and underside). Moreover, herbarium specimens of *L. lamellicola* are more robust and lighter in colour than *M. lamellatum*. Anatomically, the epithallium and subepithallial meristem are also quite distinct: 1–3 flattened epithallial cells in *L. lamellicola* (Figs 38, 39) vs 1 roundish-squarish (to slightly flattened) cell in *M. lamellatum* (Athanasiadis *et al.* 2004, fig. 100). Subepithallial meristematic cells are distinctively elongate to 17 μm long (Keats & Chamberlain 1997, table 3) in *M. lamellatum* vs to 12 μm long in *L. lamellicola* (Fig. 39, white arrows). In addition, perithallial stratification has been recorded only in *L. lamellicola* (Fig. 39, white arrowheads). A few sterile or tetrasporangial specimens of *L. lamellicola* were also found in littoral and sublittoral collections from southern Vancouver Island, which suggests that the species is probably widespread between southern California and southern British Columbia.

The generic attribution of *L. lamellicola* is based on the following character combination: (1) development of a predominantly noncoaxial hypothallium (with regular coaxial patches), (2) predominantly simple SMCs, rarely with a few branched, (3) flattened (and not flared or domed) epithallial cells, (4) carposporangial conceptacles with peripheral production of carposporangia and flattened fertile floor, and (5) development of specialized (thinner-wider) pore cells in multiporate roofs. In comparison to its NE Pacific congeners, *L. lamellicola* is distinguished by having regular patches of coaxial growth in the hypothallium; all other species of the genus lack this character entirely or develop a few coaxial cell rows sporadically. Moreover, *L. lamellicola* and *L. julieae* differ from the other NE Pacific species of *Leptophytum* in growing partly unattached and in having elongate subepithallial initials (see also Comments under *L. julieae*).



Figs. 59, 60. *Leptophyllum julieae*.

Fig. 59. Holotype specimen in UBC (UBC A38654). Note darker roof of mature multiporate conceptacles and whitish roofs of older degenerating conceptacles.

Fig. 60. Specimen with lobate margins inhabited by bryozoans on its surface (isotype in GB).

Leptophyllum julieae sp. nov.

Figs 59–75

Algae crustaceae vel foliosae, usque ad 6 cm diametro, in spongiis et algis coralloidibus prostratae; thallus in substrato adhaerens, partim libere crescens, lamellis superimpositis 100–800 μ m crassis; color thalli roseus, violaceus, rubens vel flavidus, albidus in marginibus integris lobatisque; hypothallus polystromaticus, noncoaxialis, ex cellulis 16–45 μ m longis compositus; perithallus ex cellulis minoribus gradatim ascendentibusque compositus, coaxialis partim; cellulae extimae meristematae per thalli elongatae et ovatae, 1 vel 2 cellulis epithallialibus complanatis obductae; conjunctiones cellularum contingentium vulgares; trichocytis absentes; conceptacula multiporosa, 200–770 μ m diametro externo et 100–280 μ m alta; tectum conceptaculi maturi convexum vel complanum, 30–55 μ m crassum, usque ad 105 poros habens; fila poros conceptaculorum cingentia ex 4–6 cellulis composita; cellulae versus basem porum cingentes tenuiores-latiores; cellulae subbasales porum cingentes elongatae et cellulae basales extrinsecus percurrentes; cavitates conceptaculorum 260–500 μ m diametro et 110–210 μ m altae; bisporangia 95–180 μ m longa \times 20–80 μ m lata; tetrasporophyta et gametophyta ignota.

Algae crustose to foliose, to 6 cm in diameter, prostrate on sponges and coralline algae; thallus attached to the substratum and partly growing free, with superimposed lamellae 100–800 μ m thick; colour rose to violet or reddish to yellowish with whitish margins that are entire and lobate; hypothallium polystromatic, noncoaxial, composed of cells 16–45 μ m in length; perithallium composed of smaller and gradually ascending cells, coaxial in parts; ultimate meristematic perithallial cells elongate and ovate, covered by 1 or 2 flattened epithallial cells; cell fusions between lateral cells common; trichocytes absent; conceptacles multiporate 200–770 μ m in external diameter and 100–280 μ m high; roof of mature conceptacles convex to flattened, 30–55 μ m thick, with up to 105 pores; filaments bordering the pores composed of 4–6 cells; pore cells composed of thinner-wider cells near the base; subbasal pore cells elongate, and basal pore cells projecting outwards; conceptacle chambers 260–500 μ m in diameter and 110–210 μ m high; bisporangia 95–180 μ m long and 20–80 μ m broad; tetrasporophytes and gametophytes not seen.

TYPEIFICATION: The collection UBC A38654 contains nine specimens/fragments of *Leptophyllum julieae*. The largest of the specimens has been designated as the holotype (Fig. 59) and the rest of the material as isotypes. The holotype and several isotypes are provided with multiporate (bisporangial) conceptacles.

HOLOTYPE: In UBC A38654; collected by J. W. Markham & al., 27 August 1968. (Fig. 59).

ISOTYPES: (1) In UBC A38654. (2) In GB (unnumbered) (Fig. 60). (3) In S (unnumbered). All isotypes collected by J. W. Markham & al., 27 August 1968.

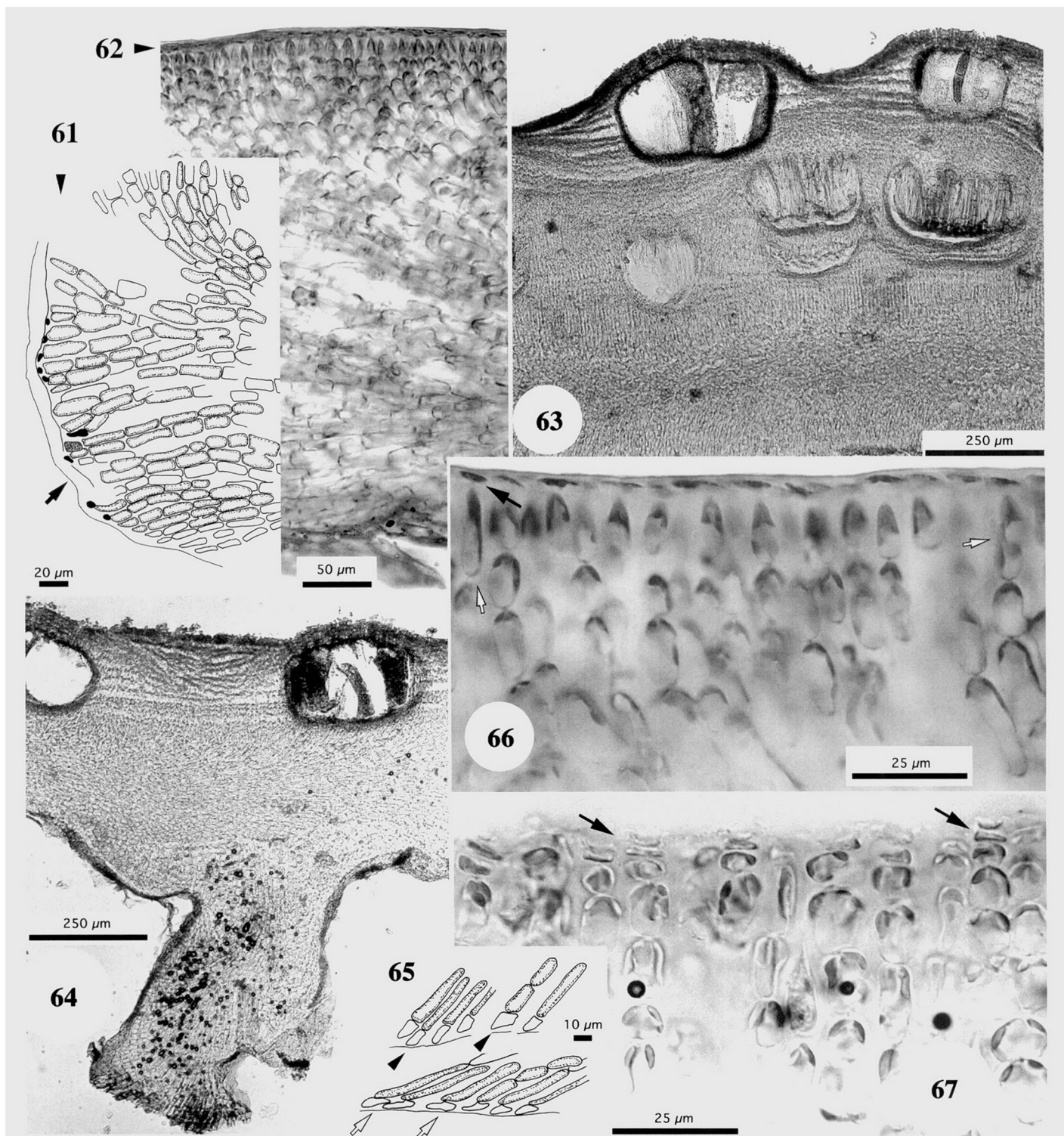
ETYMOLOGY: *Leptophyllum julieae* was identified in collections made by colleagues at UBC, including Mrs Julie Oliveira, who arranged the loan of the material.

TYPE LOCALITY: McDougal Island, Vancouver I., British Columbia, 50°10.4'N, 127°40.7'W, at 6 m depth.

HABITAT: The holotype was collected in the sublittoral zone (6 m depth) and is ventrally attached to sponges. All collections were made from 0 to 12 m depth at sheltered to moderately sheltered sites. Specimens are attached to sponges, shells, polychaete tubes, or geniculate and nongeniculate coralline algae. Two sublittoral collections (UBC A38656 and UBC A54003) are attached to a fragment of *Mesophyllum conchatum* (Setchell & Foslie) Adey and *Calharthron Manza*, respectively.

DISTRIBUTION: Known only from British Columbia: Grappler Inlet (48°N; the southernmost record), Effingham, Swiss Boy and Fleming Islands (all near Bamfield, SW Vancouver I.), and also at Numas, Kains, Solander, and McDougal Islands and Fisherman Bay (NW Vancouver I.). The northernmost record is Triple Islands (54°N).

MATERIAL EXAMINED: **Canada:** British Columbia: Vancouver Island, McDougal Island (holotype and isotypes, as described above); NE side Effingham I., off Old Indian Village, Bamfield area, 12 m, rocky, with sandy patches, moderately sheltered, bisporic, 48°52'25"N, 125°17'37"W, 17 July 1969, Baillie & Pace 26861, UBC A48006; Lighthouse Point, Kains I., 12 m, bisporic, 50°20.65'N, 128°0.2'W, 28 August 1968, Markham & al. 22690, UBC A39530; Grappler Inlet, Janeita Float, to Port Desire, Bam-



Figs. 61–67. *Leptophytum juliae*.

Fig. 61. Drawing of thallus margin in TS showing terminal darkly staining meristematic cells protected by cuticle (arrow) and noncoaxial hypothallium producing ascending perithallium. Note fusions between contiguous cells (isotype; UBC A38654).

Fig. 62. Thallus in TS showing noncoaxial hypothallium and ascending perithallium with elongate-ovate subepithallial cells (isotype).

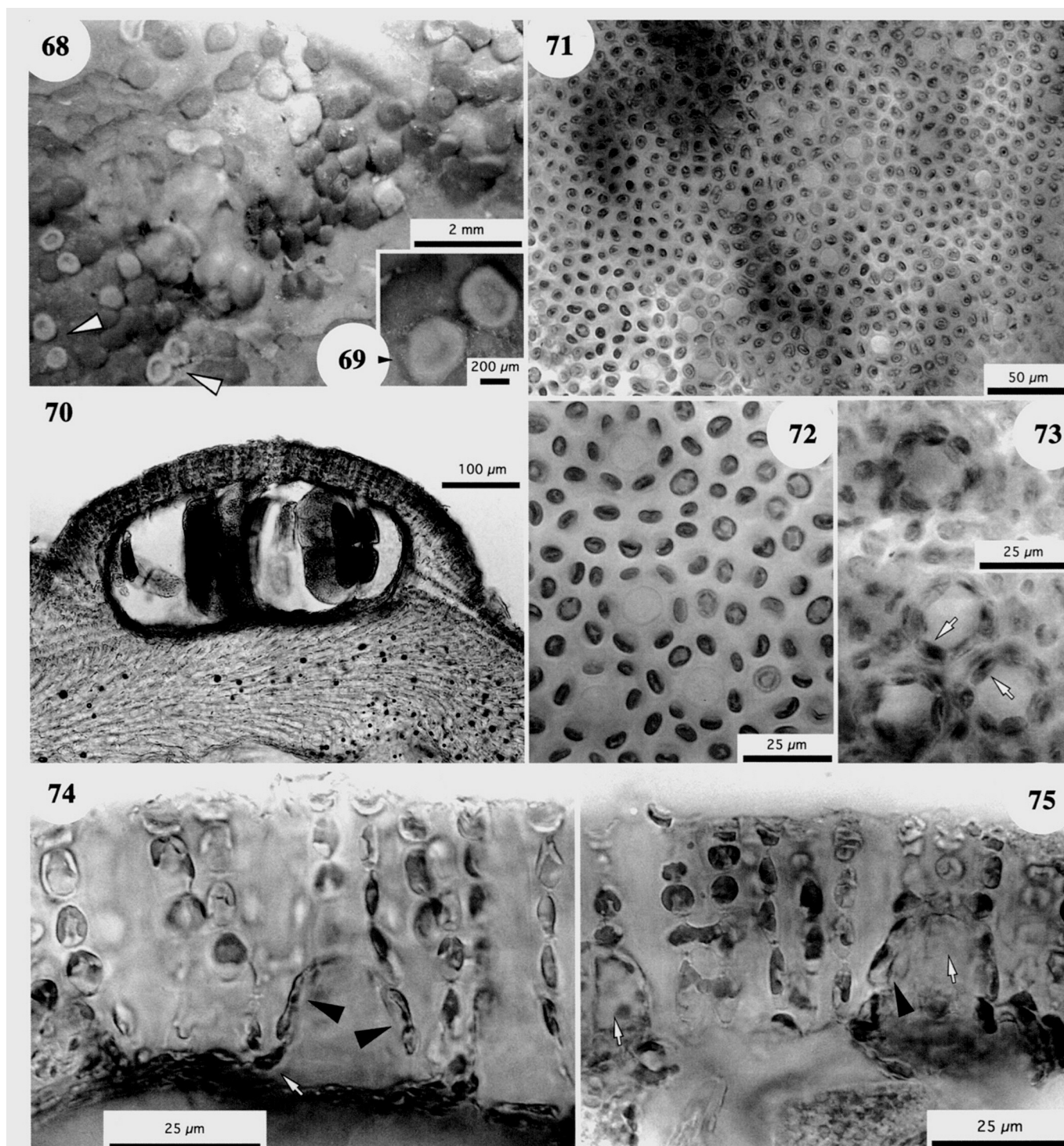
Fig. 63. Thallus in TS showing superficial and embedded conceptacles, the former with convex roofs and the latter with chambers filled with palisade cells. Observe perithallial stratification around superficial conceptacles (holotype).

Fig. 64. Thallus in TS showing ventral excrescence (isotype).

Fig. 65. Two drawings of thallus near base in TS, showing hypothallial cells ending in wedge-shaped (black arrowheads) or reniform (white arrowheads) cells (isotype).

Fig. 66. Thallus in TS showing elongate-ovate subepithallial initials (white arrows) and single flattened epithallial cells (black arrow) (isotype).

Fig. 67. Thallus in TS showing 1 or 2 (arrows) flattened epithallial cells (isotype).



Figs. 68–75. *Leptophytum juliae* (holotype).

Figs. 68, 69. Multiporate conceptacles on thallus surface. Some conceptacle roofs have collapsed (arrowheads; magnified in Fig. 69).

Fig. 70. Bisporangial conceptacle in TS.

Fig. 71. Surface view of multiporate roof with pore openings surrounded by normal epithallial cells.

Figs. 72, 73. Surface views of pores at two levels of focus showing enlarged canal near the base (Fig. 73), and thinner-wider pore cells tending to encircle the canals (arrows).

Figs. 74, 75. TSs across pore canals. Filaments bordering canals composed of specialized pore cells near base. Subbasal cells elongate and thinner (black arrowheads) -wider (Fig. 75, arrows). Note basal cells projecting outwards (Fig. 74, arrow) and conical canals.

field, 11 m, rocks, fully sheltered, bisporic, 48°49'48"N, 125°07'18"W, 31 July 1969, *Baillie & Harrison* 27302, UBC A48011; Solander I., Brooks Peninsula, 8 m, 50°07'N, 127°56'W, 25 June 1975, *Root & Johnson* 34242, UBC A54003 [mixed with *M. vanouveriense*]; reef off west end of Swiss Boy I., Bamfield area, bisporic, 48°55'15"N, 125°07'36"W, 1 August 1969, *Baillie & Harrison* 27305B, UBC A48012; west side Fleming I., Bamfield area, subtidal, bisporic, 48°50'N, 125°08'36"W, 21 June 1969, *Baillie & Pace* 25943, UBC A48002; rock reef, SW tip Fisherman Bay, 0–6 m, 50°48.2'N, 128°19.2'W, 30 August 1968, *Markham & al.* 22867, UBC A38651; rock reef, SW tip Fisherman Bay, 6–12 m, 50°48.2'N, 128°19.2'W, 30 August 1968, *Markham & al.* 22897, UBC A39993; Staples Islet, off Numas I., 3–7 m, bisporic, 50°46'2"N, 127°7'1"W, 29 August 1968, *Markham & al.* 22830, UBC A38656 [*pro parte*]; Triple Is., in Tree Nob Group, between Brown and Bell Passage, 54°18'N, 130°53'W, bisporic, growing on abalone shells, July 1978, *Golden* (unnumbered), UBC A58921 [mixed with *P. muricatum*]; Queen Charlotte Islands, Jeffrey Island Reef, 3 m, bisporic on polychaete tube, 52°21.8'N 131°11.4'W, 27 Mar. 1976, *Hart* 34277, UBC A56333.

MORPHOLOGY: Thalli encrusting to foliose, up to at least 6 cm in extent, attached to a variety of hard substrates and growing mostly unattached. Lobate proliferations developing from the margin (Fig. 60) or dorsally, growing over the parent thallus in a superimposing manner, forming at least three separate layers. Contiguous lamellae may anastomose or grow back-to-back. Thallus surface smooth, lacking perithallial protuberances; foliose proliferations can develop dorsally and encircle epiphytes. Excrescences common on the underside, usually as lamellae that grow back-to-back. Striations occurring ventrally and on the thallus surface in irregular pattern (not reflecting a coaxial hypothallium). Margins with a whitish border (cuticle). Colour of herbarium specimens varying from light pink to violet to reddish-yellow. Mature conceptacle roofs more darkly coloured (Fig. 59), becoming whitish during degeneration (Figs 59, 68).

ANATOMY: Thallus organized dorsiventrally. Individual lamellae 100–800 µm thick (Figs 61–64), composed of a polystromatic noncoaxial hypothallium, 150–300 µm thick, produced by terminal asynchronous cell divisions and elongations (Fig. 61). Terminal meristematic cells protected by a cuticle, 8–15 µm thick (Fig. 61). Patches of coaxial hypothallial cells not seen. Ascending hypothallial filaments producing the perithallium, 60–500 µm thick (Figs 62–64), while descending hypothallial filaments may produce ventral excrescences (Fig. 64) or end in wedge-shaped (Fig. 65, black arrowheads) or reniform cells (Fig. 65, white arrowheads). Hypothallial cells 16–45 µm long and 5–12 µm broad. Perithallium partly stratified (Figs 63, 64, areas next to conceptacle chambers) composed of cells 10–30 µm long and 4–8 µm broad. Epithallial cells flattened in TS, 2–3 µm long and 5–12 µm broad, and one or two present at a time (Figs 66, 67, arrows). Subepithallial meristematic cells elongate and ovate (Figs 62, 66, white arrows), at time of division distinctively longer than perithallial cells below, up to 19 µm in length and 4–11 µm broad. Cell fusions common between contiguous somatic cells. Trichocytes and secondary pit-connections not seen.

REPRODUCTIVE STRUCTURES: Multiporate conceptacles generally raised and crowded, 200–770 µm in external diameter and 100–280 µm high (Figs 59, 68). Up to four neighboring conceptacles merging. Chambers 260–500 µm in diameter (up to 700 µm when two merge) and 110–210 µm high ($n = 19$). Conceptacle roofs convex to flattened and lacking a peripheral

rim (Fig. 70). Roof perforated by 30–105 pores ($n = 14$) (up to 149 in two merged conceptacles). Pore openings surrounded by 4–8 rosette cells, which are normal epithallial cells and flush with the surface (Figs 71, 72, 74, 75). Roofs 30–55 µm thick, composed of 4- to 8-celled filaments; cells 5–15 µm long and *c.* 5 µm broad. Pore plates 200–580 µm in diameter. Pore canals conical, *c.* 12 µm in diameter at the surface and up to 17 µm at the base (Figs 72–75). Filaments bordering pore canals composed of 4–6 cells that stain more darkly near the base and are thinner (Fig. 74, arrowheads) -wider (Fig. 75, arrows), tending to encircle the canal (Fig. 73, arrows). Subbasal cells longer than other pore cells (Figs 74, 75 arrowheads), and basal cells projecting outwards (Fig. 74, arrow). Bisporangia 95–180 µm long and 20–80 µm broad. Older conceptacles losing first their colour, then their roof collapsing (Fig. 68, arrowheads; Fig. 69); subsequently, gradually disintegrating, and their chamber filling with perithallial cells. Embedded chambers filled with palisade colourless cells (Fig. 63) also occurring (the mode of embedding not seen).

COMMENTS: *Leptophytum julieae* and *L. lamellicola* have both previously been confused with *Mesophyllum lamellatum*. *Leptophytum julieae* differs from its NE Pacific congeners in lacking coaxial patches in the hypothallium and in possessing distinctively elongate-ovate subepithallial meristematic cells. Together with *L. lamellicola*, they represent the only NE Pacific species of *Leptophytum* growing with parts of their thallus unattached. In comparison to *L. lamellicola*, *L. julieae* further differs in reproducing entirely by bisporangia (not recorded in *L. lamellicola*). In the absence of sexual reproduction, its species status remains uncertain. It could represent marginal and isolated populations of a more widely distributed species, but because we do not know its sister-taxon, we recognize *L. julieae* here as a distinct species. In the absence of gametangia, its generic position in *Leptophytum* is determined by the following character combination: (1) noncoaxial hypothallium, (2) flattened (and not flared or domed) epithallial cells, and (3) thinner-wider pore cells in multiporate conceptacle roofs. Character (1) precludes a position in *Mesophyllum* whereas character (3) precludes a position in *Synarthrophyton*. Characters (2) and (3) preclude a position in *Lithothamnion* or *Phymatolithon*.

Leptophytum foecundum (Kjellman) Adey (1966, p. 325)

Figs 76–107

BAISIONYM: *Lithothamnion foecundum* Kjellman [1883, pp. 131–132 (99–100 in the English version; see Athanasiadis 1996, p. 255), pl. 5, figs 11–19 (here reproduced in Fig. 76)].

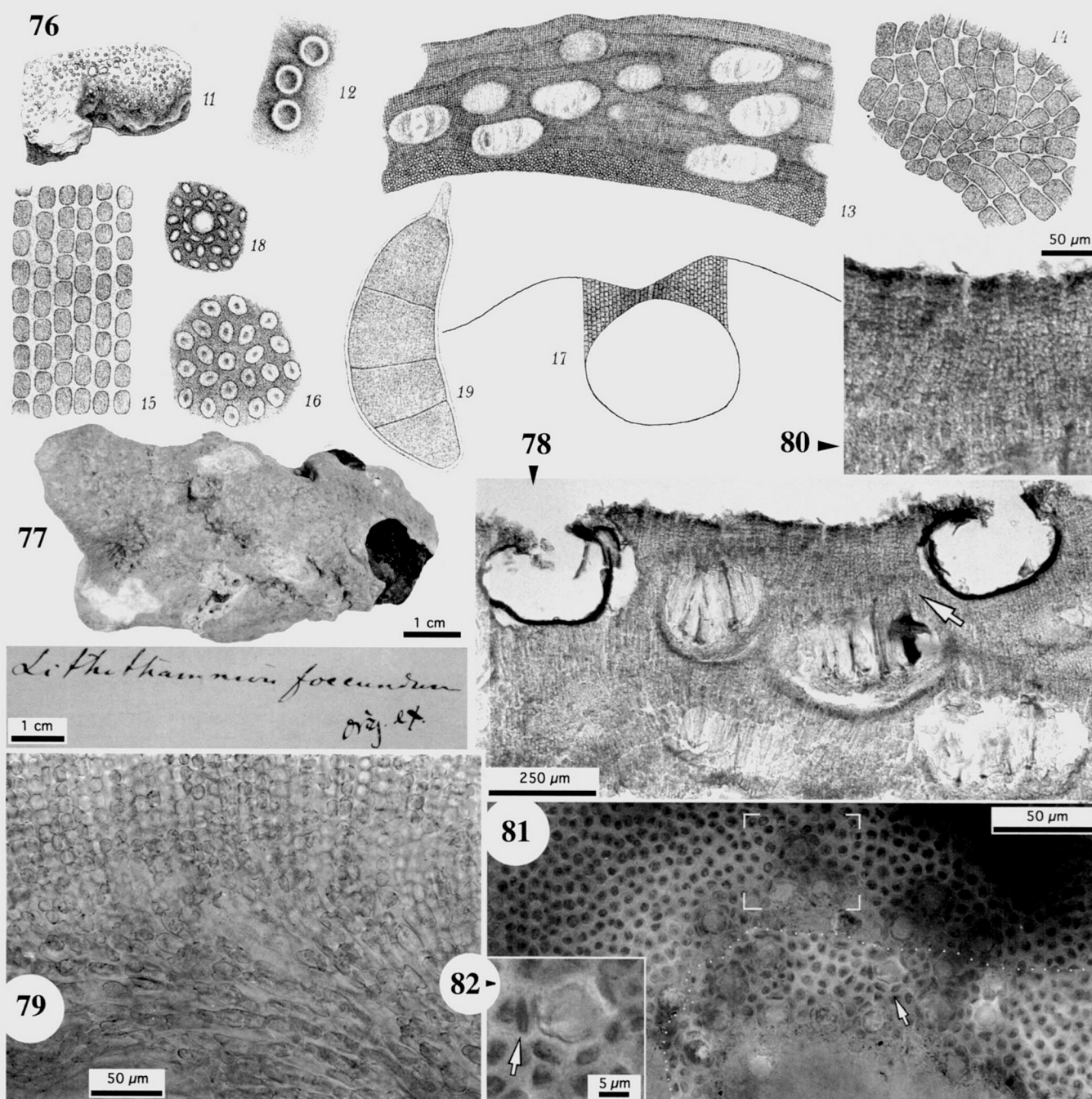
HOMOTYPIC SYNONYM: *Phymatolithon foecundum* (Kjellman) Düwel et Wegeberg (1996, p. 482).

Leptophytum foecundum var. *foecundum*

Figs 76–87

HOLOTYPE: In UPS (unnumbered and undated), collected by F. R. Kjellman, labeled '*Lithothamnion foecundum* orig. ex.' and including five slides B3:96–B3:100 labeled '*Lithothamnion foecundum* Kariska havet . . .'; previously illustrated by Düwel & Wegeberg (1996, fig. 4b) and Alongi *et al.* (2002, fig. 9) (Fig. 77).

SYNTYPE LOCALITIES: Kara Sea: Actinia Bay at 76°8'N 90°25'E and Uddebay (east coast of Novaja Zemlya) at 74.5°N.



Figs. 76–82. *Leptophytum foecundum* var. *foecundum* (type material and holotype in UPS).

Fig. 76. The 14 original illustrations included in the protologue (Kjellman 1883), here reproduced at lower (94%) magnification and showing: (11) part of specimen (size 1 : 1), (12) three rimmed conceptacles in surface view (size 2 : 1), (13) thallus in TS showing embedded conceptacles (size 40 : 1), (14) part of hypothallium in 'thin radial section' (size 400 : 1), (15) part of 'thickening system of the frond' (size 400 : 1), (16) part of 'horizontal, tangential, superficial thin' section (size 400 : 1), (17) conceptacle in TS (size 100 : 1), (18) part of roof showing pore (size 400 : 1), and (19) tetrasporangium (size 400 : 1).

Fig. 77. Holotype in UPS and Kjellman's original label (at slightly lower magnification).

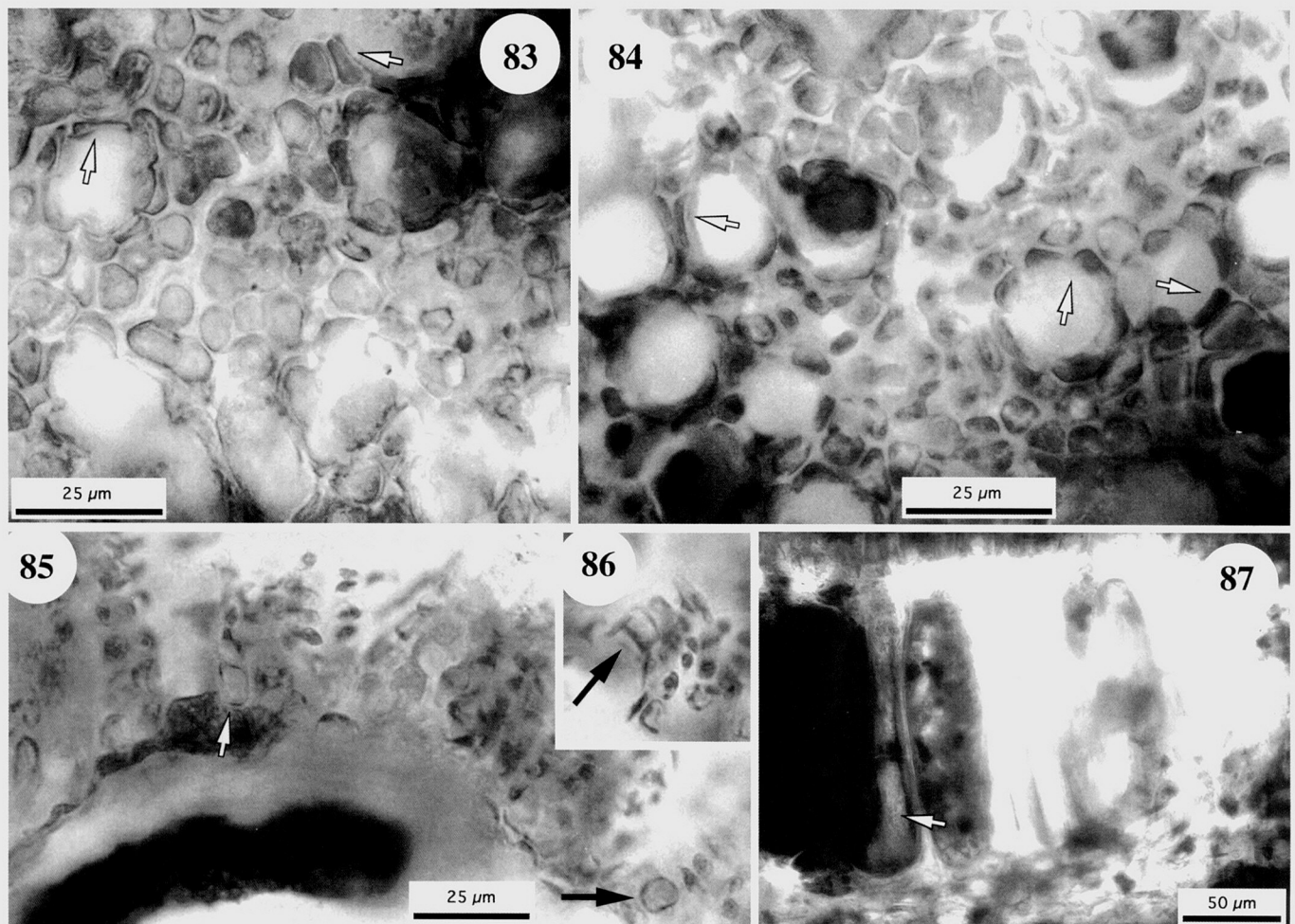
Fig. 78. Thallus in TS showing superficial and embedded conceptacles with chambers filled with palisade cells. Arrow indicates area magnified in Fig. 80 (holotype).

Fig. 79. Thallus in TS showing basal system of filaments (hypothallium) producing ascending perithallium composed of isodiametric cells (holotype).

Fig. 80. Overgrowth of conceptacle through further growth of roof filaments (detail of Fig. 78, arrow).

Fig. 81. Surface view of sunken conceptacle roof at three levels of focus (outside frame, inside frame and within dotted area). Note the specialized rosette cells (arrow; magnified in Fig. 82; holotype).

Fig. 82. Surface view of pore with thinner-wider (arrow) rosette cells (holotype).



Figs. 83–87. *Leptophytum foecundum* var. *foecundum*.

Figs. 83, 84. Surface views of multiporate roofs with pore canals, at lower levels of focus, showing thinner-wider pore cells (arrows) (Fig. 83: slide B3: 98 in UPS; Fig. 84: section of holotype fragment).

Figs. 85, 86. TSs of conceptacle roofs at two levels of focus, showing the specialized subbasal pore cells (arrows). Fig. 86 shows the canal indicated by a black arrow in Fig. 85, at a lower level of focus (holotype fragment).

Fig. 87. Embedded bisporangial conceptacle in TS showing remains of bisporangia (arrow) (slide B3: 99 in UPS).

HABITAT: Specimens from the Siberian coast (Kjellman 1883) and East Greenland (Lund 1959, p. 198) grow on pebbles and stones between 10 and 120 m depth.

DISTRIBUTION: Arctic Ocean between Alaska (Boulder Patch, Stefansson Sound; present study) and Cape Taimur on the Siberian coast (Kjellman 1883); in the North Atlantic Ocean, south to Gulf of Maine (Adey 1966), northern Iceland (Adey 1968), and northern Norway (Kjellman 1883; Foslie 1895, p. 137).

MATERIAL EXAMINED: **Russia:** Kara Sea. Holotype (as described above).

United States: Alaska. Station DS-11, Boulder Patch, Stefansson Sound, 6 m, 70°19.25'N 147°35.1'W, 27 July 1980, bisporic, R. T. Wilce A & B (2 hand-picked cobbles), in GB (unnumbered).

OBSERVATIONS ON THE PROTOLOGUE AND HOLOTYPE MATERIAL: Two localities in the Kara Sea were cited in the protologue [Kjellman 1883, pp. 9 (6), 131–132 (99–100)]: (1) Uddebay (erroneously said to be located at 76°8'N 90°25'E) and (2) Actinia Bay (said to be at about 76°N). Uddebay is located on the east coast of Novaja Zemlya (74.5°N) and is apparently the locality of a collection previously identified as *Lithothamnion polymorphum* (Kjellman 1877, p. 15) and included in

the protologue of *L. foecundum*, while Actinia Bay is situated at 76°8'N 90°25'E [as elsewhere specified by Kjellman 1883, p. 9 (7)].

The material of *Lithothamnion foecundum* in Kjellman's herbarium in UPS comprises: (1) a single undated specimen (c. 7 cm in extent; Fig. 77) annotated by Kjellman '*Lithothamnion foecundum* orig. ex.', (2) 5 slides (B3: 96, B3: 97, B3: 98, B3: 99 and B3: 100; each with the printed label 'Upsala Botan. Museum' and separately annotated by Kjellman '*Lithothamnion foecundum* Kariska havet Längd . . .', '*Lithothamnion foecundum* Kariska havet tetrasp.', '*Lithothamnion foecundum* Kariska havet Long. snitt', and '*Lithothamnion foecundum* Kariska havet fig. 4'), and (3) two specimens in a folder annotated by Kjellman '*Lithothamnion (polymorphum)* [the epithet replaced by the name] *foecundum* Kjellm. *Lithoderma fatiscens*. Sibiriska Ishafvet nära Cap. Taimur 12/8/1878. . .'. The single undated specimen (Fig. 77) has previously been examined by Chamberlain (1990, pp. 181–183, figs 2, 12–16, 30), Düwel & Wegeberg (1996, p. 478, figs 4b, 34–38), Alon-

gi *et al.* (2002, p. 144, figs 9, 10) and Sandra Lindstrom ('16 Febr. 2001'; annotation in herb.). It has been recognized as the unambiguous holotype element by all these authors.

The annotations on the five slides clearly indicate that these were used in the preparation of the protologue of *L. foecundum*. The material on these slides comprises thallus sections (B3: 96, 98–100), bisporangia (two seen on slide B3: 98, one each seen on slides B3: 97, 99), and remains of multiporate roofs (B3: 96). New fragments of the holotype were examined, and these indicate that the thallus exhibits a dorsiventral organization. Individual lamellae are 350–1000 µm thick (Figs 78–79), reaching up to 1100 µm through superimposition of two lamellae. The hypothallium is noncoaxial and relatively thin, 60–80 µm thick, composed of rectangular cells, 10–45 µm long and 5–10 µm broad [10–50 by 4–10 µm according to Chamberlain (1990)]. It produces an ascending perithallium up to 940 µm thick composed of nearly isodiametric cells 8–10 µm long and c. 10 µm broad [5–15 by 5–10 µm according to Chamberlain (1990)] (Figs 78, 79). Cell fusions between somatic cells are common. Epithallial cells and subepithallial initials were not identified with certainty, but according to Chamberlain (1990), epithallial cells are somewhat flattened. Multiporate conceptacles are generally raised, 350–620 µm in external diameter and up to 840 by 540 µm in two merged ones [340–570 µm and up to 740 µm in merged ones, according to Chamberlain (1990, fig. 13)]. They have distinctively sunken pore plates, perforated by 27–31 pores [up to 40 according to the protologue and up to 50 according to Chamberlain (1990)] (Fig. 81). Pore plates have a diameter between 130 and 220 µm and are 30–40 µm thick [composed of 5–7 cells according to Düwel & Wegeberg (1966, p. 478, fig. 37)]. The roof thickness reaches 90 µm along the periphery (including the rim). Individual pore canals have a diameter of 8–15 µm and are surrounded by 5–8 rosette cells, which are often specialized (Figs 81, 82, arrows). Pore cells lining the base of canals are generally specialized and, like certain rosette cells, thinner-wider in views from above, tending to encircle the canal (Figs 83, 84, arrows). In TSs of the roof, pore cells may appear to be 'larger' (apparently demonstrating their wider dimension) than contiguous roof cells (Figs 85, 86, arrows). Epithallial cells of the roof are roundish to angular and measure 5–11 µm in diameter. Conceptacles become embedded, and their chambers are 320–450 µm in diameter and 160–200 µm high [208–390 by 156–182 µm according to Chamberlain (1990)] (Fig. 78). Conceptacle embedding occurs through further growth of the roof filaments (Fig. 80) and not via centripetal growth of peripheral filaments. The embedded chambers are filled with palisade cells (and occasionally have bisporangial remains). Only bisporangia were seen in the material examined, and these are 170–190 µm long and 60–70 µm broad (Fig. 87, arrow). Yet, Kjellman (1883) described and illustrated tetrasporangia (120–185 by 45 µm) (Fig. 76, Kjellman's fig. 19).

The lack of annotation of place and date on the holotype, the presence of bisporangia on its thallus (Chamberlain 1990, p. 183, fig. 30; present study) and the lack of tetrasporangia raise questions about the identity of this material. Moreover, Kjellman's original illustration of 'a part of a specimen' (Fig. 76, Kjellman's fig. 11) shows an individual not concordant with the holotype in UPS. Nevertheless, the material on the five slides from the Kara Sea is anatomically concordant with

the holotype, and collectively these elements can be unambiguously associated with the protologue of *L. foecundum*. Because no other collections from the Kara Sea exist in UPS, the identity of this specimen as the holotype is here sustained.

Kjellman (1883, p. 131) cited two (syntype) localities in the protologue, viz. Uddebay and Actinia Bay, both in the Kara Sea. Uddebay is located on the east coast of Novaja Zemlya and is apparently the place of origin of a collection previously identified as *Lithothamnion polymorphum* by Kjellman (1877, p. 15) and cited in the protologue of *L. foecundum*. Uddebay was not visited during the Vega expedition in 1878–1880, when material from Actinia Bay and other places on the Siberian coast was collected [Kjellman 1883, p. 9(6)]. Therefore, the protologue of *L. foecundum* is based on two different collections (made at different places and dates), and which of them is represented by the holotype is unknown. In describing the holotype specimen, Chamberlain (1990, p. 181) considered it to be a part of the collection from Cape Taimur and therefore recognized Cape Taimur as the type locality of the species. Because Kjellman did not include Cape Taimur in the distribution of *L. foecundum*, recognizing (in the protologue) Actinia Bay as the northernmost locality of the species, the Cape Taimur collection cannot be considered as part of the type material.

Two statements in the protologue merit further comment. Kjellman described the 'basal system' (hypothallium) as coaxial, probably referring to its multiaxial structure, because in the material examined no coaxial growth was observed, and none of Kjellman's original illustrations shows coaxial growth (Fig. 76). Moreover, Kjellman noted and illustrated (Fig. 76, Kjellman's fig. 18) the pore canals of the multiporate roofs to be surrounded by 'a ring of cells different from the other cortical cells of the roof': this appears to be the earliest report of specialized pore cells in the Melobesioideae.

Leptophytum foecundum var. *sandrae* var. nov.

Figs 88–107

Varietas *Leptophyto foecundo* var. *foecundo* affinis, conceptaculis multiporosis majoribus 280–780 µm diametro externo cum cavitatibus majoribus 220–500 µm diametro et tectis ubi maturis complanis vel depressis poris extimis 150–360 µm disjunctis, ab eo diversa.

Allied to *Leptophytum foecundum* var. *foecundum*, from which this variety differs in having larger multiporate conceptacles (280–780 µm in external diameter) with larger chambers (220–500 µm in diameter) and flattened or sunken roofs when mature, with outermost pores 150–360 µm apart.

TIPIFICATION: The holotype (c. 2.5 cm in extent) is attached at the edge of a piece of wood (4 by 9.5 cm in extent) together with other sterile encrusting coralline algae.

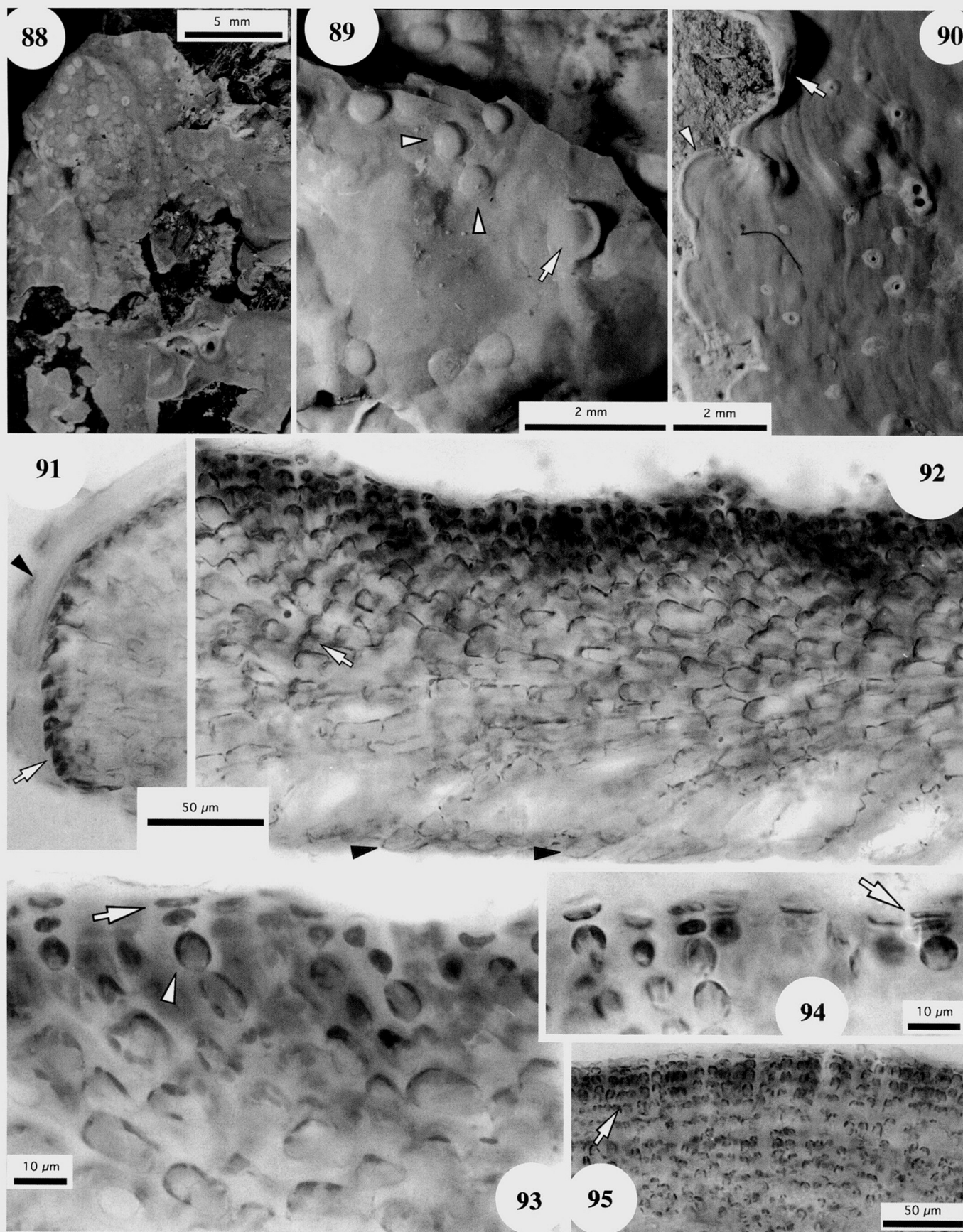
HOLOTYPE: In UBC (A48009; Pace & Baillie 26943); collected by Pace & Baillie, 19 July 1969 (Fig. 88).

ETYMOLOGY: The epithet honors our colleague Sandra Lindstrom for her kind help in arranging several loans of material from UBC.

TYPE LOCALITY: East side of Fleming Island, Bamfield area, subtidal, boulders, with sandy patches, 48°53'N, 125°07'02"W.

HABITAT: Specimens have been collected in the sublittoral zone (6–17 m depth), attached to wood fragments, shells and polychaete tubes.

DISTRIBUTION: 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).

MATERIAL EXAMINED: **Canada:** British Columbia: Vancouver Island, Daphne Point, Hardy Bay, subtidal, 50°44.7'N, 127°27'W, 18 January 1971, *LD, DP, KB, RF, JM, PN*, 28819, UBC A44187; west side of Edward King I., Bamfield area, subtidal, with some flat sandy patches, moderately exposed, on wood, 48°50'09"N, 125°12'36"W, 20 June 1969, *Pace & Chapman* 25927, UBC A48001 [growing together with *Lithothamnion* sp.]; Sproat Bay, Tzartus Island, Bamfield area, 6 m, rock w/sandy patches, fully sheltered, on wood, 48°54'21"N, 125°04'36"W, 25 June 1969, *Baillie & Harrison* 26020, UBC A48003; Sproat Bay, Tzartus Island, Bamfield area, 6 m, rock with sandy patches, fully sheltered, on wood, 48°54'21"N, 125°04'36"W, 25 June 1969, *Baillie & Harrison* 26024, UBC A48032 & *Baillie & Harrison* 26041, UBC A48004; east side of Fleming Island, Bamfield area (holotype, as described above); east side of Wizard Islet, Bamfield area, 17 m, small rocks & broken shell, moderately exposed, on polychaetes, 48°51'30"N, 125°09'36"W, 12 July 1969, *Pace & Harrison* 26753, UBC A48034; Roquefeuil Bay, Bamfield area, subtidal, rocky with sandy patches, fully sheltered, 48°51'10"N, 125°06'36"W, 22 June 1969, *Baillie & Pace* 25974, UBC A48029; Roquefeuil Bay, Bamfield area, 3 m, boulders with sandy patches, moderately sheltered, 48°51'42"N, 125°06'18"W, 22 July 1969, *Baillie & Pace* 26968, UBC A48033 [growing with *Lithothamnion* sp.]. **United States:** Washington State, Channel Rocks near Seattle, 21 May 1901, *Gardner* 654, UC 936323.

MORPHOLOGY: Thalli encrusting (Figs 88–90), up to at least 5 cm in diameter, moderately attached to pieces of wood, and strongly attached to polychaete tubes, shells and other encrusting coralline algae. Margin often attached (Fig. 90, arrowhead) and lobate; proliferations may grow free dorsally (Fig. 89, arrow) or from the margin (Fig. 90, arrow). Thallus surface smooth or occasionally provided with irregular outgrowths, which either reflect the morphology of the substrate underneath or result from conceptacle overgrowth (Fig. 107). Margin with a whitish border (cuticle) (Fig. 90, arrowhead), and surface with irregular striations. Thallus light to dark pink or violet.

ANATOMY: Thallus organization dorsiventral. Lamellae 80–300 µm thick (Fig. 92), reaching at least 1100 µm in thickness by superimposition. Hypothallium polystromatic and generally noncoaxial, produced by terminal asynchronous cell division and elongation (Fig. 91). Patches of coaxial hypothallial cells sporadically present, composed of a series of up to 6 cell arches (Fig. 92, arrow). Terminal meristematic (hypothallial) cells staining more darkly (Fig. 91, arrow) and protected by a cuticle, 10–20 µm thick (Fig. 91, arrowhead). Hypothallium 20–140 µm thick, producing an ascending perithallium, 60–200 µm thick (Figs 92–95). Descending hypothallial filaments ending in wedge-shaped cells (Fig. 92,

arrowheads). Hypothallial cells 15–32 µm long and 5–10 µm broad. Perithallium locally stratified (Fig. 95, arrow) and composed of cells 4–15 µm long and 4–8 µm broad. Epithallial cells flattened in TS, 1.5–3 µm long by 4–10 µm in diameter, one or two present at a time (Figs 93, 94, arrows). Subepithallial meristematic cells isodiametric and more or less similar or smaller in size than perithallial cells below (Fig. 93, arrowhead, Fig. 94). Cell fusions common between contiguous somatic cells. Trichocytes and secondary pit-connections not seen.

REPRODUCTIVE STRUCTURES: Multiporate conceptacles spread on the thallus surface (Fig. 96), 280–780 µm in external diameter and either flush with the surface or raised as much as 270 µm. They often develop separately, rarely two partly merge. Conceptacle roofs flattened to sunken, 40–90 µm in thickness, provided with a distinct but irregularly formed rim (Figs 96–98). Chambers 220–500 µm in diameter and 140–250 µm high ($n = 16$). Pore plates, 150–360 µm in diameter, perforated by 19–76 pores ($n = 18$). Pore openings surrounded by 5–8 rosette cells, which are flush with the surface. Rosette cells are either normal epithallial cells or thinner-wider (Figs 99, 100, arrows). Pore plates 40–65 µm thick, composed of 5- to 7-celled filaments. Pore canals having an apical opening 7–13 µm in diameter. Filaments bordering pore canals composed of 5–7 cells that are generally thinner- (Fig. 101, arrow, Figs 103, 104, white arrowheads) wider (Figs 102–105, black arrowheads), tending to encircle the canal (Fig. 101). Subbasal pore cells often more elongate, reaching c. 18 µm in length (Figs 102, 103, black arrowheads), whereas basal cells often project outwards (Figs 102, 104, arrows), forming a conical canal reaching c. 18 µm in diameter at the base. Only bisporangia seen, 100–160 µm long by 20–80 µm broad ($n = 15$) (Figs 106, 107). Older conceptacles either degenerate, losing first their pigmentation and subsequently their roof, or becoming embedded in the perithallium by peripheral filaments that grow centripetally and cover the old roof (Figs 105, 107).

COMMENTS: The Pacific specimens differ from the holotype of var. *foecundum* in several structural characters: (1) presence of patches of coaxial growth in a predominantly noncoaxial hypothallium (Fig. 92), (2) multiporate conceptacles provided with moderately sunken or flattened roofs (vs distinctively sunken in the Arctic material), (3) conceptacle embedment occurring by peripheral filaments (Fig. 105) (vs via further growth of the roof filaments themselves in the Arctic specimen; Figs 78, 80), (4) larger conceptacles (up to 780 µm vs

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Figs. 88–95. *Leptophytum foecundum* var. *sandrae*.

Fig. 88. The holotype specimen, attached at edge of piece of wood (UBC A48009).

Fig. 89. Thallus with multiporate conceptacles growing on wood. Note unattached dorsal proliferation (arrow) and rather flattened conceptacle roofs (arrowheads) (UBC A48004).

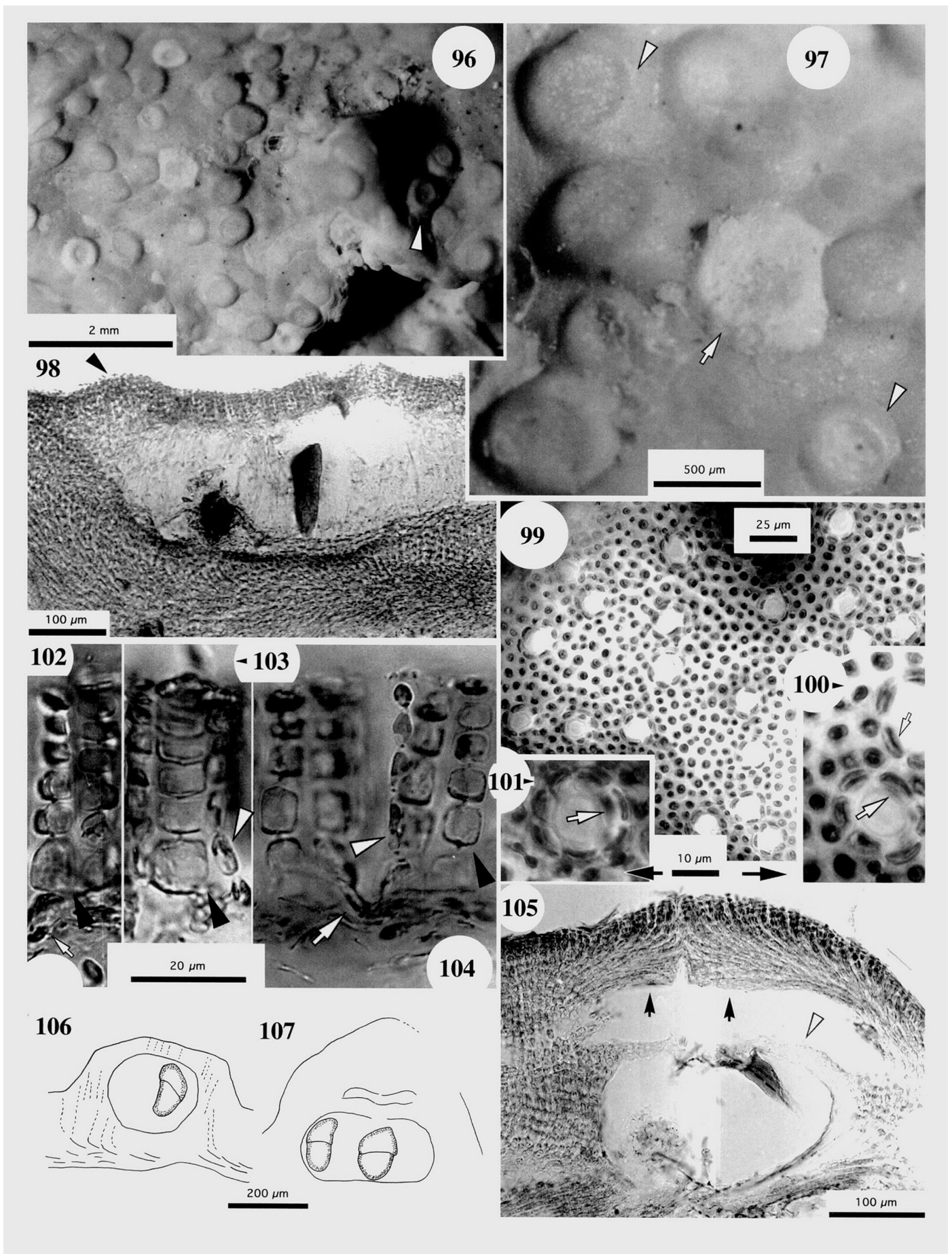
Fig. 90. Thallus margin growing attached (arrowhead) or free (arrow) and showing concentric striations on surface (holotype).

Fig. 91. Thallus margin in TS showing terminal (darkly staining) hypothallial (meristematic) cells (arrow) protected by cuticle (arrowhead) (UBC A48033).

Fig. 92. Thallus in TS showing patch of arching coaxial cells (arrow) in otherwise noncoaxial hypothallium and descending hypothallial filaments ending in wedge-shaped cells (arrowheads) (UBC A48004).

Figs. 93, 94. TSs of thalli showing ascending perithallium ending in 1 or 2 epithallial cells (arrows). Note subepithallial initials isodiametric and similar in size or smaller (arrowhead) than cells below (Fig. 94; UBC A48033; Fig. 95; UBC A48032).

Fig. 95. TS of thallus showing local perithallial stratification (arrow) (UBC A48029).



620 μm in external diameter in var. *foecundum*), (5) larger chambers (220–500 μm vs 208–450 μm in diameter, respectively), and (6) larger pore plates (150–360 μm vs 130–220 μm in diameter, respectively). After comparing these measurements with data from Arctic and North Atlantic *L. foecundum* (Foslie 1905, p. 21; Adey 1966, table IV) and new material from NW Spitsbergen (Athanasiadis, unpublished data), differences persisted in the following characters: (1) larger multiporate conceptacles in the Pacific specimens (also reflected in larger chamber and pore plate dimensions), and (2) moderately sunken to flattened conceptacle roofs (Table 1). Therefore, the Pacific specimens from Vancouver Island and Seattle are recognized to be a distinct variety of the species. Similar patterns in the mode of conceptacle embedment and in development of coaxial patches in the hypothallium of var. *sandrae* were observed in specimens of *L. foecundum* from NW Spitsbergen (Athanasiadis, unpublished data; material from Raudfjord and Møffen Islet, coll. L.-H. Jenneborg, in GB). Hence, the Pacific and Arctic varieties share a larger number of characters such as: (1) mode of thallus growth and adhesion (including superimposition and rare unattached proliferations), (2) a predominantly noncoaxial hypothallium (with coaxial patches), (3) 1–2 flattened epithallial cells, (4) subepithallial cells similar or smaller in size than perithallial cells below, (5) multiporate conceptacles with a peripheral rim, (6) embedded conceptacles, (7) specialized (thinner-wider) pore cells (including the rosette cells), and (8) bisporangia as the main type of reproduction.

The present records of var. *sandrae* suggest a higher temperature preference for this variety than var. *foecundum*. Temperature fluctuations in the distributional area of the former taxon (Vancouver Island and Seattle) range between 4° and 14°C (Hansen 1997; Lindstrom 1998), and are slightly higher or just correspond to those of the southernmost localities of var. *foecundum* in North Iceland (Adey 1968, p. 20), North Norway (Foslie 1895, p. 109; 1905, p. 21), and the Gulf of Maine (Adey 1966, p. 346) [where surface temperature ranges between 2–4° and 8–14°C (Cambridge *et al.* 1987, fig. 1, based on data from the U.S. Navy Marine Climatic Atlas)]. Whether the distribution of var. *sandrae* extends further south and/or north remains to be determined.

In comparison with its congeners in the NE Pacific, var. *sandrae* is clearly distinct in having rimmed multiporate conceptacles and specialized pore filaments bordering pore canals of multiporate roofs (the other species may show specialized pore cells at the base of canals only, whereas *L. tenue* may develop thinner-wider rosette cells; Fig. 14). Variety *sandrae* was identified in several UBC collections previously referred to *Lithothamnion californicum* Foslie and in one UC (936323)

collection identified as *L. adeyi* by Steneck & Paine (1986, p. 235). The latter material is a specimen from Channel Rocks (near Seattle) possessing: (1) rimmed multiporate conceptacles (380–600 μm in external diameter and 180–220 μm high with chambers 270–450 μm in diameter and 170–200 μm high), (2) multiporate roofs 40–50 μm in thickness, (3) patches of coaxial cells in the hypothallium, (4) superimposing lamellae (each 120–220 μm thick), (5) 5–7 rosette cells, (6) pore canals 7–11 μm in apical diameter, (7) differentiated (thinner-wider) pore cells (including rosette cells), and (8) shedding as well as embedded conceptacles (the latter filled with palisade cells). Other vegetative characters of the Channel Rocks specimen, such as length of hypothallial cells (15–30 μm long), flattened epithallial cells (2–3 μm long and 4–11 μm broad), roof filaments (5- to 7-celled), pore number (at least 36), and size of (bi-?)sporangial remains (100 \times 20 μm) are shared by both *L. tenue* and/or *L. adeyi*. Small sterile specimens of var. *sandrae* could be confused with *L. tenue*, because both taxa exhibit thallus superimposition and coaxial patches in the hypothallium. A character that could be diagnostic in such specimens is the (occasional) development of unattached margins (that apparently occurs in the former taxon only; Figs 89, 90, arrows). The following sterile UBC collections could be either of these two taxa: UBC A48031 (between Fleming and Tzaratus Islands, Bamfield area, 6 m, 5 July 1969, Pace & Harrison 26510B; *pro parte*); UBC A59244 (off Brady's Beach, Bamfield, on rock, 10 fathoms, 3 December 1978, Hansen & Garbary unnumbered, growing with a Gelidiaceae); UBC A60316 (off False Bay, San Juan Island, Washington State, on shells, 24 July 1947, Stanford unnumbered, coaxial hypothallial patches not seen but hypothallial cells up to 50 μm long); UBC A60315 (Johns Island, San Juan County, Washington State, Stanford unnumbered, coaxial hypothallial patches not seen, hypothallial cells only up to 29 μm long; could also be *L. adeyi*).

In the absence of gametangia, the generic position of *L. foecundum* within the Melobesioideae (and in particular within the complex *Synarthrophyton-Leptophytum-Mesophyllum*) is determined by the following character combination: (1) patches of coaxial cells in a predominantly noncoaxial hypothallium, (2) nonelongate subepithallial initials, (3) shallow conceptacle primordia (recorded in var. *foecundum*; Adey 1966, figs 96–98), (4) specialized (thinner-wider) pore filaments, and (5) flattened (not flared or domed) epithallial cells. Character (1) precludes a position in *Mesophyllum* whereas characters (2) and (4) preclude a position in *Synarthrophyton*. Moreover, characters (3), (4) and (5) preclude a position in the genera *Phymatolithon* or *Lithothamnion*.

The closest locality of var. *foecundum*, with respect to the

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Figs. 96–107. *Leptophytum foecundum* var. *sandrae*.

Figs. 96, 97. Multiporate and rimmed (arrowheads) conceptacles spread on thallus surface. Note degenerating conceptacle (arrow) (holotype).
Fig. 98. TS of conceptacle with distinctive peripheral rim (arrowhead) (UBC A44187).

Fig. 99. Surface view of multiporate roof showing pore canals surrounded by specialized (thinner-wider) rosette cells (holotype).

Figs. 100, 101. Surface views of pore canals at lower levels of focus showing specialized cells encircling canals (arrows) (holotype).

Figs. 102–104. Pore canals in TS at different levels of focus. Filaments bordering canals composed of thinner (white arrowheads) -wider (black arrowheads) cells. Subbasal cells elongate (arrowheads) and basal cells projecting outwards (arrows) (holotype).

Fig. 105. TS of conceptacle overgrown by peripheral filaments (arrows). Old conceptacle roof still visible (arrowhead) (UBC A48032).

Figs. 106, 107. Drawings of two bisporangial conceptacles in TS: one conceptacle (Fig. 107) embedded, resulting in an outgrowth (UBC A44187).

present NE Pacific records, is in Arctic Alaska, because we can confirm a record from Stefansson Sound (Boulder Patch, Station DS-11, 6 m, 70°19.25'N, 147°35.1'W, 27 July 1980, bisporic, *R. T. Wilce* A & B, in GB unnumbered).

Leptophytum foecundum has also been reported from Antarctica (Alongi *et al.* 2002), where it was treated as conspecific with the indigenous *Leptophytum coulmanicum*. Yet, Ross Sea specimens described by Alongi *et al.* (2002, p. 143) differ from *L. foecundum* in having smaller chambers of multiporate conceptacles (up to 280 μm in diameter vs up to 450 μm in var. *foecundum* and up to 500 μm in var. *sandrae*). Essential features (such as pore cell morphology and external morphology of multiporate conceptacles) are unknown for the Ross Sea specimens.

***Leptophytum adevi* Steneck & R. T. Paine
(1986, pp. 235–236, figs 32, 33)**

Figs 108–122

HOLOTYPE: In US 79-TIW-2; collected by R. Paine, 7 October 1979 (Figs 108–122).

HOMOTYPIC SYNONYM: *Phymatolithon adevi* (Steneck et Paine) Gabrielson in Gabrielson *et al.* (2000, p. 37).

TYPE LOCALITY: North shore of Tatoosh Island, Washington State.

HABITAT: The holotype grows on a pebble and was collected in the intertidal zone in a tidepool in a cave, below a canopy of macroalgae. Both thallus grazing and diatom fouling were reported on the thallus (Steneck & Paine 1986).

DISTRIBUTION: Known only from the type locality.

MATERIAL EXAMINED: **United States:** Washington State. Holotype as cited above.

OBSERVATIONS ON THE HOLOTYPE MATERIAL: A full description of the holotype is provided here (Figs 108–122).

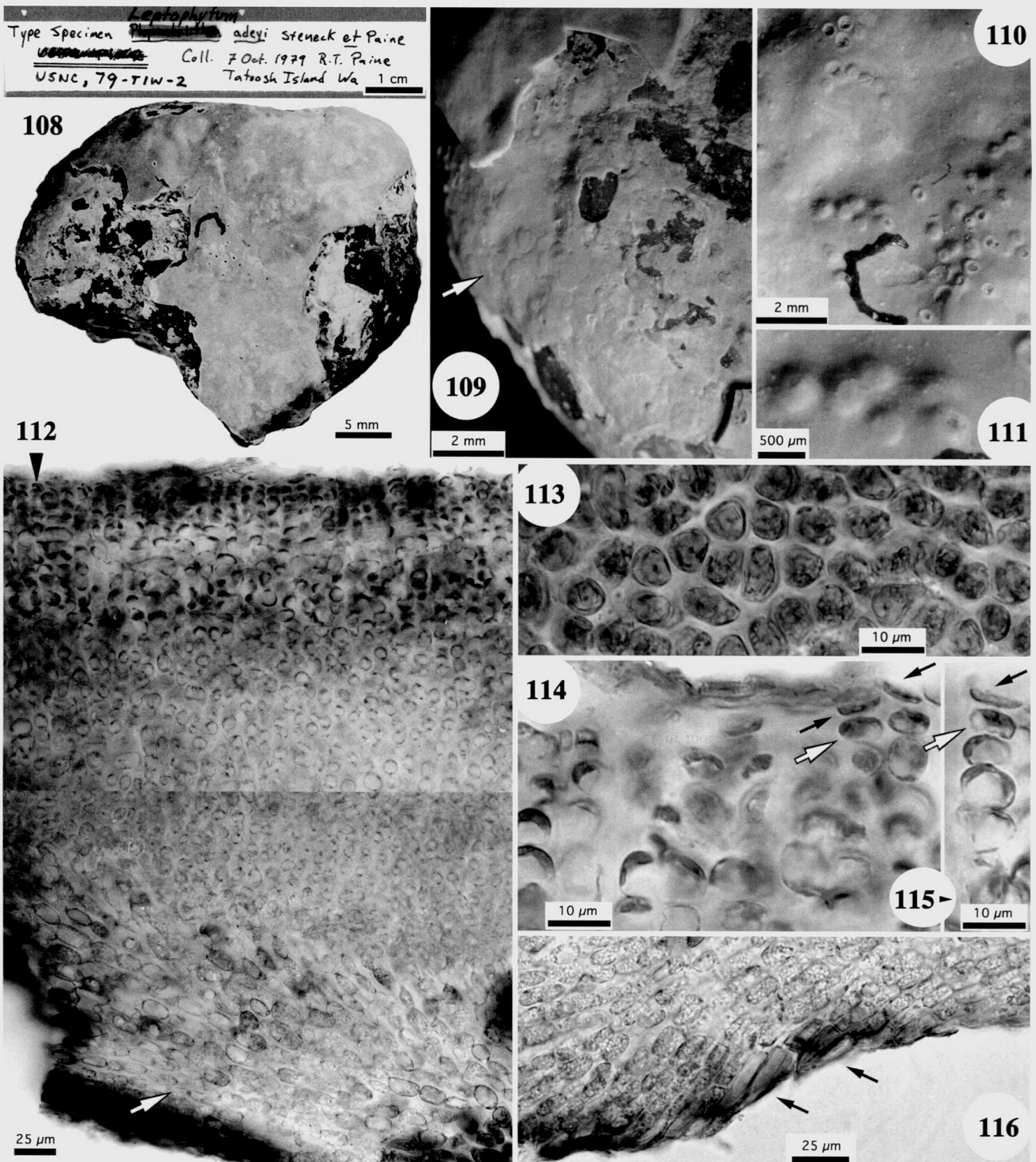
MORPHOLOGY: Thallus to 6 cm in diameter, adhering strongly to one side of a small pebble with similar diameter (Figs 108, 109). Fifteen multiporate conceptacles occurring in groups on the surface (Figs 110, 111); roofs intact or partly broken off. Dried tetrasporangia occurring on the top of some roofs. Thallus partly covering another thinner, unidentified coralline crust, which is sterile (Fig. 109, arrow). Holotype specimen bright pink in colour ('pink-purple' in the protologue), having a smooth, glossy surface with whitish regions that indicate epithallial sloughing, according to the protologue. Protuberances lacking (although 'mammilate pseudobranches' as the result of irregularities in thallus thickness are recorded in the protologue). All margins have been removed (described as 'slightly lobate' in the protologue). Several crater-like depressions, representing conceptacle remains, occurring on the thallus surface (Figs 110, 122).

ANATOMY: Thallus organized dorsiventrally, lacking superimposing growth. Individual lamellae 350–500 μm thick (420–688 μm , according to the protologue), composed of a noncoaxial polystromatic hypothallium, 160–220 thick (81–237 μm , according to the protologue), which gradually produces an ascending nonstratified perithallium 200–300 μm thick (Fig. 112). Hypothallial cells rectangular, 15–28 μm long and 5–14 μm broad. Perithallial cells nearly isodiametric, 5–12 μm long and 8–12 μm broad (5.5–12.1 $\mu\text{m} \times 4.6$ –9.4 μm , according to the protologue), ending in 1 or 2 epithallial

cells, roundish to angular in surface view (Fig. 113) and flattened in TS (Figs 114, 115, black arrows). 2–3 μm long and 8–10 μm broad (0.6–2.2 $\mu\text{m} \times 6$ –8.4 μm , according to the protologue). Subepithallial initials shorter or isodiametric, and more or less similar in size to cells below (Figs 114, 115, white arrows). Descending hypothallial filaments ending in wedge-shaped cells (Fig. 116, arrows).

REPRODUCTIVE STRUCTURES: Multiporate conceptacles 350–400 μm in external diameter (395–495 μm , according to the protologue), raised or flush with the surface. The conceptacle illustrated in the protologue reaches c. 450 μm in external diameter and is 80 μm high (Fig. 117). Pores not visible under the stereoscope [due to detrital (?) material covering the roof surface] (Figs 110, 111). Side walls of the roof meeting the thallus surface at wide angles (Fig. 117), constrictions absent. Roofs convex or flattened, lacking a peripheral rim, pierced by 22–47 pores ($n = 2$), which become apparent in decalcified material (Fig. 118). Roof 55–60 μm thick, composed of 5 or 6 cells along the periphery (Fig. 119) (33–45 μm thick and composed of more than 4 cells, according to the protologue). Pore plates 180–230 μm in diameter; individual pores with an apical opening 7–12 μm in diameter, surrounded by 7–9 rosette cells, which are normal epithallial cells (Fig. 120A). In surface views, at lower levels of focus, filaments bordering conical pore canals composed of thinner-wider cells that tend to encircle the canal, which is c. 20 μm in diameter near the base (Fig. 120C). According to the protologue, chambers are 261–311 μm in diameter; the one illustrated measuring c. 310 μm in diameter and c. 95 μm in height (Fig. 117). Old conceptacles losing their roofs, leaving crater-like depressions that are 300–350 μm in diameter (Fig. 122). These depressions apparently reflecting the diameter of chambers; their size is included here in the chamber dimension for the species. Tetrasporangia zonately divided, 70–105 μm long and 40–60 μm broad ($n = 10$) (Fig. 121), indicating the occurrence of taller (than 95 μm) chambers. Tetrasporangia occurring on the roofs of conceptacles, indicating that they have been released after the material was collected. Embedded conceptacles, secondary pit-connections and trichocytes not seen.

COMMENTS: Although recently transferred to the genus *Phymatolithon* (Gabrielson *et al.* 2000, p. 37), the original position in the genus *Leptophytum* is supported here because *L. adevi* exhibits: (1) flattened (and not domed) epithallial cells, and (2) specialized (thinner-wider) pore cells at the base of canals of multiporate roofs. In contrast, species of *Phymatolithon* generally possess domed epithallial cells (Wegeberg & Pueschel 2002) and lack specialized (thinner-wider) pore cells in multiporate roofs (see also Comments under *L. microsporum*). Nevertheless, in the absence of information on gametangial structures, the generic position in *Leptophytum* remains tentative. The present study of the holotype is in agreement with the original description provided by Steneck & Paine (1986), except that the specimen grows on a small pebble (said to be growing on rock), lacks 'mammilate pseudobranches' on its surface, and possesses tetrasporangia (not observed in the protologue). Moreover, Steneck & Paine reported the presence of slightly concave pore plates, but this feature was not evident for any of the conceptacles of the holotype. Several attempts to find new material of the species at its type



Figs. 108–116. *Leptophytum adeyi* (holotype).

Fig. 108. The holotype specimen (US, Paine # 79-TIW-2) and original label on box (in lower magnification).

Fig. 109. View of unidentified coralline specimen (arrow) growing beneath holotype.

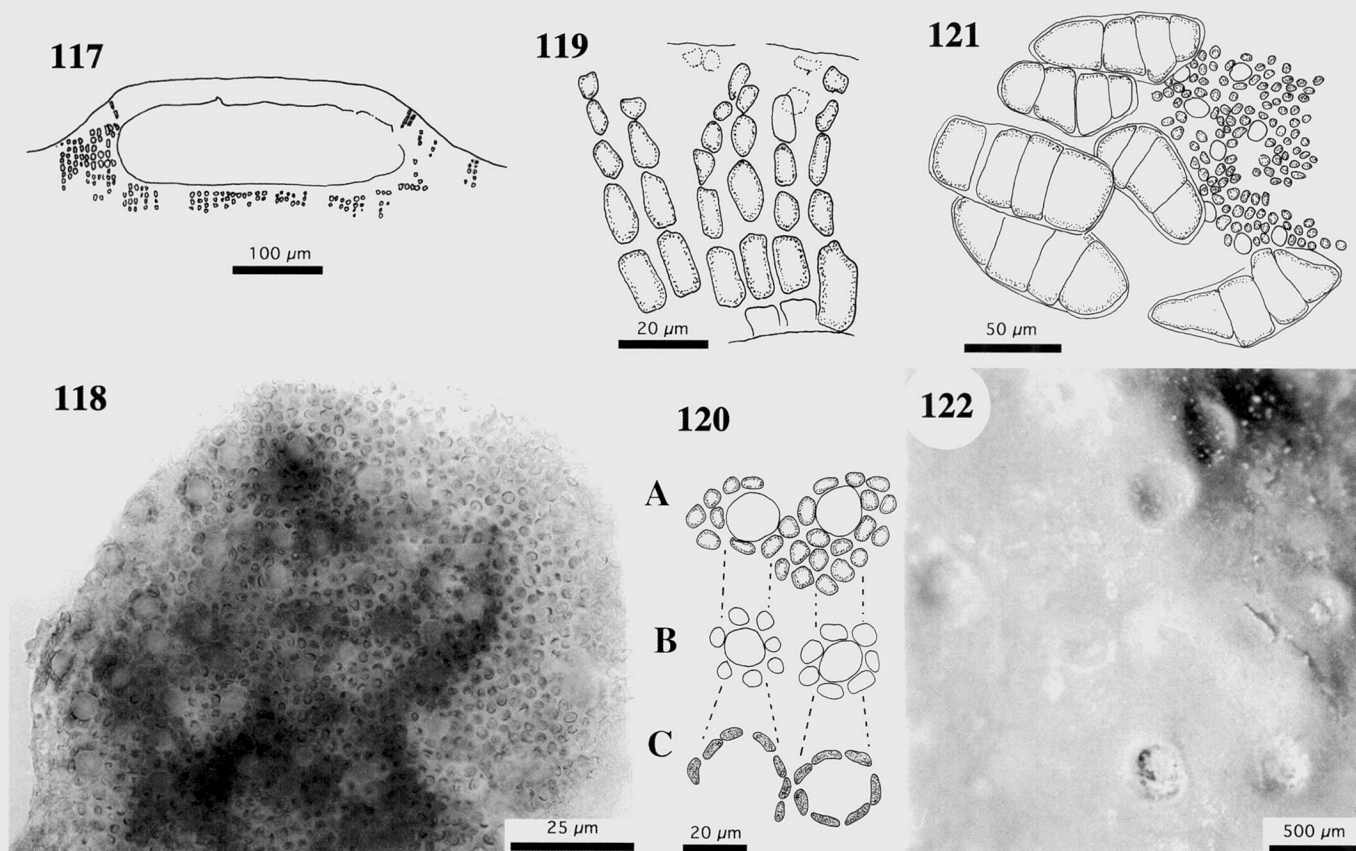
Figs. 110, 111. Surface views showing spread multiporate conceptacles. Some conceptacles (in Fig. 110) have lost their roofs, forming crater-like depressions.

Fig. 112. TS showing noncoaxial hypothallium (arrow), producing ascending perithallium of isodiametric cells.

Fig. 113. Surface view showing roundish to angular epithallial cells.

Figs. 114, 115. TSs showing flattened epithallial cells (black arrows) and short subepithallial initials (white arrows).

Fig. 116. Descending hypothallial cells ending in wedge-shaped cells (arrows).



Figs. 117–122. *Leptophytum adeyi* (holotype).

Fig. 117. Drawing of multiporate roof in TS [based on Steneck & Paine's (1986) fig. 32].

Fig. 118. Surface view of multiporate roof.

Fig. 119. Drawing of part of multiporate roof in TS.

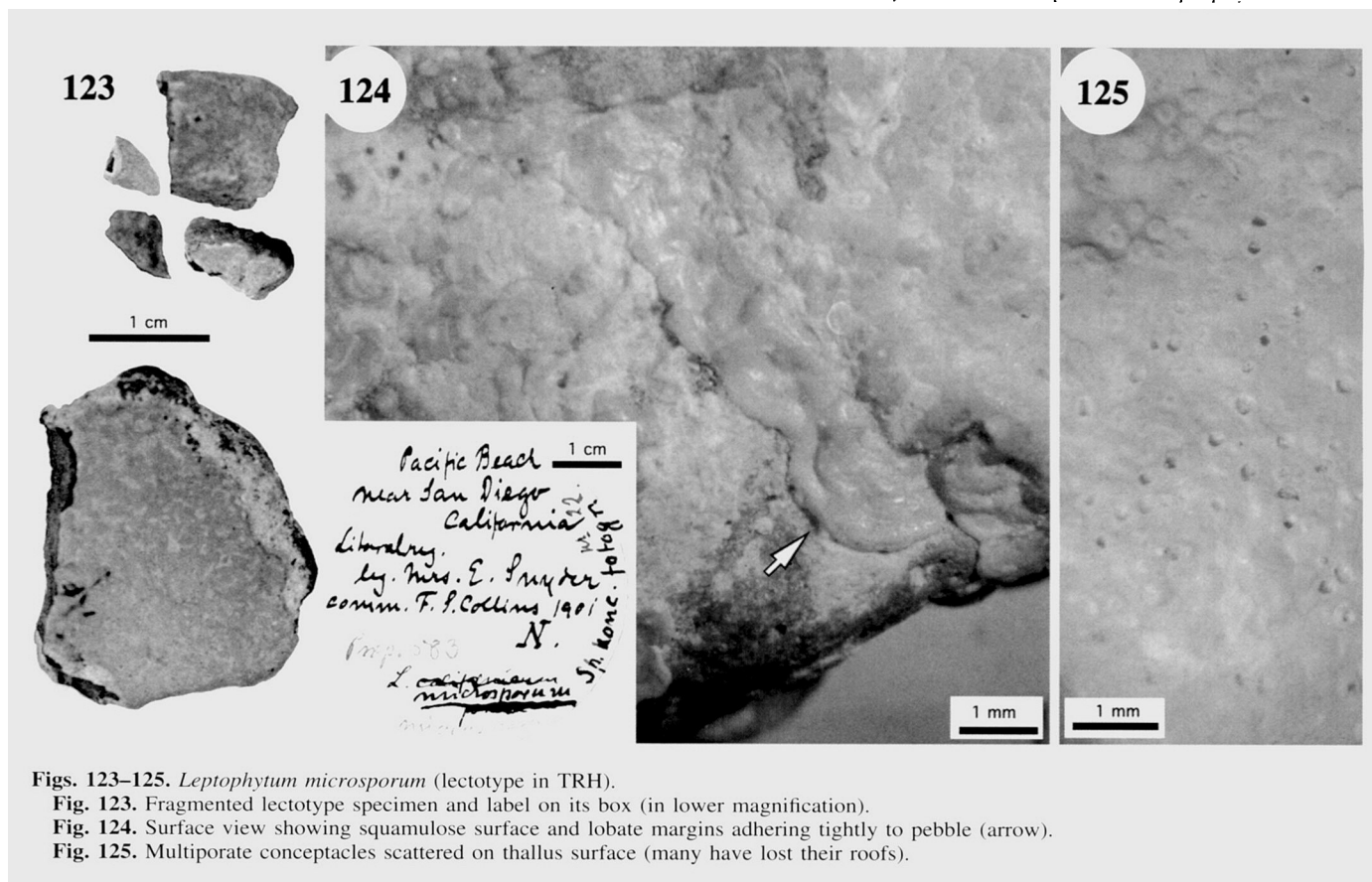
Fig. 120. Drawing of two pore canals at three levels of focus in views from above, showing: (A) rosette cells (normal epithallial cells surrounding pore openings), (B) normal roof cells surrounding pores, and (C) specialized, thinner-wider cells encircling canal near base.

Fig. 121. Drawing of tetrasporangia attached to multiporate roof.

Fig. 122. Surface view of thallus showing crater-like depressions of degenerate conceptacles.

locality (R. Paine, personal communications) have been unsuccessful, as no specimens matching the holotype were found. Therefore, the present account is based entirely on the holotype specimen. In the protologue, Steneck & Paine (1986, p. 235) cited the following five collections as 'representative specimens': (1) MAINE TIW-45, 47, collected by R. Steneck, 13 June 1980, in tidepool, at Tatoosh I., Washington, (2) MAINE TIW-10f, collected by R. Paine, October 1979, in midintertidal pool, at Tatoosh I., Washington, (3) MAINE TIW 121a & b, collected by Palumbi, June 1980, on cobbles, 33 m depth, at San Juan I. Channel, Washington, (4) UC 936323, collected by Gardner (No 654) at Channel Rocks near Seattle, 21 May 1901, and (5) UC 739472, collected by L. Roush (No 56), at East Sound, Orcas Island, Puget Sound, 7 July 1925. Unfortunately, we have been unable to examine the MAINE specimens, but we found the UC collections to belong to other species of *Leptophytum*. In particular, UC 739472 includes both carposporangial (Fig. 25) and tetrasporangial specimens (Figs 26, 27), whose vegetative and reproductive features agree well with *L. tenue* (see Comments under that species). UC 936323 differs from *L. adeyi* in possessing embedded conceptacles (filled with palisade cells),

patches of coaxial hypothallial cells, and larger (up to 600 μm in external diameter) multiporate conceptacles with flattened or sunken pore plates; these characters are collectively diagnostic for *L. foecundum* var. *sandrae* (see Comments under that species). Several UBC collections previously referred to *Lithothamnion californicum* Foslie and filed under *L. adeyi* (see Scagel *et al.* 1989, p. 205) were also found to belong to *L. foecundum* var. *sandrae* or other melobesioid species. Consequently, the distribution of *L. adeyi*, said to be between the Strait of Juan de Fuca (Puget Sound) and SE Alaska and occurring to 30 m depth, is here limited to its type locality. *Leptophytum adeyi* appears to be closely related to the North Atlantic *L. laeve*, which has also been reported from the Pacific coast of Russia, Hokkaido, the Mexican Pacific coast and also Kukak Bay in Alaska (see below under *L. laeve*). These two species differ in the external diameter of multiporate conceptacles (350–495 μm in *L. adeyi* vs 500–1000 μm in *L. laeve*), chamber diameter (261–350 μm in *L. adeyi* vs 312–700 μm in *L. laeve*), pore plate diameter (180–230 μm in *L. adeyi* vs 270–550 μm in *L. laeve*), and tetrasporangium length (70–105 μm in *L. adeyi* vs 160–225 μm in *L. laeve*; see Table 1). Sterile thalli of *L. adeyi* are apparently indistinguishable



Figs. 123–125. *Leptophyllum microsporum* (lectotype in TRH).

Fig. 123. Fragmented lectotype specimen and label on its box (in lower magnification).

Fig. 124. Surface view showing squamulose surface and lobate margins adhering tightly to pebble (arrow).

Fig. 125. Multiporate conceptacles scattered on thallus surface (many have lost their roofs).

from *L. laeve* but differ from *L. foecundum*, *L. tenue* and *L. microsporum* in lacking thallus superimposition and patches of coaxial hypothallial cells and in possessing relatively short hypothallial cells (up to 28 μm vs 50 μm in length in *L. foecundum* and *L. tenue*). On the basis of these vegetative characters, collection UBC A60315 (Johns Island, San Juan County, Washington State, 25 July 1947, sterile, Stanford unnumbered) could belong to *L. adeyi* (see also Comments under *L. foecundum* var. *sandrae*).

Leptophyllum microsporum (Foslie) comb. nov.

Figs 123–141

BASIONYM: *Lithothamnion californicum* Foslie f. *microsporum* Foslie (1902, pp. 5–6, ‘*microspora*’).

HOMOTYPIC SYNONYM: *Lithothamnion microsporum* (Foslie) Foslie in Printz (1929, p. 51).

LECTOTYPE: In TRH (unnumbered) (Fig. 123); includes 3 labels annotated by Foslie, 1 Foslie slide # 583, and 2 Lebednik slides # 583 (1&2) [one of Foslie’s labels reads ‘Pacific Beach near San Diego California Litoral reg. leg. Mrs E. Snyder comm. F. S. Collins 1901, N, prep. 583, *L. californicum* ... *microsporum*, Sp. konc. fotogr. No 22’]; collected by Mrs E. Snyder in 1901; designated by P. Lebednik in herb., February 1976.

SYNTYPES: (1) In TRH (unnumbered); includes 2 Foslie labels, 1 Foslie slide # 582, and 2 Lebednik slides # 582 (1 & 2), [one of Foslie’s labels reads ‘Pacific Beach near San Diego California litoral reg. leg. Mrs E. Snyder comm. F. S. Collins 1901, E. *L. californicum* f. ... *microsporum*, prep. 582’]. (2) In TRH (unnumbered); includes 1 Foslie label and 1 Foslie slide # 1535 [Foslie’s label reads ‘Pacific Beach near San Diego Califor. leg. Mrs E. Snyder comm. F. S. Collins 1901, # 12, *L. californicum* forma ... *microsporum*, prep. 1535’]. (3) In TRH (unnumbered); includes 1 Foslie label and 1 Foslie slide # 1534 [Foslie’s label reads ‘Pacific Beach near San

Diego California leg. Mrs E. Snyder. – Litoral reg. comm. F. S. Collins 1901, # 5, *Lithoth. californicum* Fosl. forma ... *microsporum*, prep. 1534’]. All three syntypes are designated by P. Lebednik in herb., February 1976.

TYPE LOCALITY: Pacific Beach near San Diego, California; growing on pebbles and sandstone in the littoral zone.

HABITAT: On pebbles, sandstone, and encrusting coralline algae in the littoral and sublittoral zones to at least 34–36 m depth.

DISTRIBUTION: United States and Mexico: California and Baja California. The present records range between Santa Catalina I. (southern California) and Punta Entrada (Isla Magdalena, Baja California), including Pacific Beach (San Diego), La Jolla, Isla Guadalupe, and Punta Pequeña (Bahía San Juanico, Baja California).

MATERIAL EXAMINED: **United States:** California. Pacific Beach, San Diego, littoral, 1901, *Snyder* (lectotype and syntypes in TRH, as described above); Santa Catalina Island, 1 December 1948, intertidal, rocky shore on SE side Catalina Island, Valero Sta. 1652, bisporic, on a pebble, *Dawson* 5667, LAM (AHFH, unnumbered) [*pro parte*: *L. microsporum* marked C]; ‘Beach Club’ reef, La Jolla, Temp. 18.8°C at 6 AM, bi-tetrasporic, on pebbles, 1 June 1946, *Dawson* 2043, LAM (AHFH 70380) [*pro parte*: *L. microsporum* marked EYD 2043A]. **Mexico:** Baja California. Punta Entrada, Isla Magdalena, dredged in 34–36 m, undated, on pebble, *Dawson* 6604a, LAM (AHFH 70378) [*pro parte*: *L. microsporum* is marked A]; Punta Pequeña, Bahía San Juanico, intertidal, undated, bisporic, on rock fragment, Tray 66, *Dawson* 9251a, LAM (AHFH 70381) [*pro parte*: *L. microsporum* indicated by an arrow]; Isla Guadalupe, 2.5 miles north of South Bluff, shore at –1.7’ tide, bi-tetrasporic, on pebbles, 21 December 1949, *Dawson* 8608, LAM (AHFH 70383) [*pro parte*: *L. microsporum* placed separately].

OBSERVATIONS ON TYPE MATERIAL: The type material in TRH is kept in four boxes that are identically labeled with respect to locality (Pacific Beach near San Diego California, littoral zone), collector and distributor (Mrs E. Snyder, communicated by F. S. Collins 1901) and year of collection (1901). The box-

es are further annotated by Foslie: 'E *L. californicum* forma prep. 582', 'N prep. 583 sp. Konc. Fotogr. No 22 *L. californicum* forma *microspora*', '#5 *Lith. californicum* Fosl. forma prep. 1534', and '#12 *L. californicum* f. *microspora* prep. 1535', respectively. On all labels, the specific (and forma in the last collection) epithet(s) are stricken through and replaced with the name *microsporum*.

Each of the four boxes (collections) includes one original slide (each annotated by Foslie with place, date, coll. and the numbers #582, #583, #1534 or #1535). Each of the collections 'N' and 'E' includes 2 additional slides made by P. Lebednik. The latter two collections ('N' and 'E') appear as a single entry in Adey & Lebednik (1967, p. 52). In February 1976, P. Lebednik selected the collection 'N' as lectotype and the remaining three collections as syntypes (writing the words 'Lectotypus' and 'Syntypus' on the appropriate boxes).

The lectotype is a single specimen growing on a pebble (now broken into five pieces; Fig. 123). The largest thallus reaching c. 3.3 cm in diameter. The thallus adhering strongly to the substrate and having lobate margins, which also adhere tightly (Fig. 124, arrow). Surface pinkish, provided with visible swirl-like (squamulose) contours, with a whitish border along the margin. Surface covered with multiporate conceptacles, either intact or with broken off roofs (Figs 125, 126). On a separate piece of paper, Foslie annotated 'San Diego Cal. Prep. 583. Perith. 7×7 , 9×7 , 9×6 , 6×6 , 7×6 , 6×5 , 11×7 , 11×6 , 11×9 , Hypoth. 18×7 , 18×9 , 14×7 , 14×9 , 11×7 , 18×6 , Konc (Cave) 200–300 μ ca. 25 pores'. Two further annotations on smaller pieces of paper: (1) '*L. calif.* f. . . .', and (2) '. . . prep. 583'. The lectotype is the largest specimen in the entire type collection, well-developed and showing the variation in conceptacle morphology described in the protologue, especially regarding pore number and in having roofs either slightly raised or flush with the surface.

The syntype collection marked 'E' growing on sandstone (now broken into 4 pieces), having a more irregular morphology. The few intact conceptacles having convex roofs whereas most other conceptacle remains forming crater-like depressions. On two separate pieces of paper, Foslie annotated, 'Konc. (Caves) 140–280 μ Prep. 582' and 'San Diego Cal. Prep 582 Perith. 14×7 , 11×7 , 11×9 , 7×6 , 9×7 , 7×7 , 9×9 , 6×6 , 9×6 , 11×6 Hypoth. 18×6 , 14×7 , 25×7 , 28×7 , 28×9 , 22×9 , 25×9 , 18×7 , 18×9 , 18

$\times 4$, 14×6 , 29×7 , 20×9 , 22×6 , 29×6 , 16×11 , 25×11 '.

The syntype collection marked '#5' comprising several smaller fragments (the largest up to 1.3 cm in diameter) growing on an encrusting coralline alga and on stone fragments. Specimens bearing multiporate conceptacles but roofs mostly broken off. Thallus morphology agreeing with lectotype specimen. On a separate piece of paper, Foslie annotated, 'Prep 1534, Perith. 9×7 , 7×6 , 7×7 , 11×6 , 11×7 , 6×6 , 7×9 , 9×6 , 6×7 , 6×5 , 7×5 , Hypoth. 18×6 , 22×7 , 11×6 , 20×6 , 18×7 , 18×9 , 19×6 , Sp. konc. 160–280 μ , c. 40 pores'.

The syntype collection marked '#12' comprising a single fragment, c. 1.5 cm in diameter, growing on a piece of rock. This specimen also bearing multiporate conceptacles whose morphology, like the external characteristics of the thallus, are identical to the material in the previously described collections. On a separate piece of paper, Foslie has annotated '. . . 160–300 μ . . . konc. 120–200 μ '.

The existing slides and fragments of the lectotype and syntypes indicate that the specimens are morphologically and anatomically concordant and representative of the same species. In particular, their thallus is organized dorsiventrally. Individual lamellae are 50–350 μ m thick and usually grow over the parent thallus in a superimposing manner (at least 3 layers seen, arrows, Fig. 127) so that the maximum thickness reaches 650 μ m. The hypothallium is polystromatic, 15–100 μ m thick, composed of 2–8 filaments displaying noncoaxial growth (Figs 128, 129) and having sporadic patches of few coaxial cell rows (Fig. 130, arrow). Hypothallial cells 12–22 μ m long and 5–10 μ m broad. Perithallial cells 5–12 μ m long and 4–8 μ m broad, and subepithallial initials more or less isodiametric and similar or smaller in size than cells below (Fig. 131, white arrows). Epithallial cells flattened in TS, 3–5 μ m long and 4–7 μ m in diameter, and 1 or 2 present at a time (Fig. 131, black arrows). Multiporate conceptacles spread on the surface (Fig. 126); these 175–280 μ m in external diameter (reaching 340 μ m when two merge) and either flush with the surface or raised as much as 80 μ m ($n = 14$). Those intact with convex or flattened roofs sometimes provided with an indistinct peripheral rim (Fig. 126, arrows, Fig. 130). The chambers 110–220 μ m in diameter ($n = 12$) and 70–100 μ m high ($n = 6$). Pore plates 70–155 μ m in diameter ($n = 7$) and 20–40 μ m thick, composed of 4- or 5-celled filaments (Fig. 132) and

→

Figs. 126–134. *Leptophytum microsporum* (lectotype and syntypes).

Fig. 126. Surface view of three intact and slightly rimmed multiporate conceptacles (arrows); fourth conceptacle has lost its roof (lectotype).

Fig. 127. Thallus in TS showing three superimposing layers (arrows) (syntype '5,' Foslie slide # 1534).

Fig. 128. Thallus margin in TS showing thin hypothallium composed of 2 filaments (arrow) and ascending perithallial filaments [syntype 'E,' Lebednik slide # 582(2)].

Fig. 129. Thallus base in TS showing noncoaxial hypothallium (syntype 'E,' Foslie slide # 582).

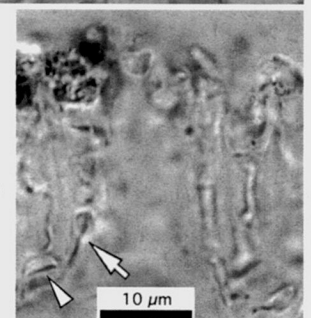
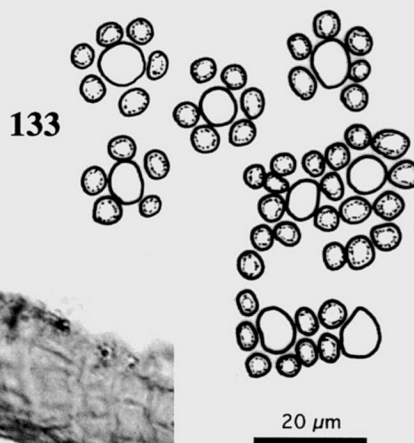
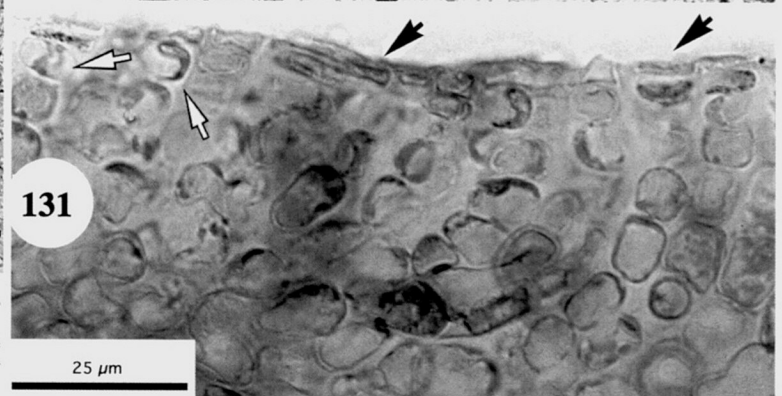
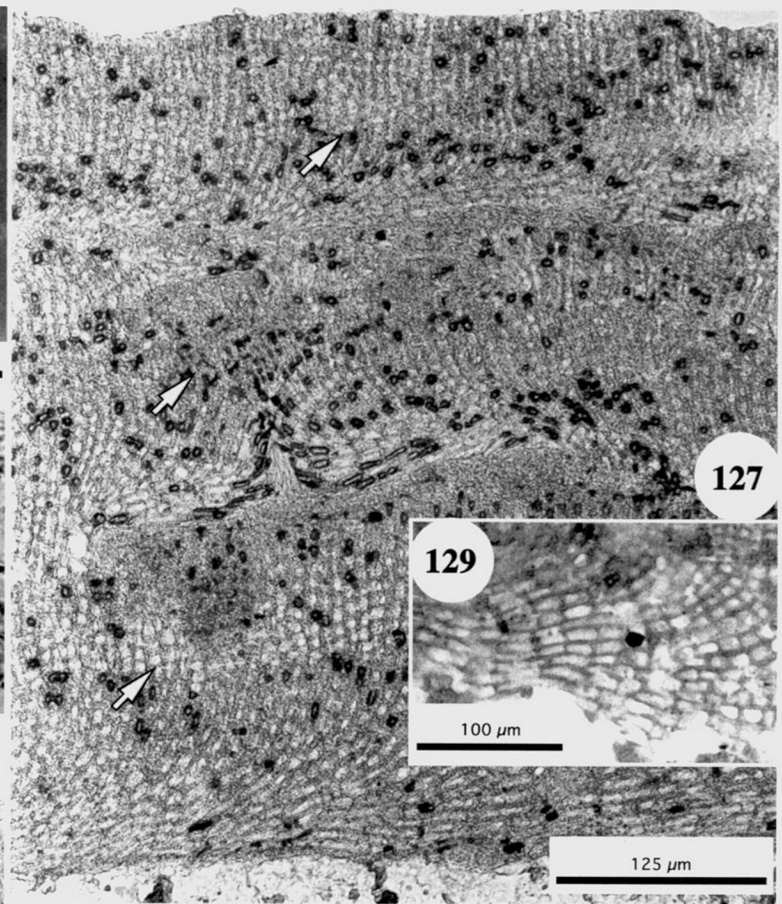
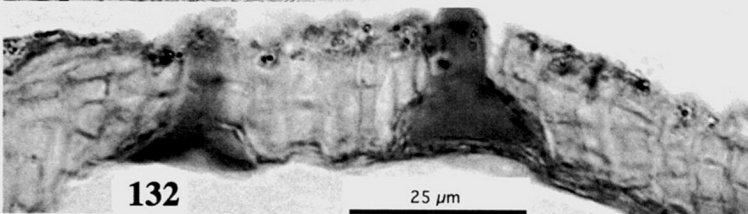
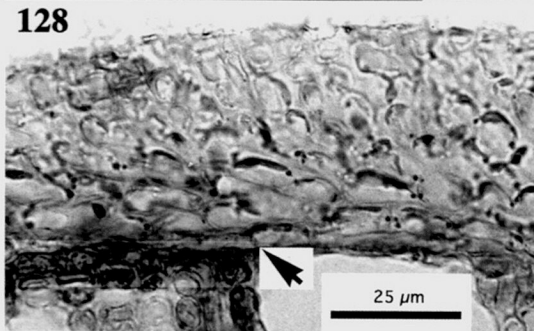
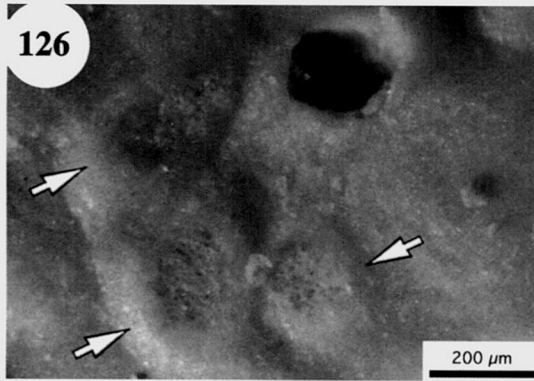
Fig. 130. Raised tetrasporangial conceptacle in TS with one tetrasporangium and hypothallium displaying coaxial cell rows (arrow) [syntype 'E,' Lebednik slide # 582(1)].

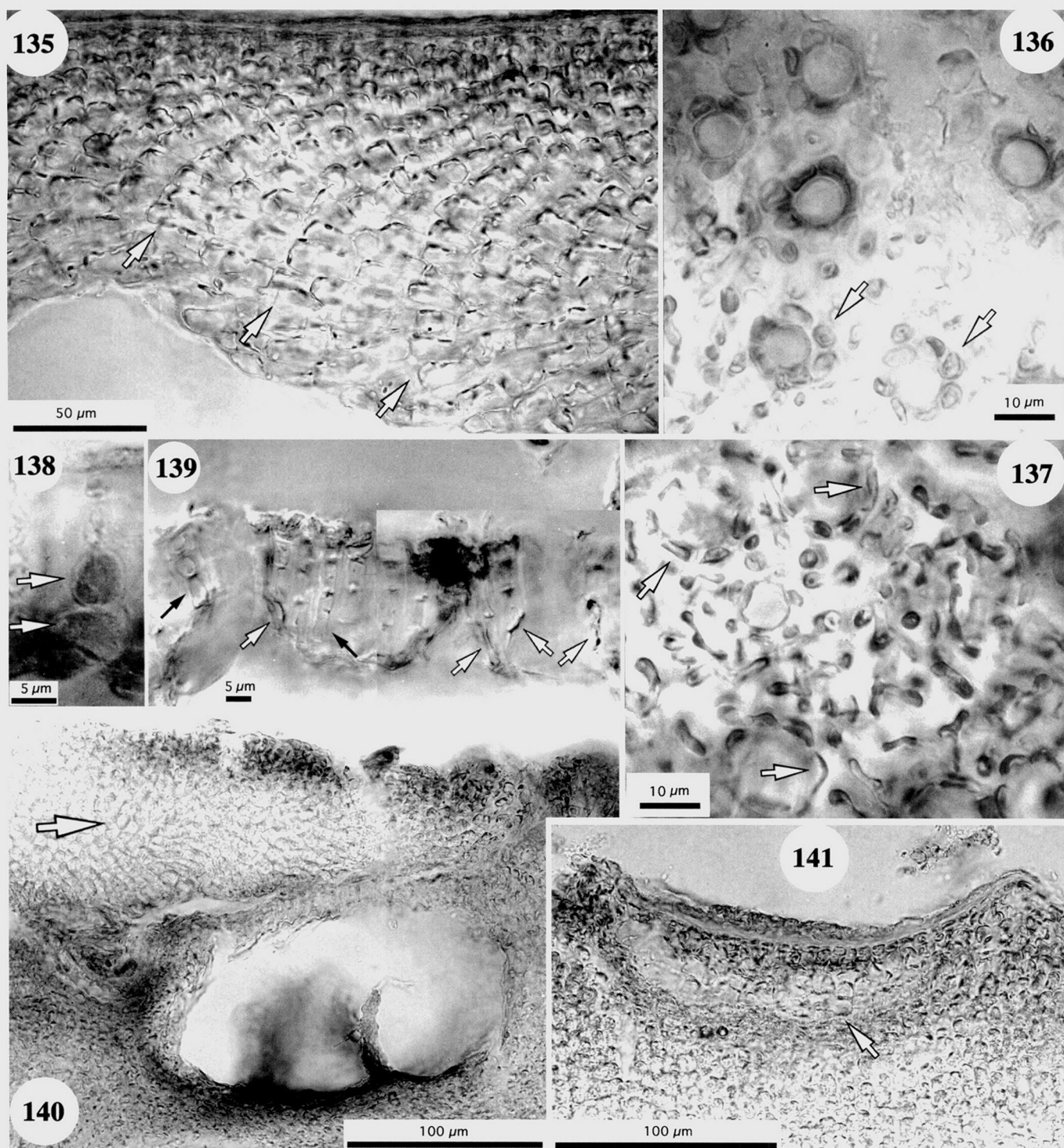
Fig. 131. Thallus in TS showing isodiametric subepithallial initials (white arrows) similar in size to or smaller than cells below and flattened epithallial cells (black arrows) [syntype 'E,' Lebednik slide # 582(2)].

Fig. 132. Conceptacle roof in TS showing two conical pore canals [syntype 'E,' Lebednik slide # 582(2)].

Fig. 133. Drawing of multiporate roof in surface view, with pores surrounded by 6 or 7 rosette cells, which are normal epithallial cells (lectotype).

Fig. 134. TS across pore canal showing the bordering cells. Subbasal cells elongate (arrow), and basal cell (arrowhead) projecting outwards (lectotype).





Figs. 135–141. *Leptophytum microsporum*.

Fig. 135. Thallus in TS showing several arches of coaxial hypothallial cells (arrows) (LAM, AHFH 70381).

Figs. 136, 137. Surface view of multiporate roof at two levels of focus, showing pores surrounded by normal epithallial cells (Fig. 136, arrows) and thinner-wider cells near base (Fig. 137, arrows) (LAM, AHFH 70378).

Fig. 138. Darkly staining basal and subbasal pore cells (arrows) in TS tangential to the pore canal (LAM, AHFH 70383).

Fig. 139. Three conical pore canals (in TS across the canals at two levels of focus), showing thinner (white arrows) subbasal cells. Normal roof cells indicated by black arrows (syntype 'E,' TRH).

Fig. 140. Conceptacle in TS embedded through thallus superimposition (arrow) (LAM, AHFH 70380).

Fig. 141. Remains of conceptacle in TS with chamber floor filled with new perithallial cells (arrow) (LAM, AHFH 70380).

perforated by 10–31 pores ($n = 7$) (up to c. 40 according to Foslie's annotations). Pores surrounded by 6–7 rosette cells, which are normal epithallial cells (Fig. 133). At their apical opening, pores 5–9 μm in diameter, becoming wider at the base and reaching c. 20 μm in diameter (Figs 132, 134). Filaments bordering conical pore canals composed of normal roof cells, except the basal and subbasal cells, which appear to be thinner (Figs 134, 139, white arrows) than normal roof cells (Fig. 139, black arrows). Subbasal cells also elongate, and basal cells projecting outwards (Fig. 134, arrowhead). One tetrasporangium observed, measuring 70 μm in length and 20 μm in breadth (Fig. 130). Older conceptacle chambers commonly filled with new perithallial cells, partly embedded in the thallus.

MORPHOLOGY: Thalli growing on pebbles, sandstone or other rock, or on other crustose coralline algae, adhering firmly to the substrate even at the margin. Thalli attaining at least 3.3 cm in diameter. The surface smooth or squamulose (with minute scales) and pinkish in colour. Perithallial protuberances lacking. Margins lobate (Fig. 124) and provided with a whitish border (cuticle?).

ANATOMY: Thallus organized dorsiventrally, consisting of lamellae 50–470 μm thick, usually growing over the parent thallus in a superimposing manner (up to at least 3 layers) so that maximum thallus thickness reaching 650 μm (Fig. 127). Hypothallium polystromatic, noncoaxial, 15–100 μm thick, composed of 2–8 filaments (Figs 128–130, 135), displaying occasional patches of coaxial growth (consisting of up to 10 cell rows) (Figs 130, 135, arrows). Hypothallial cells 12–26 μm long and 5–10 μm broad. Perithallium 25–370 μm thick. Perithallial cells 5–12 μm long and 4–8 μm broad. Subepithallial initials isodiametric, similar or smaller in size than cells below (Fig. 131, arrows). Epithallial cells flattened in TS, 2–5 μm long and 4–7 μm in diameter, 1 or 2 present (Fig. 131). Cell fusions common between contiguous somatic cells. Secondary pit-connections and trichocytes not seen.

REPRODUCTIVE STRUCTURES: Multiporate conceptacles spread on thallus (Fig. 125), either flush with the surface or slightly raised (Fig. 126), reaching 80 μm in height ($n = 22$), containing tetrasporangia or bisporangia. Conceptacles 160–280 μm in external diameter ($n = 17$; 200–300 μm , according to the protologue), two merged reaching 360 μm in diameter. Conceptacle roofs convex, flattened, or slightly concave, the latter provided with an indistinct peripheral rim (Fig. 126). Chambers 110–220 μm in diameter ($n = 21$) (up to 280 μm when two fused) and 70–110 μm high ($n = 8$). Pore plates 70–170 μm in diameter ($n = 10$) and 15–40 μm thick. Roofs composed of 4- or 5-celled filaments, perforated by 10–40 pores. Pore canals conical, 5–9 μm in diameter at the top, reaching c. 20 μm in diameter at the base (Figs 132, 134, 137); canals surrounded by 5–7 rosette cells, which are normal epithallial cells (Figs 133, 136, arrows). Filaments bordering pore canals composed of 4 or 5 normal roof cells, except near the base where pore cells are thinner-wider, tending to encircle the canal (Fig. 137, arrows); these specialized pore cells staining more darkly (Fig. 138). Subbasal cells elongate (Figs 134, 139, white arrows), and basal cells projecting outwards (Fig. 134, arrowhead), resulting in a strongly conical canal (Fig. 132). Tetrasporangia 70–90 μm long and 20–40 μm broad (n

$= 2$), bisporangia 60–110 μm long and 15–50 μm broad ($n = 6$). Older conceptacles losing their roofs and forming crater-like depressions; the latter gradually filling with new perithallial cells (Fig. 141, arrow), becoming embedded in the thallus. Other conceptacles becoming embedded through superimposition (Fig. 140, arrow). Conceptacles embedded through centripetal growth of peripheral filaments not seen. Gametangia also not seen.

COMMENTS: The presence of (1) patches of coaxial growth in a predominantly noncoaxial hypothallium, (2) flattened (and not domed or flared) epithallial cells, and (3) specialized (thinner-wider) pore cells at the base of canals of multiporate roofs collectively motivate us to transfer *Lithothamnion microsporum* to *Leptophytum*, although information from gametangia, which would confirm the new generic position, is lacking. Foslie (1902, p. 5) distinguished f. *microsporum* by the presence of small tetrasporangial conceptacles that were 'occasionally not raised above the surface of the frond.' He interpreted this feature as a kind of latent growth 'such as now and then to be seen also in other species.' Nonraised multiporate conceptacles were observed in at least two more collections, and therefore this feature appears to be a distinctive character of the species. Dawson's (1960, p. 20; 1961 p. 412, pl. 16) inclusion of *Lithothamnion microsporum* in his Pacific records of *Lithothamnion* (now *Phymatolithon*) *lenormandii* (Areschoug) Foslie caused great confusion in subsequent taxonomic surveys (Adey & Adey 1973, p. 366; Chamberlain & Irvine 1994, p. 227) because the distribution of the cold temperate *P. lenormandii* was erroneously expanded to the warm temperate NE Pacific while the identity of *L. microsporum* was obscured. The specimens described by Dawson as *Lithothamnion lenormandii* grew commonly in the littoral and sublittoral zones, and their distribution ranged from La Jolla, California, to El Salvador (Dawson 1961, p. 412). We have re-examined six Dawson collections (in LAM) referred to *Lithothamnion lenormandii* and have identified material of *L. microsporum* in five of them, the sixth collection (AHFH 70651; Dawson 2537) belonging to a species of *Lithothamnion*. Examination of another Dawson collection referred to *L. lenormandii* (US 35725, Anacapa Island, 40 m depth) by W. Adey (unpublished data) indicated that the plant is also not representative of *P. lenormandii*. No recent records of this species are known from the Pacific coast of North America.

To further support the distinction between *L. microsporum* and *P. lenormandii*, we re-examined slides of bisporangial and tetrasporangial material of *P. lenormandii* from the Swedish west coast (Herb. Suneson, GB). In this material, pore cells of multiporate roofs occasionally stain more darkly near the base of canals (Figs 142–145, arrows), and the dark-staining pore cells may have extra-thick cell walls (Figs 143, 145, arrows) and elongate cell lumens of similar thickness to contiguous roof cells (Figs 142–145, arrows). Although it is possible that different preparation and sectioning techniques could result in different cell shapes, we cannot confirm a single report of thinner pore cells in *P. lenormandii* (see further comments in Athanasiadis & Adey 2003, p. 347), as occurs in *L. microsporum* and other species of *Leptophytum* and *Mesophyllum*. Moreover, in the Scandinavian material of *P. lenormandii*, the external diameter of conceptacles ranged be-

tween 240 and 470 μm (up to 430 μm in British specimens, Chamberlain & Irvine 1994, p. 225) and their height between 40 and 140 μm (10–135 μm in specimens from the Gulf of Maine, Adey 1966, table V). Therefore *L. microsporum* and *P. lenormandii* can be separated by: (1) multiporate conceptacle height (0–80 μm in *L. microsporum* vs 10–140 μm in *P. lenormandii*), (2) multiporate conceptacle external diameter (160–280 μm in *L. microsporum* vs 240–470 μm in *P. lenormandii*), (3) patches of coaxial cells in the hypothallium (recorded in *L. microsporum* only), (4) domed epithallial cells (recorded in *P. lenormandii* only), and (5) presence of thinner-wider pore cells in *L. microsporum* (not seen in *P. lenormandii*). Dawson (1960, p. 20) reported carposporangial conceptacles, c. 300 μm in external diameter, in his Pacific material of '*L. lenormandii*', but we found no gametangia in the LAM collections.

North Pacific records of other species of *Leptophytum*

Leptophytum laeve (Foslie) Adey

On the Pacific coast of America, this species is reported with reservation by Dawson from Baja California [Dawson 1960, p. 18, as '*Lithothamnium laeve* (Strömf.) Fosl.?'; Dawson # 20481 (Neushul), southern Bahía Vizcaino, 37 m depth; Dawson # 20450a (Neushul), Isla Cedros, 18 m depth], and also from Kukak Bay (Alaska) by Saunders (1901, as *Lithothamnion laeve*). The latter material, in TRH, was cited by Adey & Lebednik (1967, p. 52) under *L. tenue*, but it was identified as *Lithothamnion laeve sensu stricto* by Foslie (Lebednik 1974). On the Pacific coast of Asia, *L. laeve* is recorded from the Commander Islands (Selivanova & Zhigadlova 1997, p. 18, 'Fertile . . . June to September, rare, epilithic, intertidal . . .'), Ozernoi Gulf in the Bering Sea (Selivanova 2002, at '7–79 m' depth), and eastern Hokkaido (Adey *et al.* 1976). We did not examine any of these collections, but we have the original data for the Hokkaido specimens (specimens # 100-18, 100-19, 102-9, 103-1B, 103-1B, 103-2A, 103-12A, 103-12B, 104-6A, 104-9A and 105-5, in herb. Adey). According to these data, the few epithallial cells present in the Japanese specimens are 5–5.5 μm long and 7.5–10 μm broad. Perithallial cells are 2–10 μm long and 5–11 μm broad, and the hypothallium is 25–100 μm thick. Roofs of multiporate conceptacles are 250–450 μm in diameter, 100–225 μm high and 40–75 μm thick. Their chambers are 400–550 μm in diameter and 190–250 μm high. Specialized pore cells in multiporate conceptacles are present in most of the specimens. Male conceptacles are 60–120 μm high and have roofs 50–75 μm thick with a central ostiole 25–50 μm in diameter. Their chambers measure 210–290 μm in diameter and are 80–130 μm high. Carposporangial conceptacles are larger and 200–250 μm high. Their roofs are 50–150 μm thick and have a central ostiole 100–160 μm in diameter. Their chambers measure 460–550 μm in diameter and are 180–340 μm high. Gonimoblasts are produced laterally. These data agree with the description of North Atlantic specimens (see Table 1), suggesting that the Hokkaido population belongs to the same morphological species.

DISCUSSION

This is the second of two investigations of types and representative specimens of taxa referred to or associated with *Mesophyllum*, *Leptophytum* and related genera from the Pacific coast of North America (Athanasiadis *et al.* 2004). Table 1 summarizes the vegetative and reproductive characters of the six species of *Leptophytum* we have found in this region (in comparison to *L. laeve* and *P. lenormandii*), and Table 2 presents a dichotomous key using their main macroscopic char-

acters. An emended description of *Leptophytum* was provided above.

Further critical studies of species, especially from the NW Pacific, Central Atlantic–Mediterranean, and the Southern Hemisphere, are needed before we can fully understand the relationships of taxa within the *Synarthrophyton*–*Leptophytum*–*Mesophyllum* complex. The main similarities and differences between these three genera have been pointed out (Athanasiadis *et al.* 2004), and the results of this study clearly support that (1) hypothallial growth (predominantly coaxial vs noncoaxial), (2) carposporangial chamber morphology (dumb-bell-shaped vs more or less elliptical with flattened floor), and (3) spermatangial morphology and development across the chamber floor (simple SMCs only vs predominantly simple with few branched SMCs) are the main diagnostic characters separating members of these genera in the Northern Hemisphere.

Because an understanding of the phylogenetic relationships among melobesoid taxa requires a thorough knowledge of the characters by which the taxa are delimited, we provide a discussion of the major characters within the context of the subfamily below.

Monoecy vs dioecy

Leptophytum tenue and *L. lamellicola* are the only species where sexual reproduction was observed, and both are monoecious in contrast to the generitype *L. laeve*, which is dioecious (Athanasiadis & Adey 2003, p. 345). These three species are the only known members of *Leptophytum* in the Northern Hemisphere to exhibit sexual reproduction, apart from a documented report of mixed phases (tetrasporangial and male conceptacles) in *L. elatum* (Chamberlain 1990, p. 191) and two unverified records of gametophytes in *L. foecundum* (Foslie 1905, p. 21; Rosenvinge 1910, p. 100). Species from the Southern Hemisphere (*L. acervatum*, *L. ferox* and *L. foveatum*) are known to be dioecious, as is usual in species of *Mesophyllum* from the Northern Hemisphere (Chamberlain & Irvine 1994, p. 204; Cabioch & Mendoza 1998; Athanasiadis *et al.* 2004). In *Synarthrophyton*, with the sole exception of dioecious *S. robbenense* Keats & Maneveldt (1997a), the species are either monoecious (Keats & Chamberlain 1997; Keats & Maneveldt 1997a) or both monoecious and dioecious (Townsend 1979, Keats & Chamberlain 1997). The latter condition is also described in a few species of *Mesophyllum* from the Southern Hemisphere (Woelkerling & Harvey 1993; Woelkerling 1996; Chamberlain 2000, pp. 371, 378), although dioecy appears to be more common (Woelkerling & Harvey 1993, p. 576). Assuming that dioecy is the apomorphic (derived) state, acquired independently across the three genera, it would appear that Pacific species of *Leptophytum* have maintained the plesiomorphic condition.

'Shallow' vs 'deep' conceptacle primordia and roof development of gametangial conceptacles

In *Leptophytum tenue* (Fig. 17), development of gametangial conceptacles occurs 3 or 4 cells below the epithallium, as previously described in (asexual and sexual) conceptacle primordia of *L. laeve* and *L. foecundum* (Adey 1966, p. 335, figs 63, 81, 96, '[asexual] conceptacle primordia . . . [derive] typically . . . from the third cell layer', 'the position of the [sex-

ual] conceptacle primordium . . . is the same as in the asexual conceptacles'). In Southern Hemisphere species of the genus, the initials are located closer to or just below the epithallium (Chamberlain & Keats 1994, figs 18, 37, 39), as in *Mesophyllum* (see Lebednik 1978, figs 2, 3, 11; 1974; Athanasiadis *et al.* 2004, figs 14, 81, 86) and *Synarthrophyton* (Harvey *et al.* 1994, fig. 14; Keats & Chamberlain 1997, figs 14, 38), but also in *Lithothamnion* and *Clathromorphum* (see Lebednik 1978, figs 8, 12). At present, this information suggests that 'shallow' gametangial primordia represent the primitive condition in the Melobesioideae, showing a gradation toward slightly deeper primordia in Northern species of *Leptophyllum* and in *Phymatolithon lenormandii* (Adey 1966, p. 335, 'five to seven cells [below the epithallium]'), and with distinctive 'deep' primordia (as the derived condition) occurring in most species of *Phymatolithon* (Lebednik 1978, fig. 8; Adey *et al.* 2001, p. 199, '8–18 cells [below the epithallium]'). The peripheral filaments, which grow centripetally and form the roof in *L. tenue*, bear terminal meristematic cells (Fig. 20), and therefore these filaments should be considered homologous to hypothallial filaments. Similar filaments with terminal meristematic cells have also been recorded in primordia of gametangial conceptacles of species of *Mesophyllum* (Woelkerling & Harvey 1992, fig. 21; 1993, figs 8A, 9 A, 22A, 23A; Athanasiadis *et al.* 2004, fig. 14), *Synarthrophyton* (May & Woelkerling 1988, fig. 32; Woelkerling & Foster 1989, fig. 25; Harvey *et al.* 1994, figs 14, 15), and in the genera *Lithothamnion* and *Phymatolithon* (see Lebednik 1978, figs 8, 9). These observations suggest that peripheral development of roof filaments in gametangial conceptacles is plesiomorphic, having an early origin in the evolution of the Melobesioideae.

Growth form

The entire thallus of *Leptophyllum tenue*, *L. adeyi* and *L. microsporum* adheres strongly to the substrate. This is also the case in *L. foecundum*, except for proliferations (either dorsal or from the margin; Figs 89, 90), which may grow unattached. Strong thallus adhesion in these species is maintained even when material becomes dry, as in herbarium specimens. In contrast, *L. julieae* and *L. lamellicola* grow mainly (*L. julieae*) or partly (*L. lamellicola*) unattached, adhering to the substrate at certain points either centrally or along the thallus periphery. As a result, most herbarium specimens of these two species are unattached (or partly attached to sponges, geniculate coralline algae and other hard substrata). An unattached mode of growth is also recorded in several species of *Mesophyllum* (see Athanasiadis *et al.* 2004), in two Arctic species associated with *Leptophyllum* (Athanasiadis 2001), and in *Synarthrophyton patena* (Hooker f. & Harvey) R. A. Townsend (1979) and *S. schielianum* Woelkerling & M. S. Foster (1989) from the Southern Hemisphere. On the other hand, and with the single exception of *L. adeyi*, thallus superimposition occurs in all NE Pacific species of *Leptophyllum*, as in the NE Pacific species of *Mesophyllum* (Athanasiadis *et al.* 2004). Species of *Mesophyllum* growing with their thallus unattached develop ventral excrescences in the form of new lamellae (Athanasiadis *et al.* 2004), and such outgrowths are also typical for *Leptophyllum julieae* (Fig. 64) and *L. lamellicola*. In *L. lamellicola*, proliferations may also grow dorsally, sometimes back-to-back, forming outgrowths resembling perithallial pro-

tuberances (Figs 30, 31). The present data suggest that similar modes of thallus growth have developed in both congeneric species and in distantly related species, and the latter cases are presently understood as parallelisms, but the events that underlie the development of these similarities are unknown.

Cuticle

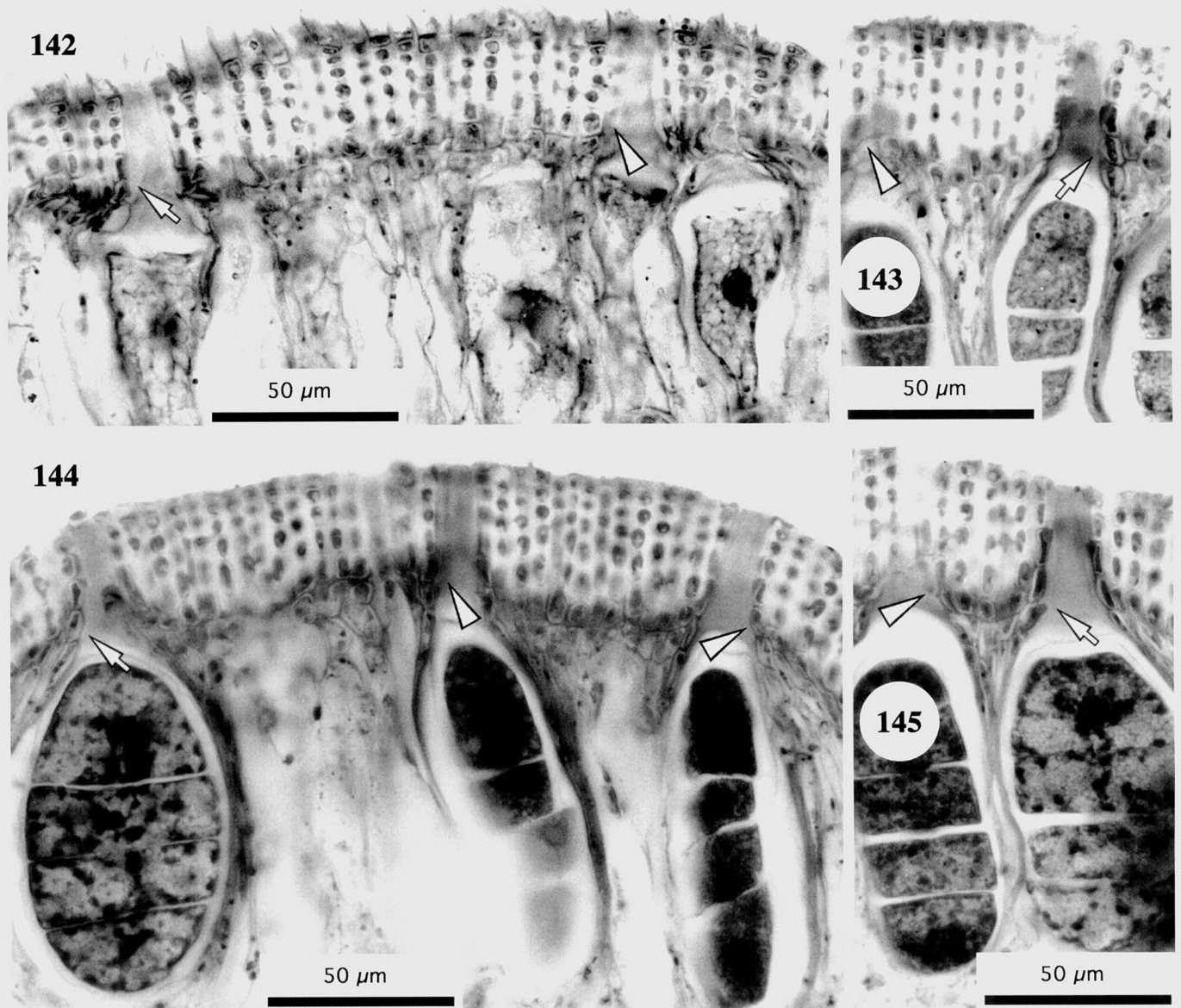
In four of the species, a gelatinous cover protecting the terminal meristematic cells was documented, as previously observed in *Clathromorphum* (Lebednik 1977b), in *Mesophyllum* (Woelkerling & Irvine 1986, fig. 18; Woelkerling & Harvey 1993, fig. 20C; Athanasiadis *et al.* 2004), and in *Synarthrophyton* (May & Woelkerling 1988, fig. 24; Woelkerling & Foster 1989, fig. 17). The terminal meristematic cells of *Leptophyllum adeyi* and *L. microsporum* were not studied, but at least in *L. microsporum* a characteristic whitish border along the thallus margin was observed. The occurrence of a cuticle in several genera of the Melobesioideae suggests that this character is plesiomorphic.

Hypothallium

Leptophyllum julieae (Figs 61–64) and *L. adeyi* (Fig. 112) seem to lack entirely any coaxial growth of the hypothallium, whereas coaxial patches of 2–15 arching cell rows may develop in the other four species. Yet, both the frequency and degree of development (number) of coaxial cell rows is variable in these species, ranging between rare with up to 4 cell rows in *L. tenue* (Figs 4, 10), rare with up to 6 cell rows in *L. foecundum* (Fig. 92), rare with up to 10 cell rows in *L. microsporum* (Figs 130, 135), and regularly present with up to 15 cell rows in *L. lamellicola* (Fig. 36). The variable expression of this character in these four species, along with the lack of any evidence of a coaxial hypothallium in other members of *Leptophyllum*, indicates that the development of coaxial patches should be regarded as a secondary (later) event in the evolution of certain members of the genus, analogous to what has been reported in two species of *Synarthrophyton* [i.e. *S. patena* (Townsend 1979, fig. 7; May & Woelkerling 1988, figs 24, 25) and *S. munimentum* Keats & Maneveldt (1997a, fig. 38)] and in one species of *Lithothamnion* (Keats *et al.* 2000, p. 388, fig. 4). On the other hand, development of coaxial patches in certain species of *Mesophyllum* from the Southern Hemisphere could be an early condition in the expression of a predominantly coaxial hypothallium, which is generally present in members of that genus from the Northern Hemisphere (Athanasiadis 2001, table 1; Cabioch & Mendoza 2003; Athanasiadis *et al.* 2004, p. 162). The taxonomic significance of the development of coaxial patches, either as an independent character or as a character state in the expression of a predominantly coaxial hypothallium, remains to be assessed cladistically.

Perithallium

Patches of coaxial growth in the perithallium (resulting in local stratification) were occasionally seen in *Leptophyllum lamellicola* (Fig. 39), *L. julieae* (Figs 63, 64) and *L. foecundum* (Fig. 95), whereas in the other three species, perithallial growth commonly occurs via asynchronous divisions and elongations of the subepithallial meristematic cells (resulting



Figs. 142–145. *Phymatolithon lenormandii*. TSs of multiporate roofs of tetrasporangial conceptacles of specimens from the Swedish west coast (Suneson slides # 583 a, in GB). Pore cells bordering canals either normal roof cells (arrowheads) or darkly staining cells (arrows), the latter occasionally elongate (Fig. 145) with extra-thick cell walls (Figs. 143, 145).

in nonstratified layers; Figs 10, 112, 135). Moreover, the subepithallial meristematic cells of *L. julieae* are distinctively elongate-ovate (Fig. 66), and those of *L. lamellicola* elongate only during division (Fig. 39) whereas those of *L. tenue* (Fig. 5), *L. foecundum* (Figs 93, 94), *L. adeyi* (Fig. 114) and *L. microsporum* (Fig. 131) are more or less isodiametric and similar to or smaller in size than cells below, as in the other species of *Leptophytum* (Adey 1966, Chamberlain 1990, Chamberlain & Keats 1994). Previous studies indicate that: (1) this character also divides the genus *Mesophyllum* (most species of which exhibit elongate initials; see Athanasiadis 2001, table 2), and (2) Arctic and subarctic species of *Leptophytum* exhibit generally short subepithallial meristematic cells. Perithallial protuberances are absent in all NE Pacific species, and such outgrowths are generally unknown in *Leptophytum*, with the single exception of the Southern Hemi-

sphere species *L. ferox* (Chamberlain & Keats 1994, p. 122). Outgrowths resulting from conceptacle embedment (Fig. 107) or back-to-back growth of dorsal lamellae (Figs 30, 31) may occur, but these structures involve hypothallial filaments and are certainly not homologous to perithallial protuberances.

Epithallium

In all species, i.e. in *Leptophytum tenue* (Fig. 5), *L. lamellicola* (Figs 38, 39), *L. julieae* (Figs 66, 67), *L. foecundum* (Figs 93, 94), *L. adeyi* (Figs 114, 115) and *L. microsporum* (Fig. 131), the epithallium is composed of 1 or 2 cells (rarely 3 in *L. lamellicola*). Moreover, the epithallial cells of the somatic thallus in all species are generally flattened (in TS) and wider than cells below and therefore can be readily distinguished from the subepithallial meristematic or other perithallial cells.

Flattened epithallial cells represent the most common type reported in *Leptophytum*, and their outer morphology probably accounts for the 'Leptophytum-type' surface that is commonly described in species of the genus (see Chamberlain & Irvine 1994, p. 165). Flattened to more or less domed epithallial cells have been recorded in a few species, i.e. in *L. bornetii* (Chamberlain 1990, p. 185), *L. ferox* (Chamberlain & Keats 1994, p. 122), and *L. elatum* (Chamberlain 1990, p. 192, fig. 25, table 1). Because the epithallium is often missing in the genus *Leptophytum*, due to sloughing (Fig. 39), most of the observed epithallial cells are probably newly formed (from the subepithallial meristematic cells) and do not belong to the original epithallium. 'Flared-like' epithallial cells, as previously seen in herbarium specimens of some Pacific species of *Mesophyllum* (Athanasiadis *et al.* 2004, figs 43, 46, 100, 130), were not observed in the present study.

Degenerate (shed) vs embedded conceptacles

In *Leptophytum tenue*, *L. adeyi* and *L. microsporum*, older conceptacles of all types gradually degenerate whereas in *L. foecundum*, *L. lamellicola* and *L. julieae* both shed and embedded multiporate conceptacles have been recorded. Embedded gametangial conceptacles were not seen in any of the species, and this condition apparently holds for all members of *Leptophytum*, where embedded conceptacles were previously observed only in one population of *L. acervatum* tetrasporophytes (Chamberlain & Keats 1994, p. 115, fig. 27). On the other hand, degenerate (shed) conceptacles have been reported in all well-studied species (Chamberlain 1990, Chamberlain & Keats 1994, Athanasiadis & Adey 2003), suggesting that this character could be a synapomorphy for members of *Leptophytum*. It needs to be emphasized that embedded conceptacles here refer to overgrowth by peripheral filaments (Fig. 105) or further growth of the roof filaments (Figs 78, 80). Embedded conceptacles that result 'passively' through thallus superimposition probably occur in all species exhibiting this mode of thallus growth, here documented only for *L. microsporum* (Fig. 140).

Pore cells of multiporate conceptacles

In all species, except *Leptophytum tenue*, pore cells bordering the base of multiporate roof canals are specialized. These cells differ from contiguous roof cells in staining more darkly and in being generally thinner-wider, tending to encircle the canal (*L. lamellicola*, Figs 44–48; *L. julieae*, Figs 73–75; *L. foecundum*, Figs 100–104; *L. adeyi*, Fig. 120; and *L. microsporum*, Figs 137–139). Moreover, in *L. foecundum*, thinner-wider pore cells occur even around the upper part of the canal, including the rosette cells (Fig. 99; as seen occasionally in *L. tenue*, Fig. 14) whereas in *L. lamellicola* (Fig. 47), *L. julieae* (Figs 74, 75), *L. foecundum* (Figs 102, 103, black arrowheads) and *L. microsporum* (Figs 134, 139, white arrows) the subbasal pore cells are elongate. Specialized pore cells are currently known in six (of the 12 well-studied) species of *Leptophytum*, and in the majority of species of *Mesophyllum* (Athanasiadis 2001, table 2; Athanasiadis *et al.* 2004), but have not been recorded in *Synarthrophyton* or other melobesoid genera (Athanasiadis 2001, table 2; but see Comments under *L. microsporum*).

Several distinct morphological types of pore cells have been

described (Keats & Maneveldt 1997b, table 1; Athanasiadis 2001, p. 109; Athanasiadis *et al.* 2004), and two of them are readily recognized in the Pacific species of *Leptophytum*: (1) pore cells with thinner-wider cell lumen, and (2) pore filaments having elongate subbasal cells. A third type, known as 'larger' pore cells, was previously described in *L. foecundum* (Düwel & Wegeberg 1996, p. 478), *Lithothamnion tenue* Rosenvinge (Düwel & Wegeberg 1996, p. 478), and *Mesophyllum aleuticum* (Athanasiadis 2001, p. 109). The present study indicates that in *L. foecundum* this is presumably based on observations of sections that expose the greater length or width of specialized pore cells (Figs 85, 103; see also Comments under *L. foecundum*) whereas in the recently described *M. aleuticum* Lebednik it is due to observations of pore cells including their extra-thick cell walls (Athanasiadis *et al.* 2004, fig. 13). Similar 'larger' pore cells, as a result of extra-thick cell walls, are shown here in *Phymatolithon lenormandii* (Figs 143, 145, arrows).

Type (2) is here recorded in certain species that simultaneously display type (1), and therefore these two morphologies should definitely be considered as two independent characters. Because both types are recorded in species of *Leptophytum* (present account) and *Mesophyllum* [Keats & Maneveldt 1997b, table 1, as regards type (2); Athanasiadis *et al.* 2004, as regards type (1)], they may have had independent origins in these two genera and are of possible diagnostic value in distinguishing groups of species within each genus.

Spermatangial structures

In both *Leptophytum tenue* (Figs 18, 19) and *L. lamellicola* (Figs 51–55), SMCs are predominantly simple and occur all over the chamber together with a few branched SMCs that are restricted either to the centre or other places on the chamber floor. Lunate SMCs (in TS) have been observed on the floor of the latter species (Fig. 55). This distinctive cell shape is currently described in several species of *Mesophyllum* [Chamberlain (2000, fig. 31); Athanasiadis *et al.* (2004, figs 48, 83, 111)], including the generitype *M. lichenoides* (Athanasiadis, unpublished data; material from North Jersey, Giffard Bay, Y. M. Chamberlain No 84/382, in GB), and in the generitype of *Leptophytum* (Athanasiadis & Adey 2003, fig. 19), suggesting that this character might be a synapomorphy for these two genera. It has been suggested that the lunate shape characterizes early stages of fertility in SMCs (Athanasiadis *et al.* 2004, p. 163) and probably results when several spermatangia are successively produced from the upper part of individual SMCs. Lunate SMCs have not been observed in *Synarthrophyton*, which exhibits branched SMCs on the chamber floor, despite thorough studies of early ontogenetic stages of male conceptacles in the generitype *S. patena* (Harvey *et al.* 1994, figs 16, 17). This suggests that the lunate shape is a distinctive feature of simple SMCs only.

The distinction made between SMCs occurring on the walls (and the roof) and those on the floor (Verheij 1992, table 1; Chamberlain & Irvine 1994: 159–162; Chamberlain & Keats 1994, table 2; Adey *et al.* 2001: 201; Athanasiadis 2001, table 2) is significant because the former derive from the peripheral (hypothallial) filaments that form the roof (Lebednik 1978: 389, figs 8–11) whereas the latter occur on normal perithallial filaments. In *Mesophyllum* and *Leptophytum*, SMCs on the

Table 1. Comparative data for the six NE Pacific species of *Leptophyllum* recognized in this study and for N. Atlantic *Leptophyllum laeve*, *Leptophyllum foecundum* var. *foecundum*, and *Phymatolithon lenormandi*. Additional data for Pacific species from ^aLebednik (1974) and ^bSteneck & Paine (1986) and for Atlantic species from ^cChamberlain (1990), ^dAdey (1966), ^eChamberlain & Irvine (1994), ^fWegeberg & Pueschel (2002), ^gAthanasiadis & Adey (2003), and ^hpresent study. Abbreviations: ND (no data), TS (transverse section). Unless specified, all measurements in micrometers.

Characters/taxa	<i>L. foecundum</i> var. <i>sandrae</i> [var. <i>foecundum</i>] ^{dh}						<i>Phymatolithon lenormandi</i> ^{deh}
	<i>L. tenue</i>	<i>L. lamellicola</i>	<i>L. juliae</i>	<i>L. aleyi</i>	<i>L. laeve</i> ^{deg}	<i>L. microsporum</i>	
Distribution	Port Clarence, Alaska	S. California, Vancouver I.	Vancouver I., Queen Charl. I.	Tatoosh I., NE Pacific	N. Atlantic, N. Pacific (?)	S. California, Baja California	N. Atlantic
Habitat	Sublittoral	Littoral and sublittoral	Littoral and sublittoral	Littoral pools in cave	Littoral and sublittoral	Littoral and sublittoral	Littoral and sublittoral
Substratum	On shells, epilithic	Epilithic, epilithic (corallines)	Epilithic, epilithic (corallines)	Epilithic (pebble)	Epilithic, epizoic	Epilithic, epilithic (corallines)	Epilithic, epiphytic (corallines)
Morphology							
Thallus growth and adhesion	Encrusting, closely adherent	Encrusting to foliose (unatt.)	Encrusting to foliose (unatt.)	Encrusting, closely adherent	Encrusting, closely adherent	Encrusting, closely adherent	Encrusting, closely adherent
Thallus diameter	Up to 3 cm	Up to 6 cm	Up to 6 cm	Up to 6 cm	Up to 5 cm	Up to 3.3 cm	Up to 8 cm ^e
Ventral outgrowths	–	+	+	–	–	–	–
Superimp. growth	+	+	+	–	–	+	+
Anatomy of the vegetative thallus							
Lamella thickness	85–200 (210 ^h)	100–2500	100–800	350–500 (688 ^b)	80–650	50–470	40–210 ^d (250 ^e)
Coax. arch. hyp.	Patches	Patches	–	Patches	–	Patches	–
Hypothall. thick.	70–130	150–800	150–300	20–140 [18 ^d –80]	14–110	15–100	14–75 ^d (100 ^e)
Perithall. thickness	50–120	150–1200	60–500	60–200 [up to 940]	50–140	25–370	ND
Stratified perith.	–	±	±	±	–	–	–
Elongate subep. in.	–	± ²	+	–	–	–	–
Terminal trich.	± ³	–	–	–	–	–	–
Hypothallial cells							
Length	12–46	10–43	16–45	15–28	8–44	12–26	8–28 ^e
Breadth	5–10 (12 ^{ai})	5–11	5–12	5–14	3.5–14.5	5–10	3–12 ^e
Perithallial cells							
Length	4–23	3–20	10–30	5–12	1.5–24	5–12	1.5–12 ^e
Breadth	3–10 (11 ^a)	3–10	4–8	(4.6 ^b) 8–12	3.5–15	4–8	2–10 ^e
Epithallium							
Number of cells	1 (2 ^a)	1–3	1–2	1–2	1–2	1–2	1 (2 ^f)
Length × breadth	2.5 × 6–10	2.5 × 4–9	2.3 × 5–12	0.6 ^b –3 × 6 ^b –10	3.9 × 6–15	2.5 × 4–7	ND
Shape (TS)	Flattened	Flattened	Flattened	Flattened	Flattened	Flattened	Domed ^{e,f} to flattened ^f
Multiporate conceptacles							
External diameter	(300 ^l) 350–720	320–680	200–770	350–400 (495 ^b)	500–1000	160–280	240–470
External height	140–270	60–200	100–280	0–270	90–270	0–80	10–135 ^d
Chamber diameter	250–500	250–530	260–500	220–500 [208 ^c –450]	312–700	110–220	122–267 ^d (333 ^c)
Chamber height	90–150	100–240	110–210	140–250 [125 ^d –200]	98–370	70–110	65 ^e –138 ^u
Convex roof	+	+	+	–	+	+	+
Flattened roof	+	+	–	+	+	+	+
Concave roof	–	–	–	–	–	±	+
Roof/pore pl. th.	40–60 (80 ^l)	30–65	30–55	(33 ^b) 55–60	45–150	15–40	18 ^d –60 ^e

Table 1. Continued.

Characters/taxa	<i>L. tenue</i>	<i>L. lamellicola</i>	<i>L. julieae</i>	<i>L. foecundum</i> var. <i>sandrae</i> [var. <i>foecundum</i>] ¹	<i>L. adeyi</i>	<i>L. laevig²deg</i>	<i>L. microsporum</i>	<i>Phymatolithon</i> <i>lenormandii</i> ³
Roof/pore pl. cells	6-8	5-7	4-8	5-7	5-6 ($\geq 4^4$)	6-8	4-5	c, 6 ^c
Pore plate diam.	250-480	240-370	200-580	150-360 [130-220]	180-230	270-550	70-170	80-210 ^d
Number of pores	73-83 (85 ¹)	47-102	30-105	19-76 [27-62 ⁵]	22-47	28-150	10-40	6-34 ^d (60 ^e)
Con. canal/diam.	-/7-13	+10-14	+12-17	+7-18 [8-15]	+7-20	-/12-19	+5-20	ND
Embedded concept.	-	+	+	+	-	-	-	-
Shedding concept.	+	+	+	+	+	+	+	+
Peripheral rim	-	-	-	\pm [+]	-	-	\pm	\pm e
Bordering pore cells								
Rosette cells/spec.	(5 ¹) 6-8 \pm 5	6-8/-	4-8/-	5-8/+	7-9/-	6-8/-	5-7/-	ND/-
Cells per filament	5-7	5-6	4-6	5-7	ND	6-8	4-5	4-6
Similar to cont.	+	+	+	-	+	+	+	+ ^e
Elong. subbas. cs	-	+	+	+	ND	-	+	\pm h
Thinner-wider	-	+	+	+	+	+	+	-
Tetrasporangia								
Length	100-130 ¹	100-170	ND	ND [120-185]	70-105	160-225	70-90	70-109 ^e
Breadth	30-35	20-75	ND	ND [45]	40-60	75-135	20-40	26-65 ^e
Bisporangia								
Length	140	ND	95-180	100-160 [170-190]	ND	100-240	60-110	47-114 ^e
Breadth	25	ND	20-80	20-80 [60-70]	ND	20-140	15-50	31-57 ^e
Male conceptacles								
External diameter	200-500	270-560	ND	ND	ND	240-420	ND	400 ^e
External height	80-140	40-170	ND	ND	ND	90-225	ND	113-160 ^d
Chamber diameter	120-260	170-460	ND	ND	ND	150-400	ND	136-210 ^d
Chamber height	40-90	70-200	ND	ND	ND	64-225	ND	65-122 ^d
Roof thickness	50-100	40-180	ND	ND	ND	35-100	ND	24 ^d -73 ^e
Ostiole diameter	30-60	20-100	ND	ND	ND	22-130	ND	16-32 ^d
Bran. SMCs-floor	+	+	+	+	+	+	+	+
Bran. SMCs-roof	-	-	ND	ND	ND	-	ND	+
Simple SMCs-floor	+	+	ND	ND	ND	+	ND	+
Simple SMCs-roof	+	+	ND	ND	ND	+	ND	+
SMCs lunate	ND	+	ND	ND	ND	+	ND	+
Carposporangial conceptacles								
External diameter	300-500 (551 ²)	430-700	ND	ND	ND	800-850	ND	430 ^e
External height	100-220	130-240	ND	ND	ND	165-400	ND	113-160 ^d
Chamber diameter	270-450	250-560	ND	ND	ND	340-650	ND	97-291 ^e
Chamber height	40-150	80-250	ND	ND	ND	100-370	ND	76 ^e -160 ^d
Roof thickness	70-130	30-120	ND	ND	ND	75-300	ND	52-78 ^e
Ostiole diameter	30-130	35-100	ND	ND	ND	51-170	ND	16-40 ^d
Peripheral carposp.	ND ¹	+	ND	ND	ND	+	ND	-
Floor flattened	+	+	ND	ND	ND	+	ND	+

¹ In UC 739472.

² Elongate during cell division.

³ On the roof of conceptacles.

⁴ After the protologue (Fig. 117), but the sporangial length (up to 105 μ m) indicates the presence of higher chambers.

⁵ A few rosette cells thinner-wider than other rosette cells.

⁶ Suneson (1943, pl. 7, fig. 34).

Table 2. Dichotomous key to the six NE Pacific species of *Leptophytum*.

1. Thallus adhering to the substrate at a few points and growing partly or mainly free	2
1. Thallus adhering closely to the substrate (the margins may grow free in <i>Leptophytum foecundum</i>)	3
2. Hypothallium with regular patches of coaxial cells. Subepithallial cells elongate during putative divisions. Gametangial and tetrasporangial thalli recorded	<i>Leptophytum lamellicola</i>
2. Hypothallium noncoaxial. Subepithallial cells distinctively elongate-ovate in shape. Only bisporangial thalli recorded	<i>Leptophytum juliae</i>
3. Hypothallium with occasional patches of coaxial cells. Roof of multiporate conceptacles flattened to sunken, usually provided with a peripheral rim. Embedded conceptacles present	<i>Leptophytum foecundum</i>
3. Hypothallium noncoaxial or with occasional patches of coaxial cells. Roof of multiporate conceptacles generally convex or flattened (or slightly sunken in <i>Leptophytum microsporum</i>). Embedded conceptacles absent	4
4. Thallus lacking superimposition. Hypothallium noncoaxial	<i>Leptophytum adeyi</i>
4. Thallus superimposition. Hypothallium with occasional patches of coaxial cells	5
5. Multiporate conceptacles up to 280 μ m in external diameter, flush with the surface or slightly raised, lacking a peripheral constriction	<i>Leptophytum microsporum</i>
5. Multiporate conceptacles up to 720 μ m in external diameter, distinctively raised and provided with a peripheral constriction	<i>Leptophytum tenue</i>

roof and the walls are elongate single cells that cut off spermatangia from the entire (elongate) side that faces the interior of the chamber (Athanasiadis *et al.* 2004, figs 49, 85, 111; Fig. 52). In *Synarthrophyton*, both simple and branched SMCs have been reported on the roof (e.g. Harvey *et al.* 1994, fig. 24), and the simple ones have been illustrated either as elongate cells (May & Woelkerling 1988, fig. 37) or as isodiametric cells (Keats & Chamberlain 1997, fig. 41; Keats & Maneveldt 1997a, figs 14, 41). At present, this information suggests a gradation in the expression of simple to branched SMCs on the roof of species of *Synarthrophyton*, and limits the taxonomic value of this character in this genus to the level of species.

A 'protective' cell layer covering the SMC initials is reported in *Mesophyllum* (Suneson 1937, fig. 40B; Suneson 1943, p. 56, 'columnar spermatangium mother-cells'; Lebednik 1978, figs 2–5; Woelkerling & Harvey 1992, fig. 23; Chamberlain & Keats 1995, fig. 20; Keats & Chamberlain 1997, table 4), *Leptophytum* (Adey 1966, figs 82, 88, 89; Lebednik 1978, p. 392; Athanasiadis & Adey 2003, fig. 18), and *Synarthrophyton* (Harvey *et al.* 1994, figs 16–18; Keats & Chamberlain 1997, figs 11, 39), indicating that this character could be a synapomorphy for the entire complex.

Overall, the present studies indicate that the type of SMCs on the chamber floor is a diagnostic generic character within the *Synarthrophyton*–*Leptophytum*–*Mesophyllum* complex. In *Synarthrophyton*, only branched SMCs have been recorded whereas in *Leptophytum* simple SMCs predominate over branched SMCs, which may occur in the centre or other places on the chamber floor. In *Mesophyllum*, only simple SMCs are recorded so far, apart from a single report of a few branched SMCs in Australian specimens referred to *Mesophyllum macroblastum* (Foslie) Adey (Woelkerling 1996, p. 201; Keats & Maneveldt 1997a, p. 465). As Woelkerling & Harvey (1993, figs 20A & C, 23C) and Woelkerling (1996) also described and illustrated a noncoaxial (to coaxial) hypothallium and flattened carposporangial floors in Australian material of this species, these characters collectively support this species belonging to *Leptophytum*. Whether these Australian specimens are conspecific with the poorly known *M. macroblastum*, which

was originally described from the Mediterranean, remains to be determined.

Carposporophytes

In both *Leptophytum tenue* (Figs 21, 25) and *L. lamellicola* (Figs 56–58), where carposporophytes were found, carposporangia were recorded at the periphery of the central fertile zone, which remained more or less flattened. Peripheral development of carposporangia is apparently recorded in all members of the Melobesioideae, except in most members of *Lithothamnion* and *Phymatolithon* (Lebednik 1977a, table 4; Chamberlain & Keats 1994, table 2; Athanasiadis 2001, table 2). On the other hand, within the *Synarthrophyton*–*Leptophytum*–*Mesophyllum* complex, a flattened floor in carposporangial conceptacles is consistently recorded only in members of *Leptophytum* (Adey 1966, pl. VIII fig. 40; Chamberlain & Keats 1994, figs 17, 38, 65; Athanasiadis & Adey 2003; Figs 21, 25, 56–58), in most members of *Synarthrophyton* (Townsend 1979, figs 11, 15; May & Woelkerling 1988, fig. 34; Woelkerling & Foster 1989, figs 32, 33; Keats & Chamberlain 1997, figs 12, 17, 18, 25, 44; Keats & Maneveldt 1997a, fig. 19), and in a few species of *Mesophyllum* from the Southern Hemisphere [i.e. *M. engelhartii* (Foslie) Adey (Woelkerling & Harvey 1993, fig. 10C; Chamberlain & Keats 1995, figs 24, 25), *M. macroblastum* (Woelkerling & Harvey 1993, fig. 23C) and *M. erubescens* (Foslie) Lemoine (Keats & Chamberlain 1994, figs 24, 25)]. In contrast, species of *Mesophyllum* from the Northern Hemisphere generally display a centrally raised carposporangial floor, resulting in a dumbbell-shaped chamber. This distinctive chamber shape is formed 'through dissolution of the peripheral part of the carposporophyte and decalcification of the perithallial cells below to make space for the carposporangia' (Athanasiadis *et al.* 2004, p. 163). As this differentiation appears to be of diagnostic value in distinguishing species of *Mesophyllum* in the Northern Hemisphere, we look forward to re-examining the Southern Hemisphere species of this complex, where the few deviations have been reported.

EPILOGUE

We would be remiss not to comment on the recent paper by Woelkerling *et al.* (2002), which remains influential (see e.g. Compère 2004).

The work of Woelkerling *et al.* can be divided in two parts: the first attempts a revision of the taxonomic literature on the Melobesioideae and in particular the generic status of *Leptophytum*, whereas the second part examines two specimens considered to be the epitype of *Leptophytum* (*Lithophyllum*) *laeve* and the lectotype of *Phymatolithon* (*Melobesia*) *lenormandii*, respectively. There are problems with both parts. The taxonomic revision is flawed because Woelkerling *et al.* establish their arguments based on a few exceptions rather than the main body of data published in international peer-reviewed journals (Lebednik 1977a, 1978; Verheij 1992, table 1; Chamberlain & Irvine 1994; Chamberlain & Keats 1994, table 2; Adey *et al.* 2001; Athanasiadis 2001, table 2). Indeed, the papers of Lebednik, Verheij and Athanasiadis are not even cited.

Some of the exceptions Woelkerling *et al.* focus on follow: (1) In the discussion of branching of spermatangial filaments, they ignore the distinction made by most authors between structures occurring on the chamber floor and structures occurring on the chamber walls and roof [as illustrated by Lebednik (1978, figs 8–12), and later recognized by Verheij (1992, table 1), Chamberlain & Keats (1994, table 2), Chamberlain & Irvine (1994, pp. 159–162), Adey *et al.* (2001, p. 201), and Athanasiadis (2001, table 2)]. The taxonomic value of this distinction is also consistent with the results of our recent studies on *Mesophyllum* (Athanasiadis *et al.* 2004) and *Leptophytum* (present account). (2) In the discussion of the site of gonimoblast filament development, they also limit their data to a few exceptions rather than using evidence provided by Lebednik (1977a, table 4), Chamberlain & Keats (1994, table 2), and Mendoza & Cabioch (1998). The observations of these latter authors are also supported in the reviews of Adey *et al.* (2001, p. 198) and Athanasiadis (2001, table 2) and are consistent with our recent studies on *Mesophyllum* (Athanasiadis *et al.* 2004, p. 163) and *Leptophytum* (present account). (3) Discreditation of the taxonomic value of staining of cells lining pore canals and shape of cells lining pore canals (Woelkerling *et al.* 2002, pp. 600–602) is unsustainable in light of our recent studies on *Mesophyllum* (Athanasiadis *et al.* 2004, p. 162) and *Leptophytum* (present account), which confirm the common presence of such specialized cells only in species of *Leptophytum* and *Mesophyllum*, as previously pointed out by Chamberlain & Irvine (1994, p. 159), Keats & Maneveldt (1997b, p. 204), Chamberlain (2000, p. 373), Adey *et al.* (2001), and Athanasiadis (1999, p. 241; 2001, table 2).

Problems also exist with the specimens Woelkerling *et al.* cite as the epitype of *Lithophyllum laeve* Strömfelt in C and the lectotype of *Melobesia lenormandii* Areschoug in LD. The former, identified by them as 'Specimen EY9201-02', as we have pointed out above in Observations under NOMENCLATURE, has no nomenclatural status, because the epitypification by Düwel & Wegeberg (1996) is noneffective, the epitype being a collection rather than a specimen as required by Art. 9.7, and Art. 9.14 strictly prohibiting correction of such mistakes for epitypes. Hence, the observations of Woelkerling *et al.* on that specimen have only taxonomic value and concern *Phy-*

matolithon lenormandii, the species to which that specimen belongs, and not *Leptophytum laeve*.

Nonetheless, we tried to locate the 'epitype' specimen EY9201-02. It took more than a year to obtain the material from the Botanical Museum in Copenhagen (C) as the 'epitype' was still on loan to Woelkerling. The loan consisted of 4 specimens, labelled EY9201-01, EY9201-06, EY9201-12, and EY9201-18. Through further examination of the material and communication with the algal keeper at C, we determined that the missing specimen EY9201-02 [illustrated by Düwel & Wegeberg (1996, fig. 5) and cited by Woelkerling *et al.* (2002, figs 1, 2, 8–10)] is currently labelled EY9201-01. Because no annotations have been made on the material examined by Woelkerling *et al.* and no examined parts of the specimen(s) are included in the 'epitype' collection, the source of the observations of Woelkerling *et al.* remains unknown.

The situation of their 'lectotype' of *Phymatolithon* (*Melobesia*) *lenormandii* is even more confusing, because the specimen they list, 'LD 50674', was collected at Cherbourg in February 1854 (see Düwel & Wegeberg 1996, p. 476, fig. 2) whereas the true lectotype of *M. lenormandii* (selected by Woelkerling) is LD 50673 (Chamberlain & Irvine 1994, p. 224) and originates from Arromanches. As shown by Düwel & Wegeberg (1996, p. 476, fig. 2), the lectotype of *M. lenormandii* is indeed a collection of 3 specimens, and whether the source of information for Woelkerling *et al.* was one of these 3 elements, or just the single specimen LD 50674, is unknown. We also do not know why the lectotype of *Melobesia lenormandii* was selected amongst collections in the Botanical Museum at Lund (LD) and not from Areschoug's herbarium at the Riksherbarium in Stockholm (S).

Nevertheless, we have taken seriously the reports of Woelkerling *et al.* of 'thinner-wider' pore cells in *P. lenormandii* and tried to confirm this character by re-examining a series of slides of material from the Swedish west coast (Figs 142–145). As we discussed above (see Comments under *L. microsporum*), no evidence of 'thinner' pore cells could be established in this species, and no such cells have so far been reported in any other member of *Phymatolithon* (Adey *et al.* 2001, p. 198), which indicates that this character, even if present in *P. lenormandii*, should be regarded as an autapomorphy. On the other hand, we observed the rare presence of darkly staining (and elongate subbasal) pore cells in this species (Figs 143–145, arrows), but because no similar pore cells have been described in any other member of *Phymatolithon*, we consider this character to be a homoplasy and not homologous with the commonly occurring specialized cells in several species of *Leptophytum* and *Mesophyllum*.

For additional comments, see Athanasiadis & Adey (2003, pp. 347–350).

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