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

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We have re-examined the types and representative collections of taxa previously associated with or closely related to the genus *Mesophyllum* in the NE Pacific. The following five species are distributed between the Aleutian Islands and southern California (La Jolla): *M. aleuticum* Lebednik, *sp. nov.*, *M. vancouveriense* (including *Lithothamnion phymatodeum* f. *aquilonium*), *M. conchatum, M. lamellatum* and *M. crassiusculum* (Foslie) Lebednik, *comb. nov.* (including *Lithothamnion aculeiferum*). All species exhibit a predominantly coaxial arching hypothallium, superimposing growth of new lamellae, a cuticle that covers the terminal meristem, raised conceptacles, and simple (unbranched) spermatangial structures. The five species differ in the following characters: (1) growth form (*M. lamellatum* and *M. conchatum* occur mainly epiphytically with the larger part of their thallus unattached, whereas the other species grow mainly attached, adhering strongly to the substrate); (2) perithallial stratification (not seen in *M. lamellatum*); (3) size of subepithallial meristematic cells (distinctly longer than cells below in *M. conchatum, M. lamellatum* and *M. crassiusculum*); (4) epithallial cell shape (roundish to squarish in *M. lamellatum* and *M. conchatum*, but generally flattened in the other three species); (5) perithallial protuberances (present in *M. vancouveriense* and *M. crassiusculum*); (6) degenerating conceptacles (in *M. aleuticum, M. conchatum* and *M. lamellatum*); (7) embedded conceptacles (in *M. vancouveriense, M. crassiusculum* and *M. conchatum*); and (8) the pore cell morphology of multiporate conceptacles. In addition, we have observed dumbbell-shaped carposporangial chambers displaying peripheral development of carposporangia in four of the species and lunate (in transverse section) spermatangial mother cells in *M. vancouveriense, M. conchatum* and *M. lamellatum*; we suggest that these distinctive morphologies may be new characters in the taxonomy of the genus. Each species is formally described and its features are illustrated, tabulated and discussed. A dichotomous key is given, and we emphasize the need for further examinations to establish the reproductive structures of gametangial plants of *M. crassiusculum*, and the distribution of this species and *M. lamellatum*.

INTRODUCTION

The first records of crustose coralline algae from the NE Pacific are those made by Dickie (1868) and Farlow (1875, 1877), who reported a total of four nongeniculate species [*Melobesia verrucata* Lamouroux, *M. membranacea* (Esper) Lamouroux, *M. farinosa* Lamouroux and *M. pustulata* Lamouroux], none of which is currently recognized to occur on this part of the American coast (Scagel *et al.* 1989). Kjellman (1889) and later Foslie (1897, 1901, 1902, 1903, 1906b) described the first local species from Alaska, British Columbia and California, and their accounts included the first species later recognized to be members of the genus *Mesophyllum* Lemoine (Adey 1970; Lebednik 1974; Steneck & Paine 1986). In his revision of several coralline genera, Adey (1970) referred fifty species to the genus *Mesophyllum*, two of which, *M. conchatum* (Setchell & Foslie) Adey and *M. lamellatum* (Setchell & Foslie) Adey, were originally described from California. In his thesis and later publications, Lebednik (1974, 1977a, 1978) recognized a new species of *Mesophyllum* from the Aleutian Islands and also transferred several other species to this genus, but did so without validating the new names or combinations. A third species, *M. vancouveriense* (Foslie) Steneck & Paine (Steneck & Paine 1986) from Washington

and British Columbia, was identified after clarifying a misconception of type elements.

In this paper, after studying the types and representative collections of all NE Pacific taxa referred to *Mesophyllum* by the above authors, we recognize five species in this region. We formally describe *M. aleuticum* Lebednik, *sp. nov.* and transfer one more species to the genus: *M. crassiusculum* (Foslie) Lebednik, *comb. nov.* Our work is part of a revision of the genus *Mesophyllum* that currently accommodates more than 60 species worldwide.

The generitype *M. lichenoides* (Ellis) Lemoine (Lemoine 1928), known from the Mediterranean and the NE Atlantic, has been described by Suneson (1937), Cabioch (1972), Adey & Adey (1973), Woelkerling & Irvine (1986), Woelkerling & Harvey (1993, figs 17, 18) and Chamberlain & Irvine (1994). Descriptions of three other European species are given by Woelkerling & Harvey (1993, figs 30, 31), Cabioch & Mendoza (1998) and Athanasiadis (1999). The Caribbean and SW Atlantic species are imperfectly known and information is largely confined to original papers (Adey 1970; Mendoza 1977; Athanasiadis 1999) and floras (e.g. Littler & Littler 2000). Species from South Africa have been studied by Keats & Chamberlain (1994), Keats & Maneveldt (1997b) and Chamberlain (2000). Some information of the remaining Indian Ocean species appears in the bibliographic account of Silva *et al.* (1996). In southern Australia, the genus *Meso-*

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phyllum has been studied by Woelkerling & Harvey (1993) and Woelkerling (1996). Pacific species from the tropics remain imperfectly known (Adey *et al.* 1982; Verheij 1993; Keats & Chamberlain 1997, p. 73; Payri *et al.* 2000), whereas records from the temperate Pacific coast of South America are summarized by Ramírez & Santelices (1991). Two Arctic species formerly placed in *Mesophyllum* have recently been examined, and a possible affiliation with the genus *Leptophytum* Adey has been suggested (Athanasiadis 2001).

Mesophyllum is also well known from the fossil record, and several species have been described from deposits in Europe, Africa, Asia, and the Indo-Pacific (Lemoine 1928, 1939, 1977; Ishijima 1942; Maslov 1962; Basso 1995; Basso *et al.* 1998), dating from the Eocene (38–54 mya) to the Recent (Johnson 1962; Basso 1995; Basso *et al.* 1998). These taxa, although important in the phylogenetic context, remain imperfectly known as regards several characters of their thallus structure and reproduction.

MATERIAL AND METHODS

Herbarium collections, including slides, were made available through generous loans from TRH, UBC and UC (herbarium abbreviations follow Holmgren *et al.* 1990) and the private herbaria of W. Johansen, P. Lebednik and R. Paine. Fragments of thalli were decalcified using acetic acid (45%, 5–24 hours) and then stained and hardened in aniline blue (1–5% solution with alcohol) for up to 4 (or more) weeks before being sectioned in Hamilton's freezing solution (1 g gum arabic–30 g sucrose–one crystal of thymol–100 ml distilled water) using a Kryomat 1700 freezing microtome (Leitz, Stuttgart, Germany), at a thickness of 30–50 μm. Observations were made by light microscopy and photographs were taken using a Zeiss Axiophot 2 (Zeiss, Jena, Germany). Permanent slides were mounted in 60–80% Karo syrup (Best Food Division CPC International, Englewood Cliffs, NJ, USA). Drawings were made using a camera lucida. Terminology is in agreement with our previous publications (see, for example, Lebednik 1974, 1977a, b; Adey *et al.* 2001; Athanasiadis 2001). Cell length is the distance between primary pit connections. In most cells, where breadth more or less equals thickness, cell breadth (or diameter) is the thickness of the cell lumen (i.e. excluding the cell walls). In *M. vancouveriense, M. conchatum* and *M. lamellatum,* we observed specialized, 'thinner-wider' pore cells, as previously described in other species of *Mesophyllum* and *Leptophytum* (Athanasiadis 1999, as 'slender'; Adey *et al.* 2001, also as 'slender–wider' or 'wider–slender'). These pore cells exhibit different thickness and breadth. In perpendicular sections (in relation to the length of such cells), cell thickness applies to the thinner dimension of the cell lumen, and cell breadth to the wider dimension (which is slightly arching; Fig. 45, arrowheads). In longitudinal sections, depending on the level of section or focus, different pore cells may demonstrate either cell length × cell thickness (and hence the pore cells appear to be thinner; Fig. 103, arrowheads) or cell length × cell breadth (and hence the pore cells appear to be wider; Fig. 103, arrows). The length of subepithallial meristematic cells was studied in several sections and refers to the maximum size that occurs during putative cell divisions. Pore plate diameter defines the length between the most remote pores of

multiporate conceptacle roofs. In *M. vancouveriense, M. lamellatum* and *M. crassiusculum,* we occasionally observed 'flared-like' epithallial cells (more frequently in the last species) and we use this term to distinguish them from true flared cells (which are known to occur regularly in the epithallium of species of *Lithothamnion* Heydrich and other genera). Flared cells consistently have a characteristic rim (along the periphery of the upper part of the anticlinal cell wall), seen as a protrusion (in transverse section) on each side wall (Fig. 25, arrowheads). The abbreviations TS (transverse section) and SMC (spermatangial mother cell, plural SMCs) are used throughout this article. Illustration legends that describe section(s) refer to TS. Certain characters from type specimens are documented in more than one illustration to provide unequivocal evidence. The laboratory methods applied in the preparation of most of the second author's specimens (Figs 3, 5–7, 9, 13–19, 81, 82, 86–88, 138–140, 143–147) are described in Lebednik (1977b).

OBSERVATIONS

Mesophyllum Lemoine (1928, p. 251)

TYPE SPECIES: *Mesophyllum lichenoides* (Ellis) Lemoine (1928, p. 251); designated by Ishijima (1942, p. 174).

HETEROTYPIC SYNONYM: *Polyporolithon* Mason [1953, p. 316; type species: *P. conchatum* (Setchell & Foslie) Mason (1953, p. 316); see Adey (1970, pp. 23, 27)].

COMMENTS: The literature on *Mesophyllum* is extensive, and a monograph of this relatively large genus of worldwide distribution has yet to be published. Therefore, we provide here a brief summary of the current understanding of the genus to identify the key characters that we have used to classify the species described in this paper. Since Lemoine's (1928) original account and prior to 1978, *Mesophyllum* had been distinguished from other genera of the Melobesioideae primarily on the presence of a coaxial hypothallium and simple spermatangial structures (Suneson 1937, pp. 67, 68, 1943, p. 58). In 1978, Lebednik showed that, amongst the nonmonotypic genera of the Melobesioideae having simple spermatangial structures only (i.e. *Mesophyllum, Melobesia* Harvey and *Clathromorphum* Foslie), *Mesophyllum* could also be distinguished in having conceptacle roofs formed through centripetal growth of peripheral filaments, and that *Mesophyllum* and *Leptophytum* were the only genera within the Melobesioideae possessing a protective layer of cells above the spermatangial initials (Lebednik 1978, p. 392, figs 10–12). More recently, Keats *et al.* (2000, p. 397) considered nine characters that could collectively distinguish *Mesophyllum* from *Lithothamnion* only. Athanasiadis (2001, table 2) compared 16 characters among the nonmonotypic genera of the Melobesioideae and observed that, whereas the segregation of *Mesophyllum* from *Lithothamnion, Phymatolithon* Foslie, *Melobesia* or *Clathromorphum* was unequivocal, the distinction between *Mesophyllum, Leptophytum* and *Synarthrophyton* Townsend was problematic and largely based on a combination of characters including the presence or absence of (1) a coaxial hypothallium in patches (present only in certain species of *Synarthrophyton* and *Mesophyllum*); (2) a predominantly coaxial hypothallium (present only in several species of *Mesophyllum*); (3) elongate subepithallial initials (present only in *Synarthrophyton* and in most species of *Mesophyllum*); (4) specialized pore cells in multiporate conceptacles (present only in most species of *Mesophyllum* and *Leptophytum*); and (5) dendroid (branched) SMCs (present only in *Synarthrophyton* and *Leptophytum*).

According to these observations, which are based on a large number of previous studies (Adey 1966; Lebednik 1977a, b, 1978; Verheij 1992, table 1; Woelkerling & Harvey 1993; Chamberlain & Irvine 1994; Chamberlain & Keats 1994, table 2; Woelkerling 1996, and

references therein), *Mesophyllum* is unequivocally distinguished from *Leptophytum* and *Synarthrophyton* in possessing simple (unbranched) SMCs only (on the floor, roof and walls of the chamber). Moreover, in several species of *Mesophyllum* (including the generitype *M. lichenoides*) a predominantly coaxial hypothallium is found, and it is on the basis of these two unique characters (and a new one recognized here: i.e. dumbbell-shaped carposporangial chambers) that we refer the five NE Pacific species to *Mesophyllum*; the remaining characters that we have examined are shared with *Leptophytum, Synarthrophyton,* or both.

Mesophyllum aleuticum Lebednik, *sp. nov.*

Figs 1–19

Alga crustacea, usque ad 10 cm diametro, in saxis et aliis corallinis algis prostrata; thallus foliosus protuberationibus nullis, in substrato firme adhaerens; margines nitidi, ad substratum arcte adhaerentes; lamellis superimpositis usque ad 1.5 mm crassis; hypothallus coaxialis, 60–155 μm crassus, e 9–15 files compositus, cellulis basalibus cuneatis; cellulae hypothalli 9–42 μm longae, 4–11 μm latae; perithallus 40–1200 μm crassus, cellulis 5–14 μm longis, 4–8 μm latis; cellulae epithalli 0–2, 2–5 μm longae et 5–9 μm latae; trichocyti (?) adsunt in filis perithalliis; conjunctiones cellularum lateralium vulgares; tecta conceptaculorum omnium elevatae; conceptacula sporangifera 525–1400 μm diametro externis; lumina conceptaculorum sporangiferorum maturorum 420–720 μm lata, 165–320 μm alta, basin vs cellulis tenuioribus elongatisque poros cingentibus, tectis sine ore, et pori usque ad 130; tetrasporangiae 90–290 μm longae et 20–125 μm crassae; gametophyta dioica; lumina conceptaculorum marium maturorum 235–785 μm lata, 40–175 μm alta; lumina conceptaculorum cystocarporum maturorum 435–720 μm lata, 205–290 μm alta; cassa conceptacula non in thallo infodiunt; spermatangia, procarpia et carposporophyta ut vulgo in genere.

Alga crustose, to 10 cm in diameter, prostrate on rocks and other coralline algae; thallus foliose, lacking protuberances, strongly attached to the substratum; margins glossy, adhering tightly to the substrate; with superimposed lamellae each up to 1.5 mm thick; coaxial hypothallium 60–155 μm thick, composed of 9–15 filaments, with wedge-shaped basal cells; hypothallial cells 9–42 μm long and 4–11 μm broad; perithallium 40–1200 μm thick, perithallial cells 5–14 μm long and 4–8 μm broad; epithallial cells 0–2 and 2–5 μm long and 5–9 μm broad; hair cells (trichocytes?) present on perithallial filaments; cell fusions between lateral cells common; all conceptacle roofs raised; sporangial conceptacles 525–1400 μm in external diameter; chamber of mature sporangial conceptacles 420–720 μm wide and 165–320 μm high, with thinner and elongate cells surrounding the pores basally, roof without a rim, and with up to 130 pores; tetrasporangia 90–290 μm long and 20–125 μm broad; gametophytes dioecious; chambers of male conceptacles 235–785 μm wide and 40–175 μm high; chambers of carposporangial conceptacles 435–720 μm wide and 205–290 μm high; empty conceptacles not embedded in the thallus; spermatangia, procarps and carposporophytes as for the genus.

HOLOTYPE: In UBC, unnumbered (Lebednik #AM-68-4, 15) (Figs 1, 2, 4, 8, 10–12), collected by *Phillip A. Lebednik,* 22 September 1968.

ISOTYPE: In GB, unnumbered (a fragment from the holotype specimen).

TYPE LOCALITY: Constantine Harbor, Jones Creek, Amchitka Island (Aleutian Islands, Alaska), c. 5 m depth, 51°24.5′N, 179°17′E.

TYPIFICATION: We designate as holotype a tetrasporangial specimen, c. 3.5 cm in extent, that is presently unattached (Fig. 1). Fragments of the same collection partly grow on a sandstone, which suggests

that the holotype was originally attached. The holotype is not the same specimen illustrated by Lebednik (1974, pl. 44, fig. 1).

HABITAT: According to Lebednik (1974), *M. aleuticum* is a common saxicolous coralline alga in the littoral and sublittoral zones of the Aleutian Islands to a depth of at least 60 m.

DISTRIBUTION: Alaska. Aleutian Islands, from Shemya Island to Goloi Island (Lebednik 1974).

MATERIAL EXAMINED: USA, Alaska. Amchitka Island, Kirilof Rocks, 51°26.9′N, 179°11.7′E, –60 ft (18 m), on cobble, 24 December 1968, *Lebednik* AM-C-60, 12-68-1, 5B, UBC; Amchitka Island, Bat Island, 51°28.57′N, 179°14.5′E, –110 ft (33 m), 9–12 September 1969, *Lebednik* AM-BI-110, 9-69-34, 5, 2, herb. Lebednik (slides); Amchitka Island, Bat Island, 51°28.57′N, 179°14.5′E, –110 ft (33 m), 9–12 September 1969, *Lebednik* AM-BI-110, 9-69-40, 8, 1, herb. Lebednik (slides); Amchitka Island, Kirilof Rocks, 51°24.36′N, 179°18.18′E, –40 ft (12 m), 2–3 May 1969, *Lebednik* AM-C-40, 5-69-7, 6, 2, herb. Lebednik (slides); Amchitka Island, Bird Cape, 51°39.8′N, 178°39.2′E, –15 ft (4.5 m), 27 September 1969, *Lebednik* AM-BC, 6-69-20, herb. Lebednik; Amchitka Island, Kirilof Rocks, 51°24.36′N, 179°18.18′E, –120 ft (36 m), 17 September 1969, tetrasporic, *Lebednik* AM-C-120, [9]-69-35, 2N, UBC; Amchitka Island, Kirilof Rocks, 51°26.9′N, 179°11.7′E, –40 ft (12 m), 24 December 1968, *Lebednik* AM-C-40, 12-68-1, 4D, herb. Lebednik (slides); Amchitka Island, St Makarius Point, 51°21.7′N, 179°12.7′E, intertidal, 11 June 1969, *Lebednik* AM-MP-1, [5]-69-11, 10, 1, GB (slides), herb. Lebednik (slides); Amchitka Island, Kirilof Rocks, 51°24.36′N, 179°18.18′E, –60 ft (18 m), tetrasporic, 12 September 1968, *Lebednik* AM-68-1, 60 13K, UBC; Amchitka Island, Constantine Harbor, Jones Creek, 51°24.5′N, 179°17′E, –15 ft, (4.5 m), 22 September 1968, *Lebednik* AM-68-4, 15, UBC (holotype), GB (slides); Amchitka Island, Kirilof Rocks, 51°26.9′N, 179°11.7′E, –20 ft (6 m), 24 December 1968, *Lebednik* AM-C-20, 12-68-1, 1A, 6D, 1, GB (slides), herb. Lebednik (slides); Amchitka Island, Kirilof Rocks, 51°26.9′N, 179°11.7′E, –20 ft (6 m), 24 December 1968, *Lebednik* AM-C-20, 12-68-1, 1, UBC; Amchitka Island, St Makarius Point, 51°23.6′N, 179°12.5′E, –30 ft (9 m), 28 December 1968, *Lebednik* AM-SM-30, 12-68-3, 8F, GB (slide); Amchitka Island, Kirilof Rocks, 51°24.36′N, 179°18.18′E, –20 ft (6 m), 17 April 1970, *Lebednik* AM-C-20, 4-70-3, 8, GB (slide); Amchitka Island, Kirilof Rocks, 51°24.36′N, 179°18.18′E, –60 ft (18 m), 17 April 1970, *Lebednik* AM-C-60, 4-70-3, 8H, UBC.

MORPHOLOGY: Plants are encrusting, to 10 cm in diameter and generally adhere tightly to the substrate, or rarely grow as unattached fragments, the margins of which may bend inwards and grow back-to-back (Figs 1, 2). The surface lacks protuberances, but some surface undulation can be observed, and white streaks may be present on plants when rocks are moved by wave action. The colour is usually bright red, sometimes becoming brownish. The margin is characteristically adherent and entire (Fig. 2), though sometimes it may be quite free and lobate when growing over other corallines. Marginal areas tend to be somewhat glossy, and the thin edge of the crust is easily seen as a narrow (less than 1 mm wide) whitish border.

ANATOMY: Thalli may reach 3 mm thick, due to superimposing, whereas individual lamellae are 100–1500 μm thick (Figs 3, 4). The internal organization is dorsiventral. The hypothallium is polystromatic and predominantly coaxial, 60–155 μm thick, and composed of 9–15 filaments that grow

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Figs 1–8. *Mesophyllum aleuticum.*
Fig. 1. The holotype specimen in UBC. Notice the multiporate conceptacles on its surface (older conceptacles are bleached) (Lebednik #AM-68-4, 15).
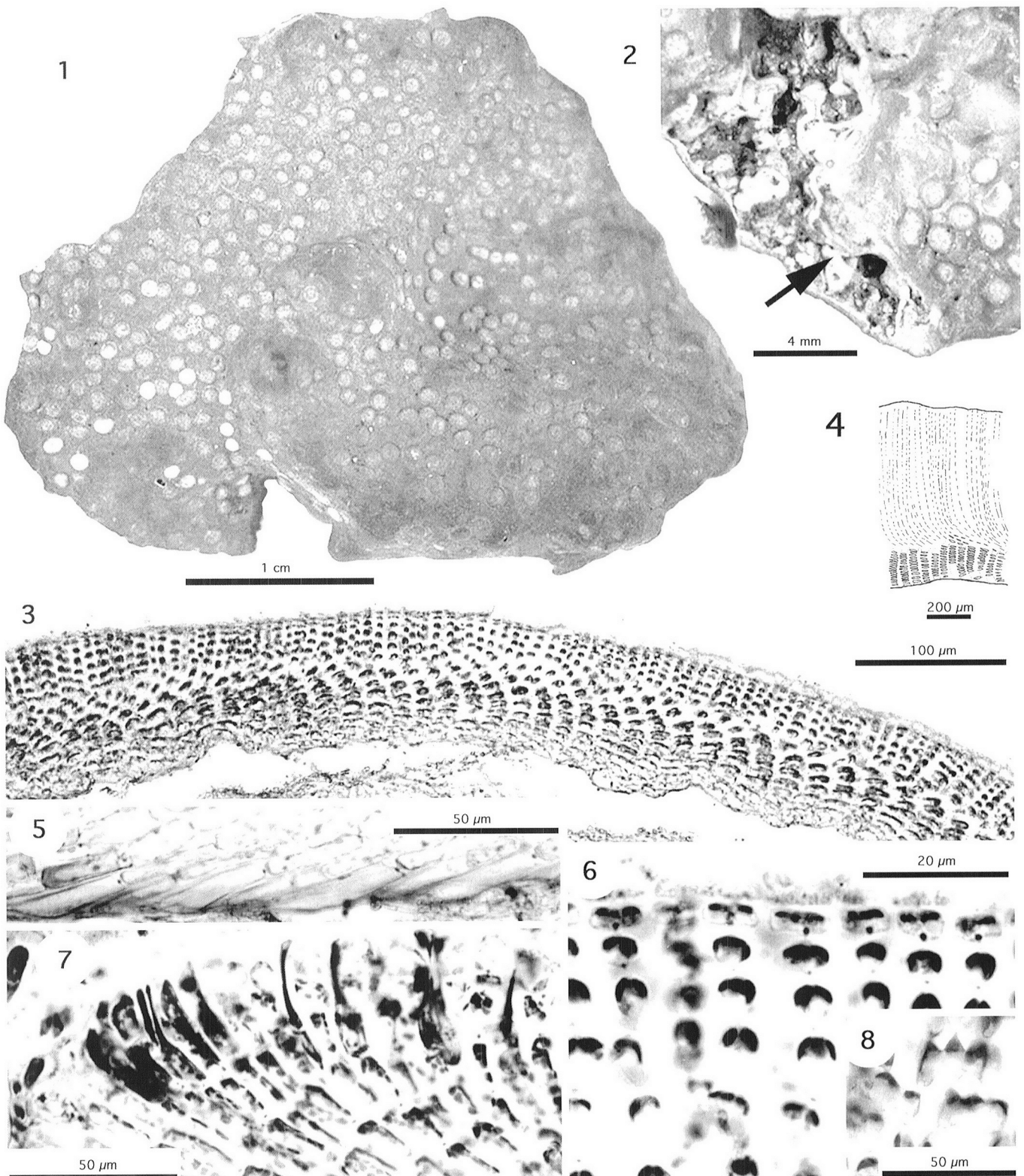
Fig. 2. Ventral view of the holotype specimen showing folding near the margin and back-to-back growth (arrow).
Fig. 3. Section of a young thallus showing a coaxial, arching hypothallium and an ascending perithallium (Lebednik #AM-BI-180, 9-69-40).
Fig. 4. Drawing of a thallus section with thick perithallial growth (holotype).
Fig. 5. Section near the base showing wedge-shaped terminal cells [reproduced from Lebednik (1974, pl. 44, fig. 4)].
Fig. 6. Section near the surface showing flattened epithallial cells and subepithallial meristematic cells more or less similar in size to cells below (Lebednik #AM-BC-15).
Fig. 7. Section near the margin showing hair-like cells (Lebednik #AM-MP-I, 6-69-11).
Fig. 8. Thallus section showing cell fusions between perithallial cells (holotype).
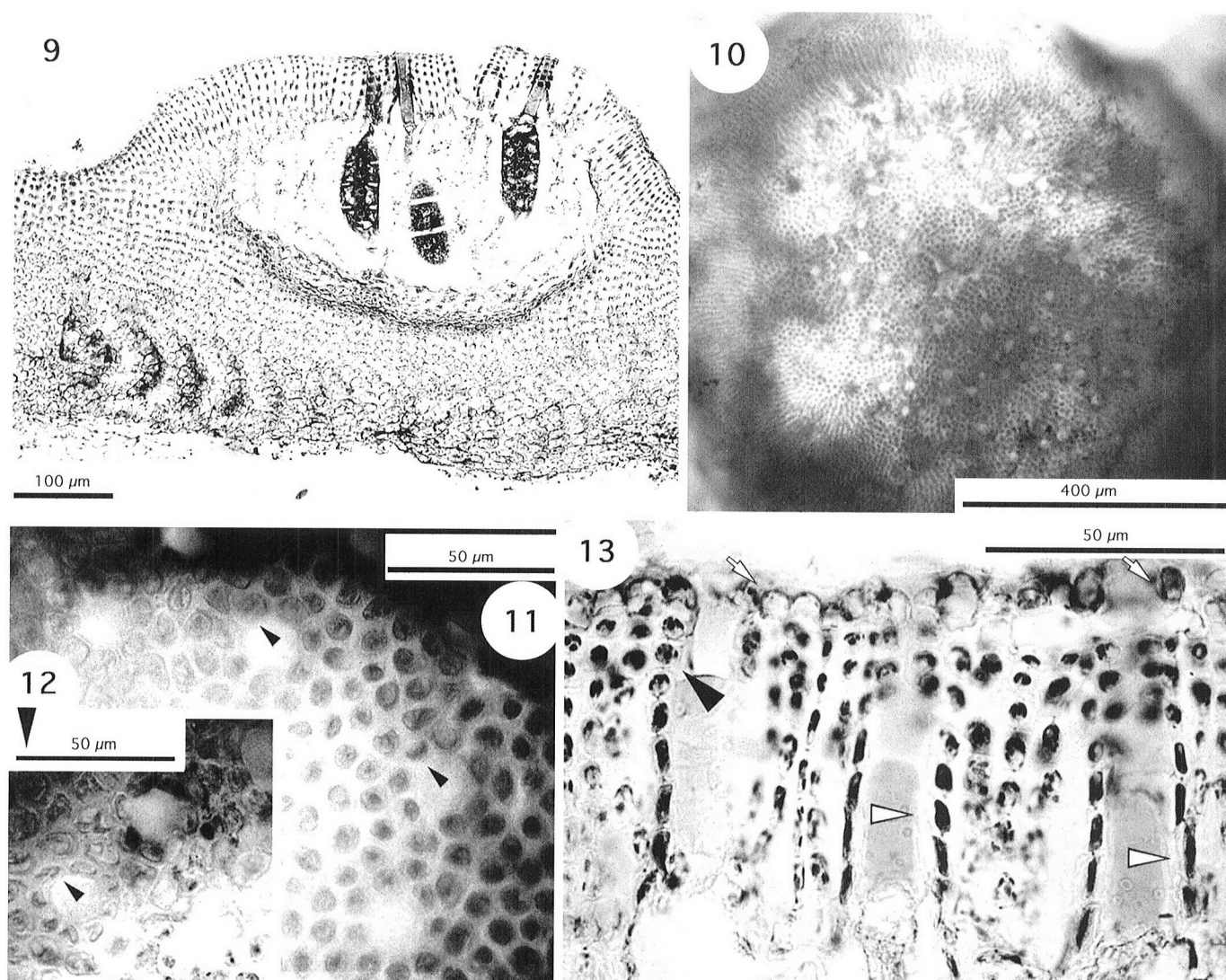
Figs 9–13. *Mesophyllum aleuticum.*
Fig. 9. Tetrasporangial conceptacle with mature tetrasporangia (Lebednik #AM-BI-110, 9-69-34).
**Fig. 10.** Surface view of a multiporate conceptacle roof (holotype).
Figs 11, 12. Surface views of a multiporate roof, showing pores surrounded by rosette cells (arrowheads) that are normal epithallial cells (holotype).
Fig. 13. Section of a multiporate roof showing filaments bordering pore canals. The filaments are composed of normal roof cells at the top (black arrowhead) and specialized cells near the base. The latter cells are elongate and thinner but have extra-thick walls (white arrowheads). Note that epithallial cells are roundish (arrows) (Lebednik #AM-C-20, 12-68-1).

centrifugally via terminal meristematic divisions, forming distinct cell arches that bend downwards and upwards. A cuticle covers the terminal meristematic cells. Descending hypothallial filaments may grow into depressions in the substrate. Hypothallial cells are 9–42 μm long and 4–11 μm broad. Basal cells of descending filaments end on the substrate at a rather high angle in wedge-shaped cells (Fig. 5). Ascending hypothallial filaments give rise to the perithallium that is 40–1200 μm thick and composed of cells that are 5–14 μm long and 4–8 μm broad. Subepithallial meristematic cells are 4–8 μm long and 4–7 μm broad, more or less similar in size to cells below, and may divide synchronously in patches producing stratification (Fig. 6). Yet stratification does not occur regularly in the perithallium. The epithallium is composed of up to two cells per perithallial filament. In TS, epithallial cells

are flattened, 2–5 μm long and 5–9 μm broad and generally wider than the perithallial cells below (Fig. 6). They also stain darker than the perithallial cells. Elongate, tapering, dark-staining hair cells (trichocytes?) develop frequently near the surface, projecting outwards (Fig. 7). These cells are produced subdichotomously from subepithallial cells and subsequently become embedded in the perithallium as it increases in thickness. Cell fusions are common in the perithallium (Fig. 8) and hypothallium. Secondary pit connections were not observed.

REPRODUCTIVE STRUCTURES: The species is dioecious with raised, prominently conical, uniporate gametangial conceptacles and oblongate multiporate conceptacles. Multiporate conceptacles are widespread over the thallus surface and measure 525–1400 μm in external diameter and 100–390 μm in height

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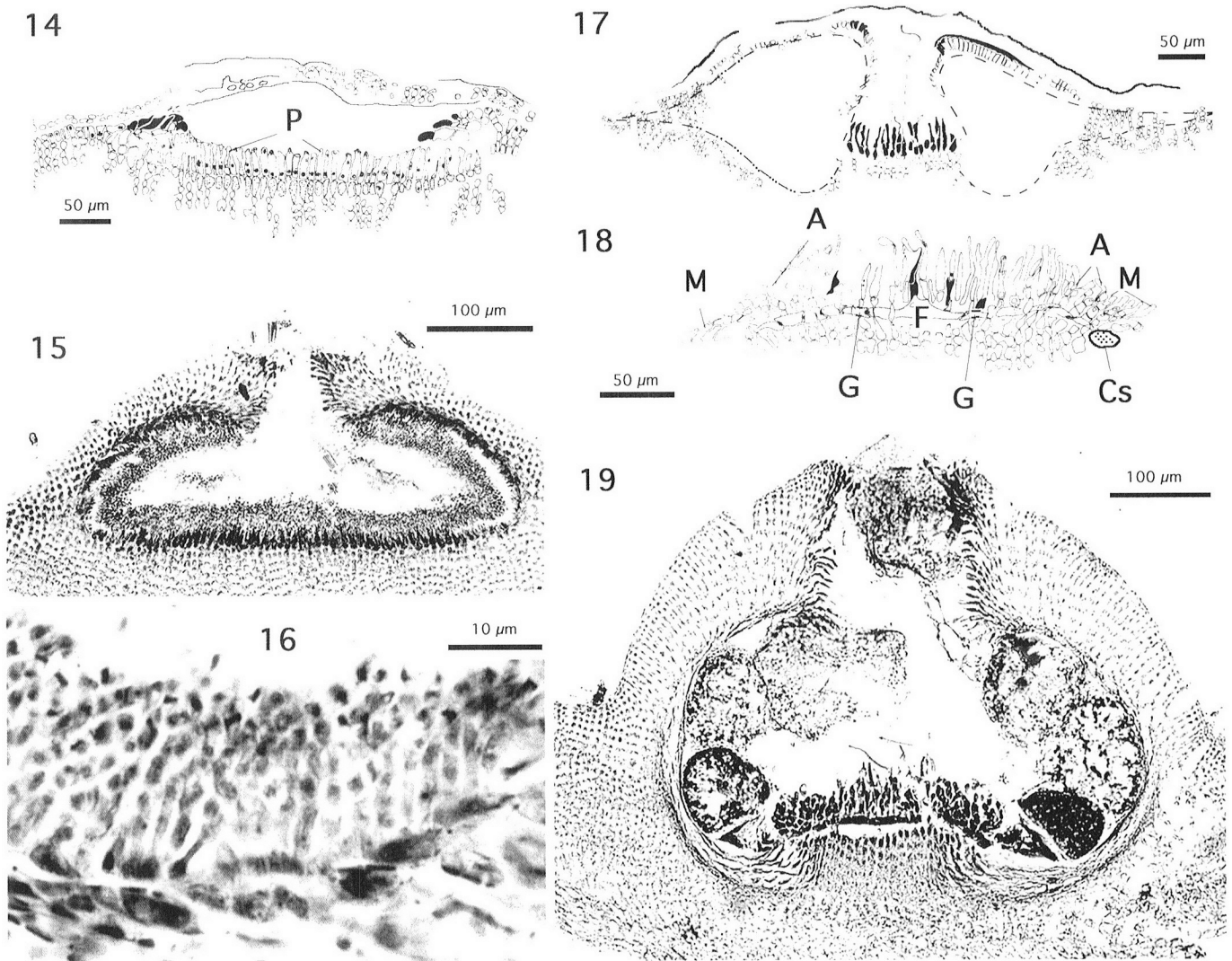
Figs 14–19. *Mesophyllum aleuticum.*

Fig. 14. Male conceptacle initials developing just below the epithallium and exhibiting spermatangial initials situated below elongate protective cells (P) with nuclei (in black) near their base [reproduced from Lebednik (1978, fig. 4)].

Fig. 15. Mature male conceptacle with unbranched spermatangial structures developing on the floor, roof and walls [reproduced from Lebednik (1978, fig. 6)].

Fig. 16. Magnification of spermatangial structures of the chamber floor [reproduced from Lebednik (1978, fig. 7)].

Fig. 17. Early stage in the development of a female conceptacle [reproduced from Lebednik (1977a, fig. 8)].

Fig. 18. Postfertilization stage showing a fusion cell (F) with lateral gonimoblast filaments (G) producing terminal carpospores (CS). Note the peripheral filaments (A) that lack carpogonia and the peripheral dense groups of small-celled branches (M) [reproduced from Lebednik (1977a, fig. 11)].

Fig. 19. Mature carposporangial conceptacle showing peripheral development of carposporangia and the central pedestal resulting from decalcification of the peripheral nonfertile area [reproduced from Lebednik (1977a, fig. 17)].

(Fig. 1). Their chambers are 420–720 μm in diameter and 165–320 μm high. They are provided with a convex (to flattened) roof that is perforated by 37–130 pores (Figs 9, 10). A peripheral rim is absent. Pore plates have an external diameter of between 460 and 845 μm, are 50–95 μm thick (Figs 9, 13) and are composed of filaments five to nine cells long (including the epithallial cell). Surface views show that pores are surrounded by a group of six to nine rosette cells (Figs 11, 12) that are normal epithallial cells. TS of the roof show that canals are not conical and are bordered by six- to nine-celled filaments composed of thinner and more elongate cells near the base (Fig. 13). These lower pore cells stain darker than adjacent roof cells and appear to have extra-thick cell walls.

Towards the top, pore cells are normal roof cells ending in roundish to hemispherical epithallial cells that are flush with the surface (Fig. 13). Tetrasporangia are zonately divided, 90–290 μm long and 20–125 μm broad (Fig. 9). Following spore release, roofs bleach, become sunken and finally break off, leaving a crater-like depression that is filled by new vegetative cells. Cavities of conceptacles embedded in the perithallium were not observed.

One immature male conceptacle was observed. At this stage, a patch of empty cells representing the thallus surface has been cast off above the meristem, suggesting that conceptacles develop two to four cells below the epithallium (Fig. 14). The central area of the conceptacle is occupied by elon-

gate cylindrical cells which are devoid of cytoplasm and whose nuclei are located in the basal portion of the cells (Fig. 14). These cylindrical cells form a protective layer over the cells below that have a denser cytoplasm. The latter cells are smaller than the cylindrical protective cells but much larger than the perithallial cells below. It is very likely that these dark-staining cells are the spermatangial initials that will develop into SMCs on the conceptacle floor. The sterile filaments immediately adjacent to the fertile zone are beginning to bend inwards and branch and will form the conceptacle roof ending in characteristic elongate cells lining the ostiole (Fig. 15). Mature SMCs form simple (unbranched) spermatangial structures on the roof and the walls, as well as on the floor of the chamber with up to three or more spermatangia cut off from individual SMCs (Fig. 16). SMCs form a part of the chamber walls. Spermatangia cut off spermatia at the apex by oblique divisions (Fig. 16). Mature male conceptacles are 380–1060 μm in external diameter and 70–235 μm high. Their chambers are 235–785 μm in diameter and 40–175 μm high; they are covered by a roof that is 40–145 μm thick and provided with a central conical ostiole, 10–125 μm in diameter (n = 28 from 14 plants).

A young female conceptacle with unfertilized carpogonial branches was observed (Fig. 17). At this stage several trichogynes extend through the ostiole. The fertile area with carpogonial branches occurs in the centre of the conceptacle and is 125 μm in diameter. Carpogonial branches are two-celled and develop singly (rarely in twos) from the supporting cell that is connected to a basal cell. There are also filaments peripheral to the fertile area but these do not form trichogynes and their function is unknown. The remaining area in the conceptacle (dashed lines in Fig. 17) is nonstaining and encircles the fertile zone. A thick layer of wall and detrital material, with a few shedding epithallial cells, overlies the young conceptacle (Fig. 17). The presence of epithallial cells suggests that the conceptacle initials arise at or slightly below the level of the meristem. After fertilization, a fusion cell develops at approximately the level of the pit connections between the basal and supporting cells of carpogonial branches (Fig. 18). Gonimoblast filaments (connecting filaments *sensu* Lebednik 1977a) with large pit plugs between the cells extend outside the periphery of the fusion cell, and carposporangia are produced at their tips. Near the periphery of the fusion cell, in the area of the nonfunctional carpogonial filaments and above the specialized filaments, there are dense groups of small-celled branches (modified auxiliary cell branches *sensu* Lebednik 1977a), which stain differently from the old carpogonial branches (Fig. 18). These branches apparently develop after fertilization because they are not seen in young conceptacles. Their staining properties, orientation and time of formation suggest that they have a specialized function, which so far is unknown (Lebednik 1977a, p. 391). The central zone of the mature carposporangial conceptacle is often located on a pedestal of (presumably calcified) cells which arise from the dissolution of the calcified cell walls peripheral to and beneath the fertile zone (Fig. 19). Hence, the chamber becomes dumb-bell-shaped, as in other species of the genus (see below). Carposporangia develop along the periphery of the fertile zone (Fig. 19). Mature carposporangial conceptacles are 520–1000 μm in external diameter and 175–350 μm high (rather conical). The chambers are 435–720 μm in diameter, 205–290 μm

high and covered by a roof that is 115–255 μm thick and that exhibits a centrally placed ostiole with a diameter of 115–175 μm (n = 10).

COMMENTS: The suite of characters described for *M. aleuticum* readily supports its accommodation in the genus *Mesophyllum*. The new species possesses simple spermatangial structures only and a predominantly coaxial growth in the hypothallium, features that are unique for *Mesophyllum* or certain of its members (including the generitype). Moreover, the new species exhibits dumbbell-shaped carposporangial chambers, as also described in the generitype and several other congeneric species (see Carposporophytes in the Discussion). At the species level, *M. aleuticum* is clearly distinct from its NE Pacific congeners in possessing: (1) hair cells (trichocytes?) that become embedded in the perithallium; and (2) the largest (sexual and asexual) conceptacles (Table 1). Moreover, *M. aleuticum* possesses a unique character combination that also distinguishes it from all other species of *Mesophyllum* that have been described in a modern context (Woelkerling & Harvey 1993; Chamberlain & Irvine 1994; Keats & Chamberlain 1994; Cabioch & Mendoza 1998; Athanasiadis 1999; Chamberlain 2000). We have not searched for its potential sister taxon, awaiting a phylogenetic analysis of the genus. The presence of both gametophytes and tetrasporophytes in our collections indicates that *M. aleuticum* reproduces sexually; hence, its species status is supported. We have found variation in mean hypothallial cell length in three specimens (24 μm in AM-MP-I, 6-69-11, 28 μm in AM-C-60, 4-7-3, and 31 μm in AM-68-4) after counting the length of 25–37 coaxial arches. We have no data for this species outside the Aleutians and no other species of *Mesophyllum* or *Leptophytum* from the Aleutian Islands have been recorded. The name *M. aleuticum* was originally proposed by Lebednik (1974) in his thesis and later appeared in several papers (Lebednik 1977a, 1978) but without a Latin description or holotype citation.

Mesophyllum vancouveriense (Foslie) Steneck & Paine (1986, p. 233)

Figs 20B, 26–53

BASIONYM: *Lithophyllum vancouveriense* Foslie [1906b, p. 21 (reprint, p. 5)].

LECTOTYPE: In TRH, unnumbered (Fig. 20B, Figs 26–28); collected by *Yendo* in June–July 1901; designated here.

PARATYPE: In UC 397503; examined by Steneck & Paine (1986, p. 233, figs 27, 29, 31, referred to as lectotype).

TYPE LOCALITY: Port Renfrew (Port San Juan), Vancouver Island.

HETEROTYPIC SYNONYM: *Lithothamnion phymatodeum* Foslie f. *aquilonium* Foslie (1907, p. 4, '*aquilonia*'); type locality: Puget Sound, Fort Casey, Whidbey Island, Washington; holotype: in TRH, unnumbered (Figs 29–32) including two slides (#1447 and #1448), 'Amerika Algae of Puget Sound No 652 on holdfast of *Laminaria*, Fort Casey, Whidbey Island, Wash. 1901 Setchell and Gardner Monograph pl. 4, fig. 12 *Lithoph. phymatodeum* f. *aquilonia* prep. 1447–48', *N.L. Gardner*, 18 June 1901.

HABITAT: Epiphytic on *Laminaria* holdfasts and coralline algae, on limpets and on rocks in the littoral zone.

DISTRIBUTION: USA and Canada. Strait of Juan de Fuca, Tatoosh Island, Washington State, USA, to Hedley Island, British Columbia, Canada; but given its commonness at Tatoosh Island, its southern distribution is probably more extended. The northernmost collection

(Hedley Island) is from Queen Charlotte Strait, 50°54.4'N, 127°34.5'W (UBC A19493).

MATERIAL EXAMINED: **Canada, British Columbia.** Vancouver Island, 6 July 1901, *K. Yendo*, TRH (includes slides #724 & #725) [mixed gathering, but includes the lectotype; Foslie's label reads '*Lithoph. vancouveriense* North America, Port Renfrew (Port San Juan), Vancouver Isl. 6–7. 1901, leg. K. Yendo, Störste . . . *Lithoph. vancouver*. pl. 54 f. 22']; Vancouver Island, SW shore, Whiffin Spit, 48°21'N, 123°43'W, 7 July 1967, *Chamut & Baillie* 16033, UBC A33812; Vancouver Island, SW shore, Whiffin Spit, 11 June 1967, *Baillie & Chamut* 15757, UBC A33078; Vancouver Island, SW shore, Whiffin Spit, 5 August 1967, *Baillie & Chamut* 16562, UBC A33877; Vancouver Island, SW shore, Whiffin Spit, 25 October 1968, *Pace & Harrison* 23886, UBC A40296; Vancouver Island, SW shore, Whiffin Spit, mid-intertidal, 22 November 1968, *Pace & Harrison* 24155, UBC A40300; Vancouver Island, SW shore, Whiffin Spit, low intertidal, tetrasporic, 18 January 1969, *Pace & Baillie* 24235, UBC A40302; Vancouver Island, SW shore, Whiffin Spit, tetrasporic, 15 April 1968, *Chamut & Chihara* 18020, UBC A33979; Vancouver Island, SW shore, Whiffin Spit, multiporate, 3 November 1967, *Chamut et al.* 17134, UBC A33083; Vancouver Island, SW shore, Whiffin Spit, 25 October 1968, *M.C., D.P., B.B.* 19814, UBC A34583 [p.p.]; Vancouver Island, SW shore, Whiffin Spit, 20 July 1967, *Baillie & Chamut* 16333, UBC A33881; Vancouver Island, SW shore, Whiffin Spit, 13 May 1968, *P.C., K.B., B.B., P.H., D.P.* 18395, UBC A33981; Vancouver Island, W coast, Point no Point, 48°23'N, 123°59'W, 10 June 1967, *Chamut & Baillie* 15702, UBC A30581 [p.p.]; Vancouver Island, W coast, Point no Point, 11 July 1968, *Chamut et al.* 19154, UBC A33984; Vancouver Island, W coast, Point no Point, tetrasporic, 20 December 1967, *Baillie & Chihara* 17284, UBC A33085; Vancouver Island, W coast, Point no Point, 18 August 1967, *Chamut & Baillie* 16864, UBC A33876; Vancouver Island, W coast, Point no Point, 24 May 1967, *Baillie & Chamut* 15423, UBC A29804; Vancouver Island, 48°25'N, 123°14'W, 12 June 1968, *Chamut & Baillie* 19194, UBC A33985 (A); Vancouver Island, Box Island, 49°04'N, 125°47'W, tetrasporic, 16 March 1968, *Baillie & Harrison* 17829, UBC A33079; Vancouver Island, Discovery Island, 48°25'N, 123°14'W, 17 July 1968, *Baillie & Pace* 19933, UBC A34589; Vancouver Island, Staples Islet, off Numas Island, 50°46'2"N, 127°7'1"W, low intertidal, sterile, 4 September 1968, *Markham et al.* 23568, UBC A39524; Vancouver Island, Staples Islet, 3–7 m, male, 29 August 1968, *Markham et al.* 22830, UBC A38656 [p.p.]; Vancouver Island, Staples Islet, high intertidal, sterile, 4 September 1968, *Markham et al.* 23567, UBC A39995; Vancouver Island, Bamfield, Rock of Deadman Cove, 48°46'54"N, 125°11'54"W, 12 m, rock, sand and shell, moderately exposed, *Pace & Harrison* 25602, UBC A48028; Queen Charlotte Strait, Numas Island, 50°46.1'N, 127°4.7'W, low intertidal, sterile, 19 April 1968, *Markham* 24346, UBC A39992; Queen Charlotte Strait, Hedley Island, 50°54.4'N, 127°34.5'W, sterile, 3 July 1962, *Widdowson* 6509, UBC A19493. **USA, Washington State.** Puget Sound, Whidbey Island, Fort Casey, 18 June 1901, *N.L. Gardner* 652 (distributed by W.A. Setchell & N.L. Gardner), TRH (includes slides #1447 and #1448) (holotype of f. *aquilonium*; Foslie's label reads 'Amerika Algae of Puget Sound No 652 on holdfast of *Laminaria*, Fort Casey, Whidbey Island, Wash. 1901 Setchell and Gardner . . . f. *aquilonia* . . .'); Tatoosh Island, tetrasporic on patty #47A, intertidal, 28 January 1991, *Paine*, GB; Tatoosh Island, tetrasporic on *Acmaea mitra*, January 1991, *Paine*, GB; Tatoosh Island, intertidal, male, on *Acmaea mitra*, 23 July 1994, *Paine*, GB; Tatoosh Island, low intertidal, 23 May 1989, *Paine*, GB; Tatoosh Island, tetrasporic, intertidal, 11 March 1993, *Paine*, patty #80, GB; Tatoosh Island, tetrasporic, intertidal, 29 March 1987, *Paine*, patty #72, GB; Tatoosh Island, tetrasporic, intertidal, 11 March 1993, *Paine*, patty #12, GB; Tatoosh Island, tetrasporic, intertidal, 11 March 1993, *Paine*, patty #98 South, GB; Tatoosh Island, tetrasporic, intertidal, 22 November 1988, *Paine*, patty #63, GB; Tatoosh Island, tetrasporic, intertidal, 20 November 1995, *Paine*, patty #39, GB.

OBSERVATIONS ON TYPE MATERIAL AND NEOLECTOTYPIFICATION: The collection of *Lithophyllum vancouveriense* in TRH that was selected as lectotype by Mason [1953, p. 341, 'Spec-

imens examined . . . Port Renfrew, July 6, 1901, Yendo (= Lectotype of *Lithothophyllum vancouveriense*, Herb. Mus. Nidaros.)'] is placed in a single box annotated '*Lith. vancouveriense* North. Amerika Port Renfrew (Port San Juan) Vancouver Isl. 6–7. 1901 leg. K. Yendo . . .' (Fig. 20). It has previously been examined by Adey & Lebednik (1967, p. 18) and Woelkerling (1993, p. 232). As shown below, this collection comprises elements that belong to at least two different taxa and, therefore, we refer to it as a type collection. It comprises (1) three large (Fig. 20A–C) and four smaller specimens (Fig. 20D–G); (2) two round boxes annotated '724' and '725' (Fig. 20H) with fragments of the material used to prepare two sections, each on slide #724 and #725; and (3) two paper sheets with a handwritten English manuscript (probably in the hand of Setchell) and with annotations (written by Foslie on the back of the sheets) of measurements of hypothallial and perithallial cells (taken from the two slides). Foslie's annotations read 'Prep. [Slide] 724. Perith. 9×7, 7×6, 7×7, 9×6, 11×6, 11×7, Hypoth. 22×7, 11×6, 14×6, 18×7, 14×7, 25×6, 22×6, 32×6, 18×6 *Lithoph. vancouveriense*' and 'Prep. 725. Perith. 9×6, 9×7, 7×7, 7×6, 11×9, 9×6, $5–6 \times 5–6$ i kanten [near the margin] 14×7, Hyp 22×7, 18×7, 11×6, 14×7, 11×7, 14×6, 25×6, 29×6'. These measurements correspond to those reported in the Norwegian protologue that reads (in translation): '*Lithophyllum vancouveriense* Fosl. mscr. Thallus attached to rocks or stones and shells of molluscs, encrusting, up to 0.5 mm thick, the surface rough or usually provided with warty branches with roundish top, up to 2 mm high and 1–1.5 mm thick; hypothallium rather well developed forming partly long arches of cells 14–25 or up to 32 μm long and 6–8 μm broad; perithallial cells subsquarish, *c*. 7 μm in diameter, or more usually vertically elongated up to 12 μm long and 6–8 μm broad; cystocarpic conceptacles convex or subconical 350–400 μm in diameter. The species resembles in habit certain forms of *Lithophyllum farlowii* and also comes close to *Phym. muricatum*. Young specimens come close to *Lithoph. whidbeyense*. Northwest coast of America: Port Renfrew (Port San Juan), Vancouver Island (Yendo) and west coast of Whidbey Island (Setchell and Gardner, no 657).'

All specimens (except specimen C in Fig. 20) bear erect terete protuberances and are sterile (or lack apparent raised conceptacles), although in the protologue, Foslie described the presence of carposporangial conceptacles as convex to subconical, 350–400 μm in external diameter. Of the two specimens illustrated by Printz [1929, pl. 54, figs 22, 23, as *Lithophyllum* (?) *vancouveriense*], the largest one is shown here in Fig. 20A, whereas the second specimen growing on a limpet is not included in the type collection and, according to Woelkerling (personal communication), is kept in the second collection 'in drawer A3 of the Foslie herbarium . . . listed under *Lithophyllum vancouveriense* in Adey & Lebednik (1967, p. 18)'. We have not examined the material on the limpet.

Examination of the two slides showed that the thallus is up to 2.2 mm thick, composed of a thick perithallium or superimposing lamellae (Fig. 21). Young lamellae are 200–250 μm in thickness. The hypothallium is poorly developed (100–200 μm thick) and a coaxial hypothallium is not evident in these sections. Some extensive coaxial growth is present in what apparently represents a horizontal section through the hypo-
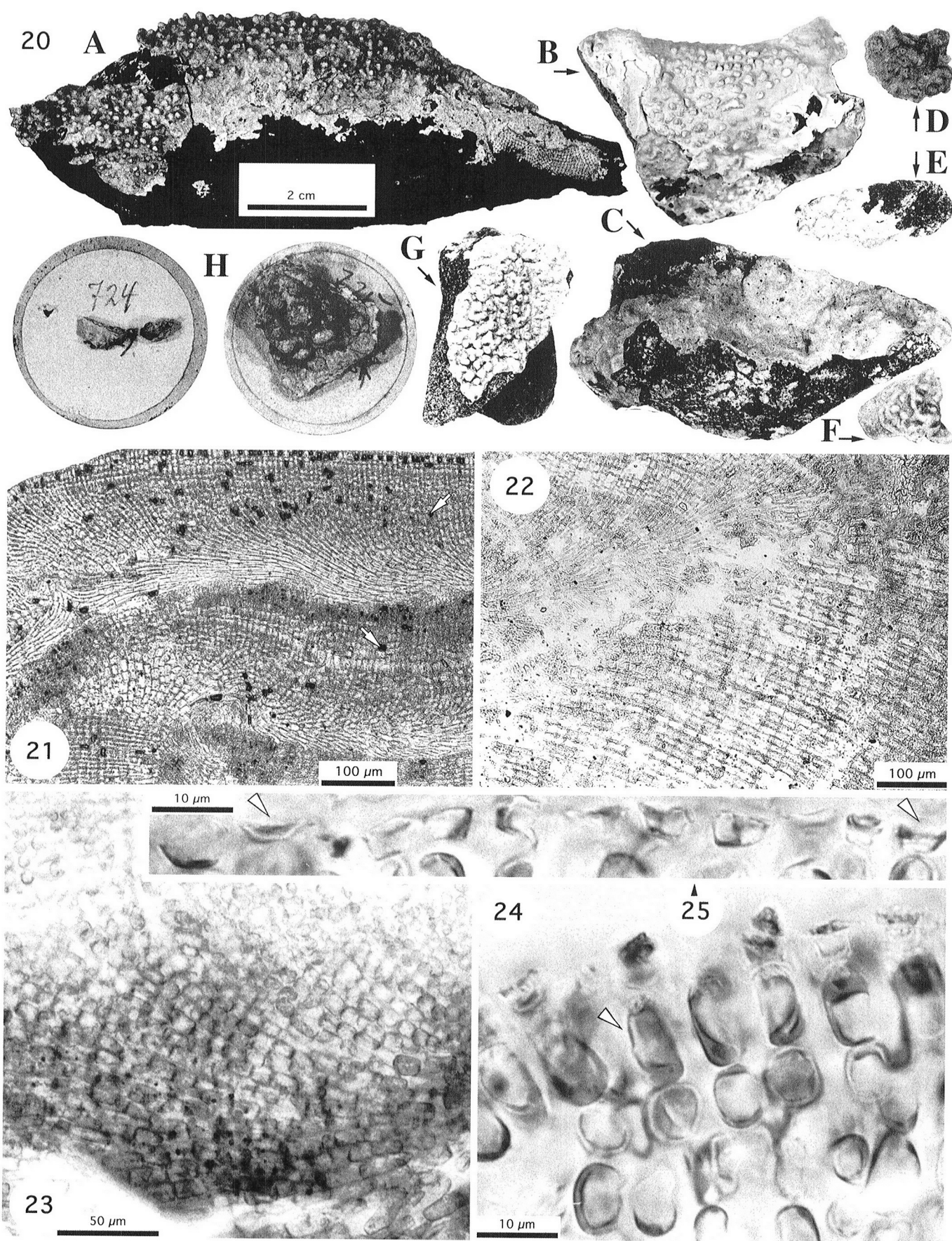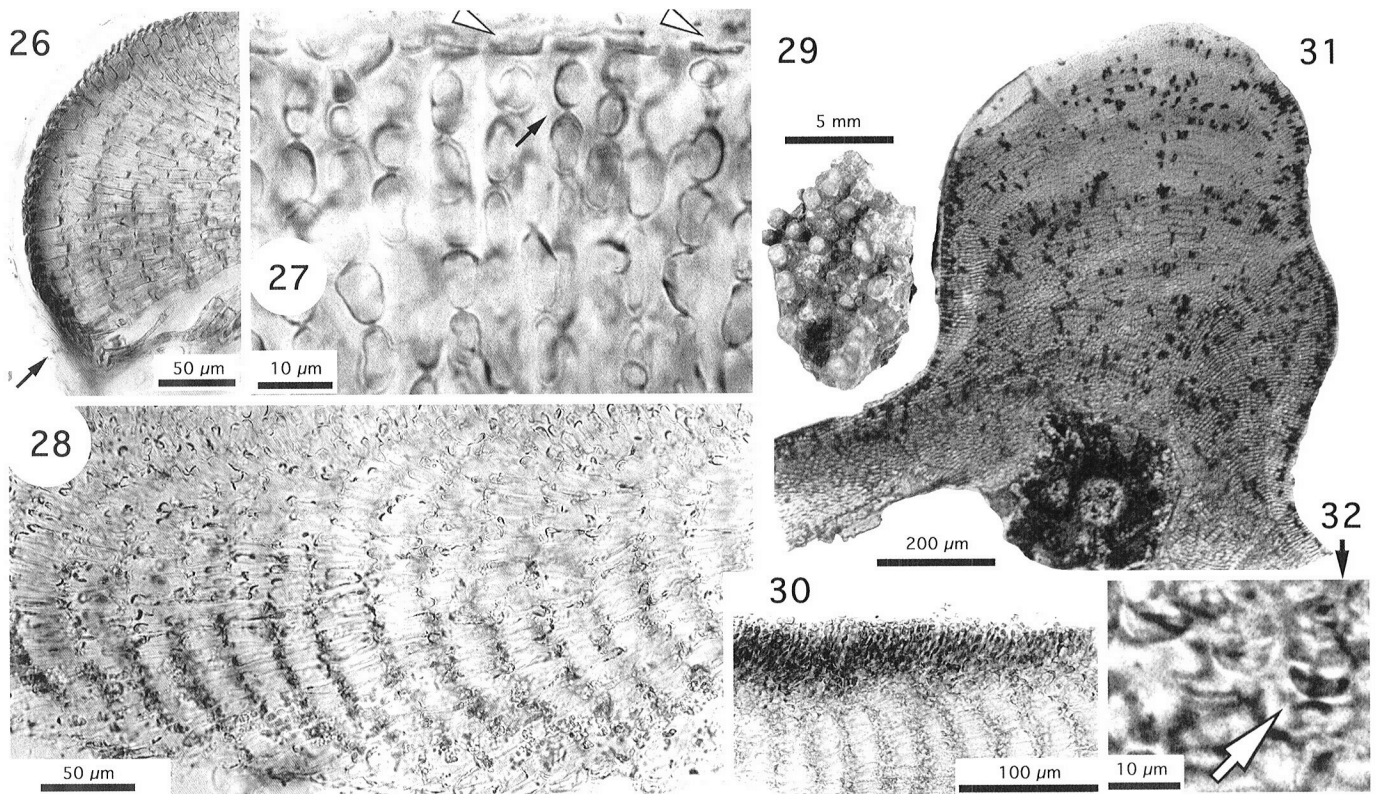
Figs 26–32. *Mesophyllum vancouveriense.*
  Figs 26–28. Lectotype of *Lithophyllum vancouveriense* in TRH.
    Fig. 26. Section at the growing margin showing a cuticle (arrow) protecting the terminal meristem and several arches of coaxial hypothallial cells.
    Fig. 27. Section near the thallus surface showing flattened epithallial cells (arrowheads) and subepithallial meristematic cells (arrow) more or less similar in size to cells below.
    Fig. 28. Section at the base showing a predominantly coaxial, arching hypothallium.
  Figs 29–32. Holotype of *Lithothamnion phymatodeum* f. *aquilonium* in TRH.
    Fig. 29. One of the largest fragments with erect protuberances.
    Fig. 30. Section of the thallus showing a predominantly coaxial, arching hypothallium.
    Fig. 31. Section showing an erect perithallial protuberance (slide #1448 in TRH).
    Fig. 32. Section at the floor of a uniporate conceptacle showing lunate SMCs (arrow).

thallium (Fig. 22), as judged from the length of cells ($\bar{x} = 24$ μm long, in 10 successive arches). The thallus surface is not well preserved and only a few terminal cells, squarish in shape, were located. Their identity as epithallial cells was not established. The ascending perithallium shows stratification in some parts of the thallus, and contiguous perithallial cells show fusions. Measurements of vegetative cells correspond to those given by Foslie in the protologue (hypothallial cells 14–32 × 6–8 μm; perithallial cells 7–12 × 6–8 μm). We have not established the identity of the material on these two slides, although it is apparent that the coaxial growth (Fig. 22) and

the size of hypothallial cells correspond to those found in the lectotype selected here (see below).

We examined further two of the specimens (A and B in Fig. 20) and a third diminutive fragment (not illustrated) of the remains of the type material. Specimen A is greyish in colour and adheres strongly to the substrate (detached fragments retained a thin layer of stone underneath). The erect terete protuberances are up to 1.2 mm long and 1–1.6 mm in diameter. The encrusting thallus reaches *c.* 7.5 cm in extent and is composed of a noncoaxial hypothallium, giving rise to a gradually ascending stratified perithallium (Fig. 23) ending in subepi-

Figs 20–25. Elements of the heterogenous type collection of *Lithophyllum vancouveriense* in TRH.
  Fig. 20. The seven larger specimens (A–G) and the two boxes with minor fragments (H) included in the type material in TRH. Specimen B is designated here as the lectotype.
 **Fig. 21.** Section showing superimposition of two independent lamellae (arrows) running in opposite directions (slide #724 in TRH).
  Fig. 22. An apparently horizontal section through the hypothallium showing coaxial growth (slide #724 in TRH).
  Fig. 23. Section near the base of the thallus showing a noncoaxial hypothallium (specimen A in TRH).
  Fig. 24. Section near the surface of the thallus showing elongate subepithallial cells (arrowhead) (specimen A in TRH).
  Fig. 25. Section at the thallus surface showing several flared epithallial cells (arrowheads) (specimen A in TRH).
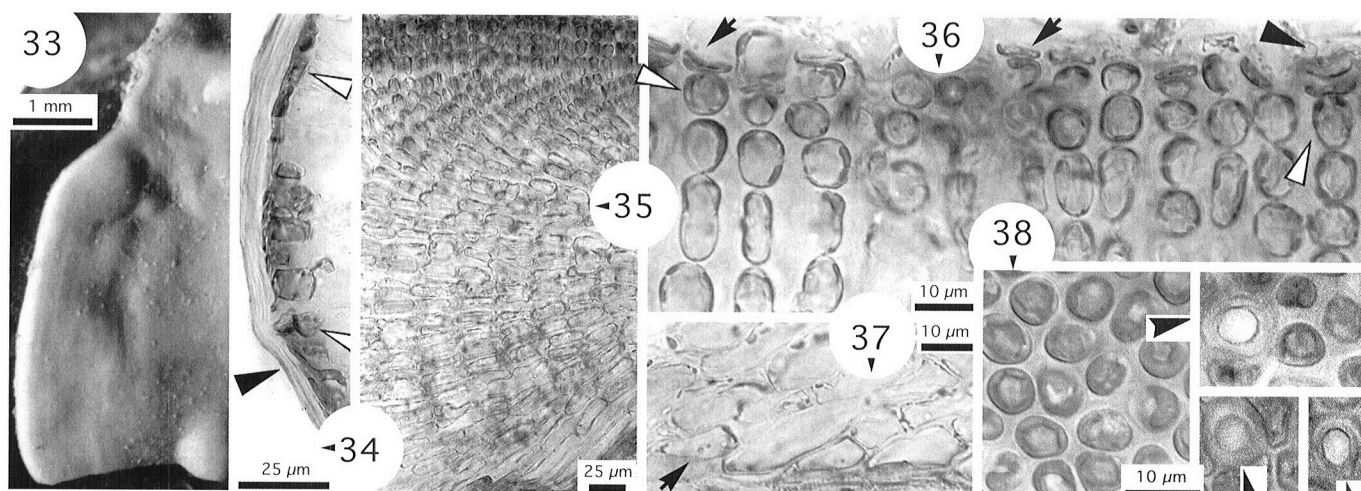
Figs 33–38. *Mesophyllum vancouveriense.*
Fig. 33. Surface view of an unattached margin with whitish border (UBC A34589).
Fig. 34. Section at the margin showing terminal meristematic cells (white arrowheads) covered by a cuticle (black arrowhead) (UBC A34583).
Fig. 35. Section of thallus near the margin showing a coaxial hypothallial growth and an ascending stratified perithallium (UBC A34583).
Fig. 36. Section near the surface showing single (arrows) or paired (black arrowhead) flattened epithallial cells and subepithallial meristematic cells of about size similar to cells below (white arrowheads) (UBC A34583).
Fig. 37. Section near the thallus base showing wedge-shaped terminal hypothallial cells (arrow) (UBC A34583).
Fig. 38. Surface view of epithallial cells (surface walls are sunken in some of them) and three presumed trichocytes (that have lost their projecting extension leaving a characteristic apical opening; arrowheads) (Paine #47A).

thallial initials that are longer than the cells below (Fig. 24). The hypothallium is 120–200 µm thick and composed of cells that are 11–23 µm long and 5–11 µm broad. The perithallium is up to 350 µm thick or more (not including protuberances) and composed of cells that are 7–18 µm long and 5–11 µm broad. Epithallial cells are usually damaged, but those that are intact are generally flared, 2–3 µm long and 5–7 µm broad (Fig. 25). Cell fusions are common between contiguous perithallial or hypothallial cells. Apparent raised conceptacles are lacking, although some crater-like depressions indicate that the specimen has been fertile. The elongate subepithallial initials, the noncoaxial hypothallium and the flared epithallial cells indicate that specimen A belongs to the genus *Lithothamnion*, most likely to *L. phymatodeum* that exhibits a similar habit and is common in this region (Steneck & Paine 1986, p. 231).

Specimen B is bleached and moderately attached to a (broken) piece of stone. Its thallus reaches *c.* 4.5 cm in extent and is 200–250 µm thick near the margin. Fragments can be easily removed using a scalpel, exposing a strongly coaxial hypothallium (in views from above or the side under a stereoscope). The margins are lobate and may grow free for a few mm. The thallus overgrows another encrusting coralline, the identity of which was not established. The terete protuberances are 0.6–1.3 mm in diameter and up to 0.8 mm high. They lie either apart (usually at a distance of 0.2–1 mm) or may coalesce (reaching 2.1 mm in diameter). In TS, the coaxial hypothallium is even more prominent, composed of long series of arching cells (Figs 26, 28). The terminal meristematic cells are protected by a cuticle (Fig. 26). The hypothallium gradually produces an ascending and partly stratified perithallium ending in subepithallial initials that are more or less similar in length to cells below (Fig. 27). New lamellae may develop from the perithallium (i.e. thallus regeneration) and

overgrow the parent thallus. The hypothallium is 150–250 µm thick and composed of cells that are 15–39 µm long and 5–8 µm broad. The perithallium is 60–100 µm thick (not including protuberances) and composed of cells that are 5–19 µm long and 5–8 µm broad. Epithallial cells are generally flattened, 3–4 µm long and 5–10 µm in diameter (Fig. 27). Cell fusions are common between contiguous perithallial or hypothallial cells. The presence of a predominantly coaxial arching hypothallium composed of longer cells (15–39 µm vs 11–23 µm found in specimen A), nonelongate subepithallial initials and flattened epithallial cells clearly indicate that specimen B is not conspecific with specimen A.

In the third fragment we examined, we also found a coaxial hypothallium (in parts of the thallus), elongate hypothallial cells (up to 45 µm long), and subepithallial meristematic cells more or less similar in size to the cells below. Epithallial cells are squarish or flattened, *c.* 2 µm long and 6–7 µm broad, or rarely 'flared-like'. Collectively, these characters suggest that this material is probably conspecific with specimen B.

From the above observations, we have concluded that the original type collection comprises specimens belonging to at least two different taxa, and therefore selection of a single type element is required. We designate specimen B as the lectotype because it agrees with parts of Foslie's protologue (the length of hypothallial cells and the presence of a coaxial hypothallium, as also seen in Fig. 22) and later accounts of the species (Steneck & Paine 1986; Scagel *et al.* 1989).

Despite the absence of reproductive structures in the lectotype, we consider its vegetative features (i.e. a predominantly coaxial, arching hypothallium, flattened epithallial cells, perithallial protuberances and the size of the somatic cells including subepithallial initials) sufficient to identify it as *M. vancouveriense*. Because no other local species could
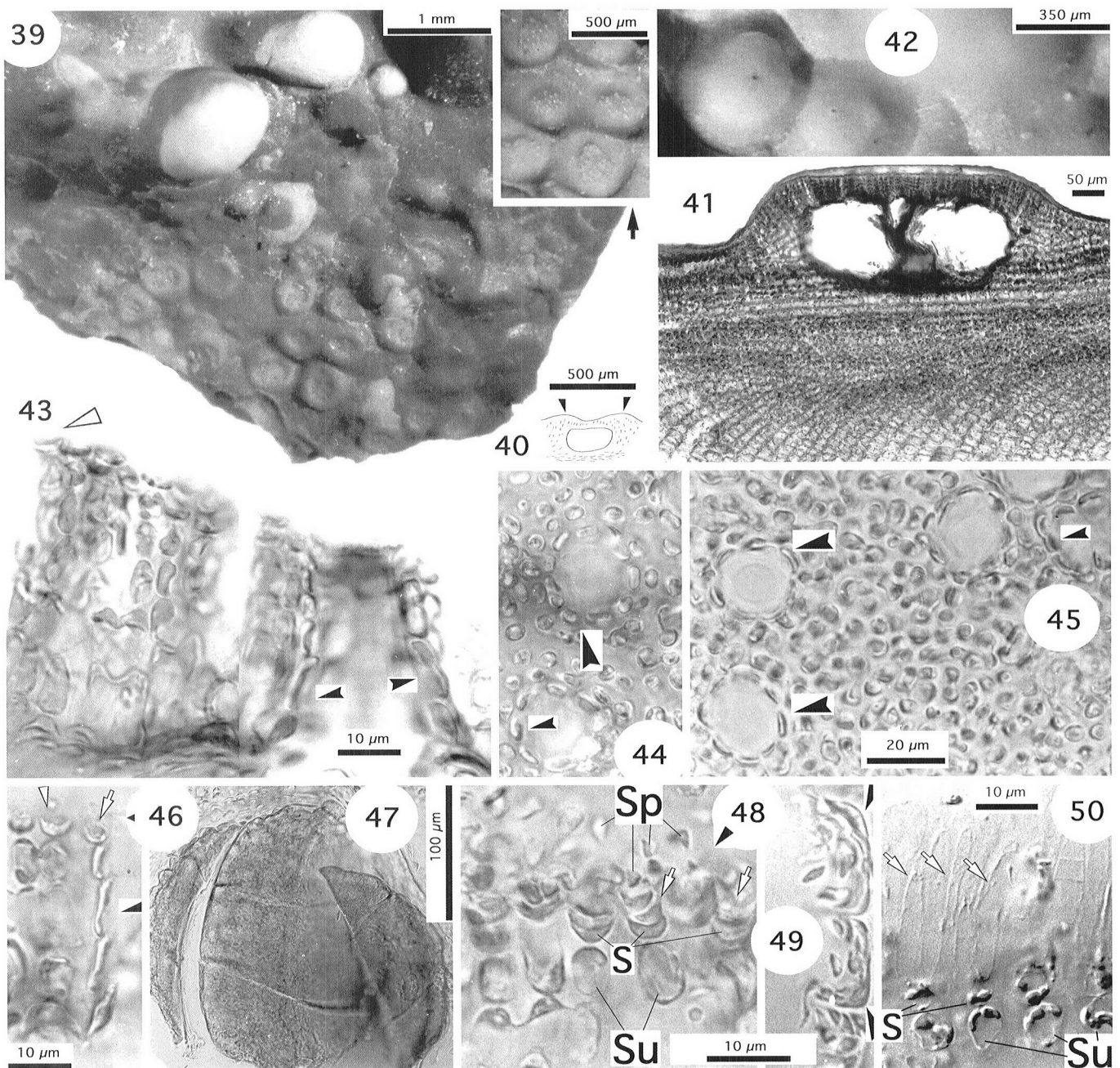
Figs 39–50. *Mesophyllum vancouveriense.*

Fig. 39. Thallus surface of a tetrasporophyte with numerous conceptacles, each provided with a distinct peripheral rim (magnified in the enclosed area; arrow) (Paine #80).

Fig. 40. Drawing of a section of a multiporate conceptacle with distinct rim (arrowheads) (Paine #80).

Fig. 41. Section of a multiporate conceptacle with less distinct rim. Note the coaxial hypothallial growth (UBC A33083).

Fig. 42. Male conceptacles (Paine #23 July 1994).

Fig. 43. Section of a multiporate roof showing the sunken pore plate and a conical pore canal where thinner pore cells (black arrowheads) are lining the canal near the base (Paine #47A). Note the 'flared-like' epithallial cell (white arrowhead).

Fig. 44. Surface view of a multiporate roof with two pores each surrounded by normal epithallial cells (arrowheads) (scale as in Fig. 45; Paine # January 1991).

Fig. 45. View of pores at a lower level of focus, showing thinner and wider cells (arrowheads) that tend to encircle the canal (Paine #47A).

Fig. 46. Section of a multiporate roof showing thinner cells (black arrowhead) bordering the left side of the canal. Note the roundish (arrow) and 'flared-like' (white arrowhead) epithallial cells that are flush with the surface (Paine #47A).

Fig. 47. Section of a multiporate conceptacle showing zonately divided sporangia (Paine #47A).

Fig. 48. Section of a male conceptacle at the floor showing supporting cells (Su) bearing single lunate SMCs (S). The SMCs support several spermatangia (arrows) that cut off spermatia (Sp) (Paine #23 July 1994).

Fig. 49. Section at the wall of a male conceptacle showing elongate SMCs (arrowheads) (Paine #23 July 1994).

Fig. 50. Section of an older male conceptacle at the floor showing supporting cells (Su) bearing roundish SMCs (S) with elongate residual walls of older spermatangia (arrows) (UBC A33979).
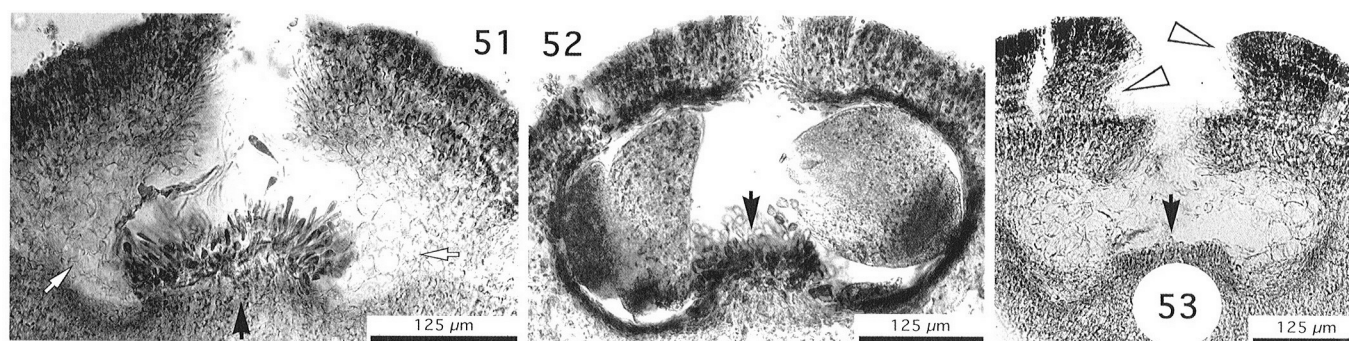
Figs 51–53. *Mesophyllum vancouveriense.*
 Fig. 51. Unfertilized carpogonial conceptacle where the central fertile zone (black arrow) is raised. Colourless cells fill up the peripheral region (white arrows) (UBC A33979).
 Fig. 52. Carposporangial conceptacle showing peripheral production of carposporangia around a raised central zone (arrow) (UBC A33979).
 Fig. 53. Older empty carposporangial conceptacle being embedded by further growth of filaments (arrowheads). Note the centrally raised zone (arrow) and the colourless cells that fill the chamber (UBC A33979).

be confused with the lectotype, we do not consider it necessary to select an epitype at present.

The material in UC (#397503) was studied by the second author (P.A.L.). This specimen is similar in morphology to that of the lectotype and a distinct coaxial hypothallium is visible with a hand lens in a fracture of this material. These observations are consistent with those of Steneck & Paine (1986, p. 233, figs 27, 29, 31). UC #397503 is labelled 'ex herb. Foslie' and should therefore be considered as part of the original material in TRH. It is possible that this element is an isolectotype (being a fragment of the lectotype), but until this can be demonstrated it should be recognized as a paratype.

The type material of *Lithothamnion phymatodeum* f. *aquilonium* survives as a single collection now 'badly fragmented . . . and detached from the host [*Laminaria* holdfast]' (Woelkerling 1993, p. 30). This has been illustrated by Printz (1929, pl. 4, fig. 12). The largest of the fragments (Fig. 29) is placed separately in a smaller box, whereas the rest of the material (minor fragments and three pieces of *Laminaria* holdfasts) are placed in a larger box together with three small paper sheets that read (1) 'Algae of Puget Sound, No 652 Distributed by W. A. Setchell and N. L. Gardner on holdfast of *Laminaria* Fort Casey, Whidbey Island, Wash. N. L. G. June 18, 1901' (printed); (2) 'Prep. 1448. Perith. 7 × 7, 9 × 7, 11 × 7, 14 × 6, 14 × 7, 11 × 9, 9 × 9, 9 × 6, 7 × 6, 18 × 7, 18 × 6, 18 × 9, Hypoth. 22 × 7, 18 × 7, 18 × 6, 22 × 6, 18 × 9, 14 × 7, 11 × 6, 11 × 7' (annotated in Foslie's hand); and (3) 'Emp. Konc. 150–400 μ. Ingen sp. [No sp.] Prep. 1447. Perith. 9 × 7, (11 × 7), 7 × 7, 7 × 7, 5 × 4, 6 × 6, 7 × 6, Hypoth. . . . 22 × 9, 14 × 7, 18 × 7, 18 × 6' (annotated by Foslie). The entire collection has been recognized as the holotype by Woelkerling (1993, p. 30).

Foslie's (1907, pp. 4, 5) description of f. *aquilonium* is in Norwegian and reads (in translation): 'It forms 180–400 μm thick crusts on *Laminaria*-roots, here and there with branch-like outgrowths 0.8–1.5 mm high and 0.6–0.8 mm in diameter, partly with thicker top up to 1 mm in diameter; carposporangial (?) conceptacles subconical, 250–400 μm in diameter. The crusts generally follow the substrate underneath. The hypothallium is relatively strongly developed, with [coaxial] arches, and forms short extensions upwards and downwards. The cells are mostly 18–22 μm long and 6–7, occasionally up to 9 μm broad. Perithallial cells are partly subsquarish, about

7 μm in diameter, partly and more usually vertically elongated, 9–18 μm long and 6–7, occasionally up to 9 μm broad. The conceptacles, that are few, are weakly developed and empty. This form looks in habit like a weakly developed *Phym. polymorphum*. It is possible that it represents an independent species, which cannot be judged until fully developed conceptacles are examined. The cells are often somehow longer and relatively thinner than in the typical *Lithoth. Phymatodeum*; but otherwise they are essentially similar. North coast of America: Puget Sound . . .'.

A coaxial hypothallium is clearly seen under a stereoscope in most fragments of the material, and in the sections (Fig. 30). In the largest fragment, protuberances (composed of perithallial cells) are up to 1.4 mm high and 1–1.4 mm in diameter; they are also evident in the Foslie slide (#1448; Fig. 31). Individual lamellae are 180–500 μm thick and are composed of a coaxial hypothallium up to 300 μm thick and an ascending perithallium up to 200 μm thick. Cells in the coaxial hypothallium reach 22 μm in length. The uniporate conceptacles in the two Foslie slides have empty chambers, c. 200 μm in diameter. However, in a sectioned fragment, conceptacles proved to be male, having chambers c. 250 μm in diameter and c. 80 μm high, with a c. 50 μm thick roof. Simple spermatangial structures are dispersed over the entire chamber, and lunate SMCs bearing spermatangia are present (in TS, Fig. 32) (see detailed description of this character below). Collectively, the data from the protologue and the new observations (i.e. a predominantly coaxial, arching hypothallium and unbranched spermatangial structures) indicate that f. *aquilonium* belongs to the genus *Mesophyllum*. Forma *aquilonium* exhibits the same vegetative and reproductive characters attributed here to *M. vancouveriense*, and therefore we consider the two taxa to be conspecific.

MORPHOLOGY: Plants reach at least 7 cm in extent and often adhere strongly to rocks, limpets (*Acmaea mitra* Rathke), *Mytilus* Linnaeus and *Laminaria* Lamouroux holdfasts, but become less adherent and finally detach from soft substrates (seen in herbarium specimens). Margins can be less adherent and sometimes even free (Fig. 33), and have a whitish border (cuticle) (Fig. 34). The thallus usually develops protuberances on its surface, at a distance of several millimeters from the margin, but individuals may also have a smooth surface (e.g.

UBC A33083 & UBC A34589). Protuberances develop from the perithallium, spaced about 1–4 mm apart. They are knobby, terete with roundish apices, usually unbranched, up to 4 mm long and 0.6–2.1 mm broad and composed of perithallial cells. The rest of the thallus surface is generally smooth, becoming glossy when dried. Ventral excrescences may develop when the thallus grows unattached; new lamellae develop adaxially from the perithallium and overgrow the parent thallus. The colour varies considerably, being bleached in old dried specimens to reddish-brown and even dark violet in dried fresh collections. Multiporate conceptacles usually have a prominent whitish rim and hence the pore plates are more or less sunken. The coaxial, arching hypothallium is clearly seen in thallus fragments under a stereoscope.

ANATOMY: The thallus is organized dorsiventrally and is up to at least 1 mm thick. It expands centrifugally along the periphery, whereas young lamellae may also develop from the upper part of the perithallium (hypothallial regeneration) and add to the thickness of the thallus. Terminal meristematic cells are covered by a cuticle (Figs 26, 34) and produce a predominantly coaxial hypothallium (Figs 28, 30, 35) that forms long series of arches (at least 30 can be seen in single sections; Fig. 41). The hypothallium gives rise to an ascending, more or less stratified, perithallium (Figs 35, 41) covered by one or two epithallial cells (Figs 27, 36). Subepithallial meristematic cells, prior to their division, are more or less similar in size to cells below (Figs 27, 36). Individual lamellae are 180–850 μm thick. The hypothallium is 100–400 μm thick; the perithallium is 40–550 μm thick (except of protuberances). Hypothallial cells are 14–50 μm long and 6–12 μm broad; those ending at the substrate are characteristically wedge-shaped (Fig. 37). Perithallial cells are 5–19 μm long and 5–10 μm broad. One or two epithallial cells develop on each perithallial filament and are generally flattened, 2–4 μm long and 5–10 μm in diameter; occasionally their surface wall is sunken and even 'flared-like' (Figs 43, 46, white arrowheads). Trichocytes (identified by their larger size and the characteristic apical opening after damage of the projecting extrusion) may rarely occur terminally (Fig. 38). Fusions are common between contiguous somatic cells. Secondary pit connections are absent.

REPRODUCTIVE STRUCTURES: The species is dioecious. Multiporate conceptacles are more or less raised or even flush with the surface (Figs 39–41); uniporate conceptacles are generally raised (Fig. 42). Multiporate conceptacles are 280–600 μm in external diameter and reach 140 μm in height. Neighbouring conceptacles may coalesce, reaching 900 μm in diameter. They have more or less sunken pore plates that are usually surrounded by a distinctive peripheral rim (Figs 39–41). Chambers are oblongate, 220–510 μm in diameter (up to 580 μm when two coalesce) and 120–300 μm high (n = 38). Conceptacle roofs are composed of five- to eight-celled filaments, reaching 55 μm in thickness at the periphery and 35–45 μm across the pore plate (Fig. 43), which is 160–400 μm in diameter. Conceptacle roofs are perforated by 9–66 pores (n = 36). Apical pore openings are c. 18 μm in diameter (Fig. 44) and generally wider towards the base (Figs 43, 45). Hence, the canals are conical. In surface view, pores are surrounded by 7–10 rosette cells that are normal epithallial cells flush with the surface (Figs 44, 46). In transverse roof sections, pore canals are bordered by five- to seven-celled filaments. Pore

cells near the base become thinner (Figs 43, 46, black arrowheads) and wider (Fig. 45, arrowheads), tending to encircle the canal (Fig. 45). Epithallial cells of the roof are flattened or roundish to hemispherical (Fig. 46, arrow), or even 'flared-like' (Figs 43, 46, white arrowheads). Zonately divided tri-(?)sporangia and tetrasporangia are 170–210 μm long and 50–100 μm broad (Fig. 47). Bisporangia are 160–180 μm long and 30–35 μm broad. Older conceptacles become gradually overgrown by peripheral filaments and finally embedded. Their chambers are then partly filled with nonstaining palisade cells.

Male conceptacles are up to 400 μm in external diameter and up to 50 μm high (Fig. 42). Chambers are 230–370 μm in diameter and 70–100 μm high (n = 5). The roof is c. 60 μm thick and has a central ostiole c. 40 μm in apical diameter. Mature conceptacles contain simple (unbranched) spermatangial structures on all surfaces of the chamber. On the floor and roof, supporting cells usually develop single lunate (in TS) SMCs that in their turn bear one or two spermatangia (Fig. 48). SMCs on the walls appear as elongated cells and usually support more than two spermatangia (Fig. 49). At the end of their fertility, SMCs become roundish or irregularly shaped and support cell wall remains of old spermatangia (Fig. 50).

Carposporangial conceptacles are 560–680 μm in external diameter and may project as much as 150 μm above the surface (n = 6). Their chambers are 380–590 μm in diameter and 160–240 μm high (n = 7). The roof is 50–110 μm thick and characteristically thicker near the centre where it has a conical ostiole, c. 30 μm in diameter at the apex and up to 120 μm in diameter at the base. In both fertilized and unfertilized conceptacles, the chambers become dumbbell-shaped, with the central fertile zone forming a pedestal (Figs 51–53). This presumably results from decalcification and dissolution of the peripheral cells of the floor, making space for the carposporangia (Fig. 52). Carposporangia are up to 180 μm in length and 70–120 μm broad. Older conceptacles become gradually embedded (Fig. 53) and their chambers are partly filled with palisade cells (Fig. 51).

COMMENTS: Steneck & Paine (1986) reported a seasonal presence of tetrasporangial and gametangial plants (the former occurring in winter and the latter in summer). The development of protuberances is apparently a variable character because we have also found individuals lacking such outgrowths. According to R. Paine (personal communication), the protuberances are a morphological response against grazing or are induced by competitive contact with another crust. Therefore, a smooth thallus may just signal that the plant has not yet been disturbed. Counting the mean length of a series of 20–35 coaxial arches, we observed considerable variation in hypothallial cell length within and between specimens: 25–33.5 μm in a single individual (Paine #39), and from 22 μm (UBC A33083 & A39995), 23.5 μm (UBC A38656), 32 μm (lectotype), to 39 μm (UBC A34583) between individuals. Among the new characters observed, we emphasize the presence of dumbbell-shaped carposporangial chambers and the presence of lunate SMCs in TS. The sporadic presence of 'flared-like' epithallial cells on the vegetative thallus or the multiporate roof (Figs 43, 46, white arrowheads) is probably an artefact resulting from the sunken surface wall that occurs

in degenerated cells. We have not observed typical flared cells in fresh material, and such cells are not reported by Steneck & Paine (1986, p. 234). Sterile foliose plants lacking protuberances resemble species of *Leptophytum* that we have also recorded in UBC collections mixed with *M. vancouveriense*. *Leptophytum* generally lacks a predominantly coaxial hypothallium that is clearly evident in all NE Pacific species of *Mesophyllum*. *Mesophyllum vancouveriense* differs from its NE Pacific congenerics in possessing three unique characters: (1) multiporate conceptacles with sunken pore plate and a distinct peripheral rim; (2) small (up to 400 μm in external diameter) male conceptacles; and (3) trichocytes in the outer perithallium (Table 1). Several UBC collections of *M. vancouveriense* have previously been referred to *M. lamellatum*, but we have not confirmed the presence of the latter species north of California. Collections UBC A40297, UBC A33986 and UBC A33985 (*pro parte*) belong to other melobesioid or mastophoroid species.

Mesophyllum conchatum (Setchell & Foslie) Adey (1970, p. 23)

Figs 54–91

BASIONYM: *Lithothamnion conchatum* Setchell & Foslie in Foslie (1902, p. 6).

HOMOTYPIC SYNONYMS: *Lithothamnion conchatum* f. *conchatum* (Foslie 1906a, p. 6, '*typicum*'); *Polyporolithon conchatum* (Setchell & Foslie) Mason (1953, p. 317).

LECTOTYPE: In TRH, unnumbered (Figs 54–64) including two slides (#729 and #1578); collected 10 January 1899, on *Calliarthron* (collector not indicated); previously illustrated by Mason [1953, pp. 317, 318, as *Polyporolithon*, '*Lectotype* – On '*Cheilosporum*' [*Calliarthron*], Pyramid Point near Pacific Grove, Monterey County, California, 8 January 1899, *Gibbs & Setchell 3057 a* (Herb. Mus. Nidaros.) ...'].

ISOLECTOTYPE: In UC 737624; designated by Mason (1953, p. 318, referred to as isotype).

TYPE LOCALITY: Point Joe, Monterey County, California.

HABITAT: Plants grow exclusively on geniculate corallines (*Calliarthron* Manza, *Bossiella* Silva, *Corallina* Linnaeus), more often found on *Calliarthron* in the littoral zone to at least 10 m depth (Adey & Johansen 1972, p. 160).

DISTRIBUTION: Confirmed only from the Pacific coast of North America. The species is reported from California (type locality), Oregon (Doty 1947, as *Lithothamnion*) and Washington, and the northernmost limit is defined at Langara Island, Queen Charlotte Islands, British Columbia (Hawkes *et al.* 1978, p. 103). The southern limit is Cambria, San Luis Obispo County, California (Mason 1953, p. 318, as *Polyporolithon*). In the NW Pacific Ocean, Zinova (1954, p. 360, as *Lithothamnion*) reported the species on *Amphiroa* Lamouroux from Tartar Strait, west of Sakhalin Island, and also from the Sea of Japan (Lebednik 1974), but these records have not been confirmed. Tasmanian plants referred to *M. incisum* (Foslie) Adey by Woelkerling (1996, fig. 84E, F) may belong to *M. conchatum* and re-examination of this material is also required (see Comments below).

MATERIAL EXAMINED: USA. California, Monterey, 10 January 1899, (collector not indicated), TRH [lectotype; Foslie's label (one of three) reads 'Amerika Monterey, Cal. 10.I.1899 *Lithoph. Conchatum* ... Setch. + Gibbs mscr ...']; California, Pigeon Point, 22 May 1966, *Johansen* 66-5-19, GB; California, Pescadero Point, C. California, 12 May 1968, *Johansen* 68-6-2, GB; Washington State, Tatoosh Island, epiphytic on *Calliarthron tuberculosum*, 26 October 2000, *Paine*, GB; Washington State, Tatoosh Island, collected in 'urchin barrens', 10 May 2001, *Paine*, GB. Canada, British Co-

lumbia. Vancouver Island, Staples Islet, off Numas Island, 50°46'2"N, 127°7'1"W, 3–7 m, tetrasporic, 29 August 1968, *Markham et al.* 22830, UBC A38656 [p.p.]; Vancouver Island, Lynne Point, 1.5° east of Hanna point, San Joseph Bay, 50°39.9'N, 128°19.1'W, 6 m, 31 August 1968, *Markham, PC & KB* 23111, UBC A39068; Vancouver Island, Cape Beach, Bamfield, rock west of Mud Cove, 48°47'48"N, 125°12'48"W, subtidal, rocky, moderately exposed, uniporate and multiporate, 13 June 1969, *Baillie & Pace* 25556, UBC A47985 [p.p.]; Vancouver Island, W coast, Arab Cove, 49°12'N, 123°57'W, low intertidal, 17 May 1969, *Baillie & Pace* 24598, UBC A40272.

OBSERVATIONS ON TYPE MATERIAL: The type material in TRH survives as a collection of several specimens placed in three typical Foslie boxes and including two slides (#729 and #1578). The entire collection has been designated as lectotype by Mason (1953, p. 317). Each of the boxes is separately annotated by Foslie: (a) '*Lithoth. conchatum* Monterey, Cal. Sp. konc. Foto ... 64 ...'; (b) '*Lithoth.* Monogr. Pl. X, figs 3–6'; and (c) 'Amerika Monterey, Cal. 10.I.1899 *Lithoph. conchatum* ... Setch. + Gibbs mscr *Lithoth. conchatum* Setch. + Fosl. Prep. 729 & 1578 Lithoth. Monogr. pl. X, figs 3–6'.

Box (a) includes a single fragment, box (b) includes the four specimens illustrated by Printz (1929, pl. 10, figs 3–6) (Fig. 54A–D), whereas the larger box (c) includes some fragments and five paper sheets with the following annotations in Foslie's handwriting: (1) 'Sp. konc. 500–800 μ in diameter ... 60–70 pores och Cyst. Konc.'; (2) (an illustration of a tetrasporangium with the annotation) '230 × 120 *L. conchatum*'; (3) '*Lithophyllum conchatum* Setchell + Gibbs mscr Monterey, Cal. Jan 10 89.'; (4) 'Prep. 729 500–700 μ 60–70 pores'; and (5) 'Prep. 729, California *L. conchatum* Perith. 18 × 9, 22 × 9, (29 × 11), 14 × 9, 11 × 9, 14 × 7, 14 × 11, 25 × 14, 18 × 11, 25 × 8, 25 × 10, 25 × 9, 25 × 11, 14 × 9, 29 × 9, 14 × 10, Hypoth. 25 × 9, 29 × 9, 26 × 9, 43 × 11, 40 × 11, 43 × 14, 36 × 11, 18 × 9, 14 × 9, 32 × 14, 32 × 9, 22 × 9, 29 × 18, 32 × 11, 25 × 11', (on the reverse side) 'Perith. cell mindre ... prep. 728'.

Three of the four specimens in box (b) (Fig. 54A, B, D) match Printz's (1929, pl. 10) figs 3, 4 and 5, whereas the fourth specimen in Printz (1929, fig. 6) survives only as a fragment (Fig. 54C). The plants are fertile and are attached to *Calliarthron*, either from their margin or ventrally, occasionally encircling the geniculate frond. All bear multiporate conceptacles, whereas specimen D (Fig. 54D) bears in addition uniporate (male) conceptacles and probably represents two individuals growing side by side.

A tetrasporangial and a sterile fragment from the third box (c) were examined anatomically. The thallus is *c.* 250 μm thick near the margin, reaching at least 550 μm in well-developed parts, consisting of a predominantly coaxial hypothallium with cells forming decumbent arches in long series (Figs 55, 56). Terminal meristematic cells are protected by a cuticle (Fig. 55, arrow). Hypothallial cells are 17–40 μm long and 8–15 μm broad, progressively giving rise to an ascending perithallium. Perithallial filaments end in single epithallial cells (Figs 57, 58) that are more or less roundish in TS, 4–8 μm long and 3–10 μm in diameter (Figs 57, 58). Descending hypothallial filaments end in wedge-shaped cells (Fig. 59). The perithallium has subepithallial meristematic cells that are distinctively longer prior to their division than the cells below (Fig. 57).
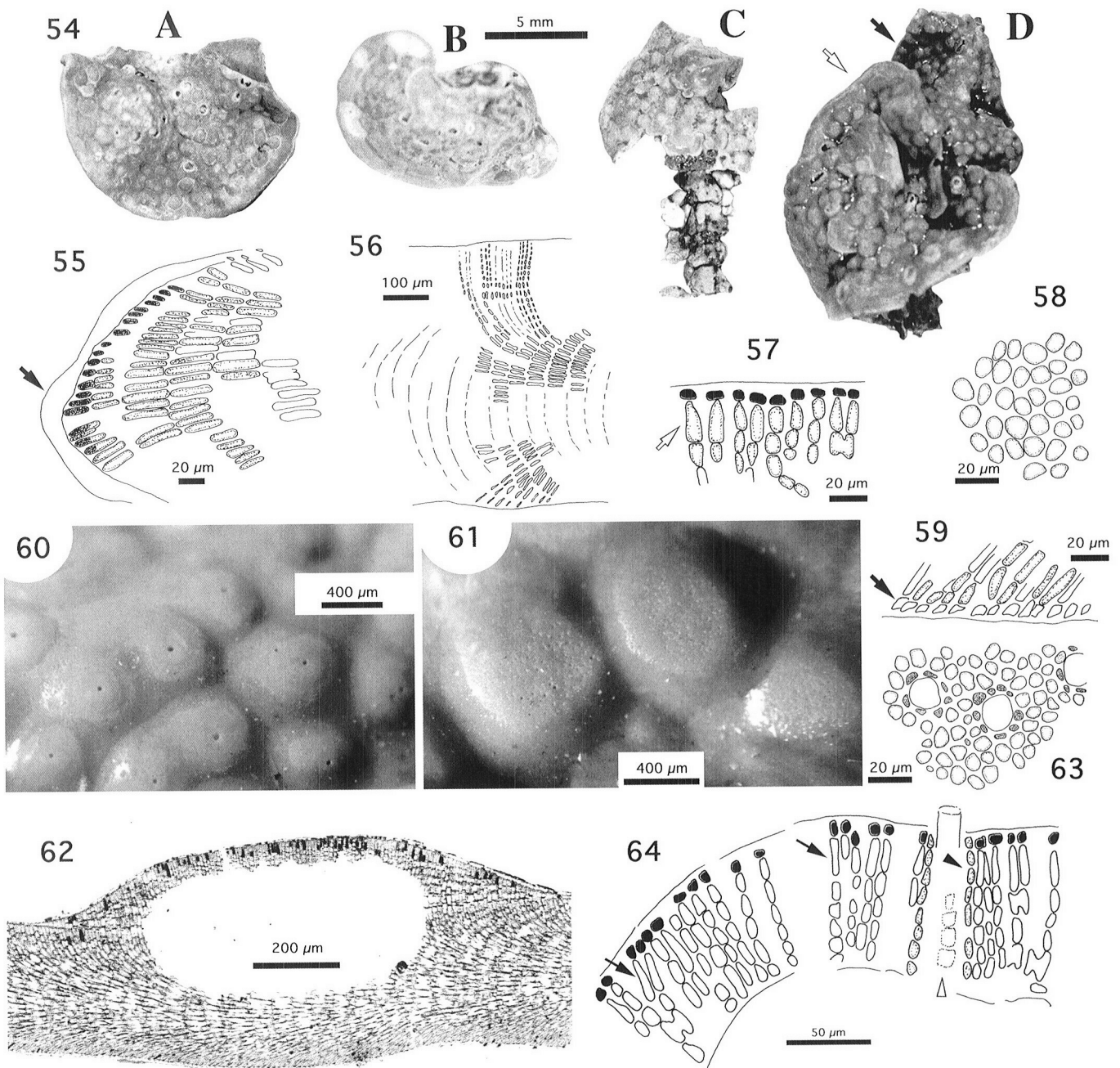
Figs 54–64. *Mesophyllum conchatum* (lectotype in TRH).
Fig. 54. The four specimens (A–D) illustrated in Printz (1929). Specimen D (two individuals?) bears both multiporate (white arrow) and uniporate (male) conceptacles (black arrow).
Fig. 55. Drawing of a section at the margin showing a cuticle (arrow) protecting the terminal meristematic cells (shadowed). Note the coaxial hypothallium.
Fig. 56. Drawing of a section of a well-developed thallus showing the coaxial, arching hypothallium and the ascending perithallium.
Fig. 57. Drawing of a section at the surface showing the elongate subepithallial meristematic cells (arrow) supporting roundish epithallial cells (in black).
Fig. 58. Drawing of epithallial cells of the vegetative thallus in surface view.
Fig. 59. Drawing of a section at the base of the thallus showing hypothallial cells ending in wedge-shaped cells (arrow).
**Fig. 60.** Uniporate (male) conceptacles from the individual in Fig. 54D indicated by the black arrow.
Fig. 61. Multiporate conceptacles from the individual in Fig. 54D indicated by the white arrow.
Fig. 62. Section of a multiporate conceptacle (slide #1578 in TRH).
Fig. 63. Drawing of the surface of a multiporate roof showing pores surrounded by normal epithallial and smaller cells (both types are shaded).
Fig. 64. Drawing of a section of a multiporate roof showing the cells (arrowheads) bordering a pore canal and elongate subepithallial meristematic cells (arrows). The roundish epithallial cells are indicated in black.
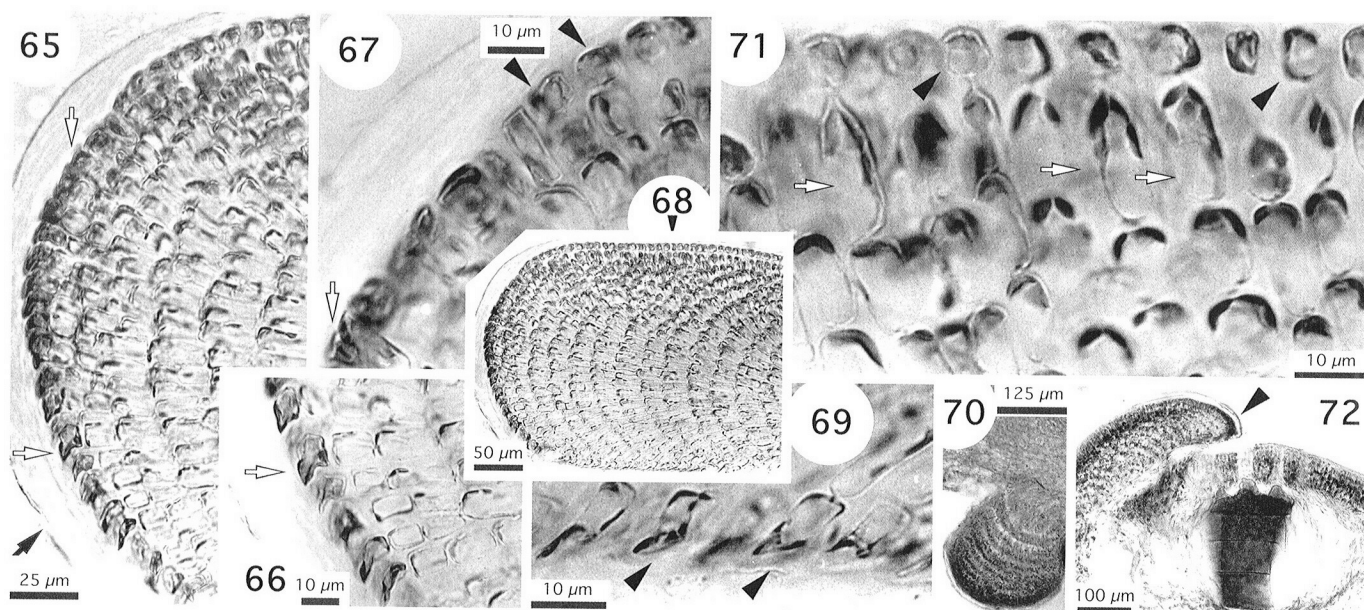
Figs 65–72. *Mesophyllum conchatum.*

Figs 65–67. Sections of the margin showing a cuticle (black arrow) protecting the terminal meristematic cells (white arrows) that produce a coaxial hypothallium. Note the early formation of epithallial cells (black arrowheads) from meristematic cells in Fig. 67 (UBC A39068).

Fig. 68. Section showing a series of coaxial arches of hypothallial cells (UBC A39068).

Fig. 69. Detail of the base showing the wedge-shaped terminal hypothallial cells (arrowheads) (UBC A39068).

Fig. 70. Formation of a ventral lamella (Paine #10 May 2001).

Fig. 71. Section at the surface showing the roundish epithallial cells (black arrowheads) and the elongate subepithallial meristematic cells (arrows) (UBC A39068).

Fig. 72. A tetrasporangial conceptacle being overgrown by a young lamella (arrowhead) (UBC A39068).

Uniporate (male) and multiporate conceptacles are generally crowded (Figs 60, 61), resulting in deformation of their typically circular outline. Male conceptacles are 250–560 μm in external diameter and slightly elevated (or even flush with the surface) (Fig. 60). Information about their content was obtained after removing one roof and investigating the conceptacle floor, which was flat and covered with spermatangial remains. Multiporate conceptacles are 500–1000 μm in external diameter ($n = 4$) and project slightly, having gently sloping side walls. They have convex to flattened roofs (Figs 61, 62) that are 70–85 μm thick, composed of five to seven cells and perforated by at least 63 pores ($n = 2$). Their chambers are 470–650 μm in diameter and 250–300 μm high ($n = 2$) (Fig. 62). Pores are 15–17 μm in apical diameter and are surrounded by 7–10 rosette cells that are either normal epithallial cells or smaller (Figs 63, 76). Smaller epithallial cells are also sporadically spread over the roof surface (Fig. 63). Epithallial cells of the vegetative thallus appear to be larger in diameter (Fig. 58). Filaments bordering pore canals are composed of gradually smaller cells towards the top (Fig. 64), which differ from contiguous roof cells. Tetrasporangia are 220–260 μm long and 50–150 μm broad ($n = 3$).

MORPHOLOGY: Plants reach 3 cm in diameter and are composed of subcircular or broadly lobate and usually superimposing lamellae (Fig. 54). Margins have a whitish border that represents a gelatinous layer (cuticle) (Fig. 65). Zonations that mirror the coaxial growth of the hypothallium are not evident on the thallus surface (or ventrally), although circular striations can be present at irregular intervals on the ventral side. Living plants are characteristically dark violet dorsally, becoming bleached as old herbarium specimens.

ANATOMY: The thallus is organized dorsiventrally, reaching at least 1 mm in thickness [said to be up to 1.5 mm thick in the protologue (Foslie 1902, p. 6)]. Individual lamellae are usually 250–600 μm thick, composed of a predominantly coaxial, arching hypothallium 190–400 μm thick [up to 800 μm according to Lebednik (1974)] (Figs 65, 68). The hypothallium is produced by terminal meristematic cells that are generally protected by a cuticle, 10–20 μm thick (Figs 65–67). Ascending hypothallial filaments progressively give rise to a stratified perithallium, whereas descending hypothallial filaments end in wedge-shaped cells (Fig. 69) or may develop ventral proliferations (Fig. 70). Hypothallial cells are 17–41 μm long and 7–15 μm broad [13–42 × 8–14 μm according to Lebednik (1974)]. The perithallium is 20–350 μm thick [up to 700 μm thick according to Lebednik (1974)] and is composed of cells that are 15–20 μm long and 7–11 μm broad [8–15 × 6–8 μm according to Lebednik (1974)]. Subepithallial meristematic cells [15 × 5–7 μm according to Adey & Johansen (1972)] are distinctively longer than cells below (Fig. 71). The epithallium is composed of one [or two according to Lebednik (1974)] roundish (in TS) cell, 4–9 μm long and 3–10 μm in diameter (Fig. 71). Cell fusions between contiguous perithallial or hypothallial cells are common (Adey & Johansen 1972, fig. 7). Dark-staining, hair-like cells embedded in the somatic thallus have been reported by Lebednik (1974). Secondary pit connections and terminal trichocytes are absent.

REPRODUCTIVE STRUCTURES: The species is dioecious and all conceptacles are raised. Older conceptacles become embedded in the thallus or lose their roofs and degenerate, or may even become embedded through thallus superimposition (Fig. 72).
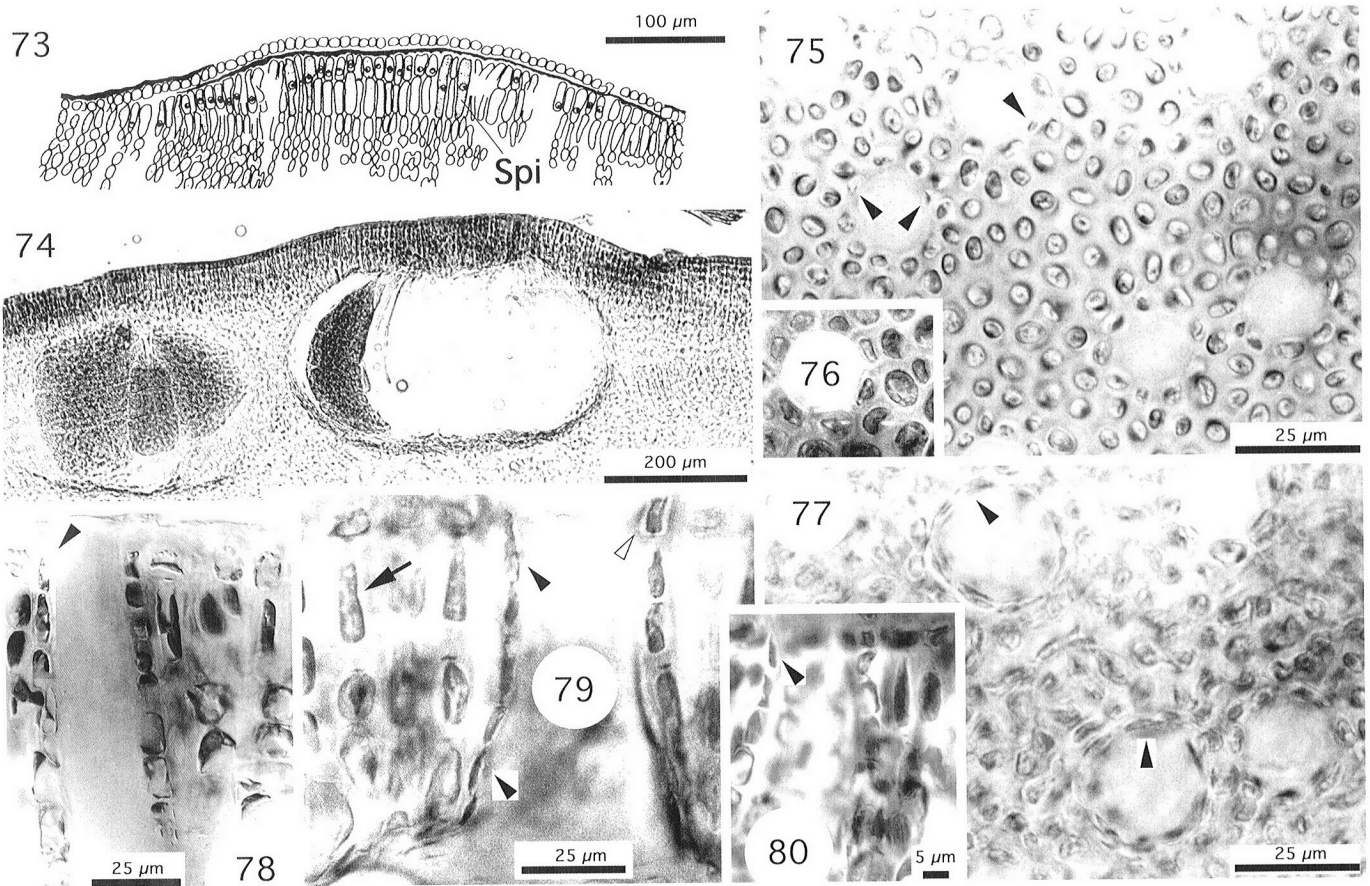
Figs 73–80. *Mesophyllum conchatum.*
Fig. 73. Early stage in the development of a multiporate conceptacle with sporangial initials (Spi) located below the epithallium [reproduced from Lebednik (1974, pl. 49, fig. 1)].
Fig. 74. Section showing two tetrasporangial conceptacles (UBC A40272).
Fig. 75. Surface view of a multiporate roof showing pores surrounded by normal epithallial and diminutive cells (arrowheads) (UBC A40272).
**Fig. 76.** Surface view of a pore from the lectotype material (scale as in Fig. 75).
Fig. 77. Surface view of the multiporate roof of Fig. 75 at a lower level of focus showing larger basal openings surrounded by thinner and wider cells (arrowheads) (UBC A40272).
Figs 78–80. Sections of multiporate roofs through pore canals, showing the variation in shape and size of cells bordering the canals: both thinner (black arrowheads) and normal roof cells (white arrowhead) may occur. Note that pore cells gradually diminish in size towards the apex, and may end below neighbouring epithallial cells (Figs 78, 80) and the elongate subepithallial meristematic cells (black arrow) (Fig. 78: Paine #10 May 2001; Fig. 79: UBC A40272; Fig. 80: Paine #26 October 2000).

Conceptacles are crowded, becoming partly overgrown by new conceptacles (hence some roofs appear to be sunken). Primordia of multiporate conceptacles occur just below the epithallium (Fig. 73; Lebednik 1974). Mature multiporate conceptacles have convex or flattened roofs, lack a peripheral rim and project moderately (Fig. 74). They are 500–1200 μm in external diameter ($n = 8$) [said to be 500–1300 μm by Mason (1953) and 445–825 μm by Lebednik (1974, table 32), whereas a mean value of 685 μm is reported by Adey & Johansen (1972, fig. 66)]. They reach 180 μm in height. Pore plates have an external diameter of between 250 and 510 μm and are 55–85 μm thick [72–103 μm thick according to Lebednik (1974, table 34), whereas Adey & Johansen (1972, fig. 66) reported a mean thickness of 62 μm]. The number of pores in individual conceptacles is 16–96 ($n = 13$) [said to be $c.$ 80 in the protologue, 60–70 in Foslie's unpublished notes, and between 30 and 70 according to Mason (1953)]. The apical pore opening is 15–18 μm in diameter (Figs 75, 76), becom-

ing wider towards the base (Figs 77, 79). Hence, pore canals are more (Fig. 79) or less (Fig. 78) conical. Each pore is surrounded by 7–10 rosette cells that either are similar in size to contiguous epithallial cells or distinctively smaller (Figs 63, 75). These two types of rosette cells are also seen in TS, where the smaller cells appear thinner and generally sunken below the surface (Figs 78–80, black arrowheads). Near the basal opening, pore cells may also be thinner (Fig. 79) and wider tending to encircle the canal (Fig. 77). In TS, roof filaments bordering the pore canals are usually composed of six to eight cells, whereas normal roof filaments are four- to seven-celled; this indicates that the bordering filaments consist of shorter cells, and these gradually diminish in size towards the apex (Fig. 78). Chambers are 410–780 μm in diameter (reaching 900 μm in two merging conceptacles) and 180–300 μm high. Tetrasporangia are 180–260 μm long (250–350 μm according to the protologue) and 50–150 μm broad. Both tetrasporangia and quadrinuclear bisporangia have been report-
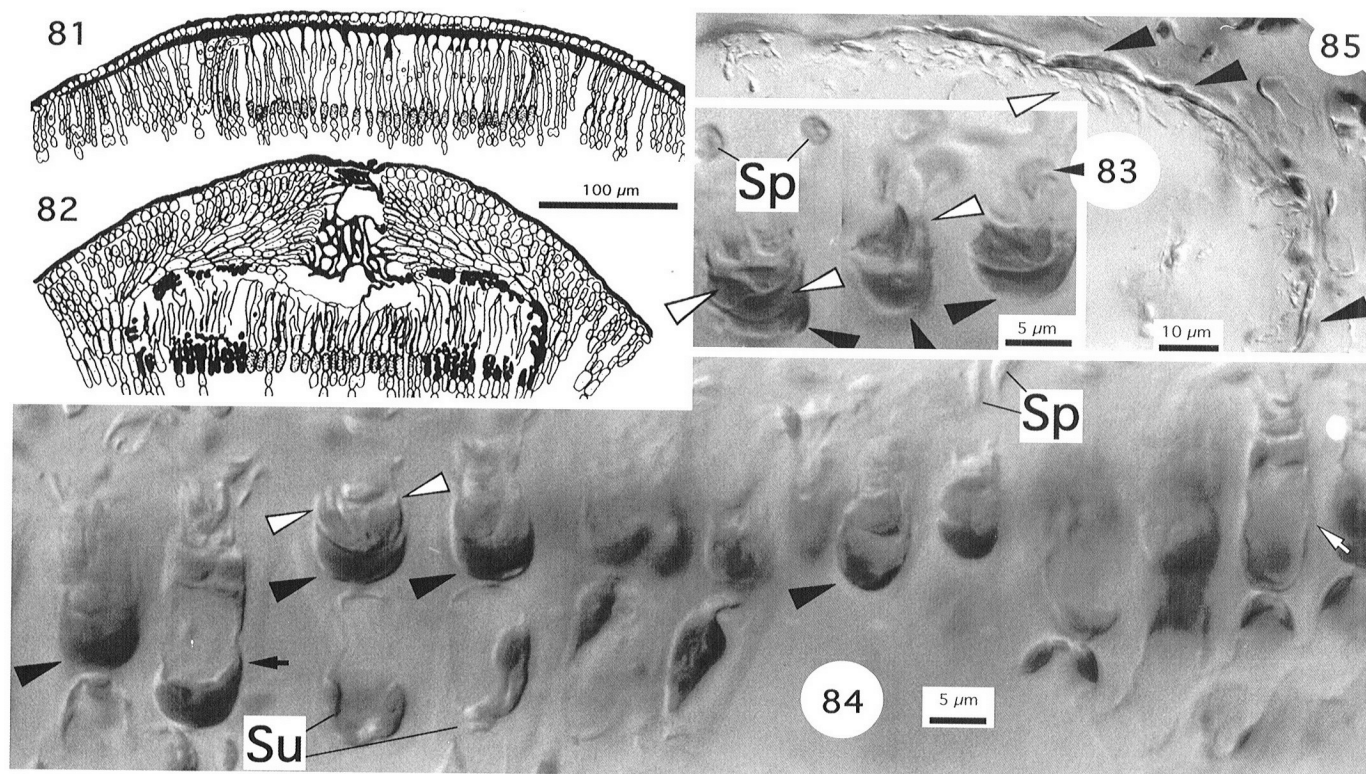
Figs 81–85. *Mesophyllum conchatum.*
Fig. 81. Early stage in the development of a male conceptacle. The initial cells (shaded) that will eventually produce SMCs are covered by a protective layer of elongate colourless cells [reproduced from Lebednik (1978, fig. 3)].
Fig. 82. Male conceptacle showing development of unbranched male structures on the floor, the walls and the roof [reproduced from Lebednik (1978, fig. 5)].
Figs 83, 84. Mature male structures on the floor showing lunate SMCs (black arrowheads) bearing several spermatangia (white arrowheads) which cut off spermatia (Sp) (Paine #10 May 2001). Note that some, apparently older, SMCs have fused with their supporting (Su) cell (Fig. 84, black arrow) to produce a colourless fusion cell (Fig. 84, white arrow) (Paine #10 May 2001).
**Fig. 85.** Male conceptacle roof showing elongate SMCs (black arrowheads) and wall residuals of spermatangia (white arrowhead) (Paine #10 May 2001).

ed by Adey & Johansen (1972, p. 170). Old multiporate conceptacles lose their roof and the resulting crater-like depressions are subsequently filled with cells.

Male conceptacles originate just below the epithallium, and the chamber is formed by the breaking down of elongate somatic (columnar) cells (Fig. 81). Adey & Johansen (1972, figs 46–49) have interpreted these columnar cells as the 'fertile area' of the conceptacle, but the spermatangial initials (that will develop into SMCs) comprise the darker-staining cells immediately below the columnar cells, which represent the protective layer (Lebednik 1978). At the periphery of this meristematic zone, there are those filaments that will form the roof of the chamber that appears after the degeneration of the columnar cells. SMCs are first produced on the floor in a ring, midway between the centre and the periphery, and extending to the periphery (Fig. 82). Mature spermatangial structures on the floor consist of typical lunate (in TS) SMCs, individually connected to normal perithallial (supporting) cells (Figs 83, 84). SMCs cut off several spermatangia. Spermatangial structures along the walls and the roof consist of SMCs that appear as elongate cells (Fig. 85). At later stages of their development, SMCs may fuse with their supporting cell (Fig. 84, black arrow) to produce colourless elongate fusion cells (Fig. 84, white arrow). Male conceptacles are 250–850 μm in ex-

ternal diameter and up to 210 μm high [278–721 × (–41)–154 μm according to Lebednik (1974, table 35)]. Their chambers are 320–470 μm in diameter and 50–120 μm high (*n* = 14) [186–443 × 72–154 μm according to Lebednik (1974, table 35)]. The roof is 60–100 μm thick [62–113 μm according to Lebednik (1974, table 35)], characteristically thicker near the centre where a conical ostiole measures *c*. 100 μm at the base and *c*. 20 μm across the apical opening [21–103 μm in diameter according to Lebednik (1974, table 35)]. Old male conceptacles become embedded in the perithallium.

Early stages in the development of female conceptacles are similar to male ones (Fig. 86; Lebednik 1974), starting with the transformation of subepithallial initials into an actively dividing zone. Mature carpogonial branches occur in the centre of the conceptacle, whereas nonfunctional carpogonial filaments occur at the periphery. The carpogonial branch is two-celled (Fig. 87) and the hypogynous cell may occasionally support two carpogonia. After presumed fertilization, the supporting cell fuses with adjacent cells, forming a fusion cell (Fig. 88). Gonimoblast filaments (connecting filaments *sensu* Lebednik 1977a) are produced from the fusion cell laterally and form carposporangia peripherally (Fig. 88). Adey & Johansen (1972, p. 176) have interpreted these filaments as a part of the fusion cell. Carposporangial conceptacles are 650–
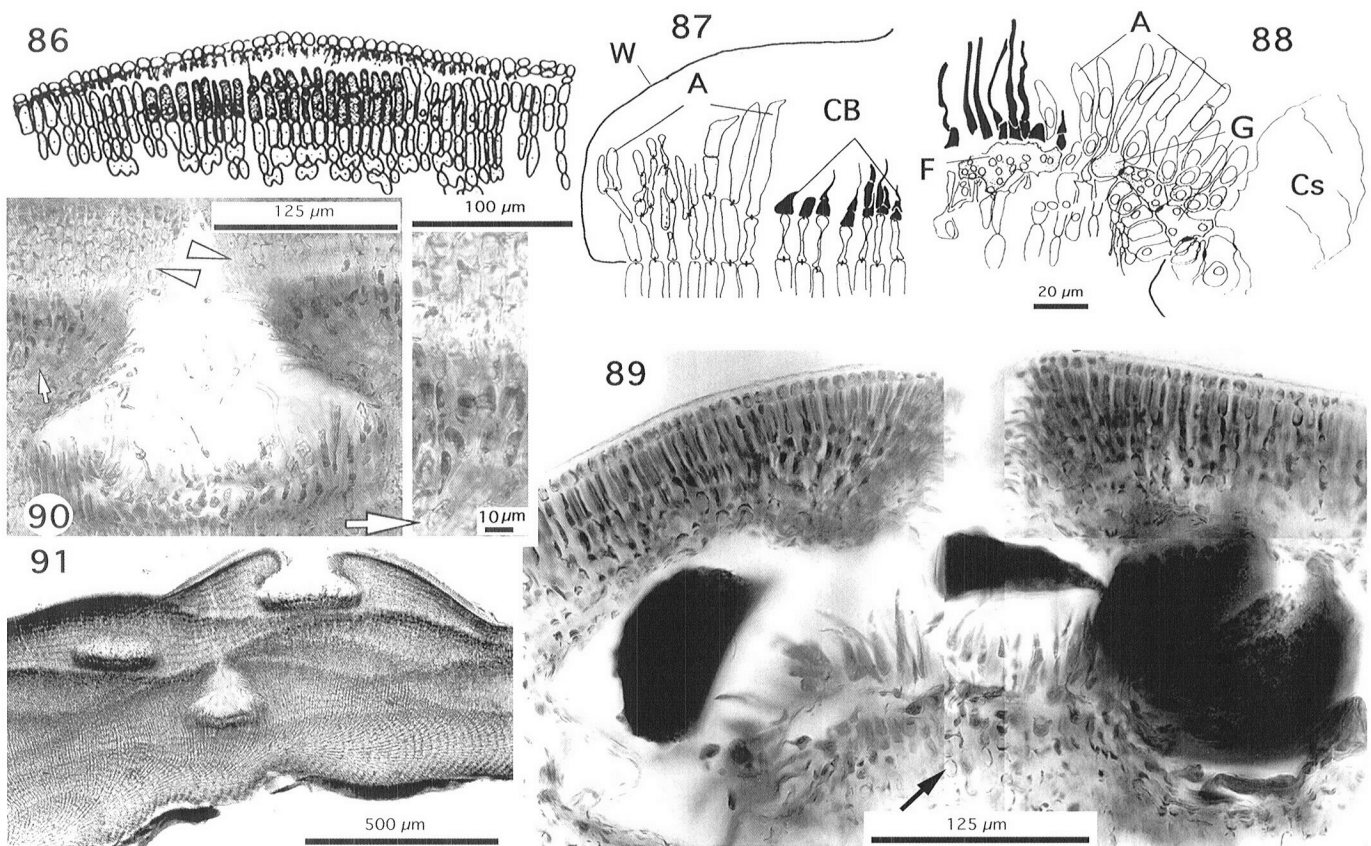
Figs 86–91. *Mesophyllum conchatum.*
Fig. 86. Carpogonial conceptacle initials (shaded) developing below the epithallium [reproduced from Lebednik (1977a, fig. 2)].
Fig. 87. Carpogonial branches (CB) and nonfunctional carpogonial filaments (A) developing on the floor and near the side wall (W) of the chamber [reproduced from Lebednik (1977a, fig. 7)].
Fig. 88. Postfertilization stage showing a central fusion cell (F) below the fertilized carpogonium, gonimoblast filaments (G) cutting off carposporangia (Cs) in the periphery of the fusion cell and the peripheral sterile filaments (A) [reproduced from Lebednik (1977a, fig. 12)].
Fig. 89. Mature carposporangial conceptacle with central pedestal (arrow) and peripheral carposporangia (Paine #10 May 2001).
Figs 90, 91. Embedded unfertilized carpogonial conceptacles (UBC A40272). Note that roof embedment (arrowheads in Fig. 90) is a result of further growth of the roof filaments. The left part of the roof (small arrow in Fig. 90) is magnified on the right (large arrow).

800 μm in external diameter and 70–150 μm high ($n = 8$) [371–670 × 0–113 μm according to Lebednik (1974, table 36), whereas a mean dimension of 900 μm is reported by Adey & Johansen (1972, fig. 69)]. Their chambers are distinctively dumbbell-shaped because the central part of the fertile zone forms a pedestal resulting from decalcification and dissolution of the peripheral cells of the floor to make space for the carposporangia (Fig. 89). Carposporangial chambers are 360–540 μm in diameter and 100–230 μm in height ($n = 8$) [278–515 × 165–247 μm according to Lebednik (1974, table 36)]. The roof is 60–110 μm thick [72–124 μm according to Lebednik (1974, table 36)], characteristically thicker near the centre where a conical ostiole measures 60–100 μm at the base and *c.* 20 μm at the apex [41–134 μm according to Lebednik (1974, table 36)]. Carposporangia are 50–150 μm in diameter. Unfertilized and old carposporangial conceptacles become embedded in the perithallium (Figs 90, 91).

COMMENTS: Two collections were cited in the original description of the species (Foslie 1902, p. 6): one from Monterey and the second one collected by *Yendo* at Vancouver Island (Mason 1953, p. 318). Later, Foslie (1906a, p. 6) described *Lithothamnion conchatum* f. *reclinatum* [now *Clathromor-*

phum reclinatum (Foslie) Adey] based on the Vancouver Island specimens. Apparently, some of these specimens were erroneously retained in the drawer containing the remains of the material of *L. conchatum* in TRH (Adey & Lebednik 1967, p. 68) that was designated as lectotype by Mason (1953, p. 317). She cited the type locality as Pyramid Point, Monterey County, California, now officially known as Point Joe (Smith 1944, p. 8). Mason erroneously gave the date of collection of the lectotype as 8 January (Adey 1970, p. 23; Woelkerling 1993, p. 57). Mason's selection of *Lithothamnion conchatum* as the generitype of *Polyporolithon* (Mason 1953, p. 316) has rendered this genus a junior synonym of *Mesophyllum* (Adey 1970). We have found little variation of hypothallial cell length, ranging from 22 μm (UBC A39068) and 24 μm (UBC A38656) to 27 μm (Paine #10 May 2001), counting the mean length of a series of 20–30 coaxial arches in three individuals. Conceptacle embedment apparently results either from thallus superimposition (Fig. 72) or from further growth of the perithallial filaments on the conceptacle roof (Fig. 90, arrowheads). The presence of both embedded (gametangial) and degenerated (tetrasporangial) conceptacles in *M. conchatum* indicates that these two processes are independent and not mu-

tually exclusive. According to Lebednik (1974, 1977a, p. 391, fig. 14), zygote transfer from the carpogonium occurs via a transfer tube that develops from the base of the carpogonium and leads to the supporting cell (that subsequently fuses with adjacent cells to form a large fusion cell). The nature and origin of the embedded hair-like cells in the somatic thallus (Lebednik 1974) remain to be clarified, but these structures are not considered here to be homologous to the terminal hair cells of *M. aleuticum* or the trichocytes of other species of *Mesophyllum*. Amongst its NE Pacific congenerics, *M. conchatum* is clearly distinguished by its subcircular thallus growing on articulated corallines. The species most closely resembles *M. lamellatum*, which differs in having an irregularly foliose thallus with apparent periclinal zonations on its margin. Tetrasporangial plants are easily distinguished because in *M. conchatum* the conceptacles are moderately projected, larger and perforated by a greater number of pores than in *M. lamellatum*. The morphology of pore cells is similar in both species.

Collections UBC A40394 and UBC A42792, referred previously to *M. conchatum*, belong to *Clathromorphum reclinatum*. This and *C. parcum* (Setchell & Foslie) Adey are the only other species epiphytic on *Calliarthron* likely to cause confusion in identification. However, *Clathromorphum* generally possesses nonraised, smaller conceptacles and lacks a coaxial hypothallium; *C. parcum* additionally has a prominent ventral attachment (Adey & Johansen 1972).

Illustrations of a Tasmanian collection (LTB 13235) from the upper sublittoral (1–2 m), referred to *M. incisum* by Woelkerling (1996, fig. 84E, F), show the type of pore cells (progressively shorter and thinner) and the shape of epithallial cells (roundish) typical of *M. conchatum*. It should be noted that *M. incisum* is also common on geniculate corallines and exhibits a subcircular thallus but anatomically possesses elongate subbasal pore cells and flattened epithallial cells (Woelkerling & Harvey 1993, fig. 14D).

Mesophyllum lamellatum (Setchell & Foslie) Adey (1970, p. 25)

Figs 92–118

BASIONYM: *Lithothamnion lamellatum* Setchell & Foslie in Foslie (1903, p. 4).

LECTOTYPE: In TRH, unnumbered (Figs 92, arrows, 94–107); collected by *Setchell & Gibbs* (#3075), 9 January 1899; previously illustrated by Printz (1929, pl. 8, fig. 4, as *Lithothamnion, pro parte*); designated herein.

PARATYPES: In UC 266384; referred to as isotype by Mason (1953, p. 330, as '*Lithothamnium*'). In UC 737622; illustrated by Mason (1953, pl. 33, fig. d, pl. 36, fig. A, as '*Lithothamnium*', referred to as isotype) and Lebednik (1974, pl. 56, figs 1–3, referred to as isotype). In TRH, unnumbered (Fig. 93); previously illustrated by Printz (1929, pl. 8, fig. 5, as *Lithothamnion*).

TYPE LOCALITY: Cypress Point, Monterey County, California.

HABITAT: The type material was collected in the littoral zone, growing on geniculate coralline fronds (and stones according to Foslie's protologue and annotations in TRH). The lectotype is attached to a species of Gelidiaceae and a species of *Leptophytum*. All other examined material is from the low littoral zone, and several specimens were found growing together with the same species of *Leptophytum*.

DISTRIBUTION: We confirm the presence of *M. lamellatum* only in Monterey County, California, although the species is widely reported from littoral and sublittoral habitats from Isla Asuncion, Baja

California (Dawson 1960, p. 18, as '*Lithothamnium*'), north to Duxbury Reef, Marin County, California (Mason 1953, as '*Lithothamnium*'), off Mendocino City, California (Dawson 1965, as '*Lithothamnium*'), in Oregon north to Boiler Bay (Doty 1947, as '*Lithothamnium*'), and to Barkley Sound (Scagel 1973, as '*Lithothamnium*') and Melville Island (Hawkes *et al.* 1978, p. 103), both in British Columbia. Dawson (1960, p. 19, as '*Lithothamnium*') mentioned that the species is abundant in the deep sublittoral in the southern part of its range and he also reported the species at 21 m depth off Mendocino City, California (Dawson 1965, p. 26, as '*Lithothamnium*'). All these records are in need of verification. We have studied over 40 UBC collections from British Columbia referred to *M. lamellatum* and found that these are misidentified *M. vancouveriense* or other melobesioid and mastophoroid species.

MATERIAL EXAMINED: **USA, California.** Monterey County, Cypress Point, 9 January 1899, *Setchell & Gibbs* 3075, TRH [lectotype & paratype; Foslie's two (of three) labels read '#3075 *Lith. lamellatum* Setch. & Fosl. Kalifornien Cypress Point Monterey 9.I.1899 leg. W.A. Setchell & R.E. Gibbs . . .' and '*Lithoth. lamellatum* Setchell & Fosl. . . . *Lithophyllum fragile* Ms . . . on stones and corallines. Cypress Point, Monterey County. W.A.S. and R.E. Gibbs, 9 January 1899']; Monterey County, Cypress Point, 9 January 1899, *Setchell* 3075, UC 266384 (paratype: the two labels read: 'Isotype of *Lithothamnion lamellatum* Setchell & Foslie . . .' and '*Lithothamnion lamellatum* Setchell & Foslie On stones and corallines, Cypress Point, Monterey Cou. W.A. Setchell 3075 January 9, 1899'); Monterey County, Pyramid Point, Pacific Grove, December 1906, *Nichols* 131, UC 745618 [p.p.]; Monterey County, Cypress Point, Pacific Grove, near mean low water, January 1919, *Gardner* 3583, UC 745601; Monterey County, Cypress Point, tetrasporic, 13 October 1928, *Roush* 111, UC 739466 [p.p.]; Monterey County, Point Lobos, male, 13 October 1928, *Roush* 104, UC 739469 [p.p.].

OBSERVATIONS ON TYPE MATERIAL AND LECTOTYPIFICATION: The original collection in TRH is placed in a round box annotated in Foslie's handwriting '#3075 *Lith. lamellatum* Setch. & Fosl. Kalifornien Cypress Point Monterey 9.I.1899 leg. W.A. Setchell & R. E. Gibbs, Prep. 825, 826. Lith. monogr. pl. 8, fig. 4–5'. It includes three specimens, smaller fragments, and three labels each annotated by Foslie: (1) 'Sp. konc. 350–600 μm Skorp. tjock [Crust thick] . . . 300–700 μm, Hyp. cell 18–36 μm 5–9 μm bred . . . Per. cells 8–14 μm 6–7 μm bred . . . (undersidan & apikal 15-22-24 . . . 6–10 μm brede'; (2) 'Skört [Fragile] hypothallium'; and (3) '*Lithoth. lamellatum* Setchell & Fosl. [and then in a different handwriting (Setchell?)] . . . *Lithophyllum fragile* Ms . . . on stones and Corallines. Cypress Point, Monterey County. W.A.S. and R.E. Gibbs. Jan. 9, 1899' (Fig. 93, arrow). Two of the specimens grow side by side (Fig. 92) and appear as a single one in Printz (1929, pl. 8, fig. 4), whereas the third specimen (Printz 1929, pl. 8, fig. 5; Fig. 93) survives only as a part (and possible minor fragments left in the box). Of the two specimens growing together, the largest is a tetrasporophyte and is designated here as the lectotype (Fig. 92, arrows). The specimen that is attached to the lectotype (Fig. 92, arrowheads) is sterile and belongs to a different taxon that will be described elsewhere as a new species of *Leptophytum*. The third specimen is also a tetrasporophyte and is recognized here as a paratype (Fig. 93); it is not a part (duplicate) of the lectotype and differs from it at least by its colour (see below). The two Foslie slides (#825 and #826) mentioned in Foslie's annotations (see also Woelkerling 1993, p. 135) were not found in the original collection. Because the type material belongs to at least two different taxa, it is possible that the protologue was based on heterogeneous material. However, only the lectotype and the paratype are tetrasporophytes and because Foslie used tetrasporangial characters to describe the species, the lectotype se-
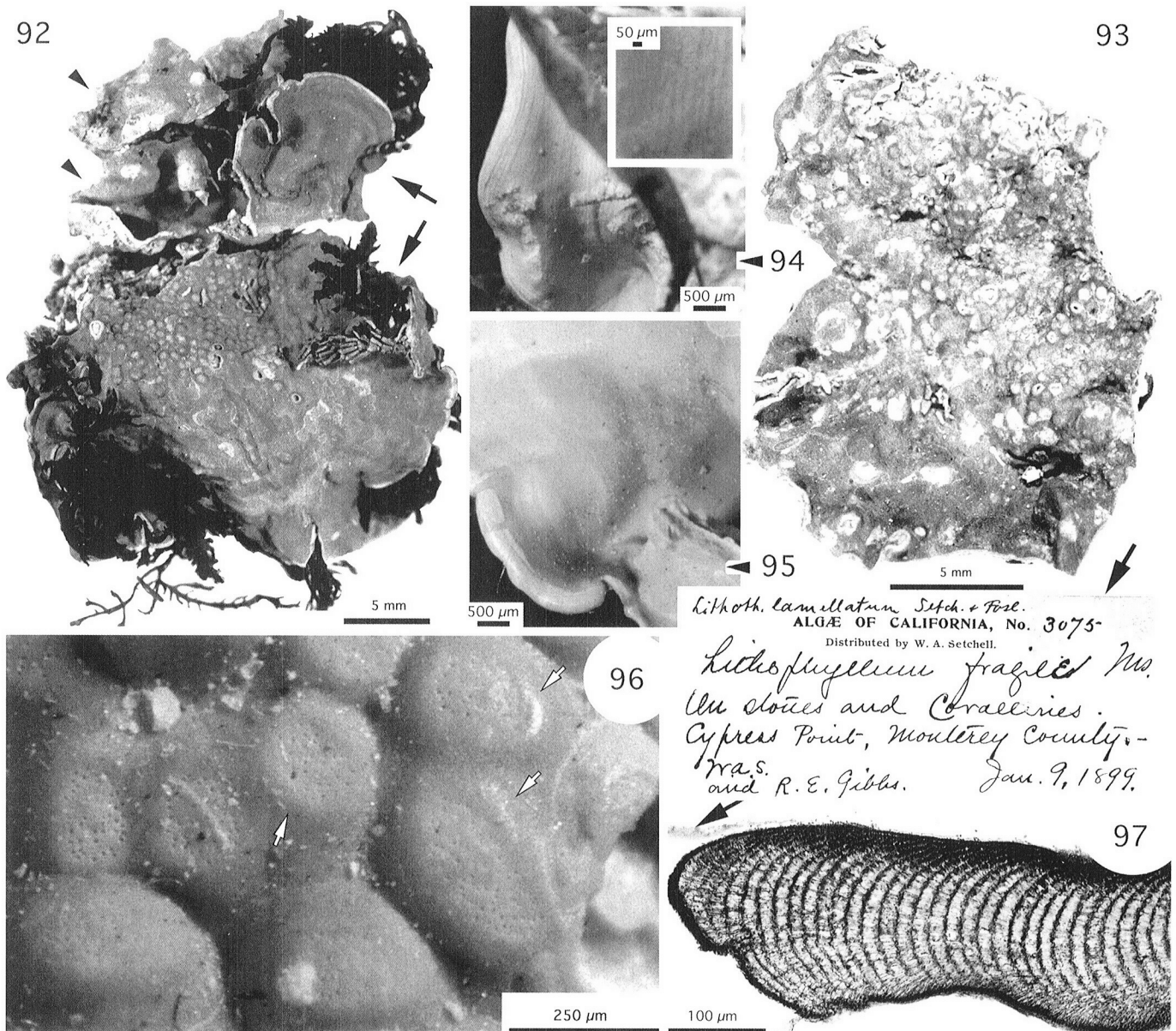
Figs 92–97. *Mesophyllum lamellatum.* Elements of the type collection in TRH.
    Fig. 92. The lectotype specimen in TRH (arrows). Arrowheads indicate a species of *Leptophytum* growing attached to the lectotype.
    Fig. 93. The paratype specimen in TRH. The label below (arrow) is one of the three found in the type collection.
    Fig. 94. Ventral view near the margin of the lectotype specimen, showing apparent periclinal zonations (see magnification in the enclosed area).
    Fig. 95. Surface view near the margin of the lectotype specimen, showing vague periclinal zonations and a whitish border (cuticle).
   **Fig. 96.** Surface view of multiporate conceptacles of the lectotype specimen, showing flattened pore plates surrounded by an indistinct rim (arrows).
    Fig. 97. Section of a young thallus showing a cuticle (arrow) protecting the terminal meristem, and a coaxial hypothallium (lectotype in TRH).

lected here represents one of the two tetrasporophytes found in the original material.

    The lectotype, as also illustrated by Printz (1929, pl. 8, fig. 4), reaches *c.* 3 cm in extent and is nearly intact apart from the side where multiporate conceptacles occur (from where a smaller fragment was also removed for the present study). Its thallus has a smooth surface, becoming irregular where it follows the substrate. The thallus lacks erect protuberances and has entire lobate proliferations that have a distinctive whitish border (cuticle) (Figs 92, 95). Marginal proliferations may overgrow the parental thallus partly attached to a species of Gelidiaceae. An apparent coaxial hypothallial growth is evident in side views of the thallus (under a stereoscope); zonations (which mirror the coaxial growth) are clearly evident on the ventral side (Fig. 94) and vaguely on the surface (Fig. 95). Ventral excrescences are present. Multiporate conceptacles occur in the central part of the thallus and are crowded (Fig. 96). The colour of the vegetative thallus is dark brownish-red. Individual lamellae are organized dorsiventrally and are 350–520 μm thick; they consist of a predominantly co-
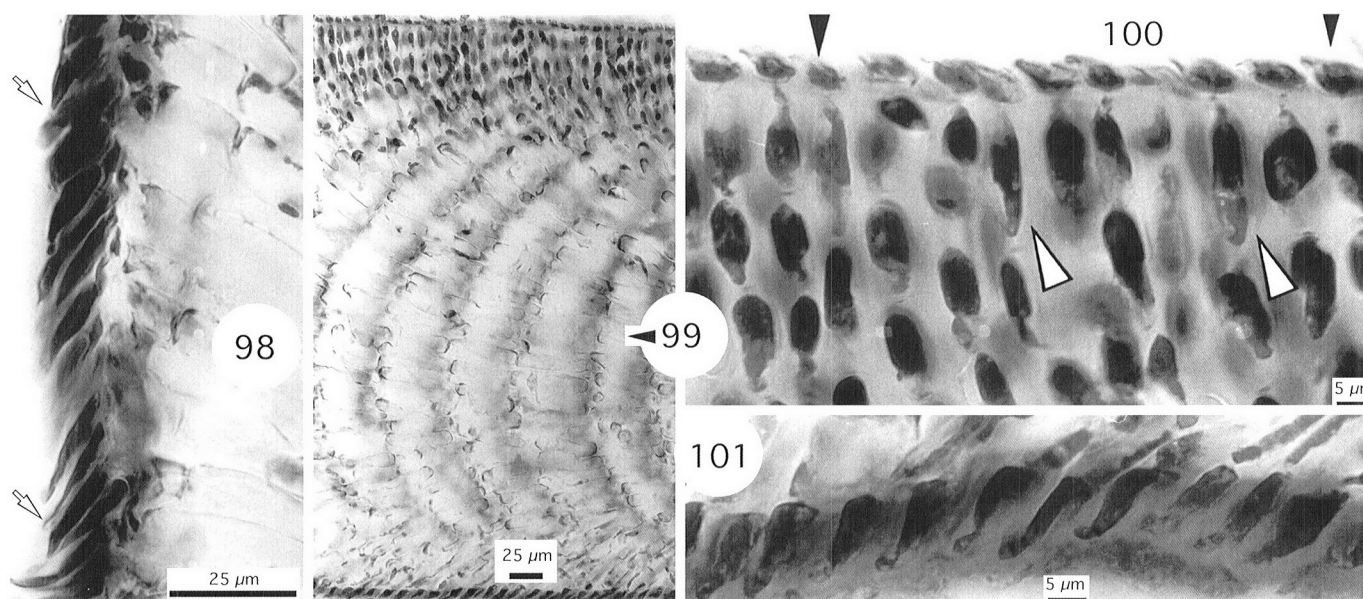
Figs 98–101. *Mesophyllum lamellatum* (lectotype in TRH).
Fig. 98. Section of the margin showing the terminal meristematic cells (arrows).
Fig. 99. Section a few cell rows behind the margin showing the coaxial arching hypothallium.
Fig. 100. Section at the surface showing a nonstratified perithallium and squarish to flattened epithallial cells (black arrowheads) supported by distinctively elongate meristematic cells (white arrowheads). Note that several epithallial cells look 'flared-like'.
**Fig. 101.** Section near the base showing the terminal wedge-shaped hypothallial cells.

axial hypothallium (Fig. 97), 170–320 μm thick, in which cells form decumbent arches in long series and grow by terminal synchronous divisions and elongations (Figs 98, 99). Hypothallial cells are 20–47 μm long and 10–12 μm broad and give rise to a gradually ascending perithallium (Figs 99, 100) and descending hypothallial filaments that terminate in wedge-shaped, dark-staining cells, 8–15 μm long and 6–8 μm broad (Fig. 101). Terminal meristematic cells are characteristically elongated and covered by a cuticle (Figs 97, 98). The perithallium is generally poorly developed, 80–150 μm thick and represented by up to three or four layers near the margin (Fig. 99). Subepithallial meristematic cells are longer prior to their division than cells below (Fig. 100). Perithallial cells are 6–20 μm long and 5–7 μm broad, terminating in single epithallial cells that are squarish (to slightly flattened), 6–8 μm in diameter, and may look 'flared-like' (Fig. 100).

Multiporate conceptacles (Fig. 96) are 510–800 μm in external diameter and are either flush with the surface or raised (up to 180 μm in height) (*n* = 8). Their roofs are irregularly flattened (to convex) and occasionally provided with an indistinct peripheral rim (Fig. 96, arrows). Twenty-seven to 71 pores were counted in some of the multiporate roofs that are lighter coloured (yellow-whitish) than the rest of the thallus surface. Chambers are 370–540 μm in diameter and 200–310 μm high (*n* = 11) (Fig. 102). The roof is 65–80 μm thick and composed of 7–10 cells (Figs 103, 106). Pores have an apical diameter of 14–17 μm and are surrounded by 8–12 rosette cells (*n* = 9) that either are similar in size or smaller than neighbouring epithallial cells (Figs 104, 105). When smaller, the rosette cells are sunken below the neighbouring epithallial cells (Fig. 106). In TS, roof filaments bordering pore canals are occasionally divided basally and composed of seven to eight cells that tend to be smaller towards the apex (Figs 103, 106). Near the base, pore cells become thinner (Fig. 103, ar-

rowheads) and wider (Fig. 103, arrows) tending to encircle the canal. Tetrasporangia are zonately divided, 140–190 μm long and 50–120 μm wide (Fig. 107). Embedded conceptacles are absent.

In the original illustration (Printz 1929, pl. 8, fig. 5) the paratype is *c*. 2.5 cm in diameter but is now only 1.8 cm (Fig. 93). It is an unattached, irregularly undulate to foliose thallus lacking protuberances on its surface and having few lobate margins. Like the lectotype, it has apparent zonations that mirror the coaxial hypothallial growth, on both its surface and ventral side near the margin. A predominantly coaxial hypothallial growth is clearly visible in side views of the thallus under a stereoscope. The ventral side is provided with lamellate outgrowths that develop horizontally to the main thallus or may grow back-to-back. Multiporate conceptacles are irregularly crowded in parts of the thallus and are coloured similarly to the rest of the thallus, except that older roofs are slightly yellowish-whitish. The colour of the vegetative surface is red-pinkish and thus differs from the lectotype, which is more brownish. Multiporate conceptacles are 220–700 μm in external diameter and are either raised or flush with the surface; they have irregular, more or less flattened roofs. An indistinct peripheral rim is occasionally present. Pore plates are 200–380 μm in diameter and perforated by 7–58 pores (*n* = 10). Pores are surrounded by 8–10 rosette cells that are either normal epithallial cells or smaller cells sunken below the surface. Canals are lined by filaments composed of seven to nine cells that tend to be smaller towards the apex, whereas near the base become thinner and wider and tend to encircle the canal. The roof is 65–85 μm thick and composed of six-to nine-celled filaments. Chambers are roundish to elliptical, 320–400 μm in diameter and 170–300 μm high. They contain tetrasporangia that are 160–240 μm long and 90–120 μm broad. Older conceptacles lose their roofs, leaving crater-like
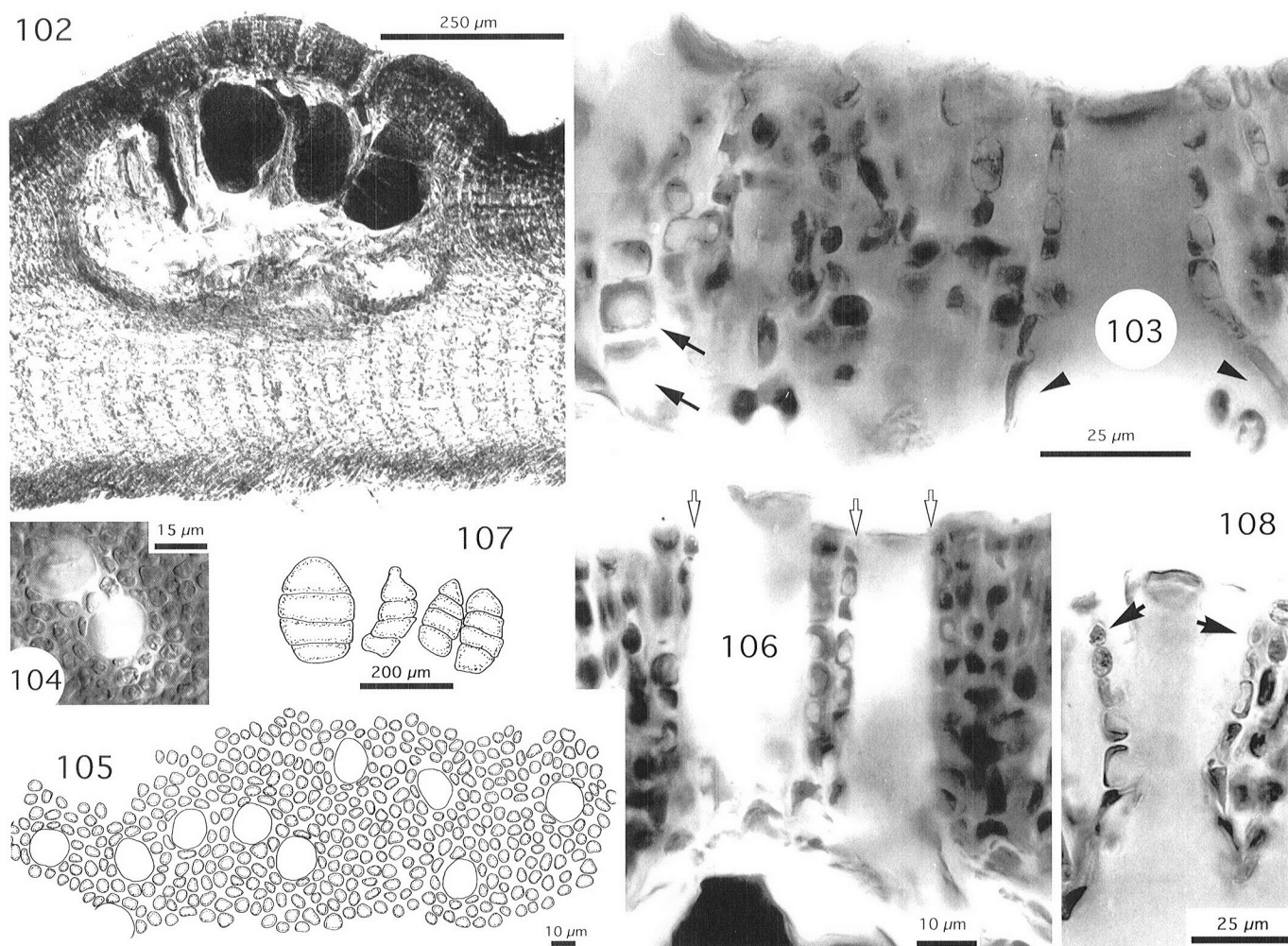
Figs 102–108. *Mesophyllum lamellatum.*
Fig. 102. Tetrasporangial conceptacle (lectotype in TRH).
Fig. 103. Section of the multiporate roof through two pore canals, showing pore cells that are wider (arrows) and thinner (arrowheads). Observe that pore cells become shorter towards the apex (arrows) (lectotype in TRH).
Figs 104, 105. Surface views of a multiporate roof (lectotype in TRH).
Fig. 106. Section of a multiporate roof through pore canals, showing small terminal pore cells (arrows) sunken below the neighbouring epithallial cells (lectotype in TRH).
**Fig. 107.** Drawing of tetrasporangia (lectotype in TRH).
Fig. 108. Section of a multiporate roof through a pore canal, showing pore cells becoming shorter towards the apex (arrows) (paratype, UC 266384).

depressions. The latter are apparently filled with new perithallial cells. Embedded conceptacles are absent. The paratype is considered here to be conspecific with the lectotype, although they differ by at least their colour.

The third specimen in the type collection, attached to the lectotype (Fig. 92, arrowheads), is a fragment c. 1 cm in extent and c. 550 μm thick. It is ventrally attached to a species of *Corallina*. It differs morphologically from the lectotype and the paratype in being lighter in colour (pinkish to purple) and in lacking the apparent periclinal zonations on its surface and ventral side. Anatomically, its thallus is organized dorsiventrally with a polystromatic noncoaxial hypothallium 250–300 μm thick, running horizontally and gradually producing an ascending perithallium up to 250 μm thick. Subepithallial meristematic cells are more or less similar in size to cells below and cut off one to two flattened epithallial cells. Hy-

pothallial cells are 11–30 μm long and 5–8 μm broad, perithallial cells are 3–10 μm long and 3–6 μm broad and epithallial cells are 2–5 μm long and 2–7 μm broad. After studying several other collections from California (in UC) and British Columbia (in UBC), we have concluded that this specimen belongs to a new species that will be described elsewhere as a member of the genus *Leptophytum*. Woelkerling (1993, p. 135) has previously considered the entire collection of *L. lamellatum* in TRH as the holotype, but because the material is representative of two separate species, the lectotypification proposed here is justified.

The material from UC 266384 that we have examined is badly fragmented. Its colour matches perfectly the lectotype in TRH. All fragments examined exhibit a predominantly coaxial, arching hypothallium and are anatomically identical to the lectotype. Lamellae are 200–550 μm thick (perithallium,
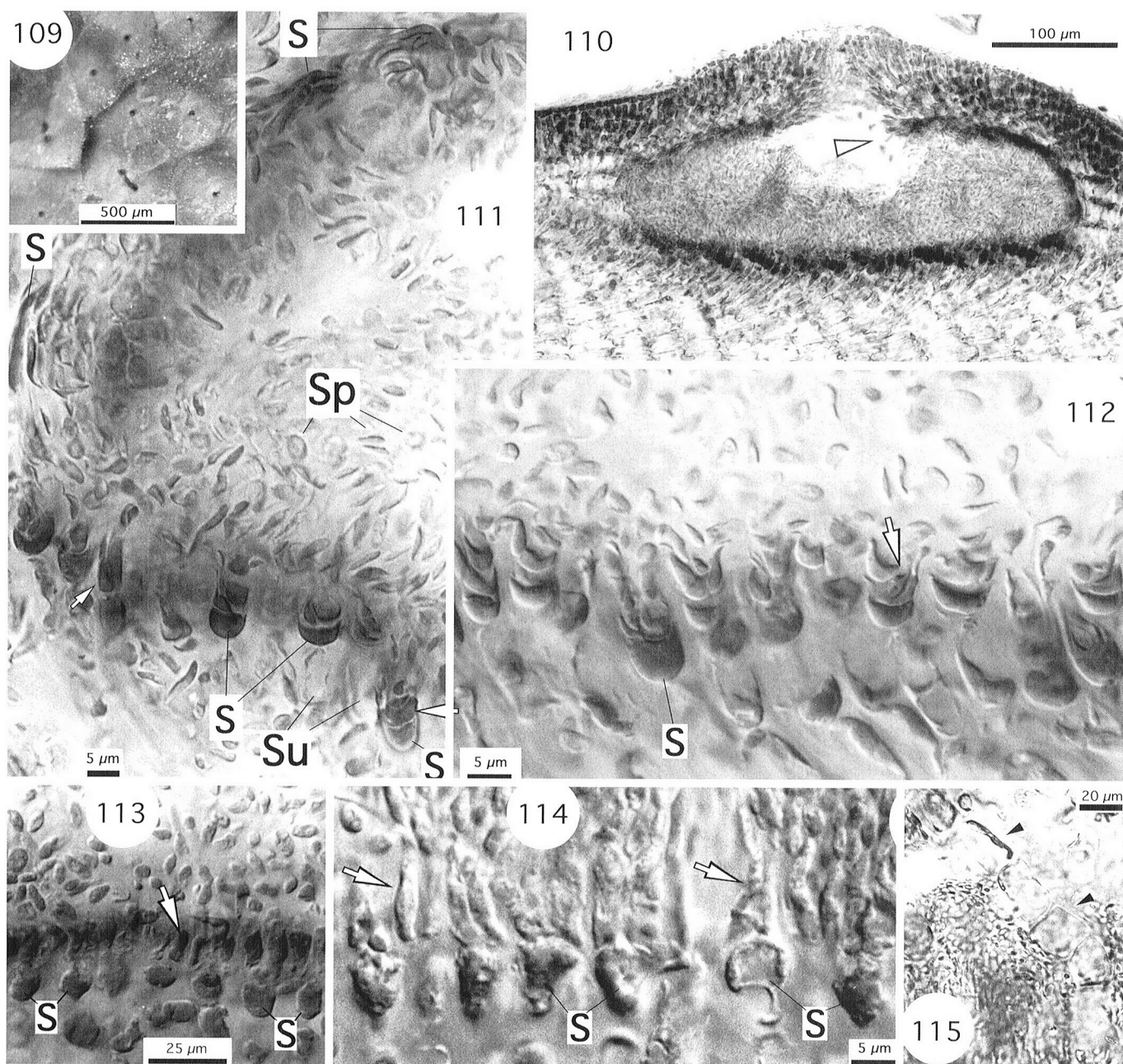
Figs 109–115. *Mesophyllum lamellatum.*

Fig. 109. Surface view of uniporate (male) conceptacles (UC 745601).

Fig. 110. Section of a mature male conceptacle. Note the projecting filaments in the ostiole (arrowhead) (paratype, UC 266384).

Figs 111, 112. Sections at the side wall and the floor of the chamber of a mature male conceptacle, showing lunate SMCs (S) on the floor and more elongate SMCs on the wall and the roof. Spermatangia (arrows) produce spermatia (Sp), whereas supporting cells (Su) are normal perithallial cells (paratype, UC 266384).

Fig. 113. Section at the floor of a male conceptacle at an older stage showing roundish SMCs (S), and more elongate spermatangia (arrow) still producing spermatia (UC 745601).

Fig. 114. Section of the floor at a later stage when the production of spermatia is cut down and the spermatangia appear as colourless (nonstaining) elongate cells (arrows) connected to rectangular–trapezoid SMCs (S) (UC 745601).

Fig. 115. Section of an old male conceptacle, showing a vegetative filament connecting the roof with the floor (arrowheads) (UC 745601).

50–200 μm; hypothallium, 150–340 μm). Multiporate conceptacles are 420–700 μm in external diameter and up to 150 μm high. Their chambers are 340–460 μm in diameter and 210–330 μm high, and the roof is 70–80 μm thick. Filaments bordering pore canals are composed of cells that tend to be smaller towards the apex (Fig. 108). Tetrasporangia are 180–

200 μm long and 70–110 μm broad. In addition, the UC collection contains male plants. Uniporate conceptacles are raised up to 130 μm above the surface, and measure 450–700 μm in external diameter (Fig. 109). Their chambers are 340–380 μm in diameter and 90–110 μm high (*n* = 3), and are covered by a 50–70 μm thick roof, characteristically thicker around
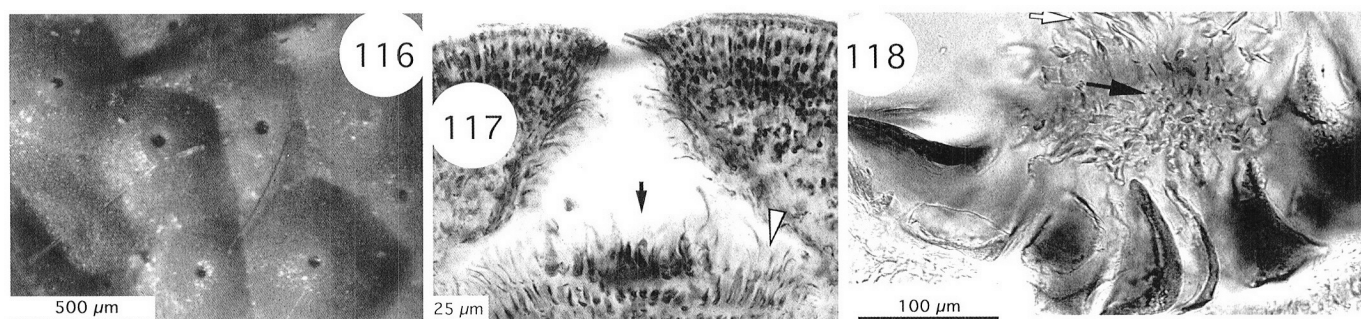
Figs 116–118. *Mesophyllum lamellatum* (UC 745618).
Fig. 116. Surface view of uniporate (carposporangial) conceptacles.
Fig. 117. Section of a young carpogonial conceptacle showing mature carpogonial branches in the centre (black arrow) surrounded by nonstaining filaments (white arrowhead).
Fig. 118. Mature carposporangial conceptacle showing carposporangia produced from the periphery of the centrally raised fertile zone (black arrow) with rests of carpogonial branches (white arrow).

the ostiole. Mature spermatangial structures cover the entire chamber (Fig. 110). On the floor, up to three spermatangia develop in succession (?) on single lunate (in TS) SMCs, each borne on a supporting cell (Figs 111, 112), whereas on the walls and the roof the SMCs appear as elongated cells (Fig. 111). UC 266384 and UC 737622 are recognized here as paratypes rather than isolectotypes because we do not know if they represent plants of the same gathering. Keats & Chamberlain (1997, p. 72, as isotype) have previously examined one of these two collections without citing the relevant UC number. UC 737622 was not examined in this study.

MORPHOLOGY: Plants are foliose, up to at least 4 cm in extent, weakly attached and grow with major parts of their thallus unattached. Herbarium specimens become loose and fragmented. The thallus is provided with lobate proliferations along the margins (Fig. 92, arrows) that may grow over the parent crust. The surface of the young thallus is smooth. Erect perithallial protuberances are lacking, although diminutive excrescences (Fig. 93) and upright (foliose) proliferations may occur. The margins are always free and have a whitish border (cuticle). Zonations (that mirror the coaxial growth of the hypothallium) are evident on the surface and ventral side (more prominently near the margin; Figs 94, 95), whereas the coaxial hypothallium is clearly seen in side views of broken lamellae. Plants growing on geniculate corallines develop ventral excrescences of irregular shape that grow around the segments of the host. The colour varies from dark brownish-red to reddish-pink.

ANATOMY: The thallus is organized dorsiventrally and reaches 2–3 mm in thickness through superimposition. Individual lamellae are 200–700 thick and composed of a predominantly coaxial hypothallium, 150–500 μm thick, where cells form arching decumbent tiers in long series (at least 35 can be followed in single sections) and give rise to an ascending perithallium 50–200 μm thick that is not stratified (Figs 97, 99, 100). Descending hypothallial filaments end in wedge-shaped, dark-staining cells (Fig. 101). A 40–50 μm thick cuticle covers the growing margin (Fig. 97). Hypothallial cells are 20–47 μm long and 6–12 μm broad; perithallial cells are 3–20 μm long and 3–7 μm broad. Epithallial cells develop singly and are roundish-squarish (to slightly flattened), 2–8 μm in diameter [4–6 μm according to Keats & Chamberlain (1997)];

these may look 'flared-like' (Fig. 100). Subepithallial meristematic cells prior to their division are longer than perithallial cells below (Fig. 100). Large cell fusions between contiguous somatic cells are common. Narrow cell fusions are not obvious but have been illustrated (Keats & Chamberlain 1997, fig. 81A). Trichocytes and secondary pit connections are absent.

REPRODUCTIVE STRUCTURES: The species is dioecious, with more or less raised uniporate and multiporate conceptacles. All conceptacle types are aggregated and contiguous ones may coalesce. Multiporate conceptacles are 220–800 μm in external diameter and may be flush with the surface or raised by as much as 180 μm. They are provided with irregularly flattened or slightly convex roofs and occasionally an indistinct peripheral rim (Fig. 96). Pore plates are 200–380 μm in diameter and are perforated by 7–71 pores. The roof is 65–85 μm thick composed of six- to 10-celled filaments. Pore canals have an apical diameter of 14–17 μm and are surrounded by 8–12 rosette cells (Figs 104, 105) that are either normal epithallial cells or smaller, and slightly sunken below the surface (Fig. 106). Pore canals are lined by filaments composed of seven to nine cells that tend to be shorter towards the apex (Figs 103, 108), whereas near the base they become thinner and wider, tending to encircle the canal that is either conical (Fig. 103) or straight (Fig. 106). Chambers are roundish to elliptical, 320–580 μm in diameter and 170–330 μm high (n = 22). Tetrasporangia are 160–250 μm long and 70–180 μm broad. Older conceptacles lose their roofs and form crater-like depressions that are subsequently filled with perithallial cells. Embedded conceptacles do not occur in the thallus.

Male conceptacles are 450–750 μm in external diameter and up to 130 μm high (Fig. 109). At maturity their chambers are elliptical to oblongate, 270–400 μm in diameter (up to 590 μm in merging ones) and 80–110 μm high (n = 12). The roof is 50–110 μm thick, being characteristically thicker around the ostiole where short filaments project near the basal opening (Fig. 110). The ostiole is conical and 40–70 μm in diameter. One to three spermatangia are generally borne on single lunate (in TS) SMCs (Figs 111, 112). SMCs on the walls and the roof appear as elongated cells (Fig. 111). In later stages of their fertility, SMCs change shape to become roundish (Fig. 113) and finally rectangular to trapezoid (Fig. 114). At the same time, spermatangia become more elongate
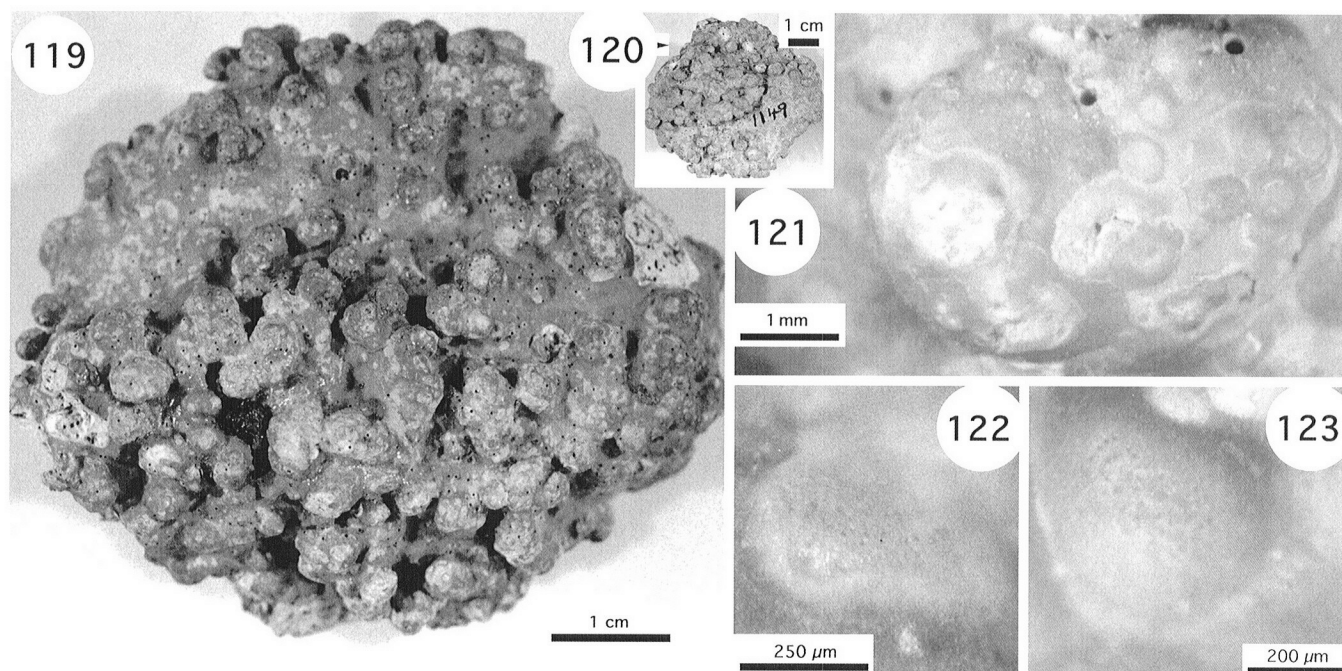
Figs 119–123. *Mesophyllum crassiusculum* (lectotype in TRH).
  Fig. 119. Surface view of the lectotype.
  Fig. 120. The reverse side of the lectotype, annotated with Setchell's number 1149.
  Fig. 121. Surface view of a protuberance with multiporate conceptacles.
  Figs 122, 123. Surface views of multiporate conceptacles with convex roof.

(Figs 113, 114). On the floor, the supporting cells of SMCs are normal perithallial cells and do not stain (Figs 110–112). Spermatangia liberate numerous spermatia (no extra cell walls surrounding them could be seen) that fill the entire chamber (Fig. 110). In a few older conceptacles, vegetative filaments were seen connecting somatic cells of the roof with the floor (Fig. 115), but their nature (whether indigenous or alien) or function was not established.

Carposporangial conceptacles are 400–600 μm in external diameter and up to 200 μm high (Fig. 116). Carpogonial conceptacles are generally smaller, with chambers up to 300 μm in diameter (Fig. 117). Numerous carpogonial branches develop in the centre of the chamber, and usually one carpogonial branch is borne from a supporting cell. Unfertilized carpogonial conceptacles occur amongst carposporangial ones and are recognized by their smaller size and their staining carpogonial branches. Following fertilization, the central fertile area forms a pedestal, as the peripheral cells of the carposporophyte and the calcified cells below dissolve to make space for the carposporangia, which are 30–50 μm in diameter (Fig. 118). Carposporangial chambers are distinctively dumbbell-shaped, 250–460 μm in diameter and 120–280 μm high. The roof of carposporangial conceptacles is 70–120 μm thick, being characteristically thicker around the ostiole, which is conical and 40–100 μm in diameter. Embedded gametangial conceptacles in the thallus were not seen.

COMMENTS: Our observations indicate that *M. lamellatum* has previously been confused with a species of *Leptophytum* in California and with both *Leptophytum* and *M. vancouveriense* in British Columbia. This is also documented by data in the literature, for example Mason's (1953, p. 330, as '*Lithothamnium*') statement that the epithallium of *M. lamellatum*

is two to three layers thick, composed of flattened cells, 1–2 × 3–4 μm. On the other hand, her account of male plants is based on type material (Mason 1953, p. 330, pl. 36, fig. a) and is in agreement with our observations. Our results are also in agreement with Foslie's protologue and the data provided by Keats & Chamberlain (1997, tables 3, 4, figs 80–91, paratype in UC). Counting the mean length of hypothallial cells in a series of 20–35 coaxial arches, we have found variation between 27.8 and 30 μm in a single specimen (UC 739469) and up to 41.7 μm in the lectotype. Morphologically, *M. lamellatum* is easily distinguished from its NE Pacific congeneries and from the species of *Leptophytum* found together with it in many collections, by its strongly coaxial hypothallium that forms periclinal zonations on its dorsal and ventral surfaces (particularly near the margin). It most closely resembles *M. conchatum* and a further comparison is given under the comments about that species. In comparison to the species of *Leptophytum* growing together with it, the thallus of *M. lamellatum* is more fragile and darker coloured (brownish-red). We have examined over 40 UBC collections referred to *M. lamellatum* from various sites around Vancouver Island, and found that these plants belong to *M. vancouveriense*, to species of *Leptophytum* or to *Phymatolithon muricatum* Foslie (whose current generic position remains unclear).

Mesophyllum crassiusculum (Foslie) Lebednik, *comb. nov.*

Figs 119–149

BASIONYM: *Lithothamnion rugosum* Foslie f. *crassiusculum* Foslie (1901, p. 4, '*crassiuscula*').

HOMOTYPIC SYNONYMS: *Lithothamnion pacificum* (Foslie) Foslie f. *crassiusculum* (Foslie) Foslie (1906a, p. 10, '*crassiuscula*'); *Lith-*
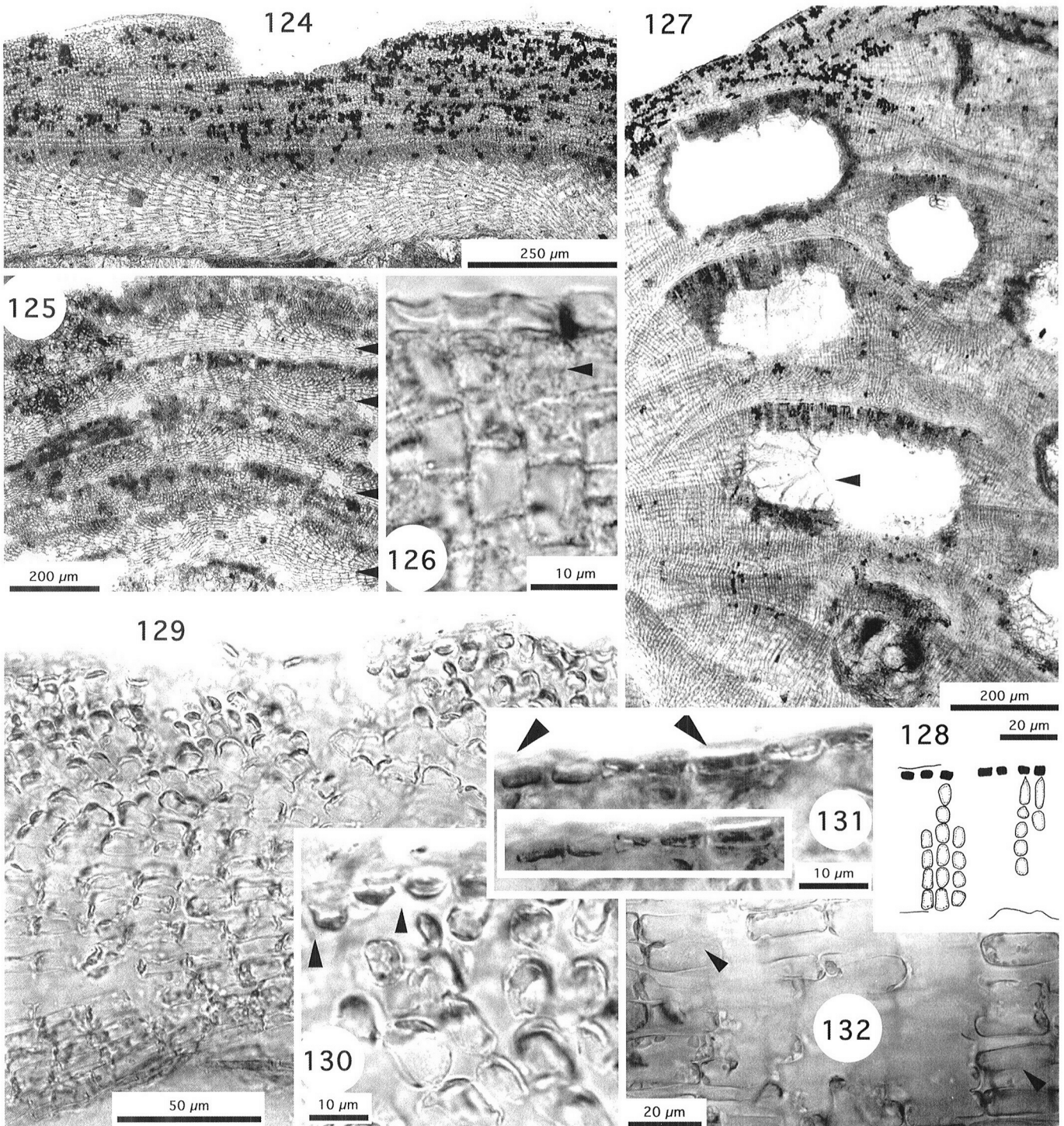
Figs 124–132. *Mesophyllum crassiusculum* (lectotype in TRH).

Fig. 124. Section of a thallus showing a predominantly coaxial hypothallium and perithallial stratification (slide #205 in TRH).

Fig. 125. Thallus section showing superimposing growth with four distinct lamellae (arrowheads; slide #205 in TRH).

Fig. 126. Thallus section near the surface showing 'squarish' remains of epithallial cells and subepithallial cells (arrowhead) similar in size to cells below (slide #205 in TRH).

Fig. 127. Thallus section showing distinct layers of empty embedded multiporate conceptacles. Observe the filaments (running centripetally) covering the embedded roofs and the partly filled chamber (arrowhead) (slide #205 in TRH).

Fig. 128. Drawing of a section of a part of a multiporate conceptacle roof showing two elongate subepithallial meristematic cells (slide #205 in TRH).

Figs 129, 130. Section of a young thallus with limited perithallial development, short subepithallial meristematic cells (or similar in size to cells below) and 'flared-like' epithallial cells (arrowheads in Fig. 130).

Fig. 131. Section at the thallus surface at two levels of focus showing typical flattened epithallial cells (arrowheads).

Fig. 132. Section near the thallus base showing a coaxial hypothallium and cell fusions between contiguous cells (arrowheads).
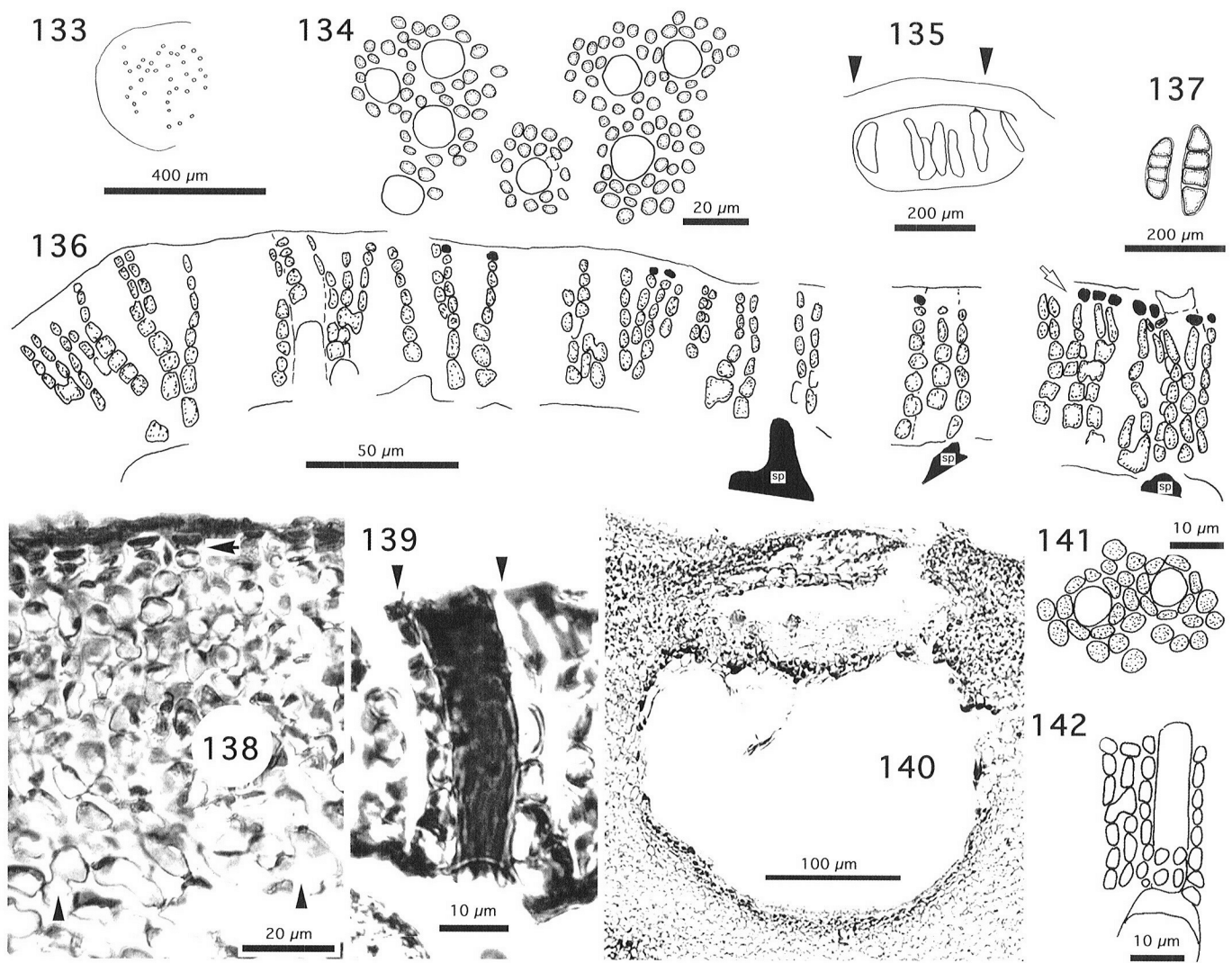
Figs 133–142. *Mesophyllum crassiusculum.*

Figs 133, 134. Drawings of a multiporate conceptacle roof in surface view. Pores are surrounded by normal epithallial cells (lectotype in TRH).

Figs 135, 136. Drawings of a section of an entire multiporate roof (as indicated by arrowheads in Fig. 135). Cells bordering pore canals are normal roof cells and roof filaments are generally composed of gradually smaller cells towards the surface. Notice the few elongate subepithallial meristematic cells (arrow), the sporangial rests (sp) and the roundish epithallial cells (in black) (lectotype in TRH).

Fig. 137. Drawing of tetrasporangia (lectotype in TRH).

Fig. 138. Section of thallus at the surface showing short subepithallial meristematic cells, cell fusions (arrowheads) and two epithallial cells (arrow) (paratype, UC 736373).

Fig. 139. Section through a multiporate roof showing the pore cells bordering the canal. Note that basal cells are larger than those towards the surface. Terminal cells (arrowheads) are flush with the surface (paratype, UC 736373).

Fig. 140. Multiporate conceptacle being covered by peripheral filaments [paratype, UC 736373; reproduced from Lebednik (1974, pl. 54, fig. 3)].

Figs 141, 142. Drawings of pores in surface view and in section. Notice that cells surrounding the apical opening and those bordering the canal are normal roof cells (paratype, UC 736367; provided by Y.M. Chamberlain).

othamnion crassiusculum (Foslie) Mason in Setchell & Mason (1943, p. 93, '*Lithothamnium*').

LECTOTYPE: In TRH, unnumbered (Figs 119–137) including a Foslie slide (#205); collected in December 1895 by *W.A. Setchell* (#1149); previously illustrated by Printz (1929, pl. 4, fig. 13, as *L. pacificum* f. *crassiusculum*); designated by Mason [1953, p. 329, as '*Lithothamnium*', '*Lectotype. – On pebbles moving freely with the waves, Whites Point, San Pedro, Los Angeles County, California, Dec. 23, 1895 Jan. 10, 1896, W. A. Setchell 1149* (Herb. Mus. Nidaros).'].

PARATYPES: In UC 736373 (Setchell #1149 B); collected between 23 December 1895 and 10 January 1896 by *W.A. Setchell;* illustrated by Lebednik (1974, pl. 54, fig. 1, referred to as isotype). In

UC 736367 (Setchell #1149); collected between 23 December 1895 and 10 January 1896, in a small inlet in the reef at Whites Points by *W.A. Setchell;* illustrated by Mason (1953, pl. 35b, larger specimen on the left, referred to as isotype).

TYPE LOCALITY: Whites Point, San Pedro, Los Angeles County, California; growing on pebbles in tide pools and in a small inlet in the reef.

HETEROTYPIC SYNONYM: *Lithothamnion aculeiferum* Mason *in* Setchell & Mason [1943, p. 94, '*Lithothamnium*'; type locality: Whites Point, San Pedro, Los Angeles County, California; holotype: in UC 739410 (Setchell #1496a) including seven slides made by Lebednik (#1–4, #6 8) and one slide made by Setchell annotated '..TYPE',
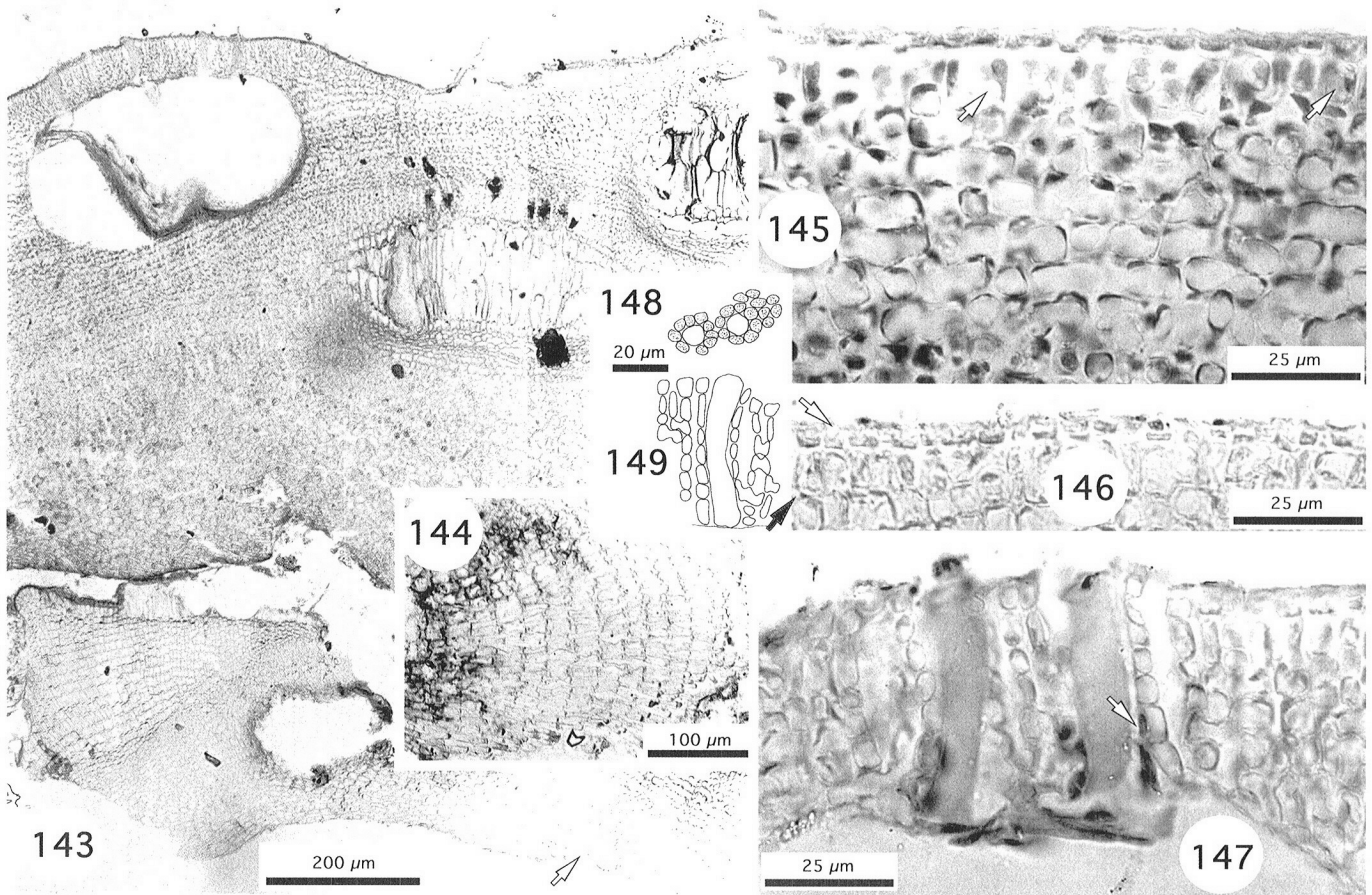
Figs 143–149. *Mesophyllum crassiusculum.* Holotype of *Lithothamnion aculeiferum* (UC 739410, slides).
Figs 143, 144. Sections of thallus showing superficial and embedded multiporate conceptacles, perithallial stratification and a coaxial hypothallium (arrow; magnified in Fig. 144).
Fig. 145. Section at the surface showing elongate subepithallial meristematic cells (arrows) and more or less flattened epithallial cells.
Fig. 146. Section of thallus at the surface showing flattened epithallial cells (white arrow) and subepithallial cells (black arrow) similar in size to cells below.
Fig. 147. Section of a multiporate roof showing pore cells bordering canals. Notice that cell size increases towards the basal opening (arrow) and that the canals are straight.
Figs 148, 149. Drawings of pores of multiporate roofs in surface view (Fig. 148) and in section (Fig. 149) (provided by Y.M. Chamberlain).

collected 6 December 1896 by *W.A. Setchell,* illustrated by Mason (1953, pl. 33c) and Masaki (1968, pl. 2, fig. 5); paratype: in TRH unnumbered including a Foslie slide (#203), collected in January 1896 in tide pools by *W.A. Setchell* (#1496 A)].

HABITAT: On pebbles in the littoral zone, in tide pools and in the surf, moving freely with the wave motion.

DISTRIBUTION: USA, California. Lebednik (1974) did not find any specimens of *M. crassiusculum* north of California, and the distribution of the species on the basis of our examinations is limited to the type locality and La Jolla, California. The name *Lithothamnion crassiusculum* has been applied for rhodoliths in the Gulf of California (Rivera *et al.* 1998, p. 50), but no material has been examined in a modern context. Masaki (1968, p. 10, pls 2, 41) reported *L. aculeiferum* in Japan, but he observed dendroid spermatangial filaments in his material, and therefore his record is doubtful. Several Californian records of *L. crassiusculum* and *L. aculeiferum* cited by Mason belong to species of *Lithothamnion* (see Comments below).

MATERIAL EXAMINED: **USA, California.** Whites Point, San Pedro, on pebbles, December 1895, *Setchell* 1149, TRH, including one Foslie slide #205 [lectotype; Foslie's label reads 'Kalifornien Whites Point San Pedro Dec. 1895 Setchell, No 1149 on pebbles . . . f. *crassiuscula* . . .']; Whites Point, near San Pedro, on pebble in small inlet in the reef, 23 December 1895 to January 1896, *Setchell* 1149, including three other labels, UC 736367 (data provided by Y.M.

Chamberlain); Whites Point, San Pedro, on pebbles in small inlet in the reef, 23 December 1895 to 10 January 1896, *Setchell* 1149, including four slides made by Lebednik, in UC 736373 (Setchell's label reads: 'Isotype of *Lithothamnion rugosum* f. *crassiusculum* Foslie'); San Pedro, *Setchell* 1496A, TRH, including a Foslie slide (#203) [Foslie's label (one of four) reads 'Setchell No 1496 A. San Pedro, Kalifornien *L. rugosum* f. *crassiuscula* [stroked through and replaced with] *pacificum* (f. *crassiuscula*?) Prep. 203']; San Pedro, *Setchell* 1496a, slides #1–3, 6 made by P.A. Lebednik from UC 739410 (holotype of *Lithothamnion aculeiferum*); San Pedro, October 1907, *Monks,* UC 739490; La Jolla, Devil's Slide, 31 May 1907, *Nichols* 382, UC 745667; La Jolla, Bird Rock, 30 May 1907, *Nichols* 349, UC 745635.

OBSERVATIONS ON TYPE MATERIAL: In the protologue, Foslie (1901, p. 4) cited two Setchell collections (#1149 and #1496 A) without designating a type. Mason (in Setchell & Mason 1943, p. 93) referred the former collection (#1149) to *L. crassiusculum,* whereas the latter (#1496a in UC) was made the holotype of the new species *L. aculeiferum* Mason *in* (Setchell & Mason 1943, p. 94). Later, Mason (1953, p. 329) selected the Setchell collection (#1149) in TRH as lectotype of *L. crassiusculum* and designated three isotypes (UC 736367, UC

Table 1. Comparative data for the five NE Pacific species of *Mesophyllum* recognized in this study.[1,2]

Characters/taxa	*M. aleuticum*	*M. vancouveriense*	*M. conchatum*	*M. lamellatum*	*M. crassiusculum*
Distribution	Aleutians	St of Juan de Fuca to Hedley I. (BC)	California to Langara I. (BC)	California	California
Habitat	littoral and sublittoral to 60 m	littoral	littoral to at least 10 m	littoral	littoral
Substratum	epilithic (rarely unattached)	epilithic, epizoic, epiphytic	epiphytic (nongeniculate corallines)	epilithic, epiphytic (Corallina, Gelidiaceae)	epilithic (rhodolith)
Morphology					
Thallus growth	encrusting	encrusting	mainly unattached	mainly unattached	encrusting
Thallus diameter	up to 10 cm	up to at least 7 cm	up to 3 cm	up to at least 4 cm	up to 7 cm
Ventral outgrowths	−	+	+	+	−
Perithallial protuberances	−	±	−	−	±
Superimposing growth	+	+	+	+	+
Colour	bright red-brownish	reddish-brown, dark violet	dark violet	dark brownish red to red-pinkish	violet to pinkish
Anatomy of the vegetative thallus					
Lamella thickness	100–1500	180–850	250–600(> 800[3])	200–700	150–1000(2500[3])
Hypothallium thickness	60–155	100–400	190–400(800[3])	150–500	(52[3])100–300
Perithallium thickness	40–1200	40–550	20–350(700[3])	50–200	50–800
Predominantly coaxial arching hypothallium	+	+	+	+	+
Stratified perithallium	±	+	+	−	±
Elongated subepithallial initial	−	−	+	+	+
Terminal trichocytes	−[4]	+	−[5]	−	−
Hypothallial cells					
Length	9–42	14–50	(13[3])17–41(42[3])	20–47	10–31
Breadth	4–11	6–12	7–15	(5[3])6–12	5–13
Perithallial cells					
Length	5–14	5–19	(8[3])15–20	3–20	4–23
Breadth	4–8	5–10	(6[3])7–11	3–7	4–9
Epithallium					
Number of cells	1 or 2	1 or 2	1(or 2[3])	1	1–3
Length × breadth	2–5 × 5–9	2–4 × 5–10	4–9 × 3–10	2–8 × 2–8	2–5 × 3–9
Shape (TS)	flattened	flattened	roundish	roundish to squarish	flattened
Asexual (multiporate) conceptacles					
External diameter	525–1400	280–600	(445[3])500–1200	220–800	300–600(636[3])
External height	100–390	up to 140	up to 180	up to 180	up to 160
Chamber diameter	420–720	220–510	(340[3])410–780	(203[3])320–580	250–410
Chamber height	165–320	120–300	180–300	170–330	130–190
Convex roof	+	−	+	+	+
Roof/pore plate thickness	50–95	35–55	55–85(103[3])	65–85	40–70
Roof/pore plate cells	5–9	5–8	4–7	6–10	6–10
Pore plate diameter	460–845	160–400	250–510	200–380	170–300
Number of pores	37–130	9–66	16–96	7–71	36–50
Conical canal	−	+	±[6]	±	+
Embedded conceptacles	+	+	−[7]	−	−
Conceptacles degenerate	+	−	+	+	−
Peripheral rim	−	+	−	±	−

Table 1. Continued

Characters/taxa	M. aleuticum	M. vancouveriense	M. conchatum	M. lamellatum	M. crassiusculum
Bordering pore cells					
Rosette cells	6–9	7–10	7–10	(7[6])8–12	6–10
Rosette cells sunken	–	–	±	±	–
Cells per filament	6–9	5–7	6–8	7–9	6–8
Similar to contiguous	+ (at the top)	+ (at the top)	+ (at the top)	+ (at the top)	+
Smaller than contiguous	–	–	+ (at the top)	+ (at the top)	–
Thinner and wider	ND[8]	+ (at the base)	+ (at the base)	+ (at the base)	–
Bi/tetrasporangia					
Length	90–290	160–210	180–260	(104[6])160–250	110–200
Breadth	20–125	30–100	50–150	(52[6])70–180	25–70
Male conceptacles					
External diameter	380–1060	up to 400	250–850	450–750	ND
External height	70–235	up to 50	(–41[3,9])–210	up to 130	ND
Chamber diameter	235–785	230–370	(186[3])320–470	(208[6])270–400	ND
Chamber height	40–175	70–100	50–120(154[3])	80–110	ND
Roof thickness	40–145	c. 60	60–100(113[3])	50–110	ND
Ostiole diameter	10–125	c. 40	20–100(103[3])	40–70	ND
Branched SMCs–floor	–	–	–	–	–[3]
Branched SMCs–roof	–	–	–	–	–[3]
Simple SMCs–floor	+	–	+	+	+[3]
Simple SMCs–roof	+	+	+	+	+[3]
SMCs lunate	ND	+	+	+	ND
Carposporangial conceptacles					
External diameter	520–1000	560–680	(371[3])650–800(900[10])	400–600	ND
External height	175–350	up to 150	(0[3])70–150	up to 200	ND
Chamber diameter	435–720	380–590	(278[3])360–540	250–460	ND
Chamber height	205–290	160–240	100–230(247[3])	120–280	ND
Chamber shape	dumbbell	dumbbell	dumbbell	dumbbell	ND
Roof thickness	115–255	50–110	60–110(124[3])	70–120	ND
Ostiole diameter	115–175	30–120	20–100(134[3])	40–100	ND

[1] ND, no data; TS, transverse section.
[2] Unless specified otherwise all measurements are in micrometers.
[3] Complementary data from Lebednik (1974).
[4] Dark-staining hair cells (trichocytes?) develop frequently near the surface and subsequently become embedded in the perithallium.
[5] Dark-staining hair-like cells are occasionally seen buried in the vegetative thallus (Lebednik 1974).
[6] Complementary data from Keats & Chamberlain (1997).
[7] Embedded gametangial and carposporangial conceptacles present.
[8] Thinner-elongate (at the base); no data about width.
[9] The negative sign indicates that the conceptacles are sunken below the thallus surface.
[10] Complementary data from Adey & Johansen (1972).

Table 2. Dichotomous key to the five NE Pacific species of *Mesophyllum*.

1.	Thallus lacking erect protuberances, adhering to the substrate at a few points only and growing mainly free 2
1.	Thallus with or without erect protuberances, adhering entirely to the substrate (the margins may grow free); in unattached fragments the margins bend inwards and grow back-to-back 3
2.	Thallus irregularly foliose, up to at least 4 cm in extent, growing on a variety of substrates including geniculate corallines. Regular periclinal zonations on its surface and ventral side present. Multiporate conceptacles up to 800 μm in external diameter, with convex or flattened roof occasionally with an indistinct peripheral rim .... *Mesophyllum lamellatum*
2.	Thallus subcircular to irregularly foliose, less than 3 cm in extent, exclusively growing on geniculate corallines. Regular periclinal zonations absent from its surface and ventral side. Multiporate conceptacles up to 1200 μm in external diameter, with convex or flattened roof lacking a peripheral rim .... *Mesophyllum conchatum*
3.	Thallus lacking protuberances. Multiporate conceptacles up to 1400 μm in external diameter, with convex roof lacking a peripheral rim. Older conceptacles degenerate .... *Mesophyllum aleuticum*
3.	Thallus smooth along the margin, usually producing knobby protuberances centrally. Multiporate conceptacles up to 635 μm in external diameter, with convex, flattened, or sunken roof with or without a peripheral rim. Older conceptacles embedded in the thallus 4
4.	Plants generally attached to rocks, limpets, shells or macroalgae. Roof of multiporate conceptacles sunken, with a peripheral rim .... *Mesophyllum vancouveriense*
4.	Plants generally attached to pebbles forming rhodoliths. Roof of multiporate conceptacles convex or flattened, lacking a peripheral rim .... *Mesophyllum crassiusculum*

736369 and UC 736373), presumably from the remains of Setchell's original collection (#1149 in UC). These three UC collections are considered here to be paratypes because their date of collection is not identical to the lectotype in TRH. Moreover, only UC 736367 and UC 736373 include material that we consider to be representative of *M. crassiusculum*.

The lectotype in TRH has been illustrated by Printz (1929, pl. 4, fig. 13). It is a single specimen growing on a pebble, to *c.* 6 cm in extent, annotated with the number 1149 (Figs 119, 120). It is placed in a single round box annotated by Foslie 'Kalifornien Whites Point San Pedro Dec. 1895 Setchell, No 1149 on pebbles, moving freely with the wave motion. *L. rugosum* [stroked through and replaced by] f. *crassiuscula* Lithoth. monogr. pl. 4, fig. 13 Prep. 205'. Apart from the lectotype specimen, the box includes several smaller fragments, a smaller box annotated 'Prep. 205 af störste eks . . . pl.' (slide 205 from the largest specimen), one slide numbered '205' and three labels: (1) 'Sp. 4 dell' (sporangia divided in four); (2) 'Konc./Tetrasp. 300–500–(600) μ Perith. 9×7, 7×7, 11×7, 9×9, 9×5, 5×7, 5×5, 14×7, 18×7, Konc. . . . (prep. 203)'; and (3) '1149 – *Lithothamnion* the pebbles moving freely with the wave motion, White's Point, San Pedro, California W.A. Setchell – Dec. 1895.'

The lectotype covers the entire pebble, adheres strongly to it and bears prominent lumpy protuberances, up to 3 mm long and 3 mm in diameter. Multiporate conceptacles are crowded on the protuberances (Fig. 121) and are generally raised by up to 85 μm above the surface. They measure 300–600 μm in external diameter. They have convex or flattened roofs 300–350 μm in diameter, and lack a peripheral rim (Figs 122, 123). A pore plate diameter of between 200 and 240 μm was measured in a detached conceptacle (*c.* 320 μm in external diameter). The material on the Foslie slide (#205) shows a section up to 4 mm thick with erect protuberances up to 2.9 mm long composed of perithallial cells. The basal part of the section shows (in at least one part) a predominantly coaxial hypothallium up to 300 μm thick, where cells form arching decumbent tiers in long series, giving rise to an ascending perithallium up to 700 μm thick (Fig. 124). Up to four superimposed layers (individual lamellae) are present in parts of the section (Fig. 125). Hypothallial cells are 18–30 μm long and 7–10 μm broad, and perithallial cells are 5–12 μm long and 5–8 μm broad. Subepithallial cells are similar in size or slightly longer than cells below and support flattened to squarish epithallial cells (Fig. 126). Embedded conceptacles occur in the thallus (Fig. 127) and in some of them multiporate roofs are evident. Chambers of embedded conceptacles are 300–410 μm in diameter and 130–190 μm high, and are either empty or partly filled (Fig. 127). Conceptacle roofs are 40–70 μm thick and composed of seven- or eight-celled filaments. In one roof, a few subepithallial meristematic cells are distinctively longer than cells below (Fig. 128). Conceptacle roofs are overgrown by peripheral filaments that subsequently produce new conceptacles, so that up to three fertile layers can be seen (Fig. 127). Further sections and surface views of smaller fragments from the lectotype revealed that in young lamellae, the coaxial hypothallium dominates (being *c.* 100 μm thick) over the perithallium (*c.* 50 μm thick) (Fig. 129). Perithallial filaments support single epithallial cells that are rarely 'flared-like' (Fig. 130) or more often flattened, 3–4 μm long and 3–9 μm in diameter (Fig. 131). Subepithallial cells are similar to or

slightly longer or shorter than cells below (Figs 129, 130). Fusions are common between perithallial or hypothallial cells (Fig. 132). Pore plates distinctively differ in colour (yellow-whitish) from the rest of the thallus surface (violet to pinkish). Conceptacle roofs are 50–65 μm thick and perforated by at least 36 pores (Fig. 133). Pores are 10–14 μm in apical diameter, surrounded by 8–10 rosette cells ($n = 8$) that are normal epithallial cells (Fig. 134). Roof filaments are composed of six to eight cells that generally diminish in size towards the surface, ending in roundish or squarish epithallial cells (Figs 135, 136). Filaments bordering pore canals are composed of cells that are similar to contiguous roof cells. A few distinctively elongate subepithallial meristematic cells were observed in a roof section (Fig. 136, white arrow), but in the vegetative thallus subepithallial cells are more or less similar in size to cells below and support more often flattened epithallial cells. Tetrasporangia are zonately divided, 110–180 μm long and 25–50 μm in diameter ($n = 15$) (Fig. 137).

The paratype collection UC 736373 is in a box containing several crusts on cobbles and minor fragments (R. Moe, personal communication). This material has previously been investigated by Mason (1953, p. 329) and Lebednik (1974, pl. 54, figs 1–3), and several slides and a note in Mason's handwriting document this case (R. Moe, personal communication). Mason's note reads '*Lithothamnion pacificum* f. *crassiuscula* 20–30 pores, spores 2-paired sometimes. Also *Lithophyllum imitans* (shiny)'. We had available for examination: (1) two Mason slides, both representative of a species of *Lithophyllum*; (2) four slides made by P. Lebednik; and (3) the actual paratype specimen examined by Lebednik (1974). This specimen is placed in a box annotated 'Isotype of *Lithothamnium rugosum* f. *crassiuscula* Foslie in: Foslie, New Melobesieae 4, 1901 (in part)' and 'Herbarium of the University of California Algae of California *Lithothamnium rugosum* f. *crassiuscula* Foslie On pebbles in small inlet in the reef at White's Pt., San Pedro. W.A. Setchell 1149 Dec. 23, 1895 to Jan. 10, 1896'. The paratype specimen grows on a cobble (c. 14 cm in extent) and is partly overgrown by two specimens of *Lithophyllum*. Lebednik's slides are separately labelled by him #1149 A (for the *Lithophyllum* sp.; *L. imitans* Foslie according to him) and #1149 B (for the paratype specimen of *M. crassiusculum*). The paratype is up to 7 cm in diameter and 2 mm thick, with irregular terete protuberances that are unbranched, 1–2 mm high and composed of perithallial cells. Young lamellae along the periphery have roundish, moderately glossy edges, with a distinct whitish border (cuticle), and are free or adherent. The rest of the thallus strongly adheres to the pebble and generally follows the contour of the substrate (i.e. stone and polychaete tubes). The smooth surface and the protuberances are covered with multiporate conceptacles that are crowded and generally raised. Anatomically, a coaxial growth is evident in the hypothallium and a cuticle covers the terminal meristem. One or two epithallial cells are present [up to three according to Lebednik (1974)] and they are flattened in TS, 2–5 μm long and 4–8 μm broad [2–4 × 5–8 μm according to Lebednik (1974)] (Fig. 138). Pore canals in multiporate roofs are tube-like and pore cells are similar in shape and size to contiguous roof cells, tending to be smaller towards the surface (Fig. 139). A pore plate diameter between 170 and 210 μm was measured in a detached conceptacle (c. 420 μm in external diameter). Old conceptacles are embedded

in the thallus by peripheral filaments that grow over the old roof that remains intact (Fig. 140). The paratype is nearly identical to the lectotype and we consider the two specimens to be conspecific. A more detailed description of the paratype is given by Lebednik (1974), whose data are included in our account of the species.

The paratype collection UC 736367 comprises two specimens that have been illustrated by Mason (1953, pl. 35b). This collection includes four labels: (1) '*Lithothamnion pacificum* Foslie #1149 = quoted by Foslie, algologiske notiser II p. 10 . . .'; (2) '*Lithothamnium crassiusculum* (Foslie) L.R. Mason in Setchell and Mason. New or Little known Crustaceous Corallines of Pacific North America. Proc. Nat. Acad. of Sci. V. 29 nos 3–4, 89–91, 1943, 1149 W.A.S. White's Pt., near San Pedro, Calif. Dec. 23, 1895 to Jan 10, 1896, on pebbles in small inlet in the reef at White's Pt.'; (3) 'Foslie cites W.A.S. 1149 as the type of *Lithoth. rugosum* f. *crassiuscula*. This specimen may be an isotype and the true type may be in Foslie's herbarium at Trondheim'; and (4) 'Photographed! UC. Berkeley #736367 = Plate 35 b in Mason 1953'. The larger of the two specimens is a tetrasporophyte with prominent protuberances (Mason 1953, pl. 35b, specimen on the left). Pore cell characteristics (Figs 141, 142) and other data provided by Y. Chamberlain (personal communication) indicate that this element is conspecific with the paratype UC 736373.

The paratype collection UC 736369 comprises a single specimen on a stone (up to 2.5 cm in extent) and includes three labels: (1) '*Lithothamnion rugosum* f. *crassiusculum* Foslie sent to Foslie partly #1149 WAS'; (2) 'a piece of this one also sent to Foslie Feb. 96 under #1149'; and (3) '1149 spec|ime|n very much like this one sent to Foslie Feb. 1896'. According to Y. Chamberlain (personal communication), this material belongs to a species of *Lithophyllum*, probably *L. proboscideum* (Foslie) Foslie. There is also one slide in UC annotated '*Lithothamnion rugosum* f. *crassiusculum* Foslie isotype! WAS 1149 . . .' that comprises sections of a species with uniporate asexual conceptacles that is probably conspecific with UC 736369.

The lectotype of *M. crassiusculum* in TRH (Fig. 119) is morphologically identical to the paratype UC 736367 (Mason 1953, pl. 35b, specimen on the left), but differs from the paratype UC 736373, which is coarser and similar to the holotype of *L. aculeiferum* (Mason 1953, pl. 33c) (see below). Anatomically, the three type elements of *M. crassiusculum* are indistinguishable and we consider them to be conspecific. In particular, they all exhibit a coaxial hypothallium, a partly stratified perithallium, flattened epithallial cells in the somatic thallus, subepithallial cells of similar size to cells below (except in conceptacle roofs where some distinctively elongate subepithallial initials are present in the lectotype), superimposing growth of new lamellae, embedded conceptacles, nonspecialized pore cells and multiporate roofs composed of cells that tend to be smaller towards the surface.

The holotype of *L. aculeiferum* (UC 739410) also grows on a pebble (Mason 1953, pl. 33c; Masaki 1968, pl. 2, figs 5, 6), and it has been re-examined by Masaki (1968, p. 10) and Lebednik (1974, pl. 52, tables 37, 38). Lebednik considered the holotype to be identical to the paratype UC 736373 of *M. crassiusculum*, except that the holotype grows over '. . . other calcareous crusts . . . not *Lithophyllum imitans*' and 'the apparent protuberances [are] not as coarse as in the specimens

of *M. crassiusculum*'. He also noted that none of the three characters used by Mason (1953, pp. 326, 329) to separate the two species is valid. In particular, sporangial partition (*L. aculeiferum* is said to have bisporangia, whereas there are tetrasporangia in *L. crassiusculum*) was not diagnostic because Masaki (1968) found that the holotype of *L. aculeiferum* was tetrasporic. The second character used by Mason, i.e. multiporate conceptacle diameter (said to be 140–165 μm in *L. aculeiferum* vs 170–230 μm in *L. crassiusculum*), was strongly underestimated for both taxa because Mason included material of other species in her accounts (see Comments below), and much larger conceptacles (up to 636 μm) were observed in the holotype of *L. aculeiferum* (Lebednik 1974, table 37). Lebednik (1974) concluded that 'the only remaining distinguishing feature . . . was that of protuberance size and shape, a character which alone is generally considered . . . insufficient . . . to distinguish species'. In view of the variable degree of protuberance size and shape that we have observed in the lectotype and paratypes of *M. crassiusculum*, this character cannot be diagnostic. Four UC slides with sections of the holotype of *L. aculeiferum* (made by P. Lebednik) and several other slides made of the same specimen and kept in the private herbarium of P. Lebednik were available for re-examination. These show a dorsiventrally organized thallus, at least 2.2 mm thick, consisting of a coaxial, arching hypothallium, up to 200 μm thick [128–162 μm thick, composed of 16–18 filaments, according to Lebednik (1974, table 38)], and a gradually ascending, more or less stratified perithallium up to at least 800 μm thick (Figs 143, 144). Hypothallial cells are 10–31 μm long and 5–13 μm broad (Lebednik 1974, table 38), and perithallial cells are 4–10 μm long and 4–7 μm broad with subepithallial meristematic cells that are distinctively longer than (Fig. 145) or similar in size to cells below (Fig. 146). Epithallial cells are flattened to domed in the vegetative thallus and borne singly or two in sequence, 2–4 μm long and 5–8 μm broad (Figs 145, 146). Several epithallial cells look 'flared-like', but this is probably due to the collapse of the outer wall, producing a 'compressed' and sometimes 'flared' appearance. These observations of the epithallium are consistent with the unpublished note made by P. Lebednik in 1972–1974. Trichocytes and secondary pit connections are absent. Multiporate conceptacles are 380–636 μm in external diameter and have convex roofs, 233–403 μm in diameter and 40–55 μm thick (Lebednik 1974, table 37). A peripheral rim is lacking (Fig. 143). Conceptacle roof filaments are composed of seven to nine cells that tend to be smaller towards the surface (Fig. 147) and terminate in squarish epithallial cells (Figs 147, 149). Pores are surrounded by eight or nine rosette cells (Fig. 148), and filaments bordering the canal are normal roof cells (Figs 147, 149). Tetrasporangia are up to 200 μm long and 70 μm broad. Conceptacle chambers are embedded in the thallus and filled with palisade cells (Fig. 143). Anatomically, the holotype of *L. aculeiferum* is indistinguishable from the lectotype of *M. crassiusculum*, and therefore we consider the two taxa to be conspecific, in agreement with Lebednik (1974).

A further collection exists in TRH annotated by Foslie: 'Setchell no 1496 A. San Pedro, Kalifornien *L. rugosum* f. *crassiuscula* [the two epithets are stroked through and replaced by] *pacificum* (f. *crassiuscula?*) Prep. 203'. This collection includes a Foslie slide (#203) and three separate labels.

Two are annotated by Foslie: 'Prep . . . 203 *L. sonderi?* . . . Jfr . . .' and 'Prep. 203. Konc. Tetrasp. 240–400(500) μ Perith. 9 × 7, 7 × 7, 7 × 5, 11 × 7, 5 × 7, 11 × 5, 9 × 5, 14 × 7, 14 × 9 . . . *L. sonderi*'. The third one has the partly printed text 'Herbarium of the University of California 1496A . . . *Lithothamnion rugosum* f. *crassiusculum* Fosl. . . . In tide pools, San Pedro. Collected by W.A. Setchell Jan. 1896'. This collection has been considered to be an isotype of *L. aculeiferum* by Woelkerling (1993, p. 18), but its date (January 1896) is different from that of the holotype (6 December 1896), and therefore it must be recognized as a paratype. The collection comprises a single specimen, violet in colour, growing on a broken pebble up to 4 cm in diameter. Multiporate conceptacles are 360–600 μm in external diameter and have yellow-whitish roofs with pore plates 220–300 μm in diameter. Conceptacle roofs are convex and pierced by up to 50 pores. Pores are 10–14 μm in diameter and surrounded by six to eight rosette cells that are similar in size and shape to contiguous epithallial cells. The material on the Foslie slide (#203) shows embedded conceptacles, superimposed lamellae and sporadic 'flared-like' epithallial cells. Morphologically, the specimen is identical to the paratype UC 736373 of *M. crassiusculum* which, like the holotype of *L. aculeiferum*, lacks prominent protuberances. We consider this specimen to be conspecific with *M. crassiusculum*.

MORPHOLOGY: Thalli are up to 7 cm in diameter, growing on pebbles and adhering strongly to the substrate. The thallus surface is moderately glossy and smooth to lumpy, with irregular terete protuberances up to 3 mm long and 1–3 mm broad, which remain unbranched (Fig. 121) and are composed of perithallial cells. Margins have a distinct whitish border (cuticle) and grow free or are adherent. The colour of the thallus is violet to pinkish, whereas the conceptacle roofs are yellow-whitish.

ANATOMY: The thallus is organized dorsiventrally and can reach at least 4 mm in thickness through superimposition. Individual lamellae are 150 μm to at least 1000 μm thick [up to 2.5 mm according to Lebednik (1974)], and consist of a predominantly coaxial, arching hypothallium, 100–300 μm thick, and an ascending more or less stratified 50–800 μm thick perithallium (Figs 124, 129, 143, 144) producing protuberances. Superimposition of the thallus is common (at least four successive layers seen; Fig. 125). Hypothallial cells are 10–31 μm long and 5–13 μm broad; perithallial cells are 4–23 μm long and 4–9 μm broad. One or two (sometimes three) epithallial cells are present; these are generally flattened in TS on the vegetative thallus (Figs 131, 145, 146) or 'flared-like' (Fig. 130), 2–5 μm long and 3–9 μm broad, but are square or roundish on conceptacle roofs (Figs 128, 136, 142, 147). Prior to their division, subepithallial meristematic cells are longer than perithallial cells below (Fig. 145), probably resulting in two daughter cells of about similar size (Fig. 146). Fusions between perithallial or hypothallial cells are common. Trichocytes and secondary pit connections are absent.

REPRODUCTIVE STRUCTURES: Multiporate conceptacles are generally raised and occur commonly on the protuberances (Figs 121–123) or on the smooth surface of the thallus (Fig. 143). Conceptacles are 300–600 μm in external diameter and up to 160 μm high [382–636 μm in diameter according to

Lebednik (1974, table 37)]. Multiporate conceptacles develop tetrasporangia or bisporangia within chambers that are 250–410 μm long and 130–190 μm high. Conceptacle roofs are 233–403 μm in diameter (Lebednik 1974, table 37); they are 40–70 μm thick (40–55 μm across the 170–300 μm diameter pore plate), lack a peripheral rim and are perforated by 36–50 pores (Figs 133, 136). Pores are 10–14 μm in apical diameter and are surrounded by 6–10 rosette cells that are similar in size and shape to contiguous epithallial cells (Figs 141, 148). Roof filaments are composed of 6–10 cells that can be divided basally (Fig. 136); cells are generally smaller towards the surface, ending in roundish or squarish epithallial cells (Figs 136, 142, 147, 149). Filaments bordering pore canals are composed of six to eight normal roof cells; pore canals are straight (Figs 136, 142, 147, 149). Tetrasporangia are zonately divided, 110–200 μm long and 25–70 μm broad (Fig. 137). Old conceptacles become embedded in the perithallium and are usually filled with palisade cells (Fig. 143). The chambers are overgrown by peripheral filaments that may produce new conceptacles, so that up to three fertile layers can be seen (Fig. 127). During the embedding process, peripheral filaments form a rim-like structure around the pore plate that becomes first sunken and then totally covered.

COMMENTS: According to Lebednik (1974, and unpublished data), male conceptacles are raised and develop simple (unbranched) spermatangial structures all over the chamber (specimens attached to pebbles at Whites Point). Collectively, the presence of a predominantly coaxial, arching hypothallium (at least in parts of the thallus) and the presence of simple spermatangial structures and flattened epithallial cells are sufficient characters to support the transfer of the species to the genus *Mesophyllum*. The occurrence of 'flared-like' epithallial cells in herbarium material may be an artefact due to the collapse of the outer cell wall. Whether typical flared epithallial cells occur in living specimens is unknown. The variable length of subepithallial cells has also been noted by Lebednik (1974, pl. 53, fig. 1). It is assumed here that meristematic cells become longer prior to their division than cells below, and eventually result in two daughter cells of about equal size. *Mesophyllum crassiusculum* is best distinguished from its NE Pacific congenerics by its (exclusive?) growth on pebbles, forming rhodoliths, and in possessing nonspecialized pore cells in multiporate conceptacle (whose roofs are generally composed of smaller cells towards the surface).

Collections UC 736336 (Nichols #575), UC 736362 (Nichols #487) and UC 745628 (Minnie Reed #93) originally referred to *L. crassiusculum* by Mason [Nichols #575 even being included in the list of specimens cited by Mason (1953, p. 329)] belong to a species of *Lithothamnion* with small multiporate conceptacles (180–420 μm in external diameter). This explains the unusual small conceptacle size reported for *L. crassiusculum* by Mason (1953, p. 329). A fourth collection (UC 745635) referred to *L. crassiusculum* was only available as small fragments, and our examination showed the presence of empty uniporate conceptacles and a coaxial hypothallium. Three other collections, UC 736354 (Nichols #126), UC 745678 (Nichols #62) and UC 745683 (Nichols #151), referred to *L. aculeiferum* and included in the list of specimens cited by Mason (1953, p. 327), also belong to *Lithothamnion* (the specimens having distinctive flared epithallial cells, non-

coaxial hypothallium and nonembedded conceptacles). A fourth collection, UC 745676 (Nichols #162), referred to *L. aculeiferum* by Mason (1953, p. 327), belongs to the same species of *Leptophytum* found in the type material of *M. lamellatum*.

DISCUSSION

This is the first part of an investigation of types and representative collections of species previously referred to or associated with the genera *Mesophyllum* and *Leptophytum* from the Pacific coast of North America (Adey 1970; Adey & Johansen 1972; Lebednik 1974, 1977a, 1978; Steneck & Paine 1986). In this paper, we recognize five species of *Mesophyllum*: *M. aleuticum* from the Aleutian Islands, representing the northernmost record of the genus; *M. vancouveriense*, recorded between the Strait of Juan de Fuca (Steneck & Paine 1986) and Hedley Island (Queen Charlotte Strait, Vancouver Island, 50°54′N); *M. conchatum*, recorded between Cambria [San Luis Obispo County, California; Mason (1953, as *Polyporolithon*)] and Langara Island [Queen Charlotte Islands, British Columbia; Hawkes *et al.* (1978)]; *M. lamellatum*, previously more widely reported, but only records from Monterey County in California are confirmed here; and *M. crassiusculum*, whose occurrence is only confirmed from Whites Point (San Pedro) and La Jolla in southern California.

The vegetative and reproductive characters of each species are summarized in Table 1, and the main macroscopic characters that separate them are used to prepare a dichotomous key in Table 2. From these two tables, it can be concluded that these taxa are easily distinguished from each other, particularly when fertile, but they can be confused with members of the genus *Leptophytum*, represented by several species between San Diego (California) and Port Clarence (Alaska). However, *Leptophytum* lacks both a predominantly coaxial hypothallium (certain species may possess coaxial patches only, according to our unpublished observations) and dumbbell-shaped carposporangial chambers (see below), and exhibits both simple and dendroid (branched) spermatangial structures.

The relationships between the five NE Pacific species of *Mesophyllum* described here remain speculative, awaiting a phylogenetic analysis of the genus. We can report that these taxa exhibit the single diagnostic feature of *Mesophyllum* (only unbranched SMCs, developing on the floor, roof and the walls) and show a close relationship to the generitype (with respect to the strongly coaxial, arching hypothallium and the dumbbell-shaped carposporangial chambers). On the basis of these characters, it is possible to hypothesize the existence of a distinct boreal subgroup within *Mesophyllum*; this is supported by the distribution of these species being restricted to the NE Pacific or the NE Atlantic and the Mediterranean Sea. This hypothesis can be tested by studying the phylogeny of the *Mesophyllum–Leptophytum–Synarthrophyton* complex, and any taxonomic relationships established should also be used to evaluate our key (Table 2), which should reflect natural relationships. Some of the characters that we have used in the description of the five NE Pacific species are discussed below.

Growth form

Mesophyllum aleuticum, *M. vancouveriense* and *M. crassiusculum* grow generally attached to the substrate and adhere strongly, although herbarium specimens of *M. vancouveriense* growing on algae (e.g. *Laminaria* holdfasts) become unattached. The margin of these three species is also less adherent and may even grow free. *Mesophyllum lamellatum* and *M. conchatum* grow mainly epiphytically with most of their thallus unattached, adhering to the substrate only at a few points. Superimposition of new lamellae on the parent thallus is evident in all species, whereas ventral excrescences in the form of new lamellae have been recorded in *M. vancouveriense*, *M. conchatum* and *M. lamellatum*.

Cuticle

In all species, we have consistently found a gelatinous cover around the thallus margin protecting the terminal meristematic cells, as previously observed in *Clathromorphum* (Lebednik 1977b) and *M. lichenoides* (Woelkerling & Irvine 1986, fig. 18). We have concluded that this cuticle is responsible for the 'whitish' border seen around the margin of the thallus.

Hypothallium

In all five species, we have observed a predominantly coaxial, arching hypothallium. Obviously, our observations do not imply that noncoaxial patches are lacking in these species, and the extent to which the coaxial regions dominate over the noncoaxial ones in each species has not been clarified (and may differ between individuals). In *M. lamellatum*, the coaxial growth is also detectable on both sides of the calcified thallus in the form of zonations (Fig. 94). The coaxial hypothallium generally develops via synchronous divisions and elongations of the terminal meristematic cells (Figs 26, 65, 98). Keats *et al.* (2000, p. 397) recently proposed that '. . . the possession of a coaxial [hypothallium is] no longer . . . diagnostic of *Mesophyllum* . . .', especially because coaxiality was found to be entirely lacking in two species referred to this genus [i.e. *M. macedonis* Athanasiadis and *M. ornatum* (Foslie & Howe) Athanasiadis (Athanasiadis 1999)]. We would rather emphasize the fact that a coaxial hypothallium is described in the vast majority of species of *Mesophyllum*, and therefore the lack of this character in a few members may either indicate later reduction or an affiliation with the related genera *Leptophytum* and *Synarthrophyton* that usually lack this character.

Perithallium

Stratification that reflects areas of simultaneous cell division and elongation (i.e. a coaxial growth in the perithallium) is evident in *M. aleuticum* (Fig. 3), *M. vancouveriense* (Fig. 41), *M. conchatum* (Fig. 91) and *M. crassiusculum* (Fig. 142), whereas in *M. lamellatum* (Fig. 100) perithallial cells divide and elongate individually. In *M. aleuticum* (Fig. 6) and *M. vancouveriense* (Fig. 36), subepithallial meristematic cells are more or less similar in size to cells below, whereas in *M. conchatum*, *M. lamellatum* and *M. crassiusculum* subepithallial cells prior to their division are conspicuously elongated. In addition, *M. vancouveriense* and *M. crassiusculum* develop perithallial protuberances that remain unbranched.

Epithallium

In *M. aleuticum* (Fig. 6), *M. vancouveriense* (Fig. 36) and *M. crassiusculum* (Figs 131, 138), epithallial cells of the somatic thallus are generally flattened and one or two (up to three in *M. crassiusculum*) are present at a time. Epithallial cells of conceptacle roofs in these species tend to be roundish (Figs 13, 46, 136), as in *M. conchatum* and *M. lamellatum*, where the epithallial cells develop singly (rarely in twos in *M. conchatum*) and are generally roundish (to squarish in *M. lamellatum*).

Degenerated vs embedded conceptacles

These two types of conceptacle evolution are clearly distinct. Conceptacle degeneration starts with the loss of pigmentation from the roof and small contiguous patches nearby. First, the conceptacle loses its roof and then the walls, leaving a crater-like depression that is subsequently filled with new perithallial cells. If perithallial growth continues, it is possible to detect the position of older conceptacles in thallus sections.

Embedded conceptacles may result from two different processes: either through thallus superimposition (Fig. 72) or when new filaments develop from the periphery of the conceptacle (Fig. 140) or the roof (Figs 53, 90) and overgrow the old structure (Figs 127, 140, 143). We have reported conceptacle embedment through superimposition only for *M. conchatum*, but it probably occurs in all species exhibiting superimposing growth and will not be discussed further. Conceptacle embedment that involves the active growth of the perithallium around the conceptacle (or the conceptacle roof) needs further comment. The presence of both embedded (gametangial) and degenerated (tetrasporangial) conceptacles in *M. conchatum* indicates that these two characters are independent and not mutually exclusive, although in the other species of *Mesophyllum* that we have examined only one of these two types was observed. It is therefore possible that embedment of gametangial conceptacles (at least in *M. conchatum*) is controlled by a different genetic mechanism (e.g. to produce new reproductive organs in a superimposing manner and prolong the fertility period of the species) and is not related to the fate of tetrasporangial conceptacles. Embedded cavities are filled with colourless palisade cells (Fig. 143) or remain empty (Fig. 147).

Pore cells of multiporate conceptacles

In all species except *M. crassiusculum*, we have observed specialized pore cells lining the base of the canals. These cells stain darker than contiguous roof cells and also differ morphologically, being either more elongate and thinner (*M. aleuticum*, Fig. 13) or thinner and wider, tending to encircle the canal (*M. vancouveriense*, Figs 43, 45; *M. conchatum*, Figs 77, 79; *M. lamellatum*, Fig. 103). Moreover, in *M. conchatum* (Fig. 78) and *M. lamellatum* (Figs 103, arrows, 108), pore cells become gradually shorter towards the surface, the uppermost ones often sunken below the neighbouring epithallial cells (Figs 78–80, 106). Similar specialized pore cells occur in several other species of *Mesophyllum* and *Leptophytum* and 'presumably function as secretory cells assisting in the release of the pore plug . . . or the passage of the [much wider] sporangia through the pore' (Adey *et al.* 2001, p. 198). The de-

velopment of such specialized cells is probably an evolutionary advancement, like the conical canal shape seen in certain species; but the reason why such specializations evolved only in certain genera or species is unknown.

Spermatangial structures

We have observed distinctive lunate (in TS) SMCs on the conceptacle floor in three of the species (Figs 48, 83, 84, 111), and we believe that this is a new character to be used in the taxonomy of the genus. We have also observed an apparent ageing of SMCs, resulting in deformation (Figs 48, 112) of their typical lunate shape to a roundish, rectangular or trapezoid shape (Figs 50, 113, 114); in some instances this resulted from the fusion of the SMC with its supporting cell (Fig. 84). We propose that lunate SMCs are the fully developed stage in their ontogeny and suggest that they may also exist in other species of the genus. The presence of empty spermatangial cell walls attached to older SMCs (Figs 50, 85) indicates that spermatangia degenerate after their fertility period. It is also suggested that spermatangia cut off or liberate spermatia because no extra cell walls could be seen enclosing them (Figs 111, 112).

Carposporophytes

In four of the species (all except *M. crassiusculum*, in which we did not examine carposporophytes), we have observed peripheral carposporangia produced around the central fertile zone that forms a pedestal (Figs 19, 52, 89, 118). This results in a distinctive dumbbell-shaped chamber in TS, and is achieved through dissolution of the peripheral part of the carposporophyte and decalcification of the perithallial cells below to make space for the carposporangia. A similarly 'elevated' central zone has been demonstrated in the generitype *M. lichenoides* (Woelkerling & Irvine 1986, fig. 25), in the second NE Atlantic–Mediterranean species *M. alternans* (Foslie) Cabioch & Mendoza (Cabioch & Mendoza 1998, fig. 12) and in *M. capense* (Rosanoff) Chamberlain (Chamberlain 2000, fig. 11). In other species of *Mesophyllum* from the Southern Hemisphere, the 'elevation' seems to be less prominent (see, for example, Woelkerling & Harvey 1993, figs 10A–C, 23C), whereas in the genera *Leptophytum* (Adey 1966, pl. 8, fig. 40; Chamberlain & Keats 1994, figs 17, 38, 65) and *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), the carposporangial floor remains more or less flat and lacks any circumferential depression. The formation of a dumbbell-shaped chamber in species of *Mesophyllum* apparently has evolutionary value in allowing the development of larger carpospores. It requires a specialized dissolution of previously formed cellular, high-magnesium calcite. Such dissolution is common in coralline algae; it occurs in the formation of the ubiquitous 'cell fusions' in some genera and during the ontogeny of conceptacles of most genera. However, as a circumferential depression in conceptacles of the Melobesioideae, it appears to be unique to species of *Mesophyllum*. In both *Mesophyllum* and *Leptophytum*, as also in *Synarthrophyton*, carposporangia are produced peripherally.

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